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Resilient biotic response to long-term climate change in the Adriatic Sea

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5

6 **Resilient biotic response to long-term climate change in the Adriatic Sea**

7

8 *Running head:* Resilience in the Adriatic fossil record

9

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23

Abstract

25 Preserving adaptive capacities of coastal ecosystems, which are currently facing the ongoing
26 climate warming and a multitude of other anthropogenic impacts, requires an understanding of
27 long-term biotic dynamics in the context of major environmental shifts prior to human
28 disturbances. We quantified responses of nearshore mollusc assemblages to long-term climate
29 and sea level changes using 223 samples (~71300 specimens) retrieved from latest Quaternary
30 sediment cores of the Adriatic coastal systems. These cores provide a rare chance to study coastal
31 systems that existed during glacial lowstands. The fossil mollusc record indicates that nearshore
32 assemblages of the penultimate interglacial (Late Pleistocene) shifted in their faunal composition
33 during the subsequent ice age, and then reassembled again with the return of interglacial climate
34 in the Holocene. These shifts point to a climate-driven habitat filtering modulated by dispersal
35 processes. The resilient, rather than persistent or stochastic, response of the mollusc assemblages
36 to long-term environmental changes over at least 125 thousand years highlights the historically
37 unprecedented nature of the ongoing anthropogenic stressors (e.g., pollution, eutrophication,
38 bottom trawling, and invasive species), that are currently shifting coastal regions into novel
39 system states far outside the range of natural variability archived in the fossil record.

40

Keywords

42 Climate Change, Mediterranean Basin, Mollusc, Glacial-Interglacial Cycle, Conservation
43 Palaeobiology, Italy.

44

Introduction

46 Predicting the impact of climate change on the structure and composition of biological
47 communities is a major goal of conservation biology (Fredston-Hermann et al., 2018; Friedman

48 et al., 2020). Simplified models based on thermal tolerances of individual taxa fail to capture the
49 response of communities because they cannot incorporate many other processes that influence
50 species distributions (Doney et al., 2012; Griffith et al., 2017; Trisos et al., 2020; Steger et al.,
51 2022). A long-term perspective on the variability and resilience of communities is becoming
52 increasingly important, as conservation strategies are faced with accelerating global change
53 (Barnosky, 2017). Geobiological archives, such as well-resolved, fossil rich sedimentary
54 successions, can extend records of ecosystem responses to climatic shifts far beyond the limited
55 timescales of direct ecological monitoring typically restricted to the most recent decades (e.g.,
56 Harnik et al., 2012; Kidwell, 2015; Dillon et al., 2020; Tomašových et al., 2020). In particular,
57 the late Quaternary geological record, which archives repeated landward-seaward migrations of
58 coastal environments during glacio-eustatic cycles, can potentially provide direct documentation
59 of long-term dynamics of marine ecosystems. These natural experiments allow for contrasting
60 empirical patterns against conceptual models of community response (Fig. 1). For example, a
61 community structure can exhibit persistence (resistance *sensu* Grimm & Wissel, 1997), if it
62 continues through the perturbation without rearranging into a different state (Grime et al., 2008;
63 Davies et al., 2018; Hyman et al., 2019; Fig. 1a,d). Alternatively, the reorganization of communities
64 can indicate resilience (also called engineering resilience), if a community shifts to an alternate
65 state after perturbation but then reassembles (Nikanorov & Sukhorukov, 2008; O’Leary et al.,
66 2017; Davies et al., 2018 and references therein; Fig. 1b,e). Finally, communities during intervals
67 of climate change can display highly variable composition resulting from the stochastic processes
68 of ecological drift and individualistic responses of species (stochastic pattern in Fig. 1c,f) that can
69 lead to novel or no-analog communities (Graham et al., 2014; Slišković et al., 2021).

70 Our understanding of long-term community dynamics in shallow-marine environments during
71 the late Quaternary climate oscillations is mostly based on fossil assemblages representing sea-

72 level highstands associated with warm interstadial and interglacial periods (e.g., Pandolfi, 1996;
73 Kowalewski et al., 2015; Martinelli et al., 2017; Davies et al., 2018). In contrast, few studies have
74 explicitly investigated marine faunal dynamics in comparable depositional environments under
75 both glacial and interglacial conditions (e.g., Tager et al., 2010; Aronson & Precht, 2016;
76 Kitamura et al., 2020), even though such data are necessary for distinguishing between alternative
77 models of community change. In this study, we describe the structure of mollusc benthic
78 assemblages (bivalves, gastropods and scaphopods) populating shallow, fluvially-influenced
79 marine systems during three specific time intervals: (1) the penultimate interglacial (LIG,
80 between ~125-110 kyr cal BP), (2) the subsequent last glacial (LG, between ~18-12 kyr cal BP),
81 and (3) the Holocene interglacial (CIG, between ~7 kyr cal BP and pre-1750 CE). This approach
82 allows for tracking the dynamics of faunal assemblages from analogous depositional settings, but
83 during different climate and sea-level states thus providing a historical perspective on biotic
84 response to long-term climate change. Here, we used the latest Quaternary fossil record of the
85 Adriatic coastal systems (Text S1; Table S1; Appendixes S1-S2) to evaluate if shallow-marine
86 mollusc assemblages display a persistent, resilient, or stochastic pattern (Fig. 1) when responding
87 to major climatic and sea-level shifts over the last ~125 kyr (Fig. S1).

88 **Materials and Methods**

89 The fossiliferous deposits of both interglacial periods are preserved in the subsurface of the
90 present-day Po coastal plain. In contrast, those of the last glacial period are situated in the central
91 and southern Adriatic, more than 250 km southeast of the studied interglacial deposits, at the edge
92 of the Mid Adriatic Deep and connected basins, where the shoreline was located during the last
93 sea-level lowstand (see Text S1; Fig. S1).

94 *Data selection criteria*

95 Distribution and preservation of macrobenthic remains in sedimentary successions representing
96 coastal habitats are controlled by a multitude of environmental parameters and sedimentary
97 processes (e.g., Rakocinski et al., 1991; Nawrot et al., 2018). To ensure comparability in terms
98 of environmental context, sedimentation rates and taphonomic regime we restricted the analyses
99 to samples from aggrading-prograding lower shoreface to foreshore sedimentary bodies
100 characterised by varying degrees of fluvial influence (hereafter referred as nearshore; Fig. S2).
101 This environmental classification of samples was mainly based on previously published
102 sedimentological and micropalaeontological inferences and was thus independent from the
103 composition of the mollusc assemblages (see Table S2 for environmental and chronostratigraphic
104 information). The samples (0.150 to 0.375 dm³ each; further details in Appendixes S1-S2) were
105 wet-sieved with 1 mm screen and the remains identified to species level whenever possible. To
106 account for disarticulation of bivalves, the number of isolated valves was divided by two.
107 Multiple ecological descriptors of the studied assemblages (species dominance, sample-
108 standardised richness, relative abundance, and occurrence frequency), present-day biogeographic
109 distribution of constituent species (data after Poppe & Goto 1991; 1993), and multivariate
110 methods were used to compare samples representing the three selected time intervals (i.e., last
111 interglacial-LIG, last late glacial-LG and current interglacial-CIG; Tables S1-S2). The results
112 were compared to a conceptual framework depicting possible patterns of community change
113 across a glacial-interglacial cycle (persistent, resilient, and stochastic pattern; Fig. 1). A
114 comparative assessment of ecological dynamics encompassing the entire land-to-deep-sea
115 depositional profile is not possible due to lack of preservation or limited sampling of different
116 segments of the bathymetric gradient. Freshwater/terrestrial species occasionally recovered in the
117 targeted samples were excluded from the analyses. The dataset for multivariate analyses was

118 further restricted to samples with at least 25 specimens. To check the sensitivity of the results, a
119 more conservative sample size threshold of 60 specimens was also used.

