



1 European pollen-based REVEALS land-cover reconstructions for the 2 Holocene: methodology, mapping and potentials

3
4 Esther Githumbi^{1,2}, Ralph Fyfe³, Marie-Jose Gaillard², Anna-Kari Trondman^{2,4}, Florence Mazier⁵, Anne-
5 Birgitte Nielsen⁶, Anneli Poska^{1,7}, Shinya Sugita⁸, Martin Theuerkauf⁹, Jessie Woodbridge³, Julien
6 Azuara¹⁰, Angelica Feurdean^{11,12}, Roxana Grindean¹², Vincent Lebreton¹⁰, Laurent Marquer¹³, Nathalie
7 Nebout-Combourieu¹⁰, Migle Stancikaite¹⁴, Ioan Tanțău¹², Spassimir Tonkov¹⁵, Lyudmila
8 Shumilovskikh¹⁶, and LandClimII data contributors¹⁷⁺.

9
10 ¹Department of Physical Geography and Ecosystem Science, University of Lund, 22362 Lund, Sweden

11 ²Department of Biology and Environmental Science, Linnaeus University, 39182 Kalmar, Sweden

12 ³School of Geography, Earth and Environmental Sciences, University of Plymouth, PL4 8AA Plymouth, United Kingdom

13 ⁴Division of Education Affairs, Swedish University of Agricultural Science (SLU), 23456 Alnarp, Sweden

14 ⁵Environmental Geography Laboratory, GEODE UMR 5602 CNRS, Université de Toulouse Jean Jaurès, 31058 Toulouse,
15 France

16 ⁶Department of Geology, Lund University, 22100 Lund, Sweden

17 ⁷Department of Geology, Tallinn University of Technology, 19086 Tallinn, Estonia

18 ⁸Institute of Ecology, Tallinn University of Technology, 10120 Tallinn, Estonia

19 ⁹Institute of Botany and Landscape Ecology, EMAU Greifswald, 1748 Greiswald, Germany

20 ¹⁰Département Homme et Environnement, UMR 7194 Histoire Naturelle de l'Homme Préhistorique, 75013 Paris, France

21 ¹¹Senckenberg Biodiversity and Climate Research Centre (BiK-F), 60325 Frankfurt am Main, Germany

22 ¹²Department of Geology, Faculty of Biology and Geology, Babeş-Bolyai University, 400084 Cluj-Napoca, Romania

23 ¹³Department of Botany, University of Innsbruck, 6020 Innsbruck, Austria

24 ¹⁴Institute of Geology and Geography, Vilnius University, Vilnius, LT-03101 Vilnius, Lithuania

25 ¹⁵Department of Botany, Sofia University St. Kliment Ohridski, 1164 Sofia, Bulgaria

26 ¹⁶Department of Palynology and Climate Dynamics, Georg-August-University, 37073 Göttingen, Germany

27 ¹⁷⁺Team list

28 +A full list of authors appears at the end of the paper.

29

30 *Correspondence to:* Esther Githumbi (esther.githumbi@lnu.se)



31 **Abstract.** Quantitative reconstructions of past land-cover are necessary for research into the processes involved in climate-
32 human-land interactions. We present the first temporally continuous pollen-based land-cover reconstruction for Europe over
33 the Holocene (last 11,700 cal yr BP). We describe how vegetation cover has been quantified from pollen records at a 1°x1°
34 spatial scale using the ‘Regional Estimates of VEgetation Abundance from Large Sites’ (REVEALS) model. REVEALS has
35 been applied to 1128 pollen records across Europe and part of the Eastern Mediterranean-Black Sea-Caspian-Corridor (30°-
36 75°N, 25°W-50°E) to reconstruct the cover of 31 plant taxa assigned to 12 plant functional types (PFTs) and three land-cover
37 types (LCTs). A new synthesis of relative pollen productivities (RPPs) available for European plant taxa was performed for
38 this reconstruction. It includes > 1 RPP values for 39 taxa, and single values for 15 taxa (total of 54 taxa). As an illustration,
39 we present maps of the results for five taxa (*Calluna vulgaris*, *Cerealia-t*, *Picea abies*, *Quercus* deciduous and *Quercus*
40 evergreen) and three LCTs (open land (OL), evergreen trees (ET) and summer-green trees (ST)) for 8 selected time windows.
41 We discuss the reliability of the REVEALS reconstructions and issues related to the interpretation of the results in terms of
42 landscape openness and human-induced vegetation change. We then describe the current use of this reconstruction and its
43 future potential utility and development. The REVEALS data presented here can be downloaded from
44 <https://doi.pangaea.de/10.1594/PANGAEA.937075?format=html#download>.



45 **1 Introduction**

46 The reconstruction of past land cover at global, continental and sub-continental scales is necessary for the evaluation of climate
47 models, land-use scenarios and the study of past climate – land cover interactions. Vegetation plays a significant role within
48 the climate system through biogeochemical and biogeophysical feedbacks and forcings (Foley, 2005; Gaillard et al., 2010,
49 2015, 2018; Strandberg et al., 2014). Land use has modified the land cover of Europe over Holocene timescales at local,
50 regional and continental scales (e.g. Roberts et al., 2019; Trondman et al., 2015; Woodbridge et al., 2014). Concerted efforts
51 have been made to model land-use and land-cover change (LULCC) over Holocene time scales (e.g. HYDE 3.2 (Klein
52 Goldewijk et al., 2017) and KK10 (Kaplan et al., 2011)). KK10 has been used to assess the impact of the scale of deforestation
53 between 6000 and 200 cal yr BP in Europe on the regional climate in the climate modelling study of Strandberg et al (2014).
54 The KK10-inferred land-cover change resulted in cooling or warming of the regional climate by 1° to 2° depending on the
55 season (winter or summer) and/or geographical location. Major changes in the forest cover of Europe over the Holocene may
56 therefore have had a significant impact on past regional climate, particularly those driven by deforestation since the start of
57 agriculture. Estimating past land-cover change can enable quantification of the scale at which human impact on terrestrial
58 ecosystems perturbed the climate system. This in turn allows us to consider when environmental changes moved beyond the
59 envelope of natural variability (Ruddiman, 2003; Ruddiman et al., 2016). We focus here on the role of LULCC in the climate
60 system; anthropogenic land-cover change can have broader consequences on other processes and changes, such as erosion and
61 fluvial systems (Downs and Piégay, 2019), biodiversity loss (Barnosky et al., 2012), nutrient cycling (Guiry et al., 2018;
62 McLauchlan et al., 2013), habitat exploitation by megafauna (Hofman-Kamińska et al., 2019) and wider ecosystem functioning
63 (Ellis, 2015; Stephens et al., 2019).

64 The Earth System Modelling (ESM) community use LULCC model scenarios, along with dynamic vegetation models, to
65 understand interactions between different components of the earth system in the past (e.g. Gilgen et al., 2019; Smith et al.,
66 2016; He et al., 2014; Hibbard et al., 2010). Disagreement between LULCC scenarios suggests that their evaluation is needed
67 using independent, empirical datasets (Gaillard et al., 2010). Pollen-based reconstruction of past land cover represents probably
68 the best empirical data for this purpose, as a direct proxy for vegetation, and for the ubiquity of data across the continent of
69 Europe (e.g. Gaillard et al., 2010, 2018). Moreover, the ‘Regional Estimates of VEgetation Abundance from Large Sites’
70 (REVEALS) model developed by Sugita (2007a) makes it possible to quantify plant cover from pollen records at a regional
71 spatial scale of ca. 100 km x 100 km (e.g. Hellman et al., 2008a). The first pollen-based REVEALS reconstruction of plant
72 cover over the Holocene covering a large part of Europe (Trondman et al., 2015) was used for the assessment of LULCC
73 scenarios (Kaplan et al., 2017), and helped to evaluate climate model simulations using LULCC scenarios (Strandberg et al.,
74 2014). A comparison between REVEALS-based open land cover from pollen records and Holocene deforestation as simulated
75 by HYDE 3.1 and KK10 showed that the REVEALS reconstructions were more similar to the KK10 scenarios than the HYDE
76 3.1 ones (Kaplan et al., 2017). Therefore, estimates of past plant cover from pollen are essential to both test and constrain
77 LULCC models, and also provide alternative inputs to Earth System Models (ESMs), Regional Climate Models (RCMs) and



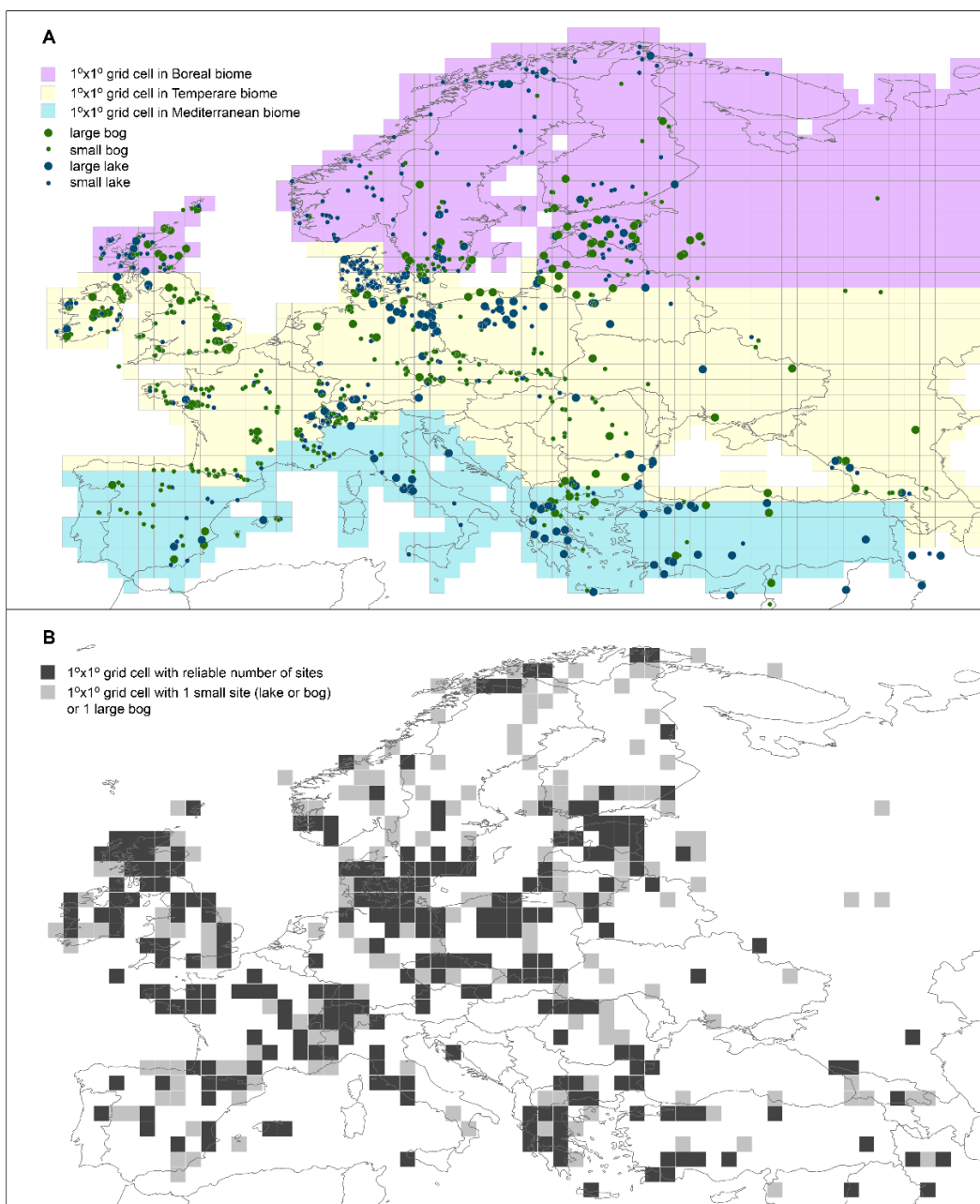
78 ecosystem models (Gaillard et al., 2018; Harrison et al., 2020). This allows improved assessments of biogeophysical and
79 biogeochemical forcings on climate due to LULCC over the Holocene (Gaillard et al., 2010; Harrison et al., 2020; Ruddiman
80 et al., 2016; Strandberg et al., 2014).

81 Europe is of particular interest as one of the regions of the globe that has experienced major human-induced land-cover
82 transformations. Europe has large N-S and W-E gradients in modern and historical climate and land use (Marquer et al., 2014,
83 2017). Early agriculture dates from the start of the Holocene in the SE Mediterranean region (Roberts et al., 2019; Shennan,
84 2018), and human impact on vegetation across most of Europe is characterized by early land-cover changes through agriculture
85 (e.g. Marquer et al., 2014; Trondman et al., 2015). There is therefore a clear need to extend quantitative vegetation
86 reconstruction to the whole of Europe, including for the first time the Mediterranean region and additional areas of Eastern
87 Europe, and to cover the whole Holocene to capture transient vegetation change at sub-millennial time scales. Europe has a
88 deep history of pollen data production (Edwards et al., 2017) and an open-access repository for pollen records (the European
89 Pollen Database (EPD): (Fyfe et al., 2009)), resulting in abundant pollen records that can be used for data-driven
90 reconstructions of past vegetation patterns at continental scales. Vegetation reconstructions for Europe based on pollen data
91 have used community-level approaches (Huntley, 1990), biomization methods (Davis et al., 2015; Prentice et al., 1996),
92 modern analogue technique (MAT; Zanon et al., 2018), and pseudobiomization (Fyfe et al., 2015). These approaches capture
93 the major trends in vegetation patterns over the course of the Holocene (Roberts et al., 2018) and biomization methods have
94 proved useful for evaluation of climate model results (e.g. Prentice and Webb III, 1998). The results of these forms of pollen
95 data manipulation either classify pollen data into discrete classes (e.g. biomization, pseudobiomization) or are semi-
96 quantitative, providing at best rough estimates of the relationship between forest and open-land cover (e.g. MAT). They cannot
97 achieve reconstructions of the cover of e.g. evergreen versus summer-green trees, or the cover of individual tree and herb taxa.
98 They are thus of limited use when differentiation of plant functional types (PFTs) is essential (e.g. Strandberg et al., 2014).
99 Moreover, forest cover over the Holocene inferred from pollen records using these approaches differs from forest cover
100 obtained with REVEALS (Roberts et al., 2018); these differences indicate that biases due to the non-linearity of the pollen-
101 vegetation relationship are not fully corrected by MAT or (pseudo -) biomization approaches.

102 In this paper we present the results of the second generation of REVEALS-based reconstruction of plant cover over the
103 Holocene in Europe, the first generation being the reconstruction published by Trondman et al. (2015). This second generation
104 reconstruction is, to date, the most spatially and temporally complete estimate of plant cover for Europe across the Holocene.
105 As with the Trondman et al. (2015) reconstruction, this new dataset is specifically designed to be used in climate modelling.
106 It is performed at a spatial scale of $1^\circ \times 1^\circ$ (ca. $100 \text{ km} \times 100 \text{ km}$) across $30^\circ\text{-}75^\circ\text{N}$, $25^\circ\text{W-}50^\circ\text{E}$ (Europe and part of the Eastern
107 Mediterranean-Black Sea-Caspian-Corridor) (Fig. 1). The number of pollen records used (1128), the area covered and time
108 length (entire Holocene) are a significant advance on the results presented in Trondman et al. (2015), which used 636 pollen
109 records covering NW Europe (including Poland and the Czech Republic and excluding western Russia and the Mediterranean
110 area), and produced estimates for five time windows (in cal yr BP, hereafter abbreviated BP): 6200-5700, 4200-3700, 700-



111 350, 350-100 BP and 100 BP to present. Marquer et al. (2014, 2017) produced continuous REVEALS reconstructions over the
112 entire Holocene, however only for transects of individual sites (19 pollen records) and groups of grid cells around them.



113
114 **Figure 1: Study region, A.) Site coverage. B.) Grid cell reliability dependent on number and type of pollen records.**

115 The 1° × 1° scale corresponds approximatively to the spatial extent of pollen-based REVEALS reconstructions as evaluated
116 by empirical studies in Europe (Hellman et al., 2008b; Soepboer et al., 2010): the REVEALS estimated abundances of plant



117 taxa (in percentage cover) correspond most closely to the plant abundances in an area of ca. 100 km x 100 km or larger (see
118 Li et al., 2020 for further discussion of the spatial scale of REVEALS reconstructions). This spatial scale is appropriate for
119 climate models that typically use spatial scales of 0.25° to 1° (Gaillard et al., 2010). REVEALS is a mechanistic model that
120 transforms pollen count data to produce quantitative reconstructions of regional vegetation (Sugita, 2007a). The model was
121 first tested and validated in southern Sweden (Hellman et al., 2008a, 2008b) and later in other parts of Europe and the world
122 (Soepboer et al., 2010; Sugita et al., 2010).

123 2 Methods

124 2.1 REVEALS model and parameters

125 Following the equation below, the REVEALS model calculates estimates of regional vegetation abundance in proportions or
126 percentage cover using fossil pollen counts from large lakes (Sugita, 2007a).

$$127 \hat{V}_i = \frac{n_{i,k} / \hat{\alpha}_i \int_R^{Z_{\max}} g_i(z) dz}{\sum_{j=1}^m \left(\frac{n_{j,k}}{\hat{\alpha}_j \int_R^{Z_{\max}} g_j(z) dz} \right)} = \frac{n_{i,k} / \hat{\alpha}_i K_i}{\sum_{j=1}^m (n_{j,k} / \hat{\alpha}_j K_j)}$$

- 128 • \hat{V}_i is the estimate of the regional vegetation abundance for taxon i (proportion or percentage).
- 129 • $n_{i,k}$ is the pollen count of taxon i at site k .
- 130 • $\hat{\alpha}_i$ is the estimate of pollen productivity (relative pollen productivity, RPP) for taxon i .
- 131 • z is the distance between the centre of the sedimentary basin and the pollen source.
- 132 • $g_i(z)$ is the pollen dispersal/deposition function for taxon i expressed as a function of distance z . Fall speed of pollen
133 (FSP), wind speed and atmospheric conditions are parameters needed to calculate this function.
- 134 • R is the radius of the sedimentary basin.
- 135 • Z_{\max} is the maximum distance within which most pollen originates (i.e. the maximum spatial extent of the regional
136 vegetation).
- 137 • m is the total number of taxa included,
- 138 • $K_i = \int_R^{Z_{\max}} g_i(z) dz$ is the “pollen dispersal-deposition coefficient” of taxon i from the border of the study site
139 (distance from the pollen sample corresponding to the radius R of the lake) to Z_{\max} .

140



141 The REVEALS model was developed for pollen records from large lakes and the assumptions of the model are listed in Sugita
142 (2007a). The model was tested and validated in Europe (Hellman et al., 2008a; Mazier et al., 2012; Soepboer et al., 2010) and
143 northern America (Sugita et al., 2010). Sugita (2007a) demonstrated using simulations that, in theory, the model can also be
144 applied on pollen records from multiple small lakes; the REVEALS estimates will however generally have larger standard
145 errors than those based on pollen data from large lakes. Moreover, although the application of the model on pollen data from
146 bogs violates the model assumption that no plants grow on the basin, REVEALS can be applied using models of pollen
147 dispersal and deposition for lakes or bogs. The Prentice’s model (Prentice, 1985; 1988) describes deposition of pollen at a
148 single point in a deposition basin and is suitable for pollen records from bogs. Sugita (1993) developed the “Prentice-Sugita
149 model” that describes pollen deposition in a lake, i.e. on its entire surface with a subsequent mixing in the water body before
150 deposition at the lake bottom. The original versions of both models use the Sutton model of pollen dispersal, i.e. a Gaussian
151 plume model from a ground-level source under neutral atmospheric conditions (Sutton, 1953). A Lagrangian stochastic model
152 of dispersion has also been introduced as an alternative for the description of pollen dispersal in models of the pollen-vegetation
153 relationship in general, and in the REVEALS model in particular (Theuerkauf et al., 2013; 2016). It is difficult, in both theory
154 and practice, to eliminate the effects of pollen coming from plants growing on sedimentary basins (e.g. Poaceae and
155 Cyperaceae) on regional vegetation reconstruction. Previous studies have assessed the impacts of the violation of this
156 assumption on the REVEALS outcomes (Mazier et al., 2012; Sugita et al., 2010; Trondman et al., 2016, 2015). An empirical
157 study in southern Sweden (Trondman et al., 2016) indicated that REVEALS estimates based on pollen records from multiple
158 small sites (lakes and/or bogs) are similar to the REVEALS estimates based on pollen records from large lakes in the same
159 region. The results also suggested that increasing the number of pollen records significantly decreased the standard error of
160 the REVEALS estimates, as expected based on simulations (Sugita, 2007a). It is therefore appropriate to use pollen records
161 from small bogs to increase the number of pollen records included in a REVEALS reconstruction, following the protocol of
162 the first generation REVEALS reconstruction for Europe (Mazier et al., 2012; Trondman et al., 2015).

163 The inputs needed to run the REVEALS model are: original pollen counts; relative pollen productivity estimates (RPPs) and
164 their standard deviation; fall speed of pollen (FSP); basin type (lake or bog); size of basin (radius); maximum extent of regional
165 vegetation; and wind speed (m/s) and atmospheric conditions. FSP can be calculated using measurements of the pollen grains
166 and the Stokes’ law (Gregory, 1973). RPPs of major plant taxa can be estimated using datasets of modern pollen assemblages
167 and related vegetation and the Extended R-Value model (Mazier et al., 2008). RPPs exist for a large number of European plant
168 taxa, and syntheses of FSPs and RPPs were published earlier by Broström in 2008 and Mazier in 2012 (Broström et al., 2008;
169 Mazier et al., 2012). The latter was used in the “first generation” REVEALS reconstruction (Trondman et al., 2015). A new
170 synthesis of European RPPs was performed for this “second generation” reconstruction. Preparation of data from individual
171 pollen records, and the values of model parameters used, are described below (sections 2.2 and 2.3).



172 2.2 Pollen records – data compilation and preparation

173 1128 pollen records from 29 European countries and the Eastern Mediterranean-Black Sea-Caspian-Corridor were obtained
174 from databases and individual data contributors. The contributing databases include: the European Pollen Database (Fyfe et
175 al., 2009; Giesecke et al., 2014); the Alpine Palynological database (ALPADABA; Institute of Plant Sciences, University of
176 Bern; now also archived in EPD); the Czech Quaternary palynological database (PALYCZ; Kuneš et al., 2009); PALEOPYR
177 (Lerigoleur et al., 2015); and datasets compiled within synthesis projects from the Mediterranean region (Fyfe et al., 2018;
178 Woodbridge et al., 2018) and the Eastern Mediterranean-Black Sea-Caspian-Corridor (EMBSeCBIO project; Marinova et al.,
179 2018) (see Fig. 1 for map, Data availability section for data location and team list for individual pollen data contributors). We
180 followed the protocols and criteria published in Mazier et al. (2012) and Trondman et al. (2015) for selection of pollen records
181 and application of the REVEALS model. Available pollen records were filtered based on criteria including basin type (to
182 exclude archaeological sites and marine records) and quality of chronological control (excluding sites with poor age-depth
183 models or fewer than three radiocarbon dates). This resulted in 1128 pollen records from lakes and bogs, both small and large.
184 The rationale behind the use of pollen records from small sites is based on the knowledge that REVEALS estimates based on
185 pollen records from multiple sites provide reasonable approximations of the regional cover of plant taxa (e.g. Trondman et al.,
186 2016; see details under section 2.1 on the REVEALS model).

187 The taxonomy and nomenclature of pollen morphological types from the 1128 pollen records were harmonised. The pollen
188 morphological types were then consistently assigned to one of 31 RPP taxa (Table 1; see section 2.3 for details on the RPP
189 dataset used in this study), following the protocol outlined in Trondman et al. (2015: SI-2). This process takes into account
190 plant morphology, biology, and ecology of the species that are included in each pollen morphological type (see Trondman et
191 al., 2015 for examples of harmonization between pollen-morphological types and RPP taxa). In this way, RPP-harmonized
192 pollen count data were produced for each of the 1128 pollen records. It should be noted that the EMBSeCBIO data does not
193 contain pollen counts from cultivars, i.e. pollen from cereals and cultivated trees were deleted from the pollen records
194 (Marinova et al., 2018). Therefore, the cover of agricultural land (represented by Cereals in this reconstruction) will always be
195 zero in the Eastern Mediterranean-Black Sea-Caspian-Corridor in grid cells including only pollen records from EMBSeCBIO,
196 although agriculture did occur in the region from early Neolithic.

197 For application of REVEALS, an age-depth model (in cal yr BP) is required for each pollen record. We used the author's
198 original model, the model available in the contributing database or, where necessary, a new age-depth model constructed
199 following the approach in Trondman et al. (2015). The age-depth model for each pollen record is used to aggregate RPP-
200 harmonised pollen count data into 25 time windows across the Holocene following a standard division used in Mazier et al.
201 (2012) and Trondman et al. (2015), later adopted by the PAGES LandCover6k working group (Gaillard et al., 2018). The first
202 three time windows (present–100 BP (where present is the date of coring), 100–350 BP; 350–700 BP) capture the major human-
203 induced land-cover changes since Early Middle Ages. Subsequent time windows are contiguous 500-year long intervals (e.g.
204 700–1200 BP, 1200–1700 BP, 1700–2200 BP, etc.) with the oldest interval representing the start of the Holocene (11200–11700



205 BP). The use of 500-year long time windows is motivated by the necessity to obtain sufficiently large pollen counts for reliable
206 REVEALS reconstructions. Since the size of the error on the REVEALS estimate partly depends on the size of the pollen
207 count (Sugita, 2007a), the length of the time window should be a reasonable compromise to ensure both a useful time resolution
208 of the reconstruction and an acceptable reliability of the REVEALS estimate of plant cover (Trondman et al., 2015).



