Rediscovering lost Cenozoic tree diversity in Western and Central Europe

Vincent Wilkens[1,*], Anna Walentowitz[1,2], Sebastian Teichert[3], Lisa Hülsmann[2,4], Nicolai Nürk [2,5], Ole R. Vetaas[6], Carl Beierkuhnlein[1,2,7,8]

[1] Department of Biogeography, University of Bayreuth, Bayreuth, Germany

[2] Bayreuth Center of Ecology and Environmental Science (BayCEER), Bayreuth, Germany

[3] GeoZentrum Nordbayern, Friedrich-Alexander-Universität Erlangen-Nürnberg (FAU), Erlangen, Germany

[4] Ecosystem Analysis and Simulation (EASI) Lab, University of Bayreuth, Bayreuth, Germany

[5] Plant Systematics, University of Bayreuth, Bayreuth, Germany

[6] Department of Geography, University of Bergen, Bergen 5020, Norway

[7] Geographical Institute Bayreuth, GIB, Universitätsstraße 30, 95447 Bayreuth, Germany

[8] Departamento de Botánica, Campus Universitario de Fuentenueva 18071, University of Granada, Granada, Spain

* Correspondence: vincent.wilkens@uni-bayreuth.de

Abstract

Paleoclimatic changes during the late Cenozoic led to substantial losses of tree diversity in Western and Central Europe. A complete overview of what taxa were lost, the timing of these losses, and their implications for the adaptation of the region's forest ecosystems to ongoing climate change is needed. Here, we compiled a dataset of fossil occurrences of tree genera from Western and Central Europe to analyze tree diversity changes during the Cenozoic (66 Ma – present). We found that tree genus richness declined 75% after its peak in the Miocene (23 – 5.3 Ma), with most losses already occurring during the Plio-Pleistocene transition (ca. 2 – 3 Ma). We then used genus-level niche models to explore how these changes unfolded within climate space. Our results show how the current regional tree flora was progressively filtered towards the colder and drier margins of climate space. This coincided with the losses of most heat-tolerant lineages, including many temperate genera that could have profited under modern climate warming (e.g., *Castanea*, *Juglans, Aesculus*). We foresee several ways in which our analyses of paleoecological data can inform forest management to increase regional tree diversity and enhance forest resilience under climate change.

Introduction

Current patterns of taxonomic, functional, and phylogenetic diversity in trees (i.e., tree diversity) across the Holarctic realm have been shaped by paleoclimatic changes (Svenning et al., 2015). As global temperatures declined and polar ice sheets reformed during the late Cenozoic (66 Ma – present), temperate trees gradually succeeded subtropical and tropical trees at middle to high latitudes (Mai, 1994; Mosbrugger et al., 2005; Westerhold et al., 2020). In Western and Central Europe, temperate tree

39   diversity remained high leading up to the Plio-Pleistocene transition (2 − 3 Ma; Lang, 1994; Svenning,
40   2003). However, over the Pleistocene, repeated glaciations triggered regional extinctions of many
41   temperate tree taxa that persisted in other parts of the Holarctic realm (Ricklefs & He, 2016). The
42   prevailing explanation is that east-west oriented geographic barriers, such as the European Alps or the
43   Mediterranean Sea, impeded the south- and northward range shifts of trees in response to paleoclimatic
44   changes (Gray, 1878; Reid, 1935; Huntley, 1993). Today, in contrast with temperate forests in North
45   America and Eastern Asia, forests in Western and Central Europe are a global cold spot of tree diversity
46   (Latham & Ricklefs 1993). A complete overview of tree diversity changes during the Cenozoic—detailing
47   what taxa were lost, the timing of these losses, and their implications for the adaptation of Western and
48   Central European forests to future climate—is still missing.

49   Recent episodes of tree mortality linked to severe droughts (Senf et al., 2020) and insect outbreaks (Hlásny
50   et al., 2021; Washaya et al., 2024) highlight the widespread vulnerability of temperate European forests
51   to ongoing climate change (Lindner et al., 2010; Forzieri et al., 2021). Post-disturbance reorganization of
52   these forests towards more resilient assemblages will probably require changes in species composition
53   (Seidl & Turner, 2022). However, the capacity for both managed and passive species turnover is limited
54   by the pool of tree species (i.e., the "option-space") expected to remain suitable under future climate
55   scenarios. Although modeling studies have identified both climate change 'winners' and 'losers' among
56   native tree species (Dyderski et al., 2018), the option-space for forestry is forecasted to narrow
57   substantially over the coming century (Wessely et al., 2024). This presents a complex problem for forest
58   management in Western and Central Europe, potentially limiting the establishment of resilient,
59   productive, and biodiverse forests using only native species. Considering that this problem has likely been
60   exacerbated by tree diversity changes during the Cenozoic, a paleoecological perspective connecting past
61   losses to current deficits is needed. While species-level identification of tree fossil data is typically not
62   possible, such data can provide insights as to what tree genera were present in Western and Central
63   Europe in the past.

64   Here, we contribute a paleoecological perspective on the dwindling option-space for forestry in Western
65   and Central Europe under climate change. First, we compiled a dataset of published fossil occurrences of
66   tree genera (see Methods for definition) in Western and Central Europe to explore tree diversity changes
67   throughout the Cenozoic (Fig. 1a). We also identified fossil occurrences precisely dated to five temperate
68   stages and interglacial periods within the Pleistocene, improving the temporal resolution of our dataset
69   in the geologically recent past. Using this dataset, we address two questions:

70   a) How did tree diversity change over the Cenozoic in Western and Central Europe?
71   b) Which tree genera became regionally extinct during the Pleistocene?

72   Next, we aimed to understand the impact of past tree diversity changes on the reorganizing capacity of
73   Western and Central European forests amid ongoing climate change. We fitted phylogenetic generalized
74   linear mixed models (PGLMMs) of climatic centers and thermal limits for all tree genera that had a
75   presence in Western and Central Europe during the Cenozoic (Fig. 1b). Models were fitted using modern
76   species occurrences and climate data (1981 − 2010) under a Bayesian framework to account for different
77   sources of uncertainty (see Methods for detailed explanation). These hierarchical models were used to
78   estimate genus-level averages of niche parameters while incorporating species-level phylogenetic

covariance and correcting for sampling bias. With respect to Western and Central Europe, we compared niche parameters of regionally extinct genera and extant genera (both estimated using all available tree species within each genus globally) against the backdrop of different warming scenarios. Additionally, we fitted niche models for all extant genera using only species native to the region, referred to here as the Holocene regional tree flora. These models were included in our comparisons to represent the reorganizing capacity of current Western and Central European forests as well as to assess how the regional species pools within extant genera are offset from global averages. With this analysis, we address the following question:

c) How have tree diversity changes over the Cenozoic impacted the reorganizing capacity of current Western and Central European forests?
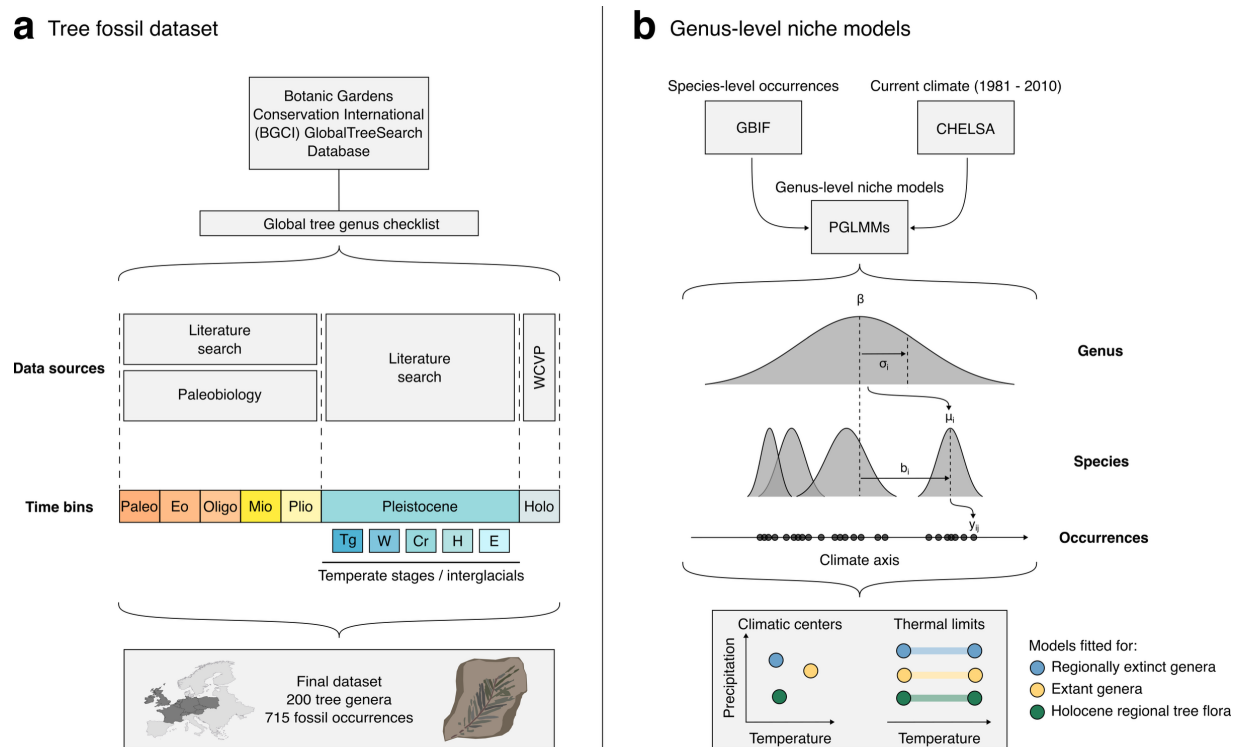

Fig. 1: **Overview of tree fossil dataset and genus-level niche models. a**, Fossil occurrences of tree genera during the Cenozoic (66 Ma – present) from Western and Central Europe (including Austria, Belgium, Czechia, France, Germany, Ireland, Luxembourg, Netherlands, Poland, Switzerland, and United Kingdom) were compiled using the Paleobiology Database (PBDB) and literature. Time bin abbreviations are as follows: Paleo – Paleocene, Eo – Eocene, Oligo – Oligocene, Mio – Miocene, Plio – Pliocene, and Holo – Holocene. For the Pleistocene, additional fossil occurrences dated to five temperate stages and interglacial periods were included: Tg – Tiglian, W – Waalian, Cr – Cromer, H – Holstein interglacial, and E – Eem interglacial. Holocene occurrences were obtained from the World Checklist of Vascular Plants (WCVP). **b**, Species-level occurrence data from the Global Biodiversity Information Facility (GBIF) were combined with climate data from CHELSA (Climatologies at high resolution for the Earth's land surface areas; Karger et al., 2017; 2018) to fit phylogenetic generalized linear mixed models (PGLMMs) of genus-

101   level climatic centers and thermal limits. These models were used to estimate genus-level averages (β) of
102   niche parameters while accounting for different sources of uncertainty.

Results

Tree diversity changes during the Cenozoic

105   We started by summarizing major trends in tree genus richness during the Cenozoic based on fossil
106   occurrences, highlighting differences between angiosperms and gymnosperms. For all analyses shown,
107   we defined a tree genus as having at least 30% of its accepted species recognized as tree-forming (see
108   Methods for details).