120 *Sample bathymetric estimates*

121 We obtained estimates of the bathymetric distribution of extant species from the Italian mollusc
122 census database (Bedulli et al., 1984). The Italian mollusc database reports, among others, water
123 depth (meters) and specimen abundance (tallied separately for live and dead individuals) for most
124 common mollusc species thriving along the Italian Peninsula. We used these data to estimate
125 preferred water depth for species commonly found in the cored sediments. For those species, its
126 preferred bathymetry was estimated as the abundance-weighted average depth. Then water depth
127 estimate for each sample was computed by the mean preferred depth of the species found in a
128 sample weighted by their specimen abundances (Wittmer et al., 2014).

129 *Multivariate analyses*

130 Prior to multivariate analyses the species occurring in one sample only were removed.
131 Subsequently, the sample-by-species matrix was converted to relative abundances and 4th-root
132 transformed to reduce the effect of hyper-abundant taxa. Other commonly used transformation
133 and standardization techniques (e.g., log-transformation, Wisconsin double-relativisation)
134 produced comparable ordination outcomes (Fig. S3; Table S3).

135 The indirect ordination was performed by non-metric multidimensional scaling (NMDS) using
136 Bray-Curtis (BC) distance measure (k=2 dimensions). Permutation-based multivariate analysis
137 of variance (PERMANOVA) based on the same distance matrix was employed to evaluate
138 differences in the locations of the multivariate groups of samples from the three compared time
139 intervals.

140 *Comparison of assemblage composition and model testing*

141 Pairwise comparisons of samples using BC dissimilarity were employed to assess the
142 resemblance between nearshore assemblages from the three periods (i.e., LIG, LG and CIG). In
143 addition, the observed mean BC distance for each of the comparisons was contrasted against a
144 sampling distribution of means obtained by randomization (based on 1000 iterations) under the
145 null hypothesis that the samples came from the same system. For each pairwise comparison, the
146 randomization procedure involved pooling all samples and then randomly reassigning them to
147 one of the three time intervals, thus mimicking the sampling structure of the actual data. For each
148 of the 1000 randomized iterations mean BC distance was computed and added to the resulting
149 resampling distribution predicted under the null hypothesis.

150 A similar approach was used in the pairwise evaluation of total species abundances obtained by
151 pooling all samples within each of the three examined time intervals. Each of the three pairwise
152 comparisons (i.e., LIG vs. LG, LIG vs. CIG, LG vs. CIG) was contrasted against a randomized
153 data permutation model depicting a homogenous system based on the pooled species abundances
154 for data combined across all compared time intervals. For each pairwise comparison, specimens
155 were sampled from the pooled species distribution into the sample structures (i.e. the same
156 number of samples and sample sizes as observed) of the compared time intervals. The simulation
157 was repeated 1000 times. For each of the three pairwise comparisons, the resulting 1000 pairs of
158 abundance values (one of each of the two compared time intervals) were obtained for each of the
159 species considered. The modeled distributions of species abundances, predicted under the null
160 hypothesis that samples came from a single underlying species abundance, were plotted together
161 with the observed values.

162 *Bivariate analyses*

163 Spearman's rank correlation coefficient was used to measure the strength of correlation between
164 NMDS sample scores and sample-standardised species richness (rarefied to 25 and 60
165 specimens), biogeographic affinity (relative abundance of Mediterranean-to-Lusitanian and West
166 African species in each sample), and sample water depth estimates. Lastly, we used information
167 on the present-day biogeographic distribution of the species as an indicator of their climatic
168 affinity to better understand the relationship between shifts in species composition and
169 palaeoclimatic changes (Fig. S1). In this approach, relative abundances of species grouped
170 according to their current biogeographic distributions were plotted to evaluate changes in the
171 biogeographic and climatic affinity of the macrofaunal stock across glacial-interglacial
172 transitions.

173 *Software and Data Access*

174 Specific details on the parameters and bivariate and multivariate statistical test and procedures
175 implemented in this study are given in the captions of figures, tables and relevant supplementary
176 online materials. All analyses were performed in R (R Development Team, 2018, v 4.0.5) and
177 Excel. The “vegan” package (Oksanen et al., 2018) was used to carry out ordinations and
178 PERMANOVA. Resampling models were written using standard base functions available in R.
179 Codes and data are provided in the supporting information.

180 **Results**

181 To evaluate macrobenthic assembly dynamics during climatic shifts we used 223 nearshore
182 samples from 18 stratigraphically well-constrained sediment cores (Appendix S1). The samples
183 yielded cumulatively 113 species and 71282 fossil specimens subdivided into three datasets: 21
184 LIG samples including 11413 fossils and 45 species, 32 LG samples including 3381 fossils and
185 60 species, and 170 CIG samples including 56488 fossils and 78 species (Appendixes S1-S2;

186 Table S1). To develop cross-validation assessments, we contrasted the results with outcomes of
187 empirically calibrated resampling models simulating patterns expected under the null hypothesis
188 that the recovered assemblages originated from the same regional pool of species (see model
189 testing in Material and Methods). In the NMDS ordination projection, CIG and LIG sample
190 groups overlapped strongly, whereas LG samples plotted separately (Fig. 2a). NMDS axis 1
191 scores were negatively correlated with sample-standardised diversity estimates (Spearman's rank
192 correlation $\rho = -0.81$, $p < 0.001$; Fig. 2b) and positively correlated with the proportion of
193 Lusitanian specimens ($\rho = 0.84$, $p < 0.001$; Fig. 2c), defined as those specimens that belonged to
194 species for which the present-day geographic ranges do not extend northward beyond the warm-
195 temperate Lusitanian province. In addition, quantitative bathymetric estimates based on faunal
196 composition were highly congruent with the independently derived estimates of water depth (Fig.
197 S2; Table S2), confirming that all sampled assemblages represented shallow-water (<10 m)
198 habitats (Fig. 2d). These results suggest that LG samples represented habitats and water depths
199 comparable to those of the LIG and CIG interglacial samples but were characterised by higher
200 species richness and depressed abundance of exclusively Mediterranean-to-Lusitanian species
201 when compared to the interglacial samples (Figs 2b-d, S4). In contrast, the interglacial samples
202 were strongly dominated by *Lentidium mediterraneum*—an infaunal filter feeder, representing
203 more than 85% of specimens in both interglacial groups of samples (Table S4).

