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3 **Current climate, but also long-term climate changes and human impacts,**
4 **determine the geographic distribution of European mammal diversity**

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6 **Running title:** Determinants of European mammal diversity

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50 **Biosketch:** Ana M. C. Santos is interested in community ecology, island biogeography and
51 macroecology. Her current work focuses on cross-scale variations of community assembly and
52 structure, and on the impacts of global change on ecosystem functioning. All co-authors work in
53 macroecology and biogeography.

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57 **Abstract:**

58 **Aim.** Historical climate variations, current climate and human impacts are known to influence
59 current species richness, but their effects on phylogenetic and trait diversity have been seldom
60 studied. We investigated the relationship of these three factors with the independent variations of
61 species, phylogenetic and trait diversity of European mammals. Considering the position of the
62 0°C isotherm in the Last Glacial Maximum as a tipping point, we tested the following
63 hypotheses: northern European assemblages host less species than southern European ones;
64 northern areas harbour **trait and** phylogenetically clustered assemblages, while the more stable
65 southern areas host random or overdispersed assemblages; and, species richness increases with
66 human influence, while phylogenetic and trait diversity show clustered patterns in areas with
67 stronger human influence.

68 **Location.** Western Palearctic.

69 **Time period.** Current and Late-Pleistocene effects on present-day diversity.

70 **Major taxa studied.** Terrestrial mammals.

71 **Methods.** We used a novel analytical approach based on distance matrices to separate the
72 independent variations of species, phylogenetic and trait diversity, and assessed their
73 relationships with current climate, climate stability and human influence through structural
74 equation models.

75 **Results.** The species-poor assemblages from northern Europe show higher phylogenetic and trait
76 clustering than the more stable richer southern areas. However, no assemblage presented trait nor
77 phylogenetic overdispersion. Current climate is the primary driver of phylogenetic and trait
78 diversity, while species richness is affected similarly by both current and past climates. Higher

79 human influence correlates positively with species richness and trait diversity, both directly and
80 by mediating indirect effects of present climate.

81 **Main conclusions.** Current climate, climate stability and human influence affect the studied
82 aspects of diversity, although the form and magnitude of their effects varies through space.

83 Importantly, higher levels of human disturbances correlate with more speciose and trait diverse
84 assemblages, an apparently counterintuitive result that deserves further study.

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86

87 **Keywords:** Community structure, functional traits, glaciations, global change, human impact,
88 phylogenetic diversity, species richness, structural equation models, trait diversity.

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91 **1. Introduction**

92 Geographic patterns of biodiversity result from evolutionary and ecological processes determining
93 the increase, maintenance and depletion of species, lineages and ecological traits through time
94 (Wiens & Donoghue, 2004). Species distributions are affected by different abiotic factors,
95 including climatic conditions and historical events, biotic interactions and human impacts (e.g.
96 Faurby & Svenning, 2015; Hortal, Lobo, & Jiménez-Valverde, 2012). Understanding the
97 importance of each one of these factors on the distribution of biodiversity is fundamental for
98 managing [the](#) current biodiversity crisis (Kerr, Kharouba, & Currie, 2007). However, most
99 research efforts have focused on species richness, with much still to be explored in what concerns
100 other facets of biodiversity, such as phylogenetic or trait diversity. These two aspects of
101 biodiversity may reflect the potential of species to maintain ecosystem functioning and acquire
102 novel evolutionary pathways for coping with environmental changes (Díaz et al., 2013; Violle,
103 Reich, Pacala, Enquist, & Kattge, 2014; Schipper et al., 2016).

104 Current climate is strongly associated with species richness, mainly through energy and
105 water budgets (e.g. Currie, 1991; Whittaker, Nogués-Bravo, & Araújo, 2007), and also with trait
106 [\(i.e., functional\)](#) and phylogenetic diversity (e.g. Barreto, Graham, & Rangel, 2019; Safi et al.,
107 2011). These factors are important drivers of the geographic distribution of different groups of
108 organisms, either acting through primary productivity (e.g. Araújo et al., 2008; Barreto et al., 2019;
109 Fløjgaard, Normand, Skov, & Svenning, 2011; Safi et al., 2011), filtering on species climatic
110 tolerances –particularly at higher altitudes and latitudes (Hawkins et al., 2003; Hortal et al., 2011),
111 or affecting mutation and speciation rates (Wiens & Donoghue, 2004). Pleistocene climatic
112 oscillations also left a strong imprint on the current distribution of many species (Sandel et al.,
113 2011) – particularly in high latitudes (Dynesius & Jansson, 2000), as well as on extinction rates

114 (Nogués-Bravo, Ohlemüller, Batra, & Araújo, 2010) and community structure (Rowan, Kamilar,
115 Beaudrot, & Reed 2016; see also Svenning, Eiserhardt, Normand, Ordonez, & Sandel, 2015).
116 These effects are particularly evident in Europe (Araújo et al., 2008; Calatayud et al., 2016, 2019;
117 Gouveia, Hortal, Cassemiro, Rangel, & Diniz-Filho, 2013; Hortal et al., 2011; Ordonez &
118 Svenning, 2016; Svenning & Skov, 2004; Svenning et al., 2015), where many species went extinct
119 in the glaciated northern latitudes during the ice ages. However, species holding certain traits and
120 belonging to particular clades were either able to persist in those areas (for example, by regulating
121 body temperature), or to survive in southern, more climatically stable refugia (e.g. Rodríguez,
122 2006). Many of these species recolonised northern Europe after the glaciers retreated (Hewitt,
123 1999), resulting in varying distribution patterns that are thought to be mainly associated with their
124 dispersal capacity, ability to occupy multiple and fragmented habitats and/or physiological
125 tolerance limits (Hortal et al., 2011; Ordonez & Svenning, 2015; Svenning & Skov, 2004).
126 Therefore, biotas from areas that underwent profound Pleistocene climate changes tend to show
127 clustered phylogenetic and trait structure, i.e. communities from these areas include species that
128 tend to be more similar in terms of phylogenetic relationships and traits than expected by chance
129 (e.g. Calatayud et al., 2019; Ordonez & Svenning, 2015; Pinkert et al., 2018). As a consequence,
130 the 0°C isotherm at the Last Glacial Maximum (LGM, around 21,000 yr bp) is still the northern
131 limit of the distribution of different taxonomic groups in Europe today (e.g. Araújo et al., 2008;
132 Hortal et al., 2011). Indeed, the past location of this isotherm roughly coincides with the shift in
133 the sign of the species–energy relationship for mammals (Whittaker et al., 2007).

134 Human activities also affect biodiversity, altering the functioning of ecosystems (Pimm et
135 al., 2014) and promoting changes in the Earth's climate and environmental conditions (Zalasiewicz
136 et al., 2008). Importantly, they have changed current diversity patterns (Faurby & Svenning, 2015),

137 highlighting the importance of including human-related effects on large-scale studies focusing on
138 diversity drivers. These human impacts are not restricted to post-industrial times (Polaina,
139 González-Suárez, & Revilla, 2019). Instead, humans have long been an important driver of species
140 range contractions and extinctions (Sandom, Faurby, Sandel & Svenning, 2014). The interaction
141 between increasing human pressure and climate changes during the Late Quaternary led to the
142 extinction of many Holarctic large mammals from particular lineages and with specific traits (e.g.
143 Davis, Faurby & Svenning, 2018; Lorenzen et al., 2011; Nogués-Bravo, Rodríguez, Hortal, Batra,
144 & Araújo, 2008; Wan et al. 2019). Indeed, some mammal traits reflect the species' susceptibility
145 to anthropogenic pressures (Fritz et al., 2009; Wan et al. 2019), so that the current patterns of trait
146 and phylogenetic diversity may have been shaped by non-random human-driven extinctions
147 (Faurby & Svenning, 2015). Paradoxically, human presence is positively correlated with mammal
148 species richness in many regions, including Europe (Araújo, 2003; Luck, 2007; Torres-Romero &
149 Olalla-Tarraga, 2015; but see Barbosa, Pautasso & Figueiredo, 2013). Both humans and other
150 mammals have for long held larger and more diverse populations in areas that currently show
151 higher productivity or certain climates (Balmford et al., 2001; Fjeldså & Burgess, 2008), or that
152 had higher climate stability during the Pleistocene (Fjeldså & Rahbek, 1998, cf. Araújo, 2003).

