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# Consequences of consumer origin and omnivory on stability in experimental food web modules

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Running Title: Consumer origin, omnivory and stability

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## Abstract

1. Food web stability, a fundamental characteristic of ecosystems, is influenced by the nature and strength of species interactions. Theory posits that food webs are stabilized by omnivory and disrupted by novel consumers, owing to the latter's potentially higher consumption rates and prey naïveté.
2. To test the effects of secondary consumer origin and trophic level on basal resource stability, we used four congeneric species of crayfish (*Faxonius* spp., formerly *Orconectes*), two from native populations (*F. propinquus* and *F. virilis*) and two from non-native populations (*F. limosus* and *F. rusticus*), and surgical manipulations to create omnivore food web and predator food chain modules. Here we were focused on temporal stability using measures of the coefficient of variation of the basal resource.
3. Consistent with theoretical and empirical predictions, food web modules with omnivory had the lowest coefficient of variation. However, contrary to expectations we did not find consistently higher coefficients of variation among non-native species. Rather, we found a lower coefficient of variation in one of the non-native species (*F. rusticus*) and one of the native species (*F. virilis*), owing to stronger interactions between the crayfish and their prey, which suppressed prey growth.
4. The results suggest that indeed omnivory is stabilizing and that very weak interactions or very low attack rates of the consumer on the basal resource can be unstable. Taken together we demonstrate that omnivores may have different impacts than predators when introduced into a novel ecosystem, differences that can supersede the effect of species identity.

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**Key words:** community dynamics; trophic ecology; interaction strength; invasive species; consumer-resource interactions.

## Introduction

Food web stability, here defined as temporal constancy, is a fundamental characteristic of ecosystems (Worm & Duffy, 2003) that can be profoundly affected by the presence of omnivores – organisms that feed on more than one trophic level (Pimm & Lawton, 1978; Pimm, 1982). Omnivory is common in food webs across a broad range of habitats, including freshwater systems (Thompson et al., 2007; Thompson, Dunne & Woodward, 2012; Wootton, 2017). Omnivores reduce the strength of consumer-resource links by shunting some of the energy up the omnivore-resource pathway and away from the consumer-resource pathway (McCann et al., 1998). A form of omnivory that has been the focus of theoretical and empirical investigations on stability is intraguild predation (IGP), where an omnivore feeds on an intermediate consumer in addition to one of the prey's resources (Polis, Myers & Holt, 1989; Holt & Polis, 1997). Through predation (Fig. 1A), the omnivore increases the mortality of the common resource, thereby preventing the latter from experiencing overshoot population dynamics (McCann, 2012); for example, if the population of the intermediate consumer suddenly declines, the population of the common resource is prevented from increasing in response by omnivore predation.

Experimental studies of the dynamics of simple three- or four-species food webs with and without omnivores (especially IGP) reveal that omnivory is stabilizing (Lawler & Morin, 1993; Morin & Lawler, 1995). One of the few direct experimental tests of food web stability as a function of the degree of omnivory was conducted on arthropod assemblages by Fagan (1997), who found that a high degree of omnivory stabilized community dynamics following disturbance; however, the omnivore and predator species used in this experiment comprised

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different genera and, consequently, the effects of omnivory on community stability were confounded by potential species effects.

There are also reasons to expect consumer origin to influence food web stability. Non-native consumers generally have stronger negative effects than trophically-similar natives on native prey populations (Salo et al., 2007; Paolucci et al., 2013). These effects are thought to result, at least in part, from prey naïveté wherein prey have not had selective pressures to adapt defences to novel predator traits (Cox & Lima, 2006). Moreover, non-native populations of predators and consumers tend to have higher resource consumption rates and can thus exert greater impacts on food resources (Bollache et al., 2008; Morrison & Hay, 2011; Dick et al., 2013; Iacarella et al., 2015). Such mechanisms can produce strong interactions that are destabilizing (McCann, Hastings & Huxel, 1998). Barrios-O'Neill et al. (2014) suggested that non-native species may disrupt food webs by being stronger interactors than functionally similar natives, or by eliminating other species, consequently increasing the average interaction strength within a food web.

Crayfishes are among the most common omnivores in freshwater ecosystems and their activities can structure littoral food webs (Olsen et al., 1991; Dorn & Wodjak, 2004; Nilsson et al., 2012; Twardochleb, Olden & Larson, 2013). Non-native crayfishes have been widely introduced in lakes and rivers, where they can replace native crayfishes (Lodge, 1987; Lodge et al., 2000), significantly reduce macroinvertebrate grazer densities (Dorn, 2013) so as to cause trophic cascades (Charlebois & Lamberti, 1996), and trigger other complex indirect effects that can lead to changes in the structure of communities and food webs (Taylor & Redmer, 1996, Nystrom et al., 1996; Lodge et al., 2000; Wilson et al., 2004; Twardochleb et al., 2013). Recognizing crayfishes as potentially valuable model organisms for studying food web

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dynamics, we used individuals from two native and two non-native populations, and surgically manipulated their mouthparts to alter their trophic guild, to test the effects of secondary consumer origin and trophic level on stability in an experimental tri-trophic food web. We hypothesized that 1) omnivory in the food web will mute the oscillations in the resource and result in greater stability – indicated by a lower coefficient of variation in the resource; and 2) strong interactions involving non-native species will produce a higher coefficient of variation in the resource compared to native crayfishes, owing to extinction of the primary consumer and concomitant release of top-down control on the resource.