209 **Table 1: Land-cover types (LCTs) and Plant Functional Types (PFTs) according to Wolf et al. (2008) and their corresponding pollen**
 210 **morphological types. Fall speed of pollen (FSP) and the mean relative pollen productivity (RPP) estimates using the new RPP**
 211 **synthesis (see section 2.3 and Appendices A-C for details) with their standard errors in brackets (see text for more explanations).**
 212 ***The FSP values of *Quercus* evergreen t. and Mediterranean Ericaceae according to the original study (Mazier, unpublished) are**
 213 **0.015 and 0.051, respectively (see Appendix B, Table B.3). The value of 0.035 (FSP of *Quercus* deciduous t.) and 0.038 (FSP of boreal-**
 214 **temperate Ericaceae) were used instead (see discussion in section 4.2 for explanation).**
 215

Land-cover types (LCTs)	PFT	PFT definition	Plant taxa/Pollen-morphological types	FSP (m/s)	PPE (SD)
Evergreen trees (ET)	TBE1	Shade-tolerant evergreen trees	<i>Picea abies</i>	0.056	5.437 (0.097)
	TBE2	Shade-tolerant evergreen trees	<i>Abies alba</i>	0.12	6.875 (1.442)
	IBE	Shade-intolerant evergreen trees	<i>Pinus sylvestris</i>	0.031	6.058 (0.237)
	MTBE	Mediterranean shade-tolerant broadleaved evergreen trees	<i>Phillyrea</i>	0.015	0.512 (0.076)
			<i>Pistacia</i>	0.03	0.755 (0.201)
			<i>Quercus evergreen t.</i>	0.035*	11.043 (0.261)
	TSE	Tall shrub, evergreen	<i>Juniperus communis</i>	0.016	2.07 (0.04)
	MTSE	Mediterranean broadleaved tall shrubs, evergreen	Ericaceae*	0.038*	4.265 (0.094)
<i>Buxus sempervirens</i>			0.032	1.89 (0.068)	
Summer green trees (ST)	IBS	Shade-intolerant summer-green trees	<i>Alnus glutinosa</i>	0.021	13.562 (0.293)
			<i>Betula</i>	0.024	5.106 (0.303)
	TBS	Shade-tolerant summer-green trees	<i>Carpinus betulus</i>	0.042	4.52 (0.425)
			<i>Carpinus orientalis</i>	0.042	0.24 (0.07)
			<i>Castanea sativa</i>	0.01	3.258 (0.059)
			<i>Corylus avellana</i>	0.025	1.71 (0.1)
			<i>Fagus sylvatica</i>	0.057	5.863 (0.176)
			<i>Fraxinus</i>	0.022	1.044 (0.048)
			<i>Quercus deciduous t. *</i>	0.035	4.537 (0.086)
			<i>Tilia</i>	0.032	1.21 (0.116)
<i>Ulmus</i>	0.032	1.27 (0.05)			
TSD	Tall shrub, summer-green	<i>Salix</i>	0.022	1.182 (0.077)	
Open land (OL)	LSE	Low shrub, broadleaved evergreen	<i>Calluna vulgaris</i>	0.038	1.085 (0.029)
	GL	Grassland - all herbs	<i>Artemisia</i>	0.025	3.937 (0.146)
			Amaranthaceae/Chenopodiaceae	0.019	4.28 (0.27)
			<i>Cyperaceae</i>	0.035	0.962 (0.05)
			<i>Filipendula</i>	0.006	3 (0.285)
			<i>Poaceae</i>	0.035	1 (0)
			<i>Plantago lanceolata</i>	0.029	2.33 (0.201)
			<i>Rumex acetosa-t</i>	0.018	3.02 (0.278)
	AL	Agricultural land - cereals	<i>Cerealia-t</i>	0.06	1.85 (0.380)
<i>Secale cereale</i>			0.06	3.99 (0.320)	

216



217 2.3 Model parameter setting

218 For the purpose of this study, a new synthesis of the RPP values available for European plant taxa was performed in 2018-
219 2019 based on the latest synthesis by Mazier et al. (2012) and additional RPP studies published since then (Appendix A-C). It
220 provides new alternative RPP datasets for the whole of Europe, including or excluding plant taxa with dominant entomophily,
221 with the important addition of plant taxa from the Mediterranean area (Table A1). The location of studies included in the RPP
222 synthesis are shown in Fig. C1 and related information is provided in Table C1. The selection of RPP studies, RPP values
223 (shown in Appendix B, Tables B1 and B2) and calculation of mean RPP and their standard error (SD) for Europe are explained
224 in Appendix C. The synthesis includes a total of 54 taxa for which RPP values are available (Tables B1 and B2), 39 taxa from
225 studies in boreal and temperate Europe, and 15 taxa from studies in Mediterranean Europe of which seven include exclusively
226 sub-Mediterranean and Mediterranean taxa: *Buxus sempervirens*, *Carpinus orientalis*, *Castanea sativa*, Ericaceae
227 (Mediterranean species), *Phillyrea*, *Pistacia* and *Quercus* evergreen type. RPP values are available from both boreal/temperate
228 and Mediterranean Europe for seven taxa: i.e. Poaceae (reference taxon), *Acer*, *Corylus avellana*, Apiaceae, *Artemisia*,
229 *Plantago lanceolata* and Rubiaceae (Table B2). Table A1 presents the new RPP dataset for the 54 plant taxa and, for
230 comparison, the mean RPP values from Mazier et al. (2012) and from the recent synthesis by Wieczorek & Herzs Schuh (2020).
231 Moreover, comparison with the RPP values of three studies not used in our synthesis is shown in Table A2. For the REVEALS
232 reconstructions presented in this paper, we excluded strictly entomophilous taxa, which resulted in a total of 31 taxa (Table 1).
233 The excluded taxa are Compositae SF Cichorioidae, *Leucanthemum* (*Anthemis*)-t., *Potentilla*-t., *Ranunculus acris*-t., and
234 Rubiaceae. We included entomophilous taxa that are known to be characterised by some anemophily, e.g. *Artemisia*,
235 Chenopodiaceae, Rubiaceae, and *Plantago lanceolata*. We excluded plant taxa with only one RPP value except
236 Chenopodiaceae, *Urtica*, *Juniperus*, and *Ulmus*, and the seven exclusively sub-Mediterranean and Mediterranean taxa
237 mentioned above.

238 The FSP values (Tables 1 and A1) for boreal and temperate plant taxa were obtained from the literature (Broström et al., 2008;
239 Mazier et al., 2012); these values were in turn extracted from Gregory (1973) for trees, and calculated based on pollen
240 measurements and Stokes' law for herbs (Broström et al., 2004). FSPs for Mediterranean taxa (*Buxus sempervirens*, *Castanea*
241 *sativa*, Ericaceae (Mediterranean species), *Phillyrea*, *Pistacia*, and *Quercus* evergreen type) were obtained by using pollen
242 measurements and Stokes' law (Mazier et al., unpublished); the FSP of *Carpinus betulus* (Mazier et al., 2012) was used for
243 *Carpinus orientalis* (Grindean et al., 2019).

244 The site radius was obtained from original publications where possible. Sites in the EMBSecBIO were classified as small
245 (0.01-1 km²), medium (1.1-50 km²) or large (50.1-500 km²). These were assigned radii of 399m, 2921m and 10000 m,
246 respectively. Where a site's radius could not be determined from publication, it was geolocated in Google Earth and the area
247 of the site was measured. A radius value was extracted assuming that a site shape is circular (Mazier et al., 2012). A constant
248 wind speed of 3 m/s, assumed to correspond approximatively to the modern mean annual wind speed in Europe, was used
249 following Trondman et al. (2015). Z_{\max} (maximum extent of the regional vegetation) was set to 100 km. Z_{\max} and wind speed



250 influence on REVEALS estimates has been evaluated earlier in simulation and empirical studies (Gaillard et al., 2008; Mazier
251 et al., 2012; Sugita, 2007a). Atmospheric conditions are assumed to be neutral (Sugita, 2007a).

252 **2.4 Implementation of REVEALS**

253 REVEALS was implemented using the REVEALS function within the LRA R-package (Abraham et al., 2014; see Code
254 availability, section 6). The function enables the use of deposition models for bogs (Prentice's model) and lakes (Sugita's
255 model), and two dispersal models (a Gaussian plume model, and a Lagrangian stochastic model taken from the DISCOVER
256 package (Theuerkauf et al., 2016). Within this study the Gaussian plume model was applied. The REVEALS model was run
257 on all pollen records within each $1^\circ \times 1^\circ$ grid cell across Europe. The REVEALS function runs lake and bog sites separately
258 within each $1^\circ \times 1^\circ$ grid cell, and combines results (if more than one pollen record per cell) to produce a single mean cover
259 estimate (in proportion) and mean standard error (SE) for each taxon. The formulation of the SE can be found in Appendix A
260 of Sugita (2007a). The REVEALS SE takes into account the standard deviations on the relative pollen productivities for the
261 individual pollen taxa (Table 1) and the number of pollen grains counted in the sample (Sugita, 2007a). The uncertainties of
262 the averaged REVEALS estimates of plant taxa for a grid cell are calculated using the delta method (Stuart and Ord., 1994),
263 and expressed as the SEs derived from the sum of the within- and between-site variations of the REVEALS results in the grid
264 cell. The delta method is a mathematical solution to the problem of calculating the mean of individual SEs (see Li et al., 2020,
265 Appendix C, for the formula and further details). Results of the REVEALS function are extracted by time window, producing
266 25 matrices of mean REVEALS estimates of cover and 25 matrices of corresponding mean SEs for each of the 31 RPP taxa
267 and each grid cell. The 31 RPP taxa are also assigned to 12 plant functional types (PFTs) and three land-cover types (LCTs)
268 (Table 1) and their mean REVEALS estimates calculated. These PFTs follow Trondman et al. (2015), with the addition of two
269 PFTs for Mediterranean vegetation not reconstructed in earlier studies: Mediterranean shade-tolerant broadleaved evergreen
270 trees (MTBE) and Mediterranean broadleaved tall shrubs, evergreen (MTSE). The mean standard errors for LCTs and PFTs
271 including more than one plant taxon are calculated using the delta method (Stuart. and Ord., 1994), as explained above.

272 **2.5 Mapping of the REVEALS estimates**

273 To illustrate the information that the new REVEALS reconstruction provides, we present and describe in section 3 maps of
274 the REVEALS estimates (% cover) and their associated SEs for the three LCTs (Fig. 2 to 4) and five taxa for eight selected
275 time windows: the five taxa are *Cerealia-t* and *Picea abies* (Fig. 5 and 6), and *Calluna vulgaris*, deciduous *Quercus*, and
276 evergreen *Quercus* (Fig. D1-D3). The selection of the five taxa and eight time windows is motivated essentially by notable
277 changes in spatial distribution of these taxa through time, with higher resolution for recent times characterised by the largest
278 and most rapid human-induced changes in vegetation cover. For visualisation purposes the estimates are mapped in nine %
279 cover classes. These fractions are the same for the three LCTs (Figures 2-4), and the mapped output can therefore be directly
280 compared. In contrast, the colour scales used for the five taxa vary between maps depending on the abundance of the PFT/taxon
281 (Fig. 5 and 6, D1-D3). Different taxa thus have different scales and maps cannot be directly compared. We visualise uncertainty



282 in our data by plotting the SE as a circle inside each grid cell; it is the coefficient of variation (CV, i.e. the standard error
283 divided by the REVEALS estimate). Circles are scaled to fill the grid cell if the SE is equal or greater than the mean REVEALS
284 estimate (i.e. $CV \geq 1$). Grid-based REVEALS results that are based on pollen records from just large bogs, or single small
285 bogs or lakes, provide lower quality results (see section 2.1 on the REVEALS model, and discussion section 4.1). Grid cells
286 for which this is the case are detailed in Table GC_quality_by_TW (see section 5, Data availability), by time window. It
287 should be stressed that the percentage scale ranges we use here are different from those used in the maps of Trondman et al.,
288 (2015) and, therefore, the data visualisation we present cannot be directly compared with that of the 2015 study.

289 **3 Results**

290 The full results, or REVEALS dataset, include mean REVEALS values (in proportions) and their related mean SE for 31
291 individual tree and herb taxa, twelve PFTs and three LCTs for each grid cell in 25 consecutive time windows of the Holocene
292 (11.7 k BP to present) (see Data availability section). Here, results are illustrated by maps of the three LCTs (Fig. 2-4) and five
293 taxa (Fig. 5-6, D1-D3). The presented maps are not part of the published dataset archived in Pangea (see Data availability,
294 section 5), they are examples of how the data can be presented and what they can be used for.

295 **3.1 Land-cover types**

296 The three land-cover types are evergreen trees (ET), summer-green trees (ST) and open land (OL). ET includes six PFTs which
297 are composed of nine pollen-morphological types (here after referred to as taxa). ST includes four PFTs which are composed
298 of eleven taxa while OL includes three PFTs that are in turn composed of nine taxa (Table 1).

299 **3.1.1 Open Land (OL)**

300 At the start of the Holocene, OL (Fig. 2) is higher in western Europe where it generally exceeds 80% cover, compared with
301 central Europe where it is more typically ~60%. There is a general decline in OL cover through the early Holocene. At 5700-
302 6200 BP most grid cells in central Europe have OL cover values between 10-50%. In western Europe, whilst OL is generally
303 reduced, several grid cells on the Atlantic fringe of northern Scotland persistently maintain 80-90% OL cover. OL increases
304 from the mid-Holocene, and by 2700-3200 BP the British Isles, France, Germany and the Mediterranean region have grid cells
305 recording OL values >70%. In central, northern and eastern Europe grid cells OL values vary between 10 - 70% at 2700-3200
306 BP. Time windows from the last two millennia show a consistent increase in OL with values >60% across most of central,
307 southern and western Europe and 20-70% in northern Europe.

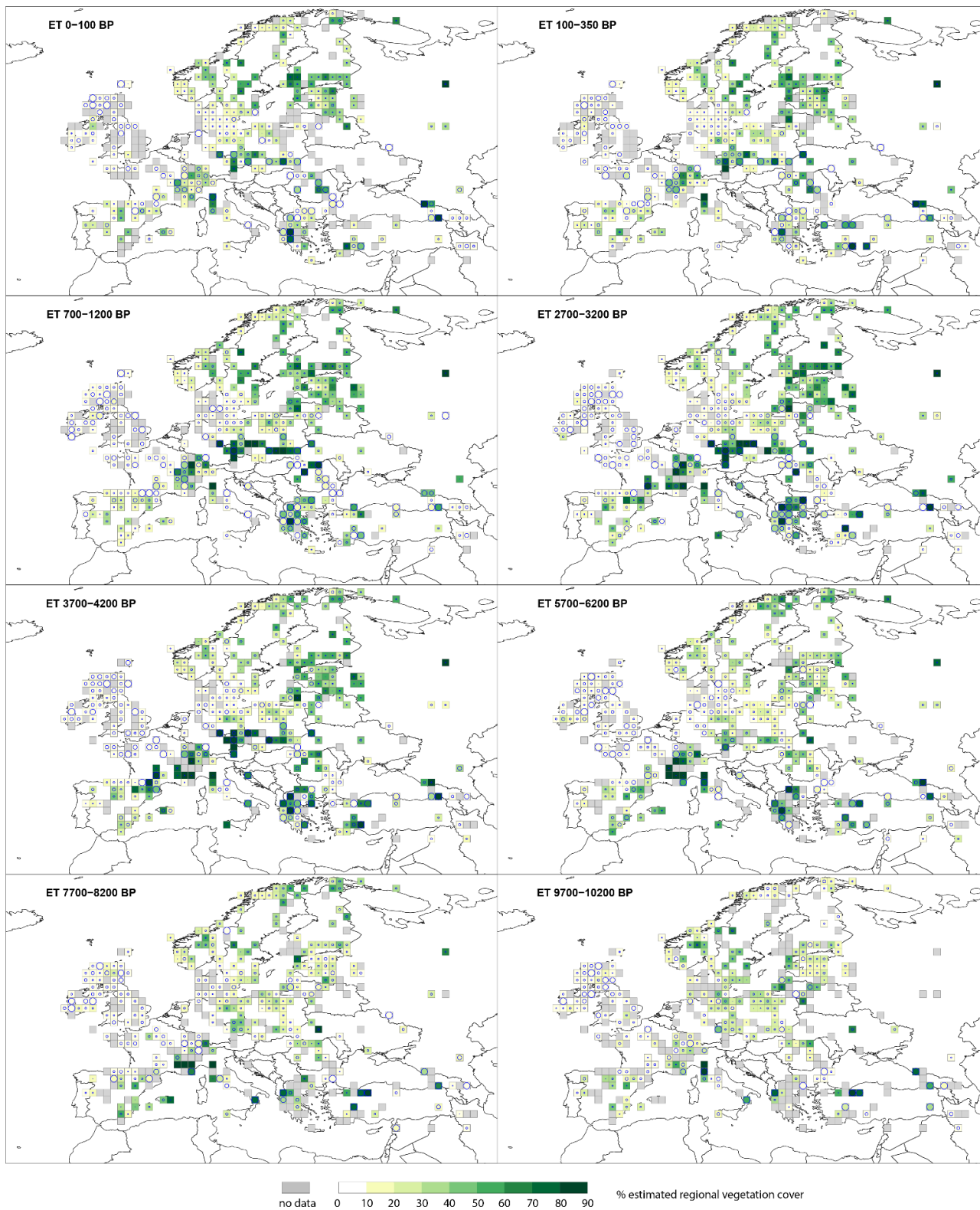




309 **Figure 2. Grid-based REVEALS estimates of Open Land (OL) cover for eight Holocene time windows. Percentage cover of open**
310 **land in 10% intervals represented by increasing shades of green. Grey cells: cells without pollen data for the time window, but with**
311 **pollen data in other time windows. Circles in grid cells represent the coefficient of variation (CV; the standard error divided by the**
312 **REVEALS estimate). When $SE \geq$ REVEALS estimate, the circle fills the entire grid cell and the REVEALS estimate is not different**
313 **from zero. This occurs mainly where REVEALS estimates are low.**

314 **3.1.2 Evergreen Trees (ET)**

315 Evergreen tree (ET) cover (Fig. 3) at 9700-10200 BP is <30% across Europe, and by 7700-8200 BP fewer than 30 grid cells
316 show ET >50%. ET percentage cover slowly increases through the early Holocene and at 5700-6200 BP groups of grid cells
317 in southern Europe record >80%, while in northern Europe ET cover ranges between 10% and 60%. There is a consistent
318 increase in ET cover over Europe during the mid- and late-Holocene with ET cover peaking at 2700-3200 BP before starting
319 to reduce. Across western parts of Europe, including the British Isles, western France, Denmark, and the Netherlands ET never
320 exceeds 20% cover.

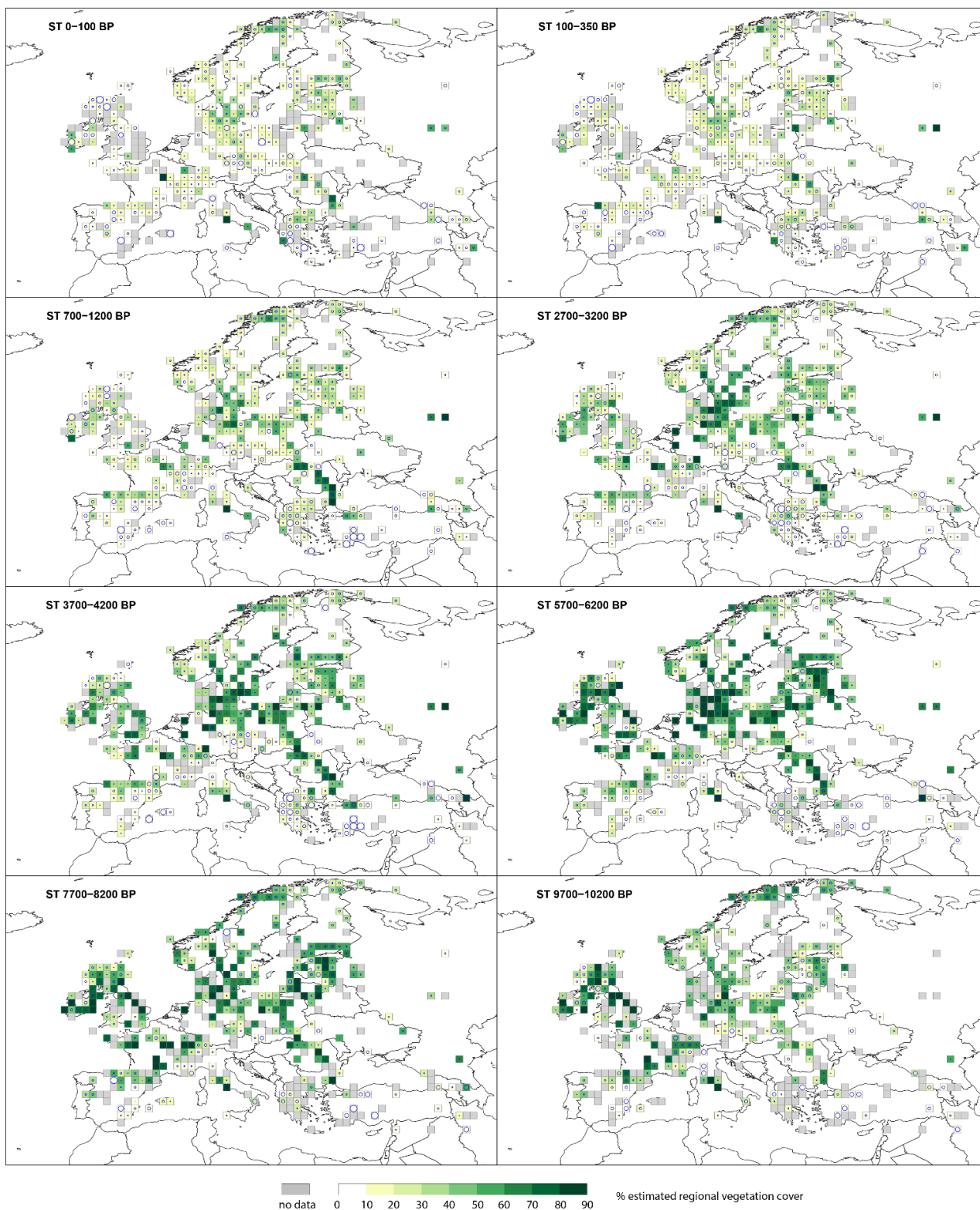




322 **Figure 3. Grid-based REVEALS estimates of Evergreen Tress (ET) cover for eight Holocene time windows. See caption of Figure 2**
323 **for more explanations.**

324 **3.1.3 Summer-green Trees (ST)**

325 The estimate of cover of summer-green trees (Fig. 4) in the early Holocene at 9700-10200 BP is >40% across Europe. A small
326 number (<10) of grid cells in northern, western, central and southern Europe have cover >60%. This significantly increases to
327 5700-6200 BP, at which time ST cover is >60% in central Europe, and 40-60% in northern Europe. ST cover remains <20%
328 in southern Europe. From 5700-6200 BP there is a steady decline in ST cover across Europe. At 2700-3200 BP only central
329 Europe has ST cover >50% while the rest of Europe exhibits values <50%. There is a consistent decline over the last two
330 millennia BP. Most of Europe has ST cover <30% in the most recent time windows (100-350 and 100 BP-present), except for
331 a group of grid cells in the southern Baltic states and scattered records elsewhere.





