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Are impacts of the invasive alien plant *Crassula helmsii* mediated by detritus? A litter experiment in a temperate pond

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Abstract Because of the high growth rates often achieved by invasive alien macrophytes, their establishment in recipient ecosystems may alter the abundance and composition of litter entering detrital pathways, representing a significant—but often overlooked—ecological effect of these invasions. *Crassula helmsii* (Kirk) Cockayne (New Zealand pygmyweed) is an invasive alien macrophyte, notorious for its profuse growth in invaded waterbodies. *C. helmsii* is perennial and often forms dense stands, producing abundant detritus. To investigate whether some of *C. helmsii's* impacts are mediated by this detritus, we conducted an 85-day litterbag experiment comparing decomposition of *C. helmsii* with that of *Callitriche stagnalis* Scop. (water-starwort), a commonly co-occurring native macrophyte. Macroinvertebrate assemblage composition was comparable between macrophyte species throughout the experiment, but shifted as plants decayed. Litterbags were initially dominated by the invasive shredder *Crangonyx pseudogracilis* Bousfield, 1958 and later by *Euglesa casertana* (Poli, 1791), an interstitial suspension feeder. *C. helmsii* litter decomposed more slowly, with proportionally less invertebrate-mediated breakdown, but was ultimately colonised by more abundant macroinvertebrates, including more *C. pseudogracilis*. Decomposition may be slowed by *C. helmsii's* high carbon: nitrogen ratio. These results suggest that *C. helmsii* invasion may impact macroinvertebrate assemblages via the production of long-lasting and relatively unpalatable detritus.

Keywords Biological invasion · Detritivory · Ecosystem function · Macroinvertebrate · Submerged macrophyte · Facilitation

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Introduction

Invasive species are proliferating worldwide, aided by human vectors of dispersal and anthropogenic change to recipient ecosystems (Seebens et al., 2017; IPBES, 2023). Establishing the factors which govern the ecological impacts of invasion is a key research goal in invasion biology and could enable problematic invasions to be pre-empted and acted against (Simberloff et al., 2005, 2013). Self-evidently, interactions

between invasive species and recipient biota are key determinants of both ecosystem resilience to invasions, and the impacts of successful invasion (Maron & Vilà, 2001; Simberloff et al., 2013). Because of the foundational role of macrophytes (macroscopic green plants and macroalgae) in terrestrial, freshwater and marine systems, macrophyte invasions may cause far-reaching impacts on recipient ecosystems (Vilà et al., 2011; Maggi et al., 2015; Tasker et al., 2022). In freshwaters, much attention has been paid to determining the rules governing interactions between alien macrophytes and herbivores, mostly due to herbivory's potential role in fostering ecosystem resilience through biotic resistance, wherein invasions may be suppressed by interactions with native biota (Parker & Hay, 2005; Morrison & Hay, 2011; Grutters et al., 2017; Oliveira et al., 2019). In contrast, relatively little research has focussed on interactions between alien macrophytes and detritivores (but see Cuassolo et al. 2020; Dekanová et al. 2021). Whilst detritivory clearly cannot play a direct role in biotic resistance, it may be instrumental to the wider ecosystem impacts of invasive macrophytes. Aquatic macrophytes are generally more frequently consumed as detritus than whilst alive, and macrophyte litter decomposition (conducted in part by detritivores) strongly influences freshwater nutrient cycling and energy flows (Newman, 1991; Shilla et al., 2006; Bakker et al., 2016; Dekanová et al., 2021; Thornhill et al., 2021). Impacts of a macrophyte invader on detritivores are therefore likely to be more significant than impacts on herbivores in determining the invasion's impacts on the recipient ecosystem.

The freshwater decomposition of vascular plant detritus can be thought of as a 3-part process, consisting of (1) leaching; (2) microbial decomposition and (3) mechanical/invertebrate fragmentation (Webster & Benfield, 1986). Leaching of water-soluble compounds leads to considerable early mass loss (Gessner et al., 1999; Pope et al., 1999; Carvalho et al., 2015), concurrent with the beginnings of colonisation by microbes (e.g. bacteria, hyphomycete fungi) and fragmentation of detritus by invertebrate detritivores and/or mechanical action (e.g. by current or abrasives) (Webster & Benfield, 1986; Santonja et al., 2018). The latter two processes act in a positive feedback loop: microorganisms 'condition' the detritus, making it more palatable and nutritious for detritivores (Anderson et al., 2017). Resulting

detritivore fragmentation increases the surface area of the detritus, promoting further microbial colonisation and decomposition (Newman, 1991; Longhi et al., 2008). The rate of decomposition is influenced by detritus traits (Cebrian & Lartigue, 2004), detritivore assemblage composition (Jonsson & Malmqvist, 2000; Gessner et al., 2010) and physical and chemical factors including temperature, pH, oxygen concentration and waterbody trophic state (Webster & Benfield, 1986).

