Palaeontology
The Palaeontological Association
www.palass.org
[Palaeontology, 2024, e12696]

Response of Mediterranean Sea bivalves to Pliocene–Pleistocene environmental changes

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Typescript received 22 June 2023; accepted in revised form 12 February 2024

Abstract: The Mediterranean Sea is recognized as a hotspot of marine biodiversity. Analysing its past biodiversity can help in understanding species' response to climate change. We built a species-level dataset of bivalve occurrences across the Zanclean–Calabrian interval, a time characterized by significant changes in climate, and by bivalve extinctions. The dataset includes more than 400 species distributed from the eastern to the western Mediterranean Sea. We measured changes in richness and turnover through time, for the entire dataset, and for different palaeoenvironments and combinations of tiering and feeding categories to test if specific environmental conditions and different lifestyles were correlated to species extinction or survival through time. We also compared niche breadth, geographical range size, and species abundance of extinct and extant species, to test which of these parameters potentially affected extinction risk. Our results confirm a loss of biodiversity between 3 Ma and the Early Pleistocene, although this loss was less intense and more gradual than previously estimated. We also found significant differences in niche breadth and geographical range size between extinct and extant species. Suspension feeders lost a higher proportion of species and suffered a higher reduction of geographical range compared to infaunal deposit feeders. Species loss was more protracted and higher on the shoreface than on the shelf, which is probably related to the reduction of shallow-water vegetated environments and to the disaggregation of heterozoan carbonate ramp habitats with cooling and sea-level drop at the onset of the northern hemisphere glaciation.

Key words: bivalve, biodiversity, Mediterranean Sea, species richness, extinction risk, climate change.

THE Pliocene–Pleistocene transition is an important target time interval for both palaeoclimatologists and palaeontologists interested in understanding the role of climate on faunal change. The Pliocene is considered to be the most recent epoch of Earth history with global temperatures and carbon dioxide levels comparable to future predictions (Lisiecki & Raymo 2005; Fedorov *et al.* 2013; Prista *et al.* 2015; Beltran *et al.* 2021), whereas the Early Pleistocene was an epoch characterized by intense climatic oscillations due to the onset of the northern hemisphere glaciation (Pagani *et al.* 2010). Past climatic variability and related sea-level changes are considered the main causes of regional extirpations among marine macrofauna and megafauna that occurred after the mid-Piacenzian (Jablonski *et al.* 2017; Pimiento *et al.* 2017). Changes in temperature controlled changes in marine ecosystems on million-year, millennial, and centennial timescales, as observed during the mid-Piacenzian Warm Period and during the Late Pliocene and Pleistocene high-frequency climate cycles (Dominici & Danise 2023; Tomašových *et al.* 2023).

It has been widely demonstrated that past climatic variability drove faunal extinctions in the Mediterranean area during the Pliocene–Pleistocene transition (Monegatti & Raffi 2001). The Mediterranean Sea is recognized as a hotspot of marine biodiversity. Unfortunately, this diversity is currently threatened by global warming that may impact marine communities and trophic relationships among organisms (Albano *et al.* 2021). Investigating how species responded to environmental disturbances in the geological past helps us to predict to what degree marine species are vulnerable to recent and future climate change.

Previous studies focused on the Mediterranean area estimated a strong biodiversity loss of bivalves at the transition from Pliocene warmer and moister conditions to Pleistocene colder and drier climate regimes, with a peak of extinction at 3 Ma (Raffi *et al.* 1985; Monegatti & Raffi 2001). Nonetheless, these studies focused on taxonomic species loss only, without focusing on macroevolutionary dynamics linked to species turnover. At the same

time, the potential response of different tiering and trophic categories to Pliocene–Pleistocene climate and environmental change received little attention. Also of potential interest is the role of water depth in species extinction or survival. Tomašových *et al.* (2014), for instance, observed temporal turnover in Neogene molluscan communities along the onshore–offshore gradients when looking at long temporal scales. To fill this gap, we analysed the effect of potential extinction drivers in determining bivalves' extinction risk taking into account different lifestyles and palaeoenvironments distributed across an onshore-offshore gradient. Although several biological/ecological traits have been identified as correlating with species extinction risk (i.e. body size, geographical extent, population density), we tested the role of geographical range size, niche breadth, and abundance as determinants of bivalve survival or extinction. It has been demonstrated that habitat specialists with a narrow geographical range and low abundance can be extremely vulnerable even to modest environmental change (Roberts & Hawkins 1999; Raia *et al.* 2016). Furthermore, niche breadth and geographical range size are statistically interrelated and may reinforce each other (Dulvy *et al.* 2004), although singling out their effect on extinction is a hard task. Saupe *et al.* (2015) suggested that, in the western Atlantic, geographical range played a predominant role for mollusc extinction waves at the Pliocene–Pleistocene transition, whereas niche breadth apparently had a secondary role. Abundance is also thought to influence extinction risk, although little is known about its relationship to extinction rates over geological time. Simpson & Harnik (2009) found a non-linear relationship between abundance and extinction risk, with rare and abundant genera exhibiting a higher extinction rate compared to moderate abundant genera. In contrast, Harnik *et al.* (2012) found that local abundance had little effect in determining extinction.

For this purpose, in this study we assembled a new dataset of bivalve fossil occurrences from literature data which spans the entire Mediterranean area, the North Sea, and the eastern Atlantic coast, and ranges in time from the Zanclean to the Calabrian (5.33 to 0.78 Ma). Our aims were to: quantify biodiversity changes through time combining a taxonomical (species level) and functional diversity (tiering and feeding categories) approaches; compare species change through time in different palaeoenvironments (shoreface vs shelf) testing if extinction rates were different across the bathymetric gradient; and investigate the role of geographical range size, niche breadth, and abundance on bivalve survival and extinction. This approach allowed us to test for potential functional shifts in Mediterranean Sea bivalves under intense climate and environmental change.

MATERIAL AND METHOD

Species-level dataset

Expanding on the work of Danise & Dominici (2023), which included only information on the families Veneridae, Pectinidae and Lucinidae, the present dataset includes Pliocene–Pleistocene fossil occurrences of all bivalve families from the Mediterranean area, the North Sea and the eastern Atlantic coast. Mediterranean Sea occurrences were used to estimate species diversity through time in the basin. Those from the North Sea and the eastern Atlantic were only used for calculating species' geographical range size, to avoid the underestimation of species' geographical extent (see below).

For each species, individual occurrence data include information about geographical location (geographical coordinates and locality), chronostratigraphic attribution, lithology, lithostratigraphic level from which the species come from or name of the analysed sample (if specified) and palaeoenvironment. We subdivided the latter into five categories across an onshore–offshore siliciclastic gradient (brackish–estuarine, shoreface, inner shelf, outer shelf and slope). Calcarenite occurrences were included only when specific indications about the palaeobathymetry were provided by the authors.

As regards the chronostratigraphic attribution of each site, we reported minimum and maximum ages derived from the literature or the boundary ages of the geological stage associated with each occurrence (i.e. for a fossil site that is Zanclean in age, we considered a time frame spanning from 5.33 to 3.6 Ma). The midpoint of this range was used to assign a point age to each occurrence.

To gather fossil occurrences of bivalve species, we re-examined bivalve lists published in the literature (e.g. Monegatti & Raffi 2001) and integrated them with more recent publications. We revised the bivalve fossil lists in terms of species presence/absence and accounted for the most recent taxonomic and systematic attributions. Indeed, recent articles provided new clarification about bivalve nomenclature and taxonomy (Mikkelsen & Bieler 2003; La Perna & D'Abramo 2011; La Perna *et al.* 2018; Pimentel *et al.* 2021; Brunetti & Della Bella 2022a). Moreover, we modified the chronological attribution of some fossil sites according to recent biochronological evidence. For instance, some sites previously dated relying on planktonic foraminiferal biostratigraphic correlations were revised according to the more recent Mediterranean Neogene planktonic foraminifer biozonation and biochronology published in Lirer *et al.* (2019). Other chronological revisions were made after considering recent fossil site re-evaluations. For instance, Dominici & Forli (2021) recently assigned the Camino Tondo (Tuscany, Italy) site

to Zanclean rather than middle Piacenzian age (as in Monegatti & Raffi 2001), based on a correlation with the nearby Arcille succession recently attributed to the Lower Pliocene (Bianucci *et al.* 2019; Dominici & Forli 2021).

