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4 **Population density modifies the ecological impacts of invasive species**

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23 **Abstract**

24 In assessments of ecological impact in invasion ecology, most studies compare un-invaded
25 sites with highly invaded sites, representing the ‘worst-case scenario’, and so there is little
26 information on how impact is modified by the population density of the invader. Here, we assess
27 how ecological impact is modified by population density through the experimental development
28 of density-impact curves for a model invasive fish. Using replicated mesocosms and the highly
29 invasive *Pseudorasbora parva* as the model, we quantified how their population density
30 influenced their diet composition and their impacts on invertebrate communities and ecosystem
31 processes. The density-impact curves revealed both linear and non-linear density-impact
32 relationships. The relationship between *P. parva* density and zooplankton body mass was
33 represented by a low-threshold curve, where their impact was higher at low densities than
34 predicted by a linear relationship. In contrast, whilst the relationship between density and
35 zooplankton biomass and abundance was also non-linear, it was high-threshold, indicating a
36 lower impact than a linear relationship would predict. Impacts on diversity and phytoplankton
37 standing stock were linear and impacts on benthic invertebrate abundance and decomposition
38 rates were represented by s-shaped curves. These relationships were underpinned by *P. parva*
39 dietary analyses that revealed increasing reliance on zooplankton as density increased due to
40 depletion of other resources. We caution against the common assumption that ecological impact
41 increases linearly with invader density and suggest that increased understanding of the
42 relationship between invader population density and ecological impact can avoid under-
43 investment in the management of invaders that cause severe problems at low densities.

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45

46 **Introduction**

47 Biological invasions have substantial adverse economic and environmental consequences
48 worldwide (Pejchar and Mooney 2009; Pyšek and Richardson 2010; Vilá et al. 2011) and,
49 therefore, research on their management receives considerable attention (e.g. Epanchin-Niell and
50 Hastings 2010; Britton et al. 2011a; Januchowski-Hartley et al. 2011; Larson et al. 2011).
51 Invasive species have been associated with declines in biodiversity and negative effects on
52 ecosystem processes (e.g. Elgersma and Ehrenfeld 2011; Jackson et al. 2014). The impact of
53 invaders, however, varies considerably among species and habitats, and is often context
54 dependent (Larson et al. 2011; Kumschick et al. 2012).

55 It is commonly assumed that the effect of invasion increases proportionally as invader
56 abundance increases (Yokomizo et al. 2009; Elgersma and Ehrenfeld 2011). However, impact
57 studies tend to compare scenarios of high invader density (i.e. representing the ‘worst case
58 scenario’) with those where the invader is absent. Consequently, there is little evidence to
59 support this assumption, despite the fact that the abundance of a species can vary considerably
60 across its invasive range (Hansen et al. 2013). Evidence suggests that ecological impacts can
61 vary across invasion densities in a non-linear manner (Elgersma and Ehrenfeld 2011), with a
62 recent study revealing that the impact of the ponto-caspian goby *Neogobius melanostomus*
63 declines at higher densities due to increased intraspecific interactions (Kornis et al. 2014).

64 A limited number of studies have examined the density-dependent ecological impacts of
65 invasive species and they detected both linear and non-linear relationships between population
66 density and ecological impact (e.g. Li et al. 2007; Kulhanek et al. 2011; Thomsen et al. 2011
67 Green and Crowe 2014; Kornis et al. 2014; Wilkie et al. 2014). For example, Elgersma and

68 Ehrenfeld (2011) found that the cascading impacts of an invasive shrub (Japanese barberry,
69 *Berberis thunbergii*) were linear on decomposition rates but non-linear on microbial community
70 structure. Whilst animal invasions are generally less well studied when compared to plant
71 invasions, especially in aquatic environments (Lowry et al. 2013), evidence suggests that
72 invasive animals often have cascading impacts on lower trophic levels in lakes and rivers (e.g.
73 Baxter et al. 2004; Ellis et al. 2011), with invasive fish altering primary productivity and
74 decomposition rates (Zavaleta et al. 2001; Simon and Townsend 2003; Baxter et al. 2004).
75 However, we are unaware of any studies that have examined how the population density of an
76 invasive fish alters these cascading effects. Freshwater biodiversity is often considered
77 proportionally the most at risk to environmental change on a global scale (Jenkins 2003) and,
78 therefore, it is of paramount importance to deepen our understanding of relationships between
79 aquatic invader densities and impacts. The population density of aquatic invasive animals is
80 important in shaping not only their direct ecological impacts through their trophic links and
81 competitive interactions, but also their indirect impacts by influencing the strength of trophic
82 cascades. The strength of trophic cascades may be modified through influencing prey grazing
83 pressure (Baum and Worm 2009), intraspecific competition and invader diet (Svanbäck and
84 Bolnick 2007), or the feeding behaviour of the prey (Figueredo and Giani 2005).

