



Deposited via The University of Leeds.

White Rose Research Online URL for this paper:

<https://eprints.whiterose.ac.uk/id/eprint/138808/>

Version: Accepted Version

---

**Article:**

Doherty-Bone, TM, Dunn, AM, Jackson, FL et al. (2019) Multi-faceted impacts of native and invasive alien decapod species on freshwater biodiversity and ecosystem functioning. *Freshwater Biology*, 64 (3). pp. 461-473. ISSN: 0046-5070

<https://doi.org/10.1111/fwb.13234>

---

© 2018 John Wiley & Sons Ltd. This is the peer reviewed version of the following article: Doherty-Bone, TM, Dunn, AM, Jackson, FL et al. (1 more author) (2018) Multi-faceted impacts of native and invasive alien decapod species on freshwater biodiversity and ecosystem functioning. *Freshwater Biology*. ISSN 0046-5070, which has been published in final form at <https://doi.org/10.1111/fwb.13234>. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Use of Self-Archived Versions.

**Reuse**

Items deposited in White Rose Research Online are protected by copyright, with all rights reserved unless indicated otherwise. They may be downloaded and/or printed for private study, or other acts as permitted by national copyright laws. The publisher or other rights holders may allow further reproduction and re-use of the full text version. This is indicated by the licence information on the White Rose Research Online record for the item.

**Takedown**

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing [eprints@whiterose.ac.uk](mailto:eprints@whiterose.ac.uk) including the URL of the record and the reason for the withdrawal request.

1 **Multi-faceted impacts of native and invasive alien decapod species on freshwater**  
2 **biodiversity and ecosystem functioning**

3 Thomas M. Doherty-Bone<sup>1,2,3¶</sup>, Alison M. Dunn<sup>2,3</sup>, Faye L. Jackson<sup>1†</sup>, Lee E. Brown<sup>1,3</sup>

4 <sup>1</sup> School of Geography, University of Leeds, Leeds, West Yorkshire, United Kingdom

5 <sup>2</sup> School of Biology, University of Leeds, Leeds, West Yorkshire, United Kingdom

6 <sup>3</sup> water@leeds, University of Leeds, Leeds, West Yorkshire, United Kingdom

7 ¶ Current address: Conservation Programmes, Royal Zoological Society of Scotland,  
8 Edinburgh, United Kingdom

9 † Current address: Marine Scotland Science Freshwater Fisheries Laboratory, Scottish Government,  
10 Faskally, Perthshire, United Kingdom

11 \* Corresponding author: Lee E. Brown, School of Geography, University of Leeds, Leeds,  
12 West Yorkshire, LS2 9JT, Email: [l.brown@leeds.ac.uk](mailto:l.brown@leeds.ac.uk), Tel: +44 (0)113 3433302, Fax: +44  
13 (0) 113 34 33302

14

15 Running title: Native and invasive decapod impacts

16

17 **Keywords:** *Pacifastacus leniusculus*; *Eriocheir sinensis*; *Austropotamobius pallipes*;  
18 biodiversity; ecosystem functioning

19

## 20 Summary

21 1. Changes to species composition, such as biological invasions and extinctions, have  
22 the potential to alter ecosystems. Invaders often replace taxonomically similar species,  
23 resulting in potentially redundant impacts. For example, freshwater decapod  
24 crustaceans are pervasive invasive alien species but they often extirpate native  
25 decapods. This study addresses whether or not these compositional shifts lead to  
26 impacts on the structure of the macroinvertebrate community, key ecosystem functions  
27 such as decomposition rates and primary productivity and freshwater properties such  
28 as turbidity.

29 2. In a controlled outdoor mesocosm experiment that ran for 33 days, impacts on  
30 biodiversity, ecosystem functioning and properties were compared between a native,  
31 endangered crayfish (*Austropotamobius pallipes*) and two invasive alien decapods:  
32 the crayfish *Pacifastacus leniusculus* and crab *Eriocheir sinensis*. Equal densities of  
33 these decapod species were compared between mesocosms, with a replicated array of  
34 decapod free controls. Measurements included macroinvertebrate densities,  
35 decomposition of leaf litter, production of biofilms, plankton, macrophytes, gross  
36 primary productivity, turbidity and dissolved nutrients.

37 3. While taxonomic richness of non-decapod macroinvertebrates was marginally higher  
38 in the invasive alien treatments, differences in Shannon diversity were negligible, and  
39 beta diversity was higher for the invasive alien crab. Gastropod density was reduced  
40 in the benthos of invasive alien treatments. This was associated with increased  
41 primary productivity of periphyton, particularly in the presence of *P. leniusculus*.  
42 Increased turbidity was however inversely correlated with periphyton primary  
43 productivity in the *E. sinensis* treatment. Nitrate concentration was significantly lower  
44 in invasive compared to native crayfish mesocosms, but similar to decapod free

45 controls. This reflects the potential for this species to act as a nitrogen sink, mediated  
46 through both enhanced periphyton and reduced nitrogen recycling. Other processes,  
47 such as decomposition rates, sediment respiration, community respiration and gross  
48 primary productivity did not differ between treatments.

49 4. This study demonstrates impacts of both native and invasive alien decapod species on  
50 certain aspects of benthic biodiversity and ecosystem processes, but with many of  
51 these parameters unaffected. This assumes equal densities of each species in its  
52 environment. The enhanced gastropod predation and associated trophic cascade by  
53 invasive decapods are likely explained through higher consumption rates, metabolism  
54 and activity. These per-capita impacts are likely to be exacerbated further *in-situ* due  
55 to typically higher densities of invasive compared to native crayfish.

## 56 **Introduction**

57 The change of species composition within and its impact on ecosystems is a critical issue in  
58 environmental management (Loreau et al., 2001, Balvanera et al., 2006). Biological invasions  
59 are a prime driver of changes to species composition and are one of the most widespread and  
60 damaging pressures on freshwater ecosystems (Strayer and Dudgeon, 2010, Ricciardi and  
61 MacIsaac, 2011). The mechanisms by which invasive alien species influence ecosystems are  
62 frequently complex and challenging to predict (Simberloff et al., 2013). Invasive alien  
63 decapods (crabs and crayfish) are common invaders of freshwater ecosystems globally,  
64 causing changes to ecosystem services (Lodge et al., 2012). Conversely, numerous freshwater  
65 decapods are threatened with extinction, including by invasive alien species of other  
66 decapods (Richman et al., 2015). A major question then is whether native and alien species  
67 are ecologically redundant. For example, where an invader is functionally similar to a native  
68 species, it would either extirpate or co-occur with the native species, exerting no novel  
69 impacts that would otherwise cause ecosystem change. Alternatively replacement of a native

70 by a non-redundant invasive species would drive changes in ecosystems through novel  
71 trophic and engineering interactions (Rosenfeld, 2002, Magoulick and Piercy, 2016).

72 Freshwater decapods are omnivorous, consuming leaf litter, plants, smaller animals and  
73 carrion (Emmerson and McGwynne, 1992, Gladman et al., 2012, Dunoyer et al., 2014,  
74 Rosewarne et al., 2016). These trophic interactions can result in cascades leading to changes  
75 in periphyton production (Nyström et al., 2001, Jackson et al., 2014, Rosewarne et al., 2016)  
76 and detritus decomposition (Dunoyer et al., 2014, Lagrue et al., 2014). Decapods also  
77 modify physical habitats through bioturbation of sediments, resulting in increased turbidity  
78 and suspended material (Harvey et al., 2013), as well as changes to dissolved nutrient  
79 concentrations in water columns through excretion (Evans-White & Lamberti, 2005,  
80 Doherty-Bone et al., 2018). Invasive alien decapods and the extinction of native decapods  
81 therefore have the potential to impact freshwater biodiversity and ecosystem processes at  
82 multiple trophic levels.

83 Studies on the ecological consequences of replacement of native decapods species by non-  
84 native species have found both redundant and non-redundant outcomes in microcosms,  
85 mesocosms and the field (Twardochleb et al., 2013, Lagrue et al., 2014, Ercoli et al., 2015).  
86 For example, redundancy has been reported between invasive and native crayfish based on  
87 field observations and *in-situ* enclosure experiments (Ercoli et al., 2014, Lagrue et al., 2014).  
88 Meta-analyses have found invasive decapods tend to exert stronger effects on lower resources  
89 such as detritus and prey compared to native species (Twardochleb et al., 2013, James et al.,  
90 2014). Native decapod species also exert strong top-down impacts, with implications for both  
91 extinctions and conservation translocations (Rosewarne et al., 2013, James et al., 2014).  
92 Some experiments have however shown non-redundant impacts of various species of  
93 invasive crayfish on invertebrates and ecosystem processes (Dunoyer et al., 2014, Jackson et  
94 al., 2014). The literature is dominated by North American examples, with European invasion

95 syndromes limited to loss of Noble Crayfish (*Astacus astacus*, Astacidae) (e.g. Nystöm et al.,  
96 1999, Ercoli et al. 2014, 2015), as opposed to other native European species such as  
97 *Austropotamobius* (Astacidae). Many of the studies in published meta-analyses also only  
98 compared experiments involving only one decapod separately as opposed to those exposing  
99 the native and invasive to the same experimental conditions (James et al., 2014).

100 This study reports the results of a field-based mesocosm experiment to compare the impacts  
101 of a formerly widespread European-native crayfish and two invasive alien decapods on  
102 community structure and ecosystem functioning. Field-based mesocosm studies (use of  
103 water tanks or flumes) have the advantage of increased complexity than laboratory  
104 microcosms but can be replicated to avoid confounding factors that disparate field sites might  
105 generate (Schindler, 1998, Ledger et al., 2009). For decapod invasions, consistent effects  
106 have been reported across experimental venues from laboratory to mesocosm to field, but so  
107 far these have been restricted to studies on impacts on invertebrates and macrophytes  
108 (Nyström et al., 1999, Lodge et al., 1998, Twardochleb et al., 2014, Ercoli et al., 2014, 2015).

109 The study system incorporates the European native White Clawed Crayfish  
110 (*Austropotamobius pallipes*, Astacidae) and invasive alien species that often replace it: the  
111 American Signal Crayfish (*Pacifastacus leniusculus*, Astacidae); and the Chinese Mitten  
112 Crab (*Eriocheir sinensis*, Varunidae). *Austropotamobius pallipes* is classified as  
113 “Endangered” by the IUCN, and is threatened primarily by invasive alien crayfish species  
114 (Füreder et al., 2010), especially *P. leniusculus* (Holdich and Reeve, 1991). *Eriocheir*  
115 *sinensis* is also invading rivers in the former range of *A. pallipes* (Almeida et al., 2014).

