Marine Environmental Research 196 (2024) 106422

Contents lists available at ScienceDirect

Marine Environmental Research

journal homepage: www.elsevier.com/locate/marenvrev

Transient species driving ecosystem multifunctionality: Insights from competitive interactions between rocky intertidal mussels

Claudia Betancourtt [a,b,*], Alexis M. Catalán [c], Diego F. Morales-Torres [a], Daniela N. Lopez [d,e], Valentina Escares-Aguilera [a], Luis P. Salas-Yanquin [f], Joseline A. Büchner-Miranda [a], Oscar R. Chaparro [a], Jorge Nimptsch [a], Bernardo R. Broitman [g,h,i], Nelson Valdivia [a,j]

[a] Instituto de Ciencias Marinas y Limnológicas, Facultad de Ciencias, Universidad Austral de Chile, Campus Isla Teja, Valdivia, Chile
[b] Programa de Doctorado en Biología Marina, Facultad de Ciencias, Universidad Austral de Chile, Valdivia, Chile
[c] Centro de Investigación en Ecosistemas de la Patagonia, CIEP, Coyhaique, Chile
[d] Instituto de Ciencias Ambientales y Evolutivas, Universidad Austral de Chile, Valdivia, Chile
[e] Center of Applied Ecology and Sustainability (CAPES), Pontificia Universidad Católica de Chile, Santiago, Chile
[f] Universidad Nacional Autónoma de México, Facultad de Ciencias, Unidad Multidisciplinaria de Docencia e Investigación, Sisal, Mexico
[g] Instituto Milenio en Socio-Ecología Costera (SECOS), Chile
[h] Núcleo Milenio UPWELL, Chile
[i] Facultad de Artes Liberales, Universidad Adolfo Ibañez, Viña Del Mar, Chile
[j] Centro FONDAP de Investigación de Dinámicas de Ecosistemas Marinos de Altas Latitudes (IDEAL), Chile

ARTICLE INFO

Keywords:
Biodiversity
Dominance
Species identity
Physiological variables
BEF research
Ecosystem functioning

ABSTRACT

Anthropogenic biodiversity loss poses a significant threat to ecosystem functioning worldwide. Numerically dominant and locally rare (i.e., transient) species are key components of biodiversity, but their contribution to multiple ecosystem functions (i.e., multifunctionality) has been seldomly assessed in marine ecosystems. To fill this gap, here we analyze the effects of a dominant and a transient species on ecosystem multifunctionality. In an observational study conducted along ca. 200 km of the southeastern Pacific coast, the purple mussel *Perumytilus purpuratus* numerically dominated the mid-intertidal and the dwarf mussel *Semimytilus patagonicus* exhibited low abundances but higher recruitment rates. In laboratory experiments, the relative abundances of both species were manipulated to simulate the replacement of *P. purpuratus* by *S. patagonicus* and five proxies for ecosystem functions—rates of clearance, oxygen consumption, total biodeposit, organic biodeposit, and excretion—were analyzed. This replacement had a positive, linear, and significant effect on the combined ecosystem functions, particularly oxygen consumption and excretion rates. Accordingly, *S. patagonicus* could well drive ecosystem functioning given favorable environmental conditions for its recovery from rarity. Our study highlights therefore the key role of transient species for ecosystem performance. Improving our understanding of these dynamics is crucial for effective ecosystem conservation, especially in the current scenario of biological extinctions and invasions.

1. Introduction

Three decades of empirical work demonstrates that biodiversity loss can impair a wide array of ecosystem functions such as energy flow, nutrient cycling, and biomass production (Adler et al., 2012; Cardinale et al., 2012; Harris et al., 2018; Matías et al., 2018). Most of these studies focus on the effects of biodiversity on single function (Hooper et al., 2005, Stachowicz et al., 2007, Cardinale et al., 2012). However, recent evidence indicates that the consequences of biodiversity loss can be exacerbated when several functions are analyzed simultaneously (Hector and Bagchi, 2007; Cardinale et al., 2012; Manning et al., 2018). Therefore, the concept of ecosystem "multifunctionality" was coined to represent the simultaneous performance of multiple functions (Byrnes et al., 2014). While multifunctionality has been widely studied in terrestrial habitats, less research has been conducted in marine ecosystems, which are being severely threatened by anthropogenic biodiversity loss.

Biodiversity can influence ecosystem multifunctionality by means of

---

* Corresponding author. Instituto de Ciencias Marinas y Limnológicas, Facultad de Ciencias, Universidad Austral de Chile, Campus Isla Teja, Valdivia, Chile.
E-mail address: c.betancourttm@gmail.com (C. Betancourtt).

https://doi.org/10.1016/j.marenvres.2024.106422
Received 27 November 2023; Received in revised form 20 February 2024; Accepted 21 February 2024
Available online 27 February 2024

between-species niche differences that allow for more efficient resource use in the community (e.g., Tilman et al., 1997). For example, differential habitat use by marine soft-bottom species have been suggested to increase several ecosystem functions simultaneously (Beauchard et al., 2023). These "complementarity effects" can be overridden, however, by the effect of species with strong effects on energy flows and nutrient cycling, as shown for marine encrusting communities elsewhere (e.g., Valdivia et al., 2009). Importantly, such "identity effects" can be exacerbated by species with large relative abundances (i.e., dominant species; Grime, 1998).

Dominant species largely contribute to multiple ecosystem functions (Smith and Knapp, 2003; Dangles and Malmqvist, 2004; Winfree et al., 2015). In this line, the mass ratio hypothesis predicts that the abundance of species with strong functional effects is a better predictor of ecosystem functioning than the number of species per se (Grime, 1998). However, this may not always apply, because even rare species can strongly influence energy flows and nutrient cycling (Hooper et al., 2005; Cardinale et al., 2012). Therefore, the contributions of complementarity and dominant species to ecosystem functioning are still unclear.

Along with dominants, species can be categorized as subordinates and transients according to their relative abundances (Grime, 1998). In a certain habitat, subordinate species show low relative abundance and appear in association with dominants (Valone and Balaban-Feld, 2018). Transients encompass species with low relative abundance that can be dominant or subordinate elsewhere or under different environmental conditions (Grime, 1998; Magurran and Henderson, 2003). Subordinates and transients can still significantly influence community functioning due to high recruitment, resource consumption, and growth rates under suitable environmental conditions (Gouhier et al., 2011; Bracken and Low, 2012). An important feature of dominant species, particularly sessile, is that they function as foundation species that change the local environment and resource availability through their own physical structure and metabolic activity (Dayton, 1972; Jones et al., 1994; Catalán et al., 2021).

The diverse set of sessile filter-feeding species that inhabit the rocky intertidal zones of temperate environments provides an ideal system for testing the effects of dominant and transient species on ecosystem multifunctionality; their feeding activity mediates the coupling and energy transfer between the water column and the benthos (Asmus and Asmus, 1991; Gili and Coma, 1998; Largaespada et al., 2012). For instance, mussels living in temperate intertidal tidepools can directly or indirectly influence microalgae cover, dissolved organic matter, and net primary productivity, along with abiotic environmental variables like light availability and seawater temperature and pH (Fields and Silbiger, 2022). The mid-intertidal zone of wave-exposed rocky shores is characterized by large patches of competitively dominant mussel species (Paine, 1974; Broitman et al., 2001), while the abundance of subdominant and transient species can exhibit broad fluctuations over multiple temporal scales (Underwood and Jernakoff, 1981; Menge et al., 1994; Capelle et al., 2023).

