



AperTO - Archivio Istituzionale Open Access dell'Università di Torino

Spatial patterns and broad-scale weather cues of beech mast seeding in Europe

This is a pre print version of the following article:

Original Citation:

Availability:

This version is available <http://hdl.handle.net/2318/1652932> since 2017-11-24T10:22:30Z

Published version:

DOI:10.1111/nph.14600

Terms of use:

Open Access

Anyone can freely access the full text of works made available as "Open Access". Works made available under a Creative Commons license can be used according to the terms and conditions of said license. Use of all other works requires consent of the right holder (author or publisher) if not exempted from copyright protection by the applicable law.

(Article begins on next page)

1 **Spatial patterns and broad-scale weather cues of beech mast seeding in Europe**

2 Giorgio Vacchiano^{*^1}, Andrew Hacket-Pain^{2,3}, Marco Turco^{4,5}, Renzo Motta¹, Janet
3 Maringer^{6,7}, Marco Conedera⁷, Igor Drobyshev^{8,9}, Davide Ascoli¹⁰

4

5 ¹ DISAFA, University of Turin. Largo Braccini 2, 10095 Grugliasco (TO), Italy. Currently at
6 European Commission, Joint Research Centre, D1 Bio-economy, Via Fermi 2749, Ispra VA,
7 Italy

8 ² St. Catherine's College, Manor Road, Oxford, OX1 3UJ, UK

9 ³ Fitzwilliam College, Storeys Way, Cambridge, CB3 0DG, UK

10 ⁴ Department of Applied Physics, University of Barcelona, Av. Diagonal 647, 08028
11 Barcelona, Spain

12 ⁵ Barcelona Supercomputing Center (BSC), c/ Jordi Girona 29, 08034 Barcelona, Spain□

13 ⁶ Institute for Landscape Planning and Ecology, University of Stuttgart, Keplerstr. 11, 70174
14 Stuttgart, Germany

15 ⁷ Swiss Federal Institute for Forest, Snow, and Landscape Research WSL, a Ramél 18, CH-
16 6953 Cadenazzo, Switzerland

17 ⁸ Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences,
18 P.O. Box 49, 230 53 Alnarp, Sweden

19 ⁹ Chaire industrielle CRSNG-UQAT-UQAM en aménagement forestier durable, Université
20 du Québec en Abitibi-Témiscamingue, 445 Boulevard de l'Université, Rouyn-Noranda,
21 Québec J9X 5E4, Canada

22 ¹⁰ Dipartimento di Agraria, University of Naples Federico II, via Università 100, 80055
23 Portici, Napoli, Italy

24 [^]equal contribution

25 *corresponding author. +39 329 6497188; giorgio.vacchiano@unito.it; currently at European
26 Commission, Joint Research Centre, Directorate D – Sustainable Resources - Bio-Economy
27 Unit, Ispra (VA), Italy. Twitter: @forestsci

28

29 Word count for the main body of the text (Introduction, Materials and Methods, Results,
30 Discussion, and Acknowledgements): 6113

31 Word counts for each section: Summary 194, Introduction 634, Materials and Methods 2057,
32 Results 1013, Discussion 2375

33

- 34 • Number of figures: 6 (in color: Fig. 1, 3, 4, 5, 6)
35 • Number of tables: 3
36 • Number of supporting information: 13 Figures, 2 Tables, 1 script

37

38 **Summary**

- 39 ▪ Mast seeding is a crucial population process in many tree species, but its spatio-
40 temporal patterns and drivers at the continental scale are still unknown.
- 41 ▪ Using a large dataset (8,000 masting observations across Europe for years 1950-2014)
42 we analyzed the spatial pattern of masting across the entire geographical range of
43 European beech, how it is influenced by precipitation, temperature, and drought, and
44 the temporal and spatial stability of masting-weather correlations.
- 45 ▪ Beech masting exhibited a general distance-dependent synchronicity and a pattern
46 structured in three broad geographical groups consistent with continental climate
47 regimes. Spearman's correlations and logistic regression evidenced a general pattern
48 of beech masting correlating negatively with temperature in the summer two years
49 prior to masting, and positively with summer temperature one year before masting
50 (i.e., 2T model). The temperature difference between the two previous summers
51 (DeltaT model) was also a good predictor. Moving correlation analysis applied to the
52 longest eight chronologies (74 to 114 years) revealed stable correlations between
53 temperature and masting, confirming consistency in weather cues across space and
54 time.
- 55 ▪ These results confirm widespread dependency of masting on temperature and lend
56 robustness to the attempts to reconstruct and predict mast years using temperature
57 data.

58

59 **Key words:** *Fagus sylvatica* L. (beech), mast seeding, Moran effect, population ecology,
60 seed production, synchronization, weather cues

61

62

63

64 **Introduction**

65

66 Mast seeding (or masting) is the synchronous and highly variable production of fruits and
67 seeds (Pearse *et al.*, 2016), and is a crucial population process in many grass, shrub and tree
68 species (Kelly & Sork, 2002). As a form of information-mediated interaction, masting
69 synchrony has important implications for broader ecological patterns emerging at the
70 community and ecosystem levels (Mescher & Pearse, 2016). The synchrony of masting
71 varies across species (Norden *et al.*, 2013), time (Drobyshev *et al.*, 2010), and space (Suzuki
72 *et al.*, 2005), with cascading effects on plant regeneration (Ascoli *et al.*, 2015), community
73 composition (Lichti *et al.*, 2014), nutrient fluxes (Zackrisson *et al.*, 1999), carbon allocation
74 (Müller-Haubold *et al.*, 2013), and trophic cascades (Blackwell *et al.*, 2001), including those
75 that involve organisms that carry human infectious diseases (e.g., Hantaviruses: Clement *et*
76 *al.*, 2010; Lyme disease: Ostfeld & Keesing, 2000).

77

78 Describing and predicting masting is therefore critical to better understand population
79 dynamics, assess present and future ecosystem resilience, and design adaptive forest
80 management strategies (Wagner *et al.*, 2010). In recent decades, the temporal pattern of
81 masting has been described for several species in boreal, temperate, and tropical biomes
82 (Koenig & Knops, 2000). A growing body of research has elucidated some of the
83 environmental and physiological cues of masting (e.g., Kelly, 1994; Kelly & Sork, 2002;
84 Kelly *et al.*, 2013; Miyazaki *et al.*, 2014; Pearse *et al.*, 2016), and suggested several
85 mechanisms responsible for the synchronization of masting in individual species from the
86 stand to the regional scale (Satake & Iwasa, 2000; Koenig & Knops, 2013; Koenig *et al.*,
87 2015).

88

89 The oldest and simplest hypothesis for masting states that seed crops vary in response to
90 weather variation (Büsgen *et al.*, 1929; Kelly, 1994). In particular, temperature and
91 precipitation in the years previous to seed production have been consistently related to
92 masting (e.g., in grasses: Schauber *et al.*, 2002; shrubs: Mayer & Pendleton, 2015; trees: Bisi
93 *et al.*, 2016). The nature of such relationships can be either correlative, i.e., weather is a “cue”
94 that triggers other processes and that plants are able to sense (e.g., Kelly & Sork, 2002; Kelly
95 *et al.*, 2013), or causal, in the case that weather directly influences resources and other
96 proximate causes of masting (Monks *et al.*, 2016; Pearse *et al.*, 2016) (correlative analysis on
97 its own cannot distinguish these models, and we hereafter use the word “cue” in a broad

98 sense without addressing underlying mechanisms). Several studies have assessed masting at
99 the scale of a plant's distribution range (e.g., Kelly *et al.*, 2000; Schauber *et al.*, 2002; Masaki
100 *et al.*, 2008), but few have tested whether such cues are constant in space and time across the
101 range. In other words, do spatial and temporal variations in masting emerge from (a)
102 variations in weather, or (b) differences in local plant response to the same weather patterns,
103 e.g. as a consequence of inter-population differences and adaptations in genes that regulate
104 flowering (Tan and Swain, 2006)? Addressing this question will provide important
105 information on predicting masting both in the short and at the long term, such as in the case
106 of masting responses to climate change and the consequences on large-scale ecosystem
107 processes.

108

109 The aims of this paper are to: i) describe the spatial pattern of masting across the entire
110 distribution of European beech (*Fagus sylvatica* L.), one of the most important European
111 forest species (Fig. 1a); ii) measure the strength of the relationship between beech masting
112 and weather, using alternative models built with variables previously found relevant for
113 masting in plants, and beech in particular, i.e., precipitation, temperature, and drought, either
114 using monthly values, or aggregating both by season and to express two-year differences
115 ("delta" models); iii) assess the stability of masting-weather correlations through space (i.e.,
116 whether the strength, timing, and relative importance of weather cues vary across
117 geographical space) and time.

118

119 Materials and methods

120

121 *Beech masting data*

122

123 To address such questions, we used a recently available, long-term, large-scale database of
124 masting for European tree species (MASTREE: Ascoli *et al.*, 2017). Each observation was
125 characterized by the following measurements: the date of inclusion in the database, the
126 masting proxy considered (e.g., seed, pollen), the scale of measurement of the original data
127 (continuous or ordinal), the year of measurement, the NUTS-1 (Nomenclature of Territorial
128 Units for Statistics version 2013, level 1, i.e., European administrative subdivisions
129 corresponding to macro-regional aggregations) [data source: GISCO – Eurostat (European
130 Commission)] where the observation was recorded (Fig. 1b), the start and end year of the
131 series, and the length of the continuous recording series to which each observation belongs

132 (range: 1-191 years). Non-EU countries where beech masting data were recorded (i.e.,
133 Ukraine, Serbia, Switzerland, Bosnia and Herzegovina) were also included in the database
134 with dummy NUTS-1 codes. Observations where NUTS-1 location was uncertain were
135 excluded from further analysis.

136

137 All database records belonging to series with length ≥ 5 years were associated to a 5-class
138 ordinal measurement (ORDmast) from (1) very poor masting to (5) very abundant masting
139 (Ascoli et al., 2017). To build our target variable we extracted values of ORDmast for beech
140 in the period 1950-2014 (for spatial pattern analysis and Spearman's correlations) or 1901-
141 2014 (for ordinal regression and moving correlation analysis), because antecedent
142 observations were sparse and unevenly spread across the continent. Pollen and flowering data
143 were excluded, as pooling different masting proxies may introduce some noise, such as
144 would happen should flowers' crops not mature into fruits owing to environmental
145 constraints. A total of 769 individual series covering 7983 annually resolved observations
146 from 22 European countries was selected for further analyses.

147

148 *Data treatment*

149

150 To obtain long masting series with a minimum amount of missing data, individual masting
151 series were aggregated into 61 NUTS-1 chronologies (NC) by using the most frequently
152 observed masting class for each year (Table S1). The highest masting class was used in case
153 of multi-modality, but the impact of a different choice would be negligible (mean
154 Spearman's correlation between NC calculated using highest and lowest masting class in
155 case of multi-modality = 0.91, range = 0.68 to 1.00). All forests within a NUTS-1 should
156 have homogenous climatic and ecological characteristics; the assumption was tested by
157 computing the mean Spearman's correlation coefficient between individual weather series
158 (see "Weather cues analysis", period 1901-2014) and between individual masting series in
159 each NUTS-1 (henceforth "intra-NUTS correlations") with ≥ 7 years of observation in
160 common. This sample size was chosen as a trade-off between the need for robustness (critical
161 value for Spearman's correlation with $n=7$ and $p=0.05$: rho = 0.79) and data inclusion (i.e.,
162 keeping at least 60% of all NUTS-1 into the analysis). Possible inflation of cross-correlation
163 values due to temporally autocorrelated series was corrected by calculating adjusted degrees
164 of freedom according to Dutilleul *et al.* (1993). Correlation coefficients computed on <30
165 observation pairs were corrected according to Hotelling's (1953) second-order

166 transformation. NUTS-1 indeed showed high internal consistency of both weather series (rho
167 > 0.9, except for precipitation) and masting series (of 36 NUTS-1 with at least two masting
168 series sharing ≥ 7 elements, 30 had a significantly positive intra-NUTS correlation, with an
169 average value of 0.66) (Fig. S1; Table S2).