Overall, the dataset counts 4938 fossil occurrences belonging to 68 bivalve families distributed over 137 fossil localities (Appendices S1–S3).

After collecting the data, we classified the species as either extant (i.e. still living in the Mediterranean Sea today) or extinct. The latter refers to species globally extinct or locally extirpated from the Mediterranean area during the Pliocene–Pleistocene interval. For each species, we further tallied information on feeding and tiering, as reported in Nawrot *et al.* (2017) and in the Paleobiology Database (https://paleobiodb.org/). Accordingly, we chose from seven combinations of feeding and tiering categories: infaunal deposit feeder, infaunal suspension feeder, epifaunal suspension feeder, boring suspension feeder, carnivorous, chemosymbiotic and commensal.

To verify potential changes of species richness over time, we split the Pliocene–Pleistocene bivalve dataset into four temporal bins, identifying an early Zanclean temporal window (from 5.3 to 4 Ma; bin 1), a middle Zanclean to Piacenzian temporal range which includes the mid-Piacenzian Warm Period (from 3.9 to 3 Ma; bin 2), a late Piacenzian to Gelasian interval (from 2.9 to 2 Ma; bin 3), and a fourth, youngest time-interval which includes the terminal part of Gelasian and the Calabrian (1.9 to 0.7 Ma; bin 4).

Measures of species richness and turnover

Richness was measured using three different approaches. The first is raw richness counts (the number of species sampled in each time bin). To account for biases related to sampling intensity, we recalculated raw species richness by considering range-through data (Appendix S4). This procedure takes into account missing species in a certain time bin that were presumably present in the basin, as they are found in the previous and the successive time bin (i.e. if a species occurs in time bins 1 and 3, it is also added to the intermediate time bin 2). For this, we considered a species as present during the Early Pliocene if it had already appeared in the Mediterranean as a fossil during the Miocene (Monegatti & Raffi 2001; Appendix S3). Similarly, we counted a species in the Late Pleistocene if it currently lives in Mediterranean Sea (Nawrot *et al.* 2017). Since the number of sites (and occurrences) is uneven across the four-time bins, we further rarefied the data to make them comparable. We adopted the coverage-based rarefaction approach described in Chao & Jost (2012). First, we converted all the occurrences into an incidence matrix to determine the presence/absence of species in each site and time bin. Then, we rarefied the data by using the sample coverage associated with the less sampled temporal bin as minimum sample size (Close *et al.* 2018). Changes in richness through time, by rarefaction, were also investigated by comparing the shoreface and the shelf (given by inner and outer shelf occurrences together), which are the most occurrence-rich environments in the dataset, and by comparing trends in the most abundant feeding/tiering categories (infaunal deposit, infaunal suspension and epifaunal suspension feeders). Rarefaction was performed using the iNEXT R package (v3.0.0; Hsieh *et al.* 2022).

To explore rates of species turnover between time bins we quantified the proportion of species gain and species loss passing from a temporal bin to the next. Specifically, we calculated the proportion of species turnover, appearance, and disappearance using the codyn R package (v2.0.5; Hallett *et al.* 2016). We repeated the analysis for both raw data and range-through data, separately.

Geographical range size, niche breadth and occurrence frequency

Geographical range size was estimated for each species by computing the area of the minimum convex polygon (MCP; Carotenuto *et al.* 2010) enclosing all the species occurrences. Singletons and very rare species were excluded because MCP has a minimal requirement of five occurrences to be computed. For the species that were widespread beyond the Mediterranean area, we added the record from the North Sea and eastern Altantic to avoid the underestimation of their geographical extent. MCPs were further calculated separately for extinct and extant species. We tested whether extant and extinct MCP distributions differ by means of paired samples with the Wilcoxon test, which does not rely on any assumption regarding the original distribution of the data (Mann & Whitney 1947). The entire procedure was repeated by looking at the full dataset and then merging the occurrence of the first two time-bins (BIN1, hereafter) and those of the other two more recent bins (BIN2, hereafter) to avoid small sample size limitations and spurious outputs. MCP calculations were performed by applying the mcp function embedded in the adehabitatHS R package (v0.3.15; Calenge 2006).

We estimated the niche breadth for extinct and extant species using the Levins' niche breadth index (LI; Feinsinger *et al.* 1981), which measures the degree of similarity between the frequency distribution of palaeoenvironments used by species and the frequency distribution of all palaeoenvironments available to it. LI uses the relative occurrences of each species in each palaeoenvironment and ranges from 0 to 1, where a value of 1 indicates generalist taxa that are equally abundant across palaeoenvironments,

and 0 indicates specialist taxa that favour specific palaeoenvironments. This index was calculated for each species after removing species whose niche cannot be confidently measured because they fall below the limit of quantification due to low counts and sparse, random distribution across samples (Finn *et al.* 2020). As with MCPs, we computed LI by considering the full dataset first and then splitting the data in BIN1 and BIN2. The differences between LI values associated with extinct and extant species were evaluated by applying the non-parametric Wilcoxon two-sample test.

We estimated species occurrence frequencies by counting the number of occurrences of each species. This parameter was used as a proxy of species abundance since it is strongly correlated to it (Gaston *et al.* 2000). We adopted the same MCP and LI approach to compare the distributions of species occurrence frequencies of extinct and extant species and quantified the differences of these distributions over time.

Finally, differences in geographical range size, niche breadth, and abundance between extant and extinct species were also measured for the three main feeding/tiering categories separately.

RESULTS

Structure of the dataset

All the analyses, except the estimates of MPCs, were performed using only bivalve occurrences restricted to the Mediterranean Sea (N = 4389). In the dataset, 45 out of 68 families count more than 10 fossil occurrences (Appendix S2). Pectinidae (S = 42, N = 688), Veneridae (S = 40, N = 561), and Cardiidae (S = 27, N = 329) are the most abundant families in terms of both number of species (S) and occurrences (N) (Appendix S2). Time bin 4 has the highest number of occurrences (N = 1534; Table 1; Fig. S1), time bins 1 and 2 have more than 1000 occurrences, while time bin 3 has the lowest number (N = 494; Table 1; Fig. S1). The number of occurrences of extinct species gradually decreases over time, while extant species show an almost opposite pattern, although bin 3 is the poorest (Fig. S2A). In particular, we found a large decline in the occurrences of both extinct and extant species passing from bin 2 to bin 3 (Fig. S2A). Since bin 3 is poorly sampled, we merged occurrences of time bins 1 and 2, and time bins 3 and 4, creating two larger time-bins, BIN1 and BIN2, respectively. After this procedure, the drop in extinct species continues to be detectable, but there is no drop for extant species (Fig. S2B). Similar trends were found when considering changes in the number of extinct and extant species through time. Specifically, the raw richness of extinct species decreases after time bin 2 and remains constant during time bins 3 and 4 (Fig. S2C). Furthermore, the total richness of BIN2 is almost two thirds that of BIN1 (Table 1; Fig. S2C). On the other hand, species richness of extant species is the highest in bin 4 and the lowest in bin 3 (Table 1; Fig. S2C). We find no detectable difference when time is merged into only two time-bins (BIN1 and BIN2; Fig. S2D).

TABLE 1. Number of bivalve fossil occurrences in each time bin in the Mediterranean Sea.

Time_bin	No. occurrences	No. localities	No. extinct species	No. extant species
1	1171	35	116	165
2	1190	32	121	154
3	494	15	69	123
4	1534	39	71	207

As for geographical range size, fossil localities from the Zanclean to the mid-Piacenzian are uniformly distributed over the entire study area (Figs 1A, S3). After that, there is a reduction in the spatial distribution of localities, since we have no record for the western part of the basin starting from the Gelasian (i.e. Iberian Peninsula and North Africa). In addition, there are no fossil sites from the North Sea in the Calabrian stage (Figs 1A, S3).