109   Compiled fossil data from Western and Central Europe showed a steady increase in tree genus richness
110   throughout most of the Cenozoic, followed by a significant decline after the Miocene (Fig. 2a, b). This
111   increase was interrupted only by a small decrease over the Eocene-Oligocene boundary, during which
112   angiosperms (11% decrease) and gymnosperms (53% increase) responded differently. In the Miocene,
113   tree genus richness reached an overall peak of 151 genera, including 122 angiosperms and 29
114   gymnosperms. Tree genus richness subsequently decreased 27% in the Pliocene, followed by a further
115   58% decrease in the Tiglian stage of the Early Pleistocene. During the Pleistocene, tree genus richness
116   remained comparatively stable, but reached an overall low of 29 genera in the Holstein and Eem
117   interglacials. When taken as a whole, Western and Central Europe hosted 60 tree genera in the
118   Pleistocene (45% decrease from the Pliocene). Of the 200 tree genera found in the fossil record of Western
119   and Central Europe during the Cenozoic, only 37 have a native presence in the region today. Altogether,
120   tree genus richness decreased 75% from its peak in the Miocene to the Holocene, with gymnosperms
121   (79% decrease) more impacted than angiosperms (75% decrease). We conducted sensitivity analyses to
122   evaluate how varying the minimum threshold for classifying a genus as a tree genus, defined by the
123   proportion of species within the genus known to be tree-forming, affects these findings (Supplementary
124   Figs. 1 – 3). These analyses confirmed the robustness of all trends, though the absolute numbers of genera
125   varied.

126   Next, we calculated turnover (β_{TURN}) and nestedness (β_{NEST}) components of ß-diversity (β_{TOTAL}) between all
127   consecutive time bins using the Sørensen dissimilarity index (Fig. 2c). Total ß-diversity exhibited two peaks
128   during the Cenozoic, both driven primarily by the nestedness component, reflecting large losses or gains
129   of genera with few replacements. The first peak was the Paleocene-Eocene transition (β_{TOTAL} = 0.494, β_{TURN}
130   = 0.024, β_{NEST} = 0.470), which coincided with the emergence of 78 genera in the fossil record. The second
131   peak was the Pliocene-Tiglian transition (β_{TOTAL} = 0.423, β_{TURN} = 0.022, β_{NEST} = 0.401), over which 65 genera
132   disappeared from Western and Central Europe (52 permanently). During the Eocene-Oligocene transition
133   (β_{TOTAL} = 0.356, β_{TURN} = 0.345, β_{NEST} = 0.011), turnover was the dominant component, indicating that
134   changes in total ß-diversity resulted largely from genera being replaced by others. This timespan was
135   marked by the first appearances of many temperate tree genera (e.g., *Picea*, *Betula*, *Fagus*) as well as the
136   first losses of tropical tree genera, including palms (e.g., *Areca*, *Livistona*, *Serenoa*) and mangroves (e.g.,
137   *Nypa*, *Xylocarpus*, *Excoecaria*). During the Pleistocene, total ß-diversity trended downwards. However,
138   absolute gains and losses of tree genera were small, and compositional changes were strongly influenced
139   by intermittent gaps in the fossil record. Sensitivity analyses showed that both trends and absolute
140   changes in ß-diversity were not dependent on the definition of a tree genus, with some breakdown

141 observed at the most conservative threshold proportion of 1.0, which is attributable to the limited
142 numbers of genera meeting this criterion (Supplementary Figs. 4 – 6).
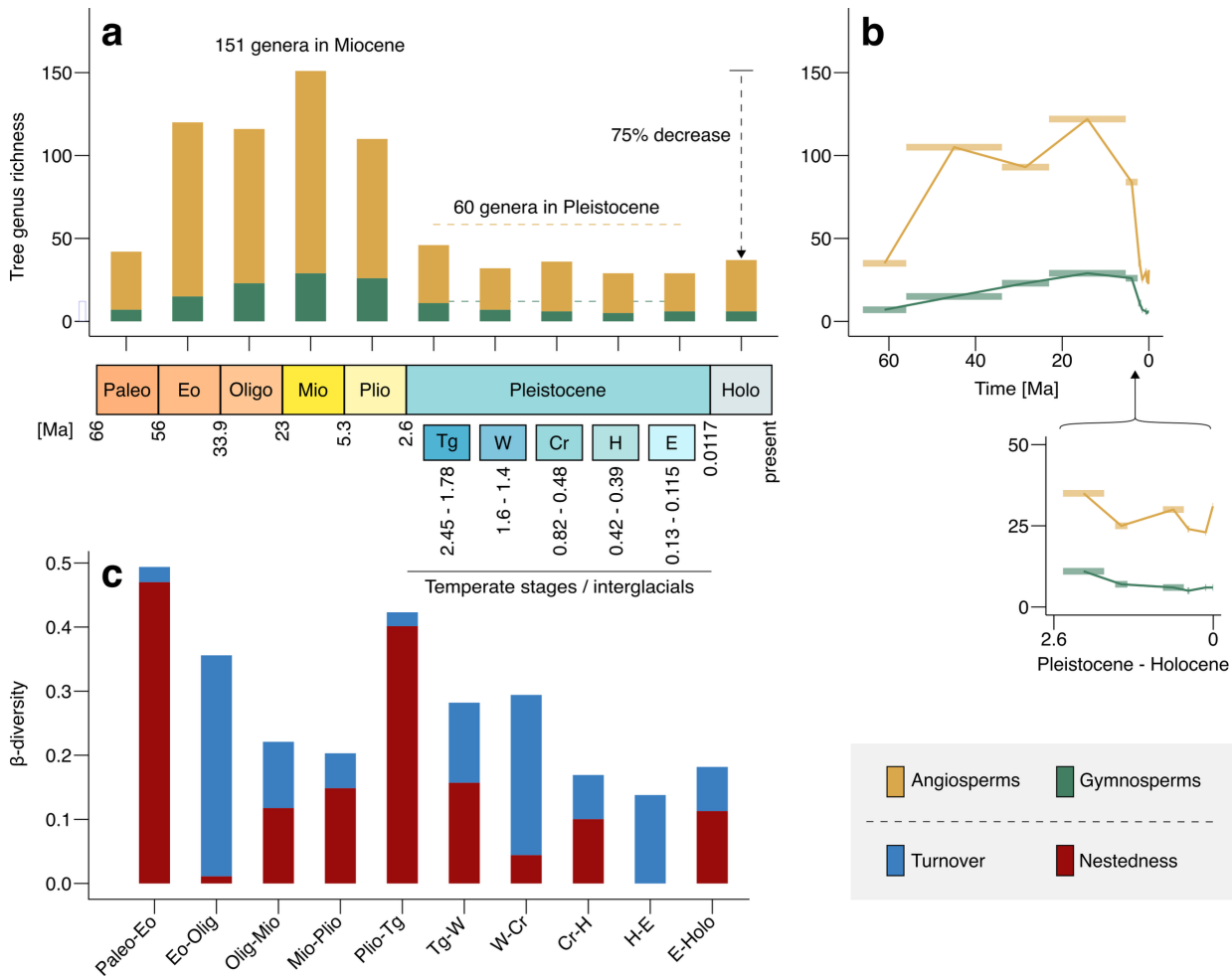

143

Fig. 2: **Tree genus diversity changes in Western and Central Europe over the Cenozoic (66 Ma – present)**
based on compiled fossil occurrences. a, Tree genus richness changes over 11 time bins, highlighting
differences between angiosperms (orange) and gymnosperms (green). Time bin abbreviations are as
follows: Paleo – Paleocene, Eo – Eocene, Oligo – Oligocene, Mio – Miocene, Plio – Pliocene, and Holo –
Holocene. For the Pleistocene, additional fossil occurrences dated to five temperate stages and
interglacial periods were included: Tg – Tiglian, W – Waalian, Cr – Cromer, H – Holstein interglacial, and E
– Eem interglacial. **b**, Tree genus richness changes on a linear timescale. Lines connect the midpoints of
each time bin from **a**, with a closer look at the Pleistocene-Holocene interval (2.6 – present). **c**, Total ß-
diversity changes between consecutive time bins, broken down into nestedness (red) and turnover (blue)
components.

Most regional extinctions of tree genera in Western and Central Europe took place during the Plio-
Pleistocene transition or earlier (Fig. 2a). Compiled fossil data revealed only 27 tree genera that went
regionally extinct during the Pleistocene (Fig. 3). During the Tiglian stage, 13 tree genera were lost,
including several currently found in temperate forests of North America and Eastern Asia, such as
redwood (*Sequoia*), arborvitae (*Thuja*), and swamp cypress (*Taxodium*). Certain temperate genera,

159 including hemlock (*Tsuga*) or hickory (*Carya*), maintained a presence into the Waalian or Cromer stage,
160 respectively. Other genera that disappeared from Western and Central Europe during the Middle
161 Pleistocene, such as chestnut (*Castanea*), horse chestnut (*Aesculus*), walnut (*Juglans*), laurel (*Laurus*), and
162 pistachio (*Pistacia*), maintain native populations in the Mediterranean basin today. From the Holstein
163 interglacial to the Holocene, only three additional genera were lost: olive (*Olea*), wingnut (*Pterocarya*),
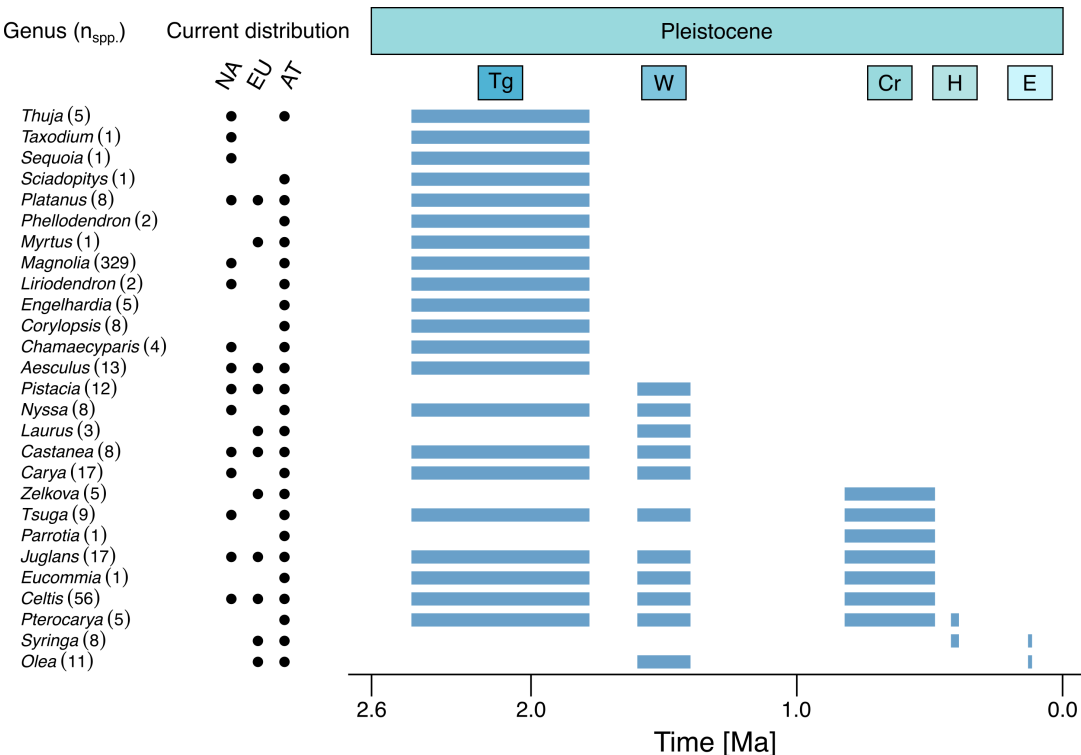164 and lilac (*Syringa*).

165

Fig. 3: **All regionally extinct tree genera in Western and Central Europe (WCE) that disappeared during**
the **Pleistocene.** The number of accepted tree species according to Botanic Gardens Conservation
International (BGCI) GlobalTreeSearch database are given. Current distribution in NA: North America, EU:
Europe (excluding WCE), and AT: temperate Asia based on continental distribution data from World
Checklist of Vascular Plants. Pleistocene interglacials and temperate stages are abbreviated as follows: Tg
– Tiglian, W – Waalian, Cr – Cromer, H – Holstein interglacial, and E – Eem interglacial.

