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, but 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 independent, 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). In addition, the functional consequences of biodiversity loss can be exacerbated at regional spatial scales, which are relevant for conservation or policy (Isbell et al., 2017). To our best knowledge, however, the correlations of multiples dimensions of stability have not been assessed at large spatial scales yet (Gonzalez et al., 2020).

Each dimension of stability can be assessed either for aggregate ecosystem properties performed by the whole community, such as productivity, community biomass, or cover (functional stability), or for the combination of species identities and abundances in the community (compositional stability; Micheli et al., 1999). The relationship between both domains of stability sheds light into the contribution of particular combinations of species to the aggregate function. For example, if the community is characterised by asynchronous species dynamics, in which the decay of some species is compensated by

proportional increases of others, then the community could maintain relatively stable aggregate properties over time (Yachi and Loreau, 1999; Gonzalez and Loreau, 2009). This implies that a low compositional stability can sustain a high functional stability (Tilman, 1996; Micheli et al., 1999). In these cases, negative or null correlations between functional and compositional aspects of stability can be observed (e.g., Hillebrand et al., 2018; Hillebrand and Kunze, 2020). The stabilising role of such asynchronous or compensatory species dynamics is supported by several studies (Gonzalez and Loreau, 2009; Valencia et al., 2020). However, 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).

Within the functional and compositional domains, 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 be independent of each other or can be correlated. Several models suggest that most stability dimensions are positively correlated (e.g., Scheffer et al., 2009; Radchuk et al., 2019). For instance, communities with low invariability (i.e., highly variable functioning or composition over time) can show low resistance against disturbances, because of the increased risk of extinctions of species with small population sizes (Lande et al., 2003). In those cases, stability is unidimensional and conservation decisions could maximise both aspects of stability, i.e., enhancing resistance

would also enhance invariability. However, negative correlations among dimensions can be also observed. Resistance, for example, can be negatively related with resilience when disturbance has a strong impact on the community and intrinsic growth rates are high: Larger initial disturbances can allow for faster recovery trajectories in function or composition (Harrison, 1979; Hillebrand et al., 2018). Negatively correlated stability dimensions imply that policy trade-offs would be needed to maintain either one or another aspect of stability. Finally, chronic disturbances, like the loss 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.

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). 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

112 were functionally and evolutionary distinct and included the red corticated alga *Mazzaella*
113 *laminarioides,* chthamalid barnacles (mixture of *Jehlius cirratus* and *Notochthamalus*
114 *scabrosus*), and the purple mussel *Perumytilus purpuratus* (hereafter referred to as
115 *Mazzaella*, barnacles, and *Perumytilus,* respectively; Table 1). This setup allowed us to test
116 the following three hypotheses.

117 *H1: The magnitude of the stability response will depend on the identity of the removed*
118 *dominant species.* The three dominant species use the settlement substratum in different
119 ways: *Perumytilus* is able to monopolise almost the 100 % of primary substratum, while the
120 barnacle complex occurs in combination with bare rock and filamentous algae (Table 1;
121 Broitman et al., 2001; Moreno, 2001; Lagos et al., 2005). *Mazzaella*, on the other hand, uses
122 a smaller proportion of the primary substratum, but generates a large canopy-like
123 structure above the rock (Hoffmann and Santelices, 1997). Thus, the removal of these
124 species should trigger different responses of the ensuing assemblages (see also next
125 paragraph, below).

126 *H2: Across sites, the removal of the dominant species will elicit negative or neutral*
127 *correlations between functional and compositional stability dimensions due to prevailing*
128 *compensatory dynamics.* The removal of *Perumytilus* triggers the compensation between
129 subordinate taxa: fast-growing ephemeral macroalgae such as *Ulothrix* sp. and *Pyropia* spp.
130 dominate the assemblage during the first two months after the removal, then they are
131 replaced by barnacles and *Ulva* sp., and eventually by *Mazzaella* (Aguilera and Navarrete,
132 2012; Tejada-Martinez et al., 2016). Barnacles facilitate small grazers; therefore, the
133 removal of barnacles leads to increased abundances of microalgae but decreased
134 abundances of perennial macroalgae (Harley, 2006; Mrowicki et al., 2014; Whalen et al.,

2016). Finally, the removal of *Mazzaella* is associated with the decay of the red alga *Gymnogongrus furcellatus* (*Asterfilopsis furcellata*), but the increase in the abundance of *Ulva rigida*, *Lithophyllum* spp., and the ephemerals *Petalonia fascia* and *Scytosiphon lomentaria* (Jara and Moreno, 1984)—these dynamics are ascribed to shading effects of *Mazzaella* on the understorey (Moreno and Jaramillo, 1983; Nielsen and Navarrete, 2004).

H3: Across sites and within the stability domains (functional and compositional), the stability dimensions will be correlated with each other. According to previous modelling work (Radchuk et al., 2019), the stability dimensions will show positive pairwise correlations. The exception will be negative correlations of resistance-resilience, because stronger impacts can allow faster recovery rates, and resilience-invariability, because a faster recovery is expected to be associated with more variable temporal trajectories in function and composition (Hillebrand et al., 2018).

Materials and methods

Study province

The study was conducted at multiple field sites on the extremes of a large transitional biogeographic province that extends between the Peruvian and Magellan provinces along the Chilean sector of the South East Pacific (Camus, 2001; Thiel et al., 2007; Lara et al., 2019). We used eight study sites that where evenly split between the northern and southern extremes of the province (around 30.23ºS and 39.9º, respectively)—each region encompassing ca. 200 km of shoreline (see Fig. 1). Therefore, the experimental design considered four spatial scales: The province encompassed two regions; each region included four sites. Then, each site contained several replicated plots. A plot was a fixed

158 location where the abundance of macrobenthic sessile species was estimated over time.
159 There were two types of plots, either control or disturbed in which the dominant species
160 was removed. Within each site, each stability metric was calculated for randomly paired
161 plots (one of each type of plot). Depending on the tested hypothesis, the analyses were
162 conducted at the scale of individual plots, paired plots, or after aggregating these data
163 according to the identity of the removed species, which was a site-level attribute.

164 The northern region is characterised by semi-permanent coastal upwelling activity,
165 which coincides with a significant transition in abiotic (Hormazabal et al., 2004; Garreaud
166 et al., 2011; Tapia et al., 2014) and biotic conditions (Valdivia et al., 2015). Compared with
167 neighbour locations, this upwelling point has been associated with more persistent abiotic
168 environmental conditions, more synchronous species fluctuations, and lower invariability
169 in total cover (Valdivia et al., 2013).

170 The southern region presents significant correlations between Chlorophyll-*a*
171 concentration, riverine inputs, and runoff from forestry and agricultural activities (Van
172 Holt et al., 2012; Lara et al., 2019). In this region, upwelling activity is weaker and more
173 intermittent than the sector equatorward from Concepción, which is dominated by strong
174 seasonal upwelling (ca. 37S; Atkinson et al., 2002; Letelier et al., 2009; Pinochet et al.,
175 2019).

