Global Ecology and Biogeography

WILEY

Global Ecology and Biogeography | A Journal of Macroecology

RESEARCH ARTICLE

Two Decades of Community Responses Reveal a Consistent Increase in Species Occurrences in South-Eastern Pacific Rocky Shores

Mauricio H. Oróstica[1,2] | Paulina A. Arancibia[3] | Otso Ovaskainen[3,4] | Sergio A. Navarrete[2,5,6,7] | Bernardo R. Broitman[2,8]

[1]Universidad Católica del Maule, Vicerrectoría de Investigación y Postgrado, Centro de Investigación de Estudios Avanzados del Maule (CIEAM), Talca, Chile | [2]Instituto Milenio en Socio-Ecología Costera, SECOS, Santiago, Chile | [3]Department of Biological and Environmental Sciences, University of Jyväskylä, Jyväskylä, Finland | [4]Faculty of Biological and Environmental Sciences, University of Helsinki, Helsinki, Finland | [5]Estación Costera de Investigaciones Marinas, Las Cruces, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Santiago, Chile | [6]Millenium Nucleus for Ecology and Conservation of Temperate Mesophotic Reefs Ecosystems (NUTME), Pontificia Universidad Católica de Chile, Santiago, Chile | [7]Centro de Investigación Oceanográfica COPAS COASTAL, Universidad de Concepción, Concepción, Chile | [8]Departamento de Ciencias, Facultad de Artes Liberales, Universidad Adolfo Ibáñez, Viña del Mar, Chile

Correspondence: Mauricio H. Oróstica (morostica@ucm.cl)

Received: 14 February 2025 | **Revised:** 10 November 2025 | **Accepted:** 21 November 2025

Handling Editor: Jonathan Belmaker

Keywords: community assembly | environmental drivers | multi-taxa | species-responses | species-taxonomy | species-traits

ABSTRACT

Aim: Understanding how diverse communities respond to environmental fluctuations is a central challenge in ecology. Here, we assessed how communities responded to environmental variation over the past 23 years and evaluated the extent to which these responses can be associated with taxonomic relationships, as well as biological and ecological species traits.

Location: Central portion of the Humboldt Upwelling Ecosystem, with 22 rocky shore survey sites spanning 8° of latitude (28° S–36° S).

Time Period: 2000–2023.

Major Taxa Studied: Intertidal zone communities.

Methods: We used joint species distribution models to integrate quantitative survey data, satellite sea surface temperature (SST) as a proxy for environmental conditions, taxonomic information and species biological traits along a latitudinal gradient with heterogeneous thermal conditions.

Results: Our proxy for environmental variation revealed weak and non-significant SST cooling at central sites, whereas sites near 30° S showed slight warming trends. Taxonomic relationships and individual species traits were weakly associated with their collective responses to SST variability. However, we identified a consistent increase in the occurrence of both macroalgal and invertebrate species across the region. The occurrence of macroalgal species was more sensitive to SST variation than invertebrates, with responses shifting from positive at equatorward sites to increasingly negative at poleward sites. Patterns of species co-occurrence were strongly dependent on spatial scale, particularly among invertebrates.

Main Conclusions: Species occurrences increased across the region, but these responses were not significantly associated with taxonomic relatedness or with easily assigned species traits. This pattern likely indicates comparatively low niche conservatism

Mauricio H. Oróstica and Paulina A. Arancibia should be considered joint first authors.

within these communities in relation to SST responses, while other structuring processes—such as species interactions—are not well captured by the traits examined. As other studies have detected slight cooling trends over the past two decades, our results suggest that the lack of community-wide reorganisation reflects the absence of a clear environmental driver.

1 | Introduction

Understanding how multiple co-occurring and interacting species respond to environmental change is a central quest in biogeography, macroecology and evolutionary ecology (Wiens et al. 2010). Species respond to environmental variability either by migrating or adjusting their physiological and overall individual performance (Green et al. 2022). In many cases, these responses to environmental variation are conserved among species within lineages (Wiens and Graham 2005), generating correlated responses among related species (Wiens et al. 2010). On the other hand, species traits can modulate interactions within a community, as well as responses of the species to environmental stress, thus helping to explain patterns of community structure across environmental gradients (Herrera et al. 2023). Rapid environmental change is reshaping local communities as species shift ranges, alter their ecological performance and form novel assemblages, thereby altering ecological interactions (Fossheim et al. 2015; Pinsky et al. 2020; Vergés et al. 2019). Consequently, identifying community responses to environmental variation requires data across diverse taxa and matching the relevant spatial and temporal scales.

Temperature influences multiple physiological and ecological processes, both directly and indirectly (Bowler et al. 2017; Koussoroplis and Wacker 2016). Shifts in temperature—whether in average long-term values, ranges, extreme events, or overall thermal regimes—can compromise local population abundance and viability by limiting propagule production, reproduction and offspring survival (Bowler et al. 2017). For instance, in some species, survival declines at high temperatures, while reproduction can fail at low ones, so population growth peaks at intermediate temperatures, dropping at the extremes (Koussoroplis and Wacker 2016). In marine systems, seawater temperature also covaries with many other physical–chemical variables, such as inorganic nutrients, pH and dissolved oxygen (Mann and Lazier 2006). Ocean temperature, driven primarily by water movement, influences propagule dispersal and key ecological processes—both bottom-up (e.g., productivity) and top-down (e.g., predation)—that shape community structure (Menge et al. 2003; Sanford 1999).

Coastal upwelling in temperate eastern boundary regions is driven by equatorward winds that bring cold, nutrient-rich deep water to the surface (Bakun 1973; Mann and Lazier 2006). Global warming has strengthened land-ocean pressure gradients (Bakun 1990), intensifying upwelling and causing nearshore cooling in ecosystems like the Humboldt Current (García-Reyes et al. 2023; Sydeman et al. 2014). In situ and satellite datasets reveal modest but significant cooling trends from central Perú down to southern Chile, which are attributed to a poleward change in the position of the South Pacific Anticyclone (Aguirre et al. 2018; de la Maza et al. 2024; García-Reyes et al. 2023; Schneider et al. 2017; Weidberg et al. 2020).

The rocky shores of the Humboldt Current have served as key sites for studying the role of environmental processes on species adaptation, interactions and community dynamics in the intertidal system (Broitman et al. 2001; Castilla 1999; Navarrete et al. 2005; Santelices and Marquet 1998). So far, long-term shifts in species occurrences remain rare (Aguilera et al. 2020). Experimental manipulations have evidenced the strong influence of top-down processes in shaping local community structure, while regional-scale variation in bottom-up forcing drives shifts in community regulation pathways (Castilla 1999; Navarrete et al. 2022, 2005). These communities are taxonomically, trophically and functionally diverse, and include species with varying life histories (Castilla 1999). Given this complexity, understanding how Humboldt Current intertidal communities respond to environmental change requires examining how species' traits and taxonomic identities contribute to broader patterns of community assembly (Herrera et al. 2023).

Estimating temperature's direct effects on species traits is challenging due to its strong covariance with other environmental variables (Koussoroplis and Wacker 2016) and its influence on species interactions (Sanford 1999). Because temperature affects competitors and predators differently, and can result in measurable changes in species occurrences, single-species responses rarely scale up to communities. Moreover, trait-based responses to temperature may vary widely among species unconstrained by phylogeny. Understanding these responses requires examining multiple biological traits locally, and integrating them across broader spatial scales. Merging taxonomic, trait-based and environmental data offers a powerful framework for understanding community assembly (Ovaskainen et al. 2017), especially under the current scenario of global change. Nevertheless, applying integrative approaches to species-rich, taxonomically diverse communities is more complex than in homogeneous systems (Ford and Roberts 2020; Weigel et al. 2023). This complexity underscores the need for long-term, high-resolution ecological datasets across broad phylogenetic and taxonomic groups to capture shifts in species occurrences and their consequences for community assembly (Ovaskainen et al. 2017).

Unlike the global trend of warming, the Humboldt system's regional cooling presents a unique opportunity to explore how diverse communities respond to long-term environmental variability across a latitudinal gradient. We analysed 23 years of standardised, multi-site, ecological surveys using joint species distribution models, integrating taxonomy, species traits and sea surface temperature. We asked: (1) Can species traits predict their responses to environmental variation in macroinvertebrates and macroalgae? (2) Do related species share occurrence patterns and respond similarly to environmental variability, and thus show a broad form of niche conservatism? (3) Are community responses spatially structured along latitude, and do producers and consumers respond similarly? (4) Do species co-occurrence patterns vary across spatial scales, and how can such variation inform our understanding of

underlying ecological processes? Our goal is to assess whether species' occurrences share trends of increase or decline, and to examine how taxonomy, species traits and environmental variation jointly structure long-term community response patterns.

2 | Methods

2.1 | Study Region

Stretching over 6000 km (5°–56° S), the south-eastern Pacific coast spans multiple ecoregions with distinct biota (Herrera et al. 2023). Coastal upwelling is a mesoscale process (10–100 s of km) that, along the Humboldt region, exposes benthic organisms to cold, nutrient-rich, but low-oxygen and low-pH waters (Strub et al. 1998). This persistent oceanographic process shapes both local community dynamics and the biogeographical patterns in this region (Lara et al. 2019; Navarrete et al. 2005).

2.2 | Surveys, Data Collection and Local Environmental Filters

We compiled a long-term dataset from 22 sampling sites along the Chilean coast (28.09° S–36.07° S), sampled between 2000 and 2023. It includes extensive surveys from 2003 to 2005 (Broitman et al. 2011), unpublished data from 2012 to 2021–2023, and partial sampling from other years (2000–2002, 2006–2011, 2013–2020). In total, the dataset comprises 5536 sampling units collected mostly during spring and summer, with some additional samples obtained in winter and autumn. While broad in geographic and temporal scope, the dataset remains incomplete due to variability in sampling effort across years and sites (see Appendix S1 in Supporting Information: Figure S1.1).