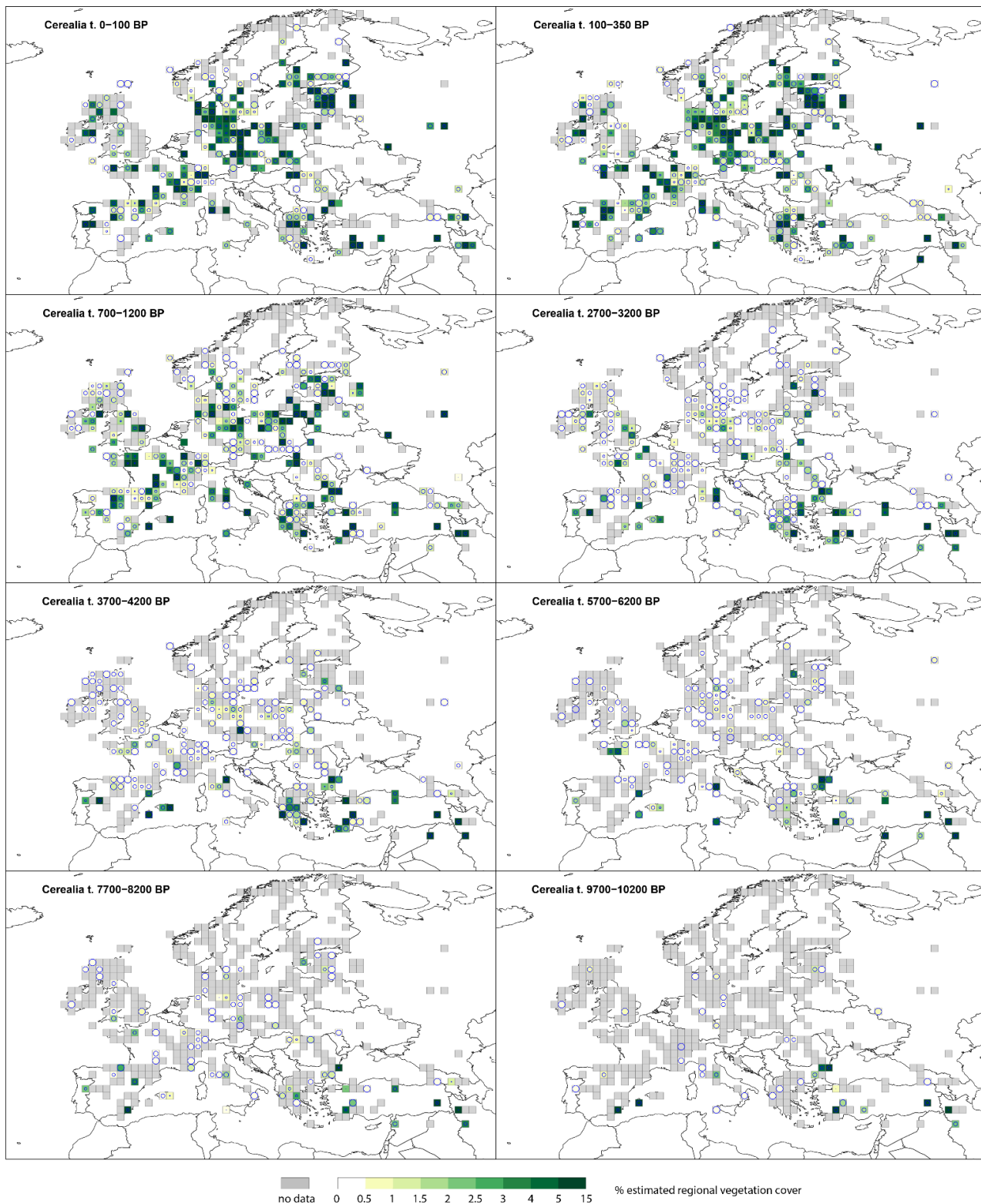
333 **Figure 4. Grid-based REVEALS estimates of Summer-green Trees (ST) cover for eight Holocene time windows. See caption of**
334 **Figure 2 for more explanations.**

335 **3.2 Selected taxa**

336 In terms of PFTs, *Cerealia-t* is assigned to agricultural land (AL), *Picea abies* to shade tolerant evergreen trees (TBE1: *Picea*
337 *abies* is the only taxon in this PFT), *Calluna vulgaris* to low evergreen shrubs (LSE: *Calluna vulgaris* is the only taxon in this
338 PFT), deciduous *Quercus* to shade tolerant summer-green trees (TBS), and evergreen *Quercus* to Mediterranean shade-tolerant
339 broadleaved evergreen trees (MTBE) (Table 1).

340 **3.2.1 *Cerealia-t*.**

341 *Cerealia-t*. (Fig. 5) is recorded at low proportions throughout the Holocene with 10-15% as the maximum cover. *Cerealia-t*.
342 is present in southern Europe at 9700-10200 BP with several grid cells recording >5 to 10%. Whilst such values are rare, there
343 are scattered grid cells in central and western Europe recording the presence of *Cerealia-t*. at very low levels (0.5-1%). These
344 values have high SE (greater than the REVEALS estimate) and are therefore not different from zero; they correspond to single
345 findings of *Cerealia-t*. By 5700-6200 BP, grid cells in Estonia and France record 3-5% cover, and several regions within central
346 and western Europe record 0-5% (0.5-1%), although with high SEs. At 2700-3200 BP, *Cerealia-t*. is recorded across central
347 and western Europe in the British Isles, France, Germany, and Estonia with low values. In Norway, Sweden and Finland it has
348 0-1% cover with high SEs. The highest cover (>5%) is observed across Europe from 1200 BP.

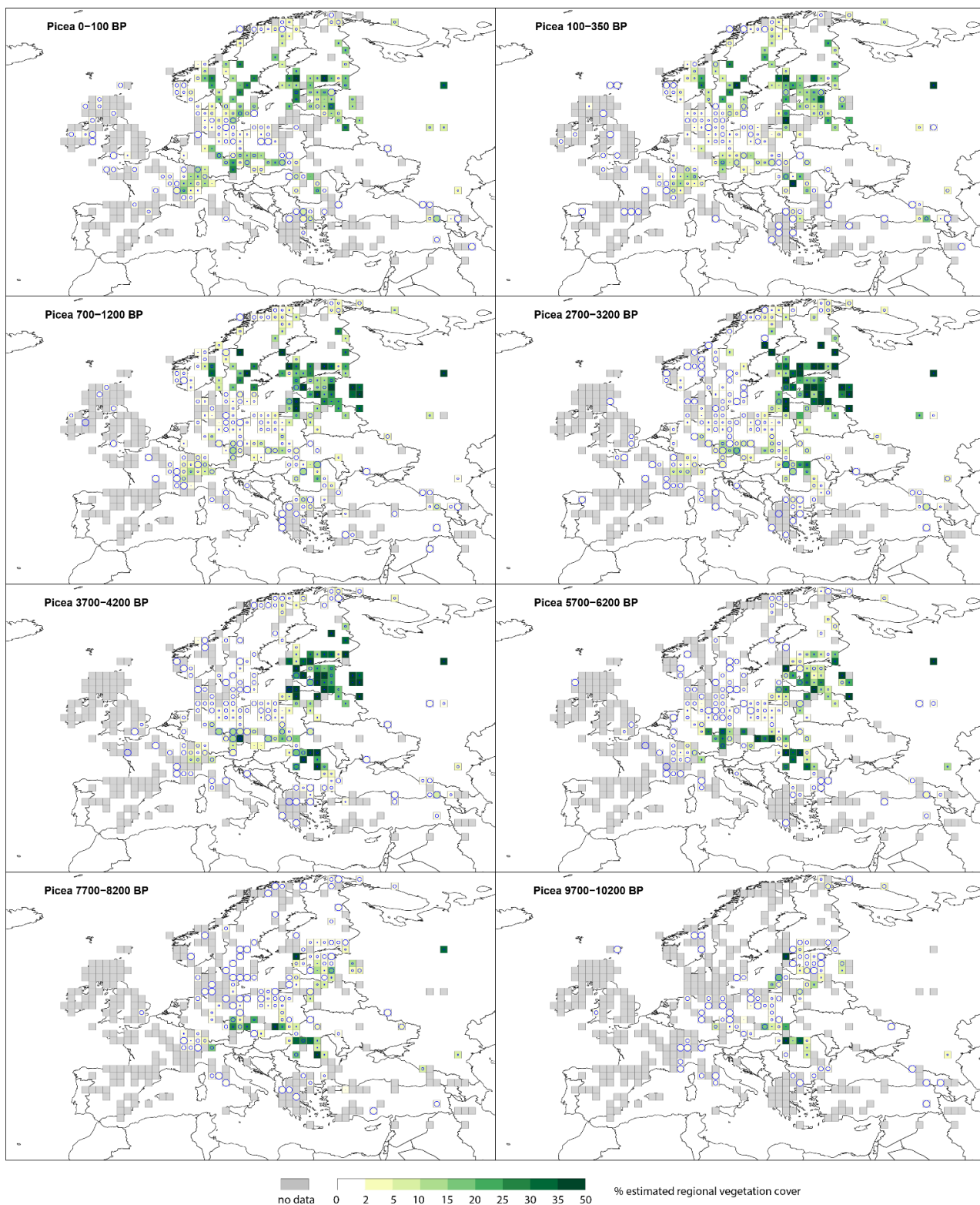




350 **Figure 5. Grid-based REVEALS estimates of Cerealia - t cover for eight Holocene time windows. Percentage cover in 0.5% intervals**
351 **between 0 and 3%, 1% intervals between 3 and 5, and 5% interval between 5 and 10%. See caption of Figure 2 for more explanations.**

352 **3.2.2 *Picea abies***

353 *Picea abies* (Fig. 6) cover is low (1-2%) at 9700-10200 BP, although a number of grid cells in central and eastern Europe
354 record values between 30 and 50%. By 7700-8200 BP, grid cells recording 30-50% cover are observed in more regions of
355 central and eastern Europe than earlier (Russia, Estonia, Romania, Slovakia and Austria). At 5700-6200 BP, almost all central
356 Europe has consistent but low cover of *Picea abies*; values are higher towards northeast Europe (Russia, Estonia, Latvia,
357 Belarus and Lithuania), up to 30-50%. By 2700-3200 BP the cover of *Picea abies* has increased across central (ca. 10%) and
358 northeast Europe (>30%). From 1200 BP, *Picea abies* is recorded in northern Europe, particularly in Norway and Sweden with
359 some grid cells recording 25-50% cover.





361 **Figure 6. Grid-based REVEALS estimates of *Picea* cover for eight Holocene time windows. Percentage cover in 1% interval between**
362 **0 and 2%, 3% interval between 2 and 5%, 5% intervals between 5 and 30%, and 20% interval between 30 and 50%. See caption of**
363 **Figure 2 for more explanations.**

364 3.2.3 *Calluna vulgaris*

365 During the Holocene, *Calluna vulgaris* cover (Fig. D1) peaks at 50%, and is largely distributed in a central European belt from
366 the British Isles across to the southern Baltic States. At 9700-10200 BP, it is recorded in only a few grid cells, mostly in central
367 and Western Europe, and at levels <10%. Cover slowly increases and by 7700-8200 BP, there are several grid cells with cover
368 >25% within the British Isles, and with 10-20% cover within Denmark. At 5700-6200 BP grid cells in coastal locations in
369 northwest Europe (particularly France, Germany and Denmark) have 50% *Calluna vulgaris* cover. Cover steadily increases
370 within the same grid cells and by 2700-3200 BP, cover has increased in northern and Eastern Europe e.g. Norway, Estonia,
371 with values up to 20% cover. The highest cover of *Calluna vulgaris* is recorded in the last two millennia. Although some grid
372 cells in southeast Europe record low cover values, these have high SE.

373 3.2.4 *Quercus deciduous*

374 *Quercus deciduous* (Fig. D2) is recorded in central and western Europe at 9700-10200 BP at low levels (<10%), while in
375 southern Europe (Italy) there are several grid cells recording >20% cover. By 7700-8200 BP cover in central and western
376 Europe is between 1-10% while in northern and eastern Europe grid cells it is <2% with high SEs. During the mid-Holocene
377 (5700-6200 BP) most of Europe, with the exception of some grid cells at the northern and southeast extremes, record *Quercus*
378 deciduous cover values between 2-15%. By 2700-3200 BP, the cover in the same grid cells has decreased to values between
379 2-10%. Thereafter, the number of grid cells recording *Quercus deciduous* cover remains similar; however, the percentage
380 cover slowly decreases and at 350-100 BP, the number of grid cells with *Quercus deciduous* cover above 5% is very low.

381 3.2.5 *Quercus evergreen*

382 The spatial distribution of *Quercus evergreen* (Fig. D3) remains the same throughout the Holocene. Cover of >30% is restricted
383 to only a few grid cells and time windows. At the start of the Holocene *Quercus evergreen* is recorded with values <15% in
384 southern Europe (Spain, Italy, Greece and Turkey) with high SEs. Cover of *Quercus evergreen* does not exceed 15% until
385 6700-7200 BP (not shown), in grid cells located in Turkey, Greece and Italy. From 6700-7200 BP there is an increase in the
386 number of grid cells recording *Quercus evergreen* in southern Europe but most exhibit low cover values (<15%), and have
387 high SEs.



388 4 Discussion

389 The results presented here are the first full-Holocene grid-based REVEALS estimates of land-cover change for Europe
390 spanning the Mediterranean, temperate and boreal biomes, and highlighting the spatial and temporal dynamics of 31 taxa, 12
391 PFTs and 3 LCTs across Europe over the last 11700 years. Previous studies have demonstrated major differences between
392 REVEALS results and pollen percentages (e.g. Marquer et al., 2014; Trondman et al., 2015), and it is not the scope of this
393 paper to evaluate the results in that context. This discussion focuses on the reliability and potential of this second generation
394 of REVEALS reconstruction for Europe for use by the wider science community.

395 4.1 Data reliability

396 The REVEALS results are reliant on the quality of the input datasets, namely pollen count data, chronological control for
397 sequences, and the number and reliability of RPP estimates used (further discussion on RPPs under 4.2). The standard errors
398 (SEs) can be considered a measure of the precision of the REVEALS results, and of reliability\quality (Trondman et al., 2015).
399 Where SEs are equal or greater than the REVEALS estimates (represented in the maps of Fig. 2-6 and D1-D3 as a circle that
400 fills the grid), caution should be applied in the use of the REVEALS estimates, as it implies that they are not different from
401 zero when taking the SEs into account. Whilst this is possible within an algorithmic approach that includes estimates of
402 uncertainty, it is conceptually impossible to have negative vegetation cover. If $SEs \geq \text{mean REVEALS value}$ it is therefore
403 uncertain whether the plant taxon has cover within the grid cell. Cover may either be very low or the taxon may be absent
404 within region (grid cell in this case).

405 The size of pollen counts impacts on the size of REVEALS SEs (Sugita, 2007a); larger counts result in smaller SEs.
406 Aggregation of samples from pollen records to longer time windows results in larger count sizes and thus lower SEs (see
407 sections 2.2 above and 4.2 below). Our input dataset includes more than 59 million individual pollen identifications, organised
408 here into 16711 samples from 1128 sites, where a sample is an aggregated pollen count for RPP taxa for a time window at a
409 site. 77% of samples have count sizes in excess of 1000, which is deemed most appropriate for REVEALS reconstructions
410 (Sugita, 2007a). The mean count size across all samples is 3550. Samples with count sizes lower than 1000 are still used, but
411 result in higher SEs. More than half of the pollen records used in the study were sourced from databases (see section 2.2). Note
412 that the EMBSecBIO taxonomy has been pre-standardised, and the data compilers have removed *Cerealia*-type. This means
413 that for grid cells within the Eastern Mediterranean-Black Sea-Caspian-Corridor, caution is advised in the interpretation of
414 *Cerealia*-type. Nevertheless, pollen from e.g. ruderals often related to agriculture such as *Artemisia*,
415 *Amaranthaceae/Chenopodiaceae*, and *Rumex acetosa* type are included in the land-cover type open land; therefore, changes in
416 cover of open land in the Eastern Mediterranean-Black Sea-Caspian-Corridor may be related to changes in agricultural land
417 (see also discussion below, re agricultural, section 4.3).

418 Aggregation of pollen counts to time windows depends on age-depth models. We have used the best age-depth models
419 available to us, based on the chronologies presented in Giesecke et al. (2014) for EPD sites, and through liaison with data



420 contributors. Nevertheless, future REVEALS runs may draw on improvements to age-depth modelling, which may result in
421 some original pollen count data being assigned to different time windows.

422 The REVEALS results here are provided for $1^\circ \times 1^\circ$ grid cells across Europe. The size and number of suitable pollen records
423 is an important factor in the quality of the REVEALS estimates for each grid cell. The REVEALS model was developed for
424 use with large lakes (>100-500 ha) that represent regional vegetation (Sugita, 2007a). Grid cells with multiple large lakes will
425 thus provide results with the highest level of certainty and reflect best the regional vegetation. These grid cell results comprising
426 of one or more large lakes are considered “high quality” (dark grey grids in figure 1B). It has been shown both theoretically
427 (Sugita, 2007a) and empirically (Fyfe et al., 2013; Trondman et al., 2016) that pollen records from multiple smaller (<100 ha)
428 lakes will also provide REVEALS estimates that reflect the regional vegetation. However, SEs may be larger if there is high
429 variability in pollen composition between records. We therefore also consider grid cells with multiple sites “high quality”.
430 Application of REVEALS to pollen records from large bogs violates assumptions of the model (see section 2.1 above).
431 Therefore, REVEALS estimates for grid cells including large bogs or single small sites (lake or bog) may not be representative
432 of regional vegetation, particularly in areas characterised by heterogeneous vegetation. We consider such estimates as “lower
433 quality” (light grey grids in figure 1B), although they may still provide first-order indications on vegetation cover, and represent
434 an improvement on pollen percentage data (Marquer et al., 2014). Our results provide REVEALS estimates for a maximum of
435 420 grid cells per time window. The number and type of pollen records in a grid cell can change between time windows: not
436 all pollen records cover the entire Holocene. It is therefore important to consider not just the number and type of pollen records
437 in the total dataset, but how this changes between time windows, to assess the reliability of individual results. Results for a
438 maximum of 143 grid cells are based on three or more sites, 65 on two sites, and a minimum of 212 grid cells on a single site.
439 The results of a maximum of 67 grid cells are based on single small bogs (<400 m radius), 68 on single small lakes (<400 m
440 radius), and 82 on single large bogs. It implies that about half the grid cells with REVEALS results should be considered as
441 “lower quality” results.

442 **4.2 Role of RPPs and FSP in REVEALS results**

443 A key assumption of the REVEALS model is that RPP values are constant within the region of interest, and through time
444 (Sugita, 2007a). Nevertheless, it has been suggested that RPPs may vary between regions, with the variation caused by
445 environmental variability (climate), vegetation structure, or methodological design differences (Hellman et al., 2008a; Mazier
446 et al., 2012; Li et al., 2020; Wiczorek and Herzschuh, 2020). Wiczorek and Herzschuh (2020) have shown that inter-taxon
447 variability in RPP values is generally lower than intra-taxon variability, lending support to application of the approach we used
448 in the new synthesis of RPP in Europe (Appendix A-C), i.e. calculation of mean RPPs using all available RPP values that can
449 be considered as reliable. Nevertheless, some RPP taxa still present a challenge, for example, Ericaceae, where Mediterranean
450 tree forms have a greater number of inflorescences and hence may have a higher RPP than low-growth form Ericaceae in
451 central and northern Europe. As we are using a single RPP dataset with the RPP of Ericaceae obtained in the Mediterranean
452 region (more explanations below), the effect of higher pollen producing Ericaceae in the Mediterranean might result in



453 underrepresentation of Ericaceae cover in Central-North Europe. Unfortunately, we have only unique RPP values for Ericaceae
454 in both boreal-temperate Europe and Mediterranean Europe, and therefore the large difference in RPP between the two biomes
455 remains to be confirmed with more RPP studies.

456 Currently there is higher confidence in the boreal and temperate RPP values that are based on a wider set of studies increasing
457 the spread of values and hence reliability of the mean RPP values used (Mazier et al., 2012; Wieczorek and Herschuh, 2020),
458 whilst RPP values for Mediterranean taxa are based on fewer empirical RPP studies. The new RPP datasets for Europe
459 produced for this study (Appendix A-C) can be used in different ways. The RPPs provided in Table A1 can be used for entire
460 Europe, including entomophilous taxa or not, and including all values from the Mediterranean area or only the values for the
461 strictly sub-Mediterranean and/or Mediterranean taxa. If one uses all RPPs from the Mediterranean area, there will be taxa for
462 which there is both a RPP value obtained in boreal/temperate Europe and a RPP value obtained in Mediterranean Europe.
463 Application of both RPP values in a single REVEALS reconstruction is not straightforward to achieve, because the border
464 between the two regions has shifted over the Holocene. In the REVEALS reconstruction presented in this paper, we chose to
465 use the RPPs from Mediterranean Europe only for the sub-Mediterranean and/or Mediterranean taxa (including Ericaceae)
466 (Table 1 and A1), and for all other taxa we used the RPPs from boreal/ temperate Europe. The major issue with this choice is
467 the RPP value of Ericaceae. Using only the large value from Mediterranean Europe may lead to an under-representation of
468 Ericaceae (*Calluna* excluded), in particular in boreal Europe, but perhaps also in temperate Europe. Using only the small value
469 from boreal/temperate Europe may lead to an over-representation of Ericaceae in Mediterranean Europe.

470 Until we have more RPP values for each taxon, it is not possible to disentangle the effect of all factors influencing the
471 estimation of RPPs and to separate the effect of methodological factors from those of factors such as vegetation type, climate
472 and land use. The only way to evaluate the reliability of RPP datasets is to test them with modern or historical pollen
473 assemblages and related plant cover (Hellman et al., 2008a, 2008b). We argue that RPP values of certain taxa may not vary
474 substantially within some plant families or genera, while they might be variable within others, depending on the characteristics
475 of flowers and inflorescences that may be either very different or relatively constant within families or genera (see discussion
476 in (Li et al., 2018)). Therefore, we advise to use compilations of RPPs at continental or sub-continental scales rather than
477 compilations at multi-continental scales as the North Hemisphere dataset proposed by Wieczorek and Herzs Schuh (2020). We
478 consider the RPP selection used within this work as the most suitable for Europe to date, but expect revised and improved RPP
479 values as more RPP empirical studies are published. Moreover, experimentation in REVEALS applications will allow future
480 studies to evaluate the effects of using different RPP datasets on land-cover reconstructions (e.g. Mazier et al., 2012).

481 The role of FSP values in the pollen dispersal and deposition function ($g_i(z)$) in the equation of the REVEALS model, section
482 2.1) has been discussed by Theuerkauf et al. (2012). In this application of REVEALS we used the Gaussian Plume Model
483 (GPM) of dispersion and deposition as most existing RPP values have been estimated using this model. The GPM approximates
484 dispersal as a fast-declining curve with distance from the source plant, which implies short distances of transport for pollen
485 grain with high FSP compared to other models of dispersion and deposition (Theuerkauf, 2012). We have used the FSP values
486 obtained for *Quercus* deciduous (0.035 m/s) and boreal-temperate Ericaceae (0.037 m/s) for *Quercus* evergreen and



487 Mediterranean Ericaceae, respectively, although the FSP values of those two taxa were estimated to 0.015 and 0.051 in the
488 Mediterranean study (Table 1 and A1). The possible effect of using the lower FSP for *Quercus* evergreen (0.015 m/s) and the
489 high FSP for Mediterranean Ericaceae (0.051 m/s) may be lower cover of *Quercus* evergreen and higher cover of
490 Mediterranean Ericaceae than our results suggest. This hypothesis however requires further testing.

491 **4.3 Use of the REVEALS results**

492 The second generation dataset of pollen-based REVEALS land cover in Europe over the Holocene (this paper) is currently
493 used in two major research projects: LandClimII, and PAGES LandCover6k. LandClimII is a development of LandClimI
494 (Strandberg et al., 2014; Trondman et al., 2015) and studies the difference in the biogeophysical effect of land-cover change
495 on climate at 6000, 2500 and 200 BP (Githumbi et al., 2019). PAGES LandCover6k focuses on providing datasets on past
496 land-cover/land-use for climate modelling studies (Gaillard et al., 2018; Harrison et al., 2020). The first generation REVEALS
497 land-cover reconstruction (Marquer et al., 2014, 2017; Trondman et al., 2015) were used to evaluate other pollen-based
498 reconstructions of Holocene tree-cover changes in Europe (Roberts et al., 2018) and scenarios of anthropogenic land-cover
499 changes (ALCCs) (Kaplan et al., 2017) (see also section 1). The Trondman et al. (2015) reconstructions were used to create
500 continuous spatial datasets of past land cover using spatial statistical modelling (Pirzamanbein et al., 2014, 2018, 2020).
501 Spatially explicit datasets/maps based on the second generation of REVEALS reconstruction are currently being produced
502 within PAGES LandCover6k and used to evaluate and revise the HYDE (Klein Goldewijk et al., 2017) and KK10 (Kaplan et
503 al., 2009) ALCC scenarios. Moreover, LandCover6k archaeology-based reconstructions of past land-use change (Morrison et
504 al., 2021) will be integrated with the datasets of REVEALS land-cover. Besides the uses listed above, the second generation
505 of REVEALS reconstruction for Europe offers great potential for use in a large range of studies on past European regional
506 vegetation dynamics and changes in biodiversity over the Holocene (Marquer et al., 2014, 2017) and the relationship between
507 regional plant cover, land use, and climate over millennial and centennial time scales. Moreover the data can be used to create
508 all sorts of maps of plant cover that can serve in various contexts.

509 Several papers have discussed in depth the issues that need to be taken into account when interpreting REVEALS
510 reconstructions of past plant cover, in particular Trondman et al. (2015) and Marquer et al. (2017). The interpretation in terms
511 of human-induced vegetation change is one of the major challenges. The cover of open land (OL) may be used to assess
512 landscape openness, but is not a precise measure of human disturbance, as OL will include plant taxa characterizing both
513 naturally-open land and agricultural land that has been created by humans through the course of the Holocene with the
514 domestication of plants and livestock. Natural openness can occur in arctic and alpine areas, in wet regions, in river deltas and
515 around large lakes, as well as in eastern steppe areas. It is a particular challenge in the Mediterranean region where natural
516 vegetation openness represents a larger fraction of the land cover than in temperate or boreal Europe (Roberts et al., 2019).
517 Agricultural Land (AL) is the only PFT that includes cultivars; nevertheless, it is restricted to cereal cropping, and many other
518 cultivated crop types that can be identified through pollen analysis do not yet have RPP values (e.g. *Linum usitatissimum*
519 (common flax), *Cannabis* (hemp), *Fagopyrum* (buckwheat), beans, etc.). Moreover, the *Cerealia-t.* pollen morphological type



520 includes pollen from wild species of Poaceae, especially when identification relies essentially on measurements of the pollen
521 grain and its pore and does not consider exine structure and sculpture (Beug, 2004; Dickson, 1988).
522 The maps presented and described in section 3 as an illustration of the results show similar changes in spatial distributions and
523 quantitative cover of plant taxa and land-cover types through time, between 6000 BP and present, as the results published in
524 Trondman et al., (2015). The much greater potential of the new REVEALS reconstruction resides in its larger spatial extent,
525 covering not only boreal and temperate Europe but also southern and eastern Europe, and its contiguous time windows across
526 the entire Holocene, from 11700 BP to present. The quality of results is also higher in a number of grid cells in comparison to
527 Trondman et al (2015), where new pollen records have been included, which may in several cases decrease the standard error
528 on the REVEALS estimates.

