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Friends of mine: an invasive freshwater mussel facilitates growth of invasive macrophytes and mediates their competitive interactions

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Abstract

1. Increasing rates of invasions in ecosystems worldwide necessitate experiments to determine the role of biotic interactions in the success and impact of multiple alien species. Here, we examined competitive and facilitative interactions among various combinations of three widespread and often co-occurring invaders: the zebra mussel *Dreissena polymorpha*, and the macrophytes *Elodea canadensis* and *Elodea nuttallii*.
2. Using a mesocosm-based, factorial experimental design, we assessed the effect of interspecific competition on macrophyte growth rates in the absence and presence at varying biomass of *D. polymorpha*.
3. Growth rates (wet grams day⁻¹) of *E. canadensis* and *E. nuttallii* were similar when grown in isolation. When grown together, in the absence of *D. polymorpha*, *E. canadensis* growth was not significantly reduced in the presence of *E. nuttallii* and vice versa. In the presence of *D. polymorpha* (26.0 ± 1 mm), monocultural growth of *E. canadensis* was largely unaffected, while *E. nuttallii* growth was strongly enhanced. Low (2.64g) and medium (3.96g) mussel biomass led to negative interspecific effects between *E. canadensis* and *E. nuttallii*; at high (5.28g) mussel biomass, the effect of interspecific competition was negated.
4. Overall, *D. polymorpha* alleviated competitive interactions between the two invasive macrophytes when all three species co-occurred, and substantially enhanced growth of *E. nuttallii* with increasing mussel biomass, thereby suggesting a possible influence on the relative dominance of these macrophytes in the field.
5. Our study demonstrates how facilitations can cause shifts in dominance among closely-related invaders. The consequences of such facilitations for the structure and function of communities remain to be explored generally.

1. Introduction

Despite burgeoning studies that demonstrate the influence of invasive alien species on ecosystems, community dynamics and native biodiversity, progress toward a predictive understanding of invader impact has been limited (Ricciardi *et al.* 2013; Dick *et al.* 2017). Globally, ecosystems are being invaded at accelerating rates, resulting in rapid accumulations of alien species (Ricciardi 2006; Ricciardi & MacIsaac 2011; Seebens *et al.* 2017; Seebens *et al.* 2018) and increased opportunities for competitive and facilitative interactions that may generate variation in invader success and impact across space and time (Mony *et al.* 2007; Relva *et al.* 2010; Gallardo and Aldridge 2015; Meza-Lopez & Siemann 2015; O’Loughlin & Green 2017). Identification and quantification of these interactions across multiple context-dependencies is essential to developing effective management protocols (Ricciardi *et al.* 2013; Dick *et al.* 2017; Strayer *et al.* 2017).

Among the most complex context-dependencies are interspecific interactions of multiple invaders. Over the past two decades, studies have examined the community-level phenomenon of ‘invasional meltdown’, whereby facilitative interactions among invasive species promote their mutual establishment, persistence, and intensification of their impacts on recipient ecosystems (Simberloff & Von Holle 1999; Ricciardi 2001; Simberloff 2006). A variety of studies have suggested that invasive species can singularly or synergistically modify recipient ecosystems in a manner that mediates the establishment and impact of additional invaders through, for example, habitat formation, enhanced foraging opportunities, provision of shelter, and displacement of predators (Adams *et al.* 2003; Green *et al.* 2011; Kobak *et al.* 2016; Sheppard *et al.* 2018). Several experimental studies have provided strong evidence of negative population-level impacts, amplified by facilitative interactions (e.g. Relva *et al.* 2010; Montgomery *et al.* 2011). However, these complex interactions are often poorly defined, equivocal, or underexplored, and typically overlooked in risk analysis and management

strategies (Simberloff 2006; Roy *et al.* 2014; Gallardo & Aldridge 2015; O’Loughlin & Green 2017). For example, there may be many instances where an invader can facilitate some resident species while inhibiting others within the invaded community (Ricciardi 2001; Ward & Ricciardi 2007, 2013; Relva *et al.* 2010; Montgomery *et al.* 2011), and such differential effects could have significant impacts on the structure and functional ecology of the community (O’Dowd *et al.* 2003; Green *et al.* 2011; Montgomery *et al.* 2011).

