

Interactive effects of resource quality and temperature drive differences in detritivory among native and invasive freshwater amphipods

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Abstract

1. Invasive non-native species and climate change are two of the greatest pressures facing freshwater communities; however, how they interact to impact ecosystem function remains poorly understood despite the potential for impacts on key functional behaviours, such as detritivory, which could have wide-reaching impacts.
2. We quantified the rates of detrital processing and survival of one U.K. native (*Gammarus pulex*) and two invasive non-native (*Dikerogammarus villosus* and *Dikerogammarus haemobaphes*) freshwater amphipod species, across three temperatures (8°C, 14°C, and 20°C), and three leaf diets of varying resource quality (oak, sycamore, and alder) in laboratory microcosms. We also compared amphipod survival across the different temperature and diet treatments.
3. Rates of detrital processing varied between the native and invasive non-native amphipod species, with native *G. pulex* having a faster processing rate than both invasive non-native species at the lower temperatures. However, as the temperature treatments increased, between-species differences decreased, while the effects of leaf diets became more apparent. Although the survival probability did not vary with amphipod species, amphipod survival was higher at lower temperatures and in treatments containing higher quality leaf diets.
4. We propose that the invasive non-native *Dikerogammarus* species will affect native communities through lower rates of detrital processing; however, this impact may change under predicted climatic warming and be increasingly similar to native amphipod species.

KEYWORDS

Detritivory, *Dikerogammarus*, ecosystem functioning, *Gammarus pulex*, invasive non-native species

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1 | INTRODUCTION

Biological invasions can negatively impact communities (Gallardo et al., 2016; Gurevitch & Padilla, 2004; Simberloff et al., 2013; Závorka et al., 2018) through direct interactions such as predation, and, indirectly, for example through altering the ecosystem's energy and nutrient dynamics (Kenis et al., 2009; Salo et al., 2007). The rate of biological invasions has increased in recent years and shows no sign of slowing (Seebens et al., 2017). While the impacts of biological invasions have received much research attention, our understanding of how these impacts may vary with respect to abiotic factors, such as changing temperature and resource availability, remains incomplete (Bellard et al., 2016; Sorte et al., 2013). Freshwater systems are particularly at risk from biological invasions with their connectivity and flow regimes having the potential to facilitate species spread (Moorhouse & Macdonald, 2015).

Many freshwater communities gain the majority of their nutrient input from allochthonous sources, often in the form of organic detrital matter (e.g. Leberfinger et al., 2011). The largest of these sources is the windfall of leaves in autumn, which results in an annual organic matter nutrient input *pulse*. Leaves are quickly colonised by microbial biofilms (e.g. hyphomycete fungi) and macroinvertebrates (e.g. shredders) (McArthur & Barnes, 1988), which break down the leaves from coarse particulate organic matter (CPOM, >1mm) to fine particulate organic matter (FPOM, <1mm). This early stage of the detritus pathway is essential as, for the vast majority of the freshwater community, the CPOM remains a largely inaccessible resource. Cuffney et al. (1990) demonstrated the importance of leaf shredding macroinvertebrates by measuring a decline of 50%–74% in leaf litter processing rates and an associated 33% decline in FPOM production when macroinvertebrates were removed from streams by an insecticide treatment. Macroinvertebrate shredders are therefore important keystone species and play an important role in facilitating energy flow within freshwater communities (Wallace & Webster, 1996).

Dikergammarus villosus and *Dikergammarus haemobaphes*, two larger freshwater invasive species, have spread through Europe (e.g. Aldridge, 2013; MacNeil et al., 2010) and now dominate many of the invaded waterbodies (Dick & Platvoet, 2000), often outcompeting native amphipods such as *Gammarus pulex*. Despite being omnivorous, much research attention has been given to the predatory impacts of *D. villosus* and *D. haemobaphes* invasion (e.g. Dodd et al., 2014; Warren et al., 2021). Both *Dikergammarus* species have been shown to have a greater preference for animal tissues over allochthonous organic matter (Bacela-Spychalska & Van Der Velde, 2013) in addition to showing reduced rates of detrital processing, when compared to native species. For example, MacNeil et al. (2011) show that *D. villosus* undertake detrital processing at lower rates than native *G. pulex* when provided with sycamore (*Acer pseudoplatanus*) leaves (See also Little & Altermatt, 2018). In contrast, at least some *D. villosus* populations show shredding behaviours comparable to their native counterparts (e.g. Hellmann

et al., 2015; Koester et al., 2016). However, there have been few studies of the detritivorous behaviour (the mechanical breakdown of detrital matter) of *D. haemobaphes* (Constable & Birkby, 2016). Furthermore, the effect of temperature on the detritivorous behaviours of invasive non-native amphipods, including *D. villosus* and *D. haemobaphes*, has been rarely studied despite expected warming due to climate change. It is possible that non-native amphipod invasions could result in wider impacts in freshwater systems via changes in nutrient availability, specifically, via the breakdown of CPOM into FPOM with temperature variation having the potential to exacerbate or mitigate these changes. Despite FPOM metrics providing valuable insights in previous freshwater ecology studies (e.g. Fernandes et al., 2015 and López-Rojo et al., 2018), much of the previous invasion ecology literature has focussed on CPOM loss as a metric for detrital processing and as a proxy measure for nutrient availability. FPOM measures could provide a greater level of detail of the potential impacts of amphipod invasions to the wider freshwater community as FPOM is the resource available to the majority of freshwater species (Doherty-Bone et al., 2018). FPOM generation simultaneously increases nutrient availability for the wider community (Crowl et al., 2001) and increases the surface area of detrital matter for increased rates of microbial breakdown.