When looking at palaeoenvironments, most species occurrences are associated with shoreface and shelf (inner and outer) settings (about 85% of total occurrences and 70% of species; Table S1A; Fig. S4). This trend holds constant over time (Table S1B). Consequently, we restricted further analyses to these environments only. Concerning feeding/tiering categories, we decided to focus on infaunal deposit, infaunal suspension, and epifaunal suspension feeders because most of the species are associated with these categories (about 90% of total occurrences and 86% of total species; Table S2A–B; Fig. S5).

Species richness and turnover

Bivalve rarefied species richness declines through time. In detail, bins 1 and 2 show a higher richness compared to time bins 3 and 4, with a main decline from time bin 2 to 3 (Figs 1B, S5). Range-through data confirm this pattern pointing to a maximum species richness during time bin 2 (N = 340; Fig. 1B) and a minimum richness during time bin 3 (N = 307; Fig. 1B). Raw data show a slightly different pattern, with a big drop in species richness in time bin 3, but similar number of species in time bins 1, 2 and 4 (Fig. S6).

Changes in rarefied species richness through time of the main feeding/tiering categories show that both infaunal and epifaunal suspension feeders followed the

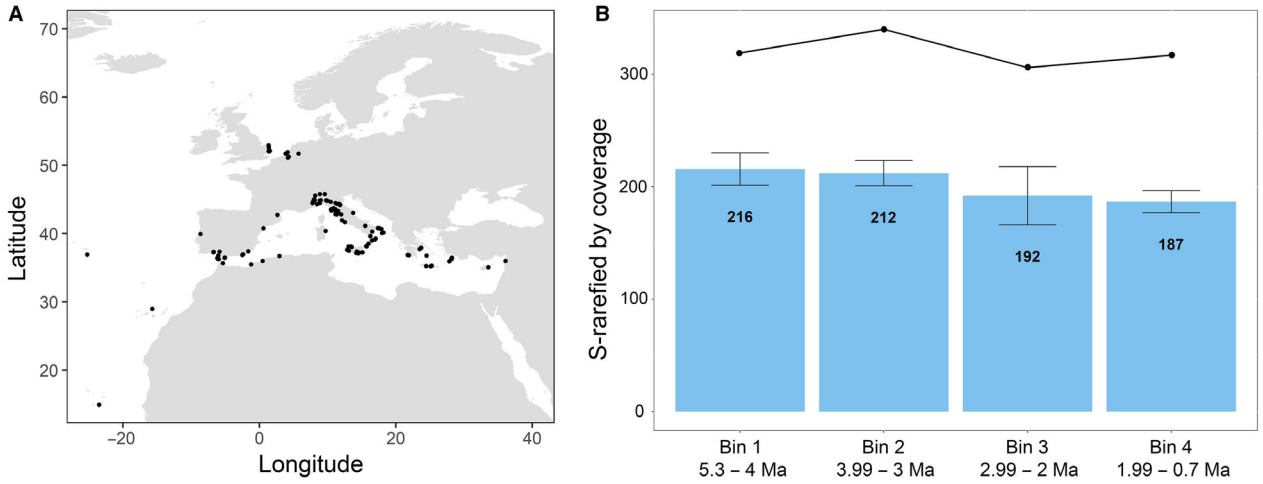

FIG. 1. A, geographical distribution of Zanclean–Calabrian bivalve fossil sites included in the dataset. B, species richness through time; blue bars indicate rarefied species richness; continuous line represents range-through species richness; range bars are 95% confidence intervals.

previous described general trend, with higher richness during bins 1 and 2 (Fig. 2A, B). Infaunal deposit feeders, instead, show a slight and gradual increment of richness over time (Fig. 2C). Range-through data almost confirm these trends even if they suggest a marked drop in species richness for epifaunal suspension feeders passing from bin 2 to bin 3 (Fig. 2A).

Looking at changes in richness across the shoreface and the shelf through time, a gradual reduction over time in terms of richness is observed for species that lived on the shelf from time bin 1 to 3 (Fig. 3B). In contrast, the shoreface shows the highest number of species in time bin 2 instead of bin 1, and the gradual decline is postponed compared to the shelf (Fig. 3A).

In terms of turnover through time, the highest species disappearance is between time bins 2 and 3 (13.3%; Table 2A), whereas the highest appearance occurs between time bins 3 and 4 (13.5%; Table 2A). These patterns are similar when raw data are considered, even if the magnitude of turnover in range-through data is lower compared to raw data (Table S3). For both infaunal and epifaunal suspension feeders, turnover follows the same general trends, with high disappearances (>10%) and low appearance (<5%) between time bins 2 and 3 (Table S4A, B). In contrast, the highest appearance for the infaunal deposit feeders occurred between time bins 3 and 4 while the disappearance is very low over all time bin transitions (<10%; Table S4C).

Geographical range size, niche breadth and occurrence frequency

In terms of geographical range size, MCPs of extant species are significantly larger than MCPs of extinct species ($Z = -5.064$, $p < 0.001$; Fig. 4). When analysing the geographical range size of BIN1 and BIN2, we observed however that this has not always being the case: during the first time-bin (up to 3 Ma), extinct and extant species had a similar geographical distribution ($Z = -1.667$, $p = 0.095$; Fig. 4). In contrast, extant species have a higher geographical distribution than extinct ones after 3 Ma ($Z = -4.234$, $p < 0.001$; Fig. 4).

When looking at trends in MCP by mode of life for the entire dataset, the geographical range of extinct epifaunal suspension feeders is similar to that of extant ones ($Z = -1.452$, $p = 0.146$), especially during BIN1 (Fig. 5A–C). When looking at the entire dataset, extinct infaunal suspension feeders instead have a lower MCP than extant ones ($Z = -3.989$, $p < 0.001$; Fig. 6A), but this is not the case for BIN1 ($Z = -1.466$, $p = 0.142$, Fig. 6B). Infaunal deposit feeders differ from the other two categories because the geographical range of extant species is always larger than that of extinct ones (Fig. 7A–C).

Overall, extant species show wider niche breadths than extinct species ($Z = -2.285$; $p = 0.022$; Fig. 4D). When time bins are merged, there is no significant difference between extinct and extant species during time BIN1 ($Z = -2.256$, $p = 0.082$; Fig. 4E), but there is during BIN2 ($Z = -2.773$, $p = 0.005$; Fig. 4F). A similar trend is observed for infaunal species, both deposit and suspension feeders (Figs 6, 7), with a drastic change in LI values passing from BIN1 to BIN2 for infaunal suspension feeders (BIN1: $p = 0.347$, BIN2: $p = 0.016$; Fig. 6E, F). In contrast, for epifaunal species there is no statistical difference in the niche breadth between extinct and extant species over time ($Z = 0.561$, $p = 0.574$; Fig. 5D). In fact, the median LI value of extinct species during BIN1 is slightly larger than that of extant ones (Fig. 5).

