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**LETTER**

# Species Removal Dampens the Scale Dependency of Ecological Determinism and Stochasticity in Coastal Communities

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## ABSTRACT

Deterministic and stochastic processes control community dynamics. However, the responses of both processes to the loss of foundation species, which strongly influence community dynamics across spatial scales, are unclear. We experimentally examined how spatial extent and foundation species removal affect rocky-intertidal community dynamics over 3 years in eight field sites spanning ~1000 km along the southeastern Pacific. The normalised stochasticity ratio (*NST*), which distinguishes between stochastic (> 50%) and deterministic (< 50%) community dynamics, decreased with spatial extent for sessile and mobile species, with consistently lower values under foundation species removal for sessile communities. The effect of foundation species removal on *NST* was strongest in smaller sessile communities and diminished as spatial extent increased, while mobile communities showed no significant response to the disturbance. Our experimental results demonstrate that the loss of foundation species disrupts the scale dependency of ecological mechanisms, highlighting its negative implications for biodiversity conservation and ecosystem functioning.

## 1 | Introduction

Temporal variation in population abundance is an inherent property of ecological communities. It can be represented as temporal β-diversity, the variation in the identities and abundances of taxa in an assemblage over two or more time points (Magurran et al. 2019). Quantifying temporal variation allows us to understand how populations, communities and ecosystems respond to natural and anthropogenic disturbances (Lamy et al. 2021). Hence, untangling the mechanisms controlling temporal β-diversity is a central aim of ecological research. An emerging consensus indicates that community dynamics are controlled by an interplay of deterministic and stochastic processes (HilleRisLambers et al. 2012; Vellend 2016; Thompson et al. 2020). Another prediction arising from this recent theoretical synthesis suggests that the effect of stochastic processes on population and community dynamics decreases as spatial extent and total community abundance increase (e.g., Vellend 2016). However, empirical evidence demonstrating such scale dependency remains elusive (but see Graco-Roza et al. 2022; Xu et al. 2024). Understanding this relationship is crucial for predicting future states of ecosystems in the face of natural or anthropogenic disturbances.

Deterministic mechanisms—like niche partitioning and environmental filtering—depend on the breadth of species' environmental tolerances, such as density-independent physiological responses to abiotic conditions and density-dependent biological interactions like competition, predation and facilitation (MacArthur and Levins 1967; Keddy 1992; Belyea and Lancaster 1999; Somero 2010). On the other hand, stochasticity shapes community dynamics by altering demographic rates (birth, reproduction and mortality), along with dispersal and colonisation processes (MacArthur and Wilson 1967; MacArthur 1972; Drake 1991; Hubbell 2001; Fukami 2004; Shoemaker et al. 2020; Reijenga et al. 2021). Environmental stochasticity is another relevant source of community or population stochasticity: importantly, the temporal pattern of an environmental variable is composed of both a deterministic trend (e.g., seasonality) and temporally uncorrelated environmental variation that usually occurs at smaller temporal scales, which can be analytically used as a proxy for environmental stochasticity. Environmental heterogeneity—that is persistent environmental differences between sites within a region—is a central element of niche-based processes with scale-dependent effects on biodiversity (Pianka 1966; MacArthur and Wilson 1967; MacArthur 1972; Drake 1991; Hubbell 2001; Fukami 2004; Reijenga et al. 2021; Graco-Roza et al. 2022). It is possible, therefore, to compare the relative contribution of predictable and unpredictable environmental patterns on temporal β-diversity as proxies for deterministic and stochastic environmental processes, respectively. A predominant influence of stochastic processes on community dynamics can generate temporal β-diversity patterns that are indistinguishable from ecological drift (Zhou et al. 2014; Ning et al. 2019; Liang et al. 2020). However, empirical evidence shows that press disturbances, such as habitat degradation due to anthropogenic activities, can diminish the influence of temporal stochasticity—this strengthens the role of deterministic environmental filtering and biotic interactions in shaping temporal β-diversity (Li et al. 2021).

How does spatial scale influence the effects of deterministic and stochastic processes on temporal β-diversity? On one side, environmental heterogeneity can increase with increasing spatial extent, as shown in habitats like oceanic islands, freshwater lakes and rocky shores (Blanchette et al. 2008; Fenberg et al. 2015; Chase et al. 2019). Deterministic processes like niche differences could maintain populations of species that can exploit different environmental niches distributed over larger spatial scales (Whittaker 1972; Tilman 1980; Chase et al. 2019; Wang et al. 2019; Li et al. 2020). On the other side, the strength of stochasticity is density-dependent: communities with more individuals are less affected by random demographic and environmental events than smaller communities (Lande 1993; Orrock and Watling 2010; Vellend 2016; Shoemaker et al. 2020; Segrestin and Leps 2022). Similarly, across larger regions, niche differences maintained by environmental heterogeneity can override the effects of stochasticity on temporal community dynamics (Orrock and Watling 2010). If larger areas incorporate or 'sample' greater environmental heterogeneity and harbour larger populations, the influence of deterministic processes on temporal β-diversity should increase—and the effects of stochastic processes should decrease—as spatial extent increases.

The scale dependency of community structuring processes can be influenced by large and persistent disturbances, such as the local extinction of numerically dominant species that have strong effects on community dynamics (e.g., Gaylord et al. 2011). Foundation species, which are usually numerically dominant, have a large influence on community dynamics because they form biogenic habitats that ameliorate environmental extremes (Dayton 1971; Cole and McQuaid 2010; Ellison 2019; Lamy et al. 2020; Catalán et al. 2023). Therefore, the loss of foundation species can have strong negative ecological consequences, leading to delayed but predictable extinctions within the remnant habitats (Tilman et al. 1994). Foundation species, like mussels in rocky shore systems, amplify the effect of environmental stochasticity on the temporal dynamics of subdominant species (Wootton 2010). Moreover, theory indicates that the temporal variation in abundance of numerically dominant species largely contributes to the variation of the whole community (de Mazancourt et al. 2013; Loreau and de Mazancourt 2013). The loss of a foundation species in a community should therefore decrease the contribution of stochasticity to temporal β-diversity. However, the loss of biogenic habitat and the concomitant extinction or reduction in population size of other species can stimulate the settlement of pioneer organisms characterised by stochastic population dynamics (Stroud et al. 2024), leading to an increase in stochasticity across spatial extent. Indeed, classic successional models explicitly incorporate stochasticity over time (e.g., priority effects) to predict compositional dynamics after disturbance (Connell and Slatyer 1977). Accordingly, the effects of foundation species on the balance between ecological determinism and stochasticity are still unclear.

