

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_w) 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⁻² y⁻¹, 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 0.25×0.25 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 Δ 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 Δ 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 (ρ) 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 (ρ) 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 (ρ) 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 ΔBIC . 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 ΔBIC , 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 ΔBIC . 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 ± 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_w (i.e., associated to dry and cool winters), but fruit production in
328 broadleaved species was positively correlated with NAO_{sp} (associated with warm and dry
329 springs) and negatively correlated with NAO_a (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_{sp} 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_a⁻) 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_{sm}⁺) 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_{sm} 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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543 tropical forest. - *Ecology* 80: 1632–1647.

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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.

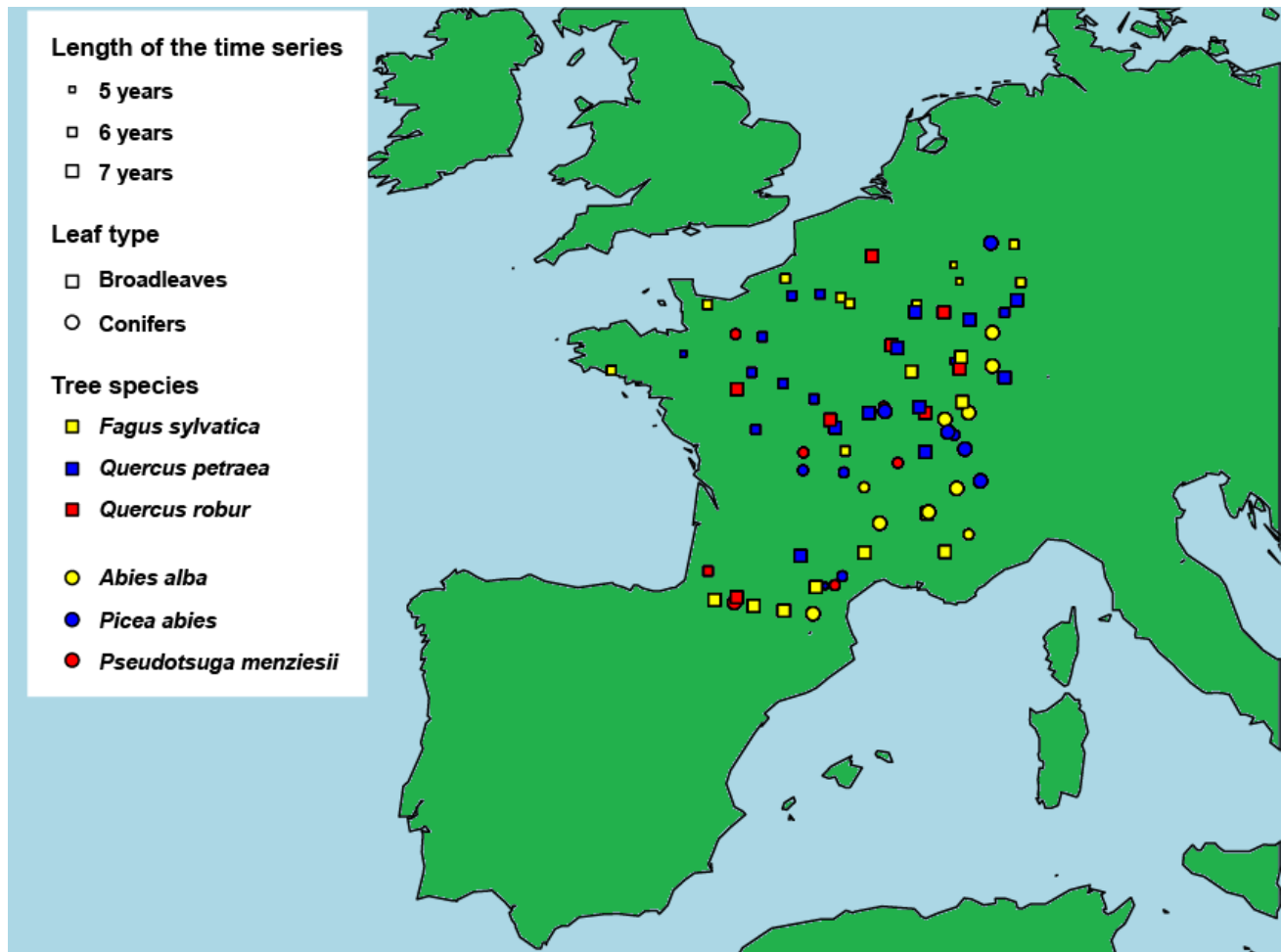
549 **Figure 2:** Relationships between the seasonal North Atlantic Oscillation (NAO) indices and
550 weather for 2002–2010. Positive (+) and negative (-) symbols after NAO indicate positive and
551 negative phases of the index. Values are β weights calculated using generalised linear mixed
552 models 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**

