Environmental Context Dependency in Species Interactions

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Journal Guidelines:

- Maximum 3500 words main text (excluding introductory pa ragraph/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').

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)

FIGURES

Time series of study species Example attractor? (in supplementary) CCM results

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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

33 under which they are performed. As an alternative, we utilize empirical dynamic modeling
34 applied to a 30-year time series to estimate species interaction strengths across a wide range
35 of environmental conditions in a coastal marine ecosystem. By including large-scale climate
36 indices, sea surface temperature, and a measure of physical disturbance in analyses, we show
37 that environmental context influences the strength and direction of species interactions. In
38 so doing, we are able to confirm and extend results from previous studies, as well as identify
39 potentially important but understudied interactions. The significant context dependency in
40 species interactions found in this study argues for a greater utilization of long-term data and
41 empirical dynamic modeling in studies of ecosystem dynamics.

Introduction

42

43 Interactions between species drive patterns of diversity, stability, resilience, and productivity
44 in nature[1–4]. In any ecosystem, the collection of species interactions determines community
45 dynamics. Until recently, most studies viewed these dynamics—e.g., the bleaching and
46 recovery of a coral reef, or the assembly and disassembly of terrestrial plant communities—as
47 processes resulting from static, predictable species interactions. However, the observation
48 that species interactions are not spatiotemporally uniform[5–8] calls into question assumptions
49 of interaction stability.

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

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

64 A solution to these difficulties is to a) utilize ecological observations collected over a long time
65 period, across a large range of environmental contexts, with b) an analytical method to directly
66 estimate context-dependent species interactions from those observations. Such an approach
67 could help to characterize environmental contingencies in species interactions and explicitly
68 examine interaction variability. Here, we use empirical dynamic modelling (EDM,[15]) to
69 estimate a varying species interaction network and establish environmental context dependency
70 in interaction strength and direction. Empirical dynamic modelling uses information from
71 single or multiple time series to empirically model relationships between variables through
72 the reconstruction of dynamic attractors (https://youtu.be/8DikuwwPWsY). The general

73 modelling framework for all EDM methods is readily adaptable to many different sorts of
74 time series variables, including environmental variables manifesting at different scales[16–18].
75 Because the methods are specifically designed for nonlinear dynamic systems, EDM—in
76 theory—should be able to illuminate context-dependent patterns in species interactions.

77 Recently-developed EDM methods exist for uncovering dynamic species interactions from time
78 series data[15], but these methods have insofar been applied only to simulated and planktonic
79 communities, and their utility to the study of other ecological systems remains untested.
80 We focus here instead on giant kelp forests in southern California, a diverse and temporally
81 dynamic ecosystem in which many important species interactions are well-documented[19–21].
82 The study of kelp forests has been foundational to ecological theory, especially regarding the
83 relative influence of top-down and bottom-up structuring forces in ecosystems[22–26]. Recently,
84 however, findings from long-term kelp forest research programs have begun to challenge many
85 long-held beliefs about the drivers of kelp forest ecosystem dynamics[27]. In particular, a
86 longer-term perspective has led to a recognition of the critical importance of environmental
87 context—such as level of physical disturbance or the current state of El Niño conditions—for
88 understanding kelp forest processes[28–31]. In this study we utilize monitoring data from one
89 such effort at San Nicolas Island, a small, remote member of the California Channel Islands
90 in the northeast Pacific[32].

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

Results and discussion

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

In southern California, *Macrocystis* population dynamics can be driven by nutrient availability and physical disturbance[26,30]. The availability of nitrate is inversely related to seawater temperature[42] 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 mapping[33] (CCM) to the set of six biological and five physical variables, we find a relatively dense interaciton network (Figure 1). 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 methods[30] 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.

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 6); rather, the site has transitioned from an urchin barren[41] 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 species[20].

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-maps[15,34] (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 5). 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.