116 The aims of this study were to measure the impacts of decapod invasion and extinction on  
117 macroinvertebrate community structure, autogenic and allochthonous ecosystem processes  
118 and properties (aquatic physicochemistry). The following hypotheses were tested: (H<sub>1</sub>)

119 decapod presence would result in increased consumption of resources, especially by invasive  
120 species (Haddaway et al., 2012, Rosewarne et al., 2016), particularly slow moving species  
121 such as gastropods and other invertebrates, leading to (H<sub>2</sub>) reduced grazing pressure and an  
122 increase in primary and gross primary production. It was also expected that (H<sub>3</sub>)  
123 decomposition rates would be maintained or even enhanced in invasive species treatments,  
124 despite depletion of shredding invertebrates, due to high omnivory amongst decapods (Usio  
125 et al., 2000, Dunoyer et al., 2014, Doherty-Bone et al. 2018); and (H<sub>4</sub>) invasive alien  
126 decapods would alter water quality through changes to dissolved nutrients from excretal  
127 products (Evans-White & Lamberti, 2005, Usio et al. 2006, Doherty-Bone et al., 2018,  
128 Fritschie & Olden, 2018), increased turbidity from bioturbation (Harvey et al., 2013) and  
129 particulate carbon from detritivory (Doherty-Bone et al., 2018).

## 130 **Materials & Methods**

### 131 *Experimental set-up*

132 To investigate the ecological consequences of replacement of native by invasive alien  
133 decapod species on lentic freshwater ecosystems, an array of outdoor mesocosms was  
134 established (Supp. Fig. 1). These consisted of 16 plastic water tanks 0.65 m deep, 1 m  
135 diameter and 0.78 m<sup>2</sup> in area dug into the ground. These were located on the University of  
136 Leeds Field Research Unit, Spen Farm near Tadcaster, West Yorkshire. To prevent decapod  
137 escape, water tanks were covered with mesh (20 mm aperture), gravel covered the ground  
138 between water tanks to suppress weeds and enhance desiccation of escaping invertebrates,  
139 and a plastic fence (~0.3 m deep, 1 m high) surrounded the array.

140 Each mesocosm was filled with water from a nearby borehole up to *c.* 0.002 m<sup>3</sup>. A substrate  
141 of a 9:1 mix of sand and Aquasoil and gravel of ~ 3 cm depth was then added to each  
142 mesocosm. Microbial communities were added (09 Apr 2013 – 73 days prior to the

143 experiment) through the addition of 1 litre inoculum from a homogenate of water originating  
144 from a broad range of nearby freshwater habitats so far un-invaded by alien decapods. Native  
145 macrophytes in the mesocosm consisted of *Ceratophyllum demersum* (Ceratophyllaceae), 115  
146 g wet mass rinsed with deionised water to remove large numbers of passenger invertebrates,  
147 plankton and microbes. This species was chosen because it is abundant in lentic freshwaters  
148 in the UK and Europe (Duigan et al., 2007). These were planted in the middle of the water  
149 tank (11 Apr 2013 – 72 days prior to the experiment) in pots containing gravel and 1 ml of  
150 aquatic plant compost (Aquasol®). To allow a standard surface for the sampling of algal  
151 biofilm, an unglazed tile was placed on the sediment surface of each mesocosm so it would  
152 receive the same light exposure. To provide a resource for the “brown” compartment of the  
153 food web, leaf litter detritus was added in the form of 10g Alder (*Alnus glutinosa*,  
154 Betulaceae) and 40g Oak (*Quercus robur*, Fagaceae) which had been air dried following  
155 abscission before weighing. In addition, three packs of pre-weighed (5 g) oven dried Alder  
156 leaves with coarse mesh (20 mm aperture) were added to each mesocosm to enable  
157 decomposition rates to be estimated. These were accompanied with a single fine pack (0.5  
158 mm aperture, to exclude most macroinvertebrate shredders) of Alder leaves to differentiate  
159 microbial from macroinvertebrate breakdown.

160 Macroinvertebrates with limited colonization abilities were added to each mesocosm 30 days  
161 prior to addition of decapods to the experiment: chironomid larvae (*Chironomus* sp.,  
162 Chironomidae ~ 1500 individuals); *Gammarus pulex* (Gammaridae, 100 individuals); *Asellus*  
163 *aquaticus* (Asellidae, 100 individuals); *Baetis rhodani* (Baetidae, 50 individuals); Cased-  
164 caddis larvae, *Sericostoma* sp. (Sericostomatidae, 10 individuals); and six species of  
165 gastropod (100 individuals of *Radix peregra* Lymnaeidae, 10 *Planorbarius corneus*  
166 Planorbidae, 10 *Lymnaea stagnalis* Lymnaeidae, 10 *Lymnaea palustris* Lymnaeidae, 20  
167 *Physa fontinalis* Physidae, 10 *Bithynia tentaculata* Bithyniidae). Other invertebrates

168 colonised naturally. Collectively, the water tanks held 47 taxa of 12,075 individuals by the  
169 end of the experiment. The most dominant species (by percentage of individuals) were  
170 gastropods (39%), chironomid larvae (37%) and *A. aquaticus* (13%). The water tanks were  
171 also colonised by water boatmen (*Micronecta* sp. Corixidae and *Notonecta* sp. Notonectidae).  
172 A full list of invertebrate species occurring in the mesocosms and their origin is listed in  
173 Supp. Table 1. General water quality parameters are given in Supp. Table 2.

174 For the decapod treatments, *A. pallipes* were obtained from Porter Brook, Sheffield, UK  
175 (Natural England licence # 20122661), *P. leniusculus* from Loch Ken, Dumfriesshire and *E.*  
176 *sinensis* from the River Thames at Chiswick. To the authors' knowledge, any relationship  
177 between the decapod habitat of origin and subsequent functional process impacts has not  
178 been tested. Despite this, acclimatization (> 3 months) was undertaken to reduce any risks of  
179 confounding the effects of relocation on the decapod impacts. Decapods were subsequently  
180 introduced to the mesocosms following 24 hours of no feeding.

### 181 *Experimental design*

182 The experiment ran from 21 Jun 2013 when the decapods were added, to 22 Jul 2013 (33  
183 days total). Treatments were arranged in a randomised factorial design, with four replicates  
184 each of native crayfish (*A. pallipes*), invasive alien crayfish (*P. leniusculus*), invasive alien  
185 crab (*E. sinensis*) treatments, and a control with no decapods. Each mesocosm (with the  
186 exception of the controls) had two sub-adult (sexually immature, *sensu* Rosewarne et al.,  
187 2016 and citations therein) decapods (carapace length:  $31.78 \pm 3.07$  mm for *A. pallipes*;  $34.08$   
188  $\pm 2.31$  mm for *P. leniusculus*;  $29.37 \pm 3.56$  mm for *E. sinensis*). This produced a decapod  
189 density of  $2.56 \text{ m}^{-2}$ , generally within the range of densities observed in field sites (Nyström,  
190 2002, Rudnick et al., 2003).

### 191 *Macroinvertebrate sampling*

192 At the end of the experiment, invertebrates were sampled using a hand-net (250  $\mu\text{m}$  aperture  
193 mesh) swept repeatedly through the mesocosm's water for one minute, including scraping the  
194 sides of the water tank and disturbing the sediment surface. Leaf packs were also removed to  
195 sample invertebrates. Debris from the nets was placed in labelled plastic zip lock bags and  
196 treated with  $\sim 70\%$  EtOH solution to kill and preserve invertebrates. Invertebrates from these  
197 samples and the leaf packs were later sorted from debris in the laboratory, identified to  
198 species level where possible (using Dobson et al., 2012 and references therein) and  
199 enumerated.

#### 200 *Ecosystem functioning*

201 Leaf packs were removed at the end of the experiment, rinsed with deionised water and oven  
202 dried at  $50^\circ\text{C}$  to constant mass, weighed then ashed at  $500^\circ\text{C}$  to calculate ash-free dry mass  
203 (AFDM). Decomposition rates were calculated as the change in estimated AFDM (following  
204 Benfield, 2006). Fine particulate organic matter (FPOM) in the water column & benthos was  
205 sampled using suction from a 20 cm diameter, 70 cm length cylindrical tube, stored in a  
206 plastic sample bag and treated with methylated spirit solution for later processing. These  
207 samples were filtered first through 10mm mesh, then through  $0.7 \mu\text{m}$  GF/F filter discs, oven  
208 dried at  $105^\circ\text{C}$  for 24 hours, weighed following cooling, and then ashed at  $500^\circ\text{C}$  to calculate  
209 AFDM.

210 Macrophytes were rinsed in deionised water to remove invertebrates and other material, and  
211 dried for 24 hours or until constant mass at  $50^\circ\text{C}$ , then ashed at  $500^\circ\text{C}$  to estimate AFDM.  
212 Filamentous algae was abundant in all the mesocosms but not measured due to time  
213 constraints and the difficulty in separating other matter to obtain reliable estimates of mass.  
214 Biofilms (bacteria, fungi and periphyton) were sampled from the tiles using a nylon brush  
215 and stored at  $-20^\circ\text{C}$  prior to processing. Biofilm biomass was measured as for FPOM

216 described above. Primary productivity (measured as chlorophyll *a*) of periphyton from a 5 ml  
217 sub-sample was measured using the filtration and spectrometric method of Steinman et al.  
218 (1996). Water samples were collected from the surface water for plankton and stored at -20°C  
219 until processing where a 5ml sub-sample measured for chlorophyll *a* and biomass measured  
220 as for biofilms.

221 Community respiration and gross primary productivity of the mesocosms was measured 30  
222 days into the experiment using the diel oxygen technique, where probes recorded changes in  
223 dissolved oxygen (D.O.) every 15 minutes for 24 hours using a YSI Environmental  
224 ProODO™ logger, following Bott (1996). The premise of this technique is that changes in  
225 D.O. are linked to the extent of both photosynthesis and respiration by the community, with  
226 daily respiration estimated from the change in oxygen in darkness (reduction of  
227 photosynthetically active radiation verified using a Delta QS-5 quantum sensor connected to  
228 a Campbell® CR800 data logger). D.O. was corrected for re-aeration from wind-induced gas  
229 exchange with the surface water and atmosphere by measuring wind speed (using an  
230 anemometer connected to a Campbell® CR800 data logger) every 15 minutes, *sensu* Staehr  
231 et al. (2010). From these measurements, community respiration ( $\mu\text{g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ ), gross primary  
232 productivity ( $\mu\text{g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ ), and net primary productivity ( $\mu\text{g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ ) were calculated.  
233 Sediment respiration was measured *in-situ* in enclosed 350 ml chambers using O<sub>2</sub>  
234 consumption over time (3 hours), assuming equal day and night respiration (Bott et al., 1985,  
235 Doering et al. 2011).

### 236 *Ecosystem properties*

237 Physicochemical measurements included pH (using a Hanna pH meter) and turbidity (using a  
238 Model 2100 A Turbidimeter, CAMLAB, Cambridge). Dissolved oxygen was measured on  
239 day 30 using the probes when using the diel technique mentioned above. Analysis of water

240 samples collected on day 33 were subsequently analysed with a Skalar SAN ++ continuous  
241 flow auto-analyser for ammoniacal nitrogen (NH<sub>3</sub>-N), nitrates (N-NO<sub>3</sub>) and soluble reactive  
242 phosphorus (PO<sub>4</sub>-P).

