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The North Atlantic Oscillation synchronises fruit production in western European forests

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1 **The North Atlantic Oscillation synchronises fruit production in western**  
2 **European forests**

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19 **Abstract**

20 Weather and its lagged effects have been associated with interannual variability and  
21 synchrony of fruit production for several tree species. Such relationships are used often in  
22 hypotheses relating interannual variability in fruit production with tree resources or favourable  
23 pollinating conditions and with synchrony in fruit production among sites through the Moran  
24 effect (the synchronisation of biological processes among populations driven by meteorological  
25 variability) or the local availability of pollen. Climatic teleconnections, such as the North Atlantic  
26 Oscillation (NAO), representing *weather packages*, however, have rarely been correlated with  
27 fruit production, despite often being better predictors of ecological processes than is local  
28 weather. The aim of this study was to test the utility of seasonal NAO indices for predicting  
29 interannual variability and synchrony in fruit production using data from 76 forests of *Abies*  
30 *alba*, *Fagus sylvatica*, *Picea abies*, *Pseudotsuga menziesii*, *Quercus petraea*, and *Q. robur*  
31 distributed across central Europe. Interannual variability in fruit production for all species was  
32 significantly correlated with seasonal NAO indices, which were more prominently important  
33 predictors than local meteorological variables. The relationships identified by these analyses  
34 indicated that proximal causes were mostly responsible for the interannual variability in fruit  
35 production, supporting the premise that local tree resources and favourable pollinating  
36 conditions are needed to produce large fruit crops. Synchrony in fruit production between  
37 forests was mainly associated with weather and geographical distance among sites. Also, fruit  
38 production for a given year was less variable among sites during warm and dry springs  
39 (negative spring NAO phases). Our results identify the Moran effect as the most likely  
40 mechanism for synchronisation of fruit production at large geographical scales and the  
41 possibility that pollen availability plays a role in synchronising fruit production at local scales.  
42 Our results highlight the influence of the NAO on the patterns of fruit production across  
43 western Europe.

44 **Keywords:** synchrony, seeds, weather lagged effects, tree reproduction

## 46 1. Introduction

47 Production of fruit and seeds is an essential step in the life cycle of plants that allows  
48 individuals to transmit their genes to the next generation and to colonise new territories.  
49 Reproduction, however, has important implications beyond the plant itself, especially if it  
50 concerns the key species of a community: production of fruit can alter entire ecosystems by  
51 producing cascading effects throughout food webs (Elkinton et al. 1996, Ostfeld and Keesing  
52 2000), even affecting the transmission of diseases such as Lyme disease to humans (Ostfeld  
53 1997). Different patterns of fruit production can thus have a range of different consequences  
54 for ecosystems.

55 Two of the most studied hypotheses attempting to account for interannual variability in fruit  
56 production are the *resource matching* and the *pollination efficiency* hypotheses. The  
57 mechanistic *resource matching* hypothesis (Norton and Kelly 1988, Sork et al. 1993, Kelly and  
58 Sork 2002) suggests that plants produce fruit as a direct response to the available resources  
59 (Table 1). The *pollination efficiency* hypothesis (Norton and Kelly 1988, Smith et al. 1990,  
60 Koenig and Ashley 2003), however, states that synchronised and intermittent flowering  
61 increases the success of pollination in wind-pollinated species because it ensures a high rate  
62 of successful pollination during years of extensive flowering (Table 1). Both hypotheses can be  
63 indirectly related to meteorological variability, because weather can influence both the  
64 acquisition of tree resources (e.g. by increased photosynthesis) and environmental conditions  
65 associated with effective pollination.

66 Similarly to interannual variability, synchrony in fruit production has also mostly been explained  
67 by two hypotheses. Moran's theory (Moran 1953, Ranta et al. 1997) states that synchrony in  
68 fruit production is controlled by synchrony in meteorological conditions, which prompt trees to  
69 divert resources into reproduction or, mechanistically, to producing more fruit when weather is  
70 favourable for acquiring more resources (Table 1). Because meteorological conditions can also  
71 be spatially synchronous (Koenig 2002), the Moran effect has also been hypothesised to  
72 synchronise of fruit production over large geographical areas (Koenig and Knops 2013). The  
73 *pollen coupling* hypothesis (Satake and Iwasa 2002), however, suggests that the available  
74 pollen from neighbouring trees can generate synchrony in fruit production among individuals

75 by interacting with the resources available to the trees (Table 1, i.e., extensive maturation of  
76 female flowers after a massive pollinating event (when enough pollen is available) would  
77 deplete the resources of all trees at the same time, increasing synchronisation of fruit  
78 production within the population among years in the long run).

79 Most studies that have tested these hypotheses have based their conclusions on the  
80 relationship between meteorological conditions and interannual variability and synchrony in  
81 fruit production, due to the importance of meteorological variability to plant productivity (Sork et  
82 al. 1993, Fernández-Martínez et al. 2012, Koenig and Knops 2013). Recent studies have  
83 highlighted the possible role of temperature as a meteorological cue (Kelly et al. 2013, Kon  
84 and Saito 2015), although another study has suggested that temperature likely acts mainly as  
85 a proximal cause for the prediction of fruit crop size (Pearse et al. 2014). In any case,  
86 temperature variability would also explain synchrony in fruit production, because changes in  
87 temperature occur at wide geographical scales (Koenig 2002). Other meteorological variables  
88 (e.g., precipitation or water stress), however, could also be used as meteorological predictors  
89 of interannual variability and synchrony in fruit production (Sork et al. 1993, García-Mozo et al.  
90 2007, Espelta et al. 2008, Fernández-Martínez et al. 2012).

91 Weather at continental scales is mostly driven by general patterns of atmospheric circulation.  
92 Climatic teleconnections can influence weather strongly over very large areas. The El  
93 Niño/Southern Oscillation affects the weather of the entire planet (Grove 1998, NOAA 2012),  
94 and the North Atlantic Oscillation (NAO, the dipole connecting the Icelandic low with the  
95 Azores high) strongly affects the Atlantic basins of Europe and North America (Hurrell et al.  
96 2002, 2003). Ecosystems may accordingly also be affected by teleconnections (Straile 2002,  
97 Menzel et al. 2005, Martínez-Jauregui et al. 2009, Hódar et al. 2011), and some studies have  
98 suggested that teleconnection indices often predict ecological processes better than local  
99 weather (Ottersen et al. 2001, Stenseth et al. 2003, Hallett et al. 2004) because they  
100 aggregate meteorological conditions over large spatial scales. The NAO index may thus be an  
101 excellent meteorological cue. Nonetheless, the role of such climatic teleconnections, has rarely  
102 been explored in studies focused on fruit production (but see Wright et al. (1999)). Additionally,  
103 most of the published literature exploring the effects of the NAO on ecosystems has focused  
104 on the values of the index in winter (Ottersen et al. 2001), which can limit usefulness of the

105 approach, because different biological processes might be influenced by weather in different  
106 seasons.

107 Fruit production in some species has been strongly correlated with weather in warm seasons  
108 (Sork et al. 1993, Fernández-Martínez et al. 2012, 2015, Kelly et al. 2013, Pearse et al. 2014),  
109 for which the winter NAO (NAO<sub>w</sub>) may have little influence. Tree species with contrasting leaf  
110 habits (evergreen and deciduous) may be sensitive to meteorological conditions during  
111 different seasons. Winter-deciduous species must accumulate enough resources prior to  
112 winter for spring leaf unfolding and flowering, so autumn weather likely has some influence on  
113 next year's productivity. Winter meteorological variability, however, may play a role in  
114 determining plant productivity during the next year, because evergreen species preserve their  
115 leaves during the winter. Exploring the effects of the NAO index for other seasons may also  
116 provide interesting results and even improve the prediction capacity of the models.

117 We tested the ability of seasonal NAO indices to predict interannual variability in fruit  
118 production by constructing statistical models, including local meteorological (temperature and  
119 precipitation) variables and NAO indices for the previous autumn, winter, spring, and summer  
120 seasons, using data from 76 forests of *Abies alba*, *Fagus sylvatica*, *Picea abies*, *Pseudotsuga*  
121 *menziesii*, *Quercus petraea*, and *Q. robur* distributed across Europe. We also identified the  
122 environmental variables that could account for synchrony in fruit production among forests  
123 within species. Finally, we discuss the plausibility of various hypotheses addressing  
124 interannual variability and synchrony in fruit production based on our statistical results.

