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ARTICLE

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Stable isotopes reveal an invasive plant contributes more than native sources to anuran larvae diets

Milica Radanovic ^a, Joseph R. Milanovich^a, Kyle Barrett^b and John A. Crawford ^c

^aDepartment of Biology, Loyola University Chicago, Chicago, IL, USA; ^bDepartment of Forestry and Environmental Conservation, Clemson University, Clemson, SC, USA; ^cNational Great Rivers Research and Education Center, East Alton, IL, USA

ABSTRACT

Foraging theory suggests organisms increase their fitness through dietary and energetic choices. In nature, organisms choose to consume balanced optimal diets but as exotic plants invade ecosystems, new foraging options become available. Often these plants have different traits and can negatively affect fitness of foragers by lowering survival or growth due to toxicity. Wetland habitats are highly susceptible to plant invasions which can have negative effects on nutrient cycling. The purpose of this study was to examine whether invasion of purple loosestrife (*Lythrum salicaria*) alters tadpole foraging preference thus potentially impacting their survivorship and fitness. We designed a common garden experiment and utilized stable isotopic signatures to investigate the contribution of purple loosestrife and native hardwood detritus to larval wood frog (*Rana sylvatica*) and southern leopard frog (*Rana sphenoccephala*) diets. Tadpoles derived a higher percentage of resources from purple loosestrife compared to native hardwood detritus when presented with both options, despite its high concentration of toxic secondary compounds. It is unknown if tadpoles can detect competing fitness signals that may be associated with higher nutrient and toxicity levels in purple loosestrife. Discovering the presence or absence of such signals will promote a greater understanding of selective foraging in changing environments.

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Introduction

Foraging theory is used to explain the behaviors organisms exhibit when selecting food sources to increase fitness (Mangel & Clark 1986; Schoener 1987). Organisms are faced with choices of dietary composition, where to search for the optimal sources, how much time to spend foraging, and how far to move between nutrient sources when attempting to maximize their individual fitness (Pyke 1984; Searle et al. 2005; Bartumeus & Catalan 2009). Organisms selectively choose food sources to meet their preferred and balanced dietary needs (Bryant & Kuropat 1980; Sedinger & Raveling 1984; Felton et al. 2016), but selection can be influenced by other factors, such as predation risk and abundant food choices within their diverse habitat (Marco-Méndez et al. 2016), altering the effect the choices have on their fitness and survival. To achieve a balanced diet, organisms choose to consume sources that maximize energy (Felton et al. 2016), are nutrient rich (Felton et al. 2009; Rothman et al. 2011), and are void of toxins (Bryant & Kuropat 1980). Thus, organisms will discriminate against unpalatable and hard-to-digest foods, unless no other option is available (Felton et al. 2009,

2016) and to compensate for limited availability of highly nutritious food sources, organisms will consume excess amounts of the available low-quality resources (Cruz-Rivera & Hay 2000; Simpson et al. 2004; Robbins et al. 2007; Felton et al. 2016). Therefore, additional studies are required to explain complex foraging behavior in larger varieties of organisms and ecosystems.

Non-native invasive plants are an increasing feature of many ecosystems (Farnsworth & Ellis 2001; Wang et al. 2015). In cases where these novel resources have nutritive and toxic qualities that are unfamiliar to herbivores, it is unclear how (or if) foraging preferences will shift in invaded areas (Pyke 1984; Ehrenfeld et al. 2003; Marco-Méndez et al. 2016). The impact of invaders to wetlands is vigorously debated. Many studies argue that invasions have purely negative impacts on wetlands by reducing biodiversity, causing shifts in organismal consumption patterns, and altering the availability of nutrients (Ehrenfeld et al. 2003; Yakimowski et al. 2005; Roura-Pascual et al. 2011). Alternatively, a few studies suggest that invasions have a small or no impact on ecosystems and that it benefits from the added nutrients (Vilà et al. 2011). Purple loosestrife (*Lythrum salicaria*) is an invasive plant that has had negative impacts on different wetland systems such as decreases in biodiversity due to its high seed dispersion capabilities and fast growth rate (Farnsworth & Ellis 2001; Yakimowski et al. 2005). Additionally, purple loosestrife is composed of higher concentrations of secondary compounds (phenolic acid, tannins, etc.) compared to native species, which could negatively affect aquatic ecosystems (Rauha et al. 2001). Thus, ecologists need a better understanding of aquatic invaders' influence on ecosystem processes – especially as it relates to the potential for invasive plants to alter organismal foraging decisions.

Current rates of extinction resemble rates experienced during the previous five great extinction events leading to massive decreases in biodiversity and ecosystem services (Barnosky et al. 2011; Hocking & Babbitt 2014; Ceballos et al. 2015). Wetland taxa such as amphibians are especially vulnerable (Sodhi et al. 2008; Wake 2012; Hocking & Babbitt 2014). Of the more than 7000 species of amphibians, approximately 41% are facing extinction due to global change (Hocking & Babbitt 2014). Larval anurans (tadpoles) are uniquely positioned to be important in wetland ecosystems because they are typically found in large numbers, consume a variety of detrital resources, promote nutrient cycling and decomposition, and are consumed by many predators (Schiesari et al. 2009; Hocking & Babbitt 2014). Many amphibians have bi-phasic life cycles and are strongly connected to wetland environments due to their reliance upon aquatic systems for breeding sites, nutritional sources, and habitat increasing the impact plant invasions can have on their foraging patterns (Huckembeck et al. 2014; Burgett & Chase 2015).

