Turf facilitation in global marine forests

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Abstract

The Stress Gradient Hypothesis (SGH) predicts primary producer competition and facilitation is related to environmental stress. Despite being well-documented in terrestrial systems, facilitation is rarely integrated into our understanding of the dynamics in marine forests. Critical coastal habitats created by canopy-forming seaweeds have recently been seen to transition to less biodiverse regimes dominated by turf algae and populations are predicted to increasingly transition based on the paradigm that turf algae negatively affect canopy seaweeds. Meta-analysis was used to estimate the effect of turfs on canopy species using experimental and observational data. We found that turf species do compete with marine canopies in subtidal kelp forests, however, these interactions become increasingly facilitative at shallower depths and high latitude, supporting the SGH. This work provides new insight into the dynamics of a highly-studied ecosystem, and emphasizes the need to re-assess the importance of facilitation when predicting the response of systems to global change.

Introduction

Competitive interactions among primary producers have been widely shown to shift to facilitative when conditions become stressful, as predicted by the Stress Gradient Hypothesis (SGH; Bertness & Callaway 1994; Bruno et al. 2003; He et al. 2013). For example, in a study of alpine plant interactions, identically and globally replicated experiments demonstrated that interactions shifted from competitive at low elevations to facilitative at higher, more stressful, elevations (Callaway et al. 2002). This shift from competitive to facilitative interactions along gradients of stress has likewise been shown for arid plants and nurse shrubs (Armas et al. 2011), pitcher plants and spiders (Lim et al. 2018), and alpine herbivores (Barrio et al. 2013), among others. Similar to terrestrial elevational shifts from negative to positive interactions, species interactions among marine and limnal taxa have also been shown to shift from competitive to facilitative in 1) drier, more stressful tidal elevations (intertidal marsh plants: Bertness & Hacker 1994; barnacles and mussels: Kawai & Tokeshi 2007), and in 2) warmer, more stressful latitudes (Bennett et al. 2015; McAfee et al. 2016). Despite being well-documented in terrestrial and brackish ecosystems, the SGH has not been tested in marine forests, and instead competition is thought to be the dominant structuring mechanism (though see Bennett et al. 2015). In this study, marine forest ecosystems were used to examine influences of species facilitation, positive interactions and principles of the SGH in structuring algal communities.

The past decade has seen dramatic declines in marine forest cover (Ling et al. 2015; Krumhansl et al. 2016; Wernberg et al. 2016; Vergés et al. 2016). Foundation species provide habitat and energy to associated organisms (Dayton 1972), ultimately increasing biodiversity. Foundation species persistence is critical for understanding the dynamics of the systems they sustain. One of the most well studied, conspicuous groups of foundation species are canopy-forming brown seaweeds, belonging primarily to the orders Laminariales (kelp) and Fucales (fucoids). Many disturbed marine forests are shifting from canopy-dominated to systems dominated by turf-forming or crustose algae (Filbee-Dexter & Scheibling 2014; Filbee-Dexter & Wernberg 2018), an example of alternative stable states (Dayton & Tegner 1984). With a suite of abiotic and biotic

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stressors contributing to the decline of kelp forests, their recovery is thought to be prevented, in part, by competition with algal species that live in the understory (Filbee-Dexter & Scheibling 2014; Filbee-Dexter & Wernberg 2018).

Negative effects of algal turfs on canopies are well supported from long-term subtidal research programs and experimental studies (Dayton et al. 1984; Hernández -Carmona et al. 2005; Gorman & Connell 2009). Although many canopy-forming species are dominant competitors (Dayton et al. 1984), abiotic and biotic disturbance can lead to the dominance of turf algae, if those turf algae compete with the canopy (Fig. 1A). For example, the co-occurrence of El Niño-driven warm temperatures, nutrient depletion, and unusually strong storms devastated more than 500 hectares of kelp forest in southern California (Dayton & Tegner 1984). In the wake of massive loss of kelp adults and kelp recruitment failure, a new, turf-dominated community emerged, comprised of turf species and subdominant understory kelp. Algal turfs, unaffected by the El Niño disturbances, inhibited the recruitment of new canopy kelp, slowing the kelp forest recovery (Dayton et al. 1984). Although the kelp forest generally recovered after this El Niño, the kelp-dominated community never returned at its southernmost range edge (Hernández-Carmona et al. 2005). The dominance of these turf species, particularly herbivore-resistant coralline algae, is often maintained by the presence of kelp grazers (Vergés et al. 2016), forming the classic coralline algae/urchin barren alternative stable state (Filbee-Dexter & Scheibling 2014). The assumption of competitive exclusion by the turf now forms the basis of recommended restoration practices (Hernandez-Carmona et al. 2005) and even predictions for the future of canopy-forming marine ecosystems (Connell et al. 2013). For example, in the turf-as-competitors framework (Fig. 1A), as coralline turfs are expected to decline with ocean acidification, kelp abundance would be expected to increase under ocean acidification, due to the assumed release from competition and physiological effects from increased$p$ CO_2 (Harley et al. 2012). Despite the dominance of the competition framework in the study of marine forests, many examples exist of canopy facilitation by turfs (Fig. 1B). These examples of facilitation have yet to be comprehensively incorporated into our understanding of canopy-turf dynamics or marine forest alternative stable states.

