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Cover: Fossil oyster (*Ostrea conchaphila*) specimens from San Pedro, CA, Palos Verdes Sand, Late Pleistocene. Specimens curated by Los Angeles County Museum Invertebrate Paleontology department.

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Reconstructing oyster paleocommunity structure over the last 3.6 million years: A southern California case study

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We culled abundance record data from the NSF-funded TCN, Eastern Pacific Invertebrate Communities of the Cenozoic (EPICC), including all southern California localities that recorded the presence of oysters from the last 3.6 million years to document how oyster communities change through time. In total, over 120,000 specimens from 78 localities throughout southern California (i.e., Los Angeles, Orange, and San Diego counties) were examined. The data were broken down into four-time bins: late Pliocene, middle Pleistocene, late Pleistocene, and Holocene. Using multivariate statistics, several statistically coherent groups based on occurrences and abundances through time were identified. Results indicate that the late Pliocene coherent groups possessed a loose, facultative, individualistic community structure that allowed taxa to shift their latitudinal gradients as they tracked shifting environments. The dominant oyster—*Dendrostrea vespertina*—as well as other taxa, became extinct at the Plio-Pleistocene boundary. Afterwards, community structure changed, as did the dominant oyster. We suspect that the onset of northern hemisphere glaciation at the Plio-Pleistocene boundary changed both the magnitude and rate of sea surface temperatures such that local extinction occurred causing changes in dominance within marine communities. During the middle Pleistocene, *Ostrea conchaphila (lurida)* appeared and remained dominant throughout the Holocene. In addition, distinct spatial groups existed causing reduced migration along the coast of southern California. Perhaps southern California marine communities responded to the water-mass differences associated with the mid-Pleistocene transition from a mild, 41 ka glacial-interglacial cycle to the more variable ~100 ka glacial-interglacial cycle reducing migration along the coast of southern California. The loose, individualistic community structure seen in the late Pliocene returned during the late Pleistocene and continued through the Holocene allowing marine communities the flexibility to track shifting environments.

Keywords: Late Pliocene, Pleistocene, *Ostrea*, *Dendrostrea*, Los Angeles Basin, San Diego Embayment

INTRODUCTION

Through recent digitalization efforts by the NSF-funded Eastern Pacific Invertebrate Communities of the Cenozoic (EPICC) TCN—a collaboration of 10 natural history museums and academic institutions—fossil marine invertebrate data that were otherwise only accessible to a limited few can now be accessed. A small fraction, 3% to 4% of fossil localities worldwide, are currently accounted for in literature-based digital data repositories like the Paleobiology Database (www.paleobiodb.org).

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Digitization of the nine institutions' holdings of Cenozoic marine invertebrate collections from California, Oregon, and Washington reveal that museum data represents 23 times the number of unique fossil localities than are currently recorded in the Paleobiology Database (Marshall et al. 2018). Once all EPICC data are mobilized fully, 1.6 million specimen records will be available for paleontologists to make inferences about the patterns and processes of past evolutionary and ecological changes across environmental gradients, which can be of great scientific value, especially in this age of rapid global change.

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This study utilizes EPICC data digitized from the Natural History Museum of Los Angeles County Invertebrate Paleontology (LACMIP) collection (Hendy et al. 2020). The LACMIP team has worked to increase taxonomic quality control and produce strategies for increasing fitness of use and trust in aggregated data (Estes-Smargiassi et al. 2018, Hendy and Wiedrick 2019). We focused on collections containing oysters and limited our geographic reference to southern California. Southern California fossils provide an excellent laboratory for examining past evolutionary and ecological changes particularly from the most recent geological past. Sedimentary basins within the region contain a well-preserved and extensive fossil record particularly within the last 65 million years (Yerkes et al. 1965). However, examining biotic patterns from approximately the last ~4.0 million years (late Pliocene through Holocene) provides a suitable analog to modern biotic patterns for several reasons. First, by the Pliocene epoch, continents and oceanic basins had nearly reached their present-day configuration (Blakey and Ranney 2018). Second, the Pliocene through the Holocene records a climatic shift from a sustained warming period to a subsequent cooling period. The Pliocene specifically provides an accessible example of what models estimate climate could be in the late 21st century, a climate in which atmospheric CO₂ concentrations are estimated to be higher than pre-industrial values resulting in a more equitable temperature gradient between high and low latitudes (Haywood et al. 2011, Jansen et al. 2007, Salzmann et al. 2011). And third, over 75% of the California Province living molluscan species, which extend from Point Conception, California to Cedros Island, Baja California, are also present as Pleistocene fossils, including common and ecologically important species like *Macoma nasuta* Conrad (1837) and *Callianax biplicate* Sowerby (1825) (Woodring and Bramlette 1946, Valentine 1966, 1989, Deméré 1983, Valentine and Jablonski 1993, Roy 2001, Squires et al. 2006, Powell et al. 2009, Squires 2012, Vendrasco et al. 2012).

Today, there is only one native oyster species, the Olympia oyster, *Ostrea lurida* (Carpenter, 1864). It lives along the North American West Coast, from Alaska to central Baja, Mexico. Within the last century *O. lurida* was a widely distributed habitat-forming species in bays and estuaries, including in California, and was exploited as a food resource by California Native Americans. In the early 1900s, some combination of over-harvesting, pollution, and habitat loss/degradation led to significant declines throughout this species' range. Oyster beds are now absent in California estuaries (Polson and Zacherl

2009b). Currently, restoration ecologists are exploring how to create native *O. lurida* beds within southern California (Fuentes et al. 2019, Zacherl et al. 2015) that support a diverse community of marine species (Champieux 2015, Walker 2015). Their goal is to restore a past ecological niche that is more ecologically functional and resilient to changing environmental conditions to aid in bay tideland and shoreline protection. However, no quantitative data describing oyster abundances and their associated community structure prior to their modern decline in southern California exist. Utilization of new data sources, like EPICC, can help develop paleoecological baselines and provide a critical foundation for restoration efforts (Froyd and Willis 2008). Examining past oyster communities, from the late Pliocene through the Holocene, will help establish pre-human oyster community baselines and provide insight into how oyster communities respond to changing climatic conditions within the southern California region. Here we reconstruct species occurrence patterns by determining relationships among taxa through time and space. We aim to document how coherent taxonomic groups vary through time and how coherent taxa vary between, and within, local areas within a particular time interval.

MATERIALS AND METHODS

Data acquisition and treatment

The majority of data was culled from the EPICC database, which contains fossil abundance data of all counted and identified fossil specimens from one specific collection area or locality. Few collection sites remain accessible, or even exist, at present due to urbanization. We searched the database for all localities within southern California containing the presences of oysters over the span of the last 3.6 million years. In addition to the EPICC data, we screen-washed, counted, and identified fossils from two locations: 1) a Holocene section within Newport Bay, Orange County, CA (Vreeland 2014) and, 2) the late Pleistocene Palos Verdes Sands on Knoll Hill, San Pedro, California (undergraduate thesis work completed by Jolene Ditmar and Brian Rue). In total, we analyzed over 120,000 specimens and 825 mollusc species from 62 samples within Los Angeles, Orange, and San Diego Counties (Fig. 1). It is important to note that since extreme morphological plasticity prevents differentiation between *Ostrea lurida* and *O. conchaphila* (Polson et al. 2009a), we lumped abundance counts for these two species into one taxonomic group that we termed: *O. conchaphila (lurida)*. Historically, they were described as

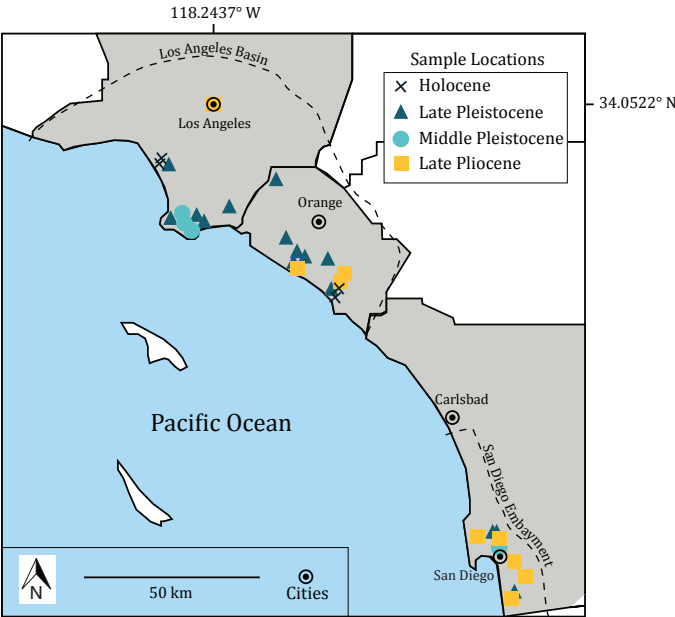


Figure 1. Regional map depicting fossil sample site locations. Fossils were derived from different time intervals within two separate sedimentary basins. Dashed lines represent the general outline of the Los Angeles Basin and the San Diego Embayment. The solid lines represent county line divisions: Los Angeles, Orange, and San Diego counties.

two species (Carpenter 1857, 1864), then synonymized as *O. conchaphila* by Harry (1985), but subsequent molecular evidence re-established them as separate species (Polson et al. 2009a, Raith et al. 2015).

Although the numerical age of formations in southern California that span the Plio-Pleistocene boundary remains uncertain due to how the data were originally collected and current refinement of the biostratigraphy, we broke the data down into four-time bins: Holocene (0–11,700 yBP), late Pleistocene (11,700–126,000 yBP), middle Pleistocene (126,000–781,000 yBP), and late Pliocene (~2.6–3.6 Ma) (Fig. 2) (Woodring and Bramlette 1946, Yerkes et al. 1965, Bowersox 2005, Buczek et al. 2020).

