High dimensionality of the stability of a marine benthic ecosystem

Nelson Valdivia[1, 2, *], Moisés A. Aguilera[3, 4], Bernardo R. Broitman[5]

[1]Instituto de Ciencias Marinas y Limnológicas, Facultad de Ciencias, Universidad Austral de Chile, Campus Isla Teja, Valdivia, Chile

[2]Centro FONDAP de Investigación de Dinámicas de Ecosistemas Marinos de Altas Latitudes (IDEAL)

[3]Departamento de Biología Marina, Facultad de Ciencias del Mar, Universidad Católica del Norte, Larrondo 1281, Coquimbo, Chile

[4]Centro de Estudios Avanzados en Zonas Áridas (CEAZA), Universidad Católica del Norte, Ossandón 877, Coquimbo, Chile

[5]Departamento de Ciencias, Facultad de Artes Liberales & Bioengineering Innovation Center, Facultad de Ingeniería y Ciencias, Universidad Adolfo Ibáñez, Av. Padre Hurtado 750, Viña del Mar, Chile

*Corresponding author Tel.: +56632221557, Fax: +56632221455, E-mail: nelson.valdivia@uach.cl

Nelson Valdivia ORCID ID: https://orcid.org/0000-0002-5394-2072

Bernardo R. Broitman ORCID ID: http://orcid.org/0000-0001-6582-3188

Moisés A. Aguilera ORCID ID: https://orcid.org/0000-0002-3517-6255

Abstract

Stability is a central property of complex systems and encompasses multiple dimensions such as resistance, resilience, recovery, and invariability. How these dimensions correlate among them is focus of recent ecological research; yet, empirical evidence at regional scales, at which conservation decisions are usually made, remains absent. Using a field-based manipulative experiment conducted in two marine intertidal regions, we analyse the correlations among different aspects of stability in functioning (community cover) and composition of local communities facing a press disturbance. The experiment involved the removal of the local space-dominant species for 35 months in eight sites under different environmental regimes in northern- and southern-central Chile (ca. 30ºS and 40ºS, respectively). After the disturbance, the magnitude of the initial responses and the recovery patterns were similar among communities dominated by different species, but varied between the functional and compositional response variables, and among four dimensions of stability. The recovery trajectories in function and composition remained mostly uncorrelated across the system. Yet, larger initial functional responses were associated with faster recovery trajectories—high functional resilience, in turn, was associated with both, high and low variability in the pattern of recovery. Finally, the compositional stability dimensions were independent from each other. The results suggest that varying community compositions can perform similar levels of functioning, which might be the result of strong compensatory dynamics among species competing for space in these communities. Knowledge of several, and sometimes orthogonal, aspects of stability is mandatory to fully describe the stability of complex ecological systems.

Introduction

Anthropogenic environmental change is disrupting the functioning and composition of ecosystems over multiple spatiotemporal scales (De Laender et al., 2016;Isbell et al., 2017). Understanding the capacity of ecosystems to absorb and respond to such disturbances is challenging, because stability is a multifaceted property characterised by several dimensions (Pimm, 1984;Ives and Carpenter, 2007;Donohue et al., 2013). Recent theoretical and empirical advances provide the framework to assess this dimensionality through correlations between multiple aspects of stability such as resistance, resilience, recovery, and invariability (Donohue et al., 2013;Hillebrand et al., 2018;Radchuk et al., 2019). Most scientific research to date has focused on either one or two dimensions, which has impaired our capacity to fully understand the stability of complex ecological systems (Donohue et al., 2016;Kéfi et al., 2019). The functional consequences of biodiversity loss can be exacerbated at large spatial scales that are relevant for conservation or policy (Isbell et al., 2017). Yet, empirical tests of stability dimensionality conducted at ecologically relevant scales are, to our best knowledge, still missing.

The dimensions of stability include, but are not limited to, *resistance*, or the degree to which an aggregate function or species composition remains unchanged after a disturbance, *resilience*, or the speed of community recovery after the disturbance, *recovery*, or the degree to which the community recovers from the disturbance, and *invariability*, or the degree of constancy of the function or composition around the temporal recovery trend (Grimm and Wissel, 1997;Hillebrand et al., 2018). These aspects of stability can well be independent of each other or can be correlated. Recent models suggest that most stability dimensions are positively correlated (Radchuk et al., 2019). For instance, communities

with low invariability (i.e. highly variable functioning over time) can show low resistance against disturbances following the increased risk of local stochastic extinction for species with small population sizes (Lande et al., 2003). In those cases, stability is unidimensional and conservation decisions could maximise both aspects of stability. However, resistance can be negatively related to resilience when disturbance has a strong impact on functioning and intrinsic growth rates are high (Harrison, 1979;Hillebrand et al., 2018). Resistance can also negatively correlate with invariability in mesocosm experiments (Pennekamp et al., 2018). Negatively correlated stability dimensions imply that policy trade-offs would be needed to maintain either one or another aspect of stability. Strong disturbances, such as the local extinction of dominant species, can lead to uncorrelated dimensions of stability (Donohue et al., 2013). The lack of correlation among stability dimensions (i.e. a high dimensionality) indicates that multiple aspects need to be quantified simultaneously to fully characterise the overall stability of the ecosystem.

The responses to disturbances can be assessed either for aggregate ecosystem properties performed by the community, such as productivity or total abundance (functional stability), or for the combination of species identities and abundances in the community (compositional stability; Micheli et al., 1999). Asynchronous or compensatory species dynamics have been shown to stabilise (in terms of invariability) ecosystem properties of species-rich communities, because different community compositions can achieve similar levels of functioning (Tilman, 1996;Yachi and Loreau, 1999;Gonzalez and Loreau, 2009). Therefore, functional compensation between species could lead to negative or null correlations between functional and compositional aspects of stability. By implication, the recovery of functioning will not necessarily need a full recovery of

community composition. While several studies support the role of species compensation in stabilising community functioning (reviewed in Gonzalez and Loreau, 2009), it is less clear how functional and compositional stabilities will be correlated in communities facing the widespread chronic disturbances experienced by ecosystems (Guelzow et al., 2017).

In this study, we analyse the results of a field-based manipulative experiment in which a press disturbance, i.e. the chronic extinction of the locally dominant species, was simulated to assess the dimensionality of stability within the functional and compositional domains of rocky intertidal sessile communities. To this end, we used total community cover as a relevant metric of ecosystem functioning. For communities of sessile species, this function expresses the degree to which competing species use the space as a limiting resource and thus, its relevant to understand both functional and compositional stability (Paine, 1980;Dunstan and Johnson, 2006;Stachowicz et al., 2008). Multiple sites spanning a large environmental gradient (Fig. 1) were used to assess the dimensionality of stability at an ecologically relevant spatial scale (Isbell et al., 2017). Without incurring in a large replacement in species identities, our experimental design involved that the locally dominant species varied among sites, which allowed us to enhance the generality of our findings (e.g. Arnillas and Cadotte, 2019). These dominant species were functionally and evolutionary distinct and included the red corticated alga *Mazzaella laminarioides,* chthamalid barnacles (mixture of *Jehlius cirratus* and *Notochthamalus scabrosus*), and the purple mussel *Perumytilus purpuratus* (hereafter referred to as *Mazzaella*, barnacles, and *Perumytilus,* respectively; Table 1). This setup allowed us to test the following three hypotheses.

