

## Competitive and demographic leverage points of community shifts under climate warming

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# Competitive and demographic leverage points of community shifts under climate warming

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Accelerating rates of climate change and a paucity of whole-community studies of climate impacts limit our ability to forecast shifts in ecosystem structure and dynamics, particularly because climate change can lead to idiosyncratic responses via both demographic effects and altered species interactions. We used a multispecies model to predict which processes and species' responses are likely to drive shifts in the composition of a space-limited benthic marine community. Our model was parametrized from experimental manipulations of the community. Model simulations indicated shifts in species dominance patterns as temperatures increase, with projected shifts in composition primarily owing to the temperature dependence of growth, mortality and competition for three critical species. By contrast, warming impacts on two other species (rendering them weaker competitors for space) and recruitment rates of all species were of lesser importance in determining projected community changes. Our analysis reveals the importance of temperature-dependent competitive interactions for predicting effects of changing climate on such communities. Furthermore, by identifying processes and species that could disproportionately leverage shifts in community composition, our results contribute to a mechanistic understanding of climate change impacts, thereby allowing more insightful predictions of future biodiversity patterns.

## 1. Introduction

Climate change has already led to widespread alterations of biological systems [1], and higher rates of global warming are predicted in the next century [2]. Ecosystem impacts of climate change include alterations to community composition: as species' ranges shift poleward [1,3,4], particular locations have, in general, seen increases in low-latitude species and decreases in high-latitude species [3,5,6]. However, observations and manipulative experiments have highlighted the idiosyncrasy of species' responses [7–10], indicating that categorizing species based on single characteristics, such as their current geographical affinities, is inadequate for forecasting future community structure. Thus, the most insightful predictions of future changes in species' abundances and community composition require an understanding of the principal mechanisms underlying warming effects. Here, we take a whole-community approach to mechanistically evaluate impacts of climate warming on multiple component species and their interactions.

Studies of the biological impacts of climate change have focused largely on direct effects on single species [10,11], despite evidence that including species interactions can greatly improve the accuracy of predicted impacts [8,12]. Furthermore, interspecific interactions themselves are often dependent on environmental conditions [13–17]. For example, competitive outcomes may reverse along gradients in surface topography [18], moisture availability [19], nutrient availability [12], CO<sub>2</sub> [20], salinity [21] and temperature [8,22,23]. Climate-driven changes in species dominance hierarchies could lead to marked differences in the

composition of strongly competitive communities, such as assemblages of foundational plants and invertebrates. Species interactions, along with demographic processes, are likely to underlie community responses that have been observed in *in situ* warming experiments [7,12,19,24,25]. However, the relative importance of individual mechanisms (e.g. changes in survival rate versus competitive ability) is not easily discernible in such studies.

We used a simulation modelling approach to predict impacts of climate warming on the composition of a marine community, and we combined these simulations with a sensitivity analysis to assess the primary mechanisms underlying predicted compositional shifts. Our marine study system is composed of sessile invertebrates that inhabit subtidal hard substrata, including human-made structures (e.g. docks and piers). We evaluated effects of climate warming on five species of sessile invertebrates that collectively occupy the majority of available space in our Bodega Harbor (California, USA) study system, comprising four colonial tunicates (*Botrylloides violaceus*, *Didemnum vexillum*, *Diplosoma listerianum* and *Distaplia occidentalis*) and an encrusting bryozoan (*Watersipora subtorquata*); for brevity, all are referred to hereafter by genus. Because they are subtidal and space-limited [26,27], species in this community are likely to respond to increasing ocean temperature via changes in processes responsible for space acquisition and maintenance. We adapted a community model developed by Crowley *et al.* [28] so that it described our study system, and we parametrized this model with data collected in field and laboratory microcosm experiments.

