



# Functional Ecology

## 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.

## Data accessibility

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### Abstract

1. Much of the morphological and ecological diversity present on earth is believed to have arisen through the process of adaptive radiation. Yet, this is seemingly at odds with substantial evidence that niches tend to be similar among closely related species (i.e., niche conservatism). Identifying the relative importance of these opposing processes in driving niche evolution under different circumstances is therefore essential to our understanding of the interaction between ecological and evolutionary phenomena.
2. In this study, we make use of recent advances in our understanding of the phylogeny of kelps (*Laminariales*) to investigate niche evolution in one of the most ecologically significant groups of benthic habitat-forming organisms on the planet. We quantify functional traits and use community sampling data from a kelp diversity hotspot to determine which traits are responsible for the habitat ( $\beta$ ) niche of kelps and whether they are labile or conserved across the kelp phylogeny.
3. We find that combinations of functional traits have evolved convergently across kelp subclades and that these functional traits are significant predictors of community

structure. Specifically, traits associated with whole-kelp structural reinforcement and material properties were found to be significantly correlated with species distributions along a gradient of wave disturbance and thus predict the outcome of environmental filtering. However, kelp assemblages were made up of species that are more phylogenetically distinct than expected (i.e., phylogenetic overdispersion), suggesting that niche partitioning along this gradient of wave disturbance has been an important driver of divergence between close relatives.

4. These results are consistent with the hypothesis that environmental filtering associated with wave disturbance plays an essential role in determining the habitat niche of kelps across local communities and further suggest that this process can drive phenotypic divergence and niche partitioning between close relatives. We propose that parallel adaptive radiation of kelp subclades has shaped the diversity and species composition of kelp forests in the Northeast Pacific and we discuss how evidence from the literature on incipient or ongoing speciation events support this hypothesis.

## Introduction

A major challenge among ecologists is to understand how community- and ecosystem-level processes influence the macroevolution of lineages (Webb et al. 2002, Emerson and Gillespie 2008, Gerhold et al. 2015). Local environmental gradients serve as the environmental context in which both ecological and evolutionary processes occur and can thus serve as a starting point to address this challenge. Stress and/or disturbance from the environment can exceed the tolerances of some species, causing them to be excluded from certain communities (e.g. van der Valk 1981, Menge and Sutherland 1987, Webb et al. 2002, Cornwell and Ackerly 2009, Kraft et al. 2014). Thus environmental gradients can serve as “environmental filters”, resulting in

communities of species that share phenotypic traits necessary to survive in a particular environment (Reich and Oleksyn 2004, Swenson and Enquist 2007, Kraft et al. 2011, 2014, Cavalheri et al. 2015, Ulrich et al. 2017). Over evolutionary timescales, environmental gradients can influence the phenotypic evolution of community members by serving as strong sources of selective pressure (Cavender-Bares et al. 2004a, Demes et al. 2013, Gerhold et al. 2015). Thus, community assembly dynamics along environmental gradients depend strongly on the interplay of these ecological and evolutionary processes. Yet, disentangling the factors at play has been an ongoing challenge (Cavender-Bares et al. 2009).

Depending on the evolutionary history of the species pool and the evolutionary lability of underlying phenotypes, we might expect very different patterns of relatedness among the species found in local communities subject to environmental filtering. Many studies have found that closely related species tend to share similar phenotypes and ecological niches (Webb 2000, Webb et al. 2002, Silvertown et al. 2006a, Kraft et al. 2007, Wiens et al. 2010) due to processes that promote retention of ancestral characteristics (“niche conservatism”; Losos 2008, Wiens et al. 2010) or due to a lag caused by a shared ancestor and slowly evolving traits (Wiens 2008, Losos 2008). This pattern that closely related species tend to be more similar to each other than they are to distantly related species (hereafter “phylogenetic signal”) is remarkably common (Darwin 1859, Webb et al. 2002, Losos 2008, Vamosi et al. 2009, Wiens et al. 2010), leading many researchers to assume that it is true, even in the absence of any phenotypic data (see Gerhold et al. 2015 for a review). When phenotype and phylogeny are correlated, closely related species are often clustered in space because close relatives with similar traits tend to experience similar outcomes from strong environmental filtering (Fig 1a; Webb et al. 2002, Cavender-Bares et al. 2009). However, the many studies showing evidence for niche conservatism and phylogenetic signal (reviewed by Losos 2008, Wiens et al. 2010) stand in contrast to another body of work on the process of adaptive radiations wherein lineages are known to spread out across environmental gradients (hereafter “niche partitioning”) to move into open niches as they diversify (MacArthur 1958, Hector and Hooper 2002). This process would be expected to result in the opposite community pattern: communities made up of

distantly related species that share a set of convergently evolved traits (Fig 1b; Cavender-Bares et al. 2004a, Silvertown et al. 2006a, 2006b, Cavender-Bares et al. 2018). While true patterns are likely to reflect a combination of processes that both support and constrain ecological divergence, it is necessary to determine the relative importance of these seemingly opposing evolutionary forces in various lineages and circumstances to understand how and when particular processes dominate phenotypic evolution. The relative importance of these different processes can be inferred by identifying the patterns of phenotypic variation across the phylogeny of a given lineage and by determining how this phenotypic variation relates to the sorting of species into ecological communities (Lopez et al. 2016).

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

evolution of phenotypic traits across rocky shores, but ecological and evolutionary processes have yet to be linked across any major lineage that occupies this environment.

Kelps (order Laminariales) are the largest and most productive macroalgae in the ocean and dominate approximately 25% of coastlines globally (Wernberg et al. 2019). Kelps increase the productivity of cool, temperate nearshore ecosystems and their presence can substantially alter the composition of biotic communities (Steneck et al. 2002, Graham 2004, Teagle et al. 2017, Hind et al. 2019) by forming three-dimensional habitats called ‘kelp forests’ (Wernberg and Filbee-Dexter 2019). In spite of their global importance, we still have a limited understanding of the processes underlying the evolution of kelps. While recent advances in phylogenetics have dramatically improved our understanding of the relationships between species and the evolution of some key morphological features (e.g., Lane et al. 2006, Kawai et al. 2013, Jackson et al. 2017, Starko et al. 2019b), our understanding of how niche structure has evolved across this ecologically diverse clade is limited. Kelps diversified in the North Pacific following a major global cooling event (Starko et al. 2019b), possibly as a result of ecological opportunity that arose as the North Pacific became increasingly temperate over the past 30 million years (Starko et al. 2019b, Vermeij et al. 2019). While kelps are found globally, they are most phylogenetically diverse in the Northeast Pacific (Bolton 2010, Starko et al. 2019b) and it remains largely unclear what processes have allowed for the production of such high sympatric diversity in this part of the ocean.

