The role of nutrients, productivity, and climate in determining tree fruit production in European forests

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Summary

Fruit production (NPP), the amount of photosynthates allocated to reproduction (%GPP) and their controls for spatial and species-specific variability (e.g., nutrient availability, climate) are poorly studied in forest ecosystems. We characterised fruit production and its temporal behaviour for several tree species and resolved the effects of gross primary production (GPP), climate, and foliar nutrient concentrations.

We used data for litterfall and foliar nutrient concentration from 126 European forests and related it to climatic data. GPP was estimated for each forest using a regression model.

Mean NPP ranged from approximately 10 to 40 g C m\(^{-2}\) y\(^{-1}\) and accounted for 0.5-3% of the GPP. Forests with higher GPPs produced larger fruit crops. Foliar zinc (Zn) and phosphorus (P) concentrations were associated positively with NPP, while foliar Zn and K were negatively related to its temporal variability. Maximum NPP and interannual variability of NPP was higher in Fagaceae than in Pinaceae species.

NPP and %GPP were similar amongst the studied species despite the different reproductive temporal behaviour of Fagaceae and Pinaceae species. We report, for the first time, that foliar concentrations of P and Zn play an important role in determining %GPP, NPP and its temporal behaviour.

Keywords: crop size, fertility, fruiting, reproductive effort, seeds, spatial variability
Reproductive behaviour in plant species is a crucial part of ecosystem functioning, and, therefore, patterns of production of fruit has received much attention from a wide range of ecologists (Koenig & Knops, 2005). *Masting* is a reproductive behaviour, presented mostly by anemophilous and long-lived plant species, consisting on the synchronised alternation of years with extremely large fruit crops and years with little or no fruit production (Kelly & Sork, 2002). Because of the consequences that masting can entail on the ecosystems (e.g., important cascading effects throughout the food web (Ostfeld & Keesing, 2000)), a large array of studies have tried to understand how and why this extreme interannual variability in fruit production happens (Fernández-Martínez et al., 2016b). Nonetheless, it remains unclear why some species or populations produce larger fruit crops or have more temporally variable fruit production than others. Most theories have focused on the ultimate causes (e.g., avoiding seed predation) for these particular life-history traits (Silvertown, 1980; Kelly, 1994), but the proximate causes (e.g., the mechanistic effect of temperature on pollination) of the spatial variability in fruit production and its temporal behaviour have rarely been explored. Some authors have suggested that the size of the fruit crop from trees subjected to poor growing conditions (e.g. extreme or highly variable climates or poor soil properties such as low nutrient availability) should exhibit higher interannual variability (Kelly & Sork, 2002) because of the benefits of the economy of scale (Norton & Kelly, 1988; Smith et al., 1990). However, little empirical evidence has yet been found to confirm that high interannual variability in fruit production is associated with poor growing conditions, such as drought (Fernández-Martínez et al., 2012) or nutrient limitations.

Most of the studies focusing on fruit or seed production have quantified the number of fruits produced per tree (Sork et al., 1993; Espelta et al., 2008; Crone et al., 2011; Fernández-Martínez et al., 2015), and only few have provided data in units of mass produced per area (Campioli et al., 2010; Herbst et al., 2015; Pérez-Ramos et al., 2015). This is essential for elucidating the contribution of reproduction to ecosystemic net primary production (NPP), which is the sum of aboveground (wood, leaves, fruits) and belowground (roots) biomass production, root exudates and the emission or organic volatile compounds. The lack of a quantitative assessment of C allocation to fruit production has been an important drawback for correctly estimating fruit NPP (NPP) and total biomass production in, for instance, synthesis.
studies on plant carbon allocation (e.g. Vicca et al., 2012; Campioli et al., 2015a). Given that
the mean residence time of carbon is very dependent on the compartment where carbon is
allocated to (Fernández-Martínez et al., 2016a), measures of NPP, and the percentage of
gross primary production (GPP, which equals net ecosystem photosynthesis) allocated to
reproduction would facilitate carbon balance closure in forest ecosystems and would improve
in-depth understanding of plant strategies under different environmental conditions and
responses to changes in e.g., climate and nutrient availability.

Endogenous factors such as stand age, basal area, or taxonomical family and exogenous
factors such as climate, nutrient availability, and anthropogenic impacts have been
demonstrated to largely control GPP, NPP and carbon allocation to different NPP fractions at
the global scale (Vicca et al., 2012; Campioli et al., 2015), and different components of NPP
(e.g. foliage, stems, or roots) may be controlled by different factors (Fernández-Martínez et al.,
802014a). These endogenous and exogenous factors may thus also have an effect on NPP.
Nutrient availability, in particular, may play an important role in determining NPP, and its
temporal behaviour, because fruits and seeds are nutrient-richer (mostly in nitrogen [N],
phosphorus [P], and potassium [K]) than vegetative tissues (Reekie & Bazzaz, 1987). Fruit
production may thus have stronger relationships with nutrient availability than vegetative
tissues (Sala et al., 2012). Nitrogen, for example, is the primary limiting nutrient for vegetative
growth (Elser et al., 2007; LeBauer & Treseder, 2008) and has also been positively correlated
with investment in reproduction (Han et al., 2013; Miyazaki et al., 2014). Nitrogen deposition
has been suggested to increase forest productivity (Luyssaert et al., 2010; de Vries et al.,
892014), but when combined with sulphur (S) deposition, the acidification of soils can have a
negative impact on productivity and soil processes (Oulehle et al., 2011; Büntgen et al., 2013).
Plants growing in P-deficient environments may also have a lower investment in sexual
reproduction than those living in P-rich environments (Fujita et al., 2014). Other macro- and
micronutrients, often rarely studied in wild plants, may also play an important role in
determining fruit production and its temporal behaviour (Swietlik, 2002).

While elemental concentrations are important, the ratios between the various elements may be
even more relevant. The foliar N:P ratio was suggested as an important indicator of plant
nutritional status and vegetative (Güsewell, 2004; McGroddy et al., 2004; Sardans et al., 2012,
982016b) and reproductive (Fujita et al., 2014) production. For example, species with low foliar
99N:P ratios tend to be fast-growing and more competitive for soil resources than species with 100higher N:P ratios (Willby et al., 2001; Elser et al., 2003; Peñuelas et al., 2013). Other studies 101have suggested that, within the same species, plants or shoots producing flowers may have 102lower N:P ratios than those that do not produce flowers (Eckstein & Karlsson, 1997; Güsewell, 1032004). Other elemental stoichiometries, such as C:N or C:P ratios, may also indicate 104limitations of soil nutrients (Fernández-Martínez et al., 2014b) and may therefore also be 105associated with reproductive behaviour in plants.

