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RESEARCH ARTICLE

Changes in biodiversity and species associations along a latitudinal gradient

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Abstract. Biodiversity is currently threatened at local, regional, and global scales, and identifying the species that are vulnerable to these changes is essential for conservation efforts. For example, the breadth of species' ranges may offer important clues to their susceptibility to loss, as widespread species may be more resistant to loss than species with a narrower range breadth. To determine the potential for shifts in community interactions along the latitudinal geographic ranges of species, we examined pair-wise associations between narrow-range endemic and widespread rocky intertidal species. We surveyed rocky intertidal species composition at eight sites along the California coast from San Diego to Cape Mendocino. Four sites were south of Point Conception, and four sites were north of Point Conception. Point Conception is a major biogeographic feature for coastal marine species, where sea surface temperatures transition from cool temperate waters in the north to warm temperate waters in the south. To determine whether pair-wise species associations were significant, we compared the observed communities' standardized effect size to a null model to determine which species occurred together more or less often than by chance. Across all sites, widespread species were considerably more abundant than narrow-range endemic species, and the majority of species were widespread. However, total species richness was unrelated to the number of widespread species, and was, instead, determined by the number of narrow-range endemic species present at a site. Our analyses suggest that species are more aggregated than segregated south of Point Conception, but the opposite is true north of Point Conception. Additionally, we found that species associations between narrow-range endemics drove the overall patterns in species associations. One possible explanation for these patterns is that positive interactions, especially those involving narrow-range endemic species, are more important in southern California's more thermally stressful intertidal habitats.

Key words: Biogeography, California, communities, latitudinal gradient, Point Conception, rocky intertidal, species associations

Introduction

Global biodiversity is currently threatened by a variety of stressors, including climate change (Pecl et al. 2017). As environmental conditions continue to change, species are faced with limited response options: undergo a geographic range shift, adapt to the new conditions, increase use of facilitative habitats, or go locally extinct (Bellard et al. 2012, Singer et al. 2013, Kadowaki et al. 2016, Jurgens and Gaylord 2018). Biodiversity declines have increased in the last century due to strong human impacts (Barnosky et al. 2011, Ceballos et al. 2015), and these declines are likely to alter the functioning of ecosystems (Naeem et al. 2012). It is essential to understand the potential for global change to impact biodiversity so that better decisions can be made regarding conservation and restoration of ecosystems, habitats, and species (Bellard et al. 2012).

Not all species are likely to respond to global changes in the same way. For example, widespread species, with broad biogeographic distributions and tolerances to a wide variety of environmental conditions, might be less susceptible to the effects of climate change. In contrast, narrow-range endemic species tend to have limited geographic ranges because of their restricted physiological tolerances to abiotic conditions, recent evolutionary history, or dispersal barriers. These attributes of narrow-range endemic

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species make local extinctions and range shifts more likely (Malcolm et al. 2006). As temperatures continue to rise, some narrow-range endemic species, such as vertebrate and plant species, have been declining in abundance, causing shifts in community assembly and structure (Malcolm et al. 2006). These losses can potentially have strong cascading effects within the ecosystem, causing shifts in species interactions along latitudinal gradients (Travis 1996, Leonard 2000, Pennings and Silliman, 2005, Freestone et al. 2010, Freestone and Osman 2011). It is essential to understand the relationships between species' distributions, interactions, and susceptibility to loss in order to predict species- and community-level responses to global change (Sorte 2013, Maguire et al. 2015).

Interactions between species can change along latitudinal gradients because of changes in environmental conditions (Leonard 2000, Freestone and Osman 2011). For example, a negative interaction under benign conditions may shift to a facilitative interaction when the interacting species live in a harsh environment. Leonard (2000) found that the canopy-forming seaweed *Ascophyllum nodosum* increased the survival of barnacle recruits south of Cape Cod, Massachusetts, where temperatures were high. However, this facilitative effect disappeared at cooler northern sites. Climate change is also likely to change species' interactions because of differences in the responses of individual species. Sorte et al. (2010) found that many species have undergone poleward range shifts, but the speed of these shifts differs among species. At more local scales, an increase in temperature can lead to a change in the competitive abilities of species, resulting in a shift in the dominant species in a community (Sorte and White 2013). For these marine species, the exposure to warmer air and water temperatures can have strong impacts on species dispersal, development, and stress tolerance. Kelly and Eernisse (2007) found that larval development is faster at warmer locations within a species range, leading to reduced dispersal of those genotypes. Additionally, the expression of heat-shock proteins has also been shown to differ across a species range with higher expression at the range edge than at the center of the distribution (e.g., Sorte and Hoffman 2004).

