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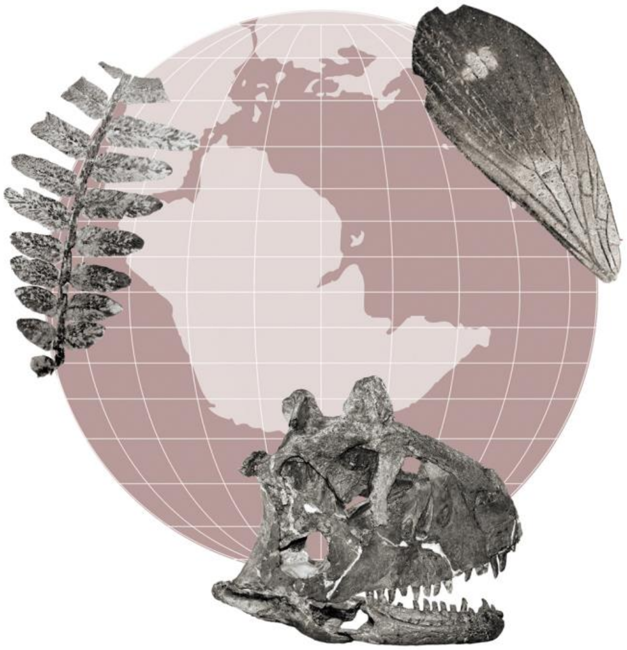

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# Conservation paleobiology of intertidal molluscs: detecting human impacts in San Antonio Bay, Northern Patagonia

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Running header: ARCHUBY and ROCHE: Conservation paleobiology in patagonian marine intertidal

Short Description: Mollusc biodiversity variation along natural and anthropogenic environmental gradients is evaluated through the study of death assemblages

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**Abstract.** This study evaluates the usefulness of molluscan dead shell assemblages accumulated in the intertidal zone as ecological indicators in San Antonio Bay, located in northern San Matías Gulf, Argentine Patagonia. Based on quantitative sampling and comprehensive multivariate analyses, changes in molluscan biodiversity were assessed in relation to natural (subaerial exposure and hypersalinity) and anthropogenic (eutrophication) environmental gradients. In addition, a taphonomic fidelity assessment was performed using a presence/absence matrix. Two intertidal channels were studied: one affected by anthropogenic eutrophication and another with minimal human influence. The results show that species abundances of death assemblages accurately reflect environmental gradients, particularly the stress derived from distance to the bay, which determines variations in aerial exposure, salinity, and temperature. More distal communities exhibit lower species richness and dominance of *Heleobia australis*, whereas proximal ones are more diverse and even. Differences between channels are significant but moderate, with *Agathistoma patagonicum*, a well-known intertidal to shallow subtidal herbivore being abundant where anthropogenic eutrophication occurs. Beta diversity analysis suggests that death assemblages retain information on pre- and post-impact community configurations, from the unexpectedly high contribution of a proximal site in the eutrophicated channel, and a higher influence of turnover in the same channel, in comparison with the non-impacted, in which a nestedness pattern seems to explain the reduction of alpha diversity upstream. Based on a presence/absence comparison, death assemblages differ from the living community, although both follow the environmental gradients. Molluscan death assemblages thus provide effective, inexpensive, and non-invasive tools for conservation paleobiology, enabling reconstruction of the recent history of benthic ecosystems and early detection of anthropogenic alterations, thereby offering key information for designing conservation strategies in Patagonian marine environments.

**Keywords**. Molluscan shell assemblages. Taphonomic fidelity. Environmental gradients. Eutrophication. Benthic biodiversity. Argentine Patagonia. Conservation paleobiology. Multivariate analysis.

**Resumen**. *Paleobiología de la conservación con moluscos intermareales: detección de impactos antrópicos en la Bahía de San Antonio, Northern Patagonia*.Este estudio evalúa la utilidad de los ensambles de conchas de moluscos acumulados en la franja intermareal como indicadores ecológicos en la Bahía de San Antonio, ubicada en el norte del golfo San Matías, Patagonia argentina. A partir de muestreos cuantitativos y análisis multivariados exhaustivos, se evaluaron los cambios de la biodiversidad de moluscos en función de gradientes ambientales naturales (exposición subaérea e hipersalinidad) y antropogénicos (eutrofización). Además, se realizó una evaluación de la fidelidad tafonómica utilizando una matriz de presencia/ausencia. Se estudiaron dos canales intermareales: uno afectado por eutrofización antropogénica y otro con influencia humana mínima. Los resultados muestran que las abundancias de especies de los ensambles de muerte reflejan con precisión los gradientes ambientales, particularmente el estrés generado por la distancia a la bahía, que determina diferencias en exposición aérea, salinidad y temperatura. Las comunidades más distales exhiben menor riqueza de especies y dominancia de *Heleobia australis*, mientras que las proximales son más diversas y equitativas**.** Las diferencias entre los canales son significativas pero moderadas, con *Agathistoma patagonicum*, un conocido herbívoro intermareal a submareal somero, siendo abundante donde ocurre la eutrofización antropogénica. El análisis de la diversidad beta sugiere que los ensambles de muerte retienen información sobre configuraciones de las comunidades pre y post-impacto, que se deduce de la inesperadamente alta contribución de un sitio proximal en el canal eutrofizado (PV), y mayor influencia de turnover en el mismo canal comparado con el no impactado, donde el patrón de anidamiento explica la reducción de la diversidad alfa aguas arriba. Molluscan death ensamblajes así proporcionan herramientas efectivas, económicas y no invasivas para la paleobiología de la conservación, habilitando reconstrucción de la historia reciente de ecosistemas bentónicos y detección de alteraciones antropogénicas, ofreciendo así información clave para diseñar estrategias de conservación en los ambientes marinos patagónicos.

**Palabras clave**. Ensambles de conchas de moluscos. Fidelidad tafonómica. Gradientes ambientales. Eutrofización. Biodiversidad bentónica. Patagonia argentina. Paleobiología de la conservación. Análisis multivariado.

## Introduction

The current biodiversity crisis—driven by climate change, habitat destruction, overexploitation, invasive species, and pollution (Conservation Paleobiology Workshop, 2012; Dietl et al., 2015; López-Gappa, 2022a; Narvarte et al., 2022)—demands comprehensive biotic inventories and long-term monitoring. However, surveys of living communities, which often rely on space-for-time substitution as baselines (Avaca et al., 2008; Güller & Zelaya, 2017; Roche et al., 2020), capture only recent ecosystem states and preserve little historical information about temporal dynamics. While modern impacts have been documented for the last decades to a few centuries, long-term biodiversity records remain scarce, and past disturbances are difficult to quantify (Halpern et al., 2008). The geohistorical record is crucial for reconstructing ecosystem changes, identifying past human impacts, and informing conservation plans. For example, Tomašových & Kidwell (2017) demonstrated how 19th-century livestock expansion drove siltation and local extinction of shell-gravel ecosystems off California.

The marine benthic ecosystems of the ca. 3,000 km of Patagonian Atlantic coast are little known. Exhaustive surveys in a supposedly pristine or little impacted region (Cuevas et al., 2006; Güller & Zelaya, 2017; Olivier et al., 1966; but see Orensanz et al., 2002; Rechimont et al., 2013), are scarce. In any case, available species lists are relatively recent and include effects of early human occupations as well as of modern human impacts and global warming. The shifting baseline syndrome  (Pauly, 1995; Tyler & Schneider, 2018) is a common problem for almost any conservation plan: the target ecosystem changed recently and is in a trend of change. Conservation plans need to disentangle the original composition of communities from human effects.

Originally concerned in evaluating the fidelity of fossil assemblages to former communities, and how these entities vary according to paleoenvironments, actualistic taphonomy developments found that: 1. Assemblages of dead remains record the composition of living communities with acceptable fidelity more often than not. 2. These assemblages are an average of the successive compositions (Kidwell, 2001; Kidwell & Flessa, 1996), usually weighted by the more recent (Kowalewski, 2009; Archuby et al., 2023) . Some consequences of these findings allow us to infer that death assemblages are *a priori*, proper proxies of the living communities they come from, and thus can be good surrogates of baseline communities.

### *Mollusc death shells assemblages as proxies of ecological information.*

Even when in the cases in which the species compositions of the death assemblages show high fidelity to the communities from which they originate, these two synecological entities are not identical. Death assemblages are time-averaged , *i.e*, an admixture of specimens found together that did not live at the same time. This distortion becomes a methodological advantage as it incorporates information on previous configurations of the communities, eventually including those prior to anthropogenic impacts (Archuby et al., 2015; Archuby & Roche, 2019; Kidwell, 2001; Tomašových & Kidwell, 2009a). A related advantage of temporal averaging of death assemblages is that they are less affected by short-term drastic fluctuations in the composition of living communities. For example consider as an example of this is the local extinction of the yellow clam (*Amarilladesma mactroides*) on the coasts of Brazil, Uruguay and Argentina between 1993 and 1995, which eliminated the most abundant species in soft-bottom communities in just a few weeks (Dadón, 2005; Fiori & Cazzaniga, 1999; Vázquez et al., 2016). The populations recovered quickly, but without reaching the pre-mortality densities. The species composition of these communities varied drastically from the configuration before the event, to the immediate aftermath, and to the post-recovery phase, so that samples at any of these three stages would have yielded different results from one other. The composition of the death shell assemblages is refractory to such changes, which is valuable for studying natural population expansions and contractions of benthic species. Interestingly, cases in which great differences are found between dead-shell assemblages and the living assemblage allow hypothesizing the presence of recent, strong changes (such as anthropogenic impact; Kidwell, 2007a) that otherwise would not be detectable in the absence of systematic long-term sampling of living communities(e.g., Dietl & Flessa, 2011; Kidwell & Tomašových, 2013; Martinelli et al., 2013; Tomašových & Kidwell, 2017).

The correspondence between death assemblages and the living communities is a principle that allows the use of the former as tools to approximate biodiversity and composition, and their changes over time. This fact is based on two concepts. The first states that certain groups of species in marine habitats, such as polychaetes, crustaceans and molluscs among others, can be confidently taken as surrogates of the communities they come from (Magierowski & Johnson, 2006; Mellin et al., 2011; Terlizzi et al., 2005; Tyler & Kowalewski, 2017, 2025; Warwick & Light, 2002). The second suggests that molluscs, in addition to being appropriate surrogates of marine benthic communities, develop good levels of taphonomic fidelity, *i.e.*, preserve significant information on biodiversity and its changes following environmental gradients (Archuby et al., 2015; Kidwell, 2007a, 2008; Olszewski & Kidwell, 2007; Smith, 2005; Tomašových & Kidwell, 2009b; Tyler & Kowalewski, 2017). Furthermore, mollusc death assemblages are more abundant and diverse with respect to living communities (Kidwell, 2009); their survey is cheaper and simpler, and working with them is far less invasive and harmful to communities (Kowalewski, 2009). Finally, death assemblages record the average composition of living communities over time and are sometimes vital to identify anthropogenic impacts that altered communities before the existence of any exhaustive record of the features of ecosystems -one pillar of the conservation paleobiology (Scarponi et al., 2023; Kidwell et al., 2025).

Conservation paleobiology requires that the transfer of ecological information from living communities to death and fossil assemblages be known to some extent and modelled (Archuby et al., 2023). While studies based on examples of ecosystems with anthropogenic impacts of the northern hemisphere (or Global North) are abundant (Kidwell, 2007a and references included in the article and in supplementary online material: Kidwell, 2007b), there still exist latitudes that almost lack this kind of information (notable exceptions are Simoes *et al*. (2009), Rivadeneira & Nielsen (2022), Assumpção *et al*. (2022) and Rojas et al. (2025)). Such is the case of the ecological information stored in the death assemblages of the Atlantic Patagonian coast. An exception that illustrates the general pattern is the work of Kidwell (2007a) that includes three case studies in the opening of the Beagle Channel, a trait that connects the Atlantic and Pacific Oceans, at the southern boundary between Argentina and Chile, more than two thousand kilometres from San Antonio Bay, along the coast.

### *Benthic Mollusc Diversity in San Matías Gulf: Background*

Orensanz et al. (2002) concluded that little is known of the coastal Patagonian biota. In their report on invasive species from southern Brazil to the southernmost end of the continent in Tierra del Fuego Province, Argentina, the authors faced the problem of the poor documentation of the living and fossil species in order to identify invasions. Archuby et al. (2015) evaluated large-scale taphonomic fidelity in rocky shores along 1,500 km of the Argentine Patagonian coast, from Punta Mejillón in the north of the San Matías Gulf to Puerto Deseado (from 40º to 48º south latitude). This work found that, based on death assemblages, it is possible to distinguish between different biogeographical provinces. The precision of the study was low to assess fidelity at finer scales: life and death assemblages had been collected at different times and not exactly in the same locations. In addition, samples of death assemblages were collected by hand, which implies a bias against small species and a reduction in taphonomic fidelity in different ways (Kidwell, 2002; Olszewski & Kidwell, 2007). Archuby & Roche (2019) surveyed the death assemblage of a rocky shore in a single site, Punta Mejillón, in the north of San Matías Gulf, where they found surprisingly high levels of alpha diversity, if compared with studies based on living fauna. These authors demonstrated that diversity distributes differentially along the intertidal belt and that sieving is a requisite to correctly sample diversity. Besides these, other studies based on intertidal death assemblages are few, mainly focused on biotic interactions (Archuby & Gordillo, 2018; Gordillo & Archuby, 2012, 2014; Martinelli et al., 2013). For instance, based on predation rates, Martinelli et al. (2013) hypothesized the occurrence of the effect of human eutrophication in Playa Unión, placed a few tens of kilometres south of Península Valdés, on Golfo Nuevo.

