Non-native Chinese mystery snail (*Bellamya chinensis*) supports consumers in urban lake food webs

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Abstract.   Non-native species are widely regarded as threats to ecosystem structure and function; however, these species may also provide benefits to ecosystems that have lost former functions to environmental degradation. This study evaluated whether non-native species provide prey resources or induce trophic cul-de-sacs (by diverting basal energy away from higher trophic levels) in developed ecosystems where native prey are in decline. We used stable isotopes of ^{13}C, ^{15}N, and ^{2}H to assess whether non-native Chinese Mystery snail (*Bellamya chinensis*) provides a prey resource to consumers, and maintains the integration of benthic resources into food webs of lakes subjected to lakeshore development. Regardless of *Bellamya* presence, consumers in undeveloped lakes were supported primarily by benthic resources, and lakeshore development dramatically reduced consumer reliance on these resources. This was at least partly due to a reduction in the availability of native snails, a high-quality prey item, to the dominant littoral consumer, molluscivorous pumpkinseed sunfish (*Lepomis gibbosus*). In developed lakes with non-native *Bellamya*, generalist yellow perch (*Perca flavescens*) and piscivorous largemouth bass (*Micropterus salmoides*) consumed benthic resources in proportions similar to undeveloped lakes, and pumpkinseed sunfish consumed *Bellamya* in higher proportions than in undeveloped lakes. Thus, *Bellamya* provided a prey substitute in developed lakes where native snail populations were depressed; and *Bellamya*'s influence extended to higher trophic-level consumers. Our study provides evidence that non-native species can ameliorate some effects of environmental degradation, and we suggest that future research considers how the effects of non-native species, either positive or negative, may vary across human-modified landscapes.

Key words: *Bellamya chinensis*; context-dependent impact; introduced species; invasive; *Lepomis gibbosus*; *Micropterus salmoides*; *Perca flavescens*; prey subsidy; urban development.

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INTRODUCTION

Debate over the role of non-native species in contemporary landscapes has emerged in recent years (Schlaepfer et al. 2011, Vitule et al. 2012). On one side, non-native species are widely recognized as threats to native species, biodiversity, and ecosystem structure and function (Simberloff 2011, Ricciardi et al. 2013), and their effects may be magnified by other anthropogenic disturbances, including habitat modification and climate change (Didham et al. 2007, Rahel and Olden 2008). Alternatively, non-native species may provide food, habitat, or engineering processes to ecosystems that have lost former functions to environmental degradation and

other human activities, and thus could benefit native species in invaded ecosystems (e.g., Foster and Robinson 2007, Griffiths et al. 2010, Carroll and Peterson 2013). Examples include non-native mammals supporting native predatory birds in urban environments (Cava et al. 2012); non-native macrophytes benefiting fish by increasing prey production in coastal areas where native habitat has been destroyed (Martin and Valentine 2011); and non-native crayfish subsidizing wetland bird diets in rice fields (Tablado et al. 2010). Although non-native species can provide prey resources to consumers (Pintor and Byers 2015), it is unknown whether the quality of non-native prey can be equivalent to native prey that they replace and sufficient to support consumers. Further, research has yet to identify the environmental context in which non-native species may subsidize or replace existing prey resources.

Non-native species that are predator-resistant or have low nutritional value may be of little benefit to native consumers. For example, native rusty crayfish (*Orconectes rusticus*) and pumpkinseed sunfish (*Lepomis gibbosus*) exhibit low predation rates on non-native zebra mussels (*Dreissena polymorpha*) in laboratory settings (Naddafi and Rudstam 2014), and Vinson and Baker (2008) demonstrated that rainbow trout (*Oncorhynchus mykiss*) lose body mass when fed on non-native New Zealand mudsnails (*Potamopyrgus antipodarum*). Low-quality prey may induce what have been termed as trophic cul-de-sacs (*sensu* Bishop et al. 2007) by out-competing other prey species for preferred resources and ultimately diverting basal energy away from consumers and back to lower trophic levels in the form of detritus (Bishop et al. 2007, Power et al. 2008). Non-native species may also have high feeding rates and be released from predation (Colautti et al. 2004, Dick et al. 2014), further increasing the likelihood of trophic cul-de-sacs. Alternatively, non-native species that are susceptible to predators may provide suitable prey resources in human-impacted environments where native prey have been extirpated or are in low abundance (Tablado et al. 2010, Cava et al. 2012).

Our study is the first to evaluate whether non-native species provide prey resources or induce trophic cul-de-sacs across a gradient in native prey availability due to human disturbance, and to explore the implications for higher trophic levels in freshwater ecosystems.

Freshwater ecosystems are particularly susceptible to human land use because they are highly connected to and reliant on adjacent terrestrial habitats that provide inputs of nutrients, habitat structure, and food resources (Allan 2004). Thus, degradation of the surrounding terrestrial environment disrupts supplies of organic material and habitat that support aquatic food web production (Brauns et al. 2011, Larson et al. 2011). Freshwater ecosystems are also subjected to ongoing species introductions that are positively associated with land use change (Strayer 2010), making freshwater food webs well suited for studying the potential for non-native species to ameliorate or magnify the effects of environmental degradation on ecosystems.