Linking past losses to current deficits in forest reorganization

173 We used PGLMMs to determine the average locations of Cenozoic tree genera within a bivariate climate
174 space of mean annual temperature and annual precipitation (Fig. 4a). Our results show how most extant
175 genera as well as the Holocene regional tree flora are distinctly clustered towards the colder and drier
176 margins of climate space (e.g., *Acer*, *Fagus*, *Picea* in Fig. 4a). Incorporating the last known fossil occurrence
177 of each genus from Western and Central Europe further revealed that this clustering is linked to a strong
178 directional pattern of filtering across time (Fig. 4b). In contrast, most regionally extinct genera (e.g., *Areca*,
179 *Meliosoma*, *Eugenia*, *Ziziphus*, *Phoenix* in Fig. 4a) occupy much warmer and wetter conditions. Regionally
180 extinct genera also collectively span the broadest range in climatic conditions, including tropical,
181 subtropical, and temperate climates, but are more absent towards the colder and drier margins.

182 Compared with extant genera, corresponding genera in the Holocene regional tree flora (representing
183 only native species from Western and Central Europe) show a general shift towards on average colder and
184 drier locations in climate space (e.g., compare *Acer* and *Acer*$_{nat}$ in Fig. 4a). Both regionally extinct and
185 extant genera are evenly distributed across temperate parts of climate space, but extant genera in these
186 parts typically contain more tree species per genus than regionally extinct genera.
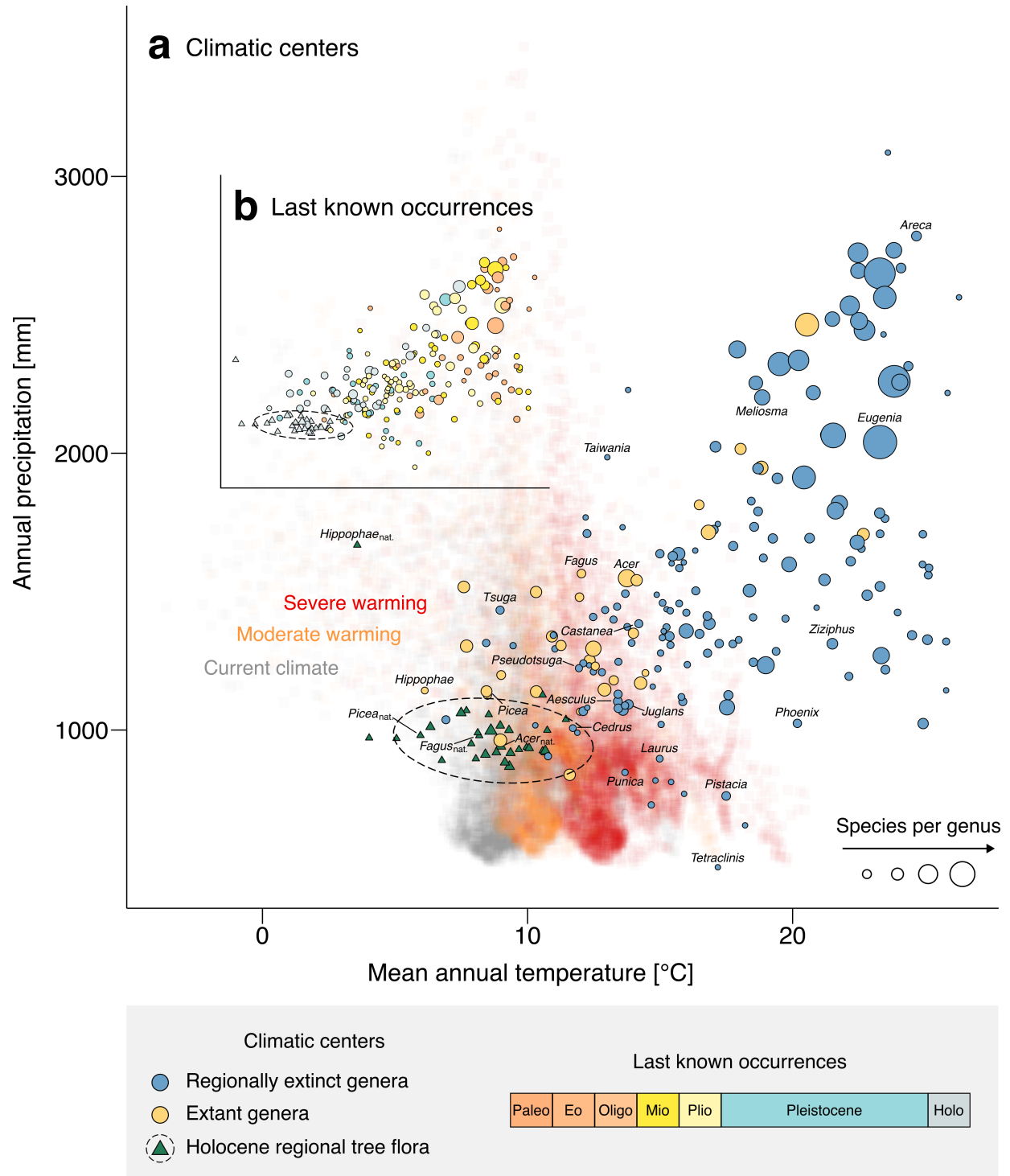
187

a Climatic centers

b Last known occurrences

Annual precipitation [mm]

3000

2000

1000

Areca

Meliosma

Eugenia

Taiwania

*Hippophae*nat.

Fagus

Acer

Severe warming

Moderate warming

Current climate

Tsuga

Castanea

Pseudotsuga

Ziziphus

Hippophae

Aesculus

*Picea*nat.

Picea

Juglans

Phoenix

*Fagus*nat.

*Acer*nat.

Cedrus

Laurus

Punica

Pistacia

Tetraclinis

Species per genus

0   10   20

Mean annual temperature [°C]

Climatic centers

● Regionally extinct genera
● Extant genera
▲ Holocene regional tree flora

Last known occurrences

| Paleo | Eo | Oligo | Mio | Plio | Pleistocene | Holo |

188

Fig. 4: **Average locations in climate space of Cenozoic tree genera from Western and Central Europe. a**, Estimated climatic centers of 200 tree genera, comparing regionally extinct genera (blue) and extant genera (yellow). Climatic centers of the Holocene regional tree flora (green), comprising the same genera as in extant genera but modelled using only native species, were also estimated. The Gelman-Ruben criterion ($\hat{R}$) was used to assess Bayesian model convergence, with values closer to 1.0 indicating

194 successful convergence. Altogether, of the 232 models fitted, seven were excluded from the plot ($\hat{R} > 1.05$
195 or number of divergent transitions > 40). Current and future climate scenarios for Western and Central
196 Europe have been underlaid, with each square representing a 625 km^2 (25 x 25 km) terrestrial grid cell.
197 Current climate: 1981 – 2010. Moderate warming: SSP1-2.6 (+ 1.3 – 2.4 °C by 2100). Severe warming:
198 SSP5-8.5 (+ 3.3 – 5.7 °C by 2100). **b**, Estimated climatic centers of 200 tree genera as well as the Holocene
199 regional tree flora (same as in **a**), with colors corresponding to the timing of the last known fossil
200 occurrence of each genus in Western and Central Europe. **a**, **b**, Point size scales with the number of
201 accepted tree species within each genus.

202 To compare the thermal tolerances of Cenozoic tree genera, we used PGLMMs to estimate upper and
203 lower thermal limits, defined here as the genus-level averages of mean daily maximum temperature of
204 the warmest month and mean daily minimum temperature of the coldest month, respectively (Fig. 5; see
205 Supplementary Fig. 7 for full figure). Genera were arranged by increasing upper thermal limit (bottom to
206 top), since this niche parameter will be relevant under ongoing climate warming. Overall, the Holocene
207 regional tree flora exhibits the lowest tolerances for on average higher temperatures compared to almost
208 all extant and regionally extinct genera. The Holocene regional tree flora also exhibits the greatest cold
209 tolerances, though many regionally extinct and extant genera show similar capacity to tolerate on average
210 colder temperatures while still maintaining high upper thermal limits (e.g., *Robinia* or *Tilia* in Fig. 5).
211 Compared to the Holocene regional tree flora, corresponding genera within extant genera show much
212 higher upper thermal limits (e.g., compare *Pinus* and *Pinus*$_{nat}$ in Fig. 5). Future warming scenarios in
213 Western and Central Europe will shift heat extremes further towards these upper limits (Fig. 5).
214 Furthermore, including the last known fossil occurrence of each genus reveals that most genera with high
215 thermal limits disappeared from Western and Central Europe, particularly from the Miocene onwards (Fig.
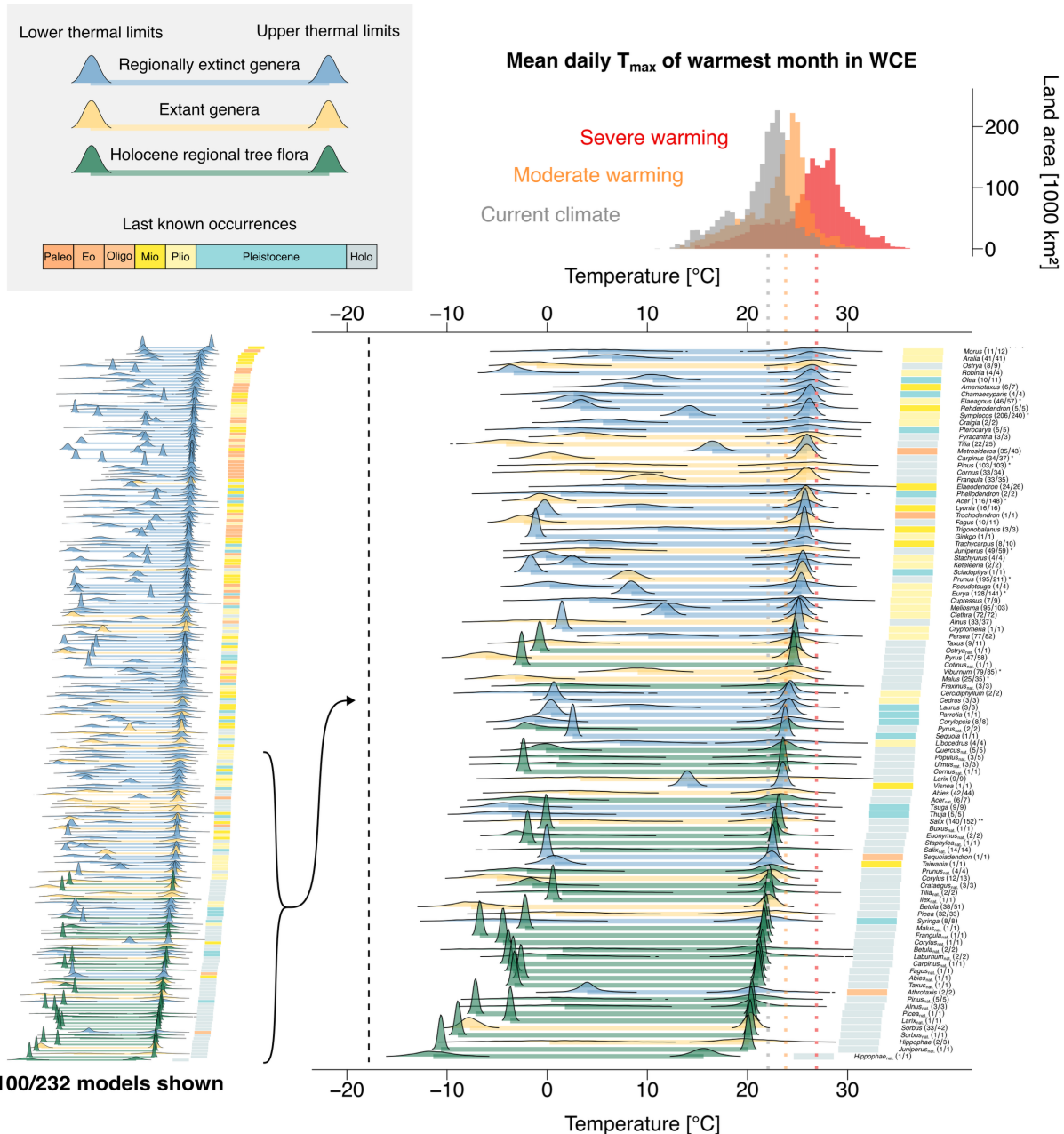216 5).