176 Rocky-shore communities inhabiting the mid-intertidal zone across the province are
177 composed of a diverse set of mobile and sessile species, where human harvesting and
178 environmental context modulate ecological interactions (Broitman et al., 2001; Lagos et al.,
179 2005; Caro et al., 2010; Broitman et al., 2011). The sessile communities are dominated by
180 green macroalgae like *Ulva compressa* and *U. rigida*, red macroalgae like *Mazzaella*

181 *laminarioides* and *Gelidium chilense*, or filter feeders like the barnacles *Jehlius cirratus*,
182 *Notochthamalus scabrosus,* and *Perumytilus purpuratus* (reviewed in Aguilera et al., 2019).
183
184 *Experimental design and setup*
185 At each site, we conducted a manipulative experiment with dominant-species
186 removal as a fixed factor. The experiments were conducted between October 2014 and
187 August 2017 in the southern region, and between December 2014 and September 2017 in
188 the northern region—in both cases, the prolonged time span (ca. three years) allowed us to
189 fully capture the seasonal and intra-annual variation in abiotic conditions and species
190 composition. Prior to the start of the experiment, we estimated relative species abundances
191 in ten 30 x 30 cm plots haphazardly located on the mid-intertidal zone to determine locally
192 dominant species as those with the highest relative abundances at each site (see also
193 Valone and Balaban-Feld, 2018). At each site, quadrats were located within an alongshore
194 transect (ca. 3 m wide) covering ca. 50 m of the coastline. The red corticated alga *Mazzaella*
195 *laminarioides* and chthamalid barnacles (a mixture of *Jehlius cirratus* and *Notochthamalus*
196 *scabrosus*) were the dominant taxa in the northern region; chthamalid barnacles and the
197 purple mussel *Perumytilus purpuratus* were the dominant species in the southern region
198 (hereafter referred as *Mazzaella*, barnacles, and *Perumytilus,* respectively; Table 1). Before
199 the manipulations, mean percentage cover of dominant species ranged from ca. 30 % for
200 *Mazzaella* in the northern region to 100 % for *Perumytilus* in the southern region.
201 Simpson's concentration index varied between 0.4 and 0.9 in the northern and southern
202 region, respectively, picturing a higher evenness in species abundance distribution in the
203 former than the latter region (Table 1).

204 Following site characterization, we started identical field experiments. We used 30 x
205 30 cm experimental plots on the mid-intertidal zone of each site, which were permanently
206 marked with stainless-steel bolts. The size of the experimental unit was selected to
207 minimise the impact on the local intertidal communities. For logistic reasons, we deployed
208 10 replicate plots in the sites located on the northern sector and 20 replicates in the
209 southern sites. Experimental plots were haphazardly located within areas of high
210 abundance of the locally dominant species and relatively flat and horizontal rocky surfaces.
211 Thus, we avoided crevices, tide-pools, and vertical surfaces to reduce biotic variation
212 related to local spatial heterogeneity.

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

222 All plots were sampled immediately before the removal of local dominants, 1-2
223 months after the manipulation, and then approximately every three months until the end of
224 the experiment. All macroalgae and sessile macro-invertebrates (> 5 mm) occurring in each
225 plot were identified *in situ* and classified to the lowest possible taxonomic level (usually
226 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):

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

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

where f_i is the percentage cover of species i, F is the equivalent aggregate community-level function (total community cover), and $\sigma_{f_i}^2$ and σ_F^2 are their respective temporal variances. The index is standardised between 0 (perfect asynchrony, i.e., most species' abundances are negatively correlated over time) and 1 (perfect synchrony, i.e., most species'

abundances are positively correlated). Since φ is independent of the magnitude and distribution of species abundances and variances, it allows us to quantitatively compare communities with different numbers of species (Loreau and de Mazancourt, 2008).

Stability dimensions

Stability was assessed according to the metrics for resistance, resilience, recovery, and invariability described by Hillebrand et al. (2018). Each metric was estimated by randomly pairing one control and one disturbed plot in each site. In this way, we obtained replicate estimations within each site. The stability metrics in the functional domain were calculated on the basis of total community cover (F), and the stability metrics in the compositional domain were calculated on the basis of Bray-Curtis similarities (sim) between the disturbed and control plots (C).

Resistance (a) was estimated for function as the log-response ratio (LRR) calculated after the disturbance took place (1-2 months after the removal of local dominants):

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

where F_{dist} is total community cover in the dominant-removed plot, and F_{con} is the same 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 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

289 reflect low functional recovery; thus, the absolute value of functional *c* was analysed in the
290 test of hypotheses H1 and H3 (see *Statistical analyses*).
291 *Invariability* (*d*) was calculated as the multiplicative inverse of the standard
292 deviation of residuals (*resid*) from the regression slope *b* as:

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

293 Larger values de *d* denote smaller temporal variations around the trend of recovery
294 in function or composition (Hillebrand et al. 2018). Note that invariability is termed as
295 *Temporal stability* by Hillebrand et al. (2018). However, we have preferred to use
296 *Invariability* to avoid confusions with the term *Stability* (see also Radchuk et al., 2019).
297
298 *Statistical analyses*
299 For simplicity, hereafter the community in each site will be referred to according to
300 the identity of the locally dominant species that was removed (i.e., *Mazzaella*-, barnacle-, or
301 *Perumytilus*-dominated communities). This means that the plots and sites will be grouped
302 into each of the three community types in some of the statistical analyses.
303
304 *H1: The magnitude of the stability response will depend on the identity of the removed*
305 *dominant species*
306 To test this hypothesis, we first used *t*-tests for each community and within each
307 stability domain (either functional or compositional) to determine if resistance, resilience,
308 and recovery significantly differed from the reference values. Secondly, we used separate
309 general lineal models (LMM) to compare the magnitude of each stability dimension among

310 the three communities. Accordingly, we used the absolute value of functional resistance
311 and recovery to focus on their magnitudes. The models included the identity of the
312 removed dominant species as fixed effect, and site as random effect. Nevertheless, site was
313 removed from the models of the compositional domain due to singularity (i.e. variance
314 nearly zero).
315
316 *H2: Across sites, the removal of the dominant species will elicit negative or neutral*
317 *correlations between functional and compositional stability dimensions due to prevailing*
318 *compensatory dynamics*
319 First, we used one-tailed *t*-tests to determine whether φ was significantly lower
320 than 1 (i.e., perfect synchrony in species fluctuations) for each community. In addition, we
321 used a generalised linear mixed model (GLMM) to determine if the removal of the locally
322 dominant species decreased φ (i.e., increased the degree of species compensation within
323 the community). For the model we used a Gamma structure of errors and a log link
324 function; the model included the identity of the dominant species in each site and the
325 removal treatment (removal or control) as crossed and fixed factors, and the site (eight
326 levels) as random factor. After initial the fit, however, site was removed due to singularity.
327 Second, Pearson product-moment correlations were calculated between functional
328 and compositional dimensions of stability. Correlations were calculated separately for each
329 community and stability dimension. In these correlations, we used the absolute value of
330 every functional stability dimension to assess the magnitude, rather than the direction, of
331 these responses. The absence of statistically significant correlations, in addition to near-

