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PLANT-ANIMAL INTERACTIONS - ORIGINAL PAPER

Extracts of the invasive shrub *Lonicera maackii* increase mortality and alter behavior of amphibian larvae

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Abstract Water-soluble phytochemicals produced by invasive plants may represent novel elements of invaded ecosystems that can precipitate a variety of direct and indirect effects on native organisms. Phenolic compounds in particular are a common plant defense, and these compounds may have disproportionate impacts on amphibians compared to other taxa. We coupled an exploration of invasive plant extract effects on larvae of four amphibian species (the salamander *Ambystoma maculatum*, the toad *Anaxyrus americanus*, and the frogs *Hyla* sp. and *Lithobates blairi*) with behavioral observations designed to determine whether behavior can ameliorate the negative effects of exposure to invasive plant extracts. Larvae were reared in extracts of the widespread invasive Amur honeysuckle (*Lonicera maackii*), mixed native leaf litter, and a water control. *Anaxyrus americanus* tadpoles reared in *L. maackii* extracts were more likely to die than tadpoles reared in native extracts, but differences in mortality following rearing in native and exotic extracts were not significant for the other three species. *Anaxyrus americanus* and *L. blairi* tadpoles made more trips to the surface in *L. maackii* extracts than in native extracts, consistent with the hypothesis that exotic extracts may interfere with respiratory physiology and suggesting that *L. blairi* can behaviorally ameliorate the negative effects of *L. maackii* extracts. Our study highlights both a direct and indirect pathway by which invasive plant extracts may alter the ecological dynamics of native fauna.

Keywords Allelopathy · Invasive species · Missouri · Respiration · Tadpoles

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Introduction

Invasive species alter the ecosystems in which they are introduced through many pathways, including trophic interactions with native organisms (Levine et al. 2004), alteration of disturbance regimes (Brooks et al. 2004), and transformation of habitat structure (Crooks 2002). Accumulating evidence attests to the importance of indirect and/or cryptic effects of invasive species on native organisms, as in refuge-mediated apparent competition (Orrock et al. 2008; Orrock et al. 2010), invasional meltdown (Simberloff and Von Holle 1999), and invasive-induced trophic cascades (Kimbro et al. 2009). Many invasive plants produce allelopathic chemicals that may be bioavailable to native taxa, and exposure to novel chemical compounds produced by invasive plants may represent cryptic threats to native fauna (Maerz et al. 2005; Brown et al. 2006; Canhoto and Laranjeira 2007; Watling et al. 2010). To quantify the impacts of invasive plant extracts on organisms with which they share no trophic connection, we conducted a laboratory study to determine whether larvae of four species of native amphibians differed in survival, growth, or behavior in exotic plant extracts compared with native plant extracts.

Exposure to water-soluble secondary compounds produced by invasive plants may affect amphibian larvae through both direct and indirect pathways. The mortality of American toad (*Anaxyrus americanus*) larvae was found to be much greater in tadpoles reared in exotic Purple Loosestrife (*Lythrum salicaria*) leachate than in those reared in extracts from native Broad-Leaf Cattail (*Typha latifolia*; Maerz et al. 2005). Although untested, Maerz et al. (2005) hypothesized that increased mortality in exotic plant extracts may be the result of oxygen deprivation because *L. salicaria* contains a greater concentration of phenolic compounds than *T. latifolia*, and phenolics are known to interfere with gill functioning in fish (Temmink et al. 1989). Because *A. americanus* are essentially an obligate gill-breathers (Wassersug and Feder 1983), they may be particularly sensitive to plant extracts containing elevated phenolic concentrations. However, amphibian larvae are highly variable in terms of respiratory anatomy and physiology, and not all species rely on gills for respiration (Ultsch et al. 1999), suggesting that tadpoles of different species may vary in their response to phenolics. A common behavioral adaptation to oxygen-poor environments is to increase the time spent in relatively oxygen-rich water near the surface (Wassersug and Seibert 1975), so we may expect that tadpoles exposed to elevated concentrations of phenolic compounds would attempt to ameliorate oxygen stress by engaging in more surfacing behavior than tadpoles in more benign environments. Many tadpoles reduce activity in the presence of predators (Skelly 1995); consequently, changes in water chemistry that result in greater levels of activity and/or increased surfacing behavior may expose individuals to increased predation risk, representing an indirect pathway by which invasive plants may affect larval amphibians (White et al. 2006).

