

Competition between co-occurring invasive and native consumers switches between habitats

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Abstract

1. The introduction of a non-native species frequently has adverse direct effects on native species. The underlying mechanisms, however, often remain unclear, in particular where native and invasive species are taxonomically similar.
2. We found evidence of direct competitive interactions between a globally distributed invasive species (the Pacific oyster, *Magallana gigas*) and its native counterpart (the European oyster, *Ostrea edulis*). We also discovered that the competitive outcome differed between different habitat types and orientation by identifying context-dependent responses driven by environmental conditions and stress (i.e. intertidal compared to subtidal habitats; and vertical versus horizontal substratum). This is particularly important because the European oyster is threatened, or in decline, throughout most of its range, and restoration efforts are underway in many regions.
3. We combined experimental manipulations and stable isotope analysis (SIA) to identify the direct effects of competition and the mechanisms by which the invasive and native species compete. We identified negative effects of the invasive species on the native oyster, but these were limited to the subtidal habitat (lower stress environment) and determined by substratum orientation (habitat structure). Crucially, we found that effects of the invasive species on the native species were not always negative and under certain conditions (e.g. on vertical substrata) were positive. Shifts in isotopic niches of both species when co-occurring, alongside mixing models, indicate that exploitative competition for food is most likely to underpin niche partitioning between both species.
4. We have identified different foraging strategies under different contexts, and our findings highlight the importance of exploitative competition as a driving mechanism behind the co-occurrence of two seemingly functionally similar consumers.

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The combination of experimental manipulations with SIA is a powerful tool, and we illustrate how this approach should be incorporated, into multiple environmental contexts at appropriate scales, to more accurately predict impacts of the spread of invasive species on native communities.

KEYWORDS

competition, ecological niche, invasive species, orientation, oysters, stable isotope analysis, temperate reefs

1 | INTRODUCTION

The accelerating spread of invasive species has a global impact on biodiversity and ecosystem functioning, which has a considerable economic cost to society (Pimentel, Zuniga, & Morrison, 2005; Vitousek, 1990). Moreover, endangered species may be further threatened by non-native species acting as predators or competitors (Katsanevakis et al., 2014; Wilcove, Rothstein, Dubow, Phillips, & Losos, 1998). Invasion success is predicted to be greater where invaders present novel functional traits, which enables them to exploit marginal or vacant niches and limits interaction potential between native and invasive species (Escoriza & Ruhí, 2016). In contrast, invasion success where host communities include seemingly functionally similar native species can be attributed to just one or two superior traits of the invader, such as greater growth rates or a faster assimilation of nutrients (Krasso, Brown, Bishop, Kelaher, & Summerhayes, 2008). Differing abiotic conditions may enhance or compromise these traits (Krasso et al., 2008; Ruesink, 2007). Environmental context, thus, plays a major role in shaping communities and species interactions and is often neglected when impacts of invaders are quantified (Bruno, Stachowicz, & Bertness, 2003; Papacostas et al., 2017; Vye, Emmerson, Arenas, Dick, & O'Connor, 2015).

Competition between species with overlapping ecological niches is generally driven by resource limitation, such as food, space or shelter (Connell, 1983; Ferguson, White, & Marshall, 2013; Pianka, 1981). Competition for shared resources or interference between species increases with functional similarity and can lead to a displacement of the native species and a possible loss of associated functional traits (Dick et al., 2017; Didham, Tylanakis, Hutchison, Ewers, & Gemmel, 2005; Elton, 1958; Wardle, Bardgett, & Callaway, 2011). Superior competitors access limited resources more efficiently and can thus directly reduce the fitness of inferior competitors (Elton, 1958; Pianka, 1981). The introduction of a competitively superior non-native species could, therefore, lead to a loss of native species. This may result in a loss of diversity and shifts in assemblage structure and further endanger the recovery or conservation of already threatened species (Britton, Ruiz-Navarro, Verreycken, & Amat-Trigo, 2018; Gurevitch & Padilla, 2004; Molnar, Gamboa, Revenga, & Spalding, 2008).

In terrestrial systems, native competitors have been shown to curb the spread of ecologically closely related invasive species (Levine, Adler, & Yelenik, 2004), but competitive interactions in aquatic systems appear to be weaker and less likely to limit invasion

success (Bando, 2006; Papacostas et al., 2017). Abiotic stressors, such as desiccation or shear stress, can enhance the negative impact of invasions when occurring at unprecedented rates or magnitude (Macdougall & Turkington, 2005). However, competitive interactions can also be mitigated by abiotic stress, which enables resource partitioning that may result in the coexistence of species with similar ecological niches (Carbonell et al., 2017; Krasso et al., 2008). Biological interactions are further modified by habitat heterogeneity, which determines the strength of competitive effects based on the ecological niche requirement of invasive and native competitors (Bando, 2006; Bulleri, Bruno, Silliman, & Stachowicz, 2016). It is currently unclear how abiotic stress affects the impacts of invasive species, where native communities include morphologically similar species, or how such interactions may differ between benign and harsh environmental conditions.

Originating from Japan, the Pacific oyster, *Magallana gigas* (formerly *Crassostrea gigas*), is an extremely versatile invader that has established global and extensive wild populations in predominantly intertidal habitats following its direct introduction for aquaculture purposes (Kochmann, O'Beirn, Yearsley, & Crowe, 2013). In contrast, populations of the previously dominant native European flat oyster, *Ostrea edulis*, have declined dramatically in recent decades owing primarily to overfishing and habitat destruction and remaining populations are found mainly in subtidal areas (Riesen & Reise, 1982; Thurstan, Hawkins, Raby, & Roberts, 2013). Although the decimated state of most *O. edulis* populations coincided with the introduction and spread of *M. gigas*, a perceived difference in their preferred habitats allayed initial concerns about negative effects of the introduced species on the recovery of native populations. Recent studies in Europe show, however, that both species now co-occur, albeit often at low densities, in intertidal and shallow subtidal zones where they may fulfil similar functions in the ecosystem and could compete for shared resources; thus, there is potential for direct competition (Tully & Clarke, 2012; Zwerschke et al., 2017; Zwerschke, Emmerson, Roberts, & O'Connor, 2016; Zwerschke, Hollyman, et al., 2018). While in Australia, *M. gigas* has already been shown to limit the distribution of the morphologically similar native Sydney rock oyster, *Saccostrea glomerata*, to high intertidal areas of the shore where *M. gigas* is present (Bishop et al., 2010; Krasso et al., 2008). More recently, it has been suggested that trophic niches of *O. edulis* and *M. gigas* may overlap (Green et al., 2017; Nielsen, Hansen, & Vismann, 2017; N. Zwerschke, D.