204 Permutational multivariate analysis of variance (PERMANOVA) provided further evidence for
205 the distinct species composition of the LG assemblages and strong similarities between the two
206 interglacials (Table S5). However, PERMANOVA results can be sensitive to the unbalanced
207 sampling design (Anderson & Walsh, 2013). Therefore, we also compared the observed BC
208 dissimilarities between individual samples from different time intervals with the predictions of
209 the resampling models (Fig 3a-b). Only in the LIG vs. CIG comparison, the observed mean

210 pairwise BC dissimilarity fell within the sampling distribution of means expected if the samples
211 from the two interglacial periods came from a species pool with a homogenous composition and
212 comparable abundance structure (Fig. 3b). In contrast, the average dissimilarity between LG
213 samples and samples from either of the studied interglacials departed significantly from the null
214 model predictions and was much higher than the observed mean pairwise distance between LIG
215 and CIG samples (Fig. 3a,c; $p = 0.001$). Moreover, when individual samples were pooled together
216 in each time interval (Fig. 4a-c), the two interglacials were also characterised by a very similar
217 species abundance structure, with a positive Spearman's rank correlation ($\rho = 0.51$; $p < 0.001$,
218 Fig. 4c and Table S6). On the other hand, species abundances in LG and either of the interglacials
219 were not significantly correlated ($\rho < 0.035$ and $p > 0.70$ in both cases; Fig. 4a,b and Table S6).
220 Lastly, a comparable stock of species dominated the Adriatic nearshore settings during both
221 interglacials (Table 1), with seven of the most dominant species recovered from the CIG interval
222 also belonging to the top ten species in the LIG samples (Table S4). On the other hand, LG group
223 of samples shared only four of the top ten most abundant species with the CIG (Tables 1, S4).

224 Relative abundances of species with different biogeographic affinities (Fig 5) were comparable
225 between the two interglacials, but differed from those observed in the LG. Specifically, the LIG
226 and CIG samples were dominated by species restricted to Mediterranean and Lusitanian
227 provinces (>88% of specimens; Fig. 5a,c). The relative abundance of this group decreased down
228 to 26% during the LG period. In contrast, cosmopolitan species, today occurring in both
229 (sub)tropical and cold-temperate East Atlantic regions, increased in relative abundance from less
230 than 7% in both interglacials to 54% in the LG period. The LG samples are also characterised by
231 a higher relative abundance (19%; Fig. 5b) of Boreal species (ranging from the Mediterranean to
232 the cold-temperate NE Atlantic), compared to the interglacial samples (5% and 3% in the LIG
233 and CIG, respectively).

234 Discussion*235 Nearshore biotic response to glacial-interglacial cycles*

236 The macrobenthic assemblages from the two interglacials are statistically indistinguishable in
237 terms of species composition (Figs 2-5; Table 1) and characterised by high dominance and low
238 richness both at the scale of individual samples (Figs 2b, S4) and the regional species pool (Fig.
239 S6; Tables 1, S4). However, they remain distinct from more species-rich glacial assemblages
240 representing similar shallow-marine habitats. These results indicate that Late Pleistocene
241 interglacial nearshore associations of the Adriatic transitioned to a different state during the last
242 glacial period, but when interglacial climatic conditions were reestablished in the Holocene, these
243 mollusc associations shifted back to the species composition and abundance structures
244 characteristic of the previous interglacial. Minor differences between the current and previous
245 interglacial assemblages suggested by the ordination analysis (Fig. 2a) are likely driven by
246 sampling effects (see NMDS results limited to larger samples only; Fig. S5). Despite high spatial
247 and temporal variability of deltaic habitats, the similarity of the two interglacial assemblages
248 suggests that large-scale, long-term environmental drivers overwhelmed local effects of changing
249 coastal physiography or distance to the river or distributary channel mouths. Overall, the observed
250 palaeoecological pattern of nearshore assemblages is consistent with the resilient model of long-
251 term community response to glacial-interglacial climate and sea-level cycles (Fig. 1a,d).

252 The observed resilient response of mollusc assemblages from dynamic, fluvially-influenced
253 nearshore settings (McKinney, 2007) is also consistent with patterns observed in other marine
254 systems. Deep-sea benthic foraminiferal assemblages of the Santa Barbara Basin (USA) exhibited
255 a similar repetitive faunal turnover in response to millennial-scale variations in oxygen
256 concentrations related to Dansgaard-Oeschger climatic cycles (Cannariato & Kennett, 1999).
257 Pleistocene coral-reefs of Papua New Guinea, were characterised by recurring coral associations

258 during sea-level highstands and compositionally distinct lowstand assemblages over the past 416
259 kyr (Pandolfi, 1996, Tager et al., 2010). Interestingly, the variable composition of lowstand coral
260 associations contrasts with the persistence of microbenthic and calcareous algal assemblages from
261 the same reef ecosystem (Tager et al., 2010). Finally, the resilient response of onshore
262 macrobenthic associations together with higher turnover in offshore environments was
263 documented in the deep-time fossil record during higher-order sea-level fluctuations over
264 millions of years (Danise & Holland, 2017). On the other hand, some late Cenozoic marine
265 mollusc faunas underwent continuous gradual changes in species composition during past climate
266 oscillations, in spite of cyclic recurrence of similar environments (Stanton & Dodd, 1997). Such
267 a pattern is similar to the substantial shifts in plant and vertebrate communities frequently
268 observed in Quaternary terrestrial ecosystems, which have been linked to differential responses
269 of individual species to highly dynamic environmental changes (Jackson & Blois, 2015). Thus,
270 rather not surprisingly, biotic responses to naturally occurring climate changes during the
271 Quaternary appear to have varied greatly across ecosystem types and organismal groups.

272 Taken together, the results of this and previous studies suggest that resilient patterns can
273 be scale invariant, and more prevalent in communities that inhabit environmentally unstable
274 habitats and may thus be pre-adapted to cope with long-term climate and sea-level changes.
275 Indeed, the studied nearshore system is dominated by r-selective eurythermal species capable of
276 rapid re-colonization whenever favorable environmental conditions return. In addition, a large
277 suite of more vulnerable (i.e., less thermally tolerant) Pliocene Mediterranean taxa had been
278 previously extirpated in a series of regional extinctions (Monegatti & Raffi, 2001). Therefore, the
279 impact of the Quaternary climate shifts has been attenuated in the Mediterranean Sea by a long
280 history of major climatic fluctuations that had shaped the regional pool of taxa in this region.

