Of olives and carp: interactive effects of an aquatic and a terrestrial invader on a stream-riparian ecosystem

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Abstract. Multiple invasive species may interact, influencing one another and generating synergistic effects on food webs and ecosystem processes. We investigated the interaction between two non-native species widespread in the western USA: common carp (Cyprinus carpio) and Russian olive (Elaeagnus angustifolia), an invasive riparian tree associated with di-nitrogen fixation. Deep Creek, Idaho, was an International Biological Program site in the early 1970s; at that time, carp were rare and Russian olive was absent. Subsequently, Russian olive was introduced and established a dense stand, increasing allochthonous inputs and nitrogen-rich benthic organic matter. Since 1971, carp density has increased ~4× (an increase our bioenergetic analysis suggests could not have been sustained in the absence of Russian olive). Carp gut contents in 2013–2014 revealed, on average, ~40% olives, and, similarly, stable isotope analyses revealed ~58% of carp tissues were derived from olives. A small-scale, short-term experimental exclusion of these subsidized carp caused ~3× increases in macrophytes and chlorophyll-a, suggesting they may limit algae and macrophyte biomass. Moreover, carp that consumed olives excreted more nitrogen (~2× more ammonium, ~2× more total dissolved nitrogen, and ~3× more total nitrogen) compared to those that had not, which may amplify recycling and export from streams invaded by both species. This scenario is characteristic of an “invasional meltdown,” with attendant changes in food webs and ecosystem processes.

Key words: common carp; Cyprinus carpio; Elaeagnus angustifolia; invasional meltdown; nutrient dynamics; Russian olive.

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INTRODUCTION

As the number of biological invasions continues to increase, many ecosystems now host multiple non-native species, and in some environments, the number of non-native species outnumbers native taxa (Johnson et al. 2009, Jackson et al. 2014, Turbelin et al. 2017). However, studies of non-native invasive species’ effects on one another are relatively few, and multiple invaders may be involved in a variety of complex interactions that could lead to consequences for native communities and ecosystems (Simberloff and Von Holle 1999, Jackson 2015). Invaders may negatively affect one another through competition and/or predation, positively influence one another through facilitative interactions, or have no effect on each other (Simberloff and Von Holle...
Depending on the interaction, their combined influence on native communities and ecological impacts may be diminished (Ross et al. 2004, Liu et al. 2018) or amplified (Beggel et al. 2016, Crego et al. 2016). The latter, in addition to ecosystem impacts, could enhance establishment and spread of invaders (Ricciardi 2001, Grosholz 2005). The scenario of potential facilitation and possible increased magnitude of impact are characteristic of an “invasional meltdown” (Simberloff and Von Holle 1999). An “invasional meltdown,” whereby interspecific facilitation leads to an accelerating increase in the number of introduced species (i.e., secondary invaders) and their impact, has received limited attention with relatively little empirical support (Simberloff 2006, Green et al. 2011, O’Loughlin and Green 2017).

Biological invasions are numerous in freshwater systems and include a wide variety of species that can develop enormous populations, which can strongly alter native populations, community structure, and ecosystem processes (Strayer 2010). However, there is a need for studies that address both consequences for community structure and ecosystem processes, as well as the direct and indirect effects. Invading primary consumers can dominate nutrient cycling and ingest so much primary production that they significantly affect the amount and composition of primary producers (e.g., mollusks; Hall et al. 2003). Their impacts on the amount and quality of primary production, as in the case of zebra mussels (*Dreissena polymorpha*), can affect nearly every part of an ecosystem (Strayer et al. 1999, Strayer 2009). Likewise, the spread of introduced, non-native salmonid fishes severely alters stream communities through direct predation on and competition with native species, as well as indirect effects on food webs (Flecker and Townsend 1994, Simon and Townsend 2003).

Biological invasions can interrupt resource flows, like the cycling of nutrients, and have far-reaching effects on interconnected ecosystems (Hall et al. 2003), including impacts that can propagate across the land–water interface (Baxter et al. 2004, Benjamin et al. 2011, Koel et al. 2019). Invasive species may directly affect nutrient storage and cycling through growth, and excretion or egestion (Capps and Flecker 2013, Capps et al. 2015). Nutrient recycling by a consumer is a function of the nutritional requirements of the consumer and the elemental content of its food resources. All else being equal, a consumer will release, via excretion or egestion, more of a nutrient if the proportion of that nutrient in its food is higher than its stoichiometric requirements (for growth, reproduction). For example, a diet with an increasing nitrogen (N): phosphorus (P) ratio results in increasing N:P excretion rates (Sterner and Elser 2002). As a result, species invasions may influence nutrient storage and recycling in streams by altering consumer-driven nutrient remineralization and sequestration (Capps et al. 2015), but this has only begun to be investigated (e.g., see Strayer 2012, Tronstad et al. 2015).

One of the most common woody riparian species in western North America is Russian olive, *Elaeagnus angustifolia* (Friedman et al. 2005, Nagler et al. 2011, Collette and Pither 2015), an invasive, non-native tree that was introduced to this region in the late 1800s (Katz and Shafroth 2003). It was intentionally planted as an ornamental, for windbreaks, erosion control and wildlife enhancement, and it escaped cultivation throughout the region in the 1950s (Christiansen 1963, Knopf and Olson 1984). Factors that contribute to the establishment and spread of Russian olive include horticultural cultivation, its large seed size and seed longevity, and altered flow regimes (i.e., damming and irrigation water withdrawals) (Katz and Shafroth 2003, Espeland et al. 2017). It is a deciduous tree that adds a large flux of recalcitrant allochthonous litter to streams along which it invades (Royer et al. 1999) and thus reduces the efficiency of organic matter processing within invaded stream ecosystems (Mineau et al. 2012). Russian olive also has a high capacity to fix N2 through microbial association and has been associated with changes in in-stream N dynamics (Mineau et al. 2011). Given these wide-ranging effects on aquatic ecosystems, Russian olive has the potential to interact with other invasive species in stream-riparian ecosystems, but this possibility has not yet been investigated.