Here, we investigate the separate and interactive effects of spatial extent (number of sites) and the loss of dominant—foundation—species on the contribution of ecological determinism and stochasticity to temporal β-diversity. To this end, we used the rocky intertidal ecosystem of the southeastern Pacific coast to implement a 3-year field manipulative experiment replicated across eight sites spanning ~1000 km and over 10° of latitude. We used a normalised stochasticity ratio (*NST*) as the response variable, comparing observed temporal β-diversity to null expectations (Zhou et al. 2014; Ning et al. 2019). We tested five interrelated hypotheses:

(H1) The contribution of stochastic processes to temporal β-diversity decreases with increasing spatial extent: Environmental heterogeneity increases with spatial extent, strengthening niche differences and reducing demographic stochasticity as total community abundance increases (Orrock and

**TABLE 1** | Location of the study sites in the northern and southern subregions in the southeast Pacific coast.

| Subregion | Latitude | Longitude | Site | Site code | Removed foundation species | Percent cover (mean ± SD) |
|---|---|---|---|---|---|---|
| Northern | 29.28 | 71.18 | Temblador | TEMB | Barnacles | 40.0 ± 18.1 |
| | 30.20 | 71.48 | Guanaqueros | GUAN | Barnacles | 69.0 ± 20.6 |
| | 30.45 | 71.42 | Limarí | LIMA | *Mazzaella laminarioides* | 54.3 ± 15.0 |
| | 30.54 | 71.41 | Punta Talca | PTAL | *M. laminarioides* | 31.1 ± 21.4 |
| Southern | 39.41 | 73.22 | Cheuque | CHEU | *Perumytilus purpuratus* | 100.0 ± 0.0 |
| | 39.78 | 73.39 | Calfuco | CALF | *P. purpuratus* | 100.0 ± 0.0 |
| | 39.93 | 73.59 | Chaihuín | CHAI | Barnacles | 89.0 ± 10.0 |
| | 40.54 | 73.72 | Pucatrihue | PUCA | *P. purpuratus* | 98.4 ± 3.05 |

*Note:* The foundation species experimentally removed at each site is identified. Mean (±SD) percent cover of each species, measured before the experimental removal, is given for each site.

Watling 2010; Vellend 2016; Chase et al. 2019). We predicted determinism would increase, and stochasticity decrease, from small to large communities.

(H2) Foundation species removal increases deterministic processes in temporal β-diversity: Foundation species provide habitat complexity, buffering abiotic stress and supporting less-tolerant species (Helmuth et al. 2006; Altieri and van de Koppel 2014); their removal would push temporal β-diversity towards determinism.

(H3) Alternatively, foundation species removal increases stochasticity in temporal β-diversity: Loss of less-tolerant species following the removal of foundation species may lead to colonisation by transient species that increases stochastic colonisation and demographic patterns (Stroud et al. 2024). This hypothesis predicts increased stochasticity with removal.

(H4) Foundation species removal amplifies the positive effect of spatial extent on determinism: If H2 holds, we predict removal would strengthen the positive effect of spatial extent on determinism.

(H5) Conversely, foundation species removal and spatial extent may cancel each other's effects: If H3 holds, removal would counteract the negative effect of spatial extent on stochasticity.

## 2 | Material and Methods

### 2.1 | Study Region and Experimental Design

The study was conducted at the equator- and poleward extremes of the transitional biogeographic province of the southeastern Pacific shoreline (ca. 30° S to 40° S, respectively; Lara et al. 2019; Table 1). The structure of the rocky intertidal zone communities in the region is described elsewhere (Aguilera et al. 2019; Valdivia, Aguilera, et al. 2021).

We conducted a manipulative field experiment at the mid intertidal zone of each of four sites located around 30° S (referred to as 'northern subregion'), and at four sites located around 40° S (referred to as 'southern subregion'). Each subregion spanned ca. 200 km of the shoreline (Table 1). To characterise local environmental conditions, we utilised sea surface temperature (*SST*), air temperature and wind components over time at each study site (see Supporting Information).

Foundation species such as the corticated red alga *Mazzaella laminarioides* (Bory) Fredericq 1993 and chthamalid barnacles (a mixture of *Jehlius cirratus* (Darwin 1854) and *Notochthamalus scabrosus* (Darwin 1854) were the dominant species in the northern subregion; chthamalid barnacles and the purple mussel *Perumytilus purpuratus* (Lamark 1819) dominated the southern subregion (Table 1; Valdivia, Aguilera, et al. 2021). The experimental units consisted of 30 × 30 cm plots selected on the mid-intertidal zone and within areas of high abundance of the locally dominant foundation species. The experiment involved the sustained removal of each locally dominant sessile species as a fixed factor with two levels (foundation species removal or control without manipulation). Settlers and recruits of the foundation species were removed from the removal plots approximately every 3 months. Therefore, we selectively removed the dominant species, conforming to a 'press disturbance' (e.g., Bulleri et al. 2012).

The abundance of each macrobenthic species (> 5 mm) was estimated for each plot immediately before the initial removal of foundation species, 1–2 months after, and then approximately every 3 months until the end of the experiment (Supporting Information). The experiments were conducted between October 2014 and August 2017 in the southern subregion, and between December 2014 and September 2017 in the northern subregion; that is ca. 3 years (see details in Valdivia, López, et al. 2021; Fica-Rojas et al. 2022; Catalán et al. 2023). All observations and experimental manipulations were carried out during diurnal low tides (tidal range ca. 1.5 m). Before the analyses (except *db-RDA*), species abundance data of all plots within each site were summed to exclude the within-site variation and to focus on the temporal trends of the sites and regions.