Invasion of purple loosestrife (*L. salicaria*) introduces a nutrient-rich food source (Milanovich et al. 2016) with higher concentrations of secondary compounds (Rauha et al. 2001) to wetland ecosystems as a potential food source for tadpoles. Tadpoles need to consume a highly nutritious diet to prepare for and complete metamorphosis, which could be attracting tadpoles to choose purple loosestrife as part of their optimal diet (Kupferberg 1997). Foraging theory implies that tadpole fitness will increase when consuming optimal diets (Pyke 1984; Searle et al. 2005); however, the consumption and presence of purple loosestrife has been shown to decrease tadpole survivorship (Barrett et al. Forthcoming; Brown et al. 2006; Cohen et al. 2012; Milanovich et al. 2016). Tadpoles exposed to higher concentrations of secondary compounds associated with purple loosestrife experienced changes to metamorph size and duration of the development period (Cohen et al. 2012; Milanovich et al. 2016). Within wetlands invaded by purple loosestrife, tadpoles are presented with a choice between consuming an invasive plant that is more nutritious, but toxic, or native plants that do not have the same quality of nutrients. An examination into the contribution of invasive plants to tadpole diets can be used to further assess the impact of aquatic invaders on higher trophic levels.

The primary objective of our study was to quantify the contribution of purple loosestrife and native hardwood detritus to tadpole consumers at two locations in the United States. Specifically, we used stable isotopes to determine whether purple loosestrife invasion is influencing tadpole foraging strategies that are presumably evolved to optimize growth and survivorship. We hypothesized the

larvae of southern leopard frogs (*Rana sphenoccephala*) and wood frogs (*Rana sylvatica*) would consume a higher percentage of native hardwood detritus compared to purple loosestrife to avoid negative impacts from secondary compounds despite the potential benefits of the higher nutrient concentrations in the invasive plant.

Materials and methods

Focal species

Purple loosestrife is an aquatic invasive plant introduced into North America in the early 1800s where cultivation for ornamental value has increased extensively since 1940 (Farnsworth & Ellis 2001). Currently, purple loosestrife has an extensive range across North American wetland habitats and is predicted to expand its known distribution (Lindgren & Walker 2012). Recent evidence suggests invasive purple loosestrife has higher phenolic (e.g. galic acid), nitrogen (N) and phosphorus (P) content when compared to several invasive and native aquatic plant species (Emery & Perry 1995; Templer et al. 1998; Stephens et al. 2013; Maurer 2014).

Wood frogs occur from the southern Appalachian Mountains of Georgia, north above the Arctic Circle, and west to Alaska. In Missouri (MO) and South Carolina (SC), breeding typically occurs between January and March in fish-free, ephemeral woodland pools or wetlands (Redmer & Trauth 2005). Wood frogs complete metamorphosis between 65 and 130 days; prior to metamorphosis larvae feed primarily on detritus, plant/algal material, and some zooplankton (Redmer & Trauth 2005; Schiesari et al. 2009; Schriever & Williams 2013). Southern leopard frogs are most abundant in the southeastern portion of the United States with large densities in the Appalachian Highlands (Garrett & Barker 1987; Butterfield et al. 2005). Their southern range extends to Arkansas, Tennessee, Louisiana, Mississippi, Alabama, Georgia, South Carolina, and most of Missouri (Garrett & Barker 1987; Butterfield et al. 2005). In MO, adults breed in large numbers during autumn following rainfall (Doody & Young 1995; Johnson 2000; Butterfield et al. 2005). Southern leopard frogs complete metamorphosis 50–75 days following hatching and consume green algae, diatoms, and detritus as tadpoles (Wright 2002; Hillis 1982; Butterfield et al. 2005; Williams et al. 2008).

Experimental design

Six mesocosm tanks (133 L) at Lindenwood University's Daniel Boone Field Station in St. Charles County, MO, and 12 mesocosm tanks at Clemson University's Environmental Toxicity facility in Anderson County, SC, were set up to simulate natural aquatic environments. Native hardwood detritus was collected following senescence during November 2013 from wetland sites where egg masses were collected for this study. SC native hardwood detritus consisted of scarlet oak (*Quercus occinea*), white oak (*Quercus alba*), and American sweetgum (*Liquidambar styraciflua*), while MO native hardwood detritus consisted of black oak (*Quercus velutina*), post oak (*Quercus stellata*), and white ash (*Fraxinus americana*). Whole purple loosestrife plants were collected following senescence in November 2013 from Porter County, Indiana. In December 2013, all 18 mesocosms were filled with 120 L of tap water and a 50/50 mixture of 75 g of purple loosestrife, and 75 g of native hardwood detritus similar to other experiments and left to overwinter (Stoler & Relyea 2011, 2013a). Mesocosms were covered with 60% mesh shade cloth and inoculated 24 hours later with 1 L of natural wetland water from respective sites where egg masses were collected.

In spring 2014, mesocosms were again inoculated with 1 L of natural wetland water and 5 g of Purina® Rabbit Chow approximately 10 days prior to the addition of tadpoles (Stoler & Relyea 2013b). Wood frog and southern leopard frog egg masses were collected from wetlands near the SC study site and only wood frog egg masses were collected in MO (February–March for SC and March–April for MO). The egg masses were stored in holding tanks, at both locations, until frog tadpoles hatched and reached Gosner stage 21, the desired developmental stage for tank release.