While previous studies have investigated how amphipods perform under a range of different environment conditions (e.g. Jermacz et al., 2020; Kenna et al., 2016; Truhlar et al., 2014) few studies have accounted for amphipod survival (but see Maazouzi et al., 2011). For example, any between-species per-capita difference in detrital shredding rate could either be exacerbated or negated through climate driven differences in survival rates. We aimed to quantify the individual level detrital processing rates (mg of FPOM) of three amphipod species when provided with three diets of differing resource quality across three different temperatures. We also compared amphipod survival between treatment combinations as changes in population density are likely to also impact detrital shredding rates.

We hypothesised that the rate of detrital breakdown will differ between (H₁) the amphipod species with native *G. pulex* expected to process detritus at a higher rate than both non-native *Dikergammarus* species and (H₂) between the leaf diets, with higher leaf quality leaf diets being consumed at higher rates than those of lower quality. We also expected that (H₃) leaf consumption rates would increase as temperature increased, due to higher metabolic activity. We further hypothesised that: (H₄) the survival of amphipods would vary between amphipod species and decrease as treatment temperatures rise; and (H₅) all species will have higher rates of survival when provided with a higher quality food resource in comparison to those provided with resources of lower quality. It is also unlikely that any one of these variables will act in isolation. Another of our primary aims was to explore how their synergistic effects, along with amphipod survival, impacts detrital processing.

2 | METHODS

2.1 | Amphipods

We collected invasive non-native *D. villosus* from Grafham Water, Cambridgeshire, U.K. (52.292N; 0.323W), *D. haemobaphes* from the Leeds–Liverpool canal, Saltaire, U.K. (53.839N; 1.796W), and native *G. pulex* from Meanwood Beck, Leeds, U.K. (53.830N; 1.575W). We collected amphipods during the winter (December and January) of 2017/2018. Average daily air temperatures for these months were between 4.6°C and 4.9°C in December and 4.8°C and 5.5°C in January (Met Office et al., 2022). In both months, Grafham Water had the highest average temperature (4.9°C and 5.5°C) while Leeds and Saltaire were more similar (Leeds = 4.7°C and 4.8°C and Saltaire = 4.6°C and 4.8°C). We used standard kick sampling methods for collecting *D. haemobaphes* and *G. pulex*. Due to their high abundance, we collected *D. villosus* by hand from artificial substrate.

Amphipods were kept in mixed sex groups in oxygenated 5-L tanks of dechlorinated tap water with a maximum of 50 individuals per tank. Amphipods were kept in these group tanks for between two and five days and were provided with an excess of conditioned leaves of English oak (*Quercus robur*), alder (*Alnus glutinosa*), and sycamore (*A. pseudoplatanus*; see methods section *leaf material* for details). Tanks were kept at 14°C on a 12:12 light: dark cycle in controlled temperature rooms. Prior to experimentation, amphipods were brought to the treatment temperatures at a rate of 2°C change every 6 hr in temperature-controlled incubators (MIR-254-PE, Panasonic, PHC Holdings Corporation), before being acclimatised to the treatment temperatures for 24 hr. Amphipods were then starved for a further 24 hr to empty gut contents.

2.2 | Leaf material

We collected English oak (*Quercus robur*), alder (*Alnus glutinosa*) and sycamore (*A. pseudoplatanus*) leaves from around Leeds, U.K. (53.80N; 1.55W). Leaves were collected from the ground after falling naturally from the trees. Leaf species were chosen due to their widespread and general abundance across the study area and for their varying nutritional and physiological (e.g. palatability) characteristics. For example, oak leaves are known to be tougher and have a lower C:N ratio than alder leaves (Foucreau, Puijalon, et al., 2013). We conditioned leaves in stream water, also collected from Meanwood Beck, Leeds, U.K., for 14 days at 14°C and 12:12L:D. Conditioning leaves better reflects natural processes in freshwater systems but also increases the palatability of leaves for freshwater macroinvertebrates (e.g. Bloor, 2011) via the formation and growth of microbial and fungal biofilms. We cut leaves into discs (8 mm in diameter) avoiding midribs, dabbed them dry, and weighed them before adding them to the experimental arenas.