281 *Mechanisms of change and ecosystem resilience*

282 Understanding how the structure and composition of past ecosystem change through time allows
283 us to depict hypothetical scenarios of community dynamics in the face of climate change. Broad
284 models of community assembly fall within three categories: interaction assembly, environment
285 assembly, and neutral assembly (Vellend, 2016 and references therein). Interaction assembly
286 model considers communities structured primarily by ecological locking among species due to
287 strong interspecific interactions (e.g., predation or resource competition), resulting in limited
288 membership. Environment assembly model regards community membership principally as the
289 result of deterministic species responses to the changing physical environment. Finally,
290 communities structured by stochastic (neutral) processes have no membership constraints, strong
291 hysteresis, and high variability under comparable environmental conditions.

292 Before we assess those three models of community assembly, we should first note that in the
293 semi-enclosed Adriatic basin, the transitions from interglacial to glacial periods, were
294 characterised by changes in the basin morphology, sea surface temperature, salinity and
295 circulation pattern (Piva et al., 2008; Maselli et al., 2014; Fig. S1). During the last glacial interval,
296 the targeted portion of the Adriatic experienced high sedimentation rates, eutrophic waters, and
297 frequent freshwater inflows (Asioli et al., 2001; Pellegrini et al., 2018). Although similar
298 conditions were present also during the middle-late Holocene (Amorosi et al., 2016; Pellegrini et
299 al., 2021), some of the key abiotic factors are estimated to have differed strongly between glacial
300 and interglacial periods. Salinity was lower during the LG period due to a more confined Adriatic
301 basin and higher inflow of freshwater from the Po River (Asioli et al., 2001; Pellegrini et al.,
302 2017). Moreover, the estimated sea surface temperatures (SSTs) were $\sim 6^{\circ}\text{C}$ lower during the Last
303 Glacial Maximum (LGM) compared to the Holocene climatic optimum (Capotondi 2004; but see
304 also Piva et al., 2008), an offset slightly lower than that estimated for the Adriatic between the
305 LGM and LIG (Hoffman et al., 2017, see also discussion below).

306 Shifts in the relative abundance of species with different biogeographic and climatic affinities
307 (Figs 2c, 5; Table S4) in targeted nearshore assemblages follow these environmental changes.
308 Samples from all three time intervals were dominated by molluscs that thrive in shallow-water
309 habitats with fine sand substrates in the modern Mediterranean Sea (Pérès & Picard, 1964).
310 However, during LIG and CIG, species that today are restricted to subtropical to warm-temperate
311 Mediterranean and Lusitanian provinces had much higher relative abundances (i.e., *L.*
312 *mediterraneum*, *Chamelea gallina* and *Donax semistriatus*). On the other hand, assemblages from
313 LG were characterised by higher richness and evenness and were dominated by species whose
314 present-day biogeographic ranges extend farther northward into cool-temperate regions of the
315 Eastern Atlantic (e.g., *Spisula subtruncata*, *Fabulina fabula*; Petersen, 1914). Notwithstanding
316 the different composition and diversity structure, glacial and interglacial nearshore communities
317 all share eurytopic species that thrive in fluvially-influenced settings along an onshore-offshore
318 gradient, such as *Ecrobia ventrosa* species-complex and *Varicorbula gibba*.

319 This biotic pattern is consistent with the regional palaeotemperature record (Fig. S1d; Capotondi,
320 2004; Piva et al., 2008) and suggests that nearshore Adriatic mollusc communities most likely
321 followed the environmental assembly model, where community composition is largely
322 determined by the overlap between their environmental tolerances and the local environmental
323 conditions (Jackson & Blois, 2015). Thus, in LG the dominance of cosmopolitan taxa
324 characterised by broad habitat niches and thermal tolerance (so expected to be found across
325 heterogeneous environments and more resistant to thermal stresses), suggests the predominant
326 role of environmental filtering (species sorting) in driving the shifts in the assemblage
327 composition rather than biotic perturbation related to species interactions expected during
328 community coalescence (blending of distinct communities) (Rocca et al., 2020). During the last
329 glacial period, lower temperatures limited the fitness of a subset of r-selected nearshore species

330 that are characterised by explosive population dynamics and can reach high densities in favorable
331 conditions but are less adapted to a colder climate (e.g., *L. mediterraneum*, *C. gallina*; Fig. 5b;
332 Tables 1, S4). Consequently, their abundance and occurrences in the northern regions of the
333 Mediterranean, including the Adriatic Sea, was greatly reduced, in some cases limiting their
334 distribution to the southern coasts of the basin. On the other hand, species characterised by
335 broader thermal tolerances (as suggested by their present biogeographic distribution) were able
336 to thrive under colder conditions increasing richness and evenness of LG nearshore assemblages
337 (Fig. 5). The subsequent Holocene climate warming reversed this pattern by again favoring
338 Lusitanian and Mediterranean species, which dominated highly variable shallow-marine
339 environments in the Adriatic Sea during the last interglacial period. The species that were
340 common in LG assemblages are still found in nearshore settings in northern Europe, but they
341 likely retracted to slightly deeper habitats in the Mediterranean part of their range. Such
342 bathymetric shifts are frequently documented among marine species in response to the ongoing
343 SST rise and might constitute an important driver of community reorganization (e.g., Weinberg,
344 2005; Pinsky et al., 2013).

345 *Conservation implications for the 21st century*

346 Our results together with the palaeoclimate data and climate change scenarios point to the
347 potential adaptive capacities of the Adriatic nearshore mollusc communities to the limited near-
348 future global warming. During the last interglacial, SSTs in the Northern Atlantic (above 23.5°N
349 latitude) were between 0.6 and 1.3 °C ± 0.5°C higher than during the pre-industrial times
350 (Hoffman et al., 2017). However, within the Mediterranean basin which is considered a climatic
351 hotspot sensitive to radiative forcing which amplifies climatic trends, palaeotemperature
352 estimates point toward higher values. Alkenone-derived SSTs for the late LIG in the central
353 Adriatic were estimated at ~ 22°C (see Fig. S1d), that is ~ 3.5°C higher than present-day SSTs

354 (i.e., 18.5°C, that is the mean value resulting from daily estimates obtained offshore southern
355 Marche and northern Puglia regions from July 2011 to June 2015; see Table 1 in Gizzi et al.,
356 2016). In addition, the radiative forcing of greenhouse gasses below 4.5 W/m², as predicted by
357 Representative Concentration Pathways (RCP) 2.6 and 4.5, should constrain near-future, central
358 Adriatic mean SST warming to less than 2°C (see Shaltout & Omstedt, 2014 for projected SST
359 at the end of the 21st century in the Adriatic). Therefore, the resilience of targeted assemblages
360 and strong similarities in many of the ecosystem features between the present and last interglacial,
361 suggest that efforts aimed at limiting the radiative forcing of greenhouses gasses below 4.5 W/m²
362 (i.e., RCP 4.5 scenario), should result in a limited impact on the Adriatic nearshore deltaic
363 mollusc communities. However, other anthropogenic stressors including bottom trawling
364 (Eigarrrd et al., 2017; Pitcher et al. 2022), hypoxic events (Justić, 1991), coastal landscape
365 modifications, and aquaculture (Viero et al., 2019; Sliškočić et al., 2021), have been affecting
366 community composition of the Adriatic ecosystems since at least the mid-20th century. These
367 multi-faceted impacts are shifting taxonomic and abundance structures far more strongly than
368 natural environmental drivers did during the latest Quaternary (e.g., Lotze et al., 2010;
369 Kowalewski et al., 2015; Gallmetzer et al., 2019; Tomašových et al., 2020). The ongoing human
370 restructuring of these ecosystems could push local assemblages beyond the historical range of
371 variability despite their high resilience to natural climate dynamics.

