Environmental Context Dependency in Species Interactions

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22 July, 2018

Primary target journal: Nature Ecology and Evolution

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 nature[1–4]. In any ecosystem, the collection of species interactions determines community

33 dynamics. Until recently, most studies viewed these dynamics—e.g., the bleaching and
34 recovery of a coral reef, or the assembly and disassembly of terrestrial plant communities—as
35 processes resulting from static, predictable species interactions. However, the observation
36 that species interactions are not spatiotemporally uniform[5–8] calls into question assumptions
37 of interaction stability.

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

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

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

65 Recently-developed EDM methods exist for uncovering dynamic species interactions from time
66 series data[15], but these methods have insofar been applied only to simulated and planktonic
67 communities, and their utility to the study of other ecological systems remains untested.
68 We focus here instead on giant kelp forests in southern California, a diverse and temporally
69 dynamic ecosystem in which many important species interactions are well-documented[19–21].
70 The study of kelp forests has been foundational to ecological theory, especially regarding the
71 relative influence of top-down and bottom-up structuring forces in ecosystems[22–26]. Recently,
72 however, findings from long-term kelp forest research programs have begun to challenge many
73 long-held beliefs about the drivers of kelp forest ecosystem dynamics[27]. In particular, a
74 longer-term perspective has led to a recognition of the critical importance of environmental
75 context—such as level of physical disturbance or the current state of El Niño conditions—for

76 understanding kelp forest processes[28–31]. In this study we utilize monitoring data from one
77 such effort at San Nicolas Island, a small, remote member of the California Channel Islands
78 in the northeast Pacific[32].

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

89 Results

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

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

111 Applying convergent cross mapping[33] (CCM) to the set of six biological and five physical
112 variables, we find a relatively dense interaciton network (Figure 1). Out of 90 possible
113 unidirectional links between species and between species and the environmental variables,
114 40 are significant. Adult *Macrocystis* density is driven by all five environmental variables,
115 with SWH, SST, and the NPGO showing the strongest causal signals. This finding confirms

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116 recent work by others using different methods[30] that showed that these same three variables
117 were the primary controls of giant kelp biomass dynamics across the California coast. More
118 generally, although the included physical variables show significant links to many of the
119 biological variables, the NPGO and SWH show the strongest links to almost all of the
120 biological variables. Our analysis suggests that more attention should be focused on the
121 effects of the NPGO.

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

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

144 There are two important aspects of S-maps that deserve mention. First, the S-map estimation
145 procedure, like all EDM methods, is specifically designed for nonlinear systems, and is
146 therefore an appropriate tool for investigating ecosystems exhibiting nonlinear dynamics such
147 as alternative stable states or hysteresis[15]. Secondly, because S-maps utilizes reconstructed
148 multispecies attractors, each estimated interaction is fundamentally based on observations of
149 similar past ecosystem states—in our case represented as multivariate collections of causally-
150 linked species' densites—rather than a phenomenological extrapolation of the most recent
151 dynamics. In simple terms, instead of asking, "What is our prediction for the strength of
152 herbivory based on last year's observed dynamics," S-maps is concerned with, "What is our
153 best estimate for the strength of herbivory, based on our knowledge of times in the past when
154 the ecosystem was most similar to today?"

