Science of the Total Environment 743 (2020) 140723

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Intraspecific diversity in an ecological engineer functionally trumps interspecific diversity in shaping community structure

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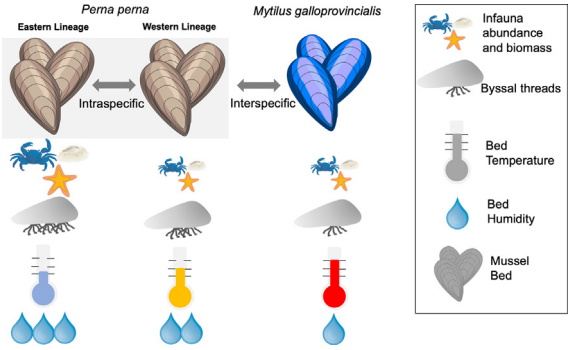
HIGHLIGHTS

- We tested whether intraspecific diversity may functionally exceed species diversity.
- We used two bioengineering mussel species, one of which displays genetic lineages.
- Associated communities, structural and environmental heterogeneity were evaluated.
- Ecosystem-level effects varied more intraspecifically than between species.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 5 April 2020
Received in revised form 29 June 2020
Accepted 2 July 2020
Available online 7 July 2020

Editor: Sergi Sabater

Keywords:
Genetic lineages
Mussel
Ecosystem functioning
Biodiversity

ABSTRACT

Can intraspecific diversity functionally supersede interspecific diversity? Recent studies have established the ecological effects of intraspecific variation on a number of ecosystem dynamics including resilience and productivity and we hypothesised that they may functionally exceed those of species diversity. We focused on a coastal ecosystem dominated by two coexisting bioengineering mussel species, one of which, *Perna perna*, displays two distinct phylogeographic lineages. A manipulative field experiment revealed greater habitat structural complexity and a more benign microscale environment within beds of the eastern lineage than those of the western lineage or the second species (*Mytilus galloprovincialis*); the latter two did not differ. Similarly, while infaunal species abundance and biomass differed significantly between the two lineages of *Perna*, there was no such difference between *Mytilus* and the western *Perna* lineage. The evenness and diversity of associated infaunal assemblages responded differently. Diversity differed relatively weakly between species, while evenness showed a very strong difference between conspecific lineages. Our results show that variation within a species can functionally supersede diversity between species. As the two *P. perna* lineages have different physiological tolerances, we expect them to react differently to environmental change. Our findings indicate that predicting the ecosystem-level consequences of climate change requires an understanding of the relative strengths of within- and between-species differences in functionality.

1. Introduction

Human activities are driving unprecedentedly rapid changes to environment conditions worldwide, resulting in global biodiversity loss and reshuffling (Barnosky et al., 2011; Cardinale et al., 2012). These changes

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https://doi.org/10.1016/j.scitotenv.2020.140723
0048-9697/

in biodiversity affect ecosystem functions and, in turn, the sustainability of human societies, prompting calls for increased research into understanding the consequences of such alterations (Balvanera et al., 2013; Isbell et al., 2017). Earlier research focused mainly on diversity at the species level and its effect on key ecosystem processes. The results of manipulative experiments have shown that the removal or replacement of certain species can have significant effects on the structure of communities and the functioning of the associated ecosystems (Cardinale et al., 2000; Symstad et al., 1998). More recently, research has widened the characterization of diversity to include distinct genotypic and phenotypic variation within single species. Indeed, studies in various systems have demonstrated that intraspecific phenotypic trait variation can have large ecological effects on processes such as primary productivity (Crutsinger et al., 2006; Zhu et al., 2000), nutrient cycling (Lecerf and Chauvet, 2008), but see (Crutsinger et al., 2013), species coexistence (Siefert, 2012; Spasojevic and Suding, 2012) and ecosystem resilience and resistance (Des Roches et al., 2018; Hughes and Stachowicz, 2004; Raffard et al., 2019; Reusch et al., 2005).

Nevertheless, researchers have not yet broadly quantified the general ecological importance of intraspecific variation relative to among-species variation (but see Griffiths et al., 2016). Recognising the relative functional significance of distinct levels of biodiversity is not only a central objective of evolutionary biology, it is also critical to predicting the consequences of accelerating biodiversity loss and to planning effective conservation and management activities (Santamaría and Mendez, 2012). This is particularly important in the case of species that act as ecosystem engineers, the presence of which heavily affects local and even regional levels of biodiversity (Jones et al., 1994). Such organisms modify the environment either through their own physical structure (autogenic engineering; e.g., tree shading, hydrodynamic stress attenuation by coral reefs) or by transforming living or non-living materials from one physical state to another mechanically or in other ways (allogenic engineering; e.g., burrow excavation by mammals, mound building by termites) (Hastings et al., 2007; Jones et al., 1994).

In marine intertidal habitats, mussels have a major role as ecosystem engineers (e.g., Suchanek, 1985). They modify their environment primarily through the physical structure of their aggregations (mussel beds) and simple behaviours, acting both as autogenic and allogenic ecological engineers (e.g., Bertness, 1984; Borthagaray and Carranza, 2007; Nicastro et al., 2012). The physical heterogeneity of a mussel bed matrix is determined by shell geometry and shell packing (Hughes and Griffiths, 1988) and by the intricate mat of byssal threads, secreted by mussels to adhere to the substratum, combined with shell fragments and debris trapped within the bed (e.g., Seed and Suchanek, 1992). In addition, temperature and humidity regimes within the mussel aggregation are moderated by the ability of some mussel species to gape the valves during aerial exposure (Nicastro et al., 2010b). The complex matrix of a mussel bed creates a benign environment that forms the habitat for a diverse array of associated species, or infauna. The matrix of a mussel bed relieves environmental stress by ameliorating conditions of irradiance, temperature, wave force and humidity, while at the same time generating and trapping food for the infauna. Most importantly, diversity at the species level influences the beneficial effects of the mussel-created habitat (e.g., Lathlean et al., 2016; Nicastro et al., 2012), influencing the composition of the associated community (Lintas and Seed, 1994; Seed, 1996). Coexisting mussel species with very similar biological and ecological functions are known to harbour very different faunas within the mussel bed matrix (e.g., Arribas et al., 2013).