Many studies have experimentally examined how variation in biodiversity will respond to simulated warming to try to understand how species interactions will change in the future (e.g., Sorte et al. 2010, Gruner et al. 2017). However, observational data can also help us to understand the current state of species interactions. Understanding how species associate with one another and interact can help identify how species losses could impact the community as a whole. If a species is susceptible to extinction (e.g., because of its limited tolerance to changing environmental conditions) then extinction of that vulnerable species may have a cascading effect on other species that it associates and interacts with in an ecological community. One method used to better understand community dynamics is to examine species co-occurrences, a pairwise approach to assess species associations. A species association can be defined as aggregated, segregated, or neutral. A species association is aggregated when species co-occur together more often than expected by chance. An association is segregated when species occur together less often than expected by chance. A neutral association occurs when species co-occurrence cannot be defined as segregated or aggregated (Puri et al. 2014). In this study, we apply this technique to evaluate whether there are regional differences in species associations on opposite sides of a biogeographic boundary, with a particular focus on whether narrow-range endemic and widespread species differ in their associations. Together, narrow-range endemic and widespread species are assembled into communities, but these communities change with latitude, and especially across biogeographic boundaries.

Our research aimed to determine how species associations vary across a latitudinal gradient and how species associations among narrow-range endemics and widespread species differ on along that gradient. We hypothesized that (1) variation in diversity patterns would be primarily associated with widespread species because widespread species are more likely to be present at many sites; (2) narrow-range endemic species' associations would differ from those of widespread species because widespread species are able to tolerate a wide range of physiological conditions and may not require as many facilitative interactions as narrow-range species; and (3) species associations would change with latitude, with more aggregated species at southern latitudes due to higher thermal and desiccation stresses. We predicted that narrow-range endemic species would exhibit more aggregated associations due to co-evolved relationships with other narrow-range endemic species. Additionally, we predicted that associations would differ regionally and latitudinally due to changes in abiotic conditions.

Methods

Study system

We studied the species living on California, USA, rocky intertidal shorelines (see Supporting Information, Table S1, for species list). The California coast can be divided into two biogeographic provinces, the Oregonian and the Californian, which are separated by Point Conception, a major biogeographic feature for coastal marine species on the California coast. At Point Conception, water temperatures transition from cool temperate waters in the north to warm temperate waters in the south, and larval dispersal is limited (Dawson 2001, Hohenlohe 2004, Sotka et al. 2004, Fig. 1). Many intertidal species ranges begin or end near Point Conception. To the north, the Oregonian province extends from Point Conception to Dixon Entrance at the border between Alaska (USA) and British Columbia (Canada). To the south, the Californian province extends from Point Conception to Punta Eugenia in Baja California (Mexico) (Valentine 1966, Blanchette et al. 2008).
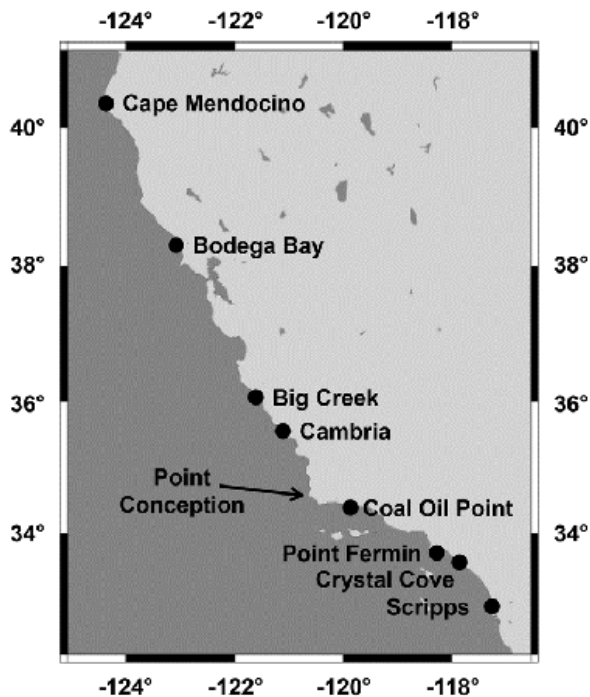
Figure 1. Eight study sites spanned the California, USA, rocky shoreline. Cape Mendocino, Bodega Bay, Big Creek, and Cambria are north of Point Conception. Coal Oil Point, Point Fermin, Crystal Cove, and Scripps are south of Point Conception.