106The general aim of this study was to characterise fruit production and its temporal behaviour 107for several of the most abundant European tree species and to distinguish species-specific 108variability from the effects of the taxonomical family, productivity, foliar nutrient concentrations, 109climate, and atmospheric deposition of N and S. We specifically aimed i) to estimate average 110NPPf and the percentage of GPP (hereafter %GPP) allocated to fruit production of various tree 111species distributed across Europe, ii) to parameterize masting by assessing the temporal 112variation of NPPf of these species by calculating the coefficient of variation (CV), the 113consecutive disparity index (D), and the temporal autocorrelation at a one-year time lag (AR1: 114the correlation between fruit production in year y and year y-1), and iii) to identify the possible 115determinants of the spatial and species-specific variability of fruit production and its temporal 116behaviour in relation to GPP, foliar nutrient (C, N, P, K, S, Fe, Mg, Ca, Zn, Mn, and Cu) 117concentrations and C:N:P stoichiometries (C:N, N:P, and C:P ratios), climate (mean annual 118temperature and precipitation and their interannual variabilities), and atmospheric deposition of 119N and S. We also explored the potential differences in fruiting behaviour between species of 120the Pinaceae and Fagaceae families.

1212. Materials and methods

1222.1. Data collection

1232.1.1. Data for litterfall and foliar nutrient concentrations

124We downloaded data for litterfall (Pitman et al., 2010) and foliar nutrient concentrations (Rautio 125et al., 2010) from the ICP Forests database (International Co-operative Programme on 126Assessment and Monitoring of Air Pollution Effects on Forest, operated under the UNECE 127Convention on Long-range Transboundary Air Pollution, http://icp-forests.net/), containing data 128for several forest species in Europe. Fruit and foliar litterfall for each site were summed over
entire years, and foliar nutrient concentrations (C, N, P, K, S, Fe, Mg, Ca, Zn, Mn, and Cu) were averaged per site. Average foliar C:N:P stoichiometries per site were calculated on a mass basis. We used foliar nutrient concentrations instead of soil nutrient availability as the measure of nutrient availability for plants because foliar nutrient concentrations often better reflect nutrient availability for plants than nutrient concentration of soils because sometimes nutrients in soils are not available for plants because of multiple factors such as bioimmobilization (Aber & Melillo, 1982) or complex formation (related to too high or too low pH; Truog, 1947; Comerford, 2005).

The original data for litterfall were available in units of g of dry weight m\(^{-2}\) y\(^{-1}\) and we used carbon concentration data (provided by the same database) to convert these data to units of g C m\(^{-2}\) y\(^{-1}\). We also used site information such as mean site diameter to calculate mean basal area, as an estimation of the mean size of the trees at each site. To avoid eventual artefacts of anomalous years dominating too short data sets, of the 210 forests originally available, we used only 126 forests with time series with four or more years of data (Figure S1). We also excluded *Ceratonia siliqua* and *Larix decidua* because of the scarcity of replicates (two and one forest, respectively), as well as 12 multi-species forests. We provided summary values for *Pinus nigra*, but did not include this species in the statistical models, because only three replicates were available. Because of missing data for some of the predictor variables, only 97 forests were finally used to fit the statistical models.

2.1.2. Climatic data

We extracted mean annual temperature and precipitation data (MAT and MAP, respectively) for our forests from the WorldClim database (Hijmans et al., 2005). This database provides climatic data with a high spatial resolution (30 arc seconds, ca. 1 km at the equator) and contains robust mean monthly climatic data derived from lengthy time series (1950-2000).

2.1.3. GPP data and the calculation of the NPP\(_f\)-to-GPP percentage

We aimed to understand the relative reproductive investment of trees (relative to GPP), but the ICP forest network did not measure GPP. We therefore developed and tested a model that predicts average GPP from independent drivers. We used a global forest database (Luyssaert et al., 2007; Fernández-Martínez et al., 2014b) containing carbon fluxes and productivity data from forests. We extracted data from sites that reported both mean GPP (mainly derived from...
eddy covariance CO₂ fluxes) and foliar NPP, as well as MAT, MAP, and leaf type. We chose this set of predictors because these variables were also available for each of the ICP-forest sites used in this study, allowing the estimation of GPP for each site. The model, containing data for 84 forests, accounted for 74% of the variance in GPP. We cross-validated the model using 75% of the data as a sampling set and the remaining 25% as the testing set and repeated this procedure 1000 times randomising both subsets. The cross-validation indicated that the model performed acceptably well: average errors of the model predictions were lower than 12% for the testing set. The model and cross-validation are summarised in the Supplementary Material (Figure S2 and Section 2: Estimating GPP). We calculated the percentage of GPP allocated to NPP (hereafter %GPP) as: %GPP = 100 × NPP × GPP⁻¹.

2.1.4. Atmospheric deposition data
We obtained data for atmospheric deposition from the EMEP gridded datasets and ICP Forests. Modelled N and S deposition data from the EMEP gridded maps were correlated with the ICP data for each forest (R=0.32 and 0.67, P < 0.001, for N and S deposition, respectively). We used the EMEP data throughout in our statistical models because the ICP data were incomplete for our database.

2.2. Data analyses
We calculated all the average metrics of fruit production per site from the annual values per site: average NPP, average %GPP, maximum NPP recorded in each forest, NPP CV, NPP D (Martín-Vide, 1986), and NPP AR1. D was calculated in addition to CV because it was recently suggested to improve the assessment of temporal variability relative to the CV, especially in negatively autocorrelated time series. Further information on the D index can be found in the Supplementary Material, Section 1: The consecutive disparity index (D). AR1 indicates the temporal correlation between fruit crop sizes for years y-1 and y. Negative AR1 values in fruit production time series may be a sign of depletion of resources after large fruit crops (Sork et al., 1993; Fernández-Martínez et al., 2015). These values of fruit CV, D and AR1 were further averaged across sites per species to characterise the temporal behaviour of NPP of that species. Using average site values as replicates, we identified differences amongst species and families using ANOVAs and Tukey's HSD tests for multiple comparisons.
We fitted linear mixed models (LMMs) to characterise the relationships of the exogenous (MAT, MAP, and N and S atmospheric deposition) and endogenous (foliar nutrient concentrations, GPP, basal area, and family – Pinaceae or Fagaceae) variables with the temporal behaviour of fruit production (mean NPP, %GPP, maximum NPP, and the CV, D, and AR1 of NPP). Using the species as a random effect (to take into account, for example, the species effect on stoichiometry), we tested whether the fruit production metrics were correlated with productivity and with forest characteristics, such as GPP, basal area, family of the species, climate, foliar nutrient concentrations, and atmospheric deposition of N and S. The saturated model used GPP, basal area, N and S deposition, MAT, MAP, the CVs of MAT and MAP, foliar concentrations of C, N, P, K, S, Fe, Ca, Cu, Mg, and Zn, and foliar C:N, N:P, and C:P ratios as fixed effects. We used D of MAT and MAP instead of the CV for the models predicting D of NPP. Variables were selected using the backwards-forwards stepwise method, starting from the saturated model. Once the most important variables were selected, we calculated the first-order interactions of the variables within the model and removed the non-significant terms. Models were fitted with the lme function of the R package “nlme” (Pinheiro et al., 2013) using restricted maximum likelihood and a Gaussian distribution. To provide a measure of goodness of fit of our models we assessed the marginal (fixed factors) and conditional (fixed + random factors) variance explained by the model (pseudo R²) using the method proposed by Nakagawa & Schielzeth (2013) implemented in the MuMIn R package (Barton, 2015). We also used generalised additive models (GAMs) to explore the non-linearities between the response variables and the predictors using spline functions. NPP and D of NPP were log-transformed to meet the assumption of normality and heteroscedasticity in the model residuals. All analyses were performed using R statistical software (R Core Team, 2015).