Lakes throughout North America have undergone extensive development characterized by removals of riparian and aquatic vegetation and coarse woody debris, which together reduce the retention of organic matter and densities of macrophytes that provide food and habitat for littoral zone invertebrates and fish (e.g., Francis et al. 2007, Larson et al. 2011). Lakeshore development can dramatically alter compositions of benthic invertebrate communities, reduce the availability of benthic prey, and shift consumer diets from reliance on terrestrial and benthic to pelagic resources (Schindler and Scheuerell 2002, Francis et al. 2007). Concurrent with lakeshore development, Chinese mystery snail (*Bellamya chinensis*; hereafter *Bellamya*) has been introduced to many North American lakes and can achieve high densities in lake littoral zones (Solomon et al. 2010). *Bellamya* is a large snail (up to 70 mm shell height; Fig. 1c), and its thick shell and hard operculum may afford protection against some predators (Olden et al. 2009). In addition, the snail's ability to filter-feed and non-selectively scrape benthic periphyton (Jokinen 1982, Olden et al. 2013) provides the potential for large competitive effects on native grazing invertebrates. Together this evidence suggests that *Bellamya* has the potential to divert basal resources from, and intensify the effects of shoreline development on, higher trophic levels. Alternatively, *Bellamya* may help maintain the integration of benthic resources in lake food webs by providing an abundant prey resource in developed lakes where native benthic prey are in low densities.
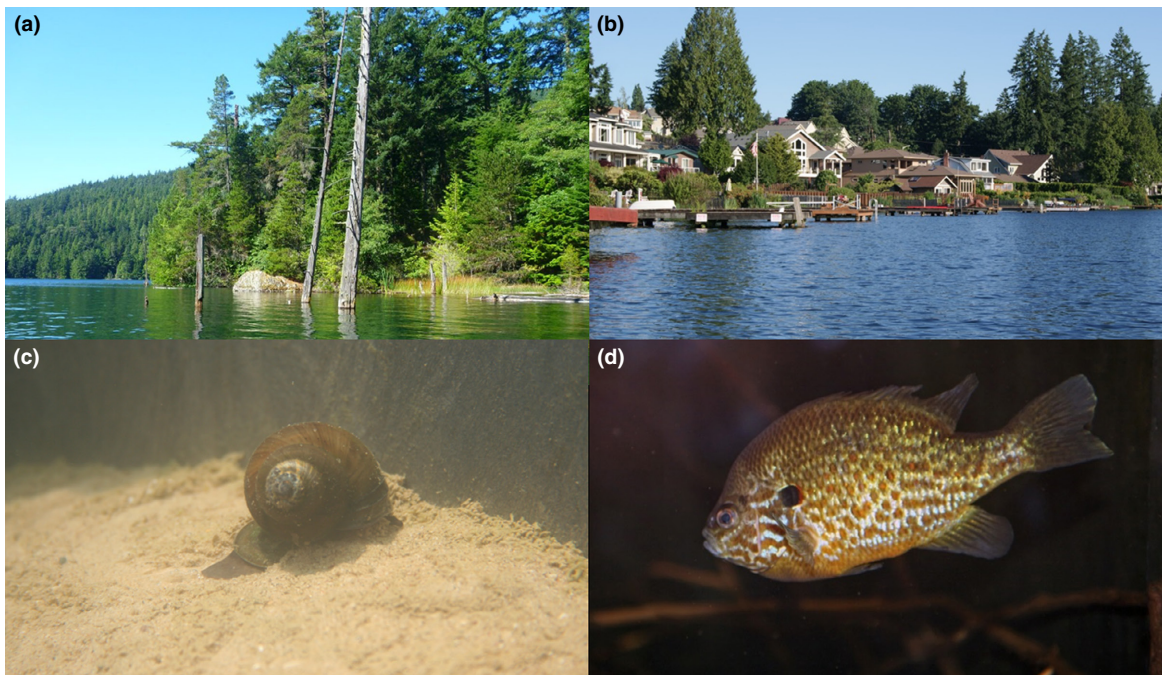
Fig. 1. (a) Undeveloped Cascade Lake, Orcas County, WA (L. Twardochleb); (b) developed Pine Lake, King County, WA (S. Linzmaier); (c) non-native Chinese mystery snail, *Bellamya chinensis* (J. Olden); (d) molluscivorous pumpkinseed sunfish, *Lepomis gibbosus* (Wikimedia Commons, M. Manske).

Our objectives were to identify whether *Bellamya* induces trophic cul-de-sacs or maintains the integration of benthic pathways in food webs, and to assess whether the ecological role of this non-native species is consistent among lakes with varying degrees of shoreline development. We predicted that *Bellamya* substitutes for declines in native invertebrates so that fish in developed lakes with *Bellamya* exhibit similar reliance on benthic resources compared with fish in undeveloped lakes; and *Bellamya* does not influence resource use by fish in undeveloped lakes due to the availability of native prey. Alternatively, if *Bellamya* induces a trophic cul-de-sac, we expected to find an increase in reliance on pelagic resources and concurrent decrease in reliance on benthic resources among fish consumers in developed and undeveloped lakes.

METHODS

Study system

We studied 11 lakes in the Puget Sound lowlands of Washington State, United States, that span a gradient of shoreline urbanization ranging from undeveloped lakes with restricted public access to developed lakes with the entire shoreline containing residential houses and little riparian vegetation (Fig. 1a,b). Shorelines of undeveloped lakes are surrounded by dense canopies of native evergreen and less abundant deciduous trees, whereas developed lakes are characterized by open space, ornamental gardens and grass lawns, non-native shrubs, and native deciduous trees that typically outnumber evergreen tree species. Lakes were selected using data from previous surveys (presented in Tamayo and Olden 2014), and by examining monthly monitoring data from King County's Lake Stewardship Program (www.kingcounty.gov), to ensure high similarity in surface area and mean depth; all lakes were small, summer stratified, and oligo- to mesotrophic (Table 1).

Lakes contained similar assemblages of fish species that include native populations of rainbow trout, and naturalized populations of yellow perch (*Perca flavescens*), largemouth bass (*Micropterus salmoides*), and pumpkinseed

Table 1. Physical characteristics, including lake surface area, mean depth, Secchi depth, a measure of water clarity, and mean epilimnetic total phosphorus concentrations for lakes in each of four sampling categories.

Lake	Surface area (km^2)	Mean depth (m)	Secchi depth (m)	Total phosphorus (μg/L)
Undeveloped – *Bellamya* absent				
Fern	0.10	4.6	4.1	10.7
Walsh	0.43	5.2	3.2	8.3
Undeveloped – *Bellamya* present				
Cascade	0.68	8.2	5.8	15.4
Padden	0.64	8.3	3.2	7.5
Wilderness	0.28	6.4	3.2	12.5
Developed – *Bellamya* absent				
Martha	0.23	7.3	4.2	10.1
Shoecraft	0.53	5.5	3.6	8.3
Sunday	0.19	2.4	1.9	27.9
Developed – *Bellamya* present				
Angle	0.42	7.6	6.5	7.7
Pine	0.35	6.1	5.5	8.2
Star	0.34	7.6	3.1	9.8

sunfish (Fig. 1d). These species were first introduced to Washington State in the late 1800s and are the most abundant species across the lakes (Washington Department of Fish and Wildlife 2005). Further, they are representative of littoral (pumpkinseed sunfish) and littoral-pelagic (yellow perch and largemouth bass) consumers in the region. Assessing resource use by a specialized molluscivore, pumpkinseed sunfish, and a dietary generalist, yellow perch, allows for an examination of *Bellamya*'s influence on consumers with differing feeding specialties; in addition, we can assess whether *Bellamya*'s effects are transmitted through the food web via intermediate consumers to a higher trophic-level consumer, largemouth bass.

