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ORIGINAL PAPER

Leaves of an invasive shrub induce mass mortality of an amphibian apex predator and its macroinvertebrate prey

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Abstract Studies of plant invasions have primarily focused on effects within shared habitats of native and invasive species. However, secondary compounds produced by terrestrial invasive plants can cross terrestrial-aquatic boundaries via senesced leaves, leading to altered patterns of aquatic biodiversity and ecosystem functioning. Impacts of phenolic compounds from senesced leaves have been characterized among relatively lower trophic groups, but effects on keystone species, such as apex predators, should have disproportionately larger effects on aquatic food webs. Using a widespread invasive species (Amur Honeysuckle, *Lonicera maackii*), we employed experimental mesocosms to examine effects of honeysuckle leaf litter addition on survival of apex predators (larval spotted salamanders, *Ambystoma maculatum*), their zooplankton and macroinvertebrate prey, indicators of primary productivity and decomposition, and abiotic variables influenced by phenolic compounds. Despite previous laboratory observations suggesting *A. maculatum* might exhibit resistance to *L. maackii* leachates, we observed near complete loss of both *A. maculatum* and benthic macroinvertebrates in experimental mesocosms, while zooplankton abundance was unaffected. Mortality was likely associated with precipitous declines in dissolved oxygen following rapid decomposition of *L. maackii* leaves, and these conditions facilitated nearly 15-fold increases in larval mosquito abundance. Our results highlight how experimental venue and methodology may alter outcomes of investigations involving senesced leaves of invasive plants. Losses of amphibian predators under quasi-natural invasion conditions indicate important influences on terrestrial-aquatic nutrient exchange, and we highlight phenological patterns of leaf senescence and breeding by aquatic organisms as important avenues for further investigation in characterizing the consequences of plant invasions.

Keywords Leaf litter · Macroinvertebrates · Plant leachates · Terrestrial-aquatic linkages · Salamander · Zooplankton

Introduction

Exotic species can become invasive, displacing native flora and fauna, and negatively impacting ecosystems (Mooney and Cleland 2001; Zedler and Kercher 2004; Didham et al. 2005; Lockwood et al. 2013; Havel et al. 2015; David et al. 2017; Stewart et al. 2021). Invasive plant species in particular are established on all seven continents, subsequently altering native ecosystems through direct and indirect pathways. Direct pathways through which invasive plants affect ecosystems include competition and associated changes in plant community

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composition (Orrock et al. 2010; Didham et al. 2005; Weidenhamer and Callaway 2010), shifts in canopy structure, shifts from herbaceous to woody plants (or vice versa), increased productivity and leaf litter deposition, changes in leaf litter mass loss, altered nutrient regimes, and increased or decreased flammability (Zedler and Kercher 2004). Some invasive plants, however, also exert ecosystem-level effects through indirect pathways, such as alteration of terrestrial and/or aquatic chemical environments (Ehrenfeld 2003; Levine et al. 2003; Wolfe and Klironomos 2005; Burrow and Maerz 2022).

Several invasive plant families alter physical and chemical environments of invaded habitats (Ehrenfeld 2003; Wolfe and Klironomos 2005; Weidenhamer and Callaway 2010), and of these, shrubs are the most common plant life form (McKinney and Goodell 2010). In much of the eastern United States, Amur Honeysuckle (*Lonicera maackii*) has invaded (Luken and Thieret 1996; Hutchinson and Vankat 1997; Miller and Gorchov 2004), creating thick shrub layers that are absent in native, uninvaded forests (Collier et al. 2002). Invasion by *L. maackii* has altered above-ground features of ground level light (McKinney and Goodell 2010), transpiration (Boyce et al. 2012), humidity (Chen and Matter 2017), pollinator visitation (McKinney and Goodell 2010), and seed germination (McEwan et al. 2010), as well as below-ground features of soil water content (Pfeiffer and Gorchov 2015), soil microbial communities (Arthur et al. 2012), and decomposition rates (Trammell et al. 2012). Such changes influence plant and animal diversity and therefore impact community composition of invaded areas (Collier et al. 2002; McKinney and Goodell 2010; Watling et al. 2011a) while creating novel ecological interactions (McNeish and McEwan 2016; Hoven et al. 2017; Martinod and Gorchov 2017; Stewart et al. 2021). *Lonicera maackii* also significantly alters soil chemistry by releasing water soluble phenolic compounds (i.e., tannins) which are toxic to many terrestrial and aquatic animals (Templer et al. 1998; Rauha et al. 2001; Watling et al. 2011b). Studies of *L. maackii* and other invasive terrestrial plants have emphasized their direct impacts on terrestrial communities, yet recent work has highlighted the apparent ease with which phenolic compounds of invasive plant species can cross terrestrial-aquatic boundaries via senesced leaves, negatively impacting both lentic (Watling et al. 2011a, b, c; Robison et al. 2021) and lotic aquatic ecosystems (McNeish et al. 2012; Borth et al. 2018; Little et al. 2021).

