Environmental Context Dependency in Species Interactions

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**Journal Guidelines**:

* Maximum 3500 words main text (excluding introductory paragraph/abstract)
* Maximum 6 display items (figures/tables)
* The introductory paragraph is typically 150 words and is unreferenced; it contains a brief account of the background and rationale of the work, followed by a statement of the main conclusions introduced by the phrase “Here we show” or some equivalent.An introduction (without heading) of up to 500 words of referenced text expands on the background of the work (some overlap with the summary is acceptable), and is followed by a concise, focused account of the findings (headed ‘Results’), and one or two short paragraphs of discussion (headed ‘Discussion’).

## Introductory paragraph (abstract)

Ecological interactions are not uniform across time, and instead vary with environmental conditions. Interactions among species are often measured with short-term controlled experiments, but these experiments are subject to the particular environmental conditions under which they are performed. As an alternative, we utilize empirical dynamic modeling applied to a 30-year time series to estimate species interactions across a wide range of environmental conditions. We show that environmental context influences the strength and direction of species interactions. In so doing, we are able to confirm and extend results from previous studies, as well as identify potentially important but understudied dynamics, including the importance of specifically studying variation rather than mean interaction outcomes. The significant context dependency in species interactions found in this study argues for a greater utilization of long-term data and empirical dynamic modeling in studies of ecosystem dynamics.

## Introduction

Interactions between species drive patterns of diversity, stability, resilience, and productivity in nature1–4. In any ecosystem, the collection of species interactions determines community dynamics. Until recently, most studies viewed these dynamics—e.g., the bleaching and recovery of a coral reef, or the assembly and disassembly of terrestrial plant communities—as processes resulting from static, predictable species interactions. However, the observation that species interactions are not spatiotemporally uniform5–8 calls into question assumptions of interaction stability.

Ecologists recognize now that important species interactions may vary over time, but this context dependency remains difficult to measure and describe. Experiments that measure interactions are generally performed over a limited spatiotemporal range, and are therefore subject to a specific environmental context that may not encompass the range of conditions experienced by that ecosystem over longer time scales9. This is worrying, since environmental context can profoundly influence the outcome of species interactions ranging anywhere from keystone predation7 to competition5,10,11, to protective symbioses12–14.

Moreover, the focus of the search for context dependency has been on mean interaction strengths, at the expense of specific examinations of interaction variance8. This focus may be misguided, as it has been shown that interactions that are variable in magnitude and direction—and therefore “weak” when averaged—may actually be some of the most important in driving community dynamics4. If key species interactions are variable in this way across environmental gradients, then many studies may be attributing important ecological phenomena to observational noise.

A solution to these difficulties is to a) utilize ecological observations collected over a long time period, across a large range of environmental contexts, with b) an analytical method to directly estimate context-dependent species interactions from those observations. Such an approach could help to characterize environmental contingencies in species interactions and explicitly examine interaction variability. Here, we use empirical dynamic modelling (EDM15) to estimate a varying species interaction network and establish environmental context dependency in interaction strength and direction. Empirical dynamic modelling uses information from single or multiple time series to empirically model relationships between variables through the reconstruction of dynamic attractors (<https://youtu.be/8DikuwwPWsY>). The general modelling framework for all EDM methods is readily adaptable to many different sorts of time series variables, including environmental variables manifesting at different scales16–18. Because the methods are specifically designed for nonlinear dynamic systems, EDM—in theory—should be able to illuminate context-dependent patterns in species interactions.

Recently-developed EDM methods exist for uncovering dynamic species interactions from time series data15, but these methods have insofar been applied only to simulated and planktonic communities, and their utility to the study of other ecological systems remains untested. We focus here instead on giant kelp forests in southern California, a diverse and temporally dynamic ecosystem in which many important species interactions are well-documented19–21. The study of kelp forests has been foundational to ecological theory, especially regarding the relative influence of top-down and bottom-up structuring forces in ecosystems22–26. Recently, however, findings from long-term kelp forest research programs have begun to challenge many long-held beliefs about the drivers of kelp forest ecosystem dynamics27. In particular, a longer-term perspective has led to a recognition of the critical importance of environmental context—such as level of physical disturbance or the current state of El Niño conditions—for understanding kelp forest processes28–31. In this study we utilize monitoring data from one such effort at San Nicolas Island, a small, remote member of the California Channel Islands in the northeast Pacific32.