153 The relationships between species richness and current climate, climate change and
154 anthropogenic effects are relatively well known (e.g. Svenning et al., 2015), whereas the effects
155 of these factors on the geographical patterns of phylogenetic and trait (i.e., functional) diversity
156 have been less studied, particularly at large spatial scales (but see, e.g., Faurby & Svenning, 2015;
157 Holt et al., 2018; Safi et al., 2011). Here we evaluate the large-scale patterns of species, trait and
158 phylogenetic diversity of native European mammals, assessing the potential effects of current

159 climate, climate changes since the LGM, and human impacts. We do this through a novel statistical
160 approach that allows disentangling the independent effects of each facet of biodiversity.

161 Europe underwent significant climatic changes during the Pleistocene, of increasing
162 intensity towards the north. Therefore, we expect that both the distribution of biodiversity and the
163 relative importance of its drivers will differ between northern and southern European biotas (as
164 delimited by the location of the LGM 0° isotherm, see above). We predict that northern areas have
165 fewer species than the more climatically-stable areas of the south (H1). Also, northern areas will
166 harbour phylogenetically clustered assemblages, due to the importance of phylogenetically
167 conserved adaptations to cold environments or related with dispersal ability (H2.1). In contrast,
168 southern assemblages were less influenced by such filters, having experienced more climatically
169 stable environments that provided longer time [periods](#) for the evolution of communities
170 (Rodríguez, 2006); therefore, in general, southern assemblages should not be phylogenetically
171 clustered, exhibiting either no particular evolutionary pattern, or even phylogenetic overdispersion
172 (i.e. include species that are less related to each other than expected by chance) (H2.2). These
173 hypotheses also apply to trait diversity: northern biotas will tend towards trait redundancy (due to
174 the selection of traits related to the ability to colonise or persist in these areas) (H3.1), whereas
175 such clustering will not occur in southern assemblages. In this latter region, we expect a random
176 trait structure, or even trait overdispersion in those areas where long-term species interactions have
177 promoted limiting similarity processes (e.g. long-term competition reduced trait overlap) (H3.2).
178 We also expect that the diversity of northern assemblages is driven mainly by past climatic
179 conditions, while in the south it is primarily driven by current climate (predictions associated with
180 H1, H2.1, H2.2, H3.1 and H3.2). Regarding human impacts, we expect that species richness will
181 be higher in areas with stronger human influence (H4.1; see above); such areas will also present

182 phylogenetic and functional homogenization, which translates into phylogenetic and trait
183 clustering (H4.2 and H4.3, respectively). Given the complexity of interactions between diversity,
184 current climate, climate stability, and human impacts, we evaluate the concurring effects of all
185 these factors using Structural Equation Models.

186

187 **2. Methods**

188 *2.1. Data*

189 Data on the distribution of native terrestrial (both volant and non-volant) mammal species were
190 obtained from IUCN (2016). We used range maps instead of Atlas data, as the latter may include
191 incomplete and uneven information on species distribution (see Hortal, 2008). We used a 100 km
192 equal-area grid in order to minimize omission and commission errors, thus balancing data quality
193 and resolution (Hortal, 2008; Hortal et al., 2011; Hurlbert & Jetz, 2007). So, range maps were
194 reprocessed to obtain the occurrence of each species in a 100 km equal-area grid (i.e. with 10,000
195 km² cells) encompassing the whole Western Palearctic, i.e. both Europe and the Mediterranean
196 region (European grid, based on the ETRS89 Lambert Azimuthal Equal-Area projection; it also
197 includes the Mediterranean Islands and Northern Africa). This region hosts 357 mammal species,
198 which constitute the regional pool of species that can potentially colonise any grid cell, and
199 therefore were used as the source pool for all community assembly analyses described below. The
200 extent of our analyses was limited to mainland Europe (comprising Great Britain and Russia up to
201 the Ural Mountains), the Anatolian Peninsula, Syria and Israel. In total, these territories host 354
202 mammal species. We excluded cells that had less than 95% of land surface. Species richness was
203 calculated as the number of species recorded in each grid cell.

204 Trait data were obtained from PanTheria database (Jones et al., 2009) and updated using
205 additional sources (as in Hidasi-Neto, Loyola, & Cianciaruso, 2015; Safi et al., 2011). The selected
206 traits relate to the type and quantity of resources used, and how and where these resources are
207 acquired (Safi et al., 2011). These include: (i) body mass (in grams), (ii) diet (i.e. vertebrates,
208 invertebrates, foliage, stems and bark, grass, fruits, seeds, flowers, nectar and pollen, roots and
209 tuber); (iii) habitat (aquatic, fossorial, ground-dwelling, aboveground dwelling, aerial) and activity
210 period (catemeral, crepuscular, diurnal, nocturnal). When trait data were missing for a given
211 species, median values for the genus were used. This occurred for 9.8% of the species, mainly in
212 Rodentia, and for less than 5% of the cells of the trait by species matrix; after this process, only
213 0.4% of the cells of this matrix had missing data (mostly in activity period). We used a dated
214 mammalian ‘supertree’ (Bininda-Emonds et al., 2007, updated by Fritz, Bininda-Emonds, &
215 Purvis, 2009), modifying it according to the IUCN Red List taxonomic nomenclature (IUCN,
216 2016). Although some parts of the mammal phylogeny are still under discussion (e.g. O’Leary et
217 al., 2013), this phylogeny remains as the most complete and stable for the whole Class (Daru et
218 al., 2019), and is widely used in macroecological studies (e.g. Saladin et al., 2019).

219 Current and historical climate data were gathered from the ECHAM3 paleoclimatic model
220 (Braconnot et al., 2007; processed as in Calatayud et al., 2016; Hortal et al., 2011), and included
221 current temperature and precipitation, and temperature and precipitation stability since the LGM.
222 These two latter variables correspond to the differences between current and LGM values, so
223 smaller values indicate higher climate stability (Araújo et al., 2008; Hortal et al., 2011).
224 Comparability between these variables was attained by extracting all information from the same
225 Atmosphere-Ocean General circulation model, i.e. using a downscaled version of the ECHAM3
226 paleoclimatic model (Braconnot et al., 2007). The impact of human activities (i.e. anthropogenic

227 effects) was measured with the Human Influence Index (HII; Sanderson et al., 2002), which
228 includes information about human population density, land use, infrastructure and human access.

229

230 *2.2. Calculating phylogenetic and trait diversity*

231 Phylogenetic and trait diversity are not entirely independent from either species richness or each
232 other (Tucker, Davies, Cadotte, & Pearse, 2018). Also, traits usually have some degree of
233 phylogenetic signal, so closely related species will tend to exhibit similar trait values (de Bello et
234 al., 2017; Díaz et al., 2013; but see de Bello et al., 2015). To disentangle the effect of these three
235 components of diversity, we calculated the phylogenetic diversity that is independent of species
236 richness, and also the trait diversity that is independent of both species richness and phylogenetic
237 diversity, using a rationale similar to de Bello et al. (2017) and Nascimento, Correia, Ruiz-Esparza,
238 & Gouveia (2018). To do this, we developed an analytical approach based on distance matrices,
239 following Diniz-Filho, Cianciaruso, Rangel, & Bini (2011) (see Fig. S1 in supporting information).
240 For each assemblage (i.e. each grid cell), we calculated phylogenetic diversity (PD) using Faith's
241 (1992) index, corresponding to the total branch length of a phylogenetic tree that connects all
242 species within an assemblage. Afterwards, we calculated net phylogenetic diversity (nPD; herein
243 called phylogenetic diversity for simplicity), i.e. the PD that is independent of species richness. To
244 do this, we first created 1000 random assemblages from the species pool with the same species
245 richness of each real assemblage, by shuffling species labels across the tips of the phylogeny.
246 Second, we calculated nPD as the difference between the observed PD and the mean PD of the
247 randomisations, divided by the standard deviation of the randomised PD values; therefore, nPD
248 corresponds to the standardised effect size of each assemblage (Gotelli & Rohde, 2002). Negative
249 nPD values correspond to assemblages with species that are phylogenetically clustered (i.e.

