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

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19**Summary**

20· Fruit production (NPP_f), the amount of photosynthates allocated to reproduction ($\%GPP_f$) and
21their controls for spatial and species-specific variability (e.g., nutrient availability, climate) are
22poorly studied in forest ecosystems. We characterised fruit production and its temporal
23behaviour for several tree species and resolved the effects of gross primary production (GPP),
24climate, and foliar nutrient concentrations.

25· We used data for litterfall and foliar nutrient concentration from 126 European forests and
26related it to climatic data. GPP was estimated for each forest using a regression model.

27· Mean NPP_f ranged from approximately 10 to 40 g C m^{-2} y^{-1} and accounted for 0.5-3% of the
28GPP. Forests with higher GPPs produced larger fruit crops. Foliar zinc (Zn) and phosphorus
29(P) concentrations were associated positively with NPP_f, while foliar Zn and K were negatively
30related to its temporal variability. Maximum NPP_f and interannual variability of NPP_f was higher
31in *Fagaceae* than in *Pinaceae* species.

32· NPP_f and $\%GPP_f$ were similar amongst the studied species despite the different reproductive
33temporal behaviour of *Fagaceae* and *Pinaceae* species. We report, for the first time, that foliar
34concentrations of P and Zn play an important role in determining $\%GPP_f$, NPP_f and its temporal
35behaviour.

36**Keywords:** crop size, fertility, fruiting, reproductive effort, seeds, spatial variability

1. Introduction

38Reproductive behaviour in plant species is a crucial part of ecosystem functioning, and, 39therefore, patterns of production of fruit has received much attention from a wide range of 40ecologists (Koenig & Knops, 2005). *Masting* is a reproductive behaviour, presented mostly by 41anemophilous and long-lived plant species, consisting on the synchronised alternation of years 42with extremely large fruit crops and years with little or no fruit production (Kelly & Sork, 2002). 43Because of the consequences that masting can entail on the ecosystems (e.g., important 44cascading effects throughout the food web (Ostfeld & Keesing, 2000)), a large array of studies 45have tried to understand how and why this extreme interannual variability in fruit production 46happens (Fernández-Martínez *et al.*, 2016b). Nonetheless, it remains unclear why some 47species or populations produce larger fruit crops or have more temporally variable fruit 48production than others. Most theories have focused on the ultimate causes (e.g., avoiding 49seed predation) for these particular life-history traits (Silvertown, 1980; Kelly, 1994), but the 50proximate causes (e.g., the mechanistic effect of temperature on pollination) of the spatial 51variability in fruit production and its temporal behaviour have rarely been explored. Some 52authors have suggested that the size of the fruit crop from trees subjected to poor growing 53conditions (e.g. extreme or highly variable climates or poor soil properties such as low nutrient 54availability) should exhibit higher interannual variability (Kelly & Sork, 2002) because of the 55benefits of the *economy of scale (Norton & Kelly, 1988; Smith et al., 1990)*. However, little 56empirical evidence has yet been found to confirm that high interannual variability in fruit 57production is associated with poor growing conditions, such as drought (Fernández-Martínez 58*et al.*, 2012) or nutrient limitations.

59Most of the studies focusing on fruit or seed production have quantified the number of fruits 60produced per tree (Sork *et al.*, 1993; Espelta *et al.*, 2008; Crone *et al.*, 2011; Fernández-61Martínez *et al.*, 2015), and only few have provided data in units of mass produced per area 62(Campioli *et al.*, 2010; Herbst *et al.*, 2015; Pérez-Ramos *et al.*, 2015). This is essential for 63elucidating the contribution of reproduction to ecosystemic net primary production (NPP), 64which is the sum of aboveground (wood, leaves, fruits) and belowground (roots) biomass 65production, root exudates and the emission or organic volatile compounds. The lack of a 66quantitative assessment of C allocation to fruit production has been an important drawback for 67correctly estimating fruit NPP (NPP_f) and total biomass production in, for instance, synthesis

68studies on plant carbon allocation (e.g. Vicca *et al.*, 2012; Campioli *et al.*, 2015a). Given that
69the mean residence time of carbon is very dependent on the compartment where carbon is
70allocated to (Fernández-Martínez *et al.*, 2016a), measures of NPP_f and the percentage of
71gross primary production (GPP, which equals net ecosystem photosynthesis) allocated to
72reproduction would facilitate carbon balance closure in forest ecosystems and would improve
73in-depth understanding of plant strategies under different environmental conditions and
74responses to changes in e.g., climate and nutrient availability.

75Endogenous factors such as stand age, basal area, or taxonomical family and exogenous
76factors such as climate, nutrient availability, and anthropogenic impacts have been
77demonstrated to largely control GPP, NPP and carbon allocation to different NPP fractions at
78the global scale (Vicca *et al.*, 2012; Campioli *et al.*, 2015), and different components of NPP
79(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_f.
81Nutrient availability, in particular, may play an important role in determining NPP_f and its
82temporal behaviour, because fruits and seeds are nutrient-richer (mostly in nitrogen [N],
83phosphorus [P], and potassium [K]) than vegetative tissues (Reekie & Bazzaz, 1987). Fruit
84production may thus have stronger relationships with nutrient availability than vegetative
85tissues (Sala *et al.*, 2012). Nitrogen, for example, is the primary limiting nutrient for vegetative
86growth (Elser *et al.*, 2007; LeBauer & Treseder, 2008) and has also been positively correlated
87with investment in reproduction (Han *et al.*, 2013; Miyazaki *et al.*, 2014). Nitrogen deposition
88has 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
90negative impact on productivity and soil processes (Oulehle *et al.*, 2011; Büntgen *et al.*, 2013).
91Plants growing in P-deficient environments may also have a lower investment in sexual
92reproduction than those living in P-rich environments (Fujita *et al.*, 2014). Other macro- and
93micronutrients, often rarely studied in wild plants, may also play an important role in
94determining fruit production and its temporal behaviour (Swietlik, 2002).

95While elemental concentrations are important, the ratios between the various elements may be
96even more relevant. The foliar N:P ratio was suggested as an important indicator of plant
97nutritional 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

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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 110NPP_f and the percentage of GPP (hereafter $\%GPP_f$) allocated to fruit production of various tree 111species distributed across Europe, ii) to parameterize masting by assessing the temporal 112variation of NPP_f 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.

121**2. Materials and methods**

122*2.1. Data collection*

123*2.1.1. Data for litterfall and foliar nutrient concentrations*

124We downloaded data for litterfall (Pitman *et al.*, 2010) and foliar nutrient concentrations (Rautio 125*et 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

129entire years, and foliar nutrient concentrations (C, N, P, K, S, Fe, Mg, Ca, Zn, Mn, and Cu)
130were averaged per site. Average foliar C:N:P stoichiometries per site were calculated on a
131mass basis. We used foliar nutrient concentrations instead of soil nutrient availability as the
132measure of nutrient availability for plants because foliar nutrient concentrations often better
133reflect nutrient availability for plants than nutrient concentration of soils because sometimes
134nutrients in soils are not available for plants because of multiple factors such as
135bioimmobilization (Aber & Melillo, 1982) or complex formation (related to too high or too low
136pH; Truog, 1947; Comerford, 2005).

137The original data for litterfall were available in units of g of dry weight m^{-2} $y^{-1}$and we used
138carbon concentration data (provided by the same database) to convert these data to units of g
139C m^{-2} y^{-1}. We also used site information such as mean site diameter to calculate mean basal
140area, as an estimation of the mean size of the trees at each site. To avoid eventual artefacts of
141anomalous years dominating too short data sets, of the 210 forests originally available, we
142used only 126 forests with time series with four or more years of data (**Figure S1**). We also
143excluded *Ceratonia siliqua* and *Larix decidua* because of the scarcity of replicates (two and
144one forest, respectively), as well as 12 multi-species forests. We provided summary values for
145*Pinus nigra,* but did not include this species in the statistical models, because only three
146replicates were available. Because of missing data for some of the predictor variables, only 97
147forests were finally used to fit the statistical models.

148*2.1.2. Climatic data*

149We extracted mean annual temperature and precipitation data (MAT and MAP, respectively) for
150our forests from the WorldClim database (Hijmans *et al.*, 2005). This database provides
151climatic data with a high spatial resolution (30 arc seconds, ca. 1 km at the equator) and
152contains robust mean monthly climatic data derived from lengthy time series (1950-2000).

153*2.1.3. GPP data and the calculation of the NPP_f -to-GPP percentage*

154We aimed to understand the relative reproductive investment of trees (relative to GPP), but the
155ICP forest network did not measure GPP. We therefore developed and tested a model that
156predicts average GPP from independent drivers. We used a global forest database (Luyssaert
157*et al.*, 2007; Fernández-Martínez *et al.*, 2014b) containing carbon fluxes and productivity data
158from forests. We extracted data from sites that reported both mean GPP (mainly derived from

159eddy covariance CO_2 fluxes) and foliar NPP, as well as MAT, MAP, and leaf type. We chose

160this set of predictors because these variables were also available for each of the ICP-forest

161sites used in this study, allowing the estimation of GPP for each site. The model, containing

162data for 84 forests, accounted for 74% of the variance in GPP. We cross-validated the model

163using 75% of the data as a sampling set and the remaining 25% as the testing set and

164repeated this procedure 1000 times randomising both subsets. The cross-validation indicated

165that the model performed acceptably well: average errors of the model predictions were lower

166than 12% for the testing set. The model and cross-validation are summarised in the

167Supplementary Material (**Figure S2** and **Section 2: Estimating GPP**). We calculated the

168percentage of GPP allocated to NPP_f (hereafter $\%GPP_f$) as: $\%GPP_f = 100 \times NPP_f \times GPP^{-1}$.