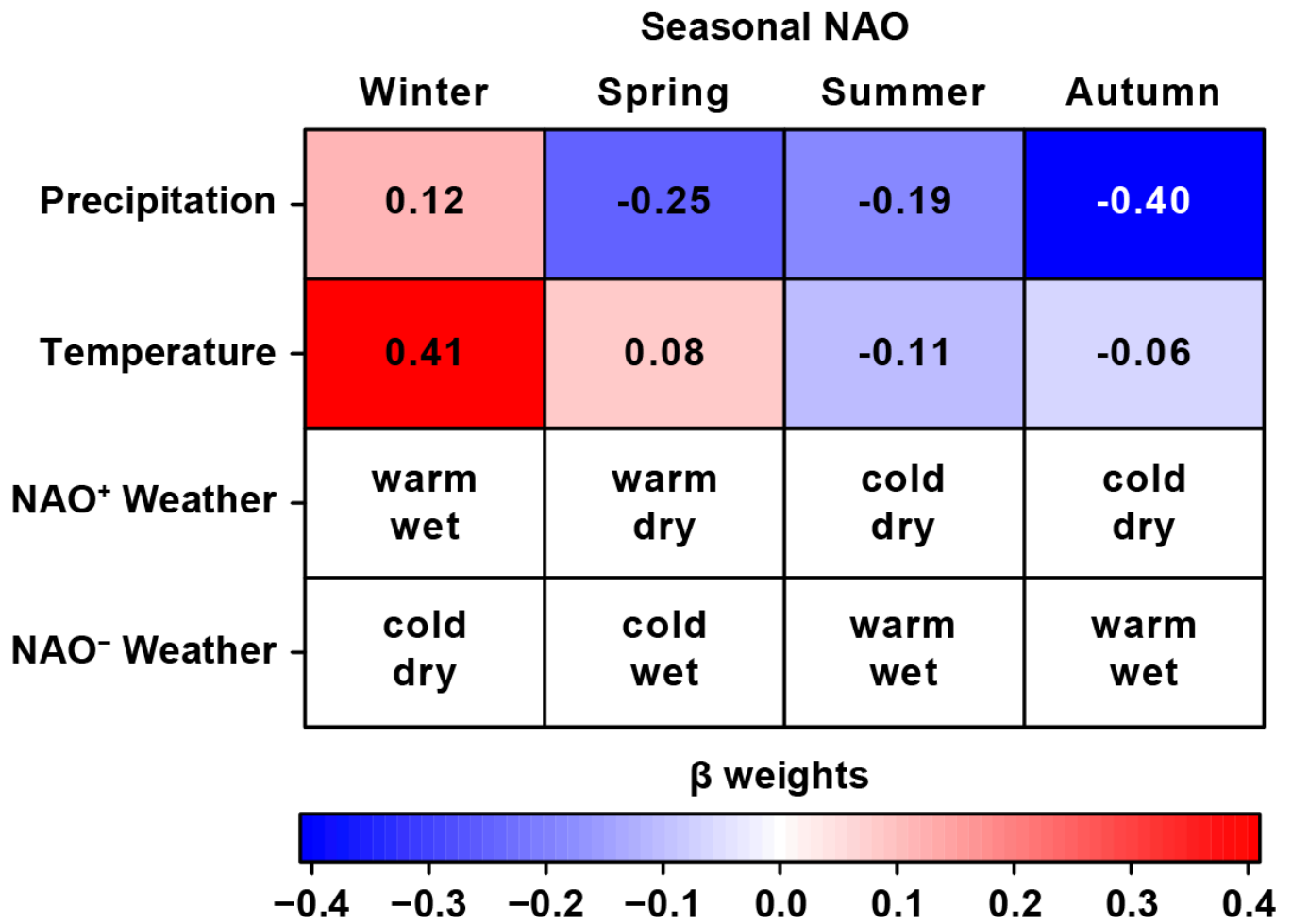


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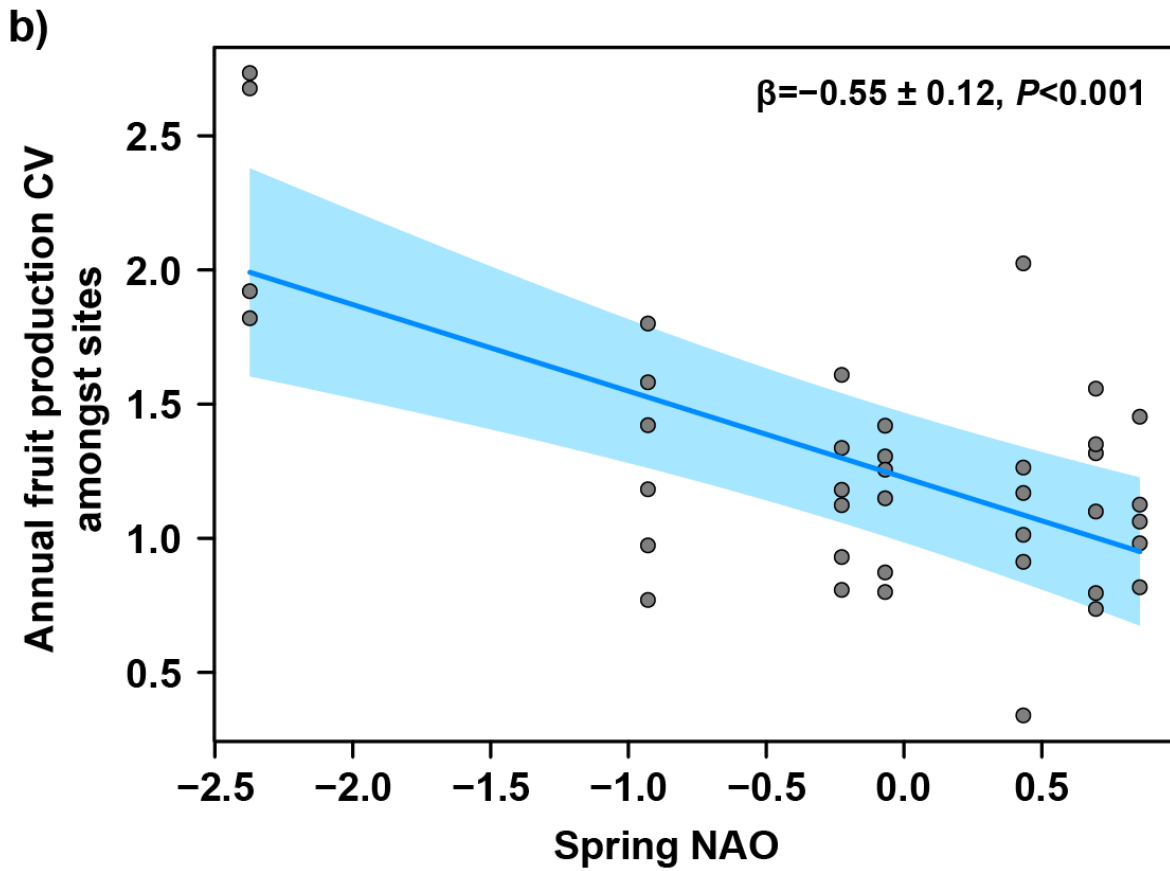
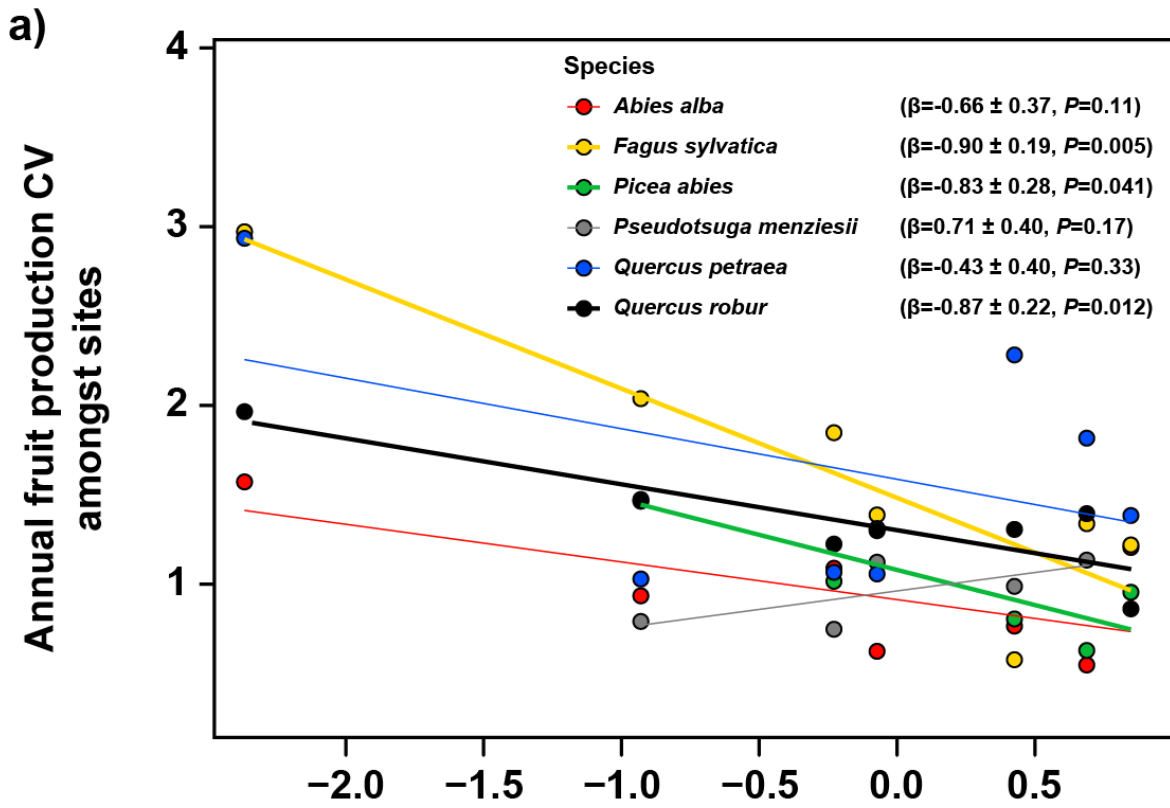
563 **Figure 2**



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565

566 **Figure 3**



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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
a) Interannual variability			
Resource matching	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.
Efficiency of pollination	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) Synchrony			
The Moran effect	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.
Pollen coupling	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.