217

218

219
220 Fig. 5: **Upper and lower thermal limits of Cenozoic tree genera from Western and Central Europe.**
221 Posteriors of upper and lower thermal limits for 200 tree genera were estimated, comparing regionally
222 extinct genera (blue) and extant genera (yellow). Posteriors of genus-level thermal limits of the Holocene
223 regional tree flora (green) were also estimated, comprising the same genera as in extant genera but
224 modelled using only native species. Models were arranged by increasing upper thermal limit (bottom to
225 top). Only the first 100 of 232 models are shown (see Supplementary Fig. 7 for full figure including all
226 models). Color stripes correspond to the last known occurrence of each genus in the fossil record of
227 Western and Central Europe. All genera have been labelled on the right-hand side of the plot, including
228 the number of species from all accepted species in each genus used to fit the models. The Gelman-Ruben
229 criterion ($\hat{R}$) was used to assess Bayesian model convergence, with values closer to 1.0 indicating
230 successful convergence. Genera with $\hat{R} > 1.01$ (*) or $\hat{R} > 1.05$ (**) were labelled as having potentially

231 unreliable estimates. The distribution of heat extremes (mean daily maximum temperature of the
232 warmest month) by land area under current and future climate scenarios in Western and Central Europe
233 is overlaid. Current climate: 1981 – 2010. Moderate warming: SSP1-2.6 (+ 1.3 – 2.4 °C by 2100). Severe
234 warming: SSP5-8.5 (+ 3.3 – 5.7 °C by 2100).

235

Discussion

237 This study combined fossil data with climatic niche models to provide an overview of past tree diversity
238 changes in Western and Central Europe as well as to explore how these changes unfolded within climate
239 space. Our results highlight current deficits in regional tree diversity and potential limitations in the
240 capacity of forests to reorganize amid climate warming, linking these to paleoecological legacies during
241 the late Cenozoic. We demonstrate how insights from the past 66 million years can improve our
242 understanding of current forest ecosystems and guide management strategies to adapt forests to future
243 climate.

244 Using our fossil dataset, we give a detailed account of the substantial decline in tree genus richness in
245 Western and Central Europe after the Miocene (23 – 5.3 Ma). We found that most losses took place before
246 the Tiglian stage of the Early Pleistocene (> 2.45 Ma), with a few regionally extinct tree genera even
247 persisting into the Middle Pleistocene (ca. 820 – 115 ka). European tree diversity has been recognized as
248 lower than other continents for a long time (e.g., Gray, 1878; Latham & Ricklefs, 1993; e.g., Svenning,
249 2003; Eiserhardt et al., 2015). Unlike previous studies, we focus on Western and Central Europe, which
250 encompasses a major portion of managed temperate forest ecosystems in Europe today. Our results
251 indicate that this region was especially impacted by late Cenozoic extinctions, as evidenced by the regional
252 losses of tree genera (e.g., *Castanea*, *Juglans*, *Aesculus*) that have persisted in other parts of Europe.
253 Furthermore, previous studies (Latham & Ricklefs, 1993 Svenning, 2003; Bhagwat & Willis, 2008;
254 Eiserhardt et al., 2015) were conducted at a much coarser temporal resolution, whereas our research
255 offers a high-resolution analysis of tree diversity changes in Western and Central Europe for the entire
256 Cenozoic, including five time bins in the Pleistocene that improve coverage when both paleoclimatic
257 variability and extinctions were at their highest. The compiled dataset is freely available and can form the
258 basis for further biogeographical studies (see Data Availability).

259 Past regional extinctions of tree genera in Western and Central Europe coincided with a strong shift in
260 favor of lineages adapted to colder and drier climates. These results are consistent with previous analyses
261 (Svenning et al., 2003; Eiserhardt et al., 2015) as well as reconstructed paleoclimatic cooling and drying
262 since the mid-Cenozoic (Westerhold et al., 2020). In the process, most heat-adapted lineages were also
263 found to have been progressively filtered from the regional tree flora. Filtering favored extant genera over
264 regionally extinct genera in addition to more cold-adapted and drought-tolerant species within extant
265 genera. Thus, our results show how past tree diversity changes in Western and Central Europe can be
266 linked to projected limitations in the capacity of the current regional tree flora to respond to ongoing
267 climate warming (Dyderski et al., 2018; Wessely et al., 2024). However, we note that our analysis does
268 not indicate regionally extinct genera exhibiting clear advantages over extant genera under future climate
269 scenarios. This suggests that lost genus-level diversity itself might not be a major barrier to forest
270 reorganization. Instead, the lack of native species within extant genera, which would be suited to warmer
271 and drier conditions in the future (Gebrechorkos et al., 2025), will be the main challenge for regional forest

272 management. While extant genera contain such species globally in other temperate zones, they are
273 missing in Western and Central Europe. Given these limitations, ongoing climate warming also risks
274 inducing interaction effects with paleoclimatic cooling that greatly amplifies future losses in regional tree
275 diversity (Mathes et al., 2021).

276 Developing niche models at taxonomic levels higher than species is an essential step towards linking
277 paleoecological data with contemporary biodiversity research (Smith et al., 2019). We used niche models
278 that leveraged phylogenetic relationships within genera to compensate for species-level differences in
279 occurrence data availability. To do this, we assumed that closely related species will tend to occupy similar
280 environmental niches (i.e., phylogenetic niche conservatism). Although this assumption is well-founded
281 (e.g., Prinzing, 2001; Svenning, 2003; Crisp & Cook 2012; Hardy et al., 2012; Hawkins et al., 2013;
282 Eiserhardt et al., 2015; Vetaas et al., 2018), it may not hold if phylogenies have not been adequately
283 resolved. Consequently, estimates for individual genera could be biased, but this would not impact the
284 overall interpretation of our findings. We also counteracted sampling biases in species occurrence data
285 by weighting the likelihood contribution of each occurrence as proportional to the sampling effort
286 required to obtain it (Zizka et al., 2021; see Methods). This approach has previously been shown to help
287 recover unbiased regression coefficients (Stolar & Nielsen, 2014). Furthermore, correlative methods
288 produce models of the realized niche, which could lead to underestimation of thermal limits when abiotic
289 and biotic constraints on the fundamental niche are not accounted for (Chevalier et al., 2024). We
290 assumed these issues would average out when modeling niches at the genus level, particularly when
291 drawing on statistical power from many species. However, while our models are more robust because of
292 this, they are less interpretable since they represent genus-level averages, whereas individual species can
293 deviate significantly from these averages.

294 Forest reorganization in Western and Central Europe will require shifts towards more heat-adapted and
295 drought-tolerant species in accordance with increasing temperatures and precipitation variability (Albrich
296 et al., 2020; Seidl et al., 2024; Pinsky et al., 2025). If compositional changes are disrupted, such as when
297 current stocks of young trees face high cultivation risk (Gass & Hülsmann, 2025), forests could degrade
298 into alternative ecosystem states with major implications for the global carbon sink, local biodiversity, and
299 ecosystem services (Bowd et al., 2023; Yang et al., 2023). Our findings highlight limitations in the capacity
300 of current Western and Central European forest ecosystems to reorganize under ongoing climate
301 warming, supporting the case for introducing non-native species to partially restore lost tree diversity and
302 enhance climate resilience. However, the ecological risks associated with these measures are
303 unpredictable and could threaten native biodiversity (Roy et al., 2024). Even if not invasive themselves,
304 non-native species can act as vectors for the spread of pests and diseases. Nevertheless, non-native tree
305 species have played important roles in forestry, arboriculture, and urban planning in Europe for centuries
306 with instances of both successful establishment (*Robinia pseudoaccacia* L.) and complete failure (*Pinus
307 strobus* L.; Pötzelsberger et al., 2020; Wohlgemuth et al., 2022). Non-native tree species currently make
308 up around 4% of European forest area (Brus et al., 2019), attributable to advantages in productivity and
309 resilience over native species (e.g., *Pseudotsuga menziesii* Mirb., which is not prone to spruce bark beetle
310 outbreaks; Thomas et al., 2022).

311 Non-native species carry substantial uncertainty regarding their population trends and dominance
312 patterns, but these risks could be mitigated with measures that incorporate insights from paleoecological
313 data (Barak et al., 2016; Grace et al., 2019; Bush et al., 2022; Goodenough & Webb, 2022). In particular,
314 species from regionally extinct genera that were present during the Pleistocene and persisted into the

315 Holocene in neighboring regions could guide assisted migrations (e.g., *Aesculus hippocastanum* L., *Juglans*
316 *regia* L., *Castanea sativa* Mill.; Kreyling et al., 2011). However, our results show that the options become
317 very limited after the Early Pleistocene. Critically, the species represented in the fossil record by these
318 genera are probably not the same species that persist today. Some species from regionally extinct genera
319 with relictual populations in the Mediterranean basin may be an exception to this (e.g., *Aesculus*
320 *hippocastanum*; Postigo-Mijarra et al., 2008). Even if their modern relatives are suitable for cultivation,
321 current forest ecosystems and their biotic interactions differ significantly from those of the Pleistocene,
322 especially due to the absence of large herbivores (Pearce et al., 2024). Therefore, further research is
323 needed to fill gaps about how lost genus-level diversity can be compensated for with non-native species
324 given the invasiveness risks and high species-level variation within many genera. Extant genera also
325 contain many non-native species from other continents or neighboring regions that will be better suited
326 to future climate, have the potential to hybridize with native species, and may carry fewer risks since these
327 genera have persisted in the region throughout the Cenozoic (Dimitrova et al., 2022). Furthermore, native
328 tree diversity in Western and Central Europe is still underutilized as most forests are species-poor due to
329 past and ongoing management rather than climatic constraints. Attempting to utilize the full option-space
330 of native tree species diversity including genetic variation (Chakraborty et al., 2024) should be a priority
331 alongside any alternative measures.

332 In summary, we document substantial losses of tree diversity in Western and Central Europe during the
333 late Cenozoic accompanied by strong paleoclimatic filtering that has shaped the regional tree flora over
334 tens of millions of years. These insights show that current challenges in regional forest management are
335 deeply entrenched in paleoecological legacies, possibly requiring significant human intervention in forest
336 ecosystems. In the end, striking a balance between the concerns of foresters and ecologists to increase
337 regional tree diversity will be critical to forest reorganization.

338

Methods

340 All data analyses were conducted in R v.4.4.2. (R Core Team, 2024).

Tree diversity changes during the Cenozoic

Obtaining fossil data

343 To analyze how tree diversity changed throughout the Cenozoic era in Western and Central Europe, we
344 first compiled a dataset of macrofossil and fossil pollen occurrences of tree genera. We conducted our
345 study at the genus level because species-level identification of tree fossils is generally not possible. This is
346 due to critical identifying features being poorly preserved or the specimens not matching any known
347 extant species. Our dataset spanned 11 time bins, corresponding to seven geological epochs in the
348 Cenozoic era (Cohen et al., 2013). The Pleistocene was further divided into five temperate stages and
349 interglacial periods, following the historical nomenclature from Lang (1994). The steps taken to compile
350 the dataset are described in detail below.

351 We obtained a global checklist of tree species from the Botanic Gardens Conservation International
352 GlobalTreeSearch database (BGCI; accessed 24/10/2024), which defines a tree in accordance with the
353 IUCN Global Tree Specialist Group definition of "a woody plant with usually a single stem growing to a

354 height of at least 2 meters, or if multi-stemmed, then at least one vertical stem five centimeters in
355 diameter at breast height". We standardized this checklist by matching all species names to the World
356 Checklist for Vascular Plants (WCVP) using the R package "U.Taxonstand" (Zhang & Qian, 2023; Zhang et
357 al., 2025). Species for which a perfect match could not be found were removed.