169*2.1.4. Atmospheric deposition data*

170We obtained data for atmospheric deposition from the EMEP gridded datasets and ICP

171Forests. Modelled N and S deposition data from the EMEP gridded maps were correlated with

172the ICP data for each forest (R=0.32 and 0.67, $P < 0.001$, for N and S deposition,

173respectively). We used the EMEP data throughout in our statistical models because the ICP

174data were incomplete for our database.

175*2.2. Data analyses*

176We calculated all the average metrics of fruit production per site from the annual values per

177site: average NPP_f, average $\%GPP_f$, maximum NPP_f recorded in each forest, NPP_f CV, NPP_f D

178(Martín-Vide, 1986), and NPP_f AR1. D was calculated in addition to CV because it was recently

179suggested to improve the assessment of temporal variability relative to the CV, especially in

180negatively autocorrelated time series. Further information on the D index can be found in the

181Supplementary Material, **Section 1: The consecutive disparity index (*D*).** AR1 indicates the

182temporal correlation between fruit crop sizes for years y-1 and y. Negative AR1 values in fruit

183production time series may be a sign of depletion of resources after large fruit crops (Sork *et*

184*al.*, 1993; Fernández-Martínez *et al.*, 2015). These values of fruit CV, D and AR1 were further

185averaged across sites per species to characterise the temporal behaviour of NPP_f of that

186species. Using average site values as replicates, we identified differences amongst species

187and families using ANOVAs and Tukey's HSD tests for multiple comparisons.

188We fitted linear mixed models (LMMs) to characterise the relationships of the exogenous (MAT, 189MAP, and N and S atmospheric deposition) and endogenous (foliar nutrient concentrations, 190GPP, basal area, and family – *Pinaceae* or *Fagaceae*) variables with the temporal behaviour of 191fruit production (mean NPP_f, $\%GPP_f$, maximum NPP_f, and the CV, D, and AR1 of NPP_f). Using 192the species as a random effect (to take into account, for example, the species effect on 193stoichiometry), we tested whether the fruit production metrics were correlated with productivity 194and with forest characteristics, such as GPP, basal area, family of the species, climate, foliar 195nutrient concentrations, and atmospheric deposition of N and S. The saturated model used 196GPP, basal area, N and S deposition, MAT, MAP, the CVs of MAT and MAP, foliar 197concentrations of C, N, P, K, S, Fe, Ca, Cu, Mg, and Zn, and foliar C:N, N:P, and C:P ratios as 198fixed effects. We used D of MAT and MAP instead of the CV for the models predicting D of 199NPP_f. Variables were selected using the backwards-forwards stepwise method, starting from 200the saturated model. Once the most important variables were selected, we calculated the first-201order interactions of the variables within the model and removed the non-significant terms. 202Models were fitted with the *lme* function of the R package "*nlme*" (Pinheiro *et al.*, 2013) using 203restricted maximum likelihood and a Gaussian distribution. To provide a measure of goodness 204of fit of our models we assessed the marginal (fixed factors) and conditional (fixed + random 205factors) variance explained by the model (pseudo R^2) using the method proposed by 206Nakagawa & Schielzeth (2013) implemented in the MuMIn R package (Barton, 2015). We also 207used generalised additive models (GAMs) to explore the non-linearities between the response 208variables and the predictors using spline functions. NPP_f and D of NPP_f were log-transformed 209to meet the assumption of normality and heteroscedasticity in the model residuals. All analyses 210were performed using R statistical software (R Core Team, 2015).

211**3. Results**

212*3.1. Species-specific variability in fruit production and its temporal behaviour*

213Mean fruit production amongst the studied species ranged from (mean ± standard error) 6.1 ± 2141.7 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,** 215**Table S1)**. In fact, mean NPP_f per year varied little amongst species and differed significantly 216only between the two above species and between *Pinus sylvestris* and *Quercus petraea* 217**(Figure 1)**. Nonetheless, when grouped *Pinaceae* species had a higher average NPP_f than 218*Fagaceae* species (23.2 ± 2.1 and 15.0 ± 1.6 g C m^{-2} y^{-1}, respectively; ANOVA, *P* = 0.003).

219Similarly, the percentage of GPP invested in NPP_f ($\%GPP_f$) varied little amongst species
220**(Figure 1)** and, on average, was <3% in all species (**Table S1**). The only differences amongst
221species were found between *P. sylvestris*, *P. menziesii*, and *Q. petraea*, with $\%GPP_f$ higher in
222*P. sylvestris* than in the other two species. On the other hand, $\%GPP_f$ was different between
223families, being higher for *Pinaceae* than *Fagaceae* forests (1.7 ± 0.2 and 1.1 ± 0.1%,
224respectively; 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**).

226Temporal variability in fruit production differed substantially across species and between
227families (**Figure 3, Table S1**). The *Fagaceae* species *Fagus sylvatica*, *Q. petraea*, and *Q.*
228*robur* had the highest temporal variabilities, with an average CV >1.3 and D >1.5 **(Table S1)**.
229Both these indices of temporal variability indicated higher variability in fruit production in
230*Fagaceae* than in *Pinaceae* forests (1.38 ± 0.05 and 0.73 ± 0.05 for CV and 1.81 ± 0.09 and
2310.85 ± 0.05 for D, respectively; $P < 0.001$). Also, the ANOVA indicated that the first
232autocorrelation coefficient (AR1) differed amongst species (**Figure 3, Table S1**). Tukey's HSD
233test, however, found significant differences in AR1 only between *P. menziesii* and *F. sylvatica*.
234The former species had almost no autocorrelation, and the latter had a strong negative
235autocorrelation. Autocorrelation in fruit production generally tended to be negative, suggesting
236that years with higher (lower) fruit production tended to be followed by a year with lower
237(higher) fruit production.

238*3.2. Determinants of fruit production and of its temporal behaviour*

239Our statistical linear mixed models (LMMs) indicated that GPP and foliar Zn and P
240concentrations **(Figure 4)** were positively associated with NPP_f within and across species
241**(Table 1)**. We also found a statistically significant positive interaction between foliar Zn and P
242concentrations ($P = 0.01$), indicating that the positive effect of Zn increased with increasing
243foliar P concentration (and vice versa) **(Figure 5)**. Our analysis thus identified a synergistic
244effect of foliar Zn and P concentrations, leading to higher fruit production when both nutrients
245occurred at high concentrations in the leaves. The LMM accounted for 56% of the variance in
246NPP_f, with 40% explained by the fixed effects (GPP, Zn and P) and 16% by differences
247amongst species.

248Similar to NPP$_f$, %GPP$_f$ was higher in forests with high foliar Zn and P concentrations **(Table 1)**. 249The interaction between foliar Zn and P concentrations was also statistically significantly 250positively associated with %GPP$_f$ (P = 0.025). The model for %GPP$_f$ explained 44% of the 251variance in %GPP$_f$, with 31% accounted for by the fixed effects and the remaining 13% by 252interspecific variability. Maximum recorded NPP$_f$ was associated positively with GPP, basal 253area and foliar Zn concentrations, and negatively with MAP and foliar N and C:P 254concentrations **(Table 1)**. Also, *Fagaceae* species presented larger maximum NPP$_f$ than 255*Pinaceae* species (P = 0.004). The model accounted for 41% of the variance in maximum 256NPP$_f$, with 31% explained by the fixed effects and 10% by interspecific variability.

257Temporal variability in fruit production differed depending on the index used to evaluate 258interannual variation (CV and D), but temporal variability in NPP$_f$ was clearly larger for 259*Fagaceae* than for *Pinaceae* species (P < 0.01 for both indices**; Table 1, Figure 4)**. The model 260predicting the temporal variability of fruit production using the CV index indicated that more 261productive forests with higher foliar Zn concentrations exhibited lower interannual variability in 262fruit production. In contrast, the model predicting D of NPP$_f$ indicated that D was higher in 263forests with larger basal areas and lower foliar K concentrations (**Table 1**). Overall, the CV and 264D models explained 62% and 56%, respectively, of the variance in the CV and D of fruit 265production, with 58% and 55% explained by the fixed effects and the remaining 4% and 1% by 266interspecific variability.

267Finally, the model that best predicted temporal AR1 indicated a tendency for more negative 268values of temporal autocorrelation in forests with high loads of N deposition than in forests less 269exposed to N deposition (P = 0.055). However, N deposition explained only 3% of the variance 270in the temporal autocorrelation of fruit production, and species-specific variability explained 27120% of the variability in AR1.

272**4. Discussion**

273*Estimates of NPP$_f$ and their role in the forest C balance*

274Our results provide the first estimates of carbon allocation to fruit production for some of the 275most abundant tree species in European forests. Despite the high variability in the estimates, 276due mainly to the differences in GPP and foliar nutrient concentrations **(Table 1)**, average NPP$_f$ 277in our sample of European forests ranged from 10 to 40 g C m^{-2} y^{-1} and accounted for 0.5-3%

278of the GPP, both being higher in *Pinaceae* than in *Fagaceae* species. These estimates of NPP_f

279and GPP allocation are lower than those in previous studies. Herbst et al. (2015) reported

280mean NPP_f estimates of 95 ± 37 and 73 ± 25 g C m^{-2} y^{-1} for managed and unmanaged stands

281of *F. sylvatica*, respectively. GPP allocation to NPP_f averaged 6.7 ± 3.4 and 4.6 ± 2.0% in the

282managed and unmanaged stands respectively. In addition, $\%GPP_f$ reached 23% in the

283managed stand during an exceptional mast year. Campioli et al., (2010) reported an average

284NPP_f for *P. sylvestris* of 76 ± 8 g C m^{-2} y^{-1} and an average $\%GPP_f$ of 6.0 ± 0.6%.

