

Foundation species promote community stability by increasing diversity in a giant kelp forest

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Abstract. Foundation species structure communities, promote biodiversity, and stabilize ecosystem processes by creating locally stable environmental conditions. Despite their critical importance, the role of foundation species in stabilizing natural communities has seldom been quantified. In theory, the stability of a foundation species should promote community stability by enhancing species richness, altering the population fluctuations of individual species, or both. Here we tested the hypothesis that the stability of a marine foundation species, the giant kelp *Macrocystis pyrifera*, increased the stability of the aggregate biomass of a phylogenetically diverse assemblage of understory algae and sessile invertebrates that compete for space beneath the giant kelp canopy. To achieve this goal, we analyzed an 18-yr time series of the biomass of giant kelp and its associated benthic community collected from 32 plots distributed among nine shallow reefs in the Santa Barbara Channel, USA. We showed that the stability of understory algae and sessile invertebrates was positively and indirectly related to the stability of giant kelp, which primarily resulted from giant kelp's direct positive association with species richness. The stability of all community types was positively related to species richness via increased species stability and species asynchrony. The stabilizing effects of richness were three to four times stronger when algae and invertebrates were considered separately rather than in combination. Our finding that diversity–stability relationships were stronger in communities consisting of species with similar resource requirements suggests that competition for shared resources rather than differential responses to environmental conditions played a more important role in stabilizing the community. Increasing threats to structure-forming foundation species worldwide necessitates a detailed understanding of how they influence their associated community. This study is among the first to show that dampened temporal fluctuations in the biomass of a foundation species is an important determinant of the stability of the complex communities it supports.

Key words: biodiversity; community stability; diversity–stability relationship; environmental heterogeneity; foundation species; kelp forests; species asynchrony.

INTRODUCTION

Foundation species have garnered considerable attention by ecologists over the years for their disproportionate role in providing habitat for other species and structuring the communities they live in (Dayton 1972, Ellison et al. 2005). Much of the research on this topic has focused on the capacity of foundation species to influence communities by reducing environmental stress and increasing resource availability and habitat complexity (Bertness and Bruno 2001, Angelini et al. 2011, Kikvidze et al. 2015). By contrast, the effects of foundation species on the stability of their associated communities

has received relatively little attention (Bulleri et al. 2012), despite the fact that community stability was central to the original definition of foundation species (Dayton 1972). This may be due in part to a traditional focus on long-lived foundation species that vary little in abundance or biomass from year to year (e.g., trees, desert shrubs; Ellison et al. 2005, Lindbladh and Foster 2010, Peters and Yao 2012). However, many structure-forming foundation species (e.g., bivalves, grasses, kelps) have relatively short life spans (i.e., <10 yr) or display substantial intra-annual variability in abundance or biomass (Altieri and Witman 2006, Rodhouse et al. 2014, Miller et al. 2018). In ecological systems defined by such dynamic foundation species, it has not yet been established whether the stability of the foundation species enhances the stability of the entire community of organisms. Resolving this research gap will help determine the

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extent to which the stability of a foundation species can simultaneously benefit the broader community they define.

The stability of natural communities, and its relationship to species richness in particular, has captured the attention of ecologists for decades, spawning considerable debate about the direction and strength of the relationship between diversity and stability (MacArthur 1955, Goodman 1975, McNaughton 1977, McCann 2000, Ives and Carpenter 2007). Theory predicts that diversity enhances the stability of aggregate community properties (e.g., total biomass, primary production) via a variety of mechanisms, most notably compensatory dynamics, overyielding, evenness, and statistical averaging (Doak et al. 1998, Tilman 1999, Yachi and Loreau 1999, Lehman and Tilman 2000, Loreau and de Mazancourt 2008, Thibaut and Connolly 2013). A large number of experimental studies, primarily conducted in grasslands and aquatic mesocosms, have confirmed that species richness can promote community stability and lead to positive diversity–stability relationships (DSR; Tilman and Downing 1994, Tilman 1999, Tilman et al. 2006, Isbell et al. 2009, Hector et al. 2010, Cardinale et al. 2013). However, more recent results derived from field studies in a wide range of natural systems are less definitive regarding the importance of diversity in stabilizing communities (Campbell et al. 2011, Houlahan et al. 2018), as compelling evidence for a positive DSR was found in approximately half of the natural communities examined in a recent meta-analysis across multiple ecosystems and taxa (Houlahan et al. 2018). It has been argued that abiotic factors make compensatory dynamics rare in nature, which might disrupt DSRs (Houlahan et al. 2007). Consequently, accounting for the abiotic factors known to influence the diversity and abundance of organisms is key to understanding the relationship between diversity and stability in natural systems.

The stability of a foundation species may promote community stability by either enhancing species richness, altering the population dynamics of individual species, or both. The stabilizing path involving species richness is supported in part by observations of increased diversity in the presence of foundation species (Kikvidze et al. 2015, Miller et al. 2018). Other lines of evidence show that foundation species reduce abiotic stress (Kikvidze et al. 2015), alter resources (Castorani et al. 2018), provide refuge from predators and competitors (Dayton 1975, Stachowicz 2001, Canion and Heck 2009), and provide nursery habitat (Heck et al. 2003) for many species. Thus, foundation species have the capacity to promote community stability by directly enhancing the stability of individual species and the degree of asynchronous fluctuations among them.

