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1 **Can people change the ecological rules that appear general across space?**

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24

25 **Abstract**

26 **Aim:** The projections of human impact on the environment and biodiversity patterns are crucial
27 if we are to prevent their destruction. Such projections usually involve the assumption that the
28 same human activities always affect biodiversity in the same way either in geographically distant
29 areas within the same time scale or in the same areas in different periods. In this paper, plant and
30 snail fossils from Central Europe that cover the last 12,000 years provide evidence against this
31 assumption.

32 **Location:** Central Europe

33 **Methods:** We examined fossil data on central European plants and snails, and extracted **time**
34 **series** of (i) local species richness (alpha - diversity) at a scale of approximately 300×300
35 meters and decays of (ii) Jaccard index and (iii) Simpson beta with increasing distance (up to
36 approximately 400 Km) through time.

37 **Results:** We show that two vital biodiversity patterns follow neither oxygen-isotope nor borehole
38 temperature proxies, but instead vary between archaeologically known periods, with the most
39 noticeable and irreversible breaks (i) when arable agriculture was introduced into **Central**
40 **Europe**, (ii) when the Roman Empire collapsed, and (iii) during the event known as the 12th
41 century colonization in Central Europe. The patterns computed from data across time sometimes
42 contradicted the patterns computed across space.

43 **Main conclusion:** We therefore infer that people can, and sometimes have, contributed to
44 temporal changes in ecological rules that are seemingly general across space. Our findings
45 indicate that the changes in ecological rules are so substantial that efforts to project future

46 biodiversity based on space-for-time substitution might fail, unless we gain knowledge about
47 how these general rules are altered.

48

49 Introduction

50 Hartley (1953) famously remarked that “the past is another country,” and ecologists have often
51 taken the dictum almost literally, using analyses of spatial variation in biodiversity and its drivers
52 to draw inferences about likely temporal dynamics in response to projected environmental
53 change (Thuiller *et al.*, 2005; Kerr *et al.*, 2007; Algar *et al.*, 2009; Kharouba *et al.*, 2009;
54 Svenning *et al.*, 2009; Blois *et al.*, 2013a; ESKILDSEN *et al.*, 2013; Kerr & Dobrowski, 2013). This
55 approach depends on the tacit assumption of uniformitarianism (Gould, 1965; Thuiller *et al.*,
56 2005; Kharouba *et al.* 2009; Blois *et al.*, 2013ab; ESKILDSEN *et al.*, 2013), that responses to
57 environment remain invariant over time. While the palaeontological history of life in deep time
58 (e.g., Jablonski *et al.*, 2006; Tomášových & Kidwell, 2010) and its responses to environmental
59 drivers are increasingly well documented (e.g., Rose *et al.*, 2011; Mayhew *et al.*, 2012; Huang *et al.*
60 *et al.*, 2014; Mannion *et al.*, 2014; Fraser *et al.*, 2014; Tomášových *et al.*, 2015, Lyons *et al.*, 2016),
61 less attention has been given to changes of biodiversity rules and mechanisms in Europe during
62 the Holocene (but see Feurdean *et al.*, 2010; and Lyons *et al.*, 2016; or Shuman *et al.*, 2012;
63 Blois *et al.*, 2013ab; Blarquez *et al.*, 2014 for the North American Holocene). This is despite the
64 fact that the European Holocene has a well-documented history, during which people started
65 gradually changing their environment by increasingly complex and intensive agricultural
66 management. The European Holocene can therefore be seen as a pseudo-experiment, showing
67 the responses of ecological rules to the long-term pressure of different agricultural technologies.

68 Central Europe (i.e., the focal area; Fig. 1) has experienced several culturally defined
69 periods and two main climate periods since the last Ice-Age. In short, during the transition period
70 between the Last Ice Age and the Holocene, the temperature was generally increasing (see Bond
71 *et al.*, 1997 for short term exceptions) and reached approximately the present level by around

72 9,500 calBP (Alley *et al.*, 1995). Since then, temperature has stagnated showing relatively
73 shallow variations (Wanner *et al.*, 2008). In general, nearly all known temperature proxies show
74 these two periods, but the detailed variation at finer temporal scale is a subject of debate.

75 Just after the Last Glacial Maximum (approximately 20,000 calBP; all temporal data are
76 hereafter calibrated and expressed in years before present), the focal area was re-settled by
77 hunters and gatherers (Lowe *et al.*, 1994; Svoboda, 1999). The first settlements where people
78 practiced small-scale horticulture are documented from about 7,500 calBP in the lowlands of the
79 focal area (Bogaard, 2004). Arable agriculture is considered to have arrived in the region shortly
80 after 6,000 calBP (Bogaard, 2004). From then, settlement spatial patterns were stable with only
81 limited breaks such as rebellions against Rome, which expanded to the south of this area and
82 attempted to control the adjoining territory. This period of relative prosperity ended in 1,626
83 calBP when the Great Migration in Europe began and the collapse of the Roman Empire
84 commenced. During the Great Migration in Europe, many different tribes of northern and eastern
85 origin settled successively in the focal region. Most importantly, some of them were of a
86 nomadic lifestyle and survived on pastoralism (Fouracre, 2006) so that the extent of arable
87 agriculture was demonstrably lower than in the previous period. New peasants practicing arable
88 agriculture gradually settled in the focal region after approximately the 8th century AD (ca. 1,300
89 calBP). In the late 12th and early 13th centuries AD (850-950 BP), the population of the region
90 increased rapidly, because the king encouraged farmers and shepherds from overpopulated parts
91 of Europe to settle in the [region](#) (Barlett, 1993).