332 zero values of φ were used as evidence of species compensation after the removal of
333 dominant species.
334 Third, to identify the species driving compensation (or the lack thereof), we used
335 Similarity Percentage Routines (SIMPER; Clarke, 1993) that partitioned the contribution of
336 each species to the between-treatment dissimilarity in each community.
337
338 *H3: Across sites and within the stability domains (functional and compositional), the stability*
339 *dimensions will be correlated with each other*
340 Pearson product-moment correlations were used to test this hypothesis. Within the
341 functional and compositional domains, analyses were conducted combining all sites and
342 communities to test for a tendency between these dimensions to correlate independently
343 of the ecological context and species identities.
344 All analyses, calculations, and plots were done in R programming environment
345 version 4.0.2 and the R-packages *lme4, MuMIn, sjPlot, tidyverse,* and *vegan* (Bates et al.,
346 2015; Oksanen et al., 2019; Wickham et al., 2019; Bartoń, 2020; Lüdecke, 2020; R Core
347 Team, 2020), except for Fig. 1, which was made using MatLab R2014a and data from
348 MODIS-Aqua.
349
350 **Results**
351 *H1: The magnitude of the stability response will depend on the identity of the removed*
352 *dominant species*
353 The different communities significantly responded to the experimental disturbances
354 within both functional and compositional domains (Figs. 2A, C, E, G and B, D, F, H,

355 respectively; Table A1 in the Appendix). The exception was the functional resilience of the
356 barnacle- and *Perumytilus*-dominated communities, which did not differ from zero (Table
357 A1, Fig. 2C). When we compared the magnitude of the responses among communities, the
358 three communities exhibited remarkably similar stability responses to the experimental
359 disturbance for both domains (Fig. 2). Accordingly, we did not detect statistically
360 significant differences among the communities, with the exception of functional resilience
361 (GLMM contrasts in Table A2: *Mazzaella* > barnacles; Fig. 2C).
362
363 *H2: Across sites, the removal of the dominant species will elicit negative or neutral*
364 *correlations between functional and compositional stability dimensions due to prevailing*
365 *compensatory dynamics*
366 The low values of the proxy for species synchrony, φ, indicated that species
367 compensation was common across communities and removal treatments (Fig. 3). The
368 parameter was on average 0.11 (0.06 – 0.16), 0.30 (0.21 – 0.40), and 0.17 (0.12 – 0.21) for
369 *Mazzaella*, barnacles, and *Perumytilus* communities respectively (mean [95% CI]). These
370 values were significantly lower than 1 in each community (one-tailed *t*-tests: t_9 = -42.2, t_{16} =
371 -17.5, and t_{28} = -38.2 for *Mazzaella,* barnacles, and *Perumytilus,* respectively; $P < 0.001$).
372 However, the response of these dynamics to the dominant removal varied among
373 communities. The press disturbance increased the strength of species compensation in the
374 *Perumytilus* communities, but not in the others (GLM: R^2 = 0.45, $P < 0.001$ for an 80-%
375 decrease in φ in the *Perumytilus* communities, see Figure 3). In these communities, the
376 strengthening of species compensation was accounted for by the overshoot in the
377 abundance of Ulvoids (mixture of *Ulva rigida* and *U. compressa*) during the first half of the

experiment (late 2014 - early 2016; see Fig. A1 in the Appendix); this taxon was replaced by chthamalid barnacles over time, which remained relatively stable until the end of the experiment in mid-2017 (Fig. A1).

About seven (TEMB and GUAN) and ten (PTAL) taxa accounted for ca. 90 % of the dissimilarities between treatments in the northern region; about three (CALF) and five (CHAI) taxa explained the 90 % of the multivariate differences between treatments in the southern metacommunity (Table A3). Across both regions, these species included encrusting, filamentous, and corticated macroalgae, in addition to barnacles (e.g., *Austromegabalanus psittacus*; Table A3). The lichen *Verrucaria* sp. accounted for a relatively important percentage of between-treatment dissimilarities in the northern region (TEMB, GUAN, and PTAL; Table A3).

According to the high prevalence of species compensation, we observed almost no statistically significant correlation between functional and compositional stabilities across communities (Fig. 4). Separately for the three community types, we observed non-statistically significant, correlations for resistance (Fig. 4A; Table A4 in the Appendix). For resilience, only the communities in which barnacles were removed showed a significant, and negative, correlation between the functional (absolute value) and compositional domains (green symbols in Fig. 4B; Table A4). Similarly, the barnacle-dominated communities exhibited a negative correlation between functional (absolute value) and compositional recoveries (green symbols in Fig. 4C; Table A4). Finally, functional invariability was uncorrelated from compositional invariability (Fig. 4D; Table A4).

H3: Across sites and within the stability domains (functional and compositional), the stability dimensions will be correlated with each other

Our results did not support this hypothesis, yet we detected some significant correlations (Fig. 5; Table A5 in the Appendix). In the functional domain, statistically significant correlations were found between resistance and resilience (negative; Fig. 5A; Table A5), resistance and invariability (positive; Fig. 5D; Table A5), and resilience and invariability (negative; Fig. 5E; Table A3). In the compositional domain, we did not detect statistically significant correlations among stability dimensions (Fig. 6; Table A5).

Discussion

This study showed that the stability of rocky intertidal communities in a broad biogeographical province of the SE Pacific shore is a multidimensional property. After the removal of locally dominant species, the magnitude of the effect of the disturbance and the temporal pattern of recovery were surprisingly similar among communities but varied between functional and compositional response variables, and among the four dimensions of stability examined here; namely, resistance, resilience, recovery, and invariability. Only in the functional domain we still observed significant correlations between resistance and resilience (negative), resistance and invariability (positive), and resilience and invariability (negative). The high prevalence of species compensation and asynchronous dynamics could explain the general lack of correlation between functional and compositional stability domains, indicating that functional recovery may not involve a fully compositional recovery in this study system. Our results are in line with recent evidence of the multifaceted nature of ecological stability (Donohue et al., 2016; Hillebrand et al., 2018;

423 Pennekamp et al., 2018; Kéfi et al., 2019; Radchuk et al., 2019), which we further discuss
424 below.
425
426 *Different communities exhibited similar initial and long-term stability responses to local*
427 *extinction*
428 The disturbance elicited significant stability responses within both the functional
429 and compositional domain regardless of the dominant species identity, with the exception
430 of functional resilience, which was indistinguishable from zero in the case of the
431 invertebrate-dominated communities. Despite these differences, no community fully
432 recovered in the end of the experiment, 35 months after the start of the disturbance.
433 Importantly, the consistently negative compositional resilience provides further support
434 for a persistent departure of these assemblages from the reference state (i.e. control plots),
435 as shown in phytoplankton mesocosm experiments (Hillebrand et al., 2018). This result
436 may indicate that the recovery, and restauration, of this ecosystem may need a longer time
437 span than here considered. Long-term (i.e., 20 years) monitoring of rocky intertidal
438 communities suggests the existence of cyclic succession after severe disturbances, with the
439 alternation of dominant species every ca. two years (Benincà et al., 2015). These non-
440 equilibrium dynamics can well be amplified by environmental stochasticity, as shown by
441 experimental removals of dominant mussels (Wootton, 2010). Thus, the non-equilibrium
442 and near-chaotic nature of coastal systems may obstruct our ability to restore disturbed
443 coastal ecosystems. Indeed, a major review of restoration strategies indicates that
444 functional and compositional recovery of coastal systems may reach on average a 34 % in
445 12 years, even when active restoration is enforced (Moreno-Mateos et al., 2020).