3. Results

3.1. Species-specific variability in fruit production and its temporal behaviour

Mean fruit production amongst the studied species ranged from (mean ± standard error) 6.1 ± 1.7 g C m⁻² y⁻¹ in Pseudotsuga menziesii to 40.6 ± 9.9 g C m⁻² y⁻¹ in Pinus nigra (Figure 1, Table S1). In fact, mean NPP per year varied little amongst species and differed significantly only between the two above species and between Pinus sylvestris and Quercus petraea (Figure 1). Nonetheless, when grouped Pinaceae species had a higher average NPP than Fagaceae species (23.2 ± 2.1 and 15.0 ± 1.6 g C m⁻² y⁻¹, respectively; ANOVA, P = 0.003).
Similarly, the percentage of GPP invested in NPP$_f$ ($\%$GPP$_f$) varied little amongst species (Figure 1) and, on average, was <3% in all species (Table S1). The only differences amongst species were found between P. sylvestris, P. menziesii, and Q. petraea, with $\%$GPP$_f$ higher in P. sylvestris than in the other two species. On the other hand, $\%$GPP$_f$ was different between families, being higher for Pinaceae than Fagaceae forests (1.7 ± 0.2 and 1.1 ± 0.1%, respectively; ANOVA, $P = 0.004$). Maximum NPP$_f$ was similar across species and averaged at 22546.9 ± 3.1 g C m$^{-2}$ y$^{-1}$ (Figure 2, Table S1).

Temporal variability in fruit production differed substantially across species and between families (Figure 3, Table S1). The Fagaceae species Fagus sylvatica, Q. petraea, and Q. robur had the highest temporal variabilities, with an average CV >1.3 and D >1.5 (Table S1). Both these indices of temporal variability indicated higher variability in fruit production in Fagaceae than in Pinaceae forests (1.38 ± 0.05 and 0.73 ± 0.05 for CV and 1.81 ± 0.09 and 1.05 ± 0.05 for D, respectively; $P < 0.001$). Also, the ANOVA indicated that the first autocorrelation coefficient (AR1) differed amongst species (Figure 3, Table S1). Tukey’s HSD test, however, found significant differences in AR1 only between P. menziesii and F. sylvatica. The former species had almost no autocorrelation, and the latter had a strong negative autocorrelation. Autocorrelation in fruit production generally tended to be negative, suggesting that years with higher (lower) fruit production tended to be followed by a year with lower (higher) fruit production.

### 3.2. Determinants of fruit production and of its temporal behaviour

Our statistical linear mixed models (LMMs) indicated that GPP and foliar Zn and P concentrations (Figure 4) were positively associated with NPP$_f$ within and across species (Table 1). We also found a statistically significant positive interaction between foliar Zn and P concentrations ($P = 0.01$), indicating that the positive effect of Zn increased with increasing foliar P concentration (and vice versa) (Figure 5). Our analysis thus identified a synergistic effect of foliar Zn and P concentrations, leading to higher fruit production when both nutrients occurred at high concentrations in the leaves. The LMM accounted for 56% of the variance in NPP$_f$, with 40% explained by the fixed effects (GPP, Zn and P) and 16% by differences amongst species.
Similar to NPP, %GPP was higher in forests with high foliar Zn and P concentrations. The interaction between foliar Zn and P concentrations was also statistically significantly positively associated with %GPP, (P = 0.025). The model for %GPP explained 44% of the variance in %GPP, with 31% accounted for by the fixed effects and the remaining 13% by interspecific variability. Maximum recorded NPP was associated positively with GPP, basal area and foliar Zn concentrations, and negatively with MAP and foliar N and C:P concentrations. Also, Fagaceae species presented larger maximum NPP than Pinaceae species (P = 0.004). The model accounted for 41% of the variance in maximum NPP, with 31% explained by the fixed effects and 10% by interspecific variability.

Temporal variability in fruit production differed depending on the index used to evaluate interannual variation (CV and D), but temporal variability in NPP was clearly larger for Fagaceae than for Pinaceae species (P < 0.01 for both indices; Table 1, Figure 4). The model predicting the temporal variability of fruit production using the CV index indicated that more productive forests with higher foliar Zn concentrations exhibited lower interannual variability in fruit production. In contrast, the model predicting D of NPP indicated that D was higher in forests with larger basal areas and lower foliar K concentrations (Table 1). Overall, the CV and D models explained 62% and 56%, respectively, of the variance in the CV and D of fruit production, with 58% and 55% explained by the fixed effects and the remaining 4% and 1% by interspecific variability.

Finally, the model that best predicted temporal AR1 indicated a tendency for more negative values of temporal autocorrelation in forests with high loads of N deposition than in forests less exposed to N deposition (P = 0.055). However, N deposition explained only 3% of the variance in the temporal autocorrelation of fruit production, and species-specific variability explained 20% of the variability in AR1.

### Discussion

Estimates of NPP and their role in the forest C balance

Our results provide the first estimates of carbon allocation to fruit production for some of the most abundant tree species in European forests. Despite the high variability in the estimates, due mainly to the differences in GPP and foliar nutrient concentrations (Table 1), average NPP in our sample of European forests ranged from 10 to 40 g C m⁻² y⁻¹ and accounted for 0.5-3%
of the GPP, both being higher in *Pinaceae* than in *Fagaceae* species. These estimates of NPP, and GPP allocation are lower than those in previous studies. Herbst et al. (2015) reported mean NPP estimates of 95 ± 37 and 73 ± 25 g C m⁻² y⁻¹ for managed and unmanaged stands of *F. sylvatica*, respectively. GPP allocation to NPP averaged 6.7 ± 3.4 and 4.6 ± 2.0% in the managed and unmanaged stands respectively. In addition, %GPP reached 23% in the managed stand during an exceptional mast year. Campioli et al., (2010) reported an average NPP for *P. sylvestris* of 76 ± 8 g C m⁻² y⁻¹ and an average %GPP of 6.0 ± 0.6%.

Various reasons might be behind the differences between our results and previous reports of NPP and allocation to fruit. Differences in the endogenous characteristics of the stands, such as GPP or foliar nutrient concentrations, are of major importance for fruiting NPP (Figure 4, Table 1). Moreover, exogenous factors such as the management of the stand can also influence carbon allocation to fruiting (Herbst et al., 2015). The assessment of average values, however, is very dependent on the period of measurement due to the high irregularity of fruit production, especially when analysing relatively short time series of masting species such as those of the *Fagaceae* family. Different sampling methodologies could also be responsible for these differences in average NPP.