The San Matías Gulf (SMG) has been considered as a hot-spot of diversity (Güller & Zelaya, 2017) based on the record of high levels of marine mollusc species richness. The Gulf is in the transition zone between the Magellanic and Argentine biogeographic provinces (Balech & Ehrlich, 2008; Zaixso et al., 2015) so life and death assemblages include species typical from both biogeographical entities (Archuby et al., 2015; Archuby & Roche, 2019). San Matías Gulf has been proposed as a relevant place for conservation (Machado-Schiaffino et al., 2011). However, most studies restrict to mollusc species worth for exploitation such as mussels (*Mytilus edulis platensis, Aulacomya atra*), scallops (*Aequipecten tehuelchus*), razor clams (*Ensis macha*), oysters

(*Ostrea puelcha*), clams (*Amiantis purpurata, Ameghinomya antiqua, Atrina seminuda, Panopea abbreviata*), whelks (*Buccinanops deformis*) and volutes (*Zidona dufresnei*) and the patagonian octopus (*Octopus tehuelchus*).

Avaca et al. (2008) provided two databases of live specimens sampled from subtidal habitats on the northern and northwestern margins of San Matías Gulf. Zaixso et al. (Zaixso et al., 1998) exhaustively surveyed the San José Gulf, that opens to the SMG. The aforementioned Güller & Zelaya (2017) work described high levels of mollusc diversity in the San Matías and San José Gulfs. These authors compiled 85 sampling points, from the intertidal to depths of 25 m, as well as some samples from greater depths, accounting for 30,481 specimens of molluscs. The survey accounted for 119 species of molluscs, including bivalves (49) and gastropods (70). When other studies are added by the authors, the figure reaches 141 species (60 bivalves and 81 gastropods) , several recorded only from shells (questionably assumed to be alive in the communities; Scarabino *et al*., 2016). Although this figure is important, the potential of death shell assemblages is even more surprising if one considers that Archuby & Roche (2019) in their study based on death assemblages in a single locality, and only the intertidal and supratidal, identified 70 species of molluscs. Recently, Avaca *et al*. (2025) conducted a detailed study of molluscan biodiversity along the two main tidal channels of San Antonio Bay, with the aim of evaluating diversity changes across an environmental gradient associated with depth. The authors detected higher diversity and evenness in the less impacted eastern channel, and lower diversity in the inner (proximal) localities compared with the distal ones, in both channels. Overall, the current understanding of the benthic diversity of the San Matías Gulf is far from being comprehensive (Roche et al., 2020).

With all, there are not to date studies centred in the composition and structure of shallow marine benthic communities that allow the development of a gulf-scale picture in terms of diversity. Is the Gulf a true biodiversity spot or just the addition of species due to the superposition of two biogeographical provinces? (and eventually species that do not live now, i.e. collected as only shells). Are species recorded only from empty shells living in the same place? Is there a shift in the distribution of species due to global warming?

*Potential human-driven changes in Patagonian benthic ecosystems.*

Patagonia is a large, little populated region with agricultural activities of low intensity due to its almost xeric climate (López-Gappa, 2022; Orensanz et al., 2002). However, far from being home to a set of pristine ecosystems, it has abundant evidence of human impacts. With the exception of sandy beaches, Patagonian shores host invasive species with significant biological impacts (Orensanz et al., 2002). *Balanus glandula* was introduced by the 1960's in Mar del Plata City, approximately 700 km north east of San Antonio Bay, and spread rapidly along the Patagonian coast(Zaixso et al., 2015). *Crassostrea gigas* was intentionally introduced 1982 in Bahía Anegada, 200 km north east of San Antonio Bay for aquaculture activities. *C. gigas* populations expand, although they still did not reach San Matías Gulf (Mendez et al., 2015; Orensanz et al., 2002; Wörner et al., 2019). Besides, a large list of non-native species, including macro and microalgae, hydroids, polychaetes, sea slugs, amphipods, shrimps, crabs, bryozoans, ascidians and fishes, are present in the Patagonian coasts (Schwindt et al., 2018).

Eutrophication, the consequence on ecosystems of the arrival of nutrients to the sea, either from waste waters of human populations or agricultural activities releasing excesses of fertilizers (Cloern, 2001; Fricke et al., 2016), was described for different places in Patagonia (Esteves et al., 1997; Fricke et al., 2016; Helbling et al., 2010; Teichberg et al., 2010). Human impacts to the benthic communities of the San Matías Gulf are mainly related to the eutrophication caused by the releasing of sewage waters to the ocean, especially relevant in San Antonio Oeste and Las Grutas cities, the widespread fishing activities by bottom trawling, and the artisanal fishing in the intertidal to shallow subtidal belts (López-Gappa, 2022; Narvarte et al., 2022).

San Antonio Bay (Fig. 1) is surrounded by two urban areas and a small town close to a harbour. The region is subject of an intense touristic activity during summer (Roche et al., 2020). Previous works identified the occurrence of human-derived eutrophication of the San Antonio Oeste (SAO) Channel, that runs along the San Antonio Oeste City, consisting in high levels of nitrogen coming mainly from domestic wastewaters. The wastewater origin of nutrients is supported by evidence: the reduction in the salinity during ebbtides, and the higher concentrations of nitrogen and the enrichment in $^{15}N$ in the eutrophicated channel (Martinetto et al., 2010). In addition to the domestic wastewater discharge, a fish processing factory placed in the city, also discharges fluids with nutrients to the coast (Martinetto et al., 2011).

Figure 1.

Kidwell (2009) describes a clear relationship between the degree of anthropogenic eutrophication of shallow marine ecosystems and the decrease in the similarity between death assemblages and living communities from which they come from, in such a way that human eutrophicated ecosystems develop low levels of taphonomic fidelity. In the case of highly impacted communities, the composition of the death assemblages is a good proxy (perhaps the only available) of the pre-impact configuration of the biota.

In this contribution we seek to evaluate how the assemblages of modern benthic mollusc remains (shells) record the environmental gradients and the recent anthropogenic modifications, in the benthic intertidal communities of the San Antonio Bay, located north of the San Matías Gulf, in the northernmost tip of the Argentine Patagonian coast. We also seek to improve the knowledge about the potential usefulness of mollusc death assemblages to establish baselines and identify anthropogenic impacts in the shallow benthic communities. Additionally, we checked the fidelity of life to death assemblages with a presence-absence species matrix. The survey was conducted in two tidal flats associated with two tidal channels of the San Antonio Bay, Argentina. The western channel, or SAO channel, placed along the town of San Antonio Oeste, is a human impacted (eutrophicated) water body, characterised by high levels of nutrients and an abundant community of macroinvertebrates. The eastern channel or SAE channel mirrors the SAO channel towards the east. It has a similar extension and features, except the fact that it is sensibly less impacted by human activities (Avaca et al., 2019). The SAE lacks any human population nearby, with the exception of a very small village built on the coast, around 2 km from the channel. Martinetto et al. (2010) evaluated another channel of the bay, not influenced by human activities, and found no indications of excess of nutrients nor algae in large amounts, which suggests that the movement of water of the tidal cycle does not deliver them to other places in the Bay.

We expect that mollusc death assemblages will follow the gradient of stress caused by salinity and subaerial exposure in terms of species composition and diversity. We also hypothesize that there will be differences between the communities of the channels, due to the effect of eutrophication in one of them. This study advances the field of near-time Conservation Paleobiology (Dietl et al., 2015), which contributes to the knowledge of current ecosystems providing evidence from relatively young death and fossil assemblages.

## Materials and methods

The San Matías Gulf (GSM) is the northernmost gulf of the Argentine Patagonian Atlantic coast (Fig. 1). It has an irregular outline, with an extension of around 150 km in the latitudinal sense and 160 in the longitudinal sense, approximately 18,000 square km of surface and a perimeter, around the coast, of 570 km. Biologically, it is placed in the Argentine Biogeographic Province, but in wide overlap with the south Atlantic Magellan Province, and is therefore characterized by a mix of species from both biogeographic entities (Balech & Ehrlich, 2008; Güller & Zelaya, 2017).

The San Antonio Bay is an 80 $km^2$ bay placed in the northern part of the San Matías Gulf. During high tides the bay covers ca. 120 $km^2$, leaving 81% exposed during low tides (Martinetto et al., 2011). The region is characterised as having a temperate climate, arid to semi-arid, with total annual precipitation no higher than 250 mm (Paruelo et al., 1998; Teichberg et al., 2010). The San Antonio Bay is subject to a macrotidal regime, with up to 9 m semidiurnal tides (Daleo et al., 2006; Piola & Scasso, 1988). During low tides, a wide intertidal belt populated by sand, mud and pebbles, and marshes dominated by *Sporobolus alterniflora* (Isacch et al., 2006) is exposed. The northern part of the gulf, where San Antonio Bay is placed, has salinities higher than in the southern part, due to the effect of desiccation under highly arid conditions (Genchi et al., 2010; Piola & Scasso, 1988). Salinities higher than 34 ppt were reported (Piola & Scasso, 1988), while Fricke et al., (2016) described values above 37 ppt in two channels of San Antonio Bay. One of the authors of this work (AR) observed salinities above 40 ppt in the water of the distal portions of the channels. In the summer, a temperature and density stratification of the gulf is established. Sea surface temperature is around 18º C in summer (February) and 11º C in winter (August). Agricultural activities are minor in the region, which is characterized as a semi-desert (Isacch et al., 2006). The Bay receives almost no freshwater via precipitation. The city of San Antonio Oeste had more than 19,000 inhabitants by 2022 (Instituto Nacional de Estadísticas y Censo. Argentina, 2022). Together with the neighbourhoods that surround the city, it reaches around 27.000 inhabitants. In addition, the area receives tourists during the summer period.

Samples were collected along two channels that discharge into San Antonio Bay, during 2018 and 2019. Seabed at sampling spots were relatively homogeneous, characterized by sedimentary grain sizes ranging from coarse sand to gravel (Avaca et al., 2025). The western channel is placed along the San Antonio City and has high levels of eutrophication (Teichberg et al., 2010). The eastern channel mirrors the former towards the east, and is almost free from direct human influence. Death assemblages in both channels were sampled at three different distances, in places accessible to the surveys, four times a year, one per season (as a part of a wider study focused on the living communities; Fig. 1; Table 1). In all cases, samples were taken from middle intertidal at the lowest tide. More distal localities suffer longer subaerial exposure and are subject to changes in salinity (hypersalinity caused by desiccation) and high temperatures and are, therefore, more stressed.

The west (San Antonio Oeste) channel was characterized as eutrophic in comparison with a nearby channel, used as control (Fricke et al., 2016; Martinetto et al., 2010, 2011). The concentration of dissolved inorganic nitrogen (DIN) of the western channel during the low tide (88.6 ± 5.6 µM; Teichberg et al., 2010) is two times the observed in a recognized eutrophic water body, the Venice Lagoon (43.5 ± 56.2 µM; Martinetto et al., 2010). This is the case despite the fact that the San Antonio Bay experiences a remarkable water exchange due to its wide tidal amplitude. Evidence convincingly suggests that, in the SAO channel, macroalgae are able to obtain human-derived nutrients to support a growth rate higher than observed in other eutrophicated coastal settings (Martinetto et al., 2011). Authors observed that, contrary to other coastal ecosystems with anthropogenic impacts, SAO channel does not experience loss of biodiversity linked to excess nutrients. It seems that the large amount of exchange of water due to the macrotidal regime keeps the water oxygenated, and allows a diverse macroinvertebrate fauna to develop.

Table 1.

Localities of the western channel, from distal to proximal places are: Arboleda (AR), Instituto (IN) and Punta Verde (PV). Punta Verde receives tourists, especially during summer. Localities in the eastern channel, from distal to proximal, are Saco Viejo (SV), Las Tejas (LT) and Punta Perdices (PP). Each sample consisted of eight replicates. In each replicate, all living and dead specimens from the surface and top 2 cm of a 0.5 × 0.5 m quadrat were collected. Replicates per sample were pooled for the purposes of this study. The sediments were sieved in a 2 mm aperture mesh. Empty shells and living specimens were separated *in situ*. Sampling was performed four times a year (one per season). Living specimens were identified to the species level and recorded as presence per locality (Roche et al., 2020). Dead specimens were identified to the species level and counted. In the case of disarticulated dead bivalve species, the number of individuals was calculated as the total of shells/2. The analysis fidelity of the death assemblages with respect to the life assemblages was based on a presence/absence matrix of living and dead individuals per locality (Table 2 in Roche et. al, 2020, P/A matrix of species per locality, pooling seasonal data into single composite sample per site; total number of live specimens 56,767). The ecological analysis of death assemblages used a matrix of species counts per locality, treating seasonal counts as replicates. This decision is based on Avaca et al (2019) that described a minor influence of seasonality (although in their article of 2025 they found some differences in the eastern channel (Avaca et al., 2025)). In our study, based on time-averaged assemblages with smaller sample sizes, seasons did not show statistical differences (PERMANOVA, $p>0.05$ in all cases). Two samples, A_Su (Arboleda summer) and PP_A (Punta Perdices autumn) were excluded from the analysis due to their very small sample size (3 and 14 respectively).