Here, we assess the effects of intraspecific versus interspecific diversity on infaunal communities in a coastal ecosystem dominated by two key bioengineers. We focused on the intertidal mussels *Mytilus galloprovincialis* and *Perna perna*, the latter represented by two distinct evolutionary genetic lineages. Previous studies have shown not only spatial segregation and behavioural divergence between *M. galloprovincialis* and *P. perna*, they have also highlighted fundamental differences between *P. perna* lineages in behavioural traits known to affect survival along large- and small-scale environmental gradients(Zardi et al., 2015a; Zardi et al., 2011); critically, these distinct behaviours are likely to lead to microclimate differences within mussel aggregations, influencing their roles as bioengineers (Zardi et al., 2015a). On this basis, we hypothesised that the effects of intraspecific diversity (i.e., between genetic lineages) on environmental properties and infaunal assemblages would differ from those of interspecific diversity (i.e., *P. perna* versus *M. galloprovincialis*). Specifically, we used a manipulative field experiment to test the prediction that differences in the strength of bioengineering effects would be greater between genetic lineages than between species. The effects of intra or interspecific diversity on ecosystem functioning were assessed in terms of (a) shaping the associated infaunal community of invertebrates, (b) moderating the microclimate within the mussel aggregation in terms of temperature and humidity and (c) modifying habitat structural complexity in terms of the number of byssal threads.

2. Materials and methods

2.1. Study species

Perna perna and *Mytilus galloprovincialis* show clear geographic and intertidal distributional patterns (Fig. 1a). The southern African coastline can be divided into three major biogeographic regions: the cool-temperate west coast, the warm-temperate south coast, and the

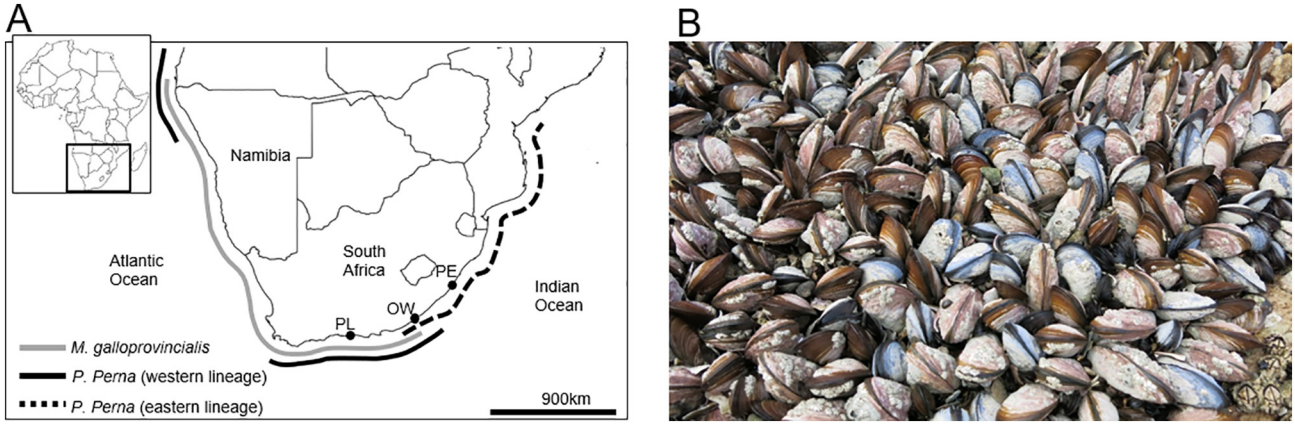

Fig. 1. (a) Experimental location (OW: Old Woman's River) and sampling sites (PL: Plettenberg Bay: PE: Port Edward) along the South African coastline and distributional ranges of *Perna perna* lineages and *Mytilus galloprovincialis*: (b) structurally complex mixed bed of *P. perna* and *M. galloprovincialis* at PL.

subtropical east coast (Emanuel et al., 1992). *P. perna* dominates the sub-tropical and warm-temperate bioregions. It is absent from the cold waters of the upwelling-dominated west coast of South Africa, and reappears in central Namibia, extending along the west coast of Africa into the Mediterranean (Lourenço et al., 2012; Cunha et al., 2014). *M. galloprovincialis* invaded southern Africa in the late 1970s and soon became the most successful marine invasive species spreading along more than 2800 km of coast; it now dominates the cool-temperate west coast bioregion (Robinson et al., 2005). On the warm-temperate south coast, the two species coexist, compete for space and show partially overlapping intertidal zonation with *M. galloprovincialis* dominating the high mussel zone and *P. perna* the lower shore, with mixed species beds in the middle (Bownes and McQuaid, 2006; Rius and McQuaid, 2006; Rius and McQuaid, 2009). Importantly, analyses of *P. perna* mitochondrial and nuclear DNA show a sharp phylogeographic break at the warm-temperate/subtropical transition on the southeast coast of South Africa, with distinct western and eastern genetic lineages (Cunha et al., 2014; Zardi et al., 2007a; Zardi et al., 2015a). The two lineages overlap in their distributions on the southeast coast of South Africa over a distance of approximately 200 km.

These species and lineages have evolved suites of adaptations to cope with the stresses of emersion and wave action that are crucial for the occurrence and dynamics of the associated infauna. During aerial exposure, *P. perna* alternates opening and closing of the valves (gaping behaviour) in order to maintain aerobic respiration, while *M. galloprovincialis* keeps the valves closed and undergoes anaerobic respiration (Nicastro et al., 2010b). The gaping behaviour of *P. perna* has no effect on the body temperatures of isolated individuals, but when surrounded by conspecifics, evaporative cooling effects emerge for the mussel bed as a whole (Nicastro et al., 2012). The intensity of the behaviour also changes intraspecifically, with the eastern *P. perna* lineage gaping more than the western one (Zardi et al., 2015a).

The ability of a mussel to survive wave action is largely due to the byssus which allows mussels to attach firmly to the substratum and to form beds (Waite, 1992). This provides a complex habitat that supports recruiting mussels and an array of other species (Seed, 1996; Suchanek, 1985). The number of byssal threads is known to be greater in *P. perna* individuals than in *M. galloprovincialis* (Zardi et al., 2006) and, within *P. perna*, higher in the eastern than the western lineage (Zardi et al., 2015a). Morphologically, *M. galloprovincialis* has a wider shell (scaled to shell length) than *P. perna*, while the two *P. perna* lineages do not show phenotypic shell differences (Zardi et al., 2006).