Between-site environmental differences could have generated "unexplained" variability in the stability responses, precluding our ability to detect differences among the dominant species. Nevertheless, our analyses suggest that the factors (other than dominant's identity) associated to between-site differences may have little influence on the stability measurements (compare the pseudo-R^2 between fixed factors and full models in Table A2). In the case of functional stability, between-site differences accounted for small, but non-zero, amount of variation in the stability responses. Dampened environmental variability in sites under the influence of persistent upwelling could have influenced the invariability in community cover (Valdivia et al., 2013). Sea water temperature patterns define the phenology of most intertidal organisms (Sanford, 2002; Baldanzi et al., 2018), which, mediated through larval dispersal processes, can influence overall population growth rates, and thus functional resilience and recovery (Svensson et al., 2005). In the case of compositional stability, on the contrary, site accounted for almost no variation in Bray-Curtis dissimilarity. If site differences seemly accounted for a small variation in stability responses, then, to what degree the stability observed at the local scales can scale up to regional and seascape scales?

The area-invariability relationship indicates that stability should increase from local to regional scales due to asynchronous dynamics among sites within the landscape, and also among species within sites (Wang and Loreau, 2014; Zhang et al., 2018). Moreover, increased beta diversity (i.e. between-site differences in species composition) is expected to increase the spatial asynchrony in functioning among sites, and thus the stability of the whole landscape (Wang and Loreau, 2016). According to the high prevalence of asynchronous species dynamics (this study; Valdivia et al., 2013) and high beta diversity

469 (Broitman et al., 2001; Valdivia et al., 2015; Valdivia et al., 2017), predictions based on the
470 area-invariability relationship should hold in our study system. Albeit the extension of this
471 theory to other stability dimensions and the compositional domain still needs further
472 development, we suggest that maximising protected areas, rather than focusing on patches
473 that contain unique assemblages, should be a conservation goal to maintain the functioning
474 in the analysed ecosystem (see also Economo, 2011; Ospina-Alvarez et al., 2020).
475
476 *Compensatory dynamics were common within the system, leading to null or negative*
477 *function-composition correlations*
478 In agreement with our prediction, asynchronous and compensatory species
479 dynamics were strong in the study region. The strength of these dynamics, however, varied
480 among the three analysed community types. In particular, the removal of *Perumytilus*
481 reduced the synchrony in species abundances following compensatory dynamics between
482 ulvoid algae and barnacles, according to the facilitation model of ecological succession
483 (Connell and Slatyer, 1977). In addition to competitive species replacement during
484 succession, asynchronous species dynamics can also reflect differential species
485 environmental responses, population compensatory cycles, species-wise variations in
486 dispersal, and neutral, zero-sum dynamics (e.g. Lehman and Tilman, 2000; Chesson et al.,
487 2001; Loreau et al., 2003; Loreau and de Mazancourt, 2008). At global scales, asynchronous
488 dynamics can have stronger effects on stability than species richness (Valencia et al., 2020).
489 Accordingly, evidence of the central role of species synchrony in the stability of ecosystem
490 functions is supported by studies across ecosystems and taxonomic groups (reviewer by
491 Gonzalez and Loreau, 2009).

492 The lack of correlation between functional and compositional measurements of
493 stability could well reflect the effects of species compensation. For instance, high resistance
494 and recovery (i.e., near-zero log-response ratios) in the functional domain were observed
495 along ample ranges of both metrics in the compositional domain, and the negative function-
496 composition correlations detected for resilience and recovery further reinforce the notion
497 of functional compensation within these communities (Guelzow et al., 2017; Hillebrand et
498 al., 2018; Hillebrand and Kunze, 2020). This indicates that a given level of functioning could
499 be performed by communities with different compositions, which may have important
500 consequences for ecosystem restauration (Fig. 7A; Borja et al., 2010).
501
502 *The stability dimensions were mostly uncorrelated across community types and stability*
503 *domains*
504 In the functional domain, the correlations among the different dimensions of
505 stability ranged from negative to null and to positive. We were able to detect negative
506 correlations between functional resistance and resilience and between resilience and
507 invariability. Negative functional resistance-resilience and resilience-invariability
508 correlations have been also observed in modelling and experiments conducted on
509 experimental phytoplanktonic mesocosm communities (Hillebrand et al., 2018), and have
510 been associated to comparatively high growth rates that allow faster recovery rates with
511 stronger initial impacts (Harrison, 1979). Similarly to aquatic ciliate communities
512 (Pennekamp et al., 2018), larger initial functional responses (i.e. lower resistance) were
513 associated with more temporally stable functioning, which could respond to a positive

514 relationship between species' invariability and relative abundance (Grman et al., 2010;
515 Lamy et al., 2020).
516 In the compositional domain, on the other hand, no statistically significant
517 correlation between stability dimensions was detected. This high dimensionality implies
518 that the four aspects of compositional stability analysed in this study are fully orthogonal
519 and are mandatory to completely describe the response of these communities to an
520 ecologically realistic disturbance akin to our press removal of the dominant species.
521 Uncorrelated stability dimensions have been highlighted by previous work when ecological
522 communities face severe environmental disturbances (Allison, 2004; van Ruijven and
523 Berendse, 2010; Donohue et al., 2013; Hillebrand et al., 2018). Contrarily, most empirical
524 research has been based on one or two stability dimensions; the temporal coefficient of
525 variation has been widely used to assess the stability in aggregate ecosystem functions in
526 the absence of major disturbances (reviewed by Kéfi et al., 2019). Yet, restoration
527 assessment after pulse and press disturbances would largely benefit from considering
528 multiple components of stability, because, as we have shown, these components may well
529 be decoupled during the process of recovery (Fig. 7B; Donohue et al., 2016; Moreno-Mateos
530 et al., 2020).
531 Perhaps, percentage cover would have been too coarse to detect differences stability
532 among community types and positive correlations among the stability dimensions. Albeit
533 we considered the multi-layered nature of macrobenthic communities in our in-situ
534 estimations, it would be the case that between-plot variations in the tri-dimensional
535 projection of the communities would have generated unwanted variation in the stability
536 responses. However, our results are well supported by previous work assessing other