In this study, we approach competition and facilitation in marine forests within the framework of the SGH and the well-documented patterns seen in terrestrial systems. We examine the longstanding hypothesis that the effect of turf algae on canopy-forming species is competitive, using a new global dataset of marine turf-canopy interactions. We used meta-analysis to answer the following questions: a) What is the overall effect of the turf on canopy-forming seaweeds? b) Does this effect differ among turf functional groups? c) Does the effect of turfs on the canopy vary along stress gradients, i.e. depth? d) Does the effect of turfs on the canopy vary latitudinally?, and d) Does herbivory modify the effect of turfs on the canopy? We expand the number of studies previously included in a meta-analysis of kelp-turf interactions four-fold, and broaden the scope from the effect only on recruitment to the effect on all life-history stages of canopy forming species (O'Brien & Scheibling 2018). We show that the previously well-documented competitive effects of turf species on canopy species are part of a continuum of positive to negative interactions that depend predictably on stress.

Methods

Study Systems

Marine forests generally are created by the large, three-dimensional structure of brown seaweeds in the class Phaeophyceae, primarily the "kelps" (order Laminariales) and fucoids (order Fucales). Generalized terms used to describe functional groups within these systems are not consistent, thus, for the sake of clarity we will use "canopy-forming species" to describe brown seaweeds that create three-dimensional habitat. This includes all canopy species referred to as floating, stipitate, and prostrate canopies in Dayton et al. (1984), also termed surface, understory, and bottom canopies (Schiel & Foster 2015). Algal turfs are a diverse functional group that includes species from all three algal phyla, but refer to shrub-like, filamentous, and branched species that can be opportunistic and provide very little structure (Filbee-Dexter & Wernberg 2018). Alternately, algal crusts are low-lying, prostrate species that closely adhere to the substrate (Steneck & Dethier 1994). These two functional groups can further be divided by whether or not the species is calcified (Steneck & Dethier 1994). These delineations result in four functional groups that interact with canopy-forming species:

coralline turf, coralline crust, non-coralline turf, non-coralline crust. Throughout the manuscript, we often refer to "turfs", given their increasing importance in transforming coastal environments (Filbee-Dexter & Wernberg 2018), but we consider the interactions of each of these four functional groups that live below the canopy.

Data Compilation

We searched the ISI Web of Science database (26 October 2017) and ProQuest Dissertation & Theses database (25 November 2017) to find studies of the effects of turf algae on canopy algal species (see Appendix S1 in Supporting Information for a list of search terms). These searches resulted in 1,916 unique manuscripts. Of these results, studies were included if they met the following inclusion criteria:

- Study type: empirical (no theoretical or modeling papers were included)
- Species studied: canopy-forming algae and understory algae (crustose or turf-forming)
- Treatment: presence/absence of understory algae or gradient of understory abundance

- Responses: canopy algae fitness or population growth in the presence/absence of understory algae, including: density of recruits, population size, mechanical strength, survival, survival
- Comparator: appropriate controls for experimental studies, non-understory algal substrates (when comparing kelp fitness when associated with understory substratum)
- Mean and variance for both experimental and control treatments were reported

A list of the total papers assessed, and whether each was included, can be found in Appendix S1 Table S1. We supplemented these records with additional studies that met our inclusion criteria, obtained via personal communication and literature cited sections of papers. This resulted in included studies from 41 manuscripts (some manuscripts included multiple studies with unique response variables or treatment types). For each study, we recorded the treatment and control effect sizes and variance, the sample sizes, latitude, longitude, study year, response type (count, percent cover, rate, etc.), experiment type (turf removal, substrate comparison), plot size (meters^2) or container volume (milliliter), whether or not herbivory was experimentally tested, the life-history stage of the canopy species, species identities, and depth (in meters relative to mean lower low water, "MLLW"). When the latitude and longitude was not provided for a study, we used GEO-Locate to estimate the location from locality (*http://www.museum.tulane.edu/geolocate/*). When a depth range was reported, the midpoint was recorded. For studies where depth was not reported, we imputed depth as follows. Using information provided in the text, if the study was described as low or mid intertidal, we assigned a depth of +0 and +1.0 m MLLW, respectively (Appendix S1). Generally, "intertidal" refers to studies at depths shallower than 0 m MLLW, while "subtidal" are the zones deeper than the lowest low tide (m MLLW < 0). For four studies, no depth or zone was reported and additional information from the literature was sought to assign depth (Appendix S1). When plot sizes were not standardized among replicates (only Gunnill 1980), plot area was recorded as the midpoint between the two sizes.

When papers reported results from studies replicated at multiple sites or time points, we recorded data from each replicated study in our database. When an experiment tested the effect of multiple factors, we included data from only the treatment most similar to ambient or natural conditions (e.g., a no-nutrient addition treatment, or a canopy-intact treatment). In two studies, the effect of artificial turfs on the canopy was measured. These effects did not differ from the effect of "live" turfs (Appendix S2) and were thus included. When raw data or means and variance estimates were not available in text or tables, we extracted data from figures using 'digitize' for R (Poisot 2011; R Core Team 2019).

