Environmental stress, facilitation, competition, and coexistence

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Abstract. The major theories regarding the combined influence of the environment and species interactions on population and community dynamics appear to conflict. Stress/disturbance gradient models of community organization, such as the stress gradient hypothesis, emphasize a diminished role for competition in harsh environments whereas modern coexistence theory does not. Confusion about the role of species interactions in harsh environments is perpetuated by a disconnect between population dynamics theory and data. We linked theory and data using response surface experiments done in the field to parameterize mathematical, population-dynamic competition models. We replicated our experiment across two environments that spanned a common and important environmental stress gradient for determining community structure in benthic marine systems. We generated quantitative estimates of the effects of environmental stress on population growth rates and the direction and strength of intra- and interspecific interactions within each environment. Our approach directly addressed a perpetual blind spot in this field by showing how the effects of competition can be intensified in stressful environments even though the apparent strength of competition remains unchanged. Furthermore, we showed how simultaneous, reciprocal competitive and facilitative effects can stabilize population dynamics in multispecies communities in stressful environments.

Key words: Bugula neritina; competition; competition coefficients; environmental stress; facilitation; filter-feeding bryozoans; marine invertebrates; multispecies communities; Ricker model; stress gradient hypothesis; Watersipora subtorquata.

INTRODUCTION

Because environmental variation is ubiquitous, understanding how changes in the environment influence species interactions is crucial for predicting population and community dynamics. Many classic (e.g., Connell 1978, Grime 1979, Huston 1979) and modern (e.g., derivatives of the Menge and Sutherland [1987] stress gradient hypothesis; Callaway 2007) theories of community dynamics continue to emphasize a diminished role for competition in harsh environments, but modern species coexistence theory does not (Chesson and Huntly 1997, Chase et al. 2002, Violle et al. 2010, Fox 2012). Understanding how these theories can mutually inform each other is therefore an important goal.

Stress gradient models (commonly called “stress gradient hypotheses,” SGH) of community organization have been important for simplifying the enormous context dependency of species interactions across environmental gradients (Menge and Sutherland 1987, Bertness and Callaway 1994, Angelini et al. 2011). These theories specifically predict that the frequency and/or strength of competition declines and facilitation increases with increasing environmental stress (Bruno et al. 2003, Callaway 2007, Maestre et al. 2009). Empirical support has been generated through estimates of the strength of interspecific interactions between individuals or surveys of community-wide patterns in the frequency of positive and negative interactions along environmental gradients (Callaway 2007, Maestre et al. 2009). This work has been useful for identifying common patterns in the strength and direction (positive vs. negative) of species interactions among disparate communities, and for highlighting the role of facilitation in community dynamics (Stachowicz 2001, Bruno et al. 2003). However, these conceptual theories and the empirical methods used to support them are rarely suited to understanding the consequences of changes in the strength and direction of species interactions for the regulation of populations, and therefore for species coexistence (Freckleton et al. 2009, Siepielski and McPeek 2010). For example, stress gradient hypotheses are often framed in terms of the commonness of particular types of interactions (Maestre et al. 2009), but the commonness of an interaction type across an entire community provides little information on the density-dependent regulation of populations within those communities. Furthermore, intraspecific competitive effects are rarely estimated in these studies even though it is the ratio of the strength of population-level intra- to interspecific effects that determines the outcome.

Modern coexistence theory, in contrast, tends to explain community structure as a consequence of the influence of the environment on interspecific interactions, but also on density-independent processes and intraspecific interactions (Chesson 2000, Snyder 2008, Levine and HilleRisLambers 2009). These mathematical theories demonstrate that environmental gradients, including stress and disturbance gradients, can promote coexistence (Caceres 1997, Bolker and Pacala 1999, Chesson 2003, Adler et al. 2006, Snyder 2008). Furthermore, modern coexistence theory does not preclude changes in the strength, direction, or frequency of particular types of interspecific interactions in different environments such as those suggested by stress gradient hypotheses (e.g., Sears and Chesson 2007). However, coexistence theory provides no a priori predictions about the outcome of those interactions (Chase et al. 2002). In particular, the strength of an interaction cannot be used to determine the importance of an interaction for population regulation (Freckleton et al. 2009). This is because the direct density-independent effects of a harsh environment can make a population less tolerant of competition, which means that competitive exclusion can occur more readily in harsh environments even though the intensity of competition may be weaker (Chesson and Huntly 1997). Ultimately, coexistence depends on how the environment affects the relative strengths of both intra- and interspecific interactions, and the direct density-independent effects of the environment on a species’ tolerance to competition (Chesson 2000). Importantly, independent changes in each of these variables depend strongly on species-specific responses to the environment (Angert et al. 2009), an area recently identified as being crucial for improving stress gradient models of community organization (Maestre et al. 2009).

The foci and underlying motivations behind stress gradient hypotheses (e.g., Callaway 2007) and modern, population dynamic coexistence theories (e.g., Chesson 2000) are therefore different, but their predictions are not necessarily mutually exclusive. Where possible, the conclusions of these theories might mutually inform each other. One step toward this goal is to determine the consequences of individual-level changes in the direction, frequency, and strength of interspecific species interactions (the domain of stress gradient theories of community organization) for population dynamics (the domain of modern, population-dynamic, coexistence theories). This requires quantification of the direct effects of the environment on density-independent processes, as well as the indirect effects of the environment on populations as mediated through changes in both intra- and interspecific interactions. However, estimating both direct and indirect effects of the environment on the population-level outcome of species interactions is a challenge that is rarely met empirically (Chesson and Huntly 1997, Freckleton et al. 2009, Siepielski and McPeek 2010).

Approaches that allow formal links between mathematical population demographic theory and data are ideally suited for quantifying the strength and direction of species interactions and for determining how these changes affect population dynamics (Inouye 2001, Levine and HilleRisLambers 2009). However, such approaches are rarely replicated across stress gradients. Using a classic model system for studying competition—benthic marine invertebrates—we replicate a powerful but rarely used experimental design in the field in two strongly contrasting environments that span an important natural stress gradient in marine systems. Using our experimental field data, we parameterize a mathematical model of competitive population dynamics to provide quantitative estimates of the direct effects of environmental conditions on density-independent rates of increase, and the indirect effects of the environment on population dynamics via changes in the direction and strength of both intra- and interspecific interaction coefficients. We test the predictions of stress gradient models by evaluating how the strength and direction of species interactions vary depending on environmental harshness, and we show that the consequences of these changes for competitive population dynamics are not straightforward.

**Materials and Methods**

**Assemblage, study species, and the environment**

We studied population dynamics in diverse, subtidal, sessile marine invertebrate assemblages in which strong interactions, both competitive and facilitative, are a distinctive feature (Buss 1990, Stachowicz and Byrnes 2006). We were explicitly interested in interactions among early-successional invasive species before they were largely outcompeted by later-successional dominants (typically after four to six weeks). Therefore, we studied competition between two filter-feeding bryozoans: an encrusting species, *Watersipora subtorquata*, and an arborescent species, *Bugula neritina*. Both species are invasive and widespread globally and often dominate recruitment of recently exposed substrata at our field site, such that there is strong potential for interactions between these species to be important determinants of their success in early-successional assemblages. We quantified competitive population dynamics between a single cohort of genetic individuals and, consistent with the mathematical theory that we apply, our response variable was the production of a new generation of genetic individuals. Our approach was deliberately phenomenological; our results include the effects of all mechanisms of competition/facilitation and all density-independent influences on our study species.

We studied interactions in two habitats that encompass one of the most important environmental gradients for determining community structure in marine systems:
vertical and horizontal (facedown) habitats (Miller and Ron 2008). These habitats vary in several environmental variables, including rates of sediment and UV exposure, which are two major sources of stress for many species of filter-feeding sessile invertebrates (Irving and Connell 2002). Definitions of environmental stress are often problematic because they rarely take into account species-specific responses to the environment (Maestre et al. 2009). Therefore we defined stress in terms of the direct response of our study species to the environmental conditions (sensu Sears and Chesson 2007). Based on our observations of performance of Bugula and Watersipora, we specified the vertical habitat as more stressful a priori, which is also consistent with reduced development and lower productivity of assemblages on vertical habitats at our field site. Our estimates of density-independent performance ($\lambda'$) were used to confirm that the vertical habitat was intrinsically stressful for both species. Additional information on the life histories of our study species and the natural history and location of our study system is provided in Appendix A.

