1	Inter-annual and decadal changes in teleconnections drive continental-scale synchronization of tree
2	reproduction
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35 Abstract

36	Climate teleconnections drive highly variable and synchronous seed production (masting) over large-scales.
37	Disentangling the effect of high-frequency (inter-annual variation) from low-frequency (decadal trends)
38	components of climate oscillations will improve our understanding of masting as an ecosystem process.
39	Using century-long observations on masting (the MASTREE database) and data on the Northern Atlantic
40	Oscillation (NAO), we show that in the last sixty years both high-frequency summer- and spring-NAO and
41	low-frequency winter NAO components are highly correlated to continent-wide masting in European beech
42	and Norway spruce. Relationships are weaker (non-stationary) in the early 20 th century. This finding
43	improves our understanding on how climate variation affects large-scale synchronization of tree masting.
44	Moreover, it supports the connection between proximate and ultimate causes of masting: indeed, large-
45	scale features of atmospheric circulation coherently drive cues and resources for masting, as well as its
46	evolutionary drivers, such as pollination efficiency, abundance of seed dispersers, and natural
47	disturbance regimes.
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53 Masting, the synchronous and highly variable production of seeds by a population of plants, may 54 periodically synchronize over large portions of a species distribution range¹⁻³, with major cascading effects 55 on ecosystems functioning⁴. Large-scale masting events rely on the spatial synchronization (Moran effect) of proximate mechanisms of masting (here after "proximate causes")⁵, such as those promoting resource 56 57 accumulation and floral induction in the previous one to two years, and cross-pollination in the mast year⁴. 58 Over longer timescales, several studies report periods with frequent large masting events that alternate with periods of rare masting, and attribute this fluctuation to decadal trends in broad climate patterns^{7,8}. 59 60 Indeed, the interplay of proximate causes leading to masting may occur at both annual and longer time scales, e.g. by increasing the sensitivity of trees to a flowering-inducing cue during extended periods of 61 higher resource availability due to a favourable climate trend^{4,5,6,9}. Disentangling the effects of climate 62 63 oscillations on masting at high- (inter-annual) versus low- (decadal) frequencies would therefore result in 64 an improved understanding of masting as an ecosystem process and its causes.

Teleconnections are broad climate patterns that produce spatially correlated weather conditions at both inter-annual and decadal time scales^{10,11}. Indices describing the phase of a teleconnected climate system integrate several weather variables¹², which makes them good candidates for explaining the large-scale synchronization of ecological processes¹³, including masting^{1,14,15}.

69 Several teleconnection indices were found to correlate to tree masting and its proximate causes, such as the El Niño Southern Oscillation in East Asia and Oceania^{1,2,16}, the North Pacific Index in North America¹⁴, 70 and the North Atlantic Oscillation in Europe^{8,15,17}. However, due to limitations of masting data in time 71 and/or space, none of these studies tested for the effect of the low-frequency component of the 72 73 teleconnection. Likewise, no assessment was made on whether the effects were consistent through time. In this paper, we take advantage of long-term masting observations (the MASTREE database)¹⁸, covering 74 75 most of the Fagus sylvatica L. (European beech) and Picea abies (L.) H. Karst (Norway spruce) distribution. 76 We used MASTREE to assess the effect of inter-annual and decadal variations of the North Atlantic 77 Oscillation (NAO) on large-scale masting in both species, and the stability of such effects through time.

Beech and spruce may display synchronized reproduction over a large portion of their distribution area^{3,15}. 78 79 Previous studies found a relationship between NAO and beech masting in some regions of Central-Northern 80 Europe, but uncertainties emerge regarding the timing and direction of this relationship (Table 1). Positive 81 NAO in the winter of the year prior to fruit ripening (Y_{M-1}) favoured beech masting in Southern England¹⁷. 82 Negative NAO in the summer two years before fruit ripening (Y_{M-2}), followed by a positive summer-NAO in year Y_{M-1} , enhanced beech masting in Southern Sweden⁸, while positive NAO in the spring during flowering 83 (Y_M) synchronized masting in Germany, France, and Luxemburg¹⁵. This final relationship is also reported for 84 spruce¹⁵. Hence, no strong evidence of a spatially and temporally consistent influence of NAO on beech and 85 86 spruce masting has emerged at the continental scale. We argue that inconsistencies in previous studies 87 arise from: a) failure to analyze the whole period during which climate affects proximate causes of masting in beech (three years from Y_{M-2} to Y_{M})³ and spruce (two years from Y_{M-1} to Y_{M})¹⁹, b) inability to test the 88 89 effects of decadal NAO components as a potential common influence on masting, c) disregarding that the 90 relationship between masting and NAO may have changed through time.

In order to get a broader understanding in the relationship between masting and NAO, we address the
following questions: 1) Do all NAO components reported as relevant for masting in previous studies (Table
1) exert a significant effect on beech and spruce synchronous seed production at the European scale? 2) Do
both inter-annual and decadal variations of NAO affect beech and spruce masting? 3) Are NAO-masting
relationships consistent with weather patterns known to determine masting in both species? 4) Are these
relationships stationary through time?