85 Density-impact curves describe the relationship between the population density of an
86 invader and its economic or ecological impact. Recently, they have been recognised as a valuable
87 tool in the impact-assessment and management of invaders (Yokomizo et al. 2009), but they
88 have rarely been applied. Yokomizo et al. (2009) described four potential relationships,
89 including the linear relationship (Fig. 1) that is generally assumed by managers when data
90 relating density and impact are absent. The occurrences of low-threshold and high-threshold

91 curves are particularly important as they indicate that impact is either more or less severe than
92 predicted by the linear relationship, respectively (Fig. 1). Finally, s-shaped curves occur when
93 impact is more or less severe than predicted at low or high invasion densities and vice versa (e.g.
94 Fig. 1; Yokomizo et al. 2009). Here, we adopt the approach of Yokomizo et al. (2009) with
95 application to the ecological impact of an invasive fish. The shape of density-impact curves can
96 depict which invaders have acute impacts at low densities and those whose populations have
97 little ecological consequences other than at their highest population densities.

98 To develop the density-impact curves in this study, we use a mesocosm experiment to
99 examine the density-dependent impacts of a model invasive fish. Although mesocosm
100 experiments might lack the ‘realism’ of natural experiments or observations, they provide
101 controlled environments where mechanistic relationships can be more easily quantified and
102 scaled-up to represent larger-scale processes (Spivak et al. 2011). Further, mesocosm
103 experiments have proved useful in numerous ecological impact studies on climate change
104 (Stewart et al. 2013) and invasive species (e.g. Rudnick and Resh 2005; Ho et al. 2011; Jackson
105 et al. 2014). The model species was the Southeast Asian fish topmouth gudgeon *Pseudorasbora*
106 *parva* which is now present across much of Europe (Gozlan et al. 2010a). While studies have
107 determined factors influencing their invasion success (Copp et al. 2007; Britton and Gozlan
108 2013; Jackson et al. 2013) and interactions with native fish (e.g. Beyer et al. 2007; Jackson and
109 Britton 2013), their density dependent impacts are unknown. Our objectives were to (1)
110 experimentally determine how *P. parva* population density modified (i) their diet composition,
111 (ii) invertebrate community structure, and (iii) ecosystem processes; and (2) develop ecological
112 relevant density-impact curves for the invasive fish. We hypothesise that the impact of the

113 invader will increase linearly with population density, causing a shift in diet as preferred
114 resources become depleted.

115

116 **Materials and methods**

117 In their native range, *P. parva* are present in both lentic and lotic systems. However, in
118 much of their invasive range in Europe, their highest abundances tend to occur in relatively small
119 lentic systems, with rivers used primarily for natural dispersal into waters downstream on the
120 floodplain (Gozlan et al. 2010a). To represent these small lentic habitats, we used replicated
121 outdoor pond mesocosms which were away from tree cover, located in Southern England, of
122 1000 L volume and 1.0 m⁻² surface area. We chose to quantify *P. parva* impact in mesocosms as
123 their relatively simple ecosystems enable accurate inferences to be drawn on impact without the
124 additional complexity of including a broad range of native species that could represent
125 experimental confounds. The experiment comprised four treatments; low, medium and high
126 densities of *P. parva* (8, 24 and 48 individuals, respectively), and an un-invaded control. These
127 fish numbers provided population densities within the range encountered in their invasive
128 populations in Europe, including England where densities have been recorded to 65 m⁻², levels
129 far in excess of native fishes (Britton et al. 2008, Britton et al. 2010b, Jackson and Britton 2013).
130 Treatments were randomly assigned to mesocosms, all fish were female to avoid reproduction
131 and maintain population density, and were of 48 to 68 mm starting fork length. Although *P.*
132 *parva* may invade systems with other fish present, it was necessary for our study to use single
133 populations in order to isolate their impacts and create density-impact curves.

134 The experiment commenced in July 2012 and ran for 120 days. We established the
135 mesocosms 10 days prior to fish introduction with filling of water from an adjacent fishless pond

136 with a zooplankton community dominated by copepods; 1000 L was added to each mesocosm to
137 ensure that the zooplankton community was equally represented in each mesocosm. Each
138 mesocosm was provided with clean gravel substrates, fish refuge (a 30cm length of 65 mm
139 diameter drain pipe), a pond lily (*Nymphoides peltata*) and were seeded with equal aliquots of
140 chironomid larvae and *Asellus aquaticus*. These species were chosen as: (i) they would mimic a
141 simple pond food web commonly invaded by *P. parva*; (ii) Chironomid larvae, copepod species
142 and *N. peltata* are commonly encountered in their invasive and native range: and (iii) *A.*
143 *aquaticus* are encountered regularly in their diet in their invasive range (e.g. Rosecchi et al.
144 1993; Declerck et al. 2002). To quantify leaf litter breakdown rates, we attached a plastic mesh
145 bag (5mm mesh size) containing a known mass (~1.5g) of dry leaf litter from a native tree
146 (*Fagus sylvatica*) to the benthos of each mesocosm. The leaf litter decomposition rates were
147 determined using their exponential decay rate coefficient (k ; see Heiber and Gessner 2002) and
148 calculated using the start and end dry weights of the packs.