Interspecific competition between plant species, whereby one species constrains or interferes with the ability of others to acquire resources, is a common determinant of invader success (Gioria & Osborne 2014; Ellawala & Kodithuwakku 2017; Paolacci *et al.* 2018a,b) and is often related to differential tolerance to resource scarcity or asymmetries in resource acquisition (Mony *et al.* 2007; Paolacci *et al.* 2016; Ellawala & Kodithuwakku 2017). Opportunistic use of available nutrients can result in a competitive advantage and enhanced growth (Dawson *et al.* 2011; Paolacci *et al.* 2016), in accordance with theory that predicts a higher Relative Growth Rate (RGR) in successful invaders compared to competitors (Funk & Vitousek 2007). Moreover, under nutrient enriched conditions, some plants may rapidly outcompete co-occurring species. Exploitation of differential niches within the same environment can ensure improved access to resources, and a competitive advantage over species unable to exploit multiple niches (Evans and Edwards 2001). On the other hand, ecological or phylogenetic similarity between existing and new invaders (as found within the same genus) can facilitate invader success, perhaps owing to direct facilitation or weaker competitive interactions (Sheppard *et al.* 2018), although even congeneric species can display differential RGRs under the same environmental conditions (Paolacci *et al.* 2016, 2018a). Accordingly, examination of how both native and invasive species exploit resources for rapid growth will enhance understanding of invasion dynamics (Paolacci *et al.* 2018b); however,

there is a paucity of studies that examine competitive interactions between multiple invaders, especially plants (Kuebbing *et al.* 2013; Sheppard *et al.* 2018).

Elodea canadensis Rich. In Michx. (1803) and *Elodea nuttallii* (Planch) H. St. John, 1920 are congeneric aquatic macrophytes native to North America (Barrat-Segretain *et al.* 2002; Vernon & Hamilton 2011) and invasive in Europe, Asia and Australasia. Both species were likely initially introduced through the aquarium and ornamental trades. These rooted, submerged, perennial species typically inhabit lakes, ponds and slow-moving rivers (Barrat-Segretain *et al.* 2002; Champion *et al.* 2010). Both *Elodea* spp. increase flood risk, devalue adjacent property, disrupt navigation, confound water extraction, and impede irrigation and recreational activities (Hussner *et al.* 2017). Although non-native, since first being recorded present in 1836, *E. canadensis* had become widespread in both Britain and Ireland prior to the introduction of *E. nuttallii* in 1966 (Simpson 1984). However, *E. nuttallii* can rapidly dominate invaded ecosystems and significantly alter freshwater communities (Champion *et al.* 2010; Zehnsdorf *et al.* 2015; Thouvenot & Thiébaud 2018; but see Kelly *et al.* 2015). Following its establishment, *E. nuttallii* has often been observed to displace *E. canadensis* (Simpson 1990). Although the displacement of *E. canadensis* by *E. nuttallii* is not readily explained by most physiological parameters, it appears that under resource-enriched conditions the ability of *E. nuttallii* to accumulate phosphorus is greater than that of the former (Robach *et al.* 1995; Barrat-Segretain *et al.* 2002; Josefsson 2011). Equally, comparative elongation of *E. nuttallii* stems may give it a competitive advantage in canopy formation, thus shading and inhibiting *E. canadensis* growth (Kelly *et al.* 2015).