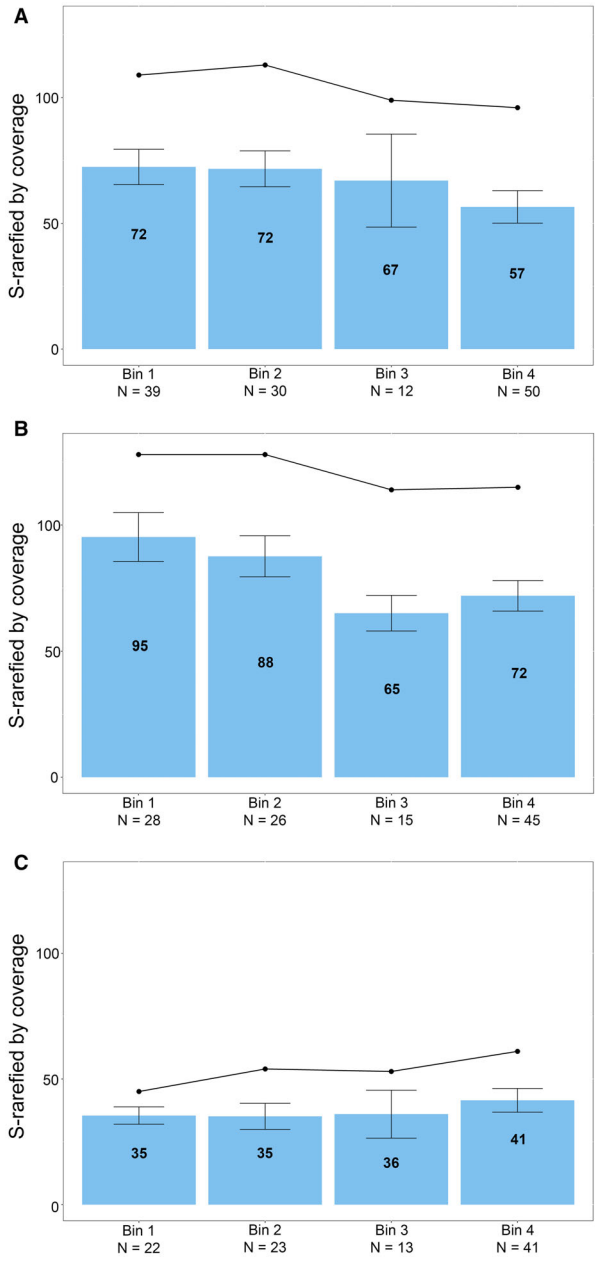

FIG. 2. Richness over time for different tiering and feeding categories. A, epifaunal suspension feeders. B, infaunal suspension feeders. C, infaunal deposit feeders. Blue bars indicate species richness after rarefying the data; continuous line represents range-through species richness; N indicates the number of fossil sites in each time bin; range bars are 95% confidence intervals.

Finally, extant bivalves are more abundant than extinct bivalves. This trend is constant over time (Fig. 4G–I) although this difference increases after 3 Ma, as also observed when the dataset is split into the three different modes of life (Figs 5–7).

DISCUSSION

Geological constrains on the fossil bivalve dataset

We note that not all time-bins are equally represented through time in terms of number of occurrences or number of fossil sites, with time bin 3 being the least well represented (Table 1). After 3 Ma, the Mediterranean fossil record becomes restricted to the Italian Peninsula and to the eastern Mediterranean area, with no western fossiliferous sites available in the literature (Fig. S3). The decrease in the areal extent and in the number of Late Pliocene to Gelasian sites can be explained by the interplay of tectonic and eustatic drivers. Regional tectonic uplift (Marinelli 1975) of the central Tyrrhenian margin (i.e. Tuscany) led to the emersion of many marine basins in central Italy, with the establishment of fully continental conditions during the Gelasian (Cosentino *et al.* 2009; Benvenuti *et al.* 2014; Bianchi *et al.* 2015; Riforgiato *et al.* 2005). Similarly, along the Cadiz coast in southwestern Spain, tectonic activity caused important palaeogeographical changes through local uplift and progressive regression, with a consequent reduction of marine deposition, restricted to shoreline environments (Gutiérrez-Mas & Mas 2013). Furthermore, cooling, linked to the intensification of the northern hemisphere glaciation (Lisiecki & Raymo 2005) resulted in strong glacio-eustatic sea level changes with a main Gelasian sea level drop of 70 m at 2.15 Ma registered in the Mediterranean Sea (Rohling *et al.* 2014). Global sea level drop during the Gelasian also caused a change from marine to continental sedimentation in the North Sea (Vandenberghe *et al.* 2004). Marine sedimentation persisted instead, during the Pleistocene, in sedimentary basins characterized by high subsidence rates such as, amongst the others, the Po Plain – Adriatic foredeep, in Italy (Dominici 2001), the Crotone Basin, a Neogene–Quaternary depocentre developed along the Ionian margin of Calabria, in Italy (Zecchin *et al.* 2012), and some basins of the Hellenic Arc, such as the Creta Basin, in Greece (Mantovani *et al.* 2022).

Bivalve biodiversity changes through time

The Zanclean was characterized by prolonged climatic warm conditions with a peak of warming known as the Pliocene Climatic Optimum (PCO; 4.4–4 Ma) when global mean temperature was roughly 4°C higher than estimated for the pre-industrial period (Fedorov *et al.* 2013) and sea-level was 23.5 m above modern sea-level (Dumitru *et al.* 2019). After the first spike of the northern hemisphere glaciation around 3.6 Ma (Mudelsee & Raymo 2005), temperature increased during the

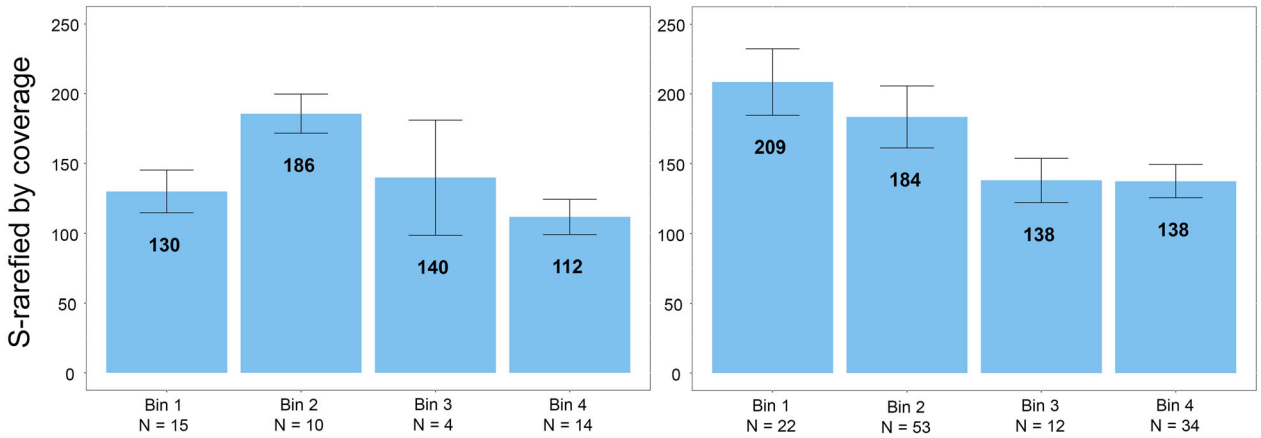

FIG. 3. Richness over time bins for species living in shoreface (left) and shelf (right) environments. Blue bars indicate species richness after rarefying the data; continuous lines represent range-through species richness; N indicates the number of fossil sites in each time bin; range bars are the 95% confidence intervals.

TABLE 2. Bivalve species turnover among consecutive time bins using range-through data: A, occurrences divided into four time-bins (bins 1–4); B, occurrences divided into two time-bins (BIN1 and BIN2).

Time	Turnover	Appearance	Disappearance
A			
bin 1–2	0.185	0.121	0.063
bin 2–3	0.172	0.04	0.133
bin 3–4	0.239	0.135	0.104
B			
BIN1-BIN2	0.311	0.146	0.165

mid-Piacenzian Warm Period (3.3–3.0 Ma), getting 2–3°C higher than pre-industrial values, and global sea-level rose 16.2 m above modern sea-level (Dumitru *et al.* 2019). This warm interval was followed by a deterioration of climate after 3 Ma (Herbert *et al.* 2015) with a stronger intensification of northern hemisphere glaciation waves starting from 2.7 Ma (Kaboth-Bahr *et al.* 2021).

Our data indicate that the highest species richness occurred during the mid-Pliocene (i.e. time bin 2), while the highest decrease of species richness and turnover are registered after 3 Ma (Fig. 1). This evidence suggests that the onset of long-term global cooling and regional changes in surface water conditions (Marlow *et al.* 2000) represent an important driver of bivalve extinction or extirpation, corroborating the conclusions of Monegatti & Raffi (2001). However, we found that the wave of extinction was less intense and more gradual than previously thought. The latter authors identified a large drop in the number of species of Pliocene Mediterranean bivalves around 3 Ma (loss of 80 species out of 338, 24% of the total). Although our raw data show a species loss of 83 species after 3 Ma (Fig. S6), the more reliable range-through estimates show a species loss of 34 species (about 11%; Fig. 1), while resampling techniques lower this value to 20 (9.4%; Fig. 1). If we use range-through data, after splitting the dataset into two time-bins only (i.e. following the same time resolution of Monegatti & Raffi 2001), we get even more conservative estimates, with a species loss of around 17% at 3 Ma (Table 2B). This discrepancy is probably due to multiple causes, such as the description of new fossil localities since 2001, recent revisions of bivalve taxonomy, and new chronostratigraphic attributions of some fossil sites in recent years, as explained above. Furthermore, the Monegatti & Raffi (2001) study was only based on fossil localities from Italy, whereas the present work provides a more exhaustive view of temporal changes in biodiversity by including localities from the entire Mediterranean area (see Danise & Dominici (2023) for further details).

