

1 **Quantifying the effect of testate amoeba**
2 **decomposition on peat-based water-table**
3 **reconstructions**

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24 **Abstract**

25 Testate amoebae are a widely-used tool for palaeohydrological reconstruction from peatlands.
26 However, it has been observed that weak idiosomic siliceous tests (WISTs) are common in uppermost
27 peats, but very rarely found as subfossils deeper in the peat profile. This taphonomic problem has been
28 noted widely and it has been established that WISTs disaggregate and/or dissolve in the low pH
29 condition of ombrotrophic peatlands. Here we investigate the effect of this taphonomic problem on
30 water-table reconstructions from thirty European peatlands through the comparison of reconstructions
31 based on all taxa and those with WISTs removed. In almost all cases the decomposition of WISTs does
32 not introduce discernible bias to peatland water-table reconstructions. However, some discrepancy is
33 apparent when large abundances of *Corythion-Trinema* type are present (9-12 cm deviation with 50-60
34 % abundance of this particular taxon). We recommend that WISTs should be removed before carrying
35 out water-table reconstructions, and that the minimum count of testate amoebae per sample should
36 exclude WISTs to ensure the development of robust reconstructions.

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47 **Keywords:** Palaeoecology; Peatlands; Protists; Taphonomy; Testate amoebae; Water-table
48 reconstruction

49 Introduction

50 Testate amoebae have become an important tool for reconstruction of palaeohydrology from temperate
51 (Booth 2002; Galka et al. 2013; Hendon and Charman 2004), tropical (Swindles et al. 2018, 2016,
52 2014), and high latitude (Sim et al. 2019; Swindles et al. 2015; Zhang et al. 2018) peatlands. Some
53 testate amoeba taxa produce proteinaceous tests (amorphous, e.g. *Hyalosphenia* spp.; or plate-like, e.g.
54 *Arcella* spp.), which can be reinforced with agglutinated extraneous material (xenosomes, e.g. *Diffflugia*
55 spp.), whereas others form self-secreted siliceous or calcareous plates/scales (idiosomes, e.g. *Euglypha*
56 spp.; *Paraquadrula* spp.), or siliceous plates recycled from consumed prey (e.g. *Nebela* spp.). Certain
57 taxa incorporate both idiosomes and xenosomes (e.g. *Netzelia* spp.), or xenosomes and recycled
58 siliceous plates (e.g. *Heleopera* spp.) in test construction (see Charman et al. 2000).

59

60 The reliability of all microfossil-based palaeoenvironmental reconstructions is limited by the quality of
61 the primary data. Differential preservation of microfossils is a particular problem in micropalaeontology
62 as it can severely alter the original assemblage composition, which may lead to erroneous
63 palaeoenvironmental inferences (e.g. Jonasson and Patterson, 1992). In peatlands, several authors have
64 noticed that weak idiosomic siliceous tests (WISTs) from species of the genera *Euglypha*, *Corythion*,
65 *Sphenoderia*, *Trinema* and *Tracheleuglypha* are not readily preserved in older peats (Booth and
66 Jackson, 2003; Mitchell et al., 2008; Wilmschurst et al., 2003). Swindles and Roe (2007) and Payne
67 (2007) carried out laboratory-based experiments to examine the preservation of testate amoebae in
68 peatlands. These studies showed that some testate amoeba taxa (primarily WISTs) were particularly
69 vulnerable to decomposition in low pH conditions or through desiccation. However, Mitchell et al.
70 (2008), using small regional-scale transfer function models, suggested that differential test preservation
71 has little impact on palaeohydrological reconstruction from *Sphagnum*-dominated peatlands.

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73 Here we build upon Mitchell et al. (2008) and examine the effects of WIST preservation on water-table
74 depth reconstructions using a new large database of 30 European peatlands (Swindles et al., 2019). We

75 use the state-of-the-art pan-European transfer function which is based on ~1300 samples from 18
76 countries (Amesbury et al., 2016) to carry out the reconstructions.

77

78 **Material and Methods**

79 We used published testate-amoeba subfossil data from 30 European peatlands (Fig. 1, Table 1). The
80 pan-European transfer function of Amesbury et al. (2016) was applied to each dataset to generate water-
81 table depth reconstructions (expressed as a water-table position in cm below peatland surface). The best
82 performing model was determined by the R^2 and root mean square error of prediction (RMSEP),
83 calculated as apparent and leave-one-out (LOO) cross-validated measures. The model based on
84 weighted-average tolerance down-weighting with inverse deshrinking (WA-Tol_Inv) was selected as
85 the best performing model (Amesbury et al., 2016). Water-table reconstructions were carried out on i)
86 the complete assemblages; (ii) the assemblages with WISTs removed; and (iii) the assemblages with
87 WISTs removed, using a modified version of the Amesbury et al. (2016) transfer function from which
88 WISTs had also been removed. The WISTs removed comprise all taxa in the following groups from the
89 transfer function model: *Corythion-Trinema* type, *Euglypha ciliata* type, *Euglypha rotunda* type,
90 *Tracheleuglypha dentata* type and *Sphenoderia* type. Reconstructions were carried out in R (R Core
91 Team, 2018) using the package ‘rioja’ (Juggins, 2018). Sample-specific errors for the transfer function
92 reconstructions were generated from 1000 bootstrap cycles. For information regarding the age-depth
93 models for each site, see Swindles et al. (2019) (also presented in Supplementary material 1).

94

95 **Results and Discussion**

96 The difference in transfer function performance between the original and no-WIST models is negligible
97 (Table 2). The results of our analysis from peat cores are shown in Fig. 2-6 (reconstructions are based
98 on the transfer function model containing the complete assemblages). It is clear that some sites exhibit
99 a rapid disappearance of WISTs in the upper part of the peat profile (e.g. Slowinskie, Stazki), whereas
100 WISTs persist at greater depths at other sites (e.g. Lille Vildmose, Mauntschas). These differences

101 between sites may be due to variation in: (i) the original concentration of WISTs; (ii) peatland type; (iii)
102 peat properties including humification and bulk density; (iv) site hydrology; (v) the thickness of poorly-
103 decomposed upper peats (acrotelm); and (vi) microclimate.

104

105 The removal of WISTs has only a very small effect on water-table depth reconstructions generally.
106 However, greater deviation (> 5 cm water-table depth difference) occurs in Mauntschas, Lille Vildmose,
107 Butterburn and Kusowo owing to a large percentage (30-59%) of WISTs in certain samples.
108 Nevertheless, directional changes are generally the same in both reconstructions. Our results support
109 previous suggestions that WISTs are poorly preserved down-core in peats, with only 17.45% of WIST
110 occurrences found before 1500 CE and 64.45% occurring since 1800 CE (Fig. 7, Supplementary
111 material 1).

112

113 Fig 8a, b show that there is a strong relationship between the reconstructions based on the full
114 assemblages and the reconstructions with WISTs removed ($R^2 = 0.988$, $p < 0.0001$). A LOESS model
115 suggests that WIST abundance must reach >50 % to effect the reconstruction by greater than ± 5 cm;
116 such abundances occur in <1% of all samples. The greatest discrepancies occur when large abundances
117 of *Corythion-Trinema* type are present (9-12 cm deviation with 50-60 % abundance of this particular
118 taxon) (Fig. 9a). The effect of *Corythion-Trinema* type on reconstructions is comparatively greater than
119 that of *Euglypha* spp. (Figs. 9a, b) due to its relatively drier optima in the transfer function model (see
120 Amesbury et al., 2016). A strong and significant relationship is also observed between the
121 reconstructions based on the down-core assemblages with WISTs removed (using the original model
122 that includes WISTs), and the reconstructions based on the no-WIST transfer function model ($R^2 =$
123 0.988 , $p < 0.0001$) (Figs. 8c, d).

124

125 We conclude that the taphonomy of WISTs in peatlands does not introduce significant bias to the
126 interpretation peatland water-table reconstructions as palaeohydrological records. This confirms the

127 findings of a previous study using regional transfer functions (Mitchell et al. 2008), and suggests that
128 there may be no need to count WISTs in studies focussed on the reconstruction of peatland
129 palaeohydrology. WISTs can be easily overlooked by analysts because of their transparency and are
130 often difficult to identify, resulting in a large degree of grouping in standard taxonomies (e.g. Charman
131 et al., 2000; but see Roland et al., 2017). The occurrence of *Corythion-Trinema* type at the top of cores
132 but not at depth could potentially lead to an apparent dry shift in water-table reconstructions, but in
133 reality, it is merely a taphonomic artefact. We recommend that (i) the minimum count of testate
134 amoebae in peatland palaeohydrological studies (~100 individuals – see Payne and Mitchell, 2008)
135 should exclude WISTs; and that (ii) WISTs are excluded during transfer function application (i.e.
136 Swindles et al., 2019) to ensure the development of robust water-table reconstructions unaffected by
137 relatively minor, but potentially significant, taphonomic issues.

138

139 **Author contributions**

140 G.T.S., T.P.R. and M.J.A. conceived the project and carried out the research. T.G.S. and R.E.F. assisted
141 with data visualisation using R. G.T.S., M.J.A., T.P.R., M.L., M.M.K, T.G.S., R.E.F and E.A.D.M.
142 wrote the manuscript.

143

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155 of Waterloo, Canada.

156

157 **Appendix A. Supplementary data**

158 Supplementary data associated with this article can be found, in the online version, at [XXXX](#).

159

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234

235 **Figure and table captions**

236 **Fig. 1.** Location of study sites. Refer to Table 1 for site names.

237 **Fig. 2.** Water-table reconstructions from our study sites (cm below peatland surface). Blue lines are
238 reconstructions following removal of WISTs; Black lines are reconstructions based on all taxa.
239 Bootstrap errors are shown as grey lines. Red bars indicate the percentage abundance of WISTs. Sites
240 shown: Akerlanna Romosse, Altabergsmossen, Amburneaux, Ardkill, Ballyduff and Barschpfuhl.

241 **Fig. 3.** Water-table reconstructions from our study sites (cm below peatland surface). Blue lines are
242 reconstructions following removal of WISTs; Black lines are reconstructions based on all taxa.
243 Bootstrap errors are shown as grey lines. Red bars indicate the percentage abundance of WISTs. Sites
244 shown: Butterburn, Cloonoolish, Dead Island, Derragh, Gazwa and Gullbergbymossen.

245 **Fig. 4.** Water-table reconstructions from our study sites (cm below peatland surface). Blue lines are
246 reconstructions following removal of WISTs; Black lines are reconstructions based on all taxa.
247 Bootstrap errors are shown as grey lines. Red bars indicate the percentage abundance of WISTs. Sites
248 shown: Izery, Jelenia Wyspa, Keighley Moor, Kontolanrahka, Kusowo and Lappmyran.

249 **Fig. 5.** Water-table reconstructions from our study sites (cm below peatland surface). Blue lines are
250 reconstructions following removal of WISTs; Black lines are reconstructions based on all taxa.
251 Bootstrap errors are shown as grey lines. Red bars indicate the percentage abundance of WISTs. Sites
252 shown: Lille Vildmose, Linje, Malham, Mannikjarve, Mauntschas and Mechacz.

253 **Fig. 6.** Water-table reconstructions from our study sites (cm below peatland surface). Blue lines are
254 reconstructions following removal of WISTs; Black lines are reconstructions based on all taxa.
255 Bootstrap errors are shown as grey lines. Red bars indicate the percentage abundance of WISTs. Sites
256 shown: Praz Rodet, Slieveanorra, Slowinskie, Stazki, Stordalen and Taul Muced.

257 **Fig. 7.** Percentage of WISTs in each site plotted against age (Year CE) for each region and all sites.

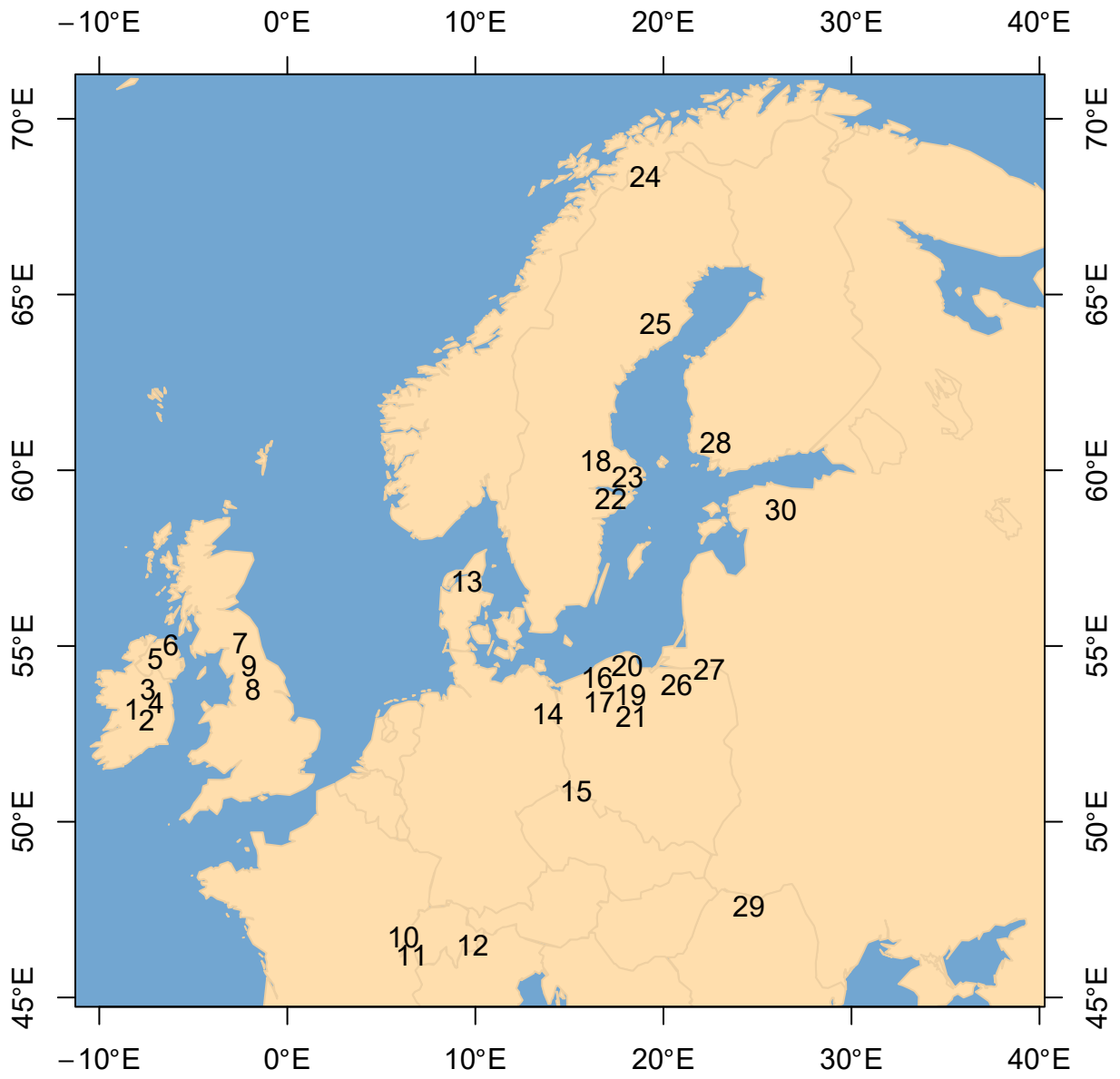
258 **Fig. 8.** Graphs showing the effect of WISTs on water-table reconstructions: (a) Water-table depth
259 reconstruction following removal of WISTs from the core samples against water-table reconstruction
260 based on all taxa (a linear regression line is shown); (b) Difference between water-table reconstructions
261 based on all taxa and water-table reconstructions following removal of WISTs from the core samples
262 against percentage of WISTs in the sample (a loess smooth is shown); (c) Water-table depth
263 reconstruction following removal of WISTs from the transfer function model against water-table
264 reconstruction based on all taxa (a linear regression line is shown); (d) Difference between water-table
265 reconstructions based on all taxa and water-table reconstruction following removal of WISTs from the
266 transfer function model against percentage of WISTs in the sample (a loess smooth is shown). Only
267 samples containing WISTs were included in the analysis.

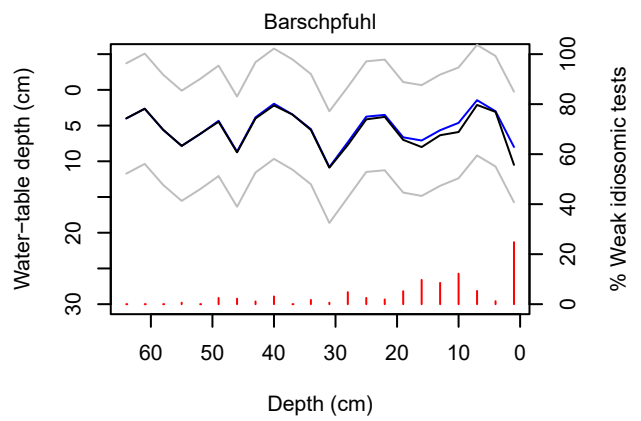
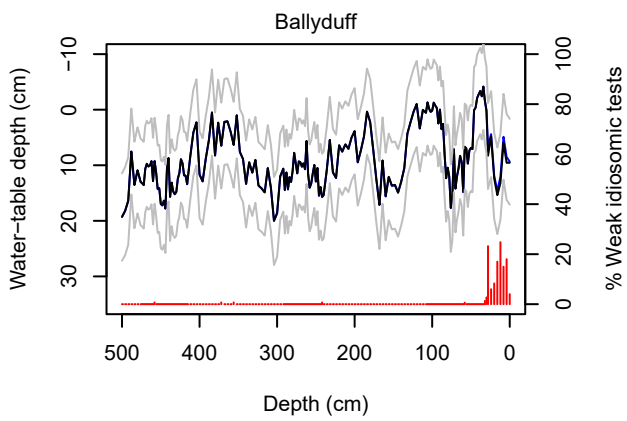
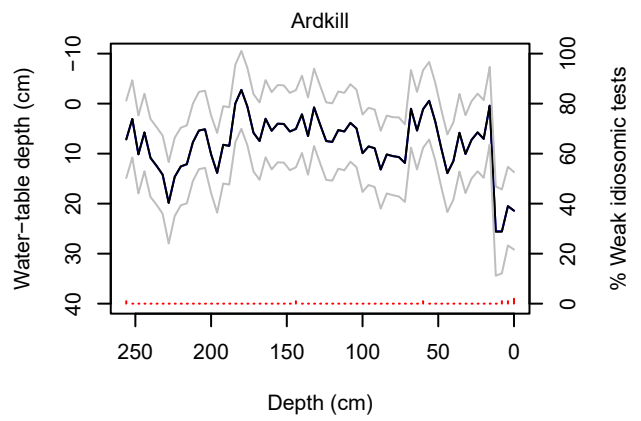
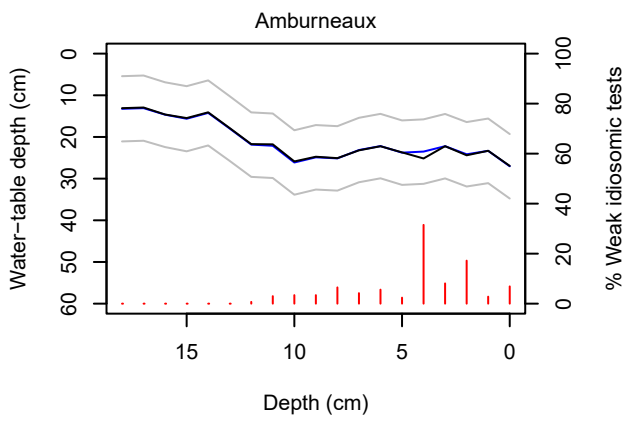
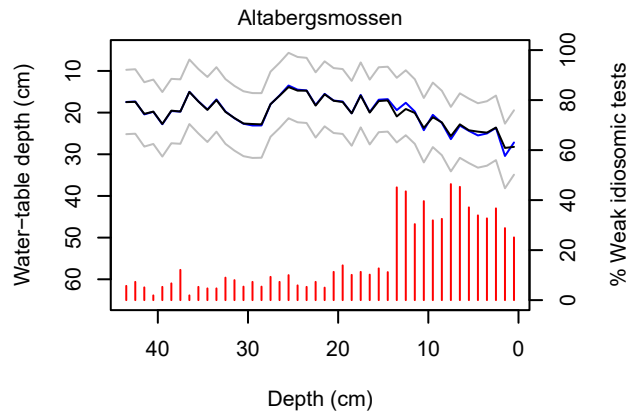
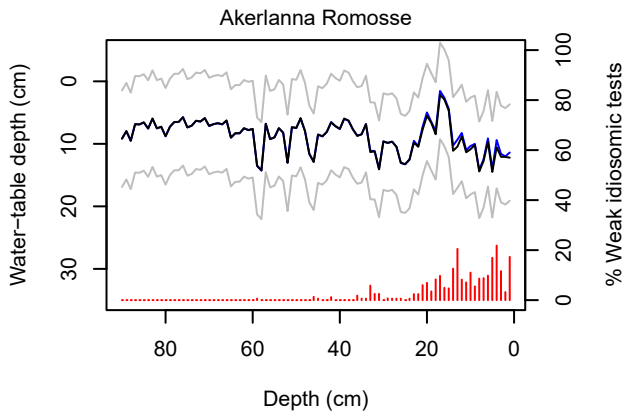
268 **Fig. 9.** Difference between water-table reconstructions based on all taxa and water-table reconstructions
269 following removal of WISTs from the core samples against percentage of WIST taxa in the sample (a
270 loess smooth is shown when there are enough data); (a) *Corythion–Trinema* type; (b) Total *Euglypha*
271 type; (c) *Sphenoderia* type; (d) *Tracheleuglypha dentata* type.

