Impact of weather cues and resource dynamics on mast occurrence in the main forest tree species in Europe

Anita Nussbaumer[a,*], Peter Waldner[a], Vladislav Apuhtin[b], Fatih Aytar[c], Sue Benham[d], Filippo Bussotti[e], Johannes Eichhorn[f], Nadine Eickenscheidt[g], Petr Fabianek[h], Lutz Falkenried[i], Stefan Leca[j], Martti Lindgren[k], María José Manzano Serrano[l], Stefan Neagu[j], Seppo Nevalainen[m], Jozef Pajtik[n], Nenad Potočić[o], Pasi Rautio[p], Geert Sioen[q], Vidas Stakėnas[r], Celal Tasdemir[c], Iben Margrete Thomsen[s], Volkmar Timmermann[t], Liisa Ukonmaanaho[k], Arne Verstraeten[q], Sören Wulff[u], Arthur Gessler[a,v]

[a] WSL, Swiss Federal Institute for Forest, Snow and Landscape Research, Birmensdorf, Switzerland
[b] Estonian Environment Agency, Tartu, Estonia
[c] Eastern Mediterranean Forest Research Institute, Tarsus/Mersin, Turkey
[d] Forest Research, Alice Holt, Farnham, Surrey, United Kingdom
[e] University of Firenze, Dept. of Agri-Food Production and Environmental Science, Firenze, Italy
[f] Nordwestdeutsche Forstliche Versuchsanstalt (NW-FVA), Göttingen, Germany
[g] Landesamt für Natur, Umwelt und Verbraucherschutz Nordrhein-Westfalen (LANUV), Recklinghausen, Germany
[h] Forestry and Game Management Research Institute, Jíloviště, Czech Republic
[i] Landesbetrieb Wald und Holz Nordrhein-Westfalen, Gelsenkirchen, Germany
[j] National Institute for Research and Development in Forestry (INCDS), Voluntari, Romania
[k] Natural Resources Institute Finland (LUKE), Helsinki, Finland
[l] ESMA Estudios Medioambientales S.L., Madrid, Spain
[m] Natural Resources Institute Finland (LUKE), Joensuu, Finland
[n] Forest Research Institute, Zvolen, Slovak Republic
[o] Croatian Forest Research Institute, Jastrebarsko, Croatia
[p] Natural Resources Institute Finland (LUKE), Rovaniemi, Finland
[q] Research Institute for Nature and Forest (INBO), Brussels, Belgium
[r] Lithuanian Research Centre for Agriculture and Forestry, Kaunas, Lithuania
[s] Department of Geosciences and Natural Resource Management, University of Copenhagen, Copenhagen, Denmark
[t] Norwegian Institute of Bioeconomy Research (NIBIO), Ås, Norway
[u] Swedish University of Agricultural Science (SLU), Umeå, Sweden
[v] ETH Zurich, Swiss Federal Institute of Technology, Zurich, Switzerland

A B S T R A C T

Mast seeding, the synchronised occurrence of large amounts of fruits and seeds at irregular intervals, is a reproductive strategy in many wind-pollinated species. Although a series of studies have investigated mast year (MY) patterns in European forest tree species at the regional scale, there are few recent evaluations at a European scale on the impact of weather variables (weather cues) and resource dynamics on mast behaviour. Thus the main objective of this study is to investigate the impact of specific weather conditions, as environmental drivers for MYs, on resources in *Fagus sylvatica* L., *Quercus petraea* (MATT.) LIEBL., *Quercus robur* L., *Picea abies* (L.) KARST. and *Pinus sylvestris* L. at a European level and to explore the robustness of the relationships in smaller regions within Europe. Data on seed production originating from the International Co-operative Programme on

Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests) were analysed. Three beta regression models were applied to investigate the impact of seasonal weather variables on MY occurrence, as well as the influence of fruiting intensity levels in the years prior to MYs. Resource dynamics are analysed at three different spatial scales (continent, countries and ecoregions).

At a European scale, important weather cues for beech MYs were a cold and wet summer two years before a MY, a dry and warm summer one year before a MY and a warm spring in the MY. For spruce, a cold and dry summer two years prior to a MY and a warm and dry summer in the year before the MY showed the strongest associations with the MY. For oak, high spring temperature in the MY was the most important weather cue. For beech and spruce, and to some extent also for oak species, the best fitting models at European scale were well reflected by those found at smaller scales. For pine, best fitting models were highly diverse concerning weather cues. Fruiting levels were high in all species two years before the MY and also high one year before the MY in the oak species and in pine. In beech, fruiting levels one year before the MY were not important and in spruce, they were inconsistent depending on the region. As a consequence, evidence of resource depletion could only be seen in some regions for spruce.

1. Introduction

Mast seeding describes the synchronised occurrence of large amounts of fruits and seeds at irregular intervals. This is a reproductive strategy in many wind-pollinated species and occurs at stand or regional scale (Nilsson and Wastljung, 1987; Kelly, 1994; Herrera et al., 1998; Koenig and Knops, 2000; Kelly and Sork, 2002; Kelly et al., 2013). However, studies of mast behaviour in various species show that the definition of years with mast seeding (mast years, hereafter MYs) is ambiguous, and there is no common view on the methodology for recognising MYs. Mostly, MYs are defined either based on visual assessments (Pearse et al., 2014; Koenig and Knops, 2014; Moreira et al., 2015; Wesolowski et al., 2015; Bisi et al., 2016; Vacchiano et al., 2017) or by derivations from quantitative parameters, e.g. from litterfall measurements (McKone et al., 1998; Curran et al., 1999; Monks and Kelly, 2006; LaMontagne and Boutin, 2009; Smaill et al., 2011; Koenig and Knops, 2014). However, independent of the applied MY definition (Nussbaumer et al., 2016) fruiting intensity and MY occurrence are strongly related.

The impact of mast seeding on ecosystems is of interest as it may have several economic implications. Mast events in fruit producing species like oak and beech can lead to decreased wildlife caused crop loss (Picard et al., 1991) and increased game populations (Wohlgemuth et al., 2016), but as a consequence, also an increased human health risk associated with zoonoses, e.g. Lyme disease or Hanta virus induced diseases (Schnurr et al., 2002; Costello et al., 2003; Vapalahti et al., 2003; Ostfeld, 2013). The role of MYs in wood production, i.e. resource allocation to seeds rather than to wood, is controversial as studies on this topic have yielded differing results. For common beech, Eichhorn et al. (2008) and Drobyshev et al. (2010) found a decrease in stem increment, whereas in oak species and Scots pine, no impact on stem increment could be found (oak species: Askeyev et al., 2005; Pérez-Ramos et al., 2010; Alla et al., 2012; Martin et al., 2015; Lebourgeois et al., 2018; pine: Martínez-Alonso et al., 2007).

The main theories discussed today describing mechanisms leading to mast seeding consist of ultimate and proximate theories (Pearse et al., 2016). The most common ultimate hypotheses are the predator satiation hypothesis, the pollination efficiency hypothesis and the environmental prediction hypothesis which all involve some aspect of economy of scale (Kelly, 1994; Pearse et al., 2016). The predator satiation hypothesis suggests that the survival rate for seeds is enhanced by surplus production and that distribution of fruits increases through the attraction of scatter-hoarding seed dispersers (Janzen, 1971; Kelly, 1994; Kon et al., 2005a; Vander Wall, 2010; Pearse et al., 2016). The pollination efficiency (or pollen coupling) hypothesis describes the advantage of coordinated flowering years in self-incompatible tree species at stand to regional scale to augment wind pollination success (Kelly, 1994; Crone and Rapp, 2014, Pearse et al., 2016). An extension of the pollination efficiency hypothesis is the concept of phenology synchrony which enables pollen coupling in the first place (Bogdziewicz

et al., 2017a). The environmental prediction hypothesis states that after wildfires the plant populations which immediately produce high amounts of seeds have a higher survival rate. This last hypothesis applies primarily to herbaceous plant species in fire-prone regions, whereas woody plants produce serotinous fruits which release seeds after wildfires (Kelly, 1994; Pearse et al., 2016).

In contrast, proximate hypotheses describe the drivers and preconditions for the occurrence of MYs. Factors studied include the influence of weather conditions both in the sensitive phases of bud meristem and primordia development in the years prior to a MY, as well as during the florescence period. Furthermore, nutritional conditions and fruit and seed production in preceding years are investigated to better understand concepts of resource dynamics.

The influence of weather on masting has recently been discussed by Pearse et al. (2016) who suggest that species perform either flowering masting or fruit maturation masting. The first strategy requires weather cues which lead to the generation of next-year flower buds in the year before the masting event while the latter requires distinct weather conditions during the flowering period to synchronise pollination and lead to fruit production. Geburek et al. (2012) investigated pollen production in several Austrian wind-pollinated tree species and found that there are two types of pollen producers: masting pollen producers and non-masting pollen producers. The first type produces high amounts of pollen only prior to a masting event, while the latter produces pollen every year and only masts when the pollination period of an individual is synchronised by benevolent weather conditions.