## Materials and methods

### Study species

Four congeneric crayfish species were used in this experiment: two species from native populations (the northern clearwater crayfish *Faxonius* (*Orconectes*) *propinquus* from the upper St. Lawrence River and the virile crayfish *F. virilis* from Ontario) and two species from non-native populations (the spinycheek crayfish *F. limosus* from the upper St. Lawrence River, and the rusty crayfish *F. rusticus* from Ontario). Both *F. limosus* and *F. rusticus* have extensive invasion histories and have caused significant impacts on recipient communities in North America and Europe (Olsen et al., 1991; Kozák et al., 2007; Hirsch, 2009; Nilsson et al., 2012). Although *F. virilis* occurs naturally over a large area of the USA and Canada encompassing the Great Lakes-St Lawrence River basin and extending to the continental divide, it has been introduced to other regions of North America (Hobbs, Jass & Huner, 1989; Phillips, Vinebrooke & Turner, 2009; Larson et al., 2010) as well as the Netherlands and the U.K. (Ahern, England, & Ellis, 2008). The northern crayfish, *F. propinquus*, has a relatively limited

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invasion history but has also caused impacts on recipient systems (Hill & Lodge, 1999; Rosenthal, Stevens, & Lodge, 2006).

**Experimental design**

Using a crayfish-snail-benthic algae food web, we created two modules (an omnivore food web and a predator food chain), each involving one of four congeneric crayfish species (*F. propinquus*, *F. virilis*, *F. limosus*, and *F. rusticus*) plus a snail-only consumer-resource interaction (Fig. 1). Each of these crayfish species includes snails in its diet (Crowl & Covich, 1990; Rosenthal et al., 2006; Twardochleb et al., 2013; A.R., pers. obs.). The experiment was conducted in 36 outdoor freshwater mesocosms (114-L plastic containers, 81 x 51.4 x 44.5 cm) located at McGill University (Montreal, Quebec). Each mesocosm received 4 L of gravel as sediment to foster natural biogeochemical cycling processes and, on 15 July 2013, mesocosms were filled with 64 L of dechlorinated tap water. Benthic algae were allowed to grow on tiles placed at the bottom of mesocosms for 21 days prior to the start of experiments. Each mesocosm was provided with 70 snails (*Physella* sp.), which acted as primary consumers of benthic algae. The snails were collected from the St. Lawrence River, which is within the native range of two of the crayfishes (*F. propinquus* and *F. virilis*) and outside the native range of the other two crayfishes (*F. limosus* and *F. rusticus*, the latter not having been recorded in the river).

Finally, each mesocosm received a single crayfish from one of the four species (*F. propinquus*, *F. virilis*, *F. limosus* and *F. rusticus*), which behaved as either an omnivore (consumed benthic algae) or a predator (did not consume benthic algae). Organism collection is

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described in the Supporting Information. Each food web module × species combination and the snail-only module were repeated four times, for a total of 36 mesocosms.

All mesocosms were arranged adjacent to each other in a single row, across which modules were distributed randomly. A refuge (PVC pipe, 10 cm length x 5 cm diameter) was also added to each mesocosm to reduce crayfish stress. Eight 10 cm x 10 cm tiles that were divided into quadrats were attached to the bottom of each mesocosm using magnets to keep them stationary during the experiment. The tiles were used as substrate on which the resource (benthic algae) would grow, and from where we would collect benthic algal samples for analysis. Mesocosms were covered with 2 $mm^2$ vinyl mesh to reduce colonization by macroinvertebrates, to minimize diurnal temperature variations, and to prevent crayfish from escaping.

**Procedures for predator conversion**

Although crayfish remove benthic algae less efficiently than snails do (Luttenton, Horgan, & Lodge, 1998), they feed on both vegetation and animals to a sufficient degree to be classified as omnivores and they exhibit a specificity in feeding structures for different resources (Holdich, 2002). To have phylogenetically-equivalent crayfish 'predators' to compare against omnivores, crayfish were manipulated surgically to prevent them from consuming algae and therefore rendering them a default predator. The transformation of crayfish from omnivores to predators was achieved by altering their "filter proper", which is comprised of the acuminate setae on the 1$^{st}$ maxilliped and maxillae (Budd, Lewis & Tracey, 1978; Holdich, 2002). Setae from the 1$^{st}$-3$^{rd}$ maxillipeds, maxilla, maxillule and mandible were removed under a microscope using microdissection scissors while crayfish were under

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anesthesia (clove oil at 1 ml/L). Crayfish selected as omnivores were also anesthetised and placed under a microscope for the same duration as the full predator conversion procedure; this was intended to reduce any manipulation effects on subsequent crayfish behaviour. Dissections were performed from 31 July to 3 August 2013 (the date of the procedure was randomised across species), after which the crayfish were kept in separate tanks during the recovery period prior to the beginning of the experiments. The manipulation of arthropod mouthparts has been used to control predation in experiments (e.g., Schmitz et al., 1997; Nelson et al., 2004), however, in these previous studies mouthparts were altered to prevent consumption of all prey, whereas in the present study mouthparts were manipulated to allow consumption of only certain resources.

