# Species insurance trumps spatial insurance in stabilizing biomass of a marine macroalgal metacommunity

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*Abstract.* Because natural ecosystems are complex, it is difficult to predict how their variability scales across space and levels of organization. The species-insurance hypothesis predicts that asynchronous dynamics among species should reduce variability when biomass is aggregated either from local species populations to local multispecies communities, or from metapopulations to metacommunities. Similarly, the spatial-insurance hypothesis predicts that asynchronous spatial dynamics among either local populations or local communities should stabilize metapopulation biomass and metacommunity biomass, respectively. In combination, both species and spatial insurance reduce variation in metacommunity biomass over time, yet these insurances are rarely considered together in natural systems. We partitioned the extent that species insurance and spatial insurance reduced the annual variation in macroalgal biomass in a southern California kelp forest. We quantified variability and synchrony at two levels of organization (population and community) and two spatial scales (local plots and region) and quantified the strength of species and spatial insurance by comparing observed variability and synchrony in aggregate biomass to null models of independent species or spatial dynamics based on cyclic-shift permutation. Spatial insurance was weak, presumably because large-scale oceanographic processes in the study region led to high spatial synchrony at both populationand community-level biomass. Species insurance was stronger due to asynchronous dynamics among the metapopulations of a few common species. In particular, a regional decline in the dominant understory kelp species Pterygophora californica was compensated for by the rise of three subdominant species. These compensatory dynamics were associated with positive values of the Pacific Decadal Oscillation, indicating that differential species tolerances to warmer temperature and nutrient-poor conditions may underlie species insurance in this system. Our results illustrate how species insurance can stabilize aggregate community properties in natural ecosystems where environmental conditions vary over broad spatial scales.

*Key words: compensatory dynamics; kelp forests; metacommunity; spatial insurance hypothesis; spatial scale; stability; synchrony.* 

# INTRODUCTION

It is well known that diverse portfolio assets stabilize financial investments. Similarly, species diversity can stabilize aggregate biomass of local communities if species vary asynchronously through time (Loreau and de Mazancourt 2013, Thibaut and Connolly 2013, Isbell et al. 2015, Donohue et al. 2016). Such a species insurance effect can arise from either interspecific competition (Doak et al. 1998, Lehman and Tilman 2000) or

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different species responses to environmental conditions (Doak et al. 1998, Klug et al. 2000, Loreau and de Mazancourt 2013). Similarly, spatial insurance can stabilize regional or metacommunity biomass—the biomass aggregated across multiple species and spatial units—if spatial dynamics among local communities are asynchronous (Wang and Loreau 2014, 2016). Limited dispersal, environmental heterogeneity, and spatial variation in species composition all contribute to increasing the asynchrony among local community dynamics (Loreau et al. 2003, Wang and Loreau 2014, 2016). Spatial insurance can also stabilize the aggregate biomass of metapopulations if the spatial dynamics of local populations are asynchronous (Liebhold et al. 2004, Walter et al. 2017, Thorson et al. 2018), and species insurance can further stabilize metacommunity biomass if the metapopulation dynamics of the constituent species vary asynchronously in time (Wang et al. 2019). Whether through local communities or metapopulations, species asynchrony, spatial asynchrony, or both should in theory stabilize metacommunity biomass (Loreau et al. 2003, Wang and Loreau 2014, 2016). However, the extent to which species and spatial asynchrony combine and interact across different hierarchical levels to stabilize metacommunity biomass is rarely measured in natural systems (but see Houlahan et al. 2007, Gonzalez and Loreau 2009, Vasseur et al. 2014, Wilcox et al. 2017, Magurran and Henderson 2018, Thorson et al. 2018, Wang et al. 2019).

Theory suggests that such insurance effects are more likely to occur when the long-term average biomass is relatively even across species or spatial units (Doak et al. 1998, Thibaut and Connolly 2013, Wang and Loreau 2016). In nature, however, many species are consistently rare and some areas consistently barren, meaning that a few dense sampling units, common species, or both, are likely to drive biomass fluctuations, potentially limiting insurance effects (Cottingham et al. 2001, Hillebrand et al. 2008, Grman et al. 2010, Sasaki and Lauenroth 2011, Thibaut and Connolly 2013). Here, we measure asynchronous species and spatial dynamics across multiple hierarchical levels of macroalgae living under the kelp forest canopy using a new method that quantifies the extent that species insurance and spatial insurance stabilize aggregate biomass in a metacommunity.

Beneath the buoyant canopy of giant kelp (*Macrocystis pyrifera*), many understory algal species compete for space and light (Santelices and Ojeda 1984, Edwards 1998, Miller et al. 2011, 2018). The strong competitive interactions among these species, and their different tolerances to local oceanographic conditions, disturbance, and substrate (Reed and Foster 1984, Dayton et al. 1992), potentially generate asynchronous species dynamics. However, regional-scale processes can synchronize species biomass in space, obscuring asynchronous species dynamics when environmental drivers operate over large spatial scales (Lamy et al. 2018).