To confirm the expected resource quality of the leaf diets we analysed their nutrient content. We oven-dried (105°C for 24 hr)

a subset of conditioned leaves of each of the three species (oak, alder and sycamore) to a constant dry mass and analysed their carbon, nitrogen, and total phosphorous content using standardised laboratory protocols (Allen, 1989). We analysed carbon and nitrogen contents with an Elementar vario MICRO cube (Elementar Analysensysteme GmbH, Langensfeld, Germany) combustion analyser (samples per leaf species analysed = 3, species = mean sample mass [mg; \pm SE]; oak = 3.926 [\pm 0.025], alder = 3.992 [\pm 0.062], sycamore = 3.949 [\pm 0.012]) and we used a Skalar SANN++ continuous-flow auto-analyser (Skalar Analytical B.V.) for the total phosphorous analysis ($n = 2$, species = mean [mg] \pm SE; oak = 199.9 [\pm 0.000], alder = 200.0 [\pm 0.000], sycamore = 200.1 [\pm 0.300]).

2.3 | Experimental microcosms

We constructed experimental arenas from two stacked 350-mL plastic containers (Solo, Lake Forest, U.S.A. Diameter = 117 mm, depth = 61 mm). We filled the experimental arenas with dechlorinated tap water (de-chlorinated using aeration over 48 hr). The base of the upper container was replaced with a 1-mm plastic mesh to retain particles larger than 1 mm (CPOM) in the upper container, while particles smaller than 1 mm (FPOM) were collected in the lower container. We provided the amphipods with a refuge (a glass bead approximately 20 mm in diameter) in the upper container in addition to a diet of 12 conditioned leaf discs of known weight. Each microcosm contained a single amphipod, except for the control treatments. The control treatments did not contain amphipods to allow the rate of leaf breakdown not attributable to amphipod shredding (e.g. microbial and fungal breakdown) to be quantified. Microcosms were not aerated or subject to water flow due to the perceived levels of disturbance such activity would have in the microcosms. The three species of amphipod were assigned one of three leaf species treatments (oak, alder, or sycamore) and one of three temperature treatments (8°C, 14°C, or 20°C). Temperature treatments were chosen to provide a representative range of current temperatures (8°C and 14°C) (Hammond & Pryce, 2007) and an extreme temperature within the boundaries of predicted climate change scenarios (20°C) (Orr et al., 2010). Experimental microcosms were arranged haphazardly in temperature-controlled incubators (MIR-254-PE, Panasonic, PHC Holdings Corporation) with each incubator assigned a single temperature treatment.

The experiment ran for 14 days with daily checks for amphipod mortality and moulting. Where individuals had moulted, the moults were removed. Where individuals had died, the day of mortality was recorded. In instances of mortality occurring within the first 24 hr of the experiment, these replicates were removed. After replicate removal and mortality of amphipods during the pre-experimental acclimatisation and gut clearing phases, each treatment combination was replicated between 14 and 30 times. At the end of the experiment, amphipods were dabbed dry and weighed. Water samples,

containing suspended FPOM, were filtered through a pre-weighed filter paper (Whatmann GF/F [Whatmann], pore size = 0.7 μm), oven-dried (105°C for 24 hr), and weighed.

2.4 | Statistical analysis

All statistical analyses were undertaken in R version 3.3.2 and RStudio version 1.0.136 (R Core Team, 2016; RStudio, 2016). We used the *AICcmodavg* R package for model comparison. Weights of the three amphipod species were significantly different (ANOVA; $F_{(2,549)} = 192.8$, $p < 0.001$), with a Tukey HSD test indicating that each pairwise comparison was significantly different ($p < 0.001$). Invasive non-native *D. villosus* individuals were the largest, while native *G. pulex* were the smallest (mean mg [\pm SE]; *D. villosus* = 85.38 [\pm 2.19], *D. haemobaphes* = 52.74 [\pm 1.26], *G. pulex* = 43.88 [\pm 0.92]).

2.5 | Amphipod detrital processing

Rates of amphipod leaf breakdown, measured as FPOM generated, were modelled while accounting for the potential effects of amphipod weight (mg) and the number of shredding days the amphipod undertook. The number of shredding days was defined as the number of days the amphipod was alive minus one as it is assumed that amphipods were likely to have displayed atypical behaviour prior to death. This correction was not applied to amphipods that survived the full duration of the experiment (14 days). The amphipod weight and shredding days terms were included in every FPOM model. The rates of detrital breakdown were analysed by generating 15 candidate general linear models with all combinations of amphipod species, diet types, and temperature as main and interaction terms. We then compared these models, using Akaike information criterion corrected for small sample size (AICc) scores, to the control model which contained only amphipod weight and number of shredding days fixed effects terms to identify the best fit model.

In some cases, our estimates of detrital processing rates were negative, apparently caused by filters weighing more prior to FPOM filtering than after. We suggest that these instances could be indicative of measurement error, with the true value being close to zero. Here we present analyses using all data, while analyses excluding negative estimates are provided in the Appendix (Figures S1 and S2 and Tables S1 and S2) and yielded similar results.

2.6 | Amphipod survival

We analysed amphipod survival using generalised linear models with binomial error structures. Similar to our other analyses, we compared 15 candidate models to a control model containing only an

amphipod weight fixed effect term using AICc scores. All candidate models contained the amphipod weight term and a combination of interaction and main effect terms of amphipod species, diet types, and temperature treatment.