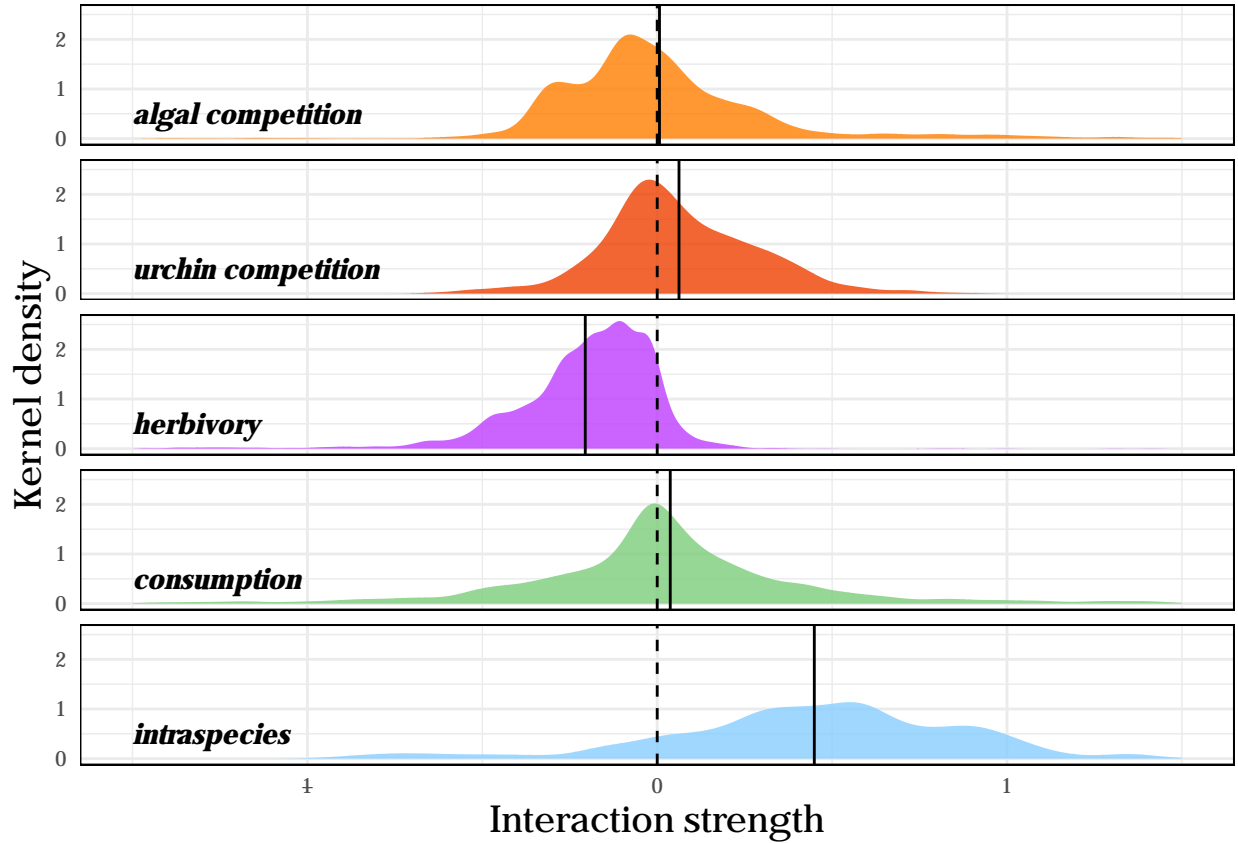There are two important aspects of S-maps that deserve mention. First, the S-map estimation

Figure 1: Reconstructed interaction web using results of convergent cross mapping
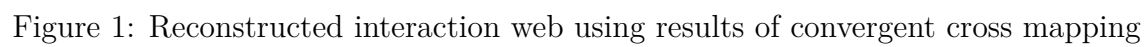
Figure 2: Distribution of estimated interaction by type

157 procedure, like all EDM methods, is specifically designed for nonlinear systems, and is
158 therefore an appropriate tool for investigating ecosystems exhibiting nonlinear dynamics such
159 as alternative stable states or hysteresis[15]. Secondly, because S-maps utilizes reconstructed
160 multispecies attractors, each estimated interaction is fundamentally based on observations of
161 similar past ecosystem states—in our case represented as multivariate collections of causally-
162 linked species' densites—rather than a phenomenological extrapolation of the most recent
163 dynamics. In simple terms, instead of asking, "What is our prediction for the strength of
164 herbivory based on last year's observed dynamics," S-maps is concerned with, "What is our
165 best estimate for the strength of herbivory, based on our knowledge of times in the past when
166 the ecosystem was most similar to today?"