We calculated model projections using parameter values corresponding to each of three temperatures: an ambient temperature (14°C), and two increased temperatures predicted by warming scenarios (+2.5°C and +4°C [2]). We used the model outcomes and results of the sensitivity analysis to address three specific questions. First, which species are likely to increase versus decrease in the community as the ocean warms? Second, what is the relative role of four key population- and community-level processes in changing predicted species dominance patterns? Third, which of the five species sustain the most significant temperature-dependent alterations in demographic rates and interaction strengths, leading to predicted dominance shifts? Identifying the most important mechanisms (i.e. processes and species) is a step towards improving predictions about trajectories of climate-driven shifts in community composition [29].

## 2. Methods

We formulated a spatially implicit community model in an open population based on the framework advanced by Crowley *et al.* [28]. The model incorporates four main processes important to dynamics in space-limited, hard substrate benthic communities of sessile organisms [30]: recruitment (of propagules), growth (i.e. lateral growth into unoccupied space), overgrowth (i.e. interspecific competition) and mortality. The model of Crowley *et al.* [28] assumed a closed population of sessile organisms, but our model also includes recruitment from an external larval pool, reflecting the dynamics of a small patch of habitat within a larger metacommunity. Our model consists of a set of coupled differential equations; following the notation of Crowley *et al.* [28], the two-species version of this model would be

$$\frac{df_i}{dt} = f_i b_i A + f_i f_j (c_{ij} b_i - c_{ji} b_j) - f_i d_i + r_i A \quad (2.1a)$$

and

$$\frac{df_j}{dt} = f_j b_j A + f_j f_i (c_{ji} b_j - c_{ij} b_i) - f_j d_j + r_j A, \quad (2.1b)$$

where  $f_i$  is the proportion of space occupied by species  $i$ ,  $b_i$  is the growth rate of species  $i$  into unoccupied space ( $b_i \geq 0$ ),  $c_{ij}$  is the overgrowth competition coefficient ( $c_{ij} \geq 0$ ) describing the reduction in growth rate experienced by species  $i$  when in contact with another species  $j$ ,  $d_i$  is the mortality rate of species  $i$  leading to a retreat from occupied space ( $d_i \geq 0$ ),  $r_i$  is the recruitment rate of species  $i$  describing the settlement of new individuals onto unoccupied space and  $A$  is the total amount of unoccupied space ( $A = 1 - f_i - f_j$ ).

We expanded the two-species framework of Crowley *et al.* [28] into a system of five equations that predict the dynamics of a five-species community. This was accomplished by adjusting the terms denoting the total occupied area ( $A = 1 - f_1 - f_2 - f_3 - f_4 - f_5$ ) and including additional terms of the form  $f_i f_j (c_{ij} b_i - c_{ji} b_j)$  in each equation to describe the 20 pairwise interactions between five competing species.

