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Coastal ecosystems on a tipping point: Global warming and parasitism combine to alter community structure and function

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Abstract

Mounting evidence suggests that the transmission of certain parasites is facilitated by increasing temperatures, causing their host population to decline. However, no study has yet addressed how temperature and parasitism may combine to shape the functional structure of a whole host community in the face of global warming. Here, we apply an outdoor mesocosm approach supported by field surveys to elucidate this question in a diverse intertidal community of amphipods infected by the pathogenic microphallid trematode, *Maritrema novaezealandensis*. Under present temperature (17°C) and level of parasitism, the parasite had little impact on the host community. However, elevating the temperature to 21°C in the presence of parasites induced massive structural changes: amphipod abundances decreased species-specifically, affecting epibenthic species but leaving infaunal species largely untouched. In effect, species diversity dropped significantly. In contrast, four degree higher temperatures in the absence of parasitism had limited influence on the amphipod community. Further elevating temperatures (19–25°C) and parasitism, simulating a prolonged heat-wave scenario, resulted in an almost complete parasite-induced extermination of the amphipod community at 25°C. In addition, at 19°C, just two degrees above the present average, a similar temperature–parasite synergistic impact on community structure emerged as seen at 21°C under lower parasite pressure. The heat-wave temperature of 25°C per se affected the amphipod community in a comparable way: species diversity declined and the infaunal species were favoured at the expense of epibenthic species. Our experimental findings are corroborated by field data demonstrating a strong negative relationship between current amphipod species richness and the level of *Maritrema* parasitism across 12 sites. Hence, owing to the synergistic impact of temperature and parasitism, our study predicts that coastal amphipod communities will deteriorate in terms of abundance and diversity in face of anticipated global warming, functionally changing them to be dominated by infaunal species.

KEYWORDS

amphipod host community, climate change, *Maritrema novaezealandensis*, mesocosm experiment, microphallid trematode, parasite vulnerability, species diversity, species richness, temperature sensitivity, temperature–parasitism synergy

1 | INTRODUCTION

The forecast global warming is bound to affect the performance and distribution of organisms worldwide, in turn changing the composition of species assemblages and modifying ecosystem properties and function (Harley et al., 2006; IPCC 2014; Parmesan & Yohe, 2003; Walther et al., 2002). However, predicting exactly how populations, communities, and ultimately ecosystems will respond to these already ongoing climate changes is a major scientific challenge. Based on knowledge of present species distributions, the basic ecology of individual species and their temperature tolerances, seemingly robust forecasts could be elaborated. However, apart from the fact that global climate change is not solely a matter of temperature, there is mounting evidence across ecosystems that temperature significantly influences the strength and outcome of species interactions (Araújo & Luoto, 2007; Gilman, Urban, Tewksbury, Gilchrist, & Holt, 2010; Traill, Lim, Sodhi, & Bradshaw, 2010; Tylianakis, Didham, Bascompte, & Wardle, 2008; Walther, 2010). Given that species interactions are among the decisive forces structuring ecological communities, the general validity of single-species models can be questioned.

One species interaction that has received increasing attention in recent years is that between host and parasite. Parasites are ubiquitous components of the biosphere and many play a community-structuring role either directly by regulating specific host populations, or indirectly by altering the abundance or phenotype of a keystone host species (Hatcher, Dick, & Dunn, 2012; Larsen & Mouritsen, 2014; Minchella & Scott, 1991; Mouritsen & Haun, 2008; Mouritsen & Poulin, 2005; Thomas, Renaud, & Guégan, 2005; Tompkins et al., 2002; Wood et al., 2007). Interestingly, for a wide range of parasites, in particular some flatworms (Trematoda), the transmission of infective stages is highly temperature dependent, which means that the strength of the host–parasite interaction and in turn the parasites' ecological roles will be sensitive to climate fluctuations (Hernandez, Poole, & Cattadori, 2013; Marcogliese, 2001; Mouritsen & Poulin, 2002a; Paull, Lafonte, & Johnson, 2012; Poisot, Gueveneux-Julien, Fortin, Gravel, & Legendre, 2017; Poulin, 2006). This has been evidenced especially in coastal ecosystems where pathogenic microphallid trematodes from both the northern and southern hemispheres have been forecast to drive populations of their main crustacean second intermediate hosts to the brink of extinction under global warming (Mouritsen, Tompkins, & Poulin, 2005; Studer, Poulin, & Tompkins, 2013). Microphallids are engaged in three host life cycles including a vertebrate definitive host, a gastropod first intermediate host, and a crustacean second intermediate host. They show little host specificity towards their second intermediate host (and definitive host alike), being capable of infecting a taxonomically very diverse group of crustaceans that possess an important ecological role in coastal ecosystems (Mouritsen & Poulin, 2002b). In addition, different lines of evidence suggest that the guild of secondary host species differ markedly in their susceptibility to infection or in the infection intensity-dependent pathology inflicted by the parasites (Jensen, Jensen, & Mouritsen, 1998; Koehler, Gonchar, & Poulin, 2011; Koehler & Poulin, 2010; Larsen, Jensen, & Mouritsen, 2011). Given (a) temperature-dependent parasite transmission, (b) the absence of strong host specificity, and (c) species-specific parasite susceptibility, one may raise the intriguing hypothesis that microphallid parasitism in concert with temperature increases associated with global warming will cause unprecedented changes to the structure and function of coastal communities of crustaceans. Additive and synergistic effects of climate change and species interactions on community properties have been documented recently in the case of grazing (e.g. Dangal et al., 2016), predation (e.g. Miller, Matassa, & Trussell, 2014), and competition (e.g. Stenseth et al., 2015). Parasitism, on the other hand, has not yet received the same level of attention.

Here, we explore the above hypothesis by using the intertidal microphallid trematode *Maritrema novaezealandensis* and its amphipod host community as a model system. *M. novaezealandensis* uses the mud snail *Zeacumantus subcarinatus* as its only first intermediate host species from where infective larvae (cercariae) are released with the purpose of infecting the crustacean second intermediate host (Martorelli, Fredensborg, Mouritsen, & Poulin, 2004). Red-billed gulls *Larus novaehollandiae* (or any other crustacean-eating bird) serve as definitive hosts reached by trophic transmission. Sexual reproduction occurs within the shorebirds' digestive tract, and trematode eggs, infective to the snails, are distributed in the intertidal habitat via the birds' droppings. The transmission of *Maritrema* cercariae from first to second intermediate host is known to be strongly temperature dependent (Fredensborg, Mouritsen, & Poulin, 2005; Studer, Thieltges, & Poulin, 2010; Studer et al., 2013). We utilized a mesocosm experimental design—supported by field investigations—to assess how different levels of temperature and infection combine to influence amphipod community structure and diversity. We hypothesized that elevated temperatures and parasitism would be particularly detrimental to the amphipods but in a highly species-specific manner, leading to the creation of a differently structured community. Our study provides the first attempt to unravel the combined effect of parasitism and global warming on a diverse host community.

2 | MATERIALS AND METHODS

2.1 | Study sites

Mesocosm experiments, associated field investigations and collection of experimental organisms were conducted during the austral summer 2006/2007 in Otago Harbour and adjacent inlet, South Island, New Zealand. Experiments were performed at the Portobello Marine Laboratory (45°49′41″S, 170°38′29″E), whereas field investigations and collections of experimental material were carried out on the nearby intertidal sand flats of Hoopers Inlet (45°51′33″S, 170°40′10″E) and Lower Portobello (45°49′55″S, 170°40′15″E). In

addition, 12 well-separated bays within the ca. 20 km long Otago Harbour were sampled during 2001/2002 and 2003/2004 to test for an in situ relationship between amphipod community structure and parasitism.

2.2 | Collection of experimental material

2.2.1 | Amphipods

In order for the experiments to be based on a naturally occurring uninfected amphipod community, experimental crustaceans were collected in Hoopers Inlet. The mud snail *Zeacumantus subcarinatus* that serves as the only first intermediate host to the microphallid trematode *M. novaezealandensis* is absent here, and hence, also the parasite (Bryan-Walker, Leung, & Poulin, 2007; Fredensborg, Mouritsen, & Poulin, 2004).

Prior to experimental collections, a thorough investigation was conducted in Hoopers Inlet aiming to establish the range of amphipod species present, the relative distribution of microhabitats (unvegetated bare sand and beds of sea lettuce, *Ulva lactuca*) within which they were found, and the relative density of each species within each microhabitat (Appendix S1). Based on this survey, the experimental mesocosms were constructed to match exactly the structure of a naturally occurring amphipod community and the microhabitats supporting it. Six species of amphipods were found in significant densities of which two were highly abundant free-swimming species (*Paracalliope novizealandiae* and *Paramoera chevreuxi*), two were benthic mainly sedentary species (*Heterophoxus stephenseni* and *Paracorophium lucasi*), and two were rare tube-building species associated with sea lettuce only (*Aora* sp. and *Lembos* sp.) (Table 1, Appendix S1). All six species serve as second intermediate hosts for *M. novaezealandensis* (Koehler & Poulin, 2010; Koehler et al., 2011; this study).

