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RESEARCH ARTICLE

Parasitism dramatically alters the ecosystem services provided by freshwater mussels

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Abstract

1. Parasites can indirectly affect ecosystem function by altering host phenotype, but the trait-mediated impacts of parasitism at an ecosystem level remain poorly characterised. However, understanding the influence of parasites is central to understanding the ecosystem services provided by host species, especially in an era of global environmental change.
2. We examined the effect of native (the trematode *Rhipidocotyle campanula*) and invasive (the bitterling fish *Rhodeus amarus*) parasites, and their interaction, on the clearance rates of unionid mussels, a dominant ecosystem-engineering group that modify freshwater ecosystems worldwide. We used a combination of field experiments, laboratory experiments and ecological simulations to demonstrate the phenotypic impact of parasites on the functional response of two mussel species across an environmental gradient (suspended particle concentration), and extended this with host and parasite community data to demonstrate the consequences for a real-world ecosystem, the Old West River in Cambridgeshire, England.
3. Both parasites altered the clearance rates of their hosts but in contrasting fashion: while *R. campanula* increased host clearance rates relative to uninfected conspecifics under all conditions, *R. amarus* supressed clearance rates at high suspended particle concentrations (eutrophic conditions) but elevated them otherwise. The parasites displayed different infection patterns in the two host species, and the invasive *R. amarus* rarely co-infected mussels with *R. campanula*.
4. Given their disparate effects, the parasites' distributions reversed the relative filtration capacity of the two host species under high vs. low concentrations of suspended particles, demonstrating how differences between the infection patterns of native and invasive parasites, as well as their individual effects, need to be considered. Overall, the proportion of daily river discharge filtered by the combined mussel community changed by up to 96% in the presence of parasites. By incorporating multiple host species and multiple parasite species, we provide ecologically relevant evidence for the trait-mediated effects of parasites on ecosystem processes.
5. Our study demonstrates that parasitism can significantly alter wider ecosystem processes through changing the phenotype of their host. Future work on

ecosystem function should take parasitism into account, and consider both trait-mediated and density-mediated effects.

KEYWORDS
clearance rate, ecosystem engineer, eutrophication, filtration, functional response, invasive species, trait-based effect, unionid

1 | INTRODUCTION

Parasites are an important and often underappreciated component of global ecosystems (Carlson et al., 2020; Hudson et al., 2006; Lafferty et al., 2008). In an era of unprecedented global change, parasite abundances and distributions may be altered through multiple mechanisms. For example, increased temperatures are predicted to increase the prevalence of some parasites and diseases, such as helminths (Cohen et al., 2020). In addition, a general trend of biotic homogenisation facilitates parasite spread to previously unoccupied regions (Olden et al., 2004); this can also be enhanced by environmental conditions and lead to outbreaks of previously low-abundance invaders (Spear et al., 2021). Host species may therefore encounter higher prevalence and intensities of native parasites, as well as increasing numbers of invasive parasites. The consequences of this redistribution of parasite pressure, and the degree to which it applies to different parasite species with different life-history strategies, remain to be fully characterised (but see Dunn et al., 2012). While the effects of parasites at an individual level are well known for a broad range of host taxa (Sánchez et al., 2018), parasites may also affect ecosystem functioning (Wood & Johnson, 2015) and can be considered as cryptic ecosystem engineers (Selbach et al., 2022). Despite many suggestions that parasites can affect ecosystem functioning (Hatcher et al., 2012) and theoretical evidence for this (Vannatta & Minchella, 2018), empirical evidence for the impact of parasites on ecosystem-level processes remains rare (Fischhoff et al., 2020; but see Pascal et al., 2020).

Parasites affect ecosystems through three mechanisms: direct biomass effects, density-mediated effects and trait-mediated effects (Dunn et al., 2012; Fischhoff et al., 2020; Hatcher et al., 2006, 2014). Biomass effects occur when the parasite directly contributes significantly to the standing biomass of the ecosystem (e.g. Kuris et al., 2008; Preston et al., 2021) and, for example, acts as an important carbon or food source (Morley, 2012). Density-mediated effects occur when parasites alter the mortality or reproductive rates of one or more host species, thus altering community structure or the total biomass of the system (e.g. Bojko et al., 2019, 2020; Chantrey et al., 2014; Friesen et al., 2020). Finally, trait-mediated effects occur when parasites alter the phenotype of their hosts, such as increasing metabolism and feeding rates (Dick et al., 2010; Nadler et al., 2021), bioturbation rate (Dairain et al., 2020) or nitrogen excretion rate (Mischler et al., 2016). For both density- and trait-mediated mechanisms, impacts are more likely to scale to the ecosystem level if hosts have strong engineering effects. Despite this sound framework, evidence for the different mechanisms is unevenly distributed. There is high support for density-mediated effects, with a large focus on how host death affects ecosystems (Borer et al., 2021; Coen & Bishop, 2015). There is much less support for trait-mediated effects scaling to an ecosystem level (Fischhoff et al., 2020), and studies that do support this mechanism are largely drawn from rocky shore and estuarine environments (e.g. Dairain et al., 2020; Mouritsen & Poulin, 2010; Wood et al., 2007). In general, a recent review found that understanding the trait-mediated ecosystem-level effects of parasitism across a range of systems is highly underdeveloped and an important research frontier (Fischhoff et al., 2020).

Understanding the trait-mediated effects of parasitism requires consideration of two issues. The first is the underlying environmental conditions on which the host phenotype exerts an effect. For example, Fielding et al. (2003) found that infection with the acanthocephalan parasite *Echinorhyncus truttae* reduced the feeding rate of the amphipod *Gammarus pulex*, while Dick et al. (2010) found that an infection increased the feeding rate of the host in the same system. This discrepancy is explained by the fact that the first study only offered low prey densities to *G. pulex*, while the latter study offered a range of prey densities where elevated feeding could be observed (Dick et al., 2010). A functional response analysis is therefore desirable, to avoid drawing erroneous conclusions based only on a 'snapshot' assessment of the conditions (Dick et al., 2014). Analysing the effect of parasites on host functional responses is also highly relevant given the changing global environmental conditions, as it effectively allows for comparison across a range of possible scenarios (e.g. Williams et al., 2019). However, few studies apply a functional response analysis to the trait-mediated impacts of parasitism, and those that have (e.g. Stier et al., 2015) do not consider the ecosystem-level implications.

The second issue requiring careful consideration in studying the trait-mediated effects of parasitism on ecosystem functioning is the role of variable host–parasite and parasite–parasite interactions. Most studies on the ecosystem-level effects of parasitism consider a one-host, one-parasite system, but this accords poorly with ecological reality (Preston et al., 2016). Different species host different parasites (Dallas et al., 2019), or may host the same parasites at varying prevalence (Mills & Reynolds, 2002a). These differences between hosts may be caused by different shared evolutionary histories with available parasites (Blasco-Costa et al., 2021), environmental conditions and dispersal limitation (Moss et al., 2020), or interactions between parasites, which can facilitate or inhibit one another to varying degrees (Clay et al., 2019; Sweeny et al., 2020). The relative importance of these factors may vary between parasite species; for

example, some brood parasites in particular may use a sophisticated range of evolutionary and ecological cues to determine host quality and actively select host species (Mills & Reynolds, 2002a), which may include avoiding depositing in hosts infected with conspecific or heterospecific parasites (Vyas et al., 2019). Such host specificity or host preference, caused by both passive and active factors, means that parasite-mediated phenotypes may be expressed in different host species in ways that could not be predicted from the underlying parasite prevalence alone. A comprehensive understanding of the ecosystem effects of parasites thus requires understanding how the environmental conditions interact with parasite-mediated effects, and how those effects are distributed by multiple parasites within and between host species.