We used the data from the 11 successive surveys conducted after the initiation of the experiment—spanning ca. 3 years—to estimate temporal community trends separately for sessile and mobile species. Since we were interested in the response of the remaining community to the local extinction of foundation species, the latter were removed from the dataset before the analyses.

## 2.2 | Spatial Scaling of Communities

To assess the relationship between spatial extent (area: *A*) and community dynamics, individual sites ($n = 8$) were aggregated into groups of cumulative numbers of communities (i.e., 1–8). This method resembled the aggregation of sites or samples in type-III species–area curve, where the curve is defined by the mean species richness under all possible permutations of samples (Scheiner 2003; Ugland et al. 2003; Wang et al. 2017). In our study, we aggregated data by summing the observed abundances of each species across sampling times within each site aggregation, resulting in a time series of each species for each site combination and removal treatment. Accordingly, *A* was expressed as the number of sites included in the calculation of temporal community patterns (see further details in the Supporting Information).

Temporal β-diversity was estimated as Bray–Curtis dissimilarities among sampling times and for each site combination (from one to eight sites). It was calculated from all possible pairwise similarities between sampling times for every site combination, treating the three-monthly region-wide community matrices as a metacommunity. Null models were used to assess temporal ecological stochasticity: Bray–Curtis dissimilarity was compared to null expectations, assuming deterministic processes could make communities more similar or dissimilar than expected by chance (Chase et al. 2009; Zhou et al. 2014; Ning et al. 2019; Li et al. 2021). Null communities for each site combination were generated by randomising the observed species abundance matrix 100 times using the '*PF*' algorithm, which maintains fixed taxon richness per sample and assigns taxa occurrence probabilities proportional to total occurrences at each site aggregation (Gotelli 2000; Chase et al. 2019; Ning et al. 2019).

## 2.3 | Temporal β-Diversity

To assess the relative contributions of deterministic and stochastic processes to community dynamics, we used the *NST* based on the selection strength (*SS*) proposed by Zhou et al. (2014). For each pairwise comparison, *SS* is a proportion calculated as the difference between observed dissimilarity and null expected dissimilarity, divided by the observed dissimilarity. The mean *SS* across all pairwise comparisons is then used as *NST* (Zhou et al. 2014). *NST* is bounded between 0 and 1, with values above 0.5 (50%) indicating predominantly stochastic assembly and values below 0.5 indicating predominantly deterministic assembly (Ning et al. 2019; see the equations in Supporting Information).

## 2.4 | Statistical Analyses

We used general linear mixed models (*LMMs*) to test our hypotheses, analysing separately the *NST* of sessile or mobile species as response variables. Spatial extent (*A*, eight levels: one to eight sites) and foundation species removal (two levels: control or removed) were included as fixed, crossed effects. Alpha diversity varied between subregions (see Section 3), so species richness was added as a fixed effect. Linear and quadratic orthogonal contrasts were applied to *A* and species richness to account for potential nonlinear *NST* patterns. Data for *A* and species richness were standardised and centred before model fitting.

Each model incorporated an autoregressive-moving average (*ARMA*) structure to address residual non-independence in space from site grouping. Model improvement was assessed by visually inspecting autocorrelation and partial autocorrelation functions (*ACF*, *pACF*, Figure S1) and conducting log-likelihood ratio (*LR*) tests comparing naïve models to *ARMA*-inclusive models. First- and second-order correlation structures were tested sequentially. For sessile species, first-order *ARMA* did not improve the naïve model ($LR = 0.18$, $p = 0.66$), but second-order ARMA did ($LR = 13.1$, $p < 0.001$). For mobile species, both first- and second-order *ARMA* improved model fit ($LR = 61.8$, $p < 0.001$; $LR = 7.2$, $p = 0.007$, respectively). Thus, second-order *ARMA* was used for both sessile and mobile species models. It should be noted that the incorporation of *ARMA* in the improved model did not affect the calculation of temporal *NST*, as this calculation was independent from the statistical model formulation. Therefore, controlling spatial autocorrelation did not increase the likelihood of detecting stochastic temporal patterns in our analyses.

The Akaike information criterion, corrected for small samples (*AICc*), was used to evaluate the strength of empirical support for the global and all possible nested models. Model selection was based on Delta Akaike ($\Delta_i$) and the probability of each model ($w_i$), given the observed data and the model family. Model averaging was applied to account for uncertainty when no single 'best' model could be identified (Burnham and Anderson 2004; Symonds and Moussalli 2011), using only models with $\Delta_i < 6$ (see statistical details in the Supporting Information).

Variance partitioning analyses were conducted to assess the contribution of the abiotic environment to community dynamics at site and regional scales (Bray–Curtis dissimilarities). For each environmental variable, we first calculated the mean value for each spatial scale and then the first-order difference was computed as a proxy for uncorrelated environmental variability (environmental stochasticity). Both raw and stochasticity-proxy environmental variables were used as predictors in variance partitioning analyses (Peres-Neto et al. 2006). This allowed partitioning of temporal variation in community structure into 'pure' effects of deterministic trends and stochastic environmental variability, using adjusted $R^2$ and distance-based redundancy analyses (*db-RDA*; Peres-Neto et al. 2006). Confidence intervals (95% CI) for adjusted $R^2$ were obtained via 1000 bootstrap resamples.

Multivariate trends in community structure were analysed using *db-RDA* and *PERMANOVA*, based on Bray–Curtis dissimilarities, separately for each site. Models included removal treatment and sampling time as fixed, crossed factors. *PERMANOVAs* were conducted with 1000 permutations of raw data, restricted within each fixed plot to account for repeated measurements.

Temporal coefficients of variation (*CV*) were visualised for the abundance of the removed foundation species (*M. laminarioides*, barnacles and *P. purpuratus*) along spatial extent (*A*). Temporal *CV* was also calculated for understorey species showing strong responses to removal treatments: green macroalgae of the Ulvoid group and mobile grazers such as the molluscs *Scurria* spp. (Gray 1847) and *Siphonaria lessonii* Blainville, 1827 (Valdivia, López, et al. 2021; Fica-Rojas et al. 2022). For foundation species, we used data from control plots; for understorey species, we included both control and disturbed-plot data. Temporal *CVs* were calculated as the temporal standard deviation divided by the temporal mean in percent cover.