92 The principle of uniformitarianism is applied in different fields of biology with slightly
93 different meanings and terminology. Palaeobiologists and ecologists use the assumption of
94 space-for-time substitution [to mean](#) the stability of [the](#) environmental requirements of individual

95 species (i.e. fundamental niche, see Williams *et al.*, 2007) across time (e.g., Kharouba *et al.*,
96 2009; Walker *et al.*, 2010). Paleobiologists *sometimes* refer to the assumption of space-for-time
97 substitution as ‘the assumption of uniformitarianism’, and employ it when making an inference
98 about the past environment from the presence of recently living species in the fossil archive (e.g.,
99 Mannion *et al.*, 2014; Faurby and Svenning, 2015; Lyons *et al.*, 2016). Unlike palaeobiologists,
100 ecologists use the assumption of space-for-time substitution when projecting future species
101 spatial ranges, and spatial variation of diversity under different climatic scenarios (see Williams
102 *et al.*, 2007). The assumption of uniformitarianism, however, originally referred to the stability
103 of laws, rules or patterns across time (Gould, 1965), which links the assumption with the concept
104 of generality (Lawton, 1999), that is the invariance of ecological *laws and mechanisms that*
105 *underpin them* across space (White *et al.*, 2006; Šizling & Storch, 2007), time (White *et al.*,
106 2006) and taxa (White *et al.*, 2006; Šizling & Storch, 2007; Storch & Šizling 2008; Harte *et al.*,
107 2009). Here we focus on the assumption of uniformitarianism for biodiversity rules (Mannion *et*
108 *al.*, 2014; Faurby and Svenning, 2015; Lyons *et al.*, 2016), and we therefore add a third
109 dimension to the recently used concept of changing climate, and constant or changing
110 fundamental niches (Williams *et al.*, 2007).

111 Macroecological research has demonstrated and theoretically supported a number of
112 biodiversity patterns that would have good claims to being deemed general ecological *rules or*
113 *even laws* (Lawton, 1999). *Amongst these are the repeated findings that* local diversity, as well
114 as species spatial turnover (i.e. a measure of dissimilarity) are higher in productive and warm
115 environments (Currie *et al.*, 2004; Drakare *et al.*, 2006; Storch *et al.*, 2005; Dornelas *et al.*,
116 2014), and *that* similarity between assemblages decreases with diversity (Lennon *et al.*, 2001;
117 Koleff & Gaston, 2002) and distance (Nekola & White, 1999; Azaele *et al.*, 2009). If these

118 relationships hold constant across space, time and taxa, they could be used for further
119 specification of biodiversity patterns projected under different climate scenarios (e.g., Kerr *et al.*,
120 2007; Kharouba *et al.*, 2009; Dornelas *et al.*, 2013). Alternatively, a variation of spatial
121 biodiversity patterns across time would raise questions such as: ‘Can methods of biodiversity
122 projection produce results that agree with observed spatial biodiversity patterns?’ or ‘Does
123 temporal variation in spatially and/or taxonomically general rules also imply changes in their
124 underlying mechanisms?’ or ‘What is a proper meaning of the biodiversity patterns that vary
125 across time?’

126 Here, we examine temporal behaviour of spatial biodiversity patterns that might be
127 considered rules or even laws. We do this by analysing fossil data on Central European plant
128 (Kuneš *et al.*, 2009; Dudová *et al.*, 2010; Žák *et al.*, 2010; Břízová, 2009; Stebich & Litt, 1997;
129 Hahne, 1992; Skrzypek *et al.*, 2009) and land snail (Horáčková *et al.*, 2014) assemblages (Fig. 1,
130 see S1 for details on the datasets) that cover the past 14.3 thousand years. These analyses of plant
131 and snail assemblages map two different but complementary environments; plant communities
132 were compiled from pollen grains that are mostly preserved in acidic environments, whereas
133 snail communities were extracted from shells that are preserved only in carbonaceous
134 environments.

135

136

137 **Methods**

138 *Patterns to track biodiversity*

139 To examine changes in spatial patterns of biodiversity through the Postglacial period (i.e., the
 140 Late Glacial and the Holocene), we will assess both shifts in local species richness (hereafter S),
 141 and two different indices of assemblage similarity: the Jaccard index (hereafter J , $J \stackrel{\text{def}}{=} S_{A \cap B} / (S_A + S_B - S_{A \cap B})$;
 142 $S_{A \cap B} / S_{A \cup B}$; Gaston *et al.*, 2007) and Simpson beta ($\beta_{Sim} \stackrel{\text{def}}{=} S_{A \cap B} / \min(S_A, S_B)$); where S_A , S_B ,
 143 $S_{A \cap B}$ and $S_{A \cup B}$ are species richnesses of the sites A and B, and shared and common species
 144 richness of the sites, respectively; for more see S2; Gaston *et al.*, 2007) or rather one minus
 145 Simpson beta (hereafter β'_{Sim}) to ensure that higher values reflect higher similarity (Fig. S2A).

146 The indices S , J and β'_{Sim} (i) are increasingly understood to be key aspects of biodiversity
 147 change (e.g., Gaston *et al.*, 2007; Šizling *et al.*, 2009; Keil *et al.*, 2012; Gaston, 2003; Tuomisto,
 148 2010, Dornelas *et al.*, 2014), (ii) cannot be calculated from each other, so that we can increase
 149 the information on the focal assemblages by combining these indices (Fig. S2B), and (iii) they
 150 are linked to several other biodiversity patterns (e.g., Koleff & Gaston, 2002; Šizling & Storch,
 151 2004; Tjørve & Tjørve, 2008; Šizling *et al.*, 2009; Jost, 2010; Dornelas *et al.*, 2014). For
 152 example, J tends to increase with increasing S (Koleff & Gaston, 2002; Jost, 2010) and is one of
 153 two crucial drivers of species-abundance distribution (Šizling *et al.*, 2009). J and β'_{Sim} capture
 154 the proportion of species shared by two different assemblages; however, J relates the species
 155 overlap to the *total* S across both assemblages whereas β'_{Sim} relates the overlap to the size of the
 156 *smaller* assemblage (S2). Consequently, J is a symmetric measurement of similarity between
 157 two assemblages, while β'_{Sim} reflects the degree to which the less species rich assemblage is
 158 nested within the more speciose community (S2).

159 While J and β'_{Sim} carry information about the structure of an assemblage, their spatial
 160 decays provide information on the spatial autocorrelation in assemblage similarity. Apparently,

161 the focal region may be more species rich than expected from local S , even if the similarity of
 162 two adjacent assemblages is high. This happens if there is considerably lower spatial
 163 autocorrelation in assemblage similarity at large distances than at short distances, and therefore
 164 the decay in the values of the similarity indices is steep (Fig. 2, compare the distance decays of
 165 plant J values between the three time windows_5,100, 6,900 and 14,300 calBP). As a rover would
 166 say: ‘I do not see big changes as I go, but every evening I find myself on absolutely different
 167 land’. Indeed, high similarity between adjacent areas does not imply high similarity between two
 168 non-adjacent areas (Šizling *et al.*, 2011), because the ratio between the short-distance similarity
 169 and long-distance similarity depends on the range of the forces that cause spatial autocorrelation.
 170 Here we examine similarities between several pairs of assemblages scattered across a landscape.
 171 The distance between the assemblages in each pair therefore varies. As J and β'_{Sim} decay with
 172 distance between assemblages (Nekola & White, 1999), we explore the rates of distance decays
 173 to control for the effect of distance on the focal indexes.

