

# Leaves and litterbugs: how litter quality affects amphipod life-history and sexually selected traits

Rickey D. Cothran<sup>1,2,5</sup>, Aaron B. Stoler<sup>1,3,5</sup>, and Rick A. Relyea<sup>1,4</sup>

<sup>1</sup>Department of Biological Sciences and Pymatuning Laboratory of Ecology, University of Pittsburgh, 4249 Fifth Avenue, Pittsburgh, Pennsylvania 15260 USA

**Abstract:** Resources that cross ecosystem boundaries (subsidies) are common in nature, but we have little knowledge of how such resources affect individual traits and, consequently, ecological interactions. In wetlands, leaf litter is an important resource subsidy that regulates ecological processes including the production of consumer biomass. However, litter quality is highly variable and depends on local plant species diversity. Many aquatic consumers are highly nutrient limited, so differences in nutrients and other chemical components in litter are likely to affect numerous individual traits of consumers including life-history and sexually selected traits. We tested whether the species of tree leaf litter consumed by freshwater amphipods affected survival, growth, and development of sexually selected traits. Amphipods had higher survival, attained larger body sizes, and had larger male sexual traits when reared on litter that was relatively nutritious and low in plant secondary and structural compounds. Such widespread trait changes suggest that changing forest composition could have substantial effects on wetland ecology and the evolution of sexual traits over ecological time scales.

**Key words:** allochthonous input, *Hyalella*, phenotypic plasticity, resource quality, resource subsidy, ecological stoichiometry

The flow of resources across ecosystem boundaries (subsidies) can have dramatic effects on consumer biomass and density and, consequently, on ecosystem functioning (Polis et al. 1997, Richardson et al. 2009, Stoler and Relyea 2011). In temperate forests, leaf litter is an important subsidy, particularly in wetlands where rapid litter decay leads to high levels of consumer production (Rubbo et al. 2006). Interspecific and annual differences in foliar chemistry are a tremendous source of variation in the quality of litter subsidies (Webster and Benfield 1986). As the composition of plants in forests changes because of disturbance and succession, interspecific differences in foliar chemistry alter resource quality for litter consumers (Webster and Benfield 1986). Despite the increasing rate of these changes caused by human activity (Bunker et al. 2005), few investigators have examined the effects of leaf-litter quality on consumer phenotypes (Reiskind et al. 2009, Danger et al. 2013, Stoler and Relyea 2013).

Changes in leaf-litter diversity affect consumers through changes in the supply of essential nutrients and secondary compounds that decrease nutrient availability (Webster and Benfield 1986). The process of litter decomposition is

coupled with microbial activity on the litter, which increases digestibility of the litter (softens the leaf) and makes the litter more nutritious by mineralizing nutrients (Kausik and Hynes 1971, Bärlocher and Kendrick 1975a, b, Howarth and Fisher 1976, Facelli and Pickett 1991). Leaf litter generally is a nutrient-poor resource (Cross et al. 2003, 2005), but concentrations of nutrients can vary by an order of magnitude across litter species (Ostrofsky 1997). Nutrient availability also may vary depending on the presence of plant secondary and structural compounds. For example, lignin is a structural compound found in varying concentrations across leaf species that can bind to nutrients and make them difficult for microbes to extract and digest (Melillo et al. 1982). Therefore, litter species with high concentrations of lignin generally have poor nutritional quality and tend to deter consumers. Polyphenolics, secondary compounds found in most litter species, can reduce microbial growth on the litter surface and directly interfere with consumer physiology, both of which can deter feeding activity (Maerz et al. 2005, Ardón and Pringle 2008). Nutrient-rich leaves that are low in plant secondary and structural compounds are colonized more quickly by mi-

E-mail addresses: <sup>2</sup>Present address: Department of Biological Sciences, Southwestern Oklahoma State University, 100 Campus Drive, Weatherford, Oklahoma 73096 USA, rdcotran@gmail.com; <sup>3</sup>Present address: Department of Biological Sciences, Oakland University, 2200 North Squirrel Road, Rochester, Michigan 48309 USA, abstoler@gmail.com; <sup>4</sup>relyea@pitt.edu; <sup>5</sup>Joint first authors

crobes and decompose faster than recalcitrant, toxic, and nutrient-poor leaves (Taylor et al. 1989, Gessner and Chauvet 1994) and are preferred by consumers (Kaushik and Hynes 1971).

Litter is a nutrient-poor resource, so detritivores face one of the greatest stoichiometric imbalances (difference in C:nutrient ratios between a consumer and its food; Cross et al. 2003, 2005) in nature. Such imbalances should strongly affect life-history traits that depend on rare nutrients (e.g., growth is often strongly limited by P; Sterner and Elser 2002, Elser et al. 2003). Most investigators that have demonstrated life-history penalties associated with an imbalanced diet have focused on herbivores, which generally consume food that is much more balanced than that consumed by detritivores (Frost and Elser 2002, Frost et al. 2006, Elser et al. 2003). We know less about how imbalances affect the life history of detritivores, particularly those species that consume leaf litter. Moreover, the variable nutrient profiles and secondary compounds, which affect the microbial conditioning of leaves, should contribute to the severity of stoichiometric imbalance between leaf litter and consumer (Taylor et al. 1989, Gessner and Chauvet 1994). The few investigators who have addressed the effect of leaf-litter quality on consumer traits have discovered large effects on life-history traits (Iversen 1974, Tuchman et al. 2002, Reiskind et al. 2009, Cohen et al. 2012, Danger et al. 2013, Stephens et al. 2013, Stoler and Relyea 2013). Despite these studies, we still know very little about how stoichiometric imbalances affect the life history of detritivores and other species that consume leaf litter as part of their diet.

