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

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Word count for the main body of the text (Introduction, Materials and Methods, Results, Discussion, and Acknowledgements): 6113
Word counts for each section: Summary 194, Introduction 634, Materials and Methods 2057, Results 1013, Discussion 2375

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

Summary

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

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

Introduction

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

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

The oldest and simplest hypothesis for masting states that seed crops vary in response to weather variation (Büsgen *et al.*, 1929; Kelly, 1994). In particular, temperature and precipitation in the years previous to seed production have been consistently related to masting (e.g., in grasses: Schauber *et al.*, 2002; shrubs: Mayer & Pendleton, 2015; trees: Bisi *et al.*, 2016). The nature of such relationships can be either correlative, i.e., weather is a "cue" that triggers other processes and that plants are able to sense (e.g., Kelly & Sork, 2002; Kelly *et al.*, 2013), or causal, in the case that weather directly influences resources and other proximate causes of masting (Monks *et al.*, 2016; Pearse *et al.*, 2016) (correlative analysis on its own cannot distinguish these models, and we hereafter use the word "cue" in a broad sense without addressing underlying mechanisms). Several studies have assessed masting at the scale of a plant's distribution range (e.g., Kelly *et al.*, 2000; Schauber *et al.*, 2002; Masaki *et al.*, 2008), but few have tested whether such cues are constant in space and time across the range. In other words, do spatial and temporal variations in masting emerge from (a) variations in weather, or (b) differences in local plant response to the same weather patterns, e.g. as a consequence of inter-population differences and adaptations in genes that regulate flowering (Tan and Swain, 2006)? Addressing this question will provide important information on predicting masting both in the short and at the long term, such as in the case of masting responses to climate change and the consequences on large-scale ecosystem processes.

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

Materials and methods

Beech masting data

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

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

Data treatment

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

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

Spatial analysis of masting patterns

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

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

We used coordinates of NUTS-1 centers to compute the geographical distance matrix for the Mantel test, and the index of Suzuki *et al.* (2005), a metric derived from Spearman's correlation coefficient, for the masting dissimilarity matrix. Only NC pairs with an overlap of ≥7 consecutive years of observation were included in the latter. Alongside the Mantel correlation coefficient, we computed a Mantel correlogram (Oden and Sokal, 1986) by binning distances and calculating the mean pairwise correlation between NC for pairs in each distance class. Significance of each Mantel correlation coefficient was computed by a randomization approach (2000 permutations) in which the rows and/or columns of the distance matrices are randomly rearranged (Mantel, 1967), and corrected for multiple comparison according to Holm (1979) in the case of Mantel correlograms. Furthermore, we ran two unidirectional Mantel tests and correlograms as a function of distance along longitude (Dlon) and latitude (Dlat) only, by fixing the other coordinate to its mean value across all NUTS-1, to scrutinize the structure of masting along the two orthogonal geographical directions. Mantel tests and correlograms were run with package *ncf* version 1.1 (Bjornstad, 2015) for the R statistical framework (R Core Team, 2016).