111 *H1: The three dominant species use the settlement substratum in different ways; upon*
112 *removal, the ensuing communities will exhibit different magnitudes of stability responses.*
113 *Perumytilus* is able to monopolise almost the 100 % of primary substratum, while the
114 barnacle complex occurs in combination with bare rock and filamentous algae (Table 1;
115 Broitman et al., 2001;Moreno, 2001;Lagos et al., 2005)—*Mazzaella*, on the other hand, uses
116 a smaller proportion of the primary substratum, but generates a large canopy-like
117 structure above the rock (Hoffmann and Santelices, 1997). In addition, different ecological
118 mechanisms are suggested to lead to species compensation in the dynamics these
119 communities experience after the extirpation of the dominant species (*Perumytilus*:
120 facilitation-competition over succession; barnacles: facilitation of grazers and macroalgae;
121 *Mazzaella*: light attenuation, see below).
122 *H2: Across sites, the removal of dominant species will elicit negative or neutral*
123 *correlations between functional and compositional stability dimensions due to prevailing*
124 *compensatory dynamics.* The removal of *Perumytilus* triggers the compensation between
125 subordinate taxa: fast-growing ephemeral macroalgae such as *Ulothrix* sp. and *Pyropia* spp.
126 dominate the assemblage during the first two months after the removal, then they are
127 replaced by barnacles and *Ulva* sp., and eventually by *Mazzaella,* in line with Connell and
128 Slatyer (1977) facilitation successional model (Aguilera and Navarrete, 2012;Tejada-
129 Martinez et al., 2016). Barnacles facilitate small grazers; therefore, the removal of barnacles
130 leads to increased abundances of microalgae, but decreased abundances of perennial
131 macroalgae (Harley, 2006;Mrowicki et al., 2014;Whalen et al., 2016). Finally, the removal of
132 the corticated macroalga *Mazzaella* is associated with an increase in the abundance of *Ulva*
133 *rigida*, *Lithophyllum* spp., the colonisation by the ephemerals *Petalonia fascia* and

134 *Scytosiphon lomentaria* (Jara and Moreno, 1984), but a decrease in *Gymnogongrus*
135 *furcellatus*—these dynamics are ascribed to negative effect of *Mazzaella* cover on light
136 availability (Moreno and Jaramillo, 1983;Nielsen and Navarrete, 2004).
137 *H3: Across sites and stability domain (functional and compositional stability), the*
138 *stability dimensions will be correlated with each other.* According to previous modelling
139 work (Radchuk et al., 2019), the stability dimensions will show positive pairwise
140 correlations. The exception will be negative resistance-resilience and resilience-
141 invariability correlations (Hillebrand et al., 2018).
142
143 **Materials and methods**
144 *Study region*
145 The study was conducted at multiple field sites on the extremes of a large
146 transitional biogeographic province that extends between the Peruvian and Magellan
147 provinces along the Chilean sector of the South East Pacific (Camus, 2001;Thiel et al.,
148 2007;Lara et al., 2019). We used eight study sites that where evenly split between the
149 northern and southern extremes of the province (around 30.23ºS and 39.9º,
150 respectively)—each region encompassing ca. 200 km of shoreline (see Fig. 1).
151 The northern region is characterised by semi-permanent coastal upwelling activity,
152 which coincides with a significant transition in abiotic (Hormazabal et al., 2004;Garreaud et
153 al., 2011;Tapia et al., 2014) and biotic conditions (Valdivia et al., 2015). Upwelling activity
154 in the region has been suggested to increase community-wide synchrony in species'
155 abundance fluctuations, and thus to decrease community invariability (Valdivia et al.,
156 2013). Rocky-shore communities inhabiting the mid-intertidal zone across the province are

157 composed of a diverse set of mobile and sessile species, where human harvesting and
158 environmental context modulate ecological interactions (Broitman et al., 2001;Lagos et al.,
159 2005;Caro et al., 2010;Broitman et al., 2011).

160 The southern region presents a persistent relationship between Chlorophyll-*a*
161 concentration, riverine inputs, and runoff from forestry and agricultural activities (Van
162 Holt et al., 2012;Lara et al., 2019). In this region, upwelling activity is weaker and more
163 intermittent than the sector equatorward from Concepción, which is dominated by strong
164 seasonal upwelling (ca. 37S; Atkinson et al., 2002;Letelier et al., 2009;Pinochet et al., 2019).
165

166 *Experimental design and setup*

167 At each site, we conducted a manipulative experiment with dominant-species
168 removal as a fixed factor. The experiments were conducted between October 2014 and
169 July-August 2017 in the southern region, and between December 2014 and August-
170 September 2017 in the northern region—in both cases, the prolonged time span (ca. three
171 years) allowed us to fully capture the seasonal and intra-annual variation in abiotic
172 conditions and species composition. Prior to the start of the experiment, we estimated
173 relative species abundances in ten 30 x 30 cm plots haphazardly located on the mid-
174 intertidal zone to determine locally dominant species as those with the highest relative
175 abundances at each site (see also Valone and Balaban-Feld, 2018). At each site, quadrats
176 were located within an alongshore transect (ca. 3 m wide) covering ca. 50 m of the
177 coastline. The red corticated alga *Mazzaella laminarioides* and chthamalid barnacles (a
178 mixture of *Jehlius cirratus* and *Notochthamalus scabrosus*) were the dominant taxa in the
179 northern region; chthamalid barnacles and the purple mussel *Perumytilus purpuratus* were

180 the dominant species in the southern region (hereafter referred as *Mazzaella*, barnacles,
181 and *Perumytilus,* respectively; Table 1). Before the manipulations, mean percentage cover
182 of dominant species ranged from ca. 30 % for *Mazzaella* in the northern region to 100 %
183 for *Perumytilus* in the southern region—unevenness in species abundance distribution,
184 expressed as Simpson's concentration index, varied between 0.4 and 0.9 in the northern
185 and southern region, respectively (Table 1).

186 Following site characterization, we started identical field experiments. We used 30 x
187 30 cm experimental plots on the mid-intertidal zone of each site, which were permanently
188 marked with stainless-steel bolts. The size of the experimental unit was selected to
189 minimise the impact on the local intertidal communities. For logistic reasons, we deployed
190 10 replicate plots in the sites located on the northern sector and 20 replicates in the
191 southern sites. Experimental plots were haphazardly located, avoiding crevices, tide-pools,
192 and vertical surfaces to reduce biotic variation related to local spatial heterogeneity and
193 within areas of high abundance of the locally dominant species.

194 At the onset of experimental manipulations (i.e. October and December 2014 in the
195 southern and northern regions, respectively), we haphazardly selected half of the plots at
196 each site and completely removed the dominant species with scrapers and chisels. The
197 remaining half of the experimental units remained un-manipulated and assigned to the
198 control level. Settlers and recruits of the dominant species were further removed
199 approximately every three months, i.e. the press disturbance treatment (see also Bulleri et
200 al., 2012). Prior field studies on recruitment patterns in the region suggest that the three-
201 month window between manipulations allows to functionally exclude dominant species
202 (Aguilera et al., 2013;Valdivia et al., 2013;Valdivia et al., 2015).

All plots were sampled immediately before the manipulations, 1-2 months after the removal of local dominants, and then approximately every three months until the end of the experiment. All macroalgae and sessile macro-invertebrates (> 5 mm) occurring in each plot were identified *in situ* and classified to the lowest possible taxonomic level (usually species). For each plot, we used a 0.09-m^2 frame, divided in 25 equal fields with a monofilament line, to estimate sessile species abundances as percentage cover (1 % resolution). We quantified the organisms growing on both primary and secondary substrata (i.e. rock and other organisms, respectively), which allowed total community cover to increase beyond 100 %. This protocol has been used in several studies of benthic diversity along Chile and elsewhere (see Broitman et al., 2011;Bulleri et al., 2012). The data obtained during the 11 successive surveys, conducted after the first removal, were used to estimate four dimensions of stability, i.e. resistance, resilience, recovery, and invariability. Since we were interested in the response of the remaining community to the local extinction of dominants, the latter were removed from the dataset when we assessed community stability.