Amur honeysuckle (*Lonicera maackii*) is a shrub of Asian origin that has invaded much of the USA east of the Rocky Mountains, where it occurs primarily in disturbed areas and forest edges (Hutchinson and Vankat 1997; Bartuszevige et al. 2006; Watling and Orrock 2010). This shrub produces phenolic compounds (tannins) in its leaves and roots (Dorning and Cipollini 2006; Cipollini et al. 2008) that are toxic to native plant taxa (Dorning and Cipollini 2006) and deter generalist herbivores (Cipollini et al. 2008). *Lonicera maackii* can be abundant in urban and suburban forested wetlands (Swab et al. 2008; Cutway and Ehrenfeld 2009), and its broad distribution in the eastern and central USA overlaps the geographic ranges of many native amphibians. Because the phytochemicals produced by *L. maackii* are water-soluble (Cipollini et al. 2008), they may be bioavailable to aquatic organisms occurring in invaded wetlands. Thus, the changes in water quality caused by *L. maackii* may represent a potentially important yet cryptic chemical change in the environment that is capable of altering ecological dynamics relative to uninvaded conditions (Watling et al. 2010).

Interspecific variation in responses to invasive plant extracts may alter the outcome of competition, predation, and indirect interactions in real communities. Within this framework, we wanted to test for tadpole responses to plant extracts across multiple taxa. We hypothesized that individuals reared in *Lonicera* extracts would have a lower survival rate and reach a smaller body size than individuals in native extracts and water controls. In addition to monitoring survival, we made behavioral observations of individual tadpoles to determine whether behavior is capable of ameliorating the negative effects of *Lonicera* extracts. We expected that individuals reared in *Lonicera* extracts would make more trips to the surface than those reared in native and control extracts. By coupling our exploration of plant extract effects to multiple taxa that interact as both competitors and predators with behavioral observations, we gain insight into the ways that changes in survival and/or behavior induced by exotic plant leachates may affect native food webs.

Methods and material

Leaf material was obtained from several individual *L. maackii* shrubs located throughout the August A. Busch Memorial Conservation Area (hereafter Busch Conservation Area or BCA, 38°45′N, 91°21′W) in St Charles county, Missouri in November 2008 and stored in a freezer at −20°C until use. The leaves were obtained as the *L. maackii* shrubs were beginning to drop their leaves, while the shrubs of native taxa had already dropped their leaves by the collection period (late November). Consequently, dried, recently fallen leaves (the top-most layer of litter) representing a mix of native taxa (mostly *Quercus* spp. and Shagbark hickory *Carya ovata*) were obtained from throughout the BCA. In a separate field study using leaf litter and soil from the BCA, we found differences in the concentration of total phenolics consistent with the differences we describe below (Watling et al. 2010), so it is unlikely that differences in the origin of leaf material confounded our results. Extracts were prepared according to the procedure described by Maerz et al. (2005). Leaves were dried to constant mass after which extracts were prepared by soaking 5 g of dried leaves in 1 L of room-temperature, dechlorinated tap water for 48 h. Leaf material was then removed, and the extracts were stored in opaque plastic containers at 4°C. Controls were prepared using dechlorinated water treated and stored similarly to the leaf extracts. All experiments were run using three types of extracts: *L. maackii* (referred to as *Lonicera* when in the description of the extract treatment), mixed native litter (Native), and dechlorinated water (Control). We measured the concentration of substances reducing Folin phenol reagent (e.g., total phenolics) using spectrophotometry following standard procedures for water quality analysis (Clesceri et al. 1998). Differences in the concentration of total phenolics between *Lonicera*, Native, and Blank extracts were analyzed using a one-way analysis of variance (ANOVA), and pairwise comparisons were made using Tukey's honestly significant difference post hoc test.