Whilst the aquatic decomposition of invasive riparian, emergent and floating plant litter has been subject to some investigation (Chimney & Pietro, 2006; Saulino et al., 2018; Cuassolo et al., 2020; Dekanová et al., 2021), to our knowledge the decomposition of alien submerged plant litter has rarely been studied to date (Carpenter & Adams, 1979; Shilla et al., 2006). Given the importance of detritus to freshwater nutrient and energy flows, the availability and palatability of invasive macrophyte detritus is likely to strongly influence recipient ecosystems (Cebrian & Lartigue, 2004; Saulino et al., 2018). Detritus availability may vary according to macrophyte phenology and biomass production, and the rate of microbial decomposition. Palatability may vary according to nutrient concentrations, particularly nitrogen and phosphorus, and the retention of defensive chemicals, such as phenolic compounds, or structures, such as trichomes and sclerophylly (Webster & Benfield, 1986; Newman, 1991; Chimney & Pietro, 2006; Hanley et al., 2007). The overall rate of decomposition, and impacts on the invaded ecosystem, will be mediated by match/mismatch between these plant traits and the traits present in the recipient detritivore assemblage (Tiegs et al., 2013; Carvalho et al., 2015).

Crassula helmsii (New Zealand pygmyweed) is an alien aquatic plant, originally from Australasia, which has spread widely across small lentic waterbodies throughout NW Europe since its introduction in the mid-twentieth century (Smith & Buckley, 2020). Small waterbodies are particularly threatened by biological invasions due to their insular, island-like nature, with high endemism and species turnover between basins (Davies et al., 2008; Moorhouse & Macdonald, 2015). *C. helmsii* is notorious for the production of profuse biomass in the margins of these waterbodies, up to 1.5 kg m^{-2} (Dawson & Warman, 1987). As plants within these dense stands senesce, they can be expected to produce considerable volumes

of litter (Carpenter & Lodge, 1986; Newman, 1991). Because *C. helmsii* is perennial and retains above-ground biomass throughout the year in many areas (Hussner, 2009; Smith & Buckley, 2020), this material is likely to be available almost permanently.

Prior field surveys (Tasker et al., 2024) revealed marked shifts in the taxonomic and functional composition of macroinvertebrate detritivores within *C. helmsii*-invaded sites compared to uninvaded waterbodies. In particular, alien detritivores were more abundant in sites invaded by *C. helmsii*, and traits associated with detritivory drove differences in functional assemblage composition between invaded and uninvaded sites. These results suggest that the impacts of *C. helmsii* invasion on detritivores are a major determinant of the plant's impacts on ecosystem structure and function (Petchey & Gaston, 2006; Schmera et al., 2016), but *C. helmsii* decomposition has not been studied to date.

In order to investigate the mechanisms underpinning the impacts of *C. helmsii* on macroinvertebrate detritivores, we designed a field experiment to compare *C. helmsii* litter breakdown with that of an architecturally similar co-occurring native macrophyte. Litterbags were deployed in a *C. helmsii*- invaded pond in West Cornwall, UK, containing either *C. helmsii* or the widespread co-occurring native macrophyte, *Callitriche stagnalis* (common water-starwort). Through this experiment, we aimed to evaluate whether *C. helmsii* impacts recipient macroinvertebrate assemblages via its detritus, as suggested by Tasker et al. (2024).

We sought to address this question by assessing the decomposition rate of alien *C. helmsii* litter versus native *C. stagnalis* litter, and the composition of macroinvertebrate assemblages colonising *C. helmsii* vs. *C. stagnalis* during decomposition. We hypothesised that the rate of litter breakdown would differ between *C. helmsii* and *C. stagnalis,* as a result of their colonisation by distinct detritivore assemblages.

Methodology

Field experiment: detritus colonisation and breakdown

Experiment site

The field experiment was conducted in a circumneutral permanent pond with an area of 0.11 ha (pH 5.85, conductivity 141 µS/cm (May 2021)), surrounded by grassland and heathland in Sancreed, west Cornwall, United Kingdom (50° 06′ 18″ N, 005° 38′ 03″ W, altitude 180 m). The pond is artificial, having been dug in 1997, and has a mean depth of 1 m. It is fishless and well vegetated with submerged macrophytes throughout, including abundant *Crassula helmsii* amongst a mosaic of other macrophytes over a silt substratum. We did not record *Callitriche stagnalis* from the waterbody during our trial, although it occurs widely in similar habitats across the region, including at Sancreed (NBN Trust, 2023). Marginal areas are partly shaded by extensive riparian *Salix* L. The study was conducted between April and June 2023, during which time local monthly temperatures averaged 13.1 °C (mean daily max. 16.1 °C, min. 10.2 °C) (Met Office, 2023).

Experimental procedure

Crassula helmsii and *Callitriche stagnalis* were collected from Cadover Bridge, Dartmoor (50° 27′ 55″ N 4° 02′ 09″ W, March 2023), thoroughly rinsed to remove epiphytes and air-dried at a temperature of 26 ± 3 °C for 2 weeks. Once plants had attained constant mass, they were split into 5 ± 0.1 g portions and placed into 20×30 cm mesh litter bags ($n = 42$). Of these, 24 coarse mesh bags ($n = 12$ for each macrophyte species) had a 700 µm mesh base and 7 mm mesh on the upper side (adapted from Bedford, 2004), permitting access for macroinvertebrate detritivores. The remaining 18 fine mesh bags ($n = 9$ for each macrophyte species) were composed entirely of 700 µm mesh, for the quantification of microbial and meiofaunal decomposition in the absence of macroinvertebrates. Upon arrival at the experimental site, bags were weighted down with cleaned glass marbles, shut with cable ties (coloured to indicate the plant species within) and secured in groups to randomly