537 functional proxy, such as consumption rates and biomass (Ghedini et al., 2015; Hillebrand
538 et al., 2018; Valencia et al., 2020). Percentage cover in sessile communities is the results of
539 the complex interaction between preemptive competition, disturbance, and recolonisation
540 (Paine, 1980), which makes it a good proxy for functioning.
541
542 *Conclusion and future directions*
543 Our results allow us to conclude that ecological stability of the analysed intertidal
544 communities is a multidimensional and complex phenomenon. The experimental removal
545 of locally dominant species elicited significant, and similar in magnitude, stability
546 responses of communities in a large biogeographical province of the SE Pacific shore. These
547 responses varied between functional and compositional domains, likely due to pervasive
548 and strong asynchronous species dynamics.
549 Still is necessary to determine how different types and aspects of disturbances can
550 influence stability dimensionality in these ecosystems. Albeit recent modelling work
551 indicates that disturbance types such as random, species-specific, or local disturbances can
552 have similar effects on stability dimensionality (Radchuk et al., 2019), contrasting the
553 effects of pulse and press disturbances can enhance our mechanistic understanding of the
554 ecological consequences of current climate crisis (Kéfi et al., 2019)—anthropogenic climate
555 change involves the interdependent effects of both types of disturbances over multiple
556 spatiotemporal scales (Harris et al., 2018). Regional manipulative experiments considering
557 a more ample range of environmental filters and dispersal limitations would allow us
558 model the role of spatial aspects of disturbance (Zelnik et al., 2018; 2019) in how stability
559 dimensionality scales from sites to entire regions; to our best knowledge, the scale

560 dependence of stability has been investigated only for single aspects of stability (Wang et
561 al., 2017). In summary, realising that stability is indeed a multidimensional concept will
562 enhance our ability to predict the response of communities and metacommunities to future
563 and ongoing anthropogenic disturbances.
564

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582

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856

857

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. Sea surface temperature and Chlorophyll-a data were not included in the statistical analyses and are shown here to describe the environmental conditions across the province.

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) recovery are shown as absolute values in order to compare magnitudes, rather than directions of effects. Values are mean ± 95 % confidence intervals. Dashed lines represent maximum resistance and recovery; solid grey lines represent 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*).

893 Fig. 3

894 Community-wide synchrony among subordinate species in each community type

895 (*Mazzaella-,* barnacle-, or *Perumytilus*-dominated community). The range of φ is [0, 1], with

896 1 = perfectly synchronous species fluctuations and 0 = perfectly asynchronous,

897 compensatory species fluctuations. Values are mean ± 95 % confidence intervals. All

898 communities statistically differed from 1 (one-tailed *t*-tests: t_9 = -42.2, $P < 0.001$; t_{16} = -17.5,

899 $P < 0.001$; t_{28} = -38.2, $P < 0.001$, respectively), indicating prevalent compensatory dynamics

900 across the region. The removal of the dominant species systematically increased the

901 strength of species compensation in the *Perumytilus* communities, but not in the others

902 (Gamma GLM, R^2 = 0.45, P < 0.001 for *Perumytilus*).

903

904 Fig. 4

905 Pairwise associations between functional and compositional dimensions of stability. In

906 these analyses, all functional dimensions were used as absolute values in order to

907 correlated magnitudes, rather that directions of effects. Dashed lines represent maximum

908 resistance and recovery; solid grey lines represent minimum resilience. Only (B) resilience

909 and (C) recovery of the barnacle-dominated communities (green symbols and trend lines ±

910 95 % confidence intervals) showed significant function-composition correlations (r = -0.52

911 and r = -0.57, respectively; P < 0.05).

912

913 Fig. 5

914 Associations among four dimensions of functional stability. Dashed lines represent

915 reference values for maximum resistance and recovery; solid grey lines represent

916 reference values for minimum resilience. Across communities, statistically significant
917 correlations were detected for the resistance-resilience, resistance-invariability, and
918 resilience-invariability pairs (trend lines ± 95 % confidence intervals; r = -0.38, r = 0.39,
919 and r = -0.36, respectively; P < 0.01).
920
921 Fig. 6
922 Associations among four dimensions of compositional stability. Dashed lines represent
923 maximum resistance and recovery; solid grey lines represent minimum resilience. No
924 statistically significant correlation was detected across communities.
925
926 Fig. 7
927 Summary of scenarios based on correlations between (A) functional and
928 compositional stability domains and (B) stability dimensions. Different scenarios have
929 different scenarios for ecosystem conservation and management. Panel A: Systems
930 exhibiting positive functional-compositional stability correlations may need a full recovery
931 in species composition to achieve a full recovery in functioning (yellow quadrant); if not, no
932 functional recovery would be possible (orange quadrant). Contrarily, negative functional-
933 compositional correlations (e.g., barnacle communities in this study) imply that the altered
934 community may be able to compensate the functioning of the pre-disturbance community,
935 but also that restored communities are unable to recover pre-disturbance functional
936 values. Panel B: A positive correlation between two aspects of stability (e.g., functional
937 resistance and invariability; this study) indicates that and conservation decisions could
938 improve both aspects of stability; a negative correlation (e.g., functional resistance and

resilience; this study) implies that policy trade-offs will be crucial to maintain either one or another aspect of stability. The lack of correlation among stability dimensions (e.g., all compositional dimensions in this study) indicates that, due to high uncertainty, multiple aspects are mandatory to characterise the stability of the ecosystem.

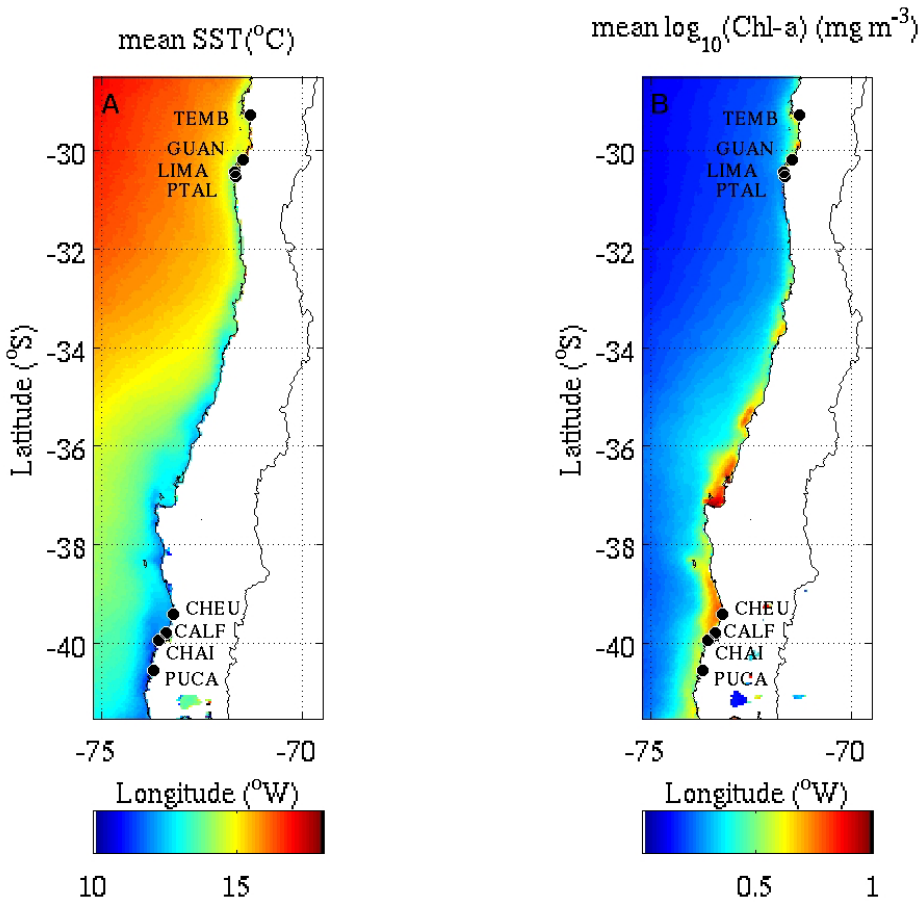


Fig. 1 Valdivia et al.