The zebra mussel *Dreissena polymorpha* (Pallas, 1771), native to the Black and Caspian sea basins, is a prolific invasive bivalve that can dominate freshwater ecosystems and cause myriad ecological and economic impacts (Ricciardi *et al.* 1998; Higgins & Vander Zanden 2010; Ward & Ricciardi 2013; Sousa *et al.* 2014). In particular, *D. polymorpha* has displaced native mussel

species, increased water clarity, altered nutrient cycling, and caused shifts in macrophyte assemblages and blooms of filamentous macroalgae (Ricciardi *et al.* 1998; Rosell *et al.* 1999; Ricciardi 2003; Ward & Ricciardi 2013). Possible mutualistic interactions between *D. polymorpha* and invasive macrophytes, such as *Myriophyllum spicatum* and *Potamogeton crispus*, have been observed (MacIsaac 1996; Skubinna *et al.* 1995), as have a range of commensalistic interactions whereby *D. polymorpha* promotes establishment and persistence of a variety of invaders (Bially and MacIsaac 2000; Ricciardi 2001). In essence, *D. polymorpha* appears to be disproportionately involved in facilitative interactions with other invaders (DeVanna *et al.* 2011). Therefore, *Dreissena* could potentially alter competitive interactions between congeneric invasive *Elodea* species. Notably, the displacement of *E. canadensis* by *E. nuttallii* has been observed to occur more rapidly in areas containing relatively high *D. polymorpha* densities (KC *pers. obs.*). Although some juvenile *D. polymorpha* can be found adhering to plant leaves and stems, the majority of the mussels reside on the benthic substrate. Hence, we propose that the presence of *D. polymorpha* can accelerate the competitive replacement of *E. canadensis* by *E. nuttallii*, likely through the latter's more efficient use of available nutrient resources excreted by *D. polymorpha*.

We thus used laboratory-based mesocosm experiments to examine the effect of interspecific competition – and the role of *D. polymorpha* in mediating such competition – on the growth rates of *E. canadensis* and *E. nuttallii*. As dead mussel shells adsorb phosphate (Xiong *et al.* 2011), the impact of non-living mussel shells on plant growth was also considered. We therefore tested the effect of the presence of non-living zebra mussel shells and varied living mussel densities on the growth rates of each *Elodea* species when grown alone (single species) and together (both species experiencing interspecific competition). Based on field observations and pilot studies (Crane, 2019), we hypothesised that: 1) *E. nuttallii* would have a higher growth rate than *E. canadensis*; 2) interspecific competition will reduce growth rates of both

species, especially negatively affecting *E. canadensis* growth; and that 3) *D. polymorpha* would facilitate enhanced *Elodea* spp. growth, especially for *E. nuttallii*, principally through favourable changes in habitat conditions including water chemistry parameters.

2. Methods

2.1 Specimen collection

Elodea canadensis was collected from Tully Mill Lough (54°15'32.1"N; 7°42'50.4"W) in August 2017. *Elodea nuttallii* was collected from Lough Erne, Northern Ireland (54°18'12.1"N; 7°37'20.8"W) in August 2017. Lough Erne is a naturally eutrophic lake and its water chemistry reflects the underlying geology of limestone and sandstone which gives rise to carbonate-rich, slightly acidic waters. Strands of each species were cut just above the level of the roots and were transported in source water to Queen's Marine Laboratory (QML), School of Biological Sciences, Queen's University Belfast, Portaferry, Northern Ireland, UK. In addition, 80 L of lake water was collected from Lough Erne at the same time. This water was later used for mesocosm experiments.

Dreissena polymorpha was collected from Lough Erne, Northern Ireland (54°17'07.89"N 7°32'52.61"W) in August 2017. Mussels were detached from rocky substrates by clipping byssal threads and transported in a cooler filled with source lake water. Only large adult mussels with a shell length 24-30mm were selected and placed into an aerated 20-L tank for 48 hours.

All plant and mussel specimens were housed in aerated aquaria filled with source water, maintained at a constant temperature of 12°C. Source water for experimental use was kept aerated and likewise maintained under laboratory conditions. Organisms were acclimated for a minimum of 48 hours prior to experimental use.

2.2 Experimental design

Plant fragments were randomly selected from holding aquaria and apical fragments were cut to a length of 60mm. Specimens were cut immediately below the final node 16 hours prior to the start of the experiment and washed in dechlorinated tap water to remove any debris. In all cases, apical fragments were harvested from mature plants. Where possible, fragments were cut from unbranched sections of stem; however, if present, axillary side shoots were removed. Excess liquid was gently removed by manually spinning individual fragments in a handheld centrifuge (Westmark), ten times clockwise followed by ten spins counter-clockwise. Fragment wet weight (mg) was recorded using a Mettler Toledo AB104. The base of each individual fragment was protected using a small piece of cotton wool before being wrapped with a 60 × 5mm lead weight to keep the base of the fragment at the bottom of the mesocosm and the apical section positioned vertically.

