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# Reports

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# The duality of ocean acidification as a resource and a stressor

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*Abstract.* Ecologically dominant species often define ecosystem states, but as human disturbances intensify, their subordinate counterparts increasingly displace them. We consider the duality of disturbance by examining how environmental drivers can simultaneously act as a stressor to dominant species and as a resource to subordinates. Using a model ecosystem, we demonstrate that $CO_2$-driven interactions between species can account for such reversals in dominance; i.e., the displacement of dominants (kelp forests) by subordinates (turf algae). We established that $CO_2$ enrichment had a direct positive effect on productivity of turfs, but a negligible effect on kelp. $CO_2$ enrichment further suppressed the abundance and feeding rate of the primary grazer of turfs (sea urchins), but had an opposite effect on the minor grazer (gastropods). Thus, boosted production of subordinate producers, exacerbated by a net reduction in its consumption by primary grazers, accounts for community change (i.e., turf displacing kelp). Ecosystem collapse, therefore, is more likely when resource enrichment alters competitive dominance of producers, and consumers fail to compensate. By recognizing such duality in the responses of interacting species to disturbance, which may stabilize or exacerbate change, we can begin to understand how intensifying human disturbances determine whether or not ecosystems undergo phase shifts.

*Key words:* *calcifying herbivores; climate change; $CO_2$; kelp forest; phase shift; turf algae.*

## Introduction

Ecosystem states can be maintained or created by ecological dominants (e.g., kelp forests and coral reefs), but as human disturbances intensify these habitats are increasingly displaced by their competitive subordinates (e.g., mats of turf algae; Steneck et al. 2002, Hughes et al. 2007). The mechanisms through which this occurs generally center on the role of disturbance in suppressing competitive dominants and the subsequent release of subordinates from competition (Tilman and Lehman 2001). Yet, this paradigm overlooks the duality by which some forms of disturbance such as elevated $CO_2$ operate, specifically that it can provide opportunities for one competitor (i.e., acting as a resource) while constraining the other (i.e., acting as a stressor). Resource enhancement can thus reverse competitive dominance by increasing productivity of subordinates, which then may replace dominants (Bertness et al. 2002, Connell et al. 2013, Yan et al. 2014). These effects can be further enhanced when stressors impede the functional role of consumers (e.g., herbivores), that ordinarily keep subordinates in check (Ghedini et al. 2015).

Resources and stressors that mediate the productivity of producers can also determine consumer response (Chase et al. 2002). Indeed, the balance between changing resource availability to primary producers and the intensity with which they are consumed is a critical tension in the stability of ecosystem states (Connell and Ghedini 2015). For example, nutrient pollution acts as a resource to trigger community shifts (Scheffer et al. 2001), but when it is accompanied by a countervailing increase in herbivory (Cottingham and Schindler 2000), these bottom-up effects can be neutralized (i.e., trophic compensation; Ghedini et al. 2015). In cases where increased consumption indirectly negates the direct effect of disturbance, the competitive hierarchy, and ultimately community stability, can be maintained through compensation (Post and Pedersen 2008). In contrast to stability, ecosystem change (i.e., phase shift) occurs when stressors suppress consumers or resources boost producers, normally subordinate plants are then released from consumer control or resource

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limitations (Vitousek et al. 1997, Scheffer et al. 2001). When consumption is suppressed, subordinate producers may gain an advantage as they may be released from their subordinate status and exert a significant competitive effect on the normally dominant species (Chapin et al. 1997, Post and Pedersen 2008).

The effects of resources and stressors are likely to be unequal among species, generating potential shifts in species dominance where some species gain a relative advantage over their competitors (Monaco and Helmuth 2011). An emerging concern is the duality of effects of increasing concentrations of anthropogenic carbon dioxide ($CO_2$), which can act as a resource (positive effect; Connell et al. 2013) via the provision of inorganic carbon as a nutrient for primary producers, or, conversely, as a stressor (negative effect; Orr et al. 2005) to calcifying consumers via ocean acidification. Elevated $CO_2$ can therefore create competitive imbalances in communities by affecting one primary producer more than another and changing the intensity of their consumption by herbivores (Ghedini and Connell 2016). This, in turn, may drive shifts in community composition.