Twenty tadpoles were randomly distributed to the each of the 18 experimental tanks at this stage and were allowed to complete metamorphosis. A 0.5 m × 0.1 m piece of floating foam was placed in each tank during metamorphosis to provide habitat for the metamorphic individuals. Tanks were checked daily to collect metamorphic individuals and the experiment ended when two weeks passed without a metamorphic individual found in each tank. The first two and last two individual wood frogs and southern leopard frogs from each tank were euthanized in a benzocaine solution (Oragel[®], 1 g/L) and were placed in a 60 °C oven until dried (approximately seven days). Gut content analysis was not performed on metamorphic individuals; however, stable isotope analysis provides biomass accumulations from long-term dietary patterns (Rudnick & Resh 2005; Araújo et al. 2007). Prior to addition to the mesocosm tanks, five native hardwood leaves and five samples of whole purple loosestrife plants were randomly selected and dried at 60 °C. Dried tadpoles and dried plant samples were homogenized with a ball mill and sent to the University of Georgia Analytical Chemistry Laboratory (Athens, Georgia) for carbon (¹³C) and nitrogen (¹⁵N) stable isotope analyses following the methods of Milanovich et al. (2012). Lipid proportions of tadpoles are known to be less than 5%; therefore, we did not conduct lipid processing or correct for lipid content (Post et al. 2007; Jefferson et al. 2014). Stable isotopic values are expressed in parts per thousand (‰).

Stable isotope mixing models

Proportional isotopic contributions of native hardwood versus purple loosestrife detritus to the isotopic composition of the tadpoles in each treatment were estimated using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Specifically, a Bayesian mixing model software package, MixSIAR (version 2.1.3), was used for stable isotopic analysis to represent the contribution of different sources of plant material to the isotopic composition of wood frog and southern leopard frog tadpoles up to metamorphosis (Stock & Semmens 2013). The Markov Chain Monte Carlo parameters were set at the very long test length (chain length = 1,000,000; burn = 700,000; thin = 300; chains = 3). Unlike other organisms, tadpoles' gut lengths differ based on the nutritional quality that they are exposed to during their larval period (Latney & Clayton 2014). Tadpoles presumably forage more on nutrient-rich resources during their larval periods in order to maximize energy for growth and development (Schiesari et al. 2009). To account for the differences in the quality and utilization of purple loosestrife and native hardwood detritus, we corrected for trophic enrichment between plant material resources and tadpoles by using a range of calculated discrimination factors: (a) 0.0‰ and 0.0‰; (b) 1.2‰ and 2.6‰; (c) 1.69‰ and 1.98‰; and (d) 2.0‰ and 2.4‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively (Schiesari et al. 2009; Jefferson et al. 2014; J. C. Maerz, University of Georgia, unpublished data). Fractionation factors show the degree to which lighter isotopic values are being used by biological functions and assimilated in the consumer's biomass. Changing those values results in different ratios and concentrations of heavy to light isotopes in the consumer's isotopic signature. If tadpoles are primarily consuming purple loosestrife, then the changing fractionation factors should not drastically alter their isotopic signatures (O'Leary 1981). If the mixing models show tadpoles are still deriving the majority of their nutrients from purple loosestrife after correcting the fractionation values, then tadpoles are most likely consuming purple loosestrife and rapidly utilizing its higher nutritional values for biological development leading to higher concentrations of lighter isotopes in its biomass (Schiesari et al. 2009).

MixSIAR and other mixing models use Bayesian inference to help solve linear mixing models, which can determine diet composition of consumers based on the isotopic signatures of the consumers and their sources (Parnell et al. 2010). In short, these models are fit using MCMC sampling which generates proportions of the consumer's diet based on the isotopic signatures of the consumers and their sources (McClellan et al. 2010). Mixing models use isotopic values and discrimination factors to account for the organism's assimilated diet and thus estimate what portions of the diet compose its separate or combined tissues (Parnell et al. 2010; Phillips 2012). Using fractionation values improves accuracy, but does add additional variability (Parnell et al. 2013). The MixSIAR

program is equipped to handle concentration dependence, uncertainties regarding consumer–source discrimination, uncertainties due to isotopic variability, multiple sources of nutrients, and model error options (process error or process and residual error; Semmens & Moore 2008). Although Bayesian mixing model software has improved, issues can still be associated with stable isotope analysis. Such analyses require extensive prior information for the models to give a correct output (Phillips et al. 2014). For example, all the sources available to the consumer should be present and the fractionation values unique to the study organism must be known (Semmens & Moore 2008; Caut et al. 2009). Ecological systems are complex and it is difficult to account for all errors and uncertainties without the proper prior information (Semmens & Moore 2008).

Results

In the SC treatments, the $\delta^{15}\text{N}$ of purple loosestrife detritus was significantly enriched (121%; $t_{(5,353)} = -3.504$, $p = 0.015$) compared to native hardwood detritus; whereas the $\delta^{13}\text{C}$ signature of purple loosestrife detritus is only 1.74% higher than that of native hardwood detritus and not significantly different ($t_{(7,98)} = -1.694$, $p = 0.129$). Similar differences were documented in the MO treatments, with a marginally significant difference of 90.17% in $\delta^{15}\text{N}$ between purple loosestrife and native hardwood detritus ($t_{(5,789)} = -2.137$, $p = 0.078$), and a non-significant difference of -0.06% in $\delta^{13}\text{C}$ ($t_{(7,409)} = 0.05$, $p = 0.961$). Isotopic signature plots of ^{13}C and ^{15}N at the SC and MO treatments were similar (Figure 1(A–L)), but show tadpoles and both detritus sources are misaligned – suggesting a source outside of the two primary detritus sources was contributing to tadpole biomass. Tadpole stable isotope concentrations were more enriched in ^{15}N for both frog species compared to available detritus sources at Clemson and Lindenwood (Figure 1(A–L)).

