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# Predators and invasive plants affect performance of amphibian larvae

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Exotic ecosystem engineers induce structural and qualitative habitat changes in invaded landscapes, yet studies rarely examine the effects of both of these changes on native taxa. We used a factorial experiment in natural, predator-containing environments to determine whether performance of amphibian larvae was affected by predators and/or changes in habitat structure or chemistry associated with the invasive shrub *Lonicera maackii*. Invertebrate predators significantly reduced survival of American toad *Anaxyrus americanus* larvae, whereas tadpole development was accelerated in pools inoculated with the chemical signature of *L. maackii*. The significant effect of *L. maackii* chemistry on *A. americanus* larvae suggests that invasive species may have non-intuitive effects even on native taxa with which they share no trophic connection, and may represent cryptic components of the multiple, interactive drivers of biodiversity change.

Invasive species represent important threats to biodiversity because they can disrupt key biotic interactions such as competition and predation (Levine et al. 2004), alter disturbance regimes (Brooks et al. 2004), and change the structure and quality of habitat in a landscape (Crooks 2002). Habitat-forming invasive species may have particularly far-reaching impacts in the ecosystems they invade because they can alter interactions among organisms (Gribben et al. 2009) and create novel indirect effects (White et al. 2006, Orrock et al. 2010). Although habitat-forming invasive species may provide structure themselves (Orrock et al. 2008a, 2010), they may also alter habitat quality via the addition of novel chemicals, as when exotic plants produce allelopathic compounds (Hierro and Callaway 2003). In some cases, water-soluble secondary compounds can alter water quality in landscapes where plants invade (Gordon 1998, Ehrenfeld 2003). Although these chemical and structural changes may have important and potentially interactive consequences for organisms in invaded habitats, large-scale field experiments capable of disentangling structural and chemical effects of invasive engineers have not been conducted. We used a landscape experiment to test for invasive plant impacts on survival and development of larval amphibians by comparing tadpole performance in water bodies with and without invasive plants present.

Physical and chemical changes to breeding habitat may have important consequences for amphibians because larval survival and development can influence amphibian population dynamics and persistence (Vonesh and De la Cruz 2002). Changes in habitat structure induced by invasive ecosystem engineers can alter ambient temperatures and levels of ultraviolet radiation and temperature, both of which can affect amphibian growth and survival (Newman 1998, Calfee et al. 2006). Amphibian larvae are also susceptible to changes in water chemistry, and may be particularly sensitive to water-soluble phenolic compounds (Kerby et al. 2010) that may be produced by exotic plants and become bioavailable to aquatic organisms, (Maerz et al. 2005, Canhoto and Laranjeira 2007). The structural and qualitative habitat changes caused by invasive species can also influence aquatic invertebrates (Canhoto and Laranjeira 2007), many of which are predators that affect performance of amphibian larvae (Werner and McPeek 1994, Hammond et al. 2007). Because there are few studies describing impacts of allelopathy on trophically-unrelated organisms in general (Wardle et al. 1998), it remains unclear if changes in water chemistry induced by invasive plants are important in natural, predator-containing water bodies and whether synergistic interactions between habitat structure and chemistry exist.

Amur honeysuckle *Lonicera maackii* is an exotic shrub that occurs in much of the United States east of the Rocky Mountains. In the midwestern United States, *L. maackii* provides a dense shrub layer that is not present in uninvaded oak-hickory forest. In addition to providing a novel dimension of vegetation structure in the forests it invades, *L. maackii* produces water-soluble phenolic compounds in its roots and leaves that have been shown to inhibit growth and survival of native plants (Dorning and Cipollini 2006, Cipollini et al. 2008). *Lonicera maackii* extracts are lethal to *Anaxyrus americanus* tadpoles reared without predators in laboratory studies (Watling et al. 2011). However, *A. americanus* tadpoles also make more trips to the surface in *L. maackii* extracts compared with extracts of native leaf litter and water controls (Watling et al. 2011), potentially making them more susceptible to predators (Moore and Townsend 1998). We manipulated the location and quality of artificial water bodies in plots invaded and uninvaded by *L. maackii*, and allowed invertebrate predators access to pools to investigate how an invasive ecosystem engineer changes the environment in ways that affect performance of *A. americanus* larvae in predator-containing water bodies.