372 The long-term perspective offered by geohistorical archives is fundamental for defining
373 ecological baselines, which in turn, should inform conservation actions aimed at sustaining highly
374 dynamic coastal ecosystems. However, restoration of environments and resource stocks to the
375 pristine or pre-industrial conditions may not be feasible given the socio-economic contexts of
376 these densely populated areas. Long-term conservation practices, therefore, should focus on
377 maintaining connectivity among areas of relatively unaffected, natural habitats that could act as

378 a buffer against ecosystem shifts due to ongoing climate warming. Such low impact areas increase
379 habitat heterogeneity across different climatic zones and can serve as potential thermal refugia,
380 and thus promote resilience to climate change (Bernhardt & Leslie, 2013). Maintaining and
381 possibly improving the quality of marine refugia in the Mediterranean Sea (Mu & Wilcove, 2020)
382 is thus necessary to preserve the structure and resilience of coastal communities and their
383 ecosystem services (Schneider, 2018).

384 In summary, this study suggests that the Adriatic nearshore assemblages have alternated naturally
385 between two community states over the last ~125 kyr and thus demonstrated a remarkable
386 resilience in face of major, long-term environmental perturbations. The observed resilience
387 during the most recent interglacial-glacial transitions is not consistent with stochastic or
388 interaction-based community assembly models. Instead, the high similarity between assemblages
389 representing the two interglacial periods and distinct composition observed in the glacial faunas
390 suggest that, over millennial timescales, shallow-marine benthic assemblages have been primarily
391 structured by environmental forcing. Over the last century, however, pollution, eutrophication,
392 trawling, and invasive species have been affecting coastal ecosystems. Our findings suggest that
393 if these impacts can be controlled, the targeted nearshore communities of the Adriatic should be
394 resilient to the limited rise of sea surface temperatures predicted for the near future. In addition
395 to the international policies addressing global warming, we stress here the importance of the
396 mitigation of the threats associated with human activities in the coastal areas at the local and
397 regional levels.

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605 RN, MK, MA; Writing—review & editing: MK, RN, DS, CP, FG, FT.,

606

607 **Figure and table legends**

608 **Figure 1. Conceptual framework.** Idealized outcomes representing patterns of community
609 response to glacial-interglacial changes at the regional scale, evaluated by means of ordination
610 analyses (NMDS) and correlation between abundances of species (black: pairwise comparison
611 between the two interglacial units, green: comparisons between glacial and interglacial units).
612 Each column shows one of the three idealised scenarios. Persistent pattern (**a** and **d**): communities
613 maintain species composition and diversity through environmental perturbations even though
614 populations of constituent species shift spatially in concert with sea-level changes. Resilient
615 pattern (**b** and **e**): communities shift to an altered state during the glacial period but return to
616 previous composition with the re-establishment of interglacial conditions. Stochastic pattern (**c**
617 and **f**) unique species associations characterise communities from all three-time periods.

618 **Figure 2. Gradient and rank correlation analyses:** **a**) NMDS ordination of nearshore samples
619 containing at least 25 specimens (see also Fig. S5 for a NMDS output based on sample size
620 threshold of 60 specimens). Relative abundance of species was 4th-root transformed. Samples are
621 colour-coded according to the climatic interval: Green—current interglacial (CIG), Light
622 blue—last interglacial (LIG), and Dark red—last glacial (LG). The size of each point is
623 proportional to sample size. Convex hulls delimit the ordination space occupied by each group of
624 samples. **b**) Correlation between NMDS axis 1 sample scores (NMDS1) and species richness
625 rarefied to 25 specimens. Standardised species richness for relatively small samples tends to be
626 primarily driven by evenness, so the two measures are strongly correlated. **c**) Correlation between

627 NMDS1 and relative abundance of Mediterranean-to-Lusitanian and West African species
628 recovered in each sample. **d)** Correlation between NMDS1 and the sample water depth estimates
629 based on species bathymetric preferences (see Material and Methods for details). In **b-d** panels,
630 rank correlation coefficient ρ is shown also for NMDS axis 2 sample scores.