149 At the end of the experimental period, we recaptured the *P. parva*, with an overall
150 recapture rate of 86 %. All fish were over-anaesthetised (MS-222) before a dorsal muscle sample
151 was taken from a maximum of eight fish ($n = 3-8$) from each mesocosm for carbon and nitrogen
152 stable isotope analyses to determine diet composition. We also collected putative fish-food
153 resources (algae, benthic invertebrates and zooplankton; $n = 3-9$ of each) from each mesocosm
154 for stable isotope analyses. All samples were oven dried overnight at 60°C before analysis at the
155 Cornell Isotope Laboratory, New York, USA. The data outputs were in the format of delta (δ)
156 isotope ratios expressed per mille (‰) and were used to calculate the fish standard ellipse areas
157 (SEA_c; Jackson et al. 2012) using the *siar* (Jackson et al. 2011) package in R (R Core Team

158 2013). These provide a bivariate estimate of a population's core isotopic niche and the subscript
159 'c' indicates that a small sample size correction was applied (Jackson et al. 2011).

160 On the final day of the experiment, we sieved 2L of water from each mesocosm through a
161 250µm sieve. Zooplankton densities and body sizes were determined using microscopy of the
162 sieved water, with all individuals identified and counted to obtain abundance and diversity
163 (Shannon's diversity index) estimates. Body mass estimates were derived using image analysis
164 software (KLONK Image Measurement) where up to 20 randomly selected individuals per
165 species were measured and their mass derived using length-weight regression equations (Bottrell
166 et al. 1976). The total body-mass of all measured individuals of each species were used to
167 estimate total zooplankton biomass. For the size spectra analysis, body mass is expressed in units
168 of carbon (µg, C; assuming 40% of total weight is C; Reiss and Schmid-Araya 2008). To
169 estimate macro-invertebrate abundance, we counted the number of Chironomids and *A.*
170 *aquaticus* in each leaf litter bag as a standard measure.

171 As a proxy for primary productivity, we measured phytoplankton standing stock on the
172 final day of the experiment by filtering a 0.5L water sample from each mesocosm through GF/C
173 filters (Whatman[®], Maidstone, UK) before adding 5ml of 90% acetone. After 24 hours the
174 samples were centrifuged and the supernatant was used for spectrophotometry to determine
175 chlorophyll-*a* concentration (see Jeffrey and Humphrey 1975; values expressed as mg ml⁻¹).

176 Data were $\log_{10}(x+1)$ transformed to meet the assumptions of parametric tests. We used
177 analysis of variance to test for differences between treatments in all variables. When using
178 multiple response variables per mesocosm (e.g. isotope data), mesocosm identity was included as

179 a random factor, nested within treatment. If between-treatment effects were significant, post-hoc
180 tests were performed (Tukey's HSD).

181 To develop the density-impact curves we related each transformed replicate response
182 variable to invasive fish density using linear and non-linear (quadratic and cubic) models in the
183 'R' computing program (R Core Team 2013). Akaike's Information Criterion (corrected for
184 small sample sizes; AIC_c) was used to select the model that best fit the data. The best fit model
185 was then plotted as the density-impact curve for each response variable.

186

187 **Results**

188 *Invasive fish diet composition*

189 With increased population density, there was a significant dietary shift to resources with
190 lower carbon isotope values ($F_{2,68} = 27.39$, $P < 0.001$; Fig. 2; cf. Supplementary Material
191 Appendix 1). Since zooplankton had the lowest carbon signatures of the food resources, this
192 suggests an increased reliance on this resource with increased density (Fig. 2). At low densities,
193 *P. parva* isotope values were more closely associated with benthic invertebrates and algae (Fig.
194 2). There were no significant differences between the treatments in fish $\delta^{15}N$ ($F_{2,68} = 0.78$, $P =$
195 0.48) or trophic niche width (SEA_c ; $F_{2,9} = 0.07$, $P = 0.93$).

196 *Direct impacts*

197 Overall, 2260 individual zooplankton were identified and 537 measured. Body mass
198 ranged from 0.006 to 4.08 μg C in the un-invaded control compared to a reduced range of 1.48 to
199 3.70 in the high density treatments. Average zooplankton body mass was significantly higher in
200 the medium and high density mesocosms compared to the control and low density mesocosms

201 ($F_{3,531}=14.02$, $P<0.001$; Fig. 3A). The relationship between invasive population density and
202 zooplankton body mass was represented by a low threshold curve (Fig. 4A; Table 1).

203 Zooplankton diversity was significantly reduced at medium and high invasion densities
204 compared to the un-invaded control and, for the latter, compared to the low density invasion
205 scenario ($F_{3,12} = 7.05$, $P = 0.005$; Fig. 3B). The relationship between invasive population density
206 and zooplankton diversity was linear (Fig. 4B; Table 1). Zooplankton abundance and biomass
207 were reduced at high invasion densities compared to all other treatments (abundance: $F_{3,12} =$
208 11.98 , $P = 0.001$; biomass: $F_{3,12} = 11.55$, $P = 0.001$; Fig 3C, 3D). The relationships between
209 invasive population density and zooplankton abundance and biomass were high threshold (Fig.
210 4C, 4D; Table 1).

