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Highlights

- Rocky intertidal communities' response to El Niño in a latitudinal transect
- Community changes driven by ecological processes rather than thermal tolerance
- Biogeographical patterns are persistent to El Niño

Abstract

The Peruvian coast experiences the largest interannual variability of sea surface temperature in the world due to the combined influence of the coastal upwelling and El Niño Southern Oscillation (ENSO). Although biological impacts of El Niño events have been widely reported, their effects on rocky intertidal communities remains largely unknown in Peru. Herein, we analyze the results of two biological surveys of rocky intertidal communities, conducted along 1400 km of the Peruvian coast. The first survey was conducted in 2015 yielding a snapshot of the distribution of rocky intertidal communities after 17 years of stable La Niña-like conditions. The second survey was carried in

October 2017, after the 2015-16 and the 2017 El Niño events, which produced warm sea surface temperature (SST) anomalies up to 6°C on the Peruvian coast. We find no changes throughout the latitudinal transect in taxonomic richness but an important turnover of species, especially marked in the transition zone (~4-8°S) between the Panamic and the Humboldt provinces. Temperature-related southward migration of species was evidenced in a few sites but did not explain the large-scale change in communities observed from 2015 to 2017, primarily driven by large changes in the distribution of a few ecologically important species across the Panamic and Humboldt provinces. A primary environmental impact on some ecologically key species likely triggered a chain of secondary impacts through ecological relationships which lead to a complex change independent from SST gradients. Further studies are needed to better characterize and disentangle the seasonal and interannual variability of the rocky intertidal communities and their drivers. When this interannual variability is integrated, the nine study sites show a highly persistent community structure determined by the latitudinal SST gradient along the Peruvian coast.

1. Introduction

El Niño Southern Oscillation (ENSO) is responsible for approximately 85% of the interannual climatic variability along the Peruvian coast (Carré *et al.*, 2013). El Niño, the warm phase of ENSO, generates sea surface temperature (SST) anomalies that are larger in Peru than anywhere else in the world, with widespread effects on marine ecosystems. During ENSO-neutral conditions of oceanic circulation and considering the low latitude, coastal waters are relatively cold (16-20°C) due to coastal upwelling. During El Niño events, the thermocline deepens in the Eastern Pacific preventing the upwelling of deeper cold and nutrient-rich waters to the surface. As a result, primary productivity is reduced and SST increases considerably between 3 to 18 months depending on the magnitude of the event (Wyrtki, 1975; Cane, 1983). Temperature anomalies can reach up to 8°C during extreme

events like those that occurred in 1982/83 and 1997/98 (Carré *et al.*, 2013). These interannual marine temperature anomalies are the largest in the world and, coupled with others abiotic cofactors (e.g., rainfall and salinity changes), can have significant impacts on the coastal biodiversity either directly or indirectly (Barber and Chavez, 1983; Paredes *et al*., 1998; Espino, 1999; Arntz *et al.*, 2006; Camus, 2008). The opposite phase of ENSO referred to as La Niña, is characterized by cooler conditions related to a shallower thermocline and an intensification of the coastal upwelling. These cold anomalies have lower amplitude, favor primary productivity, and are generally not considered as stressful conditions for the coastal Peruvian ecosystem (Wang and Fiedler, 2006).

To date, no continuous, periodic and comparable observations of rocky shores biological communities along the Peruvian coast and continental margin are available. Several studies document the biological effects of El Niño in Peruvian coastal ecosystems during the extreme 1982-83 and the 1997-98 events (Arntz, 1986; Glynn, 1988; Castilla and Camus, 1992; Arntz *et al.*,1988; Tarazona *et al*., 1988a; Tarazona *et al*., 1988b; Tarazona *et al*., 2003; Thiel *et al*., 2007; Camus, 2008) but focus on site specific variability. Information about the influence of ENSO on rocky intertidal benthic fauna and flora in Peru is thus scarce and has never been investigated along a latitudinal gradient.

Recently, Ibañez-Erquiaga *et al*. (2018) proposed a biogeographic zonation of rocky intertidal communities along the Peruvian coast based on a latitudinal survey performed from February to May 2015 in 41 coastal sites. The authors defined three biogeographic units: (1) a tropical, Panamic province (3.5 - 4.5° S), (2) a transitional zone (5 - 5.5° S), and (3) a temperate, Humboldt province (6 - 13.5°S). The model proposed by Ibañez-Erquiaga *et al.* (2018) provides a snapshot of the latitudinal distribution of rocky intertidal communities after 17 years of relatively cool and stable La Niña-like conditions after the strong 1997-98 El Niño event. Herein, we add data from a survey performed in October 2017 at 9 sites (among those sampled by Ibañez-Erquiaga *et al*., 2018) distributed along 1400 km of the Peruvian coast (from 3.7 to 13.9° S) (Figure 1). Thus, we assumed that ecosystems

had fully recovered from the 1998 El Niño disturbance and were under the long-term influence of La Niña conditions in Peru.

Two El Niño events occurred between surveys. The 2015-16 El Niño is considered among the most powerful of the last decade (Huang *et al*., 2016), with a maximum anomaly located in the central Pacific region and a moderate warming in the Eastern tropical Pacific and in the Peruvian coast (Figure 2). Soon after, a short-lasting El Niño event occurred from January to May 2017 (known as coastal El Niño), characterized by a much larger temperature anomaly but restricted to the coast off Peru and Ecuador (Echevin et al., 2018; Garreaud, 2018). In central Peru, SST anomalies reached 6° C (Figure 2) and together with catastrophic rainfall and floods across the coast (Rodríguez-Morata *et al.*, 2018). Although not as severe as the extreme 1982-83 and 1997-98 events, the 2017 coastal El Niño event has been considered as a strong but localized event for the amplitude of the temperature anomaly on the Peruvian coast (Echevin et al., 2018; Garreaud, 2018). Our second survey was conducted in October, about 4 months after the end of this event. Therefore, this second survey is ideal to assess long-lasting impacts of El Niño environmental variability in biological communities after a long period of being predominantly under rather cool neutral or La Niña conditions.

Ibañez-Erquiaga *et al*. (2018) showed that temperature and nutrients are strongly linked with the biogeographic zonation of benthic rocky communities. Since surface warm water masses are also characterized by low nutrient concentration, here we use SST anomalies as an integrated indicator of the oceanographic state on the Peruvian coast. We expected long-lasting impacts of El Niño on the rocky shore communities including changes in the species diversity and in the latitudinal pattern of community composition due to mortality, southward migration, and a southward shift in species recruitment.

The objective of this study is twofold. First we aimed to evaluate the cumulative impact of the 2015-16 and 2017 El Niño events on species diversity and geographic distribution of benthic rocky intertidal communities across the Peruvian Pacific coast, by assessing changes in the characteristics

and latitudinal patterns in the communities before and after the El Niño events in relationship with SST anomalies along the coast. Because earlier systematic records of rocky shore communities are not available in Peru, our approach lacks referential observations, but is also the first study of rocky intertidal communities' response to El Niño in a latitudinal transect. Our second aim was to assess the robustness of the bioregionalization to inter-annual variability, as well as the relative influence of mean SST conditions versus El Niño-related SST anomalies as long-term abiotic drivers of the biogeographic zonation of rocky intertidal species along the Peruvian coast, comparing the biogeographic zonation of rocky shore communities with latitudinal gradients in long-term statistics of coastal SST including ENSO-related variability.

2. Materials and Methods

2.1. Study area, site selection and sampling design

We studied nine rocky shore sites of the Peruvian coast, from Acapulco (3.74° S, 80.77° W) to La Mina (13.91º S, 76.31° W) encompassing a 1400 km stretch of coastline (1200 km in direct line), or a variation of 11.63° latitude and 6.14° longitude (Figure 1). These nine sites were selected among the 41 sites survey performed between February and May of 2015 by Ibañez-Erquiaga *et al*. (2018) allowing a direct comparison in these localities. Sites were separated by 0.5 to 2.8° of latitude with a shorter distance between northern sites where gradients are steeper and where the transition between the Panamic and the Humboldt ecoregion was reported (Figure 1, Table 1). Fishing, recreational, or urban areas were avoided to minimize the anthropogenic influence in community composition. Selected sites were rocky shore, with wave-exposed platforms from 25 m^2 to ~1000 m^2. The slope of the rock platform did not exceed 45°. Caves and crevices were not surveyed to keep a homogeneous flat sampling area. At each site, observations were performed in a representative sample of the intertidal zone through a total of 16 quadrats distributed in four haphazardly-distanced (in a range of

3-10m) transects of four quadrats distributed from the upper intertidal to the lower intertidal zones. We used a 0.25 m^2 quadrat of 0.50 m x 0.50 m with a 100-intersection grid. In each transect 4 intertidal fringes were identified according to the presence of litorinids (upper), sessile barnacles (mid-high), mussels (mid-low) and macroalgae and anemones (low) following the sampling method presented in Broitman *et al*. (2001), Rivadeneira and Fernandez (2005) and Ibañez-Erquiaga *et al*. (2018). Within each fringe and along the transect, one quadrat was randomly placed on plain rock surface. We used a 0.25 m2 quadrat of 0.50 m x 0.50 m with a 100-intersection grid. Each site sampling cover thus a total surface area of 4 m² and 1600 point-intersects, which is similar to previous rocky shore studies in the Pacific (Broitman et al., 2001; Blanchette et al., 2008; Rivadeneira and Fernandez, 2005; Ibañez-Erquiaga et al., 2018). Sampling was conducted during the lowest tide at daytime and lasted about 3 hours per site.

Table 1. Study sites coordinates and sampling dates

Site name	Sitecode	Latitude °N	Longitude °E	1st sampling	2nd sampling
Acapulco	ACA	-3.74	-80.77	22/02/2015	2/10/2017
PuntaVeleros	PVE	-4.17	-81.14	21/02/2015	6/10/2017
PuntaBalcones	PBA	-4.68	-81.32	1/03/2015	5/10/2017
Yacila	YAC	-5.12	-81.16	3/03/2015	3/10/2017
PuntaAguja	PAG	-5.80	-81.08	15/03/2015	4/10/2017
Puemape	PUE	-7.51	-79.54	10/03/2015	7/10/2017
Tamborero	TAM	-10.32	-78.05	8/04/2015	8/10/2017
Pucusana	PUC	-12.47	-76.79	17/04/2015	13/10/2017
La Mina	MIN	-13.91	-76.31	8/05/2015	18/10/2017

The zonation pattern for the region sampled has been described in Paredes (1974) for the central coast, and further characterized by Ibanez-Erquiaga et al. (2018). These authors describe for the rocky intertidal of the Panamic Province, the predominance of *Jehlius cirratus* and *Austrolittorina araucana* for the upper intertidal level, Ulva spp. for the middle level, and *Semimytilus algosus* with

Grateloupia filicina in the low level. In the Transition Zone, *J. cirratus* and *Echinolittorina* spp. are predominant in the upper intertidal level, *Ulva* spp. and *Phragmatopoma* spp. characterize the middle level, and *G. filicina* with *Ahnfeltiopsis durvillaei* are predominant in the lower level. For the Humboldt ecoregion, *J. cirratus* and *Echinolittorina* spp. are predominant in the upper intertidal level, *Perumytilus purpuratus* and *Ulva* spp. characterize the middle level, and *S. algosus* the lower level.