2.2. Transplant experiment

To determine the effects of lineage and species on infaunal assemblages, artificial mussel beds were deployed at Old Woman's River (OW, 33°28′59″ S, 27°08′47″ E) on the warm-temperate south coast of South Africa (Fig. 1a). This area is situated within the contact zone of the two genetic lineages of *Perna perna* (Zardi et al., 2007a), where individuals from both eastern and western lineages as well as *M. galloprovincialis* naturally co-occur. Shores at OW are flat, gently sloping sandstone platforms with uniform topography.

The manipulative experiment consisted of three treatments: (a) 100% eastern lineage *P. perna* (hereafter eastern), (b) 100% western lineage *P. perna* (hereafter western) or (c) 100% *M. galloprovincialis* individuals. Each *P. perna* treatment was made up of mussels collected from one of two locations outside the overlap zone, known to support pure genetic lineages (Fig. 1a; PL: Plettenberg Bay; PE: Port Edward). *Mytilus galloprovincialis* does not occur east of the overlap region, and was collected at the same locations as the western lineage of *P. perna*, Plettenberg Bay. Mussels were acclimated in tanks in a controlled environment room set at 20 °C (±0.5 °C) under a 12/12 h (light/dark) light regime, for three weeks before deployment in the field. Two day before field deployment shells were carefully scrubbed and cleaned of fouling organisms in order to limit contamination from pre-existing infaunal.

All mussels were deployed in the field on November 16th, 2018; mussels (shell length 3.5–4.5 cm measured before starting the experiment and randomly allocated across treatments) were placed in 15 × 15 cm metal quadrats ($n = 4$ for each treatment), secured by large washers and screws into rawl plugs, in previously drilled holes, and then covered with a strong plastic mesh (mesh size: 16 mm), so that they could re-attach firmly to the substratum (as in Zardi et al., 2011). Twenty-five mussels were placed in each quadrat covering the entire area. This density (1111 mussels m^{-2}) is representative of co-occurring natural beds (McQuaid and Mostert, 2010). Previous manipulative experiments at the same experimental location (OW) and with the same species showed that the mesh does not affect the temperature or humidity experienced by mussels (Zardi et al., 2011). Each artificial patch was placed in a flat area cleared on the mid-shore, at the same intertidal height as natural beds between 60 and 80 cm from the nearest existing patches. To avoid loss of mussels due to wave action or storm events, the mesh was left on the artificial mussel patches for the duration of the experiment, which lasted for three months.

To assess infaunal communities, mussels and all associated fauna were collected at the end of the experiment. Samples were preserved in ethanol, then washed and separated through a sieve with 1 mm mesh. All invertebrate macrofauna >1 mm were sorted, counted, identified to the lowest taxonomic level possible, decalcified in nitric acid if necessary, dried for two days at 60 °C and then weighed.

To assess the degree of modification of the physical environment due to ecosystem engineering (Fig. 1b), within-bed interstitial temperature and relative humidity were recorded in three haphazardly selected beds ($n = 3$) for each treatment. Collection of temperature and humidity data started on the dropping tide, as soon as the artificial mussel beds were out of water, and continued for 90 min. Recordings were taken every 5 min. Interstitial temperature was measured with digital thermocouples (thermometer 800024, SPER SCIENTIFIC Ltd.) carefully placed within beds but not in contact with any mussel shell. Interstitial humidity was recorded with a data logger (iButtons®, Maxim Integrated Products, USA). The periphery of each bed was avoided to limit possible edge effects. The measurements were replicated on two days during spring tide (November 23rd and November 22nd 2018), during the last month of the experiment.

As a proxy of within-bed architectural complexity, the mean number of byssal threads in five mussels from each of three quadrats per treatment (eastern and western *P. perna*, *M. galloprovincialis*; n = 3) was assessed at the end of the experiment. Previous studies showed that, for these species, thread counts from five mussels are representative of an entire quadrat for a given mussel length and hydrodynamic condition (Nicastro et al., 2010a; Zardi et al., 2007b; Zardi et al., 2006).

2.3. Data analyses

The comparison of inter- vs intra-specific effects was made by comparing the strengths of two contrasts. The effect of interspecific variation (Contrast 1) was assessed by comparing all *P. perna* treatments (Eastern + Western) versus the *M. galloprovincialis* treatment. The effect of intraspecific variation (Contrast 2) was derived by comparing *P. perna* Eastern versus *P. perna* Western.

2.3.1. Habitat structural complexity and environmental heterogeneity

The effects of inter and intraspecific variations on habitat complexity and on mussel bed microclimate was assessed using two methods of statistical analysis.

First, orthogonal contrasts were used for mean number of byssal threads per quadrat, and within-bed air temperature and relative humidity after 30, 60 min and 90 min. Environmental data for each day and time point were analysed separately.

Second, the effect size was calculated for each orthogonal contrast analysed and used to compare the magnitudes of the effects between inter (Contrast 1) and intraspecific variation (Contrast 2). Given the

sample sizes (<20), Hedges' g was chosen over Cohen's d (Grissom and Kim, 2005). Descriptors for magnitudes based on Cohen (1992) and adapted according to Sawilowsky (2009) were used. Confidence interval for the effect size with a confidence coefficient of 95% was calculated (Hedges and Olkin, 2014).

2.3.2. Effects of inter- and intraspecific variation on associated macrofauna

We employed three methods of statistical analysis.

First, the effects of inter and intraspecific variations were quantified using orthogonal contrasts of Margalef richness (d), Pielou's evenness (J′), and Shannon-Wiener diversity (H′ natural log-transformed).

Second, the effect size was calculated for each index and used to compare the magnitudes of the effects between inter (Contrast 1) and intraspecific variation (Contrast 2). Hedges' g and 95% confidence coefficients were used as above. Third, multivariate one-way PERMANOVA analyses (Anderson, 2001) were performed to test the effects of inter- and intraspecific variability (i.e., the two contrasts) on (1) species abundance and (2) species biomass. These tests were performed with either Contrast 1 (effect of interspecific variability) or Contrast 2 (effect of intraspecific variability) as a fixed factor and (1) infaunal species counts or (2) biomass as the dependent variables. For each PERMANOVA analysis, a Bray-Curtis dissimilarity matrix for square root transformed multivariate data was used. Significance of F-ratios was determined from 9999 randomizations of the data (Anderson, 2005). When only a restricted number of permutations was possible, we used Monte Carlo *p*-values (p(mc)) rather than permutational *p*-values (p(perm)). Permutation tests of multivariate dispersion (PERMDISP; Anderson, 2004) were used to check the homogeneity in the average dissimilarities of samples from the central location of their group. A similarity percentage analysis (SIMPER) was then used to determine the percentage contribution that each variable (species counts or biomass) made to the Bray-Curtis dissimilarities. Species were ranked by their contribution to overall dissimilarity and included up to an accumulated total of 50% of average dissimilarity.