97 We show that in the last sixty years the inter-annual variation of NAO in summer and spring as well as 98 decadal trends in the winter NAO are highly correlated to continent-wide masting in beech and spruce. This 99 finding highlights the role of teleconnections in affecting large-scale synchronization of tree masting and 100 provides insights on its evolutionary drivers.

- 102 Results
- 103 Raw seasonal NAO indices vs masting index model

104 The large-scale masting index (M index) for beech in Central-Northern Europe (Supplementary Fig. 2, left) 105 displayed the highest values (above 95th percentile) in years 1773, 1811, 1846, 1858, 1869, 1888, 1900, 106 1909, 1918, 1926, 1948, 1958, 1995, 2006 and 2011. From 1950 to 2014, the spruce M index was 107 significantly correlated with the beech M_index (Pearson=0.58, p<0.001, two-sided test) and several 108 synchronized large-mast events were shared by both species (e.g. 1974, 1990, 1992, 1995, 2000, 2004, 109 2006, 2011) (Fig. 1). For both species, the period used for model building showed transitions between prolonged high (i.e. in early '50s, early '90s of the 20th century, and in 2010s) and prolonged low M index 110 111 (e.g. 1961 to 1986) (Fig. 1). Interestingly, this last period coincided with a reduced and non-significant 112 correlation between the two series (Pearson=0.35, p=0.12). 113 All the raw seasonal NAO indices tested separately and at a regional scale by previous studies (Table 1) 114 significantly affected beech masting when analysed simultaneously. The model explained a high portion of the variability of the beech M index between 1952 and 2015 at the sub-continental scale (pseudo- R^2 = 115 116 0.55, Supplementary Table 1). The summer-NAO Y_{M-2} was negatively correlated with M_index, while the 117 winter-NAO Y_{M-1} and summer-NAO Y_{M-1} , and the spring-NAO Y_{M} , correlated positively. The effect of the 118 autoregressive factor (AR1) was significant, with a negative effect (Supplementary Table 1). For spruce, only winter-NAO Y_{M-1} and the spring-NAO Y_M were significant and positively correlated to M index (pseudo-R² = 119

- 120 0.27, Supplementary Table 1).
- 121 Low-frequency domain of NAO and masting relationships

122 Wavelet analysis showed that all seasonal NAO indexes exhibited coherence with beech and spruce

- 123 masting at similar low-frequency domains, although relationships displayed a different level of significance
- 124 for different seasonal indices. In the second half of the 20th century, all winter-NAO indices (NOAA for 1950-
- 125 2015 Fig. 2A; Hurrell 1899-2015 Fig. 2B; Jones 1826-2015 Fig. 2C) showed significantly positive
- 126 coherence with beech masting in the frequency domain of 7 to 16 years. A similar wavelet coherence
- 127 existed between the winter-NAO using the NOAA index (1950-2015) and the spruce M_index

128 (Supplementary Fig. 5A).

129 Long-term analyses (>50 years) on beech data revealed that coherence between the beech M index and 130 winter-NAO varied through time. In the first half of the 20th century both the Hurrell (Fig. 2B) and the Jones 131 (Fig. 2C) indices did not show any significant coherence with M index, and only in the second half of the 19th century an in-phase influence of winter-NAO on the beech M_index emerged, again with a frequency 132 133 domain of 7 to 16 years (Fig. 2C). Summer-NAO and M index of both species were significantly coherent for 134 a short period around 1980 (Supplementary Fig. 5B and Supplementary Fig. 6A and 6C), but for beech the signal in the domain of 7 to 16 years remained throughout the 20th century (albeit weakly). Finally, a 135 136 significant coherence between spring-NAO and beech M index was found using both NOAA and Hurrell 137 indices since 1985 at frequencies of about 8 to 16 years, but this was mostly out of the cone of influence 138 (Supplementary Fig. 6B and 6D). For spruce, a coherence with spring-NAO remained weak around 11 years for the second half of the 20th century (Supplementary Fig. 5C). 139

Despite major differences in significance and stationarity between the winter-NAO and the summer- and spring-NAO, we opted for further testing of the low-frequency component of all seasonal NAO indices. In the final regression models, low frequency indices with a periodicity of 11 years (i.e. the midpoint between

143 7 and 16 years) were included for both species.