Naturally occurring wild densities of *D. polymorpha* were estimated as living population biomass (soft and hard tissues; wet weight g m⁻²) at ten locations in Lough Erne. For the experimental treatments, three relative biomass categories were used: low (300g m⁻²), medium (450g m⁻²) and high (600g m⁻²). Biomass estimates for *D. polymorpha* were similar to those reported for *Dreissena* spp. inhabiting lakes in North America and Europe (Custer & Custer 1993; Cleven & Frenzel 1993; Karatayev *et al.* 2014; Ginn *et al.* 2017). In Lake Erie, for example, the average biomass for mixed populations of *D. polymorpha* and a functionally similar congener bivalve, the quagga mussel *D. rostriformis bugensis*, ranged from (mean ± SE) 55.4 ± 11.8 to 588.8 ± 94.4 g m⁻² amongst different sites (Karatayev *et al.* 2014). However, biomass is highly variable in relation to stage of invasion or age of population, and can be impacted by changes to biotic and abiotic conditions (see Karatayev *et al.* 2014).

In addition, the biomass of non-living *D. polymorpha* shells was recorded with shells being collected and scraped as clean as possible from each site (Table 1). Mean biomass of dead

shells was then calculated from across all sites, and a representative biomass was selected (100g m⁻²). Mesocosms (1.5L: high-density polyethene) had a surface area of 88 cm², thus mussel treatments were scaled to replicate naturally occurring biomass i.e. zero mussels (representing their absence), dead shells (0.88 g; an entire adult mussel 26.0 ± 1 mm, scraped clean), Low (2.64g; 1 adult mussel 26.0 ± 1 mm), Medium (3.96g; 2 adult mussels 26.0 ± 1 mm) and High (5.28g; 3 adult mussels 26.0 ± 1 mm) densities (Table 1). Mussels were placed directly on the base of the mesocosms, but were free to reposition themselves within the mesocosm at all times. Mesocosms did not contain any additional substrate.

Elodea fragments were placed in the mesocosms which acted as a proxy for a shallow lake ecosystem. As above, lake water obtained from Lough Erne was used to ensure plants had sufficient nutrients for growth and *D. polymorpha* had sufficient seston to filter feed (Vanderploeg 2017). Each mesocosm had two individual growing strands of *Elodea*; either comprising a single species (i.e. two strands of *E. canadensis* or two strands of *E. nuttallii*), representing the absence of interspecific competition; or both species together (i.e. one strand of *E. canadensis* with one strand of *E. nuttallii*), representing the presence of interspecific competition. These were combined in a factorial design with mussel treatments (zero, shells only, low, medium and high density). Control mesocosms of water only were also used, i.e. no plants or mussels added. Mesocosm water was exchanged for fresh, aerated lake water every three days to ensure *D. polymorpha* had sufficient food, whilst air lines delivered oxygen and water motion for the duration of the experiment. In total, the experiment was conducted over twelve days, with four water cycles lasting three days each (see below). All experimental groups were replicated in triplicate. Light of 30μmol photons m⁻² s⁻¹ was supplied by four 52 W Arcadia 1200mm Marine Stretch LED lamps under a 16:8 hour light: dark regime; 30μmol photons was considered sufficient for photosynthesis (Mielecki & Pieczyńska 2005). All waste invasive plant material was destroyed after the experiment by autoclaving.

2.3 Plant growth rates

Elodea biomass increase or growth rate (GR) was estimated following Van Echelpoel (2016):

$$GR = \frac{(fWW - iWW)}{t}$$

Equation 1

where fWW = final wet weight (g), iWW = initial wet weight and t = time interval.