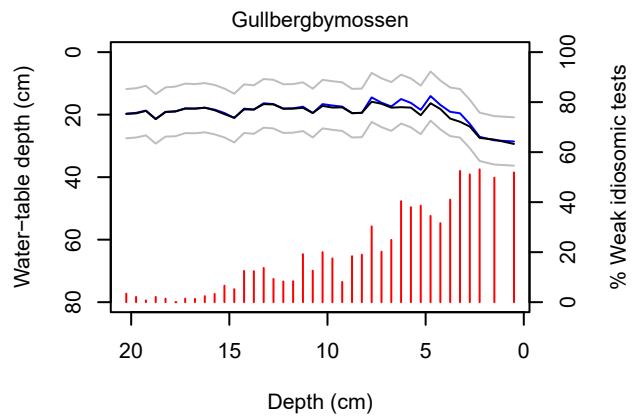
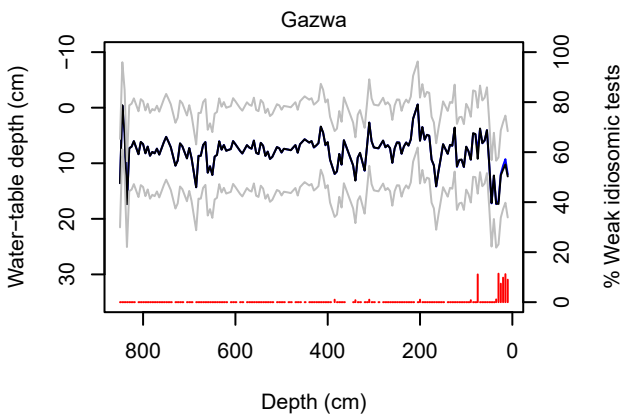
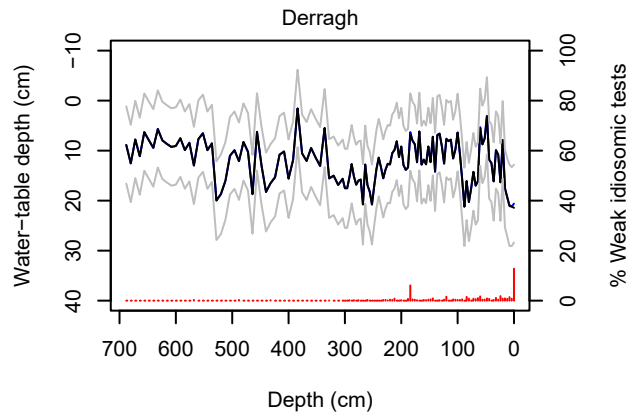
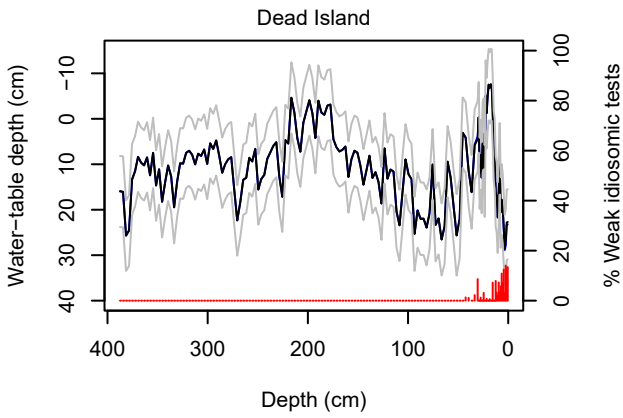
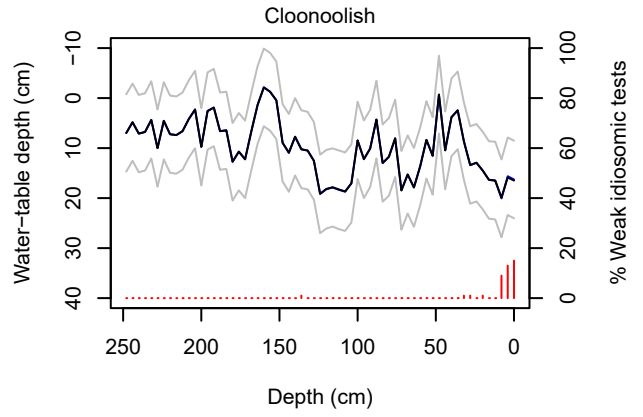
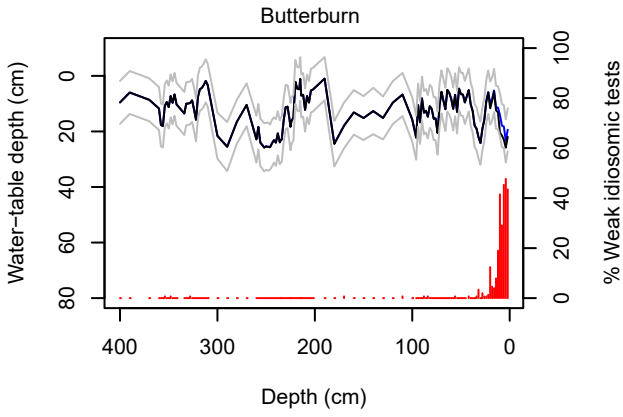
272 **Table 1.** Study sites.

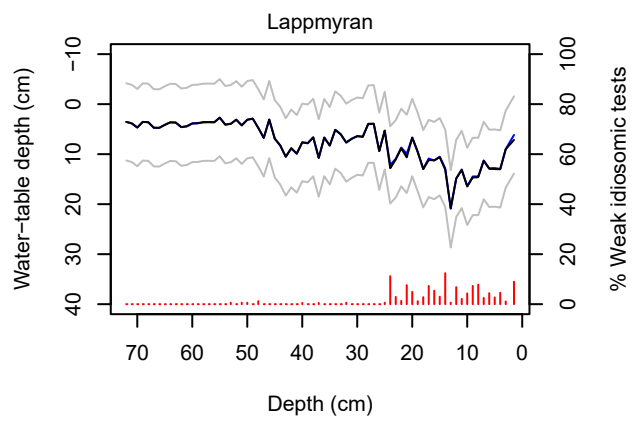
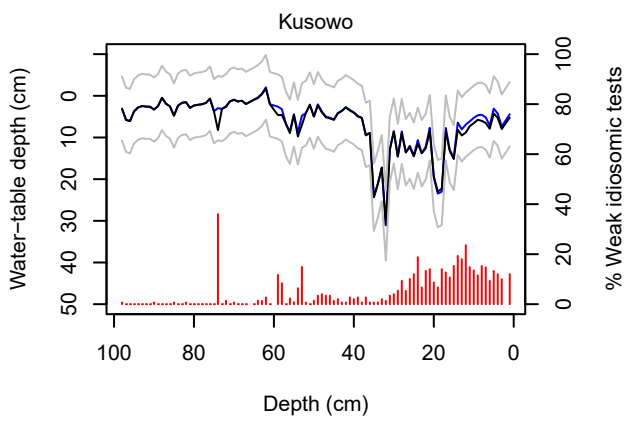
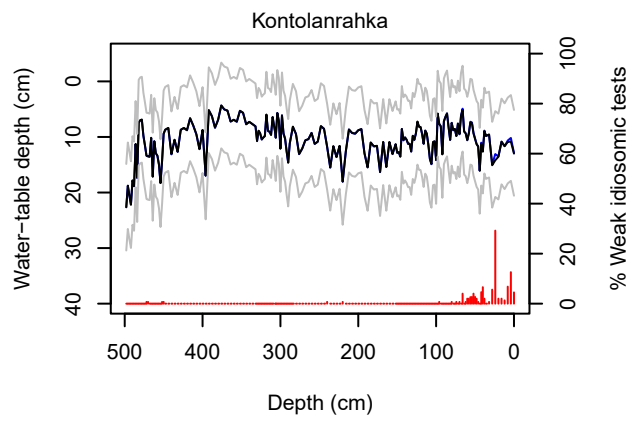
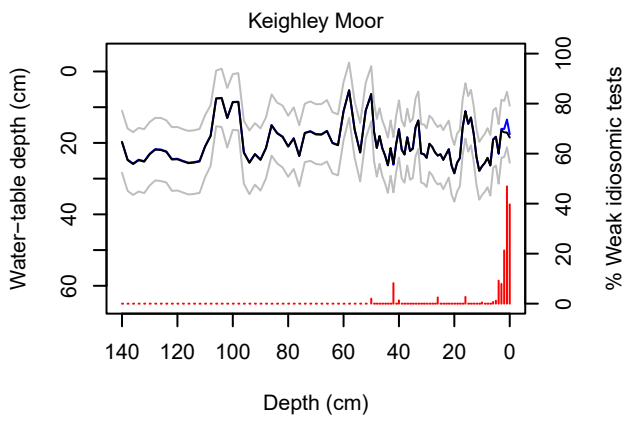
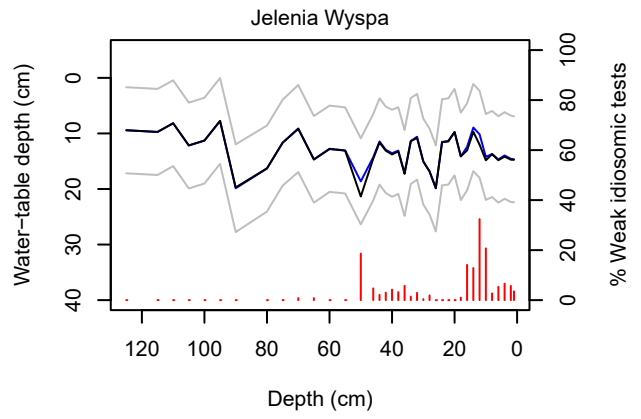
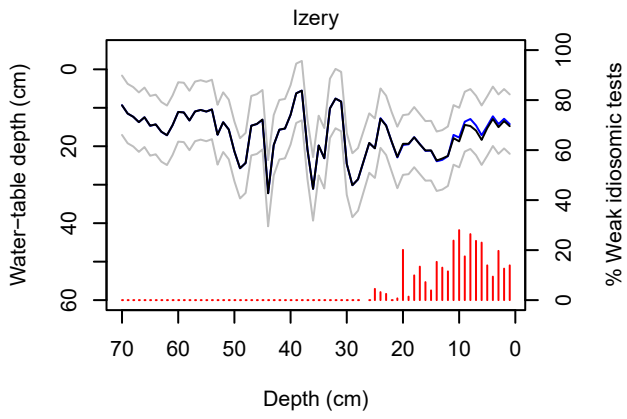
273 **Table 2.** Transfer function performance for the full and no-WISTs training sets. The transfer function
274 model is based on weighted averaging-tolerance downweighted regression (with inverse deshrinking).
275 The values derived from “leave-one-out” (LOO) cross-validation are shown. The results show that the
276 difference between the two models is negligible.

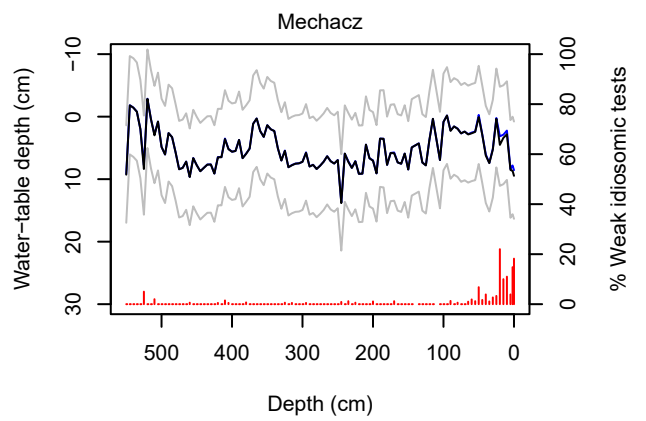
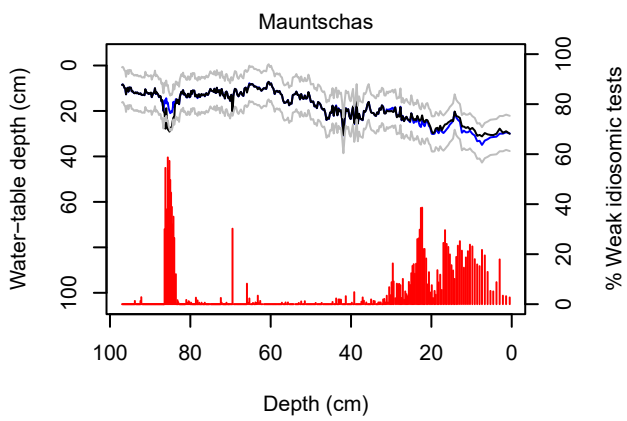
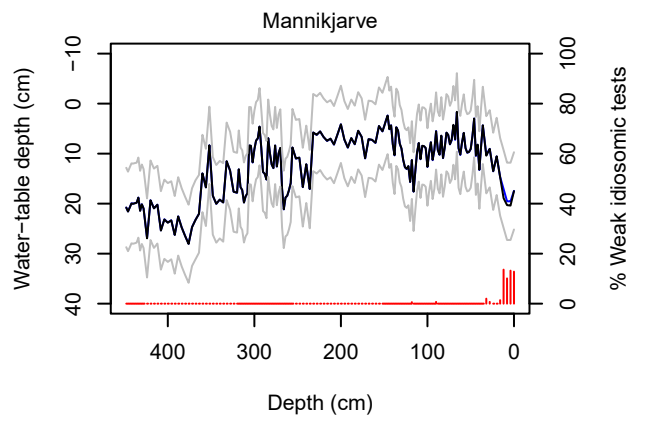
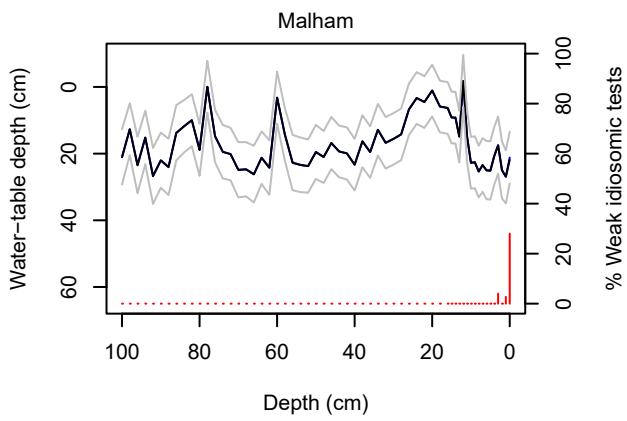
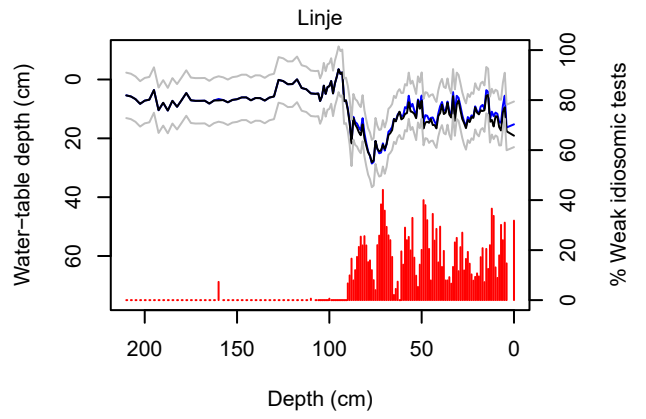
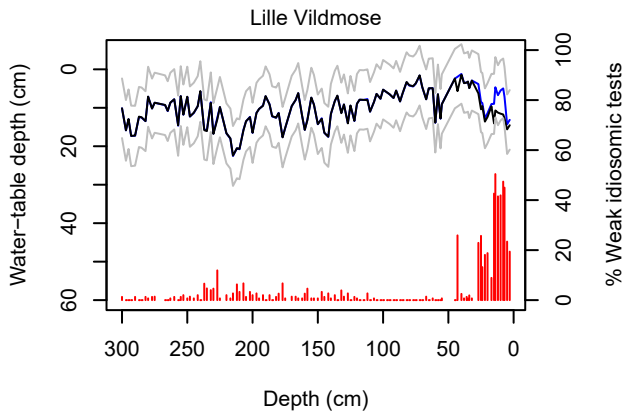
277 **Supplementary material 1.** Bayesian age-depth models for each site. Please see Swindles et al. (2019)
278 for information regarding the methods used and the site chronologies.

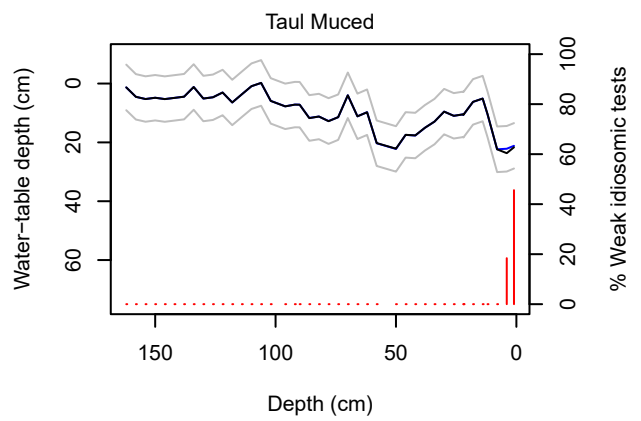
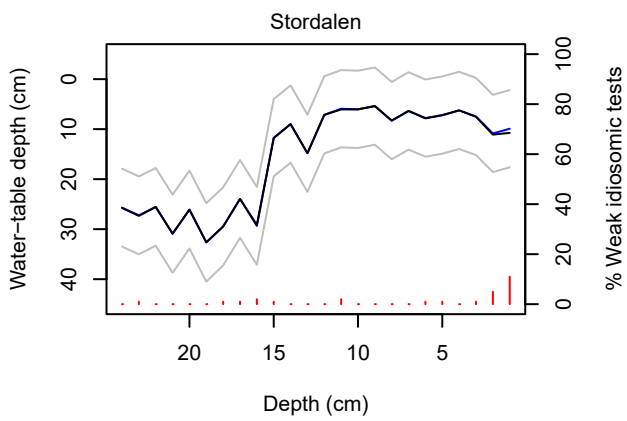
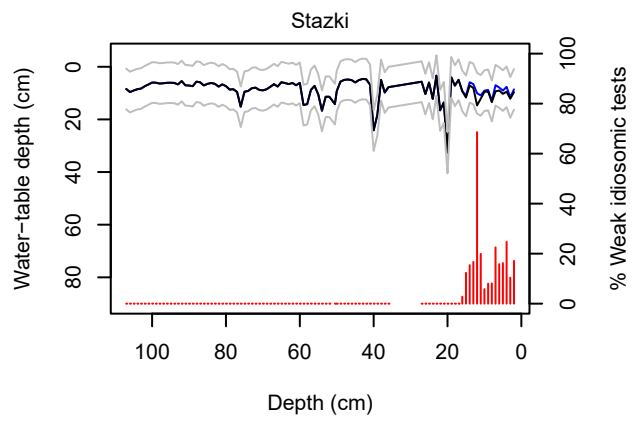
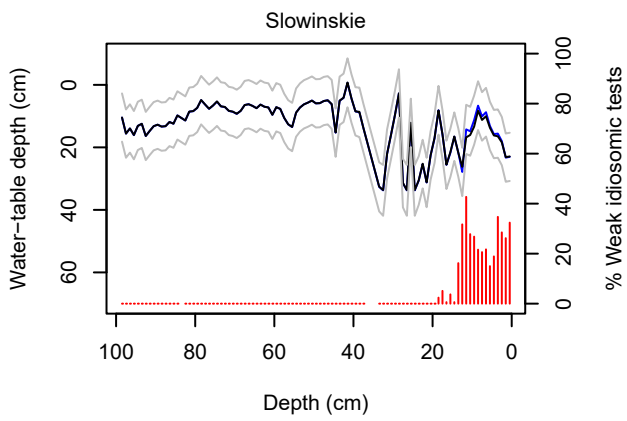
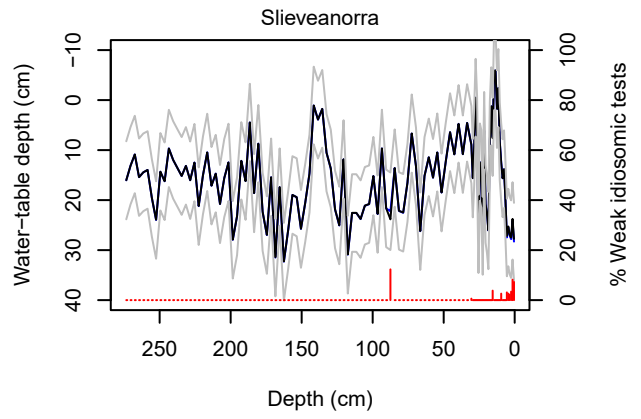
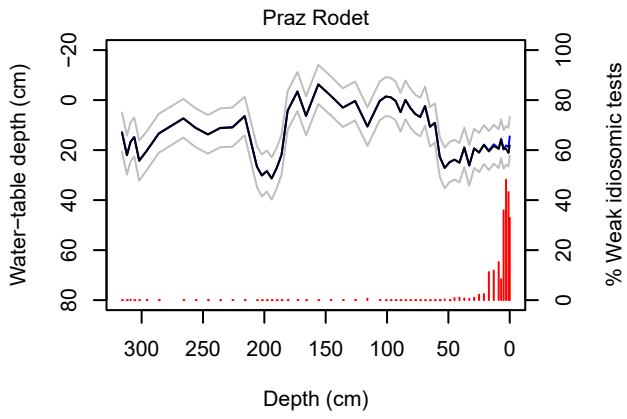




