

# A hierarchical Bayesian model to investigate trade-offs between growth and reproduction in a long-lived plant

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Running headline: **Trade-off between growth & reproduction**

## 1 Abstract

A trade-off between growth and fecundity, reflecting the inability of simultaneously investing in both functions when resources are limited, is a fundamental feature of life history theory. This particular trade-off is the result of evolutionary and environmental constraints shaping reproductive and growth traits, but it remains difficult to pinpoint in natural populations of long-lived plants. We developed a hierarchical Bayesian model to estimate the inter-individual correlation among growth and reproduction, using observations at individual level over several years combined with resource simulations from an ecophysiological-based model (CASTANEA). In the Bayesian model, the resource, simulated by CASTANEA and incorporated as a latent variable, is allocated to tree growth, reproductive buds initiation and fruit maturation. Then, we used individual random effects correlated among energetic sinks to investigate potential trade-offs. We applied this original approach to a Mediterranean coniferous tree, Atlas Cedar (*Cedrus atlantica*), at two contrasted levels of competition, high versus low density population. We found that trees initializing many reproductive buds had a higher growth. Moreover, a negative correlation was detected between growth and fruit survival during maturation. Finally, trees investing more resource to mature fruits initiated less reproductive buds. The level of competition did not impact the sign of these three correlations, but changed the level of resource allocation: low density population favored growth whereas high density favored reproduction. The level of resource have an impact on individual strategies. This new modeling framework allowed us to detect various individual strategies of resource allocation to growth versus late-stage reproduction on the one hand, and to early- versus late-stage reproduction on the other hand. Moreover, the sign of the correlation between growth and reproductive traits depends on the stage of reproduction considered. Hence, we suggest that the investigation of potential trade-offs between growth and reproduction requires to integrate the dynamics of resource and sink's phenology, from initiation to maturation of reproductive organs.

**Keywords:** *Cedrus atlantica*, conifer, masting, mechanistic model, resource allocation, trade-off, tree growth

## 2 Introduction

Trade-offs between life-history traits are expected to be ubiquitous throughout the living world. Although the concept of trade-off is used in many disciplines, we will follow here the definition in evolutionary ecology proposed by Stearns (1989): "trade-offs represent the costs paid in the currency of fitness when a beneficial change in one trait is linked to a detrimental change in another". In this sense, a trade-off corresponds to a negative correlation between two traits related to fitness, which are observed on a set of individuals, or at different life-stages for a given individual. In particular, trade-offs between traits may occur when the resources, i.e. energy and nutrients, are limited. In this case, trade-offs are the results of resource allocation to different sinks sharing a common pool of resources. Thus, some of the trade-offs observed within a population may result from the variation in allocation strategies among individuals and/or among life-stages. The inter-individual variability of allocation strategies, as any other phenotypic trait, is expected to be driven by a combination of environmental and genetic factors (Garland and Carter, 1994). The theoretical model of van Noordwijk and de Jong (1986) demonstrated that the patterns of resource acquisition versus resource allocation can change the sign of the correlation between two life history traits: when resource acquisition is highly variable among individuals while the fraction allocated to each life history traits is similar, the between-trait correlation is positive. In the reverse case, when resource allocation is highly variable among individuals, but not resource acquisition, the correlation becomes negative. To better track trade-offs, one solution is to account for the variability of resources acquisition and allocation between individuals together with the measurement of life history traits: this approach requires combining ecophysiology with population ecology (Olijnyk and Nelson, 2013).

Trade-offs between reproduction and growth-related life-history traits have received much attention (Bell, 1980; Lovett Doust, 1989), in particular in annual and perennial plants (Obeso, 2002; Thomas, 2011; Lauder *et al.*, 2019). Most studies investigated trade-offs through the phenotypic correlations between growth and reproduction at individual or population level, and reported either positive, negative or no correlations (Sánchez-Humanes *et al.*, 2011; Thomas, 2011; Wu *et al.*, 2020). Four main hypotheses related to resource allocation have been advanced

77 to explain such idiosyncratic patterns (Pulido *et al.*, 2014): resource allocation to growth and  
78 reproduction can be either (i) based on a hierarchy, where the resource is first allocated to repro-  
79 duction and then to growth (Wardlaw, 1990; Suzuki, 2001) or (ii) linked to different resource  
80 pools, so that the resource allocated to growth is independent from that allocated to reproduction  
81 (Cremer, 1992; Yasumura *et al.*, 2006; Knops *et al.*, 2007; Żywiec and Zielonka, 2013) or (iii)  
82 linked to a single resource pool, with a constant fraction of resource allocated to each sink  
83 (Despland and Houle, 1997; Pérez-Ramos *et al.*, 2010; Berdanier and Clark, 2016; Lebourgeois  
84 *et al.*, 2018) or, finally, (iv) linked to a single resource pool with competition for resources  
85 allocated to different sinks (Koenig and Knops, 1998; Martín *et al.*, 2015; Lebourgeois *et al.*,  
86 2018). Only in cases (i) and (iv) the expected trade-off can be observed, while cases (ii) and (iii)  
87 can lead to positive or non significant correlation. Besides resource allocation schemes, climatic  
88 conditions can have contrasted direct effects on reproduction and growth and generate negative  
89 environmental correlation without functional trade-off, for instance when favorable conditions  
90 for growth are unfavorable for reproduction (Knops *et al.*, 2007; Mund *et al.*, 2020).

91

92 Trade-off can also occur between early and late stages of reproduction. This is well illus-  
93 trated by the *Quercus sp* study by Knops *et al.* (2007), where the meaningful trade-off occur  
94 between current and future reproduction. Indeed, due to the high reproductive costs in trees,  
95 an important seed production in a given year can decrease the level of resource to invest in  
96 future reproduction, explaining why less seeds are produced the year after (Sala *et al.*, 2012).  
97 This trade-off between current and future reproduction was confirmed by removal experiments,  
98 where removing fruits increase the number reproductive buds and increase fruit production in  
99 the following year (Elmqvist *et al.*, 1991; Fox and Stevens, 1991; Fox, 1995; Santos-del Blanco  
100 and Climent, 2014).

101

102 Another important trade-off in monoecious plants may occur between male and female re-  
103 production. Studies investigating the cost of reproduction usually neglect the male function and  
104 in particular the abortion of reproductive flowers. The major assumption supporting this simpli-  
105 fication is that male function needs fewer resources than female function (Elmqvist *et al.*, 1991;

106 Obeso, 2002) and is not limiting for reproduction. However, this hypothesis may no longer hold  
107 under changing climate (Schermer *et al.*, 2019). In trees, studies of the trade-off between male  
108 and female reproduction are rare due to the difficulty to measure male reproductive biomass.  
109 But studying reproduction only from the female point of view may underestimate the initial  
110 reproductive effort and lead to a wrong estimate of correlation between growth and reproductive  
111 traits (Knops *et al.*, 2007; Knops and Koenig, 2012). Hence, two hypotheses are commonly  
112 used: male biomass is relatively constant across years whereas reproductive female biomass  
113 follows available resource (Knops and Koenig, 2012), or both male and female biomass co-vary  
114 through time (Houle, 2001).

