

# ARCHIVIO ISTITUZIONALE DELLA RICERCA

# Alma Mater Studiorum Università di Bologna Archivio istituzionale della ricerca

Abundance-diversity relationship as a unique signature of temporal scaling in the fossil record

This is the final peer-reviewed author's accepted manuscript (postprint) of the following publication:

Published Version: Tomašových, A., Kowalewski, M., Nawrot, R., Scarponi, D., Zuschin, M. (2024). Abundance-diversity relationship as a unique signature of temporal scaling in the fossil record. ECOLOGY LETTERS, 27(7), 1-15 [10.1111/ele.14470].

Availability: This version is available at: https://hdl.handle.net/11585/995285 since: 2024-10-31

Published:

DOI: http://doi.org/10.1111/ele.14470

Terms of use:

Some rights reserved. The terms and conditions for the reuse of this version of the manuscript are specified in the publishing policy. For all terms of use and more information see the publisher's website.

This item was downloaded from IRIS Università di Bologna (https://cris.unibo.it/). When citing, please refer to the published version.

(Article begins on next page)

- 1 Abundance-diversity relationship as a unique signature of temporal scaling in the fossil
- 2 record
- 3
- 4 Adam Tomašových<sup>1</sup>\*, Michał Kowalewski<sup>2</sup>, Rafał Nawrot<sup>3</sup>, Daniele Scarponi<sup>4</sup>, Martin
- 5 Zuschin<sup>3</sup>

- <sup>1</sup>Earth Science Institute, Slovak Academy of Sciences, 84005, Bratislava, Slovakia, ORCID:
  0000-0002-0471-9480
- 9 <sup>2</sup>Florida Museum of Natural History, University of Florida, 1659 Museum Road, Gainesville,
- 10 FL, ORCID: <u>0000-0002-8575-4711</u>
- <sup>11</sup> <sup>3</sup>Department of Palaeontology, University of Vienna, Josef-Holaubek-Platz 2, 1090 Vienna,
- 12 Austria, ORCID: <u>0000-0002-5774-7311</u>, <u>0000-0002-5235-0198</u>
- <sup>4</sup>Dipartimento di Scienze Biologiche, Geologiche e Ambientali, University of Bologna, Via
- 14 Zamboni 67, 40126 Bologna, Italy, ORCID: <u>0000-0001-5914-4947</u>
- 15 \*Corresponding author: Adam Tomašových, geoltoma@savba.sk

- 17 Keywords: paleoecology, macroecology, species diversity, species-time relationship,
- 18 Holocene, time averaging
- 19 Author Contributions: A.T, M.K., R.N., D.S. and M.Z. designed research, collected data,
- 20 and performed analyses; A.T wrote the initial draft, and A.T, M.K., R.N., D.S. and M.Z.
- 21 contributed to the final version.
- 22 Competing Interest Statement: The authors declare no competing interest.
- 23 Running title: Temporal scaling of fossil-record diversity
- 24 Abstract: 149 words
- 25 Main Text: 5126 words
- 26 Number of figures: 6

- 27 Number of references: 81
- 28 Supporting text
- 29 Figures S1-S11
- 30 Tables S1-S5 (separate files)
- 31 SI references
- 32 Data files and scripts at Dryad-Zenodo:
- 33 https://doi.org/10.5061/dryad.fttdz0903
- 34 <u>https://doi.org/10.5281/zenodo.11664933</u>
- 35
- 36

# 37 Abstract

38 Species diversity increases with the temporal grain of samples according to the species-time 39 relationship, impacting paleoecological analyses because the temporal grain (time averaging) 40 of fossil assemblages varies by several orders of magnitude. We predict a positive relation 41 between total abundance and sample size-independent diversity (ADR) in fossil assemblages 42 because an increase in time averaging, determined by a decreasing sediment accumulation, 43 should increase abundance and depress species dominance. We demonstrate that, in contrast 44 to negative ADR of non-averaged living assemblages, the ADR of Holocene fossil 45 assemblages is positive, unconditionally or when conditioned on the energy availability gradient. However, the positive fossil ADR disappears when conditioned on sediment 46 47 accumulation, demonstrating that ADR is a signature of diversity scaling induced by variable 48 time averaging. Conditioning ADR on sediment accumulation can identify and remove the 49 scaling effect caused by time averaging, providing an avenue for unbiased biodiversity 50 comparisons across space and time.

## 52 INTRODUCTION

53 In recent years, ecologists have become increasingly interested in biodiversity dynamics 54 across timescales, achieving new insights through the integration of neo- and paleoecological 55 data (Buma et al. 2019; Benito et al. 2020; Pandolfi et al. 2020; Patrick et al. 2021; Dornelas 56 et al. 2023; Rillo et al. 2022). However, differences in temporal grain of fossil assemblages 57 and their consequences for diversity patterns need to be accounted for to avoid invalid 58 inferences (Powell and Kowalewski 2002; Bush and Bambach 2004; Balseiro and Waisfeld 59 2014; Carlucci and Westrop 2015; Finnegan et al. 2019). Species diversity increases with the 60 temporal grain of samples as predicted by eco-evolutionary models and observed in 61 neoecological and paleoecological time series according to the species-time relationship 62 (STR, Figure 1, Preston 1960, Rosenzweig 1998). Temporal grain of paleoecological samples 63 is equal to time averaging that corresponds to the cumulative amount of time during which the 64 individuals forming a fossil assemblage have lived (Kidwell 2013). Estimates of species 65 diversity thus depend on the time span over which a given assemblage is observed in 66 neoecological surveys (Adler and Lauenroth 2003; Fridley et al. 2006; Castillo-Escrivà et al. 2020; O'Sullivan et al. 2021) or over which it is incorporated into the stratigraphic record 67 68 (Scarponi and Kowalewski 2007; Tomašových and Kidwell 2010a). As marine and terrestrial 69 environments are characterized by variability in sediment accumulation rate, in disintegration 70 rate of organismal (typically skeletal) remains, and in their mixing by burrowers (Aller 1982; 71 Kidwell 1986), time averaging of fossil assemblages in a single paleoecological time series 72 can vary by several orders of magnitude, from years or decades to multiple millennia or 73 longer (Scarponi et al. 2013; Tomašových et al. 2016; Ritter et al. 2023). This large variability 74 in time averaging magnifies the importance of the scaling effect generated by the STR in 75 paleoecological, as opposed to neoecological time series, in which the temporal grain of 76 sampling units can be directly controlled.

In contrast to neoecological data, estimation of time averaging is challenging in the fossil record as the accuracy of geochronological tools is limited. Fluctuations in diversity observed in the fossil record across series of assemblages, which slide up and down along the STR continuum according to their time averaging, can be thus difficult to distinguish from changes driven by eco-evolutionary processes. To address this problem, here we formulate a simple prediction regarding the effect of the variability in temporal grain on the diversity observed in the fossil record. This prediction, which ultimately can be used to filter out 84 scaling effects on diversity, postulates that the relation between the total fossil abundance and 85 diversity estimated with methods that remove its dependency on sample size (ADR; Hurlbert 1971; Chao et al. 2014, 2020) will be pulled towards positive values in fossil assemblages 86 87 (Figure 2). This prediction relies on the negative effect of sediment accumulation rate on both 88 (1) the abundance of fossils (total abundance of individuals standardized to sediment mass or 89 volume) and (2) the time averaging of fossil assemblages themselves, which influences the 90 shape of the species-abundance distribution (Figure 2A, Tomašových and Kidwell 2010b) and 91 thus species diversity (Šizling et al. 2009; Alroy 2015; Chase et al. 2018; McGlinn et al. 92 2021).

93 First, in the absence of variability in sedimentation and disintegration, fossil 94 abundance is a function of both standing abundance and mortality of living populations that 95 eventually enter as dead individuals into the sediment (Figure 2A). Fossil abundance 96 integrates this flux of dead individuals into historical layers over variable durations of time 97 averaging. A decrease in sediment accumulation rate (i.e., in the input of non-skeletal 98 sediment) will increase the abundance of individuals in fossil assemblages (Kidwell 1986). 99 Although fossil abundance is also reduced by disintegration rate (Figure 2A), this prediction 100 is supported empirically as fossil concentrations are associated with stratigraphic surfaces that 101 result from reduced accumulation rates (Kidwell 1989; Abbott 1997; Egenhoff and Maletz 102 2007). Second, although the time averaging of fossil assemblages will decline with skeletal 103 disintegration and will increase with mixing (Figure 2A), the sediment accumulation rate is a 104 first-order control of time averaging in most settings (Scarponi et al. 2013; Tomašových et al. 105 2023). Therefore, species diversity of assemblages, measured with indices that are 106 independent of sample size or use sample size-based or coverage-based rarefaction, will 107 increase with declining sediment accumulation rate as species dominance and the slope of the 108 rank-abundance distribution decline with increasing time averaging (steep gray solid lines 109 scale to flatter dashed lines, right column in Figure 1). This prediction primarily applies to 110 taxa with high preservation potential in the fossil record (such as calcareous foraminifers, 111 ostracods or molluscs).

Here, we evaluate whether the abundance-diversity relation in fossil assemblages
(ADR<sub>F</sub>) in the Holocene record of molluscs in the northern Adriatic Sea is positive,
unconditionally or when conditioned on the energy availability gradient (i.e., water depth),
and thus whether it carries the signature of variable time averaging. The abundance-diversity

116 relation independently documented in living assemblages (ADR<sub>L</sub>) provides a benchmark for

- 117 abundance and diversity not affected by time averaging that can be compared with the  $ADR_F$
- 118 observed in the fossil record. Based on 26 age-dated sediment cores, we assess the hypotheses
- 119 positing (1) that sediment accumulation covaries negatively with fossil abundance and species
- 120 diversity, (2) that fossil abundance and species diversity are positively related, either
- 121 unconditionally or when conditioned by the energy availability that shapes the ADR<sub>L</sub> in the
- 122 northern Adriatic Sea (Figure 2B-I), and (3) are independent when conditioned on sediment
- 123 accumulation (Figure 2J-M). To determine whether our findings apply to other taxa, we assess
- 124 the  $ADR_L$  and  $ADR_F$  in marine benthic foraminiferal assemblages from different areas
- 125 worldwide using data from the Biodeeptime database (Smith et al. 2023).
- 126

# 127 CONCEPTUAL FRAMEWORK: PREDICTIONS FROM SPECIES-TIME 128 RELATIONSHIP INDEPENDENT OF SAMPLE SIZE

129 The STR is assessed in terms of how the raw species richness increases as a function of 130 accumulation of temporally-segregated samples. In this approach, diversity increases not only 131 as a function of increasing temporal grain (time averaging) but also as a function of increasing 132 sample size. This effect leads to the positive slope of the STR even when the increase in 133 diversity is driven purely by sampling. Although the contribution of sampling to the STR 134 slope can be segregated from the ecological processes that induce temporal turnover in species composition (White et al. 2004, 2006), the STRs can be assessed on the basis of a 135 sample-size independent diversity, i.e., the Hill-transformed probability of interspecific 136 encounter (PIE). In Figure 1, we summarize the scaling of this measure as a function of 137 138 increasing time averaging in two distinct dispersal-limited metacommunity models. They 139 differ in the degree of niche equivalence and density-dependence but nevertheless generate 140 positive STRs by changing the shape of rank-abundance distributions as a consequence of 141 increasing time averaging. On the one hand, species have equal demographic rates on a per 142 capita basis in a neutral model, leading to steady-state diversity and an evolving 143 metacommunity species pool in drift-speciation equilibrium (following Hubbell 2001). On the 144 other hand, species differ in density-independent niche breadth (standard deviation of the Gaussian response equal to 0.1 and 0.5 relative to the gradient length of one) and the strength 145 146 of interspecific competitive interactions ( $\alpha_{ij} = 0.5$  or 0.95, relative to intraspecific  $\alpha_{ii}$  of 1) in 147 non-neutral models with constant metacommunity richness (following Thompson et al. 2020).

148 Figure 1 visualizes the model predictions under these scenarios (source scripts in R Core 149 Team (2021) in the Supplement). Namely, the increase in diversity is associated with the 150 decline in species dominance and the flattening of rank-abundance distributions (e.g., reducing its slope when fitted by the geometric, power-law or power-bend distributions), with 151 152 rank abundance distributions of non-averaged assemblages (1 year) being steeper than those of assemblages time-averaged to 1,000 years. The ADR<sub>F</sub> is predicted to mimic the species-153 154 time relationships because the total abundance is proportional to the product of standing 155 abundance and the inverse of lifespan, with abundance along the x-axis stretched or squeezed 156 depending on the lifespan of organisms.

157 The Hill-transformed diversity based on PIE should remain constant with increasing time averaging only when local assemblages represent random samples from a static 158 159 metacommunity pool (sampling model of Coleman, 1981) or from an evolving 160 metacommunity pool sampled over time spans that are shorter than the time scale of 161 metacommunity diversification (e.g., over 1,000 years when the mean time of species 162 originating in a metacommunity is 10,000 years, black lines in Figure 1A). This scenario is 163 captured by the neutral model and thus can occur when species extinctions due to ecological drift are in equilibrium with speciation (Hubbell 2001; McGill et al. 2005). The STR slope 164 165 will be positive in all other scenarios, determined by processes such as density dependence, dispersal limitation, or turnover related to habitat filtering (White et al. 2006; Carey et al. 166 167 2007; McGlinn and Palmer 2009; Raia et al. 2011). Once the scale of time averaging approaches the time scale of metacommunity diversification, even randomly assembled 168 169 metacommunities will exhibit a positive ADR<sub>F</sub>. The estimates of diversity independent of 170 sample size (such as the diversity based on PIE) or standardized to the same sampling 171 completeness (Alroy 2010, Chao et al. 2020) will thus invariably increase with increasing 172 time averaging. This scaling effect does not necessarily increase the evenness measures that 173 have species richness in the denominator as the sensitivity of these indices to time averaging 174 depends on the ratio of higher-order diversity relative to species richness.

The theoretical predictions visualized in Figure 1 and in the path diagrams in Figure 2 provide a framework for interpreting the empirical ADR<sub>F</sub>. The ADR can be measured in the logarithmic space as a regression coefficient specifying the effect of logged abundance on logged diversity or as a Pearson correlation coefficient between these variables (empirical species-time relations tend to be power law-like, White et al. 2006). The effects of increasing

180 time averaging that pulls the ADR<sub>F</sub> towards positive values can be visualized in cartoons 181 depicting the abundance-diversity space and path diagrams in Figure 2. These cartoons assume that assemblages are subjected to random time averaging that varies by four orders of 182 magnitude, that the scaling exponent for the Hill-transformed PIE-based diversity is 0.1, and 183 that the individual lifespan is one year. The abundance and diversity will be positively related 184 in fossil assemblages varying in time averaging if abundance is unrelated to diversity in living 185 186 assemblages (Figure 2B). However, when standing abundance and diversity exhibit a 187 nonrandom relationship in living assemblages (Chase and Leibold 2002; Storch et al. 2018), 188 the resulting  $ADR_F$  is a combination of (1) ecological processes driving the  $ADR_L$  (e.g., 189 energy or resource availability affecting both variables at yearly or generational scales) and 190 (2) STR scaling effects (Figure 2B-D). Conditioning the  $ADR_F$  on the gradient in energy availability that forces the positive or negative ADR<sub>L</sub> will lead to the positive ADR<sub>F</sub> if the 191 192 scaling STR effects contribute to variability in diversity (Figure 2F-H). Therefore, the positive 193 ADR<sub>F</sub>, either unconditional or conditioned on the energy availability gradient, can be a 194 criterion for detecting variability in diversity induced by variability in time averaging in the 195 fossil record. However, the effect of temporal scaling can be confirmed by conditioning the 196 ADR<sub>F</sub> on sediment accumulation: if this conditioning leads to the independency between 197 fossil abundance and diversity, the variability in diversity is likely truly triggered by variability in time averaging (Figure 2J-L). Finally, conditioning the ADR<sub>F</sub> on sediment 198 199 accumulation only can be used to infer the original ADR<sub>L</sub> as determined by ecological 200 processes unrelated to temporal scaling.

201

#### 202 MATERIAL AND METHODS

203 Study system – macrofaunal assemblages in the Adriatic Sea. The northern Adriatic Sea is 204 one of the few regions where both living assemblages and age-dated, volume-standardized 205 fossil assemblages were extensively sampled at the scale of the whole basin. We compiled 206 information on the total standing abundance and diversity of living molluscan communities from published surveys performed in the late 20<sup>th</sup> and early 21<sup>st</sup> century at water depths 207 208 between intertidal and 70 m (Figure S1). This dataset includes 1,150 living assemblage samples represented by Van Veen grabs (0.1 m<sup>2</sup>) or sediments from 1 m<sup>2</sup> quadrats collected 209 210 by scuba divers (Table S1). Data on 489 molluscan fossil samples were compiled from 26 211 sediment cores collected in the northern Adriatic Sea and Po coastal plain and documented in 212 our former studies (Table S2). Eleven 1-1.5 m-long piston and gravity cores were collected at 213 12-44 m water depth (Gallmetzer et al. 2016). These cores were split into 4-5 cm-thick 214 increments; assemblages from all increments were surveyed. Fifteen cores (> 10 m-long) 215 from the Po coastal plain were split into 5 and 10-cm increments sampled either at 1-3 m 216 intervals or more densely in the case of frequent facies shifts. Age data for 26 cores were 217 compiled from the original reports (at least 6 dated levels per core or at least 2 dated levels 218 per systems tract, Figures S2-S3) and analyzed with Bayesian age-depth models (Blaauw and 219 Christen 2011) to compute variability in estimates of sediment accumulation rate (cm/y) (see 220 Supporting Information, Figure S4-S5).

221

Living and fossil macrofaunal assemblages. In all compiled studies, samples of living and 222 223 fossil molluscan assemblages were all sieved with a 1 mm mesh size. The abundance of living molluscan individuals was standardized to 1 m<sup>2</sup>. The fossil abundance was estimated as the 224 225 total number of all identifiable molluscan specimens based on exhaustive counting of all 226 specimens in each increment, or by extrapolating to the total increment volume from sample 227 splits, and splits standardized to the number of specimens per 1 dm<sup>3</sup> of sediment. Species diversity was estimated as the Hill-transformed PIE (Hsieh et al. 2016). The minimum raw 228 229 (unstandardized) sample size is 10 individuals and the median sample size is 139 individuals.