Dissolution of phenolic compounds can result in maladaptive behavioral changes and increased mortality of some aquatic animals (McNeish and McEwan 2016; Stewart et al. 2021; Burrow and Maerz 2022). Native species are adversely affected by phenolic compounds produced by invasives because of short evolutionary histories of co-occurrence, which limit evolution of resistance to novel toxins ("novel weapons hypothesis"; Callaway and Ridenour 2004). Lethal and sub-lethal effects of phenolic compounds on aquatic taxa negatively impact population-, community-, and ecosystem-level patterns and processes (reviewed in McNeish and McEwan 2016; Burrow and Maerz 2022), yet previous studies of *L. maackii* invasion impacts on aquatic animals have been taxonomically limited primarily to: (a) macroinvertebrates in lotic systems; and (b) herbivorous anuran larvae (i.e., tadpoles) in lentic systems. These groups tend to occupy relatively low trophic positions, and thus further investigation is needed to predict the broader impacts of invasion by *L. maackii* in aquatic systems (Weidenhamer and Callaway 2010; Watling et al. 2011c). Specifically, assessments of invasion impacts on secondary and/or higher order consumers are particularly warranted, as their responses to phenolic compounds may alter trophic cascades and resulting aquatic community structure.

Within many aquatic habitats, larval salamanders are apex predators that dramatically alter community structure and generate strong trophic cascades (Morin 1983a, b; Cortwright and Nelson 1990; Holomuzki et al. 1994; Petranka 1998). Therefore, disparate responses to *L. maackii* among larval salamanders and their invertebrate prey could alter resulting trophic dynamics and ecosystem functions. Previous studies of larval amphibian exposure to leaf extracts of invasive species have observed widely varying responses, ranging from increased mortality, to altered behavior without reduced survivorship, to relatively no impact, to positive effects (Watling et al. 2011a, b, c; Stephens et al. 2013, Martin et al. 2015). Watling et al. (2011b) showed larval spotted salamanders (*Ambystoma maculatum*: Ambystomatidae) did not experience increased mortality from exposure to leachate from *A. maackii* relative to native leaf litter, yet syntopic *Anaxyrus americanus* tadpoles experienced increased mortality under the same conditions;

similar species-specific responses occur in response to other invasive plants (Maerz et al. 2005). Such taxon-specific effects extend to predator–prey interactions, as Robison et al. (2021) demonstrated most macroinvertebrate taxa consumed by larval *A. maculatum* are reduced drastically when exposed to *L. maackii*, while zooplankton prey were unaffected.

Prior assessments of amphibian responses to *L. maackii* exposure have elucidated several possible mechanisms of increased mortality, such as inhibition of respiration (Watling et al. 2011b) or induction of behaviors that increase predation risk (Hickman and Watling 2014). However, the use of controlled lab studies, while critical in identifying the mechanistic bases of mortality, may underestimate rates of in situ mortality and associated consequences for aquatic communities. For example, studies of animal responses to invasive plants often employ leaf leachates as sources of phenolic compounds as opposed to whole leaves, yet such approaches do not incorporate potential additive or synergistic effects of leachates and leaf litter decomposition on survival. Leaves of *L. maackii* decompose more rapidly than many native plant species (Arthur et al. 2012; McNeish et al. 2012; Trammell et al. 2012), potentially leading to increased hypoxia that may exacerbate effects of leachates on respiration predicted to occur through coating of respiratory structures (Maerz et al 2005; Watling et al. 2011b; Hickman and Watling 2014). Also, native plants produce their own phenolic compounds, often in higher concentrations than invasive plants generally (Kim and Lee 2011) and *L. maackii* specifically (Watling et al. 2011b), and aquatic systems are unlikely to consist solely of leaf litter from *L. maackii* even in heavily-invaded habitats (Watling et al. 2011c). Therefore, natural or quasi-natural observational and/or experimental approaches employing mixed leaf litter (sensu Watling et al. 2011c; Barrett et al. 2017; Robison et al. 2021) are needed to improve our understanding of the broader ecological consequences of *L. maackii* invasion for aquatic ecosystems. Within this context, we employed an experimental mesocosm design to assess the consequences of *L. maackii* leaf litter addition for growth and survival of predatory larval *A. maculatum*. We concurrently characterized invertebrate prey community structure and indices of ecosystem function (leaf litter decomposition, dissolved oxygen, relative fluorescence, and biofilm formation) that are sensitive to changes in invertebrate abundance and community composition. We hypothesized that if larval *A. maculatum* persisted following addition of *L. maackii* leaves, they would experience negative growth and survival consequences if macroinvertebrate prey densities decreased. Larval *Ambystoma* exhibit ontogenetic dietary shifts from zooplankton to macroinvertebrate prey (Freda 1983; McWilliams and Bachmann 1989), and therefore we predicted that persistence of zooplankton following *L. maackii* invasion (Robison et al. 2021) would not offset losses in macroinvertebrate abundance or prevent resultant decreases in larval growth and survival. We also predicted that reductions in densities of larval salamanders and predatory macroinvertebrates would facilitate increased abundances of their shared zooplankton prey. Such changes in community structure were hypothesized to decrease rates of decomposition (due to the loss of shredding taxa) and primary production (due to increased densities of herbivorous zooplankton). By characterizing responses of trophic groups with varying sensitivities to *L. maackii* leaf litter, we hoped to gain insight into how species-specific tolerances to invasion might alter community structure and ecosystem function.

