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Manuscripts

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

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36

37 **Summary**

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

54
55 **Key words:** *Fagus sylvatica* L. (beech), mast seeding, Moran effect, population ecology,
56 seed production, synchronization, weather cues

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59

60 **Introduction**

61

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

73

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

84

85 The oldest and simplest hypothesis for masting states that seed crops vary in response to
86 weather variation (Büsgen *et al.*, 1929; Kelly, 1994). In particular, temperature and
87 precipitation in the years previous to seed production have been consistently related to
88 masting (e.g., in grasses: Schauber *et al.*, 2002; shrubs: Mayer & Pendleton, 2015; trees: Bisi
89 *et al.*, 2016). The nature of such relationships can be either correlative, i.e., weather is a “cue”
90 that triggers other processes and that plants are able to sense (e.g., Kelly & Sork, 2002; Kelly
91 *et al.*, 2013), or causal, in the case that weather directly influences resources and other
92 proximate causes of masting (Monks *et al.*, 2016; Pearse *et al.*, 2016). In the absence of
93 manipulative experiments, we cautiously consider weather variables as cues. However, few

94 studies have tested whether such cues are constant in space and time across an entire species'
95 distribution range (e.g., Masaki *et al.*, 2008). In other words, do spatial and temporal
96 variations in mast seeding emerge from (a) variations in weather, or (b) differences in local plant
97 response to the same weather patterns, e.g. as a consequence of inter-population differences
98 and adaptations in genes that regulate flowering (Tan and Swain, 2006)? Addressing this
99 question will provide important information on predicting mast seeding both in the short and at the
100 long term, such as in the case of mast seeding responses to climate change and the consequences
101 on large-scale ecosystem processes.

102

103 The aims of this paper are to: i) describe the spatial pattern of mast seeding across the entire
104 distribution of European beech (*Fagus sylvatica* L.), one of the most important European
105 forest species (Fig. 1a); ii) measure the strength of the relationship between beech mast seeding
106 and selected weather variables referring to precipitation, temperature, and drought; iii) assess
107 the stability of mast seeding-weather correlations through space (i.e., whether the strength, timing,
108 and relative importance of weather cues vary across geographical space) and time.

109

110 **Materials and methods**

111

112 *Beech mast seeding data*

113

114 To address such questions, we used a recently available, long-term, large-scale database of
115 mast seeding for European tree species (MASTREE: Ascoli *et al.*, 2017). Each observation was
116 characterized by the following measurements: the date of inclusion in the database, the
117 mast seeding proxy considered (e.g., seed, pollen), the scale of measurement of the original data
118 (continuous or ordinal), the year of measurement, the NUTS-1 (Nomenclature of Territorial
119 Units for Statistics version 2013, level 1, i.e., European administrative subdivisions
120 corresponding to macro-regional aggregations) [data source: GISCO – Eurostat (European
121 Commission)] where the observation was recorded (Fig. 1b), the start and end year of the
122 series, and the length of the continuous recording series to which each observation belongs
123 (range: 1-191 years). Non-EU countries where beech mast seeding data were recorded (i.e.,
124 Ukraine, Serbia, Switzerland, Bosnia and Herzegovina) were also included in the database
125 with dummy NUTS-1 codes. Observations where the country was known but the precise
126 geographical location was uncertain were assigned a NUTS-0 attribution (i.e., country level).

127

128 All database records belonging to series with length ≥ 5 years were associated to a 5-class
129 ordinal measurement (ORDmast) from (1) very poor masting to (5) very abundant masting
130 (Ascoli et al., 2017). To build our target variable we extracted values of ORDmast for beech
131 in the period 1950-2014 (for spatial pattern analysis and Spearman's correlations) or 1901-
132 2014 (for ordinal regression and moving correlation analysis), because antecedent
133 observations were sparse and unevenly spread across the continent. Pollen and flowering data
134 were excluded, as pooling different masting proxies may introduce some noise, such as
135 would happen should flowers' crops not mature into fruits owing to environmental
136 constraints. A total of 769 individual series covering 7983 annually resolved observations
137 from 22 European countries was selected for further analyses.

138

139 *Data treatment*

140

141 To obtain long masting series with a minimum amount of missing data, individual masting
142 series were aggregated into 61 NUTS-1 chronologies (NC) by using the most frequently
143 observed masting class for each year (Table S1). The highest masting class was used in case
144 of multi-modality, but the impact of a different choice would be negligible (mean
145 Spearman's correlation between NC calculated using highest and lowest masting class in
146 case of multi-modality = 0.91, range = 0.68 to 1.00). All forests within a NUTS-1 should
147 have homogenous climatic and ecological characteristics; the assumption was tested by
148 computing the mean Spearman's correlation coefficient between individual weather series
149 (see "Weather cues analysis", period 1901-2014) and between individual masting series in
150 each NUTS-1 (henceforth "intra-NUTS correlations") with ≥ 7 years of observation in
151 common. This sample size was chosen as a trade-off between the need for robustness (critical
152 value for Spearman's correlation with $n=7$ and $p=0.05$: $\rho = 0.79$) and data inclusion (i.e.,
153 keeping at least 60% of all NUTS-1 into the analysis). Possible inflation of cross-correlation
154 values due to temporally autocorrelated series was corrected by calculating adjusted degrees
155 of freedom according to Dutilleul *et al.* (1993). Correlation coefficients computed on <30
156 observation pairs were corrected according to Hotelling's (1953) second-order
157 transformation. Intra-NUTS weather correlations were always higher than 0.9, except for
158 precipitation (higher than 0.6). Of 36 NUTS-1 with at least two masting series sharing ≥ 7
159 elements, 30 had a significantly positive intra-NUTS correlation, with an average value of
160 0.66 (Fig. S1; Table S2).

161

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

166

167 *Spatial analysis of masting patterns*

168

169 To address our first objective, we analyzed the spatial structure of masting synchrony at the
170 continental scale by running a Mantel test (2000 permutations) on NC. This test measures the
171 correlation between two dissimilarity matrices containing measures of geographical and
172 ecological distance. Here, it addresses the hypothesis that masting chronologies farther apart
173 would be less similar to one another (de-synchronized) than closer ones.

174

175 Time series of seed production may exhibit lagged negative temporal autocorrelation (e.g.,
176 Koenig & Knops, 2000) and non-stationarity (i.e., temporal trends; Allen *et al.*, 2014). Both
177 may alter cross-correlation analyses. Therefore, all NC were checked for temporal
178 autocorrelation (max order =1, excluding segments with <7 consecutive years of observation
179 which may bias the autocorrelation function; Sork *et al.*, 1993) by fitting a Cumulative Link
180 regression Model (CLM: Agresti, 2002) (probit link with 2000 iterations) against NC of the
181 previous year (NC_{t-1}). Of 47 NUTS-1 chronologies with ≥ 7 consecutive years of observation,
182 21 had a significantly negative autocorrelation at lag 1 (Table S2). NC that exhibited
183 significant temporal trends (i.e., slope of linear regression against year of observation
184 significant at $p \leq 0.05$) were detrended by extracting regression residuals (negative trend: ITI,
185 SI0; positive trend: DEA, DEB, DEC, PL1, PL2, PL5, PL6).

186

187 We used coordinates of NUTS-1 centers to compute the geographical distance matrix for the
188 Mantel test, and the index of Suzuki *et al.* (2005), a metric derived from Spearman's
189 correlation coefficient, for the masting dissimilarity matrix. Only NC pairs with an overlap of
190 ≥ 7 consecutive years of observation were included in the latter. Furthermore, we ran two
191 unidirectional Mantel tests as a function of distance along longitude (Dlon) and latitude
192 (Dlat) only, by fixing the other coordinate to its mean value across all NUTS-1, to scrutinize
193 the structure of masting along the two orthogonal geographical directions. Mantel tests were
194 run with package *ncf* version 1.1 (Bjornstad, 2015) for the R statistical framework (R Core
195 Team, 2016).

196

197 Secondly, we assessed the geographic pattern of beech masting in Europe by running a
198 hierarchical cluster analysis on NC using Ward's minimum variance method (Murtagh &
199 Legendre, 2014), which minimizes within-cluster distances relative to between-cluster
200 distances (Ward, 1963). Only NC pairs sharing ≥ 7 consecutive years of observation were
201 included in the dissimilarity matrix. NUTS-1 not satisfying such condition when paired
202 against every other NUTS-1 were filtered out. Dissimilarities between individual NC pairs
203 with an insufficient number of observations (4.9% of all NC pairs) were simulated by a linear
204 model of the form $a_0 + a_1 D_{lon} + a_2 D_{lat}$ ($a_0 = 18.41$, $a_1 = 1.61 \times 10^{-5}$, $a_2 = 1.54 \times 10^{-5}$, adjusted
205 $R^2 = 0.35$; F-statistic = 709.9 on 2 and 2672 degrees of freedom, p-value < 0.001). We
206 determined the optimal number of clusters by maximizing the index by Dunn (1974) with the
207 R package *NbClust* (Charrad *et al.*, 2014), and computed cluster stability by nonparametric
208 bootstrap with the R package *fpc* (Hennig, 2015). The validity of each cluster was also
209 assessed by checking that the mean Spearman correlation between all NC pairs in each
210 cluster was higher than the mean correlation between all pairs from two different clusters.

211

212 *Weather cues analysis*

213

214 To measure the strength of weather cues of masting, we calculated Spearman's correlations
215 between each NC (filtered on ≥ 7 years of observation, after detrending if needed: see above)
216 and the following variables: Mean monthly temperature (MEAN), monthly mean of daily
217 maximum temperature (MAX), monthly mean of daily minimum temperature (MIN),
218 monthly precipitation (PRE), three-months Standardized Precipitation Index (SPI3; McKee *et al.*,
219 1993), and three-months Standardized Precipitation and Evaporation Index (SPEI3;
220 Vicente-Serrano *et al.*, 2010). Weather series were obtained by averaging monthly data
221 across all cells included in each NUTS-1 from the gridded database CRU TS 3.23 (0.5°
222 resolution; years 1901-2014) (Harris *et al.*, 2014), and detrended before all subsequent
223 analysis by running a linear filter on each individual monthly variable for the timespan
224 selected (1901-2014 or 1950-2014). SPI3 was calculated using the nonparametric approach
225 described by Hao *et al.* (2014), in which the probability distributions are calculated
226 empirically (Gringorten, 1963), rather than by fitting a parametric distribution function.
227 SPEI3 was calculated from the difference between available water (i.e., three-month sum of
228 PRE) and the potential evapotranspiration, which is based on the FAO-56 Penman–Monteith
229 estimation (Allen *et al.*, 1998) and directly gridded by the CRU. The difference was fit to a

230 log-logistic probability distribution to transform the original values to standardized units
 231 (Vicente-Serrano *et al.*, 2010). SPEI3 measures the climatic water balance and therefore
 232 provides a more reliable and spatially comparable measure of drought severity than
 233 precipitation alone (Vicente-Serrano *et al.*, 2013). Data extraction and calculation of drought
 234 indices were performed with the R packages *cruts* (Taylor and Parida, 2016) and *SPEI*
 235 (Begueria and Vicente-Serrano, 2013). Correlations (years 1950-2014) were computed for all
 236 36 months of a three-year period, including the calendar year of seed production and the two
 237 years prior (lag -1 and -2). After preliminary scrutiny of the most significant correlations, we
 238 also ran correlations against aggregated summer (June-July) weather variables of one and two
 239 years prior to masting, and against the difference (Delta) between values of each weather
 240 variables measured one and two years prior (e.g., Delta Temperature, Kelly et al. 2013). The
 241 absence of non-linear relationships was visually checked before running all correlations. For
 242 each correlation, significance was tested at the 95% confidence level, with a simple
 243 Bonferroni correction, i.e. adjusting the required alpha value according to the number of
 244 comparisons (0.05/36), to account for multiple comparisons. Finally, to assess the role of
 245 weather in determining the spatial pattern of masting in Europe, we ran a hierarchical cluster
 246 analysis of all six weather variables for the period 1950-2014, using Suzuki's dissimilarity
 247 index and three optimal clusters, and compared them against masting clusters by computing
 248 the overall proportion of matches between masting and weather clusters.