All experiments were run with egg masses or tadpoles collected at the BCA and transported to the laboratory. We selected four taxa representing two amphibian orders (Anura and Caudata) and four families (Ambystomatidae, Bufonidae, Hylidae, Ranidae) that are common both at our study site and throughout much of the eastern and central USA. These taxa interact as both predators (Ambystomatidae) and competitors (Bufonidae, Hylidae, and Ranidae) and, therefore, provide a breadth of information on the consequences of invasive-induced changes in food web structure that are impossible to examine using a single species. A short description of the details on the handling of each species is provided in the following paragraphs.

Ambystoma maculatum

Egg masses were obtained on 13 March 2009 ($n = 2$) and 15 April 2009 ($n = 1$) and transported to the laboratory where they were placed in 1.8-L plastic buckets with dechlorinated tap water and stored in climate chambers under a 10/14-h light/dark photoperiod at 15°C and 65% humidity. (Note: these chamber conditions apply for all larval experiments described subsequently and are typical of laboratory experiments with amphibian larvae; Harkey and Semlitsch 1988; Hickman et al. 2004). Approximately 48–72 h after hatching, *A. maculatum* larvae were randomly assigned to individual 1.8-L plastic buckets filled with 1 L of extract (*Lonicera*, Native, or Control). Larvae were provided with a mixture of frozen shrimp and dried shrimp pellets at 6- to 10-day intervals for the first two feedings and then with blood worms for the duration of rearing. In all experiments, the water was not changed during the duration of the experiment, but dechlorinated water was added to containers as necessary to maintain water volume near 1 L.

Anaxyrus americanus

Recently hatched individuals (Gosner stage 25 or below) of *A. americanus* were obtained from several roadside ditches from throughout the BCA on 14 May 2009 and transferred to 1.8-L plastic buckets containing the chosen treatment extract and stored in the climate chamber on 18 May 2009. Tadpoles were fed approximately every 6–10 days with ground dehydrated algal pellets (approximately 10 mg; feeding procedure is the same as that described below).

Lithobates blairi

Ova from three separate eggs masses were obtained in the field on 7 April 2009 and transported to the laboratory. Approximately 72 h after hatching, individual tadpoles were transferred to 1.8-L plastic buckets containing the chosen treatment extract, and placed in the growth chamber. Because of limited access to materials, nine individuals were housed in 4.1-L plastic buckets.

Hyla chrysocelis/versicolor

Tadpoles and egg masses of the Gray Treefrog are indistinguishable morphologically, and we refer to this taxon as *Hyla* hereafter. Three egg masses were obtained in the field on 14 May 2009 and transferred to the laboratory. Because of the small size of recently hatched tadpoles, we waited approximately 96 h after hatching to transfer individuals to individual 1.8-L plastic buckets that contained the chosen treatment extract.

Monitoring growth and survival

Larvae were monitored over a 45-day period. Individuals were checked at least twice per week to determine survival, and the date on which dead individuals were encountered was recorded. To make our growth data comparable to those of Maerz et al.'s (2005) study on invasive plant effects on larval amphibians, on day 21 of the experiment we took digital photographs of surviving individuals (body size measurements of *A. maculatum* individuals were obtained on day 32 of rearing because of their longer larval period relative to other taxa included in the study). Animals were photographed against a 0.5 × 0.5-cm grid from which body length data were obtained using the ImageJ program (Rasband 2009). Body size data were analyzed using a one-way ANOVA with extract as a factor (*Lonicera*, Native, Control) and body size (millimeters) as the dependent variable. Survival data were analyzed using Cox Regression with day as the independent variable and survival as the response.

