

# 1 Environmental Context Dependency in Species 2 Interactions

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6 **Journal Guidelines:**

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

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## 17 **Introductory paragraph (abstract)**

18 Ecological interactions are not uniform across time. They commonly vary with environmental  
19 conditions. Yet, interactions among species are often measured with short-term controlled  
20 experiments whose outcome can depend greatly on the particular environmental conditions  
21 under which they are performed. Running experiments repeatedly to address this context  
22 challenge is an inefficient solution at best. As an alternative, we utilize empirical dynamic  
23 modeling applied to a 30-year time series from coastal kelp forests to estimate species  
24 interactions across a wide range of environmental conditions. We show that environmental  
25 context greatly alters the strength and direction of species interactions. In so doing, we confirm  
26 and extend results from previous studies on the power of empirical dynamic modeling. We  
27 identify potentially important but understudied kelp forest dynamics, including the importance  
28 of specifically studying variation in interaction strength rather than mean interaction outcomes.  
29 The significant context dependency in species interactions found in this study argues for  
30 a greater utilization of long-term data and empirical dynamic modeling in studies of the  
31 dynamics of other ecosystems.

## 32 Introduction

33 Interactions between species drive patterns of diversity, stability, resilience, and productivity  
34 in nature<sup>1–4</sup>. In any ecosystem, the collection of species interactions determines community  
35 dynamics. Until recently, most studies viewed these dynamics—e.g., the bleaching and  
36 recovery of a coral reef, or the assembly and disassembly of terrestrial plant communities—as  
37 processes resulting from static, predictable species interactions. However, the observation  
38 that species interactions are not spatiotemporally uniform<sup>5–8</sup> calls into question assumptions  
39 of interaction stability.

40 Ecologists recognize now that important species interactions may vary over time, but this  
41 context dependency remains difficult to measure and describe. Experiments that measure  
42 interactions are generally performed over a limited spatiotemporal range, and are therefore  
43 subject to a specific environmental context that may not encompass the range of conditions  
44 experienced by that ecosystem over longer time scales<sup>9</sup>. This is worrying, since environmental  
45 context can profoundly influence the outcome of species interactions ranging anywhere from  
46 keystone predation<sup>7</sup> to competition<sup>5,10,11</sup>, to protective symbioses<sup>12–14</sup>.

47 Moreover, the focus of the search for context dependency has been on mean interaction  
48 strengths, at the expense of specific examinations of interaction variance<sup>8</sup>. This focus  
49 may be misguided, as it has been shown that interactions that are variable in magnitude  
50 and direction—and therefore “weak” when averaged—may actually be some of the most  
51 important in driving community dynamics<sup>4</sup>. If key species interactions are variable in this way  
52 across environmental gradients, then many studies may be attributing important ecological  
53 phenomena to observational noise.

54 A solution to these difficulties is to a) utilize ecological observations collected over a long time  
55 period, across a large range of environmental contexts, with b) an analytical method to directly  
56 estimate context-dependent species interactions from those observations. Such an approach  
57 could help to characterize environmental contingencies in species interactions and explicitly  
58 examine interaction variability. Here, we use empirical dynamic modelling (EDM<sup>15</sup>) to  
59 estimate a varying species interaction network and establish environmental context dependency  
60 in interaction strength and direction. Empirical dynamic modelling uses information from  
61 single or multiple time series to empirically model relationships between variables through  
62 the reconstruction of dynamic attractors (<https://youtu.be/8DikuwwPWsY>). The general  
63 modelling framework for all EDM methods is readily adaptable to many different sorts of  
64 time series variables, including environmental variables manifesting at different scales<sup>16–18</sup>.  
65 Because the methods are specifically designed for nonlinear dynamic systems, EDM—in  
66 theory—should be able to illuminate context-dependent patterns in species interactions.

67 Recently-developed EDM methods exist for uncovering dynamic species interactions from  
68 time series data<sup>15</sup>, but these methods have to date been applied only to simulated and  
69 planktonic communities, and their utility to the study of other ecological systems remains  
70 untested. Here we extend the exploration of dynamic species interactions using EDM to  
71 giant kelp forests in southern California, a diverse and temporally dynamic ecosystem in  
72 which many important species interactions are well-documented through experimental and

73 comparative studies<sup>19–21</sup>. The study of kelp forests has been foundational to ecological theory,  
74 especially regarding the relative influence of top-down and bottom-up structuring forces in  
75 ecosystems<sup>22–26</sup>. Recently, however, findings from long-term kelp forest research programs  
76 have begun to challenge many long-held beliefs about the drivers of kelp forest ecosystem  
77 dynamics<sup>27</sup>. In particular, a longer-term perspective has led to a recognition of the critical  
78 importance of environmental context—such as level of physical disturbance or the current  
79 state of El Niño conditions—for understanding kelp forest processes<sup>28–31</sup>. In this study we  
80 utilize monitoring data from one such effort at San Nicolas Island, a small, remote member  
81 of the California Channel Islands in the northeast Pacific<sup>32</sup>.