**Experimental methods**

We studied competitive population dynamics using a response surface experimental design in which we manipulated densities of our study species across a range of density combinations such that each species occurred at both different densities and relative abundances (Appendix B; for detailed descriptions of response surface designs, see Inouye [2001], Damgaard [2008]). Our design closely replicates the experience of species in real communities where densities and relative abundances can take a wide range of values in space and time. Most importantly, data generated using this approach can be fit statistically to theoretical models of competition (Law and Watkinson 1987, Inouye 1999, 2001). We extended the use of the response surface approach by replicating the experiment in the field across multiple environments. Our extension enabled us to estimate and directly compare population growth rates and interaction coefficients for both species in both benign and stressful environments in a way that directly links empirical field data with mathematical population dynamic theory.

We used standard methods to collect individuals of Watersipora and Bugula that were less than five days old and of similar size, and to manipulate recruit densities (Hart and Marshall 2009, Hart et al. 2012; see Appendix A). We attached individual recruits of each species haphazardly within a 50 × 50 mm square in the center of 110 × 110 mm settlement plates according to 16 combinations of conspecific and heterospecific densities (Appendices B and C). To generate accurate parameter estimates with an efficient experimental design we followed the recommendations of Inouye (2001) to include a wide range of density combinations, including, as recommended, densities above and below densities of recruits commonly observed in the field (typically 0.25–0.75 individuals/cm²; Appendices A and B).

In the field we attached and randomly arranged two full sets of the 16 density combinations (i.e., 2 × 16 settlement plates) on each of four 800 × 800 mm, 6 mm thick, PVC backing panels. Backing panels were suspended from floating pontoons at a depth of 1 m in either a facedown horizontal (benign) or vertical (stressful) orientation, with two backing panels in each orientation. In total, there were 2144 recruits divided by two species distributed across 128 settlement plates across four backing panels. This arrangement meant that there were two backing panels statistically nested within each of the two environments such that there were two replicates of each of our environment treatments. Within each replicate of the environment, there were two replicates of each of the 16 density combinations (Appendix C).

Competition between our focal species occurred in the field where other biotic (e.g., settlement and growth of other species, predation) and abiotic factors (e.g., temperature, disturbance, water flow) were allowed to vary naturally. We maintained densities of the focal species by removing new recruits each week. After one month in the field, we recorded mortality and measured colony size and fecundity of all surviving individuals. To estimate size and fecundity of Watersipora, we took a high-resolution digital photograph of each colony and used image processing software (ImageJ; Rasband 1997–2008) to estimate colony area and to count embryos (embryos in Watersipora are visible as spherical pink structures behind zooid frontal walls; Hart and Keough 2009). To estimate size in Bugula, we counted the number of bifurcations on each colony’s longest branch and converted this metric into zooid number using standard methods (Keough and Chernoff 1987). To estimate fecundity in Bugula, we used a dissecting microscope to count all embryos, which are individually brooded in specialized, highly visible zooids called oovicells.

**Analytical methods: competition model analyses**

Our main goal was to determine how the environment affects density-independent population growth and the strength and direction of intra- and interspecific interaction coefficients, and to predict how these changes were likely to influence the outcome of the species’ interactions. To do this we first fitted our data to seven different competition models and used a model selection procedure to choose a single model that best described dynamics in our system. Candidate models and the details of model selection are provided in Appendices A and D. Second, using only the best model, we used a model simplification procedure to determine which model parameters were required to describe the dynamics in our system.

The primary response variable for our competition model analyses was per capita embryo production.
(fecundity), which we used to quantify the per capita contribution to population size at time \( t + 1 \). Consistent with the original formulation of the population dynamic models that we apply, this single response variable includes any effects of the environment or species interactions on mortality and growth as well as any other demographic rate that affects fecundity.

Of the seven candidate competition models, dynamics were best described by a Ricker model (Ricker 1954):

\[
\frac{N_{i,t+1}}{N_{j,t}} = \lambda_{\text{env},i} \exp\left(-a_{ij,\text{env}}/N_{i,t} - a_{ij,\text{env}}/N_{j,t}\right)
\]

where \( N_{i,t} \) and \( N_{j,t} \) are the initial densities of recruits of species \( i \) and \( j \), respectively, \( N_{i,t+1} \) is the total reproductive output of species \( i \) at the end of the experiment, \( \lambda \) is the density-independent growth rate, and \( a_{ij} \) and \( a_{ij} \) are the absolute intra- and interspecific competition coefficients, respectively. We fit the experimental data to the Ricker model and estimated parameter values using nonlinear least-squares estimation (see Appendix A for details). Importantly, we included environment as a two-level categorical grouping factor in our model fits such that the subscript \([\text{env.}]\) indicates that parameter estimates are allowed to vary between benign and stressful environments. Including environment as a factor allowed us to simultaneously fit all of our experimental data for each species using a single model, which resulted in separate parameter estimates and therefore separate competition surfaces estimated for each environment. The full model has six parameter estimates for each focal species (i.e., three demographic parameters \([\lambda, a_{io}, \text{and } a_{ij}]\) in each of two environments [benign, stressful]).

To determine the most parsimonious form of the Ricker model, we used likelihood ratio tests (LRT) to compare versions of the Ricker model with and without each individual parameter such that we removed all terms that did not improve model fit at a significance level of 0.10. These tests included comparisons of models with separate estimates of a population parameter in each environment to a simpler (reduced) model with only a single estimate of the same parameter across both environments. When these tests were not significant, we compared models with and without the population parameter of interest to determine if each individual parameter should be included to describe dynamics. We repeated these tests separately for each parameter \([\lambda, a_{io}, \text{and } a_{ij}]\). For each parameter in the final, most parsimonious model, we constructed likelihood profiles, which we then used to calculate 95% confidence intervals around each estimate using standard methods (for a detailed explanation of this procedure, see Venables and Ripley 2002, Bolker 2008, Ritz and Streibig 2008).

Linking mathematical competition theory with empirical field data is difficult and we relied on some reasonable assumptions to justify our approach. The competition model is a discrete-time population model that typically relies on comparisons between population sizes at time \( t \) and \( t + 1 \). To accommodate this feature, we studied competition among a single cohort of new recruits in early-successional assemblages before they were largely excluded by later-successional dominants. Ideally, our response variable would have been the number of recruits of our study species to the same habitats at time \( t + 1 \). However, the minute and dispersive larval phase in our study species’ life histories makes this difficult. Therefore, we used our integrative measure of per capita reproduction at four weeks as the response variable in our competition model analyses. Estimates of interaction coefficients \([a_{ij} \text{ and } a_{ij}]\) are not affected by this response variable under two assumptions, the first of which is that reproduction at week four is linearly related to the number of recruits at time \( t + 1 \). Data from our research group suggest that fecundity at week four is linearly related to lifetime fecundity in our experimental species (For \textit{Watersipora}, \( R^2 = 0.30, F_{1,161} = 69.9, P < 0.001\); for \textit{Bugula}, \( R^2 = 0.73, F_{1,22} = 63.11, P < 0.001\); Marshall et al. 2003, Marshall and Monro 2013), but the relationship between fecundity and recruitment is unknown because this requires an estimate of planktonic mortality. However, a linear relationship should again be a good approximation when density-independent processes determine larval survival in the plankton, which is a reasonable assumption for species such as ours that are unlikely to compete in the plankton (as we will describe) and do not mass spawn (Hughes et al. 2002). The second assumption is that we captured the major period of competition, which should also be reasonable, given that competition is unlikely among the planktonic, non-feeding larvae of these species. We did not quantity the effects of interactions between benthic adults and settling larvae, assuming that recruitment at time \( t + 1 \) is to newly disturbed habitat and thus generations are nonoverlapping. We address this caveat in the Discussion.

