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

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Summary

1. Changes to species composition, such as biological invasions and extinctions, have the potential to alter ecosystems. Invaders often replace taxonomically similar species, resulting in potentially redundant impacts. For example, freshwater decapod crustaceans are pervasive invasive alien species but they often extirpate native decapods. This study addresses whether or not these compositional shifts lead to impacts on the structure of the macroinvertebrate community,key ecosystem functions such as decomposition rates and primary productivity and freshwater properties such as turbidity.
2. In a controlled outdoor mesocosm experiment that ran for 33 days, impacts on biodiversity, ecosystem functioning and properties were compared between a native, endangered crayfish (Austropotamobius pallipes) and two invasive alien decapods: the crayfish Pacifastacus leniusculus and crab Eriocheir sinensis. Equal densities of these decapod species were compared between mesocosms, with a replicated array of decapod free controls. Measurements included macroinvertebrate densities, decomposition of leaf litter, production of biofilms, plankton, macrophytes, gross primary productivity, turbidity and dissolved nutrients.
3. While taxonomic richness of non-decapod macroinvertebrates was marginally higher in the invasive alien treatments, differences in Shannon diversity were negligible, and beta diversity was higher for the invasive alien crab. Gastropod density was reduced in the benthos of invasive alien treatments. This was associated with increased primary productivity of periphyton, particularly in the presence of P. leniusculus. Increased turbidity was however inversely correlated with periphyton primary productivity in the E. sinensis treatment. Nitrate concentration was significantly lower in invasive compared to native crayfish mesocosms, but similar to decapod free

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

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

Introduction

The change of species composition within and its impact on ecosystems is a critical issue in environmental management (Loreau et al., 2001, Balvanera et al., 2006). Biological invasions are a prime driver of changes to species composition and are one of the most widespread and damaging pressures on freshwater ecosystems (Strayer and Dudgeon, 2010, Ricciardi and MacIsaac, 2011). The mechanisms by which invasive alien species influence ecosystems are frequently complex and challenging to predict (Simberloff et al., 2013). Invasive alien decapods (crabs and crayfish) are common invaders of freshwater ecosystems globally, causing changes to ecosystem services (Lodge et al., 2012). Conversely, numerous freshwater decapods are threatened with extinction, including by invasive alien species of other decapods (Richman et al., 2015). A major question then is whether native and alien species are ecologically redundant. For example, where an invader is functionally similar to a native species, it would either extirpate or co-occur with the native species, exerting no novel impacts that would otherwise cause ecosystem change. Alternatively replacement of a native by a non-redundant invasive species would drive changes in ecosystems through novel trophic and engineering interactions (Rosenfeld, 2002, Magoulick and Piercy, 2016).

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

Studies on the ecological consequences of replacement of native decapods species by non-native species have found both redundant and non-redundant outcomes in microcosms, mesocosms and the field (Twardochleb et al., 2013, Lagrue et al., 2014, Ercoli et al., 2015). For example, redundancy has been reported between invasive and native crayfish based on field observations and in-situ enclosure experiments (Ercoli et al., 2014, Lagure et al., 2014). Meta-analyses have found invasive decapods tend to exert stronger effects on lower resources such as detritus and prey compared to native species (Twardochleb et al., 2013, James et al., 2014). Native decapod species also exert strong top-down impacts, with implications for both extinctions and conservation translocations (Rosewarne et al., 2013, James et al., 2014). Some experiments have however shown non-redundant impacts of various species of invasive crayfish on invertebrates and ecosystem processes (Dunoyer et al., 2014, Jackson et al., 2014). The literature is dominated by North American examples, with European invasion syndromes limited to loss of Noble Crayfish (Astacus astacus, Astacidae) (e.g. Nystöm et al., 1999, Ercoli et al. 2014, 2015), as opposed to other native European species such as Austropotamobius (Astacidae). Many of the studies in published meta-analyses also only compared experiments involving only one decapod separately as opposed to those exposing the native and invasive to the same experimental conditions (James et al., 2014).

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

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

The aims of this study were to measure the impacts of decapod invasion and extinction on macroinvertebrate community structure, autogenic and allochthonous ecosystem processes and properties (aquatic physicochemistry). The following hypotheses were tested: (H_1)

decapod presence would result in increased consumption of resources, especially by invasive species (Haddaway et al., 2012, Rosewarne et al., 2016), particularly slow moving species such as gastropods and other invertebrates, leading to (H_2) reduced grazing pressure and an increase in primary and gross primary production. It was also expected that (H_3) decomposition rates would be maintained or even enhanced in invasive species treatments, despite depletion of shredding invertebrates, due to high omnivory amongst decapods (Usio et al., 2000, Dunoyer et al., 2014, Doherty-Bone et al. 2018); and (H_4) invasive alien decapods would alter water quality through changes to dissolved nutrients from excretal products (Evans-White & Lamberti, 2005, Usio et al. 2006, Doherty-Bone et al., 2018, Fritschie & Olden, 2018), increased turbidity from bioturbation (Harvey et al., 2013) and particulate carbon from detritivory (Doherty-Bone et al., 2018).