115

116 The aim of this study is to detect the trade-off between growth and reproduction at different  
117 stages of the reproduction cycle and considering different functions (male and female) within a  
118 tree population. To tackle this objective, we developed a new and original methodological ap-  
119 proach by combining two different models for resource acquisition and allocation, respectively.  
120 On the one hand, we used an ecophysiological model to simulate the acquisition of resource  
121 at the individual tree level (Net Primary Production, NPP). This ecophysiological model simu-  
122 lates climate effects through several processes such as tree photosynthesis, respiration and soil  
123 evaporation. On the other hand, we developed a hierarchical Bayesian model based on resource  
124 allocation processes, which simultaneously accounts for (i) the timing of growth and reproduc-  
125 tive processes, and (ii) the variation among individuals and years in resource allocation and in  
126 the phenotypic gender, both considered as latent variables. This approach allows to estimate  
127 the inter-individual correlation between growth and reproduction while accounting for resource  
128 heterogeneity between trees.

## 129 **3 Material and Methods**

### 130 **3.1 Hierarchical Bayesian model**

131 We developed a Bayesian hierarchical model linking resource to three energetic sinks: growth,  
132 reproductive buds initiation and female cones survival. Potential correlations between these

133 sinks are accounted for by correlated random effects. The model is composed of two layers (see  
134 Fig. 1 for a general overview): the process model which describes how resource is allocated  
135 to each sink, and the data model which describes the links between the process model and  
136 the observations. The observations consist in repeated counts of male and female organs to  
137 characterize the reproductive sink and repeated measure of size increment to characterize the  
138 growth sink. Description of model implementation and procedure is present in Appendix S1:  
139 Section S2. We presented prior parameters in Table S1, accuracy of the model in Table S2 and  
140 posterior distribution in Table S3.

### 141 3.1.1 Process model

142 **Resource allocation to energetic sinks:** The resource ( $NPP_{i,t}$ ) for individual  $i$  at year  $t$  deter-  
143 mines its growth ( $BAI_{i,t}$ ), the number of initiated reproductive buds ( $IB_{i,t}$ ) and the probability of  
144 female cones survival ( $p_{i,t}^{FCS}$ ). The use of correlated random effects (referred as  $\epsilon_{x,i}$ ) allowed us  
145 to investigate potential trade-offs among these three energetic sinks. We tested two alternative  
146 models of inter-individual variation for each growth and reproduction trait to identify two po-  
147 tential types of phenotypic trade-off, either driven by NPP resource or not, respectively named  
148 "model 1" and "model 2". In model 1, inter-individual variation acts on the capacity to valorize  
149 the amount of available resource (NPP), i.e. we introduced a random individual effect on the  
150 growth or reproduction trait response to NPP. In model 2, inter-individual variation is directly on  
151 the trait, i.e. we introduced a random effect on the intercept of the model. With this approach,  
152 there is no constraints on the triplet  $\{\gamma; \beta_1; \beta_2\}$ . Instead, the correlated individual random effect  
153 used here ( $\epsilon_{x,i}$ ) allow more flexibility, and possible synergies or antagonisms between sinks to  
154 emerge from the model. To determine which one of the two model is the best, we included  
155 the variable  $Y \sim \text{Bernoulli}(p_Y)$  indicating whether NPP was the only resource responsible of  
156 inter-individual correlation ( $Y = 0$ ) or not ( $Y = 1$ ):

$$\left\{ \begin{array}{l} BAI_{i,t} = (\underbrace{\gamma_d + Y * \epsilon_{1,i}}_{\text{model 1}}) * NPP_{i,t} + \underbrace{(1 - Y) * \epsilon_{1,i}}_{\text{model 2}} \\ IB_{i,t} = X_{i,t} * ((\underbrace{\beta_{1,d} + Y * \epsilon_{2,i}}_{\text{model 1}}) * NPP_{i,t} + \underbrace{(1 - Y) * \epsilon_{2,i}}_{\text{model 2}}) \\ \text{logit}(p_{i,t}^{FCS}) = \beta_0 + (\underbrace{\beta_{2,d} + Y * \epsilon_{3,i}}_{\text{model 1}}) * NPP_{i,t} + \underbrace{(1 - Y) * \epsilon_{3,i}}_{\text{model 2}} \\ \epsilon \sim \mathcal{N}_3(0, \Sigma) \end{array} \right. \quad (1)$$

157 where  $\gamma_d$  is the slope parameter that depends on the density  $d$ . In the model 1,  $\epsilon_{1,i}$  is an individual  
 158 random effect associated to the slope parameter whereas in the model 2, the individual random  
 159 effect does not constrains  $NPP_{i,t}$  on growth increment ( $BAI_{i,t}$ ). Then,  $\beta_{1,d}$  is the slope parameter  
 160 than depends on density  $d$  and  $\epsilon_{2,i}$  constrains the slope parameter (model 1) or is individual  
 161 random effect for the effect of  $NPP_{i,t}$  on bud initiation ( $IB_{i,t}$ ) (model 2). Parameter  $\beta_{2,d}$  is the  
 162 slope depending of density  $d$  and  $\epsilon_{3,i}$  is associated to the slope parameter (model 1) or is the  
 163 individual random effect for the effect of  $NPP_{i,t}$  on female cones survival ( $p_{i,t}^{FCS}$ ) (model 2).  $X_{i,t}$   
 164 is a Bernoulli variable ( $X_{i,t} \sim \mathcal{B}(p_X)$ ), indicating if individual  $i$  produced ( $X_{i,t} = 1$ ) or not ( $X_{i,t}$   
 165  $= 0$ ) reproductive buds at year  $t$ , allowing to consider null values in the observations, because  
 166 some trees never produced cones (see Fig 3). The intercept  $\beta_0$  is fixed to constrain  $p_{i,t}^{FCS} \approx 0$   
 167 when  $NPP_{i,t} = 0$ . Note that the model does not account for other possible drivers of female  
 168 cone survival such as pollen limitation.

169 This model explicitly considers that individual random effect on the three sinks,  $\{\epsilon_{1,i}; \epsilon_{2,i};$   
 170  $\epsilon_{3,i}\}$ , are related to each other through the variance-covariance matrix  $\Sigma$ . Their pairwise  
 171 correlations can thus be used to investigate constrains in resource allocation to the three sinks.  
 172 Indeed, for a given amount of resource available for an individual  $i$ ,  $NPP_{i,t}$ , the sign of the  
 173 correlation between  $\epsilon_{l,i}$ , and  $\epsilon_{k,i}$  indicates how much resource is respectively allocated to sinks  $l$   
 174 and  $k$ . Correlations were computed as  $\rho_{l,k} = \Sigma_{l,k} / (\Sigma_{l,l} \Sigma_{k,k})$ .

