



The effects of novel leaf litter deposition on competitive, predator–prey and host–parasite interactions of American toad larvae

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Abstract Wetland plant communities are changing rapidly due to a wide range of human activities. The deposition of leaf litter from novel plant communities can alter both the chemical and physical habitat of aquatic ecosystems. Lesser understood are the ecological consequences of novel leaf litter inputs in aquatic communities. Toward this goal, we used two plant invasion scenarios (comparing native black huckleberry to exotic autumn olive and native swamp loosestrife to exotic purple loosestrife) to simulate a shift in wetland plant communities. In this study, we investigated the effects of novel leaf litter leachates on three aquatic ecological interactions: intraspecific competition, predation and parasitism. We examined how leaf litter leachates influence the interactions of American toad larvae (*Anaxyrus americanus*) with their conspecifics, a dragonfly predator (*Anax spp.*) and a trematode parasite (Echinostomatidae). We

found that leaf litter type influenced competitive interactions only for the huckleberry versus autumn olive comparison. We did not detect any effects of leaf litter type on predator–prey interactions. Finally, litter type strongly influenced host–parasite interactions for both leaf litter comparisons, altering host susceptibility, parasite survival and net infection rates. These results highlight the breadth of potential ecological repercussions of shifting wetland plant communities for native ecosystems.

Keywords Echinostome · *Bufo* · *Lythrum salicaria* · *Elaeagnus umbellata* · *Gaylussacia baccata* · *Decodon verticillatus*

Introduction

Over half of the world's wetlands have been lost, primarily due to development and human activity (Davidson 2014). Those remaining face degradation from pollution, climate change, invasive species and other threats (Kingsford et al. 2016). These factors may in turn contribute to changes in wetland plant communities. For instance, invasive plants are a particularly prominent threat in wetland ecosystems (Zedler and Kercher 2004). Exotic invasive plants may outcompete natives due to rapid growth and high fecundity among other factors (Pyšek and Richardson

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2007; Dickson et al. 2012), often leading to reduced plant community diversity (Hejda et al. 2009). Changes in plant community composition alter both the chemical and physical habitat of wetlands (Bais et al. 2003). One way in which this occurs, which has garnered recent attention, is through the deposition of senescent tissues (i.e., leaf litter; as reviewed in Stoler and Relyea 2020). Leaf litter represents a major allochthonous source of nutrients in many lotic and lentic systems (Fisher and Likens 1973; Polis et al. 1997). Changes in leaf litter composition have been shown to alter wetland community composition (Stoler and Relyea 2011, 2016; Wymore et al. 2018; Montez et al. 2021) and ecosystem functioning (Cameron and LaPoint 1978; Farrer and Goldberg 2009; Ehrenfeld 2010; Earl et al. 2014; Wymore et al. 2018). As wetland plant communities continue to change under human influence, it will be essential to understand how the deposition of novel leaf litter affects wetland ecosystems.

As exotic plant invasions are a major driver of change in wetland plant communities (Zedler and Kercher 2004), instances of plant invasions represent a useful tool for examining the mechanisms by which novel leaf litter inputs may elicit changes in wetland ecosystems. At the simplest level, these impacts may stem from direct effects on specific taxa. For instance, leachates from invasive plants can have lethal and sublethal effects on sensitive taxa such as anurans (Maerz et al. 2005; Adams and Saenz 2012; Sacerdote and King 2014; Earl and Semlitsch 2015) and invertebrates (Canhoto and Laranjeira 2007; Going and Dudley 2008; Borth et al. 2018; Wilkins et al. 2020). Direct, density-mediated effects may indirectly affect other community members. For example, labile, nutrient-dense litter can promote algal growth directly, indirectly increasing the development rate of primary consumers (i.e., bottom-up effects; Cohen et al. 2014; Stephens et al. 2013). In addition, trait-mediated effects of leachates on factors such as movement (Saenz and Adams 2017; Burraco et al. 2018) and predator recognition (Dodd and Buchholz 2018) may influence ecological interactions. Finally, changes in leaf litter inputs may further alter ecological interactions via changes to the chemical or physical conditions in which they take place. For instance, novel leaf litter inputs may alter wetland surface cover, water chemistry and the structure of benthic refugia, potentially mediating chemical and visual detection, as well

as encounter frequency, between predators and prey (Stoler and Relyea 2013b; Jabiol et al. 2014). While the direct effects of various leaf litters have been documented for a wide range of wetland taxa, fewer studies have examined the effects of changes in leaf litter composition on specific ecological interactions (Stoler and Relyea 2020). Examining the impacts of these leaf litters on not only wetland organisms, but also their interactions, is critical to developing a holistic understanding of how plant communities shape diversity and ecosystem processes in aquatic systems.

The goal of this study was to investigate how a shift in wetland plant community composition can influence aquatic ecological interactions via the deposition of novel leaf litter. As exotic invasive species are a major driver of plant community change (Zedler and Kercher 2004), we examined two pairs of native and invasive plants that share similar habitat preferences (black huckleberry [*Gaylussacia baccata*–Ericaceae] versus autumn olive [*Elaeagnus umbellata*–Elaeagnaceae] and swamp loosestrife [*Decodon verticillatus*–Lythraceae] versus purple loosestrife [*Lythrum salicaria*–Lythraceae]). We utilized anuran larvae as our focal taxa for this study because previous studies have demonstrated a broad range of direct and indirect effects—ranging from sublethal (e.g., altered growth, development and behavior Brown et al. 2006; Saenz and Adams 2017; DiGiacopo et al. 2018) to lethal (i.e., reduced survival; Adams and Saenz 2012; Milanovich et al. 2016)—of changes in leaf litter composition on anurans. Therefore, in this study, we evaluated the effects of leaf litter type on amphibian ecology, including competitive, predator–prey and host–parasite interactions.

Methods

Model plants

To address our objectives, we used leaf litter from one pair of native and invasive herbaceous plants (swamp loosestrife and purple loosestrife) and one pair of native and invasive shrubs (black huckleberry and autumn olive). We chose these native and invasive pairs to evaluate the ecological impacts of shifting plant communities because they represent likely scenarios of plant invasions in wetlands of the eastern

USA. Purple loosestrife is a widespread invasive species across much of North America, known to create near monocultures in heavily invaded wetlands (Thompson et al. 1987; Weiher et al. 1996; Blossey et al. 2001). Swamp and purple loosestrife are frequently found together or occupying similar habitats, including semi-permanently flooded wetland soils (Blossey et al. 1994). Autumn olive is woody, nitrogen-fixing species prevalent in the eastern USA, which is recognized as a highly competitive and problematic invader in both open and understory habitats (Dornbos et al. 2016). While autumn olive typically invades upland communities, it has also been noted establishing in riparian habitats (Kohri et al. 2002, 2011; Church et al. 2004) and can be found along the banks of disturbed wetlands in close proximity to native black huckleberry plants (DD personal observation).

On 18 September 2017, we collected swamp loosestrife and purple loosestrife leaves from Cutler Pond (Binghamton, NY; 42° 07' 45.3" N, 75° 54' 31.2" W). On 15 October 2017, we collected leaves from black huckleberry and autumn olive from Binghamton University's Nature Preserve (42° 04' 55.6" N 75° 58' 05.0" W). At both of our study sites, leaf litter from each species is deposited into nearby water bodies. For all species, we collected leaves from plants less than one meter from the water's edge. We collected leaves directly from the plants to prevent variable degradation between leaf litter types, which may impact leaf tissue chemistry. We placed leaf litter in 100-L indoor wading pools at 25 °C on a standard 14:10 light/dark cycle to air dry for approximately one month before transferring it to plastic garbage bags for storage until the start of the mesocosm experiment.

Model amphibian

To evaluate the effect of leaf litter on competition, predator–prey and host–parasite interactions, we chose larval American toads (*Anaxyrus americanus*) as our model amphibian. American toads are native throughout much of the eastern USA and are commonly found inhabiting ponds and wetlands with our four plant species. On 16 May 2018, we collected 10 partial clutches of American toad eggs from Aqua Terra Wilderness Area in Binghamton, NY (42° 01' 55.5" N, 75° 56' 09.8" W). Eggs were reared at Binghamton University's Ecological Research

Facility (ERF) in a 100-L outdoor pools, filled with 90-L aged well water and covered with 70% shade cloth. Once hatchlings reached the free-feeding tadpole stage (Gosner stage 25; Gosner 1960), we fed them rabbit chow ad libitum until the start of the experiments.