distributed stakes in the margins of the waterbody (depth < 1 m). Fine and coarse mesh bags containing *C. helmsii* or *C. stagnalis* were distributed evenly across these stakes, so that for each retrieval date, an even number of bags of both macrophyte species were retrieved from each stake, negating potentially confounding variation in abiotic conditions across the waterbody. 14 bags (4 coarse, 3 fine for each macrophyte species) were extracted from the waterbody on each of 3 retrieval dates, after 10 (d10), 35 (d35) and 83 (d83) days. Retrieval dates were selected to encompass all stages of litter decay (rapid early mass loss through to slow breakdown of recalcitrant litter components), and collect macroinvertebrates associated with each stage of decomposition (Carvalho et al., 2015). Individual bags were retrieved using a large 500 μm mesh bag to prevent loss of plant material or invertebrates. Upon retrieval, litterbags were placed singly in 1 l pots containing 70% industrial denatured alcohol (for invertebrate fixation) and transferred to the laboratory for processing.

In the laboratory, macroinvertebrates were separated from plant material, which was then air-dried to constant mass and weighed (to the nearest milligramme: Adam Equipment PW254). Macroinvertebrates were then identified and counted. Where possible, specimens were identified to species level using a range of resources (Hammond et al., 1985; Elliott et al., 1988; Savage, 1989; Wallace et al., 1990; Edington & Hildrew, 1995; Nilsson, 1996; Foster & Friday, 2011; Dobson et al., 2012; Foster et al., 2014; Brochard et al., 2016; Smallshire & Swash, 2018; Rowson et al., 2021), with the exception of Bivalvia (species/genus), Diptera (subfamily) and Annelida (subclass).

Carbon: nitrogen analysis

To assess carbon:nitrogen (C:N) ratios, litter was freeze-dried, ground and passed through a 180 μm sieve. We weighed out ca. 5 mg of resulting powders into tin cups for C:N analysis in an elemental analyser (Elementar, Langensolbold, Germany, see Epstein et al., 2019). To minimise contamination by invertebrates and extraneous detritus, we included only litter from fine mesh bags in this analysis.

Data analysis

Decomposition rate was calculated based on the exponential decay model (Petersen & Cummins, 1974; Bärlocher, 2005; Thornhill et al., 2021), using the formula:

$$-k = \frac{\ln\left(\mathrm{DM}_1/\mathrm{DM}_0\right)}{d},$$

where DM_0 is initial dry mass, DM_1 is dry mass upon recovery and d is the number of days submersed. For convenience, $-k$ is expressed positively hereafter.

Differences in mass loss and C:N ratio between *C. helmsii* and *C. stagnalis* litter were assessed using linear models. *Microbial decomposition* was assessed by analysing rates of decomposition in fine mesh bags, whilst *invertebrate-mediated decomposition* was assessed by calculating the difference in coarse mesh mass loss and average fine mesh mass loss per macrophyte species per retrieval date, and analysing these values (Dekanová et al., 2021). Differences in the taxon richness and abundance of macroinvertebrates associated with coarse litter bags were assessed using generalised linear models (packages *lme4* (Bates et al., 2015) and *MASS* (Venables & Ripley, 2002)). Finding that the invasive *Crangonyx pseudogracilis* and native *Euglesa casertana* were by far the most abundant macroinvertebrates in our samples, we constructed additional generalised linear models to individually assess differences in the abundance of these species. Model assumptions were checked graphically, and generalised least squares fits (package *nlme* (Pinheiro et al., 2023)) used where issues with homogeneity of variance were evident. For all models, homogeneity of response (equivalence of breakdown slopes) was tested using Type III (simultaneous) ANCOVA (package *car* (Fox & Weisberg, 2018)). If no significant interaction between retrieval date and macrophyte species was observed, Type I (sequential) ANCOVA was used for significance testing of main effects, whereas results of Type III ANCOVA were reported where interactions were significant. Values of $P < 0.05$ were considered statistically significant.

Differences in taxonomic assemblage composition of macroinvertebrates associated with *C. helmsii* and *C. stagnalis* litter bags during breakdown were assessed using permutational multivariate analysis of variance (PERMANOVA) on a Bray–Curtis

dissimilarity matrix (package *vegan* (Oksanen et al., 2022)). For this purpose, abundance data were square-root transformed to down-weight the influence of dominant taxa.

To assess differences in functional assemblage composition, we constructed a functional trait database using fuzzy-coded data (Tachet et al., 2010; Schmidt-Kloiber & Hering, 2015) encompassing 3 biological traits with 24 modalities: food, feeding type and maximal body size (Table 1). We then constructed a community weighted means (CWM) matrix by crossing our functional trait and taxon abundance databases (package *ade4* (Thioulouse et al., 2018)), and used this to compute an ordination using fuzzy principal components analysis (FPCA) (Guareschi et al., 2021).

All analyses were conducted in the R computing environment (R Core Team, 2023).