Almost pure cultures of both *H. stephenseni* and *P. lucasi* could be obtained by core sampling in Hoopers Inlet. The remaining four species, mostly associated with sea lettuce (Table 1, Appendix S1), were collected by rinsing a large amount of *U. lactuca* in a seawater-filled bucket and then straining the water. In all cases, a 500 μm sieve was used to extract the animals that subsequently were brought to the laboratory for sorting and species identification under a dissection microscope. To minimize mechanical damage to the more than 23,000 amphipod individuals eventually sorted out by hand for the experiments, all handling was done using pipettes. When not processed in the laboratory, animals were stored in containers supplied with 16–17°C filtered running seawater.

To verify the absence of microphallid trematode infections in the collected amphipod community, 30 haphazardly chosen individuals of each amphipod species were dissected for trematodes and all were found uninfected. To establish the overall size distribution of the experimental amphipods, another subsample of each species was extracted just prior to experimentation and measured from rostrum to telson under a dissection microscope (Table 1). All animals were preserved in 4% formaldehyde prior to measurements and dissection.

2.2.2 | Snails

As a source of parasites for the experiments, medium-sized mud snails (*Zeacumantus subcarinatus*) were collected by hand in a midintertidal area at Lower Portobello where the infection prevalence is relatively high (see Fredensborg et al., 2004, 2005). Snails were kept in laboratory aquaria supplied with 16–17°C running filtered

TABLE 1 The experimental amphipod community listed according to the species relative field abundance in Hoopers Inlet (this study) in association with their preferred microhabitat, ecotype, feeding type, general behaviour, source of ecological information, mean body length (*SE*, *n*; this study), and the number of individuals added to each experimental mesocosm unit

Species	Family	Microhabitat and ecotype	Feeding type and behaviour	Source	Body length (mm)	No. in mesocosms
Paracalliope novizealandiae	Paracalliopiidae	Macroalgae, epibenthic, free-swimming	Epiphytic/epibenthic grazer, highly active and mobile	Barnard (1972), Cummings, Pridmore, Thrush, and Hewitt (1995)	3.5 (0.12, 50)	205
Paramoera chevreuxi	Eusiridae	Macroalgae, free-swimming	Omnivore, highly active and mobile	Clason, Duquesne, Liess, Schulz, and Zauke (2003)	4.3 (0.20, 50)	103
Heterophoxus stephenseni	Phoxocephaliidae	Benthic, free-living	Infaunal predator, slow moving	Dauby, Scailteur, Chapelle, and De Broyer (2001)	3.8 (0.09, 50)	83
Paracorophium lucasi	Corophiidae	Benthic, tube-building	Surface detritus feeder, microalgae grazer and Sedentary	Ellis, Nicholls, Craggs, Hofstra, and Hewitt (2004)	2.9 (0.19, 50)	34
Aora sp.	Aoridae	Macroalgae, tube-building	Epiphytic grazer, detritus feeder, slow moving and sedentary	Dixon and Moore (1997)	3.9 (0.19, 45)	25
Lembos sp.	Aoridae	Macroalgae, tube-building	Epiphytic grazer, detritus feeder, slow moving and sedentary	Dixon and Moore (1997)	5.4 (0.23, 15)	10

seawater and ad libitum *U. lactuca* as a food source until further processing. To establish their infection status, snails were placed individually in seawater-filled Petri dishes at 25°C under illumination for a minimum of 5 hr. Under these conditions, snails with mature *Maritrema* infections start shedding cercariae, the infective larval stage of the parasite (Fredensborg et al., 2005; Keeney, Waters, & Poulin, 2007). To verify absence of infection, snails scored as uninfected (no cercarial emission) were screened again after 7 days as well as immediately prior to experimentation. *Z. subcarinatus* was occasionally found infected by other trematode species than *M. novaezealandensis* but only snails harbouring the latter as well as uninfected snails were used in the experiments. These snails measured on average 13.1 mm in shell height (range: 10.5–16.0 mm, $n = 224$).

To guide establishment of realistic snail densities in the mesocosms, the density of *Zeacumantus* across the various microhabitats present on the Lower Portobello sand flat (bare sand, sea lettuce bed, and eelgrass bed) was investigated prior to collection of the experimental specimens (see Appendix S1).

2.2.3 | Sea lettuce

As a source of food as well as substrate for snails and some species of amphipods during the experiments (see Table 1, Appendix S1), sea lettuce was collected in Hoopers Inlet and brought to the laboratory. Here, the thallus was rinsed thoroughly with filtered seawater to remove associated faunal organisms and then stored in containers supplied with filtered running seawater. As in the case of amphipods and snails, the abundance of sea lettuce in Hoopers Inlet (g wet weight per m^2) was estimated prior to collection, with the purpose of supplying mesocosms with field-relevant amounts (Appendix S1).

2.2.4 | Sediments

As a substrate for the two burying amphipods, *H. stephenseni* and *P. lucasi*, sediment was collected from the sandy high-intertidal area of Lower Portobello. Here, these benthic species were found to be largely absent, which excluded the risk of contaminating the experimental mesocosms with juvenile individuals. The collected substrate was sieved through a 500 μm mesh to remove any other macrofaunal organisms present and brought to the laboratory for storage (16–17°C filtered running seawater). In addition to this base sediment (medium-fine sand), diatom-rich silty surface sediment was also collected from Hoopers Inlet and sieved through a 250 μm mesh to remove juvenile *Paracorophium* present. The purpose of including this fine and diatom-rich sediment in the mesocosms was to provide the detritus feeding and epibenthic-grazing amphipods with a high-quality food source (see Table 1 for relevant species). Light microscopy of small sediment samples confirmed the presence of a range of epipelic diatoms in high abundance (genera *Amphora*, *Gyrosigma*, *Navicula*, *Nitzschia*, *Plagiogramma*). Apart from the community of microphytobenthos, a range of meiofaunal groups were also present (ciliates, nematodes, copepods, ostracods, and rotifers), thus providing the predatory *H. stephenseni* with food items.

2.3 | Experimental design and protocol

During January and February, two temporally separated outdoor mesocosm experiments both lasting 14 days were carried out. The first experiment aimed at simulating a standard global-warming scenario under moderate parasite pressure (standard-warming experiment). The second aimed at an extreme warming or heat-wave scenario under high parasite pressure (extreme-scenario experiment). The outdoor setting provided greater realism but did not allow for temperature levels to be precisely fixed (see next section).

Both experiments involved four treatments each: lower temperatures with and without parasites and higher temperatures with and without parasites. The dichotomous treatment structure rather than multiple treatment levels (see Rohr et al., 2011) was dictated by the substantial labour involved in establishing the replicated mesocosms prior to experimentation (see below).

The experimental mesocosm unit was a transparent circular PVC container, 25 cm in inner diameter and 21 cm in height resulting in a 491 cm^2 bottom surface area and a water volume of 9 L (Figure S1). About 3 cm below the top of the container, four evenly dispersed holes (each c. 1 cm^2) covered with a 500 μm polyethylene mesh functioned as water outflow. Silicon tubes, 1 m in length and an inner diameter of 5 mm, were used to supply each container with running filtered seawater (salinity: 33–34) at the desired experimental temperature (see below). The seawater supply was filtered solely through gravel and therefore contained small naturally occurring planktonic organisms. A constant flow rate of 18 L/hr was established in each container, corresponding to a full exchange of water every half hour. This relatively high flow rate served to (a) obtain the required temperature treatments, (b) keep the water body and sediment fully oxygenated, and (c) secure a steady supply of planktonic organisms serving as a food source for some of the experimental animals.

The water supply system consisted of two large PVC tanks used as seawater reservoirs, one heated and one unheated. The heated seawater tank (h = 1.0 m, d = 0.8 m) contained ca. 500 L and supplied half of the experimental containers. To maintain the desired water temperature during the experiments, a thermostat-controlled heater was submerged into the tank. The second seawater tank (h = 1.0 m, d = 0.5 m) contained ca. 200 L and supplied the other half of the experimental containers with unheated seawater. Both water tanks were supplied with the same source of running filtered seawater, whose inflow rate was controlled by a float valve. This setup was sufficient to establish the two temperature treatments in the first standard-warming experiment. However, for the subsequent extreme-scenario experiment, the temperature of the previously unheated seawater reservoir also had to be increased. This was accomplished by directing water from the heated reservoir into the unheated one through a shunt equipped with a valve to control the flow.

One litre of base sediment was added to each mesocosm container equivalent to a depth of 2 cm substrate. On top of this, a 1–2 mm layer of the silty diatom-rich surface sediment was then added

as a food source for some of the experimental amphipods. The containers were subsequently connected to their water supply and left for suspended sediment particle to settle prior to addition of the experimental organisms. From this point and until commencement of the experiments, all mesocosm units were supplied with a flow of filtered unheated seawater (16–17°C).