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

Weather cues analysis

To measure the strength of weather cues of masting, we calculated Spearman's correlations between each NC (filtered on ≥ 7 years of observation, after detrending if needed: see above) and the following variables: Mean monthly temperature (MEAN), monthly mean of daily maximum temperature (MAX), monthly mean of daily minimum temperature (MIN), monthly precipitation (PRE), three-months Standardized Precipitation Index (SPI3; McKee *et* *al.*, 1993), and three-months Standardized Precipitation and Evaporation Index (SPEI3; Vicente-Serrano *et al.*, 2010). Weather series were obtained by averaging monthly data across all cells included in each NUTS-1 from the gridded database CRU TS 3.23 (0.5° resolution; years 1901-2014) (Harris *et al.*, 2014), and detrended before all subsequent analysis by running a linear filter on each individual monthly variable for the timespan selected (1901-2014 or 1950-2014). SPI3 was calculated using the nonparametric approach described by Hao *et al.* (2014), in which the probability distributions are calculated empirically (Gringorten, 1963), rather than by fitting a parametric distribution function. SPEI3 was calculated from the difference between available water (i.e., three-month sum of PRE) and the potential evapotranspiration, which is based on the FAO-56 Penman–Monteith estimation (Allen *et al.*, 1998) and directly gridded by the CRU. The difference was fit to a log-logistic probability distribution to transform the original values to standardized units (Vicente-Serrano *et al.*, 2010). SPEI3 measures the climatic water balance and therefore provides a more reliable and spatially comparable measure of drought severity than precipitation alone (Vicente-Serrano *et al.*, 2013). Data extraction and calculation of drought indices were performed with the R packages *cruts* (Taylor and Parida, 2016) and *SPEI* (Begueria and Vicente-Serrano, 2013). Correlations (years 1950-2014) were computed for all 36 months of a three-year period, including the calendar year of seed production and the two years prior (lag -1 and -2). After preliminary scrutiny of the most significant correlations, we also ran correlations against aggregated summer (June-July) weather variables of one and two years prior to masting, and against the difference (Delta) between values of each weather variables measured one and two years prior (e.g., Delta Temperature, Kelly et al. 2013). The absence of non-linear relationships was visually checked before running all correlations. For each correlation, significance was tested at the 95% confidence level, with a simple Bonferroni correction, i.e. adjusting the required alpha value according to the number of comparisons (0.05/36), to account for multiple comparisons. Finally, to assess the similarity of weather spatial patterns to those of masting, we applied hierarchical cluster analysis to each weather variable, using the same settings and period (1950-2014) as the analysis run on masting, and compared the consistency of masting vs. weather clusters by computing the overall proportion of NUTS-1 that were classified into the same cluster under both analyses.

Spatio-temporal stability of weather cues

To test for spatial stability of masting-weather relationships, we fitted a linear model of Spearman's correlation coefficient between masting and MAX of June, July, and August of the one and two years prior, and latitude. Subsequently, we modeled the eight longest NC (DE1, DE2, DE9, DEF, DK0, NL1, SE2, UKJ – including 74 to 115 yearly observations in the period 1901-2014) as a function of detrended weather variables, using ordinal logistic regression within the R package *rms* (Harrell, 2016). In this analysis, NC_{-1} was used as an additional independent variable, to account for potential temporal autocorrelation resulting e.g. from resource depletion (Davis, 1957) or resource switching (Kelly & Sork, 2002). All models were fitted with 44-65 observations (years 1950-2014), and validated using both a new prediction interval (years 1901-1949, 30-41 observations for each NC except NL1 with 10), and a bootstrapped leave-one-out cross-validation run on the calibration time period. Weather variables (i.e., MAX and PRE in June and July -1 and -2, hereafter MAX_{JUN-1}, MAX_{JUL-1}, MAX_{JUN-2}, $MAX_{JUL-2,}$ PRE_{JUN-1}, PRE_{JUL-1}, PRE_{JUN-2}, PRE_{JUL-2}) were selected based on the previous correlation analysis and evidence from literature on beech masting (e.g., Piovesan and Adams, 2001; Drobyshev *et al.*, 2010). The absence of non-linear univariate relationships was visually checked before running the models. All independent variables were z-transformed to ensure comparability of effect sizes within models; to account for collinearity among weather variables, optimal models were selected using backward stepwise selection based on the Akaike Information Criterion (AIC). Nagelkerke R^2 was used to compare models for different NC.

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

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

Results

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

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

Correlations between NC and PRE were weaker and much less consistent than with temperature (Fig. S7). Significantly positive correlations with PRE in two summers prior and negative in one summer prior emerged locally (e.g., in Germany, UK, France, and Switzerland), although a clear distinction between clusters was not evident. Correlations with summer$_{-2}$ were on average stronger than with summer$_{-1}$. SPI3 and SPEI3 were similar to MAX, with strong and significant correlations in summer$_{-2}$ and, less strongly, summer$_{-1}$ (Fig. S8; Fig. S9), albeit on a more restricted geographic extent (Germany, Denmark, United Kingdom, Belgium, Sweden). Spring water balance (PRE, SPEI3) was generally uncorrelated to masting in beech (except a positive correlation of $\mathrm{PRE}_{\mathrm{APR-1}}$ in France and $\mathrm{PRE}_{\mathrm{APR0}}$ in Croatia).