Extract effects on surfacing behavior

We made observations of focal individuals to test for behavioral shifts consistent with decreased respiratory ability in individuals exposed to *Lonicera* extracts. We used the number of trips to the surface as our behavioral metric because surfacing behavior is associated with low oxygen levels (Wassersug and Seibert 1975), and these oxygen deprivation behaviors would be expected if the compounds in *L. maackii* cause damage to gill tissue as has been hypothesized (Maerz et al. 2005). Surfacing behavior was calculated from digital video after the animals had been measured on day 21. To prevent observer disruption, a digital video camera was positioned above 500-mL test chambers inside the climate-controlled room where the tadpoles were reared. Test chambers were filled with 300 mL of extract at the same concentration (5 g/L) used for rearing; the extracts were stored at 4°C prior to use. Animals were gently added to test chambers following the acclimation of water temperature to the climate controlled room (15°C). Behavioral observations of individuals were made in the same type of extract (*Lonicera*, Native, Control) that they had been reared in. Animals were allowed to acclimate for approximately 15 min prior to behavioral assays. A single observer (CRH) measured the number of trips to the surface over a 300-s period. Trips to the surface were defined as the moment the animal moved to the top quarter section of the chamber; subsequent surface scores were only made if animals dropped below the top quarter of the chamber. We tested for differences in the number of trips to the surface among extracts using a generalized linear model with a negative binomial error distribution. Methodological difficulties precluded behavioral observations of *A. maculatum* larvae, so we were only able to make behavioral observations of the three anuran species, *A. americanus*, *Hyla*, and *L. blairi*.

Results

Phenolic concentration

There was a significant difference in the concentration of total phenolics among extracts ($F_{2,9} = 77.96$, $P < 0.001$, and post hoc tests indicated that all pairwise treatment combinations were significantly different from one another ($P \leq 0.05$ in all cases). The concentration of total phenolics [mean ± 1 standard error (SE)] was 12.77 ± 1.07 mg/L in Native extracts, 3.35 ± 0.64 mg/L in *Lonicera* extracts, and 0.48 ± 0.18 mg/L in Control extracts. Although we did not observe phenolic concentrations in the range of 12–13 mg/L in the field, samples from small (diameter 1 m) pools created for an experimental field manipulation revealed concentrations approaching those observed in the laboratory study (range in total phenolics = 0.02–4.82 mg/L in native pools versus 0.00–1.50 mg/L in *L. maackii* pools; Watling et al. 2010). The results of our laboratory study are therefore likely to be most relevant in relatively small, ephemeral pools (e.g., vernal pools) that can be important breeding habitats for some amphibians (Brooks and Hayashi 2002; Van Buskirk 2003).

Survival and growth

Ambystoma maculatum larvae reared in *Lonicera* or Native extracts were more likely to die than those reared in Control extracts ($z = 3.67$, $P < 0.001$ and $z = 2.75$, $P = 0.006$; Fig. 1a), but there was no difference in the survival of

