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Weather and trade-offs between growth and reproduction regulate fruit production in European forests

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Abstract

Some tree species have a highly variable year-to-year pattern of reproduction which has repercussions for the entire ecosystem. Links between meteorological variability, fruit production and crown cover, and trade-offs between reproduction and vegetative growth, remain elusive, despite a long history of research. We explored how meteorological conditions determined variations in fruit production and crown cover and how remotely sensed vegetation indices, such as the enhanced vegetation index (EVI), may be used to characterize the fluctuations in fruit production. We used data for fruit production from six European tree species (*Abies alba*, *Picea abies*, *Pseudotsuga menziesii*, *Fagus sylvatica*, *Quercus petraea* and *Q. robur*) growing in monospecific stands, EVI and seasonal meteorological variables (precipitation and temperature) for 2002-2010. Weather accounted for fruit production better than EVI. Deciduous trees were more responsive to weather than evergreens, most notably to different seasonal temperatures, which was positively correlated mainly with crown cover and fruit production in deciduous species. Our results also suggested different patterns of relationships between fruit production, crown cover and weather, indicating different strategies of resource management. These patterns indicated a possible internal trade-off in evergreens, with resources allocated to either growth or reproduction. In contrast, in deciduous species we found no evidence for such a trade-off between vegetative growth and reproduction.

Keywords: Variability, fruit production, EVI, crown cover, weather, trade-off.

1. Introduction

Seed and fruit production are key functions for both plants and ecosystems. They are essential parts of the biological cycle of individual plants, because they allow them to reproduce and thus transmit their genes to the next generation and disperse the species. However, fruit production is variable from year to year, and some species might even show an extremely erratic pattern of low and massive fruit production among years (Espelta et al. 2008; Kelly et al. 2013). Fruiting variability will thus have an impact on the entire ecosystem by affecting various processes. For example, a variable supply of seeds and fruits will entail a bottom-up cascade of trophic responses by causing fluctuations in the population densities of fruit and seed consumers. By extension, this will affect the population densities of their predators and competitors (Ostfeld and Keesing, 2000; Espelta *et al.*, 2008, 2017; Bogdziewicz *et al.*, 2016).

Determining the factors that drive fruit production has been the focus of many studies in recent decades (Kelly 1994; Koenig and Knops 2000; Kelly and Sork 2002; Pérez-Ramos et al. 2015; Fernández-Martínez et al. 2017b), and various hypotheses have been proposed to account for fluctuations from year to year. The most commonly accepted theories accounting for the proximal causes of fruit production involve tree resources: the hypothesis of *resource matching* [also known as the hypothesis of *weather tracking* (Kelly 1994; Kelly and Sork 2002; Pearse et al. 2016)], the hypothesis of *resource accumulation* (Isagi et al. 1997; Satake and Iwasa 2000; Camarero et al. 2010; Fernández-Martínez et al. 2015; Pearse et al. 2016) and the hypothesis of *resource switching* (Norton and Kelly 1988; Kelly and Sork 2002; Sánchez Humanes and Espelta Morral 2011). These hypotheses stipulate that fruit production is driven by the levels of resources in trees (e.g. carbohydrates and nutrients), which in turn are regulated to some extent by meteorological conditions such as temperature or rainfall, even though these conditions can also act as synchronizing cues (Kelly and Sork 2002; Sala et al.

2012; Ichie et al. 2013; Bogdziewicz et al. 2017; Fernández-Martínez et al. 2017a). The resource-matching hypothesis proposes that fruit production would indirectly respond to meteorological conditions by the availability of resources, with reproduction likely positively correlated with growth. Years of good weather would thus favor photosynthesis, so more resources would be available for both vegetative and secondary growth and for reproduction (Kelly, 1994; Kelly and Sork, 2002; Fernández-Martínez *et al*., 2015; Pearse *et al*., 2016). The resource-accumulation hypothesis, though, refers to the accumulation of resources up to a threshold. Massive fruit production is then triggered and thus the exhaustion of the accumulated resources when the threshold is reached, usually decreasing vegetative and secondary growth as a trade-off (Pearl and Verma, 1988; Kelly, 1994; Fernández-Martínez *et al.*, 2015; Bogdziewicz *et al*., 2016). This hypothesis implies that resource reserves would be severely depleted after an episode of high fruit production, which could also entail a negative autocorrelation in annual fruit production (Kelly, 1994; Fernández-Martínez *et al.*, 2012, 2015). Finally, resource switching hypothesis states that there is a trade-off between reproduction and vegetative growth from year to year (Sánchez Humanes and Espelta Morral, 2011).

These hypotheses suggest that the resource levels should vary among trees. Previous studies have inferred these changes by monitoring the dynamics of the crown cover (Camarero et al. 2010; Fernández-Martínez et al. 2015). These studies tested this inference using remotely sensed vegetation indices such as the normalized difference vegetation index [NDVI, (Camarero et al. 2010)] and the enhanced vegetation index [EVI, (Fernández-Martínez et al. 2015)]. These indices are useful in comparative studies of spatial and temporal variations in the crown cover and, by extension, of variations in the photosynthetic capacity of forests (Huete *et al*., 2002; Garbulsky *et al*. 2013; Fernández-Martínez *et al*. 2019).

The aim of our study was thus to determine the influence of meteorological conditions on fruit production and crown cover in monospecific forests of *Abies alba*, *Picea abies*, *Pseudotsuga menziesii*, *Fagus sylvatica*, *Quercus petraea* and *Q. robur* distributed across Europe. We also evaluated the ability of remotely sensed vegetation indices to account for the temporal and spatial variability of fruit production in these forests. We hypothesized that variations in crown cover, estimated using EVI, could reliably monitor fruit production in forests. We also hypothesized that evergreen and deciduous trees would have different strategies of resource management, indicated by their relationships between fruit production, crown cover and weather.

We achieved these goals by first identifying the differences among species in the average and interannual variability of fruit production and EVI. We then determined the spatial relationship between the variations in fruit production and EVI and the relationships between annual variations in fruit production, EVI and meteorological variables. Finally, we determined the direct and indirect effects of meteorological and EVI variables on fruit production.

2. Materials and methods

2.1 Data collection

2.1.1 Data for fruit production

We used data for fruit production from 76 European forests distributed over France, Luxemburg and Germany (Figure 1). All sites were monospecific stands of deciduous species: *F. sylvatica* (21 sites), *Q. petraea* (20 sites) or *Q. robur* (9 sites), and evergreen species: *A. alba* (10 sites), *P. menziesii* (6 sites) or *P. abies* (10 sites). All species are producers of dry fruits.

The data for fruit production were obtained from the ICP Forests database (International Co-operative Program 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 data were gathered using the methods for litterfall sampling described by ICP Forests (Ukonmaanaho *et al.*, 2016). Litterfall was collected using nets or litterbags distributed uniformly over the sampling areas to ensure that entire plots were represented in the samples, not just the dominant trees; more collectors may have been used for deciduous species, because their leaves are more affected by air turbulence. The litter was then separated into fractions (leaves, fruits and branches). The data contained records of fruit net primary production (fNPP) from 2002 to 2013 in units of $gDW \times m^{-2} \times y^{-1}$ that were then converted to $gC \ \times m^{-2} \times y^{-1}$ using the data for C concentration provided by the same database and then used to calculate the average fNPP per year for each site. The database contained many more sites, but only monospecific forests with fNPP records for at least five years (the longest available record was seven years) were selected to avoid artifacts in the results.