3 | RESULTS

3.1 | Leaf nutrient content

Alder leaves diet contained the highest concentration of nitrogen, and had a lower carbon: nitrogen ratio (percentage composition by mass) than both the oak and sycamore (mean C:N [\pm SD]; alder = 22.16 [\pm 0.24], sycamore = 40.12 [\pm 0.34] and oak = 40.93 [\pm 2.46]). The amount of total phosphorus (mg/g) was the lowest in the alder leaves and highest in the sycamore leaves (mean total phosphorus [mg/g; \pm SD]; alder = 0.22 [\pm 0.00], oak = 0.33 [\pm 0.02], and sycamore = 0.50 [\pm 0.04]).

3.2 | Detrital shredding rates

Control treatments showed negligible FPOM production (species = mean FPOM [mg; \pm SD]; oak = -0.694 [\pm 2.370], alder = -0.167 [\pm 2.96], sycamore = -0.526 [\pm 2.83]), suggesting that leaf breakdown in amphipod treatments was primarily attributable to amphipod shredding.

Compared to a control model accounting for only amphipod weight and the number of shredding days, including the main effects of leaf diet, temperature and amphipod species separately substantially improved the control model (Δ AICc = 230.08, 107.82 and 10.96, respectively). We found that the *best fit* model (AICc weight = 1 and Δ AICc = 0.00) contained the three-way interaction term of the experimental treatments (amphipod species \times leaf diet \times temperature), suggesting that effect of each of the treatments on FPOM production depended on the combination of the other two treatment variables (Tables 1 and 2 and Figure 1). For example, assuming average amphipod weight (per species) and seven shredding days, the model predicted that when provided with an alder leaf diet and kept at 8°C, *D. haemobaphes* produced 112% less FPOM and *D. villosus* 70% less than *G. pulex* under the same conditions. However, when maintained at 20°C, *D. haemobaphes* produced only 5.7% less FPOM while *D. villosus* produced 4% less than *G. pulex* also at the same conditions (Figure 1). This relative change between species-temperature treatments is driven by larger increases in FPOM production by both *Dikerogammarus* species. As temperature increases the difference in FPOM production between amphipod species decreases while conversely, differences between leaf diets increases (Figure 1). Increasing values of the control terms, amphipod mass and the number of shredding days, were both associated with increasing FPOM generation levels.

TABLE 1 Second-order Akaike information criterion (AICc) scores, Δ AICc, and associated weights (AICc Wt.) for each of the 15 candidate models for the analyses of the rate of fine particulate organic matter (FPOM) production (mg) and amphipod survival.

Model	FPOM production (mg)			Amphipod survival		
	AICc	Δ AICc	Weight	AICc	Δ AICc	Weight
~CV	3986.580	564.267	0.000	557.350	40.793	0.000
~Amphipod species	3975.619	553.306	0.000	554.764	38.207	0.000
~Temperature	3878.756	456.443	0.000	544.519	27.962	0.000
~Leaf diet	3756.499	334.186	0.000	534.520	17.963	0.000
~Amphipod species + temperature	3866.847	444.534	0.000	541.884	25.327	0.000
~Amphipod species + leaf diet	3732.266	309.953	0.000	531.131	14.575	0.000
~Temperature + leaf diet	3596.460	174.147	0.000	520.291	3.734	0.069
~Amphipod species + temperature + leaf diet	3567.315	145.002	0.000	517.037	0.480	0.354
~Temperature \times leaf diet	3548.635	126.322	0.000	519.678	3.121	0.094
~Temperature \times amphipod species	3853.863	431.551	0.000	549.390	32.833	0.000
~Amphipod species \times leaf diet	3727.501	305.188	0.000	536.384	19.827	0.000
~Amphipod species + temperature \times leaf diet	3516.014	93.702	0.000	516.557	0.000	0.449
~Leaf diet + temperature \times amphipod species	3536.016	113.704	0.000	524.515	7.958	0.008
~Temperature + amphipod species \times leaf diet	3554.993	132.680	0.000	522.395	5.839	0.024
~Amphipod species \times temperature \times leaf diet	3,422.313	0.000	1.000	539.746	23.189	0.000

Note: The control model, denoted by CV (control variables), contained the amphipod wet weights (mg) and, for survival models, the number of shredding days undertaken by each amphipod. All subsequent models contained these control variables. Δ AICc values are the relative difference between each model and the *best fit* model. Each of the *best fit* models is indicated in bold.

3.3 | Amphipod survival

Temperature, leaf diet, and amphipod species terms improved the control model (Δ AICc = 12.83, 22.83 and 2.59). The *best fit* model contained an amphipod species term in addition to an interaction between the water temperature and leaf species terms. This *best fit* model, therefore, suggested that the species of the amphipod was important in determining amphipod survival while the effect of leaf species diet was dependent on the water temperature treatment. Generally, amphipod survival declined with increasing temperature with this decline greatest in amphipods provided with oak leaves (Table 2 and Figure 2). For example, survival probability of native amphipods (*G. pulex*) supplied with an oak leaf diet decreased as the temperature treatments increased (survival probability at 8°C = 0.91 [\pm 0.03], 14°C = 0.78 [\pm 0.05], and 20°C = 0.58 [\pm 0.09]) while *G. pulex* supplied with alder leaves showed a slight increase in survival probability between the 8 and 14°C treatments and only a minor decrease into the 20°C treatment (8°C = 0.91 [\pm 0.04], 14°C = 0.94 [\pm 0.02], and 20°C = 0.88 [\pm 0.04]). *D. villosus* showed higher survival probability than the other two species (Figure 2).