170

171 The analyses were carried out according to the following scheme: we used Mantel (1967)
172 tests and hierarchical clustering to analyze spatial patterns, Spearman's correlations and
173 ordinal logistic regression to measure the relationship between masting and weather, and
174 moving correlation analysis to assess the temporal stability of such relationship.

175

176 *Spatial analysis of masting patterns*

177

178 To address our first objective, we analyzed the spatial structure of masting synchrony at the
179 continental scale by running a Mantel test on NC. This test measures the correlation between
180 two dissimilarity matrices containing measures of geographical and ecological distance.

181 Here, it addresses the hypothesis that masting chronologies farther apart would be less similar
182 to one another (de-synchronized) than closer ones.

183

184 Time series of seed production may exhibit lagged negative temporal autocorrelation (e.g.,
185 Koenig & Knops, 2000) and non-stationarity (i.e., temporal trends; Allen *et al.*, 2014). Both
186 may alter cross-correlation analyses. Therefore, all NC were checked for temporal
187 autocorrelation (max order = 1, excluding segments with < 7 consecutive years of observation
188 which may bias the autocorrelation function; Sork *et al.*, 1993) by fitting a Cumulative Link
189 regression Model (CLM: Agresti, 2002) (probit link with 2000 iterations) against NC of the
190 previous year (NC₋₁). Of 47 NUTS-1 chronologies with ≥ 7 consecutive years of observation,
191 21 had a significantly negative autocorrelation at lag 1 (Table S2). NC that exhibited
192 significant temporal trends (i.e., slope of linear regression against year of observation
193 significant at $p \leq 0.05$) were detrended by extracting regression residuals (negative trend: ITI,
194 SI0; positive trend: DEA, DEB, DEC, PL1, PL2, PL5, PL6).

195

196 We used coordinates of NUTS-1 centers to compute the geographical distance matrix for the
197 Mantel test, and the index of Suzuki *et al.* (2005), a metric derived from Spearman's
198 correlation coefficient, for the masting dissimilarity matrix. Only NC pairs with an overlap of
199 ≥ 7 consecutive years of observation were included in the latter. Alongside the Mantel

200 correlation coefficient, we computed a Mantel correlogram (Oden and Sokal, 1986) by
201 binning distances and calculating the mean pairwise correlation between NC for pairs in each
202 distance class. Significance of each Mantel correlation coefficient was computed by a
203 randomization approach (2000 permutations) in which the rows and/or columns of the
204 distance matrices are randomly rearranged (Mantel, 1967), and corrected for multiple
205 comparison according to Holm (1979) in the case of Mantel correlograms. Furthermore, we
206 ran two unidirectional Mantel tests and correlograms as a function of distance along
207 longitude (Dlon) and latitude (Dlat) only, by fixing the other coordinate to its mean value
208 across all NUTS-1, to scrutinize the structure of masting along the two orthogonal
209 geographical directions. Mantel tests and correlograms were run with package *ncf* version 1.1
210 (Bjornstad, 2015) for the R statistical framework (R Core Team, 2016).

211

212 Secondly, we assessed the geographic pattern of beech masting in Europe by running a
213 hierarchical cluster analysis on NC using Ward's minimum variance method (Murtagh &
214 Legendre, 2014), which minimizes within-cluster distances relative to between-cluster
215 distances (Ward, 1963). Only NC pairs sharing ≥ 7 consecutive years of observation were
216 included in the dissimilarity matrix. NUTS-1 not satisfying such condition when paired
217 against every other NUTS-1 were filtered out. Dissimilarities between individual NC pairs
218 with an insufficient number of observations (4.9% of all NC pairs) were simulated by a linear
219 model of the form $a_0 + a_1 Dlon + a_2 Dlat$ ($a_0 = 18.41$, $a_1 = 1.61 \times 10^{-5}$, $a_2 = 1.54 \times 10^{-5}$, adjusted
220 $R^2 = 0.35$; F-statistic = 709.9 on 2 and 2672 degrees of freedom, p-value < 0.001). We
221 determined the optimal number of clusters by maximizing the index by Dunn (1974) with the
222 R package *NbClust* (Charrad *et al.*, 2014), and computed cluster stability by nonparametric
223 bootstrap with the R package *fpc* (Hennig, 2015). The validity of each cluster was also
224 assessed by checking that the mean Spearman correlation between all NC pairs in each
225 cluster was higher than the mean correlation between all pairs from two different clusters.

226

227 *Weather cues analysis*

228

229 To measure the strength of weather cues of masting, we calculated Spearman's correlations
230 between each NC (filtered on ≥ 7 years of observation, after detrending if needed: see above)
231 and the following variables: Mean monthly temperature (MEAN), monthly mean of daily
232 maximum temperature (MAX), monthly mean of daily minimum temperature (MIN),
233 monthly precipitation (PRE), three-months Standardized Precipitation Index (SPI3; McKee *et*

234 *al.*, 1993), and three-months Standardized Precipitation and Evaporation Index (SPEI3;
235 Vicente-Serrano *et al.*, 2010). Weather series were obtained by averaging monthly data
236 across all cells included in each NUTS-1 from the gridded database CRU TS 3.23 (0.5°
237 resolution; years 1901-2014) (Harris *et al.*, 2014), and detrended before all subsequent
238 analysis by running a linear filter on each individual monthly variable for the timespan
239 selected (1901-2014 or 1950-2014). SPI3 was calculated using the nonparametric approach
240 described by Hao *et al.* (2014), in which the probability distributions are calculated
241 empirically (Grimorten, 1963), rather than by fitting a parametric distribution function.
242 SPEI3 was calculated from the difference between available water (i.e., three-month sum of
243 PRE) and the potential evapotranspiration, which is based on the FAO-56 Penman–Monteith
244 estimation (Allen *et al.*, 1998) and directly gridded by the CRU. The difference was fit to a
245 log-logistic probability distribution to transform the original values to standardized units
246 (Vicente-Serrano *et al.*, 2010). SPEI3 measures the climatic water balance and therefore
247 provides a more reliable and spatially comparable measure of drought severity than
248 precipitation alone (Vicente-Serrano *et al.*, 2013). Data extraction and calculation of drought
249 indices were performed with the R packages *cruts* (Taylor and Parida, 2016) and *SPEI*
250 (Begueria and Vicente-Serrano, 2013). Correlations (years 1950-2014) were computed for all
251 36 months of a three-year period, including the calendar year of seed production and the two
252 years prior (lag -1 and -2). After preliminary scrutiny of the most significant correlations, we
253 also ran correlations against aggregated summer (June-July) weather variables of one and two
254 years prior to masting, and against the difference (Delta) between values of each weather
255 variables measured one and two years prior (e.g., Delta Temperature, Kelly *et al.* 2013). The
256 absence of non-linear relationships was visually checked before running all correlations. For
257 each correlation, significance was tested at the 95% confidence level, with a simple
258 Bonferroni correction, i.e. adjusting the required alpha value according to the number of
259 comparisons (0.05/36), to account for multiple comparisons. Finally, to assess the similarity
260 of weather spatial patterns to those of masting, we applied hierarchical cluster analysis to
261 each weather variable, using the same settings and period (1950-2014) as the analysis run on
262 masting, and compared the consistency of masting vs. weather clusters by computing the
263 overall proportion of NUTS-1 that were classified into the same cluster under both analyses.

264
265 *Spatio-temporal stability of weather cues*
266

267 To test for spatial stability of masting-weather relationships, we fitted a linear model of
268 Spearman's correlation coefficient between masting and MAX of June, July, and August of
269 the one and two years prior, and latitude. Subsequently, we modeled the eight longest NC
270 (DE1, DE2, DE9, DEF, DK0, NL1, SE2, UKJ – including 74 to 115 yearly observations in
271 the period 1901-2014) as a function of detrended weather variables, using ordinal logistic
272 regression within the R package *rms* (Harrell, 2016). In this analysis, NC₋₁ was used as an
273 additional independent variable, to account for potential temporal autocorrelation resulting
274 e.g. from resource depletion (Davis, 1957) or resource switching (Kelly & Sork, 2002). All
275 models were fitted with 44-65 observations (years 1950-2014), and validated using both a
276 new prediction interval (years 1901-1949, 30-41 observations for each NC except NL1 with
277 10), and a bootstrapped leave-one-out cross-validation run on the calibration time period.

278 Weather variables (i.e., MAX and PRE in June and July -1 and -2, hereafter MAX_{JUN-1},
279 MAX_{JUL-1}, MAX_{JUN-2}, MAX_{JUL-2}, PRE_{JUN-1}, PRE_{JUL-1}, PRE_{JUN-2}, PRE_{JUL-2}) were selected
280 based on the previous correlation analysis and evidence from literature on beech masting
281 (e.g., Piovesan and Adams, 2001; Drobyshev *et al.*, 2010). The absence of non-linear
282 univariate relationships was visually checked before running the models. All independent
283 variables were z-transformed to ensure comparability of effect sizes within models; to
284 account for collinearity among weather variables, optimal models were selected using
285 backward stepwise selection based on the Akaike Information Criterion (AIC). Nagelkerke
286 R² was used to compare models for different NC.

287
288 To test for temporal stability of masting-weather relationships, each of the 8 long NC was
289 fitted against the four most important weather variables selected by logistic models and
290 correlation analysis (i.e., MAX_{JUN-1}, MAX_{JUL-1}, MAX_{JUN-2} and MAX_{JUL-2}), using year as an
291 interaction factor. If the year x MAX interaction is significant, that will suggest a temporal
292 change in masting sensitivity to maximum summer temperatures. Moreover, to test also for
293 non-linear trends in correlation values, we additionally ran a moving correlation analysis
294 (MCA) between MAX_{JUN-1}, MAX_{JUL-1}, MAX_{JUN-2} and MAX_{JUL-2}, and the same 8 NC. MCA
295 was conducted on detrended weather variables using Spearman's rank correlation and a
296 window size of 28 years, i.e., the largest window giving 4 independent intervals for the
297 period 1901-2014. Most series had some missing values, but a minimum of 15 values (i.e.,
298 >50% of years observed) was required for any window.

299
300 The R code used for analyses is provided in Supplementary Information Notes S1.

301

302 **Results**

303

304 Graphical analysis of mapped NUTS-1 chronologies (Fig. S2) suggested a certain degree of
305 spatial structuring, except when most of the continent exhibited high seed production (e.g. in
306 1995). The existence of spatial aggregation in masting was confirmed by significantly
307 positive ($p < 0.01$) Mantel correlation coefficients ($M = 0.53, 0.31$, and 0.42 for the isotropic,
308 latitude-only, and longitude-only tests, respectively) and correlograms (Fig. 2, Fig. S3).

309 Hierarchical clustering of NC produced three relatively stable clusters broadly corresponding
310 to southern (SO, cluster stability = 56%), northern (NO, 68%), and eastern Europe (EA, 71%)
311 (Fig. 3; Fig. S4). Further dendrogram subdivisions suggested differences between Romania,
312 Poland, and all other NUTS-1 in EA, between Mediterranean (central Italy) and all other
313 NUTS-1 in SO, and between Atlantic (France, United Kingdom) and central NUTS-1 in NO.
314

315 Correlation analysis revealed consistently positive correlations between NC and previous
316 summers' temperature at the NUTS-1 level across the species distribution (and in all three
317 clusters), especially when using seasonal summer weather or two-year differences (Fig. 4).
318 Correlations were generally strongest for MAX and MEAN (Fig. S5), and to a lesser degree
319 MIN (Fig. S6) (mean correlation across all NUTS-1: 0.38, 0.36, 0.39, -0.21, and 0.28, 0.24,
320 0.28, -0.13, respectively against MAX, MIN, MEAN, and PRE in June-July of two years
321 prior and one year prior). MAX_{AUG-1} was not a consistent signal across Europe. One third of
322 NUTS-1 did not have significant correlations ($R \geq 0.35$ with a sample size of $n=61$) either
323 with MAX_{JUN-1}, MAX_{JUL-1} or MAX_{AUG-1}, especially those in the Netherlands, Italy, and the
324 Carpathian region (the latter were based on shorter records). Temperature in the summer two
325 years prior to masting was negatively correlated with NC across the species distribution (Fig.
326 4), and particularly in cluster NO. Consequently, DeltaT usually produced significant
327 correlations with masting. Weaker (and rarely significant) correlations were found for the
328 autumn and early winter two years prior to masting (negative MAX_{NOV-2} in Austria, Czech
329 Republic, Poland and Germany, positive MAX_{DEC-2} in Mediterranean France) and for the late
330 winter and spring of the year before masting (negative MAX_{FEB-1} in Belgium and United
331 Kingdom, positive MAX_{MAR-1} in Austria, Poland, and Croatia, negative MEAN_{APR-1} in Italy
332 and France). No consistent pattern of correlations was found between NC and temperature in
333 the year of masting, although some regional patterns during spring were found (e.g. positive
334 correlations with MAX_{FEB} in Poland and United Kingdom, or with MAX_{MAY} in Poland).

