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ARTICLE

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Community stability on built and natural intertidal habitats: Implications for coastal urban management

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Abstract

Coastal built structures often support benthic communities that differ in species diversity and composition from those found in natural reference habitats. However, most research has been conducted over short periods, limiting comprehensive analysis of long-term community trajectories and the potential for temporal convergence with natural habitats. Whether impoverished communities in novel habitats experience large fluctuations or maintain stability over time remains largely unexplored. Community composition and species abundances were studied annually over a 20-year period following the construction of a wave-exposed breakwater and compared with two adjacent natural rocky habitats in northern Chile (20° S) to determine whether the built structure develops a more variable community or converges with natural communities. Our long-term analysis of mid-intertidal community fluctuations using stability metrics, alongside short-term field experiments, revealed persistent differences in community composition between the built structure and natural rocky platforms, with transient convergence in the abundance and identity of key functional groups around 11–13 years post-construction. Due to lower abundances of foundation species, especially the absence of mussels, the built structure exhibited significantly lower species richness, greater community variability, and higher species synchrony than natural rocky platforms. Our findings suggest that communities in novel coastal habitats undergo distinct successional stages during the initial decades, indicating that the efficacy of ecological interventions is time-dependent. Supporting the rehabilitation of built structures through eco-engineering, specifically targeted early during succession or at transient saturation points, provides a strategic framework for urban coastal management. This approach is crucial for mitigating the ecological footprint of escalating coastal urbanization and successfully rehabilitating community functioning.

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KEYWORDS
artificial coastal structures, breakwaters, eco-engineering, foundation species, novel habitats, species synchrony, temporal stability

INTRODUCTION

Urban expansion is currently threatening terrestrial and aquatic biodiversity worldwide (Moreno-García et al., 2025; Seto et al., 2012), by reducing the extent and connectivity of natural habitats (Lindenmayer et al., 2023; Piano et al., 2020) and promoting the onset of "novel built habitats" that support abiotic or biotic conditions with no historical analog (Bulleri et al., 2020; Hobbs et al., 2013; Kennedy et al., 2013). Despite the broad recognition of the importance of enhancing or redesigning urban habitats to preserve biodiversity amid global anthropogenic changes (Evers et al., 2018; Kowarik, 2011), our understanding of the natural and human-driven processes that regulate the structure and functioning of these novel habitats is still limited (Andrade et al., 2021).

Built habitats are proliferating on coastal areas worldwide, as a consequence of land reclamation and increasing need to protect properties and infrastructure (Airoldi et al., 2025; Bugnot et al., 2021; Firth et al., 2016; Gittman et al., 2015). In general, the deployment of seawalls, breakwaters, groynes, or other built structures at the marine–terrestrial interface can be considered a "press disturbance" (Bender et al., 1984). Benthic communities on these built structures are exposed to altered environmental conditions (e.g., thermal, light and chemical pollution, nutrient enhancement, and mechanical disturbance) and high rates of non-native species introduction (e.g., Firth et al., 2016; Todd et al., 2019). Most of the ecological research on these novel habitats has assessed the mechanisms underpinning differences in patterns of species distribution and abundance in comparison with natural rocky environments (see Firth et al., 2016; Firth, Bone, et al., 2024 for reviews). In contrast, few studies have focused on their ecological functioning (Mayer-Pinto et al., 2018) and to the best of our knowledge, none has assessed how the temporal stability of functions differs between built versus natural habitats.

The diversity–stability hypothesis has attracted the attention of ecologists since at least the mid-20th century (MacArthur, 1955) and more intensively over the past three decades (e.g., Isbell et al., 2026; Ives & Carpenter, 2007; Loreau & de Mazancourt, 2013; Tilman, 1999), since predicting how species loss impinges on a natural system ability to guarantee stable provisioning of goods and service is key to designing sound conservation strategies. The diversity–stability relationship posits that higher species richness would enhance ecosystem ability to resist and recover from disturbances, maintaining functionality over time (Donohue et al., 2013; Hao et al., 2024; Kéfi et al., 2019). Within this framework, asynchronous fluctuations in species abundance and species dominance contribute to the temporal variability of aggregated community properties, such as total abundance or biomass, productivity, nutrient cycling, resistance to invasions or to physical disturbances (Donohue et al., 2013; Isbell et al., 2026; Sasaki et al., 2019). Asynchrony is the product of intrinsic differences in species' life traits and responses to disturbances and natural fluctuations in environmental conditions and it is directly related to species compensatory dynamics (Loreau & de Mazancourt, 2013; Tilman et al., 1998). In addition, the temporal variability of community properties is influenced by the way dominant species in the community respond to changes in the frequency or intensity of disturbances or stressful conditions (e.g., Navarrete & Berlow, 2006; Wootton, 2010). Thus, the role of dominant species on community dynamics could change over time depending on the specific environmental context in which species interactions take place (MacDougall et al., 2018; Ren et al., 2023; Valdivia et al., 2017).

Age since construction can underpin a differential structure of benthic assemblages supported by coastal built structures (Baxter et al., 2023; Burt et al., 2011; Perkol-Finkel et al., 2006). For example, 2 years after deployment, rock-boulder breakwaters supported lower invertebrate species richness and abundances than natural rocky shores (Mamo et al., 2021). Dominance by foundation species (sensu Dayton, 1985) such as fucoid macroalgae or mussels, has been recorded on some built structures after 15–20 years (e.g., concrete blocks; Cooper et al., 2025; Hawkins et al., 1983; Southward & Orton, 1954) or more (Firth, Forbes, et al., 2024) since their construction. Thus, variations in species composition and richness between built and natural structures could be expected to reduce with time (Dong et al., 2016; Yu et al., 2025). On the other hand, intense and frequent disturbance due to wave impacts, sand scouring, or intense grazing, together with the lack of topographic microhabitats (Bauer et al., 2024), has been widely shown to prevent communities from developing beyond early to mid-successional stages (Firth et al., 2016; Hill et al., 2021; Jonsson et al., 2006). Therefore, the magnitude of between-habitat differences in species composition could

decrease or increase over time, depending on local disturbance regimes, presence of dominant species, and the physical and spatial features of the habitat types.

Lack of foundation species and lower species richness are expected to promote temporal variability in intertidal communities supported by built structures (Inouye & Tilman, 1995; Ives & Carpenter, 2007; Loreau & de Mazancourt, 2008). In natural rocky habitats, foundation species such as mussels, oysters, or kelps, by providing refuges from stressful conditions and consumer pressure (i.e., acting as ecosystem engineers; Jones et al., 1994), can enhance species diversity and ecosystem functioning (Benoit et al., 2026; Firth et al., 2021), potentially sustaining the temporal stability of benthic community abundances (Bulleri, Benedetti-Cecchi, et al., 2012; Miner et al., 2021). The effect of habitat-forming species on community stability is, however, likely to depend on local environmental conditions. For example, exposure to more intense thermal stress caused by the experimental removal of dominant foundation species, such as the intertidal purple mussel *Perumytilus purpuratus* or the macroalga *Mazzaella laminarioides*, increased the asynchrony of temporal fluctuations in the abundances of associated species at lower to intermediate latitudes (Fica-Rojas et al., 2022; Valdivia et al., 2021). In contrast, on European rocky shores, removal of intertidal macroalgal canopies at low latitudes decreased asynchrony of species fluctuations, and consequently reduced temporal stability, while it had weak effects at higher latitudes. Thus, the interplay between biological (e.g., facilitation, competition) and physical (e.g., desiccation, humidity) forcing can influence the role of species synchrony or dominance in the temporal fluctuations of intertidal rocky shore communities (Bulleri, Benedetti-Cecchi, et al., 2012; Valdivia et al., 2021).