Site selection

Lakes were selected from each of four categories contrasting developed versus undeveloped and invaded versus uninvaded by *Bellamya*. Three lakes were assigned to each of the following categories, "undeveloped/*Bellamya*", "developed/non-*Bellamya*", and "developed/*Bellamya*". Two lakes were included as "undeveloped/non-*Bellamya*" lakes due to low sample sizes of fish consumers in a third lake sampled from this category (Table 1). Lakes were considered undeveloped if 40% or less of the shoreline buffer (10 m from the water edge) was developed; developed lakes had greater than 60% shoreline development (Fig. 1a,b). Percentage of

development was determined using aerial photographs combined with validation using direct field observations. Invasion categories were determined using presence/absence data for *Bellamya* from a 2009 survey (Olden, *unpublished data*). Our 2012 survey confirmed these category assignments with the exception of recently discovered populations of *Bellamya* in Martha and Sunday lakes (both developed), with mean densities of 0.08 and 0.17 individuals/m^2, respectively. Each population was restricted to a single sampling location exhibiting very low abundances and thus is likely to impart minimal food-web scale impacts. Consequently, these lakes were assigned to the "developed/non-*Bellamya*" category.

Sampling

At each lake, we collected allochthonous (terrestrial detritus) and autochthonous (aquatic macrophytes, periphytic algae) basal resources, benthic invertebrates, zooplankton, and fish, during July–August in 2012 and 2013. The lake's physical and chemical characteristics were also assessed, including water temperature, dissolved oxygen, conductivity (YSI Model 85), and pH. We estimated lake clarity using Secchi depth (m), a standard limnological method to characterize water transparency. In addition, we collected duplicate water samples for analysis of total phosphorus concentrations (TP; μg/L) from the epilimnion using a Van Dorn

bottle (Wetzel and Likens 1991). Water samples were transferred unfiltered to acid-washed polyethylene bottles, frozen, and analyzed at the University of Washington, School of Oceanography's Marine Chemistry Laboratory. Analysis of TP followed methods of Valderrama (1981).

To estimate the importance of pelagic, benthic, and terrestrial pathways to consumers, we sampled all major primary and secondary producers for stable isotope analysis of $\delta^{13}C$, $\delta^{15}N$, and $\delta^{2}H$. Each lake was divided into four quadrants (according to the cardinal directions) to distribute the following sampling effort evenly. In each lake, we deployed four hoop nets (7.9 m wing length and five hoops each 0.8 m in diameter) and 20 galvanized steel minnow traps (41.0 cm long with two 2.5 cm openings and 6.4 mm mesh size) for 24 h to sample littoral fish. Two benthic, multi-mesh gill nets (58.5 m length × 1.8 m height, six panels each being 9.8 m long with mesh-sizes 25, 32, 38, 51, 64, 76 mm, stretched mesh) were set perpendicular to shore overnight to collect littoral and pelagic fish. Fish were identified to species, measured for total length (mm), and weighed (g).

Pelagic zooplankton were sampled using oblique net tows (35 cm diameter opening, 73 μm mesh cod end) prior to sunrise. We sampled invertebrates for isotopic analysis and community indices by sweeping a D-frame net (25 cm × 35 cm opening, 500 μm mesh) over the lake bottom within a 1 m^2 quadrat at depths between 0 and 1 m, and using a Ponar Grab (0.023 m^2 opening) at depths between 1 to 4 m. Within each quadrant, we selected randomly 10 sites representing all habitat types (woody debris, macrophytes, gravel and cobble, sand) to sample invertebrates. In addition, we hand-collected *Bellamya* and snails in the genus *Physella*, the most abundant native snail across the lakes, from sediment, logs, and vegetation. All benthic samples were sieved through a 500 μm-mesh bucket, and samples taken for community indices (n = 24 per lake) were preserved in 90% ethanol. Stable isotope samples (n = 16 per lake) were put on ice in the field and frozen at −20°C in the laboratory. Leaves from dominant evergreen and deciduous tree species surrounding each lake were collected to represent terrestrial end-members.

Environmental water contributes substantially to consumer $\delta^{2}H$ signature (Soto et al. 2013); therefore, we obtained water samples for $\delta^{2}H$ signatures from each lake with a Van Dorn bottle lowered to 0.5 m depth. Environmental water samples were filtered through GF/F 0.7 μm filters to remove organisms and particulate organic matter (POM) (Solomon et al. 2011). All isotope samples were returned to the laboratory on ice and frozen at −20°C until preparation for analysis.

Laboratory preparation

Benthic invertebrate community samples were processed according to EPA Bioassessment Benthic Macroinvertebrate Protocols. We developed a morphospecies curve using a high volume sample to estimate the minimum number of randomly selected individuals needed to detect all morphospecies in a sample. On the basis of this curve, we sub-sampled each sample until 300 (± 20%) individuals were counted. Samples containing fewer than 240 individuals were processed in entirety. In addition, we sorted *Bellamya* from the entire volume of each sample to estimate densities. Organisms were identified to genus (sub-family for Chironomidae) with an 80X dissecting microscope using published and online taxonomic guides (Merritt and Cummins 1996, Thorp and Covich 2001).

We prepared stable isotope samples by extracting plugs of dorsal muscle tissue from fish. Snail shells and opercula were removed from soft tissues prior to drying. Benthic invertebrate samples were sorted by order, and zooplankton samples were separated from POM. Small individuals were aggregated to reach target weights for isotopic analysis. Aquatic and terrestrial plants were sorted to genus. All samples were dried at 55°C for 24 h and ground to a fine powder with a mortar and pestle. Samples were weighed and encapsulated in tin for analysis of $\delta^{15}N$ and $\delta^{13}C$ and in silver capsules for analysis of $\delta^{2}H$.