175 **Male and female reproduction:** The model considers that initialized buds ( $IB_{i,t}$ ) develop  
 176 into a number of initiated male cones ( $IMC_{i,t}$ ) and a number of initiated female cones ( $IFC_{i,t}$ )  
 177 according to the phenotypic gender ( $PG_{i,t}$ ) of individual  $i$  at year  $t$ , using the following model:

$$\begin{cases} \text{logit}(PG_{i,t}) \sim \mathcal{N}(\bar{P}G, \sigma_{PG}) \\ IMC_{i,t} = PG_{i,t} * IB_{i,t} \\ IFC_{i,t} = (1 - IMC_{i,t}) \end{cases} \quad (2)$$

178 Here, phenotypic gender thus correspond to maleness, i.e. the ratio of male vs male and female  
179 initiated cones.

### 180 3.1.2 Data model

181 The model uses repeated observations of growth, male reproduction and female reproduction,  
182 such as presented in our case in the section 3.3. We assume that observed growth ( $BAI_{i,t}^{\text{obs}}$ ) is  
183 related to the latent growth variable of the process model ( $BAI_{i,t}$ ) through :

$$BAI_{i,t}^{\text{obs}} \sim \mathcal{N}(BAI_{i,t}, \sigma_{BAI}) \quad (3)$$

184 The number of initiated male cones ( $IMC_{i,t}$ ) is a continuous variable while the observed abun-  
185 dance of male cones ( $IMC_{i,t}^{\text{obs}}$ ) is a categorical ordered variable as described in section 3.3. To  
186 link  $IMC_{i,t}$  and  $IMC_{i,t}^{\text{obs}}$  we used the following observational model:

$$\begin{cases} \boldsymbol{\pi}_{i,t} = [F(s_0), F(s_1) - F(s_0), F(s_2) - F(s_1), F(s_3) - F(s_2), 1 - F(s_3)] \\ IMC_{i,t}^{\text{obs}} \sim \text{Multinomial}(\boldsymbol{\pi}_{i,t}, 1) \end{cases} \quad (4)$$

187 where  $F(\cdot)$  denotes the cumulative distribution function of a normal distribution with mean  
188  $IMC_{i,t}$  and variance  $\sigma_{IMC}$ .  $\{s_0, s_1, s_2, s_3\}$  is a set of fixed thresholds determining the boundaries  
189 between each value of the notation, and are derived from  $F(\cdot)$ . Note that this approach is  
190 equivalent to consider a probit link in the case of binary data.

191 Finally, the observed count of female cones ( $FC_{i,t}^{\text{obs}}$ ) is linked to the latent variable describing  
192 number of current bud initiated ( $p_{i,t}^{FCS}$ ) and previous year reproduction (bud initiation,  $IB_{i,t-1}$ ,  
193 female cones initiation,  $IFC_{i,t-1}$ ) through the following Poisson observational model:

$$FC_{i,t}^{\text{obs}} \sim \mathcal{P}(p_{i,t}^{FCS} * IFC_{i,t-1} * IB_{i,t-1}) \quad (5)$$



## 194 **3.2 Study species and site**

195 We applied this model to Atlas cedar, *Cedrus atlantica* (Manetti ex Endl.) Carrière, a Mediter-  
196 ranean coniferous tree species. This monoecious species reaches its sexual maturity between  
197 15 and 30 years old (Toth, 1978), and carries male and female organs irregularly dispersed  
198 on the crown of the tree. Male reproduction, from reproductive bud initiation to pollen mat-  
199 uration, is achieved within one year, whereas female reproduction, from initiation to cone  
200 maturation, spreads over two years (Fig. 2). Reproductive buds are initiated during summer  
201 (June-July for male buds and late August for female buds) at year  $t-1$ , followed by pollination  
202 in September, when female cones open and receive pollen. Female cones close their scales in  
203 October-November, when male cones fall down. A time lag between pollination and fecunda-  
204 tion characterizes coniferous species (Williams, 2009), with a duration of nine months for *C.*  
205 *atlantica*. Pollen germinates in spring at year  $t$ , then ovules are fertilized and seeds begin to  
206 mature until autumn of the same year, and mature seeds are dispersed in year  $t+1$  (Toth, 1978).  
207 Hence, two generations of female cones may co-exist on a tree and it is possible to distinguish  
208 green one-year cones from brownish two-year cones. *Cedrus atlantica* can be referred to as a  
209 masting species, characterized by a seed production highly variable among years and synchro-  
210 nized among individuals (Kelly and Sork, 2002; Krouchi *et al.*, 2004).

211  
212 The study site is a 35 years-old experimental plantation located in Mont-Ventoux in France, a  
213 Mediterranean mountain, at 1170 meters of elevation (44°07' 05" N, 5°20' 38" E). All the trees  
214 were planted in similar pedo-climatic conditions. The initial tree density was 2700 stems ha<sup>-1</sup>.  
215 In this experiment, two thinning strategies had been applied leading to contrasted competitor  
216 densities at the time of observations: high (1200 stems ha<sup>-1</sup>) versus low density (250 stems ha<sup>-1</sup>).  
217 More details on the silviculture experiment and tree growth response are available in Guillemot  
218 *et al.* (2015).

## 219 **3.3 Observations of growth and reproduction**

220 We monitored 40 individual trees in the high-density stand and 31 individual trees in the low-  
221 density stand. These individuals were randomly sampled within each stand and measured each

222 year from 2002 to 2005 (except for growth, with a longer dataset from 1989 to 2015). We first  
223 measured the diameter at 1.3 meters ( $DBH_{i,t}$ ) for each individual tree  $i$  and each year  $t$ . Annual  
224 basal area increment ( $BAI_{i,t}^{obs}$ ) was computed as:  $BAI_{i,t}^{obs} = (\pi \times DBH_t^2/4) - (\pi \times DBH_{t-1}^2/4)$   
225 Male cones abundance ( $M_{i,t}$ ) was recorded as a qualitative ordered variable, consisting in a  
226 score ranging from 0 to 4: "0" means no male cone is observed; "1" means few male cones are  
227 dispersed in the canopy; "2" means male cones are abundant in one branch; "3" means male  
228 cones are abundant on two branches and "4" means male cones are abundant over the whole tree  
229 canopy. These scores were converted into multinomial observations  $IMC_{i,t}^{obs}$  as follows:

$$\left\{ \begin{array}{l} M_{i,t} = 0 \Rightarrow IMC_{i,t}^{obs} = [1, 0, 0, 0, 0] \\ M_{i,t} = 1 \Rightarrow IMC_{i,t}^{obs} = [0, 1, 0, 0, 0] \\ M_{i,t} = 2 \Rightarrow IMC_{i,t}^{obs} = [0, 0, 1, 0, 0] \\ M_{i,t} = 3 \Rightarrow IMC_{i,t}^{obs} = [0, 0, 0, 1, 0] \\ M_{i,t} = 4 \Rightarrow IMC_{i,t}^{obs} = [0, 0, 0, 0, 1] \end{array} \right. \quad (6)$$

230 Female cones ( $FC_{i,t}^{obs}$ ) were individually counted over the whole canopy from the ground with  
231 binoculars and at two seasons each year (in spring then in late summer) to discriminate one-year  
232 versus two-year female cones based on their color. The identification and distinct count of  
233 one-year versus two-years cones allowed us to determine the number of cones produced each  
234 year. The raw relationship between  $FC_{i,t}^{obs}$  and  $BAI_{i,t}^{obs}$  in Fig. 3 shows a positive correlation  
235 between growth and female reproduction and individual variation.