We used annual biomass of 56 understory macroalgal species from 39 widely distributed plots over 14 yr to evaluate the relative importance of asynchronous species and spatial dynamics in reducing the interannual variability in the aggregate biomass of the macroalgal metacommunity. To do this, we quantified variability and synchrony at multiple hierarchical levels including two levels of organization (population and community) and two spatial scales (local plots and region). We then compared observed variability and synchrony to null models of independent species or spatial dynamics based on cyclic-shift permutation. Finally, to explain differences between theoretical predictions and our observations, we assessed the importance of the uneven biomass distribution across species and space by determining the contributions of single species and plots. We found that compensatory dynamics among a few common species contribute to a species insurance effect, whereas largescale spatial environmental processes, likely linked to oceanographic and climate conditions, limited the spatial insurance effect.

### MATERIALS AND METHODS

### Ecological surveys

The Santa Barbara Coastal Long Term Ecological Research program (SBC-LTER) annually measures the abundance (density or percent cover) and size of all understory macroalgae species found in 39 fixed 80-m<sup>2</sup> plots distributed across 11 shallow (4–12 m depth) rocky reefs in the Santa Barbara Channel, California, USA (Reed 2018; Appendix S1: Fig. S1). We converted understory macroalgae abundance into biomass (g decalcified dry mass/m<sup>2</sup>, hereafter g/m<sup>2</sup>) using species-specific allometric relationships developed by Harrer et al. (2013).

# Partitioning metacommunity variability across different hierarchical levels

We focused on the summer biomass of all understory macroalgal species recorded from 2004 to 2017 (N = 56species; Appendix S1: Table S1) and assessed the coefficient of temporal variation (CV) in biomass at two levels of organization, population and community, and two spatial scales, local plot and region (Fig. 1). We calculated regional, or metacommunity variability (CV<sub>MC</sub>) as the temporal CV of aggregate metacommunity biomass, and metapopulation variability (CV<sub>MP</sub>) as the weighted average temporal CV of metapopulation biomass across all species. Local community variability (CV<sub>LC</sub>) was calculated as the weighted average temporal CV of local community biomass across all plots, and local population variability  $(CV_{LP})$  as the weighted average temporal CV of local population biomass across all species and plots (see Wang et al. 2019 and Appendix S1: Text S1 for mathematical definitions). Six synchrony indices (defined in Table 1) serve as scaling factors that measure how variability is reduced when biomass is aggregated from one hierarchical level to the next (Thibaut and Connolly 2013, Wang and Loreau 2014, Wang et al. 2019). These synchrony indices are adapted from the Loreau and de Mazancourt (2008) original definition (Wang et al. 2019), and range between 0 and 1. These indices are close to 1 (perfectly synchronous dynamics among species or space) when variability at a higher hierarchical level mirrors variability of its constituent levels, and are close to 0 (perfectly asynchronous dynamics among species or space) when constituent levels fluctuate in such a way that variability at the higher hierarchical level is null. We compared synchrony indices across levels of organization and spatial scales, and also between species synchrony and spatial synchrony.



FIG. 1. Partitioning the interannual variability in understory macroalgal metacommunity biomass into its lower hierarchical levels of variability and their degree of synchrony. The different hierarchical levels of variability correspond to local population (CV<sub>LP</sub>), local community (CV<sub>LC</sub>), metapopulation (CV<sub>MP</sub>), and metacommunity (CV<sub>MC</sub>), respectively. CV is within parentheses. The four synchrony indices,  $\phi_{P \to C,L}$ ,  $\phi_{C,L\rightarrow R}$ ,  $\phi_{P,L\rightarrow R}$  and  $\phi_{P\rightarrow C,R}$ , measure how variability is reduced from one hierarchical level to the next. For illustrative purposes, we represent a metacommunity of three local plots and three species. Understory macroalgal CV<sub>MC</sub> is 18%, which results from the scaling of local population variability (CV<sub>LP</sub>) either through local communities based on the degree of species synchrony within plots and spatial synchrony among local communities  $(120\% \times 0.490 \times 0.312)$ , or through metapopulations based on the degree of spatial synchrony across species and metapopulation synchrony ( $120\% \times 0.542 \times 0.282$ ).

# Quantifying the effect size of species and spatial insurance effects

We compared the observed degree of synchrony to null models of independent species or spatial dynamics based on cyclic-shift permutation (Hallett et al. 2014, Magurran and Henderson 2018). For each synchrony index, this permutation preserved the observed temporal autocorrelation within lower constituent hierarchical levels, but separated correlation among species at either local  $(\phi_{P \to C, k} \text{ and } \phi_{P \to C, L})$  or regional  $(\phi_{P \to C, R})$  scales and correlation among either local populations of a given species ( $\varphi_{i,L\rightarrow R}$  and  $\varphi_{P,L\rightarrow R}$ ) or local communities  $(\phi_{C,L\rightarrow R})$  (Table 1; Appendix S1: Fig. S2). Cyclic-shift permutation preserves temporal autocorrelation, therefore acknowledging the importance of density-dependence and adding ecological realism. For instance, to quantify the strength of the stabilizing effect of space on the metapopulation variability of the *i*th species, the cvclic-shift permutation selects a random start date for each local population time series within each plot, thus maintaining the same local population variability and temporal autocorrelation, but generating new distributions of metapopulation variability given spatially independent dynamics across local populations (Appendix S1: Fig. S2). We used similar approaches to test the other synchrony indices as summarized in Table 1. For each synchrony metric, we performed 999 permutations to provide a null distribution, from which we computed a standardized effect size ( $\varphi$ SES) as:

$$\varphi SES = \frac{(\varphi - \mu_{null})}{\sigma_{null}} \tag{1}$$

with  $\mu_{null}$  and  $\sigma_{null}$  the mean and standard deviation of the null distribution obtained from the permutations. For a normally distributed SES, the 95% confidence interval should roughly range between 2 and -2, and  $\phi$ SES above this interval indicate more synchronous dynamics (weaker stabilizing effects) while  $\phi$ SES below this interval indicate more asynchronous dynamics (stronger stabilizing effects). We used the same permutations to quantify the resulting percent increase or decrease in variability at each hierarchal level as  $(\phi - \mu_{null})/\phi$ .