Another invasive, non-native species common to streams along which Russian olive are spreading is the common carp (*Cyprinus carpio*), one of the most pervasive and destructive invasive...
fishes (Zambrano et al. 2006). Millions of dollars are spent annually by natural resource agencies to control common carp populations in the United States (Cole 2005). They were initially imported into the United States in 1831 (DeKay 1842) and were first introduced to Bear Lake and Oneida Counties, Idaho, in 1882 (American Fisheries Society 2013). Carp are highly fecund; a single female is capable of laying over a million eggs in a year (Bajer and Sorensen 2010). In the Midwestern United States, common carp have been reported to reach especially high densities (up to 1000 kg/ha), likely making up the majority of the fish biomass in the region (Bajer and Sorensen 2010). In Europe, invasive common carp appear to achieve only about one-tenth of the superabundance observed in the United States, causing many to speculate as to why some regions are better suited than others for this highly invasive fish (Crivelli 1983). Studies identifying processes that might explain their restricted pattern of superabundance are generally lacking (Bajer and Sorensen 2010). Common carp can influence water quality and nutrient dynamics and can reduce aquatic macrophytes and macroinvertebrate abundance (Parkos et al. 2003, Matsu zaki et al. 2007). Through their benthic feeding, carp affect bottom-up processes, modifying nutrient and turbidity concentrations and primary producer abundance and diversity, but may also exert top-down effects by preying upon invertebrates or changing the foraging condition for other fishes (Weber and Brown 2009), as has been shown in the context of invasive Asian carps (e.g., Collins and Wahl 2017). Additionally, carp can have strong direct and indirect impacts on nutrient dynamics and littoral community structure through their bioturbation and excretion (Matsu zaki et al. 2007). Similar to Russian olive, the deleterious impacts of common carp on aquatic ecosystems have been well documented, and these effects are, in part, mediated by their widespread invasions and potential for large densities in invaded ecosystems. Following this, it is likely that the effects of these species, when present together, may interact.

We investigated whether and how a terrestrial (Russian olive) invasive species and an aquatic (common carp) invader interact to have important subsequent effects on stream ecosystems. Our study was conducted through a combination of comparative and field experiment studies at Deep Creek, located in southeast Idaho, USA. Multiple reaches of Deep Creek were intensively studied when it served as a representative cool-desert stream during the International Biological Program (IBP) in the early 1970s (Minshall et al. 1972, 1973, Minshall 1978). The same reaches were recently studied after Russian olive invaded one of these sites (Mineau et al. 2011, 2012). We hypothesized that the invasion of Russian olive facilitates the invasion of the common carp and that the synergistic impacts of these subsidized carp include consequences for in-stream primary producers, organic matter standing stocks, and nutrient dynamics. Our specific objectives were to: (1) quantify the spread of Russian olive at the study site; (2) examine and compare carp abundance pre- and post-Russian olive invasion; (3) evaluate the contribution of Russian olive to the diets and population size of carp; (4) determine the effects of carp that are subsidized by Russian olive on stream macrophytes, periphyton, and organic matter standing stocks; and (5) investigate the influence of carp consuming Russian olive on the nutrient content and stoichiometry of carp nutrient excretion rates and ratios.

**Methods**

**Study site**

Deep Creek, of southeast Idaho, is a spring fed stream located in the sagebrush steppe ecoregion in the northern Great Basin watershed (42.11° N, 112.67° W; elevation 1457 m). It is typical of most streams in the Intermountain West that are spring influenced, including a common assemblage of species, as well as a legacy of withdrawal for irrigation, and land use (particularly cattle grazing). Multiple sites were studied during the IBP studies in the 1970s, but at one site (IBP “site 2”), Russian olive was introduced for bank stabilization in the 1980s and subsequently spread to form a dense stand (Fig. 1). Mean annual water temperature at this site is 18°C and the mean annual discharge is 0.635 m³/s, including periods of low flow in the summer during irrigation withdrawals. Patterns of water use have remained consistent throughout the decades of study at the site. We focus on this site because of the Russian olive invasion and because previous work on its effects (e.g., increases in allochthonous inputs and benthic...
organic matter, and changes in nutrient dynamics) was also conducted at this site (Mineau et al. 2011, 2012). Fish population data were collected during the IBP, and our general observation of an increase in carp subsequent invasion of Russian olive was also part of the motivation for this study.

**Russian olive at Deep Creek**

To assess spread of Russian olive through time, coverage of the total area of Russian olive was estimated and compared over a 20-yr period using historical imagery (1992, from Google Earth) and more recent digital imagery (2011) from the National Agriculture Imagery Program (NAIP). Riparian vegetation along a 4500 m stream transect was digitized using ArcGIS. After polygons from the 2011 NAIP image were digitized, the 1992 image was georeferenced and also digitized. To assess the differences between the digitized polygons, total shape areas and average shape areas were quantified, and presence/absence along the transect was calculated.

Fig. 1. Deep Creek, Idaho, USA (UTM coordinates: 362143 4663403), prior to Russian olive invasion (1970, top) and after (2014, bottom). 1970 Photo credit: G. Wayne Minshall.
Carp population