167 In the San Nicolas kelp forest, we find a striking prevalence of neutral and positive species
168 interactions (Figure 2). After grouping species interactions by type, only herbivory (the effect
169 of urchins on algae species) is predominantly negative. Conversely, the effect of the algae
170 species on the urchins has the flattest distribution, with occasional strong negative and strong
171 positive interactions. Likewise, contrary to our expectations, interactions between the algae
172 species and between the urchin species are not always antagonistic. These results suggest that
173 facilitation is common in kelp forests when context is considered. Since there is evidence here
174 of strong herbivory, for example, then the indirect facilitative effects between algae species
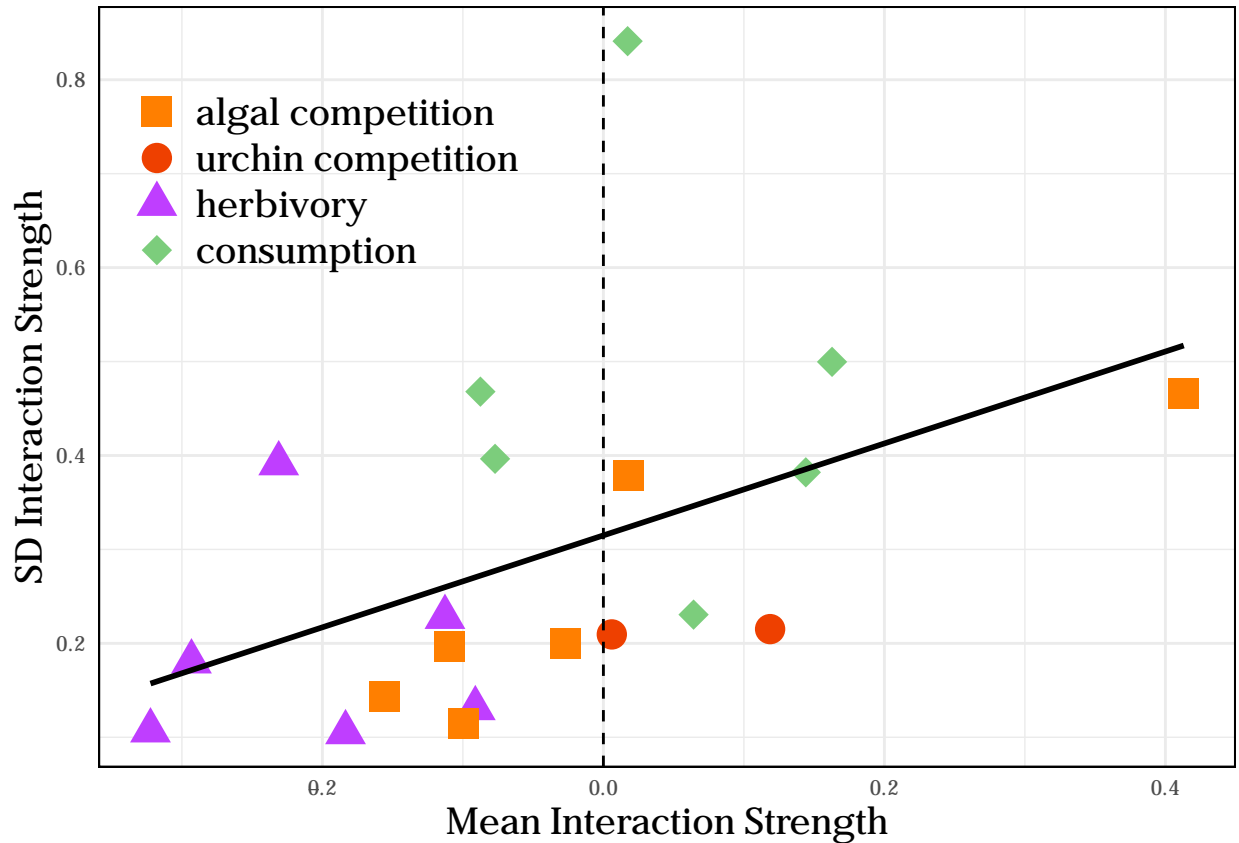
Figure 3: Mean and standard deviation of each estimated unidirectional species interaction