In this study, we investigate the phylogenetic patterns of habitat ( $\beta$ ) niche structure across geographically co-existing species of kelp in the Northeast Pacific, one of the most diverse stretches of coastline for kelps and their likely center of origin (Starko et al. 2019b). We begin by presenting a dataset of quantitative traits for 17 species of kelp and testing for phylogenetic signals on these traits. We use an ancestral state reconstruction approach to determine whether particular trait combinations share a common origin or whether they have convergently arisen in different subclades. Next, we test whether environmental filtering is an important driver of community assembly and determine how this relates to the phenotypic and

phylogenetic structure of communities. We do so by making use of a community dataset that spans a gradient of wave action, an important driver of nearshore community composition and a known filter of the kelp species pool (Duggins et al. 2003, Burel et al. 2019). By teasing apart the evolution of phenotypic features from patterns of phylogenetic community structure, our results lend critical insights into the evolution of niche structure across one of the most ecologically important groups of foundations species found anywhere in the ocean and shed light on how ecological and evolutionary forces interact to shape marine communities.

## Materials & Methods

### *Quantifying phenotypic traits*

Our sampling of kelps ( $n = 17$  species) included a majority of all species found throughout the Northeast Pacific (Guiry and Guiry 2008, Bolton 2010) and approximately 80% of species found in southern British Columbia, with the unsampled species considered to be uncommon or rare (Gabrielson et al. 2018, Druehl and Elliot 1996). Seven quantitative traits were compared for all kelp species of interest, many of which are analogous to commonly measured traits in land plants; these included two traits describing whole individual biomass allocation (stipe mass fraction or SMF, holdfast mass fraction or HMF) and five traits describing mechanical and structural properties of blade tissues. SMF and HMF describe the proportion of total biomass that is stipe or holdfast material, respectively. HMF is analogous to root-shoot ratios in land plants. Organs (holdfast, blades, stipes) of individual kelps ( $n = 5$  per species) were carefully separated and dried in a 50–60°C drying oven (Starko and Martone 2016b). Blade mass per area (BMA; analogous to leaf mass per area) was defined as the amount of dry biomass per unit area of blade tissue and therefore depends both on tissue thickness and density. BMA has been inversely linked to productivity (as “thallus mass per area” by Sakanishi et al. 2017), as has the analogous trait in land plants (e.g., Reich et al. 1991, He et al. 2009). Dry matter content (DMC) was defined as the ratio of dry weight to wet weight and is therefore the inverse of total water content. Both BMA and DMC were measured by taking hole punches of standardized area (28 mm<sup>2</sup>) out of the blades and measuring the wet mass and dry mass of each hole punch. Hole punches were taken from young tissue near the base of the blade, 2–3 cm from the edge.

Mechanical properties of blade material: breaking stress ( $\sigma$ ), stiffness ( $E$ ) and extensibility ( $\varepsilon$ ), were measured using an Instron (model 5500R, Instron Corp., Canton, Massachusetts, USA), a portable tensometer (described in Martone 2006), or were taken from the literature (Tables S1-S2). With the exception of these few material properties measurements taken from the literature, trait data represent average measurements taken from adult individuals of populations in southern British Columbia (Barkley Sound, Port Renfrew, Vancouver or Victoria; see Tables S1-S2).

We used a principal components analysis to collapse trait combinations into fewer axes of correlated traits. Then, to determine whether any major PCA axis correlates with the ability of kelps to resist dislodgement, we tested for correlations, using PGLS models, between PCA axes and tenacity-area scaling relationships quantified previously (Starko and Martone 2016a) for the 8 species included in that study. Tenacity-area scaling relationships describe the slope of the relationship between maximum dislodgement force and thallus size and are therefore an effective measure of wave tolerance.

#### *Phylogenetic reconstruction*

The phylogeny of kelps, has been studied previously in considerable detail (Lane et al. 2006, Jackson et al. 2017, Starko et al. 2019b). In this study, the time-calibrated phylogeny inferred by Starko et al. (2019b) was used to represent phylogenetic divergence in millions of years for the 17 co-occurring Northeast Pacific kelp species of interest. This time-calibrated phylogenomic analysis is the most well supported and comprehensive to date and included all 17 species except *Laminaria setchellii*, which was incorporated into the analysis by substituting it for *L. digitata*, which is not found in the Northeast Pacific but was included in the phylogenomic analysis. This substitution relies on the assumption that *L. setchellii* has an equivalent divergence time from *Laminaria ephemera* as *L. digitata*, which is well supported by previous work on intrageneric relationships between *Laminaria* species, showing less than 1 million years difference in divergence time between *L. ephemera* and *L. setchellii* vs. *L. digitata* (Rothman et al. 2017). Phylogenetic signal of traits was measured using Blomberg's K (Blomberg

et al. 2003) and Pagel's  $\lambda$  (Pagel 1999). We also tested for correlations between trait distance and phylogenetic distance using Mantel tests.

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

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

#### *Community dataset*

To determine how trait or phylogenetic differences influence community assembly, we used a community dataset of intertidal kelp distributions in Barkley Sound, British Columbia that was published in a Parks Canada technical report (Druehl and Elliot 1996). Barkley Sound is located on southern Vancouver Island and offers a broad gradient of wave exposure that is spatially dispersed across the region (Starko et al. 2019a). Data from sites sampled in 1995 ( $n = 87$  sites), the most extensive year of this survey, were combined into a data matrix that included all of the species examined in the trait analysis except two (*Laminaria ephemera* and *Cymathae triplicata*). While a coarse categorical abundance measurement is given in their report, only presence and absence data were used. Although resurveys were conducted at some of these sites, recent work demonstrated that kelp forests have been lost from several of these sites, likely as a result of the 2014-2016 heatwave (Starko et al. 2019a). Thus, only historical data were used to reconstruct niche structure before large-scale declines in Barkley Sound kelp communities.