82 To characterize environmental context dependency in kelp forest interactions between species,  
83 we take three general steps (see Methods). First, we use empirical dynamic modeling causality  
84 tests called convergent cross-mapping<sup>33</sup> to construct a kelp forest species interaction network  
85 directly from time series data. In so doing, we test for all unidirectional causal signals between  
86 five common kelp forest species, as well as between five exogenous environmental variables  
87 and those species. Second, for each identified causal link between species, we reconstruct the  
88 actual species interactions over time, using another EDM tool called multivariate S-maps  
89 (sequential locally weighted global linear maps)<sup>15,34</sup>. Finally, we show how variability in key  
90 species interactions can be related back to the environmental context under which they took  
91 place.

## 92 Results

93 Our analyses focus on the dynamics of five common southern California kelp forest species,  
94 whose interactions are thought to be important in structuring kelp forest ecosystems<sup>19,21,35</sup>.  
95 The giant kelp *Macrocystis pyrifera* is the eponymous foundation species<sup>36</sup>, the primary  
96 canopy- and habitat-forming kelp along most of the central and southern coast of California<sup>20</sup>.  
97 The monitoring data include young *Macrocystis* recruits (sporophytes identified as *Macrocystis*  
98 but less than 1 meter tall<sup>32</sup>). We explore *Macrocystis* dynamics and its interactions with  
99 two presumptive competitors and two abundant herbivores. The understory kelp species  
100 *Laminaria farlowii* and *Pterygophora californica* compete with *Macrocystis* for space, light,  
101 and nutrients<sup>37–39</sup>. The two herbivores—the purple sea urchin *Strongylocentrotus purpuratus*  
102 and the red sea urchin *Mesocentrotus franciscanus*—are thought in many places to control  
103 *Macrocystis* density and can sometimes wipe out entire giant kelp forests, leading to the  
104 alternative ecosystem state known as an urchin barren<sup>40,41</sup>.

105 In southern California, *Macrocystis* population dynamics can be driven by nutrient availability  
106 and physical disturbance<sup>26,30</sup>. The availability of nitrate is inversely related to seawater  
107 temperature<sup>42</sup> and, over longer time scales, is associated with oscillations in patterns of  
108 upwelling and oceanic currents. Accordingly, we include five environmental variables in our  
109 analyses to test their relationship to kelp forest species dynamics and interactions: sea surface  
110 temperature (SST), physical disturbance (measured by maximum seasonal wave height,  
111 SWH), and three indices of low-frequency climate modes: the Multivariate El Niño Index  
112 (MEI)<sup>43</sup>, the Pacific Decadal Oscillation (PDO)<sup>44</sup>, and the North Pacific Gyre Oscillation  
113 (NPGO)<sup>45</sup>.

114 Applying convergent cross mapping<sup>33</sup> (CCM) to the set of six biological and five physical  
115 variables, we find a relatively dense interaciton network (Figure 1). Out of 90 possible  
116 unidirectional links between species and between species and the environmental variables,  
117 40 are significant. Adult *Macrocystis* density is driven by all five environmental variables,  
118 with SWH, SST, and the NPGO showing the strongest causal signals. This finding aligns  
119 with recent work by others using different methods<sup>30</sup> that showed that these same three  
120 variables were the primary controls of giant kelp biomass dynamics across the California  
121 coast. More generally, although the included physical variables show significant links to many  
122 of the biological variables, the NPGO and SWH show the strongest links to almost all of  
123 the biological variables. Our analysis suggests that more attention should be focused on the  
124 effects of the NPGO.

125 Interestingly, in turn, adult *Macrocystis* shows strong causal links to every other biological  
126 variable. This is despite the fact that the study site at San Nicolas Island does not have a  
127 stable giant kelp forest (see raw time series, Figure 6); rather, the site has transitioned from  
128 an urchin barren<sup>41</sup> to a *Pterygophora* and *Laminaria*-dominated state, to a *Macrocystis* forest  
129 at various times throughout the 30-year time series. The implication is that, despite not  
130 maintaining dominance in the typical ecological sense of word (large abundance and biomass),  
131 *Macrocystis* remains a key foundation species in this ecosystem, because its dynamics are  
132 fundamentally important in driving the dynamics of all the other kelp forest species<sup>20</sup>.

133 CCM analysis confirms that the system studied represents a complex array of significant  
134 interactions between algal species and their herbivores. However, CCM alone does not  
135 elucidate the direction and magnitude of species interactions. To obtain estimates of the  
136 interactions themselves, we use multivariate S-maps<sup>15,34</sup> (see Methods). S-maps reconstruct  
137 dynamic “attractors” by casting the abundances of causally-related species into state space.  
138 For a set of causally-related species, a point in multivariate space can be plotted using each  
139 species’ abundance as an axis. The attractor is then created by tracing this multispecies  
140 trajectory forward in time (see example attractor in Figure 5). For each point along the  
141 attractor, S-maps computes a Jacobian matrix, the elements of which are the estimated  
142 partial derivatives between species. These interaction matrix elements are our measure of  
143 species interactions. Because Jacobians are computed sequentially for every point along  
144 reconstructed attractors, we obtain estimates of interaction strength that vary with ecosystem  
145 state.

146 Dynamic ecosystems are analogous to a landscape of variable topography, where our position  
147 on the landscape represents the current ecosystem state. In this analogy, each cardinal  
148 direction represents the density of a different species (i.e., axis in state-space), and our  
149 movement across the landscape through time represents movement along the multivariate  
150 attractor as species densities change. S-maps are simply our reconstructed topographic maps  
151 of these ecosystem landscapes. At a given point in time as we move across the landscape,  
152 we may be on top of a steep pinnacle, on a flat plain, or in a shallow valley. Regardless,  
153 it is the slope of the landscape in each direction (the partial derivative) that defines the  
154 local interaction strength between species: a steep upward slope represents a strong positive  
155 interaction between species, while a flat surface is a neutral interaction and a slight downward  
156 slope is a weak negative interaction.