Carbon and nitrogen samples were analyzed at UC Davis Stable Isotope Facility on a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Samples were compared with in-house laboratory standards calibrated against Vienna PeeDee Belemnite for

carbon and air for nitrogen. The measurement error reported by UC Davis is the long-term standard deviation of 0.2‰ for $\delta^{13}C$ and 0.3‰ for $\delta^{15}N$. Hydrogen samples were analyzed at the Colorado Plateau Stable Isotope Laboratory (Northern Arizona University) on a 1400 C thermal-chemical elemental analyzer coupled to a Thermo-Electron Delta Plus XL mass spectrometer. Samples were equilibrated for exchangeable hydrogen using a bench top equilibration technique, and raw data were corrected after analysis using the calibration standards and techniques of Wassenaar and Hobson (2003). Calibration standards were Caribou hoof ($\delta^2H = -197‰$), Keratin ($\delta^2H = -121.1‰$), and Kudo horn ($\delta^2H = -54.1‰$). We report stable isotope values in standard delta notation,

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 10^3, \qquad (1)$$

where X is the mass of the heavier isotope of the element, and R is the ratio of the heavy to light isotope in the sample and standard. The δ value is the amount of heavy and light isotopes in a sample.

Isotopic analyses

We used a Bayesian isotope mixing model (MixSIR; Moore and Semmens 2008) implemented in the R programming language (R Development Core Team 2014) to estimate contributions of benthic, pelagic, and terrestrial resources to consumer diets, and assess direct contributions of *Bellamya* to pumpkinseed sunfish diets. We modified MixSIR following the methods of Solomon et al. (2011) to account for contributions of environmental water to consumer δ^2H signatures. Environmental water has a compounding effect with trophic position, such that tissues of higher trophic-level consumers reflect the environmental water that they ingest and the environmental water ingested by their prey; we accounted for the effect of environmental water on consumer δ^2H by calculating the total contribution of environmental water to consumer tissue as:

$$\omega_{compound} = 1 - (1 - \omega)^\tau, \qquad (2)$$

where ω is the per trophic-level contribution of environmental water and τ is the trophic position of the consumer. We estimated an ω

value of 0.29 ± 0.11 (mean ± 1 SD) based on published experimental values (Solomon et al. 2009, Graham et al. 2014); trophic discrimination factors of 0.4 ± 1.3‰ per trophic level for $\delta^{13}C$ and 3.4 ± 1‰ for $\delta^{15}N$ (Post 2002), and 0‰ for δ^2H (Solomon et al. 2009). Consumer trophic positions were estimated according to Post (2002), and primary consumers were assigned a trophic position of 1.5. Consumer δ^2H signatures were then calculated as:

$$\delta^2H_{consumer} = \omega_{compound} \times \delta^2H_{water} + (1 - \omega_{compound})$$
$$\times (\phi_1 \times \delta^2H_1 + \phi_2 \times \delta^2H_2 + \phi_3 \times \delta^2H_3), \qquad (3)$$

where δ^2H_1, δ^2H_2, and δ^2H_3 refer to the isotopic signatures of individual resources and φ is the proportion of the consumer's diet derived from each resource. Signatures of δ^2H_{water} were similar across lakes, so we used a value of −60.10 ± 6.93‰ (mean ± 1 SD) in mixing models.

We examined the importance of resources from each habitat to juvenile and adult pumpkinseed sunfish, yellow perch, and largemouth bass diets, and included terrestrial detritus, zooplankton, and benthic invertebrates, amphipods and isopods, which were the most common prey items across all study lakes, as representative end-members. Pumpkinseed sunfish included as consumers ranged from 6.5 to 17.5 cm total length (TL), corresponding to sizes at which they feed on gastropods (Osenberg and Mittelbach 1989, Huckins 1997). We included yellow perch between 9 and 27 cm TL, corresponding to sizes at which yellow perch consume mixed pelagic-benthic prey (Graeb et al. 2005, Fullhart et al. 2011, L. Twardochleb, *unpublished data*). Finally, we included largemouth bass 10 to 30 cm TL as consumers in mixing models. Young of year and small juvenile fish were excluded from mixing models because fish are limited to zooplanktivory early in ontogeny (Mittelbach and Persson 1998).

We also compared the contribution of *Bellamya* to pumpkinseed sunfish in undeveloped and developed lakes by parameterizing mixing models with terrestrial detritus, zooplankton, and the benthic invertebrate groups: collectors (amphipods and isopods), odonates, native snails *Physella*, and *Bellamya* as potential

sources. We did not estimate the contribution of *Bellamya* to either largemouth bass or yellow perch diets because these species have a wide diet breadth, and mixing models that estimated the contributions of individual prey items to these two consumer species would not converge on a solution. We were unable to obtain isotope data for native snails from two lakes (Angle and Wilderness) in 2012 and instead parameterized mixing models using snail data sampled from the same lakes in 2009 (J. Olden, *unpublished data*). We ran two-sample *t*-tests to determine whether native snail isotopic signatures from other lakes included in mixing models differed significantly between 2009 and 2012, and found no significant differences between years (δ^{13}C, $t_{21} = -2.04$, $P > 0.05$; δ^{15}N, $t_{21} = 1.49$, $P > 0.05$). In addition, we used Welch's two-sample *t*-tests to assess differences between *Bellamya* and *Physella* in their δ^{13}C, δ^{15}N, and δ^2H isotopic signatures. We found that isotopic signatures between these taxa were significantly different (Appendix S1), and therefore included them as separate sources in mixing models. Finally, we specified uninformative priors on source contributions in all MixSIR models.

Statistical analyses

Lake size and transparency can influence the importance of benthic vs. pelagic and terrestrial energetic pathways to lake food webs (Vadeboncoeur et al. 2003, Larson et al. 2011); therefore, we tested for differences in lake surface area (km^2), epilimnetic TP (µg/L) and transparency as measured by Secchi depth (m) among lake categories using separate two-way analysis of variance (ANOVA). We tested for differences in densities of *Bellamya*, native snails, and the overall assemblage of non-molluscan invertebrates between lakes with developed and undeveloped shorelines using two-sample *t*-tests. Alpha levels were set at 0.05, all invertebrate data were log ($x + 1$) transformed prior to analyses, and data assumptions of homoscedasticity and normality were met for all analyses.

We assessed differences in the proportion of consumer diets derived from benthic resources across lakes, with lakes treated as replicates, using ANOVAs with binomial error structure with development and *Bellamya* presence/absence as categorical predictor variables. ANOVA models were weighted as a function of the variance in the posterior estimates of benthic resource use (as determined by Bayesian isotope mixing models) for each lake. In addition, we ran weighted, one-way ANOVAs with binomial error structure to test the contribution of native snails and *Bellamya*, respectively, to pumpkinseed sunfish diets in undeveloped and developed lakes, with development as the categorical predictor variable. Three models were considered to explain the proportion of benthic resource use by consumers: individual main effects of lake development and *Bellamya* presence, and models including main and additive effects. Model selection was performed with maximum-likelihood values from ANOVA models using modified Akaike's Information Criterion (AICc) for small sample sizes. All statistical analyses were implemented in the R programming language (R Development Core Team 2014).