2.2. Data collection at the rocky intertidal habitat

A commonly used minimum size of 0.5 cm was chosen as size limit for individuals to be counted. Mobile species (e.g. limpets, snails, crabs, mobile polychaetes) were counted as individuals present within the quadrats (4m² in total), and their abundance was reported in number of individuals per square meter. The abundance of sessile species (e.g. mussels, barnacles, algae, anemones, sessile polychaetes) was measured as a percentage of coverage using a 100-point grid within quadrats (1600 intercept points in total). Percentage of rocky and sandy substratum was also quantified. When full taxonomic identification was not achieved *in situ*, specimens were collected in 96% alcohol (invertebrates) or 4% formalin (algae) for further examination in the laboratory. Some genera include species that cannot be differentiated visually in the field, such as *Scurria* or *Ulva*, which means that their identification and quantification in the laboratory would require the collection of all individuals in the field. This option was not chosen because of its high environmental impact, so that these genera are not resolved here to the species level. *Scurria* species have been shown to be separated by small scale processes rather by large scale biogeographic features (Aguilera et al. 2013), so that this taxonomic limitation is not expected to induce any significant bias in our study. Collected samples were deposited at the collection of the Marine Biology Laboratory of the Universidad Peruana Cayetano Heredia in Lima, Peru. In the laboratory, a stereoscope or microscope was used to sort

specimens into major taxa and then identified to the lowest possible taxonomic level. When possible, Holothurian ossicles were extracted and observed to identify to the species level. Where the taxonomic uncertainty persisted, species were pooled into genera. Taxonomic identification was double checked for consistency.

2.3. Temperature data

Sea surface temperature (SST) data was obtained from the Multi-scale Ultra-high Resolution (MUR) SST Analysis fv04.1, Global, 0.01°x0.01° (Vazquez *et al.*, 1998; JPL MUR MEaSUREs Project, 2015). The monthly time series covers the period from June 2002 to April 2018. This dataset was chosen because coastal features can be captured by the ultra-high spatial resolution of ~1 km. In figure 3, we show maps of (A) mean annual SST, (B) annual SST range, (C) mean July SST, (D) mean February SST, and (E) the influence of ENSO estimated by the variance (squared standard deviation) of SST anomalies. SST statistics were calculated over the 2002-2018 period. Monthly anomalies were calculated in reference to the 2003-2016 period. For all these variables, the trend observed along the coastline was plotted *vs*. latitude. Monthly time series of SST anomalies calculated for each sampling sites are shown in figure 2. The map of SST anomalies observed in March 2017 (Figure 3F) shows the spatial pattern of the maximum temperature stress of the 2017 Coastal El Niño event.

2.4. Data analysis

A sampled based rarefaction analysis (Gotelli and Colwell, 2001) was performed to assess the sampling representativeness for the nine sampled localities. Taxa composition (presence/absence), abundance (number of individuals per square meter for mobile species, or percentage of coverage for

sessile species) and the Chao2 estimator of species richness (Chao et al., 2009) were calculated for each site and each survey. Chao2 index values were calculated with presence/absence data of all taxa using the R package SpadeR (Chao et al., 2016).

Non-metric multi-dimensional scaling (nMDS) was used to build ordination plots calculated from the Sorensen-Dice similarity matrices. The nMDS analyses were conducted with the presence-absence data set of sessile and mobile species using the R package 'vegan' (Oksanen *et al.*, 2010). The nMDS analysis was first applied to the full 2015 presence/absence dataset (41 sites) together with the 2017 dataset (9 sites) to assess the dissimilarity between these two periods and test if the samples from 2017 fit in the 2015 latitudinal pattern. The same analysis was repeated without singletons (taxa that have been recorded in only one site and one year) to assess the effect of rare species (Supplementary information). The difference between abundance data and presence-absence data in the sites surveyed in 2015 and 2017 was calculated to detect species with large changes in their abundance or spatial distribution (Tables S1 and S2). We evaluated the median latitude of the distribution before and after the El Niño events for each species observed both in 2015 and 2017. We compared median latitudes in 2015 to those observed in 2017 using a paired t-test to assess a potential latitudinal shift in species distributions.

Observations of 2017 were then combined with those obtained in 2015 in the same sites to test whether the biogeographical zonation is robust to interannual variability. A second nMDS analysis was performed for the combined dataset using the same methodology (Bray–Curtis similarity matrices using presence-absence data). The influence of temperature on the rocky intertidal biogeography was evaluated by least square linear regressions between the principal axis of this second nMDS ordination and SST statistics calculated over the 2002-2018 period (annual mean, February mean, July mean, and the variance of SST anomalies).

A power analysis was performed using the G*Power 3.1 software (Faul et al., 2009) when no correlation was detected between two variables. Post hoc evaluations were performed for bivariate regression assuming normal distribution, using a 0.05 α significance level, and correlation coefficient R = 0 as null hypothesis. We report $R_{P0.8}$, the minimum value of the true correlation coefficient so that the dataset statistical power is above 0.8. In other words, $R_{P0.8}$ represents the correlation coefficient that the dataset can reject with a type II error probability less than 0.2, which is the recommended threshold in statistical power analysis (Peterman, 1990). We also report the achieved post-hoc power.

Linear correlations were tested for spatial autocorrelation by evaluating the significance of the Moran's I coefficient through Monte Carlo and normal distribution (Supplementary information). When strong autocorrelations were found, generalized least squares (GLS) models were calculated so the influence of the spatial structure was incorporated into the linear regression model through the residual terms (Diniz-Filho et al., 2003). Different correlation spatial structures were tested, and the best fitting model was defined using the lowest Akaike Information Criterion (AIC) along with the less negative Log-Likelihood (LogLik) values (Supplementary information). Finally, a cluster analysis using Sorensen-Dice index was performed, using the software 'PAST' (Hammer *et al*., 2000), to study the similarity between study sites using presence-absence data of mobile and sessile species. Robustness of tree topologies was assessed through 10000 bootstrap replications. All statistics, except when noted, were done using R 3.5.0 (R-Core Team, 2018), through the *spdep* (Bivand et al., 2013), *nlme* (Pinheiro et al., 2018), and *MuMIn* (Barton, 2020) packages.

3. Results

Sites are listed in table 1 and hereafter referred to in the text and figures by their acronym and latitude. The 2017 dataset is composed of 1076 observations (an observation being the

documentation of the presence of any given species within a set quadrat) resulting in 79 taxa, while 924 observations, resulting in 69 taxa were obtained in the same sites in 2015. Due to spring tides, hazardous swell or other logistic constrains, data from 13 quadrats (1 in PVE[4.17°S], 3 in TAM[10.32°S], and 8 in PUC[12.47°S], representing 9.0% of the sampled surface) in 2015 and data from one quadrat (PBA[4.68°S], representing 0.7 % of the sampled surface) in 2017 could not be sampled. Observations obtained in 2015 and 2017 for the nine analyzed sites are reported in the online supplementary data Table S1 as abundance data and in Table S2 as presence/absence data. The complete 2015 dataset (41 sites) is available online in Ibañez-Erquiaga *et al*. (2018). Sampled-based rarefaction analysis showed that the number of taxa is reasonably close to the asymptotic maximum in the nine locations and both surveys, indicating that sampling effort was enough for obtaining an acceptable representation of the taxonomic richness (Figure 4), thus supporting the validity of the following analyses.

3.1. Species incidence and abundance

In this study 104 taxa were identified, of which 79 were identified to the species level. 40 species were observed only once in the 9 study sites.

The most abundant sessile species was the barnacle *Jehlius cirratus* (19.5% of total coverage in 2015 and 13.6% in 2017). Other species with high abundance include the green algae *Ulva* spp., and the encrusting algae *Lithophyllum* spp.. The most abundant mobile species were the periwinkle *Echinolittorina* spp. (accounting for 46.8% of total abundance in 2015 and 24.3% in 2017, reaching top densities of 521.3 individuals per m^2 in TAM[10.3°S] in 2015, the limpet *Scurria* spp.. The periwinkle *Austrolittorina araucana*, highly abundant and characteristic of the upper intertidal zone in 2015 had disappeared in these sites in 2017 (Table S1).

Among the 24 most abundant taxa (each representing over 1% of the total abundance or coverage), a majority was ubiquitous: *Echinolittorina* spp., *Jehlius cirratus*, *Scurria* spp., *Ulva* spp., *Tegula* spp.,

Lithophyllum spp., *Corallina officinalis*, encrusting brown algae. The anemone *Oulactis concinnata* was the most abundant sessile species in the two northernmost sites ACA[3.7°S] and PVE[4.2°S]. Taxa with high abundance and only occurring in the Humboldt province include the mussel *Perumytilus purpuratus*. Taxa with high abundance occurring only in the transition zone were the snail *Stramonita haemastoma* and the red algae *Gelidium pusillum*.

We now report changes in taxa presence, abundance, and distribution between 2015 and 2017. 44 taxa have been identified both in 2015 and 2017. 25 taxa were observed in 2015 in those sites but not in 2017, while conversely, 35 taxa were only observed in 2017. Among those 60 taxa that appeared or disappeared, most (65%) are rare (observed only once). However, some of them, were widespread and/or abundant in one of the surveys.

Among the taxa that disappeared, 3 were widespread in 2015. The most notorious is *Austrolittorina araucana*, abundant in all sites of the northern and central coast of Peru in 2015 in the upper intertidal zone. The macroalgae *Grateloupia filicina*, abundant in 2015 in the central coast, from 5 to 10°S, was not observed in 2017. The snails *Diloma nigerrimum* and *Prisogaster niger*, present in 2015 in the southern sites, disappeared in 2017. *Polysiphonia spp*. observed in 3 sites at different latitudes in 2015 was absent in 2017. Important taxa whose distribution was strongly reduced in 2017 include the limpet *Siphonaria* spp. which disappeared from 5 sites but curiously appeared in great abundance in 2017 in PAG[5.8°S]. The algae *Gymnogongrus durvillei*, the anemone *Phymanthea pluvia*, and the mussel *Semimytilus algosus* disappeared from 4 sites, which shifted their distribution southward by 4.8°, 6.4°, and 1.8° of latitude, respectively. *Jehlius cirratus*, the most abundant sessile species of the Peruvian rocky shores, showed a decreased coverage in most sites in 2017.