2.4 Water chemistry parameters

Dissolved oxygen (mg L^{-1}), pH (pH Units), Total Dissolved Solids (mg L^{-1}), temperature ($^{\circ}\text{C}$) and Conductivity ($\mu\text{S cm}^{-1}$) were recorded before and after every water change using a YSI 556 MPS multi-parameter field meter. Water samples were taken from the source water prior to every water change, and from each mesocosm at the end of each 3-day water cycle. These samples were tested for nitrate ($\mu\text{mol L}^{-1}$), nitrite ($\mu\text{mol L}^{-1}$), ammonium ($\mu\text{mol L}^{-1}$) and phosphate ($\mu\text{mol L}^{-1}$) using a Bran+Luebbe AutoAnalyser 3. Samples were taken by syringe with each syringe rinsed with 18Ω high purity water twice between samples to avoid contamination. A total of four water replacements were carried out throughout the course of the experiment.

For each mesocosm, nutrient change was established in relation to the difference in nutrient concentrations between both the immediate beginning and end of each 3-day water cycle. In all cases, due to inherent minor fluctuations of probe readings, a mean value of five consecutive measurements was obtained from each mesocosm for every sampling point. Overall nutrient flux throughout the lifetime of the experiment was determined as the mean of nutrient changes across all 3-day water cycles. Overall, initial nutrient concentrations of the lake water used to

replenish each mesocosm every three days were (mean $\pm$ SE): phosphate, 1.2 ± 0.1 ; nitrate, 5.3 ± 0.5 ; nitrite, 1.0 ± 0.1 ; ammonium, 5.2 ± 0.4 ($\mu\text{mol L}^{-1}$).

2.5 Statistical Analyses

The frequency distribution of macrophyte growth rate (the dependent variable in all tests) was assessed using a Kolmogorov-Smirnov test and was not significantly different from a normal distribution ($KS = 0.075$, $p=0.200$), thus parametric tests were used for analyses. The experimental design focused on key questions, principally: is growth of one invasive plant influenced by the presence of another, and does a third invader facilitate or inhibit the interaction of the first two? Thus, our statistical approach focused on answering these specific and allied questions by utilising pairwise comparisons or comparisons of specific treatment groups. A single global model including all main effects and possible interactions was initially constructed, but its complexity and the nuance of its interpretation detracted from the clear messages that emerged from a simpler statistical approach. Thus, pairwise comparisons between any two experimental treatment groups were tested using *t*-tests, whilst comparisons across multiple groups i.e. three or more experimental treatments were tested using one-way Analysis of Variance (ANOVA). The effect of interspecific competition (0/1 = absent or present), mussel treatment (none, shells only, low, medium and high density), and their interaction term, on *Elodea* growth rates was tested using a two-way ANOVA.

Water nutrient flux was examined separately for nitrate, nitrite, ammonium and phosphate by examining Plant and Mussel treatments and their interaction using a two-way ANOVA. Least Significant Difference (LSD) *post-hoc* tests between treatment levels was used to identify pairwise effects. All statistical analyses were performed using IBM SPSS v25.

3. Results

In the absence of *D. polymorpha*, the growth rates of *E. canadensis* (mean $\pm$ SE: 0.012 ± 0.003 wet g day⁻¹) and *E. nuttallii* (0.011 ± 0.001 wet g day⁻¹) did not differ when grown in monocultures ($t_{df=10} = 0.378$, $p=0.714$; Fig. 1a). Further, *E. canadensis* growth was not reduced in the presence of *E. nuttallii* (Fig. 1b), and *vice versa* (Fig. 1c). In the presence of non-living mussel shells, monoculture growth of *E. canadensis* was significantly reduced ($t_{df=10} = 2.227$, $p=0.050$; Fig. 1d), whereas that of *E. nuttallii* was unaffected (Fig. 1e). When grown together in the presence of mussel shells, growth rates of both plants did not differ (Fig. 1b & 1c).