Nutritional conditions and fruit and seed production in the preceding years are discussed in concepts of resource dynamics such as resource matching, resource depletion or resource switching (Crone and Rapp, 2014; Pearse et al., 2016). The resource matching hypothesis states that MYs occur when environmental conditions are favourable and resources are available, and thus growth and reproduction in individual trees would be positively correlated. Synchrony occurs due to spatially consistent weather cues (Kelly, 1994; Pearse et al., 2016). The resource depletion hypothesis describes the occurrence of MYs through accumulation and storage of resources which will lead to a MY once a specific threshold is reached and that MYs are spatially synchronised through environmental factors such as large-scale weather conditions. According to this hypothesis, mast seeding will lead to resource depletion and then the specific threshold needing to be reached again through resource accumulation; therefore, subsequent MYs are less probable (Janzen, 1971; Hacket-Pain et al., 2015; Pearse et al., 2016). In the resource switching hypothesis it is assumed that trees annually invest a steady amount of resources which are reallocated from growth to reproduction when weather conditions are favourable for flowering (Kelly, 1994; Pearse et al., 2016). As a consequence, the resource depletion hypothesis would demand low fruiting levels in the year before a MY whereas the resource matching and resource switching hypotheses prescribe no influence of fruiting levels in previous years on MY occurrence. These concepts were tested in recent studies for

different species using resource budget models which involve both resource and environmentally related parameters (Isagi et al., 1997; Satake and Iwasa, 2000; Masaka and Maguchi, 2001; Monks and Kelly, 2006; Crone and Rapp, 2014; Abe et al., 2016; Pearse et al., 2016; Pesendorfer et al., 2016; Venner et al., 2016; Bogdziewicz et al., 2018).

In recent studies on proximate mechanisms, masting behaviour was found to differ between forest tree species of the family *Fagaceae*. For *Fagus sylvatica*, Lebourgeois et al. (2018) found that the production of high seed volumes depends on temperature in the two years prior to the MY, and Bogdziewicz et al. (2017a,b) found that pollen abundance and subsequent MYs show a significant correlation. At the same time, growth was low in MYs in these studies (Lebourgeois et al., 2018) which supports the resource switching hypothesis. The findings of Bogdziewicz et al. (2017a,b) suggest that beech is a mast flowering species, i.e. flowering will ultimately lead to mast seeding. In contrast to beech, two *Quercus* species (*Quercus petraea* and *Q. robur*) showed high seed production after short but intensive pollination seasons and were dependent on high spring temperatures to synchronise flowering, thus supporting the pollination coupling and phenology synchrony hypotheses (Pesendorfer et al., 2016; Bogdziewicz et al., 2017a,b; Lebourgeois et al., 2018). For oak species, unfavourable weather conditions during the flowering season can act as a veto for fruit production (Bogdziewicz et al., 2017a,b; Lebourgeois et al., 2018) and can consequently lead to asynchronous flowering, preventing a MY (Pesendorfer et al., 2016). Furthermore, growth and seed production correlated positively in *Q. petraea* and *Q. robur* which supports the resource matching hypothesis.

To understand the future challenges in forest management with respect to natural regeneration strategies, it is crucial to understand the factors influencing mast patterns in forest tree species, especially in populations at their natural limits which are most susceptible to regional extinction, e.g. in Mediterranean or alpine climates (Pérez-Ramos et al., 2010; Fernández-Martínez et al., 2012). For beech, Övergaard et al. (2007) and Paar et al. (2011) showed that in recent years MYs have occurred more frequently in southern Sweden and Germany and therefore proposed an impact of changing temperature and precipitation patterns as a result of climate change. Hilton and Packham (2003), however, could not find a significant impact of

climate change on MY occurrence in their study of a 200-year long record of beech MYs from different Northwestern European countries. Two more recent studies on long-term data series did not support the assumption that MY frequency is increasing but rather showed that periods with more and less frequent MYs are common over the last few centuries (Drobyshev et al., 2014; Ascoli et al., 2017). Furthermore, in a recent pan-European study changes in MY frequency were found to be inconsistent between different regions for four tree species groups (Nussbaumer et al., 2016).

Several studies investigating the impact of weather variables (weather cues) on the occurrence of MYs in a multitude of species (Sork et al., 1993; Smaill et al., 2011; Kelly et al., 2013; Pearse et al., 2013; Koenig and Knops, 2014; Holland and James, 2015; Moreira et al., 2015; Bisi et al., 2016; Monks et al., 2016). Kelly et al. (2013) found the difference in summer temperature between the two previous years triggered a MY, rather than absolute temperature, and they concluded that as such climate change may not affect MY frequency. Other studies, however, found weather conditions in years prior to MYs, but not temperature differences between years, to be a main driver for mast occurrence (Moreira et al., 2015; Smaill et al., 2011; Monks et al., 2016; Pearse et al., 2014; Bisi et al., 2016; but see Holland and James, 2015) indicating that climate change can have an impact on MY frequency. A weather phenomenon investigated for its impact on MYs is the North Atlantic Oscillation (NAO) which influences macro-weather situations. Ascoli et al. (2017) and Fernández-Martínez et al. (2016) found that some of these macro-weather conditions lead to mast synchronisation in *Fagus sylvatica* and *Picea abies* in parts of Europe.

Europe is topographically diverse and shows a huge variety of climates in a relatively small area. In the last two decades many studies have been published which investigate weather impact on mast events for several European tree species (Table 1). However, there are no previous studies that investigate weather influence on MYs using harmonised methods for several forest tree species at a continental scale across the same time period.

In this study we investigate the impact of specific weather conditions as environmental drivers for MYs and the associated resource dynamics in the main European forest tree species: common beech (= beech, *Fagus sylvatica* L.); sessile and pedunculate oak (= oak

Table 1
List of recent studies on weather cues concerning mast years in European forest tree species. Abbreviations see abbreviation key.

Species	Region	Weather cue	Effect	Reference
Fagus sylvatica	Europe	NAO	Various	Ascoli et al. (2017)
Fagus sylvatica	Poland	Warm summer (lag1)	Positive	Bogdziewicz et al. (2017b)
Fagus sylvatica	Southern Sweden	Cold summer (lag2), warm summer (lag1)	Positive	Drobyshev et al. (2010, 2014)
Fagus sylvatica	France, Germany, Luxembourg	NAO	Various	Fernández-Martínez et al. (2016)
Fagus sylvatica	Southern England	Cold summer (lag2), warm summer (lag1)	Positive	Hacket-Pain et al. (2015)
Fagus sylvatica	Poland	Warm summer (lag1) and dry spring (lag0)	Positive	Kasprzyk et al. (2014)
Fagus sylvatica	France	Cold summer (lag2), warm summer (lag1)	Positive	Lebourgeois et al. (2018)
Fagus sylvatica	Germany	Warm (and dry) summer (lag1)	Positive	Müller-Haubold et al. (2013, 2015)
Fagus sylvatica	Europe	Cold summer (lag2), warm and dry summer (lag1)	Positive	Piovesan and Adams (2001)
Fagus sylvatica	Europe	Cold summer (lag2), warm summer (lag1)	Positive	Vacchiano et al. (2017)
Quercus ilex	Southern France	Drought	Negative	Pérez-Ramos et al. (2010)
Quercus ilex, Q. pubescens	North-eastern Spain	Water stress	Negative	Fernández-Martínez et al. (2012)
Quercus petraea	France, Germany, Luxembourg	NAO	Various	Fernández-Martínez et al. (2016)
Quercus petraea, Q. robur	Poland	Warm spring (lag0)	Positive	Bogdziewicz et al. (2017b)
Quercus petraea, Q. robur	France	Warm spring (lag0)	positive	Lebourgeois et al. (2018)
Quercus robur	France, Germany, Luxembourg	NAO	Various	Fernández-Martínez et al. (2016)
Quercus robur	Poland	Wet summer (lag1) and wet spring (lag0)	Positive	Kasprzyk et al. (2014)
Quercus robur	Poland	Wet spring (lag0)	Negative	Wesolowski et al. (2015)
Picea abies	Europe	NAO	Various	Ascoli et al. (2017)
Picea abies	Alps	Cold summer (lag2), warm summer (lag1)	Positive	Bisi et al. (2016)
Picea abies	Southern Sweden	Cold summer (lag2), warm summer (lag1), no spring frost (lag0), dry	Positive	Selås et al. (2002)
Picea abies	Norway	Warm (and dry) summer (lag1)	Positive	Solberg (2004)
Picea abies	Poland	Wet spring (lag0)	Not significant	Wesolowski et al. (2015)
Pinus sylvestris	Alps	Unclear	Unclear	Bisi et al. (2016)
Pinus sylvestris	Catalonia (Spain)	Drought	Negative	Vilà-Cabrera et al. (2014)

species, *Quercus petraea* (MATT.) LIEBL. and *Q. robur* L.); Norway spruce (=spruce, *Picea abies* (L.) KARST.) and Scots pine (=pine, *Pinus sylvestris* L.). We investigate these relationships at a European scale and further explore whether these findings hold across regional scales. We used the collaborative database of the crown condition survey carried out with harmonized methods (UNECE ICP Forests PCC (ed.), 2016) in the frame of the International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests) under the auspices of the UNECE Convention on Long-Range Transboundary Air. This survey includes pan-European annual assessments of various parameters concerning tree health and vitality, e.g. defoliation and fruiting intensity, and is conducted based on harmonised methods (Eichhorn et al., 2016).