250 evolutionarily closer than expected by chance), whereas positive values indicate phylogenetically
251 overdispersed assemblages (i.e. more distant than expected by chance).

252 Trait (functional) diversity was calculated using Petchey & Gaston's (2002) FD (herein
253 named FD). This metric is conceptually similar to PD, and thus involves producing a distance
254 matrix from a trait matrix (using a modified version of Gower's distance; Pavoine, Vallet, Dufour,
255 Gachet, & Daniel, 2009), converting it into a dendrogram (using UPGMA), and calculating the
256 sum of branch lengths across it. In this case, the dendrogram was built using trait information of
257 all mammal species present in the species pool. We also calculated net trait diversity (nFD), i.e.
258 the FD that is independent of species richness, in the same way as nPD. Finally, we calculated
259 phylogenetically-independent trait diversity from the residuals of the regression between the trait
260 and phylogenetic distance matrices (using absolute distance values). These residuals were then
261 used to construct a new dendrogram, which in turn was used to calculate the net phylogenetically-
262 independent trait diversity (npiFD; herein trait diversity), following the same steps as for nPD and
263 nFD. As in the case of nPD, negative values of npiFD indicate assemblages with species that are
264 functionally clustered (i.e. species with trait values more similar than expected by chance),
265 whereas positive values indicate trait overdispersed assemblages (i.e. more different than expected
266 by chance).

267

268 2.3. Statistical analyses

269 Data on species richness, net phylogenetic diversity (nPD) and net phylogenetically-independent
270 trait diversity (npiFD) per grid cell were divided into two subsets that differentiate between areas
271 that were most affected by glacial conditions in the past from those that were less affected. These
272 two subsets, herein named Northern and Southern Europe, were defined as the grid cells located

273 respectively north or south of the 0° C isotherm at the LGM (see Fig. 1), following Araújo et al.
274 (2008) and Hortal et al. (2011) (see also Hewitt, 1999; Whittaker et al., 2007). All analyses were
275 conducted separately for each one of these subsets. Differences in species richness, nPD and npFD
276 between northern and southern assemblages were assessed through a t-test for the comparison of
277 two independent groups (parametric assumptions were tested visually; not shown), using
278 Dutilleul's method (Dutilleul, 1993) that allows correcting the number of degrees of freedom to
279 account for the pseudoreplication derived from the degree of autocorrelation in the variables.
280 Further, we made a preliminary assessment on whether the relationship between each predictor
281 variable and species richness, nPD or npFD was either linear or quadratic through ordinary least
282 squares (OLS) regressions (see Table S1), in order to decide the type of relationship that should
283 be included later on in subsequent analysis (see below). The relationship between HII and the
284 different diversity variables was tested using a Pearson correlation and applying Dutilleul's
285 correction (Dutilleul, 1993). All predictors were standardised to mean = 0 and standard deviation
286 = 1.

287 Finally, we applied multigroup structural equation modelling (SEM; Grace, 2006; Shipley,
288 2000) to analyse the differences in the causal structure between current climate, climate stability,
289 human influence and each response variable (i.e. species richness, nPD and npFD). SEMs are
290 particularly appropriate for testing whether multiple hypotheses hold up, as they allow evaluating
291 a priori hypotheses describing the latent structure of the relationships among variables (Grace,
292 2006). In this type of analysis, a model with the same causal structure (i.e. same number and
293 direction of relationships between variables) is fitted from all subsets simultaneously (in this work,
294 the northern and southern biotas), but parameter values are allowed to vary freely between these
295 subsets. We combined temperature and precipitation variables using composite variables (Grace

296 2006) to evaluate the aggregated effect of current climate and climate stability. Composite
297 variables in SEMs are built by bringing together the paths of the component variables to the
298 composite, and then creating a path between the composite and the response variable. This newly
299 created path summarises the joint effect of the component variables on the response variable, and
300 provides a way to measure the importance of conceptual variables that cannot be directly measured
301 (in this case, climate as a whole).

302 To take into account spatial autocorrelation we included in the SEM model a set of spatial
303 eigenvectors obtained through spatial eigenvector mapping (Diniz-Filho et al., 2008; Legendre &
304 Legendre, 2012). To avoid high type I error rates related to eigenvector estimation, we first selected
305 the eigenvectors that minimised the autocorrelation in model residuals, based on Moran's I (MIR
306 *sensu* Bauman, Drouet, Dray, & Vleminckx, 2018). Including all these eigenvectors in the
307 structural model would result in overparametrizing the model, inflating its degrees of freedom.
308 This is one of the main problems to avoid when constructing SEM models (see Grace 2006). Thus,
309 we solved the trade-off between minimising spatial autocorrelation and avoiding
310 overparametrization by including in the SEM model only those eigenvectors that were
311 significantly correlated (at $p < 0.05$) with the response variables. This assures that all spatially-
312 structured variation in the dependent variables that is not accounted for by the predictors is
313 included in the model while calculating its parameters. All parameters of the SEM model were
314 estimated in presence of these eigenvectors, thereby avoiding potential problems due to spatial
315 autocorrelation. Because the eigenvectors were used exclusively to account for spatial
316 autocorrelation, their path coefficients are not shown. The final coefficients of determination (R^2
317 values) for all other paths in the model were calculated without the eigenvectors (following Diniz-
318 Filho et al., 2008) because including them would have spuriously inflated the explained variability.

319 To fit the model, we first designed an *a priori* model in which we included the set of
320 relationships that were theoretically important (see Fig. S2a). This initial *a priori* model did not fit
321 the data well, so we re-specified the model by adding new relationships using modification indices
322 as guidance. Modification indexes provide an estimate of the amount by which the chi-square
323 would be reduced if a new relationship between two of the variables is added to the model. We
324 sequentially added new relationships until an adequate model fit was achieved (Grace, 2006),
325 taking into account only the relationships that have biological meaning. In this case, adding the
326 correlations between the residuals of both species richness and trait diversity, and trait and
327 phylogenetic diversity was sufficient to achieve a good model fit. After fitting the final model, we
328 evaluated the stability of parameter estimation through a bootstrap. These procedures were
329 repeated using alternative *a priori* models (Fig. S2b,c) that expressed different relationships
330 between HII and species richness; models rendering higher Akaike's Information Criterion scores
331 were ignored (i.e. the model depicted in Fig. S2b, where diversity affects HII, but not vice-versa).
332 All SEM models were fitted using AMOS (Arbuckle, 2014). Complete SEM results can be found
333 in the Appendix S2 in supporting information.