335

336 Correlations between NC and PRE were weaker and much less consistent than with
337 temperature (Fig. S7). Significantly positive correlations with PRE in two summers prior and
338 negative in one summer prior emerged locally (e.g., in Germany, UK, France, and
339 Switzerland), although a clear distinction between clusters was not evident. Correlations with
340 summer₂ were on average stronger than with summer₁. SPI3 and SPEI3 were similar to
341 MAX, with strong and significant correlations in summer₂ and, less strongly, summer₁ (Fig.
342 S8; Fig. S9), albeit on a more restricted geographic extent (Germany, Denmark, United
343 Kingdom, Belgium, Sweden). Spring water balance (PRE, SPEI3) was generally uncorrelated
344 to masting in beech (except a positive correlation of PRE_{APR-1} in France and PRE_{APR0} in
345 Croatia).

346

347 Overall, most NC conformed to a general pattern of negative correlations with temperature in
348 the summer two years prior to masting, and positive correlations with temperature in the
349 summer one year prior to masting (Table 1), with no substantial differences in the response of
350 masting to weather among geographical clusters. Precipitation and drought indices were less
351 strongly and consistently correlated with NC than temperature. Additionally, neither
352 temperature nor precipitation in the year of masting was consistently correlated with NC,
353 except for a positive influence of early spring temperature in northern Europe. The
354 geographical pattern of weather variables in the period 1950–2014 was very similar to that of
355 masting, with rates of agreement between masting and weather clusters ranging from 62%
356 (TMN) to 87% (PRE) (Table 2).

357

358 Latitude was not a significant driver of the correlation between masting and MAX (Fig. S10).
359 Ordinal logistic models fitted to the eight longest NC had medium to high explanatory power
360 (range of Nagelkerke R²: 0.33– 0.72, mean = 0.57). Stepwise AIC selection isolated between
361 three and six independent variables (Fig. 5), which corroborated the results of weather
362 correlations computed for NUTS-1. The most commonly selected terms were MAX_{JUL-1}
363 (selected in all models) and MAX_{JUL-2} (all but one). MAX_{JUN-1} or MAX_{JUN-2} were
364 additionally selected in five and six models, respectively. NC₋₁, with a negative coefficient,
365 was selected in five models. Precipitation terms were selected less frequently than
366 temperature, and only half of the models included any precipitation term. Standardized
367 coefficients for precipitation were generally lower than those for temperature, indicating a
368 smaller effect on masting. Model validation produced a mean Nagelkerke R² of 0.46 after

369 bootstrapped leave-one-out cross-validation (range = 0.53-0.65), and 0.40 after extrapolation
370 to 1901-1950 (0.21-0.55), indicating that models were partially able to reproduce masting
371 variation outside of the training dataset (Table 3). Clusters SO and EA were represented by
372 only one model each, with the latter showing a lower explanatory power and weaker summer
373 effects.
374

375 Temporal trends in masting were significant in NL1, DE1 (negative trend), DE2, and DE9
376 (positive); however, the interaction between time and summer MAX was significant only in 3
377 out of 32 cases (Table 3). MCA applied to the longest eight chronologies revealed generally
378 stable correlations between temperature and masting, particularly for MAX_{JUL-1} and MAX_{JUL-2}
379 (Fig. 6, Fig. S11), except for DK0 and DE9 (increasingly stronger correlation through time).
380 Most NC showed decade-long periods when correlations with MAX were non-significant,
381 although the timing of these periods was not synchronized across Europe. Some NC showed
382 evidence of “switching” between July and June temperature (i.e., periods of reduced
383 correlations with MAX_{JUL} corresponded to increased correlations with MAX_{JUN}, e.g. DK0),
384 but in others the temporal variations in the strength of all four correlations were homogenous
385 (e.g., UKJ). Some NUTS-1 showed “parallel” correlation trends with year-1 and year-2, i.e.,
386 a decreasing importance of positive MAX₁ corresponding to an increasing importance of
387 negative MAX₂, especially in DE1 and DE2; however, the dataset is too sparse to strongly
388 generalize such evidence.
389

390 Discussion

391 Using a distribution-wide dataset with around 8,000 individual observations, we have shown
392 that a strong spatial structure exists in masting patterns of *F. sylvatica* across its distribution
393 range. Synchrony was higher between neighboring populations (Fig. S1), particularly in
394 northern Europe, and strongly declined with distance (Fig. 2), consistent with previous
395 findings for other temperate species (Koenig & Knops, 2000; Garrison *et al.*, 2008; Gallego
396 Zamorano *et al.*, 2016). While synchrony generally declined with distance (e.g., “typical”
397 years with partial masting at the continental scale such as 2002 or 2009; Fig. S2), continental-
398 scale mast years occurred on several occasions, e.g. twice in the last 40 years (1976 and
399 1995, with less comprehensive but still widespread events in 1992, 2006 and 2011; Fig. S2).
400 This is consistent with what has been previously reported for beech at both continental
401 (Nussbaumer *et al.*, 2016) and regional scale (e.g., Hilton & Packham, 2003), and it is based

403 on an unprecedented sample size. These distribution-wide mast events may have important
404 implications for large-scale, long-distance ecological processes, such as forest regeneration
405 after large disturbances (Peters *et al.*, 2005; Ascoli *et al.*, 2015; Funk *et al.*, 2015), pollen-
406 and seed-related gene flow (Kremer *et al.* 2012), bird migration (Koenig & Knops, 2001),
407 predator-prey population dynamics (Blackwell *et al.*, 2001), pest and disease diffusion
408 (Liebhold *et al.*, 2000), biological invasions (Harper, 2005), forest species range shift
409 (Takenaka, 2005), and climate resilience (Mustin, 2013). Even if masting synchrony had little
410 impact over and above the local effects through predator satiation and/or enhanced
411 pollination, and is simply a result of the weather cues used locally, when the latter co-vary
412 across large areas the ecosystem consequences may be far-reaching.

413

414 Furthermore, the temporal variability of masting in beech showed a distinct spatial structure
415 during the last 65 years, with three clusters located in northern, southern and eastern Europe
416 (Fig. 3). These clusters correspond closely to weather patterns (Fig. S12), and broadly to
417 regions of Europe influenced by different climate regimes: the northern cluster corresponds
418 to the region of western Europe associated with an oceanic climate strongly influenced by the
419 Atlantic (Cfb according to Peel *et al.*, 2007), the southern cluster overlaps with the
420 Mediterranean region (Csa), while the eastern cluster is the most continental one and is less
421 influenced by Atlantic weather (roughly corresponding to Dfb). Indeed, the longitude-based
422 Mantel-test showed a lower correlation coefficient than the latitude-based test, which may be
423 a consequence of weather events characterized by a longitude-based spatial pattern prompting
424 synchronized masting (Fernández-Martínez *et al.*, 2016a). Similar spatial structuring in beech
425 has been found by local masting studies, which explained it by an increasing influence of
426 spring frost in more continental areas (Gross, 1934), but also by tree-ring studies, which
427 linked contrasting growth patterns to the different influence of climate teleconnections, e.g.
428 between the eastern and western Mediterranean basin (Chen *et al.*, 2015; Seim *et al.*, 2015).

429

430 Numerous studies have demonstrated that mast years in many tree species are associated with
431 specific weather conditions (“weather cues”) prior to mast events (Koenig & Knops, 2014;
432 Roland *et al.*, 2014), and particularly with summer temperatures one and two years prior to
433 masting (Schauber *et al.*, 2002; Kelly *et al.*, 2013). We found similar results in this study,
434 showing that a small number of weather variables act as strong cues for masting in almost all
435 European beech populations, despite large climatic, genetic, and environmental differences.
436 Indeed, individual NC where this typical set of cues was not detected were often based on a

437 limited number of observations. We found no substantial differences in these weather cues of
438 masting among regions or clusters using either correlation analysis (Fig. 4, Fig. S10) or
439 regression models (Fig. 5), nor any significant effect of latitude (Fig. S10). This demonstrated
440 that, across the distribution, the cues for masting are highly spatially consistent, with positive
441 correlations for MAX_{JUL-1} (and to a lesser degree MAX_{JUN-1}), and negative for MAX_{JUL-2} and
442 MAX_{JUN-2}, with some local specificities. Combining June and July clearly improved the
443 consistency of strong (and significant) correlations, as did using DeltaT as a synthetic index
444 of temperature differences from year to year (Kelly et al. 2013). In some cases, the seasonal
445 analysis accounted for regional differences in the strongest individual month; AT1-3 were
446 good examples, as they responded more strongly to June temperatures than July (in contrast
447 to most other chronologies). In particular, DeltaT led to improved correlations in cases where
448 correlations with MAX_{summer-1} and MAX_{summer-2} had the expected signal, but were both
449 relatively weak (e.g. DE2, PL2, PL4), or where one individual correlation was much stronger
450 than the other (e.g. DE1, DE2, DEE, SE2, FR6). In the regression models for the NUTS-1
451 with the most data, a large proportion of the variance was explained by summer temperature
452 in years -1 and -2, suggesting that other signals are not very important.

453

454 Therefore, we suggest that the observed spatial organization of masting is more dependent on
455 weather variation across space, rather than on different sensitivities of beech population to
456 the weather cues, in contrast to what Masaki *et al.* (2008) found for *Fagus crenata*. In other
457 words, traits related to masting seems to be the same across the whole beech distribution
458 range, with the exception of small regional differences – e.g., a shift of the most important
459 summer month along a latitudinal gradient, or an increased role of temperatures in the months
460 associated with flowering, pollination and seed maturation (Hase, 1964) in northern Europe.

461

462 While the well-known relationship between general summer weather and masting in beech
463 was well supported by our results, we were also able to disentangle the relative importance of
464 temperature and precipitation as the dominant cue of masting. Wachter (1964) and Piovesan
465 and Adams (2001) suggested that summer precipitation or drought, along with or rather than
466 temperature, were the main cue of masting in beech, while Drobyshev *et al.* (2010) found no
467 relationship between masting and summer precipitation or drought (but did find a strong
468 temperature signal). We have shown that summer precipitation in the two years prior to
469 masting was an important predictor of mast events in some regions (Fig. 4, Fig. 5), and that
470 summer drought was correlated with NC in some regions (Fig. S9), but that both precipitation

and drought were clearly of secondary importance to temperature as a cue of masting. An additional analysis of the relationship between summer MAX and summer SPEI across Europe showed correlations ranging from -0.3 to -0.5 (Fig. S13), suggesting that drought could be more effective in predicting masting in certain locals than in others, hence the contrasting evidence for previous year's drought effects in the literature. The effect of spring precipitation appeared generally negligible, contrary to findings in more Mediterranean species (Fernández-Martínez *et al.*, 2015). Additionally, the importance of precipitation did not appear to vary systematically with latitude, e.g., in northern vs. southern regions where summer drought stress may be limiting (average correlation between latitude and Spearman's coefficient for MAX_{JUN-1}, MAX_{JUL-1}, and MAX_{AUG-1} = -0.13; MAX_{JUN-2}, MAX_{JUL-2}, and MAX_{AUG-2} = 0.05; PRE_{JUN-1}, PRE_{JUL-1}, and PRE_{AUG-1} = 0.07; PRE_{JUN-2}, PRE_{JUL-2}, and PRE_{AUG-2} = 0.09). Instead, summer temperatures in the previous two years, particularly in July, were always the main cue of masting, with mast years associated with a cool summer two years prior to masting, and warm temperatures in the summer prior to masting. This is highly consistent with previous findings on the sensitivity to summer temperatures in both *Fagus* and *Nothofagus* (two years prior: Gruber, 2003; Richardson *et al.*, 2005; Smaill *et al.*, 2011, Kelly *et al.*, 2013; one year prior: Hase, 1964; Wachter, 1964; Schauber *et al.*, 2002; Suzuki *et al.*, 2005; Övergaard *et al.*, 2007; Masaki *et al.*, 2008). Recent analyses of the climate sensitivity of beech diameter increment have also showed that cool, moist summers have a positive effect on the growth of the same year, favoring a resource accumulation hypothesis (Dorado Liñan *et al.*, 2017), while high summer temperatures have a negative effect on growth of the following year throughout the whole geographic distribution, including in northern and central regions (Hacket-Pain *et al.*, 2016), which could be interpreted as a growth vs. reproduction tradeoff if masting was triggered in those years (Monks and Kelly, 2006; Hacket-Pain *et al.*, 2015).