The current abundance and size structure of carp in the Deep Creek study section was estimated using a combination of electrofishing and visual (underwater and bankside) surveys from 2012 to 2014, and these estimates were compared to historic data collected during the IBP in 1971–1972. Fish were sampled using a minimum three-pass removal procedure using a backpack electrofisher (LR24; Smith-Root, Vancouver, Washington) in the summer and fall of 2012 and 2013. Sample reaches (same locations as those sampled during the IBP) were approximately 100 m in length and were blocked at the upstream and downstream ends using 4.8-mm mesh nets. Captured fish were measured (total length and fork length; nearest mm), weighed (mass; g), and then returned to the stream. The IBP studies employed this method, but only documented abundance. Therefore, density was used as the basis of comparison between IBP studies and the present density. Electrofishing surveys (approximately 2 months apart) encompassed only short reaches, and we were interested in a broader assessment of the population throughout the study section and throughout the year. Because nearly all carp were large adults and water clarity was high, we were able to complement electrofishing surveys with monthly bankside counts during both years of our study, which increased the frequency and the coverage of counts with minimal in-stream disturbance. Bankside point counts were conducted along 18 randomly located, 20-m reaches of the stream for a 5-min period by at least two observers in 2013 and 2014. Further, in spring 2014 we conducted monthly underwater surveys via mask and snorkel (Li and Li 2006) for three randomly located 100-m reaches of the stream. To reduce double-counted or missed fish, counts were conducted by two snorkelers, one fixed at the upstream end of the reach, and one who started at the downstream end and worked upstream. Comparisons of carp population estimates among all three techniques (when surveys overlapped) were conducted, and differences did not exceed 10% (mean = 5%). Population size was determined by averaging the estimates from the three techniques throughout the study, but only using the bankside count when surveys overlapped.

Biomass of carp, both current and historic, was estimated by multiplying population estimates by the mean weight of carp collected. Carp during the IBP studies were described as predominantly large adults, similar in size to the current resident carp (G. W. Minshall, Idaho State University, personal communication), so we used the current mean weight to estimate the historic population biomass. This assumption may represent a source of bias in our study; however, we evaluated the sensitivity of our findings to the assumption and found it would not substantially impact our finding that carp biomass increased unless the differences in individual fish size between 1970 and 2012 was over 3x greater, which is highly unlikely given our observations and our communications with those who were involved in the studies during the 1970s. Further, the greater source of error in our calculations is likely associated with our estimates of carp abundance to determine the entire population (if anything, these are likely to be conservative estimates, given our techniques). Therefore, though subtle changes in mean weight and population size could result in differing estimates, we judged that this would not change the overall findings.

Carp diets and stable isotope analyses

Resource use by carp was determined by diet analysis and C, N, and H stable isotopes. For diet analyses, carp were collected from Deep Creek seasonally during electrofishing surveys in 2013 and 2014 (63 total guts). Fish guts were removed in the field, immediately placed on ice, and transported to the laboratory for analysis. Diet analysis was conducted using methods similar to Higgins et al. (2006). The foremost 1/5 of gut contents were processed using a dissecting microscope and contents sorted into the following categories: Russian olive material, other terrestrial plant material, aquatic plant material, detritus of unknown origin (hereafter “amorphous detritus”), and aquatic macroinvertebrates. Materials from each category were dried at 60°C for 48 h and weighed to obtain dry mass (g) and determine percentage contributions of each to gut contents.

To supplement gut content data and determine the extent to which Russian olive material was assimilated by carp, we conducted stable isotope
analyses. In the spring of 2014, we collected carp muscle tissue, as well as samples of the major items present in carp guts for analyses. Russian olive material (olives) was collected from trees, the dominant aquatic macrophyte (Potamogeton spp.; syn. Stuckenia spp.; hereafter “Potamogeton”) from the streambed, and macroinvertebrates were collected using a kick net and sorted visually in the field. Filamentous algae (Cladophora spp.) and other periphyton were rarely observed in carp guts, so we did not include them as potential basal resources in our analyses. All tissue samples were dried at 60°C for 48 h, then cooled in a desiccator. Once dried, samples were homogenized using a mortar and pestle and were weighed and encapsulated for isotopic analysis of 13C, 15N, and 2H on an isotope ratio mass spectrometer (ECS 4010 elemental analyzer, Idaho State University Interdisciplinary Laboratory for Elemental and Isotope Analysis).

Estimate of food consumption by carp

To compare and evaluate whether or not the current carp population’s demand could be met by resources available prior to Russian olive invasion, we estimated the demand for food resources by the carp present in Deep Creek and compared it to estimates of available resources pre- and post-Russian olive invasion at the site. We used published values of carp bioenergetics (Huisman 1976, Lupatsch et al. 1998) to determine the organic matter requirements of individual carp at Deep Creek. Scaling these values to the entire study reach at Deep Creek, thus treating the reach as an ecosystem (totaling 13,440 m²), we calculated the demand for the entire population at Deep Creek and compared this to the availability of resources before and after Russian olive invasion. Availability of resources was calculated from organic matter production and standing stock estimates for Deep Creek during the IBP and post-Russian olive invasion, after Mineau et al. (2012). Further, daily consumption by carp was calculated (using methods from Bajkov 1935) and compared to resource availability. Daily consumption ($D$) was calculated as:

$$D = A \left( \frac{24}{n} \right)$$

Daily food consumption by fish in the field was estimated from the average amount of food ($A$) in the gut at the time of sampling (which we measured) and the number of hours ($n$) necessary for complete gastric evacuation (which we estimated, based upon published values).