2.1.2 Crown-cover estimates (satellite data) and meteorological data

We preferentially used EVI rather than NDVI for estimating crown cover, because EVI is more sensitive to structural variations of the crown and has provided good results in previous studies (Fernández-Martínez *et al*., 2015). EVI time series for each forest were obtained from the MOD13Q1 MODIS (Moderate Resolution Imaging Spectroradiometer, <https://modis.gsfc.nasa.gov/>) product for 18 February 2000 to 16 November 2016, with a spatial resolution of 250 × 250 m and a temporal resolution of 16 days. We only used the central pixels of the forest stand in our analysis. Because of this, we were not able to select single crowns.

Time series for precipitation and temperature were extracted from the meteorological database of the MARS unit AGRI4CAST/JRC (<http://agri4cast.jrc.ec.europa.eu/>), with a spatial resolution of 0.25 × 0.25°, for 2002-2010, which provided monthly mean temperatures and total precipitation.

We used monthly values for both the EVI and meteorological data to estimate average values of EVI, temperature and precipitation per season for each year: October-December for autumn of the year previous to fruit ripening, January-March for winter, April-June for spring and July-September for summer. We then calculated the seasonal means for each site using the yearly averages previously calculated. Finally, we estimated the anomalies associated with EVI, temperature and precipitation for each year by subtracting the seasonal mean per site to the yearly seasonal value. We only used the values between 2002 and 2008 for the EVI data to maintain consistency between the EVI and meteorological data. We decided to use only weather conditions for the year of, or previous to fruit ripening based on previous studies suggesting that the selected time frame is very important for explaining variations in fruit production (Kelly *et al.* 2013; Fernández-Martínez *et al*. 2017a).

2.2 Statistical analyses

We first determined the differences in annual means and interannual variability in fNPP and EVI among species by calculating the average EVI per year and its associated standard error (SE) using the seasonal values of EVI in our data. We then calculated the average EVI per site using the average annual EVI. The SE for EVI per site was estimated by propagating the SE for average annual EVI, following the error-propagation method:

$$\delta C = \sqrt{(\delta A)^2 + (\delta B)^2}$$

Where δ is the standard error for variables A, B, and C. The same procedure was used to calculate the average EVI per species, using the average EVI per site and propagating its SE across sites. The fNPP data contained annual values, which were used to calculate the average fNPP per site and its associated SE. We then calculated the average fNPP per species using the average fNPP per site and propagating its SE.

The interannual variabilities of fNPP and EVI were assessed by calculating the proportional variability index [PV, see section 1 in Supplementary Materials (method S1) (Heath, 2006)] and the disparity index [D, see section 2 in Supplementary Materials (method S2) (Martín-Vide 1986; Fernández-Martínez et al. 2017b, 2018)]. Both PV and D provide a more robust assessment than the coefficient of variation ($CV = SD \times mean^{-1}$) of the temporal variability, because they are much less sensitive to changes in the mean of the time series, among other properties (Martín-Vide, 1986; Heath, 2006; Fernández-Martínez *et al.*, 2017a). PV and D are similar in concept, but D differs from PV in that D takes into account the chronological order of the values of the time series, but PV is insensitive to the order (Fernández-Martínez *et al.*, 2017b). Estimating site and species-specific variability allowed us to differentiate the behavior of fNPP and EVI between sites and species. These indices for EVI were first estimated for the annual average EVI using the seasonal EVI values. Annual values of these indices were then averaged per site, and the associated SEs were calculated. Finally, the values of the indices per species were estimated by calculating the mean of the average indices per site and propagating its SE. PV and D for fNPP were first estimated for the average fNPP per site using the annual fNPP values. The values of the indices per site were then averaged per species, and their associated SEs were calculated.

We tested for differences among species by first performing analyses of variance (ANOVAs) using generalized linear mixed models (GLMMs) from the “nlme” R package (Pinheiro *et al*., 2018). Average fNPP and EVI (separately) per site were the response variables, species was the explanatory variable and sampling site was the random factor. We fitted linear models for PV and D in which the average indices per site were the response variables and species was the explanatory variable. We then performed Tukey’s honestly significant difference (HSD) tests at $P < 0.05$ for multiple comparisons on each model. These analyses allowed us to determine whether species could be grouped by reproductive behavior.

We also identified the spatial relationships between the variations in fNPP and EVI to determine whether greener sites (i.e. those with higher EVIs) also had higher average fruit production. We used average values per site and fitted a GLMM, with average fNPP per site as the response variable, average EVI per site as the explanatory variable and species as the random factor, using the “nlme” R package (Pinheiro et al. 2018). We also similarly tested each species individually by fitting a linear model and correlating average fNPP with the average EVI for each species separately.

We estimated the relationships between the annual variations of fNPP, EVI and meteorological variables by fitting one GLMM per species, where fNPP was the response variable, and anomalies of yearly seasonal averages of EVI, temperature and precipitation (see subsection 2.1.2) were the explanatory variables (e.g. $Fruit\ NPP\ year\ i \sim EVI\ autumn\ year\ i-1 + EVI\ winter\ year\ i + \cdots$). Site was the random factor. We applied a natural logarithm to the response variable in this model to maintain a normal distribution of the residuals. Variables were selected using the stepwise backward-forward method, starting from the full model (containing all possible variables and interactions) and using the Bayesian information criterion (BIC). The stepwise model selection used the “stepAIC” function of the “MASS” R package (Venerables and Ripley, 2002). ΔBIC was then calculated as the difference between the BICs of the full model and the model without the target variable as a measure of variable importance. The collinearity of the variables was evaluated using the variance inflation factor (VIF) and the “vif” function in the “car” R package (Fox and Weisberg, 2011): VIF was approximately 1 for each variable, indicating no problems of multicollinearity. The model results were visualized using partial-residual plots in the “visreg” R package (Breheny and Burchett, 2017). The variances explained by the fixed factors (marginal coefficient of determination, R^2_m) and both fixed and random factors (conditional coefficient of determination, R^2_c) were calculated using the “rsquaredGLMM” function of the “MuMIn” R package (Barton, 2018).

Finally, we determined the direct and indirect effects of the seasonal meteorological variables and EVI on fNPP for each species by path analyses, using the method of directed separation (d-separation). D-separation is a type of path analysis that uses directed acyclic graphs (DAGs) and that specifies sets of variables (represented by nodes in a DAG), for which independence is conditioned by a third variable (Pearl and Verma, 1988; Voyer and Garamszegi, 2014). That is, two variables, A and B, may be correlated using a third variable, C; A and B are d-separated by C if the knowledge of A, having established C, does not provide more information of B. The independence of A and B is thus conditioned by the nature of C. This method allowed us to fit path analyses while taking into account site as the random factor. We then defined the paths. Seasonal meteorological variables were defined as exogenous variables, i.e. they could potentially have a direct effect on both fNPP and EVI and an indirect effect on fNPP through EVI. fNPP and seasonal EVI variables were defined as endogenous variables, i.e. seasonal EVI variables could potentially be directly affected by meteorological variables and directly affect fNPP. The total effect of a variable on fNPP was calculated by adding its direct effect on fNPP to its indirect effect on fNPP multiplied by the direct effect of the intermediary variable on fNPP. That is, variable A directly affects variable B and C, and variable B directly affects variable C; the total effect of A on C is due to the direct effect of A on C plus the effect of A on B multiplied by the effect of B on C (i.e. the indirect effect of A on C). These analyses used R script, which is available upon request.