144 Inter-annual and decadal NAO vs masting index model

145 In the final model explaining the variability of beech and spruce M index, the high frequency (i.e. inter-146 annual) components of all seasonal NAO indices were significant (p<0.05, two-sided test), except winter-NAO Y_{M-1} for both species and the summer-NAO Y_{M-2} for spruce (Table 2). Conversely, among the low-147 148 frequency (i.e. decadal trends) components, only winter-NAO was significant (p<0.001) and displayed a 149 strong positive effect on both species. Of all two-way interactions, low-frequency winter-NAO x high-150 frequency summer-NAO Y_{M-1} was significant (p<0.05, beta = +0.24) in the beech model, but reduced the 151 model AIC by only 3 points (Table 1). The beech model accurately described (pseudo- R^2 =0.59) the observed 152 M_index between 1952 and 2015 (Fig. 2), correctly reproducing most individual peaks (e.g. 1960, 1995, 153 2000, 2014), and prolonged periods of high (e.g. 1989-1995) or low M index (e.g. 1961-1985). The spruce 154 model performed less well (pseudo-R²=0.42) and failed to reproduce some peaks (e.g. 1974, 1995, 2004,

155	2006, 2009). Models residuals generally showed no systematic bias and patterns (Supplementary Fig. 7),
156	except that the precision of the model increased for higher AR1. This is expected, as after high masting
157	there is often low masting, but the opposite is not the case. The leave-one-out cross validation (LOOCV)
158	was successful for beech (r=0.76) but less successful for spruce (r=0.48). However, both models accurately
159	captured the shift in the frequency of large-scale masting events that occurred around 1985, from a period
160	characterized by low M_index with relatively infrequent peaks, to a period of more regular large-scale
161	masting events with high M_index. However, residual patterns (Fig. 1 and Supplementary Fig. 7) and
162	LOOCV (Fig. 3) revealed that the model failed to predict the masting peak in 1958 for beech, highly
163	underestimated the peaks in 1974, 2004, and 2011 for both species, and highly overestimated the low
164	value in 1997.
165	NAO-masting relationships and weather patterns
166	The correlation between seasonal NAO indexes and temperature and precipitation anomalies in Central-
167	Northern Europe (Fig. 4) were consistent with weather patterns described in previous studies ^{10,12} . Positive
168	winter-NAO was correlated to positive anomalies in both temperature and precipitation. Positive spring-
169	NAO corresponded to mild temperatures and dry weather, while positive summer-NAO to positive
170	anomalies in temperature and negative anomalies in precipitation throughout Central-Northern Europe.
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172	Discussion
173	In this study, we provide the evidence of a long-term relationship between masting in trees and inter-
174	annual variation and decadal trends of a climate teleconnection. Several seasonal indices of NAO are jointly
175	responsible for synchronizing beech and spruce masting in Central-Northern Europe. While previous
176	studies ^{8,15,17} focused on specific seasonal NAO series and regions (Table 1), our results show that NAO acts
177	over multiple seasons and years synchronizing beech and spruce masting over a large part of their
178	distribution, extending from 44°N-3.5°W to 58°N-26°E and 46°N-3.5°W to 61°N-30°E for beech and spruce,
179	respectively. As a further step in comparison to previous studies, we tested the contribution of both the
180	high- (inter-annual) and low- (decadal) frequency components of seasonal NAO indices. The group of

181 significant high-frequency seasonal NAO predictors, and the direction of their influence, were consistent 182 with previous findings based on raw seasonal NAO series. Negative NAO in the summer two years before fruit ripening, followed by a positive summer-NAO in the subsequent year⁸ and by a positive spring-NAO 183 during flowering¹⁵, promotes beech masting. Spruce masting seems to be driven by the same high-184 185 frequency NAO components as for beech, except for a lack of influence of the summer two years before 186 fruit ripening. Masting intensity of the previous year had a negative effect on both beech and spruce 187 masting, which confirms that masting series display negative autocorrelation – indicative of resource depletion after large fruit crops^{4,5} – even at a sub-continental scale, such as in the widespread masting 188 failure in 1996, one year after the large masting event in 1995 (highlighted in Supplementary Fig. 1). Our 189 190 models failed to predict poor masting in 1997; such overprediction decreased when we included an 191 autoregressive term with a lag of -2 years in both models (-29% and -28% for beech and spruce, 192 respectively). This term had a negative significant effect (p<0.05, two-sided test) in both models, suggesting 193 a long-lasting resource depletion after the large mast of 1995. 194 Among low-frequency components, only winter-NAO was significant, but displayed a strong positive effect 195 on both beech and spruce masting in the frequency domain from 7 to 16 years. This shows that during 196 prolonged periods of positive winter NAO, the occurrence of widespread masting events on beech and 197 spruce increases. Although the model for beech performed better in comparison to the model for spruce, it 198 is notable that disentangling the high-frequency (i.e. inter-annual) and the low-frequency (i.e. decadal) NAO 199 components markedly improved the spruce model when compared to testing the raw NAO series (pseudo-200 R² of 0.42 vs. 0.27). 201 Many studies have discussed both the seasonal effects of NAO on Central-Northern European

weather^{10,11,12} and the effect of seasonal weather patterns on proximate causes of masting in the *Fagaceae*and *Pinaceae* families^{3,8,19,20,21,22}. Our results highlight the link between seasonal NAO and weather patterns
known to determine seed masting. Negative summer-NAO is associated with cool-wet summers in CentralNorthern Europe (Fig. 4, see also Folland *et al.*¹¹ and Bladé *et al.*¹²), a weather pattern strongly correlated
with beech masting when occurring two years before fruiting³, and commonly interpreted as increasing