4 | DISCUSSION

We have shown that invasive non-native species can undertake less key functional behaviour than their native counterpart, but under current climate change projections the between species differences

may reduce and become increasingly driven by the resource diets available. We have also demonstrated the benefits of quantifying detrital shredding behaviours by using the amount of FPOM produced rather than CPOM consumed, thereby directly measuring the nutritional resources provided by shredding behaviours.

We found that the combined effects of invasive non-native species, climate extremes, and resource quality can change the detrital processing regime and therefore the energy flow throughout a freshwater system. In addition to our use of FPOM as a measurement of detrital processing (over previously used CPOM), we have advanced previous studies through the quantification of detrital processing and survival rates for three amphipod species (*G. pulex*, *D. villosus*, and *D. haemobaphes*), when provided with three different leaf diets and at three water temperature treatments. In accord with previous studies (e.g. Kenna et al., 2016; Piscart et al., 2011) and after accounting for between amphipod mass, we find that detrital processing is undertaken at a higher rate by native *G. pulex* than by both *D. villosus* and *D. haemobaphes* (H_1). Our between-species differences account for a species-wide trend that larger amphipods produce more FPOM than smaller individuals. This effect will probably result in our reported between species differences being exacerbated as both *Dikerogammarus* species are, in general, larger than native *G. pulex*. We develop on the previous work in this area (e.g. Constable and Birkby, 2016; Kenna et al., 2016; Piscart et al., 2011) by including both U.K. non-native *Dikerogammarus* species, *D. villosus* and *D. haemobaphes*, thereby allowing for their direct comparison with native *Gammarus pulex*. We found that differences in detrital

Model term	Level	Model	
		FPOM (mg)	Amphipod survival
Amphipod weight		0.064 (0.011)	-0.002 (0.005)
Shredding days		0.783 (0.059)	
Amphipod species	DH	-5.085 (1.433)	0.745 (0.301)
	DV	-2.629 (1.427)	0.792 (0.369)
Temperature	8°C	-5.017 (1.517)	
	14°C		1.102 (0.466)
	20°C	-1.655 (1.699)	2.048 (0.477)
Leaf diet	Sycamore	3.508 (1.384)	-0.710 (0.647)
	Alder	9.176 (1.374)	0.019 (0.542)
Amphipod species × Temperature	DH:8°C	0.007 (0.004)	
	DV:8°C	-1.191 (2.155)	
	DH:20°C	2.642 (2.325)	
	DV:20°C	-1.270 (2.333)	
Amphipod species × Leaf diet	DH:Sycamore	2.991 (2.068)	
	DV:Sycamore	0.065 (2.004)	
	DH:Alder	0.036 (2.024)	
	DV:Alder	11.409 (1.993)	
Temperature × Leaf diet	8°C:Sycamore	-0.614 (2.282)	
	14°C:Sycamore		-0.193 (0.761)
	20°C:Sycamore	0.865 (2.439)	-1.058 (0.798)
	8°C:Alder	3.568 (2.225)	
	14°C:Alder		-1.608 (0.716)
	20°C:Alder	7.908 (2.375)	-1.753 (0.716)
Amphipod species × Temperature × Leaf diet	DH:8°C:Sycamore	-1.277 (3.218)	
	DV:8°C:Sycamore	0.850 (3.178)	
	DH:20°C:Sycamore	-0.166 (3.381)	
	DV:20°C:Sycamore	3.347 (3.303)	
	DH:8°C:Alder	-9.147 (3.151)	
	DV:8°C:Alder	-18.132 (3.124)	
	DH:20°C:Alder	2.919 (3.270)	
	DV:20°C:Alder	-9.411 (3.311)	

Note: Model coefficients for each model term are shown with their associated standard errors. All survival models contained an amphipod wet weight (mg) term while all FPOM models also contained the number of shredding days undertaken by each amphipod. For both models the native *Gammarus pulex* was the reference level for amphipod species and oak the reference level for the leaf diet treatment. To facilitate interpretation of hypotheses the 14°C temperature treatment was used as the reference level for the FPOM generation model and the 8°C temperature treatment for the amphipod survival model. Specifically, it was considered possible that amphipod survival would decrease with increasing temperatures while FPOM creation may be greatest within the current range of experienced temperatures (14°C).

Abbreviations: GP, *Gammarus pulex*; DH, *Dikerogammarus haemobaphes*; DV, *Dikerogammarus villosus*.

processing between *D. villosus* and *D. haemobaphes* were not consistent and instead varied between leaf diet and temperature treatments. Our use of multiple leaf diets, spanning a range of nutritional qualities is more representative of field systems but is also in contrast to the majority of previous studies, which often favour a single

resource diet (e.g. alder in Piscart et al., 2011 and sycamore in Kenna et al., 2016).