Species compensation

The degree of species compensation was measured by assessing community-wide synchrony in species abundances. To this aim, we used the φ statistic (Loreau and de Mazancourt, 2008):

$$\varphi = \frac{{\sigma^2}_F}{\left(\sum_{i=1}^{N} \sigma_{f_i}\right)^2}$$

224 $$F = \sum_{i=1}^{N} f_i,$$

225 where f_i is the percentage cover of species i, F is the equivalent aggregate community-level
226 function (total community cover), and $\sigma_{f_i}^2$ and σ_F^2 are their respective temporal variances.
227 The index is standardised between 0 (perfect asynchrony; i.e. most species' abundances are
228 negatively correlated over time) and 1 (perfect synchrony; i.e. most species' abundances
229 are positively correlated). Since φ is independent of the magnitude and distribution of
230 species abundances and variances, it allows us to quantitatively compare communities with
231 different numbers of species (Loreau and de Mazancourt, 2008).
232
233 *Stability dimensions*
234 Stability was assessed according to the metrics for resistance, resilience, recovery,
235 and invariability described by Hillebrand et al. (2018). Each metric was estimated by
236 randomly pairing one control and one disturbed plot in each site. In this way, we obtained
237 replicate estimations within each site. The stability metrics in the functional domain were
238 calculated on the basis of total community cover (F), and the stability metrics in the
239 compositional domain were calculated on the basis of Bray-Curtis similarities (sim)
240 between the disturbed and control communities (C).
241 *Resistance* (a) was estimated for function as the log-response ratio (LRR) calculated
242 after the disturbance took place (1-2 months after the removal of local dominants):

243 $$a = ln\left(\frac{F_{dist}}{F_{con}}\right),$$

244 where F_{dist} is total community cover in the dominant-removed plot, and F_{con} is the same
245 property in the control plot. A value of a = 0 indicates maximum resistance of the

community to the disturbance, $a < 0$ indicates low resistance due to underperformance, and $a > 0$ low resistance due to overperformance relative to controls, respectively (Hillebrand et al. 2018). This means that both initially increased and decreased functioning will reflect low functional resistance. For that reason, we used the modulus (absolute value) of resistance in some hypothesis tests as described below (see *Statistical analyses: H1* and *H2*).

The resistance of composition (a) was calculated on the basis of Bray-Curtis similarities between the disturbed and the control plots:

$$a = \left(\frac{C_{dist}}{C_{con}}\right),$$

Where C_{dist} and C_{con} are the species-abundance matrices in the dominant-removed and control plots, respectively. Maximum similarities of $a = 1$ indicate 100 % of similarity between disturbed and control plots and thus maximum resistance. Minimum similarities of $a = 0$ indicate 0% of similarity between both conditions and thus extremely low resistance.

Resilience (b) was calculated for each plot as the slope of the linear regression of *LRR* calculated for each sampling event (Hillebrand et al. 2018):

$$ln\left(\frac{F_{dist}}{F_{con}}\right) = i + b * t,$$

$$dis\left(\frac{C_{dist}}{C_{con}}\right) = i + b * t$$

where *i, b,* and *t* are the intercept, slope, and time, respectively. A *b*-value equalling zero indicates no recuperation over time, $b > 0$ indicates faster recuperation in case of a negative initial effect of disturbance on the function or composition, and $b < 0$ indicates further deviation from control in case of negative initial effects. When the disturbance generates

positive effects on functioning (i.e. $a > 0$), $b > 0$ is interpreted as further deviation from control and vice versa.

Recovery (c) was estimated as the *LRR* and similarity calculated at the end of the experiment. c-values equal to zero denote maximum recovery, $c < 0$ incomplete recovery, and $c > 0$ overcompensation relative to control. Like for resistance, both $c < 0$ and $c > 0$ reflect low functional recovery; thus, the modulus of functional c was analysed in the test of hypotheses H1 and H3 (see *Statistical analyses*).

Invariability (d) was calculated as the multiplicative inverse of the standard deviation of residuals (*resid*) from the regression slope b as:

$$d = \left(\frac{1}{sd(resid_b)}\right).$$

Larger values de d denote smaller temporal variations around the trend of recovery in function or composition (Hillebrand et al. 2018). Note that invariability is termed as *Temporal stability* by Hillebrand et al. (2018). However, we have preferred to use *Invariability* to avoid confusions with the term *Stability* (see also Radchuk et al., 2019).

Statistical analyses

For simplicity, hereafter the community in each site will be referred to according to the identity of the locally dominant species that was removed (i.e. *Mazzaella*-, barnacle-, or *Perumytilus*-dominated communities). This means that the sites will be grouped into each of the three community types in some of the statistical analyses.

H1: The magnitude of the stability response will depend on the identity of the removed dominant species

To test this hypothesis, we first used *t*-tests for each community and within each stability domain (either functional or compositional) to determine if resistance, resilience, and recovery significantly differed from the reference values. Secondly, we used separate general lineal models (LMM) to compare the magnitude of each stability dimension among the three communities. Accordingly, we used the modulus of functional resistance and recovery to focus on their magnitudes. The models included the identity of the removed dominant species as fixed effect, and site as random effect. Nevertheless, site was removed from the models of the compositional domain due to singularity (i.e. variance nearly zero).

H2: The removal of dominant species will elicit negative or neutral correlations between functional and compositional stability dimensions due to prevailing compensation in the community dynamics

First, we used one-tailed *t*-tests to determine whether φ was significantly lower than 1 (i.e. perfect synchrony in species fluctuations) for each community. In addition, we used a generalised linear mixed model (GLMM) to determine if the removal of the locally dominant species decreased φ (i.e. increased the degree of species compensation within the community). For the model we used a Gamma structure of errors and a log link function; the model included the identity of the dominant species in each site and the removal treatment (removal or control) as crossed and fixed factors, and the site (eight levels) as random factor. After initial the fit, however, site was removed due to singularity.

Second, Pearson product-moment correlations were calculated between functional and compositional dimensions of stability. Correlations were calculated separately for each community and stability dimension. In these correlations, we used the modulus of every functional stability dimension to assess the magnitude, rather than the direction, of these responses. The absence of statistically significant correlations, in addition to near-zero values of φ were used as evidence of species compensation after the removal of dominant species.

Third, to identify the species driving compensation (or the lack thereof), we used Similarity Percentage Routines (SIMPER; Clarke, 1993) that partitioned the contribution of each species to the between-treatment dissimilarity in each community.

H3: The stability dimensions will be correlated across sites and within each of the stability domains

Pearson product-moment correlations were used to test this hypothesis. Within the functional and compositional domains, analyses were conducted combining all sites and communities to test for a tendency between these dimensions to correlate independently of the ecological context and species identities.

All analyses, calculations, and plots were done in R programming environment version 3.6.1 and the R-packages *lme4, MuMIn, sjPlot, tidyverse,* and *vegan* (R Core Team, 2019), except for Fig. 1, which was made using MatLab R2014a and data from MODIS-Aqua.

Results

333 *H1: The magnitude of the stability response will depend on the identity of the removed*
334 *dominant species*
335 The different communities significantly responded to the experimental disturbances
336 within both functional and compositional domains (Figs. 2A, C, E, G and B, D, F, H,
337 respectively; Table A1 in the Appendix). The exception was the functional resilience of the
338 barnacle- and *Perumytilus*-dominated communities, which did not differ from zero (Table
339 A1, Fig. 2C). When we compared the magnitude of the responses among communities, the
340 three communities exhibited remarkably similar stability responses to the experimental
341 disturbance for both domains (Fig. 2). Accordingly, statistical analyses did not reveal
342 statistically significant differences among the communities, with the exception of functional
343 resilience (GLMM contrasts in Table A2: *Mazzaella* > barnacles; Fig. 2C).
344
345 *H2: The removal of dominant species will elicit negative or neutral correlations between*
346 *functional and compositional stability dimensions due to prevailing compensation in the*
347 *community dynamics*
348 The low values of the proxy for species synchrony, φ, indicated that species
349 compensation was common across communities and removal treatments (Fig. 3). The
350 parameter was on average 0.11 (0.06 – 0.16), 0.30 (0.21 – 0.40), and 0.17 (0.12 – 0.21) for
351 *Mazzaella*, barnacles, and *Perumytilus* communities respectively (mean [95% CI]). These
352 values were significantly lower than 1 in each community (one-tailed *t*-tests: t_9 = -42.2, t_{16} =
353 -17.5, and t_{28} = -38.2 for *Mazzaella,* barnacles, and *Perumytilus,* respectively; $P < 0.001$).
354 However, the response of these dynamics to the dominant removal varied among
355 communities. The press disturbance increased the strength of species compensation in the