At a subset of sites ( $n = 55$ ) that could be located by photographs in the 1996 report, the upper limit of barnacles was measured in the summers of 2018-2019 and these values were used as a continuous proxy for wave exposure. The upper limit of barnacles is an effective proxy of wave run-up and is known to increase in elevation at more wave exposed sites (Harley and Helmuth

2003, Neufeld et al. 2017). Although the absolute height of barnacles at each site may differ between 1995 and 2018-2019 due to interannual variation in weather (Harley 2003) or the oscillation in lunar declination (Burnaford et al. 2014), the relative wave exposure of sites likely remains unchanged over time because offshore swell can only enter Barkley Sound from one direction (the opening faces southwest). The upper limit of barnacles was measured by using a stadia rod and sight level, along with tide predictions from Bamfield Inlet (N 48.83596°, W -125.13614°) Effingham Island (N 48.87669°, W -125.312102°), or Mutine Point (N 48.94308°, W -125.03244°), depending on proximity. A categorical, qualitative measure of wave exposure was also provided by Druehl & Elliot (1996) and based on criteria from Topinka et al. (1981). This metric was used for analysis of all 87 sites. Past studies in Barkley Sound have found concordance between these different metrics as well as with additional cartographical measures of wave exposure (Neufeld et al. 2017, Starko et al. 2019a). Barnacle upper limit was significantly different between these wave exposure categories (ANOVA:  $F_{2,52} = 19.5815$ ,  $P < 0.0001$ ) with significant differences between all means (Tukey HSD  $< 0.05$ ), further demonstrating agreement between these two measures of wave exposure. Using the range of barnacle upper elevation data (that spanned approximately 3 to 5.5 m above Mean Lower Low Water Large Tide - MLLWLT), we created a “wave exposure index” by subtracting 3 meters from each measurement and then dividing by 2.5 (the approximate range of barnacle upper limits), resulting in an index that varied from 0 to 1.

#### *Quantifying species co-occurrence*

To test for correlations between taxa, we compared our observed community matrix to simulations and null models. First, to determine whether non-neutral processes were required to explain the distribution of species across communities, we tested whether our community matrix was significantly different from randomly shuffled communities. We did so by comparing our observed checkerboard score (i.e., c-score; Stone and Roberts 1990), a measure of association between species pairs, to randomly simulated communities using EcoSim (Gotelli and Entsminger 2001). Next, in order to test for significant associations between individual species, observed co-occurrence probabilities were calculated for each pair of species and

compared to null expectations of species co-occurrences that were generated using randomizations that considered only the number of sites at which each species was found. In cases where species were expected to co-occur at less than one site because one or both species were found at low frequencies, these species pairs were excluded due to insufficient data. Deviations from expectations were measured using a log response ratio of observed vs. expected outcomes, hereafter “co-occurrence index”. Calculated as:

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

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

#### *Phylogenetic community structure*

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

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

Where  $X_{net}$  is the average phylogenetic distance between members of a community, and  $X_{null}$  and  $SD_{null}$  represent the mean and standard deviation, respectively, of simulated random draws from the species pool. NTI is similar to NRI but considers the average distance between each

species and its closest relative. Specifically,  $X_{\text{net}}$  from equation 2 is replaced with  $X_{\text{min}}$  which is defined as the average distance between each species and its closest relative, such that:

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

For NTI,  $X_{\text{null}}$  and  $SD_{\text{null}}$  represent the mean  $X_{\text{min}}$  and associated standard deviation from random draws of the species pool, similar to calculations of NRI (Webb 2000). As a consequence of differences in the underlying metric of interest ( $X_{\text{net}}$  versus  $X_{\text{min}}$ ), NRI is more sensitive to phylogenetic clustering deeper into the phylogeny, while NTI is more sensitive to clustering near the tips of the phylogeny. We calculated these metrics using 10,000 random simulations using a null model that constrains site-level richness but determines species identity from random draws of the regional species pool. This model is appropriate because richness differs across the wave exposure gradient (Ding et al. 2012). Significance of phylogenetic community structure was evaluated in two ways. First, at a community level, sites (i.e. individual communities) were considered to be significantly structured by phylogeny if NRI or NTI values ranked among the 500 most extreme values (97.5th or 2.5th percentiles) of the 10,000 randomly generated pseudo-communities. A second approach was used to determine if, across the whole dataset, there were significant trends in phylogenetic community structure. NRI and NTI are both expected to be approximately normally distributed with a mean of zero, therefore in order to determine whether the mean of the distribution of kelp communities differed from this null expectation, t-tests were also performed, treating sites as replicates (as in Cooper et al. 2008).

#### *Wave exposure and community assembly*

We measured the relationship between species presence and wave exposure using the subset of sites ( $n = 57$ ) for which continuous wave exposure (barnacle upper limit) had been measured. This subset did not include any sites with *S. latissima*, which was therefore excluded from these analyses. It also included only one observation of *P. palmaeformis* at one of the most wave-exposed sites in our dataset. This species is well known to occur only on the most wave-exposed shores (Paine 1988, Nielsen et al. 2006) and so this site was deemed representative of the niche of *P. palmaeformis*. However, to better improve our estimate of average wave

exposure for this species, we measured the upper limit of barnacles at two sites on the nearby outer coast (Cape Beale) that consistently have *Postelsia palmaeformis* populations. All three sites were very high exposure (upper limit of barnacles: 5.2 - 5.8 m above MLLWLT). To assess the relationship between traits and species' habitat use, average wave exposure was measured for each species from all sites in which that species was present. A phylogenetic least squares (PGLS) regression was then used to test for an effect of principal component axes and all seven quantitative traits on average wave exposure. In order to further visualize differences in species habitat use, the probability of species presence was plotted against wave exposure (i.e., the upper limit of barnacles) as modeled using polynomial, binomial generalized linear models. This modelling approach allows for an optimal wave exposure rather than forcing saturation. This was done separately for members of the two subclades with the most species included here, the families Arthrothamnaceae and Alariaceae. We then tested for a phylogenetic signal on habitat niche by measuring Blomberg's K and Pagel's  $\lambda$  for average wave exposure (mean wave exposure index of all sites at which a species was found). Finally, to determine whether sites of different wave exposure also have different kelp communities, we conducted a PERMANOVA with the wave exposure categories described above as a predictor variable.