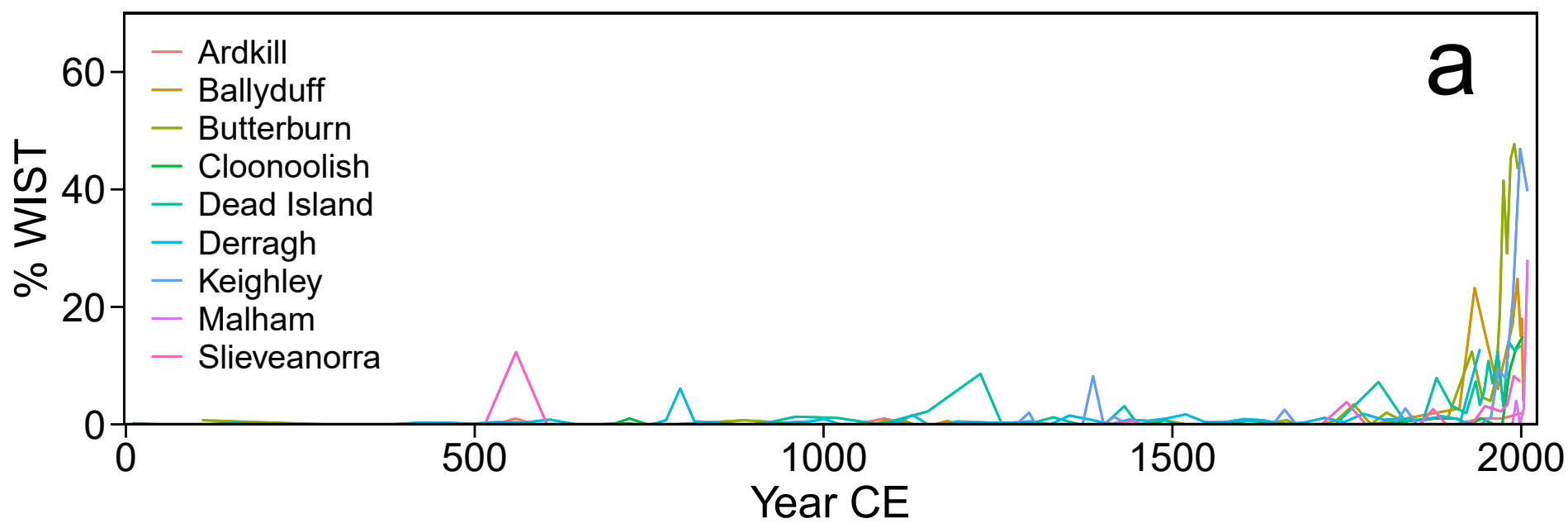




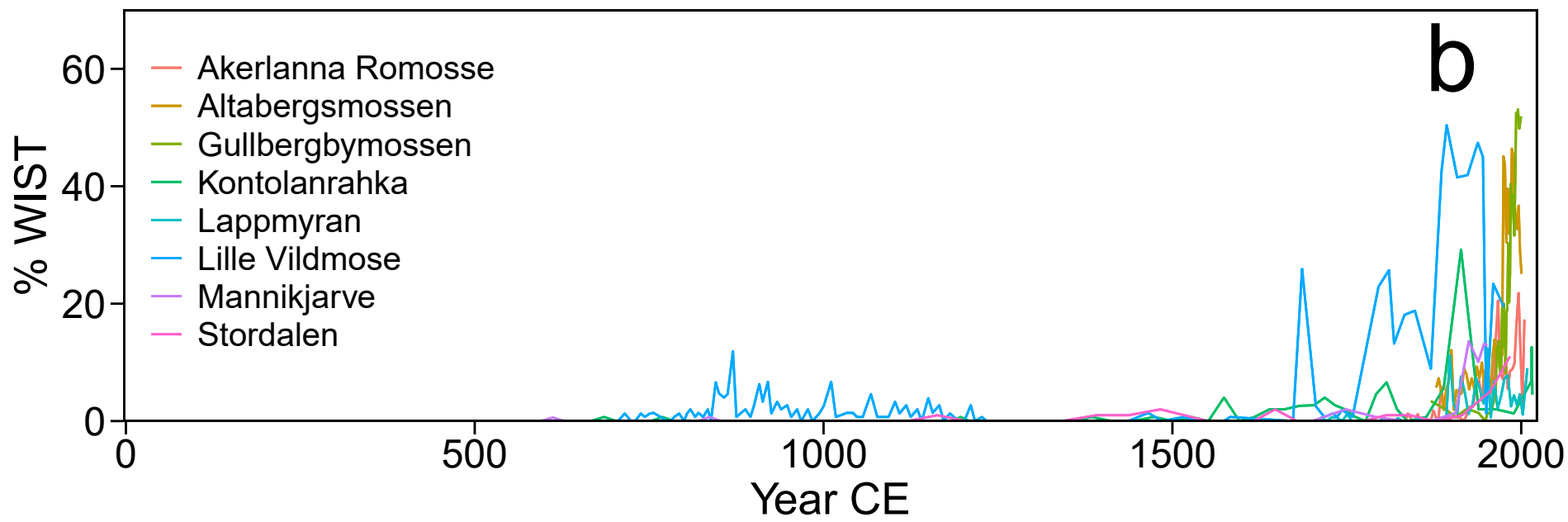




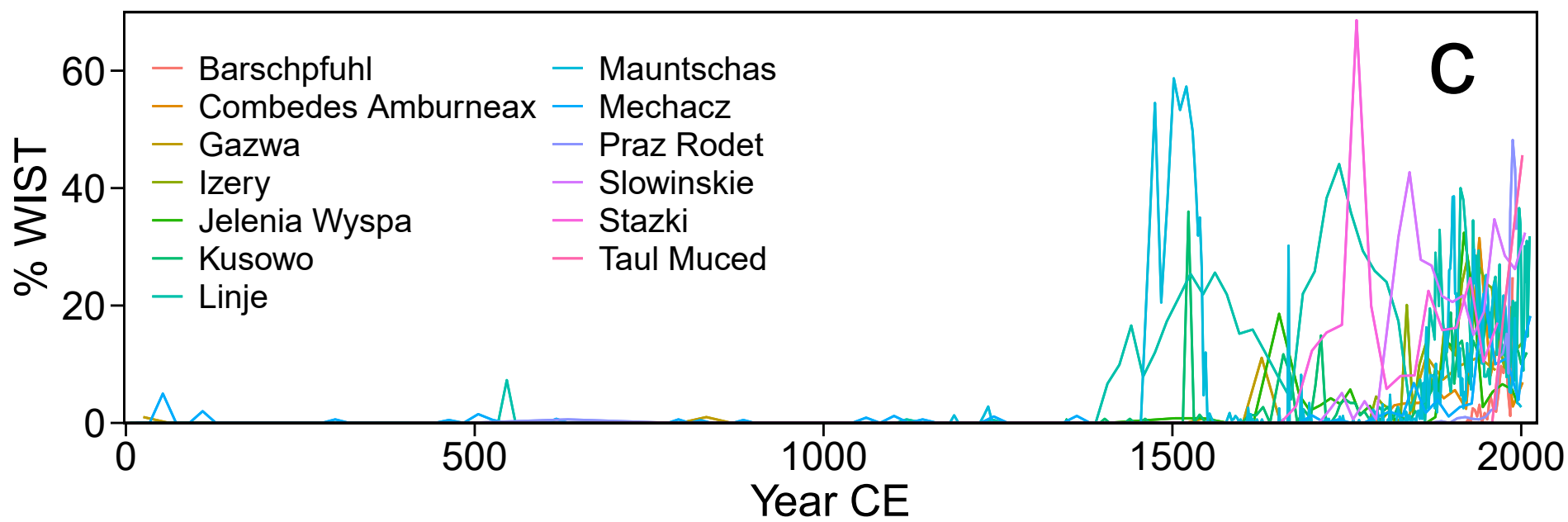
Britain and Ireland



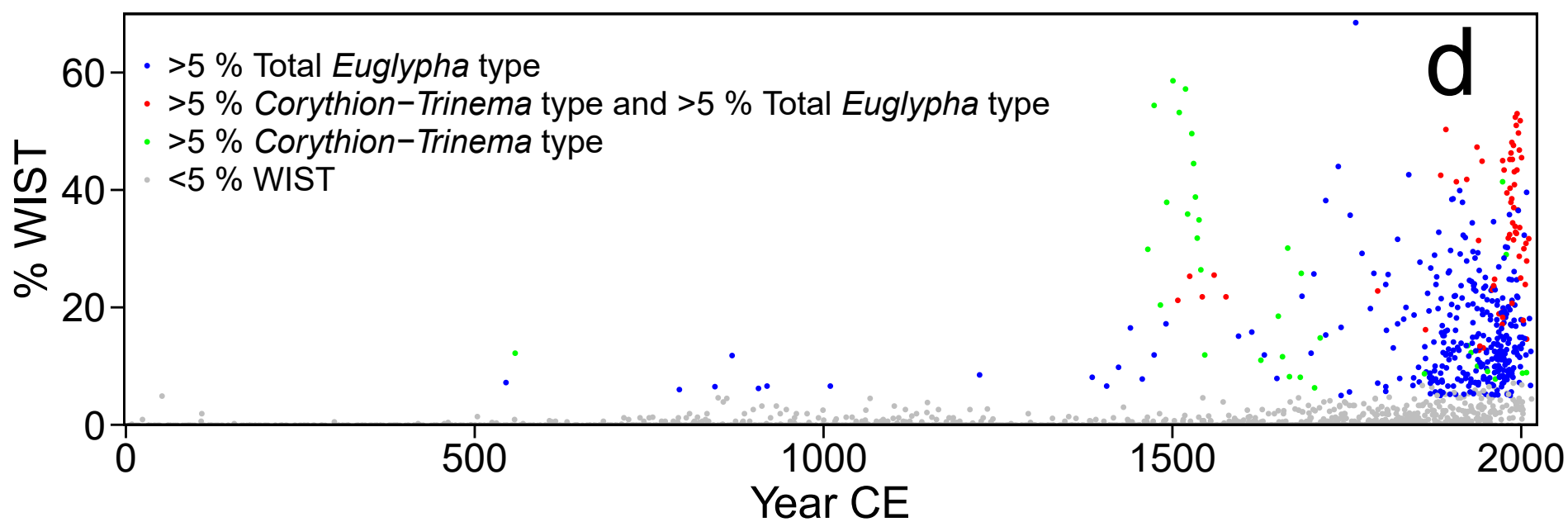
Scandinavia and Baltics

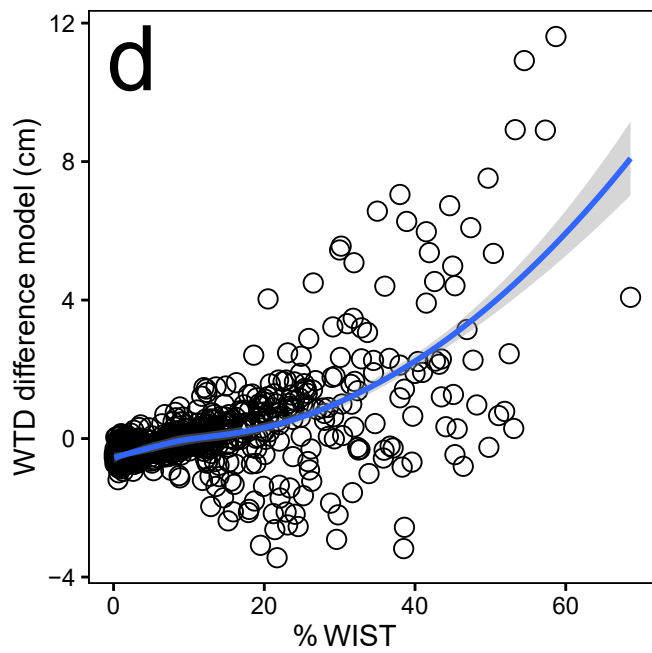
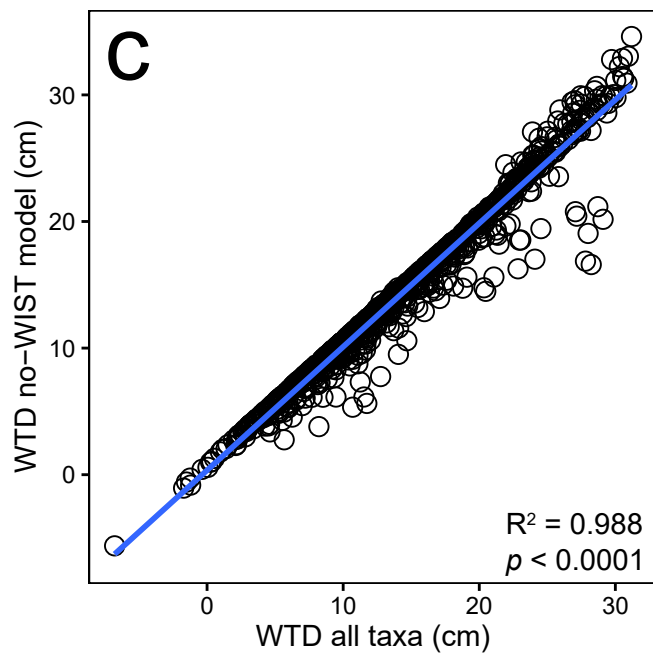
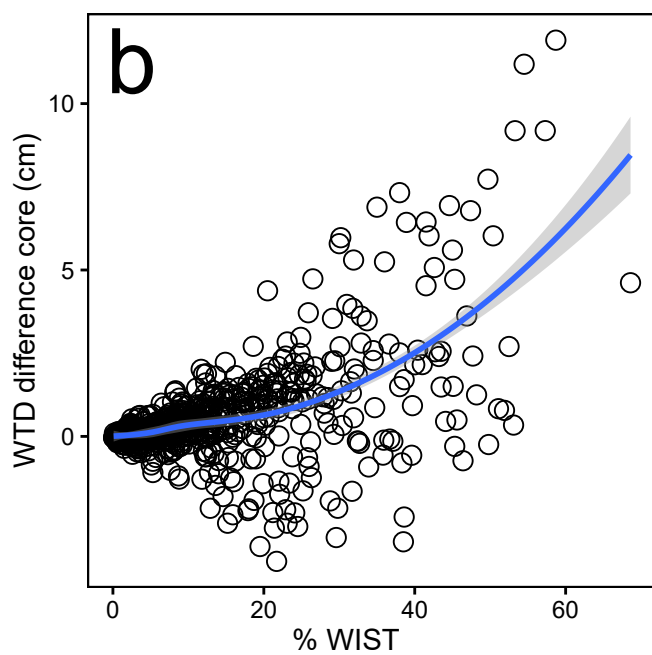
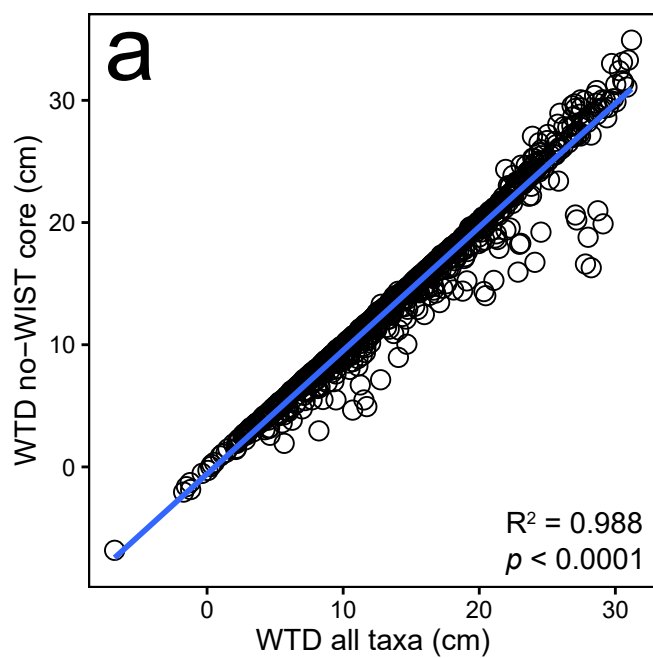


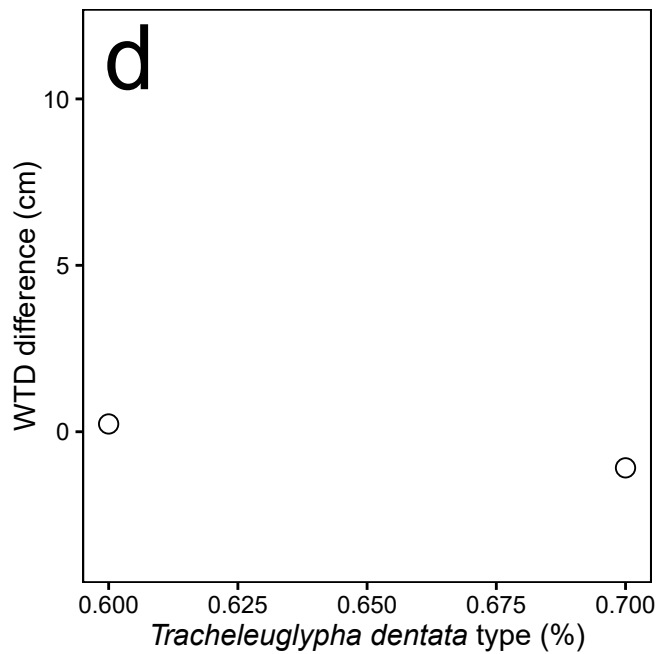
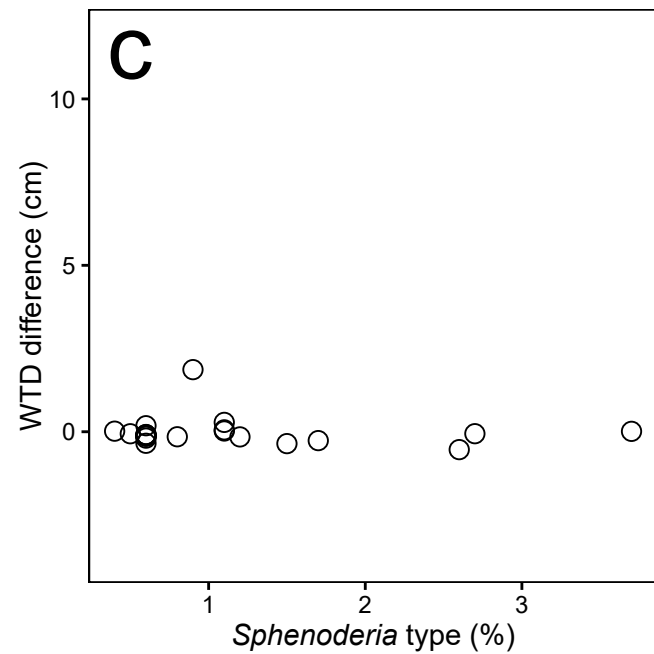
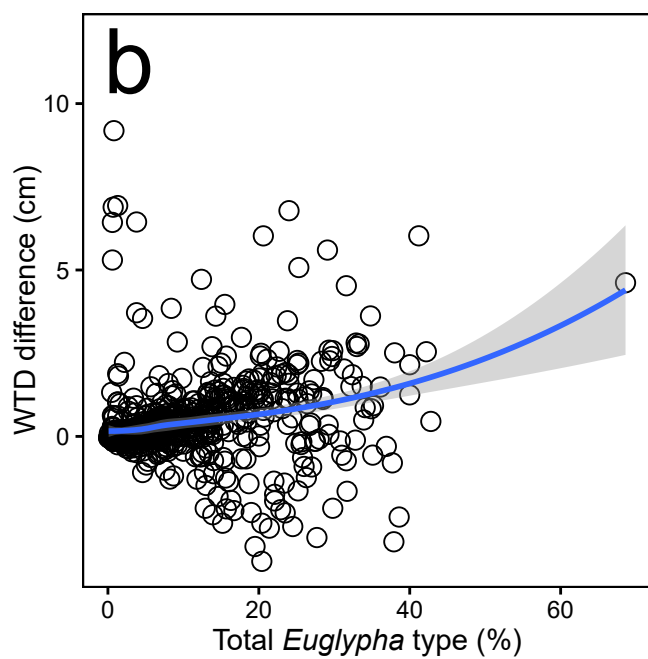
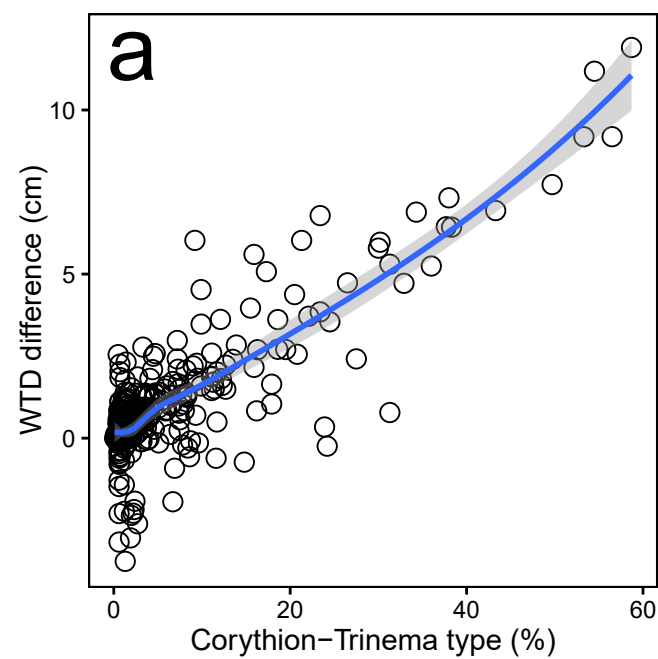
Continental Europe