155 In the San Nicolas kelp forest, we find a striking prevalence of neutral and positive species
156 interactions (Figure 2). After grouping species interactions by type, only herbivory (the effect
157 of urchins on algae species) is predominantly negative. Conversely, the effect of the algae
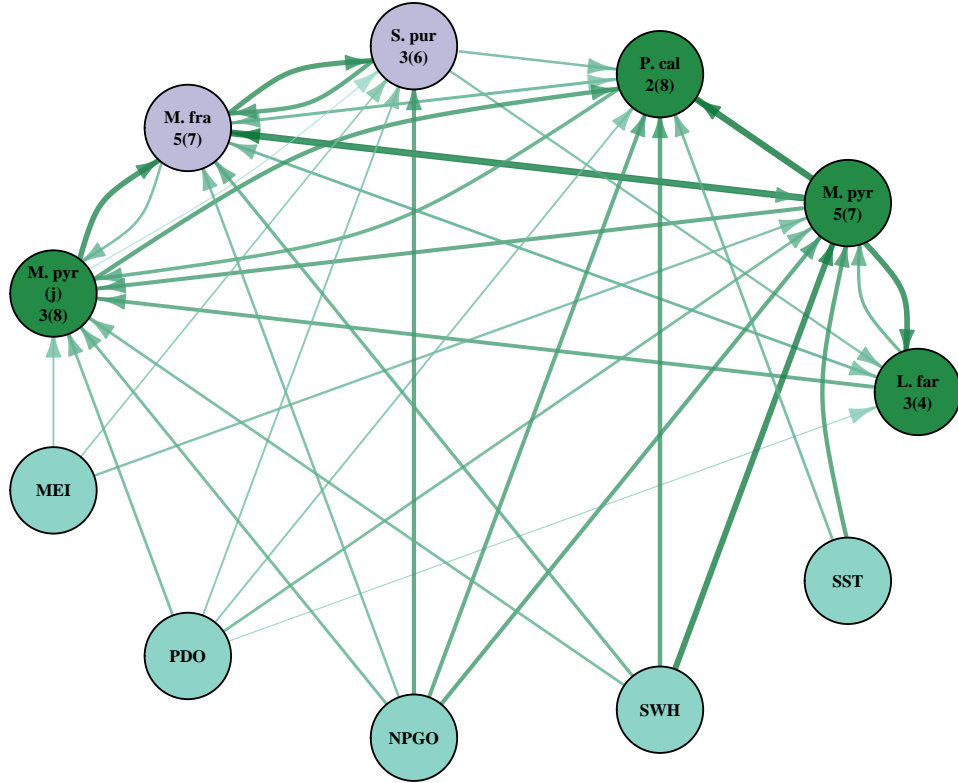158 species on the urchins has the flattest distribution, with occasional strong negative and strong