The 2017 survey also showed remarkable increases in some taxa. 4 taxa appeared in 3 to 6 sites in 2017: the snails *Mitrella baccata* and *Stramonita biserialis* in the northern sites, the cucumber

Patallus mollis in the south, and the sea anemona *Phymactis clematis* from 4.7° to 13.9°S. *Fissurella* spp., restricted to 2 northern sites in 2015, spread in 5 sites down to the southernmost site. The chiton *Acanthopleura echinata* was observed in 3 more sites. The limpet *Scurria spp.*, as well as the algae *Corallina officinalis* and the encrusting brown algae (possibly *Ralfsia* sp.) became more widespread and abundant and tend to expand their distribution northward.

We thus observe that some taxa shifted their distribution southward while others shifted northward. The average latitudinal shift (estimated by the change in the median latitude of taxa presence) of all taxa is not significant (t-test). Among the 9 main taxa that showed an increased abundance and distribution, 6 are mobile and 3 are sessile. On the contrary, among the 8 main taxa that showed a decreased abundance and distribution, a majority is sessile (5) and a minority is mobile (3).

Table 2. Summary of taxa richness and changes from 2015 to 2017

Number of taxa	ACA* [3.7°S]	PVE [4.2°S]	PBA [4.7°S]	YAC [5.1°S]	PAG [5.8°S]	PUE [7.5°S]	TAM [10.3°S]	PUC [12.5°S]	MIN [13.9°S]
In 2015 (N_0)	24	26	14	25	16	18	25	20	21
In 2017 (N_1)	9	26	25	22	23	22	22	15	25
appearing (N_a)	5	13	18	7	13	14	7	7	12
disappearing (N_d)	20	13	7	10	6	10	10	12	8
persisting	4	13	7	15	10	8	14	8	13
net change	-15	0	11	-3	7	4	-3	-5	4
turnover % **	75.8	50	64.1	36.2	48.7	60	36.2	54.3	43.5

* This site was not representative of the rocky intertidal in 2017

** $100(N_a+N_d)/(N_0+N_1)$

3.2. Species richness and species turnover

The differences in the Chao2 richness estimator from 2015 to 2017 does not show any clear geographical pattern. When considering all sites together, no significant difference was detected in species richness between 2015 and 2017, neither for mobile, sessile taxa, or all taxa together (Wilcoxon signed rank test, and t-test, $p>0.95$ in all cases). Thus, at regional scale, no significant

increase nor decrease in the taxonomic richness as estimated by the Chao2 index was detected four months after the El Niño events.

Some substantial changes were site specific. A strong reduction of species richness is observed in 2017 in ACA[3.7°S], which can be explained by a significant increase of sand coverage (t-test, $p<0.05$) in this site and the subsequent reduction of the rocky intertidal (only two mobile species were registered while 8.5 mobile species per site were registered in average). In other sites, rock coverage did not vary among sampling sets (Wilcoxon signed ranks test, $p=0.91$), and sand coverage of the rocky shore areas was zero south of 5° S. This change in ACA[3.7°S] was possibly the result of coastal geomorphological dynamics due to increased river discharge and sandbank movement during the 2017 El Niño event (Rodríguez-Morata *et al*., 2018).

The large decrease in species richness observed in the southern site PUL[12°S] is likely related to the incomplete sampling in 2015 when only 8 out of 16 quadrats could be sampled because of logistics constraints. This results in a large data dispersal in the Chao2 index for 2015. A significant increase in species richness is observed in PAG[5.8°S], a site that lies in the biogeographic transition zone. The number of taxa recorded in this site increased from 16 in 2015 to 23 in 2017 (Table 2). This net increase is composed by a loss of 6 species (2 mobile and 4 sessile) and a gain of 13 species (7 mobile, 6 sessile). The largest net increase in the number of species is observed in PBA[4.7°S] with 11 additional species in 2017 (2 mobile, 9 sessile) compared to 2015. However, the small difference in the Chao2 index values suggest this may mainly result from under-representation of the 2015 sample.

The turnover of taxa from 2015 to 2017 is relatively high (Table 2), from 36% taxa in TAM[10.3°S] (17 taxa appearing or disappearing in the record) to 64% taxa in PBA[4.7°S] (25 taxa appearing or disappearing in the record). One of the largest change in taxa is observed in the northern site PVE[4.2°S], with 13 taxa that disappeared and 13 new species in the 2017 record compared to 2015.

3.3. Dissimilarities of rocky intertidal communities between 2015 and 2017

In the first nMDS ordination analysis, samples from 2017 are dissimilar to 2015 along axis 2, while both datasets are similarly distributed along axis 1 (Figure 6A). This latter result suggests that, in 2015 like in 2017, the communities are primarily structured by the same environmental factors. For instances, sites observed in 2017 after the El Niño events are similar along axis 1 as also observed for 2015. The axis 1, which explains 54% of the variability of the complete dataset, is clearly related to the latitudinal mean SST gradient (Figure 6B). The sites surveyed in 2017 are aligned along a similar relationship with mean annual SST as the 41 sites surveyed in 2015 (Figure 6B) confirming that the rocky intertidal communities are latitudinally structured, as already shown by Ibañez-Erquiaga et al. (2018), and that this latitudinal gradient persisted after the El Niño events.

The axis 2, which explains 33% of the variability, seems largely driven by the difference between 2015 and 2017. All the sites surveyed in 2017 show a positive shift along axis 2 since 2015 (arrows in figure 6A). Because a large proportion of taxa have been observed only once (~40%), we performed a nMDS analysis excluding singletons, which showed a similar pattern (Supplementary information). The separation of the 2015 and 2017 dataset along axis 2 is therefore not related to the occurrence of rare and potentially seasonal species, but rather to the changes in the distribution of important species described in section 3.1. The disappearance of *Austrolittorina araucana*, *Prisogaster niger*, and *Grateloupia filicina* in the 2017 samples together with the widespread apparition of *Mitrella baccata*, *Stramonita biserialis*, and *Phymactis clematis* played in particular a major role. As a consequence, the dissimilarity between the 2015 and 2017 surveys is likely due to environmental factors which may be related to El Niño or to seasonal variations since the 2015 observations were made between February and April while 2017 observations were made in October.

The similarity of the 9 sites surveyed in 2017 compared to the 41 sites surveyed in 2015 is observed in a cluster analysis (Figure 7). Besides two 2105 sites separated because of anthropogenic impact (ANC and BAR) and ACA[3.7°S] which was covered in sand in 2017, the sites are distributed in 4 groups, which, despite low bootstrap values, are biogeographically consistent. The northernmost site of 2017 PVE[4.2°S] (pink branch), the Peruvian Panamic province (orange branches) in which PBA[4.7°S] and PAG[5.8°S] are included in 2017, the transition zone (red) as defined in 2015, and the Humboldt province in which 4 sites of 2017 are grouped together. All sites of the Humboldt province in 2015 belong to the Humboldt province of 2017, except for the northernmost, PAG[5.8°S], which appears in the Panamic province group in 2017. The cluster analysis indicates that 2017 samples tend to group together within their respective ecological province, which confirms that the change in rocky intertidal communities from 2015 to 2017 does not correspond to a replacement of Humboldt communities by Panamic communities, but rather to the emergence of new taxa assemblages. The outside position of PVE[4.2°S] in 2017 suggests the record of a dissimilar Panamic community in northern Peru in 2017. This is supported by the fact that among the 13 new taxa observed in PVE[4.2°S] in 2017, 8 have not been observed in any other site, and 2 were only observed further north in ACA[3.7°S] in 2015.

3.4. The latitudinal structure of rocky intertidal communities

Whatever their cause, the differences between 2015 and 2017 evidence a strong seasonal to interannual variability of rocky shore communities. The 2017 observations were pooled with the 2015 observations from the same sites and analyzed to test the robustness of the biogeographical zonation found in rocky intertidal communities by Ibañez-Erquiaga et al. (2018) to this interannual variability. The nMDS ordination analysis of the pooled dataset provided a pattern that is consistent with the site latitudinal sequence (Figure 8A). The nMDS analysis showed a slight horseshoe effect,

which is common in ordination techniques due to the fact that the axes are forced to be uncorrelated, but are not necessarily independent (Legendre and Gallagher, 2001). The first axis explained 84% of the ordination and the second axis 1%.

We evaluated the relationship between the long-term persisting geographical structure of the rocky intertidal communities with long-term SST statistics. The fist axis was significantly and strongly correlated with mean annual SST (R=0.93, p=0.001) (Figure 8B) and mean SST of July (winter) (R=0.89, p=0.001). Statistically significant spatial autocorrelations ($p<0.05$) were observed between these two variables and the first axis, however, in both cases GLS maintain significant correlations (p=0.0001 for the mean annual SST and p=0.004 for the mean SST of July) with lower AIC values (23.29 and 23.92, respectively) improving the explanatory power of the model (Supplementary information). The correlation observed between the first axis and with mean SST of February (summer) (R=0.77, p=0.195, $R_{P0.8}$= 0.79, power=0.87) was not significant, suggesting that summer temperatures are less determinant than winter temperatures in the biogeography of rocky intertidal species. On the other hand, no correlation was observed between the ordination´s first axis and long-term ENSO-related variability (R=0.10, p=0.82, $R_{P0.8}$= 0.79, power=0.06) (Figure 8C) nor with the mean seasonal SST range (R=0.06, p=0.872, $R_{P0.8}$= 0.79, power=0.05).

The cluster analysis of the pooled incidence dataset (Euclidian cluster, R=0.93) confirms that the latitudinal organization of rocky intertidal communities found in the snapshot observation of 2015, is maintained when the interannual variability is integrated (Figure 9). Locations were grouped into two main branches: the northern branch, corresponding to warm conditions of the Panamic province includes ACA[3.7°S] and PVE[4.2°S]. The southern branch is itself devided in two groups: the transition zone, which includes three sites located to the north of the Illescas Peninsula, PBA[4.7°S], YAC[5.1°S] and PAG[5.8°S], and the Humboldt province which includes the 4 remaining southernmost sites. High bootstrap scores indicate a robust structure.