3. Results

3.1 Differences in average fruit production and EVI and their variability between species

Our analyses identified significant differences in fruit production between species ($P < 0.001$) when testing for differences between species. *A. alba* and *P. abies* had the highest fNPPs (Figure 2). EVI was lower for *A. alba* and *P. abies* than the other species (Figure 2, Table S1). PV and D had different patterns, with generally higher values for the deciduous species, *F. sylvatica*, *Q. petraea* and *Q. robur* (Figure 2), i.e. the deciduous species varied more year to year than the evergreen species, *A. alba*, *P. abies* and *P. menziesii*. fNPP generally had higher variability indices than EVI, particularly for D (Figure 2, Table S1). Both PV and D had more similar values for EVI than fNPP (Figure 2, Table S1).

When testing for spatial relationships between variations in fNPP and EVI, average fNPP and EVI did not differ significantly among the sites, both when using all sites and using each species individually ($P > 0.05$, for both linear models and GLMMs). Sites with more variable EVIs were not correlated with sites with more variable fNPP ($P > 0.05$). The spatial variability of EVI was therefore not linked to the spatial variability of fNPP in our database. Therefore, it is not conclusive whether a lower or higher fruit production is related to the site being greener.

3.2 Relationships among weather, EVI and fruit production

The path analyses identified a positive effect of winter temperature on spring EVI for all species (Figure 3). Winter temperature also had a positive effect on winter EVI for all three deciduous species (*F. sylvatica*, *Q. petraea* and *Q. robur*). Spring temperature also had a positive effect on spring EVI for *F. sylvatica* and *Q. petraea* (Figure 3d and e) and for the evergreen species *P. abies*. Spring temperature, however, negatively affected spring EVI for *P. menziesii* (Figure 3b and c). Spring EVI for *F. sylvatica* was favored by precipitation in winter (Figure 3d). Autumn EVI was affected negatively by autumn precipitation for *Q. petraea* and positively by autumn temperature for *Q. robur* (Figure 3e and f). Spring precipitation had a positive effect, and summer temperature had a negative effect, on summer EVI for *Q. robur* (Figure 3f).

Winter temperature was the most recurrent meteorological variable associated with fNPP. Winter temperature was associated negatively with fNPP for *A. abla* and *P. menziesii* and positively for *Q. petraea* (Figure 3a, c, and e). fNPP for both oaks, *Q. petraea* and *Q. robur*, responded similarly to the meteorological variables. Autumn temperature had a positive effect on fNPP for both species (Figure 3e and f). fNPP was also positively correlated with high summer temperature in both species. This result differs from those for *P. menziesii* where fNPP was negatively correlated with high summer temperature (Figure 4). fNPP for *Q. robur* was positively correlated with high precipitation in summer and high temperatures in autumn (Table 1, Figure 4). *F. sylvatica* and *P. abies* had similar associations: fNPP for both species was correlated negatively with precipitation in spring and positively in winter (Figure 4). The GLMM analyses identified some similarities among the evergreen species: fNPP for both *A. alba* and *P. abies* was negatively correlated with winter temperature (Table 1, Figure 4).

fNPP was correlated with EVI for *A. alba*, *F. sylvatica* and *Q. petraea* (Table 1, Figure 5). The response for *F. sylvatica* was more similar to the responses for the evergreen species than to the responses for the other deciduous species. fNPP was negatively correlated with summer EVI for both *A. alba* and *F. sylvatica*. fNPP was correlated positively with autumn EVI and negatively with spring EVI for *F. sylvatica* (Figure 5). This outcome was similar to the outcome of the path analyses for *P. menziesii*: fNPP was correlated positively with autumn EVI and negatively with spring EVI (Figure 3). The response differed for *Q. petraea*: fNPP was positively correlated with spring EVI (Figure 5). fNPP was not significantly correlated with the EVI variables for *P. abies*, *P. menziesii* or *Q. robur* (Table 1). Seasonal EVI (spring) directly affected fNPP in the path analyses only for *P. menziesii* and *Q. petraea* (Figure 3c and e): positively for *Q. petraea* and negatively for *P. menziesii*.

P. menziesii and *Q. petraea* were the only species with indirect effects of the meteorological variables on fNPP through EVI in addition to the direct effects of the meteorological variables. Spring EVI for both species was correlated with winter and spring temperatures that in turn were correlated with fNPP. Winter temperature negatively affected fNPP, with both negative direct and indirect effects through spring EVI. Spring temperature did not have a direct effect on fNPP but was negatively correlated with it through spring EVI, leading to a small positive total effect (Figure 3c, Table 2). Winter and spring temperatures had a positive direct and indirect effect on fNPP through spring EVI, leading to a positive total effect on fNPP (Figure 3e, Table 2), in contrast to *P. menziesii.*

4. Discussion

4.1 Weather as a driver of crown cover and fruit production

Precipitation was positively correlated with crown cover of the following season for *F. sylvatica* and *Q. robur* (winter precipitation for spring EVI and spring precipitation for summer EVI, Figure 3d and f, respectively). Fruit production responded positively to precipitation in the autumn previous to fruit ripening for *Q. petraea* and to precipitation in winter for *P. abies* and *F. sylvatica* (Figure 4). In contrast, fruit production was negatively correlated with spring precipitation for *P. abies*, *F. sylvatica* and *A. alba* (Figures 3 and 4). Precipitation generally has a positive effect on crown cover and fruit production, because it can increase the photosynthetic capacity of trees and nutrient mineralization in dry soils. Especially wet autumns and winters may increase fruit production by the replenishment and accumulation of mineral resources. More resources would then be available for fruit production in the next productive season [especially N (Sardans and Peñuelas 2007; Smaill et al. 2011; Bogdziewicz et al. 2017)].

Crown cover in the summer was negatively correlated with summer temperature for *Q. robur.* Fruit production for this species was also positively correlated with summer precipitation (Figure 4). When combined with precipitation shortages, warm temperatures, particularly soon after the end of dormancy and the start of the growing season, will accelerate soil drying and thereby negatively affect photosynthetic activity and slow vegetative growth, while respiration rates may increase (Martín-Benito et al. 2008; Adams et al. 2009; Carevic et al. 2010; Olivar et al. 2011; Estiarte and Peñuelas 2015). These effects would decrease the internal resources available for fruit production and could also cause premature fruit abscission (Carevic et al. 2010; Fernández-Martínez et al. 2012, 2015; Bogdziewicz et al. 2017).