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.
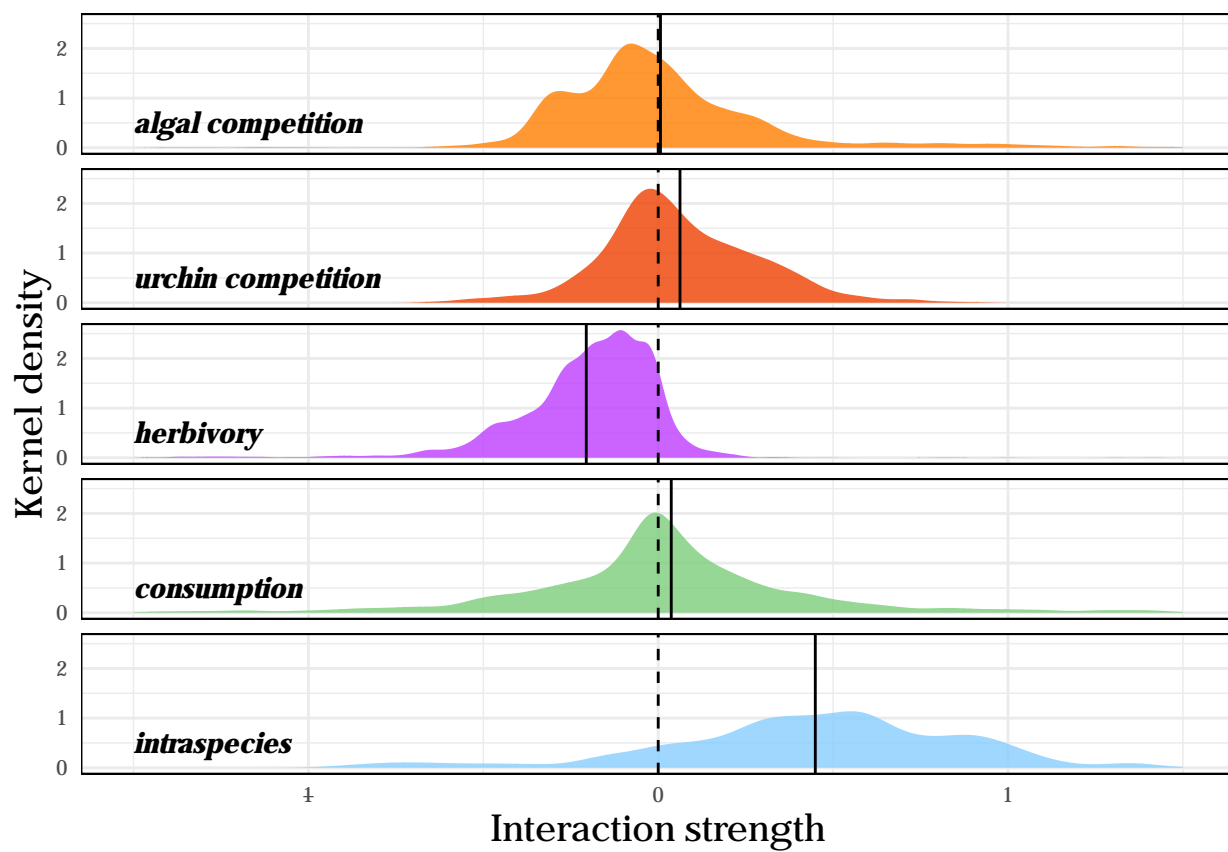
Figure 2: Smoothed kernel density histograms of estimated interactions by type. Solid lines denote means across all estimated interactions of that type.
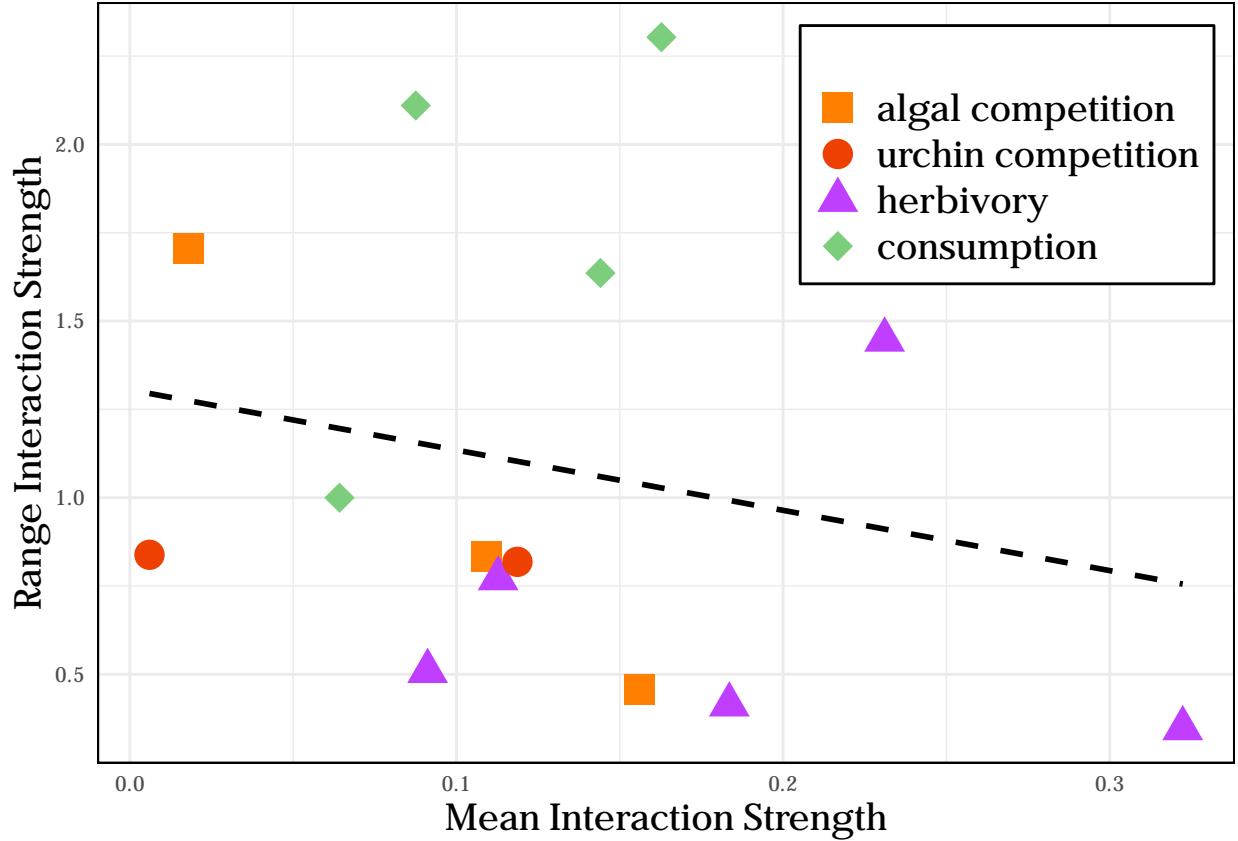
Figure 3: Mean and standard deviation of each estimated unidirectional species interaction (excluding intraspecies effects)