Manipulative experiment

To investigate the impacts of subsidized carp on stream ecosystem organic matter resources, we conducted a carp exclusion experiment in Deep Creek. The experiment was conducted in 2013 and lasted for a two-month period in the spring, when carp densities were highest. We sampled on day 30 (mid-point) and day 60 (end point). The experiment was modeled after a similar study that investigated the ecological role of Prochilodus, a detritivore that dominated fish assemblage biomass in a tropical stream (Flecker 1996). Like Prochilodus, carp in Deep Creek could be selectively excluded from portions of the stream because nearly all of the carp present were large adults, which were substantially larger than other fish and invertebrates in this system. In order to quantify the effects of carp, the experiment was set up with two treatments ($n = 7$): carp exclusion, and an open cage (control). Cages were 2 × 2 m in dimension, constructed of poultry wire (25 mm mesh size, allowing for access by the other stream organisms) and supported by fence posts (Fig. 2). Cages were built without floors so that the bottom of each cage was natural streamed and control cages were open on the downstream side to allow visitation of carp. An exclusion cage and control pair were placed at seven sites along the stream, each site at least 100 m from the other. Cages were at least 20 m apart with exclusion and control randomly assigned to be upstream or downstream. Sampling events consisted of depth and velocity measurements and estimation of substrate composition and macrophyte cover within each cage. In each cage, three locations were randomly selected for a core sample in which we collected periphyton and benthic organic matter. First, a stovepipe corer was inserted carefully onto the stream bottom, we gently stirred the water to suspend only the superficial organic matter without greatly disturbing the larger mineral sediment (Hall et al. 2011). A small sample was
collected and filtered (glass fiber filters; 1.6 µm particle retention size) for periphyton and placed on ice in the field and later frozen until laboratory analysis of ash-free dry mass (AFDM) and chlorophyll-a following standard methods (APHA 1995). After the periphyton sample was taken, all enclosed core material was removed with a cup to a depth of ~10 cm into the substrata and placed into a bucket. Material within the bucket was stirred and elutriated through a 250-µm sieve until no particulate organic material remained in the bucket. All matter retained on the 250-µm sieve was rinsed into a plastic bag and preserved with ~70% ethanol. Substrata composition and sample volume were estimated for each core sample based on materials in the bucket. We also sampled very fine particulate organic matter (VFPOM, < 250 µm). A ~250 mL subsample from the initial elutriated stovepipe core sample was collected in a cup as it passed through the 250-µm sieve. Total volume of the sample was recorded, and the contents within the bucket and sieve discarded. All VFPOM samples were placed in a cooler on ice to reduce decomposition until they were processed.

In the laboratory, we rinsed samples through stacked 1-mm and 250-µm sieves to separate coarse (>1 mm) fractions from fine (<1 mm, >250 µm). Coarse fractions were examined in a sorting tray under a Fiber-Lite® MI-150 high-intensity illuminator and all macroinvertebrates were removed. We sorted coarse particulate organic materials (CPOM) into Russian olive material, aquatic vegetation, leaves, sticks, bark, seeds, and amorphous detritus. Any unrecognizable material was placed into a miscellaneous CPOM category. Coarse particulate organic materials and FPOM subsamples were dried at 60°C for 48 h. Samples were then cooled in a desiccator, weighed to the nearest 0.001 g, and ashed in a muffle furnace at 500°C for >4 h. Samples were returned to the desiccator, cooled, reweighed to estimate ash-free dry mass (AFDM), and corrected for area sampled to yield g·AFDM·m⁻².

In the laboratory, within 24 h of field collection, VFPOM samples were homogenized and a subsample was filtered through a glass fiber filter (particle retention size = 1.6 µm). Filtered VFPOM samples were processed using the same method as FPOM and CPOM and corrected for subsampling to yield g·AFDM·m⁻².

Fig. 2. Photograph showing the two treatments at the start of the carp exclusion experiment. The control has the downstream end open so that carp have access.
Carp nutrient release

To address the hypothesis that carp subsidized by Russian olive influence nutrient recycling, we measured N and P nutrient release rates. All excretion experiments were conducted following methods similar to those of Schaus et al. (1997). Carp were collected from Deep Creek via electrofishing during three sample periods in early, mid, and late spring of 2013 and 2014 (n = 33). We also compared excretion by individual carp with variation in occurrence of Russian olive in their guts (excretion and gut contents were quantified for 26 individual carp). Additionally, in early and late Spring 2013 (to coincide with Deep Creek sampling), a small number of carp (n = 10) were collected at a nearby site from a similar, spring influenced stream, the Portneuf River; this site had no Russian olive, so it provided a comparison of excretion by carp that had likely never consumed Russian olive vs. those at Deep Creek. Carp were first placed in a holding tank for observation (~20 min) to allow for recovery after their capture. Next, carp were transferred to a cooler with 19.9 L of filtered, bottled water whose conductivity was adjusted to match in-stream conductivity by addition of small amounts of salt. Fish were incubated in excretion containers for approximately 30 min. Water samples for nutrient analyses were collected 5 min after placing each fish into excretion containers (to allow for a short adjustment period and to account for any non-excretion nutrients present) and again after the 30-min incubation time. Both filtered (0.45 μm) and non-filtered samples were collected and analyzed for the following: filtered—NH₄, soluble reactive phosphorus (SRP), total dissolved nitrogen (TDN), and total dissolved phosphorus (TDP); non-filtered—total N, and total P (SmartChem® 200 Discrete Analyzer, Idaho State University Center for Ecological Research and Education). Excretion rates were calculated as the difference in nutrient concentrations from the initial 5-min incubation nutrient concentration and post-fish incubation and expressed as mg of a given nutrient per kg of fish per hour. We did not notice any fecal production during incubations; however, leaching of fecal nutrients might have contributed to our estimates of excretion rates. To account for any effect of the coolers themselves, control samples were also collected from coolers without carp (n = 5).

Statistical analyses

Pre- and post-Russian olive invasion carp population density was compared with one-way analysis of variance (ANOVA). Diets and isotopes were analyzed using the mixing model software SIAR 4.0 (Parnell et al. 2010) in Rv4.0.5 to calculate the relative assimilation by carp of carbon, nitrogen, and deuterium from different sources using a literature based (Xia et al. 2013) trophic transfer shift of 1.43 ± 1.36 per mil for δ¹³C (± 1 SD) and 3.88 ± 1.19 per mil for δ¹⁵N. δ²H values for all of the basal resources were also obtained from Mineau (2011), and we assumed trophic fractionation to be negligible (Doucette et al. 2007). The three-source model was run using the siarolomcmcv4 command for single organisms with the default parameters (iterations = 500,000, burn-in = 50,000, thinby = 15). The end point data from the carp exclusion experiment were also analyzed using ANOVA with treatment as the independent variable. If ANOVA indicated significant differences for a response metric, we incorporated the mid-point data and conducted a repeated-measures ANOVA to test for effects of time and treatment × time interactions. Linear regression was used to examine the relationship between carp excretion of nutrients and the amount of Russian olive in their guts using data for fish that consumed RO. Comparisons of nutrient excretion by carp that did vs. did not consume Russian olive were analyzed with ANOVA for all excreted nutrients and the NH₄:SRP, TDN:TDP, and TN:TP ratios. If an effect on nutrient excretion was detected, an analysis of co-variance (ANCOVA) was also conducted with excreted nutrients as the dependent variable and date, temperature, and fish size as covariates. When appropriate, data were transformed using logarithms to reduce heteroscedasticity, and analyzed using PROC GLM in SAS (version 5; SAS Institute, Cary, NC, USA). Because P-values describe a “continuous measure of evidence” and are influenced by small sample size (Gelman 2013), we used a graded, weight of evidence approach to describe our certainty that results differed from what would be expected by chance alone (Wasserstein et al. 2019). Based upon this rationale, P-values <0.05 were considered significant, while those between 0.05 and 0.1 were considered marginally significant, but of potential
ecological importance considering our study’s small sample sizes.