In addition to weather cues, we also found that masting was strongly affected by negative temporal autocorrelation, i.e., masting category in the previous year (NC₋₁). Ordinal logistic regressions models were consistently able to predict mast years with accuracy (mean R² = 0.57) using summer temperature (and in some case precipitation) in the two previous years, plus information on previous year's masting. Negative temporal autocorrelation with a lag of one or two years is one of the defining characteristics of masting time-series (Davis, 1957; Sork *et al.*, 1993; Selås *et al.*, 2002; Koenig *et al.*, 2003), and is the mathematical expression of the rarity of consecutive mast years (category 4 or 5 in our dataset; consecutive years of

505 low masting category were instead common). The existence of negative autocorrelation in
506 masting time series has been traditionally interpreted as evidence for resource depletion, i.e.,
507 trees deplete most resources in the mast year, which limits reproduction in the following year
508 and makes consecutive heavy seed crops very rare (Davis, 1957; Sork *et al.*, 1993; Kelly &
509 Sork, 2002). However, recent studies have showed that negative temporal autocorrelation
510 would also emerge if masting were controlled by DeltaT only (Kelly *et al.*, 2013; Kon &
511 Saito, 2015; but see also Koenig *et al.*, 2015 for criticism of such model).

512

513 The strong correlations between masting and weather found by this study do not provide any
514 conclusive evidence to the debate on whether temperature is a “cue” for trees to trigger high
515 seed crops or whether it acts instead through intermediate steps indicative of a direct
516 mechanistic connection to seed production (Pearse *et al.*, 2014). Koenig & Knops (2000)
517 found that spatial autocorrelation in seed production of northern-hemisphere tree species
518 occurred at the same spatial scale as autocorrelation in rainfall and temperature, consistent
519 with the underlying effect of climatic factors on masting. However, they also found that seed
520 production had much higher variability than the weather factors, implying the existence of
521 non-linearities in weather effects, or of drivers for masting which remain unaccounted for.

522

523 While strong climate differences exist across the distribution of beech, the majority of
524 populations analyzed herein responded similarly to weather (e.g., negative response to
525 temperature and positive to precipitation two years before masting; Table 1). The negative
526 correlation with MAX_{JUL-2} could be related to resource accumulation in cooler years
527 (“priming” the trees to respond to increased temperature one year later, *sensu* Richardson *et*
528 *al.*, 2005), an interpretation that is consistent with a model of masting that includes an
529 element of carbon and/or nitrogen limitation (Sala *et al.*, 2012; Muller-Haubold *et al.*, 2015;
530 Monks *et al.*, 2016; Abe *et al.*, 2016; Pearse *et al.*, 2016). Indeed, a higher soil moisture due
531 to more precipitation and lower summer temperatures has been shown to increase litter mass
532 loss and N mineralization and uptake (Gessler *et al.*, 2005; Smaill *et al.*, 2011), which favors
533 masting in beech (Han *et al.*, 2014; Miyazaki *et al.*, 2014).

534

535 High temperatures in the summer prior to masting (MAX_{JUL-1}) have been linked to flower
536 primordia differentiation (Wachter, 1964; Gruber, 2003; see also: Merkle *et al.*, 1980 for
537 oaks, Allen *et al.*, 2014; Miyazaki *et al.*, 2014), in particular via an increase in endogenous
538 gibberellins (Turnbull, 2011; Pearse *et al.*, 2016). Following this reasoning, we might expect

539 the phenology of primordia differentiation to vary with latitude, creating a geographical
540 gradient in the timing of the previous summer cue similar to the pattern we found in some
541 southern European NUTS-1 (Fig. 4). Additionally, we also found correlations with weather
542 during the periods associated with other known processes that influence flowering
543 phenology, pollen production (Kasprzyk *et al.*, 2014; Pearse *et al.*, 2015), and seed
544 maturation in the year of masting, such as late winter frost (Matthews, 1955; Wachter, 1964),
545 at least in northern Europe. The resource priming in year₋₂ can therefore interact with the
546 MAX cue in summer₋₁ via a resource pulse that boosts an already favorable flower initiation.
547

548 Finally, the analysis of some of the longest series available showed that the sensitivity of
549 beech masting to the most important weather cues (MAX_{JUL-1} and MAX_{JUL-2}) was
550 substantially consistent through time in the last century (Fig. 6), with one possible exception
551 (DE9 with the strongest MCA trend of masting, and logistic model with poorest predictive
552 power). While many studies have reported associations between weather cues and mast years,
553 very few had the length of record required to test whether these cues are consistent through
554 time. Additionally, regression models fitted using data from the period 1950–2014
555 successfully described mast years in the first half of the 20th century (Fig. 5) – although we
556 did not switch the periods due to insufficient sample size for model calibration. This is an
557 important result, as there is little existing information on whether climate change affects the
558 sensitivity of masting to weather cues, or whether the timing of cues shifts seasonally as a
559 response to changing temperatures, as it has been demonstrated for leaf and flower phenology
560 (Menzel *et al.*, 2006). Assessing the effects of changing climate on the frequency and timing
561 of mast years is challenging (McKone *et al.*, 1998; Drobyshev *et al.*, 2014). Despite the
562 preeminent role of summer MAX, our analysis did not provide any strong evidence to
563 suggest that the relationships between weather and masting were sensitive to 20th century
564 warming (contrary to Övergaard *et al.*, 2007), as predicted by the theoretical model of Kelly
565 *et al.* (2013). This lends robustness to the attempts to reconstruct and predict mast years using
566 temperature data (e.g., Drobyshev *et al.*, 2014). However, this should be tested more
567 thoroughly. In particular, it is still unclear whether both gradual and abrupt (e.g., extreme
568 events) components of climate change influence masting frequency and spatial synchrony
569 within and across species or phylogenetic groups (Koenig *et al.*, 2016), for example through
570 changes in resource levels (Miyazaki, 2013; Allen *et al.*, 2014), pollen availability (Koenig *et*
571 *al.*, 2015), coexistence of species with different biomass allocation strategies (Perez-Ramos

572 *et al.*, 2015), and in the interactions between the processes of resource accumulation and
573 flower induction (Monks *et al.*, 2016).

574

575 **Acknowledgements**

576 The authors acknowledge Laura McGarty for language editing, and Dr. Dave Kelly and an
577 anonymous reviewer for their insightful comments to the preliminary version of this
578 manuscript.

579

580 **Author contributions**

581 GV and AHP analyzed the data and wrote the manuscript; DA designed the research,
582 provided and analyzed masting data, and wrote parts of the manuscript; MT provided and
583 interpreted weather data; ID, MC, JM, and RM contributed to research design and data
584 interpretation.

585

586 **References**

587

588 **Abe T, Tachiki Y, Kon H, Nagasaka A, Onodera K, Minamino K, Han Q, Satake A.**589 **2016.** Parameterisation and validation of a resource budget model for masting using590 spatiotemporal flowering data of individual trees. *Ecology Letters* **19**(9):1129-1139.591 **Agresti A.** 2002. *Categorical data*. New York: John Wiley & Sons.592 **Allen RB, Hurst JM, Portier J, Richardson SJ.** 2014. Elevation-dependent responses of593 tree mast seeding to climate change over 45 years. *Ecology and Evolution* **4**(18):3525-3537.594 **Allen RG, Pereira LS, Raes D, Smith M.** 1998. *Crop evapotranspiration. Guidelines for*595 *computing crop water requirements*. FAO Irrigation and drainage paper 56. Rome: FAO.596 **Ascoli D, Maringer J, Hacket-Pain A, Conedera M, Drobyshev I, Motta R, Cirolli M,**597 **Kantorowicz W, Zang C, Schueler S, et al.**, 2017. Two centuries of masting data for598 European beech and Norway spruce across the European subcontinent. *Ecology*, in press. doi:

599 10.1002/ecy.1785.

600 **Ascoli D, Vacchiano G, Maringer J, Bovio G, Conedera M.** 2015. The synchronicity of601 masting and intermediate severity fire effects favors beech recruitment. *Forest Ecology and*602 *Management* **353**:126-135.603 **Beguería S, Vicente-Serrano SM.** 2013. *SPEI: Calculation of the Standardised*604 *Precipitation-Evapotranspiration Index. R package version 1.6*. [WWW document] URL605 <https://CRAN.R-project.org/package=SPEI>. [accessed 1 September 2016].606 **Bisi F, von Hardenberg J, Bertolino S, Wauters LA, Imperio S, Preatoni DG,**607 **Provenzale A, Mazzamuto MV, Martinoli A.** 2016. Current and future conifer seed608 production in the Alps: testing weather factors as cues behind masting. *European Journal of*609 *Forest Research* **135**:743-754.610 **Bjornstad ON.** 2015. *ncf: Spatial Nonparametric Covariance Functions. R package version*611 *1.1-6*. [WWW document] URL <https://CRAN.R-project.org/package=ncf>. [accessed 1

612 September 2016].

613 **Blackwell GL, Potter MA, Minot EO.** 2001. Rodent and predator population dynamics in614 an eruptive system. *Ecological Modeling* **142**:227–245.615 **Büsgen M, Münch E, Thomson T.** 1929. *The structure and life of forest trees*. London:

616 Chapman & Hall.

- 617 **Casalegno S, Amatulli G, Bastrup-Birk A, Durrant TH, Pekkarinen A.** 2011. Modelling
618 and mapping the suitability of European forest formations at 1-km resolution. European
619 *Journal of Forest Research* **130**(6):971-981.
- 620 **Charrad M, Ghazzali N, Boiteau V, Niknafs A.** 2014. NbClust: an R Package for
621 determining the relevant number of clusters in a data set. *Journal of Statistical Software*.
622 **61**(6):1-36.
- 623 **Chen K, Dorado-Liñán I, Akhmetzyanov L, Gea-Izquierdo G, Zlatanov T, Menzel A.**
624 2015. Influence of climate drivers and the North Atlantic Oscillation on beech growth at
625 marginal sites across the Mediterranean. *Climate Research* **66**(3):229-242.
- 626 **Clement J, Maes P, de Strihou CV, van der Groen G, Barrios JM, Verstraeten WW,**
627 **van Ranst M.** 2010. Beechnuts and outbreaks of *Nephropathia epidemica* (NE): of mast,
628 mice and men. *Nephrology Dialysis Transplantation* **25**(6):1740-1746.
- 629 **Davis LD.** 1957. Flowering and alternate bearing. *Proceedings of the American Society of*
630 *Horticultural Science* **70**:545-556.
- 631 **Dorado Liñán I, Zorita E, Martínez-Sancho E, Gea-Izquierdo G, Di Filippo A,**
632 **Gutiérrez E, Levanic T, Piovesan G, Vacchiano G, Zang C, Zlatanov T, Menzel M.**
633 2017. Large-scale atmospheric circulation enhances the Mediterranean East-West tree growth
634 contrast at rear-edge deciduous forests. *Agricultural and Forest Meteorology* **239**:86-95.
- 635 **Drobyshev I, Niklasson M, Mazerolle MJ, Bergeron Y.** 2014. Reconstruction of a 253-
636 year long mast record of European beech reveals its association with large scale temperature
637 variability and no long-term trend in mast frequencies. *Agricultural and Forest Meteorology*
638 **192**:9-17.
- 639 **Drobyshev I, Overgaard R, Saygin I, Niklasson M, Hickler T, Karlsson M, Sykes MT.**
640 2010. Masting behaviour and dendrochronology of European beech (*Fagus sylvatica* L.) in
641 southern Sweden. *Forest Ecology and Management* **259**: 2160-2171.
- 642 **Dunn JC.** 1974. Well-separated clusters and optimal fuzzy partitions. *Journal of Cybernetics*
643 **4**(1):95-104.
- 644 **Dutilleul P, Clifford P, Richardson S, Hemon D.** 1993. Modifying the t test for assessing
645 the correlation between two spatial processes. *Biometrics* **49**:305-314.