211 Benthic macro-invertebrate abundance was significantly higher in the low density
212 mesocosms compared to the medium and high invasion density mesocosms ($F_{3,12} = 17.83$, $P <$
213 0.001 ; Fig. 3E). The relationship between invasive population density and macro-invertebrate
214 abundance was represented by an s-shaped curve (Fig. 4E; Table 1).

215 *Indirect impacts*

216 Water chlorophyll-a concentrations, used as a measure of phytoplankton standing stock,
217 were significantly higher in the high density treatment when compared to the low density
218 treatment ($F_{3,12} = 11.89$, $P = 0.001$; Fig. 3F). The relationship between invasive population
219 density and phytoplankton standing stock was linear (Fig. 4F; Table 1). Leaf litter decomposition
220 rates were significantly higher in the low density treatment compared to the high and medium
221 density treatments ($F_{2,9} = 5.26$, $P = 0.03$; Fig. 3G). The relationship between invasive population
222 density and decomposition rates was represented by an s-shaped curve (Fig. 4G; Table 1).

223

224 **Discussion**

225 The ecological impacts of invasive species are complex and context-dependent (Thomson
226 et al. 2011; Wilkie et al. 2014). Our study adds to a growing body of evidence that impact does
227 not always increase proportionally with invader density (Thiele et al. 2010; Elgersma and
228 Ehrenfeld 2011) and in the case of Staska et al. (2014), the relationship was counter-intuitive,
229 with decreased impact at high density. In addition, our study illustrates that density-impact
230 relationships are response-dependent, as each of the four response types described by Yokomizo
231 et al. (2009) were identified for impacts caused by a single invasive species. This variation
232 between different variables highlights the complexity of predicting the ecological consequences
233 of biological invasions. Our data suggest that assuming linear density-impact relationships is
234 likely to result in poorly directed management efforts that lack prioritisation according to
235 realised, rather than perceived, impact (Yokomizo et al. 2009).

236 In contrast to the un-invaded control and low density populations, the medium and high
237 invasive *P. parva* populations depleted the benthic invertebrate and zooplankton communities,
238 resulting in two trophic cascades. Phytoplankton standing stock increased due to reduced grazing
239 pressure and decomposition rates decreased due to a decline in shredding invertebrates. In
240 contrast, low density invasive populations caused no statistically distinguishable impacts
241 compared to the control. Similarly, evidence suggests that *P. parva* only have a detectable
242 impact on native fish when present in high invasion densities (Britton et al. 2010b). However,
243 this is independent of the negative consequences for the native fish caused by the rosette agent
244 *Sphaerothecum destruens* for which *P. parva* is a healthy host (Andreou et al. 2012). In contrast,
245 Kornis et al. (2014) found that the impact of the invasive round goby (*Neogobius melanostomus*)
246 diminished at higher densities and attributed this to increased intraspecific interactions.

247 Nevertheless, where *S. destruens* is either not present or is assessed as causing negligible
248 consequences, direct management intervention on *P. parva* may only be necessary when they are
249 present at high densities when there are measurable impacts on ecosystem functioning.
250 Cascading, indirect consequences for ecosystem functioning as a result of invasions are
251 sometimes considered to be more important from a management prospective than direct impacts
252 (Gozlan et al. 2010b) because they indicate that consequences of the invasion are spreading
253 throughout the food web (e.g. Baxter et al. 2004).

254 Invasive species management often relies on the principle that the effect of invasion
255 diminishes proportionally as abundance decreases (Yokomizo et al. 2009; Elgersma and
256 Ehrenfeld 2011). For some aspects of ecological impact, our data supports this assumption:
257 linear relationships were apparent between invasive fish density and zooplankton diversity and
258 phytoplankton standing stock. The linear increase in phytoplankton standing stock with
259 increasing fish density resulted from reduced grazing pressure caused by the truncated size
260 range, and reduced biomass, abundance and diversity of zooplankton. This trophic cascade is
261 already well documented in many native and invasive fish communities (e.g. Carpenter et al.
262 2001; Ellis et al. 2011). Native cyprinid fish are also managed on account of their ecological
263 impacts on plankton through biomanipulation (e.g. Mehner et al. 2002; Hansson et al. 1998;
264 Tátrai et al. 2009) and, therefore, density-impact curves for cyprinid fish might have resonance
265 beyond invasive ecology. Indeed, the finding that *P. parva* were invoking cascading impacts in
266 these mesocosm experiments is consistent with other mesocosm experiments that have shown
267 similar cascading impacts of native fish (e.g. Havens 1993; Vakkilainen et al. 2004). Vakkilainen
268 et al. (2004) found that native fish were more important in regulating zooplankton biomass, and
269 subsequent cascades to phytoplankton, than nutrients. Additionally, there have been documented

270 cases of common carp (*Cyprinus caprio*; Khan et al. 2003), rainbow trout (*Oncorhynchus*
271 *mykiss*; Buria et al. 2010) and largemouth bass (*Micropterus salmoides*; Carpenter et al. 1987),
272 all of which are invasive in parts of the world, causing similar cascading impacts to *P. parva* on
273 phytoplankton or periphyton. However, a major difference between *P. parva* and native cyprinid
274 fishes, in England at least, is the ability of *P. parva* to form very high population densities,
275 sometimes even higher than those used in our high density treatment, and far in excess of those
276 recorded naturally in native species such as roach (*Rutilus rutilus*; Britton et al. 2010b).
277 Consequently, whilst the densities used in our experiment were applicable to *P. parva*, and most
278 likely to other small, invasive fishes that can form similar population densities (Pinder and
279 Gozlan 2003), they will be less relevant to native fishes.