Because of the large amount of amphipods processed, addition of the different species to the mesocosms was performed over 2 days. Firstly, the two benthic amphipod species were sorted out and simultaneously added to the experimental containers, followed by the remaining four species mainly associated with sea lettuce (Table 1). The number of individuals of each amphipod species eventually added to each mesocosm (Table 1) corresponded to their natural densities in Hoopers Inlet (Appendix S1). Due to shortage of *Lembos* specimens during establishment of the extreme-scenario experiment, six instead of the planned ten individuals were added to each mesocosm.

After addition of the amphipod community, eight mud snails were placed in each container corresponding to their natural density at Lower Portobello (Appendix S1). In neither experiments were there any significant difference in average snail shell height between mesocosm units (standard-warming experiment: One-way ANOVA, $F_{23/168} = 0.161$, $p = 1.000$; extreme-scenario experiment: One-way ANOVA, $F_{27/196} = 0.121$, $p = 1.000$). To avoid escape of snails from the water column, a thin layer of grease was smeared out just above the water surface at the top of each experimental container. Along with the addition of snails, 10 g *U. lactuca* thallus was also placed in each mesocosm, corresponding to its abundance in Hoopers Inlet (Appendix S1). Finally, a temperature logger was submerged in a haphazardly chosen mesocosm at each of the two applied temperature treatments just prior to the onset of the experiments.

The four experimental treatments (see next section) were fully randomized across the mesocosms arranged in a quadratic grid in drained PVC trays elevated from the ground. Each treatment was replicated six times in the first standard-warming experiment and seven times in the subsequent extreme-scenario experiment.

2.4 | Experimental treatment settings

In the standard-warming mesocosm experiment we aimed at a lower temperature treatment of 17°C, approximating present sea surface summer temperature in Otago Harbour (Studer & Poulin, 2012), and a higher temperature treatment of 21°C in the light of ongoing climate changes (IPCC, 2014). In the subsequent extreme-scenario experiment, we aimed at temperature treatments of 19 and 25°C that are frequently encountered even at present in tide pools during summer low tides in Otago Harbour (Studer & Poulin, 2012). However, because the entire experimental setup was placed outside for both experiments, the mesocosms were subject to uncontrolled but natural diurnal variation in ambient temperature and sun radiation. This created overlying diurnal as well as day-to-day variation in the mesocosms' water temperature as recorded by the submerged temperature loggers. Hence, in the standard-warming experiment the realized mean temperature reached 16.9°C (range: 14.6–25.4°C) in the low-temperature treatment and 21.2°C (range: 17.8–26.5°C) in the high-temperature treatment (Student's t test, $t_{1427} = 53.64$, $p < 0.0005$). In the subsequent extreme-scenario experiment, these figures equalled 19.4°C (range: 16.8–26.5°C) and 25.1°C (range: 22.7–29.0°C), respectively (Student's t test, $t_{154} = 24.50$, $p < 0.0005$). Note that these experimental temperature ranges are all within values measured in situ (Studer & Poulin, 2012). For simplicity, these four temperature treatments will be denoted 17, 21, 19, and 25°C, respectively.

Regarding levels of parasitism in the standard-warming experiment, three of the eight added mud snails (37.5%) were infected by *M. novaezealandensis* in the parasite treatments, whereas no snail was infected in no-parasite treatments. The 37.5% prevalence of infection corresponds roughly to the grand mean across Otago Harbour bays in the immediate vicinity of our study sites (see Fredensborg, Mouritsen, & Poulin, 2006; Studer & Poulin, 2012). In the extreme-scenario experiment, six of the eight mud snails were infected in the parasite-treatments creating an infection prevalence of 75%. This high level of parasitism corresponds roughly to values recorded in the highly parasitized Lower Portobello Bay (Fredensborg et al., 2006; Studer & Poulin, 2012; unpublished data).

Owing to the technical difficulties involved and the need to keep experimental units undisturbed, no attempt was made to measure transmission success during the experiments (i.e. total number of metacercariae successfully established in the amphipod populations). Hence, by using a number of infected first intermediate snail hosts as the source of parasitism, the premise of the experimental design is that infective parasite larvae are released to the water column in numbers proportional to the abundance of infected snails. A further premise is that a part of these infective larvae is transmitted to the amphipod secondary hosts causing intensity-dependent mortality. In agreement with previous studies of microphallid trematode transmission, we also expect that the rate of cercarial emission from snail hosts and in turn the transmission rate are positive functions of temperature within the experimental temperature range we used (Fredensborg et al., 2005; Mouritsen, 2002; Mouritsen & Jensen, 1997; Studer et al., 2010, 2013). Consequently, lower postexperimental amphipod abundance in parasite-exposed treatments relative to non-exposed treatments will be ascribed to parasite-induced mortality, and at elevated temperatures, any excess mortality will be ascribed to temperature-dependent increase in parasite transmission (and/or temperature-dependent exacerbation of infection pathology). Note that although a gradual increase in temperature at the beginning of our experiments may have resulted in slightly different patterns of cercarial output than the sharp rise used especially in the extreme-warming experiment (see Morley & Lewis, 2013), the contrast in parasite pressure between treatments will be comparable.

2.5 | Postexperimental protocol

After termination of the experiments, remaining pieces of sea lettuce were thoroughly rinsed within each mesocosms to release any

attached animals. Water and sediment were then sieved through a 500 μm mesh from each container separately and retained animals were preserved in 4% formaldehyde. The retrieved amphipods were then sorted according to species and enumerated. Furthermore, a number of individuals of each species from each of the four experimental treatments were measured (rostrum to telson) and dissected to establish parasite loads (no. metacercariae per ind.). These specimens were haphazardly chosen across individual mesocosm units aiming to process as even a number of amphipods per unit as possible. In total, 841 amphipods specimens were measured in the standard-warming experiment (31–200 ind. per species) and 722 in the extreme-scenario experiment (36–180 ind. per species). Systematic dissections of amphipods for infections were only carried out in the standard-warming experiment (n = 323; 31–60 ind. per species). Due to extraordinarily high mortality in the extreme-warming experiment, which limited sample sizes and the value of parasite loads as a measure of transmission success (see emphasis in Results), only a few amphipod individuals (≤5 ind. per species) were scored positive for infection to verify presence of transmission.

In addition to the above protocol, a laboratory experiment was conducted to unravel the vertical distribution of *M. novaezealandensis* cercariae when released to the water column (Appendix S2). Their distributional pattern may influence the amphipods' vulnerability to infection.

2.6 | Field relationship between amphipod community and parasitism

Combined data on amphipod community structure and infection prevalence in the sympatric population of mud snails *Z. subcarinatus* were obtained from intertidal flats of 12 separate bays within Otago Harbour during 2001/2002 and 2003/2004. Amphipods were collected by sieving sediment core samples (0.012 m^2, n = 15 per bay) through a 500 μm mesh, followed by preservation, species identification, and enumeration in the laboratory (for methodological details, see Mouritsen & Poulin, 2010). Similarly, mature *Zeacumantus* snails (>6 mm in shell height) were retrieved by collecting surface sediment in haphazardly chosen 0.1 m^2 areas followed by sieving, preservation, and dissection for trematode infections in the laboratory (n = 98–442 snails per bay; see Fredensborg et al., 2005, 2006 for details). Based on these data, the relationship between amphipod species richness/diversity and the infection prevalence in the first intermediate host population was analysed and contrasted with the experimental results. See Fredensborg et al. (2006) for names and locations of the Otago Harbour bays sampled.

2.7 | Data analyses

Statistical analyses were performed using Statistical Package for the Social Sciences (SPSS). All parametric tests were preceded by evaluation of assumptions. If violated, data were rank-transformed to meet the assumptions or nonparametric statistics were applied. For the extreme-scenario experiment, the planned two-way ANOVA was abandoned in favour of pairwise contrasts (Student's t test or Mann–Whitney test) because error variances could not be stabilized through standard transformations (log, square root or rank). This applied also to species richness data from both experiments. In all other cases, Turkey post hoc test were applied following successful ANOVA's. Calculation of species diversity index (Shannon–Wiener) followed Krebs (1999) and is expressed in units of species ($2^{H'}$; $H' = -\Sigma(p_i)(\log\ p_i)$). Multidimensional scaling analyses (MDS) were performed in PRIMER on square-root transformed data, resulting in stress values below 0.05 that are indicative for excellent two-dimensional visualization.