Experiment 1: effects of leaf litter on competitive interactions

To understand the effect of leaf litter on competitive interactions, we conducted a four (swamp loosestrife, purple loosestrife, black huckleberry or autumn olive litter) x two (low vs. high competition) mesocosm experiment. We replicated each of these treatments 12 times for a total of 96 experimental units. Experimental units were spatially randomized, 19 L mesocosms (plastic pails with a diameter of 32 cm and height of 36 cm) covered with 70% shade cloth lids. On 27 April, we filled each mesocosm with 17 L of well water and added 17 g of dried swamp loosestrife, purple loosestrife, black huckleberry or autumn olive leaf litter to each mesocosm and did not disturb mesocosms until 20 May to allow litter to begin naturally breaking down. We used a litter concentration of 1 g L⁻¹ to mimic those found in natural wetland settings (Maerz et al. 2005; Rubbo et al. 2008; Stoler and Relyea 2013b).

We then introduced periphyton and phytoplankton communities to the mesocosms on 20 May in 500-mL aliquots of filtered pond water from Binghamton University's nature preserve. On 28 May, the average dissolved oxygen concentration in low density mesocosms was 1.14 mg L⁻¹. As *Anaxyrus* tadpoles exhibit may experience stress (Wassersug and Seibert 1975) or reduced survival (Maerz et al. 2005) below 4 mg L⁻¹, we chose to accelerate the natural increase in dissolved oxygen concentrations by adding oxygenated well water to each mesocosm on 4 June (0.5 L) and 6 June (1 L). On 7 June, the average dissolved oxygen concentrations were 4.40 ± 0.41 mg L⁻¹ for autumn olive, 3.08 ± 0.30 mg L⁻¹ for black huckleberry, 3.72 ± 0.52 mg L⁻¹ for purple loosestrife and 2.20 ± 0.28 mg L⁻¹ for swamp loosestrife. Next, on 8 June, we added 100 mL aliquots of water containing zooplankton (cladocerans and copepods) collected from a nearby pond (42° 07' 33.3" N 75° 54' 34.6" W). Finally, on 11 June, we size-selected 576 tadpoles from common garden pools and added four and eight

individuals to the low competition and high competition treatments, respectively. Both densities are well within the range of *Anaxyrus americanus* larval densities found in natural wetlands (Brockelman 1969; Petranks 1989). To ensure that tadpole handling did not cause mortality in our experiments, we similarly handled 20 additional individuals and assessed their survival after 24 h (we found 100% survival). Initial tadpole snout-vent length “SVL” was 7.39 ± 0.15 mm (average $\pm$ standard error) and Gosner (i.e., developmental) stage was 29.65 ± 0.29 (Gosner 1960).

Throughout the experiment, we monitored water chemistry and the abundance of phytoplankton and periphyton in all treatments (see Electronic Supplementary Material for extended methods and results). On 27 June, we drained all mesocosms, euthanized surviving tadpoles and measured SVL and Gosner stage. However, a subset of tadpoles ($n = 114$) from the low density treatments were first transferred to the laboratory to be used in an additional 24-h experiment (see “Experiment 3: Effects of leaf litter on host-parasite interactions”) before being euthanized.

Statistical analysis To understand the impacts of leaf litter on amphibian metrics at both high and low tadpole densities, we conducted separate multivariate analyses of variance (MANOVA) for each leaf litter pair, with percent survival, SVL and Gosner stage as dependent variables. We rank-transformed these data for nonparametric analysis because they did not meet assumptions of normality. To further investigate any significant multivariate effects, we conducted univariate ANOVAs (Pituch and Stevens 2015). For all significant univariate effects, we conducted Bonferroni-adjusted pairwise comparisons. We included the subset of animals that were preserved 24 h later in these statistical analyses because it is highly unlikely that the additional time and treatments (24 h parasite exposure; described in Experiment 3) significantly altered SVL or Gosner stage (on average, tadpoles only grew by 2.2% of their initial length and developed an additional 1.6% of their initial Gosner stage each day, from 12 to 27 June).

Experiment 2: effects of leaf litter on predator–prey interactions

To understand the effect of leaf litter on predator–prey interactions, we conducted a two-phase experiment. In

the first phase, we raised tadpoles in mesocosms with swamp loosestrife, purple loosestrife, black huckleberry or autumn olive litter. Concurrent with the competition experiment, we generated 12 replicates of each leaf litter community (48 mesocosms total), using the identical methods described for the “low competition” treatment in Experiment 1. In the second phase, we conducted a predation assay by evaluating the susceptibility of tadpoles reared in different litter communities to predation by a damselfly nymph (*Anax spp.*). *Anax* are common predators of larval anurans and rely heavily on visual detection of prey, such that increases in tadpole movement increase predation risk (Skelly 1994). Relative to other anurans, the high activity level and high tail beat frequency, low propulsion efficiency and minimal axial musculature make *Anaxyrus* tadpoles highly susceptible to predation by odonate nymphs (Wassersug and Hoff 1985; Chovanec 1992).

For the predation assay, on 30 May 2018 we collected 60 *Anax* nymphs from the Finch Hollow Nature Preserve in Binghamton, NY ($42^{\circ} 04' 49.9''$ N $75^{\circ} 59' 11.1''$ W) and separated them into individual 1-L containers filled with aged well water. We fed dragonflies one laboratory-reared wood frog (*Lithobates sylvaticus*) tadpole every two days and conducted water changes once per week, until the start of the predation experiment.

Before introducing predators, on 26 June, we counted the number of surviving tadpoles in each predation mesocosm. To facilitate monitoring predatory events, we strained 10 L of litter water from each mesocosm through a fine-mesh aquarium net into a 17-L tub and placed the surviving tadpoles into these units. Because *Anax* nymphs rely primarily on movement to initiate strikes, and because encounters with other tadpoles might influence activity, we only utilized mesocosm replicates with 100% tadpole survival ($n = 10$ for autumn olive, $n = 8$ for black huckleberry, $n = 4$ for purple loosestrife, $n = 2$ for swamp loosestrife). Because of the low replicate availability in purple and swamp loosestrife treatments, we excluded the purple loosestrife versus swamp loosestrife comparison from predation trials. After a one-hour acclimation period, we added 1 *Anax* nymph to each experimental unit. The average weight of predators in each treatment was 0.642 ± 0.038 g (autumn olive) and 0.645 ± 0.041 g (black huckleberry). After six hours, we removed and euthanized all

surviving tadpoles. We chose this time based on pilot studies that showed 50% mortality at six hours. During the six hours, we directly monitored capture events.

Statistical analysis To analyze differences in survival between leaf litter treatments preceding the addition of predators, we compared the proportion of tadpoles surviving for each leaf litter pair using Mann–Whitney U tests. We then conducted separate Mann–Whitney U tests to assess whether leaf litter influenced tadpole predator avoidance (for autumn olive versus black huckleberry only). We utilized nonparametric tests because the data did not meet assumptions of normality.

Experiment 3: effects of leaf litter on host–parasite interactions

To understand the effects of leaf litter on host–parasite interactions, we used trematodes (Echinostomatidae) which are common parasites of amphibian larvae. The Echinostomatidae are a widespread family of trematode flatworms, with a complex life cycle that utilizes multiple hosts (Smyth and Halton 1983). We focus on the free-swimming cercarial stage of the parasite which emerges from snails (first intermediate hosts) and encysts in the kidneys of larval amphibians (second intermediate host). Cercariae locate amphibians via physical (e.g., water turbulence and shadows) or chemical (i.e., chemotaxis) cues (Haas 2003; Sears et al. 2012). Symptoms of echinostomatid infections are dose-dependent and include hemorrhaging, edema and in some cases mortality (Huffman and Fried 2012). *Anaxyrus* tadpoles can be found in wetlands containing echinostomatid-infected snails and are relatively susceptible to echinostomatid infection compared to other amphibians native to the eastern USA (Rohr et al. 2010; Sears et al. 2012).