Understanding the extent to which built habitats vary in community composition and diversity over time—and, more broadly, how community assembly proceeds in these systems—is highly relevant for the rehabilitation of biodiversity on built structures through eco-engineering (Firth, Bone, et al., 2024). However, a comprehensive analysis of the stability of community-aggregated properties is hindered by the lack of long-term studies (over 10 years) encompassing the time needed for species to complete multiple generations (Firth, Forbes, et al., 2024).

Here, using data from a 20-year semicontinuous monitoring, we characterized and contrasted the temporal dynamics of total species abundance (i.e., sessile and mobile species) between intertidal communities on a rock-boulder breakwater and adjacent natural rocky platforms at a subtropical locality. We asked the following questions: (1) How does the extent of differences in species composition between natural and built habitats change through time? (2) Given the lower foundation species abundance, is temporal stability of aggregate community properties (i.e., total species abundance) lower in communities on the built structure than on the natural rocky platforms (O'Shaughnessy et al., 2023)? (3) Do the effects of species richness on community temporal stability differ between the built and the natural habitat? (4) Does synchronicity of species fluctuations differ between the built and the natural habitat? We complemented the long-term monitoring with short-term (573 days) field experiments. We hypothesized that, in the study system, species fluctuations would be more synchronous and community temporal stability lower on the built structure than on natural platforms, driven by the reduced abundance of foundation species (Miner et al., 2021; Valdivia et al., 2021). A positive relationship between species richness and community stability, operating via species asynchrony or foundation species abundances (Craven et al., 2018; Loreau & de Mazancourt, 2013), was predicted for the natural habitat.

MATERIALS AND METHODS

Study area and coastal habitats characteristics

The long-term community survey was conducted in Iquique (20° S), on the coastal fringe of the Atacama Desert in northern Chile. The breakwater, made of granite boulders (ca.100 m long, mean boulder size = 1.4 ± 0.11 m^2 SE), was constructed in 2005 (March–April) onto a rocky substrate in a wave-exposed shore, located in a small urban Peninsula ("Peninsula Cavancha"), to protect a coastal promenade and buildings from wave surge (Appendix S1: Section S1, Figure S1). The structure faces west and is directly exposed to southwest swells, has a steep slope (≥35°), and is connected with natural rocky platforms at both ends (Appendix S1: Figure S1). The natural rocky platforms face west and are also directly exposed to southwest swells, have an extensive intertidal fringe (~8–12 m from the high to the low intertidal fringe) and a gentler slope (~10°) (Aguilera et al., 2014) (Appendix S1: Figure S2). Mid-intertidal levels (i.e., 1.2–1.5 m above Mean Low Water (MLW)) in the natural habitat support a high abundance of the mussel *P. purpuratus* which provides habitat to juvenile and adult grazing mollusks (e.g., *Scurria* spp., *Chiton granosus, Siphonaria lessoni*), polychaetes, and opportunistic algae that settle directly onto mussel shells (e.g., *Pyropia* sp., Ulvoids, *Petalonia fascia*). The barnacles *Jehlius cirratus* and *Nothochthamalus scabrosus* are

also abundant from mid to high intertidal levels (~1.2–2.5 m MLW). The extended natural rocky platforms at this location have a high frequency of mid-intertidal tide pools, which host high species richness (Aguilera et al., 2022); among others, sponges, holothurians, spirorbid worms, ascidians, small fishes, bryozoans, decapod crustaceans, the brown algae *Colpomenia phaeodactyla*, *C. sinuosa*, and the crustose alga *Corallina officinalis*, are especially abundant inside tide pools. The built structure is not colonized by mussels, likely reflecting the abiotic and biotic mechanisms discussed later (see *Discussion*). Independently, the built structure also lacks tide pools, since the interstices between boulders are hollow and do not retain water. Because these topographic features do not occur on the built structure, our comparison was between the built structure as a whole, including its structural limitations, and the natural rocky platforms, rather than between structurally matched microhabitats within each. Together with the absence of mussels, this contributes to the built structure supporting significantly lower species diversity than natural rocky platforms (Aguilera et al., 2014). Nonindigenous species were not recorded in the mid-intertidal zone at either habitat during the 20-year monitoring period.

Given that manipulation of this riprap breakwater was not allowed by local authorities, field experiments were conducted in the mid-intertidal level (~1.2–1.5 m MLW) on an equivalent rock-boulder breakwater and adjacent natural rocky platform present in Antofagasta (23° S), approximately 400 km south (Appendix S1: Figure S1). This built structure (constructed in 2002) shared similar wave exposure and extent (120 m long) with the study site of the long-term monitoring, had a comparably steep slope (26.5° ± 1.46 SE), and lacked mussel beds. By contrast, the adjacent natural rocky platform had a gentler slope (9.64° ± 0.12 SE) and a high percentage cover (~60%–70%) of *P. purpuratus* characterizing its mid-to-high intertidal levels (Castilla et al., 2014) (Appendix S1: Figure S3).

Long-term benthic communities monitoring

Mid-intertidal assemblages on the breakwater at Iquique (20° S) and two adjacent natural rocky platforms, about 25 and 45 m apart, were first sampled in May 2005 (~1.5 months after the rock-boulder deployment). Twelve fixed contiguous quadrats with 81 intersection points were deployed along two permanent 10-m-long transects ($n = 24$ quadrats) that were randomly marked in each habitat. Transects were established parallel to the shoreline, running along the mid-intertidal fringe, and were permanently fixed for the duration of the long-term monitoring (2005–2025). Within each quadrat, species were identified at the lowest possible taxonomic levels. Percentage cover of algae, sessile invertebrates, and bare space, and density of mobile species, was estimated in situ in each quadrat. The percentage area of rock pools, crevices, and other topographic features was also measured in each quadrat.

After the first sampling in 2005, access to the breakwater and the rocky platforms was limited by the construction of a promenade and buildings until the end of 2008. Surveys restarted in January 2009. From this date, we also took photographs using a digital camera positioned directly above each quadrat. Each photograph was cropped to focus solely on the quadrat and analyzed using the programs ImageJ (http://imagej.nih.gov/ij/download.html) and CPCe (Coral Point Count with Excel extensions) (Kohler & Gill, 2006) to estimate the percentage cover of sessile organisms and the density of mobile organisms. To quantify percentage cover, we randomly projected 25 dots onto each photo and assigned a value of 4% to each organism located under a dot. This complementary method helped reduce bias in field estimations of algae and sessile invertebrate cover (Foster et al., 1991), particularly during periods of high wave action.

Regular surveys were conducted annually from 2009 to 2025, except for 2014. The surveys were carried out in summer (December–late February) and winter (early July–late August), and exceptionally in autumn (May or June) and/or spring (September–late November). Thus, community samplings included at least two or three seasons per year. During 2014, the region was hit by two earthquakes (8.2 and 7.7 Mw) and one tsunami. Although the built structure was not affected by these events, access was forbidden by local authorities for safety reasons. No upgrade or maintenance of the built structure has been made since its construction.

Community removal field experiments

We conducted a manipulative experiment in which the entire community was removed from mid-intertidal levels on a rock-boulder breakwater and on an adjacent natural rocky platform (~10 m away) located in Antofagasta (23°39' S–70°24' W). The "removal" treatment simulated a mechanical disturbance ("pulse") in which the dominant intertidal foundation species (*P. purpuratus* and barnacles) and associated algae and invertebrates were removed. Notably, mussels were absent from the breakwater prior to the experiment, consistent with patterns observed in the long-term monitoring at Iquique.