NPP is usually a relatively small component of the carbon balance of forest ecosystems, but high interannual variability in masting species, such as *F. sylvatica* or *Quercus* sp., identifies NPP as an important component to consider for a better assessment of the ecosystem carbon balance (Herbst et al., 2015) or the cascading effects that fruit NPP can entail on the entire food web of an ecosystem (Ostfeld & Keesing, 2000). Mean maximum NPP was 2- to 3-fold higher than mean NPP for all species (Table S1). %GPP can thus increase substantially in years with large fruit crops. Further analyses with longer time series are clearly needed to obtain more robust estimates of the role of fruit production in the forest carbon cycle. Nonetheless, our results do provide new insights on the fate of photosynthesised C in forest ecosystems. However, because of the way in which we estimated GPP for our sites and the error propagation, our estimates of %GPP may be subjected to larger error estimates than those we calculated by mean ± SE. Therefore, any interpretation of the values we report should take that uncertainty into consideration.

The role of nutrients in NPP and its temporal behaviour
Our forests were in the lower range of mean concentrations of foliar Zn (Table S2), indicating that some of the forests might have been Zn deficient (Swietlik, 2002). Zn deficiency has been well studied in agricultural crops, but to the best of our knowledge, we are the first to report a potential role in forest ecosystems. Zn deficiency usually occurs in plants growing on alkaline soils because of the reduced bioavailability of Zn (Ma & Lindsay, 1990), but can also occur in acidified weathered soils (Alloway, 2009). Zn limitation can have a negative impact on plant vegetative growth and especially fruit yield (Swietlik, 2002), because of the roles Zn plays in several key metabolic processes such as protein synthesis (as a component of ribosomes, Prask and Plocke, 1971) or in metalloenzymes such as carbonic anhydrases (Dell & Wilson, 1985) involved in the conversion of carbon dioxide and water to bicarbonate and protons (photosynthesis and biomass production). Cakmak and Marschner (1988) found that Zn deficiency in Gossypium hirsutum, Triticum aestivum, Lycopersicon esculentum, and Malus domestica increased the exudation of K, amino acids, sugars, and phenolics from roots because of increased membrane permeability. By exuding more carbon-rich compounds in the soil, Zn-deficient plants may thus have less photosynthates available for aboveground compartments (Vicca et al., 2012; Fernández-Martínez et al., 2014b, 2016a) and fruit production (Figures 5 and 6). These processes may also be responsible for increased temporal variability in seed production, because carbon reserves in Zn-limited trees might be insufficient for regular production of large fruit crops (Isagi et al., 1997).

However, despite foliar Zn concentrations have an effect within species, the effect of foliar Zn is also associated to the different reproductive behaviour amongst taxonomical families, since Pinaceae species present higher foliar Zn concentrations than Fagaceae species (Table S3) and both families exhibit different patterns of fruit production (i.e., Pinaceae species invest more on reproduction [Figure 1] while Fagaceae species present higher interannual variability in NPP,[Figure 3]). In that sense, high foliar Zn concentrations may be related to fast growing species (opportunistic, the r-selected species), producing fruits every year, while low foliar Zn concentrations may be linked to slow growing species (good competitors, the k-selected species) investing more heavily in fewer reproducing events. Thus, masting behavior could be related to an evolutionary strategy of the k-selected species that would confer an evolutionary advantage over their competitors (Kelly & Sork, 2002).
Forests with higher foliar P concentrations had higher mean fruit production and allocation to fruit production in our study, supporting the finding by Fujita *et al.* (2014). P had the strongest effect in forests with high foliar Zn concentrations (*Table 1*). This synergistic effect of foliar P and Zn concentrations could be a consequence of an induced limitation of one nutrient when the other is increased, (Elser *et al.*, 2007) in agreement with von Liebig’s law of the minimum (Von Liebig, 1840). The close association of P (Elser *et al.*, 2003) and Zn (Prask & Plocke, 1971) with ribosomes, and therefore with metabolism and biomass production, further supports a positive interaction between these elements. Our results also point out that both families, *Pinaceae* and *Fagaceae*, present a similar relationship between foliar P concentrations and NPP, despite their morphological and functional differences. These results also agree with previous reports suggesting that higher foliar P concentrations enable larger fruit crops compared to those with lower concentrations (e.g. in olive trees (Erel, 2008) and amongst multiple plant species (Fujita *et al.*, 2014)) or, more generally, that P limitation constrains NPP in forests (Perkins, 2004; Plassard & Dell, 2010) and in freshwater, marine, and other terrestrial ecosystems (Elser *et al.*, 2007; Peñuelas *et al.*, 2013). Additionally, higher foliar C:P ratios in our study were associated with lower maximum NPP (Table 1). This finding is also consistent with P limitation for fruit production: P-deficient forests may not be able to produce as large fruit crops as those with sufficient P availability.

According to our statistical models, trees with higher foliar N concentrations not only did not have higher NPP, but had lower maximum NPP than those with lower N concentrations (*Table 1*). This is intriguing given the fact that foliar N concentrations are higher in *Fagaceae* species than in *Pinaceae* species (*Table S2*), despite the latter presents lower maximum NPP (Table 1). This may suggest that the negative relationship between foliar N concentration and maximum NPP happens only within species and not amongst species. N has been identified as the primary limiting nutrient for vegetative growth (Elser *et al.*, 2007; LeBauer & Treseder, 2008) and reproduction (Han *et al.*, 2013; Miyazaki *et al.*, 2014), but the lack of association between foliar N concentration and NPP might be a consequence of other nutrients limiting production, such as Zn or P. Most of Europe is exposed to high rates of N deposition, which may increase N availability for plants, as indicated by the relatively high average values of foliar N concentrations in European forests (*Table S2*).
The negative relationship between atmospheric N deposition and AR1 of NPP may indicate that forests with higher N reserves are able to produce fruits crops with a periodic recurrence when other factors are not limiting growth during a particular year (such as weather, other nutrients such as Zn or P, or a combination of both (Fernández-Martínez et al., 2015). On the other hand, our analyses revealed that foliar K concentration were negatively related to interannual variability in fruit production (Table 1). This relationship may not remain amongst species because foliar K concentrations were lower in the Pinaceae family, which presents significantly lower interannual variability (Table 1). Foliar K concentrations are related to plant water regulation, thus being an important nutrient especially in arid environments, where water availability is amongst the most important factors driving fruit and secondary production (Ogaya & Peñuelas, 2007; Pérez-Ramos et al., 2010; Garbulsky et al., 2013). K bioavailability increases with increasing annual precipitation, but, through conservation mechanisms such as resorption, plants can increase their K concentrations (Sardans & Peñuelas, 2015). Hence, we hypothesise that trees with higher foliar K concentrations produce fruits more regularly because they can cope better with eventual reduced water availability and are thus less sensitive to interannual changes in water availability (Fernández-Martínez et al., 2015).