All sites







Site number	Site name	Region	Country	Latitude	Longitude
1	Cloonoolish	Britain & Ireland	Ireland	53.1865	-8.2569
2	Ballyduff	Britain & Ireland	Ireland	53.0807	-7.9925
3	Derragh	Britain & Ireland	Ireland	53.7667	-7.4083
4	Ardkill	Britain & Ireland	Ireland	53.3653	-6.9532
5	Dead Island	Britain & Ireland	Ireland	54.8862	-6.5487
6	Slieveanorra	Britain & Ireland	Ireland	55.0848	-6.1921
7	Butterburn	Britain & Ireland	England	55.0875	-2.5036
8	Malham	Britain & Ireland	England	54.0964	-2.1750
9	Keighley	Britain & Ireland	England	54.4253	-2.0369
10	Praz-Rodet	Continental Europe	Switzerland	46.5667	6.1736
11	Combe des Amburnex	Continental Europe	Switzerland	46.5397	6.2317
12	Mauntschas	Continental Europe	Switzerland	46.4900	9.8544
13	Lille Vildmose	Scandinavia	Denmark	56.8391	10.1896
14	Barschpfuhl	Continental Europe	Germany	53.0558	13.8494
15	Izery	Continental Europe	Poland	50.8519	15.3602
16	Slowinskie	Continental Europe	Poland	54.3619	16.4785
17	Bagno Kusowo	Continental Europe	Poland	53.8078	16.5872
18	Akerlanna Romosse	Scandinavia	Sweden	60.0167	17.3667
19	Jelenia Wyspa	Continental Europe	Poland	53.5918	17.9821
20	Stazki	Continental Europe	Poland	54.4244	18.0833
21	Linje	Continental Europe	Poland	53.1880	18.3098
22	Gullbergbymossen	Scandinavia	Sweden	59.6333	18.4333
23	Altabergsmossen	Scandinavia	Sweden	59.9667	18.6833
24	Stordalen	Scandinavia	Sweden	68.3568	19.0484
25	Lappmyran	Scandinavia	Sweden	64.1647	19.5828
26	Gazwa	Continental Europe	Poland	53.8726	21.2201
27	Mechacz	Continental Europe	Poland	54.3314	22.4419
28	Kontolanrahka	Scandinavia	Finland	60.7833	22.7833
29	Taul Muced	Continental Europe	Romania	47.5739	24.5450
30	Mannikjarve	Scandinavia	Estonia	58.8667	26.2500

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-

WA.inv.tol	RMSEP_{LOO}	R²_{LOO}	Average bias_{LOO}	Maximum bias_{LOO}
Original model (A)	7.72	0.59	0.01	18.66
No WIST model (B)	7.82	0.58	0.02	19.23
<i>Difference (B-A)</i>	<i>0.10</i>	<i>-0.01</i>	<i>0.01</i>	<i>0.57</i>

Supplementary Section

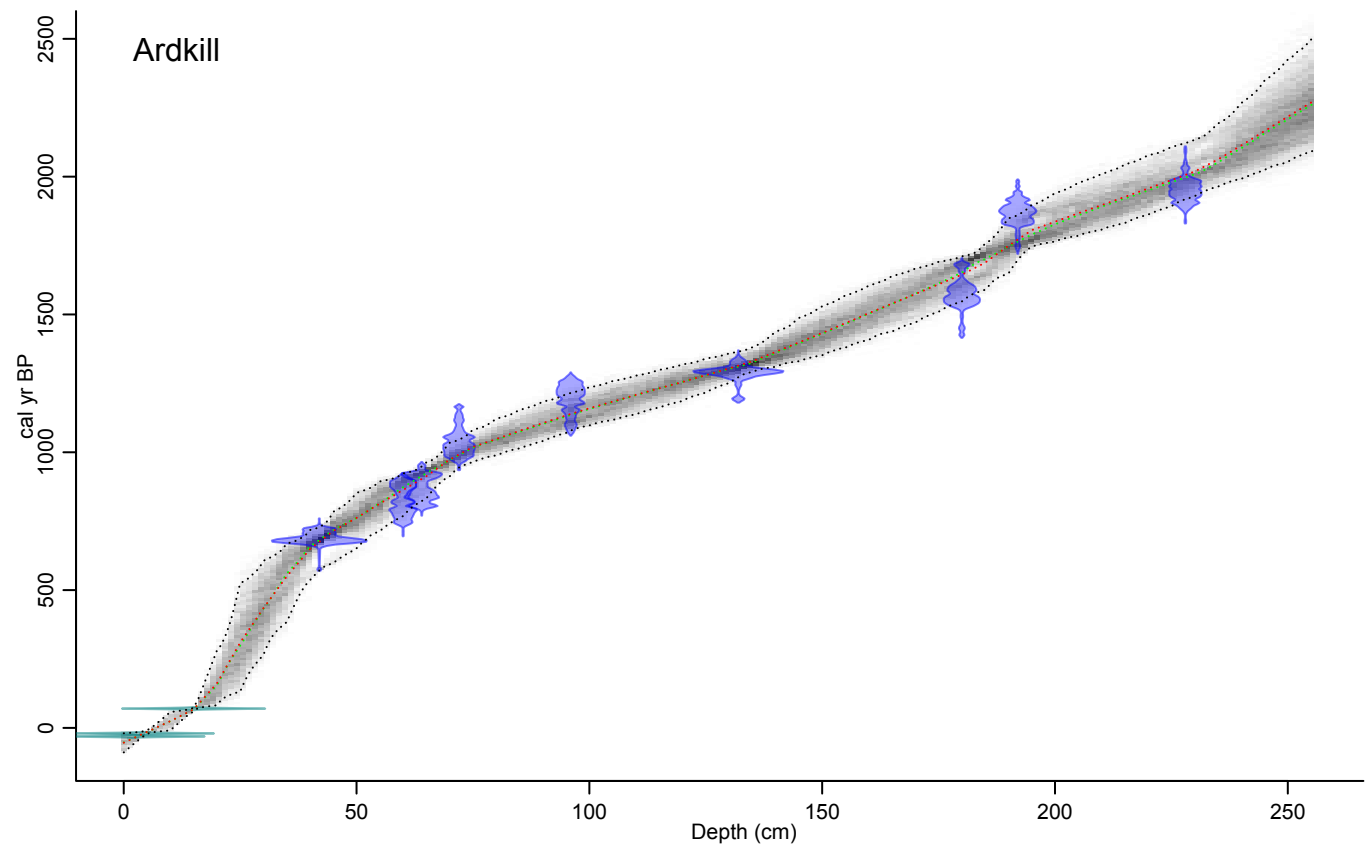
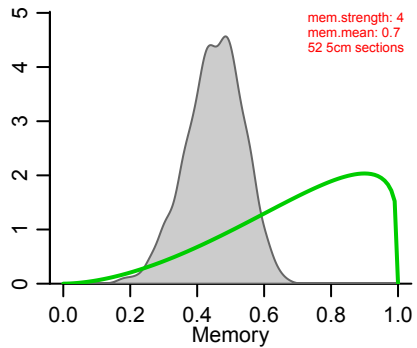
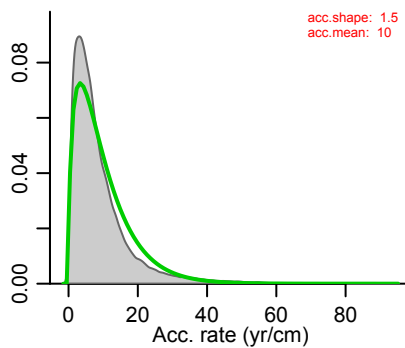
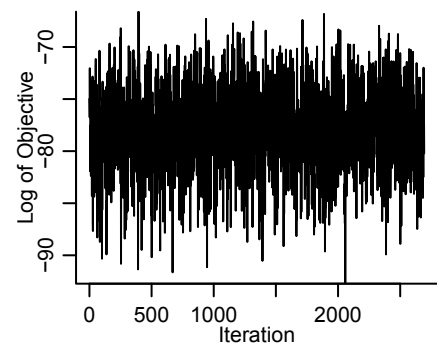
Bayesian age-depth models

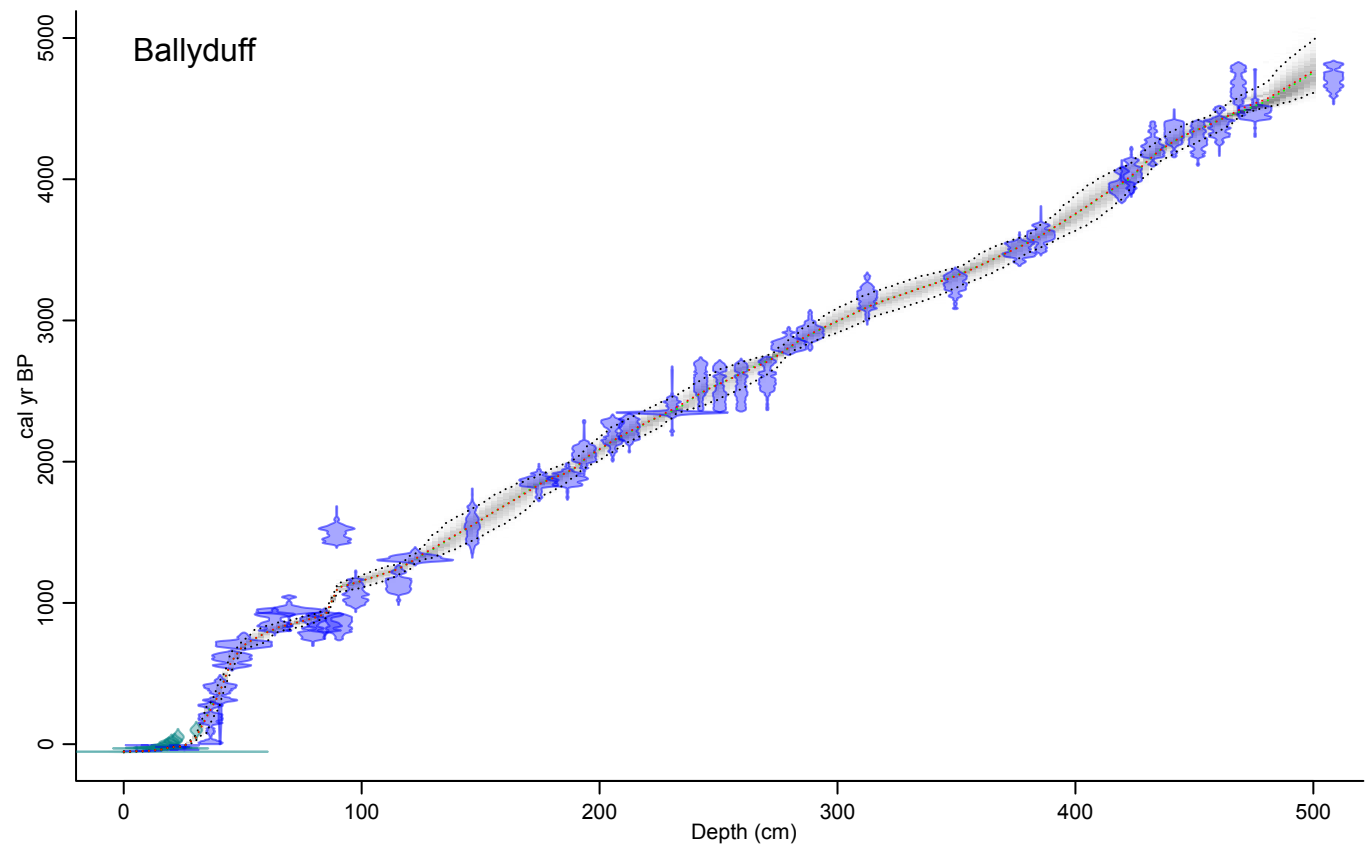
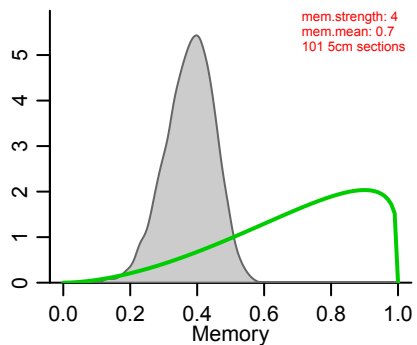
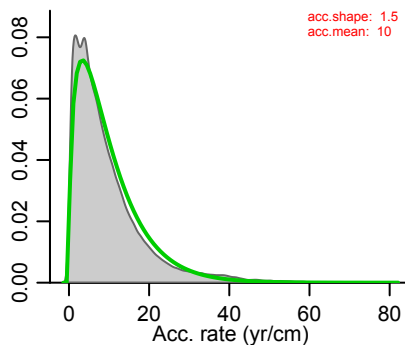
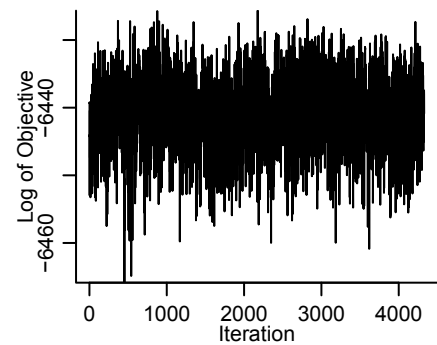
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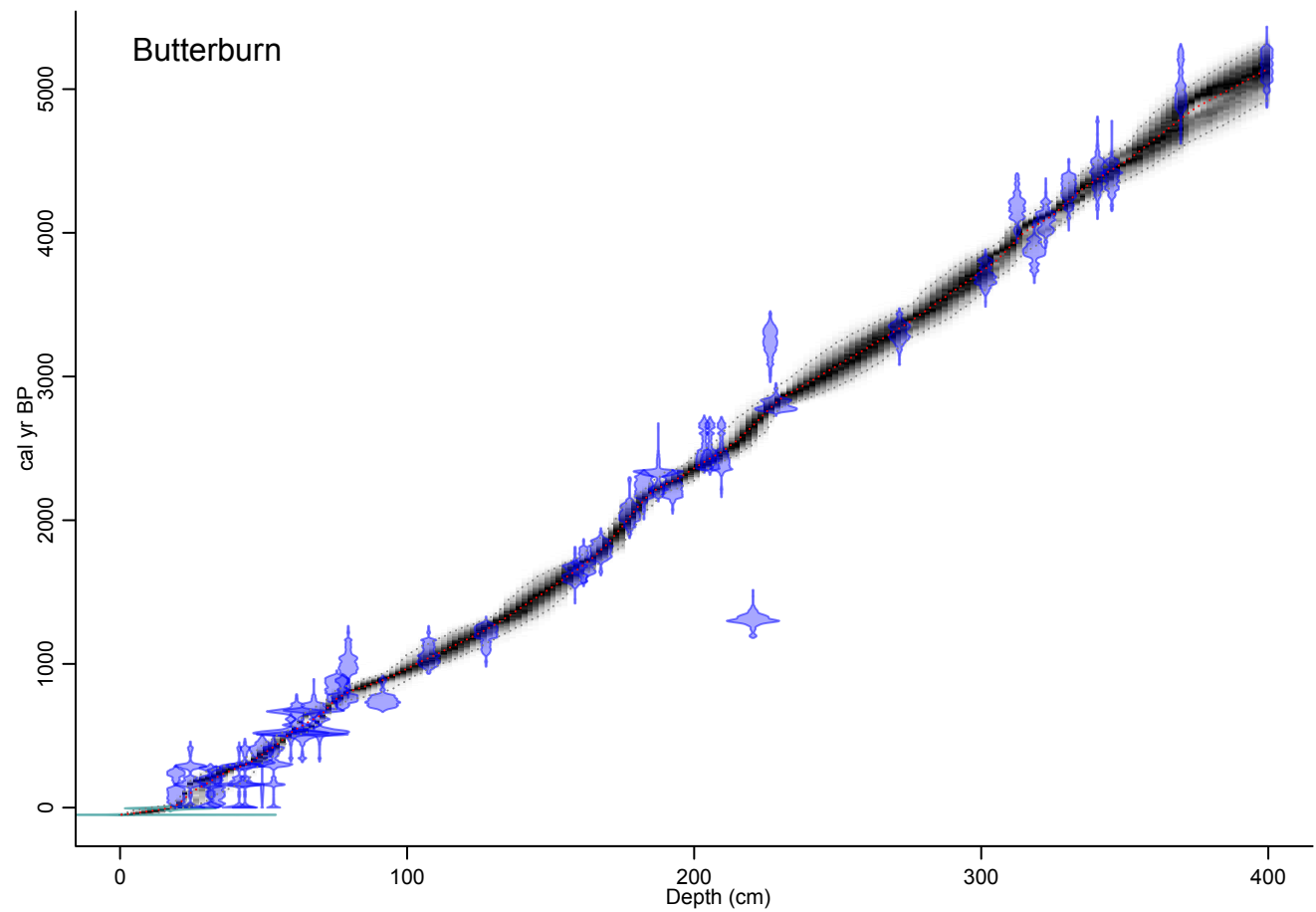
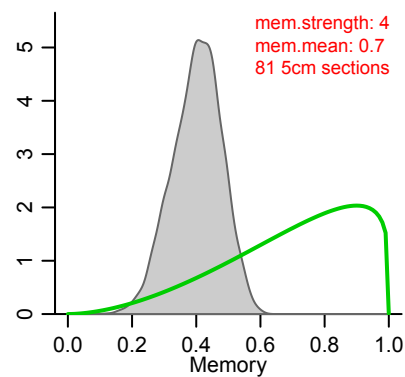
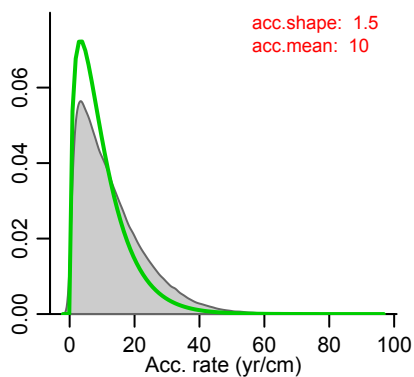
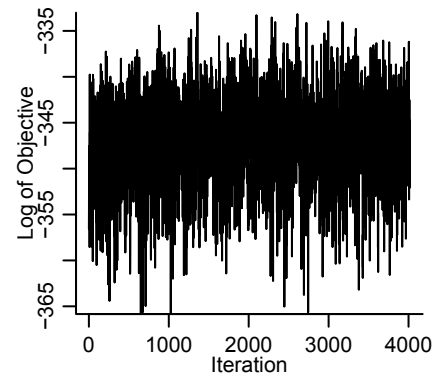
Upper panels depict the MCMC iterations (left; good runs show a stationary distribution with little structure among neighbouring iterations), the prior (green curves) and posterior (grey histograms) distributions for the accumulation rate (middle panel) and memory (right panel). Bottom panel shows the calibrated ^{14}C dates (transparent blue) and the age-depth model (darker greys indicate more likely calendar ages; grey stippled lines show 95% confidence intervals; red curve shows single 'best' model based on the mean age for each depth).