230 Water depth was measured for living assemblages during sampling and indirectly 231 estimated for fossil assemblages based on a compositional gradient in non-metric 232 multidimensional scaling (NMDS). The first axis of NMDS based on the Chord distances and the proportional abundances of molluscan species orders the Holocene fossil assemblages 233 234 along a bathymetric gradient (Figure S6-S7), as documented in former studies (e.g., Wittmer 235 et al. 2014). To visualize differences in total abundance and diversity between living and 236 fossil assemblages, we partition living assemblages (shallower and deeper than 10 m) and 237 fossil assemblages (two main groups detected by a cluster analysis based on the same 238 abundance data, Figure S8) into two equivalent, onshore (sandy intertidal and fluvially-239 influenced nearshore) and offshore (muddy offshore transition and distal prodelta) segments. 240

Abundance-diversity relationship in macrofaunal assemblages. We estimate regression
 coefficients specifying the effect of abundance on diversity using the linear mixed-effect

models (all variables normalized to z-scores). The effect of fossil abundance on fossil 243 244 diversity (ADR<sub>F</sub>) will vary not only as a function of time averaging but also as a function of 245 ecological variables (such as energy or resource availability) that jointly affect standing abundance and diversity of living assemblages (ADR<sub>L</sub>, Figure 2B-D). We use water depth as 246 247 such a variable as it affects the diversity and standing abundance of benthic invertebrates 248 (Tumbiolo and Downing 1994; Cusson and Bourget 2005). Water depth can also covary with 249 sediment accumulation and thus can confound the effects of sediment accumulation on fossil 250 diversity or abundance. The effect of water depth is thus partialled out in the assessment of 251 the two hypotheses postulating that sediment accumulation reduces diversity and abundance 252 of fossil assemblages. We then assess the corollaries that correspond to three levels of 253 conditioning (three rows in Figure 2): (1) ADR<sub>F</sub> is unconditionally positive, (2) ADR<sub>F</sub> is 254 positive when conditioned on an energy availability gradient; and (3) ADR<sub>F</sub> disappears when 255 the effect of sediment accumulation on ADR<sub>F</sub> is partialled out. The third level is equal to a 256 structural equation model that finds that the model that incorporates the effect of abundance 257 on diversity is not better than the model where the covariance between abundance and 258 diversity is set to zero.

259 To estimate the effect of abundance on diversity, we use the linear mixed-effect 260 models that account for heterogeneity among cores (with random intercepts and slopes) and within-core temporal autocorrelations (with a covariate represented by a stratigraphic depth 261 262 and the within-core correlation structure modelled by the autoregressive process of order 1, using the nlme package, Pinheiro et al. 2023). The variation in sediment accumulation, 263 264 abundance, and diversity is markedly smaller within cores than among cores (Figure S9), and 265 the majority of cores in offshore environments were deposited under slow net sediment 266 accumulation. Therefore, the fixed effects covary with random effects, violating the 267 assumption of the mixed-effect models. We thus partitioned the fixed effects into within and 268 between-core effects of abundance and sediment accumulation on diversity in these models (van de Pol and Wright 2009). Although this approach increases the number of parameters, 269 270 the between-core effect of abundance on diversity can be expected to mirror the scaling effect when time averaging varies primarily among cores. Finally, we use generalized additive 271 272 models to visualize the shape of the dependency of abundance and diversity on water depth 273 and a two-line test to assess whether this dependency along the whole bathymetric gradient is 274 U-shaped (Simonsohn 2018). We transformed fossil abundance, diversity, and sediment 275 accumulation to natural logarithms as the empirically documented STRs tend to be

approximately linear in the logarithmic space (White et al. 2006) and such transformation alsoreduces the skewness of residuals.

278

Abundance-diversity relationship in microfaunal living and fossil assemblages. To assess 279 280 the ADR<sub>L</sub> and ADR<sub>F</sub> in another clade, we compiled from the literature (1) 30 surveys of 281 abundance and diversity in living benthic foraminifers (Table S3); and (2) 73 surveys of 282 abundance and diversity in fossil benthic foraminifers in Holocene-Pleistocene cores, using 283 the Biodeeptime database (Smith et al. 2023). We restricted the data to surveys with at least 284 10 samples with volume- or mass-standardized counts per geographic region or per time 285 series (Table S4). We quantified the ADR<sub>L</sub> in 30 regions and the ADR<sub>F</sub> at the scale of (1)individual cores (73 series) and (2) at the scale of larger regions that consist of at least two 286 287 cores (25 series). As the ADR<sub>L</sub> is based on modern spatial surveys whereas the ADR<sub>F</sub> is 288 assessed on the basis of spatio-temporal stratigraphic record, we use a simple Pearson 289 correlation to compare the ADR<sub>L</sub> and ADR<sub>F</sub> of microfaunal assemblages (generalized least-290 squares accounting for temporal autocorrelation led to similar results). All data are available 291 at https://doi.org/10.5061/dryad.fttdz0903 and R language scripts at

292 <u>https://doi.org/10.5281/zenodo.11664933</u>.

293

#### 294 **RESULTS**

295 Effects of sediment accumulation on macrofaunal abundance and diversity. Sediment 296 accumulation in the northern Adriatic Sea declines from  $\sim 10$  cm/y in onshore deltaic 297 environments to only  $\sim 0.001$  cm/y at offshore locations. As predicted, fossil abundance is 298 affected negatively by sediment accumulation when water depth (energy availability) is 299 partialled out in mixed-effect models ( $\beta = -0.18$ , p < 0.0001, Figure 3A, Table 1). Similarly, 300 fossil diversity is negatively affected by sediment accumulation in mixed-effect models ( $\beta = -$ 301 0.18, p < 0.0001, Figure 3D). Although molluscan abundance declines with water depth in living assemblages ( $\beta$  = -0.47, p < 0.0001, Figure 3B), fossil abundance is invariant to water 302 depth ( $\beta = 0.02$ , p = 0.37, Figure 3C). The PIE-based diversity increases with water depth in 303 304 both living ( $\beta = 0.3$ , p < 0.0001, Figure 3E) and fossil assemblages ( $\beta = 0.33$ , p = <0.0001, 305 Figure 3F).

*Macrofaunal abundance-diversity relation.* The ADR<sub>L</sub> is negative ( $\beta = -1.17$ , p < 0.0001, 307 308  $\beta_{depth} = -0.7$ , p < 0.0001, Figure 4A). In contrast, the unconditional ADR<sub>F</sub> is generally positive  $(\beta = 0.72, p = 0.03)$  but rather complex, U-or V-shaped (two-line test with a breakpoint at 309 diversity = 1.9 separates a negative segment from a positive segment, with p < 0.05). The two 310 311 maxima in fossil abundance correspond to (1) almost monospecific assemblages in onshore 312 environments and (2) diverse assemblages in offshore environments (Figure 4B). The linear 313 mixed-effect model shows that the between-core effect of abundance on diversity is positive 314 when conditioned on water depth ( $\beta_{depth} = 0.73$ , p < 0.0001, Figure 4C) whereas the within-315 core abundance effect on diversity is negative ( $\beta_{depth} = -0.023$ , p = 0.029). This contrast 316 between among-core and within-core abundance effects on diversity is striking when analyses 317 are limited to offshore environments ( $\beta_{between} = 0.33$ , p < 0.001,  $\beta_{within} = -0.11$ , p = 0.001, Figure 4D). The unconditional ADR<sub>F</sub> is thus a composite of two patterns: the fossil diversity 318 does not systematically change with abundance in onshore environments ( $\beta = 0.61$ , p = 0.66, 319 320 light gray points in Figure 5A), whereas it increases with abundance in offshore environments  $(\beta = 0.99, p < 0.0001, \text{ light gray points in Figure 5B})$ , ascending in parallel with increasing 321 322 time averaging (contours in Figure 5B).

323

324 Macrofaunal abundance-diversity relation conditioned by sediment accumulation. The positive effect of between-core abundance on diversity in mixed-effect models disappears 325 when conditioned on sediment accumulation ( $\beta = 0.11$ , p = 0.77,  $\beta_{depth} = 0.15$ , p = 0.4). The 326 within-core abundance has weak negative effects on diversity ( $\beta$ =-0.025, p = 0.08,  $\beta_{depth}$  = -327 328 0.03, p = 0.029, Table 1). Given that the effect of abundance on diversity is not positive and 329 that the AIC of the full model that includes the effect of fossil abundance on fossil diversity 330 (AIC = -3244.6) is only 1.9 units smaller than the AIC of the model that does not incorporate this effect (AIC = -3242.7), the positive relation between the abundance and diversity of fossil 331 332 assemblages is accounted for by the confounding effect of sediment accumulation (Table 1).

334 *Microfaunal abundance-diversity relation.* ADR<sub>L</sub> does not show any preference for positive 335 values (median r = -0.18), with six datasets exhibiting a significantly negative ADR<sub>L</sub> and two

- datasets (7%) exhibiting a significantly positive ADR<sub>L</sub> (Figure 6, Table S3). 30% of 73
- 337 Holocene-Pleistocene cores exhibit a significantly positive (unconditional) ADR<sub>F</sub> (median r
- 338 =0.08, Figure 6, Table S4). This estimate also incorporates environments with low variability

in sediment accumulation where the positive ADR<sub>F</sub> is not expected to develop, and thus the 339 340 danger of misattributing the observed diversity fluctuations to ecological processes rather than 341 to the scaling effects is low. When the analyses are restricted to the cores with high variability in time averaging and abundance, 12 cores exhibit significantly positive ADR<sub>F</sub>, 11 cores show 342 343 insignificant ADR<sub>F</sub>, and one core shows significantly negative ADR<sub>F</sub>, thus increasing the percentage of significantly positive ADR<sub>F</sub> to 50% (Figure S10). Expanding the spatial scale of 344 345 microfossil datasets to those with more than one core reduces the number of all datasets to 16 346 (median r = 0.16), among which 50% show a significantly positive ADR<sub>F</sub> (Figure S11).

347

## 348 **DISCUSSION**

# 349 Slow sediment accumulation (high time averaging) enhances fossil abundance and

350 *diversity.* Our results are consistent with the two predictions positing that both abundance and diversity decline with increasing sediment accumulation. Therefore, first, time-averaged fossil 351 352 abundance is primarily controlled by the lack of dilution by non-skeletal sediment rather than 353 by ecological forcing of standing abundance of living assemblages at yearly (or generational) 354 scales covarying with slow sediment accumulation. This conclusion is supported (1) by the 355 highest abundance of living molluscan assemblages in the Adriatic Sea occurring in the 356 onshore environments subjected to high sediment accumulation, (2) by the total abundance of 357 fossil assemblages exceeding that of living assemblages not affected by time averaging by two orders of magnitude, and by (3) linear mixed-effect models that indicate that the negative 358 effects of sediment accumulation on fossil abundance are not confounded by other factors. 359 Second, the decline in sediment accumulation increases the diversity of fossil assemblages in 360 361 accordance with the STR. This effect is primarily observed in offshore environments with 362 variable sediment accumulation where fossil diversity exceeds the standing living diversity by a factor of  $\sim 2-3$ . 363

364

365 *Positive ADR<sub>F</sub> as a signature of temporal scaling.* As sediment accumulation reduces both 366 abundance and diversity, and the positive  $ADR_F$  disappears when conditioned on sediment 367 accumulation, the variability in abundance and diversity of fossil assemblages is uniquely 368 driven by variability in time averaging. The negative  $ADR_L$  also indicates that the  $ADR_F$  that 369 is unconditionally positive or positive when conditioned on the energy availability is simply a 370 consequence of variable sediment accumulation that plays a major role in modulating the 371 abundance and diversity of fossil assemblages. The effects of STR on the diversity patterns 372 resulting from variable time averaging of paleontological samples are significant, especially 373 in offshore environments (i.e., deeper than 10 m), and thus cannot be neglected in diversity 374 analyses. When cores systematically differ in sediment accumulation (and thus in time averaging) but within-core variability in sediment accumulation remains relatively low as in 375 376 this study, the mixed-effect models effectively separate the scaling effects of time averaging 377 on the among-site diversity patterns from the ecological effects of abundance on diversity 378 unrelated to temporal scaling.

379

**Regional** ADR<sub>F</sub> shaped by onshore-offshore gradients in time averaging. When standing 380 abundances and diversities of communities are negatively related as in our molluscan dataset 381 382 and time averaging differs between onshore and offshore environments (Figure 5A-B), 383 regional-scale ADR<sub>F</sub> patterns can be complex. In two scenarios in Figure 5C, the initial, 384 regional-scale  $ADR_L$  is negative in non-averaged assemblages, as observed along the 385 bathymetric gradient in the Adriatic Sea. In the first scenario, assemblages in four 386 environments are equally time-averaged and thus the regional-scale  $ADR_F$  can remain 387 negative due to the absence of variability in temporal scaling (i.e., dashed light-gray arrows in in Figure 5C). Such ADR<sub>F</sub> can be diagnostic of conditions when the weakly time-averaged 388 389 fossil record deposited in eutrophic or oxygen-deficient environments exhibit individual-rich 390 but species-poor fossil assemblages dominated by opportunistic species (Filipsson and 391 Nordberg 2004; Tsujimoto et al. 2008). In the second scenario, fossil assemblages in offshore environments, initially with the smallest abundance, are time-averaged to 2000 years, whereas 392 393 assemblages in onshore environments are time-averaged to two years only, leading to the 394 positive ADR<sub>F</sub> (a dashed dark-gray arrow in Figure 5C). The negative ADR<sub>L</sub> can thus be 395 reverted into the positive ADR<sub>F</sub> when the most productive assemblages are the least time-396 averaged, as observed in our Adriatic data. This indicates that the positive ADR<sub>F</sub> is also 397 determined by the tendency of individual-rich but species-poor assemblages dominated by 398 opportunistic species to occur in environments least prone to time averaging. Despite this 399 additional complexity, the positive ADR<sub>F</sub> is still diagnostic of diversity variability controlled 400 by the temporal scaling effect.

402 Using ADR to extract ecological signals from fossil assemblages. Even in the absence of 403 variability in time averaging, abundance and diversity can be positively associated if they 404 share a common ecological cause such as the total energy availability, leading to both diverse and individual-rich assemblages (Hurlbert 2004; Pautasso et al. 2011; Edgar et al. 2017; 405 406 Thompson et al. 2020). Therefore, the positive ADR<sub>L</sub> can lead to a false positive result with 407 respect to the role of time averaging in modulating diversity. However, several lines of 408 evidence indicate that local-scale ADR<sub>L</sub> is typically not positive. First, our analyses of 409 molluscan and foraminiferal assemblages and previous studies (Bolam et al. 2002; Covich et 410 al. 2004; Reiss et al. 2010; Leduc et al. 2012; Schonberg et al. 2014; van der Plas 2019; Dee 411 et al. 2023; Maureaud et al. 2019; Clare et al. 2022) show that the ADR<sub>L</sub> at local scales is 412 either negative or close to zero (Figure 6). Second, the ADR<sub>F</sub> of molluscan assemblages 413 conditioned on sediment accumulation is not positive. Although both total abundance and 414 biomass are constrained by energy availability that can affect species diversity at local scales, 415 they are also linked by tradeoffs that can lead to a complex ADR (Kadmon and Benjamini 416 2006, Dornelas 2010). For example, marine benthic communities dominated by small-sized species with high abundance tend to be less diverse than communities dominated by larger but 417 less numerous species (Warwick 1986; Warwick and Clarke 1994). Moreover, species 418 diversity at local scales is not a simple function of local energy availability because species 419 420 extinction is modulated by population sizes at regional scales of species geographic ranges 421 (attaining few 100s of km or more in marine benthic species). The relationships between 422 diversity and total number of individuals thus tend to be positive only in studies with regional 423 and biogeographic sampling grains (Chase and Ryberg 2004; Storch and Okie 2019; Storch et 424 al. 2018 Craven et al. 2020). The total abundance at local scales is swamped by source-sink 425 factors and tradeoffs between abundances and biomass and thus local ADR<sub>L</sub> does not simply 426 scale down from biogeographic ADR<sub>L</sub>. The ADR<sub>F</sub> that is positive unconditionally or when 427 conditioned on energy availability is thus a useful tool for the detection of scenarios where 428 variability in diversity at local scales is determined by variability in time averaging. Our 429 analyses of macro- and microfossil records suggest that this scaling effect is a common, 430 taxon-independent feature of the fossil record (Fig. 5, Table S4) and thus needs to be 431 considered when assessing paleoecological data.

The effects of temporal scaling can be expected to contribute to fluctuations in local diversity at longer, million-year time scales not only owing to long-term changes in sediment accumulation but also owing to secular changes in mixing and disintegration (Kidwell and 435 Brenchley 1994). Time averaging documented in the Cenozoic marine fossil record can attain 436 more than 100 kyr (Zimmt et al. 2022), further magnifying the scaling effects because time averaging attaining the scales of species diversification will accelerate species richness 437 accumulation in the logarithmic STR space (Rosenzweig 1998). Although pooling 438 439 assemblages with variable time averaging into million-year (macroevolutionary) bins with 440 approximately equivalent temporal grain size can alleviate the scaling STR effect, the cost of 441 such a procedure is the loss of spatial and temporal resolution. The stratigraphic records of 442 fossil assemblages with well-resolved age models can use sediment accumulation as a 443 conditioning variable that (1) can remove the biasing effects of differential diversity scaling 444 caused by variable time averaging and (2) can be used in the mixed-effect models to separate 445 the scaling STR effect from the original ADR<sub>L</sub> driven by ecological covariance between total abundance and diversity unrelated to scaling. Conditioning ADR on sediment accumulation 446 447 can thus both identify and correct for the scaling effect induced by time averaging when 448 comparing fossil biodiversity across space and time.