### 243 *Data analysis*

244 Macroinvertebrate parameters calculated included densities (per m<sup>2</sup> of mesocosm) of prey  
245 species (gastropods, isopods and chironomid larvae), taxonomic richness and Shannon  
246 diversity.  $\beta$  diversity within treatments was calculated using Jaccard's Index of similarities  
247 and compared between treatments. The remaining statistics were analysed using R (R  
248 v.3.1.0.; R Development Core Team, 2014). To contrast macroinvertebrate community  
249 structure between treatments, square root transformed invertebrate abundance data were  
250 subjected to ordination analysis using non-metric dimensional scaling (NMDS) plots of Bray-  
251 Curtis dissimilarities (formula: metaMDS, library: vegan) to view dispersion of similarities,  
252 and using PERMANOVA (formula: adonis, library: vegan) to test significance between  
253 treatments. Generalized linear models (GLMs, formula: glm) were used to identify  
254 differences between treatments for all response variables (invertebrates, ecosystem  
255 functioning and properties), with the data family selected based on maximum likelihood  
256 estimates (library: MASS, formula: fitdistr) and *post hoc* Tukey tests applied (library:  
257 multcomp, formula: glht).

258 Biofilm primary productivity was found to vary with treatment based on the GLM described  
259 above. Therefore to differentiate causality *post hoc* of top-down regulation of grazing  
260 gastropods by decapods from bottom-up factors such as turbidity, GLMs were used with  
261 primary productivity as a response with treatment as a factor with gastropod abundance,  
262 turbidity, and nitrates as covariates. Because the quasipoisson data family does not produce

263 Akaike's Information Criterion (AIC) values to estimate the best performing GLM, Gaussian  
264 data family had to be used.

## 265 **Results**

### 266 *Macroinvertebrate diversity and abundance*

267 Macroinvertebrate taxonomic richness was significantly lower in the presence of *A. pallipes*  
268 compared to the control, but there were no significant difference in richness between the  
269 control and invasive decapod treatments (Table 1, Fig. 1a, independent to individual  
270 invertebrates, Fig. 1b). Shannon index did not differ significantly between treatments (Table  
271 1, Fig. 1c). Community ordination (NMDS) plots showed more dispersed community  
272 structure in both invasive treatments compared to control or native crayfish treatments, also  
273 with less overlap (Fig. 2) but there was no significant difference in community structure  
274 (PERMANOVA:  $P > 0.05$  both among treatments and through pairwise comparisons).  
275 However, beta diversity was significantly greater for *E. sinensis* compared to controls and *A.*  
276 *pallipes* in the benthos (Table 1, Fig. 1d). There was no difference between treatment in the  
277 overall richness and density of key decapod prey such as *A. aquaticus* and Chironomidae  
278 (Figs. 1g-h). However, gastropods were significantly less abundant in the invasive decapod  
279 species treatments compared to the control and to the native crayfish treatments (Fig. 1f,  
280 Table 1), though richness of gastropods did not differ (Fig. 1e).

### 281 *Ecosystem functioning*

282 All ecosystem process variables measured showed no significant difference between  
283 treatments, with the exception of primary productivity (chlorophyll *a*) of algal biofilms  
284 (Table 2, Figs. 3a-e, Supp. Fig. 2). Biofilm primary productivity was higher for *P. leniusculus*  
285 treatments than *A. pallipes* and *E. sinensis*, but similar to controls (Fig. 3b). Subsequent

286 modelling found that the interaction between decapod treatment and the abundance of  
287 gastropods was a significant factor influencing primary productivity of biofilms and provided  
288 the strongest model (Table 3). The interaction of treatment and turbidity showed a marginally  
289 significant ( $p = 0.05$ ) effect on biofilm productivity, but there was no significant effect of the  
290 interaction between turbidity and gastropods on biofilm productivity (Table 3). Primary  
291 productivity of algal biofilms showed a significant, positive relationship with gross primary  
292 productivity (glm  $p = 0.003$ , Pearson's correlation coefficient=0.62, Supp. Fig. 3). Other  
293 primary producers (phytoplankton and submerged macrophytes) showed no significant  
294 relationship with gross primary productivity (GPP).

#### 295 *Ecosystem properties*

296 Turbidity differed significantly between the treatments (Table 2) and was higher in the  
297 invasive decapod treatments, particularly *E. sinensis* in relation to the control and *A. pallipes*  
298 (Fig. 4a). Nitrate differed between treatments ( $p = 0.02$ ) and was highest in native crayfish  
299 treatments compared to the control, with *E. sinensis* treatments also high, and *P. leniusculus*  
300 similar to controls (Fig. 4d). pH was marginally significant ( $p = 0.05$ ), being lower in all  
301 decapod treatments and *post-hoc* tests grouping *A. pallipes* and *E. sinensis*, similar to the  
302 pattern for nitrate (Fig. 4b). The other physicochemical parameters did not differ significantly  
303 with experimental treatments (Figs. 4 c,e,f).

#### 304 **Discussion**

305 This study has identified the potential for both ecological redundancy and non-redundancy  
306 for various ecological parameters among the invasive alien (*P. leniusculus* and *E. sinensis*)  
307 and the native decapod species (*A. pallipes*) in a replicated controlled mesocosm facility. This  
308 experimental setting provided a more realistic, complex environment to appraise potential  
309 impacts of an invasion syndrome occurring across Western Europe. Previous studies on this

310 invasion syndrome had been limited to laboratory-based experiments or indirect comparisons.  
311 This system reflected a functioning lentic ecosystem, with a realistic diversity of  
312 invertebrates and trophic elements, such as detritus, biofilms, plankton and plants in the  
313 presence of dynamic environmental variables.

#### 314 *Impacts on macroinvertebrate community*

315 Invertebrate communities as a whole (Shannon diversity, community composition assessed  
316 with NMDS) did not respond to invasive alien decapods in the water tank mesocosms.  
317 However, gastropod densities in the benthic zone were reduced by invasive alien decapods,  
318 while  $\beta$  diversity was higher for *E. sinensis*. Stronger impacts might have been detected had  
319 the time period of the experiment been longer than 33 days, thereby allowing the decapods to  
320 consume more gastropods and physically alter the habitat of the mesocosm through additional  
321 bioturbation. The mesocosms in this study did not consistently sustain amphipod, leech or  
322 ephemeropteran populations that have been found to decline in the presence of decapods in  
323 other laboratory, mesocosm and field studies (Stenroth & Nyström, 2003, Rosewarne et al.,  
324 2016, Mathers et al., 2016). This suggests that effects on invertebrate communities might be  
325 stronger had this mesocosm array supported more species vulnerable to decapod predation.

326 Given the depletion of gastropods by the invasive alien decapods, the lower taxonomic  
327 richness of invertebrates in native crayfish mesocosms compared to the two invasive species  
328 and controls was unexpected. The factors causing this are unclear, with several beetle species  
329 apparently assembling with the two invasive species mesocosms. This could be the result of  
330 invasive decapods creating a trophic cascade through the increased provision of FPOM  
331 (*sensu* Doherty-Bone et al., 2018), which is then consumed by prey of these beetles. The  
332 negligible impacts on Shannon diversity in response to both native and invasive alien  
333 decapods are in accord with Rosewarne et al. (2013, 2016). However, the study contrasts to

334 the significant reduction of taxonomic richness in mesocosms with *P. leniusculus* observed  
335 by Jackson et al. (2014). Examples of decreases in invertebrate taxonomic richness and  
336 Shannon diversity in rivers and lakes invaded by *P. leniusculus* (Stenroth and Nyström, 2003,  
337 Crawford et al., 2006, Ercoli et al., 2015), may reflect the higher densities of invasive versus  
338 native decapods in the field. The study's community assembly also contrasts to field  
339 observations of *P. leniusculus* invasions (compared to the uninvaded, crayfish-free sites),  
340 where invertebrate community structure differed considerably between invaded and un-  
341 invaded sites (Crawford et al., 2006, Mathers et al 2016).

342 Strong regulation of invertebrate communities by *E. sinensis* has been demonstrated in other  
343 mesocosm studies (Rudnick and Resh, 2005, Rosewarne et al., 2016). However, this is the  
344 first study to directly compare the impact of *E. sinensis* with native crayfish in mesocosms,  
345 showing increases in gastropod predation and greater taxonomic richness and  $\beta$  diversity for  
346 *E. sinensis*.  $\beta$  diversity was greater for *E. sinensis* compared to controls and *A. pallipes*,  
347 suggesting more stochastic community assembly in the presence of this invasive alien  
348 species. This is unexpected as increased predation and changes to physicochemical attributes  
349 would be expected to cause more deterministic community assembly, characterised by  
350 reduced  $\beta$  diversity (*sensu* Chase et al., 2009).

351 The reduced gastropod abundance in all invasive alien species treatments was expected from  
352 previous studies that showed higher rates of predation by invasive than native species on  
353 gastropod prey (Nystrom et al 1999, Haddaway et al., 2012, Taylor & Dunn, 2018). Previous  
354 mesocosm studies of these two invasive decapod species also showed similar impacts on  
355 gastropods (Rosewarne et al., 2016) or other benthic molluscs (Rudnick & Resh, 2005). The  
356 negligible difference in chironomid abundance between treatments was not expected.  
357 Previous laboratory and mesocosm studies demonstrated higher predation of chironomids by  
358 invasive alien decapods (Haddaway et al., 2012, Jackson et al., 2014, Rosewarne et al. 2016).

359 Studies on crayfish-prey interactions have found increased abundance of prey species in  
360 microhabitats with limited access to crayfish (Dunoyer et al., 2014). It is likely that the  
361 habitat complexity of the mesocosms in this study permitted co-existence of vulnerable prey  
362 species such as chironomid larvae with invasive alien decapod species. In addition, the  
363 presence of more easily captured prey (gastropods) in sufficient abundance is likely to have  
364 deferred the predation pressure on more mobile invertebrates such as chironomids. This  
365 demonstrates that inferences from scaling homogenous lab experiments to environments with  
366 more heterogeneous resources can be limited (Schindler 1998), although they have held for  
367 gastropod predation (Lodge et al., 1998). The consequences of replacement of *A. pallipes* by  
368 *P. leniusculus* and/or *E. sinensis* at equivalent densities in the field would thus be expected to  
369 cause reduced gastropod densities in the benthos. This impact will likely be amplified by  
370 increased densities of these invaders, as observed in other alien crayfish invasions (Hansen et  
371 al., 2013).