### *Life/death assemblages' comparison*

The fidelity death to life assemblages was evaluated with different techniques, from a presence/absence matrix. The life-death matrix consisted of 44 species distributed into 12 samples: living and dead along six localities, three per channel. In a first approximation, an ordination with correspondence analysis was carried out. The evaluation of the distribution of sites was based on graphs with scaling 1 (designed to assess the distribution of sites according to species). The plots were enriched by the projection of the variable distance as a vector and as smooth surfaces, and the drawing of convex hulls combining type of sample and the variable channel (west channel dead, west channel live, east channel dead, east channel live). In turn, to evaluate the distribution of the species, a scaling 2 graph was used (Borcard et al., 2018). Correspondence analysis was performed with function *cca* of the package *vegan* (Oksanen et al., 2021). Permutational multivariate analysis of variance (PERMANOVA) with percentage difference distance (aka Bray Curtis) was used to compare distance, sample type (life vs. death assemblages), and channel (adonis2 function; 999 permutations; Oksanen et al., 2021).

*Distribution of death assemblages*

For the analysis of the death assemblages, samples per season were used as repetitions. The matrix of the death assemblages consisted in the species abundances across 24 samples (four repetitions per six localities) with 27 species. The matrix of explanatory variables used includes: distance in meters of each locality to the San Antonio Bay, and channel (either west or east). Distances were estimated with Google Maps as the distance from the locality to the mouth of the channel to the San Antonio Bay, along the channel. The zero distance was placed in Punta Delgado in the west channel and Punta Perdices in the east channel, in such a way that proximal localities of both channels are not equivalent in terms of distance (e.g., the most proximal locality in the west channel, PV, is farther from the Bay than the middle locality of the east channel).

Samples were ordinated with principal coordinates analysis or PCoA with *cmdscale* function of package *stats* in R version 4.1.2 (R Core Team, 2025), calculated on the percentage difference distance matrix, in turn obtained with the function *vegdist* of the package *vegan* (Oksanen et al., 2021). Explanatory variables were added to the plots, and their association with the ordination was evaluated with permutation tests. Those that were significant ($p<0.05$) were chosen to be projected *a posteriori* with *envfit* function (*vegan* package). *Envfit* projects the variables as vectors or objects into the ordination plots, and estimates the significance of the r2 of the regression of these environmental variables on the axes of the ordination (Borcard et al., 2018). Species that are close to each other have similar frequencies along the objects and the proximity of a species to a site is associated with the probability of the species to be found in that site. PCoA ordination was run both, once on the dataset consisting on the proportions of species per sample and once on a arcsine of square root of the proportions matrix.

PERMANOVA was used to evaluate the effect of the explanatory variables “channel” and “distance” on the species composition of samples. It was run with the percentage difference distance matrix calculated either with the raw counts and the square root of proportions. The same test was applied to the variable Sites (factor like category with one level per locality), followed by a pairwise comparison (pairwise.adonis function with Bonferroni correction; Martinez Arbizu, 2020).

Redundancy analysis (RDA), or rather transformation-based RDA (*sensu* Borcard et al., 2018) was used to assess the relationship between explanatory variables, i.e., channel and distance from the base, and the matrix of species abundances. It was performed with the function *rda()* of the aforementioned package *vegan* of R. The species per site matrix was transformed with the Hellinger transformation previous to RDA, following Legendre & Gallagher (2001) and Borcard et al. (2018). The model was evaluated with a global test of the RDA result (999 permutations). The significance of the canonical axes was also tested with permutations (999 permutations). To assess the difference in species composition between both channels, a partial RDA with channel (west vs. east) as factor and distance as covariable was performed. The rationale of the analysis is that differences between death assemblages in eutrophicated vs. non eutrophicated habitats is tested as if distance remained constant (variability of other variables is put aside).

Hill numbers (Hill, 1973), also known as true-diversity indices (Borcard et al., 2018; Jost, 2006) were calculated. These indices rely on a number called *a* (Borcard et al., 2018) or *q* (Jost, 2006), that ranges from 0 to infinite, decreasing the weight given to rare species as it grows. In this way, when a equals 0, the diversity index is equivalent to species richness (N0, number of species present in the sample). A value of 1 (a=1, N1) gives an estimation conceptually equivalent to the entropy-based Shannon-Wiener index (equals exp(H)) that incorporates the abundance per species and thus weighing those that are numerically more represented. Finally, if a equals 2 (N2), the index is equivalent to the inverse of the Simpson's concentration index and is expected to be more sensitive to evenness (Borcard et al., 2018; Hill, 1973; Jost, 2006). Besides, we estimated all three Hill’s diversities by means of the rarefaction method with iNEXT R Package (Chao *et al*., 2014; Hsieh *et al*., 2025; Hurlbert, 1971; Sanders, 1968) with sample sizes of 100 and 500.

Beta diversity provides measures of variation in species composition that complement the evaluation of alpha diversity, as it incorporates the identity of all species (Baselga & Orme, 2012). Multiplicative Whittaker’s Beta diversity was calculated for the whole sample, for the samples of every channel, and for each site. To further analyse this topic, we estimated the local contribution of sites to beta diversity (LCBD) with the Var(Y) approach (Borcard et al., 2018). Higher levels of LCBD are characteristic of sites that are singular concerning their species composition, that can reflect either polluted or pristine ecosystems (Legendre & De Cáceres, 2013). Finally, we evaluated the patterns of beta diversity change along the channels with the Betapart R package (Baselga et al., 2025), with the aim of testing the relative incidence of turnover vs. nestedness (Baselga & Orme, 2012). Multiple-site beta diversity (Sorensen dissimilarity) was partitioned into turnover (species replacement; $\beta$SIM) and nestedness-resultant dissimilarity (species loss; $\beta$SNE) components. Presence-absence community matrices were generated from raw species abundance data. Core dissimilarity matrices were computed with betapart.core(), followed by total multiple-site measures using beta.multi(). To account for unequal sampling effort across localities, we performed balanced resampling with beta.sample(betapart.core(), sites=10, samples=100). This procedure randomly subsampled 10 sites from each channel's community matrix across 100 iterations, generating null distributions of βSOR, βSIM, and βSNE that control for differences in sample size while preserving species incidence patterns.

Two samples were excluded from PCoA, RDA and partial RDA due to their small sample size, Arboleda (AR) locality in summer and Punta Perdices (PP) in autumn.

## Results

### *Comparison of life and death assemblages*

Occurrence of living and abundances of dead species per site is shown in Table 2. Out of 44 species identified, 17 were found only alive, all of which correspond to species that are very rare according to Roche *et al*. (2020). This is related to the higher density of living species with respect to dead remains (almost five times). Four species were detected only dead: *Calliostoma militaris* is present alive in the Bay, although not detected in this survey (Roche, personal communication); a single specimen of the pulmonate *Siphonaria lessoni* was found in Punta Verde; the small infaunal bivalve *Diplodonta patagonica* was found in 5 out of 6 localities, but with low frequencies; finally, the oyster *Ostrea puelchana* is present dead in four sites with a single specimen. The ordination plot of the correspondence analysis (Fig. 2 (**a**)) shows that the samples are mostly ordered according to the distance to the bay, with distal ones (*i.e*. AR, IN and SV) to the left, and proximal (PP, LT and PV) to the right (Fig. 2 (**b**) (**c**)). Also, sets of samples of the same type and channel do not overlap much (Fig. 2 (**b**)). PERMANOVA was statistically significant for the three explanatory variables (Channel, p=0.018; Type, p=0.005, Distance, p=0.002). The departure of LT_L (Las Tejas life) from the remaining sites (Fig. 2 (**a**)- (**c**)) can be explained by the exclusive presence of five species at this locality (Fig. 2 (**d**), scaling 2 plot). In particular, species whose distribution is restricted to a single site occur in life assemblages at proximal localities, with the exception of a single specimen of *Siphonaria lessoni* in PV_D. These locally restricted species can be partly explained by the greater density of living than dead specimens in most of the samples. Interestingly, the West Channel set of life assemblages is not organized according to the distance gradient but rather perpendicular to it.

Table 2.

Figure 2.

*Mollusc death assemblages and environmental variables*

12,954 specimens distributed into 27 species (20 gastropod and 7 bivalve species) were recorded along the 24 samples, of which the majority corresponded to gastropods (12,846; 99%). The list of species included in the study and the complete database are accessible in the Appendices 1 and 2. A simplified (pooled per site) version of the database can be seen in Table 2. The bivalve species were more represented in the eastern channel than in the SAO channel. The eastern channel is characterized by a higher species richness (s=26) and lower sample size (n=4,458) than the western channel (S=20, n=8,496).

Multivariate ordinations with PCoA show that localities do not overlap significantly, i.e. they are distinct (Fig. 3, (**a**)-(**f**)). The variable distance from the San Antonio Bay is a strong factor organizing the multivariate space, and the influence of the variable channel is moderate to low (Fig. 3). Proximal samples such as Punta Verde (3.981 km from the Bay), Punta Perdices (0 km from the Bay) and Las Tejas (2.800 km from the Bay) separate from distal samples, and almost do not overlap among themselves. Sites with higher values of distance, *i.e*. IN (6.970 km from the Bay), AR (9.672 km from the Bay) and SV (7.850 km from the Bay), join together with high similarity (Fig. 3, clearer in (**b**), (**d**) and (**f**), right column plots). The variable distance contributed significantly to the ordination of both, the analysis with transformed and untransformed data (projection of explanatory variables with function *envfit*, p=0.001 in both cases), while channel was statistically non-significant (*envfit*, p=0.209 and p=0.201 respectively.

Figure 3.

Redundancy analysis, which includes as explanatory variables channel and distance, resulted statistically significant (permutation test, p=0.001). Only the first axis was significant (p=0.001), that accounted for more than 50% of the variability. The adjusted $r^2$ was 0.520. More distal localities are positively associated with the species *Heleobia australis*, so that death assemblages in localities farther from San Antonio Bay are enriched in this species (Fig. 4 (**a**)). In the other side of the plot, two groups of species place at low distance from the San Antonio Bay, one of them associated with the west channel (*Anachis isabellei*, *Agathistoma patagonicum*, *Costoanachis sertularium* and *Carditamera plata*) and a second with the east channel (*Olivella tehuelcha*, *Turbonilla rushii*, *Bostryocapulus odites* and *Fargoa bushiana*). These two groups of species vary together along the plot (Fig. 4 (**b**)). There is almost no relationship between the channels and the abundance of *Heleobia australis* (Fig. 4 (**a**)). West and east channels differ significantly in their species composition and abundances (partial RDA, including distance as covariable; p=0.010).

Figure 4.

The PERMANOVA analysis calculated from the matrix of relative frequencies (proportions) was significant for distance (p=0.001) and channel (p=0.031). The comparison of species composition between the sites resulted statistically significant (p=0.001). Multiple comparisons among sites are provided in Table 3. All localities in the eastern channel differ from each other, although LT and PP are only marginally different. In the western channel AR and IN differ marginally although both differentiate with respect to PV. SV and IN, that are placed at similar distances from the San Antonio Bay (6790 and 7850 m respectively) are not statistically different. AR, that is even farther (9672 m), is different from LT and SV. The lack of difference between AR and PP might be due to sample size (one replication of each locality was eliminated from the analysis because their sample sizes were too small, giving place to a comparison from just three per site). PV and PP do not differ. These two localities are the most proximal of both channels, although are at different distances from the Bay.

Table 3.

The PERMANOVA analysis applied to the transformed matrix (arcsine of the square root of proportions) was statistically significant for distance (p=0.001) and channel (p=0.038). The species composition of the six localities were also statistically different (p=0.001). Pairwise comparisons can be observed in Table 4. Results of the comparisons of localities of the same channel are similar to the comparisons based on the proportions matrix, except that PP and LT in the east channel, and IN and AR in the west channel do not differ. Contiguous localities are expected to be more similar in habitat and species composition. In the eastern channel, PP and LT do not differ, but SV departs significantly from LT. Interestingly, SV is twice as far from LT than this from PP. Conversely, in the western channel PV is different from IN.

Figure 5.

Table 4.

Alpha diversity was estimated for each of the 22 samples (Supplementary Online Information 3). Sample size is not positively correlated with any of the diversity indices used (real N0, N1, N2 and their estimations via  rarefaction to 100 and 500).

Correlations between sample size and diversity indices are negative in all cases, although low to moderate, and non-significant for N0, N1 and N0 rarefied to n= 100 (Supplementary Online Information 3). This result indicates that the estimations of diversity are not affected by sample size. The significant negative correlation can be explained from the higher density of shells in the distal localities that develop in a highly stressed habitat, with lower levels of diversity. Alpha diversity decreases from proximal to distal sites and is slightly higher in the eastern channel (Fig. 5). Spearman correlations between distance from the Bay and alpha diversity indices are all statistically significant and negative, i.e., the more distance to the San Antonio Bay, the lower the diversity (Table 5). Beta diversity is slightly smaller in the eastern channel (Table 6). The per-site local contribution to beta diversity is shown in Fig. 7. The non-impacted eastern channel shows a growing level of LCBD from distal to proximal locations. The AR and IN sites provide little to the beta diversity but, on the contrary, PV contributes exceedingly more than the rest.