Materials & Methods

Experimental set-up

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

Each mesocosm was filled with water from a nearby borehole up to c .0.002 m^3. A substrate of a 9:1 mix of sand and Aquasoil and gravel of ~ 3 cm depth was then added to each mesocosm. Microbial communities were added (09 Apr 2013 – 73 days prior to the experiment) through the addition of 1 litre inoculum from a homogenate of water originating from a broad range of nearby freshwater habitats so far un-invaded by alien decapods. Native macrophytes in the mesocosm consisted of Ceratophyllum demersum (Ceratophyllaceae), 115 g wet mass rinsed with deionised water to remove large numbers of passenger invertebrates, plankton and microbes. This species was chosen because it is abundant in lentic freshwaters in the UK and Europe (Duigan et al., 2007). These were planted in the middle of the water tank (11 Apr 2013 – 72 days prior to the experiment) in pots containing gravel and 1 ml of aquatic plant compost (Aquasol®). To allow a standard surface for the sampling of algal biofilm, an unglazed tile was placed on the sediment surface of each mesocosm so it would receive the same light exposure. To provide a resource for the “brown” compartment of the food web, leaf litter detritus was added in the form of 10g Alder (Alnus glutinosa, Betulaceae) and 40g Oak (Quercus robur, Fagaceae) which had been air dried following abscission before weighing. In addition, three packs of pre-weighed (5 g) oven dried Alder leaves with coarse mesh (20 mm aperture) were added to each mesocosm to enable decomposition rates to be estimated. These were accompanied with a single fine pack (0.5 mm aperture, to exclude most macroinvertebrate shredders) of Alder leaves to differentiate microbial from macroinvertebrate breakdown.

Macroinvertebrates with limited colonization abilities were added to each mesocosm 30 days prior to addition of decapods to the experiment: chironomid larvae (Chironomus sp., Chironomidae ~ 1500 individuals); Gammarus pulex (Gammaridae, 100 individuals); Asellus aquaticus (Asellidae, 100 individuals); Baetis rhodani (Baetidae, 50 individuals); Cased-caddis larvae, Sericostoma sp. (Sericostomatidae, 10 individuals); and six species of gastropod (100 individuals of Radix peregra Lymnaeidae, 10 Planorbarius corneus Planorbidae, 10 Lymnaea stagnalis Lymnaeidae, 10 Lymnaea palustris Lymnaeidae, 20 Physa fontinalis Physidae, 10 Bithynia tentaculata Bithyniidae). Other invertebrates colonised naturally. Collectively, the water tanks held 47 taxa of 12,075 individuals by the end of the experiment. The most dominant species (by percentage of individuals) were gastropods (39%), chironomid larvae (37%) and A. aquaticus (13%). The water tanks were also colonised by water boatmen (Micronecta sp. Corixidae and Notonecta sp. Notonectidae). A full list of invertebrate species occurring in the mesocosms and their origin is listed in Supp. Table 1. General water quality parameters are given in Supp. Table 2.

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

Experimental design

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

Macroinvertebrate sampling

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

Ecosystem functioning

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

Macrophytes were rinsed in deionised water to remove invertebrates and other material, and dried for 24 hours or until constant mass at 50°C, then ashed at 500°C to estimate AFDM. Filamentous algae was abundant in all the mesocosms but not measured due to time constraints and the difficulty in separating other matter to obtain reliable estimates of mass. Biofilms (bacteria, fungi and periphyton) were sampled from the tiles using a nylon brush and stored at -20°C prior to processing. Biofilm biomass was measured as for FPOM described above. Primary productivity (measured as chlorophyll a) of periphyton from a 5 ml sub-sample was measured using the filtration and spectrometric method of Steinman et al. (1996). Water samples were collected from the surface water for plankton and stored at -20°C until processing where a 5ml sub-sample measured for chlorophyll a and biomass measured as for biofilms.

Community respiration and gross primary productivity of the mesocosms was measured 30 days into the experiment using the diel oxygen technique, where probes recorded changes in dissolved oxygen (D.O.) every 15 minutes for 24 hours using a YSI Environmental ProODO™ logger, following Bott (1996). The premise of this technique is that changes in D.O. are linked to the extent of both photosynthesis and respiration by the community, with daily respiration estimated from the change in oxygen in darkness (reduction of photosynthetically active radiation verified using a Delta QS-5 quantum sensor connected to a Campbell® CR800 data logger). D.O. was corrected for re-aeration from wind-induced gas exchange with the surface water and atmosphere by measuring wind speed (using an anemometer connected to a Campbell® CR800 data logger) every 15 minutes, sensu Staehr et al. (2010). From these measurements, community respiration ($\mu g\ O_2\ m^{-2}\ d^{-1}$), gross primary productivity ($\mu g\ O_2\ m^{-2}\ d^{-1}$), and net primary productivity ($\mu g\ O_2\ m^{-2}\ d^{-1}$) were calculated. Sediment respiration was measured in-situ in enclosed 350 ml chambers using O_2 consumption over time (3 hours), assuming equal day and night respiration (Bott et al., 1985, Doering et al. 2011).

Ecosystem properties

Physicochemical measurements included pH (using a Hanna pH meter) and turbidity (using a Model 2100 A Turbidmeter, CAMLAB, Cambridge). Dissolved oxygen was measured on day 30 using the probes when using the diel technique mentioned above. Analysis of water samples collected on day 33 were subsequently analysed with a Skaler SAN ++ continuous flow auto-analyser for ammoniacal nitrogen (NH_3-N), nitrates (N-NO_3) and soluble reactive phosphorus (PO_4-P).