The synthetic framework developed by Thibaut and Connolly (2013) has considerable merit for exploring the effects of foundation species on community stability as it explicitly links community stability to population stability and clarifies their dependency on species richness.

Importantly, Thibaut and Connolly showed that community stability is the product of two quantities: (1) the weighted average stability of the populations of the community's constituent species, and (2) the amount of asynchrony in the temporal fluctuations of these species (i.e., species asynchrony). This framework is particularly useful for investigating DSRs, as it is robust to idiosyncratic changes in species' mean abundances, variances, and covariances with increasing diversity that typically occur in nature.

In this study, we used the Thibaut and Connolly framework to explore the bounds of DSRs in nature and the role of foundation species in underpinning them. We focused on a taxonomically and phylogenetically diverse assemblage of primary space holders (understory algae and sessile suspension-feeding invertebrates) on temperate rocky reefs that thrive beneath the canopy of the giant kelp (*Macrocystis pyrifera*), an iconic foundation species (Graham 2004, Castorani et al. 2018, Miller et al. 2018). We hypothesized that aggregate community biomass should be more stable on reefs where giant kelp biomass is also more stable. To test this hypothesis we surveyed the biomass of both the giant kelp and its associate assemblage of understory algae and sessile invertebrates over 18 yr across 32 plots to examine (1) how the stability of the benthic community relates to its species richness (DSR), (2) how species richness relates to species stability and asynchrony to determine community stability, and (3) how the stability of the dynamic foundation species relates to the overall stability of the community through its relationships with species richness and species dynamics. Because environmental heterogeneity can alter or modulate these relationships (Houlahan et al. 2007) we accounted for a suite of environmental variables known to influence the abundance and species composition of reef organisms in our analyses. We also evaluated the contribution of individual species to community stability to obtain a more detailed understanding of their relative importance in contributing to the DSR.

METHODS

Study system

The giant kelp *Macrocystis pyrifera* is a dynamic foundation species whose complex structure and high productivity enhance and define a diverse community of space holders on temperate rocky reefs in both the northern and southern hemispheres (Graham 2004, Castorani et al. 2018, Miller et al. 2018). Space holders on reefs occupy different trophic levels, which enhances the phylogenetic and functional diversity of the community. Understory algae are primary producers that derive their nutrition from sunlight and dissolved nutrients, whereas sessile invertebrates are consumers that filter plankton and other organic matter from the water column. The amount of light available to understory algae is greatly

influenced by shading from the taller canopy of giant kelp (Reed and Foster 1984, Santelices and Ojeda 1984), which fluctuates in space and time because of physical disturbance, grazing, variable growth conditions, and intrinsic demographic processes (reviewed in Carr and Reed 2015, Schiel and Foster 2015). Fluctuations in the biomass of giant kelp have also been shown to alter competition for space between understory algae and sessile invertebrates (Arkema et al. 2009) and significantly influence the trophic structure and species composition of the benthic community (Byrnes et al. 2011, Castorani et al. 2018, Miller et al. 2018).

Data collection

Annual community surveys in the Santa Barbara Channel were conducted from 2001 to 2018 by the Santa Barbara Coastal Long Term Ecological Research program. During summer (late July–early August) of each year, divers recorded the abundances (percent cover or density) and sizes of benthic algae and sessile suspension-feeding invertebrates within 32 fixed 40 × 2 m plots distributed among nine rocky reef sites located along an 80-km stretch of the mainland coast of the Santa Barbara Channel, USA (120.333 W to 119.542 W and 34.392 N to 34.459 N). We converted abundance and size data to biomass density (g dry mass/m²) using species-specific relationships between size and mass developed by Harrer et al. (2013) for understory algae, Reed et al. (2016) for invertebrates, and Rassweiler et al. (2018) for giant kelp. We lumped organisms that were difficult to identify to the species level underwater (e.g., crustose coralline algae, small filamentous red or brown algae) into higher taxonomic or morphological classifications and treated them as a single taxon in our analyses. We ensured that every species was consistently assigned to only one taxon. As such, our data underestimate rather than overestimate the total number of species sampled. We included a total of 53 taxa of understory algae, 61 taxa of sessile invertebrates, and one species of seagrass (*Zostera marina*) in our analysis (Appendix S1: Table S1). A complete description of the sampling methods, geographic and taxonomic coverage, and links to the data and metadata are described in Reed (2018).

Diversity and community stability

We summed the number of species and biomass of understory algae (including the seagrass *Z. marina*) and epilithic sessile invertebrates (hereafter referred to as algae and invertebrates, respectively) within each plot and year combination to obtain annual means over the 18-yr study period of species richness and benthic community biomass (i.e., the biomass of algae and invertebrates aggregated across all constituent species). We calculated stability of aggregate community biomass (hereafter referred to as community stability) as the

inverse coefficient of variation (μ/σ) in community biomass over the 18-yr study period, which standardizes the temporal variability in community biomass to its temporal mean such that higher values of μ/σ reflect higher stability. We evaluated the DSR of the benthic community by comparing community stability to mean species richness across the 32 plots.