358 Next, to establish a robust definition of a tree genus, we first calculated the proportion of tree species
359 within each genus. We initially explored two approaches: either classifying a genus as a tree genus if it
360 contained at least one tree-forming species or if it consisted entirely of tree-forming species. However,
361 we noticed that the first approach tended to include many genera consisting predominantly of herbaceous
362 or shrubby species, only a few of which are known to be tree-forming (e.g., *Erica*, *Vaccinium*,
363 *Chenopodium*), while the second approach inadvertently excluded many widely recognized tree genera
364 (e.g., *Salix*, *Quercus*, *Pinus*) since they also contain shrubby species. To address this, we conducted
365 sensitivity analyses (Supplementary Figs. 1 − 6) to evaluate the impact of different thresholds on
366 downstream analyses. Based on these results, we selected a threshold of 0.3 (at least 30% of species
367 should be tree-forming) for all further analyses. By applying this threshold to our global checklist of tree
368 species, we derived a global checklist of 3,354 tree genera.

369 We downloaded fossil occurrence data for Europe from the Paleobiology Database (PBDB; accessed
370 26/06/2025; see Data Availability). We filtered these occurrences to only include fossils dated to the
371 Cenozoic era (excluding the Pleistocene and Holocene) and which had been assigned to genera contained
372 in our global tree genus checklist. Furthermore, we filtered occurrences to only include fossils from
373 Western and Central Europe, defined in this study to encompass the following countries: Austria, Belgium,
374 Czechia, France, Germany, Ireland, Luxembourg, Netherlands, Poland, Switzerland, and United Kingdom.
375 This study area was chosen because it forms the core of the European temperate zone, contains heavily
376 managed forest ecosystems, and has been disproportionately impacted by paleoclimatic changes due its
377 geographical configuration.

378 We supplemented database occurrences with additional records identified through literature searches
379 (search string: e.g., "*Quercus*" AND "fossil") in Web of Science and Google Scholar. We thoroughly scanned
380 studies for additional fossil occurrences, including occurrences of genera not contained within PBDB. We
381 did not constrain this search to Europe, as studies from other continents often proved to be reliable
382 sources for thorough reviews of the global fossil records of certain genera or families. Occurrence data
383 for the five temperate stages and interglacial periods in the Pleistocene were acquired almost exclusively
384 through literature, which included several major monographs on the vegetation history of Europe (e.g.,
385 Lang, 1994).

386 The final dataset comprised 711 fossil occurrence records from PBDB and literature for 200 tree genera.
387 In the last step, we incorporated Holocene occurrences by generating a checklist of accepted native tree
388 genera in Western and Central Europe using WCVP, accessed via the "rWCVP" R package (Brown et al.,
389 2023). When generating this checklist, we included an additional filter that excluded any genera that were
390 listed as only native to France. This resulted in tree genera that are atypical in Western and Central
391 European temperate forests but have a limited presence in the Mediterranean coastal region of Southern
392 France (e.g., *Laurus*, *Pistacia*, *Celtis*) being classified as non-native. Furthermore, tree genera were only
393 included for the Holocene if they had previously occurred in the fossil record of Western and Central
394 Europe. This was done to rule out the possibility that new genera (without a previous presence during the

395 Cenozoic) could have emerged during the Holocene, reducing biases inherent to comparing fossil
396 occurrence data with modern country-level botanical checklists.

397 **Analyzing tree diversity changes**

398 We analyzed changes in tree genus richness and beta diversity throughout the Cenozoic era based on
399 compiled fossil data. Tree genus richness was calculated based on the number of unique tree genera
400 recorded within each time bin. Total ß-diversity as well as its nestedness and turnover components were
401 calculated for all consecutive time bins in our fossil dataset using the Sørensen dissimilarity index with the
402 "betapart" R package (Baselga & Orme, 2012). Compositional changes driven by turnover result from the
403 replacement of genera by others, whereas changes driven by nestedness occur when genera are gained
404 or lost.

405 *Building niche models of tree genera*

406 **Species occurrence data**

407 Species occurrence data was downloaded from the Global Biodiversity Information Facility (GBIF) for all
408 tree species belonging to genera in the final fossil occurrence dataset (n = 9,407 species). Only occurrences
409 with the following basis of record were included: "OBSERVATION", "OCCURRENCE",
410 "HUMAN_OBSERVATION", "PRESERVED_SPECIMEN". Occurrence data was filtered to remove entries with
411 missing coordinates, erroneously recorded coordinates, and coordinates with high or missing GPS
412 uncertainty (> 10,000 m). Remaining occurrence data for each species was then spatially thinned to a
413 common 0.25° (~ 25 km) resolution grid using the "GeoThinneR" R package (Mestre-Tomás, 2025).

414 **Climate data**

415 Global climate data was obtained from CHELSA (Climatologies at high resolution for the Earth's land
416 surface areas; Karger et al., 2017; 2018). We used the high resolution (1 km) climatologies based on GFDL-
417 ESM4 (GFDL Earth System Model Version 4.1), following recommendations of the ISIMIP3b protocol.
418 Climate data was resampled to a 0.25° spatial resolution to match species occurrence data. We used the
419 "terra" R package (Hijmans et al., 2022) to extract climate data at each species occurrence point.

420 **Accounting for sampling bias**

421 Geographical biases in species occurrence data present a major challenge for environmental niche
422 modeling. Sampling efforts that generate this data tend to be heterogeneously distributed due to
423 differences in human accessibility across landscapes. We counteracted this bias by weighting the
424 likelihood contribution of each species occurrence point in proportion to the estimated sampling effort
425 required to obtain that point. We used the "sampbias" R package (Zizka et al., 2021) to calculate weights
426 based on a spatial projection of the estimated sampling rate across all species occurrence points. For this,
427 we used the default gazetteers for cities, airports, roads, and rivers.

428 **Model fitting**

429 Following the recommendations of Smith et al. (2019) for estimating niches at taxonomic levels above
430 species, we fitted phylogenetic generalized linear mixed models (PGLMMs) of climatic centers and
431 thermal limits for 200 tree genera. We distinguished between regionally extinct and extant genera in our
432 analysis. Additionally, we fitted PGLMMs for extant genera using only species native to Western and

433   Central Europe, which we refer to as the Holocene regional tree flora. This resulted in a total of 232 models
434   of both climatic centers and thermal limits, respectively.

435   With PGLMMs, we take advantage of partial pooling, which is a feature of hierarchical models that allows
436   for information sharing across grouping variables. Partial pooling can improve the reliability of parameter
437   estimates when some groups have sparse data. In our analysis, species-level parameters are adjusted
438   toward genus-level estimates, which compensates for species with sparse occurrence data and reflects
439   shared evolutionary history and ecological limits within genera. In PGLMMs, the degree of information
440   sharing is inversely proportional to phylogenetic distance between species, which is regulated by a
441   phylogenetic variance-covariance matrix. We calculated the phylogenetic variance-covariance matrix ($\mathbf{A}$)
442   of each genus with the "ape" R package (Paradis et al., 2019). Phylogenies were generated with
443   "U.PhyloMaker" using the "GBOTB.extended.WCVP" mega tree (Smith & Brown, 2018; Jin & Qian, 2022;
444   2023; Zanne & Qian, 2023). Species that were not included in the mega tree were bound to the basal node
445   of each genus as polytomies.

446   The models were specified as intercept-only PGLMMs, including a genus-level fixed intercept and species-
447   level random intercept with phylogenetic covariance structure. If a genus was monospecific, we instead
448   fitted an intercept-only model without the species-level random intercept term. For climatic centers, we
449   selected mean annual temperature (BIO1) and annual precipitation (BIO12) as response variables,
450   representing the central tendencies of genus-level climatic distributions. For thermal limits, we selected
451   mean daily maximum temperature of the warmest month (BIO5) and mean daily minimum temperature
452   of the coldest month (BIO6) to capture the upper and lower bounds of genus-level thermal tolerances.
453   Although we treat responses of both climatic centers and thermal limits as multivariate in the modeling
454   framework for convenience, mathematically they are modeled independently without correlation of
455   residuals.

456   For a given genus, with species i and observations j, the temperature response (i.e., BIO1, BIO5, and BIO6)
457   at each occurrence point, denoted y_{ij}, was modeled using a normal distribution conditional on a species-
458   level random intercept b_i with phylogenetic variance-covariance matrix $\mathbf{A}$ (1):

459    $$y_{ij} \mid b_i \sim \mathcal{N}(\mu_i, \sigma_\epsilon^2)$$

460    $$\mu_i = \beta + b_i \tag{1}$$

461    $$b_i \sim \mathcal{N}\left(0, \sigma_b^2 \mathbf{A}\right)$$

462   where σ_b^2 and σ_ϵ^2 are the between-species and within-species variances, respectively, and β is the genus-
463   level fixed intercept. For annual precipitation, since it is continuous non-negative, we instead used a
464   Gamma distribution with the mean μ_i and shape α parameterization (2):

465    $$y_{ij} \mid b_i \sim \text{Gamma}(\mu_i, \alpha)$$

466    $$\mu_i = \beta + b_i \tag{2}$$

467    $$b_i \sim \mathcal{N}\left(0, \sigma_b^2 \mathbf{A}\right)$$

468   For each genus, we aimed to estimate the fixed intercepts β, which represented our average genus-level
469   climatic centers and thermal limits. We fitted the models under a Bayesian framework using the "brms"
470   R package (Bürkner, 2017). We used Markov chain Monte Carlo sampling with four chains of 2000

iterations each (1000 warm-up per chain), resulting in 4000 iterations post-warm-up. To improve model convergence, we specified the following broad priors for β (3) − (6):

$$\beta_{BIO1} \sim \mathcal{N}(10, 5^2) \tag{3}$$

$$\beta_{BIO12} \sim \mathcal{N}(1000, 500^2), lower\ bound = 0 \tag{4}$$

$$\beta_{BIO5} \sim \mathcal{N}(25, 5^2) \tag{5}$$

$$\beta_{BIO6} \sim \mathcal{N}(5, 5^2) \tag{6}$$

For all other parameters, we used the default weakly informative priors. The likelihood contribution of each occurrence point was weighted as described in the previous section. We set the maximum tree depth to 12 and adapted delta (the target average acceptance probability of the sampler) to 0.99 for all models. Final model convergence was assessed using the Gelman-Rubin criterion ($\hat{R}$). Most models were found to converge without any issues ($\hat{R} \approx 1.0$). For climatic centers, we excluded any models with $\hat{R} > 1.05$ or substantial divergent transitions (> 40) from plots. But for thermal limits, we instead labeled models that exceeded common $\hat{R}$ thresholds (*: $\hat{R} > 1.01$ or **: $\hat{R} > 1.05$; all models had < 40 divergent transitions).

References

Albrich, K., Rammer, W., & Seidl, R. (2020). Climate change causes critical transitions and irreversible alterations of mountain forests. *Global Change Biology*, *26*(7), 4013-4027.

Barak, R. S., Hipp, A. L., Cavender-Bares, J., Pearse, W. D., Hotchkiss, S. C., Lynch, E. A., ... & Larkin, D. J. (2016). Taking the long view: integrating recorded, archeological, paleoecological, and evolutionary data into ecological restoration. *International Journal of Plant Sciences, 177*(1), 90-102.

Baselga, A., & Orme, C. D. L. (2012). betapart: an R package for the study of beta diversity. *Methods in Ecology and Evolution*, *3*(5), 808-812.

BGCI. (2024). GlobalTreeSearch online database. Botanic Gardens Conservation International. Richmond, UK. Available at https://tools.bgci.org/global_tree_search.php. Accessed on (24/10/2024).

Bhagwat, S. A., & Willis, K. J. (2008). Species persistence in northerly glacial refugia of Europe: a matter of chance or biogeographical traits? *Journal of Biogeography*, *35*(3), 464-482.

Bowd, E. J., McBurney, L., & Lindenmayer, D. B. (2023). The characteristics of regeneration failure and their potential to shift wet temperate forests into alternate stable states. *Forest Ecology and Management, 529*, 120673.

Brown, M. J., Walker, B. E., Black, N., Govaerts, R. H., Ondo, I., Turner, R., & Nic Lughadha, E. (2023). rWCVP: a companion R package for the World Checklist of Vascular Plants. *New Phytologist*, *240*(4), 1355-1365.