**Sampling benthic algal density and snail abundance**

The experimental period lasted 61 days (5 August – 6 October 2013). Benthic algal density was sampled every second day over the experimental period. On each sampling day, benthic algae were scraped from a single quadrat within a single tile from the bottom of each mesocosm; the quadrat was chosen randomly for each mesocosm and sampled once over the experimental period. The benthic algae were then added to 30-mL of dechlorinated tap water, and the concentration of chlorophyll-*a* in each sample was determined using fluorometry (FluoroProbe, bbe-Moldaenke, Kiel, Germany). Thus, chlorophyll-*a* concentration was used as a proxy measure of benthic algal density. Data from eight tiles were collected from a total of four replicates for all crayfish species for each module, except for the *F. rusticus* predator food chain module, where data was collected from only three mesocosms owing to crayfish mortality.

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**Statistical analyses**

To measure snail mortality (including loss due to crayfish predation) across treatments, the day at which 75% of snails were lost in each mesocosm (LD75) was estimated by fitting a binomial model with a logit link function to the snail density time series data. Here we use LD75 in an analogous way to toxicity studies – as the LD75 decreases the rate of mortality increases. Treatments with a lower LD75 suffered higher mortality (a more rapid onset of 75% mortality) than higher LD75 values. A two-way analysis of variance (ANOVA) was then performed on mean LD75 using food web module and species as fixed factors.

Owing to the high degree of spatial variation within the mesocosms, for each tile in a mesocosm, we calculated the net algal density change, i.e.

$$(D_f - D_o) / L$$

where $D_f$ = density on the last day that tile was sampled, $D_o$ = density on the first day that tile was sampled, and L = length of sampling in days. We then averaged across the 8 values per mesocosm to obtain the mean net algal density change for each mesocosm. A two-way analysis of variance (ANOVA) was performed on the mesocosm net algal density change using food web module and species as fixed factors.

To assess the stability of benthic algal density, analyses were focused on temporal stability using measures of the coefficient of variation within tiles across time (Pimm, 1991; Tilman et al., 2006; Ives & Carpenter, 2007). Coefficient of variation, equal to the standard deviation divided by the mean, is a scale-independent measure of variability that is used in ecological studies (Haddad et al., 2011; Schindler et al., 2010; Howeth & Leibold, 2010;

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Kratina et al., 2012). A two-way analysis of variance (ANOVA) was then performed on the mean coefficient of variation for each mesocosm using food web module and species as fixed factors. All statistics and figures were performed using R (R Core Team, 2017).

## Results

The rate of snail mortality was greater in the omnivore food web module than the predator food chain and snail-only modules (ANOVA, Tukey HSD, $P = 0.0247$, $P<0.001$, Fig. 2A; see Fig. S1 in Supporting Information, for estimated snail abundances over time in each module). It was also greater in the predator food web module than in the snail-only module (ANOVA, Tukey HSD, $P = 0.001$). Contrary to our prediction, consumer origin had no consistent effect on snail consumption. Snails suffered a higher rate of mortality in the presence of non-native *F. rusticus* compared to either non-native *F. limosus* or native *F. propinquus* (ANOVA, Tukey HSD, $P =0.0010$, $P=0.0331$, Fig. 2A, Table S1 in Supporting Information), and in the presence of native *F. virilis* compared to non-native *F. limosus* (ANOVA, Tukey Test, $P =0.0083$). Evidence of predation was provided by fragments of crushed shells found only in the presence of crayfish. Snail mortality in the snail-only treatment was presumed to result from intraspecific competition.

Algal densities tended to be higher in the predator food web module compared with the omnivore food web module (Fig. 2B, ANOVA, Tukey HSD, $P = 0.0957$), but not the snail-only module (ANOVA, Tukey HSD, $P = 0.9897$). There was no difference in net algal density change between the predator and the snail-only modules (ANOVA, Tukey HSD, $P = 0.2921$). There was no significant difference in net algal density change among species (Table S2 in Supporting Information).

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As predicted, algal densities were more variable in the predator food chain module than in the omnivore food web module (Fig. 3, ANOVA, Tukey HSD, $P$ = 0.0429); but they were not more variable compared to the snail-only module (ANOVA, Tukey HSD, $P$ =0.8345). No difference was observed between the predator and snail-only food web modules (ANOVA, Tukey HSD, $P$ =0.5441). There was also a significant difference in the coefficient of variation between *F. rusticus* and *F. limosus* (Fig. 3, ANOVA, Tukey HSD, $P$ = 0.0023) and *F. virilis* and *F. limosus* (Tukey HSD, $P$ = 0.0213), but there was no difference between other species pairs (Table S3 in Supporting Information).

