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Paleorecords reveal the increased temporal instability of species diversity under biodiversity loss

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Abstract

Ongoing climate change threatens biodiversity and directly affects the stability of plant-animal communities. However, it is unclear how the species diversity of biological communities responds to natural climate warming, and whether the temporal stability of biodiversity in the face of climate warming varies with environmental gradients in different communities due to the lack of long-term data. We present three high-resolution records of terrestrial mollusk fossils dating back 25 kyr along a climatic and vegetation gradient from southeast to northwest across the Chinese Loess Plateau. The records show that deglacial warming increased the mollusk diversity by ~30% in species-poor steppe communities; however, in high-diversity forest-steppe communities, the effect was less, and diversity's dynamic stability was even maintained. The high-diversity communities adjusted their composition by substituting thermo-humidiphilous taxa for cold-tolerant taxa, with the compositional turnover reaching ~60%. The mollusk diversity of species-poor communities is shown to be more sensitive to the last deglacial warming and associated with the strengthening of the East Asian Summer monsoon than that of diverse communities. The increased temporal instability and sensitivity of biodiversity in species-poor communities in the face of climate disturbances, from a long-term perspective, highlights the potential risk of collapse of soil communities under future anthropogenic biodiversity loss.

Highlights

- ~2°C of natural warming was generally able to sustain or increase mollusk diversity.
- The response of mollusk diversity to deglacial warming is not homogeneous in different diversity-levels communities.
- The temporal stability of mollusk diversity decreased in semi-arid low-diversity communities.
- The high-diversity communities adjusted their composition to maintain diversity as the climate warms.

1. Introduction

Biodiversity provides the basis for the resilience of plant and animal communities to environmental perturbations (Isbell et al., 2011; Kiessling, 2005). The ongoing modern biodiversity crisis (Beaugrand et al., 2015; Panetta et al., 2018; Urban, 2015) highlights the urgent need to better understand the extent to which ecosystems will be resistant to future environmental perturbations. Several assessments have predicted that ~15-35% of plant and animal species will become extinct as global average temperatures rise ~2-3 °C above pre-industrial levels (Thomas et al., 2004; Urban, 2015). Many empirical studies have linked recent climate change to the temporal trajectory of biodiversity change (Harrison et al., 2015; Steinbauer et al., 2018); however, contrary to expectations, attempts to determine whether biodiversity tracks climatic warming over time have indicated both increases and decreases in biodiversity during recent decades (Brown et al., 2001; Harrison et al., 2015; Ricklefs, 1987). In the context of natural warming, it is still unclear how the species diversity of biological communities responds to climate change, and whether, and how these effects vary across contrasting ecosystems or along environmental gradients.

Most records of the effects of environmental drivers (e.g., climatic warming, drought, climatic variability) on biodiversity are based on decadal-scale ecological data (Engels et al., 2020). In many natural settings, it has proven difficult to disentangle natural variability from the effects of human-induced ecosystem change (Willis and Birks, 2006), as a result of the short timescales typically employed. Considering that modern biodiversity patterns are the product of long-term climate changes in the geological past, appropriate empirical assessments of the rate at which communities respond to climate change require long-term surveys of species communities (Willis and Birks, 2006). However, such surveys are scarce (Kidwell and Tomasovych, 2013; Martin and PelÁEz-Campomanes, 2014; Willis and Birks, 2006), and in particular it remains unclear whether

85   the degree of species diversity loss and compositional turnover is mediated by the

86   climatological context.

87   Paleorecords that cover much longer timescales, such as several centuries to millennia,

88   provide a broader temporal context for examining the extent to which biodiversity varies

89   with spatiotemporal changes in climate (Engels et al., 2020; Martin and PelÁEz-

90   Campomanes, 2014; Willis and Birks, 2006). Recent research has revealed a rapid and

91   significant increase (~35%) in plant diversity in eastern Colombia during the Paleocene-

92   Eocene Thermal Maximum (Jaramillo et al., 2010). In addition, a well-dated fossil record

93   from northern California indicated a relatively minor reduction in small mammal

94   diversity (~20%) and the increasing dominance of generalist species in response to

95   climate change during the last deglacial (Blois et al., 2010). These findings provide

96   important knowledge of the responses to natural warming on geological time scales with

97   a large resolution, focusing mainly on mammals and plants. Therefore, the fossil record

98   that preserves high-resolution and greater number of taxa, especially invertebrates, and

99   provides information on community dynamics, such as on whether individual species are

100   added to or lost from communities, is also needed. Among the terrestrial invertebrates,

101   terrestrial mollusks as the important decomposers within soil communities (Mason, 1970)

102   are a diverse and abundant group of invertebrates inhabiting various soil environments

103   (Dong et al., 2019; Nekola, 2003). They are abundantly preserved as fossils, for example

104   in loess sediments, and they can be identified at the species level (Horsák et al., 2018;

105   Richter et al., 2019; Rousseau and Wu, 1997; Sümegi et al., 2015; Wu et al., 2002).

106   These characteristics make mollusks a unique model taxon for exploring past shifts in

107   biodiversity (Rousseau et al., 1993) and their long-term linkages with climate change.

108   Here we present three high-resolution mollusk fossil sequences dating back 25 kyr,

109   along with environmental gradients in the Chinese Loess Plateau (CLP) (Fig. 1). Our aim

110   was to determine the response of mollusk communities to the last deglacial, which was

111   characterized by rapid and frequent climatic fluctuations but an overall warming trend.

112   During the last glacial maximum (LGM), mean annual temperatures were as much as ~5-

113   7 °C colder than today, but by ~16 kyr B.P. the climate began to warm. Holocene

114   climates were relatively stable, with temperatures ~2 °C higher than today during ~8-4

115 kyr B.P. (the Holocene climatic optimum) (Shakun et al., 2012), which is equivalent to

116 modern warming predicted for the current century.