Although estimates of interaction coefficients should be unaffected by our approach, we did not estimate true rates of density-independent increase, \( \lambda \) (Inouye 1999). To precisely predict population dynamics, our estimates of \( \lambda \), which we call \( \lambda' \), must be adjusted by an unknown linear term \( \theta(1 - m) \), where \( \theta \) is a constant relating fecundity at week four (our response variable) to lifetime fecundity, and \( m \) quantifies the proportional (value between 0 and 1) mortality of larvae in the plankton, and thus \( 1 - m \) gives the proportion of all embryos counted that survive to settlement at time equals \( t + 1 \). True values of lambda are then equal to \( \theta(1 - m) \lambda' \). In the absence of estimates for \( \theta \) and \( m \), our parameter \( \lambda' \) provided a relative estimate of the direct effects of the environment on density-independent population growth rates. Our conclusions will hold when the observed differences in fecundity are maintained across the life cycle, and when planktonic mortality of the similar-sized larvae of these species is random with respect to species.
identity. We examine the sensitivity of our results to these assumptions in Appendix E.

We explored some of the consequences of our competition model results for population dynamics by assessing the relative capacity for population growth between environments as a function of competitor density, density-independent growth rates, and competition coefficients. In Appendix E, we expand this assessment by constructing phase planes with vector fields to show the trajectories (direction and relative magnitude) of population change across a range of densities of both species.

**Analytical methods: survival and size in response to environment and competition**

To understand the extent to which differences in survival and/or individual size contributed to the observed outcomes of the competition model analyses, we assessed the influence of the environment and competition on survival and colony size. It should be noted that the effects of the environment and competition on the response variable in our competition model analyses implicitly include the effects of changes in survival and colony size in so far as these two demographic rates ultimately influence per capita fecundity. Therefore, our univariate analyses of survival and size complement, but should not be considered independently of, our competition model analyses.

Survival of *Watersipora* was high (>95%) in all environment-density combinations, so these data were not analyzed. We assessed survival of *Bugula* using a generalized linear mixed model (GLMM) with binomial errors and a logit link function. Environment was a categorical independent variable, density was a continuous independent variable, and environment was a fixed categorical independent variable. Where necessary, we transformed data to meet the assumptions of the analytical methods. We sequentially removed higher-level nonsignificant terms at alpha ≥ 0.30. Analyses were done using R v. 2.13.0 (R Development Core Team 2011). More details of our analytical methods and results are provided in Appendix A (supplementary materials and methods) and Appendix E (phase plane construction and analysis).

**Results**

**Parameter estimates from the Ricker competition model and influence of environment**

Competitive population dynamics between nonoverlapping generations of *Watersipora* and *Bugula* settling on bare (e.g., recently disturbed) substrata can be described using a Ricker competition model. The dynamics of both species were dominated by the direct effects of the environment on population growth rates (Table 1, Fig. 1; $z$ intercept at *Bugula* = 0 and *Watersipora* = 0). There was a large, negative effect of the vertical environmental conditions on $\lambda'$ that was proportionally similar in magnitude for both species. For *Watersipora*, $\lambda'(benign) = 24.7$ vs. $\lambda'(harsh) = 4.3$ (likelihood ratio test (LRT) comparing a model with a single estimate of $\lambda'$ to a model with a separate estimate of $\lambda'$ for each environment: $\chi^2 = 81.098$, df = 1, $P < 0.0001$). For *Bugula*, $\lambda'(benign) = 59.7$ vs. $\lambda'(harsh) = 15.7$ (LRT: $\chi^2 = 7.839$, df = 1, $P = 0.0051$). This result confirmed our a priori expectation that the vertical habitat was intrinsically more stressful than the horizontal habitat for both species.

In *Watersipora*, intraspecific competition $\alpha_{ww}$ (subscript on parameters show “w” for *Watersipora* and “b” for *Bugula*) was an order of magnitude stronger in benign environments (for $\alpha_{ww}$, benign = 0.025, harsh = 0.004; LRT comparing single estimates vs. separate estimates for each environment, $\chi^2 = 4.082$, df = 1, $P = 0.0433$; Table 1, Fig. 1). Indeed, although there were negative effects of intraspecific competition in benign environments, intraspecific competition in harsh environments did not differ significantly from zero ($t_{0.05}$ = 0.46, $P = 0.645$). In contrast, intraspecific competition in *Bugula* was strong and did not differ between environments ($\alpha_{bb}$ across both environments = 0.032; LRT comparing single vs. separate, environment-dependent estimates, $\chi^2 = 0.005$, df = 1, $P = 0.94$; LRT comparing presence vs. absence of $\alpha_{bb}$ in the model, $\chi^2 = 4.763$, df = 1, $P = 0.0291$). These tests indicated a need to retain $\alpha_{bb}$ in the model (Table 1).

Interspecific competition by *Bugula* on *Watersipora* did not differ between environments (LRT, $\chi^2 = 2.211$, df = 1, $P = 0.137$; Table 1) and was relatively weak ($\alpha_{wb}$ = 0.012; LRT, $\chi^2 = 3.518$, df = 1, $P = 0.0607$; Fig. 1, Table 1). In contrast, the effects of *Watersipora* on *Bugula* differed dramatically between environments (LRT comparing single vs. separate, environment-dependent estimates of $\alpha_{bw}$, $\chi^2 = 4.922$, df = 1, $P = 0.0265$), indicating that separate estimates are necessary (Table 1). There was a large negative competitive effect of *Watersipora* on *Bugula* in benign environments ($\alpha_{bw} = 0.034$). However, in harsh environments, *Watersipora* strongly facilitated *Bugula* population growth ($\alpha_{bw} = -0.043$; note that a negative “competition” coefficient indicates facilitation).

**Implications for population dynamics**

The parameterized model can be used to understand some important features of competitive population dynamics between nonoverlapping generations of *Watersipora* and *Bugula* settling on bare substrata. The term $e^{\alpha_N}$ in the Ricker model gives the per capita growth rate of species $i$ in the presence of competition from $N$ individuals of species $j$, relative to the density-
of intra- and interspecific competition separately gives sides of the Ricker equation and considering the effects both species (Table 1). Taking the natural log of both larger consequence for persistence when density-inde-
rate caused by species interactions (Fig. 2) will have a environments (Fig. 2b).

Watersipora of conspecifics have large effects on growth rates in can double growth rates in the harsh environment
environments) can halve the growth rates of Bugula

Table 1. Estimates and 95% profile-likelihood confidence intervals for parameters describing competition between two invasive marine bryozoans, Watersipora subtorquata and Bugula neritina, from the best-fit, most parsimonious Ricker competition model.

<table>
<thead>
<tr>
<th>Model</th>
<th>Parameter</th>
<th>Estimate</th>
<th>Lower</th>
<th>Upper</th>
<th>RSE/df</th>
</tr>
</thead>
<tbody>
<tr>
<td>Watersipora subtorquata, $F = \lambda e^{-\alpha_w N_i - \alpha_b N_j}$</td>
<td>$\lambda$ benign</td>
<td>24.679</td>
<td>20.237</td>
<td>29.966</td>
<td>0.140/91</td>
</tr>
<tr>
<td></td>
<td>$\lambda$ harsh</td>
<td>4.331</td>
<td>1.745</td>
<td>6.917</td>
<td>0.128/91</td>
</tr>
<tr>
<td></td>
<td>$\alpha_w$ benign</td>
<td>0.025</td>
<td>0.007</td>
<td>0.003</td>
<td>0.008/91</td>
</tr>
<tr>
<td></td>
<td>$\alpha_w$ harsh</td>
<td>0.004</td>
<td>-0.021</td>
<td>0.021</td>
<td>0.008/91</td>
</tr>
<tr>
<td></td>
<td>$\alpha_{bw}$</td>
<td>0.012</td>
<td>-0.0008</td>
<td>0.024</td>
<td>0.008/91</td>
</tr>
<tr>
<td></td>
<td>$\lambda$ benign</td>
<td>59.717</td>
<td>38.209</td>
<td>107.705</td>
<td>1.196/91</td>
</tr>
<tr>
<td></td>
<td>$\lambda$ harsh</td>
<td>15.718</td>
<td>8.546</td>
<td>28.565</td>
<td>0.947/91</td>
</tr>
<tr>
<td></td>
<td>$\alpha_b$</td>
<td>0.032</td>
<td>0.002</td>
<td>0.062</td>
<td>0.016/91</td>
</tr>
<tr>
<td></td>
<td>$\alpha_{bw}$</td>
<td>0.034</td>
<td>-0.015</td>
<td>0.085</td>
<td>0.016/91</td>
</tr>
<tr>
<td></td>
<td>$\alpha_{bw}$ harsh</td>
<td>-0.043</td>
<td>-0.092</td>
<td>0.008</td>
<td>0.016/91</td>
</tr>
</tbody>
</table>

