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

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Introduction

Reproductive behaviour in plant species is a crucial part of ecosystem functioning. Therefore, patterns of production of fruit have 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, involving the synchronized alternation of years with extremely large fruit crops and years with little or no fruit production (Kelly & Sork, 2002). Because of the consequences of masting on ecosystems (e.g. important cascading effects throughout the food web; Ostfeld & Keesing, 2000), a large array of studies have attempted to understand how and why this extreme interannual variability in fruit production occurs (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) of 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 the elucidation of the contribution of reproduction to ecosystem net primary production (NPP), which is the sum of aboveground (wood, leaves, fruits) and belowground (roots) biomass production, root exudates and the emission of organic volatile compounds. The lack of a quantitative assessment of carbon (C) allocation to fruit production has been an important drawback for the correct estimation of fruit NPP (NPPf) and total biomass production in, for instance, synthesis studies on plant C allocation (e.g. Vicca et al., 2012; Campioli et al., 2015). Given that the mean residence time of C is very dependent on the compartment to which C is allocated (Fernández-Martínez et al., 2016a), measures of NPPf and the percentage of gross primary production (GPP, which equals net ecosystem photosynthesis) allocated to reproduction would facilitate C balance closure in forest ecosystems, and would...
improve our in-depth understanding of plant strategies under different environmental conditions and responses to changes in, for example, climate and nutrient availability.

Endogenous factors, such as stand age, basal area and taxonomic family, and exogenous factors, such as climate, nutrient availability and anthropogenic impacts, have been demonstrated to largely control GPP, NPP and C 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., 2014a). These endogenous and exogenous factors may thus also have an effect on NPP. Nutrient availability, in particular, may play an important role in the determination of NPP and its temporal behaviour, because fruits and seeds are richer in nutrients (mostly in nitrogen (N), phosphorus (P) and potassium (K)) than vegetative tissues (Reeke & Bazzaz, 1987). Fruit production may thus have stronger relationships than vegetative tissue production with nutrient availability (Sala et al., 2012). N, 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). N deposition has been suggested to increase forest productivity (Luyssaert et al., 2010; de Vries et al., 2014), 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 the determination of fruit production and its temporal behaviour (Swietlik, 2002).

Although elemental concentrations are important, the ratios between the various elements may be even more relevant. The foliar N : P ratio has been suggested to be an important indicator of plant nutritional status and vegetative (Güsewell, 2004; McGroddy et al., 2004; Sardans et al., 2012, 2016b) and reproductive (Fujita et al., 2014) production. For example, species with low foliar N : P ratios tend to be fast growing and more competitive for soil resources than species with higher N : P ratios (Willby et al., 2001; Elser et al., 2003; Peñuelas et al., 2013). Other studies have suggested that, within the same species, plants or shoots producing flowers may have lower N : P ratios than those that do not produce flowers (Eckstein & Karlsson, 1997; Güsewell, 2004). Other elemental stoichiometries, such as C : N and C : P ratios, may also indicate limitations of soil nutrients (Fernández-Martínez et al., 2014b) and may therefore also be associated with reproductive behaviour in plants.

The general aim of this study was to characterize fruit production and its temporal behaviour for several of the most abundant European tree species, and to distinguish species-specific variability from the effects of the taxonomic family, productivity, foliar nutrient concentrations, climate and atmospheric deposition of N and S. We specifically aimed: (1) to estimate average NPP, and the percentage of GPP (hereafter %GPP) allocated to fruit production of various tree species distributed across Europe; (2) to parameterize masting by assessing the temporal variation of NPP of these species by calculating the coefficient of variation (CV), the consecutive disparity index (D) and the temporal autocorrelation at a 1-yr time lag (AR1, the correlation between fruit production in year y and year y – 1); and (3) to identify the possible determinants of the spatial and species-specific variability of fruit production and its temporal behaviour in relation to GPP, foliar nutrient (C, N, P, K, S, iron (Fe), magnesium (Mg), calcium (Ca), zinc (Zn), manganese (Mn) and copper (Cu)) concentrations and C : N : P stoichiometries (C : N, N : P and C : P ratios), climate (mean annual temperature (MAT) and precipitation (MAP), and their interannual variabilities) and atmospheric deposition of N and S. We also explored the potential differences in fruiting behaviour between species of the Pinaceae and Fagaceae families.