#### *Statistical software*

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

## Results

### *Phenotypic traits are convergent across taxa*

Principal component analysis resulted in seven component axes with the first two explaining 63.9% of the variation in trait values (Fig 2A). Principal component 1 (PC1) correlated with structural characteristics of the whole kelp (HMF and SMF), as well as the blade (DMC, BMA), which were themselves all positively correlated (Fig S1). Principal component 2 explained mainly the properties of materials ( $\sigma$ ,  $E$  and  $\epsilon$ ). These two components explained 35.3% and

28.6% of the total variation in functional traits respectively. Principal component 1 was correlated with tenacity-area scaling relationships (Fig S2; PGLS model:  $F = 11.92$ ,  $df = 1$  and  $6$ ,  $P = 0.0136$ ,  $R^2 = 0.665$ ) suggesting a link between the traits underlying PC1 and tolerance of fluid force. There was no significant phylogenetic signal on any of the traits investigated in this study, including principal components (Table 1, Fig 2B), indicating no correspondence between the phylogeny and trait variation. In fact, of all the traits that we assessed, only SMF had a possible but not significant phylogenetic signal (Blomberg K: 0.860,  $P = 0.063$ ; Pagel's  $\lambda = 1.128$ ,  $P = 0.085$ ). Some pairs of closely related species were somewhat similar in at least some traits (e.g. *Pleurophycus gardneri* and *Pterygophora californica*), but for the most part, closely related species differed as much or more than distantly related ones (Fig 2B). This observation was confirmed by the lack of a significant relationship between PC1 and PC2 trait distances and phylogenetic distance (PC1 Mantel test:  $Z = 6450.835$ ,  $P = 0.589$ ; PC2 Mantel test:  $Z = 6449.193$ ,  $P = 0.691$ ). Ancestral state reconstructions indicate that trait combinations have evolved repeatedly across the kelps with clear patterns of phenotypic convergence (Fig S3).

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

The community matrix was significantly non-random with a c-score that exceeded the range of values from random simulations (Fig S4). There were also several significant associations between individual species (Fig 3). Positive and negative species associations occurred between both closely and distantly related species pairs. For example, closely related species *Macrocystis pyrifera* and *Nereocystis luetkeana* were negatively associated with each other, while sister taxa, *Pleurophycus gardneri* and *Pterygophora californica*, were positively associated (Fig. 3). Moreover, *Egregia*, the most phylogenetically distinct genus from the family Arthrothamnaceae, was positively associated with some members of three other families (Alariaceae, Agaraceae, Laminariaceae) and negatively associated with a member of one (Agaraceae).

Despite clear evidence of non-random community assembly, there was no effect of phylogenetic distance on the probability of co-occurrence between species. The only significant

predictor of pairwise non-random co-occurrence (measured as “co-occurrence index”) was distance in PC1 between species pairs (Linear regression:  $F = 5.075$ ,  $df = 69$  and 1,  $P = 0.02746$ ; Fig 3C). Phylogenetic distance (Linear regression:  $F = 0.2392$ ,  $df = 69$  and 1,  $P = 0.6263$ ; Fig 3B) and PC2 distances (Linear regression:  $F = 0.3037$ ,  $df = 69$ ,  $P = 0.5833$ ; Fig 3D) did not significantly correlate with the pairwise co-occurrence of species.

There was a significant relationship between average wave exposure of a species and its value of PC1 (Linear model:  $F = 6.809$ ,  $df = 1$  and 12,  $P = 0.0228$ ; PGLS model:  $t = 3.9823$ ,  $df = 14$  and 2,  $P = 0.002$ ; Fig 4), but not PC2 (Linear model:  $F = 0.1225$ ,  $df = 1$  and 12,  $P = 0.732$ ; PGLS model:  $t = 0.8316$ ,  $df = 14$  and 2,  $P = 0.4219$ ), such that structurally reinforced species tended to be found at more wave exposed sites. This relationship was significant even when removing *Postelsia palmaeformis*, the strongest and most wave tolerant species, from the analysis (Linear model:  $F = 5.161$ ,  $df = 1$  and 11,  $P = 0.0441$ ; PGLS model:  $t = 3.0250$ ,  $df = 13$  and 2,  $P = 0.0116$ ). The only traits that significantly correlated with the average wave exposure of a species on their own were HMF and  $\varepsilon$  (Table 2). There was a possible, but not significant negative correlation between blade stiffness and average wave exposure.

#### *Kelp species are phylogenetically overdispersed across local communities*

Use of phylogenetic indices demonstrate that no communities examined were significantly phylogenetically clustered and most communities trended towards phylogenetic overdispersion relative to simulations (Fig 5). Although only a few sites were significantly overdispersed (NRI:  $n = 3$ , NTI = 7; Fig 5), average phylogenetic NRI and NTI values were significantly different from zero (NRI: t-test:  $t = 3.917$ ,  $df = 86$ ,  $P = 0.00018$ ; NTI: t-test:  $t = 9.4708$ ,  $df = 86$ ,  $P < 0.0001$ ). The few communities that trended towards phylogenetic clustering were composed of only a small number of species ( $n = 2$  or 3; Fig 5). Yet, comparing across all communities with equally low diversity, there was no clear directional effect of phylogeny on community assembly (NTI and NRI approximate zero).

Binomial models of species presence and absence along a continuous wave exposure axis further demonstrate how species in each subclade have convergently adapted to different regimes of wave exposure (Fig. 6). Individual species clearly varied in distribution across the gradient of wave exposure and closely related species (e.g. *Nereocystis luetkeana* and *Macrocystis pyrifera*) tended to specialize in different wave exposure regimes. The clear exception here is the species pair *Pterygophora californica* and *Pleurophycus gardneri* that are sisters and had nearly identical distributions across the wave exposure gradient but differed only in niche width (sensu MacArthur 1968, Slobodkichoff and Schulz 1980; Fig 6). There was a significant effect of wave exposure category on community composition (PERMANOVA:  $F = 13.205$ ,  $P < 0.001$ ; Fig S5), indicating that differences in species distributions across the wave exposure gradient scale up to community level differences in species composition at wave exposed versus wave sheltered sites. However, there was no significant phylogenetic signal on the average wave exposure index of species (Blomberg's  $K = 0.483$ ,  $P = 0.749$ ; Pagel's  $\lambda < 0.01$ ,  $P > 0.99$ ).