We tested for the displacement of competitively dominant kelp by competitively subordinate turf algae using natural $CO_2$ vents. Competition between kelps and turfs has an intensive history of research internationally (for a review, see Strain et al. [2014]) and especially in Australasia (Gorman et al. 2009). An increase in limiting nutrients has been shown to drive displacement of kelp forests by turfs, whereby turfs rapidly expand, dominate space (Russell et al. 2009), and inhibit kelp recruitment (Gorman and Connell 2009) to generate the conditions for a phase shift (Connell et al. 2008). In turn, processes that oppose turf expansion, such as herbivory, enable kelp replenishment and persistence. For herbivory to compensate for resource disturbance, however, herbivory must proportionally increase to match the rate of expansion of the competitively subordinate primary producers (Ghedini et al. 2015). We investigated whether $CO_2$ enrichment at natural vents could act unequally as a resource for kelp (*Ecklonia radiata*) and turf and whether the functional role of grazers (gastropods, *Eatoniella mortoni* and urchins, *Evechinus chloroticus*) could maintain the dominant role of kelps by compensating for changes in turf productivity. We then tested our predictions by comparing whether the turf phase occurred more frequently and extensively than the normally dominant phase (i.e., mosaic of kelp forest and urchin barren) at site with near-future $CO_2$ concentrations.

## Methods

### *Study site and species*

We assessed responses of algal habitats and their inhabitants to natural $CO_2$ vents at Te Puia o Whakaari (White Island), Bay of Plenty, New Zealand (37°31.013′ S, 177°11.649′ E). Our study area represents a rocky reef habitat characterized by a mosaic of kelp (*E. radiata*), turf algae (see Appendix S1) and sea urchin barrens devoid of vegetation (Connell and Irving 2008). Consumers comprised a gastropod (*E. mortoni*) and a sea urchin (*E. cholorticus*) for which urchins are usually the primary cause of barrens through the consumption of kelps and turfs (Shears and Babcock 2002) and together are most abundant herbivores at Whakaari.

Two independent vents (north and south) and two independent and interspersed control sites (north and south) were sampled along the northeastern coast of the island (Appendix S1: Fig. S1). The $CO_2$ plumes at vent sites extended ~24 × 20 m from the source at 6–8 m depth and represented approximate end-of-the-century projections in pH reduction (Bopp et al. 2013) without confounding differences in temperature (Appendix S1: Table S1a,b). Previous studies of Whakaari have demonstrated a pH gradient from vents to ambient conditions at these scales using uranium concentrations as a tracer of seawater pH in biogenic carbonate (Doubleday et al. 2017; Appendix S1). A detailed description of sites and their water chemistry is also provided (Appendix S1) as related to pH concentrations of RCP 8.5 "business-as-usual" projections (Bopp et al. 2013). Differences in pH among these sites (i.e., vents vs. controls) have been linked to variation in abundance of primary, secondary, and tertiary producers (Nagelkerken et al. 2016, Connell et al. 2017) that have been replicated in controlled macrocosms manipulating $CO_2$ (and thus pH) alone (Goldenberg et al. 2018).

### *Relating simplified habitat mosaics to change in productivity*

We tested the prediction that turfs dominate vent sites (i.e., elevated $CO_2$) and natural mosaics of kelp forests and urchin barrens dominate control sites (i.e., contemporary $CO_2$). In February 2015, we sampled across these this mosaics of habitat ($n$ = 25 transects per site × 4 sites [2 vents, 2 controls]; $N$ = 100 transects) in which percentage cover of kelps and turfs was calculated from within randomly positioned 1 × 15 m transects (see Connell et al. 2008 for technique).