449

# 450 Acknowledgements

- 451 We thank three reviewers for detailed and critical comments. This research was supported by
- 452 the Slovak Research and Development Agency (APVV17-0555, APVV22-0523), Slovak
- 453 Scientific Grant Agency (VEGA 02/0106/23), and by the Austrian Science Fund (FWF)
- 454 (grant number P24901).

455

#### 456 **References**

- 457 Aller, R.C., 1982. Carbonate dissolution in nearshore terrigenous muds: the role of physical
- 458 and biological reworking. *Journal of Geology*, 90, 79-95.
- 459 Alroy, J. 2010. The shifting balance of diversity among major marine animal
- 460 groups. Science, 329, 1191–1194.
- 461 Alroy, J., 2015. The shape of terrestrial abundance distributions. *Science Advances*, *1*,
  462 e1500082.
- 463 Bell, A., and Kelvyn J. 2015. Explaining Fixed Effects: Random Effects Modeling of Time-
- 464 Series Cross-Sectional and Panel Data. *Political Science Research and Methods* 3: 133–53.

- 465 Abbott, S.T., 1997. Mid-cycle condensed shellbeds from mid-Pleistocene cyclothems, New
- 466 Zealand: implications for sequence architecture. *Sedimentology*, *44*, 805-824.
- Adler, P.B. and Lauenroth, W.K., 2003. The power of time: spatiotemporal scaling of species
  diversity. *Ecology Letters*, *6*, 749-756.
- 469 Buma, B., Harvey, B.J., Gavin, D.G., Kelly, R., Loboda, T., McNeil, B.E., Marlon, J.R.,
- 470 Meddens, A.J.H., Morris, J.L., Raffa, K.F. and Shuman, B., 2019. The value of linking
- 471 paleoecological and neoecological perspectives to understand spatially-explicit ecosystem
- 472 resilience. *Landscape Ecology*, *34*, 17-33.
- 473 Balseiro, D. and Waisfeld, B.G., 2014. Evenness and diversity in Upper Cambrian–Lower
- 474 Ordovician trilobite communities from the Central Andean Basin (Cordillera Oriental,
- 475 Argentina). Palaeontology, 57, 531-546.
- 476 Benito, B.M., Gil-Romera, G. and Birks, H.J.B., 2020. Ecological memory at millennial time-
- 477 scales: the importance of data constraints, species longevity and niche features. *Ecography*,
  478 43, 1-10.
- 479 Blaauw, M. and Christen, J.A., 2011. Flexible paleoclimate age-depth models using an
- 480 autoregressive gamma process. *Bayesian Analysis* 6:457-474.
- 481 Bolam, S.G., Fernandes, T.F. and Huxham, M., 2002. Diversity, biomass, and ecosystem
- 482 processes in the marine benthos. *Ecological Monographs*, 72, 599-615.
- 483 Bush, A.M. and Bambach, R.K., 2004. Did alpha diversity increase during the Phanerozoic?
- 484 Lifting the veils of taphonomic, latitudinal, and environmental biases. *Journal of*
- 485 *Geology*, *112*, 625-642.
- 486 Carey, S., Ostling, A., Harte, J. and del Moral, R., 2007. Impact of curve construction and
  487 community dynamics on the species–time relationship. *Ecology*, *88*, 2145-2153.
- 488 46.
- 489 Carlucci, J.R. and Westrop, S.R., 2015. Trilobite biofacies and sequence stratigraphy: an
- 490 example from the Upper Ordovician of Oklahoma. *Lethaia*, 48, 309-325.
- 491 Castillo-Escrivà, A., Mesquita-Joanes, F. and Rueda, J., 2020. Effects of the temporal scale of
- 492 observation on the analysis of aquatic invertebrate metacommunities. *Frontiers in Ecology*
- 493 *and Evolution*, *8*, 561838.

- 494 Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K. and Ellison, A.M.,
- 495 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and
- 496 estimation in species diversity studies. *Ecological Monographs*, 84, 45-67.
- 497 Chao, A., Kubota, Y., Zelený, D., Chiu, C.H., Li, C.F., Kusumoto, B., Yasuhara, M., Thorn,
- 498 S., Wei, C.L., Costello, M.J. and Colwell, R.K., 2020. Quantifying sample completeness and
- 499 comparing diversities among assemblages. *Ecological Research*, *35*, 292-314.
- 500 Chase, J.M. and Leibold, M.A., 2002. Spatial scale dictates the productivity-biodiversity
- 501 relationship. *Nature*, *416*, 427-430.
- 502 Chase, J.M. and Ryberg, W.A., 2004. Connectivity, scale-dependence, and the productivity-
- 503 diversity relationship. *Ecology Letters*, 7, 676-683.
- 504 Chase, J.M., McGill, B.J., McGlinn, D.J., May, F., Blowes, S.A., Xiao, X., Knight, T.M.,
- 505 Purschke, O. and Gotelli, N.J., 2018. Embracing scale-dependence to achieve a deeper
- understanding of biodiversity and its change across communities. *Ecology Letters*, 21, 1737-1751.
- 508 Chase, J.M., McGill, B.J., Thompson, P.L., Antão, L.H., Bates, A.E., Blowes, S.A., Dornelas,
- 509 M., Gonzalez, A., Magurran, A.E., Supp, S.R. and Winter, M., 2019. Species richness change
- 510 across spatial scales. Oikos, 128, 1079-1091.
- 511 Clare, D.S., Culhane, F. and Robinson, L.A., 2022. Secondary production increases with
- 512 species richness but decreases with species evenness of benthic invertebrates. *Oikos*, e08629.
- 513 Coleman, B.D. 1981. On random placement and species-area relations. *Mathematical*
- 514 Biosciences, 54, 191-215.
- 515 Covich, A.P., Austen, M.C., Bärlocher, F., Chauvet, E., Cardinale, B.J., Biles, C.L., Inchausti,
- 516 P., Dangles, O., Solan, M., Gessner, M.O. and Statzner, B., 2004. The role of biodiversity in
- 517 the functioning of freshwater and marine benthic ecosystems. *BioScience*, 54, 767-775.
- 518 Craven, D., van der Sande, M.T., Meyer, C., Gerstner, K., Bennett, J.M., Giling, D.P., Hines,
- 519 J., Phillips, H.R., May, F., Bannar-Martin, K.H. and Chase, J.M., 2020. A cross-scale
- 520 assessment of productivity-diversity relationships. Global Ecology and Biogeography, 29,
- 521 1940-1955.

- 522 Cusson, M. and Bourget, E., 2005. Global patterns of macroinvertebrate production in marine
- 523 benthic habitats. *Marine Ecology Progress Series*, 297, 1-14.
- 524 Dee, L.E., Ferraro, P.J., Severen, C.N., Kimmel, K.A., Borer, E.T., Byrnes, J.E., Clark, A.T.,
- 525 Hautier, Y., Hector, A., Raynaud, X. and Reich, P.B., Wright A.J., Arnillas C.A., Davies K.F.,
- 526 MacDougall A., Mori A.S., Smith M.D., Adler P.B., Bakker J.D., Brauman K.A., Cowles J.,
- 527 Komatsu K., Knops J.M.H., McCulley R.L, Moore J.L., Morgan J.W., Ohlert T., Power S.A.,
- 528 Sullivan L.L., Stevens C., and Loreau M. 2023. Clarifying the effect of biodiversity on
- 529 productivity in natural ecosystems with longitudinal data and methods for causal
- 530 inference. *Nature Communications*, 14, 2607.
- 531 Dornelas, M., 2010. Disturbance and change in biodiversity. *Philosophical Transactions of*
- 532 *the Royal Society*, B365, 3719-3727.
- 533 Dornelas, M., Chase, J.M., Gotelli, N.J., Magurran, A.E., McGill, B.J., Antão, L.H., Blowes,
- 534 S.A., Daskalova, G.N., Leung, B., Martins, I.S. and Moyes, F., 2023. Looking back on
- 535 biodiversity change: lessons for the road ahead. Philosophical Transactions of the Royal
- 536 *Society B*, *378*, 20220199.
- 537 Edgar, G.J., Alexander, T.J., Lefcheck, J.S., Bates, A.E., Kininmonth, S.J., Thomson, R.J.,
- 538 Duffy, J.E., Costello, M.J. and Stuart-Smith, R.D., 2017. Abundance and local-scale processes
- 539 contribute to multi-phyla gradients in global marine diversity. *Science Advances*, *3*, e1700419.
- 540 Egenhoff, S., and Maletz, J. 2007. Graptolites as indicators of maximum flooding surfaces in
- 541 monotonous deep-water shelf successions. *Palaios*, 22, 373–383.
- 542 Filipsson, H.L. and Nordberg, K., 2004. A 200-year environmental record of a low-oxygen
- 543 fjord, Sweden, elucidated by benthic foraminifera, sediment characteristics and hydrographic
- 544 data. Journal of Foraminiferal Research, 34, 277-293.
- 545 Finnegan, S., Gehling, J.G. and Droser, M.L., 2019. Unusually variable paleocommunity
- 546 composition in the oldest metazoan fossil assemblages. *Paleobiology*, 45, 235-245.
- 547 Fridley, J.D., Peet, R.K., Van der Maarel, E. and Willems, J.H., 2006. Integration of local and
- 548 regional species-area relationships from space-time species accumulation. *American*
- 549 Naturalist, 168, 133-143.

- 550 Frignani, M. and Langone, L., 1991. Accumulation rates and<sup>137</sup>Cs distribution in sediments
- 551 off the Po River delta and the Emilia-Romagna coast (northwestern Adriatic Sea, Italy).
- 552 Continental Shelf Research, 11, 525-542.
- 553 Gallmetzer I., Haselmair A., Stachowitsch M. And Zuschin M. 2016. An innovative piston
- corer for large-volume sediment samples. Limnology and Oceanography: Methods 14:698–717.
- 556 Hsieh, T.C., Ma, K.H. and Chao, A., 2016. iNEXT: an R package for rarefaction and
- extrapolation of species diversity (H ill numbers). *Methods in Ecology and Evolution*, 7,
  1451-1456.
- 559 Hubbell, S.P., 2001. The unified neutral theory of biodiversity and biogeography. In *The*
- 560 Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press.
- 561 Hurlbert, S.H., 1971. The Nonconcept of Species Diversity: A Critique and Alternative
- 562 Parameters. Ecology 52:577-586.
- Hurlbert, A.H., 2004. Species–energy relationships and habitat complexity in bird
  communities. *Ecology Letters*, 7, 714-720.
- 565 Kadmon, R. and Benjamini, Y., 2006. Effects of productivity and disturbance on species
- 566 richness: a neutral model. American Naturalist, 167, 939-946.
- 567 Kidwell, S.M., 1986. Models for fossil concentrations: paleobiologic
- 568 implications. *Paleobiology* 12, 6-24.
- 569 Kidwell, S.M., 1989. Stratigraphic condensation of marine transgressive records: origin of
- 570 major shell deposits in the Miocene of Maryland. Journal of Geology, 97, 1-24.
- 571 Kidwell, S.M. and Brenchley, P.J., 1994. Patterns in bioclastic accumulation through the
- 572 Phanerozoic: changes in input or in destruction? *Geology*, 22, 1139-1143.
- 573 Kidwell, S.M., Best, M.M. and Kaufman, D.S., 2005. Taphonomic trade-offs in tropical
- 574 marine death assemblages: differential time averaging, shell loss, and probable bias in
- 575 siliciclastic vs. carbonate facies. *Geology*, *33*, 729-732.
- 576 Kidwell, S.M., 2013. Time-averaging and fidelity of modern death assemblages: building a
- 577 taphonomic foundation for conservation palaeobiology. *Palaeontology*, 56, 487-522.

- 578 Labra, F.A., Hernández-Miranda, E. and Quinones, R.A., 2015. Dynamic relationships
- 579 between body size, species richness, abundance, and energy use in a shallow marine
- 580 epibenthic faunal community. *Ecology and Evolution*, *5*, 391-408.
- 581 Leduc, D., Rowden, A.A., Bowden, D.A., Probert, P.K., Pilditch, C.A. and Nodder, S.D.,
- 582 2012. Unimodal relationship between biomass and species richness of deep-sea nematodes:
- 583 implications for the link between productivity and diversity. *Marine Ecology Progress*
- 584 Series, 454, 53-64.
- 585 Maureaud, A., Hodapp, D., Van Denderen, P.D., Hillebrand, H., Gislason, H., Spaanheden
- 586 Dencker, T., Beukhof, E. and Lindegren, M., 2019. Biodiversity–ecosystem functioning
- 587 relationships in fish communities: biomass is related to evenness and the environment, not to
- 588 species richness. *Proceedings of the Royal Society B*, 286, 20191189.
- 589 McGill, B.J., Hadly, E.A. and Maurer, B.A., 2005. Community inertia of Quaternary small
- mammal assemblages in North America. *Proceedings of the National Academy of Sciences*, *102*, 16701-16706.
- 592 McGlinn, D.J. and Palmer, M.W., 2009. Modeling the sampling effect in the species–time– 593 area relationship. *Ecology*, *90*, 836-846.
- 594 McGlinn, D.J., Engel, T., Blowes, S.A., Gotelli, N.J., Knight, T.M., McGill, B.J., Sanders,
- 595 N.J. and Chase, J.M., 2021. A multiscale framework for disentangling the roles of evenness,
- 596 density, and aggregation on diversity gradients. *Ecology*, *102*, e03233.
- 597 O'Sullivan, J.D., Terry, J.C.D. and Rossberg, A.G., 2021. Intrinsic ecological dynamics drive
- 598 biodiversity turnover in model metacommunities. *Nature Communications*, *12*, 3627.
- 599 Pandolfi, J.M., Staples, T.L. and Kiessling, W., 2020. Increased extinction in the emergence
- 600 of novel ecological communities. *Science*, *370*, 220-222.
- 601 Patrick, C.J., McCluney, K.E., Ruhi, A., Gregory, A., Sabo, J. and Thorp, J.H. 2021. Multi-
- scale biodiversity drives temporal variability in macrosystems. *Frontiers in Ecology and the*
- 603 Environment, 19, 47-56.
- 604 Pautasso, M., Böhning-Gaese, K., Clergeau, P., Cueto, V.R., Dinetti, M., Fernández-Juricic,
- 605 E., Kaisanlahti-Jokimäki, M.L., Jokimäki, J., McKinney, M.L., Sodhi, N.S. and Storch, D.,
- 606 2011. Global macroecology of bird assemblages in urbanized and semi-natural
- 607 ecosystems. *Global Ecology and Biogeography*, 20, 426-436.

- 608 Pinheiro J, Bates D, R Core Team (2023). nlme: Linear and Nonlinear Mixed Effects Models.
- 609 R package version 3.1-164, <u>https://CRAN.R-project.org/package=nlme</u>.
- 610 Powell, M.G. and Kowalewski, M. 2002. Increase in evenness and sampled alpha diversity
- 611 through the Phanerozoic: comparison of early Paleozoic and Cenozoic marine fossil
- 612 assemblages. *Geology*, *30*, 331-334.
- 613 Preston, F.W., 1960. Time and space and the variation of species. *Ecology*, 41, 612-627.
- 614 Reiss, H., Degraer, S., Duineveld, G.C., Kröncke, I., Aldridge, J., Craeymeersch, J.A.,
- 615 Eggleton, J.D., Hillewaert, H., Lavaleye, M.S., Moll, A. and Pohlmann, T., 2010. Spatial
- 616 patterns of infauna, epifauna, and demersal fish communities in the North Sea. ICES Journal
- 617 *of Marine Science*, 67, 278-293.
- 618 R Core Team (2021). R: A language and environment for statistical computing. R Foundation
- 619 for Statistical Computing, Vienna, Austria. URL <u>https://www.R-project.org/</u>.
- 620 Raia, P., Carotenuto, F., Meloro, C., Piras, P. and Barbera, C. 2011. Species accumulation
- over space and time in European Plio-Holocene mammals. *Evolutionary Ecology*, 25, 171-188.
- Rillo, M.C., Woolley, S. and Hillebrand, H., 2022. Drivers of global pre-industrial patterns of
- 624 species turnover in planktonic foraminifera. *Ecography*, 2022, e05892.
- 625 Ritter D.N.M., M., Erthal, F., Kosnik, M.A., Kowalewski, M., Coimbra, J.C., Caron, F. and
- 626 Kaufman, D.S., 2023. Onshore-offshore trends in the temporal resolution of molluscan death
- 627 assemblages: how age-frequency distributions reveal quaternary sea-level
- 628 history. Palaios, 38, 148-157.
- 629 Rosenzweig, M.L., 1998. Preston's ergodic conjecture: The accumulation of species in space
- 630 and time. In *Biodiversity dynamics*, 311-348. Columbia University Press.
- 631 Scarponi, D. and Kowalewski M. 2007. Sequence stratigraphic anatomy of diversity patterns:
- 632 Late Quaternary benthic mollusks of the Po Plain, Italy. *Palaios*, 22, 296-305.
- 633 Scarponi, D., Kaufman, D., Amorosi, A. and Kowalewski, M., 2013. Sequence stratigraphy
- and the resolution of the fossil record. *Geology*, *41*, 239-242.