Table 1 Macroinvertebrate functional traits included in our trait database (taken from Tachet et al. (2010), extracted using www.freshwaterecology.info)

Trait	Modality
Food	Micro-organisms
	Detritus < 1 mm
	Dead plants > 1 mm
	Live microphytes
	Live macrophytes
	Dead animals > 1 mm
	Live microinvertebrates
	Live macroinvertebrates
	Vertebrates
Feeding type	Absorber
	Deposit feeder
	Shredder
	Scraper
	Filter feeder
	Piercer
	Predator
	Parasite
Maximal body size	< 0.25 cm
	> 0.25–0.5 cm
	> 0.5–1 cm
	> 1–2 cm
	> 2–4 cm
	> 4–8 cm
	> 8 cm

Results

Litter decomposition

Mass loss

In our field trial, invertebrate-mediated decomposition was significantly greater in *C. stagnalis* litter than in litter of *C. helmsii*. Microbial decomposition was also significantly greater in *C. stagnalis* litter than *C. helmsii* litter (Table 2).

Averaged across the entire trial, rates of microbial (fine mesh) and invertebrate-mediated decomposition were approximately twice as high in *C. stagnalis* compared with *C. helmsii* (Table 3). After 83 days of decomposition, only 21.1% of *C. stagnalis*' mass remained across coarse and fine mesh litter bags, whilst *C. helmsii* retained 49.1% of its original mass. (Fig. 1).

Carbon: nitrogen ratio

C. helmsii litter had a significantly higher carbon: nitrogen ratio than *C. stagnalis* litter, but litter carbon: nitrogen ratios did not change significantly throughout our experiment (Table 3, Fig. 2).

Table 2 Results of linear models assessing decomposition rate and carbon: nitrogen (C:N) ratio of *Crassula helmsii* vs. *Callitriche stagnalis* litter

		df	F	P
Microbial decomposition (Type I LM)	Retrieval date	1, 15	54.670	< 0.001
	Plant	1	18.435	< 0.001
Invertebrate-mediated decomposition (Type I LM)	Retrieval date	1, 21	8.193	0.009
	Plant	1	9.843	0.0498
C:N ratio (Type I LM)	Retrieval date	1, 21	1.541	0.228
	Plant	1	70.860	< 0.001

Mass loss in fine mesh bags used to calculate microbial decomposition; difference in mass loss between coarse and fine mesh bags used to calculate invertebrate-mediated decomposition. Type I (sequential) LM fits assessed with F test

df degrees of freedom, *F* F-statistic, *p* probability

Table 3 Decomposition rates (k d^{-1}) of *Crassula helmsii* and *Callitriche stagnalis*

| | Leaf processing rate (k d^{-1})$\pm$SE | | |
	Overall	Microbial	Invertebrate
Crassula helmsii	0.0205 ± 0.0033	0.0155 ± 0.0028	0.0050 ± 0.0011
Callitriche stagnalis	0.0333 ± 0.0028	0.0223 ± 0.0018	0.0111 ± 0.0018

Mass loss in fine mesh bags used to calculate microbial decomposition; difference in mass loss between coarse and fine mesh bags used to calculate invertebrate-mediated decomposition
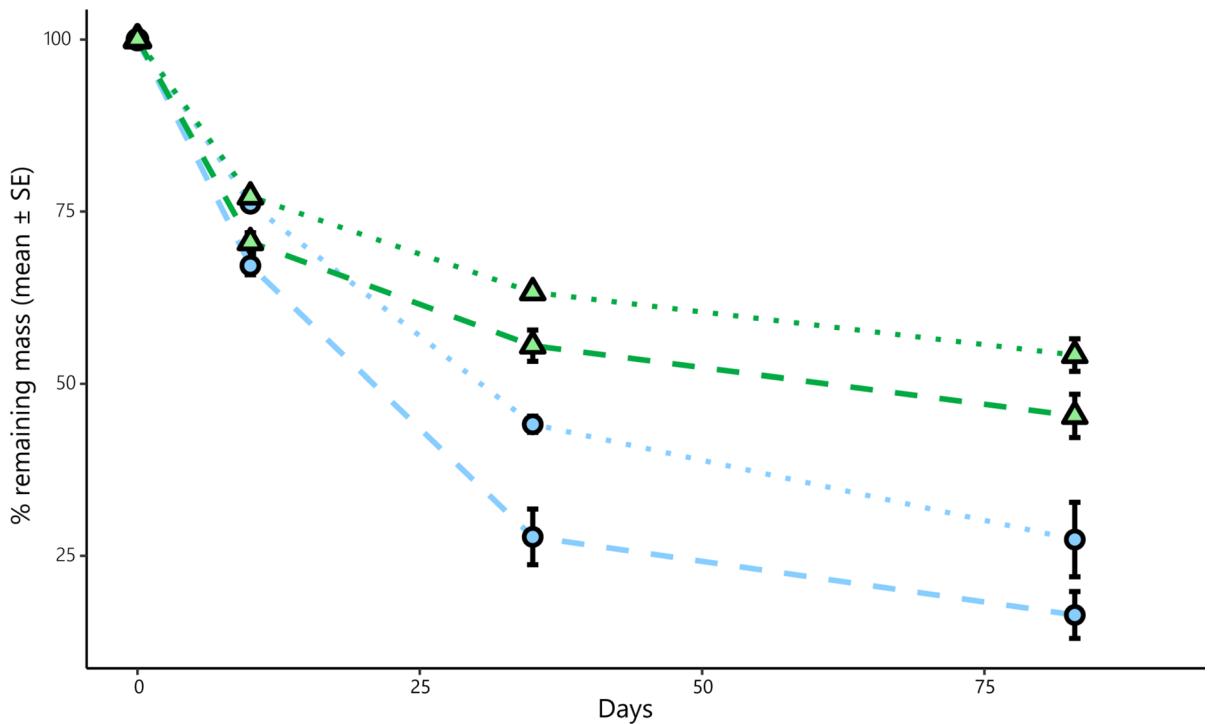
Fig. 1 Mass loss (mean$\pm$SE) of *Crassula helmsii* (▲) and *Callitriche stagnalis* (◉) over 83 days. Dotted bars=fine mesh; dashed bars=coarse mesh