Methods

We established 30 experimental mesocosms (1136-L cattle tanks) in a 5 × 6 array at Taylor Fork Ecological Area (TFEA), Eastern Kentucky University (EKU, Madison County, Kentucky, USA). Leaves from *L. maackii* and native trees (*Acer rubrum*, *Platanus occidentalis*, *Carya* spp. and *Quercus* spp.) were collected following natural senescence in November–December 2017 and dried for five days to obtain constant dry mass (DM). Mesocosms in the “mixed-leaf” treatment received 199.5 g DM of native leaves and 7.5 g DM of *L. maackii* leaves (~ 3% invasive leaf litter content, or 0.007 g/L *L. maackii* leachate concentration), and “native” leaf treatments received ~ 208 g DM of native leaf litter ($N = 15$ replicate mesocosms each). Mesocosms were randomly assigned to treatment, and the mesocosm array was positioned in a flat, open field to eliminate the possible confounding impacts of aspect and/or variable canopy cover. Zooplankton were collected from a cistern and natural pond at TFEA with an 80-μm conical zooplankton net and added to a spare mesocosm, and 3-L aliquots from this concentrated sample were added to each experimental mesocosm. Sediment was collected from a pond at TFEA, homogenized, and distributed in 2-L aliquots to each mesocosm. Each mesocosm also received 950 mL of a concentrated phytoplankton and filamentous green algae sample from an unused mesocosm. Mesocosms remained uncovered for two months (early-March to early-May) to promote colonization by volant aquatic invertebrates. Many invertebrate taxa colonized mesocosms independently; however, three snails (Mollusca: Physidae) and three larval zygopterans (Odonata: Coenagrionidae) were added to each mesocosm prior to introduction of amphibian larvae, since it appeared unlikely these groups would self-colonize before the start of the experiment.

To monitor biofilm formation in experimental mesocosms, an unglazed ceramic tile (4.7×4.7×0.5 cm) was affixed to the south-facing side of each mesocosm, suspended ~2.5 cm above leaf litter and sediment. To assess rates of leaf litter decomposition, a nylon mesh bag (27 cm×17 cm, 0.5-cm mesh) containing 5 g DM of dried native leaf litter (*Acer rubrum, Platanus occidentalis, Carya* spp. and *Quercus* spp., Boulton and Boon 1991) was placed in each mesocosm. In addition, one bag containing 5 g DM of dried *L. maackii* leaf litter was added to each mixed-leaf treatment mesocosm. All leaf litter bags were placed on top of benthic material on the mesocosm's south-facing side.

Egg masses (~20) of *A. maculatum* were collected on March 23, 2018 at Miller-Welch Central Kentucky Wildlife Management Area (Waco, Kentucky, USA). Egg masses were initially housed in the EKU vivarium facilities and maintained in environmental chambers at 11.4 °C and under a 12L:12D photoperiod until hatching, which occurred between March 30 and April 20. On April 20 all larvae were added to a single unused mesocosm and homogenized, and groups of 30 larvae were haphazardly assigned to experimental mesocosms. Larvae were photographed for subsequent measurement and transported to mesocosms, acclimated within mesocosms in transport containers for 40 min, and released.

After 45 days, three 40 cm×25 cm×25 cm minnow traps were placed in each mesocosm for 24 h, and all larval salamanders captured were photographed for measurement of snout-vent length (SVL) with Image J (Schneider et al. 2012; Mott and Steffen 2014) to determine growth rate and abundance; individuals were returned to their respective mesocosms. After larval sampling was completed, leaf litter bags were removed, dried for 120 h at 65 °C, and weighed to determine leaf litter loss. Algal tiles were removed from mesocosms and scraped with razor blades, with contents preserved in 2% glutaraldehyde, dried for 48 h at 80 °C, and weighed to estimate biomass (Rosemond et al. 1993). We also recorded relative fluorescence, dissolved oxygen, and temperature from each mesocosm. Benthic macroinvertebrates were collected using one haul of a 1215-cm^3 grab (Fieldmaster Mighty Grab, Wildlife Supply Company, Yulee, Florida). Samples were preserved in 70% ethanol and Rose Bengal stain. Macroinvertebrates were enumerated and identified under 35×dissection microscopy to the lowest useful taxonomic level and functional group using Merritt and Cummins (2008). We also opportunistically sampled larval mosquito (Culicidae: genus *Aedes*) populations in mesocosms after observing large adult emergence events from mesocosms prior to the scheduled end of the experiment. One 500-mL sample of surface water was collected from each mesocosm, with counts of larvae conducted under 35×dissection microscopy. Zooplankton samples were collected using a single vertical dip of an 80-µm conical zooplankton net, with samples preserved in 70% ethanol stained with Rose Bengal. A 1-mL subsample from each sample was pipetted onto a Sedgewick-Rafter counting chamber (Wildlife Supply Company, Yulee, Florida), and under 32×dissection microscopy, zooplankters were enumerated and identified to order (Smith 2001). After salamanders in experimental mesocosms began to show signs of metamorphosis (i.e., loss of gills and tail fins, development of eyelids and juvenile coloration; Petranka 1998), metamorphs were removed from mesocosms, photographed and measured, and anesthetized and euthanized by immersion in a 250 mg L^{-1} aqueous solution of benzocaine.