Rates of oxygen production (i.e., $O_2{\cdot}cm^{-2}\ min^{-1}$) for kelps and turfs were determined at all control and vent sites in February 2015 (Appendix S1). To obtain representative estimates of production, samples of each taxon were randomly chosen. For kelp, these rates were quantified using a photorespirometer (30 cm wide × 41 cm high cylinder) designed to quantify oxygen production in situ of an entire kelp, *E. radiata* (Rodgers et al. 2015; $n$ = 6 randomly chosen kelp per site, $N$ = 24 kelp). During incubations, dissolved oxygen and temperature were measured inside photorespirometers using an optical dissolved oxygen logger (D-OptoLogger; Envco, Auckland, New Zealand). Photosynthetically active radiation (PAR) was measured using a PAR logger (Odyssey Photosynthetic Irradiance Recording System; Dataflow Systems, Christchurch, New Zealand) that was calibrated on land against a LI-190 quantum sensor (LI-COR Biosciences, Lincoln Nebraska, USA). To compare estimates of oxygen production between vents and controls, we standardized production at the scale of 1 $m^2$ ($n$ = 6 kelp·$min^{-1}$ $m^{-2}$). For turf, samples were scraped from rock (i.e., 6.4 cm diameter) washed free of attached animals and detritus ($n$ = 25 for each control and $n$ = 26 for each vent site). Net oxygen production was then quantified using optical oxygen spots and probe (Fibox 4, PreSens, Regensburg, Germany). Turf photorespirometry was done

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in watertight cylinders (400 mL) to compare oxygen production under ambient pH (pH 8.10) and RPC 8.5 forecasts (pH 7.65). Samples were then dried for 24 h at 60°C and weighed to obtain dry biomass for both kelp and turfs. For a detailed account of methods, see Appendix S1.

### *Relating simplified habitat mosaics to change in herbivory*

To estimate the association between gastropod abundance and turf cover, we observed rates of colonization by gastropods on roughened tiles (15 × 15 cm) attached to rock. We quantified the number of gastropods per tile after the cover of turfs reached 100% across all sites (i.e., 28 d). Tiles were then collected, sealed in a plastic bag, and gastropods were counted after removal. Replication of tiles was even across all sites ($n$ = 12 per site, $n$ = 2 controls, and $n$ = 2 vents; $N$ = 48). The abundance of urchins was instead estimated at controls and vents within randomly sampled 1-$m^2$ quadrats ($n$ = 10 per site, $n$ = 2 controls, and $n$ = 2 vents; $N$ = 40).

To visualize how change in turf production and consumption sum to net productivity between vents and controls, we estimated net production as areal expansion of turf in February–March 2016, the mechanism by which turfs inhibit kelp recruitment (Gorman and Connell 2009). These estimates were derived from rates of areal turf growth (i.e., percentage cover) across experimental substratum (15 × 15 cm tiles; $n$ = 12 tiles per site, $n$ = 2 controls, $n$ = 2 vents; $N$ = 48 tiles). To quantify consumption of turf, which facilitates kelp recruitment by creating free space (Connell and Russell 2010), we estimated the per capita rates of removal of turf (per $cm^2$) by each of the two grazers using inclusion cages (i.e., cages with no grazers vs. cages with set density of grazers; Appendix S1). For gastropods, we allowed 30 individuals (see Connell et al. 2017 for description of natural densities) to graze for 3 d on caged tiles (3 × 3 cm) with 100% cover of turf; i.e., 21 d of turf growth ($n$ = 5 per control and vent; $N$ = 10 cages). For urchins, we used a technique developed for this species (Ayling 1981), which entailed placing a single urchin on a caged tile (20 × 20 cm) coated with 100% cover of black paint and quantifying the removal of paint by the characteristic star-shaped bite marks after 24 h ($n$ = 5 per control and vent; $N$ = 10 cages). Estimates of consumption for both taxa were calculated by multiplying the density of grazers by the rate of removal ($cm^{-2}{\cdot}d^{-1}{\cdot}grazer^{-1}$) for each species.