We grouped rocky intertidal species on the California coast based on whether their ranges crossed the biogeographic boundary at Point Conception. We defined widespread species as those that had geographic ranges that spanned Point Conception. For example, the range of the California mussel, *Mytilus californianus*, extends from the Aleutian Islands in Alaska to Baja California, spanning Point Conception, as well as other biogeographic boundaries (Morris et al. 1980). In contrast, we defined narrow-range endemic species as those with narrow biogeographic ranges that did not extend past Point Conception. For example, the brown seaweed *Fucus gardneri* ranges from Washington to Point Conception, and its range does not cross a major biogeographic boundary (Abbott and Hollenberg 1992). These species are typically adapted to a more limited range of abiotic conditions; species at higher latitudes are typically more adapted to cooler conditions, whereas species at lower latitudes are usually adapted to warmer temperatures.

Study sites

We performed a latitudinal survey of sites spanning 1,044 km of the California rocky shoreline between March and September of 2015. We surveyed eight sites, ranging from Cape Mendocino in northern California to Scripps Reserve in southern California: Cape Mendocino (CM; 40.34° N, 124.36° W), Bodega Bay (BB; 38.32° N, 123.07° W), Big Creek (BC; 36.07° N,

121.61° W), Cambria (CAM; 35.56° N, 121.08° W), Coal Oil Point (COP; 34.41° N, 119.88° W), Point Fermin (PF; 33.71° N, 118.29° W), Crystal Cove (CC; 33.58° N, 117.84° W), and Scripps (SCR; 32.88° N, 117.26° W; Fig. 1). Four of our sites were north and west of the biogeographic boundary at Point Conception (34.45° N, 120.40° W), and four were south and east of Point Conception.

Survey methods

At each site, we laid down 10 transects perpendicular to the water line. We surveyed species composition in a 0.25 m^2 quadrat positioned every vertical 0.5 m on each transect, starting at the mean lower-low water level. Sampling effort varied due to site topography, with quadrats sampled at each site ranging from 14 to 40 as follows: CM = 33, BB = 40, BC = 33, CAM = 30, COP = 14, PF = 24, CC = 25, SCR = 30. Locations at each site were chosen haphazardly based on where a 50 m transect could be placed parallel to the water's edge. Most sites were relatively consistent in the number of quadrats sampled. We estimated the percent cover of sessile invertebrates and algae using 100 evenly spaced grid points. All mobile invertebrates were counted within each quadrat. In most cases, we were able to identify organisms to species in the field. When species were identified only to a higher taxonomic level (e.g., genus), then we determined the possible species that could have been present and assigned the appropriate distribution based on all possible species within that group. For example, *Phyllospadix* spp. was identified as widespread because both *P. torreyi* and *P. scouleri* are found from Canada to Baja California (Phillips and Meñez 1988).

Statistical analyses

To examine community associations between species, we calculated standardized effect sizes (SES) of pair-wise species associations (Sfenthourakis et al. 2006). A SES score is a comparison of mean co-occurrence of species pairs to a null model. We defined a SES value as significant if it was at least one standard deviation (± 1.96) from the mean. SES values are calculated from presence-absence matrices, so we converted our abundance and percent cover data into presence-absence. Simulations and analyses were conducted in R using the community ecology package, vegan (version 2.3-2). We calculated SES values for every species pair on each transect (n = 10) at each site. The number of significant associations was normalized by the number of possible associations at each site. Most associations were not significant; therefore, the percentage of significant associations was small, ranging from 0.1 to 4.1% (Table 1). We identified a total of 86 taxa in our surveys, which corresponds to a total of 3,655 (= [86^2 -86]/2) potential pairwise interactions if every species were able to interact with every other species. Approximately 5% of all possible species pairs, or 183 pairs, could be expected to show a deviating association by chance. However, the total

Table 1. Number of species associations at each site: total, narrow-narrow, narrow-widespread, and widespread-widespread

Site	Total	Narrow-narrow	Narrow-widesperad	Widespread-widespread
Scripps	496	6	7	6
Crystal Cove	378	2	11	9
Point Fermin	378	2	10	14
Coal Oil Point	861	1	13	37
Cambria	465	1	12	18
Big Creek	595	0	5	14
Bodega	741	0	4	11
Cape mendocino	595	0	4	19

number of observed significant pairwise associations (206) was greater than 183 (Table 1).

To determine how latitude influenced species associations, we used linear regression to determine the effect of latitude on the number of significant species associations, the number of significant associations between narrow-range endemic and widespread species, and the number of significant associations between widespread species. We also used t-tests to determine whether there were regional differences in aggregations and segregations.

Results

Species abundance and richness

Our surveys identified an average (±SEM) of 25 (± 1) widespread species and 10 (± 2) narrow-range endemic species at each site (Fig. 2).

Most of the species at each site were widespread, except at Cambria where the species richness was split evenly between widespread and narrow-range endemic species (Fig. 3a). Across all sites, narrow-range endemic species were significantly lower in abundance than widespread species (Fig. 3b). At the three most northern sites (Big Creek, Bodega Bay, and Cape Mendocino), relative narrow-range endemic species abundance was only 2 to 8% (Fig. 3b).