Data analysis

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

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

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

Results

Macroinvertebrate diversity and abundance

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

Ecosystem functioning

All ecosystem process variables measured showed no significant difference between treatments, with the exception of primary productivity (chlorophyll a) of algal biofilms (Table 2, Figs. 3a-e, Supp. Fig. 2). Biofilm primary productivity was higher for P. leniusculus treatments than A. pallipes and E. sinensis, but similar to controls (Fig. 3b). Subsequent modelling found that the interaction between decapod treatment and the abundance of gastropods was a significant factor influencing primary productivity of biofilms and provided the strongest model (Table 3). The interaction of treatment and turbidity showed a marginally significant ($p = 0.05$) effect on biofilm productivity, but there was no significant effect of the interaction between turbidity and gastropods on biofilm productivity (Table 3). Primary productivity of algal biofilms showed a significant, positive relationship with gross primary productivity (glm $p = 0.003$, Pearson's correlation coefficient=0.62, Supp. Fig. 3). Other primary producers (phytoplankton and submerged macrophytes) showed no significant relationship with gross primary productivity (GPP).

Ecosystem properties

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

Discussion

This study has identified the potential for both ecological redundancy and non-redundancy for various ecological parameters among the invasive alien (P. leniusculus and E. sinensis) and the native decapod species (A. pallipes) in a replicated controlled mesocosm facility. This experimental setting provided a more realistic, complex environment to appraise potential impacts of an invasion syndrome occurring across Western Europe. Previous studies on this invasion syndromehad been limited to laboratory-based experiments or indirect comparisons. This system reflected a functioning lentic ecosystem, with a realistic diversity of invertebrates and trophic elements, such as detritius, biofilms, plankton and plants in the presence of dynamic environmental variables.

Impacts on macroinvertebrate community

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

Given the depletion of gastropods by the invasive alien decapods, the lower taxonomic richness of invertebrates in native crayfish mesocosms compared to the two invasive species and controls was unexpected. The factors causing this are unclear, with several beetle species apparently assembling with the two invasive species mescososms. This could be the result of invasive decapods creating a trophic cascade through the increased provision of FPOM (sensu Doherty-Bone et al., 2018), which is then consumed by prey of these beetles. The negligible impacts on Shannon diversity in response to both native and invasive alien decapods are in accord with Rosewarne et al. (2013, 2016). However, the study contrasts to the significant reduction of taxonomic richness in mesocosms with P. leniusculus observed by Jackson et al. (2014). Examples of decreases in invertebrate taxonomic richness and Shannon diversity in rivers and lakes invaded by P. leniusculus (Stenroth and Nyström, 2003, Crawford et al., 2006, Ercoli et al., 2015), may reflect the higher densities of invasive versus native decapods in the field. The study's community assembly also contrasts to field observations of P. leniusculus invasions (compared to the uninvaded, crayfish-free sites), where invertebrate community structure differed considerably between invaded and un-invaded sites (Crawford et al., 2006, Mathers et al 2016).

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

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

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

Impacts on ecosystem functioning

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

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

Plankton biomass and primary productivity were not affected by either decapod treatment, explained by greater decapod influence on benthic as opposed to pelagic habitats (Strayer, 2010). Biomass of the submerged macrophyte (Ceratophyllum) was expected to be reduced compared to controls and native crayfish treatments through direct consumption or shredding by omnivorous decapods: this pattern was observed but was not significant (Fig. 3d). This absence of impact on macrophytes has also been observed by Rosewarne et al. (2016), but other studies have found depletion of macrophytes by P. leniusculus (Nyström et al., 1996, Nyström et al., 2001, Nyström and Strand, 2003). The presence of more nutritious food items, such as animal prey, is likely to be a factor in this observation (Whitledge & Rabeni, 1997, Magoulick and Piercey, 2016). Incorporation of a demographically representative composition of adults, sub-adults and juveniles (as with Nyström et al., 2001), might also have created similarly differential usage of resources in this experiment, based on ontogenetic dietary preferences (Usio et al., 2009, Rosewarne et al., 2013).

Impacts on ecosystem properties

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

The increased nitrate concentration in decapod treatments suggests nitrification of ammonia excreted by decapods. Isolation of these species in the laboratory has shown a similar pattern of ammoniacal nitrogen (NH_3-N) production for each species, with similar values for A. pallipes and E. sinensis and lower values for P. leniusculus (Doherty-Bone et al., 2018). The lower ammonia excretion by P. leniusculus, leading to lower NO_3–N production suggests this species is likely to be a greater nutrient sink (sensu Vanni, 2002) compared to A. pallipes, through consuming and assimilating more nitrogen and reducing its availability to other organisms (particularly absorbing species such as primary producers). This suggests that invasions by P. leniusculus and the extirpation/translocation of A. pallipes could affect nitrogen cycling and community structure in N-limited ecosystems. A similar relationship has been observed for the replacement of the native Japanese crayfish Cambaroides japonicas (Cambaridae) by P. leniusculus (Usio et al., 2006).