Statistical analyses

We use non-metric multidimensional scaling (nMDS) to help explore relative abundance patterns based on 4th-root transformed abundances of taxa and Bray-Curtis dissimilarities between samples. To help confirm abundance patterns of samples (Q-mode) and taxa (r-mode) through time, we utilized a similarity profile (SIMPROF) permutation test. Given that difference in taxa abundance and composition drive differences among groups, SIMPROF analysis enabled us to establish significant, coherent taxonomic groups through null hypothesis

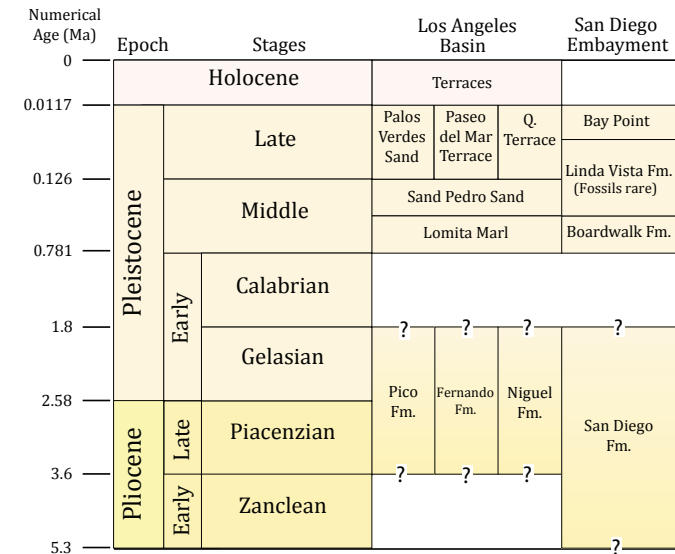


Figure 2. Lithostratigraphic correlations of rock units within the Los Angeles Basin and San Diego Embayment spanning the Holocene through the Pliocene (modified from Buczek et al. 2020). The age of Pico, Fernando, Niguel and San Diego Formations is heavily debated with estimates ranging from early Pliocene to early Pleistocene. Microfossil biostratigraphy analyses result in conflicting interpretations. However, recent work suggests that these formations range into the Gelasian stage of the early Pleistocene Epoch (Buczek et al. 2020).

testing. SIMPROF analysis conducts Q- and r-mode analyses within a non-metric multivariate framework and works through three successional steps, or types. Type 1 SIMPROF uses the Bray-Curtis index to calculate resemblances for a sample-based (Q-mode) analysis and tests the null hypothesis that samples are homogenous and lack multivariate structure. This test is used to determine whether there is evidence for multivariate structure within samples; rejecting the null hypothesis suggests structure exists and thus further analysis of our dataset is warranted. Prior to taxa-based (r-mode) analysis, Type 2 SIMPROF uses the Index of Association coefficient to construct similarity profiles to assess whether there is statistical support for concluding that patterns among variables, in this case taxa, are interpretable; rejecting the null hypothesis suggests that there are genuine, non-random, associations between taxa. If the test rejects the null hypothesis, then further investigation into taxa relationships is supported. Type 2 SIMPROF also calculates the departure of the observed similarity profile from simulated similarity profile. Excess of lower similarity values than expected imply that species have a negative association; that is, taxa occur at entirely different sites or samples and thus suggest taxonomic turnover. Excessive higher similarity values than expected imply that some species are genuinely positively associated and occur

in generally the same sites or samples (Somerfield and Clarke 2013). Having rejected a null hypothesis of “no association among taxa” in Type 2 SIMPROF, then Type 3 SIMPROF can be used to determine which taxa are associated and form coherent groups. Type 3 computes the species based (r-mode) analysis and tests the null hypothesis that species are coherently associated. As with most multivariate analyses examining species patterns, we excluded rare species by examining the 30 “most important” species—that is, those species accounting for $\geq 5\text{--}9\%$ of the total abundance in two or more samples, to reduce noise within the data. Type 3 SIMPROF is used in association with hierarchical agglomerative clustering, based on taxa association, and tests each node within the dendrogram for statistical support for divisions. If the test fails to reject the null hypothesis of coherent association among taxa at a particular node, differences among the taxa below that node should not be considered meaningful. Since the Type 3 SIMPROF analysis tests for coherence within and between species, coherent groups within a specific time interval can be interpreted as a rough estimate of taxonomic assemblages or communities. A full description of the method is described in (Clarke et al. 2008). Figure captions denote specific data treatment and reduction measures per analysis. All statistical analyses were conducted using PRIMER V7 (PRIMER-E, Plymouth, UK).

RESULTS

Species variation through time

At first glance, our dataset containing all 62 samples with time intervals superimposed on each sample site, reveals that Holocene, late Pleistocene, and middle Pleistocene sites overlap with one another (left of the plot) and the late Pliocene samples plot separately (right of the plot) along the horizontal axis (Fig 3A). When analyzed using the SIMPROF Type 1 test, a more complex group structure emerges within each time interval and as a result, 30 groups are defined at a $p\text{-value} \leq 0.001$ (Fig. 3B). Therefore, we reject the hypothesis that samples are homogeneous. Instead, we conclude that there is evidence for multivariate structure within our set of sample sites and that each of the 30 groups are significantly different from each other but internally homogeneous. Such evidence warrants further analysis of species variation (i.e., Type 2 and Type 3 SIMPROF analyses).

The Type 2 SIMPROF similarity profile for the entire dataset, based on species interactions, is highly significant ($\pi=1.885$, $p\text{-value} \leq 0.001$) suggesting that there is

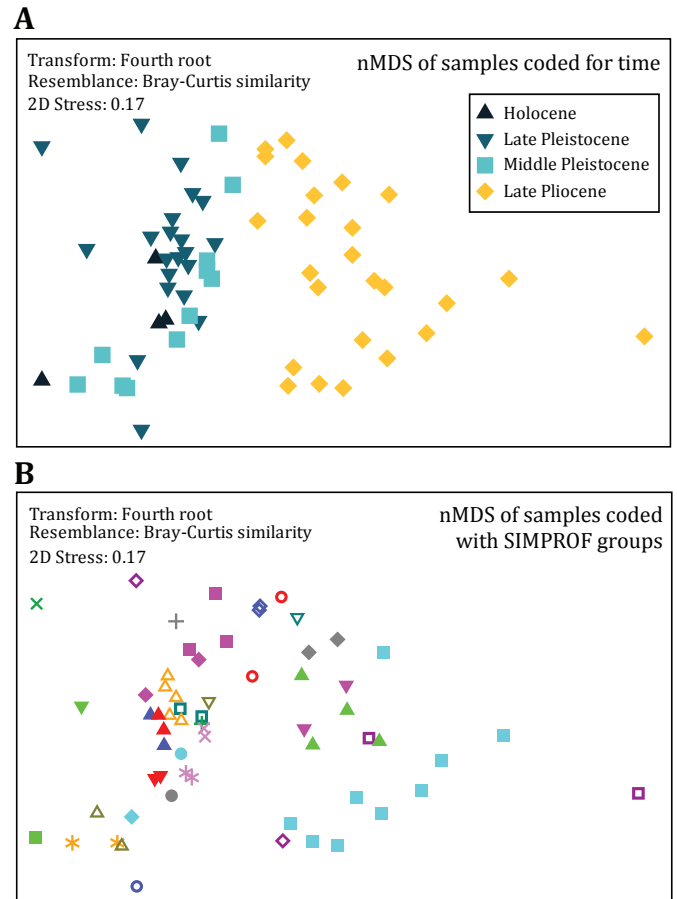


Figure 3. Non-metric Multidimensional Scaling (nMDS) sample plots for all 62 samples with any taxa contributing less than 5% of the sample removed. Analysis based on a 4th root transformation and Bray-Curtis similarities between samples. **A.** nMDS coded for time. Based on this plot it seems reasonable to suggest at least two groupings exist: group 1: The late Pliocene samples and group 2: Holocene, middle Pleistocene, and late Pleistocene samples. **B.** Each colored shape represents nMDS coded for each significant group identified by SIMPROF Type 1 test ($p\text{-value}=0.001$). The SIMPROF test indicates that it is permissible to interpret a finer level of structure within the late Pliocene and further subdivision of the Holocene, middle Pleistocene, and late Pleistocene samples.

statistical support for concluding that patterns among species are interpretable. Thus, we can reject the null hypothesis that species are not associated with each other. When examining the departure of the actual profile from the permuted profile, there is an excess of high resemblance values suggesting that species are positively associated with each other; and thus low species turnover occurs throughout the entire time frame examined (Fig 4). The long tail of zero rank values indicates there are many species that occur as one or two individuals in a single sample and thus strengthen the case for omitting rare species when running a Type 3 SIMPROF analysis.

Figure 5 depicts the dendrogram produced by

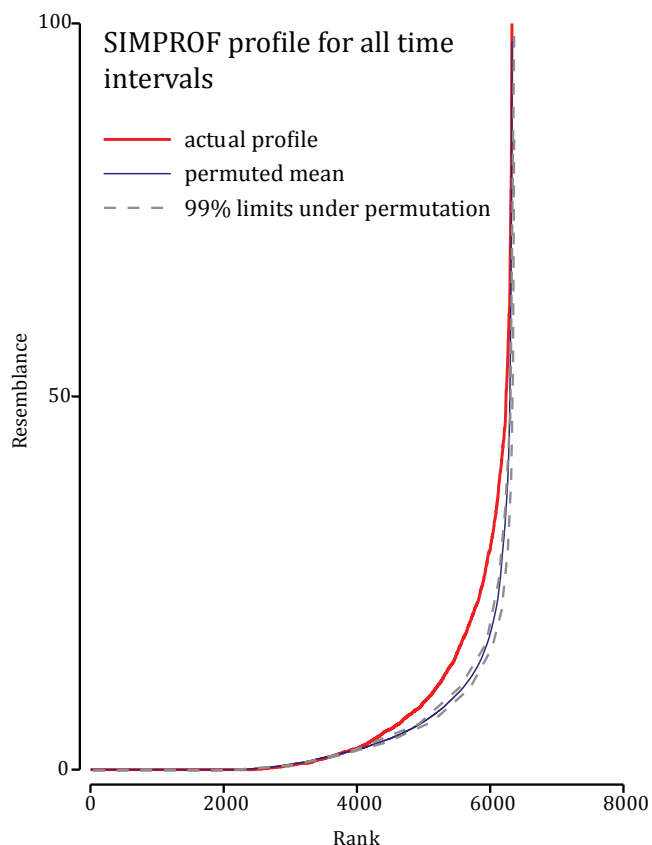


Figure 4. Similarity profiles from Type 2 SIMPROF test for all data based on Index of Association as resemblance measure calculated among 62 samples with any taxa contributing less than 5% of the sample removed. Actual profile data, plotted in bold red, represents the full set of pairwise resemblance ordered from the smallest to the largest (y-axis) plotted against their rank (x-axis). Fine blue line represents the modeled mean based on 1000 permutations and dashed lines represent the predicted range for 99% of resemblances, for any given rank, under the null hypothesis of no association among species. P -value=0.001 indicates that there are genuine associations to interpret among species.

hierarchical agglomerative clustering, coupled with a Type 3 SIMPROF test. According to the Type 3 SIMPROF, seven coherent groups (A–G) exist, with four groups containing three or more species (B, C, E, and G), two species comprise groups A, D, and F, and three single-species groups exist at the p -value ≤ 0.001 . Accordingly, we can reject the hypothesis that species are coherently associated and state that species within group B, C, E, and G vary coherently across samples. However, we cannot reject the null hypothesis for groups A, D, and F because when a pair of species form an isolated group in the dendrogram, SIMPROF cannot reject the null hypothesis because they vary differently and plots them as outliers (Clarke et al. 2008, Somerfield and Clarke 2013). Although four oyster species occur within the entire data set, only three oyster species occur in abundance within

