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

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27 Biotic resistance, facilitation, mutualism, biotic interactions, interspecific competition,
28 invasional meltdown

29 **Abstract**

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

53

54 **1. Introduction**

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

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

79 strategies (Simberloff 2006; Roy *et al.* 2014; Gallardo & Aldridge 2015; O’Loughlin & Green
80 2017). For example, there may be many instances where an invader can facilitate some resident
81 species while inhibiting others within the invaded community (Ricciardi 2001; Ward &
82 Ricciardi 2007, 2013; Relva *et al.* 2010; Montgomery *et al.* 2011), and such differential effects
83 could have significant impacts on the structure and functional ecology of the community
84 (O’Dowd *et al.* 2003; Green *et al.* 2011; Montgomery *et al.* 2011).

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

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

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

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

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

144 We thus used laboratory-based mesocosm experiments to examine the effect of interspecific
145 competition – and the role of *D. polymorpha* in mediating such competition – on the growth
146 rates of *E. canadensis* and *E. nuttallii*. As dead mussel shells adsorb phosphate (Xiong *et al.*
147 2011), the impact of non-living mussel shells on plant growth was also considered. We
148 therefore tested the effect of the presence of non-living zebra mussel shells and varied living
149 mussel densities on the growth rates of each *Elodea* species when grown alone (single species)
150 and together (both species experiencing interspecific competition). Based on field observations
151 and pilot studies (Crane, 2019), we hypothesised that: 1) *E. nuttallii* would have a higher
152 growth rate than *E. canadensis*; 2) interspecific competition will reduce growth rates of both

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

156

157 **2. Methods**

158 *2.1 Specimen collection*

159 *Elodea canadensis* was collected from Tully Mill Lough (54°15'32.1"N; 7°42'50.4"W) in
160 August 2017. *Elodea nuttallii* was collected from Lough Erne, Northern Ireland (54°18'12.1"N;
161 7°37'20.8"W) in August 2017. Lough Erne is a naturally eutrophic lake and its water chemistry
162 reflects the underlying geology of limestone and sandstone which gives rise to carbonate-rich,
163 slightly acidic waters. Strands of each species were cut just above the level of the roots and
164 were transported in source water to Queen's Marine Laboratory (QML), School of Biological
165 Sciences, Queen's University Belfast, Portaferry, Northern Ireland, UK. In addition, 80 L of
166 lake water was collected from Lough Erne at the same time. This water was later used for
167 mesocosm experiments.

168 *Dreissena polymorpha* was collected from Lough Erne, Northern Ireland (54°17'07.89"N
169 7°32'52.61"W) in August 2017. Mussels were detached from rocky substrates by clipping
170 byssal threads and transported in a cooler filled with source lake water. Only large adult
171 mussels with a shell length 24-30mm were selected and placed into an aerated 20-L tank for
172 48 hours.

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

177

178 2.2 *Experimental design*

179 Plant fragments were randomly selected from holding aquaria and apical fragments were cut
180 to a length of 60mm. Specimens were cut immediately below the final node 16 hours prior to
181 the start of the experiment and washed in dechlorinated tap water to remove any debris. In all
182 cases, apical fragments were harvested from mature plants. Where possible, fragments were
183 cut from unbranched sections of stem; however, if present, axillary side shoots were removed.
184 Excess liquid was gently removed by manually spinning individual fragments in a handheld
185 centrifuge (Westmark), ten times clockwise followed by ten spins counter-clockwise. Fragment
186 wet weight (mg) was recorded using a Mettler Toledo AB104. The base of each individual
187 fragment was protected using a small piece of cotton wool before being wrapped with a 60 ×
188 5mm lead weight to keep the base of the fragment at the bottom of the mesocosm and the apical
189 section positioned vertically.

190 Naturally occurring wild densities of *D. polymorpha* were estimated as living population
191 biomass (soft and hard tissues; wet weight g m⁻²) at ten locations in Lough Erne. For the
192 experimental treatments, three relative biomass categories were used: low (300g m⁻²), medium
193 (450g m⁻²) and high (600g m⁻²). Biomass estimates for *D. polymorpha* were similar to those
194 reported for *Dreissena* spp. inhabiting lakes in North America and Europe (Custer & Custer
195 1993; Cleven & Frenzel 1993; Karatayev *et al.* 2014; Ginn *et al.* 2017). In Lake Erie, for
196 example, the average biomass for mixed populations of *D. polymorpha* and a functionally
197 similar congener bivalve, the quagga mussel *D. rostriformis bugensis*, ranged from (mean ±
198 SE) 55.4 ± 11.8 to 588.8 ± 94.4 g m⁻² amongst different sites (Karatayev *et al.* 2014). However,
199 biomass is highly variable in relation to stage of invasion or age of population, and can be
200 impacted by changes to biotic and abiotic conditions (see Karatayev *et al.* 2014).