available resources by enhancing litter mass loss and nutrient uptake due to high soil moisture^{20,23,24,25}. In 207 208 contrast, positive summer-NAO is associated with warm-dry summers in Central-Northern Europe (Fig. 4). This weather pattern is also correlated with both beech³ and spruce¹⁹ masting when occurring the year 209 before fruit ripening, as it induces hormonal translocation for flower primordial differentiation²¹. Finally, 210 211 positive spring-NAO is associated with mild-dry weather (Fig. 4), which favours wind pollination and the related fruit-set in the seed production year^{15,19,22}. With regards to the low-frequency component of winter-212 213 NAO, prolonged positive winter-NAO phases are associated with warm-wet winters (Fig. 4) with delayed positive effects on growing season temperatures²⁶. Positive NAO in winter causes an earlier leafing out of 214 beech in Central-Northern Europe²⁷, which lengthens the growing season. Moreover, positive winter-NAO 215 enhances the primary production of Central-Northern European forests^{28,29}, which is indicative of available 216 resources for reproduction in temperate trees³⁰. Consequently, we speculate that during prolonged 217 positive phases of the winter-NAO, such as in the early '50s and in '90s of the 20th century¹⁰, more 218 219 resources were consistently available for beech and spruce masting throughout Central-Northern Europe. 220 Finally, the positive and significant interaction between the high-frequency component of summer-NAO of 221 the year before masting and the low-frequency component of winter-NAO we found in the beech model 222 could be interpreted as a higher sensitivity of the species to high temperatures inducing flowering during periods of increased resources^{5,9}. However, the low Δ AIC of the interaction factor in the regression model, 223 224 and the fact the interaction was not significant in the spruce model, advocates caution in interpreting this result. Indeed, few previous studies found such interaction, either in *Fagaceae*²⁰ or in other taxonomic 225 groups³¹. In addition, in our study this interaction could be explained by a lagged effect of the winter-NAO 226 227 on summer temperatures. Previous studies report that summer heat waves in Central-Northern Europe are strong and wide-ranging when positive summer-NAO occurs in years of positive winter-NAO²⁶. For example, 228 229 this was the case in 1994 prior to the beech masting in 1995, the largest event in the period 1952-2015 (Fig. 230 1). Interestingly, model residuals for year 1995 were reduced by including the interaction factor among 231 predictors.

232 Whichever way this interaction is interpreted, our results show that seasonal and annual variations, and 233 decadal trends in the NAO affect both short- and long-term patterns of tree masting in Central-Northern 234 Europe, although these relationships are weak in some years and periods (i.e. non-stationary through time). 235 Indeed, the NAO is the leading climate mode in Europe, but the Euro-North Atlantic region is also 236 influenced by other large-scale atmospheric modes of variability, which oscillate at both inter-annual and 237 decadal time scales replacing NAO influence on European weather patterns. This could explain model 238 errors in given years, i.e., when the NAO-based models of both species had a lower explanative power (e.g. 239 1958, 2004). Here, weather patterns inducing masting might have been influenced by other broad-scale 240 climate modes, such as the Scandinavian Pattern or the East-Atlantic and West Russian pattern³², 241 particularly in summer. For example, the summer 1957 was characterized by a severe heat wave in Central-Northern Europe, with locally record-breaking temperatures³³. While, generally, positive summer-NAO 242 values are associated with high temperature in this region¹² (Fig. 4), the 1957 temperature positive 243 244 anomaly coincided with a below-average summer-NAO. The atmospheric patterns associated with the 245 1957-heatwave are instead attributed to two clusters of geopotential anomaly³⁴, a first extending over 246 most of the Scandinavian Peninsula and the second centred mostly over France and linked to the European summer blocking³⁵. Similarly, the heatwave in summer 2003 coincided with a low summer-NAO index, and 247 was attributed to tropical Atlantic forcing³⁵ in conjunction with a marked soil water deficit throughout the 248 249 European continent³⁶.

250 From 1850 to 1900 and from 1960 to 2000, decadal winter-NAO and beech masting showed a significant 251 coherence within a frequency domain of 7 to 16 years (Fig. 2), and a similar pattern was observed for the 252 spring-NAO after 1985 (Supplementary Fig. 6 right). However, even the low-frequency components of 253 winter- and spring-NAO were not always coherent with beech masting in the past two centuries. This is consistent with previous findings of a non-stationary influence of NAO over European weather patterns^{10,35} 254 and related ecological processes¹³. Our analyses confirm that in the long-term beech masting alternates 255 256 between periods of frequent large-scale events and periods when such events are rare, thus generalizing the results of a previous study in Sweden⁸. We suggest this could be partly due to variability in the strength 257

of NAO influence on the synchronization of weather patterns determining masting at the continental scale,
 which themselves appear to be largely stable through time³.