285Various reasons might be behind the differences between our results and previous reports of

286NPP_f and allocation to fruit. Differences in the endogenous characteristics of the stands, such

287as GPP or foliar nutrient concentrations, are of major importance for fruiting NPP **(Figure 4,**

288**Table 1)**. Moreover, exogenous factors such as the management of the stand can also

289influence carbon allocation to fruiting (Herbst *et al.*, 2015). The assessment of average values,

290however, is very dependent on the period of measurement due to the high irregularity of fruit

291production, especially when analysing relatively short time series of masting species such as

292those of the *Fagaceae* family. Different sampling methodologies could also be responsible for

293these differences in average NPP_f.

294NPP_f is usually a relatively small component of the carbon balance of forest ecosystems, but

295its high interannual variability in masting species, such as *F. sylvatica* or *Quercus* sp., identifies

296NPP_f as an important component to consider for a better assessment of the ecosystem carbon

297balance (Herbst *et al.*, 2015) or the cascading effects that fruit NPP can entail on the entire

298food web of an ecosystem (Ostfeld & Keesing, 2000). Mean maximum NPP_f was 2- to 3-fold

299higher than mean NPP_f for all species **(Table S1)**. $\%GPP_f$ can thus increase substantially in

300years with large fruit crops. Further analyses with longer time series are clearly needed to

301obtain more robust estimates of the role of fruit production in the forest carbon cycle.

302Nonetheless, our results do provide new insights on the fate of photosynthesised C in forest

303ecosystems. However, because of the way in which we estimated GPP for our sites and the

304error propagation, our estimates of $\%GPP_f$ may be subjected to larger error estimates than

305those we calculated by mean ± SE. Therefore, any interpretation of the values we report

306should take that uncertainty into consideration.

307*The role of nutrients in NPP_f and its temporal behaviour*

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

327 However, despite foliar Zn concentrations have an effect within species, the effect of foliar Zn
328 is also associated to the different reproductive behaviour amongst taxonomical families, since
329 *Pinaceae* species present higher foliar Zn concentrations than *Fagaceae* species (Table S3)
330 and both families exhibit different patterns of fruit production (i.e., *Pinaceae* species invest
331 more on reproduction [Figure 1] while *Fagaceae* species present higher interannual variability
332 in NPP$_f$ [Figure 3]). In that sense, high foliar Zn concentrations may be related to fast growing
333 species (opportunistic, the r-selected species), producing fruits every year, while low foliar Zn
334 concentrations may be linked to slow growing species (good competitors, the k-selected
335 species) investing more heavily in fewer reproducing events. Thus, masting behavior could be
336 related to an evolutionary strategy of the k-selected species that would confer an evolutionary
337 advantage over their competitors (Kelly & Sork, 2002).

338Forests with higher foliar P concentrations had higher mean fruit production and allocation to 339fruit production in our study, supporting the finding by Fujita *et al.* (2014). P had the strongest 340effect in forests with high foliar Zn concentrations (**Table 1**). This synergistic effect of foliar P 341and Zn concentrations could be a consequence of an induced limitation of one nutrient when 342the other is increased, (Elser *et al.*, 2007) in agreement with von Liebig's law of the minimum 343(Von Liebig, 1840). The close association of P (Elser *et al.*, 2003) and Zn (Prask & Plocke, 3441971) with ribosomes, and therefore with metabolism and biomass production, further supports 345a positive interaction between these elements. Our results also point out that both families, 346*Pinaceae* and *Fagaceae*, present a similar relationship between foliar P concentrations and 347NPP$_f$ despite their morphological and functional differences. These results also agree with 348previous reports suggesting that higher foliar P concentrations enable larger fruit crops 349compared to those with lower concentrations (e.g. in olive trees (Erel, 2008) and amongst 350multiple plant species (Fujita *et al.*, 2014)) or, more generally, that P limitation constrains NPP 351in forests (Perkins, 2004; Plassard & Dell, 2010) and in freshwater, marine, and other 352terrestrial ecosystems (Elser *et al.*, 2007; Peñuelas *et al.*, 2013). Additionally, higher foliar C:P 353ratios in our study were associated with lower maximum NPP$_f$ (**Table 1)**. This finding is also 354consistent with P limitation for fruit production: P-deficient forests may not be able to produce 355as large fruit crops as those with sufficient P availability.

356According to our statistical models, trees with higher foliar N concentrations not only did not 357have higher NPP$_f$ but had lower maximum NPP$_f$ than those with lower N concentrations (**Table 3581)**. This is intriguing given the fact that foliar N concentrations are higher in *Fagaceae* species 359than in *Pinaceae* species **(Table S2)**, despite the latter presents lower maximum NPP$_f$ (**Table 3601)**. This may suggest that the negative relationship between foliar N concentration and 361maximum NPP$_f$ happens only within species and not amongst species. N has been identified 362as the primary limiting nutrient for vegetative growth (Elser *et al.*, 2007; LeBauer & Treseder, 3632008) and reproduction (Han *et al.*, 2013; Miyazaki *et al.*, 2014), but the lack of association 364between foliar N concentration and NPP$_f$ might be a consequence of other nutrients limiting 365production, such as Zn or P. Most of Europe is exposed to high rates of N deposition, which 366may increase N availability for plants, as indicated by the relatively high average values of 367foliar N concentrations in European forests (**Table S2**).

368The negative relationship between atmospheric N deposition and AR1 of NPP_f may indicate
369that forests with higher N reserves are able to produce fruits crops with a periodic recurrence
370(Isagi *et al.*, 1997) when other factors are not limiting growth during a particular year (such as
371weather, other nutrients such as Zn or P, or a combination of both (Fernández-Martínez *et al.*,
3722015). On the other hand, our analyses revealed that foliar K concentration were negatively
373related to interannual variability in fruit production (**Table 1**). This relationship may not remain
374amongst species because foliar K concentrations were lower in the *Pinaceae* family, which
375presents significantly lower interannual variability (**Table 1**). Foliar K concentrations are related
376to plant water regulation, thus being an important nutrient especially in arid environments,
377where water availability is amongst the most important factors driving fruit and secondary
378production (Ogaya & Peñuelas, 2007; Pérez-Ramos *et al.*, 2010; Garbulsky *et al.*, 2013). K
379bioavailability increases with increasing annual precipitation, but, through conservation
380mechanisms such as resorption, plants can increase their K concentrations (Sardans &
381Peñuelas, 2015). Hence, we hypothesise that trees with higher foliar K concentrations produce
382fruits more regularly because they can cope better with eventual reduced water availability and
383are thus less sensitive to interannual changes in water availability (Fernández-Martínez *et al.*,
3842015).

385Our results thus indicate that nutrient-rich forests produce more fruits, allocate a larger fraction
386of the GPP to fruit production, and produce fruit more regularly than nutrient-limited forests.
387This supports previous findings that suggested higher C allocation to aboveground NPP in
388nutrient-rich forests (Vicca *et al.*, 2012; Fernández-Martínez *et al.*, 2014b, 2016a), as well as
389theory and observations suggesting that high interannual variability in fruit production is more
390pronounced in environments where resources are scarce (Kelly & Sork, 2002; Fernández-
391Martínez et al., 2012). Nutrient availability may thus limit NPP_f even more than it limits
392vegetative NPP, because fruits are more nutrient-demanding than vegetative tissues (Reekie &
393Bazzaz, 1987). Amongst all investigated nutrients, foliar Zn and P concentrations were most
394strongly associated with higher fruit production. However, trees growing on soils with low
395nutrient availability might be forced to be more conservative in the use of nutrients and thus
396present higher concentrations in their tissues, acting like nutrient pools. Hence, further
397research is needed to disentangle the effects of soil nutrient availability and foliar nutrient
398concentrations on ecosystem functioning.

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Other determinants of NPP$_f$ and its temporal behaviour

400Nutrient availability and stoichiometry played a very important role in determining NPP$_f$ and its 401temporal behaviour, but site productivity and the taxonomical family were also key factors. 402Higher photosynthesis (GPP) was associated with higher NPP$_f$, higher maximum NPP$_f$, and 403lower temporal variability (CV). This result is logical, because forests with larger GPP fluxes 404also typically have larger NPP fluxes (Fernández-Martínez *et al.*, 2014a). Whether all NPP 405components increase equally with increasing GPP, however, remains unresolved. In addition, 406higher GPP might reduce the CV of fruit production because more photosynthates can be 407allocated to storage to later be used for reproduction and allowing more regular production of 408fruit crops. However, due to the positive relationship between NPP$_f$ and GPP and the 409dependence of the CV on the mean, this relationship might be spurious. This second 410hypothesis is supported by the lack of a relationship between D (which is less sensitive to the 411mean than the CV (**Supplementary Information 1: The consecutive disparity index**) of fruit 412production and GPP. A larger basal area, however, was also associated with higher maximum 413NPP$_f$, perhaps due to the competitive advantage of large trees to acquire various resources 414(e.g. nutrients, water, and sunlight).