3 | RESULTS

3.1 | Standard-warming experiment

3.1.1 | Infection abundance

As expected, surviving amphipods were found infected by *M. novaezealandensis* solely in the parasite treatments, where parasite loads varied according to experimental temperature and species of amphipod. The two free-swimming species, *P. novizealandiae* and *P. chevreuxi*, were the most heavily infected. *Paracalliope* harboured a mean metacercarial abundance of 3.8 and 7.8 individual^{-1} (range: 0–15) at low and high temperature, respectively, whereas *Paramoera* reached 40.1 and 28.4 individual^{-1} (range: 3–96), respectively. More moderate infection levels were found in the benthic tube-builder *Paracorophium lucasi* (0.93 and 2.5 individual^{-1}, respectively; range: 0–7). The other infaunal species, *H. stephenseni*, was entirely uninfected. The two amphipod species associated with sea lettuce were weakly infected: *Aora* sp. had no metacercarial infections at all, whereas *Lembos* sp. had 1.3 individual^{-1} on average (range: 0–6) at low temperature and none at high temperature. Statistically, main infection parameters (metacercarial prevalence and load) were either greatest in the high temperature treatment (21°C) or similar between temperature treatments (Table S1). Note that recorded infection characteristics do not necessarily reflect realized parasite pressure/transmission at the two temperature treatments, as the figures may be heavily skewed by intensity-dependent host mortality and/or recruitments. Similarly, species-specific parasite loads can solely be taken as a very rough indication of the relative susceptibility of the different amphipod species to *M. novaezealandensis*.

3.1.2 | Amphipod abundance

The six species of amphipods responded differently to the temperature–parasite treatments (Figure 1, Table 2). The two free-swimming amphipods, *P. novizealandiae* and *P. chevreuxi*, showed particularly high mortality rates when exposed to parasites at elevated temperatures where more than 80% in both species were eliminated relative to the low temperature/no parasites treatment (Figure 1a,b). Elevated temperatures per se had in comparison limited negative impact on survival, but of the two species, *P. novizealandiae* was clearly the

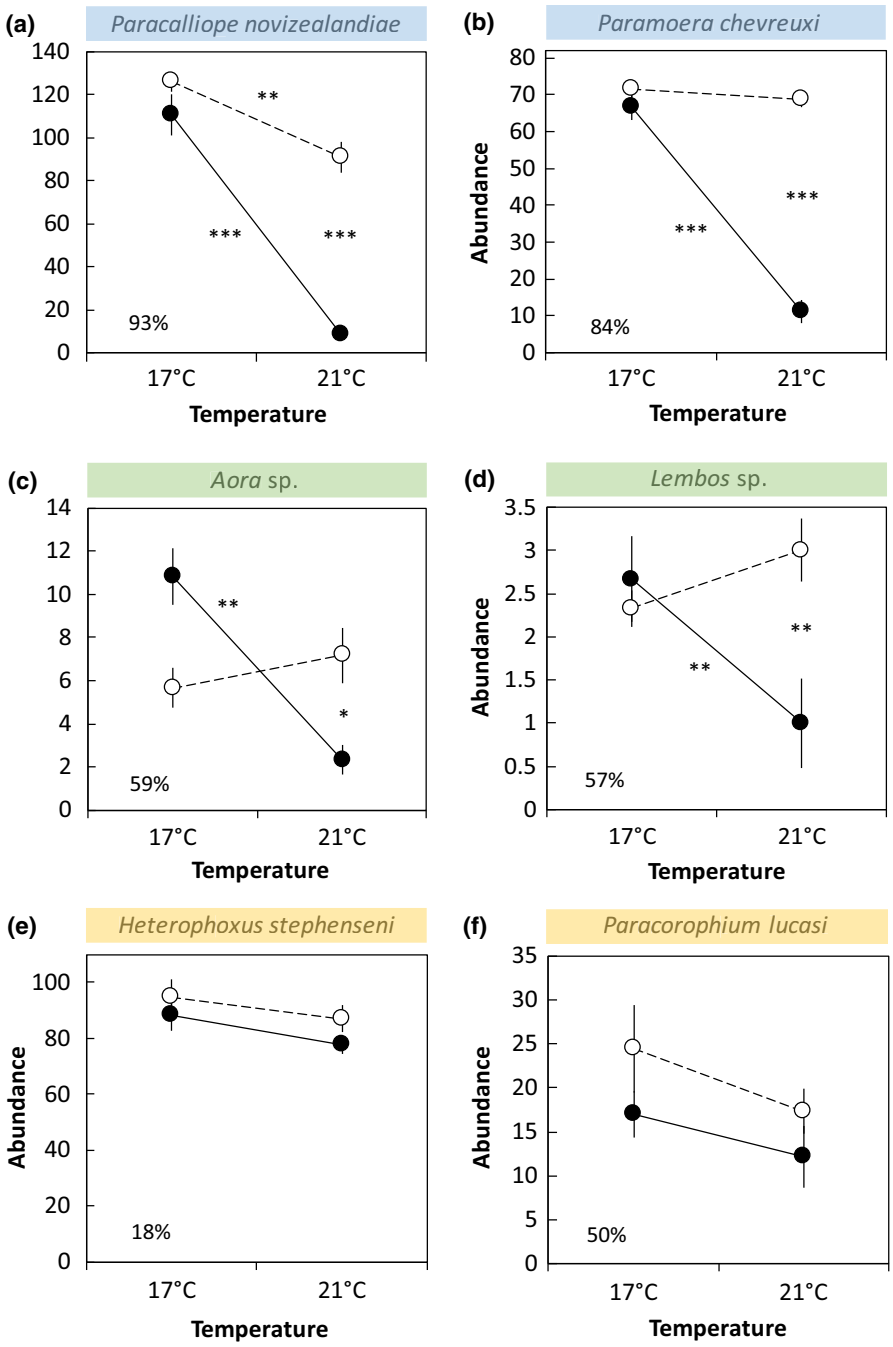

FIGURE 1 Standard-warming experiment. The postexperimental abundance of amphipod species according to temperature–parasite treatments (mean ind. per mesocosm ± *SE*; $n = 6$). Dashed line and ○: parasites absent; full line and ●: parasites present. Significance levels according to Tukey post hoc tests of treatment pairs are indicated by asterisks between markers (*$p < 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$); see Table S2 for exact *p*-values. Inserted percentages indicate proportional reduction in the number of individuals in the 21°C/parasites present treatment compared to the 17°C/parasites absent treatment, that is, a standardized measure of the synergistic impact of temperature and parasitism. Colour bars indicate the amphipod species affinity for microhabitat (blue, panel a,b: free-swimming; green, panel c,d: tube-building on vegetation; brown, panel e,f: sediment burrowers; see Table 1 and Appendix S1 for details). Note that inserted lines do not indicate linear relationships but serve to highlight the level of interaction

most temperature sensitive. Together this creates highly significant temperature–parasite interactions (Table 2) underlining that elevated temperatures and parasitism combined are detrimental to these two amphipod species.

Aora and *Lembos* associated with the vegetation likewise showed significant temperature–parasite interaction (Figure 1c,d, Table 2), driven by especially high mortalities in the high-temperature/parasites treatment but also by a tendency to benefit from increased temperature itself. The latter effect was not statistically significant in any of the two species though (Figure 1c,d). Hence, the two *Ulva*-residing aoriids were also particularly vulnerable to the high-temperature/parasite combination. However, they were so to a lesser extent than the free-swimming species as their abundance in the high-temperature/parasites treatment was reduced by just under 60% in comparison to the low-temperature/no parasites treatment (Figure 1c,d).

Contrary to the epibenthic species, the two infaunal species, *H. stephenseni* and *P. lucasi*, proved remarkably resilient to experimental manipulations. No statistically significant temperature–parasite interaction or main temperature/parasite effects were evident (Figure 1e,f, Table 2). Albeit nonsignificant, both species showed consistently lower abundances in the parasite treatments regardless of temperature (particularly *P. lucasi*) as well as lower abundances at high temperature regardless of parasite level (particularly

TABLE 2 The standard-warming experiment. Summary statistics of full-model two-way ANOVAs including postexperimental amphipod abundance (no. per mesocosm) as dependent variable and the dichotomous factors parasitism (present/absent) and temperature (17/21°C) as independent variables. Data are untransformed for all species but *Aora* sp. that were rank-transformed to meet requirements. *p*-values in bold denote statistically significant effects and * denotes that main effect *F*- and *p*-values originate from a reduced model ANOVA excluding the nonsignificant interaction term. In the latter case, the degrees of freedom are 2/21 (treatments/error), whereas in the remaining cases *df* = 3/20

	Source of variation					
	Parasitism		Temperature		Interaction	
Species	*F*	*p*	*F*	*p*	*F*	*p*
Paracalliope novizealandiae	55.674	**<0.0005**	110.298	**<0.0005**	26.118	**<0.0005**
Paramoera chevreuxi	131.528	**<0.0005**	112.716	**<0.0005**	91.824	**<0.0005**
*Heterophoxus stephenseni**	2.679	0.117	3.508	0.075	0.079	0.782
*Paracorophium lucasi**	3.308	0.083	2.969	0.100	0.107	0.746
Aora sp.	0.057	0.814	3.649	0.071	8.015	**0.010**
Lembos sp.	4.032	0.058	1.452	0.242	7.903	**0.011**

H. stephenseni; see Table 2 for *p*-values). In terms of temperature–parasite synergy, the benthic amphipods were affected the least of all species; especially so *H. stephenseni* that attained only 18% lower abundance in the high-temperature/parasites treatment than in the low-temperature/no parasites treatment. *Paracorophium lucasi* was somewhat more affected, reduced by 50% relative to the low temperature/no parasites.