117   The three loess sites (Linxia, Jingchuan, and Yaoxian) are located in temperate steppe

118 along a climatic and vegetation gradient from southeast to northwest, spanning ranges of

119 ~4 °C and 300 mm in mean annual temperature and precipitation, under the influence of

120 the East Asian summer monsoon (EASM) (Liu, 1985). The northernmost site (Linxia)

121 lies at the northern limit of the EASM and is characterized by low-diversity mollusk

122 communities. For each site, we sampled mollusk fossils at 3-cm intervals from loess-

123 paleosol profiles spanning the last 25 kyr (Figs. S1 and S2). We used a multiple index

124 definition of biodiversity (the number of species, S; Shannon-Wiener index, H') that

125 includes components of species richness and evenness, together with redundancy analysis

126 (RDA), to explore the rate and magnitude of diversity changes along the specified

127 environmental gradients.

128 **2. Materials and Methods**

129

130 *2.1. Study area and Sites*

131   The Chinese Loess Plateau (CLP) is located in the northern marginal zone of the East

132 Asian summer monsoon (EASM) and is characterized by a steep climatic gradient. At

133 present, mean annual temperature (T_{ann}) increases from ~6 to ~13 °C, and mean annual

134 precipitation (P_{ann}) from ~300 to ~650 mm from northwest to southeast (Fig. 1). About

135 70% of the precipitation falls in the summer and autumn seasons when the EASM

136 circulation transports tropical and subtropical moisture inland (Qian, 1991).

137   The three loess-palaeosol sections, Linxia (35°38′N, 103°09′E, 2179 m a.s.l., P_{ann} =

138 400 mm, T_{ann} = 6.7 °C), Jingchuan (35°15′N, 107°43′E, 1244 m a.s.l., P_{ann} = 500 mm, T_{ann}

139 = 9.5 °C), and Yaoxian section (34°53′N, 108°58′E, 673 m a.s.l., P_{ann} = 650 mm, T_{ann} =

140 12.3 °C) are located along a northwest-southeast transect across the CLP (Fig. 1). The

141 transect conforms to a climatic gradient with ranges of ~4 °C and 300 mm range in mean

142 annual temperature and precipitation, respectively (Fig. 1). Their associated plant

143 communities also lie along a gradient with higher numbers of woody plants at the

144 southeastern sites (Wang et al., 2011). The natural vegetation types can be divided into

145 different zones from north to south: steppe (Linxia), forest-steppe (Jingchuan and

146 Yaoxian), respectively (Fig. 1). Notably, the southeastern sites have more complex soil

147 environments with higher water availability and thus higher plant diversity than the

148 northwestern sites.

149 *2.2. Loess sequences and chronology*

150   The three profiles are geographically located in 'Yuan' areas (flat-topped loess

151 highlands, covered with thick loess deposits), one of the major topographic units in the

152 CLP (Liu, 1985). Sampling was undertaken on (i) the upper part of loess unit L1 (L1-1)

153 which was deposited since marine isotope stage 2 (MIS2); and (ii) the lower part of the

154 Holocene paleosol unit (S0). L1 consists of light greyish-yellow silt with thicknesses of

155 ~240 cm, ~230 cm and ~126 cm at Linxia, Jingchuan and Yaoxian, respectively (Fig.

156   S1). S0 consists of brown to dark brown silt with thicknesses ranging from 84 to 180 cm

157   (Fig. S1).

158   The chronology of the Jingchuan and Yaoxian loess-paleosol sequences is based on 24

159   optically stimulated luminescence (OSL) ages (Jingchuan, n=9; Yaoxian, n=15) (Figs. S2

160   and S3) (Dong et al., 2015). The chronology of the Linxia loess-paleosol sequence is

161   based on the high resolution OSL dating referenced from Lai and Wintle (2006). The

162   OSL sampling intervals were 20 cm for the S0 paleosol unit and 20–40 cm for the upper

163   part of the L1 loess unit. The 45–63 μm grain-size fraction was extracted and prepared

164   for equivalent dose (D_e) determination. The measurements were conducted at the

165   Luminescence Dating Laboratory at Peking University, China. The age-depth model for

166   each loess sequence was established using a polynomial fit through a number of

167   successive OSL dates and it provided the necessary chronostratigraphic framework to

168   contextualize changes in magnetic susceptibility (MS) (Fig. S3). Here, MS is the measure

169   of induced magnetization of objects in an artificial weak magnetic field (Liu, 1985).

170   Monsoon precipitation and related humidity control the formation of magnetic minerals

171   in the Chinese loess; high MS indicates a strong monsoon circulation and more

172   precipitation, MS thus can serve as a proxy of EASM intensity (An et al., 1991). Fig. S3

173   demonstrates the goodness of fit achieved using the age-depth model. The three loess

174   profiles span the past 21 kyr, including the Last Glacial Maximum (LGM), Last

175   deglacial, and Holocene (Dong et al., 2015).

176   *2.3. Mollusk sample collection*

177   The studied loess sections were first prepared by cleaning a 1.6-m-wide face in the

178   field in order to identify and log the stratigraphic units (Fig. S2). A sampling of each

179   profile was conducted at 3-cm intervals which equates to an average temporal resolution

180   of ~200-300 years per sample. A total of 255 samples were taken from the L1 and S0

181   strata. Each sample comprised ~15 kg of soil material, and the overall volume of the

182   excavated material was ~5.51 m^3. All samples were washed and sieved in the field using

183   a 0.5-mm mesh sieve to remove fine soil (Fig. S2). The mollusk shells were then picked

184   and identified under a binocular microscope. The identifiable mollusk remains were

185 counted following Rousseau and Wu (1997). The identification procedures followed Yen

186 (1939), and Chen and Gao (1987). All individual mollusks were identified to species

187 level.

188 *2.4. Quantifying terrestrial mollusk community structure*

189 To characterize the species structure and diversity patterns through time, we first

190 identified all mollusk taxa in the deposits and counted the number of identified specimens

191 at each site. We then used these data to calculate species diversity (Species number and

192 Shannon-Weiner index), and turnover (Bray-Curtis index) (Magurran, 1988) and their

193 variations through time. We used the Species number (S) and Shannon-Wiener index

194 [$$H' = -\sum_{i=1}^{n} (Pi \times \ln Pi)$$] to represent species diversity where p_i is the proportion of the

195 *i*th species, ln is the natural log, and *S* is the total number of species. Species number and

196 Shannon-Wiener index are widely used. The Shannon-Wiener index is a measure of the

197 relative dominance of different species within a community, because the metric

198 incorporates abundance, which may be a more sensitive indicator of community change

199 than species number (S). Species number (S) and Shannon-Wiener ln-based index were

200 calculated using PRIMER (Plymouth Routines in Multivariate Ecological Research)

201 version 5.0 (Clarke and Gorley, 2006).