- 646 **Fernández-Martínez M, Garbulsky M, Peñuelas J, Peguero G, Espelta JM.** 2015.
647 Temporal trends in the enhanced vegetation index and spring weather predict seed production
648 in Mediterranean oaks. *Plant Ecology* **216**(8):1061-1072.
- 649 **Fernández-Martínez M, Vicca S, Janssens IA, Espelta JM, Peñuelas J.** 2016a. The North
650 Atlantic Oscillation synchronises fruit production in western European forests. *Ecography*.
651 doi: 10.1111/ecog.02296.
- 652 **Fernández-Martínez M, Vicca S, Janssens IA, Espelta JM, Peñuelas J.** 2016b. The role
653 of nutrients, productivity and climate in determining tree fruit production in European forests.
654 *New Phytologist*. doi: 10.1111/nph.14193.
- 655 **Funk KA, Koenig WD, Knops JM.** 2015. Fire effects on acorn production are consistent
656 with the stored resource hypothesis for masting behavior. *Canadian Journal of Forest
657 Research* **46**(1):20-24.
- 658 **Gallego Zamorano J, Hokkanen T, Lehikoinen A.** 2016. Climate driven synchrony in seed
659 production of masting deciduous and conifer tree species. *Journal of Plant Ecology*. doi:
660 10.1093/jpe/rtw117.
- 661 **Garrison BA, Koenig WD, Knops JM.** 2008. Spatial synchrony and temporal patterns in
662 acorn production of California black oaks. In: Merenlender A, McCreary D, Purcell KL, eds.
663 *Proceedings of the sixth symposium on oak woodlands: today's challenges, tomorrow's
664 opportunities*. Albany, USA: USDA Forest Service, Pacific SW Forest and Range
665 Experiment Station, General Technical Report PSW-GTR-217, 343-356.
- 666 **Gessler A, Jung K, Gasche R, Papen H, Heidenfelder A, Börner E, Metzler B, Augustin
667 S, Hildebrand E, Rennenberg H.** 2005. Climate and forest management influence nitrogen
668 balance of European beech forests: microbial N transformations and inorganic N net uptake
669 capacity of mycorrhizal roots. *European Journal of Forest Research* **124**(2):95-111.
- 670 **Gringorten II.** 1963. A plotting rule for extreme probability paper. *Journal of Geophysical
671 Research* **68**(3):813–814.
- 672 **Gross H.** 1934. Die Rotbuche in Ostpreußen. *Zeitschrift für Forst- Und Jagdwesen* **66**:662-
673 651.
- 674 **Gruber R.** 2003. Control and forecasting of the fructification of European beech (*Fagus
675 sylvatica* L.) for the stand Zierenberg 38A and the level I stand in Hessen by climate factors.
676 *Allgemeine Forst Und Jagdzeitung* **174**(4):67-79.

- 677 **Hacket-Pain AJ, Cavin L, Friend AD, Jump AS. 2016.** Consistent limitation of growth by
678 high temperature and low precipitation from range core to southern edge of European beech
679 indicates widespread vulnerability to changing climate. *European Journal of Forest Research*
680 **135(5):897-909.**
- 681 **Hacket-Pain AJ, Friend AD, Lageard JGA, Thomas PA. 2015.** The influence of masting
682 phenomenon on growth-climate relationships in trees: explaining the influence of previous
683 summers' climate on ring width. *Tree Physiology* **35**:319–330.
- 684 Han Q, Kabeya D, Iio A, Inagaki Y, Kakubari Y. **2014.** Nitrogen storage dynamics are
685 affected by masting events in *Fagus crenata*. *Oecologia* **174**(3):679-687.
- 686 **Hao Z, AghaKouchak A, Nakhjiri N, Farahmand A. 2014.** Global integrated drought
687 monitoring and prediction system. *Scientific Data* **1**:1–10.
- 688 **Harper GA. 2005.** Heavy rimu (*Dacrydium cupressinum*) mast seeding and rat (*Rattus spp.*)
689 population eruptions on Stewart Island/Rakiura. *New Zealand Journal of Zoology* **32**:155–
690 162.
- 691 **Harrell FE. 2015.** *rms: Regression Modeling Strategies. R package version 4.3-1.* [WWW
692 document] URL <https://CRAN.R-project.org/package=rms>. [accessed 1 September 2016].
- 693 **Harris IP, Jones PD, Osborn TJ, Lister DH. 2014.** Updated high-resolution grids of
694 monthly climatic observations—the CRU TS3.10 dataset. *International Journal of
695 Climatology* **34**(3):623-642.
- 696 **Hase W. 1964.** Die Buchenmast in Schleswig-Holstein und ihre Abhängigkeit von der
697 Witterung. *Mitteilungen des Deutschen Wetterdienstes* **31**:1–52.
- 698 **Hennig C. 2015.** *fpc: Flexible Procedures for Clustering. R package version 2.1-10.* [WWW
699 document] URL <https://CRAN.R-project.org/package=fpc>. 2015. [accessed 1 September
700 2016].
- 701 **Hilton GM, Packham JR. 2003.** Variation in the masting of common beech (*Fagus
702 sylvatica* L.) in northern Europe over two centuries (1800–2001). *Forestry* **76**(3):319-328.
- 703 **Holm S. 1979.** A simple sequentially rejective multiple test procedure. *Scandinavian Journal
704 of Statistics* **6**:65–70.
- 705 **Hotelling H. 1953.** New light on the correlation coefficient and its transforms. *Journal of the
706 Royal Statistical Society Series B (Methodological)* **15**(2):193-232.

- 707 **Kasprzyk I, Ortyl B, Dulska-Jeż A.** 2014. Relationships among weather parameters,
708 airborne pollen and seed crops of *Fagus* and *Quercus* in Poland. *Agricultural and Forest
709 Meteorology* **197**:111-122.
- 710 **Kelly D, Geldenhuys A, James A, Penelope Holland E, Plank MJ, Brockie RE, Cowan
711 PE, Harper GA, Lee WG, Maitland MJ, Mark AF.** 2013. Of mast and mean: differential-
712 temperature cue makes mast seeding insensitive to climate change. *Ecology Letters* **16**(1):90-
713 98.
- 714 **Kelly D, Harrison AL, Lee WG, Payton IJ, Wilson PR, Schaub EM.** 2000. Predator
715 satiation and extreme mast seeding in 11 species of *Chionochloa* (*Poaceae*). *Oikos*
716 **90**(3):477-88.
- 717 **Kelly D, Sork VL.** 2002. Mast seeding in perennial plants: why, how, where?. *Annual
718 Review of Ecology and Systematics* **1**:427-447.
- 719 **Kelly D.** 1994. The evolutionary ecology of mast seeding. *Trends in Ecology & Evolution*
720 **9**(12):465-470.
- 721 **Koenig WD, Alejano R, Carbonero MD, Fernández-Rebolledo P, Knops JM, Marañón T,
722 Padilla-Díaz CM, Pearse IS, Pérez-Ramos IM, Vázquez-Piqué J, Pesendorfer MB.** 2016.
723 Is the relationship between mast-seeding and weather in oaks related to their life-history or
724 phylogeny?. *Ecology* **97**(10):2603-2615.
- 725 **Koenig WD, Kelly D, Sork VL, Duncan RP, Elkinton JS, Peltonen MS, Westfall RD.**
726 2003. Dissecting components of population-level variation in seed production and the
727 evolution of masting behavior. *Oikos* **102**(3):581-591.
- 728 **Koenig WD, Knops JM.** 1998. Scale of mast-seeding and tree-ring growth. *Nature* **396**:225-
729 226.
- 730 **Koenig WD, Knops JM.** 2000. Patterns of annual seed production by northern hemisphere
731 trees: a global perspective. *American Naturalist* **155**:59–69.
- 732 **Koenig WD, Knops JM.** 2001. Seed-crop size and eruptions of North American boreal seed-
733 eating birds. *Journal of Animal Ecology* **70**(4):609-620.
- 734 **Koenig WD, Knops JM.** 2013. Large-scale spatial synchrony and cross-synchrony in acorn
735 production by two California oaks. *Ecology* **94**:83-93.

- 736 **Koenig WD, Knops JM. 2014.** Environmental correlates of acorn production by four species
737 of Minnesota oaks. *Population Ecology* **56**:63-71.
- 738 **Koenig WD, Knops JM, Carmen WJ, Pearse IS. 2015.** What drives masting? The
739 phenological synchrony hypothesis. *Ecology* **96**(1):184-192.
- 740 **Kon H, Saito H. 2015.** Test of the temperature difference model predicting masting
741 behavior. *Canadian Journal of Forest Research* **45**:1835-1844.
- 742 **Kremer A, Ronce O, Robledo-Arnuncio JJ, Guillaume F, Bohrer G, Nathan R, Bridle
743 JR, Gomulkiewicz R, Klein EK, Ritland K, et al. 2012.** Long-distance gene flow and
744 adaptation of forest trees to rapid climate change. *Ecology* **15**(4):378-392.
- 745 **Lichti NI, Steele MA, Zhang H, Swihart RK. 2014.** Mast species composition alters seed
746 fate in North American rodent-dispersed hardwoods. *Ecology* **95**(7):1746-1758.
- 747 **Liebold A, Elkinton J, Williams D, Muzika RM. 2000.** What causes outbreaks of the
748 gypsy moth in North America? *Population Ecology* **42**(3):257-266.
- 749 **Mantel N. 1967.** The detection of disease clustering and a generalized regression approach.
750 *Cancer Research* **27**(2 Part 1):209-220.
- 751 **Masaki T, Oka T, Osumi K, Suzuki W. 2008.** Geographical variation in climatic cues for
752 mast seeding of *Fagus crenata*. *Population Ecology* **50**(4):357-366.
- 753 **Matthews JD. 1955.** The influence of weather on the frequency of beech mast years in
754 England. *Forestry* **28**(2):107-116.
- 755 **McKee TB, Doesken NJ, Kleist J. 1993.** The relationship of drought frequency and duration
756 to time scales. In: *Proceedings of the 8th Conference on Applied Climatology*. Boston, MA,
757 USA: American Meteorological Society, 179-183.
- 758 **McKone MJ, Kelly D, Lee WG. 1998.** Effect of climate change on mast-seeding species:
759 frequency of mass flowering and escape from specialist insect seed predators. *Global Change
760 Biology* **4**(6):591-596.
- 761 **Menzel A, Sparks T, Estrella N, Koch E, Aasa A, Ahas R, Alm-Kübler K, Bissolli P,
762 Braslavská O, Briede A, et al. 2006.** European phenological response to climate change
763 matches the warming pattern. *Global Change Biology* **12**:1969-1976.
- 764 **Merkle SA, Feret PP, Croxdale JG, Sharik TL. 1980.** Development of floral primordia in
765 white oak. *Forest Science* **26**:238-250.