Sexually selected traits (recently considered under the umbrella of 'life-history traits') may be particularly sensitive to changes in leaf-litter quality (Badyaev and Qvarnström 2002, Kokko et al. 2006). Sexually selected traits (i.e., ornaments and weapons used to procure mates) are often energetically expensive to produce and maintain. Thus, they are sensitive to resource stress (David et al. 2000, Cothran and Jeyasingh 2010, Cothran et al. 2012). Changes in sexual traits are particularly important because their effects may persist far longer than the supply of resource subsidy because of altered patterns of mating success. This situation could occur if sexual-trait variation available for sexual selection depended on resource quality (David et al. 2000, Cotton et al. 2004, Cothran and Jeyasingh 2010). Leaf-litter species vary in nutrient content and nutrient availability (Webster and Benfield 1986, Ostrofsky 1997), so changes in leaf-litter composition may affect the opportunity for sexual selection.

We tested the hypothesis that leaf-litter species will affect survival, growth rate, and sexual-trait development in a common wetland consumer, *Hyaella* amphipods. *Hyaella* are abundant (densities typically range from hundreds to thousands/m<sup>2</sup>) in a wide range of permanent freshwater environments from small springs to large lakes

(Wellborn 1994). They are grazers and detritivores, and they are important prey for many invertebrate and vertebrate predators (Wellborn 1994). We reared amphipods from 1<sup>st</sup> instar to maturity on 1 of 4 species of leaf litter that varied in nutrition and plant secondary and structural compounds, are dominant in the temperate forests of the northeastern USA, and are associated with contemporary shifts in forest tree diversity. For example, we used black cherry (*Prunus serotina*), which is currently gaining widespread dominance in many regions, and elm (*Ulmus* sp.), which has been decimated by Dutch elm disease (Abrams 1998, 2003, Moser et al. 2009). We predicted that amphipods would show greater survival, larger body size, and larger sexually selected traits when reared on litter species with relatively high nutrients (N and P) and relatively low lignin and polyphenolics.

## METHODS

We conducted the experiment during summer 2011 at the Donald S. Wood Field Laboratory at the University of Pittsburgh's Pymatuning Laboratory of Ecology in northwestern Pennsylvania. We reared 1<sup>st</sup>-instar amphipods to maturity on 1 of 4 species of conditioned leaf litter: bigtooth aspen (*Populus grandidentata*), black willow (*Salix nigra*), black cherry, and elm. These tree species are common in the study area, and we expected them to differ substantially in nutrient, lignin, and polyphenolic content.

We collected *Hyaella* from Conneaut Marsh in Crawford County, Pennsylvania (lat 41.537541, long -80.362368). In North America, *Hyaella* comprises a species complex with many undescribed species (Wellborn and Broughton 2008). Based on species-specific color patterns (Cothran et al. 2013b), we used a species from the B clade, designated in recent phylogenies (Wellborn and Broughton 2008). We reared amphipods individually in plastic cups (45-mm diameter, 20-mm height) in C-filtered, ultraviolet light (UV)-irradiated water. We ran the experiment at 22 ± 0.2°C (SD) on a 14:10 day:night cycle.

## Leaf-litter chemistry

We collected leaf litter from local forests immediately after abscission in autumn 2008. We air-dried the litter for 1 wk after collection and stored it through the winter. In spring before the experiment, we ground samples of dried litter to <0.5-mm particles with a Wiley mill and analyzed the particles for total N, total P, lignin, and total phenolics. N and P were analyzed at the Duke Environmental Stable Isotope Laboratory via stable isotope ratio mass spectrometry. We used 72% sulfuric acid to extract lignin and measured the difference between initial and final mass of leaf litter to quantify lignin content (modified method of C fractionation; Moorhead and Reynolds 1993). We used the Folin-Ciocalteu method to measure total phenolics (Graça et al. 2005). All analyses of leaf-

litter samples were done in triplicate to assess the consistency of our analytical procedures.

### Effects of leaf-litter species on amphipod life history and sexually selected traits

We conditioned the leaf litter outdoors in 200-L pools filled with 150 L of well water and inoculated with 400 mL of pond water from 5 ponds. We added 200 g of leaf litter from 1 of the 4 tree species to each pool. The pond water served as a common source of periphyton (algal and microbial assemblages that would increase in abundance over time), which plays an important role in conditioning leaves for macroinvertebrates (Kaushik and Hynes 1971, Bärlocher and Kendrick 1975a, b, Howarth and Fisher 1976). We conditioned leaf litter for 49 d before feeding it to amphipods to allow accumulation of a microbial biofilm on the leaf surface, which must occur for detritivores to consume the litter (Kaushik and Hynes 1971, Bärlocher and Kendrick 1975a, b, Howarth and Fisher 1976, Facelli and Pickett 1991). We collected leaves from the appropriate pool and used a hole punch to cut out 6-mm-diameter disks to feed to amphipods. Each amphipod received 3 leaf-litter disks every 3 d until they were 24 d old.