Autumn temperature was positively correlated with crown cover in autumn for *Q. robur* and with fruit production for both oak species (Figures 3 and 4). Temperature and photoperiod are principal regulators of foliar senescence in autumn. A warm autumn before fruit ripening would delay foliar senescence and abscission and provide a longer period of photosynthetic activity, which would provide more time for trees to accumulate resources and to reabsorb nutrients from leaves before they fall (Staaf and Stjernquist 1986; Doi and Takahashi 2008; Estiarte and Peñuelas 2015), increasing the availability of nutrients for fruit production in the next growing season. These responses are consistent with the resource-matching hypothesis (Kelly and Sork 2002; Pearse et al. 2016).

Winter temperature was positively correlated with winter crown cover for all deciduous species, even though they do not have leaves during this season. The greenness detected in winter with EVI may be due to the presence of evergreen shrubs and perennial plants in the understory and not to the foliage of the deciduous trees. The positive effect of winter temperature on winter crown cover may thus be an artifact, with the trees exposed to longer and warmer autumns and springs. Winter temperature had a positive effect on crown cover in spring for all species (Figure 3). Warm winters and springs positively affect crown cover by advancing the period of foliar flushing, for deciduous species, and generally extending the growing period (Estiarte and Peñuelas 2015). Warmer winters and springs could also allow an early onset of pollination, extending the pollination period and thus potentially positively affecting fruit production (Frenguelli and Bricchi 1998; Fernández-Martínez et al. 2012). Evergreen trees will lower their metabolic rate to a minimum during winter, maintaining a minimal rate of primary production. They are thus able to accumulate and store resources during unfavorable winter conditions (Havranek and Tranquillini 1995; Falge et al. 2002; Pérez-Ramos et al. 2015). Shorter and warmer winters will shorten winter dormancy, with an increase in metabolic activity and an earlier renewal of growth that will be indicated by spring crown cover (Havranek and Tranquillini 1995), which would also imply higher respiration costs. Fewer resources will therefore remain available for reproduction at the end of winter, which would negatively affect reproduction rates (Havranek and Tranquillini 1995; Fernández-Martínez et al. 2017a), as indicated by the results for *P. menziesii* and *A. alba*, where winter temperature was negatively correlated with fruit production (Figures 3 and 4).

4.2 EVI and fruit production

Average fruit production was not significantly spatially correlated with EVI for any species, perhaps due to the low spatial resolution of our crown-cover data. Other factors, such as the heterogeneous meteorological conditions among the sampling sites, the structure and age of the forests or nutrient availability, which are important determinants of the spatial variability of fruit production, however, may have obscured a possible connection (Fernández-Martínez et al. 2017b).

Autumn temperature had a positive effect on fruit production of the next growing season for both oaks, *Q. petraea* and *Q. robur* (Figure 3). Fruit production was also positively correlated with autumn crown cover for *F. sylvatica* (Table 2). As stated above, temperature is a main regulator of foliar senescence in autumn, so warmer meteorological conditions are often found to extend the growing period (Estiarte and Peñuelas 2015). A greener crown cover in autumn would allow trees to store more resources that could be invested in fruiting in the following growing season. The weather had both direct and indirect effects on fruit production for *Q. petraea* through EVI. Both winter and spring temperatures had a positive effect on spring EVI, which in turn was positively correlated with fNPP (Figure 3), leading to a positive total effect from both temperatures on fruit production (Table 1). Fruit production was also positively correlated with spring EVI (Figure 5). Higher winter and spring temperatures could trigger an earlier phenology, which in turn would increase photosynthesis and thus favor reproduction.

This scenario is consistent with the resource-matching hypothesis, where favorable meteorological conditions would increase the accumulation of resources and their subsequent allocation to both growth and reproduction (Kelly and Sork 2002; Fernández-Martínez et al. 2012; Pearse et al. 2016).

P. menziesii, however, behaved differently. Winter temperature had an overall negative effect on fruit production (Table 1) and a positive effect on spring crown cover, which both negatively correlated with fruit production (Figure 3). This finding was described by Kelly (1994) as “resource switching”, common in genera such as *Abies*, *Picea*, *Pseudotsuga* and *Fagus* (Kelly and Sork 2002). Switching refers to the mechanism of reallocating resources from vegetative growth or storage to reproduction (Kelly 1994; Pearse et al. 2016), i.e. the internal trade-off between vegetative growth or storage and reproduction (Sánchez Humanes and Espelta Morral 2011). Our results for *P. menziesii* were similar to those for *A. alba* and *F. sylvatica*: winter and spring temperatures had a direct negative effect on fNPP and a positive effect on spring EVI for *A. alba* and *F. sylvatica*, respectively, with no obvious relationship between fNPP and spring EVI. fNPP was also negatively correlated with summer EVI for both species and with spring EVI for *F. sylvatica* (Table 2), suggesting that trees would prioritize growth and storage over reproduction when meteorological conditions were favorable for photosynthesis. When meteorological conditions deteriorated, the allocation of resources would shift to favor reproduction (Kelly and Sork 2002; Pearse et al. 2016). These results are consistent with those obtained for *P. menziesii* and with the resource-switching model. More conclusive results, however, would be needed for confirmation. Greener *P. abies* crown covers in spring were correlated with warm winters and springs, and fruit production was larger after warm summers, i.e. meteorological conditions that may favor photosynthesis in these species (Figure 3). The reproductive behavior of *P. abies* is consistent with the resource-matching hypothesis, in contrast to the other evergreen species.

The relationships between the meteorological variables, crown cover and fruit production could not be clearly distinguished between the evergreen and deciduous species. Some patterns among some of the evergreens and *F. sylvatica*, however, recurred, distinguishing them from the oaks. This similarity of *F. sylvatica* with the evergreens could be due to the difference in distribution of the species. *F. sylvatica* and the evergreens inhabit more humid and cooler zones than the oaks. *Q. petraea*, *Q. robur* and *P. abies* had similar clear patterns of a resource-matching strategy. In contrast, *A. alba* and *P. menziesii* favored more conservative strategies of resource management, i.e. the resource-switching model. This strategy may include increased nutrient-use efficiency, reducing nutrient loss by favoring the development of long-lasting tissues over reproduction and only occasionally inversing the trade-off (Aerts 1995; Sánchez Humanes and Espelta Morral 2011).

5. Conclusions

Crown cover was clearly influenced by meteorological conditions (especially temperature and particularly winter temperature). Its responses, however, depended on the species, particularly whether they were evergreen or deciduous. Fruit production was also sensitive to environmental conditions, mainly winter and spring temperatures. Crown cover and fruit production were correlated for *A. alba*, *F. sylvatica* and *Q. petraea*, although crown cover directly affected fruit production only for *P. menziesii* and *Q. petraea*.

The main differences observed between the species of this study were in the relationships between fruit production, crown cover and meteorological conditions and in the influence of seasonal meteorological conditions. Our results suggested that resource matching may occur in both *Quercus* species and *P. abies*. We instead observed a trade-off between growth and reproduction, following the resource-switching model, for *A. alba, P. menziesii* and *F. sylvatica*. This response could be due to a strategy to increase nutrient-use efficiency by prioritizing the production of long-lasting tissues. Though there seemed to be reoccurring patterns, there was no obvious differences between evergreen and deciduous trees. We would need a wider sample of species to conclude on whether there is indeed a separation in the patterns used by each.