Here, we analyze how the interaction between a dominant and a transient species influences ecosystem multifunctionality. We used the purple mussel *Perumytilus purpuratus* (dominant species; hereafter referred to as *Perumytilus*) and the dwarf mussel *Semimytilus patagonicus* (transient species; hereafter referred to as *Semimytilus*) as biological models. *Perumytilus* inhabits the coast from Ecuador to the Strait of Magellan in Chile, and the southern coast of Argentina (Prado and Castilla, 2006). This species is a strong competitor that numerically dominates the mid intertidal zone in the SE Pacific coast (Fig. 1, Fuentes and Brante, 2014; Caro et al., 2011, Pacheco and Andrade, 2020), forming multi-layered matrices that harbor abundant and species-rich communities (Prado and Castilla, 2006; Valdivia et al., 2014). *Semimytilus* inhabits the Pacific coast from Ecuador to the Gulf of Ancud in Chile (Cárdenas et al., 2008), and exhibits broad seasonal abundance fluctuations (Fig. 1, Navarrete et al., 2002; Belapatiño, 2007). Both

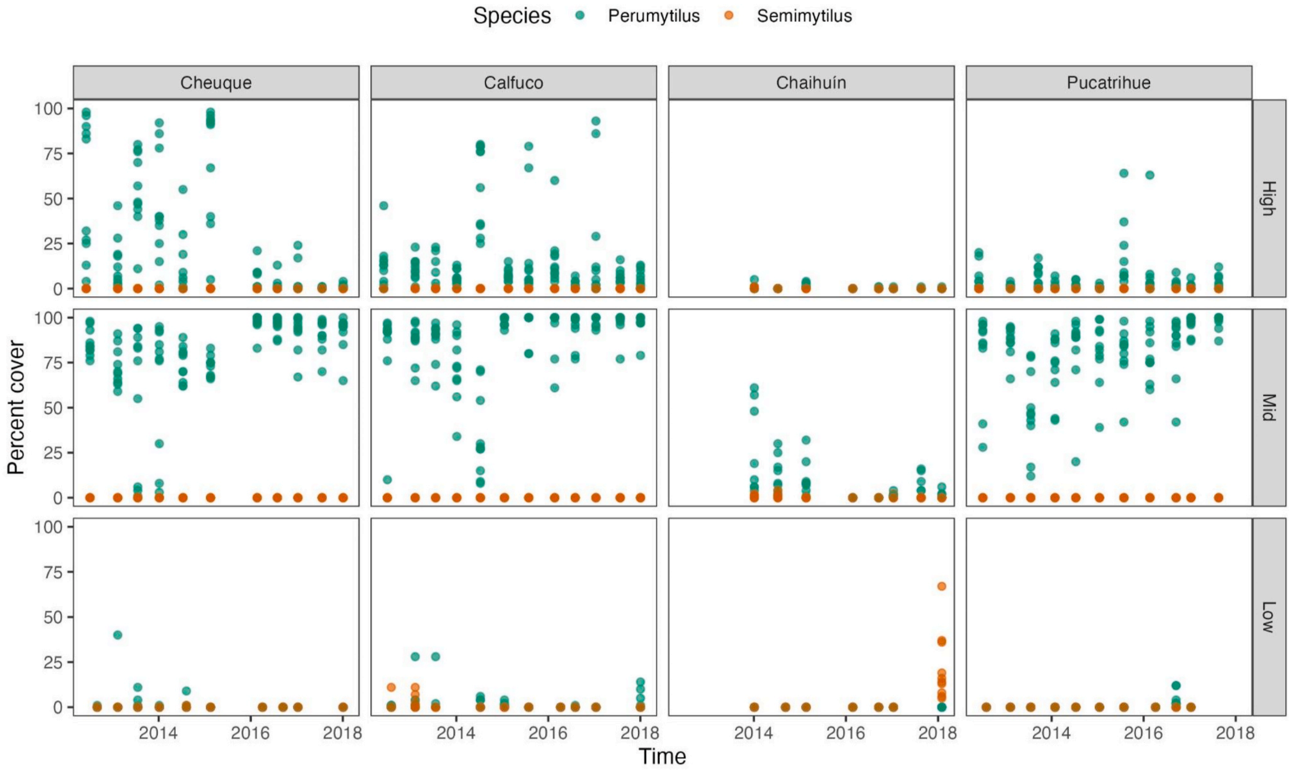

Fig. 1. Percent cover of *Perumytilus purpuratus* and *Semimytilus patagonicus* in high, mid, and low intertidal zones of four sites spanning ca. 200 km of the SE Pacific coast. Species percent covers were measured between June 2012 and January 2018 in Cheuque (39.4° S), Calfuco (39.8° S), Chaihuín (39.9° S), and Pucatrihue (40.5° S). Each dot is a 0.25 m^2 plot.

species have external fertilization and planktotrophic larvae with high dispersal potential (Ramorino and Campos, 1983; Briones et al., 2013). In the intertidal zone, individuals of *Semimytilus* can be observed within *Perumytilus* matrices (Caro and Castilla, 2004; Caro et al., 2008), and these transient mussels can form dense beds in the low intertidal zone where *Perumytilus* is absent (Fuentes and Brante, 2014). In addition, *Semimytilus* exhibits broad fluctuations in recruitment, even surpassing that of *Perumytilus* (Fig. 2). Accordingly, the observed differences in relative abundances between these dominant and transient mussels are not exclusively explained by recruitment failure—competitive asymmetries in resource use, which strongly influences ecosystem functioning, could well account for these differences. In this study, we used a synthetic-assemblage laboratory experiment—in which species identities and relative abundances were manipulated—to assess three competing hypotheses:

H1) Superior competitive abilities allow *Perumytilus* to outperform *Semimytilus* (Fuentes and Brante, 2014), leading to numerical dominance of the former (Fig. 1). If competitive abilities and functioning are positively correlated (Godoy et al., 2020), we predict that the replacement of *Perumytilus* by *Semimytilus* will decrease multiple ecosystem functions.

H2) Alternatively, the ability to recover from rarity, owing to high recruitment rates (Fig. 2), allows *Semimytilus* to invade the mid-intertidal zone under favorable environmental conditions (Pinochet et al., 2018; Skein et al., 2018). Thus, the increase in the relative abundance of this species along with the decrease in *Perumytilus* will boost multiple ecosystem functions.

H3) Owing to niche differences, complementarity effects result in species-rich communities performing better than species-poor communities, independently of species identity (Godoy et al., 2020). Therefore, mixtures of *Perumytilus* and *Semimytilus* in equal proportions should exhibit higher values of multiple ecosystem functions than monocultures of each species in isolation or dominance.

2. Material and methods

2.1. Study species and sampling sites

We measured the relative abundances of adult *Perumytilus* and *Semimytilus* every ca. six months between June 2012 and January 2018 in four rocky intertidal sites along ca. 200 km of the SE Pacific coast (39.4° S - 40.5° S). The four study sites (Cheuque [39.4° S], Calfuco [39.8° S], Chaihuín [39.9° S], and Pucatrihue [40.5° S]) represent wave-exposed shores in a study region characterized by important variation in environmental conditions at the scale of 10s–100s of km (Valdivia et al., 2017). At each site and sampling time, percent cover of *Perumytilus* and *Semimytilus* was quantified in ten 0.25 m^2 plots arranged in 20-m alongshore transects. The transects were deployed on the high, mid, and low intertidal zones. The upper limit of the high-intertidal zone was defined by the presence of the barnacle *Jehlius cirratus*, which is a sessile and perennial species that occurs highest on these shores. For each plot, we used a 50 × 50 cm frame (divided into 25 equal fields) to visually estimate the percent cover (1 % resolution).