Whereas the highest disappearance rate is at 3 Ma, the highest rate of appearance of species (14%) is recorded at around 2 Ma, at the passage from bin 3 to bin 4 (Table 2A). The Gelasian and Calabrian immigration into the Mediterranean of cold-water species coming from northern Europe and the Atlantic coast through the Strait of Gibraltar (Malatesta & Zarlenga 1986) played an important role in driving this pattern (the so-called 'boreal guests' include *Arctica islandica* (Linnaeus, 1767), Dominici 2001, Crippa *et al.* 2019; *Mya truncata* Linnaeus, 1758, Raffi 1986; *Macoma obliqua* (J. Sowerby, 1817), Sami & Taviani 1996). This high appearance rate, combined with a disappearance rate of 10%, made the transition from bin 3 to 4 the interval with the highest turnover (Table 2A), suggesting that the Lower Pleistocene was a time interval of drastic changes for Mediterranean bivalve communities.

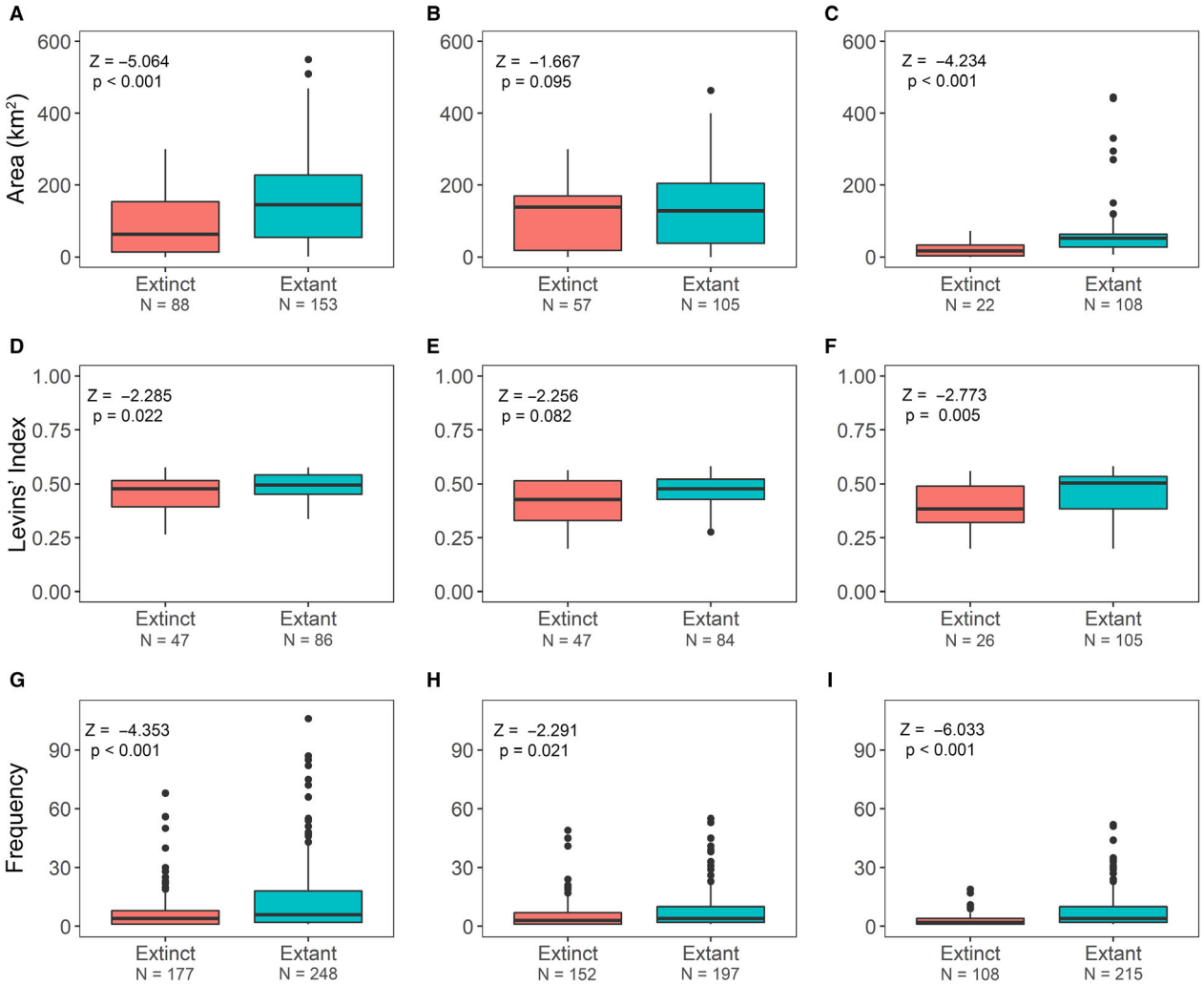

FIG. 4. Comparison of species extinction drivers over time between extinct (red) and extant (blue) species. Boxplots show difference in geographical range size (A–C), Levins' niche breadth index (D–F), and number of frequency occurrence distributions (G–I) between past and living species using the entire fossil record (A, D, G) and after splitting the dataset into two time-bins: BIN1 (B, E, H) and BIN2 (C, F, I). Statistic and p-values are reported in each plot.

Regime shift at the Pliocene–Pleistocene transition

Our results demonstrate that geographical range and niche breadth are valid predictors of extinction risk in fossil bivalves. We found significant differences between extinct and extant species when considering the entire bivalve dataset. After dividing the data into two time-bins, geographical range and niche breadth values support a scenario in which a warm, relatively stable climate during the Zanclean to early Piacenzian interval (BIN1) guaranteed a phase of ecological equilibrium for bivalves. Indeed, we did not detect any significant difference in terms of geographical range size and niche breadth between extant and extinct species during this time interval (Fig. 4B, E). Lower Pliocene bivalves were apparently adapted to the warm subtropical conditions that occurred at this time (8–10°C higher than today in the Mediterranean Sea; Tzanova & Herbert 2015). This is supported by the evidence that around 50% of the species of our dataset already existed in the Late Miocene, and they were possibly adapted to even higher water temperatures (i.e. sea surface water at high latitudes during the Late Miocene was 10–15°C higher than today: Burls *et al.* 2021). Warm and less seasonal climatic conditions favoured the geographical expansion of guest-species from the tropical zone, promoting the establishment of warm-adapted bivalve communities marked by particularly high species-richness at shoreface and onshore environments during the Piacenzian (Fig. 2). Such increase in richness might also have been favoured by the increase in