260 Although we showed a non-stationary influence of NAO on tree masting at both inter-annual and decadal 261 time scales, we also highlighted that NAO components have synchronized masting across Central-Northern 262 Europe for long periods. According to our interpretation, NAO synchronizes the proximate causes of 263 masting over large areas (Moran effect) at multiple stages of the reproductive cycle, such as resource 264 accumulation, flower differentiation, and cross-pollination. This raises the question of the ecological 265 meaning of the link between synchronous seed production and NAO patterns: is large-scale masting just a 266 coincidental consequence of NAO controlling proximate causes, or does such synchronization also provide 267 competitive advantages due to one or more economies of scale, hinting at the evolutionary factors of masting? Recently, Pearse *et al.*⁵ theorised a complementarity between proximate (i.e. mechanism driving 268 269 masting) and ultimate causes (i.e. evolutionary drivers) of masting. Several evolutionary hypotheses have 270 been proposed as ultimate causes of masting in beech and spruce, including: (i) pollination efficiency: 271 percent of seed set is higher in high-flowering years^{15,37}. (ii) Predator-dispersal: seed predators are attracted to a large fruit crop increasing dispersal-related fitness benefits^{38,39}, particularly by birds^{40,41}. (iii) 272 Environmental prediction: masting anticipates favourable conditions for seedling establishment^{19,42}. 273 Notably, seasonal NAO patterns identified by this and other studies^{8,15,17} are consistent with all these 274 275 ultimate causes. Influences of positive spring-NAO on the pollination efficiency were already discussed by Fernández-Martínez et al.¹⁵. Regarding the predator-dispersal hypothesis, some studies found a positive 276 277 relationship between winter-NAO and peaks in population dynamics of beech nuts dispersers such as Columba palumbus, Fringilla coelebs, Pica pica and Parus major^{43,44,45} and spruce dispersers such as 278 279 Carduelis spinus⁴⁶. Interestingly, a study in North America found that antiphased climate anomalies (i.e. 280 dipoles such as NAO) modulate consistently both broad-scale seed-eating bird irruptions and widespread masting¹⁴ resulting in birds anticipating the resource pulse, and this might be relevant also for beech and 281 282 spruce seed dispersers.

283 A coherent picture can also be set for the environmental prediction hypothesis, although this theory has 284 received less support, particularly when dealing with the prediction of future climate conditions favouring seedlings (e.g. wet seasons)⁴⁷. Many studies demonstrated beech and spruce recruitment failure after a 285 mast year because of thick litter or a closed tree canopy, typical of undisturbed stands^{48,49}. However, 286 regeneration is highly favoured in both species by mixed severity disturbances^{49,50,51}, particularly when 287 masting closely follows the disturbance^{52,53,54}. Notably, periods of positive winter-NAO are associated with 288 major damaging storms in Central-Northern Europe⁵⁵, while pressure patterns indicative of positive 289 summer-NAO favour drought^{10,26,35} and have been associated with fire activity in Southern Sweden⁵⁶ and 290 291 Southern England⁵⁷. Consequently, the teleconnection patterns that we show in this study to favour 292 masting may also be associated with disturbance events that create conditions favouring seedling 293 establishment. This is a different interpretation of the environmental prediction hypothesis, that does not require the prediction of future weather conditions criticised by previous studies⁴⁷. 294 After Pearse et al.⁵, we suggest a coherent ecological-evolutionary theory using teleconnections as a bridge 295 296 linking proximate and ultimate causes of masting. Previous studies used teleconnection indices to interpret the adaptive functioning of some ecological processes linked to climate oscillations¹³, and this was 297 proposed also for masting¹⁶. We do not imply that NAO has been the sole driver exerting a selective 298 299 pressure on tree masting in Central-Northern Europe, as we found a non-stationary link between NAO and 300 masting. Moreover, masting in the Fagaceae and Pinaceae families probably evolved before European 301 weather and NAO relationships established. However, alternating large-scale features of atmospheric 302 circulation with a significant impact on ecological and geophysical processes (e.g. resource cycles, animal 303 populations, natural disturbances) at any place and time might have exerted a selective pressure by 304 influencing both the proximate and ultimate causes of masting. Finally, our findings can improve the ability to predict masting based on NAO forecasts⁵⁸, particularly for 305 306 beech, assuming that the non-stationarity in the NAO-masting relationships can be taken in consideration. 307 To this extent, we suggest that studies linking climate change to tree masting should focus on how climate

308 change affects NAO patterns⁵⁹ and their relationships with proximate causes of masting.