4. Discussion

4.1. Changes in taxonomic diversity

The effects of El Niño on intertidal communities depend on the intensity and magnitude of the event. Although, the coupled oceanographic-atmosphere variability is similar, the biological responses are not always predictable (Arntz *et al*. 2006). Some responses are similar among events, strong El Niño (1982-83 and 1997-98) increased the diversity of macrobenthos on hypoxic soft-bottoms due to the increase of oxygen concentration, and colonization by low latitude immigrant species in central Peru (Tarazona *et al*. 1988a,b). Also, neritic fish assemblages would add tropical species and cold-adapted fish would extend their distributional ranges down to central Chile (Sielfeld *et al*. 2010). In rocky shore communities the most important change documented is the mass mortality of kelp beds (Martínez *et al*. 2003) which could open rocky primary space in Peru and northern of Chile. This could trigger the colonization and recovery of communities via immigration and settlement of surviving species, but there is no available evidence on how this could affect diversity patterns. Our results indicate that, at the scale of the north-central Peruvian coast, the 2015-2016 and the 2017 El Niño events did not promote an overall change in the taxonomic richness of rocky intertidal communities. The disappearing of species between the two surveys was in average compensated by the occurrence of new species. We tested whether this could mask spatial contrasts related to the fact that the 2017 El Niño SST anomaly was not of equal amplitude along the latitudinal transect of our study. SST anomalies peaked everywhere during March 2017 (Figure 2), but were highest (5-6°C) along the central coast between 5 and 9°S (Figure 3F), and limited to 1-2°C in the northernmost and southernmost sites. No significant relationship is observed between the amplitude of the El Niño 2017 SST anomaly and the Chao2 estimator change, nor with the level of taxa turnover, which may be partly due to the low statistical power resulting from the limited number of sites. However, the

largest increase in Chao2 index was observed in PAG[5.8°S], the largest net increase in taxonomic richness in PBA[4.7°S], and the largest turnover in PBA[4.7°S] and PUE[7.5°S]. All these sites experienced El Niño SST anomalies larger than 5°C, supporting some level of impact of the 2015 and 2017 El Nino events on rocky intertidal diversity, especially in the transition zone.

4.2. Changes in species distribution

The warm anomaly associated to an El Niño event may be a stressor for some species and may favour others, while some El Niño adapted species would show no response at all (e.g. Barahona *et al*. 2019). Overall, it could be predicted that El Niño produces a southward shift of species, either by inducing mortality in the northern limit of their distribution where conditions would exceed some physiological or ecological threshold, or by favouring a migration towards higher latitudes (Riascos et al., 2009; Sotil et al., 2008; Carstensen et al., 2010). Here, we found that the average shift of incidence median latitude is non-significant for mobile or sessile taxa (t-test). The large distribution changes observed for some taxa were not all directed southward.

Based on presence/absence analysis a pattern among sites and years emerge. Mobile gastropods such as *Fissurella* spp., *Mitrella baccata*, *Scurria* spp., *Stramonita biserialis*, and the sea anemone *Phymactis clemactis* were present in most of the sites sampled in 2017 but almost absent in 2015. These species are mobile and while they can inhabit exposed rocky surfaces, they can also move into crevices and sheltered areas of the habitat. Thus, these species may undergo undetected during sampling, but it is unlikely that this may have happened at multiple sites. The same reasoning applies to those taxa present in 2015 but absent or strongly reduced in 2017: gastropods *Austrolittorina araucana*, *Prisogaster niger*, *Siphonaria* spp., the anemone *Phymanthea pluvia*, but not for the mytilid *Semimytilus algosus*, and algae *Grateloupia filicina*, *Gymnogongrus durvillei*, *and Polysiphonia* spp.. *G. filicina* is considered an annual species, with plants showing higher

abundances and sizes during summer, and re-growing from the perennial attachment disc in spring after overwintering (Irvine 1983). The absence of *G. filicina* during 2017 spring could be explained by the fact that the perennial attachment disc is difficult to identify in the field or by the small size of young plants growing from it. In contrast, *G. durvillei* is usually found all year in central and north-central coast of Peru (Hidalgo et al. 2008; Li-Alfaro and Zafra-Trelles 2012; Pisfil-Farro 2014; Rojas-Paredes 2014). Its absence in multiple sites during spring 2017 could not be attributed to seasonality and is likely linked to El Niño events. *S. algosus* (Tarazona *et al*. 1985) and other mytilids (e.g., Gamarra and Cornejo 2002; Avendaño and Cantillanez 2011) have been reported to experience mortality and recruitment failure during and after strong El Niño events.

The ecology and seasonality of most marine species from Peru remains unknown. In the absence of long-term control observations, we cannot clearly attribute the observed changes in distribution and abundance to seasonal processes or to El Niño perturbations (Paine, 1986). Sessile taxa should, however, exhibit less seasonal variation in the presence/absence data and may thus reflect more closely direct or indirect El Niño impacts. Among widespread sessile species, 2 were completely absent in 2017 (*G. filicina*, *Polysiphonia spp*.) and 3 were strongly reduced (*G. durvillei* , *P. pluvia*, and *S. algosus*) and all shifted south, which is consistent with a SST-related stress. Some sites reveal some interesting changes: the fact that PAG[5.8°S] taxon assemblage belonged to the Humboldt province in 2015 and to the transition branch after the El Niño events in 2017 (Figure 7) suggests that the new rocky intertidal community in this site is at least partly due to southward species migration facilitated by El Niño conditions from 2015 to 2017. The occurrence of 8 new Panamic species in PVE[4.2°S] in 2017, which places this northernmost assemblage outside the cluster analysis (Figure 7), also supports a southward migration of species consistent with the expected impact of El Niño events.

Some taxa, on the other hand, do not fit in this scenario. The three sessile taxa that widely spread from 2015 to 2017 (*Corallina officinalis, encrusting brown algae, Phymactis clematis*) are not warm water taxa but ubiquitous taxa, that expanded in both Panamic and Humboldt provinces. A few species also show an interesting northward expansion (brown algae *Colpomena tuberculata*, *Colpomena sinuosa*). The expansion of those species was therefore not caused by favourable physical conditions during El Niño events, but was more likely an indirect consequence of those events through a modified ecological network.

4.3. El Niño impacts on community structure

Changes in community structures between 2015 and 2017 are evidenced in the nMDS (Figure 6) and the cluster analysis (Figure 7). These changes are linked to large changes in the latitudinal distribution of a few widespread species, likely caused, at least for some of them, by El Niño regional environmental anomalies occurred in 2015-2016 and 2017. Quantifying how much of the community change can be attributed to El Niño and how much to seasonal variations will require additional surveys in those sites.

The change in the communities from 2015 to 2017 was not characterized by a shift along a temperature-related axis (axis 1 of nMDS analysis, Figure 6) as one could expect from El Niño impacts. The 2017 communities are thus not simply the result of the southward migration of species and the replacement of "temperate" taxa by "Panamic" taxa. This process, which has been reported for earlier extreme El Niño events (Tarazona et al. 1988a,b; Arntz et al. 2006) was only secondary here, possibly because the amplitude and duration of the temperature anomaly was not as large than in those extreme events. The primary process responsible for the 2015 to 2017 community change might thus be ecological.

Since some of the taxa impacted here are major component of the rocky intertidal communities, we can speculate that their local disappearing or expansion produced a secondary positive or negative impact on other taxa that had not been directly affected by the physical or chemical anomalies associated to the El Niño events. In this view, the physico-chemical conditions of El Niño may have only been the trigger of a chain of impacts across the ecological network of Peruvian rocky shores. A detailed study of the ecological interactions between the most impacted species would be needed to test this hypothesis.

4.4. Robustness of the biogeographic zonation

Merging the 2015 and 2017 dataset integrates part of the seasonal and interannual variability which therefore provides us with a dataset that is more representative of the long-term biogeographical features. The nMDS (Figure 8) and the Euclidian cluster (Figure 9) analyses on the merged dataset showed a latitudinally coherent pattern of the rocky shore communities, coinciding with the biogeographic zonation proposed by Ibañez-Erquiaga *et al*. (2018) based on a snapshot picture of the rocky shore communities before the El Niño event. The coastal sites are divided in 3 groups belonging to the Panamic province in the north, the Humboldt Province in the central coast, and a transition zone that shares more similarity with the Humboldt province than with the Panamic province (Figure 9). The zonation obtained with the joint dataset suggests that the exposition to the 2015-16 and 2017 El Niño events and the change in communities described above did not alter the biogeographical structure of rocky intertidal species along the Peruvian coast. The dominant axis that structures the sites in the nMDS analysis is strongly correlated with mean surface temperature (Figure 8B), especially winter temperature. This is consistent with the fact that the community change from 2015 to 2017 is described by nMDS axis 2, which is independent from axis 1 related to mean SST (Figure 6).

No correlation is observed with long-term ENSO variance (Figure 8C). This shows that interannual temperature anomalies, although very high in Peru for the influence of ENSO, do not play a primary role in the latitudinal structure of rocky intertidal communities in the northern and central coast of Peru. Additional environmental factors besides SST, wave impact, water oxygen content, nutrient concentration and air temperature, may be determinant in the biogeographical distribution of the intertidal rocky communities and require further studies. Broitman *et al*. (2001) showed that more than mean SST and latitude, the influence of coastal upwelling cells was the driving force in the geographic patterns in the rocky intertidal of Central Chile. Another comprehensive study in Chile (assessing about 24° of latitude between 18°S and 42°S) showed a mid-latitudinal peak (at 30-32°S) in species diversity (Rivadeneira *et al*., 2002) that could be due to a combination of regional environmental conditions and local ecological interactions. In the same sense, Ibañez-Erquiaga *et al*. (2018) found phosphate concentrations to be one of the main potential drivers of biogeographic patterns at the intertidal communities at the Peruvian coast. Further work, increased sampling resolution, analysis of additional variables, and long-term ecological records are needed in Peru to describe more precisely the role of upwelling cells and ecological relationships in the rocky intertidal communities and disentangle these variables from the SST which is strongly linked to the coastal upwelling in this region.