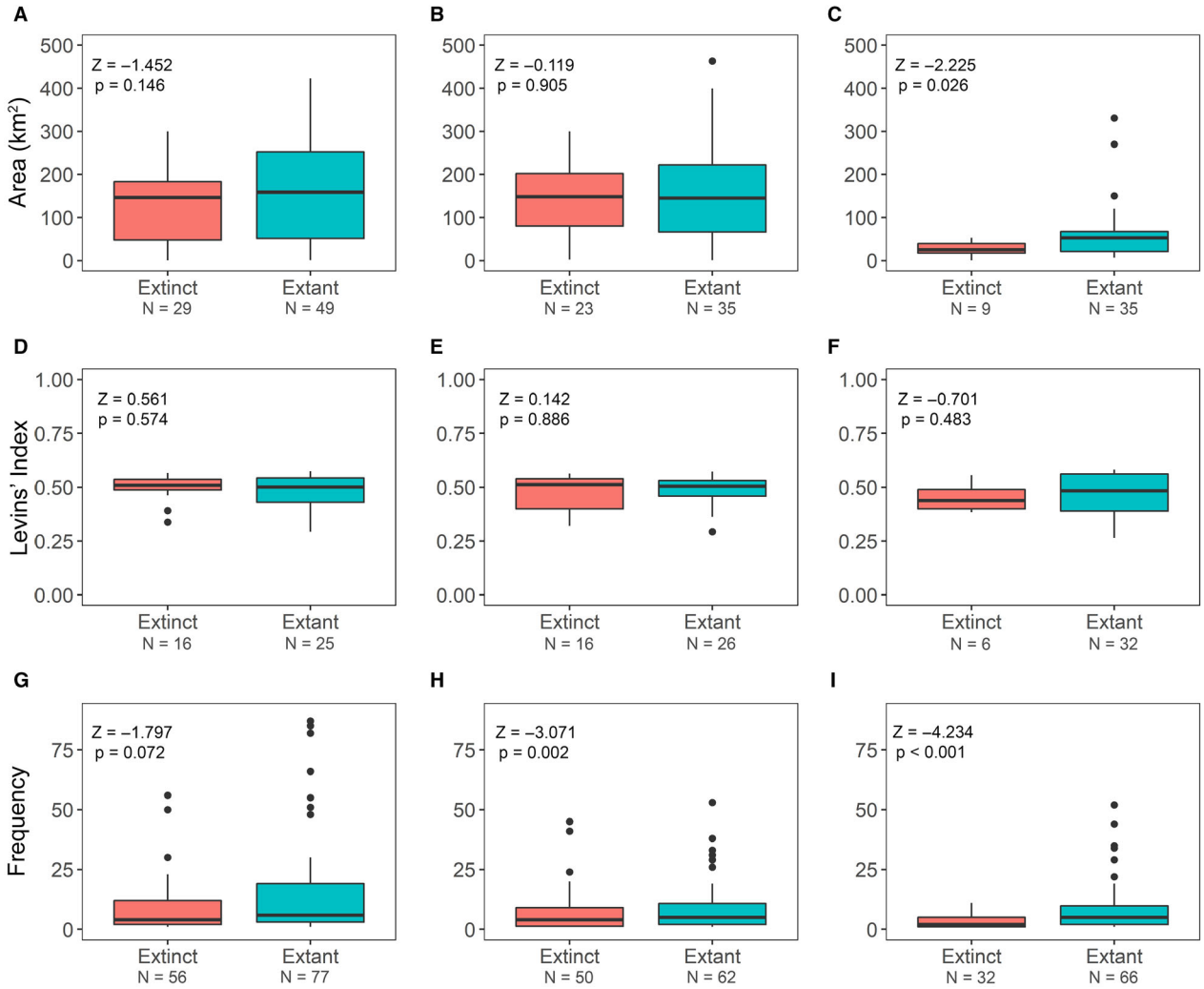

FIG. 5. Comparison of extinction drivers for epifaunal suspension feeder species over time, divided between extinct (red) and extant (blue) species. Boxplots show difference in geographical range size (A–C), Levins' niche breadth index (D–F), and number of frequency occurrence distributions (G–I) between past and living species using the entire fossil record (A, D, G) and after splitting the dataset in two time-bins: BIN1 (B, E, H) and BIN2 (C, F, I). Statistic and p-values are reported in each plot.

extent and complexity of Mediterranean *Posidonia oceanica* meadows and coralligenous formations during this time-interval (Dominici & Danise 2023).

The successive late Piacenzian to Early Pleistocene phase, characterized by global cooling and sea-level fluctuations, played a role in periodically reducing the habitable area at shallower depth (see Holland & Christie 2013), and contributed to the demise of carbonate ramp environments (Nalin *et al.* 2016; Cau *et al.* 2019; Dominici & Danise 2023). This translated into a reduction in bivalve richness in shoreface sandstones and inner shelf calcarenites (Fig. 3). Indeed, geographical range and niche breadth associated with extant species are significantly larger than those associated with extinct species after the 3 Ma threshold only (Fig. 4A–C). Rather, the number of occurrences of extant species is always higher than that of extinct ones over time (Fig. 4G–I) suggesting that abundant species suffered less due to climate-environmental change compared to rare species.

MCP, niche breadth and abundance trends jointly indicate that species which survived beyond the Pliocene–Pleistocene transition and vanished during the Pleistocene had narrow geographical ranges and lived in a small range of marine environments. The loss of niches specific to shallow-water and carbonate ramp bottoms is very likely to have increased the risk of extinction for tropical warm-adapted bivalves, with the consequent decline of thermophilic species (Monegatti & Raffi 2001). Notwithstanding, some species survived the first extinction wave at 3 Ma, finding a temporary refugium in the warmer,

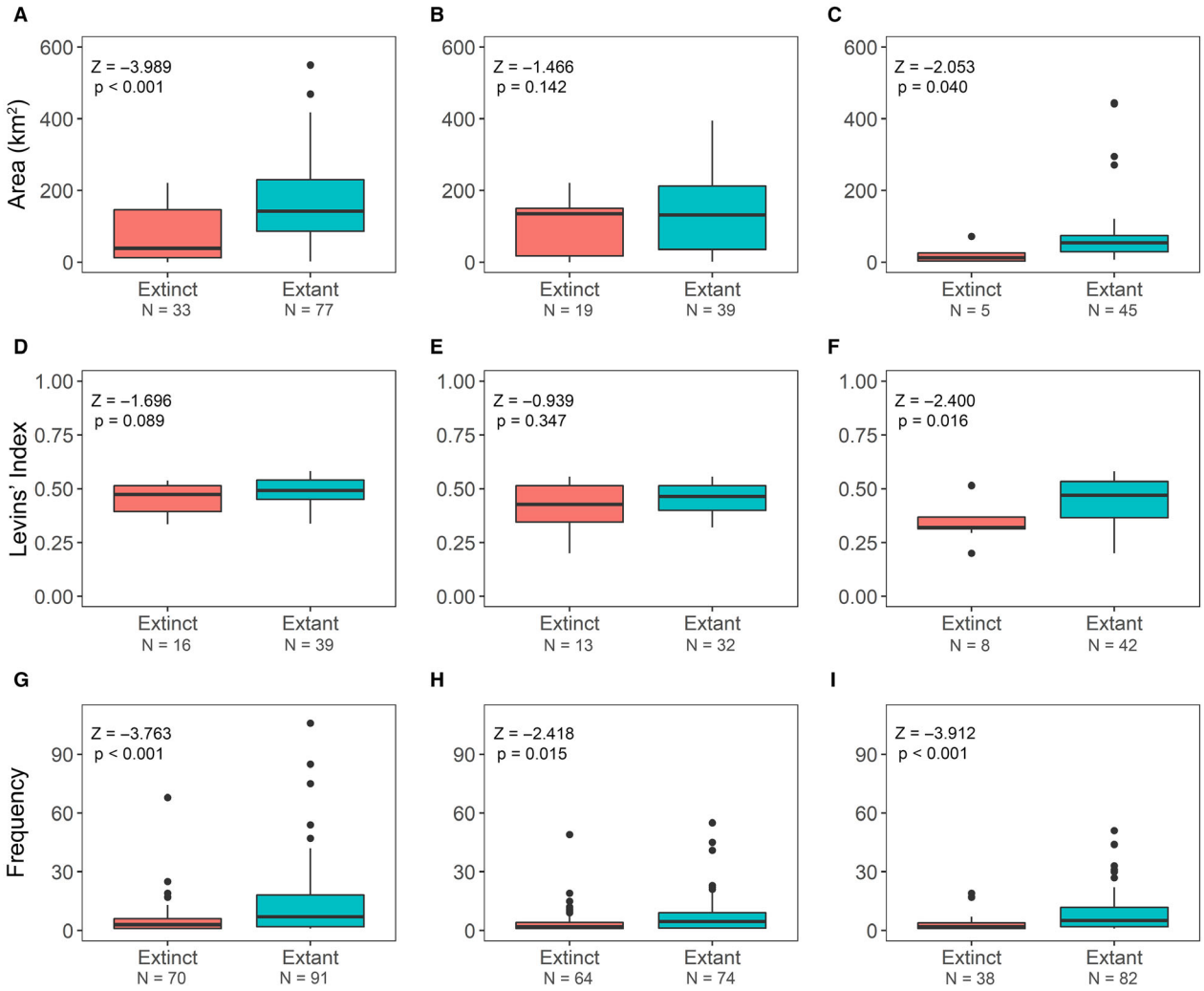

FIG. 6. Comparison of extinction drivers for infaunal suspension feeder species over time, divided between extinct (red) and extant (blue). Boxplots show difference in geographical range size (A–C), Levins' niche breadth index (D–F), and number of frequency occurrence distributions (G–I) between past and living species by using the entire fossil record (A, D, G) and after splitting the dataset in two time-bins: BIN1 (B, E, H) and BIN2 (C, F, I). Statistic and p-values are reported in each plot.

eastern Mediterranean area during the Early Pleistocene (Garilli 2011; Danise & Dominici 2023).