**RESULTS**

*Temporal changes in Russian olive and carp populations*

Russian olive cover in Deep Creek increased by ~3x between 1992 and 2011 (Fig. 3). The total area of the polygons digitized from the 1992 image (Google Earth) was 22,109 m², the average polygon area was ~221 m², and Russian olive was found along 3584 m of the study section. The total area of the polygons digitized from the 2011 NAIP image was 66,521 m², the average polygon area was ~426 m², and Russian olive was found along 4477 m of the section. From 1992 to 2011, we estimated the area of Russian olive cover had increased, on average, ~2323 m²/yr. The average size of Russian olive stands in 2011 was ~2x larger than those in 1992, indicating that both cover and size of continuous stands had increased.

Subsequent to the Russian olive invasion, carp density increased ~4x, from 0.03 ± 0.02 (carp m⁻² ± 1 SE) in the early 1970s to 0.10 ± 0.02 in 2013–2014 \( (F_{1,12} = 7.82, \ P = 0.016) \). Numbers were highest during the late winter and early spring of 2013–2014 and were lowest during the summer period of lower flow associated with

![Fig. 3. 1992 and 2011 images with associated polygons digitized using ArcGIS to show the total area of Russian olive cover.](image-url)
irrigation withdrawal. Carp in Deep Creek were predominantly adults, and size of carp varied little. The mean length ($\pm 1$ SD) was 49.5 ± 5.4 cm TL ranging from 44.0 to 61.5 cm, and average weight ($\pm 1$ SD) was 1.5 ± 0.5 kg ranging from 1.0 to 2.6 kg.

**Diets and stable isotopes**

Carp gut contents consisted of ~40% Russian olive material (Fig. 4). On average, guts contained 2500 ± 600 mg AFDM ($\pm 1$ SE) of Russian olive material (almost exclusively the olives themselves). When inputs of olives were highest in late winter and early spring, the percentage of olives in the guts also increased (up to 97%). Amorphous detritus (of unknown origin) was the second most dominant item, also making up ~40%, followed by aquatic macrophytes (~20%), aquatic macroinvertebrates (~5%), terrestrial vegetation (<1%), and rock/shell fragments (<1%).

The median of plausible mixing model outcomes requires between 2.0 g AFDM$^{-1}$ to sustain the carp population in the early 1970s and 3.2 g AFDM$^{-1}$ to sustain the 2013–2014 population.

**Carp consumption**

Using values from the literature, we determined that one adult carp in Deep Creek requires between 2.0 g AFDM$^{-1}$ (based on values from Lupatsch et al. 1998) and 3.2 g AFDM$^{-1}$ (based on values from Huism an 1976). Conservatively, we estimated the organic matter requirements for the entire population at Deep Creek: 1200 ± 200 g AFDM$^{-1}$ to sustain the carp population in the early 1970s and 3500 ± 800 g AFDM$^{-1}$ to sustain the 2013–2014 population.

Based upon energy and organic matter budgets created for Deep Creek pre- and post-Russian olive invasion (Minshall 1978, Mineau et al. 2012), we estimated the availability of resources to be 1800 g AFDM$^{-1}$ in the early 1970s and 12,200 g AFDM$^{-1}$ in 2013–2014 for the total stream segment for which the carp population was estimated. Nearly all of the difference was attributable to Russian olive inputs, of which ~30% are olives, totaling 3700 g AFDM$^{-1}$. Our calculations suggest that the organic matter required to sustain the current population of carp is ~2× greater than the available resources in the early 1970s, and that only with addition of resources like the Russian olive inputs would the current availability of resources be sufficient to support the current carp population.

Daily consumption ($D$) of Russian olive material by a carp, using the average amount of RO found in carp guts at Deep Creek ($A = 2515$ mg AFDM) and a gastric evacuation rate of $2.7$% h$^{-1}$ ($n = 37$ h within a temperature range of 12.5–20°C; Kevern 1966, Donner 2011), totaled 1.6 g AFDM$^{-1}$ of Russian olive material. Therefore, the daily consumption of Russian olive for the entire carp population at Deep Creek is approximately 2800 g AFDM$^{-1}$, which falls within our estimation of available resources.

**Effects of subsidized carp**

Over the course of our short-term experimental exclusion of carp, physical characteristics in exclosures and controls did not differ. Average depth in exclosures was 21.8 ± 2.6 cm, and in controls 23.3 ± 2.5 cm. Average velocity in exclosures was 0.13 ± 0.4 m/s, and in controls 0.14 ± 0.5 m/s. Substrate composition in exclosures was made up of 77 ± 11% fine particles (sand/silt), and in controls 76 ± 15%.
Carp exclusion caused a 3× increase in macrophyte biomass after 60 d, with marginal treatment, time, and treatment × time interaction effects (treatment: $F_{1,12} = 2.48, P = 0.10$; time: $F_{1,12} = 4.11, P = 0.06$; treatment × time: $F_{1,12} = 4.11, P = 0.06$) (Fig. 6a). Exclusion of carp also resulted in ~3× higher periphyton chlorophyll-α biomass, with significant treatment and time effects (treatment: $F_{1,12} = 14.00, P = 0.002$; time: $F_{1,12} = 7.69, P = 0.016$). Chlorophyll-α exhibited
a decrease over the duration of the experiment, but there was no treatment × time interaction (Fig. 6b). Total benthic organic matter biomass did not differ between treatment and control (Table 1). Russian olive made up ~30% of the CPOM portion of the benthic organic matter in both exclosures and controls, suggesting that during the experiment, carp apparently did not forage for olives in the streambed. The VFPM portion was ~2× greater in carp exclosures compared to controls with a significant treatment and time effect (treatment: $F_{1,12} = 6.54, P = 0.025$; time: $F_{1,12} = 14.02, P = 0.003$) (Fig. 6c).