In this study, we leverage a two-host, two-parasite system to comprehensively explore how parasites affect ecosystem function. Unionid mussels are prodigious filter-feeders in freshwater ecosystems worldwide, and can significantly alter their environments (Tankersley & Dimock Jr, 1993; Vaughn, 2018). They are also afflicted by a range of parasites which may interfere with this engineering service, though this has been hitherto unexplored (Brian & Aldridge, 2019). As common techniques exist for examining the functional response and clearance rates of freshwater mussels (e.g. Kemp et al., 2018), and given the importance of this response in global freshwater ecosystems, this system provides an excellent and significant opportunity to further knowledge on the trait-mediated impacts of parasitism.

The native digenean trematode *Rhipidocotyle campanula* is commonly observed inside the host unionid mussel *Anodonta anatina*. While the partial or complete castrating impacts of this parasite (and hence a possible density-mediated effect) are well documented (Brian et al., 2021; Müller et al., 2015), there is indirect evidence, such as shell morphology changes in infected mussels (Zieritz & Aldridge, 2011), that trematodes may also affect the filtering phenotype of the host. *R. campanula* appears to only infect mussels of the genus *Anodonta* (Brian & Aldridge, 2019), but this is unlikely to be due to active choice by the trematode given the low selective ability of its infective stage (miracidia). In contrast, both *A. anatina* and the sympatric *Unio pictorum* are infected by the invasive fish parasite *Rhodeus amarus*, which lays its embryos in the gills of freshwater mussels (Aldridge, 1999). *R. amarus* invaded the UK from the Ponto-Caspian region in the 20th century (Damme et al., 2007), and there is an evidence the mussel hosts are still evolutionarily naïve (Reichard et al., 2006). Bitterling embryos compete with mussels for oxygen (Methling et al., 2019; Spence & Smith, 2013) and deform the gills (Mills et al., 2005), and so could also affect the filtration rate of mussels. Bitterling are also highly discriminatory and can select hosts based on a variety of cues (Mills & Reynolds, 2002a; Smith et al., 2001), and thus may avoid depositing embryos in hosts previously parasitised by trematodes (Brian & Aldridge, 2021a). This system therefore allows us to test the importance of variable parasite distributions, incorporating both native and invasive parasites and two different life-history strategies, as well as parasite impacts on the ecosystem-level effects of mussels, using a combination of field surveys, field experiments, laboratory experiments and ecological simulations.

Scaling parasite effects to the ecosystem level requires integrating observational field data on host density and parasite prevalence with *per-capita* measurements of infected and uninfected mussels, and the relative role of the host in the ecosystem of interest (Preston et al., 2016). We therefore make and test four predictions: (1) bitterling will avoid depositing embryos in *A. anatina* infected with trematodes; (2) trematodes will reduce the clearance rate of *A. anatina*, its preferred host; (3) bitterling embryos will reduce the clearance rate of *U. pictorum*, its preferred host; and (4) parasites alter the rate at which unionids filter the river water where they reside. We test Prediction 1 with a field experiment, Predictions 2 and 3 with laboratory experiments, and Prediction 4 with a combination of field surveys and a simple ecological model. We show that parasites, through their impact on the host mussel trait of clearance rate, alter the filtered proportion of daily discharge of a sampled river by up to 96%, but that this effect varies with host species and may even reverse based on the nutrient profile of the river.

2 | MATERIALS AND METHODS

No permission for fieldwork was required in this study, and ethical approval was not required as manipulations only involved non-cephalized invertebrates.

We first carried out preliminary sampling to characterise our system. On the 7th of May 2019, we sampled 60 *A. anatina* and 30 *U. pictorum* from the Old West River (OW), the focal river of our study, at Stretham Old Engine (52.3343°N, 0.2243°E). We completely characterised the macroparasite communities of all sampled mussels, following procedures outlined in Brian and Aldridge (2021a). Our sampling revealed that bitterling infection was mainly observed in *U. pictorum*, while trematode infection was only observed in *A. anatina* (see Section 3). Furthermore, coinfection between trematodes and bitterling was absent.

2.1 | Prediction 1: Bitterling will avoid *A. anatina* infected with trematodes in the field

2.1.1 | Field experiment establishment

On the 14th of May 2021 we sampled 150 *A. anatina* from the River Great Ouse at King's Dyke (KD; 52.5397°N, −0.1753°E); this sampling location was selected as it has a high prevalence of the castrating trematode *R. campanula*. We non-destructively assessed all mussels for trematode infection by extracting gonadal fluid using a hypodermic needle and examining it under a compound microscope (Brian & Aldridge, 2021b). *R. campanula* was identified using Gibson et al. (1992); furthermore, it is the only digenean trematode reported using UK freshwater mussels as a first intermediate host (Brian & Aldridge, 2019). Once all mussels had been assessed, 30

trematode-infected mussels were measured using Vernier callipers to the nearest 0.1 mm, and each was paired with a non-infected mussel of identical size (within 1 mm; average length difference between pairs of infected and non-infected mussels = 0.46 mm). This was to control for the potential effect of host size on bitterling choice. The average length of mussels (±*SE*) was 72.2 mm ± 0.97 mm. We did not explicitly consider mussel sex, given the extreme female bias in this river (>95% of mussels possessing female trait of marsupia; Brian et al., 2021).

We placed each pair of mussels inside a ceramic plant pot filled with river sediment (i.e. 30 pots in total), each with a diameter of 18 cm, and attached each mussel to the pot using ~30 cm of twine that was carefully superglued on to both the pot and the mussel shell, following zu Ermgassen and Aldridge (2010). Attaching mussels to pots with string does not affect mussel valve movements or opening. Pots were buried in the sediment with the top ~5 cm exposed in OW, at a water depth of ~1 m. Pots were placed at intervals of ~4 m along the river, to ensure that no two pots were likely to be within the same male bitterling territory (zu Ermgassen & Aldridge, 2010). Pots were left for the natural bitterling population in the river to infect the experimental mussels for a period of 1 month, which maximises the chance of observing bitterling infection while minimising the possibility of deposited bitterling embryos fully developing and leaving the mussel before being observed (Aldridge, 1999). The experiment commenced on the 24th of May 2021, during the bitterling spawning season, and was terminated on the 24th of June 2021.

After the experiment ended, we recovered as many pots and mussels as possible, carrying out repeated sweeps of the experiment area. We returned all mussels to the laboratory and immediately dissected them, counting all bitterling embryos present in the gills and identifying their stage of development as 'a' to 'e' (following Aldridge, 1999), where 'a' is the least developed and 'e' the most developed. We also dissected the gonad of all experimental mussels, and verified via compound microscopy that in all cases our non-destructive diagnosis of mussels as trematode infected or uninfected was accurate. These dissections, in addition to those described in Section 2.2.2 (below), did not reveal infection with any other digenean trematodes (e.g. *Echinoparyphium recurvatum*), which has the strongest negative correlational relationship with *R. amarus* aside from *R. campanula* (Brian & Aldridge, 2021a).