Differences between assemblages were visualized using (1) non-metric multidimensional scaling (nMDS) ordinations and (2) hierarchical cluster analysis using the complete linkage method. Both methods were based on Bray-Curtis similarity matrices for infauna of either species abundance or species biomass. A similarity profile (SIMPROF) test was used to define groups of samples in the hierarchical cluster analysis with similar assemblage compositions.

3. Results

3.1. Habitat structural complexity and environmental heterogeneity

Relative humidity declined and air temperature increased with time during aerial exposure (Fig. S1a, b). No difference was detected at time zero for any day or environmental variable indicating that there was no pre-existing initial effect (day 1 humidity: $t(6) = -0.925$, $p = 0.391$ and $t(6) = 0.057$, $p = 0.956$ for Contrasts 1 and 2 respectively; day 2 humidity: $t(6) = -0.615$, $p = 0.561$ and $t(6) = 0.966$, $p = 0.371$ for Contrasts 1 and 2 respectively. Day 1 temperature: $t(6) = 2.449$, $p = 0.05$ and $t(6) = 2.121$, $p = 0.078$ for Contrasts 1 and 2 respectively; day 2 temperature: $t(6) = 0.177$, $p = 0.866$, $t(6) = 0.919$, $p = 0.394$ for Contrasts 1 and 2 respectively).

On days 1 and 2 (Fig. 2a,b), after 30, 60 and 90 min, humidity differed significantly between species (Contrast 1; after 30 min: day 1 $t(6) = 9.194$ and day 2 $t(6) = -12.513$; after 60 min: day 1 $t(6) = -44.396$ and day 2 $t(6) = -26.874$; after 90 min: day 1 $t(6) = -10.676$ and day 2 $t(6) = -6.768$; $p = 0.001$ in all cases) and within species (Contrast 2; after 30 min: day 1 $t(6) = 10.532$ and day 2 $t(6) = 10.419$; after 60 min: day 1 $t(6) = 49.605$ and day 2 $t(6) = 27.854$; after 90 min: day 1 $t(6) = 12.132$ and day 2 $t(6) = 7.978$; $p = 001$ in all cases).

In general, temperature also differed between species (Fig. 2c, d; Contrast 1; after 30 min: day 2 $t(6) = 3.894$, $p = 0.008$; after 60 min: day 1 $t(6) = 8.053$, $p = 0.001$ and day 2 $t(6) = 7.188$, $p = 0.001$; after 90 min: day 1 $t(6) = 11.526$, $p = 0.001$ and day 1 $t(6) = 6.083$, $p = 0.001$) and within species (Contrast 2; after 30 min: day 2 $t(6) = -2.942$, $p = 0.026$; after 60 min: day 1 $t(6) = -8.102$, $p = 0.001$ and day 2 $t(6) = -3.511$, $p = 0.013$; after 90 min: day 1 $t(6) = -12.125$, $p = 0.001$ and day 2 $t(6) = -4.734$, $p = 0.003$).

However, after 30 min on day 1 there was no significant effect for either contrast (Day 1: Contrast 1 $t(6) = 0.843$, $p = 0.431$, Contrast 2 $t(6) = -0.365$, $p = 0.728$).

Overall, effect sizes were above 1.2 (i.e., very large), with the exception of air temperature day 2 after 30 min, when, for both contrasts, values were below 0.8 (i.e., large) and had a non-significant CI 95% (Table 1). Effect of sizes between lineage were always relatively higher than between species. The average effect size for humidity was 21.4 and 1.8 for intra and interspecific variation. The average effect of size for air temperature was 3.4 and 0.02 for intra and interspecific variation.

The number of byssal threads per mussel differed significantly between (Contrast 1: $t(6) = -24.127$, $p = 0.001$) and within species (Contrast 2: $t(6) = 11.171$, $p = 0.001$). Effect sizes were huge for both contrasts but the Hedges' g was smaller for interspecific variation ($g = 2.02$) than for intraspecific variation ($g = 8.666$; Table 1).

3.2. Effect of treatment on associated macrofauna

A total of 46 invertebrate species were recorded from the experimental mussel beds, with 25 species associated with the eastern lineage of *P. perna*, 19 with the western lineage and 32 with *M. galloprovincialis*. Only nine species were common to all treatments (Table S1).

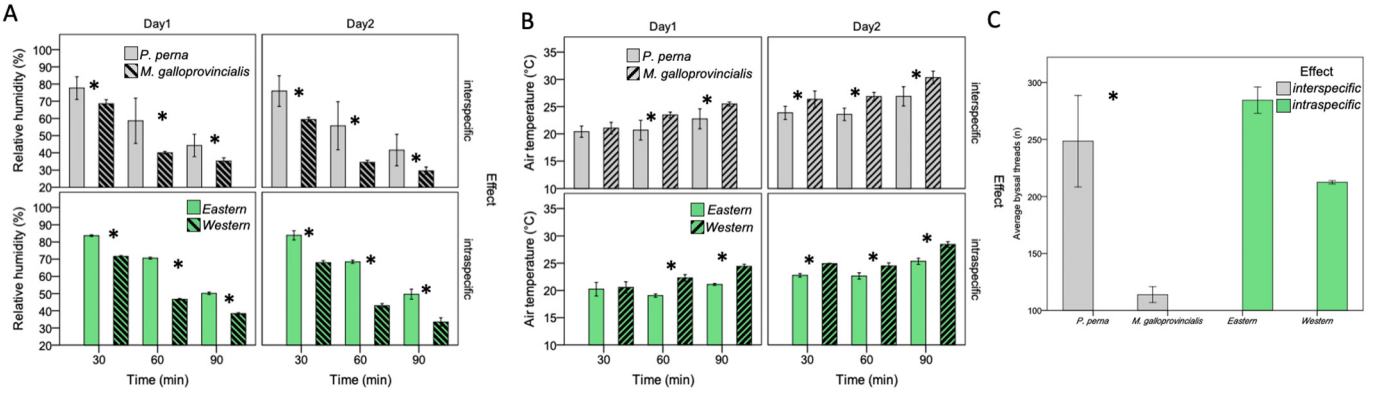

Fig. 2. Bar-plots between species (Contrast 1) and between lineages (Contrast 2) for (a) mean relative humidity (±SD) day 1, (b) mean humidity (±SD) day 2, (c) mean temperature (±SD) day 1, (d) mean temperature (±SD) day 2 and mean number of byssal threads (±SD). Asterisk denotes significant effects ($p < 0.05$).

