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Convergent evolution of niche structure in Northeast Pacific kelp forests

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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 (β) 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 supports this hypothesis.

KEYWORDS
adaptive radiation, diversification, environmental filtering, functional morphology, laminariales, niche partitioning, phylogenetic community assembly, phylogenetic overdispersion

1 | INTRODUCTION

A major challenge among ecologists is to understand how community- and ecosystem-level processes influence the macroevolution of lineages (Emerson & Gillespie, 2008; Gerhold, Cahill, Winter, Bartish, & Prinzing, 2015; Webb, Ackerly, McPeek, & Donoghue, 2002). 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. Cornwell & Ackerly, 2009; Kraft et al., 2014; Menge & Sutherland, 1987; van der Valk, 1981; Webb et al., 2002). Thus environmental gradients can serve as 'environmental filters', resulting in communities of species that share phenotypic traits necessary to survive in a particular environment (Cavalheri, Both, & Martins, 2015; Kraft et al., 2011, 2014; Reich & Oleksyn, 2004; Swenson & Enquist, 2007; Ulrich, Sewerniak, Puchałka, & Piwczyński, 2017). Over evolutionary time-scales, environmental gradients can influence the phenotypic evolution of community members by serving as strong sources of selective pressure (Cavender-Bares, Ackerly, Baum, & Bazzaz, 2004; Demes, Pruitt, Harley, & Carrington, 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, Kozak, Fine, & Kembel, 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 (Kraft, Cornwell, Webb, & Ackerly, 2007; Silvertown, Dodd, Gowing, Lawson, & McConway, 2006; Webb, 2000; Webb et al., 2002; 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 (Losos, 2008; Wiens, 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; Losos, 2008; Vamosi, Heard, Vamosi, & Webb, 2009; Webb et al., 2002; 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 (Figure 1a; Cavender-Bares et al., 2009; Webb et al., 2002). 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

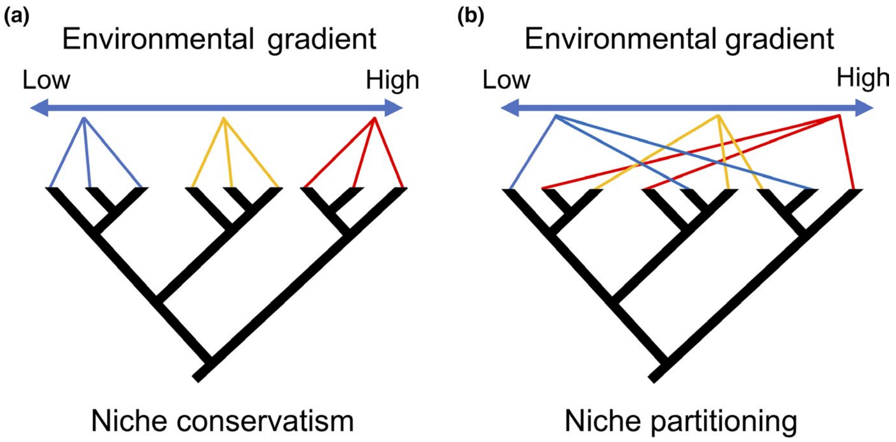

FIGURE 1 Theoretical extremes of how communities might be phylogenetically structured along environmental gradients under different dominant evolutionary processes. Lines are drawn from tips of the phylogeny to one of the three communities situated along a theoretical disturbance gradient. Colours indicate 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, Ackerly, et al., 2004). True community patterns are likely to fall between these two theoretical extremes

gradients (hereafter 'niche partitioning') to move into open niches as they diversify (Hector & Hooper, 2002; MacArthur, 1958). 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 (Figure 1b; Cavender-Bares, Ackerly, et al., 2004; Cavender-Bares et al., 2018; Silvertown, Dodd, et al., 2006; Silvertown, McConway, et al., 2006). 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 (Cavender-Bares et al., 2009; Emerson & Gillespie, 2008), most marine lineages are poorly studied in this respect (Best & Stachowicz, 2013; Verbruggen et al., 2009). 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 & 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 & Littler, 1984; Martone, 2007; Starko & Martone, 2016a; Steneck & Dethier, 1994). 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 (Demes et al., 2013; Denny, 1985; Denny & Gaylord, 2002; Gaylord, Blanchette, & Denny, 1994). 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 (Roberson & Coyer, 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, Krumhansl, Filbee-Dexter, & Pedersen, 2019). Kelps increase the productivity of cool, temperate nearshore ecosystems and their presence can substantially alter the composition of biotic communities (Graham, 2004; Hind et al., 2019; Steneck et al., 2002; Teagle, Hawkins, Moore, & Smale, 2017) by forming three-dimensional habitats called 'kelp forests' (Wernberg & 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. Jackson, Salomaki, Lane, & Saunders, 2017; Kawai, Hanyuda, Ridgway, & Holser, 2013; Lane, Mayes, Druehl, & Saunders, 2006; Starko, Soto Gomez, et al., 2019), 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, Soto Gomez, et al., 2019), possibly as a result of ecological opportunity that arose as the North Pacific became increasingly temperate over the past 30 million years (Starko, Soto Gomez, et al., 2019; Vermeij et al., 2019). While kelps are found globally, they are most phylogenetically diverse in the Northeast Pacific (Bolton, 2010; Starko, Soto Gomez, et al., 2019) 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 (β) niche structure across geographically coexisting species of kelp in the Northeast Pacific, one of the most diverse stretches of coastline for kelps and their likely centre of origin (Starko, Soto Gomez, et al., 2019). 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 (Burel et al., 2019; Duggins, Eckman, Siddon, & Klinger, 2003). 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.

2 | MATERIALS AND METHODS

2.1 | Quantifying phenotypic traits

Our sampling of kelps ($n = 17$ species) included a majority of all species found throughout the Northeast Pacific (Bolton, 2010; Guiry & Guiry, 2008) and approximately 80% of species found in southern British Columbia, with the unsampled species considered to be uncommon or rare (Druehl & Elliot, 1996; Gabrielson, Widdowson, & Lindstrom, 2018). 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 & 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, Kasai, & Tanaka, 2017), as has the analogous trait in land plants (e.g. He et al., 2009; Reich, Uhl, Walters, & Ellsworth, 1991). 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^2) 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 (σ), stiffness (E) and extensibility (ε), were measured using an Instron (model 5500R, Instron Corp.), a portable tensometer (described in Martone, 2006), or were taken from the literature (Tables S1 and 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 and 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 phylogenetic least squares (PGLS) models, between PCA axes and tenacity-area scaling relationships quantified previously (Starko & Martone, 2016a) for the eight 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 a measure of wave tolerance that directly considers ontogeny.

2.2 | Phylogenetic reconstruction

The phylogeny of kelps, has been studied previously in considerable detail (Jackson et al., 2017; Lane et al., 2006; Starko, Soto Gomez, et al., 2019). In this study, the time-calibrated phylogeny inferred by Starko, Soto Gomez, et al. (2019) 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*, is well supported by previous work on intrageneric relationships between *Laminaria* species, thus showing <1 million years difference in divergence time between *L. ephemera* and *L. setchellii* versus *L. digitata* (Rothman, Mattio, Anderson, & Bolton, 2017). Phylogenetic signals of traits were measured using Blomberg's K (Blomberg, Garland, & Ives, 2003) and Pagel's λ (Pagel, 1999). We also tested for correlations between trait distance and phylogenetic distance using Mantel tests.