## 125 **2. Materials and methods**

### 126 *2.1. Data collection*

#### 127 *2.1.1. Data for litterfall and foliar nutrient concentration*

128 We downloaded litterfall data from the ICP Forests database (International Co-operative  
129 Programme on Assessment and Monitoring of Air Pollution Effects on Forest, operated under  
130 the UNECE Convention on Long-range Transboundary Air Pollution, <http://icp-forests.net/>).  
131 The dataset contained information about fruit-production for several forest tree species in  
132 Europe for 2002–2010. Fruit litterfall was totalled per plot and year. Because the original data  
133 for litterfall was available in units of g of dry weight m<sup>-2</sup> y<sup>-1</sup>, we used fruit carbon (C) content

134 data (provided by the same database) to calculate litterfall in units of  $\text{g C m}^{-2} \text{y}^{-1}$  (as fruit net  
135 primary production [NPP]). Although data from 210 forests were available in the database we  
136 used only data from 76 single-species forests with time series records of five or more years to  
137 ensure that we had reliable records of single-species fruit production suitable for analysis of  
138 interannual variation. These selected forests consisted of *A. alba*, *F. sylvatica*, *P. abies*, *Ps.*  
139 *menziesii*, *Q. petraea*, and *Q. robur* and were distributed over France, Germany, and  
140 Luxemburg (**Figure 1**).

### 141 2.1.2. Meteorological data

142 We extracted meteorological time series for our forests from the interpolated meteorological  
143 data of the MARS unit AGRI4CAST/JRC (<http://agri4cast.jrc.ec.europa.eu/>), with a resolution  
144 of  $0.25 \times 0.25$  degrees (latitude, longitude). This database provided monthly mean  
145 temperatures and total precipitation for 2001 to 2010. We also downloaded the NAO index  
146 time series for daily data, covering the period from 1 January 1950 to 31 December 2014, from  
147 the Climate Prediction Center of the National Weather Service (NOAA,  
148 <http://www.cpc.ncep.noaa.gov/>). We then calculated the seasonal NAO indices, temperatures,  
149 and precipitation for winter, spring, summer, and autumn. We calculated the winter values as  
150 the average (for temperature and NAO) or the sum (for precipitation) of January, February, and  
151 March; spring comprised the months of April, May, and June; summer comprised the months  
152 of July, August, and September, and autumn comprised the months of October, November,  
153 and December. The seasonal NAO indices were standardised ( $[(x_i - \bar{x}) \cdot SD^{-1}]$ ) for the period  
154 1950–2014.

## 155 2.2. Data analyses

### 156 2.2.1. Interannual variability of fruit production

157 Table 2 summarizes the analyses performed in this study. We evaluated the influence of the  
158 seasonal NAO indices on local seasonal weather (temperature and precipitation) by fitting  
159 generalised linear mixed models (GLMMs) with the *nlme* R package (Pinheiro et al. 2013),  
160 using restricted maximum likelihood (REML) and a Gaussian distribution, where the site was  
161 the random factor and the seasonal NAO indices were related to seasonal temperature and  
162 precipitation.

163 We assessed the correlations between the seasonal NAO indices and fruit production using  
164 Spearman correlations for each site between the seasonal NAO indices and fruit-production  
165 time series. We then calculated the average correlations between fruit production and the  
166 seasonal NAO indices per species. We next fitted the GLMMs using REML and a Gaussian  
167 distribution, where the site was the random factor. We accounted for the effect of the previous  
168 fruit crop by also including in the models an autoregressive term for lag 1 (ARMA [1,0], crop  
169 year  $i \sim$  crop year  $i-1$ ). Saturated models (models including all possible predictors) predicting  
170 interannual variability in fruit production included temperature, precipitation, and the NAO  
171 indices for the autumn, winter, spring, and summer previous to fruit ripening (e.g. fruit crop  
172 year  $i \sim$  autumn temperature year  $i-1$  + winter temperature year  $i$  +...). The variables for each  
173 model were selected using the *dredge* function in the MuMin R package (Barton 2015) using  
174 the best subset model selection and using the Bayesian Information Criterion (BIC) as the  
175 measure of model adjustment (the best model had the lowest BIC). We also calculated the  
176 variance explained by the fixed factors (marginal variance,  $R^2_m$ ) and by the entire model  
177 (conditional variance,  $R^2_c$ ) for the final models using the methodology proposed by Nakagawa  
178 & Schielzeth (2013), also implemented in the MuMIn R package (Barton 2015) by the function  
179 *r.squaredGLMM*. The difference between the marginal and conditional variances explained  
180 was the variance explained by the random factors. We assessed the importance of the  
181 predictors within the models by calculating their  $\Delta$ BICs as the difference between the BIC of  
182 the final model and the BIC of the model without the predictor of interest. The higher the  $\Delta$ BIC,  
183 the larger the importance of the predictor within the model. Fruit NPP was log-transformed to  
184 meet the assumptions of normality and heteroscedasticity in the model residuals. We also  
185 used mixed models with random slopes to test the effect of the seasonal NAO indices on  
186 temperature and precipitation, using site as the random factor.

187 Relationships between fruit production and meteorological variables that can be associated  
188 either with successful pollination (supporting the *pollination efficiency* hypothesis) or higher  
189 tree productivity (indirectly supporting the *resource matching* hypothesis) would indicate an  
190 effect of weather on fruit production by proximal causes. If the relationship between weather  
191 and fruit production cannot be correlated with well-established physiological responses (e.g.,  
192 warm and wet conditions normally increase tree productivity [Fernández-Martínez et al. 2014]),  
193 the results may be supporting the role of weather as a cue for fruit production.



194 2.2.2. *Synchrony of fruit production among forests*

195 We first tested whether higher variability in meteorological conditions among sites was  
196 associated with higher variability in fruit production for a given year. We calculated the annual  
197 coefficient of variation ( $CV = \text{standard deviation} \cdot \text{mean}^{-1}$ ) amongst sites of seasonal (winter,  
198 spring, summer, and autumn) temperature and precipitation and of annual fruit production for  
199 each species for each of the years with records for more than five forests per species. We then  
200 used GLMMs with species as the random factor to determine the significance of the  
201 association between the CVs for annual fruit production and weather among sites and the  
202 seasonal NAO indices. Positive associations between the CVs for annual fruit production and  
203 weather would further support the Moran-effect hypothesis, and no association would indicate  
204 that other mechanisms, such as pollen coupling, might be involved in synchronising fruit  
205 production.

206 We then calculated the degree of synchrony in fruit production among all sites using  
207 Spearman's correlations ( $\rho$ ) for all sites with data for at least the same five years, and  
208 calculated the mean correlation of fruit production per species and among species. We then  
209 identified the main controls of synchrony in fruit production among forests within species by  
210 first calculating the synchrony ( $\rho$ ) for weather (seasonal temperatures and precipitation) among  
211 forests of the same species, and used linear models to identify the relationships of synchrony  
212 in weather and synchrony in fruit production with geographical distance. The Moran effect  
213 would be supported if the slope between distance and synchrony in seasonal temperature or  
214 precipitation among sites was as high as or higher than the slope between distance and  
215 synchrony in fruit production among sites (similar slopes using a  $t$ -test,  $P > 0.05$ ). If the slopes  
216 differed or fruit production was not spatially synchronous among forests, the results would  
217 indicate that the synchrony was at more local scales and thus provide indirect evidence  
218 supporting the *pollen coupling* hypothesis (Table 1).

219 We constructed linear models in which the response variable was the synchrony ( $\rho$ ) of fruit  
220 production between two forests and the predictor variables were the geographical distance  
221 between sites and the correlation between winter, spring, summer, and autumn temperatures  
222 and precipitation for the two forests. We next selected the model using the *dredge* function in  
223 the MuMin R package (Barton 2015) using the best subset model selection and using BIC as  
224 the measure of model adjustment. The best model was then assumed to have the lowest BIC

225 with all variables significant at the 0.05 level and with no negative coefficients for the  
226 meteorological variables (because negative associations between synchrony in fruit production  
227 and in meteorological variables would be nonsensical). The percentage of variance explained  
228 by the predictors was assessed using the proportional marginal variance decomposition metric  
229 *pmvd* from the *relaimpo* R package (Grömping 2007).

230 Similar to the results for interannual variability, significant relationships between synchrony in  
231 fruit production and synchrony in meteorological variables from periods potentially associated  
232 with tree productivity would indicate the Moran effect as a result of proximal causes of weather  
233 on fruit production. If meteorological variables associated with synchrony in fruit production  
234 were also be associated with spring conditions, during pollination, the *pollen coupling*  
235 hypothesis would be supported (Table 1). If meteorological predictors of fruit synchrony could  
236 not be associated with the pollinating period nor with higher tree productivity, the results would  
237 support the Moran effect with weather acting as a cue for the trees.

238 We used the *visreg* R package (Breheny and Burchett 2015) to visualise the regression  
239 models using partial plots. All data treatments and analyses were conducted using R (R Core  
240 Team 2015).