202 To determine whether there were temporal trends in the species diversity, we first

203 plotted all diversity metrics against time. We then fitted a linear model of each metric

204 against time, within each site, and calculated the slope of the trend. We then divided each

205 site into three large blocks based on the results of constrained cluster analysis (a

206 multivariate method for quantitative definition of stratigraphic zones) (Fig. 2): >17 ka

207 (LGM), 17-9 ka (last deglacial) and <9-3 ka (early-mid Holocene) in order to detect the

208 overall trends of diversity in three stages: cold glacial, deglacial warming, and warm

209 Holocene. A T-test was carried out to assess the statistical significance of the differences

210 in diversity for each of the blocks.

211 *2.5.Relationships between snail assemblages, pollen composition, and their correlations*

212 *with climate*

9

213   Numerous pollen records of varying quality are available for the study region. We first

214   selected the pollen sequence most proximal to our study site from the late Quaternary

215   pollen dataset of eastern continental Asia (Li et al., 2003; Jiang and Ding, 2005; Jiang et

216   al., 2013; Sun et al., 1997). These selected fossil pollen records are from the 'Yuan' loess

217   sections, which benefit from reliable dating control of suitably high resolution, covering

218   all or most of the last 22 kyr. The age model was calculated on the basis of OSL ages in

219   relation to the pedostratigraphy of each profile. Individual taxa for each pollen sequence

220   were interpolated for each 500-year interval using the linear integration function.

221   To ensure that the time-averaging of mollusk records and pollen sequences was

222   similar, we linearly interpolated both mollusk and pollen sequences at 500-year intervals.

223   Redundancy analysis (RDA) was then conducted to identify the role of different

224   environmental factors in determining the mollusk-pollen community structure (Ter Braak

225   and Šmilauer, 1998). We analyzed four environmental variables, all of which were

226   considered to be potentially significant influences on community structure: 1) Northern

227   Hemisphere average temperature (Nor. AT) (Shakun et al., 2012); 2) magnetic

228   susceptibility (MS), a proxy of EASM intensity; 3) arboreal pollen percentages (Ptree)

229   (Li et al., 2003; Jiang and Ding, 2005; Jiang et al., 2013; Sun et al., 1997); and 4) age.

230   These environmental variables were linearly interpolated at the same 500-year intervals

231   to ensure a reliable comparison with community structure. RDA was performed using

232   CANOCO (Ter Braak and Šmilauer, 1998).

233   **3.   Results**

234   *3.1. Temporal trend of mollusk species diversity since the last deglacial warming*

235   We analyzed 255 mollusk fossil samples from three loess sections (81, 90 and 84

236   samples from Linxia, Jingchuan, and Yaoxian, respectively), comprising 28 mollusk

237   species and 54,400 individuals (Figs. 2 and 3). We used previously established

238   chronological frameworks, based on 24 optically stimulated luminescence (OSL) dates

239   (Fig. S3), which ensured that the fossil records spanned the Last Glacial Maximum

240   (LGM), the last deglacial warming, and the Holocene epoch (Dong et al., 2015), with an

241   average temporal resolution of ~200-300 years per sample (Fig. 2).

242   The records reveal substantial temporal instability in mollusk diversity among the sites.

243   The mollusk assemblages at Linxia in the far north of the transect, proximal to the desert

244   steppe ecotone, yielded a low species richness (mean of ~2-3 species) during the LGM,

245   with an increase to a relatively high level (~5-6 species) after ~17 kyr BP, which was

246   sustained until ~4 kyr BP (Figs. 2 and 4). The Shannon-Wiener index (H') also

247   significantly increased until the early-mid Holocene, reaching a higher level than that of

248   today (an increase of ~30%) (Fig. 4). The higher H' index for the early-mid Holocene

249   indicates that there was a greater number of species and that their abundance was more

250   evenly distributed than was the case for both the LGM and the present day.

251   The mollusk fauna in the 'intermediate-diversity' steppe community at Jingchuan

252   (average of ~6-7 mollusk species) show major fluctuations in species richness but no

253   marked increase since the last deglaciation. The H' index also varied during the interval

254   of ~17-8 kyr BP (H' ~1.08-1.77) (Fig. 4), but the mean H' values were only slightly

255   higher for the early-mid Holocene than for the last glacial period.

256   The most diverse community, at Yaoxian, also shows no long-term trends in mollusk

257   diversity over the last 25 kyr, with an average of 9-10 mollusk species, although there

258   were short-term fluctuations. The H' value of the LGM communities was almost the same

259   (~1.79±0.09) as that of the Holocene communities (~1.78±0.17) (Fig. 4 and Fig. S4).

260   Overall, the temporal variation of diversity in different communities decreased

261   significantly as diversity increased, with a larger proportional effect in low-diversity

262   communities than in high-diversity communities, in response to climate change

263   reconstructed by proxy data such as magnetic susceptibility since the last deglaciation.

264

265   *3.2. Mollusks adjust their community structure to maintain species diversity*

266   To explore the different patterns of mollusk diversity dynamics, we determined which

267   species either appeared in or disappeared from the communities. All of the mollusk

268   species identified in the Chinese loess sequences that have persisted through past glacial-

269   interglacial cycles have modern equivalents. The relevant taxa can be grouped primarily

270   into cold-aridiphilous (CA) and thermo-humidiphilous (TH) groups, as well as a small

271   number of cool-humidiphilous and eurytopic groups (Chen and Gao, 1987; Wu et al.,

272   2002; Wu et al., 2018) (Fig. 2). At the northwestern locality (Linxia), the glacial fauna

273   primarily comprised CA species, such as *Vallonia tenera*, *Cathaica richthofeni* and

274   *Pupilla* cf. *turcmenica*, which persisted into the early-mid Holocene. The addition of new

275   species (mostly TH taxa: e.g., *Punctum orphana*, and *Vallonia* cf. *pulchella*) during the

276   last deglacial warming resulted in a significant increase in overall mollusk species

277   diversity.