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

203 shells was then calculated from across all sites, and a representative biomass was selected (100g
204 m⁻²). Mesocosms (1.5L: high-density polyethene) had a surface area of 88 cm², thus mussel
205 treatments were scaled to replicate naturally occurring biomass i.e. zero mussels (representing
206 their absence), dead shells (0.88 g; an entire adult mussel 26.0 ± 1 mm, scraped clean), Low
207 (2.64g; 1 adult mussel 26.0 ± 1 mm), Medium (3.96g; 2 adult mussels 26.0 ± 1 mm) and High
208 (5.28g; 3 adult mussels 26.0 ± 1 mm) densities (Table 1). Mussels were placed directly on the
209 base of the mesocosms, but were free to reposition themselves within the mesocosm at all
210 times. Mesocosms did not contain any additional substrate.

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

228

229 2.3 Plant growth rates

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

231

$$232 \quad GR = \frac{(fWW - iWW)}{t}$$

233

Equation 1

234

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

236

237 2.4 Water chemistry parameters

238 Dissolved oxygen (mg L^{-1}), pH (pH Units), Total Dissolved Solids (mg L^{-1}), temperature ($^{\circ}\text{C}$)

239 and Conductivity ($\mu\text{S cm}^{-1}$) were recorded before and after every water change using a YSI

240 556 MPS multi-parameter field meter. Water samples were taken from the source water prior

241 to every water change, and from each mesocosm at the end of each 3-day water cycle. These

242 samples were tested for nitrate ($\mu\text{mol L}^{-1}$), nitrite ($\mu\text{mol L}^{-1}$), ammonium ($\mu\text{mol L}^{-1}$) and

243 phosphate ($\mu\text{mol L}^{-1}$) using a Bran+Luebbe AutoAnalyser 3. Samples were taken by syringe

244 with each syringe rinsed with 18Ω high purity water twice between samples to avoid

245 contamination. A total of four water replacements were carried out throughout the course of

246 the experiment.

247 For each mesocosm, nutrient change was established in relation to the difference in nutrient

248 concentrations between both the immediate beginning and end of each 3-day water cycle. In

249 all cases, due to inherent minor fluctuations of probe readings, a mean value of five consecutive

250 measurements was obtained from each mesocosm for every sampling point. Overall nutrient

251 flux throughout the lifetime of the experiment was determined as the mean of nutrient changes

252 across all 3-day water cycles. Overall, initial nutrient concentrations of the lake water used to

253 replenish each mesocosm every three days were (mean \pm SE): phosphate, 1.2 ± 0.1 ; nitrate, 5.3
254 ± 0.5 ; nitrite, 1.0 ± 0.1 ; ammonium, 5.2 ± 0.4 ($\mu\text{mol L}^{-1}$).

255

256 2.5 Statistical Analyses

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

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

276

277

278 3. Results

279 In the absence of *D. polymorpha*, the growth rates of *E. canadensis* (mean \pm SE: 0.012 ± 0.003
280 wet g day⁻¹) and *E. nuttallii* (0.011 ± 0.001 wet g day⁻¹) did not differ when grown in
281 monocultures ($t_{df=10} = 0.378$, $p=0.714$; Fig. 1a). Further, *E. canadensis* growth was not reduced
282 in the presence of *E. nuttallii* (Fig. 1b), and *vice versa* (Fig. 1c). In the presence of non-living
283 mussel shells, monoculture growth of *E. canadensis* was significantly reduced ($t_{df=10} = 2.227$,
284 $p=0.050$; Fig. 1d), whereas that of *E. nuttallii* was unaffected (Fig. 1e). When grown together
285 in the presence of mussel shells, growth rates of both plants did not differ (Fig. 1b & 1c).

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

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

303 effect that negated growth inhibition caused by interspecific competition on *E. nuttallii* (Fig.
304 1m).