At the end of the 24-d experiment, we measured the head length of each amphipod. Head length is a reliable indicator of body size (Edwards and Cowell 1992) and is an important determinant of male mating success, female fecundity, and survival (Wellborn 1994, 1995). For male amphipods, we also measured posterior gnathopods (a large, claw-like appendage) and 2<sup>nd</sup> antennae. The posterior gnathopod is under sexual selection in *Hyaletella*—males with larger gnathopods have higher mating success (Wellborn 1995). No direct evidence exists that the 2<sup>nd</sup> antenna is under sexual selection in *Hyaletella*, but the trait is sexually dimorphic in this group (males have larger antennae than females) and is under sexual selection in isopods that share a similar mating biology (Bertin and Cézilly 2003, Wellborn and Cothran 2004, Cothran et al. 2012). We measured posterior gnathopod size as the maximum width of the propodus. We measured the 2<sup>nd</sup> antenna as the length of the 3<sup>rd</sup> peduncle, which is correlated with total antennal

length and the number of antennal segments. We made all measurements to a resolution of 0.024 mm with the aid of a stereomicroscope equipped with an ocular micrometer.

### Statistical analyses

We included ‘family’ (siblings originating from the same female) as a random effect in all analyses to account for potential genetic effects. We used a generalized linear model with a binomial distribution and a logit-link function to test for differences in survival across litter treatments. We did not include sex in the model because many of the amphipods died before reaching sexual maturity, and sex of immatures cannot be determined.

Differential survival among litter treatments led to an unbalanced design in tests for effects of litter on morphology. We used generalized linear mixed models based on restricted maximum likelihood methods, which provide better parameter estimates than general linear models for unbalanced data (SPSS 2005). We used the first model to test for effects of litter species, sex (individuals that survived the 24-d experiment were included in this analysis), and their interaction on body size (as head length). We used 2 additional models to test whether litter species affected development of male sexual traits, with head length as a covariate to account for allometric growth. We adjusted significance levels for multiple comparisons with the sequential Bonferroni method.

## RESULTS

### Leaf-litter chemistry

Leaf-litter species differed in nutrient, lignin, and polyphenolic content (Table 1). Differences were generally consistent with previous literature (Ostrofsky 1993, 1997). We expected some variation because of annual variation in climate, soil chemistry, and other growth factors. Elm was relatively nutritious and low in polyphenolics and lignin. Black cherry and black willow were relatively high in nutrients (N and P, respectively) and in plant secondary compounds (polyphenolics and lignin, respectively). Aspen was relatively nutrient poor and high in lignin.

Table 1. Chemical composition of the leaf species (mean molar ratio of nutrients and mean % dry mass of secondary compounds  $\pm$  1 SD) fed to amphipods. Analyses are based on triplicate measurements of pooled leaf powder.

Leaf species	C : N	C : P	Polyphenolics	Lignin
Elm	36.51 $\pm$ 0.61	823.03 $\pm$ 90.17	1.1 $\pm$ 0.01	4.9 $\pm$ 6.3
Black willow	47.11 $\pm$ 1.54	1074.93 $\pm$ 14.72	9.68 $\pm$ 0.03	12 $\pm$ 7.3
Black cherry	35.95 $\pm$ 1.37	1246.87 $\pm$ 72.78	3.5 $\pm$ 0.04	20.7 $\pm$ 4
Bigtooth aspen	56.27 $\pm$ 1.73	1206.88 $\pm$ 155.81	1.92 $\pm$ 0.03	23.9 $\pm$ 3.8

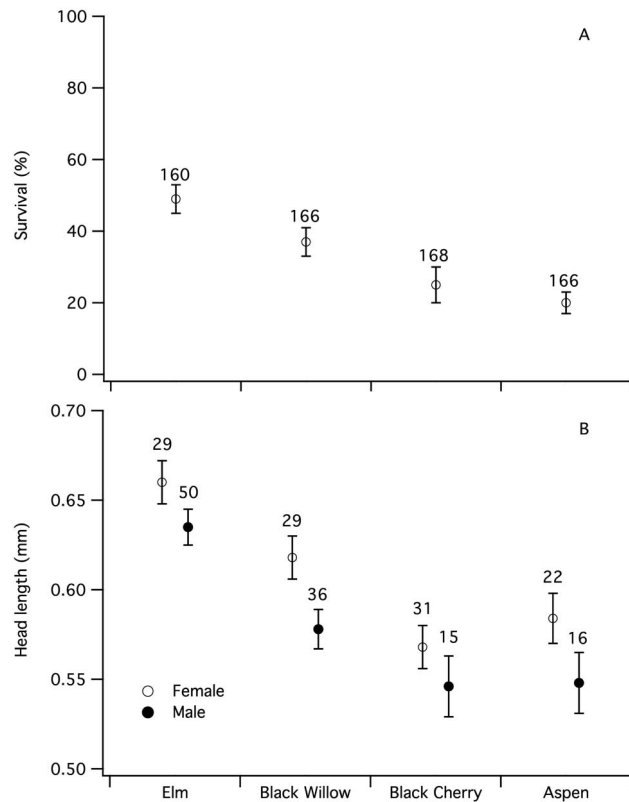


Figure 1. Mean ( $\pm 1$  SE) % survival until the end of the 24-d experiment (A) and head length (B) of amphipods reared on 4 leaf-litter species. Mean head length reflects differences in growth rates because all amphipods were the same age (24 d). Leaf-litter species are ordered on the  $x$ -axis from relatively high (high nutrient and low lignin and polyphenolic content) to low (low nutrient and high in lignin and polyphenolic content) quality. Sample size is shown above each marker.