Species stability and species asynchrony

Following Thibaut and Connolly (2013), we defined weighted average population stability (hereafter referred to as species stability or S_s) as the inverse of the weighted mean coefficient of variation in the biomass of all constituent species within a plot, with

$$S_s = 1 / \sum_i \frac{\mu_i \sigma_i}{\mu_c \mu_i}, \quad (1)$$

where μ_i and σ_i denote the 18-yr mean and standard deviation of biomass of constituent species i , and μ_c represents the 18-yr mean community biomass. We quantified species asynchrony in each plot as the complement of the Loreau and de Mazancourt (2008) synchrony index ϕ , with

$$\phi = \sigma_c^2 / (\sum_i \sigma_i)^2, \quad (2)$$

where σ_c^2 is the annual variance of community biomass and $(\sum_i \sigma_i)^2$ is the squared sum of the standard deviations of the constituent species' biomass. This measure of species asynchrony ($1 - \phi$) is bounded by 0, which indicates fluctuations in species biomass are perfectly synchronized, and 1, which indicates fluctuations in species biomass are perfectly asynchronized.

Direct and indirect drivers of community stability

To characterize the mechanisms underpinning the DSR in our study system, we examined the direct response of community stability, species stability, and species asynchrony to variation in species richness using linear regression. We also used linear regression to examine the amount of variation in species richness and community stability explained by the stability of the biomass of the foundation species (hereafter referred to as giant kelp stability). Because we were interested in exploring whether DSRs were consistent across different assemblages of rocky reef organisms, we conducted separate analyses for the understory algal community (which included the seagrass *Z. marina*), the invertebrate community, and the combined community of algae + invertebrates. We then used ANCOVA to compare the slopes of these relationships among the three types of communities.

We used structural equation modeling (SEM) to examine the direct and indirect paths through which giant kelp stability may influence the stability of the

benthic reef community. We first fitted a full model in which community stability was directly influenced by species stability, species asynchrony, and species richness. In this model, we also incorporated a direct path from giant kelp stability to community stability to account for any additional effects. In a second step, we examined the influence of the five environmental variables described below on giant kelp stability, species richness, species stability, species asynchrony, and community stability. Our goal was to control for the effects of environmental heterogeneity on these factors and the relationships among them. We tested for path significance using a Satorra–Bentler corrected likelihood ratio test. We assessed adequacy of our SEM models using a chi-squared test and the root-mean-square error of approximation (RMSEA). We constructed independent models for the combined community of algae + invertebrates and for communities consisting of only algae or invertebrates. All SEM models were fitted in R version 3.5.1 (R Development Core Team 2018) using the package lavaan (Rosseel 2012) following the same rationale.

Environmental heterogeneity

We evaluated the environmental heterogeneity along the mainland coast of the Santa Barbara Channel by assessing five environmental variables that are known to influence reef organisms (Miller et al. 2018). These variables were (1) the mean percent cover of rock (i.e., bed-rock and boulders >25 cm diameter) measured at 80 uniformly spaced points in each plot annually from 2001 to 2018 (range = 8.4–98.8%), (2) mean depth estimated from 160 uniformly spaced points within each plot in 2010 (range = 2.9–11.0 m), (3) topography, measured as the coefficient of variation of depth across the 160 uniformly spaced points and expressed as a percentage (i.e., $\sigma/\mu \times 100$; range = 1.0–21.2%), and (4) grazing pressure as estimated by the mean biomass of sea urchins (*Strongylocentrotus purpuratus*, *Mesocentrotus franciscanus*, and *Lytechinus pictus*) within each plot annually from 2001 to 2018 (range = 1–143 g/m²). These four variables were computed for each of the 32 plots. In addition, we also recorded bottom temperature every 15 min using two submersible temperature loggers from 2002 to 2018 at each of the nine rocky reef sites. We assumed that transects within each rocky reef site experienced similar long-term bottom temperature over the time period. Bottom temperatures averaged over the 18-yr study at the nine reefs ranged between 14.4 and 15.2°C.

Importance of individual species

We conducted a leave-one-out analysis to assess the importance of giant kelp stability as compared to any other species. In this analysis, we treated giant kelp not as an external driver, but as an additional member of the benthic community of understory algae and sessile

invertebrates. We computed the slope of the DSR for this larger community including giant kelp, and computed the percent decrease or increase in the slope of the DSR associated with the removal of each species (giant kelp, invertebrates, or algae). We hypothesized that if giant kelp was a particularly strong driver of community stability, then we expected the strongest decline in the slope of the DSR when giant kelp was removed as compared to any other species. Finally, we computed two species-specific metrics to investigate how individual species contributed to community stability. These metrics were computed by evaluating how (1) the mean biomass and (2) the stability of each species responded to variation in species richness using linear regression. We focused only on the species of algae and invertebrates detected in at least 10 of the 32 plots.

RESULTS

Diversity, asynchrony, and stability

The mean species richness of understory algae + invertebrates in the 32 plots averaged over the 18-yr study ranged from 11 to 27 species. We found a positive relationship between the stability of the combined community of algae + invertebrates and the mean species richness in this taxonomically complex assemblage of reef organisms (positive DSR; Fig. 1A). A gain of 16 species along the diversity gradient of the 32 plots was associated with a 75% increase in community stability. As expected from the Thibaut and Connolly (2013) theoretical framework, community stability was positively related to both the weighted stability of the community's constituent species (S_s ; Fig. 1B) and the degree of asynchrony in their biomass fluctuations ($1 - \phi$; Fig. 1C). The role of species richness in determining the strength of these two properties, however, differed, as only species stability was significantly related to species richness (Fig. 2A), whereas species asynchrony was not (Fig. 2B).