529 **5. Data availability**

530 All data files reported in this work which were used for calculations, and figures are available for public download at
531 <https://doi.pangaea.de/10.1594/PANGAEA.937075?format=html#download> (Fyfe, Ralph M; Githumbi, Esther; Trondman,
532 Anna-Kari; Mazier, Florence; Nielsen, Anne Birgitte; Poska, Anneli; Sugita, Shinya; Woodbridge, Jessie; LandClimII
533 contributors; Gaillard, Marie-José (2021): A full Holocene record of transient gridded vegetation cover in Europe. PANGAEA,
534 <https://doi.org/10.1594/PANGAEA.931856>). The data and the DOI number are subject to future updates and only refer to this
535 version of the paper. The data available in Pangaea includes: 1) REVEALS reconstructions and their associated standard errors
536 for the 25 time windows; 2) Metadata of the 1128 pollen records used; 3) LandClimII contributors listing the data
537 contributors\collectors\databases. 4) The list of FSP and RPP values used for the reconstructions and 5) Grid cell quality
538 information (in terms of available pollen data, which influences the result quality: mean REVEALS estimate of plant cover)
539 for all grid cells.

540 **6. Code availability**

541 REVEALS was implemented using the REVEALS function within the LRA R-package (Abraham et al., 2014), available at
542 <https://github.com/petrkunes/LRA>.
543 Example code for data preparation and implementation of REVEALS, using two grid cells from SW Britain, is available at
544 <https://github.com/rmfyfe/landclimII>.

545 **7. Conclusions**

546 The LRA REVEALS and LOVE models (Sugita, 2007a, 2007b) are the only current land-cover reconstruction approaches
547 based on pollen data that incorporate assumptions that reduce the biases caused by the non-linear pollen-vegetation



548 relationship, differences in sedimentary archives and spatial scales. The application of the REVEALS model to 1128 pollen
549 records distributed across Europe has produced the first full-Holocene estimates of vegetation cover for 31 plant taxa in $1^\circ \times$
550 1° grid cells. These data are made available for use by the wider science community, including aggregation of results to PFTs
551 and LCTs. The REVEALS model assumptions are clearly stated to allow interpretation and assessment of our results and
552 several of the assumptions have been tested and validated. We can therefore use the land-cover reconstructions to test the role
553 of climate and humans on the Holocene vegetation at the regional scale in terms of changes in plant cover over time and space.
554 The overview of land-cover change across Europe over the Holocene can be used to track the timing and rate of vegetation
555 shifts which is useful in discerning the drivers of the observed change (Marquer et al., 2014; 2017). We can also study the
556 effect of human-induced changes in regional vegetation cover on climate, i.e. study land use as a climate forcing (e.g. Gaillard
557 et al., 2010; Strandberg et al., 2014; Gaillard et al., 2018; Harrison et al., 2020). Local reconstructions (LOVE) can be a
558 complementary approach to archaeological surveys as fine-scale human use of the landscape cannot be distinguished using
559 REVEALS (regional estimates). The LOVE model requires that regional plant cover is known: the REVEALS reconstructions
560 are therefore needed for this purpose as well, and gridded reconstructions may be a way to perform LOVE reconstructions,
561 although other strategies can be chosen (e.g. Cui et al., 2013; Mazier et al., 2015). Questions such as the degree of vegetation
562 openness through the Holocene in Europe, or on changes in the relationship between summer-green and evergreen tree cover
563 through time can now and in the future be answered and validated with fossil pollen data via the REVEALS approach. We
564 expect that in the future imprecision can be further reduced in terms of both the quality, and spatial extent, of REVEALS
565 estimates, as more pollen records are incorporated, and work on RPPs develops.

566 **Appendices**

567 **Appendix A - New RPP dataset for Europe**

568 **A.1 New synthesis of European RPPs**

569 Table A1 is the result of the new synthesis of RPPs available in Europe we have performed for the REVEALS reconstruction
570 presented in the paper. It includes RPPs for 39 plant taxa from studies in boreal and temperate Europe of which 22 (Poaceae
571 included) are herbs or low shrubs, and for 22 plant taxa from studies in the Mediterranean area. The two regions have RPP
572 values for 7 plant taxa in common. These RPPs are compared to those from two syntheses published earlier, Mazier et al.
573 (2012) and Wieczorek and Herzschuh (2020). The number of selected RPP values (n) for Poaceae is larger than the total
574 number of RPP (tn), i.e. $n = tn + 1$. This is due to the fact that the study of Bunting et al. 2005 does not include a value for
575 Poaceae and the RPP values are related to *Quercus* (Bunting et al., 2005); therefore, RPPs related to Poaceae were calculated
576 by assuming the RPP value for *Quercus* (related to Poaceae; $Quercus_{(Poaceae)}$) was the same in this study region than the mean
577 of $Quercus_{(Poaceae)}$ RPPs from all other available studies.



578 The ranking of RPPs for 23 tree taxa, from the largest (13.56) to the smallest (0.240), is as follows (Poaceae included for
579 comparison with herbs): *Alnus*> *Quercus* evergreen (M)> *Abies alba*> *Pinus*> *Fagus sylvatica*> *Picea abies*> Ericaceae (M)>
580 *Betula*> *Quercus*> *Carpinus betulus*> *Populus*> *Juniperus*> *Corylus avellana*> *Castanea sativa*> *Sambucus nigra*-t.> *Ulmus*>
581 *Tilia*> *Salix*> *Fraxinus*> Poaceae (=1)> *Acer*> *Pistacia* (M)> *Phillyrea* (M)> *Carpinus orientalis* (M). All tree taxa have mean
582 RPPs larger than 1 except *Acer* (0.8), *Pistacia* (0.755), *Phillyrea* (0.512) and *Carpinus orientalis* (0.240). The ranking of RPPs
583 for 24 herb and low shrub taxa, from the largest (10.52) to the smallest (0.10), is as follows: *Urtica*> Chenopodiaceae> *Secale*>
584 *Artemisia*> Rubiaceae> *Rumex acetosa*-t.> *Filipendula*> *Plantago lanceolata*> *Trollius*> Ranunculaceae (M)> *Ranunculus*
585 *acris*-t.> Cerealit-t.> *Potentilla*-t.> *Plantago media*> *Calluna vulgaris*> Poaceae (=1)> Cyperaceae> *Plantago montana*>
586 Fabaceae (M)> Rosaceae (M)> Apiaceae> Compositae SF. Cichorioideae> *Empetrum*> *Leucanthemum* (*Anthemis*)-t.. Only
587 six herb taxa have RPPs larger than 3, while 12 tree taxa have RPP > than 3.
588 The two studies in the Mediterranean area provide single RPP values for 16 taxa, five herb taxa (Poaceae included) and 11 tree
589 taxa of which six are sub-Mediterranean and/or Mediterranean, and three include both temperate and Mediterranean taxa
590 (Cupressaceae, Ericaceae, *Fraxinus*) (Table B2). The RPP of herb taxa are significantly different between the study of
591 Grindean et al. (2019) and our synthesis, except for *Artemisia* (5.89 and 3, 94, respectively). The RPP of *Corylus avellana*
592 from the study of Mazier et al. (unpublished) (3.44) is double as large as the mean RPP in our synthesis (1.71), and the mean
593 RPP of *Quercus* (deciduous species) in our synthesis (4.54) is four times as large as the RPP from the study of Grindean et al.
594 (2019) (1.10).
595



596 **Table A1: New synthesis of European RPPs: mean RPPs with their SDs in brackets, and mean RPPs from the**
597 **syntheses by Mazier et al. (2012) (St2 values) and Wieczorek and Herzschuh (2020), for comparison. This synthesis:**
598 **values in bold are new mean RPPs compared to Mazier et al. (2012). The RPP values from studies in the**
599 **Mediterranean area are indicated with “M” in the second column. The values emphasized in grey are the mean RPPs**
600 **used in the new REVEALS reconstruction for Europe (this paper). The values of fall speed of pollen (FSP) are from**
601 **Mazier et al. (2012) except those in italic, i.e. FSPs for *Chenopodiaceae*, *Urtica* and *Sambucus nigra*-t. (Abraham and**
602 **Kozáková, 2012), and *Populus* (Wieczorek and Herzschuh, 2020) and the new FSPs for Mediterranean taxa. For the**
603 **three syntheses, the number of selected RPP values (n) included in the calculation of the mean RPP estimate is**
604 **indicated with the total number of available RPP values (tn) in brackets. The reason why the number of selected**
605 **RPP values (n) for Poaceae is larger than the total number of RPP (tn) is provided in section A1. For explanation of**
606 **symbols, see captions below.**

607
608 * Separate mean RPP values for *Calluna vulgaris*, *Empetrum*, and Ericaceae (*Calluna* and *Empetrum* excluded) in this
609 synthesis, a single mean RPP values for all Ericales in Wieczorek and Herzschuh (2020)

610 ** Separate mean RPP values for Cerealia type (*Secale* excluded) and *Secale* in this synthesis, a single mean RPP for all cereals
611 in Wieczorek and Herzschuh (2020)

612 *** Separate mean RPP values for Compositae SF Cichorioidae and *Leucanthemum* (*Anthemis*) type in this synthesis, a single
613 mean RPP for all Asteraceae in Wieczorek and Herzschuh (2020). Note that there are no RPP for Asteraceae (Compositae SF
614 Cichorioidae and *Leucanthemum* (*Anthemis*) type excluded) in our synthesis

615 ^ Separate mean RPP values for *Filipendula* and *Potentilla* type in this synthesis, a single mean RPP for all Rosaceae in
616 Wieczorek and Herzschuh (2020); note that there are no RPP for Rosaceae (*Filipendula* and *Potentilla*-t. excluded) in our
617 synthesis; moreover *Filipendula* and *Potentilla*-t. are classified as herbs, while Rosaceae is classified as tree in Wieczorek and
618 Herzschuh (2020)

619 ^^ Separate mean RPP values for *Plantago lanceolata*, *P. media* and *P. montana* in this synthesis, a single mean RPP for all
620 Plantaginaceae in Wieczorek and Herzschuh (2020); note that there are no RPP for Plantaginaceae (*Plantago lanceolata*, *P.*
621 *media* and *P. montana* excluded) in our synthesis

622 ^^ Separate mean RPP values for *Ranunculus acris* type and *Trollius* in this synthesis, a single mean RPP for all
623 Ranunculaceae in Wieczorek and Herzschuh (2020); note that there are no RPP for Ranunculaceae (*Ranunculus acris*-t and
624 *Trollius* excluded) in our synthesis.



Study n (tn), FSP, RPP	This paper, synthesis			Mazier et al. 2012 St 3		Wieczorek & Herzs Schuh 2020 Europe version 2			Notes
	n (tn)	FSP	RPP (SE)	n (tn)	RPP (SE)	n(tn)	RPP (SE)		
HERB TAXA									
Poaceae (Reference taxon)	16(15)	0.035	1.00 (0.00)	9(8)	1.00 (0.00)	14(12)	1.00 (0.00)		
Herb taxa									
Amaranthaceae/Chenopodiaceae	1(1)	0.019	4.280 (0.270)	none	none	1(1)	<u>4.28 (0.27)</u>	Same value as in this synthesis	
Apiaceae	1(1)	0.042	0.260 (0.010)	1(1)	0.26 (0.01)	3(3)	2.13 (0.41)		
Apiaceae	M 1(1)	0.042	5.910 (1.230)						
<i>Artemisia</i>	3(3)	0.025	3.937 (0.146)	1(1)	3.48 (0.20)	2(2)	4.33 (1.59)		
<i>Artemisia</i>	M 1(1)	0.014	5.890 (3.160)						
Asteraceae <i>Leucanth. (Anthemis) -t***</i>	1(1)	0.029	0.100 (0.010)	1(1)	0.10 (0.01)			see Asteraceae all***	
Asteraceae Cichorioideae***	3(3)	0.051	0.160 (0.020)	3(3)	0.16 (0.02)	8(10)	0.22 (0.02)	Asteraceae all***	
Asteraceae Cichorioideae	M 1(1)	0.061	1.162 (0.075)						
Asteraceae (Asteroideae + Cichorioideae)	M 1(1)	0.029	0.160 (0.100)						
<i>Calluna vulgaris*</i>	2(4)	0.038	1.085 (0.029)	2(4)	1.09 (0.03)			see Ericales all*	
Cerealia-t**	3(7)	0.060	1.850 (0.380)	2(4)	1.18 (0.04)	4(6)	2.36 (0.42)	Cereals all**	
Cerealia-t (<i>Triticum t., Secale, Zea</i>)	M 1(1)	0.060	0.220 (0.120)						
Cyperaceae	4(6)	0.035	0.962 (0.050)	4(6)	0.83 (0.04)	6(8)	0.56 (0.02)		
<i>Empetrum*</i>	1(2)	0.038	0.110 (0.030)	1(2)	0.11 (0.03)			see Ericales all*	
Ericaceae*	1(1)	0.038	0.070 (0.040)	1(1)	0.07 (0.04)	7(9)	0.44 (0.02)	Ericales all*	
Fabaceae	M 1(1)	0.021	0.400 (0.070)						
<i>Filipendula^</i>	3(3)	0.006	3.000 (0.285)	2(3)	2.81 (0.43)	4(6)	0.97 (0.11)	Rosaceae all ^	
<i>Plantago lanceolata^^</i>	4(6)	0.029	2.330 (0.201)	3(4)	1.04 (0.09)	8(10)	2.49 (0.11)	Plantaginaceae all^^	
<i>Plantago lanceolata</i>	M 1(1)	0.029	0.580 (0.320)						
<i>Plantago media^^</i>	1(1)	0.024	1.270 (0.180)	1(1)	1.27 (0.18)			see Plantaginaceae all^^	
<i>Plantago montana^^</i>	1(1)	0.030	0.740 (0.130)	1(1)	0.74 (0.13)			see Plantaginaceae all^^	
<i>Potentilla -t^</i>	2(3)	0.018	1.720 (0.200)	2(3)	1.72 (0.20)			see Rosaceae all^	
Ranunculaceae	M 1(1)	0.020	2.038 (0.335)						
<i>Ranunculus acris -t^^^</i>	2(2)	0.014	1.960 (0.360)	2(2)	1.96 (0.36)	3(5)	0.99 (0.12)	Ranunculaceae all^^^	
Rosaceae (Filipend., Pot. t., Sanguisorba)	M 1(1)	0.018	0.290 (0.120)						
Rubiaceae	2(3)	0.019	3.710 (0.340)	2(3)	3.71 (0.34)	3(5)	1.56 (0.12)		
Rubiaceae	M 1(1)	0.019	0.400 (0.070)						
<i>Rumex acetosa -t</i>	3(4)	0.018	3.020 (0.278)	3(3)	0.85 (0.05)	3(4)	0.58 (0.03)		
<i>Secale **</i>	3(3)	0.060	3.990 (0.320)	1(1)	3.02 (0.05)			see Cereals all**	
<i>Trollius ^^</i>	1(1)	0.013	2.290 (0.360)	1(1)	2.29 (0.36)			see Ranunculaceae all^^^	
<i>Urtica</i>	1(1)	0.007	10.520 (0.310)	none	none	1(1)	<u>10.52 (0.31)</u>	Same value as in this synthesis	
TREE TAXA									
<i>Abies alba</i>	2(2)	0.120	6.875 (1.442)	2(2)	6.88 (1.44)	2(2)	<u>6.88 (1.44)</u>	Same value as in this synthesis	
<i>Acer</i>	2(2)	0.056	0.800 (0.230)	2(2)	0.80 (0.23)	3(3)	0.23 (0.04)		
<i>Acer</i>	M 1(1)	0.056	0.300 (0.090)						
<i>Alnus</i>	5(7)	0.021	13.562 (0.293)	3(3)	9.07 (0.10)	4(6)	8.49 (0.22)		
<i>Betula</i> (mainly <i>B. pubescens</i> , <i>B. pendula</i>)	7(9)	0.024	5.106 (0.303)	6(6)	3.99 (0.17)	6(8)	4.94 (0.44)		
<i>Buxus sempervirens</i>	M 1(1)	0.032	1.890 (0.068)						
<i>Carpinus betulus</i>	2(4)	0.042	4.520 (0.425)	2(2)	3.55 (0.43)	3(5)	3.09 (0.28)		
<i>Carpinus orientalis</i>	M 1(1)	0.042	0.240 (0.070)						
<i>Castanea sativa</i>	M 1(1)	0.010	3.258 (0.059)						
<i>Corylus avellana</i>	4(4)	0.025	1.710 (0.100)	3(3)	1.99 (0.20)	3(4)	1.05 (0.33)		
<i>Corylus avellana</i>	M 1(1)	0.025	3.440 (0.890)						
Cupressaceae (<i>Juniperus</i> 3 species)	M 1(1)	0.020	1.618 (0.161)					See <i>Juniperus</i>	
Ericaceae (<i>Arbutus unedo</i> , <i>Erica</i> 3 species)	M 1(1)	0.051	4.265 (0.094)						
<i>Fagus sylvatica</i>	3(6)	0.057	5.863 (0.176)	4(4)	3.43 (0.09)	3(3)	2.35 (0.11)		
<i>Fraxinus excelsior</i>	5(6)	0.022	1.044 (0.048)	3(3)	1.03 (0.11)	5(5)	2.97 (0.25)		
<i>Fraxinus</i> (<i>F. excelsior</i> , <i>F. ornus</i>)	M 1(1)	0.022	2.990 (0.880)						
<i>Juniperus communis</i>	1(2)	0.016	2.070 (0.040)	1(2)	2.07 (0.04)	1(1)	7.94 (1.28)		
<i>Phillyrea</i>	M 1(1)	0.015	0.512 (0.076)						
<i>Pistacia</i>	M 1(1)	0.030	0.755 (0.201)						
<i>Picea abies</i>	4(8)	0.056	5.437 (0.097)	4(6)	2.62 (0.12)	4(6)	1.65 (0.15)		
<i>Pinus</i> (mainly <i>P. sylvestris</i>)	6(9)	0.031	6.058 (0.237)	3(5)	6.38 (0.45)	4(6)	10.86 (0.80)		
<i>Populus</i>	1(1)	0.025	2.660 (1.250)	none	none	1(1)	3.42 (1.60)		
<i>Quercus</i> (mainly <i>Q. robur</i> , <i>Q. petraea</i>)	6(8)	0.035	4.537 (0.086)	4(4)	5.83 (0.15)	5(7)	2.42 (0.10)		
<i>Quercus</i> deciduous (mainly <i>Q. peduncul.</i>)	M 1(1)	0.035	1.100 (0.350)						
<i>Quercus</i> evergreen (<i>Q. ilex</i> , <i>Q. coccifera</i>)	M 1(1)	0.015	11.043 (0.261)						
<i>Salix</i>	5(5)	0.022	1.182 (0.077)	3(4)	1.79 (0.16)	3(4)	0.39 (0.06)		
<i>Sambucus nigra -t</i>	1(1)	0.013	1.300 (0.120)	none	none	1(1)	<u>1.30 (0.12)</u>	Same value as in this synthesis	
<i>Tilia</i>	4(5)	0.032	1.210 (0.116)	1(1)	0.80 (0.03)	3(4)	0.93 (0.09)		
<i>Ulmus</i>	1(2)	0.032	1.270 (0.050)	1(1)	1.27 (0.05)	none			



626 A.2 Comparison of the new synthesis with two earlier syntheses (Table A1)

627 Of the 39 plant taxa for which we have a mean RPP in our new synthesis (N), 21 have a new mean RPP value compared to the
628 earlier synthesis of Mazier et al. (2012) (M), 18 taxa have the same mean RPPs in both syntheses. There are three new taxa for
629 which there were no RPP in M, i.e. Chenopodiaceae, *Sambucus nigra*-t. and *Urtica*. The mean RPPs are comparable between
630 the two syntheses N and M, except for *Plantago lanceolata* (2.33 in N/1.04 in M), *Alnus* (13.56/9.07), *Betula* (5.11/3.09),
631 *Carpinus betulus* (4.52/3.55), *Fagus* (5.86/3.43), *Picea* (5.44/2.62) and *Quercus* (4.54/5.83). *Abies alba* has the same RPP in
632 all three syntheses. Chenopodiaceae, *Sambucus nigra*-t. and *Urtica* have the same single RPP values in the synthesis of
633 Wieczorek and Herzsuh (2020) (W&H) and N. N and W&H also have comparable mean RPP values for *Artemisia*, Cereals
634 (Cereals, *Secale* excluded in N, all Cereals in W&H), Compositae (SF Cichorioideae in N, all Asteraceae in W&H), Cyperaceae,
635 *Plantago* (*P. lanceolata* in N, all Plantaginaceae in W&H), *Betula*, *Corylus*, *Populus* and *Tilia*. There are relatively large
636 differences in mean RPPs in W&H and N for 16 plant taxa, although the ranking of the plant taxa in terms of their mean RPPs
637 is almost the same. Mean RPP is larger in W&H than in N for Apiaceae (2.13/0.26), Ericales (0.44 in W&H) – *Empetrum*
638 (0.11) and Ericaceae (0.07) in N, *Fraxinus* (2.97/1.04), *Juniperus* (7.94/2.07), *Pinus* (10.86/6.06). Mean RPP is smaller in
639 W&H than in N for *Filipendula* (0.97/3.00), Rubiaceae (1.56/3.71), *Rumex acetosa* (0.58/2.02), *Acer* (0.23/0.80), *Alnus*
640 (8.49/13.56), *Carpinus* (3.09/4.52), *Fagus* (2.35/5.86), *Picea* (1.65/5.44), *Quercus* (2.42/4.54) and *Salix* (0.39/1.18).
641 The larger differences between the mean RPPs in N and W&H than between N and M have not been examined in detail. It is
642 due to a slightly different selection of studies, i.e. the study of Theuerkauf et al. (2013) is not included in W & H and we did
643 not include in N (boreal and temperate Europe, Mediterranean area excluded) the studies of Bunting et al. (2013), Kuneš et al.
644 (2019) and Grindean et al. (2019). Another important influencing factor is the selection of RPP values for calculation of the
645 mean RPP. Although the rules used to select RPP values are very similar between the syntheses, there are obvious differences
646 between N and W&H that are sometimes very significant (e.g. *Juniperus*).

647 A.3 Comparison of the new synthesis with three additional individual studies (Table A2)

648 The RPPs from Twiddle et al. (2012) (T) for *Pinus*, *Betula* and *Calluna* are considerably larger than the mean RPPs in our
649 synthesis (N). This is probably due to the assumption made on the RPP of *Picea* related to Poaceae. The RPP of *Picea* varies
650 greatly between the selected studies in N, from 0.57 to 8.43 (eight values available). If we assumed that the RPP of *Picea*
651 related to Poaceae in the study region of T was the mean RPP of the five smallest RPPs, i.e. 1.57, the RPP of the three taxa
652 would be 4.8 for *Pinus*, 3.4 for *Betula*, and 3.3 for *Calluna*, which is more comparable to the mean RPPs in N.
653 Three taxa in Bunting et al. (2013) (B) have a RPP comparable to the mean RPP in N, i.e. for Cyperaceae, *Ranunculus acris*-
654 t., and *Rumex acetosa*-t. (*R. acetosa* in B). The other taxa have a RPP in B smaller than the mean RPP in N, except *Plantago*
655 *maritima* that has a larger RPP (5.8) in B than the mean RPP for *P. lanceolata* in N.
656 Of nine taxa, three have a RPP in Kuneš et al. (2019) (K) that is comparable to the mean RPP in N, i.e. for *Plantago lanceolata*,
657 *Ranunculus acris*-t. and *Rumex acetosa*-t.. The other six taxa have a RPP larger than the mean RPP in N (Compositae SF



658 Cichorioideae, Cyperaceae and *Leucanthemum* (*Anthemis*)-t., or smaller (Chenopodiaceae, Rubiaceae) to considerably smaller
659 (*Urtica*). Of the 14 tree taxa, only four have a RPP in K comparable to the mean RPP in N, i.e. for *Corylus*, *Fraxinus*, *Salix*,
660 and *Ulmus*. For the other 10 tree taxa, the RPP in K is much smaller than the mean RPP in N for *Abies alba*, *Alnus*, *Carpinus*,
661 *Fagus*, *Picea*, *Pinus*, smaller for *Quercus*, and larger for *Acer* and *Tilia*.

662 Most of the RPP values of the three studies T, B and K are in the range of the values selected from the studies included in our
663 synthesis (N) except for *Urtica*, *Abies alba*, *Carpinus*, and *Pinus* in K. The Lagrangian Stochastic Model is used in K instead
664 of the Gaussian Plume Model in N, which may be one of the factors behind the lower RPPs in K, in particular (but not only)
665 for taxa with heavy pollen grains.