Table 5.

Figure 6.

Beta diversity partitioning revealed contrasting community disassembly patterns between channels (Table 7 and Fig. 7). In the WCh, total Sorensen dissimilarity (βSOR = 0.787) was partitioned into turnover (βSIM = 0.524; 66.6%) and nestedness-resultant dissimilarity (βSNE = 0.263; 33.4%), indicating species replacement as the primary driver of community differentiation along the habitat gradient. In turn, the ECh exhibited slightly lower total dissimilarity (βSOR = 0.752) but a more even distribution of nestedness (βSNE = 0.329; 43.8%) and turnover (βSIM = 0.423; 56.2%).

Table 6

Table 7

Figure 7

## Discussion

### *Live-dead comparisons*

Live assemblages in this study exhibit higher species richness than death assemblages, which can be explained by the lower density of the latter's remains (life assemblages sample size= 56,767; death assemblages sample size= 12,954). This fact does not coincide with what was expected from other works (e.g., Archuby & Roche, 2019; Kidwell, 2009 and references cited therein). Samples were taken from the sides of the channels at the level of the middle intertidal fringe, in places with little or no shell accumulation, which might explain this departure from the expectations. This low shell density is a distinctive feature of this case, indicating fewer dead remains than living specimens.

Death assemblages differ statistically from life assemblages in terms of species presences and absences. This result is *a priori* not surprising, because the former, even in the case of a pristine ecosystem, is the summation of remains of dead animals along a certain time, during which species abundances do not usually equal those present in the communities (Kidwell & Tomašových, 2013). Groups of samples of the same type (live or dead) and channel, organised primarily according to the variable distance from the San Antonio Bay, that represents a proxy of stress (correspondence analysis plot in Fig. 2 (**b**)(**c**)). Las Tejas life assemblage partly departs from this pattern, most probably due to the occurrence of five species exclusively in this sample (Fig. 2 (**d**)). The importance given to rare species, exaggerated with the use of presence-absence data, might be the cause of this unexpected departure. The variable channel (west vs. east) also influences the species composition of the assemblages, although to a lesser extent than the distance and the type of sample, but it is still statistically significant. Interestingly, the life assemblages of the west channel do not follow the general pattern: they seem to be independent (perpendicular) to the distance to the bay (Fig. 2 (**b**)). This unexpected pattern is not followed by the death assemblages that organize according to the distance. This might be a consequence of a recent alteration of the ecosystems that is still not reflected in the death assemblages.

In general, changes in death assemblages' species composition and abundances assessed from the P/A matrix follow expectations associated to the gradient of habitat stress (*i.e.* distance from the SAB) and agree with a recent study based on the living community at the same localities (Avaca et al., 2025). This is despite the significant differences between life and death assemblages described before. The result might be reasonable: death assemblages are modified by taphonomic factors but still preserve the environmental signal. It is possible that the degree of time-averaging is low for the former, but the comparison based on presence/absence data imposes a limitation to these inferences.

### *Mollusc death assemblages' changes following a stress gradient.*

Mollusc death assemblages of the both channels included in this study closely follow the environmental gradient imposed by their distance from San Antonio Bay, irrespective of  whether they are affected by eutrophication or not. The signal of the stress produced by the degree of the subaerial exposure and the excess of salinity in the benthos surpass the effect of other environmental gradients. Intertidal communities in the Atlantic Patagonian coasts are exposed to harsh physical conditions caused by the action of strong and dry winds that provoke desiccation (Bertness et al., 2006), a feature that is more intense in protected shores such as San Antonio Bay (López-Gappa, 2022a). Subordinately, species composition of the DAs in the eutrophicated west channel differ from that of the less impacted east channel.

Shell accumulations found in the intertidal fringe usually incorporate species that live in that habitat, as well as some subtidal species (Archuby & Roche, 2019). These accumulations are produced in part by the effect of storms, and include the stranding of live specimens that inhabit deeper settings (López et al., 2008). It is worth noting that the diversity recorded in these accumulations usually exceeds that obtained in the sampling of live fauna (Archuby & Roche, 2019). However, the configuration of the channels sampled for this contribution, *i.e*. protected from waves and storms, is not suitable for a widespread transport of shells from deeper subtidal bottoms of the San Antonio Bay, unless just along a limited area. Important levels of spatial mixing can be ruled out since contiguous localities differ significantly in their species composition for almost all paired comparisons (see tables 3 and 4).

The variable distance from the San Antonio Bay was statistically significant in the comparisons in all the analyses (PCoA, RDA, PERMANOVA), implying that the species compositions of the DAs change mostly according to this variable. Sites that are farther from the San Antonio Bay are enriched in the mud snail *Heleobia australis,* and impoverished in other species. *Heleobia australis* has been described as associated with the cordgrass *Sporolobus alterniflora* and the perennial glasswort *Sarcocornia perennis*, common in the salt marshes around the channels (Zaixso et al., 2015). The snail establishes a positive biotic interaction with *S. alterniflora*, that has been interpreted as a strategy to cope with the intense abiotic stress typical of the salt marshes (Canepuccia et al., 2007). Common and abundant in the restricted coastal habitats, *H. australis* looks for shelter in vegetated areas and shoals (Carcedo & Fiori, 2011). In the three most distal sites, AR (9672 m), IN (6970 m) and SV (7850 m) *H. australis* constitutes more than 95% of the specimens. There is a significant positive correlation between this species' percentage per site and the distance from the San Antonio Bay (Spearman's r=0.830; p=0.001; n=6). Interestingly, from the analysis of Fig. 4 (**b**) comes that *H. australis* is not associated with any of the channels, suggesting that the stress due to distance imposes a stronger control on the benthic life, and that this species is able to thrive with the effect of eutrophication.

The three most distal sites, IN, SV and AR, show very low levels of species richness (Fig. 5 A and B) and especially low levels of equitability (see flat boxplots in Fig. 5 C and D). All alpha diversity indices are negatively correlated with distance (Table 5), implying that distal, more stressed communities, are characterized by low richness and high dominance. Species present in these three localities other than *Heleobia australis* appear in very low abundances. Even so, species richness is higher in SV, placed in the non-impacted channel, than in IN and AR, in the western channel. Conversely, proximal localities bear higher levels of species richness and equitability (Fig. 5). RDA triplots (Fig. 4) indicate that eight species are associated with the less stressed habitats. Among them, those that characterize the west channel are predators (*Anachis isabellei*, *Costoanachis sertularium*), herbivores (*Agathistoma patagonicum*), and filter feeders (*Carditamera plata*). Species that differentiate the east channel are predators (*Olivella tehuelcha*), ectoparasites (*Turbonilla rushii* and *Fargoa bushiana*) and filter feeders (*Bostryocapulus odites*). All these eight species are present in both channels. Avaca *et al*. (2025) arrived at similar findings in their study based on living fauna .

*Eutrophication and its signal in mollusc death assemblages.*

Species composition differs significantly between the eutrophicated western channel and the eastern one. This is evident in all statistical analysis. Partial-RDA, including distance as covariate, is conclusive in this respect. *Agathistoma patagonicum*, present in five of the six localities, is more abundant in the proximal ones (PP, LT and PV). This species has been described as a common inhabitant of shallow subtidal (1-5 meters) settings, but is also present in lower intertidal and deeper subtidal habitats (Rechimont et al., 2013). *A. patagonicum*, a medium-sized grazer (herbivore) gastropod, is especially abundant in the proximal locality of the western channel (PV), where the effect of eutrophication was already demonstrated (Teichberg et al., 2010), and the distance from the San Antonio Bay is not as high as to infer harsh conditions for life. In fact, the frequency of *A. patagonicum* in PV is much higher than expected if the distance from this locality with the San Antonio Bay is considered (Fig. 8).

Figure 8

Seven species are present in the east, non-impacted channel, that are absent in the west, eutrophicated one. These taxa are little represented: the gastropods *Crepipatella dilatata* (n=2), *Turbonilla strebeli* (n=11), *Carolesia blakei* (n=13), *Turbonilla uruguayensis* (n=1), *Acteocina candei* (n=2) and the bivalves *Darina solenoides* (n=6) and *Endodesma patagonicum* (n=1). Of these, *C. dilatata, C. blakei* and *D. solenoides* are present in the life assemblage of the west channel. Conversely, just one species of gastropod, the siphonate *Siphonaria lessoni* (n=1), is present only in the west channel. This difference in species richness can be associated, at least in part, to the human impact in the west channel. An alternative explanation is the fact that two localities in the west channel, AR and IN, are placed in highly stressed distal positions while in the eastern channel two sites are in less stressed proximal positions (PP and LT) with higher diversity levels. Sample size of the west channel is more than two times the east one, although these specimens are concentrated in the distal localities, with little species richness. The presence of live specimens absent in the death assemblages can be explained by the higher of life specimens in relation to shells (sample sizes: LA= 56,767, DA= 12,846. AR, personal communication).

Local contribution to beta diversity analysis suggests that PV locality provides most of the variability of the samples included in this study in terms of species composition (see Fig. 6). The four samples of PV, display a very high dispersion (Fig. 2 (a) to (d)). Differences between samples reflect the intrinsic variability of the site, which is also evident in the plots of diversity of Fig. 4 and 5. Interestingly, the LT locality displays similar variability between samples in alpha diversity as PV, likely due to their similar values of distance from the Bay (LT: 2800 m; PV: 3981 m), although it contributes less than PV to the beta diversity.. The anomalous contribution of PV to the beta diversity suggests that there might be a different cause shaping this pattern. A plausible explanation is that this locality's death assemblage includes species present in the communities both, previously and after the inception of the eutrophication. In a research developed in the same channel, Martinetto et al. (2010), observed an increase in diversity and abundance of macroinvertebrates caused by eutrophication. The authors proposed a causal effect between algal blooms and high nutrient concentrations derived from the wastewater from the city of San Antonio Oeste. The high availability of food would have increased the abundance and diversity of macroinvertebrates. Oxygen depletion, typical of other highly eutrophic cases, was not observed due to the high rate of water exchange caused by tides.

The relatively higher incidence of the turnover component of beta diversity in the west channel in comparison with the east one suggests that human impact (excess of nutrients) drives species replacement rather than simple nested loss, potentially reflecting substitution of impact-tolerant taxa for sensitive species (see Fig. 7 and Table 7). In contrast, a relatively higher proportion of the nestedness in the east channel indicates progressive species loss along natural environmental gradients, where distal sites represent impoverished subsets of proximal assemblages. The west channel seems to reflect the superimposition of a turnover due to the human eutrophication over a basic nested pattern caused by the filtering of species associated with the increase in salinity along the channel. Avaca et al., (2025) found for the west channel a pattern of turnover between IN and AR localities and complete nestedness for the rest. Conversely, these authors found a mixed although turnover dominated pattern for the east channel. Their results are not completely comparable because they assimilated middle localities of both channels (IN and LT) regardless of their distance to the San Antonio Bay.

Ectoparasitic *Turbonilla* spp, *Fargoa bushiana*, and *Careliopsis bahiensis* might have distributions related to those of their anemone hosts. Although variable, their host-specific nature leads to infer that changes in the distribution of hosts can influence their parasites' occurrences. If this were true, ectoparasitic species should be more diverse in the east channel, where their hosts are actually more diverse. Out of eight pyramidellid species detected in this study, seven were found alive and five also dead in the east channel. Conversely, the west channel, less diverse, pyramidellid richness is lower. The living communities have three species alive, of which two were also found dead. More interestingly, *Turbonilla rushii* in the west channel was detected only dead (n=7, only in Punta Verde). This species is abundant live and dead in both proximal localities of the east channel, PP and LT, suggesting that findings in PV_D are relics of former distributions. As mentioned before, the general differences in diversity between channels can be explained at least partially by differences in localities distance from the bay, being the excess of nutrients an additional contributor.

Teichberg et al. (2010) described the presence of important phenomena of growth of dense, fast growing opportunistic seaweeds in the West Channel, linked to the anthropogenic enrichment in dissolved inorganic nitrogen. Fricke et al. (2016), in a field and experimental study found substantial differences in the composition and succession of benthic algae between the SAO channel and a control channel, and explained these differences based on the higher abundance of nutrients in the former. Algal species composition of the SAO channel was typical of eutrophicated waters (such as foliose Ulvales). Fricke et al., (2016) suggested that the high mobility of the water in the SAO channel guaranteed mixing and prevented anoxia, but did not deliver the nutrients to the bay, as the effect on algae was observed only in the SAO channel. The authors observed that macroinvertebrates consume large amounts of macroalgae (65% of *Ulva lactuca*), significantly more than in other eutrophicated coasts. They identified a sort of control of algal blooms by a well-nourished community of polychates, crabs, amphipods and molluscs. In a study associated to this one, aimed to evaluate the benthic macrofauna of the tidal channels of San Antonio Bay, Avaca *et al*. (2019) showed that molluscs are more abundant but less diverse in the SAO channel, in comparison with the *hidden* channel (in this work named as eastern channel), and suggest that the difference is associated to the human eutrophication. Conversely, Avaca *et al.* (2025) assumed similar characteristics for both channels, arguing that the strong effect of tides contribute to dilute the anthropic contamination (nutrients).