249

250 *Spatio-temporal stability of weather cues*

251

252 To test for spatial stability of masting-weather relationships, we fitted a linear model of
 253 Spearman's correlation coefficient between masting and MAX of June, July, and August of
 254 the one and two years prior, and latitude. Subsequently, we modeled the eight longest NC
 255 (DE1, DE2, DE9, DEF, DK0, NL1, SE2, UKJ – including 74 to 115 yearly observations in
 256 the period 1901-2014) as a function of detrended weather variables, using ordinal logistic
 257 regression within the R package *rms* (Harrell, 2016). In this analysis, NC_{-1} was used as an
 258 additional independent variable, to account for potential temporal autocorrelation resulting
 259 e.g. from resource depletion (Davis, 1957) or resource switching (Kelly & Sork, 2002). All
 260 models were fitted with 44-65 observations (years 1950-2014), and validated using both a
 261 new prediction interval (years 1901-1949, 30-41 observations for each NC except NL1 with
 262 10), and a bootstrapped leave-one-out cross-validation run on the calibration time period.
 263 Weather variables (i.e., MAX and PRE in June and July -1 and -2, hereafter MAX_{JUN-1} ,

264 MAX_{JUL-1} , MAX_{JUN-2} , MAX_{JUL-2} , PRE_{JUN-1} , PRE_{JUL-1} , PRE_{JUN-2} , PRE_{JUL-2}) were selected
265 based on the previous correlation analysis and evidence from literature on beech masting
266 (e.g., Piovesan and Adams, 2001; Drobyshev *et al.*, 2010). The absence of non-linear
267 univariate relationships was visually checked before running the models. All independent
268 variables were z-transformed to ensure comparability of effect sizes within models; to
269 account for collinearity among weather variables, optimal models were selected using
270 backward stepwise selection based on the Akaike Information Criterion (AIC). Nagelkerke
271 R^2 was used to compare models for different NC.

272

273 To test for temporal stability of masting-weather relationships, each of the 8 long NC was
274 fitted against the four most important weather variables selected by logistic models and
275 correlation analysis (i.e., MAX_{JUN-1} , MAX_{JUL-1} , MAX_{JUN-2} and MAX_{JUL-2}), using year as an
276 interaction factor. If the year x MAX interaction is significant, that will suggest a temporal
277 change in masting sensitivity to maximum summer temperatures. Moreover, to test also for
278 non-linear trends in correlation values, we additionally ran a moving correlation analysis
279 (MCA) between MAX_{JUN-1} , MAX_{JUL-1} , MAX_{JUN-2} and MAX_{JUL-2} , and the same 8 NC. MCA
280 was conducted on detrended weather variables using Spearman's rank correlation and a
281 window size of 28 years, i.e., the largest window giving 4 independent intervals for the
282 period 1901-2014. Most series had some missing values, but a minimum of 15 values (i.e.,
283 >50% of years observed) was required for any window.

284

285 The R code used for analyses is provided in Supplementary Information Script S1.

286

287 **Results**

288

289 Graphical analysis of mapped NUTS-1 chronologies (Fig. S2) suggested a certain degree of
290 spatial structuring, except when most of the continent exhibited high seed production (e.g. in
291 1995). The existence of spatial aggregation in masting was confirmed by significantly
292 positive ($p < 0.01$) Mantel correlation coefficients ($M = 0.53$, 0.31 , and 0.42 for the isotropic,
293 latitude-only, and longitude-only tests, respectively) (Fig. 2, Fig. S3). Hierarchical clustering
294 of NC produced three relatively stable clusters broadly corresponding to southern (SO,
295 cluster stability = 56%), northern (NO, 68%), and eastern Europe (EA, 71%) (Fig. 3; Fig. S4).
296 Further dendrogram subdivisions suggested differences between Romania, Poland, and all

297 other NUTS-1 in EA, between Mediterranean (central Italy) and all other NUTS-1 in SO, and
 298 between Atlantic (France, United Kingdom) and central NUTS-1 in NO.

299

300 Correlation analysis revealed consistently positive correlations between NC and previous
 301 summers' temperature at the NUTS-1 level across the species distribution (and in all three
 302 clusters), especially when using seasonal summer weather or two-year differences (Fig. 4).
 303 Correlations were generally strongest for MAX and MEAN (Fig. S5), and to a lesser degree
 304 MIN (Fig. S6) (mean correlation across all NUTS-1: 0.38, 0.36, 0.39, -0.21, and 0.28, 0.24,
 305 0.28, -0.13, respectively against MAX, MIN, MEAN, and PRE in June-July of two years
 306 prior and one year prior). MAX_{AUG-1} was not a consistent signal across Europe. One third of
 307 NUTS-1 did not have significant correlations ($R \geq 0.35$ with a sample size of $n=61$) either
 308 with MAX_{JUN-1} , MAX_{JUL-1} or MAX_{AUG-1} , especially those in the Netherlands, Italy, and the
 309 Carpathian region (the latter were based on shorter records). Temperature in the summer two
 310 years prior to masting was negatively correlated with NC across the species distribution (Fig.
 311 4), and particularly in cluster NO. Consequently, DeltaT usually produced significant
 312 correlations against masting. Weaker (and rarely significant) correlations were found for the
 313 autumn and early winter two years prior to masting (negative MAX_{NOV-2} in Austria, Czech
 314 Republic, Poland and Germany, positive MAX_{DEC-2} in Mediterranean France) and for the late
 315 winter and spring of the year before masting (negative MAX_{FEB-1} in Belgium and United
 316 Kingdom, positive MAX_{MAR-1} in Austria, Poland, and Croatia, negative $MEAN_{APR-1}$ in Italy
 317 and France). No consistent pattern of correlations was found between NC and temperature in
 318 the year of masting, although some regional patterns during spring were found (e.g. positive
 319 correlations with MAX_{FEB} in Poland and United Kingdom, or with MAX_{MAY} in Poland).

320

321 Correlations between NC and PRE were weaker and much less consistent than with
 322 temperature (Fig. S7). Significantly positive correlations with PRE in two summers prior and
 323 negative in one summer prior emerged locally (e.g., in Germany, UK, France, and
 324 Switzerland), although a clear distinction between clusters was not evident. Correlations with
 325 $summer_2$ were on average stronger than with $summer_1$. SPI3 and SPEI3 were similar to
 326 MAX, with strong and significant correlations in $summer_2$ and, less strongly, $summer_1$ (Fig.
 327 S8; Fig. S9), albeit on a more restricted geographic extent (Germany, Denmark, United
 328 Kingdom, Belgium, Sweden). Spring water balance (PRE, SPEI3) was generally uncorrelated
 329 to masting in beech (except a positive correlation of PRE_{APR-1} in France and PRE_{APR0} in
 330 Croatia).

331

332 Overall, most NC conformed to a general pattern of negative correlations with temperature in
333 the summer two years prior to masting, and positive correlations with temperature in the
334 summer one year prior to masting (Table 1), with no substantial differences in the response of
335 masting to weather among geographical clusters. Precipitation and drought indices were less
336 strongly and consistently correlated with NC than temperature. Additionally, neither
337 temperature nor precipitation in the year of masting was consistently correlated with NC,
338 except for a positive influence of early spring temperature in northern Europe. The
339 geographical pattern of weather variables in the period 1950-2014 was very similar to that of
340 masting, with rates of agreement between masting and weather clusters ranging from 62%
341 (TMN) to 87% (PRE) (Table 3).

342

343 Latitude was not a significant driver of the correlation between masting and MAX (Fig. S10).
344 Ordinal logistic models fitted to the eight longest NC had medium to high explanatory power
345 (range of Nagelkerke R^2 : 0.33–0.72, mean = 0.57). Stepwise AIC selection isolated between
346 three and six independent variables (Fig. 5), which corroborated the results of weather
347 correlations computed for NUTS-1. The most commonly selected terms were MAX_{JUL-1}
348 (selected in all models) and MAX_{JUL-2} (all but one). MAX_{JUN-1} or MAX_{JUN-2} were
349 additionally selected in five and six models, respectively. NC_{-1} , with a negative coefficient,
350 was selected in five models. Precipitation terms were selected less frequently than
351 temperature, and only half of the models included any precipitation term. Standardized
352 coefficients for precipitation were generally lower than those for temperature, indicating a
353 smaller effect on masting. Model validation produced a mean Nagelkerke R^2 of 0.46 after
354 bootstrapped leave-one-out cross-validation (range = 0.53-0.65), and 0.40 after extrapolation
355 to 1901-1950 (0.21-0.55), indicating that models were partially able to reproduce masting
356 variation outside of the training dataset (Table 2). Clusters SO and EA were represented by
357 only one model each, with the latter showing a lower explanatory power and weaker summer.
358 NC_{-1} effects.

359

360 Temporal trends in masting were significant in NL1, DE1 (negative trend), DE2, and DE9
361 (positive); however, the interaction between time and summer MAX was significant only in 3
362 out of 32 cases (Table 2). MCA applied to the longest eight chronologies revealed generally
363 stable correlations between temperature and masting, particularly for MAX_{JUL-1} and MAX_{JUL-2}
364 (Fig. 6, Fig. S11), except for DK0 and DE9 (increasingly stronger correlation through time).

365 Most NC showed decade-long periods when correlations with MAX were non-significant,
 366 although the timing of these periods was not synchronized across Europe. Some NC showed
 367 evidence of “switching” between July and June temperature (i.e., periods of reduced
 368 correlations with MAX_{JUL} corresponded to increased correlations with MAX_{JUN}, e.g. DK0),
 369 but in others the temporal variations in the strength of all four correlations were homogenous
 370 (e.g., UKJ). Some NUTS-1 showed “parallel” correlation trends with year-1 and year-2, i.e.,
 371 a decreasing importance of positive MAX₋₁ corresponding to an increasing importance of
 372 negative MAX₋₂, especially in DE1 and DE2; however, the dataset is too sparse to strongly
 373 generalize such evidence.