In November 2022, twelve 25 × 25 cm plots were permanently marked with stainless steel bolts in each habitat type. Plots were randomly assigned to either control or total removal treatments (Appendix S1: Section S2). Experimental plots were distributed across representative microhabitat types such as boulder sides or tops in the breakwater and on rock ledges and horizontal areas in the natural rocky platform, including, if present, tide pools and crevices. The abundance of each macrobenthic species was estimated in each plot immediately before the removal procedure, and then every 3 months until the experiment ended in June 2024 (573 days after initiation). Macroalgae and sessile macroinvertebrates in each plot were identified in situ and classified to the lowest possible taxonomic level. Sessile species abundances were estimated as percentage cover by taking photographs of each plot and analyzing them using the program ImageJ, as indicated above ("*Long-term benthic communities monitoring*").

Temporal turnover, invariability, and synchrony

Stability is a multidimensional property of ecosystems, encompassing dimensions such as invariability, resistance, and resilience, among others (Hillebrand et al., 2018). However, "invariability," measured as the inverse of the CV (i.e., 1/CV), quantifies how consistently an ecosystem maintains an aggregate function (like productivity or biomass) over time (Hillebrand et al., 2018; Wang & Loreau, 2014). Because "invariability" directly reflects the degree of temporal constancy in community properties, hereafter we refer to it as "temporal stability" (Tilman, 1999) following common usage in the literature. It should be noted that these metrics are commonly applied when disturbance involves species removal within the same habitat type (Kéfi et al., 2019), as is the case in our field experiments conducted in Antofagasta (23° S). Thus, for the long-term surveys conducted in Iquique (20° S), we focus mainly on evaluating temporal stability in species abundances between the breakwater and the natural rocky platforms, along with the potential convergence in community structure (e.g., similarity in species abundance or composition through time). Thus, different community dimensions (Hillebrand et al., 2018; Loreau & de Mazancourt, 2013), such as species turnover (i.e., species replacement between time points), temporal stability (i.e., lower variability in total species abundances through time), and species synchrony (correlated fluctuations in species abundances within each habitat), were considered diagnostic tools for interpreting the level of similarity or differences in community temporal trajectories in both habitat types.

We calculated species turnover using the function "*total turnover*" implemented in the library "*codyn*" in the R-software (Hallett et al., 2016), which refers to total species turnover of the community and calculates the proportion of species that differ between time points (from consecutive samplings) as: [*Total turnover* = (*Species gained* + *Species lost*)/*Total species observed in both time points*]. Complementarily, and for the long-term monitoring, we estimated the "*Rate of directional change*" which shows how quickly species composition shifts over time (Collins et al., 2000) (Appendix S1: Section S3). Both turnover estimators were calculated for the entire community, including sessile and mobile species.

We estimated temporal stability using the *community_stability* function in "*codyn*" library in the R-environment (Hallett et al., 2016), which calculates summed species abundances (total cover or density for sessile and mobile species, respectively) within replicates (fixed transects and plots) and time, and uses these values to calculate temporal stability as the temporal mean divided by the temporal SD, which corresponds to the inverse of the CV (i.e., $\mu/\sigma = 1/\mathrm{CV}$; Tilman, 1999). In this case, this value was calculated once for each habitat type, using the two long-term transects (Iquique; 20° S) or all experimental plots (Antofagasta; 23° S). In addition, "within-year" temporal stability (i.e., seasonal samplings) was also calculated to explore the effect of species richness on community-wide abundance fluctuations at different years (i.e., from 2009 to 2025 for the long-term survey). Thus, community-level temporal stability calculated across the full 20-year time series from the long-term surveys conducted at Iquique (20° S) yields a single value per habitat and is therefore reported descriptively. In contrast, within-year stability estimates—calculated independently for each annual sampling period (2009–2025)—generate a time series of stability values per habitat, allowing formal statistical comparison of the relationship between species richness and community stability across habitats and years. Population-level temporal stability for foundation species (mussels and barnacles) and benthic grazers was also calculated as the inverse of the CV of percentage cover. In this case, larger stability means smaller temporal variations (relative to the temporal mean) of species abundances through time.

"*Community-wide synchrony*" in species abundances was calculated using the φ statistic developed by Loreau and de Mazancourt (2008), which measures the degree of species compensation: $\varphi = \frac{\sigma_F^2}{\left(\sum_{i=1}^{N} \sigma f_i\right)^2}$; $F = \sum_{i=1}^{N} f_i$, where f_i is the percentage cover of species i, and F is the total community cover; meanwhile, σf_i and σ_F^2 are their respective temporal variances. The index was calculated

using all sampling times and for each habitat type, and is standardized between 0 (perfect asynchrony, where most species' abundances are negatively correlated over time) and 1 (perfect synchrony, where most species' abundances are positively correlated) (Loreau & de Mazancourt, 2008). As with community-level temporal stability (see above), only one descriptive value of synchrony was estimated for each habitat type.

Environmental factors

Daily average sea surface temperature (SST, °C) for each specific sampling date at the study site was used to assess the relative contribution of environmental variability to long-term community dynamics (Valdivia et al., 2025). In the upwelling-dominated coastal system of northern Chile, SST serves as an integrated proxy for upwelling intensity and primary productivity (Lara et al., 2016; Wieters et al., 2003), with lower SST values reflecting stronger upwelling, higher nutrient availability, and increased larval supply—processes known to influence intertidal community dynamics and recruitment (e.g., Menge et al., 2003; Nielsen & Navarrete, 2004). Data were derived from the Modern-Era Retrospective analysis for Research and Applications, version 2 (*MERRA-2*) reanalysis obtained via the *ERDDAP* platform (https://coastwatch.pfeg.noaa.gov/erddap). SST (from the year 2009 to 2025) was included as the main exogenous variable in the structural equation modeling (see below).

Statistical analysis

Differences in species composition between communities recorded on the breakwater at different times since its construction (i.e., age of the structure) and the natural rocky platforms were visualized using nonmetric multidimensional scaling (NMDS) on Bray–Curtis's distances on square root-transformed abundances of mobile and sessile species after a Hellinger standardization was applied. This allowed us to control the influence of highly dominant species and to handle data with different units (i.e., percentages and densities). Differences in community composition between habitat types and breakwater ages (treated as a categorical factor, corresponding to discrete sampling years since construction) and their interaction were explored using a two-way crossed PERMANOVA. To account for the sampling design, permutations (i.e., 999) were restricted within "strata" (i.e., transects) to control for the random effects of the nested structure considered. To test for homogeneity of multivariate dispersions, we used the "*betadisper*" function, followed by Tukey's HSD post hoc tests to compare distances to centroids among groups (Anderson, 2001), all implemented via the "*vegan*" package in R (R Development Core Team, 2025). The average contribution of species to the overall average dissimilarity between habitat types was examined with SIMPER analysis.

Generalized additive models (GAMs) (Wood, 2017) were constructed to explore the potential nonlinear long-term dynamics of species number ("Richness") and diversity index (Shannon–Wiener *H*-index), on the breakwater and the natural rocky platforms, using data from long-term surveys conducted at Iquique (20° S). Poisson and Gaussian error family distributions were considered, respectively (Zuur et al., 2009). Summary GAM figures were performed with the libraries "*mgcviz*" and "*visreg*," and the models were fitted using R mgcv package v.1.8-42 (R Development Core Team, 2025). We compared within-year temporal stability estimated for foundation species (barnacles and mussels), grazers, and bare rock between the breakwater and the natural rocky platforms using Welch's *t* test, where each annual estimate constituted an independent observation (2009–2025). To examine the relationship between species richness and intra-year temporal stability at each habitat type (fixed and categorical) for the long-term surveys and field experiments, Gamma models with a log-link function were constructed.

