

Convergent evolution of niche structure in Northeast Pacific kelp forests

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Author contributions

This manuscript represents a chapter of S.S.'s PhD dissertation. S.S. conceived of and designed the study. S.S., K.W.D, and C.J.N. collected the data, P.T.M. provided guidance and funding. S.S. conducted analyses and wrote the first draft of the paper. All authors contributed input into the final version of the manuscript.

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3

4 Abstract

- 5 1. Much of the morphological and ecological diversity present on earth is believed to have
6 arisen through the process of adaptive radiation. Yet, this is seemingly at odds with
7 substantial evidence that niches tend to be similar among closely related species (i.e.,
8 niche conservatism). Identifying the relative importance of these opposing processes in
9 different circumstances is therefore essential to our understanding of the interaction
10 between ecological and evolutionary phenomena.
- 11 2. In this study, we make use of recent advances in our understanding of the phylogeny of
12 kelps (Laminariales) to investigate niche evolution in one of the most important groups
13 of benthic habitat-forming organisms on the planet. We quantify functional traits and
14 use community sampling data from a kelp diversity hotspot to determine which traits
15 are responsible for the habitat (β) niche of kelps and whether they are labile or
16 conserved across the kelp phylogeny.
- 17 3. We find that combinations of functional traits have evolved convergently across kelp
18 subclades and that these traits are significant predictors of community structure.
19 Specifically, traits associated with whole-kelp structural reinforcement and material
20 properties were found to be significantly correlated with species distributions along a
21 gradient of wave disturbance and thus predict the outcome of environmental filtering.
22 However, kelp assemblages were made up of species that are more phylogenetically
23 distinct than predicted from null models (i.e., phylogenetic overdispersion), suggesting
24 that niche partitioning along this gradient of wave disturbance has been an important
25 driver of divergence between close relatives.
- 26 4. These results collectively demonstrate that environmental filtering by waves plays an
27 essential role in determining the habitat niche of kelps across local communities and
28 further suggest that this community-level process can drive phenotypic divergence
29 between close relatives. We propose that parallel adaptive radiation of kelp subclades
30 has shaped the diversity and species composition of kelp forests in the Northeast Pacific
31 and we discuss how evidence from the literature on incipient or ongoing speciation
32 events support this hypothesis.

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39 Introduction

40 A major challenge among ecologists is to understand how community-level processes influence
41 the macroevolution of lineages (Webb et al. 2002, Emerson and Gillespie 2008, Gerhold et al.
42 2015). Local environmental gradients serve as the environmental context in which both
43 ecological and evolutionary processes occur and can thus serve as a starting point to address
44 this challenge. In the context of communities, stress and/or disturbance from the environment
45 can exceed the tolerances of some species, causing them to be excluded from certain
46 communities (e.g. van der Valk 1981, Menge and Sutherland 1987, Webb et al. 2002, Cornwell
47 and Ackerly 2009, Kraft et al. 2014). Thus environmental gradients can serve as “environmental
48 filters”, resulting in communities of species that share phenotypic traits necessary to survive in
49 a particular environment (Reich and Oleksyn 2004, Swenson and Enquist 2007, Kraft et al. 2011,
50 2014, Enquist et al. 2015, Cavalheri et al. 2015, Ulrich et al. 2017). Over evolutionary timescales,
51 environmental gradients can influence the phenotypic evolution of community members by
52 serving as strong sources of selective pressure (Cavender-Bares et al. 2004a, Demes et al. 2013,
53 Gerhold et al. 2015). Thus, community assembly dynamics along environmental gradients
54 depend strongly on the interplay of these ecological and evolutionary processes. Yet,
55 disentangling the factors at play has been an ongoing challenge (Cavender-Bares et al. 2009).

56

57 Depending on the evolutionary history of the species pool and the evolutionary lability of
58 underlying phenotypes, we might expect very different patterns of relatedness among the
59 species found in local communities subject to environmental filtering. Many studies have found
60 that closely related species share similar phenotypes (Webb 2000, Webb et al. 2002, Silvertown

61 et al. 2006a, Kraft et al. 2007) due to selection against phenotypic divergence (“niche
62 conservatism”) or due to a lag caused by a shared ancestor and slowly evolving traits (Wiens
63 2008, Losos 2008). This pattern is remarkably common (Darwin 1859, Webb et al. 2002, Vamosi
64 et al. 2009), leading many researchers to assume that it is true, even in the absence of any
65 phenotypic data (see Gerhold et al. 2015 for a review). When phenotype and phylogeny are
66 correlated, closely related species are often clustered in space because close relatives with
67 similar traits tend to experience similar outcomes from strong environmental filtering (Fig 1a;
68 Webb et al. 2002, Cavender-Bares et al. 2009). However, the ubiquity of studies showing
69 evidence for niche conservatism stands in contrast to another body of work on the process of
70 adaptive radiations wherein lineages are known to spread out across environmental gradients
71 (hereafter “niche partitioning”) to move into open niches as they diversify (MacArthur 1958,
72 Hector and Hooper 2002). This process would be expected to result in the opposite community
73 pattern: communities made up of distantly related species that share a set of convergently
74 evolved traits (Fig 1b; Cavender-Bares et al. 2004a, Silvertown et al. 2006a, 2006b, Cavender-
75 Bares et al. 2018). In order to reconcile this apparent disconnect between alternative
76 theoretical expectations of phylogenetic community structure, it is necessary to determine the
77 relative importance of these opposing evolutionary forces (niche conservatism versus niche
78 partitioning) in various lineages and circumstances to determine how and when particular
79 processes dominate phenotypic evolution. The relative importance of these different processes
80 can be inferred by identifying the patterns of phenotypic variation across the phylogeny of a
81 given lineage and by determining how this phenotypic variation relates to the sorting of species
82 into ecological communities (Lopez et al. 2016).

83

84 While the relatedness of species within and between communities (hereafter, phylogenetic
85 community structure) has been well explored in terrestrial taxa, particularly embryophytes
86 (Emerson and Gillespie 2008, Cavender-Bares et al. 2009), most marine lineages are poorly
87 studied in this respect (Verbruggen et al. 2009, Best and Stachowicz 2013). This is problematic
88 because evolutionary processes in the ocean may be somewhat different from those on land,
89 with generally fewer barriers to reproduction in marine environments (Buzas and Culver 1991,
90 Schluter 2000). Marine macroalgae offer an intriguing study system to explore the evolution of
91 phenotype and niche structure because morphologies, which are relatively simple, strongly
92 influence the abiotic tolerances of species (Littler and Littler 1984, Steneck and Dethier 1994,
93 Martone 2007, Starko and Martone 2016). In particular, water motion from waves and currents
94 is believed to act as an exceptionally strong environmental filter that excludes species from
95 more wave exposed sites if they are not strong enough to resist the forces that they experience
96 (Denny 1985, Gaylord et al. 1994, Denny and Gaylord 2002, Demes et al. 2013). Conversely, low
97 flow habitats may be highly stressful due to the formation of diffusive boundary layers that
98 reduce nutrient uptake and gas exchange across macroalgal thalli (Hurd 2017). Thus, low flow
99 environments may eliminate species that fail to achieve morphologies that facilitate the
100 depletion of boundary layers when water motion is low (Coyer and Roberson 2004). This
101 continuum of stress and disturbance caused by the position of local communities along
102 gradients of water motion is an essential driver of both community assembly processes and the
103 evolution of phenotypic traits across rocky shores, but ecological and evolutionary processes
104 have yet to be linked across any major lineage that occupies this environment.

105

106 Kelps (order Laminariales) are the largest and most productive macroalgae in the ocean and
107 dominate approximately 25% of coastlines globally (Wernberg et al. 2019). Kelps increase the
108 productivity of cool, temperate nearshore ecosystems and their presence can substantially alter
109 the composition of biotic communities (Steneck et al. 2002, Graham 2004, Teagle et al. 2017,
110 Hind et al. 2019). In spite of their global importance, we still have a limited understanding of
111 the processes underlying the evolution of kelps. While recent advances in phylogenetics have
112 dramatically improved our understanding of the relationships between species and the
113 evolution of some key morphological features (e.g., Lane et al. 2006, Kawai et al. 2013, Jackson
114 et al. 2017, Starko et al. 2019b), it is unknown how niche structure has evolved across this
115 ecologically diverse clade. Kelps diversified in the North Pacific following the Eocene-Oligocene
116 boundary (Starko et al. 2019b), possibly as a result of ecological opportunity that arose as the
117 North Pacific cooled over the past 30 million years. While kelps are found globally, they are
118 overwhelmingly most diverse in the North Pacific and it remains largely unclear what processes
119 have allowed for the production of such high sympatric diversity in this part of the ocean.