374

375 Discussion

376

377 Using a distribution-wide dataset with around 8,000 individual observations, we have shown
 378 that a strong spatial structure exists in masting patterns of *F. sylvatica* across its distribution
 379 range. Synchrony was higher between neighboring populations (Fig. S1), particularly in
 380 northern Europe, and strongly declined with distance (Fig. 2), consistent with previous
 381 findings for other temperate species (Koenig & Knops, 2000; Garrison *et al.*, 2008; Gallego
 382 Zamorano *et al.*, 2016). While synchrony generally declined with distance (e.g., “typical”
 383 years with partial masting at the continental scale such as 2002 or 2009; Fig. S2), continental-
 384 scale mast years occurred on several occasions, e.g. twice in the last 40 years (1976 and
 385 1995, with less comprehensive but still widespread events in 1992, 2006 and 2011; Fig. S2).
 386 This is consistent with what has been previously reported for beech at both continental
 387 (Nussbaumer *et al.*, 2016) and regional scale (e.g., Hilton & Packham, 2003), and it is based
 388 on an unprecedented sample size. These distribution-wide mast events may have important
 389 implications for large-scale, long-distance ecological processes, such as forest regeneration
 390 after large disturbances (Peters *et al.*, 2005; Ascoli *et al.*, 2015; Funk *et al.*, 2015), pollen-
 391 and seed-related gene flow (Kremer *et al.* 2012), bird migration (Koenig & Knops, 2001),
 392 predator-prey population dynamics (Blackwell *et al.*, 2001), pest and disease diffusion
 393 (Liebhold *et al.*, 2000), biological invasions (Harper, 2005), forest species range shift
 394 (Takenaka, 2005), and climate resilience (Mustin, 2013). Even if masting synchrony had little
 395 impact over and above the local effects through predator satiation and/or enhanced
 396 pollination, and is simply a result of the weather cues used locally, when the latter co-vary
 397 across large areas the ecosystem consequences may be far-reaching.

398

399 Furthermore, the temporal variability of masting in beech showed a distinct spatial structure
400 during the last 65 years, with three clusters located in northern, southern and eastern Europe
401 (Fig. 3). These clusters correspond closely to weather patterns (Fig. S13), and broadly to
402 regions of Europe influenced by different climate regimes: the northern cluster corresponds
403 to the region of western Europe associated with an oceanic climate strongly influenced by the
404 Atlantic (Cfb according to Peel *et al.*, 2007), the southern cluster overlaps with the
405 Mediterranean region (Csa), while the eastern cluster is the most continental one and is less
406 influenced by Atlantic weather (roughly corresponding to Dfb). Indeed, the longitude-based
407 Mantel-test showed a lower correlation coefficient than the latitude-based test, which may be
408 a consequence of weather events characterized by a longitude-based spatial pattern prompting
409 synchronized masting (Fernández-Martínez *et al.*, 2016a). Similar spatial structuring in beech
410 has been found by local masting studies, which explained it by an increasing influence of
411 spring frost in more continental areas (Gross, 1934), but also by tree-ring studies, which
412 linked contrasting growth patterns to the different influence of climate teleconnections, e.g.
413 between the eastern and western Mediterranean basin (Chen *et al.*, 2015; Seim *et al.*, 2015).

414

415 Numerous studies have demonstrated that mast years in many tree species are associated with
416 specific weather conditions (“weather cues”) prior to mast events (Koenig & Knops, 2014;
417 Roland *et al.*, 2014), and particularly with summer temperatures one and two years prior to
418 masting (Schauber *et al.*, 2002; Kelly *et al.*, 2013). We found similar results in this study,
419 showing that a small number of weather variables act as strong cues for masting in almost all
420 European beech populations, despite large climatic, genetic, and environmental differences.
421 Indeed, individual NC where this typical set of cues was not detected were often based on a
422 limited number of observations. We found no substantial differences in these weather cues of
423 masting among regions or clusters using either correlation analysis (Fig. 4, Fig. S10) or
424 regression models (Fig. 5), nor any significant effect of latitude (Fig. S10). This demonstrated
425 that, across the distribution, the cues for masting are highly spatially consistent, with positive
426 correlations for MAX_{JUL-1} (and to a lesser degree MAX_{JUN-1}), and negative for MAX_{JUL-2} and
427 MAX_{JUN-2} , with some local specificities. Combining June and July clearly improved the
428 consistency of strong (and significant) correlations, as did using DeltaT as a synthetic index
429 of temperature differences from year to year (Kelly *et al.* 2013). In some cases, the seasonal
430 analysis accounted for regional differences in the strongest individual month; AT1-3 were
431 good examples, as they responded more strongly to June temperatures than July (in contrast
432 to most other chronologies). In particular, DeltaT led to improved correlations in cases where

433 correlations with $MAX_{summer-1}$ and $MAX_{summer-2}$ had the expected signal, but were both
 434 relatively weak (e.g. DE2, PL2, PL4), or where one individual correlation was much stronger
 435 than the other (e.g. DE1, DE2, DEE, SE2, FR6). In the regression models for the NUTS-1
 436 with the most data, a large proportion of the variance was explained by summer temperature
 437 in years -1 and -2, suggesting that other signals are not very important.

438

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

446

447 While the well-known relationship between general summer weather and masting in beech
 448 was well supported by our results, we were also able to disentangle the relative importance of
 449 temperature and precipitation as the dominant cue of masting. Wachter (1964) and Piovesan
 450 and Adams (2001) suggested that summer precipitation or drought, along with or rather than
 451 temperature, were the main cue of masting in beech, while Drobyshev *et al.* (2010) found no
 452 relationship between masting and summer precipitation or drought (but did find a strong
 453 temperature signal). We have shown that summer precipitation in the two years prior to
 454 masting was an important predictor of mast events in some regions (Fig. 4, Fig. 5), and that
 455 summer drought was correlated with NC in some regions (Fig. S9), but that both precipitation
 456 and drought were clearly of secondary importance to temperature as a cue of masting. An
 457 additional analysis of the relationship between summer MAX and summer SPEI across
 458 Europe showed correlations ranging from -0.3 to -0.5 (Fig. S12), suggesting that drought
 459 could be more effective in predicting masting in certain locals than in others, hence the
 460 contrasting evidence for previous year's drought effects in the literature. The effect of spring
 461 precipitation appeared generally negligible, contrary to findings in more Mediterranean
 462 species (Fernández-Martínez *et al.*, 2015). Additionally, the importance of precipitation did
 463 not appear to vary systematically with latitude, e.g., in northern vs. southern regions where
 464 summer drought stress may be limiting (average correlation between latitude and Spearman's
 465 coefficient for MAX_{JUN-1} , MAX_{JUL-1} , and $MAX_{AUG-1} = -0.13$; MAX_{JUN-2} , MAX_{JUL-2} , and
 466 $MAX_{AUG-2} = 0.05$; PRE_{JUN-1} , PRE_{JUL-1} , and $PRE_{AUG-1} = 0.07$; PRE_{JUN-2} , PRE_{JUL-2} , and

467 $PRE_{AUG-2} = 0.09$). Instead, summer temperatures in the previous two years, particularly in
468 July, were always the main cue of masting, with mast years associated with a cool summer
469 two years prior to masting, and warm temperatures in the summer prior to masting. This is
470 highly consistent with previous findings on the sensitivity to summer temperatures in both
471 *Fagus* and *Nothofagus* (two years prior: Gruber, 2003; Richardson *et al.*, 2005; Smaill *et al.*,
472 2011, Kelly *et al.*, 2013; one year prior: Hase, 1964; Wachter, 1964; Schauber *et al.*, 2002;
473 Suzuki *et al.*, 2005; Övergaard *et al.*, 2007; Masaki *et al.*, 2008). Recent analyses of the
474 climate sensitivity of beech diameter increment have also showed that cool, moist summers
475 have a positive effect on the growth of the same year, favoring a resource accumulation
476 hypothesis (Dorado Liñan *et al.*, 2017), while high summer temperatures have a negative
477 effect on growth of the following year throughout the whole geographic distribution,
478 including in northern and central regions (Hacket-Pain *et al.*, 2016), which could be
479 interpreted as a growth vs. reproduction tradeoff if masting was triggered in those years
480 (Monks and Kelly, 2006; Hacket-Pain *et al.*, 2015).

481

482 In addition to weather cues, we also found that masting was strongly affected by negative
483 temporal autocorrelation, i.e., masting category in the previous year (NC_{-1}). Ordinal logistic
484 regressions models were consistently able to predict mast years with accuracy (mean $R^2 =$
485 0.57) using summer temperature (and in some case precipitation) in the two previous years,
486 plus information on previous year's masting. Negative temporal autocorrelation with a lag of
487 one or two years is one of the defining characteristics of masting time-series (Davis, 1957;
488 Sork *et al.*, 1993; Selås *et al.*, 2002; Koenig *et al.*, 2003), and is the mathematical expression
489 of the rarity of consecutive mast years (category 4 or 5 in our dataset; consecutive years of
490 low masting category were instead common). The existence of negative autocorrelation in
491 masting time series has been traditionally interpreted as evidence for resource depletion, i.e.,
492 trees deplete most resources in the mast year, which limits reproduction in the following year
493 and makes consecutive heavy seed crops very rare (Davis, 1957; Sork *et al.*, 1993; Kelly &
494 Sork, 2002). However, recent studies have showed that negative temporal autocorrelation
495 would also emerge if masting were controlled by ΔT only (Kelly *et al.*, 2013; Kon &
496 Saito, 2015; but see also Koenig *et al.*, 2015 for criticism of such model).

497

498 The strong correlations between masting and weather found by this study do not provide any
499 conclusive evidence to the debate on whether temperature is a “cue” for trees to trigger high
500 seed crops or whether it acts instead through intermediate steps indicative of a direct

501 mechanistic connection to seed production (Pearse *et al.*, 2014). Koenig & Knops (2000)
502 found that spatial autocorrelation in seed production of northern-hemisphere tree species
503 occurred at the same spatial scale as autocorrelation in rainfall and temperature, consistent
504 with the underlying effect of climatic factors on masting. However, they also found that seed
505 production had much higher variability than the weather factors, implying the existence of
506 non-linearities in weather effects, or of drivers for masting which remain unaccounted for.