**Carp nutrient release**

We observed a significant, positive correlation between the amount of Russian olive in the guts of carp and the amount of different forms of N they excreted and egested (Fig. 7). The strongest relationship we observed was between the amount of Russian olive in carp guts and total N excreted (TN; $R^2 = 0.495, P < 0.001$), followed by total dissolved N (TDN; $R^2 = 0.242, P = 0.01$), and the association with ammonium (NH4) excretion was marginally significant ($R^2 = 0.136, P = 0.06$). We observed no relationship between size of fish and proportion of Russian olive or other diet items in the gut.

Carp from Deep Creek that ate Russian olive exhibited 2–3× higher recycling rates for all forms of N than did those from the nearby Portneuf River that had not (NH4: $F_{1,18} = 8.849, P = 0.008$; TDN: $F_{1,18} = 8.706, P = 0.009$; TN: $F_{1,18} = 12.227, P = 0.003$). However, we observed no differences in the recycling rates of SRP, TDP, and TP (Fig. 8). Thus, the N:P ratio of recycled material was generally higher for carp that had consumed Russian olive. The TN:TP ratio was

**Table 1. Mean benthic organic matter (± SE) standing stocks in carp exclusion and control cages at Deep Creek.**

| BOM standing stocks | Exclusion  | Control  |
|---------------------|------------|----------|
| Total CPOM          | 373.4 (61.7) | 246.3 (57.4) |
| RO material         | 104.6 (40.6) | 71.5 (15.9) |
| FPOM                | 150.8 (22.3) | 121.2 (28.9) |
| VFPM†               | 277.6 (48.8) | 149.1 (24.7) |
| Total BOM           | 792.9 (121.2) | 525.5 (88.1) |

Note: CPOM = coarse particulate organic matter (>1 mm); RO = Russian olive; FPOM = fine particulate organic matter (<1 mm > 250 μm); VFPM = very fine particulate organic matter (<250 μm > 1.6 μm); BOM = benthic organic matter. Values are g ash-free dry mass (AFDM) m−2.
† Indicates difference ($P < 0.05$) between exclusion and control.
significantly higher for carp that consumed Russian olive ($F_{1,18} = 9.635, P = 0.007$), and differences in the TDN:TDP ratio were marginally significant ($F_{1,18} = 3.209, P = 0.092$), whereas the NH$_4$:SRP ratio was not significantly different (Fig. 8). We detected no significant effect of carp size or water temperature on excretion. Carp length ranged from 43.5 to 79.0 cm TL, carp weight from 0.9 to 2.4 kg, and water temperature ranged from 18.6 to 19.4°C. Although the slopes of the regression lines for the different dates were similar, the $Y$ intercepts were significantly different for only the forms of N (NH$_4$: $F_{1,15} = 21.96, P < 0.001$; TDN: $F_{1,15} = 8.24, P = 0.01$; TN: $F_{1,15} = 15.37, P = 0.001$; ANCOVA), such that excretion values tended to be higher at later dates in the spring.

**DISCUSSION**

Our observation of the invasion of Russian olive and subsequent facilitation of non-native carp is characteristic of an “invasional meltdown” (Simberloff and Von Holle 1999), and the combination of these two interacting invaders appears to be driving changes in food webs and ecosystem processes. In Deep Creek, Idaho, a representative cold desert stream and site of long-term studies (Minshall 1978, Mineau et al. 2012), we found that the carp population increased ~4× with Russian olive invasion. Russian olive made up nearly 40% of carp diets and, based on stable isotopic analyses, sustained over half of their tissue production. In turn, through a manipulative experiment we found these subsidized carp caused 2–3× reductions in chlorophyll-$a$, benthic organic matter, and aquatic macrophytes. Moreover, we observed that carp that consumed Russian olive recycled up to 2× more N than those that did not. Similarly, a previous study demonstrated that the combined effects of rusty crayfish (*Orconectes rusticus*) and the Chinese mystery snail (*Bellamya chinensis*) had greater consequences for native snail communities compared to when they occurred alone (Johnson et al. 2009). More recently, invasive dreissenid mussels increased growth and activity of rusty crayfish leading to lower survival of a native crayfish (Glon et al. 2017). Although few studies have directly investigated the possibility, it seems likely that multiple invasive species are involved in a variety of complex interactions. Their combined effects can differ from that of a single invader, leading to consequences for native communities and ecosystem processes, including secondary invasion (Simberloff and Von Holle 1999, Ricciardi 2001, Grosholz 2005, O’Loughlin and Green 2017, Thouvenot et al. 2017, Liu et al. 2018).

Our findings suggest that carp are being subsidized by Russian olive inputs to streams. We
observed carp consuming large amounts of Russian olives, and stable isotope analyses suggest that they assimilate this Russian olive material. We speculate that, historically, carp in Deep Creek may have relied more on consumption of aquatic macrophytes and aquatic invertebrates. Our calculations of carp demand vs. resource availability, as well as estimates of the daily consumption of Russian olive, suggest that Russian olive is needed to sustain the current carp population. Overall, we judge that the current carp population is being subsidized by Russian olive inputs based on the combination of evidence from gut content analysis, stable isotope analyses, and our bioenergetic calculations comparing carp demand vs. resource availability. Stronger evidence could be derived from a large-scale and long-term experimental manipulation (e.g., Russian olive removal) and, indeed, such an experiment is presently underway at this site. Similar studies could also be conducted at several streams throughout the western United States where Russian olive and carp invasions are widespread (Schade and Bonar 2005, Nagler et al. 2011).