The main objective of this study was to identify possible weather cues triggering MY occurrence in the five forest tree species at a continental scale and at regional scale within Europe. Furthermore, fruiting levels in former years were used to address the topic of resource dynamics assuming that fruiting levels in years prior to MYs must be low, as suggested by the resource depletion hypothesis. Although resource levels were not directly measured, fruiting levels can be used as a proxy for resource conditions on tree level. We hypothesise that

(i) there are typical weather conditions leading to MYs in our target species;
(ii) weather cues have a spatially consistent impact on MY occurrence for each species at a continental scale;
(iii) MYs occur only after years with low or no fruit production.

To test these hypotheses we used three beta regression models with seasonal weather conditions and fruiting levels from two years prior to MYs up to the MY for Europe as well as for European countries and ecoregions to analyse whether the same models apply to subsets of the European dataset.

2. Material and methods

2.1. ICP Forests plot networks

In this study, we analysed data on fruiting intensity at tree level (FR_{tree}) measured within the crown condition survey on the ICP Forests Level I and Level II plot network (Eichhorn et al., 2016). The ICP Forests Level I plots are arranged across the whole of Europe on a systematic 16×16 km^2 grid (extensive forest monitoring), whilst Level II plots represent typical forest ecosystems of each country and are therefore not systematically spatially distributed (intensive forest monitoring, UNECE ICP Forests PCC (ed.), 2016). The crown condition survey is carried out on identifiable trees that were selected based on temporally persistent criteria (minimal stem diameter, predominant/ dominant tree, sub-plot area, etc.). The dataset includes sites with oceanic, Mediterranean, temperate and continental climates, along with the alpine regions of the Pyrenees, the Alps, the Carpathians and the Borealic uplands. The geographical extent of this dataset covers the latitudinal and longitudinal range of Europe from 10° W to 30° E and 40° to 70° N and has an altitudinal range from 0 m above sea level (a.s.l.) up to the timberline (approx. 1600–2300 m a.s.l.) (Fig. 1). Mean annual temperatures of the analysed plots range from about −6 °C to 10 °C, and annual precipitation sums range from about 300 to 3100 mm.
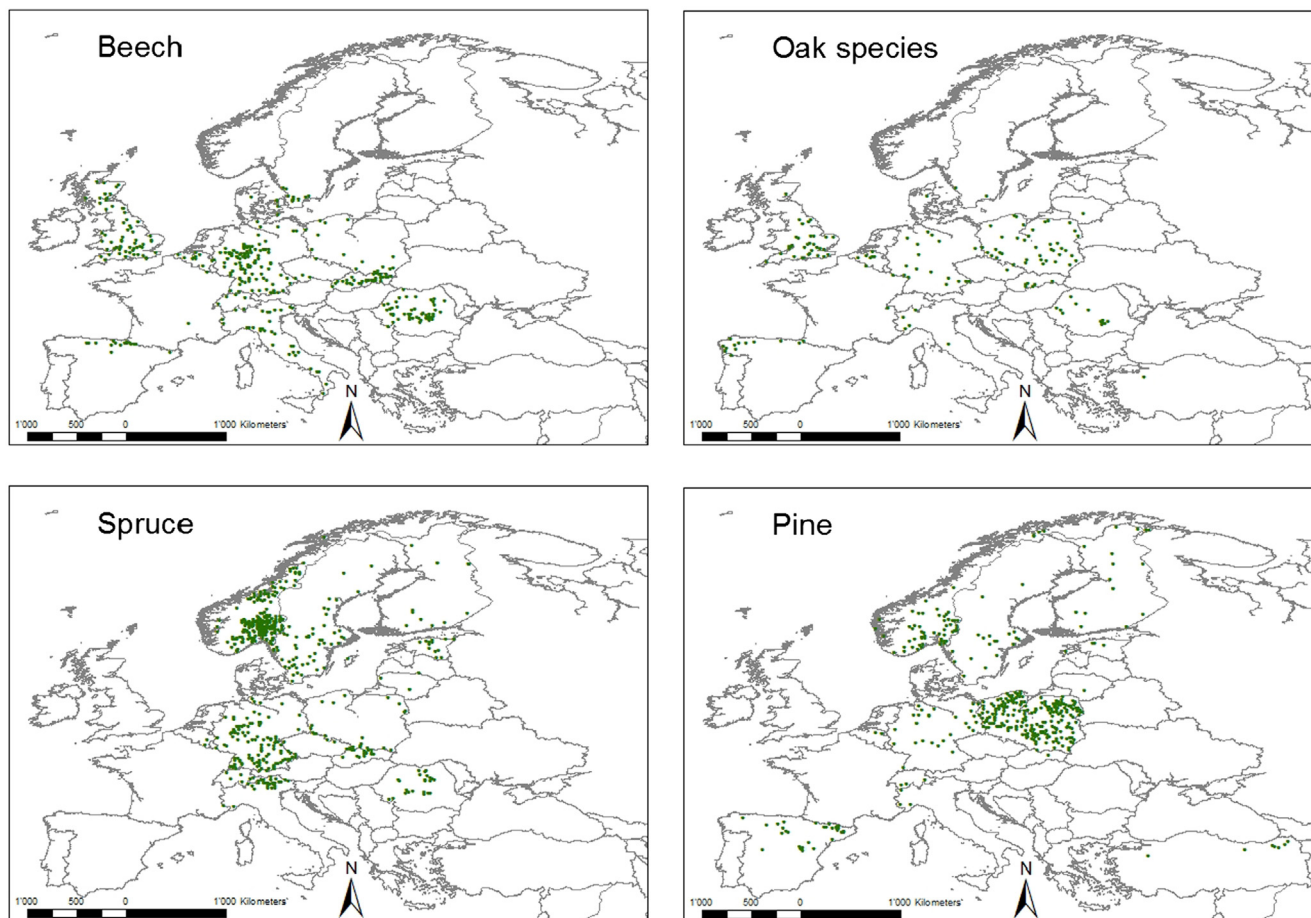

Fig. 1. Plot distribution for each of the analysed tree species. Only plots with a combination of high and low fruiting intensity, a minimum of three years of measurements and of five trees per species are shown.

2.2. Observation method and determination of fruiting intensity

The ICP Forests crown condition survey includes several parameters describing tree vitality, e.g. defoliation, damage, and fruiting, and is carried out according to harmonised methods (Eichhorn et al., 2016). Parameters are assessed annually for all selected trees during the growing season by trained field workers. The long-term quality as well as the cross-country comparability of the assessments is ensured by quality assurance and quality control procedures (Eichhorn et al., 2016).

For the assessment of FR$_{tree}$, we used the qualitative parameter 'fruiting' from the crown condition survey, which is based on a visual assessment and ranking of the fruit occurrence into 'absent', 'scarce', 'common', or 'abundant' (Eichhorn et al., 2016). For beech, the oak species and spruce, the assessed fruits (acorns, beech nuts, cones) develop following flowering in the spring of the same year. For pine, however, the green cones that are assessed in the survey originate from flowering in spring of the preceding year, therefore FR$_{tree}$ was assigned to this previous year.

Absent and scarce fruiting were combined into one category for our study due to differences in the assessment methods in the past. The ranking levels were thus encoded into the following three categories: 0 = absent or scarce fruiting, 0.5 = common fruiting, 1 = abundant fruiting. The average fruiting intensity (fr0) per plot per year for each species was calculated resulting in continuous values between 0 and 1. For each species, only plots with a minimum of five individuals, at least three years of observation and varying fr0 levels were included in the analysis. The time spans of included plot data ranged from three to 25 years (Tables 2 and A1).