### *Death assemblages, living communities and human impacts: conservation paleobiology in the Patagonian marine benthic communities.*

Our results are sufficiently solid to infer that the main factor correlated with differences in the composition of mollusc death assemblages in both channels is the distance from the San Antonio Bay. This coincides with what is expected for living communities: the increased exposure time of the biota to the extreme Patagonian climate and salinity, due to desiccation, imposes a stress that is overcome by a few species. The effect of eutrophication is subordinated to the physical stress, although it is evident: amongst the stressed sites, SV, placed in the non-impacted channel, has more species in comparison with AR and IN with sample size almost one fourth of that of both impacted localities together. The other three sites, less affected by the effect of the distance, show differences that can be explained more confidently as due to eutrophication. With minor differences, Avaca et al. (2025) arrived at similar observations in the relationship between mollusc biodiversity and the environmental gradients.

The information on the composition and structure of a community in the framework of conservation studies should reflect, at a minimum, the knowledge of it over a decade in the case of completely natural communities, and preferably from centuries to a few thousand years, if it is considered that it is necessary to know what they were like before the start of the impact of human activities (Kidwell, 2009). In this study, we were able to confidently infer the effect of eutrophication that happened during the last several decades, although this signature was subtle, probably due to the mixing of pre-impact community configurations with several generations of impact.

Human impact on the marine benthic communities of the southern Atlantic coasts probably date back to the late Pleistocene, e.g., tt was recently proposed that *Homo sapiens* caused the extinction of the Pleistocene megafauna in South America (Prates & Perez, 2021). In other parts of the world, there is evidence indicating that human activity caused the depletion of marine species used for consumption as early as 5,000 years ago (Kidwell, 2009). The deterioration of marine ecosystems from direct (excess of sedimentation and eutrophication, habitat destruction, species depletions, pandemics, biological invasion) and indirect agents (climate change) became global since several decades ago (Halpern et al., 2008). These ecological phenomena, acting at different time scales, demand the use of alternative sources of quantitative evidence of a historical nature, to acquire basic information on the state of current systems, improve ideas about baselines and about the biological consequences of human pressures on natural populations (Dietl, 2019; Kidwell, 2009).

The human presence in South America dates back to 14,000 years (more likely between 16,600 and 15,100). South America is the last continental region of the planet to be occupied by *Homo sapiens*, which makes it very attractive insofar as the anthropogenic impacts would have less temporal depth than in other regions, and would therefore be, perhaps, simpler to detect and model (Archuby et al., 2023). After a slowdown in the human population growth rate associated with the extinction of megafauna (Prates & Perez, 2021), average population densities increased around the transition between the Pleistocene and Holocene, with a maximum towards the 1000 years BP (Perez et al., 2016; Prates et al., 2020). The possible impact of mollusc consumption of human pre-Hispanic populations has been documented, for example, in the anthropogenic accumulations of molluscs on the coast of southern Brazil, known as sambaquis or shell mounds (Gaspar et al., 2014; Klokler, 2014). It has been interpreted that these human populations periodically caused the overexploitation of shellfish banks, although there are other explanations for this evidence (Klokler, 2014; Villagran Suarez et al., 2010). In the case of the San Matías Gulf, the exploitation of molluscs for consumption in archaeological times has been investigated in its northern sector (Favier Dubois et al., 2006; Favier Dubois & Borella, 2007, 2011; Favier Dubois & Scartascini, 2012), as well as in the west coast (Borella et al., 2020), and the evidence indicate that they were a regular item consumed by human populations. Still, more research is needed to the mollusc consumption by ancient patagonian populations.

The recently published cooperative international work “Identifying big questions in paleontology” (J. A. Smith et al., 2025) provided different sets of questions that hopefully will guide some research in the future. In this work we engage in questions included into “Biodiversity drivers” working group (questions BD1, BD3, BD7 and BD8) related to the way biotic and abiotic drivers shape biodiversity; “Climate change past and present” (questions CPP1, CPP3 and CPP8), that tries to reflect on how past climate changes affected the biotas and predict paths of biodiversity in the near future, facing the current climate change; “Conservation paleobiology” working group supplied relevant questions associated especially linked to this work (questions CPB2, CPB3, CPB4 and CPB5), all of them about how to integrate past biological information to the design of conservation plans; the “Looking Inward and Outward” working group results of relevance considering the unequal distribution of these types of research across the globe: our region has less publications than those inscribed in the so called Global North (questions LIO1 and LIO6). This last issue was also assessed in recent scientific articles that show the smaller representation of South America in conservation paleobiology publications (Assumpção & Ritter, 2025), and a relatively good production in actualistic taphonomy, with Argentina standing as the main contributor in the region (De Francesco et al., 2025).

Characterizing mollusc death shells assemblages accumulated in the intertidal belt, as a proxy of the yet not (fully) surveyed Patagonian benthic communities, is a promising area of research that will contribute with accurate, cheap and non-invasive techniques to get a picture of communities, as well as identify past potential human-driven impacts. To date, there are not published exhaustive biotic inventories in the San Matías Gulf, which is also true in the case of the molluscs. Taken together, the study of mollusc death assemblages in conjunction with living community surveys constitutes an important research direction that will yield relevant insights for conservation assessments.

## Final remarks

Evaluation of life and death assemblages, based on presence/absence matrix, provided some insights to taphonomic fidelity, although limited due to the nature of data. Life and death assemblages of this study differ, but still record similar biotic phenomena. Multivariate analyses group samples according to the degree of stress imposed by the distance from the San Antonio Bay, with the exception of the living samples of the west, eutrophicated channel. The lack of association of the living communities along the west channel is an evidence of recent change to the communities, provided that the death assemblages do follow the gradient of stress.

The more robust analysis based on counts of death assemblages produced meaningful findings, highlighting its importance for understanding past ecological processes. Mollusc death assemblages vary in association with natural and anthropogenic-derived differences in habitat. The stress associated with different times of exposure to harsh physical conditions, exerted a major effect on the species composition of death assemblages. Distal localities have very low levels of species richness and equitability, and are dominated by the mud snail *Heleobia australis*, while the contrary is observed in the more proximal sites (*i.e.*, higher species richness, higher equitability).

Subordinated to distance, the eutrophic nature of the San Antonio Oeste channel is also associated with differences in species composition. In proximal, stressed sites, the herbivore *Agathistoma patagonicum* stands out with higher frequency than expected. The eutrophicated west channel is characterized by lower levels of species richness.

The evaluation of the local contribution to beta diversity provides a convincing evidence of the eutrophicated nature of San Antonio Oeste channel communities: Punta Verde locality provides an exceedingly high amount of contribution to beta diversity, allowing to infer the co-occurrence of pre and post impact sets of species. In addition, the non-eutrophicated east channel combines turnover with the expected nestedness as a filtering of species in relation to the increase in stress. In the eutrophicated channel, the relative higher relevance of turnover reinforces the idea of a recent change in species composition.

Future studies should stress on the temporal mixing and a comparison with living communities, in order to assess, respectively, the degree of time-averaging and the taphonomic fidelity.

Intertidal mollusk death assemblages proved to be highly valuable proxies for assessing conservation issues in marine benthic ecosystems. This line of evidence holds great potential for disentangling the natural dynamics of these ecosystems prior to human influence, the effects of pre-Hispanic low-density occupations, and the impacts of more recent and widespread anthropogenic changes along the Patagonian coasts, from intertidal to subtidal zones. This study represents the first contribution framed within conservation paleobiology for this region.

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## Author contribution

**FA**: conceptualization (lead), data curation (lead), formal analysis (lead), investigation (equal), methodology (equal), writing – original draft (lead), writing – review and editing (equal), visualization (head), software (lead); **AR**: conceptualization (supporting), data curation (supporting), investigation (equal), fund acquisition (head), methodology (equal), writing – review and editing (equal), project administration (lead).

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## Tables

**Table 1**. Sampling sites, distances to the mouth of the channel and coordinates.

| Channel | Sampling site | Distance from the bay (m) | Latitude | Longitude |
|---|---|---|---|---|
| West | Punta Verde (PV) | 3981 | 40°43'50"S | 64°54'46"W |
| | Instituto (Ins) | 6970 | 40°43'39"S | 64°56'48"W |
| | Arboleda (Ar) | 9672 | 40°43'33"S | 64°58'36"W |
| East | Punta Perdices (PP) | 0 | 40°47'3"S | 64°50'21"W |
| | Las Tejas (LT) | 2800 | 40°47'37"S | 64°48'34"W |
| | Saco Viejo (SV) | 7850 | 40°48'18"S | 64°45'7"W |

**Table 2**. Presence (1) and absence (0) of living species (L) and abundances of dead species (D) per site. For full species names see Supplementary online Information 1. Abbreviations of the localities in Table 1. Sample sizes of death assemblages (n) and species richness (s) of all samples in the bottom.

| | West channel | | | | | | East channel | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | PV | | IN | | A | | PP | | LT | | SV | |
| | L | D | L | D | L | D | L | D | L | D | L | D |
| *DiodoraP* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *LucapinellaH* | 1 | 7 | 0 | 0 | 0 | 0 | 1 | 12 | 1 | 7 | 0 | 0 |
| *FisurellaR* | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 |
| *CrepipatellaD* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 |
| *BostrycapulusO* | 1 | 19 | 1 | 4 | 1 | 4 | 1 | 53 | 1 | 39 | 1 | 22 |
| *CrepidulaO* | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 2 | 1 | 1 | 0 | 0 |
| *SiphonariaL* | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *AgathistomaP* | 1 | 100 | 1 | 2 | 0 | 2 | 1 | 142 | 1 | 32 | 0 | 0 |
| *BuccinanopsD* | 1 | 7 | 1 | 15 | 1 | 7 | 1 | 15 | 1 | 5 | 1 | 7 |
| *HeleobiaA* | 1 | 135 | 1 | 2569 | 1 | 5338 | 1 | 453 | 1 | 231 | 1 | 2118 |
| *OlivellaT* | 1 | 29 | 0 | 7 | 0 | 2 | 1 | 192 | 1 | 114 | 1 | 1 |
| *OlivellaP* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *TurbonillaSan* | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 |
| *TurbonillaB* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *TurbonillaStr* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 9 | 1 | 2 | 0 | 0 |
| *FargoaB* | 1 | 3 | 0 | 0 | 0 | 0 | 1 | 13 | 1 | 4 | 1 | 0 |
| *CostoanachisS* | 1 | 49 | 0 | 0 | 0 | 0 | 1 | 115 | 1 | 27 | 0 | 0 |
| *SpirotropisP* | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 5 | 1 | 3 | 0 | 1 |
| *CarolesiaB* | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 11 | 1 | 2 | 0 | 0 |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *AnachisI* | 1 | 149 | 0 | 0 | 0 | 0 | 1 | 548 | 1 | 108 | 1 | 2 |
| *ParvanachisP* | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 |
| *TurbonillaMaca* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *TurbonillaU* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| *TurbonillaMulti* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *TurbonillaR* | 0 | 7 | 0 | 0 | 0 | 0 | 1 | 54 | 1 | 26 | 0 | 1 |
| *ActeocinaC* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 |
| *BooneaM* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *CalliostomaM* | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 |
| *CarditameraP* | 1 | 13 | 1 | 0 | 0 | 0 | 1 | 11 | 1 | 2 | 0 | 0 |
| *LyonsiaA* | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| *AmeghinomyaA* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *BrachidontesR* | 1 | 6 | 1 | 5 | 1 | 0 | 1 | 21 | 1 | 4 | 1 | 18 |
| *TelaniellaV* | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 |
| *CrenellaD* | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *MusculusV* | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 |
| *LassaeaA* | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| *CorbulaP* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *DarinaS* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 6 |
| *EndodesmaP* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *Mytilus* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *SemeleP* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *EntodesmaE* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| *DiplodontaP* | 0 | 3 | 0 | 2 | 0 | 3 | 0 | 3 | 0 | 3 | 0 | 0 |
| *OstreaP* | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 |
| n | - | 534 | - | 2604 | - | 5358 | - | 1664 | - | 617 | - | 2177 |
| s | 25 | 20 | 12 | 7 | 9 | 8 | 26 | 21 | 30 | 23 | 13 | 10 |

**Table 3**. PERMANOVA pairwise comparisons of species relative abundances between localities. Values in the table correspond to the probability of an F statistic higher than the observed. Abbreviations of the localities in Table 1. *, p<0.05; (*), p<0.10

| | PV | IN | Ar |
|---|---|---|---|
| PP | 0.48 | 0.038 * | 0.1 |
| LT | 0.027 * | 0.020 * | 0.026 * |
| SV | 0.025 * | 0.616 | 0.047 * |

West channel

| | PV | IN |
|---|---|---|
| Ins | 0.028 * | |

|  |  |  |
|---|---|---|
| Ar | 0.022 * | 0.066 (*) |

East channel

|  | PP | LT |
|---|---|---|
| LT | 0.063 (*) |  |
| SV | 0.035 * | 0.03 * |

**Table 4**. PERMANOVA pairwise comparisons of species abundances between localities with square root transformation of proportional abundances. Values in the table correspond to the probability of an F statistic higher than the observed. Abbreviations of the localities in Table 1.

|  | PV | IN | AR |
|---|---|---|---|
| PP | 0.557 | 0.026 * | 0.1 |
| LT | 0.033 * | 0.027 * | 0.028 * |
| SV | 0.033 * | 0.271 | 0.062 (*) |