### 241 **3. Results**

#### 242 *3.1. Effects of seasonal NAO on local weather*

243 The seasonal NAO indices were correlated with the weather at our sites (**Figure 2**). Positive  
244  $NAO_w$  phases were correlated with warm and wet winters, and positive spring NAO ( $NAO_{sp}$ )  
245 phases were correlated with warm and dry weather. Positive summer and autumn NAOs  
246 ( $NAO_{sm}$  and  $NAO_a$ , respectively) were correlated with cold and dry weather. The seasonal  
247 NAO indices, however, were not significantly correlated, either during the study period (2002–  
248 2010) or for a longer period (1950–2014). The correlations among seasonal NAO phases were  
249 generally small and not significant.

#### 250 *3.2. Interannual variability of fruit production*

251 Both changes in weather and the seasonal NAO indices were individually correlated with fruit  
252 production for all tree species (**Table 3**). Fruit crop size in both *Quercus* species and *A. alba*

253 was negatively associated with the NAO phase of the autumn prior to fruit ripening, whereas  
254 fruit production and  $NAO_w$  were strongly positively correlated for the three coniferous species.  
255 Fruit crop size was positively associated with  $NAO_{sp}$  in *A. alba*, *F. sylvatica*, and *Q. robur* and  
256 with  $NAO_{sm}$  in *P. abies* and *F. sylvatica*.

257 GLMM models predicting fruit crop size using local seasonal weather and the seasonal NAO  
258 indices also identified a relevant role of the NAO phases in predicting interannual variability in  
259 fruit production (**Table 4**). In addition, the seasonal NAO variables were usually the most  
260 important variables identified by  $\Delta BIC$ . The univariate analysis correlated fruit crop size in *A.*  
261 *alba* negatively with  $NAO_w$  and positively with  $NAO_{sp}$ . The model also identified a significant  
262 negative relationship between winter precipitation and fruit production. Based on  $\Delta BIC$ , both  
263 NAO variables were similarly important for predicting variability in fruit production and were  
264 clearly more important than winter precipitation. Large fruit crops in *P. abies* were associated  
265 with rainy winters, dry springs, and dry ( $NAO_{sm}^+$ , in positive phase) warm summers, with  $NAO_{sp}$   
266 and winter precipitation the most important variables. Fruit crop size for *P. menziesii* was  
267 positively correlated with cold and dry autumns ( $NAO_a^+$ ), warm and wet winters ( $NAO_w^-$ , in  
268 negative phase), and warm springs, being  $NAO_a$  the most important variable in the model  
269 according to  $\Delta BIC$ . Fruit production in *F. sylvatica*, as for *P. abies*, was positively correlated  
270 with cold and dry autumns ( $NAO_a^+$  and temperature) but also with dry and warm springs  
271 ( $NAO_{sp}$ ) and dry summers. Conversely, *Q. petraea* and *Q. robur* produced larger fruit crops  
272 after warm and wet autumns. Fruit production in *Q. robur* was also positively correlated with  
273 wet summers and cold winters. The best model predicting interannual variability for *Q. robur*  
274 did not identify NAO as a significant predictor, but the next model (differing only by 0.76 BIC  
275 units from the best model in **Table 4**) included  $NAO_a$  instead of winter temperature. Seasonal  
276 NAO indices were thus able to predict the interannual variability of fruit production moderately  
277 well for all tree species.

### 278 3.3. Patterns of intra- and interspecific synchrony in fruit production

279  $NAO_{sp}$  was the most highly correlated variable explaining the variability in the CVs for annual  
280 fruit production among species (**Figure 3**). The CV for annual fruit production was negatively  
281 correlated with  $NAO_{sp}$  for all species except *P. menziesii*, and the relationship was statistically  
282 significant for *F. sylvatica*, *Q. robur*, and *P. abies* ( $P=0.005$ ,  $0.012$ , and  $0.041$ , respectively).

283 *F. sylvatica* was the most synchronised species producing fruit, with a mean synchrony among  
284 sites of  $0.60 \pm 0.02$ . In contrast, synchrony in fruit production among sites was not statistically  
285 significant for *P. menziesii* (**Table 5, a**). *A. alba*, *P. abies*, *Q. petraea*, and *Q. robur* also had  
286 important synchronies in fruit production. Synchrony in fruit production, however, was  
287 significantly lower than synchrony in most of the seasonal meteorological variables  
288 (temperature and precipitation) for most of the species (**Table 5, a**). Fruit production in all  
289 species (except *P. menziesii*) showed strong spatial correlations with meteorological  
290 synchrony (**Table 5, b**), but the synchrony of fruit production was not strongly spatially  
291 dependent using univariate regressions. The slope between synchrony in fruit production and  
292 distance between plots was statistically significant only for *Q. robur*, and the slope coefficients  
293 were very close to zero for some species such as *F. sylvatica* and *Q. petraea* (**Table 5, b**) and  
294 were significantly different from most of the distance  $\times$  weather correlation slopes (*t*-tests,  
295  $P < 0.05$ ). The slopes between fruit production and distance for *A. alba*, *P. abies*, *P. menziesii*,  
296 and *Q. robur* did not differ significantly (*t*-tests,  $P > 0.05$ ) from those for most of the weather  $\times$   
297 distance relationships.

298 Amongst species, synchrony in fruit production decreased considerably compared to within-  
299 species synchrony, and some combinations were even significantly negatively correlated, such  
300 as *F. sylvatica* versus *P. menziesii* and *Q. petraea* (**Table 6**). Synchrony of fruit production  
301 amongst sites was generally similar between leaf types (**Table 6**; *t*-test,  $P > 0.05$ ).

302 Our models correlating synchrony in fruit production with synchrony in meteorological variables  
303 indicated that seasonal weather had a limited impact on intraspecific synchrony amongst sites  
304 (**Table 7**). Synchrony of meteorological conditions between sites was only a significant driver  
305 of synchrony in fruit production for *A. alba* (autumn temperature), *F. sylvatica* (winter  
306 precipitation), and *Q. petraea* (summer precipitation). The only significant relationship for  
307 synchrony in fruit production for *Q. robur* was a negative relationship with distance between  
308 sites, similar to the results of the univariate analyses (**Table 5**). Synchrony in fruit production  
309 for *P. abies* was not significantly correlated with synchrony in meteorological conditions.

## 310 **4. Discussion**

### 311 *4.1. Teleconnection indices as biological predictors*

312 Our results fully support the hypothesis that teleconnection indices are better correlated with  
313 biological processes than local weather (Ottersen et al. 2001, Hallett et al. 2004). Fruit  
314 production of all species that we considered had statistically significant relationships with  
315 seasonal NAO indices (**Figure 3, Tables 3 and 4**), highlighting the importance of the NAO as  
316 a driver of ecological processes through effects on meteorological conditions at large spatial  
317 scales (**Figure 2**). These results are thought to emerge because organisms do not respond to  
318 single environmental variables but to a combination of variables. The NAO indices are thus  
319 good predictors of *weather packages* (i.e. temperature, precipitation, humidity, wind, radiation,  
320 or pressure), reducing spatiotemporal variability in meteorological conditions into a single index  
321 (Stenseth et al. 2003) influencing weather over continental scales. The utility of the NAO (and  
322 other teleconnection indices) for characterizing weather packages influencing very large  
323 geographical scales make them suitable candidate variables for testing the Moran effect.

#### 324 4.2. Controls of interannual variability of fruit production

325 Our results highlighted a contrasting effect of seasonal NAO indices on fruit production for  
326 coniferous and broadleaved species: cone crops in coniferous species were mainly negatively  
327 correlated with NAO<sub>w</sub> (i.e., associated to dry and cool winters), but fruit production in  
328 broadleaved species was positively correlated with NAO<sub>sp</sub> (associated with warm and dry  
329 springs) and negatively correlated with NAO<sub>a</sub> (associated with warm and wet autumns)  
330 (**Tables 3 and 4**). Nonetheless, these relationships could be altered by local weather (e.g., the  
331 positive correlation between winter precipitation and fruit production for *P. abies* in **Table 4**).  
332 These differences, in part, reflect differences in the effect of leaf characteristics on when  
333 weather influences fruit production. Coniferous species in our study were all evergreen (main  
334 effect during winter) and the broadleaved species were all deciduous (main effect during  
335 spring).