#### 372 *Impacts on ecosystem functioning*

373 There was no evidence of greater leaf decomposition or derived secondary products (FPOM)  
374 in the presence of decapods in relation to the control. This is in contrast to laboratory studies  
375 (Dunoyer et al., 2014, Doherty-Bone et al., 2018) but in agreement with mesocosm studies  
376 for these species (Rosewarne et al. 2016). A reduction in decomposition was expected as a  
377 result of decapod predation on key shredders such as *A. aquaticus*. However, there was no  
378 significant difference in shredder abundance between different treatments. The lack of  
379 difference in decomposition also suggests no difference in direct shredding by the three  
380 decapod species in the mesocosms. This demonstrates another possible limitation of  
381 laboratory studies (discussed above), which have shown enhanced decomposition by  
382 decapods (e.g. Dunoyer et al. 2014), where resource availability was greatly simplified  
383 compared to the mesocosm.

384 Primary productivity of periphyton (algal biofilms), which strongly influenced the gross  
385 primary productivity of the mesocosms, was higher for *P. leniusculus* compared to *A. pallipes*  
386 and *E. sinensis* treatments. Despite experimental treatments interacting with turbidity to  
387 influence primary productivity, the trophic cascade appeared to be controlled by the top-  
388 down impact of decapod predation on gastropods. This is consistent with trophic cascades  
389 driven by grazer predation by invasive alien decapods (Jackson et al 2014, Rosewarne et al.,  
390 2016). This study has shown an invasive alien crayfish influences this trophic cascade to a  
391 greater extent than the native crayfish it replaces. However, the presence of both native and  
392 invasive decapods caused a general reduction in primary productivity of periphyton when  
393 compared to the control. As this benthic primary productivity was moderately correlated to  
394 gross primary productivity, it is possible that translocations of native crayfish into decapod  
395 free waterways, as well as invasions by *E. sinensis* might induce reductions in overall  
396 ecosystem productivity. In contrast, invasions by *P. leniusculus* could maintain primary  
397 productivity of periphyton and cascading ecosystem productivity. This would however be  
398 contingent on this species maintaining modest densities and bioturbation not interfering with  
399 turbidity. These contingencies have however not been experienced *in-situ* (Harvey et al.,  
400 2013, Almeida et al., 2014).

401 Plankton biomass and primary productivity were not affected by either decapod treatment,  
402 explained by greater decapod influence on benthic as opposed to pelagic habitats (Strayer,  
403 2010). Biomass of the submerged macrophyte (*Ceratophyllum*) was expected to be reduced  
404 compared to controls and native crayfish treatments through direct consumption or shredding  
405 by omnivorous decapods: this pattern was observed but was not significant (Fig. 3d). This  
406 absence of impact on macrophytes has also been observed by Rosewarne et al. (2016), but  
407 other studies have found depletion of macrophytes by *P. leniusculus* (Nyström et al., 1996,  
408 Nyström et al., 2001, Nyström and Strand, 2003). The presence of more nutritious food items,

409 such as animal prey, is likely to be a factor in this observation (Whitledge & Rabeni, 1997,  
410 Magoulick and Piercey, 2016). Incorporation of a demographically representative  
411 composition of adults, sub-adults and juveniles (as with Nyström et al., 2001), might also  
412 have created similarly differential usage of resources in this experiment, based on ontogenetic  
413 dietary preferences (Usio et al., 2009, Rosewarne et al., 2013).

#### 414 *Impacts on ecosystem properties*

415 This study provides a new comparison of the effect of *A. pallipes* and *E. sinensis* on water  
416 turbidity, adding to growing interest in this topic (Harvey et al., 2013). Turbidity of the water  
417 column was found to be higher in invasive alien decapod treatments than in controls or even  
418 native decapod treatments. The increased turbidity in invasive decapod treatments in the  
419 absence of correlates with phytoplankton production (which can influence turbidity) suggests  
420 increased suspended sediment via bioturbation as the most likely cause. Turbidity  
421 measurements nearer the sediment bed are likely to have been even more pronounced: rivers  
422 invaded by *P. leniusculus* show increased turbidity at the bed compared to mid water column  
423 (Harvey et al., 2013). Crayfish and other decapods increase sediment transport through  
424 burrowing, foraging, conspecific antagonistic interactions and general movement across the  
425 sediment (Harvey et al., 2011) and increased burrow density and structure (Rudnick et al.,  
426 2005). Increased turbidity in surface layers of *E. sinensis* mesocosms indicates a very high  
427 impact by this species in relation to uninvaded ecosystems.

428 The increased nitrate concentration in decapod treatments suggests nitrification of ammonia  
429 excreted by decapods. Isolation of these species in the laboratory has shown a similar pattern  
430 of ammoniacal nitrogen (NH<sub>3</sub>-N) production for each species, with similar values for *A.*  
431 *pallipes* and *E. sinensis* and lower values for *P. leniusculus* (Doherty-Bone et al., 2018). The  
432 lower ammonia excretion by *P. leniusculus*, leading to lower NO<sub>3</sub>-N production suggests this

433 species is likely to be a greater nutrient sink (*sensu* Vanni, 2002) compared to *A. pallipes*,  
434 through consuming and assimilating more nitrogen and reducing its availability to other  
435 organisms (particularly absorbing species such as primary producers). This suggests that  
436 invasions by *P. leniusculus* and the extirpation/translocation of *A. pallipes* could affect  
437 nitrogen cycling and community structure in N-limited ecosystems. A similar relationship has  
438 been observed for the replacement of the native Japanese crayfish *Cambaroides japonicas*  
439 (Cambaridae) by *P. leniusculus* (Usio et al., 2006).

440 This study indicates that invasive alien freshwater decapod species have a limited impact on  
441 macroinvertebrate community structure and ecosystem processes when occurring at low  
442 densities or densities equivalent to native crayfish, in complex habitats. Despite these limited  
443 impacts, non-redundancy was clearly demonstrated for gastropod density, primary  
444 productivity of periphyton and certain physicochemical attributes such as turbidity and  
445 nutrients. Certain traits of non-redundancy demonstrated in the laboratory did scale up to  
446 more realistic mesocosms, many others did not, such as detritivory. However, invasive alien  
447 species (including decapods, Nyström, 2002, Hansen et al., 2013) are typically characterised  
448 by achieving high densities in their host ecosystems and this could amplify the impact of the  
449 effects observed in these mesocosm experiments.

#### 450 **Acknowledgements**

451 We thank the associate editor and two anonymous reviewers for their helpful comments on  
452 that improved this paper. TMD-B was supported by a John Henry Garner Scholarship from  
453 the University of Leeds and by the Holt Educational Trust, AMD by the National  
454 Environmental Research Council (NERC G015201/1). This work was partly funded by a  
455 Research Training Support Grant from the School of Geography (University of Leeds) and by  
456 a water@leeds SPRING grant. Natural England provided licenses to collect White Clawed

457 Crayfish (#20122661), and the Port of London Authority provided access to the River  
458 Thames. The authors express their gratitude to Paul Bradly and team at PBA Ecology for  
459 assistance with acquisition of White Clawed Crayfish, and to Paul Stebbing at the Centre for  
460 Environment, Fisheries and Aquaculture Science for advice on biosecure mesocosm design.  
461 The authors also thank Stephanie Peay, Ian Marshall, the laboratory and support staff at the  
462 University of Leeds Field Research Unit and School of Geography, Alasdair Fagan, Ryan  
463 Ward, Nigel Taylor and Paula Rosewarne for assistance with the project.

464 **Conflict of interest:** The authors have no conflict of interest in production of this work.

465

466 **Literature cited**

- 467 Almeida, D., Ellis, A., England, J. & Copp, G. H. (2014). Time-series analysis of native and  
 468 non-native  
 469 crayfish dynamics in the Thames River Basin (south-eastern England). *Aquatic*  
 470 *Conservation: Marine and Freshwater Ecosystems*, 24, 192-202.
- 471 Balvanera, P., Pfisterer, A. B., Buchmann, N., He, J. S., Nakashizuka, T., Raffaelli, D. &  
 472 Schmid, B. (2006). Quantifying the evidence for biodiversity effects on ecosystem  
 473 functioning and services. *Ecology Letters*, 9, 1146-1156.
- 474 Benfield, E. (2006). Decomposition of leaf material. In: F. Richard Hauer and Gary A.  
 475 Lamberti (Eds), *Methods in Stream Ecology*, Elsevier, Oxford, UK, pp. 711-720.
- 476 Bott, T., Brock, J., Dunn, C., Naiman, R., Ovink, R. & Petersen, R. (1985). Benthic  
 477 community metabolism in four temperate stream systems: an inter-biome comparison  
 478 and evaluation of the river continuum concept. *Hydrobiologia*, 123, 3-45.
- 479 Bott, T. L. (1996). Primary productivity and community respiration. *Methods in Stream*  
 480 *Ecology*. Academic Press, San Diego, California, 533-556.
- 481 Chase, J. M., Biro, E. G., Ryberg, W. A. & Smith, K. G. (2009). Predators temper the relative  
 482 importance of stochastic processes in the assembly of prey metacommunities. *Ecology*  
 483 *Letters*, 12, 1210-1218.
- 484 Crawford, L., Yeomans, W. E. & Adams, C. E. (2006). The impact of introduced signal  
 485 crayfish *Pacifastacus leniusculus* on stream invertebrate communities. *Aquatic*  
 486 *Conservation: Marine and Freshwater Ecosystems*, 16, 611-621.
- 487 Dobson, M., Pawley, S., Fletcher, M. & Powell, A. (2012). *Guide to Freshwater*  
 488 *Invertebrates*. Freshwater Biological Association, UK.
- 489 Doherty-Bone, T.M., Dunn, A.M., Liddell, C. & Brown, L.E. (2018). Transformation of  
 490 detritus by a European native and two invasive alien freshwater decapods. *Biological*  
 491 *Invasions*.
- 492 Doering, M., Uehlinger, U., Ackerman, T., Woodtli, M. & Tockner, K. (2011).  
 493 Spatiotemporal heterogeneity of soil and sediment respiration in a river-floodplain  
 494 mosaic (Tagliamento, NE Italy). *Freshwater Biology*, 56, 1297-1311.
- 495 Duigan, C., Kovach, W. & Palmer, M. (2007). Vegetation communities of British lakes: a  
 496 revised classification scheme for conservation. *Aquatic Conservation: Marine and*  
 497 *Freshwater Ecosystems*, 17, 147-173.
- 498 Dunoyer, L., Dijoux, L., Bollache, L. & Lagrue, C. (2014). Effects of crayfish on leaf litter  
 499 breakdown and shredder prey: are native and introduced species functionally  
 500 redundant? *Biological Invasions*, 16, 1545-1555.
- 501 Emmerson, W. & McGwynne, L. (1992). Feeding and assimilation of mangrove leaves by the  
 502 crab *Sesarma meinerti* de Man in relation to leaf-litter production in Mgazana, a  
 503 warm-temperate southern African mangrove swamp. *Journal of Experimental Marine*  
 504 *Biology and Ecology*, 157, 41-53.
- 505 Ercoli, F., Ruokonen, T.J., Hämäläinen, H. & Jones, R.I. (2014). Does the introduced signal  
 506 crayfish occupy an equivalent trophic niche to the lost native noble crayfish in boreal  
 507 lakes?. *Biological Invasions*, 16, 2025-2036.
- 508 Ercoli, F., Ruokonen, T. J., Koistinen, S., Jones, R. I. & Hämäläinen, H. (2015). The  
 509 introduced signal crayfish and native noble crayfish have different effects on  
 510 sublittoral macroinvertebrate assemblages in boreal lakes. *Freshwater Biology*, 60,  
 511 1688-1698.
- 512 Evans-White, M. A. & Lamberti, G. A. (2005). Grazer species effects on epilithon nutrient  
 513 composition. *Freshwater Biology*, 50, 1853-1863.