2.3. Meteorological and regional data

Daily mean temperature and precipitation sums for each plot were extracted from the nearest grid point of the gridded meteorological observation E-OBS dataset (Version 10.0) of the European Climate Assessment and Dataset (ECA&D) with a spatial resolution of 0.25° (Haylock et al., 2008). These temperature and precipitation values were then averaged and summed, respectively, to derive (i) deviations from seasonal mean temperatures and (ii) deviations from seasonal precipitation sums from the long-term mean of 1996–2015. We defined the seasons 'spring' as April and May and 'summer' as June and July. We calculated the deviations from the seasonal mean temperatures and precipitation sums for the summer two years (*lag2*) and one year (*lag1*) prior to the fruiting assessment as well as for the spring of the actual assessment year (*lag0*). These definitions of the relevant vegetation periods are in accordance with previous studies (see Table 1). Additionally, we calculated the difference in deviations of mean summer temperatures (ΔT) as proposed by Kelly et al. (2013) using

$$\Delta T = t1 - t2$$

where t1 is the deviation of mean summer temperature of *lag1* and t2 the deviation of mean summer temperature of *lag2*.

Hence, positive values of ΔT describe a summer in *lag2* that was colder than the summer in *lag1*.

We grouped the plots at three spatial scales with (i) Europe and the two region types (ii) countries and (iii) ecoregions (according to the European Environment Agency EEA, Fig. A1) as classes. Only classes with a minimum of eight plots were analysed. Plots from countries which did not meet these conditions were integrated in the analyses at a European and/or ecoregional scale. A total of 1434 plots from 18 countries were analysed at the European, country or ecoregional scale (Tables 2 and A1; Fig. A1).

2.4. Statistical analyses

To investigate the influence of weather conditions on MY occurrence we applied beta regression models using the betareg package (Cribari-Neto and Zeileis, 2010) implemented in R (R Core Team, 2016). After checking for multicollinearity with the variance inflation factor VIF (VIF < 5) we included six weather variables within the models: deviations from long-term mean values of summer mean temperatures for *lag2* and *lag1* (t2, t1), of summer precipitation sums for *lag2* and *lag1* (p2, p1), of spring mean temperatures of *lag0* (t0) and of spring precipitation sums of *lag0* (p0). Furthermore, we included the fruiting levels of *lag2* and *lag1* (fr2, fr1) since the proximate theories explained in the introduction (e.g. resource depletion hypothesis) postulate that they influence MY occurrence (Crone and Rapp, 2014; Pearse et al., 2016).

The **basic model** included all weather variables, fr1 and fr2:

$$fr0 = fr1 + fr2 + t0 + t1 + t2 + p0 + p1 + p2 + \varepsilon \quad (1)$$

where ε is the error term to be minimised.

This model was extended with an interaction term between fr1 and t1 (hereafter **interaction model**) to include a resource-limited floral induction model introduced by Isagi et al. (1997) and further developed by Monks et al. (2016). These models are able to capture the dependence between internal resource state and external triggers such as specific weather conditions during bud development and have been proved to fit well for different wind-pollinated species (Monks et al., 2016; Bogdziewicz et al., 2017b).

$$fr0 = fr2 + t0 + t2 + p0 + p1 + p2 + fr1 \times t1 + \varepsilon \quad (2)$$

To test the **ΔT model** from Kelly et al. (2013) which assumes that temperature differences between years rather than absolute temperatures are important, we replaced t2 and t1 with ΔT:

$$fr0 = fr1 + fr2 + t0 + \Delta T + p0 + p1 + p2 + \varepsilon \quad (3)$$

All three models were tested for each species group for the whole dataset, for countries and for ecoregions. The models were fitted to data averaged over plot and year for a certain species or species group and a spatial extent. Only plots with three or more measured years were included. We used the corrected Akaike information criterion (AIC$_C$, Burnham and Anderson, 2002) to define the best fitting model of each type (basic, interaction and ΔT) using the R function 'dredge' from the MuMIn package (Barton, 2017) which calculates all possible models extracted from the full models. Models containing a maximum of five

Table 2
Number of studied plots (Level I and II) and data time range per species group and country included in at least one of the analyses. Only plots with varying FR$_{tree}$ and a minimum of three years of measurements and of five trees per species are included.

Country	No of beech plots	No of oak plots	No of spruce plots	No of pine plots	Time span
Belgium	12	7	2	2	2006–2014
Britain	64	36			1991–2007
Czechia	3	1	4		2009–2011
Denmark	4	1			2011–2015
Estonia			13	4	1996–2012
Finland			12	15	2004–2014
France	1				2009–2015
Germany	117	18	129	27	2000–2015
Italy	32	4	28	3	2006–2014
Lithuania		1	4	1	2008–2014
Norway			221	61	1997–2012
Poland	18	40	22	222	2010–2015
Romania	49	12	23		2011–2015
Slovakia	30	6	16	1	2009–2015
Spain	16	13		29	2004–2014
Sweden	9	2	55	19	2003–2013
Switzerland	6	2	6	3	2008–2014
Turkey		1		7	2009–2015
Total	361	144	535	394	1991–2015

predictors were compared and only classes with a minimum of 50 measurements were analysed to avoid over-fitting due to the high number of predictors. The best of the three model types per region and species was determined by the difference between the AIC$_C$ (ΔAIC$_C$) as well as the pseudo R^2 according to Cribari-Neto and Zeileis (2010). The pseudo R^2 computes the squared correlation between the linear predictor for the mean and the link-transformed response. The resulting best fitting models of each model type were tested for significant difference using the R function 'lrtest' from the lmtest package (Zeileis and Hothorn, 2002). The regions are subsets of the dataset used for the continental analysis and are assumed to be independent with the exception of the influence of NAO (Ascoli et al., 2017; Fernández-Martínez et al., 2016). Therefore, no further explicit validation has been performed.

The two oak species were analysed as a single species group for the following reasons: (i) fruit volumes produced in MYs for each species were tested and found to have similar quantities using data from the litterfall dataset of the ICP Forests (Nussbaumer et al., in preparation, collection technique see Pitman, 2013); (ii) recent studies on mast behaviour in *Quercus petraea* and *Q. robur* including pollen loads analysed these species as one species group since pollen cannot be determined on species level (Bogdziewicz et al., 2017b, Lebourgeois et al., 2018); (iii) these species regularly hybridise and therefore, in mixed forest stands, determination at the species level can be challenging (Muir et al., 2000).

3. Results

3.1. Common beech

For common beech, eight countries and seven ecoregions were analysed (Tables 3 and A3). There was no significant difference in performance between the best fitting basic and interaction models, and in six cases also the ΔT model, for Europe and in almost all regions. The exception being Germany where the ΔT model fitted significantly better than the two other models (Table A2). The model for Europe included the parameters fruiting level in *lag2* (fr2), spring temperatures in *lag0* (t0), summer temperatures in *lag1* and *lag2* (t1, t2) and summer

precipitation sums in *lag1* (p1). These parameters also fitted well in the region-wise evaluation. In the model for Europe, the coefficients for fr2, t1 and t0 were positive and those for t2 and p1 negative. The signature of the coefficients was also consistent for most of the weather cues in the regions with a few exceptions typically in regions where no model achieved a relatively high pseudo R^2 (> 0.5). The only weather cue with inconsistent signature of the coefficients was spring precipitation sums in *lag0* (p0) where the coefficients were positive in Poland, Spain and the Alps, and negative in Belgium, Italy and the central plains. The most important parameters were t2 which showed a significant negative impact in all regions with the exceptions of Belgium, Italy and the central plains, and fr2 which showed a positive impact on MY in ten regions, as well as t0 which was significantly positive in nine regions, but negative in Italy. Fruiting level one year before a MY (fr1) was the least important parameter with positive coefficients only in Poland, Romania and subsequently the Carpathians. Overall, the most prominent pattern of weather cues could be found to be similar across differing scales in Europe with low summer temperatures (and high precipitation sums) two years before a MY, low precipitation sums, often coupled with high temperatures in the summer before the MY, and high spring temperatures during the MY.

3.2. Oak species

For pedunculate and sessile oak, only five countries and two ecoregions were analysed (Tables 4 and A4). In six regions, none of the best fitting models was significantly different from the others, but on the eastern plains, the interaction model fitted best, and for Europe, the basic and the interaction model fitted significantly better than the ΔT model (Table A2). The pseudo R^2 achieved were generally lower than for beech. The best fitting model for Europe included fruiting levels in both *lag2* and *lag1* (fr2, fr1) and the weather cues summer temperatures in *lag2* (t2), summer precipitation sums in *lag1* (p1) and spring temperatures in *lag0* (t0). The parameters fr1, fr2, p1 and t0 had positive coefficients, whereas t2 had a negative coefficient. Although the oak dataset was spatially clustered, the two parameters fr1 and t0 were important in four and five regions, respectively, and showed the same signature as for Europe. The other parameters mostly showed no

Table 3

Most important parameters (p < 0.05) of the beta regression analyses for the **beech** regions. obs. = number of observations per region, best fit: best model type, orange = significant negative effect, purple = significant positive effect, blank = effect not significant, grey: parameter not part of the model. Abbreviations of the tested parameters see abbreviation key.