336 Cold winters may delay the growing season for evergreen species and thus the onset of  
337 flowering (Frenguelli and Bricchi 1998, García-Mozo et al. 2002, Stöckli and Vidale 2004).  
338 Delays in pollinating periods due to cold meteorological conditions have been previously  
339 reported to positively affect fruit production in the evergreen *Q. ilex* (Fernández-Martínez et al.  
340 2012). Additionally, cold winter weather may meet the chilling requirements for conifers to  
341 reach complete dormancy (Clancy et al. 1995), as is needed to survive unfavourable  
342 environmental conditions. In contrast, higher winter temperatures might entail higher metabolic

343 costs for trees, reducing the amount of reserves available to invest in reproduction. This  
344 reasoning is in line with the *resource matching* hypothesis, i.e., trees would produce fruit as a  
345 response to the available resources (**Table 1**).

346 Dry and warm spring weather (during pollination), however, can facilitate pollen dispersal,  
347 because pollen release to the atmosphere increases with temperature and precipitation  
348 removes the pollen (García-mozo et al. 2006, Fernández-Martínez et al. 2012, Kasprzyk et al.  
349 2014). We thus suggest that fruit production in deciduous broadleaved species (and *A. alba*,  
350 see **Tables 3 and 4**) was positively associated with the NAO<sub>sp</sub> phase because dry and warm  
351 weather facilitates pollen release and therefore the fertilisation of female flowers, supporting  
352 the *pollination efficiency* hypothesis (**Table 1**).

353 Fruit crop size for *Q. petraea*, (and also *Q. robur* and *A. alba*, see Table 3) was correlated with  
354 warm and wet autumns. Leaf senescence and the start of dormancy is delayed during warm  
355 and wet autumns (NAO<sub>a</sub><sup>-</sup>) because of the strong control that temperature exerts on them  
356 (Vitasse et al. 2009, Estiarte and Peñuelas 2015). Delayed leaf senescence extends the  
357 growing period, which allows trees to accumulate resources immediately after most of the fruit  
358 is matured. This additional acquisition of resources (Euskirchen et al. 2006) and tree growth at  
359 the end of the growing season could be spent during the next spring to enable more intense  
360 flowering (Fernández-Martínez et al. 2015). This mechanism would be in line with the *resource*  
361 *matching* hypothesis (**Table 1**).

362 Dry and cool summer weather (NAO<sub>sm</sub><sup>+</sup>) increased fruit crop size in *P. abies* and *F. sylvatica*  
363 (**Table 3**). Because species characteristic of colder and wetter environments are generally  
364 more sensitive to changes in temperature than in water availability (Fernández-Martínez et al.  
365 2014), high summer temperatures may lead to photoinhibition and stomatal closure and  
366 thereby reduce photosynthetic capacity, constraining resources available to allocate to ripening  
367 fruit. This reasoning mechanism potentially driven by effects of the NAO<sub>sm</sub> on fruit production  
368 provide further indirect evidence supporting the *resource matching* hypothesis for *P. abies* and  
369 *F. sylvatica* (**Table 1**).

370 In short, our results generally indicated proximal causes (weather correlated with increased  
371 productivity or better pollinating conditions), likely driven by the NAO, as amongst the most  
372 plausible mechanisms explaining interannual variability in fruit production. They also indirectly

373 suggest that the *resource matching* and *pollination efficiency* hypotheses may actually function  
374 together (**Table 1**), especially for the broadleaved species studied here, as potential drivers of  
375 interannual variability in fruit production in European forests. The different mechanisms  
376 proposed by each of these two hypotheses are likely required to a certain degree to explain  
377 the large interannual variability in fruit crops and its synchrony. The relative importance of each  
378 mechanism will surely depend on the species under study and on the site characteristics  
379 (Fernández-Martínez et al. 2012). In addition, the considerable variance explained by the  
380 models accounting for interannual variability in fruit production suggests that meteorological  
381 variability should be one of the most important factors driving interannual variability and  
382 synchrony in fruit production (Fernández-Martínez et al. 2015)

#### 383 4.3. Controls of synchrony of fruit production

384 Whether synchrony in fruit production is due to the Moran effect or pollen coupling is usually  
385 hard to determine, because both hypotheses generate similar patterns of spatial synchrony  
386 and are not mutually exclusive (Liebhold et al. 2004, Koenig and Knops 2013). Some  
387 predictions of both hypotheses, however, can help to distinguish between them. Synchrony in  
388 fruit production due to *pollen coupling* should not extend more than a few hundred kilometres  
389 at most, and the Moran effect can easily reach hundreds and even thousands of kilometres  
390 (Koenig and Knops 2013). According to this prediction, our results suggest that the Moran  
391 effect is responsible for the synchrony in fruit production among European forests, some  
392 separated by hundreds of kilometres. This inference, however, cannot completely dismiss the  
393 *pollen coupling* hypothesis, because our database consisted of forests and not individual trees,  
394 so *pollen coupling* could still be acting to amplify synchrony at the local scale.

395 The anti-synchrony in fruit production between *F. sylvatica* and *Q. petraea* (**Table 6**), two  
396 potentially co-existing species, suggests a strategy for avoiding large fruit crops in the same  
397 years. Although such a strategy would be contrary to the *predation satiation* hypothesis  
398 (Silvertown 1980, Espelta et al. 2008) but could reduce interspecific interference in pollination,  
399 because most of the pollen reaching female flowers would be from the same species in years  
400 of high intraspecifically synchronous reproduction. This hypothetical mechanism would tend to  
401 support the hypothesis that fruit production is synchronized by *pollen coupling*. Nonetheless,  
402 synchrony between non-hybridising species cannot occur by *pollen coupling*, and we found  
403 significant synchrony amongst species that do not hybridise (**Table 6**). This result further

404 supports the synchronization of reproduction through the Moran effect, especially when  
405 combined with the results from our models suggesting that the seasonal NAO indices are  
406 common drivers of interannual variability.

407 The Moran effect also predicts that distance between sites will be similarly related to both  
408 synchrony in fruit production and meteorological variables (Koenig and Knops 2013). Our  
409 results corroborate with this prediction for *A. alba*, *P. abies*, *P. menziesii*, and *Q. robur*, thus  
410 further supporting the Moran effect as an underlying cause of the patterns we have identified.  
411 Our findings for *F. sylvatica* and *Q. petraea*, however, do not support this prediction, because  
412 synchrony in fruit production for these species and meteorological variables were differently  
413 related to distance (**Table 5**). Interannual variability in fruit production for *F. sylvatica* was also  
414 linked to dry and warm spring weather, favouring pollen dispersal, so *pollen coupling* likely also  
415 plays a role synchronising fruit production in these forests and possibly also in *Q. petraea*  
416 forests given the similar relation of synchrony in fruit production and meteorological variables  
417 with distance (**Table 1**). Weather also likely plays a role in synchronising fruit crop sizes  
418 amongst sites because synchrony in meteorological conditions was correlated with synchrony  
419 in fruit production for *A. alba*, *F. sylvatica*, and *Q. petraea*. Our results must be interpreted with  
420 care, however, because none of the variables involved in predicting synchrony in fruit  
421 production also predicted interannual variability in fruit production and because the synchrony  
422 models explained only a small amount of the variance. Nonetheless, the NAO is clearly  
423 partially responsible for interannual variability in meteorological conditions over western  
424 Europe, and so we infer that 1) the NAO acts as a synchronising agent among sites and 2) the  
425 Moran effect is probably the main factor synchronising the fruit production of forests in western  
426 Europe (**Table 1**).

427 Both the Moran effect and the *pollen coupling* hypotheses may thus play a role in  
428 synchronising fruit production, but at different levels. Whereas the Moran effect is apparent at  
429 continental scales, *pollen coupling* may be restricted to local or nearby regional environments.  
430 Moreover, according to our results, evidence for the Moran effect seems to apply to more  
431 systems than does evidence for *pollen coupling*.

432 Our results generally highlight that weather packages, such as the NAO index, can improve  
433 prediction of ecological processes at wide geographical scales, which is particularly useful for  
434 testing the explanatory power of the Moran effect in particular situations. Since weather is



435 likely to affect tree resources and enable favourable meteorological conditions for pollination,  
436 we suggest that the synchronising effect of weather was more likely to be due to proximal  
437 causes driving interannual variability rather than the effect of weather as a cue for tree  
438 reproduction.

439

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544

545

546 **Figure captions**

547 **Figure 1:** Map showing the sites used in this study. The sites were located throughout France,  
548 Germany, and Luxembourg.