The stable isotope mixing models for the treatments at both sites estimate contributions from native hardwood detritus to the composition of wood frog, or southern leopard frog tadpoles' tissue was measurably lower compared to the biomass derived from purple loosestrife – despite both detritus types comprising 50% of available resources and after accounting for variation in discrimination factors (Table 1).

Discussion

Our results suggest that when given a choice, two frog species actively select resources derived from purple loosestrife over native hardwood detritus. Such a choice may result from the tadpole's ability to recognize detritus that has higher nutritive value (Pfennig 2000). Nevertheless, purple loosestrife is known to decrease survival of larval anurans due to a high concentration of secondary compounds (Maerz et al. 2005; Brown et al. 2006). Foraging theory states that organisms will make dietary choices that will increase their fitness, but frog species in this study chose to consume plant matter that is decreasing their survival rates suggesting other factors could be influencing their choices (Barrett et al. Forthcoming; Pyke 1984; Milanovich et al. 2016).

Purple loosestrife is morphologically similar to native cattails that tadpoles consume in undisturbed wetlands which can lead to the two plant species having similar environmental cues attracting tadpoles (Blossey et al. 2004). If tadpoles are choosing to consume purple loosestrife because of false environmental cues and their survival and fitness are decreasing due to that choice, then purple loosestrife invasions create putative ecological traps (Barrett et al. Forthcoming; Battin 2004; Maerz et al. 2005; Brown et al. 2006; Milanovich et al. 2016). An ecological trap can arise when an organism chooses a maladaptive habitat due to false environmental cues that leads to a decline in reproductive fitness and/or survival (Battin 2004; Robertson & Hutto 2006; Gilroy & Sutherland 2007). Ecological traps have been observed in terrestrial and aquatic ecosystems affecting a wide range of species (Dwernychuk & Boag 1972; Nordby et al. 2009; Severns 2011; Robertson 2012). Decreased habitat quality is the primary driver of ecological traps, as many habitats have been altered to the point where previously useful cues no longer offer an honest signal of environmental quality (Schlaepfer