- 635 Scheiner, S.M., Chiarucci, A., Fox, G.A., Helmus, M.R., McGlinn, D.J. and Willig, M.R.,
- 636 2011. The underpinnings of the relationship of species richness with space and
- 637 time. *Ecological Monographs*, 81, 195-213.
- 638 Schonberg, S.V., Clarke, J.T. and Dunton, K.H., 2014. Distribution, abundance, biomass and
- 639 diversity of benthic infauna in the Northeast Chukchi Sea, Alaska: Relation to environmental
- 640 variables and marine mammals. Deep Sea Research Part II: Topical Studies in
- 641 Oceanography, 102, 144-163.Simonsohn, U., 2018. Two lines: A valid alternative to the
- 642 invalid testing of U-shaped relationships with quadratic regressions. Advances in Methods and
- 643 Practices in Psychological Science, 1, 538-555.
- 644 Smith J., Rillo M.C., Kocsis Á.T., Dornelas M., Fastovich D., Huang H.H.M., Jonkers L.,
- 645 Kiessling W., Li Q., Liow L.H., Margulis-Ohnuma M., Meyers S., Na L., Penny A.,
- 646 Pippenger K., Renaudie J., Saupe E.E., Steinbauer M.J., Sugawara M., Tomašových A.,
- 647 Williams J.J., Yasuhara M., Finnegan S. and Hull P.M. 2023. BioDeepTime: A database of
- 648 biodiversity time series for modern and fossil assemblages. *Global Ecology and*
- 649 Biogeography, 32, 1680-1689.
- 650 Storch, D., Bohdalková, E. and Okie, J., 2018. The more-individuals hypothesis revisited: the
- 651 role of community abundance in species richness regulation and the productivity–diversity
- 652 relationship. *Ecology Letters*, 21, 920-937.
- Storch, D. and Okie, J.G., 2019. The carrying capacity for species richness. *Global Ecology and Biogeography*, 28, 1519-1532.
- 655 Šizling, A.L., Storch, D., Šizlingová, E., Reif, J. and Gaston, K.J., 2009. Species abundance
- distribution results from a spatial analogy of central limit theorem. *Proceedings of the National Academy of Sciences*, *106*, 6691-6695.
- 658 Thompson, P.L., Guzman, L.M., De Meester, L., Horváth, Z., Ptacnik, R., Vanschoenwinkel,
- B., Viana, D.S. and Chase, J.M., 2020. A process-based metacommunity framework linking
- 660 local and regional scale community ecology. *Ecology Letters 23*, 1314-1329.
- 661 Tomašových, A. and Kidwell, S.M., 2010a. The effects of temporal resolution on species
- turnover and on testing metacommunity models. *American Naturalist*, 175, 587-606.

- Tomašových, A. and Kidwell, S.M., 2010b. Predicting the effects of increasing temporal scale
  on species composition, diversity, and rank-abundance distributions. *Paleobiology*, *36*, 672665 695.
- 666 Tomašových, A., Kidwell, S.M. and Barber, R.F., 2016. Inferring skeletal production from
- time-averaged assemblages: skeletal loss pulls the timing of production pulses towards the
- 668 modern period. *Paleobiology*, 42, 54-76.
- 669 Tomašových, A., Kidwell, S.M. and Dai, R., 2023. A downcore increase in time averaging is
- 670 the null expectation from the transit of death assemblages through a mixed layer.
- 671 Paleobiology, 49, 527-562.
- 672 Tsujimoto, A., Yasuhara, M., Nomura, R., Yamazaki, H., Sampei, Y., Hirose, K. and
- 673 Yoshikawa, S., 2008. Development of modern benthic ecosystems in eutrophic coastal
- oceans: the foraminiferal record over the last 200 years, Osaka Bay, Japan. *Marine*
- 675 *Micropaleontology*, 69, 225-239.
- 676 Tumbiolo, M.L. and Downing, J.A., 1994. An empirical model for the prediction of secondary
- production in marine benthic invertebrate populations. *Marine Ecology Progress Series*, 114,
  165-174.
- van der Plas, F., 2019. Biodiversity and ecosystem functioning in naturally assembled
  communities. *Biological Reviews*, *94*, 1220-1245.
- van de Pol, M. and Wright, J., 2009. A simple method for distinguishing within-versus
- between-subject effects using mixed models. *Animal Behaviour*, 77, 753-758.
- Warwick, R., 1986. A new method for detecting pollution effects on marine macrobenthic
  communities. *Marine Biology*, *92*, 557-562.
- 685 Warwick, R.M. and Clarke, K.R., 1994. Relearning the ABC: taxonomic changes and
- abundance/biomass relationships in disturbed benthic communities. *Marine Biology*, *118*,
  739-744.
- 688 White, E.P., Adler, P.B., Lauenroth, W.K., Gill, R.A., Greenberg, D., Kaufman, D.M.,
- 689 Rassweiler, A., Rusak, J.A., Smith, M.D., Steinbeck, J.R., Waide, R.B. and Yao J. 2006. A
- 690 comparison of the species-time relationship across ecosystems and taxonomic
- 691 groups. Oikos, 112, 185-195.

- 692 Wittmer, J.M., Dexter, T.A., Scarponi, D., Amorosi, A. and Kowalewski, M., 2014.
- 693 Quantitative bathymetric models for late Quaternary transgressive-regressive cycles of the Po
- 694 Plain, Italy. Journal of Geology, 122, 649-670.
- 695 Zimmt, J.B., Kidwell, S.M., Lockwood, R. and Thirlwall, M., 2022. Strontium isotope
- 696 stratigraphy reveals 100 ky-scale condensation, beveling, and internal shingling of
- transgressive shell beds in the Maryland Miocene. *Palaios*, *37*, 553-573.

Abundance affected by water depth only	0.031	s.e.=0.021	p=0.14													-3589.4	9.7	4C, 4F
Abundance affected by sedim. accumulation only				-0.01	s.e.=0.010	p=0.324	-0.193	s.e.=0.046	p=<0.001							-3600.2	0	ЗA
Abundance affected by sedim. accumulation and water depth	0.018	s.e.=0.019	p=0.32	-00.09	s.e.=0.010	p=0.39	-0.186	s.e.=0.046	p=<0.001							-3599.1	1.05	4G
Diversity affected by sedim. accumulation only				-0.012	s.e.=0.016	p=0.462	-0.343	s.e.=0.081	p=<0.001							-3095	149.6	3D
Diversity affected by abundance only /unconditional ADR/										-0.019	s.e.=0.016	p=0.26	0.72	s.e.=0.31	p=0.028	-3094.2	150.4	4E
Diversity (sediment accumulation effect omitted)	0.333	s.e.=0.020	p=<0.001							-0.023	s.e.=0.012	p=0.029	0.73	s.e.=0.15	p=<0.001	-3234.4	12.1	4C, 4F
Diversity (abundance effect omitted)	0.32	s.e.=0.020	p=<0.001	0.003	s.e.=0.013	p=0.78	-0.276	s.e.=0.040	p=<0.001							-3242.7	1.9	4G
Diversity (saturated model)	0.323	s.e.=0.020	p=<0.001	0.002	s.e.=0.013	p=0.891	-0.242	s.e.=0.056	p=<0.001	-0.026	s.e.=0.012	p=0.029	0.15	s.e.=0.184	p=0.423	-3244.6	0	4G
Response Predictor	Water depth	(inverse of energy avail.)		Within-core sediment a ccumulation			Between-core sedi ment a ccumul ati on			Within-core abundance			Between-core abundance			AIC	ΔAIC	Figure

Table 1 – Summary statistics of linear mixed-effect models describing a relationship between
sediment accumulation, water depth (inverse of energy availability), fossil diversity and
abundance (visualized in figures specified on the bottom of the table). The coefficient (effect
size), its standard error and p-values are shown for each predictor. Sediment accumulation and
abundance are partitioned into within- and between-core components. The effect of betweencore abundance on diversity is unconditionally positive or positive when conditioned on the

- 706 water depth but becomes insignificant when conditioned also on between-core sediment
- 707 accumulation.



Neutral - speciation-drift equilibrium (speciation=0.0001yr<sup>1</sup>, metacommunity size=100,000 inds, dispersal = 0.1)

Low interspecific competition ( $\alpha_{\mu}$  = 1,  $\alpha_{\mu}$  = 0.25, dispersal = 0.1, metacommunity richness = 100, N patches = 25)



High interspecific competition ( $\alpha_{ii}$  = 1,  $\alpha_{ij}$  = 0.5, dispersal = 0.1, metacommunity richness = 100, N patches = 25)



709 Figure 1. The conceptual figures visualizing the dependency of species diversity on timespan of observation (species-time relationship) that flattens rank-abundance distributions and 710 711 ultimately leads to positive abundance-diversity relationship. The results are is based on outputs from two standard metacommunity models, including (A-B) neutral, spatially-implicit 712 713 metacommunity dynamics not limited (dashed gray) and limited by dispersal (solid black and 714 gray) and (C-F) non-neutral, spatially-explicit, dispersal-limited metacommunity dynamics 715 differing in species niche breadths ( $\sigma$ ) and in the strength of interspecific competition ( $\alpha_{ij}$ ). Diversity is defined based on Hill-transformed diversity of order 2, using Simpson diversity 716 717 (dotted) and PIE-based diversity (solid). The PIE-based diversity remains constant when the

neutral dynamic is not limited by dispersal (gray dashed line in A). In this scenario, no

- temporal scaling of diversity occurs because when the metacommunity pool is randomly
- sampled by the local community, the rank-abundance distribution does not change in shape
- with increasing time averaging. In all other scenarios, both neutral or non-neutral variants,
- any increase in the PIE-based diversity with increasing time averaging is associated with a
- decline in the species dominance and in the slope of the rank-abundance distribution as shown
- in the right column, where time averaging increases from 1 year (solid line) to 1000 years
- 725 (dashed line). Non-averaged and time-averaged rank abundance distributions in each scenario
- are rarefied to the same sample size (n = 300 individuals in neutral and 150 individuals in
- non-neutral models). The speciation timescale is 10,000 years and thus exceeds the maximum
- time averaging. If time averaging attains speciation timescale, diversity will exponentially
- 729 increase in logarithmic space. The construction of species-time relationship follows a moving
- 730 window approach of White et al. (2006). The simulations of neutral model are based on
- Hubbell (2001) and the simulations of non-neutral models follow Thompson et al. (2020),
- 732 with R scripts in the Supplement.





columns) and three levels of conditioning (with unconditional ADR<sub>F</sub> in B-D, ADR<sub>F</sub> 747 748 conditioned on energy availability in F-I, and ADR<sub>F</sub> conditioned on energy availability and 749 sediment accumulation in J-M). 25 fossil assemblages are subjected to random time averaging (sampled from a uniform distribution delimited by 3 and 3000 years) and zero disintegration, 750 the STR exponent is 0.1, and gray arrows correspond to the scaling expected under time 751 752 averaging. Time averaging pulls the ADR of fossil assemblages (gray circles) towards 753 positive values (upper row), although the sign of the unconditional ADR<sub>F</sub> depends on the 754 initial configuration of living assemblages (black circles). When the ADR<sub>L</sub> is ~0 (B), the 755 unconditional ADR<sub>F</sub> will be positive owing to the scaling effect. When the ADR<sub>L</sub> is negative 756 (C), the unconditional ADR<sub>F</sub> will be less negative, but the scaling effect is cancelled out by 757 the negative sign of the  $ADR_L$ . When the  $ADR_L$  is positive (D), the unconditional  $ADR_F$  will remain positive, regardless of the scaling effect. The positive effect of time averaging on 758 759 abundance and diversity emerges in all scenarios when the ADR<sub>F</sub> is conditioned on the 760 ecological variable (e.g., energy availability) that forces the negative or positive ADR<sub>L</sub> (F-H). 761 Such positive ADR<sub>F</sub> disappears when conditioned on the energy availability and sediment accumulation (J-L), providing a key insight into the contribution of time averaging to 762 763 variability in fossil abundance and diversity. The path diagrams corresponding to each row 764 are shown in the right column.



766

767 Figure 3. Sediment accumulation covaries negatively both with the abundance and diversity of fossil assemblages as predicted by the scaling effects of time averaging on both variables 768 769 (via the species-time relationship). Sediment accumulation affects negatively both abundance 770 (A) and PIE-based diversity (D) in fossil assemblages (time averaging on the top axis 771 corresponds to the inverse of sediment accumulation, neglecting the thickness of the mixed 772 layer). Abundance declines with water depth (B), whereas the PIE-based diversity increases 773 with water depth (E) in living (non-averaged) assemblages. Abundance does not covary with water depth (C), and the PIE-based diversity increases with water depth in time-averaged 774 775 fossil assemblages (F). Abundance~accumulation and diversity~accumulation relations in A

- and D are estimated with the linear mixed-effect models (Table 1). The bathymetric gradients
- in abundance and diversity in living and fossil assemblages in B-C and E-F are fitted with
- generalized additive models (with 95% confidence intervals). The insets with frequency
- distributions capture negative effects of the effects of sediment accumulation on abundance
- 780 (A) and diversity (D), based on the resampling of posterior estimates of sediment
- 781 accumulation from Bayesian age-depth models. Note: N/dm<sup>3</sup> number of individuals in fossil
- assemblages per sediment volume. Source data: Table S1-S2.



784

785 Figure 4. ADR is pulled towards the positive values as living assemblages are transformed 786 into fossil assemblages as predicted by the hypotheses postulating the effects of time 787 averaging (via sediment accumulation) on fossil abundance and diversity, and becomes 788 insignificant when conditioned on sediment accumulation. Raw (unconditional) ADR is 789 negative in living assemblages (A) and positive in fossil assemblages (B), and ADR<sub>F</sub> remains 790 positive when conditioned on the water depth (C-D). The black lines represent the fit by the 791 generalized least-square model (with spherical correlation structure) in the ADR<sub>L</sub> (A) and by 792 the linear mixed-effect model (cores as random effects and temporal autocorrelation modelled 793 by the autoregressive process of order 1) in the  $ADR_F(B)$ . The gray lines in B correspond to 794 the U-shaped fit to the ADR<sub>F</sub> by the generalized additive model. This ADR<sub>F</sub> pattern

795 represents a trace of the scaling pathway that pulled offshore assemblages (with low diversity 796 and low abundances) towards high fossil abundance and diversity. (C) Positive ADR<sub>F</sub> 797 conditioned on the water depth, with residuals of between-core abundance effect on the x axis 798 and diversity residuals on the y axis. (D) Focusing just on offshore assemblages allows for 799 plotting the actual abundances and diversities rather than their residuals. The linear mixed-800 effect model with random slopes and intercepts visualizes that within-core ADR<sub>F</sub> tends to be 801 negative whereas the between-core effect of abundance on diversity is markedly positive. (E-802 G) Path diagrams visualizing the positive relation between fossil abundance and diversity 803 (unconditional  $ADR_F$ , E), the  $ADR_F$  remains positive when conditioned on the water depth 804 (F), and the ADR<sub>F</sub> disappears when conditioned on the water depth and sediment 805 accumulation (G) on the basis of 489 fossil assemblages in the Adriatic Sea. The numbers in white boxes represent standardized regression coefficients from linear mixed-effect models 806 807 (with abundance and sediment accumulation effects corresponding to the between-core effects in Table 1), the dashed links reflect insignificant paths. The numbers in parentheses in G refer 808 809 to the model where the effect of abundance on diversity is set to zero. Source data: Table S1-810 S2.

811




814 Figure 5. Reconstructing the scaling pathway leading from the negative ADR<sub>L</sub> to the positive

- $ADR_F$  by embedding living and fossil assemblages in the same abundance-diversity space.
- 816 The small differences in abundance and diversity between living (black) and fossil

817 assemblages (gray) in onshore environments with high sediment accumulation (>0.1 cm/y) 818 and thus very low time averaging (A) contrast with the ladder-like progression of abundance and diversity in offshore environments (B), where sediment accumulation is lower than 0.1 819 cm/y and more variable, leading to the positive ADR<sub>F</sub>. The contours correspond to 820 approximate time averaging (in years) in 5 cm-increments (the inverse of sediment 821 822 accumulation in years/cm multiplied by 5), fitted by generalized additive models. The boxes 823 show mean abundance and diversity values with 95% bootstrapped confidence intervals. (C) 824 The abundance shift along the x-axis depends on the sediment accumulation, assuming no 825 disintegration and the diversity shift along the y-axis depends on the scaling slope of the 826 species-time relationship (here, STR exponent is equal to 0.15, and all molluscs are assumed 827 to have temporally-constant abundance and 1-year lifespan). The initial *local-scale*  $ADR_L$  is negative in non-averaged assemblages (four black circles, with poorly-diverse assemblages 828 829 with high abundance and highly-diverse assemblages with low abundance). The shift towards 830 the positive (regional-scale)  $ADR_F$  is magnified when species-rich but individual-poor 831 assemblages are more averaged (to 10 kyr) than species-poor and individual-rich 832 assemblages, as observed in the northern Adriatic Sea (black arrows with STR exponent = 833 0.1, with endpoints connected by the dashed black line). In the absence of variability in time averaging, the ADR<sub>F</sub> will remain negative (dashed gray lines). In A and B, as the volume of 834 fossil samples varies between  $\sim 0.8-1.3$  dm<sup>3</sup>, we standardize densities in living assemblages to 835  $N/dm^2$  in these order-of-magnitude analyses (Van Veen grabs used for sampling living 836 837 assemblages penetrate to sediment depths of 5-15 cm and are thus similar to the thickness of 838 core increments ranging between 4-10 cm). Source data: Table S1-S2.



843 Figure 6. The systematic difference in the sign of the ADR<sub>L</sub> and ADR<sub>F</sub> exhibited by benthic

844 for aminifers can reflect the effect of variable time averaging, with 29% of local FDRs and

845 50% of regional FDRs exhibiting significantly positive relation. The ADR<sub>L</sub> patterns estimated

846 on the basis of spatial surveys (n=30) are on average slightly negative. The ADR<sub>F</sub> patterns are

847 based on fossil assemblages observed in local stratigraphic series (n=73) and in regional

spatio-temporal datasets with at least two cores (n=25). Data sources: Table S3 and S4.