### Effects of leaf-litter species on amphipod life-history and sexually selected traits

Amphipod survival differed among litter species ( $F_{3,656} = 11.133$ ,  $p < 0.001$ ; Fig. 1A). Amphipods survived better when reared on elm than on aspen and black cherry (pairwise comparisons, both  $p < 0.001$ ), and they survived better when reared on black willow than on aspen ( $p = 0.003$ ). Family also explained a significant amount of variation in survival (Wald  $Z = 2.815$ ,  $p = 0.005$ ).

Body size was affected by litter species ( $F_{3,211} = 21.627$ ,  $p < 0.001$ ) and sex ( $F_{1,216} = 10.842$ ,  $p = 0.001$ ), but not their interaction ( $F_{3,219} = 0.22$ ,  $p = 0.883$ ; Fig. 1B). Averaged across sexes, amphipods were 8, 14, and 16% larger when reared on elm than on black willow, aspen, or black cherry, respectively ( $p < 0.001$ ), and amphipods reared on black willow were 7% larger than amphipods reared on black cherry ( $p = 0.013$ ). Averaged across leaf treatments, females were 5% larger than males. Family did not affect body size (Wald  $Z = 1.199$ ,  $p = 0.231$ ).

For male sexual traits, allometric slopes were similar across litter species for the posterior gnathopod (litter treatment  $\times$  body size interaction:  $F_{3,109} = 1.438$ ,  $p = 0.236$ ) and 2<sup>nd</sup> antenna ( $F_{3,109} = 0.443$ ,  $p = 0.723$ ), a result that validated use of head length as a covariate in the analysis. Size-adjusted male posterior gnathopod differed among amphipods reared on different leaf-litter species ( $F_{3,91} = 8.856$ ,  $p < 0.001$ ; Fig. 2A). Gnathopods were 18, 21, and 38% larger when amphipods were reared on elm than on black willow, black cherry, and aspen, respectively (all  $p \leq 0.027$ ). Male gnathopod size was positively correlated with male head length ( $F_{1,108} = 21.673$ ,  $p < 0.001$ ), and the effect of family was marginally nonsignificant (Wald  $Z = 1.941$ ,  $p = 0.052$ ).

Size-adjusted male 2<sup>nd</sup> antennae length differed among amphipods reared on different litter species ( $F_{3,105} = 6.566$ ,  $p < 0.001$ ; Fig. 2B). Males reared on elm had antennae that were 12, 17, and 17% larger than males reared on black willow, black cherry, and aspen, respectively (all  $p \leq 0.006$ ). Male antenna size was positively correlated with male head

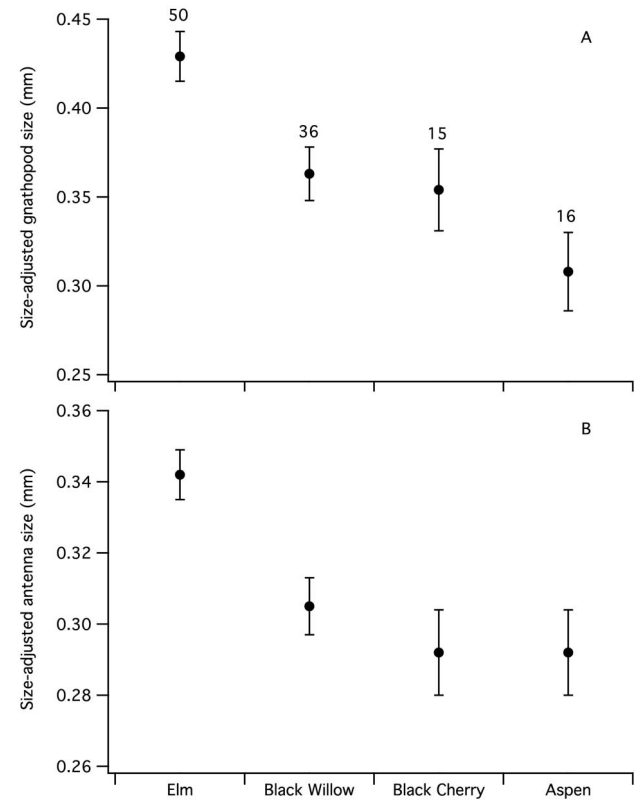


Figure 2. Estimated marginal mean ( $\pm 1$  SE) relative size (assessed at the grand mean for head length = 0.594 mm) of 2 male sexual traits, posterior gnathopods (A) and 2<sup>nd</sup> antenna (B), of amphipods reared on 4 leaf-litter species. The 2 traits were adjusted for size by including head length as a covariate in the analysis. Leaf-litter species are ordered as in Fig. 1. Sample sizes for both traits are provided on panel A.



length ( $F_{1,112} = 19.831$ ,  $p < 0.001$ ), but was not affected by family (Wald  $Z = 1.073$ ,  $p = 0.283$ ).