159 positive interactions. Likewise, contrary to our expectations, interactions between the algae
160 species and between the urchin species are not always antagonistic. These results suggest
161 that facilitation—direct or indirect—can arise in kelp forests in multiple contexts[46]. Since
162 there is evidence here of strong herbivory, for example, then the indirect facilitative effects
163 between algae species through shared herbivory avoidance[47] may sometimes outweigh their
164 direct competition. Additionally, *Macrocystis* forests can mediate current strength and as a
165 result, can also help retain reproductive propagules of other species[20]. These types of indirect
166 facilitation in kelp forests have received relatively little attention[48,49] relative to a strong focus
167 on exploitative competition between these species for light and nutrients[37,39], but similar
168 effects have been documented in other systems[???]. Our analysis does not contradict the
169 importance of competition in kelp forest ecosystems, but suggests that facilitation, especially
170 indirect facilitation, may be an additional important structuring force.

171 There is an inverse relationship between mean and range in interaction strengths (Figure
172 3). Importantly, these reported ranges in interaction strength are distinct from estimation
173 or experimental errors. They represent observed ranges across all individually-estimated
174 S-map interactions from each reconstructed attractor. While inverse mean-range relationship
175 was true overall, it varied by interaction type. For the three significant interactions between
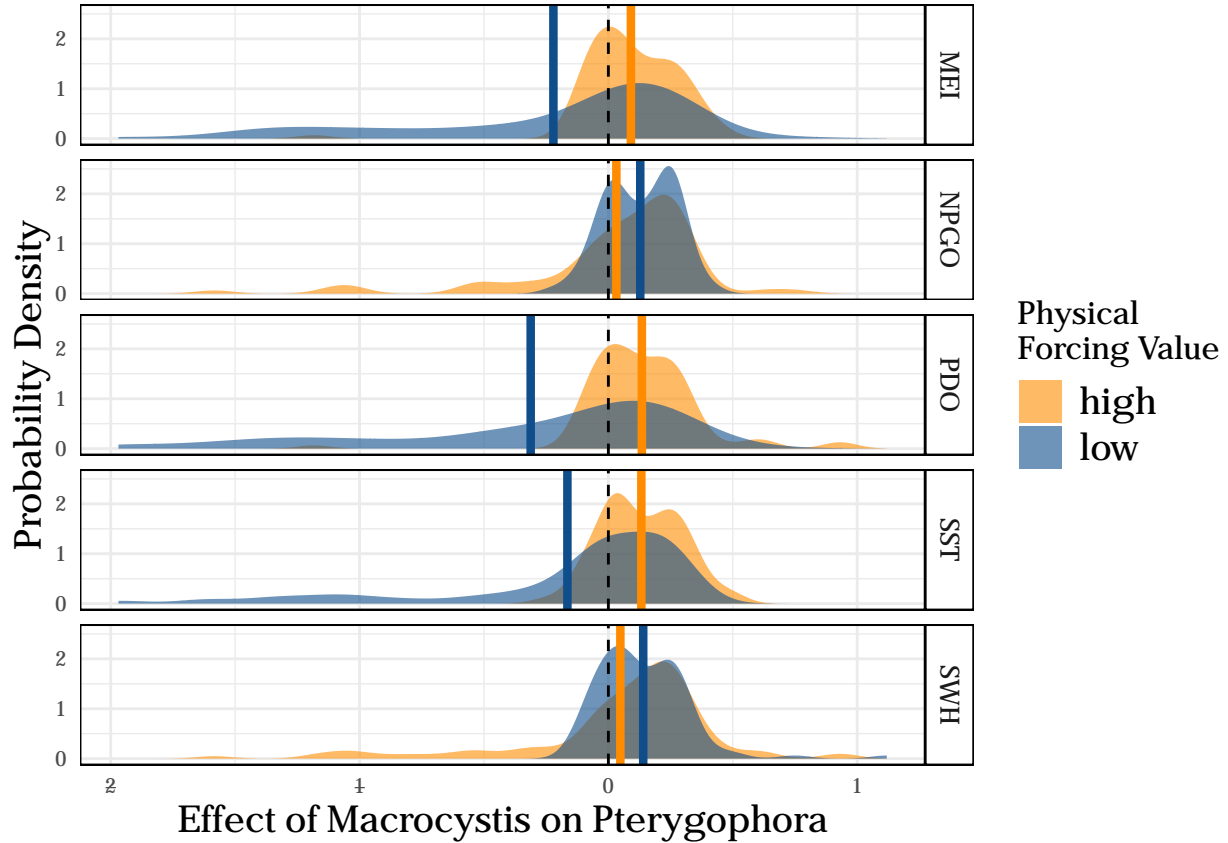
Figure 4: Distributions of *Macrocystis* effects on *Pterygophora*, under high (greater than 1) and low (less than -1) values of five normalized environmental indices (abbreviations as in Figure 1. Solid lines: mean interactions under each regime.

