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Altering species interactions outweighs the effects of experimental warming in structuring a rocky shore community

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ABSTRACT

The strength and direction of interspecific interactions governing communities is expected to change with increasing global temperatures. However, in many ecosystems it remains unclear which species interactions are most likely to be altered under increasing thermal stress and what impacts, if any, such altered interactions will have on community structure. We investigated the interactive effects of increased temperature and altered species interactions on the structure of a rocky intertidal community by deploying black and white plates in areas with or without the dominant grazer, the limpet *Cellana tramoserica*. Plates effectively manipulated substratum temperature, whilst anti-fouling paint effectively manipulated the strength of algal-herbivore interactions. Plates without *C. tramoserica* quickly developed and maintained abundant macroalgal assemblages irrespective of thermal stress. By contrast, the abundance of barnacles remained relatively low and did not differ across thermal treatments, although they were slightly more abundant in plots where *C. tramoserica* had been excluded. These results support recent findings that altered species interactions are anticipated to have greater effects on community structure than the direct impacts of warming, challenging the view community structure under warming climatic conditions can be predicted from individual responses of populations to increasing thermal stress. Based on these and other recent findings we therefore advocate for greater inclusion of biotic interactions into climate change models that aim to predict the state of future ecological communities.

1. Introduction

As global temperatures continue to rise, the relative abundance and composition of species are expected to change. This may in turn alter the strength and direction of species interactions (Sanford, 1999; Tylianakis et al., 2008; Gilman et al., 2010; Harley, 2011; Leonard, 2000), resulting in dramatically different communities governed by novel ecological processes (Blois et al., 2013; Klanderud and Totland, 2005; Urban et al., 2012; Hawkins et al., 2009). Studies undertaken within terrestrial and freshwater systems have generally found that altered biotic interactions are more important in structuring populations and communities than changes in abiotic conditions (Ockendon et al., 2014). For example, increasing temperatures have been shown to increase the relative importance of top-down versus bottom-up effects (Hoekman, 2010; Kratina et al., 2012; Carr and Bruno, 2013), strengthen plant-herbivore interactions (O'Connor, 2009), and favour positive over negative species interactions (He et al., 2013). Nevertheless, studies examining how warming influences species interactions and community structure are relatively few, and require further comparisons across multiple systems, particularly within the marine environment (but see Blake and Duffy, 2012, Mrowicki and O'Connor, 2015, Morelissen and Harley, 2007).

The significance of altered biotic interactions in shaping community responses to global climate change has only recently been appreciated. This is in part due to the predominance of studies assessing the impacts of climate change on individual species (Kordas et al., 2011; Araujo et al., 2011; Queiros et al., 2015; Kroeker et al., 2013) and the difficulty of manipulating temperatures in the field (Wernberg et al., 2012). The benefits of such in situ temperature manipulations are twofold: they test the effects of warming on whole communities and validate climate change models predicting the future state of highly complex systems. Assessing these interactions are now possible because recent advances in manipulating temperatures in the field have been made within both the marine (Smale et al., 2011; Lathlean and Minchinton, 2012; Kordas et al., 2015) and terrestrial environment (Norby and Luo, 2004; Rustad et al., 2001; Klanderud and Totland, 2005; Steinauer et al., 2015; Petchey et al., 1999; Post, 2013; Chapin et al., 1995). Such field studies have shown that increasing temperatures can produce dramatically

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different community structures. For example, four years of experimental warming and nutrient loading reduced community diversity in an alpine plant community through changes in biological interactions (Klanderud and Totland, 2005). Likewise, elevated temperatures enhanced the growth and abundance of shrubs in moist tussock tundra in Alaska but reduced the production of nonvascular plants (Chapin et al., 1995). The question remains, however, whether such changes in community structure emerge primarily from the responses of individual species to increasing temperatures or due to altered species interactions.

Rocky intertidal shores have long been used as natural laboratories to test a range of ecological theories that have been subsequently validated within other systems (e.g. Connell, 1979). More recently, rocky intertidal communities have been proposed as bellwethers of global climate change because many intertidal organisms already live at or close to their upper thermal limits (Helmuth et al., 2006; Somero, 2010). Indeed, numerous studies have reported changes in the geographical distributions and abundances of many intertidal species that correspond with increasing temperatures over time (e.g. Barry et al., 1995; Harley and Paine, 2009; Pitt et al., 2010; Southward et al., 2004). Therefore, it is not surprising that, given the ease in which biotic and abiotic factors can be manipulated, rocky intertidal systems are again considered to be useful models for understanding how climate change and altered species interactions will impact the structure and functioning of future natural communities (Harley, 2011; Miller et al., 2014).