We also observed positive DSRs when understory algae and invertebrates were considered as separate communities (Fig. 1A). The stabilizing effect of species richness on aggregate community biomass was remarkably similar for these two disparate community types ($F_{1,60} = 0.78$; $P = 0.381$), but four times greater than that of the more complex community of algae + invertebrates (Fig. 1A; $F_{2,90} = 12.66$; $P < 0.001$) as the stability of reef algae and of invertebrates increased by 219% and 323%, respectively, along the natural diversity gradient observed across plots (Fig. 1A). Both species stability (S_s) and species asynchrony ($1 - \phi$) were positively related to species richness for communities composed of either algae or invertebrates (Fig. 2A, B). Much like that observed for community stability (Fig. 1A), the positive relationships between species richness and S_s (Fig. 2A) and $1 - \phi$ (Fig. 2B) for these two community types were quite similar ($F_{1,60} = 0.02$; $P = 0.891$ and $F_{1,60} = 0.15$; $P = 0.700$ for S_s and $1 - \phi$, respectively), but each was

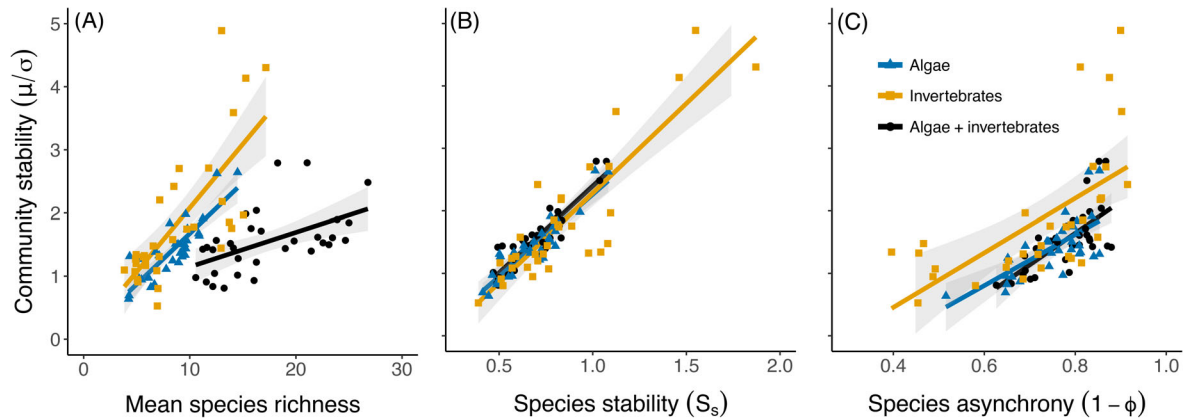


FIG. 1. Relationships between community stability and (A) mean species richness, (B) species stability, and (C) species asynchrony. Communities consisting of algae + invertebrates, algae only, and invertebrates only are pictured using black circles, blue triangles, and orange squares, respectively. Solid lines denote significant relationships and gray areas represent the 95% confidence interval of these relationships. Non-significant relationships are shown using dashed lines.

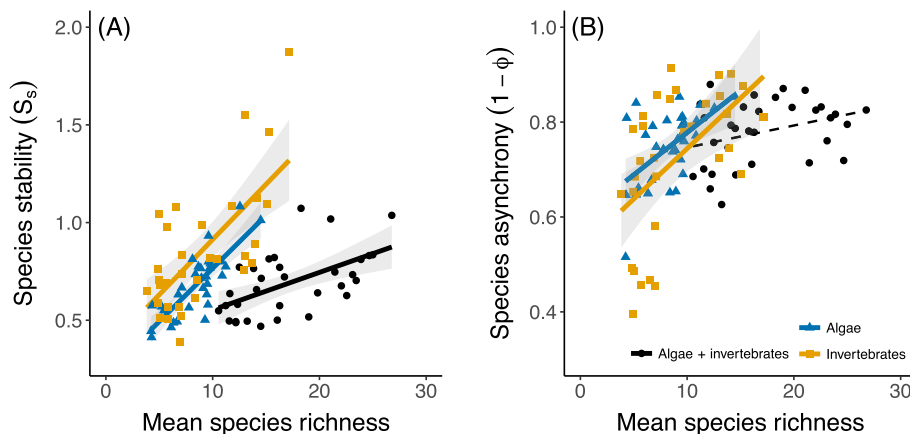


FIG. 2. Relationships between mean species richness, (A) species stability, and (B) species asynchrony. Communities consisting of algae + invertebrates, algae only, and invertebrates only are pictured using black circles, blue triangles, and orange squares, respectively. Solid lines denote significant relationships and gray areas represent the 95% confidence interval of these relationships. Non-significant relationships are shown using dashed lines.

at least three times greater than that of the more complex community composed of algae + invertebrates ($F_{2,90} = 8.12$; $P \leq 0.001$ and $F_{2,90} = 5.06$; $P = 0.008$).