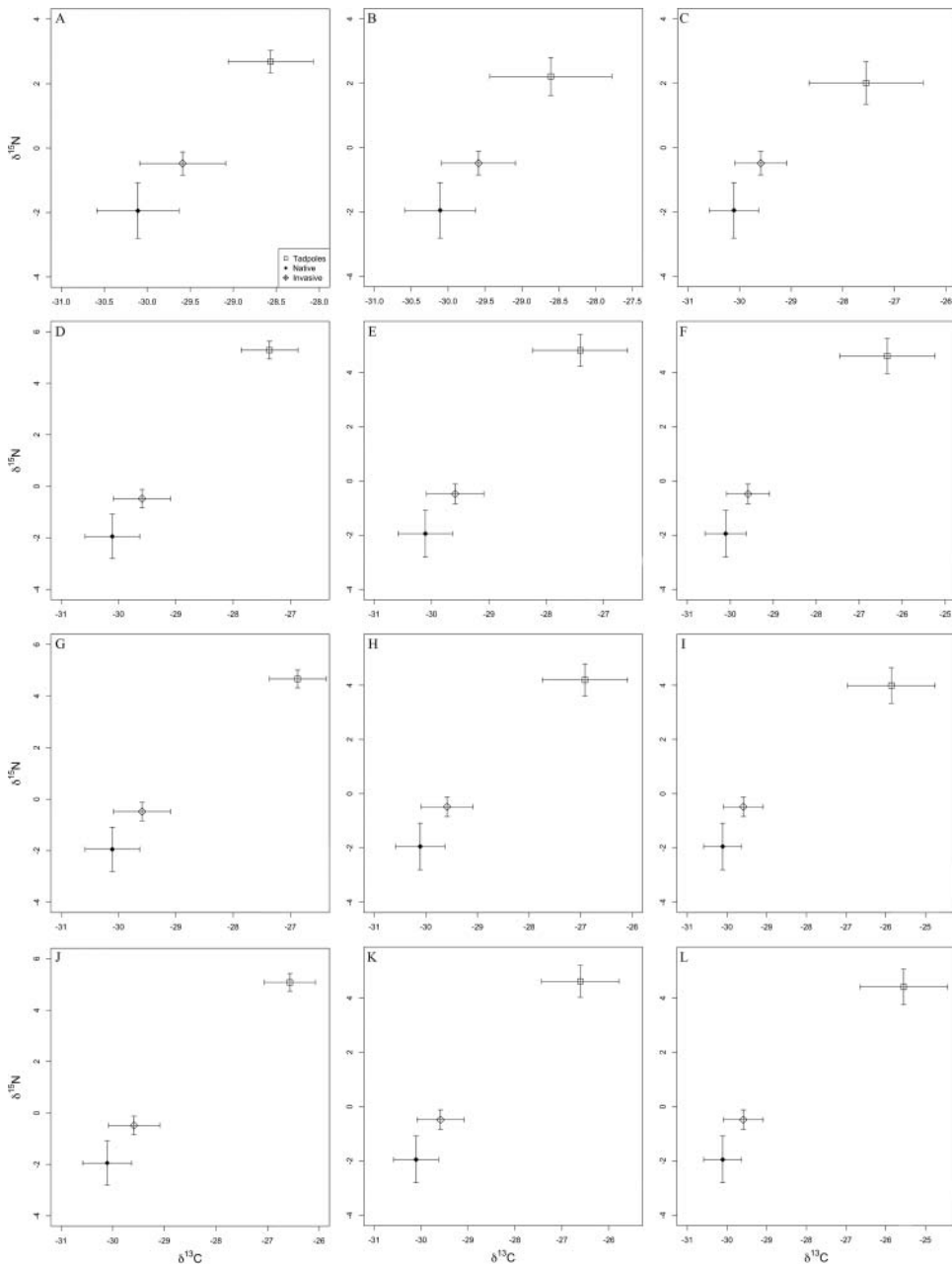


Figure 1. Dual isotope plot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures (mean \pm SE) of native and invasive detritus and tadpoles across each treatment in South Carolina (A, D, G, J for leopard frogs and B, E, H, K for wood frogs) and Missouri (C, F, I, L). (A–C) No discrimination factors for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are used; (D–F) discrimination factors of 1.2‰ and 2.6‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively, are used; (G–I) discrimination factors of 1.69‰ and 1.98‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively, are used; and (J–L) discrimination factors of 2.0‰ and 2.4‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively, are used.

et al. 2002; Battin 2004; Severns 2011; Fletcher et al. 2012; Robertson 2012; Robertson et al. 2013). Further support of this hypothesis would require evidence that the tadpoles truly can detect higher nutritive value in purple loosestrife and choose to consume it during foraging for an optimal and balanced diet (Pyke 1984; Searle et al. 2005).

Table 1. Mean percent contributions (± 1 SD) of native hardwood detritus and purple loosestrife to larval wood frog and southern leopard frog biomass derived using MixSIAR models from the Clemson (SC) and Lindenwood (MO) study sites. Four different correction factors of ^{13}C and ^{15}N are used to examine if trophic enrichment affected mean percent contributions.

Species	Correction factors							
	0.0‰ ^{13}C ; 0.0‰ ^{15}N		1.2‰ ^{13}C ; 2.6‰ ^{15}N		1.69‰ ^{13}C ; 1.98‰ ^{15}N		2.0‰ ^{13}C ; 2.4‰ ^{15}N	
	Invasive	Native	Invasive	Native	Invasive	Native	Invasive	Native
Clemson (SC)								
<i>R. sylvatica</i>	96.4% (0.037)	3.6% (0.037)	90.3% (0.094)	9.7% (0.094)	94.8% (0.137)	5.2% (0.137)	92.6% (0.131)	7.4% (0.131)
<i>R. sphenoccephala</i>	97.3% (0.027)	2.7% (0.027)	97.2% (0.027)	2.8% (0.027)	87.4% (0.303)	12.6% (0.303)	81.9% (0.348)	18.1% (0.348)
Lindenwood (MO)								
<i>R. sylvatica</i>	95.8% (0.047)	4.2% (0.047)	91.0% (0.077)	9.0% (0.077)	96.0% (0.041)	4.0% (0.041)	90.7% (0.089)	9.3% (0.089)

Tadpoles are known to be opportunistic grazers and will consume a variety of resources including algae, detritus, and zooplankton (Seale 1980; Huckembeck et al. 2014). Although we limited possible resources with respect to detritus, the mesocosms were inoculated with pond water and likely contained a variety of algae and plankton. This could explain the variation of ^{13}C values across basal resources and the disjunct nature of the ^{13}C and ^{15}N plots (Figure 1). Following correction using several reported discrimination factors, our results suggest the contribution from purple loosestrife is not solely due to consumption of plants, but potentially other sources that are deriving energy from purple loosestrife such as algae or zooplankton (Table 1; Figure 1). A consumer's ^{13}C value should align with their nutritional sources (Phillips 2012), but when the signatures do not align it can be due to carbon sources of low abundance being overlooked (Wilkinson et al. 2013). Another explanation for the ^{13}C differences could be due to how tadpoles utilize their gained nutrients and the changes in tadpole gut length due to the nutritional value of those resources (Latney & Clayton 2014). Unlike other organisms, tadpoles have limited time to reach metamorphosis and need to efficiently use their nutrients for rapid growth (Schiesari et al. 2009). The nutrients within tadpoles are reused and recycled for the tadpoles to be as efficient as possible and these processes could lead to the ^{13}C signatures not aligning completely (J. C. Maerz, University of Georgia, unpublished data). Discrimination of ^{13}C by larval anurans varies due to nutritional quality of diet (Schiesari et al. 2009; Jefferson et al. 2014). After adjusting for various correction factors, our results still suggest that purple loosestrife is the main food source despite the change in gut structure and the quality of the nutrient sources.

Despite the fact that secondary compounds found in purple loosestrife lead to a lower survival rate relative to native detritus (Barrett et al. Forthcoming; Maerz et al. 2005; Brown et al. 2006; Milanovich et al. 2016), anuran larvae are choosing to consume the invasive plant. The preference for purple loosestrife we describe here may result from the higher nutrient levels found in the plant (Milanovich et al. 2016), which promote faster times to metamorphosis and larger overall tadpoles (Milanovich et al. 2016, Barrett et al. Forthcoming). The fitness implications of the competing outcomes for growth and survivorship probabilities are realized at the individual level. Whether or not such tradeoffs can be detected by the tadpoles is an open question, and research into it will help resolve the extent to which our results are consistent with current understanding of selective foraging (Pyke 1984; Fryxell 1991).

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Disclosure statement

No potential conflict of interest was reported by the authors.

Notes on contributors


Milica Radanovic is a graduate student at Washington State University. Her research examines nitrogen and water storage and movement in soil systems.