In addition, we characterized the recruitment rates of *Perumytilus* and *Semimytilus* between May 2012 and December 2013. We deployed plastic mesh collectors (Tuffy©) in the mid intertidal of three different wave-exposed sites: “Cheuque”, “Calfuco”, and “Pucatrihue”. In each site, five collectors, separated from each other by ca. 10 m, were fastened to the rock with stainless-steel bolts. The replicate collectors were replaced every ca. 30 d.

In spring (October) 2021, we collected individuals of *Perumytilus* and *Semimytilus* from wave-exposed mid-intertidal habitats in Calfuco during low tide. Individuals were acclimatized to laboratory conditions for ten days before starting the manipulative experiment (see next section). Mean ± SD maximum shell length of *Perumytilus* and *Semimytilus* individuals was 1.50 ± 0.079 cm (n = 707) and 1.52 ± 0.082 cm (n = 693), respectively.

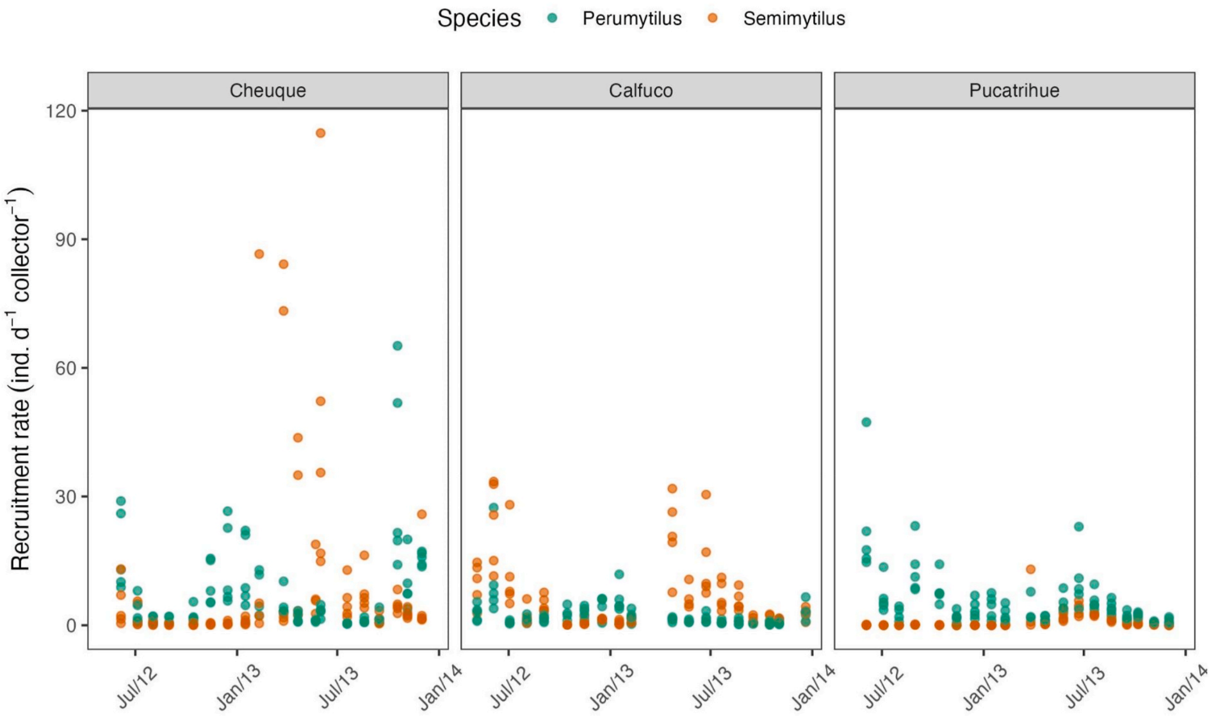

Fig. 2. Recruitment rate of *Perumytilus purpuratus* and *Semimytilus patagonicus* in Cheuque (39.4° S), Calfuco (39.8° S), and Pucatrihue (40.5° S). Five plastic-mesh collectors were deployed in each site and replaced every ca. 30 d between June 2012 and January 2014.

2.2. *Experimental design and set-up in the laboratory*

To test our predictions, we used a synthetic-assemblage laboratory experiment in which species composition is explicitly manipulated to assess the contributions of ecological processes (complementarity and selection effects) to ecosystem functions (Cottingham et al., 2001; Benedetti-Cecchi, 2004). To simulate the gradual replacement of the dominant (*Perumytilus*) by the transient (*Semimytilus*), individuals of both species were assembled along a gradient of proportional abundance of each species, ranging from a monoculture of the dominant to a monoculture of the transient (Fig. S1 in the supplementary material). Thus, the fixed factor "proportion of *Semimytilus*" was established with five levels: 0.0 (100 % *Perumytilus*), 0.2 (80 % *Perumytilus* and 20 % *Semimytilus*), 0.5 (50 % each species), 0.8 (20 % *Perumytilus* and 80 % *Semimytilus*), and 1.0 (100 % *Semimytilus*).

Ten replicates of each treatment were used, which were arranged in a randomized block design (five blocks). Each block consisted of a 50-L tank containing two replicates of each of the five treatments (ten experimental units per block). Each experimental unit consisted of a 0.5-L cylindrical aquarium. Twenty individuals were placed in each experimental unit according to our experimental design (Fig. S1).

The experiment was arranged in a temperature-controlled chamber. Seawater temperature of the experimental units was maintained at 14 °C salinity at 33 PSU and the light cycle at 12 light/12 dark h. All mussels were fed with the microalgae *Isochrysis galbana* at 30,000 cells ml^{-1} and the microalgae concentration was monitored throughout the experiment (Catalán et al., 2021).

2.3. *Ecosystem functions*

We analyzed five response variables and individual contributions to multiple ecosystem functions. Clearance, respiration, total biodeposit, organic biodeposit, and excretion rates were measured. We chose these response variables because, through the filtering of suspended matter, mussels transfer energy and nutrients from the water column to the sediment, bio-depositing organic matter, and excreting nutrients, and thus strengthening the coupling between benthic and pelagic habitats (Vaughn and Hakenkamp, 2001; Vaughn et al., 2004; Howard and Cuffey, 2006; Christian et al., 2008). These energy and nutrient subsidies cascade through the food webs and stimulate algal and macroinvertebrate production (Spooner and Vaughn, 2006; Vaughn et al., 2007, 2008).

Clearance, respiration, and biodeposition rates were measured before the start of the experiment and every seventh day until the completion of five weeks (times 0, 1, 2, 3, 4, and 5). Excretion rates were measured at the end of the experiment (time 5). Due to logistic constraints, we conducted all the physiological measurements on a subset of individuals haphazardly selected in each sampling event. The subset consisted of selecting ten—half of the—individuals from each experimental unit, but always keeping the proportion of each species constant. For example, in an 80 % *Semimytilus* experimental unit originally composed of 16 *Semimytilus* and 4 *Perumytilus*, we selected 8 individuals of the former and 2 of the latter.