Roberts, N. E. O'Connor, unpublished data) and it is expected that the invasive oyster will be the superior competitor for resources based on their demonstrated faster growth rates, younger age of maturity and high fecundity (Diederich, 2006; Eagling et al., 2017; Troost, 2010). It is not known, however, what the consequences of potential direct competition between the two suspension feeders would be for the native oyster (*O. edulis*). We designed an experiment to test directly for evidence of competition between these species by manipulating their presence in high- (intertidal) and low-stress (subtidal) environments where their distributions currently overlap. Intertidal habitats are generally subject to a greater variety of abiotic stress, such as temperature, desiccation and wave stress, limiting feeding time and increasing physiological pressure on the organisms compared to more stable conditions in subtidal habitats (McAfee, O'Connor, & Bishop, 2017). Following recent surveys that identified their overlapping distributions in these habitats (Zwerschke et al., 2017), we tested for effects of the presence of *M. gigas* on *O. edulis* (survival, growth and biomass) in intertidal (where *M. gigas* is expected to be superior based on their observed greater abundance) and subtidal (where *O. edulis* is expected to be superior based on their observed greater abundance) habitats and on vertical and horizontal substratum (representing their typical form on natural and artificial structures). Furthermore, to identify the mechanisms driving potential effects, we also compared isotopic niches of both species in monocultures with their performance where they co-occurred. For example, shifts in their isotopic niches when co-occurring would suggest exploitative competition for food which could underpin niche partitioning. Many studies have examined the impacts of invasive species, this study tests whether

the functional ecology of co-occurring species determines their interactions and whether this varies under different environmental conditions, which are analogous to high- (intertidal) and low-stress (subtidal) environments.

2 | MATERIALS AND METHODS

An experiment was conducted at Ballyhenry Bay, Strangford Lough, Northern Ireland (54°23'21.5"N 5°33'51.7"W), on a rocky intertidal shore (high abiotic stress) and the adjacent subtidal habitat at 12 m depth (low abiotic stress). During the experiment, temperature experienced by the oysters ranged from -1°C to 34.5°C (mean \pm SD = 11.5 \pm 3.6°C; HOBO® Pendant® temperature loggers [Onset Computer Corporation, Bourne, USA]) in intertidal habitats and from 6.5 to 15.1°C (11.0 \pm 2.5°C) in the subtidal habitat.

The experiment tested for effects of competition between *M. gigas* and *O. edulis* and whether this varied under different environmental contexts. It is well known that the importance of competition structuring communities varies with different levels of abiotic and biotic stress (e.g. Menge & Sutherland, 1987; Bertness & Callaway, 1994), yet this is rarely tested in invasive species studies (Ruesink, 2007). There were three factors in the experimental design: (a) experimental treatments of oyster composition (three levels: monocultures of *M. gigas*, monocultures of *O. edulis* and mixtures of both species); (b) habitat types (two levels: intertidal and subtidal); and (c) orientation of substratum (two levels: horizontal and vertical; Figure 1). Oyster density was constant in all treatments based on a fully factorial substitutive design (Balvanera et al., 2006).

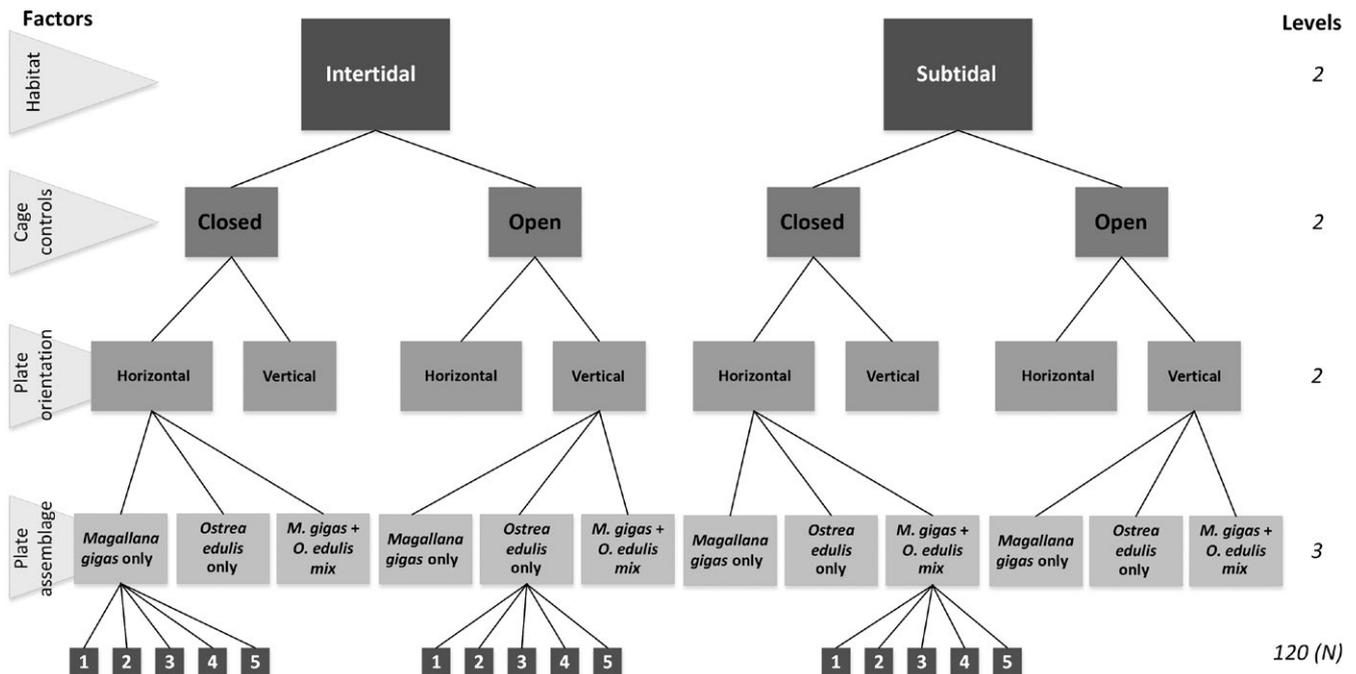


FIGURE 1 Experimental design comprised of four factors (habitat with two levels, substratum orientation with two levels, cage with two levels and experimental treatments with three levels). Each plate contained 10 oysters, thus, there were 120 experimental units and 1,200 manipulated oysters (see Supporting Information Figure S1 for illustration of experimental set-up)

To manipulate oyster presence in the field, individuals were attached to perspex plates (15 × 15 cm) with Milliput® (Dolgellau, UK) and Gorilla Super Glue® (Euxton, UK) and each plate held 10 oysters. Where both species were present, oysters were attached in an alternating pattern (five of each species). Juvenile *M. gigas* (mean length ± SD = 14.1 ± 0.2 mm) and *O. edulis* (15.1 ± 0.2 mm) were used in the experiment to incorporate scope for growth (Zwerschke et al., 2016). Oysters were sourced from local hatcheries to ensure consistent size and age. Triploid *M. gigas* were used to minimize the risk of increasing the wild spread of this non-native species (Allen & Downing, 1990).

