

# 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 g/day) 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 (2.64 g) and medium (3.96 g) mussel biomass led to negative interspecific effects between *E. canadensis* and *E. nuttallii*; at high (5.28 g) 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.

## KEYWORDS

biotic interactions, biotic resistance, facilitation, interspecific competition, invasional meltdown, mutualism

## 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 (Dick et al., 2017; Ricciardi, Hoopes, Marchetti, & Lockwood, 2013). Globally, ecosystems are being invaded at accelerating rates, resulting in rapid accumulations of alien species (Ricciardi, 2006; Ricciardi & MacIsaac, 2011; Seebens et al., 2017, 2018) and increased opportunities for competitive and facilitative interactions that may generate variation in invader success and impact across space and time (Gallardo & Aldridge, 2015; Meza-Lopez & Siemann, 2015; Mony, Koschnick, Haller, & Muller, 2007; O'Loughlin & Green, 2017; Relva, Nuñez, & Simberloff, 2010). Identification and quantification of these interactions across multiple context-dependencies is essential to developing effective management protocols (Dick et al., 2017; Ricciardi et al., 2013; Strayer et al., 2017).

Among the most complex context-dependencies are interspecific interactions of multiple invaders. Over the past 2 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 (Ricciardi, 2001; Simberloff, 2006; Simberloff & Von Holle, 1999). 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, Pearl, & Bury, 2003; Green et al., 2011; Kobak et al., 2016; Sheppard, Carboni, Essl, Seebens, & Thuiller, 2018). Several experimental studies have provided strong evidence of negative population-level impacts, amplified by facilitative interactions (e.g. Montgomery, Lundy, & Reid, 2011; Relva et al., 2010). However, these complex interactions are often poorly defined, equivocal, or underexplored, and typically overlooked in risk analysis and management strategies (Gallardo & Aldridge, 2015; O'Loughlin & Green, 2017; Roy et al., 2014; Simberloff, 2006). For example, there may be many instances where an invader can facilitate some resident species while inhibiting others within the invaded community (Montgomery et al., 2011; Relva et al., 2010; Ricciardi, 2001; Ward & Ricciardi, 2007, 2013), and such differential effects could have significant impacts on the structure and functional ecology of the community (Green et al., 2011; Montgomery et al., 2011; O'Dowd, Green, & Lake, 2003).

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 (Ellawala & Kodithuwakku, 2017; Gioria & Osborne, 2014; Paolacci, Harrison, & Jansen, 2018a; Paolacci, Jansen, & Harrison, 2018b) and is often related to differential tolerance to resource scarcity or asymmetries in resource acquisition (Ellawala & Kodithuwakku, 2017; Mony et al., 2007; Paolacci, Harrison, & Jansen, 2016). Opportunistic use of available nutrients can result in a competitive advantage and enhanced growth (Dawson, Fischer, & Kleunen, 2011; Paolacci et al., 2016), in

accordance with theory that predicts a higher relative growth rate 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 & Edwards, 2001). By contrast, 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 relative growth rates under the same environmental conditions (Paolacci et al., 2016; Paolacci, Harrison, et al., 2018a). Accordingly, examination of how both native and invasive species exploit resources for rapid growth will enhance understanding of invasion dynamics (Paolacci, Jansen, et al., 2018b); however, there is a paucity of studies that examine competitive interactions between multiple invaders, especially plants (Kuebbing, Nuñez, & Simberloff, 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, Elger, Sagnes, & Pujalon, 2002; Vernon & Hamilton, 2011) and invasive in Europe, Asia, and Australasia. Both species were probably 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, Clayton, & Hofstra, 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; Thouvenot & Thiébaud, 2018; Zehnsdorf, Hussner, Eismann, Helmut, & Melzer, 2015; but see Kelly, Harrod, Maggs, & Reid, 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 (Barrat-Segretain et al., 2002; Josefsson, 2011; Robach, Hajsek, Eglin, & Trémolières, 1995). 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 (Higgins & Vander Zanden, 2010; Ricciardi, Neves, & Rasmussen, 1998; Sousa, Novais, Costa, & Strayer, 2014; Ward & Ricciardi, 2013). 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, 2003; Ricciardi et al., 1998; Rosell, Maguire, & McCarthy, 1999; Ward & Ricciardi, 2013). Possible mutualistic interactions between *D. polymorpha* and invasive macrophytes, such as *Myriophyllum spicatum* and *Potamogeton crispus*, have been observed (Maclsaac, 1996; Skubinna, Coon, & Batterson, 1995), as have a range of commensalistic interactions whereby *D. polymorpha* promotes establishment and persistence of a variety of invaders (Bially & Maclsaac, 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 (K.C. personal observation). 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*, probably 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, Qin, Islam, Yue, & Wang, 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 (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), 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 24–30 mm were selected and placed into an aerated 20-L tank for 48 hr.