415In addition to the strong influence of foliar nutrient concentrations on NPP$_f$ and its interannual 416variability, we found a significant taxonomic effect on NPP$_f$. In particular, *Fagaceae* and 417*Pinaceae* species presented a markedly different behaviour in fruit production patterns, with 418the latter exhibiting lower maximum NPP$_f$ (probably because they are generally established 419over nutrient poor soils) and lower interannual variability in NPP$_f$. Based on our results, we can 420consider that the *Fagaceae* species studied here present a clear masting behaviour (i.e., high 421interannual variability, negative autocorrelation in fruit production (Fernández-Martínez *et al.*, 4222016b)) while it is not that clear for some of the *Pinaceae* species, especially *P. sylvestris, P.* 423*nigra* and *P. menziesii*, which present relatively low interannual variability and no negative 424autocorrelation in NPP$_f$ (**Table S1**). These differences may be related to different life-history 425traits and evolutionary strategies related to avoidance of seed predation or to different patterns 426of resource allocation. The different nature of fruits produced by the two families (cones in 427*Pinaceae* and nuts in *Fagaceae*) might be responsible for the different allocation of resources 428to fruit production in terms of biomass production. *Pinaceae* species spend many resources 429when producing cones (bearing the seeds), while in *Fagaceae* species each seed (nut) is

430usually much cheaper to produce in terms of C. This difference in the amount of resources
431needed to produce fruits between *Pinaceae* and *Fagaceae* families might be behind the
432different patterns of fruit production in our studied species. Also, the different availability of
433nutrients between families, such as N (higher in *Fagaceae*, **Table S2**) or Zn (higher in
434*Pinaceae*, **Figure 4, Table S2**), might also condition the different patterns of fruit production
435because of different nutrient-use efficiencies amongst species from different families (Sardans
436*et al.*, 2016a).

437Finally, our results also point out that masting behaviour can be well parameterised using the D
438index, because it takes into account not only the variability of the time series but also its