507

508 While strong climate differences exist across the distribution of beech, the majority of
509 populations analyzed herein responded similarly to weather (e.g., negative response to
510 temperature and positive to precipitation two years before masting; Table 1). The negative
511 correlation with MAX_{JUL-2} could be related to resource accumulation in cooler years
512 (“priming” the trees to respond to increased temperature one year later, *sensu* Richardson *et al.*,
513 2005), an interpretation that is consistent with a model of masting that includes an
514 element of carbon and/or nitrogen limitation (Sala *et al.*, 2012; Muller-Haubold *et al.*, 2015;
515 Monks *et al.*, 2016; Abe *et al.*, 2016; Pearse *et al.*, 2016). Indeed, a higher soil moisture due
516 to more precipitation and lower summer temperatures has been shown to increase litter mass
517 loss and N mineralization and uptake (Gessler *et al.*, 2005; Smaill *et al.*, 2011), which favors
518 masting in beech (Han *et al.*, 2014; Miyazaki *et al.*, 2014).

519

520 High temperatures in the summer prior to masting (MAX_{JUL-1}) have been linked to flower
521 primordia differentiation (Wachter, 1964; Gruber, 2003; see also: Merkle *et al.*, 1980 for
522 oaks, Allen *et al.*, 2014; Miyazaki *et al.*, 2014), in particular via an increase in endogenous
523 gibberellins (Turnbull, 2011; Pearse *et al.*, 2016). Following this reasoning, we might expect
524 the phenology of primordia differentiation to vary with latitude, creating a geographical
525 gradient in the timing of the previous summer cue similar to the pattern we found in some
526 southern European NUTS-1 (Fig. 4). Additionally, we also found correlations with weather
527 during the periods associated with other known processes that influence flowering
528 phenology, pollen production (Kasprzyk *et al.*, 2014; Pearse *et al.*, 2015), and seed
529 maturation in the year of masting, such as late winter frost (Matthews, 1955; Wachter, 1964),
530 at least in northern Europe. The resource priming in year₂ can therefore interact with the
531 MAX cue in summer₁ via a resource pulse that boosts an already favorable flower initiation.

532

533 Finally, the analysis of some of the longest series available showed that the sensitivity of
534 beech masting to the most important weather cues (MAX_{JUL-1} and MAX_{JUL-2}) was

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

559

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564

565 **Author contributions**

566 GV and AHP analyzed the data and wrote the manuscript; DA designed the research,
567 provided and analyzed masting data, and wrote parts of the manuscript; MT provided and

568 interpreted weather data; ID, MC, JM, and RM contributed to research design and data
569 interpretation.
570

For Peer Review

571 **References**

572

573 **Abe T, Tachiki Y, Kon H, Nagasaka A, Onodera K, Minamino K, Han Q, Satake A.**574 **2016.** Parameterisation and validation of a resource budget model for masting using575 spatiotemporal flowering data of individual trees. *Ecology Letters* **19(9)**:1129-1139.576 **Agresti A. 2002.** *Categorical data*. New York: John Wiley & Sons.577 **Allen RB, Hurst JM, Portier J, Richardson SJ. 2014.** Elevation-dependent responses of578 tree mast seeding to climate change over 45 years. *Ecology and Evolution* **4(18)**:3525-3537.579 **Allen RG, Pereira LS, Raes D, Smith M. 1998.** *Crop evapotranspiration. Guidelines for*580 *computing crop water requirements*. FAO Irrigation and drainage paper 56. Rome: FAO.581 **Ascoli D, Maringer J, Hackett-Pain A, Conedera M, Drobyshev I, Motta R, Cirolli M,**582 **Kantorowicz W, Zang C, Schueler S, et al., 2017.** Two centuries of masting data for583 European beech and Norway spruce across the European subcontinent. *Ecology*, in press. doi:

584 10.1002/ecy.1785.

585 **Ascoli D, Vacchiano G, Maringer J, Bovio G, Conedera M. 2015.** The synchronicity of586 masting and intermediate severity fire effects favors beech recruitment. *Forest Ecology and*587 *Management* **353**:126-135.588 **Beguéría S, Vicente-Serrano SM. 2013.** **SPEI: Calculation of the Standardised**589 **Precipitation-Evapotranspiration Index. R package version 1.6.** [WWW document] URL590 <https://CRAN.R-project.org/package=SPEI>. [accessed 1 September 2016].591 **Bisi F, von Hardenberg J, Bertolino S, Wauters LA, Imperio S, Preatoni DG,**592 **Provenzale A, Mazzamuto MV, Martinoli A. 2016.** Current and future conifer seed593 production in the Alps: testing weather factors as cues behind masting. *European Journal of*594 *Forest Research* **135**:743-754.595 **Bjornstad ON. 2015.** **nfc: Spatial Nonparametric Covariance Functions. R package version**596 **1.1-6.** [WWW document] URL <https://CRAN.R-project.org/package=nfc>. [accessed 1

597 September 2016].

598 **Blackwell GL, Potter MA, Minot EO. 2001.** Rodent and predator population dynamics in599 an eruptive system. *Ecological Modeling* **142**:227-245.600 **Büsgen M, Münch E, Thomson T. 1929.** *The structure and life of forest trees*. London:

601 Chapman & Hall.

- 602 **Casalegno S, Amatulli G, Bastrup-Birk A, Durrant TH, Pekkarinen A. 2011.** Modelling
 603 and mapping the suitability of European forest formations at 1-km resolution. *European*
 604 *Journal of Forest Research* **130(6)**:971-981.
- 605 **Charrad M, Ghazzali N, Boiteau V, Niknafs A. 2014.** NbClust: an R Package for
 606 determining the relevant number of clusters in a data set. *Journal of Statistical Software*.
 607 **61(6)**:1-36.
- 608 **Chen K, Dorado-Liñán I, Akhmetzyanov L, Gea-Izquierdo G, Zlatanov T, Menzel A.**
 609 **2015.** Influence of climate drivers and the North Atlantic Oscillation on beech growth at
 610 marginal sites across the Mediterranean. *Climate Research* **66(3)**:229-242.
- 611 **Clement J, Maes P, de Strihou CV, van der Groen G, Barrios JM, Verstraeten WW,**
 612 **van Ranst M. 2010.** Beechnuts and outbreaks of *Nephropathia epidemica* (NE): of mast,
 613 mice and men. *Nephrology Dialysis Transplantation* **25(6)**:1740-1746.
- 614 **Davis LD. 1957.** Flowering and alternate bearing. *Proceedings of the American Society of*
 615 *Horticultural Science* **70**:545-556.
- 616 **Dorado Liñan I, Zorita E, Martínez-Sancho E, Gea-Izquierdo G, Di Filippo A,**
 617 **Gutiérrez E, Levanic T, Piovesan G, Vacchiano G, Zang C, Zlatanov T, Menzel M.**
 618 **2017.** Large-scale atmospheric circulation enhances the Mediterranean East-West tree growth
 619 contrast at rear-edge deciduous forests. *Agricultural and Forest Meteorology* **239**:86-95.
- 620 **Drobyshev I, Niklasson M, Mazerolle MJ, Bergeron Y. 2014.** Reconstruction of a 253-
 621 year long mast record of European beech reveals its association with large scale temperature
 622 variability and no long-term trend in mast frequencies. *Agricultural and Forest Meteorology*
 623 **192**:9-17.
- 624 **Drobyshev I, Overgaard R, Saygin I, Niklasson M, Hickler T, Karlsson M, Sykes MT.**
 625 **2010.** Masting behaviour and dendrochronology of European beech (*Fagus sylvatica* L.) in
 626 southern Sweden. *Forest Ecology and Management* **259**: 2160-2171.
- 627 **Dunn JC. 1974.** Well-separated clusters and optimal fuzzy partitions. *Journal of Cybernetics*
 628 **4(1)**:95-104.
- 629 **Dutilleul P, Clifford P, Richardson S, Hemon D. 1993.** Modifying the t test for assessing
 630 the correlation between two spatial processes. *Biometrics* **49**:305-314.

- 631 **Fernández-Martínez M, Garbulsky M, Peñuelas J, Peguero G, Espelta JM. 2015.**
632 Temporal trends in the enhanced vegetation index and spring weather predict seed production
633 in Mediterranean oaks. *Plant Ecology* **216(8)**:1061-1072.
- 634 **Fernández-Martínez M, Vicca S, Janssens IA, Espelta JM, Peñuelas J. 2016a.** The North
635 Atlantic Oscillation synchronises fruit production in western European forests. *Ecography*.
636 doi: 10.1111/ecog.02296.
- 637 **Fernández-Martínez M, Vicca S, Janssens IA, Espelta JM, Peñuelas J. 2016b.** The role
638 of nutrients, productivity and climate in determining tree fruit production in European forests.
639 *New Phytologist*. doi: 10.1111/nph.14193.
- 640 **Funk KA, Koenig WD, Knops JM. 2015.** Fire effects on acorn production are consistent
641 with the stored resource hypothesis for masting behavior. *Canadian Journal of Forest*
642 *Research* **46(1)**:20-24.
- 643 **Gallego Zamorano J, Hokkanen T, Lehtikoinen A. 2016.** Climate driven synchrony in seed
644 production of masting deciduous and conifer tree species. *Journal of Plant Ecology*. doi:
645 10.1093/jpe/rtw117.
- 646 **Garrison BA, Koenig WD, Knops JM. 2008.** Spatial synchrony and temporal patterns in
647 acorn production of California black oaks. In: Merenlender A, McCreary D, Purcell KL, eds.
648 *Proceedings of the sixth symposium on oak woodlands: today's challenges, tomorrow's*
649 *opportunities*. Albany, USA: USDA Forest Service, Pacific SW Forest and Range
650 Experiment Station, General Technical Report PSW-GTR-217, 343-356.
- 651 **Gessler A, Jung K, Gasche R, Papen H, Heidenfelder A, Börner E, Metzler B, Augustin**
652 **S, Hildebrand E, Rennenberg H. 2005.** Climate and forest management influence nitrogen
653 balance of European beech forests: microbial N transformations and inorganic N net uptake
654 capacity of mycorrhizal roots. *European Journal of Forest Research* **124(2)**:95-111.
- 655 **Gringorten II. 1963.** A plotting rule for extreme probability paper. *Journal of Geophysical*
656 *Research* **68(3)**:813-814.
- 657 **Gross H. 1934.** Die Rotbuche in Ostpreußen. *Zeitschrift für Forst- Und Jagdwesen* **66**:662-
658 651.
- 659 **Gruber R. 2003.** Control and forecasting of the fructification of European beech (*Fagus*
660 *sylvatica* L.) for the stand Zierenberg 38A and the level I stand in Hessen by climate factors.
661 *Allgemeine Forst Und Jagdzeitung* **174(4)**:67-79.