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 hr 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 60 mm. Specimens were cut immediately below the final node 16 hr 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), 10 times clockwise followed by 10 spins anti-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 × 5 mm 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<sup>2</sup>) at 10 locations in Lough Erne. For the experimental treatments, three relative biomass categories were used: low (300 g/m<sup>2</sup>), medium (450 g/m<sup>2</sup>), and high (600 g/m<sup>2</sup>). Biomass estimates for *D. polymorpha* were similar to those reported for *Dreissena* spp. inhabiting lakes in North America and Europe (Cleven & Frenzel, 1993; Custer & Custer, 1997; Ginn, Bolton, Coulombe, Fleischaker, & Yerex, 2017; Karatayev et al., 2014). In Lake Erie, for example, the average biomass for mixed populations of *D. polymorpha* and a functionally similar congener bivalve, the quagga mussel *Dreissena rostriformis bugensis*, ranged from (mean ± SE) 55.4 ± 11.8 to 588.8 ± 94.4 g/m<sup>2</sup> 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

Mussel treatment	Field & mesocosm biomass (g/m <sup>2</sup> )	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		2	3.96
High		3	5.28

**TABLE 1** Mussel treatments with corresponding field and mesocosm mussel densities, specimen count, and total biomass

then calculated from across all sites, and a representative biomass was selected (100 g/m<sup>2</sup>). Mesocosms (1.5 L: high-density poly-ethene) had a surface area of 88 cm<sup>2</sup>, 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 (2.64 g; one adult mussel 26.0 ± 1 mm), medium (3.96 g; two adult mussels 26.0 ± 1 mm), and high (5.28 g; three 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 et al., 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 3 days to ensure *D. polymorpha* had sufficient food, whilst airlines delivered oxygen and water motion for the duration of the experiment. In total, the experiment was conducted over 12 days, with four water cycles lasting 3 days each (see below). All experimental groups were replicated in triplicate. Light of 30 μmol photons/m<sup>2</sup> s<sup>-1</sup> was supplied by four 52 W Arcadia 1200 mm Marine Stretch LED lamps under a 16:8 hr light: dark regime; 30 μmol 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, Boets, and Goethals (2016):

$$GR = \frac{(fWW - iWW)}{t} \quad (1)$$

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

## 2.4 | Water chemistry parameters

Dissolved oxygen (mg/L), pH, total dissolved solids (mg/L), temperature (°C), and conductivity (μS/cm) 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, nitrite, ammonium, and phosphate using a Bran + Luebbe AutoAnalyser 3. Samples were taken by syringe with each syringe rinsed with 18-Ω 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 3 days were (mean ± SE): phosphate, 1.2 ± 0.1 μmol/L; nitrate, 5.3 ± 0.5 μmol/L; nitrite, 1.0 ± 0.1 μmol/L; ammonium, 5.2 ± 0.4 μmol/L.

## 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 ( $KS = 0.075$ ,  $p = 0.200$ ), so 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 post hoc tests between treatment levels were 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  $\pm$  0.003 wet g/day) and *E. nuttallii* (0.011  $\pm$  0.001 wet g/day) did not differ when grown in monocultures ( $t_{df=10} = 0.378$ ,  $p = 0.714$ ; Figure 1a). Further, *E. canadensis* growth was not reduced in the presence of *E. nuttallii* (Figure 1b), and vice versa (Figure 1c). In the presence of non-living mussel shells, monoculture growth of *E. canadensis* was significantly reduced ( $t_{df=10} = 2.227$ ,  $p = 0.050$ ; Figure 1d), whereas that of *E. nuttallii* was unaffected (Figure 1e). When grown together in the presence of mussel shells, growth rates of both plants did not differ (Figure 1b,c).