5. Conclusions

We have presented the first insights into the response of the rocky intertidal community to two successive El Niño event in Peru (2015-16 and 2017) by analyzing the taxonomic diversity of macrobenthic species, their geographic distribution, and the latitudinal structure of communities observed in austral fall 2015 after 17 years of stable La Niña conditions and in austral spring 2017, four months after the end of the 2017 coastal El Niño event. The 2017 El Niño produced during

about three months a strong SST anomaly in the central and northern coast of Peru (Echevin et al., 2018) that reached 6°C at its maximum and triggered strong rainfalls (Rodríguez-Morata *et al*. 2018). We find that four months after this violent environmental disturbance, the taxonomic richness has not significantly changed at the regional scale, but an important turnover of species was observed everywhere, and especially in the transition zone, where the highest SST anomalies occurred. A southward migration of taxa, resulting from the southward shift of SST pattern during El Niño events in this region, has apparently occurred in some sites of northern Peru, especially in PVE[4.2°S] where eight Panamic species appeared. However, this mechanism did not trigger a strong latitudinal change on the structure of the communities. While the rocky shore communities are clearly structured along a latitudinal SST gradient, the change in species assemblages observed in 2017 occurred in a direction independent from this SST gradient. The change in species assemblages was mainly driven by the large distribution reduction of some important widespread species (*Austrolittorina araucana, Prisogaster niger, Siphonaria* spp*., Grateloupia filicina, Gymnogongrus durvillei, Phymanthea pluvia, Semimytilus algosus*) and the spread of some other species (*Fissurella* spp*., Mitrella baccata, Scurria* spp*., Stramonita biserialis, Corallina officinalis, Phymactis clematis*). In the absence of long-term record of the rocky intertidal communities in Peru, the change observed from 2015 to 2017 cannot be simply attributed to seasonal variations or to the El Niño events. However, since some of these important species are clearly not seasonal, we must conclude that at least part of these changes was caused by large scale regional environmental perturbations associated to the 2015-16 and 2017 El Niño events. The primary environmental impact on some ecologically key species likely triggered a chain of secondary impacts through ecological relationships which lead to a complex change in rocky shore communities. Further studies are needed to better characterize the seasonal and interannual variability of the rocky intertidal communities and their drivers. When this interannual variability is integrated, the 9 study sites show a very robust structure determined by the latitudinal SST gradient along the Peruvian coast.

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Author Contributions

JV and MC conceived the project idea. BI, JV and MPH carried out the field and laboratory work. BI, LW, JV, MPH and AI carried out the invertebrate identification. JAP, JV, BI and LW carried out the algae identification. JV, MC, ASP, BI, DO performed the data analysis. RSG, DO, JC, ASP aided in interpreting the results and worked on the manuscript. All authors discussed the results, provided critical feedback and contributed to the final manuscript.

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Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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FIGURE CAPTIONS

Figure 1. Map of the study area across the Peruvian Pacific coast. Black triangles show sampling locations with name, acronym and latitude. Brackets show the two biogeographic provinces.

Figure 2. SST anomalies (SSTa) from June 2002 to April 2018 for the 9 study sites, estimated from the Multi-scale Ultra-high Resolution (MUR) SST Analysis fv04.1. Note the remarkable spatial coherence of SST anomalies along the Peruvian coast. The two El Niño events of 2015/16 and 2017 are represented by the grey shaded bands. Black arrows indicate time intervals of the two sampling campaigns.

Figure 3. SST values off Peru from the Multi-scale Ultra-high Resolution (MUR) SST Analysis fv04.1. Gridded values are represented as shades in the left panels, while the values along the coastline are represented versus the latitude in the right panels. (A) mean annual SST, (B) mean seasonal SST range (shown in black and white, as it does not represent warm and cold waters), (C) mean SST for July (austral winter), (D) mean SST for February (austral summer), (E) SST anomaly variance, (F) SST anomaly of March 2017 (EN event). The 9 circles along the coastline represent sampling locations.

Figure 4. Rarefaction curves for the 9 sampling locations in 2015 (circles) and 2017 (triangles).

Figure 5. Species richness estimated by the Chao2 index in nine study sites for 2015 (blue circles) and 2017 (gray triangles).

Figure 6. (A) nMDS plot showing the pattern of dissimilarity in community structures using incidence data of the 2015 survey (Ibañez et al. 2018) (black dots, site latitude indicated as gray numbers) and the 2017 survey (blue dots, with site label). Dotted arrows show the change from 2015 to 2017 in the nine study sites. (B) Linear regression (red line) between nMDS scores (Axis 1) and sites' mean annual temperature. (see location codes in Table 1). The correlation coefficient and the p-values are indicated in red.

Figure 7. Sorensen-Dice Cluster including the 41 sites surveyed in 2015 (Ibañez-Erquiaga et al., 2018) (black labels) and the nine sites surveyed in 2017 (blue labels) using incidence data of both mobile and sessile taxa. Colors highlight the main clusters: Panamic province (orange), PVE site of 2017 (pink), the transition zone (red), and the Humboldt province (blue). Bootstrap values are indicated at each node.

Figure 8. (A) nMDS plot showing the pattern of dissimilarity in community structures of nine localities using 2015 and 2017 combined datasets. Correlation analysis between first Coordinate of nMDS graph with (B) mean annual SST and (C) ENSO-related SST variability.

Figure 9. Cluster (based on Sorensen-Dice index, R=0.93, number of bootstrap replicates: 10000) of the 9 sampling locations combining 2015 and 2017 incidence data of both sessile and mobile species. Bootstrap values are indicated at each node.

FIGURE 1

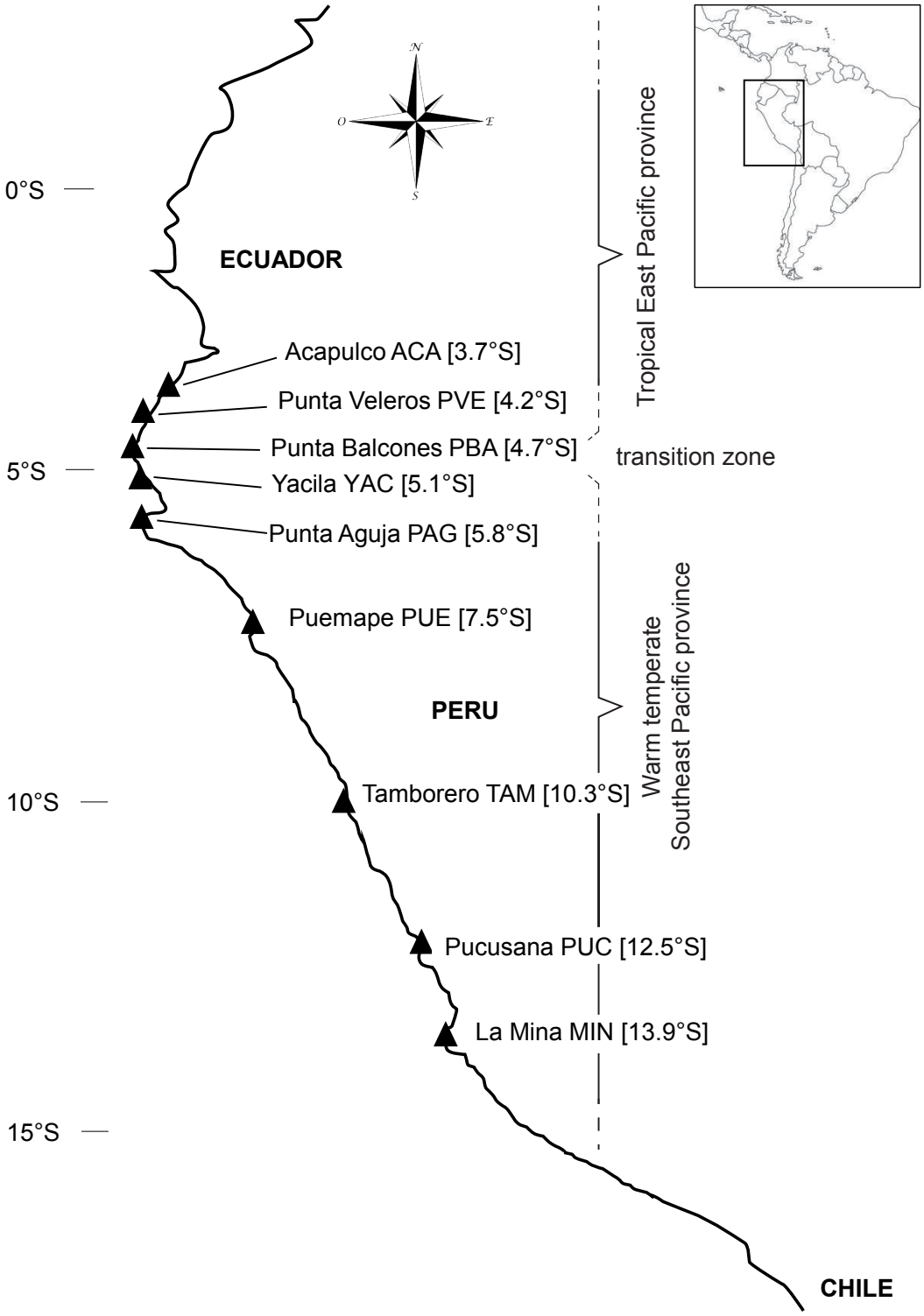

0°S
5°S
10°S
15°S
ECUADOR
PERU
CHILE
Acapulco ACA [3.7°S]
Punta Veleros PVE [4.2°S]
Punta Balcones PBA [4.7°S]
Yacila YAC [5.1°S]
Punta Aguja PAG [5.8°S]
Puemape PUE [7.5°S]
Tamborero TAM [10.3°S]
Pucusana PUC [12.5°S]
La Mina MIN [13.9°S]
Tropical East Pacific province
transition zone
Warm temperate
Southeast Pacific province

Figure 2

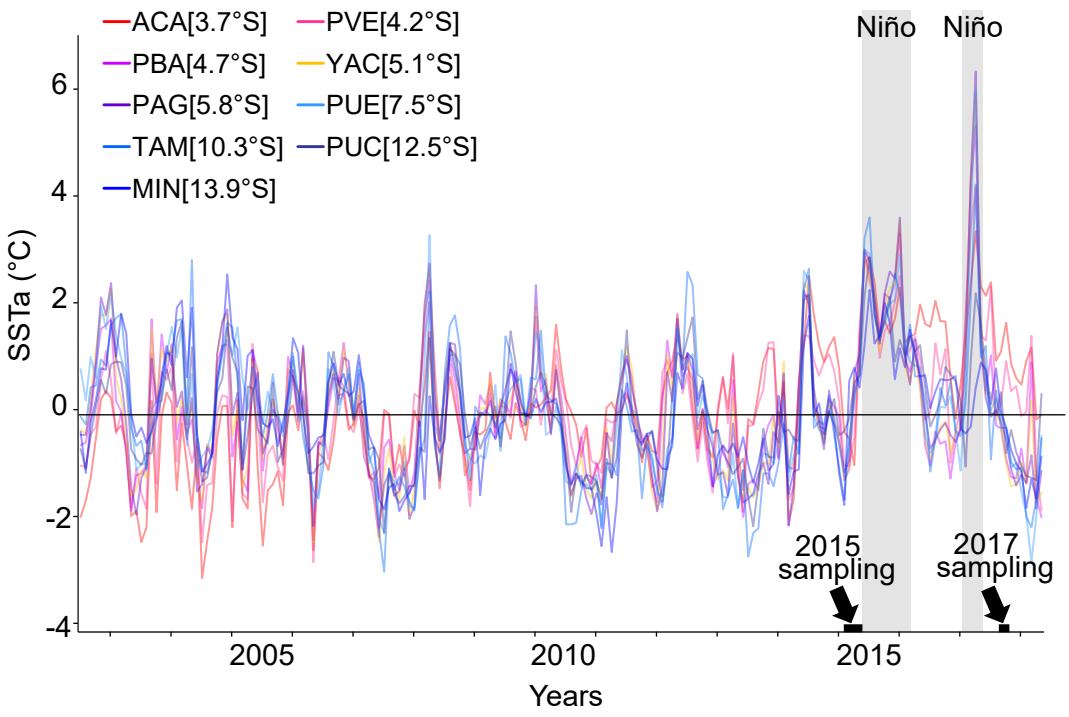

ACA[3.7°S]
PVE[4.2°S]
PBA[4.7°S]
YAC[5.1°S]
PAG[5.8°S]
PUE[7.5°S]
TAM[10.3°S]
PUC[12.5°S]
MIN[13.9°S]
Niño
Niño
SSTa (°C)
6
4
2
0
-2
-4
2015 sampling
2017 sampling
2005
2010
2015
Years