## DISCUSSION

We demonstrated that the leaf litter available to consumers can affect survival, growth, and the relative size of sexually selected traits. Amphipods reared on elm litter survived best, attained the largest body size in both sexes, and had relatively larger male sexual traits compared to amphipods raised on other litter species. This result is in agreement with our predictions. Our chemical analyses of the litter showed that elm litter had higher levels of nutrients and lower levels of plant secondary and structural compounds than the other 3 species (Ostrofsky 1997). Amphipods performed poorly on aspen litter, which was relatively nutrient poor with high lignin content, which would make aspen difficult to consume. Amphipod performance was intermediate (not as low as aspen or as high as elm) on black willow and black cherry litter, which have relatively high levels of P and N, respectively. However, black willow litter is high in polyphenolics, and black cherry litter is moderately high in both polyphenolics and lignin. We think it is likely that the moderate to high presence of these compounds explains the poorer performance of amphipods fed these 2 leaf-litter species. Collectively, the performance of amphipods on different leaf-litter species was consistent with predictions based on the nutritional quality and concentration of plant secondary and structural compounds in litter.

Our results provide data on how the stoichiometric imbalances between detritivores and their leaf-litter resource affect consumers (Cross et al. 2003, 2005). C:P and C:N of leaf litter in our experiment ranged from 823 (elm) to 1247 (black cherry) and 36 (black cherry) to 56 (bigtooth aspen), respectively. These values fall within the range of litter C:nutrient ratios found in other studies (Cross et al. 2003, 2005). We did not measure *Hyalella* C:nutrient ratios, but C:P of amphipods raised in the laboratory and collected from lakes ranged from 120 to 240 in a study by Goos et al. (2014). Based on these data, amphipods in our experiment were dealing with strong imbalances (difference in ratios between leaf litter and amphipod). If we use the highest amphipod C:P (240) estimated by Goos et al. (2014), the imbalance ranged from 583 (elm) to 1007 (black cherry). We have no data on amphipod C:N, but our results are consistent with those on other detritivores (caddisflies and craneflies) that also performed poorly on high-C:N leaf litter (Iversen 1974, Tuchman et al. 2002). This variation in the stoichiometric imbalances imposed by the leaf species in our study matches well with knowledge on the effects of P on growth and development of sexual traits (Cothran et al. 2012). Amphipods grew faster and developed larger sex-

ual traits when reared on elm, which is high in P, than on other leaf species.

Our results indicate that changes in the chemical quality of litter may induce shifts in consumer body size, which can affect several ecological interactions (Calder 1996, Werner and Gilliam 1984). In *Hyalella*, body size is an important determinant of fecundity, competitive ability, and susceptibility to predators. Fecundity and competitive ability increase with body size in *Hyalella*, and these patterns are consistent within and across species (Wellborn 1994, Cothran et al. 2013a). Shifts in body size also can alter predator-prey interactions. Whether small body size is advantageous depends on the type of predator in the environment (Wellborn et al. 1996). Therefore, changes in leaf-litter species may affect species interactions with basal resources, competitor species, and predators in aquatic food webs (Wellborn 2002).

The quality of available litter may influence sexual selection on traits in a population. Trait-based indices of a male's competitiveness or attractiveness are expected to be more informative in low- than in high-quality habitats because differences among males in quality (ability to acquire resources to develop the indicator trait) are more exaggerated in these environments (Rowe and Houle 1996, David et al. 2000). Strong empirical evidence indicates that resource quality or quantity can strongly affect the sexual-trait variation available for selection (David et al. 2000, Cotton et al. 2004) and has recently been demonstrated for *Hyalella* (Cothran and Jeyasingh 2010, Cothran et al. 2012). We have demonstrated for the first time that sexually selected traits are sensitive to changes in leaf-litter resources, probably because of differences among leaf-litter species in nutrient content and availability.

## Linking subsidies to ecosystem function and forest diversity

Our results add to a growing body of literature that highlights the importance of linking subsidy quality with consumer phenotypes to understand the effect of subsidies on nutrient cycling (e.g., Cohen et al. 2012, Stephens et al. 2013, Stoler and Relyea 2013). Shifts in the nutritional quality of leaf litter can substantially alter its palatability and nutritional value to microbes and larger consumers. We showed that these changes can have substantial effects on the growth and survival of consumers, and more subtle effects on morphological traits. Other investigators have shown that these effects can affect population dynamics (Reiskind et al. 2009), which can alter the total biomass of consumers and substantially alter the quantity of energy and nutrients processed (Batzer and Wissinger 1996). Organisms in habitats are connected with the surrounding ecosystem through processes, such as respiration, emergence, and predator-prey interactions (Beard et al. 2002,

Hoekman et al. 2011), so changes in consumer population dynamics can have ecosystem-wide consequences.

Interactions between consumer species can alter nutrient cycling and should be taken into account when considering how individual phenotypes may scale up to yield changes at the ecosystem level. Detritivores historically have been regarded as a group of redundant species, but detritivore species often show strong complementary and facilitative patterns when using leaf litter (Arsuffi and Suberkropp 1989, Graça et al. 1993a, b, Cardinale et al. 2002, Zimmer et al. 2004). Such patterns may buffer litter-based food webs from changes in forest composition. The effect of changing litter composition on other detritivore species and potential feedbacks to ecosystem processes (e.g., litter decomposition) warrants further attention (Gessner et al. 2010).