Using the long-term data set from the breakwater and the adjacent rocky platforms at Iquique (20° S), we conducted a stepwise model selection of a structural equation model (SEM) with the library "*lavaan*" in the R-environment (R Development Core Team, 2025), to test direct and indirect pathways of effects of biotic (species richness, foundation species abundances) and abiotic factors (time, seawater temperature, habitat type) on community-level within-year temporal stability. A preliminary, more complex model with both fixed and random effects was first fitted with the function "*piecewiseSEM*" in R (Lefcheck, 2016) (Appendix S1: Section S3). Then, we used bias-corrected Akaike information criterion (AIC_c) to select the minimal and best model structure using the step-Akaike information criterion (AIC) procedure. A reduced main model ($AIC_c = 320$), without random effects (using "*lavaan*" library), was finally selected. The resulting standardized path coefficients were used to determine direct and indirect effects of the different predictors using the package "*lavaangui*" implemented in *R*. Given that habitat type is represented by a single built structure and two adjacent natural platforms in this case, its effect in the SEM

should be interpreted as site-specific rather than as a generalizable contrast between habitat categories.

RESULTS

Between-habitat temporal variation and community dissimilarity

In the long-term surveys conducted in Iquique (20° S), bare space tended to be higher in the built habitat (Appendix S1: Figure S4a), while the barnacles *N. scabrosus* and *J. cirratus* were more abundant on the natural rocky platform than on the breakwater (in Appendix S1: Figure S4b). Likewise, mussels (i.e., *P. purpuratus*) were absent from the breakwater and reached higher cover (%) in adjacent natural rocky platforms (Appendix S1: Figure S4c). Also, grazing mollusks had higher densities on the rocky shore than on the breakwater, where few species dominated (e.g., *Scurria viridula*, *S. variabilis*, *C. granosus*) (Appendix S1: Figure S4d). The bare substrate was relatively stable on the breakwater compared with the natural rocky platforms (Figure 1a) (Welch's t test = 2.79; $p = 0.014$). In contrast, the abundances of foundation species, such as mussels and barnacles, were more stable over time in natural rocky habitats than on the breakwater (Figure 1b) ($t = -12.82$; $p < 0.001$). Also, the densities of grazer species were more stable in the natural rocky platforms, although no significant differences were detected when compared with the breakwater (Figure 1c) ($t = -1.76$; $p = 0.093$).

The field experiments conducted in Antofagasta (23° S) showed important differences in bare rock and foundation species cover (%) between the breakwater and the natural rocky platform (Appendix S1: Figure S5a,b), with foundation species being much less abundant (only barnacles) on the breakwater over time (Appendix S1: Figure S5b). In the breakwater, a large proportion of primary space remained bare in the removal treatment and control throughout the first 300 days (Appendix S1: Figure S5a), after which noncalcareous crustose algae (*Hildenbrandia lecannellieri, Ralfsia* spp.; ~60% cover) became dominant. In the natural rocky

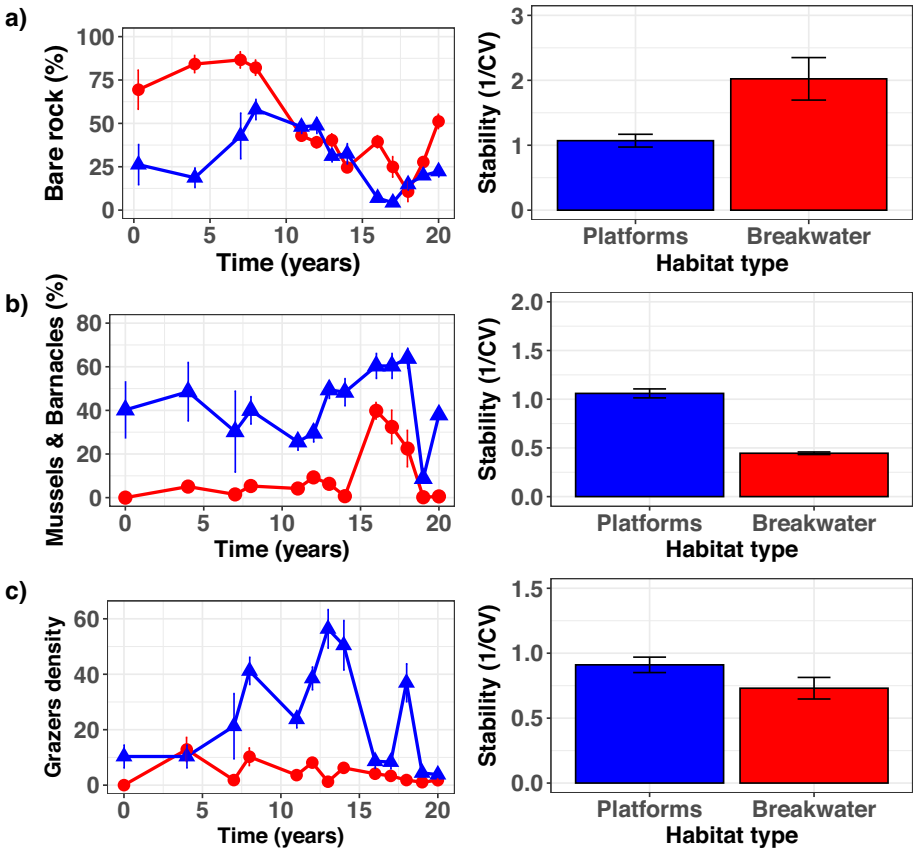


FIGURE 1 Temporal variation in the mean percentage cover (%; ±SE) of (a) bare rock, (b) foundation species (mussels and barnacles), and (c) grazer densities (indiv. ×1225 cm^{-2}), recorded in natural rocky platforms (blue) and at the study breakwater (red) in the locality of Iquique (20° S). The bar graphs to the right estimate the mean temporal stability across transects and dates for each habitat type of (a) bare rock and key taxa shown in (b) and (c), using the inverse of the CV (1/CV) of their abundance.

platform, the abundances of mussels and barnacles, and grazer increased while bare rock declined in the removal treatment (Appendix S1: Figure S5a–c), suggesting a recovery of the intertidal community.

Consistent with differences in species abundances, in the long-term surveys, significant between-habitat differences in species richness were recorded over time (Figure 2a) (GAM parametric coefficient = 0.285; $p < 0.0001$). A transient convergence in species diversity (Shannon–Wiener's H' index) was detected after about 11–13 years since breakwater construction, after which differences between communities remained stable (Figure 2b) (breakwater smooth term: estimated degree of freedom = 6.67; $p < 0.0001$). Significant compositional differences were recorded between the breakwater and natural rocky platforms at different time points since breakwater construction (*type* × *age* interaction; PERMANOVA: $R^2 = 0.19$; $p = 0.001$). Notably, at 11 and 12 years since construction (i.e., years 2016 and 2017), the breakwater community composition was more similar to that of natural rocky platforms (Figure 1c), coinciding with the convergence in the Shannon–Wiener's diversity index (Figure 1b).