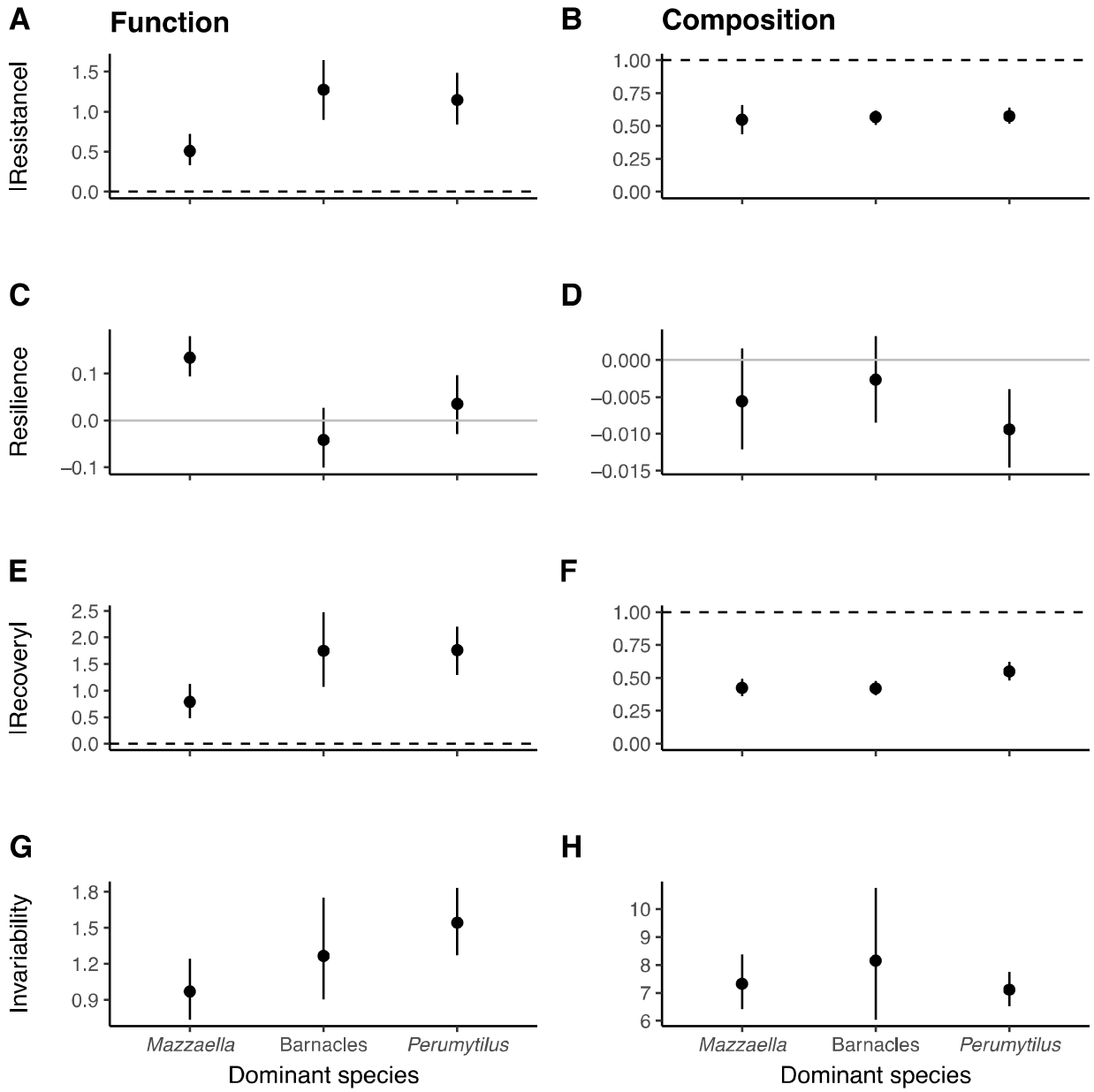
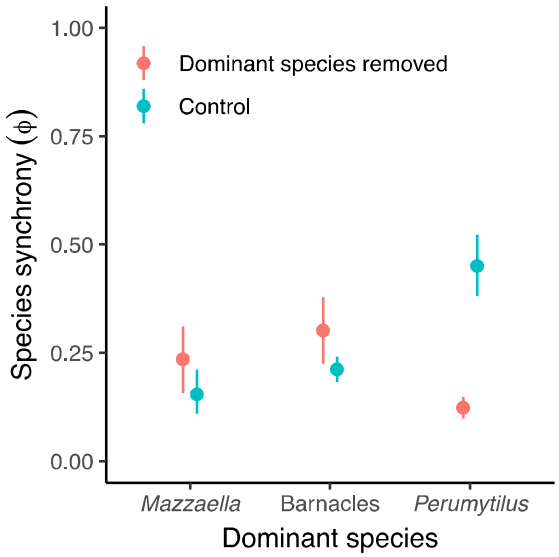


Fig. 2 Valdivia et al.