We hypothesised that (H_2) amphipods provided with higher quality resource diet would consume more and therefore produce FPOM at an increased rate. Our analyses show that the rates of

TABLE 2 ANOVA tables for the best fit models, as determined by Akaike information criterion scores, in the analyses of fine particulate organic matter (FPOM) production (mg) and amphipod survival.

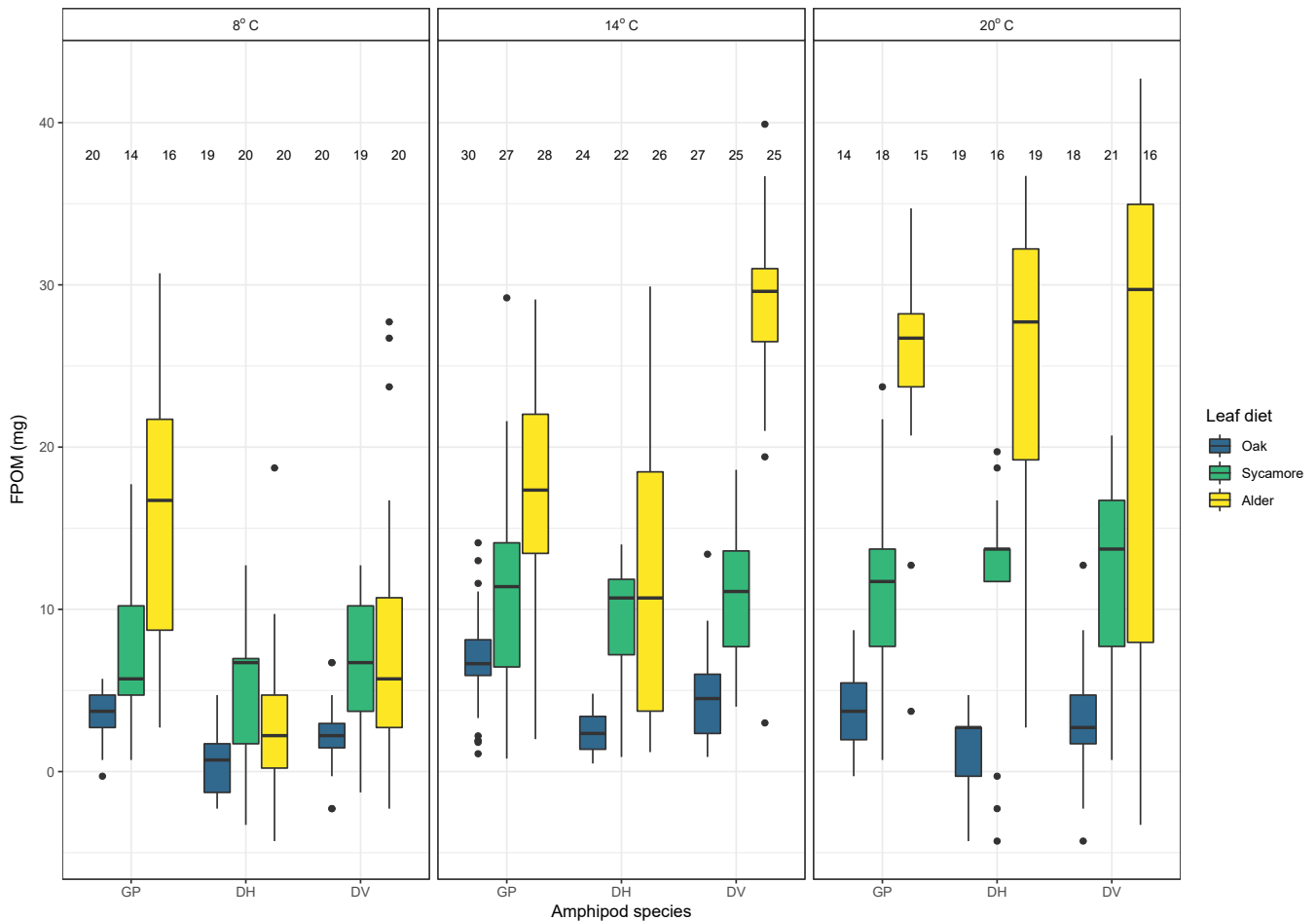


FIGURE 1 Mass of fine particulate organic matter (FPOM) generated (mg) per shredding day. DH, *Dikerogammarus haemobaphes*; DV, *Dikerogammarus villosus*; GP, *Gammarus pulex*. Numbers within the facets indicate the number of replicates within each treatment combination.

FPOM creation were the highest for amphipods on alder leaf diets and lowest for those on oak diets (H_2). Alder leaves commonly have high nitrogen content due to their nitrogen fixing fungal symbionts, which can make them a popular resource in an otherwise nutrient poor allochthonous diet (Webster & Benfield, 1986). Our analyses support this, alder leaves had the highest nitrogen content of the three leaf diets, despite also having lowest phosphorus content. Our hypothesis is also supported by high survival probabilities of with amphipods on alder leaf diets. While amphipods provided with sycamore leaves showed an intermediate level of consumption, compared to those on alder or oak, their survival was more similar to those consuming alder leaves than oak. Oak leaves are physically tough and commonly contain high levels of tannins (Foucreau, Piscart, et al., 2013; Gulis et al., 2006). In our analyses, oak leaves contained less nitrogen than the sycamore or alder leaves, which could make them a sub-optimal food resource for freshwater macroinvertebrates. Nonetheless, Foucreau, Piscart, et al. (2013) suggested that oak leaves fill an important role in detrital litter as their slower breakdown provides a long-lasting nutritional resource in the winter when most other detrital matter has been processed. Our results are consistent with those of Little and Altermatt (2018)

who similarly found amphipods preferred leaves of high resource quality. The detrital matter stoichiometry is likely to be a key determinant of food quality, in addition to the physical characteristics of the leaves such as toughness.