280 Limited budgets mean that eradication is an unattainable goal to many managers dealing
281 with invasive animals and instead, controlling abundance at relatively low densities is a common
282 and cost-effective strategy (Simberloff 2009). Nonetheless, adopting this method when the
283 density-impact relationship is non-linear may cause wasted management effort or avoidable
284 impact (Yokomizo et al. 2009). Non-linear density-impact curves indicate that ecological impact
285 is not directly proportional to invasion density and instead, the relationship between the two is
286 context dependent, varying over the density gradient (Elgersma and Ehrenfeld 2011).

287 Zooplankton body-size, abundance and biomass all had non-linear relationships with invader
288 density. Similarly, non-linear relationships between impact and invasion density have been
289 documented for locusts (*Robinia pseudoacacia*; Staska et al. 2014) and shrubs (Japanese
290 barberry, *Berberis thunbergii*; Elgersma and Ehrenfeld 2011).

291 The mean body size of zooplankton increased as fish density increased, resulting from the
292 loss of smaller cladoceran species. Whilst this was presumably as a result of preferential *P.*

293 *parva* predation, it is a counter-intuitive outcome given that a general increase in prey size is
294 usually observed with increased *P. parva* body length (Gozlan et al. 2010a). Although
295 speculative, this might relate to aspects of the biology of the larger zooplankton species to avoid
296 predation, such as their morphology deterring *P. parva* predation, as observed in juvenile bluegill
297 (*Lepomis macrochirus*) and some Daphnid species (Kolar and Wahl 1998). Nevertheless, the
298 non-linear, low-threshold relationship between the density and zooplankton body size indicated
299 that body-size was larger at lower densities than a linear relationship predicted, suggesting that
300 even at low densities, *P. parva* invasions have acute implications for zooplankton size-structure.
301 Community size-structure has an important role in maintaining food web structure (Yvon-
302 Durocher et al. 2010) and ecosystem functioning (Dossena et al. 2012) and, therefore, the
303 invasive fish have the potential to instigate whole ecosystem changes at low densities.

304 Low-threshold curves represent severe ecological impacts since the effect is apparent at
305 low densities. In contrast, high-threshold curves, such as the relationship recorded between fish
306 density and zooplankton total biomass and abundance, represent relatively minor ecological
307 impacts as they only manifest at higher densities. This is also reflected in *P. parva* diet, since the
308 reliance on zooplankton was only evident at medium and high densities, causing a cascading
309 increase in phytoplankton. *Pseudorasbora parva* had lower carbon signatures at medium and
310 high densities when compared to fish from the low density populations, indicating a greater
311 reliance on zooplankton at higher densities due to the decline in other resources, including
312 benthic invertebrates. Indeed, the distinct difference in the isotopic niche of low density
313 populations reflects the less severe impact the invaders had on lower trophic levels and thus,
314 resource availability, in the mesocosms.

315 The relationships between invasion density and benthic macro-invertebrate abundance
316 and decomposition rates were both best represented by non-linear s-shaped curves. The presence
317 of the invader in low densities appears to promote invertebrate abundance compared to the
318 control (albeit not significantly), while medium and high invasion densities caused a
319 disproportionate decline in abundance compared to that predicted by a linear relationship. This
320 promotion of invertebrate abundance at low densities caused a cascading increase in
321 decomposition rates. We speculate that invertebrate abundance may be promoted at low densities
322 due to the advantage of increased nutrient input (from fish excretion; McIntyre et al. 2008)
323 outweighing the disadvantage of predation risk. In lakes where native fish are present in
324 sympatry with invasive *P. parva*, this effect may disappear because of additional predation by
325 the native species on invertebrates. It was, however, necessary to exclude native fish from our
326 study to isolate the impacts of *P. parva*. Interactions between *P. parva* and native fish may
327 influence their density-dependent impacts and therefore further work is required in this regard.
328 Despite this, our results suggest that density-impact relationships should be taken into account in
329 management strategies to control the cascading impacts of invasive animals on lower trophic
330 levels, especially since both non-linear and linear relationships were evident when examining the
331 impact of a single species.

332 We suggest that linear approximations of density- impacts are frequently inaccurate and
333 therefore caution against the common assumption that ecological impact increases linearly with
334 invader density. Indeed, growing evidence indicates that the density-impact relationships of
335 invasions are often non-linear (Yokomizo et al. 2009; Thiele et al. 2010; Elgersma and Ehrenfeld
336 2011; Staska et al. 2014), with five out of our seven measured response variables also being non-
337 linear. Although our mesocosms represent artificial experimental conditions, this study further

338 emphasises the value of understanding the impact of invasions across density gradients,
339 especially given that management efforts are often only targeted at high-density populations. We
340 suggest that the curves can be adopted for use within existing risk assessment and management
341 frameworks to assist management decision-making (e.g. Britton et al. 2011b).