Analysis

We estimated the effect of turf species on canopy-forming species as the log-transformed response ratio (LNRR; Hedges et al. 1999). LNRR was chosen for its similarity to the calculation of non-trophic species interaction strengths from experimental data (Armas et al. 2004). The direction of effects from all studies can be interpreted as species interactions. A positive LNRR results from the negative effect that the understory has on the canopy, such that, for example, the removal of turfs results in higher canopy abundance in the

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experimental plot than in the unmanipulated control. Because several metrics resulted in a negative data point (e.g., negative growth rates), we standardized data by study by adding the minimum data value to each data point in the study to make the minimum data value zero, and then a small amount (0.001) was added to all zero means and standard deviations. We used a version of LNRR corrected for small sample size (equations 10 and 11 in Lajeunesse 2015).

We analyzed the data using mixed effects meta-regression, with random effects to account for variation within and among studies. Separate models were run for observational and experimental studies, as the methods differed significantly among the two study types. The random effect structure for both experimental and observational data allowed intercepts to vary among studies. Experimental random effects included an additional term allowing intercepts to vary among different response types (density, proportion, canopy length, growth rate), as, unlike in observational studies, experimental studies often reported the results of multiple different experiments that measured responses in multiple ways (Appendix S2).

In addition to the fundamental differences between experimental and observational methods, experimental interactions were often estimated at multiple time points. There are many ways to model repeated measures in meta-analysis (Koricheva et al. 2013). Because we were interested in whether the effect of the understory changed through time, the number of days since the start of the experiment was included in each experimental model. For certain nested models, likelihood ratio tests were used to determine whether additive or multiplicative model structures should be used (Appendix S2 Table S3). In all analyses, model coefficients are weighted by study precision (inverse variance) to give more weight to more highly replicated studies.

To quantify the overall effect of turfs on the canopy, across all studies, we used a random effects model with no fixed effects, removing studies that manipulated herbivory. To quantify the effects of our explanatory variables (functional group, depth, latitude), we used a mixed effects model with the same random effect structure as our overall effects model. To quantify the effects of herbivores, we subsetted the data to only studies that included an herbivory treatment. We also ran each experimental model separately for canopies in the order Laminariales ("kelps") and canopies in the order Fucales (Appendix S3). Other orders present in the dataset (Dictyotales and Desmarestiales) were not independently tested as there were too few samples (n Dictyotales = 2, n Desmarestiales = 5). Pseudo-R^2 was calculated for each mixed model as the proportion of total variance explained relative to a random-effects only model. Models were fit with restricted maximum-likelihood estimation and the significance of model coefficients and of linear contrasts was determined using Wald-Type Tests (Viechtbauer 2010). We conducted a series of analyses (Appendix S2) demonstrating that LNRR was not related to study year, plot size, or inclusion of artificial understory. Finally, publication bias was tested for all data (Appendix S2).

Results

We identified 41 studies that evaluated the effect of the understory on marine canopies, yielding 337 interaction estimates, spanning 46 canopy-forming species from four orders and 61 distinct turf seaweed species (Appendix S2 Figure S1). Studies were drawn from multiple biogeographic regions on five continents, as early as 1973, co-occurring with regions in which canopy-turf regime shifts have occurred (Filbee-Dexter & Scheibling 2014; Fig. 2). Overall, we found little evidence of publication bias in our dataset, supporting the results we describe below (Appendix S2).

Experimental Studies

Overall, the experimental removal of an algal understory had a mean neutral effect on the canopy (random effects model, mean $\text{LNRR}_{\text{exp}} = 1.55 \pm 0.94$, $p = 0.099$), with interactions ranging from strongly competitive to strongly facilitative (Fig. 3). The mean interaction did not change over the course of an experiment, measured as the number of days since the start of the experiment ($_{\text{days}} = 0.0012$, $p = 0.052$). The effect of turf species on the canopy varied among turf functional groups (overall Wald-type test, $\text{QM}_{[4], \text{exp}} = 17.16$, $p = 0.0018$, pseudo-$R^2 = 0.35$, Fig. 3). Specifically, the overall competitive effect of turfs on the canopy was driven by the negative effects of coralline turf and non-coralline crust ($_{\text{coralline turf}} = 3.59$, $p = 0.0009$; $_{\text{non-coralline turf}} = 2.91$, $p = 0.034$); all other turf species had no significant effect on the canopy (all $p >$

0.05; Appendix S3 Table S1). However, the effect of turf species differed among canopy types. Among kelps, non-coralline turf taxa also had a negative effect on the canopy ($_{\text{non-coralline turf}}$ = 5.04, p = 0.026). Among Fucales, all turf functional groups had an overall neutral effect on the canopy (all $p > 0.10$, Appendix S3 Table S1).