Studies addressing detrital breakdown of invasive amphipods across temperatures have been varied in their findings (Kenna et al., 2016; Truhlar et al., 2014). Specifically, Kenna et al. (2016) found that *D. villosus* showed lower detrital breakdown rates than *G. pulex* at higher water temperatures while Truhlar et al. (2014) found the opposite. Our findings support those of Kenna et al. (2016), as we have shown that FPOM generation rates varied with respect to amphipod species (H_1), leaf diet (H_2), and temperature (H_3). Based on our findings, we predict that whilst replacement of *G. pulex* by *D. villosus* and *D. haemobaphes* may lead to reduced FPOM availability at lower temperatures, this effect may be ameliorated by increased temperatures, which could be predicted under future climate change scenarios. Specifically, in warmer water bodies the two *Dikerogammarus* species are predicted to break down detrital leaf matter at similar rates to native *G. pulex*. Further studies to include a wider thermal range or short-term extreme climatic events could shed further light on these suggested differences.

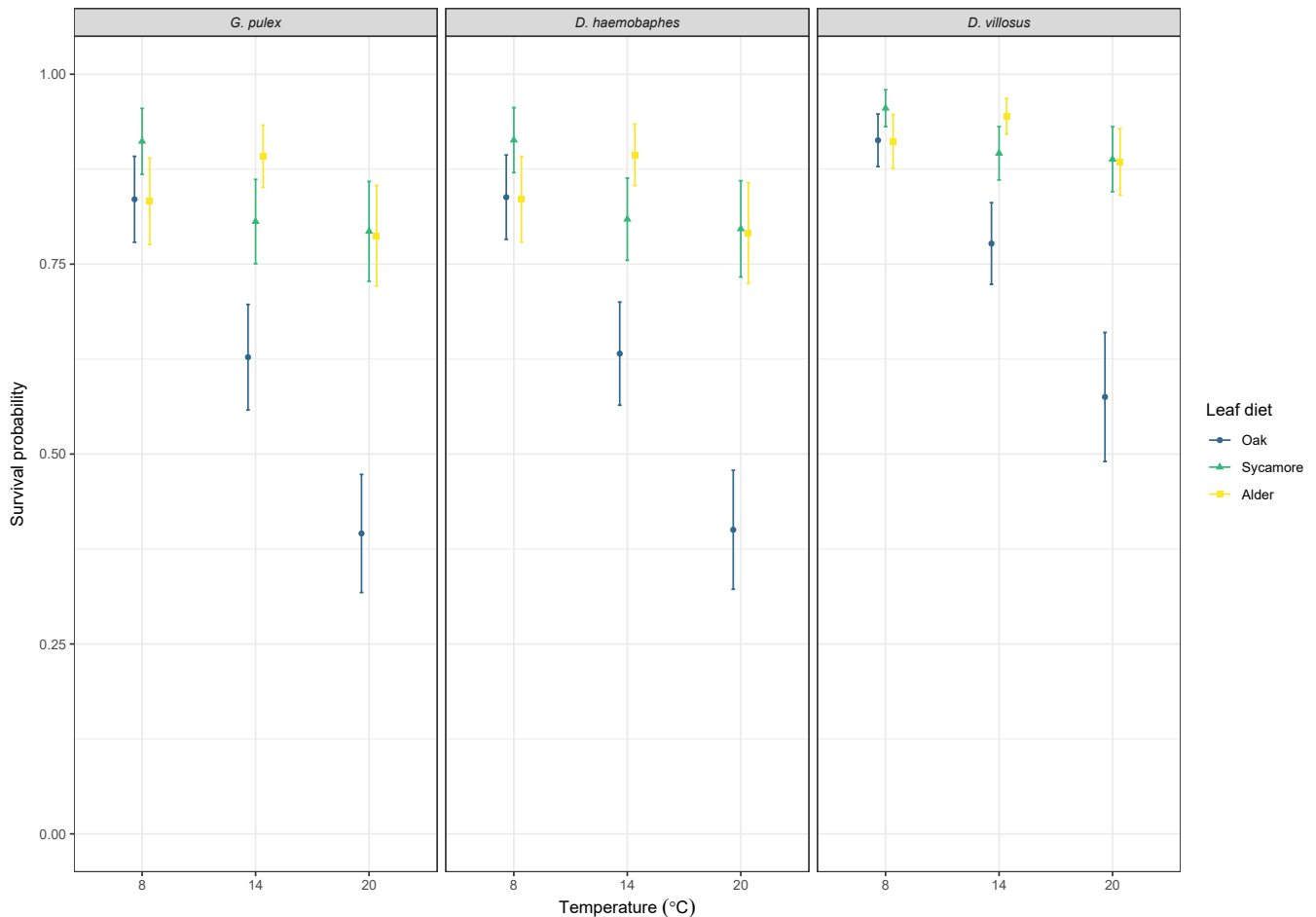


FIGURE 2 Amphipod survival, as predicted by the *best fit* model, against treatment temperature (°C), leaf diet (point shapes and colours) and amphipod species (facets). Vertical error bars show the standard error of our model predictions. The *best fit* model suggests amphipod survival varies with respect to the amphipod temperature and leaf species diet treatment combinations in addition to amphipod species. Sample sizes for these treatments are shown in [Figure 1](#).

We found that amphipod survival varied between species (H_4). This is in accord with Kenna et al. (2016), despite the differences between these studies (e.g. duration and water temperature treatments). Our finding suggests that at high temperatures the dynamic between native *G. pulex* and invasive *Dikerogammarus* species could change. Specifically, an increased probability of higher water temperatures could result in reduced population sizes of both *G. pulex* and *D. haemobaphes* and facilitate the continued spread and domination of *D. villosus*. Further to this, there was a significant difference in survival rates between leaf diet treatments (H_3). Specifically, amphipods provided with a high-quality resource (alder) diet had the highest chances of survival whereas amphipods supplied with a poor-quality resource (oak) had the lowest chances of survival. Freshwater systems are commonly reliant on allochthonous material due to many being net heterotrophic (Marcarelli et al., 2011). Current nutrient input patterns could be expected to change with leaf stoichiometry, which is known to vary within and between species (Ågren & Weih, 2012; Yuan & Chen, 2015), in addition to changes in riparian plant communities driven by climate change and invasion. The resulting resource quality impacts amphipod survival

and any changes in resource quality would also be likely to impact freshwater communities.

In this study, we quantified detrital processing using FPOM generation, rather than CPOM consumption in contrast to many previous studies (e.g. Kenna et al., 2016; Truhlar et al., 2014). We propose that FPOM provides a more direct measure of detrital processing, in terms of benefits to other species through increased nutrient availability, than CPOM which has often been used as a proxy for the former. Using FPOM measures directly could also increase our ability to identify changes at a finer scale. While microcosm experiments can rarely address the complexities of field