439temporal autocorrelation (**Table S1**). Since masting behaviour is related to high interannual
440variability and negative autocorrelation in fruit production, which is exactly what the D index
441accounts for (**Supplementary Information 1: The consecutive disparity index**), D seems to
442be a good candidate to characterise masting behaviour using a single index.

443**5. Conclusions**

444On average, NPP_f ranged from approximately 10 to 40 g C m^{-2} y^{-1} and accounted for 0.5-3% of
445the GPP, with little differences amongst species or between families (*Fagaceae – Pinaceae*).
446However, mean maximum NPP_f and interannual variability in NPP_f differed specially between
447families, being higher for *Fagaceae* than for *Pinaceae*. These differences are likely to be linked
448to different life-history traits and evolutionary strategies related to avoidance of seed predation
449or to different patterns of resource allocation, given the different nature of their fruits.

450More productive (higher GPPs) and nutrient rich forests produced larger and more regular fruit
451crops and allocated a larger percentage of photosynthates intro fruit production, which
452highlights the paramount role of available reserves of nutrients and carbohydrates to allocate
453into reproduction. Especially foliar zinc (Zn) and phosphorus (P) concentrations were
454associated positively with fruit crop size, while foliar Zn and K were negatively related to its
455temporal variability. To the best of our knowledge we report, for the first time, Zn deficiency in
456forests.

457**Acknowledgements**

463**Author contribution**

464M.F-M, S.V., I.J. and J.P planned and designed the research. M.F-M wrote the manuscript and 465analysed 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_f (upper panel) and NPP_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_f) and the CV of NPP_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_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_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_f. Blue and green colours of the response surface indicate, respectively, low and high NPP_f.
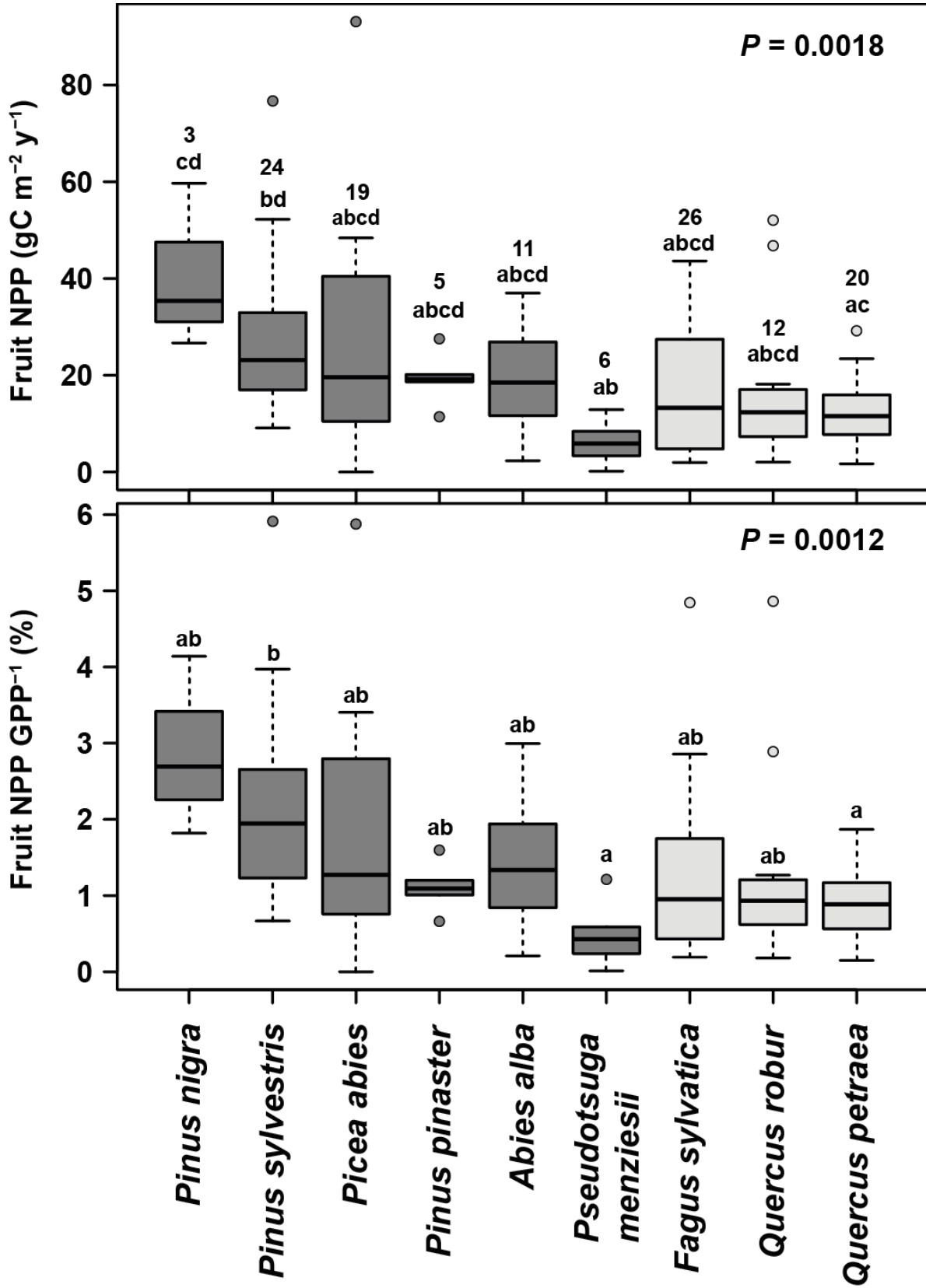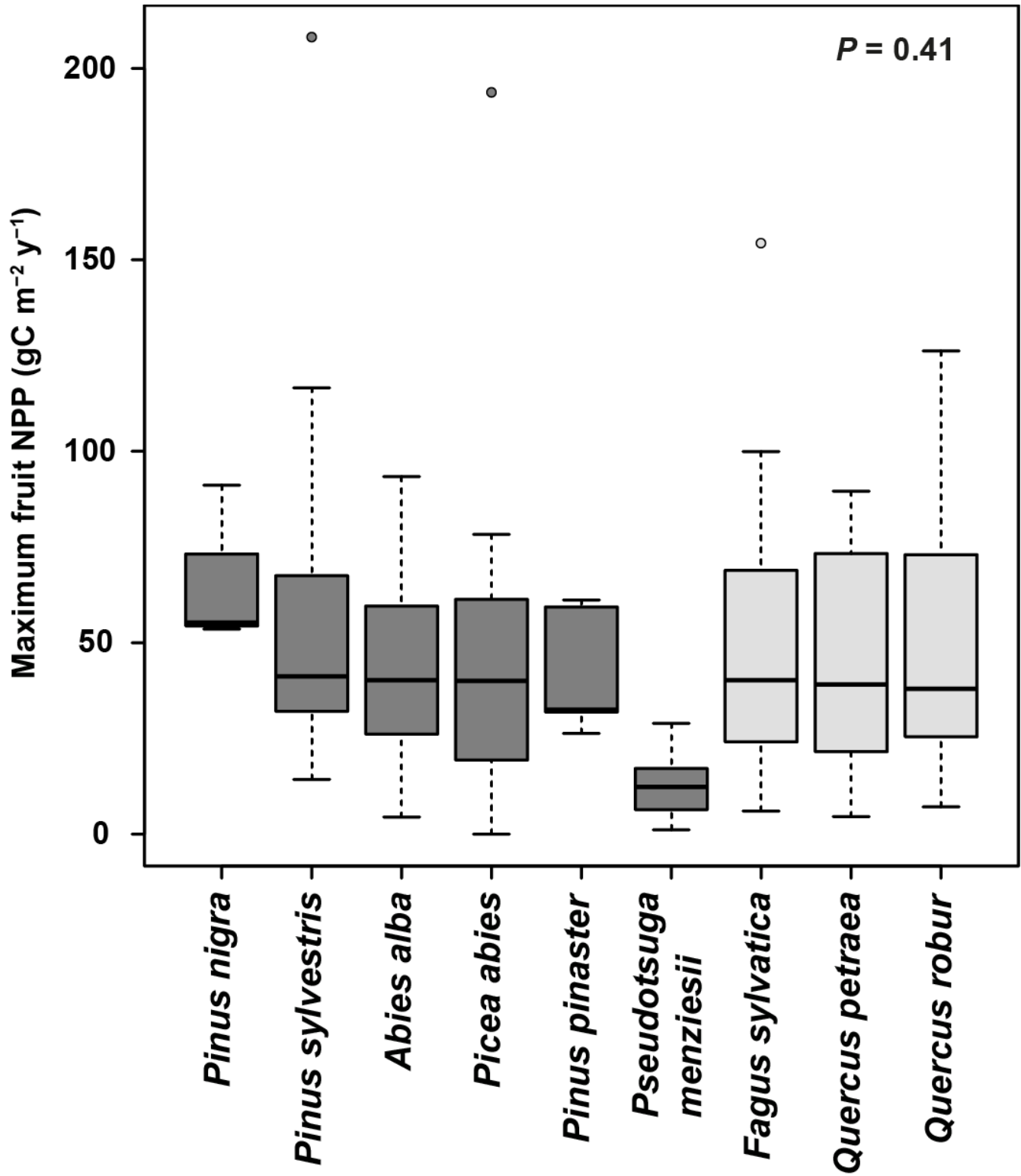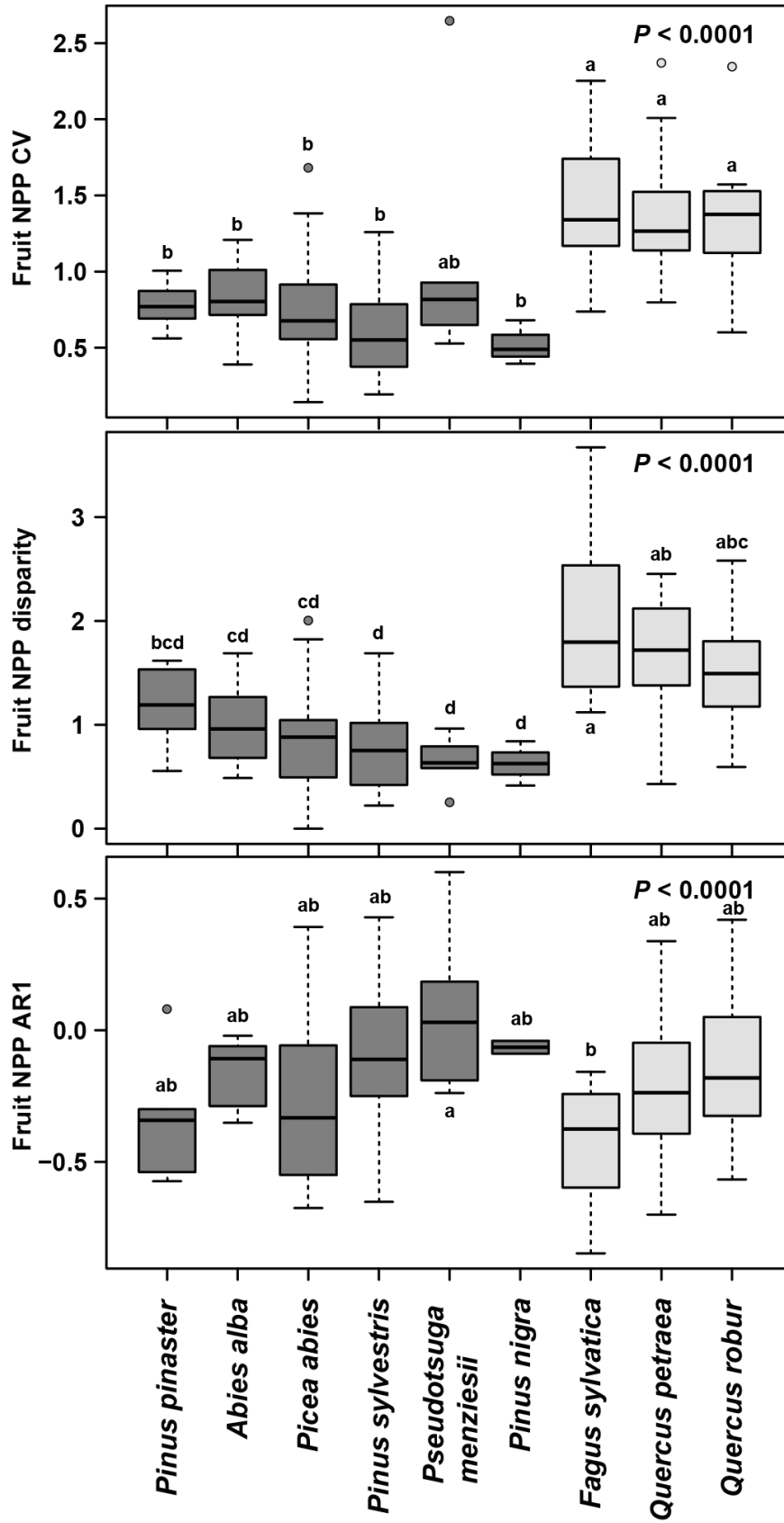
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Figure 1