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

Latitude was not a significant driver of the correlation between masting and MAX (Fig. S10). Ordinal logistic models fitted to the eight longest NC had medium to high explanatory power (range of Nagelkerke R^2: 0.33– 0.72, mean = 0.57). Stepwise AIC selection isolated between three and six independent variables (Fig. 5), which corroborated the results of weather correlations computed for NUTS-1. The most commonly selected terms were $\mathrm{MAX}_{\mathrm{JUL-1}}$ (selected in all models) and $\mathrm{MAX}_{\mathrm{JUL-2}}$ (all but one). $\mathrm{MAX}_{\mathrm{JUN-1}}$ or $\mathrm{MAX}_{\mathrm{JUN-2}}$ were additionally selected in five and six models, respectively. NC_{-1}, with a negative coefficient, was selected in five models. Precipitation terms were selected less frequently than temperature, and only half of the models included any precipitation term. Standardized coefficients for precipitation were generally lower than those for temperature, indicating a smaller effect on masting. Model validation produced a mean Nagelkerke R^2 of 0.46 after bootstrapped leave-one-out cross-validation (range = 0.53-0.65), and 0.40 after extrapolation to 1901-1950 (0.21-0.55), indicating that models were partially able to reproduce masting variation outside of the training dataset (Table 3). Clusters SO and EA were represented by only one model each, with the latter showing a lower explanatory power and weaker summer$_{-1}$ effects.

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

Discussion

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

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

Numerous studies have demonstrated that mast years in many tree species are associated with specific weather conditions ("weather cues") prior to mast events (Koenig & Knops, 2014; Roland *et al.*, 2014), and particularly with summer temperatures one and two years prior to masting (Schauber *et al.*, 2002; Kelly *et al.*, 2013). We found similar results in this study, showing that a small number of weather variables act as strong cues for masting in almost all European beech populations, despite large climatic, genetic, and environmental differences. Indeed, individual NC where this typical set of cues was not detected were often based on a limited number of observations. We found no substantial differences in these weather cues of masting among regions or clusters using either correlation analysis (Fig. 4, Fig. S10) or regression models (Fig. 5), nor any significant effect of latitude (Fig. S10). This demonstrated that, across the distribution, the cues for masting are highly spatially consistent, with positive correlations for MAX_{JUL-1} (and to a lesser degree MAX_{JUN-1}), and negative for MAX_{JUL-2} and MAX_{JUN-2}, with some local specificities. Combining June and July clearly improved the consistency of strong (and significant) correlations, as did using DeltaT as a synthetic index of temperature differences from year to year (Kelly et al. 2013). In some cases, the seasonal analysis accounted for regional differences in the strongest individual month; AT1-3 were good examples, as they responded more strongly to June temperatures than July (in contrast to most other chronologies). In particular, DeltaT led to improved correlations in cases where correlations with $MAX_{summer-1}$ and $MAX_{summer-2}$ had the expected signal, but were both relatively weak (e.g. DE2, PL2, PL4), or where one individual correlation was much stronger than the other (e.g. DE1, DE2, DEE, SE2, FR6). In the regression models for the NUTS-1 with the most data, a large proportion of the variance was explained by summer temperature in years -1 and -2, suggesting that other signals are not very important.

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

While the well-known relationship between general summer weather and masting in beech was well supported by our results, we were also able to disentangle the relative importance of temperature and precipitation as the dominant cue of masting. Wachter (1964) and Piovesan and Adams (2001) suggested that summer precipitation or drought, along with or rather than temperature, were the main cue of masting in beech, while Drobyshev *et al.* (2010) found no relationship between masting and summer precipitation or drought (but did find a strong temperature signal). We have shown that summer precipitation in the two years prior to masting was an important predictor of mast events in some regions (Fig. 4, Fig. 5), and that 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 $R^2 = 0.57$) 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 low masting category were instead common). The existence of negative autocorrelation in masting time series has been traditionally interpreted as evidence for resource depletion, i.e., trees deplete most resources in the mast year, which limits reproduction in the following year and makes consecutive heavy seed crops very rare (Davis, 1957; Sork *et al.*, 1993; Kelly & Sork, 2002). However, recent studies have showed that negative temporal autocorrelation would also emerge if masting were controlled by DeltaT only (Kelly *et al.*, 2013; Kon & Saito, 2015; but see also Koenig *et al.*, 2015 for criticism of such model).