Questions	Analyses
<i>a) Meteorological variability</i>	
Do seasonal NAO indices correlate with seasonal weather at our sites?	Generalised linear mixed models (with site as random factor) correlating seasonal temperature and precipitation with seasonal NAO indices.
<i>b) Interannual variability in fruit production</i>	
Do seasonal NAO indices correlate with fruit production?	Spearman correlations between fruit production and seasonal NAO indices per site.
Is fruit production best predicted by local meteorological variability or by seasonal NAO indices?	Generalised linear mixed models per species (with site as random factor) correlating annual fruit production with seasonal temperatures, precipitation, and NAO indices.
<i>c) Synchrony in fruit production</i>	
For a given year, is variability in fruit production amongst sites associated with variability in meteorological conditions or to seasonal NAO indices?	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.
Is fruit production (and weather) synchronised across sites within and amongst species?	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).
Is synchrony of fruit production and weather between sites spatially dependent?	Linear models correlating synchrony of fruit production and seasonal temperatures and precipitation between sites with geographical distance.
Does synchrony in fruit production between sites depend on synchrony in meteorological conditions and geographical distance?	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 _a		P		NAO _w		P		NAO _{sp}		P		NAO _{sm}		P		N	
a) Species																		
<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) Leaf type																		
Conifers	-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	
Broadleaves	-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)). Δ 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	Δ BIC	R^2_m	R^2_c
<i>Abies alba</i>				
NAO _w	-0.40 \pm 0.10	10.81		
NAO _{sp}	0.42 \pm 0.09	13.59		
P _w	-0.29 \pm 0.11	0.90		
Model			0.39	0.47
<i>Picea abies</i>				
NAO _{sm}	0.31 \pm 0.07	11.51		
P _{sp}	-0.32 \pm 0.12	2.62		
P _w	0.49 \pm 0.12	11.41		
T _{sm}	0.38 \pm 0.18	0.52		
Model			0.26	0.79
<i>Pseudotsuga menziesii</i>				
NAO _a	0.39 \pm 0.10	10.63		
NAO _w	-0.29 \pm 0.11	3.78		
T _{sp}	0.57 \pm 0.14	4.33		
Model			0.52	0.52
<i>Fagus sylvatica</i>				
NAO _a	0.48 \pm 0.07	34.37		
NAO _{sp}	0.85 \pm 0.07	88.22		
P _{sm}	-0.22 \pm 0.08	3.95		
T _a	-0.16 \pm 0.07	0.14		
Model			0.51	0.55
<i>Quercus petraea</i>				
NAO _a	-0.20 \pm 0.08	0.90		
T _a	0.35 \pm 0.08	11.89		
Model			0.21	0.21
<i>Quercus robur</i>				
P _{sm}	0.30 \pm 0.12	1.42		
T _a	0.72 \pm 0.16	14.34		
T _w	-0.38 \pm 0.15	2.45		
Model			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>
a) Synchrony (ρ)						
Fruit NPP	0.36 \pm 0.07	0.31 \pm 0.08	0.19 \pm 0.20	0.60 \pm 0.02	0.20 \pm 0.04	0.29 \pm 0.07