849	Supporting Information for
850	Abundance-diversity relationship as a unique signature of temporal scaling
851	
852 853	Adam Tomašových*, Michał Kowalewski, Rafał Nawrot, Daniele Scarponi, Martin Zuschin
854	*Corresponding author: Adam Tomašových
855	Email: geoltoma@savba.sk
856	
857	This PDF file includes:
858	
859	Supporting text
860	Figures S1 to S11
861	Tables S1 to S5
862	SI references
863	Data files and scripts:
864	https://datadryad.org/stash/share/dEfyOr0s3aBnuN3KMAloel-mi1eZ_EgfxyjlzzsXM
865	
866	
867 868	
869	
870	

#### 871 Supporting text

872

Sampling. The dataset with 1,150 living assemblages compiled from 27 studies (Figure S1, 873 Table S1) is restricted to assemblages with a minimum size of 10 individuals. In some cases, 874 875 it includes repeated bi-annual or annual sampling (such assemblages were not pooled to avoid 876 analytical time averaging). The assessment of the abundance-diversity relationship is based on 877 assemblages that were completely censused at the species level. Several surveys focused on 878 estimating the abundance of the most common species (Lentidium mediterraneum or 879 *Chamelea gallina*) in the shallowest habitats document extremely high population densities, exceeding 20,000-30,000 individuals/m<sup>2</sup>. Although they do not capture the sample total 880 881 abundance (i.e., all molluscan individuals), we use these densities as minimum estimates of 882 abundance in assessments of the depth-abundance relationship in Figure 3. Such incomplete 883 samples that lack data on abundances of other species were excluded from other analyses of 884 ADRs.

885 The 26 cores with 489 fossil assemblages span from siliciclastic deltaic settings with a 886 high sediment accumulation rate (in the NW Adriatic Sea and in the Gulf of Trieste) to 887 current-winnowed and sediment-starved, siliciclastic-carbonate settings with a low sediment 888 accumulation rate (in the NE segment). The cores archive the recentmost centuries at sites 889 with a high sediment accumulation rate (0.2-2 cm/y) or span ~9-10 kyr (corresponding to the 890 flooding of the northern Adriatic shelf) at sites with low sediment accumulation rates (<0.02 891 cm/y). These short cores were split into 4-5 cm-thick increments; assemblages from all 892 increments were surveyed. Fifteen cores (> 10 m-long) from the Po coastal plain (deposited at 893 ~ 1 cm/y during the highstand phase and at < 0.25 cm/y during the transgressive phase, 894 Scarponi et al. 2013) were split into 5 and 10 cm increments that were sampled either at 895 regular intervals separated by 1-3 m or more densely at intervals characterized by facies 896 shifts. 489 fossil assemblages cover delta front (n=105), barrier island (n=32), transgressive 897 sand sheet (n=68), prodelta (n=207), and offshore transition facies associations (n=78). Total 898 abundance refers to the total number of uniquely identifiable specimens (with umbo or hinge 899 preserved) and thus is not affected by differences in fragmentation among sites or increments. When sample sizes exceeded more than several thousands of individuals, increments were 900 901 split into fractions and the fraction-level count was multiplied by the fraction inverse to derive

- 902 the total abundance per total increment volume (e.g. if half of the sample was processed, the
- 903 total number of individuals was multiplied by two) (Gallmetzer et al. 2019).

Age models and sediment accumulation rates. Short and densely-sampled cores include 905 906 M13, M14, M20 and M21 in the proximal parts of the Po prodelta, POS514-GC-25-5 in the 907 distal parts of the Po prodelta, M28 and M29 in the Isonzo prodelta (Bay of Panzano), M38 in 908 the current-winnowed Gulf of Venice, M1 and M53 at Piran, and M44 at Brijuni. Fifteen (> 909 10 m-long) cores from the Po coastal plain include 240-S8, 205-S4, 205-S14, 205-S10, 205-S9, 205-S7, 204-S7, 205-S1, 205-S2, 256-S3, 205-S6, 204-EM-S5, 188-EM-S4, 187-EM-910 911 S12, and 187-C Goro. Sediment cores were sampled with two sampling strategies that partly 912 differ in core length, core diameter and density of increment sampling. Age models were 913 directly estimated for cores Po 3-M13, Po 4-M21, Panzano-M28, Piran-M53, and extrapolated 914 to spatially-proximate cores Po 3-M14, Po 4-M20, Panzano-M29, and Piran-M1 with highly – 915 similar lithological attributes and stratification patterns (Figure S3). In contrast to shorter 916 piston and gravity cores, age models at the coastal Po Plain are based on a smaller number of 917 age-dating levels (at least two dated levels per systems tract) (Figure S2). The core lithology 918 and fossil molluscan assemblages in these cores were described previously (Scarponi and 919 Kowalewski 2004, 2007; Kowalewski et al. 2015; Gallmetzer et al. 2017, 2019; Tomašových 920 et al. 2018; Berensmeier et al. 2023).

921The primary references for 26 cores are as follows: 240-S8 (Campo et al., 2020; Cheli922et al., 2021), 205-S4 (Scarponi et al. 2013; Amorosi et al., 2017; 2020; 2021), 205-S14

923 (Scarponi et al., 2013; Amorosi et al., 2017), 205-S10 (Sarti et al., 2009; Campo et al., 2020),

924 205-S9 (Sarti et al., 2009; Bruno et al., 2017; Amorosi et al., 2020), 205-S7 (Cibin et al.,

925 2005; Scarponi et al., 2013; Amorosi et al., 2017), 204-S7 (Calabrese et al., 2009; Amorosi et

926 al., 2017; Bruno et al., 2019), 205-S1 (Amorosi et al., 2003; Sarti et al., 2009), 205-S2

927 (Campo et al., 2020; Amorosi et al., 2021), 256-S3 (Severi et al., 2005; Campo et al., 2020),

928 205-S6 (Sarti et al., 2009; Amorosi et al., 2017, 2020), 204-EM-S5 (Amorosi et al., 2017),

929 204-EM-S4 (Amorosi et al., 2017), 188-EM-S5 (Amorosi et al., 2017), 187-EM-S12

930 (Amorosi et al., 2017), 187-C\_Goro\_I (Sarti et al., 2009), Po 3 M13, Po 3 M14, Po 4 M20, Po

4 M21 (Tomašových et al. 2018), Panzano M28 and M29 (Tomašových et al. 2017), Piran 1

932 M1 and Piran 2 M53 (Mautner et al. 2018, Tomašových et al. 2019), Venice M38 (Gallmetzer

et al. 2019), Brijuni M44 (Schnedl et al. 2018, Tomašových et al. 2022), and Poseidon core

POS514 – GC-25-5 (Berensmeier et al. 2023). The top-core age estimation of cores drilled at
the Po Plain, which was a swampy area until a few decades or centuries ago, is based either
on the year of final land reclamation of the area where the core was drilled (the cores 205-S1,
205-S2; 204 EM-S5, and 188 EM-S5 were drilled in areas that were reclaimed in 1964 AD,
the core 205-S6 was drilled in area reclaimed in 1919 AD, the core 205-S7 in area reclaimed
in 1933 AD, and the core 205-S10 in area reclaimed in 1958 AD) or on the basis of
information in geological maps and seismic profiles (Scarponi et al. 2013).

941 Bayesian age-depth models and sediment accumulation (cm/y) were estimated with 942 the Bacon function (rbacon package, Blaauw and Christen 2011, Blaauw et al. 2021) on the 943 basis of 1) single-shell radiocarbon estimates (with the mean age and age error represented by 944 standard deviation based on the radiocarbon calibration), 2) amino-acid and radiocarbon 945 estimates from multiple shells dated from the same core increment (with the mean of age 946 distribution and its standard error; the spread of within-increment ages directly reflects natural 947 time averaging of co-occurring shells as the measurement error is typically smaller than range 948 of ages induced by slow sedimentation and high mixing in these cores, Scarponi et al. 2013; 949 Tomašových et al. 2017, 2018, 2022), and 3) the timing of the boundary between the 950 highstand systems tract and the maximum flooding zone constrained on the basis of seismic 951 stratigraphy (~7,000 years BP, Amorosi et al. 2017). The calibration of amino acid and 952 radiocarbon ages and among-core correlations are presented in the references cited in the 953 previous paragraph, the input data for the Bacon function are listed in the Supplementary 954 Table 6. The parameter of the prior beta distribution for autocorrelation among sediment 955 accumulation rates within cores was set to a minimum dependency (mean=0.01) with shape = 956 100 (corresponding to a small variance in memory). The prior beta distribution for sediment 957 accumulation time (in years/cm) was set to the overall long-term sedimentation time (core 958 duration/core thickness) and the shape parameter of the beta distribution was set to 0.5 (when 959 core spanned several systems tracts) or 2 (when empirical age data do not indicate any major 960 change in sediment accumulation rate).

961 Sediment accumulation rates based on age models in these cores are moderate to high
962 (0.1-5 cm/y) in facies associations deposited in intertidal and upper shoreface environments.
963 They are more variable in lower shoreface to offshore environments, ranging from very low
964 (~0.001 cm/y) at locations affected by winnowing and sediment starvation to high (~5 cm/y)
965 at deltaic settings (Figure S4-S5). This bathymetric decline in sediment accumulation is in

accord with modern, decadal-scale estimates in deltaic settings and with the bathymetric
decline in sediment accumulation observed in the northern Adriatic Sea (Frignani and
Langone 1991).

969 The effect of sediment accumulation on abundance and diversity or conditional 970 independence between them may be assessed only when age models are based on a 971 sufficiently high number of dated intervals. When based on a few dated intervals, the 972 estimates of sediment accumulation rate will not resolve smaller-scale variability in 973 sedimentation (and thus in time averaging) when interpolating sediment accumulation rates to 974 undated levels. The estimates of sediment accumulation may be decoupled from time 975 averaging, thus potentially also not tracking the true variability in time averaging, but 976 Holocene fossil assemblages in the Adriatic Sea tend to show the close relation between 977 residence times of molluscan remains in 5-10 cm-thick increments predicted on the basis of 978 sediment accumulation and direct estimates of time averaging based on dating of at least ten 979 shells per increment (Scarponi and Kowalewski 2013, Tomašových et al. 2022).

All analyses are performed with R Core Team (2021), version 4.3.0, including the
following packages: nlme (Pinheiro et al. 2023), mgcv (Wood 2011, vegan (Oksanen et al.
2020), datawizard (Patil et al. 2020), AICcmodavg (Mazerolle et al. 2023), truncnorm
(Mesmann et al. 2018), iNEXT (Hsieh et al. 2016), piecewiseSEM (Lefcheck 2016),
synchrony (Gouhier T.C. and Guichard 2014), dplyr (Wickham 2016), ggplot2 (Wickham
2016), and rbacon (Blaauw and Christen 2011).

986

987 *The species-time relationship (STR).* The estimates of diversity that are independent of 988 sample size, such as the PIE-based diversity or rarefied species richness, will not increase with increasing time averaging when assemblages are randomly assembled (not limited by 989 990 dispersal) from metacommunities with temporally constant species-abundance distributions 991 (gray dashed line in Figures 1A). This scenario is also directly equivalent to the random 992 sampling model when an increase in species richness reflects increasing sampling from a 993 static species pool (Coleman 1981). Therefore, except in rare scenarios where the temporal 994 dynamic of assemblages is not limited by dispersal and local assemblages are random samples 995 from the metacommunity that follows a random-walk dynamic (drift-diversification, Hubbell 996 2001), diversity estimates based on sample size standardization do not correct for among-997 sample differences in time averaging. When the duration of the time series approaches the

time scale of species diversification, PIE-based diversity will increase with increasing timeaveraging even under a random metacommunity assembly.

1000 Once time averaging integrates across community assembly limited by dispersal or 1001 driven by non-neutral dynamic, different values of time averaging will produce misleading 1002 differences in diversity. We note that the scaling effect does not necessarily increase the 1003 evenness measures that have species richness in the denominator because the sensitivity of 1004 these indices to time averaging depends on the ratio of higher-order diversity relative to 1005 species richness. For example, in the absence of immigration from other regions and/or when 1006 turnover in species identity at the local scale is minor, species richness will increase with 1007 time, averaging less than the diversity of order two, thus also increasing evenness. When 1008 species richness increases with time averaging at a higher rate than the diversity of order two 1009 owing to significant turnover in species identity (as can happen in neutral models), evenness 1010 can decline with increasing time averaging.

1011

1012 Bathymetric gradients in diversity and abundance. We assess differences in abundance and 1013 diversity between living and fossil assemblages within habitats by partitioning living 1014 assemblages (shallower and deeper than 10 m) and fossil assemblages (defined by two main 1015 groups of samples in the cluster analyses that correspond to the assemblages dominated by 1016 Lentidium and Chamelea on the one hand and by species preferring offshore habitats on the 1017 other hand) into two equivalent depth segments differing not only in exposure to salinity 1018 fluctuations, in hydrodynamic conditions and grain size but also in community composition. 1019 The Bray-Curtis and Hellinger distances generate equivalent clusters and NMDS ordination 1020 patterns (Figure S6-S8). The shallower (onshore) assemblages are dominated by *Lentidium* 1021 and *Chamelea* (inhabiting nearshore environments), and the deeper (offshore) assemblages by 1022 Varicorbula, Turritellinella, Timoclea and Gouldia (thriving in offshore transition and 1023 offshore environments). This categorization allows us to assess whether the abundance and 1024 diversity of fossil assemblages exceed those of living assemblages, as predicted by the R-1025 sediment model (Kidwell 1986), and to approximate how the ADR<sub>F</sub> is shaped by time 1026 averaging while controlling for differences related to bathymetry. The analyses based on the 1027 relationship between the Hill-transformed sample size-corrected Shannon diversity (Chao et al. 2014), fossil abundance, and sediment accumulation generate almost identical results. In 1028

1029 our datasets, the PIE-based diversity also correlates strongly with Pielou's J in living ( $r = 1030 \quad 0.85$ , p<0.0001) and fossil assemblages (r = 0.91, p<0.0001).

1031 As the positive FADR patterns are predicted to be observed when fossil assemblages 1032 form under different sediment accumulation, we primarily focus on the regional-scale ADR 1033 (observed in assemblages collected in multiple sediment cores that capture larger bathymetric 1034 and geographic gradients or cover longer temporal extents than individual sediment cores) in 1035 our analyses of fossil assemblages in the northern Adriatic Sea, although we also report the 1036 local-scale ADR<sub>F</sub> (observed in individual sediment cores). The mean abundance of living 1037 assemblages declines from 4,730 at depths < 5 m to 853 at 10-20 m and to 243 at depths > 201038 m. Fossil assemblages preserved in offshore environments are on average equally rich in 1039 individuals as those from onshore environments, with mean abundance equal to 650-750 individuals/dm<sup>3</sup> on both sides of the ordination gradient. The mean PIE-based diversity 1040 1041 increases with depth both in living assemblages (r = 0.22, p < 0.0001) by a factor of ~2-3, 1042 from 3.1 at depths < 10 m to 3.2 at 10-20 m and 4.6 at depths > 20 m and in fossil 1043 assemblages (r = 0.68, p = <0.0001). The PIE-based diversity of fossil assemblages increases 1044 by a factor of ~3 when comparing onshore and offshore environments (from 2.7 in 1045 assemblages with negative scores to 8.4 in assemblages with positive scores), parallel with 1046 declining sediment accumulation. However, the diversity of fossil assemblages in offshore 1047 environments is variable, ranging from almost monospecific assemblages up to highly diverse 1048 assemblages with > 20 equally abundant species. The bathymetric decline in the dominance 1049 structure in fossil assemblages parallels the increase in evenness (r [Pielou's J] = 0.7, p < 1050 0.0001). The Hill-transformed Shannon diversity gives similar results as PIE-based diversity. 1051 The correlation between sediment accumulation and PIE-based diversity is negative when the 1052 effect of abundance is factored out. The diversity of individual-rich fossil assemblages (with 1053 more than 250 individuals/dm<sup>3</sup>) is bimodally-distributed, whereas the diversity of individual-1054 poor fossil assemblages (<250 individuals/dm<sup>3</sup>) is distributed uniformly or unimodally.

1055

1056 *Structural equation models.* In parallel with the linear mixed-effect models, we also use 1057 structural equation models (SEM, Schumacker and Lomax 2010) to assess whether a decline 1058 in sediment accumulation increases the abundance and diversity of fossil assemblages and at 1059 the same time accounts for the positive effects of abundance on diversity if conditioned by 1060 sediment accumulation. Although this simple approach does not incorporate temporal

1061 autocorrelation and heterogeneity among cores, the among-variable relationships directly 1062 parallel the setup of linear mixed-effect models. The saturated model (df=0) is compared with 1063 a reduced model without any unique effect of abundance on diversity on the basis of the 1064 Akaike information criterion and on the basis of the likelihood-ratio Chi-square statistic. The 1065 full model visualized in Figure 2B (AIC = 4182.9) explains 48% of the variation in fossil 1066 abundance by variability in sediment accumulation and water depth and 74% of the variation in diversity by variability in sediment accumulation, water depth, and fossil abundance. All 1067 1068 paths are significant at p < 0.05, except for the effect of depth on abundance (p = 0.2) and 1069 abundance on diversity (p = 0.18). 74% of the variation in diversity is also explained by 1070 variability in sediment accumulation and water depth in the model where the covariance 1071 between fossil abundance and fossil diversity is set to zero (AIC = 4183.2, likelihood-ratio 1072 test  $\chi^2 = 1.77$ , p=0.18). The unconditional positive covariance between the abundance and 1073 diversity of fossil assemblages is thus entirely accounted for by the effect of the sediment 1074 accumulation.

1075

1076 Abundance-diversity relation in molluscan fossil assemblages. The frequency and the 1077 strength of the ADR<sub>F</sub> in the stratigraphic record depends on the LADR (Figure 2A-C), on 1078 disintegration and mixing processes, on variability in time averaging, and on the magnitude of 1079 the slope of the STR, and is thus difficult to predict. The raw ADR<sub>F</sub> exhibiting the U-shaped 1080 pattern reflects the complex interaction between the negative ADR<sub>L</sub> and the time averaging 1081 effect pulling the abundance-diversity relation towards positive values (Figure 4B). When the 1082 ADR<sub>L</sub> is not random and rather negative, as in the northern Adriatic Sea, conditioning the 1083  $ADR_F$  on the main variable that covaries with the  $ADR_L$  (water depth) leads to a strongly 1084 positive relationship (Figure 4C-D). We note that in a scenario where the scaling exponent of 1085 the STR increases with depth but time averaging is equally high at all depths, offshore 1086 assemblages will be more diverse than onshore assemblages but not more rich in individuals. 1087 Therefore, the bathymetric shift in the STR slope alone, not associated with variability in time 1088 averaging, is not sufficient to generate the abundance-diversity relation.