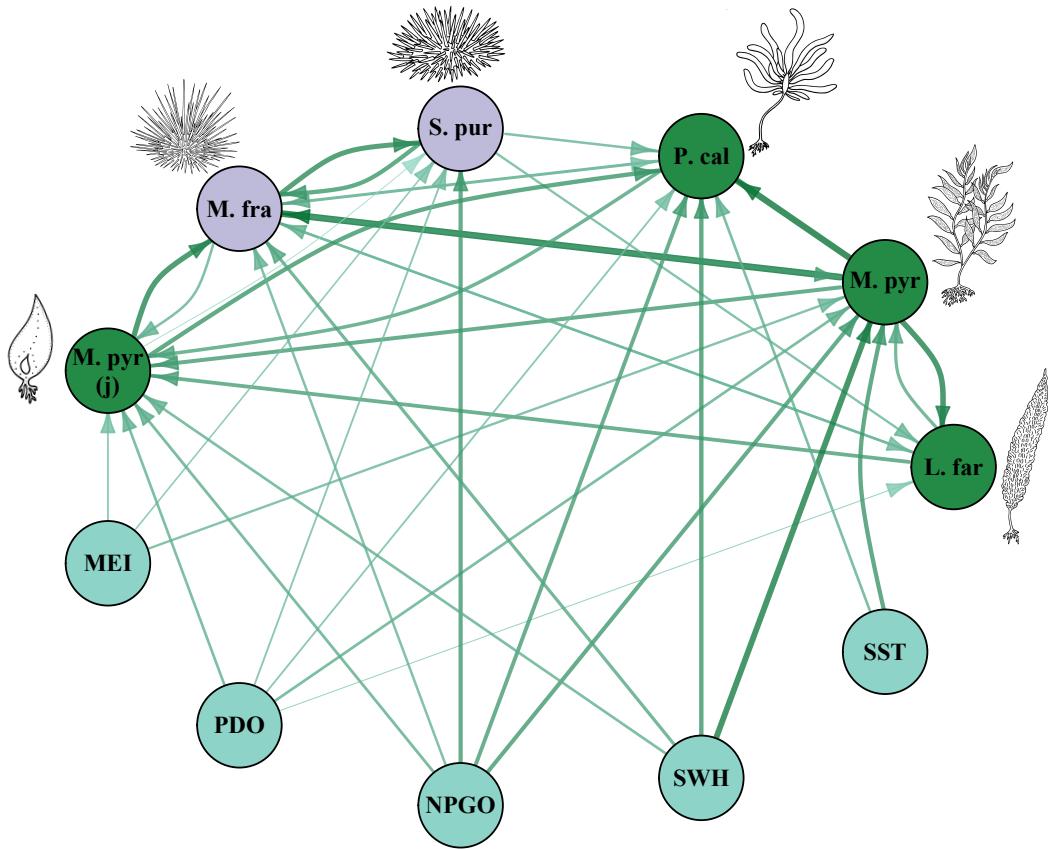


Figure 1: Reconstructed interaction web using results of convergent cross mapping. Each arrow represents a significant causal signal, and link width and opacity scale with the strength of causal forcing (see full results in Supplementary material). Species abbreviations: M. pyr: *Macrocystis pyrifera*; L.far: *Laminaria farlowii*; P.cal: *Pterygophora californica*; M.fra: *Mesocentrotus franciscanus*; S.pur: *Strongylocentrotus purpuratus*. Physical drivers: NPGO: North Pacific Gyre Oscillation; MEI: Multivariate El Nino Index; PDO: Pacific Decadal Oscillation; SST: Sea surface temperature; SWH: Significant wave height.

157 There are two important characteristics of S-maps that deserve mention. First, the S-  
158 map estimation procedure, like all EDM methods, is specifically designed for nonlinear  
159 systems, and is therefore an appropriate tool for investigating ecosystems exhibiting nonlinear  
160 dynamics such as alternative stable states or hysteresis<sup>15</sup>. Secondly, because S-maps utilizes  
161 reconstructed multispecies attractors, each estimated interaction is fundamentally based on  
162 observations of similar past ecosystem states—where each state is represented as a multivariate  
163 vector of causally-linked species' densities—rather than a phenomenological extrapolation of  
164 the most recent dynamics. For example, instead of asking, “What is our prediction for the  
165 strength of herbivory based on last year's observed dynamics,” S-maps is concerned with,  
166 “What is our best estimate for the strength of herbivory, based on our knowledge of times in  
167 the past when the ecosystem was most similar to today?”