# Species contributions to $\varphi_{P \to C,R}$ and plot contributions to $\varphi_{C,L \to R}$

To assess the importance of uneven biomass distribution across species and space, we quantified the contribution of each individual species and individual plot to metapopulation synchrony ( $\phi_{P \rightarrow C,R}$ ) and spatial community synchrony  $(\phi_{C,L\rightarrow R})$ , respectively, by computing  $\phi_{P \rightarrow C,R}$  and  $\phi_{C,L \rightarrow R}$  in the absence of respective species or plot ( $\phi'$ ). Species and plot contribution to  $\phi$  was then computed by a log response ratio  $\ln(\phi'/\phi)$ . A positive species contribution indicates that removing the species increases  $\varphi_{P \to C,R}$ , and therefore the species has a stabilizing effect by decreasing the degree of metapopulation synchrony. This can occur when the metapopulation dynamics of one species is strongly asynchronous with those of other species, and that species make up a large portion of the regional biomass and could thereby compensate for the regional variability of other species. Similarly, a positive plot contribution indicates that removing the plot increased  $\phi_{C,L\rightarrow R}$ , and therefore the plot has a stabilizing effect by decreasing the degree of spatial synchrony among local communities.

## Regional drivers of species dynamics

We used redundancy analysis (RDA) to model the temporal dynamics of macroalgal species at the regional scale. We created seven temporal variables from distance-based Moran's eigenvector maps (db-MEM: Dray et al. 2006) to represent a series of sinusoids of decreasing periods associated with smoother and shorter-term

	Symbol	$(\sigma_X)$	Numerator	$(\sum \sigma_x)$	Denominator	Null model
Spatial synchrony among local communities	$\phi_{C,L \to R}$	$\sigma_{TT}$	Temporal standard deviation of metacommunity biomass	$\sum_{k}^{m} \sigma_{\mathrm{T}k}$	Sum of temporal standard deviations of local community biomass	Is $\varphi_{C,L \to R}$ higher or lower than under independent spatial dynamics across local communities given local community dynamics?
Spatial synchrony of the <i>i</i> th species	$\phi_{i,L \to R}$	σ <sub>iT</sub>	Temporal standard deviation of metapopulation biomass of the <i>i</i> th species	$\sum_{k}^{m} \sigma_{ij}$	Sum of temporal standard deviations of local population biomass of the <i>i</i> th species	Is $\phi_{i,L \rightarrow R}$ higher or lower than independent spatial dynamics across local populations of the <i>i</i> th species given its local population dynamics?
Spatial synchrony averaged across species	$\phi_{P,L\to R} \dot{\dagger}$					Is $\varphi_{P,L \rightarrow R}$ higher or lower than under independent spatial dynamics across local populations given local population dynamics across all species?
Metapopulation synchrony	$\phi_{P \to C,R}$	$\sigma_{TT}$	Temporal standard deviation of metacommunity biomass	$\sum_{i}^{n} \sigma_{iT}$	Sum of standard deviations of metapopulation biomass	Is $\varphi_{P \rightarrow C,R}$ higher or lower than under independent species dynamics at the regional scale given metapopulation dynamics?
Species synchrony within the <i>k</i> th plot	$\phi_{P \to C,k}$	$\sigma_{\mathrm{T}k}$	Temporal standard deviation of total community biomass within the <i>k</i> th plot	$\sum_{i}^{n} \sigma_{ik}$	Sum of temporal standard deviations of local population biomass within the <i>k</i> th plot	Is $\varphi_{P \to C,k}$ higher or lower than under independent species dynamics within the <i>k</i> th plot given local population dynamics?
Species synchrony averaged across plots	$\phi_{P \rightarrow C,L} \ddagger$					Is $\varphi_{P\rightarrow C,L}$ higher or lower than under independent species dynamics within plots given population dynamics across all plots?

TABLE 1. Table of the six synchrony indices underpinning metacommunity variability.

*Notes:* These synchrony indices link the different hierarchical levels of variability to the metacommunity scale. All indices are in the form  $\varphi = \sigma_X / \sum \sigma_x$ , the square-root transformation of the Loreau and Mazancourt metric (2008), with  $\sigma_X$  the temporal standard deviation of aggregate biomass at hierarchical level X and  $\sum \sigma_x$  the sum of the standard deviations of biomass at the constituent levels making up X.  $\sigma_{ik}$  represents the most fundamental level of temporal variability; that is, the standard deviation of the *i*th species in the *k*th plot. *n* and *m* correspond to the total number of species and plots surveyed, respectively.