Field studies are necessary to assess whether our laboratory results are indicative of how differences in forest composition affect consumer populations and their ecosystems in nature. Changes in forest composition may have weak effects on wetland communities if consumer species can switch to nonlitter resources or if shifts in forest composition are complex. For example, the effect of changing litter species on amphipod populations may be mitigated by the omnivory found in this group (MacNeil et al. 1997). Moreover, changes in forest composition may include shifts to different groups of tree species rather than to monocultures (Abrams 2003). If some species in the new group are palatable, changes in forest composition may have weak effects on consumers. However, many small wetlands are likely to experience local dominance by a single tree species, so our results are still suggestive of natural phenomenon.

## Conclusions

Tremendous spatial and temporal variation exists in the composition of tree species that contribute to the leaf litter in wetlands (Ostrofsky 1997). Our work suggests that natural and human-driven changes in forest composition may alter the abundance and biomass of consumers and trait-mediated ecological and social interactions. These changes in forest composition have important implications for conserving the biota of wetlands (Stoler and Relyea 2011), but they may present an opportunity to explore some pressing ecological and evolutionary questions. For example, the evolutionary responses of wetland organisms to changes in forest composition are unexplored and may provide a powerful system to address the importance of rapid evolutionary change on ecological time scales (Post and Palkovacs 2009). Changes in the composition of leaf-litter subsidies to wetlands may provide opportunities to assess links between variation in resource quality and opportunity for sexual selection in nature. These links are well established in laboratory systems (e.g., David et al. 2000, Cotton et al. 2004, Cothran and Jeyasingh 2010, Cothran et al.

2012), but few examples are available from nature (but see Robinson et al. 2008).

## ACKNOWLEDGEMENTS

We thank S. Estrada for measuring amphipods. This research was supported by a National Science Foundation grant awarded to RAR (DEB 11-19430). We thank Associate Editor Manuel Graça, Pamela Silver, and 4 anonymous referees for constructive comments that improved the manuscript.

## LITERATURE CITED

- Abrams, M. D. 1998. The red maple paradox. *BioScience* 48: 355–364.
- Abrams, M. D. 2003. Where has all the white oak gone? *BioScience* 53:927–939.
- Ardón, M., and C. M. Pringle. 2008. Do secondary compounds inhibit microbial- and insect-mediated leaf breakdown in a tropical rainforest stream, Costa Rica? *Oecologia* (Berlin) 155: 311–323.
- Arsuffi, T. L., and K. Suberkropp 1989. Selective feeding by shredders on leaf-colonizing stream fungi: comparison of macroinvertebrate taxa. *Oecologia* (Berlin) 79:30–37.
- Badyaev, A. V., and A. Qvarnström. 2002. Putting sexual traits into the context of an organism: a life-history perspective in studies of sexual selection. *Auk* 119:301–310.
- Bärlocher, F., and B. Kendrick. 1975a. Assimilation efficiency of *Gammarus pseudolimnaeus* (Amphipoda) feeding on fungal mycelium or autumn-shed leaves. *Oikos* 26:55–59.
- Bärlocher, F., and B. Kendrick. 1975b. Leaf-conditioning by microorganisms. *Oecologia* (Berlin) 20:359–362.
- Batzer, D. P., and S. A. Wissinger. 1996. Ecology of insect communities in nontidal wetlands. *Annual Review of Entomology* 41:75–100.
- Beard, K. H., K. A. Vogt, and A. Kulmatiski. 2002. Top-down effects of a terrestrial frog on forest nutrient dynamics. *Oecologia* (Berlin) 133:583–593.
- Bertin, A., and F. Cézilly. 2003. Sexual selection, antennae length and mating advantage of large males in *Asellus aquaticus*. *Journal of Evolutionary Biology* 16:591–500.
- Bunker, D. E., F. DeClerck, J. C. Bradford, and R. K. Colwell. 2005. Species loss and aboveground carbon storage in a tropical forest. *Science* 310:1029–1031.
- Calder, W. A. 1996. Size, function, and life history. Dover Publications, Mineola, New York.
- Cardinale, B. J., M. A. Palmer, and S. L. Collins. 2002. Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature* 415:426–429.
- Cohen, J. S., J. C. Maerz, and B. Blossey. 2012. Traits, not origin, explain impacts of plants on larval amphibians. *Ecological Applications* 22:218–228.
- Cothran, R. D., K. A. Henderson, D. Schmidenberg, and R. A. Relyea. 2013a. Phenotypically similar but ecologically distinct: differences in competitive ability and predation risk among amphipods. *Oikos* 122:1429–1440.
- Cothran, R. D., and J. D. Jeyasingh. 2010. Condition dependence of a sexually selected trait in a crustacean species complex: importance of the ecological context. *Evolution* 64:2535–2546.