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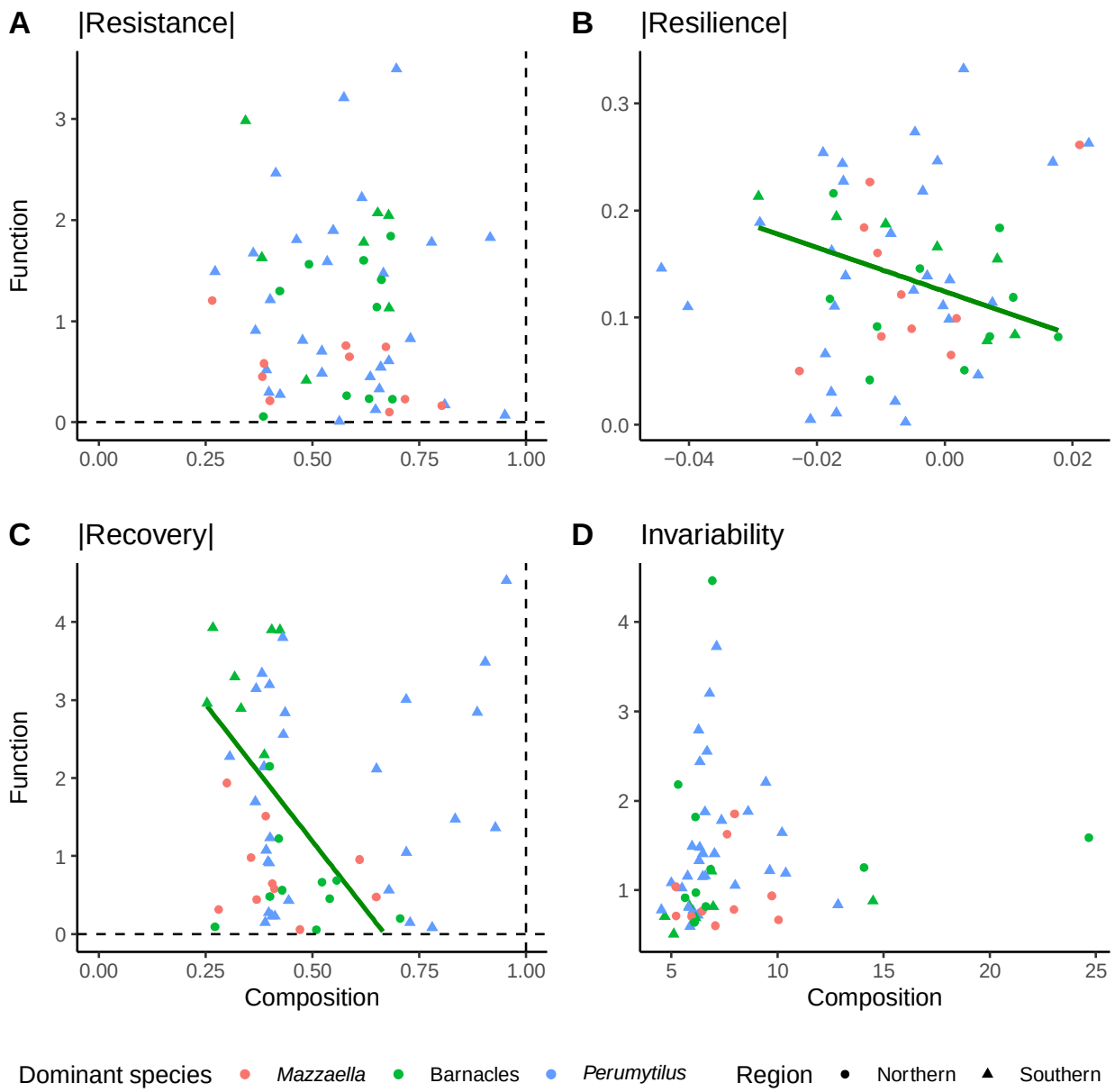

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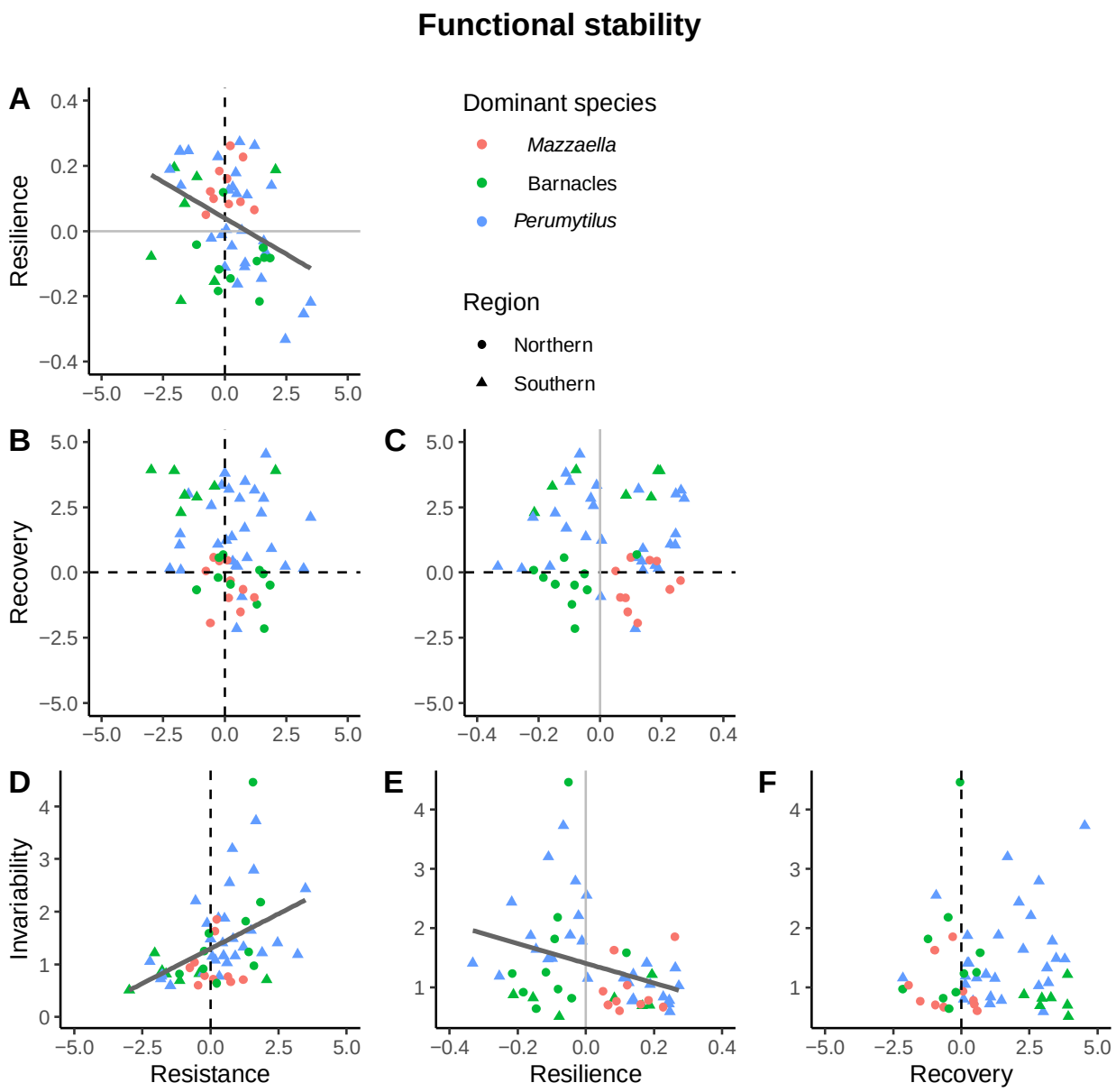