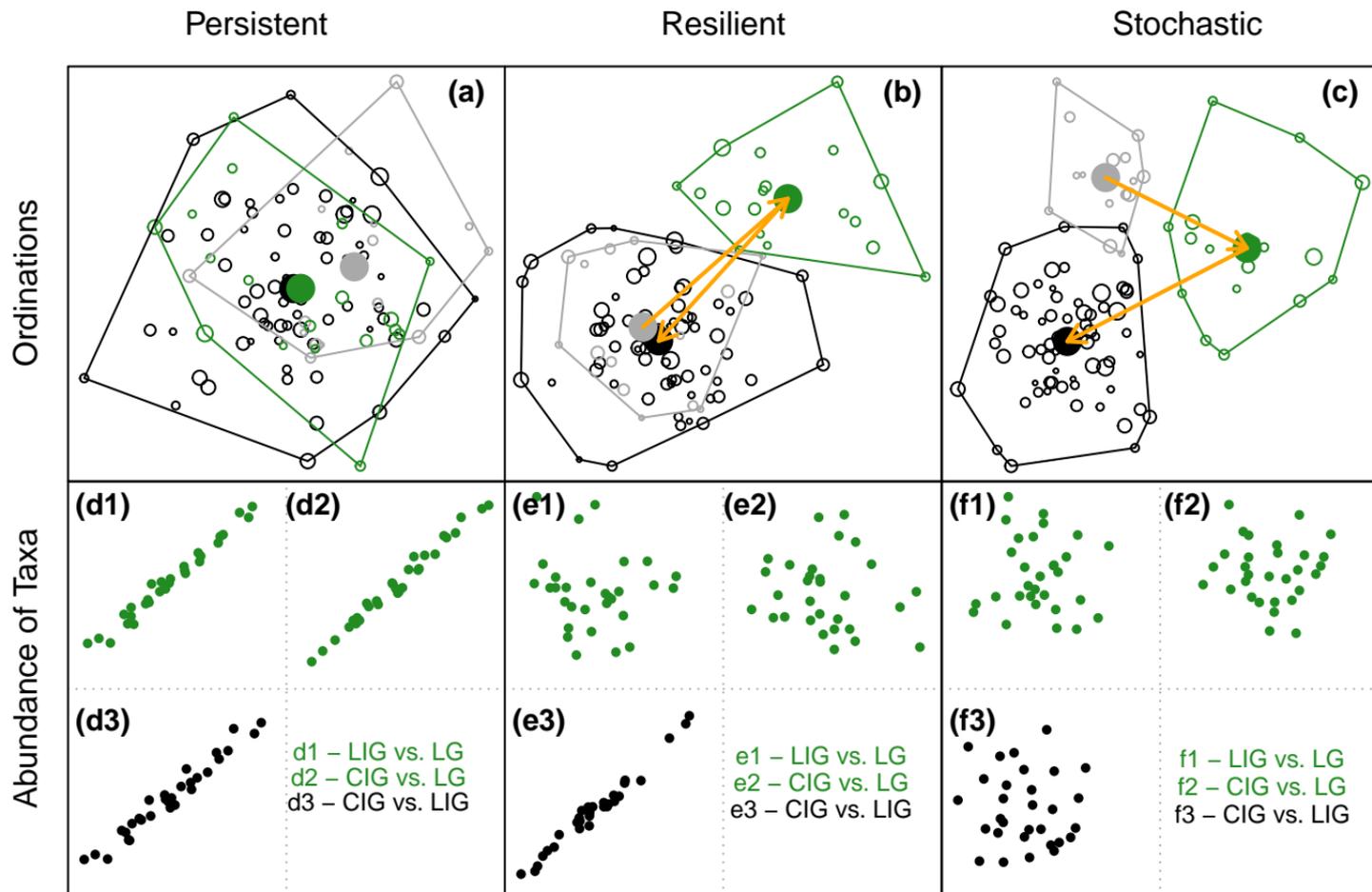
631 **Figure 3. Distribution of pairwise Bray-Curtis (BC) distances between samples representing**
632 **glacial and interglacial assemblages. a)** Current interglacial and last glacial (CIG-LG, based
633 upon 1170 pairs of compared samples). **b)** Current interglacial and last interglacial (CIG-LIG
634 based upon 975 pairs of compared samples). **c)** Last glacial and last interglacial (LG-LIG based
635 upon 270 pairs of compared samples). Red arrows mark the location of the observed mean values
636 BC distances for each frequency distribution of the three pairwise comparisons. The x-axis reports
637 BC dissimilarity range, zero value indicates that two samples have the same faunal composition,
638 one no species in common. In green sampling distributions of means based on randomization
639 (based on 1000 iterations), under the null model that the samples came from the same system.
640 Pairwise comparisons are based on the same species relative abundance matrix as the one used
641 for the NMDS ($n \geq 25$ specimens and rare species removed).

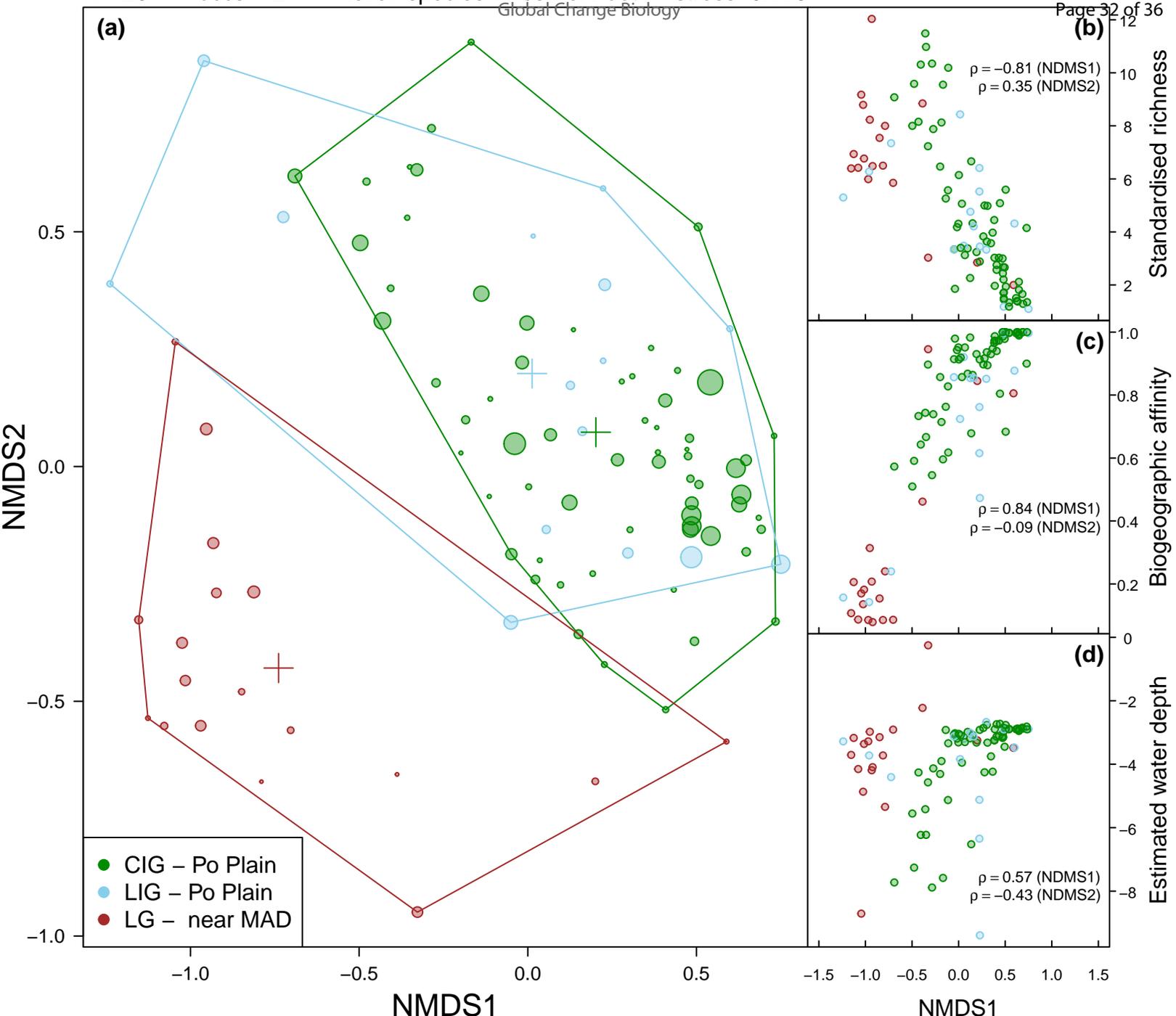
642 **Figure 4. Pairwise comparisons of species total abundances (total counts in pooled data**
643 **from each interval). a)** Current interglacial and last glacial (LIG-LG, upper-left panel). **b)**
644 Pleistocene interglacial and Last glacial (LIG-LG, upper-right panel). **c)** Holocene and
645 Pleistocene interglacials (CIG-LIG, lower panel). Species total abundances have been log-
646 transformed. The output of the randomization model based on 1000 iterations highlights the
647 portion of two-dimensional space in which the points should fall under the null model of a
648 homogenous system. Spearman's rank correlation (ρ) for each pairwise comparison is reported
649 on each panel; it is significant only for the interglacial pairwise comparison (i.e., CIG-LIG, $p <$
650 0.001; see also Table S6).