Sampling methods consisted of three to six transects at each site—carried out during daytime and at low tide—where we located seven to 20 0.25 m^2 quadrats that were distributed haphazardly along the transect. At each site and date, we aimed at sampling the three main intertidal zones (high, mid and low tidal heights). We note that using Mean Low Water, or other physical tidal benchmarks based on ocean level, is ineffective in Chile's wave-dominated intertidal zones (Flores et al. 2019). To ensure consistent delimitation of intertidal zones from the onset of the monitoring programme, we relied on well-known biological indicators: a band of the kelp *Lessonia* spp. in the low zone; extensive cover of macroalgae and/or mussel beds in the mid zone; and widespread distribution of chthamalid species or bare rock at higher levels. To standardise surveys, transects for all quadrats were established and maintained using photographs and drawings. In addition, 18 of 22 of the sites are or were part of a larval supply monitoring programme, with collectors affixed to the rock with stainless-steel bolts at two different tidal heights since 1997; we consistently utilised the permanent bolts as benchmarks for transects (Navarrete et al. 2022, 2005). To reduce among-site differences, we deployed the transects on rocky shore platforms with an area greater than 30 × 5 m, characterised by a gentle shoreward slope (~20°–30°), a flat morphology, and similar wave exposure to the prevailing southwestern swell, while avoiding crevices, tide pools and vertical walls. Full details of the sampling protocols and site locations are provided elsewhere (Broitman et al. 2001).

2.3 | Temperature Patterns and Regional Environmental Filtering

To characterise site-level thermal patterns, we used satellite-derived night-time Sea Surface Temperature data (SST, °C) from MODIS Aqua (2000–2023), sourced from NASA's Ocean colour website (http://oceancolor.gsfc.nasa.gov), and created monthly gridded composites at 0.009° spatial resolution. While satellite data may miss high-frequency variability, it correlates closely with in situ SST over different timescales (Aravena et al. 2014; Lagos et al. 2005; Tapia et al. 2009).

For each site and year, we calculated five SST metrics: the 5th, 50th and 95th quintiles, the annual mean SST (SSTM) and the standardised annual anomaly (SSTA). Due to high collinearity, we retained SSTM to represent long-term thermal regimes, and SSTA to capture interannual variability. To assess the temporal and spatial trends, we estimated rates of change (°C/year) by regressing each selected metric against year (2000–2023) and subsequently related these rates to latitude. Since surveys were not conducted for all sites in 2001, 2007 and 2020 (Appendix S1: Figure S1.1), these years were excluded from the estimation of rates of change.

2.4 | Species Identification

We surveyed macroscopic organisms (ca. > 5 mm), identifying them to the lowest possible taxonomic level, typically species, collecting specimens when necessary. When field identification was limited by mixed stands (e.g., *Gelidium chilense* and *Gelidium lingulatum*; Broitman et al. 2011) or cryptic morphology (e.g., scurrinid limpets), we recorded taxa at the genus or family level as appropriate.

2.5 | Species Biological Traits and Attributes

To take full advantage of the large phylogenetic diversity of our dataset (10 phyla), we separated it into two categories—macroalgae and invertebrates—and compiled multiple life-history-related traits based on the available literature (Table 1). To assess species' environmental responses, we used standardised categorical traits. Macroalgal attributes included life cycle and life span; invertebrate attributes included tiering position, feeding mode and larval development. In addition, maximum body size was included for both. While species attributes differed between macroalgae and invertebrates, they reflect comparable ecological strategies across groups (Table 1).

2.6 | Evolutionary Relations Among Species

In the absence of well-resolved phylogenies encompassing all species present in our communities, to account for an evolutionary correlation among species traits, we used taxonomic

TABLE 1 | Traits and attributes of intertidal species of (a) macroalgae and (b) invertebrates recorded at sites between 28° S and 36° S of the Chilean coast from 2000 to 2023.

Trait	Attribute	Description
(a)		
LC	Het	Species with the gametophyte and sporophyte of different morphology and size.
	Iso	Species with the gametophyte and sporophyte of similar morphology and size.
	Mon	Species with non-alternation of generations in morphology and size.
LS	Ann	A phenological pattern where species appear only in specific seasons/periods of the year.
	Per	A phenological pattern in which species are present throughout the entire year.
ML	Nva	Theoretical maximum length that the species would reach (cm).
(b)		
TI	Ere	Species attached to substrate with vertical growth that favours the capture of food.
	Sur	Species actively moving and adhering to intertidal substrates.
	Inf	Species living in a three-dimensional substrate matrix with unrestricted movement.
FM	Sus	Species that capture food particles from the water column by filtration.
	S De	Species that capture accumulated loose particles from a substrate.
	Gra	Species that scrape or graze algae on the substrate.
	Pre	Carnivorous organisms that actively hunt and capture prey.
LD	Plan	Larval stage that feeds on plankton favouring the duration of the larval stage and dispersal.
	Lec	Larval stages with a yolk reserve which reduces larvae duration and dispersal.
	Dir	No larval stage but with competent juveniles.
ML	Nva	Theoretical maximum length that the species would reach (cm).

Abbreviations: (a) Ann, annual; Het, heteromorphic; Iso, isomorphic; LC, life cycle; LS, life span; ML, maximum length; Mon, monomorphic; Nva, numerical variable; Per, perennial. (b) cm, centimetres; Dir, direct; Ere, erect; FM, feeding mechanisms; Gra, grazer; Inf, infaunal; LD, larval development; Lec, lecithotrophic; ML, maximum length; Nva, numerical variable; Plan, planktotrophic; Pre, predatory; S De, superficial deposit; Sur, surficial; Sus, suspension; TI, tiering.

classification as a basic approximation for phylogenetic relationships. While we recognise that taxonomy does not fully capture the complexity of evolutionary history, this approach provides a fair approximation of phylogeny across the full set of species. We confirmed the current taxonomic status of all species sampled using the World Register of Marine Species website (www.marinespecies.org; see Appendix S2: Tables S2.1 and S2.2).

2.7 | Statistical Analyses

We used the joint species distribution model Hierarchical Modelling of Species Communities (HMSC) to model intertidal community responses (Ovaskainen and Abrego 2020). We conducted separate analyses for the macroalgal and invertebrate groups. Data were modelled at the level of sampling unit ($n = 5536$ quadrats; Appendix S1: Figure S1.1). Due to the zero-inflated nature of the data, we modelled species presence–absences, assuming the probit link function and Bernoulli distribution and then abundances conditional on species presence (with linear regression on log-transformed data, with absences masked as missing data). To model environmental filtering at the local and regional scales, we included as fixed effects intertidal height (categorical predictor with three levels), season (categorical predictor with four levels), SSTM and SSTA (continuous predictors) at each site. We included tidal height in the models to account for the effects of zonation in the analyses, and consequently to allow for making appropriate comparisons of environmental responses across species groups. To assess long-term changes beyond the SST covariates mentioned above, we included 'year' as a fixed linear-trend effect. We modelled spatial structure with random effects for 'site' (22 sampling sites) and rocky shore platform (41 platforms). To capture year-to-year variation unexplained by SST or the linear year effect, we further included 'year' (21 sampling years) as a random effect. We note that as HMSC implements random effects at the community level through a latent factor approach, including these random effects also evaluates species' residual associations at these spatial and temporal levels (Ovaskainen et al. 2016). Such associations may arise from species responses to unmeasured environmental conditions, biotic interactions, stochasticity or historical contingencies (Ovaskainen and Abrego 2020).

We used published data to construct a species-by-traits matrix linking traits to environmental responses in the HMSC framework (Appendix S2, Tables S2.3 and S2.4). Macroalgal traits included life cycle (3 levels), and life span (2 levels); invertebrate traits included

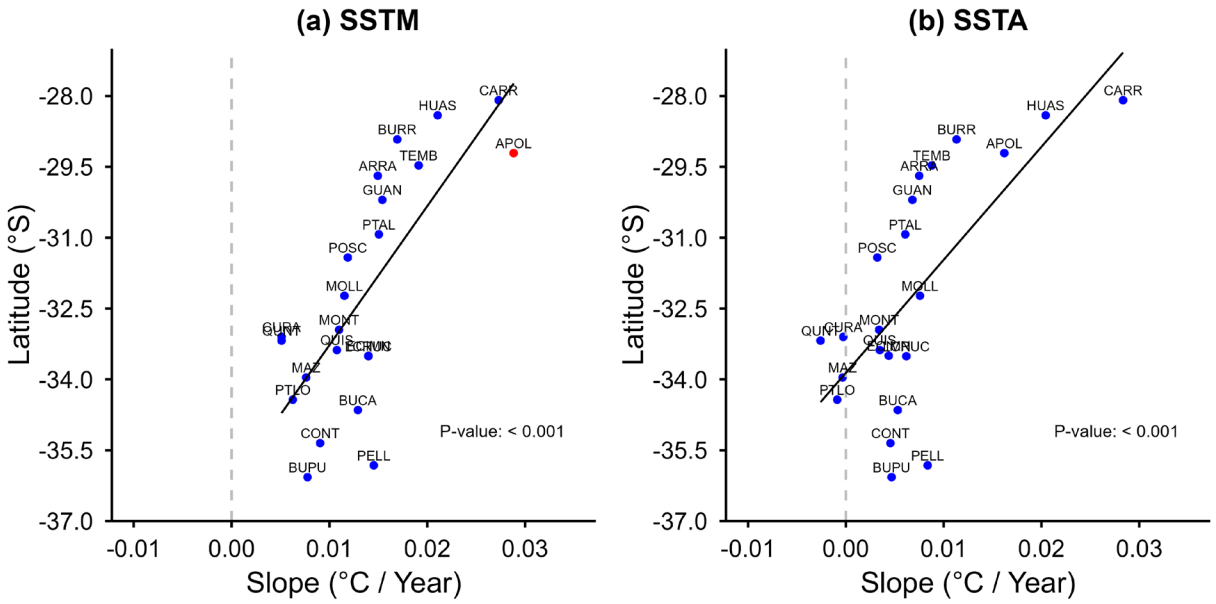

FIGURE 1 | Rate of change (°C/year) in (a) annual mean of SST (SSTM) and (b) annual SST anomalies (SSTA) across 22 sites along the central Chilean coast from 2000 to 2023 (excluding 2001, 2017 and 2020). Trend lines show the linear relationship between the rate of change and site latitude. In (a) the red dot highlights the only site (APOL) with a significant temporal trend ($p < 0.05$).