We conducted four experiments, examining the effects of leaf litter on the parasites alone and the hosts alone, as well as the net effects on their interaction in a controlled (laboratory) and a more realistic (mesocosm) setting:

Parasite survival assay (parasite infectivity) To isolate the effect of leaf litter on parasite infectivity, we exposed trematode cercariae to the four leaf litter solutions or pure well water and tracked time to death. We examined trends in survival because previous research suggests that it is a highly reliable proxy for infectivity in echinostomatids (Pechenik and Fried

1995). For this study, experimental units were 24-well plates, filled with 1945 μL of either leaf litter solution or well water plus 5 μL of Trypan Blue solution (ThermoFisher Scientific; Waltham, MA, USA) to aid in visualization of cercariae mortality (Jones et al. 2019). In each of five 24-well plates, we replicated each litter solution and a well water control four times (20 replicates per treatment for a total of 100 replicates). To obtain parasites for this study, on 24 June 2019, we collected 210 snails from a private pond in Albany, NY (see Electronic Supplementary Material for detailed methods on parasite collection and addition). We shed and pooled cercariae from the four snails with the highest infection prevalence and added 1 cercariae to each well. We checked mortality at hours one, three, five, seven, nine, 11, 12, 13, 14, 16, 20 and 24. Cercariae that were no longer moving were probed with a jet of water propelled gently from a glass pipette and were considered dead if they did not respond (Hua et al. 2016). We terminated the experiment at hour 24, which is the expected life span of these parasites at room temperature (Pechenik and Fried 1995).

Laboratory encystment experiment (host susceptibility) To isolate the effect of leaf litter on host susceptibility to parasites, on 27 June, 2018 we selected a subset of tadpoles reared in autumn olive ($n = 12$), black huckleberry ($n = 12$), purple looses-trife ($n = 12$) or swamp loosestrife ($n = 15$) mesocosms (from the low-density competition mesocosms in Experiment 1) and placed them in 1-L deli cups containing 600 mL of UV-filtered aged well water. We age-selected the youngest available individuals in each treatment to avoid the possibility of tadpoles metamorphosing during the experiment. We then added 50 cercariae to each experimental unit and allowed 24 h for the parasites to infect their hosts before euthanizing, preserving and measuring SVL and Gosner stage in all tadpoles. Previous studies indicate that 24 h is sufficient for parasites to find and encyst in the kidney (Rohr et al. 2008a). To quantify the number of parasites that successfully encysted, we dissected the tadpoles, placed the kidneys between two microscope slides and counted the number of metacercarial cysts formed (and double-checked the rest of the body for cysts in a similar manner). We kept an additional four tadpoles from each leaf litter treatment under the same conditions, but did not expose them to parasites, to serve as parasite-free controls. These

assays allowed us to isolate the effect of leaf litter on the host (i.e., susceptibility) because parasites were not exposed to leaf litter solutions.

Laboratory encystment experiment (net effects) Concurrent with the host susceptibility experiment, we assessed the net effects of leaf litter on host–parasite interactions in a similar assay. We selected a subset of tadpoles reared in autumn olive ($n = 12$), black huckleberry ($n = 10$), purple loosestrife ($n = 12$) or swamp loosestrife ($n = 13$) mesocosms (from the low density competition mesocosms in Experiment 1) and placed them in 1-L deli cups containing 600 mL of filtered leaf litter solutions from their mesocosms. We then followed the same methods for parasite exposure described in the host susceptibility section above, including four parasite-free control replicates per treatment. These assays allowed us to evaluate the effect of leaf litter on both the host and parasites (i.e., net effects) because both host and parasite were concurrently exposed to the leaf litter solutions.

Mesocosm encystment experiment (net effects) Concurrent with the other mesocosm experiments, we constructed 12 mesocosms with each of the four leaf litters ($n = 48$), following the same methodology described for the “low competition” treatment in Experiment 1. On 23 June, 2018 we added 200 cercariae into each mesocosm. After 24 h, we disassembled the mesocosms, counted, euthanized and preserved all surviving tadpoles and measured their SVL and Gosner stage. We then quantified the number of parasites that successfully encysted following the methodology described in the host susceptibility section above.

Statistical analyses—Parasite survival assay To examine the impacts of leaf litter type on parasite survival, we conducted separate survival analyses for each leaf litter pair. We utilized Wilcoxon–Gehan (life table) survival analyses, which compare survival functions across treatments and allow for right censored cases (i.e., surviving cercariae at the end of the experiment). We included the well water treatment in both analyses to understand how parasite survival in each leaf litter type compared to that in water without leaf litter leachates.

Laboratory encystment experiments To examine the impacts of leaf litter on host susceptibility to parasites, we conducted separate generalized linear models (with Poisson distributions and log links) for

each leaf litter pair, with the number of cysts per individual as the dependent variable. To understand whether patterns of encystment were associated with variation in host traits, we conducted two-tailed Pearson correlations between tadpole Gosner stage and average number of cysts for each leaf litter pair. We focused on stage here, because SVL and stage were highly correlated, and previous studies have demonstrated that developmental stage is important in parasite susceptibility (Schotthoefer et al. 2003). We conducted the same set of analyses to examine the net effects of leaf litter on host–parasite interactions (i.e., for individuals exposed to parasites in leaf litter solutions).

Mesocosm encystment experiment For encystment measures, we conducted separate independent samples t tests for each leaf litter pair, using the average number of cysts per individual within each mesocosm as the dependent variable. To understand whether patterns of encystment were associated with variation in host traits, we conducted two-tailed Pearson correlations between tadpole Gosner stage and average number of cysts for each leaf litter pair.

Results

Experiment 1: effects of leaf litter on competitive interactions

Autumn olive versus black huckleberry There was a significant overall multivariate effect of both leaf litter type (Wilk’s- λ $F_{3,41} = 73.883$, $P < 0.001$) and tadpole density (Wilk’s- λ $F_{3,41} = 13.974$, $P < 0.001$), as well as an interaction between the two (Wilk’s- λ $F_{3,41} = 3.818$, $P = 0.017$; Fig. 1) on tadpole survival, SVL and stage.

We did not find significant main effects of leaf litter type ($F_{1,43} = 1.081$, $P = 0.304$) or tadpole density on survival ($F_{1,43} = 2.852$, $P = 0.099$), nor was there an interaction between the two ($F_{1,43} = 2.656$, $P = 0.110$; Fig. 1a).

There were significant main effects of leaf litter type ($F_{1,43} = 80.931$, $P < 0.001$) and tadpole density ($F_{1,43} = 7.080$, $P = 0.011$), as well as an interaction between litter type and tadpole density ($F_{1,43} = 6.803$, $P = 0.012$) on SVL. Tadpoles reared in autumn olive were longer than those reared in black huckleberry at both high ($P < 0.001$) and low ($P < 0.001$) densities.

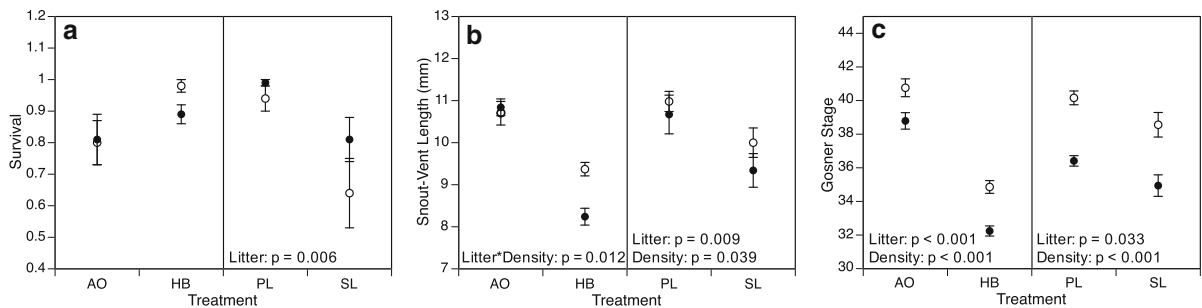


Fig. 1 Survival (as a proportion; panel a), snout-vent length (panel b) and Gosner stage (panel c) of tadpoles reared in each litter type. AO autumn olive, HB black huckleberry, PL purple loosestrife and SL swamp loosestrife. Filled circles represent individuals reared in low density treatments, while open circles

represent individuals reared in high density treatments (average $\pm$ standard error). Plaint comparisons (AO versus HB; PL versus SL) are separated by a vertical line. P-values are reported for any significant univariate main effects or interactions

In autumn olive treatments, tadpoles reared in high and low densities were the same length ($P = 0.971$), while in black huckleberry treatments, those reared at lower densities were longer than those reared at higher densities ($P < 0.001$; Fig. 1b).