Notes: Here, $F$ is per capita fecundity, which is an integrative metric that includes all density-independent and density-dependent effects on growth, survival, reproduction, and any other demographic rates that affect the contribution of an individual to population size at time $t + 1$. The density-independent rate of increase is $\lambda$, $\alpha_w$ and $\alpha_b$ are the intra- and interspecific competition coefficients, respectively, and $N_i$ is the initial density of species $i$. Subscripts on parameters represent our study species, with “w” for Watersipora and “b” for Bugula. Separate parameter estimates are provided for different levels of environmental stress (benign/ harsh) when log-likelihood ratio tests indicated that separate estimates significantly improved model fit. RSE stands for residual standard error; df is model degrees of freedom, and CI stands for confidence interval. It should be noted that, by their very nature, competition coefficients naturally take values much less than 1.

There were contrasting effects on survival between the species. Survival of Watersipora was high in both environments and across all density combinations (>95% survival). However, the environment and competitors strongly affected survival in Bugula. Surprising-
ly, survival of Bugula was actually higher in harsh environments in the absence of competition (Fig. 3);
predicted proportion surviving was 0.54 ± 0.008 (estimate ± SE) in the benign environment and 0.69 ± 0.007 in the harsh environment. However, both intraspecific and interspecific densities reduced survival of *Bugula* and there was a stronger negative effect of intraspecific (*Bugula*) densities on survival in harsh environments than in benign environments (LRT for significance of *Bugula* density × environment interaction, $\chi^2 = 9.87$, df = 1, $P = 0.002$; Fig. 3).

There were consistent negative effects of environmental harshness on the mean size of individuals of both species, but the effects of competitors varied between species (Appendix F; Fig. 4). In both *Watersipora* and *Bugula*, the mean size of individuals tended to be lower in the harsh environment, although this effect was marginally nonsignificant for *Watersipora* ($P = 0.087$). This most likely reflects a lack of power as a result of low replication at the appropriate scale (backing panel [environment], $n = 2$; Appendix F). The mean size of individuals of *Watersipora* decreased with increasing densities of both *Watersipora* and *Bugula*, and this effect was consistent in both environments (Appendix F; Fig. 4). In contrast, there were no indications of negative effects of competitor density on size in *Bugula* in either environment; indeed, the mean size of *Bugula* tended to increase with increasing densities of *Watersipora* in harsh, but not benign, environments although this effect

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**Fig. 1.** Population-level effects of intra- and interspecific competition on two invasive marine bryozoans, (a, b) *Watersipora subtorquata* and (c, d) *Bugula neritina* in benign (blue) and harsh (orange) environments. Points are observed values, and surfaces are the predicted values from the fitted model. Black and red symbols (dots and lines) indicate residuals above and below predicted surfaces, respectively. Note: to best illustrate the relationship between independent variables and the response, the axis rotation varies between (a/b) and (c/d). Also note the log response variable in panels (c) and (d).
FIG. 2. Effects of species interactions in harsh and benign environments across a range of competitor densities on population growth rates, relative to density-independent growth rates. Values on the y-axes are the factor by which density-independent growth is multiplied as a consequence of an interaction. The horizontal dotted line indicates no effect of an interaction on population growth rates.

FIG. 3. Effects of environmental stress and (a) Bugula and (b) Watersipora density on Bugula survival. Symbols and lines show observed and predicted values, respectively. Jitter has been added to observed values to distinguish overlapping data. Lines are predicted values from a GLMM with binomial errors, including environment, competitor densities, and all their interactions as independent variables. Interactions between Bugula and Watersipora density were not statistically significant, so the effect of each competitor on survival is plotted separately.
was marginally nonsignificant (environment × Watersipora interaction, $P = 0.070$; Appendix F; Fig. 4).

**DISCUSSION**

Environmental stress can have predictable effects on the intensity of species interactions, but the consequences of these changes for population dynamics are unlikely to be straightforward. Consistent with stress gradient models, the intensity of competition tended to decline and facilitation emerged in the harsh environment, and both types of interactions are expected to have strong effects on dynamics even at low densities (Table 1, Fig. 2). However, it is the interaction between each of the species-specific, density-independent (i.e., direct effects on $\lambda_i$) and density-dependent (i.e., indirect effects via $\sigma_{ii}$ and $\sigma_{ij}$) responses to the environment that determines the population-level response. For example, while the intensity of intraspecific competition in Watersipora ($\alpha_{ww}$) declined in the harsh environment, as would generally be predicted by stress gradient models, the larger proportional decline in Watersipora’s density-independent growth rate ($\lambda_w$) compensated, such that intraspecific density dependence will be lower in stressful environments, effectively increasing carrying capacity. Further, while interspecific interactions strongly modify single-species dynamics, it is the reciprocal nature of these interactions that is of overriding importance. For example, facilitation by Watersipora will benefit Bugula in the harsh environment, but the reciprocal competitive effect of Bugula on Watersipora will ultimately limit this facilitation by limiting Watersipora population growth. Our empirical approach demonstrates the importance of placing changes in the strength and direction of interactions among environments in their population-dynamic context (Freckleton et al. 2009).
The idea that the role of competition is diminished in harsh environments is deeply embedded in conceptual theory (Menge and Sutherland 1987, Bruno et al. 2003, Grime 2007) and has been used to interpret a range of ecological patterns, including species range limits (Normand et al. 2009) and patterns of diversity (Huston 1979). Our results highlight not only that the strength of competition need not always decline, but also, more importantly, that the consequences of competition for population dynamics can actually increase in harsh environments. For example, the per capita strength of interspecific competition by Bugula on Watersipora (\( k_b \)) did not differ between environments (Table 1), but the population-level consequences for Watersipora differ dramatically. The large negative effect of the harsh environment on Watersipora’s density-independent growth rate (\( \lambda_0 \); Table 1) means that Watersipora has less ability to maintain positive population growth in the harsh environment and thus is less tolerant of interspecific competition even though the strength of competition (\( \lambda_{bh} \)) is unchanged. Such a result is consistent with theoretical work that challenges the logic of traditional conceptual models for the effect of stress on competition, on the basis that these models rarely incorporate the direct negative effect of harsh environments on species’ abilities to tolerate competition (Chesson and Huntly 1997; see also Voille et al. 2010, Fox 2012). Our results do not question the veracity of conceptual stress gradient models such as the SGH (some of our data support the SGH), but instead demonstrate the importance of placing predicted changes in the strength or frequency of interactions in a population-dynamic context (Chesson and Huntly 1997, Freckleton et al. 2009).