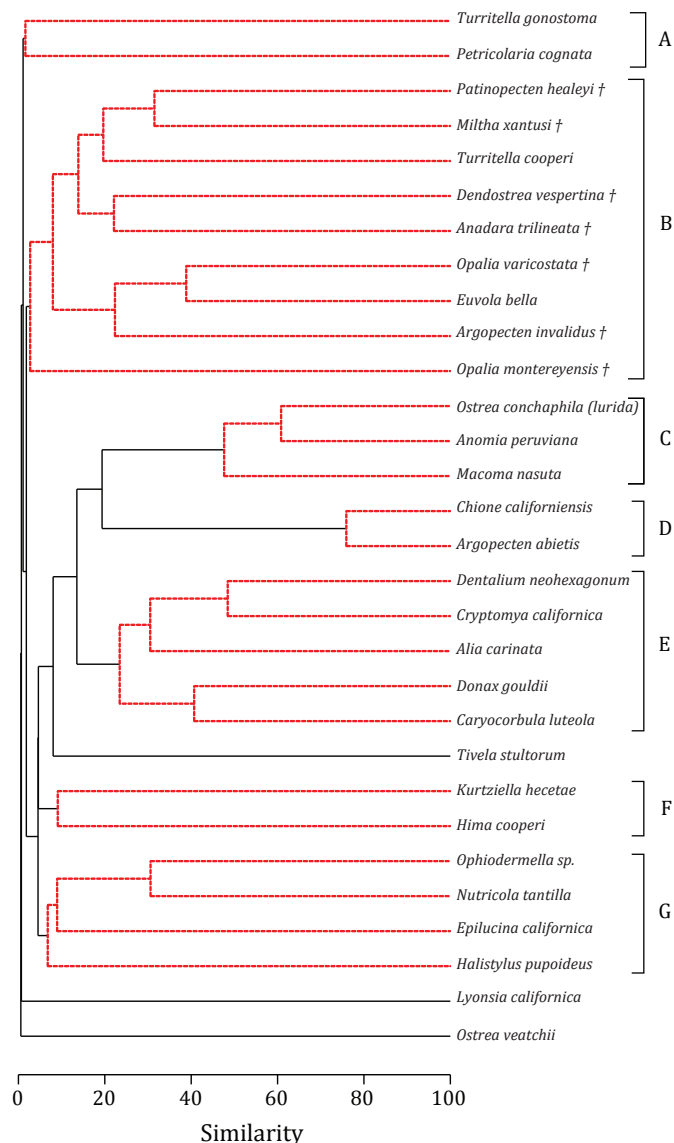


Figure 5. Dendrogram from group-averaging clustering of the 30 ‘most important species’ (i.e., those account for $\geq 9\%$ of the total abundance in two or more sample) based on Index of Association calculated among standardized (to 100%), untransformed species abundances from 62 samples. Continuous lines denote significant groups differentiated by Type 3 SIMPROF test at a p -value=0.001. Seven groups contain multiple species (A–G) and 3 groups contain single-species groups (*Tivela stultorum* Mawe (1823)—similar to group E and *Lyonsia californica* Conrad (1837) and *Ostrea veatchii*—general outliers). Dashed lines represent the substructure containing no statistical support. Dagger symbol (†) represents taxa that went extinct at the end of the late Pliocene.

our dataset; thus, when we examine the 30 ‘most important taxa’ each oyster species separates into different clusters: *Dendrostrea vespertina* Conrad (1854) fall into group B, *O. conchaphila (lurida)* occurs in group C, and *O. veatchii* Gabb (1866) clusters separate from all other species (Fig. 5).

When coherence line plots of the four main coherent

Table 1. List of taxa that comprise statically coherent groups based on all Type 3 analyses. For each taxon, we compiled its class category, ecology, and age range according www.paleobiology.org. **Min.**=minimum, **Max.**=maximum. *Age in Ma.

Taxa	Class	Locomotion	Habit	Diet	Min. Series	Max. Series	Min. Age*	Max. Age*
<i>Alia carinata</i>	Gastropoda	actively mobile	epifaunal	carnivore	upper Pliocene	upper Pleisto	3.6	0
<i>Anadara trilineata</i>	Bivalvia	facultatively mobile	semi-infaunal	suspension feeder	upper Miocene	upper Plio	11.62	2.588
<i>Anomia peruviana</i>	Bivalvia	stationary	epifaunal	suspension feeder	upper Oligocene	Holocene	28.1	0
<i>Argopecten abietis</i>	Bivalvia	facultatively mobile	epifaunal	suspension feeder	lower Plio	lower Pleisto	5.33	0.0117
<i>Argopecten invalidus</i>	Bivalvia	facultatively mobile	epifaunal	suspension feeder	lower Plio	upper Plio	5.33	2.588
<i>Argopecten ventricosus</i>	Bivalvia	facultatively mobile	epifaunal	suspension feeder	upper Miocene	Holocene	11.62	0
<i>Caecum californicum</i>	Gastropoda	actively mobile	epifaunal	grazer	middle Pleisto	upper Pleisto	0.781	0
<i>Californiconus californicus</i>	Gastropoda	actively mobile	epifaunal	carnivore	lower Plio	upper Pleisto	5.33	0
<i>Callianax baetica</i>	Gastropoda	actively mobile	epifaunal	carnivore	lower Pleisto	Holocene	2.588	0
<i>Callianax biplicata</i>	Gastropoda	actively mobile	epifaunal	carnivore	lower Plio	upper Pleisto	5.33	0
<i>Caryocorbula luteola</i>	Bivalvia	stationary	infaunal	suspension feeder	lower Miocene	upper Pleisto	23.03	0
<i>Caryocorbula ovulata</i>	Bivalvia	stationary	infaunal	suspension feeder	lower Plio	Holocene	5.33	0
<i>Cerithiopsis californica</i>	Gastropoda	actively mobile	epifaunal	grazer	upper Pliocene	Holocene	3.6	0
<i>Chione californiensis</i>	Bivalvia	facultatively mobile	infaunal	suspension feeder	upper Pliocene	Holocene	3.6	0
<i>Chione undatella</i>	Bivalvia	facultatively mobile	infaunal	suspension feeder	lower Miocene	upper Pleisto	23.03	0
<i>Crassinella pacifica</i>	Bivalvia	facultatively mobile	epifaunal	suspension feeder	upper Pliocene	upper Pleisto	3.6	0
<i>Crepidula naticarum</i>	Gastropoda	facultatively mobile	epifaunal	suspension feeder	?	Holocene	?	0
<i>Crepidula onyx</i>	Gastropoda	facultatively mobile	epifaunal	suspension feeder	upper Miocene	Holocene	11.62	0
<i>Crepidula perforans</i>	Gastropoda	facultatively mobile	epifaunal	suspension feeder	?	Holocene	?	0
<i>Crepidula princeps</i>	Gastropoda	facultatively mobile	epifaunal	suspension feeder	upper Oligocene	upper Pleisto	28.1	0.0117
<i>Crepidula lingulata</i>	Gastropoda	facultatively mobile	epifaunal	suspension feeder	upper Pliocene	Holocene	3.6	0
<i>Cryptomya californica</i>	Bivalvia	facultatively mobile	infaunal	suspension feeder	middle Miocene	Holocene	15.97	0
<i>Dendostrea vespertina</i>	Bivalvia	stationary	epifaunal	suspension feeder	upper Oligocene	upper Plio	28.1	2.588
<i>Dentalium neohexagonum</i>	Scaphopoda	slow moving	semi-infaunal	deposit feeder	lower Plio	upper Pleisto	5.33	0
<i>Diplodonta sericata</i>	Bivalvia	facultatively mobile	infaunal	suspension feeder	middle Pleisto	Holocene	0.781	0
<i>Donax californicus</i>	Bivalvia	facultatively mobile	infaunal	suspension feeder	middle Pleisto	upper Pleisto	0.781	0
<i>Donax gouldii</i>	Bivalvia	facultatively mobile	infaunal	suspension feeder	upper Pleisto	upper Pleisto	0.126	0
<i>Epilucina californica</i>	Bivalvia	facultatively mobile	deep infaunal	chemosymbiotic	upper Pliocene	upper Pleisto	3.6	0
<i>Euvola bella</i>	Bivalvia	facultatively mobile	low-level eipfaunal	suspension feeder	upper Pliocene	middle Pleisto	3.6	0.126
<i>Euvola vogdesi</i>	Bivalvia	facultatively mobile	low-level eipfaunal	suspension feeder	lower Plio	upper Pleisto	5.33	0
<i>Fissurella volcano</i>	Gastropoda	facultatively mobile	epifaunal	grazer	lower Pleisto	upper Pleisto	2.588	0
<i>Gadila aberrans</i>	Scaphopoda	slow moving	shallow infaunal	deposit feeder	upper Pliocene	upper Pleisto	3.6	0
<i>Glossaulax reclusiana</i>	Gastropoda	actively mobile	semi-infaunal	carnivore	?	Holocene	?	0
<i>Halistylus pupoideus</i>	Gastropoda	actively mobile	epifaunal	grazer	middle Pleisto	Holocene	0.781	0
<i>Hima cooperi</i>	Gastropoda	slow moving	semi-infaunal	carnivore	upper Pliocene	middle Pleisto	3.6	0.126
<i>Leopecten stearnsii</i>	Bivalvia	facultatively mobile	low-level eipfaunal	suspension feeder	lower Plio	upper Pleisto	5.33	0.0117
<i>Leptopecten latiauratus</i>	Bivalvia	facultatively mobile	epifaunal	suspension feeder	lower Plio	upper Pleisto	5.33	0
<i>Leukoma staminea</i>	Bivalvia	facultatively mobile	infaunal	suspension feeder	upper Miocene	Holocene	11.62	0
<i>Littorina scutulata</i>	Gastropoda	actively mobile	epifaunal	grazer	lower Pleisto	Holocene	2.588	0
<i>Luciniscia nuttalli</i>	Gastropoda	facultatively mobile	infaunal	chemosymbiotic	lower Miocene	upper Pleisto	23.03	0
<i>Macoma nasuta</i>	Bivalvia	facultatively mobile	infaunal	deposit feeder	upper Eocene	Holocene	37.2	0
<i>Megapitaria squalida</i>	Bivalvia	facultatively mobile	infaunal	suspension feeder	lower Plio	upper Pleisto	5.33	0
<i>Miltha xantusi</i>	Bivalvia	facultatively mobile	deep infaunal	chemosymbiotic	upper Miocene	upper Plio	11.62	2.588
<i>Mitrella gausapata</i>	Gastropoda	actively mobile	epifaunal	carnivore	lower Miocene	Holocene	23.03	0
<i>Mitrella tuberosa</i>	Gastropoda	actively mobile	epifaunal	carnivore	upper Pliocene	Holocene	3.6	0
<i>Nassarius delosi</i>	Gastropoda	slow moving	semi-infaunal	carnivore	?	Holocene	?	0
<i>Nassarius grammatus</i>	Gastropoda	slow moving	semi-infaunal	carnivore	upper Miocene	upper Plio	11.62	2.588
<i>Nassarius perpinguis</i>	Gastropoda	slow moving	semi-infaunal	carnivore	upper Pliocene	upper Pleisto	3.6	0
<i>Nutricula tantilla</i>	Bivalvia	facultatively mobile	infaunal	suspension feeder	lower Miocene	upper Pleisto	23.03	0
<i>Opalia montereyensis</i>	Bivalvia	slow moving	low-level eipfaunal	carnivore	?	Holocene	?	0
<i>Opalia varicostata</i>	Bivalvia	slow moving	low-level eipfaunal	carnivore	upper Pliocene	upper Plio	3.6	2.588
<i>Ostrea conchaphila (lurida)*</i>	Bivalvia	stationary	epifaunal	suspension feeder	middle Pleisto	Holocene	0.781	0
<i>Parvilucina tenuisculpta</i>	Bivalvia	facultatively mobile	infaunal	chemosymbiotic	upper Pliocene	upper Pleisto	3.6	0
<i>Patinopecten healeyi</i>	Bivalvia	facultatively mobile	low-level eipfaunal	suspension feeder	middle Miocene	lower Pleisto	13.82	2.588
<i>Pycnodonte erici</i>	Bivalvia	stationary	epifaunal	suspension feeder	upper Pliocene	upper Pleisto	3.6	2.588
<i>Tagelus californianus</i>	Bivalvia	facultatively mobile	infaunal	suspension feeder	lower Plio	Holocene	5.33	0
<i>Tegula eiseni</i>	Gastropoda	actively mobile	epifaunal	grazer	middle Eocene	Holocene	41.3	0
<i>Turritella cooperi</i>	Gastropoda	facultatively mobile	semi-infaunal	suspension feeder	upper Miocene	upper Pleisto	11.62	0
<i>Turritella gonostoma</i>	Gastropoda	facultatively mobile	semi-infaunal	suspension feeder	lower Miocene	upper Pleisto	23.03	0