Figure 2

Figure 3

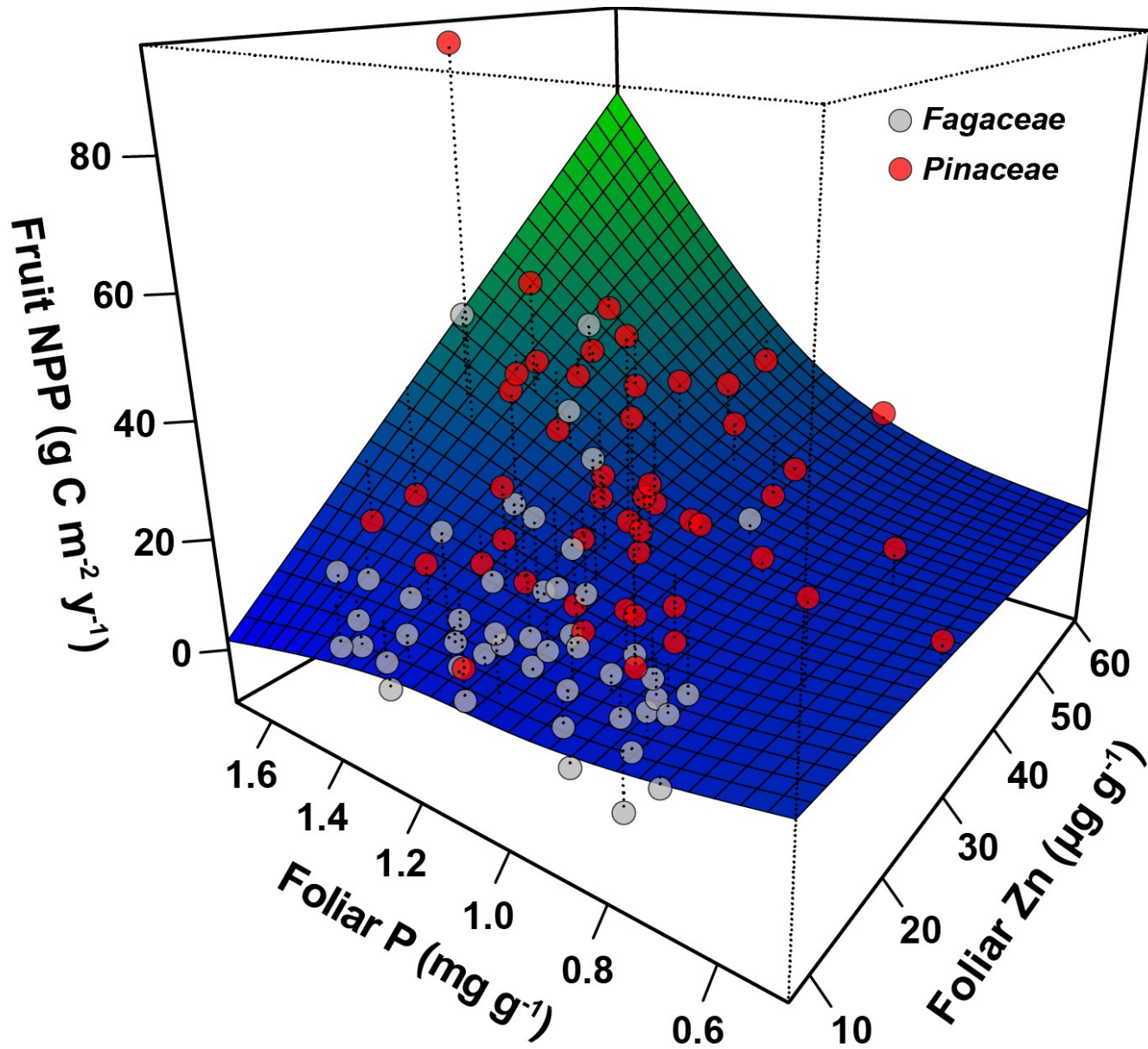**Figure 4**

Figure 5

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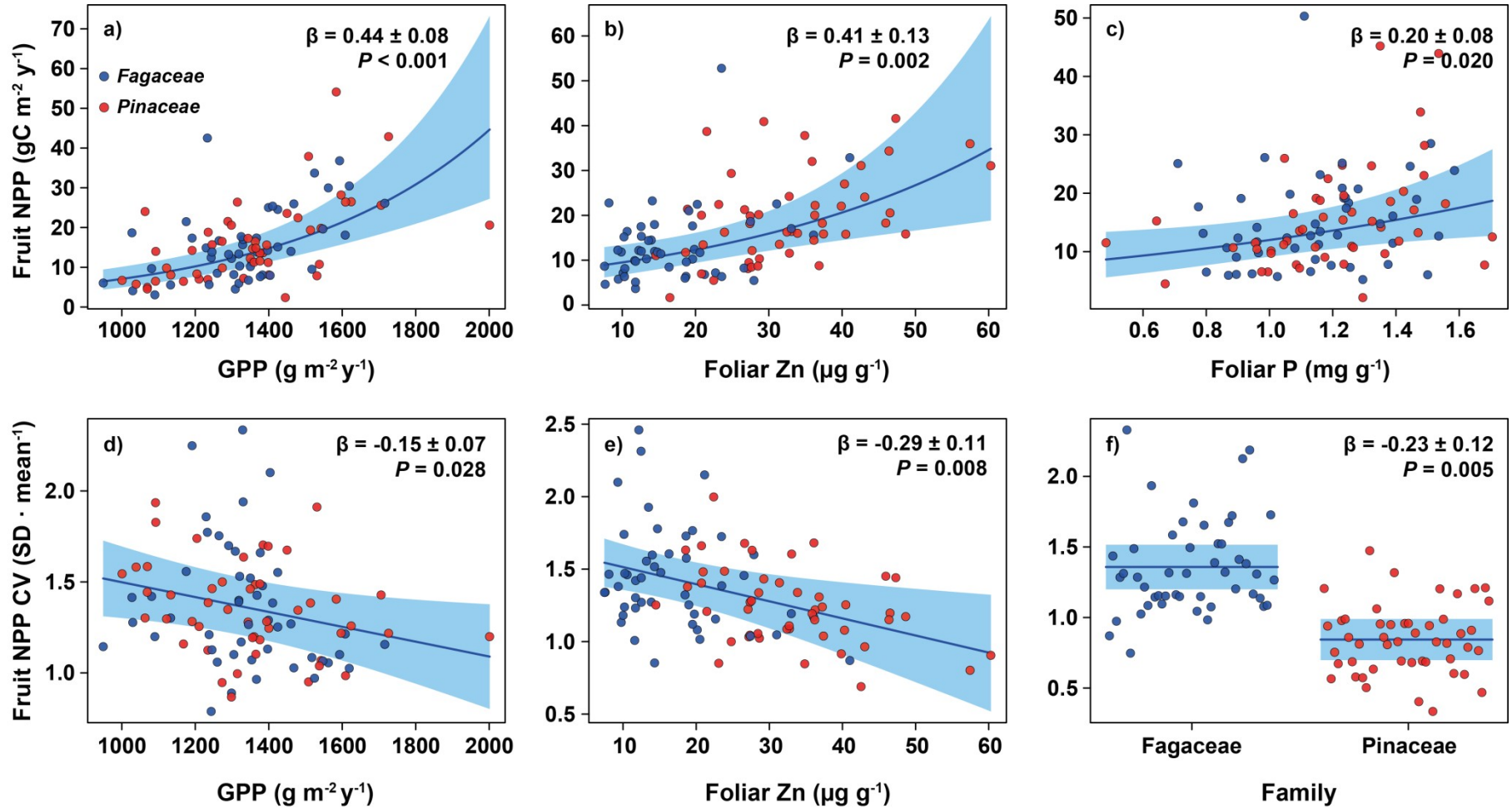
Table 1: Summary of the mixed models predicting fruit net primary production (NPP), the percentage of gross primary production allocated to NPP_f (%GPP_f), maximum NPP_f, and the CV, D, and AR1 of NPP_f. Values are beta weights ± SE. For family, the coefficient shown indicates the change from *Fagaceae* 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.

	Ln NPP_f	Ln %GPP_f	Max NPP_f	CV	D	AR1
Endogenous						
Family			- ± 0.3 **	- ± 0.1 **	- ± 0.0 ***	
GPP	0.4 ± 0.0 ***		0.2 ± 0.1 *	- ± 0.0 *		
Basal area			0.3 ± 0.1 **		0.1 ± 0.0 *	
Foliar N			- ± 0.2 *			
Foliar P	- ± 0.1	- ± 0.2 *				
Foliar Zn	- ± 0.4	- ± 0.4 *	0.3 ± 0.1 *	- ± 0.1 **		
Foliar C:P			- ± 0.1 **			
Foliar K					- ± 0.0 ***	
Exogenous						
MAP			- ± 0.1 *			
N deposition						- ± 0.1 †
Interactions						
Foliar P:Foliar Zn	1.2 ± 0.4 **	1.1 ± 0.5 **				
Variance						
Fixed factors	0.40	0.31	0.31	0.58	0.55	0.03
Interspecific	0.16	0.13	0.10	0.04	0.01	0.20
Total	0.56	0.44	0.41	0.62	0.56	0.23

673**Supplementary material**

674**Figure captions:**

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

676**Figure S2:** Observed versus predicted GPP values from the model used to estimate GPP for the study sites. See materials and 677methods and Section 1: Estimating GPP in the supplementary material for further information about model adjustment.

678**Figure S3:** Comparison of the CV and D indices using two time series with equal means and standard deviations but different 679autocorrelation structures. AR1, autocorrelation coefficient for lag 1; CV, coefficient of variation (standard deviation • mean-1); 680and D, disparity index (see **Eqs. 1 and 2** in **Supplementary Material Section 1: The consecutive disparity index (_D_)**).