**Role of competition and facilitation in interspecific population regulation**

Positive interactions are an important component of ecological theory (Stachowicz 2001, Bruno et al. 2003), and are perhaps the most prominent and influential feature of stress gradient models (Bertness and Callaway 1994, Maestre et al. 2009). However, an important gap in this field is the need to explain how populations are regulated when positive interactions can promote unbounded population growth (Holland et al. 2002). One of our most striking results suggests that the emergence of facilitation in stressful environments can be stabilized by reciprocal competitive interactions in a way that may regulate populations in multispecies communities. This is because Bugula will limit the strength of facilitation by Watersipora by limiting Watersipora population size through its own interspecific competitive effects (see Appendix E for details). Such a reciprocal interaction between facilitation and competition is analogous to consumer-resource interactions (Holland and DeAngelis 2010), where the prey contributes to population growth of the predator while the predator simultaneously reduces the density of its prey. Theory predicts that subtle interactions between facilitation and competition can fundamentally change our expectations of community dynamics (Gross 2008). Our results are distinct from Gross’s conclusions in that it is reciprocal competitive–facilitative interactions that can stabilize dynamics, rather than simultaneous competitive and facilitative effects of a benefactor species on beneficiaries. However, both studies emphasize the importance of simultaneous positive and negative interactions at the population level; further work in this area is likely to be fruitful (Holland and DeAngelis 2010).

**Life history variables and mechanisms**

Harsh environments and competition reduced population growth of both species (Fig. 1), but the mechanisms behind these effects varied between species. In Watersipora, reductions in colony size in response to both the harsh environment and competitor density appeared to cause some of the reductions in per capita reproduction (Fig. 4). This result is consistent with the idea that demographic rates in modular organisms are strongly influenced by the size of individuals (Hughes 1984, Harper et al. 1986). However, in Bugula the relationships between the population-level response and the survival and growth of individuals within those populations was less clear. Despite strong intra- (both environments) and interspecific (benign environments) competition, increasing competitor densities had no negative effect on colony size in Bugula (Fig. 4). Although this suggests that size does not strongly determine fecundity in benign environments, small increases in colony size in harsh environments (Fig. 4b) may partially explain the facilitative effect of Watersipora on Bugula. Similarly, effects on survival of Bugula were also complex and cannot be used to predict the population-level outcomes of the interactions, as described by our competition model analysis (compare Fig. 1c, d with Fig. 3). For example, although the environment had direct negative effects on per capita reproduction (\( \lambda(\text{harsh}) < \lambda(\text{benign}) \)), remembering that \( \lambda \) integrates across all density-independent effects on survival, growth, and reproduction), Bugula survival was often higher in harsh environments (Fig. 3; also see Burgess et al. 2012). Furthermore, the strength of intraspecific competition on Bugula survival was stronger in harsh environments (compare slopes in Fig. 3a), even though the overall per capita strength of intraspecific competition (\( \lambda_{bh} \)) was unchanged (Fig. 1, Table 1). These results suggest that the nature and context of an interaction can strongly determine which demographic variables are affected, and also how these variables translate to population-level effects. Choosing an appropriate metric is a critical component of studies of species interactions (Maestre et al. 2005, Snyder 2008, Freckleton et al. 2009), and our results suggest that this is even more important when comparing the
nature of interactions among environments. Integrative, population-level metrics are best, but where this is not possible, environment-specific ground-truthing of the relationship between the measured variable and the population-level response is strongly recommended (e.g., Hart and Keough 2009).

Although our approach was deliberately phenomenological, we speculate on some of the mechanisms behind our results because there is increasing evidence that *Watersipora* is an important foundation species for the development of subtidal assemblages. Stachowicz and Byrnes (2006) demonstrated that *Watersipora* creates habitat that facilitates colonization of other species. Increased colonization success cannot be the mechanism responsible for increased performance of *Bugula* in our study. We speculate that *Watersipora* may mediate the negative effects of sedimentation on *Bugula* in harsh environments, perhaps by changing patterns of water flow via generation of feeding currents (Okamura 1985, Vogel 1994). That *Watersipora* can facilitate other species by at least two mechanisms is consistent with extensions of stress gradient models that highlight the role of foundation species for providing the physical context for community development, such that communities themselves are hierarchically organized (Bruno and Bertness 2001, Altieri et al. 2010, Angelini et al. 2011).

**Limitations and future studies**

Our approach assesses dynamics in a single cohort, but takes no account of competition between adults and recruits from the plankton. *Watersipora*, for example, may affect recruitment by preempting space (a negative competitive effect), or by providing secondary space for recruitment (a positive effect; Stachowicz and Byrnes 2006). Size of *Watersipora*, and therefore space occupation, tended to be lower in harsh environments, suggesting that size-dependent positive or negative effects of *Watersipora* may be reduced in harsh relative to benign environments. Unfortunately, the net effect of these influences on population dynamics is unknown. Consequently, our results apply most strongly to nonoverlapping generations establishing on bare substrata, dynamics that are consistent with the dominance of these species in early-successional assemblages at our field site. Furthermore, our results apply when the scale of environmental variation exceeds the scale of dispersal, such that offspring recruit into an environment that is most similar to that of their parents. This is a simplifying assumption so that we could model the effects of environmental conditions on competitive population dynamics in separate environments. The alternative is certainly possible, but would require a much more complex model with experiments that include phenotypic links among life history stages.

Environmental stress can take many forms, including resource stress, physiological stress, and disturbance, and different classes of stressors are expected to have different effects on density-independent rates of increase and competition (Chesson and Huntly 1997, Kawai and Tokeshi 2007). By manipulating panel orientation we certainly modified the exposure of our study organisms to sedimentation and UV stress, but we also probably modified other variables such as food availability and predation. Indeed, multiple covarying biotic and abiotic factors are a feature of many important environmental gradients (Maestre et al. 2009). We were interested in the influence of the environment on the outcome of competition so we deliberately used a phenomenological approach. Studies that focus on the mechanisms underpinning the population-level effects would be complementary. Similarly, many of the insights of stress gradient theories of community organization and modern, population-dynamic theories of coexistence are complementary. Our approach highlights that a more comprehensive understanding of community dynamics emerges when the approaches and findings of these related theories mutually inform each other.

**Acknowledgments**

We thank Malcolm Keag, Simone Higgie, Jacquie Burgin, and David Aguirre for help in the laboratory and field, and Scott Burgess, Ed Spitznagel, and Victor Wikerhauser for statistical advice. We thank Peter Adler, Jeremy Fox, Jon Chase, Peter Chesson, Jay Stachowicz, Brian Inouye, and three anonymous reviewers for comments and suggestions that substantially improved the manuscript. Any errors remain our own. This work was funded by an Australian Research Council grant to D. J. Marshall. S. P. Hart was supported by a University of Queensland Research Scholarship.

**Literature Cited**


SUPPLEMENTAL MATERIAL

Appendix A
Supplementary materials and methods, including expanded descriptions of the study system and species’ life histories, experimental and analytical methods, and results of model selection (Ecological Archives E094-252-A1).

Appendix B
Density combinations of Watersipora subtorquata and Bugula neritina used in the response surface experiment (Ecological Archives E094-252-A2).

Appendix C
Experimental setup showing arrangement of settlement plates on backing panels in benign and harsh environments (Ecological Archives E094-252-A3).

Appendix D
Candidate competition models (Ecological Archives E094-252-A4).

Appendix E
Construction and analysis of phase planes, including zero net growth isoclines and vector fields, to describe competitive population dynamics of Watersipora and Bugula (Ecological Archives E094-252-A5).

Appendix F
Results of ANCOVA testing for the influence of environmental stress, Watersipora density, and Bugula density on mean individual size (Ecological Archives E094-252-A6).

APPENDIX A. Supplementary materials and methods, including expanded descriptions of the study system and species’ life histories, experimental and analytical methods, and results of model selection.

**Assemblage, study species and the environment**

Our study assemblage includes species from several different phyla that share important similarities in their life histories, including having a dispersive, planktonic larval stage and a sessile, filter-feeding adult stage, which grows from recently attached larval recruits. Recruitment and growth of the sessile stage in these assemblages is strongly seasonal and typically highest during summer. Complete occupation of all available space in summer is rapid, taking approximately four to six weeks, although this does not represent an ‘equilibrial’ state (Butler and Connolly 1999). Strong competition (and facilitation: Stachowicz and Byrnes 2006) on hard substrata among individuals in the sessile stage is a distinctive feature of these assemblages (Buss 1990), and studies of competition in these assemblages have been tremendously important for broader ecological understanding (Buss 1980, Keough 1984, Stachowicz et al. 1999). However, as in most other systems, population-level assessments of competition, particularly among different environments, are extremely rare.