Figure 3

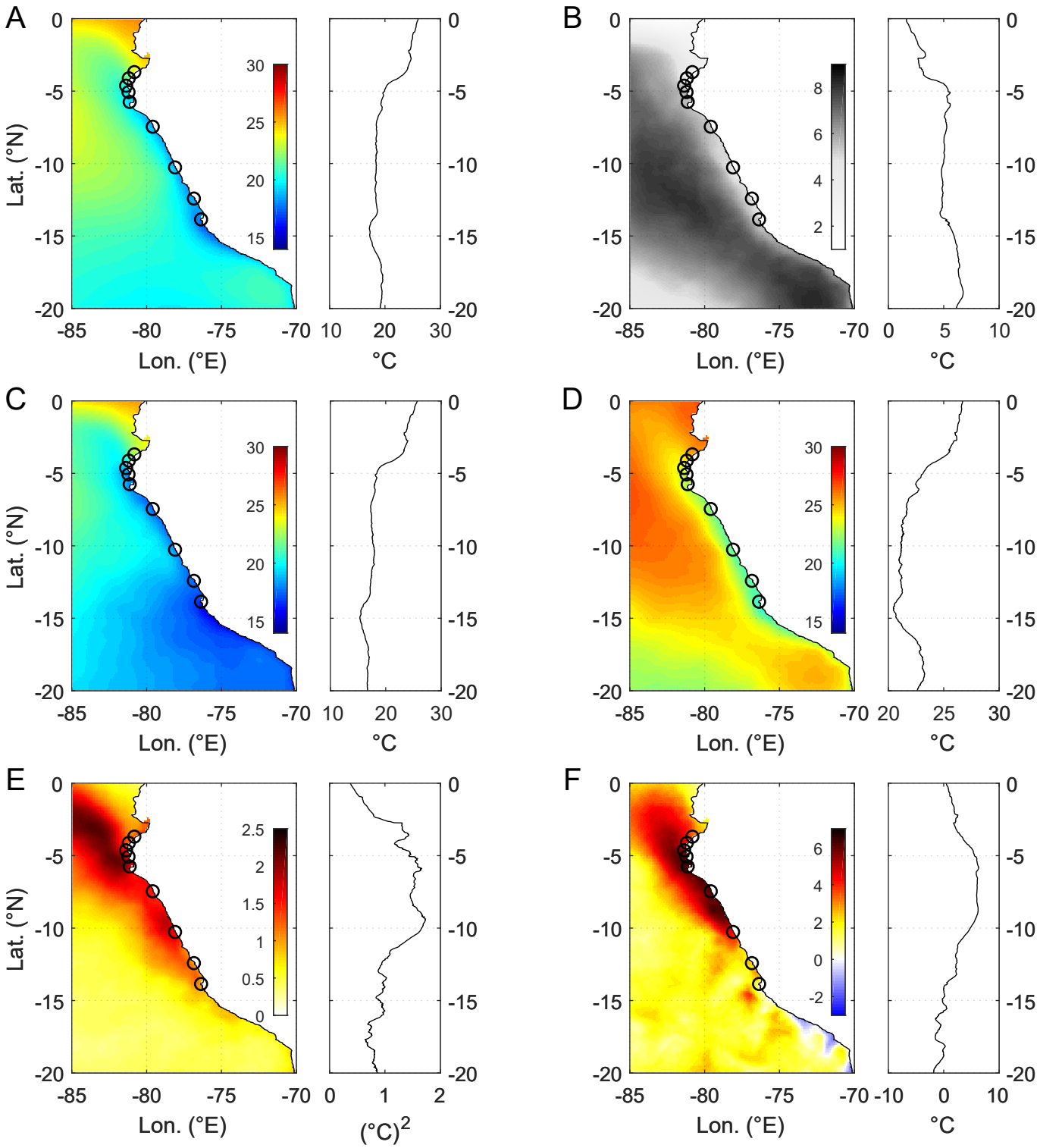

A
B
C
D
E
F
Lat. (°N)
Lon. (°E)
°C
(°C)^2
0
-5
-10
-15
-20
-85
-80
-75
-70
10
20
30
15
25
2
4
6
8
0
5
1
2
0.5
1.5
2.5
-2
-10

Figure 4

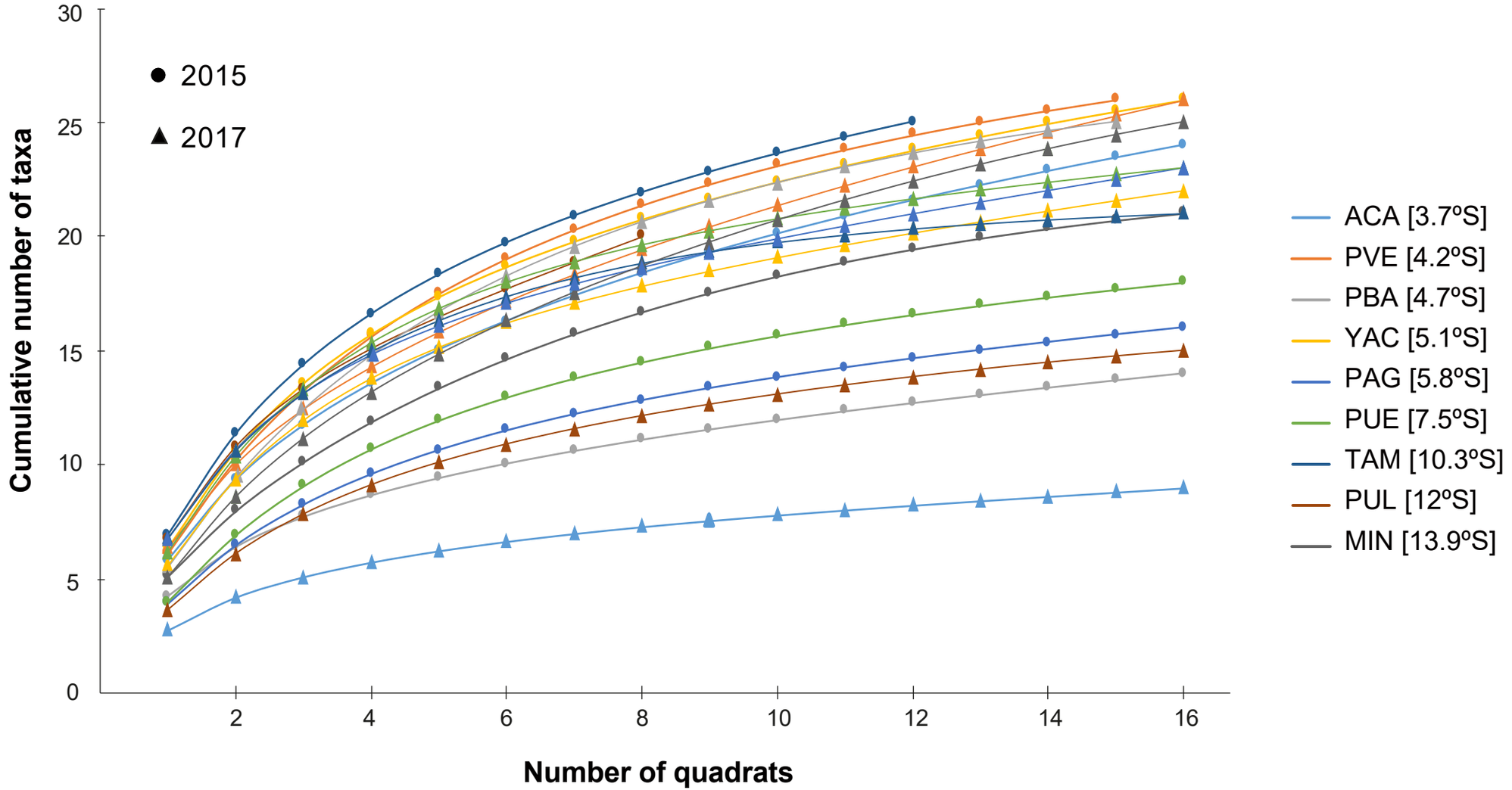

Cumulative number of taxa
Number of quadrats
2015
2017
ACA [3.7ºS]
PVE [4.2ºS]
PBA [4.7ºS]
YAC [5.1ºS]
PAG [5.8ºS]
PUE [7.5ºS]
TAM [10.3ºS]
PUL [12ºS]
MIN [13.9ºS]

Figure 5

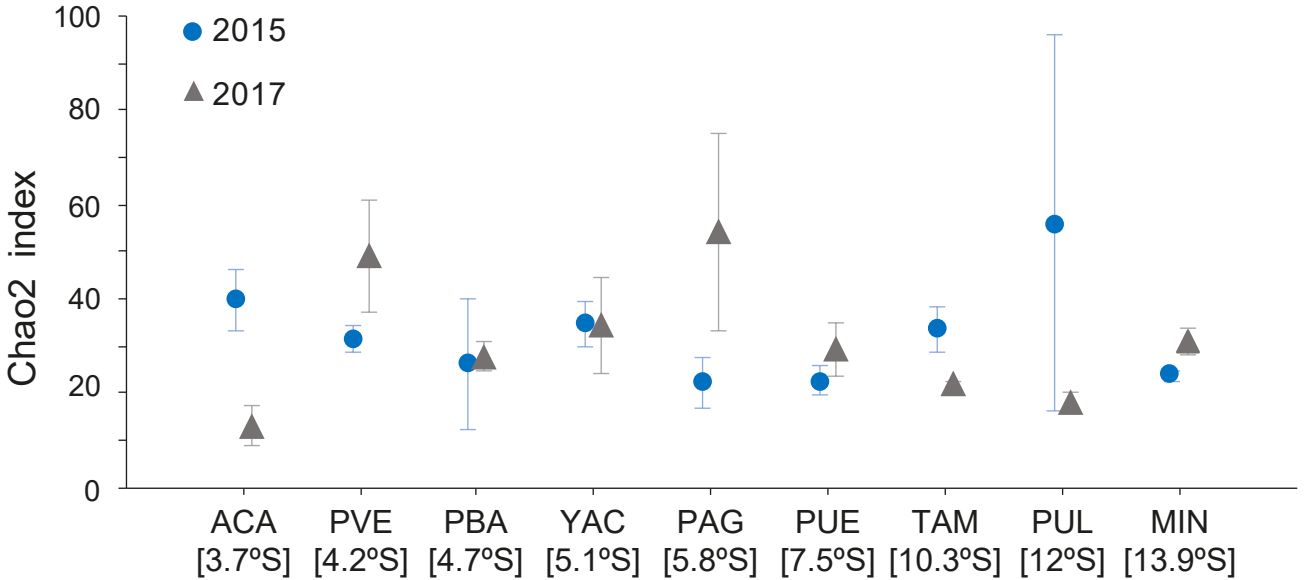

100
80
60
40
20
0
Chao2 index
2015
2017
ACA [3.7ºS]
PVE [4.2ºS]
PBA [4.7ºS]
YAC [5.1ºS]
PAG [5.8ºS]
PUE [7.5ºS]
TAM [10.3ºS]
PUL [12ºS]
MIN [13.9ºS]