### 236 3.4 Resource simulation using CASTANEA

237 We used the ecophysiological model CASTANEA to estimate the carbon resource available  
238 each year for each tree. CASTANEA aims to simulate carbon and water fluxes of monospecific  
239 forest ecosystems (Dufrêne *et al.*, 2005). The model simulates radiation transfer, photosynthesis,  
240 autotrophic respiration, carbon allocation to different tree compartments, evapotranspiration and  
241 water balance. A complete description of the model is presented in Dufrêne *et al.* (2005) with  
242 subsequent modifications described in Davi *et al.* (2009) and in Davi and Cailleret (2017). The  
243 model input data are daily climate data, soil characteristics (texture, depth and stone content), and

244 initial tree characteristics (height, diameter and age). We calibrated and validated the model for  
245 *C. atlantica* on our study site for both stand densities. The values of CASTANEA parameters,  
246 simulations design, and validation procedure are described in Appendix S1: Section S1. In  
247 the following hierarchical Bayesian model, resource was modeled for each individual through  
248 the Net Primary Productivity ( $NPP_{i,t}$ ) simulated from 1999 to 2006, and corresponding to the  
249 difference between gross primary productivity and autotrophic respiration.

## 250 **4 Results**

### 251 **4.1 Resource and phenotypic gender differences between densities**

252 The model fitted accurately male fecundity (Brier score closed to 0). We obtained a lower  
253 accuracy for both female cones production (Bayesian p-value = 0.84) and tree growth (Bayesian  
254 p-value = 0.18). The posterior predictive checks of the hierarchical Bayesian model are pre-  
255 sented in Appendix S1: Table S2. All trees had a high probability to be reproductive in both  
256 plots ( $p_X$ , posterior median [CI95%] = 0.84 [0.79; 0.88]). Remaining posterior parameters are  
257 described in the following part and in Appendix S1: Table S3. The resource  $NPP_{i,t}$  simulated  
258 with CASTANEA model varied between years (due to climate) and between individuals (due to  
259 variations in tree size and stand density; Appendix S1: section S1).  $NPP_{i,t}$  had a mean value  
260 of 11990 gC tree<sup>-1</sup> year<sup>-1</sup> (sd = 3030 gC tree<sup>-1</sup> year<sup>-1</sup>) and 8751 gC tree<sup>-1</sup> year<sup>-1</sup> (sd = 2335  
261 gC tree<sup>-1</sup> year<sup>-1</sup>), respectively for the low-density and high-density plot (Fig. 4 a).

262  
263 The phenotypic gender did not differ between the two density stands, with a mean maleness  
264 equal to 0.29 (sd = 0.04) for the high-density stand and to 0.28 (sd = 0.06) for the low-density  
265 stand (Fig. 4 b).

### 266 **4.2 Correlation between individual random effects**

267 We found that  $Y$  was equal to 0 for all iterations, meaning that the best model to infer trade-offs  
268 in resource allocation is the model 2, where the  $\epsilon_{x,i}$  are not linked to NPP. We reported the  
269 posterior distribution of correlations in Fig. 5 (a), (b) and (c) and pairwise covariations between

270 individual random effects  $\epsilon_{1,i}$ ;  $\epsilon_{2,i}$ ;  $\epsilon_{3,i}$  in Fig. 5 (d), (e) and (f).

271

272 The estimated correlation between inter-individual variations in growth ( $\epsilon_{1,i}$ ) and reproduc-  
273 tive buds initiation ( $\epsilon_{2,i}$ ) was positive ( $\rho_{1,2} = 0.54[0.32, 0.70]$  with  $pr[\rho_{1,2} > 0] = 1$ , Fig. 5  
274 a,d). Secondly, the estimated correlation between inter-individual variations in growth ( $\epsilon_{1,i}$ )  
275 and female cones survival ( $\epsilon_{3,i}$ ) was significantly negative ( $\rho_{1,3} = -0.36[-0.65, 0.24]$  with  
276  $pr[\rho_{1,3} < 0] = 0.91$ , Fig. 5 b,e) indicating a trade-off. Lastly, the estimated correlation be-  
277 tween inter-individual variations in reproductive buds initiation ( $\epsilon_{2,i}$ ) and female cones survival  
278 ( $\epsilon_{3,i}$ ) was negative ( $\rho_{2,3} = -0.85[-0.96, -0.19]$ , with  $pr[\rho_{2,3} < 0] = 0.98$ ), indicating a clear  
279 phenotypic trade-off between bud initiation and female cone survival (Fig. 5 c,f). These three  
280 correlations mainly consist in between-density correlations and within-density correlation in the  
281 high density stand (low resources), but only one within-density correlation is found in the low  
282 density stand (high level of resources) between female cone survival and bud initiation.

### 283 **4.3 Effects of stand density and phenotypic gender on individual allocation** 284 **strategies**

285 We found a higher growth response to available resource in the low density stand than in the high  
286 density stand ( $pr[\gamma_{1200} > \gamma_{250}] = 0.25$ ). However, we found a higher reproductive response,  
287 for initiation and maturation, to available resource in the high density than in the low density  
288 ( $pr[\beta_{1,1200} > \beta_{1,250}] = 0.86$  and  $pr[\beta_{2,1200} > \beta_{2,250}] = 0.94$ ). The ratio of resources allocated  
289 to growth was higher in the low density stand, whereas the ratio of resources allocated to  
290 reproduction was higher in the high density stand. Lastly, individual allocation strategies ( $\epsilon_{x,i}$ )  
291 were not affected by the phenotypic gender. Probabilities to obtain a significant correlation  
292  $P < 0.05$  between  $\epsilon_{1,i}$  and phenotypic gender ( $PG$ ) was equal to 0.25, to 0.24 with  $\epsilon_{2,i}$  and to  
293 0.16 with  $\epsilon_{3,i}$ .