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

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

Response variable	df	Residual deviance	Pr(>Chi)
Taxonomic richness	3	14.64	**0.05**
# Individuals	3	92826.00	0.84
Shannon index	3	1.36	0.31
β diversity (Jaccard)	3	0.15	**0.04**
Gastropod sp. richness	3	1.51	0.31
Gastropod density	3	27012.00	**0.01**
A. aquaticus 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

Response type	Response variable	df	Residual deviance	Pr(>Chi)
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	**0.03**
	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	**0.01**
	pH	3	0.49	**0.05**
	NH_3-N	3	0.37	0.09
	NO_3-N	3	11.05	**0.02**
	PO_4-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

Response variable	**Explanatory variable**	**Df**	**Residual deviance**	**Pr(>Chi)**	**AIC**
Biofilm primary productivity	Decapod*Gastropod	3	0.05	**0.03**	-30
	Decapod*Turbidity	3	0.06	**0.05**	-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

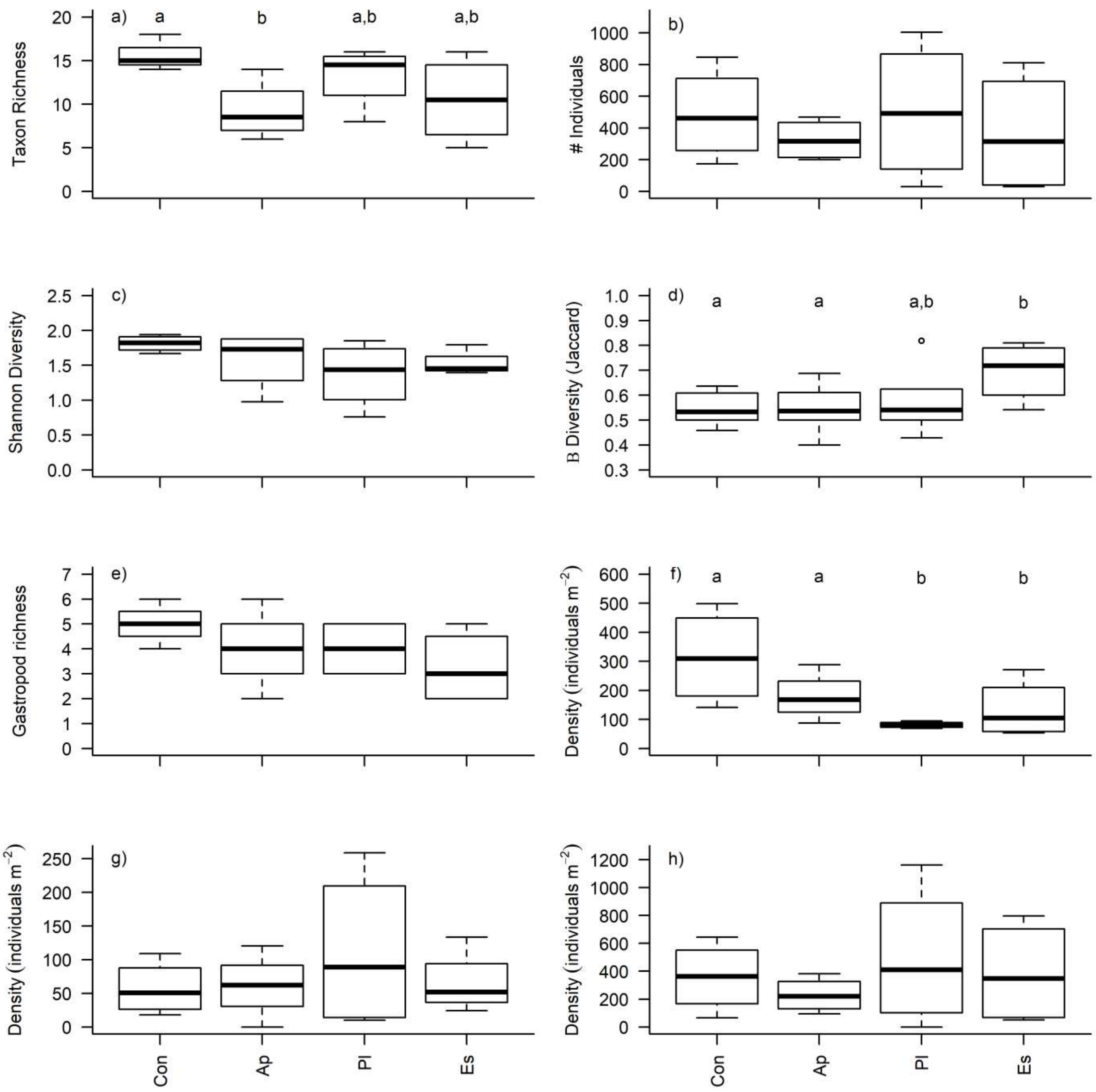
FIGURE CAPTIONS

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

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

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

Figure 4. Ecosystem properties of mesocosms: (a) turbidity (N.T.U.); (b) pH; (c) ammonium (NH_3-N); (d) nitrate (NO_3-N); (e) soluble reactive phosphorus [SRP] (PO_4-P); (f) dissolved oxygen. Letters above plots show grouping from post hoc test. Abbreviations of x-axis as with Fig. 1.