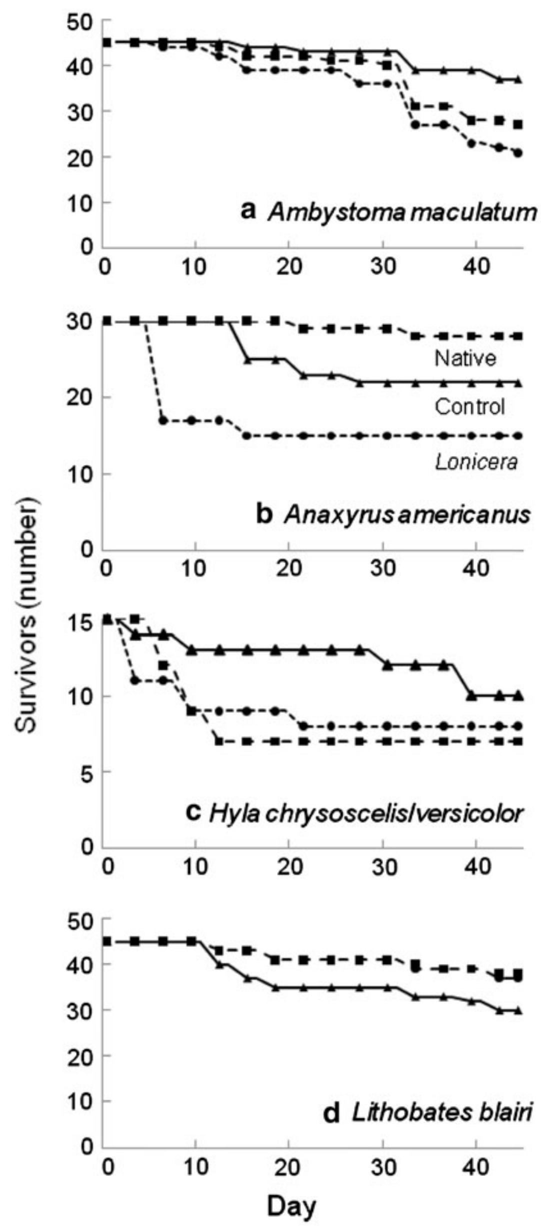

Fig. 1 Survival curves for four species of amphibian larvae (**a** *Ambystoma maculatum*, **b** *Anaxyrus americanus*, **c** *Hyla* sp., and **d** *Lithobates blairi*) reared in extracts from mixed native leaf litter (*Native*), invasive *Lonicera maackii* leaves (*Lonicera*), and dechlorinated water (*Control*) for 0–45 days. Many data points overlap during the first 10 days of the experiment, and for *L. blairii*, *Lonicera*, and Native data overlap throughout the course of the experiment

A. maculatum larvae between Native and *Lonicera* extracts ($z = 0.871$, $P = 0.380$). *Anaxyrus americanus* individuals reared in *Lonicera* extracts were 2.59-fold more likely to die than individuals reared in Control extracts ($z = 2.17$, $P = 0.03$, Fig. 1b) and 4.39-fold more likely to die than individuals in Native extracts ($z = 3.15$, $P < 0.001$). Mortality of *A. americanus* individuals in *Lonicera* extracts was rapid, with 13 of 30 individuals (43%) dying by day 4 of the experiment (Fig. 1b). Individuals reared in Native extracts were more likely to survive than individuals reared in Control extracts, but this difference was not significant ($z = -1.87$, $P = 0.062$). For both *L. blairi* and *Hyla*, there were no differences in the likelihood of survival across treatments (all $P > 0.33$; Fig. 1c, d).

Significant differences in the length of tadpoles surviving to day 21 were observed for *A. americanus* only ($F_{2,64} = 9.42$, $P < 0.001$), and pairwise comparisons indicated that individuals reared in Native extracts were larger (mean length 2.04 ± 0.21 cm) than individuals reared in the Control extracts (mean length 1.77 ± 0.25 cm; $P < 0.001$). There were no differences in the length of *A. americanus* individuals reared in *Lonicera* extracts (mean length 1.95 ± 0.17 cm) or Control extracts ($P = 0.057$), or between those reared in *Lonicera* or Native extracts ($P = 0.370$).

Respiration

The mean number of trips to the surface was significantly different among the treatments for *A. americanus* ($z = 3.56$, $P < 0.001$; Fig. 2a) and *L. blairi* tadpoles ($z = 2.80$, $P = 0.006$; Fig. 2b), but not for *Hyla* tadpoles ($z = 1.02$, $P = 0.309$; Fig. 2c). Both *A. americanus* and *L. blairi* reared in *Lonicera* extracts made more trips to the surface than those reared in Control or Native extracts (Fig. 2a, b).