120

121 In this study, we investigate the phylogenetic patterns of habitat (β) niche structure across
122 geographically co-existing species of kelp in the Northeast Pacific, one of the most diverse
123 stretches of coastline for kelps and their likely center of origin (Starko et al. 2019b). We begin
124 by presenting a dataset of quantitative traits for 17 species of kelp and testing for phylogenetic
125 signals on these traits. We use an ancestral state reconstruction approach to determine
126 whether particular trait combinations share a common origin or whether they have

127 convergently arisen in different subclades. Next, we test whether environmental filtering is an
128 important driver of community assembly and determine how this relates to the phenotypic and
129 phylogenetic structure of communities. We do so by making use of a community dataset that
130 spans a gradient of wave action, an important driver of nearshore community composition and
131 a known filter of the kelp species pool (Duggins et al. 2003, Burel et al. 2019). By teasing apart
132 the evolution of phenotypic features from patterns of phylogenetic community structure, our
133 results lend critical insights into the evolution of niche structure across one of the most
134 ecologically important groups of foundations species found anywhere in the ocean and shed
135 light on how ecological and evolutionary forces interact to shape marine communities.

136

137 **Materials & Methods**

138 *Quantifying phenotypic traits*

139 Seven quantitative traits were compared for all kelp species of interest (n=17), many of which
140 are analogous to commonly measured traits in land plants; these included two traits describing
141 whole individual biomass allocation (stipe mass fraction or SMF, holdfast mass fraction or HMF)
142 and five traits describing mechanical and structural properties of blade tissues. SMF and HMF
143 describe the proportion of total biomass that is stipe or holdfast material, respectively. HMF is
144 analogous to root-shoot ratios in land plants. Organs (holdfast, blades, stipes) of individual
145 kelps (n = 5 per species) were carefully separated and dried in a 50-60°C drying oven. Blade
146 mass per area (BMA; analogous to leaf mass per area) was defined as the amount of dry
147 biomass per unit area of blade tissue and dry matter content (DMC) was defined as the ratio of
148 dry weight to wet weight. Both BMA and DMC were measured by taking hole punches of

149 standardized area out of the blades and measuring the wet mass and dry mass of each hole
150 punch. Mechanical properties of blade material: breaking stress (σ), stiffness (E) and
151 extensibility (ϵ), were measured using an Instron (model 5500R, Instron Corp., Canton,
152 Massachusetts, USA), a portable tensometer (described in Martone 2006), or were taken from
153 the literature (Tables S1-S2). With the exception of these few material properties
154 measurements taken from the literature, trait data represent average measurements taken
155 from adult individuals of populations in southern British Columbia (Barkley Sound, Port
156 Renfrew, Vancouver or Victoria; see Tables S1-S2). We used a principal components analysis to
157 collapse trait combinations into fewer axes of correlated traits. Then, to determine whether any
158 major PCA axis correlates with the ability of kelps to resist dislodgement, we tested for
159 correlations, using PGLS models, between PCA axes and tenacity-area scaling relationships
160 quantified previously (Starko and Martone 2016) for the 8 species included in that study.
161 Tenacity-area scaling relationships describe the slope of the relationship between maximum
162 dislodgement force and thallus size and are therefore an effective measure of wave tolerance.

163

164 *Phylogenetic reconstruction*

165 The phylogeny of kelps, with more than 120 species, has been studied previously in
166 considerable detail (Lane et al. 2006, Jackson et al. 2017, Starko et al. 2019b). In this study, the
167 time-calibrated phylogeny inferred by Starko et al. (2019b) was used to represent phylogenetic
168 divergence in millions of years for the 17 co-occurring Northeast Pacific kelp species of interest.
169 This time-calibrated phylogenomic analysis is the most well supported and comprehensive to
170 date and included all 17 species except *Laminaria setchellii*, which was incorporated into the

171 analysis by substituting it for *L. digitata*, which is not found in the northeast Pacific but was
172 included in the phylogenomic analysis. This substitution relies on the assumption that *L.*
173 *setchellii* has an equivalent divergence time from *Laminaria ephemera* as *L. digitata*, which is
174 well supported by previous work on intrageneric relationships between *Laminaria* species,
175 showing less than 1 million years difference in divergence time between *L. ephemera* and *L.*
176 *setchellii* vs. *L. digitata* (Rothman et al. 2017). Phylogenetic signal of traits was measured using
177 Blomberg's K (Blomberg et al. 2003) and Pagel's lambda (Pagel 1999). We also tested for
178 correlations between trait distance and phylogenetic distance using Mantel tests.

179

180 We used the software "StableTraits" (Elliot and Mooers 2014) to reconstruct ancestral values of
181 principal component axes and the traits and to model rates of phenotypic evolution.

182 "StableTraits" samples from a heavy-tailed distribution, therefore allowing for modelling of
183 traits under selection. We ran StableTraits for 10 million generations, sampling every 1000
184 generations. Results of these analyses were visualized using the contMap function in "phytools"
185 (Revell 2012).

186

187 *Community dataset*

188 To determine how trait or phylogenetic differences influence community assembly, we used a
189 community dataset of intertidal kelp distributions in Barkley Sound, British Columbia that was
190 published in a Parks Canada technical report (Druehl and Elliot 1996). Data from sites sampled
191 in 1995 (n = 87 sites), the most extensive year of this survey, were combined into a data matrix.

192 This dataset included all of the species examined in the trait analysis except two (*Laminaria*

193 *ephemera* and *Cymathære triplicata*). Although a coarse categorical abundance measurement
194 is given in their report, only presence and absence data were used. At a subset of sites (n = 55)
195 that could be located by photographs in the 1996 report, the upper limit of barnacles was
196 measured in the summers of 2018-2019 and these values were used as a continuous proxy for
197 wave exposure. The upper limit of barnacles is an effective proxy of wave run-up and is known
198 to increase in elevation at more wave exposed sites (Harley and Helmuth 2003, Neufeld et al.
199 2017). The upper limit of barnacles was measured by using a stadia rod and sight level, along
200 with tide predictions from Bamfield Inlet, Effingham Island or Mutine Point, depending on
201 proximity. A categorical measure of wave exposure provided by Druehl & Elliot was used for
202 analyses of all 87 sites. Barnacle upper limit was significantly different between these wave
203 exposure categories (ANOVA: $F_{2,52} = 19.5815$, $P < 0.0001$) with significant differences between
204 all means (Tukey HSD < 0.05), suggesting that barnacle upper limits are an appropriate proxy
205 for wave exposure. Using the range of barnacle upper elevation data (that spanned
206 approximately 3 to 5.5 m above MLLWLT), we created a “wave exposure index” by subtracting
207 3 meters from each measurement and then dividing by 2.5 (the approximate range of barnacle
208 upper limits), resulting in an index that varied from 0 to 1. Although resurveys were conducted
209 at some of these sites, recent work demonstrated that kelp forests have been lost from several
210 of these sites, likely as a result of the 2014-2016 heatwave (Starko et al. 2019a). Thus, only
211 historical data were used to reconstruct niche structure before the large-scale degradation of
212 these kelp communities.

213

214 *Quantifying species co-occurrence*

215 First, to determine whether non-neutral processes were required to explain the distribution of
216 species across communities, we tested whether our community matrix was significantly
217 different from randomly generated communities. We did so by comparing our observed
218 checkerboard score (i.e., c-score; Stone and Roberts 1990), a measure of association between
219 species pairs, to randomly simulated communities. In order to test for significant associations
220 between individual species, observed co-occurrence probabilities were calculated for each pair
221 of species and compared to a null expectation of species co-occurrence that was generated
222 using randomizations that considered only the number of sites at which each species was
223 found. In cases where species were expected to co-occur at less than one site, these species
224 pairs were excluded due to insufficient data. Deviations from expectations were measured
225 using a log response ratio of observed vs. expected outcomes, hereafter “co-occurrence index”.
226 Calculated as:

$$227 \quad Co - occurrence\ index = Log_{10} \left(\frac{Observed}{Expected} + 1 \right) \quad Eq. 1$$

228 where “Observed” refers to the actual number of co-occurrences in the community matrix, and
229 “Expected” refers to the number of sites that species were expected to be found together given
230 the null model. Species association analyses were corrected for false detection rate and were
231 considered significant when q-values were less than 0.05. In order to determine whether
232 phylogenetic distance or trait differences (first and second trait-derived principal components)
233 influenced the co-occurrence probability of species, linear regressions were fit between each
234 predictor (phylogenetic distance, PC1 distance and PC2 distance) and co-occurrence index.

235

236 *Wave exposure and community assembly*

237 The relationship between species presence and wave exposure was measured in two ways
238 using the subset of sites ($n = 57$) for which continuous wave exposure (barnacle upper limit)
239 had been measured. This subset did not include any sites with *S. latissima*, which was therefore
240 excluded from these analyses. It also included only one observation of *P. palmaeformis* at one
241 of the most wave-exposed sites in our dataset. This species is well known to occur only on the
242 most wave exposed shores (Nielsen et al. 2006) and so this site was deemed representative of
243 the niche of *P. palmaeformis*. However, to better improve our estimate of average wave
244 exposure for this species, we measured the upper limit of barnacles at two sites on the nearby
245 outer coast (Cape Beale) that consistently have *Postelsia palmaeformis* populations. All three
246 sites were very high exposure (upper limit of barnacles: 5.2 - 5.8 m above MLLWLT). To assess
247 the relationship between traits and species' habitat use, average wave exposure was measured
248 for each species from all sites in which that species was present. A phylogenetic least squares
249 (PGLS) regression was then used to test for an effect of principal component axes and all seven
250 quantitative traits on average wave exposure. In order to further visualize differences in species
251 habitat use, the probability of species presence was plotted against wave exposure (i.e., the
252 upper limit of barnacles) as modeled using polynomial, binomial generalized linear models. This
253 modelling approach allows for an optimal wave exposure rather than forcing saturation. This
254 was done separately for members of the two subclades with the most species included here,
255 the families Arthrothamnaceae and Alariaceae. To determine whether sites of different wave
256 exposure also have different kelp communities, we conducted a PERMANOVA with the wave
257 exposure categories described above as a predictor variable.