We used the software 'StableTraits' (Elliot & 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 1,000 generations. Results of these analyses were visualized using the contMap function in 'phytools' (Revell, 2012).

2.3 | 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 & 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, Bailey, et al., 2019). 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 *Cymathaere 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, Bailey, et al., 2019). 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 & Helmuth, 2003; Neufeld, Starko, & Burns, 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, Nielsen, & Williams, 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 and Elliot (1996) and was based on the criteria from Topinka, Tucker, and Korjeff (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, Bailey, et al., 2019). 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 3–5.5 m above mean lower low water large tide—MLLWLT), we created a 'wave exposure index' by subtracting 3 m 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.

2.4 | 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 & Roberts, 1990), a measure of association between species pairs, to randomly simulated communities using EcoSim (Gotelli & 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 were 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 versus expected outcomes, hereafter 'co-occurrence index'. Calculated as:

$$\text{Co–occurrence index} = \text{Log}_{10}\left(\frac{\text{Observed}}{\text{Expected}} + 1\right), \tag{1}$$

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 <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.

2.5 | 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):

$$\text{NRI} = -\frac{X_{\text{net}} - X_{\text{null}}}{SD_{\text{null}}}, \tag{2}$$

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_{net} from Equation 2 is replaced with X_{min} which is defined as the average distance between each species and its closest relative, such that:

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

For NTI, X_{null} and SD_{null} represent the mean X_{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_{net} vs. X_{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 by conducting 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, Zang, Letcher, Liu, & He, 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, Rodríguez, & Purvis, 2008).

2.6 | 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 *Postelsia 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 (Nielsen, Blanchette, Menge, & Lubchenco, 2006; Paine, 1988) 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 *P. palmaeformis* populations. All three sites were of 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 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 modelled using polynomial and 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 λ 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.

2.7 | Statistical software

All statistical analyses were performed in R version 3.6.0, using the packages APE (Paradis, Claude, & Strimmer, 2004), PHYTOOLS (Revell, 2012), PICANTE (Kembel et al., 2010), QVALUE (Bass, Dabney, & Robinson, 2018), ECOSIMR (Gotelli, Hart, & Ellison, 2015), and COOCCUR (Griffith, Veech, & Marsh, 2016).

3 | RESULTS

3.1 | 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 (Figure 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 (Figure S1). Principal component 2 explained mainly the properties of materials (σ, *E* and ε). 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

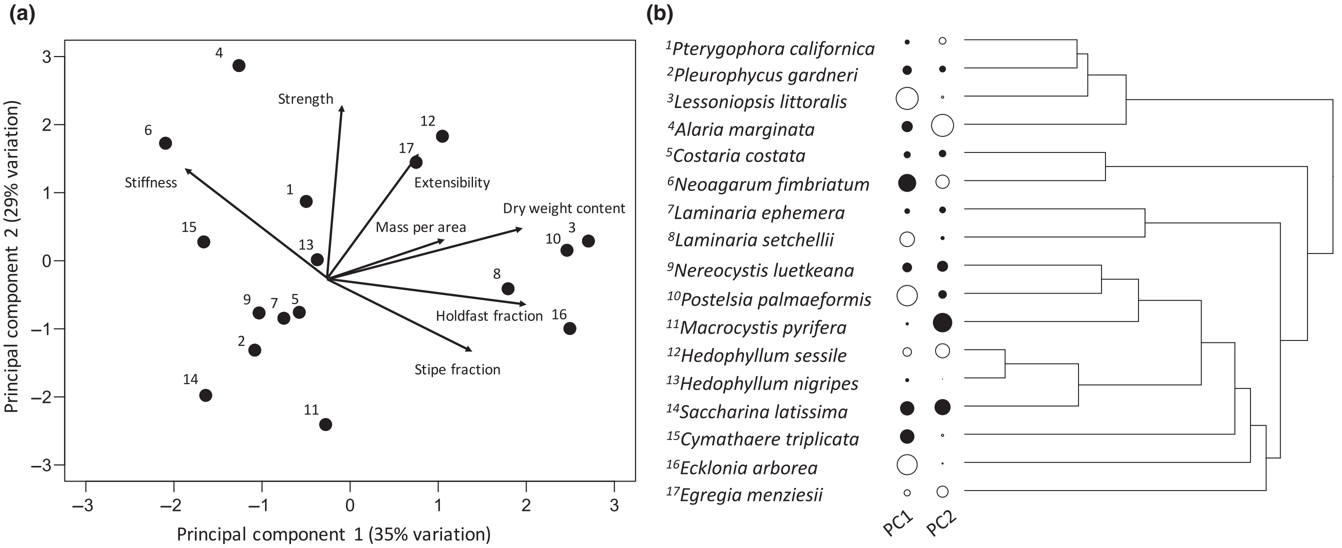

FIGURE 2 Phylogenetic distribution of trait axes in Northeast Pacific kelp species. Panel a shows the first two principal component axes. Panel b shows PC1 and PC2 plotted on the phylogeny. The size of each bubble indicates the value of each trait axis and the colour indicates whether values are positive (white) or negative (black). There is no significant phylogenetic signal in either axis (see Table 1)

TABLE 1 Statistical testing of phylogenetic signal for quantitative traits

Functional traits	Phylogenetic signal			
	Blomberg's *K*	*p* value	Pagel's λ	*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

Abbreviations: BMA, blade mass per area; DMC, dry matter content; HMF, holdfast mass fraction; SMF, stipe mass fraction.

*Trending towards statistical significance ($p < 0.10$).

relationships (Figure 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; Figure 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 (Figure 2b). This observation was confirmed by the lack of a significant relationship between PC1 and PC2 trait distances and phylogenetic distance (PC1 Mantel test: $Z = 6{,}450.835$, $p = 0.589$; PC2 Mantel test: $Z = 6{,}449.193$, $p = 0.691$). Ancestral state reconstructions indicate that trait combinations have evolved repeatedly across the kelps with clear patterns of phenotypic convergence (Figure S3).

3.2 | 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 (Figure S4). There were also several significant associations between individual species (Figure 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, *P. gardneri* and *P. californica*, were positively associated (Figure 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).

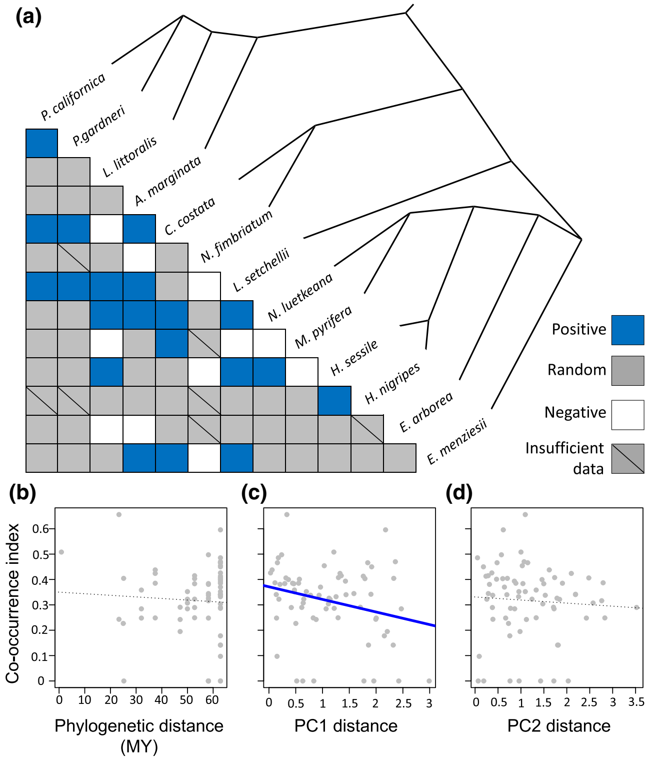

FIGURE 3 Predictors of kelp species co-occurrence. (a) Correlation matrix of species pairs. Colour in each cell indicates whether there was a significant positive or negative correlation between the occurrences of each pair of species, after correcting for false detection rate ($q < 0.05$). (b–d) Co-occurrence index [Log ((observed co-occurrence/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 ($p < 0.05$)