$$\dagger \varphi_{\mathbf{P},\mathbf{L}\to\mathbf{R}} = \sum_{i} \omega_i \cdot \varphi_{i,L\to\mathbf{R}}$$
, with  $\omega_i = \sum_{k=1}^{m} \sigma_{ij} / \sum_{i,k=1}^{n,m} \sigma_{ij}$ 

$$\ \ \phi_{P \to C,L} = \sum_k \omega_k \cdot \phi_{P \to C,k}$$
, with  $\omega_k = \sum_i^n \sigma_{ij} / \sum_{i,k}^{n,m} \sigma_{ij}$ 

temporal fluctuations. We then used forward selection (Blanchet et al. 2008) to keep only the temporal variables that successfully captured the temporal scales at which compensatory dynamics among species occurred at the regional scale. Our final RDA was based on Hellinger distance and included a general trend and the selected temporal variables (db-MEM 2, 4, and 7). Each significant canonical axis represented a distinct facet of the temporal dynamics of macroalgae at the regional scale. Therefore, to identify the environmental drivers that contributed to temporal dynamics along each significant canonical axis further, we used multiple regressions to assess how two environmental variables explained the temporal dynamics of macroalgae along each canonical axis. We used two indices that captured large-scale variations in oceanographic and climate conditions along the coast of California: The North Pacific Gyre Oscillation (NPGO) and the Pacific Decadal Oscillation (PDO). Positive NPGO values correspond with stronger wind-driven upwelling, which leads to greater nutrient concentrations, whereas positive PDO values indicate warmer sea surface temperature and nutrientpoor conditions.

All analyses were performed using R version 3.4.3 (R Core Team 2017). The RDA was performed using the *rda* function of the vegan package (Oksanen et al. 2017).

We provide an R script as Data S1 including the functions used to partition metacommunity variability and quantify effect sizes.

#### RESULTS

# Partitioning metacommunity variability across different hierarchical levels

Metacommunity biomass varied between 42.95 and 72.93 g/m<sup>2</sup> over the 14-yr period (Fig. 2). Both species and spatial effects combined to reduce the interannual variability in biomass from a temporal CV of 120% at the local population level (CV\_LP) to 18% (CV\_MC) at the metacommunity scale (Fig. 1). This stabilizing effect can be measured by multiplying species and spatial synchrony in either of two parallel paths. The local-communities path multiplies species synchrony within plots  $(\phi_{P \rightarrow C,L}$  = 0.490) with spatial synchrony among local communities ( $\varphi_{C,L\rightarrow R} = 0.312$ ), while the metapopulations path multiplies spatial synchrony across species  $(\phi_{P,L\rightarrow R} = 0.542)$  with metapopulation synchrony  $(\phi_{P \to C,R} = 0.282;$  Fig. 1). Either through local communities or through metapopulation, species insurance had a stronger stabilizing effect than spatial insurance on metacommunity biomass given the degree of natural variability observed in this system (Fig. 3).

#### Species insurance effects

At the regional scale, we found that metapopulations of different species of understory macroalgae were more asynchronous ( $\phi_{P \rightarrow C,R}$  SES = -1.71; Figs. 1, 3) than expected had they fluctuated independently of one

another. This asynchrony contributed to reducing interannual variation in metacommunity biomass ( $CV_{MC}$ ) by 40.2%. However, species insurance was weaker at the local scale, as species synchrony within plots ( $\phi_{P\rightarrow C,L}$ SES = 1.00: Figs. 1, 3) slightly increased interannual variation in local community biomass ( $CV_{LC}$ ) by 2.3% more than expected if species had fluctuated independently of one another within each plot. The strength of the species insurance effect varied among plots. The



FIG. 3. Synchrony indices and their standardized effect size (SES). Synchrony SES measures whether the stabilizing effect provided by each synchrony index is weaker (SES > 2), stronger (SES < -2) or not different (-2 < SES < 2) as compared to independent species or spatial dynamics. Grey areas represent the 95% quantiles generated based on the 999 cyclic-shift permutations, and horizontal bars represent the mean synchrony of the null distributions. Through either local communities ( $\phi_{P \rightarrow C,L}$  SES = 1.00 vs.  $\phi_{C,L \rightarrow R}$  SES = 4.21) or through metapopulations ( $\phi_{P \rightarrow C,R}$  SES = -1.71 vs.  $\phi_{P,L \rightarrow R}$  SES = 12.88), species dynamics had a stronger stabilizing effect.



FIG. 2. Regional or metacommunity biomass of understory macroalgae from 2004 to 2017. Metacommunity biomass is expressed as the averaged biomass across all plots and is divided into the contribution of the four most abundant taxa (*Ptery-gophora californica, Desmarestia ligulata, Stephanocystis osmundacea, Chondracanthus* spp.) and the remaining species.

dynamics of species biomass were more synchronous than expected in 9 of the 39 plots, resulting in 15–34% increased variability in the community biomass in these plots (Appendix S1: Fig. S3). Species dynamics were less synchronous than expected in one plot, which decreased its variability in total community biomass by 27% (Appendix S1: Fig. S3).