## 294 **5 Discussion**

295 This study revealed significant phenotypic correlations between individual tree growth and re-  
296 productive traits using an original methodology combining an ecophysiological model which  
297 simulates the yearly acquisition of resource at tree level, with a hierarchical Bayesian model  
298 which specifies how the resource is allocated to growth and reproduction throughout the pheno-  
299 logical cycle. Although similar Bayesian models have been previously developed (Buoro *et al.*,  
300 2010), this is the first time to our best knowledge that such a combined approach is used in a  
301 tree species. Considering different reproductive stage (i.e. initiation or maturation) and allowing  
302 alternatively for a driving role of NPP on the allocation scheme or not, our results shed light on  
303 the contradictory findings reported in the literature about the sign and biological meaning of the  
304 correlations between growth and reproduction (Knops *et al.*, 2007).

### 305 **5.1 Origins of the phenotypic correlations between growth and reproduc-** 306 **tion components**

307 We detected a net increase between cone production and NPP, because trees in lower density,  
308 having more NPP tends to grow and reproduce more (Appendix S1: Figure S2). We also found  
309 a positive correlation between growth and initiation of reproductive organs: trees which invested  
310 more in reproduction had also a higher growth. This result was obtained while our model does  
311 not specify any competition between sinks in case of limiting resources. Resources appeared  
312 to be invested proportionally in bud initiation and growth with a constant fraction devoted for  
313 reproduction, which is referred as the "resource matching" hypothesis. Under this hypothesis,  
314 trees both grow and reproduce more when more resources are available (Bogdziewicz *et al.*,  
315 2020).

316 Then, we found a negative correlation between growth and cone survival, suggesting that  
317 these functions of growth and cone maturation compete with each other during resource allo-  
318 cation. Similarly, a recent study in *Fagus sylvatica* demonstrated that reproduction drives the  
319 inter-annual variability of growth and that years with high reproductive effort were also years  
320 with reduced growth (Hackett-Pain *et al.*, 2018). However we cannot rule out that other processes

321 such as pollen limitation contribute to the negative correlation observed here between growth  
322 and reproduction, as showed by Knops *et al.* (2007). Indeed, in wind pollinated species, springs  
323 with high level of precipitation usually favor growth, but can reduce the efficiency of pollen  
324 release and fertilization. In these cases, negative correlation between growth and reproduction  
325 can emerge from contrasted effects of meteorological conditions, without any direct link between  
326 growth and reproduction. But we demonstrated here that resources could also contribute to this  
327 trade-off between growth and fruit maturation and it is not only dependent to pollination.

328

329 Finally, we also found a trade-off between buds initiation and female cones survival: trees  
330 investing more resource to maturate cones initiated less reproductive buds. This result is con-  
331 sistent with previously published experimental data, in particular removal experiments which  
332 demonstrated a trade-off between current and future reproduction (for instance in *Pinus halepen-*  
333 *sis*, Santos-del Blanco and Climent 2014).

334

335 The three observed correlations differ according the stand densities (Fig. 5). Trees in low  
336 density tend to allocate, proportionally, more resources to growth than in high density stand,  
337 while trees in high density tend to allocate in general more resources to bud initiation and fruit  
338 maturation than in low density stand. When resources are scarce (i.e. high density stand), trees  
339 are expected to exhibit a stronger trade-off and to invest most of their resources in reproduction  
340 whereas when resources are abundant, trees are expected to invest it preferentially for growth  
341 (Lauder *et al.*, 2019). Furthermore, correlations between growth and reproductive traits were  
342 only present in the high density stand, except for the last correlation between initiation and cone  
343 maturation, found in both densities. Our study also revealed that NPP is not the only driver to  
344 the different correlations. Additional drivers might be important too (such as reserves, nitrogen,  
345 or other sources of energy).

346

347 Finally, we found that *C. atlantica* trees were overall more females both at high and low  
348 competitor density, and that the phenotypic gender was relatively constant across years (expect  
349 in 2004 with a lower median value for low density plot, Fig 4).

## 350 **5.2 Evolutionary consequences of the observed trade-offs**

351 In the studied system, *C. atlantica* trees displayed different strategies of resource allocation:  
352 some individuals allocated resource preferentially to growth and others to cone survival; some  
353 individuals allocated resource preferentially to cone survival and other to reproductive buds  
354 initiation. These strategies were observed in an even-aged plantation where the studied indi-  
355 viduals had the same age, experiment similar climatic conditions and also similar density of  
356 competitor within stand. As trade-offs were identified through correlations between individual  
357 random effect, they integrate the genetic and plastic inter-individual variation of traits involved  
358 in growth and reproduction. The observed trade-off cannot therefore be entirely attributed to  
359 genetic factors although we expect the plastic component of trait variation to be minimized in  
360 this plantation as compared to a natural population.

361  
362 This approach could be used in natural populations, using a similar model if any proxy  
363 of spatial resource heterogeneity were available as a covariate, or a simplified model if not.  
364 Therefore, we expect that the heterogeneity of density in a natural population would also result  
365 in the coexistence of multiple allocation strategies, but along a wider range of trait values.  
366 Moreover, the heterogeneity in tree density should not only affect the amount of available  
367 resource for individuals, but also change the conditions of evolution. Finally, our study also  
368 suggests that different individual strategies are expected at the core versus the margins of natural  
369 population range (Sexton *et al.*, 2009). Indeed, we showed that trees at low-density grew  
370 more than individuals at high-density, which affected the slope (although not the sign) of the  
371 correlation between growth and reproduction. But slopes of higher values were found for  
372 low density stand. Such differences in resources acquisition could also occur across time and  
373 ontogenic stages (Thomas, 2011; Barringer *et al.*, 2013) and may affect the capacity of migration  
374 and adaptation (Aitken *et al.*, 2008).

## 375 **5.3 A new approach for modelling resource acquisition and allocation**

376 The main novelty of our approach is to combine the ecophysiological model CASTANEA to  
377 simulate resource acquisition with a hierarchical Bayesian model to account explicitly for re-



378 source allocation through latent variables (e.g.  $IB_{i,t}$ ,  $PG_{i,t}$ ). CASTANEA allowed us to obtain  
379 and validate proxys of the available resource, through the carbon Net Primary Production (NPP).  
380 The model correctly reproduced the variation in the level of resource between plots at differ-  
381 ent competitor densities. Higher NPP per individual was simulated for the low density stand,  
382 consistent with reduced competition. This positive effect of reduced competition on resource  
383 acquisition at tree level was also observed with tree growth data (Guillemot *et al.*, 2015) and  
384 simulated with another version of the CASTANEA model (Guillemot *et al.*, 2014). Based on  
385 tree ecophysiology, climate and soil conditions, variations in the levels of resource were also  
386 simulated among years. In particular, lower resources were simulated during the year 2003  
387 due to higher stress. Drought stress is known to directly impact ecosystem productivity (Ciais  
388 *et al.*, 2005) and its duration determines the growth of Mediterranean trees (Linares *et al.*, 2013;  
389 Lempereur *et al.*, 2015).