Our results thus indicate that nutrient-rich forests produce more fruits, allocate a larger fraction of the GPP to fruit production, and produce fruit more regularly than nutrient-limited forests. This supports previous findings that suggested higher C allocation to aboveground NPP in nutrient-rich forests (Vicca et al., 2012; Fernández-Martínez et al., 2014b, 2016a), as well as theory and observations suggesting that high interannual variability in fruit production is more pronounced in environments where resources are scarce (Kelly & Sork, 2002; Fernández-Martínez et al., 2012). Nutrient availability may thus limit NPP even more than it limits vegetative NPP, because fruits are more nutrient-demanding than vegetative tissues (Reekie & Bazzaz, 1987). Amongst all investigated nutrients, foliar Zn and P concentrations were most strongly associated with higher fruit production. However, trees growing on soils with low nutrient availability might be forced to be more conservative in the use of nutrients and thus present higher concentrations in their tissues, acting like nutrient pools. Hence, further research is needed to disentangle the effects of soil nutrient availability and foliar nutrient concentrations on ecosystem functioning.
Other determinants of NPP, and its temporal behaviour

Nutrient availability and stoichiometry played a very important role in determining NPP, and its temporal behaviour, but site productivity and the taxonomical family were also key factors. Higher photosynthesis (GPP) was associated with higher NPP, higher maximum NPP, and lower temporal variability (CV). This result is logical, because forests with larger GPP fluxes also typically have larger NPP fluxes (Fernández-Martínez et al., 2014a). Whether all NPP components increase equally with increasing GPP, however, remains unresolved. In addition, higher GPP might reduce the CV of fruit production because more photosynthates can be allocated to storage to later be used for reproduction and allowing more regular production of fruit crops. However, due to the positive relationship between NPP and GPP and the dependence of the CV on the mean, this relationship might be spurious. This second hypothesis is supported by the lack of a relationship between D (which is less sensitive to the mean than the CV (Supplementary Information 1: The consecutive disparity index) of fruit production and GPP. A larger basal area, however, was also associated with higher maximum NPP, perhaps due to the competitive advantage of large trees to acquire various resources (e.g. nutrients, water, and sunlight).

In addition to the strong influence of foliar nutrient concentrations on NPP, and its interannual variability, we found a significant taxonomic effect on NPP. In particular, Fagaceae and Pinaceae species presented a markedly different behaviour in fruit production patterns, with the latter exhibiting lower maximum NPP (probably because they are generally established over nutrient poor soils) and lower interannual variability in NPP. Based on our results, we can consider that the Fagaceae species studied here present a clear masting behaviour (i.e., high interannual variability, negative autocorrelation in fruit production (Fernández-Martínez et al., 2016b)) while it is not that clear for some of the Pinaceae species, especially P. sylvestris, P. nigra and P. menziesii, which present relatively low interannual variability and no negative autocorrelation in NPP (Table S1). These differences may be related to different life-history traits and evolutionary strategies related to avoidance of seed predation or to different patterns of resource allocation. The different nature of fruits produced by the two families (cones in Pinaceae and nuts in Fagaceae) might be responsible for the different allocation of resources to fruit production in terms of biomass production. Pinaceae species spend many resources when producing cones (bearing the seeds), while in Fagaceae species each seed (nut) is
usually much cheaper to produce in terms of C. This difference in the amount of resources needed to produce fruits between Pinaceae and Fagaceae families might be behind the different patterns of fruit production in our studied species. Also, the different availability of nutrients between families, such as N (higher in Fagaceae, Table S2) or Zn (higher in Pinaceae, Figure 4, Table S2), might also condition the different patterns of fruit production because of different nutrient-use efficiencies amongst species from different families (Sardans et al., 2016a).

Finally, our results also point out that mast ing behaviour can be well parameterised using the D index, because it takes into account not only the variability of the time series but also its temporal autocorrelation (Table S1). Since mast ing behaviour is related to high interannual variability and negative autocorrelation in fruit production, which is exactly what the D index accounts for (Supplementary Information 1: The consecutive disparity index), D seems to be a good candidate to characterise mast ing behaviour using a single index.

5. Conclusions

On average, NPPf ranged from approximately 10 to 40 g C m⁻² y⁻¹ and accounted for 0.5-3% of the GPP, with little differences amongst species or between families (Fagaceae – Pinaceae). However, mean maximum NPPf and interannual variability in NPPf differed specially between families, being higher for Fagaceae than for Pinaceae. These differences are likely to be linked to different life-history traits and evolutionary strategies related to avoidance of seed predation or to different patterns of resource allocation, given the different nature of their fruits.

More productive (higher GPPs) and nutrient rich forests produced larger and more regular fruit crops and allocated a larger percentage of photosynthates intro fruit production, which highlights the paramount role of available reserves of nutrients and carbohydrates to allocate into reproduction. Especially foliar zinc (Zn) and phosphorus (P) concentrations were associated positively with fruit crop size, while foliar Zn and K were negatively related to its temporal variability. To the best of our knowledge we report, for the first time, Zn deficiency in forests.

Acknowledgements
We thank the ICP Forest organisation and collaborators for providing the litterfall data used in this study. This research was supported by the European Research Council Synergy grant ERC-2013-SyG 610028-IMBALANCE-P, the Spanish Government grant CGL2013-48074-P, and the Catalan Government projects SGR 2014-274 and FI-2013. SV is a postdoctoral fellow of the Research Foundation – Flanders (FWO).

Author contribution

M.F-M, S.V., I.J. and J.P planned and designed the research. M.F-M wrote the manuscript and analysed the data. All co-authors contributed substantially in writing the paper.
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Figure captions

Figure 1: Box-and-whisker plots showing NPP\textsubscript{f} (upper panel) and NPP\textsubscript{f}-to-GPP percentage (lower panel) for nine European tree species. Dark grey boxes indicate coniferous species and light grey boxes indicate broadleaved species. The $P$ values of the ANOVAs for differences amongst species are shown inside each panel. Different letters indicate significant differences ($P < 0.05$) amongst species (Tukey's HSD test for multiple comparisons). Numbers above the letters indicate the number of replicates. Average values are presented in Table S1.

Figure 2: Box-and-whisker plot showing maximum fruit net primary production (NPP) (upper panel) for nine European tree species. Dark grey boxes indicate coniferous species and light grey boxes indicate broadleaved species. The $P$ value of the ANOVA for differences amongst species is shown inside the plot. Average values are presented in Table S1.

Figure 3: Box-and-whisker plots showing the coefficient of variation (CV, upper panel), disparity (D, middle panel), and autocorrelation coefficient for the first lag (AR1, lower panel) of fruit net primary production (NPP) for nine European tree species. Dark grey boxes indicate coniferous species and light grey boxes indicate broadleaved species. The $P$ values of the ANOVAs for differences amongst species are shown inside each panel. Different letters indicate significant differences ($P < 0.05$) amongst species (Tukey's HSD test for multiple comparisons). Average values are presented in Table S1.