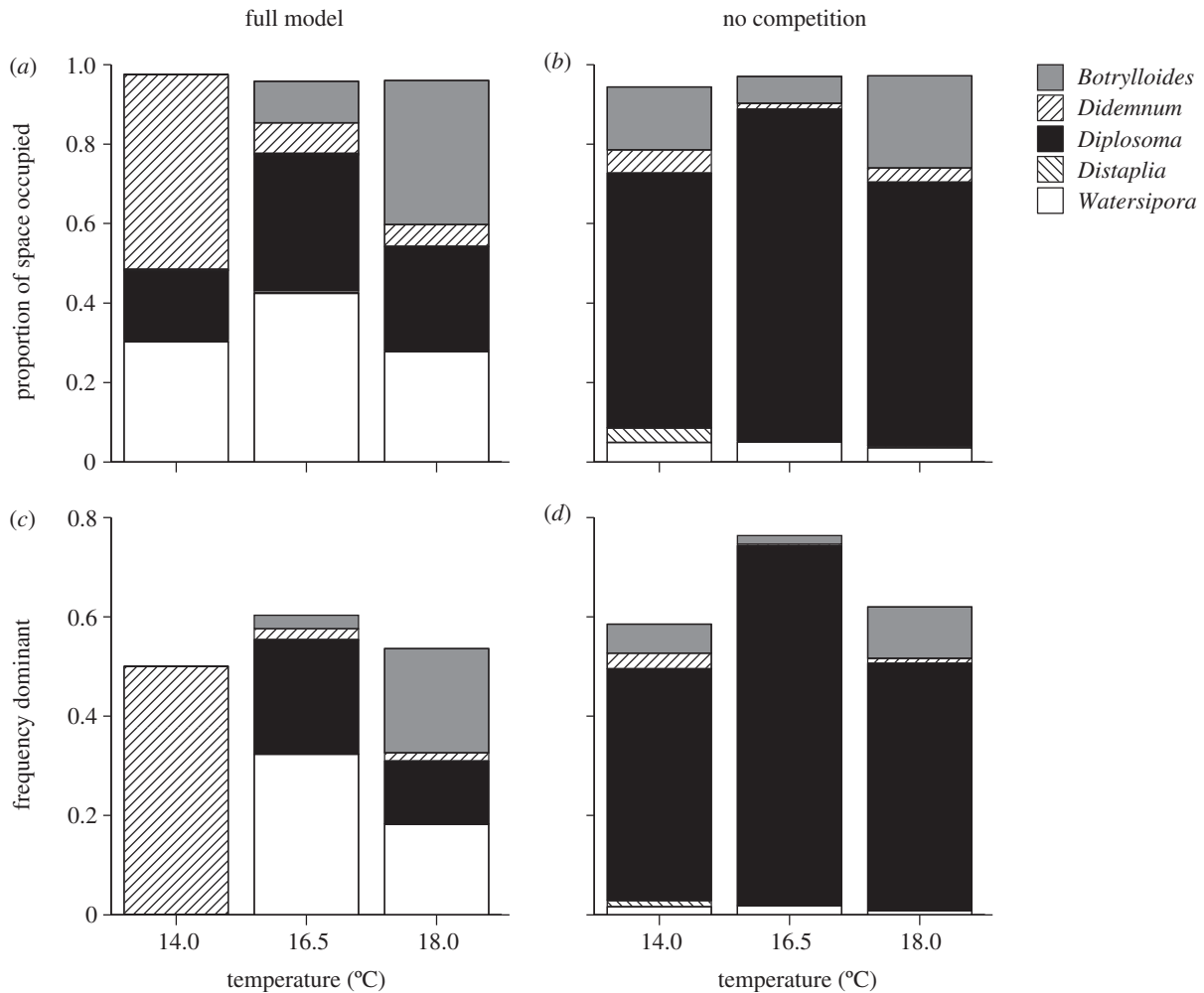
We parametrized our model using values determined via field observations for recruitment ( $r$ ) and disturbance (for which frequency and intensity were varied within each simulation), and separate laboratory experiments for growth ( $b$ ), mortality ( $d$ ) and overgrowth competition ( $c$ ) (see the electronic supplementary material, appendix S1 and table S1) [31,32]. Across  $10^5$  simulations at each temperature, we determined the mean population density of each species after 10 months (41 weeks) and the proportion of simulations in which each species was dominant (occupied greater than or equal to 90% of space in week 41). Outcomes of the model runs at ambient (14°C) temperature were compared with species' abundances on field plates deployed for the same period. To assess the importance of competition, we ran an additional set of model simulations in the absence of competition ( $c = 0$ ). Finally, we conducted a global sensitivity analysis (following the approach of Harper *et al.* [33]) to determine the relative importance of each process and species in explaining projected impacts of ocean warming on species dominance patterns.

Additional methodological details are available in appendix S1 of the electronic supplementary material.