However, total species richness at sites was unrelated to the number of widespread species at those sites (Linear Regression, $R^2 < 0.01$, $p = 0.901$; Fig. 4a). Instead, total species richness was most strongly associated with narrow-range endemic species richness (Fig. 4b; Linear Regression, $R^2 = 0.78$, $p = 0.003$). Cambria was the most diverse location, with 42 species, likely associated with its proximity to Point Conception. Big Creek had the lowest overall species richness with only 28 species. There were more
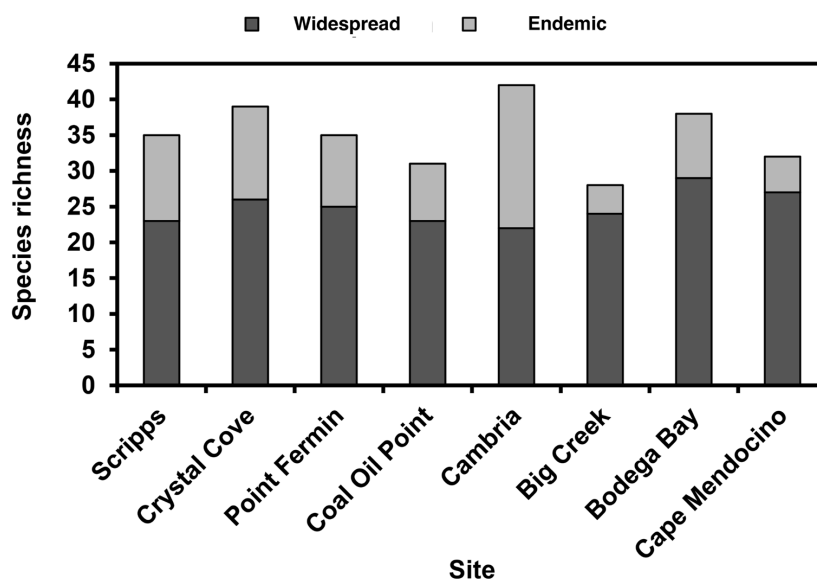
Figure 2. Diversity of narrow-range endemic and widespread species. Sites are listed latitudinally from south to north. The average (±SEM) of widespread richness was 25 (±1) species at all sites. Higher species richness (e.g., at Crystal Cove and Cambria) was primarily due to narrow-range endemic species.
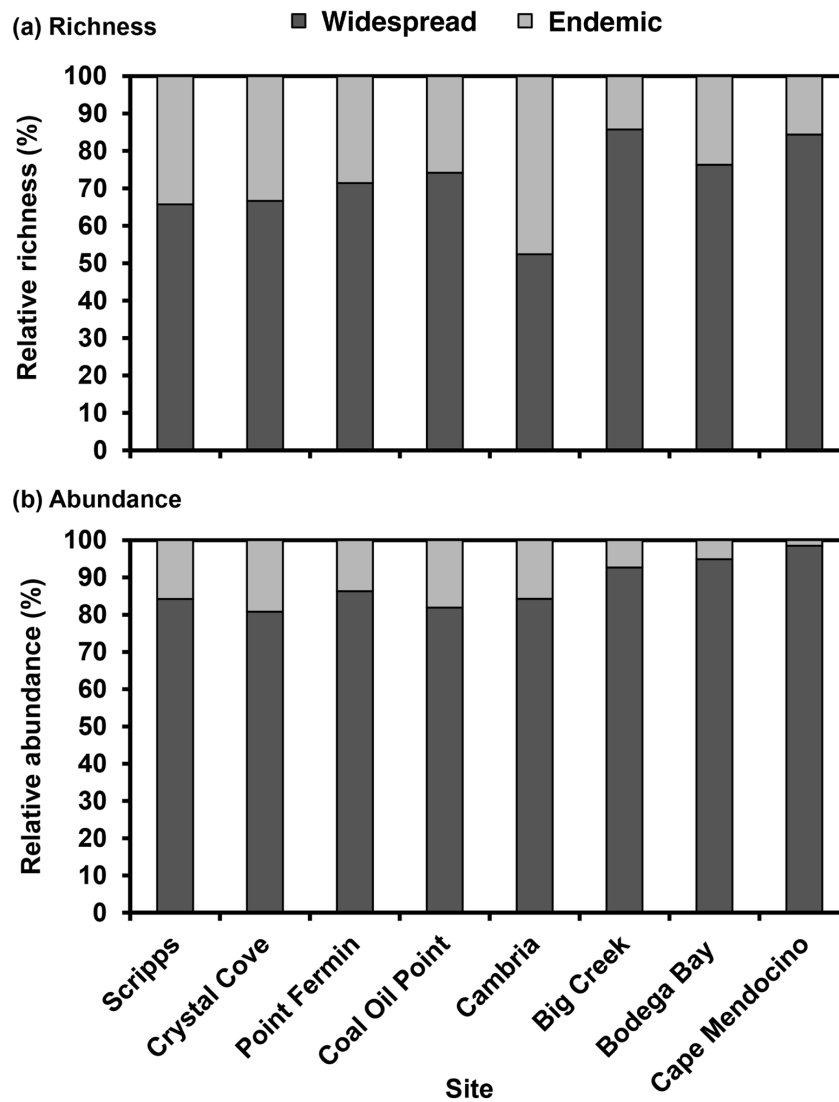
Figure 3. Relative species richness and abundance. **(a)** The majority of species were widespread species; on average, narrow-range endemic richness across sites made up less than 30% of total richness. **(b)** Narrow-range endemic species made up 20% or less of the total abundance at each site.