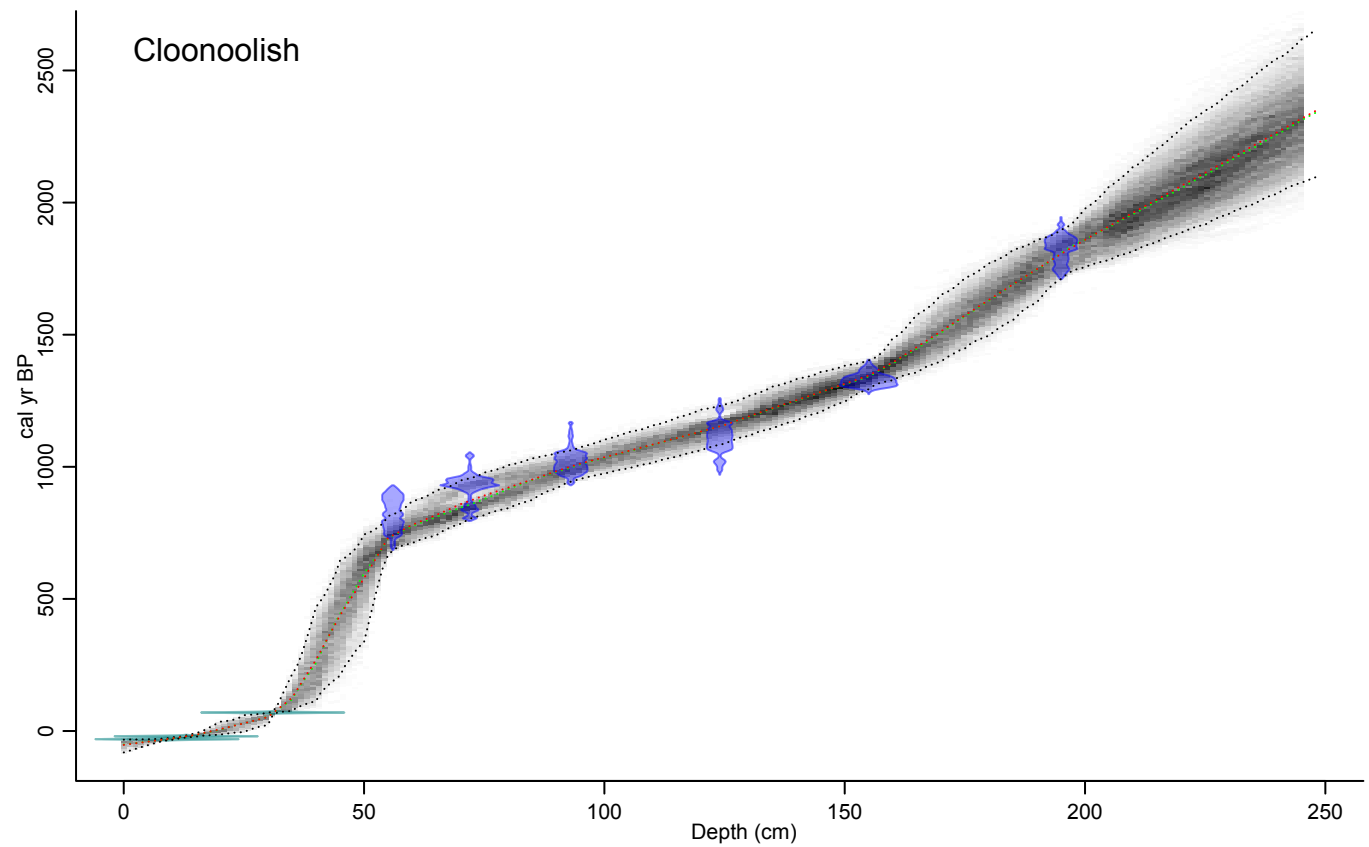
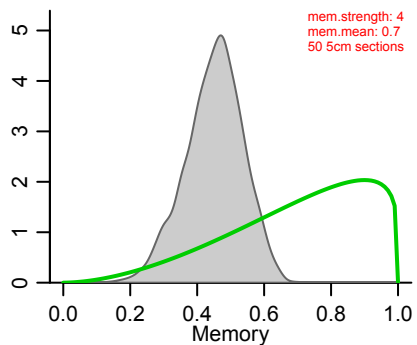
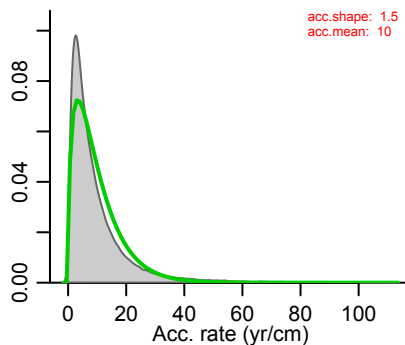
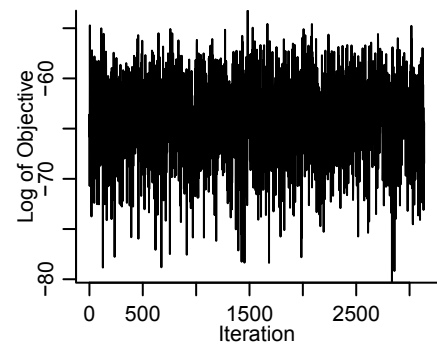
Prior information for accumulation rate and its memory or variability are shown as red text.

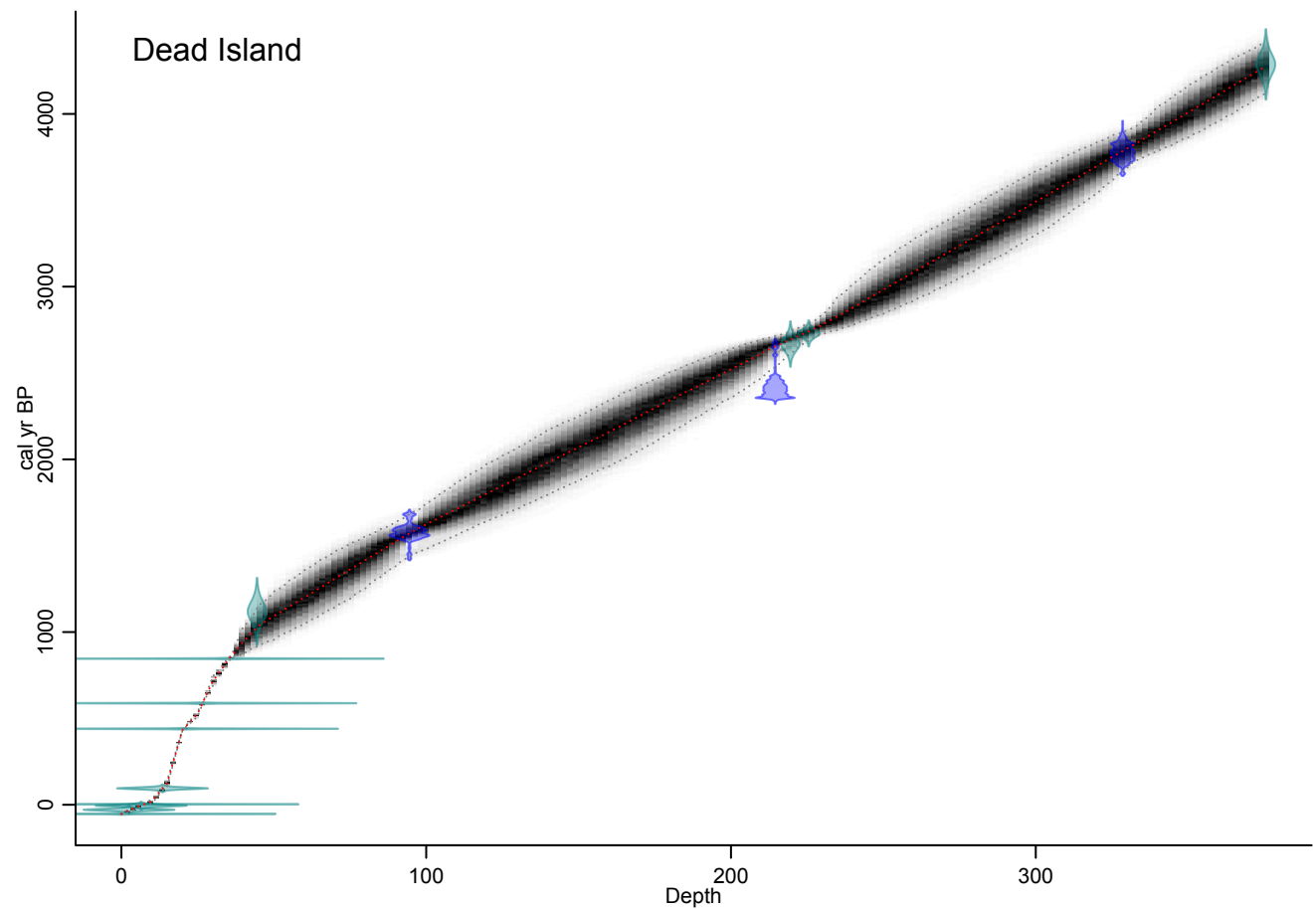
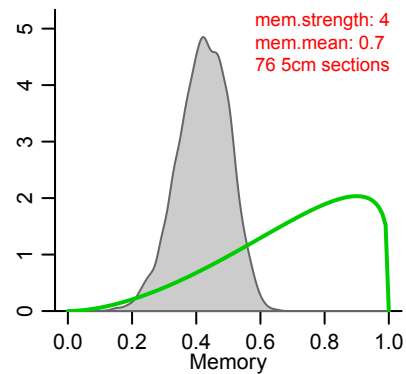
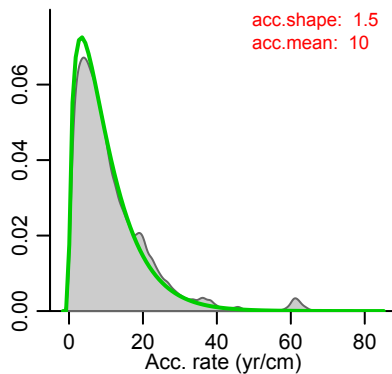
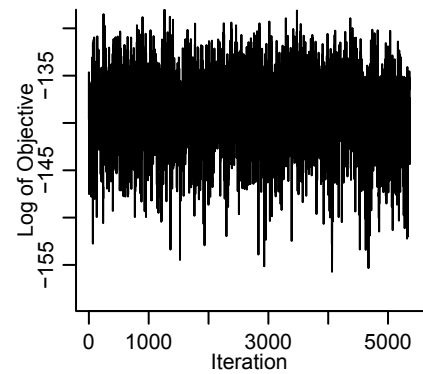
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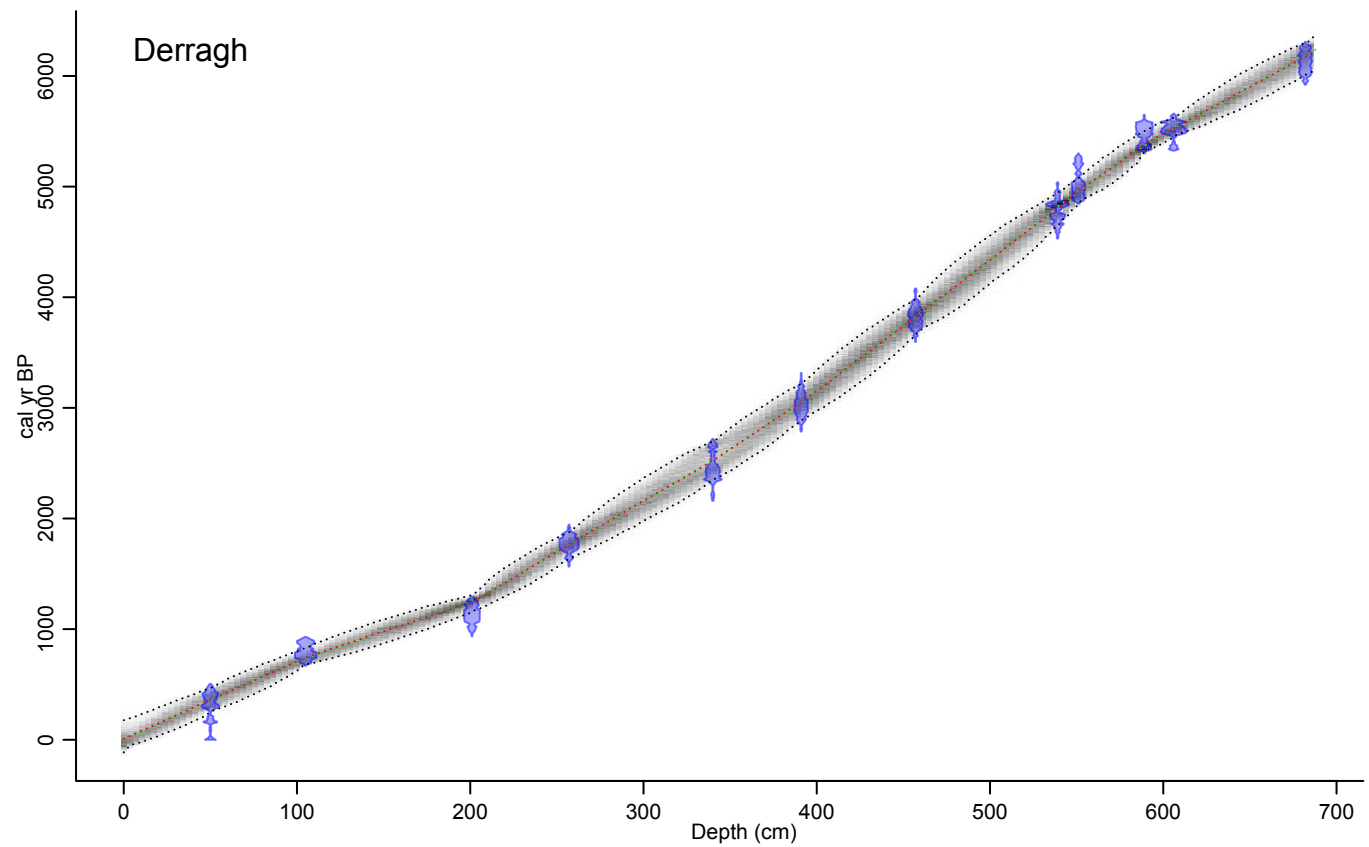
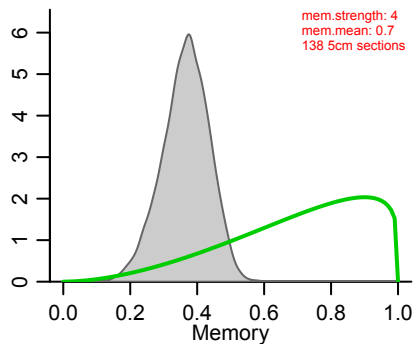
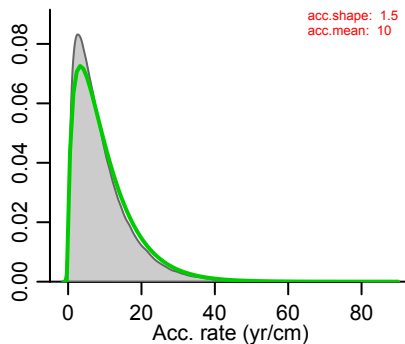
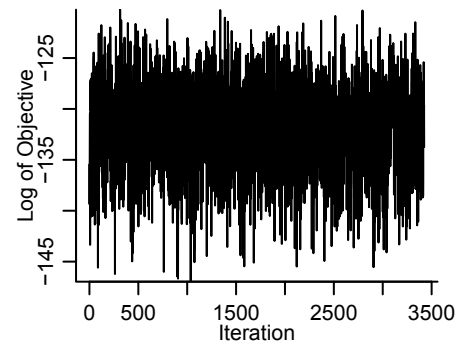


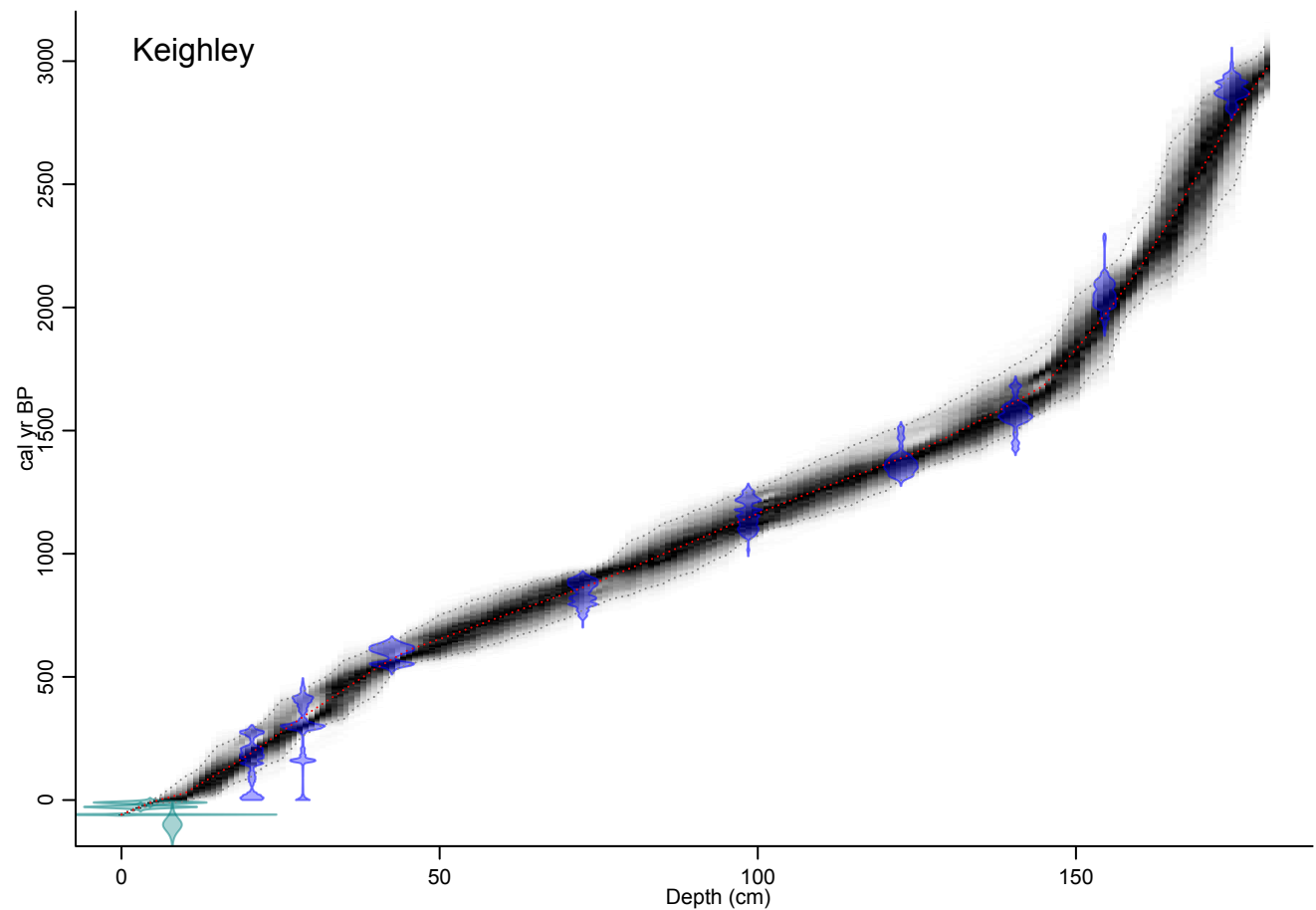
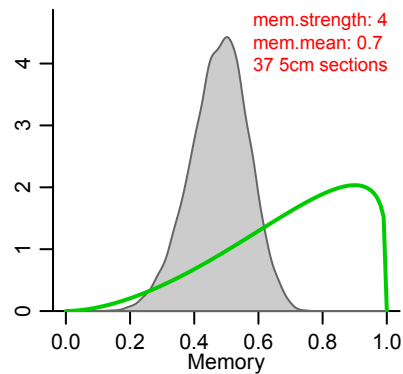
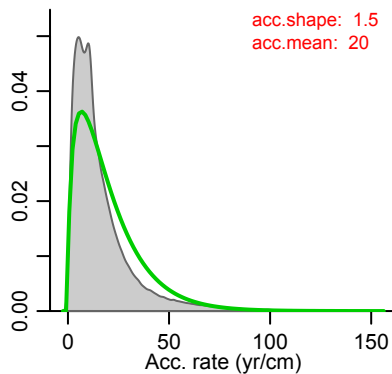
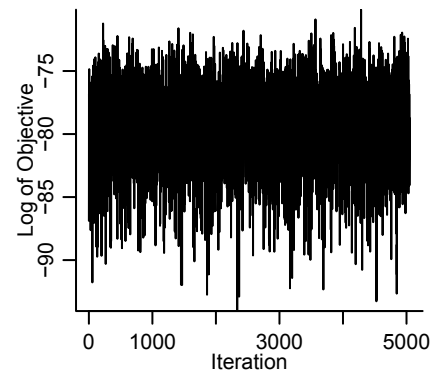