Fig. 2 Mean change to carbon: nitrogen ratio of *Crassula helmsii* (▲) and *Callitriche stagnalis* (◉) litter over 83 days in fine mesh bags. Error bars (SE) too small to be visible, so omitted
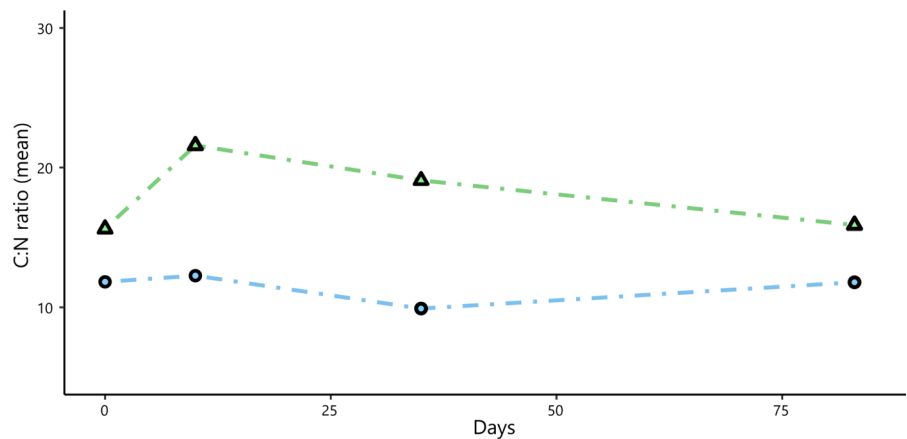
Macroinvertebrate colonisation

Abundance and taxonomic diversity

We observed a significant interaction effect of plant species and litterbag retrieval date on macroinvertebrate abundance, with *C. helmsii* litterbags containing fewer macroinvertebrates than *C. stagnalis* bags after 10 days, but more macroinvertebrates after 83 days (Fig. 3, Table 4).

Macroinvertebrate taxon richness did not differ significantly between *C. helmsii* and *C. stagnalis*, nor between litterbag retrieval dates. We found a significant interaction effect between plant and retrieval date on *Crangonyx pseudogracilis* abundance, with *C. helmsii* litterbags containing fewer *C. pseudogracilis* than *C. stagnalis* bags after 10 days, but more *C. pseudogracilis* after 83 days. *Euglesa casertana* abundance was significantly higher in litter of both

macrophyte species at later retrieval dates (Fig. 3, Table 4).

Taxonomic and functional assemblage composition

Macroinvertebrate taxonomic composition differed significantly according to retrieval date (PERMANOVA: $F_{1,18} = 4.750$, $P < 0.01$), but not according to macrophyte species (PERMANOVA: $F_{1,18} = 0.568$, $P > 0.05$). The amphipod shredder *C. pseudogracilis* was the most abundant member of d10 and d35 macroinvertebrate assemblages, whilst the suspension feeding bivalve *E. casertana* was most abundant in d83 assemblages (Table 4, Fig. 3). Consequently, functional assemblage composition shifted during litter decomposition from trait space within our FPCA ordination associated with trait modalities food: dead plants (>1 mm) and feeding mode: shredder towards space
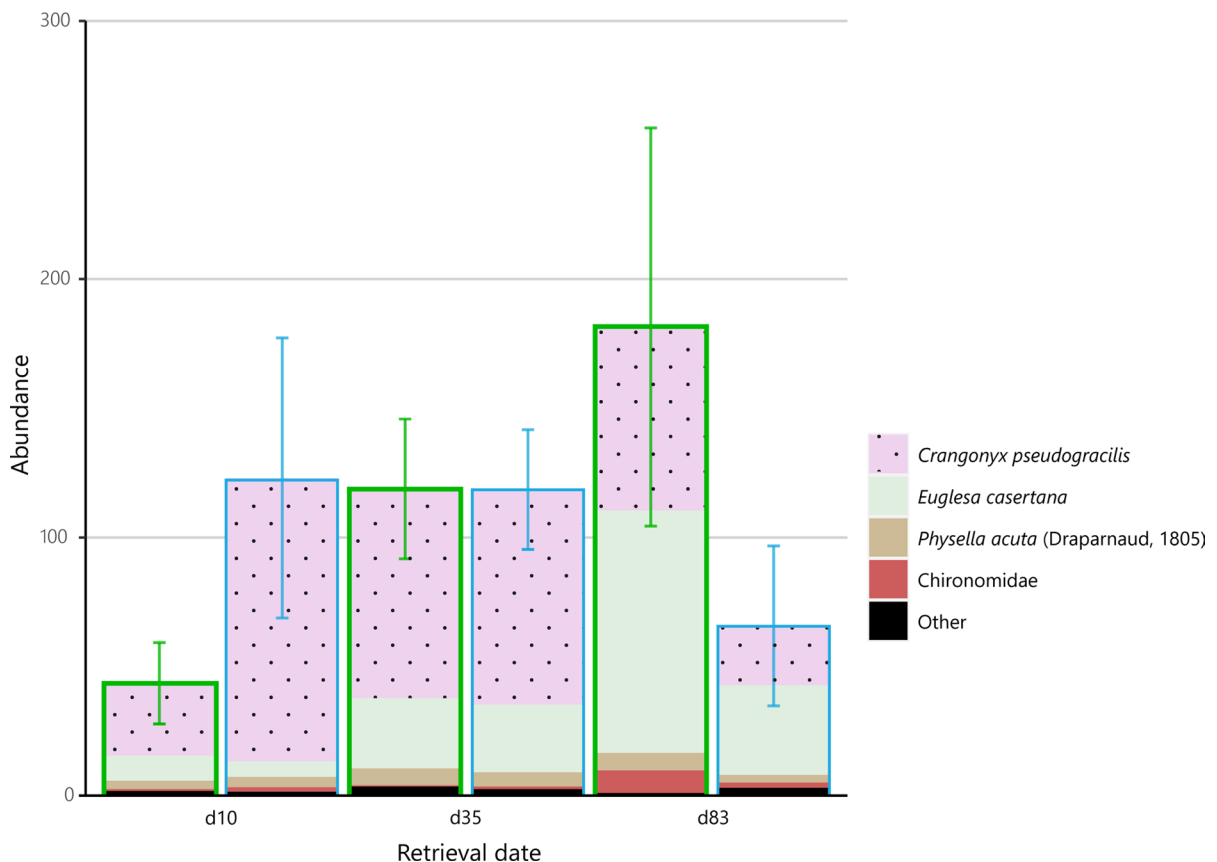