Table 1
Mean and 95% Confidence Intervals (CI) of effect sizes (g_{Hedges}) of each variable for interspecific and intraspecific variation. Asterisk indicates approaches where the relevant 95% CI of effect size does not overlap with zero. Descriptors for magnitudes are based on Cohen (Cohen, 1992) and expanded by Sawilowsky (Sawilowsky, 2009).

Variable	Interspecific variation		Intrarspecific variation	
	g_{Hedges} (lower CI – upper CI)	Descriptor	g_{Hedges} (lower CI – upper CI)	Descriptor
Relative humidity - day 1–30 min	2.256 (0.518–3.984)*	Huge	25.3 (10.896–39.705)*	Huge
Relative humidity - day 2–30 min	2.187 (0.472–3.902)*	Huge	7.584 (3.004–12.163)*	Huge
Relative humidity - day 1–60 min	1.672 (0.086–3.259)*	Ver large	47.233 (20.461–74.006)*	Huge
Relative humidity - day 2–60 min	1.798 (0.182–3.414)*	Very large	24.011 (10.332–37.69)*	Huge
Relative humidity - day 1–90 min	1.614 (0.04–3.187)*	Very large	18.332 (7.837–28.827)*	Huge
Relative humidity - day 2–90 min	1.535 (−0.022–3.091)	Very large	6.01 (2.252–9.769)*	Huge
Air temperature - day 1–30 min	1.903 (0.262–3.544)*	Very large	9.382 (3.838–14.926)*	Huge
Air temperature - day 2–30 min	0.637 (−0.78–2.054)	Medium	0.633 (−1.007–2.273)	Medium
Air temperature - day 1–60 min	3.141 (1.134–5.147)*	Huge	3.232 (0.8002–5.663)*	Huge
Air temperature - day 2–60 min	1.78 (0.168–3.392)*	Very large	2.082 (0.095–4.069)*	Huge
Air temperature - day 1–90 min	4.178 (1.802–6.554)*	Huge	5.676 (2.088–9.264)*	Huge
Air temperature - day 2–90 min	1.743 (0.14–3.346)*	Very large	2.058 (0.079–4.037)*	Huge
Average number of byssal threads	2.202 (0.483–3.921)*	Huge	8.666 (3.508–13.823)*	Huge

Orthogonal contrast analyses indicated that Shannon-Wiener diversity (H′) was lower in mussel beds composed of *P. perna* than those composed of *M. galloprovincialis* (Contrast 1: $t(9) = -2.805$, $p = 0.021$; Fig. 3), whereas species evenness and richness did not differ between the two mussel species (contrast 1: $t(9) = 0.773$, $p = 0.459$ and $t(9) = -2.01$, $p = 0.075$ for evenness and richness respectively).

Pielou's evenness J′ was significantly higher in *P. perna* eastern beds than those composed of *P. perna* western individuals (Contrast 2: $t(9) = 4.285$, $p = 0.002$) while Margalef richness (d) and H′ were not significantly different between lineages (Contrast 2: $t(9) = 0.882$, $p = 0.401$ and $t(9) = 1.971$, $p = 0.08$ for richness and diversity respectively Fig. 3)*.

Effect sizes revealed that the influence of interspecific variation on H′ was very large while that of intraspecific variation on J′ was huge (Table 2).

Infaunal abundance and biomass did not differ between species (PERMANOVA; Figs. 4a and 5a; Tables S2 and S3). nMDS plots and hierarchical clustering analyses mirrored the PERMANOVA results and did not detect any clear group separation by species. In addition, a SIMPROF test identified two different communities (Figs. 4b, 5b; $p < 0.05$), one of which comprised some *P. perna* samples and all *M. galloprovincialis samples*.

Infaunal abundance and biomass clearly differed between lineages (Figs. 4c and 5c; Tables S4 and S5). However, a significant difference was found in multivariate dispersion when testing infaunal biomass (Figs. 4c and 5c; $F_{2,9} = 17.18$; $p = 0.026$). Nevertheless, an nMDS plot showed clear grouping by lineage, indicating that the significant effect of the term is, at least partially, a result of differences among centroids and not only due to a difference in the spread of data between groups. This was confirmed by the cluster analyses, together with the SIMPROF test (Figs. 4d and 5d; $p < 0.05$), where assemblages were grouped by lineage, i.e. an intraspecific effect.

SIMPER analyses showed that the number of species that were collectively responsible for 50% of total dissimilarity between lineages was higher for abundance than for biomass (Fig. 6). In terms of abundance, recruits of *P. perna* contributed the most to the dissimilarity between the eastern and western lineages of *P. perna*, while the whelk *Burnupena lagenaria* displayed the highest contributions to the difference observed in biomass between lineages.

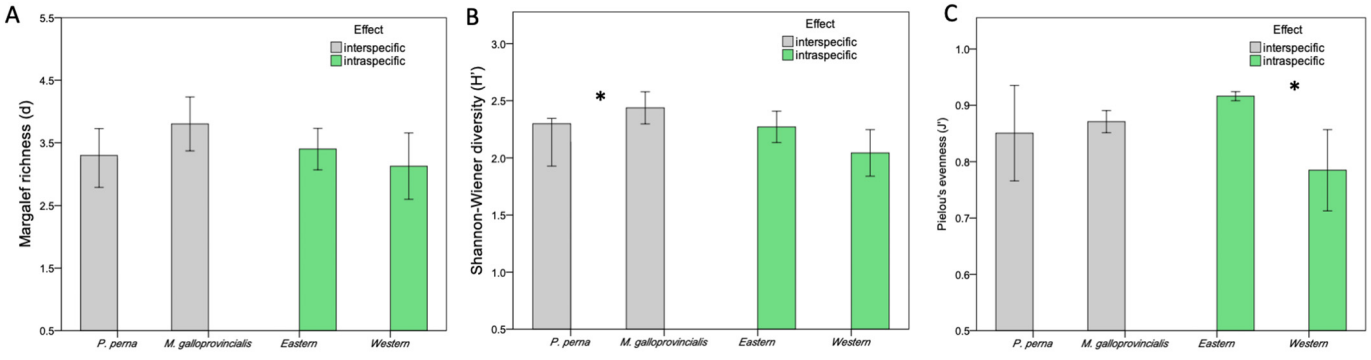

Fig. 3. Bar-plots for (a) mean species richness (±SD), (b) mean Shannon diversity (±SD) and (c) mean evenness (±SD) between species (Contrast 1) and between lineages (Contrast 2). Asterisk denotes significant effects ($p < 0.05$).