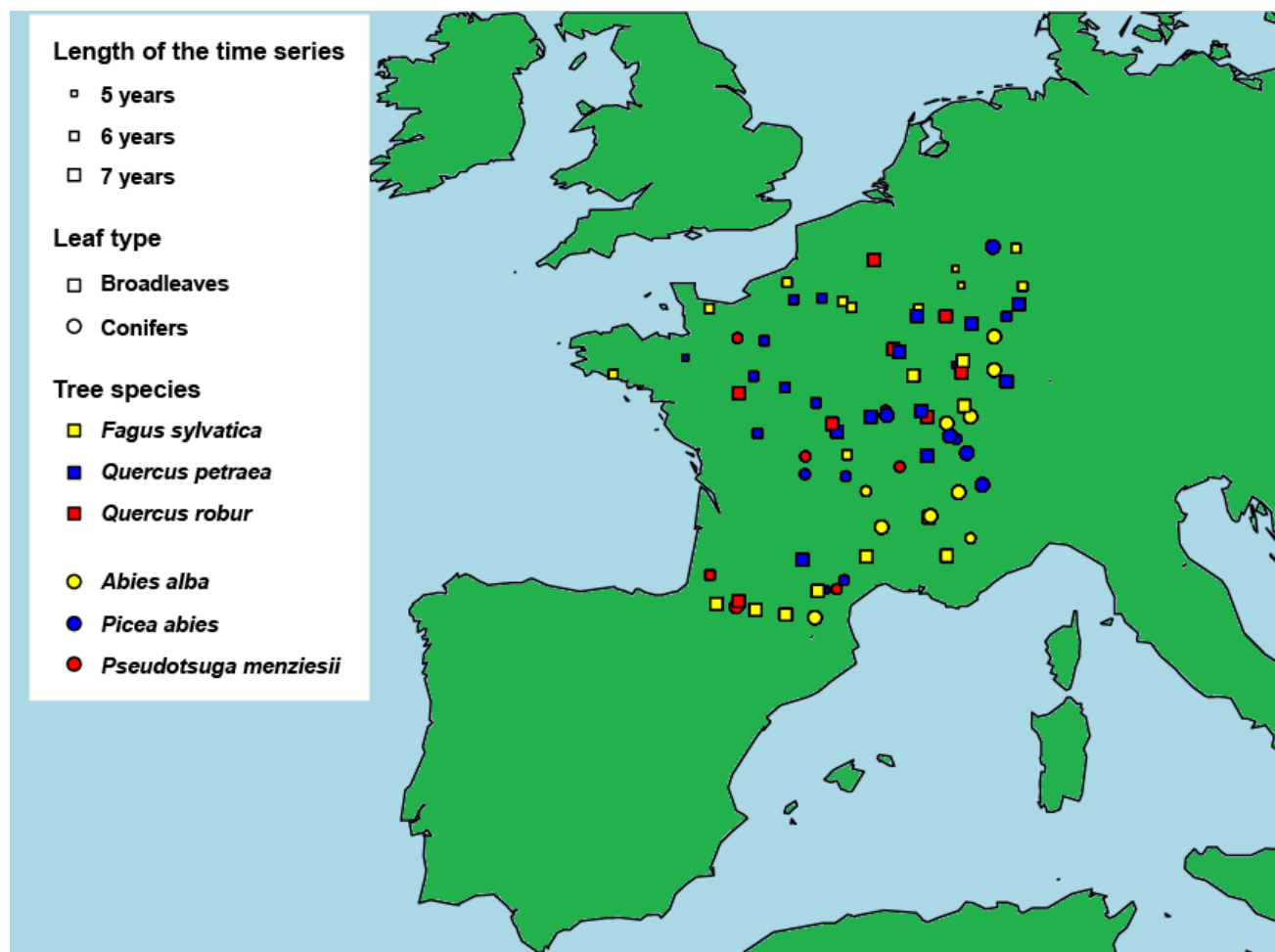
549 **Figure 2:** Relationships between the seasonal North Atlantic Oscillation (NAO) indices and  
550 weather for 2002–2010. Positive (+) and negative (-) symbols after NAO indicate positive and  
551 negative phases of the index. Values are  $\beta$  weights calculated using generalised linear mixed  
552 models with random slopes. All coefficients were significant at the 0.001 level.

553 **Figure 3:** a) Relationships between the CV of annual fruit production and the spring NAO  
554 index for the six species. Thick lines indicate significant relationships at the 0.05 level. b)  
555 Partial residuals plot showing the average relationship between the annual CV of fruit  
556 production and the spring NAO index amongst species using generalised linear mixed models.