2.4. *Clearance rate*

To measure clearance rate in each sampling time, the ten selected mussels of each experimental unit were placed in a 10-L aquarium, containing 1-μm filtered seawater at 14 °C and 32 PSU with UV-irradiated and constant aeration for water movement. Each aquarium had an initial concentration of 30,000 microalgal cells ml^{-1}. Microalgal concentration in the water was measured every hour until completing 3 h. Samples of 50 ml from each aquarium were analyzed with a Beckman Coulter Z2 counter with an aperture of 100 μm (Salas-Yanquin et al., 2018). Clearance rate was quantified as liters of water filtered per mussel tank and hour as $CR = \{V\ [(\ln C_I - \ln C_F) - a]\}/t$ (Coughlan, 1969), where CR is the filtration rate, V corresponds to the volume (L) of each aquarium, C_I is the initial concentration of microalgae, C_F is the final concentration of microalgae, t is the duration of the experiment (3 h), and a represents the average natural variation in microalgal concentration in the control aquaria without mussels: $a = (\ln C_I - \ln C_F)/t$. Clearance rate was calculated hourly and expressed as L per 10 ind.

2.5. *Oxygen consumption rate (respiration rate)*

At each sampling time, the ten selected individuals of each experimental unit were incubated in a sealed glass chamber (500 ml) filled with filtered seawater (0.5 μm, 32 PSU and UV-irradiated). The water was previously saturated by air bubbling, which was stopped 15 min before filling the chambers to facilitate the escape of microbubbles. Subsequently, the filling of the chambers, the incorporation of the mussels into the chambers, and the hermetic closure was carried out underwater to prevent air bubbles from entering the chambers from outside. During oxygen consumption measurements, the respiratory chambers were maintained in a controlled temperature bath (14 °C). Dissolved oxygen concentration was measured with a fiber-optic oxygen transmitter (FIBOX 3, PreSens) and oxygen sensing spots (PreSens GmbH, Regensburg, Germany) placed on the inner wall of the chambers (e.g., Navarro et al., 2016) at the beginning of the experiment and every 1 h until completing three measurements. Respiration rate (R) was calculated as: $R = \{[(C_I - C_F) - C_C]\ V\}/t$, where C_I is initial oxygen concentration in the chamber, C_F is final oxygen concentration in the chamber, C_C is mean value of oxygen concentration in the control chambers without mussels, V is volume (L) of seawater in the chambers (after subtracting mussel volume), t is time between measurements (3 h). Oxygen consumption rate was calculated hourly, and the results were expressed as mg h-^{1} 10 ind.-^{1}.

2.6. *Total and organic biodeposit*

After measuring the clearance rates at each sampling time, the animals were removed, and the bubbling system was stopped to allow for biodeposit decantation. The biodeposits were collected with Pasteur pipettes. Preweighed Whatman GF/C glass filters of 47 mm diameter were mounted on a vacuum pump and loaded with biodeposits. The loaded filters were then washed with distilled water to remove salts from the seawater. Each filter was then folded, labeled, and stored in aluminum envelopes to be dried for 24 h at 60 °C. The mass of each filter was obtained with a Semi Micro Balance A&D GR-202 to obtain the total dry mass of the biodeposits (precision of 0.0001 g). Once the dry mass of the biodeposits was obtained, the filters were burned in the muffle furnace at 500 °C for 3 h to determine the mass of organic and inorganic content. Biodeposit biomass (total) and the biodeposit' organic matter content were analyzed as separate variables. The results were expressed as mg h^{-1} 10 ind.$^{-1}$.

2.7. *Excretion rate*

To measure excretion rate, the ten selected mussels of each experimental unit were incubated for 2 h at 14 °C and 32 PSU in 500 ml filtered seawater (0.5 μm and UV-irradiated). Flasks containing only filtered seawater were used as controls. The principal excretion product, ammonia nitrogen, was determined according to phenol-hypochlorite methods (Solórzano, 1969), which consists of treating the water in an alkaline citrate medium (sodium hypochlorite and phenol) in the presence of sodium nitroprusside (catalyst). The result of the blue sample comes from the indophenol formed by the ammonia, which allows its analysis by spectrophotometry (Parsons et al., 1984). The excretion rate was expressed μg NH_4-N h^{-1} 10 ind.$^{-1}$.

2.8. *Statistical analyses*

We used a principal component analysis (PCA) to combine the five proxies (rates of clearance, respiration, total biodeposit, organic biodeposit, and excretion) for ecosystem functioning into a single multifunction estimator (see pairwise correlations in Fig. S2). The temporal measurements of each response variable were averaged to represent a single value for each experimental unit. Then, the mean values were combined in a PCA based on Pearson product-moment correlations. The first principal component (PC1) explained 99.6% of the overall variance of the dataset. The five variables, except both biodeposit proxies, exhibited positive loadings on PC1 (Table 1). Also, excretion rate had the strongest influence on PC1. Thus, a positive effect of the proportion of the invader on PC1 represented an overall positive effect on multifunctionality.

Mixed-effect general linear modeling (LMM) was used to test the effect of the replacement of *Perumytilus* by *Semimytilus* (i.e. "proportion of *Semimytilus*") on ecosystem multifunctionality. The model included the proportion of *Semimytilus* as a fixed explanatory variable, and PC1 scores as response variable. In addition, the model included the random block as a hierarchical effect on the slope of proportion of *Semimytilus*. Hypothesis 1 should be supported by a negative effect of the proportion of *Semimytilus* on PC1, hypothesis 2 by a positive effect of the proportion of *Semimytilus* on PC1, and hypothesis 3 by a hump-shaped effect of *Semimytilus* proportion on PC1. According to these predictions, the model included both linear and second-order orthogonal polynomials as contrasts for the effect of *Semimytilus* proportion on PC1. Marginal and conditional coefficients of determination were calculated to assess the goodness-of-fit of the fixed effects and the entire model, respectively (R_m^2 and R_c^2, Nakagawa and Schielzeth, 2013). Visual inspection of predicted-vs.-observed quantile plots and predicted-vs.-observed residual plots indicated that a gaussian error structure was appropriate for this model.

We further estimated the difference in mean growth rate between both species. Growth rate (G) of each species was calculated as $G = (L_f - L_i)/L_i$, where L_f and L_i are the final and initial maximum shell length (mm), respectively. Then, we calculated unstandardised effect sizes as between-species mean differences in G, separately for each mixture treatment in which both species were present. Mean effect sizes and confidence intervals were estimated from 1000 boostrapped values. Positive effect sizes indicated that G of *Semimytilus* was greater than that of *Perumytilus*—negative effect sizes would indicate a reversed pattern.

All data manipulation, plotting, and statistical analyses were conducted on R programming environment version 4.3.1. We used the *readxl*, *tidyverse*, *ggpubr,* and *cowplot* R packages to data reading, manipulation and plotting, the *stats* and *DHARMa* R packages for statistical analyses and diagnostics, and *bootES* for effect sizes (Wickham et al., 2019; Wilke, 2020; Wickham and Bryan, 2023; Hartig, 2022).

Table 1
Mussel physiological variables analyzed in this study. The unit, associate ecosystem function, and the loadings first principal component (PC1) of a principal component analysis combining the five proxies are shown. PC1 accounted for 99.6 % of the variation in the dataset. PC1 loading with absolute value $> 1/\sqrt{5}$ is in bold.