278   In contrast, although there was no significant change in species diversity in the

279   southeast at Jingchuan and Yaoxian, the mollusk fauna underwent a shift from the CA

280   ecological taxa to TH species. The CA taxa (mainly *V. tenera*, *P. aeoli* and *C.*

281   *pulveratrix*) were abundant (~50-60% of the assemblages) in the last glacial period but

282   they decreased after the last deglaciation, whereas the TH species (e.g., *Opeas*

283   *striatissimum*, *Macrochlamys angigyra* and *G. armigerella*) appeared and increased in

284   abundance during the last deglaciation and became the dominant species (~70-80% of the

285   assemblages) during the early-mid Holocene (Fig. 2). The results of cluster analysis

286   detected a systematic turnover (up to ~60% of assemblages) in species composition since

287   the last deglaciation (Fig. 2). Ultimately, ~2-3 dominant CA species disappeared from the

288   area, but this loss was accompanied by the appearance of TH species in the early-mid

289   Holocene epoch.

290   One intriguing aspect of these mollusk diversity dynamics is the role of cold-tolerant

291   species, which persisted at the low-diversity sites rather than being substituted since the

292   last deglaciation. Most CA species have a broader thermal tolerance than TH species and

293   currently live near these low-diversity sites (Fig. 5A), where hydrothermal conditions

294   have yet to reach or are close to their optimum for cold-tolerant species. Therefore, a

295   moderately warmer climate at a given site may enhance their abundance. In contrast, the

296   current habitat in the southeast is closer to the upper thermal limit of the CA species.

297   Therefore, the CA species in the southern community show a reduced abundance due to

298   climatic warming.

299

300 **4. Discussion**

301 *4.1. Climate-driven shift in soil-fauna-flora community composition*

302   Temperature and precipitation are the two most important factors affecting soil faunal
303 and floral communities (Chen and Gao, 1987; Wu et al., 2018). The mean temperature in
304 the Chinese Loess Plateau (CLP) has been estimated to have increased by at least ~5-7°C
305 since the last glacial maximum (LGM) to the early to mid-Holocene, which was ~2°C
306 higher compared to the present (Lu et al., 2007; Wang et al., 2001). The loess magnetic
307 susceptibility (MS) record exhibits substantial variations (~70-220×10^{-8}m^{3}kg^{-1}) which
308 reflect monsoonal rainfall, which, in concert with other quantitative palaeoclimate data
309 (e.g. bulk organic δ^{13}C, see Lu et al., 2013; Yang et al., 2015), indicate that humidity
310 increased significantly at the Pleistocene-Holocene transition. Climate oscillations from
311 cold-dry to warm-wet conditions associated with the retreat and advance of the East
312 Asian summer monsoon (EASM), respectively, are shown to have driven the
313 modification of the mollusk communities. This is roughly consistent with the observation
314 that increases in diversity and several additional TH taxa manifested in the record from
315 ~17-15 kyr BP. Notably, at the present day, these species are currently found in warmer
316 and wetter regions compared to the three localities (Dong et al., 2019; Wu et al., 2018),
317 implying that they became adapted to warm and wet climates associated with the advance
318 of the EASM. Therefore, the strengthened EASM resulted in the development of more
319 warm-mesic components in the steppe, with a concomitant restructuring of the mollusk
320 fauna from CA-dominated to TH-dominated in the warming conditions since the last
321 deglaciation.
322   Despite the observed low mollusk diversity in this semiarid steppe environment (max.
323 28 species) (Dong et al., 2019; Rousseau and Wu, 1997), the species richness and H'
324 value of high-diversity communities at the southern site were always higher than that of
325 species-poor communities at the northern sites. The southern Yaoxian mollusk fauna was
326 dominated by more diverse and abundant TH species (e.g., *O. striatissimum*, *M. angigyra*
327 and *G. armigerella*) than the northern mollusk fauna since the last deglaciation. The
328 increase in the dominant mollusk species (*P. orphana* and *G. armigerella*) in the
329 northwestern community corresponds to an increase in herbaceous plants such as Poaceae

13

330   and Fabaceae (Jiang and Ding, 2005; Jiang et al., 2013), while the appearance of *O.*

331   *striatissimum* and *M. angigyra* in the southern community is consistent with pollen

332   assemblages indicative of warmer and wetter conditions, comprising Lamiaceae and

333   *Polygonum*, and with a greater tree pollen representation (Fig. 5B) (Li et al., 2003; Sun et

334   al., 1997). The different dominant mollusk species among the three localities were

335   closely associated with the specific wet-tolerant components of their corresponding

336   vegetation zones (Fig. S5). This result is consistent with the climatic and environmental

337   gradient from southeast to northwest (Dong et al., 2019).

338   Of key importance is that the three study sites are all flat-topped ('Yuan') loess

339   deposits that lack substantive microtopographic changes and have a relatively stable

340   landscape and habitat type. This, therefore, indicates that the compositional differences

341   between the different profiles sampled were controlled mainly by climatic warming and

342   associated hydrological changes, which drove the observed ecological changes. The RDA

343   shows that EASM precipitation (based on changes in MS and $\delta^{13}C$) and Northern

344   Hemisphere average temperature (Nor. AT) is the most likely causal factors explaining

345   more than half of the variation in the mollusk-pollen data (Fig. 5B).

346

347   *4.2. Paleoecological implications for biodiversity under projected climatic warming*

348   Average global temperatures are predicted to increase during the 21st century. If

349   climate change occurs at a moderate rate (of the order of 2 °C or less per century), as in

350   the Holocene optimum period (although there were rapid and frequent temperature

351   changes of least ~5-7 °C across the late Pleistocene/Holocene transition), our records

352   suggest that mollusk species could be able to migrate and track thermal conditions that

353   match their ecological niche along the environmental gradients. The range of each

354   species shifted as a result of enhanced population growth in locations at the leading edge

355   and by reduced performance and negative population growth at the trailing edge. We

356   speculate that more warmth-adapted taxa will arrive and become dominant species under

357   sustained global warming.