- Cothran, R. D., A. R. Stiff, K. Chapman, G. A. Wellborn, and R. A. Relyea. 2013b. Reproductive interference via interspecific pairing in an amphipod species complex. *Behavioral Ecology and Sociobiology* 67:1357–1367.
- Cothran, R. D., A. R. Stiff, P. D. Jeyasingh, and R. A. Relyea. 2012. Eutrophication and predation risk interact to affect sexual trait expression and mating success. *Evolution* 66:708–719.
- Cotton, S., K. Fowler, and A. Pomiankowski. 2004. Condition dependence of sexual ornament size and variation in the stalk-eyed fly *Cyrtodiopsis dalmanni* (Diptera: Diopsidae). *Evolution* 58:1038–1046.
- Cross, W. F., J. P. Benstead, P. C. Frost, and S. A. Thomas. 2005. Ecological stoichiometry in freshwater benthic systems: recent progress and perspectives. *Freshwater Biology* 50:1895–1912.
- Cross, W. F., J. P. Benstead, A. D. Rosemond, and J. B. Wallace. 2003. Consumer-resource stoichiometry in detritus-based streams. *Ecology Letters* 6:721–732.
- Danger, M., J. A. Funck, S. Devin, J. Heberle, and V. Felten. 2013. Phosphorus content in detritus controls life-history traits of a detritivore. *Functional Ecology* 27:807–815.
- David, P., T. Bjorksten, K. Fowler, and A. Pomiankowski. 2000. Condition-dependent signalling of genetic variation in stalk-eyed flies. *Nature* 406:186–188.
- Edwards, T., and B. Cowell. 1992. Population-dynamics and secondary production of *Hyalella azteca* (Amphipoda) in *Typha* stands of a subtropical Florida lake. *Journal of the North American Benthological Society* 11:69–79.
- Elser, J. J., K. Acharya, M. Kyle, J. Cotner, W. Makino, T. Markow, T. Watts, S. Hobbie, W. Fagan, J. Schade, J. Hood, and R. W. Sterner. 2003. Growth rate–stoichiometry couplings in diverse biota. *Ecology Letters* 6:936–943.
- Facelli, J. M., and S. T. A. Pickett. 1991. Plant litter: its dynamics and effects on plant community structure. *Botanical Review* 57:1–32.
- Frost, P. C., J. P. Benstead, W. F. Cross, J. Hillebrand, J. H. Larson, M. A. Xenopoulos, and T. Yoshida. 2006. Threshold element ratios of carbon and phosphorus in aquatic consumers. *Ecology Letters* 9:774–779.
- Frost, P. C., and J. J. Elser. 2002. Growth responses of littoral mayflies to the phosphorus content of their food. *Ecology Letters* 5:232–240.
- Gessner, M. O., and E. Chauvet. 1994. Importance of stream microfungi in controlling breakdown rates of leaf litter. *Ecology* 75:1807–1817.
- Gessner, M. O., C. M. Swan, C. K. Dang, B. G. McKie, R. D. Bardgett, D. H. Wall, and S. Hattenschwiler. 2010. Diversity meets decomposition. *Trends in Ecology Evolution* 25:372–380.
- Goos, J. M., B. J. French, R. A. Relyea, R. D. Cothran, and P. D. Jeyasingh. 2014. Sex-specific plasticity in body phosphorus content of *Hyalella* amphipods. *Hydrobiologia* 722:93–102.
- Graça, M. A. S., F. Bärlocher, and M. O. Gessner. 2005. Methods to study litter decomposition: a practical guide. Springer, Berlin, Germany.
- Graça, M. A. S., L. Maltby, and P. Calow. 1993a. Importance of fungi in the diet of *Gammarus pulex* and *Asellus aquaticus* I: feeding strategies. *Oecologia* (Berlin) 93:139–144.
- Graça, M. A. S., L. Maltby, and P. Calow. 1993b. Importance of fungi in the diet of *Gammarus pulex* and *Asellus aquaticus* II: effects on growth, reproduction, and physiology. *Oecologia* (Berlin) 96:304–309.
- Hoekman, D., J. Dreyer, R. D. Jackson, P. A. Townsend, and C. Gratton. 2011. Lake to land subsidies: experimental addition of aquatic insects increases terrestrial arthropod densities. *Ecology* 92:2063–2072.
- Howarth, R. W., and S. G. Fisher. 1976. Carbon, nitrogen, and phosphorus dynamics during leaf decay in nutrient-enriched stream microecosystems. *Freshwater Biology* 6:221–228.
- Iversen, T. M. 1974. Ingestion and growth in *Sericostoma personatum* (Trichoptera) in relation to the nitrogen content of ingested leaves. *Oikos* 25:278–282.
- Kaushik, N. K., and H. B. N. Hynes. 1971. The fate of the dead leaves that fall into streams. *Archiv für Hydrobiologie* 68:465–515.
- Kokko, H., M. D. Jennions, and R. Brooks. 2006. Unifying and testing models of sexual selection. *Annual Review of Ecology, Evolution, and Systematics* 37:43–66.
- MacNeil, C., J. T. A. Dick, and R. W. Elwood. 1997. The trophic ecology of freshwater *Gammarus* spp. (Crustacea: Amphipoda): problems and perspectives concerning the functional feeding group concept. *Biological Reviews* 72:349–364.
- Maerz, J. C., C. J. Brown, C. T. Chapin, and B. Blossey. 2005. Can secondary compounds from an invasive plant affect larval amphibians? *Functional Ecology* 19:970–975.
- Melillo, J. M., J. D. Aber, and J. F. Muratore. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* 63:621–626.
- Moorhead, D. L., and J. F. Reynolds. 1993. Changing carbon chemistry of buried creosote bush litter during decomposition in the Northern Chihuahuan Desert. *American Midland Naturalist* 130:83–89.
- Moser, W. K., E. L. Barnard, R. F. Billings, S. J. Crocker, M. E. Dix, A. N. Gray, G. G. Ice, M. Kim, R. Reid, S. U. Rodman, and W. H. Williams. 2009. Impacts of nonnative invasive species on US forests and recommendations for policy and management. *Journal of Forestry* 107:320–327.
- Ostrofsky, M. L. 1993. Effect of tannins on leaf processing and conditioning rates in aquatic ecosystems: an empirical approach. *Canadian Journal of Fisheries and Aquatic Sciences* 50:1176–1180.
- Ostrofsky, M. L. 1997. Relationship between chemical characteristics of autumn-shed leaves and aquatic processing rates. *Journal of the North American Benthological Society* 16:750–759.
- Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* 147:289–316.
- Post, D. M., and E. P. Palkovacs. 2009. Eco-evolutionary feedbacks in community and ecosystem ecology: interactions between the ecological theatre and the evolutionary play. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences* 364:1629–1640.
- Reiskind, M. H., K. L. Greene, and L. P. Lounibos. 2009. Leaf species identity and combination affect performance and oviposition choice of two container mosquito species. *Ecological Entomology* 34:447–456.
- Richardson, J. S., Y. Zang, and L. B. Marczak. 2009. Resource subsidies across the land–freshwater interface and responses in