334

335 **3. Results**

336 The geographic distribution of species richness, phylogenetic diversity (nPD) and trait diversity
337 (npiFD) does not coincide in Europe. Species richness increases from the northern and southern
338 areas towards the centre of Europe, with the highest values being found close to the highest
339 mountain chains (the Alps, Pyrenees, Carpathians and the Caucasus) and in the Balkan Peninsula
340 (Fig. 1a). Southern biotas have more species than northern ones, in accordance with H1 (North: M
341 = 47.141, SD = 14.235; South: M = 55.047, SD = 15.021; t-test with Dutilleul's correction: t (12)

342 = -10.304, $p < 0.001$). nPD values are higher in southern than in northern assemblages (North: M
343 = -1.743, SD = 0.745; South: M = -1.252, SD = 0.856; t-test with Dutilleul's correction: $t(18) = -$
344 11.585, $p < 0.001$), and significant phylogenetic clustering occurs in over 30% of northern
345 assemblages (i.e. grid cells), particularly in northern Russia (Fig. 1b; see Figure S3). Although
346 Southern European assemblages are dominated by a random phylogenetic structure, 21% of the
347 cells present a significant clustered pattern. However, despite nPD values being positive in the
348 south of the Caucasus mountains, no single cell is significantly overdispersed in any region (i.e.,
349 nPD is never higher than 1.96; Fig. 1b; see Figure S3). Phylogenetic diversity results therefore do
350 not totally support hypotheses H2.1 and H2.2. The geographic pattern of trait diversity is similar
351 to that of phylogenetic diversity, as npFD values in the south are significantly higher than in the
352 north (North: M = -2.673, SD = 0.99; South: M = -1.551, SD = 0.792; t-test with Dutilleul's
353 correction: $t(9) = -24.385$, $p < 0.001$). However, in the case of **trait** structure, 75% of the northern
354 assemblages are significantly clustered (particularly north of current 0°C isotherm; Figs. 1c; see
355 Figure S3), while close to 70% of the southern assemblages present a random pattern. Note that
356 npFD values tend to increase in southern assemblages (particularly in the Iberian and Italian
357 Peninsulas, and also south of the Caucasus), but are **not** significant. Therefore, results regarding
358 **trait** diversity agree with both H3.1 and H3.2. Human influence affects most facets of biodiversity,
359 particularly in northern assemblages (Fig. 2; Table S1). However, although species richness is
360 higher in areas with higher human influence (Fig. 2a; Pearson's adj. $r^2 = 0.345$; $F(15) = 7.984$;
361 $0.05 > p > 0.01$) as initially hypothesised (H4.1), there is no relationship between phylogenetic
362 diversity and human influence (Fig. 2b; Pearson's adj. $r^2 = 0.041$; $F(21) = 0.9$; $p = 0.354$). **Also**,
363 trait clustering is higher in areas with lower human influence (Fig. 2c; Pearson's adj. $r^2 = 0.389$; F
364 $(9) = 5.866$; $0.05 > p > 0.01$), contradicting H4.2 and H4.3.

365 According to SEM results based on the model depicted in Fig. 3, the importance of the
366 direct and indirect effects of each explanatory factor also varies between northern and southern
367 Europe (Fig. 3; Fig. S4). Current climate is consistently the main driver of diversity in both
368 northern and southern regions (Fig. 3; Fig. S4), except for species richness in northern biotas,
369 which is mainly driven by climate stability. Importantly, the sign of the direct effects of current
370 climate is not constant between northern and southern biotas for both species richness and
371 phylogenetic diversity (Fig. 3; Fig. S4). Current climate has an indirect effect on all facets of
372 diversity through human influence in both northern and southern Europe, particularly over **trait**
373 diversity in the south. In contrast, climate stability affects nearly all facets of diversity (the only
374 exception is phylogenetic diversity in northern Europe), with no significant indirect effects
375 occurring in any case through human influence (Fig. 3; Fig. S4). The alternative model depicted
376 in Fig. S2c, where both HII and diversity are influenced by an unknown, common factor, presents
377 the same model fit as that of the model described above, which indicates that both models are
378 equivalent (for both models, $\chi^2 = 66.32$, AIC = 346.6).

379

380 **4. Discussion**

381 The diversity and structure of mammal biotas are not homogeneous across Europe and **diverge** in
382 areas that were differently affected by past and present climatic events and anthropogenic changes.
383 Northern European mammal assemblages have lower species richness, presenting phylogenetic
384 and, more significantly, **trait clustering**, particularly north of the current 0° isotherm. Southern
385 European assemblages, on the other hand, are richer, but have no particular pattern in neither
386 phylogenetic nor **trait** structure. Current climate is the main driver of diversity (and of human
387 influence), but climate stability also has an important effect on the species richness of northern

388 assemblages. Finally, human presence exerts direct and indirect effects on diversity, apparently
389 favoring species richness across Europe, but without leading to neither phylogenetic nor trait
390 clustering.

391 Despite the strong influence of past climate and human pressure, current climate is the most
392 important driver of large-scale gradients of European mammal diversity at the scale of our
393 analyses. Water and energy variables are known to impose constraints on species richness,
394 particularly at higher latitudes (Hawkins et al., 2003). However, the importance of different
395 climatic components may vary geographically (Gouveia et al., 2013; Hortal et al., 2011; Whittaker
396 et al., 2007). We found that such heterogeneity in the strength of the relationship between species
397 richness and current environment holds up for other aspects of diversity (see also Safi et al., 2011).
398 Indeed, current climate is highly correlated with species richness, particularly in the richer southern
399 areas, while its influence on phylogenetic and trait diversity is stronger in the species-poor
400 Northern Europe. Also, a high proportion of the variation in diversity that is accounted for by
401 current climate cannot be decoupled from human influence. Indeed, climate and primary
402 productivity can also drive the settlement of humans, which in turn impacts diversity distribution
403 (Luck, 2007). We provide additional support for the existence of these effects, as climate strongly
404 moderates human influence.

405 The general effects of current climate on the distribution of European mammals are
406 intertwined with the distinct imprint left by climate stability since the LGM. The strength of the
407 relationship between species richness and climate stability differs between northern and southern
408 biotas, becoming the most important driver of species richness in Northern Europe. These less
409 climatically stable northern areas, which were strongly affected by adverse conditions, also
410 suffered comparatively more extinctions associated with successive climate oscillations (Dynesius

411 & Jansson, 2000), which subsequently affected species distributions and led to lower species
412 richness in this region (in accordance with H1; Calatayud et al., 2016; Fløjgaard et al., 2011; Hortal
413 et al., 2011; Ordonez & Svenning, 2015; Svenning et al., 2015; Svenning & Skov, 2004). These
414 non-random extinctions lead to the disappearance of specific lineages and species with particular
415 traits, thereby selecting for generalist species and lineages. Our results support the existence of
416 such selection process, as there is a clear trend for northern European assemblages to include a
417 clustered selection of species from certain lineages and, most significantly, with specific traits (as
418 predicted by H2.1 and H3.1). Indeed, the vertebrate species that survived in this region show a
419 strong bias towards the extremes of the body size distribution (i.e., either small or large species;
420 Bhagwat & Willis, 2008), and Pleistocene climatic changes have been related to the selection of
421 large-bodied Carnivora species in northern Europe (Diniz-Filho et al., 2009). Subsequent
422 colonisation after temperatures rose and ice retreated was also dependent on the existence of
423 specific traits, including high mobility and short generation times –which are more frequent on
424 some lineages (Bhagwat & Willis, 2008; Jansson, Rodríguez-Castañeda, & Harding, 2013;
425 Ordonez & Svenning, 2016). Interestingly, the current location of the 0°C isotherm (which
426 [associates with](#) long periods of freezing temperatures throughout the year) marks a steep increase
427 in phylogenetic and, especially, trait clustering. This pattern may indicate that the constrain
428 imposed by such limit on the distribution of mammal species inhabiting the North of Europe is
429 timeless.

430 Differential survival and postglacial recolonisation would jointly explain the tendency for
431 more phylogenetically and, especially, [trait](#) clustered assemblages in northern biotas. However,
432 such trend is not a gradual decline of diversity with decreasing stability towards the north, rather
433 corresponding to distinct relationships between climate stability and both nPD and npFD in

434 northern and southern Europe (see also Hortal et al., 2011). This pattern may result from the limited
435 recolonisation of formerly glaciated areas by many species, due to limited dispersal ability and the
436 migratory barriers posed by the Pyrenees, the Alps, the Balkans, the arid areas of inner Iberian
437 Peninsula and the Mediterranean Sea (Ordóñez & Svenning, 2015, 2016; see also Hewitt, 1999).
438 Such limited recolonisation resulted in a depauperated Northern Europe, where species
439 interactions or other community-level processes have had little influence on the post-glacial
440 establishment of mammal assemblages. Therefore, differences in climate stability left no
441 significant signal on the community structure within that region, or at least are hidden within the
442 strong effects of current climate. Southern assemblages, in contrast, do not show a generalized
443 pattern of clustered phylogenetic or trait diversity. The majority of them were not different from a
444 random draw of species from the regional pool (although around a fifth of the cells in this region
445 were phylogenetically clustered), thereby providing some support to hypotheses H2.2 and H3.2.
446 Pleistocene climate changes were milder in these areas along the successive glacial-interglacial
447 cycles (Ehlers & Gibbart, 2004), and so extinctions associated with repeated environmental
448 filtering processes were probably less preeminent than in the north. Rather, these climatic
449 oscillations may have promoted speciation processes in the south due to repeated cycles of
450 vicariance and recolonisation (as in Rangel et al., 2018; see Schmitt, 2007), allowing the
451 accumulation of diverging lineages and trait configurations (Jansson & Dynesius, 2002). Such
452 combination of climatic refuge and increased diversification resulted in the higher phylogenetic
453 and trait diversity of Southern European mammals, but not in the ecological saturation of
454 landscapes that would have led to significantly overdispersed assemblages due to limiting
455 similarity processes.