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

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

High temperatures in the summer prior to masting (MAX_{JUL-1}) have been linked to flower primordia differentiation (Wachter, 1964; Gruber, 2003; see also: Merkle *et al.*, 1980 for oaks, Allen *et al.*, 2014; Miyazaki *et al.*, 2014), in particular via an increase in endogenous gibberellins (Turnbull, 2011; Pearse *et al.*, 2016). Following this reasoning, we might expect the phenology of primordia differentiation to vary with latitude, creating a geographical gradient in the timing of the previous summer cue similar to the pattern we found in some southern European NUTS-1 (Fig. 4). Additionally, we also found correlations with weather during the periods associated with other known processes that influence flowering phenology, pollen production (Kasprzyk *et al.*, 2014; Pearse *et al.*, 2015), and seed maturation in the year of masting, such as late winter frost (Matthews, 1955; Wachter, 1964), at least in northern Europe. The resource priming in year$_{-2}$ can therefore interact with the MAX cue in summer$_{-1}$ via a resource pulse that boosts an already favorable flower initiation.

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

Acknowledgements

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

Author contributions

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

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Tables

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

	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

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

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%		

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

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
$\mathrm{PRE}_{\mathrm{JUL-1}}$	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
$\mathrm{PRE}_{\mathrm{JUL-2}}$	n.s.	n.s.	0.61	n.s.	1.29	n.s.	n.s.	n.s.
$\mathrm{PRE}_{\mathrm{JUN-1}}$	n.s.	0.59	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
$\mathrm{PRE}_{\mathrm{JUN-2}}$	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0.55	n.s.
$\mathrm{MAX}_{\mathrm{JUL-1}}$	0.94	0.52	1.49	1.03	1.34	0.49	1.27	1.42
$\mathrm{MAX}_{\mathrm{JUL-2}}$	-1.06	-0.78	-1.16	-1.14	n.s.	-1.31	-1.047	-1.16
$\mathrm{MAX}_{\mathrm{JUN-1}}$	0.88	0.98	0.57	n.s.	n.s.	n.s.	0.75	0.59
$\mathrm{MAX}_{\mathrm{JUN-2}}$	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 $\mathrm{MAX}_{\mathrm{JUL-1}}$	-0.19	n.s.	0.41	n.s.	n.s.	-0.69	n.s.	n.s.
Year in $\mathrm{MAX}_{\mathrm{JUL-2}}$	n.s.	n.s.	0.47	n.s.	n.s.	-0.69	n.s.	n.s.
Year in $\mathrm{MAX}_{\mathrm{JUN-1}}$	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Year in $\mathrm{MAX}_{\mathrm{JUN-2}}$	n.s.	0.40	n.s.	n.s.	n.s.	-0.74	n.s.	n.s.
Year x $\mathrm{MAX}_{\mathrm{JUL-1}}$	-0.68	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Year x $\mathrm{MAX}_{\mathrm{JUL-2}}$	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Year x $\mathrm{MAX}_{\mathrm{JUN-1}}$	n.s.	n.s.	n.s.	n.s.	-0.53	n.s.	n.s.	n.s.
Year x $\mathrm{MAX}_{\mathrm{JUN-2}}$	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

Figure legends

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

Fig. 2 (a) Mantel correlograms for NUTS-1 masting chronologies for beech (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. 3 Hierarchical clustering of NUTS-1 masting chronologies for beech (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. 4 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

Fig. 5 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 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. Monthly weather variables: MAX maximum temperature, PRE precipitation. NC_{-1}: masting in the previous year

Fig. 6 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.