In any case, the positive ADR<sub>F</sub> can primarily emerge when abundance and diversity patterns are assessed in stratigraphic successions deposited under variable sediment accumulation. ADR<sub>F</sub> patterns within individual cores in our Adriatic dataset are rarely significantly positive because most are characterized by a limited variability in sediment

1093 accumulation and fossil abundance. Simple Pearson correlations observed within individual 1094 cores are highly variable, ranging between -0.7 and 0.63 (with significantly positive value 1095 observed in one core only). 13 out of 20 cores exhibit a range of time averaging values among 1096 5-10 cm increments that are smaller than 50 years, approximated on the basis of the inverse of 1097 sediment accumulation. The strongly positive ADR<sub>F</sub> emerges in regional-scale analysis only 1098 when assemblages within cores are time-averaged to varying degrees. Similarly, although the 1099 microfossil records show the positive ADR<sub>F</sub> also at the scale of individual cores, the 1100 proportion of datasets with significantly positive ADR<sub>F</sub> patterns increases to 50% when 1101 assessed at regional scales spanning multiple cores.

1102

1103 Microfaunal records. Our criteria used in the selection of time series with fossil assemblages 1104 from the Marben subset of the Biodeeptime database include explicit information on volume-1105 or mass-standardized estimates of per-assemblage total abundance, complete species-level 1106 census abundance counts not excluding any rare species, at least ten samples with quantitative 1107 abundance data per time series, and the associated age model. We assessed the frequency of 1108 the significantly positive ADR<sub>F</sub> patterns at the scale of individual cores (73 datasets) and at 1109 the scale of larger regions that consist of at least two cores (25 datasets). These datasets span 1110 five orders of magnitude in duration, from 10 years to more than 100,000 years. However, we 1111 also assessed the frequency of cores with a significantly positive ADR<sub>F</sub> relative to the total 1112 number of cores in settings where the preconditions for a significantly positive ADR<sub>F</sub> are met. 1113 For this purpose, we exclude the cores with low variability in time averaging and abundance 1114 in a subset of analyses focused on individual sediment cores. We use these three criteria to 1115 select this subset of cores - coefficients of variation in time averaging and in fossil abundance 1116 across the cores exceed 0.25 (i.e., time averaging and fossil abundance vary by more than 1117 25% relative to the mean abundance) and mean sediment accumulation rates are not high 1118 (with mean sediment accumulation smaller than 0.2 cm/y). When computing the coefficient of 1119 variation in time averaging between all adjacent assemblages in each core or region, we use 1120 an inverse of the sediment accumulation as a proxy for time averaging (ignoring the depth of 1121 the mixed layer). The generalized least-square models that account for temporal 1122 autocorrelation (with the same structure as in the mixed-effect models) return a similar 1123 frequency of significantly positive ADR<sub>F</sub> patterns for individual time series.

1125 *Effects of disintegration and false negatives.* The increase in fossil abundance driven 1126 by the lack of dilution can be counteracted by the disintegration of skeletal remains. 1127 Disintegration can reduce the abundance of dead individuals accumulating in the surface 1128 mixed layer to below the standing abundance of their source living assemblage (Kidwell 1129 2002). Post-mortem age-frequency distributions indicate that the disintegration of molluscan 1130 remains occurs on decadal scales in the northern Adriatic Sea (Tomašových et al., 2022). 1131 Therefore, fossil abundances observed in this setting are expected to be smaller relative to 1132 scenarios where disintegration is slower or can be neglected. However, the fossil abundance in the core samples (mean =  $730 \text{ N/dm}^2$ , max =  $7,400 \text{ N/dm}^2$ ) exceeds the living abundance 1133 observed in benthic surveys (mean =  $6 \text{ N/dm}^2$ , max =  $122 \text{ N/dm}^2$ ) by more than two orders of 1134 1135 magnitude in offshore environments. Therefore, the effect of disintegration does not cancel 1136 out the negative relation between fossil abundance and sediment accumulation. In onshore environments, the mean fossil abundance (mean =  $650 \text{ N/dm}^2$ , max =  $21,000 \text{ N/dm}^2$ ) exceeds 1137 the mean living abundance (mean =  $50 \text{ N/dm}^2$ , max =  $1,370 \text{ N/dm}^2$ ) by a smaller factor than 1138 1139 in offshore environments, probably reflecting the effect of higher dilution of molluscan 1140 remains by clastic sediments.

1141 In general, the positive ADR<sub>F</sub> can be a conservative criterion of the temporal scaling 1142 effect owing to the potential for false negatives. Even when fossil remains disintegrate 1143 rapidly, stochastic mixing by burrowers can still allow some remains to be buried into the 1144 historical layers and thus will be incorporated into the stratigraphic record. This dynamic can 1145 lead to highly time-averaged but shell-poor assemblages (Tomašových et al. 2023), leading to 1146 no differences in fossil abundance between weakly-averaged assemblages with lower 1147 diversity and highly time-averaged assemblages with higher diversity. The scenario where 1148 time averaging does not covary with fossil abundance can thus generate false negative results 1149 concerning the role of time averaging even when diversity differences among fossil 1150 assemblages are triggered by differences in time averaging.

1151

1152 Role of anthropogenic impacts. Both abundance and diversity of living assemblages

1153 collected in the late 20th and in the 21st century can be negatively affected by anthropogenic

1154 impacts, thus magnifying the differences between non-averaged living assemblages and time-

1155 averaged fossil assemblages or artificially contributing to the positive ADR<sub>F</sub> (e.g., when some

1156 weakly time-averaged assemblages have low diversity because they were sourced by

- 1157 impacted communities over the past decades). First, excluding the Anthropocene samples
- 1158 (typically represented by assemblages sourced by communities in the 20th century and
- located in the upper 20 cm of sediment cores, exceptionally in the upper 90 cm at Po Delta)
- 1160 also generates a significantly positive  $ADR_F$  in the whole northern Adriatic Sea (r = 0.46, p <
- 1161 0.0001) and also within offshore environments (r = 0.71, p < 0.0001). Second, the disparity in
- abundance between fossil and living assemblages driven by time averaging can be biased up
- 1163 because abundances of some molluscan species and the overall molluscan production have
- 1164 been depressed over the last century owing to anthropogenic eutrophication, hypoxia,
- 1165 trawling, or pollution relative to the earlier Holocene conditions (Haselmair et al. 2021).
- 1166 However, the 20<sup>th</sup>-century decline in molluscan population densities is probably not sufficient
- 1167 to generate the order-of-magnitude increase in abundance in time-averaged fossil assemblages
- 1168 relative to their living counterparts.





1172 Figure S1. Geographic distribution of living molluscan assemblages analyzed in this study 1173 visualizes the negative relation between the standing abundance of molluscs and their 1174 diversity in the northern Adriatic Sea. A. Total molluscan abundance in living assemblages 1175 (individuals/m2) tends to decline with increasing water depth. B. The Hill-transformed PIE-1176 based diversity of living assemblages tends to increase with increasing water depth. Data 1177 sources for assemblages collected alive: Ambrogi and Ambrogi 1985, Ambrogi et al. 1995, 1178 ARPAE 2010-2019, Chiantore et al. 2001, ENEA database, Forni et al. 2005, Haselmair et al. 1179 2021, ISPRA 2012, Mavric et al. 2010, Moodley et al. 1998, Nasi et al. 2020, N'Siala et al. 2008, Occhipinti-Ambrogi et al. 2002, Orel et al. 1987, Poluzzi et al. 1981, Prevedelli et al. 1180 1181 2001, Rigotti 2019, Scardi et al. 2000, Seneš 1989, Simonini et al. 2005, Solis-Weiss et al. 1182 2001, Targusi 2011, Tomašových et al. 2019, Weber and Zuschin 2013, Zavodnik and 1183 Vidakovic 1987, Zucchi Stolfa 1979. 1184

- 1185
- 1186
- 1187
- 1188



Figure S2. Age models for the Po Plain cores. Age model sources: 240-S8 (Campo et al.,
2020; Cheli et al., 2021 [sample CE]), 205-S4 (Scarponi et al. 2013; Amorosi et al., 2017;
2020; 2021), 205-S14 (Scarponi et al., 2013; Amorosi et al., 2017), 205-S10 (Sarti et al.,

1193 2009; Campo et al., 2020), 205-S9 (Sarti et al., 2009; Bruno et al., 2017; Amorosi et al.,

1194 2020), 205-S7 (Cibin et al., 2005; Scarponi et al., 2013; Amorosi et al., 2017), 204-S7

1195 (Calabrese et al., 2009; Amorosi et al., 2017; Bruno et al., 2019), 205-S1 (Amorosi et al.,

- 1196 2003; Sarti et al., 2009), 205-S2 (Campo et al., 2020; Amorosi et al., 2021), 256-S3 (Severi et
- 1197 al., 2005; Campo et al., 2020), 205-S6 (Sarti et al., 2009; Amorosi et al., 2017, 2020), 204-
- 1198 EM-S5 (Amorosi et al., 2017), 204-EM-S4 (Amorosi et al., 2017), 188-EM-S5 (Amorosi et al., 2017), 188-EM-S5 (Amorosi et al., 2017), 204-EM-S4 (Amorosi et al., 2017), 204-E
- 1199 al., 2017), 187-EM-S12 (Amorosi et al., 2017), 187-C\_Goro\_I (Sarti et al., 2009).



1201 Figure S3. Age models for the 1.5 m-long cores, with boxplots representing frequency 1202 distributions of geochronological ages (i.e., postmortem ages) of molluscan remains based on amino acid racemization calibrated by <sup>14</sup>C. The age models are partly informed by age 1203 1204 distributions but also by additional sedimentological and geochronological data (210Pb and <sup>14</sup>C of plant remains). Sources for age distributions and age models: Po 3 M13 and Po 4 M21 1205 1206 (Tomašových et al. 2018), Panzano M28 (Tomašových et al. 2018), Piran 1 M1 and Piran 2 M53 (Mautner et al. 2018, Tomašových et al. 2019), Venice M38 (Gallmetzer et al. 2019), 1207 1208 Brijuni M44 (Schnedl et al. 2018, Tomašových et al. 2022), and Poseidon core POS514 -

1209 GC-25-5 (Berensmeier et al. 2023).



1212 Figure S4. The distribution of sediment accumulation rates with respect to assemblage age.

1213 Variability in sediment accumulation rates is given by the extent of error bars corresponding

1214 to the interquartile range bracketed by the  $25^{\text{th}}$  and  $75^{\text{th}}$  percentiles (based on the posterior

1215 distribution of sediment accumulation rates).



Figure S5. The frequency distributions of the fixed effects (effects of sedimentation on
abundance and diversity in the upper row and the effect of abundance on diversity
conditioned by sedimentation or by both sedimentation and water depth in the bottom row)
expected under the repeated sampling of sediment accumulation rates from posterior
distributions derived from Bayesian age-depth models. They show that the effects of sediment
accumulation are consistently negative and the abundance effect on diversity conditioned by
sediment accumulation does not differ from zero.





Figure S6. NMDS orders fossil molluscan assemblages along a bathymetric gradient, with onshore assemblages possessing negative NMDS axis 1 scores (black circles) and offshore transition and offshore assemblages possessing positive NMDS axis 1 scores (white circles). NMDS is based on proportional abundances and Chord distance. The categorization of assemblages into onshore and offshore groups follows the clusters in Figure S8. The sizes of gray circles are scaled according to the proportional abundances of individual species.

1235



Figure S7. Sensitivity of ordinations to the underlying dissimilarity metric. The first NMDS
axis is an indicator of water depth the ordering of assemblages is highly similar on the basis of
Bray-Curtis, Hellinger and Chord distances. Onshore assemblages are represented by black
circles and offshore assemblages by white circles. The categorization of assemblages into
these two groups follows the clusters in Figure S8.



Figure S8 – Cluster analysis based on average linking method and Chord distance, separating
two main groups of assemblages, corresponding to two main environments.



1248

Figure S9. Variability in abundance, in diversity, and especially in sediment accumulation is markedly smaller within cores than among cores. Although some subset of cores from the Po coastal plain archive depositional conditions varying in sediment accumulation, the majority of cores in offshore environments were consistently deposited under low sediment

1253 accumulation.





1256 Figure S10. Local-scale (single-core) abundance-diversity relation in a selection of 25

microfossil datasets with benthic foraminifers, with mean sediment accumulation < 0.2 cm/y, 1257

1258 coefficient variation in residence time > 0.25, coefficient variation in fossil abundance > 0.5,

1259 and gamma-level PIE-based diversity exceeding five species. 12 datasets show a significantly

1260 positive relation (black), one dataset shows a significantly negative relation (gray), and 12

1261 datasets show insignificant relation (white). Data sources: Table S4.



Figure S11. Regional-scale abundance-diversity relation in 16 microfossil datasets (at least
two sites per region) with benthic foraminifers. 8 datasets show a significantly positive
relation (black), six datasets show a significantly negative relation (gray), and two datasets

1266 show insignificant relation (white). Sources: Table S4.

### 1267 Supporting tables

- 1268 Table S1 Diversity and abundance of living (non-averaged) molluscan assemblages in the
- 1269 northern Adriatic Sea, with source references. Data columns correspond to the reference,
- 1270 dataset ID (optional), latitude, longitude and water depth (m) of the assemblage, raw sample
- 1271 size and total abundance/m<sup>2</sup>. Diversity indices correspond to the effective number of species
- 1272 based on the PIE-based and Simpson index, the effective number of species based on the
- 1273 Shannon index, and evenness values based on the Pielou J and Bulla O.
- 1274 Table S2 Diversity and abundance of fossil (time-averaged) molluscan assemblages
- 1275 collected in sediment cores in the northern Adriatic Sea. Individual fossil assemblages are in
- 1276 rows, data columns correspond to the core ID, sediment depth (cm), increment thickness (cm),
- 1277 systems tract (HST highstand systems tract, MFZ maximum flooding zone, TST -
- 1278 transgressive systems tract), facies association/environment, sediment accumulation (cm/y),
- 1279 sample size, fossil abundance/dm<sup>3</sup>, Shannon H, Gini-Simpson index, Probability of
- 1280 interspecific encounter, the effective number of species (Simpson and PIE), evenness values
- based on the Pielou J and Bulla O, and the location of the assemblages along the first NMDSaxis.
- **Table S3** Abundance-diversity relations in 30 geographic datasets with benthic foraminiferal
- 1284 living assemblages (LADR), with references.
- 1285 Table S4 Abundance-diversity relations in 73 benthic foraminiferal fossil assemblages
- 1286 (FADR) in local stratigraphic series and in regional datasets, with references.
- 1287 Table S5 Input chronological data for Bacon function.
- 1288

## 1289 Supporting scripts

- 1290 R language scripts for models and species-time relation
- 1291 R language scripts for cartoons and data analyses
- 1292

# 1293 Supporting references – methods, age data, molluscan fossil assemblages

- 1294 Amorosi, A., Centineo, M. C., Colalongo, M. L., Pasini, G., Sarti, G., and Vaiani, S.C. 2003.
- 1295 Facies architecture and latest Pleistocene–Holocene depositional history of the Po Delta

- 1296 (Comacchio area), Italy. Journal of Geology 111, 39-56.
- 1297 Amorosi, A., Bruno, L., Campo, B., Morelli, A., Rossi, V., Scarponi, D., Hong, W., Bohacs,
- 1298 K.M. and Drexler, T.M., 2017. Global sea-level control on local parasequence architecture
- 1299 from the Holocene record of the Po Plain, Italy. *Marine and Petroleum Geology* 87, 99-111.
- 1300 Amorosi, A., Bruno, L., Campo, B., Costagli, B., Dinelli, E., Hong, W., Sammartino, I. and
- 1301 Vaiani, S.C., 2020. Tracing clinothem geometry and sediment pathways in the prograding
- 1302 Holocene Po Delta system through integrated core stratigraphy. Basin Research 32, 206-215.
- 1303 Amorosi A., Bruno L., Campo B., Costagli B., Hong W., Picotti V., Vaiani S.C., 2021.
- 1304 Deformation patterns of upper Quaternary strata and their relation to active tectonics, Po
- 1305 Basin, Italy. Sedimentology 68, 402-424.
- 1306 Berensmeier, M., Tomašových, A., Nawrot, R., Cassin, D., Zonta, R., Koubová, I. and
- 1307 Zuschin, M., 2023. Stratigraphic expression of the human impacts in condensed deposits of
- 1308 the Northern Adriatic Sea. Geological Society, London, Special Publications 529, 195-222.
- 1309 Blaauw, M., Christen, J.A., Lopez, M.A.A., Vazquez, J.E., Belding, T., Theiler, J., Gough, B.,
- 1310 Karney, C., Rcpp, L. and Blaauw, M.M., 2021. Package 'rbacon'. Age-depth modelling using
- 1311 Bayesian statistics. Version: 3.1.1. https://CRAN.R-project.org/package=rbacon
- 1312 Blaauw, M. and Christen, J.A., 2011. Flexible paleoclimate age-depth models using an
- 1313 autoregressive gamma process. Bayesian Analysis 6:457-474.
- 1314 Bruno L., Bohacs K.M., Campo B., Drexler T.M., Rossi V., Sammartino I., Scarponi D.,
- 1315 Hong, W., and Amorosi A. 2017. Early Holocene transgressive palaeogeography in the Po
- 1316 coastal plain (northern Italy). Sedimentology 64, 1792 1816
- 1317 Bruno, L., Campo, B., Di Martino, A., Hong, W. and Amorosi, A. 2019. Peat layer
- 1318 accumulation and post-burial deformation during the mid-late Holocene in the Po coastal
- 1319 plain (Northern Italy). *Basin Research* 31, 621-639.
- 1320 Calabrese L., Centineo M.C., Cibin U., Di Cocco I., 2009. Note Illustrative della Carta
- 1321 Geologica alla scala 1:50.000: Portomaggiore. Servizio geologico sismico e dei suoli -
- 1322 Regione Emilia Romagna, 98 pp.
- 1323 Campo B., Bruno L., Amorosi A., 2020. Basin-scale stratigraphic correlation of late
- 1324 Pleistocene-Holocene (MIS 5e-MIS 1) strata across the rapidly subsiding Po Basin (northern