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, $p = 0.02746$; Figure 3c). Phylogenetic distance (Linear regression: $F = 0.2392$, $df = 69$ and 1, $p = 0.6263$; Figure 3b) and PC2 distances (Linear regression: $F = 0.3037$, $df = 69$, $p = 0.5833$; Figure 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, $p = 0.002$; Figure 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

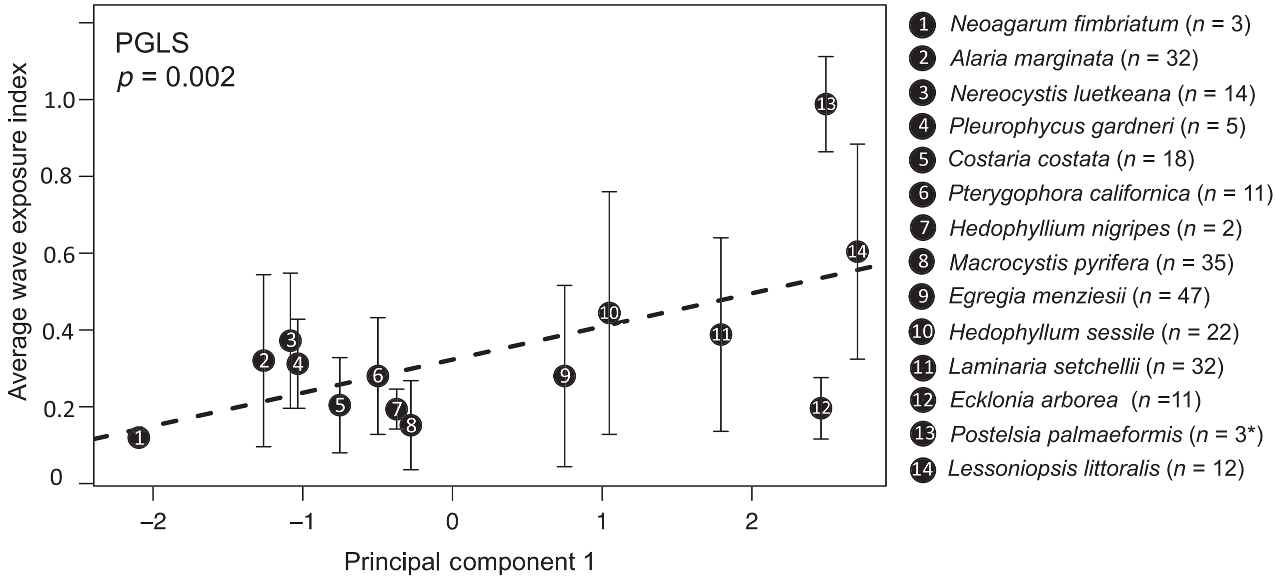

FIGURE 4 Relationship between wave exposure and structural reinforcement trait axis. Data points represent the average wave exposure that a species was found at (±variance) plotted against its value of Principal Component 1, which represents structural reinforcement traits. Numbers indicate the identity of a species and the regression line represents a phylogenetic least squares (PGLS) model

P. 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 ε (Table 2). There was a possible, but not significant negative correlation between blade stiffness and average wave exposure.

3.3 | 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 (Figure 5). Although only a few sites were significantly overdispersed (NRI: $n = 3$, NTI = 7; Figure 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; Figure 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 (Figure 6). Individual species clearly varied in distribution across the gradient of wave exposure and closely related species (e.g. *N. luetkeana* and *M. pyrifera*) tended to specialize in different wave exposure regimes. The clear exception here is the species pair *P. californica* and *P. gardneri* that are sisters and had nearly identical distributions across the wave exposure gradient but differed only in niche width (sensu MacArthur, 1968; Slobodkichoff & Schulz, 1980; Figure 6). There was a significant effect of wave exposure category on community composition (PERMANOVA: $F = 13.205$, $p < 0.001$; Figure 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 $\lambda < 0.01$, $p > 0.99$).

TABLE 2 Results of phylogenetic least squares (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**

Abbreviations: BMA, blade mass per area; DMC, dry matter content; HMF, holdfast mass fraction; SMF, stipe mass fraction.

*Trending towards significance ($p < 0.10$).

**Significant relationship ($p < 0.05$).

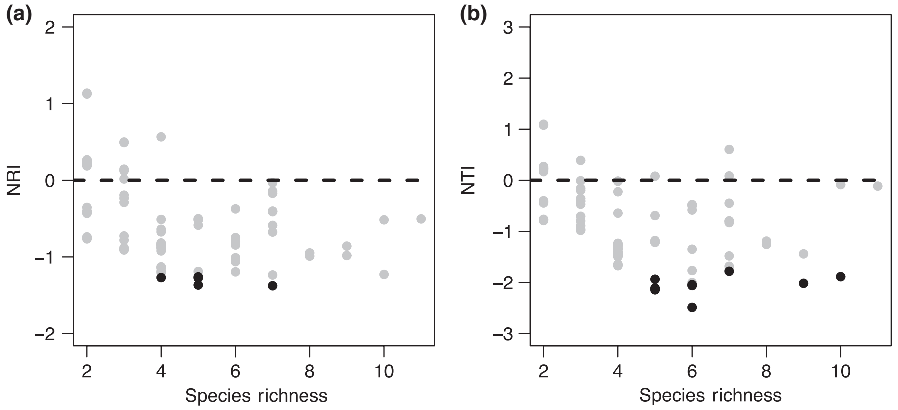

FIGURE 5 Patterns of phylogenetic community assembly across kelp assemblages. Metrics of phylogenetic community assembly [net relatedness index (NRI) and nearest taxon index (NTI)] plotted against the species richness of communities. Data points represent individual communities and significance is indicated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

