The enemy of my enemy is my friend: intraguild predation between invaders and natives facilitates coexistence with shared invasive prey

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Understanding and predicting the outcomes of biological invasions is challenging where multiple invader and native species interact. We hypothesize that antagonistic interactions between invaders and natives could divert their impact on subsequent invasive species, thus facilitating coexistence. From field data, we found that, when existing together in freshwater sites, the native amphipod *Gammarus duebeni celticus* and a previous invader *G. pulex* appear to facilitate the establishment of a second invader, their shared prey *Crangonyx pseudograscilis*. Indeed, the latter species was rarely found at sites where each *Gammarus* species was present on its own. Experiments indicated that this may be the result of *G. d. celticus* and *G. pulex* engaging in more intraguild predation (IGP) than cannibalism; when the ‘enemy’ of either *Gammarus* species was present, that is, the other *Gammarus* species, *C. pseudograscilis* significantly more often escaped predation. Thus, the presence of mutual enemies and the stronger inter- than intraspecific interactions they engage in can facilitate other invaders. With some invasive species such as *C. pseudograscilis* having no known detrimental effects on native species, and indeed having some positive ecological effects, we also conclude that some invasions could promote biodiversity and ecosystem functioning.

1. Introduction

Invasion ecologists have generated many case studies of interactions between invasive and native species, often successfully illuminating reasons for the success or failure of invaders in the context of two-species interactions (i.e. one invader/one native) [1]. However, we now face situations where multiple invader and native species have come into contact, and this makes understanding and predicting the outcomes of invasions more difficult. Thus, for example, multiple species interactions may take the form of trait-mediated indirect interactions [2,3] and multiple predator effects [4,5]. In addition, it is well known that previous invaders may facilitate subsequent invaders [6,7], that new invaders may displace previous invaders [8] and both invaders and natives can provide biotic resistance to new invaders [9]. Theoretically, however, antagonistic interactions between an invader and a native could divert their impact on a second invasive species, thus facilitating its coexistence. Here, we use field and laboratory data to test the hypothesis that an invasive and a native species, by acting as mutual enemies, facilitate invasion by a shared invasive prey species—the enemy of my enemy is my friend.

Where two species have stronger interspecific than intraspecific interactions, there is the possibility that, when together, such species may have a lesser
impact on a third species than when the former species are separate. Such disparities in inter- and intraspecific interaction strengths occur with species that engage in both cannibalism and intraguild predation (IGP) [10]. We have shown that many amphipod crustacean invaders and natives show stronger IGP than they do cannibalism [11], and hence such systems lend themselves to test our hypothesis. We thus examined the invasion success of the North American *Crangonyx pseudogracilis* in Ireland and The Isle of Man, in the face of two of its predators, the native *Gammarus duebeni celticus* and a previous invader, *G. pulex*, these latter two engaging in cannibalism and IGP. First, we ask from field survey data predation on *C. pseudogracilis* present/absence with single/mixed species heterospecific juveniles of the predator (being equivalent in size) and female (males 14–15 mm body length; juveniles 4–6 mm; these species separate Isle of Man rivers, the Crogga, Middle and Colby, [11,12]. For experiments, we collected total abundances of *G. pulex* a previous invader, *Crangonyx pseudogracilis*.