Table 2
Mean and 95% Confidence Intervals (CI) of effect sizes (g_{Hedges}) of each diversity variable for interspecific and intraspecific variation. Asterisk indicate approaches where the relevant 95% CI of effect size does not overlap with zero. Descriptors for magnitudes are based on Cohen (Cohen, 1992) and expanded by Sawilowsky (Sawilowsky, 2009).

Variable	Interspecific variation		Intrarspecific variation	
	g_{Hedges} (lower CI – upper CI)	Descriptor	g_{Hedges} (lower CI – upper CI)	Descriptor
Margalef richness (d)	1.245 (−0.055–2.544)	Very large	0.618 (−0.8–2.037)	Medium
Shannon-Wiener diversity (H′)	1.513 (0.169–2.857)*	Very large	1.31 (−0.217–2.838)	Very large
Pielou's evenness (J′)	0.286 (−0.92–1.492)	Small	2.565 (0.694–4.436)*	Huge

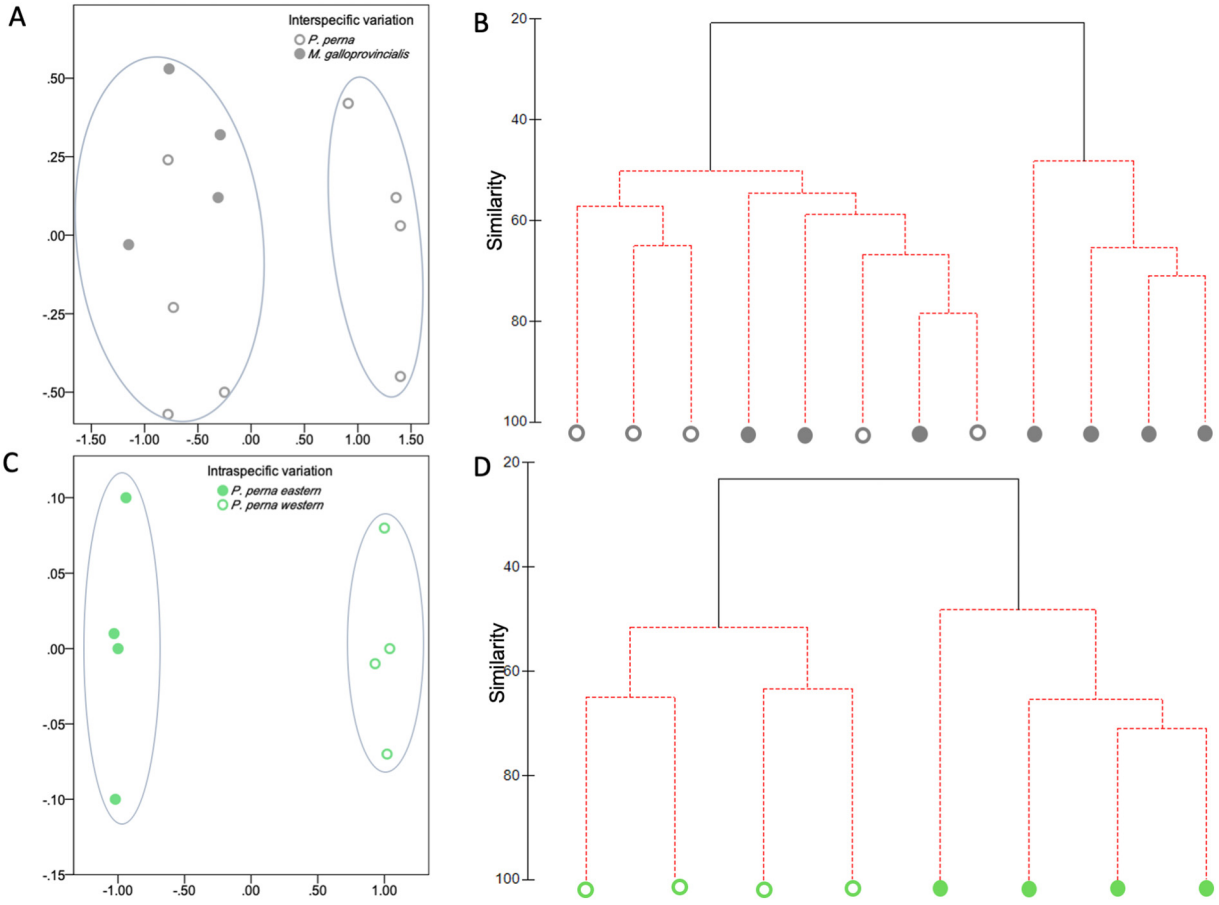

Fig. 4. The similarity in species abundance of infaunal assemblages for the effect of interspecific variation (a; b) and the effect of intraspecific variation (c; d). Non-metric multidimensional scaling (nMDS) plots (a; c) and dendrogram of the complete linkage cluster analysis (b; d). Solid branches of the dendrogram indicate significant faunal groups in which the SIMPROF test ($p < 0.05$) suggested the structure is not random. The results of clusters detected by SIMPROF test are imposed as solid lines in the nMDS plots.

4. Discussion

We found that, in terms of the effects of these mussels as bioengineers, there were greater differences between different lineages of the same species than between different species. Specifically, the effect size for habitat structural complexity, defined as the number of byssal threads produced by individual mussels within the bed, was four times greater between *P. perna* lineages than between species. For microclimate air temperature, described as air temperature of the mussel bed during emersion, effect sizes were on average (across all days and temperatures) 1.7 higher for intraspecific differences than for those between species. Similarly the average effect size for microclimate relative humidity, was more than eleven times higher between *P. perna* lineages than between the two species.