358   Our long-term records demonstrate that ~2 °C of natural warming is generally

359   conducive to either the maintenance of or an increase in soil mollusk diversity in East

360 Asia. This agrees with recent palaeoecological evidence showing that there is no globally

361 consistent trend towards lower community diversity under warming scenarios (Engels et

362 al., 2020). We suggest that the synchronous enhancement of a unique hydro-thermal

363 configuration associated with the strengthening of the EASM since the last deglaciation

364 improved the performance of the soil fauna. This implies that long-term variations in site-

365 specific factors, such as water availability, vegetation and habitat change, together with

366 rising temperature, play a significant role in regulating species diversity.

367 　　Our results suggest that the extent of the temporal variation in mollusk diversity

368 affected by a long-term climate shift is not homogeneous in communities with different

369 diversity levels within the temperate steppe and the greater biodiversity generally

370 provides greater resilience. Even if the climate shifts dramatically from cold conditions

371 analogous to the LGM to those of the warm Holocene epoch (~2 °C warmer than

372 present), species-rich mollusk communities in the forest-steppe zone appear to be capable

373 of maintaining dynamic temporal stability of diversity rendering them resilient to

374 perturbations. The equilibrium value of richness may represent the carrying capacity of

375 the local community in temperate steppe as a result of long-term adaption to a specific

376 site (Hansen et al., 2011). This provides an important baseline for assessing the number

377 of species (i.e., mollusks), which can be expected to disappear from sites due to short-

378 term climate change. Even so, ~60% of the community populations were replaced

379 unexpectedly, as warm-stenothermic taxa migrated into regions and habitats that

380 currently experience temperatures that are too low for their development.

381 　　In contrast, species-poor soil communities close to the desert-steppe ecotone are

382 deemed to be highly sensitive to external disturbances and fluctuations driven by climate

383 change. Although other soil biotas not considered here may also be responsive to climate

384 change, our results suggest an overall increase in the diversity of soil fauna under

385 projected warming associated with the enhancement of the EASM. However, it should be

386 noted that the future anthropogenic weakening of the EASM would increase the risk of

387 the collapse of these communities. Our results highlight the need for maintaining

388 complex soil environments with species-rich communities to offset the detrimental

389   effects of global warming on soil fauna diversity. Future anthropogenic reductions in

390   biodiversity will render these communities less resistant to climate change.

391

392   **5. Conclusions**

393   The biodiversity and stability of terrestrial plant and animal communities are

394   threatened by recent environmental disturbances. It is unclear whether the temporal

395   stability of biodiversity in the face of climate change varies with environmental gradients

396   in different communities due to the lack of long-term data. Here we report three

397   centennial-resolution temporal sequences of mollusk diversity changes along

398   environmental gradients in East Asia since the last deglacial warming. The results, based

399   on well-dated mollusk fossil records from loess sections dating back 25 kyr, suggest that

400   ~2°C of natural warming since the last deglaciation was generally able to sustain or

401   increase mollusk diversity in East Asia. Furthermore, we show that the response of

402   mollusk diversity to deglacial warming is differential along a climatic and vegetation

403   gradient. Although the compositional turnover reached ~60% in high-diversity forest-

404   steppe communities, with thermo-humidiphilous taxa replacing cold-tolerant taxa to fill

405   their thermal niche, these communities show no long-term trends in mollusk diversity

406   over the last 25 kyr. In contrast, the temporal stability of mollusk diversity decreased

407   along the environmental gradient towards semi-arid low-diversity communities,

408   emphasizing the important role of the environmental background and its resulting

409   diversity gradients in regulating the temporal stability of biodiversity on a long timescale.

410

Author Contributions:

Y.D., N.W., and H.L. conceived the study, Y.D., N.W., F.L., L.H., and H.L. undertook the fieldwork, Y.D., N.W., F.L., L.H., and H.L. collected the mollusk data, Y.D. and L.H. identified and counted the mollusk species, Y.D. performed statistical analyses, Y.D., N.W., F.L., L.H., H.L., and N.C.S. wrote the text; N.C.S. contributed to the interpretation of the results and writing of the text. All authors commented on the interpretation of the results and gave final approval for publication.

Competing Interest Statement: The authors declare no conflict of interest.

Data and materials availability

All the mollusk fossil remains were deposited in Key Laboratory of Cenozoic Geology and Environment, Institute of Geology and Geophysics, Chinese Academy of Sciences, China. All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Information.

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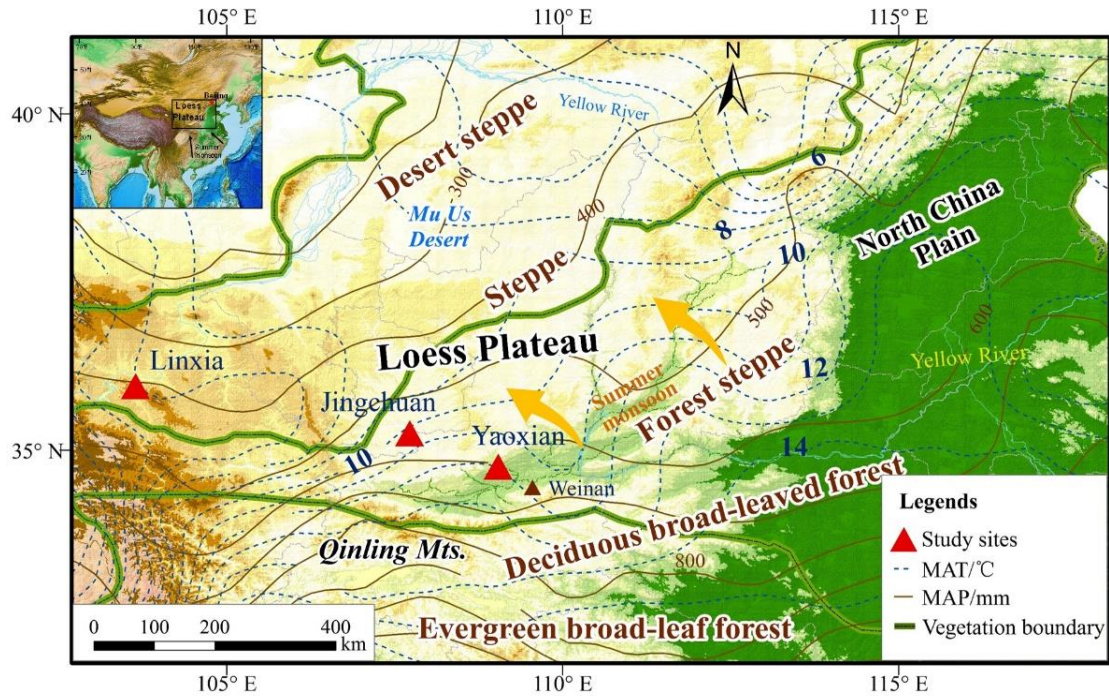
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Figures and Tables