390

391 A second advantage of our approach is the use of latent variables in the Bayesian model,  
392 which allowed us to explicitly model resource allocation (including the phenotypic gender) over  
393 the two-years reproductive cycle. This Bayesian model revealed the existence of trade-offs that  
394 could not be observed based on raw data (Fig. 3), if we look at cone production and tree growth.  
395 Many perennial species have a similar reproductive cycle over two years, with bud initiation  
396 in the first year, followed by maturation in the second year. The hierarchical Bayesian model  
397 developed in this study could thus be applied to other species, using direct measurements of  
398 resource proxys (e.g. photosynthesis), or resources estimates obtained from an ecophysiological  
399 model (for example the CASTANEA is currently calibrated for twelve European trees species).  
400 Our model can also be used in species with a shorter reproductive cycle, where female fruit  
401 mortality would occur the same year of its initiation.

402

403 Another advantage is the use of two different resource allocation schemes in the same equation  
404 (i.e. use of  $Y$ ) to identify correlation. It was possible to test if individual random effects were  
405 strictly based on NPP resource or other kinds of resources or processes. We found that for all  
406 iterations that model 2, with individual random effects outside the slope, was the best, meaning



407 that allocation to growth and reproduction are the result of not only NPP. Deeper exploration is  
408 needed to investigate what are the main limiting energies responsible of these trade-offs.

#### 409 **5.4 Towards a synthesis between models of resource allocation to repro-** 410 **duction**

411 With the Bayesian model, it was possible to test two potential models with a constrain on the  
412 resource allocation and no constrain and allowed us to identify inter-individual correlation. We  
413 found that trade-offs emerged from the estimation of the correlations between individual random  
414 effect without the inclusion of any constraints on resource allocation. This is not the case of  
415 other models that impose detailed on mechanisms driving resource acquisition and allocation,  
416 such as Dynamic Energy Budget model (DEB) or Resource Budget model (RBM). In DEB  
417 models, reserves used for growth cannot be used to increase reproduction, as direct competition  
418 occurs only among reserves used for building structure and not with those used for paying  
419 maintenance costs (Kooijman, 2009). Hence, the fraction of reserves used for growth and repro-  
420 duction is fixed. In RBM models, the resource is allocated to reproduction only when resource  
421 level exceeds a threshold (Isagi *et al.*, 1997). Indeed, RBM models consider that plants cannot  
422 have high fruit production during several years due to resource depletion (Crone and Rapp,  
423 2014). Our results support the modeling choice used in DEB and RBM models where they  
424 include allocation to reproduction. But modeling explicitly the variation of resource partition-  
425 ing between growth and reproduction across the phenological cycle could improve these models.

426  
427 We also found here that accounting for the reproductive phenology, which determines the  
428 timing of resource allocation, can improve the estimation of trade-off between growth and re-  
429 productive sinks, and can highlight the idiosyncratic correlation patterns observed in trees so  
430 far. Indeed, in the study system, the sign of the correlation between growth and reproduc-  
431 tion differs depending of the reproductive stage (initiation or maturation). But with shorter  
432 reproductive cycle, we could expect different results for the relation between growth and fruit  
433 initiation, because plants may invest resources for initiation and maturation during the same year.

434

## 435 **6 Conclusion**

436 Combining a simulation, process-based model with a Bayesian statistical estimation model can  
437 be a fruitful approach to investigate the potential trade-off between reproduction and growth.  
438 Process-based models integrate species ecology through their ecophysiological characteristics,  
439 and allow to explicitly model the effects of environmental stresses on reproduction, and in  
440 particular on reproductive phenology. However, the processes involved in tree reproduction are  
441 still not well understood and most models assume that a constant fraction of resource is allocated  
442 to reproduction (Vacchiano *et al.*, 2018). Further improvements of the resource allocation  
443 component in these models are needed to understand how tree growth and reproduction jointly  
444 respond to climate change.

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## 453 **8 Author Contribution**

454 V.J., F.L. & H.D. initiated the idea. F.L. & F.C. provided experimental data. H.D. and V.J.  
455 developed the ecophysiological model for *C. atlantica*. J.P. & E.W. designed the Bayesian  
456 model with advice from all authors. V.J., E.W. and J.P. ran simulation. V.J. started the redaction  
457 in consultation with F.L., H.D. and S.O-M. All authors contributed critically to the drafts and  
458 gave final approval for publication.

## 459 **9 Data accessibility statement**

460 Data used, CASTANEA model input simulation and hierarchical Bayesian model code are  
461 available from the Zenodo repository <<https://doi.org/10.5281/zenodo.4433892>>. The  
462 CASTANEA model is an open-source software available on the CAPSIS platform: [http:](http://capsis.cirad.fr/capsis/models)  
463 [//capsis.cirad.fr/capsis/models](http://capsis.cirad.fr/capsis/models)

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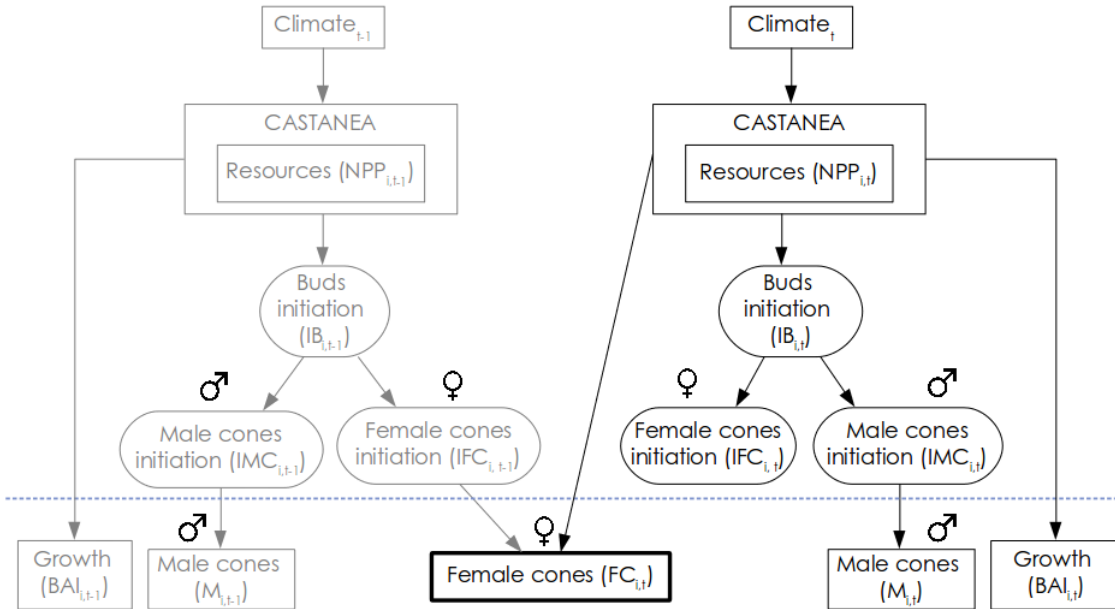
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## 616 10 List of Figures