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 species[20]. These types of indirect facilitation in kelp forests have received little attention[46; Benes2015] relative to a strong focus on exploitative competition between these species for light and nutrients[37,39], 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 important structuring factor in kelp forest ecosystems.

- 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?
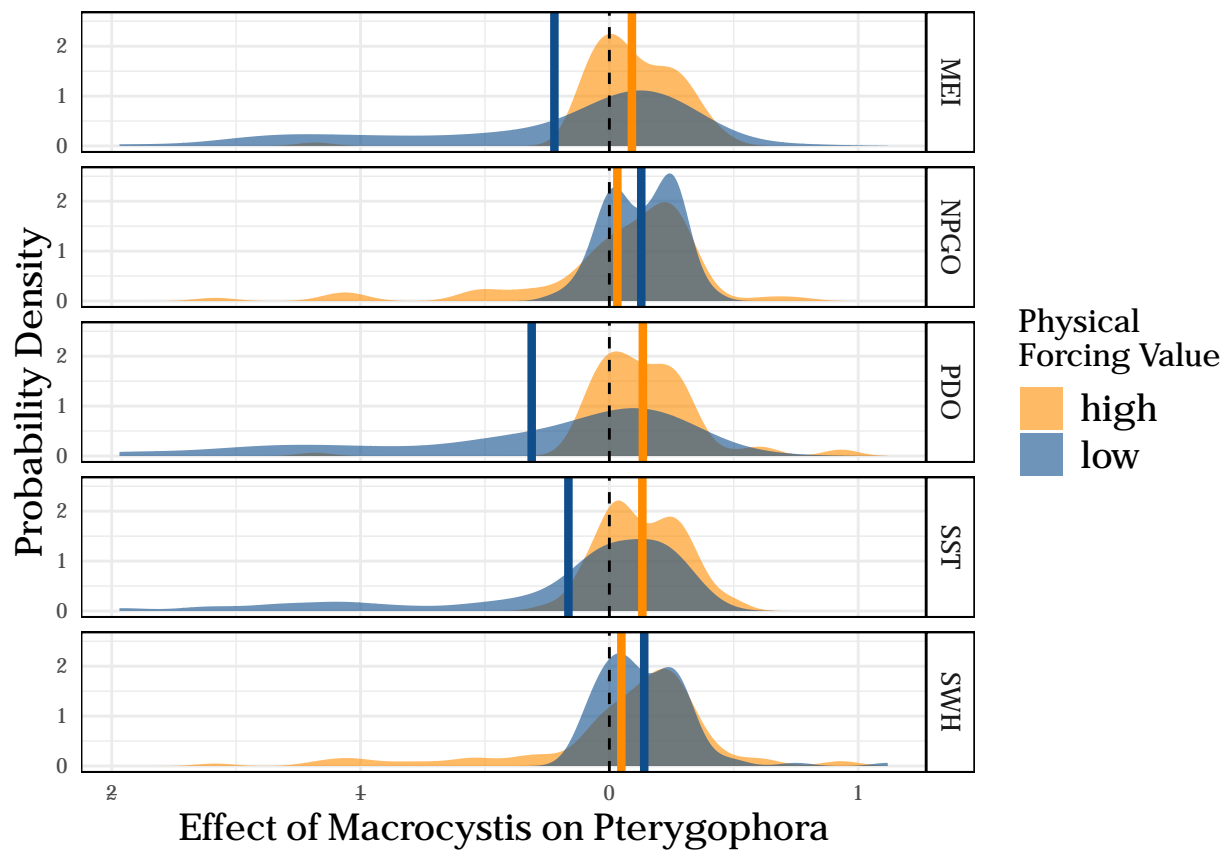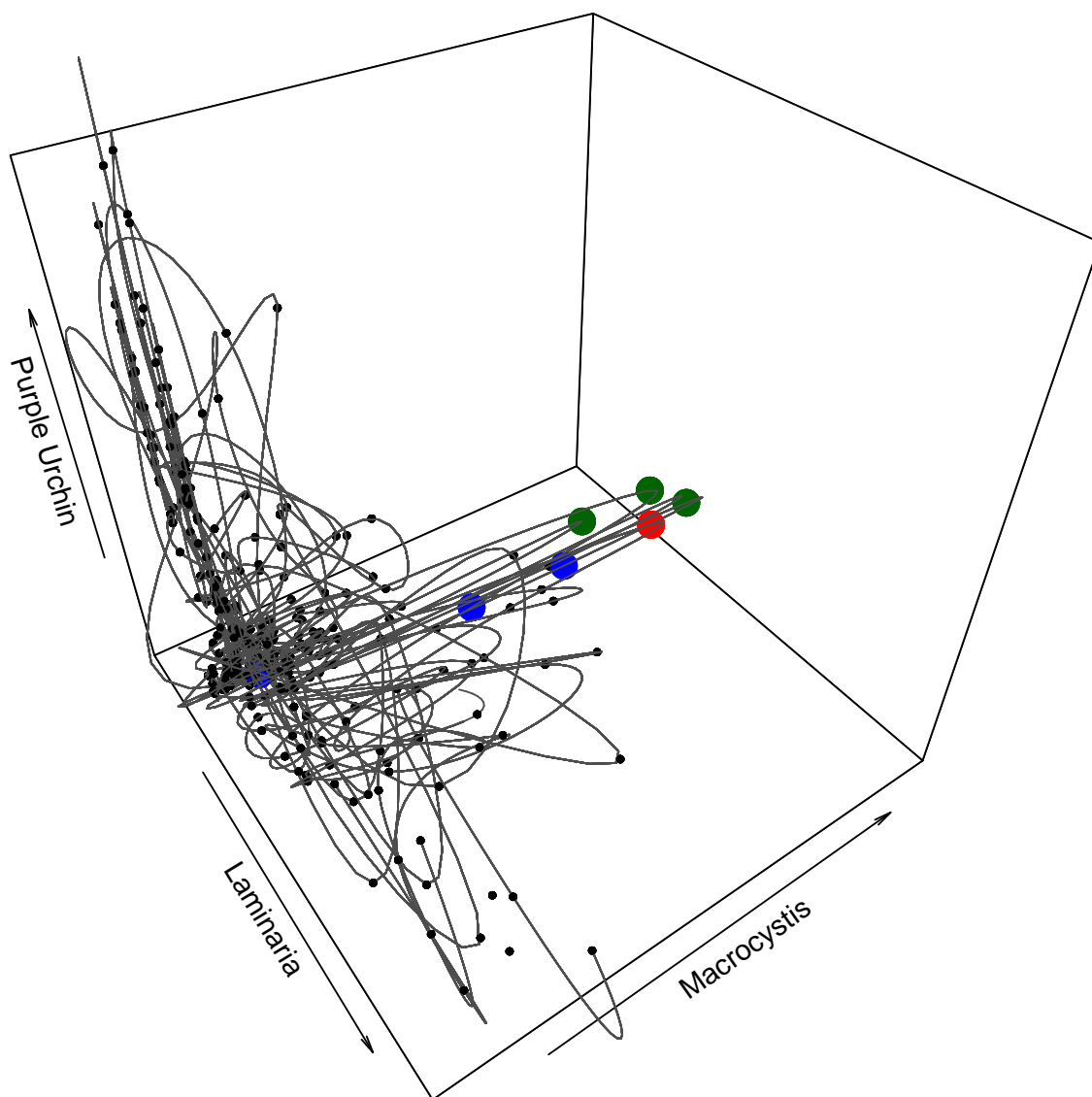
Figure 4: Macrocystis effect on Pterygophora