*Watersipora subtorquata* is a colonial encrusting bryozoan whose growth occurs by the addition of new modules (zooids) at the colony edge. Each zoid is capable of producing a single larva after which the individual zoid (but not the colony of which it is a part) senesces, which results in areas of partial mortality within genetic individuals (colonies). *Watersipora* is thought to typically compete via resource preemption and/or overgrowth and colonies of *Watersipora* are regularly observed to at least partially overgrow *Bugula stolonifera* in the field. In contrast, *Bugula stolonifera* is a colonial arborescent bryozoan in which growth occurs through the addition of zooids at the ends of branches (Keough and Chernoff 1987). Individual larvae in *Bugula* are produced by specialized zooids called ovicells. *Bugula* is expected to interact with other species by exploitative competition for resources, although the mechanism of competition in species that are not encrusting has rarely been considered in these assemblages (Buss 1979, Hart and Marshall 2012). Importantly, we take a deliberately and explicitly phenomenological approach to quantify the aggregate effects of the environment and interactions on population dynamics; we do not rely on any assumptions about mechanisms of competition, nor are such assumptions necessary for our approach.

*Bugula* and *Watersipora* can become reproductively mature after approximately 10 days to two weeks. Recruitment of these species on bare substratum ranges between approximately 0.25–0.75 individuals per cm². The life span of *Bugula* and *Watersipora* is uncertain, but individual colonies can probably live for a few months. However, at our field site both species are most common in early successional assemblages during warmer months, and subsequently their densities diminish presumably as a consequence of predation, disturbance, and competition from other species. Densities are typically less than approximately one individual per 25 cm² after approximately two months in the field. Recruitment of these species varies seasonally and at our field site, somewhat unpredictably. Our experiment describes competitive population dynamics in Summer, which tends to be when growth, reproduction and recruitment of these species is highest. Our description of competitive population dynamics among these early successional species cannot be used to explain coexistence of these species with competitively dominant later successional species. However, the dynamics we describe can be used to understand the differential success and potential coexistence of the focal species themselves when they are most common in these assemblages.
To encompass a putative stress gradient, we compared competitive outcomes between vertical and horizontal (facedown) habitats, under the a priori expectation that vertical habitats are, in general, more stressful at our field site. It should be noted that vertical habitats are not always more stressful in marine environments, but in our strongly estuarine system assemblages in vertical habitats do appear to have lower levels of productivity and slower development times. We suspect that this is partly because of higher exposure to suspended sediments, which results in a thin film of sediment to stick to these habitats and many of their attached species. We did not use horizontal, face-up habitats as thick layers of sediment rapidly accumulate in these habitats making them unsuitable habitat for almost all benthic invertebrates at our field site. However, other important environmental variables will also certainly differ between vertical and horizontal (facedown) environments. Two things should be noted about our experimental approach: (1) although we identify the vertical environment as stressful a priori based on our observations of these species and communities at our field site, we use our results to confirm this expectation; and (2) specific differences in abiotic variables between environments and the mechanisms behind our species-specific responses are not of direct interest in this study.

During our study, we allowed natural colonization and growth of other species so that we could assess the outcome of competition between our focal species in these habitats in the context of a naturally developing assemblage, and under natural levels of predation, disturbance, and other naturally varying biotic and abiotic conditions. Experiments were done at Manly Boat Harbor, Queensland, Australia (27°27´ S, 153°11´ E) in January and February (Austral Summer) 2010.

**Experimental methods**

We manipulated initial densities of recruits of *Watersipora* and *Bugula* in 16 different density combinations according to a response surface experimental design (Appendix Fig. 1). To collect individuals for the experiment we allowed natural settlement of larvae onto roughened, 0.25 mm thick PVC sheets that were attached to the underside of 6 mm thick PVC backing panels suspended from floating pontoons at a depth of 1 m. We allowed settlement to occur over five days after which we removed the PVC sheets from the backing panels and transported them to the laboratory in containers of cool seawater. In the laboratory we cut the PVC sheets around individual recruits with a scalpel (1072 recruits of each species). We then used a small amount of superglue to attach the small pieces of PVC film, each with a single recruit, haphazardly within a 50 × 50 mm square in the center of 110 × 110 mm settlement plates, according to the 16 different density combinations, with one density combination per settlement plate. These settlement plates were then attached to PVC backing panels and placed in the field as described in the methods. After one month, and in addition to estimating fecundity for each surviving individual, we also measured individual size and survival.

**Analytical methods**

There were seven commonly used mathematical models of competition in our candidate set and these included models that predict linear and nonlinear effects of density on population growth rates (Law and Watkinson 1987, Inouye 1999, Inouye 2001, Levine and HilleRisLambers 2009, Appendix Table 1). Theoretical competition models are typically parameterized in terms of carrying capacities and relative competition coefficients, where intraspecific competition is implicitly given a strength of one. These parameterizations are not always useful theoretically or empirically (Chesson 2000, Levine and HilleRisLambers 2009). Consequently, we reformulated the competition models by removing the parameter for carrying capacity (K or c in Inouye 2001), and we included an explicit parameter $\alpha_{ii}$ for intraspecific competition (Appendix Table 1). Our re-parameterizations allowed us to estimate the absolute magnitudes of $\alpha_{ii}$ and $\alpha_{ij}$. As an example, for the Ricker model, which best describes competition in our study species (see below), the original formulation is given by:

$$\frac{N_{t+1}}{N_t} = \lambda e^{-c(N_t - \alpha_{ij}N_j)}$$
where \( c \) is a constant that determines the single-species carrying capacity \((\ln(\lambda)/c)\) and \( \alpha_{ij} \) gives the strength of interspecific competition relative to intraspecific competition. The reparameterization gives:

\[
\frac{N_{t+1}}{N_t} = \lambda e^{-\alpha_{ii}N_i - \alpha_{ij}N_j}
\]

The single species’ carrying capacity in this form of the Ricker model is \( \ln(\lambda_i)/\alpha_{ii} \). A species’ tolerance to interspecific competition is \( \ln(\lambda_i)/\alpha_{ij} \), where tolerance is the maximum population size of the heterospecific competitor that a focal species at low density can tolerate. Population sizes of heterospecific competitors above this value will cause negative population growth of the focal species.

Initially we fit the competition models using maximum likelihood (using ‘nlme’ package in R) and included backing panel as a random term (i.e., nonlinear mixed effects models). However, random effects were typically very small (many orders of magnitude smaller than the residual) and did not strongly influence parameter estimates or their standard errors. Consequently, we removed random effects associated with backing panels and fit the models using nonlinear least-squares estimation, which allowed for more straightforward analyses and checking of assumptions. Using nonlinear least squares estimation, the best fit of the competition function to the experimental data is obtained by minimizing the residual sums of squares with respect to the vector of the parameters to be estimated \( \{\lambda, \alpha_{ii}, \alpha_{ij}\} \). The solution to this minimization problem, which is obtained through numerical optimization, provides the least-squares estimates of the parameters in the model (we used the ‘nls’ function, and the nl2sol adaptive nonlinear least squares algorithm, in the ‘stats’ package in R v. 2.13.0; R Development Core Team 2011).

To allow formal comparisons of parameter estimates between the two environments, we included environment (benign (i.e., horizontal) and harsh (i.e., vertical)) as a two-level categorical factor in our model fits as described in the Materials and Methods. Including environment as a factor allowed us to simultaneously fit all our experimental data for each species using a single model, which resulted in separate parameter estimates and therefore separate competition surfaces estimated for each environment (our approach is conceptually similar to an analysis of covariance [ANCOVA], where separate regression lines are estimated for each level of a categorical variable). To meet assumptions of normality and homogeneity of variance while preserving the relationship between the response and predictor variables according to the mean function we transformed both sides of the models using a Box-Cox transformation (Box-Cox constant for Watersipora = 0.2, and Bugula = 0 (i.e., log transformation)). This was done using the ‘boxcox’ function in the ‘nlrwr’ package in R. This procedure estimates the parameters in the mean function and the Box-Cox constant simultaneously using profile likelihoods (Ritz and Streibig 2008). We assessed the fit of the final model using residual plots. We also assessed the quality of the linear approximation assumption using estimates of intrinsic and parameter-effects curvature for each model (Venables and Ripley 2002). The models in the candidate set were compared using comparisons of curvature, residual standard errors and AIC.