We found significant main effects of leaf litter type ($F_{1,43} = 218.864$, $P < 0.001$) and tadpole density ($F_{1,43} = 41.479$, $P < 0.001$) on Gosner stage, but there was no interaction between the two ($F_{1,43} = 0.262$, $P = 0.611$). Tadpoles reared in autumn olive were more developed than those reared in black huckleberry ($P < 0.001$), and tadpoles reared at low densities were more developed than those reared at high densities ($P < 0.001$; Fig. 1c).

Purple loosestrife versus swamp loosestrife There was a significant overall multivariate effect of both leaf litter type (Wilk's- λ $F_{3,40} = 4.419$, $P = 0.009$) and tadpole density (Wilk's- λ $F_{3,40} = 15.051$, $P < 0.001$), but no interaction between the two (Wilk's- λ $F_{3,40} = 0.979$, $P = 0.412$) on survival, SVL and stage.

There was a significant main effect of leaf litter type ($F_{1,43} = 8.310$, $P = 0.006$), but not density ($F_{1,42} = 1.200$, $P = 0.280$), on tadpole survival. Tadpoles reared in purple loosestrife had higher survival compared to those reared in swamp loosestrife ($P = 0.006$; Fig. 1a).

There were significant main effects of leaf litter type ($F_{1,43} = 7.394$, $P = 0.009$) and tadpole density ($F_{1,42} = 4.553$, $P = 0.039$) on SVL. Tadpoles reared in purple loosestrife were longer than those reared in swamp loosestrife ($P = 0.009$), and tadpoles reared at low densities were longer than those reared at high densities ($P = 0.039$; Fig. 1b).

There were significant main effects of leaf litter type ($F_{1,43} = 4.852$, $P = 0.033$) and tadpole density ($F_{1,42} = 38.894$, $P < 0.001$) on Gosner stage. Tadpoles reared in purple loosestrife were more developed (higher Gosner stage) than those reared in swamp loosestrife ($P = 0.033$), and tadpoles reared at low densities were more developed than those reared at high densities ($P < 0.001$; Fig. 1c).

Experiment 2: effects of leaf litter on predator–prey interactions

Autumn olive versus black huckleberry: More tadpoles survived in autumn olive treatments (average proportion surviving $\pm$ SE = 1.00 ± 0.00) than black huckleberry treatments (0.90 ± 0.048) preceding the addition of predators ($U_{N=24} = 48.000$, $P = 0.033$). However, there was no impact of leaf litter type on

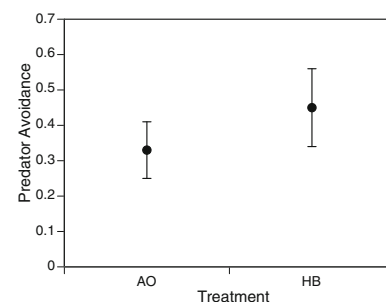


Fig. 2 Predator avoidance (proportion surviving after six-hour exposure to free-ranging *Anax*) for tadpoles reared in autumn olive (AO) and black huckleberry (HB). Only communities with 100% survival before the addition of predators were included in predation trials. Purple loosestrife and swamp loosestrife were excluded due to low replicate availability

predator avoidance ($U_{N=22} = 49.000$, $P = 0.443$; Fig. 2).

Purple loosestrife versus swamp loosestrife: There was a significant effect of leaf litter type on amphibian survival preceding predator exposure ($U_{N=24} = 23.000$, $P = 0.002$). More tadpoles survived in purple loosestrife treatments (0.81 ± 0.11) than swamp loosestrife treatments (0.23 ± 0.10).

Experiment 3: effects of leaf litter on host–parasite interactions

Parasite survival assay (parasite infectivity)—Autumn olive versus black huckleberry There was an overall effect of leaf litter type on parasite survival distributions (Wilcoxon-Gehan₂ = 16.417, $P < 0.001$). Parasite survival rates were reduced in black huckleberry compared to autumn olive ($P = 0.049$). Relative to the well water control, parasites in both autumn olive ($P = 0.008$) and black huckleberry ($P < 0.001$) exhibited significantly reduced parasite survival rates (Fig. 3a).

Parasite survival assay (parasite infectivity)—Purple loosestrife versus swamp loosestrife There was an overall effect of leaf litter type on parasite survival distributions (Wilcoxon-Gehan₂ = 8.259, $P = 0.016$). Parasite survival rates did not differ between purple loosestrife and swamp loosestrife treatments ($P = 0.181$). Compared to the well water control, purple loosestrife significantly reduced parasite survival rates ($P = 0.004$), while swamp loosestrife did not ($P = 0.116$; Fig. 3b).

Laboratory encystment experiment (host susceptibility)—Autumn olive versus black huckleberry When only the hosts were exposed to leaf litter solutions, there was a significant effect of leaf litter type on the average number of cysts per individual (Wald $\chi^2_{[1, n=24]} = 6.991$, $P = 0.008$). Tadpoles reared in autumn olive had more cysts than those reared in black huckleberry (Fig. 4a). There was a positive correlation between stage and the average number of cysts per individual ($r_{[n=24]} = 0.627$, $P = 0.001$), such that more developed individuals had more cysts (Electronic Supplementary Material, Fig. 1). We found no cysts in these, or any, parasite-free controls.

Laboratory encystment experiment (host susceptibility)—Purple loosestrife versus swamp loosestrife When only the hosts were exposed to leaf litter solutions, there was a significant effect of leaf litter type on the average number of cysts per individual (Wald $\chi^2_{[1, n=27]} = 26.535$, $P < 0.001$). Tadpoles reared in purple loosestrife had more cysts than those reared in swamp loosestrife (Fig. 4a). There was a positive correlation between stage and the average number of cysts per individual ($r_{[n=27]} = 0.568$, $P = 0.002$), such that more developed individuals had more cysts (Electronic Supplementary Material, Fig. 1).

Laboratory encystment experiment (net effects)—Autumn olive versus black huckleberry When both host and parasites interacted in leaf litter solutions, there was a significant effect of leaf litter type on the average number of cysts per individual (Wald $\chi^2_{[1, n=22]} = 27.568$, $P < 0.001$). In contrast to the

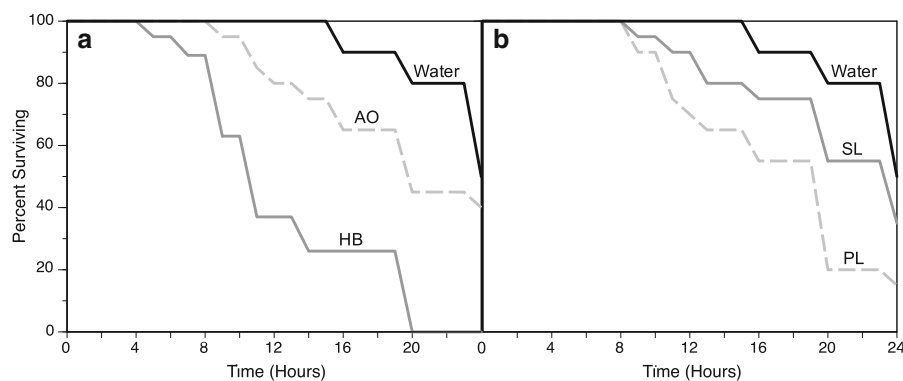


Fig. 3 24-h survival curves of cercariae exposed to one of four leaf litter solutions or a well water control. AO autumn olive, HB black huckleberry, PL purple loosestrife and SL swamp loosestrife. Panel (a) illustrates the AO (dotted gray line) versus

HB (solid gray line) comparison. Panel (b) illustrates the PL (dotted gray line) versus SL (solid gray line) comparison. Both panels include the survival curve of cercariae exposed to clean water (solid black line)