- recipient communities. *River Research Applications* 26:55–66.
- Robinson, M. R., J. G. Pilkington, T. H. Clutton-Brock, J. M. Pemberton, and L. E. B. Kruuk. 2008. Environmental heterogeneity generates fluctuating selection on a secondary sexual trait. *Current Biology* 18:751–757.
- Rowe, L., and D. Houle. 1996. The lek paradox and the capture of genetic variance by condition dependent traits. *Proceedings of the Royal Society of London Series B: Biological Sciences* 263:1415–1421.
- Rubbo, M. J., J. J. Cole, and J. M. Kiesecker. 2006. Terrestrial subsidies of organic carbon support net ecosystem production in temporary forest ponds: evidence from an ecosystem experiment. *Ecosystems* 9:1170–1176.
- SPSS. 2005. Linear mixed-effects modelling in SPSS: an introduction to the mixed procedure. SPSS technical report. SPSS, Inc., Chicago, Illinois.
- Stephens, J. P., K. A. Berven, and S. D. Tiegs. 2013. Anthropogenic changes to leaf litter input affect the fitness of a larval amphibian. *Freshwater Biology* 58:1631–1646.
- Sterner, R. W., and J. J. Elser. 2002. *Ecological stoichiometry: the biology of elements from molecules to the biosphere*. Princeton University Press, Princeton, New Jersey.
- Stoler, A. B., and R. A. Relyea. 2011. Living in the litter: the influence of tree leaf litter on wetland communities. *Oikos* 120:862–872.
- Stoler, A. B., and R. A. Relyea. 2013. Leaf litter induces morphological and developmental changes in larval amphibians. *Ecology* 94:1594–1603.
- Taylor, B. R., D. Parkinson, and W. F. J. Parsons. 1989. Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. *Ecology* 70:97–104.
- Tuchman, N. C., R. G. Wetzel, S. T. Rier, K. A. Wahtera, and J. A. Teeri. 2002. Elevated atmospheric CO<sub>2</sub> lowers leaf litter nutritional quality for stream ecosystem food webs. *Global Change Biology* 8:163–170.
- Webster, J. R., and E. F. Benfield. 1986. Vascular plant breakdown in freshwater ecosystems. *Annual Review of Ecology and Systematics* 17:567–594.
- Wellborn, G. A. 1994. Size-biased predation and prey life histories: a comparative study of freshwater amphipod populations. *Ecology* 75:2104–2117.
- Wellborn, G. A. 1995. Determinants of reproductive success in freshwater amphipod species that experience different mortality regimes. *Animal Behaviour* 50:353–363.
- Wellborn, G. A. 2002. Trade-off between competitive ability and antipredator adaptation in a freshwater amphipod species complex. *Ecology* 83:129–136.
- Wellborn, G. A., and R. E. Broughton. 2008. Diversification on an ecologically constrained adaptive landscape. *Molecular Ecology* 17:2927–2936.
- Wellborn, G. A., and R. D. Cothran. 2004. Phenotypic similarity and differentiation among sympatric cryptic species in a freshwater amphipod species complex. *Freshwater Biology* 49:1–13.
- Wellborn, G. A., D. K. Skelly, and E. E. Werner. 1996. Mechanisms creating community structure across a freshwater habitat gradient. *Annual Review of Ecology and Systematics* 27:337–363.
- Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics* 15:393–425.
- Zimmer, M., S. C. Pennings, T. L. Buck, and T. H. Carefoot. 2004. Salt marsh litter and detritivores: a closer look at redundancy. *Estuaries* 27:753–769.