Elodea canadensis growth was unaffected by *D. polymorpha* biomass in the absence of interspecific competition (Fig. 1f), but was reduced by the presence of *E. nuttallii* ($F_{df=1,21}=15.031$, $p=0.001$; Fig. 1g); the impact of interspecific competition was dependent on mussel biomass ($F_{df=2,21}=12.173$, $p<0.001$; Fig. 1h). Specifically, interspecific competition reduced *E. canadensis* growth most at low mussel biomass and to a lesser degree at medium mussel biomass. The facilitating effect of *D. polymorpha* on *E. canadensis* growth at high mussel biomass was only strong enough to negate the negative effect of interspecific competition with *E. nuttallii*, such that growth of *E. canadensis* (0.012 ± 0.003 wet g day⁻¹) precisely equalled that when it was grown in isolation without either species (Fig. 1i). Thus, *D. polymorpha* had a compensatory effect restoring *E. canadensis* growth otherwise lost due to interspecific competition with *E. nuttallii*.

In contrast, in the absence of interspecific competition with *E. canadensis*, *E. nuttallii* growth was strongly enhanced by greater *D. polymorpha* biomass ($F_{df=2,21}=18.158$, $p<0.001$; Fig. 1j). Conversely, when mussels are present, *E. nuttallii* growth was negatively affected by interspecific competition with *E. canadensis* ($F_{df=1,21}=45.010$, $p<0.001$; Fig. 1k). However, growth of *E. nuttallii* did not differ with, and was independent of, mussel biomass (Fig. 1l). Similar to that observed for *E. canadensis*, high *D. polymorpha* biomass had a compensatory

effect that negated growth inhibition caused by interspecific competition on *E. nuttallii* (Fig. 1m).

Water chemistry parameters remained consistent throughout the experiment with mean $\pm$ SE values for dissolved oxygen 13.2 ± 0.32 mg L⁻¹, pH 7.35 ± 0.01 , Total Dissolved Solids 0.15 ± 0.003 mg L⁻¹, temperature 12.4 ± 0.02 °C and Conductivity 175.1 ± 0.3 μ S cm⁻¹. Nitrate, nitrite and phosphate values differed significantly between plant treatments (Table 2), and were elevated in the presence of *Elodea* (Fig. 2a-c). Ammonium and phosphate also differed significantly between mussel treatments (Table 2). Ammonium was depressed in the presence of dead mussel shells only (Fig. 2d), whilst phosphate was depressed only at medium and high mussel densities (Fig. 2e). There was no significant interaction between Plant*Mussel treatments on any water chemistry parameters (Table 2).

4. Discussion

In the absence of *D. polymorpha*, although plant growth tended to be more reduced in *Elodea* spp. polycultures than in monocultures, growth rates did not differ. When present in plant monocultures, *D. polymorpha* enhanced the growth of *E. nuttallii* but not *E. canadensis*. However, although low and medium *D. polymorpha* biomass reduced the growth rate of co-occurring *Elodea* spp., negative effects were not evident at a high mussel biomass. The facilitation of an invader by the presence of another is consistent with invasional meltdown, even though in this case one invader was promoted over another. Further, a reduction of interspecific competition between two invasive species by the presence of an additional third invader is also consistent with the concept of invasional meltdown. In the present study, these effects were associated with significant shifts in nutrient concentrations. Baseline nutrient levels of the lake water used to replenish the mesocosms tended to increase over time, which likely reflects some die-off of phytoplankton inhabiting the water. However, baseline nutrient

levels are within the average range documented for Lough Erne by the Northern Ireland Environment Agency over a nine-year survey (2006–2014, corresponding to mean values of 6.5, 1.1, 2.8 and 0.6 $\mu\text{mol L}^{-1}$ for nitrate, nitrite, ammonium and phosphate respectively (Crane 2019).