# Spatial insurance effects

In contrast to the strong stabilizing effects of species insurance, spatial insurance was weaker-synchrony among local communities increased interannual variation in metacommunity biomass by 41.0% more than expected given independent fluctuation of local communities ( $\phi_{C,L\rightarrow R}$  SES = 4.21; Figs. 1, 3). At the population level, we found that, on average, interannual variation in metapopulation biomass (CV<sub>MP</sub>) was 51.2% more variable than expected if local populations had displayed independent spatial dynamics across plots ( $\varphi_{P,L\rightarrow R}$ SES = 12.88; Figs. 1, 3). Specifically, 36 out of the 56 species displayed more synchronous spatial dynamics than expected ( $\phi_{i,L\rightarrow R}$ ), which increased their metapopulation variability from 3 to 72% (Appendix S1: Fig. S4). Only one species, the red alga Callophyllis flabellulata, displayed less synchronous spatial dynamics than expected, decreasing its metapopulation variability by  $65\% (\phi_{i,L \rightarrow R} = 0.142; SES = -2.22).$ 

# Species contributions to $\phi_{P \to C, R}$ and regional drivers of species dynamics

Species differed in their contribution to insurance effects. The kelp Pterygophora californica, the brown algae Stephanocystis osmundacea and Desmarestia ligulata, and the red alga Chondracanthus spp. had disproportionately large effects on species insurance as their removals greatly increased metapopulation synchrony  $(\phi_{P \rightarrow C,R}$ : Appendix S1: Fig. S5) and consequently destabilized metacommunity biomass. P. californica, the dominant species of understory macroalgae, dramatically declined by 99% across all plots from 2007 (35.84 g/m<sup>2</sup>) to 2016 (0.45 g/m<sup>2</sup>: Fig. 2). Meanwhile, metacommunity biomass remained relatively constant because of compensatory increases in other understory macroalgae at the regional scale (Fig. 2). This temporal dynamic was successfully captured by the RDA, which significantly explained 60% of the temporal variation in understory macroalgae at the regional scale  $(F_{3,10} = 7.460, P = 0.001;$  Fig. 4) along the first two canonical axes. Most of the temporal variation occurred along the first canonical axis ( $R_{adj}^2 = 0.472$ , P = 0.001; Fig. 4) and suggests that declining *P. californica* biomass over time was counteracted by increases in S. osmundacea, D. ligulata, and Chondracanthus spp. from 2013 onward. The second canonical axis ( $R_{adi}^2 = 0.090$ , P = 0.002; Fig. 4) identified that increases in Cryptopleura ruprechtiana, Eisenia arborea, and Polyneura

poral variation in understory macroalgae along the first canonical axis was significantly associated with positive PDO values ( $R_{adj}^2 = 0.419$ , P = 0.007), whereas temporal variation in understory macroalgae along the second canonical axis was significantly associated with positive NPGO values ( $R_{adj}^2 = 0.474$ , P = 0.004).

## *Plot contributions to* $\varphi_{C,L \rightarrow R}$

Plots did not differ in their contribution to insurance effects, as their contributions to spatial synchrony among local communities were low (Appendix S1: Fig. S5).

# DISCUSSION

The understory macroalgae in our system form a diverse metacommunity in which biomass varies across time, space, and species. Theory and experiments predict that temporal fluctuations in aggregate biomass at the metacommunity scale should be buffered by species diversity and spatial heterogeneity (Doak et al. 1998, Tilman 1999, Lehman and Tilman 2000, Loreau and de Mazancourt 2013, Thibaut and Connolly 2013, Wang and Loreau 2014, 2016, Donohue et al. 2016). This should be no surprise given that the central limit theorem dictates that variability will decrease as biomass is aggregated from one hierarchical level to another, from local populations up to the metacommunity (Thibaut and Connolly 2013, Wang and Loreau 2014). Nevertheless, the relative importance of species and spatial stabilizing mechanisms have rarely been tested in nature (Wilcox et al. 2017), which is of relevance for management decisions aimed at maintaining the stability of natural ecosystems. A similar study found that spatial insurance was more important than species insurance for reducing variation in fish biomass from bottom trawls (Thorson et al. 2018). In contrast, we found species insurance was the main mechanism for the stability of macroalgal biomass. In particular, asynchronous metapopulation dynamics across macroalgal species had the strongest stabilizing effect on aggregate biomass dynamics at the regional scale.

The stronger stabilizing effect of asynchronous species dynamics could stem from several factors, including lifehistory trade-offs that lead to niche differentiation among species. For instance, the algae in this study have different levels of tolerance to shading (Harrer et al. 2013), causing some species to be favored over others as the giant kelp canopy waxes and wanes (Miller et al. 2011, Castorani et al. 2018). Algal species also differ in their susceptibility to removal by grazing and wave disturbance, leading to community shifts as sea urchin populations and wave events fluctuate (Ebeling et al. 1985, Harrold and Reed 1985). Other factors such as nutrient supply, suspended sediments, and water flow are also



FIG. 4. Temporal dynamics in understory macroalgae at the regional scale for 2004–2017 (Redundancy analysis biplot;  $R_{adj}^2 = 0.598$ ). Each circle represents a year in the time series and arrows represent scores of the most influential species. Temporal dynamics of understory macroalgae along the first and second canonical axis were significantly associated with positive values of the Pacific Decadal Oscillation (PDO) index and the North Pacific Gyre Oscillation (NPGO) index, respectively.

considered important in explaining the biomass dynamics of understory macroalgae (Schiel and Foster 2015), and contrasting responses to such environmental variables as well as competitive interactions may have contributed to complementarity in their biomass dynamics. Although we know most of these species are physiologically diverse (Miller et al. 2012, Harrer et al. 2013), their functional traits and ability to use complementary resources remain mostly unknown.