## Discussion

We tested a series of hypotheses relating to the relationship between phylogeny, phenotype and the environmental distributions of kelp species (Table 3). Collectively, our results provide evidence that the traits underlying the habitat niches of kelps are highly labile and suggest that this has resulted in convergent patterns of habitat use across species. Neither principal component, nor any of the individual traits that make them up, were found to be phylogenetically conserved across species (Table 1). Yet, PC1, which correlated with structural reinforcement traits, was a predictor of both pairwise species co-occurrences (Fig 3) and the position of individual species along the gradient of wave exposure (Fig 4), suggesting a role of structural traits in determining the habitat niche of species. We propose that the relationship between wave action and structural reinforcement is causal on the basis that many field studies and biomechanical models have demonstrated the role of rapid water motion as a strong selective pressure for increased tolerance to physical forces (Johnson and Koehl 1994, Duggins et al. 2003, Martone et al. 2012, Demes et al. 2013, Starko et al. 2014). Moreover, structural

reinforcement likely comes at a metabolic cost since high values of BMA can lead to reduced productivity (Sakanishi et al. 2017) and holdfasts act as carbon sinks, rather than sources, despite light pigmentation (Arnold and Manley 1985). Thus, the PC1 trait axis may represent a trade-off between tolerance to waves and maximum productivity that our data suggest determines the distribution of species across local communities.

Across communities, species co-occurrence patterns reflect the influence of environmental filtering on community composition but result in overdispersion, rather than clustering, of closely related species. Phylogenetic community indices (NRI and NTI) reveal that communities are made up of more distantly related species than predicted (Fig 5), indicative of phylogenetic overdispersion across kelp communities. Phylogenetic overdispersion of communities is commonly interpreted as phenotypic overdispersion and treated as evidence for competitive exclusion (e.g. Webb 2000, Webb et al. 2002, Cooper et al. 2008). This inference is made under the assumption that species with similar niches will be unable to co-exist if competition is an important driver of community assembly. However, in our study, species that were commonly found together also tended to be those with correlated niches, indicative of environmental filtering, not competition. For example, *Lessoniopsis littoralis* and *Hedophyllum sessile*, two distantly related species that have similar values of PC1 and specialize in wave-swept environments (Fig 6), were positively correlated across the community matrix (Fig 3). Conversely, species that specialize in different wave exposure regimes tended to be negatively correlated. For example, *Neoagarum fimbriatum*, a specialist in wave sheltered areas, and *Laminaria setchellii*, a wave exposed specialist (Fig 6), co-occurred significantly less often than predicted (Fig 3). Thus, our results suggest that kelp communities are filtered strongly but the phenotypes that allow species to pass this filter have evolved convergently in different subclades, resulting in communities of species that have similar phenotypes but come from different clades.

Past work has suggested that traits associated with habitat niche are conserved while  $\alpha$  niche traits, which result in co-existence of taxa, are more labile (Silvertown et al. 2006a, 2006b; but

see Cavender-Bares et al. 2004a). While this framework may hold in many groups of embryophytes, we show that this is not the case for kelps. Habitat niche traits in the kelps are labile and tend to be largely dissimilar among close relatives (Fig 6). While the basis of convergence in traits can be challenging to interpret and may differ across taxa, we propose that partitioning of habitats is an important means by which kelps achieve reproductive isolation and undergo speciation. Partitioning can occur either through character displacement, where competition between close relatives drives the weaker competitor to adapt to new environments (Brown and Wilson 1956), or through the splitting of a generalist niche into multiple specialized niches (Funk 1998). There is substantial evidence that simultaneous phenotypic and genetic divergence across the kelps is common and may be an important driver of diversification. In Table 4, we describe five known instances where partitioning along a gradient of wave exposure has resulted in genetic differentiation of populations or incipient speciation. The prevalence of this pattern in ongoing or incipient speciation events, lends support to our hypothesis that niche partitioning along wave exposure gradients has been a repeated driver of speciation in geographical sympatry. Taken together, data suggest that processes observed in past studies near the tips of the phylogeny scale up to explain patterns of niche evolution across the broader kelp phylogeny. Close relatives may specialize in different positions along environmental gradients, leading to parallel adaptive radiation across subclades, possibly helping to maintain coexistence of species across broad geographic scales (MacArthur 1958, Cavender-Bares et al. 2004b, 2004a, Losos 2008, Cavender-Bares et al. 2018). While many kelp species can alter their traits depending on habitat (reviewed by Koehl et al. 2008), genetic differentiation or speciation is likely to facilitate the evolution of more extreme trait differences than would be otherwise possible through plasticity (Gerard 1988, Sato et al. 2017, King et al. 2018, Augyte et al. 2018). We further hypothesize that  $\alpha$  niche traits may be more conserved than  $\beta$  niche traits across the kelps, leading to increased co-existence between distant relatives. While it is unclear exactly what traits would promote co-existence across kelp species, morphological features such as the presence of buoyant floats or long, rigid stipes may be somewhat more conserved than the traits examined here, despite multiple origins (Starko et al. 2019b). Differences in stature within the water column have been linked to competitive

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hierarchies in kelps (Edwards and Connell 2015) and may thus make up a component of species α niches.

Multiple hypotheses may explain why we observed evidence for niche partitioning but not for niche conservatism or phylogenetic signal. Kelps diversified only recently and following cooling of the global climate (Starko et al. 2019b). Kelps are much larger and more competitive than other macroalgal species (Edwards and Connell 2015) but rely on cool waters and an abundance of nutrients. Cooling of the oceans may have created an ecological opportunity for kelps, allowing them to diversify across and dominate rocky shores throughout the Northeast Pacific (Bolton 2010, Starko et al. 2019b, Vermeij et al. 2019). This ecological opportunity may have promoted selection for niche partitioning as has been documented previously in oak trees (Cavender-Bares et al. 2004a, Cavender-Bares et al. 2018), the silversword alliance (Ackerly 2009, Blonder et al. 2016) and Caribbean anoles (Losos et al. 2003). Thus, the tendency of a lineage towards niche partitioning versus niche conservatism may depend on the availability of unused ecological niche space (Losos 2008). If this is the case, then it is because of (and not in spite of) the ecological relevance of these traits that we find no phylogenetic signal. This hypothesis is further supported by recent evidence that temperature tolerance and chemical deterrent production, which determine the geographic range limits of species and the responses of species to herbivory, respectively, are also highly labile across kelps (heat tolerance: Muth et al. 2019, chemical deterrents: Starko et al. 2019b).