Response variable	Unit	Associated ecosystem function	PC1 Loading
Excretion rate	μg ammonium h^{-1} 10 ind.$^{-1}$	Resources for producers	**0.99999**
Clearance rate	L h^{-1} 10 ind.$^{-1}$	Nutrients transport	0.00152
Oxygen consumption rate	mg O_2 L^{-1} 10 ind.$^{-1}$	Carbon transport	0.00003
Total biodeposit rate	mg h^{-1} 10 ind.$^{-1}$	Resources for consumers	0.00000
Organic biodeposit rate	mg h^{-1} 10 ind.$^{-1}$	Resources for consumers	−0.00287

3. Results

Perumytilus and *Semimytilus* exhibited a clear spatial segregation across the intertidal zone of the sampling sites. *Perumytilus* (dominant) had a higher abundance in the high and mid intertidal zones of Cheuque, Calfuco, and Pucatrihue. *Semimytilus* (transient) showed sporadic abundance peaks, especially in the low intertidal of Calfuco and Chaihuín (Fig. 1).

Recruitment rate of *Perumytilus* was on average lower than that of *Semimytilus* (Fig. 2). For instance, recruitment rate of former ranged from 0.1 ind. d^{-1} collector^{-1} (Calfuco) to 65.2 ind. d^{-1} collector^{-1} (Cheuque), and that of the latter ranged from 0 ind. d^{-1} collector^{-1} (Pucatrihue) to 115.0 ind. d^{-1} collector^{-1} (Cheuque). Cheuque showed the maximum mean recruitment rate of both *Perumytilus* and *Semimytilus*, with 7.68 ind. d^{-1} collector^{-1} and 8.74 ind. d^{-1} collector^{-1}, respectively. Recruitment of *Perumytilus* peaked in austral winter (June) in the three sampling sites—additional recruitment events were observed in summer (January) in Cheuque and Calfuco (Fig. 2). *Semimytilus* reached the maximum recruitment rates in autumn (ca. April) and early winter at Cheuque, and in winter at Calfuco and Pucatrihue (Fig. 2).

In the synthetic-assemblage experiment, the increasing relative abundance of the transient had a positive, linear effect on PC1 of the five measured functions (Fig. 3, slope = 0.12 [standard error = 0.03], $P < 0.001$). Furthermore, we did not observe a statistically significant fit of the second-order polynomial contrast to PC1 ($P = 0.78$). The proportion of *Semimytilus* accounted for 19 % of the variation in PC1 ($R^2m = 0.185$), and the entire model, including also the effects of blocks, accounted for 42 % of the variation in PC1 ($R^2c = 0.423$). Since most measured functions positively influenced the PC1 (see method section and Table 1), this positive effect of increasing *Semimytilus* relative abundance represented an overall positive effect on multifunctionality. This overall pattern was mostly influenced by the patterns of excretion and oxygen consumption rates (Fig. S3).

Growth rates tended to be greater for *Semimytilus* than *Perumytilus*, as effect sizes tended to increase with the abundance increase of the former. Mean effect size (and confidence intervals) for the 0.2, 0.5, and 0.8 *Semimytilus*-proportion treatments were 0.002 mm 5 w^{-1} (week) (−0.022, 0.028), 0.012 mm 5 w^{-1} (−0.007, 0.029), and 0.010 mm 5 w^{-1} (−0.009, 0.033), respectively.

4. Discussion

Here, we analyzed the relationship of species dominance and identity with ecosystem multifunctionality in a rocky-intertidal model system. An observational study showed that the purple mussel *Perumytilus purpuratus* (dominant; hereafter referred to as *Perumytilus*) exhibited a clear pattern of numerical dominance over *Semimytilus patagonicus* (transient; hereafter referred to as *Semimytilus*) in the study sites. However, recruitment rates of *Semimytilus* surpassed those of *Perumytilus.* Then, laboratory experiments demonstrated that the gradual replacement of the dominant by the transient linearly increased multifunctionality, particularly the functions of excretion and oxygen consumption rates. High recruitment rates and resource use may confer *Semimytilus* the ability to recover from rarity and become a dominant species in scenarios where biotic and abiotic environmental conditions are more favorable. Overall, our study provides empirical evidence of the key role of transient species in the performance of multiple ecosystem functions.

Our results agree with previous studies supporting the prevalent role of species identity in mediating the relationship between biodiversity and ecosystem functioning. For example, Cardinale (2011) demonstrated that, under homogeneous environmental conditions, nutrient uptake rate of microalgal species-rich polycultures was lower than that of the most efficient species grown in monoculture (i.e., identity effects). In a homogeneous environment, thus, functioning is controlled by single species rather than several species through complementarity effects

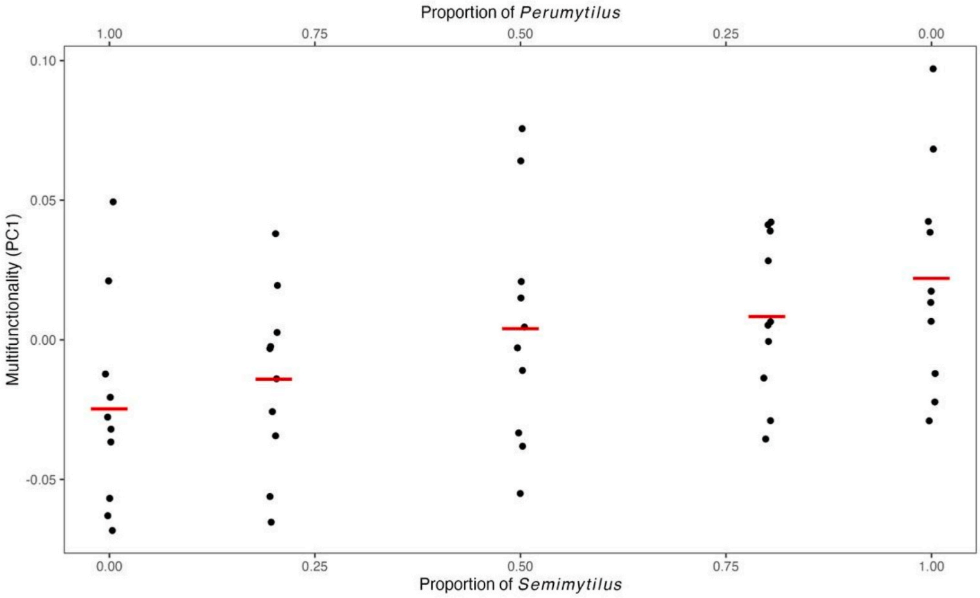

Fig. 3. Effect of increasing proportional abundance of *Semimytilus* on multifunctionality. Each dot represents an experimental unit composed of 10 mussels and the red lines indicate the mean of each group. Multifunctionality was calculated as the first principal component (PC1) of five mussel physiological proxies measured at the experimental unit scale (Table 1).

(Cardinale, 2011). Perhaps, the lack of environmental heterogeneity in our experiment could have favored identity over complementarity effects. Nevertheless, recent syntheses suggest that identity effects can be more important than complementarity effects for the functioning of both terrestrial (Ali, 2023) and marine (Gamfeldt et al., 2015) ecosystems.