Following the results of previous studies (Kochmann & Crowe, 2014), we restricted predator access to the manipulated oysters during the experiment by erecting plastic mesh cages (20 × 20 × 10 cm; mesh size: 0.5 cm) around each of the experimental plates. Pilot studies showed that juvenile oyster survival rates without protection from predators can be low; thus, we did not include plates without cages (Kochmann & Crowe, 2014). To help account for potential experimental artefacts resulting from the use of cages, a procedural cage control was included comprised of similar cages but with holes (10 × 5 cm) on three sides of the cages to allow benthic predators access (Miller & Gaylord, 2007; Figure 1, Supporting Information Figure S1).

In the mid-to-low intertidal habitat, 60 experimental plates (12 treatment combinations × 5 replicates) with 10 oysters attached to each were attached to randomly chosen boulders, either horizontally or vertically orientated as required for each treatment, and at least 1 m apart (Supporting Information Figure S1). For subtidal treatments, five customized galvanized steel frames were designed to each hold 12 experimental plates (placed 15–30 cm apart) on the seabed (see Supporting Information Figure S1 for more detail). Each frame contained a complete set of treatments (12 plates, 120 oysters) and was placed onto the seabed 10 m apart (Supporting Information Figure S1). All experimental treatments were replicated five times amounting to a total of 50 individual oysters per treatment and a total of 1,200 oysters. Experimental plates were situated at an approximately similar height on the shore or similar depth subtidally, and all experimental plates were assigned randomly to the three main experimental treatments (monocultures of *M. gigas*, monocultures of *O. edulis* and mixtures of both species); thus, any variation in background or environmental conditions is incorporated into the design (Supporting Information Figure S1). The experiment ran from August 2013 until September 2014.

Survival and growth rate of each oyster was quantified, by photographing each experimental plate with a Nikon D90 SLR camera, using a frame attached to the camera to ensure that each image was taken at a similar angle and distance (see Illustration of plain language abstract for subtidal and intertidal example, respectively). To test for evidence of competition between the oysters without disturbing the experimental set-up, the circumference of each oyster was estimated with ImageJ (following Loh & Pawlik, 2012, Schindelin, Rueden, Hiner, & Eliceiri, 2015). Oyster growth rate was estimated by comparing estimates at the start and end of the

experiment. Biomass of *O. edulis* and *M. gigas*, cleared of all epibionts, was quantified at the end of the experiment.

Putative oyster food resources, such as plankton and detritus from macroalgae, were sampled to estimate oyster isotopic niche and test for assimilation of different resources. Zooplankton were sampled using plankton nets (50 µm mesh size), based on three 30-min trawls (speed of 1 knot) per sampling event. Zooplankton were chosen both as a direct food source (oyster particle retention size ≈ 5–100 µm; Dupuy, Hassen, & LeGall, 1999) and to represent a temporally integrated measure of phytoplankton stable isotopes (Post, 2002; Vander & Rasmussen, 2001). Recent growth samples of macroalgae (*Fucus serratus*, *Fucus vesiculosus*, *Ascophyllum nodosum* and *Ulva* spp.) were taken fortnightly. Samples of brown algae (*F. serratus*, *F. vesiculosus*, *A. nodosum*) were pooled because they had similar isotopic values.

At the end of the experiment, all oysters were immediately frozen (−20°C) for later stable isotope analysis (SIA). In preparation for SIA, oysters were dissected and the digestive system was discarded from the tissue. Tissue and macroalgal samples were rinsed in deionized water, dried for 48 hr at 60°C and then ground to a fine powder. Samples were standardized to approx 1 mg for oyster tissue, and approximately 3 mg for macroalgae and plankton, into tin capsules (6 × 4 mm, Sercon Ltd) on a Mettler Toledo XS3DU Microbalance. Samples were analysed for C and N stable isotope ratios and elemental percentage concentration at Iso-Analytical, Crewe, UK, using an elemental analyser (Europe Scientific).

2.1 | Data analysis

Prior to analysis, data were tested for normality and homogeneity of variance (Zuur, Ieno, & Elphick, 2010). In the early stages of the experiment, a stark difference emerged between mortality rates in cages compared with the cage controls where very few oysters survived (Table 1; binomial glm: $F_{2,116} = 109.89$, $p < 0.001$). Therefore, all further analysis was carried out solely on data from experimental plates within closed cages to maximize ecological insight. We tested for differences between oyster composition (both monocultures and mixtures of both species), habitat type (intertidal and subtidal) and substratum orientation on oyster mortality. The factor “oyster species identity” (*O. edulis* or *M. gigas*) was added to specifically test for interspecific competitive effects on oyster mortality on plates with both oyster species. To test for difference in mortality rates, individual oyster presence/absence in all treatments was analysed using a generalized estimation equation (GEE) with a binomial distribution and a cloglog link to account for the high frequency of 1 s in the data. An exchangeable correlation structure allowed the nesting of individual plates as a random factor in treatments (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). The best model fit for the GEE models was chosen by randomly dropping interactions between factors from the model and comparing it to the original model using p -values of ANOVA (analysis of variance; Zuur et al., 2009). During the process of fitting the model, the factor “habitat type” was removed from the GEE term because its exclusion did not change the variance explained for this model.