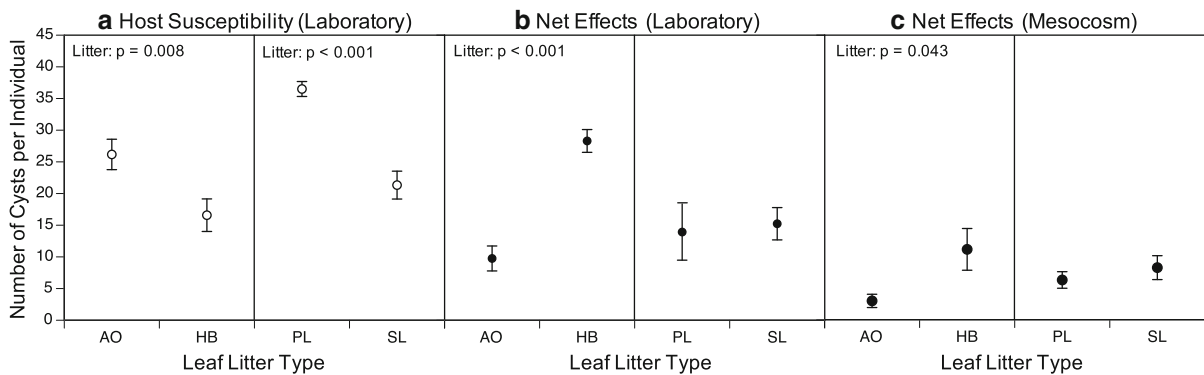


Fig. 4 Number of cysts per individual (average $\pm$ standard error) for tadpoles exposed to cerariae in 3 separate trials. *AO* autumn olive, *HB* black huckleberry, *PL* purple loosestrife and *SL* swamp loosestrife. Panel (a) illustrates the Host Susceptibility (laboratory) trial in clean water (open circles). Panel (b) illustrates the Net Effects (laboratory) trial in leaf litter

solutions (closed circles). Panel (c) illustrates the Net Effects (mesocosm) trial in leaf litter solutions (closed circles). Plant comparisons (AO versus HB; PL versus SL) are separated by a vertical line. *P*-values are reported for any significant main effects or interactions

clean water exposures, tadpoles in black huckleberry treatments now had more cysts than those in autumn olive treatments (Fig. 4b). There was no correlation between stage and the average number of cysts per individual ($r_{[n=22]} = -0.337$, $P = 0.125$; Electronic Supplementary Material, Fig. 1).

Laboratory encystment experiment (net effects)—Purple loosestrife versus swamp loosestrife When both hosts and parasites interacted in leaf litter solutions, there was no significant effect of leaf litter type on the average number of cysts per individual (Wald $\chi^2_{[1, n=25]} = 0.068$, $P = 0.794$). Tadpoles reared in purple loosestrife and swamp loosestrife had similar numbers of cysts (Fig. 4b). There was no correlation between stage and the average number of cysts per individual ($r_{[n=25]} = 0.106$, $P = 0.615$; Electronic Supplementary Material, Fig. 1).

Mesocosm encystment experiment (net effects)—Autumn olive versus black huckleberry There was a significant effect of leaf litter type on the average number of cysts per individual ($T_{18,9} = -2.164$, $P = 0.043$). Autumn olive individuals had significantly fewer cysts than black huckleberry individuals (Fig. 4c). Tadpole stage was negatively correlated with the average number of cysts per individual ($r_{[n=23]} = -0.446$, $P = 0.033$), such that more developed tadpoles had fewer cysts than less developed tadpoles (Electronic Supplementary Material, Fig. 1).

Mesocosm encystment experiment (net effects)—Purple loosestrife versus swamp loosestrife There was no effect of leaf litter type on the average number of

cysts per individual ($T_{13} = -0.561$, $P = 0.585$; Fig. 4c). Tadpole stage was not correlated with the average number of cysts per individual ($r_{[n=15]} = -0.038$, $P = 0.894$; Electronic Supplementary Material, Fig. 1).

Discussion

Experiment 1: Effects of leaf litter on competitive interactions

Our first objective was to examine how leaf litter type influenced tadpole responses to intraspecific competition. Overall, tadpoles reared in purple loosestrife and autumn olive leaf litter treatments were longer and more developed than those reared in swamp loosestrife and huckleberry, respectively. In addition, we found that interactive effects of leaf litter type and tadpole density were invasion-scenario specific. In the purple and swamp loosestrife communities, tadpoles were similarly affected by competition; those reared in high competition were smaller than those reared in low competition. In contrast, for the autumn olive versus black huckleberry communities, the effect of competition depended on leaf litter. In autumn olive treatments, tadpoles reared at both densities reached approximately the same size ($P = 0.971$), while in black huckleberry treatments, tadpoles reared at low densities were 14% longer than those at high densities ($P < 0.001$). Stoler and Relyea (2013a) similarly

demonstrated that leaf litter type mediated both the direction and magnitude of the effects of increasing competition on larval wood frog morphology. We expected that differences in the growth and development of tadpoles would be driven in a large part by differences in resource abundance (Stephens et al. 2015). This is supported by the reduced growth and development of tadpoles reared at high densities, where periphyton abundance was lower (Electronic Supplementary Material, Fig. 3c) than at low tadpole densities. However, periphyton abundance did not differ between litter types in either of the two invasion scenarios. Differences in tadpole growth and development between litter types may have been influenced by variation in phytoplankton (Electronic Supplementary Material, Fig. 3a) or alternative resource abundance, or by water quality (Quammen and Durtsche 2003; Whiles et al. 2010; Burraco et al. 2018) and requires further research. Collectively, these results suggest that changes in wetland plant community, and subsequently leaf litter subsidies, can mediate the effects of intraspecific competition between anuran larvae.

We also found that toad tadpoles in the competition study exhibited higher survival when reared in purple loosestrife than swamp loosestrife. Previous studies suggest that concurrent exposure to soluble phenolics and low dissolved oxygen levels may reduce tadpole survival (Maerz et al. 2005; Leonard 2008; Cohen et al. 2012). Both purple and swamp loosestrife are members of Lythraceae and are known to have high phenolic concentrations in their leaf tissues (Rauha et al. 2001; Maerz et al. 2005), which are known to damage amphibian gill cells (Temminck et al. 1989). This presents a major issue for American toads (Cohen et al. 2012), which are highly reliant on gill function for oxygen uptake due to late development of functional lungs (Duellman and Trueb 1994), especially in instances of low oxygen availability. In our study, oxygen concentrations were significantly lower in swamp loosestrife than purple loosestrife by about 4.4% on average (Electronic Supplementary Material, Fig. 1a), potentially contributing to the reduced survival in swamp loosestrife. Had we not increased dissolved oxygen before tadpole addition, mortality may have been higher (Maerz et al. 2005), though we cannot speculate whether this would have exacerbated or ameliorated differences in mortality between treatments without further research. While tadpole

performance (in terms of growth and survival) was poorer in swamp loosestrife than purple loosestrife, other studies have reported the opposite trend when purple loosestrife was compared with native leaf litters that were more recalcitrant or had lower phenolic concentrations, such as cattail (Blossey et al. 2001; Brown et al. 2006). This supports the notion that plant traits are a more important predictor of the impacts of changes in leaf litter composition than plant origin (Cohen et al. 2012, 2014; Stoler and Relyea 2020).

Experiment 2: effects of leaf litter on predator–prey interactions

Our second objective was to examine the top-down effects of leaf litter in our predation trials. Contrary to previous work, we did not detect an effect of leaf litter on predator avoidance. Stoler and Relyea (2013b) demonstrated increased turbidity (due to high concentrations of red maple leaf litter leachates) increased predation risk of tadpoles by a visual predator, the Eastern newt (*Notophthalmus viridescens*). In our study, while black huckleberry was more than twice as turbid as autumn olive (see Electronic Supplementary Material, Fig. 4), we saw no effect of leaf litter on tadpole predation by *Anax* dragonfly nymphs. Despite the exceptional visual acuity of odonates (Sherk 1977; Bybee et al. 2012), dragonfly larvae differ from newts in their predatory strategy (sit-and-wait vs. active pursuit, respectively; Cooper et al. 1985). Thus, future studies might consider evaluating whether leaf litter-induced shifts in turbidity are more important for particular predation styles. Tadpole behavior may have also impacted predation rates; both leachates and predator cues can affect tadpole movement, and subsequently, predation risk (Gallie et al. 2001; Hickman and Watling 2014; Saenz and Adams 2017; Burraco et al. 2018), though more work is needed to understand whether this played a role in our system. Collectively, while we found similar predation rates in two leachate solutions, it is important to consider different experimental circumstances. For instance, while we filtered out the litter prior to predator assays, variation in the quality of different litters as prey refuge may mediate the rate of prey capture (Folsom and Collins 1984; Hossie and Murray 2010). Additionally, a longer trial (compared to our six hours) may have revealed effects of leaf litter on the predator itself, as multiple studies have demonstrated impacts

of leaf litter on aquatic macroinvertebrate life history and community composition (Abelho and Graça 1996; Stoler and Relyea 2011; Cothran et al. 2014). Thus, future research should consider the role of leaf litter as physical habitat (e.g., suitability as a refuge from predators) as well as their direct impacts on predators, to better understand implications of shifts in plant communities on aquatic predator–prey interactions.