## Results

Overall, net production of turfs was nearly 10-fold higher at vents relative to controls, reflecting greater rates of primary production and reduced rates of consumption (see visual summary, Fig. 1). In contrast, control sites had negligible net productivity, having both lower rates of primary production and more intense rates of consumption by urchins (i.e., barren habitats) compared to vents. Predictively, the size-frequency distribution of turfs shifted toward more frequent larger patches (Fig. 2) in that it increased from a maximum of 6 m diameter patches at controls to a maximum of 15 m diameter patches at vents (Kolmogrov-Smirnov $Kd_{50,50}$ = 0.860, $P < 0.05$). The mosaic of barrens and kelp forest differed in the opposite direction (Fig. 2) so that both habitats were smaller at vents (most ≤ 7 m) compared to controls (up to 15 m) (barrens $Kd_{50,50}$ = 0.280, $P < 0.05$; kelp forest $Kd_{50,50}$ = 0.480, $P < 0.05$).

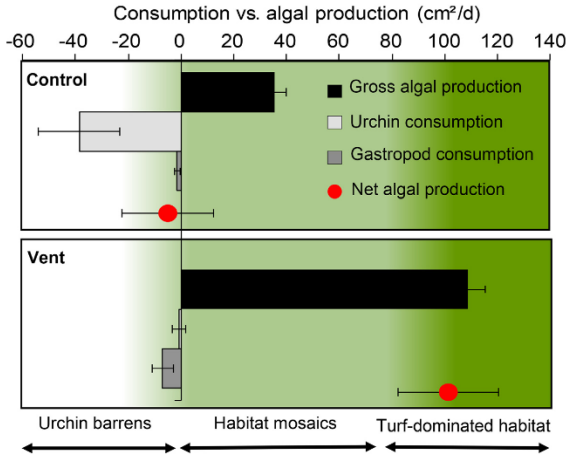



FIG. 1. A visual summary of the unequal effects (resource vs. stressor) of ocean acidification (mean ± SE): gross production of turf algae (black), consumption by urchins (light gray) and gastropods (dark gray), and net production of turf algae (red circles; sum of positive production and total negative consumption). At controls, habitat mosaics exist because net turf productivity is near zero (i.e., mosaic of kelp forest, urchin barrens, and turf mats). At vents, net production is greater because production of turfs is boosted and consumption is suppressed (i.e., turf-dominated habitat). Net production was estimated as areal expansion of turf cover (±), the mechanism by which turfs inhibit kelp recruitment (Gorman and Connell 2009).

The effect of vents (control vs. vents) on oxygen production (μmol $O_2{\cdot}cm^{-2}$ $min^{-1}$) was detected for turfs, but not for kelps (Appendix S1: Table S2). Turfs were strongly affected by vents, such that oxygen production was nearly double that at vents compared to controls (Fig. 3B; ANOVA, $F_{1,48}$ = 17.117, $P < 0.05$). In contrast, production of kelp was not detected to differ between controls and vents (Fig. 3A; ANOVA, $F_{1,1}$ = 12.77, $P > 0.49$), yet the analysis was sufficiently powerful to detect between-site variation (i.e., within the factor vents, ANOVA, vent × site $F_{1,20}$ = 9.98, $P < 0.05$) where northern and southern vent sites differed from each other (SNK tests).

The abundance of urchins was greater at controls than vents (Fig. 3C; ANOVA, $F_{1,36}$ = 57.69, $P < 0.05$) and vice versa for gastropods (Fig. 3D; ANOVA, $F_{1,30}$ = 9.39, $P < 0.05$; Appendix S1: Table S2). This opposing pattern was also evident in the feeding rates of urchins (Fig. 3E; ANOVA, $F_{1,10}$ = 17.35, $P < 0.05$) and gastropods (Fig. 3F; ANOVA, $F_{1,8}$ = 11.90, $P < 0.05$; Appendix S1: Table S2).