RESULTS

Invertebrate abundances and lake characteristics

Lake surface area, water clarity (measured as Secchi depth), and TP were comparable across lake categories (Table 1). We found no significant differences in lake surface area between developed and undeveloped lakes ($F_{1,7} = 0.57$, $P = 0.48$), between lakes with and without *Bellamya* ($F_{1,7} = 1.91$, $P = 0.21$), or any interaction therein ($F_{1,7} = 0.98$, $P = 0.36$). In addition, epilimnetic TP did not differ significantly between developed and undeveloped lakes ($F_{1,18} = 0.16$, $P = 0.69$), between lakes with and without *Bellamya* ($F_{1,18} = 0.97$, $P = 0.34$), nor was there a significant interaction ($F_{1,18} = 2.64$, $P = 0.12$). Similarly, we found no significant differences in water transparency between developed and undeveloped lakes ($F_{1,7} = 0.06$, $P = 0.82$), between lakes with and without *Bellamya* ($F_{1,7} = 2.05$, $P = 0.20$); nor did we find a significant interaction ($F_{1,7} = 0.71$, $P = 0.43$). Densities of *Bellamya* ($t_4 = -7.13$, $P < 0.01$) and native snails ($t_9 = -3.52$, $P < 0.01$) were significantly higher in undeveloped than developed lakes (Fig. 2). By contrast, lake development did not have a significant effect on non-molluscan invertebrate densities (Fig. 2; $t_9 = -0.59$, $P = 0.57$).
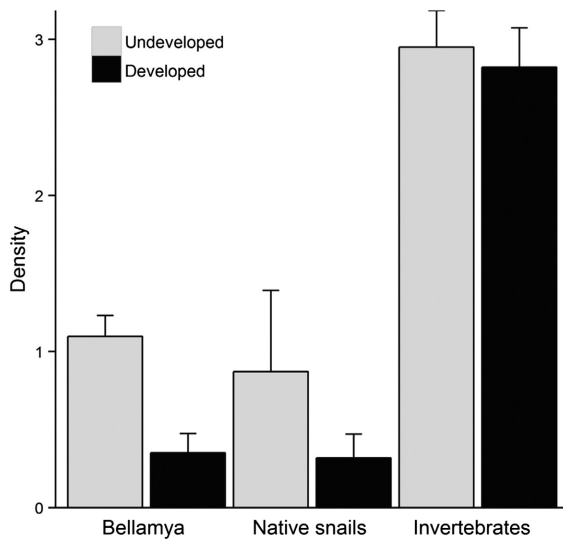
Fig. 2. Densities (log + 1 m^{-2}) of *Bellamya*, native snails, and non-molluscan invertebrates in undeveloped and developed lakes (*n* = 5 undeveloped lakes; *n* = 6 developed lakes). Error bars represent 1 standard deviation of the mean.

Benthic resource use by lake consumers

Isotope bi-plots revealed that benthic basal resources in lakes were enriched in ^{13}C compared to pelagic and terrestrial resources and that isotopic signatures of consumers in developed lakes differed between *Bellamya* and non-*Bellamya* lakes (Fig. 3). Figure 3 depicts a subset of resources and consumers for two developed lakes, Martha and Pine, to illustrate differences in carbon signatures between *Bellamya* and non-*Bellamy*a lakes. Pumpkinseed sunfish and largemouth bass were more enriched in ^{13}C in developed lakes with *Bellamya*, suggesting a higher reliance on benthic-derived resources compared with developed lakes without *Bellamya* (Fig. 3a,c); however, yellow perch were not consistently more enriched in ^{13}C in developed/*Bellamya* lakes (Fig. 3b). There were no systematic differences in consumer isotopic signatures between undeveloped lakes with and without *Bellamya*, suggesting that *Bellamya* does not have substantial influence on resource use by consumers in undeveloped lakes (*results not shown*).

Results of three-isotope mixing models suggest that all consumers relied heavily on benthic resources in undeveloped lakes and that lake development substantially reduced the proportion of benthic-derived resources, and increased the proportion of pelagic resources in diets of yellow perch and largemouth bass, but not pumpkinseed sunfish (Fig. 4). Terrestrial resource use was low for all consumers (Appendix S2), such that resources for fish were obtained directly from benthic or pelagic food webs. In addition, there was a striking pattern of higher benthic resource use by all consumers in developed/*Bellamya* lakes compared with developed/non-*Bellamya* lakes (Fig. 4). AIC$_c$ model selection on ANOVA models identified that for all consumers, a model including additive effects of lake development and *Bellamya* best explained the proportion of benthic-derived resources in consumer diets (Table 2).