Region	obs.	fr2	p2	t2	fr1	p1	t1	p0	t0	inter	ΔT	pseudo R^2	best fit
Europe	2702											0.3892	basic / interaction
Belgium	70											0.5042	none
Britain	900											0.4853	basic / interaction
Germany	855											0.5678	ΔT
Italy	187											0.2955	basic / interaction
Poland	89											0.4542	basic / interaction
Romania	234											0.2096	basic / interaction
Slovakia	176											0.5255	none
Spain	94											0.3854	none
Alps	80											0.397	basic / interaction
Carpathians	370											0.1744	none
Central highlands	631											0.5629	basic / interaction
Central plains	261											0.5596	none
Hungarian lowlands	55											0.4248	basic / interaction
Western highlands	61											0.6588	basic / interaction
Western plains	68											0.4885	none

Table 4

Most important parameters ($p < 0.05$) of the beta regression analyses for the **oak** regions. obs. = number of observations per region, best fit: best model type, orange = significant negative effect, purple = significant positive effect, blank = effect not significant, grey: parameter not part of the model. Abbreviations of the tested parameters see abbreviation key.

Region	obs.	fr2	p2	t2	fr1	p1	t1	p0	t0	inter	pseudo R^2	best fit
Europe	**1090**	purple		orange	purple	purple			purple	grey	0.0662	basic / interaction
Britain	519	purple			purple			orange	purple	grey	0.1027	none
Germany	97			orange				orange		grey	0.0999	none
Poland	200				purple	orange	orange	purple		grey	0.273	none
Romania	59								orange	grey	0.1224	none
Spain	75	purple	purple	orange	purple			purple		grey	0.2207	none
Central plains	171		orange	orange	purple	orange		purple		grey	0.4034	none
Eastern plains	75			purple	purple		orange	purple		orange	0.1878	interaction

consistent signatures or were only important in a few regions. Summer precipitation sums in *lag2* (p2) was only important in two regions and the other two parameters from *lag2*, fr2 and t2, as well as summer temperatures in *lag1* (t1), were only important in three regions. Another important parameter for the regions was spring precipitation sums in *lag0* (p0) but signatures were positive in three regions, whereas in Britain and Germany the coefficient was negative. For Romania, only t0 was significant.

3.3. Norway spruce

For Norway spruce, nine countries and seven ecoregions were analysed (Tables 5 and A5). In eight regions, either the best fitting basic and interaction models or all three model types did not differ significantly. For Europe, Germany and the Fenno-Scandian shield, the interaction model showed the significantly best fit and in five regions, the ΔT model fitted significantly better than the other two models (Table A2). The best fitting model for Europe achieved only a low pseudo $R^2 = 0.179$ whereas on regional scale pseudo R^2 of typically 0.19 to 0.41 and up to 0.77 (Sweden) were reached. This best model for Europe included summer precipitation sums and fruiting levels in *lag1* (p1, fr1), summer temperatures in *lag1* and *lag2* (t1, t2) and the interaction term. t2, p1 and the interaction term had negative coefficients,

whereas fr1 and t1 had positive ones. The most important parameters overall were t2, t1 (or ΔT), and summer precipitation sums in *lag2* (p2) and p1, all of which showed consistent signatures with negative coefficients except for t1. Although p2 was not important at a continental scale, on a regional scale a combination of low p2 and t2 were important in most of northern Europe (Norway, Sweden, Borealic uplands) as well as in the Carpathians and the central highlands and plains. For many other countries and ecoregions one of the two parameters was important but, as an exception, coefficients for p2 were positive in the Alps and in the western highlands. Weather cues in *lag0*, i.e. t0 and p0, showed inconsistent signatures, as did fruiting level in *lag1* (fr1). The latter was important in three quarters of the regions, but signatures of the coefficients were positive and negative in six regions each. Fruiting level in *lag2* (fr2) was the least important parameter and was significantly high in only five regions. Overall, the dominant weather pattern leading to MYs was low summer temperatures and often low precipitation sums two years before the MY, and high summer temperatures, coupled with low precipitation sums one year before the MY. The main differences to the results for beech were the differing importance of precipitation regimes in *lag2*, the inconsistent impact of temperatures in *lag0* on MY occurrence for spruce and the low importance of fr2.

Table 5

Most important parameters ($p < 0.05$) of the beta regression analyses for the **spruce** regions. obs. = number of observations per region, best fit: best model type, orange = significant negative effect, purple = significant positive effect, blank = effect not significant, grey: parameter not part of the model. Abbreviations of the tested parameters see abbreviation key.

Region	obs.	fr2	p2	t2	fr1	p1	t1	p0	t0	inter	ΔT	pseudo R^2	best fit
Europe	3645			orange	purple	orange	purple			grey	grey	0.179	interaction
Estonia	200	purple		orange	purple	orange	purple			grey	grey	0.2601	basic / interaction
Finland	76			grey	orange	grey	purple			grey	orange	0.355	ΔT
Germany	897		orange	purple			orange		orange	purple	grey	0.361	interaction
Italy	166	purple		orange	purple					grey	grey	0.2922	basic / interaction
Norway	1775		orange	orange	purple	orange		orange		grey	orange	0.1948	ΔT
Poland	100		orange	orange	purple	purple		purple		grey	grey	0.2218	basic / interaction
Romania	109	purple		orange		orange				grey	grey	0.1997	none
Slovakia	92		orange	orange	purple	orange		purple		grey	grey	0.2822	basic / interaction
Sweden	165		orange	orange	purple	orange	purple			grey	grey	0.7722	basic / interaction
Alps	205	purple	purple	orange	purple			purple		grey	grey	0.2927	basic / interaction
Borealic uplands	1477		orange	orange		orange		orange		grey	orange	0.1915	ΔT
Carpathians	232		orange	orange	purple	orange				grey	orange	0.1486	ΔT
Central highlands	768		orange	orange	purple	purple	purple		orange	grey	grey	0.3446	basic / interaction
Central plains	361	purple	orange	orange			orange		orange	grey	orange	0.2041	ΔT
Fenno-Scandian shield	301		orange	orange	purple		orange		orange	grey	grey	0.409	interaction
Western highlands	55		purple	purple	purple		orange			grey	grey	0.331	none

Table 6

Most important parameters (p < 0.05) of the beta regression analyses for the **pine** regions. obs. = number of observations per region, best fit: best model type, orange = significant negative effect, purple = significant positive effect, blank = effect not significant, grey: parameter not part of the model. Abbreviations of the tested parameters see abbreviation key.

Region	obs.	fr2	p2	t2	fr1	p1	t1	p0	t0	inter	pseudo R²	best fit
Europe	2284	purple		orange	purple			purple	purple	grey	0.1308	basic / interaction
Finland	78				purple		purple		orange	purple	0.1781	interaction
Germany	173		purple		purple		purple			grey	0.2035	none
Norway	573	purple		orange	purple		purple		orange	grey	0.0976	basic / interaction
Poland	1095				purple	orange	orange	purple	purple	grey	0.3038	basic / interaction
Spain	173				purple	purple	purple		orange	grey	0.1971	basic / interaction
Borealic uplands	418		purple		purple				orange	grey	0.1114	none
Central plains	895		orange		purple	orange	orange	purple		grey	0.5361	basic / interaction
Eastern plains	419	purple			purple			orange		grey	0.1956	none
Fenno-Scandian shield	168		purple		purple			purple	purple	grey	0.2462	none

3.4. Scots pine

For Scots pine, five countries and four ecoregions were analysed (Tables 6 and A6). The best models generally achieved lower pseudo R^2 values than the other species. The basic and interaction model fitted similarly well at the European level and in four regions, whereas the interaction model fitted best for Finland (Table A2). In four regions, there was no significant difference between the best fitting model types. For pine, the temporal components of the parameters correspond to the year with respect to flowering, but not to cone production (see Section 2.2). The best fitting model for mast occurrence in Europe included the parameters fruiting levels in *lag1* and *lag2* (fr1, fr2), summer temperatures in *lag2* (t2) and spring temperatures and precipitation sums in *lag0* (p0, t0), all of which had positive coefficients with the exception of t2. Furthermore fr1 was an important parameter in all regions with consistent signatures. The two most important weather cues were t0 and summer temperatures in *lag1* (t1) but both showed inconsistent signatures. t0 had positive coefficients (as in the European model) in Poland, the central plains and the Fenno-Scandian shield, and negative coefficients in Finland, Norway, Spain and the Borealic uplands, whereas t1 showed opposite signatures in these regions except for the Fenno-Scandian shield where t1 was not important. All other parameters were only important in a few regions. There was no overall prominent weather pattern for pine and the only consistent and important parameter was fr1.

