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Can strong consumer and producer effects be reconciled to better forecast
'catastrophic' phase-shifts in marine ecosystems?

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ABSTRACT

The indirect effects of climate on species interactions were initially surprising, but ecological models that account for ecosystem decline have long underestimated their ubiquity and strength. Indirect effects not only yield “unexpected results”, but also some of the strongest ecological effects (i.e. phase-shifts) that have been regarded as “catastrophes” on coral reefs, “collapses” of kelp forests and “crises” in seagrass meadows. Such effects went unanticipated because the impact of one species on another required knowledge of a third element that was inadequately understood. Subsequent debate over the causes of habitat loss has often been polarised by two extreme points of view, i.e. consumer versus producer effects. It is our perspective that these debates will persist unless we clarify the context-dependency of two kinds of indirect effect; those driven by strong *consumer* effects and those driven by strong *producer* effects. On human-dominated coasts, loss of coral, kelp and seagrass can occur as a function of change in trophic cascades (i.e. *consumer* effects) as well as change to competitive hierarchies (i.e. *producer* competition for resources). Because production and consumption are under strong physiological control by climate (providing predictable responses), there is merit in recognising the type and context of indirect effects to reduce errors associated with model-based forecasting. Indeed, forecasts of how global (e.g. elevated temperature and CO₂) and local drivers (e.g. fishing and pollution) combine to drive ecological change will often depend on the relative strength of different kinds of indirect effects (i.e. consumer effects v. producer effects). By recognising the context-dependency of the indirect effects under investigation, the information content of forecasts may not only increase, but also provide an improved understanding of indirect effects and community ecology in general.

1. INTRODUCTION

Early research into the ecological consequences of climate change has primarily focused on direct effects, reflecting the historical idea that the strongest drivers in ecosystems are direct. While readily detectable, direct effects do not necessarily play predominant roles in shaping communities relative to indirect effects (Benedetti-Cecchi, 2000). The detection of indirect effects relies heavily on experimental studies, hence their ubiquity has become increasingly appreciated since experimental ecology gained reputation (e.g. Root, 1973; Menge, 1976). Recognition of the strength of experiments reached prominence in studies of iconic ecosystems (e.g. coral reefs, kelp forests and seagrass meadows) that transition to a contrasting state under altered environmental conditions (e.g. shifts to primary producers of simpler architectural complexity; Bellwood et al., 2004; Connell et al., 2008).

As the name implies, “indirect” effects are not as simple to identify as “direct” effects and can often yield “unexpected results” (Wootton, 1994). They are often unanticipated because the impact of one species on another requires knowledge of a third species or mediating component which is poorly understood. Even when mediating components of a system are well understood, they tend to be well understood at only a few select sites (Bruno, et al., 2009) and their generalisation may be highly contingent on species-specific and system-specific factors, such as palatability of primary production, recruitment dynamics, system openness, and differences in the spatial and temporal scale of consumer population dynamics. These complexities challenge our capacity to predict the conditions in which strong indirect effects occur.

Habitats comprised of coral, kelp and seagrass have become model systems for assessing phase-shifts (e.g. Steneck et al., 2002 for kelps; Hughes et al., 2007 for corals; Eklof et al., 2008 for seagrass). In their ‘natural’ state, these habitats form three-dimensional structures that are continuously disturbed and readily reassemble after natural disturbances. When these foundation species (*sensu* Dayton, 1975) fail to regenerate after natural or human impacts (Hughes et al., 2005)

their replacements are of contrasting species identity and diversity. These replacements can bring such penetrating changes to productivity, energy flow and human economies that they have been regarded as “catastrophes” (Hughes, 1994) , “collapses” (Jackson et al., 2001) or “crises” (Bellwood et al., 2004).

In this perspective, we focus on a key contingency affecting indirect effects and consider their inclusion in ecological forecasts. The range of indirect effects is extraordinary (Menge, 1995), but can be aggregated into several classes (Strauss, 1991; Menge, 1995). We focus here on two classes: those driven by strong *consumer* effects and those driven by strong *producer* effects. The effect of consumers on phase-shifts (i.e. alterations of trophic cascades) tends to be more commonly studied than that of primary productivity (i.e. alteration of competitive dominance of space), depending on the system and its locality. Studies of consumer effects on coral reefs, kelp forests and seagrass meadows centre on the persistence of these habitats via herbivory (i.e. trophic-cascades; Bellwood et al., 2004; Steneck et al., 2002, Heck and Valentine, 2007). Studies of producer effects centre on abiotic changes that alter the relative dominance of ephemeral algae over kelps (Gorman et al., 2009), smother seagrass (Walker and McComb, 1992), or enhance seaweed control of coral reefs (Littler et al., 2006). Because phase-shifts are often a consequence of changes to a balance between primary productivity and its consumption, recognising the factors that alter this balance are key to forecasting their effects.