Figure 6

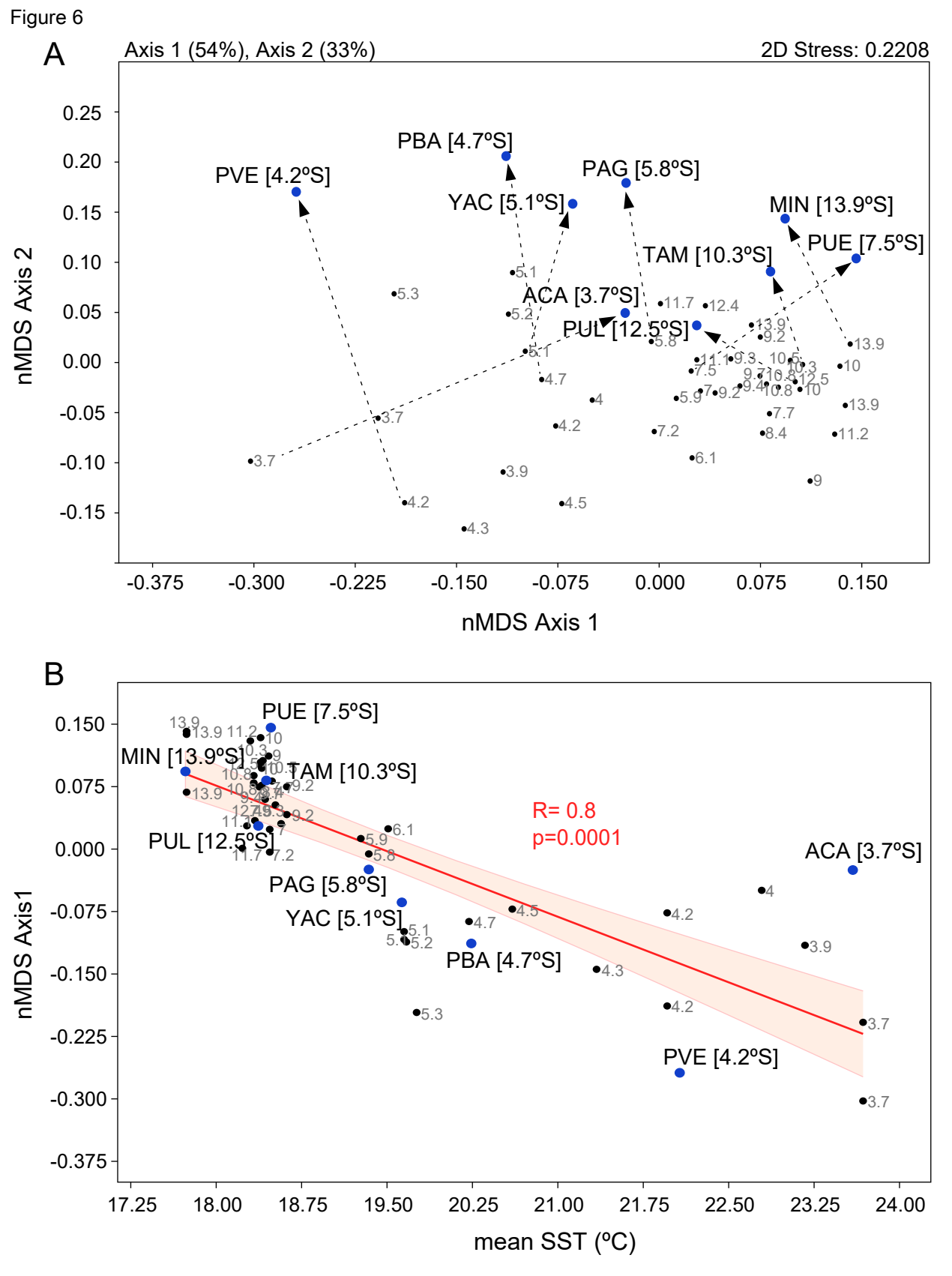

A
Axis 1 (54%), Axis 2 (33%)
2D Stress: 0.2208
PBA [4.7ºS]
PVE [4.2ºS]
PAG [5.8ºS]
YAC [5.1ºS]
MIN [13.9ºS]
PUE [7.5ºS]
TAM [10.3ºS]
ACA [3.7ºS]
PUL [12.5ºS]
nMDS Axis 2
nMDS Axis 1
B
R= 0.8
p=0.0001
nMDS Axis1
mean SST (ºC)

Figure 7

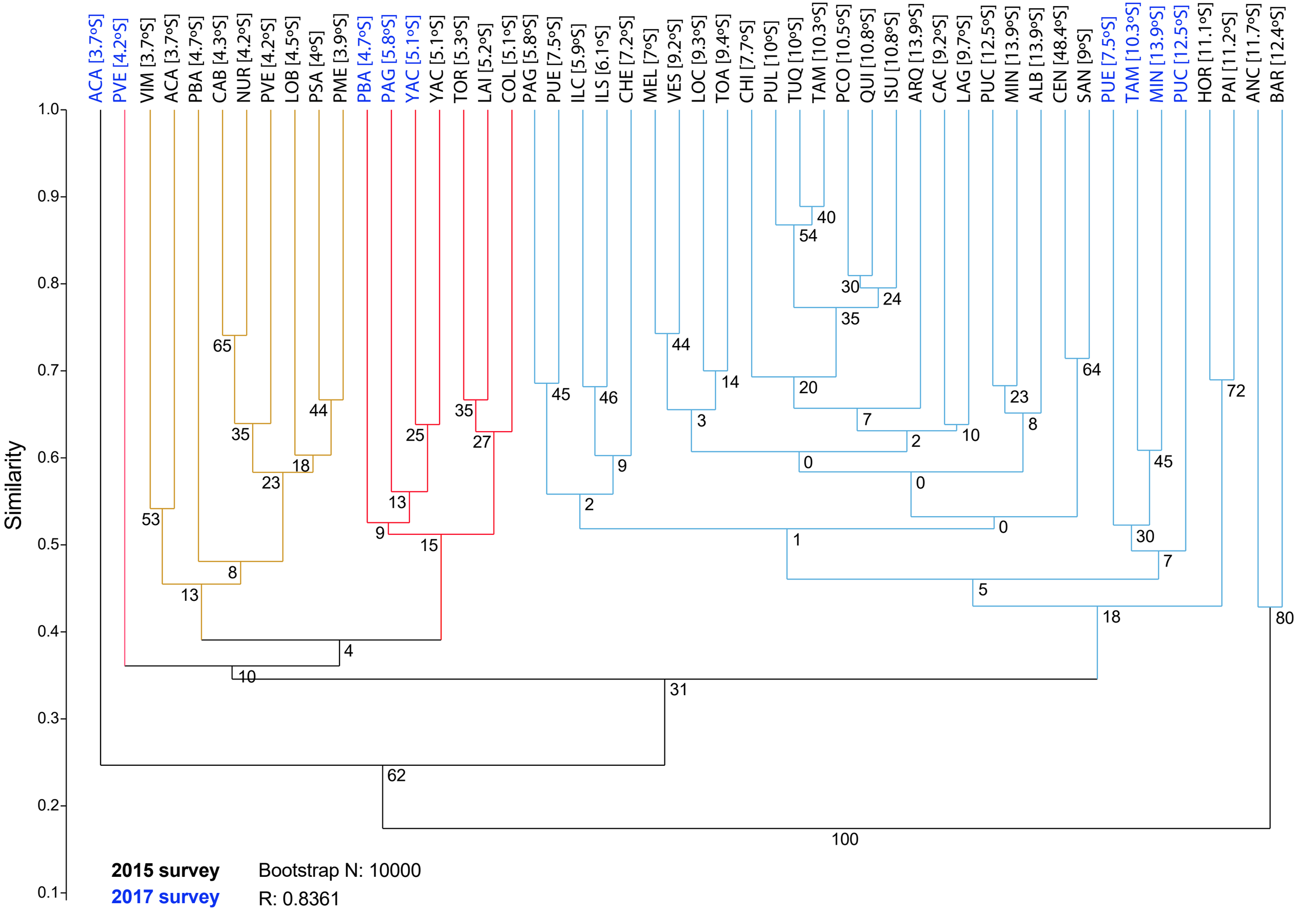

ACA [3.7°S]
PVE [4.2°S]
VIM [3.7°S]
ACA [3.7°S]
PBA [4.7°S]
CAB [4.3°S]
NUR [4.2°S]
PVE [4.2°S]
LOB [4.5°S]
PSA [4°S]
PME [3.9°S]
PBA [4.7°S]
PAG [5.8°S]
YAC [5.1°S]
YAC [5.1°S]
TOR [5.3°S]
LAI [5.2°S]
COL [5.1°S]
PAG [5.8°S]
PUE [7.5°S]
ILC [5.9°S]
ILS [6.1°S]
CHE [7.2°S]
MEL [7°S]
VES [9.2°S]
LOC [9.3°S]
TOA [9.4°S]
CHI [7.7°S]
PUL [10°S]
TUQ [10°S]
TAM [10.3°S]
PCO [10.5°S]
QUI [10.8°S]
ISU [10.8°S]
ARQ [13.9°S]
CAC [9.2°S]
LAG [9.7°S]
PUC [12.5°S]
MIN [13.9°S]
ALB [13.9°S]
CEN [48.4°S]
SAN [9°S]
PUE [7.5°S]
TAM [10.3°S]
MIN [13.9°S]
PUC [12.5°S]
HOR [11.1°S]
PAI [11.2°S]
ANC [11.7°S]
BAR [12.4°S]
Similarity
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
65
35
23
18
44
53
8
13
4
10
31
62
100
35
27
25
13
9
15
45
46
9
2
1
0
44
3
14
20
54
40
30
24
35
7
2
10
0
0
23
8
64
72
45
30
7
5
18
80
2015 survey
2017 survey
Bootstrap N: 10000
R: 0.8361