## 3 | Results

Over the sampling period, we identified 54 species: 30 sessile and 24 mobile (Table S1). Bias-corrected Chao's extrapolated richness indicated representative sampling of subregional species pools. In the southern subregion, sessile richness was 16 (observed) and 18 (extrapolated, SE = 3.73). Mobile richness was 18 (observed) and 18.49 (extrapolated, SE = 1.3) in the north, and 15 (both observed and extrapolated) in the south.

Intra-subregion variability in taxonomic coverage was slight (Figure S2 and Table S2). In the north, GUAN and LIMA had the best representation for both sessile and mobile species, with observed and extrapolated richness closely matching. PTAL also matched for mobile species, while TEMB and PTAL suggested unseen mobile species (Table S2). In the south, all sites showed tight matches between observed and extrapolated richness (Table S2).

Community structure changed significantly over time (Figures 1 and 2; Table S3). Most sites exhibited disturbance-dependent trends, except CHAI (sessile) and PTAL (mobile), where foundation species removal and time effects were independent (Table S3a,b). Sessile communities in removal plots did not converge to control conditions by the experiment's end (sampling time 11, Figure 1), indicating limited recovery over 3 years due to foundation species removal. Removal plot temporal trajectories of sessile species were longer in multivariate space, especially in PTAL, CHEU, CALF and PUCA. Mobile species trajectories were similar in magnitude between removal and control plots, except in CALF, where removal plots were shorter (Figure 2).

The effects of spatial extent (*A*) and foundation species removal on the *NST* varied between mobile and sessile species. For sessile species ($NST_s$), the full model, including *A*, removal, their interactions, and species richness had the strongest empirical support ($w_i = 0.97$; $\Delta_i$ of the second-ranked model = 6.75; Table S4a). In control groups, $NST_s$ decreased from 0.71 (CI = 0.64–0.78; fully stochastic dynamics) in single-site groups to 0.48 (0.40–0.56: moderately deterministic dynamics) in eight-site groups (Figure 3). In the removal treatment, $NST_s$ decreased from 0.57 (0.49–0.62) in small areas to 0.44 (0.37–0.52) in large areas (Figure 3). Foundation species removal negatively impacted $NST_s$, particularly in small site groups, with this effect diminishing as *A* increased (Figure 3). The slope of $NST_s$ against *A* was steeper for controls (slope = −0.98 [SE = 0.13]; Table S5a) than for removal treatments (between-group slope difference = 0.45 [0.14]; Table S5a). Species richness had a negative, nonlinear effect on $NST_s$ (Table S5a). Fixed effects (*A*, richness, and removal) explained 43% of $NST_s$ variation, while the full model explained 59% ($R^2_m = 0.43$, $R^2_c = 0.59$), indicating site-specific factors (e.g., local environment, composition) influenced baseline $NST_s$.

For mobile-species *NST* ($NST_m$), low Akaike weights of the top-ranked models indicated high uncertainty in model selection (Table S4b; $R^2_m = 0.20$, $R^2_c = 0.41$ for the full model). Model averaging revealed a significant, negative and linear effect of spatial extent on $NST_m$, regardless of removal treatment (Figure 3, Table S5b). Neither foundation species removal nor mobile species richness influenced $NST_m$ (Table S5b).

Variance partitioning analyses indicated that the contribution of 'pure' deterministic environmental trends to sessile species dynamics increased with spatial extent in control treatments (Figure 4). Foundation species removal amplified the deterministic environmental component, particularly at subregional scales, while also increasing the influence of uncorrelated environmental noise (environmental stochasticity) at small, but not large, spatial scales (Figure 4). For mobile species, environmental stochasticity's contribution decreased with spatial scale (Figure 4). These results align qualitatively with *NST* insights (Figure 3, Table S5).

Temporal variability in foundation species likely shaped these patterns, as all three species exhibited a reduced temporal coefficient of variation (CV) with increasing spatial extent in control areas (Figure 5). *M. laminarioides* showed the highest temporal variation, followed by barnacles and then *P. purpuratus* (Figure 5). Regionally, Ulvoid algae and grazer guilds were most affected by removal treatments, displaying contrasting patterns across spatial extents (Figure S3). Removal increased Ulvoids' temporal CV compared to controls, mitigating their steep decline, while reducing grazer abundance's temporal CV, with this effect slightly strengthening at larger spatial extents (Figure S3).

## 4 | Discussion

Our findings revealed an increasing role of ecological determinism—and a declining role of stochasticity—in shaping temporal β-diversity, influenced by the presence of dominant foundation species and understory species mobility in the rocky shore ecosystem of the southeastern Pacific. Experimentally removing dominant foundation species—*M. laminarioides* (red macroalgae), a chthamalid barnacle complex, and the purple mussel *P. purpuratus*—enhanced the contribution of deterministic processes to temporal β-diversity of sessile species at small scales (one to three sites) but not at larger scales. This likely resulted from stronger environmental filtering on sessile species dynamics at smaller scales, rather than reduced environmental stochasticity. Thus, foundation species removal may have intensified environmental filtering effects on sessile species, but at small spatial scales. In contrast, mobile species dynamics were primarily influenced by spatial scale, likely due to reduced environmental stochasticity. Overall, our study provides empirical evidence of the negative impacts of losing foundation species on the spatial scaling of key ecological mechanisms.