However, these overall effects marked geographical and latitudinal variation in the effect of turfs on canopies. In line with the widespread paradigm of kelp forest interactions, the effect of turfs was overall competitive in subtidal systems. Specifically, the effect of coralline turf on canopy taxa was competitive in the subtidal, and increasingly facilitative in the intertidal (Fig. 4, pseudo-R^2 = 0.16, $_{\text{depth * coralline turf}}$ = -0.61, p = 0.0003). Though found in a narrower depth range than turfs, non-coralline crust also had an increasingly positive effect on the canopy at shallower depth ($_{\text{depth * non-coralline crust}}$ = -1.33, p = 0.009). The effect of coralline crust and non-coralline turf on the canopy did not change across depth, and this pattern held for canopy kelps (Appendix S3 Table S2). Studies of canopy Fucales, conducted primarily in the intertidal zone, demonstrated no difference in interactions across depth (all functional groups, $p_{\text{functional group: depth}} > 0.05$, pseudo-$R^2$ = 0.27; Appendix S3 Table S2).

The effect of turfs on the canopy varied across latitude ($QM_{[8]}$ = 26.69, p = 0.0008, pseudo-R^2 = 0.39). In particular, the effect of non-coralline crust became more competitive at higher latitudes ($_{\text{latitude * non-coralline crust}}$ = 0.40, p = 0.027). Further, the effect of coralline turf was more facilitative at higher latitudes, with marginal significance ($_{\text{latitude * coralline turf}}$ = -0.35, p = 0.058; Appendix S3 Table S3).

Next, we looked only at variation in the interaction across life history stage of the canopy, and did not include variation across depth and latitude. The effect of turfs on the canopy differed among canopy life history stages, depending on the turf functional group and the identity of the canopy ($QM_{[31]}$ = 45.13, p < 0.0001, pseudo-R^2 = 0.13; Fig. 3). Turf species had competitive effects on the canopy, primarily at early life history stages. Coralline crust and all turfs negatively affected germling canopies (overall effect, p for linear contrasts < 0.01: $_{\text{coralline crust}}$ = 4.77, p = 0.029; $_{\text{coralline turf}}$ = 9.65, p = 0.00008; $_{\text{non-coralline turf}}$ = 5.43, p = 0.014). Further, coralline crusts negatively affected the later canopy "recruit" stage (overall effect: $_{\text{coralline crust}}$ = 4.77, p = 0.004). All other effects were not modified by life history stage of the canopy (Appendix S3 Table S4). Finally, considering only studies that manipulated herbivory (n = 28), the mean effect of turfs on the canopy did not depend on the presence or absence of herbivores (linear contrast, $_{\text{-herbivore - +herbivore}}$ = 2.84 ± 2.10, p = 0.18; pseudo-R^2 = 0.44, Appendix S3 Figure S1).

Observational studies

Observational studies of understory effects on canopy algae were mostly conducted on kelp (n Laminariales = 90, n Fucales = 1), at early life history stages (recruits or juveniles). Further, these studies were exclusively carried out in the intertidal, significantly shallower than experimental studies and at a higher mean latitude (both t-test, $p_{\text{obs - exp}}$ < 0.001). Thus, these results are comparable only to a subset of the experimental results above. Among observational studies, the absence of an algal understory had a strong negative effect on the canopy, indicating a positive interaction between the two groups (random effects model, mean LNRR_{obs} = -1.46 ± 0.74, p = 0.048). The effect of turfs on the canopy varied among turf functional groups (overall Wald-type test, $QM_{[3], \text{obs}}$ = 17.37, p < 0.0001, pseudo-R^2 = 0.71). In observational studies, most turf species had no effect on the canopy, but unlike experimental studies, coralline turf facilitated the canopy ($_{\text{coralline turf}}$ = -2.74, p = 0.0016). This effect did not change across depth or latitude (Appendix S3 Tables S5-7).

Discussion

Globally, canopy-dominated marine ecosystems are decreasing, shifting to "urchin barrens" dominated by crustose algae and herbivores (Ling et al. 2015), or turf-dominated ecosystems (Filbee-Dexter & Wernberg 2018). When canopies are lost, marine forests decline in productivity (Chapman 1981), habitat complexity (Miller et al. 2015), and diversity (Graham 2004). Given the ecological and economic importance of these systems, much attention is being paid to factors that might contribute to their decline or prevent their restoration (Gorman & Connell 2009). In particular, crustose and turf-forming algae are thought to be major barriers to the persistence of marine forests, especially under climate change (Connell & Russell

2010), given the assumption that these turf and crustose taxa compete with and exclude canopy-forming species (Connell et al. 2013).