West channel

|  | PV | IN |
|---|---|---|
| IN | 0.026 * |  |
| Ar | 0.033 * | 0.345 |

East channel

|  | PP | LT |
|---|---|---|
| LT | 0.105 |  |
| SV | 0.023 * | 0.016 * |

**Table 5**. Spearman correlations between distance from the San Antonio Bay and alpha diversity represented by effective numbers of Hill (N0, N1 and N2) raw, and from rarefaction curves standardized n= 100 and 500, calculated using the iNEXT package (Hsieh et al., 2016). rho = Spearman correlation coefficient; *p*-value determines significance (*p* < 0.05 = *, *p* < 0.01 = **, *p* < 0.001 = ***; ns = not significant).

| Index | rho | p_value | p_signif |
|---|---|---|---|
| N0 | -0.691 | 4.00E-04 | *** |
| N0_100 | -0.819 | 0.00E+00 | *** |
| N0_500 | -0.751 | 1.00E-04 | *** |
| N1 | -0.85 | 0.00E+00 | *** |
| N1_100 | -0.841 | 0.00E+00 | *** |
| N1_500 | -0.841 | 0.00E+00 | *** |
| N2 | -0.841 | 0.00E+00 | *** |
| N2_100 | -0.841 | 0.00E+00 | *** |
| N2_500 | -0.841 | 0.00E+00 | *** |

**Table 6**. Beta diversity indices for the whole sample and for every channel

|  | N0 | N1 | N2 |
|---|---|---|---|
| Whole sample | 3.356 | 1.716 | 1.46 |
| W.Channel | 3.188 | 1.776 | 1.476 |
| E.Channel | 2.648 | 1.505 | 1.387 |

**Table 7**. Multiple-site beta diversity partitioning (Sorensen dissimilarity) for the west channel (WCh) and east channel (ECh). βSOR = total beta diversity; βSIM = species turnover (replacement); βSNE = nestedness-resultant dissimilarity (species loss). Values derived from betapart::beta.multi() on presence-absence community matrices (WCh: n=11 samples; ECh: n=11 samples). Percentages indicate relative contribution to total βSOR.

| Channel | βSOR (Sorensen Beta) | βSIM (Turnover component) | βSNE (Nestedness component) |
|---|---|---|---|
| WCh | 0.787 | 0.524 (66%) | 0.263 (33.4%) |

|  |  |  |  |
|---|---|---|---|
| ECh | 0.752 | 0.423 (56.2%) | 0.329 (43.8%) |

## Figure captions

**Figure 1**. Location of the studied localities. SAB, San Antonio Bay. Abbreviations of the localities: AR, Arboleda; IN, Instituto; PV, Punta Verde; PP, Punta Perdices; LT, Las Tejas; SV, Saco Viejo. The satellite image, obtained from Google Earth, was obtained at low tide (Copyright, 2022. TerraMetrics, CNES/Airbus).

**Figure 2**. Correspondence analysis ordination plots. **A**, **B** and **C**, scaling 1 plots to evaluate the distribution of sites. **D**, scaling 2 plot, to assess the distribution of species. **A**, ordination of localities with the addition of species. Closer localities are more similar in species composition. The plot was restricted to coordinates (-2,2) to facilitate the visualization of the samples. Species that lie outside the range of the plot to the top right corner were manually moved to its margin. **B**, ordination plot with the addition of a convex hull for combinations of channel and type of sample (live or dead). Labels were displaced to avoid superposition with points of localities. **C**, scaling 1 plot with the addition of the variable distance as a vector and as smooth surfaces. Abbreviations of the localities in Figure 1. **D**: dead sample; L: live sample. The vector corresponds to the projection of the variable distance. Explained inertia values are 21.32 % (CA1) and 17.61% (CA2).

**Figure 3**. Results of principal coordinate analysis. Left and right columns correspond to the analysis performed to the database of proportions of species per sample and the arcsine of the square root of the proportions respectively. (**A**) and (**B**) include the ellipses and the projection of the distance variable as a vector. Plots (**C**) and (**D**) correspond to the same result of the first two plots but with the addition of convex hulls

instead of ellipses and the projection of the species. (**E**) and (**F**) are the plots of the PCoA with the samples. Samples from the same locality have the same colours. Points correspondences: PV, 1 to 4; IN, 5 to 8; AR, 9 to 11; PP, 12 to 14; LT, 15 to 18; and SV, 19 to 22.

**Figure 4**. Plots of the redundancy analysis. (**A**) Scaling 1 (distance triplot). The distances between sites reflect their Euclidian distance. The angles between species arrows and distance reflect their correlations. The association between a channel and species is found by projecting the centroid of the first variable on the second; (**B**) Scaling 2 (correlation tripolot). The similarity between species abundances along samples can be evaluated as the angle between these species' arrows. The projection of a site at right angle on the distance arrow or on the arrow of a species, approximates the value of the site along that variable. The angles between species and the distance variable reflect their correlation. (Borcard et al., 2018). The plots include only species that accumulate a goodness of fit of at least 0.3 (function *goodness* of *vegan* package) to facilitate the visualization. Labels: blue, explanatory variables; red, species; black, localities. Abbreviations of the localities in Figure 1. Abbreviations of seasons: Sp, spring; Su, summer; A, autumn; and W, winter.

**Figure 5**. Boxplots and stripcharts of species richness indices. Blue dots represent a single index per sample (one per season). Whiskers represent the range without outliers, the box is limited by quartiles 1 and 3 and the horizontal lines are the medians. (**A**)N0 (species richness); (**B**) rarefaction estimation of species richness with n=100. (**C**) N1; (**D**) N2. Abbreviations of the localities in Figure 1.

**Figure 6**. Boxplots and stripcharts of the local contribution of each locality to the beta diversity (LCBD). Blue dots represent a single index per sample (one per season).

Whiskers represent the range without outliers, the box is limited by quartiles 1 and 3 and the horizontal lines are the medians. Abbreviations of the localities in Figure 1.

**Fig. 7.** Violin plots with embedded boxplots showing the null distributions of Sorensen-based beta diversity partitioning from 100 balanced resampling iterations (betapart::beta.sample(sites=10, samples=100)). WCh = west channel; ECh = east channel. βSOR = total beta diversity; βSNE = nestedness-resultant dissimilarity (species loss); βSIM = turnover (species replacement). Thicker violin regions indicate higher probability density. Horizontal lines within violins represent quartiles and medians from boxplots. The elevated turnover (βSIM) in WCh suggests species replacement dominates under pollution stress.

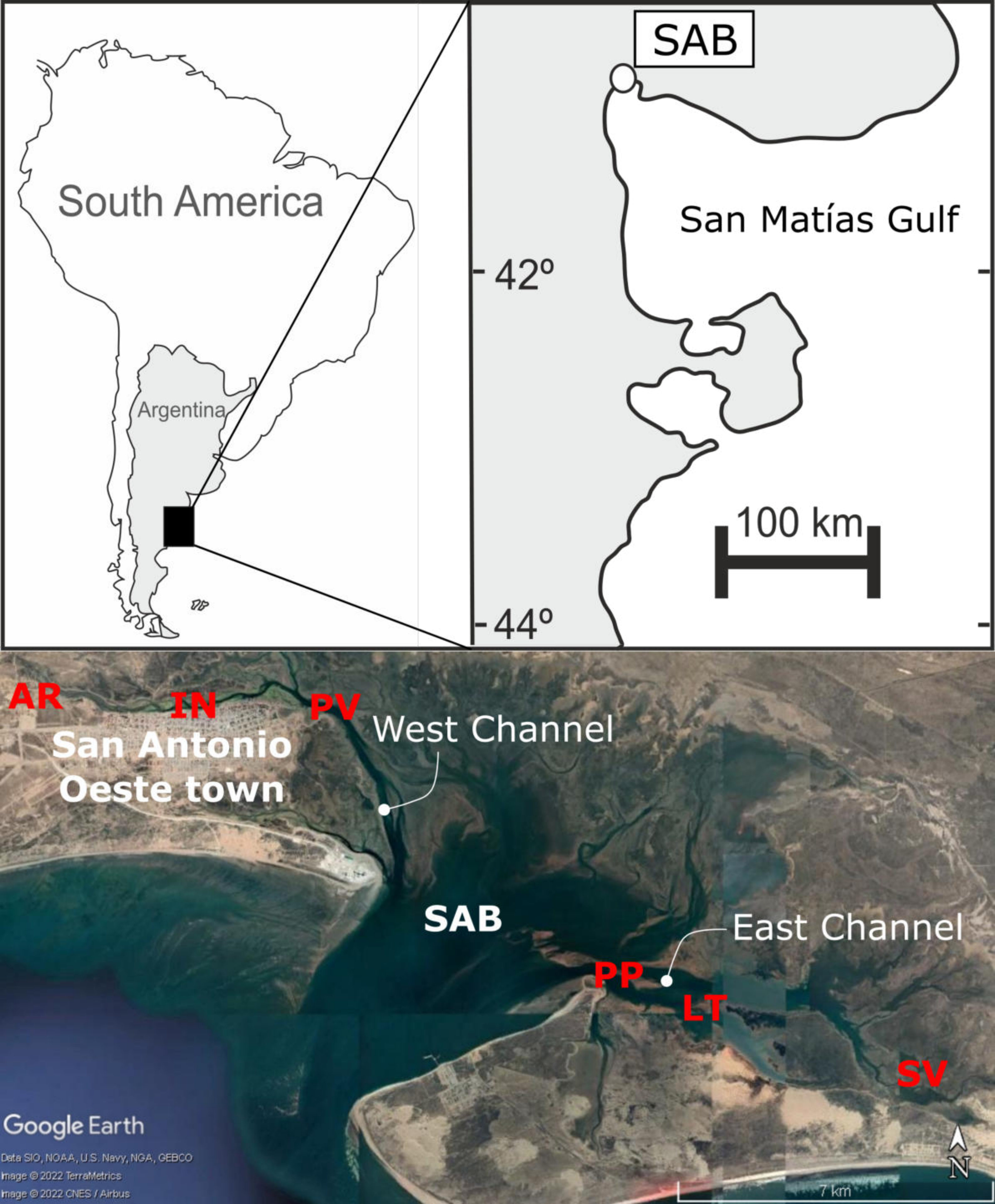
**Figure 8**. Plot of the percentage of *Agathistoma patagonicum* specimens per sample according to distance from the San Antonio Bay. Abbreviations of the localities in Figure 1.

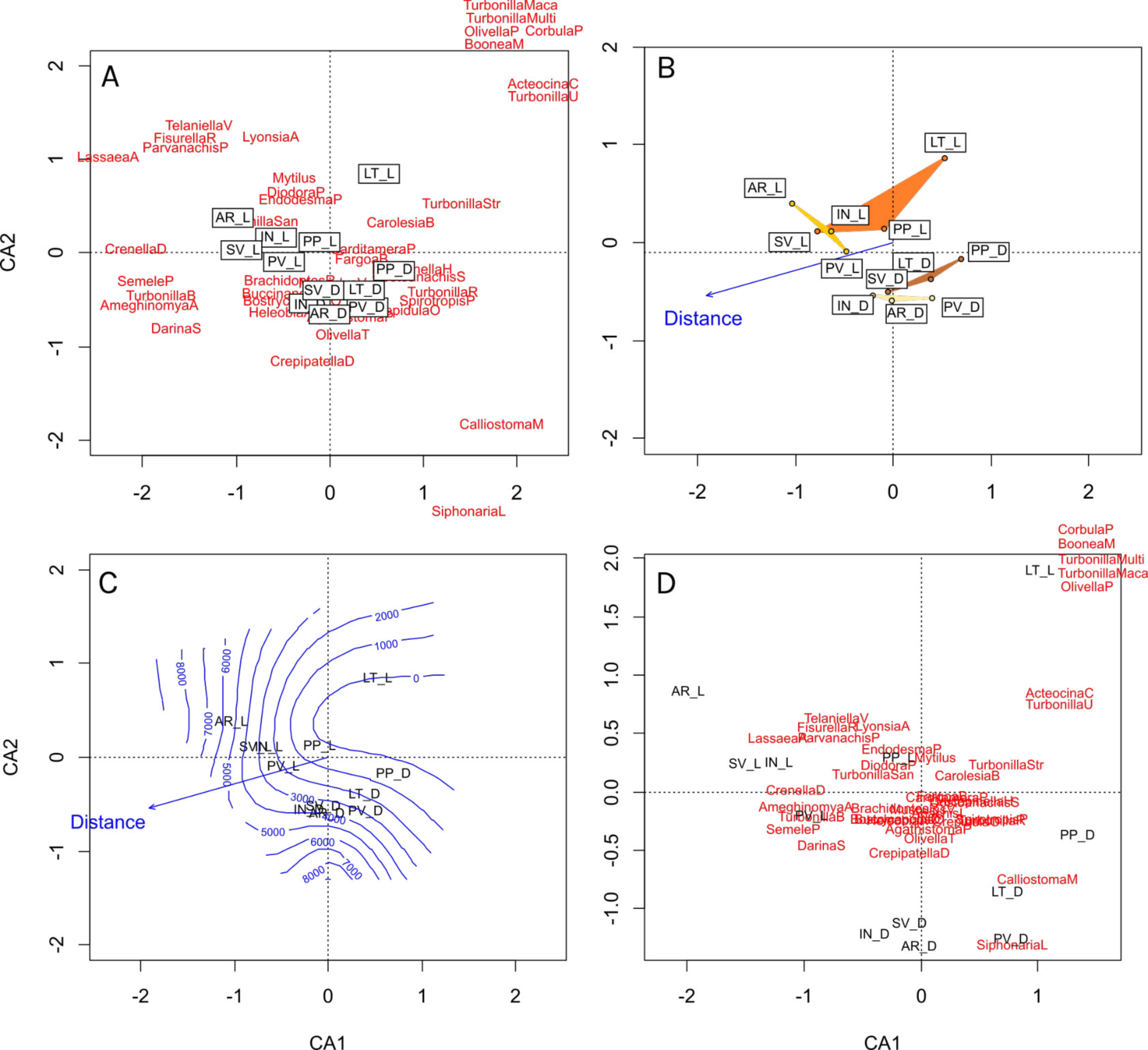
## Supplementary online information

SOI 1. List of species and their abbreviated names.