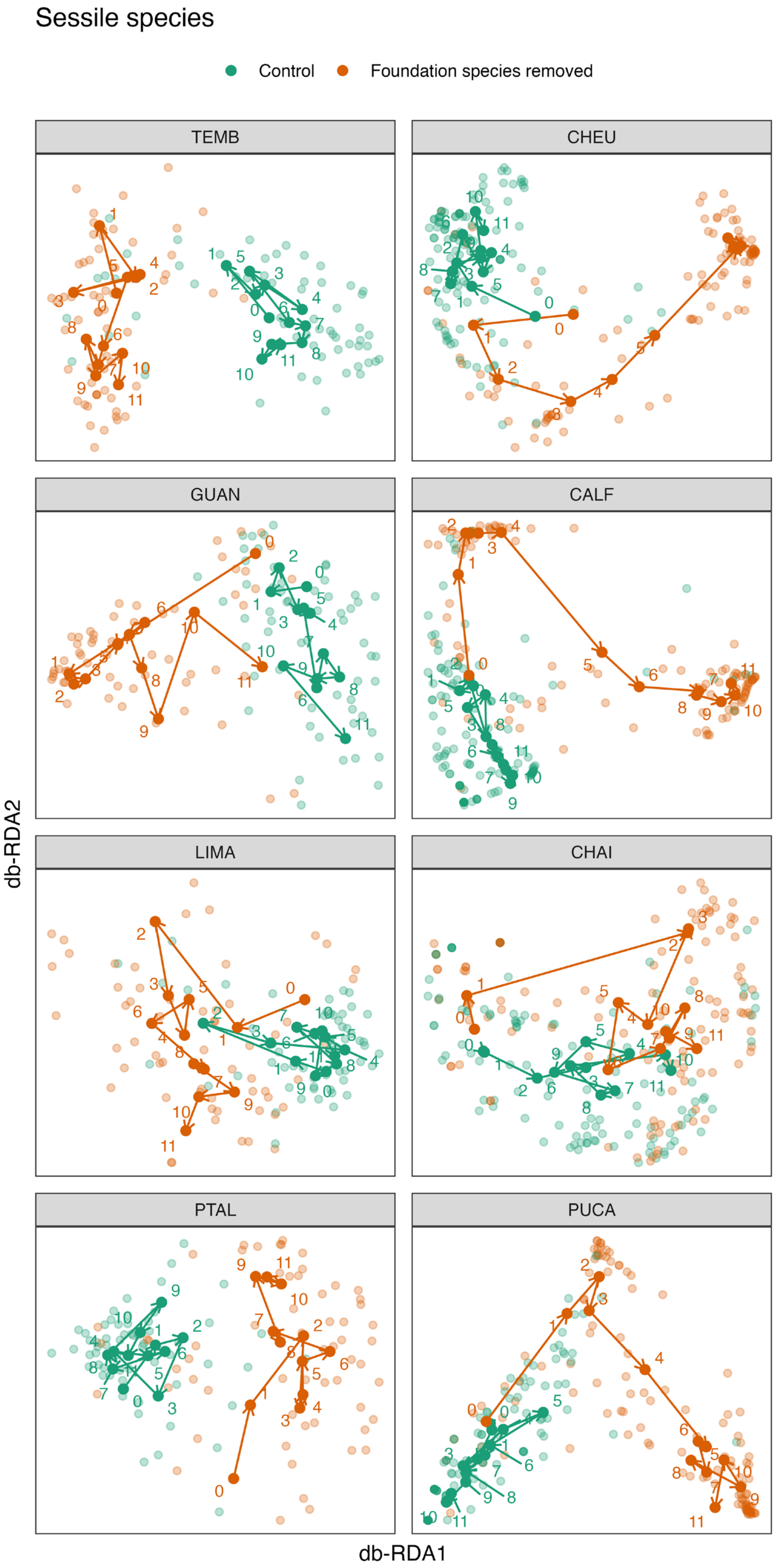

**FIGURE 1** | Legend on next page.

**FIGURE 1** | Community structure of sessile species. Separate distance-based redundancy analyses (*db-RDA*) for each experimental site. The analyses were based on Bray-Curtis dissimilarities calculated from the species-abundance matrix of each site. The model included the experimental removal of the locally dominant foundation species and sampling time. Sites were arranged in the northern and southern subregions (left and right columns, respectively).

### 4.1 | Foundation Species Removal Affected the Scale Dependency of Ecological Processes in Sessile Communities

The removal of foundation species altered the relative importance of stochastic and deterministic dynamics for subdominant sessile communities at small to mid-sized scales, supporting Hypothesis 4. This shift can be explained by two non-exclusive mechanisms. First, foundation species mitigate environmental stress in rocky intertidal habitats and regulate the structure and stability of associated communities (e.g., Watt and Scrosati 2013). Variance partitioning analyses suggested that foundation species removal increased the effects of deterministic environmental trends on sessile species dynamics, but only at subregional scales (Figure 4), aligning with observed patterns in sessile species (i.e., $NST_s$). For instance, removing the *M. laminarioides* canopy increases mean rock temperature and desiccation variability during low tide, affecting the spatial distribution of subdominant sessile species in this region (Catalán et al. 2023). Additionally, air temperature within purple mussel patches is, on average, 3°C lower than in surrounding areas at one of our southern sites ($n = 45$ and 33, respectively; A. Catalán, unpublished data). Although we lack direct evidence of environmental buffering by barnacles or mussels in our sites, studies elsewhere demonstrate their significant influence on local conditions and community structure (Harley 2006; Silliman et al. 2011; Bertocci et al. 2024). For example, field experiments show that space-dominant mussel species—ecologically similar to those in our study—amplify the impact of environmental stochasticity on subdominant species abundance over time (Wootton 2010), a pattern also observed in our system (Figure 4). Therefore, foundation species removal likely exacerbated environmental harshness for sessile species, strengthening the influence of environmental filtering on temporal β-diversity.

The environmental variables selected to characterise environmental heterogeneity significantly correlate with benthic community structure in the study region and elsewhere (Wieters et al. 2009; Lurgi et al. 2020). For instance, geographic variation in *SST* aligns with several biogeographic breaks of southeastern Pacific intertidal species (Rivadeneira and Fernandez 2005; Broitman et al. 2018; Lara et al. 2019). It should be noted, however, that unmeasured variables that also associate with the biogeographic discontinuities, such as Chlorophyll-*a* concentration and turbid river plumes, need further attention as their effects on community dynamics depend on the spatial scale (Navarrete et al. 2005; Lara et al. 2019). Air temperature can strongly influence intertidal community structure in the absence of foundation species like mussels (Silliman et al. 2011). Additionally, wind components associated with coastal upwelling and low *SST* are robust predictors of stressful conditions for calcifying invertebrates and intertidal species with limited dispersal potential (Fenberg et al. 2015; Valdivia et al. 2015; Fernández et al. 2024). Thus, the environmental heterogeneity observed in this study could drive environmental filtering in sites where abiotic conditions exceed the physiological tolerance of certain species (Portner and Knust 2007; Somero 2010; Broitman et al. 2018). Enhanced environmental filtering following foundation species removal may have intensified the influence of density-independent selective forces or altered ecological interactions (Lagos et al. 2005; Navarrete et al. 2005, 2022), leading to the observed decrease in $NST_s$ in smaller communities. Furthermore, increased environmental heterogeneity could have promoted niche partitioning as sites coalesced into larger areas, explaining the shift from more stochastic ($NST_s > 0.5$) to more deterministic ($NST_s < 0.5$) dynamics in sessile species within control communities.