168 In the San Nicolas kelp forest, we find a striking prevalence of neutral and positive species  
169 interactions (Figure 2). After grouping species interactions by type, only herbivory (the effect  
170 of urchins on algal species) is predominantly negative. Conversely, the effect of the algal  
171 species on the urchins has the flattest distribution, with occasional strong negative and strong  
172 positive interactions. Likewise, contrary to our expectations, interactions between the algal  
173 species and between the urchin species are not always antagonistic. These results suggest that  
174 facilitation—direct or indirect—can arise in kelp forests in multiple contexts<sup>46</sup>. For example,  
175 since there is evidence here of strong herbivory, then there may be indirect facilitation  
176 between algal species because of a shared herbivore<sup>47</sup>: a greater algal density in general  
177 could ameliorate the negative effect of herbivory on any one species. This sort of indirect,  
178 associative facilitation may sometimes outweigh the strength of direct algal competition.  
179 Additionally, *Macrocystis* forests can mediate current strength and as a result, can also  
180 help retain reproductive propagules of other species<sup>20</sup>. These types of indirect facilitation  
181 in kelp forests have received comparatively little attention<sup>48,49</sup> relative to the strong focus  
182 on exploitative competition between these species for light and nutrients<sup>37,39</sup>, but similar  
183 effects have been documented in other ecosystems<sup>50</sup>. Our analysis does not contradict the  
184 importance of competition in kelp forest ecosystems, but suggests that facilitation, especially  
185 indirect facilitation, may be an additional important structuring force.

186 There is an inverse relationship between mean and range in interaction strengths (Figure  
187 3). Importantly, these reported ranges in interaction strength are distinct from estimation  
188 or experimental errors. They represent observed ranges across all individually-estimated  
189 S-map interactions from each reconstructed attractor. While inverse mean-range relationship  
190 was true overall, it varied by interaction type. For the three significant interactions between  
191 algal species (excluding interactions with *Macrocystis* recruits), the effects with the smallest  
192 mean strength had the largest range across the time series. The effects of algal on urchin  
193 species were the most variable in general, and the herbivory effects the least. Additionally,  
194 the range was greater than the mean for all of these interactions, further supporting the  
195 idea that context dependency may be the rule rather than the exception in this ecosystem.  
196 The observed mean-range relationship echoes work done across a range of experimental  
197 systems<sup>4</sup>, and implies that interactions that seem weak on average may simply vary in sign  
198 and magnitude across contexts but still be important in each of those contexts nonetheless.