## Discussion

Environmental change can provoke opposing responses among species (i.e., positive resource and negative stressor; Harley et al. 2017) and, by assessing the direction and magnitude of these effects, we can unravel the ecological processes that buffer or exacerbate change. We demonstrate that ocean acidification can affect producers and consumers unequally, suppressing compensatory processes (Connell and Ghedini 2015) that would otherwise dampen the direct

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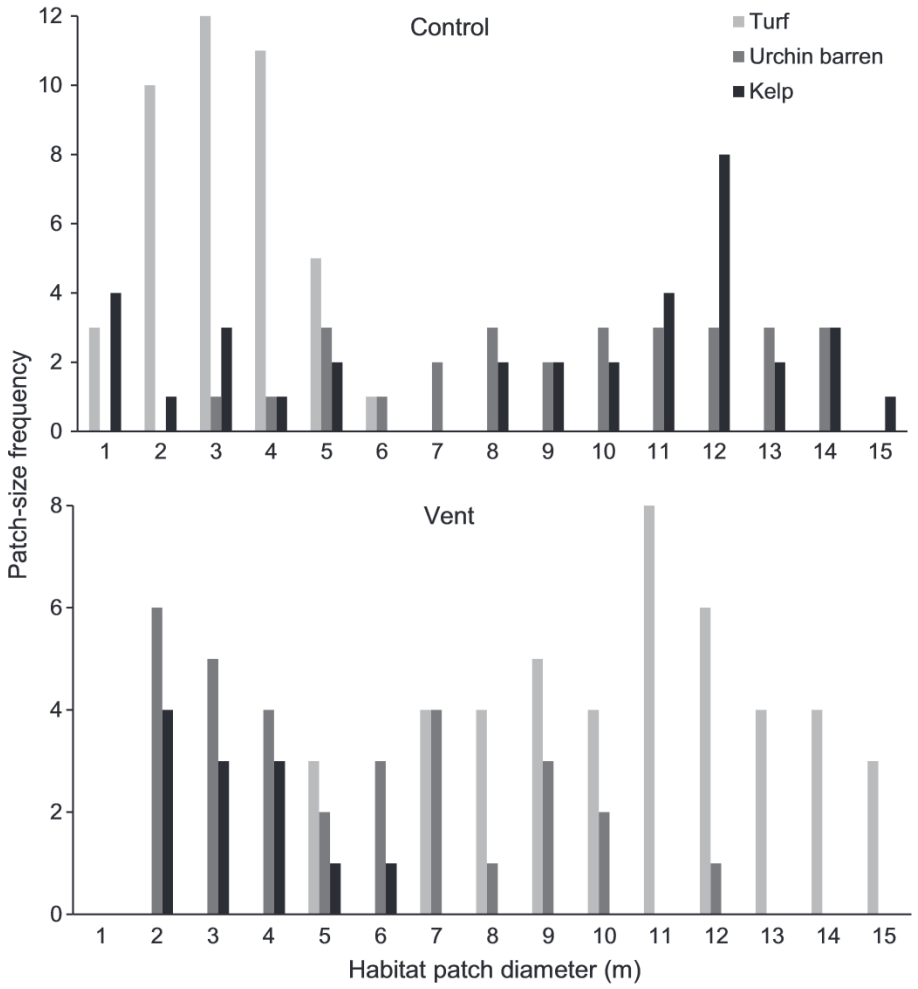



FIG. 2. Habitat mosaics homogenize into turf-dominated habitats. Frequency histogram of patch diameter of turf, barren, and kelp habitat at controls (contemporary $CO_2$ conditions) and vents (future $CO_2$ conditions). Top graph shows extensive mosaics of kelp forests and barrens (dark shades) punctuated by small turf algae (light gray) and bottom graph shows extensive monopolies of turfs (light gray) at the expense of shrinking mosaics (dark shades).