356 *Perumytilus* communities, but not in the others (GLM: $R^2 = 0.45$, $P < 0.001$ for an 80-%
357 decrease in φ in the *Perumytilus* communities, see Figure 3). In these communities, the
358 strengthening of species compensation was accounted for by the overshoot in the
359 abundance of Ulvoids (mixture of *Ulva rigida* and *U. compressa*) during the first half of the
360 experiment (late 2014 - early 2016; see Fig. A1 in the Appendix); this taxon was replaced
361 by chthamalid barnacles over time, which remained relatively stable until the end of the
362 experiment in mid-2017 (Fig. A1, see also species accounting for the between-treatment
363 dissimilarities in Table A3).
364 According to the high prevalence of species compensation, we observed almost no
365 statistically significant correlation between functional and compositional stabilities across
366 communities (Fig. 4). Separately for the three community types, we observed non-
367 statistically significant, correlations for resistance (Fig. 4A; Table A4 in the Appendix). For
368 resilience, only the communities in which barnacles were removed showed a significant,
369 and negative, correlation between the functional (modulus) and compositional domains
370 (green symbols in Fig. 4B; Table A4). Similarly, the barnacle-dominated communities
371 exhibited a negative correlation between functional (modulus) and compositional
372 recoveries (green symbols in Fig. 4C; Table A4). Finally, functional invariability was
373 uncorrelated from compositional invariability (Fig. 4D; Table A4).
374
375 *H3: The stability dimensions will be correlated across sites and within each of the stability*
376 *domains*
377 Our results did not support this hypothesis, yet we detected some significant
378 correlations (Fig. 5; Table A5 in the Appendix). In the functional domain, statistically

379 significant correlations were found between resistance and resilience (negative; Fig. 5A;
380 Table A5), resistance and invariability (positive; Fig. 5D; Table A5), and resilience and
381 invariability (negative; Fig. 5E; Table A3). In the compositional domain, we did not detect
382 statistically significant correlations among stability dimensions (Fig. 6; Table A5).
383

384 **Discussion**

385 This study showed that the stability of rocky intertidal communities in a broad
386 region of the SE Pacific shore is a multidimensional property. After the removal of locally
387 dominant species, the magnitude of the effect of the disturbance and its temporal pattern of
388 recovery were surprisingly similar among communities (Hypothesis 1) but varied between
389 functional and compositional response variables (Hypothesis 2) and among the four
390 dimensions of stability examined here; namely, resistance, resilience, recovery, and
391 invariability (Hypothesis 3). Only in the functional domain we still observed significant
392 correlations between resistance and resilience (negative), resistance and invariability
393 (positive), and resilience and invariability (negative). The high prevalence of species
394 compensation and asynchronous dynamics could explain the general lack of correlation
395 between functional and compositional stability domains, indicating that functional
396 recovery may not involve a fully compositional recovery in this study system. Our results
397 are well in line with recent evidence of the multifaceted nature of ecological stability
398 (Donohue et al., 2016;Hillebrand et al., 2018;Pennekamp et al., 2018;Kéfi et al.,
399 2019;Radchuk et al., 2019), which we further discuss below.
400

401 *Different communities exhibited similar initial and long-term stability responses to local*
402 *extinction*

403 The disturbance elicited significant stability responses within both the functional
404 and compositional domain regardless of the dominant species identity, with the exception
405 of functional resilience, which was indistinguishable from zero in the case of the
406 invertebrate-dominated communities. Despite these differences, no community fully
407 recovered in the end of the experiment, 35 months after the start of the disturbance.
408 Importantly, the consistently negative compositional resilience provides further support
409 for a persistent departure of these assemblages from the reference state (i.e. control plots),
410 as shown in phytoplankton mesocosm experiments (Hillebrand et al., 2018). This result
411 may indicate that the recovery, and restauration, of this ecosystem may need a longer time
412 span than here considered. Long-term (i.e. 20 years) monitoring of rocky intertidal
413 communities suggests the existence of cyclic succession after severe disturbances, with the
414 alternation of dominant species every ca. two years (Beninca et al., 2015). These non-
415 equilibrium dynamics can well be amplified by environmental stochasticity, as shown by
416 experimental removals of dominant mussels (Wootton, 2010). Thus, the non-equilibrium
417 and near-chaotic nature of coastal systems may obstruct our ability to restore disturbed
418 coastal ecosystems. Indeed, a major review of restoration strategies indicates that
419 functional and compositional recovery of coastal systems may reach on average a 34 % in
420 12 years, even when active restoration is enforced (Moreno-Mateos et al., 2020).

421 Between-site environmental differences could have generated "unexplained"
422 variability in the stability responses, precluding our ability to detect differences among the
423 dominant species. Nevertheless, our analyses suggest that the factors (other than

424 dominant's identity) associated to between-site differences may have little influence on the
425 stability measurements (compare the pseudo-R^2 between fixed factors and full models in
426 Table A2). In the case of functional stability, between-site differences accounted for small,
427 but non-zero, amount of variation in the stability responses. Dampened environmental
428 variability in sites under the influence of persistent upwelling could have influenced the
429 invariability in community cover (Valdivia et al., 2013). Sea water temperature patterns
430 define the phenology of most intertidal organisms (Sanford, 2002;Baldanzi et al., 2018),
431 which, mediated through larval dispersal processes, can influence overall population
432 growth rates, and thus functional resilience and recovery (Svensson et al., 2005). In the
433 case of compositional stability, on the contrary, site accounted for almost no variation in
434 Bray-Curtis dissimilarity. If site differences seemly accounted for a small variation in
435 stability responses, then, to what degree the stability observed at the local scales can scale
436 up to regional and metacommunity scales?
437 The area-invariability relationship indicates that stability should increase from local
438 to regional scales due to asynchronous and compensatory dynamics among sites within the
439 metacommunity, and also among species within sites (Wang and Loreau, 2014;Zhang et al.,
440 2018). Moreover, increased beta-diversity (i.e. between-site differences in species
441 composition) is expected to increase the spatial asynchrony in functioning among sites, and
442 thus the stability of the metacommunity (Wang and Loreau, 2016). According to the high
443 prevalence of asynchronous species dynamics (this study ;Valdivia et al., 2013) and high
444 beta-diversity (Broitman et al., 2001;Valdivia et al., 2015;Valdivia et al., 2017), predictions
445 based on the area-invariability relationship should hold in our study system. Albeit the
446 extension of this theory to other stability dimensions and the compositional domain still

needs further development, we suggest that maximising protected areas, rather than focusing on patches that contain unique assemblages, should be a conservation goal to maintain the functioning in the analysed ecosystem (see also Economo, 2011;Ospina-Alvarez et al., 2020).

Compensatory dynamics were common within the system, leading to null or negative function-composition correlations

In agreement with our prediction, asynchronous and compensatory species dynamics were strong in the study region. The strength of these dynamics, however, varied among the three analysed community types. In particular, the removal of *Perumytilus* reduced the synchrony in species abundances following compensatory dynamics between ulvoids algae and barnacles, according to the facilitation model of ecological succession (Connell and Slatyer, 1977). In addition to competitive species replacement during succession, asynchronous species dynamics can also reflect differential species environmental responses, population compensatory cycles, species-wise variations in dispersal, and neutral, zero-sum dynamics (e.g. Lehman and Tilman, 2000;Chesson et al., 2001;Loreau et al., 2003;Loreau and de Mazancourt, 2008). Accordingly, evidence of the central role of species synchrony in the stability of ecosystem functions is supported by studies across ecosystems and taxonomic groups (reviewer by Gonzalez and Loreau, 2009).