258

259 *Phylogenetic community structure*

260 To further test for an effect of phylogeny on community assembly we used indices of
261 phylogenetic community structure (Webb 2000). Net relatedness index (NRI) and nearest taxa
262 index (NTI) measure the extent to which taxa are phylogenetically clustered at a particular site
263 relative to the regional species pool. A positive value of either NRI or NTI indicates phylogenetic
264 clustering, while negative values indicate phylogenetic overdispersion. NRI measures
265 phylogenetic clustering by considering the average phylogenetic distance between all members
266 of a community. Specifically, NRI is defined as follows:

267
$$NRI = -\frac{X_{net} - X_{null}}{SD_{net}} \quad \text{Eq. 2}$$

268 Where X_{net} is the average phylogenetic distance between members of a community, and X_{null}
269 and SD_{null} represent the mean and standard deviation, respectively, of simulated random draws
270 from the species pool. We calculated these metrics using 10,000 random simulation. NTI is
271 similar to NRI but considers the average distance between each species and its closest relative.
272 Specifically, X_{net} from equation 2 is replaced with X_{min} which is defined as the average distance
273 between each species and its closest relative, such that:

274
$$NTI = -\frac{X_{min} - X_{null}}{SD_{null}} \quad \text{Eq. 3}$$

275 For NTI, X_{null} and SD_{null} represent the mean X_{min} and associated standard deviation from
276 random draws of the species pool, similar to calculations of NRI. As a consequence of
277 differences in the underlying metric of interest (X_{net} versus X_{min}), NRI is more sensitive to
278 phylogenetic clustering deeper into the phylogeny, while NRI is more sensitive to clustering

279 near the tips of the phylogeny. The significance of trends in phylogenetic structure was
280 evaluated in two ways. First, at a community level, sites (i.e. individual communities) were
281 considered to be significantly structured by phylogeny if NRI or NTI values ranked among the
282 500 most extreme values (97.5th or 2.5th percentiles) of the 10,000 randomly generated
283 pseudo-communities. A second approach was used to determine if, across the whole dataset,
284 there were significant trends in phylogenetic community structure. NRI and NTI are both
285 expected to be approximately normally distributed with a mean of zero, therefore in order to
286 determine whether the mean of the distribution of kelp communities differed from this null
287 expectation, t-tests were also performed, treating sites as replicates (as in Cooper et al. 2008).

288

289 *Statistical software*

290 All statistical analyses were performed in R version 3.6.0, using the packages “ape” (Paradis et
291 al. 2004), “phytools” (Revell 2012), “picante” (Kembel et al. 2010), “qvalue” (Bass et al. 2018),
292 “EcoSimR” (Gotelli et al. 2015), and “cooccur” (Griffith et al. 2016).

293

294 **Results**

295 *Phenotypic traits are convergent across taxa*

296 Principal component analysis resulted in seven component axes with the first two explaining
297 63.9% of the variation in trait values (Fig 2A). Principal component 1 (PC1) correlated with
298 structural characteristics of the whole kelp (HMF and SMF), as well as the blade (DMC, BMA),
299 which were themselves all positively correlated (Fig S1). Principal component 2 explained

300 mainly the properties of materials (σ , E and ϵ). These two components explained 35.3% and
301 28.6% of the total variation in functional traits respectively. Principal component 1 strongly
302 correlated with tenacity-area scaling relationships (Fig S2; PGLS model: $F = 11.92$, $df = 1$ and 6 , P
303 $= 0.0136$). There was no significant phylogenetic signal on any of the traits investigated in this
304 study, including principal components (Table 1, Fig 2B). However, our analysis revealed a
305 possible but not significant phylogenetic signal on SMF (Blomberg K : 0.860, $P = 0.063$; Pagel's
306 $\Lambda = 1.128$, $P = 0.085$). Although not significant, Blomberg's K was < 1 in all cases,
307 indicating that traits tended to be more dissimilar among close relatives than predicted from a
308 Brownian motion model. Some pairs of closely related species were somewhat similar in at
309 least some traits (e.g. *Pleurophycus gardneri* and *Pterygophora californica*), but for the most
310 part, closely related species differed as much or more than distantly related ones (Fig 2B). This
311 observation was confirmed by the lack of a significant relationship between PC1 and PC2 trait
312 distances and phylogenetic distance (PC1 Mantel test: Z -stat = 6450.835, $p = 0.589$; PC2 Mantel
313 test: Z -stat = 6449.193, $p = 0.691$). Ancestral state reconstruction demonstrates that trait
314 combinations have evolved repeatedly across the kelps with clear patterns of phenotypic
315 convergence (Fig S3).

316

317 *Kelp communities are phenotypically (not phylogenetically) clustered*

318 The community matrix was non-random with a c -score that exceeded the range of values from
319 random simulations (Fig S4). There were several significant associations between species (Fig
320 3). Positive and negative species associations occurred between both closely and distantly
321 related species pairs. For example, closely related species *Macrocystis pyrifera* and *Nereocystis*

322 *luetkeana* were negatively associated with each other, while sister taxa, *Pleurophycus gardneri*
323 and *Pterygophora californica*, were positively associated (Fig. 3). Moreover, *Egregia*, the most
324 phylogenetically distinct genus from the family Arthrothamnaceae, was positively associated
325 with some members of three other families (Alariaceae, Agaraceae, Laminariaceae) and
326 negatively associated with a member of one (Agaraceae).

327

328 Despite clear evidence of non-random community assembly, there was no effect of
329 phylogenetic distance on the probability of co-occurrence between species. The only significant
330 predictor of pairwise non-random co-occurrence (measured as “co-occurrence index”) was
331 distance in PC1 between species pairs (Linear regression: $F=5.075$, $df=69$, $P=0.02746$; Fig 3C).
332 Phylogenetic distance (Linear regression: $F=0.2392$, $df=69$, $P=0.6263$; Fig 3B) and PC2 distances
333 (Linear regression: $F=0.3037$, $df=69$, $P=0.5833$; Fig 3D) did not significantly correlate with the
334 pairwise co-occurrence of species.

335

336 There was a significant relationship between average wave exposure of a species and its value
337 of PC1 (Linear model: $F = 6.809$, $df = 1$ and 12 , $P = 0.0228$; PGLS model: $t = 3.9823$, $df = 14$ and
338 2 , $P = 0.002$; Fig 4), but not PC2 (Linear model: $F = 0.1225$, $df=1$ and 12 , $P = 0.732$; PGLS model: t
339 $= 0.8316$, $df = 14$ and 2 , $P = 0.4219$), such that structurally reinforced species tended to be
340 found at more wave exposed sites. This relationship was significant even when removing
341 *Postelsia palmaeformis*, the strongest and most wave tolerant species, from the analysis (Linear
342 model: $F = 5.161$, $df = 1$ and 11 , $P = 0.0441$; PGLS model: $t = 3.0250$, $df = 13$ and 2 , $P = 0.0116$).

343 The only traits that significantly correlated with the average wave exposure of a species on their

344 own were HMF and ϵ (Table 2). There was a possible, but not significant negative correlation
345 between blade stiffness and average wave exposure.

346

347 *Kelp species are phylogenetically overdispersed across local communities*

348 Use of phylogenetic indices demonstrate that no communities examined were significantly
349 phylogenetically clustered and most communities trended towards phylogenetic overdispersion
350 relative to simulations (Fig 5). Although only a few sites were significantly overdispersed (NRI: n
351 = 3, NTI = 7; Fig 5), average phylogenetic NRI and NTI values were significantly different from
352 zero (NRI: t-test: $t = 3.917$, $df = 86$, $p = 0.00018$; NTI: t-test: $t = 9.4708$, $df = 86$, $p < 0.0001$). The
353 few communities that trended towards phylogenetic clustering were composed of only a small
354 number of species, where clustering of species at sites appeared to be random on average (NTI
355 and NRI approximate zero).

356

357 Binomial models of species presence and absence along a continuous wave exposure axis
358 further demonstrates how species in each subclade have convergently adapted to different
359 regimes of wave exposure (Fig. 6). Individual species clearly varied in distribution across the
360 gradient of wave exposure and closely related species (e.g. *Nereocystis luetkeana* and
361 *Macrocystis pyrifera*) tended to specialize in different wave exposure regimes. The clear
362 exception here is the species pair *Pterygophora californica* and *Pleurophyucus gardneri* that are
363 sisters and had nearly identical distributions across the wave exposure gradient (Fig 6). There
364 was a significant effect of wave exposure category on community composition (PERMANOVA: F
365 =13.205, $P < 0.001$; Fig S5), indicating that differences in species distributions across the wave

366 exposure gradient scale up to community level differences in species composition at wave
367 exposed versus wave sheltered sites.