- 662 **Hacket-Pain AJ, Cavin L, Friend AD, Jump AS. 2016.** Consistent limitation of growth by
 663 high temperature and low precipitation from range core to southern edge of European beech
 664 indicates widespread vulnerability to changing climate. *European Journal of Forest Research*
 665 **135(5):**897-909.
- 666 **Hacket-Pain AJ, Friend AD, Lageard JGA, Thomas PA. 2015.** The influence of masting
 667 phenomenon on growth-climate relationships in trees: explaining the influence of previous
 668 summers' climate on ring width. *Tree Physiology* **35:**319–330.
- 669 Han Q, Kabeya D, Iio A, Inagaki Y, Kakubari Y. **2014.** Nitrogen storage dynamics are
 670 affected by masting events in *Fagus crenata*. *Oecologia* **174(3):**679-687.
- 671 **Hao Z, AghaKouchak A, Nakhjiri N, Farahmand A. 2014.** Global integrated drought
 672 monitoring and prediction system. *Scientific Data* **1:**1–10.
- 673 **Harper GA. 2005.** Heavy rimu (*Dacrydium cupressinum*) mast seeding and rat (*Rattus* spp.)
 674 population eruptions on Stewart Island/Rakiura. *New Zealand Journal of Zoology* **32:**155-
 675 162.
- 676 **Harrell FE. 2015.** *rms: Regression Modeling Strategies. R package version 4.3-1.* [WWW
 677 document] URL <https://CRAN.R-project.org/package=rms>. [accessed 1 September 2016].
- 678 **Harris IP, Jones PD, Osborn TJ, Lister DH. 2014.** Updated high-resolution grids of
 679 monthly climatic observations—the CRU TS3.10 dataset. *International Journal of*
 680 *Climatology* **34(3):**623-642.
- 681 **Hase W. 1964.** Die Buchenmast in Schleswig-Holstein und ihre Abhängigkeit von der
 682 Witterung. *Mitteilungen des Deutschen Wetterdienstes* **31:**1–52.
- 683 **Hennig C. 2015.** *fpc: Flexible Procedures for Clustering. R package version 2.1-10.* [WWW
 684 document] URL <https://CRAN.R-project.org/package=fpc>. 2015. [accessed 1 September
 685 2016].
- 686 **Hilton GM, Packham JR. 2003.** Variation in the masting of common beech (*Fagus*
 687 *sylvatica* L.) in northern Europe over two centuries (1800–2001). *Forestry* **76(3):**319-328.
- 688 **Hotelling H. 1953.** New light on the correlation coefficient and its transforms. *Journal of the*
 689 *Royal Statistical Society Series B (Methodological)* **15(2):**193-232.

- 690 **Kasprzyk I, Ortyl B, Dulaska-Jeż A. 2014.** Relationships among weather parameters,
691 airborne pollen and seed crops of *Fagus* and *Quercus* in Poland. *Agricultural and Forest*
692 *Meteorology* **197**:111-122.
- 693 **Kelly D, Geldenhuis A, James A, Penelope Holland E, Plank MJ, Brockie RE, Cowan**
694 **PE, Harper GA, Lee WG, Maitland MJ, Mark AF. 2013.** Of mast and mean: differential-
695 temperature cue makes mast seeding insensitive to climate change. *Ecology Letters* **16(1)**:90-
696 98.
- 697 **Kelly D, Sork VL. 2002.** Mast seeding in perennial plants: why, how, where?. *Annual*
698 *Review of Ecology and Systematics* **1**:427-447.
- 699 **Kelly D. 1994.** The evolutionary ecology of mast seeding. *Trends in Ecology & Evolution*
700 **9(12)**:465-470.
- 701 **Koenig WD, Alejano R, Carbonero MD, Fernández-Rebollo P, Knops JM, Marañón T,**
702 **Padilla-Díaz CM, Pearse IS, Pérez-Ramos IM, Vázquez-Piqué J, Pesendorfer MB. 2016.**
703 Is the relationship between mast-seeding and weather in oaks related to their life-history or
704 phylogeny?. *Ecology* **97(10)**:2603-2615.
- 705 **Koenig WD, Kelly D, Sork VL, Duncan RP, Elkinton JS, Peltonen MS, Westfall RD.**
706 **2003.** Dissecting components of population-level variation in seed production and the
707 evolution of masting behavior. *Oikos* **102(3)**:581-591.
- 708 **Koenig WD, Knops JM. 1998.** Scale of mast-seeding and tree-ring growth. *Nature* **396**:225-
709 226.
- 710 **Koenig WD, Knops JM. 2000.** Patterns of annual seed production by northern hemisphere
711 trees: a global perspective. *American Naturalist* **155**:59–69.
- 712 **Koenig WD, Knops JM. 2001.** Seed-crop size and eruptions of North American boreal seed-
713 eating birds. *Journal of Animal Ecology* **70(4)**:609-620.
- 714 **Koenig WD, Knops JM. 2013.** Large-scale spatial synchrony and cross-synchrony in acorn
715 production by two California oaks. *Ecology* **94**:83-93.
- 716 **Koenig WD, Knops JM. 2014.** Environmental correlates of acorn production by four species
717 of Minnesota oaks. *Population Ecology* **56**:63-71.
- 718 **Koenig WD, Knops JM, Carmen WJ, Pearse IS. 2015.** What drives masting? The
719 phenological synchrony hypothesis. *Ecology* **96(1)**:184-192.

- 720 **Kon H, Saito H. 2015.** Test of the temperature difference model predicting masting
721 behavior. *Canadian Journal of Forest Research* **45**:1835-1844.
- 722 **Kremer A, Ronce O, Robledo-Arnuncio JJ, Guillaume F, Bohrer G, Nathan R, Bridle**
723 **JR, Gomulkiewicz R, Klein EK, Ritland K, et al. 2012.** Long-distance gene flow and
724 adaptation of forest trees to rapid climate change. *Ecology* **15(4)**:378-392.
- 725 **Lichti NI, Steele MA, Zhang H, Swihart RK. 2014.** Mast species composition alters seed
726 fate in North American rodent-dispersed hardwoods. *Ecology* **95(7)**:1746-1758.
- 727 **Liebhold A, Elkinton J, Williams D, Muzika RM. 2000.** What causes outbreaks of the
728 gypsy moth in North America?. *Population Ecology* **42(3)**:257-266.
- 729 **Mantel N. 1967.** The detection of disease clustering and a generalized regression approach.
730 *Cancer Research* **27(2 Part 1)**:209-220.
- 731 **Masaki T, Oka T, Osumi K, Suzuki W. 2008.** Geographical variation in climatic cues for
732 mast seeding of *Fagus crenata*. *Population Ecology* **50(4)**:357-366.
- 733 **Matthews JD. 1955.** The influence of weather on the frequency of beech mast years in
734 England. *Forestry* **28(2)**:107-116.
- 735 **McKee TB, Doesken NJ, Kleist J. 1993.** The relationship of drought frequency and duration
736 to time scales. In: *Proceedings of the 8th Conference on Applied Climatology*. Boston, MA,
737 USA: American Meteorological Society, 179-183.
- 738 **McKone MJ, Kelly D, Lee WG. 1998.** Effect of climate change on mast-seeding species:
739 frequency of mass flowering and escape from specialist insect seed predators. *Global Change*
740 *Biology* **4(6)**:591-596.
- 741 **Menzel A, Sparks T, Estrella N, Koch E, Aasa A, Ahas R, Alm-Kübler K, Bissolli P,**
742 **Braslavská O, Briede A, et al. 2006.** European phenological response to climate change
743 matches the warming pattern. *Global Change Biology* **12**:1969-1976.
- 744 **Merkle SA, Feret PP, Croxdale JG, Sharik TL. 1980.** Development of floral primordia in
745 white oak. *Forest Science* **26**:238-250.
- 746 **Mescher MC, Pearse IS. 2016.** Communicative interactions involving plants: information,
747 evolution, and ecology. *Current Opinion in Plant Biology* **32**:69-76.
- 748 **Meyer SE, Pendleton BK. 2015.** Seedling establishment in a masting desert shrub parallels
749 the pattern for forest trees. *Acta Oecologica* **65**:1-10.

- 750 **Miyazaki Y, Maruyama Y, Chiba Y, Kobayashi MJ, Joseph B, Shimizu KK, Mochida**
751 **K, Hiura T, Kon H, Satake A. 2014.** Nitrogen as a key regulator of flowering in *Fagus*
752 *crenata*: understanding the physiological mechanism of masting by gene expression analysis.
753 *Ecology Letters* **17(10)**:1299-1309.
- 754 **Miyazaki Y. 2013. Dynamics of internal carbon resources during masting behavior in**
755 **trees. Ecological Research** **28**:143-150.
- 756 **Monks A, Kelly D. 2006.** Testing the resource matching hypothesis in the mast seeding tree
757 *Nothofagus truncata* (Fagaceae). *Austral Ecology* **31**:366-375.
- 758 **Monks A, Monks JM, Tanentzap AJ. 2016.** Resource limitation underlying multiple
759 masting models makes mast seeding sensitive to future climate change. *New Phytologist*
760 **210**:419-430.
- 761 **Müller-Haubold H, Hertel D, Leuschner C. 2015.** Climatic drivers of mast fruiting in
762 European beech and resulting C and N allocation shifts. *Ecosystems* **18(6)**:1083-1100.
- 763 **Müller-Haubold H, Hertel D, Seidel D, Knutzen F, Leuschner C. 2013.** Climate responses
764 of aboveground productivity and allocation in *Fagus sylvatica*: A transect study in mature
765 forests. *Ecosystems* **16**:1498-1516.
- 766 **Murtagh F, Legendre P. 2014.** Ward's hierarchical agglomerative clustering method: which
767 algorithms implement Ward's criterion?. *Journal of Classification* **31(3)**:274-295.
- 768 **Mustin K. 2013.** Red noise increases extinction risk during rapid climate change. *Diversity*
769 *and Distributions* **19(7)**:815–824.
- 770 **Norden N, Chave J, Belbenoit P, Caubère A, Châtelet P, Forget PM, Thébaud C. 2007.**
771 Mast fruiting is a frequent strategy in woody species of Eastern South America. *Plos One*
772 **2(10)**:e1079.
- 773 **Nussbaumer A, Waldne P, Etzold S, Gessler A, Benham S, Thomsen IM, Jorgensen BB,**
774 **Timmermann V, Verstraeten A, Sioen G, et al., 2016.** Patterns of mast fruiting of common
775 beech, sessile and common oak, Norway spruce and Scots pine in Central and Northern
776 Europe. *Forest Ecology and Management* **363**:237-251.
- 777 **Ostfeld RS, Keesing F. 2000.** Pulsed resources and community dynamics of consumers in
778 terrestrial ecosystems. *Trends in Ecology & Evolution* **15(6)**:232-237.