Joe R. Milanovich is an Assistant Professor of Biology. His research examines the impact of global change on amphibian and reptile distributions and the importance of herpetofauna to nutrient cycling and storage in terrestrial and aquatic ecosystems.

Kyle Barrett is an Assistant Professor of Wetland Ecology at Clemson University. His research program focuses on vertebrate response to large-scale stressors such as land use and climate change.

John A. Crawford is a wildlife ecologist and his research program is focused on amphibian and reptile ecology and conservation.

ORCID

Milica Radanovic  <http://orcid.org/0000-0001-6496-6099>

John A. Crawford  <http://orcid.org/0000-0002-0961-2308>

References

- Araújo MS, Bolnick DI, Machado G, Giaretta AA, dos Reis SF, Araújo MS, Bolnick DI, Machado G, Giaretta AA, dos Reis SF et al., 2007. Using delta13C stable isotopes to quantify individual-level diet variation. *Oecologia*. 152:643–654.
- Barnosky AD, Matzke N, Tomiya S, Wogan GOU, Swartz B, Quental TB, Marshall C, McGuire JL, Lindsey EL, Maguire KC et al., 2011. Has the Earth's sixth mass extinction already arrived? *Nature*. 471:51–57.
- Barrett K, Crawford JA, Reinstein Z, Milanovich JR. *Forthcoming*. Detritus quality produces species-specific tadpole growth and survivorship responses in experimental wetlands. *J Herpetol*.
- Bartumeus F, Catalan J. 2009. Optimal search behavior and classic foraging theory. *J Phys A Math Theor*. 42:434002.
- Battin J. 2004. When good animals love bad habitats: ecological traps and the conservation of animal populations. *Conserv Biol*. 18:1482–1491.
- Blossey B, Maerz JC, Brown C. 2004. Ecological indicators of detrimental impacts of invasive plants. In: Cardina J, editor. *Bridging the Gap Between Land Management and Research*. Proceedings of the Ohio Invasive Plant Research Conference; 2005 Aug. Wooster (OH).
- Brown CJ, Blossey B, Maerz JC, Joule SJ. 2006. Invasive plant and experimental venue affect tadpole performance. *Biol Invasions*. 8:327–338.
- Bryant JP, Kuropat PJ. 1980. Selection of winter forage by subarctic browsing vertebrates: The role of plant chemistry. *Annu Rev Ecol Syst*. 11:261–285.
- Burgett AA, Chase JM. 2015. Landscape context influences the abundance of amphibians and the strength of their food web interactions in small ponds. *Oikos*. 124:629–638.
- Butterfield BP, Lannoo MJ, Nanjappa P. 2005. *Rana sphenoclepla*. In: Lannoo MJ, editor. *Amphibian declines: the conservation status of United States species*. Berkeley: University of California Press; p. 586–587.
- Caut S, Angulo E, Courchamp F. 2009. Variation in discrimination factors ($\Delta^{15}\text{N}$ and $\Delta^{13}\text{C}$): the effect of diet isotopic values and applications for diet reconstruction. *J Appl Ecol*. 46:443–453.
- Ceballos G, Ehrlich PR, Barnosky AD, García A, Pringle RM, Palmer TM. 2015. Accelerated modern human-induced species losses: entering the sixth mass extinction. *Sci Adv*. 1:1–5.
- Cohen JS, Maerz JC, Blossey B. 2012. Traits, not origin, explain impacts of plants on larval amphibians. *Ecol Appl*. 22:218–228.
- Cruz-Rivera E, Hay ME. 2000. Can quantity replace quality? Food choice, compensatory feeding, and fitness of marine mesograzers. *Ecology*. 81:201–219.
- Doody JS, Young JE. 1995. Temporal variation in reproduction and clutch mortality of leopard frogs (*Rana utricularia*) in South Mississippi. *J Herpetol*. 29:614–616.