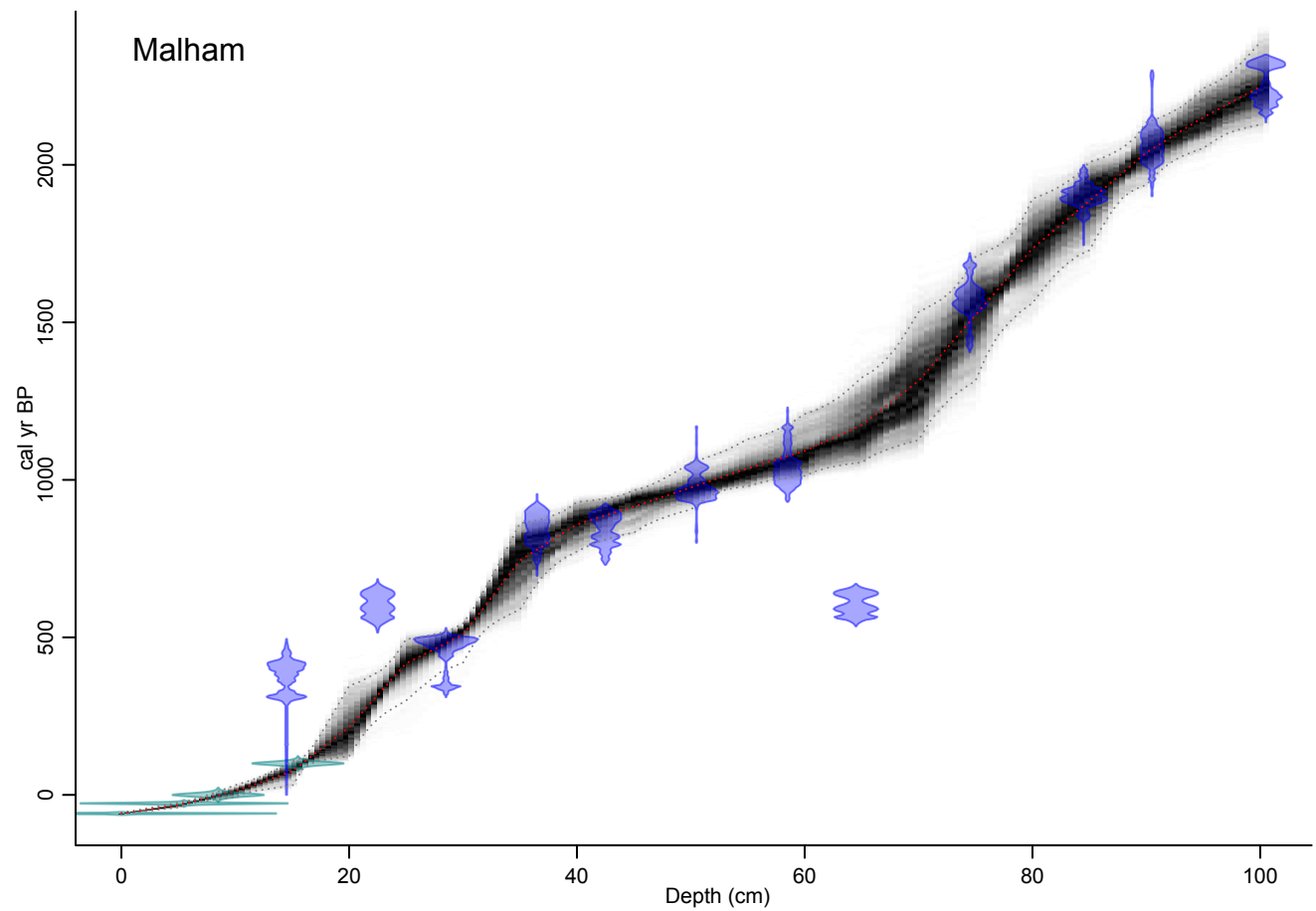
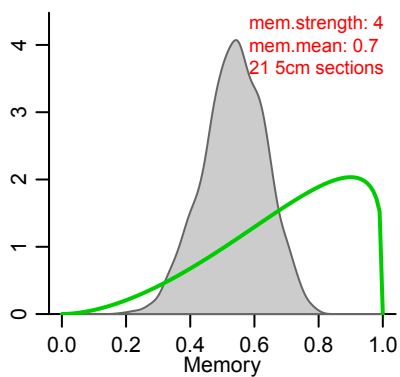
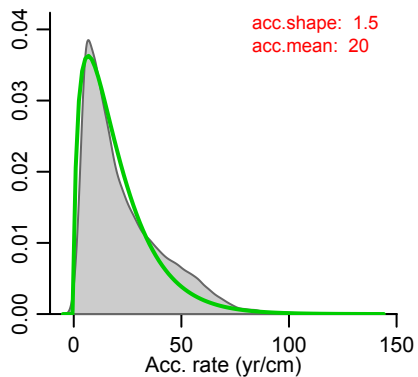
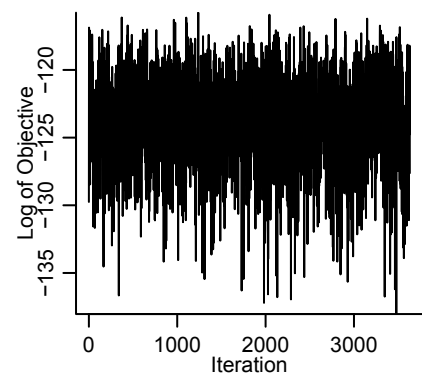


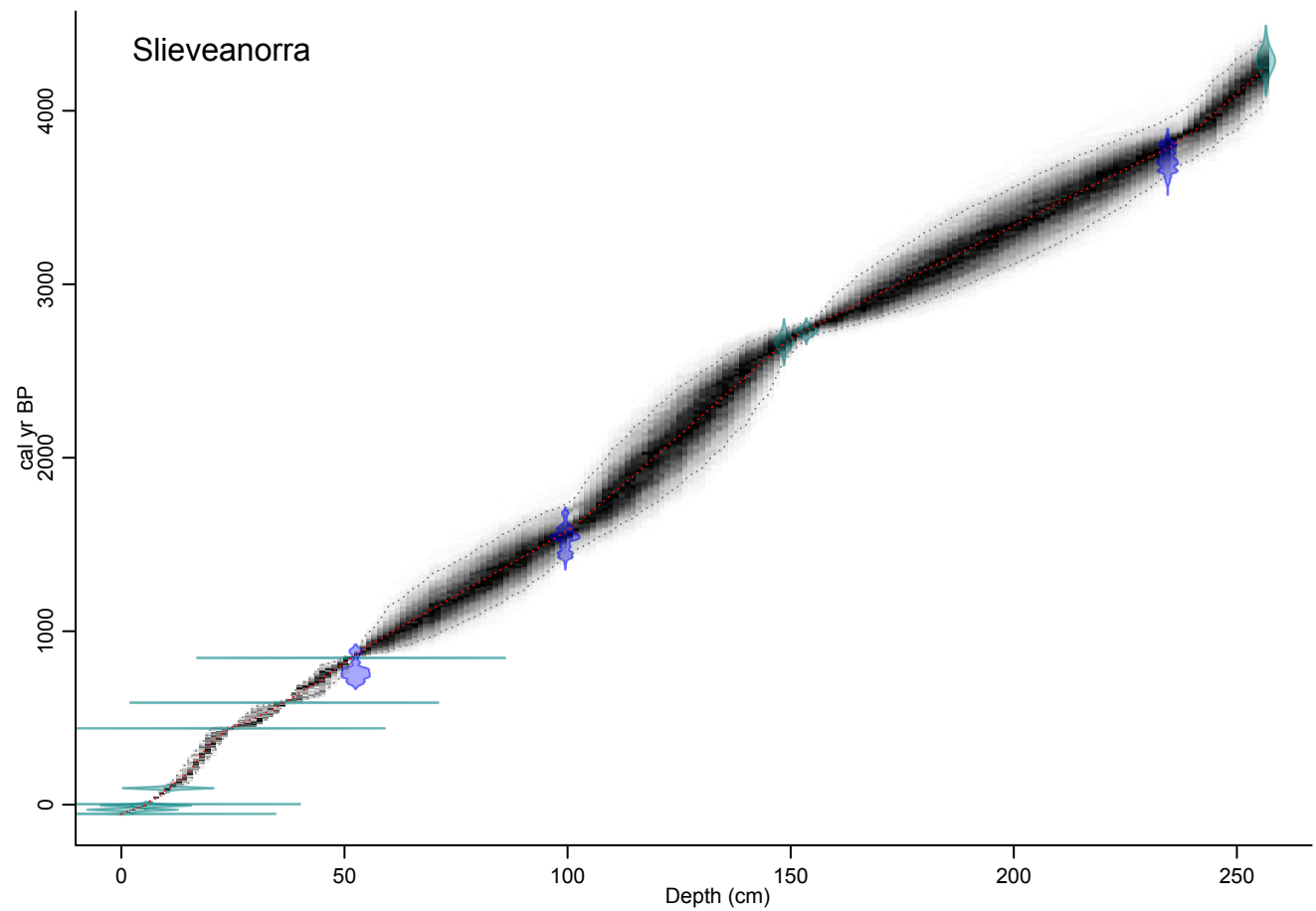
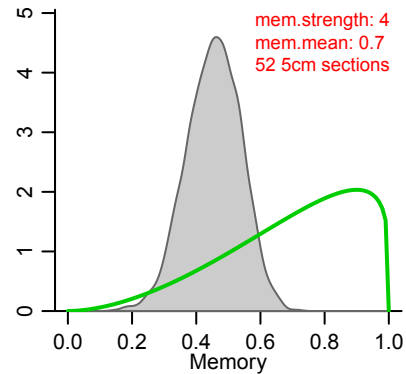
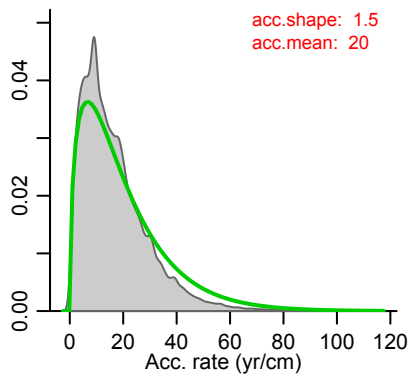
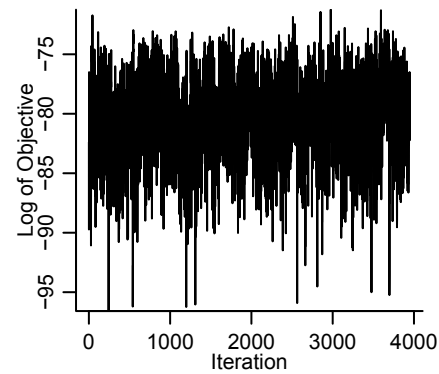


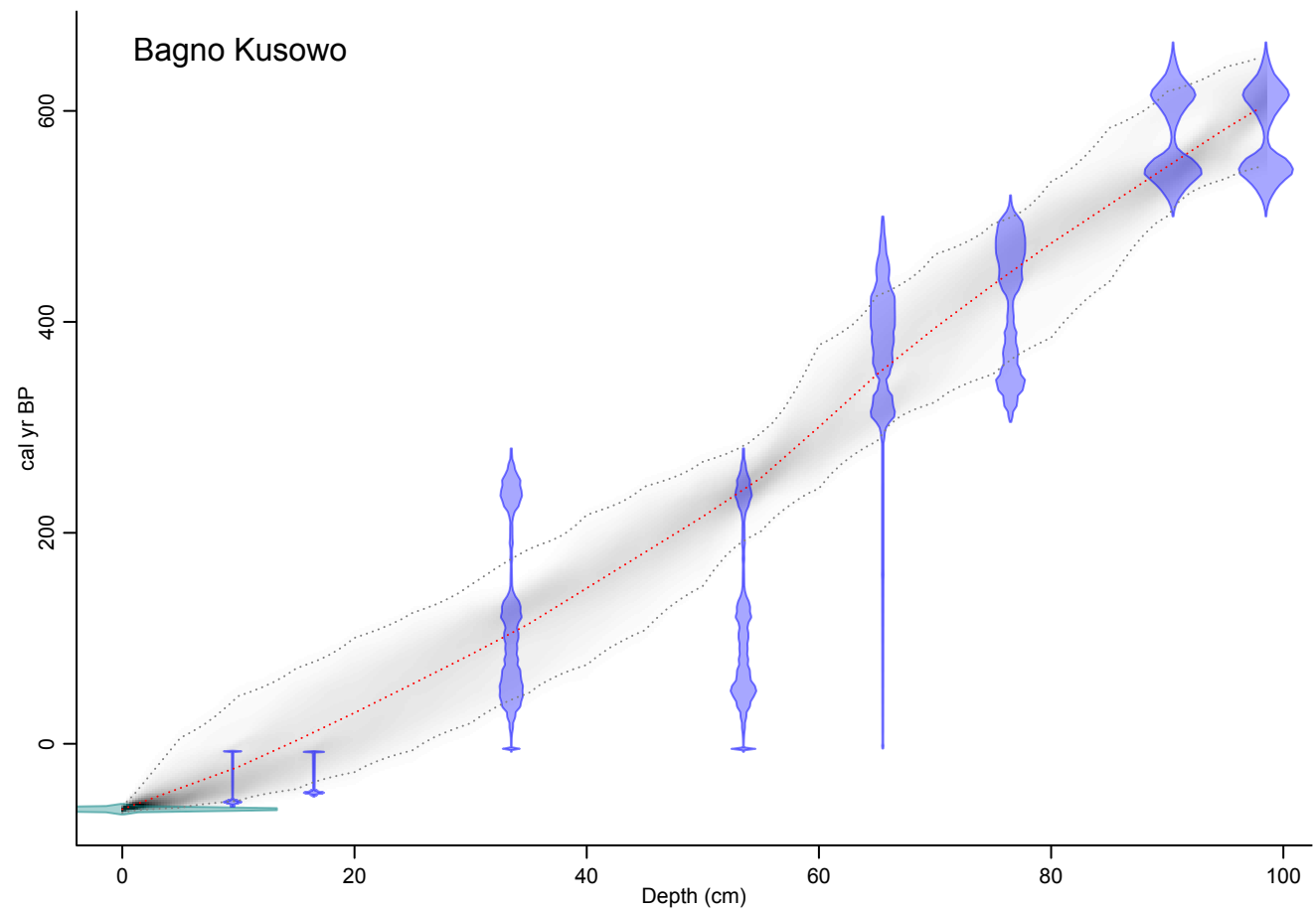
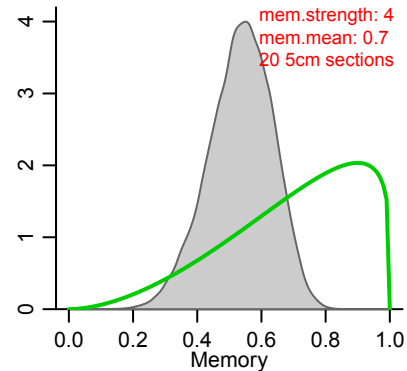
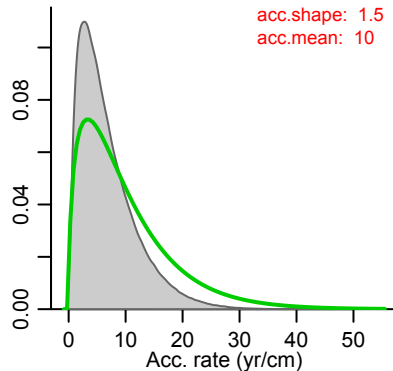
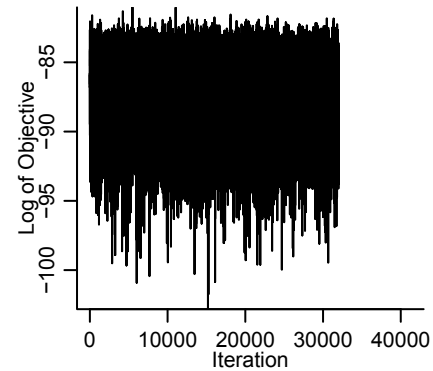


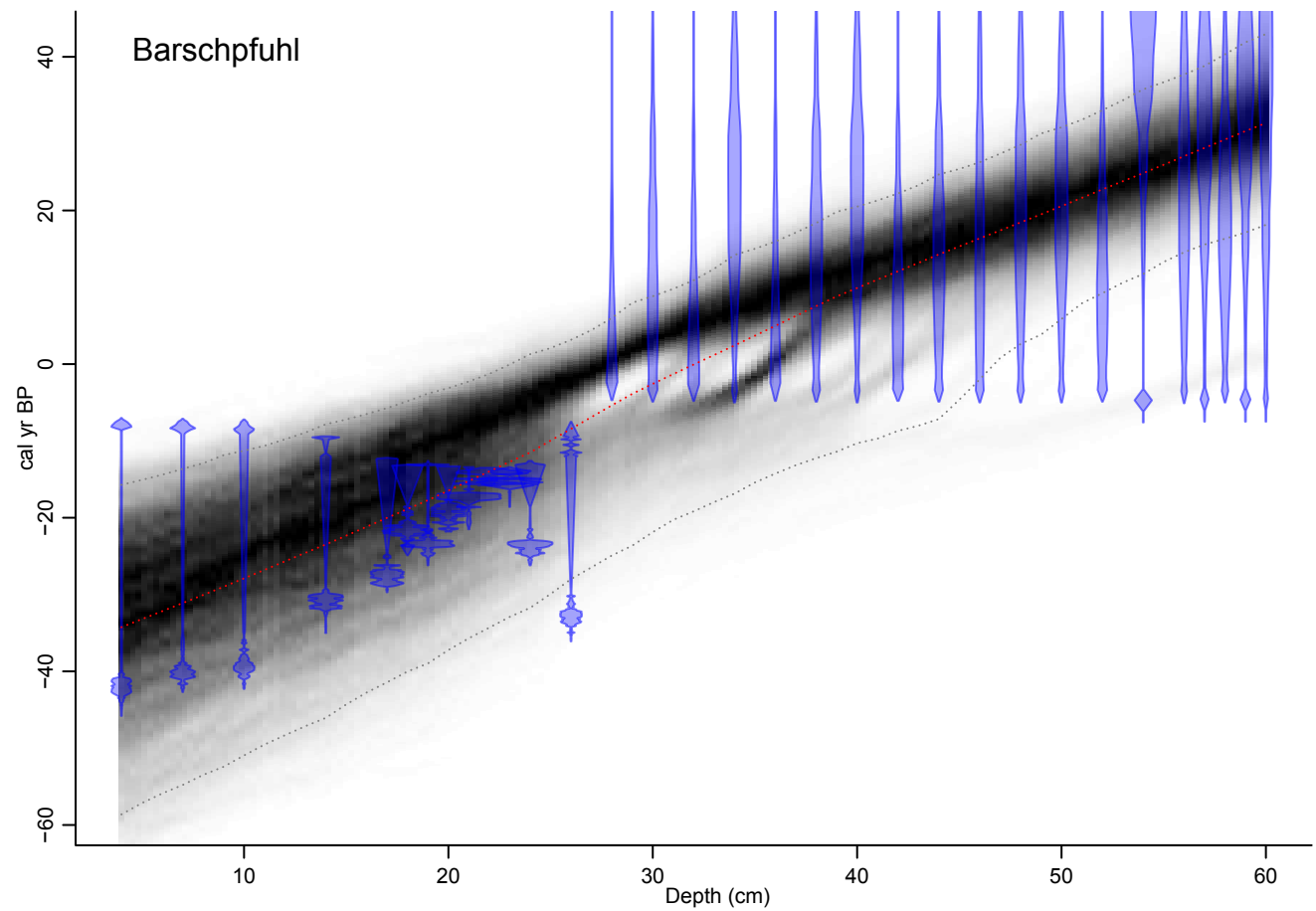
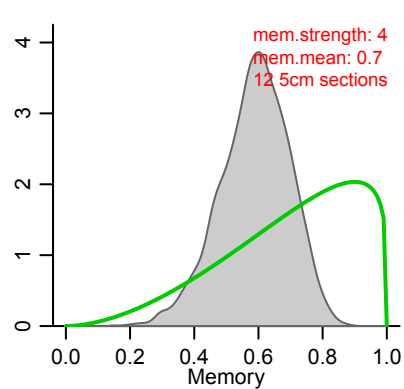
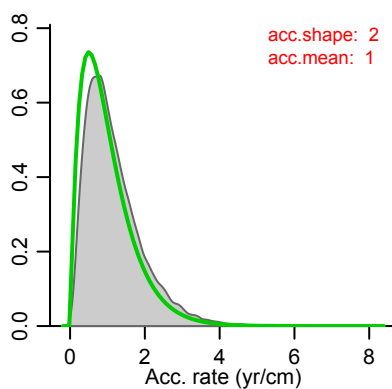
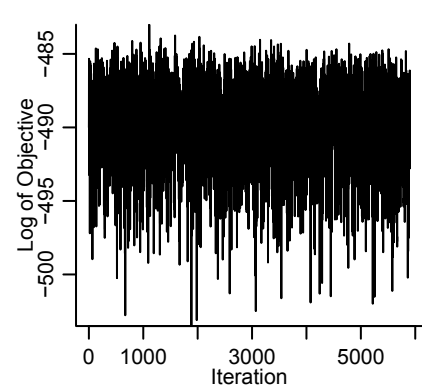