## Discussion

Theory suggests that omnivory increases stability by weakening coupling strengths that otherwise create large oscillations in organismal populations (McCann & Hastings, 1997; McCann et al., 1998; McCauley, Jenkins & Quintana-Ascencio, 2013). Two previous studies found empirical evidence of omnivory increasing stability (Fagan, 1997; Holyoak & Sachdev, 1998), but ours provides the first phylogenetically-controlled test of this phenomenon. Consistent with our first prediction, we found that the coefficient of variation was lower in food web modules with omnivory. Here, the interaction between the omnivore and benthic algae reduced the energy flux between the snail and benthic algae. Although the predation rate on snails was greater in the omnivore food web module than the predator food web module, all treatments reached the LD75 – and thus benthic algae were released from predation – within the time frame of the experiment. We posit that the predator food web modules reduced snail abundances at a slower rate owing to latent effects of the removal of the crayfish's filter proper. Nevertheless, the depletion of snails in all treatments created the potential for benthic algal

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densities to increase rapidly. However, because the omnivore could also consume the benthic algae, it prevented it growing unchecked after the removal of snails by predation. In the predator food chain module, the removal of the snails resulted in a significant increase in the net algal density change and a higher coefficient of variation. These results are consistent with theoretical predictions that if a consumer-resource interaction is excitable or shows oscillations of any sort, removing biomass can stabilize the interaction (McCann, 2012). Here, the snail-benthic algae interaction shows oscillatory potential: as the snail population decreases, the benthic algae population increases. However, in the omnivory modules benthic algae were removed, thereby weakening the relative coupling strength of the snail-benthic algae interaction. Thus, our study demonstrated the ability of an omnivore to increase temporal stability in the resource compared to a predator of the same species.

Our results did not support our predictions of the effect of species origin on stability. High resource consumption rates and efficient prey handling times are linked to the invasion success and impact potential of crayfishes (Haddaway et al., 2012; Taylor & Dunn, 2018). Therefore, we expected that non-native crayfishes would reduce stability through higher consumption rates compared with native crayfishes (Barrios-O'Neill et al., 2014). Snail mortality was higher in the presence of non-native *F. rusticus* than with native *F. propinquus* and non-native *F. limosus*, but not in comparison with native *F. virilis.* Thus, we did not find consistently higher snail consumption in non-native species, and consequently, stability was not affected by crayfish origin in our study. We propose three explanations for this. First, each of the four crayfish species used in our experiment has a history of invasion and ecological impacts beyond its native range (Wilson et al., 2004; Rosenthal et al., 2006; Twardochleb et al., 2013). Traits contributing to impacts might be conserved across conspecific populations, such

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that biogeographic origin is not as influential as other environmental factors in this context. Indeed, it has been suggested that non-native crayfish identity is less important than extrinsic characteristics of invaded ecosystems in determining their impact (Twardochleb et al., 2013), but testing this hypothesis requires multi-species and multi-site comparisons. Second, traits found to be most important for invasion success in crayfish (i.e., aggression, boldness, fecundity; Lindqvist & Huner, 1999; Gherardi & Cioni, 2004; Hudina & Hock, 2012) might not be relevant to our experiment, although they are correlated to prey consumption rates (Pintor et al., 2008). Third, the prey species (*Physella* sp.) used in our experimental food webs has evolutionary experience with *Faxonius* spp., such that it is less naïve to an unfamiliar congener than it would be to a novel predator/omnivore archetype (Cox & Lima, 2006).

We did not directly test the efficacy of our surgical manipulation. However, the contrasts between the omnivore and predator effects on algal density (Fig. 2B) suggest a differential efficiency in removing algae. It is interesting that, in this regard, the least difference was exhibited by *F. rusticus*, which is the most successful invader among the species used here (Wilson et al., 2004). In this species we observed the regeneration of the filter proper within 60 days, whereas no evidence of regeneration was observed in the other species within the experimental time frame. The regeneration of its filter proper might reflect a capacity for rapid growth and plasticity – putative traits of highly successful invaders (Crispo, 2010; Sargent & Lodge, 2014).

Although differential snail consumption across crayfish species did not produce differences in benthic algal densities, there were differences in the coefficient of variation. Stronger interaction strengths involving *F. rusticus* and *F. virilis* produced lower coefficients of variation in the basal resource than did *F. limosus*, the species with the longest LD75 – or

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ostensibly the weakest interaction strength between the crayfish, snails and benthic algae. Our results suggest that although weak to intermediate interaction strengths are stabilizing in food webs, very weak interactions are destabilizing. Here, the release of snails from predation facilitated an increase in benthic algae densities, which could not be suppressed by either predatory or omnivorous *F. limosus* individuals. This is consistent with theoretical results in Lotka-Volterra models, which show that when the attack rates are very weak the dominant eigenvalue is positive or unstable (McCann, 2012).

Taken together, our results are consistent with previous empirical work showing omnivory is stabilizing, and that the trophic position of the species, but not its origin, has an important effect on the stability of the resource population. Our study suggests that, when omnivory is weak to intermediate, non-native omnivores can also potentially stabilize the consumer-resource interactions in comparison to predators. This merits further examination, given that freshwater food webs are subject to an increasing number of introduced species, many which are omnivores (Wootton 2017).

## Data Accessibility

The complete R script for the analyses performed in the paper and associated data can be found online archived on Zenodo at the following URL: https://zenodo.org/record/1341885

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collection of crayfish. This study was funded by the National Sciences and Engineering Research Council of Canada and the Canadian Aquatic Invasive Species Network.

## Conflict of interest statement

The authors declare no conflict of interest

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## References

Ahern D., England J. & Ellis A. (2008) The virile crayfish, *Orconectes virilis* (Hagen, 1870) (Crustacea: Decapoda: Cambaridae), identified in the UK. *Aquatic Invasions* **3**, 102–104.