Another, non-mutually exclusive hypothesis is that these patterns are typical of marine macroalgae that to date have been poorly explored in this regard. Individual macroalgae are fixed in place but lineages can span broad gradients of stress and disturbance, relying only on relatively simple morphological adaptations to survive. Because traits are generally simple, the evolution of novel features may not be particularly important in determining the habitat niche of macroalgae, and thus strong selection on quantitative, heritable traits may lead to divergence being common among close relatives. This hypothesis is supported by recent work on coralline algae, showing that intense grazing by urchins (analogous to environmental

filtering) does not lead to phylogenetic clustering (Hind et al. 2019) as predicted by assumptions of niche conservatism. Regardless of the generality of our results to other marine macroalgae, we show that niche partitioning has been an important driver of kelp phenotypic evolution, highlighting the importance of divergent selection in the evolution of a lineage of marine foundation species. Future work should investigate the extent to which these patterns extend to other marine lineages in order to determine how ecological and evolutionary processes interact in the ocean.

A general limitation of our study is that we were unable to address intraspecific variation in trait values. Kelps are known to alter their morphologies in response to wave exposure (Koehl et al. 2008, Charrier et al. 2012) and thus our approach of using a single value for each species has clear caveats. The most common forms of plasticity in kelps involve blade width, ruffle and thickness (Koehl et al. 2008). Although we did not directly assess any of these traits, changes in thickness would influence BMA and possibly DMC. While the extent of intraspecific variation in trait values has never been rigorously compared to interspecific trait variation across kelps, we suspect that interspecific variation is greater than variation within any one species. For example, sister species *Nereocystis luetkeana* and *Postelsia palmaeformis* differed in holdfast investment (HMF) by over an order of magnitude and a similar pattern was observed in the Alariaceae between *Alaria marginata* and *Lessoniopsis littoralis*. This magnitude of variation has not been observed in any one species, even when assessed across habitats differing in wave exposure (Johnson and Koehl 1994, Duggins et al. 2003, Fowler-Walker et al. 2006). Moreover, common garden experiments on *Saccharina* spp. have shown greater phenotypic variation between than within species or genotypes (Gerard 1988, Sato et al. 2017, Augyte et al. 2017). Nonetheless, similar species are likely to overlap in trait values once considering populations at sites that vary in wave exposure (Duggins et al. 2003), resulting in trait overlap between some species pairs but not others. This pattern was reported recently in six non-laminarialean brown algae (Stelling-Wood et al. 2020). We speculate that quantifying phenotypic traits separately for populations at each site would result in even greater concordance between traits and environment than observed in this study, since species tend to increase structural

reinforcement when exposed to high levels of water motion (Johnson and Koehl 1994, Duggins et al. 2003, Koehl et al. 2008).

### Conclusions

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

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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 ( $P < 0.10$ )

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

<b>Functional Traits</b>	<b>t-statistic</b>	<b>P-value</b>
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 ( $P < 0.05$ )

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Table 3. Summary of hypotheses and conclusions from this study

Theme	Hypothesis	Method	Result	Conclusions
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<b>Trait evolution</b>	Traits are phylogenetically correlated	Blomberg's K and Pagel's $\lambda$ on traits; Mantel test (Fig 2, Table 1)	Not significant for any trait investigated	Hypothesis rejected
	Traits have evolved convergently	Ancestral state reconstruction (Fig S3)	Multiple origins of trait combinations	<b>Hypothesis supported</b>
<b>Species co-occurrence</b>	Communities are a random subset of the regional pool	Checkerboard simulations (Fig S4)	Community matrix is significantly more structured than expected by chance	Hypothesis rejected
	Closely related species tend to co-occur	Co-occurrence analysis (Fig 3)	No correlation between co-occurrence and phylogenetic difference	Hypothesis rejected
	Species with similar traits tend to co-occur	Co-occurrence analysis (Fig 3)	Significant correlation between co-occurrence and PC1 difference	<b>Hypothesis supported</b>
	Communities are phylogenetically structured	Net relatedness index, Nearest taxon index (Fig 5)	Communities weakly phylogenetically overdispersed on average	<b>Hypothesis supported</b>
<b>Habitat niche</b>	Habitat niches are correlated with phylogeny	Blomberg's K and Pagel's $\lambda$ on average wave exposure (Fig 6)	Not significant	Hypothesis rejected
	Habitat niches are correlated with traits	PGLS models of average trait values versus average wave exposure (Fig 4)	Significant for PC1 and some individual traits	<b>Hypothesis supported</b>

Table 4. Examples of genetic divergence between populations or incipient species 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 rachus 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	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 rbcL and cox3 (but not cox1) 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

## Figure captions

**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). True community patterns are likely to fall between these two theoretical extremes.

**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 (see Table 1).

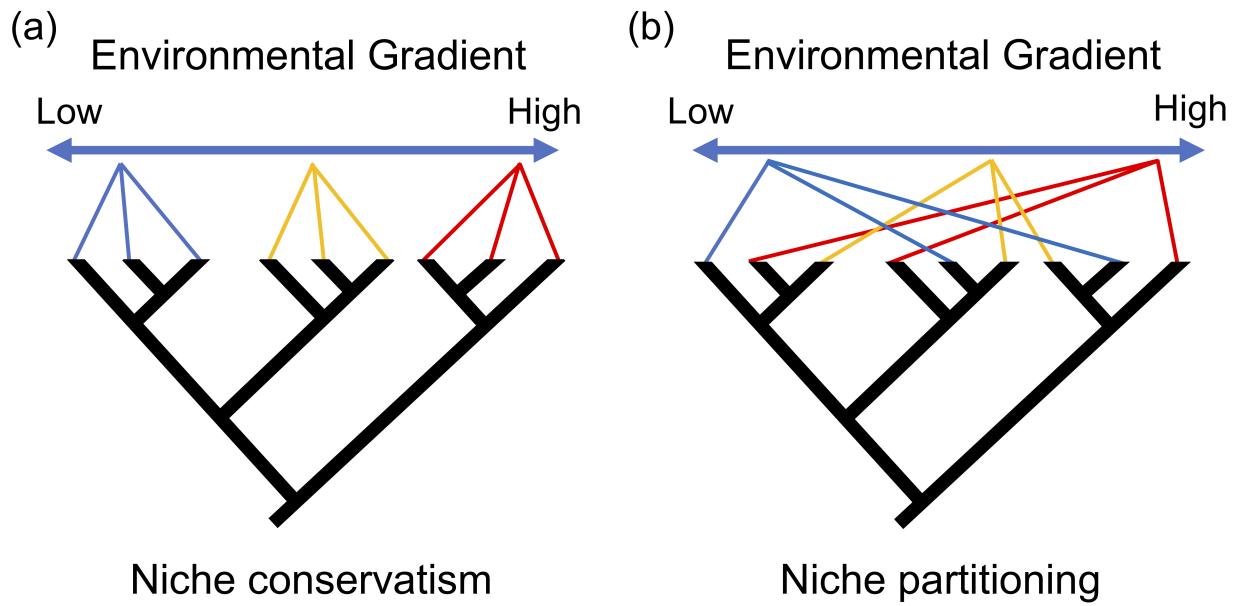
**Fig 3. Predictors of kelp species co-occurrence.** (a) Correlation matrix of species pairs. Colour in each cell indicates whether there was a significant positive or negative correlation between the occurrences of each pair of species, after correcting for false detection rate ( $q < 0.05$ ). (b-d) Co-occurrence index [ $\text{Log} ((\text{observed co-occurrence} / \text{expected co-occurrence}) + 1)$ ] versus (b) phylogenetic distance between species pairs in millions of years, (c) distance in PC1 for each species pair and, (d) 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 structural reinforcement trait axis.** Data points represent the average wave exposure that a species was found at (+/- variance) plotted against its value of Principal Component 1, which represents structural reinforcement traits. Numbers indicate the identity of a species and the regression line represents a PGLS model.