Notably, viewed across all six amphipod species, none but *Aora* sp. appeared markedly influenced by parasitism at the low 17°C (Figure 1). Strangely, the presence of parasites tended to have a positive impact on *Aora* abundance at this temperature. However, numbers are low and stochasticity may be involved.

3.1.3 | Parasite vulnerability

The additional amphipod mortality recorded in the high temperature (21°C)/parasites treatment relative to the high-temperature/no parasites treatment (%) provides an useful measure of the different species' relative vulnerability to *Maritrema* infection. This mortality-based measure will hence encompasse behavioural aspects (the parasites access to the hosts), infection success (when hosts are encountered) and the pathology each successful trematode larva inflicts. This vulnerability index clearly identifies *P. novizealandiae* and *P. chevreuxi* as the most exposed species followed by the aoriids, whereas the two sediment dwellers stand out as the least vulnerable species, especially *H. stephenseni* (Figure 2). This pattern was entirely unrelated to the experimental amphipod species mean body size (see Table 1; $r_s = 0.143$, $p = 0.787$).

3.1.4 | Diversity and community structure

The differential impact of the experimental treatments on species abundances influenced overall community structure. The Shannon–Wiener index showed a highly significant temperature–parasite interaction (Figure 3a, Table 3) resulting from a particularly low species diversity in the high temperature/parasites treatment whereas the other treatments showed very limited impact. However, elevated temperatures per se negatively influenced the Shannon–Wiener index somewhat (Figure 3a). A similar overall pattern emerged for species richness although this could not be verified statistically (no variance in all but one treatment; Figure 3b). The low species richness in the high-temperature/parasites treatment is owing largely to the extinction of the two rare species *Aora* sp. and *Lembos* sp. in some mesocosm units.

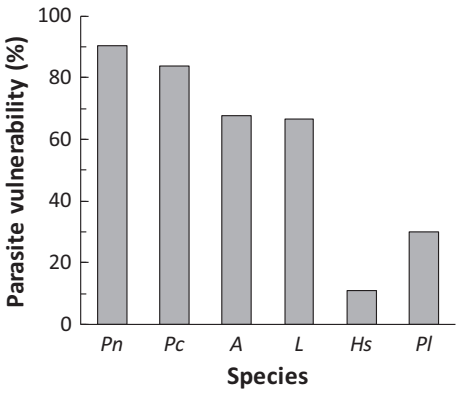

FIGURE 2 Standard-warming experiment. The six experimental amphipods species' relative vulnerability to *Maritrema novaezealandensis* infection (%) as judged by the excess mortality recorded in the 21°C/parasites treatment relative to the abundance recorded in the 21°C/no parasites treatment. *Pn*: *Paracalliope novizealandiae*; *Pm*: *Paramoera chevreuxi*; *A*: *Aora* sp.; *L*: *Lembos* sp.; *Hs*: *Heterophoxus stephenseni*; *Pl*: *Paracorophium lucasi*. Note that the here depictured proportions are not the same as those inserted in Figure 1

The impact of the experimental treatments on amphipod community structure is summarized visually in Figure 4a. Here, it is clear that the high-temperature/parasites mesocosm communities form a cluster markedly separated from the communities in the remaining treatments. Hence, elevated temperatures and parasitism act synergistically to create a uniquely different host community.

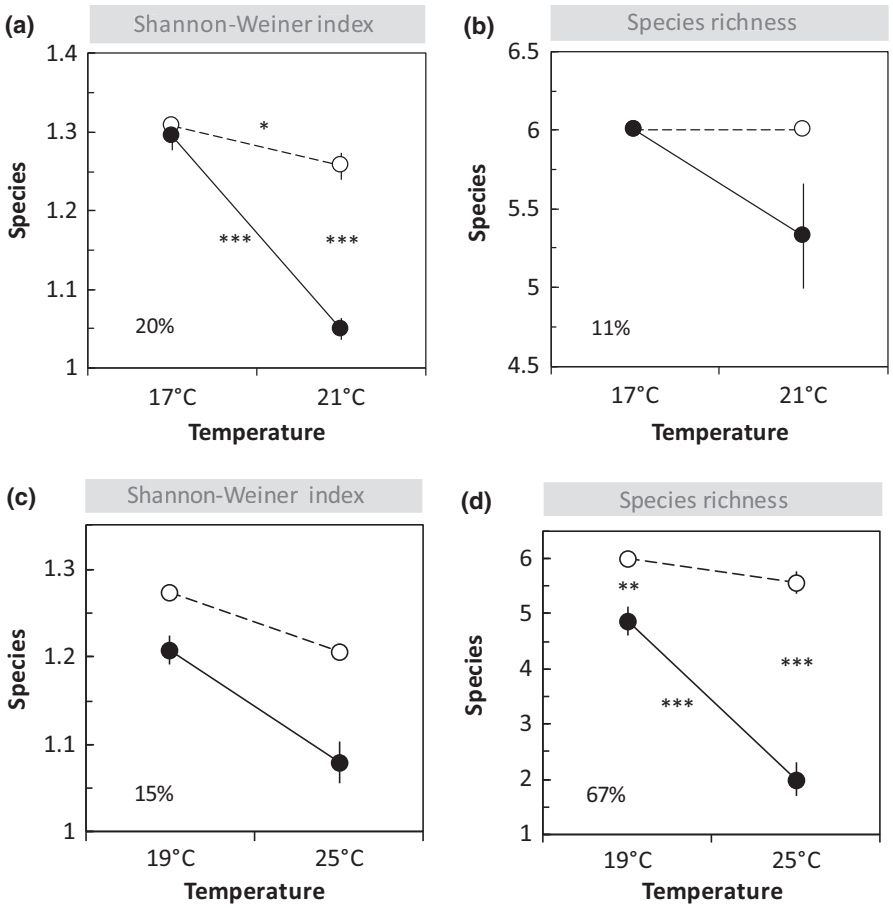

FIGURE 3 Postexperimental amphipod diversity (Shannon–Wiener index [$2^{H'}$] and species richness) according to temperature–parasite treatment in the standard-warming experiment (a, b) and the extreme-scenario experiment (c, d). Values are mean no. species per mesocosm ± *SE*; $n = 6$ (standard-warming) and $n = 7$ (extreme-scenario). Dashed line and ○: parasites absent; full line and ●: parasites present. Note that inserted lines do not indicate linear relationships but serve to highlight the level of interaction. Significance levels according to Turkey (standard-warming) and Mann–Whitney (extreme-scenario) post hoc tests of treatment pairs are indicated by asterisk between markers (*$p < 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$); see Tables S3 and S4 for exact *p*-values. Owing to absence of temperature–parasite interaction in case of the Shannon–Wiener index from the extreme-scenario experiment (Table 3) post hoc tests were redundant. Inserted percentages in panel a and b: see Figure 1. Inserted percentages in panel c and d indicate the proportional reduction in the number of species in the 25°C/parasites present treatment compared to the 19°C/parasites absent treatment

3.2 | Extreme-scenario experiment

3.2.1 | Amphipod abundance

Stepping up both temperature and parasitism had severe consequences for the amphipod community in all treatments. Most species were entirely eliminated from several mesocosm units in the high-temperature/parasites treatment, greatly reduced in numbers already in the 19°C low temperature/parasites treatment, and influenced negatively by high temperature on its own (Figure 5). Owing to the latter, the notable two-way temperature–parasitism interaction evident in the most sensitive species in the standard-warming experiment disappeared. This could not be substantiated statistically, though, due to instable error variance regardless of data transformations. Species-specific responses tended to follow the same patterns as seen in the standard-warming experiment. Mortality rates in parasite treatments relative to the low-temperature/no parasites treatment were rather high, particularly in the four epibenthic species (*P. novizealandiae* and *P. chevreuxi*, *Aora* sp., and *Lembos* sp.), and these were also greatly influenced by temperature per se (Figure 5a–d). Of the two benthic species, *P. lucasi* was the most parasite-sensitive showing quite high mortality already at 19°C. Interestingly, the previously parasite-resistant *H. stephenseni* (see Figure 1e) was strongly affected by the high parasite levels already at 19°C and suffered massive parasite-induced mortality at 25°C (Figure 5e). *H. stephenseni* was, however, the only species of the six that persisted in any significant numbers in this high-temperature/parasite treatment.

Note that percentages inserted in Figure 5 (effect size of the two statistical contrasts) differ qualitatively from those inserted in Figure 1 (effect size of the parasite–temperature synergy). Owing to almost 100% mortality in the high-temperature/parasites present treatment in the extreme-warming experiment, the latter synergy measure was considered uninformative.