Experiment 3: effects of leaf litter on host–parasite interactions

Parasites represent another important ecological enemy of larval anurans (Holland et al. 2007), and their interaction can be mediated by a variety of anthropogenic and natural factors (Koprivnikar et al. 2006; Rohr et al. 2008b). Human-mediated impacts on host susceptibility may modify host–parasite dynamics in afflicted ecosystems (Milotic et al. 2017, 2019; Buss et al. 2019; May et al. 2019). When we isolated the effects of leaf litter on host susceptibility (tadpoles were reared in leaf litter solution but exposed to parasites in clean water) tadpoles from the invasive litter treatments were more susceptible to trematode infection than tadpoles from the native litter treatments. Autumn olive tadpoles had 57.8% more cysts than black huckleberry tadpoles and purple loosestrife tadpoles had 71.1% more cysts than swamp loosestrife tadpoles. This was likely driven by accelerated tadpole development in invasive litter compared to native litter, as developmental stage and the number of cysts per individual were positively correlated for both litter pairs. This supports the findings of Rohr et al. (2010), which demonstrated that susceptibility to echinostomatid infection increases with developmental stage in American toads. Our results would suggest that while tadpoles gained the advantage of faster development in invasive leaf litter treatments, they paid the price of increased susceptibility to an ecological enemy.

However, to understand the net effect of leaf litter on host–parasite dynamics, it is important to consider not only changes in host susceptibility but also parasite survival (our proxy for infectivity). Compared to well water controls, parasite survival was unaffected by swamp loosestrife leachates, but was significantly reduced in purple loosestrife leachates. In the other plant pair comparison, both autumn olive and black huckleberry reduced parasite survival compared to clean water, but this reduction was more drastic in

black huckleberry. Previous studies have shown that anthropogenic (e.g., pesticides; Hua et al. 2016; Rohr et al. 2008a, b) and natural chemicals (e.g., microcystins; Buss et al. 2019) can be directly toxic to trematode cercariae. However, no studies to date have attempted to isolate the direct effects of leaf litter on any trematode species. In fact, to our knowledge, only two studies have examined the direct effects of leaf litter on aquatic parasites; Davidson et al. (2012) and Stoler et al. (2016a, b) demonstrated that leaf litter can affect zoospore and sporangia densities in the amphibian fungal pathogen, *Batrachochytrium dendrobatidis*. Our results demonstrate that leaf litter might similarly impact cercarial survival in echinostomatids. Parasites are important and prevalent members of natural communities (Minchella and Scott 1991), but are often overlooked in the context of environmental change (Lafferty and Kuris 1999; Johnson and Chase 2004). As wetland plant communities change (e.g., due to the introduction of exotic species), understanding their impact on host–parasite interactions will be essential. Given that parasite longevity and infectivity are major factors in disease transmission, our results highlight the importance of considering the impacts of anthropogenic change not only on hosts, but parasites as well.

While the individual impacts of changes in leaf litter on hosts and parasites provide useful mechanistic information, it was our ultimate goal to understand the net effects of leaf litter on host–parasite dynamics. Both laboratory and mesocosm trials where the host–parasite interaction occurred in leaf litter solutions yielded similar results. Despite purple loosestrife increasing tadpole susceptibility to parasites in the host exposure study, there was no difference in the number of cysts between tadpoles in purple loosestrife and swamp loosestrife when both host and parasites were exposed to leaf litter. This suggests that increased host susceptibility was counteracted by reduced parasite survival in purple loosestrife, relative to swamp loosestrife. In our other plant pair, since tadpole susceptibility was higher and cercariae lived longer in autumn olive compared to black huckleberry treatments, we might have expected that overall encystment would be much higher (i.e., additive effects) in autumn olive than black huckleberry treatments. Contrary to these predictions, tadpoles in black huckleberry treatments had 190% more cysts on average than those in autumn olive treatments. Two

possible explanations stand out to explain this disconnect: First, in black huckleberry treatments, there may have been a behaviorally-mediated increase in tadpole susceptibility to parasites not captured in the clean water trials. Tadpoles can evade trematode encystment via movement, reducing the ability for parasites to attach and crawl toward the cloaca (Daly and Johnson 2011). It is therefore possible that tadpoles moved less in black huckleberry solutions than autumn olive solutions, making it easier for parasites to encyst. For instance, Watling et al. (2011) demonstrated that American toad larvae made more trips to the surface when exposed to leachates from the invasive shrub, *Lonicera maackii*, than leachates from native plant leaf litter. Second, parasites may have been less able to locate their host in autumn olive than black huckleberry solutions, counteracting the greater cercarial mortality in black huckleberry. Echinostomatids locate hosts via chemosensory (e.g., for snail hosts) or physical cues (e.g., for fast-moving hosts like fish; reviewed by Haas 2003), but we still do not know which cues are utilized primarily for locating amphibian hosts. Ultimately, in the net effects study, tadpoles were more developed in both purple loosestrife and autumn olive, without incurring the cost of increased parasite loads. This demonstrates that while considering the effects of global change on individual organisms is imperative, accurate predictions of how ecological relationships will be affected requires examining the interactions themselves.

Conclusions

In this study, we use two invasion scenarios, comparing native swamp loosestrife with invasive purple loosestrife and native black huckleberry with invasive autumn olive, to evaluate the potential impacts of changing plant communities on three components of larval amphibian ecology. We demonstrate that tadpoles exhibited faster growth and development, equal or greater survival and equal or lower parasite loads in invasive, as compared to native, leaf litter treatments. However, it should be noted that we only compared each invasive plant to one native counterpart and used only one model amphibian, both of which play a major role in the conclusions of our study. For instance, we demonstrate that American toads exhibited more rapid growth and development in purple loosestrife than

swamp loosestrife. In contrast, previous studies have shown that American toad tadpoles develop more slowly and have lower survival in purple loosestrife than broad-leaf cattail (*Typha latifolia*) litter, while gray tree-frog (*Hyla versicolor*) performance did not differ between litter types (Maerz et al. 2005; Brown et al. 2006). Therefore, while these results clearly demonstrate that changing leaf litter inputs can have a broad range of impacts on amphibian ecology, they are not generalizable to all amphibians or invasion scenarios. This provides further support for a growing body of literature showing that considering plant traits is critical to predicting the impacts of changing leaf litter inputs (Cohen et al. 2012; Stoler et al. 2016b). While it is important to examine invasion scenarios occurring in natural ecosystems, generalities derived from examining the relationships between particular plant traits and community composition and ecosystem function may lead to stronger predictive power. To sum, results from this study emphasize the potential ecosystem-wide impacts of these invasions, including changes in water chemistry, producer communities, amphibian growth, development, survival and host–parasite interactions and suggest that plant invasions should be recognized for their ability to drive widespread ecological change.

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Authors' Contributions Both DGD and JH made substantial contributions to the design and execution of the study, analysis of the data and the writing and revision of the manuscript.

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Data Availability Data for this study are available at the Dryad Digital Repository: <https://doi.org/10.5061/dryad.np5hqbztq>.

Code Availability All statistics were conducted using SPSS (Version 24, IBM).

Declarations

Conflict of interest The authors declare no conflict of interest.

Ethics Approval Experimental vertebrate care was conducted in accordance with the Institutional Animal Care and Use Committee (IACUC) guidelines (protocol #: 809-18).