TABLE 1 Mortality of oysters at horizontal and vertical orientation in (A) caged and (B) cage control treatments over the duration of the experiment (12 months): no. of dead oysters/no. of oysters initially deployed

	<i>Magallana gigas</i>		<i>Ostrea edulis</i>	
	Horizontal	Vertical	Horizontal	Vertical
(A) Caged				
Monoculture	49/100	69/100	73/100	26/100
Mixed culture	32/50	20/50	29/50	23/50
(B) Cage control				
Monoculture	100/100	100/100	100/100	97/100
Mixed culture	50/50	50/50	49/50	50/50

Growth rate and biomass were analysed separately for each oyster species to remove large heteroscedasticity between datasets using a random intercept linear mixed-effects model (LME; Zuur et al., 2009) with the factors “oyster experimental treatment,” “habitat type” and “orientation.” Experimental plates were included as a random factor into the model to account for ecological variability in the experimental set-up. Least-square means, where *p*-values were adjusted by the Tukey method, were applied as a *post hoc* test to the LME and GEE (Lenth & Herve, 2015).

Ontogenetic dietary shifts were tested separately for oyster species using ordinary least square (OLS) regression of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values against individual mass (Supporting Information Figure S2). There were significant relationships between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values and individual body mass for *O. edulis* in both habitat types (Supporting Information Figure S2). Therefore, this ontogenetic dietary shift was corrected for by using the residuals of these regressions for further analysis.

Isotopic niches of *M. gigas* and *O. edulis* were described by both mean niche position ($\delta^{15}\text{N}$ - $\delta^{13}\text{C}$ centroid) and variance. Differences in mean isotopic niche position between monocultures and mixed assemblages were based on the Euclidean distance between treatment $\delta^{15}\text{N}$ - $\delta^{13}\text{C}$ centroids. This was compared to a null distribution obtained by 9,999 random permutations under a reduced linear model (Turner, Collyer, & Krabbenhoft, 2010). Permutations used each observation (C-N pair) as a residual vector from the overall centroid and from each group centroid (Turner et al., 2010).

Isotopic variance, representing niche width, was estimated using the same permutational approach. Changes in variance between monocultures and the mixture were based on comparison of treatments' mean nearest neighbour distances (MNN) and mean distances to treatment centroid (MNC; Layman, Arrington, Montaña, & Post, 2007; Turner et al., 2010). We also estimated isotopic niche width from Bayesian ellipse (SEA.B) using the R package SIBER (Jackson, Inger, Parnell, & Bearhop, 2011) and compared differences in niche width between monocultures and mixed assemblages by estimating the proportion of overlap of Bayesian posterior distributions.

Where significant shifts of $\delta^{15}\text{N}$ - $\delta^{13}\text{C}$ centroids from monocultures to mixed assemblages were identified, the proportional contributions of putative resources to the diets of *O. edulis* and *M. gigas* were estimated, using SIAR Bayesian mixing models (Parnell, Inger, Bearhop, & Jackson, 2010). Fractionation values for *M. gigas* were used according to Dubois, Jean-Louis, Bertrand, and Lefebvre (2007) (mean \pm SD, $\delta^{13}\text{C} = 1.9 \pm 0.2$; $\delta^{15}\text{N} = 3.8 \pm 0.2$), for all resources, with zooplankton

entered in the model a second time but using fractionation values of zero to represent a temporally integrated measure of phytoplankton stable isotopes. Elemental concentration was variable among resources and was included in all SIAR models (Philips & Koch, 2002). Differences between resource contribution estimates, from monoculture diets to diets of the mixed oyster treatment, were estimated based on the proportional overlap between posterior estimates from these two models. All data analyses were carried out with R 3.1.2 (R Core Team, 2017).

3 | RESULTS

3.1 | Oyster mortality

There was a significant interactive effect among oyster species identity (*M. gigas* or *O. edulis*), experimental treatments of oyster composition and orientation on oyster mortality rate (residuals: 594, *df* = 3, Wald = 6.35, *p* < 0.012; Supporting Information Table S1). Mortality rates of both species did not differ between habitats, and *post hoc* tests show that the identified differences were owing to a greater mortality rate of *O. edulis* in horizontal than in vertical monocultures (Figure 2).

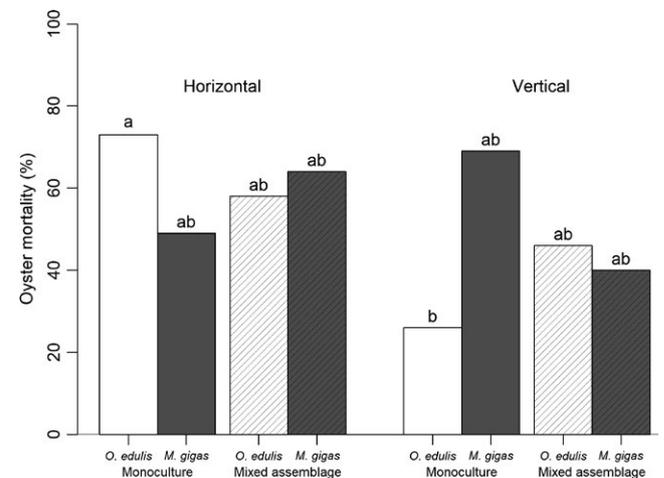


FIGURE 2 Percentage mortality of *Ostrea edulis* (white) and *Magallana gigas* (grey) in monocultures (open) and mixed assemblages (shaded) after 13 months at horizontal and vertical orientation to substratum. Data for subtidal and intertidal habitat were pooled following tests that showed their mortality rates were similar. Letters (a, b) denote groups of means that are statistically indistinguishable from each other (*p* > 0.05)

TABLE 2 Linear mixed-effects model (LMEM) testing for effects of oyster composition and substratum orientation on *Magallana gigas* and *Ostrea edulis* (A) growth and (B) biomass, in subtidal and intertidal habitats. Treatments were analysed separately between species and habitats to reduce heteroscedasticity and non-normality of data. Experimental plate was included as a random factor nested in experimental oyster treatment in the analysis. Significant results are in bold ($p < 0.05$)

	<i>O. edulis</i>				<i>M. gigas</i>			
	Subtidal		Intertidal		Subtidal		Intertidal	
	F	P	F	P	F	P	F	P
(A) Growth rate								
Intercept	238.20	<0.001	67.21	<0.001	103.14	<0.001	173.91	<0.001
Composition (C)	0.69	0.423	0.06	0.814	0.22	0.650	0.02	0.901
Orientation (O)	0.07	0.796	1.76	0.212	0.01	0.928	0.35	0.563
C*O	5.31	0.038	0.14	0.720	0.66	0.436	1.50	0.241
(B) Biomass								
Intercept	160.18	<0.001	65.55	<0.001	69.33	<0.001	169.74	<0.001
Composition (C)	0.97	0.346	0.08	0.789	0.01	0.932	0.16	0.696
Orientation (O)	2.01	0.184	0.97	0.347	0.06	0.814	0.56	0.468
C*O	1.27	0.283	0.06	0.819	0.07	0.806	10.45	0.006