2. CONSUMER VS PRODUCER EFFECTS

If ecologists are to advise on the most effective local-scale adaptations to future climate change, which necessarily involve management of non-climate impacts (e.g. fishing and pollution), then knowledge of the regional to local-scale contingencies of non-climate impacts and their interactions with changing climate are cornerstones of such advice. A key difficulty for ecologists is that the most

thoroughly researched and understood models are derived from a few select sites, and we are often in a poor position from which to judge the generality of these models, let alone their context dependencies (Connell and Irving, 2009). The following concept attempts to provide a framework within which to recognise the generality and dependences of such strong effects.

On human-dominated coasts, loss of coral, kelp and seagrass can occur as a function of change in trophic cascades (i.e. consumer effects) as well as change to competitive hierarchies (i.e. producer competition for resources). These are often regarded as top-down (i.e. trophic cascades) and bottom-up effects (i.e. resource limitation), but this dichotomy only fuels debate by focusing on polarised extremes (Graham et al., in prep). Kelp forests, coral reefs and seagrass meadows have been the focus of heated controversy about the relative strength of these alternate drivers (e.g. Hughes et al., 1999 v. Lapointe, 1999) and recent calls for critical reassessments of the generality of phase-shifts and their mechanisms (e.g. kelp forests, Foster and Schiel, 2010; coral reefs, Bruno et al., 2009; seagrasses, Heck and Valentine, 2007). We argue that confusion about the generality, locality and causes of phase-shifts maybe reconciled by recognising them as a consequence of a shift in the balance between production and consumption of key species or groups of species. This emphasis is not new. Lindeman (1942) recognised the integrative use of this basic concept in his revolutionary article that gave birth to modern ecosystems ecology.

Systems governed by strong consumer control relative to producer control are likely to be less susceptible to variation in conditions that alter primary productivity. Rather, variation in the processes that alter rates of consumption of primary productivity drive susceptibility to habitat loss. Systems under strong producer control relative to consumer control are less likely to be susceptible to variation in rates of consumption and more susceptible to variation in processes that accelerate primary production of species that facilitate loss. These effects essentially define the classical top-down vs bottom-up dichotomy, but they represent extremes of a continuum. Problematically, many localities are specifically chosen for study because they have the right combination of species and

conditions necessary for tests of particular strong effects of predilection to the researcher. The intense study of such localities tends to give the false impression of the ubiquity of the particular kind of effect under scrutiny. Hence, the global readership is unable to evaluate the representativeness of the reported effects. In this regard, we argue that authors may improve the value of their reporting by providing information on the context-dependency and representativeness of the indirect effects (i.e. relative strengths of production and consumer effects). Lack of information about representativeness is a persistent contributor to uncertainty about the generality of ecological theory, an issue that may be redressed as the discipline matures towards the explicit incorporation of the world's best understood localities into broader-scale assessments that link patterns of interest with processes of relevance (Connell and Irving, 2009).

We propose that a focus on the conditions that shift the balance between production and consumption also enables the integration of local influences into climate studies. Production and consumption are under strong physiological control by climate. They act as integrative measures of multiple effects that do not often work independently across scales. For example, increased metabolic rates in response to rises in temperature can increase consumer control of primary production under elevated nutrients (O'Connor et al., 2009). At local scales, higher nutritional quality of primary producers may propagate into faster growth rates of herbivores which accumulate larger biomass, which leads to greater rates of consumption that counter primary productivity in systems of high consumer potential. Climate change can cause similar indirect effects (Sutter et al., 2007). If production and consumption are under strong abiotic control (e.g. the effects of temperature on per capita interaction strength of herbivory; O'Connor, 2009), then these measures may also provide a common basis by which to integrate studies separated by species-specific and system-specific factors.