368

369 Discussion

370 We demonstrated evolutionary lability in the traits underlying the habitat niches of kelps and
371 suggest that this has resulted in convergent patterns of habitat use across species. Neither
372 principal component, nor any of the individual traits that make them up, were found to be
373 phylogenetically conserved across species (Table 1). In fact, for all traits, Blomberg's K was less
374 than 1, suggesting that closely related species are more dissimilar than predicted by the null
375 model (although not significant). Yet, PC1 (structural reinforcement) was a predictor of both
376 pairwise species co-occurrences (Fig 3) and the position of individual species along the gradient
377 of wave exposure (Fig 4), indicating a role of structural traits in determining the habitat niche of
378 species. We further propose that this relationship is causal on the basis that many field studies
379 and biomechanical models have demonstrated the role of rapid water motion as a strong
380 selective pressure for increased tolerance to physical forces (Johnson and Koehl 1994, Duggins
381 et al. 2003, Martone et al. 2012, Demes et al. 2013, Starko et al. 2014).

382

383 Across communities, species co-occurrence patterns reflect the influence of environmental
384 filtering on community composition but result in overdispersion, rather than clustering, of
385 closely related species. Phylogenetic community indices (NRI and NTI) reveal that communities
386 are made up of more distantly related species than predicted (Fig 5), indicative of phylogenetic
387 overdispersion across kelp communities. Phylogenetic overdispersion of communities is

388 commonly interpreted as phenotypic overdispersion and treated as evidence for competitive
389 exclusion (e.g. Webb 2000, Webb et al. 2002, Cooper et al. 2008). The idea here being that
390 species with similar niches will be unable to co-exist if competition is an important driver of
391 community assembly. However, in our study, species that were commonly found together also
392 tended to be those with correlated niches, indicative of environmental filtering, not
393 competition. For example, *Lessoniopsis littoralis* and *Saccharina sessilis*, two distantly related
394 species that have similar values of PC1 and specialize in wave-swept environments (Fig 6), were
395 positively correlated across the community matrix (Fig 3). Conversely, species that specialize in
396 different wave exposure regimes tended to be negatively correlated. For example, *Neoagarum*
397 *fimbriatum*, a specialist in wave sheltered areas, and *Laminaria setchellii*, a wave exposed
398 specialist (Fig 6), co-occurred significantly less often than predicted (Fig 3). Thus, kelp
399 communities are filtered strongly but the phenotypes that allow species to pass this filter have
400 evolved convergently in different subclades, resulting in communities of species that have
401 similar phenotypes but come from different clades.

402

403 Past work has suggested that traits associated with habitat niche are highly conserved while α
404 niche traits, which result in co-existence of taxa, are more labile (Silvertown et al. 2006a,
405 2006b; but see Cavender-Bares et al. 2004a). While this framework may hold in many groups of
406 embryophytes, we show that this is not the case for kelps. Habitat niche traits in the kelps are
407 labile and tend to be largely dissimilar among close relatives (Fig 6). While the basis of
408 convergence in traits can be challenging to interpret and may differ across taxa, we propose
409 that partitioning of habitats is an important means by which kelps achieve reproductive

410 isolation and undergo speciation. Partitioning can occur either through character displacement,
411 where competition between close relatives drives the weaker competitor to adapt to new
412 environments (Brown and Wilson 1956), or through the splitting of a generalist niche into
413 multiple specialized niches (Funk 1998). There is substantial evidence that simultaneous
414 phenotypic and genetic divergence across the kelps is common and may be an important driver
415 of diversification. In Table 3, we describe five known instances where partitioning along a
416 gradient of wave exposure has resulted in genetic differentiation of populations or incipient
417 speciation. The prevalence of this pattern in ongoing or incipient speciation events, lends
418 support to our hypothesis that niche partitioning along a wave exposure gradients has been a
419 repeated driver of sympatric speciation and that these processes observed in past studies near
420 the tips of the phylogeny scale up to explain patterns of niche evolution across the broader kelp
421 phylogeny. Close relatives may specialize in different positions along environmental gradients,
422 leading to parallel adaptive radiation across subclades, possibly helping to maintain coexistence
423 of species across broad geographic scales (MacArthur 1958, Cavender-Bares et al. 2004b,
424 2004a, Losos 2008, Cavender-Bares et al. 2018). We further hypothesize that α niche traits may
425 be more conserved than β niche traits across the kelps, leading to increased co-existence
426 between distant relatives. While it is unclear exactly what traits would promote co-existence
427 across kelp species, morphological features such as the presence of buoyant floats or long, rigid
428 stipes may be somewhat more conserved than the traits examined here, despite multiple
429 origins (Starko et al 2019b). Differences in stature within the water column have been linked to
430 competitive hierarchies in kelps (Edwards and Connell 2015) and may thus make up a
431 component of species α niches.

432
433 Multiple hypotheses may explain why phenotypic divergence, rather than niche conservatism,
434 is the dominant process behind kelp phenotypic evolution. Kelps diversified only recently and
435 following massive changes to global climate (Starko et al. 2019b). Kelps are much larger and
436 more competitive than other macroalgal species (Edwards and Connell 2015) but rely on cool
437 waters and an abundance of nutrients. Cooling of the oceans may have created an ecological
438 opportunity for kelps, allowing them to diversify across and dominate rocky shores throughout
439 the Northeast Pacific (Bolton 2010, Starko et al. 2019b, Vermeij et al. 2019). This ecological
440 opportunity may have promoted selection for niche partitioning as has been documented
441 previously, such as in oak trees (Cavender-Bares et al. 2004a, Cavender-Bares et al. 2018), the
442 silversword alliance (Ackerly 2009, Blonder et al. 2016) and Caribbean anoles (Losos et al. 2003).
443 If this is the case, then it is because of (and not in spite of) the ecological relevance of these
444 traits that we find no phylogenetic signal. This hypothesis is further supported by recent
445 evidence that temperature tolerance and chemical deterrent production, which determine the
446 geographic range limits of species and the responses of species to herbivory, respectively, are
447 also highly labile across kelps (heat tolerance: Muth et al. 2019, chemical deterrents: Starko et
448 al. 2019b). An alternative hypothesis is that these patterns are typical of marine macroalgae
449 that to date have been poorly explored in this regard. Individual macroalgae are fixed in place
450 but lineages can span broad gradients of stress and disturbance, relying only on relatively
451 simple morphological adaptations to survive. Because traits are generally simple, novelty may
452 not be particularly important in determining the habitat niche of macroalgae, and thus strong
453 selection on quantitative, heritable traits may lead to divergence being common among close

454 relatives. This hypothesis is supported by recent work on coralline algae, showing that intense
455 grazing by urchins (analogous to environmental filtering) does not lead to phylogenetic
456 clustering (Hind et al. 2019) as predicted by assumptions of niche conservatism. Regardless of
457 the generality of our results to other marine macroalgae, we show that niche partitioning has
458 been an important driver of kelp phenotypic evolution, highlighting the importance of
459 divergent selection in the evolution of a lineage of marine foundation species. Future work
460 should investigate the extent to which these patterns extend to other marine lineages in order
461 to determine how ecological and evolutionary processes interact in the ocean.

462

463 *Conclusions*

464 We demonstrate that the distribution of phenotypic traits across the kelp phylogeny represents
465 convergent evolution of niche structure. We propose that this is a consequence of niche
466 partitioning by close relatives, with wave exposure as an important axis of niche structure.
467 More broadly, our results provide clear evidence that traits are not always phylogenetically
468 conserved and that phylogenies are not proxies for ecological differences between species, but
469 instead provide an opportunity to explore how local scale processes influence
470 macroevolutionary diversification (as argued by Gerhold et al. 2015). Phenotypic divergence
471 between close relatives may be expected in particular situations and therefore understanding
472 the circumstances and spatial scales at which phenotypic conservatism or divergence are
473 expected is the critical next step for the field of phylogenetic community ecology.