4. Discussion

4.1. Model evaluation

No significant difference could be found between either the basic or the interaction model or between all three model types for all species in most regions. In only few cases for the oak species, spruce and pine did the interaction model fit significantly better than the other two model types. However, for spruce in five regions and beech in one region the ΔT model was significantly better fitting than the basic or the interaction model. Our findings therefore partly support the suggestion by Kelly et al. (2013) that the difference in summer temperatures in the two years prior to the MY has a stronger impact than the separate summer temperature conditions. However, this could only be found in one out of four species groups. This weak support is in accordance with other studies which found the ΔT model fitted less well than the interaction model (Monks et al., 2016; Bogdziewicz et al., 2017b).

4.2. Common beech

Common beech showed a clear connection between seed production and weather conditions in the previous years. Our findings for common beech i.e. that MYs are triggered by low summer temperatures with high precipitation sums two years before the MY and a warm and dry summer before the MY are in accordance with several studies within European regions and at a continental scale (Piovesan and Adams, 2001; Müller-Haubold et al., 2013; Drobyshev et al., 2014; Hacket-Pain et al., 2015; Müller-Haubold et al., 2015; Ascoli et al., 2017; Vacchiano et al., 2017). We also included spring weather conditions in our analyses which are important for pollination. We found that high temperatures during the pollination season were favourable at both the continental and regional scale, which is in accordance with previous studies for Japanese *F. crenata* (Kon et al., 2005b, 2007; Abe et al., 2016). In our dataset, when considering the ecoregional and country scale, the best fitting model was not the same for the regions as at the continental scale, although the most important weather parameters were still similar for both scales.

Concerning fruiting levels in previous years, there was no evidence for the resource depletion hypothesis as fruiting level in the year before a MY was not an important parameter in most of the regions. The lack of negative correlations could be due to carbon for fruit production not being stored in beech as found by Hoch et al. (2013). High fruiting levels two years before a MY were important at a continental scale as well as in ten regions which may support a basic 2-year fruiting cycle, as first suggested by Matthews (1955). However, the observed patterns could also be an effect of a recently observed cumulation of beech MYs in Western Europe (MYs: 2006, 2009, 2011, 2013, see Nussbaumer et al., 2016), and little support is found in the literature for a 2-year fruiting cycle in beech.

4.3. Oak species

In contrast to the findings in common beech, best fitting models for the oak species at continental and regional scale were rather diverse. The best fitting model for Europe showed that high spring temperature in the MY was the most important weather cue which was also reflected at the regional scale. This finding is in accordance with recent studies by Bogdziewicz et al. (2017a,b, 2018) and Lebourgeois et al. (2018) and can be explained as a synchronising mechanism which leads to concentrated pollination, supporting the pollen efficiency hypothesis.

At the same time, fruiting levels in the year before MYs were high at continental scale as well as in four out of seven regions which shows

that resource depletion does not apply for these species. This has also been demonstrated for *Quercus robur* in Poland by Wesolowski et al. (2015), although for the American oak species *Quercus lobata,* Pearse et al. (2014) found that resource depletion is present. Corresponding with our findings, Hoch et al. (2013) found no evidence of resource accumulation before seed production in *Quercus petraea* which supports the concept of resource matching. Previous studies have suggested that *Quercus* species show resource matching since during MYs stem growth is still enhanced (Askeyev et al., 2005; Pérez-Ramos et al., 2010; Alla et al., 2012; Martin et al., 2015; Lebourgeois et al., 2018). However, in our study we did not include growth parameters and therefore could not assess this theory. Aside from the two most prominent factors: high spring temperatures in the MY and high fruiting levels before the MY, the models showed large variation concerning the most important parameters between the regions. This would indicate that a single common theory might not suffice to explain MYs in oaks.

4.4. Norway spruce

Of the coniferous species, weather cues for Norway spruce were much more consistent than for Scots pine at the continental and the regional scale. Similar to common beech, the best fitting models for Norway spruce included summer temperature conditions in the two years before a MY (cold summer two years before and warm summer one year before the MY). However, in contrast to beech, summer precipitation sums were low in both two and one year prior to the MY. Our results are generally in accordance with Selås et al. (2002) and Solberg (2004) for southern Scandinavia, who found that a warm and dry summer leads to high fruiting intensity in the following year. The pattern of cold summer two years and warm summer one year before a MY could again be seen in Selås et al. (2002) and in Bisi et al. (2016) in the Alps. In contrast to the deciduous species in our study, weather conditions in spring of the MY were not consistent and even within adjacent regions there were often differences in the direction of the impact.

Fruiting level in the year prior to MYs showed both low and high levels in different regions, and fruiting level two years prior to the MY was only important in five regions. Spruce does not show signs of resource depletion after MYs in six out of 16 regions, including the Alps and Italy. This is supported by the findings of Bisi et al. (2016) who did not see a resource depletion effect in their study carried out in the Italian Alps. However, in six other regions, including Fenno-Scandian regions, significantly low fruiting levels in the year before a MY could be found and here, the resource depletion hypothesis is supported.

4.5. Scots pine

The best fitting models for Scots pine were the most diverse of all investigated species. In accordance with previous findings, where low precipitation rates were the strongest weather impact for inhibiting high fruiting years (Martínez-Alonso et al., 2007; Vilà-Cabrera et al., 2014), high precipitation sums in the summer before the MY was an important weather cue in Spain. The lack of common weather parameters might be a result of the atypical fruiting pattern of pine with almost no years with total absence of fruits and seeds. The same effect was found in a recent study by Bisi et al. (2016) who could not find a strong annual difference in cone production in various *Pinus* species (*P. cembra, P. mugo, P. sylvestris*). Accordingly, neither Broome et al. (2007) in Britain nor Kantorowicz (2000) in Poland were able to detect any years with a total absence of Scots pine cone production between 1951 and 1999. Pine does not follow the bimodal fruiting pattern as supposed in previous studies (Kelly, 1994; Herrera et al., 1998) and therefore, it is

important to recognise that this species may use different survival strategies with regard to climate change than species where MYs are triggered by distinct weather cues.

Fruiting levels in both years prior to the MY were high at the continental scale, which was reflected well at the regional scale for fruiting level in the year before a MY. This is again in contrast to the resource depletion hypothesis (Janzen, 1971; Hacket-Pain et al., 2015) but could also be a result of the afore-mentioned atypical fruiting behaviour. Overall, models for pine were diverse and no similarities, besides the abundantly high fruiting level in the summer previous to the MY, could be found for adjacent regions.

4.6. Masting strategies

Comparing the weather patterns leading to mast events of the investigated species reveals that the most important weather cues include summer weather conditions in the two years before the MY (beech, spruce), followed by spring weather conditions in the MY (all species). The general findings for beech and spruce agree with the results of several previous studies on these species (see Table 1). In our study, the main difference between these two species is the summer precipitation sum two years before a MY which is usually high for beech but low for spruce. The clear weather cues for beech support the findings by Bogdziewicz et al. (2017a,b) and Lebourgeois et al. (2018) that beech is a flowering masting species and will produce fruits once flowering is initiated. Due to similarly clear weather cues for spruce, it can be assumed that this species has similar masting mechanisms to beech, also supporting the definition of beech and spruce as masting pollen producers by Geburek et al. (2012). In contrast, oak species are described as fruit maturation masting species and non-masting pollen producers (Geburek et al., 2012; Pearse et al., 2016). Pine is also categorised as a non-masting pollen producer by Geburek et al. (2012) but as this species does not show typical mast behaviour it remains unclear if this species is also a fruit maturation masting species like the oak species.