Figure 4: Partial residuals plots for the models of fruit net primary production (NPP\textsubscript{f}) and the CV of NPP\textsubscript{f} without interactions. Upper panels show the relationships of gross primary production (GPP) (panel a), foliar Zn (panel b) and P (panel c) concentrations with NPP\textsubscript{f}. Lower panels show the relationships of gross primary production (GPP) (panel d), foliar Zn concentration (panel e) and family (panel f) with CV of NPP\textsubscript{f}. Beta weights ($\beta \pm SE$) and their significance ($P$) within the model without interactions are shown in each panel. Light blue shading indicates 95% confidence bands.

Figure 5: 3D plot showing the significant interaction between foliar P and Zn concentrations for predicting fruit net primary production (NPP). The response surface was calculated using a generalised additive model explaining 28% of the variance in NPP\textsubscript{f}. Blue and green colours of the response surface indicate, respectively, low and high NPP\textsubscript{f}. 

43
44
Figure 1

Fruit NPP (gC m\(^{-2}\) y\(^{-1}\))

Y-axis: Fruit NPP (gC m\(^{-2}\) y\(^{-1}\))

P = 0.0018

P = 0.0012

Y-axis: Fruit NPP GPP\(^{-1}\) (%)

Species:
- Pinus nigra
- Pinus sylvestris
- Picea abies
- Pinus pinaster
- Abies alba
- Pseudotsuga menziesii
- Fagus sylvatica
- Quercus robur
- Quercus petraea
Figure 3

Box plots showing the distribution of Fruit NPP CV, Fruit NPP disparity, and Fruit NPP AR1 for different tree species. The species are labeled as follows:

- Pinus pinaster
- Abies alba
- Picea abies
- Pinus sylvestris
- Pseudotsuga menziesii
- Pinus nigra
- Fagus sylvatica
- Quercus petraea
- Quercus robur

Significance levels are indicated by different letters above the boxes, with P < 0.0001 for all comparisons.
Table 1: Summary of the mixed models predicting fruit net primary production (NPP), the percentage of gross primary production allocated to NPP (%GPP), maximum NPP, and the CV, D, and AR1 of NPP. Values are beta weights ± SE. For family, the coefficient shown indicates the change from Fagaceae to Pinaceae. Variance explained for fixed factors corresponds to marginal $R^2$, and interspecific variance is the variance explained by the random effects. Ln indicates the response variable was transformed to the natural logarithm. Abbreviations: mean annual precipitation (MAP), coefficient of variation (CV), disparity (D), and autocorrelation coefficient at lag 1 (AR1). † $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. All models included species as a random variable.

<table>
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<th></th>
<th>Ln NPPr</th>
<th>Ln %GPPr</th>
<th>Max NPPr</th>
<th>CV</th>
<th>D</th>
<th>AR1</th>
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<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
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<tr>
<td>GPP</td>
<td>0.4 ± 0.0 ***</td>
<td>- ± 0.3 **</td>
<td>- ± 0.1 **</td>
<td>- ± 0.0 ***</td>
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<td></td>
</tr>
<tr>
<td>Basal area</td>
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<td>0.2 ± 0.1 *</td>
<td>- ± 0.0 *</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Foliar N</td>
<td></td>
<td>0.3 ± 0.1 **</td>
<td>- ± 0.2 *</td>
<td></td>
<td>0.1 ± 0.0 *</td>
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</tr>
<tr>
<td>Foliar P</td>
<td>- ± 0.1</td>
<td>- ± 0.2 *</td>
<td></td>
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<tr>
<td>Foliar Zn</td>
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<td>0.3 ± 0.1 *</td>
<td>- ± 0.1 **</td>
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<td></td>
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<tr>
<td>Foliar C:P</td>
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<td></td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td>Foliar K</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>- ± 0.0 ***</td>
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<tr>
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<tr>
<td>MAP</td>
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<td>- ± 0.1 *</td>
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<td><strong>Interactions</strong></td>
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<tr>
<td>Foliar P:Foliar Zn</td>
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<td>1.1 ± 0.5 **</td>
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<td><strong>Variance</strong></td>
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<td>Interspecific</td>
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<td>0.13</td>
<td>0.10</td>
<td>0.04</td>
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<td>Total</td>
<td>0.56</td>
<td>0.44</td>
<td>0.41</td>
<td>0.62</td>
<td>0.56</td>
<td>0.23</td>
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</table>

Supplementary material

Figure captions:
Figure S1: Map showing the location of the 126 forests monitored in this study.

Figure S2: Observed versus predicted GPP values from the model used to estimate GPP for the study sites. See materials and methods and Section 1: Estimating GPP in the supplementary material for further information about model adjustment.

Figure S3: Comparison of the CV and D indices using two time series with equal means and standard deviations but different autocorrelation structures. AR1, autocorrelation coefficient for lag 1; CV, coefficient of variation (standard deviation • mean-1); and D, disparity index (see Eqs. 1 and 2 in Supplementary Material Section 1: The consecutive disparity index (D)).
Figure S1:
Figure S2

$R^2=0.74$
RMSE=407.33

Observed GPP (g C m$^{-2}$ y$^{-1}$) vs. Predicted GPP (g C m$^{-2}$ y$^{-1}$) for Conifers and Broadleaved species.

1:1 line

- Red dots: Conifers
- Blue dots: Broadleaved
Table S1: Species (mean ± SE)

Fruit net primary production (NPP) (g C m⁻² y⁻¹), allocation to NPP (NPP \( \cdot \) GPP⁻¹ = %GPP), mean maximum NPP (Max NPP), and coefficient of variation (CV), consecutive disparity (D), and first autocorrelation coefficient (AR1) of NPP. AR1 P shows the significance of the AR1 coefficients from a t-test, and n indicates the number of sites per species. Different letters indicate significant differences (P < 0.05) amongst species (Tukey's HSD test for multiple comparisons).

<table>
<thead>
<tr>
<th>Species</th>
<th>NPP (mean ± SE)</th>
<th>Allocation</th>
<th>Max NPP</th>
<th>CV</th>
<th>D</th>
<th>AR1</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species 1</td>
<td>50 ± 2.5</td>
<td>30 ± 1.5</td>
<td>45 ± 3.0</td>
<td>0.47</td>
<td>0.89</td>
<td>-0.83</td>
<td>10</td>
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<tr>
<td>Species 2</td>
<td>40 ± 2.0</td>
<td>25 ± 1.0</td>
<td>35 ± 2.5</td>
<td>0.47</td>
<td>0.18</td>
<td>0.5</td>
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**Figure S3**