Figure 8

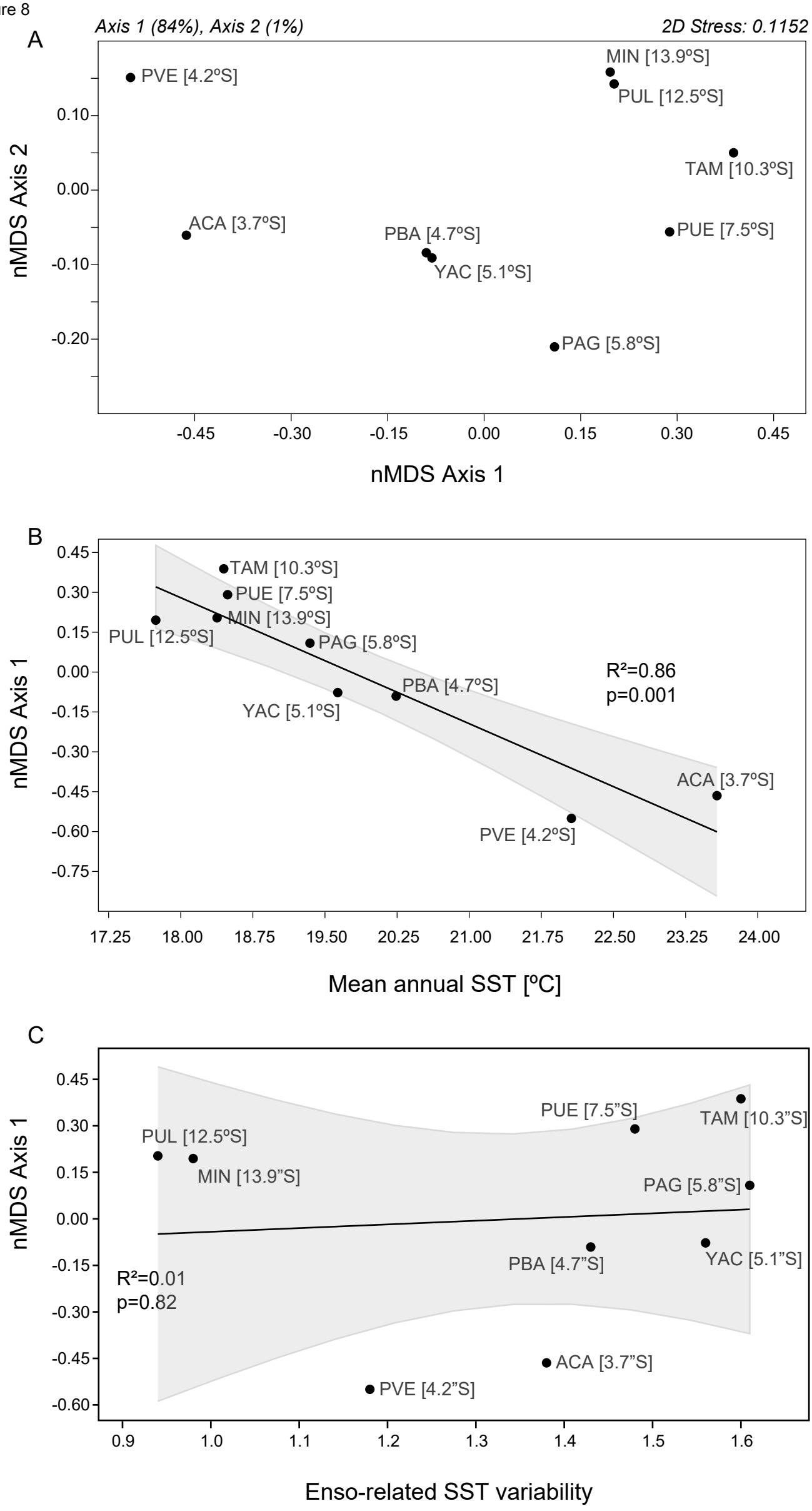
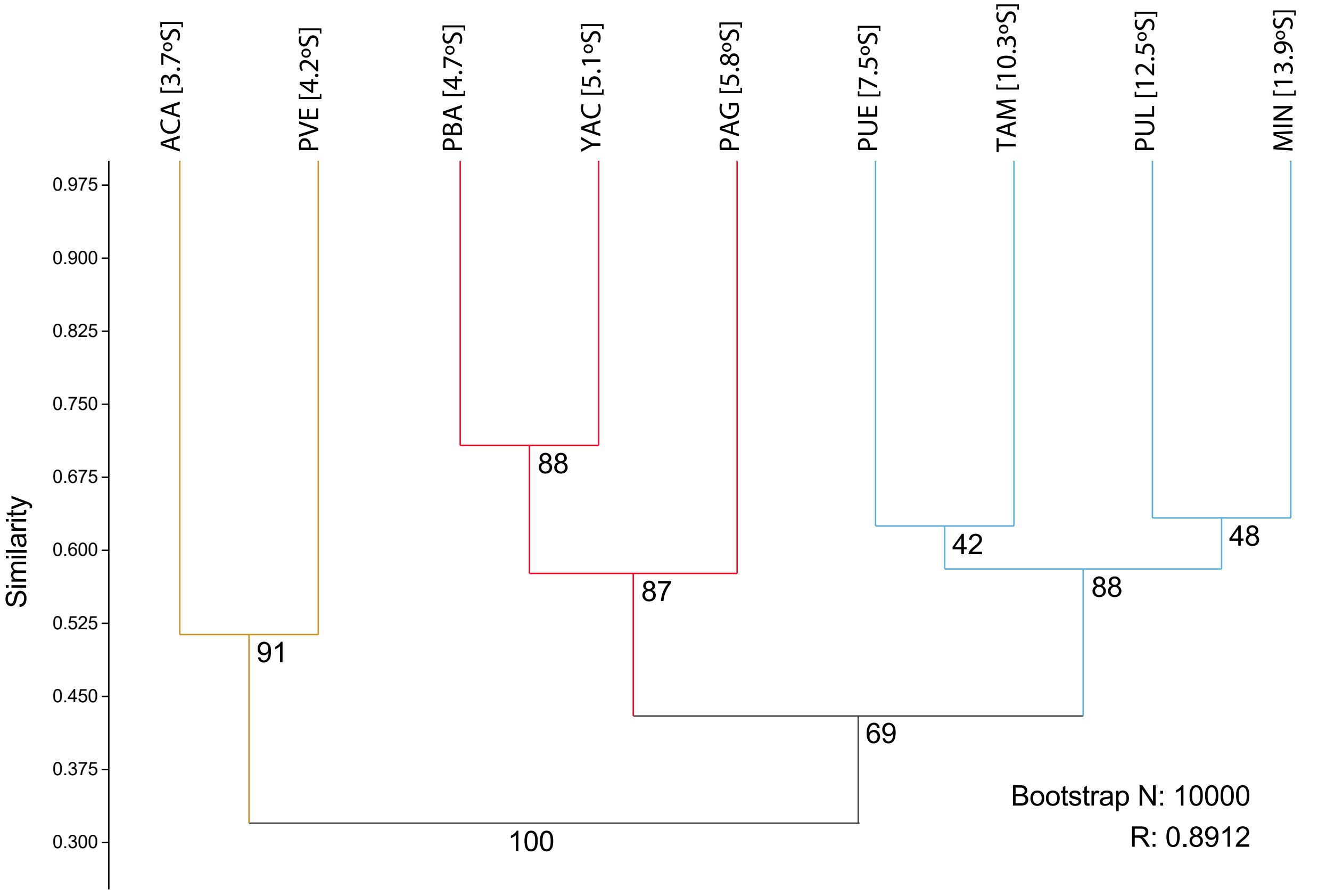

A
Axis 1 (84%), Axis 2 (1%)
2D Stress: 0.1152
PVE [4.2ºS]
MIN [13.9ºS]
PUL [12.5ºS]
TAM [10.3ºS]
ACA [3.7ºS]
PBA [4.7ºS]
PUE [7.5ºS]
YAC [5.1ºS]
PAG [5.8ºS]
nMDS Axis 2
nMDS Axis 1
B
TAM [10.3ºS]
PUE [7.5ºS]
MIN [13.9ºS]
PUL [12.5ºS]
PAG [5.8ºS]
PBA [4.7ºS]
YAC [5.1ºS]
R²=0.86
p=0.001
ACA [3.7ºS]
PVE [4.2ºS]
nMDS Axis 1
Mean annual SST [ºC]
C
PUE [7.5”S]
TAM [10.3”S]
PUL [12.5ºS]
MIN [13.9”S]
PAG [5.8”S]
PBA [4.7”S]
YAC [5.1”S]
R²=0.01
p=0.82
ACA [3.7”S]
PVE [4.2”S]
nMDS Axis 1
Enso-related SST variability

Figure 9


ACA [3.7°S]
PVE [4.2°S]
PBA [4.7°S]
YAC [5.1°S]
PAG [5.8°S]
PUE [7.5°S]
TAM [10.3°S]
PUL [12.5°S]
MIN [13.9°S]
Similarity
0.975
0.900
0.825
0.750
0.675
0.600
0.525
0.450
0.375
0.300
88
87
91
42
48
88
69
100
Bootstrap N: 10000
R: 0.8912

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

AUTHORSHIP STATEMENT

Manuscript title: Changes in rocky intertidal communities after the 2015 and 2017 El Niño events along the Peruvian coast

All persons who meet authorship criteria are listed as authors, and all authors certify that they have participated sufficiently in the work to take public responsibility for the content, including participation in the concept, design, analysis, writing, or revision of the manuscript. Furthermore, each author certifies that this study has not been and will not be submitted to or published in any other publication before its appearance in *Estuarine, Coastal and Shelf Science*.

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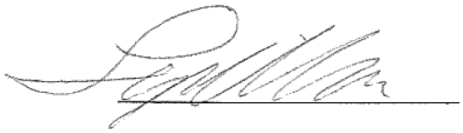
Lynn Wilbur		26/08/2020
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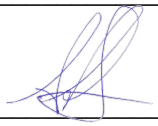
Aldo Indacochea		24/08/2020
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Supplementary Table S1

Supplementary Table S2

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Supplementary Material

Table_S2_Incidence.xlsx