Barrios-O'Neill D., Dick J.T.A., Emmerson M.C., Ricciardi A., Macisaac H.J., Alexander M.E. & Bovy, H.C. (2014) Fortune favours the bold: A higher predator reduces the impact of a native but not an invasive intermediate predator. *Journal of Animal Ecology* **83**, 693–701.

Bollache L., Dick J.T. a, Farnsworth K.D. & Montgomery W.I. (2008) Comparison of the functional responses of invasive and native amphipods. *Biology Letters* **4**, 166–169.

Budd T., Lewis J. & Tracey M. (1978) The filter-feeding apparatus in crayfish. *Canadian Journal of Zoology* **56**, 695–707.

Cox J.G. & Lima S.L. (2006) Naiveté and an aquatic-terrestrial dichotomy in the effects of introduced predators. *Trends in Ecology & Evolution* **21**, 674–80.

Crispo E., DiBattista J.D., Correa C., Thibert-Plante X., McKellar A.E., Schwartz A.K., Berner D., De León L.F., & Hendry A.P. (2010) The evolution of phenotypic plasticity in response to anthropogenic disturbance. *Evolutionary Ecology Research* **12**, 47–66.

Crowl T.A. and Covich A.P. (1990) Predator-induced life-history shifts in a freshwater snail. *Science* **247**, 949–951.

Dick J.T.A., Gallagher K., Avlijas S., Clarke H.C., Lewis S.E., Leung S., *et al.* (2013) Ecological impacts of an invasive predator explained and predicted by comparative functional responses. *Biological Invasions* **15**, 837–846.

Dorn N.J. (2013) Consumptive effects of crayfish limit snail populations. *Freshwater Science* **32**, 1298–1308.

Dorn N.J. & Wojdak J.M. (2004) The role of omnivorous crayfish in littoral communities. Oecologia **140**, 150–159.

Fagan W.F. (1997) Omnivory as a stabilizing feature of natural communities. *The American Naturalist* **150**, 554–67.

Gherardi, F. & Cioni, A. (2004) Agonism and interference competition in freshwater decapods. *Behaviour* **141**, 1297–1324.

Haddaway N.R., Wilcox R.H., Heptonstall R.E.A., Griffiths H.M., Mortimer R.J.G., Christmas M., Dunn A.M. (2012). Predatory functional response and prey choice identify predation differences between native/invasive and parasitised/unparasitised crayfish. *PLoS ONE* **7**(2), e32229.

Hudina, S. & Hock, K. (2012) Behavioural determinants of agonistic success in invasive crayfish. *Behavioural Processes* **91**, 77–81.

Hirsch P.E. (2009) Freshwater crayfish invasions: Former crayfish invader Galician crayfish hands title "invasive" over to new invader spiny-cheek crayfish. *Biological Invasions* **11**, 515–521.

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Hobbs H.H.I., Jass J.P. & Huner J. V. (1989) A review of global crayfish introductions with particular emphasis on two North American species (Decapoda, Cambaridae). *Crustaceana* **56**, 299–316.

Holdich D.M. (2002) Background and functional morphology. In: *Biology of Freshwater Crayfish*, 1st edn. (Ed. D. Holdich), pp. 14–16. Blackwell Science Ltd, Oxford, UK.

Holt R.D. & Polis G.A. (1997) A theoretical framework for intraguild predation. *American Naturalist* **149**, 745–764.

Holyoak M. & Sachdev S. (1998) Omnivory and the stability of simple food webs. *Oecologia* **117**, 413–419.

Iacarella, J.C., Dick J.T.A. & Ricciardi A. (2015) A spatio-temporal contrast of the predatory impact of an invasive freshwater crustacean. *Diversity and Distributions* **21**, 803–812.

Kozák P., Buřič M., Policar T., Hamáčková J. & Lepičová A. (2007) The effect of inter- and intra-specific competition on survival and growth rate of native juvenile noble crayfish *Astacus astacus* and alien spiny-cheek crayfish *Orconectes limosu*s. *Hydrobiologia* **590**, 85–94.

Larson E.R., Busack C.A., Anderson J.D. & Olden J.D. (2010) Widespread distribution of the nonnative virile crayfish (*Orconectes virilis*) in the Columbia River basin. *Northwest Science* **84**, 108–111.

Lawler S.P. & Morin P.J. (1993) Food-web architecture and population dynamics in laboratory microcosms of protists. *The American Naturalist* **141**, 675–686.

Lindqvist, O.V. & Huner, J.V. (1999) Life history characteristics of crayfish: What makes some of them good colonizers? *Crustacean Issues* **11**, 23–30.

Luttenton M.R., Horgan M.J., & Lodge D.M. 1998. Effects of three *Orconectes* crayfishes on epilithic microalgae: A laboratory experiment. *Crustaceana* **71**, 845–855.

McCann K.S. (2012) *Food Webs*. Princeton University Press, Princeton.

McCann K. & Hastings A. (1997) Re-evaluating the omnivory-stability relationship in food webs. *Proceedings of the Royal Society B: Biological Sciences* **264**, 1249–1254.

McCann K., Hastings A. & Huxel G.R. (1998) Weak trophic interactions and the balance of nature. *Nature* **395**, 794–798.