Materials and Methods

Data collection

Data for litterfall and foliar nutrient concentrations We downloaded data for litterfall (Pitman et al., 2010) and foliar nutrient concentrations (Rautio et al., 2010) from the ICP Forests database (International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forest, operated under the United Nations Economic Commission for Europe (UNEC) Convention on Long-range Transboundary Air Pollution, http://icp-forests.net/), containing data for 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. To sample foliar nutrient concentrations per site, five trees (at least) were randomly selected, covering the total site area. Sampled leaves were produced during the current year of sampling, were developed in light (not under shade) and were taken from the upper third of the crown (but not from the very first whorls in conifer species), attempting to represent the different orientations of the tree. Deciduous species were sampled during the second half of the growing season, before the very beginning of senescence, whereas evergreen species were sampled during the dormancy period. Further information on the experimental design of foliar nutrient concentrations can be found in Rautio et al. (2010). 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 do nutrient concentrations of soils as nutrients in soils are sometimes not available for plants for multiple reasons, 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 $g\, DW\, m^{-2}\, \text{yr}^{-1}$ so we used C concentration data (provided by the same database) to convert these data to units of $g\, C\, m^{-2}\, \text{yr}^{-1}$. 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 datasets that were too short, of the 210 forests originally available, we used only 126 forests with time series with four or more years of data (Supporting Information Fig. 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.

**Climatic data** We extracted MAT and MAP data for our forests from the WorldClim database (Hijmans et al., 2005). This database provides climatic data with a high spatial resolution (30 arc s, c. 1 km at the equator) and contains robust mean monthly climatic data derived from lengthy time series (1950–2000).

**GPP data and the calculation of the NPPf 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 (Luysaert et al., 2007; Fernández-Martínez et al., 2014b) containing C 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, randomizing 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 summarized in the Supporting Information (Fig. S2; Methods S1). We calculated the percentage of GPP allocated to NPPf (hereafter %GPPf) as: % GPPf = 100 × NPPf × GPP−1.

**Atmospheric deposition data** We obtained data for atmospheric deposition from the European Monitoring and Evaluation Programme (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 ($R^2=0.32$ 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.

**Data analyses** We calculated all the average metrics of fruit production per site from the annual values per site: average NPPf, average %GPPf, maximum NPPf recorded in each forest, NPPf CV, NPPf $D$ (Martín-Vide, 1986) and NPPf AR1. $D$ was calculated in addition to CV because it has been suggested recently to improve the assessment of temporal variability relative to CV, especially in negatively autocorrelated time series. Further information on $D$ can be found in the Supporting Information (Methods S2; Fig. S3). 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 the 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 characterize the temporal behaviour of NPPf of that species. Using average site values as replicates, we identified differences amongst species and families using analyses of variance (ANOVAs) and Tukey's honest significant difference (HSD) tests for multiple comparisons.

We fitted linear mixed models (LMMs) to characterize 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 NPPf, %GPPf, maximum NPPf and the CV, $D$ and AR1 of NPPf). Using the species as a random effect (for example, to take into account 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 CV for the models predicting $D$ of NPPf. Variables were selected using the backwards–forwards stepwise method, starting from the saturated model. Once the most important variables had been selected, we calculated the first-order interactions of the variables within the model and removed the nonsignificant terms. Models were fitted with the lme function of the R package nlme (Pinheiro et al., 2014) 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-$R^2$) using the method proposed by Nakagawa & Schielzeth (2013) implemented in the MuMIn R package (Barton, 2015). We also used generalized additive models (GAMs) to explore the nonlinearities between the response variables and the predictors using spline functions. NPPf and $D$ of NPPf 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).

**Results**

**Species-specific variability in fruit production and its temporal behaviour**

Mean fruit production amongst the studied species ranged from (mean ± SE) 6.1 ± 1.7 g C m$^{-2}$ yr$^{-1}$ in *Pseudotsuga menziesii* to

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40.6 ± 9.9 g C m⁻² yr⁻¹ in *Pinus nigra* (Fig. 1; Table S1). In fact, mean NPPf yr⁻¹ varied little amongst species and differed significantly only between the two former species and between *Pinus sylvestris* and *Quercus petraea* (Fig. 1). Nonetheless, when grouped, Pinaceae species had a higher average NPPf than Fagaceae species (23.2 ± 2.1 and 15.0 ± 1.6 g C m⁻² yr⁻¹, respectively; ANOVA, *P* = 0.003). Similarly, the percentage of GPP invested in NPPf (%GPPf) varied little amongst species (Fig. 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 %GPPf higher in *P. sylvestris* than in the other two species. However, %GPPf 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 NPPf was similar across species and averaged 46.9 ± 3.1 g C m⁻² yr⁻¹ (Fig. 2; Table S1).