456 The relationship between human influence and mammal richness is, in general, positive,
457 as initially hypothesized. Results from SEM indicate that current climate also exerts indirect
458 effects on biodiversity through its effects on human influence, suggesting that both humans and
459 other mammal species thrive in areas that currently show higher productivity and/or certain
460 climates (Balmford et al., 2001; Fjeldså & Burgess, 2008). Indeed, the spread of human
461 populations has tracked the milder climate conditions (Timmermann & Friedrich, 2016), a pattern
462 also visible in their current distribution, particularly in the north of Europe. In this region, the
463 combination of overall low productivity and the preeminence of generalist species with large
464 distribution ranges (Davies, Purvis, & Gittleman, 2009; Hortal et al., 2011) may be promoting the
465 spatial coincidence in the establishment of human populations and (relatively) diverse mammal
466 faunas. However, contrary to our expectations, the areas of high human impact do not tend to hold
467 neither phylogenetic nor functionally less diverse assemblages. Long-term human occupation
468 throughout the Pleistocene and Holocene may have increased local habitat diversity and landscape
469 heterogeneity, thus promoting higher species richness and the establishment of species with very
470 different adaptations and ecological roles (van Rensburg, Chown, & Gaston, 2002; see also Stein,
471 Gerstner, & Kreft, 2014).

472 Note, however, that these patterns correspond to the observed distribution of extant species,
473 after the extinction of those species more intolerant to humans. This effect increases the proportion
474 of species in the regional pool that can thrive in highly-impacted areas, and so these areas host
475 comparatively richer assemblages (Araújo, 2003), that still represent the overall [trait](#) and
476 phylogenetic structure of the species pool. In contrast, the imprint of human influence on
477 biodiversity does not show a direct relationship with climatic stability. This is perhaps due to the
478 highly idiosyncratic nature of mammal extinctions in Europe during the Pleistocene (see Crees et

479 al., 2016; Lorenzen et al., 2011; Santini, González-Suárez, Rondinini, & Di Marco, 2017). Some
480 species tracked climate changes, becoming extinct by humans only in periods when the extent of
481 their suitable areas was substantially reduced (e.g. woolly mammoth; Nogués-Bravo et al., 2008).
482 In contrast, other species were seemingly not affected by climatic oscillations nor human
483 colonisation (e.g. reindeer; Lorenzen et al., 2011). These species may have coped with the spread
484 of human populations partly because they did not suffer strong reductions in the extent of their
485 climatically suitable areas. They might also possess traits that allowed their persistence in
486 landscapes increasingly impacted by humans (e.g. horse; Lorenzen et al., 2011), like being evasive
487 or inconspicuous, having short generation times or being able to feed on resources that persist or
488 increase in human-transformed habitats. These traits would have contributed to the different
489 selection of species and lineages between northern and southern Europe discussed above, but
490 without generating a clear (i.e. smooth) geographic gradient of progressive influence of humans in
491 more stable areas.

492 It is also important to mention that other factors that were not specifically considered in
493 this study might be affecting both human influence and biodiversity, thereby causing the
494 correlation between them, as indicated by the similar power of the alternative SEM model (Figure
495 S2c). This model implies the existence of an extrinsic factor affecting simultaneously both
496 predictors and dependent variables in the structural equation model. Although it is hard to think of
497 a missing factor operating directly with similar intensity on the dynamics of climate, land use and
498 diversity, this serves as a cautionary note that our results should be complemented with further
499 research on the effects of other past and recent factors, such as long-term landscape dynamics or
500 the effects of pathogens and parasites (see, e.g., Ricklefs, 2015).

501 To summarise, by accounting for the effects and interactions between current and past
502 drivers of diversity, we showed that current European mammal diversity is affected by both
503 contemporary and long-term global change effects, but in spatially complex and, sometimes,
504 counterintuitive ways. The analytical approach used here allows accounting for variations in
505 species diversity, lineages and traits within a common framework, separating their largely shared
506 variations into independent variables (see de Bello et al., 2017; Nascimento et al., 2018 for similar
507 approaches). This wider and more complete overview of the factors acting behind the current
508 distribution of biodiversity allows a deeper understanding of the causes and consequences of global
509 change impacts on biodiversity (see, e.g. Mouillot et al., 2013). Indeed, the spatial idiosyncrasy of
510 the relationship between different aspects of biodiversity and climate, climate changes and human
511 impacts calls for reconsidering the common assumption that strong disturbances and harsh
512 conditions unavoidably lead to lower levels of phylogenetic and trait diversity.

513

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753 **6. Data accessibility statement:** All data used in this article comes from public sources and will
754 be archived at DIGITAL.CSIC public repository (<https://digital.csic.es/handle/10261/179077>)
755 upon acceptance of the manuscript. The final DOI of the data will eventually be included at the
756 end of the article.

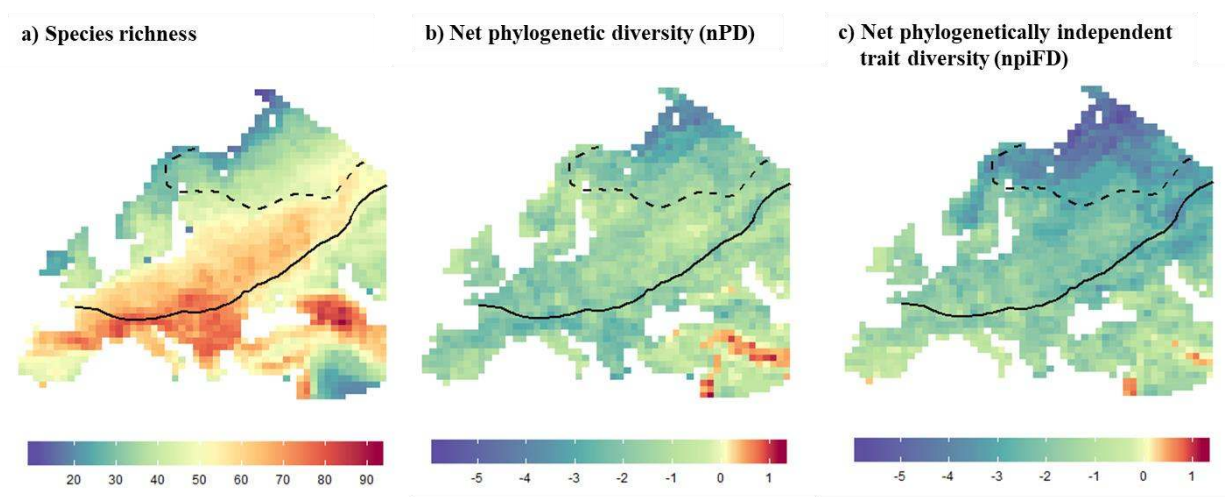
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760 **7. Figures**