Finally, the use of EVI as the sole monitoring tool could not accurately assess fluctuations in fruit production. Identifying species-specific relationships between EVI and fruit production will be needed to predict the sizes of fruit crops. The variability of the weather combined with EVI could be a useful proxy of the patterns of fruit production.

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Tables

Table 1. Summary of the GLMMs correlating fruit production with temperature (T) and precipitation (P) and for Enhanced Vegetation Index (EVI) for the autumn of the year previous to fruit ripening (au), winter (w), spring (sp) and summer (sm). Only the standardized coefficients for the most relevant variables identified by the BIC are presented. The variances explained by fixed (R2m) and random (R2c) factors are also presented.

Significance levels: *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$

Table 2. Summary of standardized total effects in the path analyses associating weather (T, temperature; P, precipitation) and Enhanced Vegetation Index (EVI) for each season (w, winter; sp, spring; sm, summer; au, autumn) with annual fruit production. Only significant (P < 0.05) values are shown.

Table 1

	$\beta \pm SE$		ΔBIC	R^2_m	R^2_c
Pinaceae					
Abies alba					
T_w	-0.382 ± 0.100	***	7.14		
EVI_{sm}	-0.282 ± 0.098	*	3.19		
Model				0.218	0.339
Picea abies					
P_w	0.203 ± 0.085	*	0.81		
P_{sp}	-0.270 ± 0.086	**	4.06		
Model				0.066	0.624
Pseudotsuga menziesii					
T_w	-0.484 ± 0.125	***	7.72		
T_{sm}	-0.432 ± 0.108	***	8.89		
Model				0.168	0.559
Fagaceae					
Fagus sylvatica					
P_w	0.344 ± 0.075	***	15.01		
P_{sp}	-0.170 ± 0.074	*	0.59		
EVI_{au}	0.203 ± 0.073	**	3.02		
EVI_{sp}	-0.276 ± 0.078	***	7.44		
EVI_{sm}	-0.247 ± 0.077	**	5.46		
Model				0.294	0.347
Quercus petraea					
T_{sm}	0.254 ± 0.083	**	4.33		
EVI_{sp}	0.479 ± 0.083	***	25.08		
Model				0.218	0.218
Quercus robur					
T_{au}	0.442 ± 0.108	***	11.57		
T_{sm}	0.272 ± 0.118	*	1.28		
P_{sm}	0.353 ± 0.117	**	4.98		
Model				0.346	0.346

Significance levels: *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$

Table 2

	Pinaceae			Fagaceae		
	A. alba	*P.menziesii*	*P. abies*	*F. sylvatica*	*Q. petraea*	*Q. robur*
Seasonal EVI						
EVI_{au}	-	0.12	-	-	-	-
EVI_{sp}	-	-0.25	-	-	0.45	-
Seasonal temperature						
T_{au}	-	-	-	-	0.5	0.34
T_{w}	-0.33	-0.24	-	-	0.51	-
T_{sp}	-	0.08	-	-0.35	0.44	-
T_{sm}	-	-	0.45	-	-	-
Seasonal precipitation						
P_{au}	-	-	-	-	0.2	-
P_{sp}	-0.24	-	-	-	-	-

Figures

Figure 1. Map of the distribution of the studied forests.

Figure 2. Box-and-whisker plots of the average fruit production (a), average Enhanced Vegetation Index (EVI) (b), proportional variability index for both fruit production (c) and EVI (d) and disparity index for both fruit production (e) and EVI (f) for each species. White boxes represent evergreen species (Abies alba, Pseudotsuga menziesii and Picea abies), and gray boxes represent deciduous species (Fagus sylvatica, Quercus petraea and Q. robur). Different letters indicate significant differences among the species. Average values and standard errors for each species are presented in Appendix Table S1. Boxes hold 50% of the data, with the bold horizontal line in the box indicating the median of the distribution. Whiskers hold the lower and higher 25% of the data, with the end of each whisker indicating respectively the minimum and the maximum value of the distribution. Dots outside the box and whiskers plot indicate outliers of the distribution.

Figure 3. Directed acyclic graphs of the d-separation path analysis for Abies alba (a), Picea abies (b), Pseudotsuga menziesii (c), Fagus sylvatica (d), Quercus petraea (e) and Q. robur (f). Each graph shows the direct effects of temperature (T), precipitation (P), and Enhanced Vegetation Index (EVI) for winter (w), spring (sp), summer (sm) and autumn (au) on annual fruit production (fNPP). The values of the effects are standardized estimates for comparing the variables within each model. Only significant paths ($P < 0.05$) are shown. Total effects on fruit production are presented in Table 1.

Figure 4. Partial-residual plots of the models correlating fruit production (fNPP) with temperature (T) and precipitation (P) for autumn (au), winter (w), spring (sp) and summer (sm) for Abies alba (a), Pseudotsuga menziesii (b and c), Picea abies (d and e), Quercus

petraea (f), Q. robur (g and h) and Fagus sylvatica (i and j). Beta weights (β ± SE) and the P values are indicated for each model. The blue lines represent the slope of the relationship, and the gray shading indicates the 95% confidence intervals. Only the two most relevant relationships between weather and fruit production are shown for Q. robur (based on the BIC); see Table 2 for detailed information.

Figure 5. Partial-residual plots of the models correlating fruit production (fNPP) with Enhanced Vegetation Index (EVI) for autumn (au), spring (sp) and summer (sm) for Fagus sylvatica (a and b), Quercus petraea (c) and Abies alba (d). Beta weights (β ± SE) and P values are indicated for each model. The blue lines represent the slopes of the relationship, and the gray shading indicates the 95% confidence intervals. Only the two most relevant relationships between EVI and fruit production are shown for F. sylvatica (based on the BIC); see Table 2 for detailed information.

Figure 1.