McCauley L.A., Jenkins D.G. & Quintana-Ascencio P.F. (2013) Reproductive failure of a long-lived wetland tree in urban lands and managed forests. *Journal of Applied Ecology* **50**, 25–33.

Morin P.J. & Lawler S.P. (1995) Food-web architecture and population dynamics: theory and empirical evidence. *Annual Review of Ecology and Systematics* **26**, 505–529.

Morrison W.E. & Hay M.E. (2011) Feeding and growth of native, invasive and non-invasive alien apple snails (Ampullariidae) in the United States: Invasives eat more and grow more. *Biological Invasions* **13**, 945–955.

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Nelson E.H., Matthews C.E. & Rosenheim J.A. (2004) Predators reduce prey population growth by inducing changes in prey behavior. *Ecology* **85**, 1853–1858.

Nilsson E., Solomon C.T., Wilson K.A., Willis T. V., Larget B. & Vander Zanden M.J. (2012) Effects of an invasive crayfish on trophic relationships in north-temperate lake food webs. *Freshwater Biology* **57**, 10–23.

Olsen T.M., Lodge D.M., Capelli G.M. & Houlihan R.J. (1991) Mechanisms of impact of an introduced crayfish (*Orconectes rusticus*) on littoral congeners, snails, and macrophytes. *Canadian Journal of Fisheries and Aquatic Sciences* **48**, 1853–1861.

Phillips I.D., Vinebrooke R.D. & Turner M.A. (2009) Ecosystem consequences of potential range expansions of *Orconectes virilis* and *Orconectes rusticus* crayfish in Canada - a review. *Environmental Reviews* **17**, 235–248.

Pimm S.L. (1982) *Food Webs*. Springer Netherlands.

Pimm S.L. & Lawton J.H. (1978) On feeding on more than one trophic level. *Nature* **275**, 542–544.

Pintor, L.M., Sih, A., & Bauer, M.L. (2008) Differences in aggression, activity and boldness between native and introduced populations of an invasive crayfish. *Oikos* **117**, 1629–1636.

Polis G.A., Myers C.A. & Holt R.D. (1989) The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics* **20**, 297–330.

Rosenthal S.K., Stevens S.S. & Lodge, D.M. (2006) Whole-lake effects of invasive crayfish (*Orconectes* spp.) and the potential for restoration. Canadian Journal of Fisheries and Aquatic Sciences **63**, 1276–1285.

Salo P., Korpimäki E., Banks P.B., Nordström M. & Dickman C.R. (2007) Alien predators are more dangerous than native predators to prey populations. *Proceedings. Biological sciences / The Royal Society* **274**, 1237–1243.

Sargent L.W., & Lodge D.M. (2014) Evolution of invasive traits in nonindigenous species: increased survival and faster growth in invasive populations of rusty crayfish (*Orconectes rusticus*). *Evolutionary Applications* **7**, 949–961.

Schmitz O.J., Beckerman A.P. & O'Brien K.M. (1997) Behaviorally mediated trophic cascades: Effects of predation risk on food web interactions. *Ecology* **78**, 1388–1399.

Taylor N.G. & Dunn A.M. (2018) Predatory impacts of alien decapod Crustacea are predicted by functional responses and explained by differences in metabolic rate. *Biological Invasion*s **20**, 2821–2837.

Thompson R.M., Dunne J. & Woodward G. (2012) Freshwater food webs: towards a more fundamental understanding of biodiversity and community dynamics. *Freshwater Biology* **57**, 1329–1341.

Thompson R.M., Hemberg M., Starzomski B.M. & Shurin J.B. (2007) Trophic levels and trophic tangles: the prevalence of omnivory in real food webs. *Ecology* **88**, 612–617.

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Twardochleb, L.A., Olden J.D. & Larson E.R. (2013) A global meta-analysis of the ecological impacts of nonnative crayfish. *Freshwater Science* **32**, 1367–1382.

Wilson K.A., Magnuson J.J., Kratz T.K., Lodge D.M., Hill A.M., Perry W.L., & Willis T.V. (2004) A long-term rusty crayfish (*Orconectes rusticus*) invasion: dispersal patterns and community change in a north temperate lake. Canadian Journal of Fisheries and Aquatic Sciences **61**, 2255–2266.

Wootton K.L. (2017) Omnivory and stability in freshwater habitats: Does theory match reality? *Freshwater Biology* **62**, 821–832.

Worm B. & Duffy J.E. (2003) Biodiversity, productivity and stability in real food webs. *Trends in Ecology and Evolution* **18**, 628–632.