- 514 Fritschie, K.J. and Olden, J.D. (2018). Estimating the effects of non-native species on nutrient  
515 recycling using species-specific and general allometric models. *Freshwater Biology*.
- 516 Füreder, L., Gherardi, F., Holdich, D., Reynolds, J., Sibley, P. & Souty-Grosset, C. (2010).  
517 *Austropotamobius pallipes*. In: IUCN 2012. IUCN Red List of Threatened Species.  
518 Version 2012.2.
- 519 Gladman, Z., Adams, C., Bean, C., Long, J. & Yeomans, W. (2012). Investigating the threat  
520 of non-native North American signal crayfish (*Pacifastacus leniusculus*) to salmon  
521 redds. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 22, 134-137.
- 522 Haddaway, N. R., Wilcox, R. H., Heptonstall, R. E. A., Griffiths, H. M., Mortimer, R. J. G.,  
523 Christmas, M. & Dunn, A. M. (2012). Predatory functional response and prey choice  
524 identify predation differences between native/invasive and parasitised/unparasitised  
525 crayfish. *PLOS ONE*, 7, e32229.
- 526 Hansen, G. J., Vander Zanden, M. J., Blum, M. J., Clayton, M. K., Hain, E. F., Hauxwell,  
527 J.,...Mikulyuk, A. (2013). Commonly rare and rarely common: comparing population  
528 abundance of invasive and native aquatic species. *PLOS ONE*, 8, e77415.
- 529 Harris, R. M., Armitage, P. D., Milner, A. M. & Ledger, M. E. (2007). Replicability of  
530 physicochemistry and macroinvertebrate assemblages in stream mesocosms:  
531 implications for experimental research. *Freshwater Biology*, 52, 2434-2443.
- 532 Harvey, G. L., Henshaw, A. J., Moorhouse, T. P., Clifford, N. J., Holah, H., Grey, J. &  
533 MacDonald, D. W. (2013). Invasive crayfish as drivers of fine sediment dynamics in  
534 rivers: field and laboratory evidence. *Earth Surface Processes and Landforms*, 39,  
535 259-271
- 536 Harvey, G. L., Moorhouse, T. P., Clifford, N. J., Henshaw, A. J., Johnson, M. F., MacDonald,  
537 D. W., Reid, I. & Rice, S. P. (2011). Evaluating the role of invasive aquatic species as  
538 drivers of fine sediment-related river management problems: The case of the signal  
539 crayfish (*Pacifastacus leniusculus*). *Progress in Physical Geography*, 35, 517-533.
- 540 Holdich, D. M. & Reeve, I. D. (1991). Distribution of freshwater crayfish in the British Isles,  
541 with particular reference to crayfish plague, alien introductions and water quality.  
542 *Aquatic Conservation: Marine and Freshwater Ecosystems*, 1, 139-158.
- 543 Jackson, M. C., Jones, T., Milligan, M., Sheath, D., Taylor, J., Ellis, A., Grey, J. (2014).  
544 Niche differentiation among invasive crayfish and their impacts on ecosystem  
545 structure and functioning. *Freshwater Biology*, 59, 1123-1135.
- 546 James, J., Slater, F. M., Vaughan, I. P., Young, K. & Cable, J. (2015). Comparing the  
547 ecological impacts of native and invasive crayfish: could native species' translocation  
548 do more harm than good? *Oecologia*, 178, 309-316.
- 549 Lagrue, C., Podgorniak, T., Lecerf, A. & Bollache, L. (2014). An invasive species may be  
550 better than none: invasive signal and native noble crayfish have similar community  
551 effects. *Freshwater Biology*, 59, 1982-1995.
- 552 Ledger, M., Harris, R., Armitage, P. & Milner, A. (2009). Realism of model ecosystems: an  
553 evaluation of physicochemistry and macroinvertebrate assemblages in artificial  
554 streams. *Hydrobiologia*, 617, 91-99.
- 555 Lodge, D.M., Stein, R.A., Brown, K.M., Covich, A.P., Brönmark, C., Garvey, J.E. &  
556 Klosiewskt, S.P. (1998). Predicting impact of freshwater exotic species on native  
557 biodiversity: challenges in spatial scaling. *Austral Ecology*, 23, 53-67.
- 558 Lodge, D.M., Deines, A., Gherardi, F., Yeo, D.C., Arcella, T., Baldrige, A.K., Barnes,  
559 M.A., Barnes, M.A., Chadderton, W.L., Feder, J.L., Gantz, C.A., Howard, G.W.,  
560 Jerde, C.L., Peters, B.W., Peters, B.W., Sargent, L.W., Turner, C.R., Wittmann, M.E.  
561 & Zeng, Y. (2012). Global introductions of crayfishes: evaluating the impact of  
562 species invasions on ecosystem services. *Annual Review of Ecology, Evolution, and*  
563 *Systematics*, 43, 449-472.

- 564 Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U.,  
565 Huston, M.A., Raffaelli, D., Schmid, B. & Tilman, D. (2001). Biodiversity and  
566 ecosystem functioning: current knowledge and future challenges. *Science*, 294, 804-  
567 808.
- 568 Magoulick, D. D. & Piercey, G. L. (2016). Trophic overlap between native and invasive  
569 stream crayfish. *Hydrobiologia*, 766, 237-246
- 570 Mathers, K. L., Chadd, R. P., Dunbar, M. J., Extence, C. A., Reeds, J., Rice, S. P. & Wood,  
571 P. J. (2016). The long-term effects of invasive signal crayfish (*Pacifastacus*  
572 *leniusculus*) on instream macroinvertebrate communities. *Science of the Total*  
573 *Environment*, 556, 207-218.
- 574 Navel, S., Mermillod-Blondin, F., Montuelle, B., Chauvet, E. & Marmonier, P. (2012).  
575 Sedimentary context controls the influence of ecosystem engineering by bioturbators  
576 on microbial processes in river sediments. *Oikos*, 121, 1134-1144.
- 577 Nyström, P. (2002). Ecology. Biology of Freshwater Crayfish, David Holdich (Ed.),  
578 Blackwell Sciences Ltd, London.
- 579 Nyström, P., Brönmark, C. & Granéli, W. (1996). Patterns in benthic food webs: a role for  
580 omnivorous crayfish? *Freshwater Biology*, 36, 631-646.
- 581 Nyström, P., Brönmark, C. & Granéli, W. (1999). Influence of an exotic and a native crayfish  
582 species on a littoral benthic community. *Oikos*, 85, 545-553.
- 583 Nyström, P. & Strand, J. (2003). Grazing by a native and an exotic crayfish on aquatic  
584 macrophytes. *Freshwater Biology*, 36, 673-682.
- 585 Nyström, P., Svensson, O., Lardner, B., Brönmark, C. & Granéli, W. (2001). The influence of  
586 multiple introduced predators on a littoral pond community. *Ecology*, 82, 1023-1039.
- 587 Ricciardi, A. & MacIsaac, H. J. (2011). Impacts of biological invasions on freshwater  
588 ecosystems. Fifty Years of Invasion Ecology: the Legacy of Charles Elton, 211-224.
- 589 Richman, N.I., Böhm, M., Adams, S.B., Alvarez, F., Bergey, E.A., Bunn, J.J., Burnham, Q.,  
590 Cordeiro, J., Coughran, J., Crandall, K.A., Dawkins, K.L., DiStefano, R.J., Doran,  
591 N.E., Edsman, L., Eversole, A.G., Füreder, L, Furse, J.M., Gherardi, F., Hamr, P.,  
592 Holdich, D.M., Horwitz, P., Johnston, K., Jones, C.M., Jones, J.P.G., Jones, R.L.,  
593 Jones, T.G., Kawai, T., Lawler, S., López-Mejía, M., Miller, R.M., Pedraza-Lara, C.,  
594 Reynolds, J.D., Richardson, A.M.M., Schultz, M.B., Schuster, G.A., Sibley, P.J.,  
595 Souty-Grosset, C., Taylor, C.A., Thoma, R.F., Walls, J., Walsh, T.S. & Collen, B.  
596 (2015). Multiple drivers of decline in the global status of freshwater crayfish  
597 (Decapoda: Astacidea). *Philosophical Transactions of the Royal Society B*, 370,  
598 20140060.
- 599 Rosenfeld, J. S. (2002). Functional redundancy in ecology and conservation. *Oikos*, 98, 156-  
600 162.
- 601 Rosewarne, P., Mortimer, R. & Dunn, A. (2013). Size-dependent impacts of the endangered  
602 white-clawed crayfish (*Austropotamobius pallipes*) (Lereboullet) on the littoral  
603 community. *Knowledge and Management of Aquatic Ecosystems*, 06.
- 604 Rosewarne, P., Mortimer, R.J., Newton, R. J., Grocock, C., Wing, C. D. & Dunn, A. M.  
605 (2016). Feeding behaviour, predatory functional responses and trophic interactions of  
606 the invasive Chinese mitten crab (*Eriocheir sinensis*) and signal crayfish  
607 (*Pacifastacus leniusculus*). *Freshwater Biology*, 61, 426-443.
- 608 Rosewarne, P. J., Svendsen, J. C., Mortimer, R. J. & Dunn, A. M. (2014). Muddied waters:  
609 suspended sediment impacts on gill structure and aerobic scope in an endangered  
610 native and an invasive freshwater crayfish. *Hydrobiologia*, 722, 61-74.
- 611 Rudnick, D. & Resh, V. (2005). Stable isotopes, mesocosms and gut content analysis  
612 demonstrate trophic differences in two invasive decapod crustacea. *Freshwater*  
613 *Biology*, 50, 1323-1336.