physiological effects of environmental change. For producers, an enriched $CO_2$ environment had a positive effect on subordinates (i.e., turf algae) and a negligible effect on competitively dominant kelp. In turn, for consumers, $CO_2$ suppressed the abundance and feeding rate of urchins, the primary grazer, but had an opposite effect on gastropods, the minor grazers. Such a disproportionate increase in one primary producer over the other, enhanced by a net reduction in consumption, can lead to community imbalance (Fig. 4). We demonstrate the potential consequence of this imbalance in a temperate rocky reef community exposed to enriched $CO_2$ conditions.

Carbon acts as a resource for primary producers (Raven and Hurd 2012) but, as observed here, not to an equal extent. Due to the fast-growing, adaptable, and weedy nature of turf algae, they appear to gain a competitive edge over kelp living in $CO_2$-enriched conditions (Connell et al. 2013). This boost to productivity overwhelms the capacity of herbivores to absorb the excess production, generating a significant increase in net production. While compensation of excess primary productivity occurs when consumption is proportional to the increase in producer biomass (Ghedini et al. 2015), near-future $CO_2$ concentrations caused a collapse in herbivory by the primary grazer, calcifying urchins. It is well documented, in the laboratory at least, that the survival, growth, and abundance of calcifying organisms is often diminished under elevated $CO_2$ conditions (Kroeker et al. 2013). At natural vent sites, we observed similar effects, where there was a reduction in both abundance and per capita rate of consumption by urchins. This suppression of a key grazer would allow turf algae, boosted from carbon enrichment, to proliferate relatively ungrazed. This observation suggests that urchins have not acclimated to enriched $CO_2$ conditions and that acclimation may not always be relied upon to strengthen the resistance of communities to change.

The duality of $CO_2$ enrichment, as stressor and resource, as shown here, is exemplified by its opposing effects on calcifying herbivores. In contrast to urchins, a heavily calcifying gastropod flourished under $CO_2$ enrichment (Connell et al. 2017). Nevertheless, the counter-intuitive response of gastropods at vent sites suggests indirect effects; more food and

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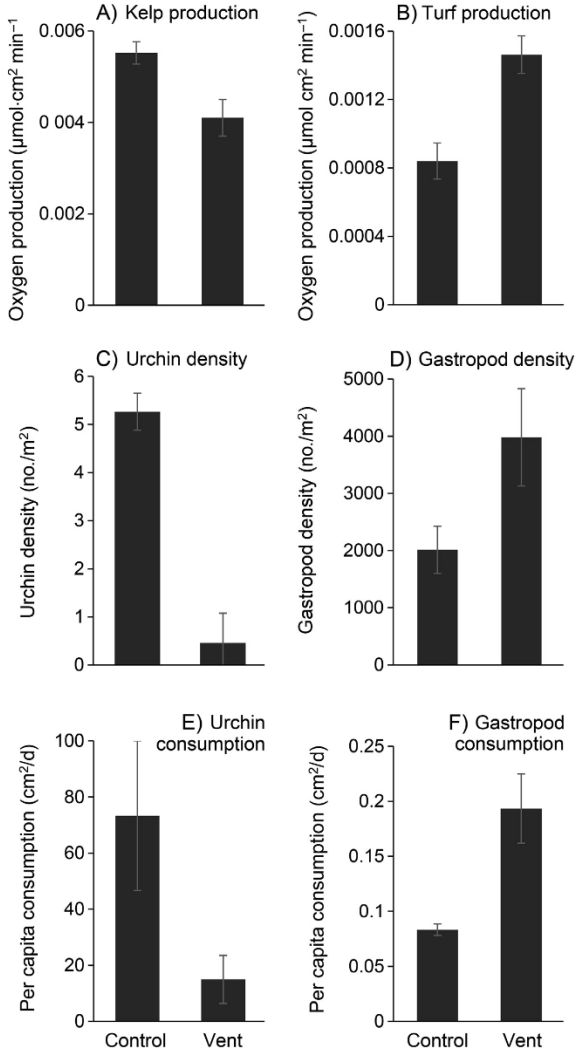