199 As a case in point, consider the interaction of adult *Macrocystis* and the understory kelp

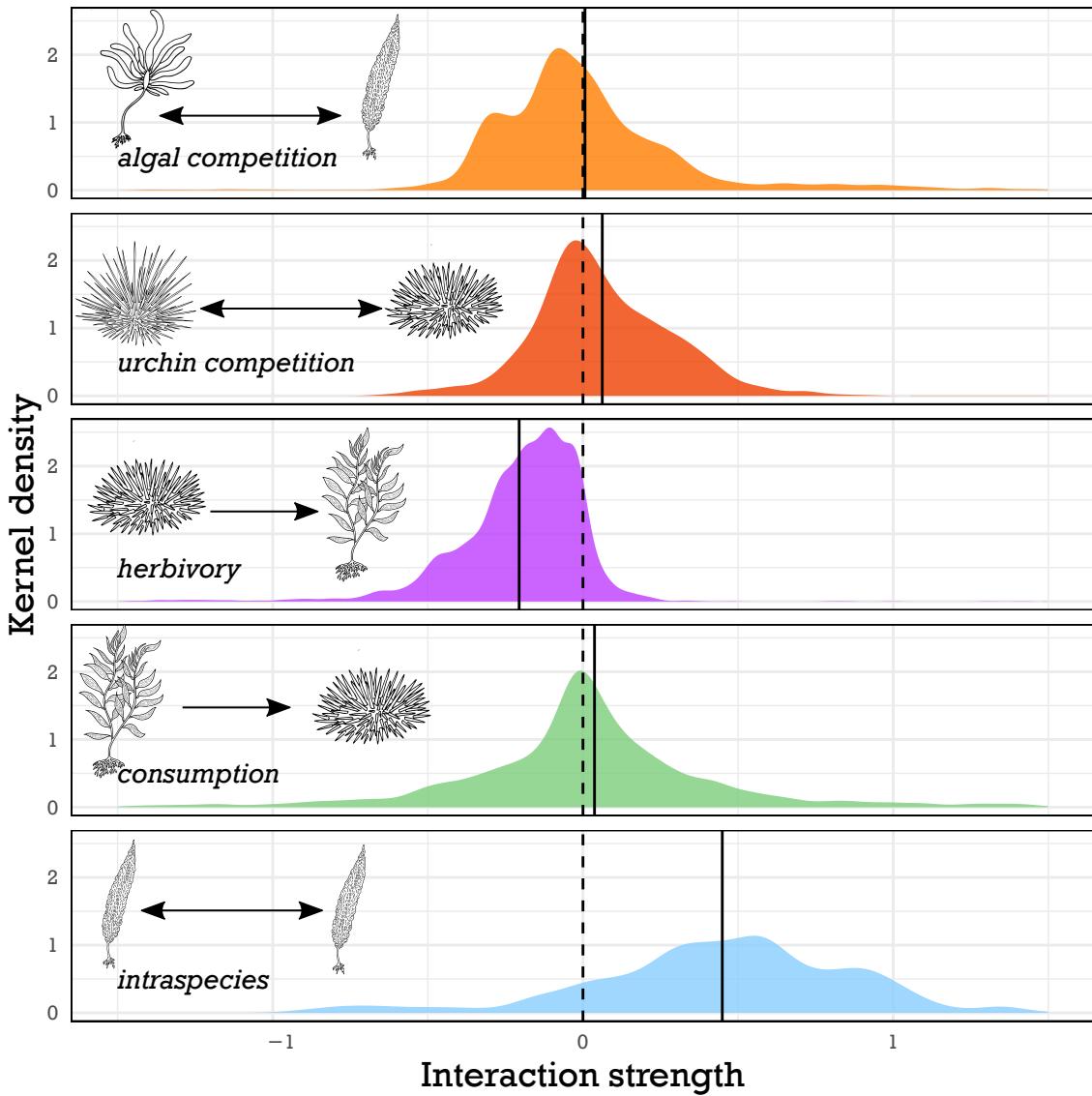


Figure 2: Smoothed kernel density histograms of estimated interactions by type. Solid lines denote means across all estimated interactions of that type.

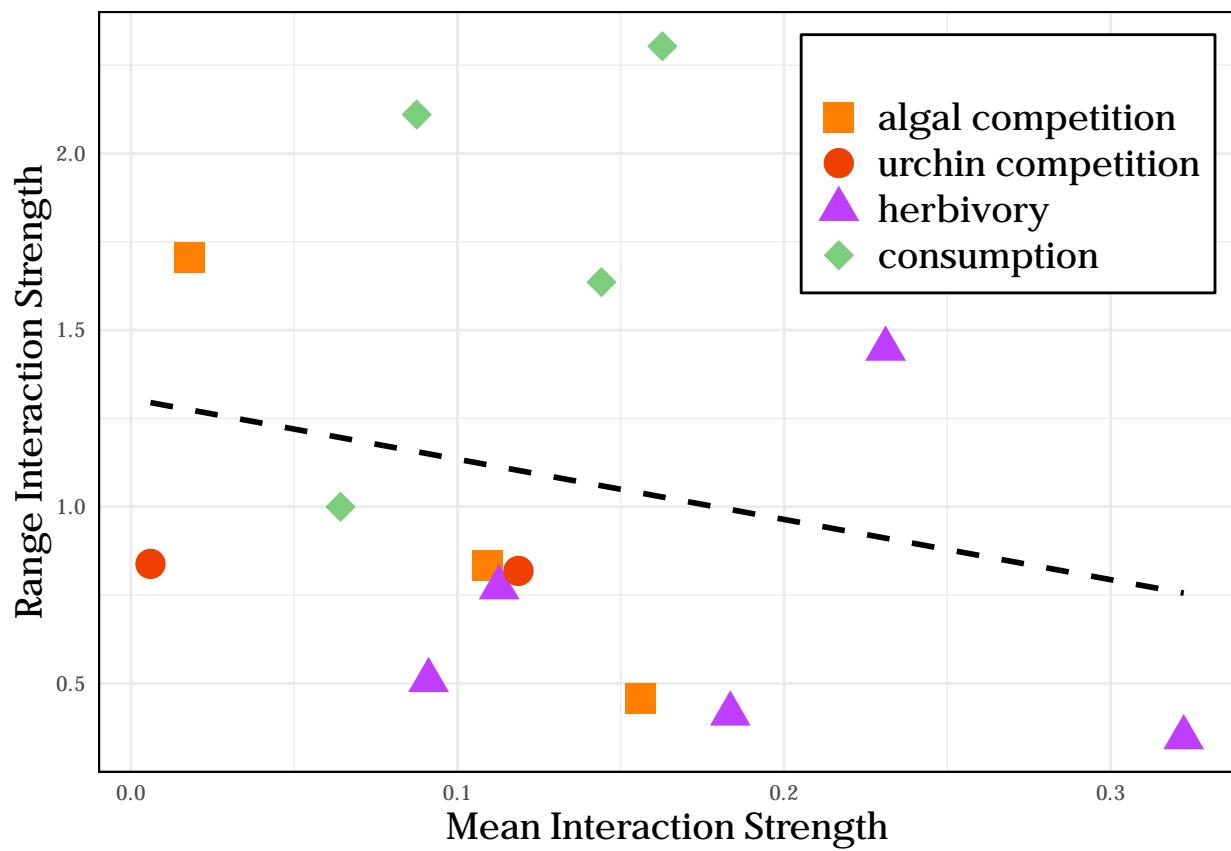


Figure 3: Mean absolute interaction strength and standard deviation for each estimated unidirectional species interaction, excluding intraspecies effects