Statistical analyses

All statistical analyses were performed using R version 4.1.0 (R Core Team 2021). We initially expected to assess treatment effects on larval salamander survival and growth at 45 days, as well as the average number of metamorphs produced, time to metamorphosis, and size at metamorphosis. However, exceedingly low survival of larval *A. maculatum*, as well as low metamorph production, in the mixed-leaf treatment precluded all but an analysis of treatment effects on larval survival at 45 days. Treatment effects on larval survival (arcsine square-root-transformed) were analyzed using a Mann–Whitney U test. After removing singletons and doubletons from the macroinvertebrate data set, treatments effects on invertebrate communities were examined using multivariate analysis of variance (MANOVA), with response variables of: (1) zooplankton densities; (2) benthic macroinvertebrate densities, (3) densities of each of the three most common benthic macroinvertebrate groups (Chironomidae, Culicidae, Oligochaeta, which collectively accounted for > 90% of all macroinvertebrate taxa); and (4) densities of larval culicids obtained from opportunistic surface sampling. All densities were square-root transformed, as these values were derived from count data using the known volumes of areas sampled. A second MANOVA was used to assess treatment effects on: (1) dissolved oxygen; and (2) relative fluorescence units (as indicators of primary production; (3) biofilm mass (as an indicator of biofilm growth); (4) leaf litter loss between native-leaf bags in the native-leaf mesocosms and mixed-leaf bags in the mixed-leaf mesocosms; and (5) leaf litter loss between native-leaf bags in both the native- and mixed-leaf treatments. The latter response was included to determine if increased rates of decomposition observed in *L. maackii* bags were specific to that species or reflective of general trends towards increased decomposition rates in the mixed-leaf treatment. Following identification of significant treatment effects from MANOVA, subsequent univariate analyses of variance (ANOVAs) were conducted for each response variable, while including Holm's adjustment for multiple comparisons.

Results

Mortality of larval *A. maculatum* was nearly 100% when exposed to leaves of *L. maackii*, and in fact, larvae were only detected in a single mixed-leaf mesocosm ($N = 2$ larvae) during minnow trapping at 45 days post-introduction, resulting in significantly lower larval survival between treatments (Fig. 1; Mann–Whitney U test, $P = 0.0006$; larvae detected in 100% of native-leaf mesocosms). However, larval growth rates could not be reliably estimated due to low sample sizes from mixed-leaf mesocosms. In addition to minnow-trapping, opportunistic observations of native- and mixed-leaf mesocosms as early as 2 days post-introduction, and repeatedly at intervals of 2–3 days/week, resulted in no observations of larval *A. maculatum* in mixed-leaf mesocosms, indicating rapid mortality. Metamorphosis of larval *A. maculatum* occurred between May 31 and September 18. Only three metamorphic *A. maculatum* emerged from mixed-leaf mesocosms (1% survival), whereas a total of 114 metamorphs emerged from native leaf mesocosms (38% survival).

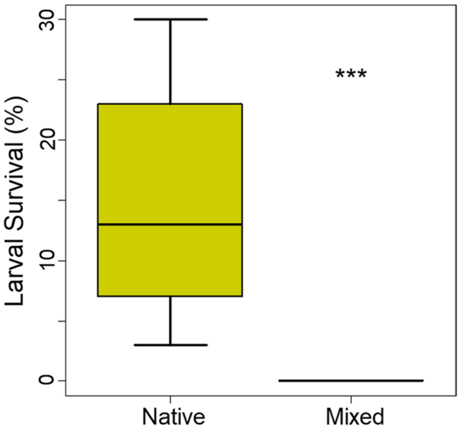


Fig. 1 Mean percent survival of larval *Ambystoma maculatum* in response to leaf litter type. The central horizontal lines within boxes represent medians, the boxes encompass quartile ranges, and whiskers represent minimum and maximum data values, with *** denoting $P < 0.01$

Addition of *L. maackii* leaves to experimental mesocosms significantly altered invertebrate communities (MANOVA $F_{6,13} = 47.568$, $P < 0.001$; Table 1). The presence of *L. maackii* leaves significantly reduced densities of macroinvertebrates collectively (by ~ 91.7%; Fig. 2a), and specifically for benthic chironomid larvae (by 87.5%; Fig. 2b) and oligochaetes (by 100%; Fig. 2c). Conversely, addition of *L. maackii* leaves increased densities of culicids at the surface of experimental mesocosms by nearly 15-fold (Fig. 2d). Densities of benthic culicid larvae (Fig. 2e) and zooplankton (Fig. 2f) were not significantly affected by addition of *L. maackii*.