We tested the widespread hypothesis that turf species in marine forests have negative effects on canopies (O'Brien & Scheibling 2018). We found that, although turf algae do compete with the canopy, competition occurs in a limited number of cases and the effect of the turfs on the canopy was highly variable, often neutral, and even facilitative in many cases (Table 1). Importantly, we found that in subtidal ecosystems, turf species do compete with the canopy (primarily kelps; Fig. 4), which supports the existing conceptualization of competition as a driving mechanism in subtidal kelp forests (Dayton et al. 1984; Reed & Foster 1984; Connell & Russell 2010; Connell et al. 2013). Further, experimental findings thought to contradict the competition paradigm (e.g., Barner et al. 2016) can be situated in a continuum of interactions that is predictable from the SGH (Bertness & Callaway 1994; Bennett et al. 2015): negative subtidal interactions shift to positive, facilitative interactions in the intertidal. The mechanisms underlying the turf-canopy interactions in this study were variable (Table 1). It is beyond the scope of this study to describe these mechanisms in detail (recently reviewed in Edwards & Connell 2012; O'Brien & Scheibling 2018), but despite the differences in the physiological, chemical, and physical processes that generate turf-canopy interactions, generalities emerged in the strength and sign of interactions.

Stress Gradient Hypothesis in marine forests

Although highly variable, the effect of turfs on the canopy was consistently facilitative in intertidal environments and at higher latitudes. Intertidal communities are characterized by extreme abiotic stress for marine organisms, primarily thermal and desiccation stress due to immersion. As predicted by the SGH (Bertness & Callaway 1994), we found that the effect of the turf species on the canopy shifted from competitive in the subtidal to facilitative in the intertidal. Specifically, coralline turfs increasingly facilitated the canopy at shallower depths in experimental studies (Fig. 4). Among the observational studies (all intertidal), both coralline and non-coralline turfs facilitated the canopy (Fig. 3). For example, coralline turfs facilitated the intertidal kelp, *Postelsia palmaeformis* , due to the cooler temperatures and higher humidity among turfs than on bare rock (Hutto 2011). Thus, turfs may be critical for ameliorating stressful abiotic conditions, therefore critical for canopy-forming species recruitment and persistence in certain cases (also reported in Bennett et al. 2015).

We also found a suggested facilitative effect of turf algae at higher latitudes. Among experimental studies alone, there was a trend of coralline turf facilitating canopy algae at higher latitudes (Fig. 5, Appendix S3, Table S3). Although non-coralline crusts had a stronger competitive effect at higher latitudes, we discuss our reservations in interpreting the effect of non-coralline crust below (section *Assumptions and limitations*). Further, observational studies were conducted at higher latitudes and demonstrated overall facilitation by turf species. When combined, these two lines of evidence support the conclusion that facilitation of the canopy may be stronger at higher latitudes. Conflicting with our results, multiple marine and terrestrial studies have demonstrated stronger facilitation at lower, warmer latitudes (Bertness et al. 1999; Pennings et al. 2003; McAfee et al. 2016). A reason for this discrepancy may be the complexity of latitudinal gradients in sea surface temperature. Many of our included studies were conducted along the Northeast Pacific coastline, where upwelling results in little change in sea surface temperature across ˜25º of latitude (Schoch et al. 2006). Ultimately, across ecosystems, the functional relationship between temperature and the strength of facilitation remains unclear. Both water depth and latitude in this study are proxies for stress, and more work needs to be done to truly isolate the effect of desiccation stress (or drought stress for terrestrial plants) and temperature on the prevalence of facilitation.

Other factors influencing interactions with marine canopies

Facilitation is also predicted to be stronger at early life history stages (Callaway & Walker 1997). The "nurse plant syndrome" has been widely demonstrated among plants, where adult "nurse" plants facilitate the recruitment and persistence of seedlings (Miriti 2006; He et al. 2013). We found conflicting evidence for the presence of this syndrome in turf/crust - canopy interactions. Experimental studies generally demonstrated

competitive effects of multiple understory species on canopies at early life history stages, while observational studies supported strong facilitation of canopy recruits by coralline turf. Overall, few studies in our meta-analysis quantify effects on the canopy across multiple life history stages (Appendix S3 Fig. S2), which precludes any strong conclusions here. Given that canopy-forming brown seaweeds produce microscopic stages as part of their recruitment process (Schiel and Foster 2006), these stages must be included in studies as they are fundamental to population recovery and persistence.

We also found little support for the hypothesis that the effect of turfs on the canopy is influenced by the presence of herbivores. Experiments that excluded herbivores demonstrated the same interaction as paired plots that included herbivores (Appendix S3 Figure S1). Herbivory should only alter the interaction if herbivores were facilitated or excluded as a function of turf removal. For example, some understory turf algae prevent the influx of sea urchins at the kelp forest boundary by limiting their movement, resulting in a positive indirect effect of turf on kelp (Konar et al. 2014). On the other hand, recruitment facilitation by turf algae of canopy herbivores can drive the emergence of kelp forest - urchin barren alternative stable states (Baskett & Salomon 2010). Marine herbivores generally have strong effects on primary producers (Poore et al. 2012), and urchin herbivory in particular is a dominant force structuring global kelp forests (Pearse 2006; Ling et al. 2015). However, few studies have explicitly examined the effect of herbivory on marine turf-canopy interactions (included in present study, $n = 14$), with factorial experiments to disentangle these interactions. Work in the Patagonian steppe has even found that the interaction among grasses was mediated by the strength of herbivory (Graff et al. 2007) - a mechanism of the SGH that may be worth exploring in marine forests. Future studies should examine the interaction of turf species with canopy herbivores to fully quantify the direct and indirect effects of competition, facilitation, and herbivory.