3.2 | Growth rate

Subtidally, there was an interaction between experimental treatments (composition and orientation), indicating that here the effect of *M. gigas* on the growth rate of *O. edulis* differed between

horizontal and vertical substrata (Table 2A, Figure 3a). Results of *post hoc* tests were not conclusive, possibly owing to the opposing directions of significant effects (Quinn & Keough, 2002). The growth rate of *O. edulis* appears lower in the presence of *M. gigas* where oysters were horizontal but contrastingly was greater in the presence

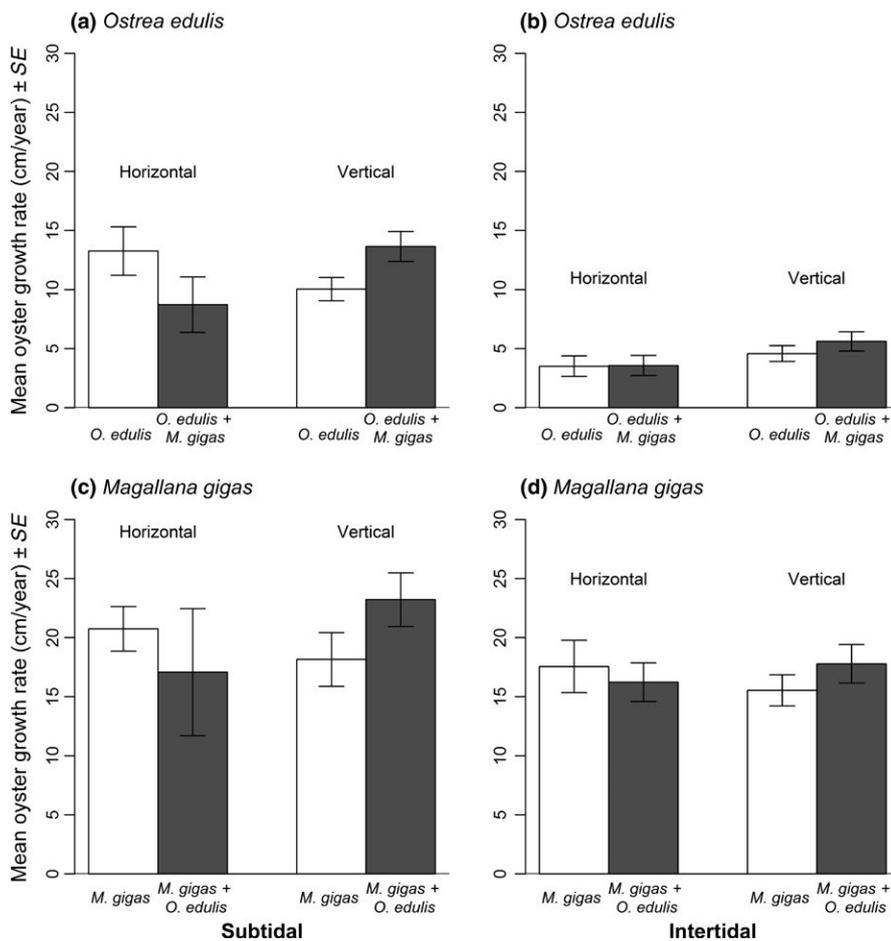


FIGURE 3 Mean growth rates (\pm S.E.) of *O. edulis* (a - b) and *M. gigas* (c - d) at horizontal and vertical orientation in single species assemblages (white) and mixed species assemblages (grey). Growth rates of oysters are shown based on means of subtidal (a, c) and intertidal (b, d) habitats consistent with the statistical model

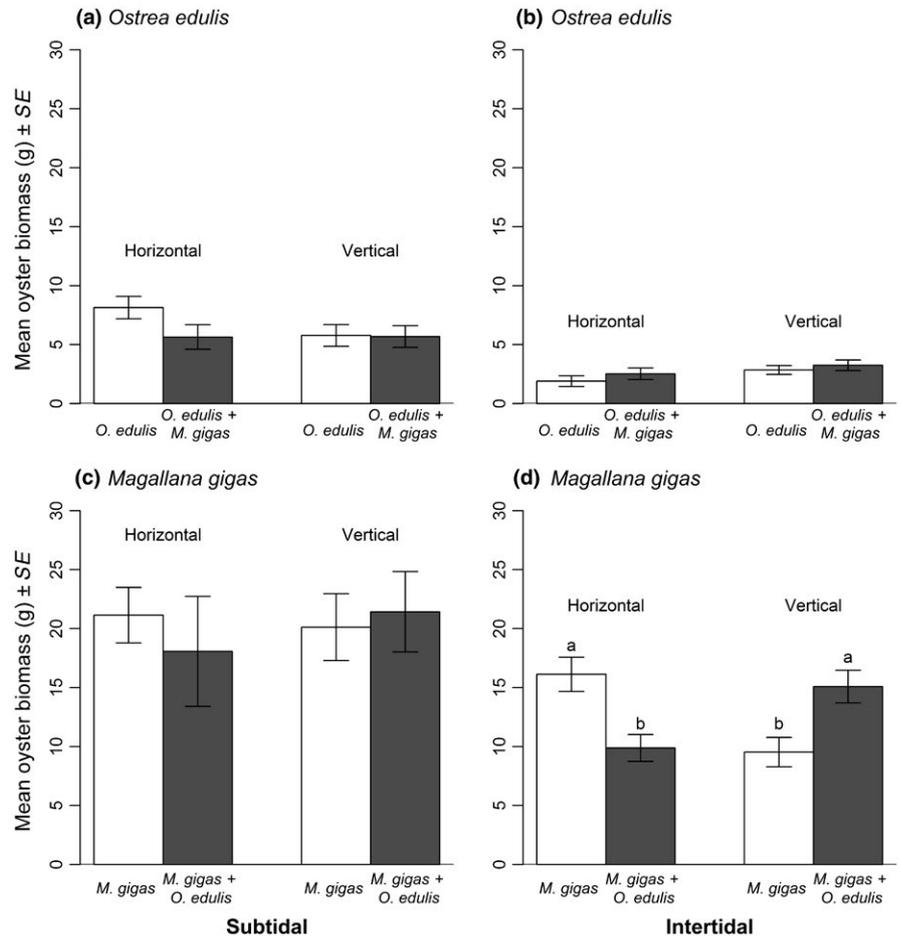


FIGURE 4 Mean biomass (\pm S. E.) for *O. edulis* (a - b) and *M. gigas* (c - d) at horizontal and vertical orientation in subtidal (a, c) and intertidal (b, d) habitats. Letters (a, b) denote groups of means that are statistically indistinguishable from each other ($p > 0.05$)

of *M. gigas*, where oysters were on vertical substrata (Figure 3a). Intertidally, there was no effect of *M. gigas* on the growth rate of *O. edulis* (Table 2A, Figure 3b). Additionally, there was no effect of *O. edulis* on the growth rate of *M. gigas* (Table 2A, Figure 3c,d).