Community-wide turnover, synchrony, and the effect of biotic components on temporal stability

Total species turnover, that is, the proportion of species that differ between time points, was relatively similar between the built structure and natural rocky platforms

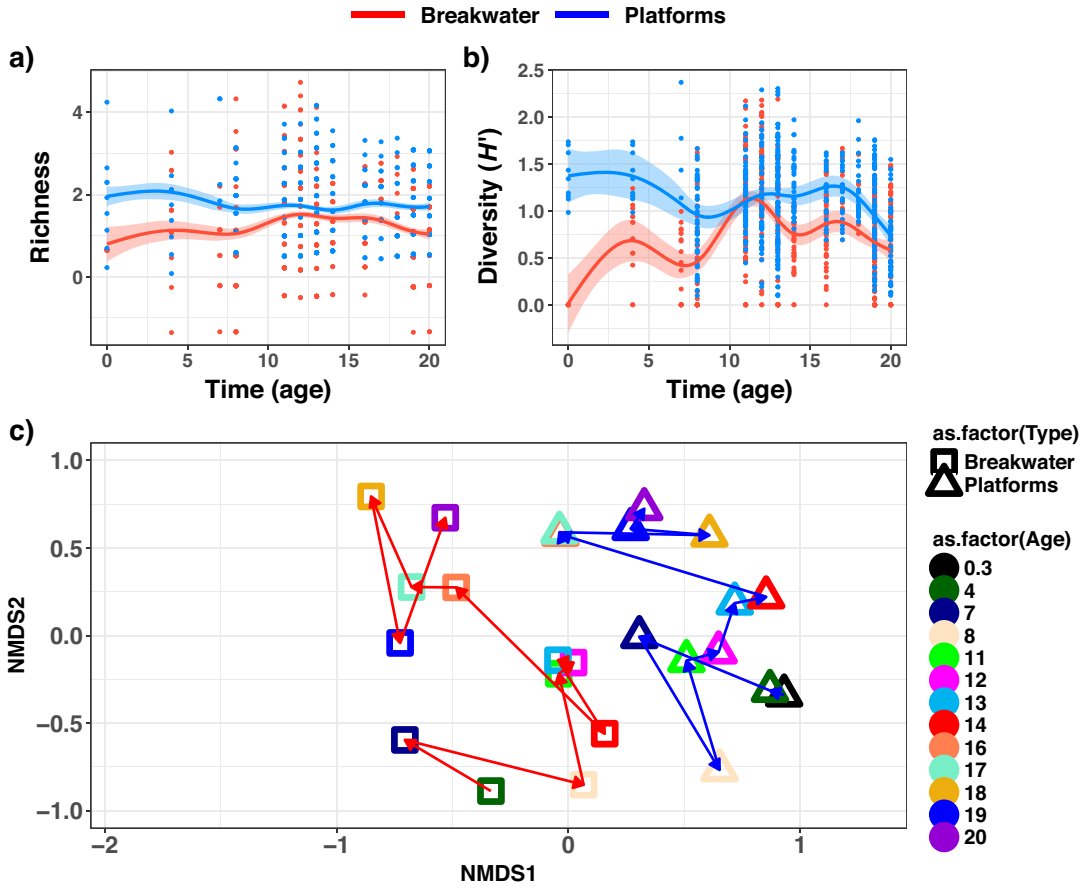


FIGURE 2 Long-term community composition over time. General additive models (GAMs) fit of (a) species richness (i.e., mean number of species per quadrat) and (b) Shannon's diversity index (H') recorded on the breakwater and natural rocky platforms, and (c) nonmetric multidimensional scaling (NMDS) of species composition (sessile and mobile species diversity) based on Bray–Curtis's distances on square root-transformed abundances of mobile and sessile species after a "Hellinger standardization" was applied. In (a) and (b), the expected values and CIs for each habitat type are presented as blue or red lines, respectively. Red and blue dots correspond to partial residuals of each model; because partial residuals combine model predictions with residual variation, they may take values outside the natural range of the response variable (e.g., slightly negative values for richness), which does not reflect actual observed counts. Arrows in (c) represent the temporal trajectories of the community for the breakwater (red) and the natural rocky platforms (blue) since the breakwater construction (black circle).

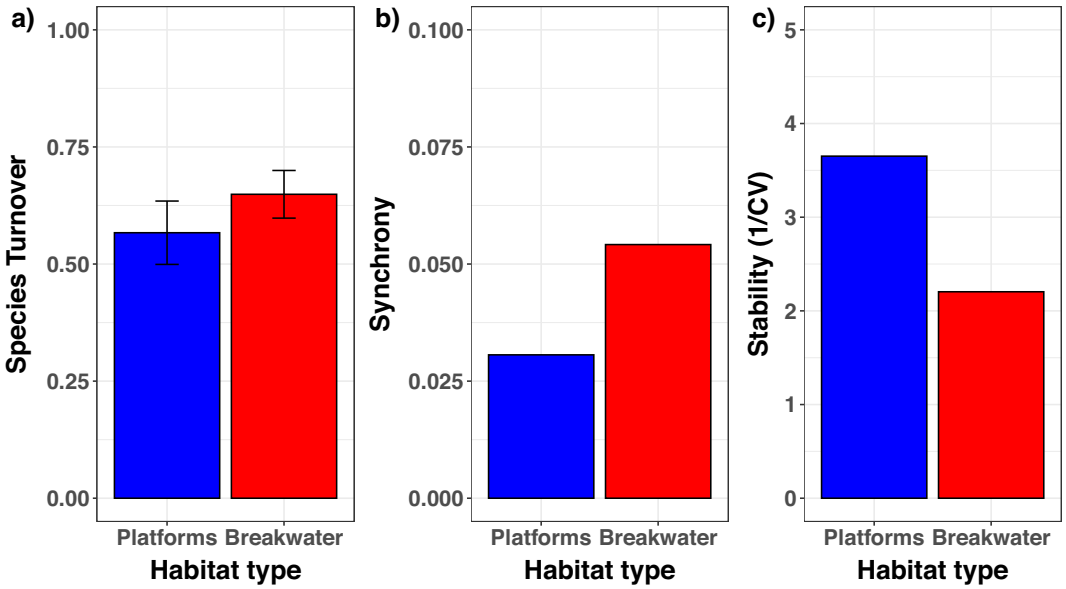


FIGURE 3 Long-term community dynamics from the long-term survey. (a) Mean (± SE) species turnover calculated across consecutive surveys, (b) synchrony, and (c) temporal stability (1/CV), estimated at two rocky platforms (blue) and at the study breakwater (red) at Iquique (20° S). Data from 2009 to 2025.

(Figure 3a) ($t = 0.969$; $p = 0.344$), suggesting no strong directional difference in turnover dynamics between habitats at this site (Appendix S1: Figure S6a). This pattern was also evident in the rate of directional change, which demonstrated similar shifts in species composition throughout the study period (Appendix S1: Figure S6b). In the long-term surveys, species synchrony was high (Figure 3b) and temporal stability was lower (Figure 3c) on the breakwater than on natural rocky platforms. Field experiments conducted in Antofagasta (23° S) corroborated these findings, showing a similar between-habitat pattern in species turnover (Figure 4a,b) but higher synchrony in the removal (disturbed) treatment and higher temporal stability in the control in both habitat types (Figure 4c–f). Nonetheless, the magnitude of community synchrony was greater on the breakwater (Figure 4c,d), whereas temporal stability was relatively equivalent in both habitat types (Figure 4e,f).

Community-wide intra-annual temporal stability estimated at the long-term surveys (Iquique; 20° S) showed a monotonic positive relationship with species richness (measured at the quadrat scale; 1225 cm^2), particularly on the breakwater (Figure 5a, Appendix S1: Table S1). A similar pattern emerged from field experiments (Antofagasta; 23° S), where temporal stability increased monotonically with species richness (estimated at 625 cm^2 scale) on the study breakwater in both treatments (Figure 5b). However, the analysis revealed a nonsignificant trend ($p = 0.09$) of species richness on temporal stability on the breakwater in this case (Appendix S1: Table S1).