narrow-range endemic species in southern California (i.e., south of Point Conception) than in northern California; 17 southern narrow-range endemic species and 10 northern narrow-range endemic species were present in our surveys.
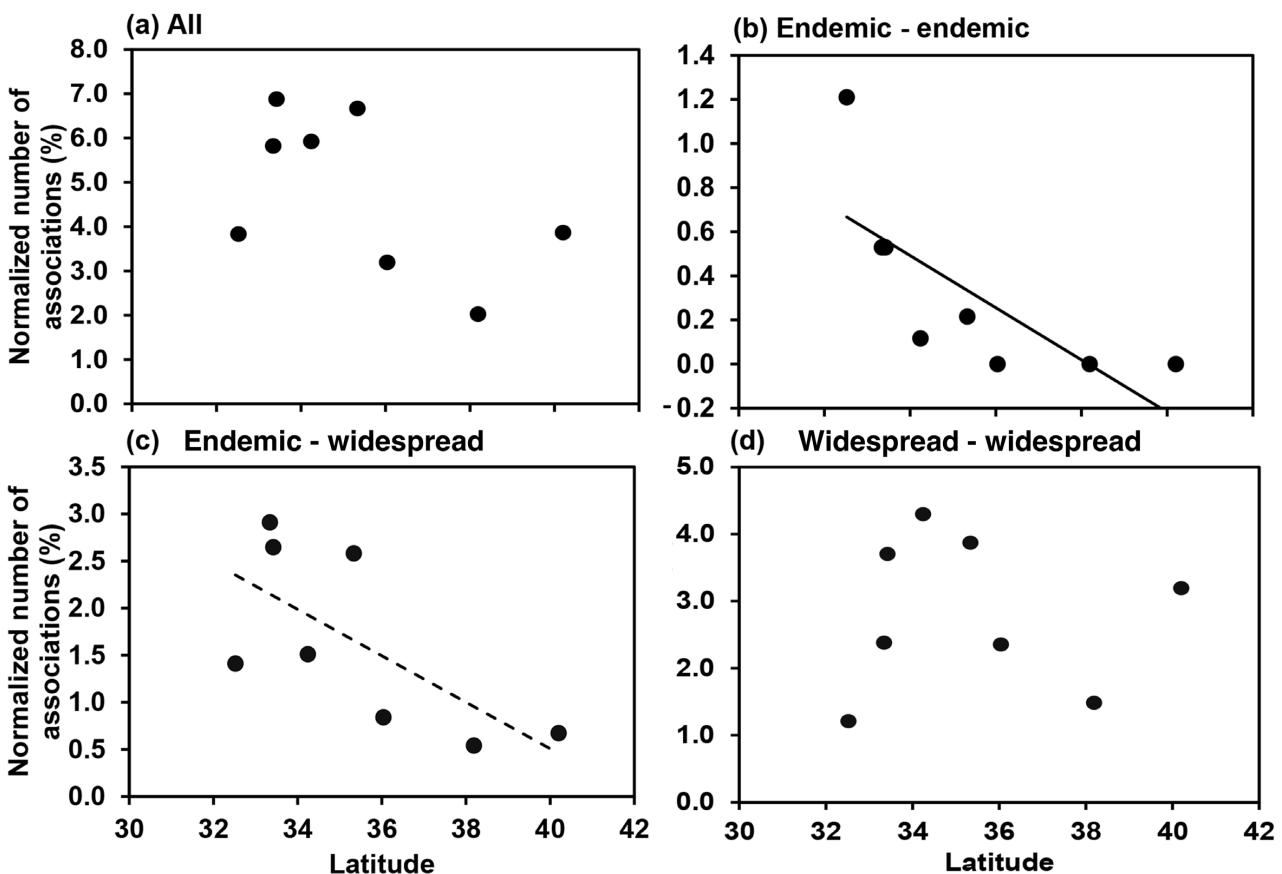
Species associations