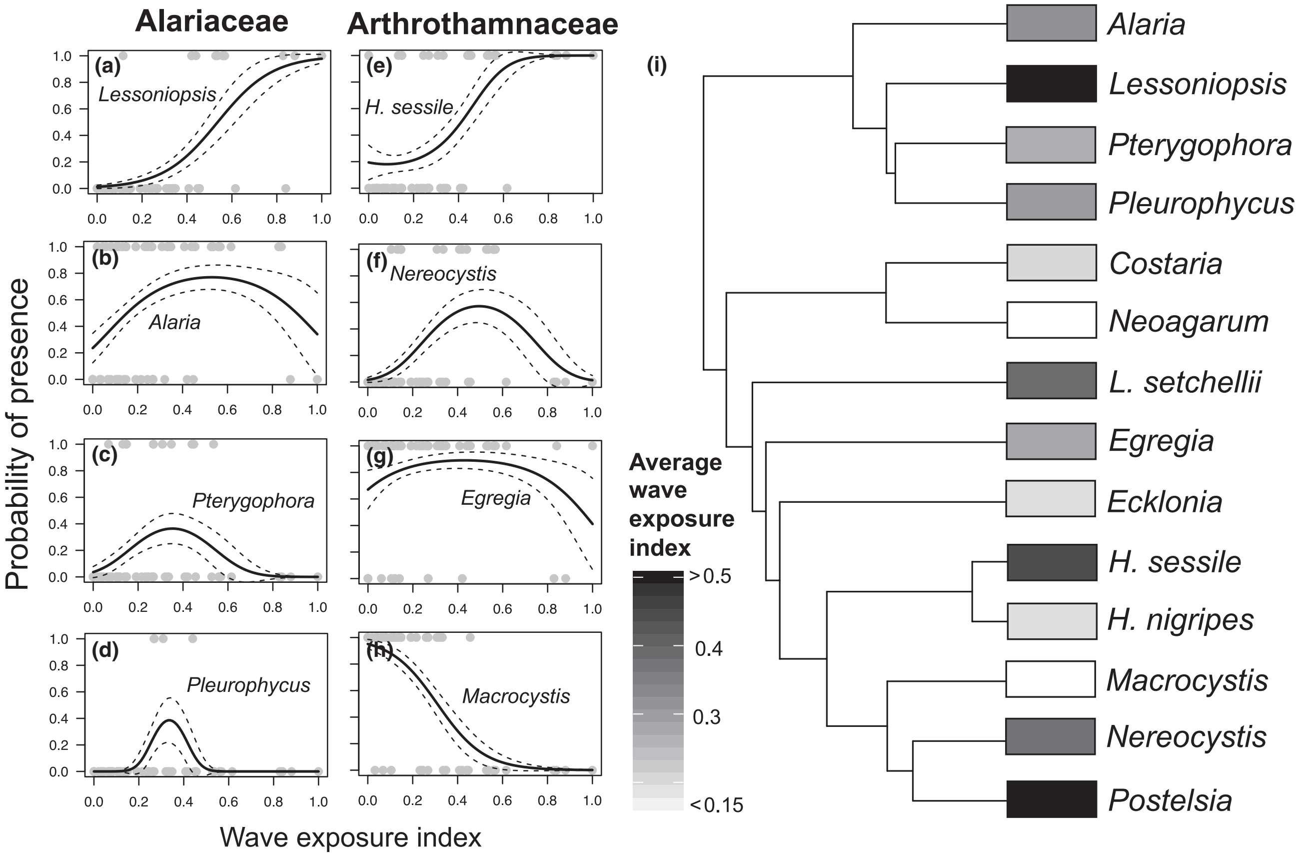

FIGURE 6 Phylogenetic distribution of habitat niches across the kelps. (a–h) Logistic polynomial regressions of species occupancy across a gradient of wave exposure. Columns represent members of two different kelp families (left = Alariaceae, right = Arthrothamnaceae). (i) Phylogeny of the kelps showing 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 $\lambda < 0.01$, $p > 0.99$). [Correction added on 28 September 2020, after first online publication: The word 'Eckonia' has been corrected to 'Ecklonia'.]

4 | 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 (Figure 3) and the position of individual species along the gradient of wave exposure (Figure 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

TABLE 3 Summary of hypotheses and conclusions from this study. Supported hypotheses are shown in bold

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

biomechanical models have demonstrated the role of rapid water motion as a strong selective pressure for increased tolerance to physical forces (Demes et al., 2013; Duggins et al., 2003; Johnson & Koehl, 1994; Martone, Kost, & Boller, 2012; Starko, Claman, & Martone, 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 & Manley, 1985). Thus, the PC1 trait axis may represent a trade-off between tolerance to waves and maximum productivity that our data suggest which 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 (Figure 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. Cooper et al., 2008; Webb, 2000; Webb et al., 2002). This inference is made under the assumption that species with similar niches will be unable to coexist 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 (Figure 6), were positively correlated across the community matrix (Figure 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 *L. setchellii*, a wave exposed specialist (Figure 6), co-occurred significantly less often than predicted (Figure 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 α niche traits, which result in coexistence of taxa, are more labile (Silvertown, Dodd, et al., 2006; Silvertown, McConway, et al., 2006; but see Cavender-Bares, Ackerly, et al., 2004). 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 (Figure 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 & 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

TABLE 4 Examples of genetic divergence between populations or incipient species across gradients of wave exposure

Species	Environmental gradient	Description	Evidence of differentiation	References
Ecklonia arborea	Wave exposure	Genetic differentiation associated with changes in blade morphology and wave exposure	M13 DNA fingerprinting	Roberson and Coyer (2004)
Egregia menziesii	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, Miner, and Gaines (2002) and Henkel, Hofmann, and Whitmer (2007)
Macrocystis pyrifera	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	Astorga, Hernández, Valenzuela, Avaria-Llautureo, and Westermeier (2012), Camus, Faugeron, and Buschmann (2018) and Kopczak, Zimmerman, and Kremer (1991)
Pelagophycus porra	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, Olsen, and Stam (2000)
Saccharina latissima sensu lato	Wave exposure	A wave-exposed specialist population from Maine was described as new species, *Saccharina angustissima*, making *S. latissima* paraphyletic	Difference in rbcL and cox3 (but not cox1) between *S. angustissima* and *S. latissima* populations from Maine; common garden revealed that blade shape is genetically determined	Augyte et al. (2018)

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 (Cavender-Bares, Ackerly, et al., 2004; Cavender-Bares, Kitajima, & Bazzaz, 2004; Cavender-Bares et al., 2018; Losos, 2008; MacArthur, 1958). While many kelp species can alter their traits depending on habitat (reviewed by Koehl, Silk, Liang, & Mahadevan, 2008), genetic differentiation or speciation is likely to facilitate the evolution of more extreme trait differences than would be otherwise possible through plasticity (Augyte, Lewis, Lin, Neefus, & Yarish, 2018; Gerard, 1988; King, McKeown, Smale, & Moore, 2018; Sato et al., 2017). We further hypothesize that α niche traits may be more conserved than β niche traits across the kelps, leading to increased coexistence between distant relatives. While it is unclear exactly what traits would promote coexistence 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, Soto Gomez, et al., 2019). Differences in stature within the water column have been linked to competitive hierarchies in kelps (Edwards & 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 following cooling of the global climate (Starko, Soto Gomez, et al., 2019). Kelps are much larger and more competitive than other macroalgal species (Edwards & 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, Soto Gomez, et al., 2019; Vermeij et al., 2019). This ecological opportunity may have promoted selection for niche partitioning as has been documented previously in oak trees (Cavender-Bares, Ackerly, et al., 2004; Cavender-Bares et al., 2018), the silversword alliance (Ackerly, 2009; Blonder, Baldwin, Enquist, & Robichaux, 2016) and Carribean 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, Graham, Lane, & Harley, 2019, chemical deterrents: Starko, Soto Gomez, et al., 2019).