groups (groups B, C, E, and G) are examined through time, the different curves display a great variety of abundances across time intervals. Particularly, species in group B, including the oyster *D. vespertina*, were present in high abundances during the late Pliocene and then almost disappear in the time intervals that follow. In contrast, most species in groups C and E replace late Pliocene species and thrive during the middle and late Pleistocene. Group C species, including the oyster species *O. conchaphila (lurida)*, then increase in abundance within the Holocene while group E decrease in abundance (Fig. 6). Interestingly, seven out of the nine species within group B are extinct taxa, including the late Pliocene oyster *D. vespertina* (Table 1). All remaining taxa within the coherence line plots, regardless of their groupings, are extant taxa (Table 1). In terms of oyster abundance, both *D. vespertina* and *O. conchaphila (lurida)* occur at lower abundances compared to the other taxa within their individual groups. *Dendrostrea vespertina* ranges between 2–35% and *O. conchaphila (lurida)* ranges between 1–27% (Fig. 6).

Species variation within time intervals and between local areas

Late Pliocene data—According to the results, late Pliocene county sites overlap (Fig. 7A) and within those sites valid multivariate structure exists within samples at a p -value ≤ 0.001 (Fig. 7A). Thus, we can reject the null hypothesis that samples are homogeneous and state that multivariate structure exists within late Pliocene sample sites. For example, within San Diego County four significant groups occur (Fig. 7A). Departure of the actual profile from the permuted profile indicates an excess of positive association between species suggesting low turnover rates within this time interval (Fig. 7B). A long tail of zero values also exists for this time interval justifying the removal of rare species during the Type 3 SIMPROF analysis. Three significant groups, containing two or more species, cluster out according to the Type 3 results at a p -value ≤ 0.001 (Fig. 7C). Two species, *Ostrea montereyensis* Dall (1907) and *O. veatchii*, plot independently of the three main groups. Group A constitutes the dominant oyster group within the late Pliocene and contains the abundant oyster *D. vespertina* and ecologically is dominated by actively mobile epifaunal carnivorous gastropods (e.g., *Alia carinata* Hinds, 1844) and facultatively mobile infaunal bivalves (e.g., *Nutricola tantilla* Gould, 1853) (Fig. 8). Infaunal bivalves (*Macoma nasuta* Conrad, 1837) and carnivorous gastropods (*Luciniscia nuttalli* Conrad, 1837) dominate group B. Group

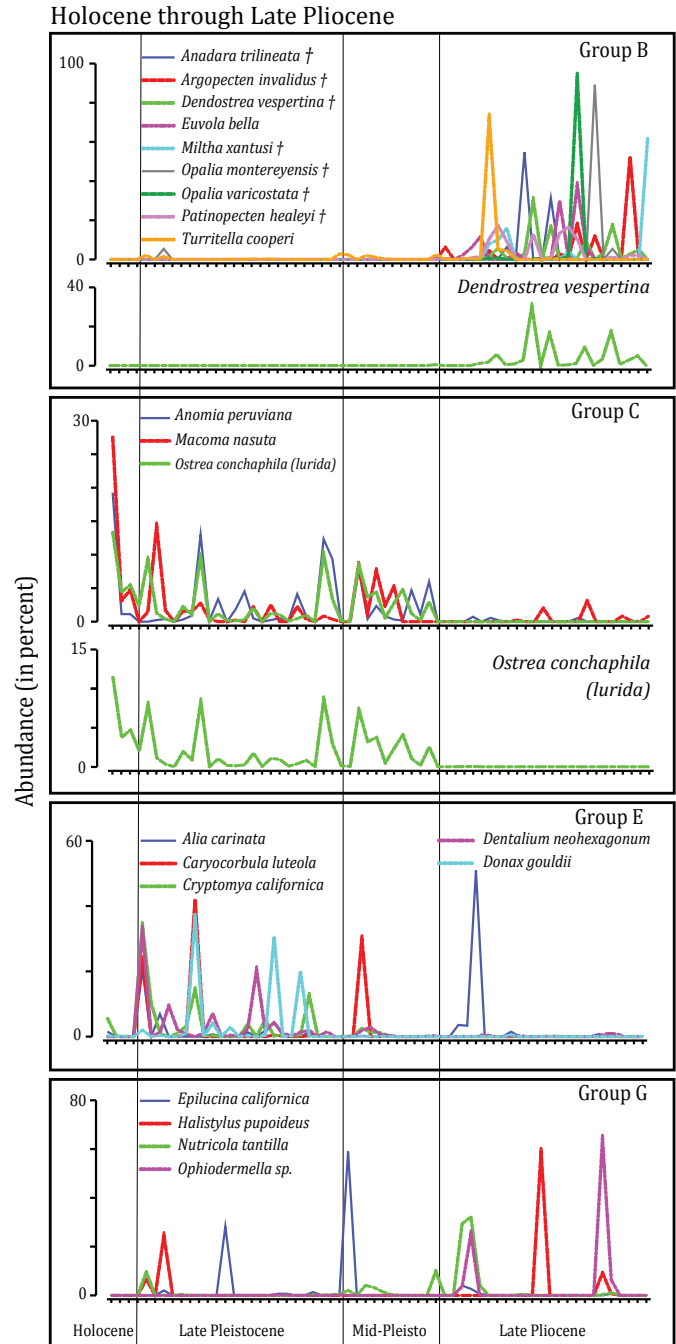


Figure 6. Coherent curves, or line plots, for groups of species identified in Figure 5. To view how coherent species groups vary through time, we rearranged the x axes according to the samples' designated time interval with the most recent (Holocene on the left) and the oldest time interval (late Pliocene) on the right. The y-axes represent percentages of the total abundance of a particular species found across the 62 samples (species are standardized but untransformed). Dagger symbol (†) represents taxa that went extinct at the end of the late Pliocene.

C contains another late Pliocene oyster, *Pycnodonte erici* Hertlein (1929), and predominantly contains epifaunal bivalves (e.g., *Patinopecten healeyi* Arnold, 1906). The