- 1325 Italy). Quaternary Science Reviews 237, 106300.
- 1326 Cheli A, Mancuso A, Azzarone M, Fermani S, Kaandorp J, Marin F, et al. 2021. Climate
- variation during the Holocene influenced the skeletal properties of Chamelea gallina shells inthe North Adriatic Sea (Italy). *PLoS ONE* 16, e0247590.
- 1329 Cibin U. et al., 2005 Note illustrative della Carta geologica d'Italia alla scala 1:50.00: Forlì-
- 1330 Cervia. Servizio geologico sismico e dei suoli Regione Emilia Romagna, 104 pp.
- 1331 Gallmetzer, I., Haselmair, A., Tomašových, A., Stachowitsch, M. and Zuschin, M., 2017.
- 1332 Responses of molluscan communities to centuries of human impact in the northern Adriatic
- 1333 Sea. Plos One 12, e0180820.
- 1334 Gallmetzer, I., Haselmair, A., Tomašových, A., Mautner, A.K., Schnedl, S.M., Cassin, D.,
- 1335 Zonta, R. and Zuschin, M., 2019. Tracing origin and collapse of Holocene benthic baseline
- 1336 communities in the northern Adriatic Sea. *Palaios* 34, 121-145.
- 1337 Gouhier T.C. and Guichard F. 2014. Synchrony: quantifying variability in space and
- 1338 time. Methods in Ecology and Evolution, 5, 524–533. R package version
- 1339 0.3.8, http://synchrony.r-forge.r-project.org.
- 1340 Haselmair, A., Gallmetzer, I., Tomašových, A., Wieser, A.M., Übelhör, A. and Zuschin, M.,
- 1341 2021. Basin-wide infaunalisation of benthic soft-bottom communities driven by
- 1342 anthropogenic habitat degradation in the northern Adriatic Sea. Marine Ecology Progress
- 1343 Series 671, 45-65.
- 1344 Hsieh, T.C., Ma, K.H. and Chao, A., 2016. iNEXT: an R package for rarefaction and
- extrapolation of species diversity (H ill numbers). *Methods in Ecology and Evolution*, 7,1451-1456.
- Hubbell, S.P., 2001. The unified neutral theory of biodiversity and biogeography. *Princeton: Princeton University Press.*
- 1349 Kidwell, S.M., 2002. Time-averaged molluscan death assemblages: palimpsests of richness,
- 1350 snapshots of abundance. *Geology*, *30*, 803-806.
- 1351 Lefcheck J.S. 2016. piecewiseSEM: Piecewise structural equation modeling in R for ecology,
- 1352 evolution, and systematics. *Methods in Ecology and Evolution*, **7**, 573-579.
- 1353 Mautner, A.K., Gallmetzer, I., Haselmair, A., Schnedl, S.M., Tomašových, A. and Zuschin,

- 1354 M., 2018. Holocene ecosystem shifts and human-induced loss of Arca and Ostrea shell beds
- 1355 in the north-eastern Adriatic Sea. *Marine Pollution Bulletin* 126, 19-30.
- 1356 Mazerolle M.J. 2023. AICcmodavg: Model selection and multimodel inference based on
- 1357 (Q)AIC(c). R package version 2.3.3, https://cran.r-project.org/package=AICcmodavg.
- 1358 Mersmann, O., Trautmann, H., Steuer, D., and Bornkamp, B. 2018. truncnorm: Truncated
- 1359 Normal Distribution. Package 'truncnorm'. *R package version* 1.0-9. R ( $\geq$  3.4.0),
- 1360 https://github.com/olafmersmann/truncnorm
- 1361 Oksanen J., Blanchet G.F., Friendly M., Kindt R., Legendre P., McGlinn D., Minchin P.R.,
- 1362 O'Hara B., Simpson G.L., Solymos P., Stevens M.H.H., Szoecs E. and Wagner H. 2020.
- 1363 vegan: Community Ecology Package. R package version 2.5-7. https://CRAN.R-
- 1364 project.org/package=vegan
- 1365 Patil I., Makowski D., Ben-Shachar M., Wiernik B., Bacher E., and Lüdecke D. 2022.
- 1366 datawizard: An R Package for Easy Data Preparation and Statistical Transformations. Journal
- 1367 of Open Source Software, 7, 4684. doi:10.21105/joss.04684.
- 1368 Pinheiro J., Bates D., R Core Team 2023. *nlme: Linear and Nonlinear Mixed Effects Models*.
- 1369 R package version 3.1-164, https://CRAN.R-project.org/package=nlme.
- 1370 Sarti G. et al., 2009 Note illustrative della Carta geologica d'Italia alla scala 1:50.00:
- 1371 Comacchio. Servizio geologico sismico e dei suoli Regione Emilia Romagna, 126 pp.
- 1372 Scarponi, D. and Kowalewski, M., 2004. Stratigraphic paleoecology: bathymetric signatures
- 1373 and sequence overprint of mollusk associations from upper Quaternary sequences of the Po
- 1374 Plain, Italy. *Geology*, *32*, 989-992.
- 1375 Scarponi, D. and Kowalewski M. 2007. Sequence stratigraphic anatomy of diversity patterns:
- 1376 Late Quaternary benthic mollusks of the Po Plain, Italy. *Palaios*, 22, 296-305.
- 1377 Scarponi, D., Kaufman, D., Amorosi, A. and Kowalewski, M., 2013. Sequence stratigraphy
- 1378 and the resolution of the fossil record. *Geology* 41, 239-242.
- 1379 Schnedl, S.M., Haselmair, A., Gallmetzer, I., Mautner, A.K., Tomašových, A. and Zuschin,
- 1380 M., 2018. Molluscan benthic communities at Brijuni Islands (northern Adriatic Sea) shaped
- 1381 by Holocene sea-level rise and recent human eutrophication and pollution. *Holocene* 28,
- 1382 1801-1817.

- 1383 Schumacker R.E., Lomax R.G. 2010. A beginner's guide to structural equation modelling.
- 1384 Routledge Taylor and Francis Group, 3<sup>rd</sup> Edition.
- 1385 Severi et al., 2005. Note illustrative della Carta geologica d'Italia alla scala 1:50.00: Rimini.
- 1386 Servizio geologico sismico e dei suoli Regione Emilia Romagna, 143 pp.
- 1387 Tomašových, A., Gallmetzer, I., Haselmair, A., Kaufman, D.S., Vidović, J. and Zuschin, M.,
- 1388 2017. Stratigraphic unmixing reveals repeated hypoxia events over the past 500 yr in the
- 1389 northern Adriatic Sea. *Geology* 45, 363-366.
- 1390 Tomašových, A., Gallmetzer, I., Haselmair, A., Kaufman, D.S., Kralj, M., Cassin, D., Zonta,

1391 R. and Zuschin, M., 2018. Tracing the effects of eutrophication on molluscan communities in

1392 sediment cores: outbreaks of an opportunistic species coincide with reduced bioturbation and

- 1393 high frequency of hypoxia in the Adriatic Sea. *Paleobiology* 44, 575-602.
- 1394 Tomašových, A., Gallmetzer, I., Haselmair, A., Kaufman, D.S., Mavrič, B. and Zuschin, M.,
- 1395 2019. A decline in molluscan carbonate production driven by the loss of vegetated habitats
- encoded in the Holocene sedimentary record of the Gulf of Trieste. *Sedimentology* 66, 781-807.
- 1398 Tomašových, A., Gallmetzer, I., Haselmair, A. and Zuschin, M., 2022. Inferring time
- averaging and hiatus durations in the stratigraphic record of high-frequency depositionalsequences. *Sedimentology* 69, 1083-1118.
- 1401 Wickham H. 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York.
- 1402 ISBN 978-3-319-24277-4, https://ggplot2.tidyverse.org.
- 1403 Wickham H., François R., Henry L., Müller K., and Vaughan D. 2023. dplyr: A Grammar of
- 1404 Data Manipulation. R package version 1.1.4,
- 1405 https://github.com/tidyverse/dplyr, https://dplyr.tidyverse.org.
- 1406 Wood S.N. 2011. Fast stable restricted maximum likelihood and marginal likelihood
- 1407 estimation of semiparametric generalized linear models. Journal of the Royal Statistical
- 1408 *Society B*, **73**, 3-36.
- 1409
- 1410 Supporting references living molluscan assemblages

- 1411 Ambrogi, R. and Ambrogi, A.O., 1985. The estimation of secondary production of the marine
- 1412 bivalve *Spisula subtruncata* (da Costa) in the area of the Po River delta. *Marine Ecology* 6,
- 1413 239-250.
- 1414 Ambrogi, R., Colangelo, M.A., Fontana, P., Gatto, M., Sei, S. and Tracanella, E., 1995. La
- 1415 demografia del bivalve *Lentidium mediterraneum* nella zona di mare antistante il delta del Po.
- 1416 Atti 6 congresso Società Italiana di Ecologia 16, 165-167.
- 1417 ARPAE 2010-2019. Valutazione dello stato delle acque marine costiere. Monitoraggio delle
- 1418 acque marino costiere e classificazione dello stato di qualità. Regione Agenzia Prevenzione
- 1419 Ambiente Energia Emilia-Romagna. https://www.arpae.it/it/temi-ambientali/mare/report-e-
- 1420 bollettini/stato-acque-marine
- 1421 https://www.arpae.it/it/temi-ambientali/mare/report-e-bollettini/stato-acque-marine
- 1422 Chiantore, M., Bedulli, D., Cattaneo-Vietti, R., Schiaparelli, S. and Albertelli, G., 2001.
- 1423 Long-term changes in the Mollusc-Echinoderm assemblages in the north and coastal middle
- 1424 Adriatic Sea. Atti della Associazione Italiana di Oceanologia e Limnologia, 14, 63-75.
- 1425 ENEA. Italian Mollusc Census Database of the Italian National Agency for New
- 1426 Technologies, Energy and Sustainable Economic Development.
- 1427 http://www.santateresa.enea.it/wwwste/malaco/home.htm.
- 1428 Forni, G. and Ambrogi, A.O., 2005. Struttura di popolazione del bivalve Lentidium
- 1429 *mediterraneum* e variazioni ambientali in Nord Adriatico. *Biologia Marina Mediterranea* 12,
- 1430 277-280.
- 1431 ISPRA (2012) Studio delle comunita' bentoniche. Monitoraggio del Terminale GNL area
- 1432 della condotta offshore Fase di esercizio provvisorio (2 E). Istituto Superiore per la
- 1433 Protezione e la Ricerca Ambientale.
- 1434 Mavrič, B., Orlando-Bonaca, M., Bettoso, N. and Lipej, L., 2010. Soft-bottom
- 1435 macrozoobenthos of the southern part of the Gulf of Trieste: faunistic, biocoenotic and
- 1436 ecological survey. *Acta Adriatica* 51, 203-216.
- 1437 Moodley, L., Heip, C.H. and Middelburg, J.J., 1998. Benthic activity in sediments of the
- 1438 northwestern Adriatic Sea: sediment oxygen consumption, macro-and meiofauna
- 1439 dynamics. Journal of Sea Research 40, 263-280.

- 1440 N'Siala, G. M., V. Grandi, M. Iotti, G. Montanari, D. Prevedelli, and R. Simonini. 2008.
- 1441 Responses of a northern Adriatic Ampelisca–Corbula community to seasonality and short-
- 1442 term hydrological changes in the Po River. Marine Environmental Research 66, 466–476
- 1443 Occhipinti-Ambrogi, A., Favruzzo, M. and Savini, D., 2002. Multi-annual variations of
- 1444 macrobenthos along the Emilia-Romagna Coast (Northern Adriatic). *Marine Ecology*, 23,
- 1445 307-319.
- 1446 Orel, G., Marocco, R., Vio, E., Del Piero, D. and Della Seta, G., 1987. Sedimenti e biocenosi
- 1447 bentoniche tra la foce del Po ed il Golfo di Trieste (Alto Adriatico). *Bulletin d'Ecologie*, 18,1448 229-241.
- 1449 Prevedelli, D., Simonini, R. and Ansaloni, I., 2001. Relationship of non-specific
- 1450 commensalism in the colonisation of the deep layers of sediment. Journal of the Marine
- 1451 Biological Association of the United Kingdom 81, 897-901.
- 1452 Pitacco, V., Mistri, M., Aleffi, I.F., Lardicci, C., Prato, S., Tagliapietra, D. and Munari, C.,
- 1453 2019. Spatial patterns of macrobenthic alpha and beta diversity at different scales in Italian
- transitional waters (central Mediterranean). *Estuarine, Coastal and Shelf Science*, 222, 126-138.
- 1456 Poluzzi, A., Sabelli, B. and Taviani, M., 1981. Auto-sinecologia dei Molluschi: dei fondi
- 1457 mobili del delta settentrionale del Po (Estate 1980). Bollettino della SocietaPaleontologica
- 1458 Italiana, 21, 169-178.
- 1459 Rigotii, L. 2019. Studio e caratterizzazione preliminari di sedimento e macrozoobenthos in
- 1460 due stazioni marine costiere in località Ca' Roman (VE). Dipartimento di Biologia,
- 1461 Universita' degli studi di Padova, Master thesis.
- 1462 Scardi, M., R. Crema, P. Di Dato, E. Fresi, and G. Orel. 2000. Le comunità bentoniche
- 1463 dell'Alto Adriatico: un'analisi preliminare dei cambiamenti strutturali dagli anni'30 ad oggi.
- 1464 Pp. 95–108 in O. Giovanardi, ed. Impact of trawl fishing on benthic communities. *Istituto*
- 1465 Centrale per la Ricerca Scientifica e Tecnologica Applicata al Mare, Rome.
- Seneš, J., 1989. North Adriatic inter-island shelf ecosystems of the Rovinj area. *Geologica Carpathica* 40, 333-354.

- 1468 Simonini, R., I. Ansaloni, A. B. Pagliai, and D. Prevedelli. 2004. Organic enrichment and
- 1469 structure of the macrozoobenthic community in the northern Adriatic Sea in an area facing
- 1470 Adige and Po mouths. ICES Journal of Marine Science 61, 871–881.
- 1471 Solis-Weiss, V., Rossin, P., Aleffi, F., Bettoso, N., Orel, G., Vrišer, B., 2001. Gulf of Trieste:
- 1472 sensitivity areas using benthos and GIS techniques. In: Özhan, E. (Ed.), *Proceedings of the*
- 1473 Fifth International Conference on the Mediterranean Coastal Environment. Ankara, Turkey,
- 1474 1567–1578. http://ipt.vliz.be/eurobis/resource?r=macroben\_lbmrev\_evco
- 1475 Targusi, M. 2011. I crostacei Anfipodi quali descrittori delle comunità bentoniche di ambienti
- 1476 marino costieri interessati da attività antropiche. Universita degli studi di Napoli Federico II,
- 1477 Dissertation thesis.
- 1478 Weber, K. and Zuschin, M., 2013. Delta-associated molluscan life and death assemblages in
- 1479 the northern Adriatic Sea: implications for paleoecology, regional diversity and
- 1480 conservation. Palaeogeography, Palaeoclimatology, Palaeoecology, 370, 77-91.
- 1481 Zucchi Stolfa M.L. 1979. Lamellibranchi recenti delle lagune di Grado e di Marano.
- 1482 Atti del Museo Friulano di Storia Naturale 1, 41-60.
- 1483 Zavodnik, D. and Vidakovic, J., 1987. Report on bottom fauna in two Northern Adriatic areas
- 1484 presumed to be influenced by inputs. Report of the FAO/UNEP Meeting on the Effects of
- 1485 Pollution on Marine Ecosystems, Food and Agriculture Organization of the United Nations,
- 1486 Fisheries Report, 352, Supplement, 263-279.

### 1488 Supporting references – living benthic foraminiferal assemblages

- 1489 Alves Martins, M.V., Hohenegger, J., Frontalini, F., Dias, J.M.A., Geraldes, M.C. and Rocha,
- 1490 F., 2019. Dissimilarity between living and dead benthic foraminiferal assemblages in the
- 1491 Aveiro Continental Shelf (Portugal). PLoS One, 14, e0209066.
- 1492 Avnaim-Katav, S., Almogi-Labin, A., Kanari, M. and Herut, B., 2020. Living benthic
- 1493 for a for a southeastern Mediterranean ultra-oligotrophic shelf habitats: Implications for
- 1494 ecological studies. Estuarine, Coastal and Shelf Science, 234, 106633

- 1495 Barras, C., Jorissen, F.J., Labrune, C., Andral, B. and Boissery, P., 2014. Live benthic
- 1496 for aminiferal faunas from the French Mediterranean Coast: Towards a new biotic index of
- 1497 environmental quality. *Ecological Indicators*, 36, 719-743.
- 1498 Dimiza, M.D., Koukousioura, O., Triantaphyllou, M.V. and Dermitzakis, M.D., 2016. Live
- 1499 and dead benthic foraminiferal assemblages from coastal environments of the Aegean Sea
- 1500 (Greece): Distribution and diversity. *Revue de Micropaléontologie*, 59, 19-32
- 1501 Dessandier, P.A., Bonnin, J., Kim, J.H. and Racine, C., 2018. Comparison of living and dead
- 1502 benthic foraminifera on the Portuguese margin: Understanding the taphonomical processes.
- 1503 Marine Micropaleontology, 140, 1-16
- 1504 Diz, P. and Francés, G., 2008. Distribution of live benthic foraminifera in the Ría de Vigo
- 1505 (NW Spain). Marine Micropaleontology, 66, 165-191
- 1506 Fentimen, R., Rüggeberg, A., Lim, A., Kateb, A.E., Foubert, A., Wheeler, A.J. and
- 1507 Spezzaferri, S., 2018. Benthic foraminifera in a deep-sea high-energy environment: the Moira
- 1508 Mounds (Porcupine Seabight, SW of Ireland). Swiss Journal of Geosciences, 111 561-572.
- 1509 Harloff, J. and Mackensen, A., 1997. Recent benthic foraminiferal associations and ecology
- 1510 of the Scotia Sea and Argentine Basin. *Marine Micropaleontology*, 31, 1-29.
- 1511 Jiang, F., Fan, D., Zhao, Q., Wu, Y., Ren, F., Liu, Y. and Li, A., 2023. Comparison of alive
- 1512 and dead benthic foraminiferal fauna off the Changjiang Estuary: Understanding water-mass
- 1513 properties and taphonomic processes. *Frontiers in Marine Science*, 10, 1114337.
- 1514 Licari, L. and Mackensen, A., 2005. Benthic foraminifera off West Africa (1° N to 32° S): Do
- 1515 live assemblages from the topmost sediment reliably record environmental variability?.
- 1516 Marine Micropaleontology, 55, 205-233
- 1517 Lutze, GF (1974): Benthische Foraminiferen in Oberflächen-Sedimenten des Persischen
- 1518 Golfes. Teil 1: Arten. Meteor Forschungsergebnisse, Deutsche Forschungsgemeinschaft,
- 1519 Reihe C Geologie und Geophysik, C17, 1-66
- 1520 Mackensen, A., Fu, D.K., Grobe, H. and Schmiedl, G., 1993. Benthic foraminiferal
- assemblages from the eastern South Atlantic Polar Front region between 35 and 57 S:
- 1522 Distribution, ecology and fossilization potential. *Marine Micropaleontology*, 22, 33-69.