Climate and oceanographic changes occurring at the Pliocene–Pleistocene boundary forced the gradual transition from warm, carbonate-rich to cool-water environments characterized by the alternation of cool-water carbonates and terrigenous-rich deposits (Cau *et al.* 2019; Pedley & Grasso 2006). As a consequence, bivalves with tropical affinities went extinct leaving room for species with either high ecological plasticity or opportunistic behaviour (Dominici & Danise 2023). In addition, the increase in the seasonality of seawater temperature and the onset of lower winter palaeotemperatures favoured the arrival of the 'boreal guests' and the dominance of opportunistic species like *Arctica islandica* and *Mya truncata* (Dominici 2001; Crippa *et al.* 2019). Finally, recent advancements in the study of biotic invasions has hypothesized the entrance of tropical species from the Red Sea, through the Suez Isthmus, into the eastern Mediterranean during Pleistocene interglacials and ensuing sea-level highstands (Albano *et al.* 2022), further complicating the reconstruction of climate–diversity relationships.

The high turnover rate detected when moving from the Pliocene to the Pleistocene confirms the concurrent actions of species gain and loss dynamics. Our results indicate that widely distributed eurythermal species, occurring both in the Mediterranean Sea and the North Sea, such as *Abra alba* (W. Wood, 1802), *Aequipecten opercularis* (Linnaeus, 1758), *Dosinia lupinus* (Linnaeus, 1758) and *Timoclea ovata* (Pennant, 1777), avoided

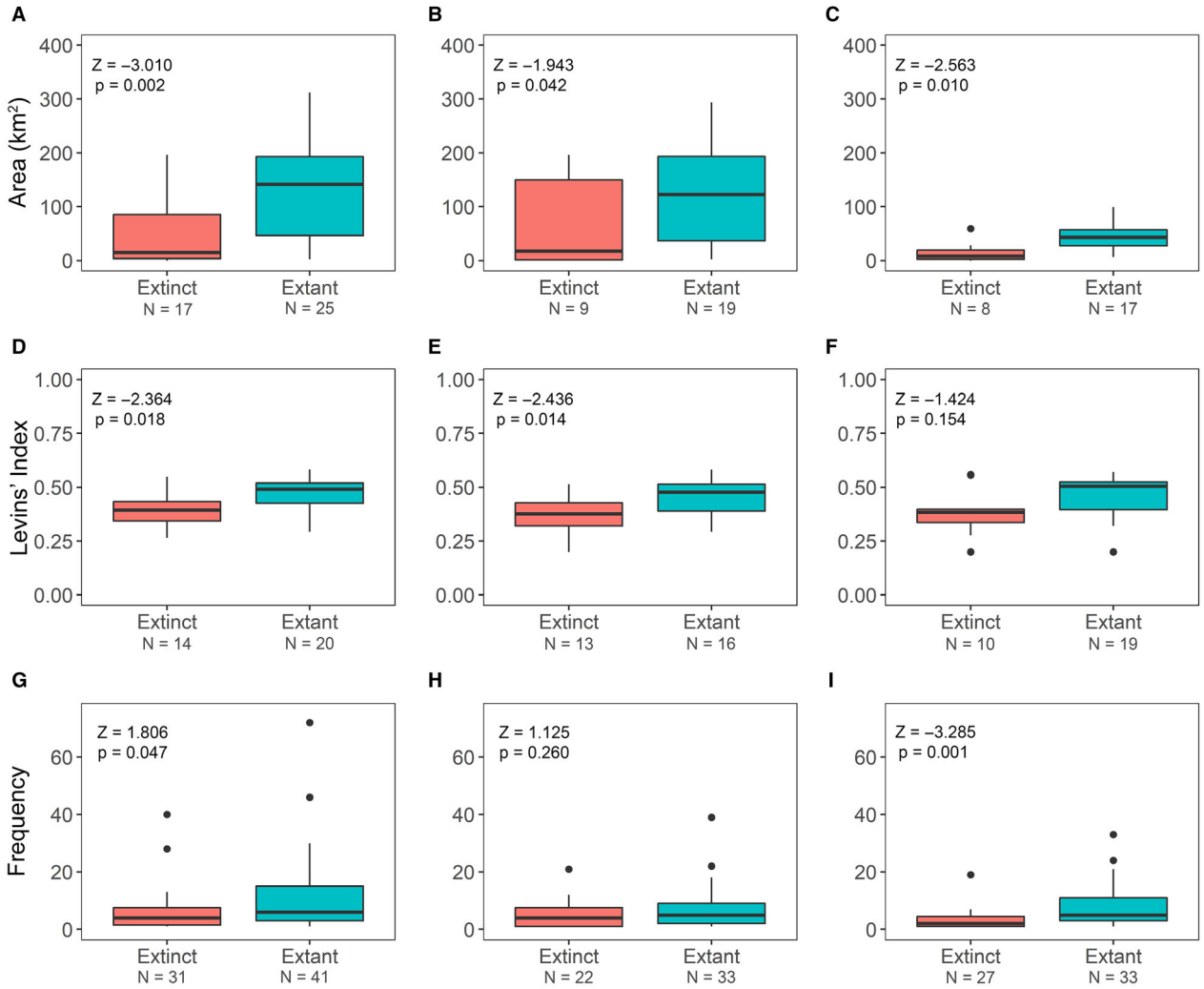

FIG. 7. Comparison of extinction drivers for infaunal deposit feeder species over time, divided between extinct (red) and extant (blue) species. Boxplots show difference in geographical range size (A–C), Levins' niche breadth index (D–F), and number of frequency occurrence distributions (G–I) between past and living species by using the entire fossil record (A, D, G) and after splitting the dataset in two time-bins: BIN1 (B, E, H) and BIN2 (C, F, I). Statistic and p-values are reported in each plot.

extinction. Niche breadth analysis indicates that extant species had higher ecological plasticity and a tendency to sustain a broader range of environmental conditions compared to extinct taxa. These ecological traits, therefore, could have represented a further advantage for extant species dealing with intense climatic changes (Saupe *et al.* 2015; Byrne *et al.* 2020). Besides that, extinction was not even when looking at the different life-habits of the studied species. The present results show that suspension feeders were more affected than species with an infaunal–depositivore lifestyle. Indeed, the latter slightly increased their richness at the passage Pliocene to the Early Pleistocene, while suspension feeders did the opposite (Fig. 2; Table S4).

After merging the data for the three main modes of life in two time bins (BIN1 and BIN2), we noted no difference in geographical range and niche breadth between extinct and extant bivalves up to 3 Ma among infaunal and epifaunal suspension feeders (Figs 5, 6). In contrast, we found several significant differences after the Pliocene–Pleistocene boundary. Ecological and environmental changes affected epifaunal species in terms of richness, abundance and geographical range size (Figs 2A, 5). The reduction in richness of epifaunal suspension feeders is probably driven mostly by the extinction (or local extinction) of some species belonging to the family Pectinidae at 3 Ma (e.g. *Aequipecten bicknelli* Sacco, 1897, *Aequipecten scabrellus* (Lamarck, 1819), *Lissochlamys excisa* (Bronn, 1831); Monegatti &

Raffi 2001; Danise & Dominici 2023). Indeed, Pectinidae represented the dominant group of the Pliocene in terms of both number of species and number of occurrences, and its richness significantly decreased after the mid-Piacenzian Warm Period (Appendix S2). Danise & Dominici (2023) noted that some extinct species were adapted to coarse sandy and gravelly bottoms in high energy shallow water environments and presumably suffered a strong reduction in habitable area with the onset of a cooler climatic regime and the reduction of carbonate heterozoan shoals. However, eurythermal species with very large bathymetric distributions among the Pectinidae (Ceregato *et al.* 2007) survived into the modern Mediterranean, including *Pecten jacobaeus* (Linnaeus, 1758) and *Talochlamys multistriata* (Poli, 1795). Indeed, extinct species that survived global cooling maintained a niche breadth comparable to that of extant species (Fig. 6).