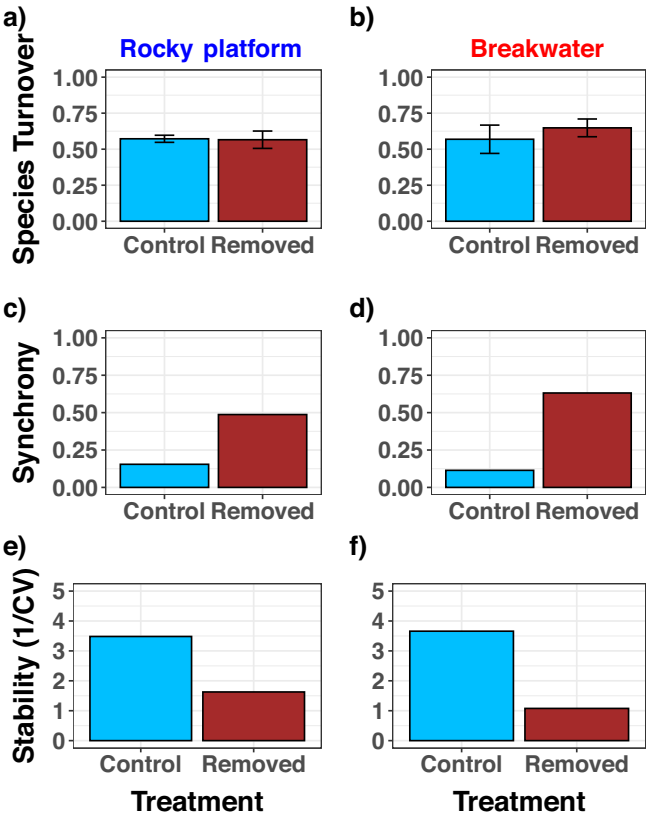


FIGURE 4 Short-term community dynamics from field experiments. Species turnover (a and b), species synchrony (c and d), and temporal stability (i.e., 1/CV) (e and f) estimated for unmanipulated control and community "removed" 25 × 25 cm areas after 573 days of experiments, in a study rocky platform and a breakwater at Antofagasta (23° S).

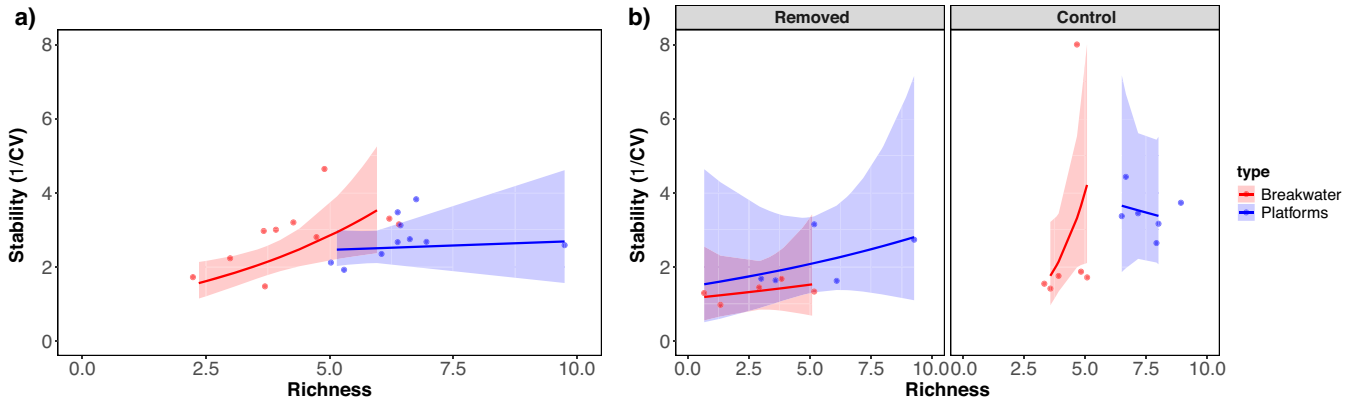


FIGURE 5 Richness–invariability relationship. Gamma models (log-link function) were fitted to the relationship between species richness and temporal stability (1/CV, "Invariability") at (a) the long-term surveys in Iquique (20° S) and (b) the short-term (573 days, ca. 19 months) field experiment conducted in Antofagasta (23° S), separately for the "Removed" and "Control" treatments. Expected values and 95% CIs are shown for the breakwater (red) and natural rocky platform(s) (blue) at each locality. Lines and confidence bands are restricted to the range of species richness observed within each group, to avoid extrapolation beyond the sampled data. Red and blue points represent observed values of temporal stability (1/CV) for each transect (a) or plot (b).

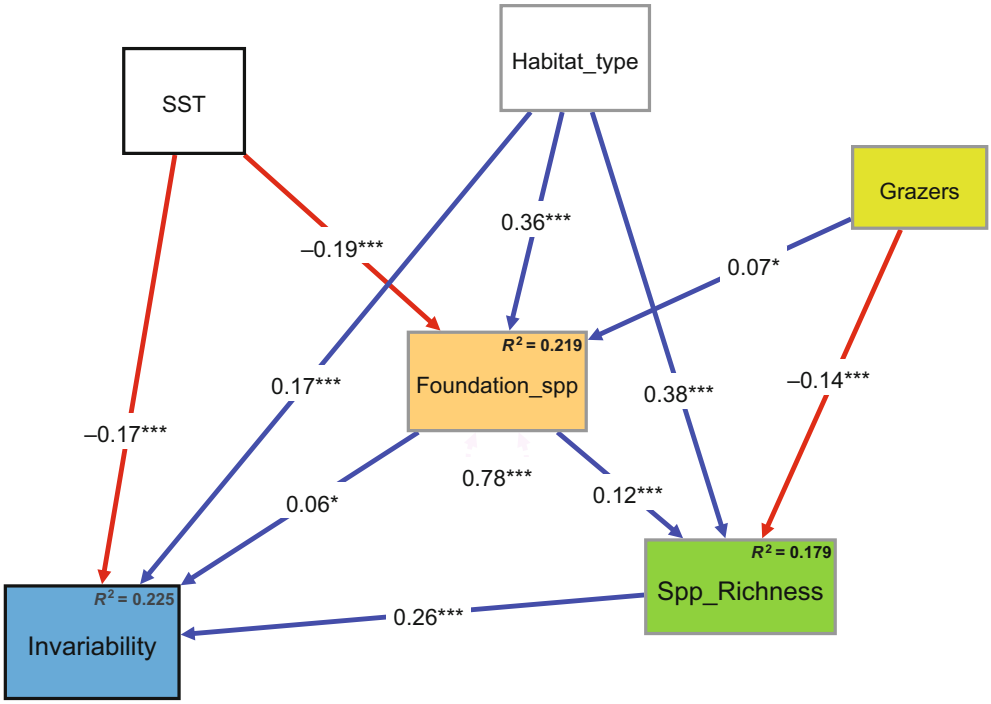


FIGURE 6 Structural equation model (SEM) showing the direct and indirect effects of different biotic and abiotic factors on the "intra-year" community invariability (i.e., 1/CV; a measure of temporal stability) at the breakwater and the natural rocky platforms. The model fits the data relatively well (Fisher's $C = 1.913$; $p = 0.167$, $n = 1156$). Blue lines represent positive effects, while red lines indicate negative effects. Values correspond to the standardized path coefficients. The variance explained by the entire model (R^2) is provided for each response variable. The categorical variable "habitat type" was coded as binary (Natural = 1, Breakwater = 0). Only statistically significant effects (*: $p < 0.05$; ***: $p < 0.001$) are depicted. SEM was fitted to the data from the long-term monitoring program. SST, sea surface temperature.