174 Several models of distance decay in assemblage similarity (Fig. 2,S3) have been
 175 proposed. Here we utilize the simplest, an exponential approach (Nekola & White, 1999; see S4),
 176 which obeys

$$S = S_0 e^{r_{a1}a + r_{\sigma1}\sigma^{-1} + r_{t1}t_{acc} + r_{N1}N + r_{E1}E}, \quad (\text{Eq. 1})$$

$$J = J_0 e^{r_{d2}d + r_{\Delta a2}\Delta a + r_{a2}a_{min} + r_{\sigma2}\sigma_{min}^{-1} + r_{\Delta\sigma2}\Delta\sigma + r_{t2}t_{acc} + r_{\Delta t2}\Delta t_{acc} + r_{N2}N + r_{E2}E}, \quad (\text{Eq. 2})$$

177 and

$$\beta'_{Sim} = \beta'_{Sim,0} e^{r_{d3}d + r_{\Delta a3}\Delta a + r_{a3}a_{min} + r_{\sigma3}\sigma_{min}^{-1} + r_{\Delta\sigma3}\Delta\sigma + r_{t3}t_{acc} + r_{\Delta t3}\Delta t_{acc} + r_{N3}N + r_{E3}E}, \quad (\text{Eq. 3})$$

178 where d is distance between the assemblages, a is altitude, N is latitude, E is longitude, σ is
 179 sampling effort (see S6 for details), and t_{acc} is time during which the focal sample has
 180 accumulated. The symbol Δ stands for the difference of respective values between the

181 assemblages. The r -values are rates of respective decays, and S_0, J_0 and $\beta'_{Sim,0}$ would be S, J and
 182 β'_{Sim} if data were ideal ($\sigma \rightarrow \infty, \Delta a = 0, \Delta \sigma = 0, t_{acc}=0, \Delta t_{acc} = 0$) and if d, N, E, a were zero.
 183 Eq. 1 does not capture a distance decay, but captures species richness (S) decay along spatial ($a,$
 184 N, E), temporal (t), and data quality (σ) gradients.

185

186 *Data standardization*

187 Our goal is not to test an hypothesis about the underlying mechanisms, but to employ a practical
 188 tool to unify heterogeneous data in order to track temporal variation in biodiversity patterns. To
 189 do so, we first standardized our data to account for differences in a, N, E, σ and t_{acc} . In the first
 190 step, we extracted the rates of the decays (i.e., parameters r) by fitting (S2) the Eqs 1-3 to data in
 191 each 200-year time window (Fig. 1). Having generated, for each predictor and each time
 192 window, a unique value of r , we were able to estimate the S, J and β'_{Sim} for any combination of
 193 predictors and any time window. We have proven that the estimated series of S, J and β'_{Sim}
 194 showed no bias along its predictors (S4,S5,S7,S8.T1; see also Xiao *et al.*, 2011 for biases caused
 195 by logarithmic transformations), thus capturing a central trend. Therefore, in the second step, we
 196 used Eqs 1-3 to compute standardized values of S, J and β'_{Sim} by setting $d = 1\text{km}; \Delta a =$
 197 $0; a_{min} = 300\text{m}; \sigma_{min} = 1,000$ specimens and 1km^2 in plants and snails, respectively (for
 198 details see S6); $\Delta \sigma = 0; t_{acc} = 1\text{year}; \Delta t_{acc} = 0; N = 50^o$ and $E = 15^o$. These nine input
 199 values define our reference point (Fig. 1).

200 For comparison, we therefore considered the Postglacial variation in the focal
 201 biodiversity measures (including rates of their distance decays; r_{d2}, r_{d3}) of two typical sites
 202 located in the middle of Central Europe (asterix in Figs. 1, S1), set 1km apart at 300m above sea

203 level. Although our standardized values would differ from the tracked measures had they been
204 observed, the lack of bias (S5,S7,S8.T1) in our model relative to the data ensures that detected
205 temporal trends will be unbiased.

206

207 *Filter to sort data: agricultural vs non-agricultural landscape*

208 In order to examine the possible impact of agriculture on changes in biodiversity drivers and
209 rules, for some analyses, we split the plant data into two sub-samples: sites with the indicators of
210 agriculture (*Avena-type*, *Castanea sativa*, *Cerealia undif.*, *Fagopyrum*, *Juglans*, *Pisum sativum*,
211 *Secale cereal*, and *Vitis* pollen; and *Zea mays* after 1492) and all others. We hereafter refer to the
212 sites with the pollen spectra containing the indicators of agriculture as agricultural sites, and
213 those without indicators of agriculture as wild sites. The wild sites may include forest where
214 people gathered firewood, established pastures or even deserted parts of landscape.

215

216 *Statistical analyses*

217 Having standardized S , J and β'_{Sim} as well as rates of distance decays, we can now assess the
218 effects of environmental drivers such as deforestation and agricultural management, employing a
219 Generalized Linear Model (GLM) (Bolker *et al.*, 2008) that utilizes all predictors in one analysis.

220 We have employed no techniques that would remove spatial or temporal autocorrelation
221 from the analyses because the autocorrelations are caused by biologically relevant effects, and
222 their statistical removal would mean a loss of the focal information (for more see Diniz-Filho *et*
223 *al.*, 2003 but for opposite opinion see Dornelas *et al.*, 2013). More specifically, the spatial

224 autocorrelation is captured by the rates of distance decay in our approach, and the temporal
225 autocorrelation is modelled by the variable of *year*, which is a proxy for successional sequences
226 (or trends caused by unobserved effects) of the *focal* parameters. The successional sequences, in
227 turn, may have been triggered by abrupt climatic events (Shuman, 2012), innovations in
228 agricultural management, or events connected with soil chemistry. We neither used an automatic
229 stepwise reduction of potential predictors (for reasons see Whittingham *et al.*, 2006; Mundry &
230 Nunn, 2009) nor a reduction of predictors based on information criteria, because we did not
231 formulate a model that provides maximum information on the system. Instead we used an ‘expert
232 based’ reduction (Flom & Cassell, 2009) of the predictors.