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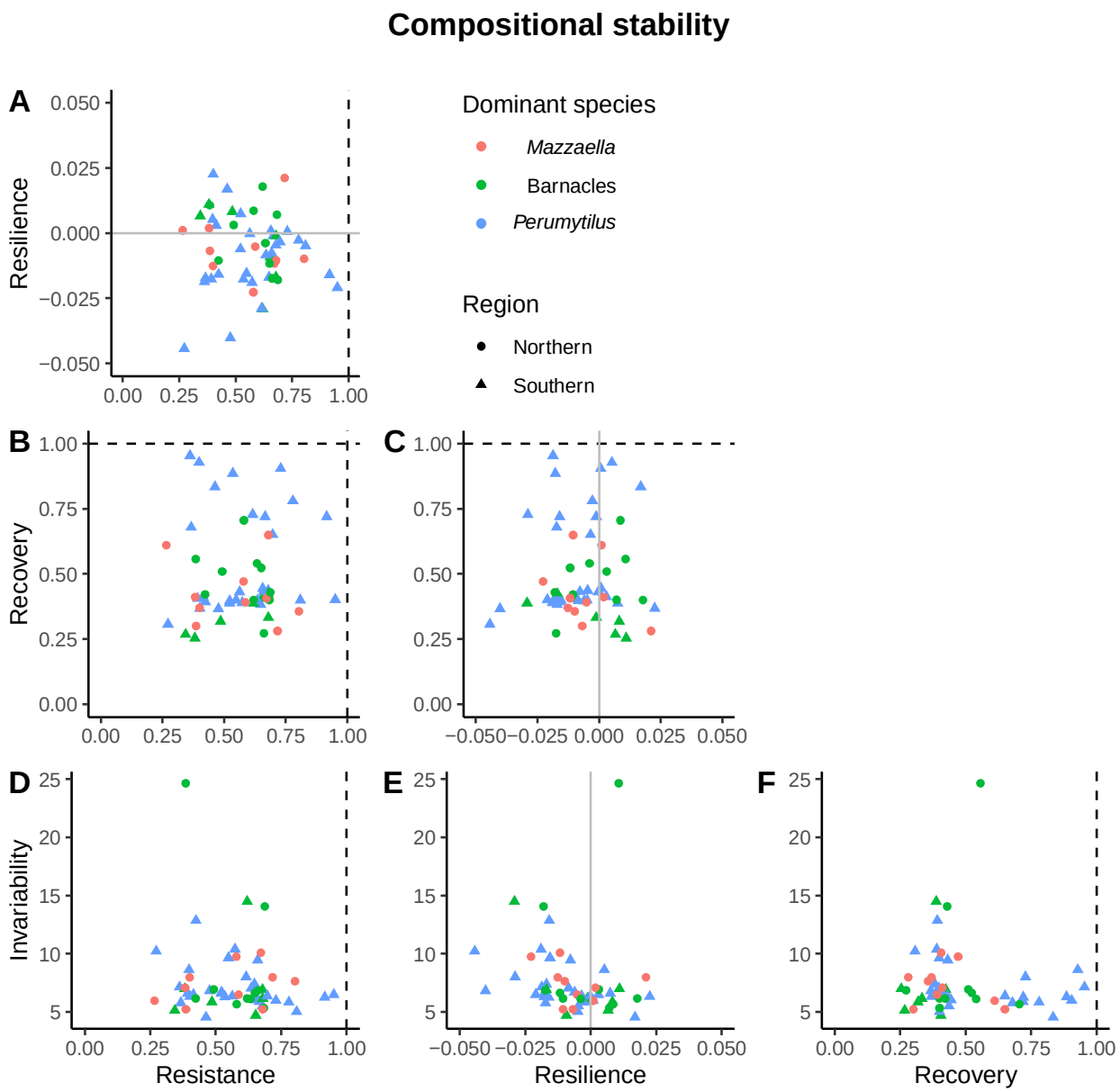

Fig. 6 Valdivia et al.

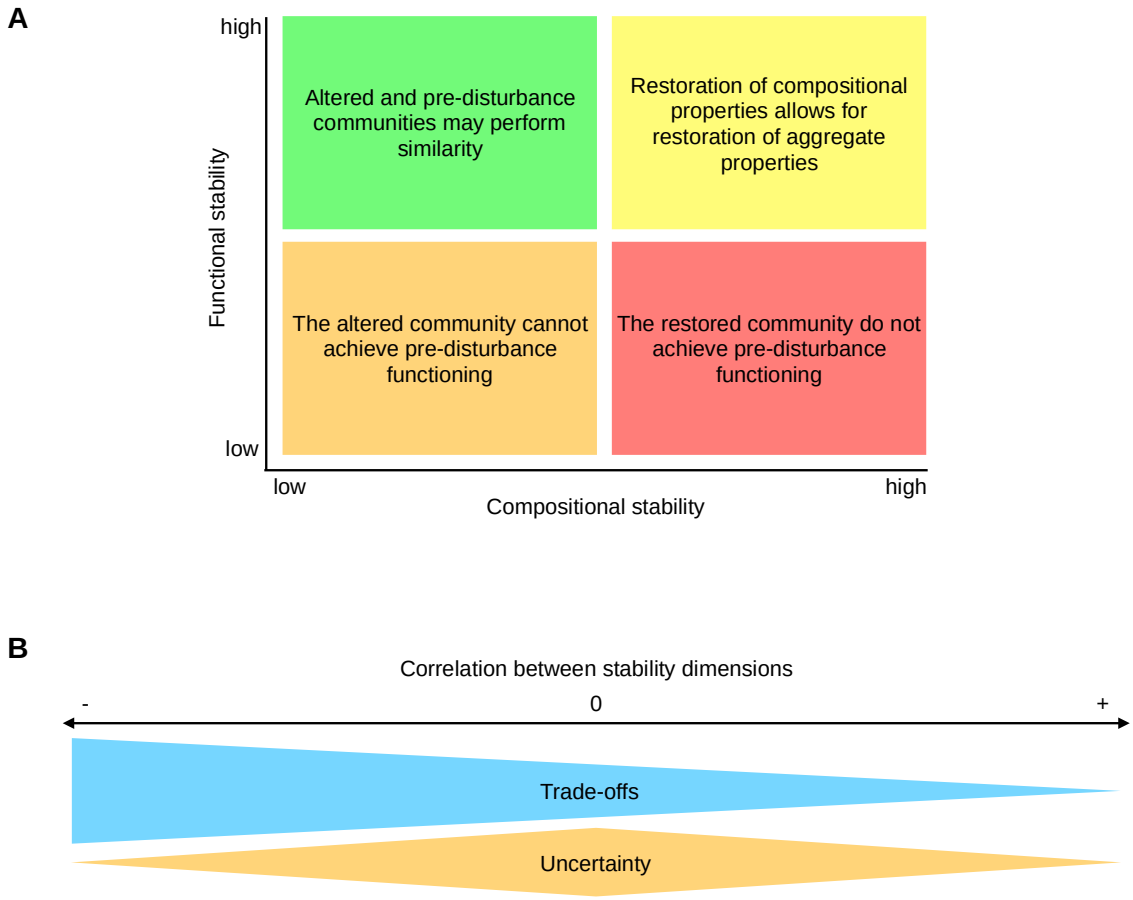

Fig. 7 Valdivia et al.