When all significant species associations were considered, we found that the total normalized number of associations was not related to latitude (Linear Regression: $R^2 = 0.18$, $F_{1,6} = 2.58$, $p = 0.185$; Fig. 5a). However, as latitude increased, the number of narrow-range endemic pair-wise species associations decreased (Linear Regression, $R^2 = 0.48$, $F_{1,6} = 7.43$, $p = 0.034$; Fig. 5b). Similarly, the number of significant associations between narrow-range endemic and

widespread species tended to decrease with increasing latitude (Linear Regression, $R^2 = 0.38$, $F_{1,6} = 5.27$, $p = 0.061$; Fig. 5c). However, there was no relationship between the number of significant associations and latitude when only associations between widespread species were considered (Linear Regression, $R^2 = 0.17$, $F_{1,6} = 0.00$, $p = 0.980$; Fig. 5d).
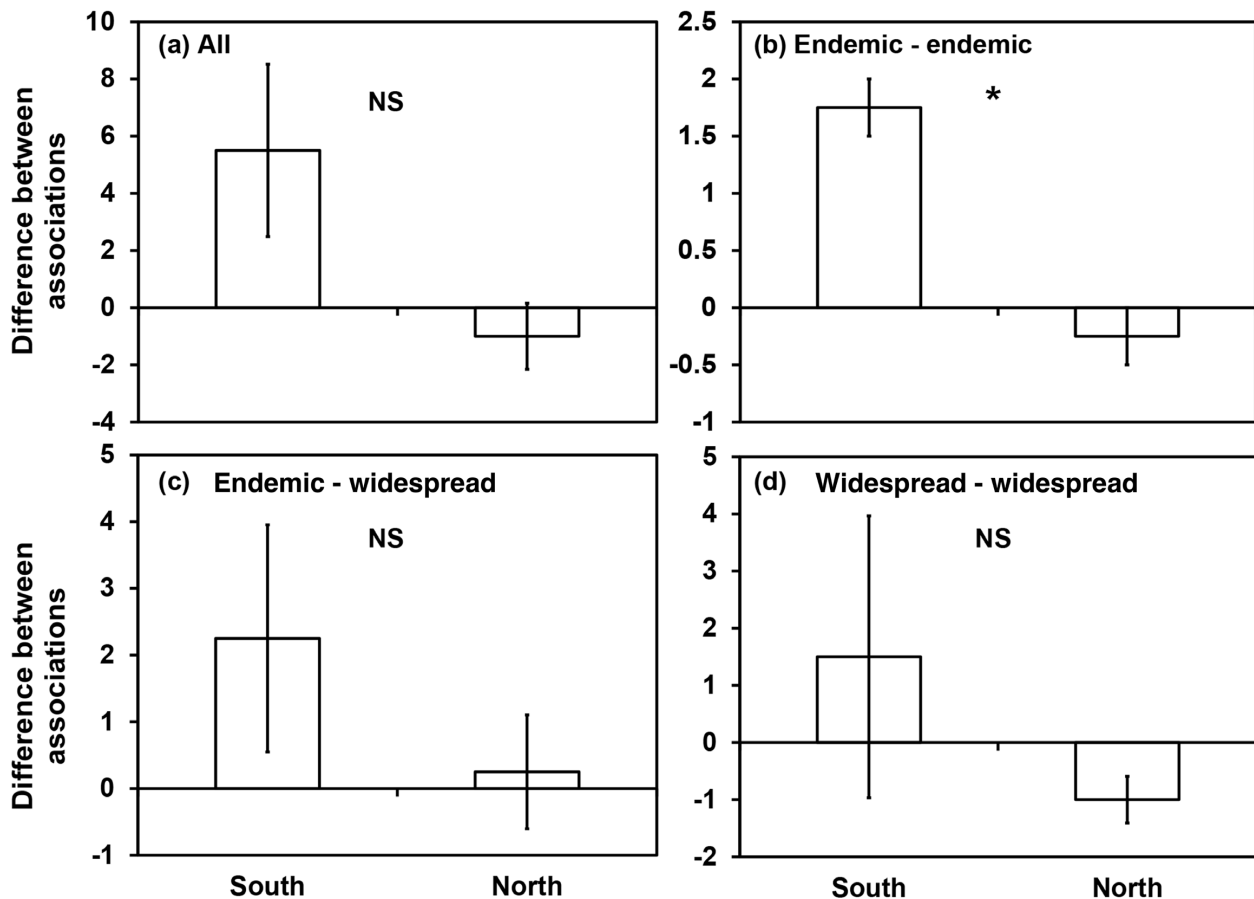
Species aggregations were more common south of Point Conception than north of Point Conception regardless of the type of species included in the analysis (Fig. 6). When all species associations were included, there was no difference between the two regions ($t = 2.01$, df = 3.86, $p = 0.117$). However, when only associations between narrow-range endemic species were included in the analysis, the difference between aggregated and segregated associations
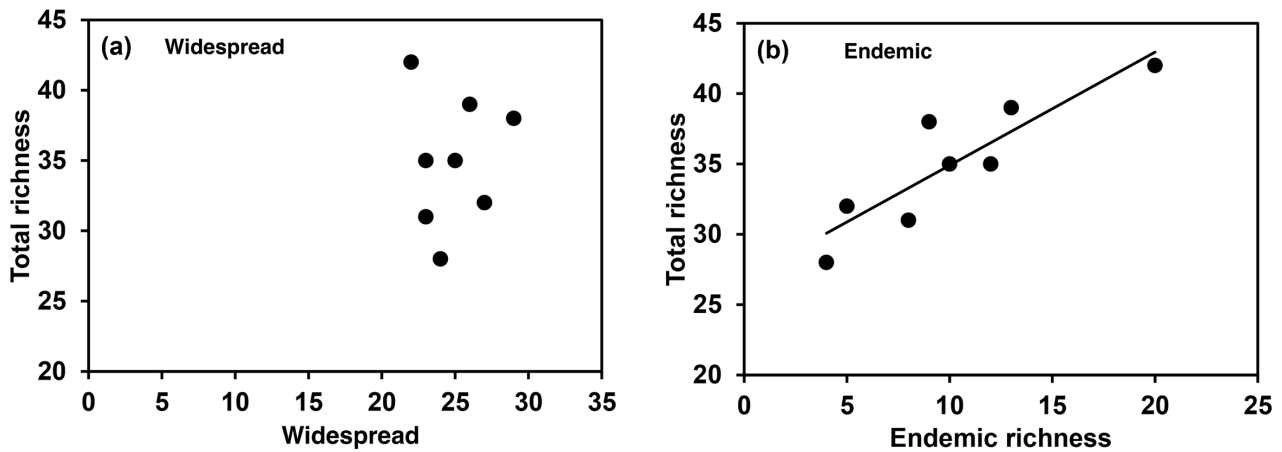
Figure 4. Relationship between species richness and the number of **(a)** widespread species and **(b)** narrow-range endemic species. Whereas the number of widespread species was unrelated to total species richness ($R^2 = 0.00$, $p = 0.901$), the number of narrow-range endemic species at a site was strongly correlated with total species richness ($R^2 = 0.78$, $p = 0.003$).