681

Figure S1:
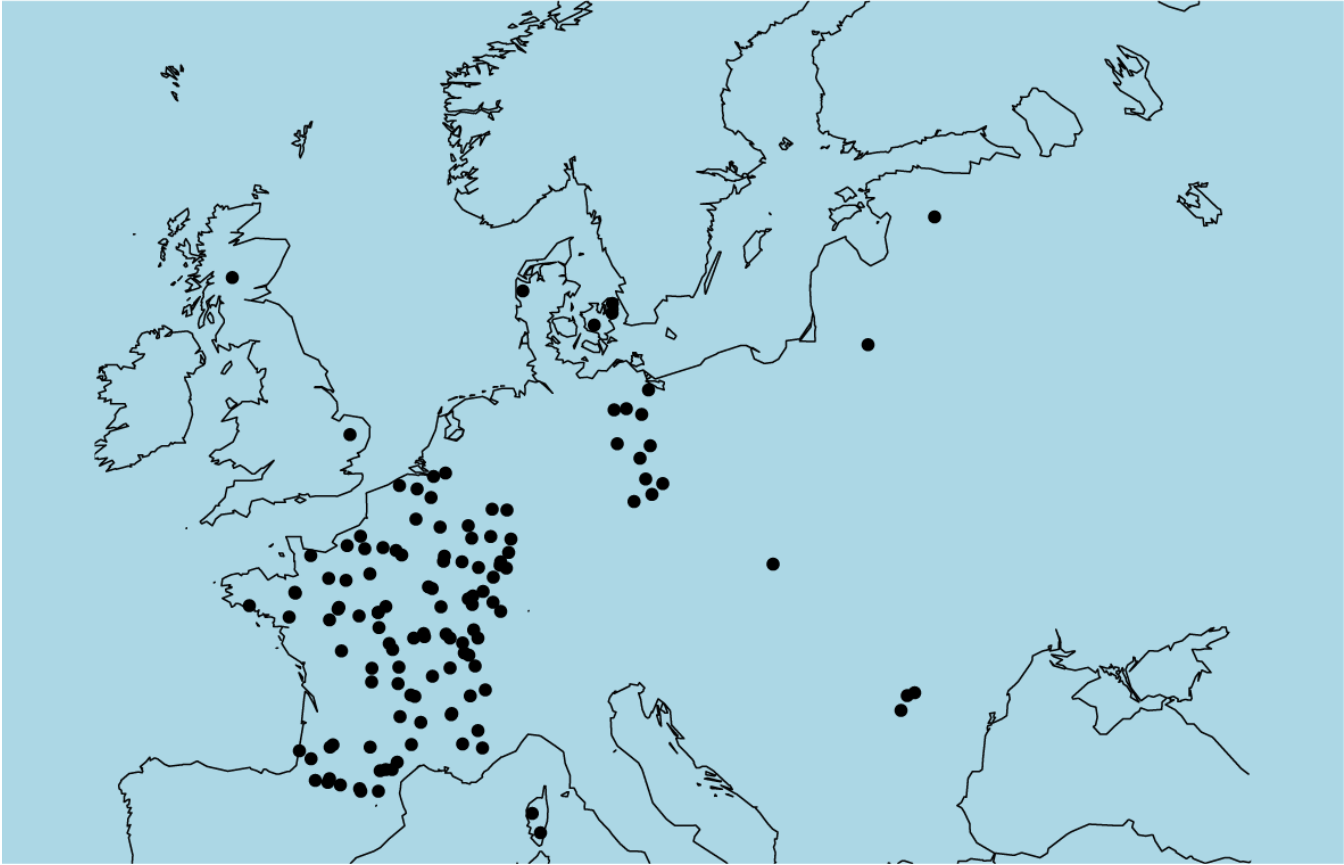
Figure S2

Figure S3
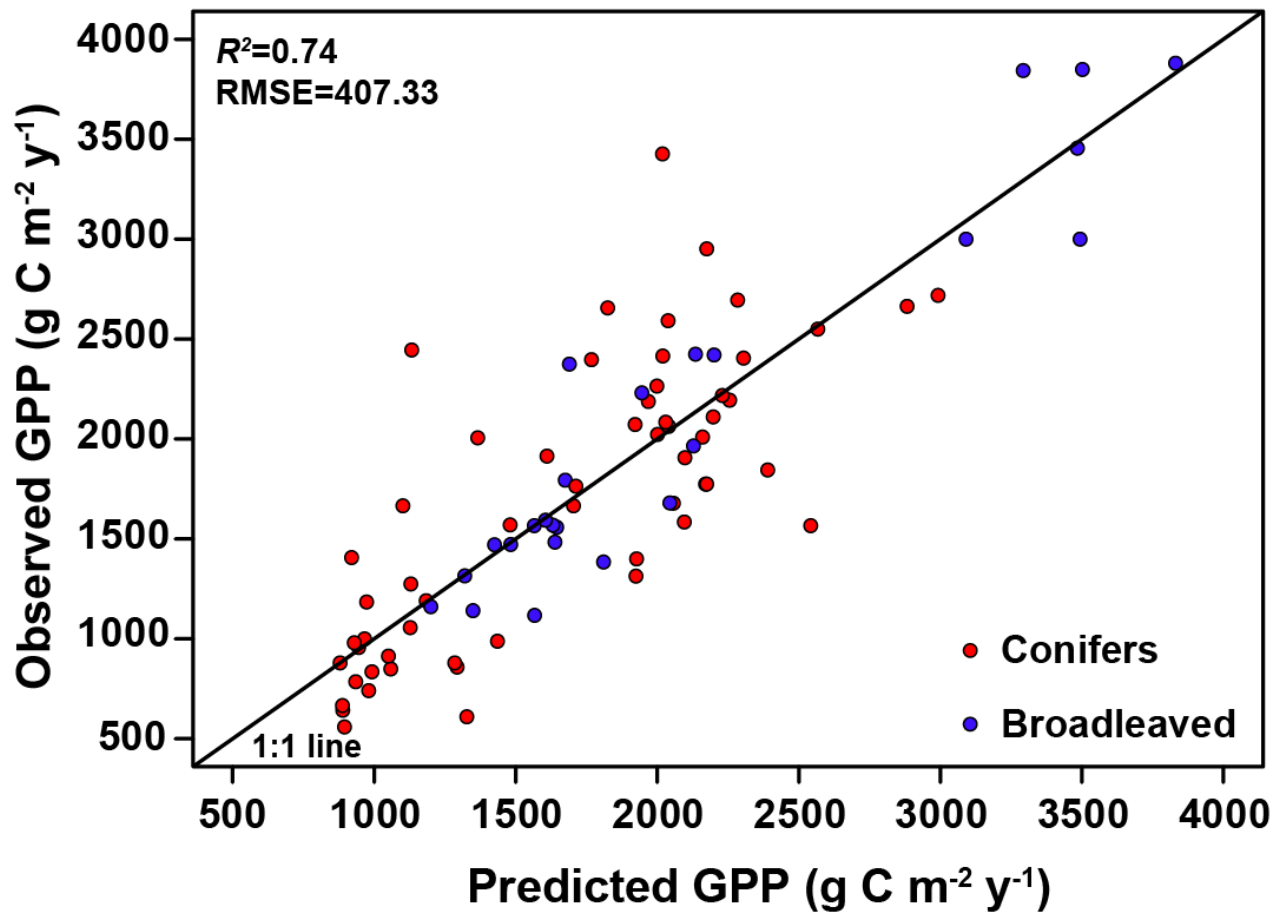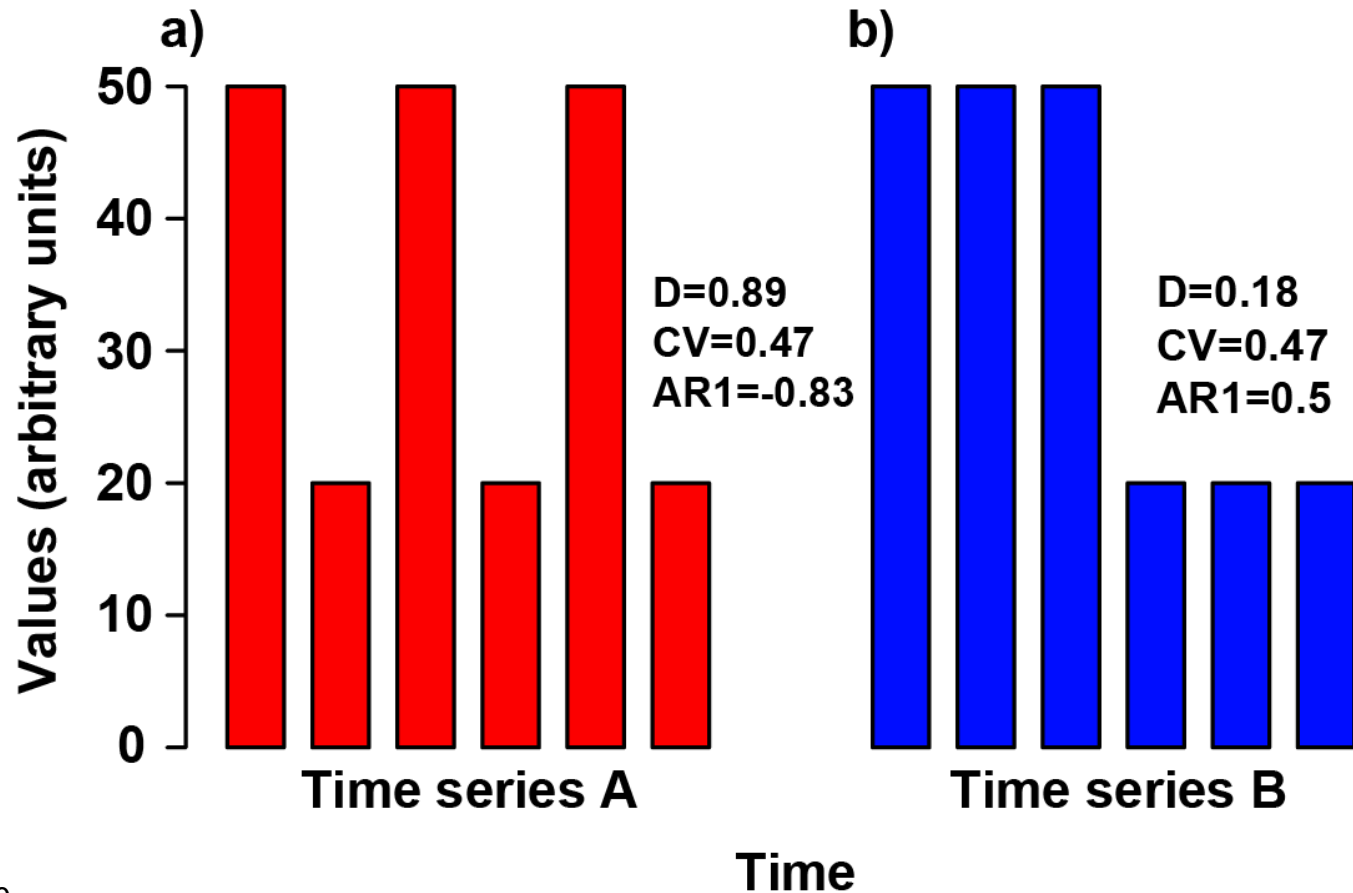
Table S1: Species (mean ± SE)
691 fruit net primary production (NPP) (g C m^{-2} y^{-1}), allocation to NPP$_f$ (NPP$_f$ · GPP^{-1} = %GPP$_f$), mean maximum NPP$_f$ (Max NPP), and
692 coefficient of variation (CV), consecutive disparity (D), and first autocorrelation coefficient (AR1) of NPP$_f$. AR1 P shows the significance of
693 the AR1 coefficients from a t-test, and n indicates the number of sites per species. Different letters indicate significant differences ($P < 0.05$)
694 amongst species (Tukey's HSD test for multiple comparisons).

	NPP_f		$\%GPP_f$		Max NPP_f		CV		D		AR1	AR1 P		n
Abies alba	18.7 ± 3.3	abcd	1.4 ± 0.3	ab	43.1 ± 7.9	a	0.83 ± 0.08	b	1.00 ± 0.11	cd	-0.15 ± 0.04	0.0717	ab	11
Fagus sylvatica	16.1 ± 2.5	abcd	1.2 ± 0.2	ab	49.0 ± 6.9	a	1.42 ± 0.08	a	2.02 ± 0.15	a	-0.42 ± 0.04	<0.0001	b	26
Picea abies	25.0 ± 5.2	abcd	1.8 ± 0.4	ab	46.2 ± 9.8	a	0.76 ± 0.09	b	0.89 ± 0.12	cd	-0.27 ± 0.08	0.0011	ab	19
Pinus nigra	40.6 ± 9.9	cd	2.9 ± 0.7	ab	66.6 ± 12.2	a	0.52 ± 0.08	b	0.63 ± 0.12	d	-0.06 ± 0.02	0.7322	ab	3
Pinus pinaster	19.4 ± 2.6	abcd	1.1 ± 0.2	ab	42.2 ± 7.4	a	0.78 ± 0.08	b	1.17 ± 0.19	bcd	-0.33 ± 0.12	0.0060	ab	5
Pinus sylvestris	26.8 ± 3.2	bd	2.1 ± 0.3	b	54.6 ± 8.3	a	0.60 ± 0.05	b	0.77 ± 0.09	d	-0.09 ± 0.06	0.1538	ab	24
Pseudotsuga menziesii	6.1 ± 1.7	ab	0.5 ± 0.2	a	13.1 ± 4.1	a	1.06 ± 0.32	ab	0.64 ± 0.10	d	0.07 ± 0.12	0.5249	a	6
Quercus petraea	12.3 ± 1.5	ac	0.9 ± 0.1	a	44.5 ± 6.2	a	1.36 ± 0.08	a	1.71 ± 0.11	ab	-0.20 ± 0.06	0.0012	ab	20
Quercus robur	16.9 ± 4.6	abcd	1.3 ± 0.4	ab	49.6 ± 10.8	a	1.35 ± 0.12	a	1.51 ± 0.16	abc	-0.10 ± 0.09	0.2431	ab	12

695

Table S2: 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.