SOI 2. Database including explanatory variables and species abundances per sample.

SOI 3. Alpha diversity indices.


South America
Argentina
SAB
San Matías Gulf
42º
44º
100 km
AR
IN
PV
San Antonio Oeste town
West Channel
SAB
East Channel
PP
LT
SV
Google Earth
Data SIO, NOAA, U.S. Navy, NGA, GEBCO
Image © 2022 TerraMetrics
Image © 2022 CNES / Airbus
7 km
N


A
B
C
D
CA1
CA2
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TurbonillaMulti
OlivellaP
CorbulaP
BooneaM
ActeocinaC
TurbonillaU
TelaniellaV
FisurellaR
ParvanachisP
LassaeaA
LyonsiaA
Mytilus
DiodoraP
EndodesmaP
TurbonillaStr
CarolesiaB
CrenellaD
SemeleP
TurbonillaB
AmeghinomyaA
DarinaS
OlivellaT
CrepipatellaD
CalliostomaM
SiphonariaL
SpirotropisP
TurbonillaR
TurbonillaSan
AgathistomaP
LT_L
AR_L
IN_L
SV_L
PP_L
PV_L
PP_D
SV_D
LT_D
IN_D
PV_D
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Distance
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7000
6000
5000
3000
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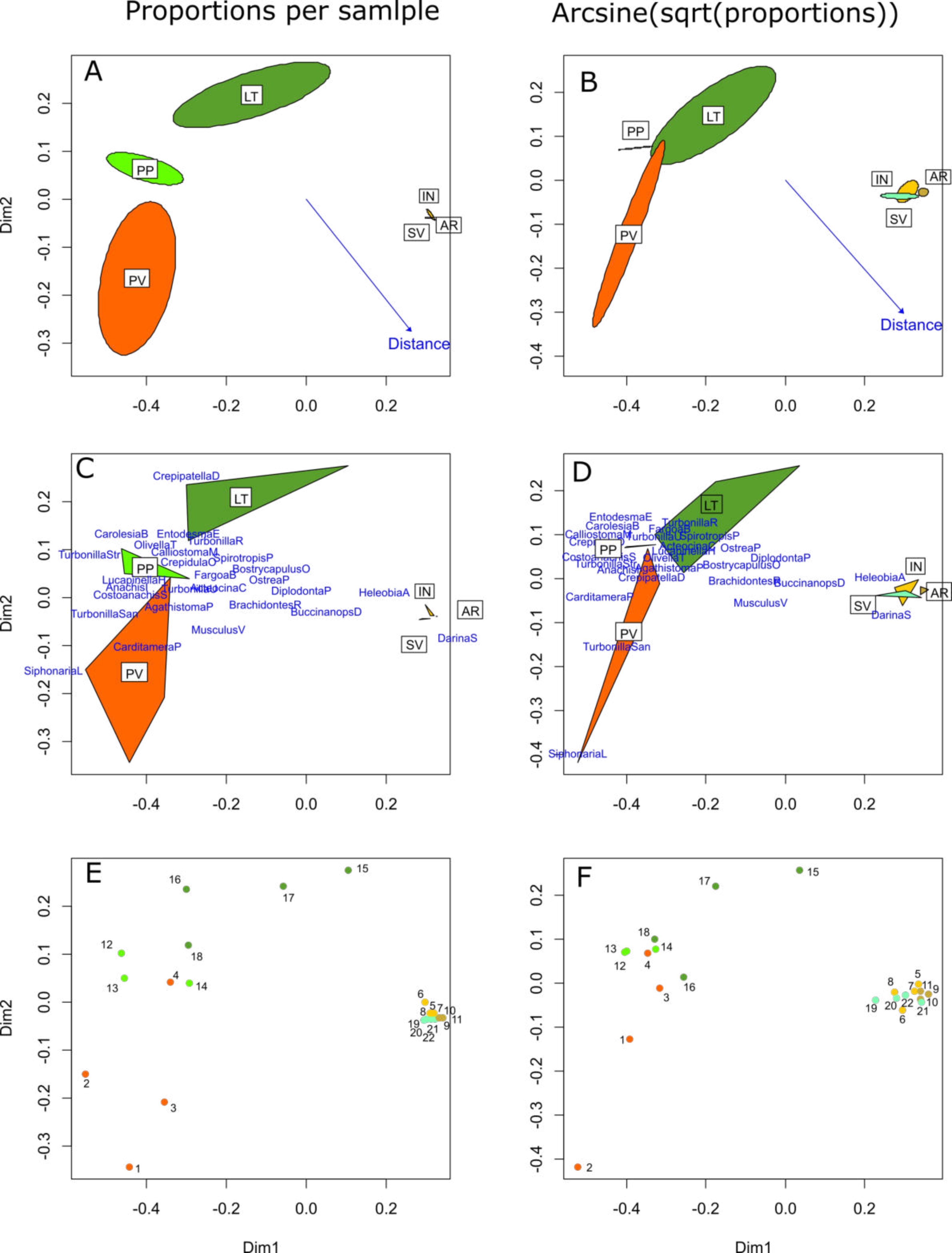
Proportions per samlple
Arcsine(sqrt(proportions))
A
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SV
Distance
Dim1
Dim2
CrepipatellaD
CarolesiaB
EntodesmaE
OlivellaT
TurbonillaR
CalliostomaM
TurbonillaStr
SpirotropisP