Identity effects can also contribute to biodiversity-ecosystem functioning relationships through selective processes such as interspecific competition, which causes dominance of species with stronger effects on ecosystem functioning (i.e., “selection effects”; Loreau and Hector, 2001). This is because functional traits can drive competitive interactions between species (Fox, 2003; Kunstler et al., 2016). Our results evidenced that, under laboratory conditions, a transient species was functionally superior than a dominant species. This, in turn, could lead to competitive exclusion provided the appropriate biotic and abiotic environmental conditions. Indeed, propagule pressure and resource use favoring *Semimytilus* can allow this species to become an invasive species elsewhere. In South Africa, for instance, *Semimytilus* is a numerically dominant invasive species, which currently covers about 500 km of the coastline and forms dense matrices that constitute a significant proportion of the total intertidal biomass (Robinson et al., 2005; Laird and Griffiths, 2008; Mead et al., 2011). Along with competitively excluding other primary substratum holders (e.g., *Aulacomya ater* and *Choromytilus meridionalis*), generating novel biogenic habitats, and supporting emerging economic activities (Robinson et al., 2007; de Greef et al., 2013), *Semimytilus* could well have a significant impact on multiple ecosystem functions in the invaded habitats, as shown in our experiments.

If our experiment suggests that *Semimytilus* would eventually outcompete *Perumytilus*, why is it not as abundant as the latter along the SE Pacific coast of southern Chile? Ruling out dispersal limitations (Fig. 2), an answer to this question would be that the individuals of *Semimytilus* were collected from a locality with suboptimal environmental conditions. Field-based experimental evidence from 37° S (Concepción), ca. 500 km to the north of our study site (39.8° S), suggests that *Semimytilus* can outperform *Perumytilus* in terms of clearance rates when suspended sand is present, and that the former can numerically dominate the mid-intertidal primary substratum during early succession and the low intertidal during mid-late succession (Fuentes and Brante, 2014; Pinochet et al., 2018). A non-exclusive answer refers to differential environmental tolerances: in the absence of interspecific competition, growth rates of *Perumytilus* are higher in the mid-intertidal, while those of *Semimytilus* are higher in the low intertidal and in presence of suspended sand (Pinochet et al., 2018). Finally, apparent competition (Holt and Bonsall, 2017) could well be operating in this system. *Acanthina monodon,* a prominent muricid predator, largely prefers *Semimytilus* over *Perumytilus* as prey, likely due to differences in shell thickness, handling time, consumption rates, and thus energetic profitability (Soto et al., 2004; Averbuj et al., 2021). Therefore, a combination of physiological performance (shown in this study), environmental tolerances, and predation would allow for coexistence between both species at the whole-intertidal spatial scale.

5. Conclusion

Using a model competitive system, this study highlights the effect of transient species on several ecosystem functions. Although environmental variability was restricted in this experiment, our results are well in line with previous evidence supporting the role of species identity in maintaining ecosystem functioning and adds the novel aspect of multifunctionality, which is not well understood in marine ecosystems particularly. Understanding these dynamics is crucial for effective conservation and management of coastal ecosystems, especially in the context of the current biodiversity loss and biological invasions.

CRediT authorship contribution statement

Claudia Betancourtt: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Alexis M. Catalán:** Methodology. **Diego F. Morales-Torres:** Writing – review & editing, Methodology. **Daniela N. Lopez:** Writing – review & editing, Methodology. **Valentina Escares-Aguilera:** Writing – review & editing, Methodology. **Luis P. Salas-Yanquin:** Writing – review & editing, Methodology. **Joseline A. Büchner-Miranda:** Writing – review & editing, Methodology. **Oscar R. Chaparro:** Writing – review & editing, Conceptualization. **Jorge Nimptsch:** Conceptualization. **Bernardo R. Broitman:** Writing – review & editing, Visualization, Conceptualization.

Nelson Valdivia: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing finantial interest or personal relationship that could hace appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

We thank all members of the Lafkenche-lab working group at Universidad Austral de Chile for their kind support during field and laboratory work. This study was financially supported by grant #1230286 from the Fondo Nacional de Desarrollo Científico y Tecnológico (FONDECYT) awarded by the Agencia Nacional de Investigación y Desarrollo (ANID) to NV and by a grant (#15150003) from the Centro FONDAP Investigación en Dinámica de Ecosistemas de Altas Latitudes (IDEAL) awarded to NV. CB was supported by ANID doctoral scholarship #21201126. Luigi Musco and two anonymous reviewers provided important criticism that improved a previous version of this paper. This study is part of the PhD dissertation of CB, supervised by NV and registered at the Universidad Austral de Chile. The authors have no conflict of interest to declare.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2024.106422.

References

Adler, P.B., Dalgleish, H.J., Ellner, S.P., 2012. Forecasting plant community impacts of climate variability and change: when do competitive interactions matter? J. Ecol. 100 (2), 478–487.

Ali, A., 2023. Biodiversity–ecosystem functioning research: brief history, major trends and perspectives. Biol. Conserv. 285, 110210.

Asmus, R.M., Asmus, H., 1991. Mussel beds: limiting or promoting phytoplankton? J. Exp. Mar. Biol. Ecol. 148 (2), 215–232.

Averbuj, A., Büchner-Miranda, J.A., Salas-Yanquin, L.P., Navarro, J.M., Pardo, L.M., Matos, A.S., Pechenik, J.A., Chaparro, O.R., 2021. Energetic trade-offs: implications for selections between two bivalves prey species by a carnivorous muricid gastropod. PLoS One 16 (4), e0250937.

Beauchard, O., Thompson, M.S.A., Ellingsen, K.E., Piet, G., Laffargue, P., Soetaert, K., 2023. Assessing sea floor functional biodiversity and vulnerability. Marine ecology Progress Series 708, 21–43.

Belapatiño, A.O., 2007. Variabilidad del asentamiento larval de mitílidos en bahía independencia, Pisco-Perú, durante el periodo. 1996–2003. Biology Degree Thesis. Universidad Nacional Mayor de San Marcos. Universidad del Perú, Perú, p. 67.

Benedetti-Cecchi, L., 2004. Increasing accuracy of causal inference in experimental analyses of biodiversity. Funct. Ecol. 18, 761–768.

Bracken, M.E., Low, N.H., 2012. Realistic losses of rare species disproportionately impact higher trophic levels. Ecol. Lett. 15 (5), 461–467.

Briones, C., Presa, P., Pérez, M., Pita, A., Guiñez, R., 2013. Genetic connectivity of the ecosystem engineer *Perumytilus purpuratus* north to the 32 S southeast Pacific ecological discontinuity. Marine Biology 160, 3143–3156.

Broitman, B.R., Navarrete, S.A., Smith, F., Gaines, S.D., 2001. Geographic variation of southeastern Pacific intertidal communities. Mar. Ecol. Prog. Ser. 224, 21–34.

Byrnes, J.E., Gamfeldt, L., Isbell, F., Lefcheck, J.S., Griffin, J.N., Hector, A., Cardinale, B. J., Hooper, D.U., Dee, L.E., Emmett Duffy, J., 2014. Investigating the relationship between biodiversity and ecosystem multifunctionality: challenges and solutions. Methods Ecol. Evol. 5 (2), 111–124.

Capelle, J.J., Hartog, E., Wilkes, T., Bouma, T.J., 2023. Seasonal variation in the balance and strength of cooperative and competitive behavior in patches of blue mussels. PLoS One 18 (10), e0293142.