References

- Abelho M, Graça MAS (1996) Effects of eucalyptus afforestation on leaf litter dynamics and macroinvertebrate community structure of streams in Central Portugal. *Hydrobiologia* 324:195–204
- Adams C, Saenz D (2012) Leaf litter of invasive Chinese tallow (*Triadica sebifera*) negatively affects hatching success of an aquatic breeding anuran, the Southern Leopard Frog (*Lithobates sphenoccephalus*). *Can J Zool* 90:991–998
- Bais HP, Vepachedu R, Gilroy S, Callaway RM, Vivanco JM (2003) Allelopathy and exotic plant invasion: from molecules and genes to species interactions. *Science* 301:1377–1380
- Blossey B, Schroeder D, Hight SD, Malecki RA (1994) Host specificity and environmental impact of the Weevil *Hylobius transversovittatus*, a biological control agent of purple loosestrife (*Lythrum salicaria*). *Weed Sci* 42:128–133
- Blossey B, Skinner LC, Taylor J (2001) Impact and management of purple loosestrife (*Lythrum salicaria*) in North America. *Biodivers Conserv* 10:1787–1807
- Borth EB, Custer KW, McEwan RW (2018) Lethal effects of leaf leachate from the non-native invasive shrub Amur honeysuckle (*Lonicera maackii*) on a model aquatic organism (*Hyalella azteca*). *Écoscience* 25:189–197
- Brockelman WY (1969) An analysis of density effects and predation in *Bufo Americanus* tadpoles. *Ecology* 50:632–644
- Brown CJ, Blossey B, Maerz JC, Joule SJ (2006) Invasive plant and experimental venue affect tadpole performance. *Biol Invasions* 8:327–338
- Burraco P, Iglesias-Carrasco M, Cabido C, Gomez-Mestre I (2018) Eucalypt leaf litter impairs growth and development of amphibian larvae, inhibits their antipredator responses and alters their physiology. *Conserv Physiol* 6:119
- Buss N, Wersebe M, Hua J (2019) Direct and indirect effects of a common cyanobacterial toxin on amphibian-trematode dynamics. *Chemosphere* 220:731–737
- Bybee SM, Johnson KK, Gering EJ, Whiting MF, Crandall KA (2012) All the better to see you with: a review of odonate color vision with transcriptomic insight into the odonate eye. *Org Divers Evol* 12:241–250
- Cameron GN, LaPoint TW (1978) Effects of tannins on the decomposition of Chinese tallow leaves by terrestrial and aquatic invertebrates. *Oecologia* 32:349–366
- Canhoto C, Laranjeira C (2007) Leachates of *Eucalyptus globulus* in intermittent streams affect water parameters and invertebrates. *Int Rev Hydrobiol* 92:173–182
- Chovanec A (1992) The influence of tadpole swimming behaviour on predation by dragonfly nymphs. *Amphibia-Reptilia* 13:341–349
- Church JM, Williard KWJ, Baer SG, Groninger JW, Zaczek JJ (2004) Nitrogen leaching below riparian autumn olive stands in the dormant season. In: Yaussy DA, Hix DM, Long RP, Goebel PC (eds) *Proceedings, 14th Central Hardwood Forest Conference*, pp 211–216
- Cohen JS, Maerz JC, Blossey B (2012) Traits, not origin, explain impacts of plants on larval amphibians. *Ecol Appl* 22:218–228
- Cohen JS, Rainford S-KD, Blossey B (2014) Community-weighted mean functional effect traits determine larval amphibian responses to litter mixtures. *Oecologia* 174:1359–1366
- Cothran RD, Stoler AB, Relyea RA (2014) Leaves and litter-bugs: how litter quality affects amphipod life-history and sexually selected traits. *Freshwater Sci* 33:812–819
- Daly EW, Johnson PTJ (2011) Beyond immunity: quantifying the effects of host anti-parasite behavior on parasite transmission. *Oecologia* 165:1043–1050
- Davidson EW, Larsen A, Palmer CM (2012) Potential influence of plant chemicals on infectivity of *Batrachochytrium dendrobatidis*. *Dis Aquat Org* 101:87–93
- Dickson TL, Hopwood JL, Wilsey BJ (2012) Do priority effects benefit invasive plants more than native plants? An experiment with six grassland species. *Biol Invasions* 14:2617–2624
- DiGiacopo DG, Meindl GA, Ryan S, Jaeger J, Wersebe M, Martin A, Robinson SA, Graham G, Palmer AR, Setteducate A, Murray I, Prior K, Hua J (2018) Interaction between invasive plant leaf litter and NaCl on two model amphibians. *Biol Invasions* 21:391–403
- Dodd CE, Buchholz R (2018) Apparent maladaptive oviposition site choice of Cope's gray treefrogs (*Hyla chrysoscelis*) when offered an array of pond conditions. *Copeia* 106:492–500
- Dornbos DL, Martzke MR, Gries K, Hesselink R (2016) Physiological competitiveness of autumn olive compared with native woody competitors in open field and forest understory. *For Ecol Manag* 372:101–108
- Duellman WE, Trueb L (1994) *Biology of amphibians*. JHU Press, New York
- Earl JE, Castello PO, Cohagen KE, Semlitsch RD (2014) Effects of subsidy quality on reciprocal subsidies: how leaf litter species changes frog biomass export. *Oecologia* 175:209–218
- Earl JE, Semlitsch RD (2015) Effects of tannin source and concentration from tree leaves on two species of tadpoles. *Environ Toxicol Chem* 34:120–126
- Ehrenfeld JG (2010) Ecosystem consequences of biological invasions. *Annu Rev Ecol Evol Syst* 41:59–80
- Farrer EC, Goldberg DE (2009) Litter drives ecosystem and plant community changes in cattail invasion. *Ecol Appl* 19:398–412
- Fisher SG, Likens GE (1973) Energy flow in bear brook, new hampshire: an integrative approach to stream ecosystem metabolism. *Ecol Monogr* 43:421–439
- Folsom TC, Collins NC (1984) The diet and foraging behavior of the larval dragonfly anax junius (*Aeshnidae*), with an assessment of the role of refuges and prey activity. *Oikos* 42:105–113
- Gallie JA, Mumme RL, Wissinger SA (2001) Experience has no effect on the development of chemosensory recognition of predators by tadpoles of the American Toad, *Bufo americanus*. *Herpetologica* 57:376–383