Diversity, stability, and foundation species

We found that the relationship between community stability and giant kelp stability differed among the community types (Fig. 3A). The stability of communities consisting of algae + invertebrates and algae only were positively related to giant kelp stability. In addition, we found that the stability of these two community types was more strongly related to the temporal standard deviation of giant kelp biomass ($F_{1,30} = 5.07$, $P < 0.05$ and $F_{1,30} = 4.463$, $P < 0.05$ for algae + invertebrates and algae only, respectively) than to the temporal mean of giant kelp biomass (non-significant relationships). In

contrast, the stability of the invertebrate community was unrelated to giant kelp stability. We observed similar differences among community types with regard to the relationship between species richness and giant kelp stability (Fig. 3B).

Direct and indirect drivers of community stability

Our SEM results revealed that species stability, species asynchrony, species richness, and giant kelp stability combined to explain at least 95% of the observed variation in community stability for all three community types (Fig. 4). Adequate model fits were indicated by non-significant chi-squared tests ($P > 0.05$) and low RMSEA (< 0.08) for all three community types. The direct path from species richness to community stability was not significant for all three types of communities.

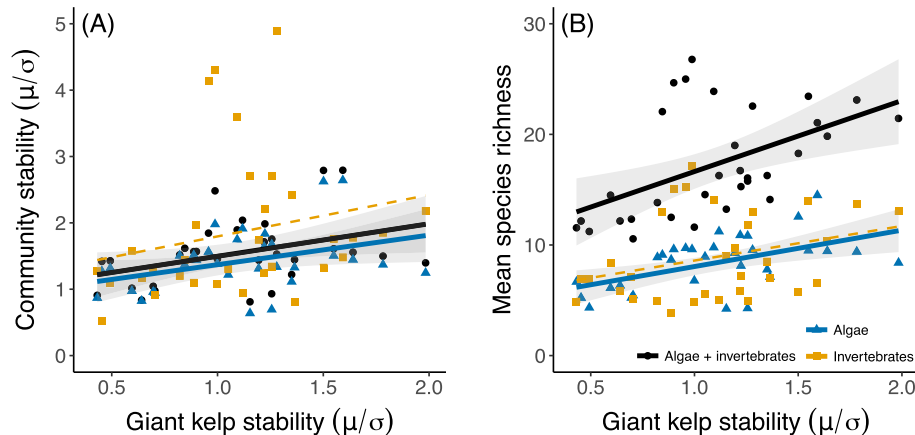


FIG. 3. Relationships between giant kelp stability, (A) community stability and (B) mean species richness. Communities consisting of algae + invertebrates, algae only, and invertebrates only are pictured using black circles, blue triangles, and orange squares, respectively. Solid lines denote significant relationships and gray areas represent the 95% confidence interval of these relationships. Non-significant relationships are shown using dashed lines.

Instead, the positive effect of species richness on community stability occurred via indirect paths through species stability (S_s) and species asynchrony ($1 - \phi$).

The positive univariate relationships between giant kelp stability and community stability observed for algae + invertebrates and algae only (Fig. 1B) were not significant in the SEMs (Fig. 4A, B). Instead, the positive association between giant kelp stability and the community stability of algae + invertebrates and algae only occurred via the indirect effects of species richness on both species stability and species asynchrony. Coefficients for indirect paths between species richness and community stability through S_s were 1.3–2.9 times larger (depending on community type) than those involving species asynchrony. We found that the direct paths between giant kelp stability and both species stability and species asynchrony were not significant for all three community types and therefore removed them from the final SEMs. We also found that direct positive paths between giant kelp stability and species richness in the SEMs were similar to those in the univariate analyses for combined community of algae + invertebrates and the community of algae only (Fig. 4 vs. Fig. 3B). In contrast, the non-significant relationship between species richness of invertebrates and giant kelp stability observed in the univariate analyses was significantly positive in the SEM (Fig. 4 vs. Fig. 3B).

Environmental heterogeneity

Accounting for environmental heterogeneity among plots greatly improved the strength of the direct and indirect relationships between giant kelp stability and the other ecological variables evaluated in the SEMs of the three community types (Appendix S1: Fig. S1 vs. Fig. 4). Plot depth, topography, and the long-term average of both sea urchin biomass and bottom temperature

were significant predictors in all SEMs (Fig. 4). We found a positive path between plot depth and species richness of algae + invertebrates and invertebrates, but a negative one for the richness of algae. We also found a positive path between topography and the richness of all three community types, as well as with the species stability of algae + invertebrates and invertebrates. Sea urchin biomass displayed a negative association with the species stability of algae + invertebrates and the species richness of algae, whereas it was positively associated with the richness of invertebrates. Lastly, bottom temperature was negatively associated with giant kelp stability, the richness of algae, and the species stability of invertebrates.

Importance of individual species

The slope of the DSR including giant kelp as part of the community was 0.082, suggesting that adding giant kelp increased the strength of the observed DSR by 33.7% (Fig. 5). Removing the dominant understory alga *Pterygophora californica* similarly decreased the strength of the DSR (by 30.4%). The effects of all other species on the DSR were substantially smaller (Fig. 5). We also found that the mean biomass of *P. californica* displayed by far the largest increase with species richness (Appendix S1: Fig. S2). Finally, the stability of 35 species, including *P. californica*, significantly increased with species richness, whereas the stability of only three species significantly decreased with species richness (Appendix S1: Fig. S2).