In Australian kelp forests, for example, there is a contrasting focus between consumer versus producer effects that reflects two different systems: those coasts affected by the Leeuwin Current

and those affected by the East Australian Current (reviewed in Connell and Gillanders, 2007). These oceanic-scale differences drive two kinds of researchers with alternate focuses (i.e. consumer vs producer effects) and little awareness or concern for their integration. We propose that on rocky coasts lacking strong herbivory (i.e. coasts of the Leeuwin Current), declining water quality is associated with increases in turf cover at the expense of kelp cover (i.e. kelps-to-turfs; Gorman and Connell, 2009; Gorman et al., 2009), and concerns about future climate change tend to focus on interactions with water quality (Russell, et al., 2009; Wernberg, et al., 2010). Conversely, on rocky coasts with strong consumer control (i.e. coasts of the East Australian Current), change in consumer abundance has strong effects on kelp loss (i.e. kelps-to-barrens; Andrew, 1993; Ling and Johnson, 2009) and concerns for kelp persistence focus on recruitment and fishing of consumers (Ling et al., 2009). Such recognition for the relative strength of producer and consumer strengths and their contingencies (e.g. associations with oceanography or biogeography) would reduce confusion over the increasing accumulation of local scale details that provide a difficult basis for the interpretation of general or broad-scale patterns.

Phase-shifts on coral reefs (i.e. coral-to-seaweed shifts) have also led researchers to focus on either alterations to consumption or production in isolation, thereby causing discussion to be polarised (e.g. Hughes et al., 1999 v. Lapointe, 1999). There now appears to be a more integrative perspective that recognises both influences (Bellwood et al., 2004), but progress on predicting the locations and conditions of coral-to-seaweed shifts may be improved. Many reefs may be consumer controlled in that they are isolated from nutrient pollution, especially isolated offshore reef systems (e.g. Greenaway and Gordon-Smith, 2006). Yet, the regulating influence of intense herbivory on macroalgae (Mumby et al., 2006) may be quite general, including some inshore reefs (Hughes et al., 2007). In such consumer-controlled localities, concerns about future climate tend to focus on the management of overfishing via marine protected areas (e.g. Hughes et al., 2007). On coral reefs in close proximity to nutrient pollution, such as many inshore reefs, we note that water quality is of increasing concern (Fabricius et al., 2004), with research and management focusing on reducing

pollution as well as loss of herbivores (Littler et al., 2006). At the extreme of strong consumer effects, substantial reduction in herbivory can lead to increases in cover of algae even if there is no change in nutrient availability (McCook et al., 2001), indicating that changes in consumption alone are sufficient for phase-shifts at many locations. At the other extreme of strong producer effects, declines in water quality in localities lacking strong herbivory are likely to be precursors to decreasing coral cover and increasing algal cover (Bellwood et al., 2004; Littler et al., 2006). Use of this conceptual framework (i.e. consumer v. producer effects) may assist researchers to reconcile the extent to which some of the most intensely studied and debated tropical localities represent anomalies (i.e. poor foundations for general models; Bruno et al., 2009) or valued insights into extremes of a continuum of responses.

Phase-shifts in seagrass meadows (i.e. seagrass-to-sand) have been intensely studied over two decades, yet there is recent concern as to whether the research focus has been appropriate, worthy of funding, or of the attention of natural resource managers (Heck and Valentine, 2007). Heck and Valentine (2007) explain broad scale agreement about the causes of seagrass loss (i.e. eutrophication), then challenge the idea by demonstrating that changes in trophic structure can explain the same patterns of loss (i.e. trophic cascades). We consider that such sudden swings of interpretations may be moderated by empirical assessments focused on shifts in both consumer and producer potential as a function of altered conditions (e.g. pollution and fishing). Coastal eutrophication is often linked to an expansion of fast-growing epiphytic algae that smother seagrass leaves and may ultimately drive a shift from seagrass habitat to bare sand through prolonged inhibition of photosynthesis (Walker and McComb, 1992; Duarte, 2002). Such strong producer effects, however, appear particularly common in locations with sparse numbers of herbivores (i.e. weak consumer potential), which may otherwise consume epiphytes to the benefit of seagrasses (Duarte, 2002). Strong consumer effects may be largely under-appreciated (Valentine and Duffy, 2006), particularly under conditions where the indirect effects of over-harvesting of fish cascades via urchins, past the initial benefits of reducing epiphyte biomass and onto the over-consumption of

seagrass. This balance between production and consumption may be altered through nutrient enrichment which can increase the palatability of seagrasses to grazers (Goecker et al., 2005), and thereby strengthen consumption (Power, 1992). Similar to studies of coral and kelp loss, it is difficult to solve the broader problem of seagrass loss through the isolated study of alternate drivers, then hoping that they may be assembled into a coherent theory.