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 (Charrier, Le Bail, & de Reviers, 2012; Koehl et al., 2008) 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 *N. luetkeana* and *P. 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 *L. littoralis*. This magnitude of variation has not been observed in any one species, even when assessed across habitats differing in wave exposure (Duggins et al., 2003; Fowler-Walker, Wernberg, & Connell, 2006; Johnson & Koehl, 1994). Moreover, common garden experiments on *Saccharina* spp. have shown greater phenotypic variation between than within species or genotypes (Augyte, Yarish, Redmond, & Kim, 2017; Gerard, 1988; Liesner, Shama, Diehl, Valentin, & Bartsch, 2020; Sato 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, Gribben, & Poore, 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 (Duggins et al., 2003; Johnson & Koehl, 1994; Koehl et al., 2008).

5 | 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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AUTHORS' 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 AVAILABILITY STATEMENT

Data are deposited in the Dryad Digital Repository http://doi.org/10.5061/dryad.18931zctg, (Starko, Demes, Neufeld, & Martone, 2020).

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REFERENCES

Ackerly, D. (2009). Conservatism and diversification of plant functional traits: Evolutionary rates versus phylogenetic signal. *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 19699–19706. https://doi.org/10.1073/pnas.0901635106

Arnold, K. E., & Manley, S. L. (1985). Carbon allocation in *Macrocystis pyrifera* (Phaeophyta): Intrinsic variability in photosynthesis and respiration. *Journal of Phycology*, *21*, 154–167.

Astorga, M. P., Hernández, C. E., Valenzuela, C. P., Avaria-Llautureo, J., & Westermeier, R. (2012). Origin, diversification, and historical biogeography of the giant kelps genus *Macrocystis*: Evidences from Bayesian phylogenetic analysis. *Revista de Biología Marina y Oceanografía*, *47*, 573–579. https://doi.org/10.4067/S0718-19572012000300019

Augyte, S., Lewis, L., Lin, S., Neefus, C. D., & Yarish, C. (2018). Speciation in the exposed intertidal zone: The case of *Saccharina angustissima* comb. nov. & stat. nov. (Laminariales, Phaeophyceae). *Phycologia*, *57*, 100–112.

Augyte, S., Yarish, C., Redmond, S., & Kim, J. K. (2017). Cultivation of a morphologically distinct strain of the sugar kelp, *Saccharina latissima* forma *angustissima*, from coastal Maine, USA, with implications for ecosystem services. *Journal of Applied Phycology*, *29*, 1967–1976. https://doi.org/10.1007/s10811-017-1102-x

Bass, J., Dabney, A., & Robinson, D. (2018). *qvalue: Q-value estimation for false discovery rate control*. R package version 2.14.0. Retrieved from http://github.com/jdstorey/qvalue

Best, R. J., & Stachowicz, J. J. (2013). Phylogeny as a proxy for ecology in seagrass amphipods: Which traits are most conserved? *PLoS ONE*, *8*, e57550. https://doi.org/10.1371/journal.pone.0057550

Blanchette, C. A., Miner, B. G., & Gaines, S. D. (2002). Geographic variability in form, size and survival of *Egregia menziesii* around point conception, California. *Marine Ecology Progress Series*, *239*, 69–82. https://doi.org/10.3354/meps239069

Blomberg, S. P., Garland, T., & Ives, A. R. (2003). Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. *Evolution*, *57*, 717–745. https://doi.org/10.1111/j.0014-3820.2003.tb00285.x

Blonder, B., Baldwin, B. G., Enquist, B. J., & Robichaux, R. H. (2016). Variation and macroevolution in leaf functional traits in the Hawaiian silversword alliance (Asteraceae). *Journal of Ecology*, *104*, 219–228. https://doi.org/10.1111/1365-2745.12497

Bolton, J. J. (2010). The biogeography of kelps (Laminariales, Phaeophyceae): A global analysis with new insights from recent advances in molecular phylogenetics. *Helgoland Marine Research*, *64*, 263–279. https://doi.org/10.1007/s10152-010-0211-6

Brown, W. L., & Wilson, E. O. (1956). Character displacement. *Systematic Zoology*, *5*, 49–64. https://doi.org/10.2307/2411924

Burel, T., Schaal, G., Grall, J., Le Duff, M., Chapalain, G., Schmitt, B., … Ar Gall, E. (2019). Small-scale effects of hydrodynamics on the structure of intertidal macroalgal communities: A novel approach. *Estuarine, Coastal and Shelf Science*, *226*, 106290. https://doi.org/10.1016/j.ecss.2019.106290

Burnaford, J. L., Nielsen, K. J., & Williams, S. L. (2014). Celestial mechanics affects emersion time and cover patterns of an ecosystem engineer, the intertidal kelp *Saccharina sessilis*. *Marine Ecology Progress Series*, *509*, 127–136. https://doi.org/10.3354/meps10876

Buzas, M. A., & Culver, S. J. (1991). Species diversity and dispersal of benthic foraminifera. *BioScience*, *41*, 483–489. https://doi.org/10.2307/1311806

Camus, C., Faugeron, S., & Buschmann, A. H. (2018). Assessment of genetic and phenotypic diversity of the giant kelp, *Macrocystis pyrifera*, to support breeding programs. *Algal Research*, *30*, 101–112. https://doi.org/10.1016/j.algal.2018.01.004

Cavalheri, H., Both, C., & Martins, M. (2015). The interplay between environmental filtering and spatial processes in structuring communities: The case of neotropical snake communities. *PLoS ONE*, *10*, e0127959. https://doi.org/10.1371/journal.pone.0127959

Cavender-Bares, J., Ackerly, D. D., Baum, D. A., & Bazzaz, F. A. (2004). Phylogenetic overdispersion in Floridian oak communities. *The American Naturalist*, *163*, 823–843. https://doi.org/10.1086/386375

Cavender-Bares, J., Kitajima, K., & Bazzaz, F. A. (2004). Multiple trait associations in relation to habitat differentiation among 17 Floridian oak species. *Ecological Monographs*, *74*, 635–662. https://doi.org/10.1890/03-4007

Cavender-Bares, J., Kothari, S., Meireles, J. E., Kaproth, M. A., Manos, P. S., & Hipp, A. L. (2018). The role of diversification in community assembly of the oaks (*Quercus* L.) across the continental U.S. *American Journal of Botany*, *105*, 565–586.

Cavender-Bares, J., Kozak, K. H., Fine, P. V. A., & Kembel, S. W. (2009). The merging of community ecology and phylogenetic biology. *Ecology Letters*, *12*, 693–715. https://doi.org/10.1111/j.1461-0248.2009.01314.x

Charrier, B., Le Bail, A., & de Reviers, B. (2012). Plant Proteus: Brown algal morphological plasticity and underlying developmental mechanisms. *Trends in Plant Science*, *17*, 468–477. https://doi.org/10.1016/j.tplants.2012.03.003

Cooper, N., Rodríguez, J., & Purvis, A. (2008). A common tendency for phylogenetic overdispersion in mammalian assemblages. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1646), 2031–2037. https://doi.org/10.1098/rspb.2008.0420

Cornwell, W. K., & Ackerly, D. D. (2009). Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs*, *79*, 109–126. https://doi.org/10.1890/07-1134.1

Darwin, C. (1859). *On the origin of species by means of natural selection* (p. 502). London, UK: Murray.