We show that the most benign beds are those composed of eastern lineage *P. perna* individuals, which are known to have a higher byssal thread production and more pronounced gaping behaviour than the other two classes of mussels, leading to amelioration of abiotic conditions at the aggregation level and increased mussel resistance to thermal stress (Nicastro et al., 2012). Bed microclimate was less favourable in beds of western lineage *P. perna* which had fewer byssal threads and exhibits more limited gaping (Zardi et al., 2015a) and still less favourable in beds of *M. galloprovincialis*, which does not gape and has the fewest byssal threads (Nicastro et al., 2012; Nicastro et al., 2010b). We predicted that such distinct differences in habitat engineering abilities could lead to second-order effects on the associated fauna. Our manipulative experiment revealed that infaunal abundance and biomass differed between the two lineages (Contrast 1; intraspecific variation) while it remained similar between the two species when *P. perna* lineages were aggregated (Contrast 2; interspecific variation).

In the face of the appreciation of key ecological effects of variation below the species level (Bolnick et al., 2011; Mimura et al., 2017; Monteiro et al., 2017; Saada et al., 2016; Weber et al., 2017; Zardi et al., 2015b), the relative contributions of intraspecific versus species effects are not well resolved. It is generally expected that for direct ecological responses (sensu Strauss, 1991 through consumption for example; Wootton, 1994), variation in effects will be consistently larger among species than within species while, for indirect ecological responses (mediated by another organism, for example), inter- and intraspecific effects are comparable (Des Roches et al., 2018 and references therein). Contrary to these expectations, our results show that inter-lineage phenotypic differentiation has stronger direct effects on associated community than those of interspecific differences with the effect size for evenness being nine times greater for differences between *P. perna* lineages than for those between species. An exception concerned heterogeneity the Shannon-Wiener diversity index for infaunal assemblages showed a stronger among- than within-species effect. This probably reflects the weaker engineering abilities of *M. galloprovincialis* (no gaping and low byssal thread production) leading to relatively weak moderation of the mussel bed microclimate. Richness and evenness are linked to different roles in community functioning and the relationship between the two remains a controversial issue in ecology from both theoretical and empirical perspectives (e.g., Jost, 2010; Soininen et al., 2012; Zhang et al., 2012). More importantly, evenness usually responds more rapidly to environmental stressors than species richness and affects ecosystem function before

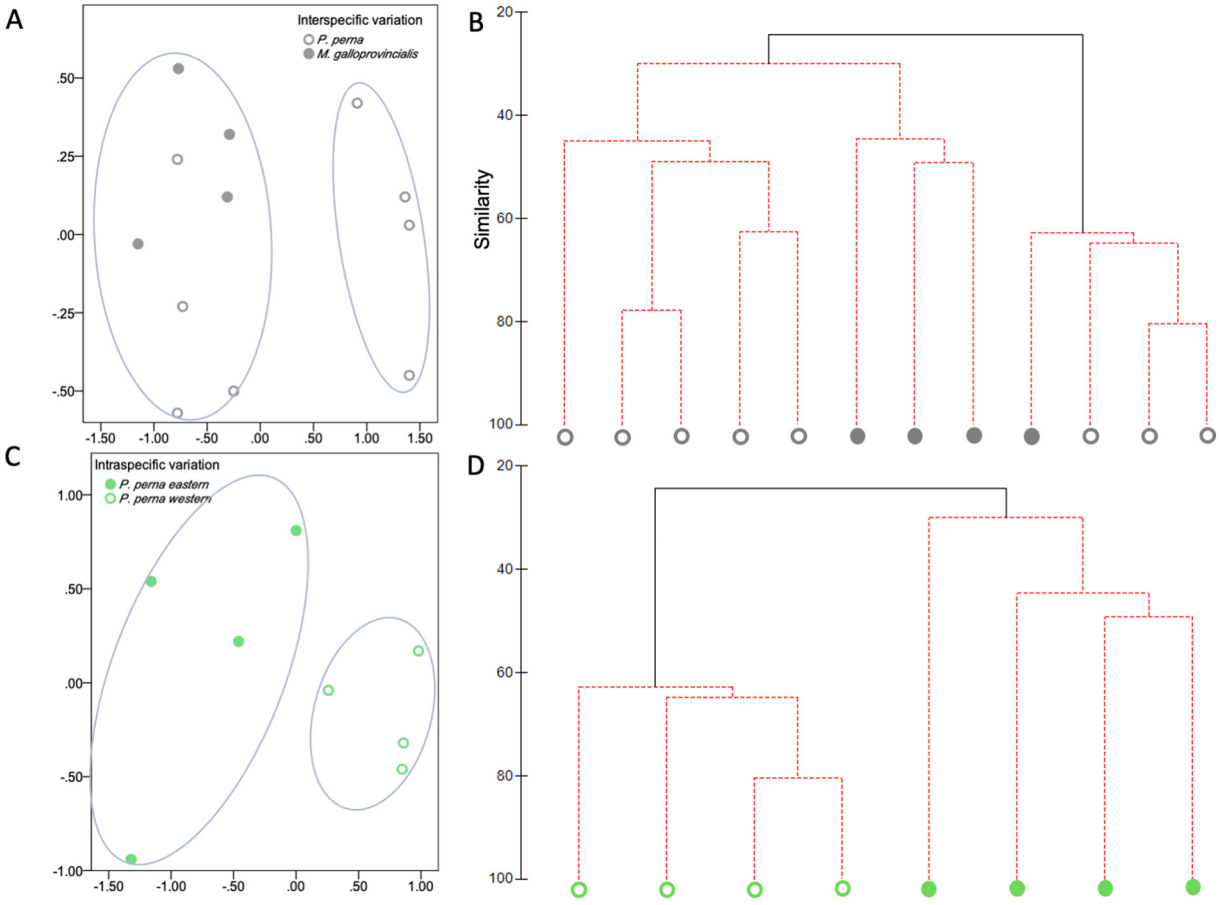

Fig. 5. The similarity in species biomass of infaunal assemblages for the effect of interspecific variation (a; b) and the effect of intraspecific variation (c; d). Non-metric multidimensional scaling (nMDS) plots (a; c) and dendrogram of the complete linkage cluster analysis (b; d). Solid branches of the dendrogram indicate significant faunal groups in which the SIMPROF test ($p < 0.05$) suggested the structure is not random. The results of clusters detected by SIMPROF test are imposed as solid lines in the nMDS plots.