CrepidulaO
BostrycapulusO
FargoaB
LucapinellaH
AnachisI
TurbonillaU
ActeocinaC
OstreaP
CostoanachisS
DiplodontaP
HeleobiaA
AgathistomaP
BrachidontesR
TurbonillaSan
BuccinanopsD
MusculusV
DarinaS
CarditameraP
SiphonariaL
0.2
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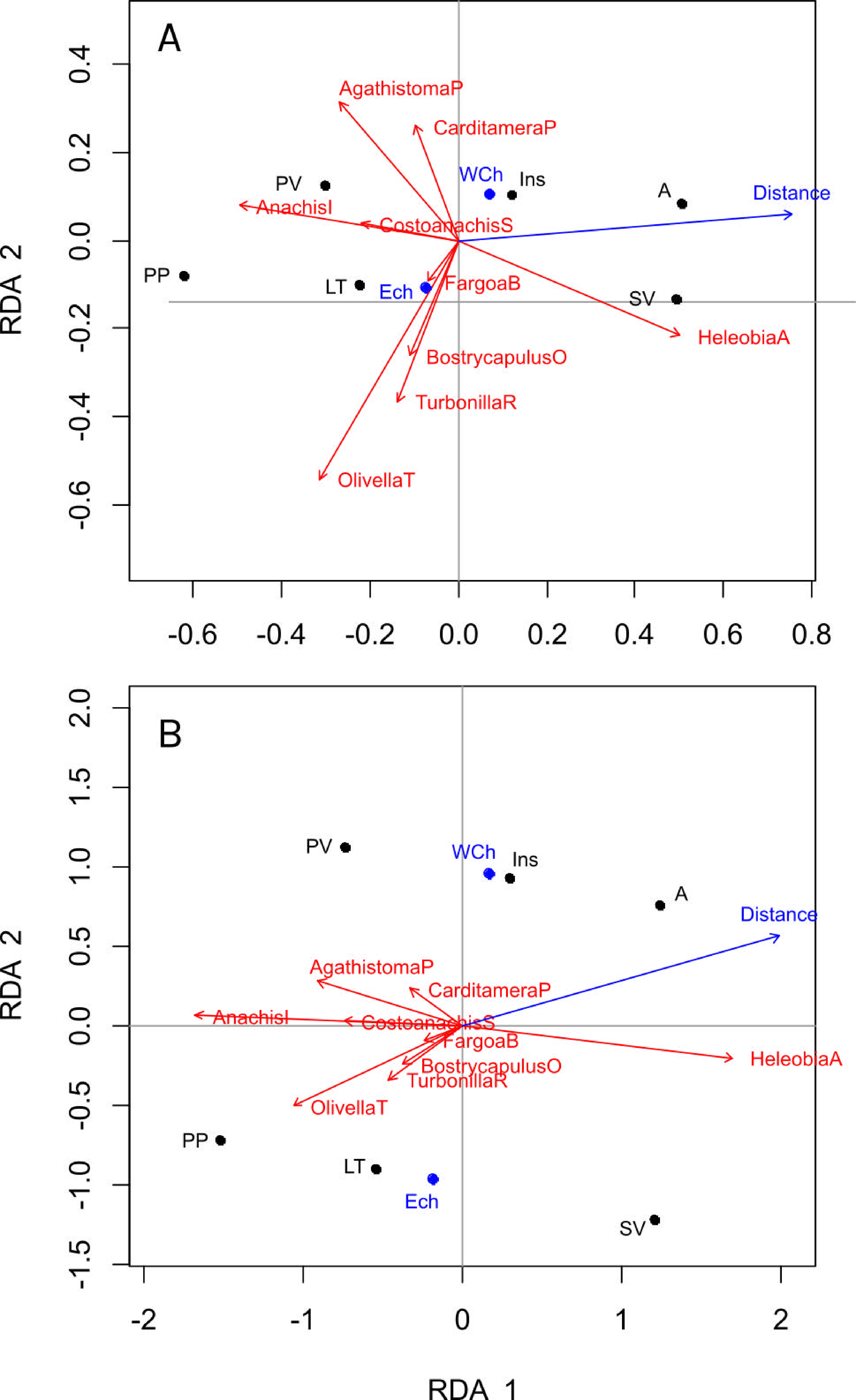
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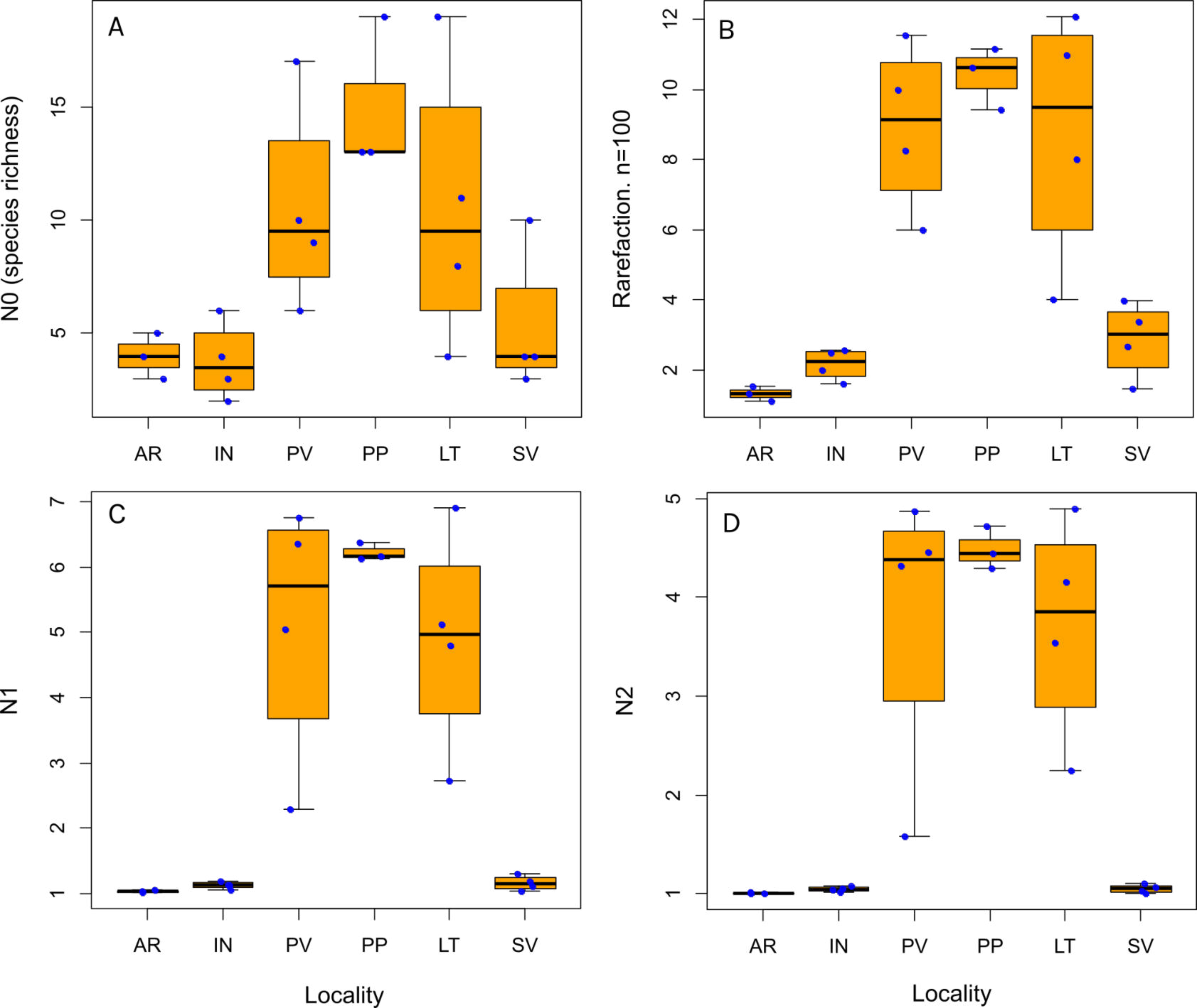
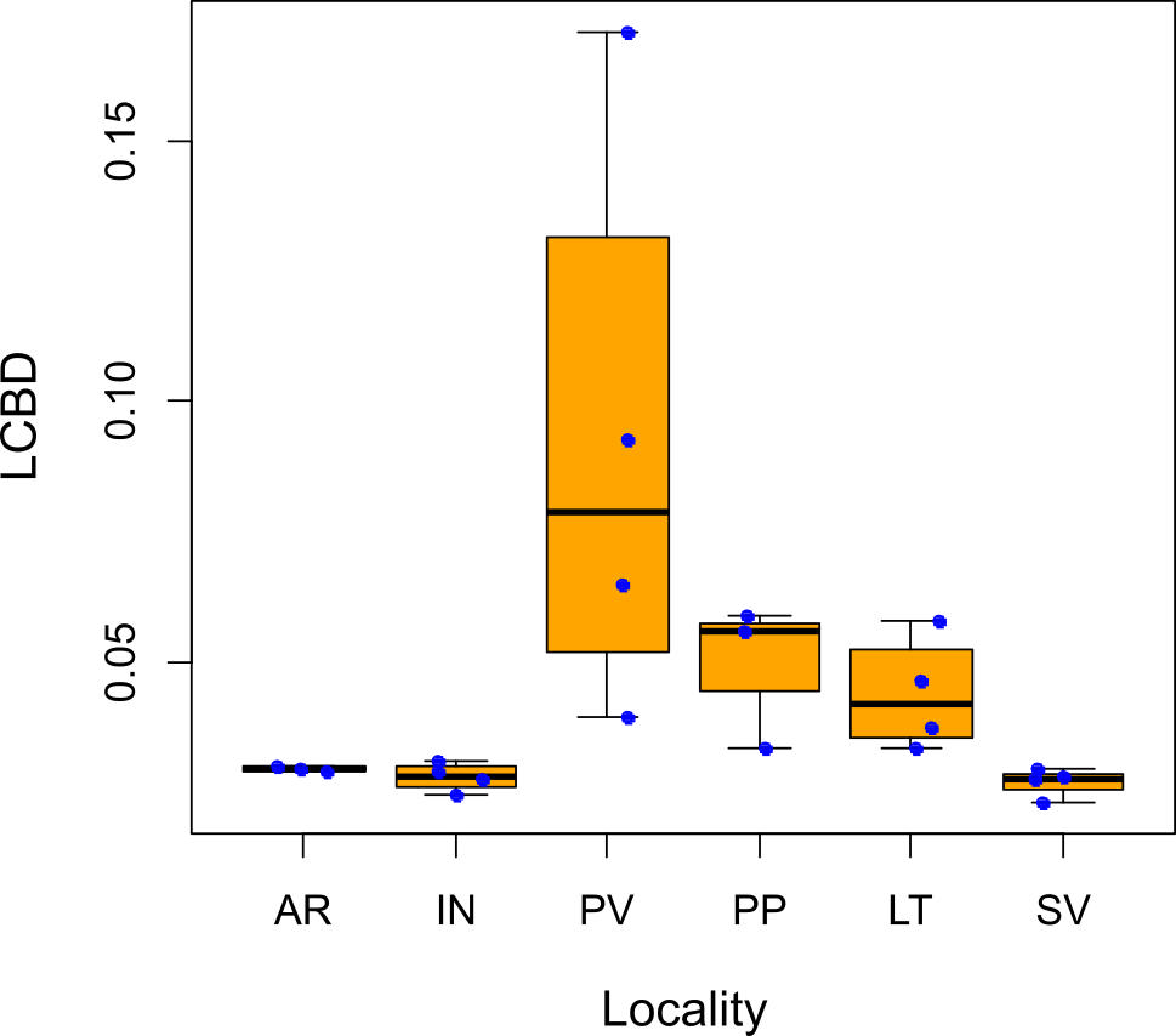
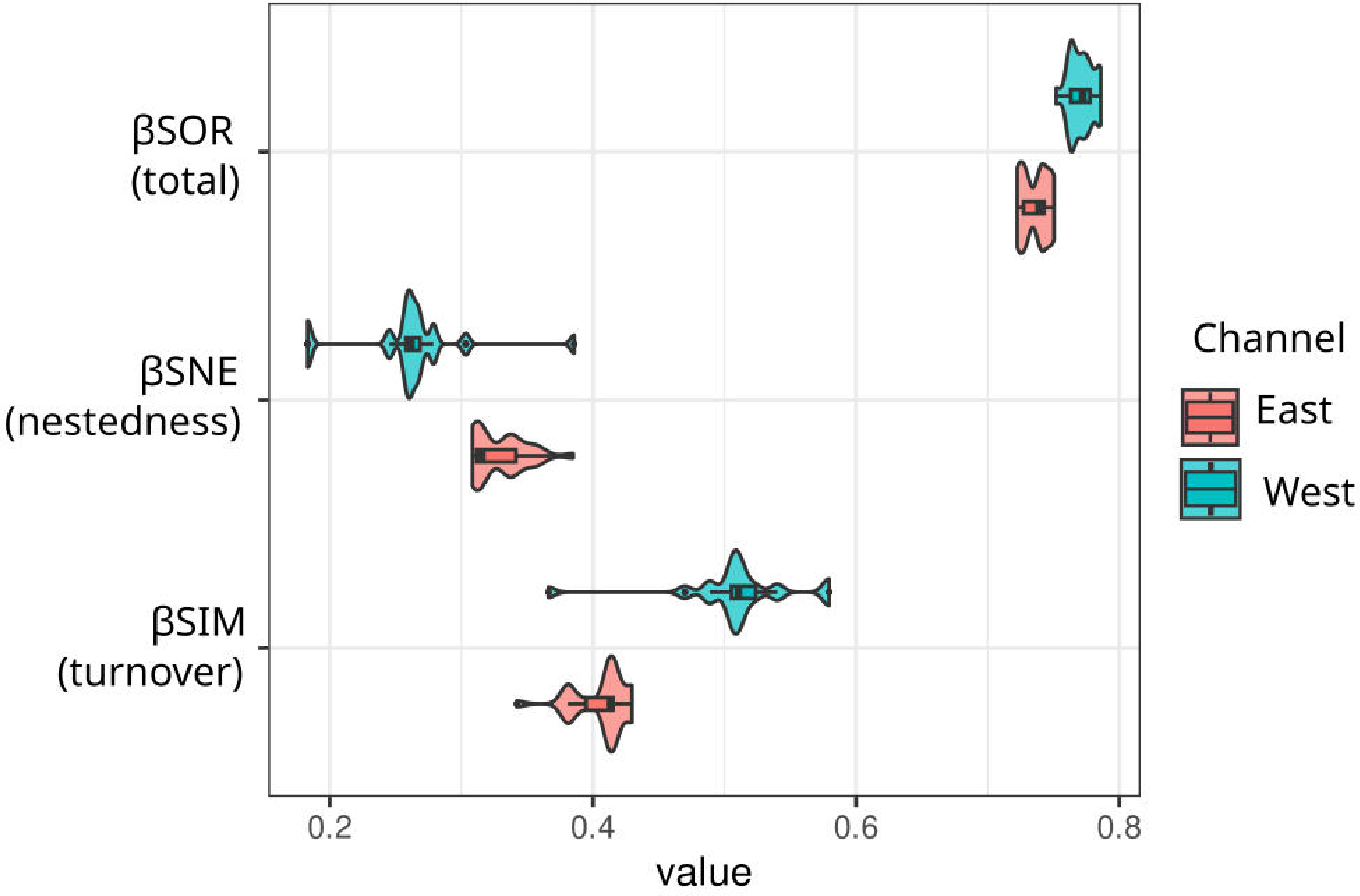
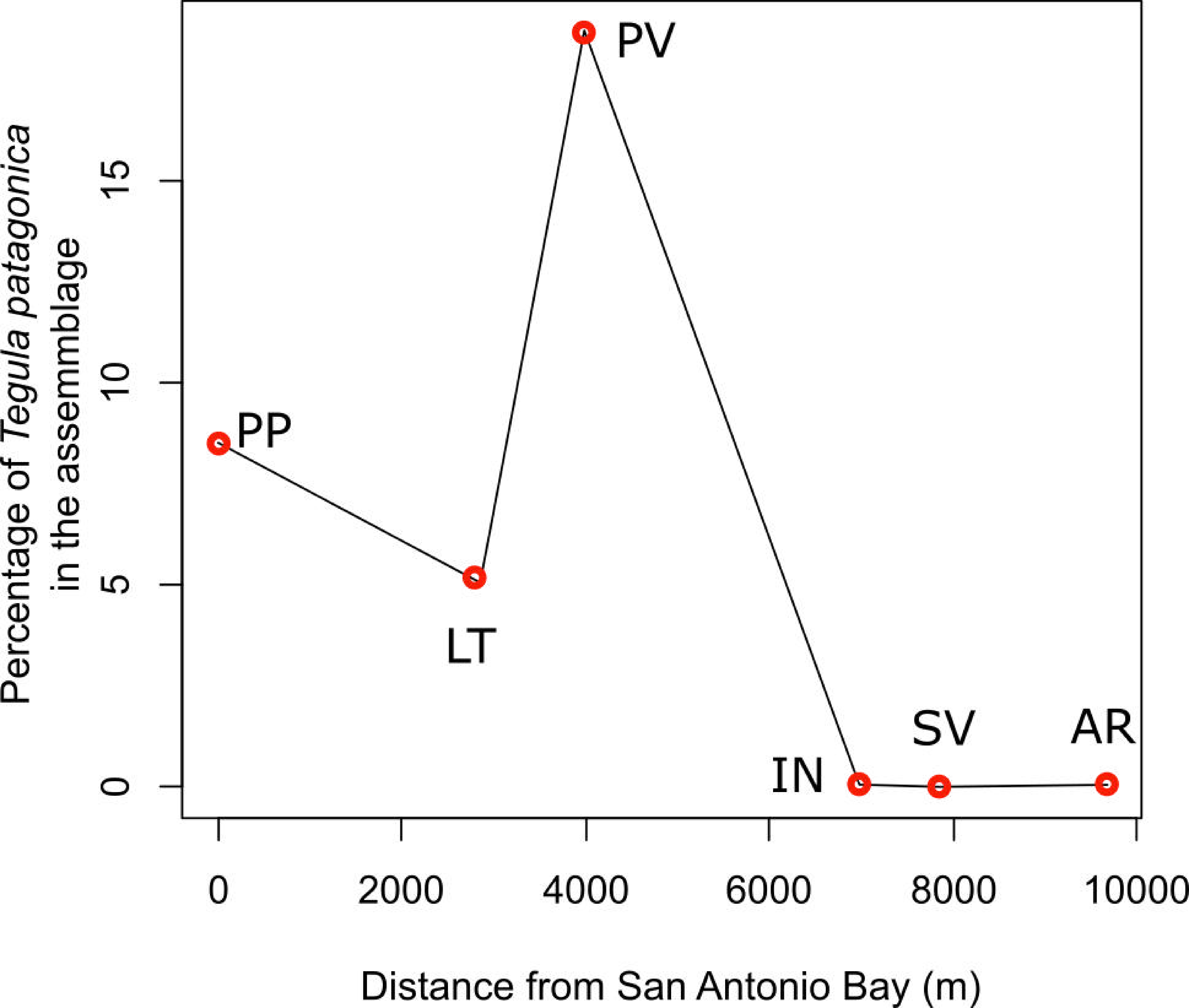
HeleobiaA
BostrycapulusO
TurbonillaR
OlivellaT
RDA 2
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6
0.8
B
PV
WCh
Ins
A
Distance
AgathistomaP
CarditameraP
AnachisI
CostoanachisS
FargoaB
HeleobiaA
BostrycapulusO
TurbonillaR
OlivellaT
PP
LT
Ech
SV
RDA 2
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2
-1
0
1
2
RDA 1


A
N0 (species richness)
5
10
15
B
Rarefaction. n=100
2
4
6
8
10
12
C
N1
1
2
3
4
5
6
7
D
N2
1
2
3
4
5
AR
IN
PV
PP
LT
SV
Locality


LCBD
0.05
0.10
0.15
AR
IN
PV
PP
LT
SV
Locality


βSOR
(total)
βSNE
(nestedness)
βSIM
(turnover)
0.2
0.4
0.6
0.8
value
Channel
East
West


Percentage of *Tegula patagonica* in the assemblage
Distance from San Antonio Bay (m)
0
5
10
15
0
2000
4000
6000
8000
10000
PP
LT
PV
IN
SV
AR