tiering (3 levels), feeding mechanisms (4 levels), and larval development (3 levels). Log-transformed maximum length was included for all species. These traits were used in the second-level regression model of HMSC, which evaluates how the traits influence the species-specific responses to the fixed effects included in the model. Then, we built the taxonomic trees with equal branch lengths across levels (i.e., kingdom, phylum, class, order, family, species). These trees were then converted into correlation matrices and used as a phylogenetic random effect in the models to examine whether closely related species show similar responses beyond what can be explained by their traits. This includes the estimation of the strength of the taxonomical signal parameter ρ, with $\rho = 1$ if species responses to the fixed effects are fully distributed according to the taxonomic relationships, and $\rho = 0$ if they are randomly distributed with respect to the taxonomy.

We fitted the models with the HMSC R package 'Hmsc', assuming the default prior distribution (Ovaskainen and Abrego 2020). We sampled the posterior distribution of each model with four Markov chain Monte Carlo (MCMC) chains, each of which was run for 37,500 iterations, of which the first 12,500 were discarded as burn-in. The chains had a thinning of 100 to yield 250 posterior samples per chain, resulting in 1000 posterior samples per model in total. We assessed MCMC convergence by examining the potential scale reduction factors of the model parameters (Gelman and Rubin 1992). We evaluated the explanatory and predictive powers of the presence-absence models through the Area Under the Curve (AUC) statistic, and of the abundance conditional on presence models through R^2; explanatory power through a model fitted to all data and predictive power through two-fold cross-validation across the sampling units (Abrego and Ovaskainen 2023).

To explore potential latitudinal changes in community-level response to the predictors, we summarised the species-specific responses to community-level metrics that described the extent to which the community showed positive versus negative responses to each predictor at each sampling site. For this, we computed the community-weighted mean response over the species, weighted either by species occurrences, that is those species that were observed at least once in the focal site, or by a measure of species incidence expressed as the number of times the species were observed in the focal site.

3 | Results

3.1 | Temperature Patterns

Annual rates of change in SST exhibited a strong positive relationship with latitude ($p < 0.001$, Figure 1). At the site level, most regressions of SST metrics against year were small in magnitude and not significant, except for APOL for SSTM (Figure 1a). Overall, some of the northern sites (28° S–30° S) showed higher positive rates of SSTM and SSTA than southern sites, and trends were nil poleward of 30° S (Figure 1a,b).

3.2 | Patterns of Species Richness

The separate HMSC models included 54 macroalgal and 57 invertebrate species. Among macroalgae, Florideophyceae were the more diverse class ($n = 32$), followed by Phaeophyceae ($n = 11$), Ulvophyceae ($n = 9$) and Bangiophyceae ($n = 1$), including one species of the Eurotiomycetes fungus class (Appendix S2: Table S2.1). Generally, the number of macroalgal species was lower towards the northern part of our study area (i.e., 28° S–30° S, except for HUAS) when compared to sites located between 30° S and 36° S (Figure 2). For invertebrates (Appendix S2: Table S2.2), the most common class was Gastropoda ($n = 22$), followed by Polyplacophora ($n = 9$), Thecostraca ($n = 7$), Malacostraca ($n = 6$), Bivalvia ($n = 3$),

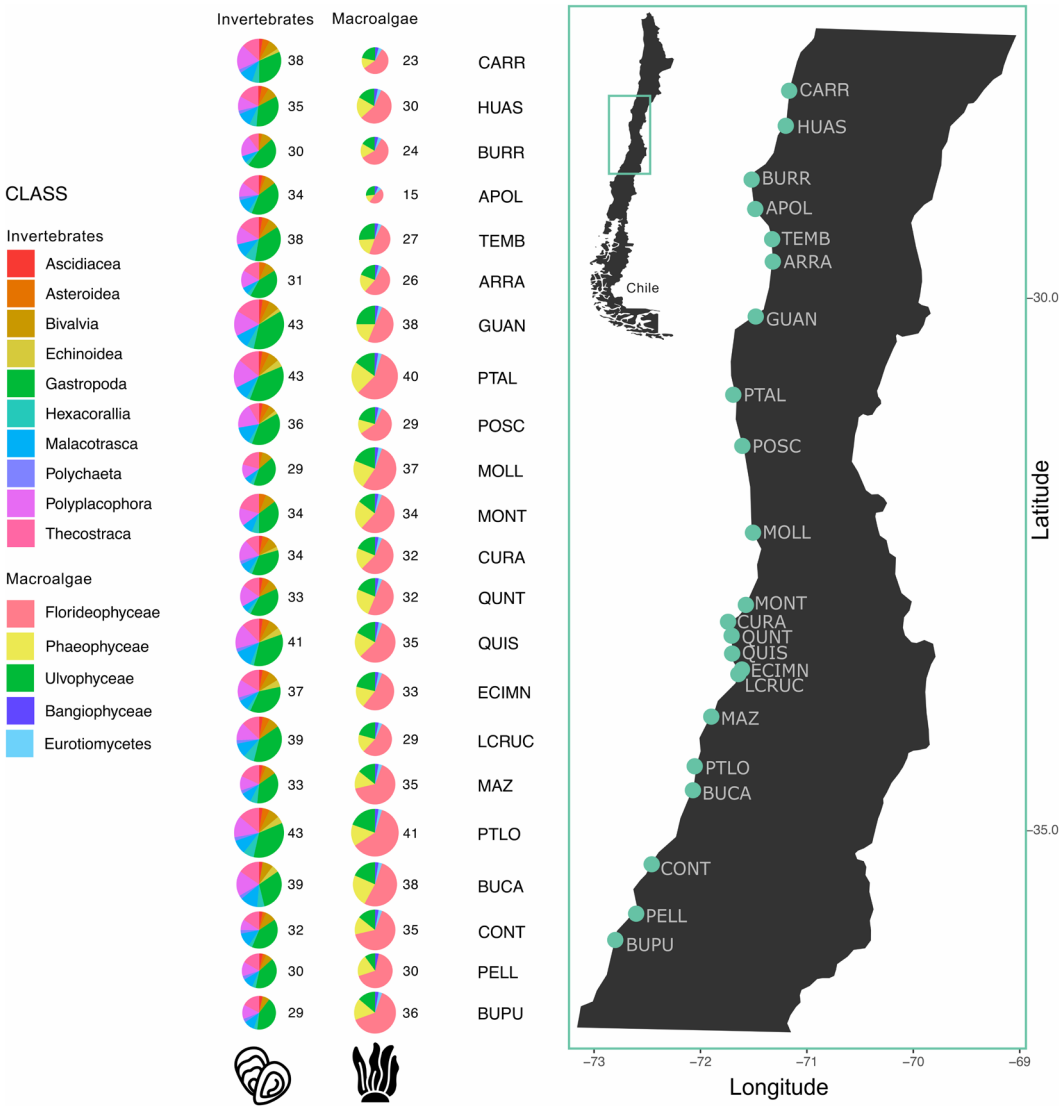

FIGURE 2 | Number of species per class of macroalgae and invertebrates recorded from 2000 to 2023 across 22 sites along the central Chilean coast (28° S–36° S). The total number of species recorded on each site per category is indicated to the right of each pie chart, and their size is proportional to this number. The Eurotiomycetes class (represented by one species) was included in the macroalgal group and in calculating the total occupied space (%) by sessile species in the field. The full names of the sites are detailed in Appendix S1: Figure S1.1.

Hexacorallia ($n = 4$), Asteroidea ($n = 2$), Echinoidea ($n = 2$), Ascidiacea ($n = 1$) and Polychaeta ($n = 1$). Unlike the spatial trend for macroalgae, the total number of invertebrate species ranged between ~30 and 45 across sites with no clear trend (Figure 2). We note here that our surveys are not designed to capture Polychaete species and other invertebrate groups (e.g., Peracarids) concealed within microhabitats, and thus the low representation in our database does not reflect the local diversity of this group. Some of the more species-rich sites were located around 30° S (GUAN, PTAL) and poleward.

3.3 | Species Traits and Attributes

In our surveys, macroalgal species mainly had an isomorphic life cycle ($n = 37$), followed by a heteromorphic cycle ($n = 14$), and only a few species showed a monomorphic life cycle ($n = 3$; Appendix S2: Table S2.3). In addition, about half of the algal taxa had a perennial life span ($n = 31$), while the rest had an annual cycle ($n = 23$). A total of 50 species of macroalgae reached a maximum length below 50 cm and only four reached large sizes (i.e., > 50 cm; Appendix S2: Table S2.3).

For invertebrates, 41 species were mobile and 16 sessile, while most live primarily on the rock surface, and five species mostly among or within kelp holdfasts (Appendix S2: Table S2.4). In terms of feeding habits, most invertebrates were grazers ($n = 32$), filter-feeders ($n = 11$), carnivores ($n = 10$) and deposit feeders ($n = 4$). Almost half of the invertebrates had a lecithotrophic larval strategy ($n = 23$), while the other half had a planktotrophic larval mode ($n = 29$), with fewer species exhibiting direct development ($n = 5$). More than half of the invertebrate species reached a maximum length of up to 10 cm ($n = 47$), while a few reached larger sizes of up to 33 cm (Appendix S2: Table S2.4).