Consistent with previous findings, SEMs constructed for the long-term surveys conducted at Iquique (20° S) showed that the cover of foundation species (%) promoted total species richness (Figure 6). This increase in richness, in turn, was associated with greater intra-annual temporal stability in species abundances (Figure 6, see blue lines). Despite a slight, although statistically significant, positive effect on foundation species percentage cover, grazer density was negatively related to species richness (Figure 6, see red lines).

Furthermore, exogenous variables such as the age of the breakwater and fluctuations in SST (Appendix S1: Figure S7) negatively affected foundation species abundances and intra-annual stability in total species abundances (Figure 6, red lines). Overall, the models suggest biotic components, like the abundance of foundation species and species richness, which were higher in natural rocky platforms at the study site, play a crucial role in promoting community temporal stability in the rocky intertidal system. In contrast, abiotic factors like SST produced a significant modulatory effect on foundation species, decreasing temporal stability.

DISCUSSION

This study provides novel evidence that, in a single-site case-study comparison (i.e., long-term surveys in Iquique; 20° S) spanning two decades, interactions between key biotic factors, including foundation species abundances, species richness, and species asynchrony, and abiotic variability (e.g., SST) shape community temporal stability across longer and more ecologically relevant timescales than typically examined. Three key findings emerged from the analyses: First, divergence in species composition between the built and adjacent natural platforms was persistent over time, but a transient convergence in species diversity and composition was observed around 11–13 years after the built structure was constructed. Second, the community on the built structure was more temporally variable than on natural platforms, a pattern associated with lower foundation species abundances, lower species diversity, and higher synchrony in species abundances. Finally, foundation species significantly influenced species richness, and the number of species per se appeared to affect community temporal stability more strongly on the built structure than on natural platforms. Field experiments conducted at an independent locality (Antofagasta, 23° S) corroborated these findings, suggesting that the observed patterns may hold across built structures sharing similar physical contexts (e.g., wave exposure), despite differences in specific site conditions.

The role of foundation species in community fluctuations

There is evidence that the presence of a dominant foundation species such as mussels or kelps, by providing refuges against stressful conditions, can enhance species diversity (Benoit et al., 2026; Firth et al., 2021), thereby stabilizing rocky shore communities (Bulleri, Benedetti-Cecchi, et al., 2012; Miner et al., 2021). In the long-term surveys conducted in Iquique (20° S), we found that the divergence in species composition and diversity between the study breakwater and the natural rocky platforms persisted over time, although a transient convergence in species numbers and composition was observed roughly 11–13 years after the deployment of the built structure. This result aligns with previous studies, which showed that similar coastal structures developed mainly "saturated" communities after about 6–8 years since construction (Yu et al., 2025), with older communities exhibiting even lower taxonomic richness (Dong et al., 2016). Our results from the long-term surveys indicated that the absence of the foundation species, *P. purpuratus*, on the built structure, along with the concurrent removal of barnacles in the "community removal" treatment of the field experiments conducted in Antofagasta (23° S), promoted higher species synchrony and, consequently, community variability. This pattern supports the positive relationship between asynchrony and stability, implying a compensatory mechanism in species abundances, which has been described across various natural and seminatural systems (Craven et al., 2018; Loreau & de Mazancourt, 2013; Valencia et al., 2020), including intertidal rocky platforms in southern Chile (Fica-Rojas et al., 2022; Valdivia et al., 2021). Our field surveys revealed that foundation species influence community stability mainly through their effects on species richness. Given topographic heterogeneity can reduce rocky shore community stability through suppression of foundation species (Sola et al., 2025), further examination of the concurrent role of different topographic (e.g., rock pools) and biogenic microhabitats in community fluctuations is needed.

Biodiversity and stability in natural and built coastal structures

There is compelling evidence linking biodiversity to community stability, driven by the combination of species asynchrony, species interactions, the stability of dominant species, and overyielding (Craven et al., 2018; Loreau & de Mazancourt, 2013; Sasaki et al., 2019). In particular, the effects of species richness on temporal community stability seem to operate through the indirect influence of species synchrony/asynchrony (Valencia et al., 2020). In this context, in the long-term surveys conducted at Iquique (20° S), we found that the number of species increased community stability more consistently in the breakwater, where high species synchrony and lower abundances of foundation species (barnacles) were observed, although the short-term field experiments conducted in Antofagasta (23° S) corroborated these

findings only partially. Therefore, the mechanisms through which species richness affected community stability seemed to differ between the two study habitat types, with the natural rocky platforms aligning with the main pattern observed in other systems, where species asynchrony (Craven et al., 2018; Valdivia et al., 2021; Valencia et al., 2020), and/or foundation species presence/absence (Bulleri, Benedetti-Cecchi, et al., 2012; Bulleri, Russell, & Connell, 2012; Miner et al., 2021; Valdivia et al., 2025) play significant roles. Conversely, on the breakwater, the positive influence of species richness on community stability could not be directly attributed to these mechanisms. The diversity–stability relationship was more evident on the breakwater than on the natural rocky platforms, contrasting with our original hypothesis, which may be related to the lower species richness on the built structure. This unexpected pattern warrants further attention in future studies.

Modulatory effects of environmental and biotic processes on community assembly

Long-term surveys conducted in Iquique (20° S) across a wave-exposed breakwater and adjacent rocky platforms revealed that biotic factors primarily influence community fluctuations. Given wave exposure modulates desiccation stress, larval supply, and substratum availability, its variation across built structure orientations and ages likely contributes to the context-dependency of community dynamics observed across studies (Bracewell et al., 2021; Mayer-Pinto et al., 2019). Beyond these factors, SST (Appendix S1: Figure S7)—acting mainly as a proxy for upwelling and primary productivity—significantly reduced "intra-annual" community stability. This suggests that environmental variability, influencing, for example, invertebrate larval availability (Lara et al., 2016), also played an important role in intertidal community dynamics across the built structure and the natural rocky platforms (Valdivia et al., 2021). In addition, since foundation species such as mussels were absent from the studied breakwater, air desiccation stress may have significantly contributed to fluctuations in subordinate species in the absence of biogenic thermal refuges. The persistent absence of mussels (*P. purpuratus*) from the study breakwater over 20 years warrants explanation. Since large mussel beds were neighboring the structures—and the mussel larvae have large dispersal and settlement correlated positively with wave height (Navarrete et al., 2005, 2015)—we cannot attribute this pattern to limitations in larval dispersal (Heino et al., 2015; Loke & Chisholm, 2023). Likewise, a "mass-effect" through "source-sink dynamics" where species are maintained in unfavorable conditions ("sinks") via immigration from source populations (Mouquet & Loreau, 2003; Pulliam, 1988; Shmida & Wilson, 1985) appears unlikely.