Deep Creek is representative of many streams in the Intermountain West that host multiple invasive, non-native species, and it provides a rare opportunity for assessing effects of multiple invaders in that it has been studied historically as non-natives have invaded. Other non-native species present in Deep Creek include New Zealand mudsnails (Potamopyrgus antipodarum), largemouth bass (Micropterus salmoides), yellow perch (Perca flavescens), and rainbow trout (Oncorhynchus mykiss), though of these only bass were numerous at the time of this study. This study did not address these additional non-native species, but we expect that other important interactions may be occurring that include them. For example, the New Zealand mudsnail, another common invader of the west (Kerans et al. 2005), was also found in the guts of carp during our study and has been documented in the diets of carp in other settings (e.g., Cross et al. 2013). Further, although we did not observe this at Deep Creek, other non-native fish could also be consuming Russian olive. For instance, Cheek (2019) found that Russian olive represents a significant subsidy to channel catfish in the San Juan River. These findings along with ours highlight the need for similar studies elsewhere.

Our short-term experimental exclusion of carp demonstrated that carp subsidized by Russian olive can cause reductions in aquatic primary
producers and alter stream organic matter dynamics. Previous investigations have shown that carp in other settings have similar effects, with a range of consequences for other animals (e.g., macroinvertebrates) (Parkos et al. 2003, Matsuzaki et al. 2007, Weber and Brown 2009). We did not investigate the full range of potential effects of subsidized carp owing to the limited temporal and spatial scales of this experiment. For example, we initially planned to evaluate impacts of carp on the invertebrate assemblage, but a preliminary assessment suggested the scale of the experiment was inadequate to properly investigate such a response. Macrophyte responses might also have been much stronger if the experiment had lasted longer. Macrophytes were apparently more abundant during the IBP studies (Minshall et al. 1973), and indeed, there is much more luxuriant macrophyte growth in Deep Creek upstream of an irrigation diversion where Russian olive occurs but carp do not (K. K. Heinrich and C. V. Baxter, personal observation). However, during this study we did not quantify the current biomass of aquatic macrophytes present at Deep Creek. Mineau et al. (2011) reported that primary production rates at Deep Creek have remained similar since Russian olive invasion, and because periphyton chlorophyll-a concentration was quickest to respond to carp exclusion, we suspect that this primary production has shifted from being dominated by macrophytes to being driven by periphyton. The experiment did not allow us to evaluate the consequences for other animals present at Deep Creek, which include not only the non-natives mentioned above but also the remaining native fish species. The speckled dace (Rhinichthys osculus), which does not appear to eat Russian olive material, has for unknown reasons experienced a substantial population decrease since the IBP studies (Minshall et al. 1973, Heinrich and Baxter, unpublished data), and the native pilose crayfish (Pacifastacus gambiai), which may consume Russian olive material, is currently rare (K. K. Heinrich, personal observation). Previous studies have demonstrated that crayfish are displaced by carp via habitat depletion and alteration in behavior (Hinojosa-Garro and Zambrano 2004). Therefore, it seems likely that subsidized carp may be having indirect effects on organisms like these as well, but this remains to be investigated.

We measured 2–3× more N recycled from carp that ate Russian olive compared to carp that did not. Previous studies have considered how introduced fishes influence ecosystem processes, but few have quantified how these changes affect nutrient dynamics in freshwater ecosystems (see Capps and Flecker 2013, Capps et al. 2015). The nutrient recycling by a consumer depends on the imbalance between its nutrient content and its food (Sterner and Elser 2002). In this case, we studied an invasive fish and a novel, invasive food source. Fish excretion has consequences for ecosystem nutrient dynamics (Vanni et al. 1997, Vanni 2002, McIntyre et al. 2008, McIntyre and Flecker 2010). Owing to its strong association with microbial di-nitrogen fixation, Russian olive has already been shown to subsidize stream ecosystems with N (Mineau et al. 2011), and here, we show that carp consuming Russian olive recycle more nitrogen within the stream. Therefore, the synergistic effects of these two invaders may lead to added or altered stoichiometric imbalances that then propagate through the ecosystem, and perhaps to downstream habitats as well. As part of a previous study at Deep Creek, Mineau et al. (2011) estimated uptake at the study section as 0.02 mg·m⁻²·min⁻¹ and <0.01 mg·m⁻²·min⁻¹ for NH₄ and SRP, respectively. If we calculate the mean excretion by carp (mg·m⁻²·min⁻¹) for the entire study section at Deep Creek, we find that carp excretion far exceeds the rate of ecosystem uptake (~4000× more for NH₄ and ~400× more for SRP). Mineau et al. (2011) observed that concentrations of N increased from up to downstream along a cumulative gradient of Russian olive exposure, and we might expect a similar response to carp distribution as well. McIntyre et al. (2008) showed that the spatial distribution of fish could generate hotspots of nutrient recycling in a tropical stream. Similarly, carp in Deep Creek typically aggregate in pools, so N concentrations are likely highest just downstream of such aggregations, a possibility to be investigated.