Contributions of Bellamya and native snails to pumpkinseed sunfish diets

Pumpkinseed sunfish consumed higher proportions of *Bellamya* in developed lakes (Pine, Angle) where native snails have declined, and consumed native snails in higher proportions in undeveloped lakes (Cascade, Padden, Wilderness) where snails were present at high densities (Fig. 5; Appendix S3). However, *Bellamya* was a measureable component of the pumpkinseed sunfish diet in all lakes, comprising 10% or more of the diet. ANOVAs indicated that pumpkinseed sunfish consumed significantly greater proportions of native snails in undeveloped lakes, and significantly greater proportions of *Bellamya* in developed lakes (Table 3). We qualitatively assessed diets from frozen pumpkinseed sunfish and yellow perch from six lakes (*n* = 5 to 9 fish lake^{-1}) in the laboratory to confirm our results, and we found evidence that pumpkinseed sunfish and yellow perch consumed *Bellamya* and native snails in undeveloped and developed lakes. Native snails were identified by the presence of thin shell fragments, and *Bellamya* were identified by the presence of the operculum, which is lacking in other snails in these lakes. Our sample size was not sufficient to make a quantitative assessment of overall dietary components, but the most common dietary components for pumpkinseed sunfish and yellow perch were *Physella*, *Bellamya*, amphipods, isopods, cladocerans, and copepods.
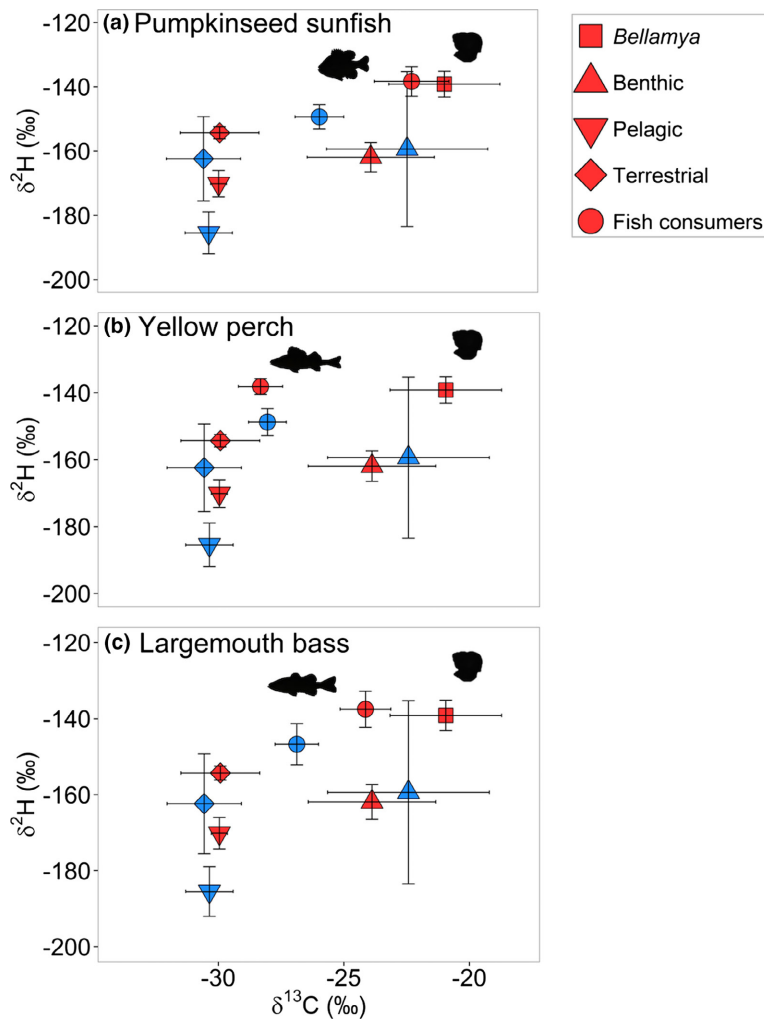
Fig. 3. Source and consumer δ^{13}C and δ^2H signatures in developed lakes Martha (*Bellamya* absent; blue symbols) and Pine (*Bellamya* present; red symbols) for (a) pumpkinseed sunfish; (b) yellow perch; and (c) largemouth bass. Note the enrichment in ^{13}C and ^{2}H for pumpkinseed sunfish and largemouth bass in the *Bellamya* compared to the non-*Bellamya* lake.

Discussion

Our study indicates that a non-native species (*Bellamya chinensis*) does not induce a trophic cul-de-sac but is accessible to fish consumers, and substitutes for native snails whose populations have declined in degraded habitats of developed lakes. We also provide evidence that the strength of the prey substitution represented by *Bellamya* is context dependent, such that *Bellamya* has greater effects on higher trophic levels in developed lakes where high-quality prey are less available to consumers. These results are consistent with a recent meta-analysis finding that non-native prey have neutral or positive effects on predators (Pintor and Byers 2015).

Overall, benthic resources were more important to food webs of undeveloped lakes than either terrestrial or pelagic resources, comprising 60–80% of fish diets. By contrast, lakes with developed shorelines had low abundances of native snails, and consumers displayed lower reliance on benthic resources and concurrently increased their use of pelagic resources. As predicted, *Bellamya* did not influence resource use in
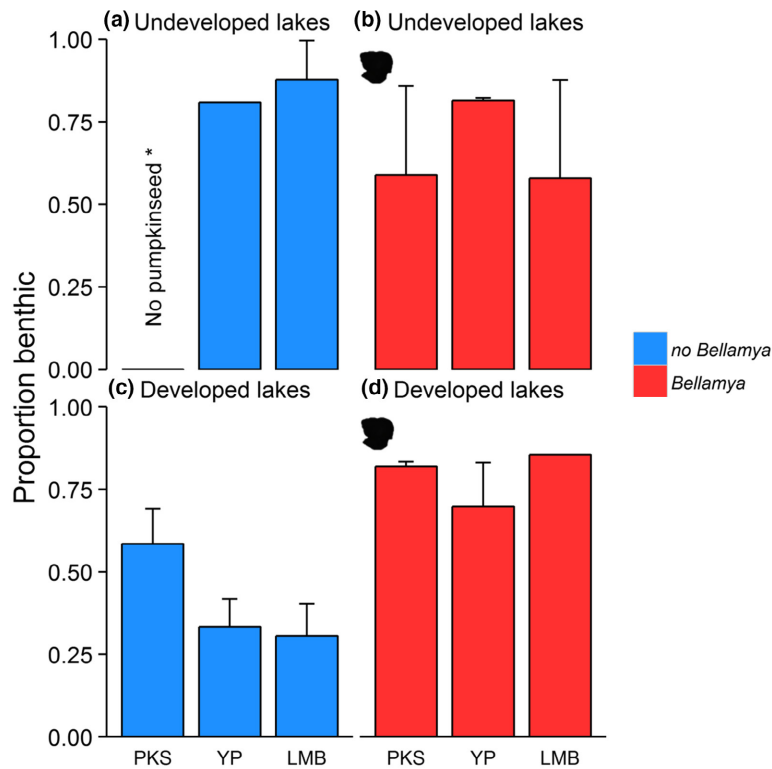
Fig. 4. Benthic resource use was high among pumpkinseed sunfish (PKS), yellow perch (YP), and largemouth bass (LMB) in undeveloped lakes (a) with and (b) without populations of non-native *Bellamya*. Benthic resource use was much lower for all fish in (c) developed lakes without *Bellamya* compared to undeveloped lakes. However, benthic resources comprised the majority of fish diets in (d) developed lakes with *Bellamya*. Bars are mean ± 1 SD estimated proportion of fish diets composed of benthic prey for each lake category. *Note that there are no populations of pumpkinseed sunfish in undeveloped lakes without *Bellamya*.