## Methods

This work took place at the August A. Busch Memorial Conservation Area in St Charles county, MO (38°42′N, 90°44′W). Structural and chemical effects of *Lonicera maackii* were manipulated independently in artificial pools located throughout the 20 km$^2$ study area. Pools were installed in forested areas between 10–29 April 2009. Twelve plots, six in forest with a high density of *L. maackii* stems (mean number of stems per 1 m radius circular plot $\pm$ 1 SD = 2.90 $\pm$ 0.80) and six in forest with few or no *L. maackii* stems (0.25 $\pm$ 0.53 stems per plot) had pitfall trap arrays sampling terrestrial amphibians in addition to the artificial pools we created. All plots were located within 100 m of pools known to be used as breeding sites by amphibians (e.g. within the core area of upland habitat use for many temperate amphibians, Semlitsch and Bodie 2003). Insofar as we know, there have been no consistent differences in land use history between invaded and uninvaded plots. At each plot four pools approximately 1 m in diameter and 1 m apart and sloping at a 40–50° angle to a maximum depth of approximately 50 cm were installed. Pools were lined with plastic sheeting and covered with topsoil; two pools in each plot were lined with soil from a site with the opposite *L. maackii* density (e.g. pools in invaded plots were lined with topsoil from an uninvaded plot and vice versa) and the other two pools were lined with the soil removed while creating them. The topsoil in pools was covered with a comparable amount of leaf litter (approximately 500 g) in accordance with the type of soil used to line the pool and pools were allowed to fill with rainwater. We collected water samples from all stocked pools in August 2009 after the termination of all field experiments and measured pH using a freshwater pH test kit and the concentration of substances reducing Folin phenol reagent (e.g. total phenols) using spectrophotometry following standard procedures for water quality analysis (Clesceri et al. 1998).

At each site, one pool of each chemical treatment (e.g. with and without the chemical signature of *L. maackii*) was stocked with tadpoles, and the other two pools were left to be colonized naturally. We did not observe oviposition during the course of this study, so only report on the results of stocked pools here. On 14 May 2009, pools were stocked with 15 American toad *Anaxyrus americanus* tadpoles at stage 25 in the Gosner classification (McDiarmid and Altig 1999) obtained at several uninvaded breeding sites throughout the BCA and mixed to create a source pool of tadpoles representing different clutches. Tadpoles were left in pools for 26 nights, and surviving individuals were removed from pools on 9 and 11 June 2009. At the same time, we recorded the occupancy of pools by larval *Hydrochara* beetles, which we have observed to prey on *A. americanus* tadpoles (see also Roth and Jackson 1987). We never observed recently metamorphosed individuals around pools during regular visits to adjacent pitfall traps, and no other aquatic tadpole predators were observed during the study.

We recorded two metrics of larval performance: survival is a key life history trait linked to population growth (Stearns 1992), whereas the developmental stage of surviving individuals influences fitness in the post-metamorphic stage via carry-over effects (Child et al. 2008). Development was scored on a four-point scale based on a modification of the Gosner staging system by condensing stages 26–30, 31–35, 36–41 and 42–46 into four stages (I, II, III and IV) representing individuals with undifferentiated hind limb buds (I), hind limbs with a distinct foot paddle but relatively undifferentiated toes (II), well differentiated toes on the hind limbs (III), and forelimbs (IV).