Cárdenas, J., Aldea, C., Valdovinos, C., 2008. Chilean marine mollusca of northern patagonia collected during the CIMAR-10 fjords cruise. Gayana 72 (2), 202–240.

Cardinale, B.J., 2011. Biodiversity improves water quality through niche partitioning. Nature 472 (7341), 86–89.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Dayli, G.C., Loreu, M., Grace, J.B., Lariguaderie, A., Srivastava, D.S., Naeem, S., 2012. Biodiversity loss and its impact on humanity. Nature 486 (7401), 59–67.

Caro, A.U., Escobar, J., Bozinovic, F., Navarrete, S.A., Castilla, J.C., 2008. Phenotypic variability in byssus thread production of intertidal mussels induced by predators with different feeding strategies. Mar. Ecol. Prog. Ser. 372, 127–134.

Caro, A.U., Castilla, J.C., 2004. Predator-inducible defenses and local intrapopulation variability of the intertidal mussel *Semimytilus algosus* in central Chile. Marine Ecolog -Progress Series 276, 115–123.

Caro, A.U., Guiñez, R., Ortiz, V., Castilla, J.C., 2011. Competition between a native mussel and a non-indigenous invader for primary space on intertidal rocky shores in Chile. Mar. Ecol. Prog. Ser. 428, 177–185. https://doi.org/10.3354/meps09069.

Catalán, A.M., Büchner-Miranda, J., Riedemann, B., Chaparro, O.R., Valdivia, N., Scrosati, R.A., 2021. Community-wide consequences of nonconsumptive predator effects on a foundation species. J. Anim. Ecol. 90 (5), 1307–1316.

Christian, A.D., Crump, B.G., Berg, D.J., 2008. Nutrient release and ecological stoichiometry of freshwater mussels (Mollusca: unionidae) in 2 small, regionally distinct streams. J. North Am. Benthol. Soc. 27, 440–450.

Cottingham, K.L., Brown, B.L., Lennon, J.T., 2001. Biodiversity may regulate the temporal variability of ecological systems. Ecol. Lett. 4 (1), 72–85.

Dangles, O., Malmqvist, B., 2004. Species richness–decomposition relationships depend on species dominance. Ecol. Lett. 7 (5), 395–402.

Dayton, P.K., 1972. Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. In: Parker, B.C. (Ed.), Proceedings of the Colloquium on Conservation Problems in Antarctica. Blacksburg, VA. Allen Press, Lawrence, KS, pp. 81–96, 10—12 Septem- ber 1971.

De Greef, K., Griffiths, C.L., Zeeman, Z., 2013. Deja vu? A second mytilid mussel, *Semimytilus algosus*, invades South Africa's west coast. Afr. J. Mar. Sci. 35 (3), 307–313.

Fields, J.B., Silbiger, N.J., 2022. Foundation species loss alters multiple ecosystem functions within temperate tidepool communities. Mar. Ecol. Prog. Ser. 683, 1–19.

Fox, J.W., 2003. The long-term relationship between plant diversity and total plant biomass depends on the mechanism maintaining diversity. Oikos 102 (3), 630–640.

Fuentes, K., Brante, A., 2014. Megadisturbances and ecological recovery in the intertidal zone: the role of interspecific competition between bioengineer mussel species. Mar. Ecol. Prog. Ser. 515, 161–172.

Gamfeldt, L., Lefcheck, J.S., Byrnes, J.E.K., Cardinale, B.J., Duffy, J.E., Griffin, J.N., 2015. Marine biodiversity and ecosystem functioning: what's known and what's next? Oikos 124 (3), 252–265.

Gili, J.M., Coma, R., 1998. Benthic suspension feeders: their paramount role in littoral marine food webs. Trends Ecol. Evol. 13 (8), 316–321.

Godoy, O., Gómez-Aparicio, L., Matías, L., Pérez-Ramos, I.M., Allan, E., 2020. An excess of niche differences maximizes ecosystem functioning. Nat. Commun. 11 (1), 4180.

Grime, J.P., 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. J. Ecol. 86 (6), 902–910.

Gouhier, T.C., Menge, B.A., Hacker, S.D., 2011. Recruitment facilitation can promote coexistence and buffer population growth in metacommunities. Ecol. Lett. 14 (12), 1201–1210.

Harris, R.M., Beaumont, L.J., Vance, T.R., Tozer, C.R., Remenyi, T.A., Perkins-Kirkpatrick, S.E., Mitchell, P.J., Nicotra, A.B., McGregor, S., Andrew, N.R., Letnic, M., Kearney, M.R., Wernberg, T., Hurley, L.B., Chambers, L.E., Fletcher, M.S., Keatley, M.R., Woodward, C.A., Williamson, G., Duke, D.M., Bowman, D.M.J.S., 2018. Biological responses to the press and pulse of climate trends and extreme events. Nat. Clim. Change 8 (7), 579–587.

Hartig, F., 2022. DHARMa: Residual Diagnostics for Hierarchical (Multi-level/mixed) Regression Models. R package version 0.4.5.

Hector, A., Bagchi, R., 2007. Biodiversity and ecosystem multifunctionality. Nature 448 (7150), 188–190.

Holt, R.D., Bonsall, M.B., 2017. Apparent competition. Annual Review of Ecology, Evolution, and Systematics 48, 447–471.

Hooper, D.U., Chapin III, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, A.J., Symstad, J., Vandermeer, D.A., Wardle, D.A., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol. Monogr. 75 (1), 3–35.

Howard, J.K., Cuffey, K.M., 2006. The functional role of native freshwater mussels in the fluvial benthic environment. Freshw. Biol. 51, 460–474.

Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. Oikos 373–386.

Kunstler, G., Falster, D., Coomes, D.A., Hui, F., Kooyman, R.M., Laughlin, D.C., Poorter, L., Vanderwel, M., Vieilledent, G., Wright, S.J., Aiba, M., Baraloto, C., Caspersen, J., Cornelissen, J.H.C., Gourlet-Fleury, S., Hanewinkel, M., Herault, B., Kattge, J., Kurokawa, H., Oanda, Y., Peñuelas, J., Poorter, H., Uriarte, M., Richardson, S., Ruiz-Benito, P., Sun, I., Stahl, G., Swenson, N.G., Thompson, J., Westerlund, B., Wirth, C., Zavala, M.A., Zeng, H., Zimmerman, J.K., Zimmermann, N.E., Westoby, M., 2016. Plant functional traits have globally consistent effects on competition. Nature 529 (7585), 204–207.

Laird, M., Griffiths, C.L., 2008. Present distribution and abundance of the introduced barnacle *Balanus glandula* in South Africa. Afr. J. Mar. Sci. 30, 93–100.

Largaespada, C., Guichard, F., Archambault, P., 2012. Meta-ecosystem engineering: nutrient fluxes reveal intraspecific and interspecific feedbacks in fragmented mussel beds. Ecology 93 (2), 324–333.

Loreau, M., Hector, A., 2001. Partitioning selection and complementarity in biodiversity experiments. Nature 412, 72–76.

Manning, P., Van Der Plas, F., Soliveres, S., Allan, E., Maestre, F.T., Mace, G., Whittingham, M.J., Fischer, M., 2018. Redefining ecosystem multifunctionality. Nature Ecology & Evolution 2 (3), 427–436.

Magurran, A.E., Henderson, P.A., 2003. Explaining the excess of rare species in natural species abundance distributions. Nature 422, 714–716.