TABLE 3 Standard-warming and extreme-scenario experiments. Summary statistics of full-model two-way ANOVAs including postexperimental amphipod diversity (Shannon–Wiener index, 2H') as dependent variable and the dichotomous factors parasitism (present/absent) and temperature (standard-warming: 17/21°C; extreme-scenario: 19/25°C) as independent variables. Degrees of freedom (*df*): 3/20 (standard-warming) and 3/24 (extreme-scenario). *p*-values in bold denote statistically significant effects

	Source of variation					
	Parasitism		Temperature		Interaction	
Experiment	*F*	*p*	*F*	*p*	*F*	*p*
Standard-warming	58.384	**<0.0005**	104.267	**<0.0005**	44.434	**<0.0005**
Extreme-scenario	46.072	**<0.0005**	50.106	**<0.0005**	0.038	0.848

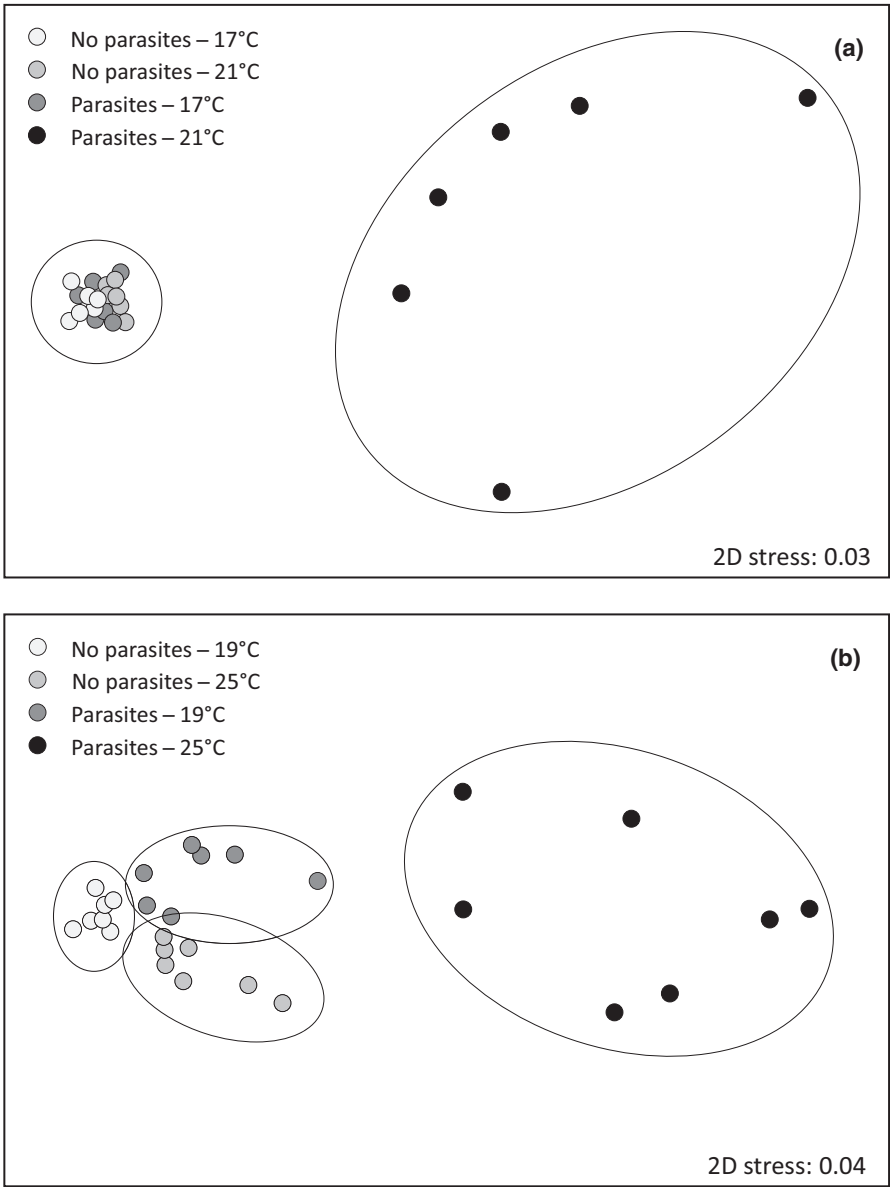

FIGURE 4 Multidimensional scaling (MDS plots) visualizing treatment-dependent displacement of amphipod community structure in (a) the standard-warming experiment and (b) the extreme-scenario experiment. Clusters of mesocosm units are encircled according to temperature–parasite treatments (see inserted keys)

3.2.2 | Diversity and community structure

The pattern in species diversity mirrors that of abundance: owing to significant reductions also in the high-temperature/no parasites treatment, no two-way temperature–parasitism interaction was evident (Figure 3c, Table 3). Instead, the main effects of temperature and parasitism were highly significant (Table 3), demonstrating that under this extreme experimental scenario both temperature and parasitism have isolated negative effects on amphipod species diversity. In case of species richness, two-way analysis could not be performed due to

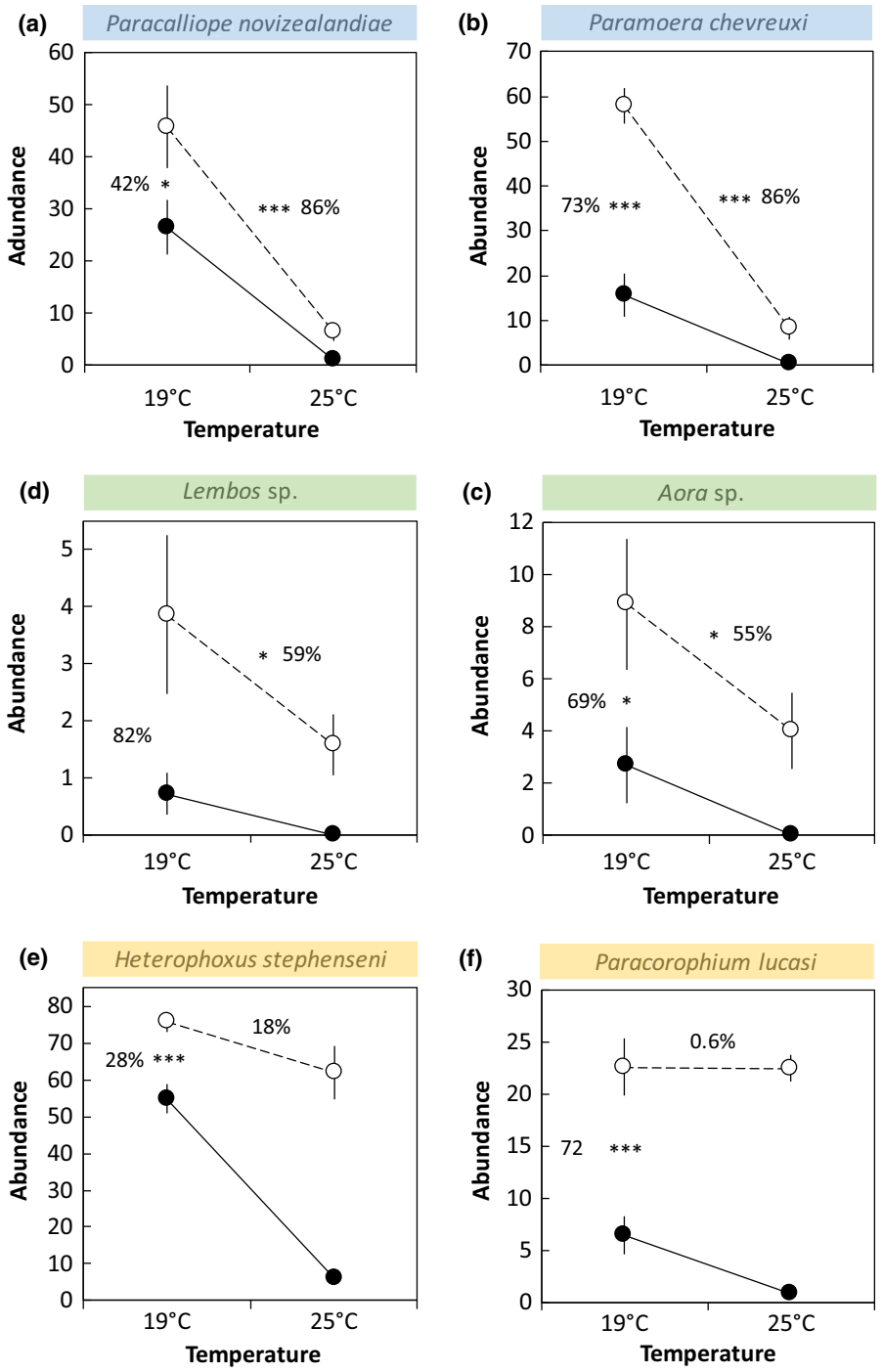

FIGURE 5 Extreme-scenario experiment. The postexperimental abundance of amphipod species according to temperature–parasite treatments (mean ind. per mesocosm ± *SE*; $n = 7$). Dashed line and ○: parasites absent; full line and ●: parasites present. No two-way ANOVAs were performed on these data, and hence, significance levels based on Student's *t* tests of treatment pairs (raw or rank-transformed data) are indicated by asterisks between markers (*$p < 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$). Note that only two statistical contrasts were performed: 19°C/parasites absent treatment against 19°C/parasites present and 25°C/parasites absent; see Table S5 for exact *p*-values. Inserted percentages indicate the proportional reduction in the number of individuals in the 19°C/parasites present and the 25°C/parasites absent treatments compared to the 19°C/parasites absent treatment. Colour bars indicate the amphipod species' affinity for microhabitat (blue, panel a,b: free-swimming; green, panel c,d: tube-building on vegetation; brown, panel e,f: sediment burrowers; see Table 1 and Appendix S1 for details). Note that inserted lines do not indicate linear relationships but serve to highlight the level of interaction

heterogeneous error variance. However, based on pairwise contrasts the temperature–parasitism interaction appears retained (Figure 3d), which indicates that contrary to the synergistic effect of high temperatures and parasitism, the applied experimental temperature ranges per se are unable to eliminate any of the amphipod species.