- 779 **Övergaard R, Gemmel P, Karlsson M. 2007.** Effects of weather conditions on mast year
780 frequency in beech (*Fagus sylvatica* L.) in Sweden. *Forestry* **80(5)**:555-565.
- 781 **Pearse IS, Koenig WD, Funk KA, Pesendorfer MB. 2015.** Pollen limitation and flower
782 abortion in a wind-pollinated, masting tree. *Ecology* **96(2)**:587-593.
- 783 **Pearse IS, Koenig WD, Kelly D. 2016.** Mechanisms of mast seeding: resources, weather,
784 cues, and selection. *New Phytologist* **212(3)**:546-562.
- 785 **Pearse IS, Koenig WD, Knops JM. 2014.** Cues versus proximate drivers: testing the
786 mechanism behind masting behavior. *Oikos* **123(2)**:179-184.
- 787 **Peel MC, Finlayson BL, McMahon TA. 2007.** Updated world map of the Köppen-Geiger
788 climate classification. *Hydrology and Earth System Sciences* **11**:1633-1644.
- 789 **Pérez-Ramos IM, Padilla-Díaz CM, Koenig WD, Maranon T. 2015.** Environmental
790 drivers of mast-seeding in Mediterranean oak species: does leaf habit matter?. *Journal of*
791 *Ecology* **103(3)**:691-700.
- 792 **Peters VS, Macdonald SE, Dale MR. 2005.** The interaction between masting and fire is key
793 to white spruce regeneration. *Ecology* **86(7)**:1744-1750.
- 794 **Piovesan G, Adams JM. 2001.** Masting behaviour in beech: linking reproduction and
795 climatic variation. *Canadian Journal of Botany* **79(9)**:1039-1047.
- 796 **R Core Team. 2016.** *R: A language and environment for statistical computing*. Vienna,
797 Austria: R Foundation for Statistical Computing. [WWW document] URL [https://www.R-](https://www.R-project.org)
798 [project.org](https://www.R-project.org) [accessed 1 November 2016].
- 799 **Richardson SJ., Allen RB, Whitehead D, Carswell FE, Ruscoe WA, Platt KH. 2005.**
800 Climate and net carbon availability determine temporal patterns of seed production by
801 *Nothofagus*. *Ecology* **86(4)**:972-981.
- 802 **Roland CA, Schmidt JH, Johnstone JF. 2014.** Climate sensitivity of reproduction in a
803 mast-seeding boreal conifer across its distributional range from lowland to treeline forests.
804 *Oecologia* **174(3)**:665-677.
- 805 **Sala A, Hopping K, McIntire EJ, Delzon S, Crone EE. 2012.** Masting in whitebark pine
806 (*Pinus albicaulis*) depletes stored nutrients. *New Phytologist* **196(1)**:189-199.
- 807 **Satake A, Iwasa YO. 2000.** Pollen coupling of forest trees: forming synchronized and
808 periodic reproduction out of chaos. *Journal of Theoretical Biology* **203(2)**:63-84.

- 809 **Schauber EM, Kelly D, Turchin P, Simon C, Lee WG, Allen RB, Payton IJ, Wilson PR,**
810 **Cowan PE, Brockie RE. 2002.** Masting by eighteen New Zealand plant species: The role of
811 temperature as a synchronizing cue. *Ecology* **83**:1214-1225.
- 812 **Seim A, Treydte K, Trouet V, Frank D, Fonti P, Tegel W, Panayotov M, Fernández-**
813 **Donado L, Krusic P, Büntgen U. 2015.** Climate sensitivity of Mediterranean pine growth
814 reveals distinct east–west dipole. *International Journal of Climatology* **35(9)**:2503-2513.
- 815 **Selås V, Piovesan G, Adams JM, Bernabei M. 2002.** Climatic factors controlling
816 reproduction and growth of Norway spruce in southern Norway. *Canadian Journal of Forest*
817 *Research* **32(2)**:217-225.
- 818 **Smaill SJ, Clinton PW, Allen RB, Davis MR. 2011.** Climate cues and resources interact to
819 determine seed production by a masting species. *Journal of Ecology* **99(3)**:870-877.
- 820 **Sork VL, Bramble J, Sexton O. 1993.** Ecology of mast-fruiting in three species of North
821 American deciduous oaks. *Ecology* **74(2)**:528-541.
- 822 **Suzuki W, Osumi K, Masaki T. 2005.** Mast seeding and its spatial scale in *Fagus crenata* in
823 northern Japan. *Forest Ecology and Management* **205(1)**:105-116.
- 824 **Takenaka A. 2005.** Local coexistence of tree species and the dynamics of global distribution
825 pattern along an environmental gradient: a simulation study. *Ecological Research* **20(3)**:297-
826 304.
- 827 **Tan FC, Swain SM. 2006.** Genetics of flower initiation and development in annual and
828 perennial plants. *Physiologia Plantarum* **128(1)**:8-17.
- 829 **Taylor BM, Parida B. 2016.** *cruts: Interface to Climatic Research Unit Time-Series Version*
830 *3.21 Data. R package version 0.3.* [WWW document] URL [https://CRAN.R-](https://CRAN.R-project.org/package=cruts)
831 [project.org/package=cruts](https://CRAN.R-project.org/package=cruts) [accessed 1 September 2016].
- 832 **Turnbull C. 2011.** Long-distance regulation of flowering time. *Journal of Experimental*
833 *Botany* **62(13)**:4399-4413.
- 834 **Vicente-Serrano SM, Beguería S, López-Moreno JI. 2010.** A multiscalar drought index
835 sensitive to global warming: the standardized precipitation evapotranspiration index. *Journal*
836 *of Climate* **23(7)**:1696-1718.
- 837 **Vicente-Serrano SM, Gouveia C, Camarero JJ, Beguería S, Trigo R, López-Moreno JI,**
838 **Azorín-Molina C, Pasho E, Lorenzo-Lacruz J, Revuelto J, Morán-Tejeda E. 2013.**

- 839 Response of vegetation to drought time-scales across global land biomes. *Proceedings of the*
840 *National Academy of Sciences* **110(1)**:52-57.
- 841 **Wachter H. 1964.** Über die Beziehung zwischen Witterung und Buchenmastjahren.
842 *Forstarchiv* **35**:69-78.
- 843 **Wagner S, Collet C, Madsen P, Nakashizuka T, Nyland RD, Sagheb-Talebi K. 2010.**
844 Beech regeneration research: from ecological to silvicultural aspects. *Forest Ecology and*
845 *Management* **259(11)**:2172-2182.
- 846 **Ward JH, Hook ME. 1963.** Application of an hierarchical grouping procedure to a problem
847 of grouping profiles. *Educational and Psychological Measurement* **23(1)**:69–82.
- 848 **Zackrisson O, Nilsson MC, Jäderlund A, Wardle DA. 1999.** Nutritional effects of seed fall
849 during mast years in boreal forest. *Oikos* **84**:17-26.
- 850

851 **Tables**

852

853 **Table 1** Common weather cues for beech masting across the species distribution range

854 relative to the year of seed production (summary of correlation analyses)

855

	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

856

857

858 **Table 2** Coefficients and statistics of ordinal logistic regression models for masting as a
 859 function of multiple weather variables in the eight longest NC (backwards stepwise selection
 860 by AIC; n.s. = non-significant at $p > 0.05$). Year and year x MAX were computed using
 861 bivariate models with one interaction term.
 862

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.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	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.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	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.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Year x MAX _{JUL-2}	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	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

863

864

865 **Table 3** Proportion of matches from the assignment of NUTS-1 into masting and weather
 866 clusters. Accuracy: rate of total matches (masting cluster = weather cluster) to total number
 867 of NUTS-1.
 868

Weather variable	Weather cluster	Masting-EA	Masting-NO	Masting-SO
TMP	EA	14	0	2
	NO	4	21	4
	SO	0	0	2
	Accuracy	78.7%		
TMN	EA	11	0	0
	NO	4	21	1
	SO	3	0	7
	Accuracy	61.9%		
TMX	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%		

869

870

871 **Figure legends**

872

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

876

877 **Fig. 2** (a) Mantel correlograms for NUTS-1 masting chronologies (1950-2014). Distance in
878 500-km wide bins. Black dots indicate significant ($p \leq 0.05$) correlations, sequentially
879 corrected for multiple testing using Holm's procedure. (b) Pairwise Spearman's correlations
880 between NUTS-1 masting chronologies (1950-2014) against raw distance in km; black line:
881 local polynomial regression smoother.

882

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

888

889 **Fig. 4** Spearman's correlation between monthly maximum temperature (1950-2014) and
890 NUTS-1 masting chronologies. NUTS-1 ordered and colored according to the cluster they
891 belong to (colors as in Fig. 3, black = excluded from clustering due to insufficient chronology
892 length). The three bottom lines show correlation against seasonal summer weather (June-
893 July) and the Delta variable (difference between weather variable in year.₂ and year.₁). The
894 sample size (number of years on record) is reported on the secondary x-axis. (.) significant at
895 $p \leq 0.05$, (*) significant at $p \leq 0.00139$ (Bonferroni-corrected). MEAN: the mean correlation
896 for the corresponding month across the study area.

897

898 **Fig. 5** Ordinal logistic models of masting (8 longest NC) as a function of weather predictors:
899 (a) model statistics for calibration (1950-2014) and validation (1901-1949). Rsq_{1950_2014}
900 is R^2 the calibration dataset, Rsq_boot is the bootstrapped R^2 from leave-one out cross-
901 validation (1000 re-samples), and Rsq_{1901_1949} is the R^2 of the predicted values for 1901-
902 1949 vs. observed (validation dataset). (b) standardized model coefficients. Only significant
903 predictors are filled in the table, with the color depending on the coefficient.

904

905 **Fig. 6** Moving Spearman's correlation (lines: 28-years timesteps) between the eight longest
906 NC and MAX (1901-2014). Thick lines represent significant ($p \leq 0.05$) correlations.
907

For Peer Review

908 **Supplementary Information**

909

910 **Script S1** R Code for the analysis carried out in the present paper

911

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

914

915 **Table S2** Intra-NUTS correlation of masting series and temporal autocorrelation in NC (n =
916 records in the chronology, including only consecutive series of ≥ 7 records; rho = mean
917 Spearman's correlation between all series in the NUTS-1; ar1 = autoregression coefficient at
918 lag (1); slope=slope of linear regression of NC vs. time; n.s. = non-significant at $p=0.05$).

919

920 **Fig. S1** Mean Spearman's rank correlation of masting series within each NUTS-1 (black: no
921 data; grey: NUTS-1 with less than 2 series or <7 years' overlap between series). ©

922 EuroGeographics for the administrative boundaries

923

924 **Fig. S2** NUTS-1 masting chronologies from year 1976 to 2014 (black: no data; grey: no data
925 for the year; orange: very poor [1]; dark green: very abundant [5]). Output clipped on beech
926 distribution (Fig. 1a)

927

928 **Fig. S3** Mantel correlograms for NUTS-1 masting chronologies (1950-2014) across latitude
929 (left) and longitude only (right). Black dots indicate significant correlations ($p \leq 0.05$),
930 sequentially corrected for multiple testing using Holm's procedure.