309

310 Methods

311 Masting index

312 To analyse the response of beech and spruce masting at the sub-continental scale we computed an annual 313 masting index for both species representing how much of the species distribution range displays a heavy 314 seed crop in each year. We used the MASTREE database¹⁸ which contains the longest available masting 315 record for European beech and Norway spruce covering most of both species distribution and including 316 annually resolved observations of beech and spruce seed production or related proxies (e.g. flowering, 317 airborne pollen, fruiting, dendrochronological reconstruction). We truncated the data to 2015 and 2014, 318 and excluded the pollen and flowering proxies for beech and spruce respectively. We limited our analysis to 319 the Central-Northern European regions, i.e. the core area of beech and spruce distribution where climate is most influenced by NAO^{10,11,12}, and where all previous studies were focused (Table 1). In total, we selected 320 321 5774 yearly observations from 337 series in 40 NUTS-1 (Nomenclature of Territorial Units for Statistics) for 322 beech, and 5119 yearly observations from 191 series in 37 NUTS-1 for spruce (Supplementary Fig. 1). For 323 each series, we extracted the 5-class ordinal masting index (from 1: very poor, to 5: very abundant) 324 provided by MASTREE (column ORDmast). To avoid oversampling in regions with multiple data-series, we 325 aggregated individual masting series into NUTS-1 chronologies by using the modal masting class for each 326 year and NUTS-1. This produced long masting series with a minimum amount of missing data³. We then 327 computed the annual masting index (M index) for both species as the difference between the proportion 328 of NUTS-1 displaying a good masting (classes 4 and 5, NC-45) and a poor masting (classes 1 and 2, NC-12) in 329 any given year. M index varies from -1, when all NUTS-1 are in class 1 and 2 (broad masting failure), to +1 330 when all NUTS-1 are in masting classes 4 and 5 synchronously. Intermediate (zero) values indicate a 331 prevalence of class-3 masting, or a balanced distribution of NC-45 and NC-12 (Supplementary Fig. 1). 332 M_index was computed on a different number of NUTS-1 each year, but covered a continuous period from 333 1760 to 2015 and 1800 to 2014 for beech and spruce, respectively (Supplementary Fig. 2).

334 Raw seasonal NAO indices vs masting index model

335 To test at the sub-continental scale the consistency of NAO-mast correlations reported by previous studies 336 at the regional scale (Table 1), we built a regression model. The building of this initial model was limited to 337 1952-2015 and 1959-2014 for beech and spruce respectively, when NUTS-1 chronologies were numerous 338 (Supplementary Fig. 2), and evenly spread across the study area³. To build the predictors, we used the 339 monthly NAO series provided by the Climate Prediction Center of the National Oceanic and Atmospheric 340 Administration (NOAA), which covers the entire period of analysis (i.e. 1950-2015). As in previous studies 341 (Table 1), we computed raw seasonal NAO indices (i.e., without extracting high- and low-frequency 342 components) by averaging monthly values as follows: December of the previous year to March (winter-343 NAO), April to May (spring-NAO), June to September (summer-NAO). The shorter window for spring-NAO 344 was justified by the fact that beech and spruce flowering and pollination in Central-Northern Europe occur 345 mostly between April and May. We then fitted M index of both species as a function of summer-NAO Y_{M-2} , winter-NAO Y_{M-1} and summer-NAO Y_{M-1} , and spring-NAO Y_M . We accounted for the effect of resource 346 depletion by previous masting events^{4,5} by adding an autoregressive term with a lag of -1 year. All 347 348 predictors were standardized and checked for the absence of collinearity (pairwise Pearson correlation 349 <0.4). Since the response was beta-distributed for both beech and spruce (Supplementary Fig. 3 left 350 column), we rescaled M index from 0 to 1 and fitted a beta regression model via maximum likelihood using the R *betareg* package⁶⁰ for the R statistical framework. 351

352 Low-frequency domain of NAO and tree masting relationships

353 To test whether low-frequency changes in NAO influence beech and spruce masting, and to extract the 354 frequency domain of such relationship, we carried out a wavelet coherence analysis using the wtc function in the R package *biwavelet*⁶¹. Wavelet analysis has often been applied to test for causality between 355 teleconnections and geophysical processes⁶², and allows assessment of whether such relationships are 356 time-stationary across the frequency domain⁶³. To avoid bias due to non-normality⁶³, M index of both 357 species was arcsine-transformed⁶⁴ prior to the wavelet analysis (Supplementary Fig. 3 right column). 358 359 Wavelet analysis for spruce was limited to the period 1950-2014, as before 1950 there were too few data 360 to calculate M_index (Supplementary Fig. 2 right), while for beech we used data extending back to 1826