474

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Tables and Figures

Table 1. Statistical testing of phylogenetic signal for quantitative traits

Functional Traits	Phylogenetic Signal			
	Blomberg's K	P-value	Pagel's Lambda	P-value
PC1	0.538	0.610	<0.01	>0.99
PC2	0.612	0.425	<0.01	>0.99
HMF	0.353	0.693	<0.01	>0.99
SMF	0.860	0.063*	1.128	0.085*
BMA	0.718	0.190	<0.01	>0.99
DMC	0.521	0.649	<0.01	>0.99
Strength	0.584	0.457	0.108	0.737
Stiffness	0.720	0.197	0.303	0.437
Extensibility	0.285	0.962	<0.01	>0.99

*Trending towards significance (P < 0.10)

Table 2. Results of PGLS models testing for correlations between traits and average wave exposure of species (df = 1,12)

Functional Traits	t-statistic	P-value
PC1	3.9283	0.0020**
PC2	0.8316	0.4219
HMF	3.8602	0.0023**
SMF	0.9203	0.3756
BMA	1.0040	0.3351
DMC	1.5138	0.1560
Strength	0.8776	0.3974
Stiffness	-2.1020	0.0573*
Extensibility	2.2003	0.0481**

*Trending towards significance ($P < 0.10$)

**Significant relationship ($P < 0.05$)

Table 3. Evidence of incipient speciation occurring across gradients of wave exposure

Species	Environmental gradient	Description	Evidence of differentiation	References
<i>Ecklonia arborea</i>	Wave exposure	Genetic differentiation associated with changes in blade morphology and wave exposure	M13 DNA Fingerprinting	Roberson & Coyer 2004
<i>Egregia menziesii</i>	Wave exposure, latitude	Difference in blade and rachis morphology at wave exposed versus sheltered sites; evidence of differential mortality depending on morphology	No direct evidence of genetic differentiation with ITS, despite parapatric overlap of populations. Reciprocal transplants suggest phenotype is genetically determined	Blanchette et al. 2002, Henkel et al. 2007
<i>Macrocystis pyrifera</i>	Wave exposure, outer versus inner coast	Difference between wave exposed and wave sheltered morphs; phenotypic-genetic correlations among juveniles suggest local adaptation and differentiation	Genetic distance in ITS2 and microsatellites; Spatially isolated (outer coast vs. Sea of Chiloe)	Kopczak et al. 1991, Astorga et al. 2012, Camus et al. 2018
<i>Pelagophycus porra</i>	Wave exposure, substrate	Two distinct morphologies known from the Channel Islands, one on wave exposed sides of islands, the other from wave protected sides. Exposed sites are rocky, sheltered sites are mixed with soft sediment	Random amplified polymorphic DNA show isolation, ITS shows no differentiation	Miller et al. 2000
<i>Saccharina latissima</i> sensu lato	Wave exposure	A wave-exposed specialist population from Maine was described as new species, <i>Saccharina angustissima</i> , making <i>S. latissima</i> paraphyletic	Difference in <i>rbcL</i> and <i>cox3</i> (but not <i>cox1</i>) between <i>S. angustissima</i> and <i>S. latissima</i> populations from Maine; common garden revealed that blade shape is genetically determined	Augyte et al. 2018

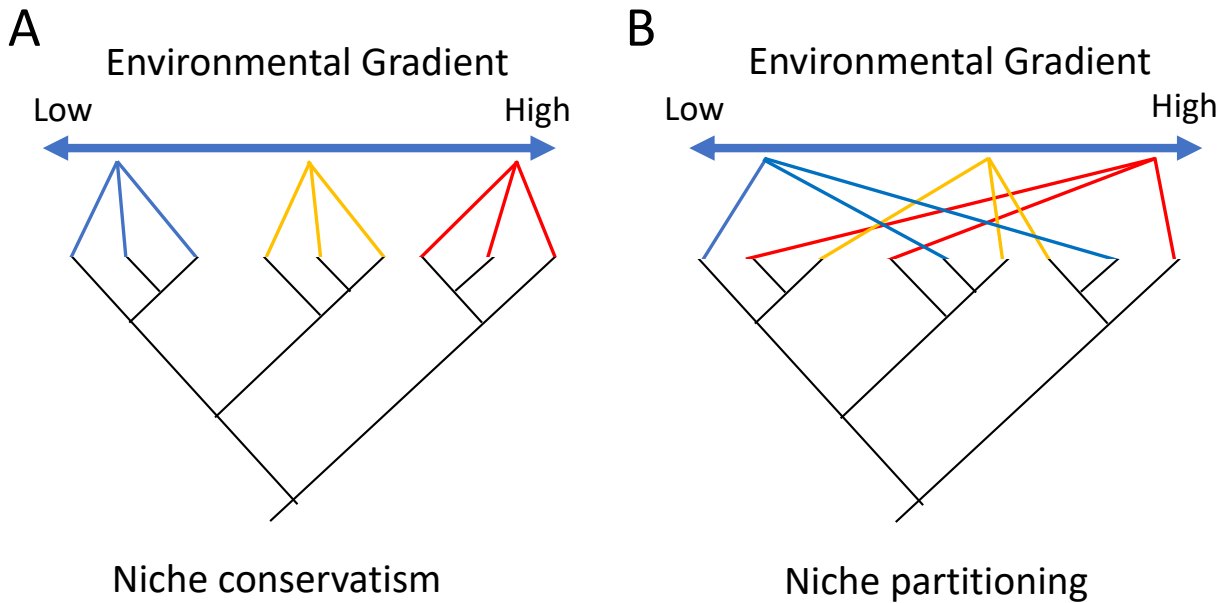


Fig 1. Theoretical extremes of how communities might be phylogenetically structured along environmental gradients under different dominant evolutionary processes. Lines are drawn from tips of the phylogeny to one of three communities situated along a theoretical disturbance gradient. Colours indicate a particular set of traits and environmental filtering drives trait clustering in both examples. If niches are conserved within subclades, then communities are expected to be clustered phylogenetically (Panel A; e.g., Webb 2000). If close relatives partition niches across the environmental gradient, then communities are expected to be phylogenetically overdispersed (Panel B; e.g., Cavender-Bares et al. 2004a).

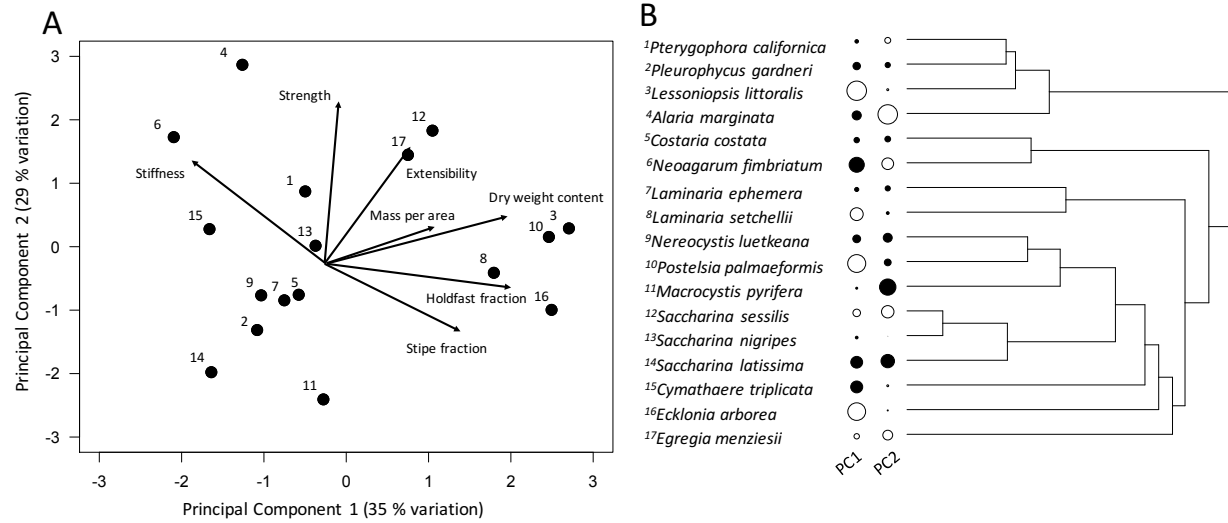


Fig 2. Phylogenetic distribution of trait axes in northeast Pacific kelp species. Panel A shows the first two principal component axes. Panel B shows PC1 and PC2 plotted on the phylogeny. The size of each bubble indicates the value of each trait axis and the colour indicates whether values are positive (white) or negative (black). There is no significant phylogenetic signal in either axis.