Brus, R., Pötzelsberger, E., Lapin, K., Brundu, G., Orazio, C., Straigyte, L., & Hasenauer, H. (2019). Extent, distribution and origin of non-native forest tree species in Europe. *Scandinavian Journal of Forest Research, 34*(7), 533-544.

Bürkner, P. C. (2017). brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software*, *80*, 1-28.

Bush, M. B., Conrad, S., Restrepo, A., Thompson, D. M., Lofverstrom, M., & Conroy, J. L. (2022). Human-induced ecological cascades: extinction, restoration, and rewilding in the Galápagos highlands. *Proceedings of the National Academy of Sciences*, *119*(24), e2203752119.

Chakraborty, D., Ciceu, A., Ballian, D., Benito Garzón, M., Bolte, A., Bozic, G., ... & Schueler, S. (2024). Assisted tree migration can preserve the European forest carbon sink under climate change. *Nature Climate Change*, 14(8), 845-852.

Chevalier, M., Broennimann, O., & Guisan, A. (2024). Climate change may reveal currently unavailable parts of species' ecological niches. *Nature Ecology & Evolution*, *8*(7), 1298-1310.

Cohen, K. M., Finney, S. C., Gibbard, P. L., & Fan, J. X. (2013). The ICS international chronostratigraphic chart. *Episodes Journal of International Geoscience*, *36*(3), 199-204.

Crisp, M. D., & Cook, L. G. (2012). Phylogenetic niche conservatism: what are the underlying evolutionary and ecological causes? *New Phytologist*, *196*(3), 681-694.

Dyderski, M. K., Paź, S., Frelich, L. E., & Jagodziński, A. M. (2018). How much does climate change threaten European forest tree species distributions? *Global Change Biology*, *24*(3), 1150-1163.

Eiserhardt, W. L., Borchsenius, F., Plum, C. M., Ordonez, A., & Svenning, J. C. (2015). Climate-driven extinctions shape the phylogenetic structure of temperate tree floras. *Ecology Letters*, *18*(3), 263-272.

Forzieri, G., Girardello, M., Ceccherini, G., Spinoni, J., Feyen, L., Hartmann, H., ... & Cescatti, A. (2021). Emergent vulnerability to climate-driven disturbances in European forests. *Nature Communications*, *12*(1), 1081.

Gass, L., & Hülsmann, L. (2025). Mapping the next forest generation–the potential of national forest inventory data for identifying regeneration gaps. Preprint at https://doi.org/10.32942/X2GS8X.

GBIF: The Global Biodiversity Information Facility (2025) *What is GBIF?*. Available from https://www.gbif.org/what-is-gbif.

Gebrechorkos, S. H., Sheffield, J., Vicente-Serrano, S. M., Funk, C., Miralles, D. G., Peng, J., ... & Dadson, S. J. (2025). Warming accelerates global drought severity. *Nature*, 1-8.

Goodenough, A. E., & Webb, J. C. (2022). Learning from the past: opportunities for advancing ecological research and practice using palaeoecological data. *Oecologia*, *199*(2), 275-287.

Grace, M., Akçakaya, H. R., Bennett, E., Hilton-Taylor, C., Long, B., Milner-Gulland, E. J., ... & Hoffmann, M. (2019). Using historical and palaeoecological data to inform ambitious species recovery targets. *Philosophical Transactions of the Royal Society B*, *374*(1788), 20190297.

Gray, A. (1878). Forest geography and archaeology. *American Journal of Science, 3*(93), 183-196.

Hardy, O. J., Couteron, P., Munoz, F., Ramesh, B. R., & Pélissier, R. (2012). Phylogenetic turnover in tropical tree communities: impact of environmental filtering, biogeography and mesoclimatic niche conservatism. *Global Ecology and Biogeography*, *21*(10), 1007-1016.

Hawkins, B. A., Rueda, M., Rangel, T. F., Field, R., & Diniz-Filho, J. A. F. (2014). Community phylogenetics at the biogeographical scale: cold tolerance, niche conservatism and the structure of N orth A merican forests. *Journal of Biogeography*, *41*(1), 23-38.

Hijmans, R. J., Bivand, R., Forner, K., Ooms, J., Pebesma, E., & Sumner, M. D. (2022). Package 'terra'. *Maintainer: Vienna, Austria*, *384*.

Hlásny, T., König, L., Krokene, P., Lindner, M., Montagné-Huck, C., Müller, J., ... & Seidl, R. (2021). Bark beetle outbreaks in Europe: state of knowledge and ways forward for management. *Current Forestry Reports*, *7*, 138-165.

Huntley, B. (1993). Species-richness in north-temperate zone forests. *Journal of Biogeography*, 20(2), 163-180.

Jin, Y. & Qian, H. (2022) V.PhyloMaker2: An updated and enlarged R package that can generate very large phylogenies for vascular plants. *Plant Diversity, 44*, 335-339.

Jin, Y., & Qian, H. (2023). U. PhyloMaker: An R package that can generate large phylogenetic trees for plants and animals. *Plant Diversity, 45*(3), 347-352.

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., ... & Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, *4*(1), 1-20.

Karger D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E, Linder, H.P., Kessler, M. (2018). Data from: Climatologies at high resolution for the earth's land surface areas. *EnviDat*.

Kreyling, J., Bittner, T., Jaeschke, A., Jentsch, A., Steinbauer, M., Thiel, D., Beierkuhnlein, C. (2011). Assisted colonization: a question of focal units and recipient localities. *Restoration Ecology*, 19(4), 433-440.

Lang, G. (1994). *Quartäre Vegetationsgeschichte Europas-Methoden und Ergebnisse*. Gustav Fischer Verlag.

Latham, R. E., & Ricklefs, R. E. (1993). Continental comparisons of temperate-zone tree species diversity. *Species diversity in ecological communities: historical and geographical perspectives*, 294-314.

Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J., ... & Marchetti, M. (2010). Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *Forest Ecology and Management*, *259*(4), 698-709.

Mai, D. H. (1995). *Tertiäre Vegetationsgeschichte Europas*. Methoden und Ergebnisse.

Mathes, G. H., van Dijk, J., Kiessling, W., & Steinbauer, M. J. (2021). Extinction risk controlled by interaction of long-term and short-term climate change. *Nature Ecology & Evolution*, *5*(3), 304-310.

571 Mestre-Tomás, J. (2025). GeoThinneR: An R Package for Efficient Spatial Thinning of Species Occurrences
572 and Point Data. Preprint at https://doi.org/10.48550/arXiv.2505.07867.

573 Mosbrugger, V., Utescher, T., & Dilcher, D. L. (2005). Cenozoic continental climatic evolution of Central
574 Europe. Proceedings of the National Academy of Sciences, 102(42), 14964-14969.

575 Paradis, E., Blomberg, S., Bolker, B., Brown, J., Claude, J., Cuong, H. S., ... & Didier, G. (2019). Package
576 'ape'. *Analyses of Phylogenetics and Evolution, version*, *2*(4), 47.

577 Pearce, E. A., Mazier, F., Fyfe, R., Davison, C. W., Normand, S., Serge, M. A., ... & Svenning, J. C. (2024).
578 Higher abundance of disturbance-favoured trees and shrubs in European temperate woodlands prior to
579 the late-Quaternary extinction of megafauna. *Journal of Ecology, 112*(12), 2813-2827.

580 Pinsky, M. L., Hillebrand, H., Chase, J. M., Antão, L. H., Hirt, M. R., Brose, U., ... & Blowes, S. A. (2025).
581 Warming and cooling catalyse widespread temporal turnover in biodiversity. *Nature, 638(*8052), 995-999.

582 Postigo-Mijarra, J. M., Gómez Manzaneque, F., & Morla, C. (2008). Survival and long-term maintenance
583 of tertiary trees in the Iberian Peninsula during the Pleistocene: first record of Aesculus
584 L.(Hippocastanaceae) in Spain. *Vegetation History and Archaeobotany*, *17*(4), 351-364.

585 Pötzelsberger, E., Spiecker, H., Neophytou, C., Mohren, F., Gazda, A., & Hasenauer, H. (2020). Growing non-
586 native trees in European forests brings benefits and opportunities but also has its risks and limits. *Current*
587 *Forestry Reports*, *6*, 339-353.

588 Prinzing, A., Durka, W., Klotz, S., & Brandl, R. (2001). The niche of higher plants: evidence for phylogenetic
589 conservatism. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *268*(1483), 2383-
590 2389.

591 R Core Team. (2024). R: A language and environment for statistical computing. R Foundation for Statistical
592 Computing. https://www.R-project.org/

593 Reid, E. M. (1935). British floras antecedent to the Great Ice Age. *Proceedings of the Royal Society of*
594 *London. Series B-Biological Sciences*, *118*, 197-241.

595 Ricklefs, R. E., & He, F. (2016). Region effects influence local tree species diversity. *Proceedings of the*
596 *National Academy of Sciences*, *113*(3), 674-679.

597 Roy, H. E., Pauchard, A., Stoett, P. J., Renard Truong, T., Meyerson, L. A., Bacher, S., ... & Ziller, S. R. (2024).
598 Curbing the major and growing threats from invasive alien species is urgent and achievable. *Nature*
599 *Ecology & Evolution*, *8*(7), 1216-1223.

600 Seidl, R., & Turner, M. G. (2022). Post-disturbance reorganization of forest ecosystems in a changing world.
601 *Proceedings of the National Academy of Sciences*, *119*(28), e2202190119.

602 Seidl, R., Potterf, M., Müller, J., Turner, M. G., & Rammer, W. (2024). Patterns of early post-disturbance
603 reorganization in Central European forests. *Proceedings of the Royal Society B, 291*(2031), 20240625.

Senf, C., Buras, A., Zang, C. S., Rammig, A., & Seidl, R. (2020). Excess forest mortality is consistently linked to drought across Europe. *Nature Communications*, *11*(1), 6200.

Smith, S.A., Brown, J.W., 2018. Constructing a broadly inclusive seed plant phylogeny. *Am. J. Bot. 105*, 302-314.

Smith, A. B., Godsoe, W., Rodríguez-Sánchez, F., Wang, H. H., & Warren, D. (2019). Niche estimation above and below the species level. *Trends in Ecology & Evolution*, *34*(3), 260-273.

Stolar, J., & Nielsen, S. E. (2015). Accounting for spatially biased sampling effort in presence-only species distribution modelling. *Diversity and Distributions*, *21*(5), 595-608.

Svenning, J. C. (2003). Deterministic Plio-Pleistocene extinctions in the European cool-temperate tree flora. *Ecology Letters*, *6*(7), 646-653

Svenning, J. C., Eiserhardt, W. L., Normand, S., Ordonez, A., & Sandel, B. (2015). The influence of paleoclimate on present-day patterns in biodiversity and ecosystems. Annual Review of Ecology, Evolution, and Systematics, 46(1), 551-572.

Thomas, F. M., Rzepecki, A., & Werner, W. (2022). Non-native Douglas fir (Pseudotsuga menziesii) in Central Europe: Ecology, performance and nature conservation. *Forest Ecology and Management, 506*, 119956.

Vetaas, O. R., Grytnes, J. A., Bhatta, K. P., & Hawkins, B. A. (2018). An intercontinental comparison of niche conservatism along a temperature gradient. *Journal of Biogeography, 45*(5), 1104-1113.

Washaya, P., Modlinger, R., Tyšer, D., & Hlásny, T. (2024). Patterns and impacts of an unprecedented outbreak of bark beetles in Central Europe: A glimpse into the future? *Forest Ecosystems*, *11*, 100243.

Wessely, J., Essl, F., Fiedler, K., Gattringer, A., Hülber, B., Ignateva, O., ... & Seidl, R. (2024). A climate-induced tree species bottleneck for forest management in Europe. *Nature Ecology & Evolution*, *8*(6), 1109-1117.