- 766 **Mescher MC, Pearse IS.** 2016. Communicative interactions involving plants: information,
767 evolution, and ecology. *Current Opinion in Plant Biology* **32**:69-76.
- 768 **Meyer SE, Pendleton BK.** 2015. Seedling establishment in a masting desert shrub parallels
769 the pattern for forest trees. *Acta Oecologica* **65**:1-10.
- 770 **Miyazaki Y, Maruyama Y, Chiba Y, Kobayashi MJ, Joseph B, Shimizu KK, Mochida
771 K, Hiura T, Kon H, Satake A.** 2014. Nitrogen as a key regulator of flowering in *Fagus
772 crenata*: understanding the physiological mechanism of masting by gene expression analysis.
773 *Ecology Letters* **17**(10):1299-1309.
- 774 **Miyazaki Y.** 2013. Dynamics of internal carbon resources during masting behavior in
775 trees. *Ecological Research* **28**:143-150.
- 776 Monks A, Kelly D. 2006. Testing the resource matching hypothesis in the mast seeding tree
777 *Nothofagus truncata* (Fagaceae). *Austral Ecology* **31**:366-375.
- 778 **Monks A, Monks JM, Tanentzap AJ.** 2016. Resource limitation underlying multiple
779 masting models makes mast seeding sensitive to future climate change. *New Phytologist*
780 **210**:419-430.
- 781 **Müller-Haubold H, Hertel D, Leuschner C.** 2015. Climatic drivers of mast fruiting in
782 European beech and resulting C and N allocation shifts. *Ecosystems* **18**(6):1083-1100.
- 783 **Müller-Haubold H, Hertel D, Seidel D, Knutzen F, Leuschner C.** 2013. Climate responses
784 of aboveground productivity and allocation in *Fagus sylvatica*: A transect study in mature
785 forests. *Ecosystems* **16**:1498-1516.
- 786 **Murtagh F, Legendre P.** 2014. Ward's hierarchical agglomerative clustering method: which
787 algorithms implement Ward's criterion?. *Journal of Classification* **31**(3):274-295.
- 788 **Mustin K.** 2013. Red noise increases extinction risk during rapid climate change. *Diversity
789 and Distributions* **19**(7):815–824.
- 790 **Norden N, Chave J, Belbenoit P, Caubère A, Châtelet P, Forget PM, Thébaud C.** 2007.
791 Mast fruiting is a frequent strategy in woody species of Eastern South America. *Plos One*
792 **2**(10):e1079.
- 793 **Nussbaumer A, Waldne P, Etzold S, Gessler A, Benham S, Thomsen IM, Jorgensen BB,
794 Timmermann V, Verstraeten A, Sioen G, et al.,** 2016. Patterns of mast fruiting of common

- 795 beech, sessile and common oak, Norway spruce and Scots pine in Central and Northern
796 Europe. *Forest Ecology and Management* **363**:237-251.
- 797 **Oden NL, Sokal RR. 1986.** Directional autocorrelation: an extension of spatial correlograms
798 to two dimensions. *Systematic Zoology* **35**:608-617.
- 799 **Ostfeld RS, Keesing F. 2000.** Pulsed resources and community dynamics of consumers in
800 terrestrial ecosystems. *Trends in Ecology & Evolution* **15**(6):232-237.
- 801 **Øvergaard R, Gemmel P, Karlsson M. 2007.** Effects of weather conditions on mast year
802 frequency in beech (*Fagus sylvatica* L.) in Sweden. *Forestry* **80**(5):555-565.
- 803 **Pearse IS, Koenig WD, Funk KA, Pesendorfer MB. 2015.** Pollen limitation and flower
804 abortion in a wind-pollinated, masting tree. *Ecology* **96**(2):587-593.
- 805 **Pearse IS, Koenig WD, Kelly D. 2016.** Mechanisms of mast seeding: resources, weather,
806 cues, and selection. *New Phytologist* **212**(3):546-562.
- 807 **Pearse IS, Koenig WD, Knops JM. 2014.** Cues versus proximate drivers: testing the
808 mechanism behind masting behavior. *Oikos* **123**(2):179-184.
- 809 **Peel MC, Finlayson BL, McMahon TA. 2007.** Updated world map of the Köppen-Geiger
810 climate classification. *Hydrology and Earth System Sciences* **11**:1633-1644.
- 811 **Pérez-Ramos IM, Padilla-Díaz CM, Koenig WD, Maranon T. 2015.** Environmental
812 drivers of mast-seeding in Mediterranean oak species: does leaf habit matter?. *Journal of
813 Ecology* **103**(3):691-700.
- 814 **Peters VS, Macdonald SE, Dale MR. 2005.** The interaction between masting and fire is key
815 to white spruce regeneration. *Ecology* **86**(7):1744-1750.
- 816 **Piovesan G, Adams JM. 2001.** Masting behaviour in beech: linking reproduction and
817 climatic variation. *Canadian Journal of Botany* **79**(9):1039-1047.
- 818 **R Core Team. 2016.** *R: A language and environment for statistical computing*. Vienna,
819 Austria: R Foundation for Statistical Computing. [WWW document] URL <https://www.R-project.org> [accessed 1 November 2016].
- 821 **Richardson SJ., Allen RB, Whitehead D, Carswell FE, Ruscoe WA, Platt KH. 2005.**
822 Climate and net carbon availability determine temporal patterns of seed production by
823 *Nothofagus*. *Ecology* **86**(4):972-981.

- 824 **Roland CA, Schmidt JH, Johnstone JF.** 2014. Climate sensitivity of reproduction in a
825 mast-seeding boreal conifer across its distributional range from lowland to treeline forests.
826 *Oecologia* **174**(3):665-677.
- 827 **Sala A, Hopping K, McIntire EJ, Delzon S, Crone EE.** 2012. Masting in whitebark pine
828 (*Pinus albicaulis*) depletes stored nutrients. *New Phytologist* **196**(1):189-199.
- 829 **Satake A, Iwasa YO.** 2000. Pollen coupling of forest trees: forming synchronized and
830 periodic reproduction out of chaos. *Journal of Theoretical Biology* **203**(2):63-84.
- 831 **Schauber EM, Kelly D, Turchin P, Simon C, Lee WG, Allen RB, Payton IJ, Wilson PR,**
832 **Cowan PE, Brockie RE.** 2002. Masting by eighteen New Zealand plant species: The role of
833 temperature as a synchronizing cue. *Ecology* **83**:1214-1225.
- 834 **Seim A, Treydte K, Trouet V, Frank D, Fonti P, Tegel W, Panayotov M, Fernández-**
835 **Donado L, Krusic P, Büntgen U.** 2015. Climate sensitivity of Mediterranean pine growth
836 reveals distinct east–west dipole. *International Journal of Climatology* **35**(9):2503-2513.
- 837 **Selås V, Piovesan G, Adams JM, Bernabei M.** 2002. Climatic factors controlling
838 reproduction and growth of Norway spruce in southern Norway. *Canadian Journal of Forest
839 Research* **32**(2):217-225.
- 840 **Smaill SJ, Clinton PW, Allen RB, Davis MR.** 2011. Climate cues and resources interact to
841 determine seed production by a masting species. *Journal of Ecology* **99**(3):870-877.
- 842 **Sork VL, Bramble J, Sexton O.** 1993. Ecology of mast-fruiting in three species of North
843 American deciduous oaks. *Ecology* **74**(2):528-541.
- 844 **Suzuki W, Osumi K, Masaki T.** 2005. Mast seeding and its spatial scale in *Fagus crenata* in
845 northern Japan. *Forest Ecology and Management* **205**(1):105-116.
- 846 **Takenaka A.** 2005. Local coexistence of tree species and the dynamics of global distribution
847 pattern along an environmental gradient: a simulation study. *Ecological Research* **20**(3):297-
848 304.
- 849 **Tan FC, Swain SM.** 2006. Genetics of flower initiation and development in annual and
850 perennial plants. *Physiologia Plantarum* **128**(1):8-17.
- 851 **Taylor BM, Parida B.** 2016. *cruts: Interface to Climatic Research Unit Time-Series Version*
852 *3.21 Data. R package version 0.3.* [WWW document] URL <https://CRAN.R-project.org/package=cruts> [accessed 1 September 2016].

- 854 **Turnbull C.** 2011. Long-distance regulation of flowering time. *Journal of Experimental*
855 *Botany* **62**(13):4399-4413.
- 856 **Vicente-Serrano SM, Beguería S, López-Moreno JI.** 2010. A multiscale drought index
857 sensitive to global warming: the standardized precipitation evapotranspiration index. *Journal*
858 *of Climate* **23**(7):1696-1718.
- 859 **Vicente-Serrano SM, Gouveia C, Camarero JJ, Beguería S, Trigo R, López-Moreno JI,**
860 **Azorín-Molina C, Pasho E, Lorenzo-Lacruz J, Revuelto J, Morán-Tejeda E.** 2013.
861 Response of vegetation to drought time-scales across global land biomes. *Proceedings of the*
862 *National Academy of Sciences* **110**(1):52-57.
- 863 **Wachter H.** 1964. Über die Beziehung zwischen Witterung und Buchenmastjahren.
864 *Forstarchiv* **35**:69-78.
- 865 **Wagner S, Collet C, Madsen P, Nakashizuka T, Nyland RD, Sagheb-Talebi K.** 2010.
866 Beech regeneration research: from ecological to silvicultural aspects. *Forest Ecology and*
867 *Management* **259**(11):2172-2182.
- 868 **Ward JH, Hook ME.** 1963. Application of an hierarchical grouping procedure to a problem
869 of grouping profiles. *Educational and Psychological Measurement* **23**(1):69–82.
- 870 **Zackrisson O, Nilsson MC, Jäderlund A, Wardle DA.** 1999. Nutritional effects of seed fall
871 during mast years in boreal forest. *Oikos* **84**:17-26.
- 872

873 **Tables**

874

875 **Table 1** Common weather cues for beech masting across the species distribution range
876 relative to the year of seed production (summary of correlation analyses)

877

	Year -2	Year -1	Year 0
Main signal	COOL summer	WARM summer	
Secondary signal	WET summer	DRY summer	
Regional signals	COOL February and April, WARM March, DRY February and autumn		WARM February and May, WET spring

878

879

880 **Table 2** Proportion of matches from the assignment of NUTS-1 into masting and weather
 881 clusters. Study species: beech. Accuracy: rate of total matches (masting cluster = weather
 882 cluster) to total number of NUTS-1. Cluster identification: EA Eastern Europe, NO Northern,
 883 SO Southern. Monthly weather variables: MEAN mean temperature, MIN minimum
 884 temperature, MAX maximum temperature, PRE precipitation, SPI3 Standardized
 885 Precipitation Index, SPEI3 Standardized Precipitation and Evaporation Index
 886

Weather variable	Weather cluster	Masting-EA	Masting-NO	Masting-SO
MEAN	EA	14	0	2
	NO	4	21	4
	SO	0	0	2
Accuracy		78.7%		
MIN	EA	11	0	0
	NO	4	21	1
	SO	3	0	7
Accuracy		61.9%		
MAX	EA	14	0	5
	NO	4	15	1
	SO	0	6	2
Accuracy		66.0%		
PRE	EA	16	2	1
	NO	2	19	1
	SO	0	0	6
Accuracy		87.2%		
SPI3	EA	14	0	1
	NO	4	21	2
	SO	0	0	5
Accuracy		85.1%		
SPEI3	EA	11	0	1
	NO	7	21	2
	SO	0	0	5
Accuracy		78.7%		

887

888

889 **Table 3** Coefficients and statistics of ordinal logistic regression models for beech masting as
 890 a function of multiple weather variables in the eight longest NUTS-1 chronologies
 891 (backwards stepwise selection by AIC; n.s. = non-significant at $p>0.05$). Monthly weather
 892 variables: MAX maximum temperature, PRE precipitation. Year and year x MAX were
 893 computed using bivariate models with one interaction term. Cluster identification: EA
 894 Eastern Europe, NO Northern, SO Southern.