### Process-model



### Data-model

Figure 1: Graphical representation of the hierarchical Bayesian model used with the process and data models. Right angles boxes represent observed variables and elliptic boxes represent unobserved variable (i.e. latent variables). We represent the previous year ( $t - 1$ ) in gray color and current year ( $t$ ) in black color. Resource (referred as  $NPP_{i,t}$ ) is simulated from the ecophysiological model (CASTANEA) with climate data. Resource is then allocated to radial growth ( $BAI_{i,t}$ ) and reproduction, which initiates buds ( $IB_{i,t}$ ). Buds differ then between male ( $IMC_{i,t}$ ) and females ( $IFC_{i,t}$ ) according to phenotypic gender (no presented in the figure,  $PG_{i,t}$ ). During the year  $t$  we have the maturation of males cones ( $M_{i,t}$ ) of the same year  $t$  and the the female cones survival based on female cones initiated the previous year  $t - 1$  (black bold box,  $FC_{i,t}$ ).

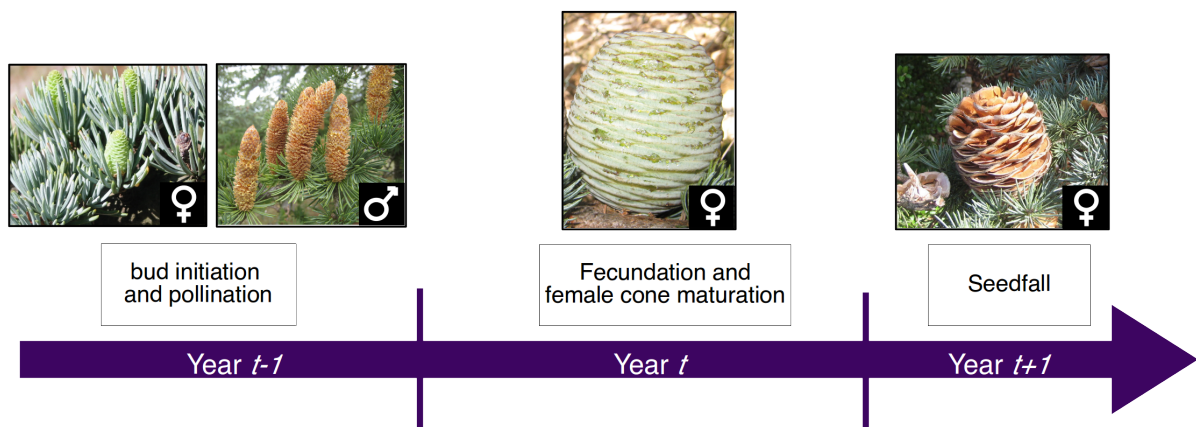


Figure 2: Overview of the general reproductive and growth cycle of *Cedrus atlantica*. Male reproduction and growth is carry on in one year. The duration of female reproduction takes two years from bud initiation during  $year_{t-1}$  followed by the maturation of female cone during  $year_t$ . Seedfall occurs during  $year_{t+1}$ .

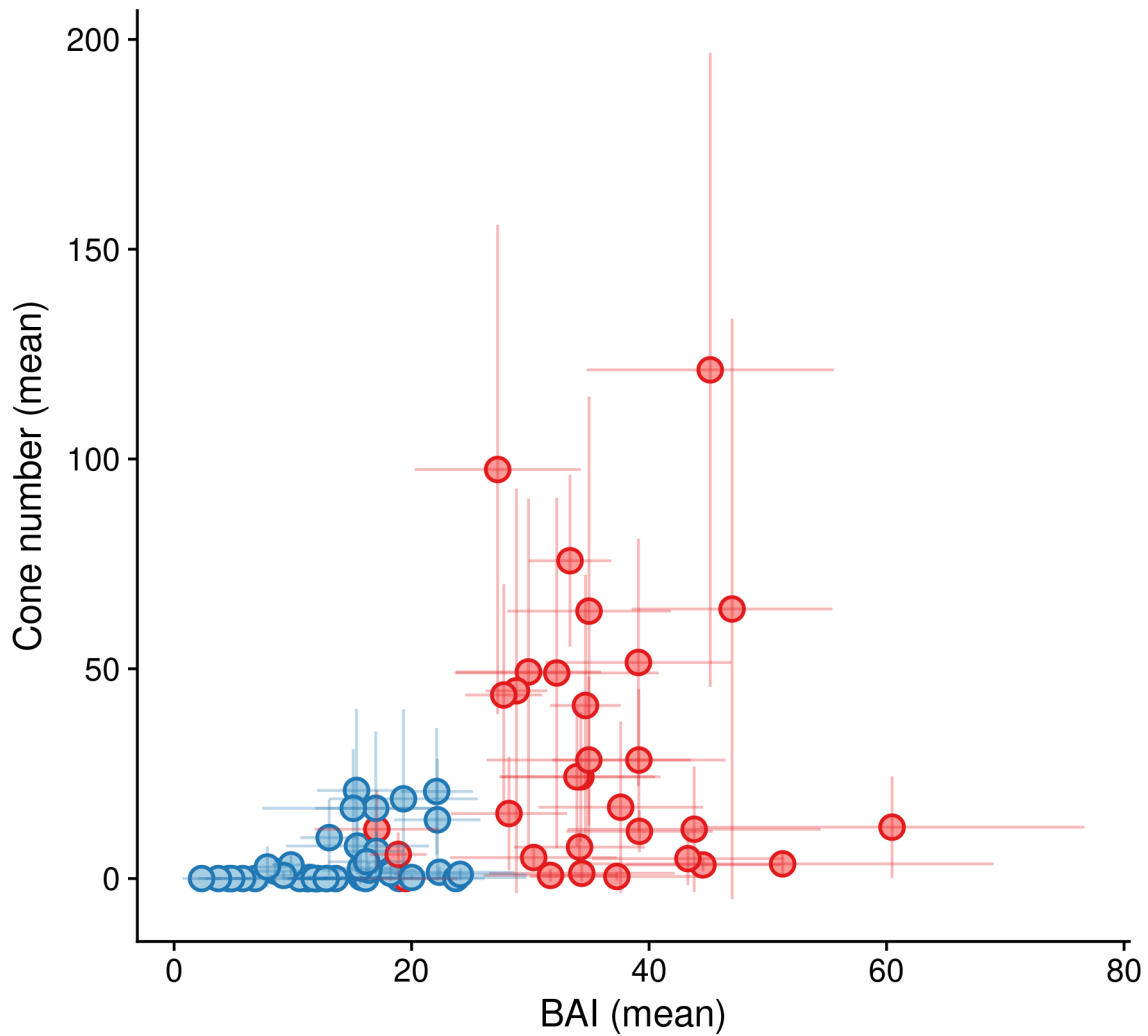


Figure 3: Raw data of female cone and growth for both density stand. Mean values with inter-annual standard deviations of female cone number ( $FC_{i,t}^{\text{obs}}$ ) and mean growth increment ( $BAI_{i,t}^{\text{obs}}$ , referred here as BAI or Basal Area Increment in  $\text{cm}^2 \text{year}^{-1}$ ) for each individuals. Blue is for high density (1200 stems  $\text{ha}^{-1}$ ) and red color for low density stand (250 stems  $\text{ha}^{-1}$ ).