Space had a weaker stabilizing effect because of more synchronous spatial dynamics at both population and community levels. Synchronous spatial dynamics can be attributed to broad-scale environmental forcing (Loreau et al. 2003, Wang and Loreau 2014, Shanafelt et al. 2015) and/or high dispersal (Kendall et al. 2000, Liebhold et al. 2004). Spore dispersal estimates for macroalgae range from a few meters to several kilometers but generally average <1 km (Gaylord et al. 2002, Kinlan and Gaines 2003). This is much shorter than the maximum distance between our plots (75 km), suggesting that dispersal alone does not explain the high degree of spatial synchrony in our system. Although it is challenging to decipher the actual mechanisms underlying spatial synchrony, our results suggest that the regional dynamics of macroalgal species was tightly linked with the PDO and NPGO indices, which capture large-scale variations in sea surface temperature and nutrient concentration along the coast of California. This result is not surprising, given that sea surface temperature has been shown to influence subtidal reef assemblages strongly over large spatial scales in the study region (Lamy et al. 2018). Because spatial autocorrelation in environmental conditions usually decays with distance (Koenig 1999), it is possible that spatial insurance becomes stronger at a greater spatial extent, and differences in spatial extent could explain why we found more spatial synchrony in macroalgal biomass than Thorson et al. (2018) found for fish biomass. Future work on how the relative importance of species and spatial insurance changes with spatial extent will help to resolve this.

The insurance value of biodiversity is frequently invoked as a main driver of stability, whereby greater species richness stabilizes community and ecosystem properties because of differential species responses to environmental fluctuations and complementary resource use (Tilman 1999, Elmqvist et al. 2003, Leary and Petchey 2009). Although early theoretical models assumed even abundance among species (Cottingham et al. 2001), skewed biomass across species can modulate how species richness affects variability in aggregate biomass (Thibaut and Connolly 2013, Wang and Loreau 2016), as shown empirically (Smith and Knapp 2003, Polley et al. 2007, Hillebrand et al. 2008, Grman et al. 2010, Sasaki and Lauenroth 2011). In nature, speciesabundance distributions are typically highly skewed, such that rare species contribute disproportionately to species richness. Under these circumstances the massratio hypothesis (Grime 1998) predicts that only a few dominant species drive community dynamics. In our system, regional dominance was driven by four species, P. californica, D. ligulata, Chondracanthus spp., and S. osmundacea, which composed 60% of the total metacommunity biomass. Notably, the understory kelp P. californica was the most dominant species overall (33%) and exhibited strongly synchronous spatial metapopulation dynamics. Furthermore, its metapopulation biomass declined by 99% between 2007 and 2016, in part because of high mortality during a 2014-2016 warming event (Reed et al. 2016). P. californica flourishes in cool water, and small embryonic stages are more sensitive to high temperature than are larger adults (Matson and Edwards 2007). Nonetheless, we observed that the precipitous decline in P. californica biomass during the 2014-2016 warming event resulted in adult mortality. Remarkably, metacommunity biomass did not decline during this period, because of a compensatory increase in the three subdominant species D. ligulata, Chondracanthus spp., and S. osmundacea. This change in hierarchical dominance between a few dominant species helped offset the otherwise weak spatial insurance. Such a response could result from species-specific differences in tolerance to large-scale variability in ocean temperature and nutrient concentrations that occurred over the 14-yr period. Indeed, P. californica was favored during years of cooler, nutrient-rich conditions, whereas the three subdominant species thrived during warmer, nutrient-poor periods. In this system, therefore, compensatory species dynamics is linked to large-scale climate patterns in the Pacific Ocean described by the NPGO and PDO and their relationships to El Niño Southern Oscillation (ENSO). Although the compensatory increase of the three subdominant algae in response to the decline of P. californica stabilized metacommunity biomass, the functioning of the understory macroalgal communities presumably changed, because the subcanopy of P. californica supports more fish (Ebeling and Laur 1985) and spiny lobster (Mai and Hovel 2007). Moreover, P. californica is consumed by numerous grazers and detritivores and the compensating increase of D. ligulata, an annual and opportunistic early successional species (Edwards 1998), is unlikely to replace its function as a food source fully because it is unpalatable to many species due to its high sulfuric acid content (Eppley and Bovell 1958, Anderson and Velimirov 1982).

This study is one of the first to investigate the respective roles of species and spatial synchrony at the metacommunity scale (Wilcox et al. 2017). It highlights how species insurance can stabilize aggregate community properties in natural ecosystems where environmental conditions vary over broader spatial scales. Without species insurance, local and regional assemblages would have larger temporal fluctuations, which could reduce the primary production and functional diversity that promote metacommunity stability. Nonetheless, species insurance against volatility in biomass of this diverse metacommunity was driven by a few dominant species rather than species richness per se. Given that most species are rare, we suspect the same will be true in most other natural communities.