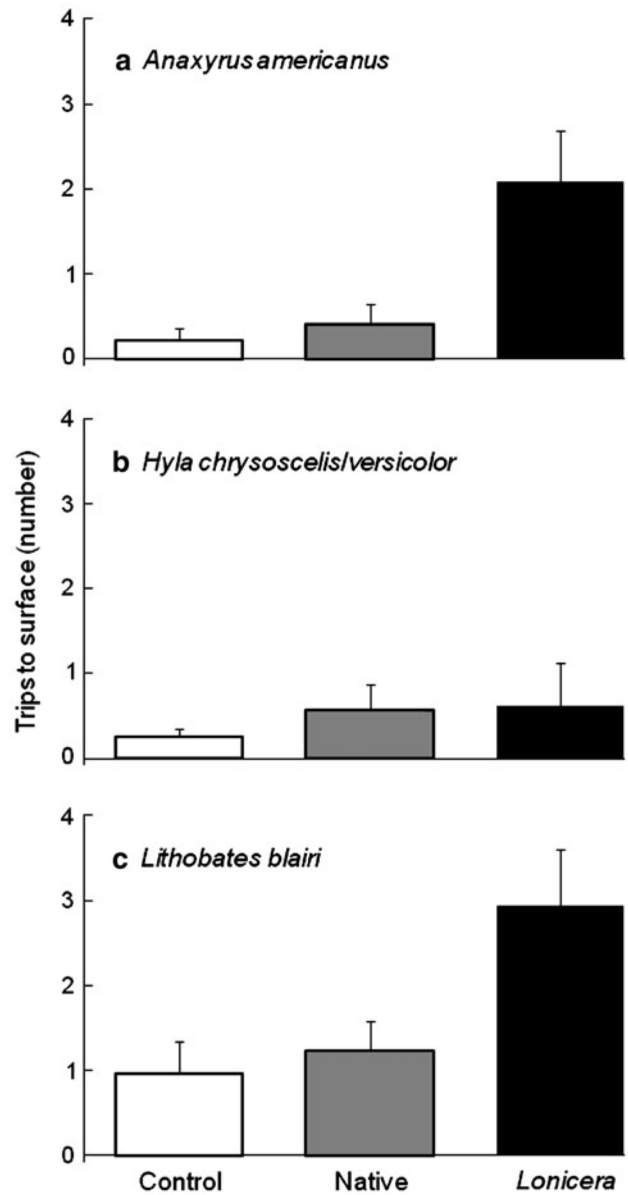

Fig. 2 Number of trips to the surface (mean ± 1 SE) during 5-min observation periods for three species of amphibian larvae in Native, *Lonicera* and Control extracts (see Fig. 2 for composition of extracts)

Discussion

The results of our study demonstrate that invasive plant extracts can reduce the survival of larval amphibians, documenting behaviors that suggest a decreased respiratory ability in exotic extracts and that behavioral shifts may ameliorate the toxic effects of exotic leachate for some species. *Anaxyrus americanus* tadpoles raised in *Lonicera* extracts were more likely to die than individuals raised in Native extracts (Fig. 1b). We observed a behavioral response (greater number of trips to the water surface) consistent with inhibited respiratory capacity in *A. americanus*. However, the observation that *L. blairi* tadpoles also increased surfacing behavior but were not more likely to die in *Lonicera* extracts suggests that they may be able to behaviorally counteract the negative effects of *Lonicera* leachate. Our results highlight two pathways by which invasive plants interact with organisms with which they share no trophic connection and suggest that amphibians may be negatively affected by plant invasions when exotic species contain toxic compounds absent in native plants.

Previous studies of invasive plant extracts on native animals have reported elevated mortality in exotic leachate containing a greater concentration of total phenolics than native leachate (Maerz et al. 2005; Brown et al. 2006; Canhoto and Laranjeira 2007). For example, the concentration of total phenolics in exotic *L. salicaria* extracts that induced mortality in *A. americanus* larvae comparable to that observed in the present study was 15.73 mg/L (Maerz et al. 2005), whereas native *Typha latifolia* contained only 0.62 mg/L (Maerz et al. 2005). In contrast, the concentration of total phenolics in the mixed native litter used in our study (12.77 mg/L) was much greater than the phenolic concentration of exotic *Lonicera* extracts (3.35 mg/L). It therefore appears that *L. maackii* is not toxic to *A. americanus* by virtue of a greater concentration of total phenolics but, rather, by virtue of both the presence and concentration of specific phenolic compounds. Studies of *L. maackii* extracts have implicated the phenolic compounds apigenin and luteolin as toxins that inhibit the growth and germination of native plants and deter herbivores (Dorning and Cipollini 2006; Cipollini et al. 2008). Our description of a rapid and substantial mortality of *A. americanus* tadpoles in *L. maackii* extracts suggests that *L. maackii* toxicity may be linked to specific compounds (e.g., apigenin and luteolin) rather than total phenolics. It is also possible that *L. maackii* toxicity is associated with other chemical or physical properties of the extracts, although we did not observe differences in dissolved oxygen levels in a subset of samples investigated in the study (Hickman, unpublished data) nor in pH in the pools utilized in a field mesocosm study of *L. maackii* effects on tadpoles (Watling et al. 2010). Amphibians have been shown to be particularly sensitive to phenolic compounds (Kerby et al. 2010), and our results suggest that more work is necessary to elucidate the link between phenolics and aquatic organisms in general. We note that although we observed a treatment effect on the survival of the *A. anaxyrus* individuals that were captured as tadpoles (the other species were obtained as egg masses), we doubt this difference in exposure affected our results because we would expect tadpoles introduced to extracts from the wild would be more resistant to leachate than naïve individuals.