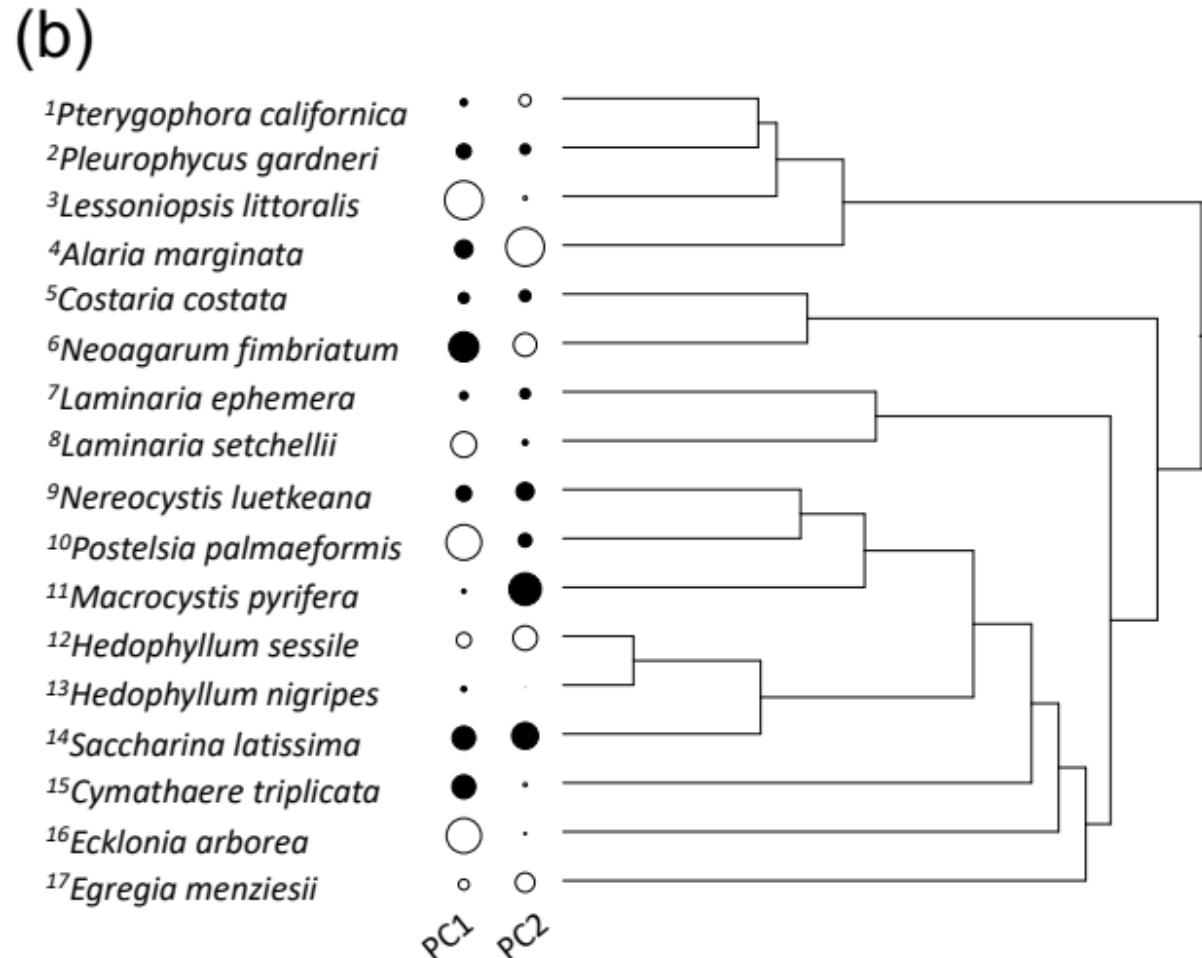
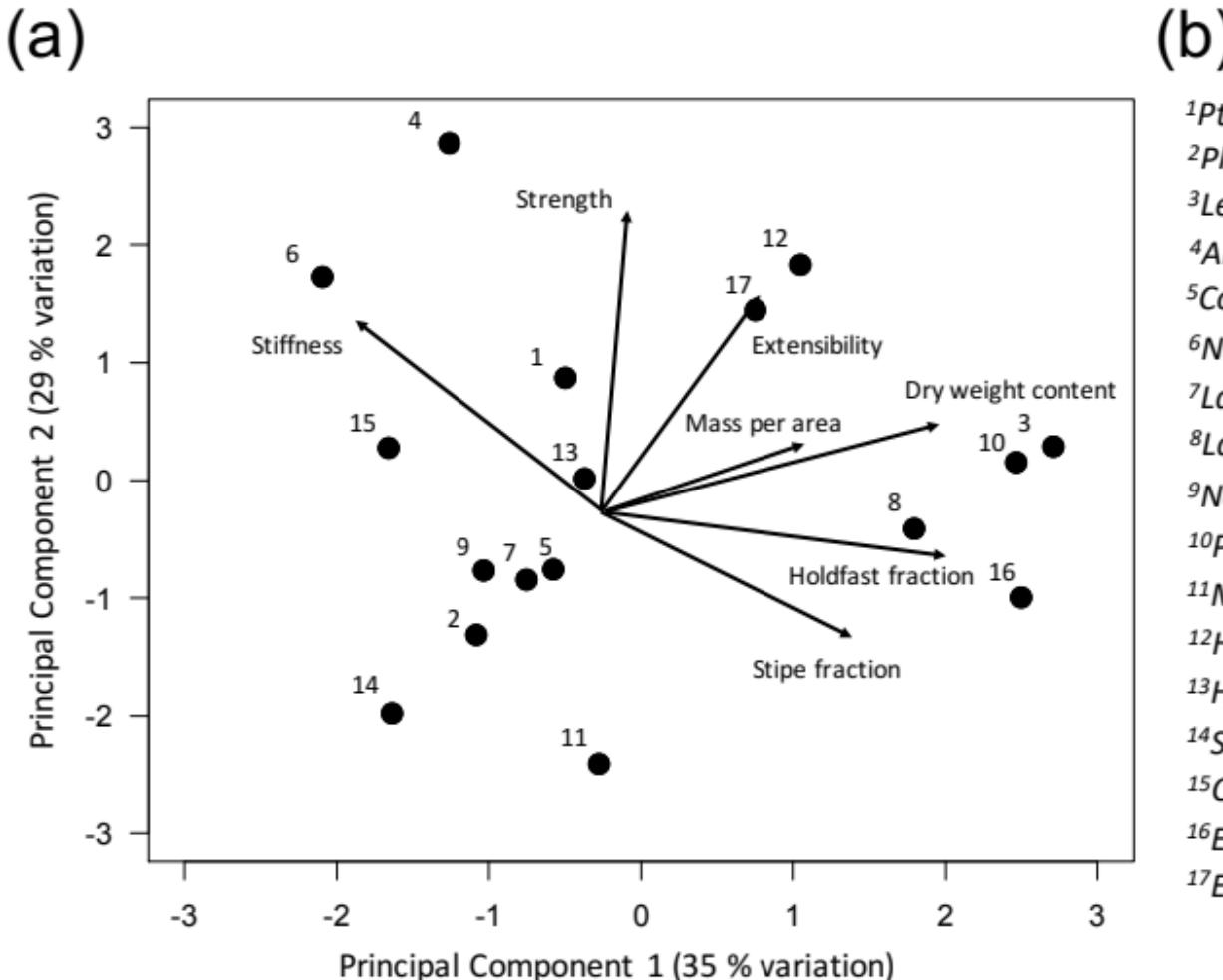
**Fig 5. Patterns of phylogenetic community assembly across kelp assemblages.** Metrics of phylogenetic community assembly (NRI and NTI) plotted against the species richness of communities. Data points represent individual communities and significance is indicated with dot colour. Black dots indicate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