176 algae species (excluding interactions with *Macrocytis* recruits), the effects with the smallest
177 mean strength had the largest range across the time series. The effects of algal on urchin
178 species were the most variable in general, and the herbivory effects the least. Additionally,
179 the range was greater than the mean for all of these interactions, further supporting the
180 idea that context dependency may be the rule rather than the exception in this ecosystem.
181 The observed mean-range relationship echoes work done across a range of experimental
182 systems[4], and implies that interactions that seem weak on average may simply vary in sign
183 and magnitude across contexts but still be important in each of those contexts nonetheless.

184 As a case in point, consider the interaction of adult *Macrocystis* and the understory kelp
185 *Pterygophora californica*, the interaction with the "weakest" mean strength of all algal
186 interactions in Figure 3. *Macrocystis* is often the dominant competitor in kelp forests
187 for nutrients and light[37,39], but in this site on average has a neutral to positive effect on
188 *Pterygophora* (Figure 4), a result seemingly incongruous with the established competitive
189 hierarchy. However, in southern California, *Macrocystis* is also known to be a better competitor
190 under cold-water, nutrient-rich conditions[38]. Although negative interactions of *Macrocystis*
191 with *Pterygophora* are rare in our study, they align with those expectations: *Macrocystis* has a

192 greater chance of flipping its interaction from positive to negative—and asserting interspecies
193 dominance—under low values of the MEI and PDO, and high values of the NPGO (Figure 4).
194 These are all climate regimes associated with increased availability of nutrients in southern
195 California[43–45]. Hence, the rare, but strong negative effects of *Macrocystis* on *Pterygophora*
196 conform to expected patterns across decadal-scale climate shifts[38,50], despite the two species'
197 weak mean interaction at this site. In this way, the prevailing environmental context at any
198 point in time is the landscape upon which species interactions occur, potentially tipping the
199 scales in favor of one species over another. Moreover, these rare competitive events may be
200 precisely what precipitates nonlinear ecosystem shifts between alternative states.

Discussion

202 Ecosystem dynamics are composed of nonlinear species relationships, played out within shifting
203 environmental contexts. A significant challenge in the study of ecosystem dynamics has been
204 the difficulty in appropriately extrapolating experimental results to real ecosystems, where
205 multiple species-species and species-environment interactions are operating simulateously. We
206 have shown in this study that empirical dynamic modeling can help to tackle this challenge,
207 using time series data to accurately reconstruct nonlinear ecosystem trajectories. Beginning
208 with a published monitoring data set from a kelp forest ecosystem, EDM methods helped to
209 elucidate causation, build interaction networks, and investigate the influence of large-scale
210 environmental drivers on interaction strength. In this particular ecosystem, our analyses
211 confirmed decades of experimental work regarding the foundation species *Macrocystis pyrifera*,
212 but also were able to contextualize those classic interactions as they apply at the study
213 site. A classic algal competitive dominance hierarchy[38] is seemingly weak at this site under
214 average conditions, but not absent—under predictable nutrient, temperature, and disturbance
215 regimes, *Macrocystis* can be dominant at this site.

216 More generally, we report evidence here of an inverse mean-range relationship in interaction
217 strengths and a strong presence of apparent facilitation under multiple environmental con-
218 texts, results that agree with previous theoretical and experimental findings across multiple
219 ecosystems[4,51–53]. An important implication is that if a goal is understanding the dynamics
220 of entire ecosystems, studying the mean outcome of single species interactions may not
221 be adequate. Indirect associations between multiple species and shifting environmental
222 contexts may give rise to rare, critical moments when fleeting strong interactions determine
223 ecosystem shifts. This idea needs further investigation in multiple systems, but if widely
224 applicable, it means that context dependency—and its role in mediating varying species inter-
225 action strengths—deserves more attention than the identification of context-averaged mean
226 interactions[8]. In a growing number of ecosystems, EDM is helping in this endeavour[15,54,55].