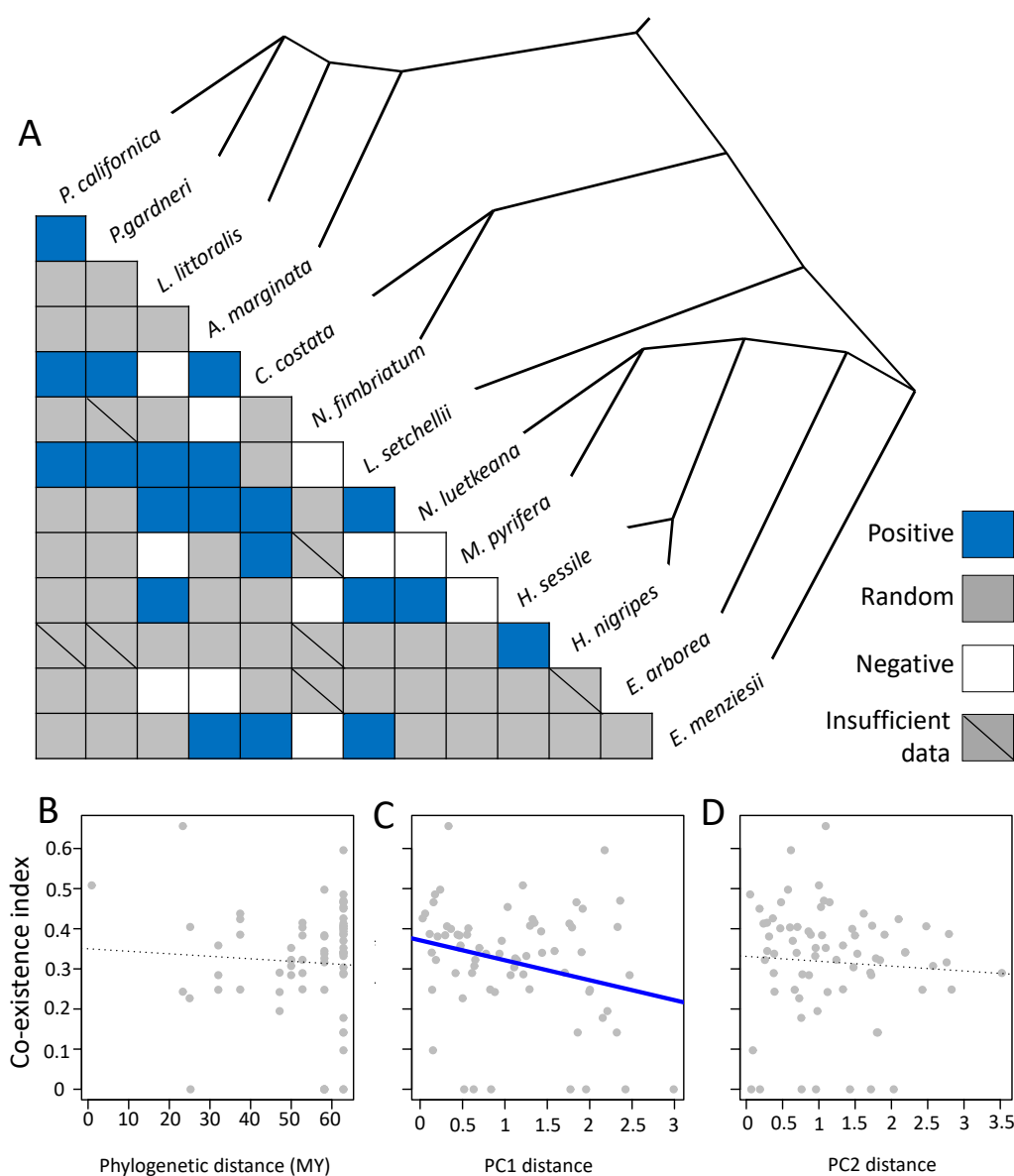


Fig 3. (A) Correlation matrix of species pairs. Colour in each cell indicates whether there was a significant positive or negative correlation between the occurrences of each pair of species, after correcting for false detection rate ($q < 0.05$). (B-D) Co-occurrence index [$\text{Log}((\text{observed co-occurrence} / \text{expected co-occurrence}) + 1)$] versus (A) phylogenetic distance between species pairs in millions of years, (B) distance in PC1 for each species pair and, (C) distance in PC2 for each species pair. Dotted lines indicate insignificant trends, while the solid blue line in panel B indicates a significant slope ($P < 0.05$).

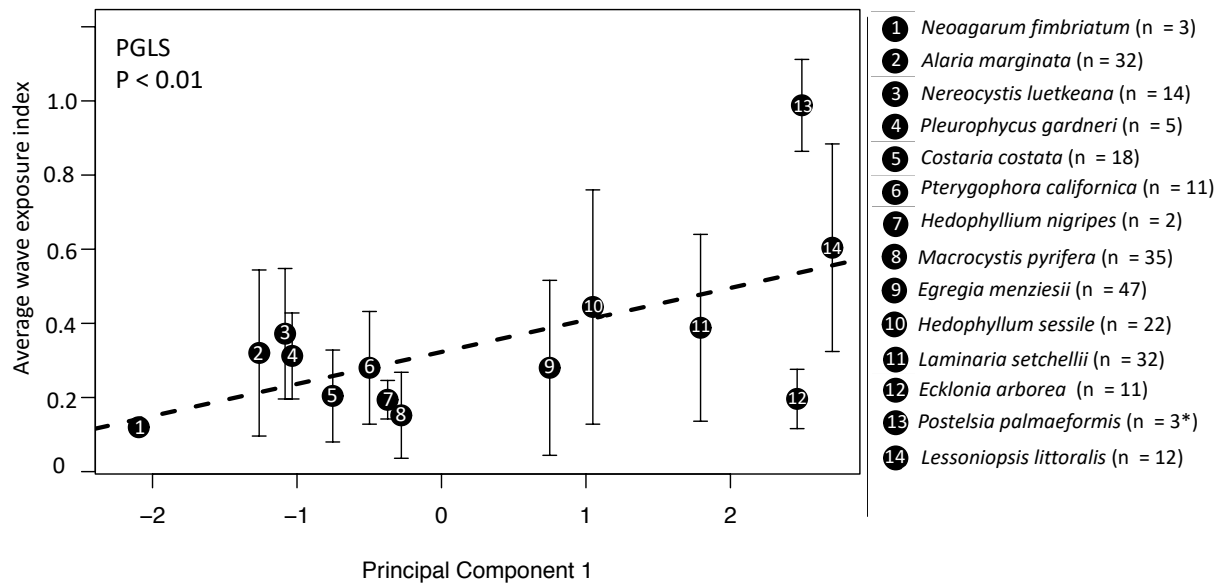


Fig 4. Relationship between wave exposure and principal component 1. Data points represent the average wave exposure that a species was found at (+/- variance) plotted against its value of PC1.

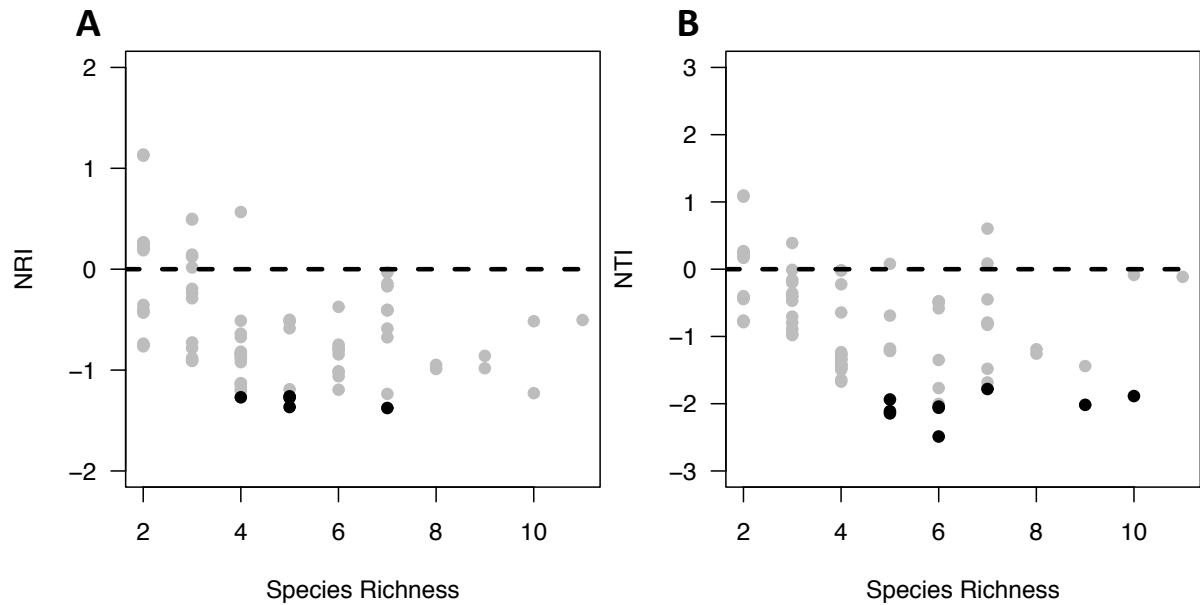


Fig 5. Metrics of phylogenetic community assembly (NRI and NTI) plotted against the species richness of communities. Data points represent individual communities and significance is indicated with dot colour. Black dots indicate that communities are significantly structured by phylogeny, while grey dots indicate no significant phylogenetic effect.