Addition of *L. maackii* leaf litter altered multiple indicators of aquatic ecosystem function in

Table 1 Results of MANOVA for overall effects of treatment type (native leaves versus native/*L. maackii* mixed leaves) on invertebrate communities, and subsequent univariate ANOVAs for each response variable

		F	*df*	*P*
MANOVA		47.568	6.13	< 0.001
ANOVAs				
	Zooplankton (total)	0.691	1.18	0.833
	Macroinvertebrates (total)	21.159	1.18	0.001
	Chironomidae	11.831	1.18	0.009
	Culicidae (benthic)	0.068	1.18	0.833
	Culicidae (surface)	328.700	1.18	< 0.001
	Oligochaeta	30.556	1.18	0.001

All response variables were square-root transformed counts of each invertebrate taxa

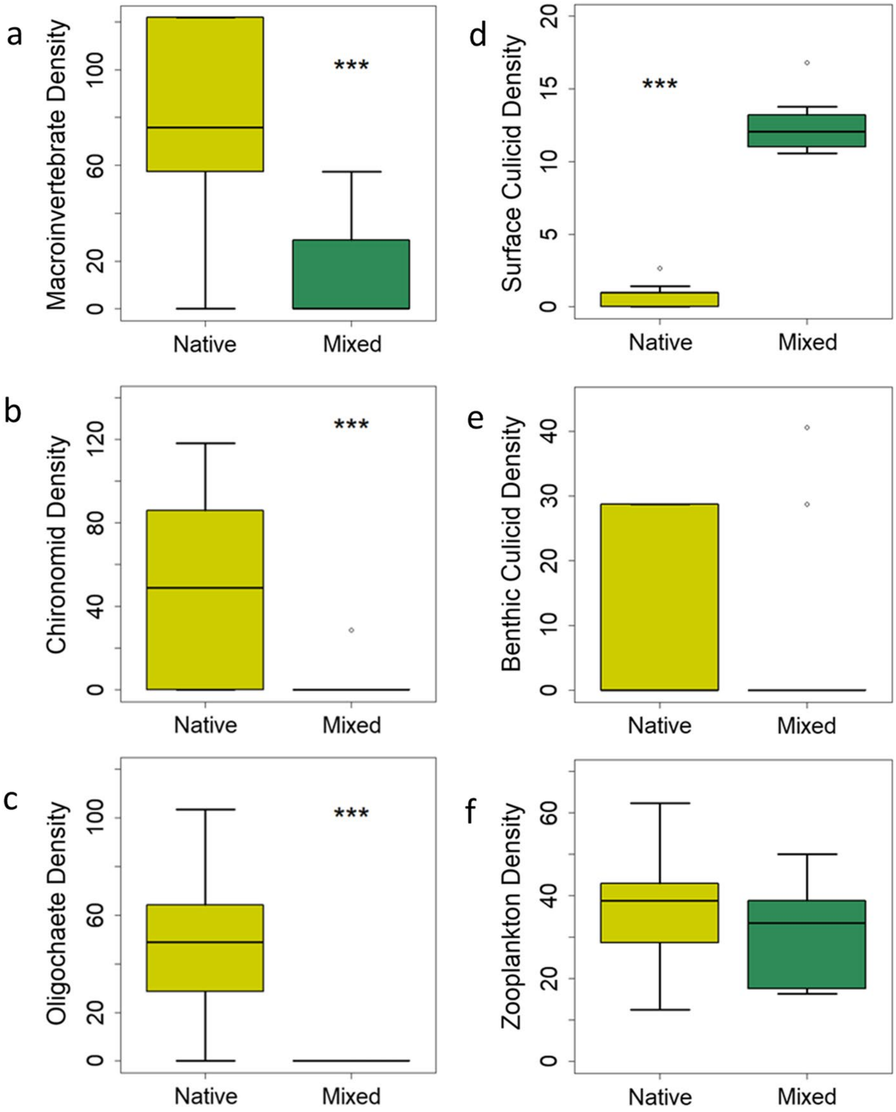


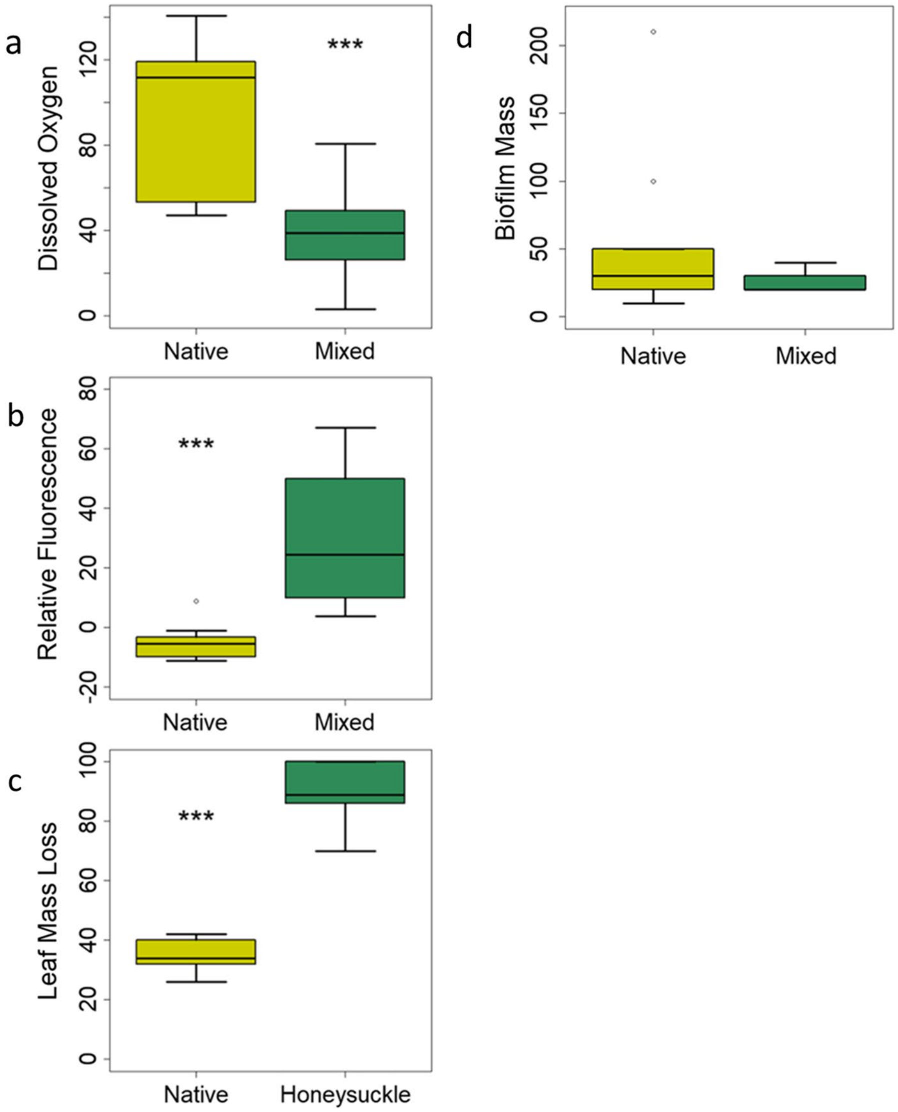
Fig. 2 Mean densities (individuals/cm^3) of all benthic macroinvertebrates combined (**a**), benthic chironomid larvae (**b**), benthic oligochaetes (**c**), surface culicid larvae (**d**), benthic culicid larvae (**e**), and zooplankton (**f**) in response to leaf litter type. The central horizontal lines within boxes represent medians, the boxes encompass quartile ranges, and whiskers represent minimum and maximum data values, with *** denoting $P < 0.01$

Table 2 Results of MANOVA for overall effects of treatment type (native leaves versus native/*L. maackii* mixed leaves) on indicators of ecosystem function, and subsequent univariate ANOVAs for each response variable

	F	*df*	*P*
MANOVA	14.788	5.14	< 0.001
ANOVAs			
Dissolved oxygen	18.568	1.18	< 0.001
Relative fluorescence units	20.673	1.18	< 0.001
Algal biomass	2.287	1.18	0.147
Leaf loss (native versus mixed)	58.229	1.18	< 0.001
Leaf loss (native versus native)	0.737	1.18	0.419

experimental mesocosms (MANOVA $F_{5,14} = 14.788$, $P < 0.001$; Table 2). Mixed-leaf mesocosms containing *L. maackii* leaves exhibited a 59.3% decrease in dissolved oxygen relative to native-leaf mesocosms, as well as a sevenfold increase in relative fluorescence (Fig. 3a, b). Leaf litter bags containing *L. maackii* leaves in mixed-leaf mesocosms exhibited nearly fourfold decreases in leaf mass (i.e., increased rates of decomposition) during the study period relative to bags containing native leaves (Fig. 3c). Native leaves in both native- and mixed-leaf mesocosms exhibited similar decreases in leaf loss (Table 2), and therefore decomposition of native leaves was not affected by the presence and/or decomposition of *L. maackii*