361 (Supplementary Fig. 2 left). From 1950 to 2015 we used seasonal NAO indices by NOAA aggregating months 362 as for the initial regression model. However, to extend the beech analysis before 1950 we used seasonal NAO indices provided by Hurrell¹⁰ and Jones *et al.*⁶⁴, which cover the periods 1899-2015 and 1826-2015. 363 364 respectively. The NOAA and Hurrell series are suited to test for coherence using all seasonal indices, because they are based on principal component analysis of sea level pressure over the North Atlantic⁶⁵. 365 366 Conversely, the Jones index is station-based (with fixed stations located in the Azores and Iceland), which makes it robust for winter NAO only¹². Consequently, the wavelet coherence analysis for 1826-1899 was 367 carried out on winter-NAO calculated from Jones et al.⁶⁴ only. 368 369 Each wavelet coherence analysis was computed using Morlet continuous wavelet transform and considering the lag -1 autocorrelation of each series⁶³. The data were padded with zeros at each end to 370 371 reduce wraparound effects. Significance of coherence within all frequency domains larger than five years 372 (i.e. low frequencies) was tested using a time-average test and 500 Monte Carlo randomizations. 373 High- and low-frequency NAO vs masting index model 374 To discriminate between low- and high-frequencies NAO components for the period 1952-2015, we fitted 375 each of the three raw seasonal NAO series (i.e. winter-, summer-, spring-NAO) with a running line smoother 376 using the "supsmu" function of the stats R package. The span of all smoothers was set to the mean 377 frequency domain at which wavelet coherence of raw seasonal NAO series against beech and spruce 378 masting was significant (considering all NAO data sources and seasons). The corresponding high-frequency 379 components were calculated by subtracting the smoothed series from the raw seasonal NAO index 380 (Supplementary Fig. 4). For the summer season, two high-frequency summer-NAO components were 381 calculated (i.e., for both Y_{M-2} and Y_{M-1}). We then fitted M_index as a function of the three low-frequency 382 components (winter-, summer-, spring-NAO), the four high-frequency components (summer-NAO Y_{M-2} , 383 winter-NAO Y_{M-1} , summer-NAO Y_{M-1} , spring-NAO Y_M), and an autoregressive term with a lag of -1 year. All 384 predictors were standardized and checked for collinearity (pairwise Pearson correlation <0.4). The period of 385 analysis was limited to 1952-2015 and 1959-2014 for beech and spruce, respectively; the response was

assumed to be beta-distributed, and the model was fitted via maximum likelihood using the *betareg* package for R⁶⁰.

388 When testing for interactions between all high- and low-frequency NAO predictors, we needed to limit

389 overfitting, due to the large number of possible bivariate interactions relative to the number of

390 observations. Following Quinn & Keough⁶⁶, we computed the residuals of the "null" model (without

391 interactions), and fitted them as a linear function of each possible two-way interaction among standardized

392 predictors. Only interactions producing a significant (p<0.05) fit against null model residuals were added to

the final model. The pseudo R-squared of the model was computed as the squared correlation between the

linear predictor for the mean and the link-transformed response⁶⁰.

395 We assessed the importance of each (standardized) predictor in the final model by calculating the

396 difference between the Aikaike's information criterion (AIC) of the models with and without the concerned

397 predictor (Δ AIC) – the higher Δ AIC, the larger the importance of the predictor in the model. The final model

398 was validated by leave-one-out cross validation.

399 NAO relationships with weather patterns determining masting

400 To test if NAO-masting relationships were coherent with weather patterns known to determine masting in

401 both beech and spruce^{3,19}, we analysed the correlation between significant NAO patterns, as in the final

402 regression model, and local weather anomalies. At each grid point of Europe, we computed the Spearman

403 correlation between seasonal NAO indexes and both precipitation and temperature series. Monthly

404 precipitation and temperature were obtained from the Climate Research Unit (CRU) database (version

405 TS4.00). CRU time series and the NAO series were aggregated to the periods DJFM (December-January-

406 February-March), AM (April-May) and JJAS (June-July-August-September) and linearly detrended. The

407 period between 1950 and 2015 was considered for the correlation analysis.

408 Data availability

409 The beech and spruce seed data that support the findings of this study are published in Ascoli et al.¹⁸, are

410 available on Ecological Archives (doi:10.1002/ecy.1785) and are accessible via the following link:

411 http://onlinelibrary.wiley.com/store/10.1002/ecy.1785/asset/supinfo/ecy1785-sup-0002-

- 412 DataS1.zip?v=1&s=2491b8cc559d5ec909f96dfc5a91397b1d7e9683 . NAO data from the Climate Prediction
- 413 Centre are available at:
- 414 <u>http://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/norm.nao.monthly.b5001.current.ascii.table;</u>
- 415 NAO data from Hurrell at the link:
- 416 <u>https://climatedataguide.ucar.edu/sites/default/files/nao_pc_monthly.txt;</u> NAO data from Jones at the
- 417 link: <u>https://crudata.uea.ac.uk/cru/data/nao/nao.dat;</u> CRU database (version TS4.00) is available at
- 418 <u>http://badc.nerc.ac.uk/data/cru/</u>.
- 419 *Code availability*
- 420 The R code used for analyses is provided as Supplementary material. We used R 3.3.1 version.

421	References
421	References

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572 End notes

- 573 Author contribution: D.A., A.H.P. and G.V. designed the research, analyzed the data and wrote the
- 574 manuscript; M.T. contributed to research design and interpreted weather data; I.D., M.C., J.M., and R.M.
- 575 contributed to research design and data interpretation.
- 576
- 577 **Competing interests:** The authors declare no competing financial interests.

579 Figures legends

580 Figure 1. Observed and predicted values of the masting indexes

- 581 Observed (blue line) and predicted (orange line) yearly values of M_index (scaled from 0 to 1) calculated for
- 582 Central and Northern Europe for beech (first row, 1950-2015) and spruce (second row, 1959-2014).
- 583 Predicted values estimated according to the final model in Table 2. Grey bars are the model residuals.