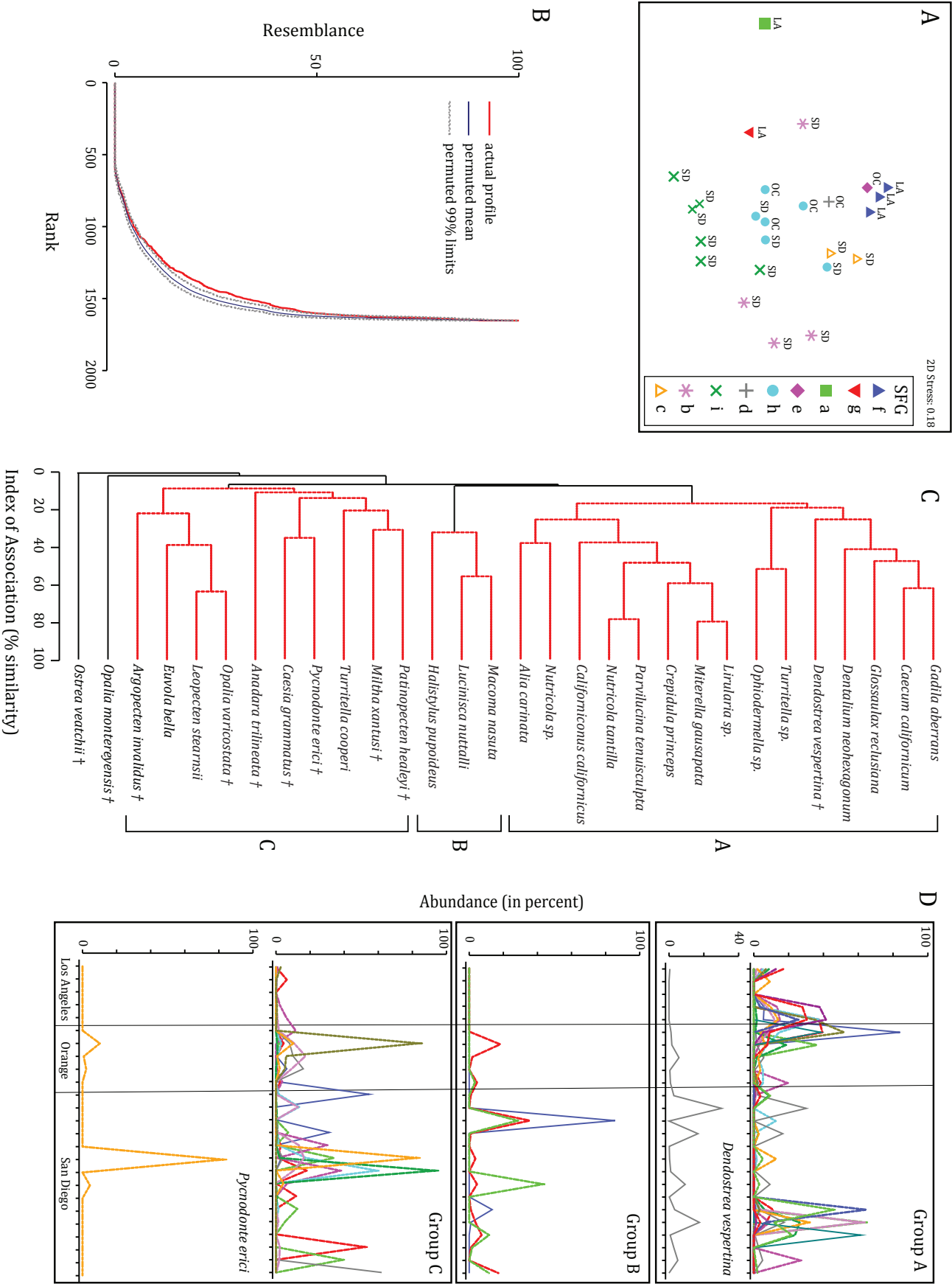


Figure 7. Caption on top of page 9.

Figure 7. Late Pliocene statistical procedures for samples (A) and species (B–D). **A.** Non-metric Multidimensional Scaling (nMDS) plot of late Pliocene samples with any taxa contributing less than 5% of the sample removed. Analysis was produced using 4th root transformed, abundances of species, and Bray-Curtis similarities between samples. Late Pliocene resemblance measure calculated among 25 samples and 58 species. Symbols represent significant groups identified by SIMPROF Type 1 test; all grouping have a p -value=0.001. **B.** Similarity profile from Type 2 SIMPROF test based on Index of Association. P -value=0.001 indicates that there are genuine associations to interpret among species. Actual profile data, plotted in bold red, represents the full set of pairwise resemblance ordered from the smallest to the largest (y-axis) plotted against their rank (x-axis). Fine blue line represents the modeled mean based on 1000 permutations and dashed lines represent the predicted range for 99% of resemblances, for any given rank, under the null hypothesis of no association among species. **C.** Late Pliocene taxonomic dendrogram from group-averaging clustering of the 30 ‘most important species’ (i.e., those account for $\geq 11\%$ of the total abundance in two or more sample) based on Index of Association calculated among standardized (to 100%), untransformed species abundances from 25 samples. Continuous lines denote significant groups differentiated by Type 3 SIMPROF test at a p -value=0.001. Dashed lines represent the substructure containing no statistical support. **D.** Late Pliocene species coherent plots, or line plots, for groups containing two or more species (see Fig. 7C). To view how coherent groups vary spatially, we rearranged the x-axes according to the samples’ latitude from North to South (See Figure 1. for county locations). The y-axes represent percentages of the total abundance of a particular species found across the 25 samples (species are standardized but untransformed). Dagger symbol (†) represents taxa that went extinct at the end of the late Pliocene.

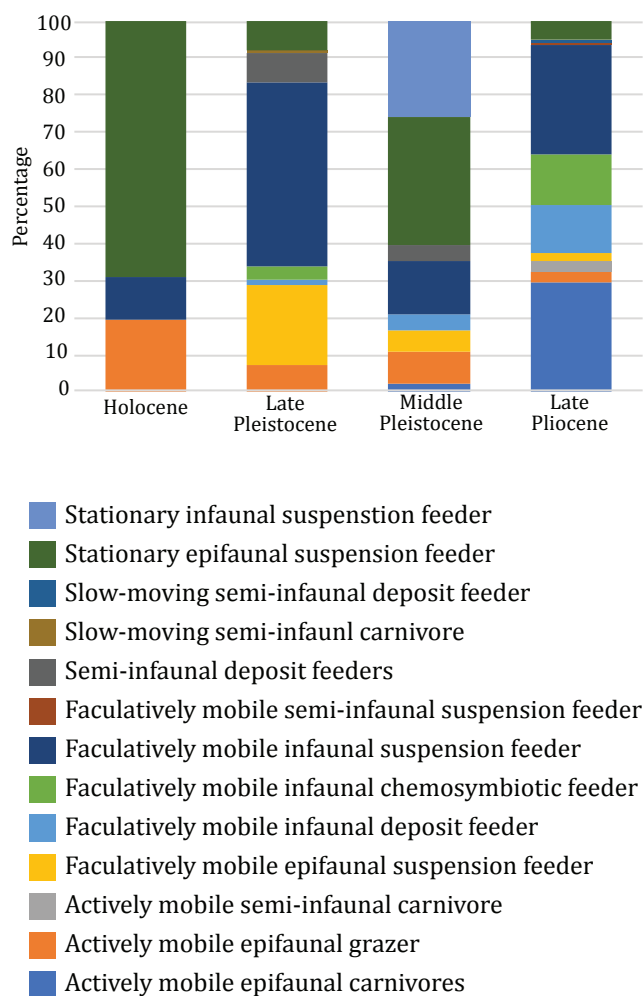


Figure 8. Ecological structure of oyster dominant coherent groups within each time interval. The late Pliocene bar graph is based on the species abundances within Group A—Figure 7. The middle Pleistocene is based on the species abundances within Group A—Figure 9. late Pleistocene bar graph is based on the species abundances within Group D—Figure 10. Holocene bar graph is based on the species abundances within Group A—Figure 11.

remaining oyster, *O. veatchii*, plots as an outlier and thus varies differently compared to all other species (Fig. 7C). Examination of the coherence line plots reveal the

biological complexity within this time interval. Each line plot represents a variety of abundance patterns across sites (Fig. 7D). Species within group A were present and abundant in most Los Angeles and Orange County sites but almost disappear in over half of the San Diego sites and occur in relatively high abundance in the other half of the San Diego sites. *Dendrostrea vespertina*, the only oyster in group A, is relatively low in abundance within Los Angeles and Orange County sites but higher in abundance within San Diego sites (i.e., 5–20%). Group B species were absent from Los Angeles County and then occurred at relatively low abundances (2–40%) except for a site-specific high peak in abundance of one particular species (i.e., *Halistylus pupoideus* Carpenter, 1864). Species within group C occurred in very low abundances within Los Angeles County sites, slightly increase in abundance within Orange County sites (1–20%), and then abundances increased more within San Diego County sites (Fig. 7D). *Pycnodonte erici*, the only oyster within the group, occurs in relatively low abundance (1–10%) throughout Los Angeles, Orange, and San Diego Counties but peaks in abundance (~80%) in one San Diego site (Fig. 7D).

Middle Pleistocene data—Figure 9A displays the nMDS plot of the middle Pleistocene sites coded for Type 1 SIMPROF groups. Three significant groups occur, at a p -value ≤ 0.001 , each designated to a specific county location. Clear division along the horizontal axis occurs between San Diego and Los Angeles sites as well as a separation within Los Angeles sites (Fig. 9A). Type 2 analysis of species reveals valid association between species at a p -value ≤ 0.001 (Fig. 9B). Departure of the actual profile from the permuted profile indicates an excess of negative association between species suggesting turnover occurred within this time interval (Fig. 9B). A long tail of zero values also exists for this time interval justifying the removal of rare species during the Type 3 SIMPROF analysis. Type 3 SIMPROF analysis reports

Figure 9. Caption on top of page 11.