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Fig. 1. Location of the study sites (solid red triangles) along modern climatic and environmental gradients from desert steppe to forest-steppe (Wu, 1994). The inset map shows the location of the Chinese Loess Plateau and the prevailing monsoon circulation. The arrows indicate the direction of the summer monsoonal winds. Brown triangle denotes location of the site referenced in the text (Wu et al., 2002). The isohyets (in millimeters/mm; gray lines) and isotherms (in degrees Celsius/°C; brown dashed lines) represent values averaged over 51 years (1951–2001) (Lin et al., 2002).

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(A) Linxia

(B) Jingchuan
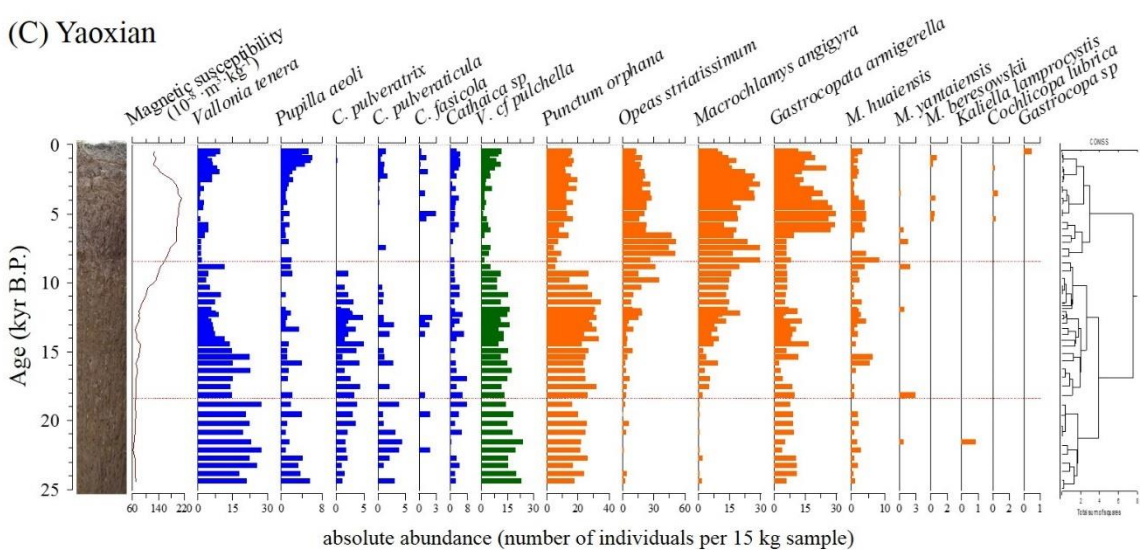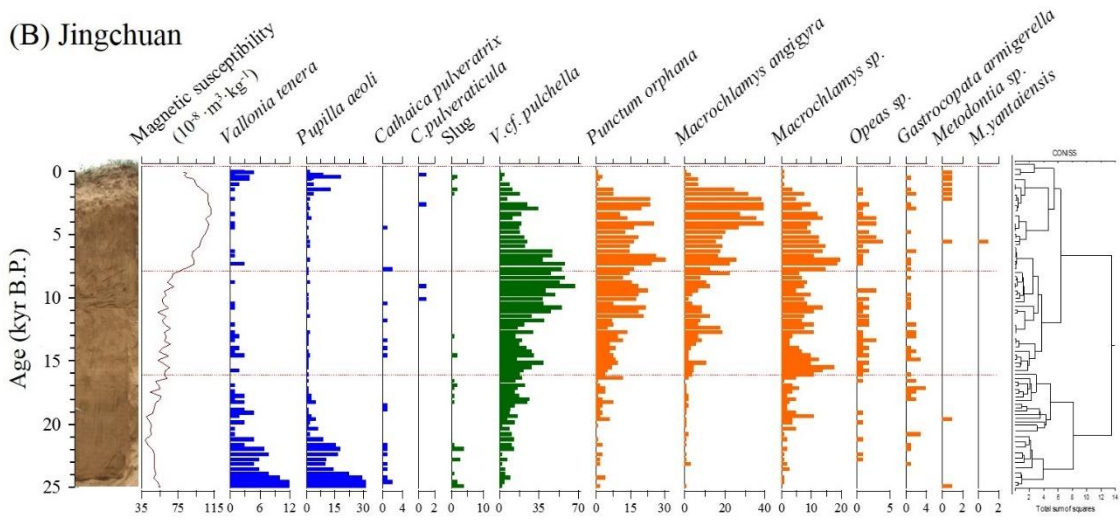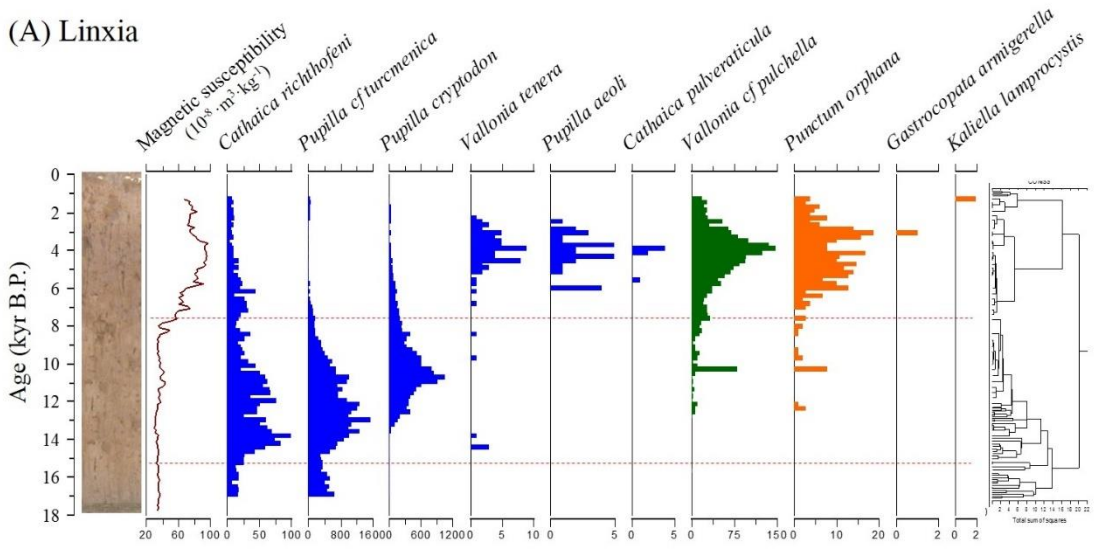
(C) Yaoxian