557

558

559 **Figure 1**

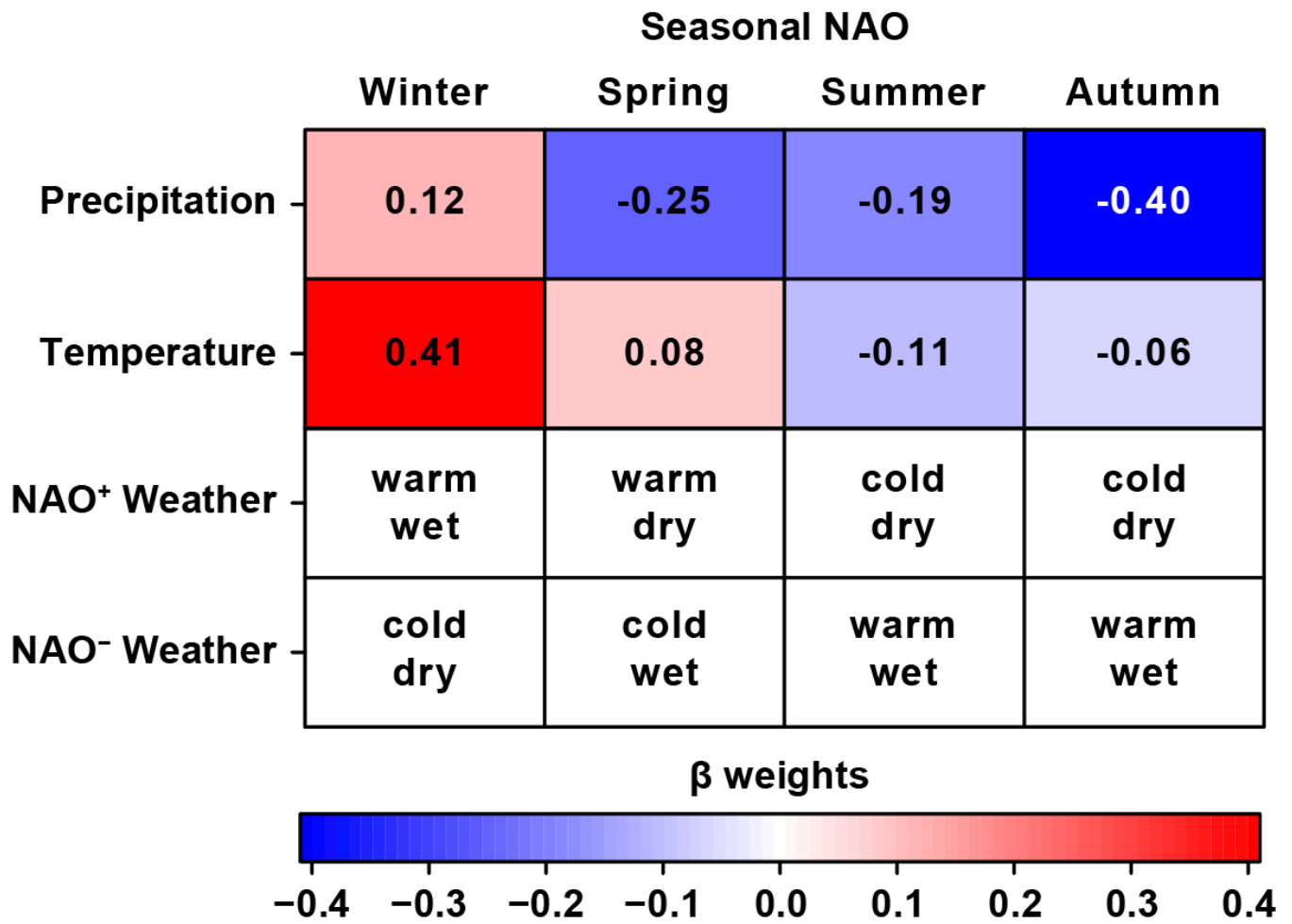


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563 **Figure 2**

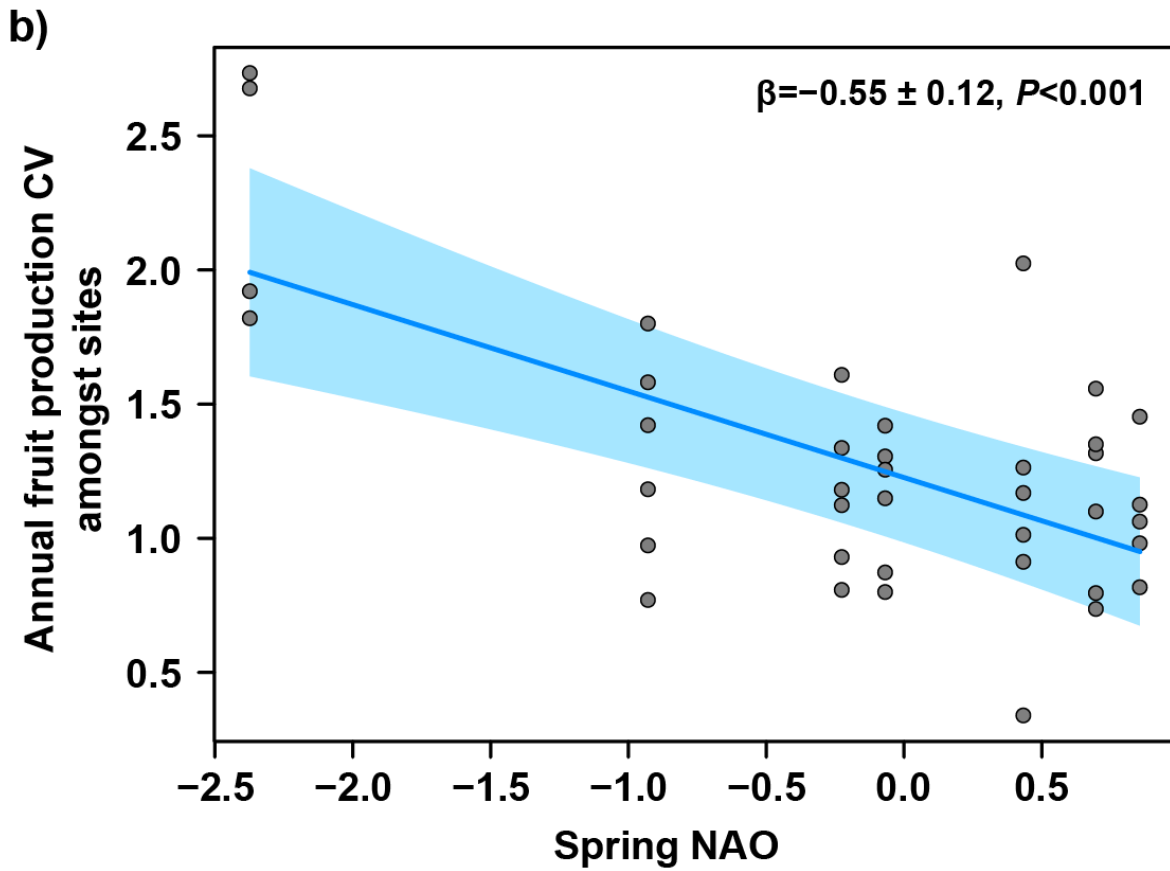
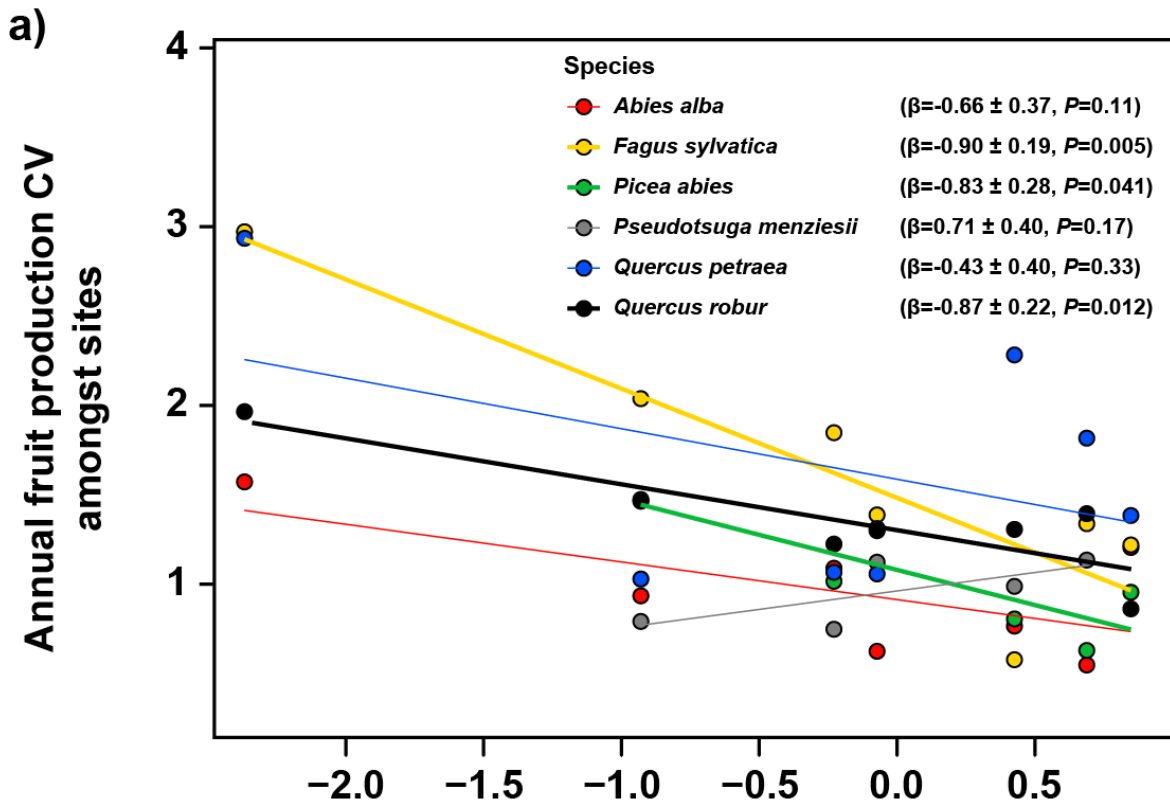


564

565

566 **Figure 3**





567

568

569 **Table 1:** Summary of the hypotheses discussed in this study for interannual variability and synchrony in fruit production. Our  
 570 analysis was focused on weather relationships with interannual variability and synchrony in fruit production, so only indirect  
 571 evidence of the weather relationships supporting or rejecting the hypotheses are presented.

Hypothesis	Summary	Indirect evidence	
		Supports	Rejects
<b>a) Interannual variability</b>			
<b>Resource matching</b>	Plants produce fruit as a direct response to the available resources.	Favourable weather for tree productivity is positively correlated with fruit production.	No correlation with weather, or weather cannot be associated with higher tree productivity.
<b>Efficiency of pollination</b>	Synchronised and intermittent flowering increases successful pollination in wind-pollinated	Favourable weather for pollination (e.g. warm and dry springs) is positively correlated with fruit production.	Favourable weather for pollination is negatively or not correlated with fruit production.
<b>b) Synchrony</b>			
<b>The Moran effect</b>	Synchrony in fruit production is driven by synchrony in meteorological conditions.	Fruit production amongst sites is correlated with the same meteorological conditions. Non-hybridising species are also synchronised.	Fruit production amongst sites is correlated with different meteorological conditions, or no significant synchrony in fruit production is found amongst sites.
<b>Pollen coupling</b>	Pollen availability from neighbouring trees can generate synchrony in fruit production amongst individuals by interacting with available resources.	Favourable weather for pollination is positively correlated with fruit production. Synchrony occurs within species at the local scale.	Unfavourable weather for pollination is correlated with fruit production. Non-hybridising species are synchronised.

572 **Table 2:** Summary of the specific aims of the study and the statistical tests performed.

<b>Questions</b>	<b>Analyses</b>
<b><i>a) Meteorological variability</i></b>	
<b>Do seasonal NAO indices correlate with seasonal weather at our sites?</b>	Generalised linear mixed models (with site as random factor) correlating seasonal temperature and precipitation with seasonal NAO indices.
<b><i>b) Interannual variability in fruit production</i></b>	
<b>Do seasonal NAO indices correlate with fruit production?</b>	Spearman correlations between fruit production and seasonal NAO indices per site.
<b>Is fruit production best predicted by local meteorological variability or by seasonal NAO indices?</b>	Generalised linear mixed models per species (with site as random factor) correlating annual fruit production with seasonal temperatures, precipitation, and NAO indices.
<b><i>c) Synchrony in fruit production</i></b>	
<b>For a given year, is variability in fruit production amongst sites associated with variability in meteorological conditions or to seasonal NAO indices?</b>	Generalised linear mixed models per species (with site as random factor) correlating annual CV of fruit production amongst sites with annual CV of seasonal temperatures and precipitation and with seasonal NAO indices.
<b>Is fruit production (and weather) synchronised across sites within and amongst species?</b>	Temporal synchrony of fruit production, temperature, and precipitation amongst sites is calculated using Spearman correlations (i.e. correlation of time series A vs. time series B).
<b>Is synchrony of fruit production and weather between sites spatially dependent?</b>	Linear models correlating synchrony of fruit production and seasonal temperatures and precipitation between sites with geographical distance.
<b>Does synchrony in fruit production between sites depend on synchrony in meteorological conditions and geographical distance?</b>	Linear models correlating synchrony of fruit production with synchrony of seasonal temperatures and precipitation and geographical distance between sites.