Beyond larval availability, multiple abiotic and biotic filters acting sequentially, from metamorphosis and settlement through post-settlement survival to reproduction (e.g., Connell, 1985; Thorson, 1966), could have prevented mussel establishment on the study breakwater. Given that the sun-exposed sides of the built structures, lacking shaded or moist shelters, can reach higher temperatures during the day (Aguilera et al., 2019; Cryan et al., 2021), increasing species evaporative cooling and desiccation stress, it may reduce post-settlement survival even of foundation species (Helmuth, 1998). In addition, thermal stress can also increase grazing pressure, likely by boosting metabolic rates (O'Connor, 2009), contributing to the persistence of bare space. In turn, reduced barnacle cover may decrease substrate roughness, limiting mussel establishment on the built structure (Berlow & Navarrete, 1997; Navarrete & Berlow, 2006; Navarrete & Castilla, 1990). Mussel larvae are known to preferentially settle on biogenic nursery habitats such as barnacle matrices (Navarrete & Castilla, 1990), or even branching algae, and articulated coralline algae (Kelaher, 2003; McQuaid & Lindsay, 2005), which were largely absent or scarce on the study breakwater. The lack of these facilitative substrata may have prevented mussel establishment independently of larval supply, suggesting that restoring foundation species on built structures may require a sequential facilitation approach; first, promoting barnacle or algal nursery habitats before mussel recruitment can be expected.

Early colonists, such as cyanophytes and opportunistic macroalgae, which can preempt space and tolerate stressful conditions, could also hinder later colonization and establishment of foundation species (Berlow, 1997; Connell & Slatyer, 1983; Fukami, 2015). The same pattern could be invoked for grazer-resistant algae species like *Hildenbrandia* and *Ralfsia*, which could preempt space under intense grazing (Bertness et al., 1983), reducing barnacle colonization and likely subsequent mussel settlement. Indeed, noncalcareous crustose algae abundance was higher in the study breakwater than in the natural rocky platforms, especially from around 12 years since construction (Appendix S1: Figure S4). Whether these taxa function as inhibitory dominants, delaying succession toward foundation-species-dominated states, or as cryptic foundation species providing thermal buffering and substratum stability for meiofauna and early recruits, remains unclear. Targeted removal experiments, combined with settlement assays, would help clarify the nature and direction of these interactions, and whether managing crustose algae during early or mid-successional

stages could enhance foundation species recruitment on built structures across different sites. Taken together, SST, desiccation stress, together with competition and consumption, might interactively explain the reduced abundances of foundation species on the study breakwater, a phenomenon that warrants further investigation combining thermal loggers and settlement assays across built structures with different wave orientations and ages.

Timing and features for the "greening of gray infrastructure"

Our 20-year dataset reveals that intertidal communities on built coastal structures do not simply converge toward natural communities over time; rather, they follow a more complex, nonlinear trajectory with at least three recognizable ecological stages (Appendix S1: Figure S8). In the first stage, (I) spanning roughly the first decade after construction, species richness increases gradually as propagules from adjacent natural communities colonize available space, a process likely dominated by stochastic events and chance arrival of settlers, a "lottery for space" in which early colonists with equivalent settlement abilities claim primary substrate (Chesson, 2000; Shinen & Navarrete, 2014). This is followed by a transient saturation stage (S), observed around 11–13 years post-construction in our system, during which species diversity peaks and community composition transiently converges with that of adjacent natural platforms. This window of maximum diversity may reflect a temporary balance between colonization and competitive exclusion, where resource partitioning and fitness differences allow high species coexistence (Schoener, 1974; Siepielski & McPeek, 2010). Eventually, however, the community enters a decline stage (D), from approximately 14–15 years onward, in which species richness decreases and bare space increases. We attribute this late-stage impoverishment to the compounding effects of desiccation stress and intensified biotic interactions, particularly grazing and competition, operating in the persistent absence of the foundation species *P. purpuratus* and of topographic microhabitats, which on natural rocky platforms buffer these stressors by creating shaded, moist refuges for subordinate species.

The increase in bare space during this decline stage (Appendix S1: Figure S8) deserves particular attention. Rather than representing a return to an early successional state, this stage likely reflects a community locked in an alternative configuration, dominated by large bare rock patches and stress-tolerant noncalcareous crustose algae. This state is characterized by high species synchrony and low temporal stability, from which rehabilitation toward a foundation-species-dominated state may be difficult without external intervention. Similar successional trajectories have been documented in built structures elsewhere (Dong et al., 2016; Yu et al., 2025), suggesting that this pattern may be a general feature of community development on artificial hard substrata.

This temporal framework has direct implications for the "greening of gray infrastructure" ("GGI") which correspond to the planned enhancement of built structures to support biodiversity (Firth, Bone, et al., 2024). The key insight is that the effectiveness of ecological interventions is time-dependent—the same action applied at different stages may produce fundamentally different outcomes. Intervening early, during the increase stage, by promoting nursery habitats and enhancing substrate complexity, and seeding or transplanting foundation species such as mussels or kelps, could redirect the successional trajectory before stochastic early colonists preempt primary space. This would not only accelerate community development but also modify the types of microhabitats available for later-arriving species (i.e., "priority effect"; Fukami, 2015), potentially preventing the decline stage altogether. Alternatively, intervening during the saturation stage, when species diversity is at its peak, could consolidate biodiversity gains and extend the window of maximum richness before the community declines. In both cases, managing competitive and consumptive interactions early in succession, for instance, by controlling grazing pressure or removing nonindigenous early colonists which tend to establish early at succession (Bulleri & Airoldi, 2005; Glasby et al., 2007; Leclerc et al., 2018), may further enhance the long-term biodiversity outcomes of built structures.

Concluding remarks

Assisting the early arrival of species in recently installed structures, or in disturbed patches of older ones, could enhance marine eco-engineering efforts by boosting biodiversity (Firth, Bone, et al., 2024). However, previous studies have shown that ecological enhancement of built structures can be highly dependent on the environmental context (Aguilera et al., 2025; Bracewell et al., 2021; Mayer-Pinto et al., 2019; Strain et al., 2021), making it more challenging to generalize these interventions. Nonetheless, some common patterns can be identified from local successional patterns of species traits and functional groups (Weidlich et al., 2021) along environmental gradients of wave and/or thermal stress, thereby enabling proper management of facilitative and antagonistic interactions (Silliman & He, 2018). Although we

found no indication of dispersal limitation for foundation species colonization at the study site, the limited species connectivity along highly urbanized coasts (Bishop et al., 2017; Vargas-Fonseca et al., 2016) may suggest that dispersal-driven processes may be key in sustaining local intertidal communities within some built structures (Loke & Chisholm, 2023). Long-term surveys and field experiments remain essential for identifying the roles of dispersal- and/or niche-driven processes in shaping natural and built coastal habitats. In a quest for general patterns, simultaneous analysis of community fluctuations across different "novel built structures" under different environmental scenarios (e.g., urbanization levels, wave exposure) may offer valuable insights for planning where, when, and how to intervene. Importantly, given that community dynamics on built structures appear to be highly context-dependent, varying with urbanization levels, wave exposure, and local species pools (Mayer-Pinto et al., 2019; Strain et al., 2021), site-specific idiosyncrasies may themselves be ecologically meaningful, rather than mere noise to be averaged out. Identifying the environmental drivers of such variability may thus be as important as searching for generalized patterns.

AUTHOR CONTRIBUTIONS

Conceptualization: Moisés A. Aguilera. *Data curation*: Moisés A. Aguilera. *Formal analysis*: Moisés A. Aguilera. *Funding acquisition*: Moisés A. Aguilera. *Methodology*: Moisés A. Aguilera. *Visualization*: Moisés A. Aguilera, and Nelson Valdivia. *Writing—original draft*: Moisés A. Aguilera, Nelson Valdivia, and Bernardo R. Broitman. *Writing—review and editing*: Moisés A. Aguilera, Nelson Valdivia, Bernardo R. Broitman, Louise B. Firth, and Fabio Bulleri.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Aguilera, 2026a) are available in Figshare at https://doi.org/10.6084/m9.figshare.33650113.v1. Code (Aguilera, 2026b) is available in Figshare at https://doi.org/10.6084/m9.figshare.33651097.v1.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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