3.3 | Biomass

There were no statistically significant effects of the presence of *M. gigas* on the biomass of *O. edulis* (Table 2B, Figure 4a,b). There was, however, an interaction between experimental treatments (composition and orientation), in intertidal habitat, on *M. gigas* biomass (Table 2B Figure 4d). *Post hoc* tests show clearly that on horizontal substrata the biomass of *M. gigas* was lower in the presence of *O. edulis* whereas where oysters were vertical the biomass of *M. gigas* was greater in the presence of *O. edulis* (Figure 4d).

3.4 | Isotopic niche position and width of *O. edulis* and *M. gigas* in monocultures

Mean isotopic niche position ($\delta^{15}\text{N}$ - $\delta^{13}\text{C}$ centroids) and isotopic niche widths (SEAc) were significantly different between *M. gigas* and *O. edulis* when in monocultures, in both intertidal (Euclidian distance = 1.23; $p < 0.0001$) and subtidal habitats (Euclidian distance = 1.40; $p < 0.0001$; Figure 5, Supporting Information Figure S3).

3.5 | Shifts in isotopic niche position for co-occurring oysters

Intertidally, *O. edulis* displayed a significant centroid shift towards ^{15}N depletion where both species were present compared to its monoculture but only when attached to horizontal substratum (Table 3, Figure 5a). *M. gigas* were relatively ^{13}C -enriched where it co-occurred with *O. edulis* compared to the monoculture but only in the vertical treatments (Table 3, Figure 5a-c). Subtidally, *O. edulis* did not shift its niche position significantly when in the presence of *M. gigas*. However, *M. gigas* co-occurring with *O. edulis* was relatively depleted in ^{15}N but only when on horizontal substratum and depleted in ^{13}C where it was vertical (Table 3, Figure 5c,d). It is possible that this shift in the horizontal treatment is because of a relatively smaller sampling size that resulted from greater mortality rates in this treatment (Supporting Information Table S2).

3.6 | Shifts in isotopic niche width for co-occurring oysters

All three measures of niche width (SEA_b, MNN nor MDC) increased significantly for *M. gigas* in subtidal horizontal mixed assemblages where the isotopic niches of *M. gigas* and *O. edulis* overlapped

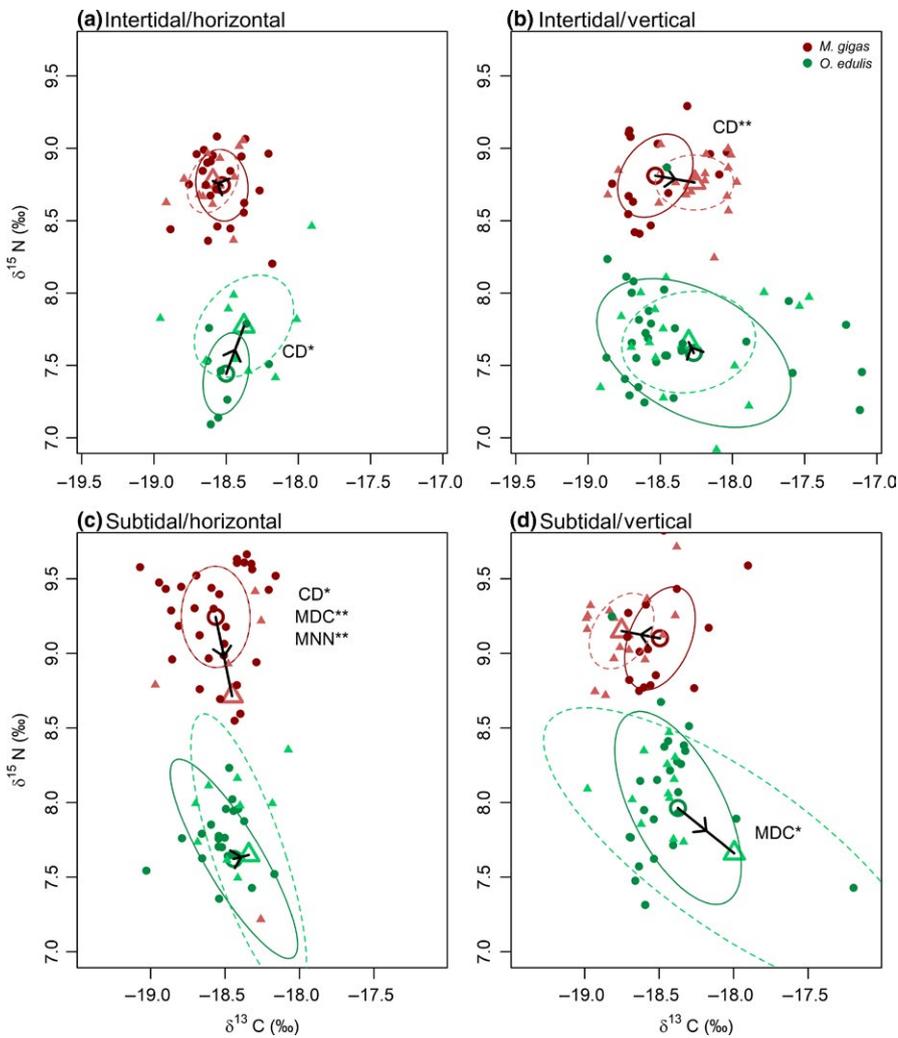


FIGURE 5 Direction (arrow), distance and significance (*) of changes in oyster $\delta^{15}\text{N}$ - $\delta^{13}\text{C}$ isotopic niche positions and widths from monocultures (circles) to mixtures of both species (triangles) for *M. gigas* (red) and *O. edulis* (green) in (a - b) intertidal and (c - d) subtidal habitats and at (a, c) horizontal and (b, d) vertical orientations. Centroids (open symbols), ellipses (SEAc) and raw data (filled symbols) for monocultures (solid line) and mixed assemblages (dashed line) are displayed. Significant differences between monoculture and mixed assemblages centroid distance (CD), mean nearest neighbour distance (MNN) and mean distance to centroid (MDC) are annotated by * ($p < 0.05$) and ** ($p < 0.01$)

