The North Atlantic Oscillation synchronises fruit production in western European forests

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Abstract

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

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

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1. Introduction

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

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

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

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

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

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

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

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

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

2. Materials and methods

2.1. Data collection

2.1.1. Data for litterfall and foliar nutrient concentration

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

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

2.1.2. Meteorological data

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

2.2. Data analyses

2.2.1. Interannual variability of fruit production

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

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

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

2.2.2. Synchrony of fruit production among forests

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

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

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

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

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

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

3. Results

3.1. Effects of seasonal NAO on local weather

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

3.2. Interannual variability of fruit production

Both changes in weather and the seasonal NAO indices were individually correlated with fruit 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).

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

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

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

4. Discussion

4.1. Teleconnection indices as biological predictors

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

4.2. Controls of interannual variability of fruit production

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

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

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

4.3. Controls of synchrony of fruit production

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

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

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

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

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

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

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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.

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544

545

Figure captions

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

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

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

557

Figure 1

563 **Figure 2**

Seasonal NAO

	Winter	Spring	Summer	Autumn
Precipitation	0.12	-0.25	-0.19	-0.40
Temperature	0.41	0.08	-0.11	-0.06
NAO⁺ Weather	warm wet	warm dry	cold dry	cold dry
NAO⁻ Weather	cold dry	cold wet	warm wet	warm wet

β weights

−0.4 −0.3 −0.2 −0.1 0.0 0.1 0.2 0.3 0.4

564

565

566   **Figure 3**

a)

Species
- *Abies alba* (β=-0.66 ± 0.37, *P*=0.11)
- *Fagus sylvatica* (β=-0.90 ± 0.19, *P*=0.005)
- *Picea abies* (β=-0.83 ± 0.28, *P*=0.041)
- *Pseudotsuga menziesii* (β=0.71 ± 0.40, *P*=0.17)
- *Quercus petraea* (β=-0.43 ± 0.40, *P*=0.33)
- *Quercus robur* (β=-0.87 ± 0.22, *P*=0.012)

b)