absolute abundance (number of individuals per 15 kg sample)

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Fig. 2. Variations in the absolute abundance of mollusk species (number of individuals per 15 kg of sediment) during the past 25 kyr at the Linxia (A), Jingchuan (B) and Yaoxian sections (C) compared with the magnetic susceptibility record. Changes in the temporal abundance of the three ecological groups are shown in blue (cold-aridiphilous), green (cool-humidiphilous) and red (thermo-humidiphilous). The three defined mollusk zones are based on the results of constrained cluster analysis, which are shown on the right of the diagram.

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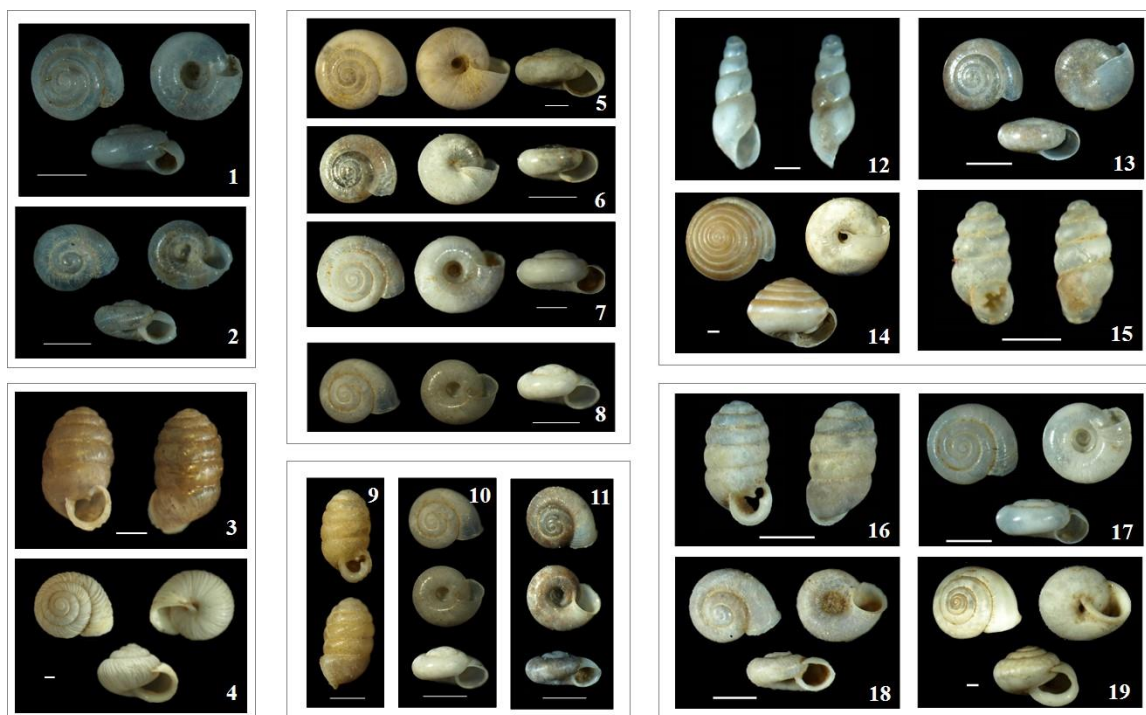
Fig. 3. Photos of representative mollusk species in the Linxia, Jingchuan and Yaoxian loess-palaeosol sequences. All scale bars are 1 mm. 1 *Punctum orphana* from Linxia S_0 paleosol; 2 *Vallonia tenera* from Linxia S_0 paleosol; 3 *Pupilla cryptodon* from Linxia L_1 loess; 4 *Cathaica richthofeni* from Linxia L_1 loess; 5 *Macrochlamys* sp. from Jingchuan S_0 paleosol; 6 *Macrochlamys angigyra* from Jingchuan S_0 paleosol; 7 *P.*

633 *orphana* from Jingchuan S_0 paleosol; 8 *Vallonia* cf. *pulchella* from Jingchuan S_0 paleosol;

634 9 *Pupilla aeoli* from Jingchuan L_1 loess; 10 *V.* cf. *pulchella* from Jingchuan L_1 loess; 11

635 *V. tenera* from Jingchuan L_1 loess; 12 *Opeas striatissimum* from Yaoxian S_0 paleosol; 13

636 *M. angigyra* from Yaoxian S_0 paleosol; 14 *Metodontia huaiensis* from Yaoxian S_0

637 paleosol; 15 *Gastrocopta armigerella* from Yaoxian S_0 paleosol; 16 *P. aeoli* from

638 Yaoxian L_1 loess; 17 *P. orphana* from Yaoxian L_1 loess; 18 *V. tenera* from Yaoxian L_1

639 loess; 19 *Cathaica pulveraticula* from Yaoxian L_1 loess.