- Dwernychuk LW, Boag DA. 1972. Ducks nesting in association with gulls – an ecological trap? *Can J Zool.* 50:559–563.
- Ehrenfeld JG, Pfennig DW, Stoler AB, Relyea RA, Latney L, Clayton LA, Wang WQ, Sardans J, Wang C, Zeng CS et al., 2003. Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems.* 6:503–523.
- Emery SL, Perry JA. 1995. Aboveground biomass and phosphorus concentrations of *Lythrum salicaria* (purple loosestrife) and *Typha* spp. (cattail) in 12 Minnesota wetlands. *Am Midl Nat.* 134:394–399.
- Farnsworth EJ, Ellis DR. 2001. Is purple loosestrife (*Lythrum salicaria*) an invasive threat to freshwater wetlands? Conflicting evidence from several ecological metrics. *Wetlands.* 21:199–209.
- Felton AM, Felton A, Raubenheimer D, Simpson SJ, Foley W, Wood J, Wallis I, Lindenmayer D. 2009. Protein content of diets dictates the daily energy intake of a free-ranging primate. *Behav Ecol.* 20:685–690.
- Felton AM, Felton A, Raubenheimer D, Simpson SJ, Krizsan SJ, Hedwall P-O, Stolter C, Robbins C, Fortin J, Rode K et al., 2016. The nutritional balancing act of a large herbivore: an experiment with captive moose (*Alces alces* L). *PLoS One.* 11:e0150870.
- Fletcher RJ, Orrock JL, Robertson BA. 2012. How the type of anthropogenic change alters the consequences of ecological traps. *Proc Biol Sci.* 279:2546–2552. doi: 10.1098/rspb.2012.0139.
- Fryxell JM. 1991. Forage quality and aggregation by large herbivores. *Am Nat.* 138:478–498.
- Garrett JM, Barker DG. 1987. A field guide to reptiles and amphibians of Texas. Austin (TX): Texas Monthly Press.
- Gilroy JJ, Sutherland WJ. 2007. Beyond ecological traps: perceptual errors and undervalued resources. *Trends Ecol Evol.* 22:351–356.
- Hillis DM. 1982. Morphological differentiation and adaptation of the larvae of *Rana berlandieri* and *Rana sphenocphala* (*Rana pipiens* complex) in sympatry. *Copeia.* 1982:168–174.
- Hocking DJ, Babbitt KJ. 2014. Amphibian contributions to ecosystem services. *Herpetol Conserv Biol.* 9:1–17.
- Huckenbeck S, Loebmann D, Albertoni EF, Hefler SM, Oliveira MCLM, Garcia AM. 2014. Feeding ecology and basal food sources that sustain the paradoxical frog *Pseudis minuta*: a multiple approach combining stomach content, prey availability, and stable isotopes. *Hydrobiologia.* 740:253–264.
- Jefferson DM, Hobson KA, Demuth BS, Ferrari MCO, Chivers DP. 2014. Frugal cannibals: how consuming conspecific tissues can provide conditional benefits to wood frog tadpoles (*Lithobates sylvaticus*). *Naturwissenschaften.* 101:291–303.
- Johnson TR. 2000. The amphibians and reptiles of Missouri. 2nd ed. Jefferson City (MO): Missouri Department Conservation.
- Kupferberg SJ. 1997. The role of larval diet in anuran metamorphosis. *Am Zool.* 159:146–159.
- Latney L, Clayton LA. 2014. Updates on amphibian nutrition and nutritive value of common feeder insects. *Vet Clin North Am Exot Anim Pract.* 17:347–367.
- Lindgren CJ, Walker D. 2012. Predicting the spread of purple loosestrife (*Lythrum salicaria*) in the Prairies. *Can Field Nat.* 126:306–319.
- Maerz JC, Brown CJ, Chapin CT, Blossey B. 2005. Can secondary compounds of an invasive plant affect larval amphibians? *Funct Ecol.* 19:970–975.
- Mangel M, Clark CW. 1986. Towards a unified foraging theory. *Ecology.* 67:1127–1138.
- Marco-Méndez C, Wessel C, Scheffel W, Ferrero-Vicente L, Fernández-Torquemada Y, Cebrián J, Heck KL, Sánchez-Lizaso JL, Hartog C Den, Thayer G et al., 2016. Lack of impact of *Posidonia oceanica* leaf nutrient enrichment on *Sarpa salpa* herbivory: additional evidence for the generalist consumer behavior of this cornerstone Mediterranean herbivore. Doi H, editor. *PLoS One.* 11:e0168398.
- Maurer MM. 2014. Variability in the phenolic content of invasive and non-invasive emergent wetland plants. Rochester (NY): Rochester Institute of Technology.
- McClellan CM, Braun-McNeill J, Avens L, Wallace BP, Read AJ. 2010. Stable isotopes confirm a foraging dichotomy in juvenile loggerhead sea turtles. *J Exp Mar Bio Ecol.* 387:44–51.
- Milanovich JR, Barrett K, Crawford JA, Platt T, Fuentes-Yaco C, Frank K, Maerz J, Brown C, Chapin C, Blossey B et al., 2016. Detritus quality and locality determines survival and mass, but not export, of wood frogs at metamorphosis. Green AJ, editor. *PLoS One.* 11:e0166296.
- Milanovich JR, Maerz JC. 2012. Assessing the use of non-lethal tail clips for measuring stable isotopes of plethodontid salamanders? *Herpetological Conservation and Biology.* 7:67–74.
- Nordby JC, Cohen AN, Beissinger SR. 2009. Effects of a habitat-altering invader on nesting sparrows: an ecological trap? *Biol Invasions.* 11:565–575.
- O'Leary MH. 1981. Carbon isotope fractionation in plants. *Phytochemistry.* 20:553–567.
- Parnell AC, Inger R, Bearhop S, Jackson AL. 2010. Source partitioning using stable isotopes: coping with too much variation. *PLoS One.* 5:e9672.
- Parnell AC, Phillips DL, Bearhop S, Semmens BX, Ward EJ, Moore JW, Jackson AL, Grey J, Kelly DJ, Inger R. 2013. Bayesian stable isotope mixing models. *Environmetrics.* 24:387–399.
- Pfennig DW. 2000. Effect of predator–prey phylogenetic similarity on the fitness consequences of predation: a trade–off between nutrition and disease? *Am Nat.* 155:335–345.
- Phillips DL, Inger R, Bearhop S, Jackson AL, Moore JW, Parnell AC, Semmens BX, Ward EJ. 2014. Best practices for use of stable isotope mixing models in food-web studies. *Can J Zool.* 92:823–835.