2.1.2 | Field experiment analysis

We compared overall bitterling prevalence (i.e. initially leaving aside the paired nature of our experiment) between trematode-infected mussels and uninfected mussels using an equality of proportions test. In addition, for pairs where both mussels were successfully recovered, we carried out Fisher's exact test to assess independence in infection prevalence between trematode-infected mussels and uninfected mussels.

2.2 | Predictions 2 and 3: Parasites will affect the clearance rates of mussels in laboratory experiments

We carried out two laboratory experiments: the first compared the filtration rates of *A. anatina* with and without trematodes, and the second compared the filtration rates of *U. pictorum* with and without bitterling embryos.

2.2.1 | Experimental subjects

In total, 30 *A. anatina* (15 infected with trematodes, 15 uninfected) and 45 *U. pictorum* (15 infected with bitterling, 30 uninfected) were used in the filtration rate experiments. Infected and uninfected *A. anatina* were identified as described above, from the same population that was sampled at KD. Experimental *U. pictorum* subjects were collected from OW on the 24th of May 2021, and taken back to the laboratory to non-destructively assess bitterling infection. We carefully opened the valves of mussels by inserting and twisting a blunt scalpel, and then examined the mussel demibranchs for evidence of bitterling embryos with the aid of a rounded probe. Before being used in experiments, mussels were maintained in the laboratory in 10 L buckets in water from their home rivers at 19° C, under constant darkness. They were able to feed on algae present at ambient concentrations in the river water but were not provided with additional food.

To calculate filtration rates, we measured the change in concentration of algae cells between the start and end of the experiment, using Chlorophyll *a* concentration as a proxy for algal concentration. We used *Chlorella vulgaris* (strain CCAP 211/12) as our algae species, as this is readily consumed by both mussel species. *C. vulgaris* was grown using 3 N-BBM+V medium and a 16:8 L:D cycle. We measured Chlorophyll *a* concentration using a handheld fluorometer (AquaFluor 8000-010) that was calibrated using serial dilutions of a Chlorophyll *a* analytical standard (Sigma Aldrich) of known concentration; the fit of the calibration curve was 97.8%.

2.2.2 | Experimental procedures

The day before the experiments, we gently scrubbed the shells of all mussels to remove organic material and placed them in clean dechlorinated water overnight. The day of the experiment, buckets were filled to 500 ml with varying amounts of clean dechlorinated water and *C. vulgaris* culture, to produce a range of Chlorophyll *a* concentrations (suspended particle concentration) between 20 and 160 µg/L. To start the experiment, mussels were placed in individual buckets and the Chlorophyll *a* concentration was immediately measured. Experiments were conducted in a constant temperature room matched to field conditions (19°C). To avoid location effects within the room, individual bucket location was randomised in terms

of both algal concentration and whether the mussel was infected or uninfected with parasites. Buckets were aerated throughout the experiment, and therefore no adjustment was required for the settling rate of algae as this effectively resuspends particles (Kemp et al., 2018). Each mussel was allowed to filter for 2 hr, and then we measured the Chlorophyll *a* concentration again and ended the experiment.

All mussels were immediately dissected to confirm infection status and intensity. Bitterling intensities were calculated as the number of bitterling embryos per mussel; trematode intensities were calculated as the percentage of the gonad filled with trematode tissue (following Brian & Aldridge, 2020). Following these dissections, one *A. anatina* that was originally thought to be trematode-free was found to be trematode infected, and three *U. pictorum* that were thought to be bitterling-infected were found to be uninfected; these mussels were therefore treated in the analyses below according to their updated infection status. After parasite diagnosis, all soft tissue from the mussels was removed, dried to constant mass (DW) and weighed to the nearest 0.0001 g.

2.2.3 | Laboratory experiment analysis

For each of the two experiments (*A. anatina* with or without trematodes; *U. pictorum* with or without bitterling), we analysed the 'consumption rate' (raw amount of algae consumed by mussels *per* gram of dry weight *per* hour) of mussels by fitting a generalised linear model (Gamma family, log link) to the response variable of Chlorophyll *a* (μg/L) consumed per g dry weight per hour. Independent variables were initial Chlorophyll *a* concentration (μg/L), infection status (infected/uninfected) and the interaction of these two factors. We also explored whether intensity of infection influenced consumption rate.

We calculated 'clearance rates' (ml of water filtered *per* g dry weight *per* hour) using Equation (1), following Kemp et al. (2018), where DW is the dry weight of mussels (to account for different sizes of mussel) and $C_{initial}$ and C_{final} are the starting and ending concentrations of Chlorophyll *a* (μg/L):

$$CR = \frac{500}{2DW} \ln\left(\frac{C_{initial}}{C_{final}}\right). \quad (1)$$

To confirm that the consumption rate of mussels followed a Type I functional response, we plotted the clearance rates for each mussel against the corresponding starting concentration of Chlorophyll *a*; the slope of this line should not be significantly different from zero (i.e. the clearance rate should be directly proportional to the amount of algae available to be consumed). We assessed departures from this assumption by fitting a Gamma-distributed generalised linear model (log link) of clearance rate against starting Chlorophyll *a* concentration, for both infected mussels and uninfected mussels.

2.3 | Prediction 4: Effects observed in the field and laboratory scale to an ecosystem level

2.3.1 | Parametrising the ecosystem model

Using the data of our field and laboratory studies, we parameterised a series of ecological simulations that scale up our results to an ecosystem level. These simulations were carried out with a bespoke function (see Supplementary Code) written in R v3.6.3. (R Core Team, 2020), and incorporated observed mussel densities and mussel size, observed parasite prevalence and distributions (what hosts they appeared in), and mussel clearance rates with and without parasites. The overall goal of these simulations was to determine how parasites influence the rate at which mussel populations filter the Old West River. Specifically, we asked what proportion of the daily summer discharge rate (calculated using the parameters of McIvor, 2004) a 1 km stretch of mussels could filter, with and without parasites. We chose this measure (proportion of daily discharge) as it captures both river volume and flow rate, and we chose this time period (summer) as this was when our observational sampling and experiment took place. We calculated this proportion for a range of possible mussel densities (1 mussel per square metre to 50 mussels per square metre), and calculated actual estimates (separately) for populations of *A. anatina* and *U. pictorum* at their observed densities. Briefly, for each density, simulations first assigned a given number of mussels as parasitised and unparasitised based on mussel species and observed parasite prevalence, assigned a clearance rate to each mussel based on the mussel species identity, clearance rate experiments and simulation set (see below), summed the clearance rate of all mussels and expressed that sum as a proportion of the daily OW river discharge.