227 EDM does not take the place of experimentation, but we argue that it can help to both
228 contextualize and guide it. Our analysis was a proof of concept: we started with simple time
229 series from a monitoring dataset in a well-studied but complex ecosystem, and showed how
230 previous experimental results play out over a longer time period. We hope that this approach
231 can be applied to many other ecosystems, where time series data exist but where important
232 interactions may not be as well-established. Where important interactions are known, EDM

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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 well[50]. 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* dominance[23]. 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

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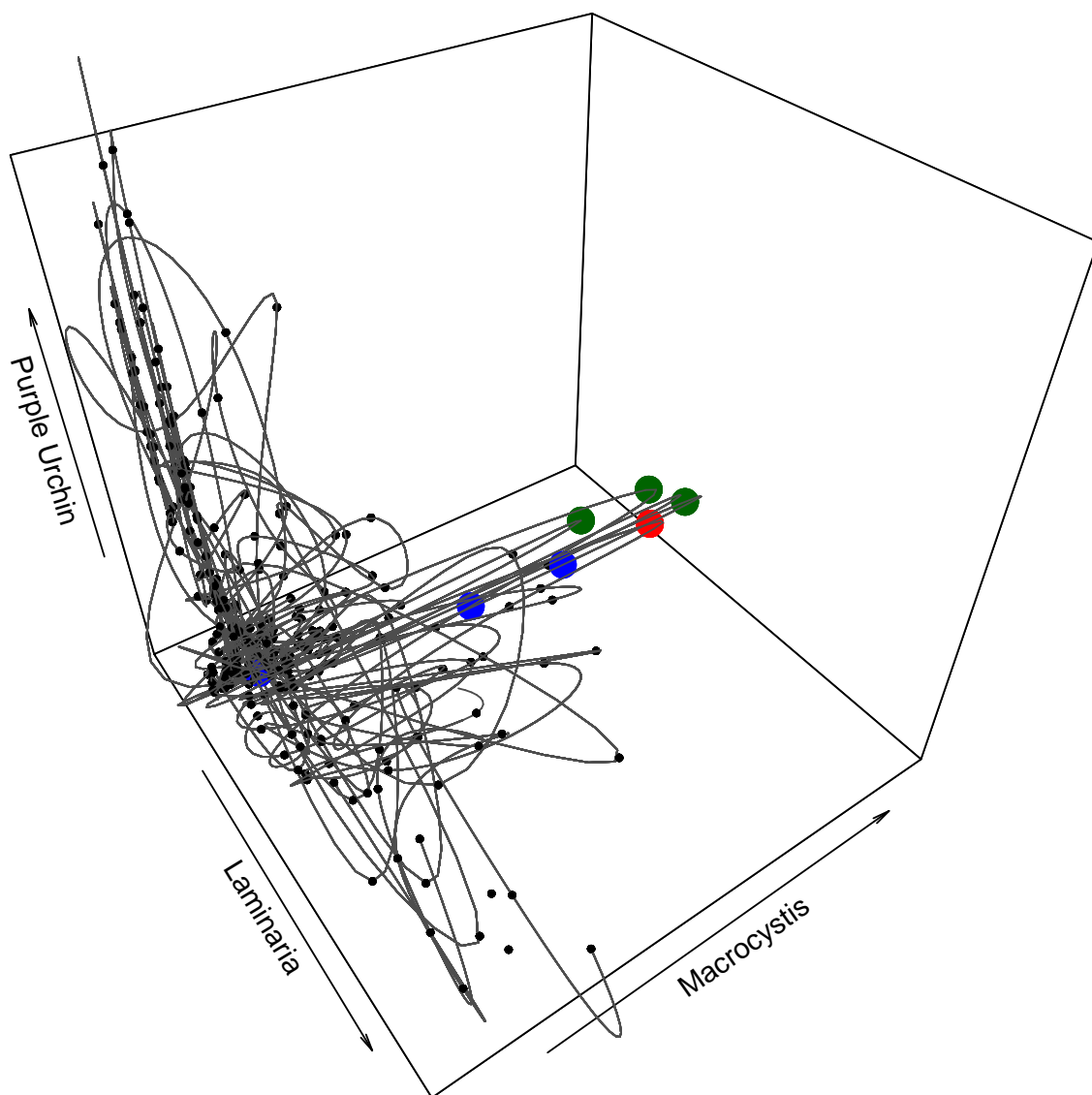2. Suttle, K. B., Thomsen, M. A. & Power, M. E. Species Interactions Reverse Grassland
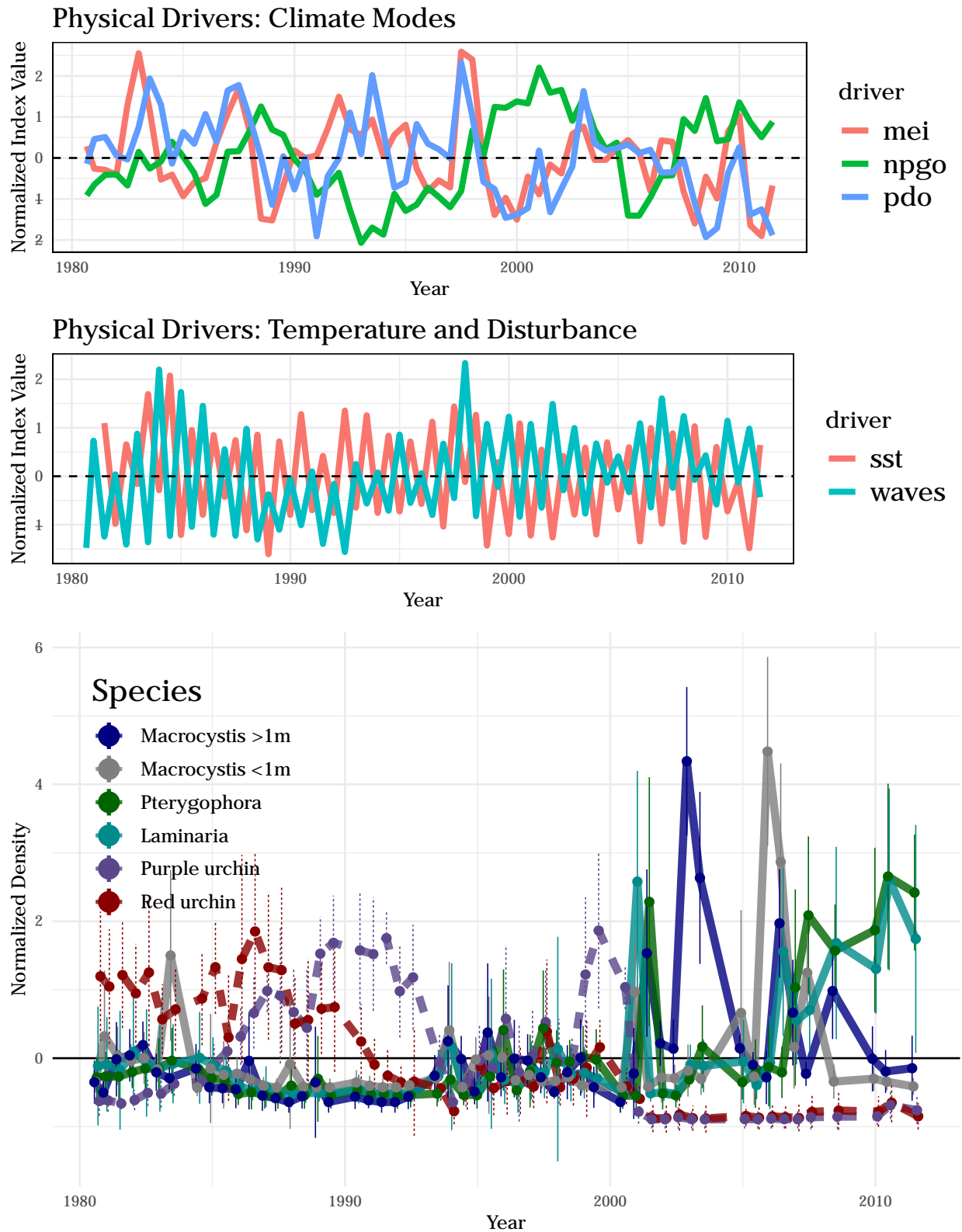
Figure 5: Example reconstructed dynamic attractor

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

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