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# Figures

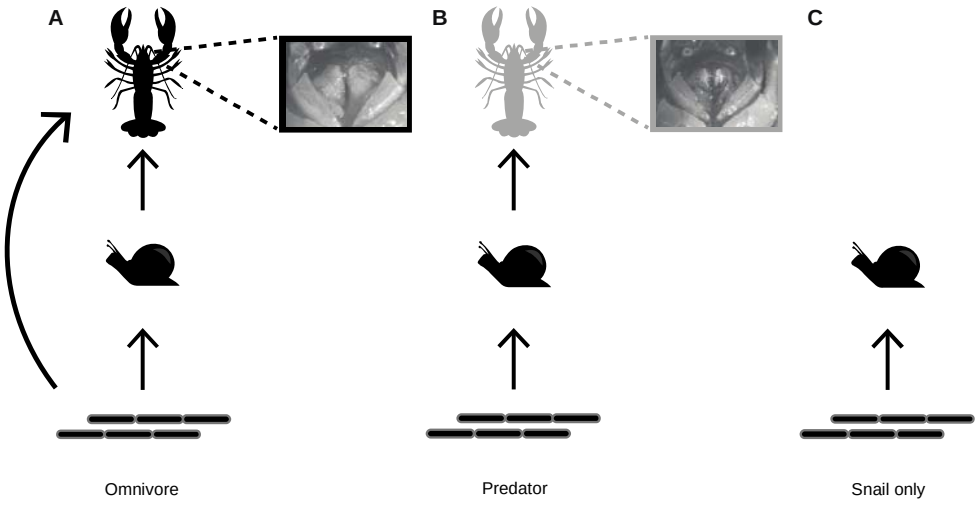


**Figure 1.** Modules used in the experiment. A. Omnivore food web module. Omnivore crayfish (black) both consumed and competed with snails for a common resource (benthic algae). B. Predator food chain module crayfish (grey) only consumed snails, which in turn consumed benthic algae. Insets depict the removal of setae in the predator treatment to prevent the consumption of benthic algae. C. Snail-only, consumer-resource interaction, treatment.

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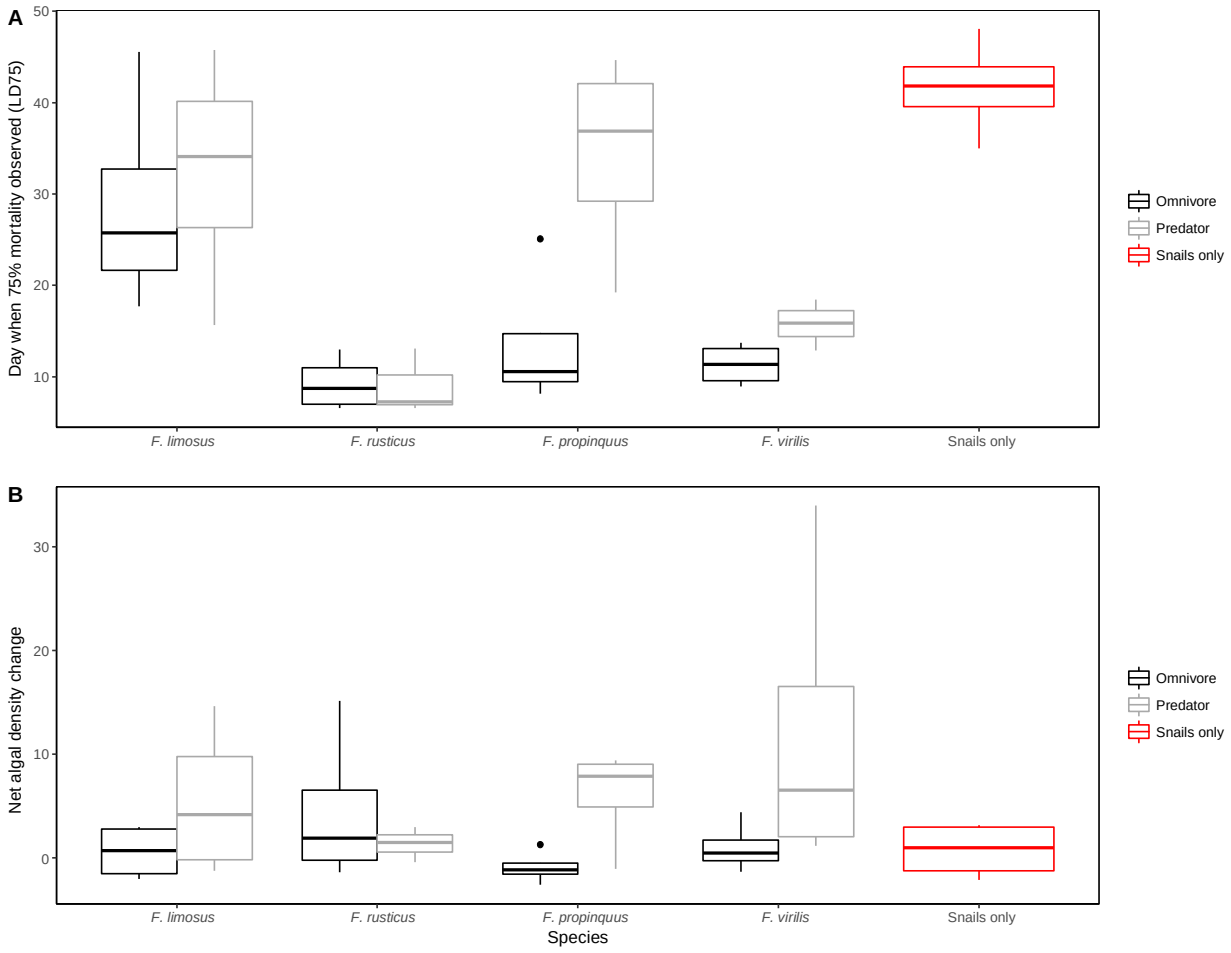