233 The ‘expert based’ reduction (Flom & Cassell, 2009) of the predictors under
234 consideration introduces an external knowledge of the predictors and logical reasoning into the
235 statistical test. To provide an example, 10 potential predictors may be weakly correlated with
236 each other and/or some of them might show a significant effect by pure chance (i.e., collinearity
237 problems are exacerbated and *p*-values are biased toward 0 in automatic stepwise methods; Flom
238 & Cassell, 2009), even if the test is designed to avoid this effect. We should therefore take into
239 consideration only the predictors (i) with statistically significant effects (there are usually more
240 of them), (ii) with effects that are supported by the ‘expert knowledge’ (to test for the effect of
241 even weak collinearity of the predictors by combining subset of predictors) , and those (iii) that
242 make up a biologically meaningful group of predictors (due to the bias of *p*-values, an automatic
243 reduction of parameters may by chance suggest a simultaneous effect of two predictors that are
244 independent or only weakly and nonlinearly correlated and therefore can be involved into the
245 same analysis but that are unlikely to act together). We used a strict level of significance
246 ($1.3 \cdot 10^{-3}$, S8.T2), but we broke the rule and used the level $1 \cdot 10^{-2}$ when the effect was

247 supported by reasoning (to include the effects that were accidentally insignificant). The
248 reasoning behind each test is summarized in the Results section and in the supplement (S8). Prior
249 to the tests, we transformed all variables to make them approach the Gaussian frequency
250 distribution (S8.T2).

251

252 **Results**

253 *Postglacial trends in biodiversity patterns*

254 A GLM analysis, **controlling** for year, number of sites and mean altitude across the sites (the
255 second and third variables vary with year; S8.T2) (i) showed a consistent trend of increasing S
256 and J toward the present (S8.T3), but (ii) showed neither increase nor decrease in β'_{Sim} . A closer
257 look at Fig. 3, however, shows that behind the stability of β'_{Sim} and the increase in S and J is
258 hidden a story of at least four different periods that match historically documented eras.

259 **12,200 - 9,600 calBP** ($\epsilon - \delta$ in Figs. 3-5) covers the Late Glacial to Holocene Transition,
260 that is, the last warming episode of the Last Glacial that ends when the oxygen-isotope
261 climatic proxies (Alley *et al.*, 1995) indicate no further post-Ice Age warming (Fig. 4).
262 During this period: (i) distance decays in plant J and β'_{Sim} became less pronounced (i.e.,
263 rates approached zero; Fig. 3C; S8.T4), (ii) snail J almost approached the level of recent
264 assemblages (Fig. 3B; S8.T4) and (iii) plant S stayed constant (Fig. 3E). This period fell
265 within what archaeologists call the Mesolithic period, the last period before agriculture
266 was introduced (Bailey & Spikins, 2008) into Central Europe. Although humans were
267 present as hunters and gatherers in the focal region, we expect they had only limited

268 impact on the environment, through for example local fire management (Kuneš *et al.*,
269 2008).

270 **9,600 – 5,800 calBP** ($\delta - \gamma$) commenced when the temperature became relatively stable
271 (Fig. 4) and ended with a sudden jump in plant J (Fig. 3A; S8.T4), which was the greatest
272 change since the end of the postglacial warming approximately 9,000 years ago. Neolithic
273 horticulture was introduced into Central Europe during this period (7,500 calBP)
274 (Bogaard, 2004) with agriculture conducted only on small fragmented grounds that more
275 closely resembled gardens rather than present fields. People could manage only light,
276 fertile soils in lowland areas (Rulf, 1991). Our data on plants and snails suggest that
277 between-assemblage similarity (J and β'_{Sim} ; Fig. 3A,B) stayed constant across time and
278 decayed only gradually with distance (small distance rates in Fig. 3C,D) during this
279 period. The apparent decrease in plant J is insignificant; but plant and snail S steadily
280 increased (Fig. 3E,F; S8.T4), and plant distance decay grew steeper (S8.T4).

281 **5,800 – 1,600 calBP** ($\gamma - \beta$) commenced when Late Neolithic people began to practice
282 arable agriculture (Bogaard, 2004) and ends suddenly with the decline of the Roman
283 Empire and events that are known in Central Europe as the Migration Period (Fouracre,
284 2006). Our data characterize this period as an era with high mean similarity between
285 neighbouring plant assemblages (J) and a steeper distance decay of J compared with the
286 preceding period (Fig. 3C; S8.T4). During this period people extended their fields within
287 the landscape, most likely founded pastures in the hills and learnt how to convert heavy
288 soil above 350 m altitude into arable fields (Bogaard, 2004). In our data, more than seven
289 sites with the indicators of agriculture had appeared by this date. We thus could examine J
290 and β'_{Sim} distance decays for the agricultural and wild sites separately. Surprisingly, the

291 sudden jump in J (Fig. 5A) at ca. 5,800 calBP occurs only in wild sites whilst the J of
292 agricultural landscapes holds roughly stable (Fig. 5A). At ca. 1,600 calBP the wild plant J
293 drops to the level shown before 5,800 calBP (Fig. 5A), signalling the end of the period.

294 ***1,600 calBP – to the present*** (β and later) After the collapse of the Roman Empire, the
295 plant J of agricultural (but not wild) sites abruptly fell to levels last seen before the advent
296 of arable agriculture, but from 800 calBP (α) onward, the index's value began to increase
297 again (Fig. 3A, S8.T4); parallel (but non-significant) shifts occur in β'_{Sim} around the same
298 time (Figs. 5A,B). The 13th century (α) is known as an era of new colonization in Central
299 and Eastern Europe. During these years, human populations increased, new regions were
300 colonized and many inventions such as three-year crop rotation and new ploughing
301 technologies were introduced (Barlett, 1993).

302

303 *Drivers of biodiversity patterns*

304 We suspected that the potential drivers were (i) year, which is a proxy for successional sequence
305 or unobserved effects, (ii) **temperature, as reflected in the borehole and oxygen isotope proxies**,
306 (iii) S , because it is a frequently reported driver of J (e.g., Lennon *et al.*, 2001; Koleff & Gaston,
307 2002), (iv) tree cover, (v) number of sites in the focal time window (not all of the 200 year time
308 windows contained a preserved sample, Fig. 1), and (vi) mean altitude across the focal samples.
309 Not all the potential drivers were, however, involved in all analyses or were considered to be
310 biologically founded (for details see S8). Some of these drivers may be directly affecting S and
311 turnover (i-ii, see S8.T2 and T5 for details), but they may also be subject to artefactual changes

312 in data quality, which would affect the predicted values (v-vi, S8.T2), and indeed the same
313 driving variable may do both (iii-iv, S8.T2).