β=−0.55 ± 0.12, *P*<0.001

Spring NAO

567

568
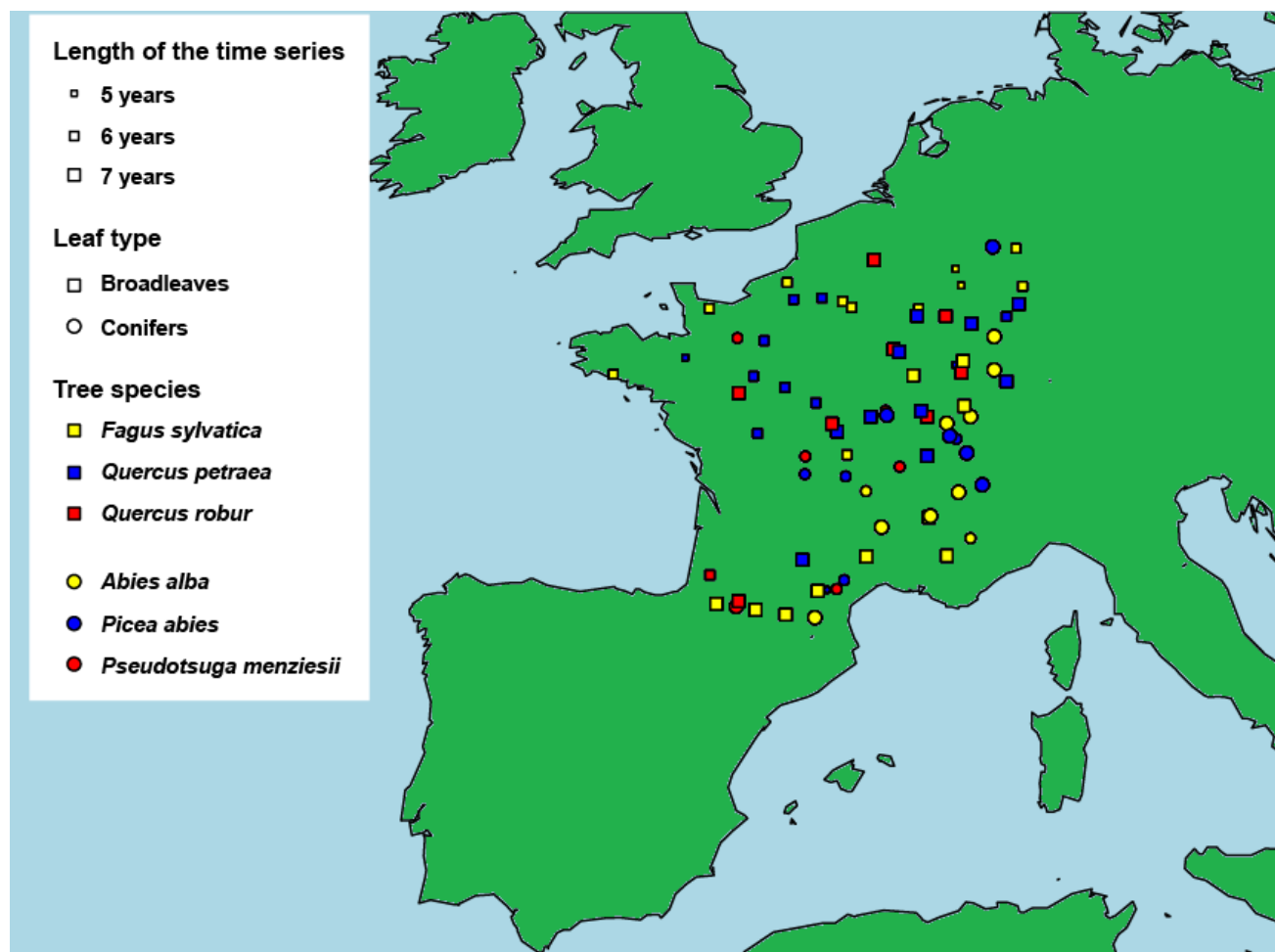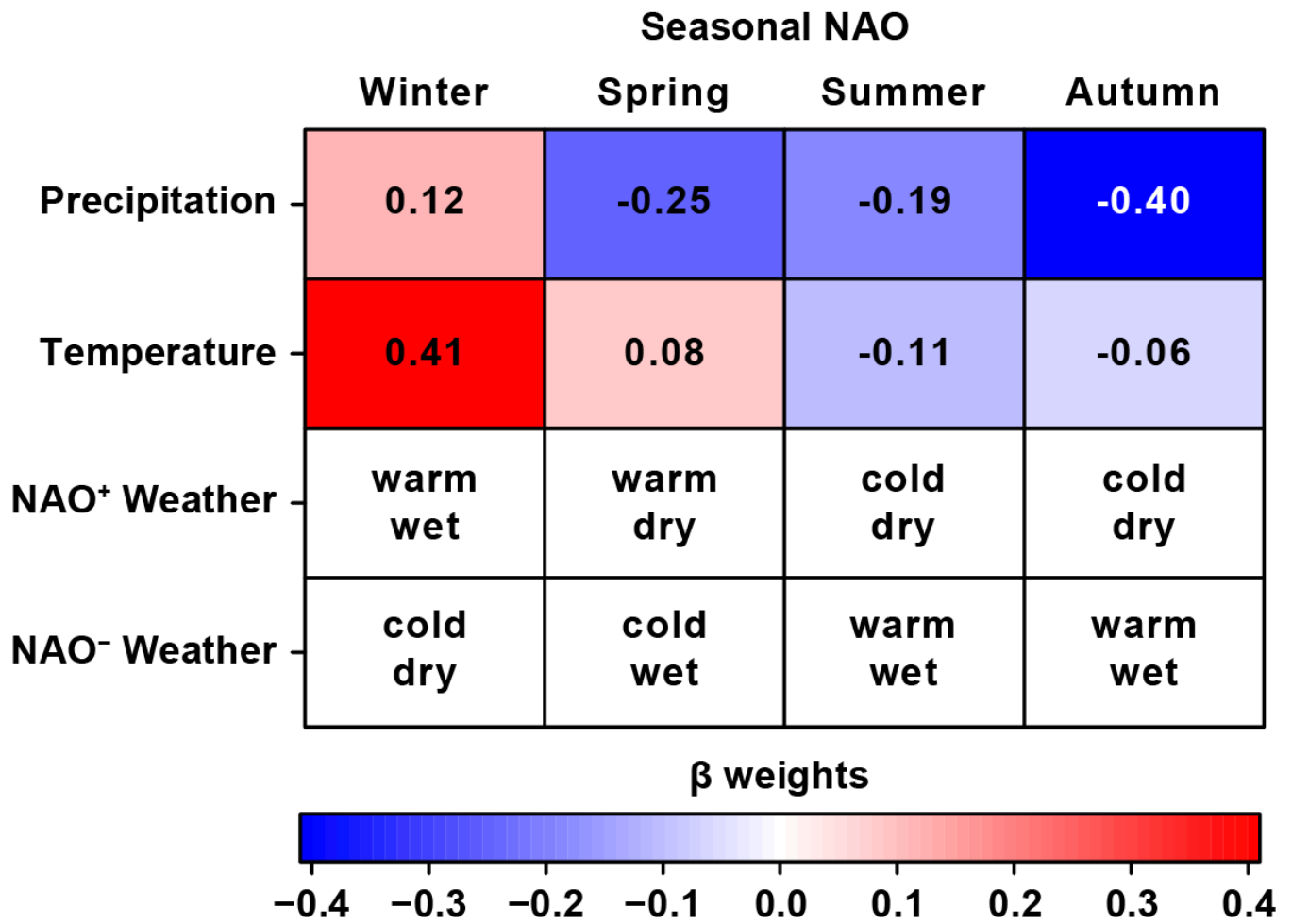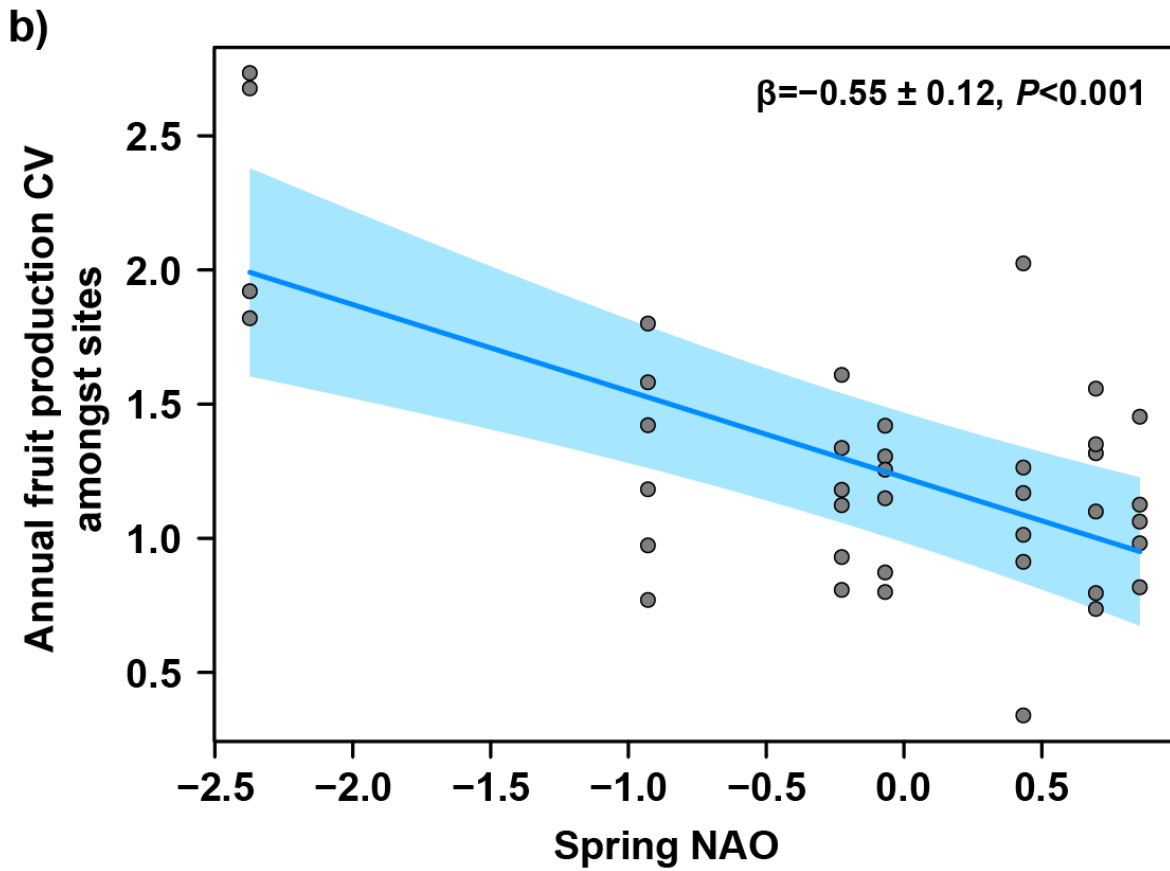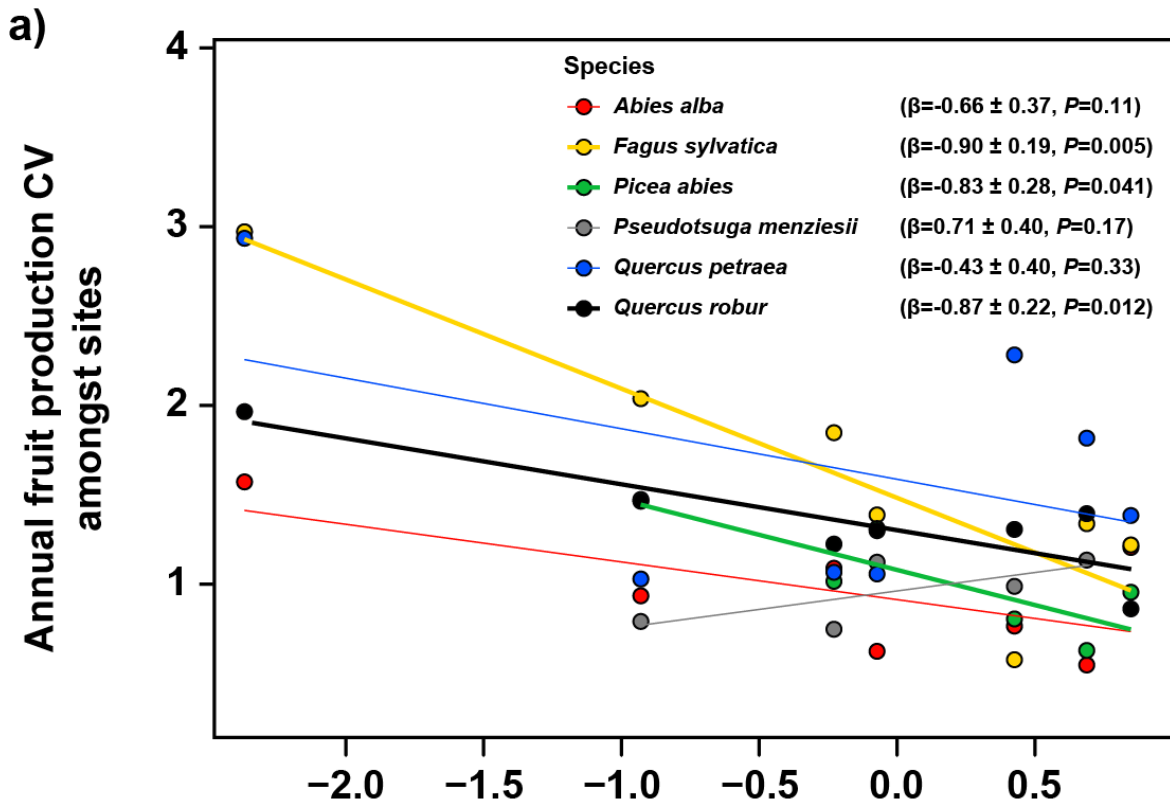
Table 1: Summary of the hypotheses discussed in this study for interannual variability and synchrony in fruit production. Our analysis was focused on weather relationships with interannual variability and synchrony in fruit production, so only indirect evidence of the weather relationships supporting 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.