Demes, K. W., Pruitt, J. N., Harley, C. D. G., & Carrington, E. (2013). Survival of the weakest: Increased frond mechanical strength in a wave-swept kelp inhibits self-pruning and increases whole-plant mortality. *Functional Ecology*, *27*, 439–445. https://doi.org/10.1111/1365-2435.12067

Denny, M. W. (1985). Wave forces on intertidal organisms: A case study. *Limnology and Oceanography*, *30*, 1171–1187.

Denny, M., & Gaylord, B. (2002). The mechanics of wave-swept algae. *Journal of Experimental Biology*, *205*, 1355–1362.

Ding, Y., Zang, R., Letcher, S. G., Liu, S., & He, F. (2012). Disturbance regime changes the trait distribution, phylogenetic structure and community assembly of tropical rain forests. *Oikos*, *121*, 1263–1270. https://doi.org/10.1111/j.1600-0706.2011.19992.x

Druehl, L. D., & Elliot, C. T. J. (1996). Parks Canada Barkley sound kelp distribution. Parks Canada Contract #K3489-3-0006.

Duggins, D. O., Eckman, J. E., Siddon, C. E., & Klinger, T. (2003). Population, morphometric and biomechanical studies of three understory kelps along a hydrodynamic gradient. *Marine Ecology Progress Series*, *265*, 57–76. https://doi.org/10.3354/meps265057

Edwards, M. S., & Connell, S. D. (2015). *Chapter 7: Competition, a major factor structuring seaweed communities. Seaweed biology: Novel insights into ecophysiology, ecology and utilization*. New York, NY: Springer.

Elliot, M. G., & Mooers, A. Ø. (2014). Inferring ancestral states without assuming neutrality or gradualism using a stable model of continuous character evolution. *BMC Evolutionary Biology*, *14*, 226. https://doi.org/10.1186/s12862-014-0226-8

Emerson, B. C., & Gillespie, R. G. (2008). Phylogenetic analysis of community assembly and structure over space and time. *Trends in Ecology & Evolution*, *23*, 619–630. https://doi.org/10.1016/j.tree.2008.07.005

Fowler-Walker, M. J., Wernberg, T., & Connell, S. D. (2006). Differences in kelp morphology between wave sheltered and exposed localities: Morphologically plastic or fixed traits? *Marine Biology*, *148*, 755–767. https://doi.org/10.1007/s00227-005-0125-z

Funk, D. J. (1998). Isolating a role for natural selection in speciation: Host adaptation and sexual isolation in *Neochlamisus bebbianae* leaf beetles. *Evolution; International Journal of Organic Evolution*, *52*, 1744–1759.

Gabrielson, P. W., Widdowson, T. B., & Lindstrom, S. C. (2018). *Keys to the seaweeds and seagrasses of Oregon and California: North of point conception*. Hillborough, NC: PhycoID, 9.

Gaylord, B., Blanchette, C. A., & Denny, M. W. (1994). Mechanical consequences of size in wave-swept algae. *Ecological Monographs*, *64*, 287–313. https://doi.org/10.2307/2937164

Gerard, V. A. (1988). Ecotypic differentiation in light-related traits of the kelp *Laminaria saccharina*. *Marine Biology*, *97*, 25–36. https://doi.org/10.1007/BF00391242

Gerhold, P., Cahill, J. F., Winter, M., Bartish, I. V., & Prinzing, A. (2015). Phylogenetic patterns are not proxies of community assembly mechanisms (they are far better). *Functional Ecology*, *29*, 600–614. https://doi.org/10.1111/1365-2435.12425

Gotelli, N. J., & Entsminger, G. L. (2001). Swap and fill algorithms in null model analysis: Rethinking the knight's tour. *Oecologia*, *129*(2), 281–291.

Gotelli, N. J., Hart, E. M., & Ellison, A. M. (2015). EcoSimR: Null model analysis for ecological data. R package version 0.1.0. https://doi.org/10.5281/zenodo.16522. Retrieved from http://github.com/gotellilab/EcoSimR

Graham, M. H. (2004). Effects of local deforestation on the diversity and structure of southern California giant kelp forest food webs. *Ecosystems*, *7*, 341–357. https://doi.org/10.1007/s10021-003-0245-6

Griffith, D. M., Veech, J. A., & Marsh, C. J. (2016). cooccur: Probabilistic species co-occurrence analysis in R. *Journal of Statistical Software*, *69*, 1–17.

Guiry, M. D., & Guiry, G. (2008). AlgaeBase. *AlgaeBase*. Retrieved from algaebase.org

Harley, C. D. G. (2003). Abiotic stress and herbivory interact to set range limits across a two-dimensional stress gradient. *Ecology*, *84*, 1477–1488. https://doi.org/10.1890/0012-9658(2003)084[1477:ASAHIT]2.0.CO;2

Harley, C. D. G., & Helmuth, B. S. T. (2003). Local- and regional-scale effects of wave exposure, thermal stress, and absolute versus effective shore level on patterns of intertidal zonation. *Limnology and Oceanography*, *48*, 1498–1508. https://doi.org/10.4319/lo.2003.48.4.1498

He, J.-S., Wang, X., Flynn, D. F. B., Wang, L., Schmid, B., & Fang, J. (2009). Taxonomic, phylogenetic, and environmental trade-offs between leaf productivity and persistence. *Ecology*, *90*, 2779–2791. https://doi.org/10.1890/08-1126.1

Hector, A., & Hooper, R. (2002). ECOLOGY: Darwin and the first ecological experiment. *Science*, *295*(5555), 639–640. https://doi.org/10.1126/science.1064815

Henkel, S. K., Hofmann, G. E., & Whitmer, A. C. (2007). Morphological and genetic variation in *Egregia menziesii* over a latitudinal gradient. *Botanica Marina*, *50*, 159–170. https://doi.org/10.1515/BOT.2007.019

Hind, K. R., Starko, S., Burt, J. M., Lemay, M. A., Salomon, A. K., & Martone, P. T. (2019). Trophic control of cryptic coralline algal diversity. *Proceedings of the National Academy of Sciences of the United States of America*, *116*, 15080–15085. https://doi.org/10.1073/pnas.1900506116

Hurd, C. L. (2017). Shaken and stirred: The fundamental role of water motion in resource acquisition and seaweed productivity. *Perspectives in Phycology*, *4*, 73–81. https://doi.org/10.1127/pip/2017/0072

Jackson, C., Salomaki, E. D., Lane, C. E., & Saunders, G. W. (2017). Kelp transcriptomes provide robust support for interfamilial relationships and revision of the little known Arthrothamnaceae (Laminariales). *Journal of Phycology*, *53*, 1–6. https://doi.org/10.1111/jpy.12465

Johnson, A., & Koehl, M. (1994). Maintenance of dynamic strain similarity and environmental stress factor in different flow habitats: Thallus allometry and material properties of a giant kelp. *The Journal of Experimental Biology*, *195*, 381–410.