Temporal variability in fruit production differed substantially across species and between families (Fig. 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 of 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 0.85 ± 0.05 for *D*, respectively; *P* < 0.001). In addition, ANOVA indicated that the first autocorrelation coefficient (AR1) differed amongst species (Fig. 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.

**Determinants of fruit production and its temporal behaviour**

Our statistical LMMs indicated that GPP and foliar Zn and P concentrations (Fig. 4) were positively associated with NPPf 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) (Fig. 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 NPPf with 40% explained by the fixed effects (GPP, Zn and P) and 16% by differences amongst species.

Similar to NPPf, %GPPf was higher in forests with high foliar Zn and P concentrations (Table 1). The interaction between foliar Zn and P concentrations was also statistically significantly positively associated with %GPPf (*P* = 0.025). The model for % GPPf explained 44% of the variance in %GPPf, with 31% accounted for by the fixed effects and the remaining 13% by interspecific variability. Maximum recorded NPPf was positively associated with GPP, basal area and foliar Zn concentrations, and negatively associated with MAP and foliar N and C : P concentrations (Table 1). In addition, Fagaceae species presented larger maximum NPPf than did Pinaceae species (*P* = 0.004). The model accounted for 41% of the variance in maximum NPPf, 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 NPPf was clearly larger for Fagaceae than for Pinaceae species (*P* < 0.01 for both indices; Table 1; Fig. 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. By contrast, the model predicting *D* of NPPf 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$_f$ and their role in the forest C balance

Our results provide the first estimates of C allocation to fruit production for some of the most abundant tree species in European forests. Despite the high variability in the estimates, mainly caused by the differences in GPP and foliar nutrient concentrations (Table 1), average NPP$_f$ in our sample of European forests ranged from 10 to 40 g C m$^{-2}$ yr$^{-1}$ and accounted for 0.5–3% of the GPP, both being higher in Pinaceae than in Fagaceae species. These estimates of NPP$_f$ and GPP allocation are lower than those in previous studies. Herbst et al. (2015) reported mean NPP$_f$ estimates of 95 ± 37 and 73 ± 25 g C m$^{-2}$ yr$^{-1}$ for managed and unmanaged stands of F. sylvatica, respectively. GPP allocation to NPP$_f$ averaged 6.7 ± 3.4% and 4.6 ± 2.0% in the managed and unmanaged stands, respectively. In addition, %GPP$_f$ reached 23% in the managed stand during an exceptional mast year. Campioli et al. (2010) reported an average NPP$_f$ for P. sylvestris of 76 ± 8 g C m$^{-2}$ yr$^{-1}$ and an average %GPP$_f$ of 6.0 ± 0.6%.
Various reasons might be behind the differences between our results and previous reports of NPP$_f$ 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 (Fig. 4; Table 1). Moreover, exogenous factors, such as the management of the stand, can also influence C...
Fig. 5 Three-dimensional plot showing the significant interaction between foliar phosphorus (P) and zinc (Zn) concentrations for predicting fruit net primary production (NPP). The response surface was calculated using a generalized additive model explaining 28% of the variance in NPPf. Blue and green colours of the response surface indicate low and high NPPf, respectively.

allocation to fruiting (Herbst et al., 2015). The assessment of average values, however, is very dependent on the period of measurement because of 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 NPPf.

NPPf is usually a relatively small component of the C balance of forest ecosystems, but its high interannual variability in masting species, such as F. sylvatica or Quercus sp., identifies NPPf as an important component to consider for a better assessment of the ecosystem C 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 NPPf was two- to three-fold higher than mean NPPf for all species (Table S1). %GPPf 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 C cycle. Nonetheless, our results provide new insights into the fate of photosynthesized C in forest ecosystems. However, because of the way in which we estimated GPP for our sites and the error propagation, our estimates of %GPPf may be subjected to larger error estimates than those calculated by mean ± SE. Therefore, any interpretation of the values reported here should take that uncertainty into consideration.

The role of nutrients in NPPf 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 played by Zn in several key metabolic processes, such as protein synthesis (as a component of ribosomes, Prask & 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 & 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 C-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 (Figs 4, 5). These processes may also be responsible for increased temporal variability in seed production, because C reserves in Zn-limited trees might be insufficient for regular production of large fruit crops (Isagi et al., 1997).