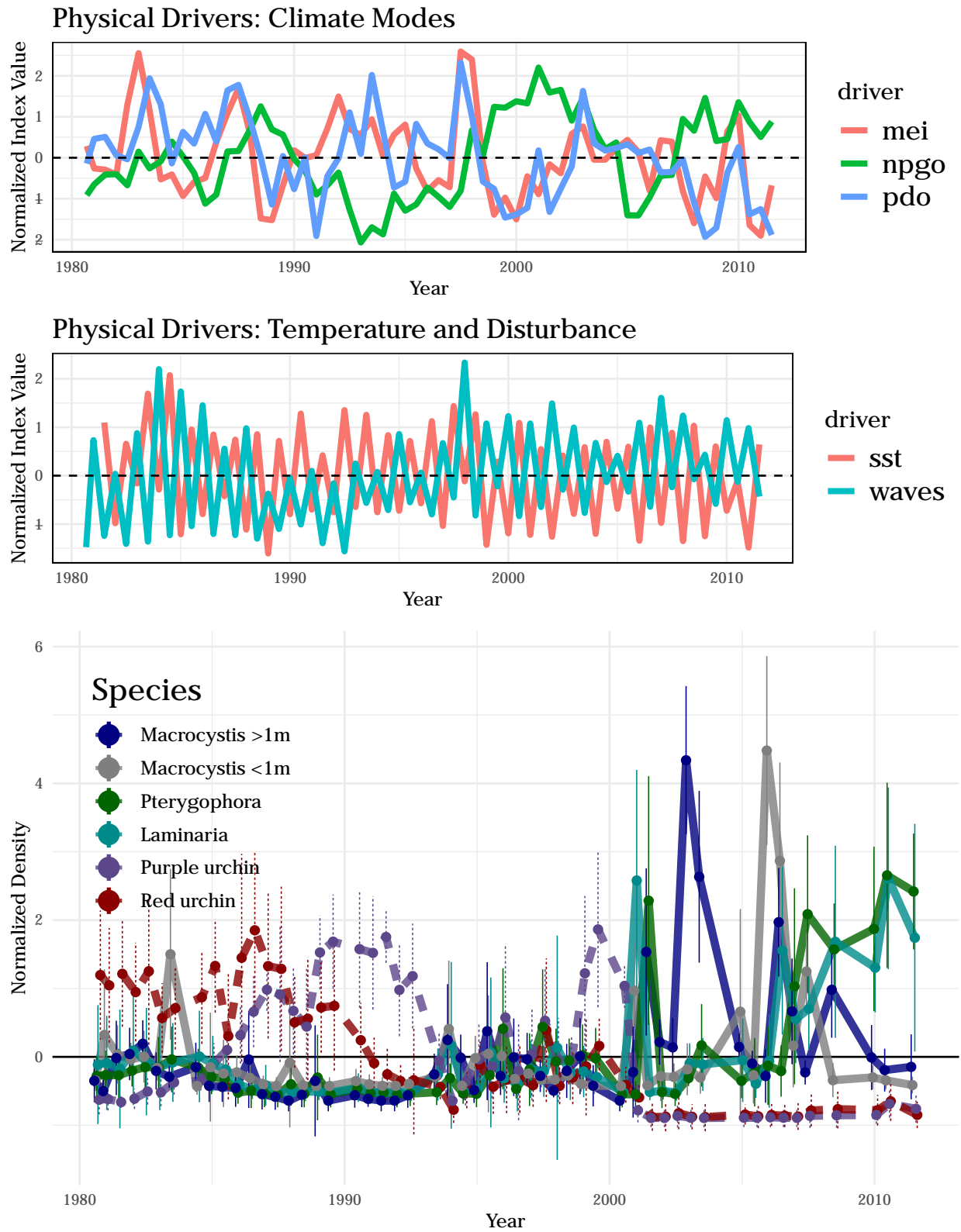Figure 5: Example reconstructed dynamic attractor

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

187 Methods

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