Kawai, H., Hanyuda, T., Ridgway, L. M., & Holser, K. (2013). Ancestral reproductive structure in basal kelp *Aureophycus aleuticus*. *Scientific Reports*, *3*, 1–7. https://doi.org/10.1038/srep02491

Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., … Webb, C. O. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, *26*, 1463–1464. https://doi.org/10.1093/bioinformatics/btq166

King, N. G., McKeown, N. J., Smale, D. A., & Moore, P. J. (2018). The importance of phenotypic plasticity and local adaptation in driving intraspecific variability in thermal niches of marine macrophytes. *Ecography*, *41*, 1469–1484. https://doi.org/10.1111/ecog.03186

Koehl, M. A. R., Silk, W. K., Liang, H., & Mahadevan, L. (2008). How kelp produce blade shapes suited to different flow regimes: A new wrinkle. *Integrative and Comparative Biology*, *48*, 834–851. https://doi.org/10.1093/icb/icn069

Kopczak, C. D., Zimmerman, R. C., & Kremer, J. N. (1991). Variation in nitrogen physiology and growth among geographically isolated populations of the giant kelp, *Macrocystis pyrifera* (Phaeophyta). *Journal of Phycology*, *27*, 149–158.

Kraft, N. J. B., Adler, P. B., Godoy, O., James, E. C., Fuller, S., & Levine, J. M. (2014). Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology*, *29*, 592–599. https://doi.org/10.1111/1365-2435.12345

Kraft, N. J., Comita, L. S., Chase, J. M., Sanders, N. J., Swenson, N. G., Crist, T. O., … Anderson, M. J. (2011). Disentangling the drivers of β diversity along latitudinal and elevational gradients. *Science*, *333*, 1755–1758.

Kraft, N. J. B., Cornwell, W. K., Webb, C. O., & Ackerly, D. D. (2007). Trait evolution, community assembly, and the phylogenetic structure of ecological communities. *The American Naturalist*, *170*, 271–283. https://doi.org/10.1086/519400

Lane, C. E., Mayes, C., Druehl, L. D., & Saunders, G. W. (2006). A multi-gene molecular investigation of the kelp (Laminariales, Phaeophyceae) supports substantial taxonomic re-organization. *Journal of Phycology*, *42*, 493–512.

Liesner, D., Shama, L. N. S., Diehl, N., Valentin, K., & Bartsch, I. (2020). Thermal plasticity of the kelp laminaria digitata (phaeophyceae) across life cycle stages reveals the importance of cold seasons for marine forests. *Frontiers in Marine Science*, *7*, 456. https://doi.org/10.3389/fmars.2020.00456

Littler, M. M., & Littler, D. S. (1984). Relationships between macroalgal functional form groups and substrata stability in a subtropical rocky-intertidal system. *Journal of Experimental Marine Biology and Ecology*, *74*, 13–34. https://doi.org/10.1016/0022-0981(84)90035-2

Lopez, B., Burgio, K., Carlucci, M., Palmquist, K., Parada, A., Weinberger, V., & Hurlbert, A. (2016). A new framework for inferring community assembly processes using phylogenetic information, relevant traits and environmental gradients. *One Ecosystem*, *1*, e9501.

Losos, J. B. (2008). Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecology Letters*, *11*, 995–1003. https://doi.org/10.1111/j.1461-0248.2008.01229.x

Losos, J. B., Leal, M., Glor, R. E., de Queiroz, K., Hertz, P. E., Rodríguez Schettino, L., … Larson, A. (2003). Niche lability in the evolution of a Caribbean lizard community. *Nature*, *424*, 542–545. https://doi.org/10.1038/nature01814

MacArthur, R. H. (1958). Population ecology of some warblers of northeastern coniferous forests. *Ecology*, *39*, 599–619. https://doi.org/10.2307/1931600

MacArthur, R. H. (1968). The theory of the niche. In *Population biology and evolution* (pp. 159–176). Syracuse, NY: Syracuse University Press.

Martone, P. T. (2006). Size, strength and allometry of joints in the articulated coralline Calliarthron. *Journal of Experimental Biology*, *209*, 1678–1689. https://doi.org/10.1242/jeb.02139

Martone, P. T. (2007). Kelp versus coralline: Cellular basis for mechanical strength in the wave-swept seaweed *Calliarthron* (Corallinaceae, Rhodophyta). *Journal of Phycology*, *43*, 882–891.

Martone, P. T., Kost, L., & Boller, M. (2012). Drag reduction in wave-swept macroalgae: Alternative strategies and new predictions. *American Journal of Botany*, *99*, 806–815. https://doi.org/10.3732/ajb.1100541

Menge, B. A., & Sutherland, J. P. (1987). Community regulation: Variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *The American Naturalist*, *130*, 730–757. https://doi.org/10.1086/284741

Miller, K. A., Olsen, J. L., & Stam, W. T. (2000). Genetic divergence correlates with morphological and ecological subdivision in the deep-water elk kelp, *Pelagophycus porra* (Phaeophyceae). *Journal of Phycology*, *36*, 862–870. https://doi.org/10.1046/j.1529-8817.2000.99233.x

Muth, A. F., Graham, M. H., Lane, C. E., & Harley, C. D. G. (2019). Recruitment tolerance to increased temperature present across multiple kelp clades. *Ecology*, *100*, e02594. https://doi.org/10.1002/ecy.2594

Neufeld, C. J., Starko, S., & Burns, K. (2017). Disturbance and diversity in a continental archipelago: A mechanistic framework linking area, height, and exposure. *Ecosphere*, *8*, e01957. https://doi.org/10.1002/ecs2.1957

Nielsen, K. J., Blanchette, C. A., Menge, B. A., & Lubchenco, J. (2006). Physiological snapshots reflect ecological performance of the sea palm, *Postelsia palmaeformis* (Phaeophycaea) across intertidal elevation and exposure gradients. *Journal of Phycology*, *42*, 548–559.

Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature*, *401*, 877–884. https://doi.org/10.1038/44766

Paine, R. T. (1988). Habitat suitability and local population persistence of the sea palm *Postelsia palmaeformis*. *Ecology*, *69*, 1787–1794. https://doi.org/10.2307/1941157

Paradis, E., Claude, J., & Strimmer, K. (2004). APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics*, *20*, 289–290. https://doi.org/10.1093/bioinformatics/btg412

Reich, P. B., & Oleksyn, J. (2004). Global patterns of plant leaf N and P in relation to temperature and latitude. *Proceedings of the National Academy of Sciences of the United States of America*, *101*, 11001–11006. https://doi.org/10.1073/pnas.0403588101

Reich, P. B., Uhl, C., Walters, M. B., & Ellsworth, D. S. (1991). Leaf lifespan as a determinant of leaf structure and function among 23 Amazonian tree species. *Oecologia*, *86*, 16–24. https://doi.org/10.1007/BF00317383

Revell, L. J. (2012). phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, *3*, 217–223. https://doi.org/10.1111/j.2041-210X.2011.00169.x

Roberson, L. M., & Coyer, J. A. (2004). Variation in blade morphology of the kelp *Eisenia arborea*: Incipient speciation due to local water motion? *Marine Ecology Progress Series*, *282*, 115–128. https://doi.org/10.3354/meps282115

Rothman, M. D., Mattio, L., Anderson, R. J., & Bolton, J. J. (2017). A phylogeographic investigation of the kelp genus *Laminaria* (Laminariales, Phaeophyceae), with emphasis on the South Atlantic Ocean. *Journal of Phycology*, *53*, 778–789.