Fig. 3 Abundance of macroinvertebrates associated with *Crassula helmsii* and *Callitriche stagnalis* litter bags after 10, 35 and 83 days (mean ± 1 SE). Thick green borders = *C. helmsii;* thin blue borders = *C. stagnalis*

Table 4 Results of GLM and GLS models assessing taxon richness, total abundance and abundance of *Crangonyx pseudogracilis* and *Euglesa casertana* associated with *Crassula* *helmsii* or *Callitriche stagnalis* litter, with litterbag retrieval date incorporated as a fixed factor

		df	F	X²	P
Taxon richness (Type I Poisson GLM)	Retrieval date	1, 21	2.944		0.101
	Plant	1	0.120		0.732
Total abundance (Type III GLS)	Retrieval date	1		2.921	0.087
	Plant	1		1.083	0.298
	Plant: retrieval date	1		5.523	0.02
C. pseudogracilis abundance (Type III negative binomial GLM)	Plant	1		3.825	0.051
	Retrieval date	1		4.950	0.03
	Plant: retrieval date	1		5.270	0.02
E. casertana abundance (Type I negative binomial GLM)	Retrieval date	1		22.407	< 0.001
	Plant	1		1.714	0.191

Type I GLS fits assessed with *F* test, Type III with Wald chi-sq. Type I GLM fits assessed with Wald chi-sq, Type III with likelihood ratio test

df degrees of freedom, *F* F-statistic, *p* probability

associated with the trait modalities food: detritus (< 1 mm) and feeding mode: filter feeder (Fig. 4). See Table S1 for a complete list of macroinvertebrate taxa recorded from litter bags.

Discussion

Given the major contribution made by detritus to aquatic energy flows and nutrient cycling (Webster & Benfield, 1986; Cebrian & Lartigue, 2004; Shurin et al., 2005), changes to the quantity and quality of
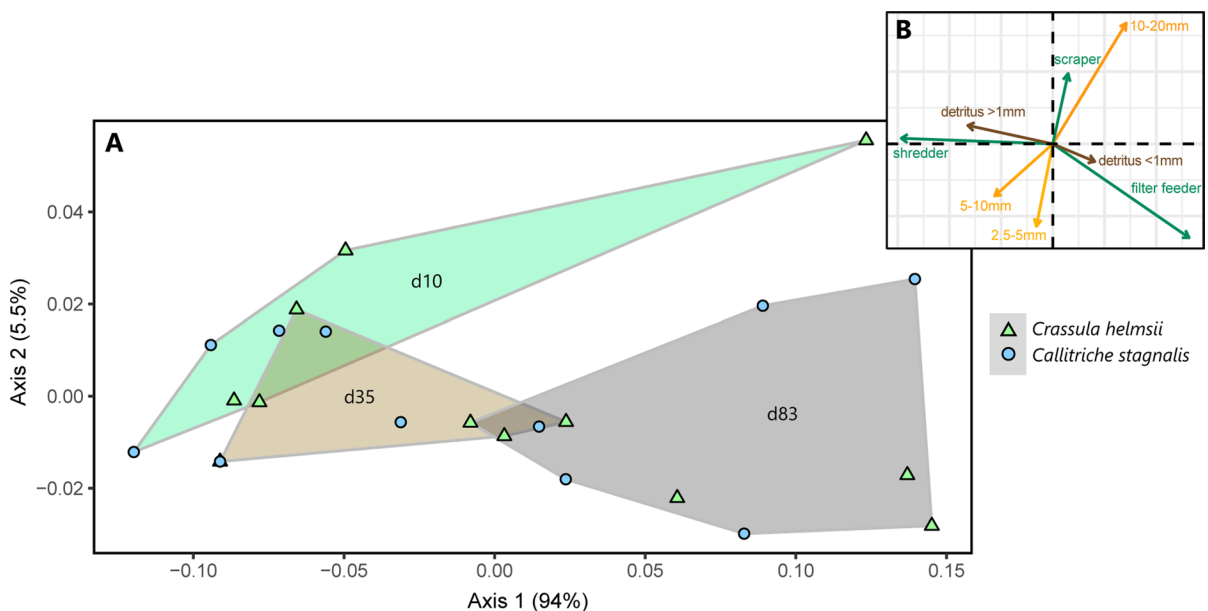