**Figure 2.** A. Median day each species consumed 75% of the snails available in each mesocosm (LD75) for each module. The lower and upper hinges correspond to the first and third quartiles (the 25th and 75th percentiles). Across all species, omnivores consumed 75% of snails in the mesocosm (i.e., reached LD75) faster than predators (ANOVA, Tukey HSD, $P$ = 0.0416) but not the snail-only module (ANOVA, Tukey HSD, $P$ = 0. 70667). B. Mean net algal density change for each food web module and species. The lower and upper hinges correspond to the first and third quartiles (the 25th and 75th percentiles). Net algal density change was significantly higher in the omnivore food web module than the predator food chain module (ANOVA, Tukey HSD, $P$ = 0.0391) but not the snail-only module (ANOVA, Tukey HSD, $P$ =

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0.0756). Crayfish are grouped by origin on the x-axis. *F. limosus* and *F. rusticus* are non-native, while *F. propinquus* and *F. virilis* are native species.

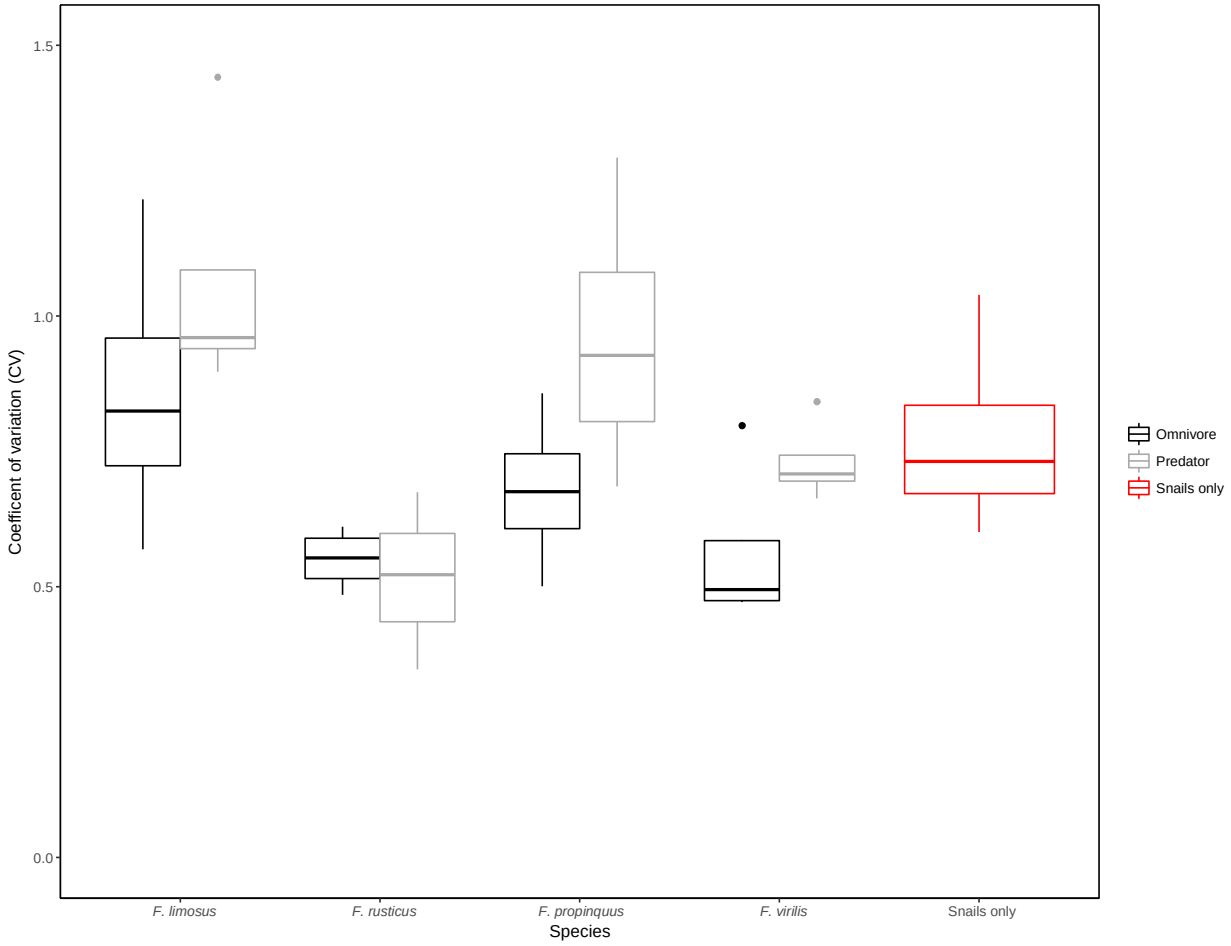


**Figure 3.** Median coefficient of variation (standard deviation/mean) for benthic algal density across the experiment for each module. The lower and upper hinges correspond to the first and third quartiles (the 25th and 75th percentiles). The coefficient of variation in the predator food chain module is significantly higher than the omnivore food web (ANOVA, Tukey HSD, $P$ = 0.0429) but not the snail-only modules(ANOVA, Tukey HSD, $P$ = 0.8345). Crayfish are grouped by origin on the x-axis. *F. limosus* and *F. rusticus* are non-native, while *F. propinquus* and *F. virilis* are native species.