For each system, such dichotomous and abruptly changing perspectives are useful in promoting debate and ideas, but inhibitory to the synthesis of general theories and the ability to forecast phase-shifts. This uncertainty seems to occur as a function of the lack of knowledge about the relative strengths of the two kinds of indirect effects (i.e. consumer v. producer) and the conditions which shift the balance of strength between the two. It is our perspective that there is interpretive value in studies that recognise this context-dependency (i.e. type and strength of indirect effect), and assess the conditions that shift this balance between production and consumption to produce phase-shifts. Further progress on generality could be prioritised if the best understood localities (i.e. high scientific evidence and agreement) were incorporated with those locations yielding problematic interpretations (i.e. where both scientific interest and uncertainty is high).

3. HABITAT LOSS THROUGH INHIBITION OF REPLENISHMENT

Loss of seagrass through overgrowth by epiphytic algae typically increases local sediment mobility, which can inhibit recruitment (Walker and McComb, 1992) and may contribute to the lengthy recovery times of disturbed seagrass meadows (decades to centuries: Kirkman and Kuo, 1990).

Alternately, loss of coral or kelp often involves rapid colonisation of new space by ephemeral and fast growing algae, which can persist for decades in both coral reefs (Hughes, 1994) and kelp forests (Connell et al., 2008). Identification of the conditions that cause these algae to change function from early successional stages to more permanent occupiers of space is often key to understanding why

corals and kelps fail to regenerate after natural or human impacts. Ephemeral algae, such as turfs, for example, are not usually competitively superior to perennial habitat formers, but can smother seagrasses (Duarte, 2002) and be competitively superior to the early life-history stages of recruiting corals (Birrell et al., 2005; Arnold et al., 2010) and kelps (Gorman and Connell, 2009). They are frequently the primary space occupiers after disturbances such as mass-bleaching events and regional out-breaks of crown-of-thorns starfish on coral reefs (Diaz-Pulido et al., 2002), and storms in kelp forests (Connell, 2005). Even in the absence of major perturbation, rates of mortality of corals and kelps are often high (corals Hughes et al., 1985; kelps Hatcher et al., 1987). Hence the loss of corals and kelps is often less about reduced resistance (i.e. perturbations cause high rates of turnover), and more about the reduced ability for these systems to recover (i.e. resilience).

‘Turfs’ are a recurring component in the reporting of phase-shifts on coral reefs, seagrass meadows, and in kelp forests, and are likely to attract attention in climate studies (e.g. Russell et al., 2009). Turfs appear to transform a pulse event (e.g. bleaching, storms) into a persistent disturbance or chronic stress that makes recovery slow or unattainable (i.e. reduced resilience). ‘Turf’, however, is one of those words that changes meaning depending on the locality or observer and is often defined in retrospect in ways that attempt to capture those taxa that otherwise would be omitted from the description of an assemblage. Hence, there is considerable work required to understand their common properties and the conditions in which they persist or facilitate latter successional stages of algae that dominate in place of corals and kelps.

What is increasingly recognised is that sediment and turfs provide positive feedbacks for each other because the life-history and physiology of turfs are better suited to nutrient overloading (Worm et al., 1999; Gorgula and Connell, 2004) and their sediment-trapping morphology enables them to rapidly recruit to and retain space under heavy coastal sedimentation (Airoldi et al., 1998). Turfs, like many fast growing and ephemeral algae, lack the ability to store nutrients and have a growth strategy that allows them to exploit sudden increases in nutrient, but collapse when resources are

depleted (Pedersen and Borum, 1996). Hence, conditions with a continuous supply of nutrients allow them to persist. Turfs are also better able to withstand the negative effects of sedimentation than their competitors (e.g. corals, Birrell et al., 2005; kelps, Airoidi and Beck, 2007). It is not clear whether it is the turfs themselves, or the sediment they trap that inhibits coral and kelp recruitment. Whether forecasted climate (e.g. elevated temperature and CO₂) represents abiotic conditions that also enable turfs to persist for longer periods of time appears to be a gap in the understanding of their future role in phase-shifts (Connell and Russell, 2010). While there is still debate surrounding whether elevated CO₂ will have direct positive effects on the productivity of macroalgae, recent experimental evidence that both temperate and tropical turfs will increase in abundance under future conditions (Table 1; Connell and Russell, 2010) illustrates the merit of increasing the breadth of consideration of elevated ocean-CO₂ beyond the effects of ocean-acidification on calcifying organisms.