The MDS visualization of these structural patterns shows, as in the standard-warming experiment, that the high-temperature/parasites mesocosms cluster together and away from the other treatments (Figure 4b). This further demonstrates the synergistic impact of temperature and parasitism in creating a uniquely different amphipod community. Furthermore, under this extreme scenario, the three remaining treatments also cluster apart from each other (Figure 4b), emphasizing that both elevated temperature and parasitism on their own affect community structure, and most intriguingly, they do so in different ways.

3.3 | Field evidence

Across the 12 investigated Otago Harbour bays, there was a highly significant negative relationship between amphipod species richness (see Table S6 for species involved) and the infection prevalence in the local mud snail population (Figure 6). Infection prevalence

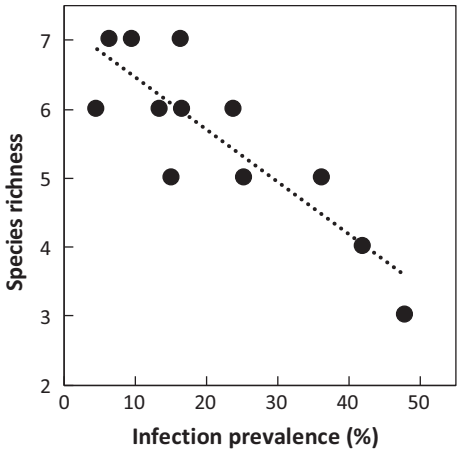

FIGURE 6 Field relationship between amphipod species richness and arcsine-transformed infection prevalence (%) by *Maritrema novaezealandensis* in the sympatric mud snail *Zeacumantus subcarinatus* population across 12 bays in Otago Harbour. Trendline and linear regression summary statistics: Richness = −0.076 Prevalence + 7.212; $r^2 = 0.741$, $p < 0.0005$. See Table S6 for amphipod species

explained 74.1% of the variation in species richness. This negative relationship remains even if potentially influential predictors other than infection prevalence are statistically corrected for. A multiple regression analysis entering also (as predictors) sediment particle diameter, sediment chlorophyll-*a* content, ghost shrimp *Callianassa filholi* abundance, New Zealand cockle *Austrovenus stutchburyi* density and cockle infection intensity (with other species of trematodes) results in a significant total regression ($r^2 = 0.922$; $p = 0.033$) but infection prevalence in mud snails emerges as the sole statistically significant predictor ($r_p^2 = 0.810$; $p = 0.014$) (Table S7).

A marginal significant negative relationship also exists between amphipod species diversity in terms of Shannon–Wiener index and snail infection prevalence ($r^2 = 0.0.336$, $p = 0.048$; data not shown). However, a multiple regression analysis, correcting for potential predictors of diversity other than prevalence, eroded this negative correlation ($r^2_p = 0.445$, $p = 0.377$).

4 | DISCUSSION

Our study suggests that under future warming scenarios as well as short-term heat waves at present, the combined action of increasing temperature and parasitism will be particularly detrimental to intertidal amphipod communities. They will face major structural changes and diversity declines, and functionally develop into assemblages dominated by infaunal species. Even these sediment dwelling amphipods risk complete elimination under more extreme, yet possible, temperature–parasitism scenarios. The study thus highlights the trematode *M. novaezealandensis* as an emerging, very potent community engineer in New Zealand intertidal ecosystems under the ongoing climate changes.

The mesocosm experiments mirrored a naturally occurring intertidal ecosystem as much as experimentally possible and thus integrated existing intra- and interspecific interactions and their responses to temperature variations. The amphipod community's reaction to the experimental manipulation of temperature and parasitism was remarkably clear. Exposure to present mean sea surface summer temperature (c. 17°C) in the absence as well as presence of moderate parasitism, and exposure to a mean temperature about four degrees higher in absence of parasitism, left the amphipod host community largely unaffected (Figures 1, 3a,b and 4a). Although the experimental temperature levels were superimposed natural diurnal fluctuations peaking around 25–26°C, this did not result in detrimental parasite transmission nor severe temperature stress in the amphipod community taken as a whole. However, the common *P. novizealandiae* showed signs of temperature sensitivity, which translated into a modest decline of the Shannon–Wiener diversity index (Figures 1a and 3a). However, combining elevated temperatures (c. 21°C) and parasitism created a potent synergism with profound consequences for the host community. Likely, the higher temperatures elicited significant *Maritrema* transmission from snails to amphipods (see Introduction) causing the latter to die-off in a highly species-specific manner, affecting especially the common free-swimming species and the rare aoriids (Figure 1). In effect, the community deteriorated in terms of diversity and marginally also species richness, and shifted structurally to become dominated by infaunal amphipods (Figures 1, 3a,b, 4a and Figure S2).

Further elevating temperature levels and parasite pressure only exacerbated the synergistic impact on the amphipod community (Figures 3c,d, 4b and 5), bringing it to the brink of extinction as a whole. Only the infaunal *H. stephenseni* remained in any significant numbers, obviously causing substantial decreases in both species diversity and richness. Interestingly, under this extreme temperature–parasite scenario the synergistic impact of the two factors on the host community manifested itself already at a mean temperature of c. 19°C, just two degrees above present sea surface temperature. Again, parasite-induced species-specific declines in host abundance resulted in marked reductions in species diversity and richness (Figures 3c,d and 5), leaving an amphipod community structurally different from that at 19°C without parasites (Figure 4b). Under the soaring temperatures of the extreme-scenario experiment peaking at 29°C, high temperatures by themselves deteriorated the community, having negative effects particularly on *P. novizealandiae* and *P. chevreuxi* but also the aoriids (Figure 5a–d), and in turn on diversity measures as well. This isolated temperature impact favouring the benthic species hence resembles the structural changes seen also for the combined temperature–parasite synergy. Regardless of this similarity, increasing temperatures do not simply exacerbate the impact of parasitism, and parasitism does not simply exacerbate the impact of increasing temperature. On their own, temperature and parasitism have inherently different structural effects on the amphipod community, evidenced by different clustering of mesocosm units according to treatments in the MDS plot (Figure 4b). Consequently, the combined action of the two factors creates a unique

community whose structure cannot easily be anticipated from these factors' separate influence.

The structural changes of the amphipod community are for the main part a result of the host species differential vulnerability to the increased number of parasite larvae expected to be released at increasing temperature (Figure 2). However, the processes leading to this species-specific vulnerability are not entirely clear. Mortality induced by microphallid trematodes (such as *Maritrema*) in amphipod second intermediate hosts is intensity-dependent, and the trematode larvae tend to accumulate in the larger host individuals of the population that then die-off at a high rate (Bates, Poulin, & Lamare, 2010; Fredensborg et al., 2004; Koehler & Poulin, 2010; Larsen & Mouritsen, 2014). This occurs either as a simple function of time (age) or because larger hosts constitute larger targets. The latter may be reflected in the body sizes of postexperimental amphipods that tend to be smallest in the high-temperature/parasitism treatments (Appendix S3). However, if size-dependent parasite susceptibility is the sole operating process across species, a positive relationship between vulnerability and the pre-experimental mean body length of different amphipod species would also be expected. Such relationship did not exist. Rather, the different vulnerabilities relate to the species overall behaviour (Table 1) in relation to that of the parasites (Appendix S2). Of the six amphipod species, the free-swimming *P. novizealandiae* and *P. chevreuxi* are particularly active and thus likely to express the highest metabolic rates. Together, this may repeatedly bring these specimens into contact with the bulk of swimming cercariae just above the sediment surface (Appendix S2), where their high ventilation rate (abdominal appendage beating) ensures a high contact rate between host and parasites (see Mouritsen & Jensen, 1997). The aoriids, in contrast, live in tubes attached to sea lettuce drifting across the sediment surface (see Figure S1), which means that some individuals may periodically be elevated above the highest concentrations of *Maritrema* cercariae. This, together with their sluggish behaviour indicating low metabolism and in turn low ventilation rate and host–parasite contact rate, argue for their somewhat lower parasite vulnerability in comparison to the free-swimming species (Figure 2). *Heterophoxus stephenseni* is, as a free-living sediment burrower, entirely beyond the reach of the swimming parasite larvae and its low vulnerability is therefore expectable. Interestingly, directly challenged by *Maritrema* cercariae outside its protective sedimentary environment, *H. stephenseni* turns out to be even more susceptible to *Maritrema* infection than *P. novizealandiae* (Koehler et al., 2011). This clearly emphasizes the importance of behavioural aspects in shaping the species-specific parasite vulnerability in the present ecosystem. It could also explain the marked *Heterophoxus* decline seen in the high-temperature/parasitism treatment of the extreme-scenario experiment: high temperature means high activity, bringing these individuals to the sediment surface more often than usually the case. In comparison, the sediment tube-building *P. lucasi* can be placed behaviourally between the aoriids and *H. stephenseni* and therefore displays an intermediate vulnerability to infection. Although the above behavioural considerations may account for the observed overall parasite vulnerability, species-specific variation in internal defence systems may also have been in play.