To characterize environmental context dependency in kelp forest interactions between species, we take three general steps (see Methods). First, we use empirical dynamic modeling causality tests called convergent cross-mapping33 to construct a kelp forest species interaction network directly from time series data. In so doing, we test for all unidirectional causal signals between five common kelp forest species, as well as between five exogenous environmental variables and those species. Second, for each identified causal link between species, we reconstruct the actual species interactions over time, using another EDM tool called multivariate S-maps (sequential locally weighted global linear maps)15,34. Finally, we show how variability in key species interactions can be related back to the environmental context under which they took place.

## Results

Our analyses focus on the dynamics of five common southern California kelp forest species, whose interactions are thought to be important in structuring kelp forest ecosystems19,21,35. The giant kelp *Macrocystis pyrifera* is the eponymous foundation species36, the primary canopy- and habitat-forming kelp along most of the central and southern coast of California20. The monitoring data include young *Macrocystis* recruits (sporophytes identified as *Macrocystis* but less than 1 meter tall32). We explore *Macrocystis* dynamics and its interactions with two presumptive competitors and two abundant herbivores. The understory kelp species *Laminaria farlowii* and *Pterygophora californica* compete with Macrocystis for space, light, and nutrients37–39. The two herbivores—the purple sea urchin *Strongylocentrotus purpuratus* and the red sea urchin *Mesocentrotus franciscanus*—are thought in many places to control *Macrocystis* density and can sometimes wipe out entire giant kelp forests, leading to the alternative ecosystem state known as an urchin barren40,41.

In southern California, *Macrocystis* population dynamics can be driven by nutrient availability and physical disturbance26,30. The availability of nitrate is inversely related to seawater temperature42 and, over longer time scales, is associated with oscillations in patterns of upwelling and oceanic currents. Accordingly, we include five environmental variables in our analyses to test their relationship to kelp forest species dynamics and interactions: sea surface temperature (SST), physical disturbance (measured by maximum seasonal wave height, SWH), and three indices of low-frequency climate modes: the Multivariate El Niño Index (MEI)43, the Pacific Decadal Oscillation (PDO)44, and the North Pacific Gyre Oscillation (NPGO)45.

Applying convergent cross mapping33 (CCM) to the set of six biological and five physical variables, we find a relatively dense interaciton network (Figure ). Out of 90 possible unidirectional links between species and between species and the environmental variables, 40 are significant. Adult *Macrocystis* density is driven by all five environmental variables, with SWH, SST, and the NPGO showing the strongest causal signals. This finding confirms recent work by others using different methods30 that showed that these same three variables were the primary controls of giant kelp biomass dynamics across the California coast. More generally, although the included physical variables show significant links to many of the biological variables, the NPGO and SWH show the strongest links to almost all of the biological variables. Our analysis suggests that more attention should be focused on the effects of the NPGO.

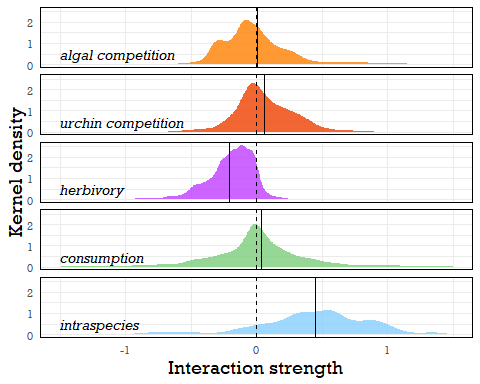
![Reconstructed interaction web using results of convergent cross mapping. Each arrow represents a significant causal signal, and link width and opacity scale with the strength of causal forcing (see full results in Supplementary material). Species abbreviations: M. pyr: ; L.far: ; P.cal: ; M.fra: ; S.pur: . Physical drivers: NPGO: North Pacific Gyre Oscillation; MEI: Multivariate El Nino Index; PDO: Pacific Decadal Oscillation; SST: Sea surface temperature; SWH: Significant wave height.](data:application/pdf;base64,)