666



667 **Table A2: Comparison of the mean RPPs in this synthesis with the RPP estimates from Britain (Twiddle, 2012),**
 668 **Greenland (Bunting et al., 2013) and Czech Republic (Kuneš et al., 2019). Explanations for symbols in the taxa list, see**
 669 **caption below Table A4. + The original paper does not provide a RPP for Poaceae and values of standard deviations**
 670 **(SDs) for the RPPs. We extracted the RPP values related to *Picea* from Table 5 in Twiddle et al. (2012). RPPs related**
 671 **to Poaceae (1.00+) were then calculated by assuming that the RPP of *Picea* was equal to the mean RPP of *Picea* in**
 672 **Europe (this synthesis) (in bold). ++ The RPPs and their SDs are not listed in the original paper, we therefore read the**
 673 **values from Figure 4 (Bunting et al., 2013) and the decimals are approximate. +++ Kuneš et al. (2019): we chose the**
 674 **RPP values that were considered best by the authors, i.e. using the lake dataset (pollen from lake sediment), ERV sub-**
 675 **model 1 and the Lagrangian Stochastic Model (for details, see Discussion section, this paper). # value for *Plantago***
 676 ***maritima* and ## two values for *Rumex acetosa* and *Rumex acetosella*, respectively (Bunting et al., 2013), for comparison**
 677 **with *Plantago* spp. and *Rumex acetosa*-t. (this paper). Underlined RPPs are close to mean RPPs (this synthesis).**
 678

Study Information on analysis	This paper, synthesis RPP (SE)	Twiddle et al. (2012)+ RPP - ERV3 random GPM	Bunting et al. (2013)++ RPP (SE) - ERV1 GPM	Kunes et al (2019)+++ RPP (SE) - R ERV1 LSM
HERB TAXA				
Poaceae (Reference taxon)	1.000 (0.000)	1.00+	1.00 (0.00)	1.00 (0.00)
Herb taxa				
Amaranthaceae/Chenopodiaceae	4.280 (0.270)			1.58 (0.74)
<i>Calluna vulgaris</i> *	1.085 (0.029)	11.42		
Comp. <i>Leucanthemum (Anthemis)</i> -t***	0.10 (0.01)			0.94 (0.43)
Comp. SF. Cichorioideae***	0.160 (0.020)			1.04 (0.64)
Cyperaceae	0.962 (0.050)		<u>0.95 (0.05)</u>	2.10 (0.88)
<i>Plantago lanceolata</i> ^^	2.330 (0.201)		5.8 (0.3)#	<u>2.24 (0.71)</u>
<i>Potentilla</i> -t^	1.720 (0.200)		0.4 (0.03)	
<i>Ranunculus acris</i> -t^^^	1.960 (0.360)		<u>2.0 (0.1)</u>	<u>1.38 (1.13)</u>
Rubiaceae	3.710 (0.340)			1.03 (0.74)
<i>Rumex acetosa</i> -t	3.020 (0.278)		<u>3.5 (0.3)/ 2.0 (0.1)##</u>	<u>1.94 (1.35)</u>
<i>Urtica</i>	10.520 (0.310)			1.16 (0.52)
TREE TAXA				
<i>Abies alba</i>	6.875 (1.442)			1.08 (0.99)
<i>Acer</i>	0.800 (0.230)			<u>1.25 (0.75)</u>
<i>Alnus</i>	13.562 (0.293)			2.44 (0.73)
<i>Betula</i> (mainly <i>B. pubescens</i> , <i>B. pendula</i>)	5.106 (0.303)	13.16	3.75 (0.4)	2.53 (0.91)
<i>Carpinus betulus</i>	4.520 (0.425)			1.36 (0.36)
<i>Corylus avellana</i>	1.710 (0.100)			<u>2.31 (1.13)</u>
<i>Fagus sylvatica</i>	5.863 (0.176)			0.88 (0.25)
<i>Fraxinus excelsior</i>	1.044 (0.048)			<u>0.79 (0.37)</u>
<i>Picea abies</i>	5.437 (0.097)	5.44		2.39 (0.93)
<i>Pinus</i> (mainly <i>P. sylvestris</i>)	6.058 (0.237)	16.32		1.55 (0.44)
<i>Quercus</i> (mainly <i>Q. robur</i> , <i>Q. petraea</i>)	4.537 (0.086)			2.08 (0.46)
<i>Salix</i>	1.182 (0.077)		0.7 (0.03)	<u>1.43 (0.62)</u>
<i>Tilia</i>	1.210 (0.116)			2.30 (1.24)
<i>Ulmus</i>	1.270 (0.050)			<u>0.96 (0.77)</u>

679



680 **Appendix B - Selection of RPP values and calculation of the mean RPPs and their SDs**

681 **B.1 Methods**

682 Tables B1 (Boreal and Temperate Europe) and B2 (Mediterranean Europe) list the RPP values from the 16 selected studies
683 according to the information on models used provided in Appendix C (Table C1) with further explanations on selection of
684 RPP studies. We followed similar procedures and rules as Mazier et al. (2012) and Li et al. (2018) to produce a new standard
685 RPP dataset for Europe. We consider that there are still too few RPP values per taxon to disentangle variability in the RPP
686 values for a particular taxon due to methodological issues, landscape characteristics, land use, or climate. We therefore use the
687 mean of selected RPP values for each taxon in the new standard RPP dataset, following Broström et al. (2008) and Mazier et
688 al. (2012). In boreal and temperate Europe, the number of RPP values per taxon varies between one and nine (*Betula*) (Table
689 B1), and in Mediterranean Europe, there is only one value per taxon (Table B2). In general, all three sub-models of the ERV
690 model were used in the RPP studies. We selected the RPP values obtained with the ERV sub-model considered by the authors
691 to have provided the best results (following the approach of Li et al., 2018). This is usually evaluated by the shape of the curve
692 of likelihood function scores (LFS), or log likelihood (LL) (see e.g. Twiddle et al., 2012) and the LFS and LL values
693 themselves. All RPPs selected for this synthesis are expressed relative to Poaceae (RPP=1). In studies that used another
694 reference taxon and calculated a RPP for Poaceae, the RPPs were recalculated relative to Poaceae. In studies that did not
695 include a RPP value for Poaceae, it was assumed that the reference taxon had a RPP related to Poaceae equal to the mean of
696 the RPP values for that taxon in the other studies (e.g. Mazier et al., 2012). For simplicity, we used the value of *Quercus* (5.83)
697 calculated by Mazier et al. (2012) for the study by Bunting et al. (2005) (*Quercus* as reference taxon, no RPP value for
698 Poaceae). We could also have used the new mean RPP for *Quercus* (4.54) using our selected RPPs (five values, instead of
699 three in Mazier et al. (2012)). The latter would not have changed our results significantly; the mean RPP for *Quercus* would
700 have been 4.28 instead of 4.54 (Table A4). For the study by Baker et al. (2016), we used the RPP values obtained with Poaceae
701 as the reference taxon, given that the RPPs relative to *Quercus* or *Pinus* were almost identical when ERV submodel 3 was
702 used. The selection of RPP values in boreal and temperate Europe for the calculation of the mean RPP values of each taxon
703 (values emphasized in green in Table S1.2, A and B) is based on the following rules:

- 704 1. We excluded the RPP values that were not significantly different from zero considering the lower bound of its SE,
705 and values that were considered as uncertain by the authors of the original publications (e.g., *Vaccinium* for Finland
706 (Räsänen et al., 2007), *Pinus* for Central Sweden (von Stedingk et al., 2008)). Moreover, some RPP values were
707 excluded as they were assumed to be outliers or unreliable based on experts' knowledge on the plants involved, the
708 pollen-vegetation dataset, and the field characteristics of the related studies. For example, the RPPs for Cyperaceae,
709 *Potentilla-t* and Rubiaceae obtained in SW Norway (Hjelle, 1998) and those for *Salix* and *Calluna vulgaris* from
710 Central Sweden (von Stedingk et al., 2008) were assumed to be too low compared to the values obtained in other
711 study areas (Mazier et al., 2012).



712 2. (i) when five or more RPP estimates of pollen productivity ($N \geq 5$) were available for a pollen type, the largest and the
713 smallest RPP values (generally outlier values) were excluded, and the mean was calculated using the remaining three
714 or more RPP estimates; (ii) when $N=4$, the most deviating value was excluded, and the mean calculated using the
715 other three RPP values; (iii) when $N=3$, the mean was based on all values available except if one value was strongly
716 deviating from the other two; and (iv) when $N=2$, the mean was based on the two values available; an exception is
717 *Ulmus* for which we excluded the value from Germany (Theuerkauf et al. 2013) given that several of the RPPs in this
718 study are considerably higher than most values in the other available studies, i.e. for *Betula* (18.7), *Quercus* (17.85)
719 and *Tilia* (12.38). The latter values were also excluded from the mean RPP, as well as the unusually high values found
720 by Baker et al. (2016) for *Betula* (13.94), *Pinus* (23.12) and *Quercus* (18.47). Baker et al. (2016) argue that the high
721 RPP values might be characteristic of temperate deciduous forests that were little impacted by human activities. More
722 studies in this type of wooded environments would be needed to confirm this assumption. In the absence of such
723 studies we consider these values as outliers.

724 The SDs for the mean RPP values were calculated using the delta method (Stuart. and Ord., 1994), a mathematical solution to
725 the problem of calculating the mean of individual SDs (see e.g. Li et al. 2020 for more details).



726 **Table B1: Europe (Mediterranean area excluded): RPP estimates and their SDs (in brackets) with the total number of**
 727 **taxa per study indicated and in brackets the number of taxa with selected RPP estimates. (A) Studies using moss**
 728 **pollsters as pollen samples. (B) Studies using surface lake sediments as pollen samples. For explanation of symbols, see**
 729 **captions below Table B1 (B).**
 730 **(A)**

Type of pollen sample Region ERV submodel	Moss polsters							
	Finland ERV 3	C Sweden ERV 3	S Sweden# ERV 3	Norway ERV 1	England## ERV 1	Swiss Jura ERV 1	Czech Rep* ERV 1	Poland** ERV 3
HERB TAXA								
Poaceae (Reference taxon)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)
Amaranthaceae/Chenopodiaceae							4.28 (0.27)	
Apiaceae				0.26 (0.009)				
<i>Artemisia</i>							2.77 (0.39)	
<i>Calluna vulgaris</i>		0.30 (0.03)	4.70 (0.69)	1.07 (0.03)				
Cerealia-t			3.20 (1.14)				0.0462 (0.0018)	
Comp. <i>Leucanthemum (Anthemis)</i> -t				0.10 (0.008)				
Comp. SF. Cichorioideae			0.24 (0.06)	0.06 (0.004)				
Cyperaceae	0.002 (0.0022)	0.89 (0.03)	1.00 (0.16)	0.29 (0.01)		0.73 (0.08)		
<i>Empetrum</i>	0.07 (0.06)	0.11 (0.03)						
Ericaceae		0.07 (0.04)						
<i>Filipendula</i>			2.48 (0.82)	3.39 (0.00)				
<i>Plantago lanceolata</i>			12.76 (1.83)	1.99 (0.04)			3.70 (0.77)	
<i>Plantago media</i>						1.27 (0.18)		
<i>Plantago montana</i>						0.74 (0.13)		
<i>Potentilla</i> -t			2.47 (0.38)	0.14 (0.005)		0.96 (0.13)		
<i>Ranunculus acris</i> -t			3.85 (0.72)	0.07 (0.004)				
Rubiaceae			3.95 (0.59)	0.42 (0.01)		3.47 (0.35)		
<i>Rumex acetosa</i> -t			4.74 (0.83)	0.13 (0.004)				
<i>Secale</i>			3.02 (0.05)					
<i>Trollius</i>						2.29 (0.36)		
<i>Urtica</i>							10.52 (0.31)	
<i>Vaccinium</i>	0.01 (0.01)							
TREE TAXA								
<i>Abies</i>						3.83 (0.37)		
<i>Acer</i>			1.27 (0.45)			0.32 (0.10)		
<i>Alnus</i>			4.20 (0.14)		8.74 (0.35)		2.56 (0.32)	15.95 (0.6622)
<i>Betula</i>	4.6 (0.70)	2.24 (0.20)	8.87 (0.13)		6.18 (0.35)			13.94 (0.2293)
<i>Carpinus</i>			2.53 (0.07)					4.48 (0.0301)
<i>Corylus</i>			1.40 (0.04)		1.51 (0.06)			1.35 (0.0512)
<i>Fagus</i>			6.67 (0.17)			1.20 (0.16)		
<i>Fraxinus</i>			0.67 (0.03)		0.70 (0.06)		1.11 (0.09)	
<i>Juniperus</i>		0.11 (0.45)	2.07 (0.04)					
<i>Picea</i>		2.78 (0.21)	1.76 (0.00)			8.43 (0.30)		
<i>Pinus</i>	8.40 (1.34)	21.58 (2.87)	5.66 (0.00)				6.17 (0.41)	23.12 (0.2388)
<i>Quercus</i>			7.53 (0.08)		5.83 (0.00)##		1.76 (0.20)	18.47 (0.1032)
<i>Salix</i>		0.09 (0.03)	1.27 (0.31)		1.05 (0.17)		1.19 (0.12)	
<i>Sambucus nigra</i> -t							1.30 (0.12)	
<i>Tilia</i>			0.80 (0.03)				1.36 (0.26)	0.98 (0.0263)
<i>Ulmus</i>			1.27 (0.05)					
Total number of taxa 39 (38)	6 (4)	10 (7)	26 (25)	12 (8)	7 (7)	11(10)	13(12)	8 (5)

731
732



733 (B)

Type of pollen sample Region ERV submodel	lake surface sediment				
	Estonia ERV 3	Denmark ERV 1	Swiss Plateau	Germany*** ERV 3	Germany ****
HERB TAXA					
Poaceae (Reference taxon)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)
<i>Artemisia</i>	3.48 (0.20)				5.56 (0.020)
<i>Calluna vulgaris</i>		1.10 (0.05)	0.00076 (0.0019)		
Cerealia-t	1.60 (0.07)	0.75 (0.04)	0.17 (0.03)	9.00 (1.92)	0.08 (0.001)
Compositae <i>Leucanthemum (Anthemis)</i> -t			0.24 (0.15)		
Cyperaceae	1.23 (0.09)				
<i>Filipendula</i>	3.13 (0.24)				
<i>Plantago lanceolata</i>		0.90 (0.23)			2.73 (0.043)
<i>Rumex acetosa</i> -t		1.56 (0.09)			2.76 (0.022)
<i>Secale</i>				4.08 (0.96)	4.87 (0.006)
TREE TAXA					
			9.92 (2.86)		
<i>Alnus</i>	13.93 (0.15)		2.42 (0.39)	15.51 (1.25)	13.68 (0.049)
<i>Betula</i>	1.81 (0.02)		4.56 (0.85)	9.62 (1.92)	19.70 (0.117)
<i>Carpinus</i>			2.58 (0.39)	9.45 (0.51)	
<i>Corylus</i>			0.76 (0.17)		
<i>Fagus</i>		5.09 (0.22)	1.39 (0.21)	5.83 (0.45)	9.63 (0.008)
<i>Fraxinus</i>				6.74 (0.68)	1.35 (0.012)
<i>Juniperus</i>			0.57 (0.16)		
<i>Picea</i>	4.73 (0.13)	1.19 (0.42)	1.35 (0.45)	1.58 (0.28)	5.81 (0.007)
<i>Pinus</i>	5.07 (0.06)			5.66 (0.00)	5.39 (0.222)
<i>Populus</i>			2.56 (0.39)	2.66 (1.25)	
<i>Quercus</i>	7.39 (0.20)			2.15 (0.17)	17.85 (0.049)
<i>Salix</i>	2.31 (0.08)				
<i>Tilia</i>				1.47 (0.23)	12.38 (0.101)
<i>Ulmus</i>					11.51 (0.101)
Total number of taxa (selected values)	23 (22)	11 (11)	7 (7)	13 (9)	13 (10)
					15 (11)

734
 735 # RPPs for herbs from Broström et al. (2004); RPPs for trees from Sugita et al. (1999) (reference taxon *Juniperus*), converted
 736 to Poaceae as reference taxon by Broström et al. (2004).
 737 ## Bunting et al. (2005), reference taxon *Quercus* and no RPP for Poaceae; RPPs relative to Poaceae calculated by Mazier et
 738 al. (2012) assuming that the RPP of *Quercus* relative to Poaceae is the same as the mean RPP of *Quercus* from three other
 739 studies in NW Europe.
 740 * New RPPs from the Czech Republic (Abraham and Kozáková, 2012).
 741 ** New RPPs from Poland. Poaceae as reference taxa (see text for more details)
 742 *** New RPPs from Germany (Matthias et al., 2012), reference taxon *Pinus*. RPPs converted to Poaceae as reference
 743 taxon. We selected the RPP estimates obtained with the dataset of vegetation cover including only the trees that had reached
 744 their flowering age (allFIDage) (for more information, see Matthias et al., 2012).
 745 **** New RPPs from Germany (Theuerkauf et al., 2013); in the original publication, the ERV analysis was performed with
 746 the Lagrangian Stochastic Model (LSM) for dispersal of pollen and with *Pinus* as reference taxon. For this synthesis, Martin



747 Theuerkauf redid the analysis with the Gaussian Plume Model for dispersal of pollen (Parsons and Prentice, 1981; Prentice
748 and Parsons, 1983) and with Poaceae as reference taxon.

749 **Green:** selected RPP estimates to be included in the mean RPP values.

750 **Red:** RPP estimates excluded because $SE \geq RPP$.

751 **Orange:** RPP estimates excluded because of a too large difference with the other available estimates and their mean (less than
752 half or more than double the mean RPP).

753 **Light blue:** RPP estimates excluded due to its extreme high value compared to the other available estimates (much over double
754 the mean of the other RPPs), i.e. from the study at Bialowice forest (Poland, Baker et al., 2016) for *Betula*, *Pinus* and *Quercus*,
755 Central Sweden (von Stedingk et al., 2008) for *Pinus*, and Germany**** (Theuerkauf et al., 2013) for *Betula*, *Quercus*, *Tilia*,
756 and *Ulmus*.



757 **Table B2: Mediterranean area: RPP estimates and their SDs from two available studies, and mean RPPs for northern**
 758 **and temperate Europe (Table A1, Appendix A), for comparison. The single RPPs emphasized in green were used in the**
 759 **REVEALS reconstruction for Europe (this paper). The plant taxa emphasized in bold are sub-Mediterranean and/or**
 760 **Mediterranean plant species and genera. The values emphasized with grey shadow are the mean RPPs that were used**
 761 **in the REVEALS reconstruction (this paper) for entire Europe (Mediterranean area included). See Appendix B for**
 762 **more details. FSP values: from Mazier et al. (2012) except (') new values from Mazier et al. (unpubl.), (") value from**
 763 **Abraham and Kózáková (2012), (""') value from (Commerford et al., 2013). *, **FSP from Mazier et al. (2012) used in**
 764 **the REVEALS reconstruction (this study) for Ericaceae (Medit)* and Quercus evergreen** instead of the new FSP**
 765 **values from Mazier et al. (unpubl.); for more explanations, see Discussion section, this paper.**
 766

Region	France Medit. (ERV3)			Roumania (ERV3)			Europe, Medit. excluded		
Study reference	Mazier et al. (unpubl.)			Grindean et al. (2019)			This paper (Tables 2A, 2B)		
	RPP	SD	FSP	RPP	SD	FSP	RPP	SD	FSP
HERB TAXA									
Poaceae (reference taxon)	1.000	0.000	0.035	1.00	0.00	0.035	1.00	0.00	0.035
Apiaceae				5.91	1.23	0.042	0.26	0.01	0.042
<i>Artemisia</i>				5.89	3.16	0.014''	3.937	0.146	0.014''
Asteraceae (Asteroideae + Cichorioideae)				0.16	0.10	0.029			
Asteraceae Asteroidae (<i>Anthemis</i> t., <i>Leucanthemum</i>)							0.10	0.01	0.029
Asteraceae Cichorioideae	1.162	0.675	0.061'				0.16	0.02	0.05
Cerealia (Cerealia t. + <i>Triticum</i> t. + <i>Secale</i> + <i>Zea</i>)				0.22	0.12	0.060			
Cerealia (Cerealia t., <i>Secale</i> excluded)							1.85	0.38	0.060
Cerealia - <i>Secale cereale</i>							3.99	0.33	0.060
Fabaceae				0.40	0.07	0.021'''			
<i>Plantago lanceolata</i>				0.58	0.32	0.029	2.33	0.20	0.029
Ranunculaceae	2.038	0.335	0.020'						
Ranunculaceae - <i>Ranunculus acris</i> t.							1.96	0.36	0.014
Ranunculaceae - <i>Trollius</i>							2.29	0.36	0.013
Rosaceae (<i>Filipendula</i> , <i>Potentilla</i> t., <i>Sanguisorba</i>)				0.29	0.12	0.018			
Rosaceae - <i>Filipendula</i>							3.00	0.28	0.006
Rosaceae - <i>Potentilla</i> t.							1.72	0.20	0.018
Rubiaceae				0.40	0.07	0.019	3.71	0.34	0.019
TREE/SHRUB TAXA									
<i>Acer</i>				0.30	0.09	0.056	0.80	0.23	0.056
<i>Buxus sempervirens</i>	1.890	0.068	0.032'						
<i>Carpinus betulus</i>							4.52	0.43	0.042
<i>Carpinus orientalis</i>				0.24	0.07	0.042			
<i>Castanea sativa</i>	3.258	0.059	0.010'						
<i>Corylus avellana</i>	3.440	0.890	0.025				1.71	0.10	0.025
Cupressaceae (<i>Juniperus communis</i> , <i>J. phoenicea</i> , <i>J. oxycedrus</i>)	1.618	0.161	0.020'						
Cupressaceae - <i>Juniperus communis</i>							2.07	0.04	0.016
Ericaceae (<i>Arbutus unedo</i> , <i>Erica arborea</i> , <i>E. cinerea</i> , <i>E. multiflora</i>)	4.265	0.094	0.051'						
Ericaceae (<i>Vaccinium</i> dominant, <i>Calluna</i> excluded)							0.07	0.04	0.038*
<i>Fraxinus excelsior</i>							1.04	0.02	0.022
<i>Fraxinus</i> (<i>F. excelsior</i> , <i>F. ornus</i>)				2.99	0.88	0.022			
<i>Phillyrea</i>	0.512	0.076	0.015'						
<i>Pistacia</i>	0.755	0.201	0.030'						
<i>Quercus evergreen</i> (<i>Q. ilex</i>, <i>Q. coccifera</i>)	11.043	0.261	0.015'						
<i>Quercus</i> deciduous (<i>Q. spp.</i> , <i>Q. peduncularis</i> dominant)				1.10	0.35	0.035			
<i>Quercus</i> deciduous (<i>Q. petraea</i> + <i>Q. rubra</i>)							4.54	0.09	0.035**
Total number of taxa	11			13					

767



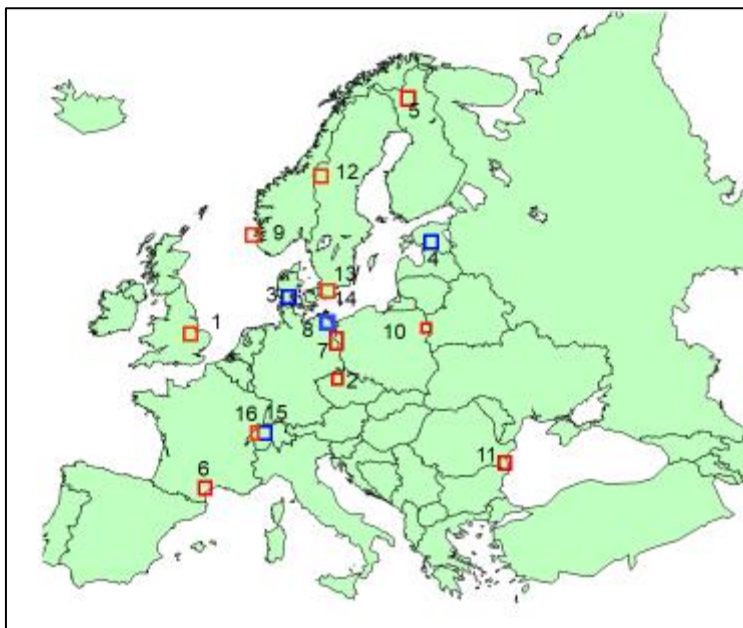
768 **Appendix C - Selection of RPP studies**

769 **C.1 Introduction**

770 The most common method to estimate RPPs involves the application of the Extended R-Value (ERV) model on datasets of
771 modern pollen assemblages and related vegetation cover. A summary of the ERV model and its assumptions, and an extensive
772 description of standardised field methods for the purpose of RPP studies are found in Bunting et al. (2013). Estimation of RPPs
773 in Europe started with the studies by Sugita et al. (1999) and Broström et al. (2004) in Southern Sweden, and Nielsen et al.
774 (2004) in Denmark. The first tests of the RPP in pollen-based reconstructions of plant cover using the LRA's REVEALS
775 (REgional VEgetation Abundance from Large Sites) model (Sugita, 2007a) were published by Soepboer et al. (2007) in
776 Switzerland and Hellman et al. (2008a and b) in South Sweden. Over the last 15 years, a large number of RPP studies have
777 been undertaken in Europe North of the Alps, but it is only recently that RPP studies were initiated in the Mediterranean area
778 (Grindean et al., 2019; Mazier et al., unpublished). Two earlier syntheses of RPPs in Europe were published by Broström et
779 al. (2008) and Mazier et al. (2012). From 2012 onwards, these RPP values have been used in numerous applications of the
780 LRA's two models REVEALS and LOVE (LOcal Vegetation Estimates) (Sugita, 2007a and b) to reconstruct regional and
781 local plant cover in Europe (Cui et al., 2013; Fyfe et al., 2013; Marquer et al., 2020; Mazier et al., 2015b; Nielsen et al., 2012;
782 Nielsen and Odgaard, 2010; Trondman et al., 2015). Recently, Wiczczonek and Herzschuh (2020) published a synthesis of the
783 RPPs available for the Northern Hemisphere; it includes new mean RPP values for Europe that were produced independently
784 from the synthesis we present here.