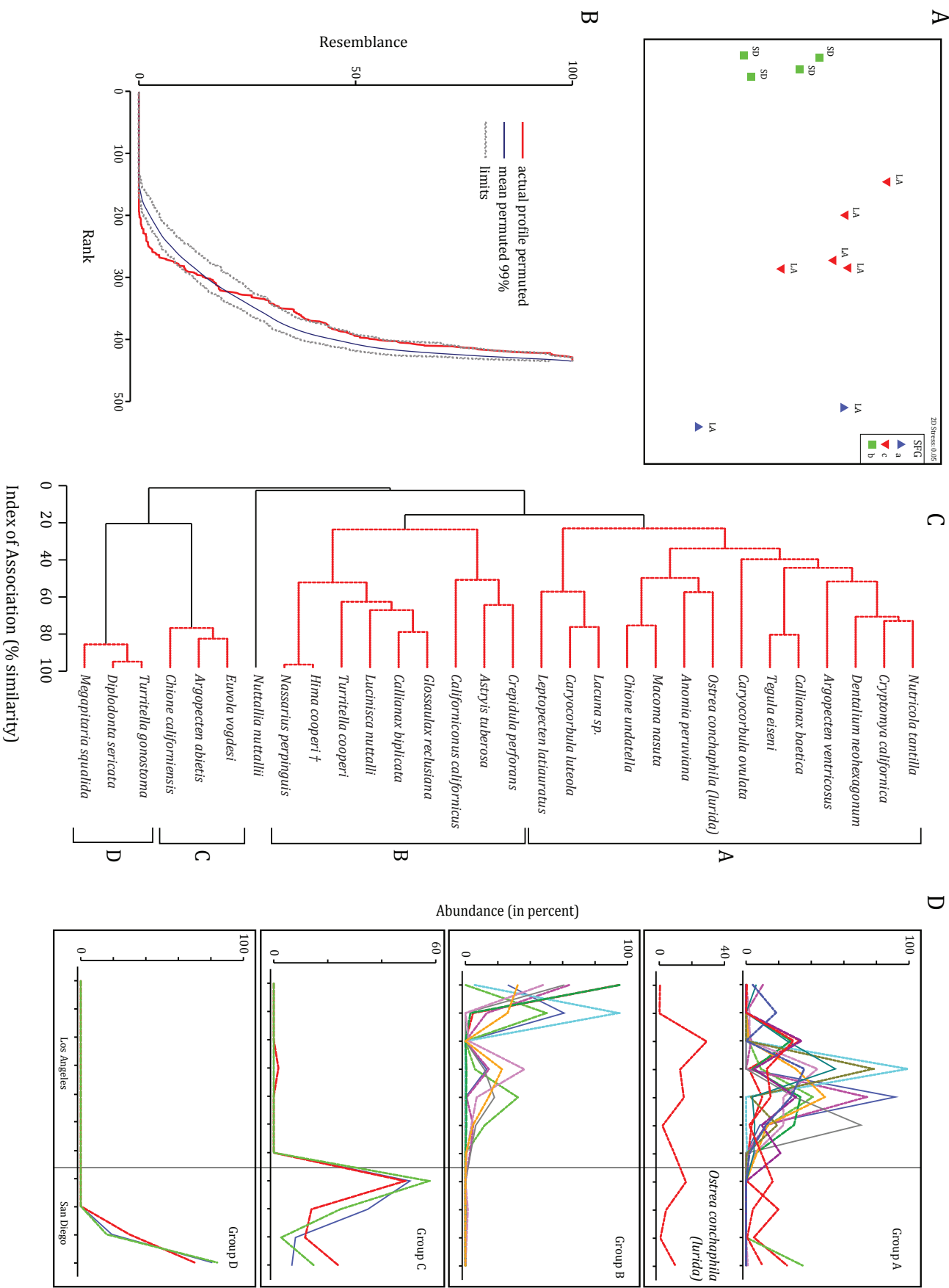


Figure 9. Middle Pleistocene statistical procedures for samples (A) and species (B–D). **A.** Non-metric Multidimensional Scaling (nMDS) plot produced using 4th root transformed, abundances of species, using Bray-Curtis similarities between samples. Any species contributing less than 5% of the total sample was removed. Middle Pleistocene resemblance measure calculated among 11 samples and 30 species. Symbols represent significant groups identified by SIMPROF Type 1 test; all grouping have a p -value=0.001. **B.** Similarity profile from Type 2 SIMPROF test based on Index of Association. P -value=0.001 indicates that there are genuine associations to interpret among species. Actual profile data, plotted in bold red, represents the full set of pairwise resemblance ordered from the smallest to the largest (y-axis) plotted against their rank (x-axis). Fine blue line represents the modeled mean based on 1000 permutations and dashed lines represent the predicted range for 99% of resemblances, for any given rank, under the null hypothesis of no association among species. **C.** Middle Pleistocene taxonomic dendrogram from group-averaging clustering of the 30 ‘most important species’ (i.e., those account for $\geq 5\%$ of the total abundance in two or more sample) based on Index of Association calculated among standardized (to 100%), untransformed species abundances from 11 samples. Continuous lines denote significant groups differentiated by Type 3 SIMPROF test at a p -value=0.001. Dashed lines represent the substructure containing no statistical support. **D.** Middle Pleistocene species coherent plots, or line plots, for groups of species identified in Figure 8C. The x-axis is rearranged according to the samples’ latitude from North to South (See Figure 1. for county locations). The y-axes represent percentages of the total abundance of a particular species found across the 11 samples (species are standardized but untransformed). Dagger symbol (†) represents taxa that went extinct at the end of the middle Pleistocene.

four significant groups with two or more species (groups A through D), and only one species—*Nuttallia nuttallii* Conrad (1837)—separating out independently at a p -value ≤ 0.001 (Fig. 9C). Accordingly, we can reject the null hypothesis and state that species within groups A, B, C, and D vary coherently across samples. The only oyster species present in this time interval is *Ostrea conchaphila* (lurida) and clusters into Group A (Fig. 9C). Stationary epifaunal bivalves dominate this group (e.g., *O. conchaphila* (lurida)) followed by stationary infaunal suspension feeding bivalves (e.g., *Caryocorbula luteola* Carpenter, 1864) and mobile infaunal suspension feeders (e.g., *Chione undatella* Sowerby, 1835) (Fig. 8). In contrast, various gastropods comprise group B, predominantly carnivorous gastropods (i.e., *Astyris tuberosa* Carpenter, 1865, *Californiconus californicus* Reeve, 1844, *Glossaulax reclusiana* Deshayes, 1839, *Callianax biplicate* Sowerby, 1825, *Hima cooperi* Forbes, 1852, and *Caesia perpinguis* Hinds, 1844), followed by suspension-feeding gastropods (i.e., *Crepidula perforans* Valenciennes, 1846 and *Turritella cooperi* Carpenter, 1864) and one chemosynthetic gastropod (i.e., *Luciniscia nuttalli* Conrad, 1837). The smaller groups C and D contain a combination of epifaunal and infaunal bivalves and one suspension feeding gastropod. Group C includes both epifaunal (*Euvola vogdesi* Arnold, 1906, *Argopecten abietis* Jordan and Hertlein, 1926) and infaunal bivalves (*Chione californiensis* Broderip, 1835) while a suspension feeding gastropod (*Turritella gonostoma* Valenciennes, 1832) and infaunal bivalves (*Diplodonta sericata* Reeve, 1850 and *Megapitaria squalida* Sowerby, 1835) constitute group D. Figure 9D reveals strong species-turnover across sites as predicted by the Type 2 SIMPROF results. Groups A, B, C, and D tend to occur only in a limited subset of sites and species within groups A and B change between more northern and southern sites. For example, group A species occur in low abundances in the northern Los Angeles County sites and peak in abundance in the more southern site.

Group B displays the opposite pattern; species in this group occur in high abundances within more northern Los Angeles County site, then decline in abundance further south within Los Angeles County (Fig. 9D). Group C and D occur predominantly within San Diego sites and clearly switch within the county sites (Fig. 9D). Although groups C and D vary within San Diego sites, site locations are essentially from the same latitude and longitude therefore trends between northern and southern sites do not exist (Fig. 9D).

Late Pleistocene data—The late Pleistocene resembles the late Pliocene in terms of its complex spatial pattern. Within most of the SIMPROF groups, multiple county sites exist indicating that a complex spatial pattern exists between sites (Fig. 10A). Type 2 SIMPROF analysis indicates that interpretable association exists between species at a p -value ≤ 0.001 (Fig. 10B). Departure of the actual profile from the permuted profile indicates an excess of positive association between species and suggests low turnover within this time interval. A long tail of zero values exists justifying the removal of rare species during the Type 3 SIMPROF analysis (Fig. 10B). Figure 10C displays the dendrogram produced via the combination of agglomerative clustering and Type 3 SIMPROF analysis. According to the Type 3 SIMPROF results, four significant groups cluster out, two contain more than two species (i.e., groups A and D), two contain a pair of species, (i.e., groups B and C) while seven species separate out independently at a p -value ≤ 0.001 (Fig. 10C). Accordingly, we can reject the null hypothesis and state that species within the group A and D vary coherently across site, while we cannot reject the null hypothesis for groups B and C. Group A is primarily comprised of gastropods, both carnivorous (i.e., *Callianax biplicate* Sowerby, 1825, *Caesia delosi* Woodring, 1946) and grazing (i.e., *Fissurella volcano* Reeve, 1849), and a deep burrowing bivalve (i.e., *Epilucina californica*) (Fig. 10C, Table 1). The only oyster present in this time interval, *Ostrea conchaphila* (lurida),

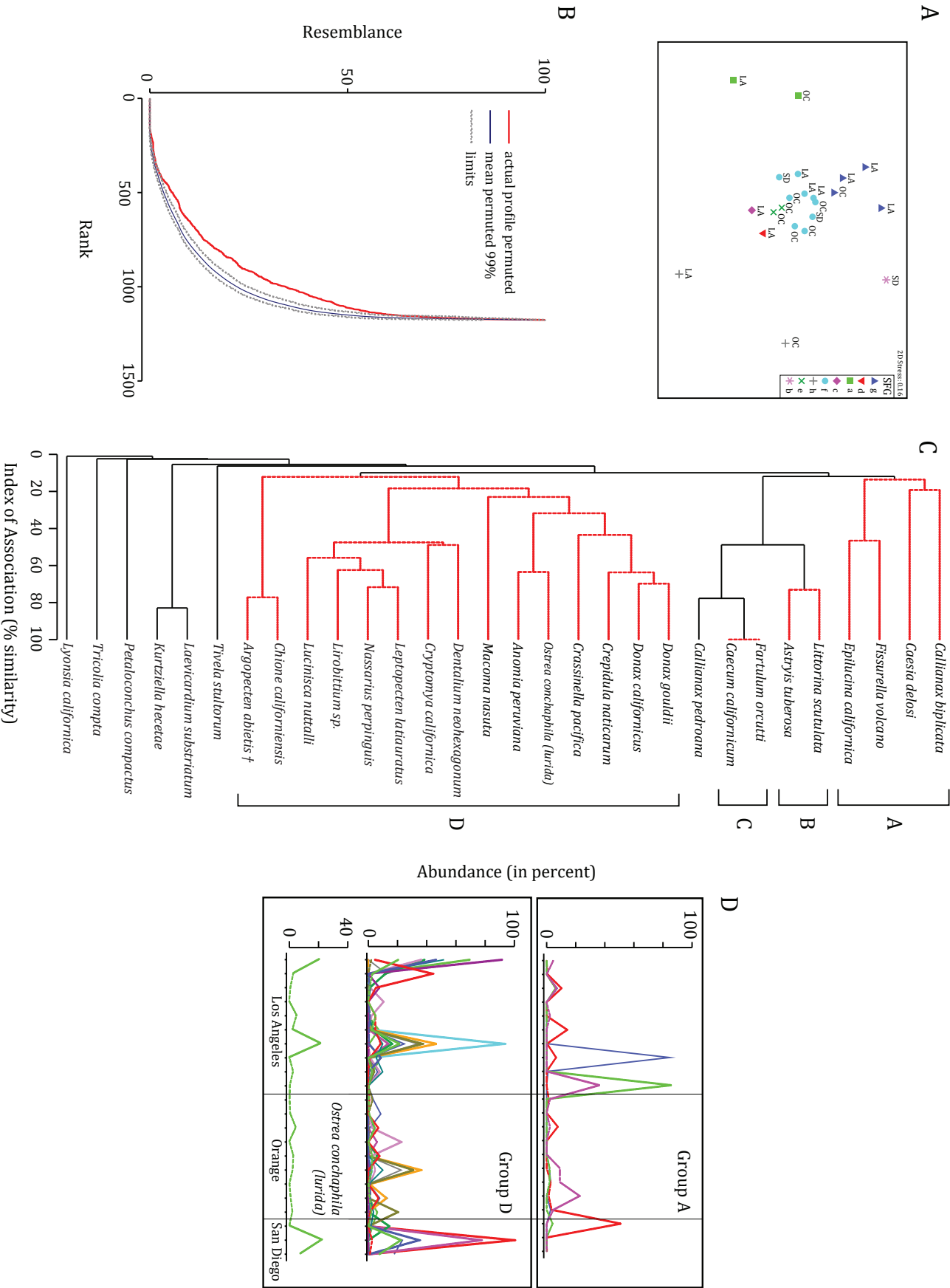


Figure 10. Caption on top of page 13.