Water quality and tadpole performance variables were analyzed using a split-plot ANOVA with structural treatment as the main plot and chemical treatment as the subplot (hereafter we refer to treatment levels as structure–invaded, structure–uninvaded, chemical–invaded and chemical–uninvaded to concisely describe the factorial combination of structural and chemical treatments). The Kenward–Rogers approximation was used to estimate appropriate degrees of freedom and variance components (Littell et al. 2006). Habitat structure, chemistry and predator occupancy were all treated as fixed effects. Water quality variables were examined using a Gaussian response distribution. The number of tadpoles alive at the end of the experiment was examined with a generalized linear model with a Poisson response distribution. Tadpole development was analyzed with a $\chi^2$-test to determine whether the frequency of most developed (stage IV) tadpoles varied as a function of habitat structure, chemistry or predator presence. For all $\chi^2$-tests, the response measured was the number of pools containing 0, 1 or 2 stage IV tadpoles (no pool contained more than two stage IV individuals) and pools with no surviving tadpoles were excluded from analyses. Because many cells had counts of less than five, significance of the $\chi^2$-test was determined by Monte-Carlo simulation; Monte-Carlo p-values confirmed standard p-values in all cases. All statistical tests were performed in SAS (SAS Inst. 2000) and means are presented $\pm$ SE.

## Results

Our experimental manipulation of leaf litter and soil in pools produced a significant change in water chemistry (habitat chemistry main effect, $F_{1,10} = 5.60$, $p = 0.040$), with the concentration of total phenolics lower in invaded pools ($0.45 \pm 0.35$ mg l$^{-1}$) than in uninvaded pools ($1.62 \pm 0.35$ mg l$^{-1}$). Phenolic concentration did not differ between pools in invaded and uninvaded plots (habitat structure main effect, $F_{1,10} = 1.24$, $p = 0.291$), and was therefore influenced only by our manipulation of soil and leaf litter. There was no interaction between habitat structure and chemistry on phenolic concentration ($F_{1,10} = 2.60$, $p = 0.138$). There was no difference in pH as a function of *L. maackii* density, chemistry or their interaction (all $p > 0.556$).

There was no main effect of habitat structure ($F_{1,6.49} = 0.08$, $p = 0.792$), chemistry ($F_{1,19} = 1.51$, $p = 0.235$) or their interaction ($F_{1,19} = 2.91$, $p = 0.104$) on tadpole survival (Fig. 1). Survival was over 50% lower in pools where predators were present (mean number of survivors = 2.04 ± 0.79) than where predators were absent (mean number of survivors = 5.34 ± 1.28; $F_{1,19} = 7.59$, $p = 0.013$; Fig. 2). The number of most-developed tadpoles did not vary between pools with and without invertebrate predators ($\chi^2 = 0.70$, DF = 2, $p_{\text{Monte Carlo}} = 1.000$); although only one stage IV tadpole was found in a pool occupied by *Hydrochara* larvae, the distribution of slow-developing tadpoles was similar between pools occupied or unoccupied by predators, resulting in a non-significant predator effect on development. The number of most-developed tadpoles did not differ between high and low *L. maackii* density treatments ($\chi^2 = 0.29$, DF = 2, $p_{\text{Monte Carlo}} = 1.000$, but there were more stage IV tadpoles in pools with the chemical signature of *L. maackii* than in pools with a native chemical signature ($\chi^2 = 7.29$, DF = 2, $p_{\text{Monte Carlo}} = 0.015$) indicating developmental acceleration in invaded pools (Fig. 3). Predator occupancy was unaffected by either habitat structure or chemistry (both $\chi^2 = 0.89$, DF = 2, $p_{\text{Monte Carlo}} = 0.645$).