3.4 | MCMC Convergence and Model Fit

The HMSC models reached adequate convergence; the median value of the potential scale reduction factors over the regression parameters in the models was 1.04 (macroalgae; presence-absence), 1.02 (macroalgae; abundance conditional on presence), 1.06 (invertebrates; presence-absence) and 1.01 (invertebrates; abundance conditional on presence). In the macroalgae model (presence–absence), the mean AUC for explanatory power was 0.91, and the mean AUC for predictive power was 0.86. In the invertebrate model (presence–absence), the mean AUC for explanatory power was 0.92, and the mean AUC for predictive power was 0.87. Thus, both models were fitted well to the data and showed no major signs of overfitting. For the abundance conditional on presence models, the mean R^2 for model fit was 0.31 for macroalgae and 0.49 for invertebrates, while the cross-validated R^2 values were 0.12 and 0.28, respectively.

3.5 | Species Responses to Environmental Predictors

In the presence–absence models, there was no evidence for the species responses being taxonomically structured: for macroalgae, the posterior probability by which the parameter ρ is positive was $\Pr[\rho>0]=0.37$, whereas for invertebrates it was $\Pr[\rho>0]=0.31$ (Figure 3). There was however a high and statistically well-supported taxonomical structure in the abundance conditional on presence models: for macroalgae $\Pr[\rho>0]=1$ and $E[\rho]=0.89$, whereas for invertebrates, $\Pr[\rho>0]=1$ and $E[\rho]=0.95$ (Appendix S1: Figure S1.2).

In the presence–absence models, year explained the largest amount of variation among the random effects for both communities (Table 2), consistent with the temporal changes in species occurrences (Figure 3). Among the fixed predictors, tidal height emerged as the most important, followed by year and SSTM, whereas season and SSTA contributed the least to explain community responses (Table 2). Except for a few taxa, macroalgae and invertebrates had higher occurrences in low and mid-intertidal zones compared to the high intertidal zone, as evidenced by consistently positive β coefficients (Figure 3). Only seven species of macroalgae (including the *Verrucaria* fungus genus) had lower occurrences at low intertidal levels than higher levels (Figure 3a). Similarly, most invertebrates had higher occurrences in the low and mid-intertidal zones (Figure 3b). The exceptions to this pattern were eight species that had their lowest occurrences at both mid and low-intertidal levels (i.e., had their highest occurrences in the high intertidal level), and another group of five species that only occurred less in low levels (Figure 3b).

Both presence–absence models showed a consistent positive temporal response, with many macroalgae and invertebrates increasing in occurrence over time (33 and 42 species, respectively; Figure 3). Only two species of macroalgae decreased in occurrence over time (Figure 3), while season had a modest effect overall, with both groups occurring less frequently in spring than in summer (Figure 3). Regarding ocean temperature, we observed that 21 species of macroalgae reduced their occurrences with increasing SSTM, especially Florideophyceae species; 22 showed no significant response, and 11 increased their occurrences (including the *Verrucaria* genus, Figure 3a). In the case of invertebrates, most species showed no statistically supported responses (33 species); however, 19 species increased their occurrences with increasing SSTM, and five species had negative responses (Figure 3b).

Community-weighted mean response (CWMR) allowed us to identify latitudinal trends in the community response to model predictors (Figure 4). The linear effect of the year was homogeneous across the region, except for the macroalgal species incidence-based metric, which showed that CWMR was slightly less positive towards higher latitudes ($p<0.001$; Figure 4i). When looking at intertidal elevations (Figure 4b,c,j,k), no latitudinal trends were evident for invertebrates (except for Figure 4k), but for macroalgae both metrics evidenced a positive relationship, indicating that species 'preference' for lower and mid intertidal levels (compared to the high intertidal level) is stronger at poleward sites ($p<0.001$). Similarly, the community response to SSTA differed between the groups: invertebrates showed weaker responses than macroalgae, which showed increased response to SSTA towards the south ($p<0.001$; Figure 4d,l). CWMR to SSTM was not uniform across the coast, and both macroalgae and invertebrates responded more negatively at increasing latitudes. Although the two groups followed the same trend, the steeper slope for macroalgae evidenced a stronger response ($p<0.005$; Figure 4e,m). Moreover, there is a clear shift in the responses of macroalgae, going from positive responses in the northern sites (~30° S) to negative responses towards the south (Figure 4e,m). For invertebrates, communities only showed positive responses with the lowest values in the most southern sites (i.e., above 35° S, Figure 4e,m). In the case of macroalgae, the latitudinal change in community responses seemed to be related to changes in community structure as in the southern sites, the proportion of species that responded negatively to SSTM increased (Figure 5). The pattern held for invertebrates but only in the southernmost sites (Figure 5). Seasonal community responses varied little across latitude. While both groups of species had generally higher prevalence in the autumn than in the summer, for macroalgae the difference decreased towards the south ($p<0.01$; Figure 4f). Macroalgae were more abundant in winter than in summer, whereas invertebrates showed the opposite pattern; both trends were consistent but not significant across latitudes (Figure 4g,o). In spring, both communities showed lower abundances than in the summer (Figure 4h,p), with the smallest difference observed for macroalgae in the south ($p<0.01$; Figure 4h).

3.6 | Species Responses to the Environment Explained by Traits

In presence–absence models of both community groups, size (maximum length) was associated with species distributional patterns across the intertidal zones, with larger individuals being more prevalent in the mid and lower than in the higher zones (Appendix S1: Figure S1.3a,c). Isomorphic macroalgae were also more prevalent in the lower and mid than high intertidal zones, while lecithotrophic invertebrates did so only in the lower zone (Appendix S1: Figure S1.3a,c). In macroalgae, large-bodied species responded especially negatively to

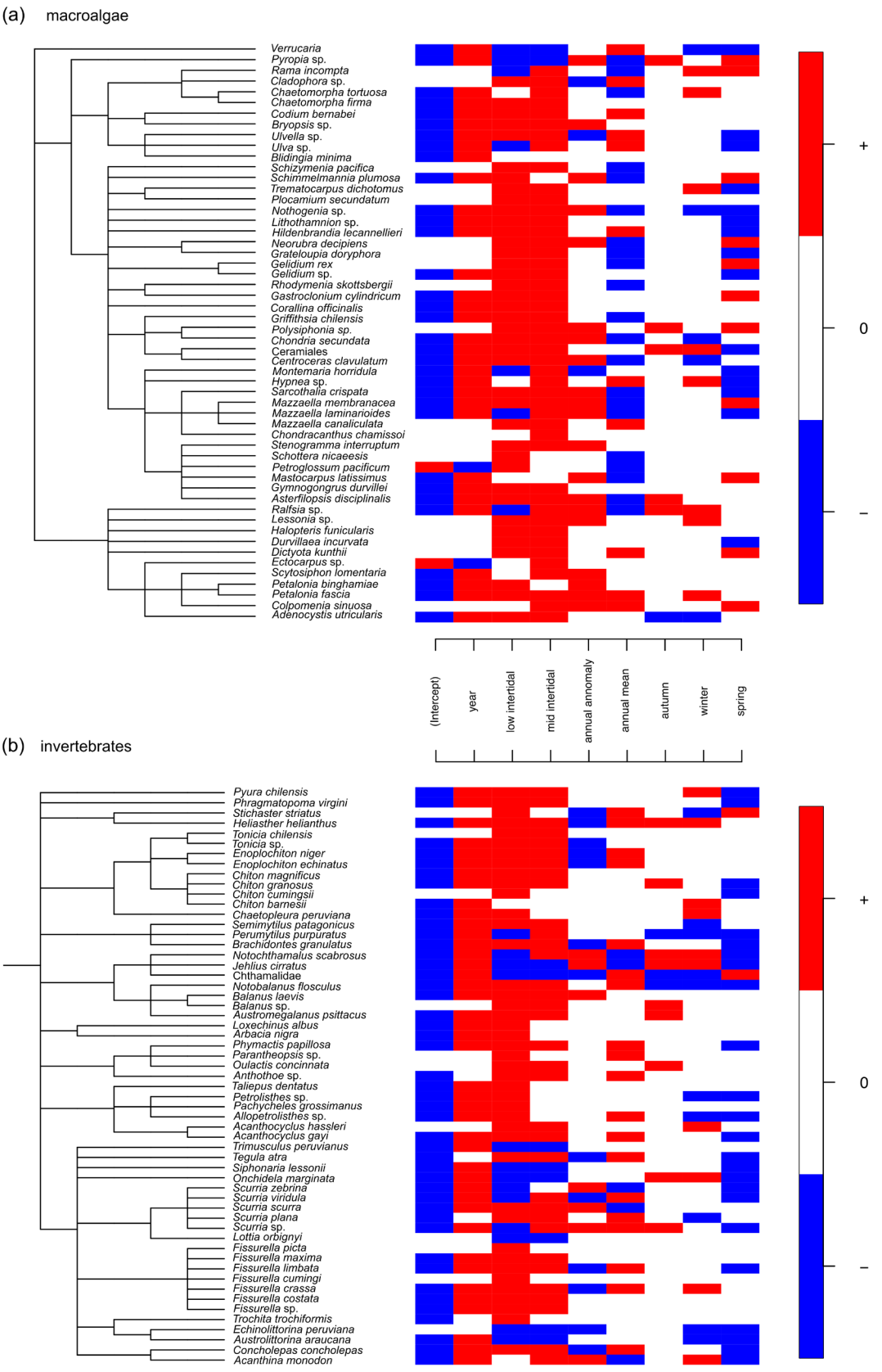

FIGURE 3 | Taxonomically structured responses of presence-absences species of (a) macroalgae and (b) invertebrates to the predictors included in the HMSC models. Red, blue and white colours represent the average estimated effect of the predictors on species' occurrence across the study region. Positive responses are shown in red, negative in blue, and responses without strong statistical support in white (less than 95% posterior probability). Responses to the categorical predictors shown on the *x*-axis, that is low intertidal and mid intertidal levels, as well as autumn, winter and spring, are shown in comparison to the reference 'high intertidal' level and 'summer', respectively. The predictor 'Year' indicates the overall linear effect of the time; and the environmental variables. SSTA, the standardised annual SST anomaly; SSTM, the yearly SST mean.