## 3. Results and discussion

Our results indicate the potential for large shifts in species dominance patterns and community composition primarily driven by the temperature dependence of growth, mortality and competitive ability for three key species. Detecting these shifts required the incorporation of species interactions. Representative model runs using mean parameter values illustrate typical community trajectories (see the electronic supplementary material, figure S1): *Diplosoma* (an early successional species [34]) initially occupied the majority of space and then was supplanted by one of the competitively dominant species (*Didemnum*, *Watersipora* or *Botrylloides*). Although compositional patterns shifted with warming, *Diplosoma* remained an effective early colonist at increased temperature.

The general dynamics shown in figure S1 of the electronic supplementary material (i.e. eventual dominance by a single species on the time scale of 1 year) are typical of results from the model; however, a range of outcomes was possible within the distribution of  $10^5$  random simulations at each temperature, as shown in figure 1. Specifically, in the model solutions with randomly drawn parameters, the mean proportion of space occupied by each species after 10 months, and the proportion of simulations in which each species was



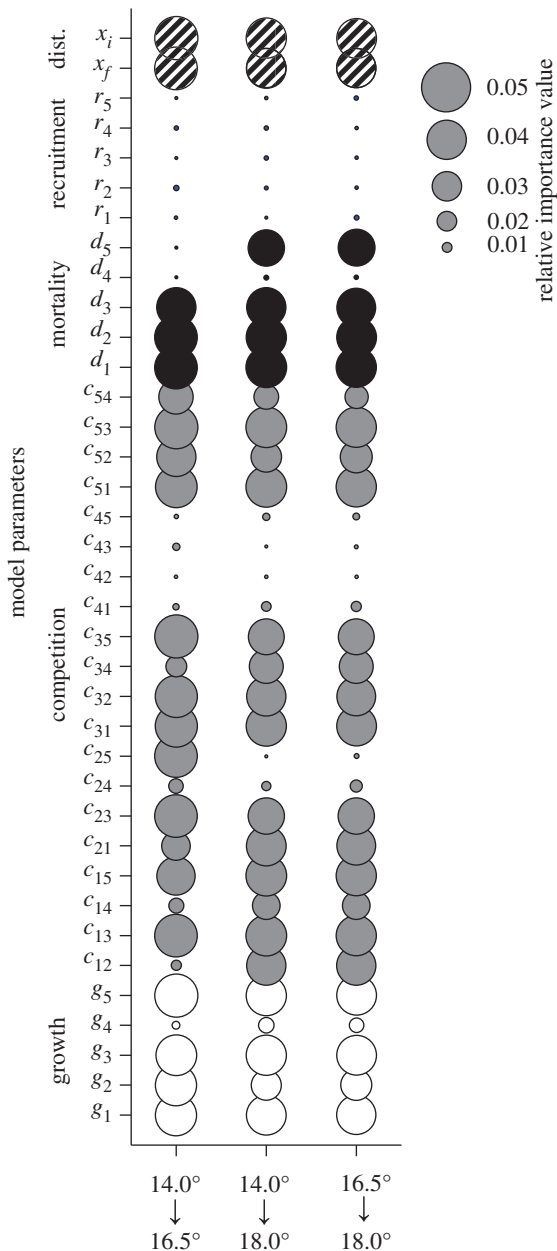
**Figure 1.** Summary of model projections with randomly varying parameter values for the three study temperatures. (a,b) Proportion of space occupied after 10 months (41 weeks; simulations were started on 1 May). (c,d) Frequency dominant is the proportion of runs ( $n = 10^5$ ) in which each species became the dominant spaceholder (occupied  $\geq 90\%$  available space). The effect of species interactions on model outcomes is evident based on differences between results for (a,c) the fully parametrized model and (b,d) projections without competition.

dominant (greater than or equal to 90% space occupied), changed with increasing temperature (figure 1a,c). In ambient temperature conditions (14.0°C), *Didemnum* attained the highest population densities. At 16.5°C, *Diplosoma* and *Watersipora* increased in density, displacing *Didemnum* as the most dominant species, whereas at 18°C, *Botrylloides* was most abundant, overtaking *Diplosoma* and *Watersipora*. Under warming, *Didemnum* dominance decreased and evenness increased (Pielou's  $J = 0.63, 0.74$  and  $0.78$  at 14, 16.5 and 18.0°C, respectively). *Distaplia* had a mean proportional density of less than 0.01 at all temperatures and was never dominant. In summary, under progressively warmer conditions, *Botrylloides* increased, *Didemnum* decreased, *Distaplia* remained at very low abundance, and densities and dominance patterns of *Diplosoma* and *Watersipora* waxed and waned across the temperature treatments.