Two sets of simulations were generated: one set assuming low Chlorophyll *a* concentrations (40 μg/L) were present in the river, and one set assuming high Chlorophyll *a* concentrations (120 μg/L) were present in the river. These two values of were chosen because they represent typical summer Chlorophyll *a* levels and highly eutrophic Chlorophyll *a* levels in English rivers, respectively (Neal et al., 2006). We ran our simulations at two values because the effect of bitterling depended on Chlorophyll *a* concentration (see Results). Each set of simulations considered four cases: an *A. anatina* population with trematodes at the observed prevalence; an *A. anatina* population with no trematode infection; a *U. pictorum* population with bitterling at the observed prevalence; and a *U. pictorum* population with no bitterling infection. Therefore, in total, we simulated eight cases. Because the effects of parasites occur at an individual level, we did not average over populations, instead, our models explicitly accounted for individual-level variation (see Section 2.3.2 below).

Population-level clearance rates are typically expressed in terms of overall mussel biomass per square metre; it was not desirable or possible to do this here as parasite prevalence cannot be expressed in this fashion, and this would not take into account the variation

among individual mussels. Instead, we calculated the average biomass of individual mussels at OW. In July 2021, we sampled 20 replicate 0.25 m^2 quadrats at OW along the riverbank and measured all mussels found. Sampling involved excavating the substrate to a depth of ~5 cm to detect mussels buried in the sediment. This process gave us average mussel densities in addition to size distributions of the populations. We used length to dry mass equations (parameterised using our May 2019 sampling where dry weights were calculated, following procedure of Coughlan et al., 2021) to work out the size of an average mussel for both populations, and thus transformed our estimated average clearance rate from ml *per g dry weight* per hour, into ml *per mussel* per hour. This assumes that mussels of all sizes are equally likely to be infected by trematodes and bitterling; this assumption has previously been shown to be sound (Brian & Aldridge, 2021a).

2.3.2 | Accounting for uncertainty

We ran 10 replicate simulations for each mussel density (1 m^{-2}, 2 m^{-2}, …, 50 m^{-2}), for each of the eight cases. In other words, for a given mussel species (e.g. *A. anatina*), at a given density (e.g. 10 m^{-2}) and a given Chlorophyll *a* concentration (e.g. 40 µg/L), we calculated the expected proportion of daily river discharge filtered 10 times, and averaged those 10 replicates. Replicates were not identical because we allowed two key parameters to vary in our model, reflecting two significant areas of uncertainty in our underlying data: estimated parasite prevalence and estimated clearance rate. To demonstrate the overall degree of uncertainty, each replicate (rather than just their average) is individually plotted on the corresponding figure.

To account for uncertainty in our field estimates of parasite prevalence, we allowed the number of mussels infected with parasites to vary according to their binomial probabilities. For example, if the simulation involved a density of 10 mussels and the observed parasite prevalence was 0.4, it would be most likely that 4 of the 10 mussels were assigned as being parasitised; however, it is also possible that other numbers of mussels were assigned as being parasitised for that particular replicate, according to their declining binomial likelihood. This accounts for the fact we cannot know the true prevalence of parasites in the whole population, as our field sampling only provides an estimate. In line with our observations (and to allow us to parameterise all clearance rates using our laboratory experiments), we limited *A. anatina* to only be infected with *R. campanula*, and *U. pictorum* to only be infected with *R. amarus*.

To account for significant variation in the estimates of mussel clearance rates (see confidence intervals in Figures 1 and 2), we allowed the clearance rate for each mussel in each replicate to vary. Specifically, we allowed the simulated clearance rate for a particular mussel to be drawn from a uniform distribution where the minimum and maximum possible values were the lower and upper bound, respectively, of the 95% confidence interval for the estimated clearance rate. Each of the eight cases (*A. anatina* and *U. pictorum* populations, with and without parasites, at low or high Chlorophyll

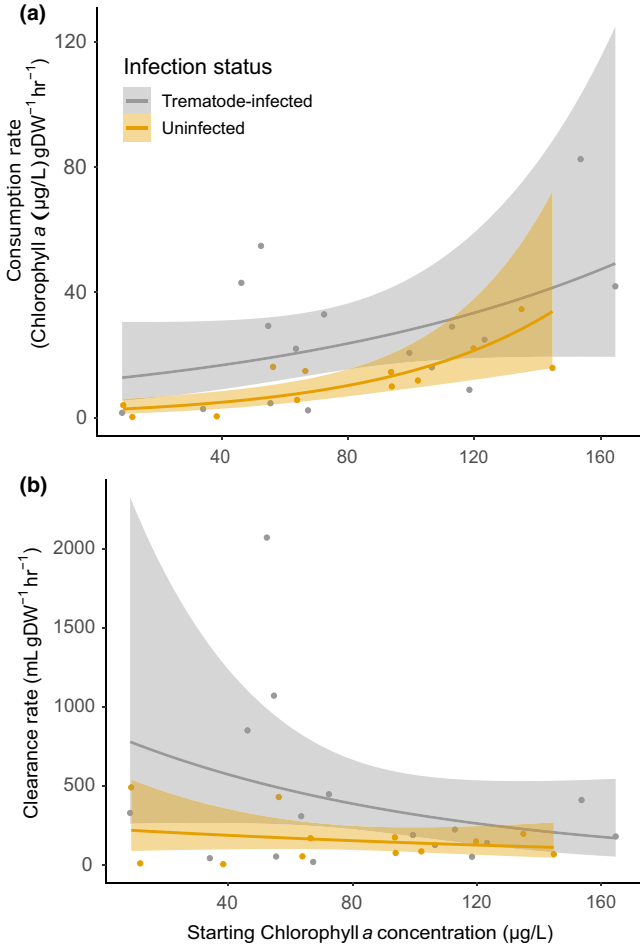

FIGURE 1 The functional filtering response of *Anodonta anatina* for trematode-infected (grey lines) and uninfected (yellow lines) mussels. Shaded regions are 95% confidence intervals around the means, which were fitted using a generalised linear model (Gamma family, log link). (a) The feeding rate of *A. anatina* [micrograms of Chlorophyll *a* consumed per litre per gram of mussel dry weight (DW) per hour] in response to different starting Chlorophyll *a* concentrations. (b) The clearance rate of *A. anatina* (millilitres per gram of dry weight per hour) in response to different starting Chlorophyll *a* concentrations.

a concentrations) had its own 95% confidence interval, calculated using the results of the clearance rate experiments. This approach was used in favour of using the overall average clearance rate for each case, which would not take into account the variation observed in the clearance rates of individual mussels.

2.3.3 | Calculating the effect across the combined mussel community

Finally, we combined the known densities of *A. anatina* and *U. pictorum* and repeated the same procedure described above at a community level. These densities were estimated using the same 20 replicate quadrats used to estimate the mean biomass of mussels at OW. We thus had four simulated cases: the mussel community with

associated parasites and without associated parasites, at environmental conditions of low and high Chlorophyll *a* concentration. The quadrats were exhaustively sampled, but it is possible that there was a sampling bias making it more likely to detect larger mussels. We do not believe this will affect our results, as very small mussels will have correspondingly small filtration rates (Kryger & Riisgård, 1988). In addition, our estimates do not include the contribution of *U. tumidus*, another freshwater mussel species also found at the site. This species does not host *R. campanula* (Brian & Aldridge, 2019), and is only rarely parasitised by *R. amarus* relative to *A. anatina* and *U. pictorum* (Reynolds et al., 1997), and so the effect of parasites on its phenotype is expected to be extremely minor.