Figure 5. Number of species associations normalized by the number of possible associations by latitude: **(a)** all species associations, **(b)** associations between narrow-range endemic species, **(c)** associations between narrow-range endemic and widespread species, and **(d)** associations between widespread species. The number of associations decreased with increasing latitude when narrow-range endemic species were included (a, b, and c). When only widespread species were includes there was no relationship between latitude and species associations.

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Figure 6. Average (±SEM) differemce between aggregated and segregated species associations south and north of Point Conception: **(a)** all species associations, **(b)** associations between narrow-range endemic species, **(c)** associations between narrow-range endemic and widespread species, **(d)** associations between widespread species. In all cases, aggregated associations were more common south of Point Conception than north. (N = 4 sites per region)

in the south was higher than the difference in the north (t = 5.65, df = 6, p = 0.001). When widespread species were included (either widespread-widespread associations or associations between widespread and narrow-range endemic species) there was no difference between sites south and north of Point Conception (widespread-widespread: t = 1.0, df = 3.16, p = 0.388; narrow-range endemic-widespread: t = 1.1, df = 4.42, p = 0.348).

Discussion

We had hypothesized that widespread species would drive patterns of abundance. This hypothesis was supported: widespread species were universally the most abundant species at our study sites (Figs. 2, 3), and they represented the majority of species across all sites (Fig. 3). We also hypothesized that widespread species would drive patterns of diversity. However, the number of species at a location was actually most strongly related to narrow-range endemic species richness; widespread richness was unrelated to total

species richness (Fig. 4). Furthermore, even though narrow-range endemic species were not highly abundant, they were involved in an unexpectedly large proportion of significant associations, indicating that, despite their low abundances, narrow-range endemic species may be disproportionately important in determining community structure (Bracken and Low 2012, Mouillot et al. 2013).