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

Questions	Analyses
a) Meteorological variability	
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.
b) Interannual variability in fruit production	
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.
c) Synchrony in fruit production	
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 (ρ ± 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																	
Abies alba	-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
Picea abies	-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
Pseudotsuga menziesii	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
Fagus sylvatica	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
Quercus petraea	-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
Quercus robur	-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

27

578 **Table 4:** Summary of the models predicting fruit production per species. Standardised
579 coefficients are shown as model estimates (β ± standard error (SE)). ΔBIC 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.

	β ± SE	ΔBIC	R^2_m	R^2_c
Abies alba				
NAO_w	-0.40 ± 0.10	10.81		
NAO_{sp}	0.42 ± 0.09	13.59		
P_w	-0.29 ± 0.11	0.90		
Model			0.39	0.47
Picea abies				
NAO_{sm}	0.31 ± 0.07	11.51		
P_{sp}	-0.32 ± 0.12	2.62		
P_w	0.49 ± 0.12	11.41		
T_{sm}	0.38 ± 0.18	0.52		
Model			0.26	0.79
Pseudotsuga menziesii				
NAO_a	0.39 ± 0.10	10.63		
NAO_w	-0.29 ± 0.11	3.78		
T_{sp}	0.57 ± 0.14	4.33		
Model			0.52	0.52
Fagus sylvatica				
NAO_a	0.48 ± 0.07	34.37		
NAO_{sp}	0.85 ± 0.07	88.22		
P_{sm}	-0.22 ± 0.08	3.95		
T_a	-0.16 ± 0.07	0.14		
Model			0.51	0.55
Quercus petraea				
NAO_a	-0.20 ± 0.08	0.90		
T_a	0.35 ± 0.08	11.89		
Model			0.21	0.21
Quercus robur				
P_{sm}	0.30 ± 0.12	1.42		
T_a	0.72 ± 0.16	14.34		
T_w	-0.38 ± 0.15	2.45		
Model			0.26	0.28

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587

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

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

595

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

	Abies alba	*Picea abies*	*Pseudotsuga menziesii*	*Fagus sylvatica*	*Quercus petraea*	*Quercus robur*
Abies alba	**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)
Picea abies	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)
Pseudotsuga menziesii	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)
Fagus sylvatica	**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)
Quercus petraea	**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)
Quercus robur	**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)

601

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 ± 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.

	A. alba	*P. abies*	*F. sylvatica*	*Q. petraea*	*Q. robur*
Distance					-0.71 ± 0.13
T_a	0.45 ± 0.15				
P_w			0.20 ± 0.08		
P_{sm}				0.20 ± 0.09	
R^2	0.20	-	0.04	0.04	0.50
Comparisons	38	22	163	135	30

609