895

Coefficients	DE1	DE2	DE9	DEF	DK0	NL1	SE2	UKJ
NC ₋₁	-1.05	n.s.	-0.79	n.s.	-1.18	n.s.	-1.25	-1.00
PRE _{JUL-1}	n.s.							
PRE _{JUL-2}	n.s.	n.s.	0.61	n.s.	1.29	n.s.	n.s.	n.s.
PRE _{JUN-1}	n.s.	0.59	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
PRE _{JUN-2}	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0.55	n.s.
MAX _{JUL-1}	0.94	0.52	1.49	1.03	1.34	0.49	1.27	1.42
MAX _{JUL-2}	-1.06	-0.78	-1.16	-1.14	n.s.	-1.31	-1.047	-1.16
MAX _{JUN-1}	0.88	0.98	0.57	n.s.	n.s.	n.s.	0.75	0.59
MAX _{JUN-2}	n.s.	-0.73	-0.68	-0.84	-1.61	-0.73	n.s.	-0.65
Model statistics								
observations	58	65	57	44	65	56	55	65
p	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
R ² (calibration)	0.54	0.33	0.70	0.46	0.66	0.47	0.72	0.63
R ² (leave one-out)	0.49	0.27	0.62	0.41	0.61	0.43	0.65	0.58
R ² (validation)	0.51	0.21	0.32	0.43	0.21	0.40	0.54	0.55
Year in MAX _{JUL-1}	-0.19	n.s.	0.41	n.s.	n.s.	-0.69	n.s.	n.s.
Year in MAX _{JUL-2}	n.s.	n.s.	0.47	n.s.	n.s.	-0.69	n.s.	n.s.
Year in MAX _{JUN-1}	n.s.							
Year in MAX _{JUN-2}	n.s.	0.40	n.s.	n.s.	n.s.	-0.74	n.s.	n.s.
Year x MAX _{JUL-1}	-0.68	n.s.						
Year x MAX _{JUL-2}	n.s.							
Year x MAX _{JUN-1}	n.s.	n.s.	n.s.	n.s.	-0.53	n.s.	n.s.	n.s.
Year x MAX _{JUN-2}	n.s.	0.58	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Cluster	SO	EA	NO	NO	NO	NO	NO	NO

896

897

898 **Figure legends**

899

900 **Fig. 1** (a) Current distribution of beech in Europe at 1-km resolution (Casalegno *et al.*, 2011,
901 filtered for cell cover $\geq 5\%$); (b) number of beech masting data series in each NUTS-1 for
902 the period 1950-2014.

903

904 **Fig. 2** (a) Mantel correlograms for NUTS-1 masting chronologies for beech (1950-2014).
905 Distance in 500-km wide bins. Black dots indicate significant ($p \leq 0.05$) correlations,
906 sequentially corrected for multiple testing using Holm's procedure. (b) Pairwise Spearman's
907 correlations between NUTS-1 masting chronologies (1950-2014) against raw distance in km;
908 black line: local polynomial regression smoother.

909

910 **Fig. 3** Hierarchical clustering of NUTS-1 masting chronologies for beech (1950-2014) based
911 on Suzuki's dissimilarity index (red: eastern cluster, green: northern, blue: southern, grey: no
912 data within beech distribution for the study period). © EuroGeographics for the
913 administrative boundaries. Output clipped on European beech distribution (Fig. 1a). Asterisks
914 indicate NUTS-1 used for analysis of long masting chronologies.

915

916 **Fig. 4** Spearman's correlation between monthly maximum temperature (1950-2014) and
917 NUTS-1 masting chronologies for beech. NUTS-1 ordered and colored according to the
918 cluster they belong to (colors as in Fig. 3, black = excluded from clustering due to
919 insufficient chronology length). The three bottom lines show correlation against seasonal
920 summer weather (June-July) and the Delta variable (difference between weather variable in
921 year₂ and year₁). The sample size (number of years on record) is reported on the secondary
922 x-axis. (.) significant at $p \leq 0.05$, (*) significant at $p \leq 0.00139$ (Bonferroni-corrected).
923 MEAN: the mean correlation for the corresponding month across the study area. JJ.2: June-
924 July, two years prior; JJ.1: June-July, one year prior; delta: JJ.2 – JJ.1

925

926 **Fig. 5** Ordinal logistic models of beech masting (8 longest NUTS-1 chronologies) as a
927 function of weather predictors: (a) model statistics for calibration (1950-2014) and validation
928 (1901-1949). Rsq_1950_2014 is R^2 of the calibration dataset, Rsq_boot is the bootstrapped R^2
929 from leave-one out cross-validation (1000 re-samples), and Rsq_1901_1949 is the R^2 of the
930 predicted values for 1901-1949 vs. observed (validation dataset). (b) standardized model
931 coefficients. Only significant predictors are filled in the table, with the color depending on

932 the coefficient. Monthly weather variables: MAX maximum temperature, PRE precipitation.

933 NC₋₁: masting in the previous year

934

935 **Fig. 6** Moving Spearman's correlation (lines: 28-years timesteps) between the eight longest

936 NUTS-1 beech masting chronologies and maximum temperature (MAX) (1901-2014). Thick

937 lines represent significant ($p \leq 0.05$) correlations.

938

939 **Supplementary Information**

940

941 **Notes S1** R Code for the analysis carried out in the present paper

942

943 **Table S1** NUTS-1 chronologies of masting from 1901 to 2016 on an ordinal scale of 1 (very
944 poor) to 5 (very abundant); dash = no data

945

946 **Table S2** Intra-NUTS correlation of masting series and temporal autocorrelation in NC

947

948 **Fig. S1** Mean Spearman's rank correlation of masting series within each NUTS-1

949

950 **Fig. S2** NUTS-1 masting chronologies from year 1976 to 2014

951

952 **Fig. S3** Mantel correlograms for NUTS-1 masting chronologies (1950-2014) across latitude
953 and longitude only

954

955 **Fig. S4** Dendrogram for the hierarchical clustering of NUTS-1 masting chronologies (1950-
956 2014)

957

958 **Fig. S5** Spearman's correlation between monthly mean temperature (1950-2014) and NUTS-
959 1 masting chronologies

960

961 **Fig. S6** Spearman's correlation between monthly minimum temperature (1950-2014) and
962 NUTS-1 masting chronologies

963

964 **Fig. S7** Spearman's correlation between monthly precipitation (1950-2014) and NUTS-1
965 masting chronologies

966

967 **Fig. S8** Spearman's correlation between monthly SPI3 (1950-2014) and NUTS-1 masting
968 chronologies

969

970 **Fig. S9** Spearman's correlation between monthly SPEI3 (1950-2014) and NUTS-1 masting
971 chronologies

972

973 **Fig. S10** Linear models of Spearman's correlation between masting and MAX in June, July,
974 or August of the one and two years prior vs. latitude

975

976 **Fig. S11** Summary of moving Spearman's correlation (1901-2014, window size: 28 years)
977 between the eight longest NC and MAX_{JUL-1} (red) and MAX_{JUL-2} (blue)

978

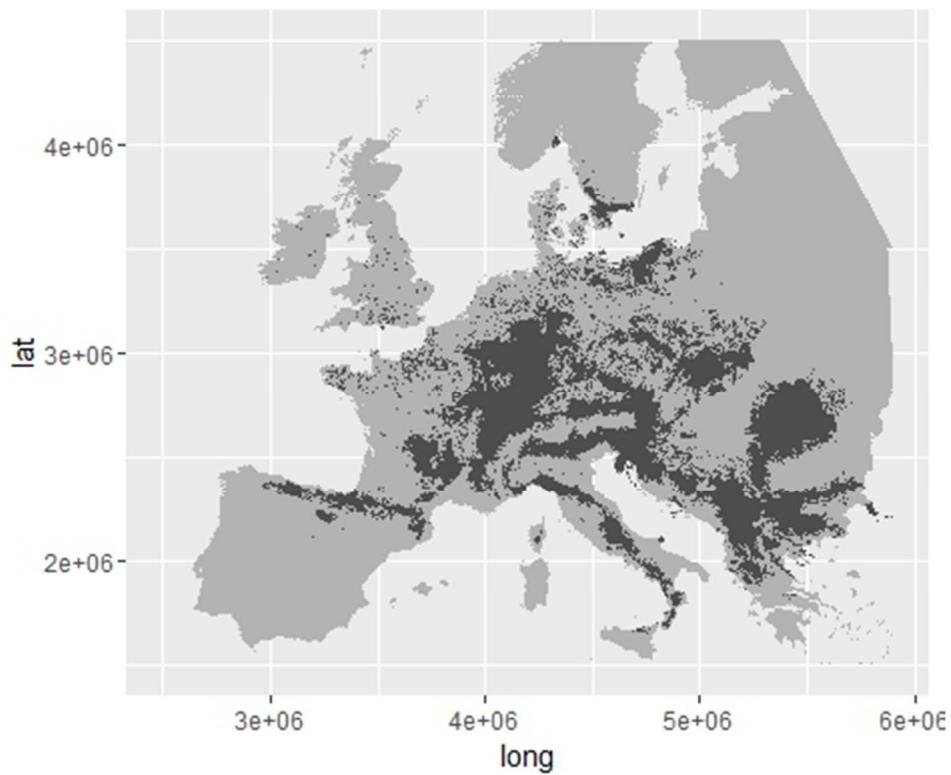
979 **Fig. S12** Hierarchical clustering of NUTS-1 weather variables (1950-2014) based on
980 Suzuki's dissimilarity index

981

982 **Fig. S13** Spearman's correlation between MAX in June-July and SPEI3 across the study area,
983 period 1901-2014

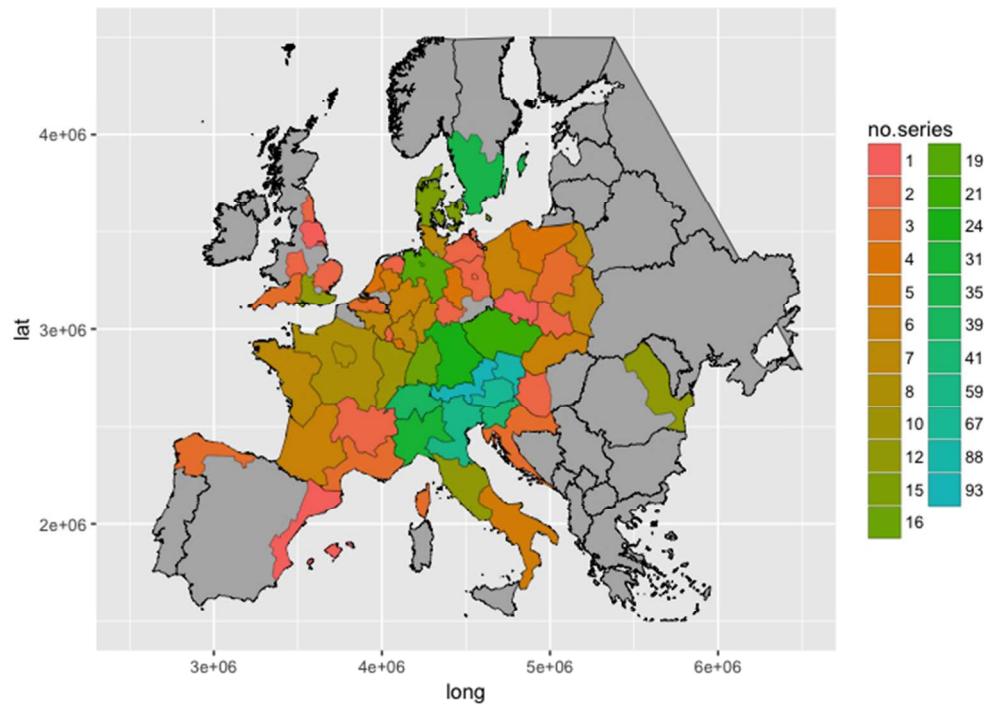
984

985



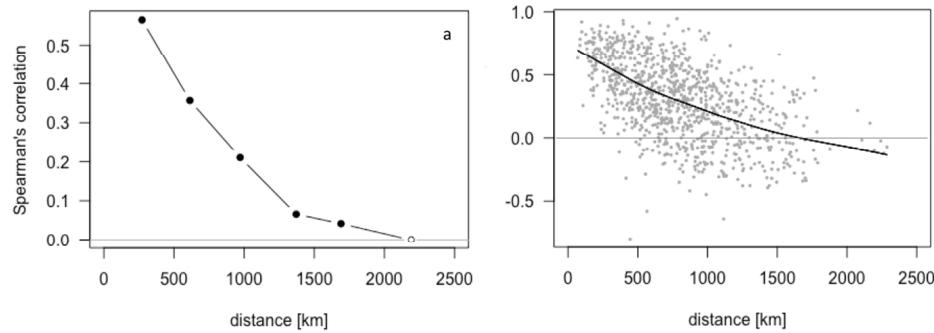
(a) Current distribution of beech in Europe at 1-km resolution (Casalegno et al., 2011, filtered for cell cover $\geq 5\%$);