The global sensitivity analysis allowed us to identify the processes and species whose responses to warming most strongly influenced predicted changes in community structure (figure 2). Across these comparisons, the mortality parameters for *Botrylloides* and *Diplosoma*, and the growth parameters for these species and *Watersipora*, were consistently among the top half of parameters that accounted for 80 per cent of the total importance. By contrast, the recruitment parameters for all species were of lower importance. The predicted changes in community composition with increasing temperature were

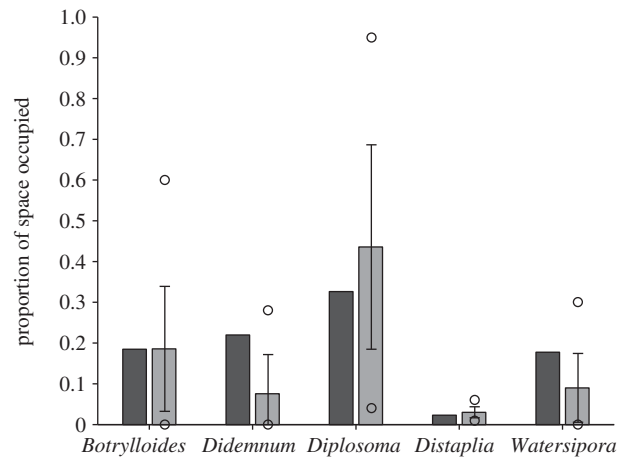
also keenly dependent on changes in interspecific interaction strengths. The competition coefficients describing the pairwise interactions between *Botrylloides*, *Diplosoma* and *Watersipora* were consistently among the one-third of parameters that represented 60 per cent of the total importance. Furthermore, when model simulations were obtained without interspecific competition, the predicted community composition was very different (figure 1b,d): *Diplosoma* was predicted to remain overwhelmingly dominant at all temperatures, with *Didemnum*, *Distaplia* and now also *Watersipora* all predicted to decline to extremely low densities under warming. Community diversity was also lower in the absence of competition when compared with the full model runs: Shannon diversity for simulations with (without) competition was 1.02 (1.01), 1.19 (0.55) and 1.26 (0.87) at 14, 16.5 and 18.0°C, respectively.

Together, these analyses testing the importance of particular processes and species underlying community alterations indicate that post-settlement space acquisition and maintenance are of great importance for determining predicted shifts with climate warming, and these processes leverage changes through particular species (i.e. *Botrylloides*, *Diplosoma* and *Watersipora*). By contrast, *Distaplia* and *Didemnum* were of less importance in explaining temperature-driven changes in the community, particularly beyond 16.5°C. Competition parameters for these latter two species had consistently low importance, and all parameters related to *Distaplia* were



**Figure 2.** For combinations of the three study temperatures, circle diameter indicates the relative importance of changes in each model parameter (from lower to higher temperature values) in determining the identity of the dominant species at the higher temperature based on a global sensitivity analysis. Circle shading denotes the type of parameter represented, and subscripts correspond to species: 1, *Botrylloides*; 2, *Didemnum*; 3, *Diplosoma*; 4, *Distaplia*; and 5, *Watersipora*.  $c_{ij}$  indicates the reduction in growth rate of species  $i$  when overgrowing species  $j$ .