The lack of correlation between functional and compositional measurements of stability could well reflect the effects of species compensation. For instance, high resistance and recovery (i.e. near-zero log-response ratios) in the functional domain were observed along ample ranges of both metrics in the compositional domain. This indicates that a given

470 level of functioning could be performed by communities with different compositions, which
471 may have important consequences for ecosystem restauration (e.g. Borja et al., 2010). In
472 this line, the negative function-composition correlations detected for resilience and
473 recovery further reinforce the notion of functional compensation within these
474 communities. These results agree with previous empirical studies showing low or negative
475 correlations between functional and compositional stability in other ecosystems (Guelzow
476 et al., 2017;Hillebrand et al., 2018;Hillebrand and Kunze, 2020).
477
478 *The stability dimensions were mostly uncorrelated across community types and stability*
479 *domains*
480 In the functional domain, the correlations among the different dimensions of
481 stability ranged from negative to null and to positive. We were able to detect negative
482 correlations between functional resistance and resilience and between resilience and
483 invariability. Negative functional resistance-resilience and resilience-invariability
484 correlations have been also observed in modelling and experiments conducted on
485 experimental phytoplanktonic mesocosm communities (Hillebrand et al., 2018), and have
486 been associated to comparatively high growth rates that allow faster recovery rates with
487 stronger initial impacts (Harrison, 1979). Similarly to aquatic ciliate communities
488 (Pennekamp et al., 2018), larger initial functional responses (i.e. lower resistance) were
489 associated with more temporally stable functioning, which could respond to a positive
490 relationship between species' invariability and relative abundance (Grman et al.,
491 2010;Lamy et al., 2020).

492 In the compositional domain, on the other hand, no statistically significant
493 correlation between stability dimensions was detected. This high dimensionality implies
494 that the four aspects of compositional stability analysed in this study are fully orthogonal
495 and are mandatory to completely describe the response of these communities to an
496 ecologically realistic disturbance akin to our press removal of the dominant species.
497 Uncorrelated stability dimensions have been highlighted by previous work when ecological
498 communities face severe environmental disturbances (Allison, 2004;van Ruijven and
499 Berendse, 2010;Donohue et al., 2013;Hillebrand et al., 2018). Contrarily, most empirical
500 research has been based on one or two stability dimensions; the temporal coefficient of
501 variation has been widely used to assess the stability in aggregate ecosystem functions in
502 the absence of major disturbances (reviewed by Kéfi et al., 2019). Yet, restoration
503 assessment after pulse and press disturbances would largely benefit from considering
504 multiple components of stability, because, as we have shown, these components may well
505 be decoupled during the process of recovery (Donohue et al., 2016;Moreno-Mateos et al.,
506 2020).
507
508 *Conclusion and future directions*
509 Our results allow us to conclude that ecological stability of the analysed intertidal
510 communities is a multidimensional and complex phenomenon. The experimental removal
511 of locally dominant species elicited significant, and similar in magnitude, stability
512 responses of communities in a large metacommunity of the SE Pacific shore. These
513 responses varied between functional and compositional domains, likely due to pervasive
514 and strong asynchronous species dynamics.

Still is necessary to determine how different types and aspects of disturbances can influence stability dimensionality in these ecosystems. Albeit recent modelling work indicates that disturbance types such as random, species-specific, or local disturbances can have similar effects on stability dimensionality (Radchuk et al., 2019), contrasting the effects of pulse and press disturbances can enhance our mechanistic understanding of the ecological consequences of current climate crisis (Kéfi et al., 2019)—anthropogenic climate change involves the interdependent effects of both types of disturbances over multiple spatiotemporal scales (Harris et al., 2018). Regional manipulative experiments considering a more ample range of environmental filters and dispersal limitations would allow us modelling the role of spatial aspects of disturbance (Zelnik et al., 2018;2019) in how stability dimensionality scales from communities to metacommunities; to our best knowledge, the scale dependence of stability has been investigated only for single aspects of stability (Wang et al., 2017). In summary, realising that stability is indeed a multidimensional concept will enhance our ability to predict the response of communities and metacommunities to future and ongoing anthropogenic disturbances.

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Tables

Table 1

Identity of the dominant species experimentally removed at each rocky shore site in each region. South latitude and West longitude (Lat. and Lon. respectively) data are provided in decimal degrees. Community-specific mean percentage (1st and 3rd quantiles parenthesised) cover of each locally space-dominant species (*Mazzaella laminarioides*, mixture of *Jehlius cirratus* and *Notochthamalus scabrosus* barnacles, and *Perumytilus purpuratus*) is provided. Simpson's concentration index (λ; range: [0, 1]) indicates the degree of unevenness in the distribution of species abundances. Community-specific mean percentage covers are in bold.

Region	Lat.	Lon.	Site	Site code	*Mazzella*	Barnacles	*Perumytilus*	λ
Northern	29.28	71.18	Temblador	TEMB	0 (0-0)	**40** (25.5-56.2)	0.2 (0-0)	0.43
	30.20	71.48	Guanaqueros	GUAN	0 (0-0)	**69** (67.5-80.2)	0.3 (0-0.8)	0.67
	30.45	71.42	Limarí	LIMA	**54.3** (41.2-65)	0.5 (0-1)	0 (0-0)	0.48
	30.54	71.41	Punta Talca	PTAL	**31.1** (19.5-48.5)	1.3 (1-2)	0.1 (0-0)	0.37
Southern	39.41	73.22	Cheuque	CHEU	2.3 (0-0)	21.9 (2-40)	**100** (100-100)	0.59
	39.78	73.39	Calfuco	CALF	7.6 (0-2.2)	4 (1-5.2)	**100** (100-100)	0.62
	39.93	73.59	Chaihuín	CHAI	7 (0-8)	**89** (84-97.2)	3.5 (1-3.5)	0.77
	40.54	73.72	Pucatrihue	PUCA	0 (0-0)	1.1 (1-1)	**98.5** (98.8-100)	0.86

Figure caption

Fig. 1

Location of study sites in the northern and southern regions in the SE Pacific shore of Chile. Colour scales denote long-term temporal mean (2003-2018) of (A) sea surface temperature and (B) $\log_{10}$ Chlorophyll-*a* concentration using L3 MODIS-aqua data (Lara et al., 2019). Site codes are in Table 1. *Mazzaella*-dominated communities: LIMA and PTAL; barnacle-dominated communities: TEMB, GUAN, and CHAI: *Perumytilus*-dominated communities: CHEU, CALF, and PUCA.

Fig. 2

Four dimensions of stability in the (A, C, E, G) functional and (B, D, F, H) compositional domains. Note that (A) functional resistance and (E) recover are shown as modulus in order to compare magnitudes, rather than directions of effects. Values are mean ± 95 % confidence intervals. Dashed lines represent reference values for maximum resistance and recovery; solid grey lines represent reference values for minimum resilience. All stability dimensions statistically differed from reference values, excepting (C) functional resilience of barnacle- and *Perumytilus*-dominated communities (t-tests: t_{16} = -1.24, P > 0.05; t_{28} = 1.28, P > 0.05, respectively). Accordingly, the three types of communities exhibited similar stability responses, excepting functional resilience (GLMM contrasts: *Mazzaella* > barnacles; *Mazzaella* > *Perumytilus*).