Why foundation species removal increased determinism (decreased $NST_s$) in areas of one to three sites but not in larger areas? Previous evidence from the same region shows that the correlation in the total abundance, along to larval supply rates of the dominant invertebrates, among sites is maximal at scales of two to three sites (Navarrete et al. 2008), implying comparatively low spatial β-diversity (Broitman et al. 2011; Valdivia, López, et al. 2021) and environmental heterogeneity (Wang et al. 2019)—high levels of this 'community-level spatial synchrony' are theoretically and empirically associated with lowered community stability in response to disturbances (Wang et al. 2019; Valdivia, López, et al. 2021). In addition, an increase in deterministic environmental effects may be counterbalanced by larger random fluctuations in dispersal, post-settlement mortality and recruitment of opportunistic colonisers after foundation species removal over larger areas (Hypothesis 5). Such compensation over larger spatial scales can explain, in part, the increase in environmental (both trend and random) effects on community dynamics at subregional scales. Therefore, this study provides important information for the management of ecosystem functioning, as key ecological processes might be severely disrupted in small-sized communities (e.g., marine protected areas). This information could help to guide managers and stakeholders in restoring highly degraded habitats at spatial scales at which determinism may predominate (Gawecka and Bascompte 2023).

Second, the experimental removal of foundation species may trigger deterministic successional dynamics in the remaining community, as shown in manipulative experiments on Mediterranean intertidal assemblages (Maggi et al. 2011). In this line, random events of reproduction, death and dispersal (i.e., demographic stochasticity) of numerically dominant foundation species can, through competitive interactions, contribute to the stochasticity of the subdominant species (Wootton 2010; de Mazancourt et al. 2013). For instance, barnacles can be very sensitive to small stochastic perturbations over time in rocky intertidal habitats (Medeiros et al. 2023), which can lead to community dynamics that differ from deterministic niche-based

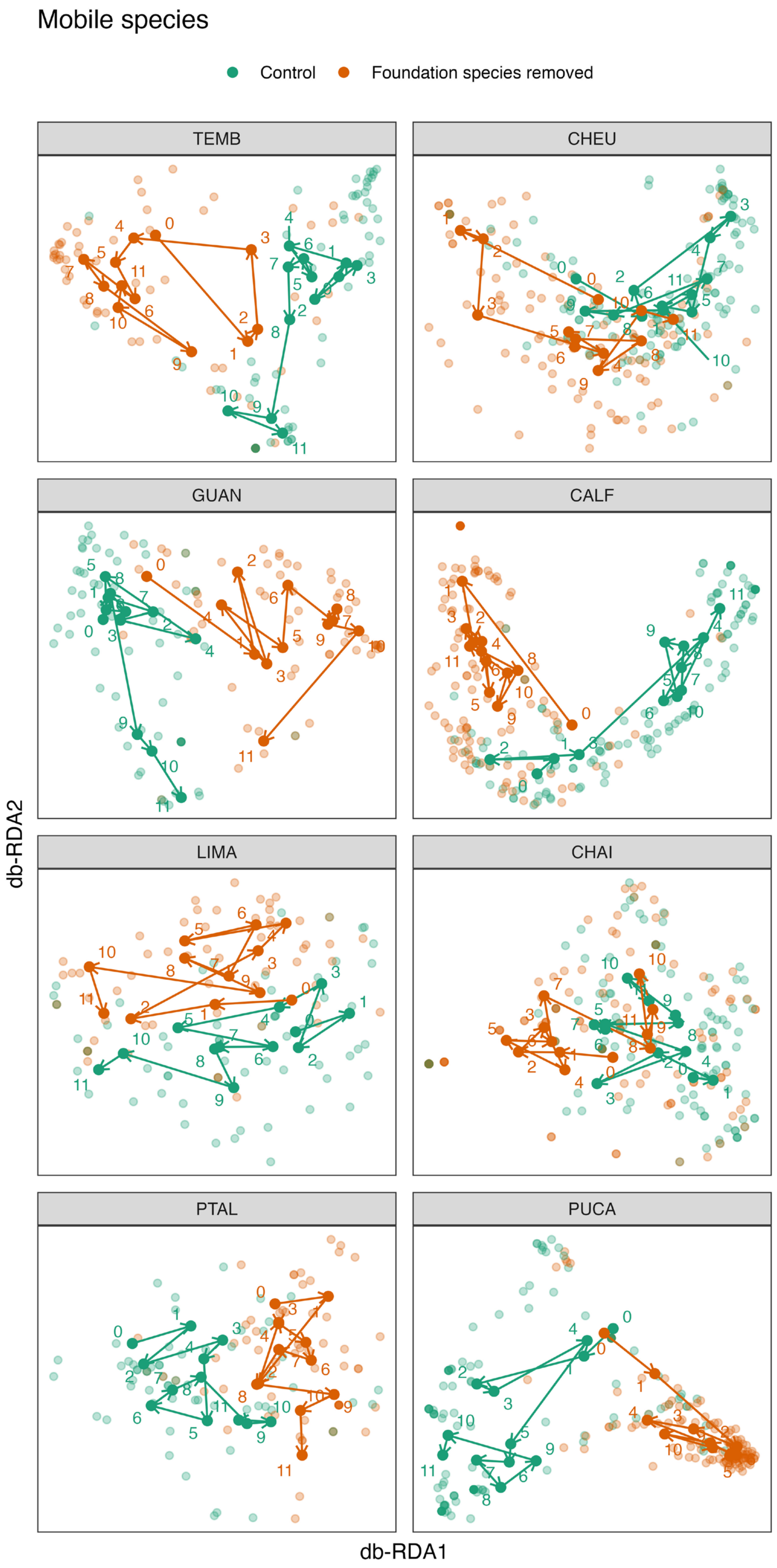

**FIGURE 2** | Legend on next page.

**FIGURE 2** | Community structure of mobile species. Separate distance-based redundancy analyses (*db-RDA*) for each experimental site. The analyses were based on Bray–Curtis dissimilarities calculated from the species-abundance matrix of each site. The model included the experimental removal of the locally dominant foundation species and sampling time. Sites were arranged in the northern and southern subregions (left and right columns, respectively).