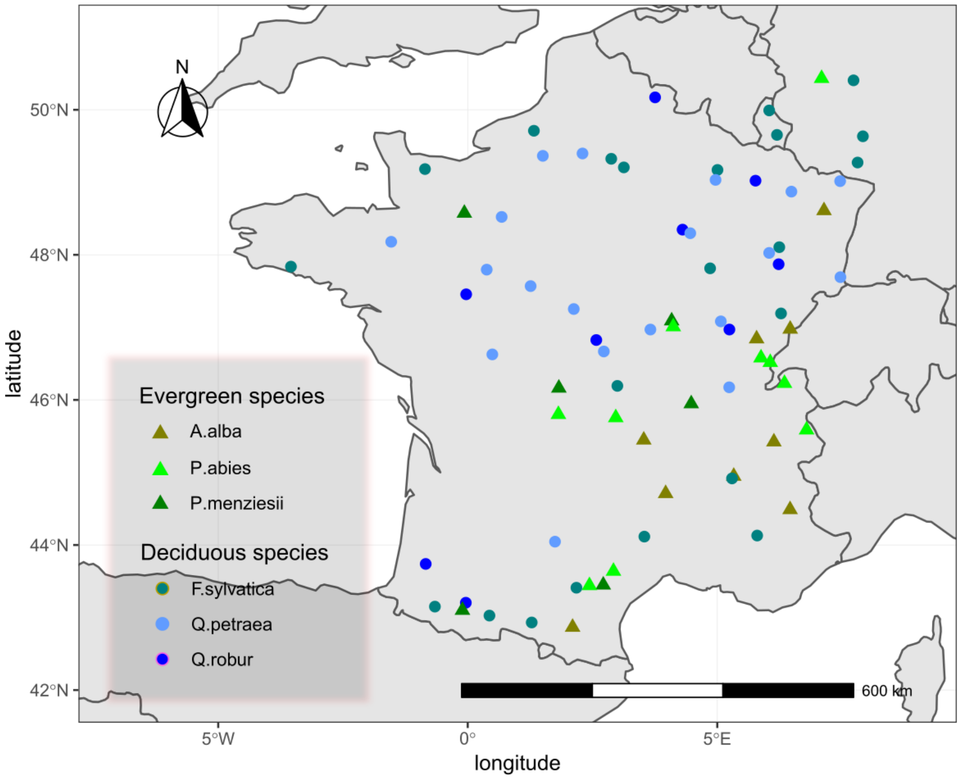

N
50°N
48°N
46°N
44°N
42°N
latitude
5°W
0°
5°E
longitude
600 km
Evergreen species
A.alba
P.abies
P.menziesii
Deciduous species
F.sylvatica
Q.petraea
Q.robur

Figure 2.

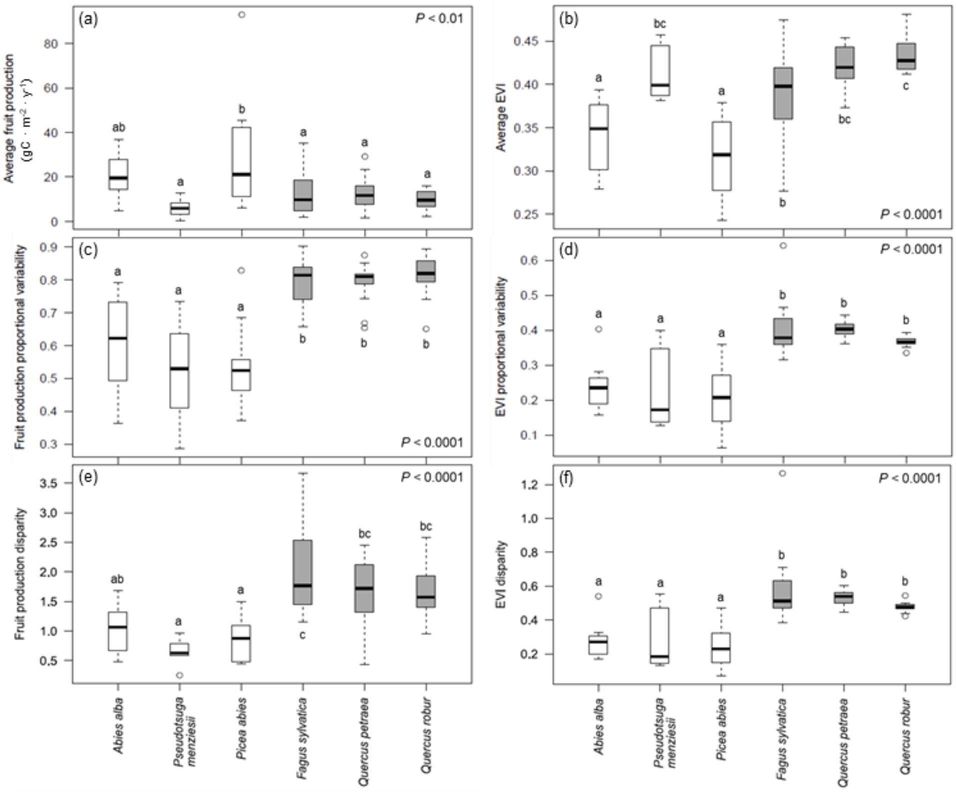

(a)
P < 0.01
Average fruit production (gC · m-2 · y-1)
0
20
40
60
80
ab
a
b
a
a
a
(b)
Average EVI
0.25
0.30
0.35
0.40
0.45
a
bc
a
b
bc
c
P < 0.0001
(c)
Fruit production proportional variability
0.3
0.4
0.5
0.6
0.7
0.8
0.9
a
a
a
b
b
b
P < 0.0001
(d)
P < 0.0001
EVI proportional variability
0.1
0.2
0.3
0.4
0.5
0.6
a
a
a
b
b
b
(e)
P < 0.0001
Fruit production disparity
0.5
1.0
1.5
2.0
2.5
3.0
3.5
ab
a
a
c
bc
bc
(f)
P < 0.0001
EVI disparity
0.2
0.4
0.6
0.8
1.0
1.2
a
a
a
b
b
b
Abies alba
Pseudotsuga menziesii
Picea abies
Fagus sylvatica
Quercus petraea
Quercus robur

Figure 3.