Temperate rocky intertidal communities of south eastern Australia generally fluctuate between two alternate states within the midshore region: those dominated by the subtropical barnacle *Tesseropora rosea* or those dominated by the limpet *Cellana tramoserica* (Underwood et al., 1983) (Fig. 1). Within the former, high densities of *T.rosea* exclude *C. tramoserica* and reduce their ability to graze on microalgae (Underwood et al., 1983). Increased *T. rosea* densities also (i) promote the growth of epiphytic algae (Jernakoff, 1985), (ii) provide thermal refugia for littorinids and other small gastropods (Creese, 1982; Jernakoff and Fairweather, 1985; Lathlean, 2014), and increase food availability for the predatory whelk *Morula marginalba* (Fairweather, 1988). By contrast, communities dominated by the limpet *C. tramoserica* are characterised by large amounts of bare rock and low densities of the barnacle *T. rosea* (Underwood et al., 1983). This is because *C. tramoserica* inadvertently ingests or dislodges newly settled barnacle larvae whilst grazing on algae. In some instances, *C. tramoserica* may indirectly facilitate barnacles via reducing the abundance of competing algae and creating free space which could be colonised by barnacle larvae (Underwood et al., 1983; Lathlean et al., 2013). Therefore, the interaction between *C. tramoserica* and *T. rosea*, and the modification of free space, is a highly influential biotic process operating on these shores. Yet how might this change under future warming?

Whilst we currently do not know the specific vulnerabilities of rocky intertidal species in southeast Australia it could be argued that mobile grazers, such as *C. tramoserica*, may be expected to spend more time seeking refuge from increased levels of heat-stress thus reducing their consumption of macroalgae and their overall fitness or may graze in areas with less thermal stress. Indeed, the homing behaviour of *C. tramoserica* and its reduced mobility compared to other mid intertidal gastropods (Underwood, 1977) may make this species more susceptible to rising temperatures. In addition, since *T. rosea* reaches its highest densities within subtropical regions of eastern Australia and declines towards its southern range limit (Lathlean et al., 2010; Lathlean et al., 2015), we might expect abundances of *T. rosea* to increase within temperate regions as air and sea temperatures continue to rise, of which the latter is more than three times faster than the global average (Lough, 2009; Ridgway and Hill, 2009; Cai et al., 2005). This in turn may displace *C. tramoserica* and reduce its competitive dominance, leading to rocky intertidal communities dominated by either barnacles or macroalgae along with reduced unoccupied primary substrata (Underwood et al., 1983).

The aim of this study was to simultaneously test the effects of increasing temperatures on the structure of mid intertidal communities in southeast Australia in the presence and absence of a key herbivore. We achieved this by deploying black and white plates to passively manipulate substratum temperatures and by manipulating the relative abundances of the dominant grazer *Cellana tramoserica*. Being released from grazing pressure, we expected areas without *C. tramoserica* to become increasingly dominated by macroalgae or barnacles, whereas areas with *C. tramoserica* were expected to remain free of macroalgae. Furthermore, where *C. tramoserica* had been excluded we expected abundances of barnacles and macroalgae to be negatively affected by

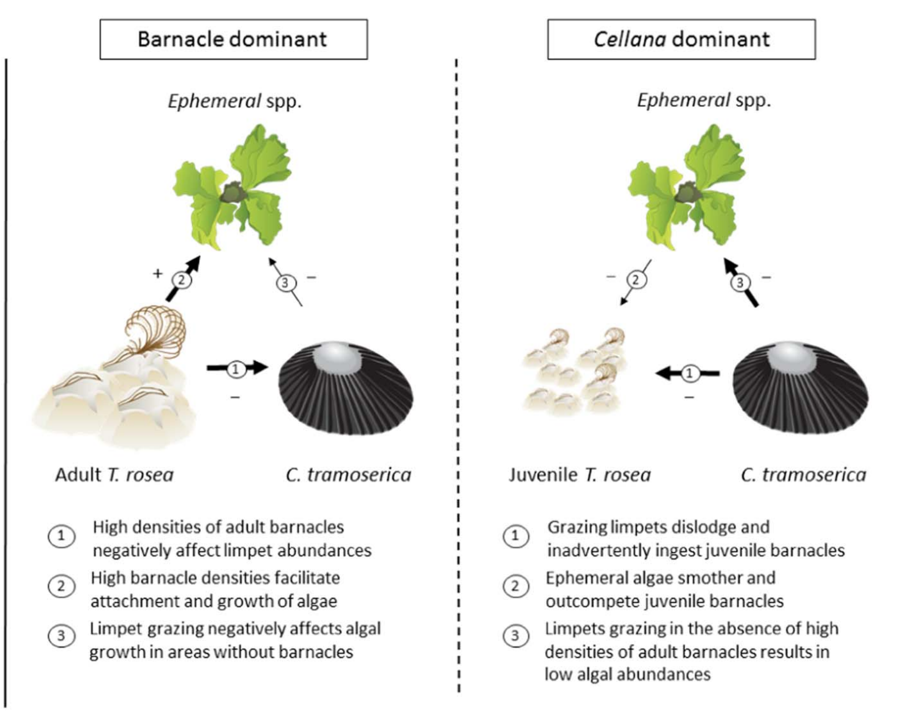

Fig. 1. Conceptual diagram illustrating the changes in the strength and direction of biotic interactions depending on the abundance/dominance of either the barnacle *Tesseropora rosea* or the limpet *Cellana tramoserica* on mid intertidal regions of rocky shores in southeast Australia.