Westerhold, T., Marwan, N., Drury, A. J., Liebrand, D., Agnini, C., Anagnostou, E., ... & Zachos, J. C. (2020). An astronomically dated record of Earth's climate and its predictability over the last 66 million years. S*cience*, *369*(6509), 1383-1387.

Wohlgemuth, T., Gossner, M. M., Campagnaro, T., Marchante, H., van Loo, M., Vacchiano, G., ... & Silva, J. S. (2022). Impact of non-native tree species in Europe on soil properties and biodiversity: a review. *NeoBiota*, *78*, 45-69.

Yang, H., Ciais, P., Frappart, F., Li, X., Brandt, M., Fensholt, R., ... & Wigneron, J. P. (2023). Global increase in biomass carbon stock dominated by growth of northern young forests over past decade. *Nature Geoscience, 16*(10), 886-892.

Zanne, A.E., Tank, D.C., Cornwell, W.K., et al., 2014. Three keys to the radiation of angiosperms into freezing environments. *Nature*, *506*, 89-92.

638 Zhang, J. & Qian, H. (2023). U.Taxonstand: An R package for standardizing scientific names of plants and
639 animals. *Plant Diversity*, *45*(1): 1-5.

640 Zhang, J., Qian, H., Wang, X. (2025). An online version and some updates of R package U.Taxonstand for
641 standardizing scientific names in plant and animal species. *Plant Diversity, 47*(1): 166-168.

642 Zizka, A., Antonelli, A., & Silvestro, D. (2021). Sampbias, a method for quantifying geographic sampling
643 biases in species distribution data. *Ecography*, *44*(1), 25-32.

644

Acknowledgements

648

Data availability

650 All data necessary to reproduce our results are freely available either on Zenodo or can be downloaded
651 online. See "data_references.docx" for further information.
652 https://zenodo.org/records/17079667

653

Code availability

655 All code used in this study is available on GitHub and Zenodo:
656 https://github.com/vfwilkens/PaleoTrees-WCE/
657 https://zenodo.org/records/17079667

658

Author contributions

660 V.W., A.W., and S.T. conceptualized the study under supervision from C.B.; V.W., A.W., L.H., and S.T.
661 developed all methods and carried out the formal analysis. V.W. wrote the first draft of the paper and C.B.,
662 A.W., S.T., L.H., N.N., and O.V. contributed substantially to the revisions.
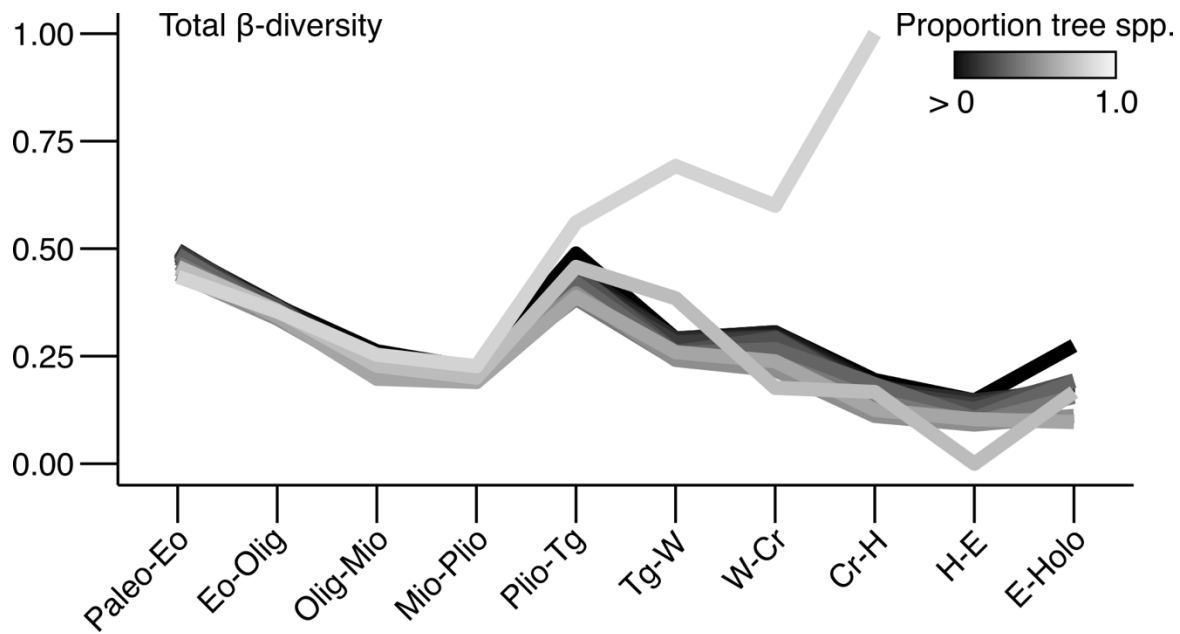
663

Supplementary Information

665
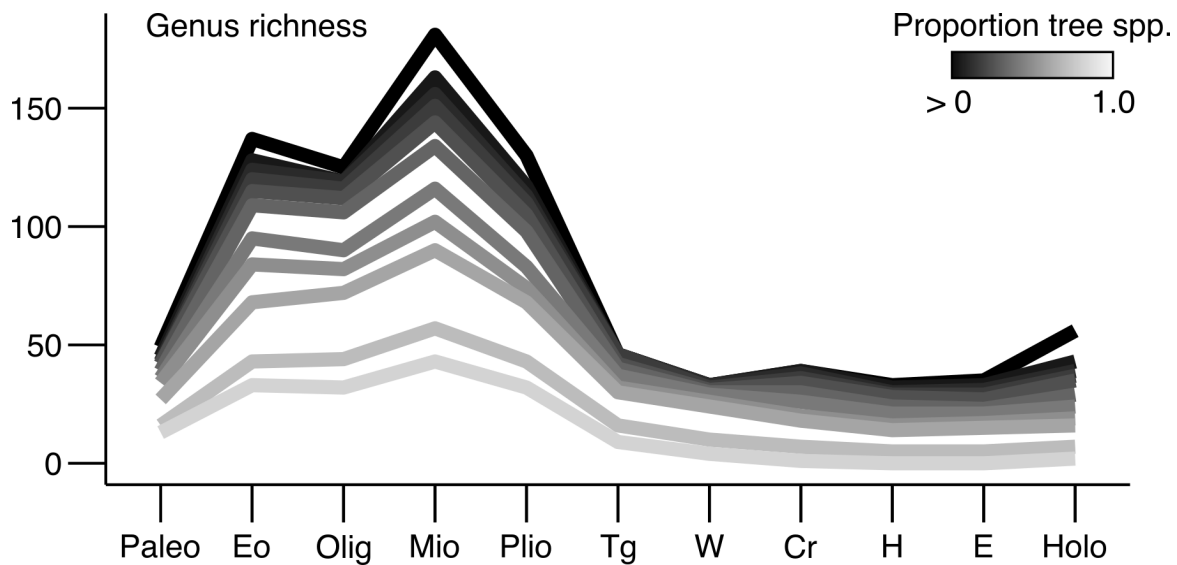
Supplementary Fig. 1: Changes in tree genus richness during the Cenozoic depending on how a tree genus is defined. We calculated the proportion of tree species (according to BGCI GlobalTreeSearch database) within each genus (from all accepted species in WCVP) and performed a sensitivity analysis around this value. Only genera containing at least 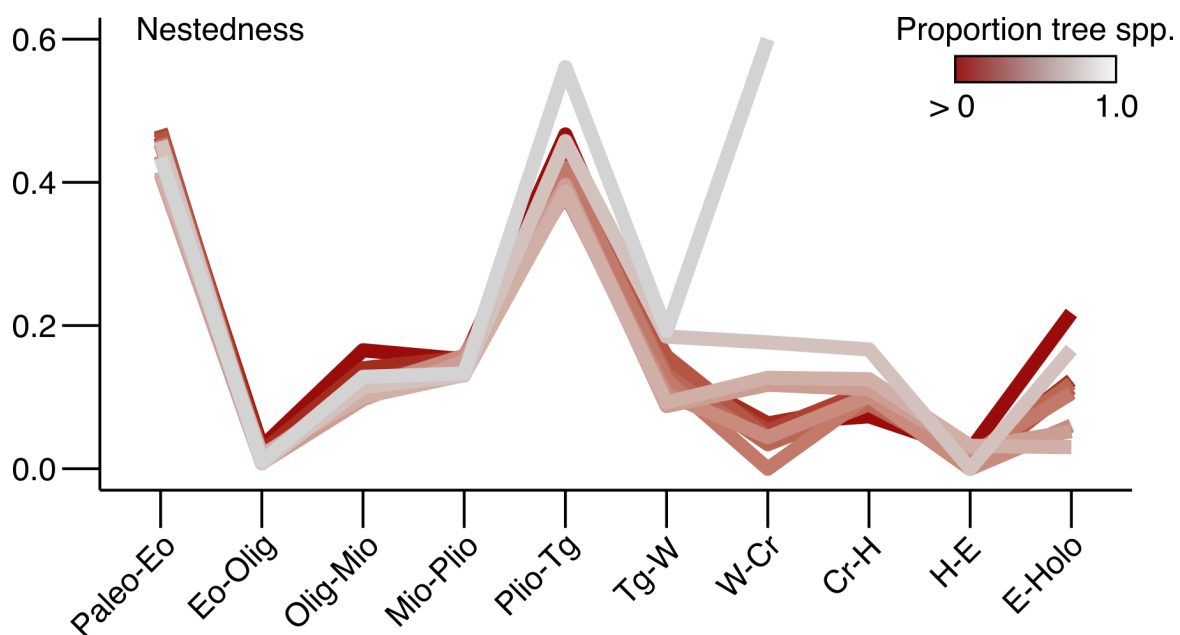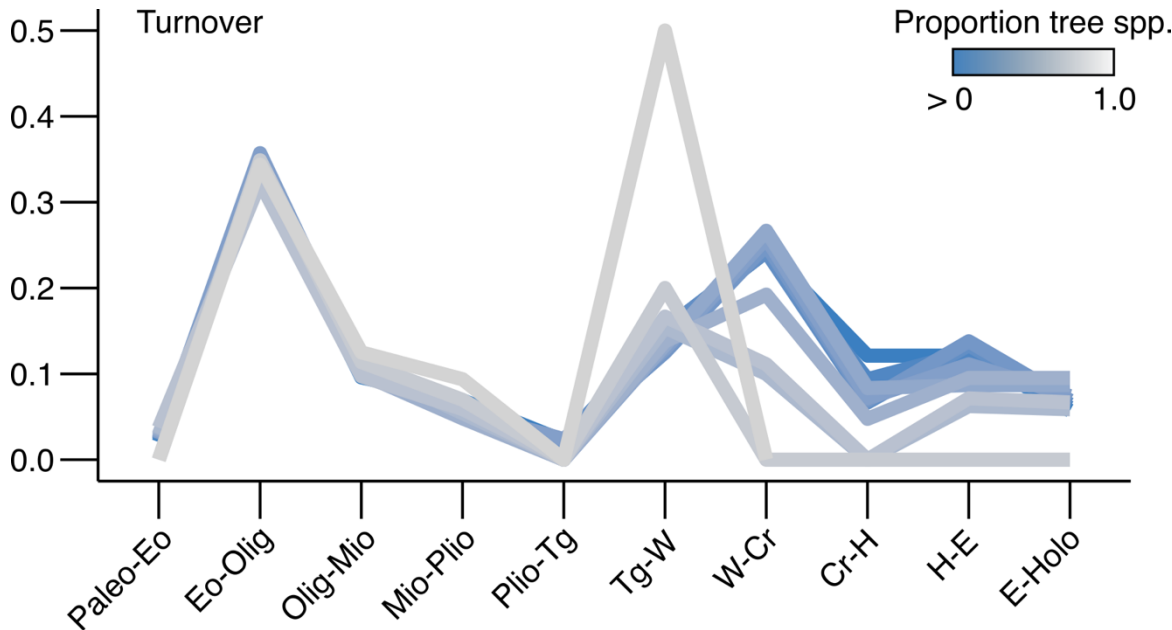a single tree-forming species were included. Time bin abbreviations are as follows: Paleo – Paleocene, Eo – Eocene, Oligo – Oligocene, Mio – Miocene, Plio – Pliocene, Tg – Tiglian, W – Waalian, Cr – Cromer, H – Holstein interglacial, and E – Eem interglacial, and Holo – Holocene.
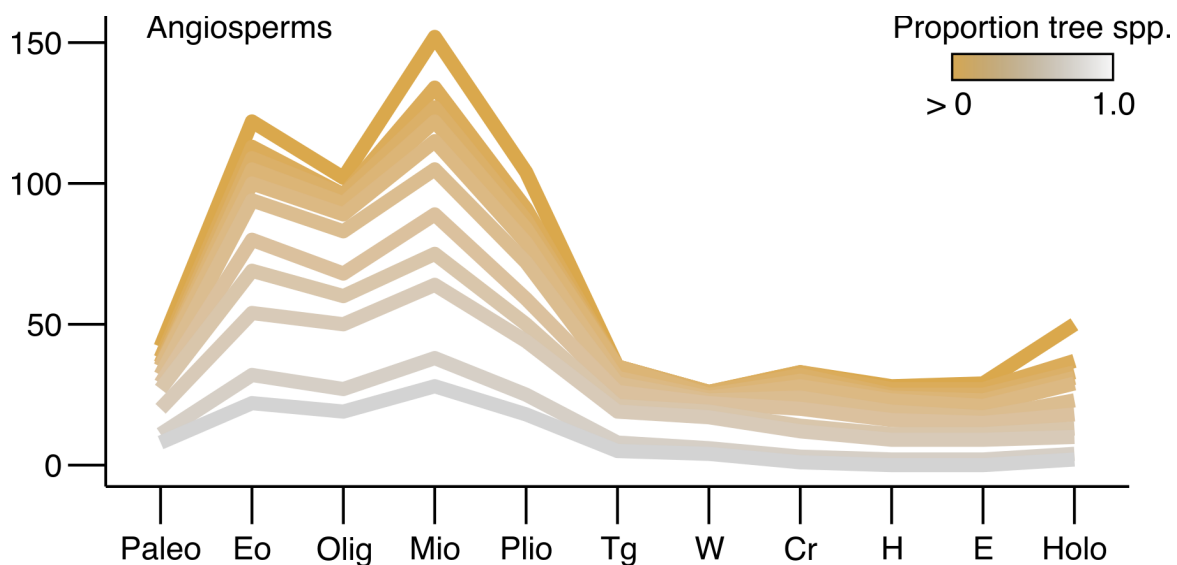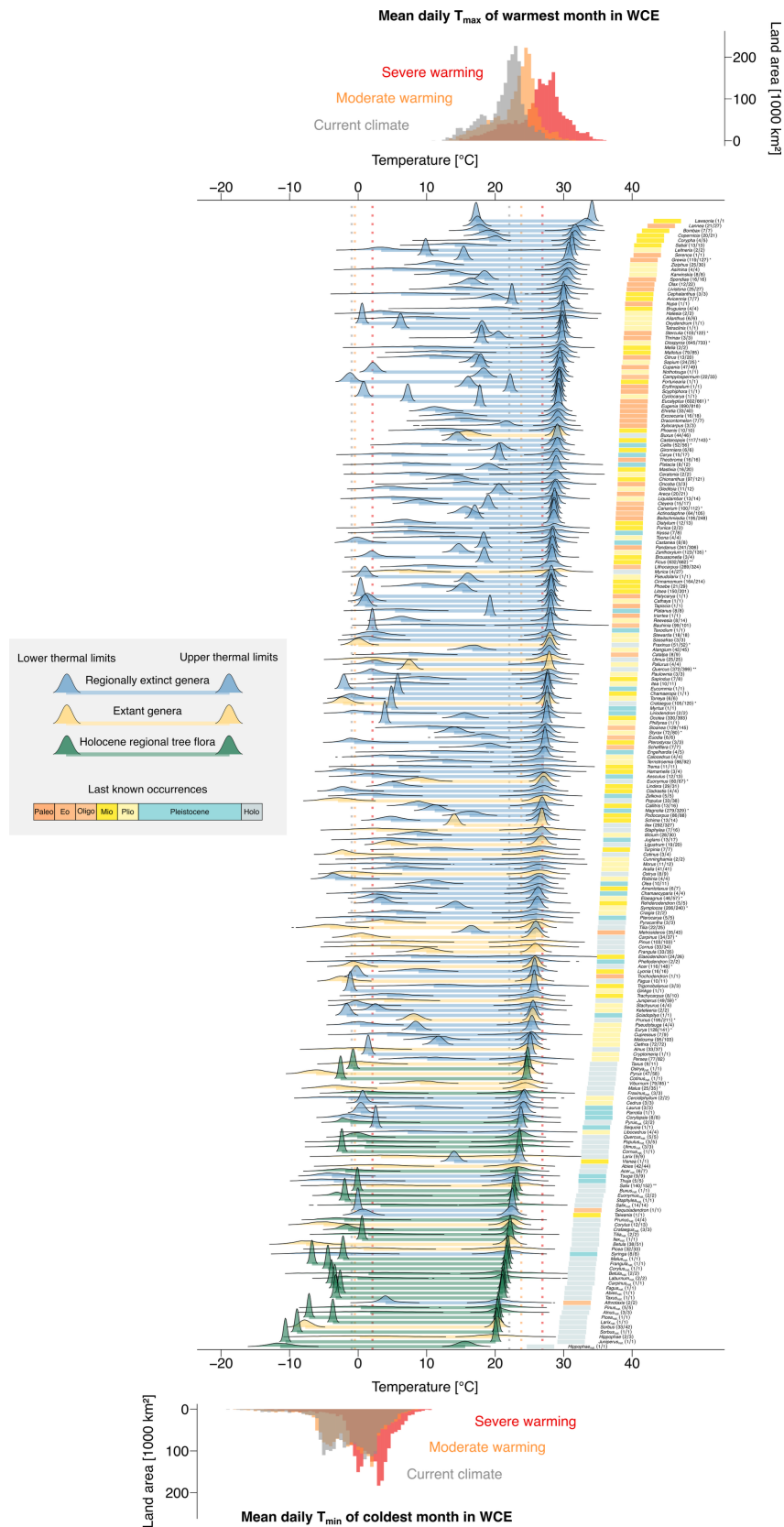