	C		N		P		K		C:N		C:P		N:P		*n*
Abies alba	52.42 ±	a	12.94 ±	b	1.16 ±	b	5.61 ±		40.02 ±		452.6 ±		11.32 ±		1
	0.11	b	0.31	c	0.04	c	0.25	bc	0.75	b	15.8	b	0.44	c	1
Fagus sylvatica	53.07 ±		24.23 ±		1.17 ±	b	7.04 ±	ab	22.11 ±		479.9 ±		21.73 ±		2
	0.43	a	0.53	a	0.05	c	0.32	c	0.53	c	18.5	b	1.02	a	6
Picea abies	51.35 ±	a	13.61 ±	b	1.34 ±		5.60 ±		38.10 ±		397.0 ±		10.48 ±		1
	0.37	b	0.30	c	0.07	b	0.25	bc	0.74	b	17.1	b	0.41	c	9
Pinus nigra	53.50 ±		14.90 ±	b	1.17 ±	b	6.37 ±	ab	41.47 ±		428.0 ±		12.47 ±		
	NA	a	3.62	c	0.11	c	0.49	c	NA	b	NA	b	2.17	c	3
Pinus pinaster	52.41 ±	a	9.06 ±		0.70 ±		4.60 ±		60.34 ±		808.1 ±		13.59 ±	b	
	0.26	b	0.55	c	0.08	c	0.81	c	5.00	a	97.3	a	1.88	c	5
Pinus sylvestris	52.51 ±	a	15.87 ±		1.28 ±		5.43 ±		34.41 ±		429.0 ±		12.67 ±		2
	0.15	b	0.58	b	0.04	b	0.13	bc	1.23	b	15.7	b	0.70	c	4
Pseudotsuga menziesii	53.02 ±	a	16.30 ±		1.21 ±		7.44 ±		32.63 ±		443.4 ±		13.65 ±	b	
	0.22	b	0.43	b	0.06	b	0.44	ab	0.77	b	23.3	b	0.83	c	6
Quercus petraea	52.38 ±	a	23.66 ±		1.10 ±	b	7.16 ±	ab	22.60 ±		502.1 ±		22.11 ±		2
	0.18	b	0.53	a	0.05	c	0.27	c	0.47	c	24.4	b	0.86	a	0
Quercus robur	52.56 ±	a	24.92 ±		1.33 ±		7.80 ±		22.35 ±		420.5 ±		19.99 ±	a	1
	0.71	b	1.47	a	0.07	b	0.76	a	1.99	c	34.8	b	1.85	b	2

702 **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},
703 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
704 for multiple comparisons), and n indicates the number of sites per species.

	S	Fe	Ca	Mg	Mn	Zn	Cu
Abies alba	0.95 ± 0.03 d	47.98 ± 3.09 b	8.33 ± 0.92 a	1.35 ± 0.10 abc	917.14 ± 305.36 b	29.42 ± 1.07 bc	4.01 ± 0.07 c
Fagus sylvatica	1.50 ± 0.04 ab	95.30 ± 3.45 ab	7.24 ± 0.69 ab	1.12 ± 0.11 abc	1390.59 ± 182.55 ab	23.91 ± 1.48 bcd	7.16 ± 0.20 a
Picea abies	0.91 ± 0.04 d	54.76 ± 3.62 b	5.14 ± 0.58 bcd	1.00 ± 0.07 abc	823.44 ± 146.23 b	22.54 ± 1.61 cd	2.98 ± 0.14 c
Pinus nigra	0.96 ± 0.19 d	89.07 ± 21.53 ab	2.79 ± 0.47 d	0.95 ± 0.18 abc	512.33 ± 150.54 b	37.15 ± 7.95 ab	4.50 ± 0.56 bc
Pinus pinaster	0.84 ± 0.04 d	53.20 ± 5.30 b	3.25 ± 0.42 d	1.48 ± 0.12 ab	182.33 ± 64.20 b	25.53 ± 3.19 bcd	3.01 ± 0.46 c
Pinus sylvestris	1.01 ± 0.04 d	59.98 ± 5.82 b	3.30 ± 0.20 d	0.83 ± 0.05 ac	621.43 ± 66.07 b	42.64 ± 1.86 a	4.18 ± 0.23 c
Pseudotsuga menziesii	1.11 ± 0.02 cd	66.14 ± 3.73 b	3.47 ± 0.33 cd	1.41 ± 0.08 abc	904.38 ± 109.14 b	22.83 ± 1.69 bcd	4.35 ± 0.28 bc
Quercus petraea	1.36 ± 0.03 bcd	89.69 ± 4.66 ab	6.40 ± 0.28 abc	1.60 ± 0.06 a	1920.72 ± 129.54 a	11.27 ± 0.59 e	6.84 ± 0.17 a
Quercus robur	1.64 ± 0.05 a	105.82 ± 7.96 a	6.84 ± 0.41 abc	1.76 ± 0.21 a	1129.10 ± 136.85 ab	14.70 ± 1.75 de	7.61 ± 0.34 a

705

706 1. The consecutive disparity index (*D*)

707

708 D assesses the consecutive variations in a time series and so is sensitive to real time-step to time-step 709 variations, conversely to the CV index, which is insensitive to temporal autocorrelation. D has been 710 used in climate research to better assess interannual variability in the highly irregular precipitation time 711 series of the Iberian Peninsula (Martín-Vide, 1986) and is calculated as:

712 $$D = \frac{1}{n-1} \cdot \sum_{i=1}^{n-1} \left| \ln \frac{p_{i+1}}{p_i} \right| \quad \text{Equation 1}$$

713 where p_i is the series value and *n* is the series length. To avoid numerical indetermination (division by 0) 714 when a time series contains zeros, we can sum a constant (*k,* usually a unit) to the entire time series 715 as:

716 $$D = \frac{1}{n-1} \cdot \sum_{i=1}^{n-1} \left| \ln \frac{p_{i+1}+k}{p_i+k} \right| \quad \text{Equation 2}$$

717 The core of D lies in the assessment of the variability by taking into account the consecutive changes in 718 a time series (see Eqs. 1 and 2). Additionally, on the contrary to CV (standard deviation · mean^{-1}), the 719 calculation of D does not take the mean of the time series into account, which makes it less dependent 720 on the mean. An easy example of the differences between the CV and the D indices can be seen in 721 **Figure S3**. Both time series have the same CV but completely opposite temporal behaviours. The first 722 time series (A) fluctuates every year, but the second time series (B) is stable during the first half and 723 then shifts to a second state. The higher consecutive interannual variability makes the D index to be 724 higher in time series A.

2. Estimating GPP

726To estimate GPP for each forest, we constructed a linear model using data from a global forest
727database (Luyssaert et al., 2007; Fernández-Martínez et al., 2014b) containing carbon fluxes and
728productivity data from forests. We extracted data from sites that reported annual GPP (mainly derived
729from eddy covariance CO_2 fluxes) and foliar NPP, as well as MAT, MAP, and leaf type. Abbreviations:
730mean annual precipitation (MAP), mean annual temperature (MAT), standard errors (SE), standardized
731coefficients (**β**), root mean squared error (RMSE), degrees of freedom (df).

732**Model summary**

	Estimate	SE	β	SE	t	Pr(>|t|)	
(Intercept)	985.637	284.828	0.000	0.000	3.46	0.000883	***
Leaf type - conifers	-239.186	236.925	-0.138	0.136	-1.01	0.315877	
MAP	-0.422	0.271	-0.484	0.311	-1.556	0.123863	
MAT	-9.244	18.794	-0.068	0.137	-0.492	0.624226	
Foliar NPP	4.627	0.798	0.517	0.089	5.795	1.42E-07	***
Leaf type - conifers:map	0.378	0.186	0.453	0.223	2.032	0.045615	*
MAP:MAT	0.035	0.013	0.829	0.303	2.734	0.007762	**

	R^2			
Leaf type	0.029		R^2	0.7374
MAP	0.219		R^2_{adj}	0.7169
MAT	0.222		**RMSE**	407.33
Foliar NPP	0.241		**Error %**	9.15%
Leaf type:MAP	0.009		**df**	77
MAP:MAT	0.016		**P**	<0.001

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

	2.50%	50%	97.50%	Mean	SE
R^2	0.636	0.707	0.767	0.706	0.033
R^2_{adj}	0.616	0.691	0.754	0.690	0.034
RMSE on crossvalidation	268.765	396.577	526.764	396.700	67.726
% error on crossvalidation	7.38%	11.52%	17.08%	11.40%	2.63%

733