Matías, L., Godoy, O., Gómez-Aparicio, L., Pérez-Ramos, I.M., 2018. An experimental extreme drought reduces the likelihood of species to coexist despite increasing intransitivity in competitive networks. J. Ecol. 106 (3), 826–837.

Mead, A., Carlton, J.T., Griffiths, C.L., Rius, M., 2011. Revealing the scale of marine bioinvasions in developing regions: a South African re-assessment. Biol. Invasions 13, 1991–2008.

Menge, B.A., Berlow, E.L., Blanchette, C.A., Navarrete, S.A., Yamada, S.B., 1994. The Keystone species concept: variation in interaction strength in a rocky intertidal habitat. Ecol. Monogr. 64, 249–286.

Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods Ecol. Evol. 4 (2), 133–142.

Navarrete, S.A., Broitman, B., Wieters, E.A., Finke, G.R., Venegas, R.M., Sotomayor, A., 2002. Recruitment of intertidal invertebrates in the southeast pacific: interannual variability and the 1997– 1998 el niño. Limnol. Oceanogr. 47, 791–802.

Navarro, J.M., Labraña, W., Chaparro, O.R., Cisternas, B., Ortíz, A., 2016. Physiological constraints in juvenile *Ostrea chilensis* fed the toxic dinoflagellate *Alexandrium catenella*. Estuar. Coast 39, 1133–1141.

Pacheco, A.S., Andrade, D.G., 2020. Decline of a non-native ecosystem engineer and its replacement with a native on rocky shores: effects on the diversity and structure of benthic communities. Mar. Biodivers. 50 (1), 2.

Parsons, T.R., Maita, Y., Lalli, C.M., 1984. A Manual of Chemical and Biological Methods for Sea Water Analysis. Pergamon. Press, p. 173.

Pinochet, J., Dominguez, J., Neira, E., Rojas, C., Acuna, E., Cancino, J.M., Brante, A., 2018. Tidal height and sand as potential drivers of the ecological interaction of the two intertidal mussels *Perumytilus purpuratus* and *Semimytilus algosus*. Marine Ecology-an Evolutionary Perspective 39, e12503.

Prado, L., Castilla, J.C., 2006. The bioengineer *Perumytilus purpuratus* (Mollusca: Bivalvia) in central Chile: biodiversity, habitat structural complexity, and environmental heterogeneity. J. Mar. Biol. Assoc. U. K. 86 (2), 417–421.

Ramorino, L., Campos, B., 1983. Larvas y postlarvas de Mytilidae de Chile (Molluscs: Bivalvia). Rev. Biol. Mar 19, 143–192.

Robinson, T.B., Branch, G.M., Griffiths, C.L., Govender, A., Hockey, P.A.R., 2007. Changes in South African rocky invertebrate community structure associated with the invasion of the mussel *Mytilus galloprovincialis*. Mar. Ecol. Prog. Ser. 340, 163–171.

Robinson, T.B., Griffiths, C.L., McQuaid, C., Rius, M., 2005. Marine alien species of South Africa—status and impacts. Afr. J. Mar. Sci. 27, 297–306.

Salas-Yanquin, L.P., Navarro, J.M., Pechenik, J.A., Montory, J.A., Chaparro, O.R., 2018. Volcanic ash in the water column: physiological impact on the suspension-feeding bivalve *Mytilus chilensis*. Mar. Pollut. Bull. 127, 342–351.

Skein, L., Alexander, M., Robinson, T., 2018. Contrasting invasion patterns in intertidal and subtidal mussel communities. Afr. Zool. 53 (1), 47–52.

Smith, M.D., Knapp, A.K., 2003. Dominant species maintain ecosystem function with non-random species loss. Ecol. Lett. 6 (6), 509–517.

Solórzano, L., 1969. Determination of ammonia in natural waters by the phenolhypochlorite metod. Limnol. Oceanogr. 14 (5), 799–801.

Soto, R.E., Castilla, J.C., Bozinovic, F., 2004. Conducta de forrajeo del gastrópodo *Acanthina monodon* Pallas, 1774 (Gastropoda: muricidae) en el intermareal rocoso de Chile central. Rev. Chil. Hist. Nat. 77 (1), 157–175.

Spooner, D.E., Vaughn, C.C., 2006. Context-dependent effects of freshwater mussels on the benthic community. Freshw. Biol. 51, 1016–1024.

Stachowicz, J.J., Bruno, J.F., Duffy, J.E., 2007. Understanding the effects of marine biodiversity on communities and ecosystems. Annual Review Ecology, Evolution and Systematics 38, 739–766.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., Siemann, E., 1997. The influence of functional diversity and composition on ecosystem processes. Science 277 (5330), 1300–1302.

Underwood, A.J., Jernakoff, P., 1981. Effects of interactions between algae and grazing gastropods on the structure of a low-shore intertidal algal community. Oecologia 48, 221–233.

Valdivia, N., de la Haye, K.L., Jenkins, S.R., Kimmance, S.A., Thompson, R.C., Molis, M., 2009. Functional composition, but not richness, affected the performance of sessile suspension-feeding assemblages. J. Sea Res. 61 (4), 216–221.

Valdivia, N., Buschbaum, C., Thiel, M., 2014. Succession in intertidal mussel bed assemblages on different shores: species mobility matters. Mar. Ecol. Prog. Ser. 497, 131–142.

Valdivia, N., Segovia-Rivera, V., Fica, E., Bonta, C.C., Aguilera, M.A., Broitman, B.R., 2017. Context-dependent functional dispersion across similar ranges of trait space covered by intertidal rocky shore communities. Ecol. Evol. 7 (6), 1882–1891.

Valone, T.J., Balaban-Feld, J., 2018. Impact of exotic invasion on the temporal stability of natural annual plant communities. Oikos 127 (1), 56–62.

Vaughn, C.C., Gido, K.B., Spooner, D.E., 2004. Ecosystem processes performed by unionid mussels in stream mesocosms: species roles and effects of abundance. Hydrobiologia 527, 35–47.

Vaughn, C.C., Hakenkamp, C.C., 2001. The functional role of burrowing bivalves in freshwater ecosystems. Freshw. Biol. 46, 1431–1446.

Vaughn, C.C., Nichols, S.J., Spooner, D.E., 2008. Community and foodweb ecology of freshwater mussels. J. North Am. Benthol. Soc. 27, 409–423.

Vaughn, C.C., Spooner, D.E., Galbraith, H.S., 2007. Context-dependent species identity effects within a functional group of filter-feeding bivalves. Ecology 88, 1654–1662.

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D.A., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Khun, M., Lin-Pedersen, T., Miller, E., Milton-Bache, S., Müller, K., Ooms, J., Robinson, D., Paige-Seidel, D., Spinu, V., Takahashi, K., Vaughan, D., Wilke, C., Woo, K., Yutani, H., 2019. Welcome to the tidyverse. J. Open Source Softw. 4 (43), 1686.

Wickham, H., Bryan, J., 2023. R Packages. O'Reilly Media, Inc.

Wilke, C.O., 2020. Cowplot: Streamlined Plot Theme and Plot Annotations for 'ggplot2'. R package version 1.0.0.

Winfree, R., W. Fox, J., Williams, N.M., Reilly, J.R., Cariveau, D.P., 2015. Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. Ecol. Lett. 18 (7), 626–635.