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#### LITERATURE CITED

- Anderson, R. J., and B. Velimirov. 1982. An experimental investigation of the palatability of kelp bed algae to the sea urchin *Parechinus angulosus* leske. Marine Ecology 3:357–373.
- Blanchet, F. G., P. Legendre, and D. Borcard. 2008. Forward selection of explanatory variables. Ecology 89:2623–2632.
- Castorani, M. C. N., D. C. Reed, and R. J. Miller. 2018. Loss of foundation species: disturbance frequency outweighs severity in structuring kelp forest communities. Ecology 99:2442– 2454.
- Cottingham, K. L., B. L. Brown, and J. T. Lennon. 2001. Biodiversity may regulate the temporal variability of ecological systems. Ecology Letters 4:72–85.
- Dayton, P. K., M. J. Tegner, P. E. Parnell, and P. B. Edwards. 1992. Temporal and spatial patterns of disturbance and recovery in a kelp forest community. Ecological Monographs 62:421–445.
- Doak, D. F., D. Bigger, E. K. Harding, M. A. Marvier, R. E. O'Malley, and D. Thomson. 1998. The statistical inevitability of stability-diversity relationships in community ecology. American Naturalist 151:264–276.
- Donohue, I., et al. 2016. Navigating the complexity of ecological stability. Ecology Letters 19:1172–1185.
- Dray, S., P. Legendre, and P. R. Peres-Neto. 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). Ecological Modelling 196:483–493.
- Ebeling, A. W., and D. R. Laur. 1985. The influence of plant cover on surfperch abundance at an offshore temperate reef. Environmental Biology of Fishes 12:169–179.
- Ebeling, A. W., D. R. Laur, and R. J. Rowley. 1985. Severe storm disturbances and reversal of community structure in a southern California kelp forest. Marine Biology 84:287– 294.

- Edwards, M. S. 1998. Effects of long-term kelp canopy exclusion on the abundance of the annual alga *Desmarestia ligulata* (Light F). Journal of Experimental Marine Biology and Ecology 228:309–326.
- Elmqvist, T., C. Folke, M. Nyström, G. Peterson, J. Bengtsson, B. Walker, and J. Norberg. 2003. Response diversity, ecosystem change, and resilience. Frontiers in Ecology and the Environment 1:488–494.
- Eppley, R. W., and C. R. Bovell. 1958. Sulfuric acid in Desmarestia. Biological Bulletin 115:101–106.
- Gaylord, B., D. C. Reed, P. T. Raimondi, L. Washburn, and S. R. McLean. 2002. A physically based model of macroalgal spore dispersal in the wave and current-dominated nearshore. Ecology 83:1239–1251.
- Gonzalez, A., and M. Loreau. 2009. The causes and consequences of compensatory dynamics in ecological communities. Annual Review of Ecology, Evolution, and Systematics 40:393–414.
- Grime, J. P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. Journal of Ecology 86:902–910.
- Grman, E., J. A. Lau, D. R. Schoolmaster, and K. L. Gross. 2010. Mechanisms contributing to stability in ecosystem function depend on the environmental context. Ecology Letters 13:1400–1410.
- Hallett, L. M., et al. 2014. Biotic mechanisms of community stability shift along a precipitation gradient. Ecology 95:1693–1700.
- Harrer, S. L., D. C. Reed, S. J. Holbrook, and R. J. Miller. 2013. Patterns and controls of the dynamics of net primary production by understory macroalgal assemblages in giant kelp forests. Journal of Phycology 49:248–257.
- Harrold, C., and D. C. Reed. 1985. Food availability, sea urchin grazing, and kelp forest community structure. Ecology 66:1160–1169.
- Hillebrand, H., D. M. Bennett, and M. W. Cadotte. 2008. Consequences of dominance: A review of evenness effects on local and regional ecosystem processes. Ecology 89:1510– 1520.
- Houlahan, J. E., et al. 2007. Compensatory dynamics are rare in natural ecological communities. Proceedings of the National Academy of Sciences USA 104:3273–3277.
- Isbell, F., et al. 2015. Biodiversity increases the resistance of ecosystem productivity to climate extremes. Nature 526:574–577.
- Kendall, B. E., O. N. Bjørnstad, J. Bascompte, T. H. Keitt, and W. F. Fagan. 2000. Dispersal, environmental correlation, and spatial synchrony in population dynamics. American Naturalist 155:628–636.
- Kinlan, B. P., and S. D. Gaines. 2003. Propagule dispersal in marine and terrestrial environments: A community perspective. Ecology 84:2007–2020.
- Klug, J. L., J. M. Fischer, A. R. Ives, and B. Dennis. 2000. Compensatory dynamics in planktonic community responses to pH perturbations. Ecology 81:387–398.
- Koenig, W. D. 1999. Spatial autocorrelation of ecological phenomena. Elsevier, Amsterdam, The Netherlands.
- Lamy, T., D. C. Reed, A. Rassweiler, D. A. Siegel, L. Kui, T. W. Bell, R. D. Simons, and R. J. Miller. 2018. Scalespecific drivers of kelp forest communities. Oecologia 186: 217–233.
- Leary, D. J., and O. L. Petchey. 2009. Testing a biological mechanism of the insurance hypothesis in experimental aquatic communities. Journal of Animal Ecology 78:1143–1151.
- Lehman, C. L., and D. Tilman. 2000. Biodiversity, stability, and productivity in competitive communities. American Naturalist 156:534–552.