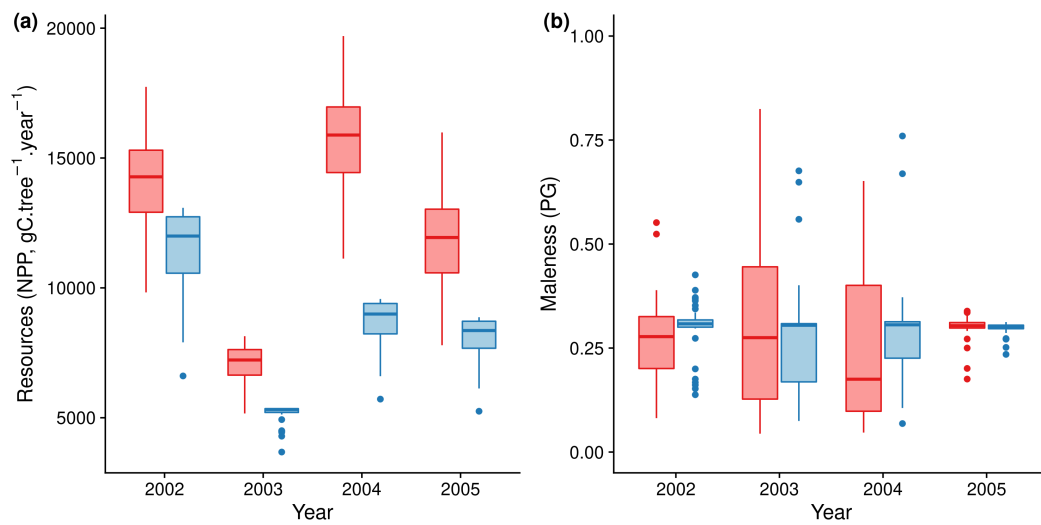


Figure 4: Output simulation of resource obtained from the ecophysiological model CASTANEA and estimation of the phenotypic gender from the hierarchical Bayesian model. (a) Boxplot of resource (Net Primary Productivity, in  $\text{gC m}^{-2} \text{year}^{-1}$ ) simulated with the CASTANEA model for both stand density and years (b) Boxplot of phenotypic gender estimated for both stand density and years, ranging in y-axis from femaleness (0) to maleness (1). For both graphics, blue color is for the high density ( $1200 \text{ stems ha}^{-1}$ ) and red for the low density stand ( $250 \text{ stems ha}^{-1}$ ).

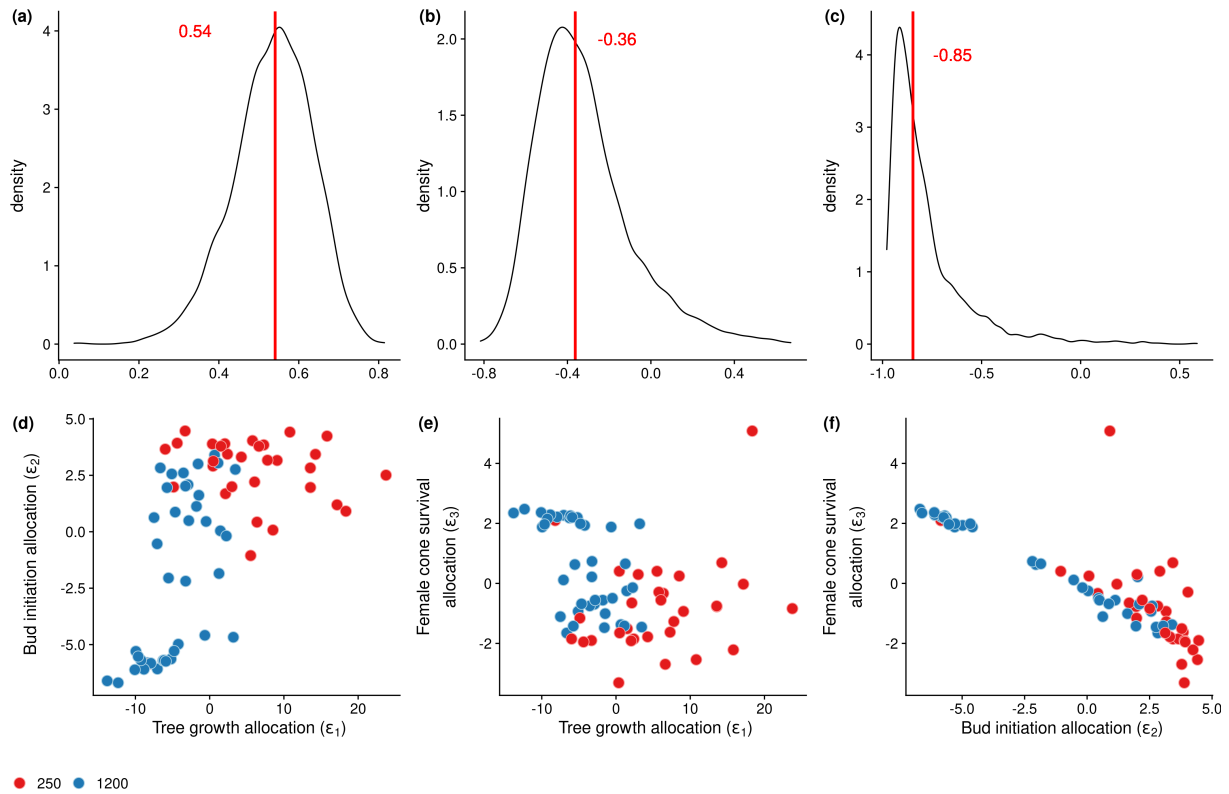


Figure 5: Correlation among sinks and their probabilities. (a) Density of the correlation  $\rho_{1,2}$  is positive (b) Density of the correlation  $\rho_{1,3}$  is negative (c) Density of the correlation  $\rho_{1,2}$  is negative. The red line represent the median posterior value for these three graphics. (d) Positive correlation between growth allocation ( $\epsilon_1$ ) and allocation to buds initiation ( $\epsilon_2$ ) (e) Negative correlation between growth allocation ( $\epsilon_1$ ) and female cone survival ( $\epsilon_3$ ) (f) Negative correlation between allocation to buds initiation ( $\epsilon_2$ ) and female cone survival ( $\epsilon_3$ ). Dots represent mean individual values, with blue and red color, respectively for high and low density of the stand.