314 For example, deforestation may influence plant diversity directly, biologically, by
315 altering the species pool of the site. However, it may also influence the distance over which
316 pollen accumulates, changing the quality of the dataset and therefore resulting in artefactual
317 shifts in measured S (Hellman *et al.*, 2009). Likewise, S may control J by a biologically relevant
318 mechanism or the S may have an artefactual effect on the observed J , e.g., the changes in S and J
319 may be simultaneously caused by the distance over which pollen accumulates. A change in this
320 distance would consequently cause artefactual bias not only in J but also in S . Our analyses show
321 that (i) tree cover (Fig. S9) only affects J , but neither its distance decay nor S (S8.T2); that (ii)
322 the abrupt change in J at about 5,800 calBP was not accompanied by an abrupt change in S ; and
323 that (iii) J did not follow S (i.e., before 9,600 calBP S remained stable, and J increased, and after
324 9,600 calBP S increased, and J remained stable). Hence, we consider the effects (if any) of tree
325 proportion and S on J as driven by biological mechanisms. Unlike the biologically founded
326 variables, the variables with possible artefactual effects were automatically (i.e., manually
327 without hesitation) removed from the analyses when significance did not support their impact.

328 At the scale of the time sequence as a whole, there are few consistent rules linking the
329 various predictors to the indices studied. For instance, the GLM indicated a significant link
330 between S and temperature in several combinations of predictors. Visual inspection, however,
331 shows that plant and snail S remained stable during the warming episode of the Last Glacial to
332 Holocene Transition (ϵ - δ in Figs. 3E,F and 4) whilst both showed increasing richness when
333 temperature stagnated (after δ). The S - temperature relationship is thus approximately L-shaped
334 during the Postglacial period, with the left part showing independence of S from temperature,

335 and the right part parallel with the y-axis. Because there are no doubts about the main periods of
336 temperature increase and later stagnation in the post ice age era, we conclude that S is practically
337 temperature independent at the Postglacial scale.

338 The role of these predictors becomes clear when the data are analysed in two categories:
339 before the introduction of arable agriculture (>5,800 calBP) and after (<5,800 calBP). Before this
340 event, S , J and the distance decay in J depended on temperature, and year or tree cover (S8.T5;
341 without possibility to distinguish between the effects of the two latter predictors) in both the
342 focal taxa. The only two exceptions were (i) the snail J , which correlated only with snail S , and
343 (ii) plant S , which correlated only with tree cover (S8.T5). After the advent of arable agriculture:
344 (i) we detected a smaller effect of temperature on our parameters than that detected in the earlier
345 period (S8.T5, Fig. S10), and (ii) plant J , a value which is no longer affected by the proportion
346 of trees, decreased with increasing S (Fig. 6, S8.T5). No difference between plants and snails
347 was detected in β'_{sim} and its rate of distance decay. Both these parameters were insensitive to any
348 tested predictor during both the pre- and post- arable agriculture periods.

349 In sum, the drivers of J and S appear to shift abruptly at about 5,800 calBP (Fig. 6),
350 which is demonstrated by the apparent break point at around 5,800 calBP (Figs. 3,5,6,S10-12).
351 Noticeably, after 5,800 calBP the plants' J -temperature relationship (Fig. 6B) becomes
352 significantly higher than for the years between 12,200-5,800 calBP (S8.T6). This signals a
353 radical switch in the forces that differentiate neighbouring assemblages around this time.

354

355 **Discussion**

356 We have demonstrated that patterns that appear general across space may, and sometimes do
357 change across time. Specifically, the increase in J with increasing S and the increase in S with
358 temperature, both of which are considered general rules in macroecology (Lennon *et al.*, 2001;
359 Koleff & Gaston, 2002; Jost, 2010; Brown, 2014) with important consequences, are spatial rules
360 that do not appear to hold across time at the Holocene scale (Faurby & Svenning, 2015; see
361 Mayhew *et al.*, 2012 for the opposite result in deep-time). Indeed, spatial decay in J determines
362 the slope of the species-area relationship (Tjørve & Tjørve, 2008), a curve that ecologists employ
363 to assess loss of S when habitat is destroyed (Pimm & Raven, 2000), and the decay in J also
364 contributes to asymmetry in species abundance distributions (Šizling *et al.*, 2009). The recently
365 observed increase in S with temperature is interpreted as having a solid basis in metabolic theory
366 (Brown, 2014; but see Currie *et al.*, 2004 for the opinion that S is driven by a form of energy,
367 which in turn correlates with temperature). Our data, however, show a decrease in plants' J with
368 increasing S occurred after arable agriculture was introduced to the focal area (Fig. 6A), and a
369 decrease in S with increasing temperature arose between the introduction of arable agriculture
370 and collapse of the Roman Empire (Fig. S10A), both periods lasting for several thousands of
371 years.

372 Freudean *et al.* (2010) and Blarquez *et al.* (2014) reported temporal variation of
373 assemblage similarity for Romania and for several regions in North America, respectively. Their
374 β -time relationships (their β scales with our J) differ from the plant's J -time relationship
375 reported here, and only Blarquez *et al.*'s (2014) data from Eastern Canadian Forests show a J -
376 time relationship that is similar to our result. We therefore suggest that agricultural management
377 and successional sequences have the power to change seemingly general ecological patterns
378 (Faurby & Svenning, 2015, Lyons *et al.*, 2016). The reason is that (i) the jumps in J , which are

379 reported here, coincide with historically documented breaks in the intensity of agricultural
380 management, (ii) that no similar jumps were reported from Romania (Freudean *et al.*, 2010),
381 where historically most people survived on pastoralism, or North America (Blarquez *et al.*, 2014)
382 where the level of agriculture during the Holocene was likely less intense than in Central Europe,
383 and (iii) that no break in assemblage similarity coincided with any abrupt change in a
384 temperature proxy or any abrupt climatic change reported by Shuman (2012).