- Liebhold, A., W. D. Koenig, and O. N. Bjørnstad. 2004. Spatial synchrony in population dynamics. Annual Review of Ecology, Evolution, and Systematics 35:467–490.
- Loreau, M., and C. de Mazancourt. 2008. Species synchrony and its drivers: neutral and nonneutral community dynamics in fluctuating environments. American Naturalist 172:E48– E66.
- Loreau, M., and C. de Mazancourt. 2013. Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. Ecology Letters 16:106–115.
- Loreau, M., N. Mouquet, and A. Gonzalez. 2003. Biodiversity as spatial insurance in heterogeneous landscapes. Proceedings of the National Academy of Sciences USA 100:12765–12770.
- Magurran, A. E., and P. A. Henderson. 2018. More than the sum of the parts: annual partitioning within spatial guilds underpins community regulation. Proceedings of the Royal Society B 285:20180659.
- Mai, T. T., and K. A. Hovel. 2007. Influence of local-scale and landscape-scale habitat characteristics on California spiny lobster (*Panulirus interruptus*) abundance and survival. Marine and Freshwater Research 58:419–428.
- Matson, P. G., and M. S. Edwards. 2007. Effects of ocean temperature on the southern range limits of two understory kelps, *Pterygophora californica* and *Eisenia arborea*, at multiple life-stages. Marine Biology 151:1941–1949.
- Miller, R. J., S. Harrer, and D. C. Reed. 2012. Addition of species abundance and performance predicts community primary production of macroalgae. Oecologia 168:797–806.
- Miller, R. J., K. D. Lafferty, T. Lamy, L. Kui, A. Rassweiler, R. L. Rongstad, and D. C. Reed. 2018. Giant kelp increases faunal diversity through physical engineering. Proceedings of the Royal Society B 285:20172571.
- Miller, R. J., D. C. Reed, and M. A. Brzezinski. 2011. Partitioning of primary production among giant kelp (*Macrocystis pyrifera*), understory macroalgae, and phytoplankton on a temperate reef. Limnology and Oceanography 56:119–132.
- Oksanen, J. et al. 2017. vegan: community ecology package. R package version 2.4-5. https://CRAN.R-project.org/package= vegan
- Polley, H. W., B. J. Wilsey, and J. D. Derner. 2007. Dominant species constrain effects of species diversity on temporal variability in biomass production of tallgrass prairie. Oikos 116:2044–2052.
- R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/
- Reed, D. C. 2018. SBC LTER: Reef: Annual time series of biomass for kelp forest species, ongoing since 2000. Environmental Data Initiative. https://doi.org/10.6073/pasta/23965abf 42954f345cfd6642fe3c4810
- Reed, D. C., and M. S. Foster. 1984. The effects of canopy shadings on algal recruitment and growth in a giant kelp forest. Ecology 65:937–948.
- Reed, D., L. Washburn, A. Rassweiler, R. Miller, T. Bell, and S. Harrer. 2016. Extreme warming challenges sentinel status of kelp forests as indicators of climate change. Nature Communications 7:13757.
- Santelices, B., and F. P. Ojeda. 1984. Effects of canopy removal on the understory algal community structure of coastal forests of *Macrocystis pyrifera* from southern South America. Marine Ecology Progress Series 14:165–173.
- Sasaki, T., and W. K. Lauenroth. 2011. Dominant species, rather than diversity, regulates temporal stability of plant communities. Oecologia 166:761–768.
- Schiel, D. R., and M. S. Foster. 2015. The biology and ecology of giant kelp forests. First edition. University of California Press, Berkeley, California, USA.

- Shanafelt, D. W., U. Dieckmann, M. Jonas, O. Franklin, M. Loreau, and C. Perrings. 2015. Biodiversity, productivity, and the spatial insurance hypothesis revisited. Journal of Theoretical Biology 380:426–435.
- Smith, M. D., and A. K. Knapp. 2003. Dominant species maintain ecosystem function with non-random species loss. Ecology Letters 6:509–517.
- Thibaut, L. M., and S. R. Connolly. 2013. Understanding diversity-stability relationships: towards a unified model of portfolio effects. Ecology Letters 16:140–150.
- Thorson, J. T., M. D. Scheuerell, J. D. Olden, and D. E. Schindler. 2018. Spatial heterogeneity contributes more to portfolio effects than species variability in bottom-associated marine fishes. Proceedings of the Royal Society B 285:20180915.
- Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. Ecology 80:1455– 1474.

- Vasseur, D. A. et al. 2014. Synchronous dynamics of zooplankton competitors prevail in temperate lake ecosystems. Proceedings of the Royal Society B 281:20140633.
- Walter, J. A., L. W. Sheppard, T. L. Anderson, J. H. Kastens, O. N. Bjørnstad, A. M. Liebhold, and D. C. Reuman. 2017. The geography of spatial synchrony. Ecology Letters 20:801–814.
- Wang, S., and M. Loreau. 2014. Ecosystem stability in space:  $\alpha$ ,  $\beta$  and  $\gamma$  variability. Ecology Letters 17:891–901.
- Wang, S., and M. Loreau. 2016. Biodiversity and ecosystem stability across scales in metacommunities. Ecology Letters 19:510–518.
- Wang, S., T. Lamy, L. M. Hallett, and M. Loreau. 2019. Partitioning ecological stability across hierarchical levels in heterogeneous landscapes: linking theory to data. Ecography. https://doi.org/10.1111/ecog.04290
- Wilcox, K. R. et al. 2017. Asynchrony among local communities stabilises ecosystem function of metacommunities. Ecology Letters 20:1534–1545.

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