TABLE 2 | Percentage (%) of variation in species occurrences explained by different groups of predictors in the presence–absence models.

	Random			Fixed				
Model	**Year**	**Site**	**Platform**	**Year**	**Height**	**SSTA**	**SSTM**	**Season**
Macroalgal	3.0	2.3	1.3	2.0	7.3	0.4	1.9	0.3
Invertebrates	2.8	1.9	1.4	1.6	7.0	0.4	1.7	0.5

Note: The values shown sum to the explanatory power of the model in units of Tjur's R^2. Values show averages over all species.
Abbreviations: SSTA, annual sea surface temperature anomaly; SSTM, annual mean sea surface temperature.

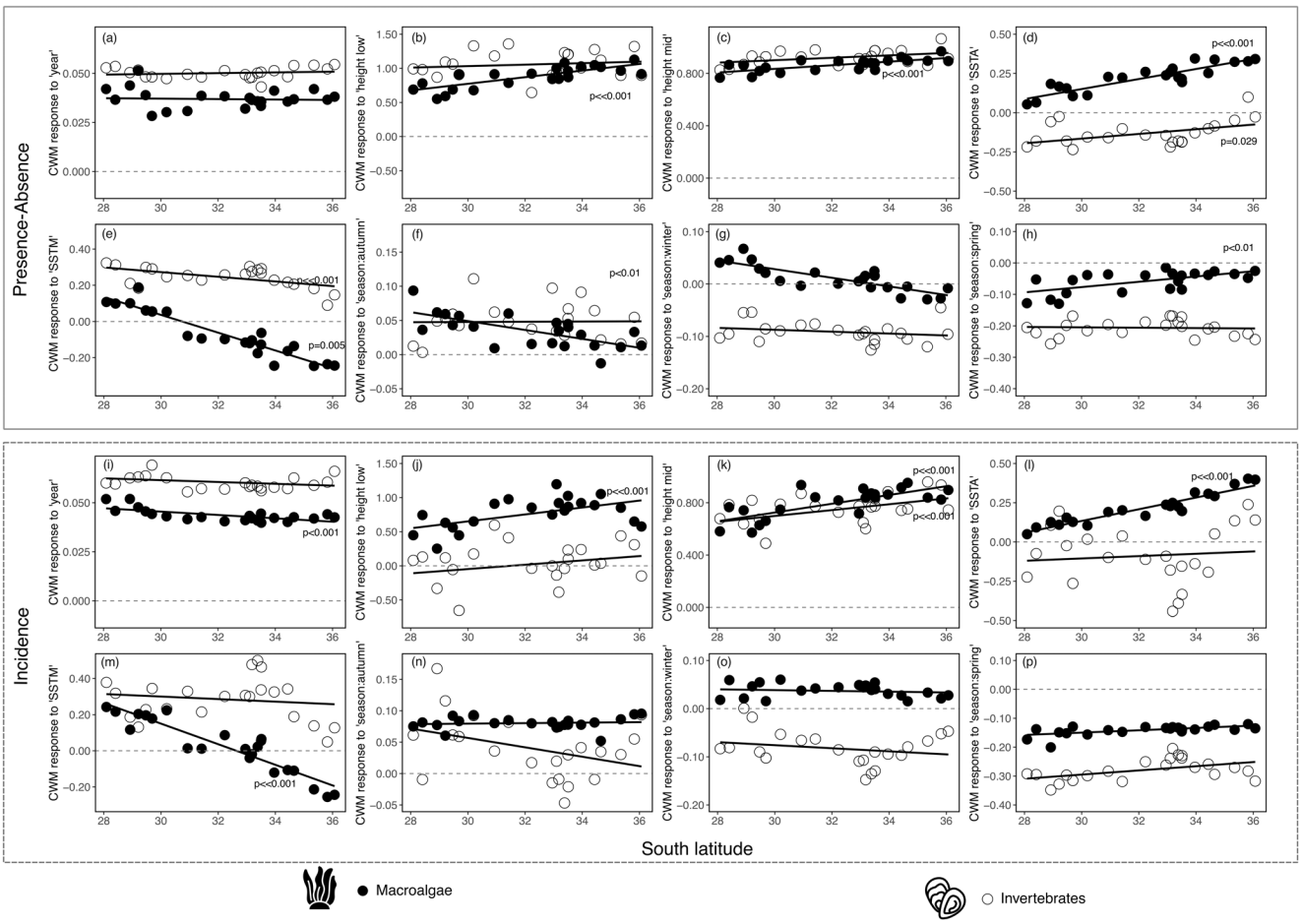

FIGURE 4 | Community-weighted mean responses (CWMR) of macroalgae (closed black circles) and invertebrates (open circles) to variations in the fixed predictors included in the HMSC models across the latitudinal gradient. Each point corresponds to a site ($n = 22$). Top panels (solid box) show community responses using a metric based on weighting by presence–absence (i.e., species that occurred at least once per site: a–h). Bottom panels (dashed box) show responses with a metric calculated based on weighting by incidence (i.e., the number of times the species was observed on each site: i–p). *p*-values are reported for significant relationships. The full name, latitude and longitude of each site are detailed in Appendix S1: Figure S1.1.

SSTM, whereas planktotrophic invertebrates responded especially negatively to SSTA (Appendix S1: Figure S1.3a,c). Traits did not significantly explain seasonal variation in macroalgae, whereas autumn negatively affected both lecithotrophic and planktotrophic invertebrates. In abundance conditional on presence models, traits did not structure the responses of macroalgae in a statistically supported manner, and in invertebrates, such responses were limited to season and SSTA (Appendix S1: Figure S1.3b,d).

3.7 | Scale-Dependent Species Co-Occurrence Patterns

Residual associations quantify patterns of species co-occurrence that persist after accounting for the species' responses to environmental predictors (Figure 6). Here, the species' residual co-occurrences had scale-dependent patterns that differed between macroalgae and invertebrates. Both groups displayed high year-to-year variation in community structure, with a large block of species

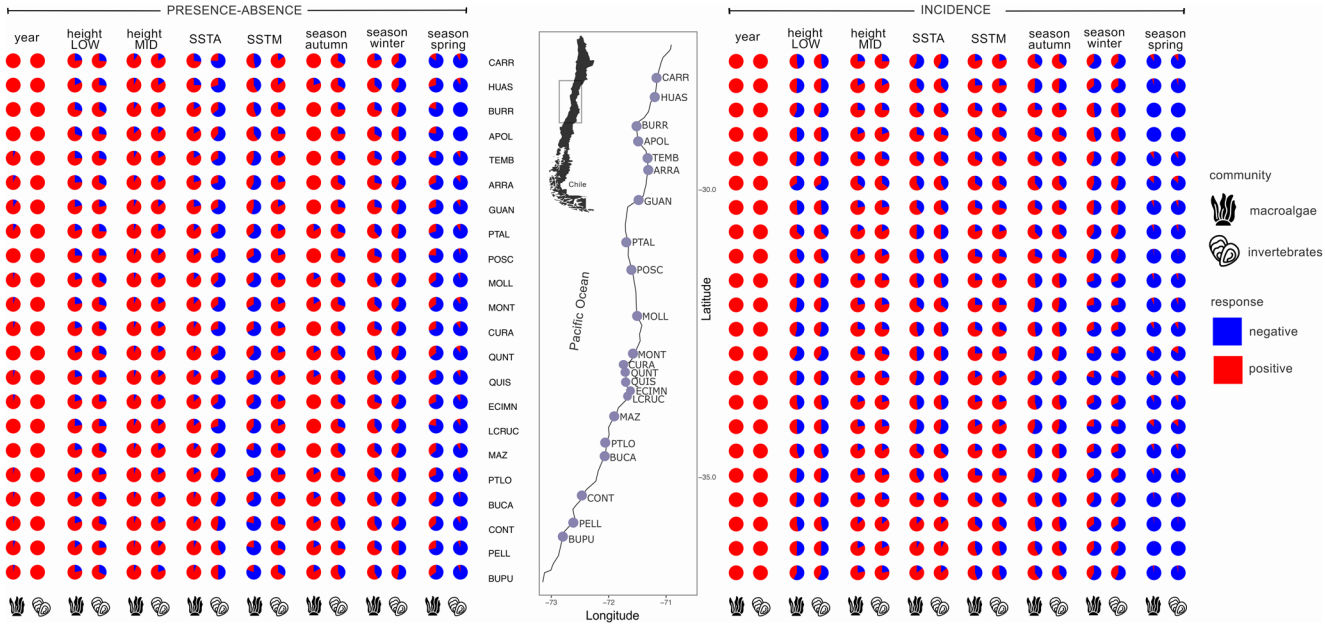

FIGURE 5 | Proportion of macroalgal and invertebrate species showing positive (red) or negative (blue) responses to variations in the fixed predictors included in the HMSC models across the latitudinal gradient. Responses were summarised to community-level metrics (Community-Weighted Mean Response, CWMR) that described the extent to which the community showed positive versus negative responses at each focal site, that is presence–absence (left panel) and incidence metrics (right panel). The full name, latitude and longitude of each site are detailed in Appendix S1: Figure S1.1.