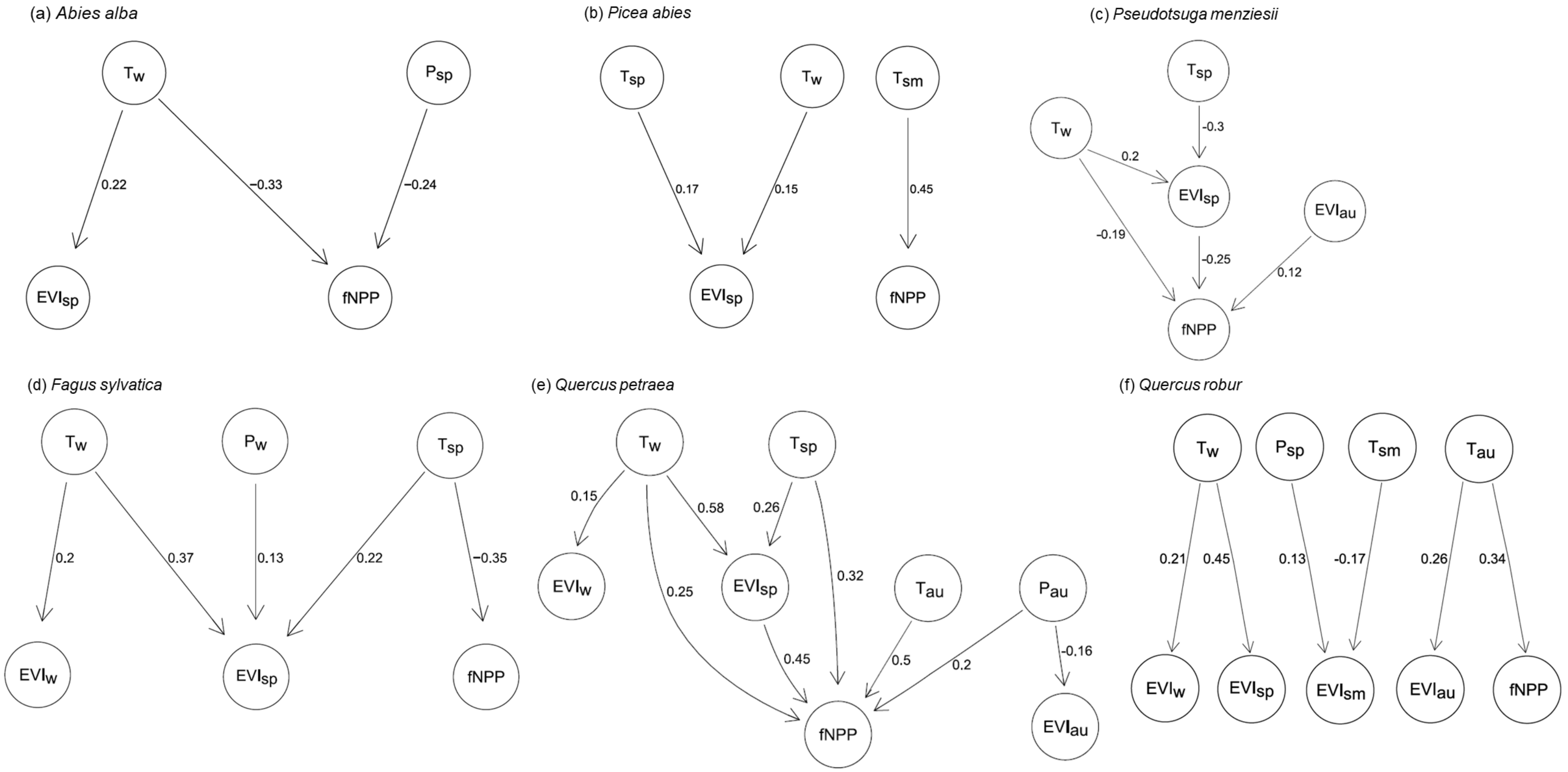

(a) Abies alba
Tw
Psp
0.22
−0.33
−0.24
EVIsp
fNPP
(b) Picea abies
Tsp
Tw
Tsm
0.17
0.15
0.45
EVIsp
fNPP
(c) Pseudotsuga menziesii
Tsp
Tw
-0.3
0.2
EVIsp
EVIau
-0.19
-0.25
0.12
fNPP
(d) Fagus sylvatica
Tw
Pw
Tsp
0.2
0.37
0.13
0.22
−0.35
EVIw
EVIsp
fNPP
(e) Quercus petraea
Tw
Tsp
0.15
0.58
0.26
EVIw
0.25
EVIsp
0.32
Tau
Pau
0.45
0.5
0.2
-0.16
fNPP
EVIau
(f) Quercus robur
Tw
Psp
Tsm
Tau
0.21
0.45
0.13
-0.17
0.26
0.34
EVIw
EVIsp
EVIsm
EVIau
fNPP

Figure 4.

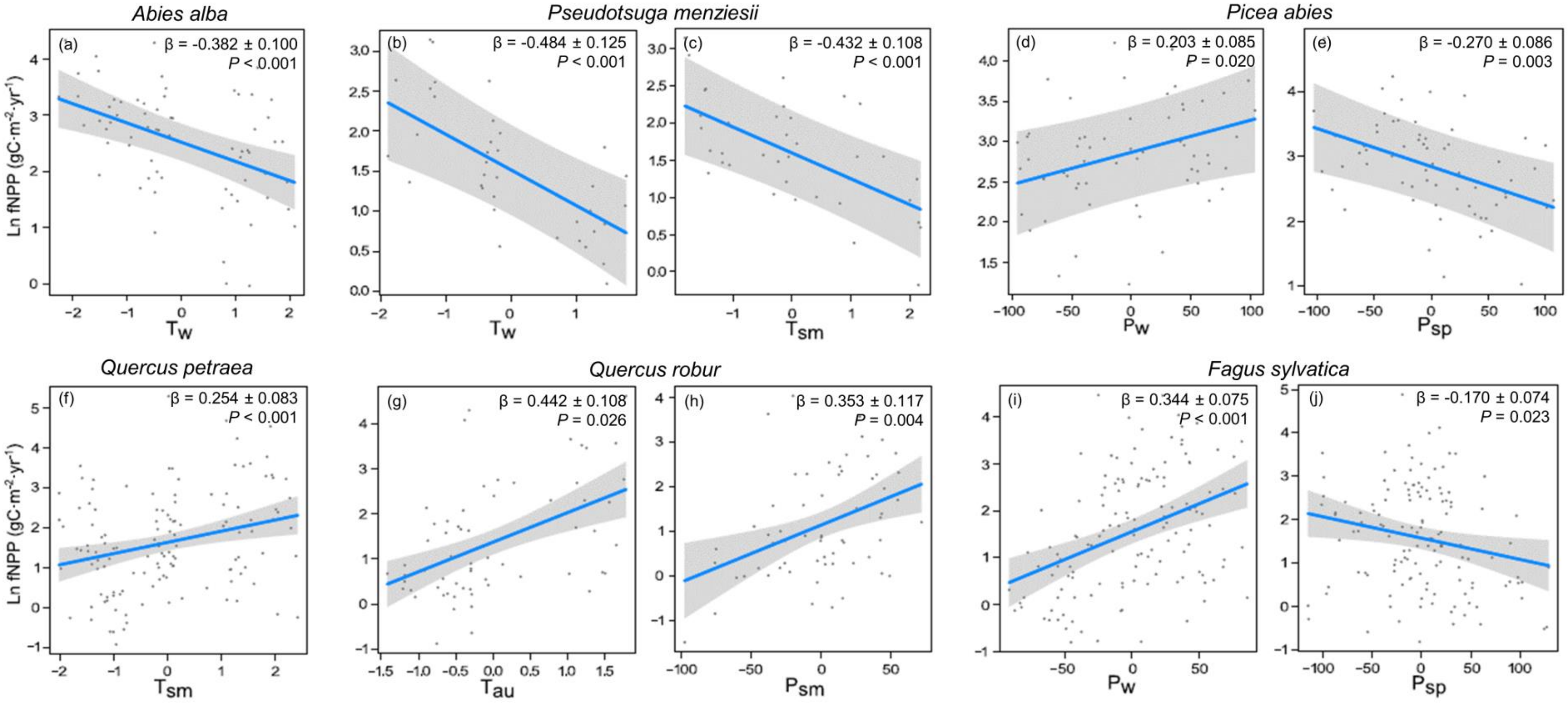
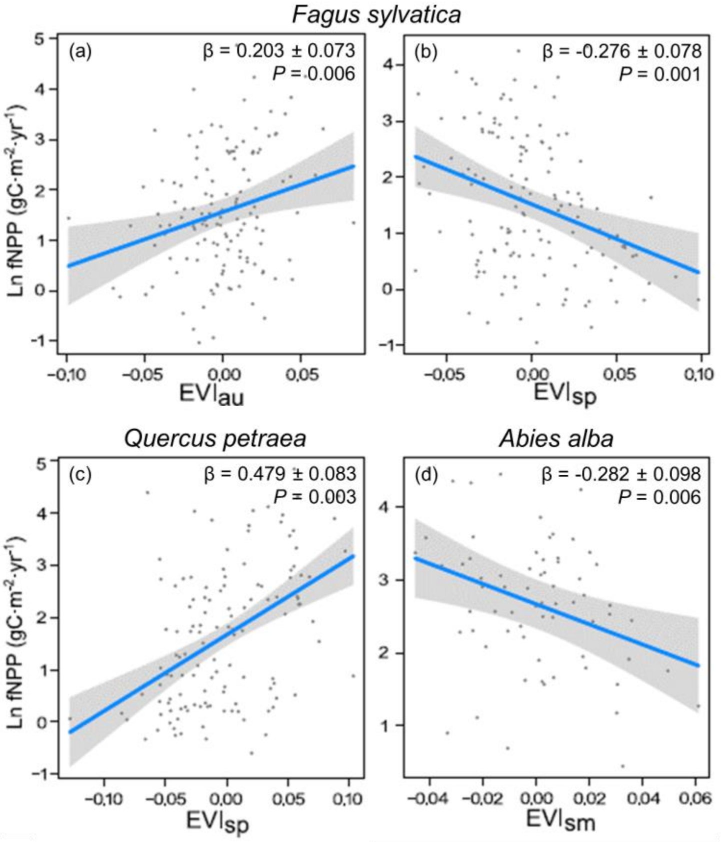