Table 2. Summary of AIC_c model selection on three ANOVA models that explain differences in benthic resource use by consumers among lake categories. K is the number of model parameters; ΔAIC_c = AIC_c of the model - AIC_c minimum of all models under consideration; w_i is the probability that the model is the best of all models under consideration; and the evidence ratio is the weight of the best fit model divided by the weight of the model under consideration. For pumpkinseed sunfish, largemouth bass, and yellow perch, the best-supported models include additive effects of the categorical variables, *Bellamya* presence and lakeshore development.

Model	K	AIC_c	ΔAIC_c	w_i	Evidence ratio
Pumpkinseed sunfish					
Bellamya presence + development	3	141.0	0.0	1.0	1.0
Bellamya presence	2	151.5	10.5	< 0.01	187.7
Development	2	175.7	34.7	< 0.01	3.5e + 7
Yellow perch					
Bellamya presence + development	3	230.4	0.0	1.0	1.0
Development	2	251.9	21.5	< 0.0001	4.7e + 4
Bellamya presence	2	258.7	28.3	< 0.0001	1.4e + 6
Largemouth bass					
Bellamya presence + development	3	378.8	0.0	1.0	1.0
Bellamya presence	2	445.5	66.7	< 0.0001	3.0e + 14
Development	2	451.8	73.0	< 0.0001	7.2e + 15

undeveloped lakes, where benthic reliance was high regardless of invasion history; however, *Bellamya* had detectable effects in food webs of developed lakes, where fish consumed higher proportions of benthic resources in the presence of *Bellamya*, and their resource use was broadly similar to that of fish in undeveloped lakes. Moreover, *Bellamya* provided an important contribution to the diet of the dominant littoral con-
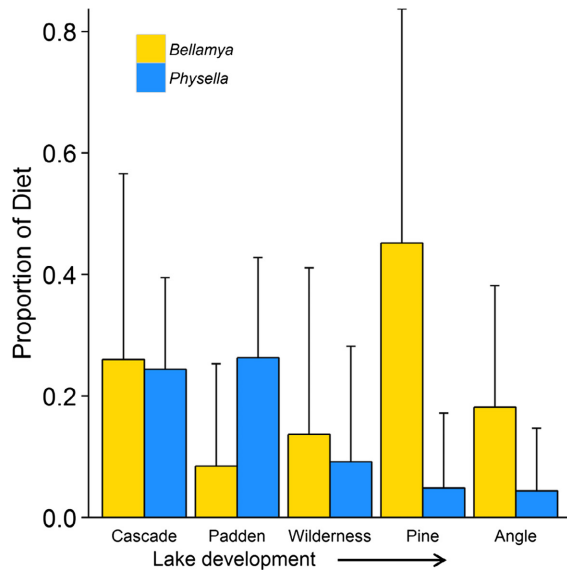

Fig. 5. Pumpkinseed sunfish consumed *Bellamya* in higher proportions in developed (Pine, Angle) than undeveloped (Cascade, Padden, Wilderness) lakes and native snails, *Physella*, in higher proportions in undeveloped lakes. Bars show mean + 95% credible intervals (uncertainty around the mean probability estimate) for the proportion of the diet composed of *Bellamya* and native snails based on outputs of three-isotope mixing models.

sumer, pumpkinseed sunfish, in developed lakes where native snails were rare.

Pumpkinseed sunfish are molluscivores with pharyngeal jaws adapted for crushing snails, and their consumption increases directly with snail abundance (Wainwright et al. 1991). Our study suggests that pumpkinseed sunfish consume native snails and *Bellamya* in proportions from 30% to as high as 60% of the diet; consistent with the work of Huckins (1997) and Osenberg and Mittelbach (1989), in which snails contributed greater than 25% and 80%, respectively, of pumpkinseed diets in lakes with high snail densities. Results from our isotope mixing models suggest that *Bellamya* is a prey substitute in developed lakes, where it constitutes a larger proportion of the pumpkinseed diet than native snails. *Bellamya* is larger-bodied (size range 4–65 mm shell height) than *Physella*, the most abundant native snail in these lakes (size range 1–6 mm; L. Twardochleb, *unpublished data*), and is highly visible on the surface of sediment and woody debris (L. Twardochleb, *personal observation*). Pumpkinseed sunfish have a higher encounter rate with large, visible snails and select positively for larger individuals that are more energetically dense (Osenberg and Mittelbach 1989). Pumpkinseed sunfish would therefore be expected to have more encounters with, and consume higher proportions of *Bellamya* than native snails in developed lakes where overall snail densities are low. Although adult *Bellamya* likely reach a size refuge from predation due to pumpkinseed gape limitation, small thin-shelled juveniles (4–7 mm shell height) fall within the range of sizes that pumpkinseed sunfish are able to consume. For example, pumpkinseed sunfish that were offered snails ranging from 2 to 11 mm shell length during feeding experiments

Table 3. Summary of one-way ANOVAs with binomial error structure testing for effect of lake development on proportion of native snails and *Bellamya* in the diets of pumpkinseed sunfish. Lake development significantly decreased the proportion of native snails in fish diets, while development significantly increased the proportion of *Bellamya* in fish diets. Z scores and P values indicate whether a parameter coefficient is different from zero.

Model	Coefficient	Estimate (SE)	Z	P
Native snails consumed	(Intercept)	−1.09 (0.14)	−7.69	<0.01
	Lake development	−1.94 (0.20)	−9.58	<0.01
Bellamya consumed	(Intercept)	−1.92 (0.16)	−11.78	<0.01
	Lake development	0.64 (0.27)	2.32	0.02

consumed snails up to 1/10 of their body length (Mittelbach 1984). Moreover, juvenile *Bellamya* are born during summer months when pumpkinseed sunfish feed actively on molluscs in lake littoral zones (Jokinen 1982, Stephen et al. 2013), and the literature suggests that even small pumpkinseeds feed on juvenile gastropods (e.g., Keast 1978). Taken together, this evidence indicates that juvenile *Bellamya* are accessible to pumpkinseed sunfish and provide a high-quantity prey resource in developed lakes.