DISCUSSION

Although previous studies have considered the role of foundation species in structuring natural communities (Bertness and Bruno 2001, Stachowicz 2001, Heck et al.

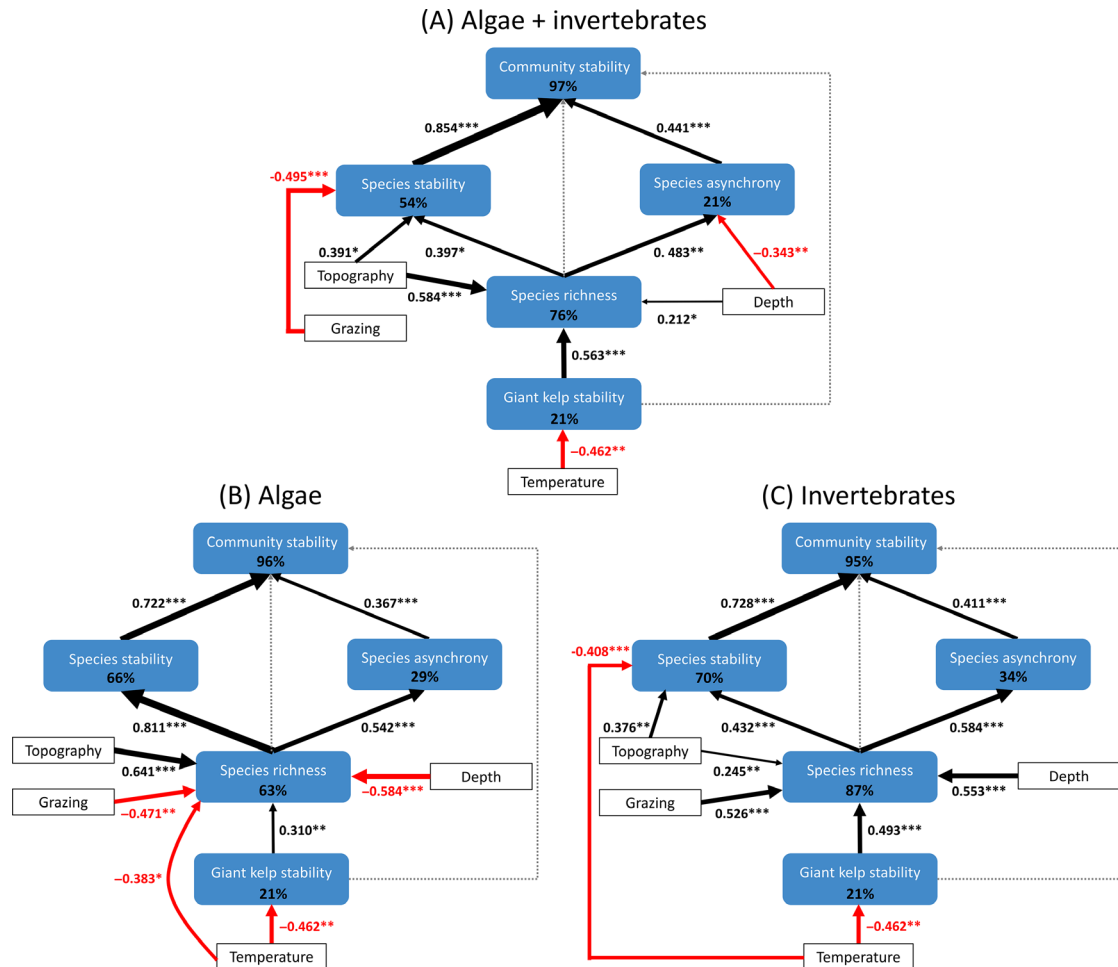


FIG. 4. The three best structural equation models (SEMs) explaining community stability for (A) algae + invertebrates, (B) algae only, and (C) invertebrates only. Values (percent) within boxes refer to the coefficient of determination of individual models. The four environmental variables retained in the final SEMs, depth, topography, grazing pressure, and bottom temperature, are shown in white boxes. The widths of the arrows scale with the magnitude of the standardized regression coefficients. Non-significant paths are shown using dashed lines. (A) $\chi^2 = 23.208$, $df = 19$; $P = 0.228$, root-mean-square error of approximation (RMSEA) = 0.083; (B) $\chi^2 = 18.782$, $df = 20$, $P = 0.536$, RMSEA = 0.001; (C) $\chi^2 = 21.491$, $df = 19$, $P = 0.310$, RMSEA = 0.064. Significance level: *** $P < 0.001$, ** $P < 0.01$ and * $P < 0.05$.

2003, Ellison et al. 2005, Canion and Heck 2009, Angelini et al. 2011, Kikvidze et al. 2015), few, if any, have explored the relationship between the stability of a foundation species and the stability of its associated community. Our study helps fill this gap by demonstrating that the stability of the aggregate biomass of a phylogenetically diverse assemblage of understory algae and sessile invertebrates was positively related to the stability of an iconic marine foundation species, the giant kelp *Macrocystis pyrifera*. Such positive relationships may be directly driven by the stability of giant kelp. More specifically, we suggest that this relationship resulted primarily from the indirect positive effect of giant kelp stability on species richness, partially corroborating our hypothesis that the stability of the foundation species should increase community stability via its effects on species

richness and/or population dynamics. With respect to the latter mechanism, our SEMs provided no evidence that dampened fluctuations in giant kelp biomass directly affected species stability and species asynchrony to stabilize the aggregate community biomass of all three community types. This result was robust to the inclusion of several variables that captured the environmental heterogeneity at the scale of our study system.