Whereas the mesocosms experimental temperature regimes can be justified by the ongoing global warming and anticipated increases in frequency, duration, and severity of heat waves (IPCC, 2014), the choice of an infection prevalence in the snail population of 75% in the extreme-scenario experiment is clearly above present average. Likely owing to the complexity of the topic, no study has yet attempted to predict how the infection prevalence by trematodes in the first intermediate snail hosts may be influenced by climate changes. Inherently, the infection prevalence in the *Zeacumantus* snail population, and probably all other snail host populations alike, is a positive function of the density of definitive bird hosts that supply the parasite eggs (Fredensborg et al., 2006). In intertidal ecosystems, climate changes can be envisaged to result in longer residence times of migratory shorebirds due to a milder winter climate, which could also benefit resident species; in addition, coastal squeeze due to sea-level rise may elevate bird densities (Ausden, 2014; Clausen & Clausen, 2014; Godet, Jaffré, & Devictor, 2011; Hughes, 2004; MacLean et al., 2008). On the other hand, some migratory shorebird populations may decrease owing to reproductive failure in the rapidly warming arctic and subarctic breeding grounds (IPCC, 2014; Wauchope et al., 2017). The snail hosts themselves, and hence the trematodes within, could benefit from higher winter temperatures through greater winter survival, but also suffer greater heat-related summer mortalities (Fredensborg et al., 2005; Mouritsen & Poulin 2002b). The latter, however, may in the present system be offset by a greater heat tolerance of trematode-infected *Zeacumantus* snails (see Bates, Leiterer, Wiedeback, & Poulin, 2011). A generally milder climate is bound to increase the activity of the poikilothermic snail host, which in turn could increase contact rates between host and parasite eggs deposited on the sediment surface in bird droppings. Combined, these purely qualitative considerations tentatively suggest that infection prevalence in the first intermediate host population could well increase rather than decrease in a future warmer world, justifying the extreme-scenario experiment's level of parasitism. In any case, the applied high prevalence does presently occur in some bays within Otago Harbour (Fredensborg et al., 2006), making our extreme scenario-experiment highly relevant, if not on a broad spatial scale in the future, then at a local scale now as well as in the future.

The fact that Otago Harbour presently supports great variation in trematode infection prevalence in local snail populations across bays, provided a unique opportunity to test the field relevance of our experimental findings of decreasing amphipod diversity with increasing parasitism. Indeed, the existence of a strong negative relationship between amphipod species richness and snail parasitism (Figure 6) underlines that our experimental predictions are in play already under the present temperature regime.

This field-validated experimental prediction of a future deterioration of the intertidal community of amphipod hosts may be challenged by the logic consequence that if the second intermediate hosts are driven more or less to extinction, the parasite life cycle will

be disrupted, thus exterminating the trematode rather than the amphipods. This scenario is unlikely, though. *M. novaezealandensis* utilizes a particularly wide spectrum of secondary host species, ranging from amphipods over isopods to decapods and allied crustaceans (Koehler & Poulin, 2010). Larger decapods in particular are tolerant of microphallid infections, generally supporting high parasite loads (Koehler & Poulin, 2010). Therefore, in the absence of a dense amphipod community the *Maritrema* life cycle may continue to exist, shunted through the decapod secondary hosts to crab-eating definitive hosts.

The mere 2 week duration of our experiments indicates that the temperature–parasitism synergy can act on a very short time scale indeed. Similar evidence is available from the northern hemisphere where a dense population of corophiid amphipods was wiped out by microphallid trematodes during a 3 week heat wave (Jensen & Mouritsen, 1992). Hence, the anticipated future increase in frequency of prolonged heat waves is bound to increasingly limit epibenthic amphipod species in particular to low-parasitism pockets in sublittoral habitats or intertidal bays where *Zeacumantus* snails are few. Owing to the tremendous selection pressure this poses on the animals, they may over evolutionary time adapt to better resist parasite infections (see Bates et al., 2010; Bryan-Walker et al., 2007)—and high temperatures per se for that matter—and eventually repopulate the intertidal flats. In the nearer future, however, this ecosystem belongs to infaunal amphipods (Figure S2).

Little comparable evidence appears to exist. Larsen et al. (2011) demonstrated that the parasite-induced elimination of an abundant corophiid amphipod during a heat wave (op. cit.) paved the way for a less abundant but parasite-resistant sibling species. Similarly, Fleury et al. (2004) showed that the impact of a parasitoid on the relative frequency of two *Drosophila* species was temperature dependent, and Brockhurst, Fenton, Roulston, and Rainey (2006) found the same for two species of bacteria in the presence of a phage. The only study on a multihost assemblage involves a fungus that seems to alter a community of freshwater zooplankton by targeting the dominant species in a temperature-dependent manner (Hoenicke, 1984).

Of course, rising temperature is only one aspect of environmental change that may interact with parasitism to alter community structure. For instance, ocean acidification is increasingly recognized as a major threat to marine ecosystems through its impacts not only on the performance of individual organisms (Kroeker, Kordas, Crim, & Singh, 2010), but also on the strength of interspecific interactions (Allan, Domenici, McCormick, Watson, & Munday, 2013; Fabry, Seibel, Feely, & Orr, 2008). In our study system, reduced seawater pH has been shown to negatively affect the snail first intermediate host of the trematode *M. novaezealandensis* and the success of its snail-to-amphipod transmission (Harland, MacLeod, & Poulin, 2015; MacLeod & Poulin, 2015). Several additional environmental changes occurring concurrently with global warming can also modulate parasitism and other interspecific interactions, with unpredictable but likely serious consequences for natural communities.

Although a limited list indeed, the above studies on temperature–parasitism synergy together with the present results emphasize its general importance for community structuring across ecosystems, bearing a potential for further scrutiny. Despite inclusion of a diverse amphipod community in the present mesocosm experiments, the wide host spectrum used by *M. novaezealandensis* suggests that the identified temperature–parasitism synergy may reach beyond amphipods: the entire intertidal crustacean community is likely to be modified by this single trematode species. To unravel the full set of winners and losers in this temperature–parasite game is a challenge for the future. Also, disentangling the complex processes determining the density of infected first intermediate snail hosts will be imperative for precise predictions of *M. novaezealandensis*' future role as an ecosystem engineer. Finally, *M. novaezealandensis* is not the sole keystone trematode haunting intertidal animals. Echinostomatid trematodes infecting the New Zealand cockle *A. stutchburyi* as secondary hosts have been shown, solely through their impact on the cockles' burying behaviour, to facilitate the intertidal crustacean community (Mouritsen & Poulin, 2005, 2010). The transmission of these trematodes is likely also temperature dependent (Poulin, 2006), and hence, the ecosystem engineering roles played by microphallid and echinostomatid trematodes may tend to counteract each other as temperatures increase. Unravelling the full parasite community's integrated impact on the intertidal community in the context of climate change will be a most challenging but also very interesting endeavour for future investigations.

Generally, specialist parasites and generalist parasites with asymmetrical impact on the host guild are believed to maintain or even boost biodiversity (Dobson & Hudson, 1986; Fenton & Brockhurst, 2008; Hatcher et al., 2012; Hudson, Dobson, & Lafferty, 2006; Larsen & Mouritsen, 2014). By targeting the often-dominant competitor or keystone species, the parasites will induce a competitive release that elevates diversity. Under average conditions, the generalist parasite *M. novaezealandensis* may indeed occupy such structuring role and participate in maintaining crustacean diversity. However, as the parasite pressure on the host community increases with increasing temperatures, a threshold or tipping point will be reached where the initially positive influence on diversity turns negative. Because many host–parasite systems appear sensitive to climate variability (e.g. Mouritsen & Poulin, 2002a), such nonlinear response may be widespread across systems.

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