a)
Taxon Richness
a
b
a,b
a,b
0
5
10
15
20
b)
Individuals
0
200
400
600
800
1000
c)
Shannon Diversity
0.0
0.5
1.0
1.5
2.0
2.5
d)
Β Diversity (Jaccard)
a
a
a,b
b
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
e)
Gastropod richness
0
1
2
3
4
5
6
7
f)
Density (individuals m^{-2})
a
a
b
b
0
100
200
300
400
500
600
g)
Density (individuals m^{-2})
0
50
100
150
200
250
h)
Density (individuals m^{-2})
0
200
400
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800
1000
1200
Con
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Es
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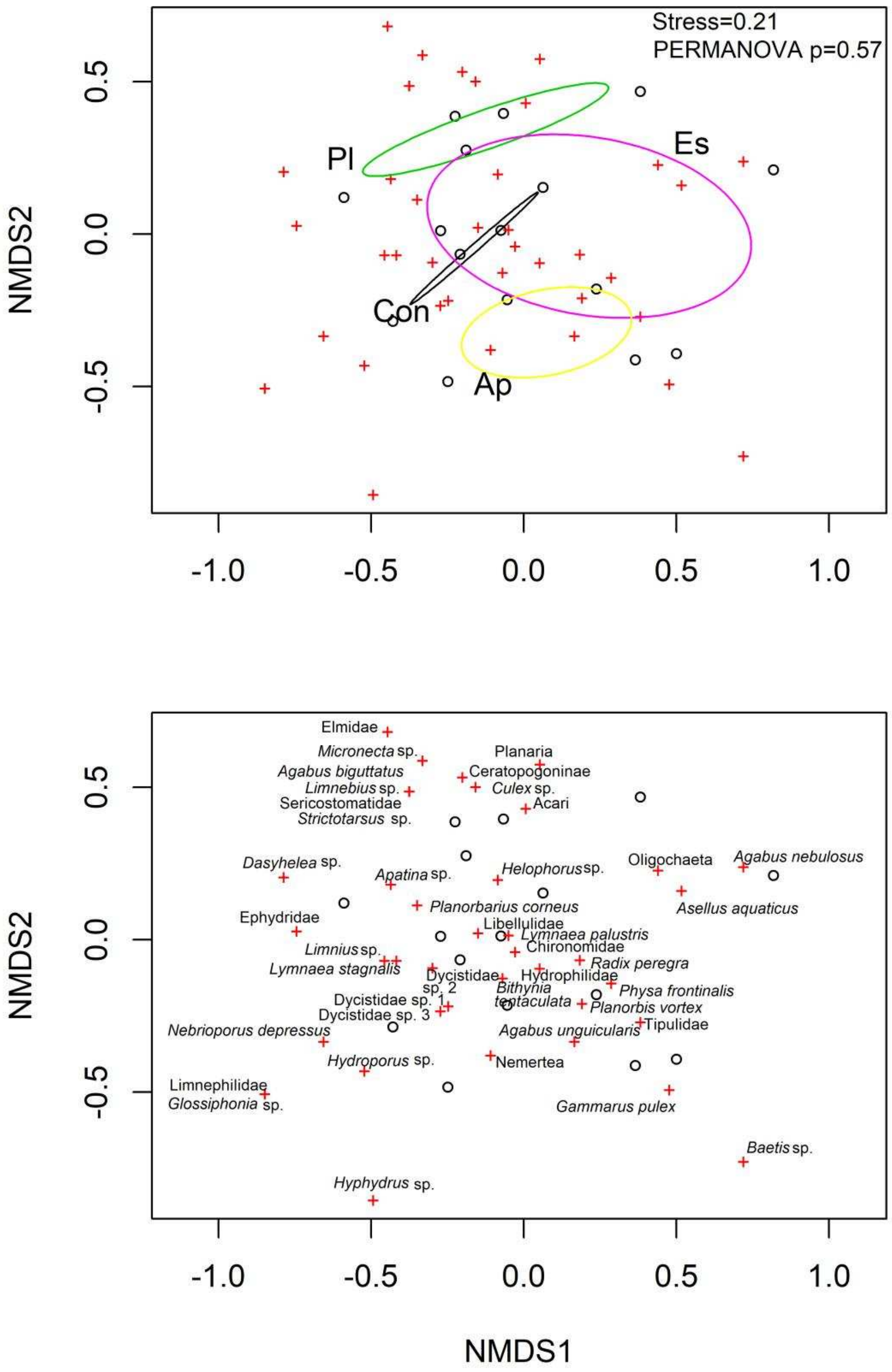
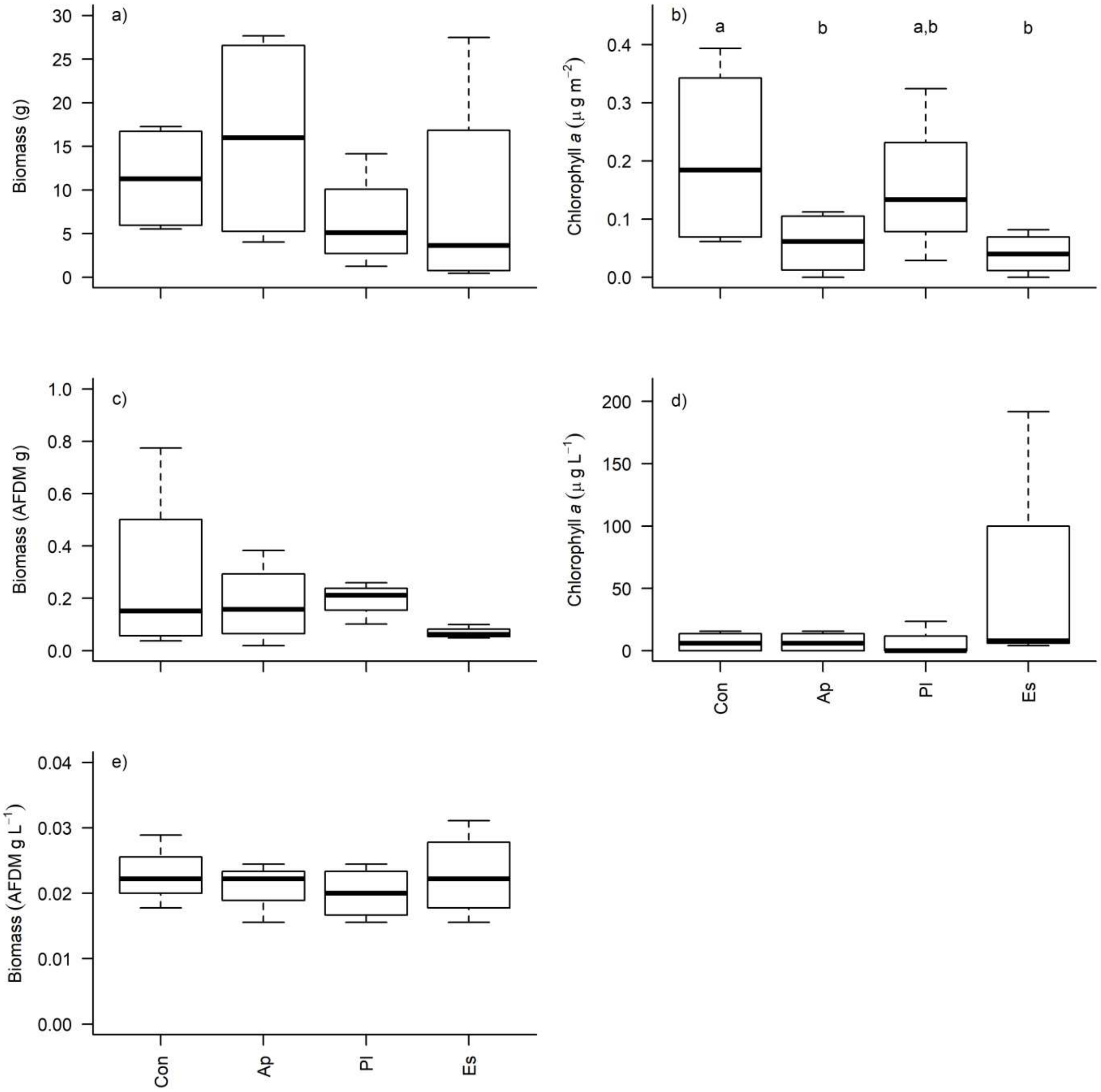
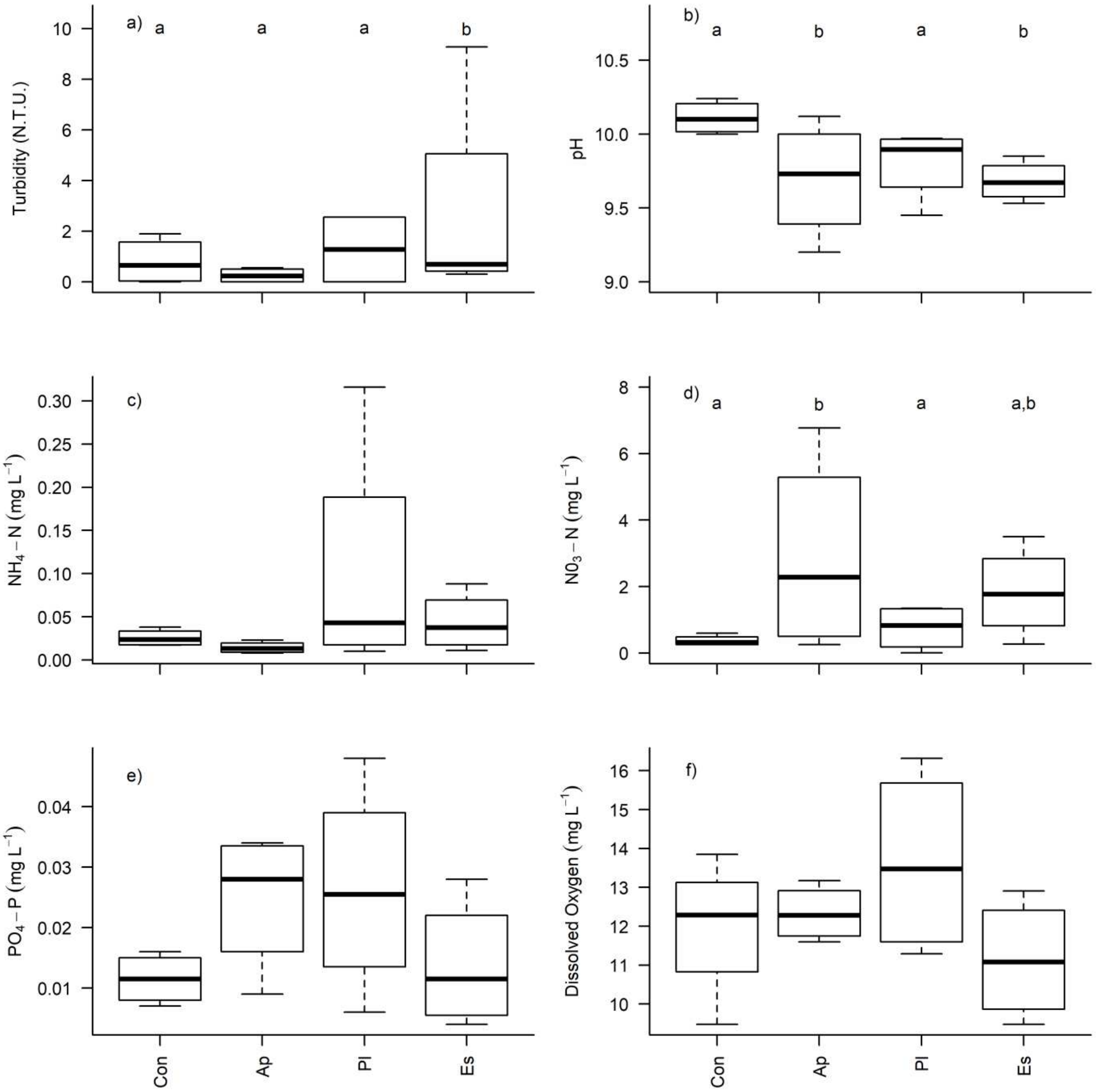