305 Water chemistry parameters remained consistent throughout the experiment with mean \pm
306 SE values for dissolved oxygen 13.2 ± 0.32 mg L⁻¹, pH 7.35 ± 0.01 , Total Dissolved Solids
307 0.15 ± 0.003 mg L⁻¹, temperature 12.4 ± 0.02 °C and Conductivity 175.1 ± 0.3 μ S cm⁻¹. Nitrate,
308 nitrite and phosphate values differed significantly between plant treatments (Table 2), and were
309 elevated in the presence of *Elodea* (Fig. 2a-c). Ammonium and phosphate also differed
310 significantly between mussel treatments (Table 2). Ammonium was depressed in the presence
311 of dead mussel shells only (Fig. 2d), whilst phosphate was depressed only at medium and high
312 mussel densities (Fig. 2e). There was no significant interaction between Plant*Mussel
313 treatments on any water chemistry parameters (Table 2).

314

315 **4. Discussion**

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

328 levels are within the average range documented for Lough Erne by the Northern Ireland
329 Environment Agency over a nine-year survey (2006–2014, corresponding to mean values of
330 6.5, 1.1, 2.8 and 0.6 $\mu\text{mol L}^{-1}$ for nitrate, nitrite, ammonium and phosphate respectively (Crane
331 2019).

332 Previous experiments have compared the growth rates of *E. canadensis* and *E. nuttallii* in
333 monoculture and sympatry (e.g. Barrat-Segretain & Arnaud 2004). Equally, the ability of *D.*
334 *polymorpha* to engineer the invaded environment has been shown by several studies (Arnott &
335 Vanni 1996; MacIsaac 1996; Ricciardi & MacIsaac 2000; Karatayev *et al.* 2002; Ricciardi
336 2003; Bykova *et al.* 2006; Higgins *et al.* 2008; Higgins & Vander Zanden 2010; Nogaro &
337 Steinman, 2014). However, this study is the first to demonstrate the potential for competitive
338 and facilitative interactions among these three invaders. Not only does the presence of *D.*
339 *polymorpha* facilitate the growth rate of *E. nuttallii*, but it also reduced competition between
340 *E. canadensis* and *E. nuttallii*. Moreover, field observations of juvenile *D. polymorpha* attached
341 to *E. nuttallii* is suggestive of a mutualistic relationship (KC *pers. obs.*), consistent with reports
342 of colonization of macrophytes by *D. polymorpha* (MacIsaac 1996; Horvath & Lamberti 1997;
343 Bodamer & Ostrovsky 2010). Mussels attached to drifting *E. nuttallii* could also benefit from
344 local dispersal (cf. Horvath & Lamberti 1997) or be transported overland attached to
345 macrophytes snagged on recreational boat trailers (Johnson *et al.* 2001). Although small
346 fragmentary propagules of *Elodea* can produce new growth, fragments tend to not to survive
347 extended periods of air exposure, e.g. < 3 hours at 20°C (Coughlan *et al.* 2018). Nevertheless,
348 rapid spread and establishment of *E. nuttallii* continues to have detrimental knock-on effects
349 on native biota, especially plants, invertebrates and algal periphyton (Kelly *et al.* 2015).
350 Overall, our results corroborate the role of *D. polymorpha* as an ecological engineer, with broad
351 influence on community dynamics and an ability to mediate interactions among invasive
352 species (Ricciardi 2001; DeVanna *et al.* 2011). Our results also highlight the need for improved

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

355 *Dreissena polymorpha* can enhance nutrient cycling through excretion and, on a lake-wide
356 basis, large populations can: 1) excrete significant concentrations of ammonia, nitrate and
357 dissolved phosphorus; 2) reduce concentrations of suspended seston, chlorophyll a,
358 phytoplankton and total phosphorus; 3) alter the structure and metabolic function of the benthic
359 bacterial community; and 4) increase water transparency (Gardner *et al.* 1995; James *et al.*
360 1997; Gardner *et al.* 2001; Matthews & Effler 2001; Lohner *et al.* 2007; Higgins *et al.* 2008).
361 A significant effect of zebra mussel metabolism is their ability to convert particulate forms of
362 nutrients into dissolved, available forms (Arnott & Vanni 1996). Although not statistically
363 evident, our results suggest a trend of greater ammonium depletion by higher mussel densities
364 when *Elodea* was present, and while *Elodea* can utilize both nitrate and ammonium the nutrient
365 of preference is ammonium (Ozimek *et al.* 1993). No significant depletion of nitrate or nitrite
366 was observed during the experimental period when plants were present. However,
367 interestingly, increasing density of living *D. polymorpha* was associated with declining
368 phosphate concentrations. Although dead mussel shells adsorb phosphate (Xiong *et al.* 2011),
369 this was demonstrably not the case in the present study. While nutrients were unlikely to be
370 limiting, our results suggest that differences in growth rate could be attributed to plant
371 competition or the presence of *D. polymorpha*, and that further work is required to specifically
372 test the role of how both *Elodea* species nutrients excreted by *Dreissena* and why phosphate
373 levels declined with increasing mussel biomass.