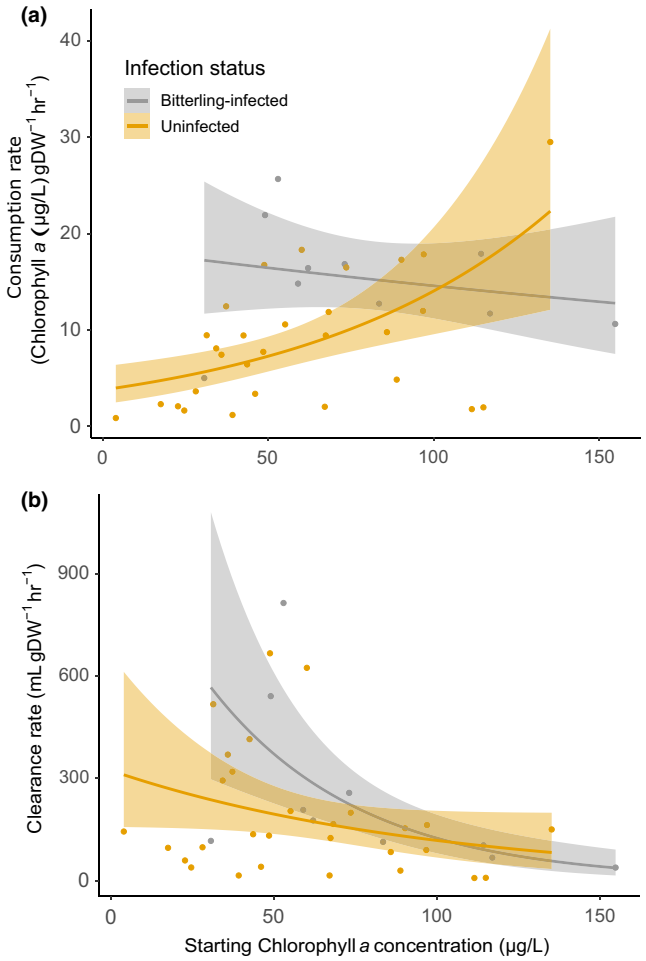

FIGURE 2 The functional filtering response of *Unio pictorum* for bitterling-infected (grey lines) and uninfected (yellow lines) mussels. Shaded regions are 95% confidence intervals around the means, which were fitted using a generalised linear model (Gamma family, log link). (a) The feeding rate of *U. pictorum* [micrograms of Chlorophyll *a* consumed per litre per gram of mussel dry weight (DW) per hour] in response to different starting Chlorophyll *a* concentrations. (b) The clearance rate of *U. pictorum* (millilitres per gram of dry weight per hour) in response to different starting Chlorophyll *a* concentrations.

3 | RESULTS

3.1 | Field observation and Prediction 1: Bitterling avoid *A. anatina* infected with trematodes

Sampling of mussels in May 2019 revealed that trematodes and bitterling displayed different infection patterns between *A. anatina* and *U. pictorum* host mussels. 27% of *A. anatina* were infected with trematodes, while no *U. pictorum* were infected with trematodes. In contrast, 66% of *U. pictorum* hosted bitterling embryos in their gills, compared to just 8% of *A. anatina*. In addition, there was no coinfection between trematode and bitterling parasites in *A. anatina*.

Recovery rates of the experimental mussels quite were low: only 28 of the 60 mussels were recovered, and out of the 30 matched pairs, both mussels in the pair were recovered on only eight occasions. We suspect that an unanticipated level of boat activity dislodged pots and caused the mussels to become unattached, as several pots were found on their sides.

Table 1 shows the overall results of the experiment. In total, 17 bitterling embryos were found in non-trematode-infected mussels (3.4 ± 0.78 bitterling per mussel, mean $\pm$ *SE*), in contrast to just three from trematode-infected mussels (1.5 ± 0.35 bitterling per mussel). However, the low sample size means that the proportion of mussels with bitterling infection did not differ between trematode-infected or non-trematode-infected mussels ($p = 0.256$). All developmental stages of bitterling were observed in mussels that did not have trematodes (Table 1), including two mussels that had very late-stage bitterling embryos, suggesting they were infected soon after the experiment commenced.

However, a slightly different pattern was observed when considering the eight recovered pairs in isolation. Here, results within the pair were always identical: either both trematode-infected and non-trematode-infected mussels had bitterling (2 pairs) or both did not

TABLE 1 The number of bitterling embryos recovered from trematode-infected and non-infected mussels. Numbers refer to the total number of bitterling embryos of each stage observed; numbers in brackets indicate the number of mussels where bitterling embryos were observed. For mussels without trematode infection, it was common for bitterling at multiple developmental stages to be observed in the same mussel, indicating multiple deposition events

Trematodes?	Total mussels recovered	Bitterling development stage					Total
		a	b	c	d	e	
Yes	13	1 (1)	0	0	2 (1)	0	3 (2)
No	15	4 (3)	6 (3)	2 (2)	1 (1)	4 (2)	17 (5)

(6 pairs). This suggests that occurrences of bitterling in trematode and non-trematode mussels are not independent (Fisher's exact test, $p = 0.036$). However, in both cases where both mussels in the pair had bitterling, the mussel that was uninfected with trematodes had a higher intensity of bitterling than the trematode-infected mussel. Nevertheless, it is clear from our study that coinfection between trematodes and bitterling is highly unlikely, with *A. anatina* disproportionately hosting trematodes and *U. pictorum* disproportionately hosting bitterling. Our results therefore focus on these discrete host–parasite combinations.

3.2 | Predictions 2 and 3: Parasites affect the clearance rates of mussels in laboratory experiments

Infection with trematodes significantly increased the consumption rate of algae by *A. anatina*, the opposite of the prediction made by Prediction 2 (Figure 1). The shape of the consumption response was the same for trematode-infected and uninfected mussels (lack of interaction between infection status and starting Chlorophyll *a* concentration, $t_{24} = 1.339$, $p = 0.193$), but trematode-infected mussels showed a significantly higher consumption rate ($t_{24} = -2.434$, $p = 0.023$; Figure 1a). This higher consumption rate was weakly correlated with the intensity of trematode infection (Figure S1), with higher intensities of infection having higher rates. The functional response was confirmed to be Type I: despite reasonably high variation, the slope of the clearance rate was not significantly different from zero when plotted against the starting concentration of algae for both trematode-infected ($t_{14} = -1.503$, $p = 0.155$) and uninfected ($t_{10} = -0.875$, $p = 0.402$) mussels, indicating the clearance rate was directly proportional to the amount of algae available (Figure 1b). The mean clearance rate (95% confidence interval) for trematode-infected mussels was 407.2 (146.9–667.5) ml/g DW/hr, and the mean clearance rate for uninfected mussels was 159.4 (72.0–246.8) ml/g DW/hr.