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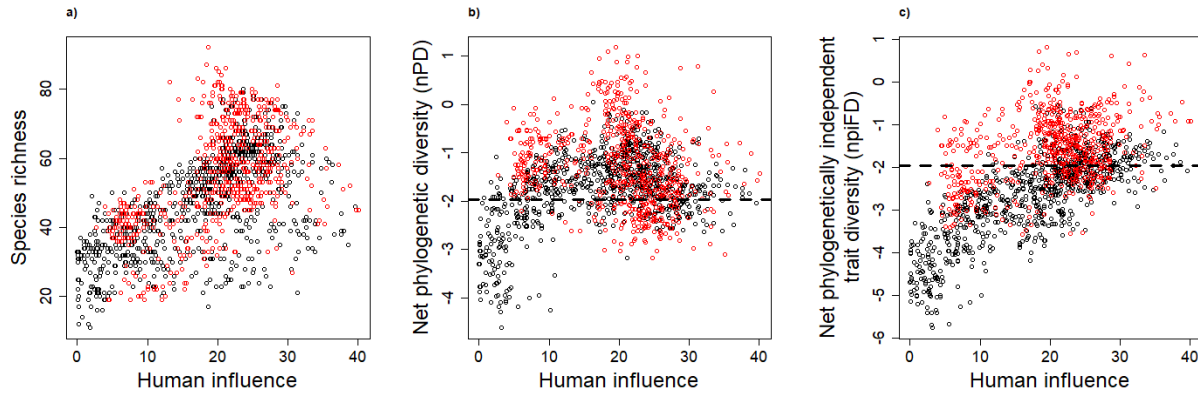


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765 Figure 1. Geographic distribution of mammal (a) species richness, (b) net phylogenetic diversity
766 and (c) net phylogenetically-independent trait diversity across Europe. The solid black line
767 indicates the position of the 0°C isotherm at LGM (21 ka), while the dashed line indicates its
768 current location. (b) and (c) are represented using the same scale, and values below -1.96 indicate
769 assemblages with phylogenetic or trait clustering, respectively.

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773 Figure 2. Relationship between human influence and (a) species richness, (b) net phylogenetic
 774 diversity (measured as nPD) and (c) net phylogenetically-independent trait diversity (measured
 775 as npiFD) in Europe (see supporting information, Table S1). Red dots represent grid cells located
 776 south of the 0° C isotherm of the [Last Glacial Maximum](#), and black dots represent those located
 777 north of that line. The dashed line indicates $SES = -1.96$, meaning that values falling below it are
 778 statistically significant (i.e. $p\text{-value} < 0.05$).

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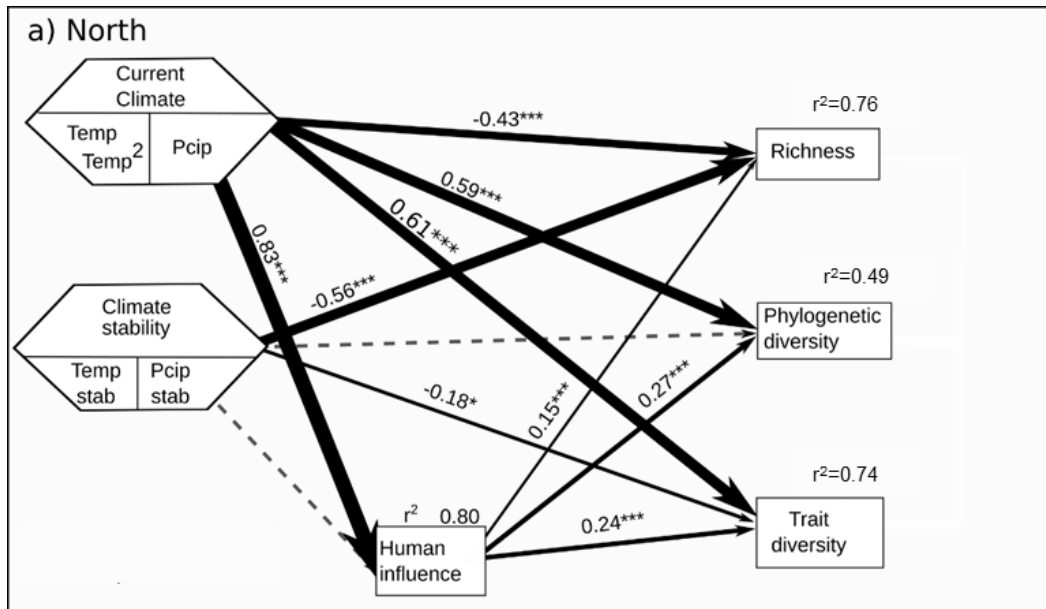
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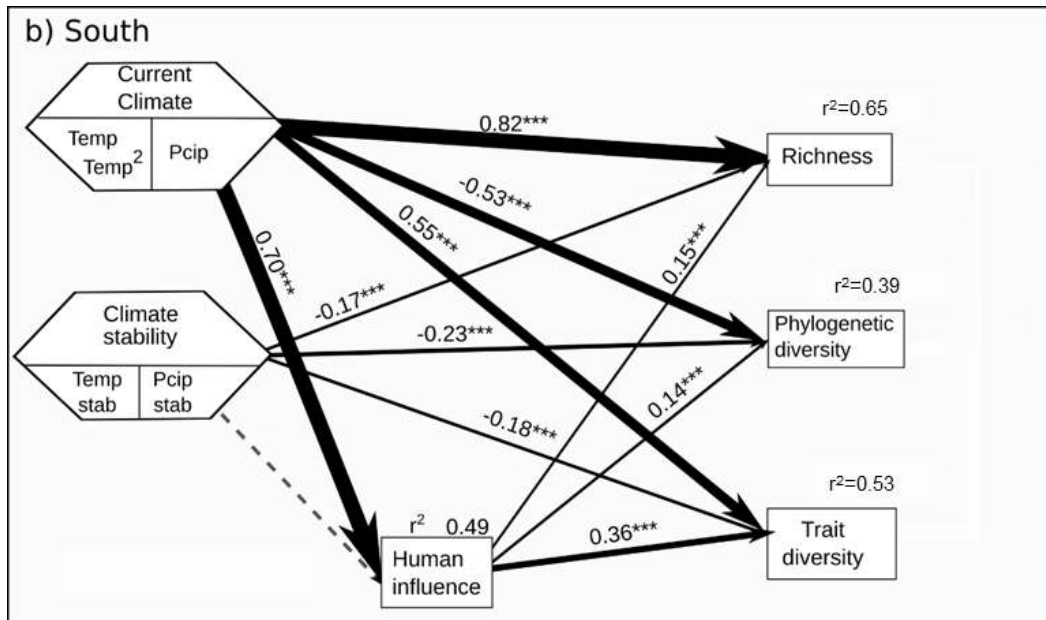
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789 Figure 3. Structural Equation models (SEMs) for the mammal diversity of (a) Northern Europe
 790 and (b) Southern Europe. Species richness was measured as number of species, phylogenetic
 791 diversity as net phylogenetic diversity (nPD) and trait diversity as net phylogenetically-
 792 independent trait diversity (npiFD) (see main text for details). Model fit parameters: $\chi^2 = 66.32$;
 793 $p = 0.53$; d.f. = 64. Numbers indicate the standardised path coefficients; arrow thickness is
 794 proportional to coefficient value; and dashed lines correspond to non-significant relationships.
 795 Coefficients of determination of endogenous variables that act as response variables are also
 796 represented. The correlations between the errors of exogenous variables are not shown.