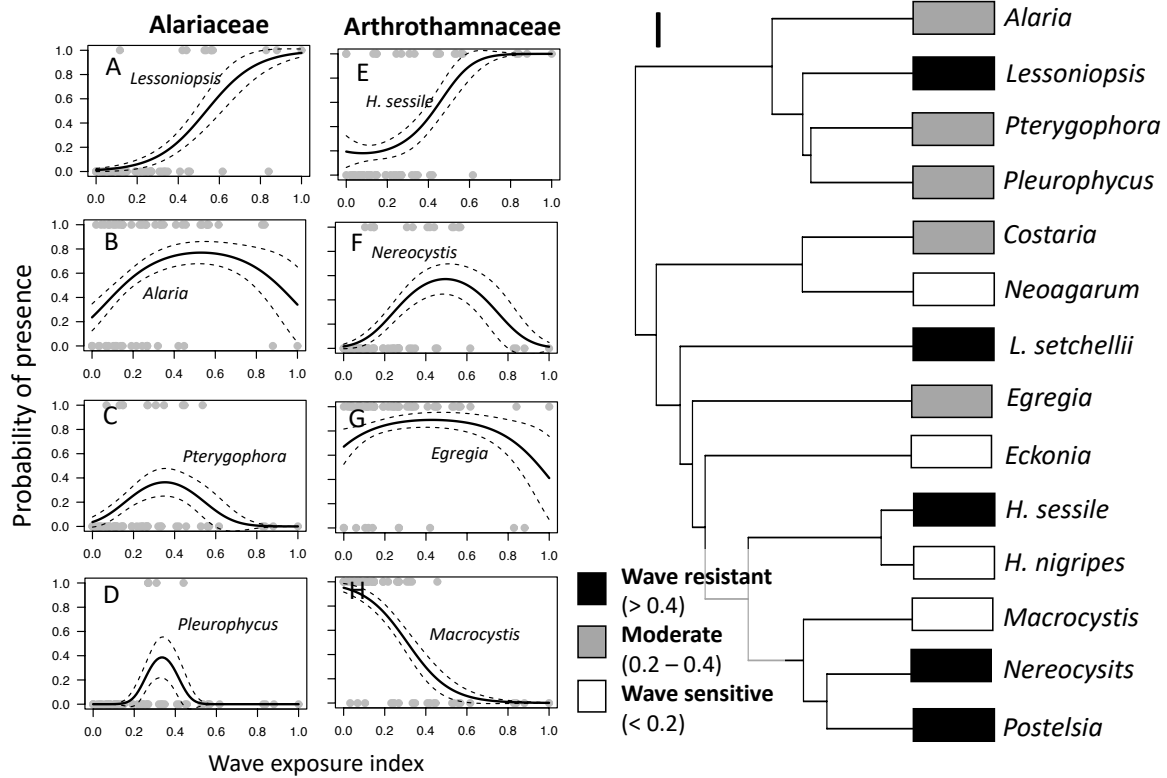


Fig 6. (A-H) Logistic polynomial regressions of species occupancy across a gradient of wave exposure. Columns represent members of two different kelp families (left = Alariaceae, right = Arthrothamnaceae). (I) Phylogeny of the kelps with average wave exposure split into three categories: wave resistant species, moderate species and wave sensitive species.

Supplemental Information for “Convergent evolution of niche structure in Northeast Pacific kelp forests”

Table S1. Locations of field sites from which trait data were collected on different species

Site Name	Location	Latitude	Longitude
Bamfield Inlet	Barkley Sound, BC	48.8345	-125.13682
Brady's Blowhole	Barkley Sound, BC	48.82329	-125.16151
Edward King Island	Barkley Sound, BC	48.82235	-125.21731
Scott's Bay	Barkley Sound, BC	48.83413	-125.14775
Prasiola Point	Barkley Sound, BC	48.81751	-125.16926
Cape Beale	Barkley Sound, BC	48.78537	-125.2165
Ogden Point	Victoria, BC	48.41399	-123.38572
Botanical Beach	Port Renfrew, BC	48.52753	-124.44877
Whytecliff Park	Vancouver, BC	49.37226	-123.29212

Table S2. Sources of trait data used in this study. σ = breaking stress, E = tensile modulus (stiffness), ϵ = extensibility, SMF = stipe mass fraction, HMF = holdfast mass fraction, DMC = dry matter content of blades, BMA = blade mass per area.

Species	Materials (σ , E & ϵ)	Biomass (SMF & HMF)	Blade Properties (DMC & LMA)
<i>Alaria marginata</i>	This study, Botanical Beach (n = 8)	Starko & Martone 2016 (n = 5)	This study, Blowhole (n = 10)
<i>Lessoniopsis littoralis</i>	This study, Brady's Blowhole (n = 5)	Starko & Martone 2016 (n = 5)	This study, Blowhole (n = 9)
<i>Pleurophyucus gardneri</i>	This study, Ogden Point (n = 5)	Starko & Martone 2016 (n = 5)	This study, Ogden Point (n = 6)
<i>Pterygophora californica</i>	This study, Botanical Beach (n = 8)	Starko & Martone 2016 (n = 5)	This study, Ogden Point (n = 2)
<i>Costaria costata</i>	This study, Whytecliff Park (n = 8)	Starko & Martone 2016 (n = 5)	This study, Scott's Bay (n = 3)
<i>Neoagarum fimbriatum</i>	This study, Whytecliff Park (n = 8)	Starko & Martone 2016 (n = 5)	This study, Bamfield Inlet (n = 4)
<i>Egregia menziesii</i>	Demes et al 2013 (n = 39)	Starko & Martone 2016 (n = 5)	This study, Scott's Bay (n = 5)
<i>Ecklonia arborea</i>	Hale 2001	This study, Scott's Bay (n = 5)	This study, Scott's Bay (n = 5)
<i>Cymathaere triplicata</i>	This study, Ogden Point (n = 7)	This study, Ogden Point (n = 5)	This study, Ogden Point (n = 5)
<i>Nereocystis luetkeana</i>	This study, Botanical Beach (n = 8)	Starko & Martone 2016 (n = 5)	This study, Scott's Bay (n = 3)
<i>Macrocystis pyrifera</i>	Hale 2001	Starko & Martone 2016 (n = 5)	This study, Scott's Bay (n = 13)
<i>Postelsia palmaeformis</i>	This study, Botanical Beach (n = 8)	Starko & Martone 2016 (n = 5)	This study, Cape Beale (n = 3)
<i>Saccharina sessilis</i>	This study, Botanical Beach (n = 8)	Starko & Martone 2016 (n = 5)	This study, Prasiola Point (n = 7)
<i>Saccharina nigripes</i>	This study, Scott's Bay (n = 6)	Starko & Martone 2016 (n = 5)	This study, Scott's Bay (n = 12)
<i>Saccharina latissima</i>	This study, Bamfield Inlet (n = 4)	Starko & Martone 2016 (n = 4)	This study, Bamfield Inlet (n = 6)
<i>Laminaria setchellii</i>	Starko et al 2018 (Blowhole) (n = 6)	Starko & Martone 2016 (n = 5)	This study, Blowhole (n = 3)
<i>Laminaria ephemera</i>	This study ((n = 4)	Starko & Martone 2016 (n = 5)	This study, Edward King (n = 4)

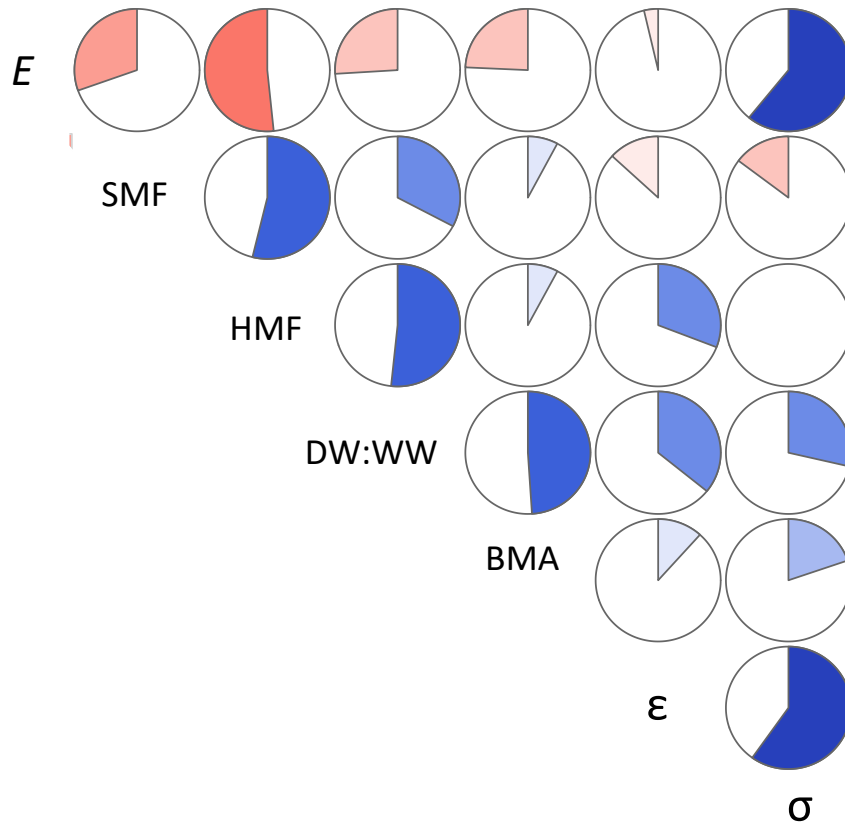


Fig S1. Correlogram of the seven functional traits examined in this study. The filled in pie slices indicate the correlation coefficient, r ($0 < r < 1$). Blue slices indicate a positive correlation between traits, while red slices indicate negative correlations.