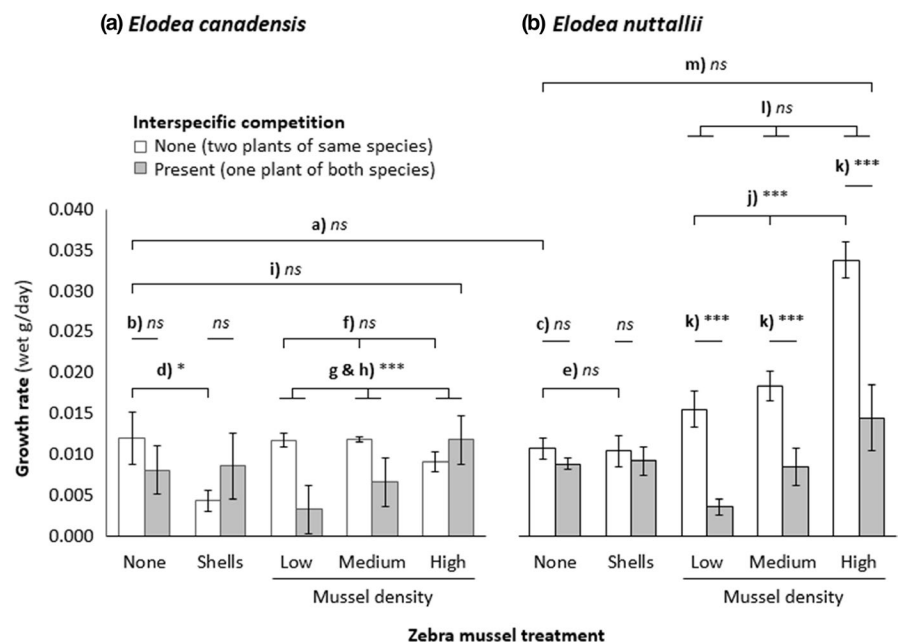
*Elodea canadensis* growth was unaffected by *D. polymorpha* biomass in the absence of interspecific competition (Figure 1f), but was reduced by the presence of *E. nuttallii* ( $F_{1,21} = 15.031$ ,  $p = 0.001$ ;

Figure 1g); the impact of interspecific competition was dependent on mussel biomass ( $F_{2,21} = 12.173$ ,  $p < 0.001$ ; Figure 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  $\pm$  0.003 wet g/day) precisely equalled that when it was grown in isolation without either species (Figure 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 ( $F_{2,21} = 18.158$ ,  $p < 0.001$ ; Figure 1j). Conversely, when mussels are present, *E. nuttallii* growth was negatively affected by interspecific competition with *E. canadensis* ( $F_{1,21} = 45.010$ ,  $p < 0.001$ ; Figure 1k). However, growth of *E. nuttallii* did not differ with, and was independent of, mussel biomass (Figure 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* (Figure 1m).

Water chemistry parameters remained consistent throughout the experiment with mean  $\pm$  SE values for dissolved oxygen 13.2  $\pm$  0.32 mg/L, pH 7.35  $\pm$  0.01, total dissolved solids 0.15  $\pm$  0.003 mg/L, temperature 12.4  $\pm$  0.02°C and conductivity 175.1  $\pm$  0.3  $\mu$ S/cm. Nitrate, nitrite, and phosphate values differed significantly between plant treatments (Table 2), and were elevated in the presence of *Elodea* (Figure 2a–c). Ammonium and phosphate also differed significantly between mussel treatments (Table 2). Ammonium was depressed in the presence of dead mussel shells only (Figure 2d), whilst phosphate was depressed only at medium and high mussel densities (Figure 2e). There was no significant

**FIGURE 1** Mean ( $\pm$ SE) comparative growth rates (wet g/day) 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 \*\*\* =  $p < 0.001$