797 **Supporting Information– Appendix S1. Long-term climate changes, current climate and**
798 **human impacts determine the geographic distribution of European mammal diversity**

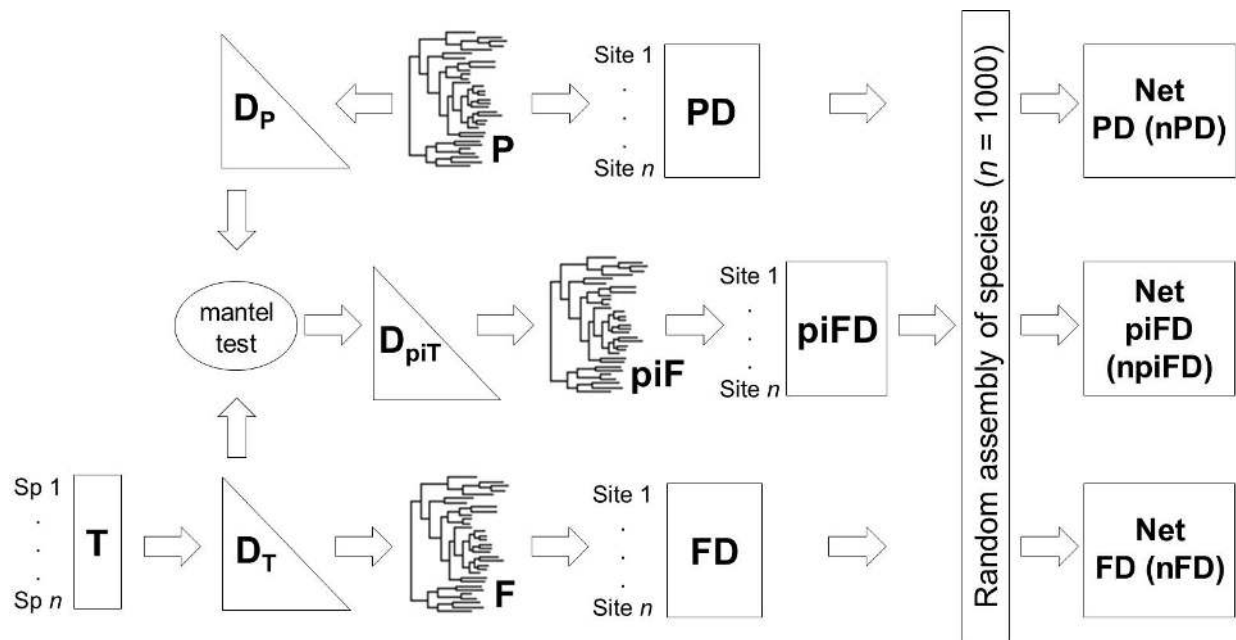
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800 Table S1. Results of the exploratory linear ordinary least squares (OLS) regressions assessing the
801 relationship between species richness, phylogenetic diversity (nPD) and trait diversity (npiFD) of
802 mammal assemblages, and several descriptors of current climate, climate stability and
803 anthropogenic effects. Quadratic terms were evaluated for all predictors, but only significant
804 relationships are shown.

Set of variables	Variable	Species richness		Phylogenetic Diversity		Trait Diversity		
		Coefficient	Adj. R ²	Coefficient	Adj. R ²	Coefficient	Adj. R ²	
Northern Europe	Current Climate	Current Temperature	1.744	-	0.094	-	0.167	-
		Current Temperature ²	-0.092	0.349***	-0.011	0.466***	-0.002	0.704***
		Current Precipitation	-0.03	0.14***	0.001	0.041***	0.001	0.033***
	Climate stability	Temperature Stability	-1.137	0.457***	-0.002	-0.001	-0.011	0.008**
		Precipitation Stability	-0.046	0.316***	3.116x10 ⁻⁵	-0.001	-0.002	0.116***
	Anthropogenic effects	Human Influence	0.958	0.375***	0.036	0.194***	0.085	0.612***
Southern Europe	Current Climate	Current Temperature	3.711	-	0.018	-	0.306	-
		Current Temperature ²	-0.171	0.331***	0.002	0.149***	-0.007	0.415***
		Current Precipitation	0.05	0.599***	-0.002	0.324***	-0.001	0.022***
	Climate stability	Temperature Stability	2.076	0.061***	-0.204	0.184***	-0.071	0.025***
		Precipitation Stability	0.055	0.122***	-0.001	0.0193***	-4.938x10⁻⁴	0.002***
	Anthropogenic effects	Human Influence	1.063	0.274***	-0.026	0.048***	0.039	0.129***

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806 *0.05 > P > 0.01; **0.01 > P > 0.001; ***P < 0.001.

807 Coefficient corresponds to the regression coefficients; Adj. R² is the adjusted R². Values in bold
808 are statistically significant.

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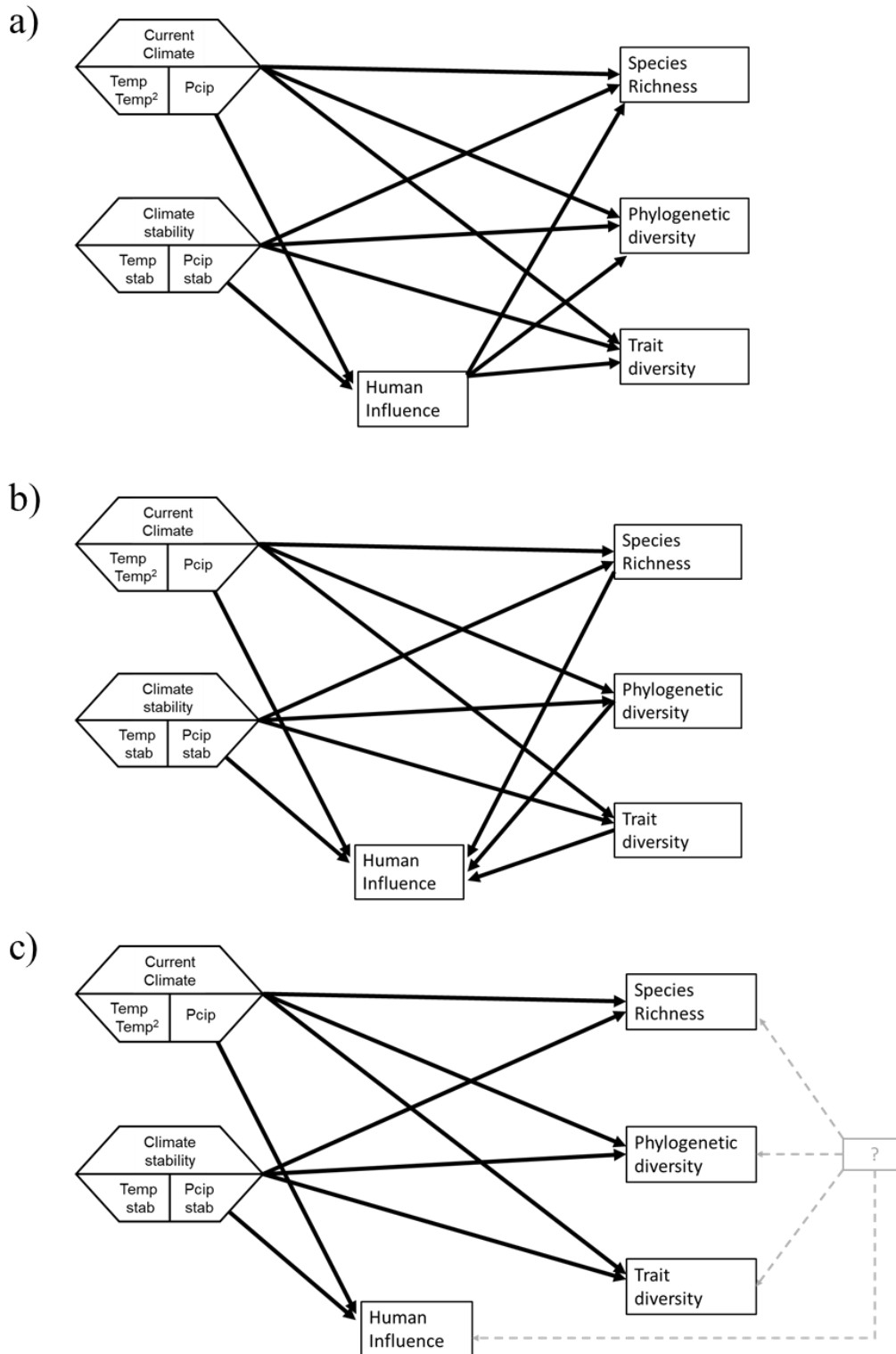


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814 Figure S1. Scheme of the hierarchical protocol used to separate the net phylogenetic and trait
 815 diversity components independent from species richness, and the net phylogenetically-
 816 independent component of trait diversity. Triangular distance matrices (D_P and D_T) based on
 817 phylogenetic (P) or trait (T) data, respectively, were obtained from either known phylogenies or
 818 trait values. Net phylogenetic diversity (PD) and trait diversity (FD) were calculated according to
 819 the branch lengths of their corresponding trees, and their richness-independent variations (nPD
 820 and nFD) were calculated as the net departure from 1000 random assemblages of the same
 821 number of species, gathered from the species present in the regional pool. Phylogenetically
 822 independent trait diversity (piFD) and net phylogenetically-independent trait diversity (npiFD)
 823 were obtained from a matrix of phylogenetically-independent trait distances (D_{piT}), calculated
 824 as the partial component of trait distances in a matrix regression between trait and phylogenetic
 825 distance matrices.