TABLE 3 Isotopic niche responses to mixed assemblages of *Ostrea edulis* and *Magallana gigas* defined by isotopic niche position (mean distance between centroid; CD) and width, for each oyster species in two different habitats at horizontal (h) and vertical (v) orientations. Measures for isotopic niche width included mean distance to centroid (MDC), mean nearest neighbour (MNN), increase (+) or decrease (-) in SEA_B from monocultures to mixed assemblages and true probability of change. Results from Bayesian analysis (SEA_B) are represented as probabilities. Significant results for frequentists' P -values are represented in bold. Permutational analysis was carried out under a reduced model with 9,999 permutations

Oyster species	Habitat	Orientation	Niche position		Niche width					
			CD	P -value	MDC	P -value	MNN	P -value	$\text{SEA}_B \pm$	Probability
<i>O. edulis</i>	Intertidal	h	0.351	0.019	0.13	0.158	0.097	0.296	+	57.1
<i>O. edulis</i>	Intertidal	v	0.083	0.875	0.14	0.469	0.031	0.759	-	82
<i>O. edulis</i>	Subtidal	h	0.103	0.912	0.188	0.785	0.175	0.226	+	93.4
<i>O. edulis</i>	Subtidal	v	0.485	0.159	0.605	0.067	0.195	0.325	+	99.9
<i>M. gigas</i>	Intertidal	h	0.069	0.648	0.029	0.58	0.003	0.959	+	92.3
<i>M. gigas</i>	Intertidal	v	0.276	0.003	0.083	0.094	0.013	0.691	-	70.5
<i>M. gigas</i>	Subtidal	h	0.542	0.011	0.338	0.006	0.5	0.006	+	> 99.9
<i>M. gigas</i>	Subtidal	v	0.263	0.021	0.071	0.321	0.062	0.079	-	68.7

(Table 3, Figure 5c). SEA_B of *O. edulis* increased significantly in subtidal vertical mixtures of both species (Table 3, Figure 5c). In the intertidal, there was no difference in SEA_B , MNN or MDC for both oyster species.

3.7 | Direction of trophic niche shifts where both oyster species co-occur

Proportional shifts in individual dietary constituents between monocultures and mixed assemblages were small and not significant at

our alpha level (probability > 95%; max difference between modal proportions = 0.04), yet two cases had a probability of >80%. Since even small dietary changes can have large effects on long-term performance, we surmised that, compared to monocultures, *M. gigas* in the presence of *O. edulis* appeared to assimilate a more ^{13}C -enriched benthic diet (increase in brown or green macroalgae) in intertidal vertical habitats. In contrast, diets of *M. gigas* in mixtures in subtidal vertical habitats appeared to be composed of more pelagic elements (increase in zoo- or phytoplankton) than in a monoculture (Table 4).

4 | DISCUSSION

We show how abiotic stress levels (intertidal vs. subtidal habitats) can indicate interaction strengths between two competitors

while substratum topography (vertical vs. horizontal substratum) can determine whether interactions are competitive or facilitative. Interestingly, in this system overall oyster mortality rates were least affected by the presence of competitors and survival was largely driven by predation and differences between substratum topography, to which the native oyster was more susceptible to in monocultures. Lower abiotic stress in subtidal habitats strengthened the effect of *M. gigas* on *O. edulis*, which switched from competitive, on horizontal substratum, to facilitative, on vertical substratum. Trophic competition (e.g. exploitative competition) between the two species and a re-organization of trophic dynamics are most likely the mechanisms behind this effect of *M. gigas* on *O. edulis*. This was revealed by their changes in isotopic niche width and overlap (Britton et al., 2018; Bulleri et al., 2016; Jackson & Britton, 2014). High abiotic stress environments in the

TABLE 4 Overall and specific proportional dietary shifts where both oyster species co-occur compared to monocultures. Mixing models were only run for treatment combinations with a significant shift of $\delta^{15}\text{N}$ - $\delta^{13}\text{C}$ centroids (CD). Model outputs with 95% credible intervals are given before a summarized increase or decrease and probability. Overall trends towards a more benthic or pelagic diet are indicated by asterisks

Overall dietary change	More pelagic	<<<<	>>>>	More benthic
	Zooplankton	Phytoplankton	Brown Algae	Green Algae
<i>Ostrea edulis</i> intertidal horizontal				
Monoculture mode	0.02	0.83	0.03	0.04
95% CI	0–0.25	0.63–0.93	0–0.07	0–0.21
Mixed assemblages mode	0.01	0.83	0.05	0.03
95% CI	0–0.2	0.63–0.93	0–0.09	0–0.23
Increase (+)/decrease (-)	-	+	+	-
Probability of difference	0.58	0.51	0.65	0.47
<i>Magallana gigas</i> intertidal vertical				
Monoculture mode	0.01	0.89	0.05	0.02
95% CI	0–0.05	0.80–0.94	0.02–0.07	0–0.14
Mixed assemblages mode	0.01	0.87	0.07	0.02
95% CI	0–0.04	0.79–0.92	0.04–0.1	0–0.13
Increase (+)/decrease (-)	-	-	+*	+*
Probability of difference	0.56	0.68	0.91	0.53
<i>M. gigas</i> subtidal horizontal				
Monoculture mode	0.06	0.85	0.04	0.04
95% CI	0.01–0.11	0.79–0.91	0.01–0.06	0–0.11
Mixed assemblages mode	0.02	0.81	0.03	0.04
95% CI	0–0.26	0.51–0.94	0–0.9	0–0.32
Increase (+)/decrease (-)	-	-	-	+*
Probability of difference	0.46	0.81	0.45	0.73
<i>M. gigas</i> subtidal vertical				
Monoculture mode	0.02	0.86	0.05	0.05
95% CI	0–0.09	0.76–0.93	0.01–0.07	0–0.16
Mixed assemblages mode	0.04	0.87	0.02	0.03
95% CI	0–0.1	0.79–0.95	0–0.04	0–0.14
Increase (+)/decrease (-)	+*	+*	-	-
Probability of difference	0.57	0.66	0.87	0.56

intertidal zone altered the strength of species interactions compared to those identified in the more benign subtidal. Contrary to our expectations based on current abundance and distribution patterns of both species (Zwerschke et al., 2017), *O. edulis* seemed to be the superior competitor in intertidal habitats and *M. gigas* in the subtidal zone. Intertidal presence of *O. edulis* seemed to affect biomass accumulation of *M. gigas*. The direction of the effect of *O. edulis* on *M. gigas*, however, was still dictated by habitat structure, with an adverse effect on *M. gigas* biomass on horizontal substratum and a facilitative effect on vertical substratum. Here, shifts in isotopic niches do not reveal a clear pattern, which would imply that *O. edulis* utilizes different mechanisms than *M. gigas* when domineering in competition.