Our study is among the first to show that dampened fluctuation in the biomass of a foundation species is an important determinant of the dynamics of the complex communities it supports. Our finding that community stability and species richness increased with giant kelp stability was driven primarily by lower interannual variation in kelp biomass (i.e., lower standard deviation) rather than by higher mean biomass averaged over the

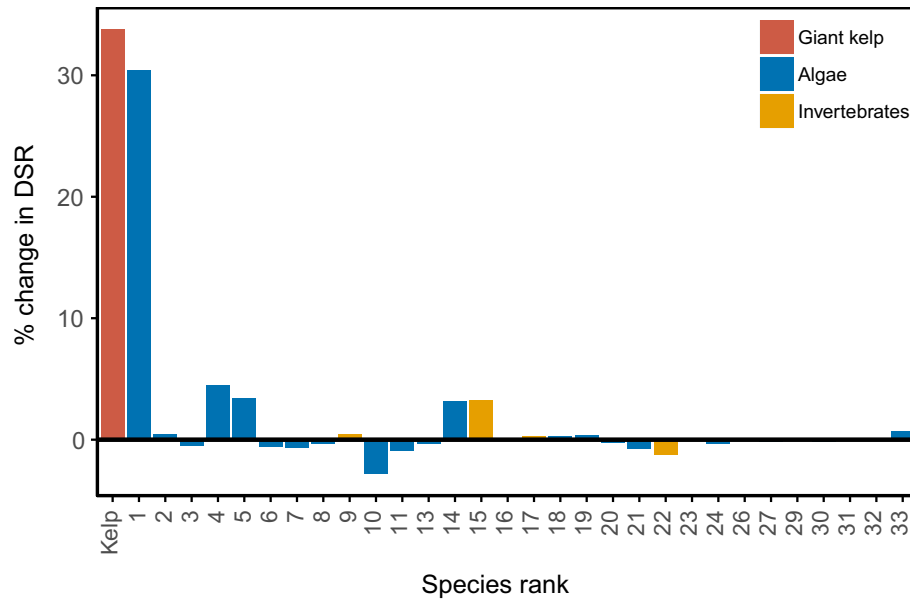


FIG. 5. Leave-one-out analysis treating giant kelp as an additional member of the benthic community of understory algae and sessile invertebrates rather than an external driver. The percent change in diversity–stability relationship (DSR) was computed as $(DSR_{\text{before}} - DSR_{\text{after}})/DSR_{\text{before}} \times 100$, where DSR_{before} and DSR_{after} are the slope of the DSR before and after removing each species (giant kelp, invertebrates, or algae) individually. All species ranked higher than 33 have percent change in DSR $<0.15\%$ (Appendix S1: Table S1).

18-yr study period. Importantly, the role of giant kelp in stabilizing the benthic community was indirect; giant kelp stability indirectly increased community stability by increasing species richness, with no direct link between giant kelp stability and community stability. Temporally stable kelp forests may harbor more species because they facilitate more consistent recruitment of species over time (Carr 1994), stabilize the availability of limiting resources (Eckman et al. 1989, Castorani et al. 2018), and provide a spatial and temporal refuge from abiotic and biotic stresses (Gaylord et al. 2007). This in turn may diminish the demographic stochasticity of resident forest species, ultimately reducing their risk of local extinction. Stable kelp forests may also enhance biodiversity by providing consistent microhabitats that allow more species to coexist over time because of niche differentiation (Bulleri et al. 2016).

Including environmental heterogeneity into our analyses did not alter our general conclusions regarding the role of giant kelp on the DSR of the reef community. However, it did increase the strength of the direct and indirect relationships between community stability and the ecological variables that define it, which enhanced our understanding of the DSR in this system and giant kelp's influence on it. For instance, bottom temperature negatively influenced giant kelp stability, which is not surprising given that the biomass dynamics of giant kelp in the region have been negatively linked to ocean temperature (Bell et al. 2015). Reef topography was positively associated with the species richness of all three community types, perhaps because topographically more

complex plots provide a greater array of microhabitat types. Reef depth was positively associated with the species richness of invertebrates and negatively associated with the species richness of macroalgae, most likely because light availability decreases with increased depth. The negative relationship between grazing pressure (as estimated by sea urchin biomass) and the species richness of algae is consistent with the direct negative effects of sea urchins on macroalgae shown in many reef systems (Ling et al. 2015), including giant kelp forests (Schiel and Foster 2015). Although previous work in our system demonstrated that sea urchins also negatively affect sessile invertebrates (Byrnes et al. 2013, Miller et al. 2018), our results show an indirect positive effect, suggesting that urchins may release invertebrates from competition for space with algae.