Figure 10. Late Pleistocene statistical procedures for samples (A) and species (B–D). **A.** Non-metric Multidimensional Scaling (nMDS) plot produced using 4th root transformed, abundances of species, using Bray-Curtis similarities between samples. Any species contributing less than 5% of the total sample was removed. Late Pleistocene resemblance measure calculated among 22 samples and 49 species. Symbols represent significant groups identified by SIMPROF Type 1 test; all grouping have a p -value=0.001. **B.** Similarity profile from Type 2 SIMPROF test based on Index of Association. P -value=0.001 indicates that there are genuine associations to interpret among species. Actual profile data, plotted in bold red, represents the full set of pairwise resemblance ordered from the smallest to the largest (y-axis) plotted against their rank (x-axis). Fine blue line represents the modeled mean based on 1000 permutations and dashed lines represent the predicted range for 99% of resemblances, for any given rank, under the null hypothesis of no association among species. **C.** Late Pleistocene taxonomic dendrogram from group-averaging clustering of the 30 ‘most important species’ (i.e., those account for $\geq 9\%$ of the total abundance in two or more sample) based on Index of Association calculated among standardized (to 100%), untransformed species abundances from 22 samples. Continuous lines denote significant groups differentiated by Type 3 SIMPROF test at a p -value=0.001. Dashed lines represent the substructure containing no statistical support. **D.** Late Pleistocene species coherent plots, or line plots, for groups of species identified in Figure 10C. The x-axis is rearranged according to the samples’ latitude from North to South (See Figure 1. for county locations). The y-axis represent percentages of the total abundance of a particular species found across the 22 samples (species are standardized but untransformed). Dagger symbol (+) represents taxa that went extinct at the end of the late Pleistocene.

clusters into the largest group, Group D. Facultatively mobile infaunal suspension feeder dominate Group D (e.g., *Donax gouldii* Dall, 1921) followed by facultatively mobile epifaunal suspension feeders and epifaunal bivalves (e.g., *Argopecten abietis*) and semi-infaunal deposit feeders (e.g., *Dentalium neohexagonum* Sharp and Pilsbry in Pilsbry and Sharp, 1897) (Fig. 8). Coherence line plots of the two main species groups reveal no discernable spatial trend between counties. Species within group A vary between a relatively lower abundance (~ 1 –40%) across sites with two site specific increases in abundance (Fig. 10D). Within Group D, three samples contain a relatively higher abundance of species, including the highest abundance of *O. conchaphila (lurida)* ($\sim 20\%$), compared to other sites. These peaks in abundance occur within Los Angeles and San Diego while species within Orange County sites remain at relatively lower abundance including *O. conchaphila (lurida)* (Fig. 10D).

Holocene data—Figure 11A presents the nMDS ordination based on all four Holocene sites, with the county location labeled on each symbol and each symbol representing the Type 1 SIMPROF groupings at a p -value ≤ 0.001 . Based on the p -value, we can reject the hypothesis that samples are homogeneous and state that multivariate structure exists within the Holocene sites. Examination of this plot reveals significant sample variation between the Orange and Los Angeles County sites along the horizontal axis and within Los Angeles County sites along the vertical axis. The Type 2 SIMPROF test based on interspecies correlation (Fig. 11B), is highly significant ($\pi=23.143$, p -value ≤ 0.001) indicating that there are valid associations to interpret between species. Thus, we can reject the null hypothesis that species are not associated with each other. Examination of the actual profile compared to the permuted profile indicates both excess of positive associations and negative associations (Fig. 11B). The tail of zero values strengthens the case for removing rare taxa prior to Type 3 SIMPROF

analyses. The dendrogram produced by agglomerative hierarchical cluster and Type 3 SIMPROF reveals further structure, with each species falling into three significant groups (A–C) p -value ≤ 0.001 . Of the three groups only two groups (A and B) contain more than two species. Group C forms an isolated group containing two species. According to the results, we can reject the null hypothesis and state that species within groups A and B vary coherently across samples; however, SIMPROF cannot reject the null hypothesis of coherence at any level of association for group C because SIMPROF tests cannot discriminate profiles when there are only two variables (or samples) to compare (Somerfield and Clarke 2013) (Fig. 11C). Coherence line plots of the two main species groups reveal a spatial difference between species. Group A species tend to occur at higher abundances within Los Angeles compared to the Orange County sites. Group A contains the only oyster which happens to be the most dominant taxon within this time period (Fig. 11C and Fig. 8). Group B species are generally lower in abundance across Los Angeles and Orange County with the exception of one Los Angeles location/sample (Fig. 11D).

DISCUSSION

At the end of the Pliocene, an abrupt transition from warmer to cooler climates occurred with the onset of major northern hemisphere glaciation ~ 2.7 million years ago. Throughout the last 2.5 million years, long-term trends of climatic cooling characterized nearshore marine environments as glacial and interglacial cycles waxed and waned in response to changes in the periodicity of Earth’s orbital configuration. Midway through the glacial and interglacial cycles, the periodicity of glacial response changes from a mild, 41 ka cycle to a more variable ~ 100 ka cycle (Lisiecki and Raymo 2005, 2007). The rapid and substantial climate change during this time undoubtedly affected marine taxa. In fact, researchers document enhanced and variable extinction and

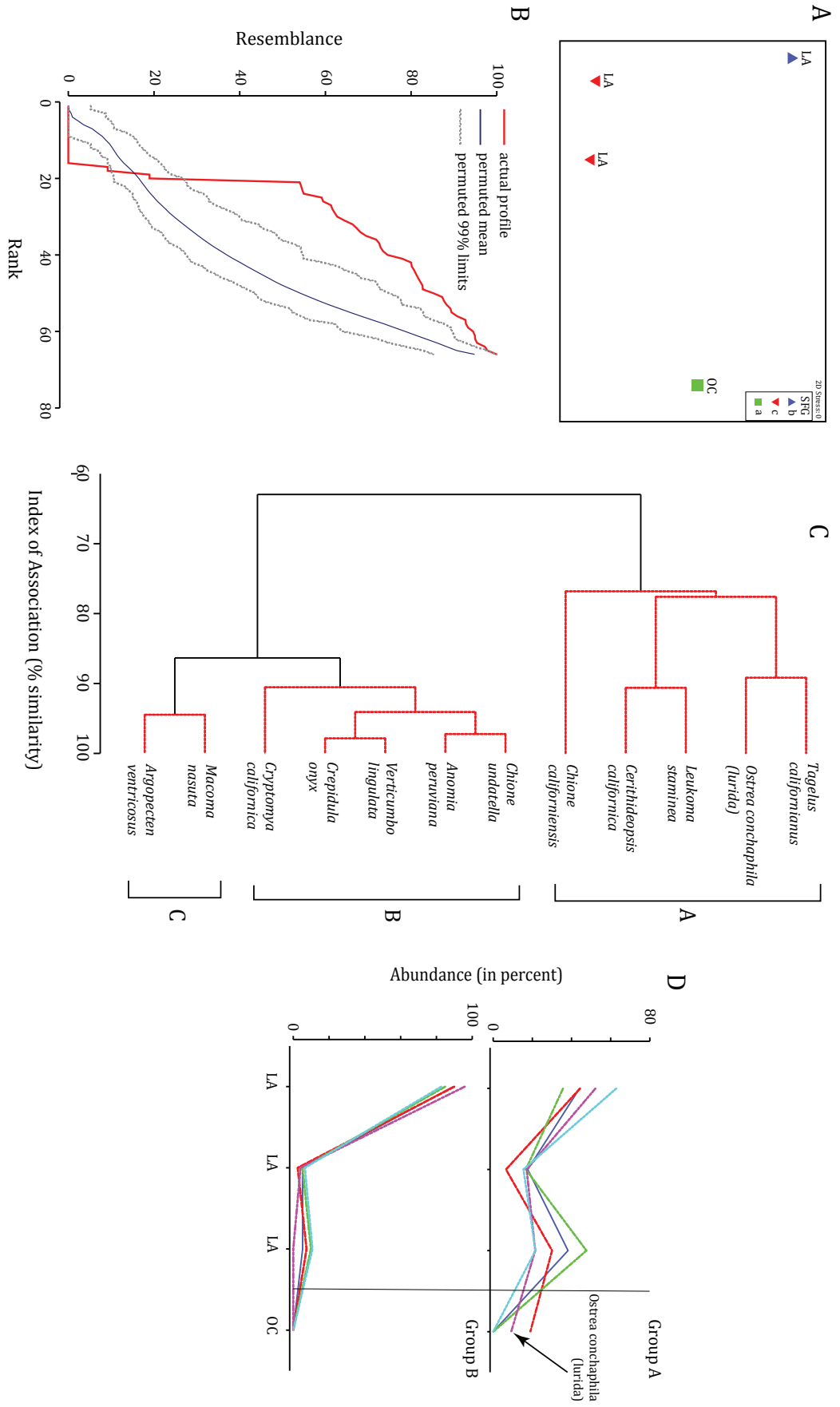


Figure 11. Caption on top of page 15.

Figure 11. Holocene statistical procedures for samples (A) and species (B–D) based on 12 species and 4 samples. **A.** Non-metric Multi-dimensional Scaling (nMDS) plot produced using 4th root transformed, abundances of species in each data set, using Bray-Curtis similarities between samples. Symbols represent significant groups identified by SIMPROF Type 1 test; all grouping have a p -value=0.001. **B.** Similarity profile from Type 2 SIMPROF test based on Index of Association. P -value=0.001 indicates that there are genuine associations to interpret among species. Actual profile data, plotted in bold red, represents the full set of pairwise resemblance ordered from the smallest to the largest (y-axis) plotted against their rank (x-axis). Fine blue line represents the modeled mean based on 1000 permutations and dashed lines represent the predicted range for 99% of resemblances, for any given rank, under the null hypothesis of no association among species. **C.** Holocene taxonomic dendrogram from group-averaging clustering of the 30 ‘most important species’ (i.e., those account for 5% of the total abundance in two or more sample) based on Index of Association calculated among standardized (to 100%), untransformed species abundances from 22 samples. Continuous lines denote significant groups differentiated by Type 3 SIMPROF test at a p -value=0.001. Four groups contain multiple species (A–D) and seven groups contain single-species groups. Dashed lines represent the substructure containing no statistical support. **D.** Holocene species coherent plots, or line plots, for groups of species identified in Figure 11C. The x-axis is rearranged according to the samples’ latitude from North to South (See Figure 1. for county locations). The y axes represent percentages of the total abundance of a particular species found across the four samples (species are standardized but untransformed). The y-axes represent percentages of the total abundance of a particular species found across the four samples (species are standardized but untransformed).

origination depending on the region studied. Across the Plio-Pleistocene boundary, much of the research focuses on the regional extinction along the Atlantic and Caribbean coast (e.g., Stanley and Campbell 1981, Jackson et al. 1993, Allmon 2001, Todd et al. 2002).