Abiotic stress may have affected the strength of the competitive interactions. Negative competitive effects are generally associated with a decrease in trophic level (Jackson et al., 2012; Vander Zanden, Casselman, & Rasmussen, 1999). At high abiotic stress in intertidal horizontal habitats, however, the trophic niche of *O. edulis* became more $\delta^{15}\text{N}$ enriched in the presence of *M. gigas*, which may indicate an increase in trophic level, while *M. gigas'* trophic niche remained stable. Contrary to the theory that niche partitioning facilitates coexistence of competitors at higher abiotic stress levels (Bulleri et al., 2016; Carbonell et al., 2017), changes in trophic niches in this context were not indicative of trophic re-organization nor of individual niche specialization (Britton et al., 2018; Costa-Pereira & Rudolf, 2018). Therefore, it is unlikely that exploitative competition was a driving factor in intertidal habitats. Additionally, both growth rate and biomass of *O. edulis* remained unaffected by the presence of *M. gigas*, which suggests a low competitive effect on the native oyster and a loss of the competitive superiority of *M. gigas* (Jackson et al., 2012; Vander Zanden et al., 1999). Interestingly, it is under the same environmental context that the biomass of *M. gigas* declines in the presence of *O. edulis*. Theory predicts that interference competition is costly on both sides, in which case it is unlikely that *O. edulis* acted as a superior interference competitor during this study, since decreased biomass of *M. gigas* was not coupled with declining performance measures of *O. edulis* (Amarasekare, 2002; Vance, 1984). However, other studies have shown that intraspecific facilitation increases in importance at high abiotic stress (Okamura, 1988; Svanfeldt, Monro, & Marshall, 2017). Greater densities of filter feeding bryozoans in high-flow environments, for example, are more efficient in locally slowing down water flow and increasing feeding efficiency than those at lower densities (Svanfeldt et al., 2017). Thus, it is possible that in high abiotic stress environments, the presence of the slightly smoother shell structure of *O. edulis* reduces *M. gigas'* intraspecific environmental amelioration capacity, such as water retention and stabilizing of temperatures (McAfee et al., 2017; Padilla, 2010). In contrast, at low abiotic stress levels in subtidal horizontal habitats *O. edulis* growth rate declined when its trophic niche overlapped with *M. gigas*. Here, *M. gigas* represents traits of a superior exploitative competitor (Vance, 1984).

Surface topography seems to consistently modify the direction of the identified species interactions. Generally, we found that negative effects of the competitively superior species (*O. edulis* in intertidal and *M. gigas* in subtidal habitats), manifested themselves at horizontal orientations, yet effects reversed to facilitative in vertical orientations. More importantly, this pattern seems unrelated to the competitive mechanism (i.e. interference and exploitation), which suggests surface topography is the primary driver underpinning the outcome of inter-specific competition. Differences in surface topography can enhance or reduce environmental stress, thereby generating different ecological niches (MacArthur, 1970; Petren, 2001). In the context of this study, horizontal substratum is more readily available for settlement of organisms, but bears a greater risk of sedimentation, predation and wave stress (Grabowski, 2004; Soniat, Finelli, & Ruiz, 2004). In contrast, vertical substratum is not only more scarce in shallow subtidal habitats but often also experiences low water flow which reduces plankton availability (Lenihan, Micheli, Shelton, & Peterson, 1999; Soniat et al., 2004). Differing species responses to these two orientations in monocultures and mixtures suggests a dependence of species interaction type (e.g. inter- or intraspecific) on substratum topography. It seems that orientation of substratum can modulate species exclusion by competition (intra-specifically on vertical and inter-specifically on horizontal substratum) or coexistence by facilitation (intra-specifically on horizontal and inter-specifically on vertical substratum). Facilitation on vertical substratum may occur through trophic niche partitioning. Here, *O. edulis* alters its niche size and *M. gigas* shifts its niche centroid in response to each other, which ultimately could allow the coexistence of both species (Gilbert, Srivastava, & Kirby, 2008). The effect of different ecological niches on species interactions has already been shown in other systems, such as grasslands and for avian communities (Carrete, Sanchez-Zapata, Tella, Gil-Sanchez, & Moleon, 2006; Pearson, Ortega, & Maron, 2017). Here, we suggest that competition success in benthic systems could also be determined by differences in ecological niches, represented as substratum topography, which underpin biological interactions.

Ultimately, the absence of co-occurrence-linked mortality suggests that both species could co-exist and suggests that weaker competitive interactions prevail in this system, which prevent the total exclusion of native or invasive species (Papacostas et al., 2017). This would suggest that the presence of *M. gigas* would only affect the recovery of native oyster populations under specific environmental context (e.g. subtidal, vertical habitats). Here, we have shown that, in the presence of a morphologically similar competitor, invasion success was determined by abiotic stress, and that surface topography drives differences in biotic interaction type. Specifically, this study has shown that niche partitioning and facilitation were primarily driven by surface topography rather than abiotic stress (Bruno et al., 2003; Carbonell et al., 2017) and suggests that differences in ecological niches, such as those created by orientation of substratum is

an under-rated factor in species interactions and should be included in future studies aiming to clarify the role of invasive competitors.

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AUTHORS' CONTRIBUTIONS

N.O.C., D.R., N.Z. and C.H. contributed to ideas and experimental design. N.Z. and H.V.R. involved in implementation and data collection. M.E., C.R., N.O.C., N.Z. and C.H. contributed to analysis and interpretation of data. N.Z. and N.O.C. involved in writing of the manuscript.

DATA ACCESSIBILITY

All data have been published in this manuscript and are made available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.581qd15> (Zwerschke, van Rein, et al., 2018).

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SUPPORTING INFORMATION

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