Fig. 3

821 Community-wide synchrony among subordinate species in each community type
822 (*Mazzaella-,* barnacle-, or *Perumytilus*-dominated community). The range of φ is [0, 1], with
823 1 = perfectly synchronous species fluctuations and 0 = perfectly asynchronous,
824 compensatory species fluctuations. Values are mean ± 95 % confidence intervals. All
825 communities statistically differed from 1 (one-tailed *t*-tests: t_9 = -42.2, $P < 0.001$; t_{16} = -17.5,
826 $P < 0.001$; t_{28} = -38.2, $P < 0.001$, respectively), indicating prevalent compensatory dynamics
827 across the region. The removal of the dominant species systematically increased the
828 strength of species compensation in the *Perumytilus* communities, but not in the others
829 (Gamma GLM, R^2 = 0.45, P < 0.001 for *Perumytilus*).
830
831 Fig. 4
832 Pairwise associations between functional and compositional dimensions of stability. In
833 these analyses, all functional dimensions were used as modulus in order to correlated
834 magnitudes, rather that directions of effects. Dashed lines represent reference values for
835 maximum resistance and recovery; solid grey lines represent reference values for
836 minimum resilience. Only (B) resilience and (C) recovery of the barnacle-dominated
837 communities (green symbols) showed significant function-composition correlations (r = -
838 0.52 and r = -0.57, respectively; P < 0.05).
839
840 Fig. 5
841 Associations among four dimensions of functional stability. Dashed lines represent
842 reference values for maximum resistance and recovery; solid grey lines represent
843 reference values for minimum resilience. Across communities, statistically significant

correlations were detected for the resistance-resilience, resistance-invariability, and resilience-invariability pairs ($r = -0.38$, $r = 0.39$, and $r = -0.36$, respectively; $P < 0.01$).

Fig. 6

Associations among four dimensions of compositional stability. Dashed lines represent reference values for maximum resistance and recovery; solid grey lines represent reference values for minimum resilience. No statistically significant correlation was detected across communities.

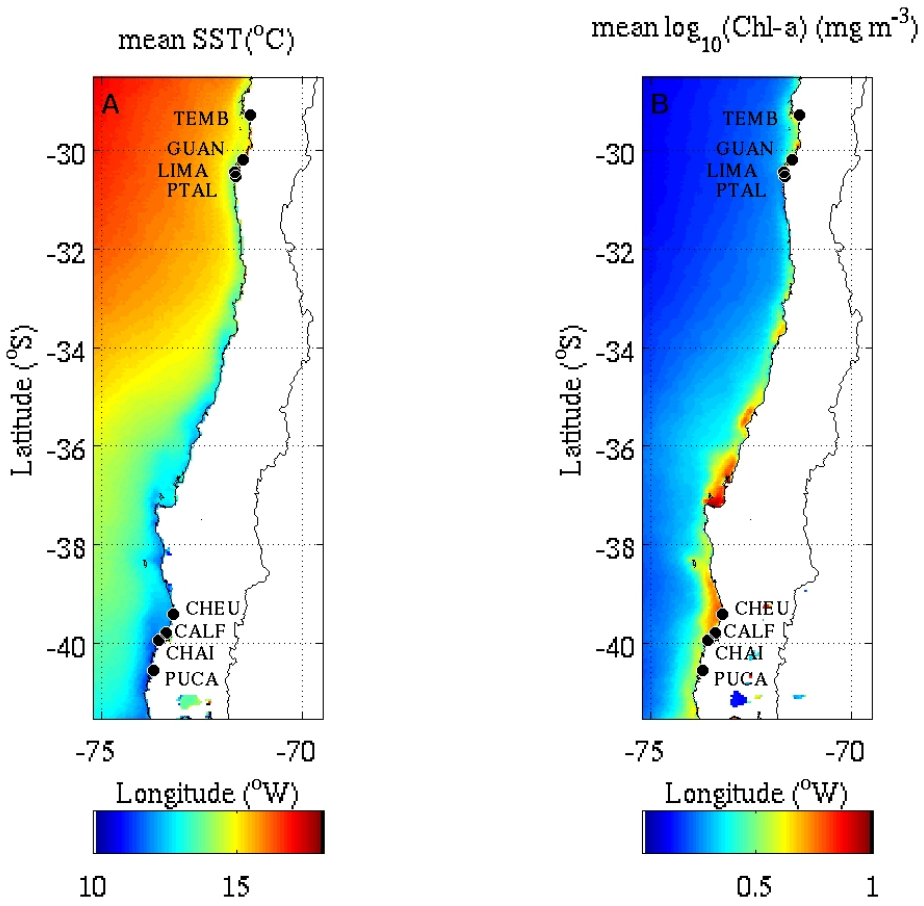


Fig. 1 Valdivia et al.