Assumptions and limitations

In addition to variability, clear patterns emerged between experimental and observational studies moving from neutral effects to facilitation of turfs on canopy species. However, it is important to note that observational studies were conducted in intertidal, shallow subtidal and/or high latitude environments, all factors that influence facilitation interactions. Thus, the different results for observational and experimental studies may be attributable instead to these confounding differences. Here, the included observational studies generally used a study design where the number of canopy individuals were counted on a given substrate (e.g., turf, crust, bare rock), scaled by the availability of that substrate ($n = 68$ out of 91 observational studies). For three pairwise interactions in this study, effects were estimated both observationally and experimentally, yielding similar effect size estimates (Appendix S3 Fig. S3). More work is needed to understand the relationship between experimental and observational effect sizes in non-trophic interactions, but the similarity here in response ratios is encouraging.

Another limitation of the present study is an imbalance in sample size among turf functional groups. Of the four groups, there are fewer estimates of the effect of non-coralline crustose algae on canopies ($n_{non-coralline\ crust} = 28$, $n_{non-coralline\ turf} = 79$, $n_{coralline\ crust} = 114$, $n_{coralline\ turf} = 102$). Estimates of the abundance and importance of these species vary in canopy-forming systems: in an Alaskan subtidal system, non-coralline crusts dominate the substrate relative to other species, while classic studies fail to mention non-coralline crusts as a component of the community (e.g., Reed & Foster 1984). The present study includes no estimates of the effect of non-coralline crusts in deep water (deepest is -5m relative to MLLW) and our finding that the non-coralline crust effect is more positive at shallower depths (Fig. 4) should be interpreted with caution.

Next steps: species interactions, global change, and regime shifts

Natural or anthropogenic disturbances may create situations in which turfs could alternately compete with or facilitate canopy-species recovery (Table 1). In particular, non-coralline turfs tend to be more resilient to disturbances such as El Niño (Filbee-Dexter & Wernberg 2018) and other disturbances (eutrophication, sedimentation, ocean acidification) actually favor the growth of non-coralline turfs over other taxa (Connell & Russell 2010; Muth et al. 2017). If turf or crustose algae inhibit canopy recruitment, then the marine

forest may never recover after disturbance. However, if facilitation occurs, canopy species may recover from a disturbance more quickly in environments with stronger or more frequent positive interactions. Previous global change predictions for marine forests were based on a negative effect of turfs on canopy-forming species (Harley et al. 2011). Undeniably, competition with turfs contributes to the globally-observed regime shift away from canopy-dominated ecosystems (Petraitis & Dudgeon 2004; Filbee-Dexter & Scheibling 2014; O'Brien & Scheibling 2018). However, in many ecosystems, facilitation creates a positive feedback that maintains contrasting system states (Kéfi et al. 2016). Given the frequency at which we observe turf and crust facilitation of canopies in this study, these positive effects may also contribute to alternative stable states in marine forests. Future work should explicitly test for positive interactions in these systems, and examine the role of facilitation in amplifying or dampening the observed global regime shift to turf- and crust-dominated marine forests.

We found that interactions in this system formed a continuum from competitive to facilitative, across a predictable stress gradient. We used latitude as a geographic proxy for temperature, as few studies in this meta-analysis included environmental data alongside interaction estimates. In the future, abiotic data, and especially temperature, should be reported and possibly experimentally manipulated in studies of marine forest interactions. We found a stress gradient effect when we combined intertidal and subtidal studies in the same analysis, though few empirical studies treat these as one system with an "elevational" gradient. We encourage more empirical work integrating the subtidal and intertidal ecosystems, especially given environmental changes that may drive species to deeper (warming) or shallower (sea level rise) water. Finally, the interactions included in this study are only a few of the diverse set of trophic and non-trophic interactions in marine forests. Herbivory, competition, facilitation, predation, and indirect effects are all interactions that shape community structure and play a role in regime shifts (Petraitis & Dudgeon 2004). Linking the effect of the canopy on turfs and crusts with the interactions in this study would be a feasible first step in understanding the emergent impact of all these interactions (Bennett et al. 2015; O'Brien & Scheibling 2018). Our results highlight the importance of testing for facilitative interactions where competition is thought to dominate, shedding new light on a well-studied interaction involved in a global regime shift.

Supporting Information

Appendix S1 - Data compilation

Appendix S2 - Supplemental analyses

Appendix S3 - Supplemental results

Reference list

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Figure legends

Figure 1. Two simplified examples of the effect of turf species on canopy-forming macroalgae. A) In this example, the canopy kelp is negatively affected by two species that live in the understory below. This competitive effect can be measured experimentally, through the removal of the turf and crust understory. If the abundance (or biomass, etc.) of the canopy increases in the absence of the turf and crust species, the interaction is estimated as competitive. B) However, if these species facilitate the canopy kelp, then the removal of turfs and algal crusts should have a negative effect on the canopy.

Figure 2. Locations of the studies included in the meta-analysis, by study type. On the right is the distribution of studies in the Northeast Pacific Ocean, where a high density of studies have been conducted.