Reconstructed interaction web using results of convergent cross mapping. Each arrow represents a significant causal signal, and link width and opacity scale with the strength of causal forcing (see full results in Supplementary material). Species abbreviations: M. pyr: ; L.far: ; P.cal: ; M.fra: ; S.pur: . Physical drivers: NPGO: North Pacific Gyre Oscillation; MEI: Multivariate El Nino Index; PDO: Pacific Decadal Oscillation; SST: Sea surface temperature; SWH: Significant wave height.

Interestingly, in turn, adult *Macrocystis* shows strong causal links to every other biological variable. This is despite the fact that the study site at San Nicolas Island does not have a stable giant kelp forest (see raw time series, Figure ); rather, the site has transitioned from an urchin barren41 to a *Pterygophora* and *Laminaria*-dominated state, to a *Macrocystis* forest at various times throughout the 30-year time series. The implication is that, despite not maintaining dominance in the typical ecological sense of word (large abundance and biomass), *Macrocystis* is “dynamically dominant”, and remains the key foundation species in this ecosystem. Its dynamics are fundamentally important in driving the dynamics of all the other kelp forest species20.

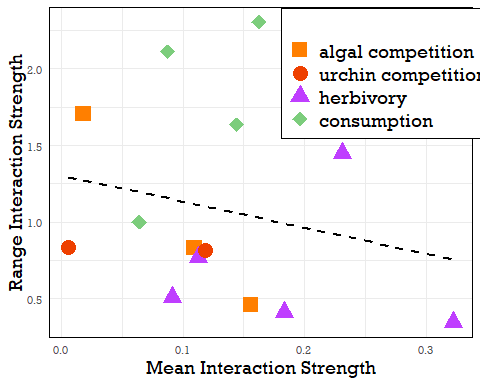
CCM analysis confirms that the system studied represents a complex array of significant interactions between algal species and their herbivores. However, CCM alone does not elucidate the direction and magnitude of species interactions. To obtain estimates of the interactions themselves, we use multivariate S-maps15,34 (see Methods). S-maps reconstructs dynamic “attractors” by casting the abundances of causally-related species into state space. For a set of causally-related species, a point in multivariate space can be plotted using each species’ abundance as an axis. The attractor is then created by tracing this multispecies trajectory forward in time (see example attractor in Figure ). For each point along the attractor, S-maps computes a Jacobian matrix, the elements of which are the estimated partial derivatives between species. These interaction matrix elements are our measure of species interactions. Because Jacobians are computed sequentially for every point along reconstructed attractors, we obtain estimates of interaction strength that vary with ecosystem state.

There are two important aspects of S-maps that deserve mention. First, the S-map estimation procedure, like all EDM methods, is specifically designed for nonlinear systems, and is therefore an appropriate tool for investigating ecosystems exhibiting nonlinear dynamics such as alternative stable states or hysteresis15. Secondly, because S-maps utilizes reconstructed multispecies attractors, each estimated interaction is fundamentally based on observations of similar past ecosystem states—in our case represented as multivariate collections of causally-linked species’ densites—rather than a phenomenological extrapolation of the most recent dynamics. In simple terms, instead of asking, “What is our prediction for the strength of herbivory based on last year’s observed dynamics,” S-maps is concerned with, “What is our best estimate for the strength of herbivory, based on our knowledge of times in the past when the ecosystem was most similar to today?”