785 **C. 2 Selection of RPP studies and related information on methods used**

786 The synthesis of mean RPPs presented here was produced in 2018 and applied in REVEALS reconstructions 2018-2020. Of
787 nineteen RPP studies available (in July 2021), we selected fifteen published between 1998 and 2018 and one unpublished
788 study in 2018 (Grindean et al., 2019). The sixteen study regions are distributed in twelve European countries (Figure C1) and
789 detailed in Table C1. Three studies are not included in our synthesis: Britain (Twiddle et al., 2012) because of the absence of
790 Poaceae in the calculated RPPs, curves of likelihood function scores exhibiting departures from theoretically correct curves,
791 and doubts expressed by the authors on the reliability of the values; Greenland (Bunting et al., 2013) because this land area
792 was not included in the REVEALS reconstruction of Holocene plant cover in Europe presented in this paper; and Czech
793 Republic (Kuneš et al., 2019) because the study was not ready when we finalized our synthesis. However, we compare the
794 RPP values from these three studies with the mean RPP values in this synthesis (Appendix A, Table A2).
795 All studies used the ERV model to calculate RPPs, and all but one study used modern pollen assemblages and vegetation; only
796 Nielsen et al. (2004; Denmark) used historical pollen and vegetation data. Eleven studies used pollen assemblages from moss
797 pollsters, five studies from lake sediments. Grindean et al. (2019; Romania) also used some pollen assemblages from surface



798
799 **Figure C1: Location of the selected studies of relative pollen productivities (RPP) in Europe. 1. Britain**, (Bunting et al., 2005); **2.**
800 **Czech Republic**, (Abraham and Kozáková, 2012); **3. Denmark**, (Nielsen, 2004); **4. Estonia**, (Poska et al., 2011); **5. Finland**, (Räsänen et
801 al., 2007); **6. France**, Mazier et al. unpublished; **7. Germany**, (Matthias et al., 2012); **8. Germany**, (Theuerkauf et al., 2013); **9. Norway**,
802 (Hjelle, 1998); **10. Poland**, (Baker et al., 2016); **11. Romania**, (Grindean et al., 2019); **12. Sweden**, (von Stedingk et al., 2008); **13. Sweden**,
803 (Sugita et al., 1999); **14. Sweden**, (Broström et al., 2004); **15. Switzerland**, (Soepboer et al., 2007); **16. Switzerland**, (Mazier et al., 2008).
804

805 soil samples. All studies used distance-weighted vegetation except two, Hjelle et al. (1998; SW Norway) and Sugita et al.
806 (1999; S Sweden). The Gaussian Plume Model (GPM) was used for pollen dispersal and deposition to distance-weight
807 vegetation, i.e. the Prentice's bog model (Parsons and Prentice, 1981; Prentice and Parsons, 1983) in studies using pollen from
808 moss pollsters, and the Sugita's lake model (Sugita, 1993) in studies using pollen from lake sediments (see also caption of
809 Table C1). In the case of the study by Theuerkauf et al. (2013), the published RPP values were calculated using the Lagrangian
810 Stochastic Model. For the purpose of this synthesis, Theuerkauf recalculated the RPPs using the GPM bog model in the
811 application of the ERV model. The distribution of sites for collection of pollen samples and vegetation data within the study
812 regions is random or random stratified in seven of the eleven studies using moss pollsters; the five remaining studies used
813 selected sites (or systematic distribution). Studies using lake sediments normally result in a systematic site distribution.
814 Broström et al. (2005) and Twiddle et al. (2012) showed that random distribution of sites provided better estimates of "relevant
815 source area of pollen" (RSAP; *sensu* Sugita, 1994) and thus of RPPs, given that the reliable RPPs are those obtained at the
816 RSAP distance and beyond. Both studies indicated that systematic distribution of sites have the tendency to result in curves of
817 likelihood function scores that do not follow the theoretical behaviour, i.e. an increase of the scores with distance until the
818 values reach an asymptote. However, the difference in RPPs between systematic and random sampling is generally not very
819 large. Nonetheless, systematic sampling may lead to uncertainty in terms of reliability of RPPs and random distribution of



820 sites is recommended and has generally been used in studies using moss pollsters or soil samples published from 2008 and
 821 onwards.

822 **Table C1: Selection of studies for the synthesis of relative pollen productivity (RPP) estimates. Emphasized in bold:**
 823 **additional, new studies compared to the studies included in the synthesis of Mazier et al. (2012). For explanation of**
 824 **symbols, see captions below the Table.**

Country	Region	No sites	Site distrib.	Pollen sample ¹	ERV sub-model	Distance weighting model ²	Reference taxon	No taxa ³	Reference
Britain	East Anglian: Norfolk woodlands	(34 + 19) [^]	selected	M	1	GPM Prentice's bog	<i>Quercus</i> Poaceae**	6	Bunting et al. 2005
Czech Republic	Central Bohemia: agricultural landscape	54	stratified random	M	1	GPM Prentice's bog	Poaceae	13	Abraham & Kóžaková 2012
Denmark	Ancient agricultural landscape ⁺	30	selected	L ⁺⁺	1	GPM Sugita's lake	Poaceae	7	Nielsen et al. 2004
Estonia	Hemiboreal forest zone: mixed woodland - agricultural landscape	40	selected	L	3	GPM Sugita's lake	Poaceae	10	Poska et al. 2011
Finland	N Finland	24	stratified random	M	3	GPM Prentice's bog	Poaceae	6	Räsänen et al. 2007
France	Mediterranean region	23	random	M	3	GPM Prentice's bog	Poaceae	11	Mazier et al. unpubl.
Germany	Eastern Germany: Brandenburg, agricultural landscape	49	selected	L	3	GPM Sugita's lake	<i>Pinus</i> Poaceae*	16	Matthias et al. 2012
	NE Germany: agricultural landscape	27	selected	L	3	LSM GPM Sugita's Lake ²	<i>Pinus</i> Poaceae*	11 (15) ³	Theuerkauf et al. 2013
Norway	SW Norway: Hordaland and Sogn og Fjordane, mown or grazed grassland and heath	39	selected	M	1	None [#]	Poaceae	17	Hjelle 1998
Poland	NE Poland: Bialowieza Forest	18	stratified random	M	3	GPM Prentice's bog	Poaceae	8	Baker et al. 2016



Romania	SE Romania: Forest-steppe region	26	random	M & S	3	GPM Prentice's bog	Poaceae	13	Grindean et al. 2019
Sweden	West- Central Sweden: Forest-tundra ecotone	30	random	M	3	GPM Prentice's bog	Poaceae	10	von Stedingk et al. 2008
	S Sweden: ancient cultural landscapes	114	selected	M	3	None [#]	<i>Juniperus</i> Poaceae*	14 (17) ³	Sugita et al. 1999
	S Sweden: unfertilized mown or grazed grasslands	42	selected	M	3	GPM Prentice's bog	Poaceae	11	Broström et al. 2004
Switzerland	Lowland: agricultural landscape	20	selected	L	3	GPM Prentice's bog	Poaceae	13	Soepboer et al. 2007
	Jura Mountain: pasture woodlands	20	(stratified) random ^{^^}	M	1	GPM Prentice's bog	Poaceae	11	Mazier et al. 2008

825

826 ¹ L=lakes; M=moss pollsters; S=surface soil

827 ² Other distance-weighting models were used in most studies, including the Gaussian Plume Model (GPM), 1/d, 1/d²
 828 (d=distance) and the Lagrangian Stochastic Model (LSM). The GPM is used in both the model developed for bogs (Parsons
 829 and Prentice, 1981; Prentice and Parsons, 1983) and lakes (Sugita, 1993). For this RPP synthesis, we chose the results from
 830 the analyses using GPM rather than 1/d or 1/d². Note: In the study of Theuerkauf et al. (2013) the LSM was used. For this
 831 synthesis, Theuerkauf recalculated his RPPs using the lake model developed by Sugita (1993).

832 ³ Number of plant taxa for which RPP was estimated, including the reference taxon. Note: In the study by Theuerkauf et al.
 833 (2013) RPPs were estimated for 17 taxa using LSM. The RPPs were recalculated using the lake model (Sugita, 1993) for 15
 834 taxa (see note under ² above) for this synthesis. In the study of Sugita et al. (1999) RPPs were calculated for 14 trees and 3
 835 herbs. We used only the values for the 14 trees in this synthesis, following the syntheses by Broström et al. (2008) and Mazier
 836 et al. (2012).

837 [^] Britain: the study includes two areas (a and b) in which RPP estimates were calculated for different sets of taxa and the two
 838 areas have different numbers of sites: a. Calthorpe (34), 5 taxa; b. Wheatfen (17), same 5 taxa and *Corylus* (6 taxa in total).

839 ^{^^} random distribution restricted to areas of the study region with existing vegetation maps (therefore no sites outside these
 840 areas); i.e. study region including separate areas (Mazier et al., 2008).

841 ⁺ Vegetation data from historical maps around 1800 CE.

842 ⁺⁺ lake sediments dated to ca. 1800.

843 ^{*} The reference taxon used in the original study is different from Poaceae. For this synthesis the RPPs were converted to values
 844 relative to Poaceae.

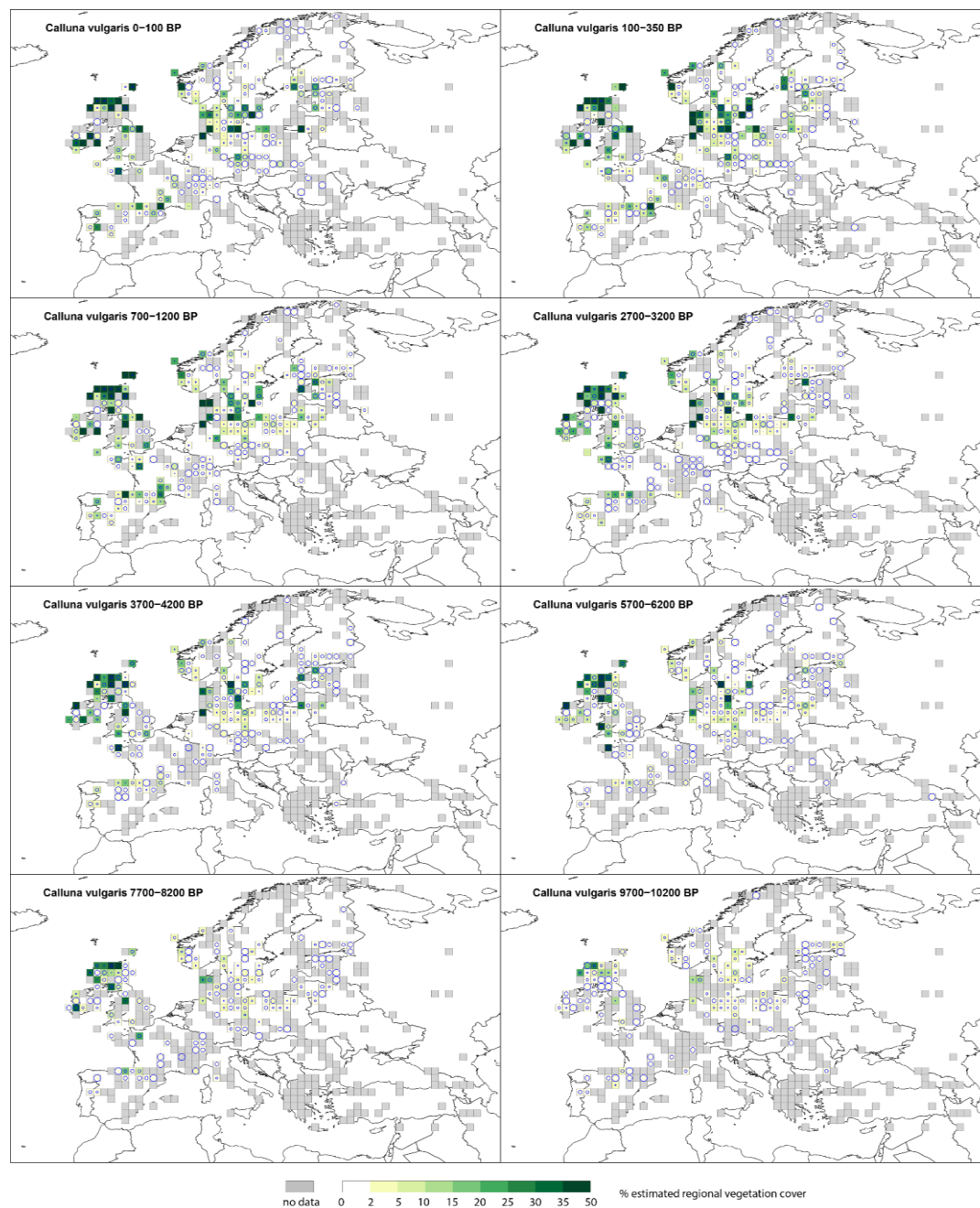


845 ** The study of Bunting et al. (2005) does not include a RPP for Poaceae. In order to calculate the RPPs relative to Poaceae,
846 it was assumed that the RPP of *Quercus* was equal to the mean of RPPs from three other studies in Europe (see Mazier et al.,
847 2012 for details). Although we have included new RPP values for *Quercus* in this synthesis, we did not recalculate the RPPs
848 from Bunting et al. (2005) with a new mean value for *Quercus*, but used the same values as in Mazier et al. (2012). For
849 comparison, the mean value for *Quercus* using the RPPs of the additional studies included in this synthesis is 4.28 (instead of
850 5.83 in Mazier et al., 2012). This would imply slightly lower RPPs in Britain also for *Alnus*, *Betula*, *Corylus*, *Fraxinus* and
851 *Salix*.

852 # no distance weighting used for vegetation data because there was no information about vegetation with increasing distance
853 from the pollen sample (Hjelle et al., 1998; Sugita et al., 1999). In the Swedish study, vegetation data within a 10² m² (herb
854 taxa) and 10³ m² quadrat (tree taxa) centred on the pollen sample was used (Sugita et al., 1999).

855 **Appendix D Maps of REVEALS cover for three plant taxa (*Calluna vulgaris*, *Quercus deciduous* and *Quercus***
856 **evergreen)**

857



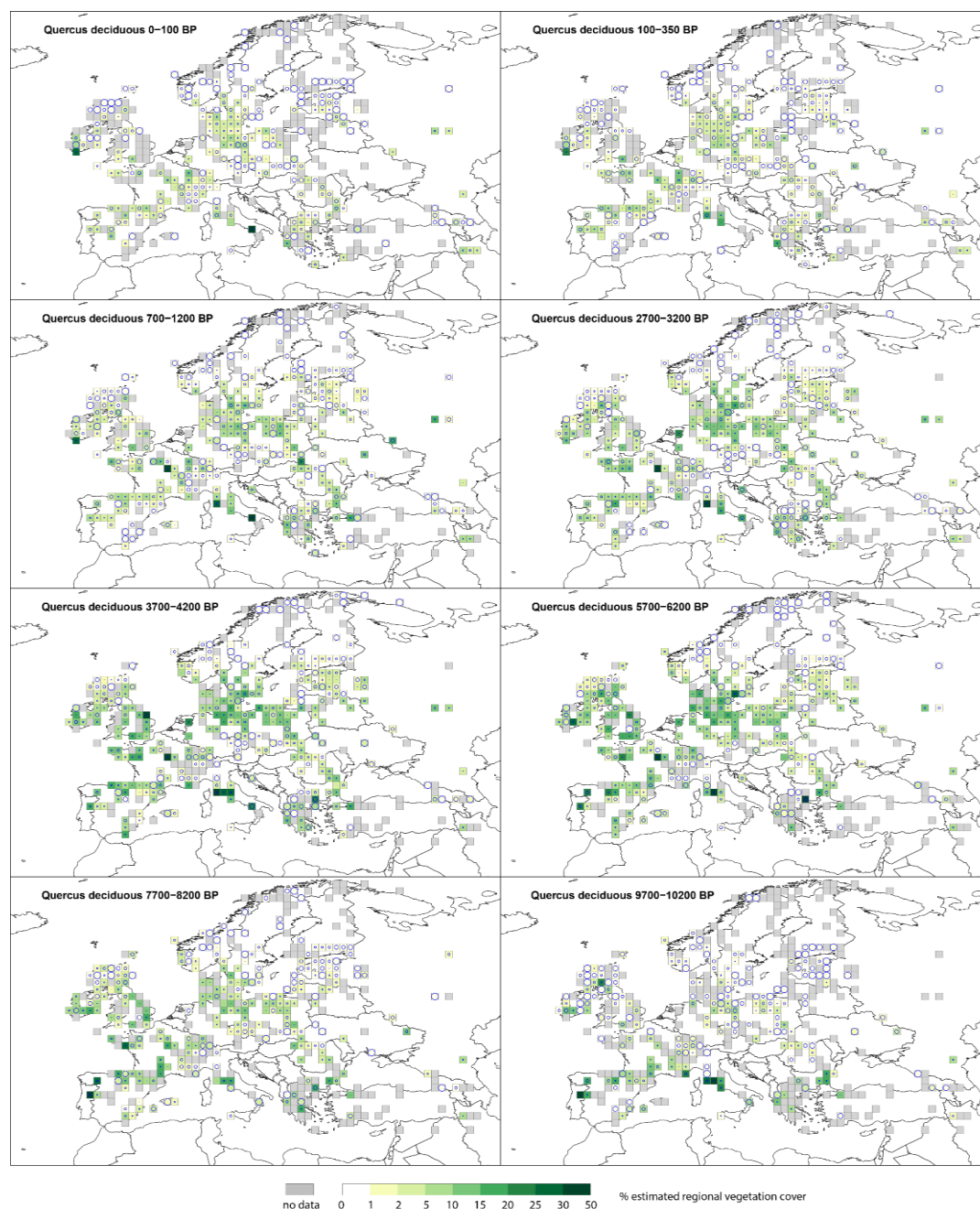
858

859 **Figure D1.** Grid-based REVEALS estimates of *Calluna vulgaris* cover for eight Holocene time windows. Percentage cover in 2%
860 interval between 0 and 2%, 3% interval between 2 and 5%, 5% intervals between 5 – 35% and 15% interval between 35 and 50%.
861 Grey grid cells have no data (pollen) for *Calluna vulgaris* in the mapped time window. The circles represent the coefficient of
862 variation (CV; the standard error divided by the REVEALS estimate). When $SE \geq$ REVEALS estimate, the circle fills the entire
863 grid cell and the REVEALS estimate is not different from zero. This occurs mainly where REVEALS estimates are low.

864

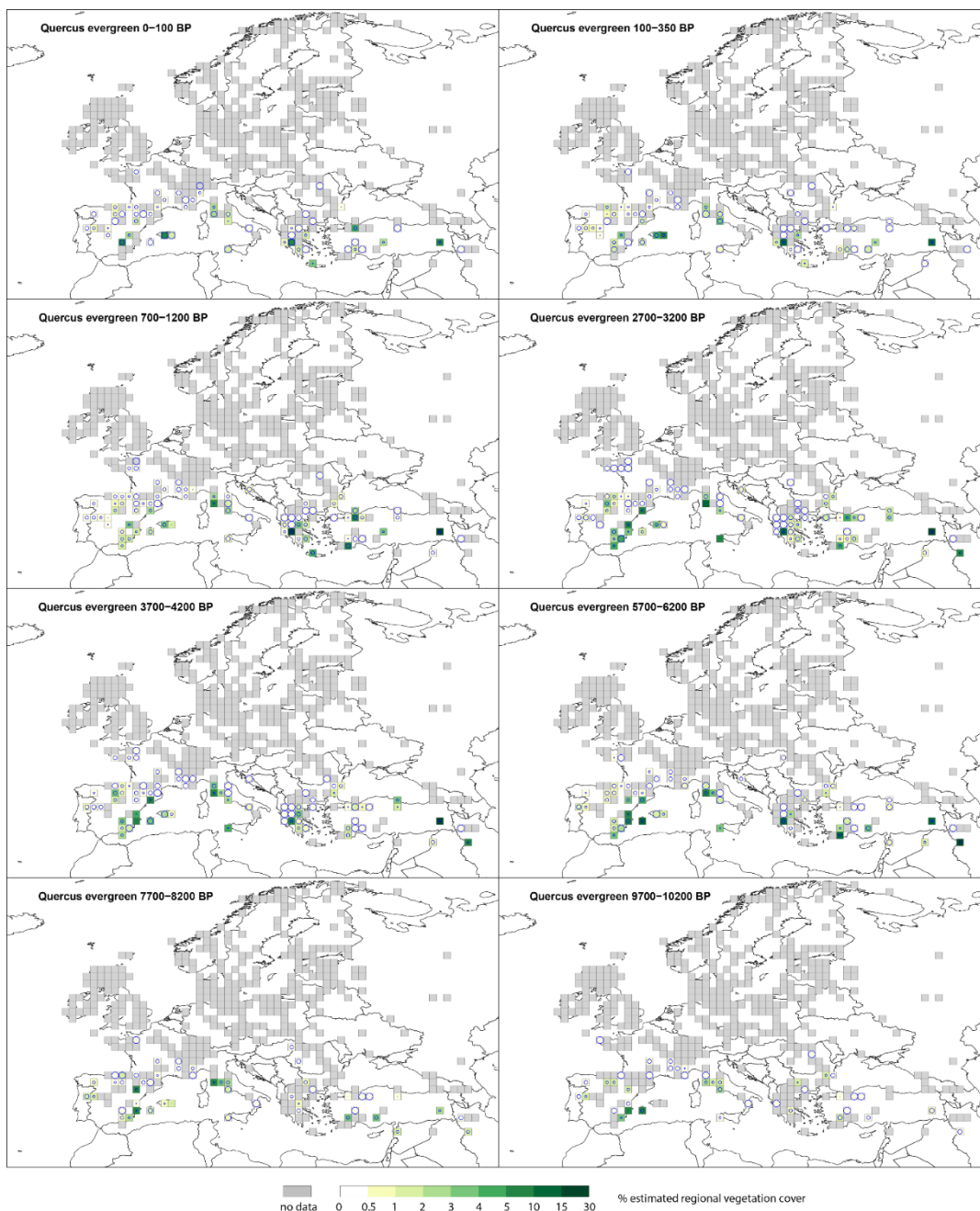


865



866
867
868
869

Figure D2. Grid-based REVEALS estimates of *Quercus* deciduous regional cover in eight Holocene time windows. Percentage cover in 1% interval between 0 and 2%, 3% interval between 2 and 5%, 5% intervals between 5 and 30% and 20% interval between 30 and 50%. See caption of Figure A1 for more explanations.



870
871
872
873

Figure D3. Grid-based REVEALS estimates of *Quercus* evergreen cover for eight Holocene time windows. Percentage cover in 0.5% intervals between 0 and 1%, 1% intervals between 1 and 5%, 5% intervals between 5 and 15 and 15% interval between 15 and 30%. See caption of Figure A1 for more explanations.