385 There is a striking contrast between the sensitivity of J to temperature and year or tree
386 cover and the lack of significant correlation between β'_{Sim} and the tested predictors. Although
387 β'_{Sim} varies along the time axis, its changes are not as pervasive as those in J . Moreover, β'_{Sim}
388 always returns close to its mean level of 0.7, suggesting the existence of a force that stabilizes
389 β'_{Sim} making the average value of the index roughly constant over time. As a result, the recent
390 differences between the plant J and β'_{Sim} are approximately 0.22, whereas they differed by
391 roughly 0.32 at about 14,000 calBP. The snail data are rather too noisy for robust conclusions.

392 Higher values of J and S (Figs. 3,S7) in the recent centuries, compared with J and S in the
393 early Holocene, suggest a process of spatial homogenization. McKinney & Lockwood (1999)
394 suggested that the process of homogenization would be accompanied by a decline in species
395 richness at large scales. Here we report evidence of a recently more homogeneous spatial pattern
396 of assemblages, accompanied by an increase in species richness at fine scales (i.e., S). In detail,
397 however, J has generally declined since 9,600 calBP with only two episodes of rapid increase at
398 approximately 5,800 and 800 calBP, drawing a picture of a landscape where a slow process of
399 'heterogenization' has been interrupted by episodes of sudden homogenization. A similar
400 pattern of interspersed periods of homogenization and heterogenization was observed in
401 Romanian Holocene plant data (Feurdean *et al.*, 2010), although the periods of homogenization

402 in Romania were not as short or as rapid as we report here for central Europe. The slow and long
403 lasting periods of homogenization in Romania may again result from the pastoral history of the
404 region.

405 The combination of constant or increased J and decreasing rate of its distance decay
406 between 9,600 and 5,800 calBP together with the rapid increase in J and no change in its rate of
407 distance decay at about 5,800 calBP (Fig. 4a,b) suggests that the changes in assemblage
408 similarity occurred simultaneously at a variety of spatial scales. Geometrically, recently higher J
409 and S , and roughly similar β'_{Sim} compared with the values for 14,000 years ago (calBP) can only
410 mean that (i) the average ratio between the number of species unique to the more species-poor
411 site and shared between pairs of sites is now similar to the historical values, and that (ii) species
412 richness of the species-poor sites on average increased.

413 Blois *et al.* (2013b) concluded that the methods of species diversity projection worked
414 poorly during the North American Holocene, i.e., after people arrived in the focal area, but that
415 these methods perform well in the pre-Holocene period. They suggest two (non-exclusive)
416 explanations : firstly, that the temporal variation in climate is smaller than spatial variation in
417 climate in North America during the Holocene, and secondly, that the observed patterns are
418 being driven by human impacts. Here we suggest a variation on their latter explanation. Blois *et*
419 *al.* (2013b) tested the power of both predictions under several assumptions, in particular the
420 assumption of space-for-time substitution applied to habitat requirements. Such a projection,
421 however, reflects the spatial variation in the size of the species pool rather than the variation in
422 local species richness. We therefore conclude that the spatial variation in local species richness is
423 shaped by ecological rules constrained by regional species pools. The combined results of this
424 study and of Blois *et al.* (2013b), might therefore tell a story of constant fundamental niches of

425 species in the species pool, but changing biodiversity rules that form local assemblages in the
426 inhabited landscapes. Still, the extent of landscape management by native Americans in the focal
427 area is not clear. However, Blarquez *et al.* (2014) reported a similar *J*-time relationship as we do
428 here, but only for the Eastern Canadian Forest and not for North-West regions, and Blois *et al.*,
429 (2013b) reported worse Holocene predictions for eastern parts of America than Pleistocene
430 predictions. Both cases suggest an impact of human activities in the Eastern regions of America.
431 Such a conclusion would also shed light on the findings of White & Kerr (2006) who reported a
432 discrepancy between population-density-species-richness relationships observed across space
433 and time. For better support for the hypothesis of constant fundamental niches and different
434 biodiversity rules under the pressure of agriculture we would, however, need detailed knowledge
435 of the regional history for each dataset separately, and we would need a test that separates the
436 assumption of space-for-time substitution (which applies on fundamental niches) from the
437 assumption of uniformitarianism (which applies on biodiversity rules).

438 The biggest change in focal patterns in our dataset took place at around 5,800 calBP.
439 What actually happened at this time? The fact that biodiversity patterns shift abruptly around the
440 time that arable agriculture was introduced to the focal region, and shift again during the great
441 migration after the fall of the Roman Empire, suggests a possible link between our findings and
442 agricultural management. However, it is not clear if agricultural management is the sole factor
443 responsible for the documented changes in biodiversity patterns. After all, no such shifts were
444 detected around 800 calBP when agriculture and population expanded abruptly during the
445 medieval Colonization of the Central European wilderness (Barlett, 1993). This should warn us
446 against the conclusion that a unique, causal link exists between agriculture and the event 5,800
447 calPB. A closer look at our data shows that (i) the nutrient-rich broadleaf forests, which was

448 dominated by *Corylus*, *Quercus*, *Ulmus*, *Tilia* and *Fraxinus*, were replaced with acidophilic
449 *Fagus* - *Abies* formations, and (ii) the snail species typical for the Early Holocene (*Discus*
450 *runderatus*, *Perpolita petronella*) withdrew from lowland to mountain areas around 5,800 calBP.
451 This suggests that the land use changes of this period were accompanied by climatic,
452 geochemical and/or biogeographical shifts (see S13 for a possible scenario).

453 The Central European landscape changed markedly around 5,800 calBP and again around
454 1,600 calBP. The first event turned the Central European plant assemblages into a ‘well tended
455 garden’ where the main driving force came to be human management in contrast to wilderness
456 where assemblages are formed by ‘natural’ processes. The second event partially returned the
457 plant assemblages to pre-agricultural conditions, and at this time plant *J* returned to values
458 similar to those before the year 5,800 calBP. However, other aspects of the community did not
459 go back to pre-agricultural patterns: the *J*-temperature relationship (Fig. 6), for example,
460 remained elevated, and the *S*-temperature relationship shifted to even higher values (Fig. S10),
461 although *S* began to increase with increasing temperature again. This suggests that the alteration
462 of ecological rules at around 5,800 calBP was not only unpredictable but also in part irreversible.
463

464 **Conclusions**

465 Some recently observed and/or theoretically supported ecological rules, such as the temperature
466 dependence of species richness and the relationship between species richness and Jaccard index
467 of species spatial turnover, do not generally hold across time. These relationships have been
468 shifted or even temporarily inverted at different times in the Holocene, and we suggest that these
469 exceptions from ‘generally expected behaviour’ are caused by intensive land use. The main

470 support for this hypothesis is that people practiced arable agriculture and that settlement was
471 dense and stable during these periods. As a possible mechanism, we suspect a permanent
472 pressure that shaped local assemblages and successional sequences, which may have been
473 triggered by changes in soil chemistry. We therefore conclude that the focal **rules** are not general
474 across time, at least in **intensively managed arable** landscapes, and that arable agriculture may
475 turn off or even irreversibly damage ecological mechanisms that underlay these **rules**, and which
476 may be vital for ecosystem functioning.