Supplementary Information

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

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

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

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

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

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

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

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

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

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

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

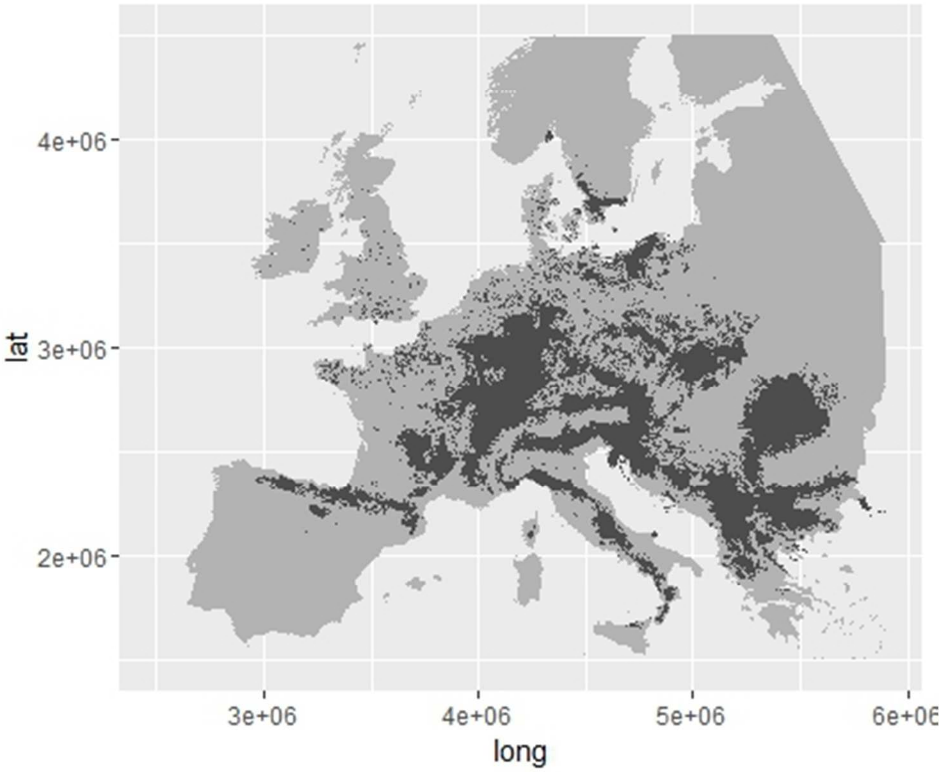
Fig. S9 Spearman's correlation between monthly SPEI3 (1950-2014) and NUTS-1 masting chronologies

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

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

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

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



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

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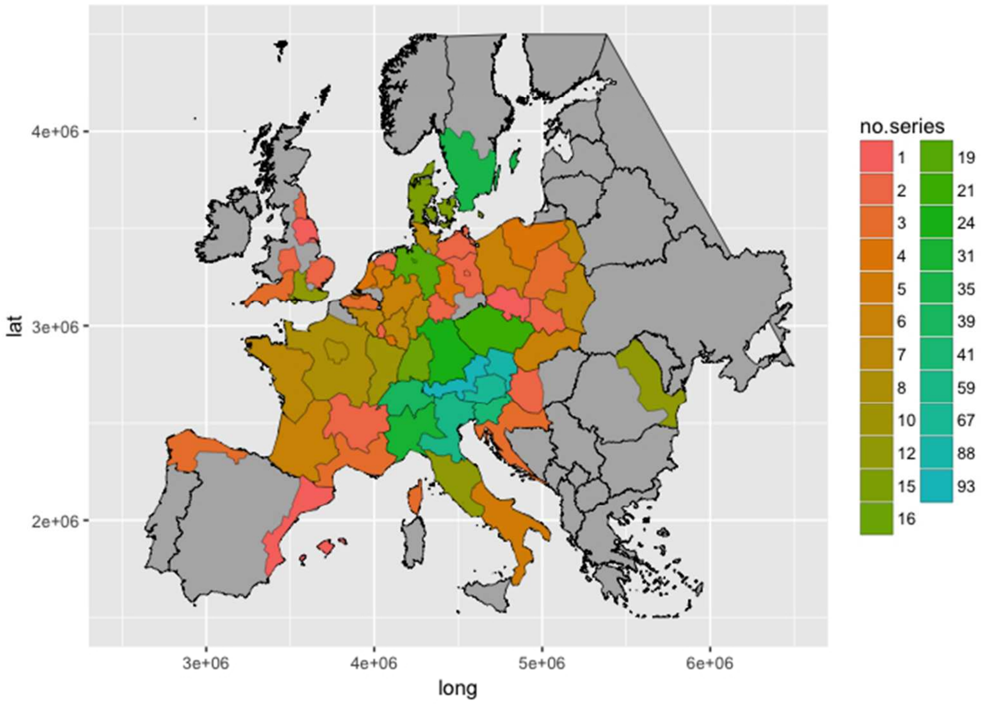