Results of model selection from candidate set

Of the seven candidate models, four could be reasonably fit to the data for both species (Appendix Table 1). Comparison of AIC among the four models indicated there was no clear best model (\( \Delta AIC < 2 \) for three of the four models for Watersipora and for all models for Bugula). We chose a modified Ricker model as the best descriptor of competitive population dynamics for both species. In all cases, this model best met the linear approximation assumptions of the nonlinear least-squares methods and so should provide the most precise parameter estimates.

Literature cited

Buss, L. W. 1979. Bryozoan overgrowth interactions - the interdependence of competition for space and


APPENDIX B. Density combinations of *Watersipora subtorquata* and *Bugula neritina* used in the response surface experiment.

**Fig. B1.** Density combinations of *Watersipora subtorquata* and *Bugula neritina* used in the response surface experiment. Population sizes are numbers of individuals in 25 cm$^2$. Our design follows recommendations by Inouye (2001) for density combinations that optimize efficiency, and accuracy and strength of inference.

**Literature cited**

APPENDIX C. Experimental setup showing arrangement of settlement plates on backing panels in benign and harsh environments.

**Fig. C1.** Experimental setup, showing arrangement of 32 settlement plates on horizontal (benign) and vertical (harsh) backing panels, and an example of the haphazard arrangement of individuals of *Watersipora subtorquata* and *Bugula neritina* in one density combination on one settlement plate. There were two replicate backing panels in each environment. Settlement plates were arranged haphazardly on backing panels.
Candidate competition models where $\lambda$ is the finite rate of increase, $\alpha_{ii}$ and $\alpha_{ij}$ are intra and interspecific competition coefficients respectively, $b$ is a parameter that allows for a more flexible fit and $N_i$ and $N_j$ are the densities of the focal and competitor species respectively. The response variable when fitting these models was $N_{t+1}/N_t$. * indicates model could be reasonably fit to the data for both species.

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<th>Competition models</th>
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<td>$\lambda e^{-\alpha_{ii} N_i - \alpha_{ij} N_j}$ *</td>
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<td>$\lambda / (1 + \alpha_{ii} N_i + \alpha_{ij} N_j)$ *</td>
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<tr>
<td>$\lambda e^{-\alpha_{ii} \ln(N_i) - \alpha_{ij} \ln(N_j)}$ *</td>
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<td>$1 + \lambda \left(1 - \alpha_{ii} N_i - \alpha_{ij} N_j\right)$ *</td>
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<tr>
<td>$\lambda / 1 + (\alpha_{ii} N_i + \alpha_{ij} N_j)^b$</td>
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<tr>
<td>$\lambda / (1 + N_i^\alpha_{ii} + N_j^\alpha_{ij})$</td>
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**Appendix E.** Construction and analysis of phase planes, including zero net growth isoclines and vector fields, to describe competitive population dynamics of *Watersipora* and *Bugula*.

We used our parameter estimates to describe qualitative differences in the nature of the interaction between our study species between environments using phase planes (Figs. E1 and E2). Phase planes can be used to graphically display zero net growth isoclines (ZNGIs, described further below) for both species, as well as the trajectories (direction and relative magnitude) of population change at species densities distant from system equilibria. In this way the information contained within the phase planes can be used to describe both equilibrial (at either intersections or intercepts of the ZNGIs) and non-equilibrial dynamics of the interaction as predicted by the results of our competition model analyses.

The axes of the phase planes (Figures E1 and E2) show the densities of species *i* and species *j*. *Watersipora* density is on the ‘x’-axis and *Bugula* density is on the ‘y’-axis in our figures. Each species has its own zero net growth isocline on each phase plane. Regardless of the form of the population model, points along the zero net growth isoclines show the specific combinations of conspecific and heterospecific densities at which the population growth rate of a focal species (the species whose zero net growth isocline is being considered) is predicted to be zero. Growth of a focal species is negative at population densities higher than its ZNGI and is positive at densities lower than its ZNGI, noting the axis that represents the focal species’ density.

With respect to the Ricker model, ZNGIs are linear. The *j*-intercept of the ZNGI for focal species *i* shows the predicted single-species carrying capacity for species *i* (for the Ricker model the *j*-intercept = $\ln(\lambda_i)/\alpha_{ii}$). The *j*-intercept of the ZNGI for focal species *i* is an indicator of the maximum tolerance of the focal species to interspecific competition as the density of the focal species itself approaches zero (for the Ricker model, the *j*-intercept = $\ln(\lambda_i)/\alpha_{ij}$). Regardless of the absolute value of the *j*-intercept, differences in the relative magnitude of this value (between environments, for example) provide information about the differences in the relative ability of the focal species to have positive population growth at low densities when its competitor is abundant – a key criterion of species coexistence. However, the ultimate arbiter of a species’ ability to increase when rare is given by a comparison between: (1) the ability of the focal species when at low densities to tolerate interspecific competition; and (2) the single-species carrying capacity of the focal species’ competitor (i.e., this is a comparison of the intercepts of the different species’ ZNGIs on the same plot axis). For species *i* in the Ricker model this involves the comparison between $\ln(\lambda_j)/\alpha_{ij}$ and $\ln(\lambda_j)/\alpha_{jj}$, noting subscripts. In general, when all absolute maximum (i.e., not per capita) intraspecific effects are stronger than absolute maximum interspecific effects (for the Ricker model, noting arrangement of subscripts and direction of inequalities: $\ln(\lambda_j)/\alpha_{ii} > \ln(\lambda_j)/\alpha_{ij}$ and $\ln(\lambda_j)/\alpha_{jj} < \ln(\lambda_j)/\alpha_{jj}$) coexistence can occur, with equilibrium densities at the intersection of the ZNGIs.

For the Ricker model, the slope of the ZNGI for species *i*, with respect to the density of focal species *i* itself, is equal to the (negative) ratio of per capita intra- to inter-specific effects (-$\alpha_{ii}/\alpha_{ij}$). As per capita intraspecific effects increase relative to per capita interspecific effects, the slope of the ZNGI with respect to changes in density of the focal species will become increasingly negative (when dealing with competition, not facilitation). Similarly, if per capita intraspecific effects ($\alpha_{ii}$) increase relative to per capita interspecific effects ($\alpha_{ij}$), the slope of the ZNGI will become less negative with respect to changes in the density of the focal species, but will simultaneously become more negative with respect to changes in the density of the competitor. Therefore, the slope of the ZNGI can be used to understand the relative influence of changes in the density of conspecifics vs. heterospecifics, including at growth rates different from zero, and therefore at species densities distant from equilibria.

We stress that our illustration of ZNGIs on the phase planes do not imply equilibrial dynamics in our system. What is most important are the relative differences in the position of the intercepts, and in the direction and magnitude of the slopes of the zero net growth isoclines for both study species between the environments. For example, differences in the slopes of the ZNGIs between environments indicate differences in the relative influence of changes in conspecific vs. heterospecific density in each environment, regardless of the absolute population densities. Differences in slopes and intercepts of the ZNGIs provide important information about the relative and combined importance of changes in density-independent and -dependent effects between environments.

In addition, non-equilibrial dynamics can also be described by vector fields, which indicate the trajectories of the combined population changes of both species at population sizes away from the ZNGIs and/or equilibria themselves. Vectors in Fig. E1 were calculated using solutions of the parameterized Ricker models (Table 1) across a wide range of combinations of population sizes of the two species. Importantly, the length of the vectors in our plots represent the relative magnitude of population change, not the absolute levels of population change across a full time step, and should be used only as an indication of the direction in which population dynamics are expected to proceed. Furthermore, the vectors and ZNGIs that we construct do not account for uncertainty around our parameter estimates, but we hope can be used to identify qualitative changes in the dynamics of the interactions of these species between environments. Differences between the environments were of primary interest in our study, not absolute values within environments.