Supplementary Fig. 2: Changes in tree genus richness of angiosperms during the Cenozoic depending on how a tree genus is defined. We calculated the proportion of tree species (according to BGCI GlobalTreeSearch database) within each genus (from all accepted species in WCVP) and performed a sensitivity analysis around this value. Only genera containing at least a single tree-forming species were
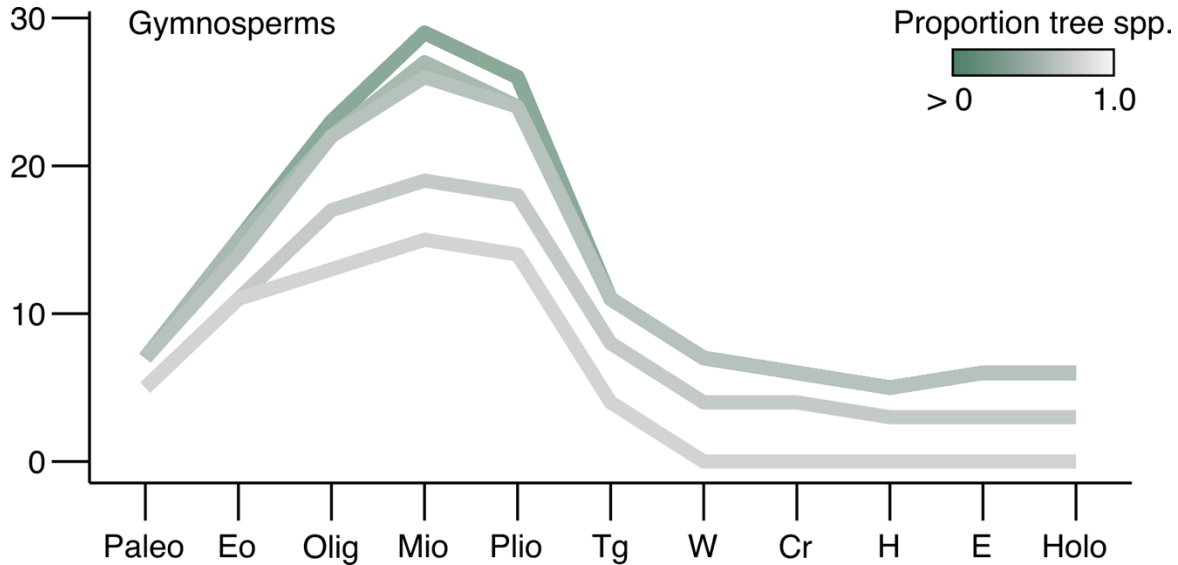
Supplementary Fig. 3: Changes in tree genus richness of gymnosperms during the Cenozoic depending on how a tree genus is defined. We calculated the proportion of tree species (according to BGCI GlobalTreeSearch databse) within each genus (from all accepted species in WCVP) and performed a sensitivity analysis around this value. Only genera containing at least a single tree-forming species were included. Time bin abbreviations are as follows: Paleo – Paleocene, Eo – Eocene, Oligo – Oligocene, Mio – Miocene, Plio – Pliocene, Tg – Tiglian, W – Waalian, Cr – Cromer, H – Holstein interglacial, and E – Eem interglacial, and Holo – Holocene.

693

Supplementary Fig. 4: Changes in total beta diversity between subsequent time bins during the Cenozoic, depending on how a tree genus is defined. We calculated the proportion of tree species (according to BGCI GlobalTreeSearch database) within each genus (from all accepted species in WCVP) and performed a sensitivity analysis around this value. Only genera containing at least a single tree-forming species were included. Time bin abbreviations are as follows: Paleo – Paleocene, Eo – Eocene, Oligo – Oligocene, Mio – Miocene, Plio – Pliocene, Tg – Tiglian, W – Waalian, Cr – Cromer, H – Holstein interglacial, and E – Eem interglacial, and Holo – Holocene.

701

702

Mean daily T$_{max}$ of warmest month in WCE

Land area [1000 km²]

Severe warming
Moderate warming
Current climate

Temperature [°C]

Lower thermal limits   Upper thermal limits

Regionally extinct genera

Extant genera

Holocene regional tree flora

Last known occurrences

| Paleo | Eo | Oligo | Mio | Plio | Pleistocene | Holo |

Temperature [°C]

Land area [1000 km²]

Severe warming
Moderate warming
Current climate

Mean daily T$_{min}$ of coldest month in WCE

724

Supplementary Fig. 7: Upper and lower thermal limits of Cenozoic tree genera from Western and Central Europe. Posteriors of upper and lower thermal limits for 200 tree genera were estimated, comparing regionally extinct genera (blue) and extant genera (yellow). Posteriors of genus-level thermal limits of the Holocene regional tree flora (green) were also estimated, comprising the same genera as in extant genera but modelled using only native species. Models were arranged by increasing upper thermal limit (bottom to top). Color stripes correspond to the last known occurrence of each genus in the fossil record of Western and Central Europe. All genera have been labelled on the right-hand side of the plot, including the number of species from all accepted species in each genus used to fit the models. The Gelman-Ruben criterion ($\hat{R}$) was used to assess Bayesian model convergence, with values closer to 1.0 indicating successful convergence. Genera with $\hat{R} > 1.01$ (*) or $\hat{R} > 1.05$ (**) were labelled as having potentially unreliable estimates. The distribution of heat extremes (mean daily maximum temperature of the warmest month) and cold extremes (mean daily minimum temperature of the coldest month) by land area under current and future climate scenarios in Western and Central Europe are overlaid. Current climate: 1981 – 2010. Moderate warming: SSP1-2.6 (+ 1.3 – 2.4 °C by 2100). Severe warming: SSP5-8.5 (+ 3.3 – 5.7 °C by 2100).

740

741

742

743

744