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

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

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

398

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408

409 **6. Author contributions**

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

414

415 **7. Data Accessibility**

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

417

418 **8. References**

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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	300	1	2.64
Medium	450	2	3.96
High	600	3	5.28

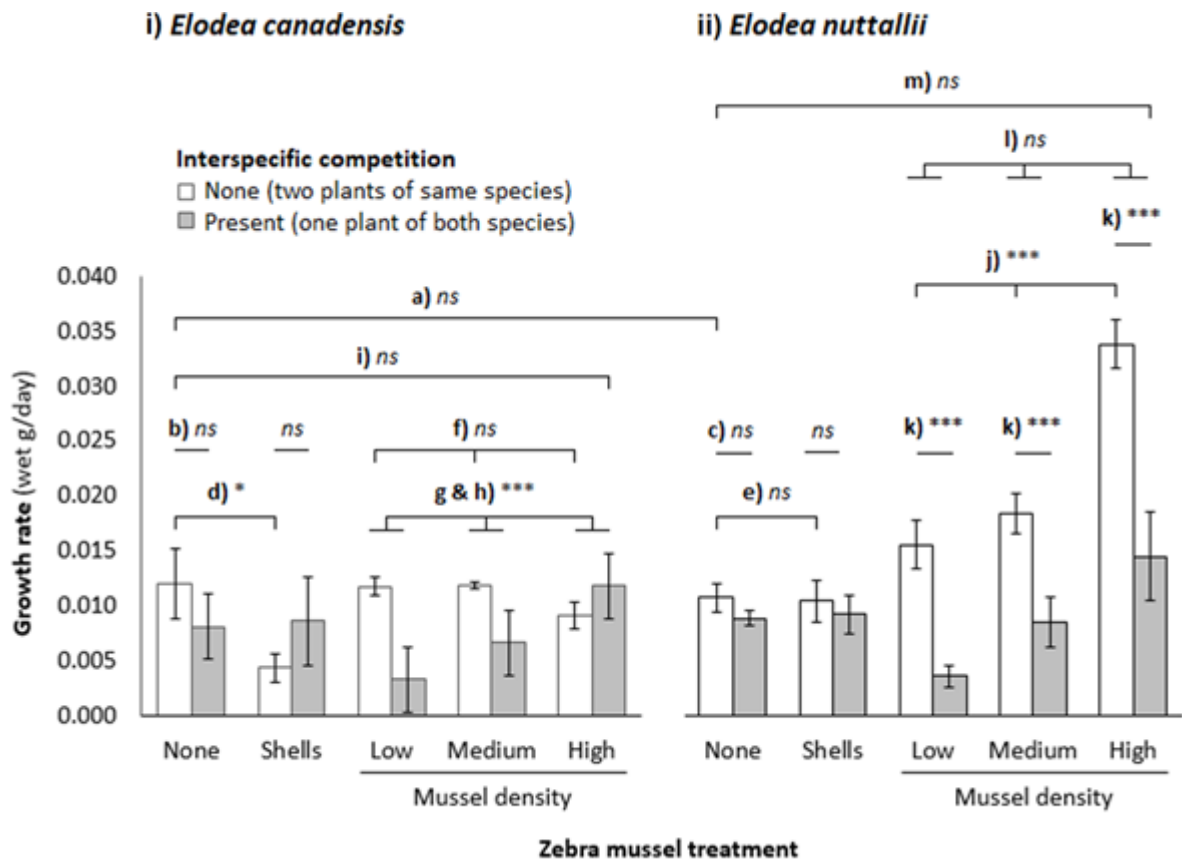


Fig. 1 Mean (\pm SE) comparative growth rates (wet g.day⁻¹) for **i) *Elodea canadensis*** (left panel) and **ii) *Elodea nuttallii*** (right panel) with (grey bars) and without (white bars) the presence of interspecific competition (paired bars) in each zebra mussel, *Dreissena polymorpha*, treatment 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	F	n.df.	d.df.	p
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