4. FORECASTING CLIMATE EFFECTS

We define “forecastable” and “predictive” ecosystem attributes as those that may allow uncertainty to be reduced to a point from which forecasts yield useful information (Clark et al., 2001). Prediction of the future has a long history (e.g. omens and prophecy) that is renowned for its variable usefulness (e.g. agricultural and economic forecasts; Bernstein, 2004), but remains highly sought after because humans are inherently interested in reducing uncertainty about the future (Van der Sijde et al., 1996). Ecologists have dedicated substantial volumes to recognising the types and uses of prediction and their possibilities and limitations (e.g. Peters, 1991; Brown, 1995; Carpenter, 2002). Despite this long history, the information content of ecological forecasts may be low. We openly admit that the dynamics of many systems are hard to predict because of difficulties in identifying thresholds, nonlinearities and synergisms (Scheffer et al., 2001), and because many events are simply unpredictable (e.g. extreme events, disease).

To date, ecological forecasts about the consequences of future climates have largely relied on species-climate envelope models which provide initial insights into how species ranges may shift or risk extinction (e.g. Araujo and Rahbek, 2006). The approach uses correlations between environmental variables (e.g. temperature) at the boundary of a species range to estimate a species 'fundamental niche space'. Assuming that the current range edge is set by some aspect of climate, future ranges are forecast by projecting future climate conditions across a landscape (or seascape). There are two separate yet interlinked limitations of these models. First, the effects of climate on the range boundaries of a species are likely to be altered by local environmental conditions at the range edge, and these conditions are likely to differ among localities as the range shifts with a changing climate. Second, they assume similar strength and direction of species interactions, which even under no change in species composition is a difficult assumption because many interactions are under strong abiotic control (O'Connor, 2009).

The type and scales of observation of proxies for climate may need more consideration than we currently allow (Hallett et al., 2004), including the failure to detect discrete extreme events (c.f. annual and monthly averages) and ecological dependences at small scales. For example, sea surface temperature may not be an effective proxy for an organism's body temperature (Helmuth et al., 2010). Even the well understood consumer-prey interaction between *Pisaster ochraceus* and *Mytilus californianus* cannot be predicted based on environmental temperature alone given site-specific differences between predator and prey body temperatures (Broitman, et al., 2009). To assist species-climate models, therefore, knowledge is needed on indirect effects and their sensitivity to climate.

Whilst the indirect effects of climate on species interactions were initially surprising (Sanford, 1999), we are starting to learn that they commonly lag behind the more intuitive and easily detectable direct effects, and can even reverse the direct effects of climate (Suttle et al., 2007). Forecasts that require assumptions about the direction and strength of species interactions can predict outcomes

consistent with reasonable expectations (e.g. increases in fishery landings via climate driven increases in the rate of primary production; Brown et al., 2010). It is sometimes both surprising and sobering that the theoretical basis of such forecasts may not be detectable (e.g. increasing rates of primary production are countered by biotic interactions under future climate conditions; Gaedke et al., 2010) and simple models which ignore indirect effects may either underestimate (e.g. where synergies occur) or overestimate (e.g. where effects are counter balanced) the effects of a changing climate.

For these reasons, the nature and scales of such effects need to be understood and such assessments require long-term experiments. Experiments offer feedback on the potential validity of mathematical and conceptual models by revealing the unanticipated effects of climate (e.g. strong indirect effects; Lensing and Wise, 2006). A recent trend for criticising analyses in favour of alternate techniques (e.g. Fidler et al., 2004; Fidler et al., 2006) has met with a thoughtful and robust defence (Hurlbert and Lombardi, 2009) that is tinged with humour and worth reading. Some of this sway in popularity of alternate schools of quantitative philosophy was anticipated four decades ago (Van Valen et al., 1974), but it would be unproductive if such repositioning diminishes the use and rigour of experimental ecology.

The challenges facing an experimentalist's contribution to forecasting have similarities to those attempting to interface experimental information with observational information across successively broader areas of space (i.e. local-regional-biogeographic scales). Heterogeneity at small scales, which represents the cumulative conditions (i.e. global, biogeographic, regional, local), suggest that organisms may not respond to overall changes in climate *per se*. Demonstrations of an effect of one or two climate variables (e.g. elevated CO₂ and temperature) without showing the local conditions in which these effects occur are difficult to interpret because they lack realism and context. This is similar to the well known challenges of scaling-up experiments, where lack of understanding of how local abiotic and biotic conditions are repeated across space stifle interpretations about the

representativeness of results and the conditions upon which they are contingent (Connell and Irving, 2009). Indeed, Carpenter's (2002) essay on ecological forecasting starts with the sentence "Ecology cannot ignore context".