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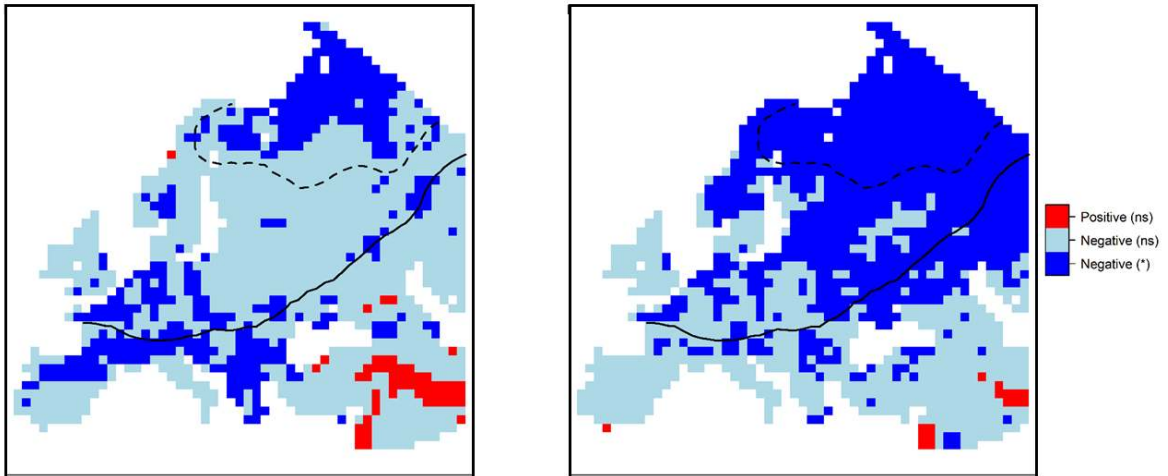


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829 Figure S2. Scheme of the *a priori* models that summarise the initial hypothesis on how
 830 endogenous (response) and exogenous (explanatory) variables are related. Model a) was the one
 831 used in the study, while b) and c) correspond to alternative models.

a) Net phylogenetic diversity (nPD)

b) Net phylogenetically independent trait diversity (npiFD)



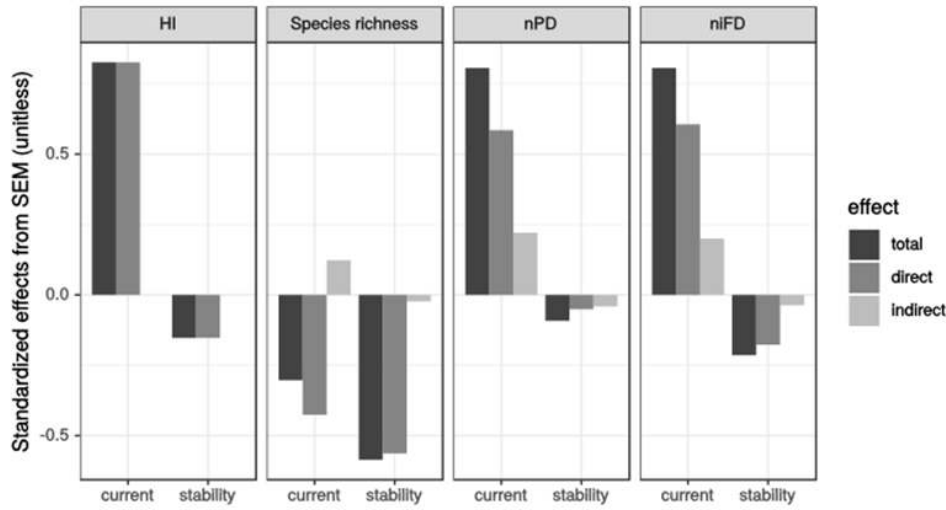
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833 Figure S3. Geographical distribution of the statistical significance of mammal (a) net
834 phylogenetic diversity (nPD) and (b) net phylogenetically-independent trait diversity (npiFD)
835 across Europe. The solid black line indicates the position of the 0°C isotherm at [the Last Glacial](#)
836 [Maximum](#) (21 ka), while the dashed line indicates its current location. Red cells indicate non-
837 significant positive values of both nPD and npiFD (i.e., $0 < \text{nPD}/\text{npiFD} < 1.96$), while grey cells
838 indicate non-significant negative values (i.e., $-1.96 < \text{nPD}/\text{npiFD} < 0$) and blue cells indicate
839 significant negative values (i.e., $\text{nPD}/\text{npiFD} \leq -1.96$).

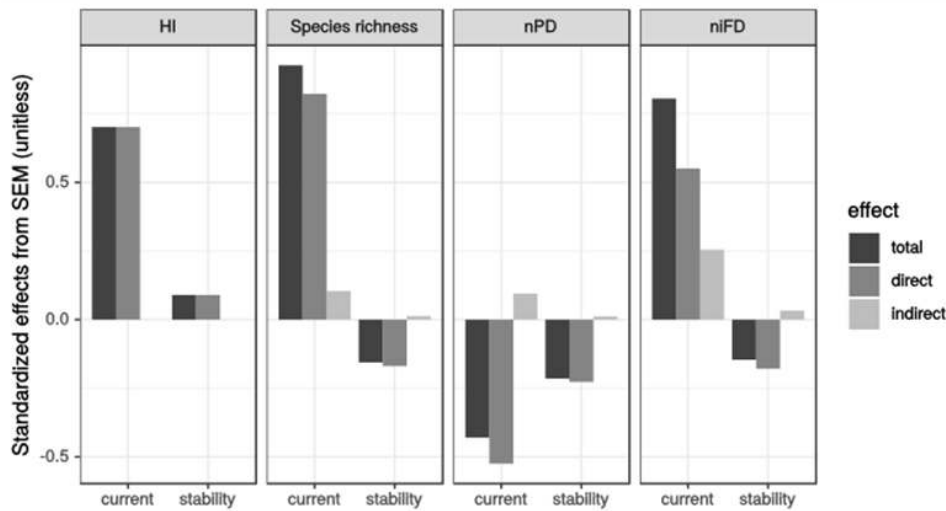
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a) North



b) South



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Figure S4. Total, direct and indirect standardised effects (through human influence) of both current climate and past climate stability, obtained from the path coefficients of the structural equation models (SEMs) for mammal diversity (species richness, phylogenetic – nPD, and trait diversity – npiFD; see main text for more details) in (a) Northern Europe and (b) Southern Europe.

850 File GEB-2019-0174.R2.xls. Appendix S2. Complete results of the SEM analysis for northern
851 and southern Europe. The document includes two sheets. The first one “Fit summary” reports the
852 results of the model before including the composite variables, and is useful for checking the
853 effects of current climate (three variables: temperature, temperature² and precipitation) and
854 climate stability (two variables: stability in temperature and precipitation) individually. The
855 second sheet “composite summary” reports the results of the model once the composite variables
856 are included, and is useful to check the effects of current climate and climate stability as a whole.
857 Both sheets include four tables. Table a: Coefficients of the relationships or regression weights;
858 table b: covariance between the exogenous variables; table c: correlation between the exogenous
859 variables; table d: percentage of explained variability or squared multiple correlations. Also, each
860 table contains two parts, the left panel shows the analysis for northern Europe and the right panel
861 shows the results of southern Europe.