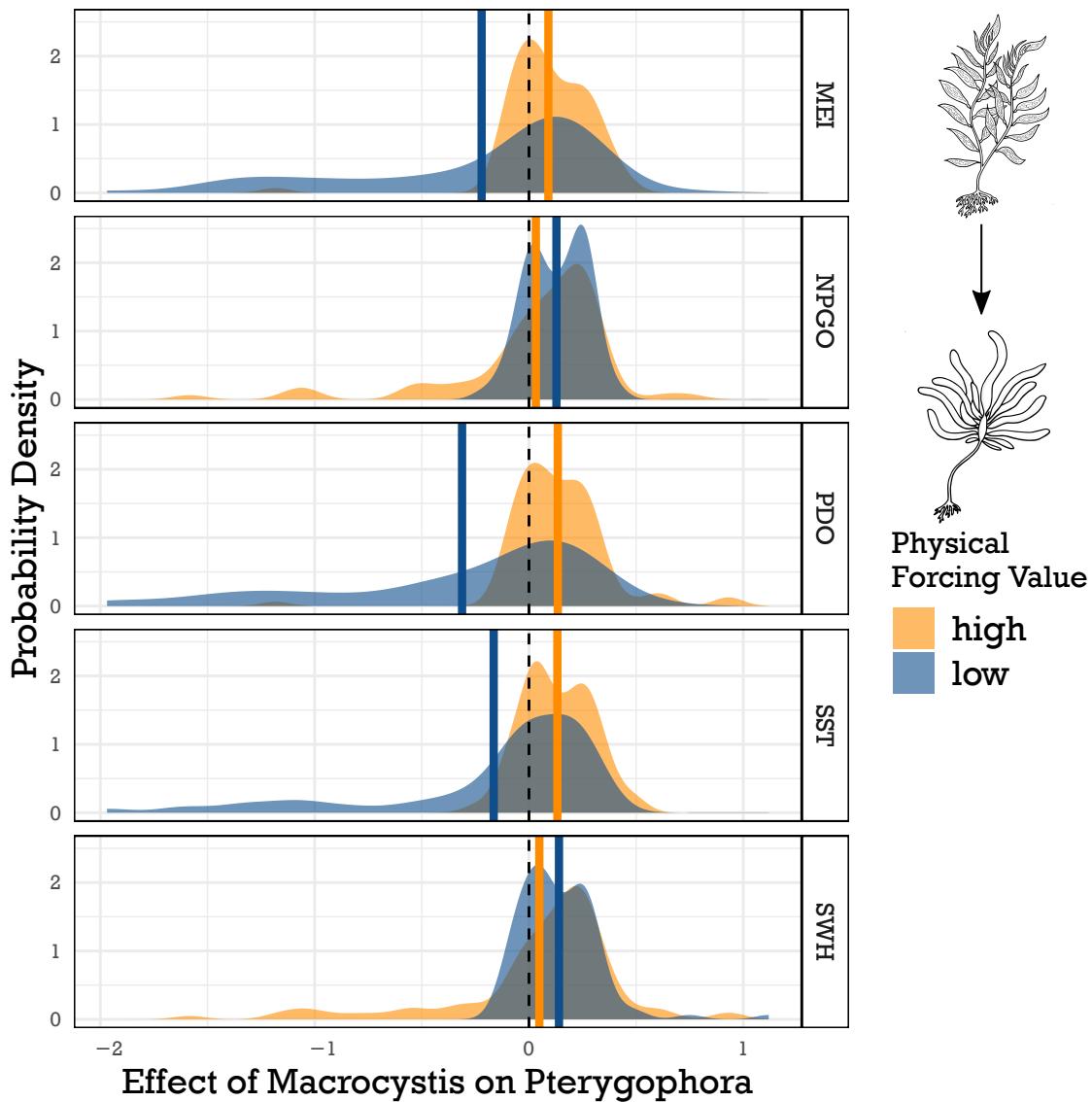


Figure 4: Distributions of *Macrocystis* effects on *Pterygophora*, under high (greater than 1) and low (less than -1) values of five normalized environmental indices (abbreviations as in Figure 1. Solid lines: mean interactions under each regime.

200 *Pterygophora californica*, the interaction with the “weakest” mean strength of all algal  
201 interactions in Figure 3. *Macrocystis* is often the dominant competitor in kelp forests  
202 for nutrients and light<sup>37,39</sup>, but in this site on average has a neutral to positive effect on  
203 *Pterygophora* (Figure 4), a result seemingly incongruous with the established competitive  
204 hierarchy. However, in southern California, *Macrocystis* is also known to be a better competitor  
205 under cold-water, nutrient-rich conditions<sup>38</sup>. Although negative interactions of *Macrocystis*  
206 with *Pterygophora* are rare in our study, they align with those expectations: *Macrocystis* has a  
207 greater chance of flipping its interaction from positive to negative—and asserting interspecies  
208 dominance—under low values of the MEI and PDO, and high values of the NPGO (Figure 4).  
209 These are all climate regimes associated with increased availability of nutrients in southern  
210 California<sup>43–45</sup>. Hence, the rare, but strong negative effects of *Macrocystis* on *Pterygophora*  
211 conform to expected patterns across decadal-scale climate shifts<sup>38,51</sup>, despite the two species’  
212 weak mean interaction at this site. In this way, the prevailing environmental context at any  
213 point in time is the landscape upon which species interactions occur, potentially tipping the  
214 scales in favor of one species over another. Moreover, these rare competitive events may be  
215 precisely what precipitates nonlinear ecosystem shifts between alternative states.

## 216 Discussion

217 Ecosystem dynamics are composed of nonlinear species relationships, played out within shifting  
218 environmental contexts. A significant challenge in the study of ecosystem dynamics has been  
219 the difficulty in appropriately extrapolating experimental results to real ecosystems, where  
220 multiple species-species and species-environment interactions are operating simultaneously. We  
221 have shown in this study that empirical dynamic modeling can help to tackle this challenge,  
222 using time series data to accurately reconstruct nonlinear ecosystem trajectories. Beginning  
223 with a published monitoring data set from a kelp forest ecosystem, EDM methods helped to  
224 elucidate causation, build interaction networks, and investigate the influence of large-scale  
225 environmental drivers on interaction strength. In this particular ecosystem, our analyses  
226 confirmed decades of experimental work regarding the foundation species *Macrocystis pyrifera*,  
227 but also were able to contextualize those classic interactions as they apply at the study  
228 site. A classic algal competitive dominance hierarchy<sup>38</sup> is seemingly weak at this site under  
229 average conditions, but not absent—under predictable nutrient, temperature, and disturbance  
230 regimes, *Macrocystis* can be dominant at this site.