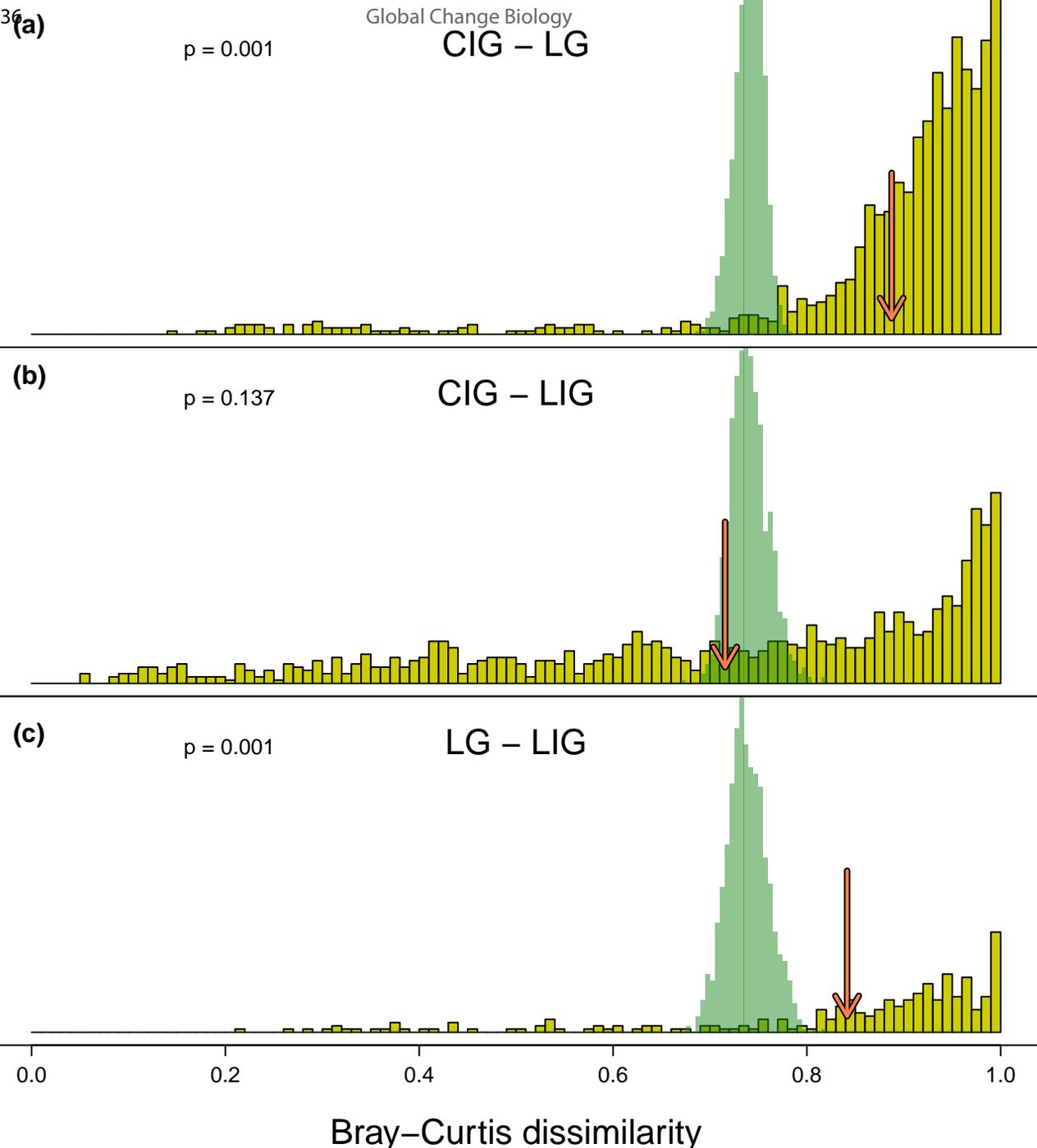
651 **Figure 5. Comparisons of species total relative abundances grouped according to their**
652 **biogeographic distribution. a)** Current interglacial—CIG; **b)** last late-glacial—LG; **c)** last
653 interglacial—LIG. Information on the geographic range of mollusc species is after Poppe and
654 Goto, (1991, 1993). Abbreviations for biogeographic affinity of species distribution: BOR =
655 species occurring in the Mediterranean, Lusitanian, and Boreal provinces; COS = species of
656 cosmopolitan distribution (i.e., occurring from West African until Boreal provinces); MED/LUS
657 = species occurring in the Mediterranean and/or Lusitanian provinces; WAF= species occurring
658 in the Mediterranean, Lusitanian and West African provinces.