931

932 **Fig. S4** Dendrogram for the hierarchical clustering of NUTS-1 masting chronologies (1950-
933 2014)

934

935 **Fig. S5** Spearman's correlation between monthly mean temperature (1950-2014) and NUTS-
936 1 masting chronologies. NUTS-1 are ordered and colored according to the cluster they belong
937 to (colors as in Fig. 3, black = excluded from clustering due to insufficient chronology
938 length). The three bottom lines show correlation against seasonal summer weather (June-
939 July) and the Delta variable (difference between weather variable in year.₂ and year.₁). The
940 sample size (number of years on record) is reported on the secondary x-axis. (.) significant at

941 $p \leq 0.05$, (*) significant at $p \leq 0.00139$ (Bonferroni-corrected). MEAN: the mean correlation
942 for the corresponding month across the study area

943

944 **Fig. S6** Spearman's correlation between monthly minimum temperature (1950-2014) and
945 NUTS-1 masting chronologies. NUTS-1 are ordered and colored according to the cluster they
946 belong to (colors as in Fig. 3, black = excluded from clustering due to insufficient chronology
947 length). The three bottom lines show correlation against seasonal summer weather (June-
948 July) and the Delta variable (difference between weather variable in year₂ and year₁). The
949 sample size (number of years on record) is reported on the secondary x-axis. (.) significant at
950 $p \leq 0.05$, (*) significant at $p \leq 0.00139$ (Bonferroni-corrected). MEAN: the mean correlation
951 for the corresponding month across the study area

952

953 **Fig. S7** Spearman's correlation between monthly precipitation (1950-2014) and NUTS-1
954 masting chronologies. NUTS-1 are ordered and colored according to the cluster they belong
955 to (colors as in Fig. 3, black = excluded from clustering due to insufficient chronology
956 length). The three bottom lines show correlation against seasonal summer weather (June-
957 July) and the Delta variable (difference between weather variable in year₂ and year₁). The
958 sample size (number of years on record) is reported on the secondary x-axis. (.) significant at
959 $p \leq 0.05$, (*) significant at $p \leq 0.00139$ (Bonferroni-corrected). MEAN: the mean correlation
960 for the corresponding month across the study area

961

962 **Fig. S8** Spearman's correlation between monthly SPI3 (1950-2014) and NUTS-1 masting
963 chronologies. NUTS-1 are ordered and colored according to the cluster they belong to (colors
964 as in Fig.3, black = excluded from clustering due to insufficient chronology length). The
965 three bottom lines show correlation against seasonal summer weather (June-July) and the
966 Delta variable (difference between weather variable in year₂ and year₁). The sample size
967 (number of years on record) is reported on the secondary x-axis. (.) significant at $p \leq 0.05$, (*)
968 significant at $p \leq 0.00139$ (Bonferroni-corrected). MEAN: the mean correlation for the
969 corresponding month across the study area

970

971 **Fig. S9** Spearman's correlation between monthly SPEI3 (1950-2014) and NUTS-1 masting
972 chronologies. NUTS-1 are ordered and colored according to the cluster they belong to (colors
973 as in Fig. 3, black = excluded from clustering due to insufficient chronology length). The
974 three bottom lines show correlation against seasonal summer weather (June-July) and the

975 Delta variable (difference between weather variable in year.₂ and year.₁). The sample size
 976 (number of years on record) is reported on the secondary x-axis. (.) significant at $p \leq 0.05$, (*)
 977 significant at $p \leq 0.00139$ (Bonferroni-corrected). MEAN: the mean correlation for the
 978 corresponding month across the study area

979

980 **Fig. S10** Linear models of Spearman's correlation between masting and MAX in June, July,
 981 or August of the one and two years prior vs. latitude, in all NUTS-1 analyzed. Black dots are
 982 significant correlations, grey dots non-significant ones. Confidence intervals computed at
 983 $p=0.05$. Boxplots represents the number of NUTS-1 where Spearman's correlation between
 984 masting and MAX is highest in selected summer months; width of the boxplots is
 985 proportional to sample size.

986

987 **Fig. S11** Summary of moving Spearman's correlation (1901-2014, window size: 28 years)
 988 between the eight longest NC and MAX_{JUL-1} (red) and MAX_{JUL-2} (blue). Timestep is one
 989 year. The colored area in each violin plot represents the range of correlation values and is
 990 shaped by a kernel density estimator, the dots represent correlation value with a color
 991 intensity proportional to the significance of correlation estimated by bootstrapping
 992 (significant at $p \leq 0.05$: more intense). Larger dots represent the median correlation value.

993

994 **Fig. S12** Spearman's correlation between MAX in June-July and SPEI3 across the study area,
 995 period 1901-2014 (black: no data). © EuroGeographics for the administrative boundaries.

996

997 **Fig. S13** Hierarchical clustering of NUTS-1 weather variables (1950-2014) based on
 998 Suzuki's dissimilarity index (red: eastern cluster, green: northern, blue: southern, grey: no
 999 data within beech distribution for the study period). © EuroGeographics for the
 1000 administrative boundaries.

1001

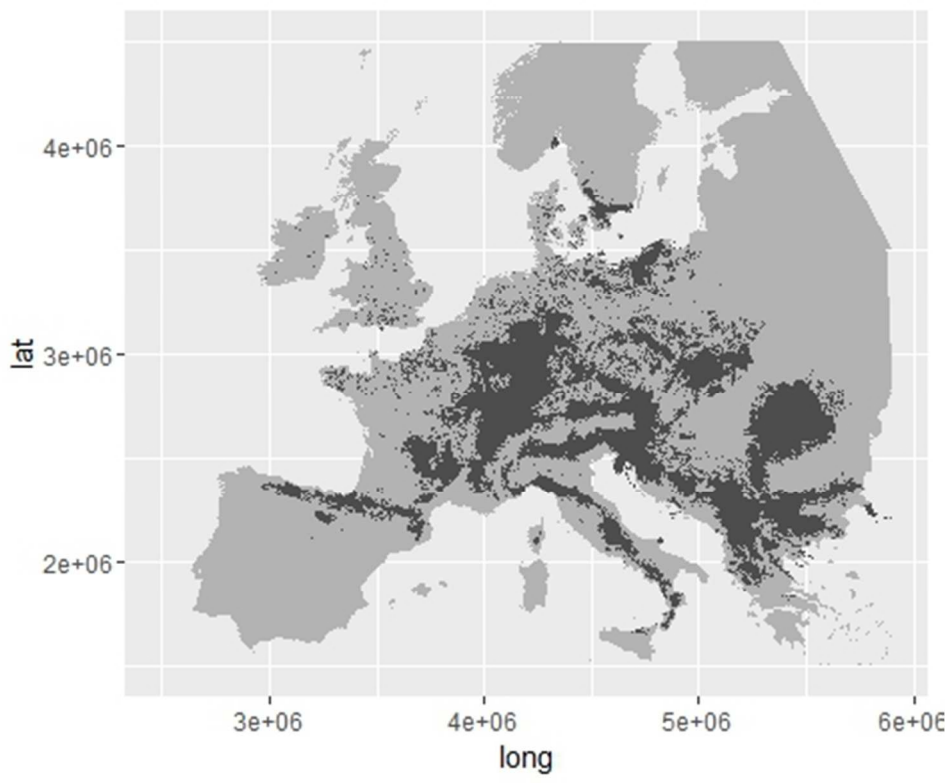


Fig. 1 (a) Current distribution of beech in Europe at 1-km resolution (Casalegno et al., 2011, filtered for cell cover $\geq 5\%$)
Fig. 1a
126x104mm (96 x 96 DPI)

view

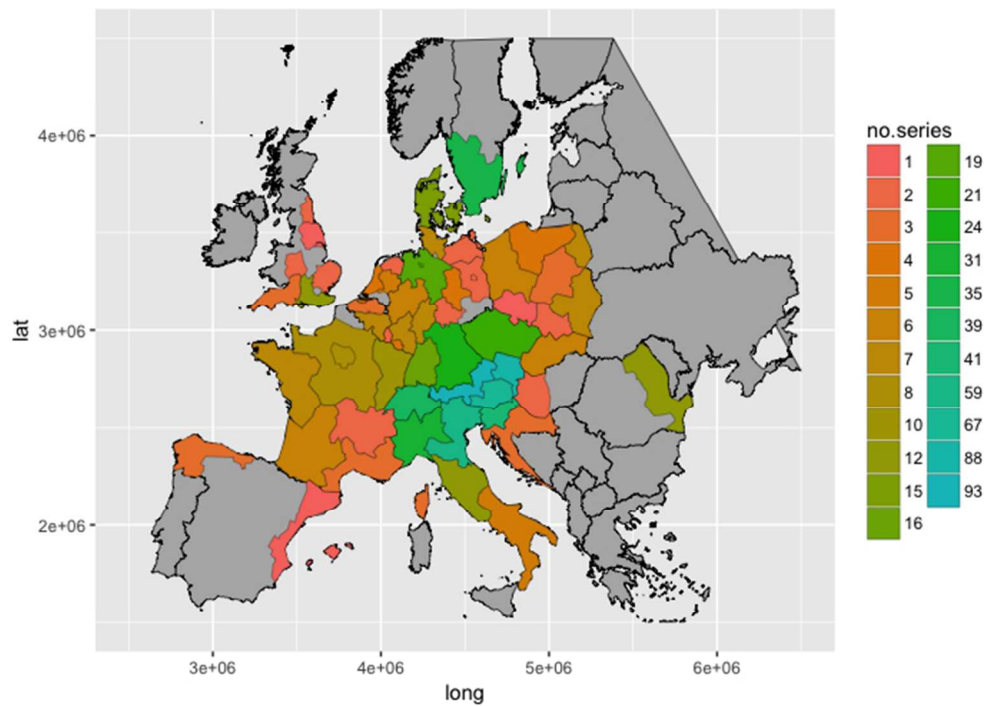


Fig. 1 (b) number of beech masting data series in each NUTS-1 for the period 1950-2014

Fig. 1b
246x176mm (72 x 72 DPI)

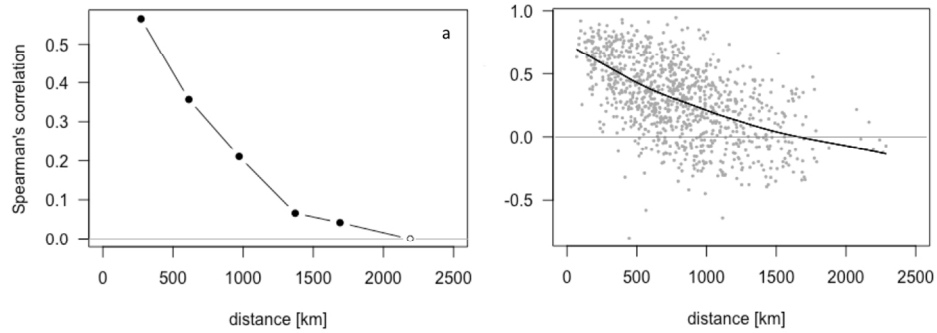


Fig. 2 (a) Mantel correlograms for NUTS-1 masting chronologies (1950-2014). Distance in 500-km wide bins. Black dots indicate significant ($p \leq 0.05$) correlations, sequentially corrected for multiple testing using Holm's procedure. (b) Pairwise Spearman's correlations between NUTS-1 masting chronologies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

Fig. 2
338x190mm (108 x 108 DPI)