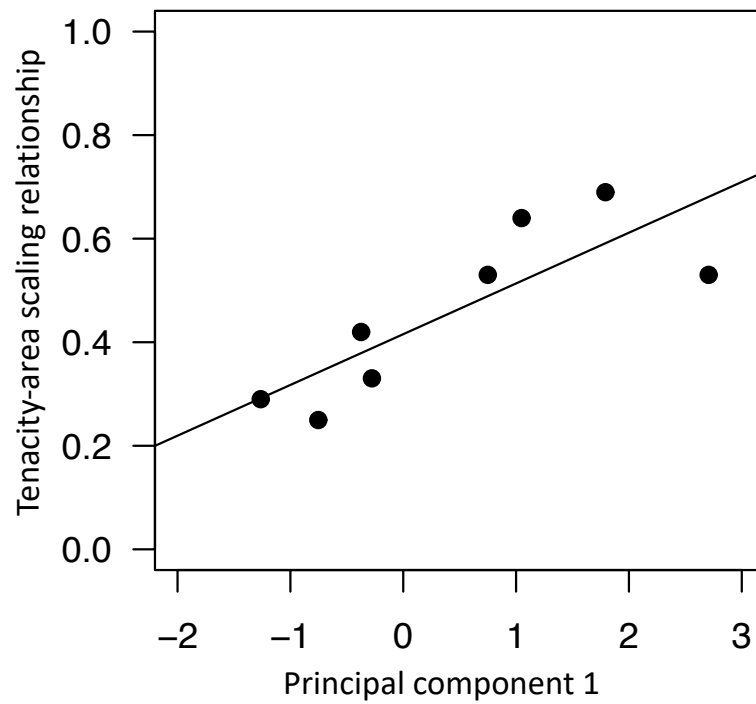


Fig S2. Correlation between principal component 1 (from this study) and tenacity-area scaling relationships (from Starko & Martone 2016).

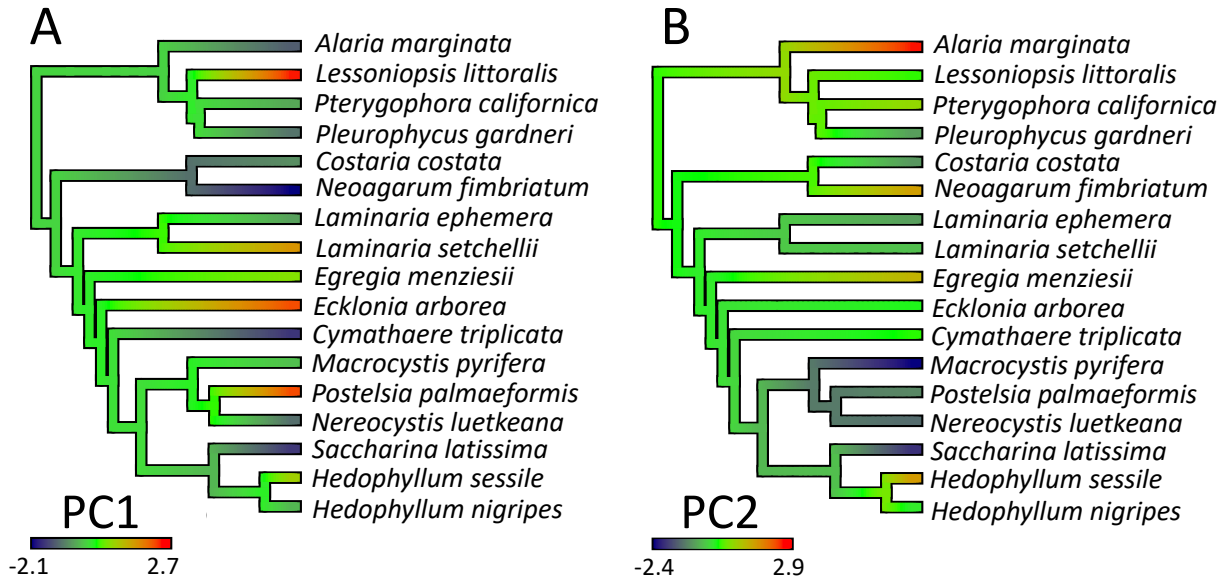


Fig S3. Ancestral state reconstruction of principal components (PC1 and PC2) computed in StableTraits and visualized using contMap. PC1 represents structural reinforcement of the whole kelp thallus, while PC2 represents a component of material properties of the blade.

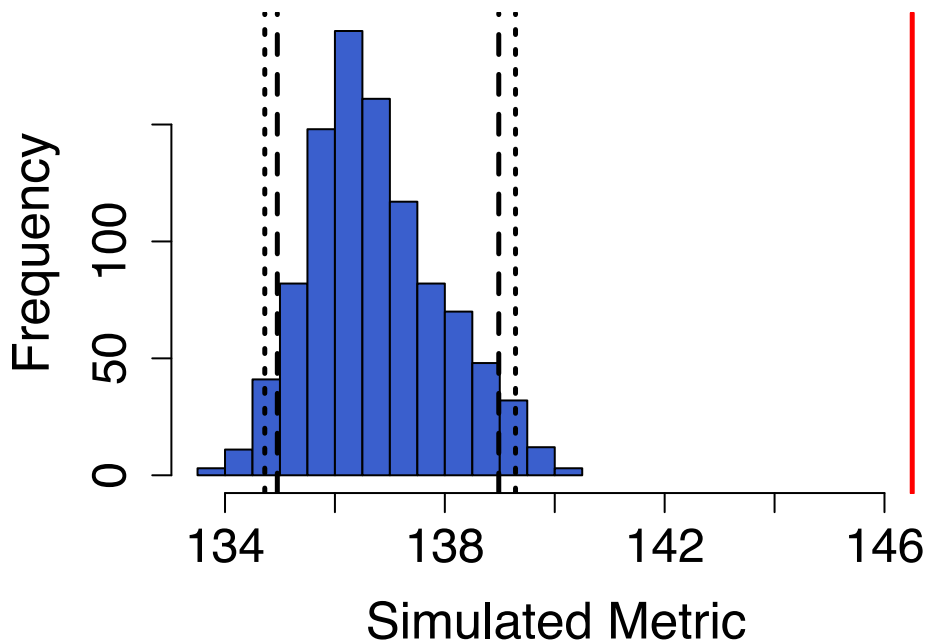


Fig S4. Observed c-score of the community matrix (red line) compared to simulated c-score values from 1000 random communities (blue histogram). Dotted lines indicate 95% confidence intervals. Analysis was conducted in the package EcoSimR.

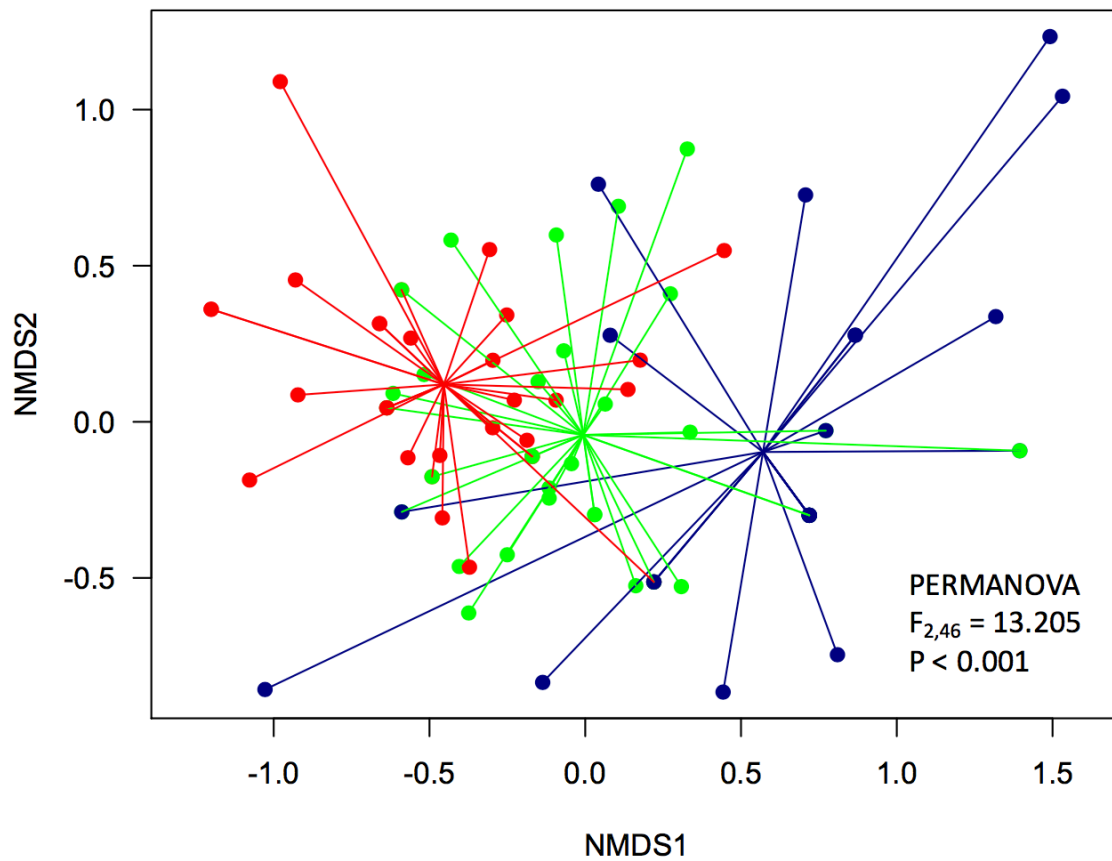


Fig S5 NMDS plot of community presence data for kelp species at 87 sites in Barkley Sound, British Columbia. Sites are coloured by wave exposure category (red = exposed, green = moderate, blue = sheltered) and lines are drawn between all sites and the centroid of its wave exposure category.