Fig. 3 Mean dissolved oxygen (%; **a**), relative fluorescence (RFU; **b**), leaf mass loss (%; **c**), and biofilm mass (mg; **d**) in response to leaf litter type. The central horizontal lines within boxes represent medians, the boxes encompass quartile ranges, and whiskers represent minimum and maximum data values, with *** denoting $P < 0.001$



leaves. Biofilm mass did not differ between native- and mixed leaf mesocosms (Fig. 3d, Table 2).

Discussion

Our study indicates senesced leaves of *L. maackii*, even at low abundances relative to native leaves, can induce mass mortality within multiple trophic levels under quasi-natural conditions in experimental aquatic mesocosms. The use of lower invasive: native leaf mass ratios compared to previous studies was intended to facilitate investigations of indirect effects of *L. maackii* leaves on apex predators through altered trophic interactions, as larval salamanders generally, and ambystomatids specifically, may be more resistant to negative effects of leaf litter composition than other larval amphibians inhabiting relatively lower trophic positions (Rubbo and Kiesecker 2004; Earl et al. 2011; Watling et al. 2011b). In contrast, we observed the near-complete loss of larval salamander apex predators and benthic macroinvertebrates, as well as any presumed ecosystem functions associated with these groups and/or their ecological interactions. Leaves of *L. maackii* exhibited increased rates of decomposition consistent with previous observations (Arthur et al. 2012; McNeish et al. 2012; Trammell et al. 2012), reducing dissolved oxygen to levels observed in other studies (Custer et al. 2017; Robison et al. 2021) despite increased relative fluorescence, and nearly extirpating larval amphibian predators and benthic macroinvertebrates while leaving zooplankton populations intact. That addition of *L. maackii* leaves reduced aquatic habitat quality was further supported by dramatic increases in abundance of larval culicids, as such taxa experience increased fitness under hypoxic conditions associated with rapid decomposition (Fish and Carpenter 1982; Yee and Juliano 2006; Chitolina et al. 2016). Beyond the broad fitness benefits of rapidly decomposing leaves of various species, *L. maackii* in particular has been linked to increased growth rates and survivorship in culicid larvae, and such effects occur following exposure to both senescent leaves and flowers (Shewhart et al. 2014).