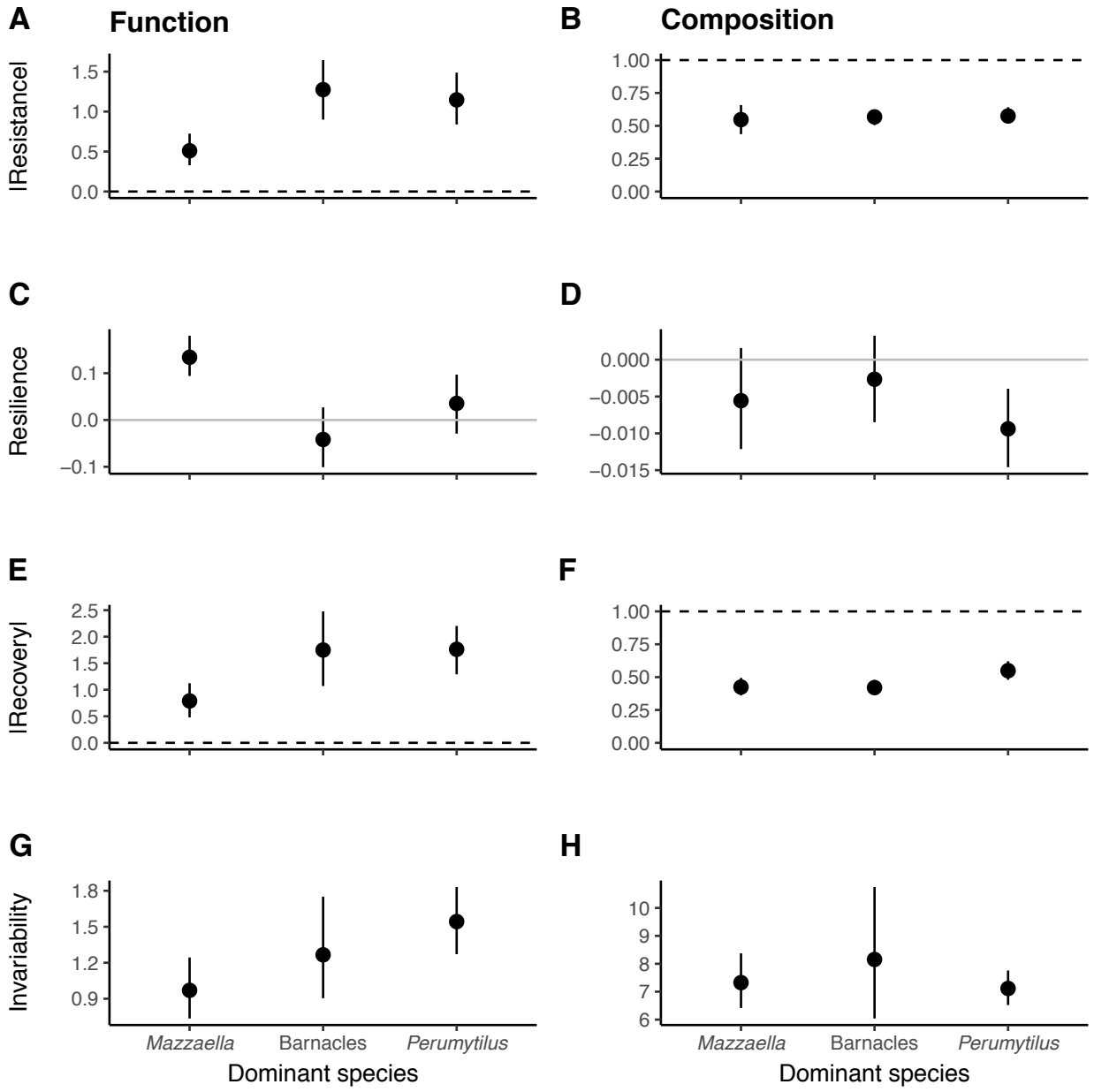
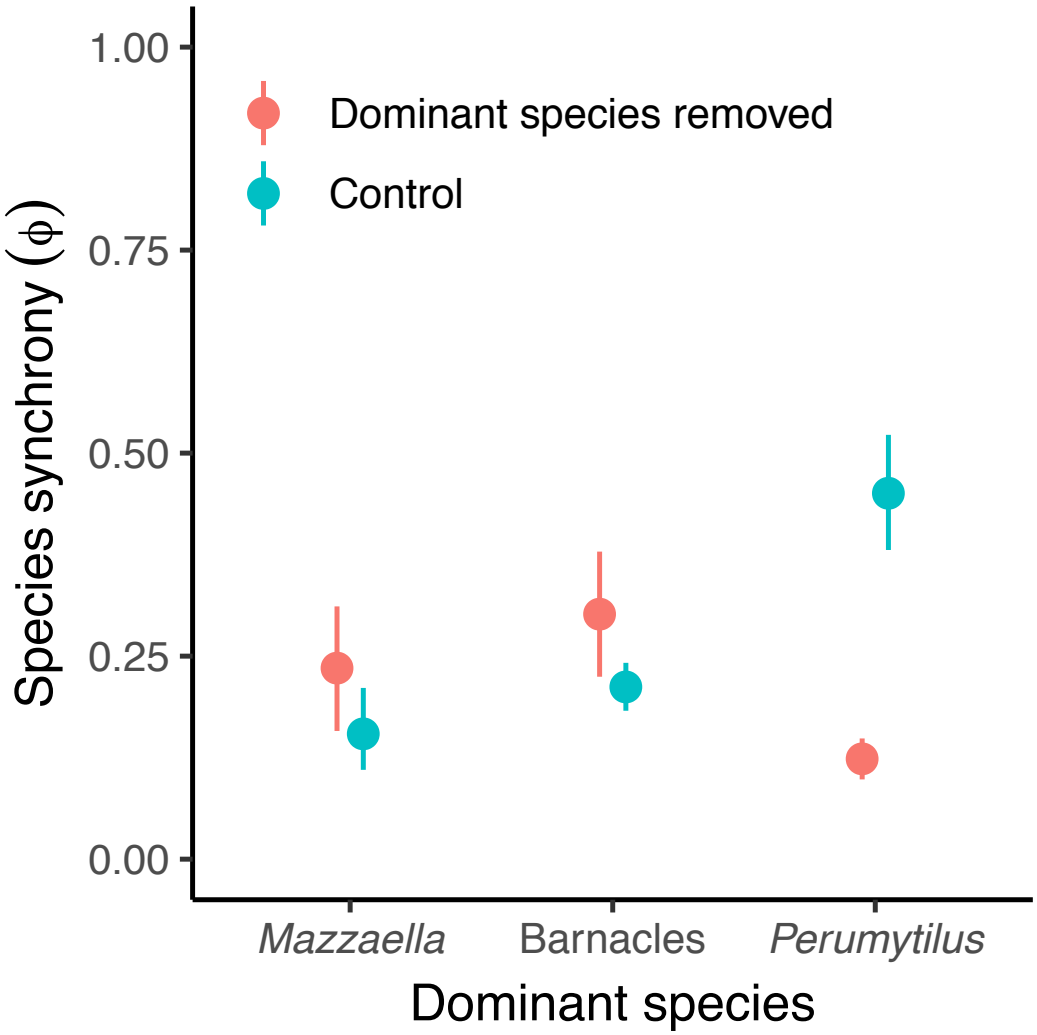


Fig. 2 Valdivia et al.



862

863 Fig. 3 Valdivia et al.

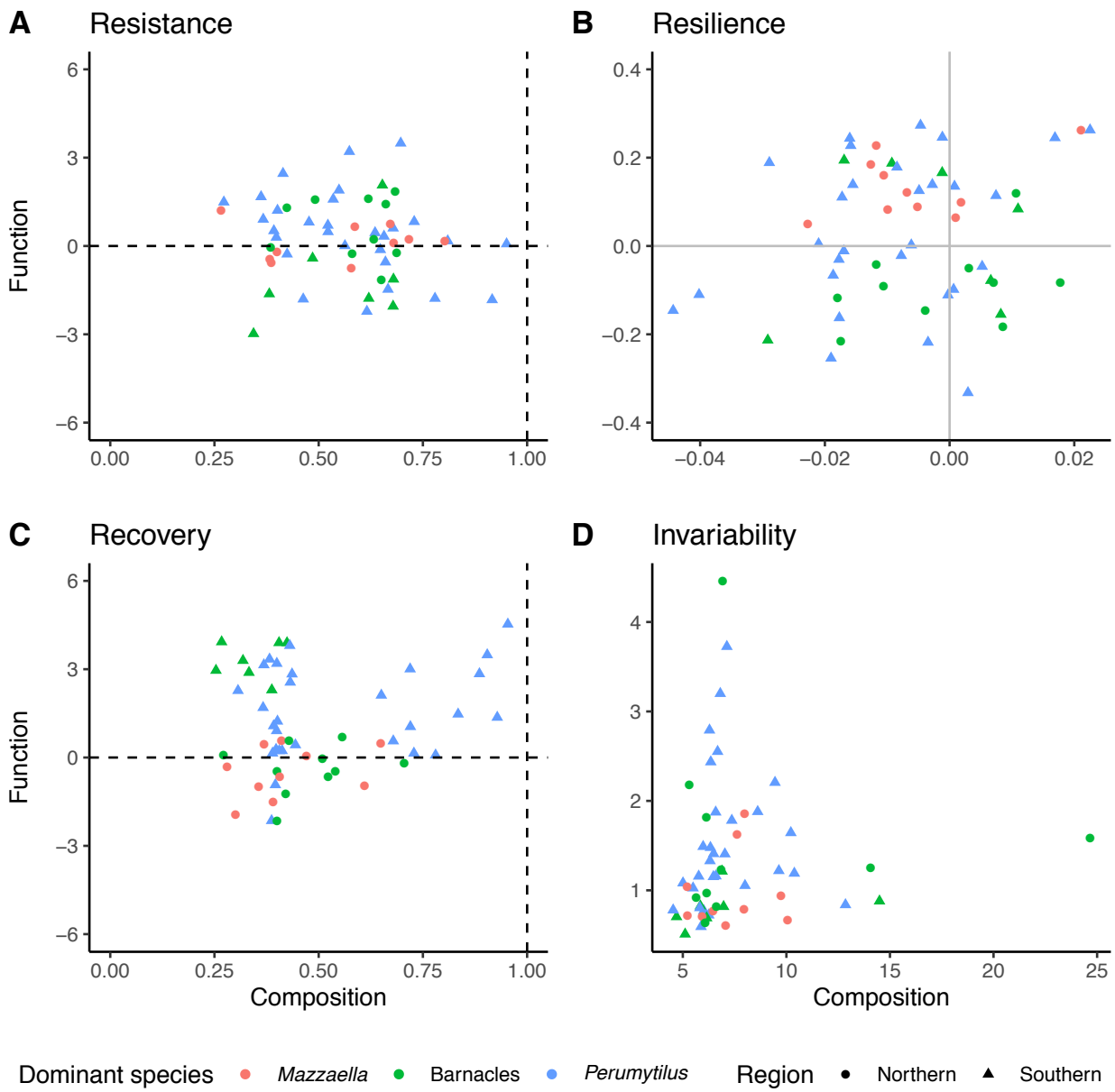


Fig. 4 Valdivia et al.