342

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505 context. – TREE. 16: 454-459.

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510 **Tables**

511

512 **Table 1.** Best fit model selection for the relationship between invasion density and each
 513 ecological response variable. The best models were selected by the lowest AIC_c value
 514 (highlighted in italics).

515

Response	Model	AIC_c	df	R-sq (adj) ⁵¹⁶
Zooplankton Body Size	Linear	-34.22	1,15	0.49 ⁵¹⁷
	<i>Quadratic</i>	<i>-35.29</i>	<i>2,14</i>	<i>0.59</i>
	Cubic	-31.04	3,13	0.56
Zooplankton Diversity	<i>Linear</i>	<i>-13.26</i>	<i>1,15</i>	<i>0.57</i>
	Quadratic	-12.89	2,14	0.58
	Cubic	-11.37	3,13	0.55
Zooplankton Abundance	Linear	61.56	1,15	0.71
	<i>Quadratic</i>	<i>58.01</i>	<i>2,14</i>	<i>0.7</i>
	Cubic	58.71	3,13	0.68
Zooplankton Biomass	Linear	71.05	1,15	0.7
	<i>Quadratic</i>	<i>67.28</i>	<i>2,14</i>	<i>0.7</i>
	Cubic	67.95	3,13	0.68
Macro-invertebrate Abundance	Linear	43.5	1,15	0.7
	Quadratic	40.2	2,14	0.68
	<i>Cubic</i>	<i>37.73</i>	<i>3,13</i>	<i>0.75</i>
Chlorophyll-a Concentration	<i>Linear</i>	<i>35.53</i>	<i>1,15</i>	<i>0.33</i>
	Quadratic	36.67	2,14	0.34
	Cubic	40.24	3,13	0.78
Decomposition Rates	Linear	-149.22	1,15	-0.002
	Quadratic	-150.72	2,14	-0.07
	<i>Cubic</i>	<i>-156.37</i>	<i>3,13</i>	<i>0.21</i>

518 **Figure legends**

519

520 **Figure 1.** The potential relationships between invasive population density and ecological
521 impacts. Re-drawn from Yokomizo et al. (2009).

522 **Figure 2.** Isotopic bi-plot showing the standard ellipse area (core isotopic niche) for each
523 mesocosm population of *P. parva* at low (dashed), medium (dark grey) and high densities
524 (black). Filled ellipses show the core isotopic range of four resources across all treatments and
525 mesocosms.

526 **Figure 3.** Zooplankton body mass (A); zooplankton diversity (B); zooplankton abundance (C);
527 zooplankton biomass (D); benthic invertebrate abundance (E); pelagic chlorophyll-*a*
528 concentration (F) and decomposition (G) in each treatment (U: un-invaded; L: low density; M:
529 medium density; H: high density). The box plot shows the median, boxed by the interquartile
530 range, and the bar charts show mean \pm standard error. Treatments statistically indistinguishable
531 from one another are grouped by lower-cased letters.

532 **Figure 4.** The invasion impact of each response variable across the *P. parva* densities used in
533 each invaded treatment (8, 24 and 48 individuals). Zooplankton body mass (A); zooplankton
534 diversity (B); zooplankton abundance (C); zooplankton biomass (D); benthic invertebrate
535 abundance (E); pelagic chlorophyll-*a* concentration (F) and decomposition (G). All response
536 values are transformed ($\log_{10}(x+1)$). Solid lines show the best fit relationship and represent the
537 density-impact curve. Where the best fit was not linear, linear regressions are shown by the
538 dotted lines for comparison. Note in graphs B, C, D, E and G the y-axis is inverted to allow
539 comparison of curves across response variables.

540

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545 three reviewers whose comments have greatly improved the manuscript.