Previous experiments have compared the growth rates of *E. canadensis* and *E. nuttallii* in monoculture and sympatry (e.g. Barrat-Segretain & Arnaud 2004). Equally, the ability of *D. polymorpha* to engineer the invaded environment has been shown by several studies (Arnott & Vanni 1996; MacIsaac 1996; Ricciardi & MacIsaac 2000; Karatayev *et al.* 2002; Ricciardi 2003; Bykova *et al.* 2006; Higgins *et al.* 2008; Higgins & Vander Zanden 2010; Nogaro & Steinman, 2014). However, this study is the first to demonstrate the potential for competitive and facilitative interactions among these three invaders. Not only does the presence of *D. polymorpha* facilitate the growth rate of *E. nuttallii*, but it also reduced competition between *E. canadensis* and *E. nuttallii*. Moreover, field observations of juvenile *D. polymorpha* attached to *E. nuttallii* is suggestive of a mutualistic relationship (KC *pers. obs.*), consistent with reports of colonization of macrophytes by *D. polymorpha* (MacIsaac 1996; Horvath & Lamberti 1997; Bodamer & Ostrovsky 2010). Mussels attached to drifting *E. nuttallii* could also benefit from local dispersal (cf. Horvath & Lamberti 1997) or be transported overland attached to macrophytes snagged on recreational boat trailers (Johnson *et al.* 2001). Although small fragmentary propagules of *Elodea* can produce new growth, fragments tend to not survive extended periods of air exposure, e.g. < 3 hours at 20°C (Coughlan *et al.* 2018). Nevertheless, rapid spread and establishment of *E. nuttallii* continues to have detrimental knock-on effects on native biota, especially plants, invertebrates and algal periphyton (Kelly *et al.* 2015). Overall, our results corroborate the role of *D. polymorpha* as an ecological engineer, with broad influence on community dynamics and an ability to mediate interactions among invasive species (Ricciardi 2001; DeVanna *et al.* 2011). Our results also highlight the need for improved

spread-prevention and population suppression methods for these damaging invaders (Crane et al. 2019; Cuthbert et al. 2019).

Dreissena polymorpha can enhance nutrient cycling through excretion and, on a lake-wide basis, large populations can: 1) excrete significant concentrations of ammonia, nitrate and dissolved phosphorus; 2) reduce concentrations of suspended seston, chlorophyll a, phytoplankton and total phosphorus; 3) alter the structure and metabolic function of the benthic bacterial community; and 4) increase water transparency (Gardner *et al.* 1995; James *et al.* 1997; Gardner *et al.* 2001; Matthews & Effler 2001; Lohner *et al.* 2007; Higgins *et al.* 2008). A significant effect of zebra mussel metabolism is their ability to convert particulate forms of nutrients into dissolved, available forms (Arnott & Vanni 1996). Although not statistically evident, our results suggest a trend of greater ammonium depletion by higher mussel densities when *Elodea* was present, and while *Elodea* can utilize both nitrate and ammonium the nutrient of preference is ammonium (Ozimek *et al.* 1993). No significant depletion of nitrate or nitrite was observed during the experimental period when plants were present. However, interestingly, increasing density of living *D. polymorpha* was associated with declining phosphate concentrations. Although dead mussel shells adsorb phosphate (Xiong *et al.* 2011), this was demonstrably not the case in the present study. While nutrients were unlikely to be limiting, our results suggest that differences in growth rate could be attributed to plant competition or the presence of *D. polymorpha*, and that further work is required to specifically test the role of how both *Elodea* species nutrients excreted by *Dreissena* and why phosphate levels declined with increasing mussel biomass.

Given that regeneration of *E. nuttallii* is higher than *E. canadensis* in the spring, and the latter is thought to have a weaker ability to compete for light (Barrat-Segretain & Elger 2004), the former may have a competitive advantage where the species co-occur (Barrat-Segretain *et al.* 2002). Szabó *et al.* (2018) found that increasing levels of light and nitrogen elicited

phenotypic responses such as stem elongation in *E. nuttallii* that were far greater than that of *E. canadensis*. They also found that under eutrophic conditions, *E. nuttallii* branched rapidly and reached the surface sooner than *E. canadensis*, thereby shading out the weaker invader and other aquatic plants. These factors could partly explain the displacement of *E. canadensis* via increased canopy formation and the eventual shading of the less vigorous species. Additionally, the ability of *D. polymorpha* to excrete available forms of nutrients, required in differing amounts by *Elodea* spp. for growth, may also help explain the increased growth of *E. nuttallii* when occurring in the absence of intraspecific competition. Similarly, the functionally similar congener *D. rostriformis bugensis* and *E. nuttallii* are hypothesized to be mutually facilitative in a German lake in which mussel filtration apparently caused an increase in water clarity, whilst macrophytes provided substrate for attachment of juvenile mussels and may have prevented summer hypoxia (Wegner *et al.* 2019).