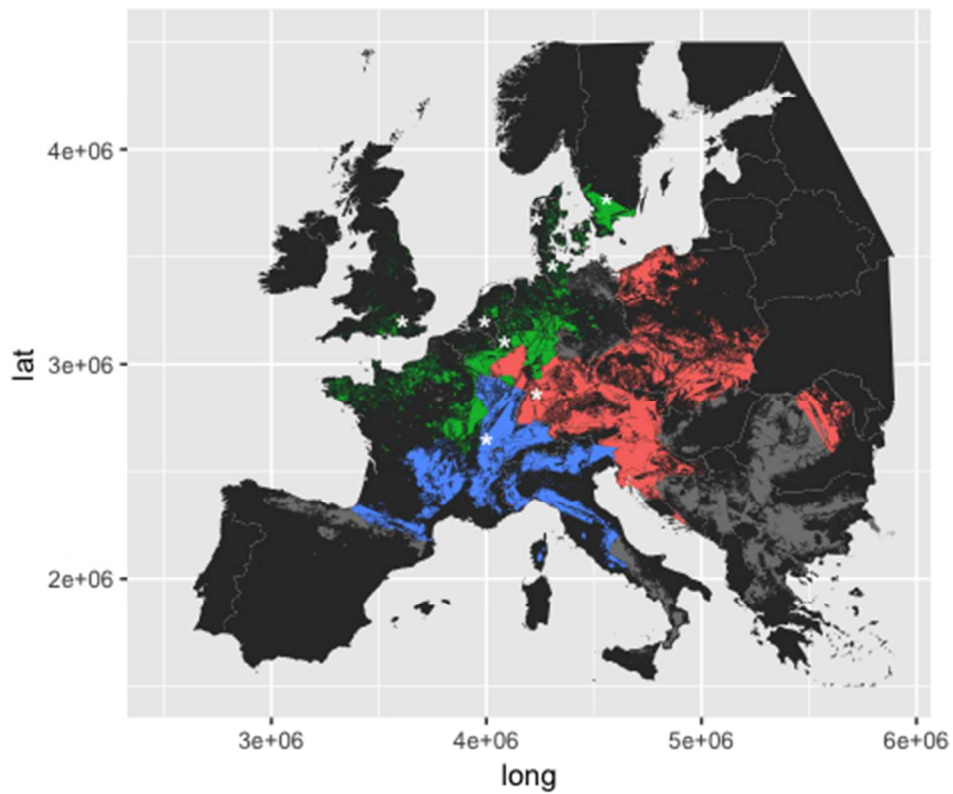


Fig. 3 Hierarchical clustering of NUTS-1 masting chronologies (1950-2014) based on Suzuki's dissimilarity index (red: eastern cluster, green: northern, blue: southern, grey: no data within beech distribution for the study period). © EuroGeographics for the administrative boundaries. Output clipped on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

Fig. 3

170x142mm (72 x 72 DPI)

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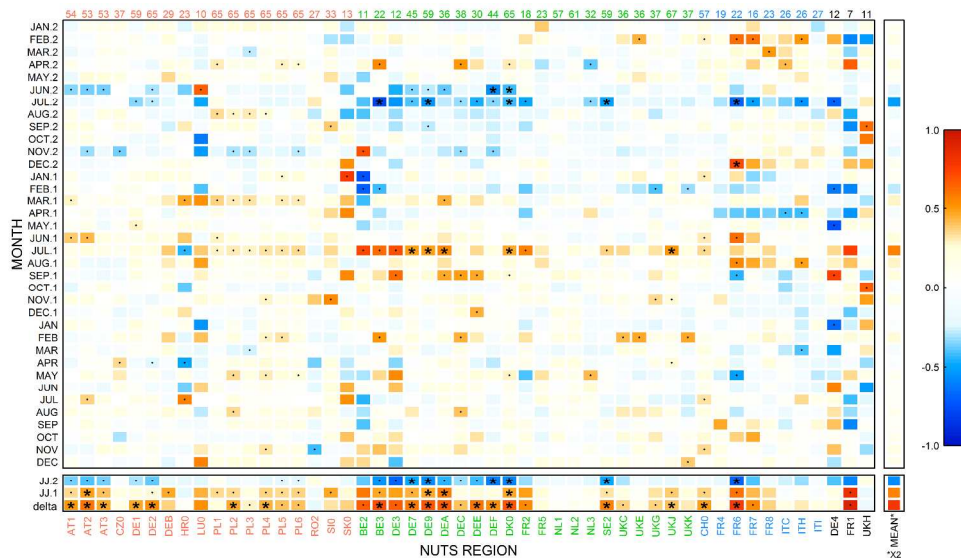


Fig. 4 Spearman's correlation between monthly maximum temperature (1950-2014) and NUTS-1 masting chronologies. NUTS-1 ordered and colored according to the cluster they belong to (colors as in Fig. 3, black = excluded from clustering due to insufficient chronology length). The three bottom lines show 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.

Fig. 4

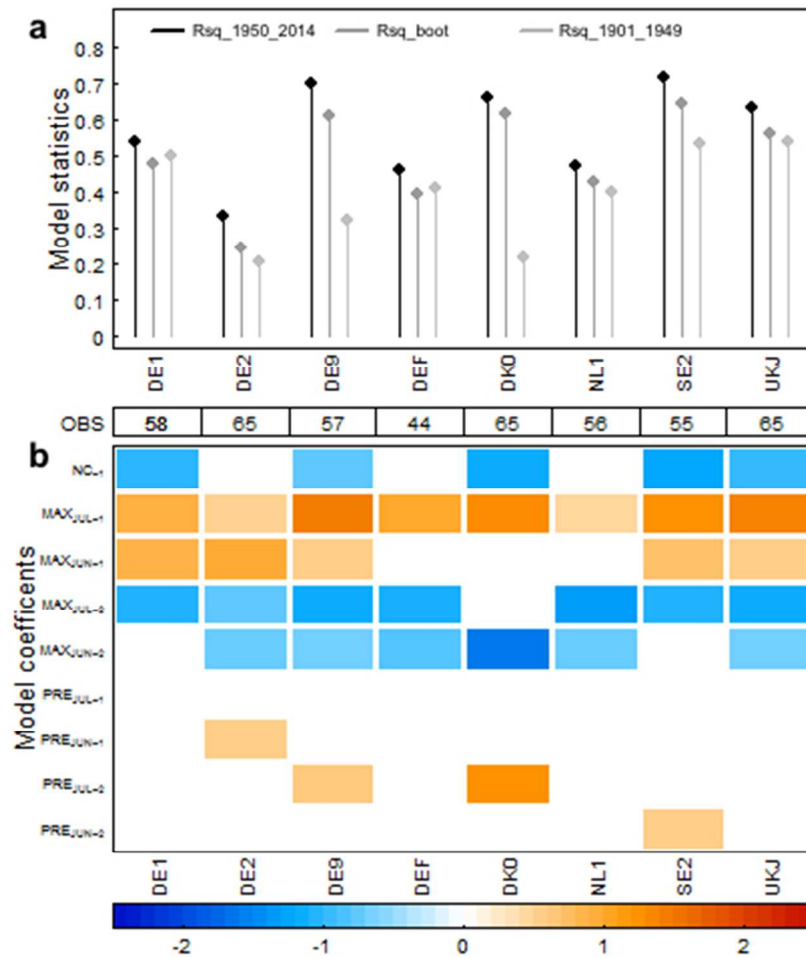


Fig. 5 Ordinal logistic models of masting (8 longest NC) as a function of weather predictors: (a) model statistics for calibration (1950-2014) and validation (1901-1949). Rsq_{1950_2014} is R^2 the calibration dataset, Rsq_{boot} is the bootstrapped R^2 from leave-one out cross-validation (1000 re-samples), and Rsq_{1901_1949} is the R^2 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.

Fig. 5

146x170mm (72 x 72 DPI)

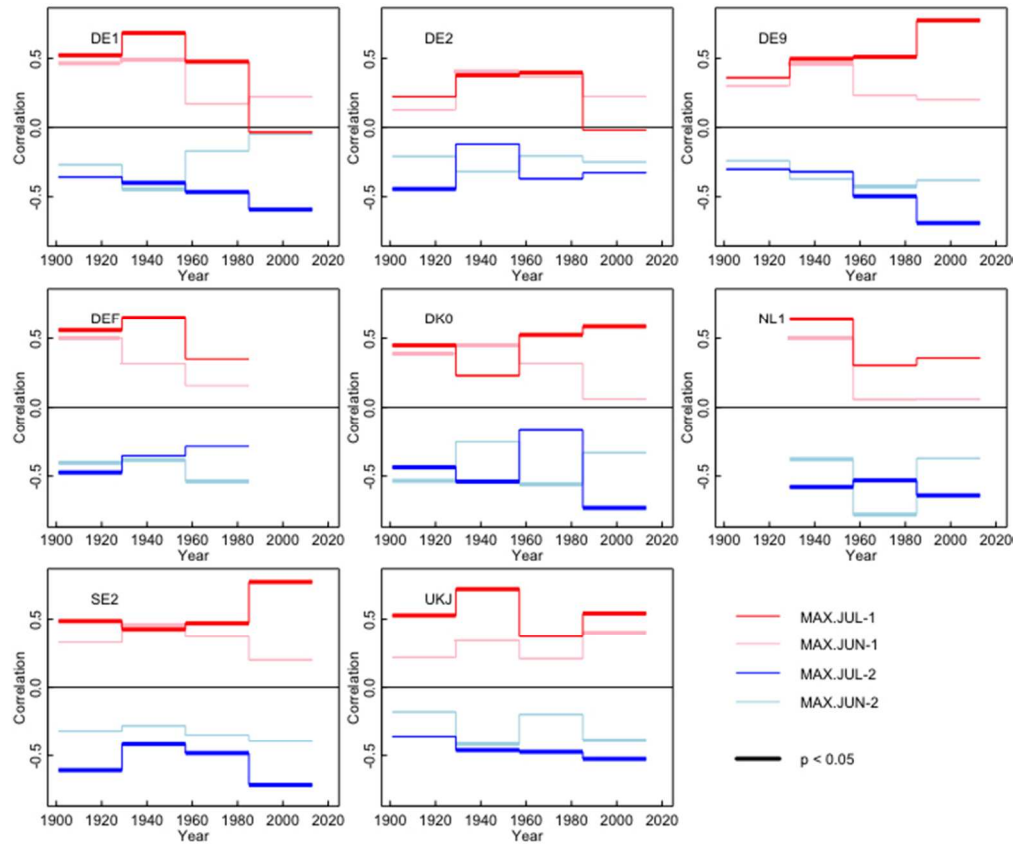


Fig. 6 Moving Spearman's correlation (lines: 28-years timesteps) between the eight longest NC and MAX (1901-2014). Thick lines represent significant ($p \leq 0.05$) correlations.

Fig. 6
251x211mm (72 x 72 DPI)