As forecasting grows in sophistication, we believe that more and more ecologists will not only improve the interpretive value of their research by revealing interactions between climate and non-climate impacts, but will also demonstrate how these effects vary according to context (i.e. variation in abiotic and biotic conditions). Forecasts of ecological responses over large geographical scales require an understanding of how environmental conditions vary at relevant scales of space and time. This requirement may encourage experimental ecologists to widen the scope of their studies rather than take refuge in studies that narrow the issues to those most resolvable. A cost involved with the rise of experimentation and its transformation of ecology from a "descriptive" to a "rigorous" science, was that it demanded rigour to the extent that ecologists sought issues most open to unambiguous and precise resolution. Hence, experimentalists avoided investing effort on issues in which uncertainty could not be easily redressed (e.g. scaling-up, Connell and Irving, 2009). If ecological forecasting is to provide greater information content, both experimental and modelling approaches will confront, rather than ignore, complexity across scales.

One fundamental challenge centres on a more explicit consideration of scale. Here, we illustrated scales of 'local' influence with examples of fishing and pollution and scales of 'global' influence with pH/CO₂ and temperature. Whilst the origin of these influences may be classified as global or local, their expression and ecological effects are unlikely to be well understood by using overly simplistic dichotomies. 'Global' conditions of pH and temperature are not uniformly expressed in space or time. 'Local' depletion of consumers may be expressed over very large scales. Similar to our arguments about research into indirect effects, we suggest that greater insights about interactions between climate and non-climate impacts are possible if we move beyond simple dichotomies (e.g. local v. global) towards integrative assessments across scales of influence.

5. CONCLUSIONS

If the causes of phase-shifts are to be understood, or even predicted, then progress centres on understanding the relative contributions of different causes of decline, particularly in realistic combinations that reflect their cumulative effect across global to local scales. Frustration with pace of progress and agreement on these issues (Pandolfi, et al., 2005) is perhaps unhelpful to progress in ecology (Littler et al., 2006) and conservation (Precht et al., 2005). Rather than being an opportunity to continually identify truly unique and novel ideas, much of this work may be painstaking, and models that account for phase-shifts will be under constant review.

Confusion has arisen when the authors of assessments of the consequences of climate and non-climate impacts have not recognised the limitations of their inferences. These limitations are often contingent on strong consumer effects (e.g. loss of consumers and its management via fishing policy) that contrast with strong producer effects (e.g. pollution and its management via water quality policy), and fail to recognise the continuum of balance between these two forces. Too much emphasis appears to have been placed on the ubiquity of certain kinds of phase-shifts (as reviewed by Bruno et al., 2009 for coral-seaweed shifts) or one kind of indirect effect at the expense of alternate causes (reviews by Heck and Valentine 2007 for seagrasses; Foster and Schiel, 2010 for kelp forests). Nevertheless, the repeated observation of phase-shifts in coral (review by McManus and Polsenberg, 2004), kelp (review by Airoidi et al., 2008) and seagrass systems (Eklof et al., 2008) means that they will continue to represent opportunities for the study of profound ecological effects.

The balance between production and consumption of species that provoke ecosystem change is often shifted by local influences that are contingent on middle-scale influences (e.g. biogeography) and together are mediated by climate. We have demonstrated that it is difficult to solve the broad problem of predicting 'catastrophic' phase-shifts through the isolated study of alternate drivers and then hoping that they may be assembled into a coherent theory. Instead, more may be achieved by

reconciling the relative strengths of producer and consumer effects which not only incorporate the study of alternate drivers, but also provide a common basis from which to integrate studies separated by species-specific and system-specific factors.

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Table 1. Forecasted CO₂ concentration (~600 ppm) reduces the space available (mean ± SE) for recruitment of corals and kelps via enhanced cover of inhibitory-turfs. Increasing CO₂ may have indirect effects (e.g. transformation of ephemeral algae into more persistent contributors to coral loss), that rival it's direct effects (e.g. ocean acidification on corals).

Availability of space for recruitment	Corals	Kelps
Under current [CO ₂]	57.8 % ± 1.5	58.0 % ± 4
Under future [CO ₂]	18.9 % ± 4.0	4.5 % ± 2.5

Data are from replicated experimental procedures on temperate and tropical seas (Russell et al., in prep.).

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