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548 **Appendices**

549 *Appendix 1: Data*

550 Table S1: Topmouth gudgeon isotope data

551 Table S2: Resource isotope data

552 Table S3: Zooplankton body size, abundance, biomass and richness

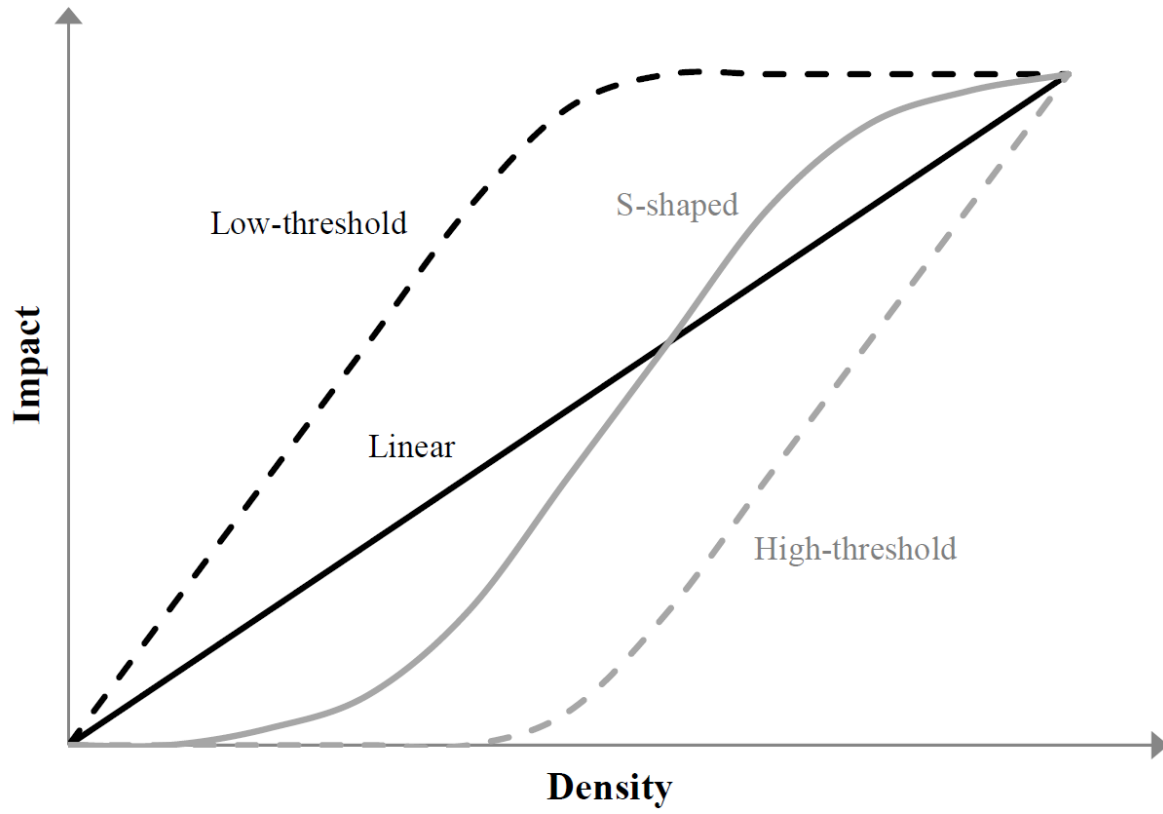
553 Table S4: Invertebrate abundance, phytoplankton standing stock and decomposition rates

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555 Fig 1

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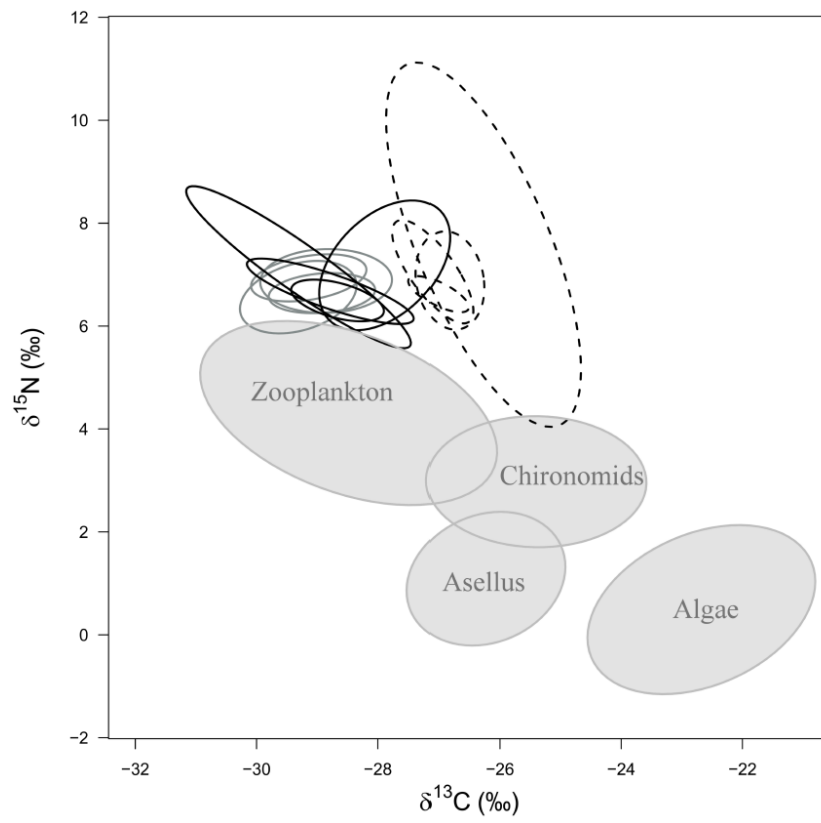