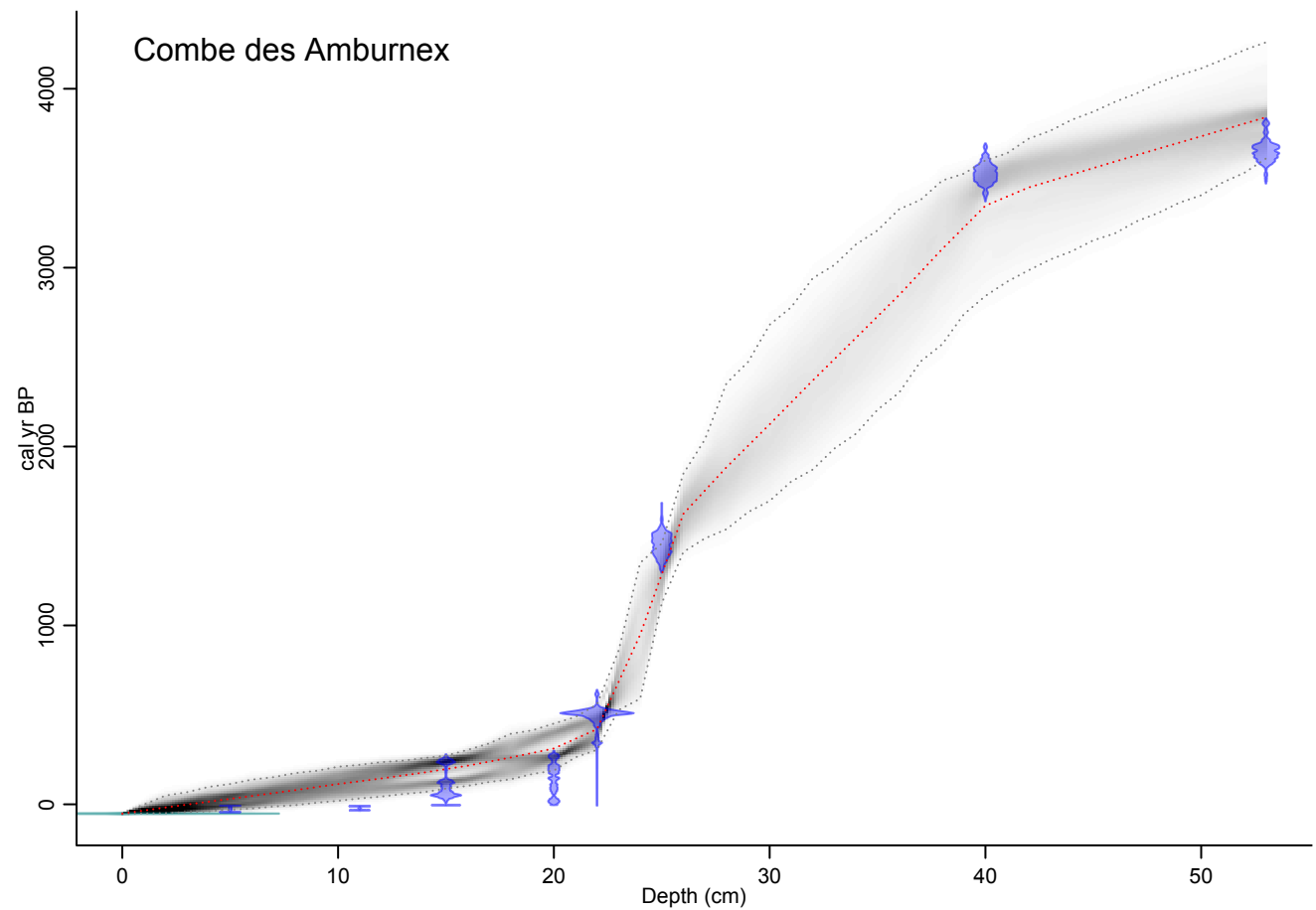
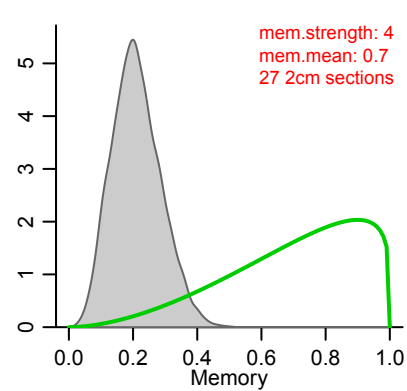
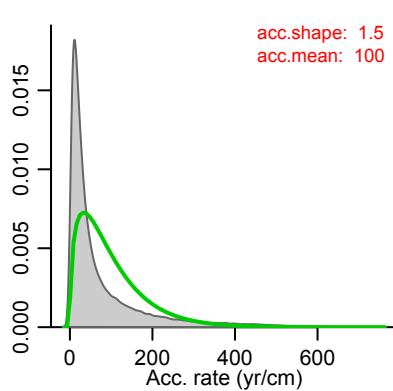
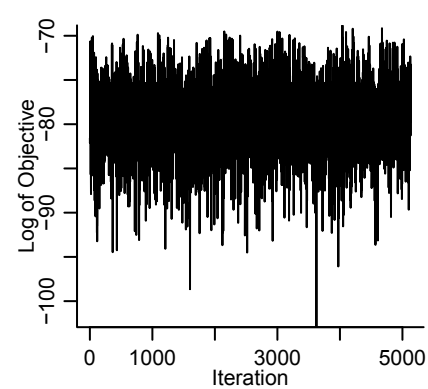


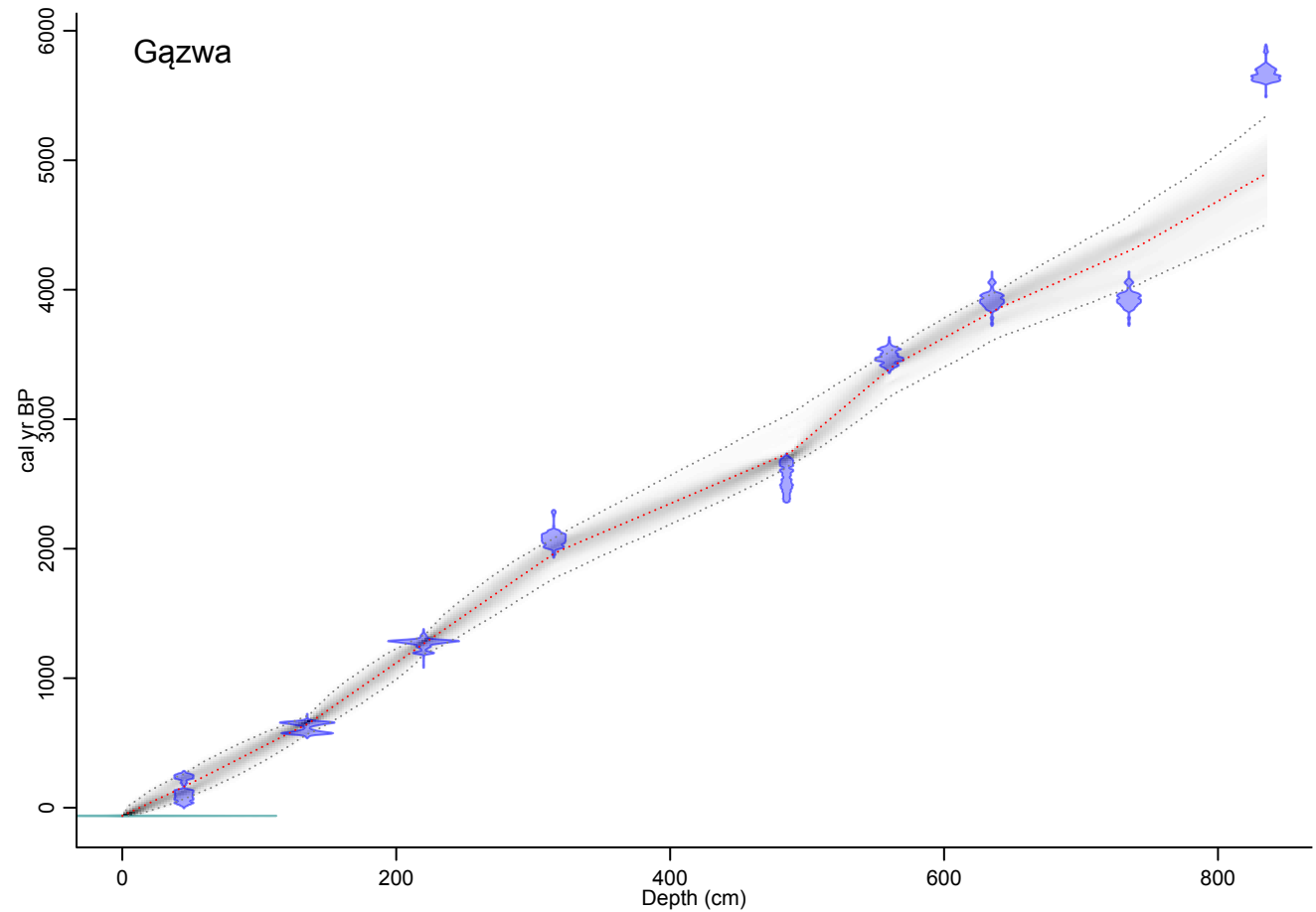
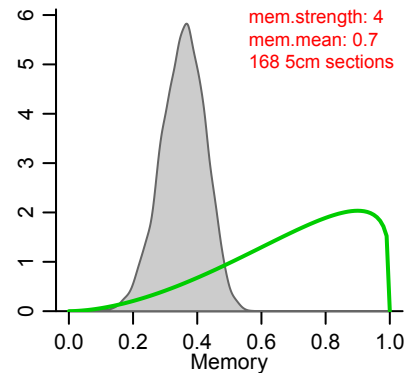
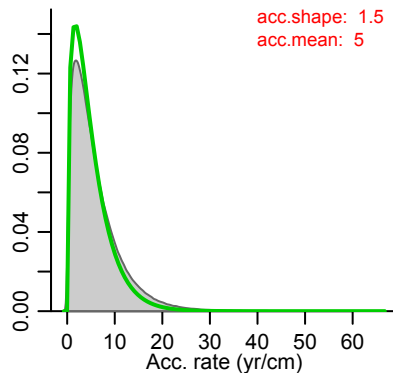
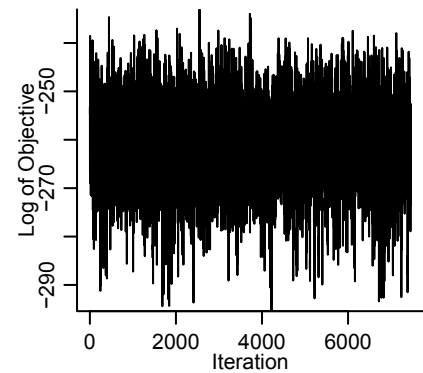


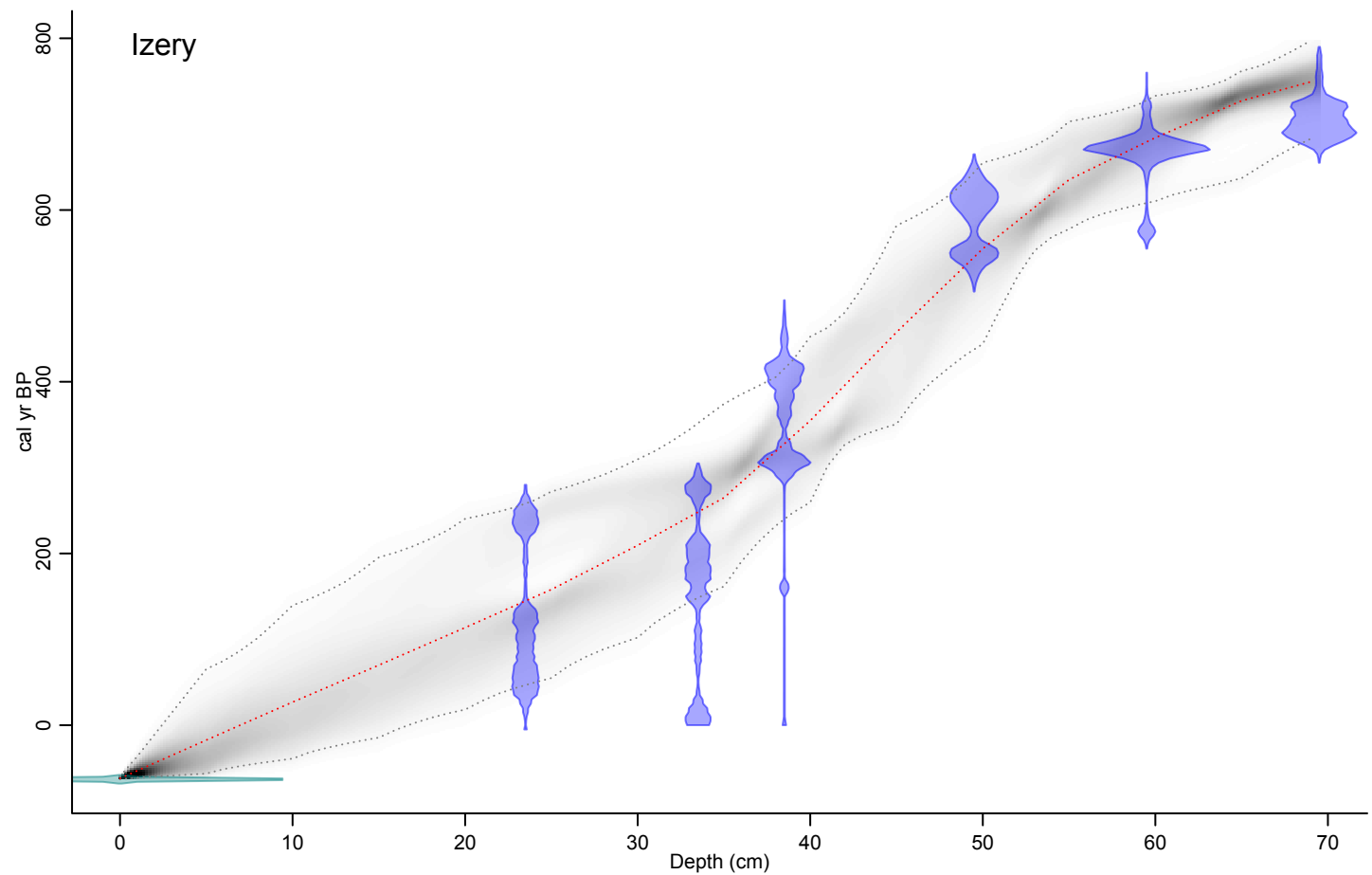
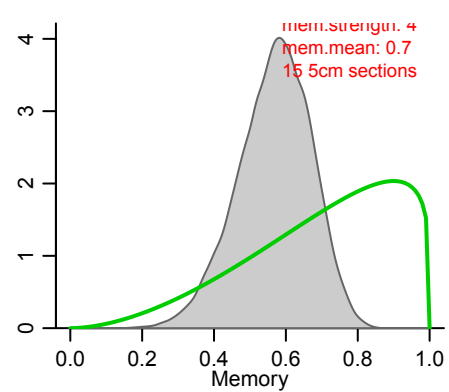
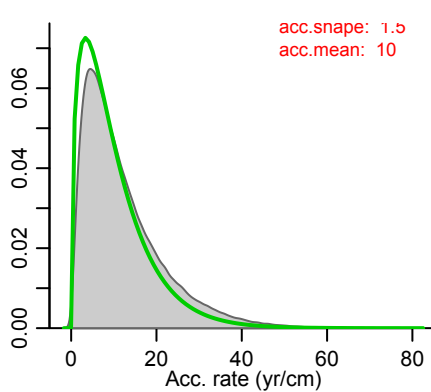
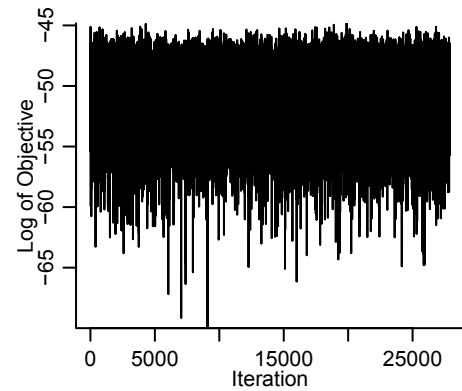


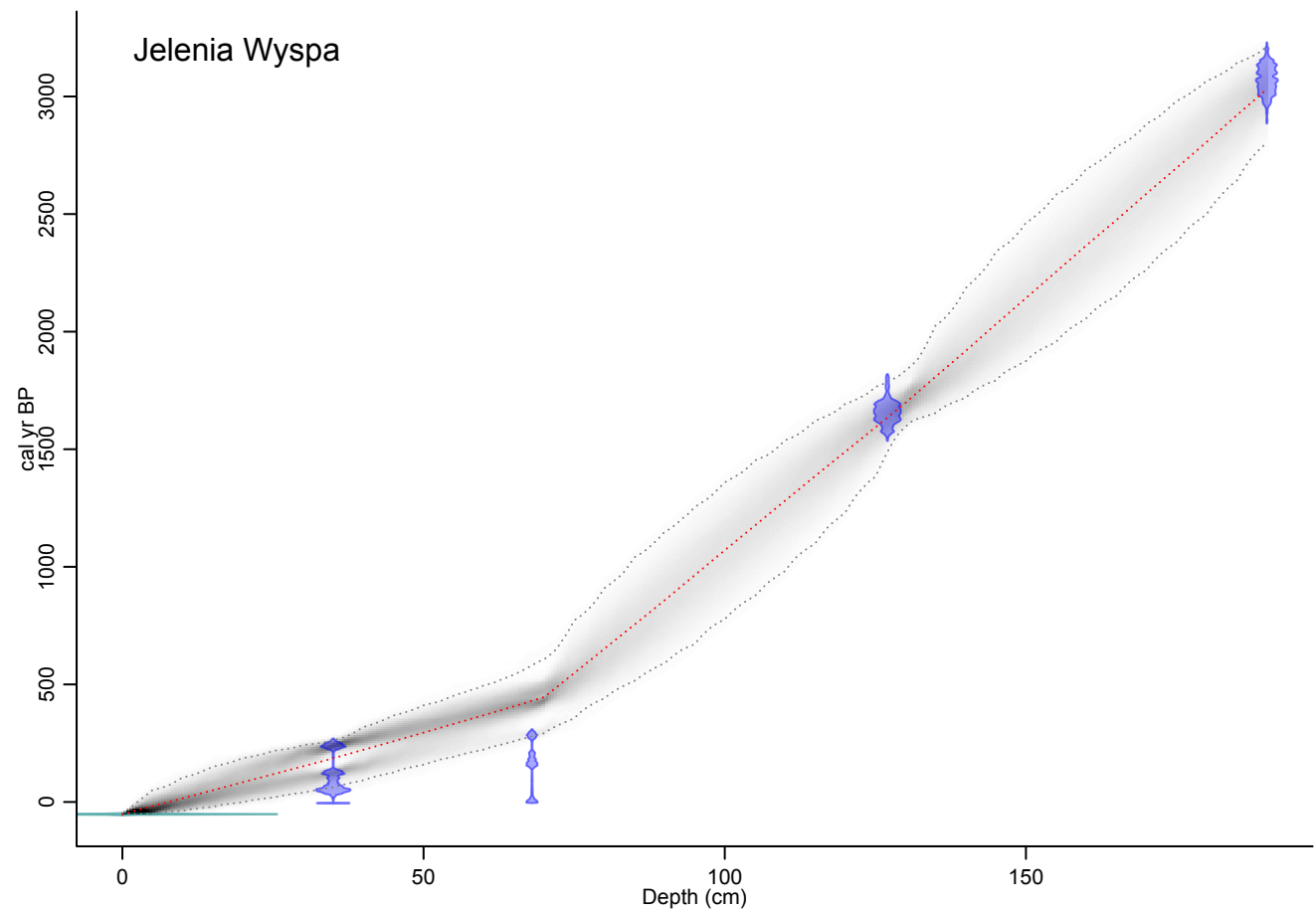
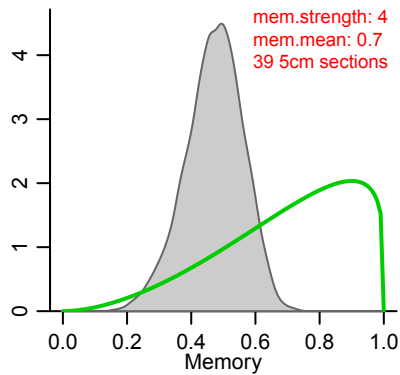
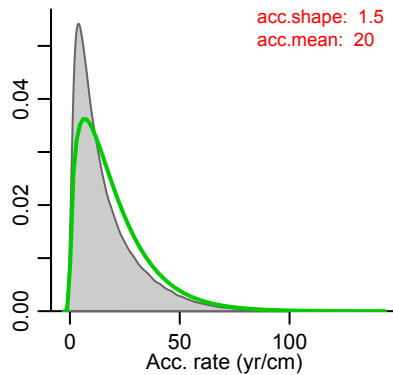
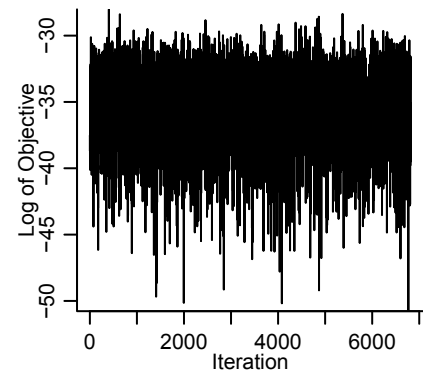