among the least important 20 per cent of processes for all three comparisons. The low importance of *Distaplia* suggests that there was a low marginal value to adding increasingly rare species to our community simulations, although it is possible that there are currently rare species that will become more common under future warming. Persistence of rare, subdominant species may occur when there are species-specific trade-offs between competition and colonization dynamics [34,35]. To some extent, we detected trade-offs within this group of five species, particularly between overgrowth rank and colonization (i.e. recruitment; electronic supplementary material, table S1). However, *Distaplia*, the species with the highest recruitment rate, had the lowest competitive ability at



**Figure 3.** Proportion of space occupied based on field data (light grey bars) and mean densities from  $10^5$  model simulations (dark grey bars) at ambient temperature. Field values are average abundances on  $n = 7 \times 10 \times 10$  cm plastic plates deployed in Bodega Harbor ( $\pm$  95% CIs; circles are maximum and minimum values). Field deployments and model simulations were started on 1 May, and population densities were assessed after 10 months.

all temperatures and was of low importance to predicted climate-driven shifts in community composition. Given that *Distaplia* is the only species among the five considered here that is native to our study system, future research should continue to address whether native species are specifically inhibited in warmer conditions when compared with non-native species [36].

Model simulations at ambient temperature ( $14^\circ\text{C}$ ) afforded a reasonably good match to field data of current community composition. The average abundance from  $10^5$  simulations for the period 1 May–15 February did not differ significantly (based on a comparison with the 95% confidence interval) from values quantified in a field experiment conducted over the same interval for four of the five species (the exception being *Didemnum*, for which proportional space occupancy was over-predicted by approx. 0.15 on average); abundances of all five species fell within the range of values observed in the field (figure 3). Although this comparison lends credibility to our choice of processes driving community structure and our empirical approach to model parametrization, we acknowledge that there are several additional processes that are likely to modify the model projections. Importantly, seasonal variability in temperature and corresponding changes to parameter values would ideally be incorporated in future forecasting models. Although we lacked appropriate data to confidently incorporate variability in our warming simulations, including seasonality improved our match between simulated and field data at ambient temperature (see the electronic supplementary material, appendix S2 and figure S2). In addition, disturbances such as predation [13] and extreme events (e.g. heat waves [37]) are expected to increase in the next century, concurrent with gradual warming, and have been shown to influence community composition [38,39]. Our analyses suggest that disturbance frequency is among the 15 per cent of most important processes determining warming-related changes in community composition, and disturbance intensity was of lower importance, but still among the upper one-third of processes that explain 50 per cent of the variation in community outcomes between temperatures. Increased disturbance could favour species best



at capitalizing on increased open space (e.g. the opportunistic species, *Diplosoma*). Alternately, disturbance could favour the most resistant species (e.g. *Watersipora* best resisted a simulated future heat wave, of our test species [40]), leading to selective mortality and consequent declines in recruitment rates as source populations of the less resistant species dwindle. It is also important to note that these models and the underlying empirical data reflect the immediate imposition of a 2.5–4°C increase in mean temperature. In reality, temperature increases of this amount are expected over a 40–90 year period of warming [2], and acclimation and adaptation have the potential to alter the temperature-dependent values used to parametrize our model.

To the degree that our model analysis—grounded in comparisons of field data to simulations run at ambient temperature—is indicative of the relative effects of future climate warming, it allows us to predict the trajectory of community composition as well as the processes and species that will most strongly affect those changes. In particular, our results underscore the importance of accounting for temperature-dependent changes in interspecific interaction strengths when making predictions about warming effects, a level of

context dependency that continues to be neglected in climate change studies and may be particularly important between species that compete for a common resource [41]. Furthermore, our analysis should promote the development of more educated hypotheses about responses to climate warming at even larger scales. For example, diverse assemblages of associated species depend on shelter and trophic subsidies provided by basal foundation species, including epibenthic marine invertebrates [42] and primary producers in analogous plant-dominated systems [43]. Our results indicate the likely trajectories for common basal species in an epibenthic community, and the mechanisms that may drive changes in these and associated species; predictions that should be tested via future experiments or baseline comparisons.

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