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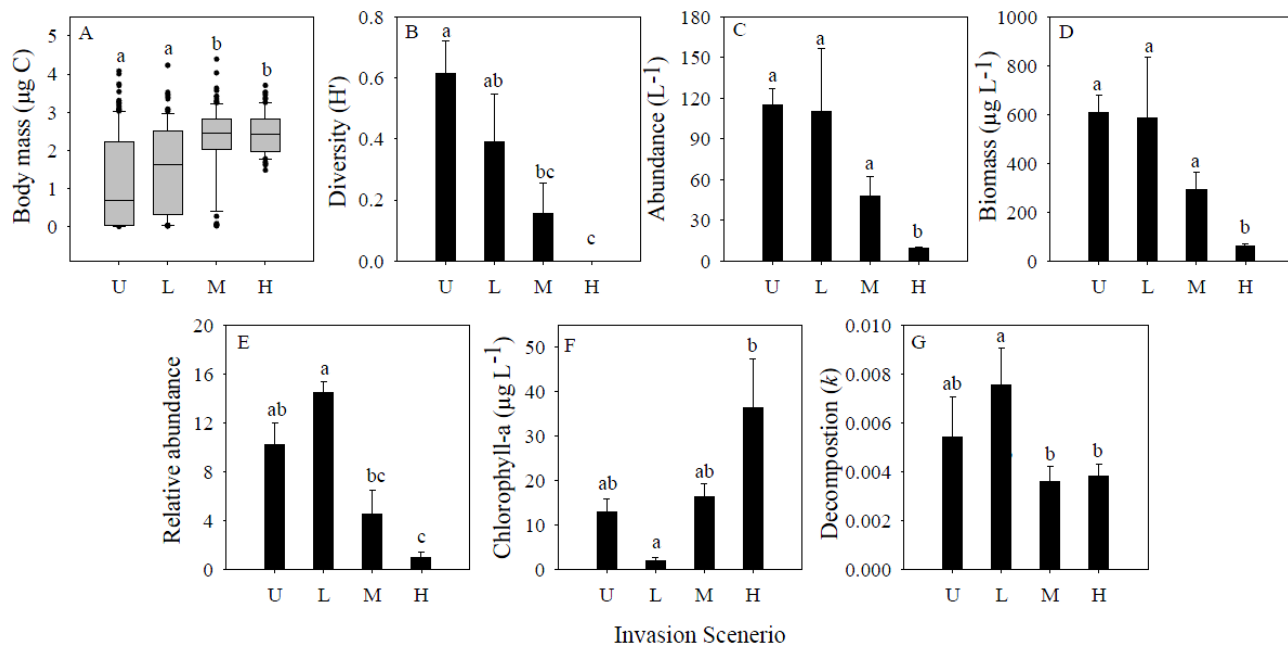
560 Fig 2

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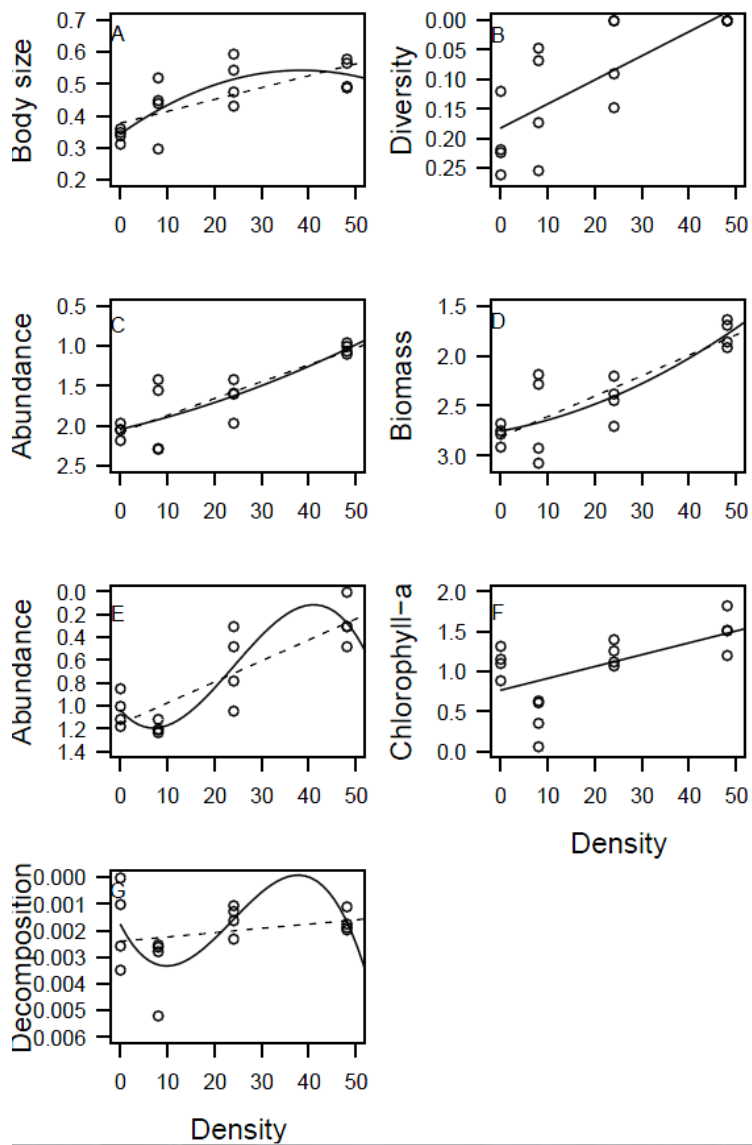
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567 Fig 4

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