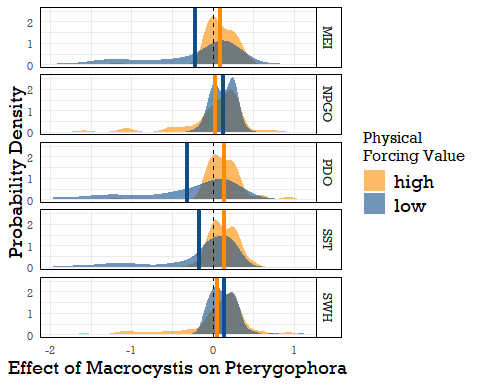
Smoothed kernel density histograms of estimated interactions by type. Solid lines denote means across all estimated interactions of that type.

In the San Nicolas kelp forest, we find a striking prevalence of neutral and positive species interactions (Figure ). After grouping species interactions by type, only herbivory (the effect of urchins on algae species) is predominantly negative. Conversely, the effect of the algae species on the urchins has the flattest distribution, with occasional strong negative and strong positive interactions. Likewise, contrary to our expectations, interactions between the algae species and between the urchin species are not always antagonistic. These results suggest that facilitation—direct or indirect—can arise in kelp forests in multiple contexts46. Since there is evidence here of strong herbivory, for example, then the indirect facilitative effects between algae species through shared herbivory avoidance47 may sometimes outweigh their direct competition. Additionally, *Macrocystis* forests can mediate current strength and as a result, can also help retain reproductive propagules of other species20. These types of indirect facilitation in kelp forests have received relatively little attention48,49 relative to a strong focus on exploitative competition between these species for light and nutrients37,39, but similar effects have been documented in other systems**???**. Our analysis does not contradict the importance of competition in kelp forest ecosystems, but suggests that facilitation, especially indirect facilitation, may be an additional important structuring force.



Mean and standard deviation of each estimated unidirectional species interaction (excluding intraspecies effects)

There is an inverse relationship between mean and range in interaction strengths (Figure ). Importantly, these reported ranges in interaction strength are distinct from estimation or experimental errors. They represent observed ranges across all individually-estimated S-map interactions from each reconstructed attractor. While inverse mean-range relationship was true overall, it varied by interaction type. For the three significant interactions between algae species (excluding interactions with *Macrocytis* recruits), the effects with the smallest mean strength had the largest range across the time series. The effects of algal on urchin species were the most variable in general, and the herbivory effects the least. Additionally, the range was greater than the mean for all of these interactions, further supporting the idea that context dependency may be the rule rather than the exception in this ecosystem. The observed mean-range relationship echoes work done across a range of experimental systems4, and implies that interactions that seem weak on average may simply vary in sign and magnitude across contexts but still be important in each of those contexts nonetheless.



Distributions of effects on , under high (greater than 1) and low (less than -1) values of five normalized environmental indices (abbreviations as in Figure . Solid lines: mean interactions under each regime.

As a case in point, consider the interaction of adult *Macrocystis* and the understory kelp *Pterygophora californica*, the interaction with the “weakest” mean strength of all algal interactions in Figure . *Macrocystis* is often the dominant competitor in kelp forests for nutrients and light37,39, but in this site on average has a neutral to positive effect on *Pterygophora* (Figure ), a result seemingly incongruous with the established competitive hierarchy. However, in southern California, *Macrocystis* is also known to be a better competitor under cold-water, nutrient-rich conditions38. Although negative interactions of *Macrocystis* with *Pterygophora* are rare in our study, they align with those expectations: *Macrocystis* has a greater chance of flipping its interaction from positive to negative—and asserting interspecies dominance—under low values of the MEI and PDO, and high values of the NPGO (Figure ). These are all climate regimes associated with increased availability of nutrients in southern California43–45. Hence, the rare, but strong negative effects of *Macrocystis* on *Pterygophora* conform to expected patterns across decadal-scale climate shifts38,50, despite the two species’ weak mean interaction at this site. In this way, the prevailing environmental context at any point in time is the landscape upon which species interactions occur, potentially tipping the scales in favor of one species over another. Moreover, these rare competitive events may be precisely what precipitates nonlinear ecosystem shifts between alternative states.