The positive relationship between giant kelp stability and community stability varied among the three community types; we found that the stability of communities consisting of algae + invertebrates and algae only was positively related to giant kelp stability, but uncoupled to giant kelp stability for communities consisting of invertebrates only. The lack of a relationship for the invertebrate community likely reflects differences in the response of understory algae and sessile invertebrates to fluctuations in kelp biomass. Many kelp forest understory algae are fast-growing opportunistic species capable of responding quickly to changes in light caused by fluctuations in giant kelp biomass (Reed and Foster 1984, Santelices and Ojeda 1984). In contrast, sessile invertebrates living in giant kelp forests tend to grow

more slowly than algae, and as heterotrophs, they are not directly affected by changes in light caused by fluctuations in giant kelp biomass. Instead, they display lagged responses to fluctuations in giant kelp that are indirectly mediated through competition for space with faster growing understory algae (Arkema et al. 2009, Miller et al. 2018). Although we did not examine the effects of giant kelp stability on the stability of mobile species, it seems reasonable that the stability of the mobile community varies with the degree to which it depends on the stability of the sessile reef community, which includes giant kelp. Indeed, recent findings show that giant kelp indirectly influences the biomass, diversity, and composition of mobile invertebrates and fishes in a manner commensurate with their dependence on the physical, trophic, and habitat resources altered by giant kelp (Castorani et al. 2018, Miller et al. 2018).

Giant kelp is a highly dynamic foundation species, and its variability across our study reefs over the 18-yr study period promoted a gradient of diversity in the benthic community that allowed us to examine diversity–stability relationships across a phylogenetically diverse range of organisms. We found that stability in aggregate community biomass was positively related to the time-averaged species richness for all community types. The strength of this relationship, however, varied considerably across the three community types as the DSR was three to four times stronger when algae and invertebrates were considered separately rather than in combination. Species asynchrony that promotes community stability can arise from competition for shared resources (Doak et al. 1998, Lehman and Tilman 2000) or differential responses to similar environmental conditions (Doak et al. 1998, Klug et al. 2000, Loreau and de Mazancourt 2013). Our finding that DSRs were stronger in less complex communities composed of species with similar resource requirements suggests that competition had the stronger influence in promoting species asynchrony.

Most studies documenting positive DSRs have focused on single trophic levels, such as plants within a grassland community competing for the same resources (Tilman et al. 2006, Isbell et al. 2009, Hector et al. 2010; but see Bulleri et al. 2012, Valdivia et al. 2013). Theory and empirical studies have shown that trophic interactions, between predators and prey or plants and herbivores, can both positively and negatively influence the stability of aggregate ecosystem properties (Thébault and Loreau 2003, Duffy et al. 2007, Ives and Carpenter 2007). In our study, understory algae and sessile invertebrates occur in distinct trophic levels of primary producers and primary consumers, respectively (Arkema et al. 2009, Miller et al. 2015, 2018), that compete for space on the reef, but do not compete for food. The effect of change in biodiversity across trophic levels is still in its infancy, and species at different trophic levels can exhibit many indirect and non-additive interactions that make predictions regarding DSRs in natural food webs complex. Nevertheless, our findings suggest that DSRs may

be strongest in communities consisting of species that share similar resource requirements as competition for limited shared resources leads to niche partitioning, which can stabilize communities (Loreau and de Mazancourt 2008). Such phenomena may help explain why DSRs in complex natural food webs can be uncommon (Jacquet et al. 2016).

Our finding that the positive relationship between species richness and community stability was driven by the effects of species richness on both species stability and species asynchrony is consistent with theoretical predictions (Doak et al. 1998, Lehman and Tilman 2000, Loreau and de Mazancourt 2008, Thibaut and Connolly 2013) and empirical observations (Tilman et al. 2006, Isbell et al. 2009, Hector et al. 2010, Cardinale et al. 2013). In our study, the indirect effect of species richness on community stability via species stability was stronger than the indirect effect through species asynchrony for all community types. The distribution of biomass among species tended to be skewed toward a few dominant species in all three community types that we examined. We found that the stability of most species increased with richness, providing support for the relationship between species richness and species stability. However, the dominant species, *Pterygophora californica*, was far and away the largest single contributor to the DSR, even though its stability did not show the greatest increase with species richness. This is because species stability in our analyses was weighted by species biomass (as per Thibaut and Connolly 2013). The disproportionately large effect of *P. californica* on community stability, therefore, reflects its disproportionately large contribution to the overall biomass of the community. Dominant species often fluctuate less over time (Lepš 2004, Steiner et al. 2005, Polley et al. 2007), which also could have contributed to the high weighted species stability of *P. californica*.

Bulleri et al. (2016) found that removing canopy-forming algae in the rocky intertidal increased temporal variability in the cover of associated algae and invertebrates over 2 yr. Our study expands on this concept by showing that the stability of a canopy-forming foundation species was an important determinant of the interannual variability in the underlying community of algae and invertebrates over an 18-yr period. The extent to which this is true for other systems requires further investigation. Many marine ecosystems are defined by structure-forming foundation species (e.g., kelps, oysters, seagrasses, corals), and identifying the conditions under which their stability matters for the rest of the community is a worthwhile endeavor given the increasing threats to these systems worldwide and the potential that conserving and restoring foundational species will benefit the ecosystem as a whole (Ellison et al. 2005).

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SUPPORTING INFORMATION

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DATA AVAILABILITY

Data are available from the Environmental Data Initiative: <https://doi.org/10.6073/pasta/23965abf42954f345cfd6642fe3c4810>