systems (Drake & Kramer, 2012), they are well adapted to quantify such processes as FPOM generation. Specifically, by limiting the sources of variation we are better able to estimate small scale processes with a higher degree of accuracy. It is possible that a greater understanding of how individual level FPOM generation and survival rates, as presented here, may be realised in complex natural systems could be achieved through addressing the known limitations of our study. Our methodologies did not allow the amphipods to demonstrate prey switching behaviour

(e.g. MacNeil and Platvoet, 2005; Pellan et al., 2016) or quantify how this might impact FPOM generation rates and amphipod survival. While our temperature treatments consisted of only three temperatures, held constant throughout the experiment, natural systems will show variation across space (e.g., north-south gradient and with water depth) and time (annual, seasonal, and diurnal). Lastly, our microcosms were designed to measure individual level FPOM generation rates and were therefore unable to account for changes in behaviour due to interactions between amphipods (e.g., competition or predation). For example, MacNeil et al. (2011) report that *D. villosus* results in reduced leaf shredding efficiency directly, through predation, and indirectly, through initiating more anti-predator behaviours in native amphipods (including *G. pulex*).

Under current climate conditions, native *G. pulex* undertake significantly more detrital processing than the invasive non-native *D. villosus* and *D. haemobaphes* but under future projected climate conditions between-species differences will change. We have shown that, generally, FPOM generation rates increased with increasing temperature, with these increases being higher in higher quality leaf diets (e.g. alder). However, we have also shown that amphipod survival rates decrease with increasing water temperature, with the largest decrease in those amphipods provided with poorer leaf diets (e.g. oak). These results suggest that any realised changes in FPOM production may be primarily driven by the leaf resources available. For example, in areas dominated by poorer quality leaf diets (e.g. oak) overall FPOM production could decrease as the decrease in survival probabilities for all amphipods appears to exceed any increase in FPOM generation. On all other leaf diets, as water temperature treatments increased, we observed the highest FPOM creation and only modest decreases in survival probability which could result in an increased rate of FPOM creation. To this end, incorporating the ability for amphipods to preferentially switch diets (for example in response to temperature treatments) could provide valuable further insight into how our results may be realised in natural systems. Ultimately, our study suggests that while currently species invasions impact the generation of FPOM and therefore the availability of nutrients to the wider community, in the future it is likely that the type of plant detrital matter available will have a far greater impact than it does currently in the present day.

AUTHOR CONTRIBUTIONS

Conceptualisation, developing methods, conducting the research, data interpretation and writing: W.F., L.B., H.R., A.D. Data analysis and preparation of figures and tables: W.F.

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DATA AVAILABILITY STATEMENT

Data are available via Zenodo <https://doi.org/10.5281/zenodo.7698365> (Fincham et al., 2023).

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SUPPORTING INFORMATION

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