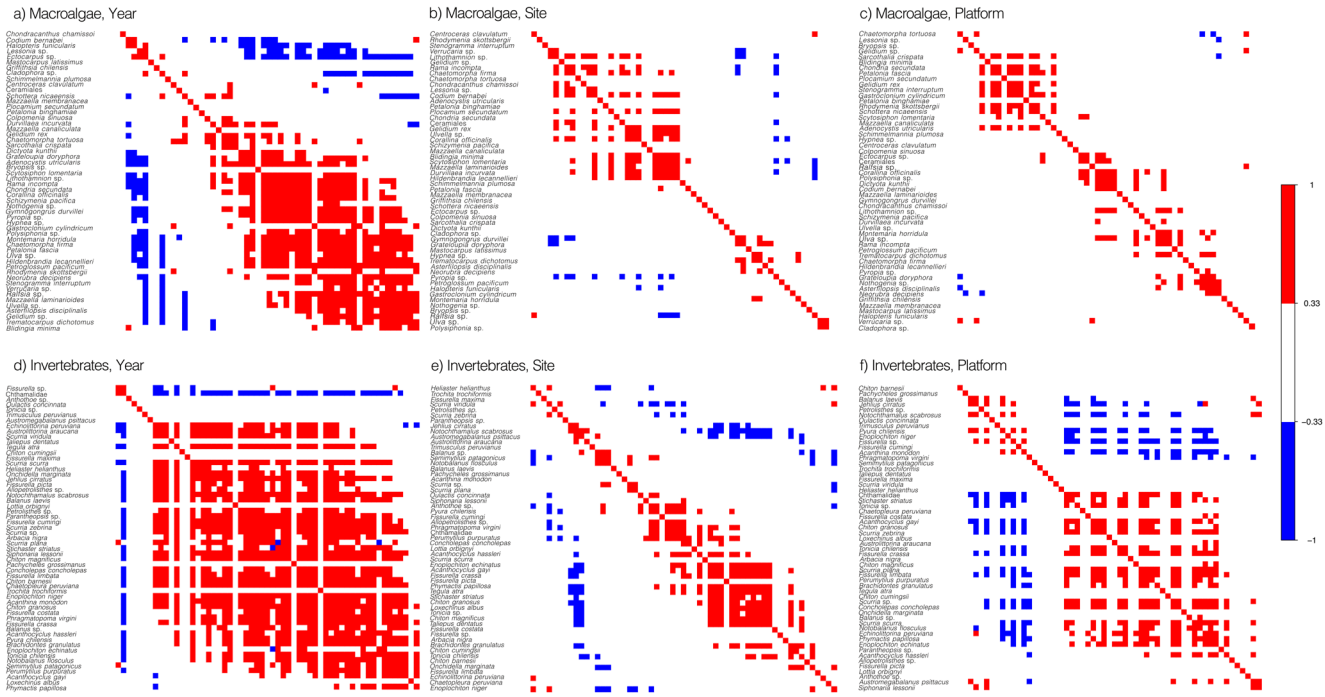

FIGURE 6 | Residual associations of (a–c) macroalgae and (d–f) invertebrate species for each random factor included in the HMSC models (presence–absence), namely year (a, d), site (b, e) and platform (c, f). In each panel, positive associations with > 90% support are shown in red, negative associations are shown in blue, and those with less than 90% posterior support are shown in white. The species are ordered separately in each panel to show clusters of co-occurring species.

that responded synchronically to yearly variations (Figure 6a,d). However, macroalgal communities had few species responding consistently at both the site and platform levels, evidenced by the low number of significant associations (i.e., colour-marked squares; Figure 6b,c, respectively). In contrast, invertebrates showed a greater number of associations at the platform level than at the site

level, with a broad cluster of species frequently co-occurring and a smaller group displaying negative associations (Figure 6e,f).

4 | Discussion

Our results show that both macroalgae and invertebrates have generally increased in the central Humboldt Upwelling Ecosystem, with variation in species occurrences responding to low-frequency environmental variability—summarised by annual sea surface temperature patterns—as well as to intertidal zonation and seasonality. Some of this variation was further explained by the species traits included in the model, such as maximum size of the species (Question 1). Beyond the effect of these traits, we did not observe a taxonomic structure in how species occurrences depended on the environmental predictors, although such a signal was evident in the abundance conditional in presence models (Question 2). Regarding latitudinal variation in species responses, macroalgae showed stronger and more spatially structured responses to SST than invertebrates, with positive responses at lower latitudes and negative ones towards the south (Question 3). Species associations were temporally consistent but varied across groups and spatial scales: macroalgae had fewer associations overall, whereas invertebrate associations were more frequent at smaller spatial scales (Question 4).

4.1 | Environmental Change and Patterns of Community Structure: A Global and Regional Outlook

Climate change has driven major shifts in marine ecosystems, including altered species interactions and poleward range shifts (Pinsky et al. 2020). Tropicalization and borealization have been reported in coastal regions (Fossheim et al. 2015; Vergés et al. 2019), yet our long-term data showed no evidence of community reorganisation across a broad latitudinal gradient that includes a biogeographical transition zone. Given the extensive spatial and temporal coverage of our study, together with the taxonomic breadth of our dataset, we anticipated detecting changes if they were occurring (Aguilera et al. 2020; Rivadeneira and Fernández 2005; Smith et al. 2006). Instead, our results highlight the long-term stability of the Humboldt Upwelling Ecosystem. Our environmental estimates relied on MODIS SST data averaged over annual scales. Moreover, satellite SST can underestimate cooling in coastal sites of intense upwelling (Meneghesso et al. 2020). Although we did not detect region-wide cooling, in line with prior evidence of cooling trends along the southeastern Pacific (Aguirre et al. 2018; de La Maza and Farías 2023; García-Reyes et al. 2023; Sydeman et al. 2014; Weidberg et al. 2020), our study region is not warming. Hence, the intensification of coastal upwelling seems to buffer coastal communities against climate-driven restructuring, and the absence of community reorganisation is not a sampling artefact. In this way, our findings establish a community-wide baseline for the region that sets a benchmark for detecting future climate impacts. Incorporating higher-resolution satellite data and long-term in situ measurements will be essential to test and predict how future changes may shape the structure of intertidal communities.

Along this line, our analyses revealed an overall increase in the occurrences of both invertebrates and macroalgae, but with contrasting latitudinal patterns. For invertebrates, this increase was consistent across latitudes and occurred without significant changes in species richness, suggesting a broader tolerance to environmental variability, and perhaps more importantly, that non-climatic drivers may play a stronger role in structuring these communities (Castilla 1999; Menge et al. 2003; Navarrete et al. 2005). In contrast, macroalgae showed a poleward increase in species richness and slight shifts in community structure, as southern communities contained a higher proportion of species responding negatively to temperature variation (Broitman et al. 2001, 2011; Santelices and Marquet 1998). These differences likely reflect how temperature extremes affect macroalgae: warm conditions increase physiological stress affecting key processes such as photosynthesis and respiration, whereas cold extremes mainly pose physical risks, such as tissue damage, which tend to be more evident in larger individuals. Since cooling in our study region remains within the thermal tolerance of most macroalgae, cold-affinity species have persisted, and their negative responses drive the community-level latitudinal signal we detected (Monteiro et al. 2022).

4.2 | Trait Selection and Interpretative Constraints

Our trait-based approach revealed limited explanatory power for species responses to SST, except for maximum size in macroalgae and planktotrophic invertebrates in the presence–absence models. Given the fundamental biological differences between macroalgae and invertebrates, we relied primarily on categorical traits rather than continuous or physiological traits. While these traits capture key life history aspects and ecological strategies, they may lack the resolution needed to detect more nuanced responses to environmental gradients. Additionally, standardised and comparable trait data across species ($n = 111$) were not always available in the literature, especially for macroalgae, which may constrain the likelihood of detecting trait signals in the species' responses. However, it is also possible that the few trait–environment associations observed reflect the absence of extreme SST events in the study region over the past two decades, resulting in more gradual or diffuse biological responses. Future studies incorporating quantitative traits (e.g., thermal tolerance, metabolic and growth rates) could provide a finer-scale understanding of species' responses.

4.3 | Macroalgal Versus Invertebrate Responses

Macroalgae not only provide food for many invertebrates but also offer protection from predators, facilitation of invertebrate recruitment, and refuge from desiccation and thermal stress (Aguilera et al. 2020; Menge and Sutherland 1987; Nielsen and Navarrete 2004). Considering the generally positive association between macroalgae and invertebrates, both assemblages should share responses to environmental gradients. However, our results indicated that macroalgae occurrences decreased towards the poleward end of the region in response to SSTM, but increased in response to SSTA, while invertebrates showed no clear latitudinal pattern. These broad differences between producers and consumers may stem from the inverse relationship

between nutrients and seawater temperature across upwelling systems (Nielsen and Navarrete 2004; Palacios et al. 2013). Warmer waters are associated with nutrient depletion, reduced macroalgal growth and diminished biomass (Navarrete et al. 2025; Vergés et al. 2019), likely affecting macroalgae more uniformly than invertebrates. Although temperature affects invertebrate physiology, activity patterns, and other vital rates (Bowler et al. 2017; Koussoroplis and Wacker 2016), its population-level impacts are usually complex. For example, recruitment is frequently decoupled from temperature yet remains crucial for local abundance. The equatorward sites that showed a positive CWMR have the lowest number of macroalgal species in the region. These positive community responses are likely driven by the match between a constrained species pool and a more stressful environment, while the opposite remains true for the poleward sites, allowing for more species to coexist (Menge and Sutherland 1987). The latter is particularly important. No major heatwaves have been reported in our study region, yet they are predicted to become more common towards the end of the century (Wang et al. 2023).