However, significant extinction occurred during the late Pliocene and middle Pleistocene along the New Zealand coast as well (Johnson and Curry 2001). Our results indicate a clear regional extinction exists in southern California at the end of the late Pliocene when ten out of the 30 most abundant species within the late Pliocene go extinct (Fig. 7C). Notably within the late Pliocene, extant taxa comprise a significant, coherent group with the now extinct oyster *Dendroostrea vespertina* (Fig. 8C: Group A). The other nine extinct taxa cluster into a separate coherent group (Fig. 8C: Group C). Spatially, the late Pliocene coherent groups wax and wane in terms of abundance without a clear spatial pattern throughout the three southern California counties (Fig. 8D).

Previous regional work indicates similar patterns of extinction within specific taxonomic groups. California pecten species indicate high levels of extinction during the Plio-Pleistocene transition (Smith and Roy 2006). Major Plio-Pleistocene molluscan extinctions reported from central and southern California within the San Joaquin Basin also occur (Bowersox 2005, 2006). Work on Plio-Pleistocene bivalves from western South America reveals an abrupt decline in the proportion of living species within the fossil record marking a ~66% decline; their results indicate that selective extinction occurred among small, epifaunal, short-ranged species (Rivadeneira and Marquet 2007). However, marine gastropods from western South America reveal a different pattern. In the absence of significant diversity changes, small, grazing gastropods replaced larger carnivore gastropods across the Plio-Pleistocene boundary (Rivadeneira and Nielsen 2017). Our data suggest ecological structural changes as well. For example, carnivorous gastropods and infaunal

bivalves share dominance with the dominant oyster, *D. vespertina*, in the late Pliocene while both infaunal and epifaunal bivalves share dominance with the dominant oyster, *Ostrea conchaphila (lurida)*, in the middle and late Pleistocene (Fig. 8). Thus, it is possible that the Plio-Pleistocene transition caused a shift in both taxonomic and ecological dominance; however, further research would need to be accomplished in order to document this pattern more rigorously.

The Plio-Pleistocene faunal turnover, in both the eastern Pacific and Atlantic regions, was related to the changing climate. Specifically, the rapid shift from warmer to cooler climates at the Plio-Pleistocene boundary affected taxa more than habitat loss via dropping sea-levels (Stanley and Campbell 1981, Stanley 1984, 1986). However, within one California basin (i.e., San Joaquin Basin) peak faunal diversity corresponds to sea-level rise while low diversity corresponds to sea-level drops (Bowersox 2005, 2006). Compared to the Atlantic marine taxa, evidence suggests that the Pacific marine taxa (including data from California, Japan and Panama) fared better, as thermally controlled provinces of the West Coast of North and Central America shift southward slow enough for faunas to migrate (Olsson 1961, Valentine 1961, Addicott 1966, Stanley 1986, Valentine et al. 2013). More recent work focuses on using marine bivalves as a model group for understanding the origins and dynamics of the latitudinal diversity gradient (LDG) (Jablonski et al. 2017). Their results indicate that regional extinction of marine bivalves across the Plio-Pleistocene boundary correlates significantly with mean annual sea-surface temperatures (Jablonski et al. 2017). In addition, the rate of temperature change between ~1.0 million-year periods correlates significantly across the Plio-Pleistocene boundary (Edie et al. 2018). Thus, the magnitude and rate of sea-surface temperature changes affect regional extinction across the Plio-Pleistocene boundary. Based on these findings, we suspect our late Pliocene oyster community

might have been susceptible to the increased magnitude and rate of changing sea-surface temperatures.

Another predictor of diversity trends during the Plio-Pleistocene climatic cooling is the geographic range size of the species at the beginning of the Pliocene, with the narrowest-ranging species most prone to regional extinction. This suggests that the species with the greater latitudinal range could tolerate and disperse at greater ranges and hence extend survival (Huang et al. 2015). Although we did not examine geographic range size of the species within this study, we hypothesize that species who survived the Plio-Pleistocene transition (e.g., *Chione californiensis*, *Californiconus californicus*, and *Caryocorbula ovulata* Sowerby, 1833) have greater geographic ranges compared to the species that disappear at the end of the Pliocene (e.g., *Opalia varicostata* Stearns, 1875, *P. erici*, and *D. vespertina*).

Over the last 2.5 million years our data reveal a much different pattern compared to patterns within the Pliocene (Figs. 3, 6). As shown in Figure 6, most coherent species within Groups C and E replace the late Pliocene Group B and remain relatively abundant from the middle Pleistocene through the Holocene. Analysis of Californian Pleistocene and recent mollusks support the relative stability we find in our data—even in light of the fluctuating glacial-interglacial cycles within the Pleistocene (Valentine and Jablonski 1991). They concluded that Pleistocene sea level change did not affect community and species continuity. Instead, species continued to shift their latitudinal ranges to track the changing ocean conditions. Further examination of eastern Pacific Pleistocene marine species reveals that species that exhibit the greatest range shifts (i.e., extraprovincial species) can be broken down into northern and southern groups. When the two groups are examined separately, results suggest that it is easier for northern species to migrate south during cooling events because cooler waters can be found in both shallow and deep environments thus limiting water-mass boundaries for northern species. In contrast, warm water expanding to the north only occurs at shallow depths producing water-mass boundaries for southern species migrating to the north (Roy et al. 1995). Evidence of species' ranges shifting suggests that the Pleistocene taxa within the eastern Pacific belong to a loose, facultative, individualistic, community structure resulting from the actual environmental and ecological instability itself. As species track shifting environments, they prevent long-term isolation and genetic differentiation and thus prevent extinction (Pease et al. 1989, Roy et al. 1996). Coral communities (Jackson and Johnson

2000) and marine ostracods (Cronin and Ikeya 1987) also exhibit evidence for individualistic species responses to climate change resulting in general community stability. Based on these conclusions, we suspect that the Pleistocene/Holocene taxa within southern California remain stable throughout this time period because the rate of sea-surface temperatures during the Pleistocene through the Holocene did not exceed the rate of change occurring at the end of the Pliocene. And, once the *O. conchaphila* (*lurida*) oyster group became established, its community structure is loose and facultative enough that it can shift with the sea-surface temperature changes associated with the glacial and interglacial cycles.

Spatial patterns of co-occurring taxa within the late Pleistocene and Holocene reveal little turnover between southern California counties much like the late Pliocene spatial pattern (Figs. 10, 11). Most of the taxa randomly appear in various abundances across the different locations, most likely representing the loose community structure described in Roy et al. (1996). However, within the middle Pleistocene significant turnover exists between dominant taxonomic groups between Los Angeles and San Diego counties (Fig. 9). The oyster group appears to vary in relative abundance across the two counties, but Group B only occurs in Los Angeles County and Groups C and D occur in San Diego County (Fig. 9). Climatically, the mid-Pleistocene marks the transition between changes in periodicity of glacial response from a 41 to ~100 ka cycle (Lisiecki and Raymo 2005, 2007). During this time the climate changed from short and mild glacial-interglacial 41 ka cycles (pre MPT >920 ka) to asymmetrical 100 ka cycles (post MPT <641 ka) (Diz et al. 2020). Perhaps this change in climate affected taxa briefly causing community isolation along the coast of southern California. Another possible explanation is that the spatial difference between middle Pleistocene localities marks a transitional, or recovery, stage between the late Pliocene extinction and the late Pleistocene stability. The Holocene also marks a difference between southern California counties and likewise, changes occur within ecological niches as epifaunal grazing gastropods share dominance with the dominant oyster, *O. conchaphila* (*lurida*). However, since our Holocene sample localities are limited, the taxonomic and ecological patterns are preliminary and subject to change as more data are collected (Figs. 8, 11).

CONCLUSIONS

Oyster communities have changed significantly along the southern California coast during the last 3.6 million

years. When we examine the 30 most abundant molluscan taxa within the entire data set, the dominant oyster, *Dendroostrea vespertina*, went extinct at the Plio-Pleistocene boundary along with six other taxa. A new oyster, *Ostrea conchaphila (lurida)*, replaced *D. vespertina* as the dominant oyster during the early Pleistocene, began its dominance in the middle Pleistocene and continued to be dominant throughout the Holocene. Once oyster communities reestablished themselves in the middle Pleistocene, the dominant taxa remained relatively stable through the Holocene; however, abundance fluctuated over time.

Examination of each time interval independently revealed how taxa fluctuate spatially and revealed details regarding paleocommunity structure during this time interval. According to our results, within the late Pliocene, late Pleistocene and Holocene, the most dominant taxa wax and wane across the various southern California locations and exhibit no real pattern associated with their spatial relationships. However, during the middle Pleistocene different taxa dominate distinct Los Angeles and San Diego sites, while *O. conchaphila (lurida)* remained at a relatively low abundance across the southern California counties. In addition to the switch in dominant oysters through time, the overall dominant taxa and ecologies within the coherent, dominant oyster groups switched too. Carnivorous gastropods and infaunal bivalves dominated the late Pliocene oyster group and then infaunal and epifaunal bivalves dominated the middle and late Pleistocene oyster groups. The Holocene marks another shift in ecology as epifaunal bivalves and grazing gastropods dominated the oyster community.

Based on the relative stability of dominant taxa in the late Pliocene, we conclude that the oyster communities possessed a loose, facultative, individualistic, community structure that allowed taxa to track shifting environments and thus shift their latitudinal gradients. At the end of the Pliocene, we suspect that the onset of northern hemisphere glaciation changed the magnitude and rate of sea-surface temperature and most likely caused a complete breakdown of late Pliocene oyster communities. Once oyster communities reestablished themselves in the middle Pleistocene, a new dominant oyster emerged, and the oyster communities varied spatially perhaps due to water-mass differences associated with the mid-Pleistocene transition between changes in periodicity of glacial response from a 41 ka to ~100 ka cycle. The relative stability of dominant taxa and the loose community structure then returned, with *O. conchaphila (lurida)* remaining as the dominant oyster in the late Pleistocene and continuing through the Holocene. The

loose, individualistic community structure allowed taxa to fluctuate in abundance and ecology spatially. Most likely the sea surface temperature changes associated with the glacial-interglacial cycles did not exceed the rate of change occurring at the end of the Pliocene. As such, late Pleistocene and Holocene species were able to track shifting environments, prevent long-term isolation, and avoid extinction.

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