231 More generally, we report evidence here of an inverse mean-range relationship in interaction  
232 strengths and a strong presence of apparent facilitation under multiple environmental con-  
233 texts, results that agree with previous theoretical and experimental findings across multiple  
234 ecosystems<sup>4,52–54</sup>. An important implication is that if a goal is understanding the dynamics  
235 of entire ecosystems, studying the mean outcome of single species interactions may not  
236 be adequate. Indirect associations between multiple species and shifting environmental  
237 contexts may give rise to rare, critical moments when fleeting strong interactions determine  
238 ecosystem shifts. This idea needs further investigation in multiple systems, but if widely  
239 applicable, it means that context dependency—and its role in mediating varying species inter-  
240 action strengths—deserves more attention than the identification of context-averaged mean

241 interactions<sup>8</sup>. In a growing number of ecosystems, EDM is helping in this endeavour<sup>15,55,56</sup>.

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

## 251 Extra notes (scratch space)

252 The disturbance effect is interesting as well<sup>51</sup>. Large disturbances can rip out entire forests  
253 (*Macrocystis* and *Pterygophora* alike) and can be the catalyst for phase shifts in ecosystem  
254 state. That is evident here in the negative tail of the effect of *Macrocystis* on *Pterygophora*.  
255 If conditions are beneficial for rapid growth, *Macrocystis* can establish more quickly than  
256 *Pterygophora* after disturbance, thereby achieving dominance and having a negative effect on  
257 *Pterygophora*.

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

262 The realized competitive niche of *Macrocystis*<sup>38</sup> may be altered at the study site, which is  
263 comprised of a low-rugosity reef highly exposed to wave disturbance, habitat characteristics  
264 that can inhibit or even reverse *Macrocystis* dominance<sup>23</sup>. The simple observation that the  
265 San Nicolas Island site has not maintained a stable kelp forest for significant periods of time  
266 further supports the lack of consistent *Macrocystis* dominance.

## 267 Work confirmed/supported/debates:

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

## 272 Suggested future research

- 273 • Predominance of mutualism- why the positive interactions of *Pterygophora* and *Macro-*  
274 *cystis*?
- 275 • Urchin grazing pressure as most important??
- 276 • Multiple stressors (e.g. herbivory, sst, wave height)

## 277 Methods

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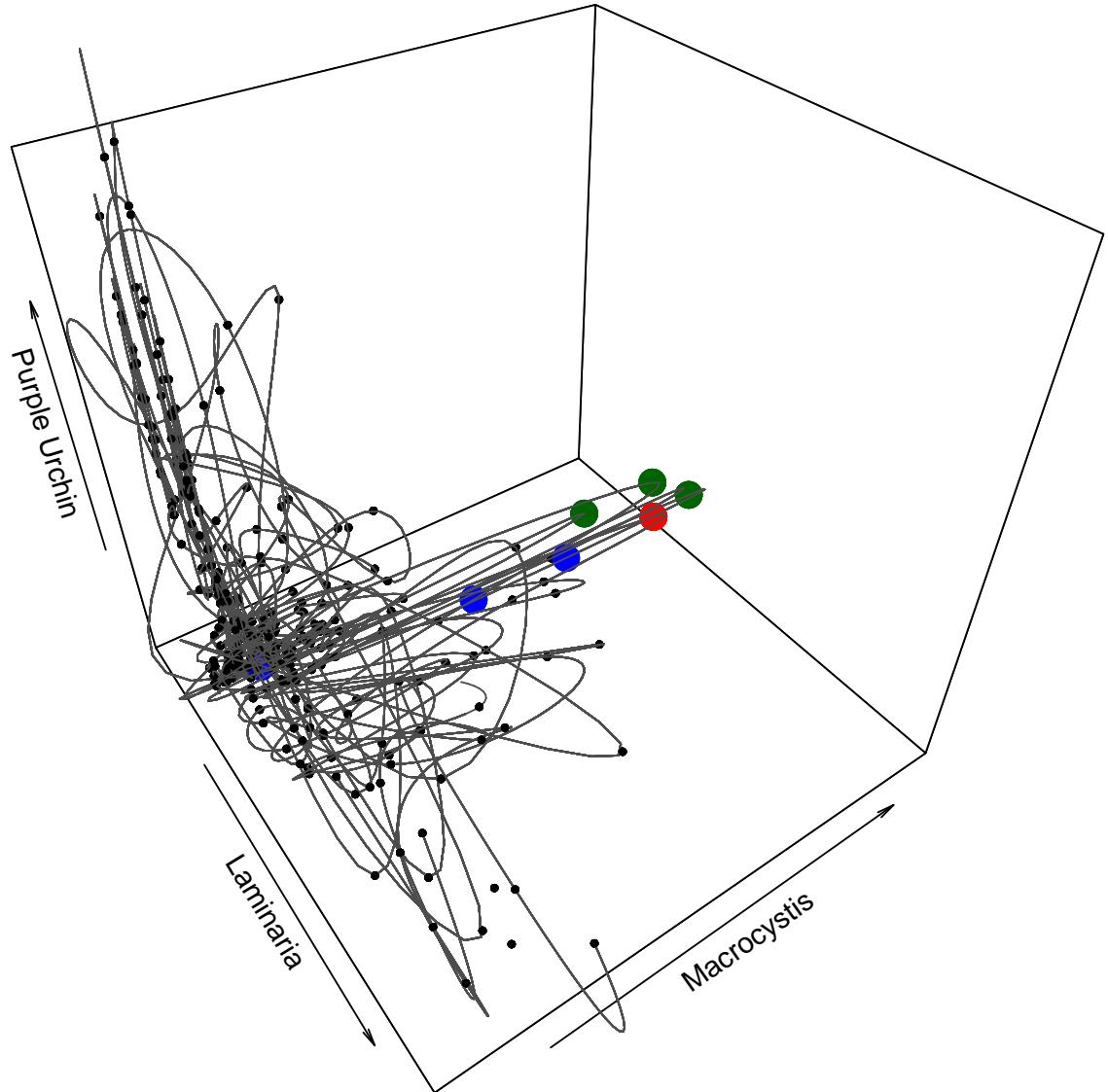