(b) number of beech masting data series in each NUTS-1 for the period 1950-2014.

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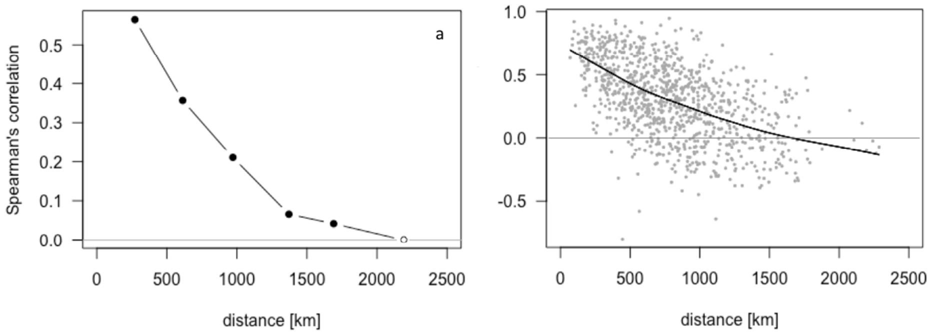
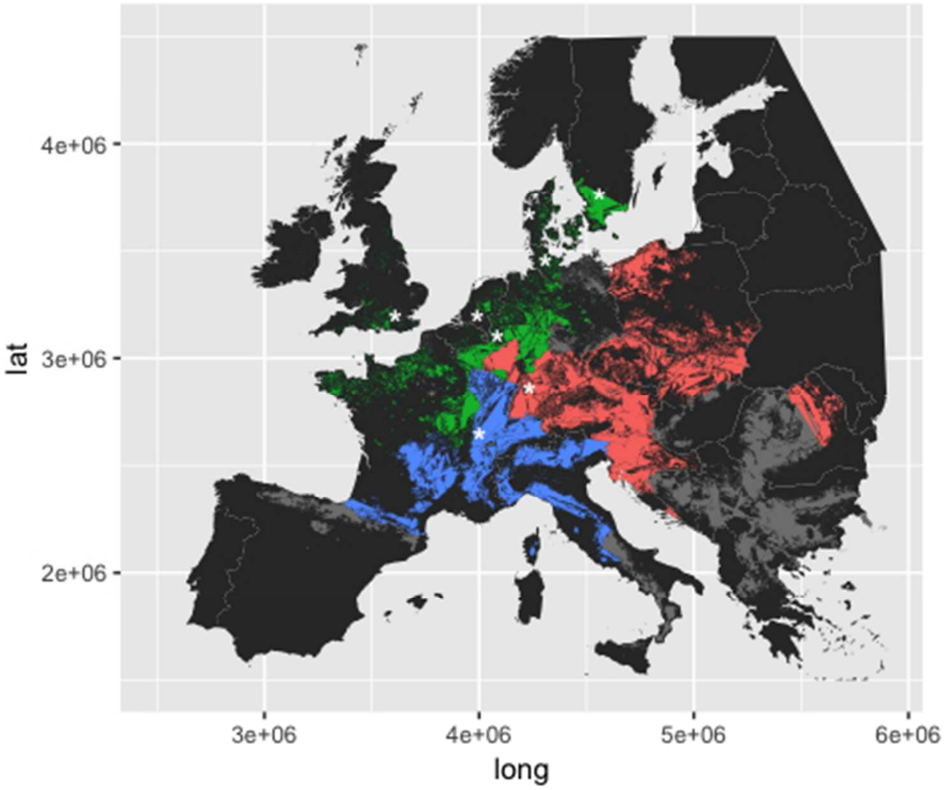


(a) Mantel correlograms for NUTS-1 masting chronologies (1950-2014). Distance in 500-km wide bins. Black dots indicate significant (p ≤0.05) correlations, sequentially corrected for multiple testing using Holm's procedure. (b) Pairwise Spearman's correlations between NUTS-1 masting chronologies (1950-2014) 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.