Stress=0.21
PERMANOVA p=0.57
Pl
Es
Con
Ap
NMDS2
0.5
0.0
-0.5
-1.0
-0.5
0.0
0.5
1.0
Elmidae
Micronecta sp.
Agabus biguttatus
Limnebius sp.
Sericostomatidae
Strictotarsus sp.
Planaria
Ceratopogoninae
Culex sp.
Acari
Dasyhelea sp.
Apatina sp.
Helophorus sp.
Oligochaeta
Agabus nebulosus
Asellus aquaticus
Ephydridae
Planorbarius corneus
Libellulidae
Lymnaea palustris
Chironomidae
Limnius sp.
Lymnaea stagnalis
Dycistidae sp. 2
Hydrophilidae
Radix peregra
Bithynia tentaculata
Physa frontinalis
Planorbis vortex
Dycistidae sp. 1
Dycistidae sp. 3
Nebrioporus depressus
Agabus unguicularis
Tipulidae
Hydroporus sp.
Nemertea
Limnephilidae
Glossiphonia sp.
Gammarus pulex
Baetis sp.
Hyphydrus sp.
NMDS1



a)
Biomass (g)
0
5
10
15
20
25
30
b)
a
b
a,b
b
Chlorophyll a (µ g m⁻²)
0.0
0.1
0.2
0.3
0.4
c)
Biomass (AFDM g)
0.0
0.2
0.4
0.6
0.8
1.0
d)
Chlorophyll a (µ g L⁻¹)
0
50
100
150
200
e)
Biomass (AFDM g L⁻¹)
0.00
0.01
0.02
0.03
0.04
Con
Ap
Pl
Es


a)
a
a
a
b
Turbidity (N.T.U.)
0
2
4
6
8
10
b)
a
b
a
b
pH
9.0
9.5
10.0
10.5
c)
$NH_4 - N$ (mg L^{-1})
0.00
0.05
0.10
0.15
0.20
0.25
0.30
d)
a
b
a
a,b
$N0_3 - N$ (mg L^{-1})
0
2
4
6
8
e)
$PO_4 - P$ (mg L^{-1})
0.01
0.02
0.03
0.04
f)
Dissolved Oxygen (mg L^{-1})
10
11
12
13
14
15
16
Con
Ap
Pl
Es
Con
Ap
Pl
Es

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

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.

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

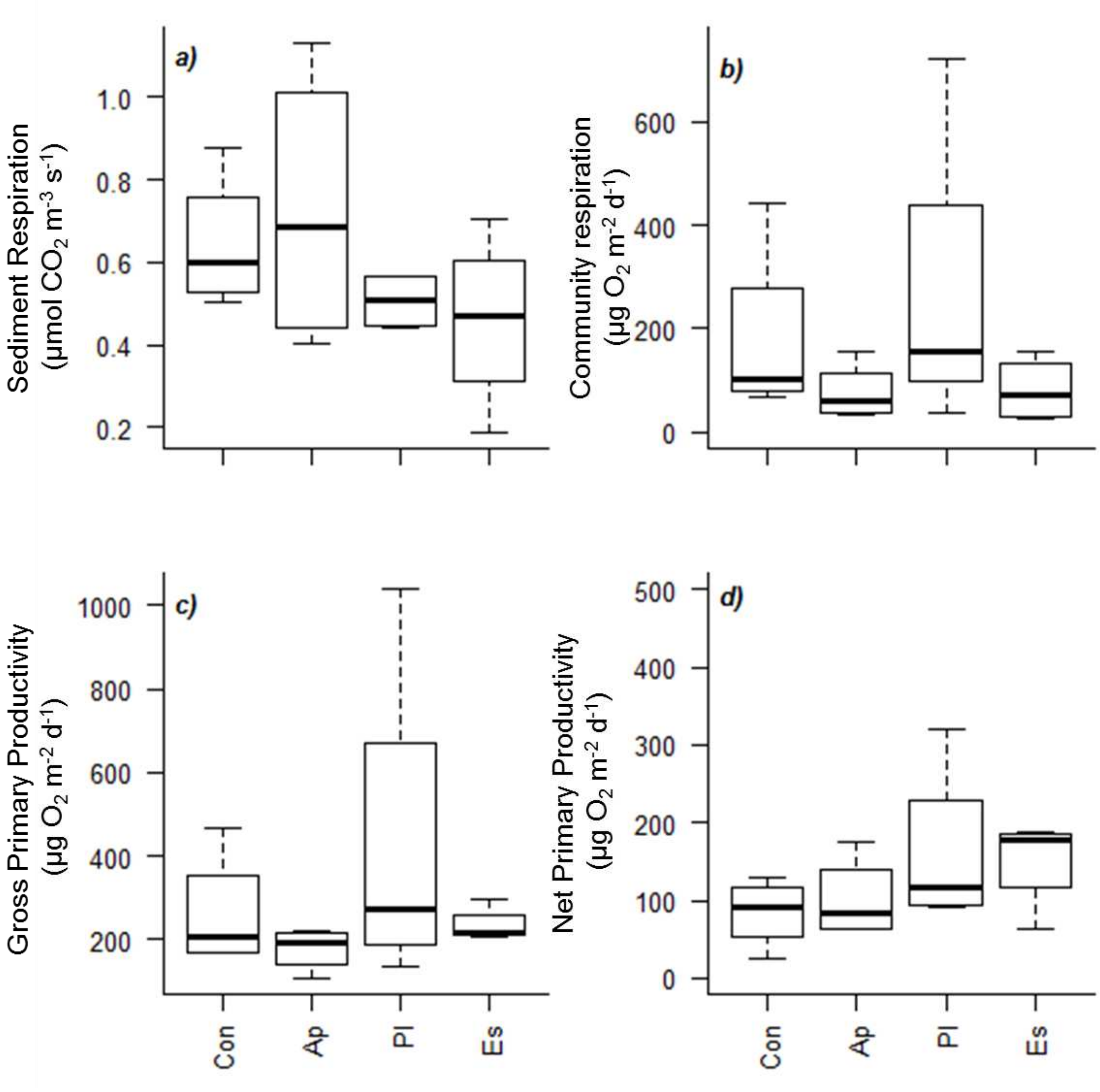
Ephydridae	Colonised
Gammarus pulex	Seeded
Glossiphonia sp.	Colonised
Halipus lineolatus	Colonised
Helophorus sp.	Colonised
Hydroporus sp.	Colonised
Hyphydrus sp.	Colonised
Hydrophilidae	Colonised
Libellulidae	Colonised
Limnebius sp.	Colonised
Limnephilidae	Colonised
Limnius sp.	Colonised
Lymnaea palustris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