573 **Table 3:** Spearman's correlations between seasonal (autumn, winter, spring, and summer seasons prior to fruit production)  
574 NAO indices and fruit production ( $\rho \pm$  standard error) per species and leaf type. The  $P$  values indicate whether average  
575 correlation coefficients differ from 0 ( $t$ -test).  $N$  indicates the number of forests per species. Only forests with five or more years  
576 of data were used in these analyses. The seasons are indicated by subscripts: w, sp, sm, and a indicate winter, spring,  
577 summer, and autumn, respectively.

	NAO <sub>a</sub>		$P$		NAO <sub>w</sub>		$P$		NAO <sub>sp</sub>		$P$		NAO <sub>sm</sub>		$P$		$N$	
<b>a) Species</b>																		
<i>Abies alba</i>	-0.34 ± 0.10	ab	0.0031	**	-0.42 ± 0.11	b	0.0007	***	0.45 ± 0.09	ab	0.0003	***	-0.07 ± 0.07	b	0.5433		10	
<i>Picea abies</i>	-0.22 ± 0.06	ab	0.0520	.	-0.42 ± 0.07	b	0.0007	***	0.13 ± 0.15	bc	0.2694		0.27 ± 0.12	ab	0.0141	*	10	
<i>Pseudotsuga menziesii</i>	0.18 ± 0.25	a	0.2163		-0.48 ± 0.12	b	0.0026	**	-0.12 ± 0.20	c	0.4400		0.00 ± 0.22	ab	0.9772		6	
<i>Fagus sylvatica</i>	0.06 ± 0.07	a	0.4089		0.03 ± 0.08	a	0.7266		0.61 ± 0.06	a	0.0000	***	0.36 ± 0.07	a	0.0000	***	21	
<i>Quercus petraea</i>	-0.39 ± 0.08	b	0.0000	***	0.09 ± 0.10	a	0.2810		0.04 ± 0.10	bc	0.6014		-0.06 ± 0.06	b	0.4676		20	
<i>Quercus robur</i>	-0.48 ± 0.11	b	0.0001	***	-0.14 ± 0.11	ab	0.2786		0.34 ± 0.11	abc	0.0092	**	-0.04 ± 0.15	b	0.7297		9	
<b>b) Leaf type</b>																		
<b>Conifers</b>	-0.18 ± 0.08	a	0.0341	*	-0.43 ± 0.06	b	0.0000	***	0.20 ± 0.09	a	0.0253	*	0.08 ± 0.08	a	0.2900		26	
<b>Broadleaves</b>	-0.21 ± 0.06	a	0.0005	***	0.02 ± 0.06	a	0.6490		0.33 ± 0.06	a	0.0000	***	0.12 ± 0.05	a	0.0250	*	50	

578 **Table 4:** Summary of the models predicting fruit production per species. Standardised  
 579 coefficients are shown as model estimates ( $\beta \pm$  standard error (SE)).  $\Delta$ BIC indicates the  
 580 variable importance of the predictors and is calculated as the difference of BIC between the  
 581 entire model and the model without the predictor of interest. Variance explained by the fixed  
 582 factors ( $R^2_m$ ) and by the entire model ( $R^2_c$ ) is also shown. All coefficients were significant at the  
 583 0.05 level. The seasons are indicated by subscripts: w, sp, sm, and a indicate winter, spring,  
 584 summer, and autumn, respectively.

	$\beta \pm$ SE	$\Delta$ BIC	$R^2_m$	$R^2_c$
<b><i>Abies alba</i></b>				
NAO <sub>w</sub>	-0.40 $\pm$ 0.10	10.81		
NAO <sub>sp</sub>	0.42 $\pm$ 0.09	13.59		
P <sub>w</sub>	-0.29 $\pm$ 0.11	0.90		
<b>Model</b>			0.39	0.47
<b><i>Picea abies</i></b>				
NAO <sub>sm</sub>	0.31 $\pm$ 0.07	11.51		
P <sub>sp</sub>	-0.32 $\pm$ 0.12	2.62		
P <sub>w</sub>	0.49 $\pm$ 0.12	11.41		
T <sub>sm</sub>	0.38 $\pm$ 0.18	0.52		
<b>Model</b>			0.26	0.79
<b><i>Pseudotsuga menziesii</i></b>				
NAO <sub>a</sub>	0.39 $\pm$ 0.10	10.63		
NAO <sub>w</sub>	-0.29 $\pm$ 0.11	3.78		
T <sub>sp</sub>	0.57 $\pm$ 0.14	4.33		
<b>Model</b>			0.52	0.52
<b><i>Fagus sylvatica</i></b>				
NAO <sub>a</sub>	0.48 $\pm$ 0.07	34.37		
NAO <sub>sp</sub>	0.85 $\pm$ 0.07	88.22		
P <sub>sm</sub>	-0.22 $\pm$ 0.08	3.95		
T <sub>a</sub>	-0.16 $\pm$ 0.07	0.14		
<b>Model</b>			0.51	0.55
<b><i>Quercus petraea</i></b>				
NAO <sub>a</sub>	-0.20 $\pm$ 0.08	0.90		
T <sub>a</sub>	0.35 $\pm$ 0.08	11.89		
<b>Model</b>			0.21	0.21
<b><i>Quercus robur</i></b>				
P <sub>sm</sub>	0.30 $\pm$ 0.12	1.42		
T <sub>a</sub>	0.72 $\pm$ 0.16	14.34		
T <sub>w</sub>	-0.38 $\pm$ 0.15	2.45		
<b>Model</b>			0.26	0.28

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586

588 **Table 5:** a) Average synchrony (average Spearman's correlation of fruit production between  
 589 sites:  $\rho \pm$  standard error) in annual fruit production (NPP), seasonal temperature (T), and  
 590 precipitation (P) between sites within species. b) Standardised slopes between synchrony and  
 591 geographical distance ( $\beta \pm$  standard error). Bold coefficients indicate values that differ from  
 592 zero at the 0.05 level ( $t$ -test).  $N$  indicates the number of pairwise comparisons. The seasons  
 593 are indicated by subscripts: w, sp, sm, and a indicate winter, spring, summer, and autumn,  
 594 respectively.