- Going BM, Dudley TL (2008) Invasive riparian plant litter alters aquatic insect growth. *Biol Invasions* 10:1041–1051
- Gosner KL (1960) A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica* 16:183–190
- Haas W (2003) Parasitic worms: strategies of host finding, recognition and invasion. *Zoology* 106:349–364
- Hejda M, Pyšek P, Jarošík V (2009) Impact of invasive plants on the species richness, diversity and composition of invaded communities. *J Ecol* 97:393–403
- Hickman CR, Watling JI (2014) Leachates from an invasive shrub causes risk-prone behavior in a larval amphibian. *Behav Ecol* 25:300–305
- Holland MP, Skelly DK, Kashgarian M, Bolden SR, Harrison LM, Cappello M (2007) Echinostome infection in green frogs (*Rana clamitans*) is stage and age dependent. *J Zool* 271:455–462
- Hossie TJ, Murray DL (2010) You can't run but you can hide: refuge use in frog tadpoles elicits density-dependent predation by dragonfly larvae. *Oecologia* 163:395–404
- Hua J, Buss N, Kim J, Orlofske SA, Hoverman JT (2016) Population-specific toxicity of six insecticides to the trematode *Echinoparyphium* sp. *Parasitology* 143:542–550
- Huffman JE, Fried B (2012) The biology of *Echinoparyphium* (*Trematoda*, *Echinostomatidae*). *Acta Parasitol* 57:199–210
- Jabiol J, Cornut J, Danger M, Jouffroy M, Elger A, Chauvet E (2014) Litter identity mediates predator impacts on the functioning of an aquatic detritus-based food web. *Oecologia* 176:225–235
- Johnson PTJ, Chase JM (2004) Parasites in the food web: linking amphibian malformations and aquatic eutrophication. *Ecol Lett* 7:521–526
- Jones DK, Davila DD, Nguyen KH, Rohr JR (2019) Effect of agrochemical exposure on *Schistosoma mansoni* cercariae survival and activity. *bioRxiv*:701060
- Kingsford RT, Basset A, Jackson L (2016) Wetlands: conservation's poor cousins. *Aquat Conserv Mar Freshwat Ecosyst* 26:892–916
- Kohri M, Kamada M, Nakagoshi N (2011) Spatial-temporal distribution of ornithochorous seeds from an *Elaeagnus umbellata* community dominating a riparian habitat. *Plant Species Biol* 26:174–185
- Kohri M, Kamada M, Yuuki T, Okabe T, Nakagoshi N (2002) Expansion of *Elaeagnus umbellata* on a gravel bar in the Naka River, Shikoku, Japan. *Plant Species Biol* 17:25–36
- Koprivnikar J, Baker RL, Forbes MR (2006) Environmental factors influencing trematode prevalence in grey tree frog (*Hyla Versicolor*) tadpoles in Southern Ontario. *J Parasitol* 92:997–1001
- Lafferty KD, Kuris AM (1999) How environmental stress affects the impacts of parasites. *Limnol Oceanogr* 44:925–931
- Leonard N (2008) The effects of the invasive exotic Chinese tallow tree (*Triadica sebifera*) on amphibians and aquatic invertebrates. University of New Orleans Theses and Dissertations
- Maerz JC, Brown CJ, Chapin CT, Blossey B (2005) Can secondary compounds of an invasive plant affect larval amphibians? *Funct Ecol* 19:970–975
- May D, Shideman G, Melnick-Kelley Q, Crane K, Hua J (2019) The effect of intensified illuminance and artificial light at night on fitness and susceptibility to abiotic and biotic stressors. *Environ Pollut* 251:600–608
- Milanovich JR, Barrett K, Crawford JA (2016) Detritus quality and locality determines survival and mass, but not export, of wood frogs at metamorphosis. *PLoS ONE* 11:e0166296–e0166296
- Milotic D, Milotic M, Koprivnikar J (2017) Effects of road salt on larval amphibian susceptibility to parasitism through behavior and immunocompetence. *Aquat Toxicol* 189:42–49
- Milotic M, Milotic D, Koprivnikar J (2019) Effects of a cyanobacterial toxin on trematode cercariae. *J Parasitol* 105:598–605
- Minchella DJ, Scott ME (1991) Parasitism: a cryptic determinant of animal community structure. *Trends Ecol Evol* 6:250–254
- Montez RD, Saenz D, Martynova-Van Kley A, Van Kley J, Nalian A, Farrish K (2021) The influence of Chinese tallow (*Triadica sebifera*) leaf litter on water quality and microbial community composition. *Aquat Ecol* 55:265–282
- Pechenik JA, Fried B (1995) Effect of temperature on survival and infectivity of *Echinostoma trivolvis* cercariae: a test of the energy limitation hypothesis. *Parasitology* 111:373–378
- Petranka JW (1989) Response of toad tadpoles to conflicting chemical stimuli: predator avoidance versus “Optimal” foraging. *Herpetologica* 45:283–292
- Pituch KA, Stevens JP (2015) Applied multivariate statistics for the social sciences: analyses with SAS and IBM's SPSS, 6th edn. London, Routledge
- Polis GA, Anderson WB, Holt RD (1997) Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annu Rev Ecol Syst* 28:289–316
- Pyšek P, Richardson DM (2007) Traits associated with invasiveness in alien plants: Where do we stand? *Biol Invasions* 193:97–125
- Quammen JK, Durtsche DRD (2003) Diet comparison in three tadpole species, *Rana sylvatica*, *Bufo americanus*, and *Pseudacris crucifer*, in a northern temperate climate. *Norse Scientist* 1:45–50
- Rauha JP, Wolfender JL, Salminen JP, Pihlaja K, Hostettmann K, Vuorela H (2001) Characterization of the polyphenolic composition of purple loosestrife (*Lythrum salicaria*). *J Biosci* 56:13–20
- Rohr JR, Raffel TR, Hall CA (2010) Developmental variation in resistance and tolerance in a multi-host-parasite system. *Funct Ecol* 24:1110–1121
- Rohr JR, Raffel TR, Sessions SK, Hudson PJ (2008a) Understanding the net effects of pesticides on amphibian trematode infections. *Ecol Appl* 18:1743–1753
- Rohr JR, Schotthoefer AM, Raffel TR, Carrick HJ, Halstead N, Hoverman JT, Johnson CM, Johnson LB, Lieske C, Piwoni MD, Schoff PK, Beasley VR (2008b) Agrochemicals increase trematode infections in a declining amphibian species. *Nature* 455:1235–1239
- Rubbo MJ, Belden LK, Kiesecker JM (2008) Differential responses of aquatic consumers to variations in leaf-litter inputs. *Hydrobiologia* 605:37–44

- Sacerdote AB, King RB (2014) Direct effects of an invasive European buckthorn metabolite on embryo survival and development in *Xenopus laevis* and *Pseudacris triseriata*. *J Herpetol* 48:51–58
- Saenz D, Adams CK (2017) Effects of Chinese tallow leaf litter on water chemistry and surfacing behaviour of anuran larvae. *Herpetol J* 27:326–332
- Schotthoefer AM, Cole RA, Beasley VR (2003) Relationship of tadpole stage to location of echinostome cercariae encystment and the consequences for tadpole survival. *J Parasitol* 89:475–482
- Sears BF, Schlunk AD, Rohr JR (2012) Do parasitic trematode cercariae demonstrate a preference for susceptible host species? *PLOS ONE* 7:e51012
- Sherk TE (1977) Development of the compound eyes of dragonflies (*odonata*). I. Larval compound eyes. *J Exp Zool* 201:391–416
- Skelly DK (1994) Activity level and the susceptibility of anuran larvae to predation. *Anim Behav* 47:465–468
- Smyth, J. D., and D. W. Halton. 1983. *The Physiology of Trematodes*. CUP Archive.
- Stephens JP, Berven KA, Tieggs SD (2013) Anthropogenic changes to leaf litter input affect the fitness of a larval amphibian. *Freshw Biol* 58:1631–1646
- Stephens JP, Berven KA, Tieggs SD, Raffel TR (2015) Ecological stoichiometry quantitatively predicts responses of tadpoles to a food quality gradient. *Ecology* 96:2070–2076
- Stoler AB, Berven KA, Raffel TR (2016a) Leaf litter inhibits growth of an amphibian fungal pathogen. *EcoHealth* 13:392–404
- Stoler AB, Burke DJ, Relyea RA (2016b) Litter chemistry and chemical diversity drive ecosystem processes in forest ponds. *Ecology* 97:1783–1795
- Stoler AB, Relyea RA (2011) Living in the litter: the influence of tree leaf litter on wetland communities. *Oikos* 120:862–872
- Stoler AB, Relyea RA (2013a) Leaf litter quality induces morphological and developmental changes in larval amphibians. *Ecology* 94:1594–1603
- Stoler AB, Relyea RA (2013b) Bottom-up meets top-down: leaf litter inputs influence predator-prey interactions in wetlands. *Oecologia* 173:249–257
- Stoler AB, Relyea RA (2016) Leaf litter species identity alters the structure of pond communities. *Oikos* 125:179–191
- Stoler AB, Relyea RA (2020) Reviewing the role of plant litter inputs to forested wetland ecosystems: leafing through the literature. *Ecol Monogr* 6:e01400
- Temmink JHM, Field JA, van Haastrecht JC, Merkelbach RCM (1989) Acute and sub-acute toxicity of bark tannins in carp (*Cyprinus carpio* L.). *Water Res* 23:341–344
- Thompson DW, Stuckey RL, Thompson EB (1987) Spread, impact and control of purple loosestrife in North American wetlands. US Fish and Wildlife Service, Washington, DC
- Wassersug RJ, Hoff KVS (1985) The kinematics of swimming in anuran larvae. *J Exp Biol* 119:1–30
- Wassersug RJ, Seibert EA (1975) Behavioral responses of amphibian larvae to variation in dissolved oxygen. *Copeia* 1975:86–103
- Watling JJ, Hickman CR, Lee E, Wang K, Orrock JL (2011) Extracts of the invasive shrub *Lonicera maackii* increase mortality and alter behavior of amphibian larvae. *Oecologia* 165:153–159
- Weiher E, Wisheu IC, Keddy PA, Moore DRJ (1996) Establishment, persistence, and management implications of experimental wetland plant communities. *Wetlands* 16:208–218
- Whiles MR, Gladyshev MI, Sushchik NN, Makhutova ON, Kalachova GS, Peterson SD, Register KJ (2010) Fatty acid analyses reveal high degrees of omnivory and dietary plasticity in pond-dwelling tadpoles. *Freshw Biol* 55:1533–1547
- Wilkins KW, Overholt E, Williamson C (2020) The effects of dissolved organic matter from a native and an invasive plant species on juvenile *Daphnia* survival and growth. *J Plankton Res* 42:453–456
- Wymore AS, Salpas E, Casaburi G, Liu CM, Price LB, Hungate BA, McDowell WH, Marks JC (2018) Effects of plant species on stream bacterial communities via leachate from leaf litter. *Hydrobiologia* 807:131–144
- Zedler JB, Kercher S (2004) Causes and Consequences of Invasive Plants in Wetlands: Opportunities, Opportunists, and Outcomes. *Crit Rev Plant Sci* 23:431–452

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