## Discussion

Invasive exotic ecosystem engineers have the potential to cause important changes in the native communities they invade (Crooks 2002), but mechanisms whereby invaders may engineer habitats are poorly understood. Using a large-scale experimental approach, we demonstrate how changes in water chemistry associated with *L. maackii* soil and leaf litter affect tadpole performance by decreasing time to metamorphosis relative to individuals in water bodies with a native chemical signature (Fig. 3C). Because there is no trophic link between *L. maackii* and *A. americanus* tadpoles, our results reveal a broad effect of invasive plant secondary compounds that extends beyond population-level interactions (Wardle et al. 1998). We also describe a significant effect of predators on survival of *A. americanus* tadpoles (Fig. 2). Thus the factors driving dynamics of larval amphibians include well-studied stressors (e.g. predation, Barnett and Richardson 2002; pesticides, Boone and James 2003; ultraviolet radiation, Calfee et al. 2006) as well as more cryptic elements such as the chemical changes associated with invasive plant secondary compounds that we describe here.

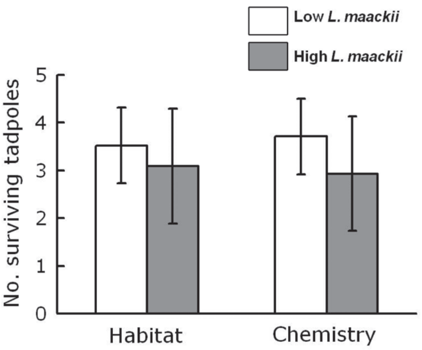

Figure 1. Number of surviving *Anaxyrus americanus* tadpoles in pools located in forest invaded or not by the shrub *Lonicera maackii* (habitat) or in pools with or without soil and leaf litter from invaded forest (chemistry).

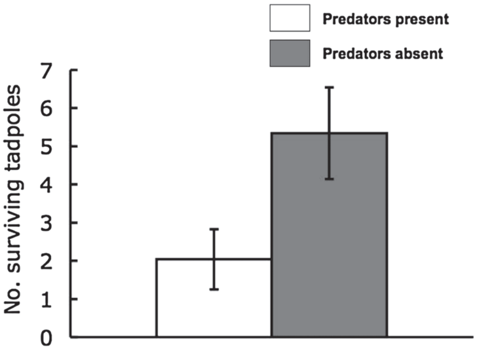

Figure 2. Number of surviving *Anaxyrus americanus* tadpoles in pools occupied or unoccupied by *Hydrochara* beetle larvae.

Whereas other studies of invasive plant extracts on aquatic organisms often report greater concentrations of total phenolic compounds in invasive compared with native plants (Maerz et al. 2005, Brown et al. 2006, Canhoto and Laranjeira 2007), *L. maackii* has a lower concentration of total phenolics than native species in our field study as well as in laboratory studies (Watling et al. 2011). Thus, *L. maackii* may not be toxic because of total phenolic concentration, but rather the presence and/or concentration of specific phenolic compounds (e.g. apigenin and luteolin in the case of *L. maackii*, Cipollini et al. 2008) that mediate toxicity of plant secondary compounds to other taxa. It is also possible that *L. maackii* leachates differ in some other chemical property from native leaves (e.g. nutrient availability) that may affect performance of larval amphibians. Given the accruing evidence suggesting that phenolic-containing invasive plants do affect native animals (Fig. 3C: Maerz et al. 2005, Brown et al. 2006, Canhoto and Laranjeira 2007) and the observation that our understanding of the complexities of phenolic effects is disproportionately low relative to their impacts on amphibian larvae (Kerby et al. 2010), future studies exploring the complexity of interactions between invasive plant chemistry and native fauna are needed.

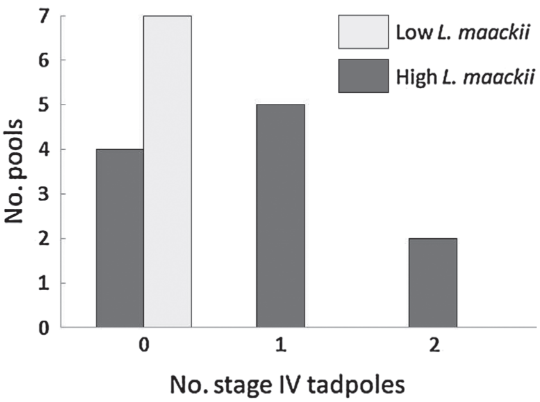

Figure 3. Number of experimental pools containing zero, one or two stage IV (most developed) *Anaxyrus americanus* tadpoles as a function of *Lonicera maackii* chemistry treatment (whether pool was lined with soil and leaf litter from plots invaded or uninvaded by *L. maackii*).