Figure 5: Example reconstructed dynamic attractor

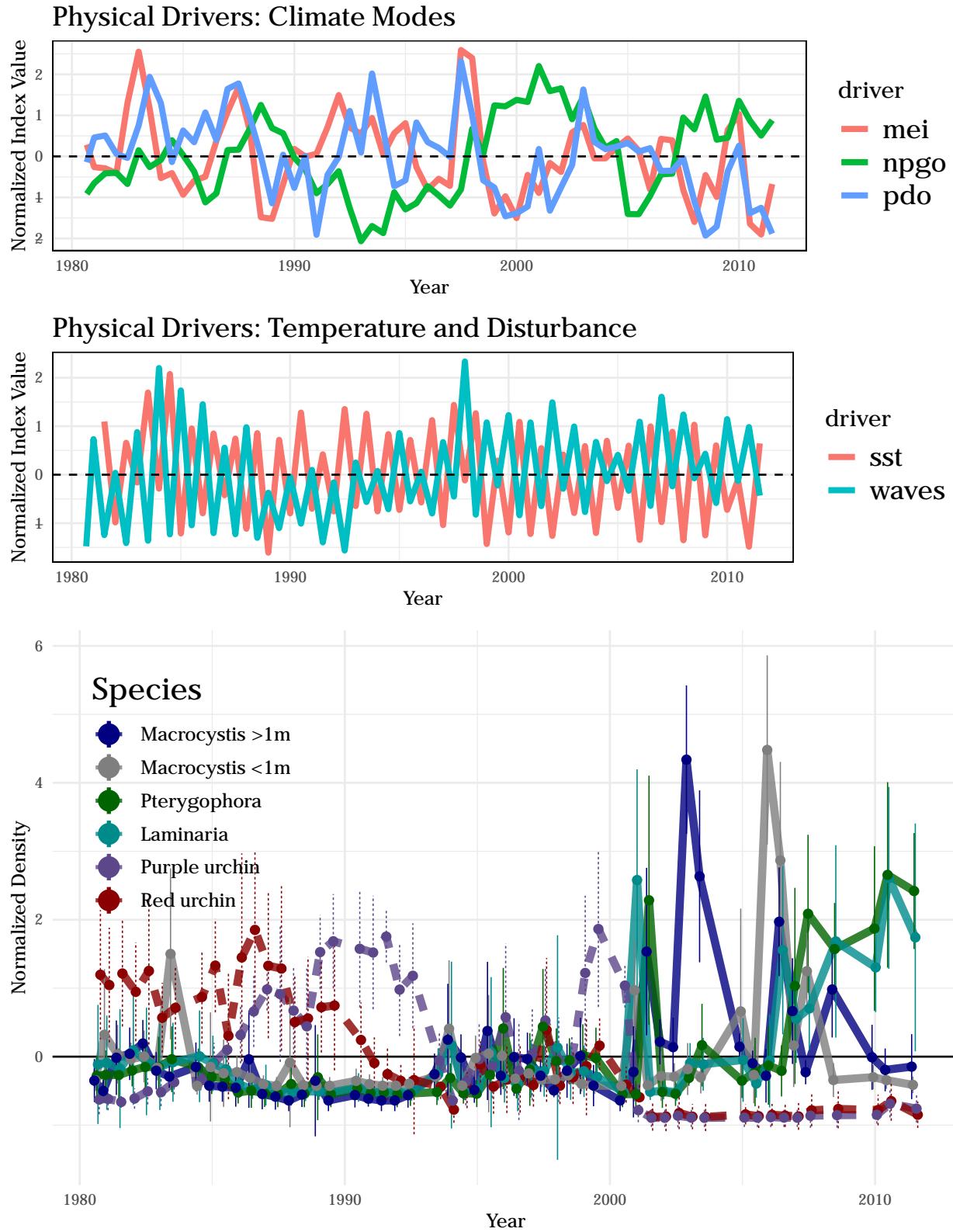


Figure 6: Raw data for species and physical drivers, normalized to zero mean and unit variance

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