874 **+Team list**

875 Åkesson Christine (School of Geography & Sustainable Development, University of St. Andrews, UK), Balakauskas Lauras
876 (Department of Geology and Mineralogy, Vilnius University, Vilnius, Lithuania), Batalova Vlada (Lomonosov Moscow State
877 University, Department of Physical geography and Landscape science, Moscow, Russia), Birks H.J.B. (Department of
878 Biological Sciences and Bjerknes Centre for Climate Research, University of Bergen, Norway), Bjune Anne. E. (Department
879 of Biological Sciences and Bjerknes Centre for Climate Research, University of Bergen, Norway), Borisova Olga (Institute of
880 Geography, Russian Academy of Sciences, Moscow, Russia), Bozilova Elissaveta (Department of Botany, Sofia University
881 St. Kliment Ohridski, Sofia, Bulgaria), Burjachs Francesc (ICREA Barcelona, Catalonia, Spain; Rovira i Virgili University
882 (URV), Tarragona, Catalonia, Spain; Institut Català de Paleoecologia Humana i Evolució Social (IPHES), Campus Sescelades
883 URV, W3, 43007 Tarragona, Spain), Cheddadi Rachid (Institut des Sciences de l'Evolution de Montpellier, Université de
884 Montpellier, CNRS-UM-IRD, Montpellier, France), Christiansen Jörg (Department of Palynology and Climate Dynamics,
885 Georg-August University, Göttingen, Germany), David Remi (Archeosciences Laboratory, UMR 6566 CReAAH, CNRS,
886 Rennes1 University, Rennes, France), de Klerk Pim (State Museum of Natural History, Karlsruhe, Germany), Dirita Federico
887 (Dipartimento di Biologia Ambientale, Università di Roma "La Sapienza", Piazzale Aldo Moro, 5, 00185, Roma, Italia), Döfler
888 Walter (Institute für Ur- und Frühgeschichte, Christian-Albrechts University, Kiel, Germany), Doyen Elise (Laboratoire
889 Chrono-Environnement, Franche-Comté University, Besançon, France), Eastwood Warren (School of Geography, Earth and
890 Environmental Sciences, University of Birmingham B15 2TT, UK), Etienne David (Savoie Mont Blanc University, Chambéry,
891 France), Feeser Ingo (Institut für Ur- und Frühgeschichte, Christian-Albrechts University, Kiel, Germany), Filipova-Marinova
892 Mariana (Museum of Natural History, Varna, Bulgaria), Fischer E. (Institute für Ur- und Frühgeschichte, Christian-Albrechts
893 University, Kiel, Germany), Galop Didier (GEODE UMR 5602, Toulouse University, Toulouse, France), Garcia Jose
894 Sebastian Carrion (Departamento de Biología Vegetal, Facultad de Biología, Universidad de Murcia, 30100 Murcia, Spain),
895 Herking Christa (Institute of Botany and Landscape Ecology, EMAU, Greifswald, Germany), Herzsuh Ulrike (Alfred-
896 Wegener-Institut Potsdam, Germany), Jouffoy-Bapicot Isabelle (Laboratoire Chrono-Environnement, Franche-Comté
897 University, Besançon, France), Kasianova Alisa (Department of Palynology and Climate Dynamics, Georg-August-
898 University, Göttingen, Germany), Kouli Katerina (Department of Geology and Geoenvironment, National and Kapodistrian
899 University of Athens, Panepistimioupolis, 15784 Ilissia, Greece), Kuneš Petr (Department of Botany, Charles University,
900 Prague, Czech RepublicCzech), Lageras Per (The Archaeologists, National Historical Museums, Lund, Sweden), Latalowa
901 Malgorzata (Department of Plant Ecology, University of Gdansk, Poland), Lechterbeck Jutta (State Office for Cultural
902 Heritage Baden-Wuerttemberg, Germany), Leroyer Chantal (Archeosciences Laboratory, UMR 6566 CReAAH, CNRS,
903 Rennes1 University, Rennes, France), Leydet Michelle (European Pollen Database, IMBE, Aix-Marseille Université, Avignon
904 Université, IRD, Aix-en-Provence, France), Lisytsina Olga (Department of Postglacial Geology, Tallinn University of
905 Technology, Tallinn, Estonia), Lukanina Ekaterina (Department of Palynology and Climate Dynamics, Georg-August-



906 University, Göttingen, Germany), Magyari Enikő (Department of Environmental and Landscape Geography, Eötvös Loránd
907 University, Budapest, Hungary), Marguerie Dominique (Archeosciences Laboratory, UMR 6566 CReAAH, CNRS, Rennes I
908 University, Rennes, France), Mariotti Marta (Dipartimento di Biologia, Università di Firenze, Via G. La Pira, 4, 50121 Firenze,
909 Italy), Mensing Scott (Department of Geography, University of Nevada, Reno, NV 89557, USA), Mercuri Anna Maria
910 (Laboratorio di Palinologia e Paleobotanica, Dipartimento di Scienze della Vita, Università di Modena e Reggio Emilia, Italy),
911 Miebach Andrea (Steinmann Institute for Geology, Mineralogy, and Paleontology, University of Bonn, Bonn, Germany),
912 Mrotzek Almut (Institute of Botany and Landscape Ecology, EMAU ,Greifswald, Germany), Milburn Paula (College of
913 Science and Engineering, University of Edinburgh, Edinburgh, Scotland), Nosova Maria (Main Botanical Garden, Russian
914 Academy of Sciences, Moscow, Russia), Overballe-Petersen Mette (Forest & Landscape, Faculty of Life Sciences, University
915 of Copenhagen, Frederiksberg, Denmark), Panajiotidis Sampson (Aristotle University of Thessaloniki, Department of Forestry
916 and Natural Environment, PO Box: 270, GR54124 Thessaloniki, Greece), Pavlov Danail (Society of Innovative Ecologists of
917 Bulgaria, Varna, Bulgaria), Persson† Thomas (Department of Geology, Lund University, Lund, Sweden), Pinke Zsolt
918 (Department of Physical Geography, Eötvös Loránd University, Budapest, Hungary), Ruffaldi Pascale (Laboratoire Chrono-
919 Environnement, Franche-Comté University, Besançon, France), Sapelko Tatyana (Institute of Limnology, Russian Academy
920 of Sciences , St. Petersburg, Russia), Schult Manuela (Institute of Botany and Landscape Ecology, EMAU, Greifswald,
921 Germany), Schmidt Monika (Department of Palynology and Climate Dynamics, Georg-August-University, Göttingen,
922 Germany), Stancikaite Migle (Institute of Geology and Geography, Vilnius University, Vilnius, Lithuania), Stivrins Normunds
923 (Department of Geography, Faculty of Geography and Earth Sciences, University of Latvia, Jelgavas iela 1, Riga, 1004,
924 Latvia), Tarasov Pavel E. (Institute of Geological Sciences, Free University of Berlin, Germany), Tonkov Spassimir
925 (Department of Botany, Sofia University St. Kliment Ohridski, Sofia, Bulgaria), Veski Siim (Department of Geology, Tallinn
926 University of Technology, Tallinn, Estonia), Wick Lucia (IPNA, University of Basel, Basel, Switzerland), Wiethold Julian
927 (INRAP, Direction interrégionale Grand-Est Nord, Laboratoire archéobotanique, Metz, France), Woldring Henk (Groningen
928 Institute of Archaeology, University of Groningen, The Netherlands), Zernitskaya Valentina (Institute for Nature Management,
929 National Academy of Sciences of Belarus, Minsk, Republic of Belarus).

930 **Author Contribution**

931 MJG coordinated the study as part of LandClim II and PAGES LandCover6k, two research projects for which she is the overall
932 coordinator and administrator. MJG, AKT, EG, FM, RF, ABN, AP and SS conceptualised the study and methodology. SS
933 developed the REVEALS model and helped with all issues related to the application of the model and interpretation of results.
934 EG, AKT, RF, FM, ABN, and AP collected new pollen records from individual authors. JW provided part of the pollen records
935 from the Mediterranean area (collected earlier for a separate project). MS and ST provided unpublished pollen records. EG
936 and AKT had the major responsibility of handling the pollen data files and collecting all related metadata. AKT collected new
937 values of relative pollen productivity estimates (RPPs) in Europe. MT provided unpublished RPP values for Germany and FM



938 for the Mediterranean area. FM, JA, VL, LM, and NNC were all involved in the unpublished RPP study in southern France,
939 and AF, RG, ABN and IT performed the RPP study in Romania. MJG performed the selection of RPP values for the new RPP
940 synthesis used in this paper, EG made the calculations of mean RPPs, and MJG wrote Appendices A, B, and C, and prepared
941 the Figures and Tables therein. RF performed the REVEALS model runs and created Figure 1 and the maps of REVEALS-
942 based plant cover (Figures 2-6 and D1-D3). EG, RF and MJG designed the manuscript, EG prepared the first draft of the
943 manuscript and all Tables, and the final manuscript for submission, RF and MJG wrote parts of the text and edited the full
944 manuscript. All the co-authors were involved in commenting the manuscript.

945 **Competing interests**

946 The authors declare that they have no conflict of interest.

947 **Figures entirely compiled by the manuscript authors:** Since such figures are part of the manuscript, they will receive the
948 same distribution licence as the entire manuscript, namely a CC BY License. No citation is needed and no reproduction rights
949 must be obtained.



950 Acknowledgements

951 This study was funded by a research project financed by the Swedish Research Council VR (Vetenskapsrådet) on
952 “Quantification of the bio-geophysical and biogeochemical forcings from anthropogenic de-forestation on regional Holocene
953 climate in Europe, LandClim II”. Financial support from the Linnaeus University’s Faculty of Health and Life Science is
954 acknowledged for Marie-José Gaillard, Anna-Kari Trondman, and Esther Githumbi. This is a contribution to the strategic
955 research areas MERGE (ModELLing the Regional and Global Earth system) and the Past Global Change (PAGES) project and
956 its working group LandCover6k (<http://pastglobalchanges.org/landcover6k>), which in turn received support from the Swiss
957 National Science Foundation, the Swiss Academy of Sciences, the US National Science Foundation, and the Chinese Academy
958 of Sciences. Anneli Poska was supported by the ESF project number PRG323. We thank Sandy Harrison (University of
959 Reading, UK) for providing the pollen records from the EMBSecBIO project.

960 References

- 961 Abraham, V. and Kozáková, R.: Relative pollen productivity estimates in the modern agricultural landscape of Central
962 Bohemia (Czech Republic), *Rev. Palaeobot. Palynol.*, 179, 1–12, doi:10.1016/j.revpalbo.2012.04.004, 2012.
- 963 Abraham, V., Oušková, V. and Kuneš, P.: Present-Day Vegetation Helps Quantifying Past Land Cover in Selected Regions of
964 the Czech Republic, edited by B. Bond-Lamberty, *PLoS One*, 9(6), e100117, doi:10.1371/journal.pone.0100117, 2014.
- 965 Baker, A. G., Zimny, M., Keczyński, A., Bhagwat, S. A., Willis, K. J. and Latałowa, M.: Pollen productivity estimates from
966 old-growth forest strongly differ from those obtained in cultural landscapes: Evidence from the Białowieża National Park,
967 Poland, *The Holocene*, 26(1), 80–92, doi:10.1177/0959683615596822, 2016.
- 968 Barnosky, A. D., Hadly, E. A., Bascompte, J., Berlow, E. L., Brown, J. H., Fortelius, M., Getz, W. M., Harte, J., Hastings, A.,
969 Marquet, P. A., Martinez, N. D., Mooers, A., Roopnarine, P., Vermeij, G., Williams, J. W., Gillespie, R., Kitzes, J., Marshall,
970 C., Matzke, N., Mindell, D. P., Revilla, E. and Smith, A. B.: Approaching a state shift in Earth’s biosphere, *Nature*, 486(7401),
971 52–58, doi:10.1038/nature11018, 2012.
- 972 Beugh, H.-J.: *Leitfaden der Pollenbestimmung für Mitteleuropa und angrenzende Gebiete.*, 2004.
- 973 Broström, A., Sugita, S. and Gaillard, M.-J. J.: Pollen productivity estimates for the reconstruction of past vegetation cover in
974 the cultural landscape of southern Sweden, *The Holocene*, 14(3), 368–381, doi:10.1191/0959683604hl713rp, 2004.
- 975 Broström, A., Nielsen, A. B., Gaillard, M.-J., Hjelle, K., Mazier, F., Binney, H., Bunting, J., Fyfe, R., Meltsov, V., Poska, A.,
976 Räsänen, S., Soepboer, W., von Stedingk, H., Suutari, H. and Sugita, S.: Pollen productivity estimates of key European plant
977 taxa for quantitative reconstruction of past vegetation: a review, *Veg. Hist. Archaeobot.*, 17(5), 461–478, doi:10.1007/s00334-
978 008-0148-8, 2008.
- 979 Bunting, M. J., Armitage, R., Binney, H. A. and Waller, M.: Estimates of ‘relative pollen productivity’ and ‘relevant source
980 area of pollen’ for major tree taxa in two Norfolk (UK) woodlands, *The Holocene*, 15(3), 459–465,
981 doi:10.1191/0959683605hl821rr, 2005.



- 982 Bunting, M. J., Schofield, J. E. and Edwards, K. J.: Estimates of relative pollen productivity (RPP) for selected taxa from
983 southern Greenland: A pragmatic solution, *Rev. Palaeobot. Palynol.*, 190, 66–74, doi:10.1016/j.revpalbo.2012.11.003, 2013.
- 984 Commerford, J. L., McLauchlan, K. K. and Sugita, S.: Calibrating Vegetation Cover and Grassland Pollen Assemblages in the
985 Flint Hills of Kansas, USA, *Am. J. Plant Sci.*, 04(07), 1–10, doi:10.4236/ajps.2013.47A1001, 2013.
- 986 Cui, Q. Y., Gaillard, M. J., Lemdahl, G., Sugita, S., Greisman, A., Jacobson, G. L. and Olsson, F.: The role of tree composition
987 in Holocene fire history of the hemiboreal and southern boreal zones of southern Sweden, as revealed by the application of the
988 Landscape Reconstruction Algorithm: Implications for biodiversity and climate-change issues, *Holocene*, 23(12), 1747–1763,
989 doi:10.1177/0959683613505339, 2013.
- 990 Davis, B. A. S., Collins, P. M. and Kaplan, J. O.: The age and post-glacial development of the modern European vegetation: a
991 plant functional approach based on pollen data, *Veg. Hist. Archaeobot.*, 24(2), 303–317, doi:10.1007/s00334-014-0476-9,
992 2015.
- 993 Dickson, C.: Distinguishing cereal from wild grass pollen: some limitations, *Circaea*, 5, 67–71, 1988.
- 994 Downs, P. W. and Piégay, H.: Catchment-scale cumulative impact of human activities on river channels in the late
995 Anthropocene: implications, limitations, prospect, *Geomorphology*, 338, 88–104, doi:10.1016/j.geomorph.2019.03.021, 2019.
- 996 Edwards, K. J., Fyfe, R. and Jackson, S. T.: The first 100 years of pollen analysis, *Nat. Plants*, 3(2), 17001,
997 doi:10.1038/nplants.2017.1, 2017.
- 998 Ellis, E. C.: Ecology in an anthropogenic biosphere, *Ecol. Monogr.*, 85(3), 287–331, doi:10.1890/14-2274.1, 2015.
- 999 Foley, J. A.: Global Consequences of Land Use, *Science (80-.)*, 309(5734), 570–574, doi:10.1126/science.1111772, 2005.
- 1000 Fyfe, R., de Beaulieu, J.-L., Binney, H., Bradshaw, R. H. W., Brewer, S., Le Flao, A., Finsinger, W., Gaillard, M.-J., Giesecke,
1001 T., Gil-Romera, G., Grimm, E. C., Huntley, B., Kunes, P., Köhl, N., Leydet, M., Lotter, A. F., Tarasov, P. E. and Tonkov, S.:
1002 The European Pollen Database: past efforts and current activities, *Veg. Hist. Archaeobot.*, 18(5), 417–424,
1003 doi:10.1007/s00334-009-0215-9, 2009.
- 1004 Fyfe, R., Twiddle, C., Sugita, S., Gaillard, M. J., Barratt, P., Caseldine, C. J., Dodson, J., Edwards, K. J., Farrell, M., Froyd,
1005 C., Grant, M. J., Huckerby, E., Innes, J. B., Shaw, H. and Waller, M.: The Holocene vegetation cover of Britain and Ireland:
1006 Overcoming problems of scale and discerning patterns of openness, *Quat. Sci. Rev.*, 73, 132–148,
1007 doi:10.1016/j.quascirev.2013.05.014, 2013.
- 1008 Fyfe, R., Woodbridge, J. and Roberts, N.: From forest to farmland: pollen-inferred land cover change across Europe using the
1009 pseudobiomization approach, *Glob. Chang. Biol.*, 21(3), 1197–1212, doi:10.1111/gcb.12776, 2015.
- 1010 Fyfe, R., Woodbridge, J. and Roberts, C. N.: Trajectories of change in Mediterranean Holocene vegetation through
1011 classification of pollen data, *Veg. Hist. Archaeobot.*, 27(2), 351–364, doi:10.1007/s00334-017-0657-4, 2018.
- 1012 Fyfe, R. M., Githumbi, E., Trondmann, A.-K., Mazier, F., Nielsen, A. B., Poska, A., Sugita, S., Woodbridge, J., Contributors,
1013 L. and Gaillard, M.-J.: A full Holocene record of transient gridded vegetation cover in Europe, *Pangaea*,
1014 doi:<https://doi.pangaea.de/10.1594/PANGAEA.931856>, 2021.
- 1015 Gaillard, M.-J., Sugita, S., Bunting, M. J., Middleton, R., Broström, A., Caseldine, C., Giesecke, T., Hellman, S. E. V., Hicks,



- 1016 S., Hjelle, K., Langdon, C., Nielsen, A.-B., Poska, A., von Stedingk, H. and Veski, S.: The use of modelling and simulation
1017 approach in reconstructing past landscapes from fossil pollen data: a review and results from the POLLANDCAL network,
1018 *Veg. Hist. Archaeobot.*, 17(5), 419–443, doi:10.1007/s00334-008-0169-3, 2008.
- 1019 Gaillard, M.-J., Kleinen, T., Samuelsson, P., Nielsen, A. B., Bergh, J., Kaplan, J. O., Poska, A., Sandström, C., Strandberg,
1020 G., Trondman, A.-K., Wramneby, A. and BACC Author Team: Second Assessment of Climate Change for the Baltic Sea
1021 Basin, edited by The BACC II Author Team, Springer International Publishing, Cham., 2015.
- 1022 Gaillard, M. J., Sugita, S., Mazier, F., Trondman, A. K., Broström, A., Hickler, T., Kaplan, J. O., Kjellström, E., Kokfelt, U.,
1023 Kuneš, P., Lemmen, C., Miller, P., Olofsson, J., Poska, A., Rundgren, M., Smith, B., Strandberg, G., Fyfe, R., Nielsen, A. B.,
1024 Alenius, T., Balakauskas, L., Barnekow, L., Birks, H. J. B., Bjune, A., Björkman, L., Giesecke, T., Hjelle, K., Kalnina, L.,
1025 Kangur, M., Van Der Knaap, W. O., Koff, T., Lageras, P., Latałowa, M., Leydet, M., Lechterbeck, J., Lindbladh, M., Odgaard,
1026 B., Peglar, S., Segerström, U., Von Stedingk, H. and Seppä, H.: Holocene land-cover reconstructions for studies on land cover-
1027 climate feedbacks, *Clim. Past*, 6(4), 483–499, doi:10.5194/cp-6-483-2010, 2010.
- 1028 Gaillard, M. J., Morrison, K. D., Madella, M. and Whitehouse, N.: Past land-use and land-cover change: the challenge of
1029 quantification at the subcontinental to global scales, *Past Glob. Chang. Mag.*, 26(1), 3–3, doi:10.22498/pages.26.1.3, 2018.
- 1030 Giesecke, T., Davis, B., Brewer, S., Finsinger, W., Wolters, S., Blaauw, M., de Beaulieu, J.-L., Binney, H., Fyfe, R., Gaillard,
1031 M.-J., Gil-Romera, G., van der Knaap, W. O., Kuneš, P., Kühl, N., van Leeuwen, J. F. N., Leydet, M., Lotter, A. F., Ortu, E.,
1032 Semmler, M. and Bradshaw, R. H. W.: Towards mapping the late Quaternary vegetation change of Europe, *Veg. Hist.*
1033 *Archaeobot.*, 23(1), 75–86, doi:10.1007/s00334-012-0390-y, 2014.
- 1034 Githumbi, E., Fyfe, R., Kjellström, E., Lindström, J., Lu, Z., Mazier, F., Nielsen, A. B., Poska, A., Smith, B., Strandberg, G.,
1035 Sugita, S., Zhang, Q. and Gaillard, M.-J.: Holocene quantitative pollen-based vegetation reconstructions in Europe for climate
1036 modelling: LandClim II. [online] Available from: [https://portal.research.lu.se/portal/en/publications/holocene-quantitative-](https://portal.research.lu.se/portal/en/publications/holocene-quantitative-pollenbased-vegetation-reconstructions-in-europe-for-climate-modelling-landclim-ii(46cc8471-f51c-4117-a7c6-cdff00638e82)/export.html)
1037 [pollenbased-vegetation-reconstructions-in-europe-for-climate-modelling-landclim-ii\(46cc8471-f51c-4117-a7c6-](https://portal.research.lu.se/portal/en/publications/holocene-quantitative-pollenbased-vegetation-reconstructions-in-europe-for-climate-modelling-landclim-ii(46cc8471-f51c-4117-a7c6-cdff00638e82)/export.html)
1038 [ccff00638e82\)/export.html](https://portal.research.lu.se/portal/en/publications/holocene-quantitative-pollenbased-vegetation-reconstructions-in-europe-for-climate-modelling-landclim-ii(46cc8471-f51c-4117-a7c6-cdff00638e82)/export.html) (Accessed 9 August 2021), 2019.
- 1039 Gregory, P.: Spores: their properties and sedimentation in still air. *Microbiology of the atmosphere. A plant science*
1040 *monograph*, 1973.
- 1041 Grindean, R., Nielsen, A. B., Tanțău, I. and Feurdean, A.: Relative pollen productivity estimates in the forest steppe landscape
1042 of southeastern Romania, *Rev. Palaeobot. Palynol.*, 264, 54–63, doi:10.1016/j.revpalbo.2019.02.007, 2019.
- 1043 Guiry, E., Beglane, F., Szpak, P., Schulting, R., McCormick, F. and Richards, M. P.: Anthropogenic changes to the Holocene
1044 nitrogen cycle in Ireland, *Sci. Adv.*, 4(6), eaas9383, doi:10.1126/sciadv.aas9383, 2018.
- 1045 Harrison, S. P., Gaillard, M. J., Stocker, B. D., Vander Linden, M., Klein Goldewijk, K., Boles, O., Braconnot, P., Dawson,
1046 A., Fluet-Chouinard, E., Kaplan, J. O., Kastner, T., Pausata, F. S. R., Robinson, E., Whitehouse, N. J., Madella, M. and
1047 Morrison, K. D.: Development and testing scenarios for implementing land use and land cover changes during the Holocene
1048 in Earth system model experiments, *Geosci. Model Dev.*, 13(2), 805–824, doi:10.5194/gmd-13-805-2020, 2020.
- 1049 He, F., Vavrus, S. J., Kutzbach, J. E., Ruddiman, W. F., Kaplan, J. O. and Krumhardt, K. M.: Simulating global and local



- 1050 surface temperature changes due to Holocene anthropogenic land cover change, *Geophys. Res. Lett.*, 41(2), 623–631,
1051 doi:10.1002/2013GL058085, 2014.
- 1052 Hellman, S., Gaillard, M.-J., Broström, A. and Sugita, S.: The REVEALS model, a new tool to estimate past regional plant
1053 abundance from pollen data in large lakes: validation in southern Sweden, *J. Quat. Sci.*, 23(1), 21–42, doi:10.1002/jqs.1126,
1054 2008a.
- 1055 Hellman, S. E. V., Gaillard, M., Broström, A. and Sugita, S.: Effects of the sampling design and selection of parameter values
1056 on pollen-based quantitative reconstructions of regional vegetation: a case study in southern Sweden using the REVEALS
1057 model, *Veg. Hist. Archaeobot.*, 17(5), 445–459, doi:10.1007/s00334-008-0149-7, 2008b.
- 1058 Hibbard, K., Janetos, A., Van Vuuren, D. P., Pongratz, J., Rose, S. K., Betts, R., Herold, M. and Feddes, J. J.: Research
1059 priorities in land use and land-cover change for the Earth system and integrated assessment modelling, *Int. J. Climatol.*, 30(13),
1060 2118–2128, doi:10.1002/joc.2150, 2010.
- 1061 Hjelle, K. L.: Herb pollen representation in surface moss samples from mown meadows and pastures in western Norway, *Veg.*
1062 *Hist. Archaeobot.*, 7(2), 79–96, doi:10.1007/BF01373926, 1998.
- 1063 Hofman-Kamińska, E., Bocherens, H., Drucker, D. G., Fyfe, R., Gumiński, W., Makowiecki, D., Pacher, M., Piličiauskienė,
1064 G., Samojlik, T., Woodbridge, J. and Kowalczyk, R.: Adapt or die—Response of large herbivores to environmental changes
1065 in Europe during the Holocene, *Glob. Chang. Biol.*, 25(9), 2915–2930, doi:10.1111/gcb.14733, 2019.
- 1066 Huntley, B.: European vegetation history: Palaeovegetation maps from pollen data - 13 000 yr BP to present, *J. Quat. Sci.*,
1067 5(2), 103–122, doi:10.1002/jqs.3390050203, 1990.
- 1068 Kaplan, J., Krumhardt, K., Gaillard, M.-J., Sugita, S., Trondman, A.-K., Fyfe, R., Marquer, L., Mazier, F. and Nielsen, A.:
1069 Constraining the Deforestation History of Europe: Evaluation of Historical Land Use Scenarios with Pollen-Based Land Cover
1070 Reconstructions, *Land*, 6(4), 91, doi:10.3390/land6040091, 2017.
- 1071 Kaplan, J. O., Krumhardt, K. M. and Zimmermann, N.: The prehistoric and preindustrial deforestation of Europe, *Quat. Sci.*
1072 *Rev.*, 28(27–28), 3016–3034, doi:10.1016/j.quascirev.2009.09.028, 2009.
- 1073 Kaplan, J. O., Krumhardt, K. M., Ellis, E. C., Ruddiman, W. F., Lemmen, C. and Goldewijk, K. K.: Holocene carbon emissions
1074 as a result of anthropogenic land cover change, *The Holocene*, 21(5), 775–791, doi:10.1177/0959683610386983, 2011.
- 1075 Klein Goldewijk, K., Beusen, A., Doelman, J. and Stehfest, E.: Anthropogenic land use estimates for the Holocene – HYDE
1076 3.2, *Earth Syst. Sci. Data*, 9(2), 927–953, doi:10.5194/essd-9-927-2017, 2017.
- 1077 Kuneš, P., Abraham, V., Werchan, B., Plesková, Z., Fajmon, K., Jamrichová, E. and Roleček, J.: Relative pollen productivity
1078 estimates for vegetation reconstruction in central-eastern Europe inferred at local and regional scales, *The Holocene*, 29(11),
1079 1708–1719, doi:10.1177/0959683619862026, 2019.
- 1080 Lerigoleur, E., Mazier, F., Jégou, L., Perret, M. and Galop, D.: PALEOPYR: un système d’information pour la gestion et
1081 l’exploitation de données palaeoenvironnementales sur le massif nord-pyrénéen. *Ingénierie des Systèmes d’Information 3*.
1082 [online] Available from: <http://paleopyr.univ-tlse2.fr/%0A>, 2015.
- 1083 Li, F., Gaillard, M.-J., Xu, Q., Bunting, M. J., Li, Y., Li, J., Mu, H., Lu, J., Zhang, P., Zhang, S., Cui, Q., Zhang, Y. and Shen,