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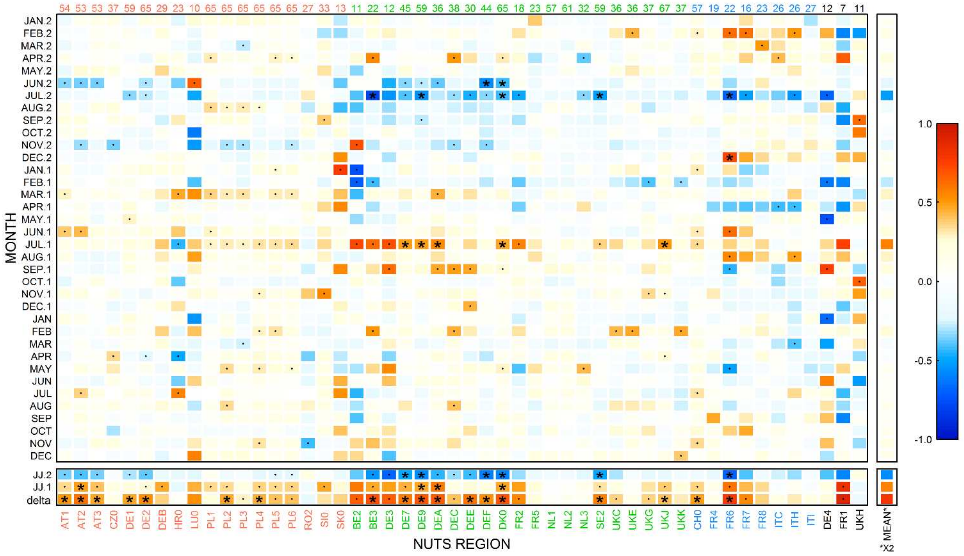
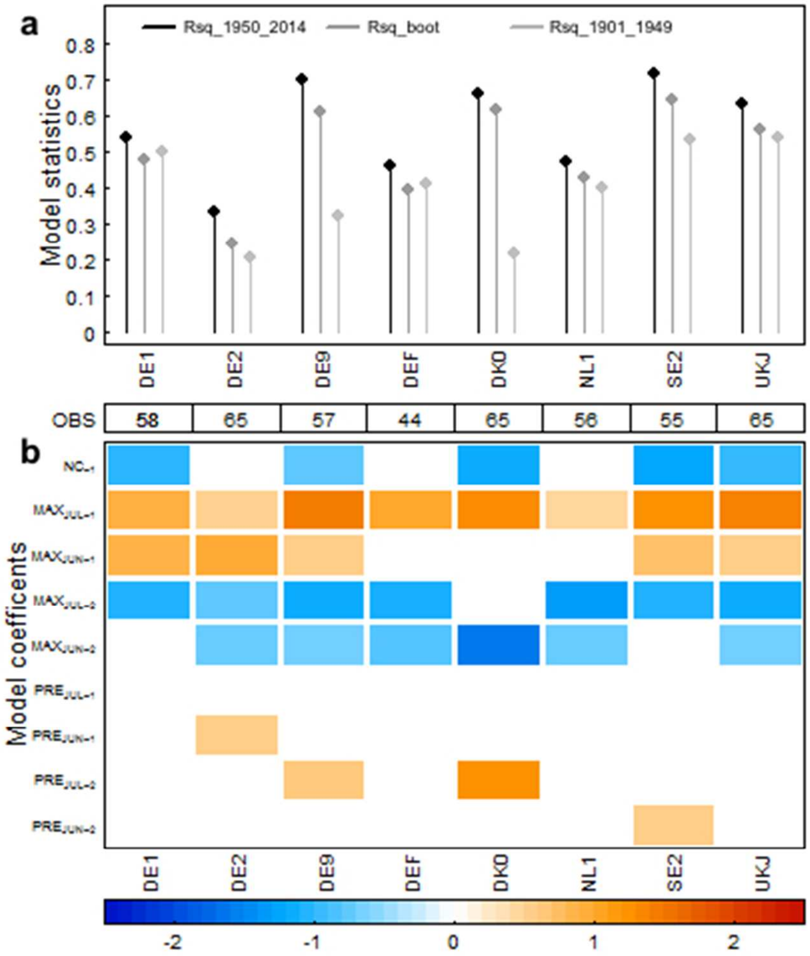