Abies alba
Pseudotsuga menziesii
Picea abies
Quercus petraea
Quercus robur
Fagus sylvatica
Ln fNPP (gC·m⁻²·yr⁻¹)
(a) β = -0.382 ± 0.100 P < 0.001
(b) β = -0.484 ± 0.125 P < 0.001
(c) β = -0.432 ± 0.108 P < 0.001
(d) β = 0.203 ± 0.085 P = 0.020
(e) β = -0.270 ± 0.086 P = 0.003
(f) β = 0.254 ± 0.083 P < 0.001
(g) β = 0.442 ± 0.108 P = 0.026
(h) β = 0.353 ± 0.117 P = 0.004
(i) β = 0.344 ± 0.075 P < 0.001
(j) β = -0.170 ± 0.074 P = 0.023
Tw
Tw
Tsm
Pw
Psp
Tsm
Tau
Psm
Pw
Psp
-2 -1 0 1 2
-1.5 -1.0 -0.5 0.0 0.5 1.0 1.5
-100 -50 0 50 100
0 1 2 3 4 5
0,0 0,5 1,0 1,5 2,0 2,5 3,0
1,5 2,0 2,5 3,0 3,5 4,0

Figure 5.


Fagus sylvatica
(a)
β = 0.203 ± 0.073
P = 0.006
(b)
β = -0.276 ± 0.078
P = 0.001
Ln fNPP (gC·m-2·yr-1)
5
4
3
2
1
0
-1
−0,10
−0,05
0,00
0,05
0,10
EVIau
EVIsp
Quercus petraea
Abies alba
(c)
β = 0.479 ± 0.083
P = 0.003
(d)
β = -0.282 ± 0.098
P = 0.006
−0,04
−0,02
0,00
0,02
0,04
0,06
EVIsp
EVIsm

Supplementary material

Table S1. Summary of average fruit production (fNPP) and Enhanced Vegetation Index (EVI) (means ± SEs) and the proportional variability (PV) and disparity (D) indices. Means were estimated per year (between 2000 and 2008) for each site and species. Different letters within a column indicate significant differences among the species (identified by Tukey's HSD test for multiple comparisons).

Species	fNPP			EVI		
	Mean	PV	D	Mean	PV	D
Pinaceae						
Abies alba	20.29 ± 0.57^{ab}	0.61 ± 0.04^{a}	1.03 ± 0.12^{ab}	0.34 ± 0.33^{a}	0.24 ± 0.06^{a}	0.28 ± 0.10^{a}
Picea abies	30.01 ± 0.51^{b}	0.54 ± 0.04^{a}	0.88 ± 0.11^{a}	0.32 ± 0.26^{a}	0.21 ± 0.06^{a}	0.24 ± 0.09^{a}
Pseudotsuga menziesii	6.08 ± 0.56^{a}	0.52 ± 0.07^{a}	0.64 ± 0.10^{a}	0.41 ± 0.32^{bc}	0.23 ± 0.03^{a}	0.28 ± 0.04^{a}
Fagaceae						
Fagus sylvatica	13.41 ± 0.99^{a}	0.80 ± 0.01^{b}	2.07 ± 0.17^{c}	0.39 ± 0.99^{b}	0.40 ± 0.06^{b}	0.57 ± 0.12^{b}
Quercus petraea	12.34 ± 1.01^{a}	0.79 ± 0.01^{b}	1.67 ± 0.13^{bc}	0.42 ± 1.02^{bc}	0.40 ± 0.06^{b}	0.54 ± 0.11^{b}
Quercus robur	9.51 ± 0.81^{a}	0.81 ± 0.02^{b}	1.69 ± 0.16^{bc}	0.43 ± 0.66^{c}	0.37 ± 0.05^{b}	0.48 ± 0.07^{b}

Method S1. The proportional variability (PV) index

PV is used to assess the variability of a time series by calculating the average difference between all possible combinations of values in the time series, ignoring the chronological order of the values. PV, however, differs from the coefficient of variation (CV) in that it is independent from the mean. That is, PV does not estimate the deviation from the mean of the series but compares all values with each other, so it is less sensitive to non-normally distributed data.

PV is calculated as:

$$C = \frac{n(n-1)}{2} \qquad (Eq. A1)$$

$$D(p) = 1 - \frac{\min(p_i, p_j)}{\max(p_i, p_j)} \qquad (Eq. A2)$$

$$PV = \frac{\sum^{p} D(p)}{C} \qquad (Eq. A3)$$

The distribution of proportional differences, $D(p)$, is first calculated using all possible combinations of values in our time series (C; Eq. A1), with each *p* representing a possible pair of values. The values are then compared by dividing the absolute proportional difference in each pair by the maximum value of each pair (Eq. A2). Finally, PV is obtained by dividing the sum of the values of $D(p)$ by the total number of possible combinations in our time series (Eq. A3).

References:

Heath JP (2006) Quantifying temporal variability in population abundances. Oikos 115:573–581

Method S2. The consecutive disparity (D) index

D is a measure of the variability of a time series that accounts for the chronological order of values in the series, which better assesses the interannual tendencies of the series. In contrast to CV, D does not depend on the mean of the time series but entirely on its chronological order.

D is calculated as:

$$E = \sum_{i=1}^{n-1} \left| ln \frac{p_{i+1}}{p_i} \right| \qquad (Eq.A4)$$

$$D = \frac{E}{n-1} \qquad (Eq.A5)$$

The disorder (E) of the time series is first assessed (Eq. A4), where p_i is a value of a series of length n. D is then calculated by dividing E by $n - 1$ (Eq. A5), which compares time series. If the time series contains a zero, a constant, k, may be added to avoid division by zero (Eq. A6):

$$D = \frac{1}{n-1} \cdot \sum_{i=1}^{n-1} \left| ln \frac{p_{i+1} + k}{p_i + k} \right| \qquad (Eq.A6)$$

References:

Fernández-Martínez M, Vicca S, Janssens IA, et al (2018) The consecutive disparity index, D, as measure of temporal variability in ecological studies. Ecosphere 9: doi: 10.1002/ecs2.2527

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