T _w	0.90 \pm 0.01	0.89 \pm 0.02	0.82 \pm 0.02	0.89 \pm 0.01	0.96 \pm 0.01	0.94 \pm 0.01
T _{sp}	0.73 \pm 0.03	0.70 \pm 0.05	0.72 \pm 0.07	0.74 \pm 0.02	0.85 \pm 0.01	0.78 \pm 0.03
T _{sm}	0.96 \pm 0.01	0.95 \pm 0.01	0.94 \pm 0.02	0.94 \pm 0.01	0.96 \pm 0.01	0.95 \pm 0.01
T _a	0.81 \pm 0.02	0.82 \pm 0.03	0.73 \pm 0.06	0.69 \pm 0.02	0.79 \pm 0.01	0.85 \pm 0.02
P _w	0.71 \pm 0.04	0.80 \pm 0.03	0.34 \pm 0.15	0.44 \pm 0.03	0.68 \pm 0.02	0.38 \pm 0.08
P _{sp}	0.62 \pm 0.04	0.56 \pm 0.07	0.62 \pm 0.08	0.53 \pm 0.03	0.58 \pm 0.03	0.67 \pm 0.03
P _{sm}	0.56 \pm 0.04	0.61 \pm 0.07	0.39 \pm 0.14	0.42 \pm 0.03	0.77 \pm 0.01	0.65 \pm 0.05
P _a	0.61 \pm 0.05	0.74 \pm 0.03	0.57 \pm 0.13	0.49 \pm 0.03	0.68 \pm 0.02	0.59 \pm 0.04
b) β with distance						
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	-0.71 \pm 0.13
T _w	-0.65 \pm 0.13	-0.69 \pm 0.16	-0.29 \pm 0.39	-0.54 \pm 0.07	-0.33 \pm 0.08	-0.79 \pm 0.12
T _{sp}	-0.62 \pm 0.13	-0.44 \pm 0.20	-0.75 \pm 0.27	-0.67 \pm 0.06	-0.70 \pm 0.06	-0.82 \pm 0.11
T _{sm}	-0.52 \pm 0.14	-0.22 \pm 0.22	-0.06 \pm 0.41	-0.41 \pm 0.07	-0.07 \pm 0.09	-0.65 \pm 0.14
T _{fall}	-0.51 \pm 0.14	-0.56 \pm 0.19	-0.02 \pm 0.41	-0.44 \pm 0.07	-0.32 \pm 0.08	-0.50 \pm 0.16
P _w	-0.86 \pm 0.08	-0.45 \pm 0.20	-0.75 \pm 0.27	-0.58 \pm 0.06	-0.21 \pm 0.08	-0.68 \pm 0.14
P _{sp}	-0.75 \pm 0.11	-0.31 \pm 0.21	-0.03 \pm 0.41	-0.35 \pm 0.07	-0.37 \pm 0.08	-0.04 \pm 0.19
P _{sm}	-0.41 \pm 0.15	-0.67 \pm 0.17	-0.54 \pm 0.34	-0.36 \pm 0.07	-0.47 \pm 0.08	-0.61 \pm 0.15
P _{fall}	-0.79 \pm 0.10	-0.64 \pm 0.17	-0.30 \pm 0.39	-0.58 \pm 0.06	-0.60 \pm 0.07	-0.79 \pm 0.12
N	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>	0.36 ± 0.07 (38)	0.07 ± 0.07 (53)	0.10 ± 0.06 (23)	0.20 ± 0.03 (161)	0.12 ± 0.03 (116)	0.26 ± 0.03 (81)
<i>Picea abies</i>	0.07 ± 0.07 (53)	0.31 ± 0.08 (22)	0.02 ± 0.06 (24)	0.08 ± 0.04 (130)	0.09 ± 0.04 (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)	-0.10 ± 0.05 (65)	-0.07 ± 0.05 (86)	-0.13 ± 0.10 (19)
<i>Fagus sylvatica</i>	0.20 ± 0.03 (161)	0.08 ± 0.04 (130)	-0.10 ± 0.05 (65)	0.60 ± 0.02 (163)	-0.12 ± 0.03 (279)	0.10 ± 0.04 (141)
<i>Quercus petraea</i>	0.12 ± 0.03 (116)	0.09 ± 0.04 (113)	-0.07 ± 0.05 (86)	-0.12 ± 0.03 (279)	0.20 ± 0.04 (135)	0.28 ± 0.04 (97)
<i>Quercus robur</i>	0.26 ± 0.03 (81)	0.04 ± 0.04 (46)	-0.13 ± 0.10 (19)	0.10 ± 0.04 (141)	0.28 ± 0.04 (97)	0.29 ± 0.07 (30)
Comparisons amongst leaf types						
Broadleaves	0.17 ± 0.02 (845)					
Conifers	0.17 ± 0.03 (168)					
All species	0.12 ± 0.01 (1830)					

600

602 **Table 7:** Summary of the models correlating synchrony (ρ) of fruit production between sites
 603 with synchrony in meteorological conditions. Coefficients are β 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>
Distance					-0.71 \pm 0.13
T_a	0.45 \pm 0.15				
P_w			0.20 \pm 0.08		
P_{sm}				0.20 \pm 0.09	
R²	0.20	-	0.04	0.04	0.50
Comparisons	38	22	163	135	30

609