![Graph showing values over time for two time series A and B.](image-url)
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<tr>
<th>Species</th>
<th>NPP$_f$</th>
<th>%GP$_f$</th>
<th>Max NPP$_f$</th>
<th>CV</th>
<th>D</th>
<th>AR1</th>
<th>AR1 <em>P</em></th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abies alba</td>
<td>18.7 ± 3.3</td>
<td>1.4 ± 0.3</td>
<td>43.1 ± 7.9</td>
<td>0.83 ± 0.08</td>
<td>b</td>
<td>1.00 ± 0.11</td>
<td>-0.15 ± 0.04</td>
<td>0.071 ± 0.04</td>
</tr>
<tr>
<td>Fagus sylvatica</td>
<td>16.1 ± 2.5</td>
<td>1.2 ± 0.2</td>
<td>49.0 ± 6.9</td>
<td>1.42 ± 0.08</td>
<td>a</td>
<td>2.02 ± 0.15</td>
<td>-0.42 ± 0.04</td>
<td>&lt;0.00 ± 0.04</td>
</tr>
<tr>
<td>Picea abies</td>
<td>25.0 ± 5.2</td>
<td>1.8 ± 0.4</td>
<td>46.2 ± 9.8</td>
<td>0.89 ± 0.09</td>
<td>b</td>
<td>0.99 ± 0.12</td>
<td>-0.27 ± 0.08</td>
<td>0.001 ± 0.08</td>
</tr>
<tr>
<td>Pinus nigra</td>
<td>40.6 ± 9.9</td>
<td>2.9 ± 0.7</td>
<td>66.6 ± 12.2</td>
<td>0.63 ± 0.08</td>
<td>b</td>
<td>0.97 ± 0.12</td>
<td>-0.06 ± 0.02</td>
<td>0.732 ± 0.02</td>
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<tr>
<td>Pinus pinaster</td>
<td>19.4 ± 2.6</td>
<td>1.1 ± 0.2</td>
<td>42.2 ± 7.4</td>
<td>0.78 ± 0.08</td>
<td>b</td>
<td>1.17 ± 0.19</td>
<td>-0.33 ± 0.09</td>
<td>0.006 ± 0.09</td>
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<tr>
<td>Pinus sylvestris</td>
<td>26.8 ± 3.2</td>
<td>2.1 ± 0.3</td>
<td>54.6 ± 8.3</td>
<td>0.77 ± 0.09</td>
<td>b</td>
<td>0.76 ± 0.09</td>
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<td>0.153 ± 0.06</td>
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<tr>
<td>Pseudotsuga menziesii</td>
<td>6.1 ± 1.7</td>
<td>0.5 ± 0.2</td>
<td>13.1 ± 4.1</td>
<td>1.06 ± 0.32</td>
<td>a</td>
<td>0.64 ± 0.10</td>
<td>0.07 ± 0.12</td>
<td>0.524 ± 0.12</td>
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<tr>
<td>Quercus petraea</td>
<td>12.3 ± 1.5</td>
<td>0.9 ± 0.1</td>
<td>44.5 ± 6.2</td>
<td>1.36 ± 0.08</td>
<td>a</td>
<td>1.71 ± 0.11</td>
<td>-0.20 ± 0.06</td>
<td>0.001 ± 0.06</td>
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<tr>
<td>Quercus robur</td>
<td>16.9 ± 4.6</td>
<td>1.3 ± 0.4</td>
<td>49.6 ± 10.8</td>
<td>1.35 ± 0.12</td>
<td>a</td>
<td>1.51 ± 0.16</td>
<td>-0.10 ± 0.09</td>
<td>0.243 ± 0.09</td>
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</table>
Species (mean ± SE) foliar C, N, P, and K concentrations and stoichiometries (C:N, C:P, and N:P). Concentrations have units of mg g⁻¹ except for C, which is per cent of dry weight. C:N, C:P, and N:P ratios are calculated on a mass basis. Different letters indicate significant differences (*P* < 0.05) amongst species (Tukey’s HSD test for multiple comparisons), and *n* indicates the number of sites per species.

<table>
<thead>
<tr>
<th></th>
<th>C</th>
<th>N</th>
<th>P</th>
<th>K</th>
<th>C:N</th>
<th>C:P</th>
<th>N:P</th>
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<tbody>
<tr>
<td><strong>Abies alba</strong></td>
<td>52.42 ± 0.11 a</td>
<td>12.94 ± 0.31 b</td>
<td>1.16 ± 0.25 c</td>
<td>5.61 ± 0.75 bc</td>
<td>40.02 ± 15.8 b</td>
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<td><strong>Fagus sylvatica</strong></td>
<td>53.07 ± 0.43 a</td>
<td>24.23 ± 0.53 a</td>
<td>1.17 ± 0.32 c</td>
<td>7.04 ± 0.53 c</td>
<td>22.11 ± 18.5 b</td>
<td>479.9 ± 10.48 b</td>
<td>11.32 ± 0.44 c</td>
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<td><strong>Picea abies</strong></td>
<td>51.35 ± 0.37 b</td>
<td>13.61 ± 0.30 c</td>
<td>1.34 ± 0.25 bc</td>
<td>5.60 ± 0.74 c</td>
<td>38.10 ± 10.48 b</td>
<td>397.0 ± 12.47 c</td>
<td>11.9 ± 0.41 c</td>
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<td><strong>Pinus nigra</strong></td>
<td>53.50 ± NA a</td>
<td>9.06 ± 0.32 c</td>
<td>0.70 ± 0.49 c</td>
<td>6.37 ± 5.00 ab</td>
<td>41.47 ± 13.59 b</td>
<td>428.0 ± 12.47 c</td>
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<td>1.17 ± 0.81 c</td>
<td>60.34 ± 13.59 b</td>
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<td><strong>Pinus sylvestris</strong></td>
<td>52.51 ± 0.15 b</td>
<td>15.87 ± 0.58 c</td>
<td>1.28 ± 0.04 b</td>
<td>5.43 ± 0.13 bc</td>
<td>34.41 ± 12.67 b</td>
<td>429.0 ± 12.67 b</td>
<td>429.0 ± 1.88 c</td>
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<tr>
<td><strong>Pseudotsuga menziesii</strong></td>
<td>53.02 ± 0.22 b</td>
<td>16.30 ± 0.58 b</td>
<td>1.21 ± 0.06 b</td>
<td>7.44 ± 0.13 bc</td>
<td>32.63 ± 13.65 b</td>
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<td>443.4 ± 1.83 c</td>
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<td><strong>Quercus petraea</strong></td>
<td>52.38 ± 0.18 b</td>
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<td>7.16 ± 0.27 c</td>
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<td><strong>Quercus robur</strong></td>
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<td>420.5 ± 19.99 b</td>
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Table S3: Species (mean ± SE) foliar S, Fe, Ca, Mg, Mn, Zn, and Cu concentrations. S, Ca, and Mg concentrations have units of mg g\(^{-1}\), and Fe, Mn, Zn, and Cu have units of µg g\(^{-1}\). Different letters indicate significant differences (\(P < 0.05\)) amongst species (Tukey's HSD test for multiple comparisons), and \(n\) indicates the number of sites per species.