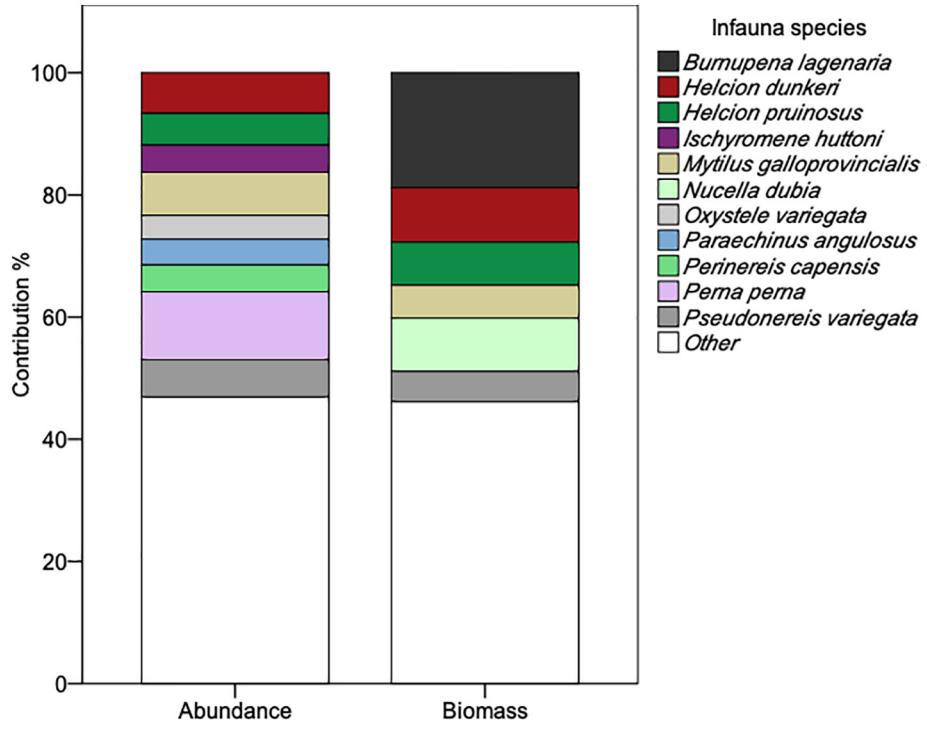

Fig. 6. SIMPER – average contributions to infaunal dissimilarity (%) for (a) abundance and (b) biomass for the effect of intraspecific variation. Cut-off for low contributions: 50% of cumulative percentage, i.e. other.

species are actually driven to extinction (Chapin et al., 2000; Rao and Larsen, 2010). Therefore, high evenness maximizes the average species survival probability in the face of demographic stochasticity (Dineen et al., 2015; Rohr et al., 2016). Critically, it has been shown that evenness is lowest in highly stressful habitats because only a minority of the species present are able to perform well, the remaining species being scarce (Scrosati and Heaven, 2007). As stress declines, more species increase in abundance, raising evenness. Experimental manipulations such as those in our study performed across a wider range of wave and thermal conditions would clarify the effects of environmental pressure on the bioengineering capabilities of intertidal mussels and the relative roles of intra- and interspecific diversity in shaping aspects of evenness and diversity.

Phenotypic variation in invasive species can affect both the adaptive potential of the species and its ecological effects on the recipient native ecosystems (Evangelista et al., 2019). This is likely to be important in our case where the recent invasion by *M. galloprovincialis* has dramatically reshaped the intertidal landscape (McQuaid et al., 2015). Our results indicate that the ability of the invasive blue mussel to moderate microclimate conditions within mussel beds and consequently influence infaunal assemblages is comparable to that of the native coexisting native *P. perna* western lineage. It is likely, however, that the ways in which the engineering functions of invasive *M. galloprovincialis* influence its associated infauna differ between native and invaded areas or even between distinct South African bioregions. Cole and McQuaid (2010) examined the habitat structure offered by *M. galloprovincialis* and *P. perna* across 3000 km and three bioregions on the South African coast. They found that the environmental conditions characterising each bioregion influenced the structure of mussel beds (the density and size of mussels) and, consequently, that of associated assemblages. Thus, the effects of ecological engineers will stem from the interaction between the ways in which they moderate environmental conditions and the broader context within which they occur. This implies that the effects of ecological engineering by *M. galloprovincialis* will differ between its native region and others that it has invaded. Moreover, on the western coast of South Africa, where *P. perna* is absent because of cold upwelled waters, *M. galloprovincialis* has become the dominant intertidal mussel, replacing the indigenous *Aulacomya ater* and *Choromytilus meridionalis*. In doing so it has massively increased the overall cover and biomass of mussels on the shore, with consequences extending to the top of the food chain (e.g., Loewenthal et al., 2015). It is, therefore, likely that along these shores the invasive blue mussel has had a larger effect on the nature of species assemblages directly depending on mussel aggregations compared to other regions where it coexists with the native *P. perna*, such as North Africa (Lourenço et al., 2017; Lourenço et al., 2020). Experimental manipulations of mussel beds under a wide range of environmental conditions are necessary to clarify how the relative bioengineering roles of coexisting dominant species vary in different regions.

4.1. Conclusion

Understanding how ecosystems are likely to respond to large scale environmental change and how ecosystem functions and services may be buffered against environmental change and loss of biodiversity requires a grasp of the variability in functional response, particularly of foundation species such as trees, corals, kelps or mussels. Contemporary climate change is profoundly affecting within-species diversity, exposing species to the potential loss of unique pools of genetic diversity and impoverishment of the adaptive potential of the species as a whole (Alsos et al., 2012; Jordan et al., 2016; Lourenço et al., 2016; Nicastro et al., 2013). Our results suggest that such rapid changes to unique portions of the species' genetic pool are likely to alter communities and the functioning of ecosystems to an unexpected degree.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2020.140723.

CRediT authorship contribution statement

Katy R. Nicastro: Conceptualization, Formal analysis, Writing - original draft. **Christopher D. McQuaid:** Methodology, Writing - original draft. **Alexia Dievart:** Investigation, Writing - review & editing. **Gerardo I. Zardi:** Conceptualization, Methodology, Investigation, Writing - original draft.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

This work is based upon research supported by the National Research Foundation of South Africa (grant number: 64801) and by Fundação para a Ciência e Tecnologia (FCT-MEC, Portugal, grant numbers: UID/Multi/04326/2019, IF/01413/2014/CP1217/CT0004). We thank three anonymous reviewers for their constructive comments.

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