5. Conclusions

Our study based on European-wide forest monitoring data showed that mast fruiting in the main forest tree species is significantly influenced by weather conditions in the previous years. However, these weather cues were only spatially consistent for beech and, to a lower extent for spruce across the regions of Europe. The most distinct weather cues for beech were a cold summer two years before a MY, a dry and warm summer in the following year, followed by a warm spring in the MY. The most distinct weather cues for MYs in spruce were a cold and dry summer two years prior to a MY, and a cold spring and warm summer in the year before the MY. In contrast to these findings for beech and spruce, only one weather precondition for MY occurrence could be found for oak species for some regions: high spring temperatures in the MY, which is thought to lead to pollen coupling (Bogdziewicz et al., 2017b; Lebourgeois et al., 2018). All other weather variables showed inconsistent or weak influence on MYs in the oak species. This may be an effect of the joint analysis of two oak species and should be further investigated. In our dataset however, the number of observations was relatively small and in mixed forest stands, identification of the species was not always possible. For pine all models had a relatively poor fit confirming that the definition of MYs might not be appropriate to describe seeding behaviour of pines at all since *Pinus* species do not show a typical pattern of high and low level fruiting years (Bisi et al., 2016; Nussbaumer et al., 2016). Indication of resource depletion after MYs i.e. a significant negative effect of intensive fruiting in the previous year (Janzen, 1971; Hacket-Pain et al., 2015; Pearse

et al., 2016), was only present in six regions for spruce. In our study the validity of this concept seems to be limited to this species. Other concepts of resource dynamics such as resource matching or resource switching might be better suited to explain the impact of fruiting levels in the years before the MY in these species but with our data, the applicability of these hypotheses could not be investigated. Our study reveals that for some species (Scots pine and to a lesser amount oak species) distinct weather cues cannot easily be found and we recommend care when spatially extrapolating these results. Our findings suggest that weather conditions during sensitive phases concerning seed production vary between forest tree species. The similarity of our results to studies investigating flowering and pollen production indicate that beech and spruce could be flowering masting species and masting pollen producers whereas the results for the oak species suggest that they might be fruit maturation masting species and non-masting pollen producers (Geburek et al., 2012; Pearse et al., 2016). Despite the differences between species and also partially at the temporal and spatial scale, this study provides a strong large-scale basis for further in-depth investigation of mast behaviour and the underlying mechanisms for the main forest tree species across Europe.

Acknowledgement
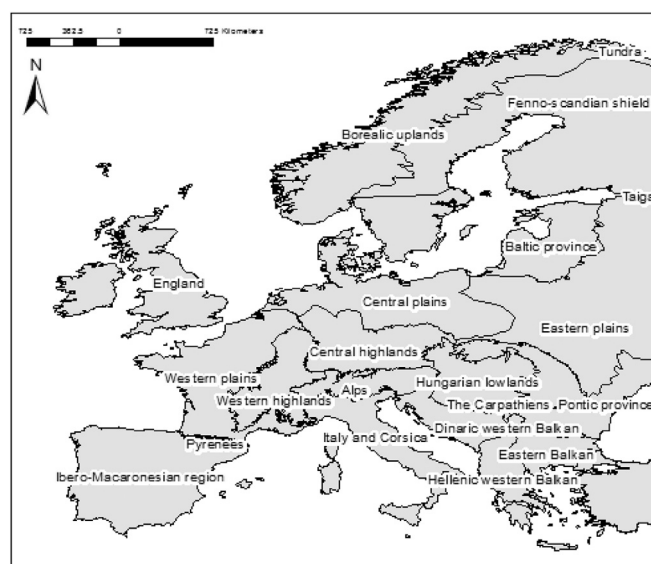
Appendix A

See Fig. A1 and Tables A1–A6.

Fig. A1. Eco-regions according to the European Environment Agency (EEA).

Table A1
Fruiting level parameters: minimum (min), maximum (max), median, and temporal range: minimum year (min) and maximum year (max) per tree species included in the analysis. n plots = number of plots.

Country	Beech						Oak						Spruce						Pine					
	Fruiting level			Temporal range		n plots	Fruiting level			Temporal range		n plots	Fruiting level			Temporal range		n plots	Fruiting level			Temporal range		n plots
	Min	Max	Median	Min	Max		Min	Max	Median	Min	Max		Min	Max	Median	Min	Max		Min	Max	Median	Min	Max	
Belgium	0.00	0.64	0.10	2006	2014	12	0.00	0.36	0.00	2006	2014	7	0.00	0.26	0.03	2008	2014	2	0.44	0.52	0.48	2010	2014	2
Czechia	0.00	0.75	0.04	2009	2011	3	0.00	0.50	0.00	2009	2011	1	0.00	0.44	0.07	2009	2011	4						
Denmark	0.00	0.54	0.12	2011	2015	4	0.00	0.25	0.07	2011	2015	1												
Estonia													0.00	0.80	0.00	1997	2012	13	0.00	0.94	0.25	1996	2011	4
Finland													0.00	0.81	0.08	2005	2014	12	0.01	0.82	0.40	2004	2013	15
France	0.00	0.92	0.00	2009	2015	1																		
Germany	0.00	1.00	0.00	2001	2015	117	0.00	0.58	0.00	2001	2015	18	0.00	1.00	0.00	2001	2015	129	0.00	0.75	0.15	2000	2014	27
Great Britain	0.00	1.00	0.13	1991	2006	64	0.00	0.98	0.01	1991	2007	36												
Italy	0.00	1.00	0.00	2009	2015	32	0.00	0.78	0.11	2009	2015	4	0.00	0.94	0.12	2009	2015	28	0.00	0.69	0.37	2008	2014	3
Lithuania							0.03	0.33	0.09	2009	2014	1	0.00	0.64	0.02	2009	2014	4	0.38	0.40	0.38	2008	2013	1
Norway													0.00	1.00	0.00	1997	2012	221	0.00	1.00	0.20	1997	2011	61
Poland	0.00	1.00	0.08	2011	2015	18	0.00	1.00	0.00	2011	2015	40	0.00	1.00	0.20	2011	2015	22	0.00	1.00	0.47	2010	2014	222
Romania	0.00	1.00	0.00	2011	2015	49	0.00	0.50	0.08	2011	2015	12	0.00	0.60	0.03	2011	2015	23						
Slovakia	0.00	0.83	0.05	2010	2015	30	0.00	0.59	0.02	2010	2015	6	0.00	0.80	0.03	2010	2015	16	0.00	0.33	0.04	2009	2014	1
Spain	0.00	0.81	0.06	2009	2014	16	0.00	0.50	0.21	2004	2014	13							0.00	0.80	0.32	2008	2013	29
Sweden	0.00	0.96	0.15	2004	2006	9	0.00	0.08	0.00	2004	2006	2	0.00	0.93	0.02	2004	2013	55	0.15	0.94	0.58	2003	2005	19
Switzerland	0.00	0.77	0.26	2009	2014	6	0.00	0.25	0.07	2009	2014	2	0.00	0.55	0.18	2009	2014	6	0.12	0.71	0.34	2008	2013	3
Turkey							0.00	0.29	0.00	2011	2015	1							0.00	0.98	0.14	2009	2014	7

Table A2

Pseudo R^2 and difference in corrected Akaike's Information criterion (ΔAIC$_C$) between models of the tested beta regression models and best fitting model per species and region (none = model types showed no significant difference ($p < 0.05$), basic/interaction = no significant difference between these model types). If ΔAIC of a model is blank, AIC$_C$ is the lowest of the three models. Model description see Section 2.4.