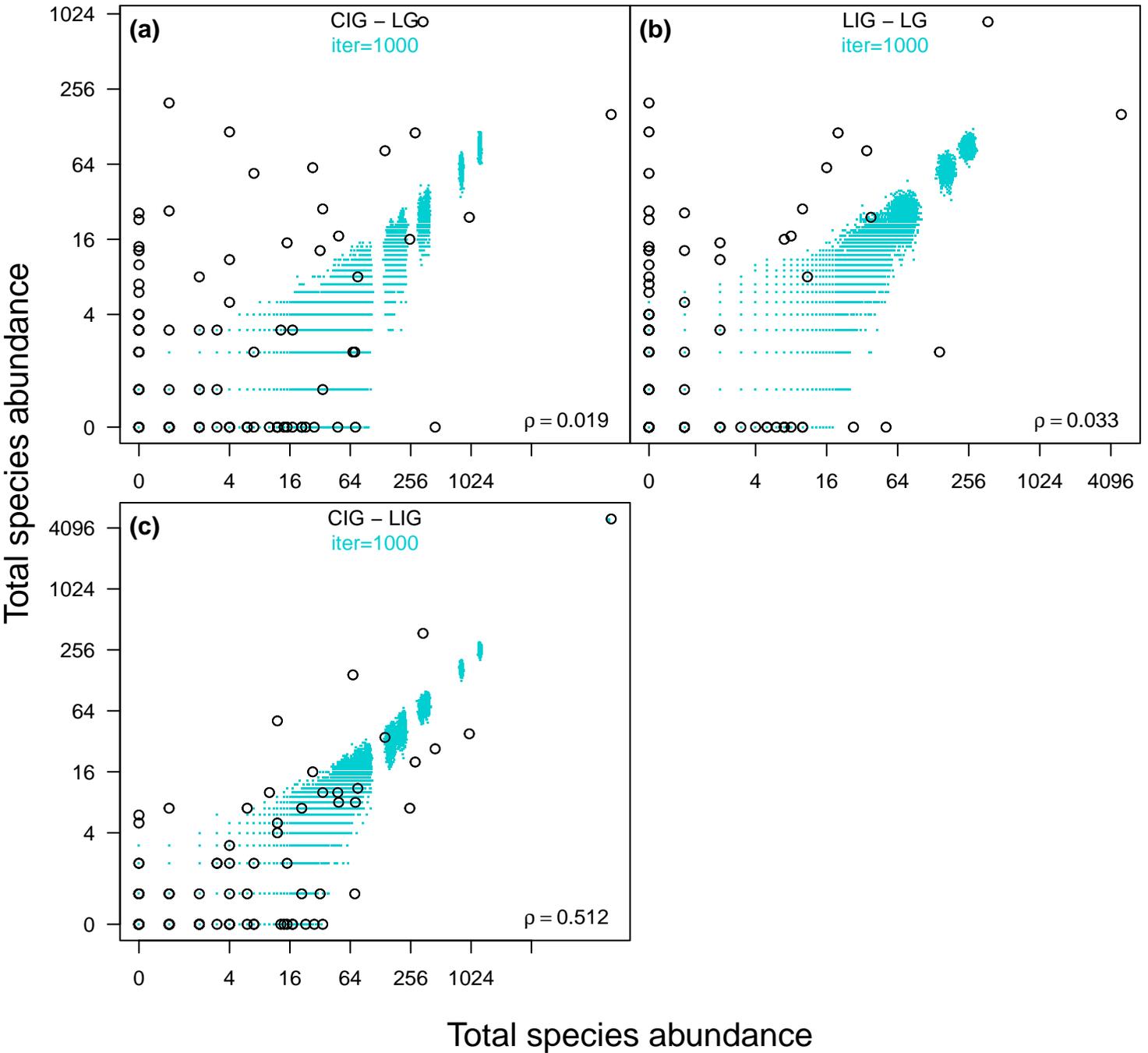
659 **Table 1. The 10 most abundant species in the current interglacial (pre-modern Era)** and
660 their ranking in the other two time periods (Pleistocene last glacial—LG and Late Pleistocene
661 interglacial—LIG). Taxonomic notes: 1 This is a group of very similar and highly variable
662 species: *Ecrobia ventrosa*, *Hydrobia acuta* and *Eupaludestrina stagnorum* not easily
663 distinguishable by the shell features; 2 *Bela formica* is considered taxon inquirendum previously
664 synonymised with *Bela nebula*; 3 commonly reported as *Tritia pygmaea* (Lamarck) a junior
665 secondary homonym of *Muricites pygmaeus* Schlotheim.

666

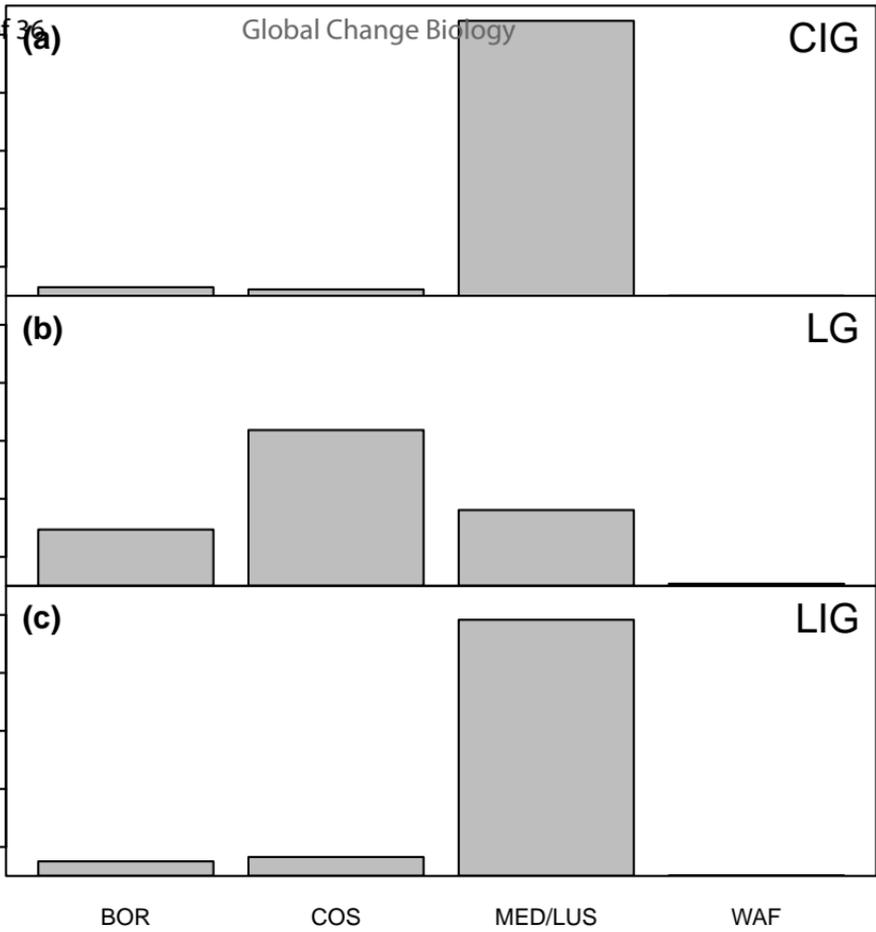








Specimen relative abundance



Species geographic range

Table 1. The 10 most abundant species in the current interglacial (pre-Modern Era)

SPECIES	AUTORSHIP	CIG	LG	LIG
(Total number of species = 113)				
<i>Lentidium mediterraneum</i>	(O.G. Costa, 1830)	1	3	1
<i>Chamelea gallina</i>	(Linnaeus, 1758)	2	12	5
<i>Donax semistriatus</i>	Poli, 1795	3	absent	7
<i>Spisula subtruncata</i>	(da Costa, 1778)	4	1	2
<i>Bittium reticulatum</i>	(da Costa, 1778)	5	5	8
<i>Varicorbula gibba</i>	(Olivi, 1792)	6	15	16
<i>Ecrobia</i> gr. <i>ventrosa</i> ¹	(Montagu, 1803)	7	6	6
<i>Bela formica</i> ²	(Nordsieck, 1977)	8	23	10
<i>Peronidia albicans</i>	(Gmelin, 1791)	9	absent	14
<i>Tritia varicosa</i> ³	(W. Turton, 1822)	10	41	32