- 614 Rudnick, D. A., Chan, V. & Resh, V. H. (2005). Morphology and impacts of the burrows of  
615 the Chinese mitten crab, *Eriocheir sinensis* H. Milne Edwards (Decapoda,  
616 Grapsoidea), in south San Francisco Bay, California, USA. *Crustaceana*, 787-807.
- 617 Rudnick, D. A., Hieb, K., Grimmer, K. F. & Resh, V. H. (2003). Patterns and processes of  
618 biological invasion: the Chinese mitten crab in San Francisco Bay. *Basic and Applied*  
619 *Ecology*, 4, 249-262.
- 620 Schindler, D. W. (1998). Whole-ecosystem experiments: replication versus realism: the need  
621 for ecosystem-scale experiments. *Ecosystems*, 1, 323-334.
- 622 Simberloff, D., Martin, J. L., Genovesi, P., Maris, V., Wardle, D. A., Aronson, J.,...Pascal,  
623 M. (2013). Impacts of biological invasions: what's what and the way forward. *Trends*  
624 *in Ecology & Evolution*, 28, 58-66.
- 625 Staehr, P. A., Bade, D., Van de Bogert, M. C., Koch, G. R., Williamson, C., Hanson, P., ...  
626 Kratz, T. (2010). Lake metabolism and the diel oxygen technique: state of the science.  
627 *Limnology and Oceanography: Methods*, 8, 628-644.
- 628 Steinman, A. D., Lamberti, G. A. & Leavitt, P. (1996). Biomass and pigments of benthic  
629 algae. In: Hauer, F.R. and G.A. Lamberti (eds.). *Methods in Stream Ecology*. Elsevier  
630 Inc. Oxford UK, pp 357-359.
- 631 Stenroth, P. & Nyström, P. (2003). Exotic crayfish in a brown water stream: effects on  
632 juvenile trout, invertebrates and algae. *Freshwater Biology*, 48, 466-475.
- 633 Strayer, D. L. & Dudgeon, D. (2010). Freshwater biodiversity conservation: recent progress  
634 and future challenges. *Journal of the North American Benthological Society*, 29, 344-  
635 358.
- 636 Taylor, N.G. & Dunn, A.M. (2018). Predatory impacts of alien decapod Crustacea are  
637 predicted by functional responses and explained by differences in metabolic rate.  
638 *Biological Invasions*, 20, 2821-2837.
- 639 Twardochleb, L. A., Olden, J. D. & Larson, E. R. (2013). A global meta-analysis of the  
640 ecological impacts of nonnative crayfish. *Freshwater Science*, 32, 1367-1382.
- 641 Usio, N. (2000). Effects of crayfish on leaf processing and invertebrate colonisation of leaves  
642 in a headwater stream: decoupling of a trophic cascade. *Oecologia*, 124, 608-614.
- 643 Usio, N., Suzuku, K., Konishi, M. & Nakano, S. (2006). Alien vs. endemic crayfish: roles of  
644 species identity in ecosystem functioning. *Archiv für Hydrobiologie*, 166, 1-21.
- 645 Usio, N., Kamiyama, R., Saji, A. & Takamura, N. (2009). Size-dependent impacts of invasive  
646 alien crayfish on a littoral marsh community. *Biological Conservation*, 142, 1480-  
647 1490.
- 648 Vanni, M. J. (2002). Nutrient cycling by animals in freshwater ecosystems. *Annual Review of*  
649 *Ecology and Systematics*, 33, 341-370.
- 650 Whitley, G.W. & Rabeni, C.F. (1997). Energy sources and ecological role of crayfishes in  
651 an Ozark stream: insights from stable isotopes and gut analysis. *Canadian Journal of*  
652 *Fisheries and Aquatic Sciences*, 54, 2555-2563.

653  
654

655

**Table 1.** Generalized linear models for macroinvertebrate biodiversity metrics with experimental treatment as the factor

<b>Response variable</b>	<b>df</b>	<b>Residual deviance</b>	<b>Pr(&gt;Chi)</b>
Taxonomic richness	3	14.64	<b>0.05</b>
# Individuals	3	92826.00	0.84
Shannon index	3	1.36	0.31
$\beta$ diversity (Jaccard)	3	0.15	<b>0.04</b>
Gastropod sp. richness	3	1.51	0.31
Gastropod density	3	27012.00	<b>0.01</b>
<i>A. aquaticus</i> density	3	26.12	0.88
Chironomidae density	3	277.04	0.75

656

**Table 2.** Generalized linear models for ecosystem functioning and water quality with experimental treatment as the factor

<b>Response type</b>	<b>Response variable</b>	<b>df</b>	<b>Residual deviance</b>	<b>Pr(&gt;Chi)</b>
Ecosystem functioning	Macroinvertebrate shredding	3	0.01	0.27
	Microbial decomposition	3	0.00	0.68
	Plant biomass	3	198.97	0.55
	Primary productivity biofilm	3	0.68	<b>0.03</b>
	Biofilm biomass accrual	3	0.00	0.27
	Primary productivity phytoplankton	3	6441.10	0.40
	Biomass of plankton	3	0.00	0.81
	Sediment respiration	3	0.00	0.26
	Community respiration	3	98932.00	0.39
	Gross Primary Productivity	3	139674.00	0.41
	Net Ecosystem Productivity	3	16709.00	0.34
Ecosystem properties	Turbidity	3	10.76	<b>0.01</b>
	pH	3	0.49	<b>0.05</b>
	NH <sub>3</sub> -N	3	0.37	0.09
	NO <sub>3</sub> -N	3	11.05	<b>0.02</b>
	PO <sub>4</sub> -P	3	0.04	0.14
	Dissolved oxygen	3	12.99	0.23

657

658

**Table 3.** Generalized linear models assessing interactions between top-down and bottom-up regulation of algal biofilms

<b>Response variable</b>	<b>Explanatory variable</b>	<b>Df</b>	<b>Residual deviance</b>	<b>Pr(&gt;Chi)</b>	<b>AIC</b>
Biofilm primary productivity	Decapod*Gastropod	3	0.05	<b>0.03</b>	-30
	Decapod*Turbidity	3	0.06	<b>0.05</b>	-24
	Decapod species	3	0.07	0.09	-20
	Turbidity	1	0.02	0.19	-19
	Nitrate	1	0.01	0.38	-18
	Gastropod abundance	1	0.00	0.67	-17
	Gastropod*Turbidity	1	0.00	0.76	-15
	Gastropod*Nitrate	1	0.00	0.80	-14
	Decapod*Nitrate	3	0.01	0.92	-13

659

660

661 **FIGURE CAPTIONS**

662

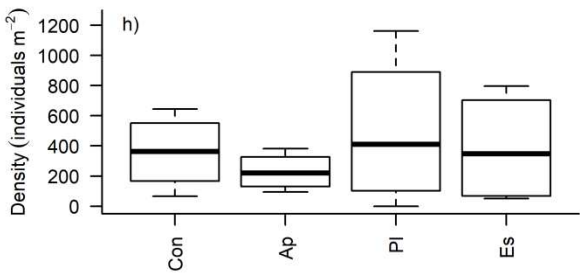
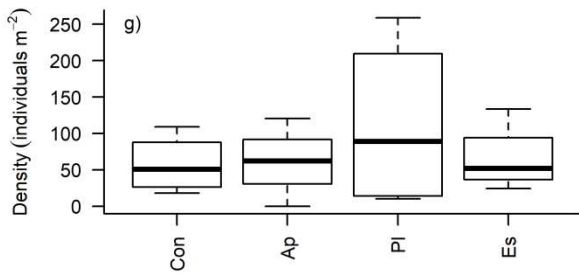
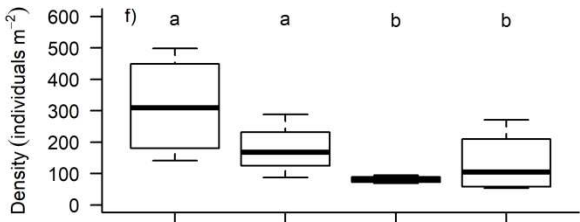
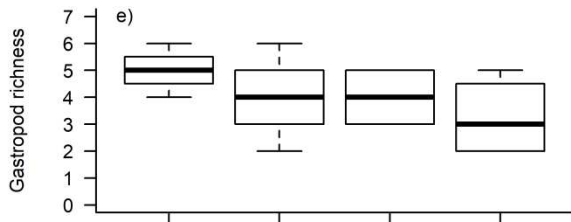
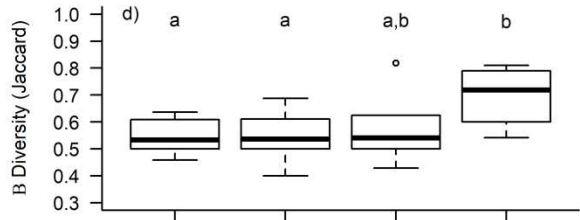
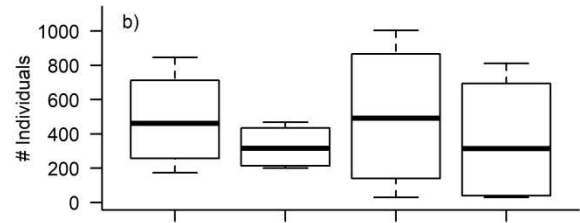
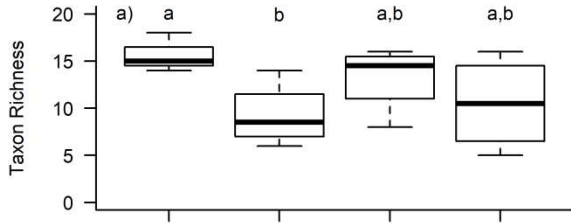
663 **Figure 1.** Macroinvertebrate community: (a) Invertebrate taxonomic; (b) the number of  
664 individuals of all invertebrate species; (c) Shannon diversity; (d)  $\beta$  diversity based on  
665 Jaccard's Index; (e) richness of gastropod species; (f) density of gastropods; (g) density of  
666 *Asellus aquaticus*; and (h) density of Chironomidae larvae. See Table 1 for statistical  
667 analyses. Letters above plots show grouping from *post hoc* test. Abbreviations of x-axis: Con  
668 – control treatments; *Ap* – *Austropotamobius pallipes*, *Pl* – *Pacifastacus leniusculus*; *Es* –  
669 *Eriocheir sinensis*.