Species	Region	Best model	Pseudo R^2			ΔAICc		
			Basic	ΔT	Interaction	Basic	ΔT	Interaction
Beech	Europe	Basic/interaction	0.3892	0.3685	0.3892		57.35	
Beech	Belgium	None	0.5042	0.5042	0.5042			
Beech	Britain	Basic/interaction	0.4853	0.4852	0.4853	0.90		0.90
Beech	Germany	ΔT	0.5520	0.5678	0.5520		21.56	
Beech	Italy	Basic/interaction	0.2955	0.2891	0.2955	1.51		1.51
Beech	Poland	Basic/interaction	0.4542	0.4239	0.4542		3.62	
Beech	Romania	Basic/interaction	0.2096	0.1461	0.2096		7.58	
Beech	Slovakia	None	0.5255	0.5096	0.5255		0.49	
Beech	Spain	None	0.3854	0.3671	0.3854	0.99		0.99
Beech	Alps	Basic/interaction	0.3970	0.3097	0.3970		2.17	
Beech	Carpathians	None	0.1744	0.1699	0.1744	0.62		0.62
Beech	Central highlands	Basic/interaction	0.5561	0.5550	0.5629		16.15	
Beech	Central plains	None	0.5694	0.5596	0.5561		4.26	
Beech	Hungarian lowlands	Basic/interaction	0.4248	0.3746	0.4248		6.10	
Beech	Western highlands	Basic/interaction	0.6415	0.5696	0.6588		7.17	
Beech	Western plains	None	0.4885	0.4885	0.4885			
Oak	Europe	Basic/interaction	0.0662	0.0573	0.0662		6.83	
Oak	Britain	None	0.1007	0.1027	0.1007	1.90		1.90
Oak	Germany	None	0.0999	0.0884	0.0999	1.35		1.35
Oak	Poland	None	0.2730	0.2327	0.2730		1.25	
Oak	Romania	None	0.1224	0.1224	0.1224			
Oak	Spain	None	0.2207	0.1921	0.2207	0.67		0.67
Oak	Eastern plains	None	0.4034	0.4034	0.4034			
Oak	Western plains	Interaction	0.1515	0.1515	0.1878	0.56	0.56	
Spruce	Europe	Interaction	0.1750	0.1770	0.1790	17.29	11.34	
Spruce	Estonia	Basic/interaction	0.2601	0.1906	0.2601		4.80	
Spruce	Finland	ΔT	0.3510	0.3550	0.3510		2.40	
Spruce	Germany	Interaction	0.3492	0.3602	0.3610	8.68		6.25
Spruce	Italy	Basic/interaction	0.2922	0.2825	0.2922		2.06	
Spruce	Norway	ΔT	0.1898	0.1948	0.1898	4.08		4.08
Spruce	Poland	Basic/interaction	0.2218	0.1314	0.2218		3.58	
Spruce	Romania	None	0.1985	0.1997	0.1985	2.05		2.05
Spruce	Slovakia	Basic/interaction	0.2822	0.2487	0.2822		0.13	
Spruce	Sweden	Basic/interaction	0.7722	0.7325	0.7722		36.24	
Spruce	Alps	Basic/interaction	0.2927	0.2478	0.2927		13.88	
Spruce	Borealic uplands	ΔT	0.1885	0.1915	0.1902	4.15	2.16	
Spruce	Carpathians	ΔT	0.1310	0.1486	0.1310	3.47		3.47
Spruce	Central highlands	Basic/interaction	0.3446	0.3431	0.3446	3.70		3.70
Spruce	Fenno-Scandian Shield	ΔT	0.2041	0.2124	0.2041	2.40		3.70
Spruce	Western highlands	Interaction	0.3839	0.3858	0.4090	1.47	0.98	
Spruce	Western plains	None	0.3304	0.3310	0.3304	1.98		1.98
Pine	Europe	Basic/interaction	0.1308	0.1301	0.1308		1.43	
Pine	Finland	Interaction	0.0940	0.0583	0.1781	4.31	7.14	
Pine	Germany	None	0.2035	0.2035	0.2035			
Pine	Norway	Basic/interaction	0.0976	0.0972	0.0976	1.55		1.55
Pine	Poland	Basic/interaction	0.3038	0.2636	0.3038		80.78	
Pine	Spain	Basic/interaction	0.1971	0.1775	0.1971		4.49	
Pine	Borealic uplands	None	0.1090	0.1114	0.1090		1.87	
Pine	Eastern plains	Basic/interaction	0.5361	0.4524	0.5361		89.87	
Pine	Fenno-Scandian Shield	None	0.1779	0.1779	0.1956	0.97	0.97	
Pine	Western plains	None	0.2462	0.2462	0.2462			

Table A3
Coefficients of the most important parameters (p < 0.05) from the beta regression analyses for the **beech** regions. obs. = number of observations per region, best fitting model per species and region (none = model types showed no significant difference, basic/interaction = no significant difference between these model types). Abbreviations of the tested parameters see abbreviation key.

Region	obs.	fr2	p2	t2	fr1	p1	t1	p0	t0	ΔT	best fit
Europe	2702	0.2364		−0.7032		−0.2456	0.3326		0.2905		basic/interaction
Belgium	70	0.5687	0.4445					−0.6674			none
Britain	900	0.5101	0.1041	−0.6969		−0.1840	0.6255				basic/interaction
Germany	855	0.1540	0.2449			−0.3043			0.2747	−0.3272	ΔT
Italy	187		0.9862					−0.1376	−1.0694		basic/interaction
Poland	89	0.1858		−0.6590	0.4318			0.6139	0.8597		basic/interaction
Romania	234	0.1228		−0.5903	0.2347	−0.1757			0.4350		basic/interaction
Slovakia	176	0.2229	0.2687	−1.1642			1.0267				none
Spain	94		−0.3084	−1.3602			0.9911	0.7480	0.7388		none
Alps	80			−1.1169		−0.3087		0.2821	0.8871		basic/interaction
Carpathians	370	0.1754		−0.6860	0.1810		0.3618		0.2738		none
Central highlands	631	0.1412	0.1692	−0.3984		−0.2882			0.5124		basic/interaction
Central plains	261	0.6183	0.2806			−0.2682		−0.4825			none
Hungarian lowlands	55	0.4502		−0.9403			0.3121				basic/interaction
Western highlands	61			−0.7127		−0.2975			1.0371		basic/interaction
Western plains	68		0.2340	−0.4055		−0.3254			0.3480		none

Table A4
Coefficients of the most important parameters (p < 0.05) from the beta regression analyses for the **oak** regions. obs. = number of observations per region, best fitting model per species and region (none = model types showed no significant difference, basic/interaction = no significant difference between these model types). Abbreviations of the tested parameters see abbreviation key.

Region	obs.	fr2	p2	t2	fr1	p1	t1	p0	t0	Inter	Best fit
Europe	1090	0.14697		−0.10576	0.09067	0.05859			0.14959		Basic/interaction
Britain	519	0.17149				0.09804		−0.11061	0.10042		None
Germany	97			−0.1871				−0.1702			None
Poland	200				0.3292	−0.2112	−0.2868	0.464	0.5713		None
Romania	59								0.3907		None
Spain	75	0.1902	0.22	−0.2657	0.3453		0.4548				None
Central plains	171		−0.4656		0.3807	−0.3238		0.3207	0.8623		None
Eastern plains	75				0.3153		−0.1437	0.4037	0.311	−0.2284	Interaction

Table A5
Coefficients of the most important parameters (p < 0.05) from the beta regression analyses for the **spruce** regions. obs. = number of observations per region, best fitting model per species and region (none = model types showed no significant difference, basic/interaction = no significant difference between these model types). Abbreviations of the tested parameters see abbreviation key.

Region	obs.	fr2	p2	t2	fr1	p1	t1	p0	t0	Inter	ΔT	Best fit
Europe	3645			−0.3012	−0.0002	−0.1119	0.3300			−0.1017		Interaction
Estonia	200	0.2833			0.1225	−0.2005	0.2432					Basic/interaction
Finland	76				−0.2752			0.3732			−0.2545	Δt
Germany	897			−0.2977	−0.1090		0.3334		0.2569	−0.1351		Interaction
Italy	166	0.2772		−0.9010	0.2546		0.7138					Basic/interaction
Norway	1775		−0.1646		−0.0836	−0.0892		−0.0501			−0.3299	Δt
Poland	100			−0.3726	0.3894	−0.2746		0.3477	0.4863			Basic/interaction
Romania	109	0.1603		−0.3093	0.2348	−0.2681	0.3667					None
Slovakia	92		−0.5185				0.6908	−0.3859	−0.6519			Basic/interaction
Sweden	165		−0.3058	−1.4092		−0.2240	0.2931	0.3011				Basic/interaction
Alps	205	0.2232	0.1844	−0.8244	0.1922				0.6924			Basic/interaction
Borealic uplands	1477		−0.1416		−0.0853	−0.0769		−0.0382			−0.3375	Δt
Carpathians	232		−0.2341		0.1509	−0.1726		−0.1588			−0.2413	Δt
Central highlands	768		−0.1003	−0.3721		−0.1490	0.2065		0.3570			Basic/interaction
Central plains	361	0.1049	−0.1800			−0.1084			−0.1222		−0.3400	Δt
Fenno-Scandian shield	301			−0.5726	−0.0793		0.7878			−0.3118		Interaction
Western highlands	55		0.1062	−0.4052	0.1672		0.3719		−0.1693			None

Table A6

Coefficients of the most important parameters (p < 0.05) from the beta regression analyses for the **pine** regions. obs. = number of observations per region, best fitting model per species and region (none = model types showed no significant difference, basic/interaction = no significant difference between these model types). Abbreviations of the tested parameters see abbreviation key.

Region	obs.	fr2	p2	t2	fr1	p1	t1	p0	t0	Inter	Best fit
Europe	2284	0.2112		−0.1633	0.3596			0.1991	0.2754		Basic/interaction
Finland	78				0.0498		0.2234		−0.1704	0.2854	Interaction
Germany	173		0.313		0.4142						None
Norway	573	0.0728		−0.115	0.2499		0.1727		−0.2171		Basic/interaction
Poland	1095				0.66086	−0.31016	−0.45152	0.34259	1.09059		Basic/interaction
Spain	173				0.4451	0.2383	0.4074		−0.3661		Basic/interaction
Borealic uplands	418		0.1273		0.2816		0.2551		−0.3587		None
Central plains	895		−0.4513		0.8762	−0.3348	−0.7204		1.7134		Basic/interaction
Eastern plains	419	0.2152			0.3799			−0.1397			None
Fenno-Scandian shield	168		0.2835		0.5405			0.5589	0.3146		None

Appendix B. Supplementary material

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.foreco.2018.07.011.

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