Finally, we also found distinct species association patterns at different spatial scales for macroalgae and invertebrates. Residual associations represent how species co-occur beyond what can be explained based on the spatio-temporal context in the model. In our study, invertebrate species showed more significant (either positive or negative) associations at small scales, while macroalgae showed fewer associations at finer resolutions. Both groups, however, displayed consistent patterns of co-occurrences across time. This temporal consistency of macroalgae and invertebrates likely reflects the persistence of long-established patterns of zonation—kelps and mussels remain restricted to the low and mid shore, respectively, and fleshy Rhodophytes remain rare at mid intertidal zones of northern sites, consistent with early observations (Broitman et al. 2001). The more frequent and structured residual associations observed among invertebrates at the platform level suggest that fine-scale ecological processes, such as microhabitat heterogeneity (e.g., crevices, shading or moisture retention), behavioural aggregation, or biotic interactions, may play a stronger role in shaping their spatial distributions. In contrast, the weaker residual associations among macroalgae at the same spatial scale may reflect their stronger reliance on broad-scale environmental drivers, such as nutrient availability, salinity and upwelling intensity, which tend to be more homogenous at the platform level. While some of this unexplained variation may reflect unmeasured environmental variables (Weigel et al. 2023), it also highlights that invertebrates may be more sensitive to localised conditions and interactions than macroalgae.

5 | Conclusions

This study provides a rare, community-wide insight into how benthic, polyphyletic assemblages in a major eastern boundary upwelling system respond to environmental variation. By integrating long-term survey data with environmental predictors, we show that neither taxonomic relatedness nor simple species traits strongly predict species responses, suggesting comparatively low niche conservatism in these communities (sensu Wiens et al. 2010). Instead, environmental context and latitude emerged as the dominant drivers of species occurrences. Macroalgae and invertebrates showed contrasting latitudinal responses: invertebrate occurrences varied across latitude without changes in species richness, whereas macroalgal occurrences and richness increased poleward but included a higher proportion of species responding negatively to temperature variation in southern communities. Our findings challenge the prevailing assumption that climate-driven community change in the coastal ocean generally follows a trajectory of tropicalization. In the Humboldt Upwelling System, stable or cooling conditions coincided with an overall increase in occurrences for both invertebrates and macroalgae, revealing that ecological trajectories under climate change are more diverse than often recognised. This highlights the importance of long-term, in situ physical and ecological monitoring for disentangling the interacting roles of environment, species interactions, and biogeographical context in shaping biodiversity in complex coastal communities.

Acknowledgements

This work was supported by grants from the Agencia Nacional de Investigación y Desarrollo (ANID-Chile), including grants to M.H.O. (85220139-SIA), B.R.B. (1221699-FONDECYT), and S.A.N. (1240851-FONDECYT; NCN19_056-NUTME; ICN 2019015-SECOS; PIA/BASAL FB0002-Center for Applied Ecology and Sustainability). O.O. was funded by the Research Council of Finland (grant nos. 336212 and 345110), and the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (grant agreement no. 856506: ERC-synergy project LIFEPLAN). M.H.O. thanks the 'Chango-lab' team, particularly M. Nuñez, J. Vera, W. Troncoso, A. Gonzalez, G. Díaz and the innumerable colleagues that have supported this study over the past two decades. Additional support to M.H.O. was provided by the University of Jyväskylä (Finland) through the Visiting Fellow Programme Grant (2023). We also thank C. Lara (Universidad Católica de la Ssma. Concepción, Chile) for supplying environmental imagery data, and H. Muller-Landau (Smithsonian Tropical Research Institute, Panama) for her insightful suggestions on an earlier draft.

Funding

This work was supported by Agencia Nacional de Investigación y Desarrollo (ANID-Chile) (1221699-FONDECYT, 1240851-FONDECYT, 85220139-SIA, ICN 2019015-SECOS, NCN19_056-NUTME, PIA/BASAL FB0002), H2020 European Research Council (856506), Jyväskylän Yliopisto, Visiting Fellow Programme Grant (2023), Research Council of Finland (336212, 345110).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in the Zenodo repository at https://doi.org/10.5281/zenodo.17253462.

References

Abrego, N., and O. Ovaskainen. 2023. "Evaluating the Predictive Performance of Presence–Absence Models: Why Can the Same Model Appear Excellent or Poor?" *Ecology and Evolution* 13: 1–11. https://doi.org/10.1002/ece3.10784.

Aguilera, M. A., N. Valdivia, B. R. Broitman, S. R. Jenkins, and S. A. Navarrete. 2020. "Novel Co-Occurrence of Functionally Redundant

Consumers Induced by Range Expansion Alters Community Structure." *Ecology* 101, no. 11: e03150. https://doi.org/10.1002/ecy.3150.

Aguirre, C., S. García-Loyola, G. Testa, D. Silva, and L. Farías. 2018. "Insight Into Anthropogenic Forcing on Coastal Upwelling Off South-Central Chile." *Elementa: Science of the Anthropocene* 6, no. 1: 59. https://doi.org/10.1525/elementa.314.

Aravena, G., B. Broitman, and N. C. Stenseth. 2014. "Twelve Years of Change in Coastal Upwelling Along the Central-Northern Coast of Chile: Spatially Heterogeneous Responses to Climatic Variability." *PLoS One* 9, no. 2: e90276. https://doi.org/10.1371/journal.pone.0090276.

Bakun, A. 1973. "Coastal Upwelling Indices, West Coast of North America, 1946–1971." In *NOAA Technical Report NMFS SSRF No. 671. National Marine Fisheries Service*. http://repository.library.noaa.gov/view/noaa/9041.

Bakun, A. 1990. "Global Climate Change and Intensification of Coastal Ocean Upwelling." *Science* 247: 198–201. https://doi.org/10.1126/science.247.4939.198.

Bowler, D. E., P. Haase, C. Hof, et al. 2017. "Cross-Taxa Generalities in the Relationship Between Population Abundance and Ambient Temperatures." *Proceedings of the Royal Society B: Biological Sciences* 284, no. 1863: 20170870. https://doi.org/10.1098/rspb.2017.0870.

Broitman, B. R., S. A. Navarrete, F. Smith, and S. D. Gaines. 2001. "Geographic Variation of Southeastern Pacific Intertidal Communities." *Marine Ecology Progress Series* 224: 21–34. https://doi.org/10.3354/meps224021.

Broitman, B. R., F. Véliz, T. Manzur, et al. 2011. "Geographic Variation in Diversity of Wave Exposed Rocky Intertidal Communities Along Central Chile." *Revista Chilena de Historia Natural* 84: 143–154. https://doi.org/10.4067/S0716-078X2011000100011.

Castilla, J. C. 1999. "Coastal Marine Communities: Trends and Perspectives From Human-Exclusion Experiments." *Trends in Ecology & Evolution* 14: 280–283. https://doi.org/10.1016/S0169-5347(99)01602-X.

de La Maza, L., and L. Farías. 2023. "The Intensification of Coastal Hypoxia Off Central Chile: Long Term and High Frequency Variability." *Frontiers in Earth Science* 10: 929271. https://doi.org/10.3389/feart.2022.929271.

de la Maza, L., E. A. Wieters, R. Beldade, M. F. Landaeta, A. Perez-Matus, and S. A. Navarrete. 2024. "Variability in Oceanographic Conditions Affecting Mesophotic Ecosystems Along the South Eastern Pacific: Latitudinal Trends and Potential for Climate Refugia." *Journal of Marine Systems* 245: 103999. https://doi.org/10.1016/j.jmarsys.2024.103999.

Flores, G., R. Cienfuegos, and S. A. Navarrete. 2019. "Beyond Tides: Surge-Dominated Submersion Regimes on Rocky Shores of Central Chile." *Marine Biology* 166: 92. https://doi.org/10.1007/s00227-019-3539-8.

Ford, B. M., and J. D. Roberts. 2020. "Functional Traits Reveal the Presence and Nature of Multiple Processes in the Assembly of Marine Fish Communities." *Oecologia* 192: 143–154. https://doi.org/10.1007/s00442-019-04555-1.

Fossheim, M., R. Primicerio, E. Johannesen, R. B. Ingvaldsen, M. M. Aschan, and A. V. Dolgov. 2015. "Recent Warming Leads to a Rapid Borealization of Fish Communities in the Arctic." *Nature Climate Change* 5: 673–677. https://doi.org/10.1038/nclimate2647.

García-Reyes, M., G. Koval, W. J. Sydeman, et al. 2023. "Most Eastern Boundary Upwelling Regions Represent Thermal Refugia in the Age of Climate Change." *Frontiers in Marine Science* 10: 1158472. https://doi.org/10.3389/fmars.2023.1158472.

Gelman, A., and D. B. Rubin. 1992. "Inference From Iterative Simulation Using Multiple Sequences." *Statistical Science* 7: 457–511. https://doi.org/10.1214/ss/1177011136.

Green, S. J., C. B. Brookson, N. A. Hardy, and L. B. Crowder. 2022. "Trait-Based Approaches to Global Change Ecology: Moving From Description to Prediction." *Proceedings of the Royal Society B: Biological Sciences* 289, no. 1971: 20220071. https://doi.org/10.1098/rspb.2022.0071.

Herrera, D. L., S. A. Navarrete, F. A. Labra, S. P. Castillo, and L. F. Opazo Mella. 2023. "Functional Biogeography of Coastal Marine Invertebrates Along the South-Eastern Pacific Coast Reveals Latitudinally Divergent Drivers of Taxonomic Versus Functional Diversity." *Ecography* 2023, no. 12: e06476. https://doi.org/10.1111/ecog.06476.