Whereas reduced survival of tadpoles in pools where we observed *Hydrochara* beetle larvae is expected given the myriad direct and indirect effects of predation (Skelly and Werner 1990, Wilbur and Fauth 1990, Nelson et al. 2004, Pressier et al. 2005, 2007, Orrock et al. 2008b), the absence of a chemical effect of *L. maackii* on *A. americanus* survival was unexpected because we have observed rapid and substantial mortality of *A. americanus* tadpoles exposed to *L. maackii* leachates in the lab (Watling et al. 2011). Several alternative mechanisms may explain these seemingly counterintuitive observations. It has been suggested that phenol accumulates to greater levels in the body at relatively lower temperatures (Brown et al. 1967), implying that the thermal environment (and therefore habitat type, time of year, and geographic location) may mediate the strength of response to *L. maackii* leachates. Studies that have described rapid and dramatic mortality of amphibian larvae in the presence of phenolic-containing invasive plant extracts used experimental arenas containing plant extracts and water only (Maerz et al. 2005, Brown et al. 2006, Watling et al. 2011). This approach does not allow leachates to interact with natural soil microbe communities and other plants and microorganisms that may mediate the strength of plant extract effects in natural systems (Abhilasha et al. 2008). As is the case with anthropogenic toxins, effects may vary depending on experimental venue and context (e.g. among laboratory, natural, and mesocosm conditions; Relyea 2006).

Our field experiment suggests that under natural conditions, alteration of the chemical environment by invasive plants induces developmental acceleration in *A. americanus* tadpoles, as we observed stage IV individuals exclusively in pools lined with soil and leaf litter from forest invaded by *L. maackii*. To our knowledge, this is the first documentation of exotic plant leachates altering the developmental trajectory of larval amphibians. Although accelerated metamorphosis has been associated with small body size (Morey 1994) which is associated with increased mortality in the terrestrial environment (Morey and Reznick 2001), susceptibility to desiccation (Child et al. 2008) and decreased locomotor performance (Beck and Congdon 2000, Ficetola and De Bernardi 2006), other studies have found neutral or positive carryover effects of reduced larval period (Smith 1987, Semlitsch et al. 1988). Longer-term studies will therefore be needed to determine the fitness consequences of the accelerated metamorphosis we describe from *L. maackii* chemistry treatments. Invasive plant effects on amphibian larvae may have large-scale population consequences: *L. maackii* occurs widely in North America east of the Rocky Mountains, and modeling suggests that performance of larvae and metamorphs may influence the persistence of amphibian populations (Vonesh and De la Cruz 2002).

Our work suggests that changes in water chemistry associated with litter and soil from forest invaded by *L. maackii* and the presence of *Hydrochara* beetle larvae affect the timing of metamorphosis and survival of *A. americanus* larvae. Although future experimental work will be necessary to fully characterize tadpole–predator–invasive plant interactions, our experiment adds to the growing evidence that invasive species may have non-intuitive effects on native biota (Orrock et al. 2008b, 2010, Gribben et al. 2009). Ultimately, the effect of invasive plants on amphibians is likely to interact with other drivers of amphibian population dynamics, including anthropogenic toxins, climate change, and disease (Collins and Storfer 2003, Sih et al. 2004). Our study suggests that an examination of multiple stressors on native animals may need to consider invasive exotic plants, because these invasive ecosystem engineers may be a cryptic component of multiple stressors on native taxa.

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