477 If we were living at the end of the Roman period, anticipating the Empire's fall, we
478 would not be able to predict the then-future (the post-fall world) simply by examining records
479 from the pre-agricultural past. Nor would we be able to use spatial variation within our
480 contemporary world to fit models that would allow such predictions. In the absence of consistent
481 ecological laws that hold constant in the face of historical shifts, such space-for-time substitution
482 becomes hazardous. Standing now at the start of the 21st century, anticipating massive changes
483 in climate, food production technologies and human populations over the next century or more,
484 are we in any better a position to project the ecological patterns of the future?

485

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492

493 **Bioscetch:** We have built up a team consisting of ecologists (ALS, ES, WK, ET, KMCT),
494 archaeobiologists (LJ, JH, VA), and quaternary scientists (PP, VL), developed new tools and
495 uncovered a hidden aspect of coevolution between human society, climate and large-scale
496 ecological rules.

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- 699

700 **Figure Legends**

701 **Fig. 1:** A schematic diagram of pollen (core at left) and snail (dug from the slope on the right)
702 samples (black squares). A black spot in the inset shows the focal area and the asterisk shows the
703 reference point to which the data are standardized (for detail see S1). Black rectangles are the
704 samples that were taken uniformly in plants and within each visually distinguishable lithological
705 layer (separated by dashed lines) in snails. Arrows indicate the samples that were radiocarbon-
706 dated. Ages of the other samples were taken from a depth-age model (Kuneš *et al.*, 2009;
707 Blaauw, 2010) using information on the dated samples, depth of the focal sample and visually
708 observable breaks in sedimentary dynamics between consecutive samples. W1-5 (separated from
709 each other by full lines) are the focal time windows (w1: 0-200 calBP, w2: 200-400 calBP, ...,
710 etc.).

711 **Fig. 2:** Distance decays of the Jaccard index (J) of assemblage similarity for plants (1st column)
712 and snails (2nd column) as observed (brown) and modelled (Eq. 2; blue). (For further
713 relationships see Figs. S3,S5,S7.) Solid and dashed lines show exponential regressions;
714 regression lines for model and data mostly overlap each other. Each relationship is characterized
715 by its initial value (intercept at zero distance) and rate of decay (negative rates suggest
716 decreasing relationship, rates close to zero suggest little or no distance decay). Ochre, blue and
717 green rows are for Palaeolithic, Mesolithic and periods when arable agriculture was practiced in
718 the focal area, respectively.