Our evidence that yellow perch consume more benthic resources in developed lakes with *Bellamya* is likely explained by the consumer's generalist feeding habits rather than a preference for snails. Yellow perch are widely considered "secondary piscivores" that feed primarily on a variety of invertebrates in proportion to their abundance and secondarily on small fish (Liao et al. 2002, Graeb et al. 2005). Previous evidence indicates that perch consume snails when available; Liao et al. (2002) found that gastropods constitute one of the three most important prey sources to yellow perch in Spirit Lake, Iowa, USA, and Cobb and Watzin (1998) counted gastropods in proportions up to 25% of perch diets in Lake Champlain, Northeastern USA and Canada. In addition, we detected snails in the gut contents of more than half of the yellow perch dissected in the laboratory. Although we were unable to estimate proportions of native snails or *Bellamya* in yellow perch diets using mixing models, the preponderance of evidence suggests that perch consume snails in Puget lowland lakes, and higher benthic resource use by perch in developed lakes with *Bellamya* may be due, in part, to the consumption of *Bellamya* as a substitute for native snails.

Bellamya also influenced benthic resource use by piscivorous largemouth bass in developed lakes, an effect that is probably mediated indirectly through prey fishes. Largemouth bass are piscivores that switch from foraging predominantly on invertebrates to fish after their first year of life (Mittelbach and Persson 1998), and display high rates of predation on pumpkinseed and bluegill sunfish (*Lepomis macrochirus*) in waterbodies where they are abundant (Olson 1996, Almeida et al. 2012). Pumpkinseed sunfish are the most abundant prey fish in our study lakes, and they display predominantly benthic isoto-

pic signatures (Figs. 2,3), with higher benthic resource use in developed lakes with *Bellamya*. The elevated benthic signature of pumpkinseed should be reflected in the isotopic signatures of their predator, largemouth bass, and consequently, our evidence that largemouth bass increase their use of benthic resources in developed/*Bellamya* lakes suggests that *Bellamya*'s effects may be transmitted up through the food web from prey fish to top consumers.

Consumers that exploit non-native prey can increase their fitness and provide biotic resistance against the population growth and spread of non-native species (Carlsson et al. 2009). King et al. (2006) showed that the threatened Lake Erie watersnake (*Nerodia sipedon insularum*) increased their growth and body size after elevating their feeding on non-native round goby (*Neogobius melanostomus*). In addition to improving their fitness, consumers that are effective at feeding on non-native prey can regulate impacts of non-native species (Carlsson et al. 2009). For example, Carlsson et al. (2011) have found that native blue crabs (*Callinectes sapidus*) exert strong predation pressure on non-native zebra mussels (*Dreissena polymorpha*) in the Hudson River estuary, and as a result, the ecosystem shows signs of recovery from intensive zebra mussel grazing. By controlling populations of non-native prey, consumers may prevent the negative ecosystem-level impacts of non-native species in lakes.

Benthic energetic pathways are critical to the maintenance of higher trophic-level consumers in lakes, and our study sheds light on the role a non-native species plays in helping maintain consumer access to benthic resources in degraded food webs. Our isotopic evidence revealed that food webs of undeveloped lakes were supported primarily by benthic pathways, which is consistent with a review by Vadeboncoeur et al. (2003) highlighting that zoobenthic prey constitute over half the diet of North American fishes, including piscivores, which derive 65% of their diets, both directly and indirectly, from benthic prey. In small, shallow lakes for which benthic production dominates, urban development reduces the efficiency of trophic transfers from benthic primary producers to higher trophic-level consumers and alters the balance of benthic and pelagic resources supporting lakes (Vadeboncoeur et al. 2003, Brauns et al. 2011). We found that develop-

ment significantly diminished the contributions of benthic resources to consumers, which can have substantial food web-level consequences such as reduced benthic-pelagic habitat coupling and lower production of pelagic fish (Schindler et al. 2000, Schindler and Scheuerell 2002). We also found that non-native prey can ameliorate some of these common, negative effects of development. Snails have high energy densities compared to other invertebrates, and fish that consume snails gain growth and competitive advantages over fish that do not (Mittelbach 1984). For example, pumpkinseed sunfish reach larger body sizes and achieve higher population sizes in lakes where they can access snails (Huckins 1997). By providing a high-quality prey resource for fish in lakes with degraded benthic pathways, *Bellamya* may help maintain fish growth and population sizes.

Our study relied on stable isotope mixing models to estimate the importance of resource pools to food webs. Mixing models can provide a range of estimates for a finite number of individual prey contributions to consumer diets (Fry 2006), and as a result we were unable to quantify the proportional contribution of *Bellamya* to consumers, yellow perch or largemouth bass that were expected a priori to consume a wide range of dietary items. However, the inclusion of hydrogen isotopes allowed us to effectively discriminate among benthic, pelagic, and terrestrial resource use by consumers (Doucett et al. 2007), and thus make inferences about how a non-native species influences broad patterns of ecosystem functioning. Future research would benefit from the integration of isotopic data with traditional diet data and emerging fatty acid analyses to allow for more detailed inferences about contributions of non-native species to consumer diets.

Non-native species are often assumed to have consistent, negative effects on ecosystems (e.g., Simberloff 2011, Ricciardi et al. 2013), whereas their emerging positive roles in contemporary landscapes are under recognized (Schlaepfer et al. 2011). We did not find evidence that *Bellamya* induced trophic cul-de-sacs; to the contrary our results show that *Bellamya* had neutral or beneficial effects on lake food webs. Further, our study highlights that *Bellamya*'s importance to the food web differed across a gradient of shoreline

development, and thus *Bellamya*'s role depended on the abiotic and biotic context of their environment. Further, because the food webs examined here were dominated by fish consumers in the families Centrarchidae (sunfishes) and Percidae (perches), we suggest that future research examine whether the role of *Bellamya* is comparable in food webs dominated by different predators. Previous studies have found evidence that non-native New Zealand mudsnails are indigestible to rainbow trout (Vinson and Baker 2008) and induce trophic cul-de-sacs in streams (Moore et al. 2012); yet Hellmair et al. (2011) showed that endangered tidewater goby, *Eucycloglobius newberryi*, consume and digest New Zealand mudsnails in estuaries. These contrasting lines of evidence indicate that extrinsic factors, such as type of ecosystem, competitors, and predators in the environment, are important for determining the roles, both positive and negative, of non-native species in present day food webs (Schlaepfer et al. 2011, Jeschke et al. 2014). Our evidence that a non-native species can ameliorate some effects of environmental degradation suggests that researchers and managers should consider the bidirectional effects of non-native species.

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