Numerous studies have shown fish can influence the spiraling and export of nutrients in streams (Vanni 2002, Hood et al. 2005, McIntyre et al. 2008). Fish with relatively high P will excrete more N compared to fish with less P demand (Sterner and George 2000, Vanni et al. 2002). Because carp are P-rich, they likely have...
higher demand for P compared to the native speckled dace present in streams like Deep Creek, and because their Russian olive food source is nitrogen-rich, they are apparently recycling even more N. If so, this may amplify the spiraling and export of nitrogen from streams invaded by both species. Our study of carp excretion was initially intended to include a controlled feeding experiment to more precisely evaluate impacts of Russian olive on this process. However, that experiment failed because carp stopped eating when held in mesocosms, and we were concerned that excretion values would not be realistic or representative under such conditions. Therefore, we compared fish within Deep Creek that had consumed variable amounts of Russian olive and those from a segment of the Portneuf River where Russian olive were not present. Factors that are known to contribute most to differences in fish excretion rates include diet, size, and temperature (Schindler and Eby 1997). The gut contents of carp from the Portneuf River were primarily composed of aquatic plant material and noticeably more macroinvertebrates than were observed in diets of Deep Creek carp (K.K. Heinrich, personal observation); the latter would be expected to result in excretion of relatively more nitrogen. Therefore, we considered the differences we observed in N recycling rates to be a conservative estimate of the effects of Russian olive consumption. Additionally, fish excretion is positively related to temperature and size of fish (Schaus et al. 1997, Vanni 2002, Vanni and McIntyre 2016). Larger fish excrete more, but at a lower mass-specific rate (Gido 2002). We controlled for size by measuring excretion from fish of similar size, and rates were scaled by weight. During the first round of measurements, Deep Creek was ~8°C warmer than the Portneuf River, but temperature was similar during the other sampling periods. Thus, excretion values for carp consuming Russian olive were ~2× higher regardless of temperature.

The majority of studies that explore stoichiometric mechanisms underpinning consequences of species loss or addition focus on measures of the recycling of inorganic forms of N and P. Both NH₄ and SRP undergo quick uptake by microbes in streams including primary producers like algae (Hall et al. 2002). However, the dissolved organic forms of N and P are also important in streams, but require further processing to be assimilated as they spiral downstream (Newbold et al. 1981). If we had only measured the inorganic forms recycled by carp, we might have missed key patterns. For instance, carp recycling of TDN was more than double that of NH₄ and differences between those that ate Russian olive vs. those that did not were stronger for TN than for NH₄. Moreover, the differences in N:P ratio recycled by carp that did vs. did not consume Russian olive were significantly different for TN and TP, were marginally significant for TDN and TDP, and were not significant for NH₄ and SRP. The precise physiological or ecological mechanisms responsible for these patterns are unknown, but warrant study.

Our study showed Russian olive may facilitate carp, but a reciprocal relationship could occur as well; carp may facilitate the spread of Russian olive, and/or other invaders. Indeed, fish are often overlooked as seed dispersers (Correa et al. 2007), although the fossil record suggests they were the first vertebrate seed dispersers (Tiffney 1986). For instance, fruit-eating Colossoma and Piaractus are very effective seed dispersers in South America (Anderson et al. 2009). Further, the common carp is known to ingest hard-coated seeds of an aquatic macrophyte, Sagittaria emer-sum, which pass through its gut, resulting in improved germination (Pollux et al. 2006). A recent study by Larkin et al. (2020) suggested carp may facilitate the spread of invasive macrophytes in Midwestern lakes. With this possibility in mind, we conducted a pilot study whereby we planted Russian olive seeds that had passed through the guts of carp, and we found that those seeds were still viable (K. K. Heinrich, unpublished). Thus, there may be potential for carp to aid in dispersal and increased germination of Russian olive, and these possibilities deserve investigation. Moreover, carp may facilitate other invaders. As mentioned above, carp consume New Zealand mudsnails and these snails can survive consumption by fish (Vinson and Baker 2008), such that consumption and movement by carp may contribute to their spread. Furthermore, owing to their high fecundity, carp may serve to subsidize invasive piscivores (e.g., largemouth bass and yellow perch), contributing to their spread and driving indirect effects on
remnant native fishes. Future studies are warranted along these lines.

Finally, susceptibility to invasion and to interactive effects (i.e., meltdown) may be mediated by legacies of land and water use, and associated changes of habitat and communities that have occurred in the past (Vitousek et al. 1997, Didham et al. 2005, 2007, MacDougall and Turington 2015). In the Intermountain West, overgrazing and water withdrawal causes habitat degradation, which sets the stage for loss of native biodiversity and spread of invasive species. Russian olives were planted throughout the west as windbreaks and to control bankside erosion, and water withdrawals (which drive loss of native riparian trees and shrubs) may have initially facilitated its spread (Christiansen 1963, Knopf and Olson 1984). Historically, native fishes in Deep Creek and other streams like it would have included large bodied cyprinids and suckers (e.g., Utah chub, *Gila atraria* and Utah sucker, *Catostomus ardens*) that could have eaten Russian olive, but these are no longer present and this loss could have created an open resource opportunity for carp. Any management solutions to invasive species like carp and Russian olive, or their interactions, should take into account these legacies (Simberloff et al. 2013).

Invasive species management and eradication efforts are expensive and labor intensive (Pimentel et al. 2005). Russian olive removal and carp eradication efforts (e.g., “carp derbies”) have become pervasive activities around the west, but are not connected to one another conceptually. Restoration efforts may yield an array of developmental pathways and habitat performances, but occur within constraints imposed by potential capacity, which in many cases has been altered from its historic character (Ebersole et al. 1997). Removal of Russian olive may not be an effective form of restoration if native species of vegetation cannot return or if interactions exist with other invaders. Very little is known regarding the effectiveness or responses to Russian olive removal as restoration (Gaddis and Sher 2012). Similarly, removal of carp may be ineffective if management does not address underlying problems that set the stage for increases in their populations. Further, understanding synergistic consequences of invaders, such as the increased nitrogen fluxes we have described accompanying Russian olive and carp invasion, should inform adaptive management of multiple invasive species. For example, large-scale removals could be designed and treated as experiments, with monitoring that extends not only to desired native species, but also other non-natives. Demonstrating tangible, but unforeseen, and far-reaching effects of invasive species such as consequences for in-stream communities and ecosystem processes will provide information critical to the understanding and application of adaptive management in the face of multiple invasive species.

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