## Discussion

Ecosystem dynamics are composed of nonlinear species relationships, played out within shifting environmental contexts. A significant challenge in the study of ecosystem dynamics has been the difficulty in appropriately extrapolating experimental results to real ecosystems, where multiple species-species and species-environment interactions are operating simulateously. We have shown in this study that empirical dynamic modeling can help to tackle this challenge, using time series data to accurately reconstruct nonlinear ecosystem trajectories. Beginning with a published monitoring data set from a kelp forest ecosystem, EDM methods helped to elucidate causation, build interaction networks, and investigate the influence of large-scale environmental drivers on interaction strength. In this particular ecosystem, our analyses confirmed decades of experimental work regarding the foundation species *Macrocystis pyrifera*, but also were able to contextualize those classic interactions as they apply at the study site. A classic algal competitive dominance hierarchy38 is seemingly weak at this site under average conditions, but not absent—under predictable nutrient, temperature, and disturbance regimes, *Macrocystis* can be dominant at this site.

More generally, we report evidence here of an inverse mean-range relationship in interaction strengths and a strong presence of apparent facilitation under multiple environmental contexts, results that agree with previous theoretical and experimental findings across multiple ecosystems4,51–53. An important implication is that if a goal is understanding the dynamics of entire ecosystems, studying the mean outcome of single species interactions may not be adequate. Indirect associations between multiple species and shifting environmental contexts may give rise to rare, critical moments when fleeting strong interactions determine ecosystem shifts. This idea needs further investigation in multiple systems, but if widely applicable, it means that context dependency—and its role in mediating varying species interaction strengths—deserves more attention than the identification of context-averaged mean interactions8. In a growing number of ecosystems, EDM is helping in this endeavour15,54,55.

EDM does not take the place of experimentation, but we argue that it can help to both contextualize and guide it. Our analysis was a proof of concept: we started with simple time series from a monitoring dataset in a well-studied but complex ecosystem, and showed how previous experimental results play out over a longer time period. We hope that this approach can be applied to many other ecosystems, where time series data exist but where important interactions may not be as well-established. Where important interactions are known, EDM can help to explore whether environmental context matters in interaction variance. Where those interactions are not as well known, EDM may be a helpful first step in identification of ecosystem links whose mechanisms can then be further established through other methods.

## Extra notes (scratch space)

The disturbance effect is interesting as well50. Large disturbances can rip out entire forests (*Macrocystis* and *Pterygophora* alike) and can be the catalyst for phase shifts in ecosystem state. That is evident here in the negative tail of the effect of *Macrocystis* on *Pterygophora*. If conditions are beneficial for rapid growth, *Macrocystis* can establish more quickly than *Pterygophora* after disturbance, thereby achieving dominance and having a negative effect on *Pterygoph ora*.

* CCM results and variable interaction network- centrality of Macrocystis
* Mean vs. variance in certain algal interactions?
* Bidirectional mean interactions (across two dimensions, A on B and B on A)?
* Frequency of positive vs. negative interactions? Across environmental gradients?

The realized competitive niche of *Macrocystis*38 may be altered at the study site, which is comprised of a low-rugosity reef highly exposed to wave disturbance, habitat characteristics that can inhibit or even reverse *Macrocystis* dominance23. The simple observation that the San Nicolas Island site has not maintained a stable kelp forest for significant periods of time further supports the lack of consistent *Macrocystis* dominance.

**Work confirmed/supported/debates**:

* Tegner et al 1997, Dayton et al 1999
* Bottom-up vs. top-down forcing? Disturbance or herbivory?
* Competition between urchin species?
* Physical drivers increase predictability of algae models!

**Suggested future research**

* Predominance of mutualism- why the positive interactions of Pterygophora and Macrocystis?
* Urchin grazing pressure as most important??
* Multiple stressors (e.g. herbivory, sst, wave height)

## Methods

![Example reconstructed dynamic attractor](data:application/pdf;base64,)

Example reconstructed dynamic attractor

![Raw data for species and physical drivers, normalized to zero mean and unit variance](data:application/pdf;base64,)

Raw data for species and physical drivers, normalized to zero mean and unit variance

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