Based on their current distribution, rate of spread, and history of successful establishment, interactions between these three invasive species are likely to occur with increasing frequency. Our findings suggest that dense *D. polymorpha* populations strongly facilitate the growth of *E. nuttallii*, but not *E. canadensis*, perhaps promoting the dominance of the former over the latter where they co-occur. This could be interpreted as a form of invasional meltdown, in which the dominance of one invader is favoured over another (e.g. Ricciardi 2001; O'Dowd *et al.* 2003; Montgomery *et al.* 2011). We expect such complex facilitative/antagonistic interactions to be common in ecosystems that are increasingly invaded.

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6. Author contributions

KC and AR proposed the study; KC designed the experiment; KC conducted the experiment; KC and LK performed chemical analysis; KC and NR performed data analysis; all authors contributed to writing the manuscript, which was jointly led by KC and NEC, and gave final approval for publication.

7. Data Accessibility

Data will be made available following acceptance for publication in Dryad digital repository.

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Table 1 Mussel treatments with corresponding field and mesocosm mussel densities, specimen count and total biomass.

Mussel treatment		Field & mesocosm biomass (g.m ⁻²)	No. of specimens in mesocosms (n)	Total specimen biomass (g)
None (control)		0	0	0.00
Shells only		100	1	0.88
Low	} Density	300	1	2.64
Medium		450	2	3.96
High		600	3	5.28

Fig. 1 Mean ($\pm$ SE) comparative growth rates (wet g.day⁻¹) for **i) *Elodea canadensis*** (left panel) and **ii) *Elodea nuttallii*** (right panel) with (grey bars) and without (white bars) the presence of interspecific competition (paired bars) in each zebra mussel, *Dreissena polymorpha*, treatment category (x -axis). Horizontal lines above bars show significance testing between selected pairs or groups of categories indicated by the span of the bars (individually cited **a-m** in Results text). $ns = p > 0.05$, $* = p < 0.05$, $** = p < 0.01$ and $*** = p < 0.001$.

Table 2 Two-way ANOVA fitting the effect of Plant and Mussel treatments and their interaction term for **a)** nitrate, **b)** nitrite, **c)** ammonium and **d)** phosphate.

Dependent variable	<i>F</i>	n.df.	d.df.	<i>p</i>
Independent variables				
a) Nitrate ($F_{df=19,40}=1.905$, $p=0.043$, $r^2=0.475$)				
Plant	5.243	3	40	0.004
Mussel	1.331	4	40	0.275
Plant*Mussel	1.261	12	40	0.278
b) Nitrite ($F_{df=19,40}=1.919$, $p=0.041$, $r^2=0.309$)				
Plant	6.262	3	40	0.001
Mussel	0.134	4	40	0.969
Plant*Mussel	1.429	12	40	0.193
c) Ammonium ($F_{df=19,40}=2.558$, $p=0.006$, $r^2=0.549$)				
Plant	1.706	3	40	0.181
Mussel	6.187	4	40	0.001
Plant*Mussel	1.562	12	40	0.143
d) Phosphate ($F_{df=19,40}=6.018$, $p<0.001$, $r^2=0.741$)				
Plant	3.948	3	40	0.015
Mussel	20.417	4	40	<0.001
Plant*Mussel	1.735	12	40	0.095

Fig. 2 Significant effects highlighted from Table 2. Mean $\pm$ 95% CIs ($\mu\text{mol L}^{-1}$) for **a)** nitrate, **b)** nitrite and **c)** phosphate showing the effect of plant treatments (right column) and **d)** ammonium and **e)** phosphate showing the effect of mussel treatments (left column). Least Significant Difference (LSD) *post-hoc* tests are shown above the bars; treatment with different letters were significantly different ($p < 0.05$). Drawings not to scale.