Extinction patterns for infaunal and epifaunal suspension feeders resemble each other, recording both a strong decrease in species richness and abundance over time (Fig. 2B), and a significant difference of geographical range size between extant and extinct species during time BIN2. Differently from the epifaunal data, we further found a significant difference in niche breadth for the infaunal suspension feeding species (Fig. 6). La Perna & D'Abramo (2011) argued that a large number of Cardiidae genera with tropical affinities were present in the Mediterranean area during the Pliocene (e.g. *Afrocardium* Tomlin, 1931; *Europicardium* Popov, 1977; *Nemocardium* Meek, 1876) and disappeared during the Early–Middle Pleistocene, although they persist outside the Mediterranean in tropical areas (Ter Poorten 2009; 2013) It is therefore plausible that climatic conditions during the Zanclean to mid-Piacenzan interval allowed the establishment of a warm-adapted Cardiidae fauna with extinct and extant species having comparable geographical ranges and similar ecological requirements, and that the onset of a new climatic regime, with stronger glacial and interglacial oscillations in the Early and Middle Pleistocene, caused their disappearance. Raffi *et al.* (1985) noted also that many bivalve taxa with tropical affinities, including members of the Veneridae and Lucinidae, disappeared from the Mediterranean Sea after the 3 Ma threshold. This is the case, for instance, for *Pelecyora brocchii* (Deshayes, 1836), *Polititapes senescens* (Cocconi, 1873), *Megaxinus transversus* (Bronn, 1831) and *Megaxinus incrassatus* (Du Bois de Montpéreux, 1831).

Besides increasing in richness, extant infaunal deposit feeders are always more geographically widespread when compared to extinct ones (Fig. 7). Patterns of niche breadth are the opposite compared to those of suspension feeders, with similar values between extinct and extant ones after 3 Ma (Fig. 7). These results are consistent with the fossil record of the Tellinidae, that represents around 26% of the species among the infaunal deposit feeders, as it has been pointed out that species richness of Pliocene Tellinidae was comparable or even lower than that of modern representatives (Monegatti & Raffi 2001; Raffi *et al.* 1985), although a recent revision argued that Pliocene species richness could be significantly underestimated (Brunetti & Della Bella 2022b). Moreover, the adaptation of many infaunal deposit feeders, such as members of the Nuculidae and Nuculanidae, to muddy bottoms during times of eustatic regression (Stanley 1986a), could have guaranteed them high survivorship during periods of intense climatic oscillations (Stanley 1986b).

Overall, our most reliable species loss estimation of about 17%, corroborates the conclusions of a recent work which estimated a 21% regime shift of marine megafauna during the same time frame (Pimiento *et al.* 2017). We also show, however, that biodiversity loss was more intense for suspension feeders in shallow-water habitats than for depositivores in deeper settings. This uneven effect of climate and eustatic sea-level changes could have led to a functional shift among bivalve communities, with the increment of species better adapted to muddy bottoms subject to high rates of terrigenous input.

The effect of climate and oceanographic changes on marine biodiversity is a relevant topic in current literature. The Mediterranean is at the same time a hotspot of marine biodiversity (Bianchi & Morri 2000) and one of the most vulnerable areas to climatic and anthropogenic change (Gorguner & Kavvas 2020). Future projections suggest considerable warming and drying trends for the area (Fraga *et al.* 2020), which will inevitably harm marine life. Indeed, dramatic biodiversity loss in marine fauna has already been documented, especially in the eastern part of the basin (Albano *et al.* 2021; Steger *et al.* 2022). In the light of this, the fossil record can help in predicting the response and the possibility of adaption of marine species to future climatic scenarios. This is supported by evidence that many endemic species at risk today, some of which are of commercial interest (e.g. *Chamelea gallina* (Linnaeus, 1758); *Pecten jacobaeus* (Linnaeus, 1758); *Flexopecten glaber* (Linnaeus, 1758); Gallagher & Albano 2023), have lived in the Mediterranean Sea since the Pliocene. Our results suggest that particular care will have to be paid to the fate of epifaunal species living in shallow waters, considering their extreme vulnerability to drastic environmental changes. From the perspective of conservation palaeobiology (Dietl *et al.* 2015; Tomašových *et al.* 2023), the present study serves as a contribution to direct the application of conservation strategies and the maintenance of Mediterranean marine functional biodiversity.

CONCLUSION

Changes in species richness and turnover rates over time confirm a significant loss in bivalve biodiversity in the Mediterranean area during the Pliocene–Pleistocene transition. Both range-through and rarefied-data approaches indicate that extinction was less intense and more gradual than previously thought. High species turnover since 3 Ma (middle–late Piacenzian) can be explained by a high proportion of both disappearance and appearance of species. The first was linked to the disappearance of species with a tropical affinity; the latter to the introduction of Mediterranean cold-water adapted taxa during Lower Pleistocene cooling. Differences in geographical range size and niche breadth between extant and extinct species become relevant after the mid-Piacenzian Warm Period, confirming that the late Piacenzian was an important turning point for extinct species. However, our results suggest that species extinction risk differed depending on species lifestyle and preferred palaeoenvironment. Species loss was high for suspension feeders, while deposit feeders were less affected. Moreover, our results show that species loss was not uniform along the bathymetric gradient. Species richness on the shelf gradually waned during the study interval, whereas in the shoreface it peaked during the Piacenzian, but remained relatively stable across the mid-Piacenzian Warm Period. Our results can contribute to predicting the response of Mediterranean bivalves to future climate and environmental change.

Acknowledgements. Funding for this publication was provided by a research contract with author AM, co-funded by the European Union – PON Research and Innovation 2014–2020 in accordance with article 24, paragraph 3(a), of law No. 240, 30 December 2010, as emended, and Ministerial Decree No. 1062 of 10 August 2021. SDa acknowledges the support of NBFC to University of Florence, Department of Earth Science, funded by the Italian Ministry of University and Research, PNRR, Missione 4 Componente 2, 'Dalla ricerca all'impresa', Investimento 1.4, Project CN00000033; SDa was also supported by the MUR, Programma per Giovani Ricercatori 'Rita Levi Montalcini'. Dr Katie Collins and an anonymous referee commented on an earlier draft of this manuscript.

Author contributions. **Conceptualization** A Mondanaro (AM), S Danise (SDa); **Data Curation** AM, SDa, S Dominici (SDo); **Formal Analysis** AM, SDa; **Funding Acquisition** SDa; **Investigation** AM, SDa, SDo; **Methodology** AM, SDa; **Project Administration** SDa, SDo; **Resources** AM, SDa, SDo; **Software** AM, SDa; **Supervision** AM; **Validation** AM, SDa, SDo; **Visualization** AM, SDa, SDo; **Writing – Original Draft Preparation** AM, SDa, SDo; **Writing – Review & Editing** AM, SDa, SDo.

Editor. Julia Sigwart

SUPPORTING INFORMATION

Additional Supporting Information can be found online (https://doi.org/10.1111/pala.12696):

Appendix S1. Raw data.
Appendix S2. Number of species and occurrences in each time-bin.
Appendix S3. Presence–absence matrix for species per time-bin.
Appendix S4. Presence–absence matrix for species per time-bin corrected for range-through.
Table S1. Number of fossil occurrences associated with each palaeoenvironment and time bin.
Table S2. Number of fossil occurrences associated with each combination of feeding and tiering category.
Table S3. Bivalve species turnover among time bins using raw data.
Table S4. Bivalve species turnover among time bins using range-through data for the most representative combinations of feeding and tiering categories.
Figure S1. Coverage-based R/E curves derived from iNext.
Figure S2. Number of occurrences and species associated with extinct and extant species over time.
Figure S3. Geographic distribution of bivalve fossil occurrences in each time bin.
Figure S4. Occurrence (A) and species (B) frequency in each palaeoenvironment.
Figure S5. Occurrence (A) and species (B) frequency in each combination of feeding and tiering category.
Figure S6. Species richness through time.

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