- Phillips DL. 2012. Converting isotope values to diet composition: the use of mixing models. *J Mamm.* 93:342–352.
- Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J, Montana CG. 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia.* 152:179–189.
- Pyke G. 1984. Optimal foraging theory: a critical review. *Annu Rev Ecol Syst.* 15:523–575.
- Rauha J-P, Olfenderb J-LW, Ekka JHA-P, Inenc S, Pihlajac K. 2001. Characterization of the polyphenolic composition of purple loosestrife (*Lythrum salicaria*). *Z Naturforsch C.* 56:13–20.
- Redmer M, Trauth SE. 2005. *Rana sylvaticus*. In: M Lannoo, editor. Amphibian declines: the conservation status of United States species. Berkeley: University of California Press; p. 590–593.
- Robbins CT, Fortin JK, Rode KD, Farley SD, Shipley LA, Felicetti LA. 2007. Optimizing protein intake as a foraging strategy to maximize mass gain in an omnivore. *Oikos.* 116:1675–1682.
- Robertson BA. 2012. Investigating targets of avian habitat management to eliminate an ecological trap. *Avian Conserv Ecol.* 7:2.
- Robertson BA, Hutto RL. 2006. A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology.* 87:1075–1085.
- Robertson BA, Rehage JS, Sih A. 2013. Ecological novelty and the emergence of evolutionary traps. *Trends Ecol Evol.* 28:552–560.
- Rothman JM, Raubenheimer D, Chapman C. 2011. Nutritional geometry: gorillas prioritize non-protein energy while consuming surplus protein. *Biol Lett.* 7:847–849.
- Roura-Pascual N, Hui C, Ikeda T, Leday G, Richardson DM, Carpintero S, Espadaler X, Gómez C, Guénard B, Hartley S et al., 2011. Relative roles of climatic suitability and anthropogenic influence in determining the pattern of spread in a global invader. *Proc Natl Acad Sci U S A.* 108:220–225.
- Rudnick D, Resh VN. Stable isotopes, mesocosms and gut content analysis demonstrate trophic differences in two invasive decapod crustacea. 2005. *Freshw Biol.* 50:1323–1336.
- Schiesari L, Werner EE, Kling GW. 2009. Carnivory and resource-based niche differentiation in anuran larvae: implications for food web and experimental ecology. *Freshw Biol.* 54:572–586.
- Schlaepfer MA, Runge MC, Sherman PW. 2002. Ecological and evolutionary traps. *Trends Ecol Evol.* 17:474–480.
- Schoener TW. 1987. A brief history of optimal foraging ecology. In: Kamil AC, Krebs JR, Pulliam HR, editors. *Foraging behaviour*. New York (NY): Plenum Press; p. 5–67.
- Schriever TA, Williams DD. 2013. Ontogenetic and individual diet variation in amphibian larvae across an environmental gradient. *Freshw Biol.* 58:223–236.
- Seale DB. 1980. Influence of amphibian larvae on primary production, nutrient flux, and competition in a pond ecosystem. *Ecology.* 61:1531–1550.
- Searle KR, Hobbs NT, Shipley LA, Lindström J. 2005. Should I stay or should I go? Patch departure decisions by herbivores at multiple scales. *Oikos.* 111:417–424.
- Sedinger JS, Raveling DG. 1984. Dietary selectivity in relation to availability and quality of food for goslings of cackling geese. *Auk.* 101:295–306.
- Semmens BX, Moore JW. 2008. MixSIR: a Bayesian stable isotope mixing model, Version 1.0. Seattle (WA): Ecology-Box, Mathematical Biology Program, Northwest Fisheries Science Center.
- Severns PM. 2011. Habitat restoration facilitates an ecological trap for a locally rare, wetland-restricted butterfly. *Insect Conserv Divers.* 4:184–191.
- Simpson SJ, Sibly R, Lee K, Behmer S, Raubenheimer D. 2004. Optimal foraging when regulating intake of multiple nutrients. *Anim Behav.* 68:1299–1211.
- Sodhi NS, Brickford D, Diesmos AC, Lee TM, Koh LP, Brook BW, Sekercioglu CH, Bradshaw CJA. 2008. Measuring the meltdown: drivers of global amphibian extinction and decline. *PloS One.* 3:e1636.
- Stephens JP, Berven KA, Tiegs SD. 2013. Anthropogenic changes to leaf litter input affect the fitness of a larval amphibian. *Freshw Biol.* 58:1631–1646.
- Stock BC, Semmens BX. 2013. MixSIAR GUI user manual, Version 1.0. Available from: <http://conserveriugo-cafeorg/user/bricesemmens/MixSIAR>.
- 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.
- Templer P, Findlay S, Wigand C. 1998. Sediment chemistry associated with native and non-native emergent macrophytes of a Hudson River marsh ecosystem. *Wetlands.* 18:70–78.
- Vilà M, Espinar JL, Hejda M, Hulme PE, Jarošík V, Maron JL, Pergl J, Schaffner U, Sun Y, Pyšek P. 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecol Lett.* 14:702–708.
- Wake, DB. 2012. Facing extinction in real time. *Science.* 335:1052–1053.

- Wang WQ, Sardans J, Wang C, Zeng CS, Tong C, Asensio D, Penuelas J. 2015. Ecological stoichiometry of C, N, and P of invasive *Phragmites australis* and native *Cyperus malaccensis* species in the Minjiang River tidal estuarine wetlands of China. *Plant Ecol.* 216:809–822.
- Wilkinson GM, Carpenter SR, Cole JJ, Pace ML, Yang C. 2013. Terrestrial support of pelagic consumers: patterns and variability revealed by a multilake study. *Freshw Biol.* 58:2037–2049.
- Williams BK, Rittenhouse AG, Semlitsch RD. 2008. Leaf litter mediates tadpole performances across forest canopy treatments. *Oecologia.* 155:377–384.
- Wright AH. 2002. Life-histories of the frogs of Okefinokee Swamp, Georgia: North American Salientia (Anura) No. 2. Ithaca (NY): Comstock Pub. Associates.
- Yakimowski SB, Hager HA, Eckert CG. 2005. Limits and effects of invasion by the nonindigenous wetland plant *Lythrum salicaria* (purple loosestrife): a seed bank analysis. *Biol Invasions.* 7:687–698.