Fig. 4 A Fuzzy principal components analysis ordination, produced using a community weighted means matrix. First two axes account for 99.5% of the variation. Convex hulls represent the location in functional trait space of macroinvertebrate assemblages from d10, d35 and d83 litterbags. **B** Trait modalities most strongly driving assemblage functional composition. Green arrows: feeding type; brown: food; orange: maximal body size

detritus are likely to be a key factor determining the impacts of alien macrophyte invasion. In our field experiment, alien *Crassula helmsii* litter decomposed at a significantly slower rate than native *Callitriche stagnalis* litter, driven in part by reduced invertebrate-mediated decomposition throughout the trial. As we hypothesised, colonisation of litter by macroinvertebrates differed between macrophyte species. Initially, *C. stagnalis* litter supported more abundant macroinvertebrates, but after 83 days, *C. helmsii* litter supported higher macroinvertebrate abundance. However, taxonomic and functional composition did not differ significantly between macroinvertebrate assemblages colonising *C. helmsii* and *C. stagnalis* litter.

Our results suggest that *C. helmsii* detritus persists for longer, and ultimately hosts more abundant detritivores. Elevated invertebrate-mediated mass loss observed in *C. stagnalis* litter suggests that the percentage of detritus consumed by detritivores per unit time is higher in *C. stagnalis* than in *C. helmsii*, indicating that *C. helmsii* may be less palatable to macroinvertebrates. However, this result might also be explained by reduced mechanical breakdown in *C. helmsii*. The composition of macroinvertebrate assemblages colonising *C. helmsii* and *C. stagnalis* litterbags did not differ significantly, indicating that *C. helmsii* detritus is processed by similar macroinvertebrates to native macrophytes. Litterbag colonisation does not necessarily directly relate to consumption, however, and processes of macroinvertebrate colonisation might be influenced by the provision of comparable refugia due to the similar physical structure of *C. helmsii* and *C. stagnalis* (Tasker et al., 2022). Differences in mass loss between *C. helmsii* and *C. stagnalis* litter in fine mesh bags are likely driven by resistance of *C. helmsii* litter to microbial decomposition (Webster & Benfield, 1986; Santonja et al., 2018). Decomposition rates could be retarded by *C. helmsii*'s low nutritional quality, as revealed by its comparatively high carbon: nitrogen ratio (Li et al., 2012).

The breakdown rate we observed for *C. helmsii* (0.018 k d^{-1}) is less than half the mean rate of 0.047 k d^{-1} calculated by Chimney and Pietro (2006) for submerged freshwater macrophytes, suggesting *C. helmsii* does indeed produce unusually recalcitrant detritus. Despite the lower percentage of *C. helmsii* detritus apparently consumed by macroinvertebrates in this trial, absolute consumption by detritivores may

be higher than that of slower growing native macrophytes such as *C. stagnalis* because of the high biomass production (and consequently high detritus production) often attained by *C. helmsii* (Dawson & Warman, 1987; Cebrian & Lartigue, 2004). In addition, *C. helmsii* is a perennial, and tends to retain aboveground biomass in winter, so will yield varying quantities of detritus throughout much of the year, as opposed to the seasonal glut typical of most native macrophytes characteristic of the shallow fluctuating waters colonised by *C. helmsii* (Carpenter & Lodge, 1986; Hussner, 2009; Smith & Buckley, 2020). The reliable supply of abundant—but perhaps somewhat unpalatable—detritus produced by *C. helmsii* is likely to drive shifts in detritivore populations within recipient ecosystems.

Crassula helmsii may facilitate further alien invasions where promoted detritivores are non-native, resulting in additional indirect impacts on recipient ecosystems (Simberloff & Von Holle, 1999). Although we detected no significant overall difference in the abundance of *C. pseudogracilis* associated with *C. helmsii* vs. *C. stagnalis* litter bags, the alien amphipod was more abundant amongst *C. helmsii* detritus by the end of the experiment. The non-native bladder snail *Physella acuta* (Rowson et al., 2021) was also present in *C. helmsii* litterbags across all removal dates. In a recent field study, Tasker et al. (2024) found that non-native detritivores (and particularly *C. pseudogracilis* and *P. acuta*) were more abundant within *C. helmsii*-invaded waterbodies than in uninvaded waterbodies, perhaps demonstrating this effect in action.