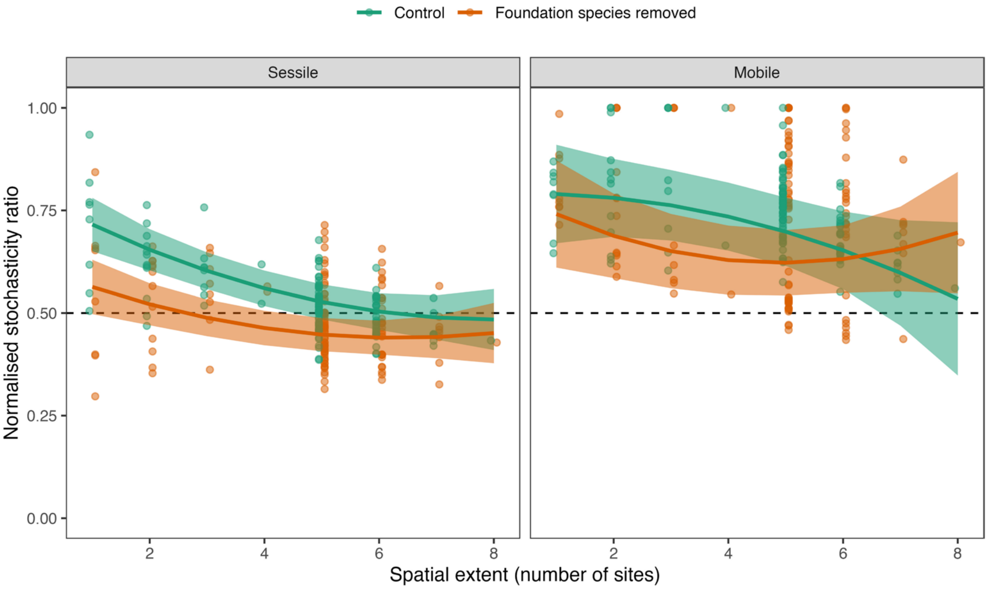

**FIGURE 3** | Effect of spatial extent (*A*, number of sites) and experimental removal of the locally dominant foundation species on *NST* of sessile and mobile rocky intertidal communities. *NST* ranges from 0 to 1, representing more deterministic and more stochastic community dynamics, respectively. The solid lines and ribbons are means and 95% confidence intervals of model predictions (Table S5).

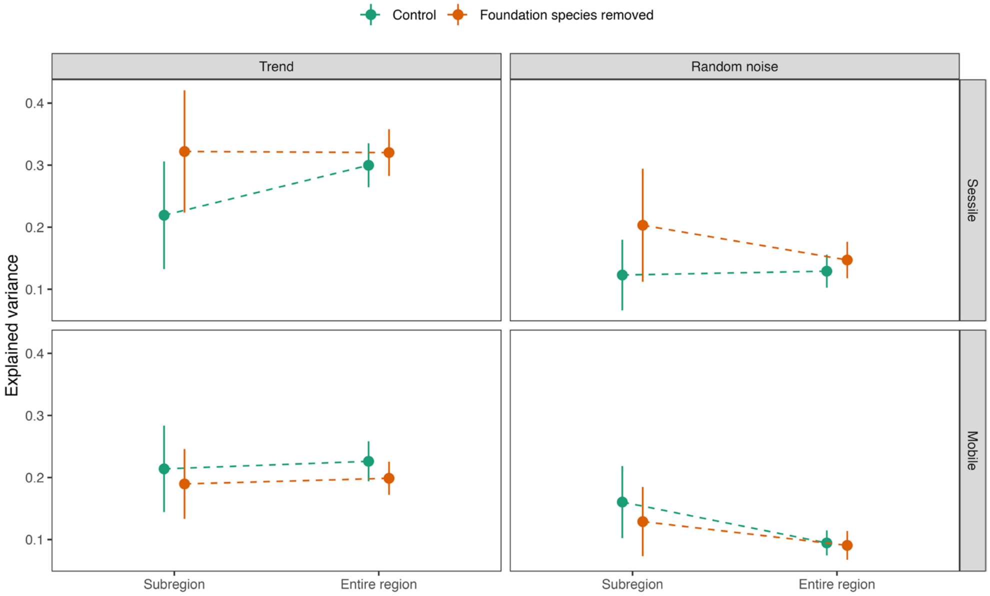

**FIGURE 4** | Summary of variance partitioning analyses of the effects of environmental variables (sea surface temperature, air temperature and wind components) on the multivariate temporal variability of sessile and mobile species. Community structure was represented as Bray–Curtis dissimilarities. Trend corresponds to the 'pure' effect of the deterministic temporal trends of the environmental drivers of community structure; random noise represents the pure effect of environmental stochasticity and was calculated as the first-order difference (i.e., detrended) of each environmental driver. The explained variance was calculated as adjusted $R^2$ after *db-RDA*. Mean and 95% confidence intervals are shown.

processes. Our results indicated that, when present, the three foundation species targeted in our study exhibited large temporal variability in small-sized communities (Figure 5), which, as predicted by theory (de Mazancourt et al. 2013), might have contributed to the large *NST* values observed for both sessile and mobile species in the control treatment at smaller spatial extents.