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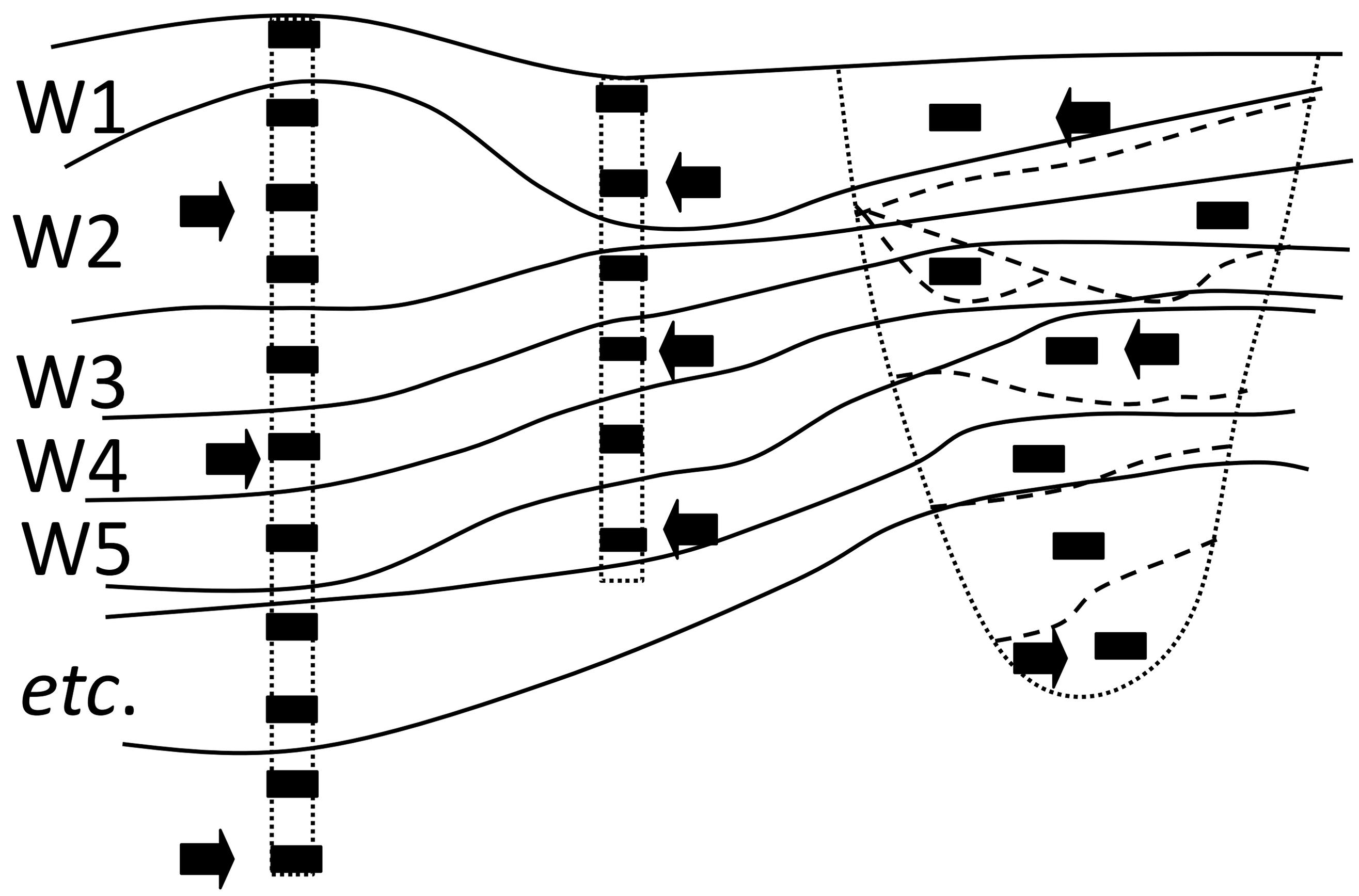
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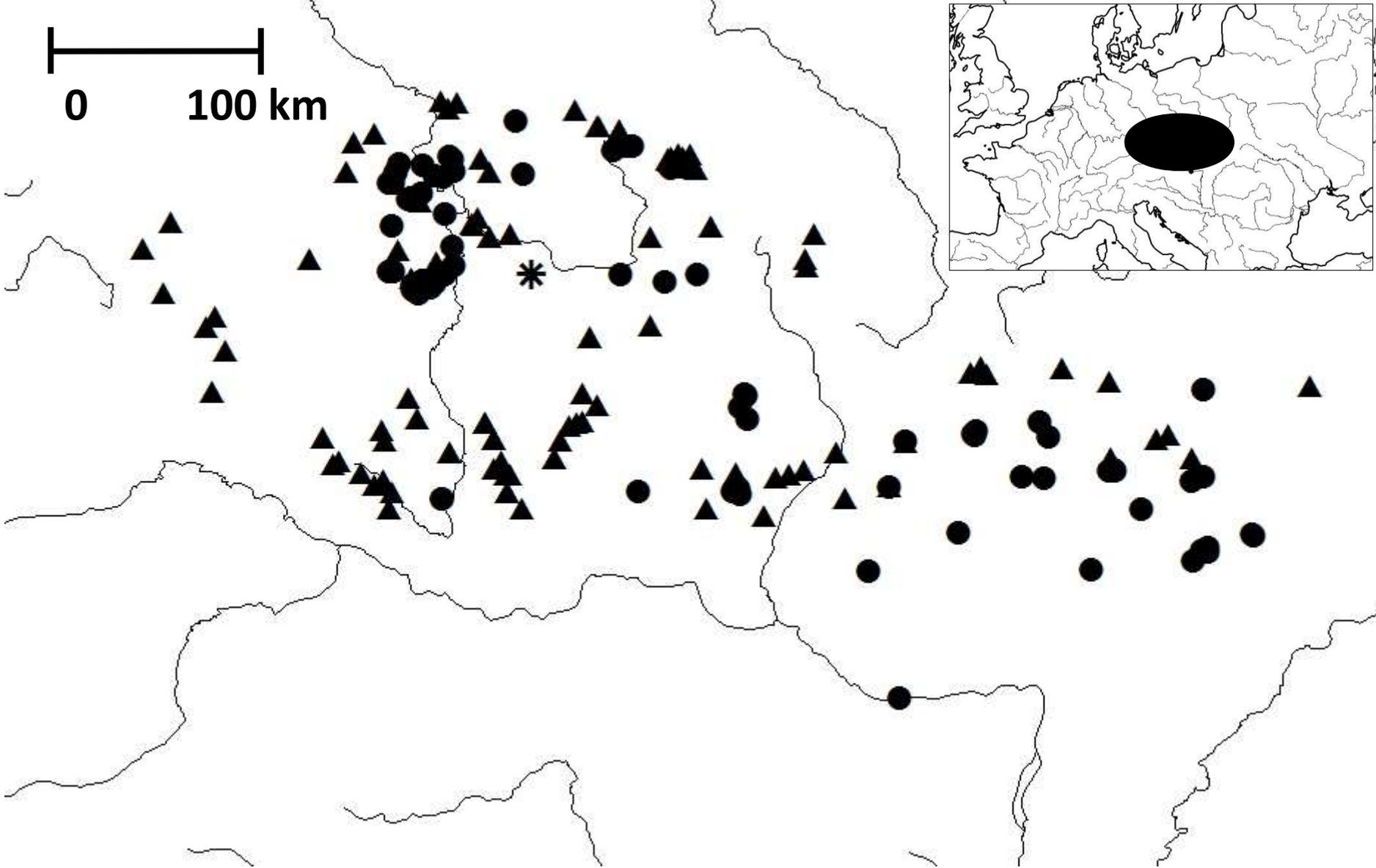
722 **Fig. 3:** Indices of assemblage similarity (A,B), rates of their distance decay (C,D) (J -brown
 723 squares, β'_{Sim} -blue circles), and S (E,F) (black) across time through the Holocene in plants (1st
 724 column) and snails (2nd column). The symbols show standardized values estimated using Eqs. 1-
 725 3, and thin lines show the particular 99% confidence intervals. Vertical lines indicate particular
 726 events: from right to left α – 800 calBP, β – 1,600 calBP, γ – 5,800 calBP, δ – 9,600 calBP and
 727 ε – 12,200 calBP.

728 **Fig. 4:** The oxygen (Alley *et al.*, 1995) (squares) and borehole (Huang *et al.*, 2008) (circles)
 729 proxies for global temperature in the northern hemisphere.

730 **Fig. 5:** Differences between the ecology of wild (brown squares) and agricultural (blue circles)
 731 landscapes as captured by the plant Jaccard index (J) of assemblage similarity (A), plant
 732 Simpson beta (β'_{Sim}) (B) and plant species richness (S) (C). The symbols show standardized
 733 values estimated using Eqs. 1-3, and thin lines show the particular 99% confidence intervals. For
 734 further relationships see Fig. S14.

735 **Fig. 6:** Responses of plant (A,B) and snail (C,D) assemblages, as measured by the Jaccard index
 736 of assemblage similarity, to variation in S (A,C) and temperature (Huang *et al.*, 2008) (B,D).
 737 Open symbols and dashed lines represent samples from periods before the year 5,800 calBP;
 738 filled symbols and solid lines represent samples from after that date. Thin dotted and full lines
 739 delimit the 95% confidence intervals. For further relationships see Fig. S11.





*** Reference Point**