To determine the robustness of our results to changes in the true value of $\lambda$, we also construct ZNGIs for a range of values of
0(1-m), where 0(1-m) determines the true value of λ (for detailed description of these terms see Materials and Methods in manuscript). In general, lower values of 0(1-m) indicate higher levels of planktonic mortality (relatively higher values of m), and higher values indicate a stronger positive relationship between our response variable and lifetime reproductive success (relatively higher values of 0).

Results: Dynamics of the interaction

Non-equilibrial dynamics are likely to most accurately describe dynamics in our study system. Consequently, we are only concerned with relative (not absolute) changes in the intercepts and slopes of the ZNGIs between environments as indicators of changes in the influence of population parameters between environments. Single-species carrying capacities (ln(λi)/αi) for Bugula were higher in benign environments and for Watersipora were higher in harsh environments (Fig. E1; ‘y’-intercepts of Bugula’s ZNGIs and ‘x’-intercepts of Watersipora’s ZNGIs, respectively). That the expected carrying capacity (ln(λw)/αw) of Watersipora was higher in the harsh environment indicates that the decline in Watersipora’s density-independent growth rate in the harsh environment is more than compensated for by an even larger proportional decline in the per capita effect of intraspecific competition (αw).

Furthermore, although the per capita effect of Bugula on Watersipora did not differ between environments (αwb, Table 1), Watersipora was less tolerant of interspecific competition from Bugula in the harsh environment than the benign environment. This is indicated by the relative difference in the value of the ‘y’-intercepts (ln(λw)/αw) of Watersipora’s ZNGIs in Fig. E1a and E1b, and occurs solely because of the lower expected density-independent growth rate of Watersipora in the harsh environment (λw(harsh)). The lower intercept (i.e., lower value of ln(λw)/αw)) indicates that Watersipora, when at low densities, will find it more difficult to maintain positive population growth when exposed to high densities of Bugula in the harsh relative to the benign environment.

The most striking change in Bugula population dynamics between environments is the change between negative competitive effects of Watersipora in the benign environment to positive facilitative effects of Watersipora in the harsh environment. This is indicated by the change from a negative to positive slope of Bugula’s ZNGI, with respect to increases in the density of Watersipora (i.e., the slope of Bugula’s ZNGI with respect to Watersipora changes from -(αbw/θwb) to +((αwb/θwb)).

Vector fields illustrate the strong influence of Watersipora on population dynamics in the benign environment and Bugula in the harsh environment (Fig. E1). The vector field describing dynamics in the harsh environment also illustrates the emergence of a negative feedback between the facilitative (positive) effect of Watersipora on Bugula and the reciprocal negative effect of Bugula on Watersipora. As Bugula densities increase (i.e., increasing Nb as one moves up the ‘y’ or Bugula-axis of the phase planes), the total negative effect of Bugula on Watersipora (i.e., αi x Ni) also increases, which has the effect of increasingly limiting Watersipora population growth. Thus, Bugula is ultimately expected to limit the magnitude of the facilitative effect of Watersipora on itself. This dynamic is illustrated by the increasingly vertical vectors at fixed densities of Watersipora but increasing densities of Bugula in Fig. E1b.

Our results suggest Watersipora will tend to be numerically dominant in the benign environment and Bugula will tend to be dominant in the harsh environment. These results remain qualitatively the same if the relative differences in our integrative response variable (per capita fecundity) observed in our experiment are maintained across the lifecycle of the two species (i.e., species have similar values for 0(1-m); see intersection of ZNGIs with the same color in Fig. E2). However, higher planktonic mortality in Watersipora (i.e., high mw), and/or a stronger positive relationship between fecundity and lifetime reproductive success in Bugula (high θw), would relatively benefit Bugula in the benign environment, whereas the opposite pattern (high mw and/or low θw) would relatively benefit Watersipora in the harsh environment (intersections of differently shaded ZNGIs in Fig. E2). See Fig. E2 caption for more details and examples.
FIG. E1. Phase planes showing zero net growth isoclines (ZNGIs) for *Watersipora subtorquata* (solid line) and *Bugula neritina* (dashed line), and vectors showing trajectories of population change at non-equilibrial densities of both species. Vectors were calculated using solutions of the parameterized Ricker model across a range of combinations of population sizes of the two species. The length of the vectors represent the relative magnitude of population change, not the absolute levels of population change across a full time step. The vectors provide a qualitative insight into the relative advantages of each species in different environments across the full range of potential density combinations of both focal species. Relative changes in the intercepts and slopes of the ZNGIs, and the direction and magnitude of vectors illustrate qualitative changes in the dynamics of species interactions among environments.

FIG. E2. Phase planes showing zero net growth isoclines (ZNGIs) for *Watersipora subtorquata* (solid line) and *Bugula neritina* (dashed line) constructed using parameter estimates from the fitted competition models. Shades of blue represent different values of the unknown quantity \( \theta(1-m) \) (see Materials and Methods for full description); darker shades represent higher planktonic mortality (relatively high \( m \)) and lighter shades indicate a stronger positive association between.
reproduction at week four and lifetime reproductive success (relatively high θ). The plots provide a qualitative insight into the relative advantages of the species in different environments and under different values of θ(1-m). Particularly in the benign environment, our conclusions about species dominance described in Figure E1 and in the manuscript are contingent on the true values of lambda (i.e., λ = θ(1-m) λ’). The relative positions of the ZNGIs in this figure show how the relative advantage of each species changes according to specific, directional departures from our assumptions (i.e., specific, directional departures in the values of θ and m). For example, Bugula’s numerical disadvantage in benign environments can be mediated when its planktonic mortality is lower than Watersipora’s, such that Watersipora’s ZNGI is a darker shade than Bugula’s ZNGI in the benign environment. However, if such a pattern was consistent between environments, such an effect would also reduce Bugula’s advantage in the harsh environment. Overall, relatively higher planktonic mortality in Watersipora (i.e., high mw, darker Watersipora ZNGIs), and/or a stronger positive relationship between fecundity and lifetime reproductive success in Bugula (high θw, lighter Bugula ZNGIs), would benefit Bugula in the benign environment, whereas the opposite pattern (relatively high mb and/or relatively low θw) would benefit Watersipora in the harsh environment.
APPENDIX F. Results of ANCOVA testing for the influence of environmental stress, *Watersipora* density, and *Bugula* density on mean individual size.

**Table F1.** Results of ANCOVA testing for the influence of environmental stress, *Watersipora* density, and *Bugula* density on mean individual size of: (a) *Watersipora*; and (b) *Bugula*. Tables show full and reduced models, where reduced models were derived through step-wise pooling of nonsignificant, higher-order terms at $\alpha > 0.30$.

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<th>SS</th>
<th>MS</th>
<th>F</th>
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<td><strong>Full model</strong></td>
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bp(env.) x *Bugula* density  
2 0.039 0.019 0.15 0.860

bp(env.) x *Water.* x *Bugula*  
2 0.083 0.041 0.32 0.725

Residuals  
80 10.245 0.128

**Reduced model**

Environment  
1 14.346 14.346 9.956 0.087

*Watersipora* density  
1 10.414 10.414 87.763 **0.000**

*Bugula* density  
1 1.510 1.510 12.723 **0.001**

backing panel (env.)  
2 2.882 1.441 12.143 **0.000**

Residuals  
90 10.680 0.119

**(b) Bugula neritina**

**Full model**

Environment  
1 26.062 26.062 26.86 **0.035**

*Watersipora* density  
1 1.538 1.538 6.32 0.128

*Bugula* density  
1 0.125 0.125 0.61 0.518

Env. x *Watersipora* density  
1 3.139 3.139 12.91 0.070

Env. x *Bugula* density  
1 0.068 0.068 0.33 0.625
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**reduced model**

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