### 2. Material and methods

We extracted data from two Irish lake surveys, Lough Neagh [11] and Lough Beg [12], on the presence of *C. pseudogracilis* at sites where either *G. d. celticus* or *G. pulex* were found separately, or where both *Gammarus* species were present together (n = 86); total abundances of *Gammarus* spp. in single and mixed species sites were similar [11,12]. We chose these lake datasets because all species have been present for several decades and hence all species have had time to potentially colonize all sites [11,12]. For experiments, we collected *G. d. celticus* and *G. pulex* (males 14–15 mm body length; juveniles 4–6 mm; these species being equivalent in size) and female *C. pseudogracilis* (7–8 mm; this species being much smaller than the *Gammarus* spp.) from separate Isle of Man rivers, the Crogga, Middle and Colby, respectively. These rivers were similar with respect to water temperature, pH, conductivity and BODs (11.9–12.1°C, 7.0–7.2, 182–219 μS cm⁻¹ and less than 2 mg l⁻¹). Each species was acclimatized separately for 4 days at 12°C on a 14 L : 10 D photoperiod, with source water, substratum, flora and fauna from their respective rivers. For experiments, aquaria were 8 cm diameter dishes containing 300 ml of aerated source water (a mix from all three sites), three glass pebbles, a 5 cm strand of pondweed (*Elodea canadensis*), a conditioned elm leaf and catfish food pellets. Single males of each *Gammarus* species (previously starved for 24 h to standardize hunger) were presented with either a conspecific or a heterospecific juvenile plus a female *C. pseudogracilis* (controls were replicates with male *Gammarus* absent; all groups n = 40). Replicates were inspected daily for a maximum of 10 days; experimental replicates were terminated when either of the two potential prey was killed. There were no cases of both prey being killed and in only 6% (9/160) of replicates there was no cannibalism or predation by day 10 and these were discarded from the dataset. We used raw frequency data in 2 × 2 contingency table χ² tests to compare: (i) for the field data, the association of *C. pseudogracilis* presence/absence with single/mixed species *Gammarus* sites and (ii) for the laboratory data, the association of predation on *C. pseudogracilis* with the presence of conspecific or heterospecific juveniles of the predator *Gammarus* species.

### 3. Results

*Crangonyx pseudogracilis* was present at significantly more sites where *Gammarus pulex* and *G. d. celticus* were both present as compared with sites where only one or other of the *Gammarus* species was present (χ² = 6.2, d.f. = 1, p = 0.013; figure 1). There were no deaths of female *C. pseudogracilis* or juvenile *Gammarus* in control groups (i.e. where *Gammarus* predators were absent). There was significantly lower *Gammarus* predation of *C. pseudogracilis* when those *Gammarus* were able to consume heterospecific as opposed to conspecific juveniles (for *G. d. celticus* predators: χ² = 23.9, d.f. = 1, p < 0.0001; figure 2a; for *G. pulex* predators: χ² = 12.8, d.f. = 1, p < 0.0005; figure 2b). This was clearly due to the *Gammarus* predators consuming more heterospecific than conspecific juveniles (figure 2c,d; the reciprocal of figure 2a,b).

### 4. Discussion

Understanding and predicting the success of biological invaders now requires examination of multiple species interactions, as invaders and natives may interact synergistically or antagonistically [6,13]. Here, we show a clear field pattern that, when together, a native and previous invader appear to facilitate the establishment of a second invader, a shared prey species. Our experimental results reveal that this is probably due to *G. d. celticus* and *G. pulex* engaging in more IGP than cannibalism, that is, when the ‘enemy’ of other *Gammarus* species is present (i.e. the other *Gammarus* species), the shared prey *C. pseudogracilis* can escape predation more often. This is consistent with the field pattern where the shared prey coexists more often with mixed *Gammarus* species assemblages than where only a single *Gammarus* species is present. Cannibalism may be lower than IGP because juvenile amphipods have evolved strategies to avoid cannibalism [14] and adults may avoid being cannibalistic to reduce the risk of parasite and pathogen transfer [15,16]. The result of relatively greater IGP is to reduce the predatory focus on *C. pseudogracilis* in mixed *Gammarus* species assemblages, whereas with only one *Gammarus* species present and low cannibalism, *C. pseudogracilis* suffers a greater predatory impact.

Numerous studies have shown that IGP can be a driving force behind the replacement of natives by invaders, such as...
G. d. celticus by G. pulex [11,17,18]. We now show a strong indirect effect of this interaction, that of facilitation of the success of another invader, C. pseudogracilis. This second invader has shown little detrimental effect on recipient freshwater communities, and indeed fulfills an important trophic role, that of detritivore [19]. This could be important for efficient energy cycling as C. pseudogracilis populations capitalize on the products of litter processing by both Gammarus species and colonize areas where native species have been lost or cannot tolerate degraded environments [20]. In addition, C. pseudogracilis presence could influence higher trophic levels, as it supplements food resources for fish, such as commercially important brown trout, by providing smaller, more manageable prey items than either co-occurring Gammarus species [21]. Thus, while ecologists must continue to appreciate the negative consequences of introduced species [22], positive ecological interactions and services could emerge where multiple invasive and native species and their prey interact. Our study thus adds to growing literature that shows introduced species could actually promote biodiversity conservation in some instances [23].

References

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