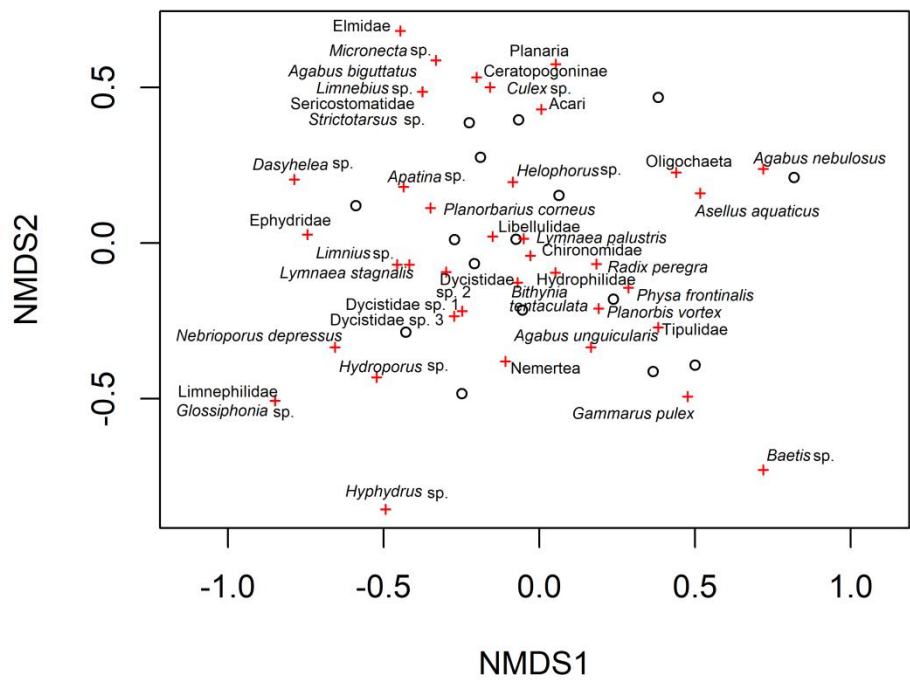
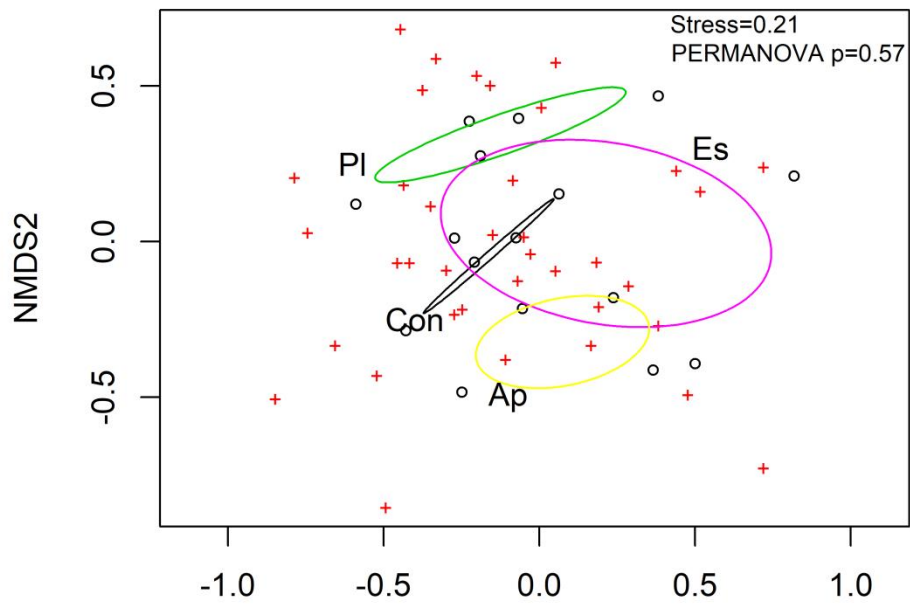
670 **Figure 2.** Non-metric dimensional scaling plots showing invertebrate community dispersion  
671 in the benthic zone of the mesocosm. Abbreviations by each ellipse are: Con – control  
672 treatments; *Ap* – *Austropotamobius pallipes*, *Pl* – *Pacifastacus leniusculus*; *Es* – *Eriocheir*  
673 *sinensis*.

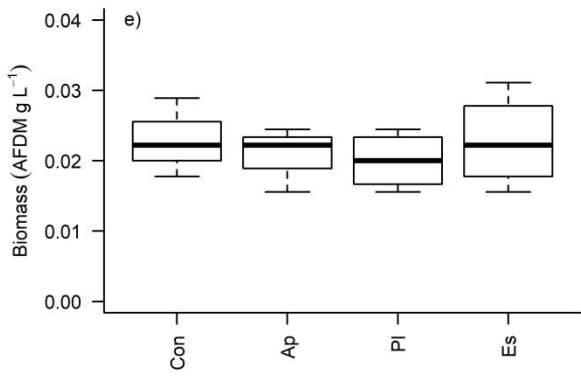
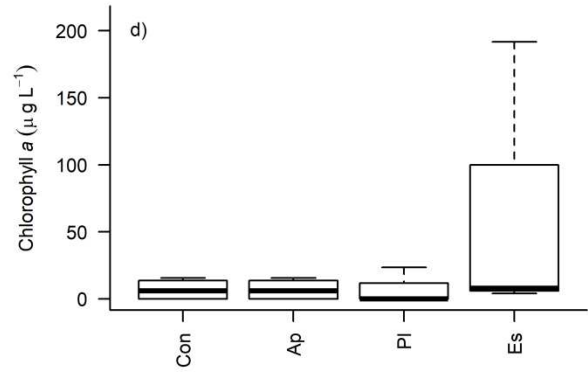
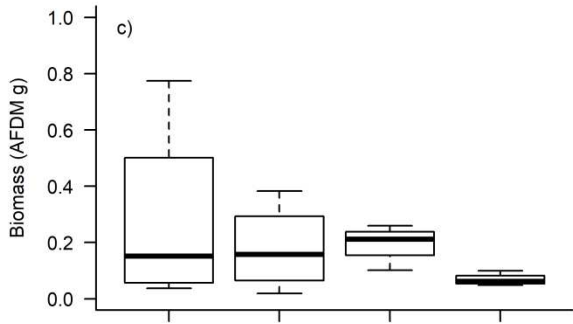
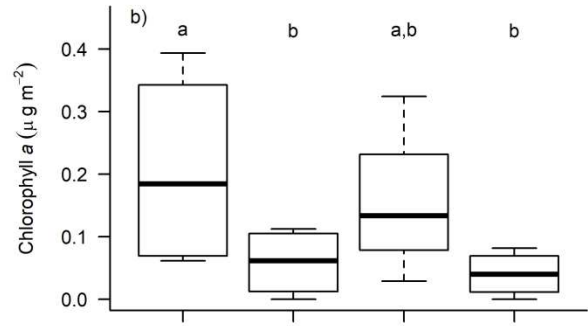
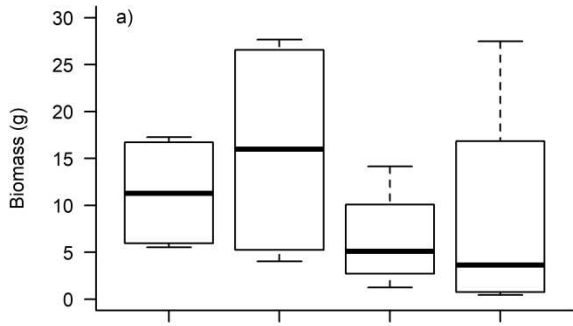
674 **Figure 3.** Primary production in mesocosms: a) biomass of submerged macrophytes; b)  
675 primary productivity of periphyton; c) biomass of biofilms; d) primary productivity of  
676 phytoplankton; e) biomass of plankton. Letters above plots show grouping from *post hoc* test.  
677 Abbreviations of x-axis as for Fig. 1.

678 **Figure 4.** Ecosystem properties of mesocosms: (a) turbidity (N.T.U.); (b) pH; (c) ammonium  
679 ( $\text{NH}_3\text{-N}$ ); (d) nitrate ( $\text{NO}_3\text{-N}$ ); (e) soluble reactive phosphorus [SRP] ( $\text{PO}_4\text{-P}$ ); (f) dissolved  
680 oxygen. Letters above plots show grouping from *post hoc* test. Abbreviations of x-axis as  
681 with Fig. 1.

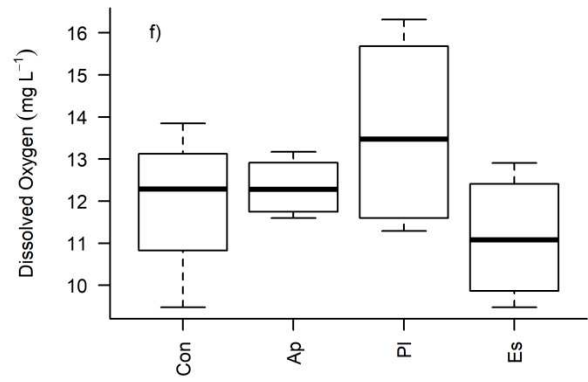
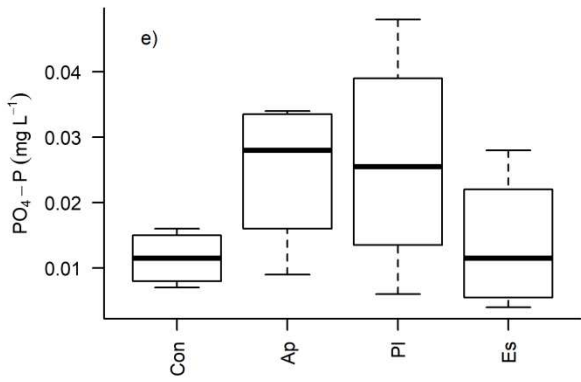
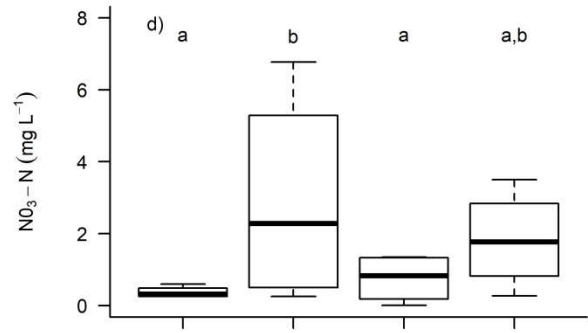
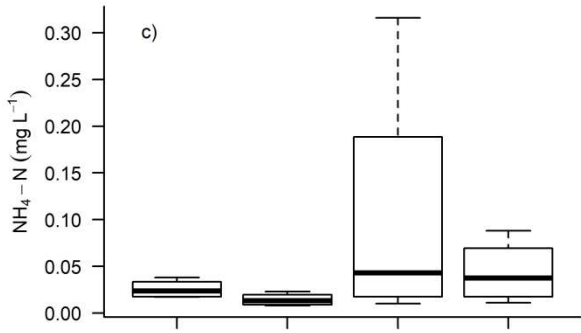
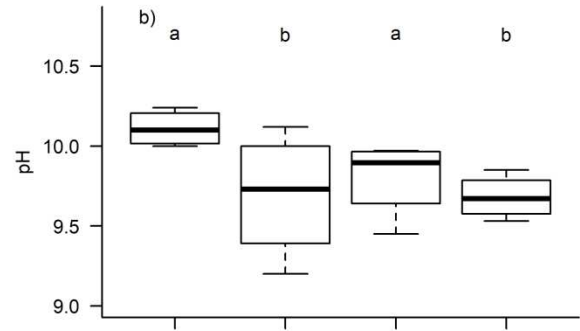
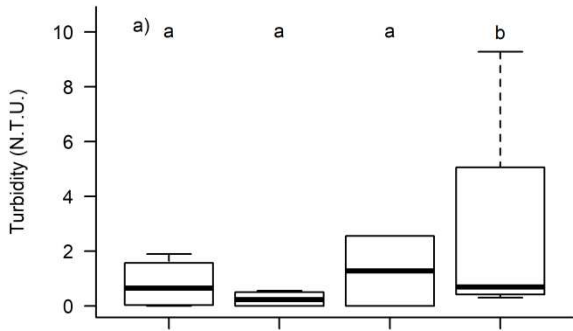
682







685  
686



687

688

689

690

691

692

693

694 **Supporting information for Doherty-Bone et al. (in review) Multi-faceted impacts of**  
695 **native and invasive alien decapod species on freshwater biodiversity and ecosystem**  
696 **functioning**

697

**Supporting Information Table 1. Macroinvertebrate inventory and origin of mesocosms.** Those species that colonised include those that arrived either through the addition of water from other water bodies or carried on the aquatic plants.