126x104mm (96 x 96 DPI)



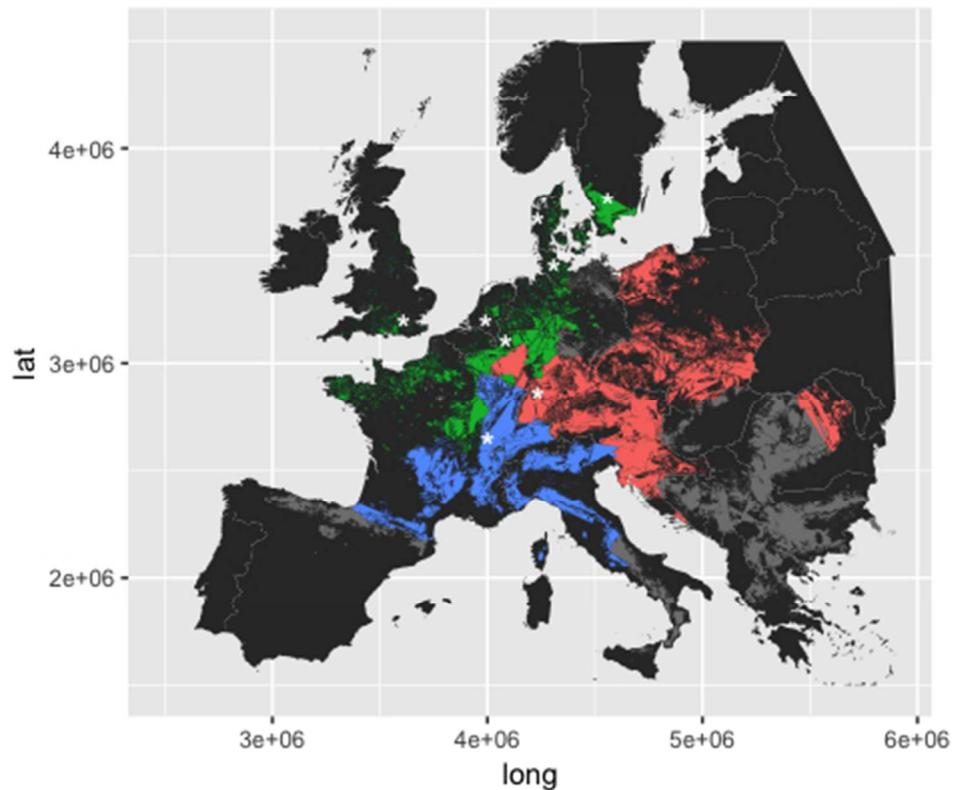
(b) number of beech masting data series in each NUTS-1 for the period 1950-2014.

246x176mm (72 x 72 DPI)



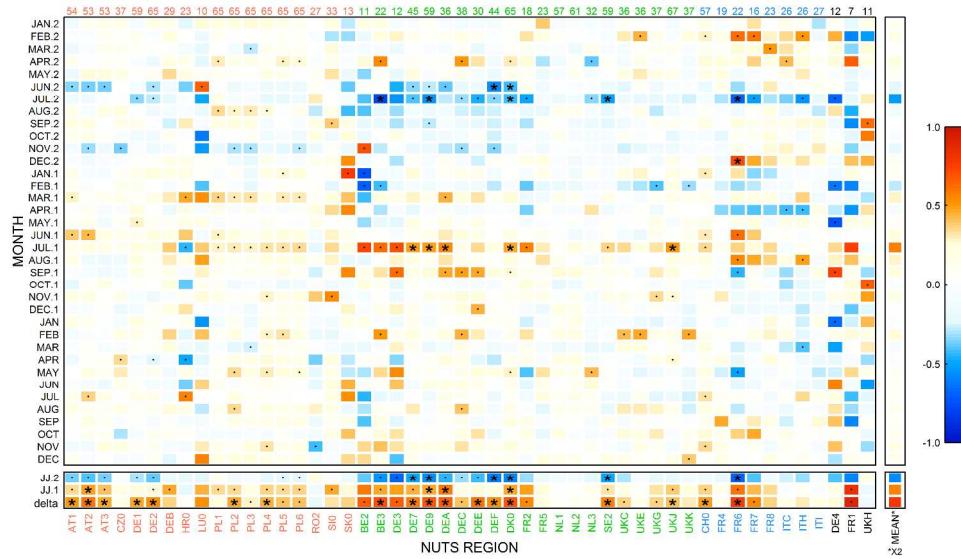
(a) Mantel correlograms for NUTS-1 masting chronologies (1950-2014). Distance in 500-km wide bins. Black dots indicate significant ($p \leq 0.05$) correlations, sequentially corrected for multiple testing using Holm's procedure. (b) Pairwise Spearman's correlations between NUTS-1 masting chronologies (1950-2014) against raw distance in km; black line: local polynomial regression smoother.

338x190mm (108 x 108 DPI)

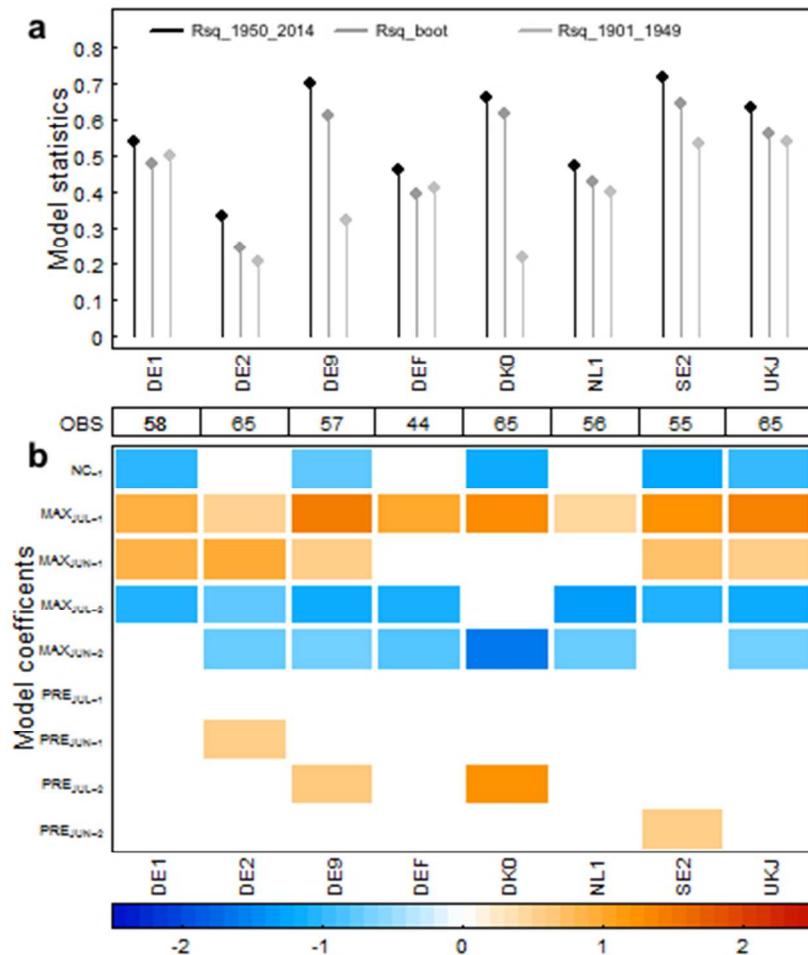


Hierarchical clustering of NUTS-1 masting chronologies (1950-2014) based on Suzuki's dissimilarity index (red: eastern cluster, green: northern, blue: southern, grey: no data within beech distribution for the study period). © EuroGeographics for the administrative boundaries. Output clipped on European beech distribution (Fig. 1a). Asterisks indicate NUTS-1 used for analysis of long masting chronologies.

170x142mm (72 x 72 DPI)

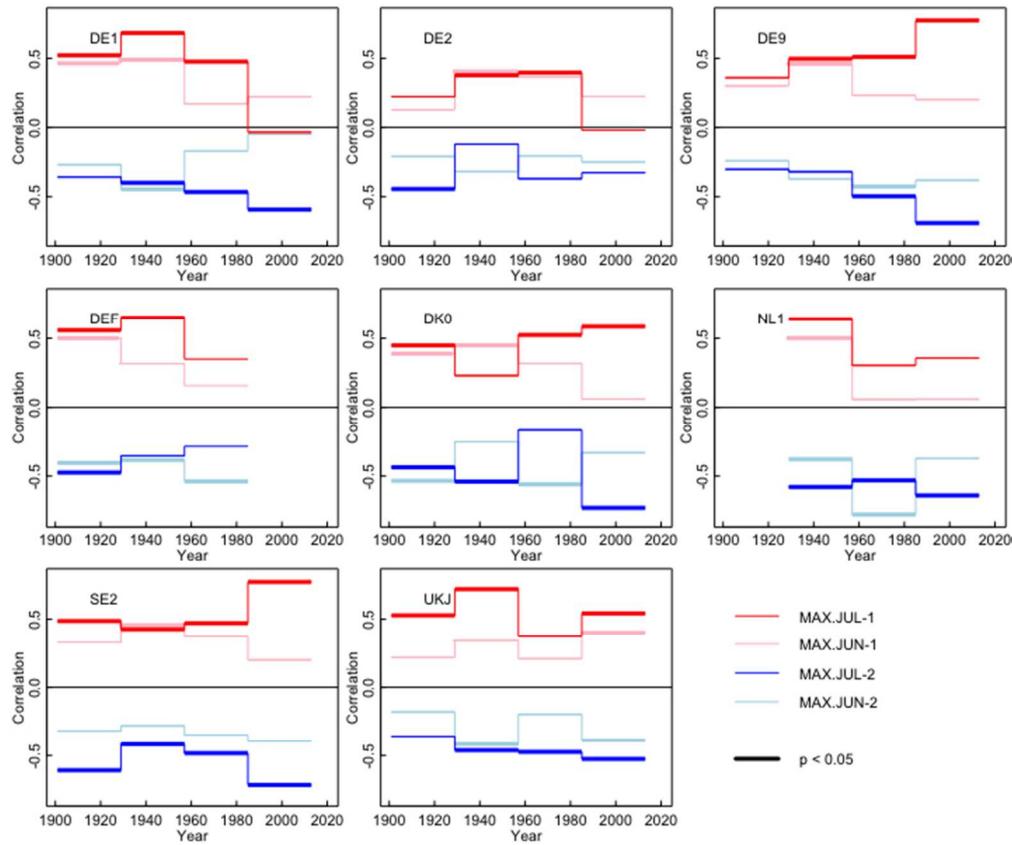


Spearman's correlation between monthly maximum temperature (1950-2014) and NUTS-1 masting chronologies for beech. NUTS-1 ordered and colored according to the cluster they belong to (colors as in Fig. 3, black = excluded from clustering due to insufficient chronology length). The three bottom lines show correlation against seasonal summer weather (June-July) and the Delta variable (difference between weather variable in year-2 and year-1). The sample size (number of years on record) is reported on the secondary x-axis. (.) significant at $p \leq 0.05$, (*) significant at $p \leq 0.00139$ (Bonferroni-corrected). MEAN: the mean correlation for the corresponding month across the study area. JJ.2: June-July, two years prior; JJ.1: June-July, one year prior; delta: JJ.2 – JJ.1



Ordinal logistic models of beech masting (8 longest NUTS-1 chronologies) as a function of weather predictors: (a) model statistics for calibration (1950–2014) and validation (1901–1949). Rsq_1950_2014 is R² the calibration dataset, Rsq_boot is the bootstrapped R² from leave-one out cross-validation (1000 resamples), and Rsq_1901_1949 is the R² of the predicted values for 1901–1949 vs. observed (validation dataset). (b) standardized model coefficients. Only significant predictors are filled in the table, with the color depending on the coefficient. Monthly weather variables: MAX maximum temperature, PRE precipitation. NC-1: masting in the previous year

146x170mm (72 x 72 DPI)



Moving Spearman's correlation (lines: 28-years timesteps) between the eight longest NUTS-1 beech masting chronologies and maximum temperature (MAX) (1901–2014). Thick lines represent significant ($p \leq 0.05$) correlations.

251x211mm (72 x 72 DPI)