The decomposition of aquatic vascular plant litter is understudied in comparison to the aquatic decomposition of allochthonous terrestrial plant material, particularly in lentic systems (Cummins et al., 1973; Gessner et al., 1999, 2010). Decomposition pathways of aquatic plant litter in lentic systems differ from better-studied processes of woody litter decomposition in lotic systems for several reasons. With the exception of some emergent species, aquatic plants typically have higher available nutrient concentrations than terrestrial plants, due largely to the absence of unpalatable structural components such as lignin, and detritus nutritional quality is strongly correlated with the percentage of detrital production which is consumed in freshwaters (Cebrian & Lartigue, 2004; Shilla et al., 2006; Bakker et al., 2016). Secondly,

differing litter properties and detritivore species pools will mean that colonising detritivore assemblages will differ between habitats (Pope et al., 1999; Cebrian & Lartigue, 2004; Carvalho et al., 2015; Bakker et al., 2016). In addition, litter decomposition in small lentic waterbodies will proceed differently to decomposition in lotic systems (or larger lakes) due to the relative insignificance of mechanical breakdown by flow or wave action (Webster & Benfield, 1986; Santonja et al., 2018). The unanticipated colonisation of our litterbags by abundant *E. casertana* might represent one such divergence from better-studied processes of lotic woody litter decomposition (Cummins et al., 1973; Petersen & Cummins, 1974; Gessner et al., 2010). The fragmentation of microbially conditioned coarse particulate organic matter (CPOM) into fine particulate organic matter (FPOM) by macroinvertebrate shredders is a well-understood and near-ubiquitous component of litter decomposition in freshwaters (Cummins et al., 1973; Webster & Benfield, 1986; Pope et al., 1999; Santonja et al., 2018; Thornhill et al., 2021), but the role of macroinvertebrate collector-gatherers and suspension feeders in detritus processing has been less well studied. To our knowledge, the mass colonisation of litter by suspension feeding *Pisidium/Euglesa* spp. has not been reported from litter experiments to date (Cummins et al., 1973; Wallace & Webster, 1996; Pope et al., 1999; Carvalho et al., 2015; Dekanová et al., 2021). *E. casertana* is a small bivalve mollusc which is thought to primarily feed in the interstices of sediment, filtering dense suspended FPOM agitated into suspension by pumping water through the pedal aperture (Lopez & Holopainen, 1987). Colonisation of litterbags by abundant *E. casertana*, particularly in the last 6 weeks of our trial, suggests that *Pisidium/Euglesa* spp. may play an underappreciated role in assimilation of detrital carbon and nutrients into macrofaunal food webs within small lentic waterbodies. Alongside direct assimilation, suspension feeding by *Pisidium/Euglesa* spp. may increase detritus particle size via egestion of faecal pellets, enabling further uptake of detrital carbon and nutrients by collector-gatherers (Wallace & Webster, 1996). Without further study, it is difficult to determine the generalisability of these findings, however.

In general, additional research on aquatic plant decomposition is much needed, given the key role of autochthonous detrital pathways in energy and nutrient flow through many freshwater ecosystems (Cebrian & Lartigue, 2004; Bakker et al., 2016), and possible contributions to carbon burial (Taylor et al., 2019). To our knowledge, whilst the role of emergent plant invasions in altering litter supply has been highlighted in previous studies (Cuassolo et al., 2020; Dekanová et al., 2021), this field experiment represents a first attempt to assess the impacts of submerged plant invasion on detritivorous macroinvertebrates. These impacts are inevitably context- and taxon-specific, so it is difficult to draw any generalisations from this experiment. In future, general trends (and a predictive framework) might be elucidated via similar litter experiments using multiple alien macrophytes alongside a suite of native comparators, with trait information incorporated into analyses (Grutters et al., 2017). These could indicate, for instance, whether facilitation of non-native detritivores—as observed in our litter experiment—is a predictable consequence of submerged alien macrophyte invasion.

Conclusion

Our field experiment indicates that the impacts of *C. helmsii* may indeed be mediated by detritus. *C. helmsii* detritus is colonised by a taxonomically and functionally similar macroinvertebrate assemblage to native macrophyte detritus, but breaks down slower, with a lower rate of invertebrate-mediated decomposition. At later stages of decomposition, *C. helmsii* may support more abundant detritivores than native macrophytes. Where present in the species pool, *C. helmsii* may facilitate the invasive amphipod *C. pseudogracilis*. Given the dense stands typically formed by *C. helmsii* (Dawson & Warman, 1987), its perennial growth (Smith & Buckley, 2020) and the recalcitrance of its litter demonstrated here, *C. helmsii* is likely to produce copious, long-lasting detritus throughout the year, driving considerable impacts on the detritivore assemblage of invaded waterbodies, and consequently upon wider ecosystem structure and functioning. Parenthetically, the colonisation of our litter bags by abundant *E. casertana* may indicate an underappreciated contribution of pea clams (*Pisidium/Euglesa* spp.) to detritus processing within these small lentic waterbodies.

Data/code availability The dataset and R script associated with this study are available from the University of Plymouth's PEARL repository (https://pearl.plymouth.ac.uk).

Declarations

Competing interests This research was conducted whilst in receipt of a PhD studentship funded by the University of Plymouth. The authors have no relevant financial or non-financial interests to declare.

Ethical approval No approval of research ethics committees was required to accomplish the goals of this study because experimental work was conducted with unregulated invertebrate species.

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