FIG. 3. Influence of vents (future $CO_2$ conditions) on primary producers and consumers (mean ± SE). Oxygen production of (A) kelps and (B) turfs; density of (C) urchins and (D) gastropods; and per capita consumption of (E) urchins and (F) gastropods. Data were pooled across sites at vents and controls. All responses, except kelp, are significantly different between $CO_2$ treatments ($P < 0.05$).

habitat (associated with turfs) shapes the abundance of this grazer more powerfully than direct negative effects (of ocean acidity; Connell et al. 2017). In tandem, their per capita feeding rates increased at vents, which can be associated with either enhanced food quality (i.e., possible increase in nitrogen content in turfs; Ghedini and Connell 2016) or reduced food quality (i.e., possible compensatory feeding for protein dilution; Raubenheimer et al. 2014). Nitrogen availability can improve growth, reproduction, and survival in herbivores (Mattson 1980) and, like carbon, may have unequal effects among species (Poorter and Navas 2003). Nonetheless, despite appearing to thrive at vent sites, gastropods alone could not adequately consume the excess turf productivity, supporting the model of competitive imbalance and an ecological shift in the seascape.

In conclusion, we highlight the duality of disturbance that jointly overwhelms compensatory processes that would have otherwise resisted ecosystem change. In our system, the probability of ecosystem collapse increases when disturbance liberates resources for one species (a primary producer) and suppresses the other (a consumer), an imbalance that inhibits compensatory processes that would otherwise resist change. This, in turn, induces a reversal in competitive dominance that defines ecosystem states. By recognizing this duality and the species interactions that stabilize or exacerbate their imbalance, we can begin to understand the ecosystem processes that counter a changing environment.

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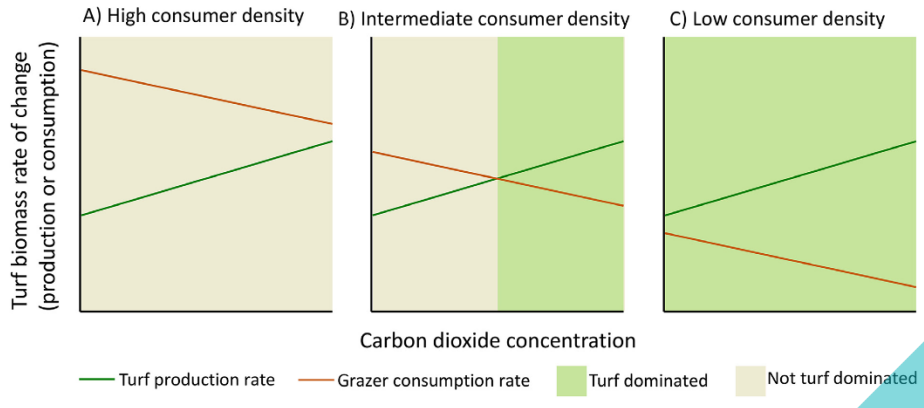



FIG. 4. The degree to which a system is dominated by a particular primary producer depends on rates of production, per capita rates of consumption, and consumer density, all of which may vary with $CO_2$ concentration. For the cases illustrated here, elevated $CO_2$ enhances primary production of turfs, but imparts a cost to consumers. At very high or very low consumer densities, turfs never (A) or always (C) dominate the system, respectively, regardless of $CO_2$. At intermediate consumer densities (B), the balance between production and consumption shifts as $CO_2$ concentration increases, and the system shifts toward turf dominance.

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