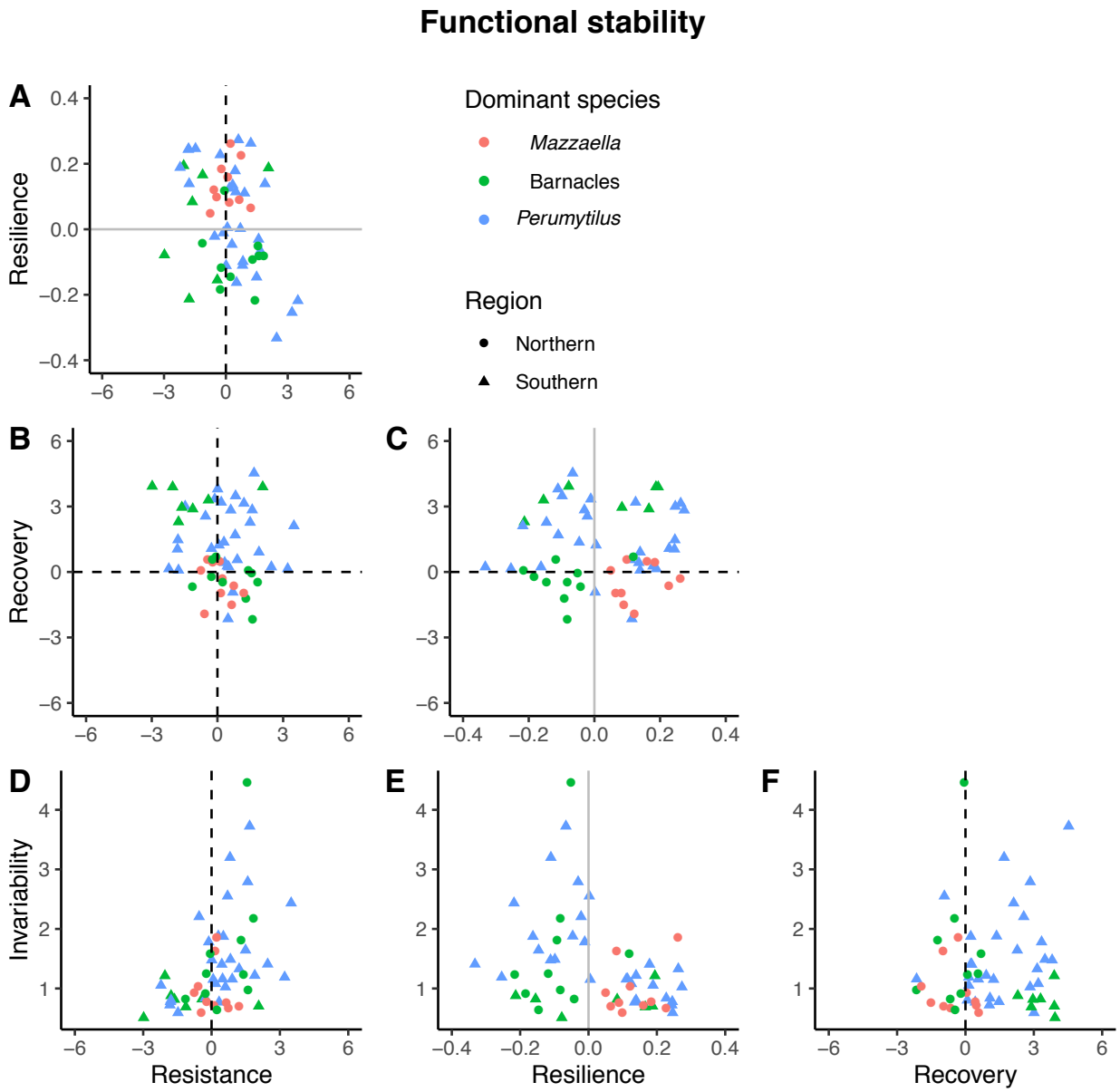


Fig. 5 Valdivia et al.

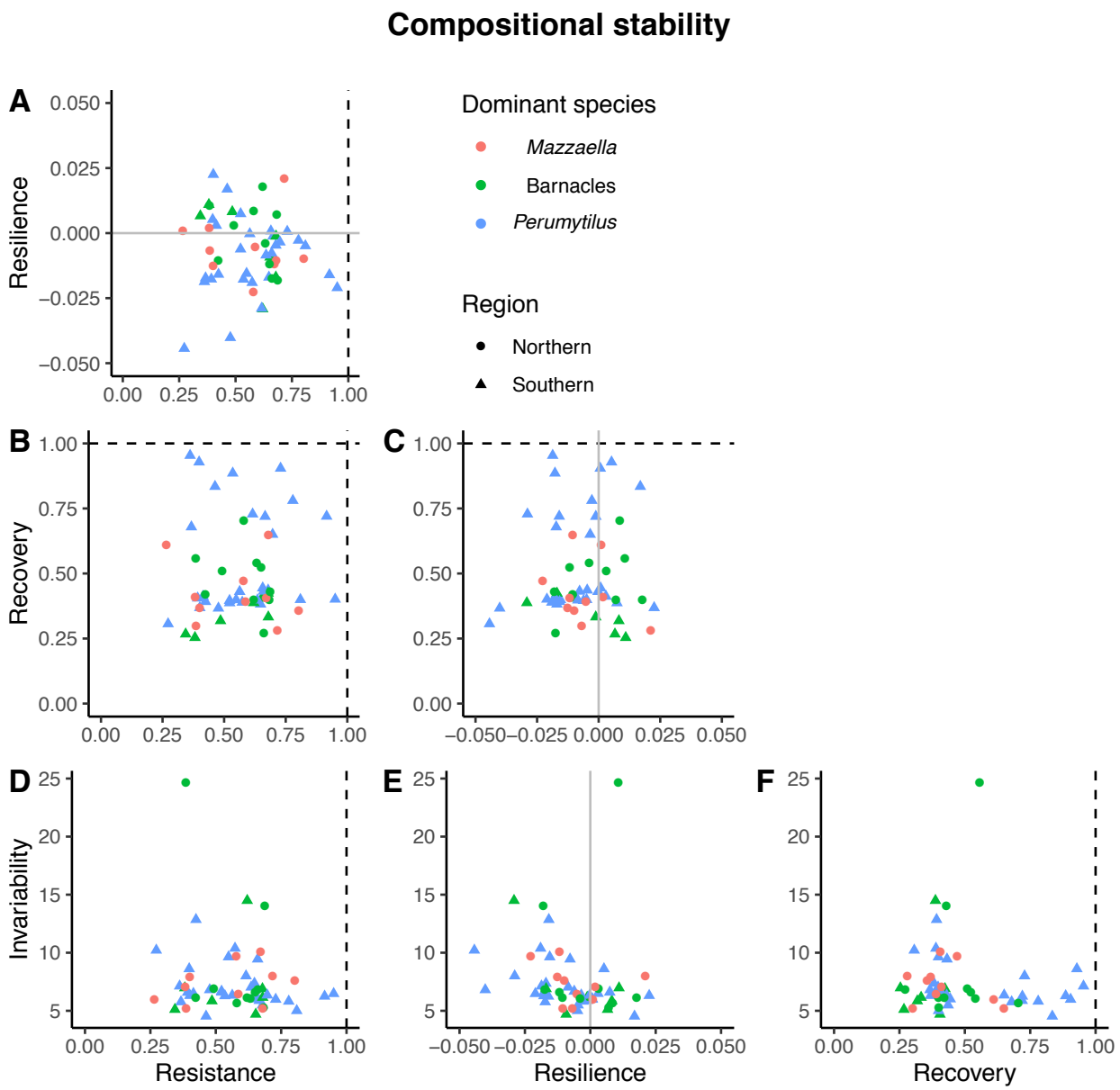


Fig. 6 Valdivia et al.