	<i>A. alba</i>	<i>P. abies</i>	<i>P. menziesii</i>	<i>F. sylvatica</i>	<i>Q. petraea</i>	<i>Q. robur</i>
<b>a) Synchrony (<math>\rho</math>)</b>						
Fruit NPP	<b>0.36 <math>\pm</math> 0.07</b>	<b>0.31 <math>\pm</math> 0.08</b>	0.19 $\pm$ 0.20	<b>0.60 <math>\pm</math> 0.02</b>	<b>0.20 <math>\pm</math> 0.04</b>	<b>0.29 <math>\pm</math> 0.07</b>
T <sub>w</sub>	<b>0.90 <math>\pm</math> 0.01</b>	<b>0.89 <math>\pm</math> 0.02</b>	<b>0.82 <math>\pm</math> 0.02</b>	<b>0.89 <math>\pm</math> 0.01</b>	<b>0.96 <math>\pm</math> 0.01</b>	<b>0.94 <math>\pm</math> 0.01</b>
T <sub>sp</sub>	<b>0.73 <math>\pm</math> 0.03</b>	<b>0.70 <math>\pm</math> 0.05</b>	<b>0.72 <math>\pm</math> 0.07</b>	<b>0.74 <math>\pm</math> 0.02</b>	<b>0.85 <math>\pm</math> 0.01</b>	<b>0.78 <math>\pm</math> 0.03</b>
T <sub>sm</sub>	<b>0.96 <math>\pm</math> 0.01</b>	<b>0.95 <math>\pm</math> 0.01</b>	<b>0.94 <math>\pm</math> 0.02</b>	<b>0.94 <math>\pm</math> 0.01</b>	<b>0.96 <math>\pm</math> 0.01</b>	<b>0.95 <math>\pm</math> 0.01</b>
T <sub>a</sub>	<b>0.81 <math>\pm</math> 0.02</b>	<b>0.82 <math>\pm</math> 0.03</b>	<b>0.73 <math>\pm</math> 0.06</b>	<b>0.69 <math>\pm</math> 0.02</b>	<b>0.79 <math>\pm</math> 0.01</b>	<b>0.85 <math>\pm</math> 0.02</b>
P <sub>w</sub>	<b>0.71 <math>\pm</math> 0.04</b>	<b>0.80 <math>\pm</math> 0.03</b>	<b>0.34 <math>\pm</math> 0.15</b>	<b>0.44 <math>\pm</math> 0.03</b>	<b>0.68 <math>\pm</math> 0.02</b>	<b>0.38 <math>\pm</math> 0.08</b>
P <sub>sp</sub>	<b>0.62 <math>\pm</math> 0.04</b>	<b>0.56 <math>\pm</math> 0.07</b>	<b>0.62 <math>\pm</math> 0.08</b>	<b>0.53 <math>\pm</math> 0.03</b>	<b>0.58 <math>\pm</math> 0.03</b>	<b>0.67 <math>\pm</math> 0.03</b>
P <sub>sm</sub>	<b>0.56 <math>\pm</math> 0.04</b>	<b>0.61 <math>\pm</math> 0.07</b>	<b>0.39 <math>\pm</math> 0.14</b>	<b>0.42 <math>\pm</math> 0.03</b>	<b>0.77 <math>\pm</math> 0.01</b>	<b>0.65 <math>\pm</math> 0.05</b>
P <sub>a</sub>	<b>0.61 <math>\pm</math> 0.05</b>	<b>0.74 <math>\pm</math> 0.03</b>	<b>0.57 <math>\pm</math> 0.13</b>	<b>0.49 <math>\pm</math> 0.03</b>	<b>0.68 <math>\pm</math> 0.02</b>	<b>0.59 <math>\pm</math> 0.04</b>
<b>b) <math>\beta</math> with distance</b>						
Fruit NPP	-0.20 $\pm$ 0.16	-0.35 $\pm$ 0.21	-0.39 $\pm$ 0.38	-0.06 $\pm$ 0.08	-0.01 $\pm$ 0.09	<b>-0.71 <math>\pm</math> 0.13</b>
T <sub>w</sub>	<b>-0.65 <math>\pm</math> 0.13</b>	<b>-0.69 <math>\pm</math> 0.16</b>	-0.29 $\pm$ 0.39	<b>-0.54 <math>\pm</math> 0.07</b>	<b>-0.33 <math>\pm</math> 0.08</b>	<b>-0.79 <math>\pm</math> 0.12</b>
T <sub>sp</sub>	<b>-0.62 <math>\pm</math> 0.13</b>	<b>-0.44 <math>\pm</math> 0.20</b>	<b>-0.75 <math>\pm</math> 0.27</b>	<b>-0.67 <math>\pm</math> 0.06</b>	<b>-0.70 <math>\pm</math> 0.06</b>	<b>-0.82 <math>\pm</math> 0.11</b>
T <sub>sm</sub>	<b>-0.52 <math>\pm</math> 0.14</b>	-0.22 $\pm$ 0.22	-0.06 $\pm$ 0.41	<b>-0.41 <math>\pm</math> 0.07</b>	-0.07 $\pm$ 0.09	<b>-0.65 <math>\pm</math> 0.14</b>
T <sub>fall</sub>	<b>-0.51 <math>\pm</math> 0.14</b>	<b>-0.56 <math>\pm</math> 0.19</b>	-0.02 $\pm$ 0.41	<b>-0.44 <math>\pm</math> 0.07</b>	<b>-0.32 <math>\pm</math> 0.08</b>	<b>-0.50 <math>\pm</math> 0.16</b>
P <sub>w</sub>	<b>-0.86 <math>\pm</math> 0.08</b>	<b>-0.45 <math>\pm</math> 0.20</b>	<b>-0.75 <math>\pm</math> 0.27</b>	<b>-0.58 <math>\pm</math> 0.06</b>	<b>-0.21 <math>\pm</math> 0.08</b>	<b>-0.68 <math>\pm</math> 0.14</b>
P <sub>sp</sub>	<b>-0.75 <math>\pm</math> 0.11</b>	-0.31 $\pm$ 0.21	-0.03 $\pm$ 0.41	<b>-0.35 <math>\pm</math> 0.07</b>	<b>-0.37 <math>\pm</math> 0.08</b>	-0.04 $\pm$ 0.19
P <sub>sm</sub>	<b>-0.41 <math>\pm</math> 0.15</b>	<b>-0.67 <math>\pm</math> 0.17</b>	-0.54 $\pm$ 0.34	<b>-0.36 <math>\pm</math> 0.07</b>	<b>-0.47 <math>\pm</math> 0.08</b>	<b>-0.61 <math>\pm</math> 0.15</b>
P <sub>fall</sub>	<b>-0.79 <math>\pm</math> 0.10</b>	<b>-0.64 <math>\pm</math> 0.17</b>	-0.30 $\pm$ 0.39	<b>-0.58 <math>\pm</math> 0.06</b>	<b>-0.60 <math>\pm</math> 0.07</b>	<b>-0.79 <math>\pm</math> 0.12</b>
<b><math>N</math></b>	38	22	8	163	135	30

596 **Table 6:** Average synchrony (Spearman's  $\rho \pm$  standard error) between sites within and amongst species. Comparisons  
 597 amongst leaf types and all sites are also shown. Bold coefficients indicate values that differ from zero at the 0.05 level ( $t$ -test).  
 598 The number of comparisons is shown in brackets below each coefficient. Only comparisons with five or more years of shared  
 599 data were used.

	<i>Abies alba</i>	<i>Picea abies</i>	<i>Pseudotsuga menziesii</i>	<i>Fagus sylvatica</i>	<i>Quercus petraea</i>	<i>Quercus robur</i>
<i>Abies alba</i>	<b>0.36 ± 0.07</b> (38)	0.07 ± 0.07 (53)	0.10 ± 0.06 (23)	<b>0.20 ± 0.03</b> (161)	<b>0.12 ± 0.03</b> (116)	<b>0.26 ± 0.03</b> (81)
<i>Picea abies</i>	0.07 ± 0.07 (53)	<b>0.31 ± 0.08</b> (22)	0.02 ± 0.06 (24)	<b>0.08 ± 0.04</b> (130)	<b>0.09 ± 0.04</b> (113)	0.04 ± 0.04 (46)
<i>Pseudotsuga menziesii</i>	0.10 ± 0.06 (23)	0.02 ± 0.06 (24)	0.19 ± 0.20 (8)	<b>-0.10 ± 0.05</b> (65)	-0.07 ± 0.05 (86)	-0.13 ± 0.10 (19)
<i>Fagus sylvatica</i>	<b>0.20 ± 0.03</b> (161)	<b>0.08 ± 0.04</b> (130)	<b>-0.10 ± 0.05</b> (65)	<b>0.60 ± 0.02</b> (163)	<b>-0.12 ± 0.03</b> (279)	<b>0.10 ± 0.04</b> (141)
<i>Quercus petraea</i>	<b>0.12 ± 0.03</b> (116)	<b>0.09 ± 0.04</b> (113)	-0.07 ± 0.05 (86)	<b>-0.12 ± 0.03</b> (279)	<b>0.20 ± 0.04</b> (135)	<b>0.28 ± 0.04</b> (97)
<i>Quercus robur</i>	<b>0.26 ± 0.03</b> (81)	0.04 ± 0.04 (46)	-0.13 ± 0.10 (19)	<b>0.10 ± 0.04</b> (141)	<b>0.28 ± 0.04</b> (97)	<b>0.29 ± 0.07</b> (30)
<b>Comparisons amongst leaf types</b>						
Broadleaves	<b>0.17 ± 0.02</b> (845)					
Conifers	<b>0.17 ± 0.03</b> (168)					
All species	<b>0.12 ± 0.01</b> (1830)					

600





602 **Table 7:** Summary of the models correlating synchrony ( $\rho$ ) of fruit production between sites  
 603 with synchrony in meteorological conditions. Coefficients are  $\beta$  weights  $\pm$  standard error.  $R^2$   
 604 indicates the total variance explained by the model. All coefficients were statistically significant  
 605 at the 0.05 level. Only comparisons with five or more years of shared data were used in the  
 606 models. The variables of seasonal temperature and precipitation are indicated by T and P,  
 607 respectively. The seasons are indicated by subscripts: w, sp, sm, and a indicate winter, spring,  
 608 summer, and autumn, respectively.

	<i>A. alba</i>	<i>P. abies</i>	<i>F. sylvatica</i>	<i>Q. petraea</i>	<i>Q. robur</i>
<b>Distance</b>					-0.71 $\pm$ 0.13
<b>T<sub>a</sub></b>	0.45 $\pm$ 0.15				
<b>P<sub>w</sub></b>			0.20 $\pm$ 0.08		
<b>P<sub>sm</sub></b>				0.20 $\pm$ 0.09	
<b>R<sup>2</sup></b>	0.20	-	0.04	0.04	0.50
<b>Comparisons</b>	38	22	163	135	30

609