In contrast, the effect of bitterling on the functional response of *U. pictorum* depended on the starting concentration of Chlorophyll *a*, as shown by a significant interaction between infection status and starting concentration ($t_{35} = 2.473$, $p = 0.018$; Figure 2a). At low concentrations, bitterling-infected *U. pictorum* showed much higher consumption rates than uninfected mussels, but this trend reversed at high concentrations. As with trematodes, this was weakly correlated with infection intensity (Figure S2), with higher bitterling loads associated with higher clearance rates. Prediction 3 was therefore not supported at low concentrations, and was supported at high concentrations. This interaction is observable in the predicted clearance rates: while uninfected *U. pictorum* also demonstrated the expected Type I functional response (clearance rate slope not different from zero; $t_{27} = -1.852$, $p = 0.075$), the clearance rates of bitterling-infected *U. pictorum* significantly decreased with increasing Chlorophyll *a* concentration ($t_8 = -4.035$, $p = 0.004$; Figure 2b). The mean clearance rate (95% confidence interval) for uninfected *U. pictorum* was 185.1 (119.8–250.4) ml/g DW/hr, while the mean clearance rate for bitterling-infected *U. pictorum* varied with algal concentration.

3.3 | Prediction 4: Effects observed in the field and laboratory scale to an ecosystem level

We extrapolated the results of our field and laboratory studies to predict the effect of parasites at an ecosystem level. First, we calculated the effect of parasites on mussel populations separately. Figure 3 shows what proportion of the daily river discharge of the Old West River could be filtered by a 1 km section of either *A. anatina* or *U. pictorum* populations of varying densities, for two different concentrations of Chlorophyll *a*: 40 µg/L (Figure 3a) or 120 µg/L (Figure 3b). Two broad scenarios were considered in each case: mussel populations with parasites present in their observed prevalence (grey lines), or mussel populations without parasites (yellow lines). Simulations were parameterised using data from the clearance rate experiments (see Section 2).

The results support Prediction 4, that parasite infection alters the ecosystem engineering capacities of mussel populations. At low Chlorophyll *a* concentrations (Figure 3a), both bitterling and trematodes increased the proportion of discharge volume filtered; in other words, they increased the ecosystem engineering capacity of mussels. At high Chlorophyll *a* concentrations (Figure 3b), while trematodes still increased the proportion filtered by *A. anatina* populations, bitterling decreased the proportion filtered by *U. pictorum*: they reduced the engineering capacity of this population. It is valuable to also compare between populations: for example, in Figure 3a, parasitised *U. pictorum* are more efficient than parasitised *A. anatina* at filtering the river, but this trend reverses in Figure 3b.

To provide a tangible example of the impact of parasites, we estimated the proportion of daily discharge of OW filtered for the observed densities of mussels present in the river (red lines and text, Figure 3). *A. anatina* were present at a density of 6 m^{-2}, with an average length of 70.3 mm (estimated average dry weight = 1.46 g). *U. pictorum* were present at a density of 38 m^{-2}, with an average length of 60.5 mm (estimated average dry weight = 1.59 g). Using these densities as examples shows that parasites can stimulate up to a 93% difference in the proportion of river discharge filtered, with a minimum of an 37% proportional difference.

Finally, we estimated the ecosystem effect of mussel parasites using the combined community density of mussel species present in OW (Figure 4). At low Chlorophyll *a* concentrations, parasites increase the proportion of daily discharge filtered by 96%, but this trend reverses at high concentrations, where parasites decrease the proportion of the same volume of water filtered by 28%.

It is also important to note the possible impact of species-specific parasite distributions on the overall number of hosts infected by parasites. At the observed species-specific prevalence (with bitterling infecting *U. pictorum* and *A. anatina* uninfected with trematodes, and trematodes infecting *A. anatina*), and observed host densities, 62% of hosts have at least one parasite, compared with a null expectation

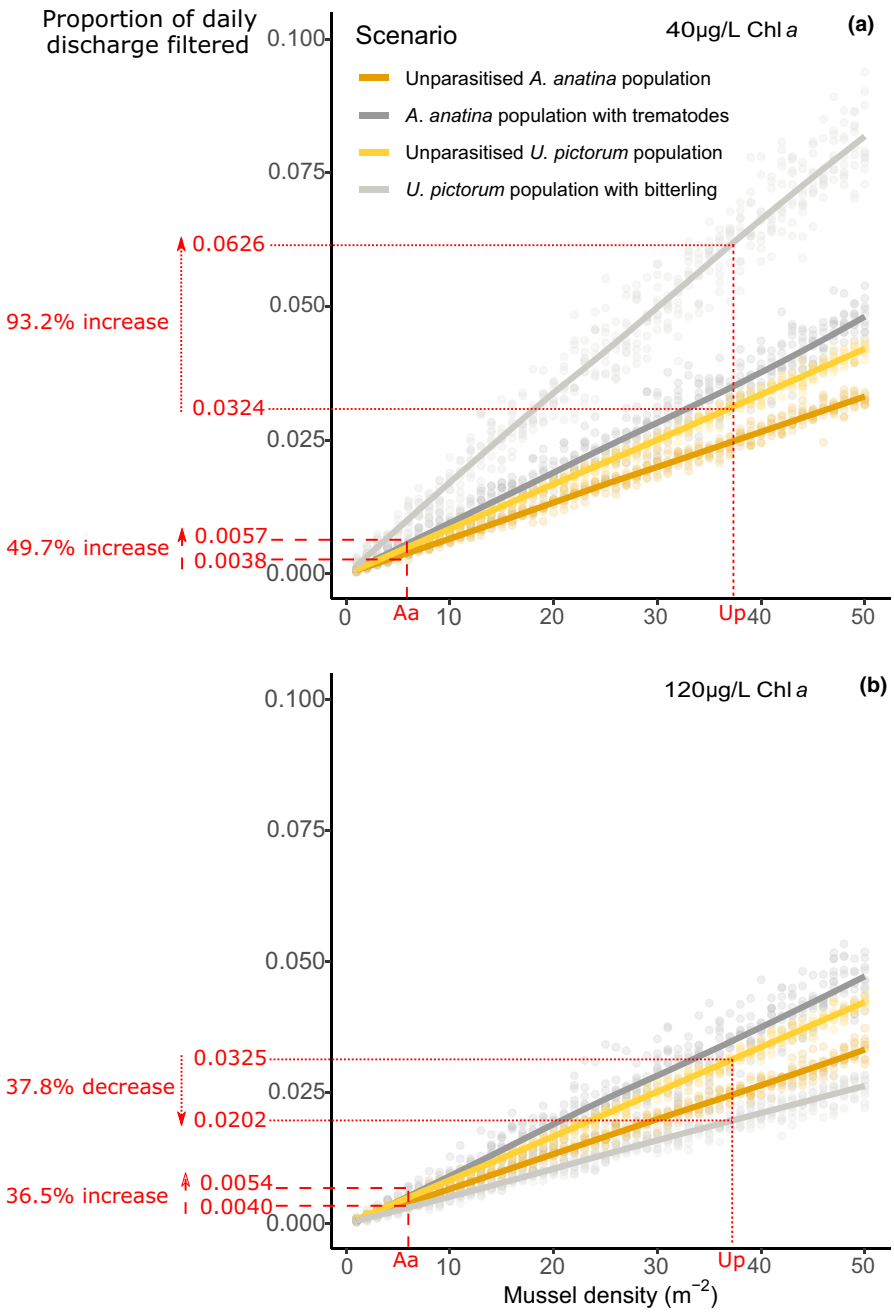

FIGURE 3 Simulated estimates for the proportion of daily discharge of the Old West River able to be filtered by a 1 km stretch of different densities of *Anodonta anatina* or *Unio pictorum*, respectively, at (a) low concentrations of Chlorophyll *a*, and (b) high concentrations of Chlorophyll *a*. Dots represent individual replicates for each case (10 replicate simulations per case per mussel density), with lines representing the average of those replicates. These simulations are based on clearance rate experiments and observed parasite prevalences (trematode prevalence of 0.27 in *A. anatina*; bitterling embryo prevalence of 0.66 in *U. pictorum*). Estimates are presented for the populations with parasites (i.e. the actual scenario), and compared with estimates for the populations in the absence of parasites. Differences in the proportion filtered between parastised and unparasitised populations are calculated and presented (red lines and text) for the actual densities of mussels present in the Old West River (*Anodonta anatina* = Aa, dashed lines, 6 mussels per square metre; *Unio pictorum* = Up, dotted lines, 38 mussels per square metre).

of just 41% if parasite infection was random with respect to host identity and coinfection.