Platycnemis sp.	Colonised
Radix peregra	Seeded
Rhantus grapii	Colonised
Sericostoma sp.	Seeded
Strictotarsus sp.	Colonised
Tipulidae	Colonised

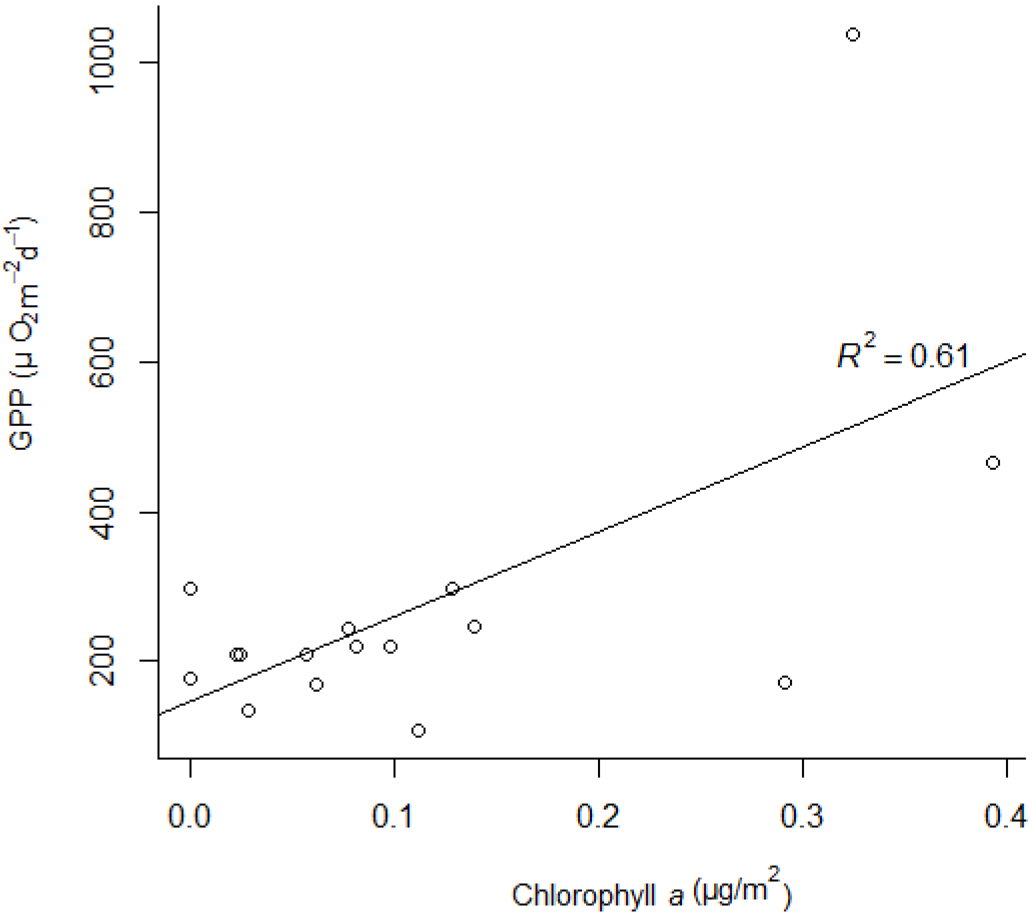
Supporting Information Table 2. Water physiochemical parameters

Parameter	Units	Mean	StDev
Dissolved oxygen	ppm	12.27	1.82
Ammonia (NH4-N)	ppm	0.05	0.08
Nitrate (NO3-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

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



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



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