Sakanishi, Y., Kasai, H., & Tanaka, J. (2017). Trade-off relationship between productivity and thallus toughness in Laminariales (Phaeophyceae). *Phycological Research*, *65*, 103–110. https://doi.org/10.1111/pre.12168

Sato, Y., Hirano, T., Ichida, H., Murakami, M., Fukunishi, N., Abe, T., & Kawano, S. (2017). Morphological and physiological differences among cultivation lines of *Undaria pinnatifida* in a common garden experiment using a tank culture system. *Journal of Applied Phycology*, *29*, 2287–2295. https://doi.org/10.1007/s10811-017-1170-y

Schluter, D. (2000). *The ecology of adaptive radiation*. Oxford, UK: Oxford University Press. 296 pp.

Silvertown, J., Dodd, M., Gowing, D., Lawson, C., & McConway, K. (2006). Phylogeny and the hierarchical organization of plant diversity. *Ecology*, *87*, S39–S49. https://doi.org/10.1890/0012-9658(2006)87[39:PATHOO]2.0.CO;2

Silvertown, J., McConway, K., Gowing, D., Dodd, M., Fay, M. F., Joseph, J. A., & Dolphin, K. (2006). Absence of phylogenetic signal in the niche structure of meadow plant communities. *Proceedings of the Royal Society B: Biological Sciences*, *273*, 39–44. https://doi.org/10.1098/rspb.2005.3288

Slobodkichoff, C. N., & Schulz, W. C. (1980). Measures of overlap. *Ecology*, *61*, 1051–1055.

Starko, S., Bailey, L. A., Creviston, E., James, K. A., Warren, A., Brophy, M. K., … Neufeld, C. J. (2019). Environmental heterogeneity mediates scale-dependent declines in kelp diversity on intertidal rocky shores. *PLoS ONE*, *14*, e0213191. https://doi.org/10.1371/journal.pone.0213191

Starko, S., Claman, B. Z., & Martone, P. (2014). Biomechanical consequences of branching in flexible wave-swept macroalgae. *New Phytologist*, *206*, 133–140. https://doi.org/10.1111/nph.13182

Starko, S., Demes, K. W., Neufeld, C. J., & Martone, P. T. (2020). Data from: Convergent evolution of niche structure in Northeast Pacific kelp forests. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.18931zctg

Starko, S., & Martone, P. (2016a). Evidence of an evolutionary-developmental trade-off between drag avoidance and tolerance strategies in wave-swept intertidal kelps (Laminariales, Phaeophyceae). *Journal of Phycology*, *52*, 54–63. https://doi.org/10.1111/jpy.12368

Starko, S., & Martone, P. T. (2016b). An empirical test of 'universal' biomass scaling relationships in kelps: Evidence of convergence with seed plants. *New Phytologist*, *212*, 719–729. https://doi.org/10.1111/nph.14120

Starko, S., Soto Gomez, M., Darby, H., Demes, K. W., Kawai, H., Yotsukura, N., … Martone, P. T. (2019). A comprehensive kelp phylogeny sheds light on the evolution of an ecosystem. *Molecular Phylogenetics and Evolution*, *136*, 138–150. https://doi.org/10.1016/j.ympev.2019.04.012

Stelling-Wood, T. P., Gribben, P. E., & Poore, A. G. B. (2020). Habitat variability in an underwater forest: Using a trait-based approach to predict associated communities. *Functional Ecology*, *34*, 888–898. https://doi.org/10.1111/1365-2435.13523

Steneck, R. S., & Dethier, M. N. (1994). A functional group approach to the structure of algal-dominated communities. *Oikos*, *69*, 476–498. https://doi.org/10.2307/3545860

Steneck, R. S., Graham, M. H., Bourque, B. J., Corbett, D., Erlandson, J. M., Estes, J. A., & Tegner, M. J. (2002). Kelp forest ecosystems: Biodiversity, stability, resilience and future. *Environmental Conservation*, *29*, 436–459. https://doi.org/10.1017/S0376892902000322

Stone, L., & Roberts, A. (1990). The checkerboard score and species distributions. *Oecologia*, *85*, 74–79. https://doi.org/10.1007/BF00317345

Swenson, N. G., & Enquist, B. J. (2007). Ecological and evolutionary determinants of a key plant functional trait: Wood density and its community-wide variation across latitude and elevation. *American Journal of Botany*, *94*, 451–459. https://doi.org/10.3732/ajb.94.3.451

Teagle, H., Hawkins, S. J., Moore, P. J., & Smale, D. A. (2017). The role of kelp species as biogenic habitat formers in coastal marine ecosystems. *Journal of Experimental Marine Biology and Ecology*, *492*, 81–98. https://doi.org/10.1016/j.jembe.2017.01.017

Topinka, J., Tucker, L., & Korjeff, W. (1981). The distribution of fucoid macroalgal biomass along central coastal maine. *Botanica Marina*, *24*, 311–320. https://doi.org/10.1515/botm.1981.24.6.311

Ulrich, W., Sewerniak, P., Puchałka, R., & Piwczyński, M. (2017). Environmental filtering triggers community assembly of forest understory plants in Central European pine stands. *Scientific Reports*, *7*, 274.

Vamosi, S. M., Heard, S. B., Vamosi, J. C., & Webb, C. O. (2009). Emerging patterns in the comparative analysis of phylogenetic community structure. *Molecular Ecology*, *18*, 572–592. https://doi.org/10.1111/j.1365-294X.2008.04001.x

van der Valk, A. G. (1981). Succession in wetlands: A Gleasonian approach. *Ecology*, *62*, 688–696.

Verbruggen, H., Tyberghein, L., Pauly, K., Vlaeminck, C., Nieuwenhuyze, K. V., Kooistra, W. H. C. F., … Clerck, O. D. (2009). Macroecology meets macroevolution: Evolutionary niche dynamics in the seaweed *Halimeda*. *Global Ecology and Biogeography*, *18*, 393–405.

Vermeij, G. J., Banker, R., Capece, L. R., Hernandez, E. S., Salley, S. O., Vriesman, V. P., & Wortham, B. E. (2019). The coastal North Pacific: Origins and history of a dominant marine biota. *Journal of Biogeography*, *46*, 1–18. https://doi.org/10.1111/jbi.13471

Webb, C. O. (2000). Exploring the phylogenetic structure of ecological communities: An example for rain forest trees. *The American Naturalist*, *156*, 145–155. https://doi.org/10.1086/303378

Webb, C. O., Ackerly, D. D., McPeek, M. A., & Donoghue, M. J. (2002). Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, *33*(1), 475–505. https://doi.org/10.1146/annurev.ecolsys.33.010802.150448

Wernberg, T., & Filbee-Dexter, K. (2019). Missing the marine forest for the trees. *Marine Ecology Progress Series*, *612*, 209–215. https://doi.org/10.3354/meps12867

Wernberg, T., Krumhansl, K., Filbee-Dexter, K., & Pedersen, M. F. (2019). Chapter 3 – Status and trends for the world's kelp forests. In C. Sheppard (Ed.), *Seas: An environmental evaluation* (2nd ed., pp. 57–78). Amsterdam, The Netherlands: Elsevier.

Wiens, J. J. (2008). Commentary on Losos (2008): Niche conservatism déjà vu. *Ecology Letters*, *11*, 1004–1005. https://doi.org/10.1111/j.1461-0248.2008.01238.x

Wiens, J. J., Ackerly, D. D., Allen, A. P., Anacker, B. L., Buckley, L. B., Cornell, H. V., … Stephens, P. R. (2010). Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters*, *13*, 1310–1324. https://doi.org/10.1111/j.1461-0248.2010.01515.x

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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