The number of significant species associations tended to decrease with latitude for all species pairs except widespread pairs (Fig. 5). This trend was only statistically significant for narrow-range endemic species pairs, which could be associated with two phenomena. First, slightly fewer narrow-range endemic species were present at sites north of Point Conception. Second, species interactions – which can underlie associations – can change with latitude. For example, Freestone and Osman (2011) found that communities at lower latitudes were more influenced by local interactions with narrow-range endemic species and those at higher latitudes were influenced by widespread species. Leonard (2000) showed that interactions

between the canopy-forming seaweed *Ascophyllum nodosum* and barnacles changed from negative to positive at southern sites where temperatures were higher. The relationship between species associations and latitude – particularly for narrow-range endemic species – suggests that these associations may be altered under future climatic conditions.

Regionally, we observed more aggregated associations in the south and more segregated associations in the north (Fig. 6). Since aggregated associations can be indicative of positive interactions, more aggregations in the south could indicate that positive interactions are more common in the more thermally stressful environment of southern California. However, aggregated associations may also indicate positive density dependence between a consumer and its resources. Therefore, these associations need to be examined on a case-by-case basis to identify the nature of the interaction between the species. These regional differences could also be due to differences in the vertical extent of the intertidal zone. Northern sites were generally characterized by broader intertidal ranges, despite similar tidal amplitudes, likely due to larger waves on the more exposed coasts north of Point Conception. With more vertical space in the intertidal zone, there is more potential for segregation.

We can use the observed associations between species pairs to infer the nature of the relationship between the two species. For example, we found that the widespread species *Mytilus californianus* (California mussel) and *Pollicipes polymerus* (gooseneck barnacle) were aggregated together more often than by chance, likely because they share a similar niche in the intertidal zone. Two chitons, *Nuttallina fluxa* and *Cyanoplax hartwegii* are narrow-range endemic species in the Californian province, and we found that they were segregated more often than by chance. *Nuttallina* typically lives higher on the shore and is more commonly found on bare rock. In contrast, *Cyanoplax* is found at intermediate tidal elevations and almost exclusively under canopies formed by the brown seaweed *Silvetia compressa*. Additionally, these two species compete for the same food source: crustose seaweeds and microalgae. This association pattern may be driven by competition for food or by physiological tolerance differences between these two species. However, the relationship between *Silvetia* and *Cyanoplax* is an example of an aggregation associated with stress amelioration; removal of the *Silvetia* canopy results in declines in *Cyanoplax* (Sapper and Murray 2003). This relationship is representative of species aggregations that are more common in southern California because of the harsher abiotic conditions associated with this region (Schoch et al. 2006).

Endemic species are a focus for conservation because they increase overall diversity and maintain community structure (Stachowicz et al. 2008). Endemic species are the targets of many conservation efforts across biomes. These species are particularly susceptible to extinctions because of their constrained geographic ranges, and the loss of these species may have cascading effects (Malcolm et al. 2005). The number of endemic species has been used to identify "biodiversity hotspots" where conservation efforts and funds should be focused (Myers et al. 2000). Our study shows that narrow-range endemic species may have a strong role in shaping rocky intertidal communities by influencing variation in diversity patterns along the California coast. Overall, we found that narrow-range endemic species were characterized by different associations compared to widespread species. Species associations changed latitudinally, with more associations south of Point Conception than in the north. Despite their low abundances, narrow-range endemic species were highly influential in these trends, highlighting their importance in rocky shore communities.

As climate change continues to affect species' geographic distributions, narrow-range endemic species may be disproportionately threatened due to their narrow biogeographic ranges and limited tolerances to abiotic conditions. Given that narrow-range endemic species were disproportionately responsible for variation in patterns of both species richness and species associations, climate-mediated shifts in their distributions are likely to alter biodiversity, species associations, and–by extension–ecosystem functioning, including shifts in interactions among species and/or changes in overall community productivity (Leonard 2000, Bracken and Low 2012, Naeem et al. 2012). Understanding how narrow-range endemics are associated with other species in ecological communities can be an important aspect to consider in conservation and management planning to maintain current ecosystem functioning. Linking biogeography, biodiversity, and species associations can help elucidate how current communities are structured and allow better predictions regarding how communities and ecosystems are likely to change in the future (Blonder et al. 2017).

Acknowledgements

Data Accessibility Statement

All data are available through the UC Natural Reserve System archives. This work was performed (in part) at sites in the University of California Natural Reserve System (Scripps Coastal Reserve, Kenneth S. Norris Rancho Marino Reserve, Landels-Hill Big Creek Reserve, Coal Oil Point Natural Reserve, and Bodega Marine Reserve. Scripps Coastal Reserve DOI: 10.21973/

N3QH2R, Kenneth S. Norris Rancho Marino Reserve DOI:10.21973/N37943, Landels-Hill Big Creek Reserve DOI:10.21973/N3NH24, Coal Oil Point Natural Reserve DOI:10.21973/N3Z07N, Bodega Marine Reserve DOI:10.21973/N32Q05

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