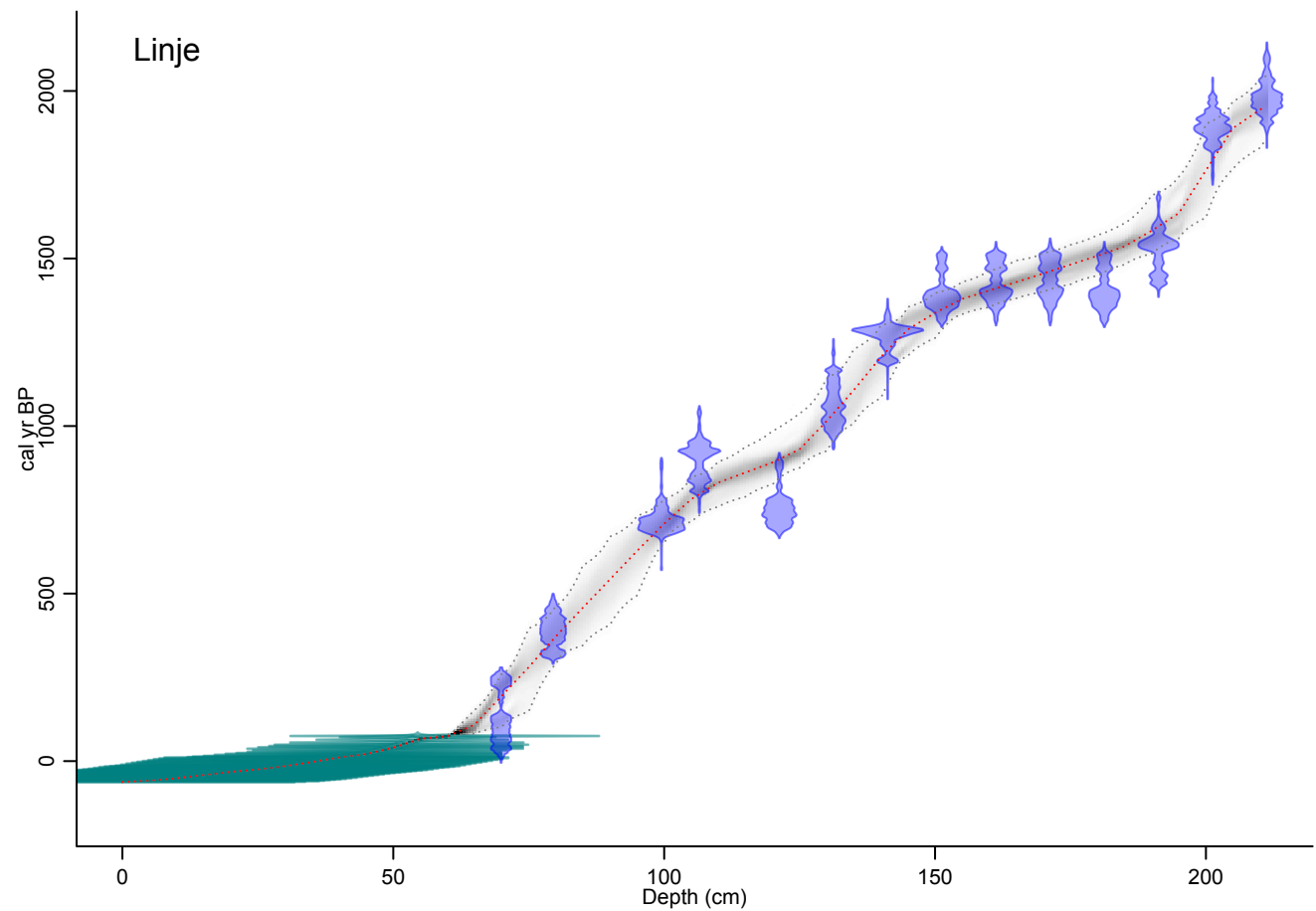
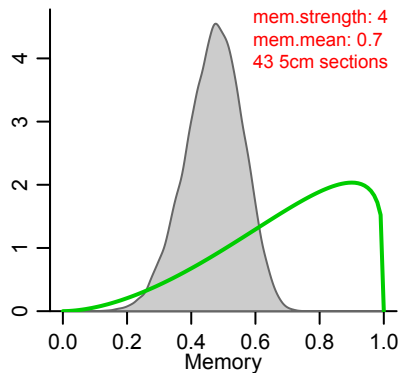
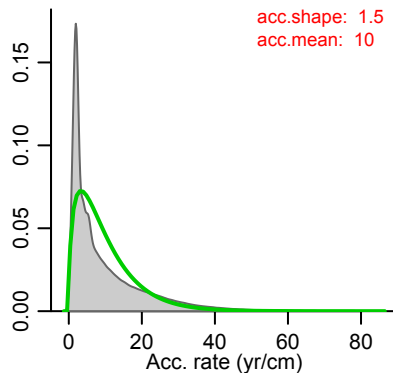
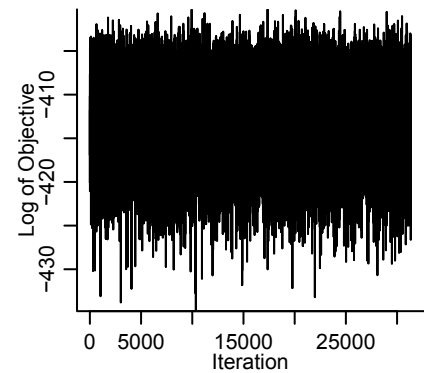


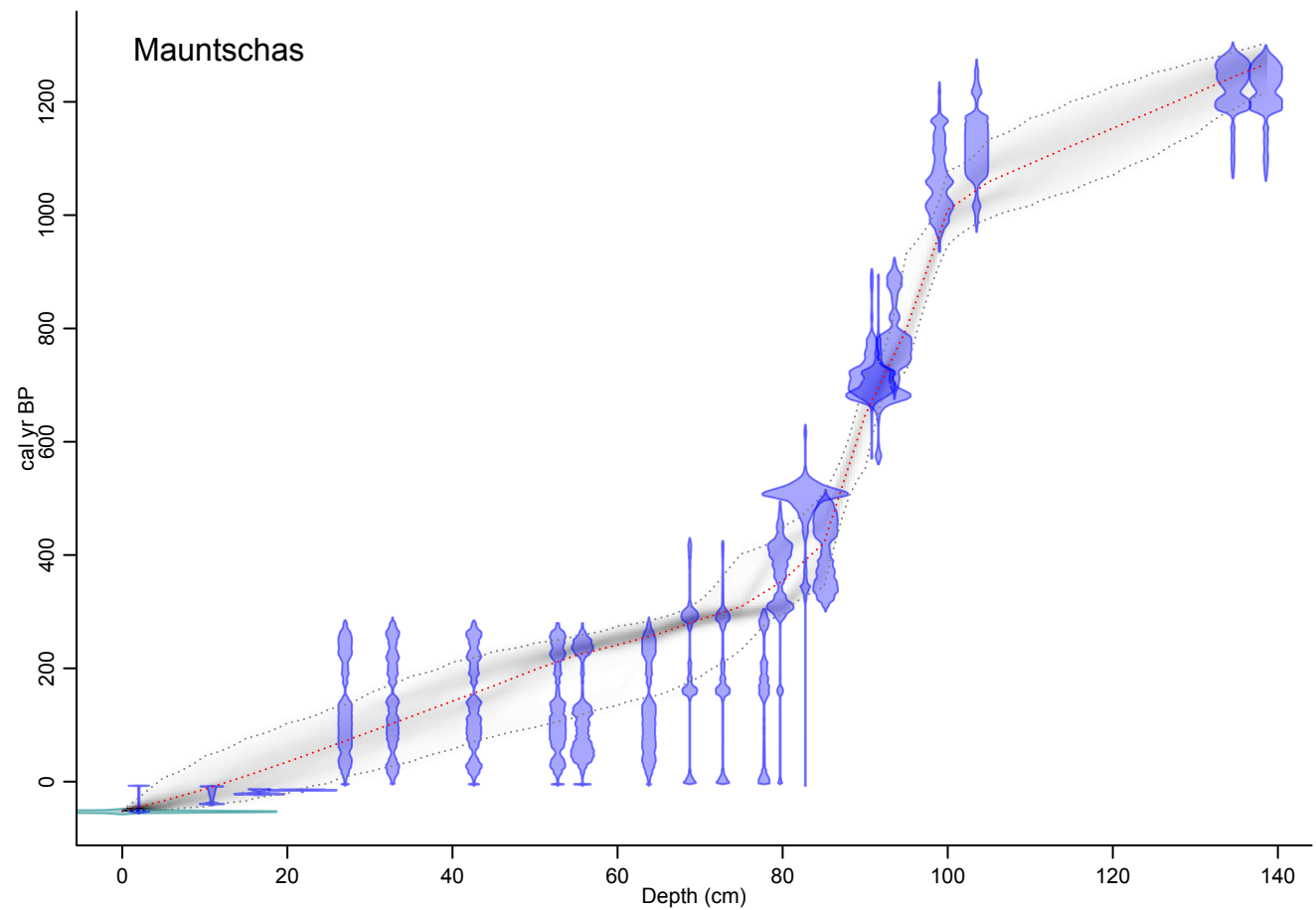
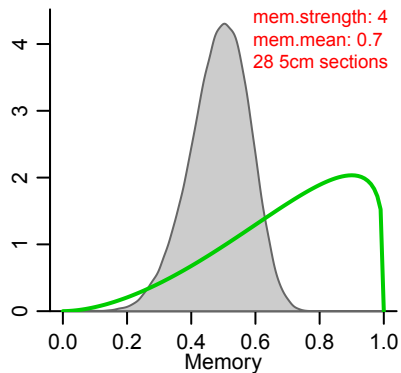
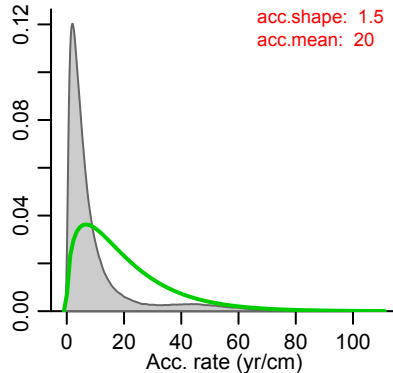
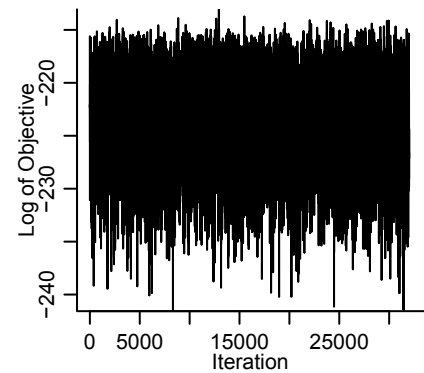


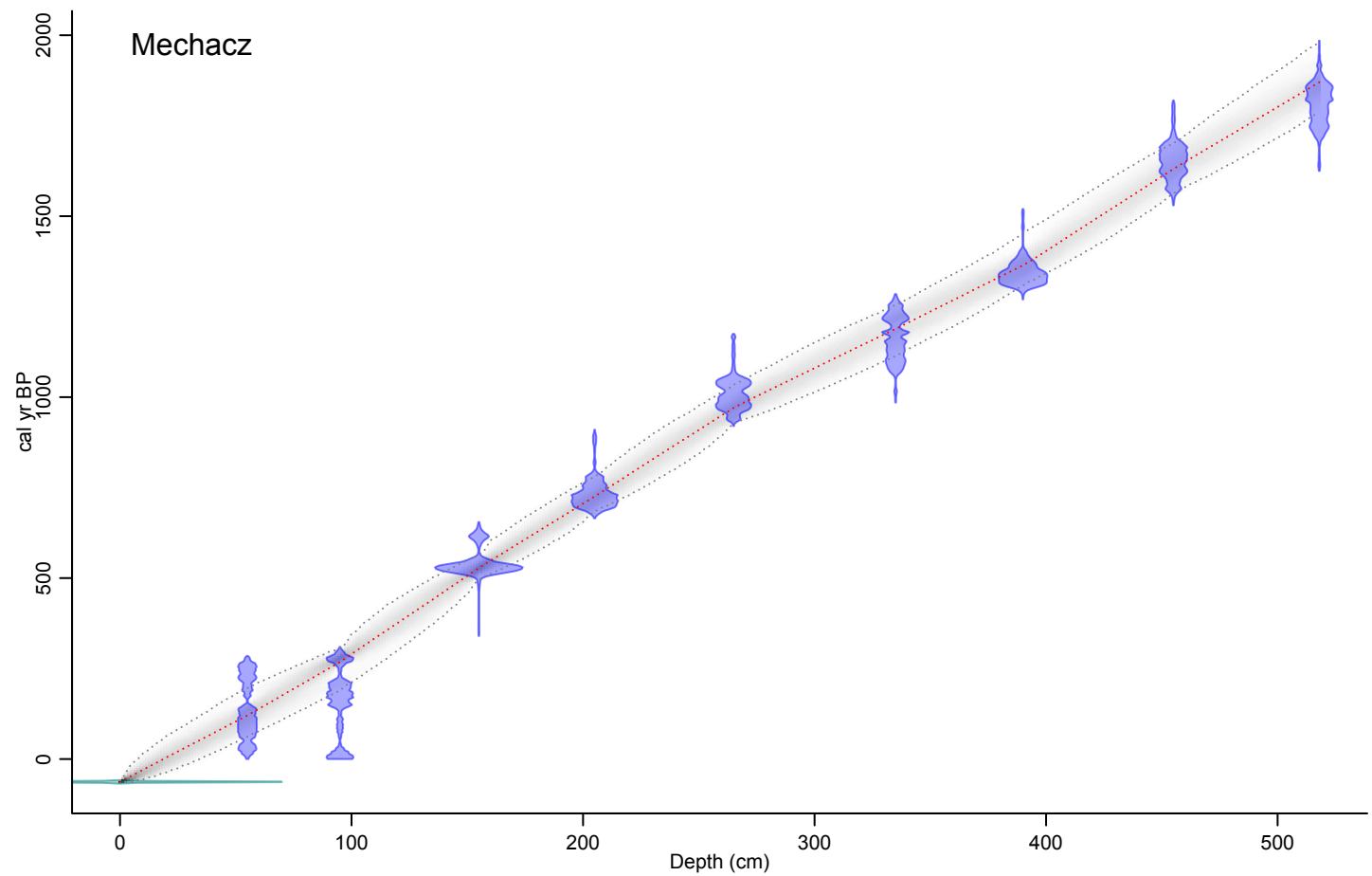
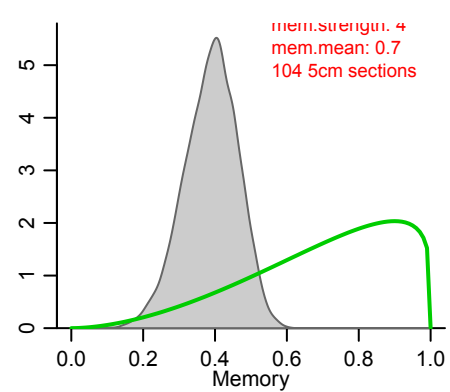
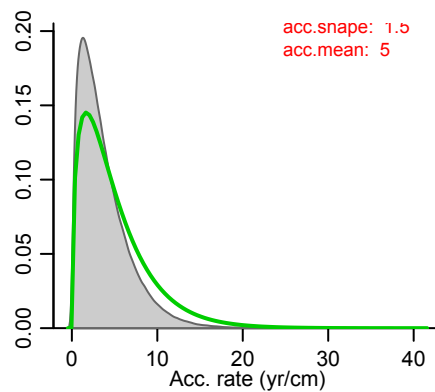
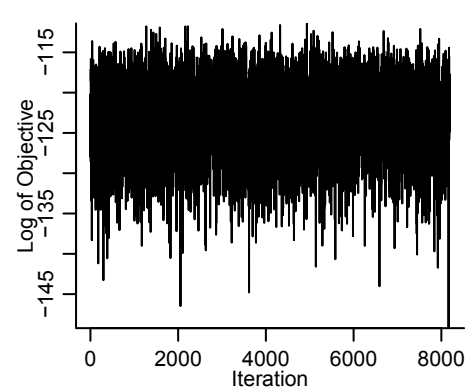


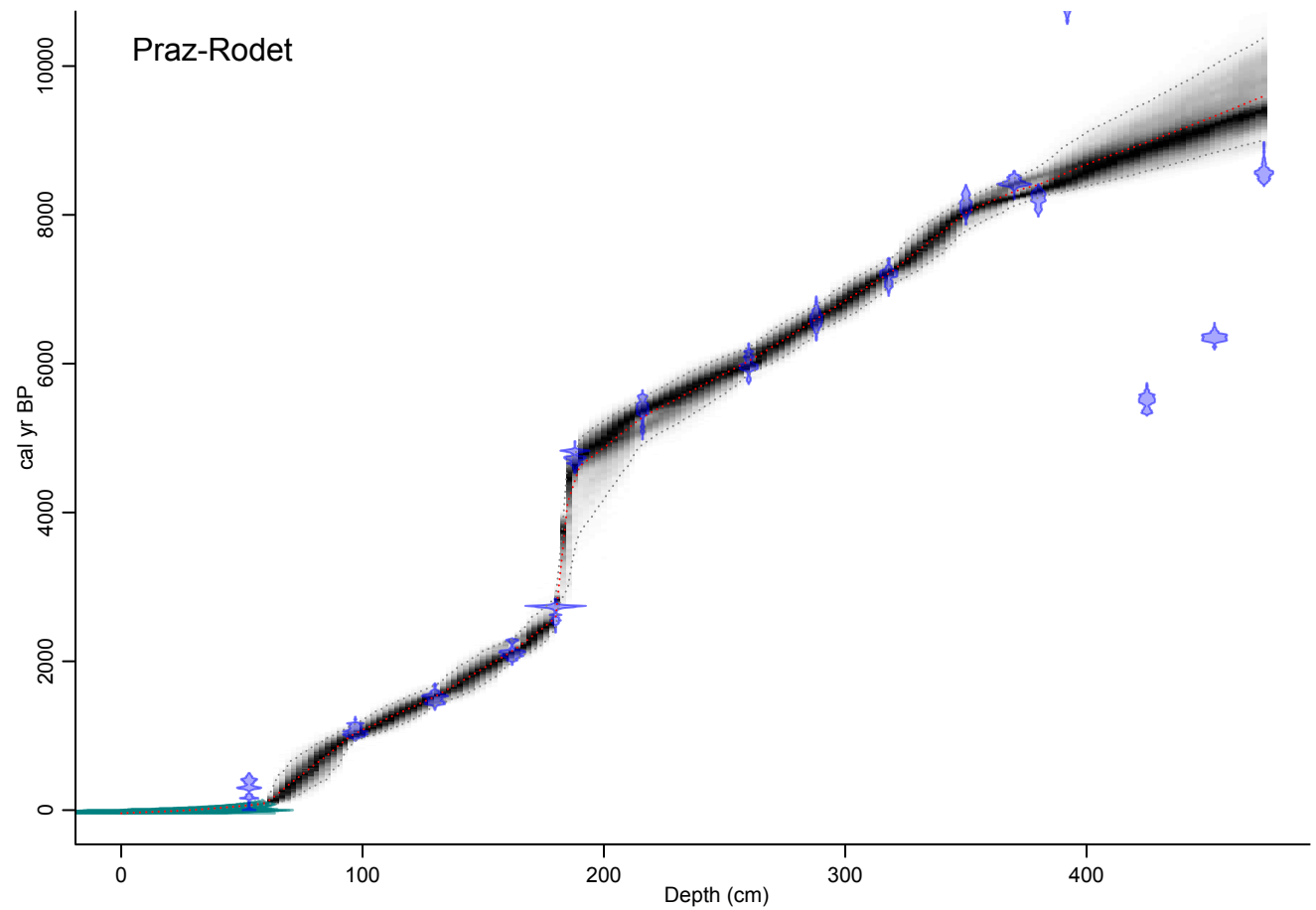
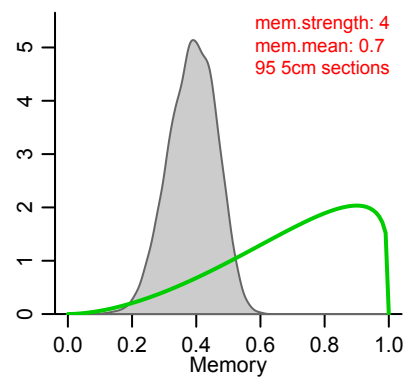
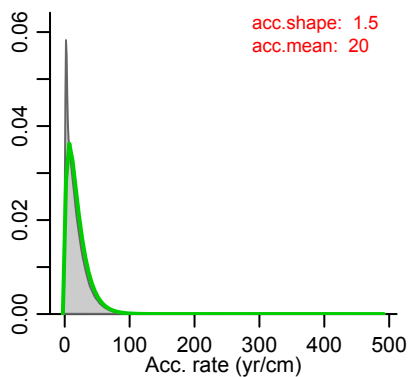
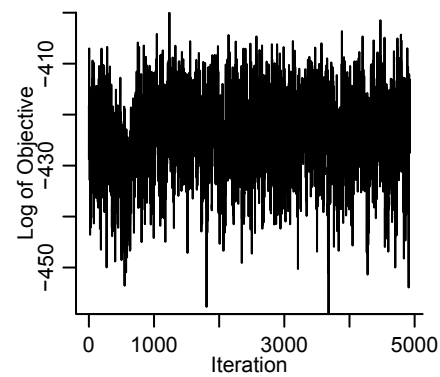


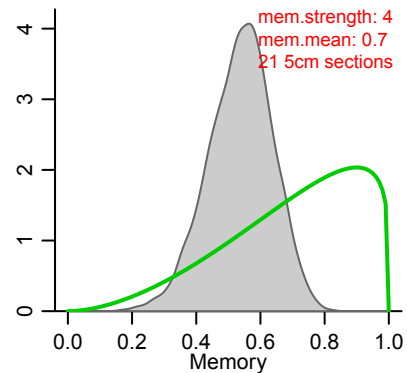
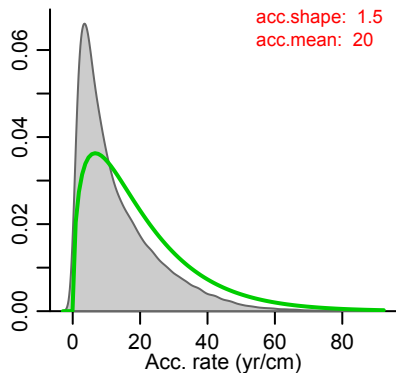
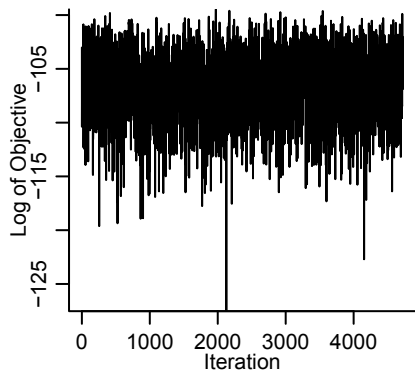












Słowińskie