Detritus-based wetlands rely heavily on autochthonous nutrient inputs, and thus chemical composition of leaf litter fall has important implications for aquatic invertebrate and amphibian communities (Yanoviak 1999; Williams et al. 2008; Kominoski et al. 2009; Earl and Semlitsch 2013; Stoler et al. 2016; Stoler and Relyea 2011, 2020). Studies of native plants have documented strong species-specific effects of leaf litter type on behavior, morphology, growth, and survival of aquatic taxa (Graça 2001; Gessner et al. 2010; Earl et al. 2012; Stoler and Relyea 2013, 2021; Earl 2021). Similar work with invasive plants suggests effects on aquatic communities are driven by specific leaf traits, and not simply non-native origins (Cohen et al. 2012; Martin and Blossey 2013), as leaf litter from some invasive species positively impacts aquatic taxa (Stephens et al. 2013; Martin et al. 2014). Negative consequences of invasive leaf litter for aquatic communities include diverse indirect, long-term effects, such as changes to nutritional quality of leaves and/or periphyton (Maerz et al. 2005), decomposition rates (Maerz et al. 2010), foraging patterns (Brown et al. 2006), surfacing behavior (Hickman and Watling 2014), and chemosensation (Stoler and Relyea 2013). However, rapid mortality such as we observed is likely indicative of more direct effects of *L. maackii*, which include decreased dissolved oxygen (Martin et al. 2014; Custer et al. 2017; Robison et al. 2021), damage to respiratory surfaces and associated reduction in absorptive capabilities (Temmink et al. 1989; Maerz et al. 2005), as well as endocrine disruption (Kudo and Yamauchi 2005). Such negative outcomes are attributable to specific phenolic compounds like apigenin and luteolin (Cipollini et al. 2008), and not necessarily heightened phenolic concentrations, as studies have repeatedly observed lower phenolic concentrations among invasive plant species relative to syntopic native species (Watling et al. 2011b; Maurer 2014; Harrison et al. 2017). While benthic taxa in our study (macroinvertebrates, salamander larvae) experienced severe mortality, persistence of zooplankton populations and increased relative fluorescence indicate potential stratification of the effects of *L. maackii* leaves and leachate. Zooplankton abundance and fluorescence were determined from the surface of mesocosms, where dissolved oxygen is often maximized in shallow ponds (Vad et al. 2013; Wauthy and Rautio 2020). We did not explore patterns of response by depth, though such approaches in future studies may help explain variable survival patterns within and among taxa based on microhabitat selection.

Mass mortality in amphibians exposed to senesced leaves of *L. maackii* in experimental mesocosms highlights complex pathways through which experimental venue and methodology may influence studies of plant invasions in aquatic ecosystems. Concentrations of invasive plant leachates employed in previous laboratory studies, including those of *L. maackii*, tend to range between 0.5 and 100 g litter/L (Maerz et al. 2005; Brown et al. 2006; Stephens et al. 2013; Borth et al. 2018; Burraco et al. 2018; Curtis and Bidart 2021), and a study of larval *A. maculatum* did not observe significant increases in mortality following exposure to leachates at a concentration of 5 g/L (Watling et al. 2011b). In contrast, we employed effective *L. maackii* and "total" (native + *L. maackii*) leachate concentrations of 0.007 g/L and 0.18 g/L, respectively, and documented catastrophic effects on larval amphibian survival. Earl et al. (2012, 2014) noted that assessments of leaf litter effects using experimental mesocosms can produce lower dissolved oxygen levels relative to similar laboratory studies (but see Custer et al. 2017 for the opposite response with fruits and flowers). Mortality of aquatic species in laboratory studies may therefore arise primarily from damage to respiratory surfaces (Maerz et al. 2005) or other chemical properties of phenolic compounds, whereas mesocosm studies would include these factors and influences of low dissolved oxygen. Studies of leachate-induced toxicity have also noted contrasting effects of tannin concentrations and larval amphibian growth and survival between lab and mesocosm approaches (Earl et al. 2012; Stephens et al. 2013). Among studies that utilize leaves rather than leachates, leaf soak times prior to introduction of focal organisms vary from hours to months (Maerz et al. 2005; Adams and Saenz 2012; Earl et al. 2014; Stephens et al. 2013), which likely affects tannin concentrations and subsequent effects on focal taxa (Earl et al. 2012; Stephens et al. 2013). In addition to initial variation in tannin and dissolved oxygen concentrations, our previous long-term (~2 years) experiment with *L. maackii* suggests invertebrate communities may recover from exposure over time, while effects on amphibian oviposition site selection remain (Robison et al. 2021), highlighting the importance of experiment duration in accurately characterizing both short- and long-term consequences of invasion.