584 Figure 2. Wavelet coherence between the standardized beech M_index and winter-NAO indices

- 585 Wavelet coherence between the standardized beech M_index and winter-NAO indices. Winter-NAO indices
- 586 used: Climate Prediction Centre-NOAA (A), Hurrell¹⁰ (B) and Jones *et al.*⁶⁴ (C). X-axes: years of analysis. Y-
- 587 axes: frequency domain of the NAO-masting relationship in years. Note that the x- and y-axes vary between
- plots. Arrows pointing up-right show in-phase behavior and y leading x, i.e. NAO leading M_index. Black
- 589 contour designates frequencies of significant coherence (p<0.1, two-sided test); the white cone of influence
- 590 shows the data space immune from distortion by edge effects. The white squares show the period of strong
- 591 coherence between 1960 and 2000.

592 Figure 3. Leave one out cross validation

- 593 Observed and predicted values of beech (left) and spruce (right) M_index from the LOOCV of the final
- 594 model. The dashed line represents the perfect match between observed and predicted values. Years with
- the largest disparity are labelled individually.

596 Figure 4. NAO and related weather patterns in temperature and precipitation

597 Correlation between NAO and temperature anomalies (first row) and between NAO and precipitation

anomalies (second row) for the seasons winter, spring, summer (columns from left to right). Regions with

- 599 significant correlations are denoted by black dots. Monthly precipitation and temperature have been
- obtained from the CRU database (version TS4.00). We aggregated these time series into seasonal time-
- 601 series and the NAO indexes according to our experiment design: winter (December-January-February-
- March, DJFM), spring (April-May, AM) and summer (June-July-August-September, JJAS). The period
- 603 between 1950 and 2015 was considered for the correlation analysis. Figure created using ggplot2 package
- 604 for R⁶⁷.

605 Tables

Table 1. Previous findings on the relationship between NAO indices and beech and spruce masting

- 607 Previous findings on the relationship between seasonal NAO indices (winter-NAO; summer-NAO; spring-
- NAO) and beech and spruce masting in different European regions. Y_M : year of masting; Y_{M-1} and Y_{M-2} : one
- and two years before masting, respectively.

Year before masting	Year before masting YM-2		YM_1	YM	
Species Beech		Beech	Beech	Beech-Spruce	
NAO season	NAO season Summer		Summer	Spring	
Correlation sign NAO season vs. masting	Negative	Positive Positive		Positive	
NAO phase (- or +) and weather in Europe	Summer-NAO- Weather: Cool-Wet	r-NAO- Winter-NAO+ Summer-NAO+ r: Cool-Wet Weather: Warm-Wet Weather: Warm-Dry		Spring-NAO+ Weather: Warm-Dry	
Previous study	Drobyshev et al. 2014	Piovesan & Adams 2001	Drobyshev et al. 2014	Fernández-M. et al. 2016	
Geographical area	Southern Sweden	Southern England	Southern Sweden	France, Germany, Luxemburg	
Studied period	1871-2006	1981-1995	1871-2006	2002-2010	

611 Table 2. Final regression model

612 Summary of the final regression model predicting the inter-annual variability of M_index of beech (period

613 1952-2015) and spruce (period 1959-2014) using both high- and low-frequency NAO components.

614 Standardized coefficients are shown as model estimates (β) ± standard error (SE). ΔAIC indicates the

615 importance of the predictors and is calculated as the difference of AIC between the full model and the

616 model without the predictor of interest. Y_{M-2} and Y_{M-1} indicate two and one years before fruit ripening,

617 respectively, while Y_M the masting year. ns = non-significant predictors.

Species	European beech			Norway spruce				
Predictor	β	SE	p-value	ΔΑΙϹ	β	SE	p-value	ΔΑΙϹ
Autoregressive term								
AR1	-0.633	0.126	0.0001	-20.11	-0.266	0.129	0.0402	-1.72
High-frequency NAO								
high summer-NAO Y _{M-2}	-0.500	0.115	0.0001	-15.37	0.158	0.116	0.17 ns	0.14
high winter-NAO Y _{M-1}	0.174	0.104	0.10 ns	-0.73	0.152	0.110	0.17 ns	0.03
high summer-NAO Y _{M-1}	0.373	0.109	0.0006	-8.92	0.286	0.121	0.0180	-3.54
high spring-NAO Y _M	0.514	0.117	0.0001	-16.33	0.364	0.122	0.0029	-6.93
Low-frequency NAO								
low winter-NAO	0.402	0.114	0.0004	-10.00	0.407	0.121	0.0008	-8.93
low summer-NAO	-0.126	0.111	0.26 ns	+1.04	-16.81	0.123	0.17 ns	0.41
low spring-NAO	-0.006	0.109	0.96 ns	+2.00	-0.128	0.111	0.24 ns	0.63
Interaction								
low winter-NAO x								
high summer-NAO Y_{M-1}	0.237	0.099	0.0170	-3.26				