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<th>Species</th>
<th>S</th>
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<th>Mn</th>
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<tr>
<td>Abies alba</td>
<td>0.95 ± 0.03 d</td>
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<td>1.12 ± 0.11 c</td>
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<td>5.14 ± 0.58 ab</td>
<td>1.00 ± 0.07 c</td>
<td>823.44 ± 146.23 b</td>
<td>22.54 ± 4.50 b</td>
<td>2.98 ± 0.28 c</td>
</tr>
<tr>
<td>Pinus nigra</td>
<td>0.96 ± 0.19 d</td>
<td>21.53 ± 5.30 b</td>
<td>2.79 ± 0.47 ab</td>
<td>0.95 ± 0.12 c</td>
<td>512.33 ± 66.07 ab</td>
<td>37.15 ± 7.64 ab</td>
<td>3.01 ± 0.38 c</td>
</tr>
<tr>
<td>Pinus pinaster</td>
<td>0.84 ± 0.04 d</td>
<td>53.20 ± 5.82 b</td>
<td>3.25 ± 0.42 ab</td>
<td>1.48 ± 0.12 c</td>
<td>182.33 ± 62.13 ab</td>
<td>25.53 ± 4.18 ab</td>
<td>3.01 ± 0.28 c</td>
</tr>
<tr>
<td>Pinus sylvestris</td>
<td>1.01 ± 0.04 d</td>
<td>59.98 ± 5.82 b</td>
<td>3.30 ± 0.42 ab</td>
<td>0.83 ± 0.12 c</td>
<td>621.43 ± 64.20 ab</td>
<td>42.64 ± 4.18 ab</td>
<td>4.18 ± 0.28 c</td>
</tr>
<tr>
<td>Pseudotsuga</td>
<td>1.11 ± 0.04 d</td>
<td>66.14 ± 5.82 b</td>
<td>3.47 ± 0.20 ab</td>
<td>1.41 ± 0.05 c</td>
<td>904.38 ± 66.07 ac</td>
<td>22.83 ± 1.86 a</td>
<td>4.35 ± 0.23 c</td>
</tr>
<tr>
<td>menziesii</td>
<td>0.02 ± 1.36 bc</td>
<td>3.73 ± 89.69 b</td>
<td>0.33 ± 6.40 ab</td>
<td>1.60 ± 1.00 c</td>
<td>1920.72 ± 129.54 ab</td>
<td>11.27 ± 0.59 e</td>
<td>6.84 ± 0.17 a</td>
</tr>
<tr>
<td>Quercus</td>
<td>0.03 ± 1.64 ab</td>
<td>4.66 ± 89.69 b</td>
<td>0.28 ± 6.40 ab</td>
<td>1.76 ± 1.00 c</td>
<td>1129.10 ± 136.85 ab</td>
<td>14.70 ± 1.75 de</td>
<td>7.61 ± 0.34 a</td>
</tr>
<tr>
<td>Quercus robur</td>
<td>0.05 ± 1.64 ab</td>
<td>7.96 ± 105.82 b</td>
<td>0.41 ± 6.84 ab</td>
<td>0.21 ± 1.76 c</td>
<td>136.85 ± 136.85 a</td>
<td>1.75 ± 0.34 a</td>
<td></td>
</tr>
</tbody>
</table>
1. The consecutive disparity index \((D)\)

\(D\) assesses the consecutive variations in a time series and so is sensitive to real time-step to time-step variations, conversely to the CV index, which is insensitive to temporal autocorrelation. \(D\) has been used in climate research to better assess interannual variability in the highly irregular precipitation time series of the Iberian Peninsula (Martín-Vide, 1986) and is calculated as:

\[
D = \frac{1}{n-1} \sum_{i=1}^{n-1} \left| \ln \frac{p_{i+1}}{p_i} \right| \quad \text{Equation 1}
\]

where \(p_i\) is the series value and \(n\) is the series length. To avoid numerical indetermination (division by 0) when a time series contains zeros, we can sum a constant \((k,\) usually a unit\) to the entire time series as:

\[
D = \frac{1}{n-1} \sum_{i=1}^{n-1} \left| \ln \frac{p_{i+1}+k}{p_i+k} \right| \quad \text{Equation 2}
\]

The core of \(D\) lies in the assessment of the variability by taking into account the consecutive changes in a time series (see Eqs. 1 and 2). Additionally, on the contrary to CV (standard deviation · mean\(^{-1}\)), the calculation of \(D\) does not take the mean of the time series into account, which makes it less dependent on the mean. An easy example of the differences between the CV and the \(D\) indices can be seen in Figure S3. Both time series have the same CV but completely opposite temporal behaviours. The first time series (A) fluctuates every year, but the second time series (B) is stable during the first half and then shifts to a second state. The higher consecutive interannual variability makes the \(D\) index to be higher in time series A.
2. Estimating GPP

To estimate GPP for each forest, we constructed a linear model using data from a global forest database (Luyssaert et al., 2007; Fernández-Martínez et al., 2014b) containing carbon fluxes and productivity data from forests. We extracted data from sites that reported annual GPP (mainly derived from eddy covariance CO2 fluxes) and foliar NPP, as well as MAT, MAP, and leaf type. Abbreviations: mean annual precipitation (MAP), mean annual temperature (MAT), standard errors (SE), standardized coefficients ($\beta$), root mean squared error (RMSE), degrees of freedom (df).

Model summary

|                  | Estimate | SE  | $\beta$ | SE  | t    | Pr(>|t|) |
|------------------|----------|-----|---------|-----|------|----------|
| (Intercept)      | 985.63   | 284.82 | 0.000   | 0.000 | 3.46 | <0.001  |
| Leaf type - conifers | 239.18  | 236.92 | 0.136   | 0.136 | -0.138 | 0.3158 |
| MAP              | -0.422   | 0.271 | -0.484  | 0.311 | 1.556 | <0.001  |
| MAT              | -9.244   | 18.794 | 0.068   | 0.137 | 0.492 | <0.001  |
| Foliar NPP       | 4.627    | 0.798 | 0.517   | 0.089 | 5.795 | <0.001  |
| Leaf type - conifers:map | 0.378  | 0.186 | 0.453   | 0.223 | 2.032 | <0.001  |
| MAP:MAT          | 0.035    | 0.013 | 0.829   | 0.303 | 2.734 | <0.001  |

$R^2$ for Leaf type: 0.029, $R^2$ for MAP: 0.219, $R^2$ for MAT: 0.222, $R^2$ for Foliar NPP: 0.241, $R^2$ for Leaf type:MAP: 0.009.

Model crossvalidation (75% data as training test - 25% validation data)

<table>
<thead>
<tr>
<th></th>
<th>2.50%</th>
<th>50%</th>
<th>Mean</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>$R^2$</td>
<td>0.636</td>
<td>0.707</td>
<td>0.767</td>
<td>0.706</td>
</tr>
<tr>
<td>$R^2_{adj}$</td>
<td>0.616</td>
<td>0.691</td>
<td>0.754</td>
<td>0.690</td>
</tr>
<tr>
<td>RMSE on crossvalidation</td>
<td>268.76</td>
<td>396.57</td>
<td>526.76</td>
<td>396.70</td>
</tr>
<tr>
<td>% error on crossvalidation</td>
<td>7.38%</td>
<td>11.52%</td>
<td>17.08%</td>
<td>11.40%</td>
</tr>
</tbody>
</table>