<b>Taxon</b>	<b>Origin</b>
Acari	Colonised
<i>Agabus biguttatus</i>	Colonised
<i>Agabus nebulosus</i>	Colonised
<i>Agabus unguicularis</i>	Colonised
<i>Apatania</i> sp.	Colonised
<i>Asellus aquaticus</i>	Seeded
<i>Baetis</i> sp.	Seeded
<i>Bithynia tentaculata</i>	Seeded
Ceratopogoninae	Colonised
<i>Chaoborus</i> sp.	Colonised
Chironomidae	Both
Coenagrionidae	Colonised
<i>Culex</i> sp.	Colonised
<i>Dasyhelea</i> sp.	Colonised
Elmidae	Colonised
<i>Elmis</i> sp.	Colonised

Ephydridae	Colonised
<i>Gammarus pulex</i>	Seeded
<i>Glossiphonia</i> sp.	Colonised
<i>Halipus lineolatus</i>	Colonised
<i>Helophorus</i> sp.	Colonised
<i>Hydroporus</i> sp.	Colonised
<i>Hyphydrus</i> sp.	Colonised
Hydrophilidae	Colonised
Libellulidae	Colonised
<i>Limnebius</i> sp.	Colonised
Limnephilidae	Colonised
<i>Limnius</i> sp.	Colonised
<i>Lymnaea palustris</i>	Seeded
<i>Lymnaea stagnalis</i>	Seeded
<i>Micronecta</i> sp.	Colonised
<i>Nebrioporus depressus</i>	Colonised
Nemertea	Colonised
<i>Notonecta</i> sp.	Colonised
<i>Odontocercum albicorne</i>	Colonised
Oligochaeta	Colonised
<i>Physa fontinalis</i>	Seeded
Planarian	Colonised
<i>Planorbis albus</i>	Seeded
<i>Planorbarius corneus</i>	Seeded
<i>Planorbis vortex</i>	Seeded

<i>Platycnemis</i> sp.	Colonised
<i>Radix peregra</i>	Seeded
<i>Rhantus grapii</i>	Colonised
<i>Sericostoma</i> sp.	Seeded
<i>Strictotarsus</i> sp.	Colonised
Tipulidae	Colonised

698

---

**Supporting Information Table 2. Water physiochemical parameters**

Parameter	Units	Mean	StDev
Dissolved oxygen	ppm	12.27	1.82
Ammonia (NH <sub>4</sub> -N)	ppm	0.05	0.08
Nitrate (NO <sub>3</sub> -N)	ppm	1.46	1.82
pH	-	9.82	0.29
Soluble reactive phosphorous	ppm	0.02	0.01
Water temperature	Celcius	23.02	0.81
Turbidity	NTU	1.26	2.31

---

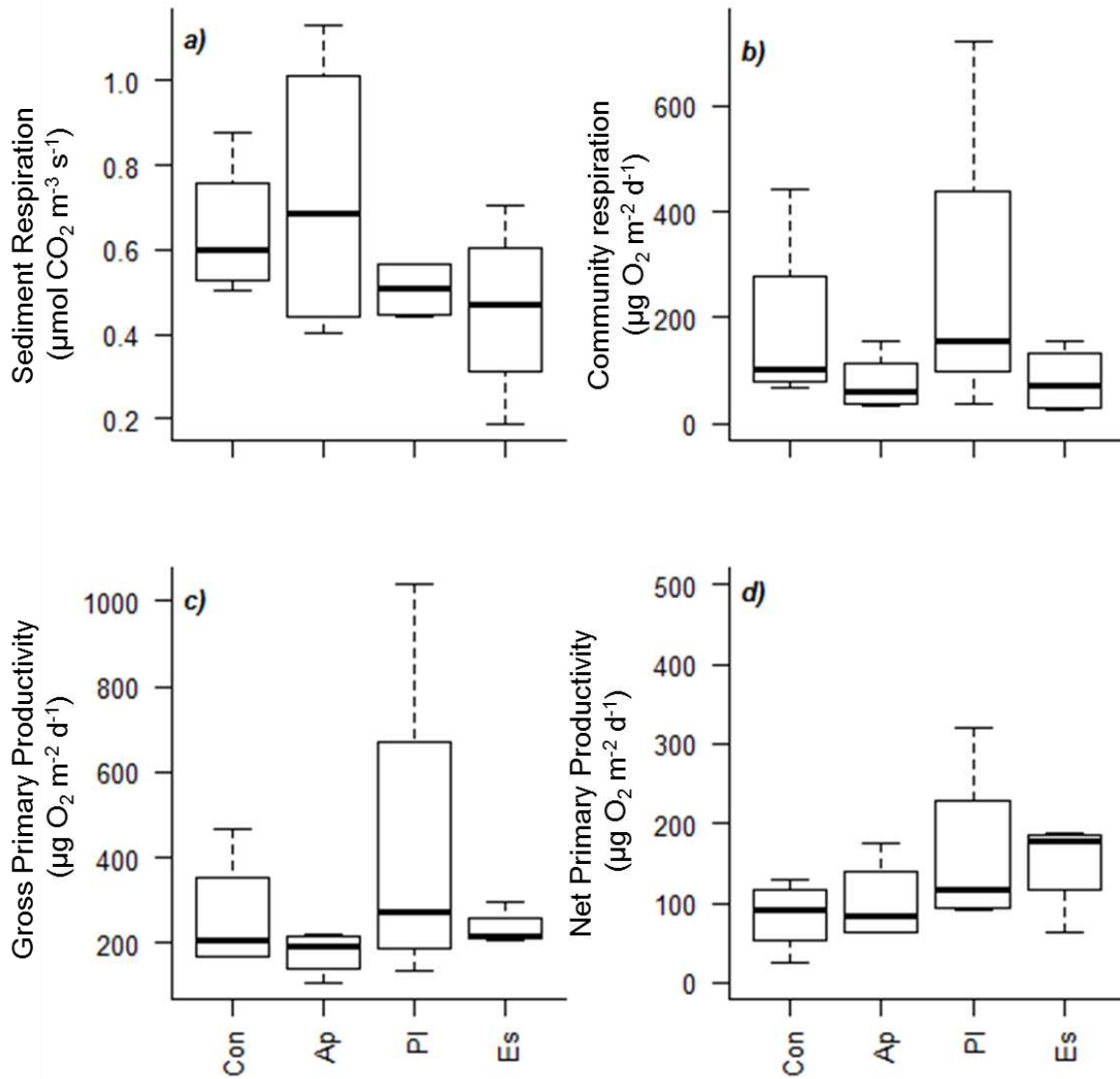
699



700

701 **Supporting Information Figure 1.** Water tank mesocosm facility used for the experiment.  
702 Shown also is the array of dissolved oxygen probes and data loggers measuring community  
703 respiration and an anemometer measuring wind speed to correct for reaeration.

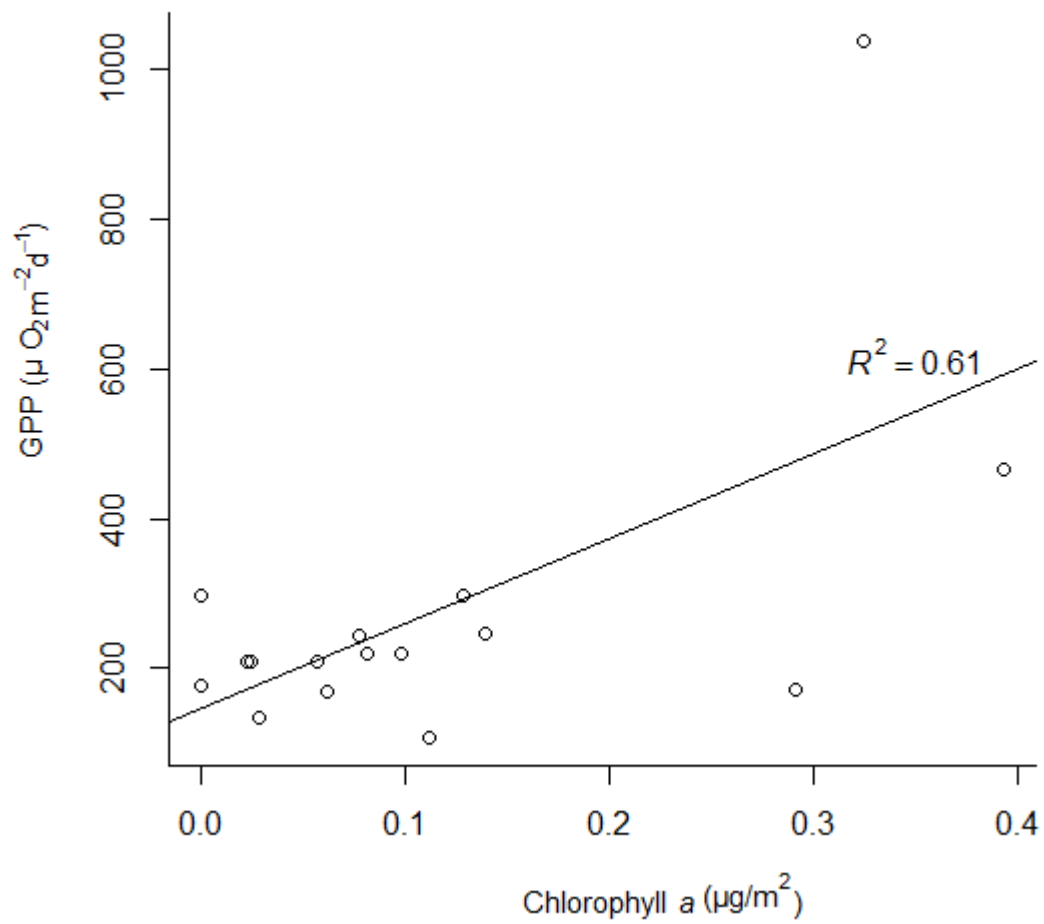
704



705

706 **Supporting Information Fig 2.** Ecosystem-scale respiration and productivity: a) Sediment  
 707 respiration; b) community respiration; c) gross primary productivity ( $\mu\text{g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ ); d) net  
 708 ecosystem productivity ( $\mu\text{g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ ). Abbreviations of x-axis as for Fig 2.

709



710

711 **Supporting Information Figure 3.** Correlation of gross primary productivity of mesocosms  
712 and primary productivity of biofilms (measured using chlorophyll *a*).

713

714

715