4 | DISCUSSION

There is a scarcity of experimental data exploring the effects of parasites on ecosystem function (Fischhoff et al., 2020; Friesen et al., 2020), and generally for how parasite-driven processes at smaller scales affect those at larger scales (Wale & Duffy, 2021). In this study, we filled this gap by integrating host densities, individual-level effects of parasitism and the distribution of both native and invasive parasites in a host community to demonstrate how parasites may influence ecosystem-level processes in a real-world system.

4.1 | Parasites affect the clearance rates of freshwater mussels in diverse ways

The individual-level effect of parasites on mussel filtration rates did not accord with all our predictions. In Prediction 2, we predicted that trematodes would reduce the clearance rates of *A. anatina*, when in fact we observed increased clearance rates (Figure 1). This is opposite to what has previously been observed for mussels (e.g. Stier et al., 2015). However, in the system of Stier et al. (2015), trematode infection was focused on the gills and palps, the organs responsible for efficient filtration (also, the trematodes were metacercariae rather than cercariae as they are in our case). In contrast, infection with *R. campanula* in our study is localised in the gonad, leaving the gills unaffected. Instead, *R. campanula* may induce oxygen

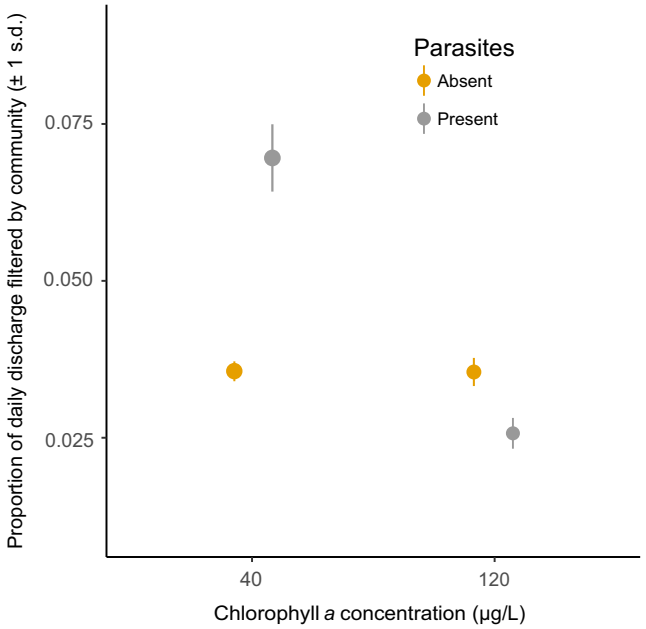

FIGURE 4 The proportion of daily discharge from the Old West river filtered by 1 km of the observed combined mussel community (*A. anatina* + *U. pictorum*), in the absence or presence of parasites, for low and high Chlorophyll *a* concentrations.

competition, meaning the filtration rate is a product of both suspended particle availability and parasitism status, with parasitised mussels having a higher rate for a given concentration of Chlorophyll *a* (Figure 1a). This is supported by MacLeod and Poulin (2016) who found that trematodes infecting the gonad in gastropods increased their host's oxygen uptake. Therefore, we suggest that trematodes could potentially enhance the filtration capacity of mussels, but that this effect is dependent on the host tissue of infection.

Our results did not fully support Prediction 3 either, that bitterling embryos would reduce the clearance rate of *U. pictorum*. At low Chlorophyll *a* concentrations, the clearance rates of infected mussels were elevated relative to uninfected mussels, but this trend reversed at high concentrations (Figure 2). This result is likely due to a combination of oxygen competition and gill deformation. Bitterling embryos compete with mussels for oxygen (Smith et al., 2004; Spence & Smith, 2013), and have been shown to increase oxygen consumption by mussels (Methling et al., 2018), so we would expect mussels to increase their filtration rates to meet elevated oxygen demands. However, bitterling also provide a physical stress by deforming the gills and disrupting their function (Methling et al., 2018; Mills et al., 2005), and so mussels may be unable to effectively increase their filtration rates to process higher concentrations of suspended particles. *U. pictorum*'s response to bitterling embryo parasitism is thus a product of both increased oxygen demand and reduced gill function. It should be acknowledged that female bitterling could have selected mussels to infect that a priori had a higher filtration rate (Mills & Reynolds, 2002b), rather than bitterling increasing clearance rates. However, previous work measuring O_2 capacity of individual mussels before and after bitterling infection definitively showed that bitterling increased oxygen demand (Methling et al., 2019), and therefore we suggest our results are the product of a bitterling-driven effect.

Trends in the field experiment testing Prediction 1 (bitterling females will avoid depositing in trematode-infected *A. anatina*) were inconclusive. We showed that it was more common for bitterling to deposit in uninfected rather than trematode-infected mussels, and that trematode-infected mussels hosted fewer bitterling embryos per mussel than uninfected ones (Table 1), though the former pattern was not statistically supported (likely due to low sample size) and the latter pattern could not be statistically tested given only two trematode-infected mussels were targeted by bitterling. Furthermore, within pairs of trematode-infected and uninfected mussels (which were spatially non-independent), infection likelihood was also not independent, with both mussels either being infected or uninfected with bitterling. This suggests that the primary driver of bitterling deposition in our experiment may not be trematode presence but microhabitat selection. Previous evidence supports the fact that bitterling prefer certain microhabitats (Reynolds et al., 1997). If bitterling microhabitat usage only weakly overlaps with a hypothetical trematode microhabitat, perhaps stimulated by hydrological factors limiting where microscopic trematode infective stages can reach, then this could also contribute to the observational field patterns. However, outside of pairs in which both mussels were recovered, we did still observe bitterling embryos in 0 of 5 trematode-infected mussels and 3 of 7 uninfected mussels, suggesting that trematode infection may be a secondary host selection filter. Further supporting this is the fact that, within the two recovered pairs that both showed bitterling infection, bitterling intensity was higher in the uninfected than in the trematode-infected mussel. This is initially surprising, as we showed that trematodes actually increase filtration rate, something female bitterling have been shown to respond positively to (Mills & Reynolds, 2002b). However, bitterling also use oxygen concentration in exhalant water as a proximate cue for oviposition choice (Smith et al., 2001). If oxygen competition is high between mussels and trematodes as we have suggested, the rate of oxygen removal in the mussel will be high, leading to oxygen-poor water flowing from the exhalant siphon. Bitterling females may therefore avoid depositing in trematode-infected mussels, much like they also avoid mussels already parasitised by bitterling embryos (Smith, 2017) and mussel species with lower inherent oxygen outflow such as *A. anatina* (Mills & Reynolds, 2002a). This highlights the need to consider the sequential nature of parasite arrival, and how this can shape parasite distributions (and thus parasite impacts) at the community scale (Karvonen et al., 2019), in addition to inherent host specificity. While the results of our field experiment remain ultimately inconclusive given low final sample size, they emphasise the need to consider the cause of observed parasite host specificity across scales (Falke & Preston, 2022; Thieltges et al., 2011), and quantify their subsequent ecosystem impacts.