Spearman's correlation between monthly maximum temperature (1950-2014) and NUTS-1 masting chronologies for beech. NUTS-1 ordered and colored according to the cluster they belong to (colors as in Fig. 3, black = excluded from clustering due to insufficient chronology length). The three bottom lines show 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 ≤0.05, (*) significant at p ≤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 re-samples), 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

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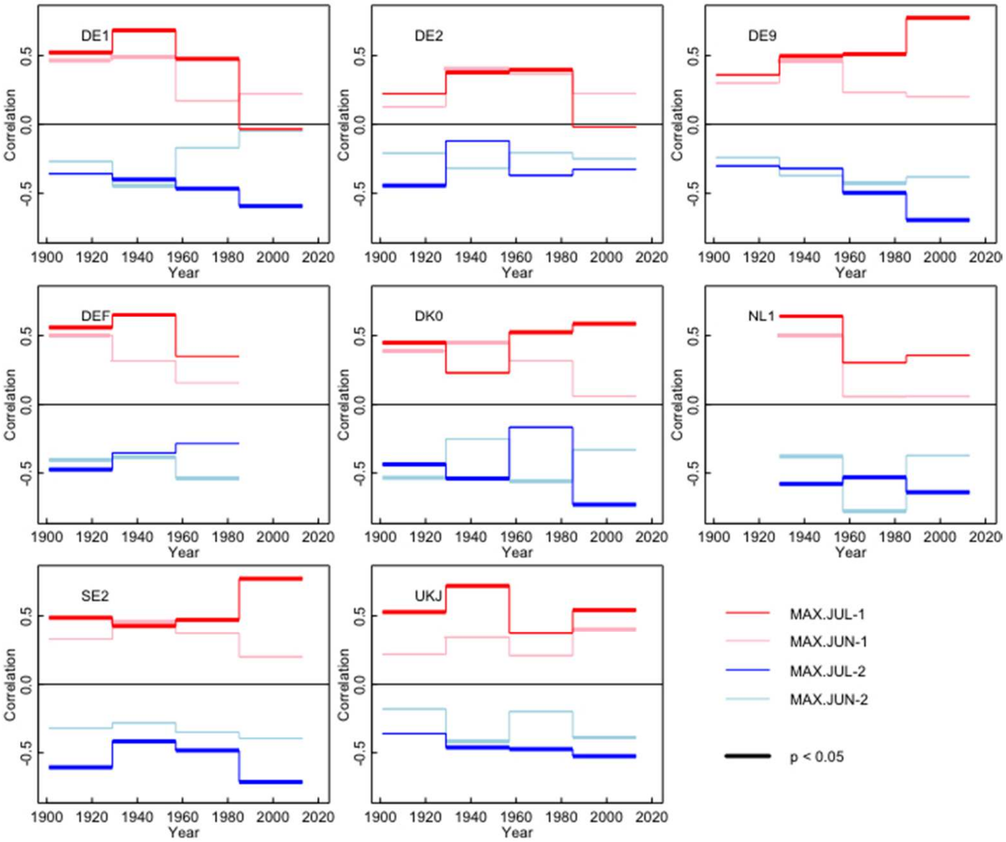

Moving Spearman's correlation (lines: 28-years timesteps) between the eight longest NUTS-1 beech masting chronologies and maximum temperature (MAX) (1901-2014). Thick lines represent significant ($p \leq 0.05$) correlations.

251x211mm (72 x 72 DPI)