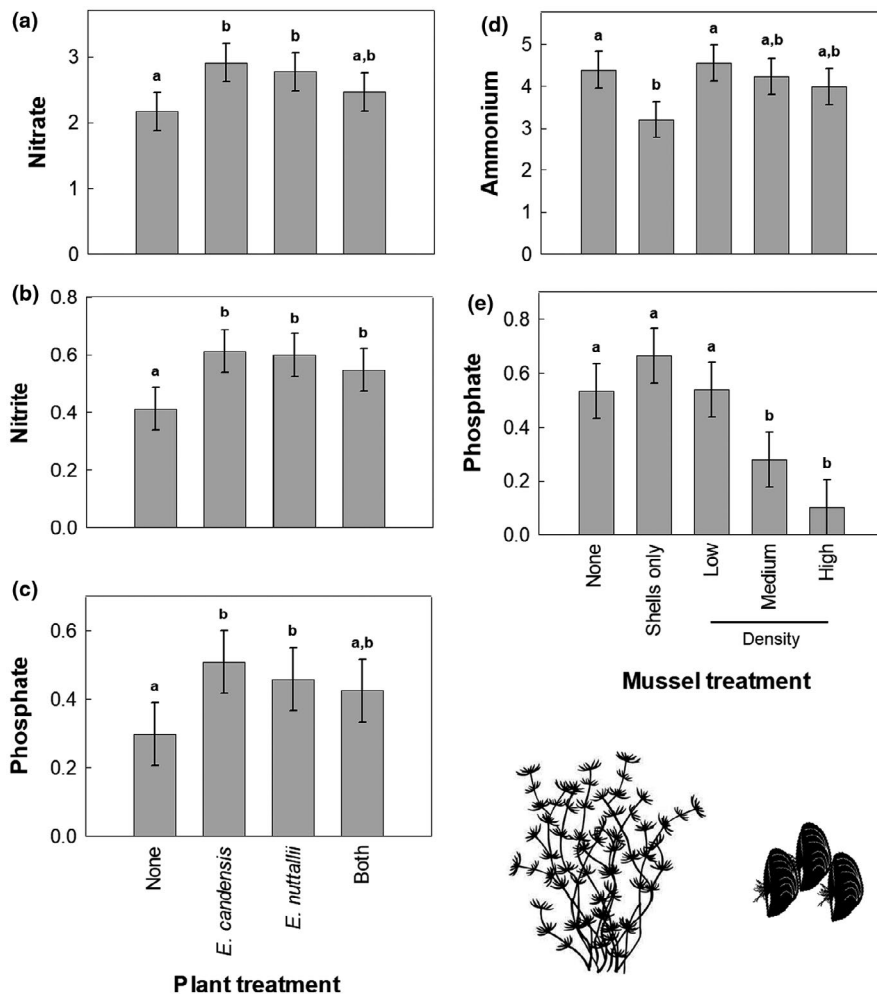
**TABLE 2** Two-way ANOVA fitting the effect of Plant and Mussel treatments and their interaction term for (a) nitrate, (b) nitrite, (c) ammonium, and (d) phosphate

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

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 probably reflects some die-off of phytoplankton inhabiting the water. However, baseline nutrient



**FIGURE 2** Significant effects highlighted from Table 2. Mean  $\pm$  95%CI ( $\mu\text{mol/L}$ ) 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 post hoc tests are shown above the bars; treatment with different letters were significantly different ( $p < 0.05$ ). Drawings not to scale

levels are within the average range documented for Lough Erne by the Northern Ireland Environment Agency over a 9-year survey (2006–2014, corresponding to mean values of 6.5, 1.1, 2.8, and 0.6  $\mu\text{mol/L}$  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; Bykova, Laursen, Bostan, Bautista, & McCarthy, 2006; Higgins, Grennan, & McCarthy, 2008; Higgins & Vander Zanden, 2010; Karatayev, Burlakova, & Padilla, 2002; MacIsaac, 1996; Nogaro & Steinman, 2014; Ricciardi, 2003; Ricciardi & MacIsaac, 2000). 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* are suggestive of a mutualistic relationship (K.C. personal observation), consistent with reports of colonisation of macrophytes by *D. polymorpha* (Bodamer & Ostrovsky, 2010; Horvath & Lamberti, 1997; MacIsaac, 1996). 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, Ricciardi, & Carlton, 2001). Although small fragmentary propagules of *Elodea* can produce new growth, fragments tend to not survive extended periods of air exposure, e.g. <3 hr at 20°C (Coughlan, Cuthbert, Kelly, & Jansen, 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 (DeVanna et al., 2011; Ricciardi, 2001). 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; Gardner, Yang, Cotner, Johengen, & Lavrentyev, 2001; Higgins et al., 2008; James, Barko, & Eakin, 1997; Lohner, Sigler, Mayer, & Balogh, 2007; Matthews & Effler, 2001). 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 utilise both nitrate and ammonium,

the nutrient of preference is ammonium (Ozimek, Donk, & Gulati, 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, Peeters, Várbíró, Borics, and Lukács (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 hypothesised 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. Montgomery et al., 2011; O'Dowd et al., 2003; Ricciardi, 2001). We expect such complex facilitative/antagonistic interactions to be common in ecosystems that are increasingly invaded.

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## AUTHOR CONTRIBUTIONS

K.C. and A.R. proposed the study; K.C. designed the experiment; K.C. conducted the experiment; K.C. and L.K. performed chemical analysis; K.C. and N.R. performed data analysis; all authors contributed to writing the manuscript, which was jointly led by K.C. and N.E.C., and gave final approval for publication.

## DATA AVAILABILITY STATEMENT

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

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