Figure 3. The overall effect of different turf functional groups on the canopy (kelps and Fucales combined). Each point in grey represents an individual measured interaction, with means and 95% confidence intervals in black. If log response ratio (LNRR) is negative, then the effect of turf species on the canopy is facilitative. If LNRR is positive, then the effect is competitive.

Figure 4. The experimental effect of different turf functional groups on the canopy, by depth. Each point is a raw data point, scaled in size by the study sample size, with 95% confidence intervals shaded around each line. Note that the slope and intercept of the coralline crust and non-coralline turf lines do not statistically differ from zero.

Figure 5. Across latitude (top), mixed evidence for increasingly facilitative interactions at higher latitudes. Below, patterns across life history stage (raw data in grey, means and 95% confidence intervals for the mean in black). For life history stage, observations were collected primarily on the recruit canopy stage (see Results: Observational studies). Plot across latitude includes only coralline turfs, plot across life history includes all canopy and turf taxa.
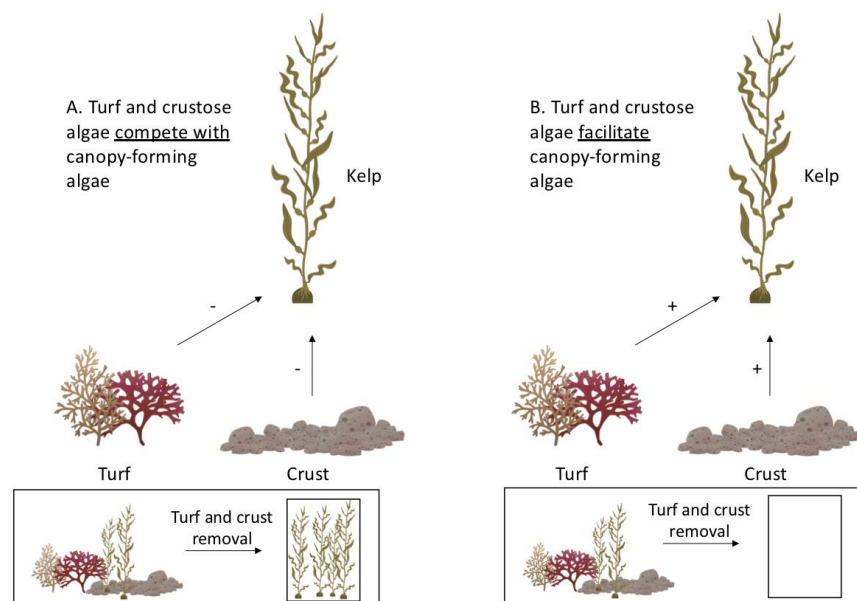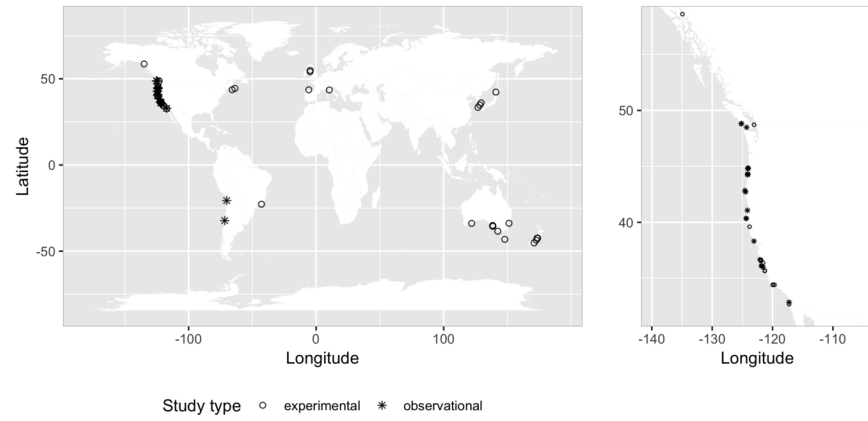
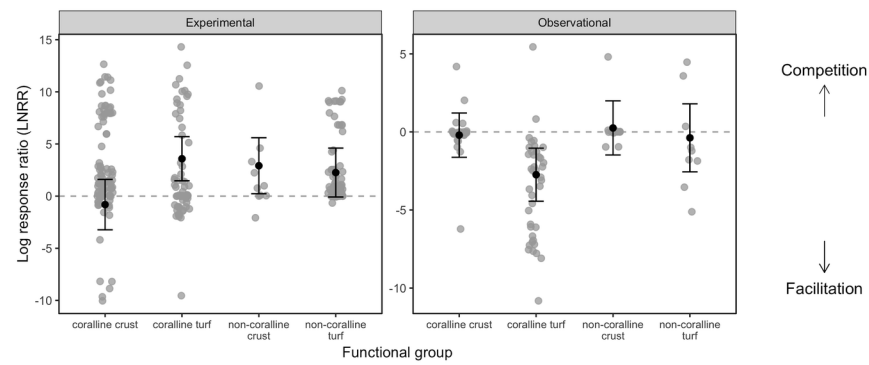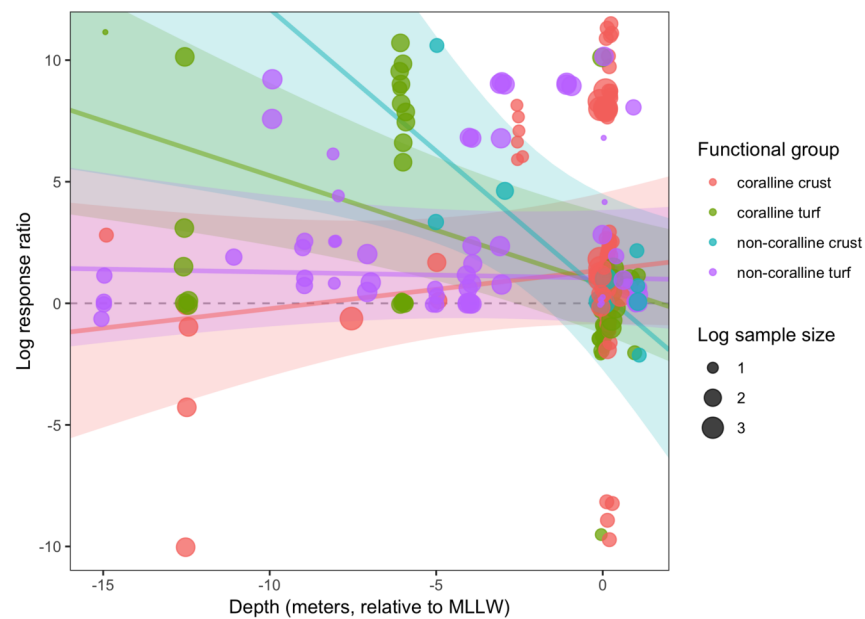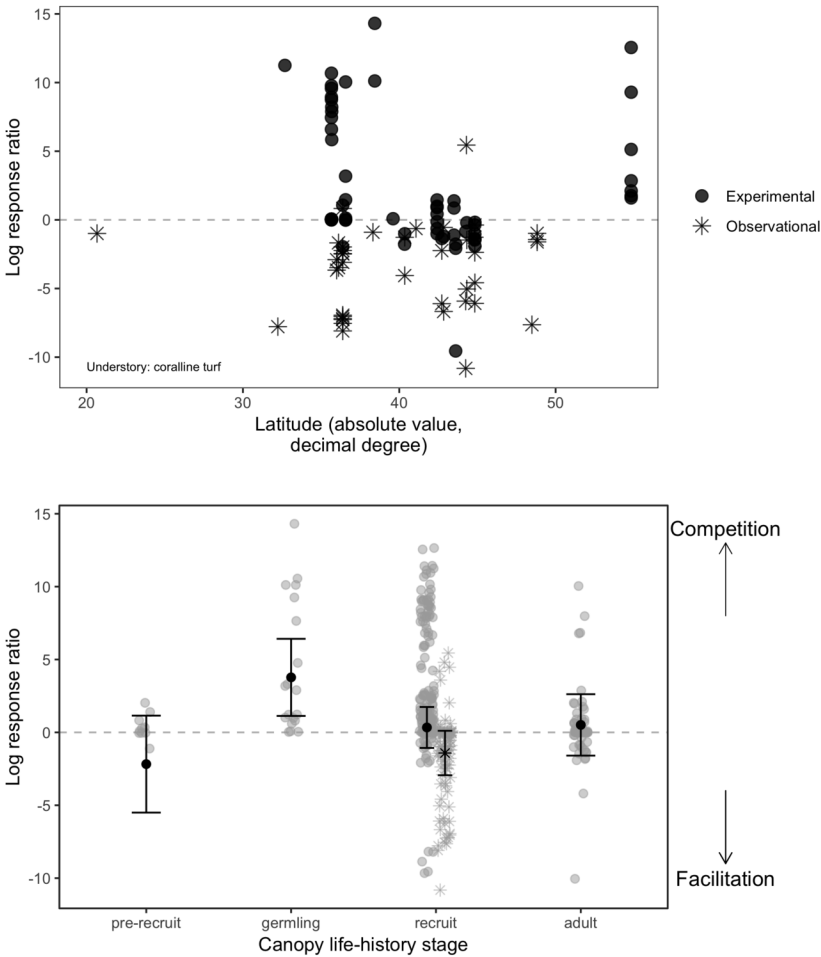*Figures*

Figure 1.

Figure 2.

Figure 3.

Figure 4.

Figure 5.

Tables

Table 1. Examples of the different interactions between the algal understory functional groups and canopy-forming species.

Effect of turf or crust on canopy	Functional group	Example mechanism
Competition	Turfs	Space limitation prevents canopy recruitment
Competition	Turfs	Abiotic disturbance (sedimentation, eutrophication) favors th
Competition	Coralline crusts	Epithelial sloughing of coralline surface cells prevents recruitm
Facilitation	Coralline turfs	Coralline turfs ameliorate desiccation stress in canopy algae
Facilitation	Turfs	Understory algae provide refuge from herbivory for canopy re