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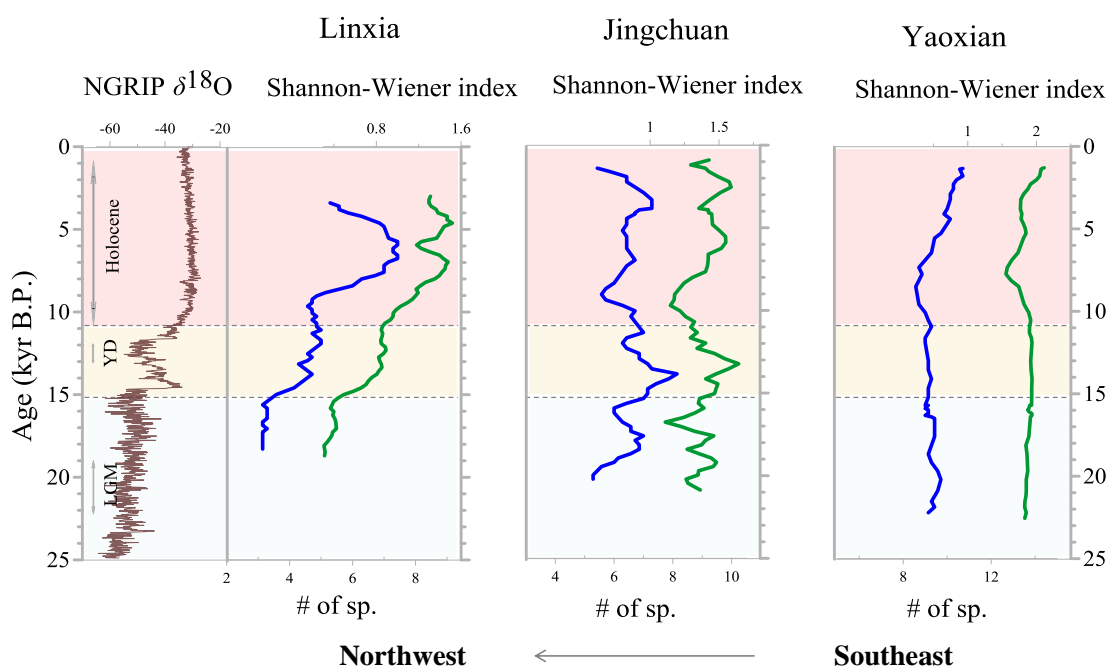
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643 **Fig. 4. Spatiotemporal variations in the number of mollusk species (S, species**

644 **richness, blue line) and the Shannon-Wiener index (H' index, green line), and**

645 **comparison with the Greenland NGRIP ice-core δ^{18}O record** (Huber et al., 2006)

646 **over the last 25 kyr.** The Holocene, Younger Dryas (YD) and LGM intervals are

647 indicated.

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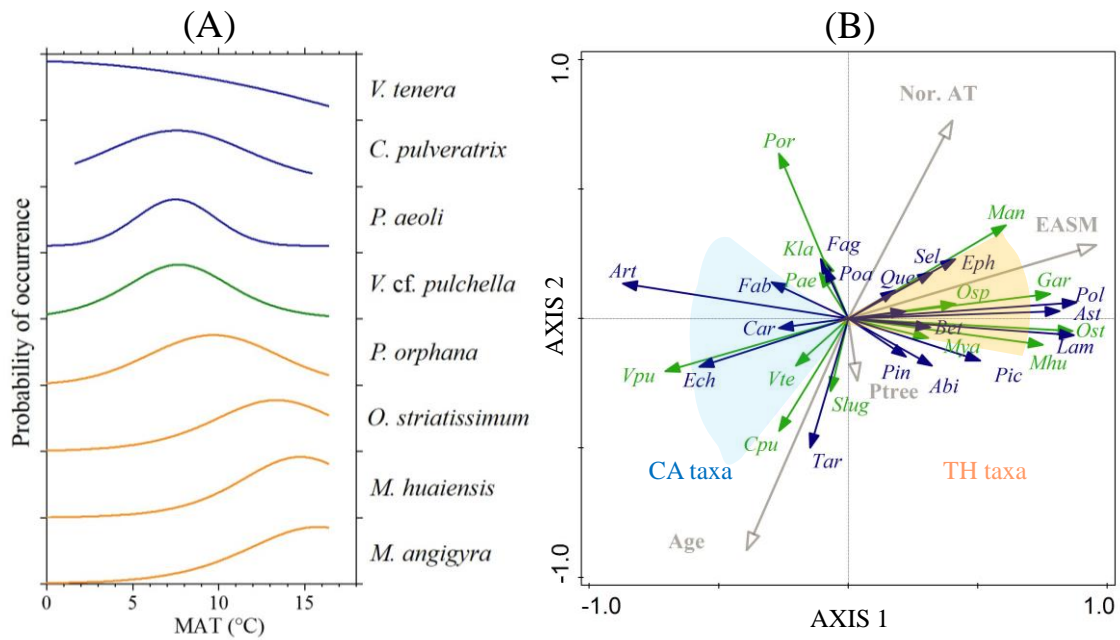
Fig. 5. Estimated mollusk thermal response curves (A) based on species current distribution ranges, and biplot based on redundancy analysis of community composition for the mollusk and pollen assemblages with respect to four environmental variables (B). MAT in x axis is defined as mean annual temperature. Mollusk species modern distribution ranges based on a field investigation of a spatial data set comprising 282 assemblages collected from surface soils across an ~800 km climatic gradient in northern China (Dong et al., 2019). The gray arrows are environmental variables, green arrows are mollusk assemblages and blue arrows are pollen components. Abbreviations for environmental variables: Nor. AT, Northern Hemisphere average temperature; EASM, East Asian summer monsoon; Ptree, arboreal pollen percentages. Abbreviations for species: Vte, *V. tenera*; Vpu, *V. cf. pulchella*; Pae, *P. aeoli*; Gar, *G. armigerella*; Cpu, *C. pulveraticula*; Por, *P. orphana*; Kla, *Kaliella lamprocystis*; Ost, *O. striatissimum*; Man, *M. angigyra*; Mhu, *Metodontia huaiensis*; Mya, *M. yantaiensis*; Pic, *Picea*; Pin, *Pinus*; Abi, *Abies*; Que, *Quercus*; Bet, *Betula*; Art, *Artemisia*; Ast, Asteraceae; Tar, *Taraxacum*-type; Ech, *Echinops*-type; Fag, *Fagopyrum*; Poa, Poaceae; Eph, *Ephedra*; Pol, Polygonaceae; Lam, Lamiaceae; Fab, Fabaceae; Car, Caryophyllaceae; Sel, *Selaginella sinensis*.