However, in addition to the effects of foliar Zn concentrations within species, the effect of foliar Zn may also be associated with different reproductive behaviour amongst taxonomic families, as Pinaceae species present higher foliar Zn concentrations than Fagaceae species (Table S3) and the two families exhibit different patterns of fruit production (i.e. Pinaceae species invest more in reproduction (Fig. 1), whereas Fagaceae species present higher interannual variability in NPPf (Fig. 3)). In this sense, high foliar Zn concentrations may be related to fast-growing species (opportunist, r-selected species), producing fruits every year, whereas low foliar Zn concentrations may be linked to slow-growing species (good competitors, k-selected species), investing more heavily in fewer reproduction events. Thus, masting behaviour 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, 1846). 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 NPPf despite their morphological and functional differences. These results also agree with previous reports...
suggesting that higher foliar P concentrations enable larger fruit crops compared with those at lower P 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 (Plazzard & Dell, 2010) and in freshwater, marine and other terrestrial ecosystems (Elser et al., 2007; Péñuelas et al., 2013). In addition, higher foliar C : P ratios in our study were associated with lower maximum NPPf (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 NPPf, but had lower maximum NPPf 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 fact that the latter present lower maximum NPPf (Table 1). This may suggest that the negative relationship between foliar N concentration and maximum NPPf occurs 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 NPPf 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 ARI of NPPf may indicate that forests with higher N reserves are able to produce fruit crops with a periodic recurrence (Isagi et al., 1997) 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). However, our analyses revealed that foliar K concentrations 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, in which water availability is amongst the most important factors driving fruit and secondary production (Ogaya & 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 & Pérez-Ramos, 2015). Hence, we hypothesize 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 GPP to fruit production and produce fruit more regularly than nutrient-limited forests. This supports previous findings which 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, which suggest that high interannual variability in fruit production is more pronounced in environments in which resources are scarce (Kelly & Sork, 2002; Fernández-Martínez et al., 2012). Nutrient availability may thus limit NPPf more strongly than it limits vegetative NPP, because fruits are more nutrient demanding than vegetative tissues (Reeke & 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 NPPf and its temporal behaviour

Nutrient availability and stoichiometry played a very important role in determining NPPf and its temporal behaviour, but site productivity and the taxonomic family were also key factors. Higher photosynthesis (GPP) was associated with higher NPPf, higher maximum NPPf 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 be used later for reproduction and to allow more regular production of fruit crops. However, because of the positive relationship between NPPf and GPP, and the dependence of 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 CV (Methods S2)) of fruit production and GPP. A larger basal area, however, was also associated with higher maximum NPPf, perhaps because of 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 NPPf and its interannual variability, we found a significant taxonomic effect on NPPf. In particular, Fagaceae and Pinaceae species presented a markedly different behaviour in fruit production patterns, with the latter exhibiting lower maximum NPPf (probably because they are generally established over nutrient-poor soils) and lower interannual variability in NPPf. 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), although this is not very 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_f (Table S1). These differences may be a result of different life history traits and evolutionary strategies related to the 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 use many resources when producing cones (bearing the seeds), whereas, 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. In addition, the different availability of nutrients between families, such as N (higher in Pinaceae, Table S2) or Zn (higher in Pinaceae; Fig. 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 indicate that masting behaviour can be well parameterized using D, because it takes into account not only the variability of the time series, but also its temporal autocorrelation (Table S1). As masting behaviour is related to high interannual variability and negative autocorrelation in fruit production, which is exactly what is accounted for by D (Methods S2), D seems to be a good candidate to characterize masting behaviour using a single index.

Conclusions
On average, NPP_f ranged from c. 10 to 40 g C m^{-2} yr^{-1} and accounted for 0.5–3% of the GPP, with little differences amongst species or between families (Fagaceae and Pinaceae). However, mean maximum NPP_f and interannual variability in NPP_f differed especially 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 to fruit production, which highlights the predominant role of available reserves of nutrients and carbohydrates to allocate to reproduction. In particular, foliar Zn and P concentrations were associated positively with fruit crop size, whereas foliar Zn and K were negatively related to its temporal variability.

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Author contributions
M.F.-M., S.V., I.A.J., J.M.E. and J.P. planned and designed the research. M.F.-M. wrote the manuscript and analysed the data. All co-authors contributed substantially to the writing of the paper.

References

**Supporting Information**

Additional Supporting Information may be found online in the Supporting Information tab for this article:

**Fig. S1** Location of the studied forests.

**Fig. S2** Model estimating gross primary production (GPP).

**Fig. S3** Example of disparity index ($D$).

**Table S1** Description of fruit production per species

**Table S2** Foliar concentrations of carbon (C), nitrogen (N), potassium (K) and phosphorus (P) per species

**Table S3** Foliar concentrations of sulphur (S), iron (Fe), calcium (Ca), magnesium (Mg), manganese (Mn), zinc (Zn) and copper (Cu) per species

**Methods S1** Model estimating gross primary production (GPP).

**Methods S2** The consecutive disparity index.

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