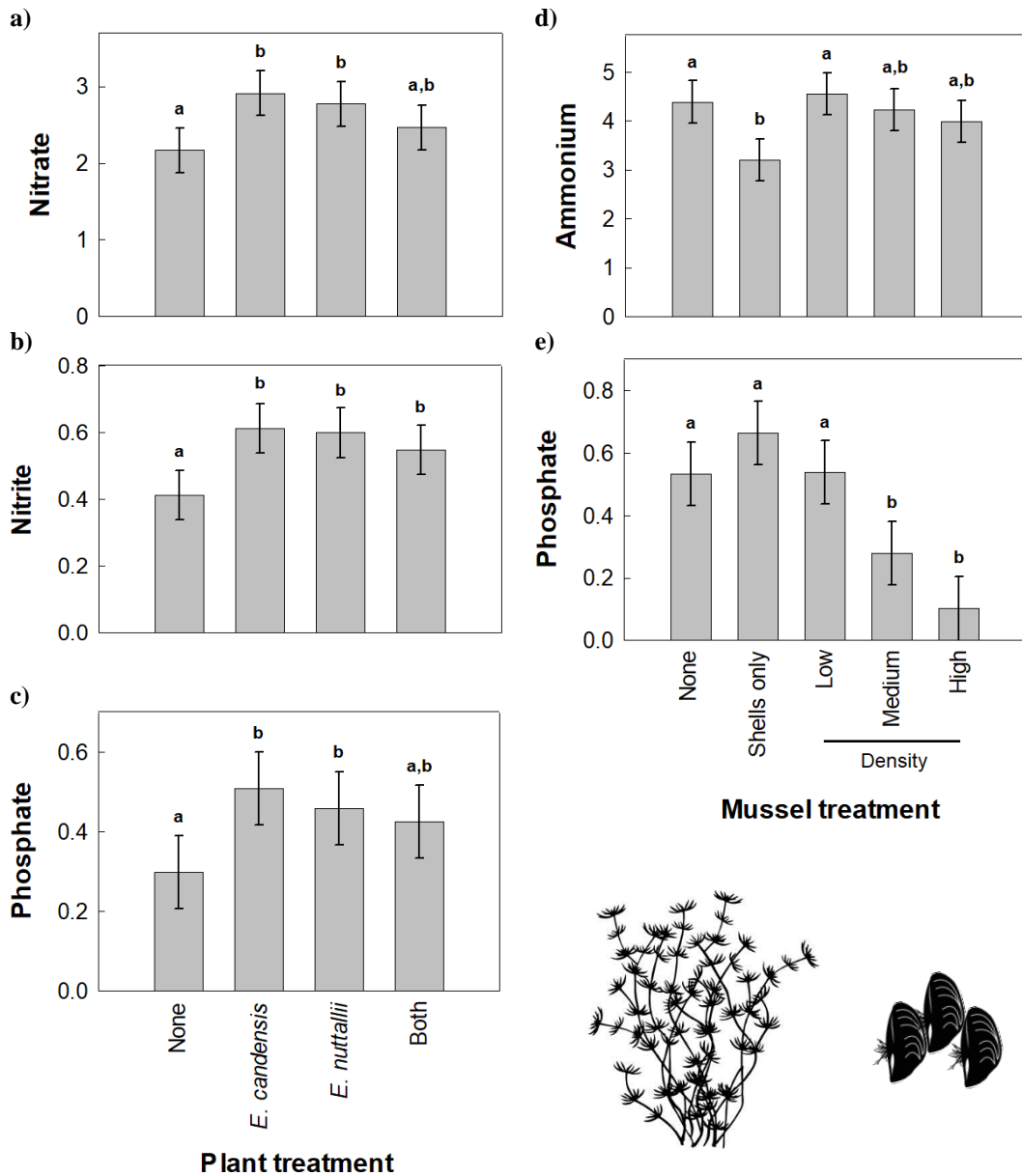


Fig. 2 Significant effects highlighted from Table 2. Mean \pm 95% CIs ($\mu\text{mol L}^{-1}$) for **a)** nitrate, **b)** nitrite and **c)** phosphate showing the effect of plant treatments (right column) and **d)** ammonium and **e)** phosphate showing the effect of mussel treatments (left column). 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.