- 1084 W.: A Review of Relative Pollen Productivity Estimates From Temperate China for Pollen-Based Quantitative Reconstruction
1085 of Past Plant Cover, *Front. Plant Sci.*, 9(September), doi:10.3389/fpls.2018.01214, 2018.
- 1086 Li, F., Gaillard, M.-J., Cao, X., Herzsuh, U., Sugita, S., Tarasov, P. E., Wagner, M., Xu, Q., Ni, J., Wang, W., Zhao, Y., An,
1087 C., Beusen, A. H. W., Chen, F., Feng, Z., Goldewijk, C. G. M. K., Huang, X., Li, Y., Li, Y., Liu, H., Sun, A., Yao, Y., Zheng,
1088 Z. and Jia, X.: Towards quantification of Holocene anthropogenic land-cover change in temperate China: A review in the light
1089 of pollen-based REVEALS reconstructions of regional plant cover, *Earth-Science Rev.*, 203(February), 103119,
1090 doi:10.1016/j.earscirev.2020.103119, 2020.
- 1091 Marinova, E., Harrison, S. P., Bragg, F., Connor, S., Laet, V., Leroy, S. A. G., Mudie, P., Atanassova, J., Bozilova, E., Caner,
1092 H., Cordova, C., Djamali, M., Filipova-Marinova, M., Gerasimenko, N., Jahns, S., Kouli, K., Kotthoff, U., Kvavadze, E.,
1093 Lazarova, M., Novenko, E., Ramezani, E., Röpke, A., Shumilovskikh, L., Tanțău, I. and Tonkov, S.: Pollen-derived biomes
1094 in the Eastern Mediterranean–Black Sea–Caspian–Corridor, *J. Biogeogr.*, 45(2), 484–499, doi:10.1111/jbi.13128, 2018.
- 1095 Marquer, L., Gaillard, M.-J., Sugita, S., Trondman, A.-K., Mazier, F., Nielsen, A. B., Fyfe, R., Odgaard, B. V., Alenius, T.,
1096 Birks, H. J. B., Bjune, A. E., Christiansen, J., Dodson, J., Edwards, K. J., Giesecke, T., Herzsuh, U., Kangur, M., Lorenz,
1097 S., Poska, A., Schult, M. and Seppä, H.: Holocene changes in vegetation composition in northern Europe: why quantitative
1098 pollen-based vegetation reconstructions matter, *Quat. Sci. Rev.*, 90, 199–216, doi:10.1016/j.quascirev.2014.02.013, 2014.
- 1099 Marquer, L., Gaillard, M.-J., Sugita, S., Poska, A., Trondman, A.-K., Mazier, F., Nielsen, A. B., Fyfe, R., Jönsson, A. M.,
1100 Smith, B., Kaplan, J. O., Alenius, T., Birks, H. J. B. J. B., Bjune, A. E., Christiansen, J., Dodson, J., Edwards, K. J., Giesecke,
1101 T., Herzsuh, U., Kangur, M., Koff, T., Latałowa, M., Lechterbeck, J., Olofsson, J. and Seppä, H.: Quantifying the effects of
1102 land use and climate on Holocene vegetation in Europe, *Quat. Sci. Rev.*, 171, 20–37, doi:10.1016/j.quascirev.2017.07.001,
1103 2017.
- 1104 Marquer, L., Mazier, F., Sugita, S., Galop, D., Houet, T., Faure, E., Gaillard, M.-J., Haunold, S., de Munnik, N., Simonneau,
1105 A., De Vleeschouwer, F. and Le Roux, G.: Pollen-based reconstruction of Holocene land-cover in mountain regions:
1106 Evaluation of the Landscape Reconstruction Algorithm in the Vicdessos valley, northern Pyrenees, France, *Quat. Sci. Rev.*,
1107 228, 106049, doi:10.1016/j.quascirev.2019.106049, 2020.
- 1108 Matthias, I., Nielsen, A. B. and Giesecke, T.: Evaluating the effect of flowering age and forest structure on pollen productivity
1109 estimates, *Veg. Hist. Archaeobot.*, 21(6), 471–484, doi:10.1007/s00334-012-0373-z, 2012.
- 1110 Mazier, F., Broström, A., Gaillard, M.-J., Sugita, S., Vittoz, P. and Buttler, A.: Pollen productivity estimates and relevant
1111 source area of pollen for selected plant taxa in a pasture woodland landscape of the Jura Mountains (Switzerland), *Veg. Hist.*
1112 *Archaeobot.*, 17(5), 479–495, doi:10.1007/s00334-008-0143-0, 2008.
- 1113 Mazier, F., Gaillard, M. J., Kunes, P., Sugita, S., Trondman, A.-K. and Brostrom, A.: Testing the effect of site selection and
1114 parameter setting on REVEALS-model estimates of plant abundance using the Czech Quaternary Palynological database
1115 Testing the effect of site selection and parameter setting on REVEALS-model estimates of plant abundance, *Rev. Palaeobot.*
1116 *Palynol.*, 187, 38–49 [online] Available from: <https://halshs.archives-ouvertes.fr/halshs-00959845>, 2012.
- 1117 Mazier, F., Broström, A., Bragée, P., Fredh, D., Stenberg, L., Thiery, G., Sugita, S. and Hammarlund, D.: Two hundred years



- 1118 of land-use change in the South Swedish Uplands: comparison of historical map-based estimates with a pollen-based
1119 reconstruction using the landscape reconstruction algorithm, *Veg. Hist. Archaeobot.*, 24(5), 555–570, doi:10.1007/s00334-
1120 015-0516-0, 2015a.
- 1121 Mazier, F., Broström, A., Bragée, P., Fredh, D., Stenberg, L., Thiere, G., Sugita, S. and Hammarlund, D.: Two hundred years
1122 of land-use change in the South Swedish Uplands: comparison of historical map-based estimates with a pollen-based
1123 reconstruction using the landscape reconstruction algorithm, *Veg. Hist. Archaeobot.*, 24(5), 555–570, doi:10.1007/s00334-
1124 015-0516-0, 2015b.
- 1125 McLauchlan, K. K., Williams, J. J., Craine, J. M. and Jeffers, E. S.: Changes in global nitrogen cycling during the Holocene
1126 epoch, *Nature*, 495(7441), 352–355, doi:10.1038/nature11916, 2013.
- 1127 Morrison, K. D., Hammer, E., Boles, O., Madella, M., Whitehouse, N., Gaillard, M.-J., Bates, J., Vander Linden, M., Merlo,
1128 S., Yao, A., Popova, L., Hill, A. C., Antolin, F., Bauer, A., Biagetti, S., Bishop, R. R., Buckland, P., Cruz, P., Dreslerová, D.,
1129 Dusseldorp, G., Ellis, E., Filipovic, D., Foster, T., Hannaford, M. J., Harrison, S. P., Hazarika, M., Herold, H., Hilpert, J.,
1130 Kaplan, J. O., Kay, A., Klein Goldewijk, K., Kolář, J., Kyazike, E., Laabs, J., Lancelotti, C., Lane, P., Lawrence, D., Lewis,
1131 K., Lombardo, U., Lucarini, G., Arroyo-Kalin, M., Marchant, R., Mayle, F., McClatchie, M., McLeester, M., Mooney, S.,
1132 Moskal-del Hoyo, M., Navarrete, V., Ndiema, E., Góes Neves, E., Nowak, M., Out, W. A., Petrie, C., Phelps, L. N., Pinke, Z.,
1133 Rostain, S., Russell, T., Sluyter, A., Styring, A. K., Tamanaha, E., Thomas, E., Veerasamy, S., Welton, L. and Zanon, M.:
1134 Mapping past human land use using archaeological data: A new classification for global land use synthesis and data
1135 harmonization, edited by J. Freeman, *PLoS One*, 16(4), e0246662, doi:10.1371/journal.pone.0246662, 2021.
- 1136 Nielsen, A. B.: Modelling pollen sedimentation in Danish lakes at c.ad 1800: an attempt to validate the POLLSCAPE model,
1137 *J. Biogeogr.*, 31(10), 1693–1709, doi:10.1111/j.1365-2699.2004.01080.x, 2004.
- 1138 Nielsen, A. B. and Odgaard, B. V.: Quantitative landscape dynamics in Denmark through the last three millennia based on the
1139 Landscape Reconstruction Algorithm approach, *Veg. Hist. Archaeobot.*, 19(4), 375–387, doi:10.1007/s00334-010-0249-z,
1140 2010.
- 1141 Nielsen, A. B., Giesecke, T., Theuerkauf, M., Feeser, I., Behre, K.-E., Beug, H.-J., Chen, S.-H., Christiansen, J., Dörfler, W.,
1142 Endtmann, E., Jahns, S., de Klerk, P., Köhl, N., Latałowa, M., Odgaard, B. V., Rasmussen, P., Stockholm, J. R., Voigt, R.,
1143 Wiethold, J. and Wolters, S.: Quantitative reconstructions of changes in regional openness in north-central Europe reveal new
1144 insights into old questions, *Quat. Sci. Rev.*, 47, 131–149, doi:10.1016/j.quascirev.2012.05.011, 2012.
- 1145 Parsons, R. W. and Prentice, I. C.: Statistical approaches to R-values and the pollen—vegetation relationship, *Rev. Palaeobot.*
1146 *Palynol.*, 32(2–3), 127–152, doi:10.1016/0034-6667(81)90001-4, 1981.
- 1147 Pirzamanbein, B., Lindström, J., Poska, A., Sugita, S., Trondman, A.-K., Fyfe, R., Mazier, F., Nielsen, A. B., Kaplan, J. O.,
1148 Bjune, A. E., Birks, H. J. B., Giesecke, T., Kangur, M., Latałowa, M., Marquer, L., Smith, B. and Gaillard, M.-J.: Creating
1149 spatially continuous maps of past land cover from point estimates: A new statistical approach applied to pollen data, *Ecol.*
1150 *Complex.*, 20, 127–141, doi:10.1016/j.ecocom.2014.09.005, 2014.
- 1151 Pirzamanbein, B., Lindström, J., Poska, A. and Gaillard, M. J.: Modelling Spatial Compositional Data: Reconstructions of past



- 1152 land cover and uncertainties, *Spat. Stat.*, 24, 14–31, doi:10.1016/j.spasta.2018.03.005, 2018.
- 1153 Pirzamanbein, B., Poska, A. and Lindström, J.: Bayesian Reconstruction of Past Land Cover From Pollen Data: Model
1154 Robustness and Sensitivity to Auxiliary Variables, *Earth Sp. Sci.*, 7(1), doi:10.1029/2018EA000547, 2020.
- 1155 Poska, A., Meltsov, V., Sugita, S. and Vassiljev, J.: Relative pollen productivity estimates of major anemophilous taxa and
1156 relevant source area of pollen in a cultural landscape of the hemi-boreal forest zone (Estonia), *Rev. Palaeobot. Palynol.*, 167(1–
1157 2), 30–39, doi:10.1016/j.revpalbo.2011.07.001, 2011.
- 1158 Prentice, C.: Records of vegetation in time and space: the principles of pollen analysis, in *Vegetation history*, pp. 17–42,
1159 Springer Netherlands, Dordrecht., 1988.
- 1160 Prentice, C., Guiot, J., Huntley, B., Jolly, D. and Cheddadi, R.: Reconstructing biomes from palaeoecological data: a general
1161 method and its application to European pollen data at 0 and 6 ka, *Clim. Dyn.*, 12(3), 185–194, doi:10.1007/BF00211617, 1996.
- 1162 Prentice, I. C.: Pollen Representation, Source Area, and Basin Size: Toward a Unified Theory of Pollen Analysis, *Quat. Res.*,
1163 23(1), 76–86, doi:10.1016/0033-5894(85)90073-0, 1985.
- 1164 Prentice, I. C. and Parsons, R. A.: Maximum Likelihood Linear Calibration of Pollen Spectra in Terms of Forest Composition,
1165 *Biometrics*, 39(4), 1051–1057 [online] Available from: [https://www-jstor-](https://www-jstor-org.proxy.lnu.se/stable/pdf/2531338.pdf?refreqid=excelsior%3A0a1269ce2e31754011525047e9760d27)
1166 [org.proxy.lnu.se/stable/pdf/2531338.pdf?refreqid=excelsior%3A0a1269ce2e31754011525047e9760d27](https://www-jstor-org.proxy.lnu.se/stable/pdf/2531338.pdf?refreqid=excelsior%3A0a1269ce2e31754011525047e9760d27), 1983.
- 1167 Prentice, I. C. and Webb III, T.: BIOME 6000: reconstructing global mid-Holocene vegetation patterns from palaeoecological
1168 records, *J. Biogeogr.*, 25(6), 997–1005, doi:10.1046/j.1365-2699.1998.00235.x, 1998.
- 1169 Räsänen, S., Suutari, H. and Nielsen, A. B.: A step further towards quantitative reconstruction of past vegetation in
1170 Fennoscandian boreal forests: Pollen productivity estimates for six dominant taxa, *Rev. Palaeobot. Palynol.*, 146(1–4), 208–
1171 220, doi:10.1016/j.revpalbo.2007.04.004, 2007.
- 1172 Roberts, C. N., Woodbridge, J., Palmisano, A., Bevan, A., Fyfe, R. and Shennan, S.: Mediterranean landscape change during
1173 the Holocene: Synthesis, comparison and regional trends in population, land cover and climate, *The Holocene*, 29(5), 923–
1174 937, doi:10.1177/0959683619826697, 2019.
- 1175 Roberts, N., Fyfe, R. M., Woodbridge, J., Gaillard, M.-J., Davis, B. A. S. S., Kaplan, J. O., Marquer, L., Mazier, F., Nielsen,
1176 A. B., Sugita, S., Trondman, A.-K. and Leydet, M.: Europe’s lost forests: a pollen-based synthesis for the last 11,000 years,
1177 *Sci. Rep.*, 8(1), 716, doi:10.1038/s41598-017-18646-7, 2018.
- 1178 Ruddiman, W. F.: THE ANTHROPOGENIC GREENHOUSE ERA BEGAN THOUSANDS OF YEARS AGO., 2003.
- 1179 Ruddiman, W. F., Fuller, D. Q., Kutzbach, J. E., Tzedakis, P. C., Kaplan, J. O., Ellis, E. C., Vavrus, S. J., Roberts, C. N., Fyfe,
1180 R., He, F., Lemmen, C. and Woodbridge, J.: Late Holocene climate: Natural or anthropogenic?, *Rev. Geophys.*, 54(1), 93–
1181 118, doi:10.1002/2015RG000503, 2016.
- 1182 Shennan, S.: *The First Farmers of Europe An Evolutionary Perspective*, Cambridge University Press, Cambridge. [online]
1183 Available from: [https://www-cambridge-org.proxy.lnu.se/se/academic/subjects/archaeology/archaeology-europe-and-near-](https://www-cambridge-org.proxy.lnu.se/se/academic/subjects/archaeology/archaeology-europe-and-near-and-middle-east/first-farmers-europe-evolutionary-perspective?format=HB&isbn=9781108422925)
1184 [and-middle-east/first-farmers-europe-evolutionary-perspective?format=HB&isbn=9781108422925](https://www-cambridge-org.proxy.lnu.se/se/academic/subjects/archaeology/archaeology-europe-and-near-and-middle-east/first-farmers-europe-evolutionary-perspective?format=HB&isbn=9781108422925), 2018.
- 1185 Soepboer, W., Sugita, S., Lotter, A. F., van Leeuwen, J. F. N. and van der Knaap, W. O.: Pollen productivity estimates for



- 1186 quantitative reconstruction of vegetation cover on the Swiss Plateau, *The Holocene*, 17(1), 65–77,
1187 doi:10.1177/0959683607073279, 2007.
- 1188 Soepboer, W., Sugita, S. and Lotter, A. F.: Regional vegetation-cover changes on the Swiss Plateau during the past two
1189 millennia: A pollen-based reconstruction using the REVEALS model, *Quat. Sci. Rev.*, 29(3–4), 472–483,
1190 doi:10.1016/j.quascirev.2009.09.027, 2010.
- 1191 von Stedingk, H., Fyfe, R. and Allard, A.: Pollen productivity estimates from the forest–tundra ecotone in west-central
1192 Sweden: implications for vegetation reconstruction at the limits of the boreal forest, *The Holocene*, 18(2), 323–332,
1193 doi:10.1177/0959683607086769, 2008.
- 1194 Stephens, L., Fuller, D., Boivin, N., Rick, T., Gauthier, N., Kay, A., Marwick, B., Armstrong, C. G., Barton, C. M., Denham,
1195 T., Douglass, K., Driver, J., Janz, L., Roberts, P., Rogers, J. D., Thakar, H., Altaweel, M., Johnson, A. L., Sampietro Vattuone,
1196 M. M., Aldenderfer, M., Archila, S., Artioli, G., Bale, M. T., Beach, T., Borrell, F., Braje, T., Buckland, P. I., Jiménez Cano,
1197 N. G., Capriles, J. M., Diez Castillo, A., Çilingiroğlu, Ç., Negus Cleary, M., Conolly, J., Coutros, P. R., Covey, R. A.,
1198 Cremaschi, M., Crowther, A., Der, L., di Lernia, S., Doershuk, J. F., Doolittle, W. E., Edwards, K. J., Erlandson, J. M., Evans,
1199 D., Fairbairn, A., Faulkner, P., Feinman, G., Fernandes, R., Fitzpatrick, S. M., Fyfe, R., Garcea, E., Goldstein, S., Goodman,
1200 R. C., Dalpoim Guedes, J., Herrmann, J., Hiscock, P., Hommel, P., Horsburgh, K. A., Hritz, C., Ives, J. W., Junno, A., Kahn,
1201 J. G., Kaufman, B., Kearns, C., Kidder, T. R., Lanoë, F., Lawrence, D., Lee, G.-A., Levin, M. J., Lindsoug, H. B., López-
1202 Sáez, J. A., Macrae, S., Marchant, R., Marston, J. M., McClure, S., McCoy, M. D., Miller, A. V., Morrison, M., Motuzaite
1203 Matuzeviciute, G., Müller, J., Nayak, A., Noerwidi, S., Peres, T. M., Peterson, C. E., Proctor, L., Randall, A. R., Renette, S.,
1204 Robbins Schug, G., Ryzewski, K., Saini, R., Scheinsohn, V., Schmidt, P., Sebillaud, P., Seitsonen, O., Simpson, I. A.,
1205 Sołtysiak, A., Speakman, R. J., Spengler, R. N., Steffen, M. L., et al.: Archaeological assessment reveals Earth’s early
1206 transformation through land use, *Science* (80-.), 365(6456), 897–902, doi:10.1126/science.aax1192, 2019.
- 1207 Strandberg, G., Kjellström, E., Poska, A., Wagner, S., Gaillard, M. J., Trondman, A. K., Mauri, A., Davis, B. A. S., Kaplan, J.
1208 O., Birks, H. J. B., Bjune, A. E., Fyfe, R., Giesecke, T., Kalnina, L., Kangur, M., Van Der Knaap, W. O., Kokfelt, U., Kuneš,
1209 P., Lataowa, M., Marquer, L., Mazier, F., Nielsen, A. B., Smith, B., Seppä, H. and Sugita, S.: Regional climate model
1210 simulations for Europe at 6 and 0.2 k BP: Sensitivity to changes in anthropogenic deforestation, *Clim. Past*, 10(2), 661–680,
1211 doi:10.5194/cp-10-661-2014, 2014.
- 1212 Stuart, A. and Ord, J. K.: *Kendall’s advanced theory of statistics, Distrib. theory*, 1 [online] Available from:
1213 <https://ci.nii.ac.jp/naid/10004597057> (Accessed 2 July 2021), 1994.
- 1214 Sugita, S.: Theory of quantitative reconstruction of vegetation I: pollen from large sites REVEALS regional vegetation
1215 composition, *The Holocene*, 17(2), 229–241, doi:10.1177/0959683607075837, 2007a.
- 1216 Sugita, S.: Theory of quantitative reconstruction of vegetation II: all you need is LOVE, *The Holocene*, 17(2), 243–257,
1217 doi:10.1177/0959683607075838, 2007b.
- 1218 Sugita, S., Gaillard, M. J. and Broström, A.: Landscape openness and pollen records: A simulation approach, *Holocene*, 9(4),
1219 409–421, doi:10.1191/095968399666429937, 1999.



- 1220 Sugita, S., Parshall, T., Calcote, R. and Walker, K.: Testing the Landscape Reconstruction Algorithm for spatially explicit
1221 reconstruction of vegetation in northern Michigan and Wisconsin, *Quat. Res.*, 74(2), 289–300,
1222 doi:10.1016/j.yqres.2010.07.008, 2010.
- 1223 Sutton, O. : *Micrometeorology.*, *Q. J. R. Meteorol. Soc.*, 79(341), 457–457, doi:10.1002/qj.49707934125, 1953.
- 1224 Theuerkauf, M., Kuparinen, A. and Joosten, H.: Pollen productivity estimates strongly depend on assumed pollen dispersal,
1225 *The Holocene*, 23(1), 14–24, doi:10.1177/0959683612450194, 2013.
- 1226 Theuerkauf, M., Couwenberg, J., Kuparinen, A. and Liebscher, V.: A matter of dispersal: REVEALSinR introduces state-of-
1227 the-art dispersal models to quantitative vegetation reconstruction, *Veg. Hist. Archaeobot.*, 25(6), doi:10.1007/s00334-016-
1228 0572-0, 2016.
- 1229 Trondman, A.-K., Gaillard, M.-J., Sugita, S., Björkman, L., Greisman, A., Hultberg, T., Lagerås, P., Lindbladh, M. and Mazier,
1230 F.: Are pollen records from small sites appropriate for REVEALS model-based quantitative reconstructions of past regional
1231 vegetation? An empirical test in southern Sweden, *Veg. Hist. Archaeobot.*, 25(2), 131–151, doi:10.1007/s00334-015-0536-9,
1232 2016.
- 1233 Trondman, A. K., Gaillard, M. J., Mazier, F., Sugita, S., Fyfe, R., Nielsen, A. B., Twiddle, C., Barratt, P., Birks, H. J. B.,
1234 Bjune, A. E., Björkman, L., Broström, A., Caseldine, C., David, R., Dodson, J., Dörfler, W., Fischer, E., van Geel, B., Giesecke,
1235 T., Hultberg, T., Kalnina, L., Kangur, M., van der Knaap, P., Koff, T., Kuneš, P., Lagerås, P., Latalowa, M., Lechterbeck, J.,
1236 Leroyer, C., Leydet, M., Lindbladh, M., Marquer, L., Mitchell, F. J. G., Odgaard, B. V., Peglar, S. M., Persson, T., Poska, A.,
1237 Rösch, M., Seppä, H., Veski, S. and Wick, L.: Pollen-based quantitative reconstructions of Holocene regional vegetation cover
1238 (plant-functional types and land-cover types) in Europe suitable for climate modelling, *Glob. Chang. Biol.*, 21(2), 676–697,
1239 doi:10.1111/gcb.12737, 2015.
- 1240 Twiddle, C. L.: Pollen Analysis : Not Just a Qualitative Tool, *Geomorphol. Tech.*, 1–11, 2012.
- 1241 Wieczorek, M. and Herzschuh, U.: Compilation of relative pollen productivity (RPP) estimates and taxonomically harmonised
1242 RPP datasets for single continents and Northern Hemisphere extratropics, *Earth Syst. Sci. Data*, 12(4), 3515–3528,
1243 doi:10.5194/essd-12-3515-2020, 2020.
- 1244 Wolf, A., Callaghan, T. V. and Larson, K.: Future changes in vegetation and ecosystem function of the Barents Region, *Clim.*
1245 *Change*, 87(1–2), 51–73, doi:10.1007/s10584-007-9342-4, 2008.
- 1246 Woodbridge, J., Fyfe, R. and Roberts, N.: A comparison of remotely sensed and pollen-based approaches to mapping Europe’s
1247 land cover, edited by M. Bush, *J. Biogeogr.*, 41(11), 2080–2092, doi:10.1111/jbi.12353, 2014.
- 1248 Woodbridge, J., Fyfe, R., Roberts, C., Trondman, A., Mazier, F. and Davis, B.: European forest cover since the start of
1249 Neolithic agriculture: a critical comparison of pollen-based reconstructions, *Past Glob. Chang. Mag.*, 26(1), 10–11,
1250 doi:10.22498/pages.26.1.10, 2018.
- 1251 Zanon, M., Davis, B. A. S. S., Marquer, L., Brewer, S. and Kaplan, J. O.: European Forest Cover During the Past 12,000
1252 Years: A Palynological Reconstruction Based on Modern Analogs and Remote Sensing, *Front. Plant Sci.*, 9(March), 1–25,
1253 doi:10.3389/fpls.2018.00253, 2018.