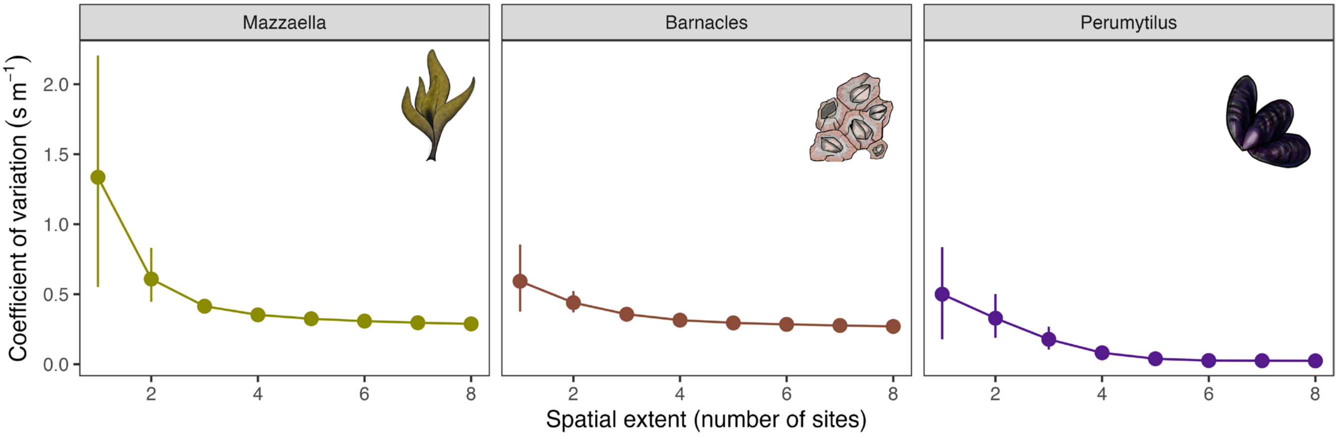

**FIGURE 5** | Temporal coefficient of variation (temporal standard deviation divided by the temporal mean of percent cover) of the experimentally removed foundation species in each site (see Table 1).

The individual traits of the three foundation species detected and manipulated in our study might, however, have different effects on community dynamics. For instance, the stalked structure of *M. laminarioides* fronds (up to 30 cm; Hoffmann and Santelices 1997) provides biogenic shelter for larger organisms (e.g., adult limpets, chitons and amphipods) compared to beds of the purple mussel or chthamalid barnacles (up to 5 and 2 cm in height, respectively). Additionally, filter-feeding invertebrates can negatively affect the recruitment of other invertebrates (including other foundation species) due to larviphagy, but positively influence opportunistic seaweeds by providing habitat and nutrients (see also Aquilino et al. 2009 for other mussels; Catalán et al. 2021). Our results might also differ from analyses of large-sized foundation species, such as giant kelp, whose influence on community dynamics—through competitive and facilitative interactions—cascades via complex networks of direct and indirect effects (Miller et al. 2018; Lamy et al. 2020; Carranza et al. 2024). For example, the temporal variation of the giant kelp appears to have a stronger effect on community-wide variability (Lamy et al. 2020) than that of *M. laminarioides* (Fica-Rojas et al. 2022). Thus, functional traits of seaweed and mussel foundation species can serve as important predictors of subdominant species' community structure (Cameron et al. 2024). The heterogeneous distribution of these foundation species across the region prevented us from conducting separate scale-dependent analyses for each species—future research could explore their potentially differential effects on subdominant community dynamics at a geographic scale.

### 4.2 | The Contribution of Environmental Stochasticity to Temporal β-Diversity of Mobile Species Decreased With Spatial Extent

In line with Hypothesis 1, *NST* of mobile species decreased with increasing spatial extent, reflecting reduced environmental stochasticity in their temporal patterns. Larger populations at regional scales are less affected by stochastic reproduction, mortality and dispersal events (Orrock and Watling 2010; Vellend 2016; Shoemaker et al. 2020).

However, species removal did not alter this pattern. This contrasts with studies showing that habitat degradation reduces stochasticity in mobile-community dynamics elsewhere (e.g., fishes: Li et al. 2021), despite using similar metrics (temporal *NST* and Bray–Curtis dissimilarities). Mobile intertidal species often exhibit variable dynamics due to their ability to relocate to optimal conditions (e.g., Aguilera et al. 2015; Catalán et al. 2023). Our removal experiment reduced macrograzers (*Chiton* spp., *Fissurella* spp.) but increased mesograzers (*S. lessonii*, *Scurria* spp., *Littorina* spp.; Fica-Rojas et al. 2022), decreasing temporal variability in mesograzer abundance, likely due to higher mean abundances. Compensatory responses among differently sized grazers (Aguilera and Navarrete 2012) may explain the null effect of removal on mobile assemblage *NST*. Such compensatory dynamics—key to community stability (Valencia et al. 2020; Valdivia, López, et al. 2021)—likely sustain stochastic dominance across scales. Protecting mobile grazers, essential for rocky shore stability, should be integrated into conservation strategies to ensure ecosystem function and human benefits (e.g., fisheries, Takashina 2021).

## 5 | Conclusion

Our study offers strong empirical evidence for the scale dependency of assembly processes in natural communities, highlighting how foundation species removal influences these processes differently for mobile and sessile species. Stochasticity decreased, and determinism increased, with spatial extent for both assemblages. However, foundation species removal weakened the effect of spatial extent on this transition for sessile, but not mobile, species. These patterns likely arose from greater abiotic heterogeneity at larger scales and stronger selective pressures on sessile species in smaller areas post-removal. Our findings suggest that the loss of dominant foundation species—for example due to anthropogenic disturbances—can significantly disrupt community structuring mechanisms, particularly at small spatial scales.

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#### Author Contributions

N.V. conceived the study; N.V. analysed the data; A.M.C., B.R.B., C.B., D.N.L., E.F.-R. and M.A.A. contributed to field work, reagents and analytical material; N.V. wrote the paper; B.R.B. and M.A.A. contributed significantly to the writing of the manuscript. All authors edited and approved the final version of the manuscript.

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## Ethics Statement

The study did not need permits because all experiments were conducted on open-access coastal areas.

## Conflicts of Interest

The authors declare no conflicts of interest.

## Data Availability Statement

The data and code that support the findings of this study are openly available in figshare at https://doi.org/10.6084/m9.figshare.28904906.v2.

## Peer Review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.70144.

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## Supporting Information

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