The behavioral shifts we observed in *A. americanus* and *L. blairi* tadpoles reared in *Lonicera* extracts are consistent with compromised respiratory ability, although they do not preclude the possibility that invasive plant extracts induce a more generalized stress response. It has been hypothesized (Maerz et al. 2005) that exotic plant extracts induce greater mortality in obligate gill breathers (e.g., *Anaxyrus* spp.) than in species that can use alternative or multiple respiratory pathways (e.g., *Lithobates* spp.; Ultsch et al. 1999). Indeed, we observed that *A. americanus* tadpoles reared in *Lonicera* extracts made more trips to the surface than individuals raised in Native or Control extracts (Fig. 2a), suggesting compromised respiratory ability of individuals reared in exotic extracts. Because *A. americanus* tadpoles lack functioning lungs until just before metamorphosis (Wassersug and Feder 1983), they may die of asphyxiation when reared in *Lonicera* leachate. In contrast, although *L. blairi* tadpoles reared in *Lonicera* extracts showed a similar tendency to make more trips to the surface than individuals reared in Native or Control extracts, the alternative respiratory pathways available to *Lithobates* spp. tadpoles (e.g., surface breathing) suggests that they are able to behaviorally ameliorate the negative effects of *Lonicera* extracts. An alternative, though not mutually exclusive possibility, is that invasive plant extracts act as a stressor that induces an increase in activity (e.g. Cooke 1971), which may be associated with increased oxygen demand.

If our behavioral observations of surfacing behavior in the laboratory are representative of behavioral shifts in natural water bodies, we may expect to see indirect effects of invasive plants on amphibian larvae. Relative to controls, many larval amphibians alter activity levels when perceived predation threat is high (Skelly 1995; Van Buskirk 2002), and this is particularly true for amphibians with cryptic predators (Hickman et al. 2004) or those occurring in habitats with limited visual detection (Mathis et al. 2003). Therefore, the increased surfacing of *A. americanus* and *L. blairi* in *L. maackii* leachates may make those tadpoles vulnerable to predation in predator-containing water bodies in the invaded forest (Moore and Townsend 1998). Increased surfacing behavior also precludes investment in resource-acquisition (e.g., foraging, Lima and Dill 1990) that could have negative indirect effects on larvae (Werner and Peacor 2003). It is becoming clear that invasive species interact with native organisms via myriad indirect pathways (White et al. 2006), and our observations suggest that while the behavioral shifts of some species of amphibian larvae may ameliorate the toxic effects of exotic extracts, these behaviors may also have negative indirect consequences via predators.

In conclusion, we describe a significant increase in the mortality of *A. americanus* tadpoles when reared in *Lonicera* extracts compared with those raised in Native extracts. In contrast to previous studies, increased mortality in *Lonicera* extracts was not associated with greater concentrations of total phenolic compounds. Both *A. americanus* and *L. blairi* showed behaviors consistent with decreased respiratory ability in *Lonicera* extracts compared with Native extracts. However, whereas oxygen deprivation may be lethal to *A. americanus* tadpoles that lack lungs as larvae, *L. blairi* may behaviorally ameliorate the negative effects of *Lonicera* extracts by making more trips to the water surface. Because increased movement may make tadpoles more vulnerable to predators, our results suggest that chemical shifts in the environment caused by plant invasion may precipitate a variety of direct and indirect effects on native organisms.

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