Koussoroplis, A. M., and A. Wacker. 2016. "Covariance Modulates the Effect of Joint Temperature and Food Variance on Ectotherm Life-History Traits." *Ecology Letters* 19: 143–152. https://doi.org/10.1111/ele.12546.

Lagos, N. A., S. A. Navarrete, F. Véliz, A. Masuero, and J. C. Castilla. 2005. "Meso-Scale Spatial Variation in Settlement and Recruitment of Intertidal Barnacles Along the Coast of Central Chile." *Marine Ecology Progress Series* 290: 165–178. https://doi.org/10.3354/meps290165.

Lara, C., G. S. Saldías, B. Cazelles, M. M. Rivadeneira, P. A. Haye, and B. R. Broitman. 2019. "Coastal Biophysical Processes and the Biogeography of Rocky Intertidal Species Along the South-Eastern Pacific." *Journal of Biogeography* 46: 420–431. https://doi.org/10.1111/jbi.13492.

Mann, K. H., and J. R. N. Lazier. 2006. *Dynamics of Marine Ecosystems: Biological–Physical Interactions in the Oceans*. 3rd ed. Wiley. https://doi.org/10.1002/9781118687901.

Meneghesso, C., R. Seabra, B. R. Broitman, et al. 2020. "Remotely-Sensed L4 SST Underestimates the Thermal Fingerprint of Coastal Upwelling." *Remote Sensing of Environment* 237: 111588. https://doi.org/10.1016/j.rse.2019.111588.

Menge, B. A., J. Lubchenco, M. E. S. Bracken, et al. 2003. "Coastal Oceanography Sets the Pace of Rocky Intertidal Community Dynamics." *Proceedings of the National Academy of Sciences of the United States of America* 100: 12229–12234. https://doi.org/10.1073/pnas.1534875100.

Menge, B. A., and J. P. Sutherland. 1987. "Community Regulation: Variation in Disturbance, Competition, and Predation in Relation to Environmental Stress and Recruitment." *American Naturalist* 130: 730–757. https://doi.org/10.1086/284741.

Monteiro, C., J. Pereira, R. Seabra, and F. P. Lima. 2022. "Fine-Scale Survey of Intertidal Macroalgae Reveals Recent Changes in a Cold-Water Biogeographic Stronghold." *Frontiers in Marine Science* 9: 880074. https://doi.org/10.3389/fmars.2022.880074.

Navarrete, S. A., M. Barahona, N. Weidberg, and B. R. Broitman. 2022. "Climate Change in the Coastal Ocean: Shifts in Pelagic Productivity and Regionally Diverging Dynamics of Coastal Ecosystems." *Proceedings of the Royal Society B: Biological Sciences* 289: 11–13. https://doi.org/10.1098/rspb.2021.2772.

Navarrete, S. A., A. E. González, J. Faúndez, et al. 2025. "Growth Rates and Response to Nutrient Variability in the Green Tide Forming Alga Ulva Stenophylloides From Algarrobo Bay, Chile." *Marine Environmental Research* 210: 107338. https://doi.org/10.1016/j.marenvres.2025.107338.

Navarrete, S. A., E. A. Wieters, B. R. Broitman, and J. C. Castilla. 2005. "Scales of Benthic-Pelagic Coupling and the Intensity of Species Interactions: From Recruitment Limitation to Top-Down Control." *Proceedings of the National Academy of Sciences of the United States of America* 102: 18046–18051. https://doi.org/10.1073/pnas.0509119102.

Nielsen, K. J., and S. A. Navarrete. 2004. "Mesoscale Regulation Comes From the Bottom-Up: Intertidal Interactions Between Consumers and Upwelling." *Ecology Letters* 7: 31–41. https://doi.org/10.1046/j.1461-0248.2003.00542.x.

Ovaskainen, O., and N. Abrego. 2020. *Joint Species Distribution Modelling: With Applications in R (Ecology, Biodiversity and Conservation)*. Cambridge University Press. https://doi.org/10.1017/9781108591720.

Ovaskainen, O., N. Abrego, P. Halme, and D. Dunson. 2016. "Using Latent Variable Models to Identify Large Networks of Species-to-Species Associations at Different Spatial Scales." *Methods in Ecology and Evolution* 7: 549–555. https://doi.org/10.1111/2041-210X.12501.

Ovaskainen, O., G. Tikhonov, A. Norberg, et al. 2017. "How to Make More out of Community Data? A Conceptual Framework and Its Implementation as Models and Software." *Ecology Letters* 20: 561–576. https://doi.org/10.1111/ele.12757.

Palacios, D. M., E. L. Hazen, I. D. Schroeder, and S. J. Bograd. 2013. "Modeling the Temperature-Nitrate Relationship in the Coastal Upwelling Domain of the California Current." *Journal of Geophysical Research: Oceans* 118: 3223–3239. https://doi.org/10.1002/jgrc.20216.

Pinsky, M. L., R. L. Selden, and Z. J. Kitchel. 2020. "Climate-Driven Shifts in Marine Species Ranges: Scaling From Organisms to Communities." *Annual Review of Marine Science* 12: 153–179. https://doi.org/10.1146/annurev-marine-010419-010916.

Rivadeneira, M. M., and M. Fernández. 2005. "Shifts in Southern Endpoints of Distribution in Rocky Intertidal Species Along the South-Eastern Pacific Coast." *Journal of Biogeography* 32: 203–209. https://doi.org/10.1111/j.1365-2699.2004.01133.x.

Sanford, E. 1999. "Regulation of Keystone Predation by Small Changes in Ocean Temperature." *Science* 283: 2095–2097. https://doi.org/10.1126/science.283.5410.2095.

Santelices, B., and P. A. Marquet. 1998. "Seaweeds, Latitudinal Diversity Patterns, and Rapoport's Rule." *Diversity and Distributions* 4: 71–75. https://doi.org/10.1046/j.1472-4642.1998.00005.x.

Schneider, W., D. Donoso, J. Garcés-Vargas, and R. Escribano. 2017. "Water-Column Cooling and Sea Surface Salinity Increase in the Upwelling Region Off Central-South Chile Driven by a Poleward Displacement of the South Pacific High." *Progress in Oceanography* 151: 38–48. https://doi.org/10.1016/j.pocean.2016.11.004.

Smith, J. R., P. Fong, and R. F. Ambrose. 2006. "Dramatic Declines in Mussel Bed Community Diversity: Response to Climate Change?" *Ecology* 87: 1153–1161. https://doi.org/10.1890/0012-9658(2006)87[1153:DDIMBC]2.0.CO;2.

Strub, P. T., J. Mesias, V. Montecino, J. Rutllant, and S. Salinas. 1998. "Coastal Ocean Circulation Off Western South America." In *The Global Coastal Ocean: Regional Studies and Syntheses*, edited by A. R. Robinson and K. H. Brink, vol. 11, 273–313. John Wiley & Sons.

Sydeman, W. J., M. García-Reyes, D. S. Schoeman, et al. 2014. "Climate Change and Wind Intensification in Coastal Upwelling Ecosystems." *Science* 345: 77–80. https://doi.org/10.1126/science.1251635.

Tapia, F. J., S. A. Navarrete, M. Castillo, et al. 2009. "Thermal Indices of Upwelling Effects on Inner-Shelf Habitats." *Progress in Oceanography* 83: 278–287. https://doi.org/10.1016/J.POCEAN.2009.07.035.

Vergés, A., E. McCosker, M. Mayer-Pinto, et al. 2019. "Tropicalisation of Temperate Reefs: Implications for Ecosystem Functions and Management Actions." *Functional Ecology* 33: 1000–1013. https://doi.org/10.1111/1365-2435.13310.

Wang, S., Z. Jing, L. Wu, et al. 2023. "Southern Hemisphere Eastern Boundary Upwelling Systems Emerging as Future Marine Heatwave Hotspots Under Greenhouse Warming." *Nature Communications* 14: 28. https://doi.org/10.1038/s41467-022-35666-8.

Weidberg, N., A. Ospina-Alvarez, J. Bonicelli, et al. 2020. "Spatial Shifts in Productivity of the Coastal Ocean Over the Past Two Decades Induced by Migration of the Pacific Anticyclone and Bakun's Effect in the Humboldt Upwelling Ecosystem." *Global and Planetary Change* 193: 103259. https://doi.org/10.1016/j.gloplacha.2020.103259.

Weigel, B., N. Kotamäki, O. Malve, K. Vuorio, and O. Ovaskainen. 2023. "Macrosystem Community Change in Lake Phytoplankton and Its Implications for Diversity and Function." *Global Ecology and Biogeography* 32: 295–309. https://doi.org/10.1111/geb.13626.

Wiens, J. J., D. D. Ackerly, A. P. Allen, et al. 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.

Wiens, J. J., and C. H. Graham. 2005. "Niche Conservatism: Integrating Evolution, Ecology, and Conservation Biology." *Annual Review of Ecology, Evolution, and Systematics* 36: 519–539. https://doi.org/10.1146/annurev.ecolsys.36.102803.095431.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** geb70176-sup-0001-Appendix1-figures.docx. **Figure S1.1:** Total number of experimental units (quadrats) across 22 sites (2000–2023). **Figure S1.2:** Taxonomically structured species abundance responses to environmental and temporal predictors. **Figure S1.3:** Trait-environment relationships for macroalgae and invertebrates from HMSC models. **Appendix S2:** geb70176-sup-0002-Appendix1-Tables.docx. **Table S2.1:** Macroalgal species recorded across 22 sites along the Chilean coast (2000–2023). **Table S2.2:** Invertebrate species recorded across 22 sites along the Chilean coast (2000–2023). **Table S2.3:** Traits of macroalgal species included in the HMSC models. **Table S2.4:** Traits of Invertebrate species included in the HMSC models.