- 1523 Mallon, J., Glock, N., and Schönfeld, J. 2012, The response of benthic foraminifera to low-
- 1524 oxygen conditions of the Peruvian oxygen minimum zone. In: Altenbach, A., Bernhard J.M.
- 1525 and Seckbach J., eds, Anoxia: Evidence for Eukaryote Survival and Paleontological
- 1526 *Strategies*, Springer, Dordrecht, 305–321.
- 1527 In: ANOXIA :. , ed. by Altenbach, Alexander V., Bernhard, Joan M. and Seckbach, Joseph.
- 1528 Cellular Origin, Life in Extreme Habitats and Astrobiology, 21
- 1529 Martins, M.V.A., Hohenegger, J., Frontalini, F., Miranda, P., da Conceição Rodrigues, M.A.
- and Dias, J.M.A., 2016. Comparison between the dead and living benthic foraminiferal
- 1531 assemblages in Aveiro Lagoon (Portugal). Palaeogeography, Palaeoclimatology,
- 1532 Palaeoecology, 455, 16-32.
- 1533 Martins, M.V.A., Hohenegger, J., Martínez-Colón, M., Frontalini, F., Bergamashi, S., Laut,
- 1534 L., Belart, P., Mahiques, M., Pereira, E., Rodrigues, R. and Terroso, D., 2020. Ecological
- 1535 quality status of the NE sector of the Guanabara Bay (Brazil): A case of living benthic
- 1536 foraminiferal resilience. Marine Pollution Bulletin, 158, 111449
- 1537 Melis, R. and Violanti, D., 2006. Foraminiferal biodiversity and Holocene evolution of the
- 1538 Phetchaburi coastal area (Thailand Gulf). *Marine Micropaleontology*, 61, 94-115.
- 1539 Mojtahid, M., Jorissen, F., Lansard, B., Fontanier, C., Bombled, B. and Rabouille, C., 2009.
- 1540 Spatial distribution of live benthic foraminifera in the Rhône prodelta: Faunal response to a
- 1541 continental-marine organic matter gradient. Marine Micropaleontology, 70, 177-200
- 1542 Oron, S., Friedlander, A.M., Sala, E. and Goodman-Tchernov, B.N., 2022. Recent shallow
- 1543 water foraminifera from the Selvagens Islands (Northeast Atlantic)–Assemblage composition
- and biogeographic significance. Estuarine, Coastal and Shelf Science, 264, 107671
- 1545 Parent, B., Barras, C., Bicchi, E., Charrieau, L.M., Choquel, C., Bénéteau, É., Maillet, G.M.
- 1546 and Jorissen, F.J., 2021. Comparison of four foraminiferal biotic indices assessing the
- 1547 environmental quality of coastal Mediterranean soft bottoms. Water, 13, 3193
- 1548 Raposo, D., Frontalini, F., Clemente, I., da Conceição Guerreiro Couto, E., Veríssimo, F. and
- 1549 Laut, L., 2022. Benthic foraminiferal response to trace elements in a tropical mesotidal
- 1550 Brazilian estuary. Estuaries and Coasts, 45, 2610-2631

- 1551 Schmidt, S. and Schönfeld, J., 2021. Living and dead foraminiferal assemblage from the
- 1552 supratidal sand Japsand, North Frisian Wadden Sea: distributional patterns and controlling
- 1553 factors. Helgoland Marine Research, 75, 6, 1-22
- 1554 Schumacher, S., Jorissen, F.J., Dissard, D., Larkin, K.E. and Gooday, A.J., 2007. Live (Rose
- 1555 Bengal stained) and dead benthic foraminifera from the oxygen minimum zone of the
- 1556 Pakistan continental margin (Arabian Sea). Marine Micropaleontology, 62, 45-73
- 1557 Szarek, R., Kuhnt, W., Kawamura, H. and Kitazato, H., 2006. Distribution of recent benthic
- 1558 for aminifera on the Sunda Shelf (South China Sea). Marine Micropaleontology, 61, 171-195
- 1559 Thies, A., 1991. Die Benthos-Foraminiferen im Europäischen Nordmeer. Doctoral
- 1560 dissertation, Christian-Albrechts-Universität Kiel.
- 1561 Timm, S., 1992. Rezente Tiefsee-Benthosforaminiferen aus Oberflächensedimenten des
- 1562 Golfes von Guinea (Westafrika)-Taxonomie, Verbreitung, Ökologie und
- 1563 Korngrößenfraktionen. Doctoral dissertation, Geologisch-Paläontologisches Institut und
- 1564 Museum Christian-Albrechts-Universität Kiel.
- 1565 Venturelli, R.A., Rathburn, A.E., Burkett, A.M. and Ziebis, W., 2018. Epifaunal foraminifera
- 1566 in an infaunal World: Insights into the influence of heterogeneity on the benthic ecology of
- 1567 oxygen-poor, deep-sea habitats. Frontiers in Marine Science, 5, 344.
- 1568 Walton, W.R., 1955. Ecology of living benthonic foraminifera, Todos Santos Bay, Baja
- 1569 California. Journal of Paleontology, 29, 952-1018.
- 1570 Wollenburg, J.E. and Mackensen, A., 1998. Living benthic foraminifers from the central
- 1571 Arctic Ocean: faunal composition, standing stock and diversity. Marine Micropaleontology,
- 1572 34, 153-185
- 1573

## 1574 Supporting references – fossil benthic foraminiferal assemblages

- 1575 Abu-Zied, R.H., Rohling, E.J., Jorissen, F.J., Fontanier, C., Casford, J.S. and Cooke, S., 2008.
- 1576 Benthic foraminiferal response to changes in bottom-water oxygenation and organic carbon
- 1577 flux in the eastern Mediterranean during LGM to Recent times. Marine
- 1578 Micropaleontology, 67, 46-68.
- 1579 Avnaim-Katav, S., Almogi-Labin, A., Schneider-Mor, A., Crouvi, O., Burke, A.A.,
- 1580 Kremenetski, K.V. and MacDonald, G.M., 2019. A multi-proxy shallow marine record for
- 1581 Mid-to-Late Holocene climate variability, Thera eruptions and cultural change in the Eastern
- 1582 Mediterranean. Quaternary Science Reviews, 204, 133-148.
- 1583 Buzas-Stephens, P., Livsey, D.N., Simms, A.R. and Buzas, M.A., 2014. Estuarine
- 1584 for aminifera record Holocene stratigraphic changes and Holocene climate changes in ENSO
- and the North American monsoon: Baffin Bay, Texas. Palaeogeography, Palaeoclimatology,
- 1586 Palaeoecology, 404, 44-56.
- 1587 Cardiff J. et al. 2019. Multidecadal Changes in Marine Subsurface Oxygenation Off Central
- 1588 Peru During the Last ca. 170 Years. Frontiers in Marine Science, 10.3389/fmars.2019.00270.
- 1589 Consolaro, C., Rasmussen, T.L. and Panieri, G., 2018. Palaeoceanographic and environmental
- 1590 changes in the eastern Fram Strait during the last 14,000 years based on benthic and
- 1591 planktonic foraminifera. *Marine Micropaleontology*, 139, 84-101.
- 1592 Dimiza, M.D., Fatourou, M., Arabas, A., Panagiotopoulos, I., Gogou, A., Kouli, K., Parinos,
- 1593 C., Rousakis, G. and Triantaphyllou, M.V., 2020. Deep-sea benthic foraminifera record of the
- 1594 last 1500 years in the North Aegean Trough (northeastern Mediterranean): A paleoclimatic
- 1595 reconstruction scenario. Deep Sea Research Part II: Topical Studies in Oceanography, 171,
- 1596 104705.
- 1597 Filipsson, H.L. and Nordberg, K., 2004. A 200-year environmental record of a low-oxygen
- 1598 fjord, Sweden, elucidated by benthic foraminifera, sediment characteristics and hydrographic
- 1599 data. Journal of Foraminiferal Research, 34, 277-293.
- 1600 Fink, H.G; Wienberg, C.; Hebbeln, D.; McGregor, H.V.; Schmiedl, G.; Taviani, M.; Freiwald,
- 1601 A. (2012): Oxygen control on Holocene cold-water coral development in the eastern
- 1602 Mediterranean Sea. Deep Sea Research Part I: Oceanographic Research Papers, 62, 89-96
- 1603 Hess, S., Alve, E., Andersen, T.J. and Joranger, T., 2020. Defining ecological reference
- 1604 conditions in naturally stressed environments–How difficult is it? *Marine Environmental*1605 *Research*, 156, 104885.
- 1606 Kaminski, M.A., Aksu, A., Box, M., Hiscott, R.N., Filipescu, S. and Al-Salameen, M., 2002.
- 1607 Late Glacial to Holocene benthic foraminifera in the Marmara Sea: implications for Black

- 1608 Sea–Mediterranean Sea connections following the last deglaciation. *Marine Geology*, 190,1609 165-202.
- 1610 Klootwijk, A.T., Alve, E., Hess, S., Renaud, P.E., S?rlie, C. and Dolven, J.K., 2021.
- 1611 Monitoring environmental impacts of fish farms: Comparing reference conditions of sediment
- 1612 geochemistry and benthic foraminifera with the present. *Ecological Indicators*, 120, 106818.
- 1613 Le Houedec, S., Mojtahid, M., Bicchi, E., de Lange, G.J. and Hennekam, R., 2020. Suborbital
- 1614 hydrological variability inferred from coupled benthic and planktic foraminiferal?based
- 1615 proxies in the southeastern Mediterranean during the last 19 ka. *Paleoceanography and*
- 1616 Paleoclimatology, 35, e2019PA003827.
- 1617 Matos, L., Wienberg, C., Titschack, J., Schmiedl, G., Frank, N., Abrantes, F., Cunha, M.R.
- and Hebbeln, D., 2017. Coral mound development at the Campeche cold-water coral
- 1619 province, southern Gulf of Mexico: Implications of Antarctic Intermediate Water increased
- 1620 influence during interglacials. *Marine Geology*, 392, 53-65.
- 1621 Melis, R. and Salvi, G., 2009. Late Quaternary foraminiferal assemblages from western Ross
- 1622 Sea (Antarctica) in relation to the main glacial and marine lithofacies. *Marine*
- 1623 Micropaleontology, 70, 39-53.
- 1624 Melis, R. and Salvi, G., 2020. Foraminifer and Ostracod Occurrence in a Cool-Water
- 1625 Carbonate Factory of the Cape Adare (Ross Sea, Antarctica): A Key Lecture for the Climatic
- and Oceanographic Variations in the Last 30,000 Years. *Geosciences*, 10, 413.
- 1627 Melis, R., Capotondi, L., Torricella, F., Ferretti, P., Geniram, A., Hong, J.K., Kuhn, G., Khim,
- 1628 B.K., Kim, S., Malinverno, E. and Yoo, K.C., 2021. Last Glacial Maximum to Holocene
- 1629 paleoceanography of the northwestern Ross Sea inferred from sediment core geochemistry
- and micropaleontology at Hallett Ridge. Journal of Micropalaeontology, 40, 15-35.
- 1631 Melis, R., Carbonara, K., Villa, G., Morigi, C., Bárcena, M.A., Giorgetti, G., Caburlotto, A.,
- 1632 Rebesco, M. and Lucchi, R.G., 2018. A new multi?proxy investigation of Late Quaternary
- 1633 palaeoenvironments along the north-western Barents Sea (Storfjorden Trough Mouth
- 1634 Fan). Journal of Quaternary Science, 33, 662-676.
- 1635 Milker, Y., Schmiedl, G. and Betzler, C., 2011. Paleobathymetric history of the Western
- 1636 Mediterranean Sea shelf during the latest glacial period and the Holocene: Quantitative

- 1637 reconstructions based on foraminiferal transfer functions. Palaeogeography,
- 1638 Palaeoclimatology, Palaeoecology, 307, 324-338.
- 1639 Mojtahid, M., Toucanne, S., Fentimen, R., Barras, C., Le Houedec, S., Soulet, G., Bourillet,
- 1640 J.F. and Michel, E., 2017. Changes in northeast Atlantic hydrology during Termination 1:
- 1641 Insights from Celtic margin's benthic foraminifera. *Quaternary Science Reviews*, 175, 45-59.
- 1642 Osterman, L.E. and Smith, C.G., 2012. Over 100 years of environmental change recorded by
- 1643 foraminifers and sediments in Mobile Bay, Alabama, Gulf of Mexico, USA. Estuarine,
- 1644 Coastal and Shelf Science, 115, 345-358.
- 1645 Osterman, L.E., Pavich, K., and Caplan, J., 2004, Benthic foraminiferal census data from Gulf
- 1646 of Mexico cores (Texas and Louisiana Continental Shelf). U.S. Geological Survey Open-File
- 1647 Report 2001-1209, 15 p.
- 1648 Pérez-Asensio, J.N., Frigola, J., Pena, L.D., Sierro, F.J., Reguera, M.I., Rodríguez-Tovar, F.J.,
- 1649 Dorador, J., Asioli, A., Kuhlmann, J., Huhn, K. and Cacho, I., 2020. Changes in western
- 1650 Mediterranean thermohaline circulation in association with a deglacial Organic Rich Layer
- 1651 formation in the Alboran Sea. *Quaternary Science Reviews*, 228, 106075.
- 1652 Pinto, A.F.S., Martins, M.V.A., Fonseca, M.C.M., Pereira, E., Terroso, D.L., Rocha, F.,
- 1653 Rodrigues, M.A.C., 2017. Late Holocene closure of a barrier beach in Sepetiba Bay and its
- 1654 environmental impact (Rio de Janeiro, Brazil). Journal of Sedimentary Environments, 2, 65-
- 1655 80.
- 1656 Polovodova Asteman, I. and Nordberg, K., 2013. Foraminiferal fauna from a deep basin in
- 1657 Gullmar Fjord: The influence of seasonal hypoxia and North Atlantic Oscillation. *Journal of*
- 1658 Sea Research, 79, 40-49.
- 1659 Polyak, L., Best, K.M., Crawford, K.A., Council, E.A. and St-Onge, G., 2013. Quaternary
- 1660 history of sea ice in the western Arctic Ocean based on foraminifera. *Quaternary Science*
- 1661 *Reviews*, 79, 145-156.
- 1662 Richwine, K.A., Marot, M., Smith, C.G., Osterman, L.E. and Adams, C.S., 2013. Biological
- and geochemical data of gravity cores from mobile Bay, Alabama. US Department of the
- 1664 Interior, US Geological Survey.

- 1665 Schmiedl, G., Hemleben, C., Keller, J. and Segl, M., 1998. Impact of climatic changes on the
- 1666 benthic foraminiferal fauna in the Ionian Sea during the last 330, 0000
- 1667 years. Paleoceanography, 13, 447-458.
- 1668 Schmiedl, G., Mitschele, A., Beck, S., Emeis, K.C., Hemleben, C., Schulz, H., Sperling, M.
- and Weldeab, S., 2003. Benthic foraminiferal record of ecosystem variability in the eastern
- 1670 Mediterranean Sea during times of sapropel S5 and S6 deposition. *Palaeogeography*,
- 1671 Palaeoclimatology, Palaeoecology, 190, 139-164.
- 1672 Takata, H., Hong, S.H., Yoo, D.G., Kim, J.C., Cheong, D. and Khim, B.K., 2022. Fossil
- 1673 benthic foraminifera in the Nakdong River Delta (southeast Korea) during the early to middle
- 1674 Holocene. Paleontological Research, 26, 283-300.
- 1675 Tetard, M., Licari, L. and Beaufort, L., 2017. Oxygen history off Baja California over the last
- 1676 80 kyr: A new foraminiferal?based record. *Paleoceanography*, 32, 246-264.
- 1677 Tsujimoto, A., Nomura, R., Yasuhara, M., Yamazaki, H. and Yoshikawa, S., 2006. Impact of
- 1678 eutrophication on shallow marine benthic foraminifers over the last 150 years in Osaka Bay,
- 1679 Japan. Marine Micropaleontology, 60, 258-268.
- 1680 Usami, K., Ohi, T., Hasegawa, S. and Ikehara, K., 2013. Foraminiferal records of bottom-
- 1681 water oxygenation and surface-water productivity in the southern Japan Sea during 160–15
- 1682 ka: associations with insolation changes. *Marine Micropaleontology*, 101, 10-27.
- 1683 Xiang, R., Yang, Z., Saito, Y., Fan, D., Chen, M., Guo, Z. and Chen, Z., 2008.
- 1684 Paleoenvironmental changes during the last 8400 years in the southern Yellow Sea: Benthic
- 1685 foraminiferal and stable isotopic evidence. *Marine Micropaleontology*, 67, 104-119.