Combining our field and laboratory results into an ecosystem model allowed us to provide clear support for Prediction 4, that

parasites significantly alter the clearance rates of freshwater mussels: we observed that the proportional river discharge filtered may change by up to 96% relative to an uninfected host community. We first inspected the ecosystem impacts from the perspective of the two mussel populations separately (Figure 3), which allowed us to compare the impact of parasites on one population's service provision relative to other species in the community; this is a key and largely unaddressed step in scaling up parasite effects to the ecosystem level (Preston et al., 2016). Our results show the importance of this approach: at low Chlorophyll *a* concentrations, the clearance rate of the parasitised *U. pictorum* population is higher than the clearance rate of the parasitised *A. anatina* population (Figure 3a), but this trend reverses at high Chlorophyll *a* concentrations (Figure 3b). The overall ecosystem service provided by the mussel community is therefore a product of the underlying environmental conditions, parasite prevalence and host community composition. In our example, densities of *U. pictorum* are ~6.5 times higher than *A. anatina* and so the community-level impact of parasites closely follows the *U. pictorum* response, with the proportion of river discharge filtered being 96% higher at low concentrations of suspended particles and 28% lower at high concentrations of suspended particles (Figure 4). However, different proportions of host species would alter these conclusions. Future work should aim to incorporate how the whole-community ecosystem effect is influenced by host and parasite density and distribution, especially as host community composition is also a strong determinant of parasite community structure (Dallas & Presley, 2014; Mihaljevic et al., 2018; Williamson et al., 2019).

4.2 | Parasitism may affect ecosystem services

Our study supports and extends previous work which have demonstrated the trait-mediated effects of parasitism. Wood et al. (2007) convincingly showed that the parasite-altered feeding rate of a snail shifted macroalgal and invertebrate community composition; however, while they hypothesised about the potential ecosystem-level consequences of this shift they did not quantify it explicitly. Mischler et al. (2016) extended work in this area by quantifying how nitrogen flow in freshwater snails, and subsequent ecosystem-level nutrient cycling, was influenced by parasites, though they only parameterised models for hypothetical water volumes and averaged across snail populations, thus not allowing for sources of stochasticity. In contrast, we explicitly quantified the effect of parasitism on a real ecosystem; furthermore, by considering multiple species in the community (as opposed to a single host species, as in previous studies), we can more convincingly contextualise the effect of parasites at this level, and see how parasitism alters their relative contribution to an important ecosystem service. While our estimates do involve scaling up from the experimentally quantified individual effects, by incorporating individual variation in our models we have shown our results to be robust to stochasticity. In addition, recent work has shown that scaling up to higher levels of organisation tends to underestimate the magnitude of change (Orr et al., 2021). We therefore consider our results to be highly reliable, and they may even be conservative.

Despite its robustness, our approach is dependent on temporal context. For example, river flow rate varies throughout the year, as does mussel filtration rate (Lurman et al., 2014). We focused on summer discharge as this was when our sampling and experimentation took place, and therefore directly extrapolating beyond this may be unreliable. However, as we emphasise the *proportional* change rather than absolute values, as long as the effect of parasites on individual mussels is reasonably consistent through the year, our results should be broadly translatable to other seasons. While *R. campanula* prevalence may vary (Taskinen et al., 1997), infection rates remain >10% throughout the year in this river (Brian et al., 2021; Brian & Aldridge, 2021a), and so we expect a qualitative effect regardless of sampling time, even if prevalence changes. Furthermore, we have also left aside the temporal density-mediated effect of parasitism; for example, trematodes can increase unionid mussel mortality under stressful conditions (Jokela et al., 2005) and reduce population-level reproductive capacity (Brian et al., 2021). Incorporating such effects into models of ecosystem function requires understanding how reproductive limitation influences long-term population dynamics. For example, does a 13% reduction in population-level glochidial output (Brian et al., 2021) directly correspond to a 13% reduction in juvenile mussel recruitment the following year? To our knowledge, such information is not yet available for freshwater mussels. However, it is a crucial area of future work, and emphasises the broader need to combine information on the trait-mediated and density-mediated effects of parasites on ecosystem-level processes.

Interactions between invasive and native parasites are predicted to become much more common under global change scenarios (Olden et al., 2004). Recent evidence suggests that the spread of invasive species has not reached a saturation point, and may even be accelerating (Seebens et al., 2017). It is therefore vital to understand the nature of these interactions and how they may affect hosts. We have shown that invasive bitterling fish infrequently co-infect with trematodes (Table 1); while our sample size was small it does provide experimental support for previous extensive observational work (Brian & Aldridge, 2021a). Therefore, the native trematode *R. campanula* not only has a clear trait-mediated effect, but it also mediates parasite patterns by possibly influencing ovipositing decisions in an invasive parasite, resulting in indirect consequences for ecosystem services. Such interactions, where native parasites alter the distribution or success of invasive parasites and vice versa, are likely to be common in this era of global change and must be included when considering the impact of parasites on the ecosystem services of their hosts.

Our results therefore have immediate and urgent implications for freshwater ecosystems. The filtration service of freshwater mussels is a key contributor to both less turbid water and nutrient deposition (Vaughn, 2018), something that is increasingly important as waters become more eutrophic (Smith et al., 1999). However,

our results suggest that, at least for the observed host community composition, parasitised populations are nearly 30% less effective at filtering an equivalent volume of water under more eutrophic conditions, possibly lowering ecosystem health. This reduction in function will be exacerbated by unionid declines (Lopes-Lima et al., 2021), especially considering the fact that parasites influencing functionally important hosts are expected to have the greatest impacts (Preston et al., 2016). In general, the effect of parasites on hosts and ecosystems may be wide ranging but also context dependent (Lange et al., 2014; Richard et al., 2021). Different parasites may show variable infection patterns and respond in different ways to environmental factors, emphasising that their life-history characteristics need to be carefully considered. As the global environment continues to change, and invasive species continue to spread, we have demonstrated that incorporating the trait-mediated impact of parasites is an essential step in predicting the shape of future ecosystem function.

AUTHORS' CONTRIBUTIONS

J.I.B. and D.C.A. conceived of and designed the study, and carried out the field components; J.I.B. and S.A.R. carried out the laboratory experiments; J.I.B. designed the ecosystem models and analysed and interpreted the data, with input from S.A.R.; J.I.B. drafted the manuscript, and all authors contributed substantially to editing and revisions.

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CONFLICT OF INTEREST

The authors declare they have no conflict of interest.

DATA AVAILABILITY STATEMENT

All data and code are archived in the digital repository Dryad Digital Repository 10.5061/dryad.b5mkkwhg6 (Brian et al., 2022).

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