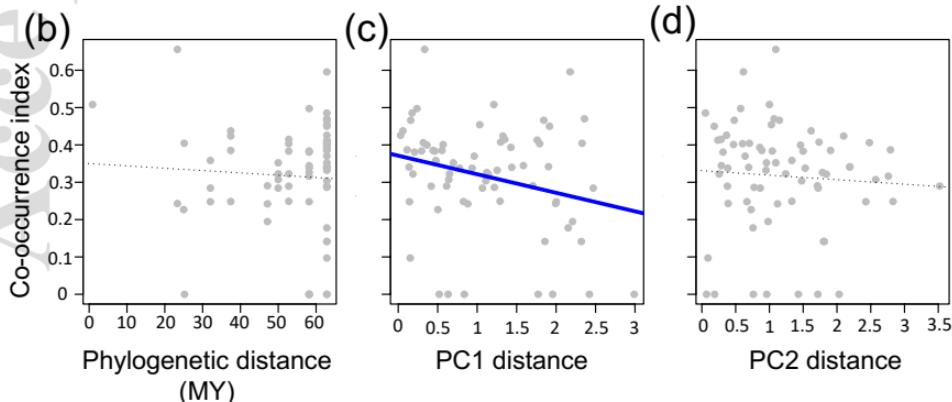
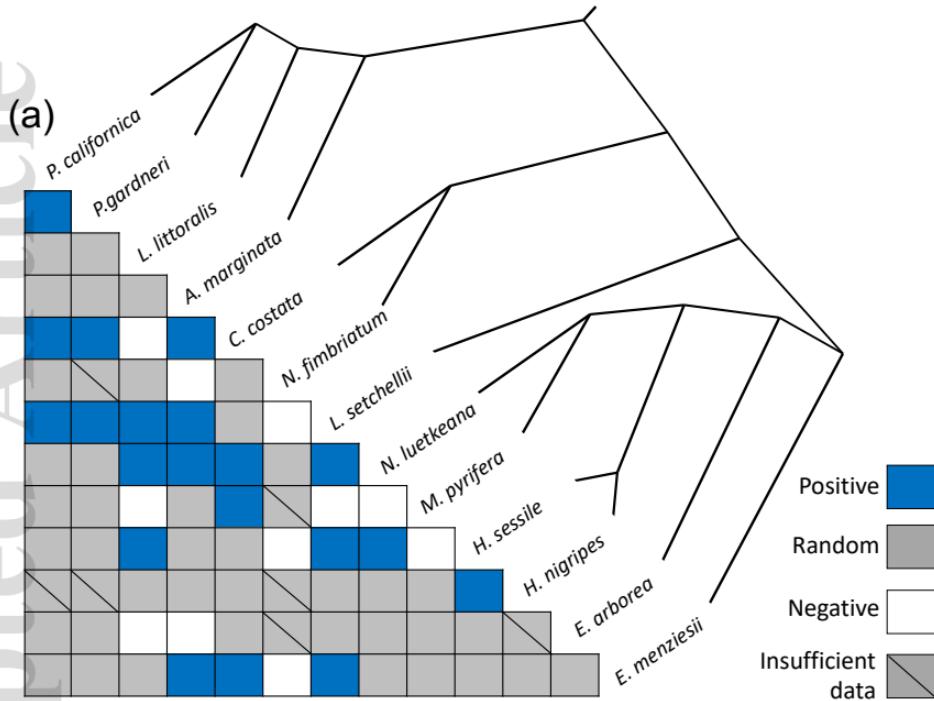
**Fig 6. Phylogenetic distribution of habitat niches across the kelps.** (A-H) Logistic polynomial regressions of species occupancy across a gradient of wave exposure. Columns represent members of two different kelp families (left = Alariaceae, right = Arthrothamnaceae). (I) Phylogeny of the kelps showing the average wave exposure of each species. There was no

significant phylogenetic signal on habitat niche (Blomberg's  $K = 0.483$ ,  $P = 0.749$ ; Pagel's  $\lambda < 0.01$ ,  $P < 0.99$  ).



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