Secondary compounds produced by invasive plants exhibit considerable temporal and/or ontogenetic variability in their chemical composition and toxicity (Ravn et al. 1994; Boege and Marquis 2005; Goodger et al. ; Elger et al. 2009). Assessments of invasion impacts must therefore consider aspects of phenology and subsequent effects on ecological interactions. *Lonicera maackii* exhibits an extended leaf phenology, undergoing leaf out and senescence earlier and later, respectively, than many native species, at least partially due to increased freeze tolerance (McEwan et al. 2009). Beyond the extended duration over which *L. maackii* may broadly impact native communities, leaf leachate toxicity varies seasonally, with peaks of toxicity at the beginning and end of the growing season (Borth et al. 2018). Proposed as a mechanism to deter herbivory during periods when fewer native leaves are available to herbivores (Fridley 2012; Borth et al. 2018), this pattern consequently increases leaf toxicity at or near senescence, coinciding with peak periods of deposition into aquatic systems. Larval amphibian and invertebrate communities also exhibit temporally staggered breeding phenologies (Petranka 1998; Dodd 2013) and differ considerably in their responses to secondary compounds of invasive plant species (Martin and Blossey 2013; DiGiacopo et al. 2019; Iglesias-Carrasco et al. 2022). Consequently, the specific timing of senescence in *L. maackii*, coupled with considerations regarding which species are present and/or vulnerable to exposure, will likely mediate net effects on aquatic communities. Larval *A. maculatum*, for example, rarely engage in cannibalism or congeneric predation (Mott and Maret 2011; Mott and Sparling 2016), yet earlier-hatching species such as *A. opacum* and *A. tigrinum* exert strong effects on larval amphibian communities via predation, cannibalism, and competition (Wilbur 1972; Stenhouse et al. 1983; Holomuzki and Collins 1987; Walls and Blaustein 1995), such that the loss of predatory/cannibalistic taxa may exert different effects on trophic cascades and resultant community structure compared to species with alternative ecological traits.

Within species, ontogenetic and/or phenological shifts in diet and microhabitat use may shape temporal vulnerability to leachate toxicity. Small and/or young larval amphibians often utilize benthic habitats as refugia from predators (Werner 1991; Brodman and Jaskula 2002; Mott and Steffen 2014). Leachate-induced reductions in dissolved oxygen, combined with general patterns of stratification wherein benthic habitats exhibit lower dissolved oxygen concentrations (Moore 1970), may place smaller individuals at heightened risks of asphyxia given their poor lung development and subsequent inability to use surface breathing (sensu Wassersug and Seibert 1975; Maerz et al. 2005). In contrast, larger larvae with advanced lung development towards surface breathing may periodically leave benthic habitats, thus potentially reducing mortality from hypoxic environments, but with increased risks of predation unless larvae have outgrown predator gape limitations (Hickman and Watling 2014). At the broadest scales, anthropogenic climate change may exacerbate effects of *L. maackii* via phenological shifts in senescence and colonization/breeding in wetlands. General trends towards progressively later dates of leaf senescence (Gill et al. 2015; Menzel et al. 2006), coupled with later and earlier breeding by fall- and spring-breeding amphibians, respectively (Todd et al. 2011), suggest leachate-induced mortality may occur when larval amphibian density and/or diversity is highest. Ultimately, additional studies are needed better characterize interactions between species-specific responses to invasive leachates and phenological patterns of leaf senescence to provide more comprehensive assessments of the potential risks of invasion.

While previous studies have observed reductions in density and diversity of macroinvertebrates in response to leachates from *L. maackii* (McNeish et al. 2017; Little et al. 2021; Robison et al. 2021), to our knowledge our results are the first report of mass mortality in an apex aquatic predator. Amphibians are particularly sensitive to the presence of phenolic compounds in aquatic habitats (Kerby et al. 2010), and amphibian population declines due to introduction of senesced leaves from invasive plants represent significant potential losses in ecosystem function. In many aquatic ecosystems, larval salamanders regulate nutrient exchange across terrestrial-aquatic boundaries, while the resulting terrestrial metamorphic individuals occupy intermediate trophic positions, serving as critical energetic links between soil invertebrates and larger vertebrate carnivores (Davic and Welsh 2004; Sánchez-Hernández 2020). Aquatic salamanders are particularly important consumers of invertebrate vectors of disease, such as mosquitos (Brodman and Dorton 2006; Rubbo et al. 2011), which is consistent with our observations of dramatic increases in mosquito abundance in the absence of larval salamanders. Shewhart et al. (2014) demonstrated only larval culicids exposed to leachates of *L. maackii*, relative to leachates from native species and controls, exhibited increased growth rates and advancement to pupation during the study period. Therefore *L. maackii* invasion may simultaneously facilitate increased insect disease vector biomass while decreasing biomass of some of their most abundant consumers. Recent investigations have linked wide-scale amphibian declines to increased incidence of insect-borne human pathogens (Springborn et al. 2022), highlighting ecologically and financially important amphibian ecosystem services. Additional studies are needed to characterize the ecological effects of leachates from invasive plants in situ, with particular focus on long-term effects of chronic exposure on species diversity, ecological interactions, and associated ecosystem services.

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Author contributions Both authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by JLB and CLM. The first draft of the manuscript was written by JLB, and both authors commented on previous versions of the manuscript. Both authors read and approved the final manuscript.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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