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## Temperature and masting control Norway spruce growth, but with high individual tree variability

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1 **Temperature and masting control Norway spruce growth, but with high**  
2 **individual tree variability**

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33 **Keywords:**

34 Picea abies, tree ring, dendrochronology, mast, super-producer, Paneveggio, growth-reproduction

35 trade-off

36

37

38 **Highlights (3-5 bullet points, 85 characters per bullet points)**

39

40 • Cone production is synchronised between trees, but dominated by “super-producers”

41

42 • Cone and seed production show no long-term temporal trend despite strong regional

43 warming

44

45 • Radial growth is lower in mast years that coincide with unfavourable climate (cool summer

46 temperature)

47

48 • Growth reductions in mast years are restricted to “super-producers”

49

50

51

52

53 **Abstract**

54 Tree growth and reproduction are subject to trade-offs in resource allocation. At the same time,  
55 they are both influenced by climate. In this study, we combined long records of reproductive effort  
56 at the individual- (29 years), population- (41 years) and regional (up to 53 years) scale, and tree ring  
57 chronologies, to investigate the effects of climate and reproductive allocation on radial growth in an  
58 Alpine Norway spruce forest.

59

60 Seed and cone production was highly variable between years (mean individual CV = 1.39, population  
61 CV = 1.19), but showed high reproductive synchrony between individuals (mean inter-tree  
62 correlation = 0.72). No long-term trend in reproductive effort was detected over four decades of  
63 observations. At the stand scale, cone production was dominated by a small number of individuals  
64 (“super-producers”), who remained dominant over three decades.

65

66 Individual tree growth responded positively to summer temperature, but the response to cone  
67 production varied between individual trees. Consequently, we found some evidence that mast years  
68 were associated with a divergence in growth between high and low cone producing individuals, and  
69 a decline in within-population growth synchrony.

70

71 At the population level we found limited evidence of a relationship between growth and  
72 reproduction. Radial growth was lower than average in some mast years, but not in others. This was  
73 partly explained by summer temperature during the year of growth, with growth reductions  
74 restricted to mast years that coincided with colder than average summers. Regional mast records  
75 and tree ring chronologies provided some support to indicate that our results were consistent in  
76 other spruce stands, although the effect of mast years on growth appeared to vary between sites.

77

78 Tree ring variation at the individual and population level, and between-tree growth synchrony are  
79 influenced by masting, and consequently dendrochronologists should consider both the occurrence  
80 of masting and the individual differences in reproductive effort when interpreting tree ring datasets.  
81 Our results also indicate that tree ring chronologies contain information to facilitate reconstruction  
82 of mast events, which will help address outstanding questions regarding the future response of  
83 masting to climate change.

## 84 1. Introduction

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85

86 Tree growth and reproduction are the endogenous processes that drive forest dynamics and tree  
87 population demography, along with mortality. Growth is strongly influenced by climate, through  
88 control on wood formation processes (Carrer *et al.*, 2017), and through complex effects on resource  
89 accumulation and availability (Hayat *et al.*, 2017; Medlyn *et al.*, 2002). Likewise, allocation to  
90 reproduction is also strongly influenced by climate, directly via climate cues (Vacchiano *et al.*, 2017)  
91 that trigger flowering and affect pollination efficiency (Koenig *et al.*, 2015), and indirectly through  
92 the regulation of available resources (PearseKoenig and Kelly, 2016; AllenMillard and Richardson,  
93 2017). Growth and reproduction are themselves related through a trade-off for resources  
94 (BarringerKoenig and Knops, 2013; Obeso, 2002), which may itself vary in strength with climate  
95 (Sletvold and Agren, 2015; Hacket-PainLageard and Thomas, 2017; Villellas and Garcia, 2018).  
96 Consequently, integrating growth and reproduction data should allow a more complete  
97 understanding of the tree growth responses to climate, including climate extremes and long-term  
98 trends (Davi *et al.*, 2016; Hacket-Pain *et al.*, 2018; Lucas-Borja and Vacchiano, 2018).

99

100 Internal reserves in mature trees may be expected to buffer against the trade-off between growth  
101 and reproduction, but growth reductions in years of high reproductive investment are frequently  
102 reported (BarringerKoenig and Knops, 2013; Hacket-PainLageard and Thomas, 2017; Monks and  
103 Kelly, 2006; Selas *et al.*, 2002). Masting species may show particularly strong trade-offs as their  
104 reproductive strategy is characterised by highly variable allocation to reproduction (Kelly and Sork,  
105 2002; MencucciniPiusi and Sulli, 1995; PearseKoenig and Kelly, 2016). Growth reductions in mast  
106 years have been reported in studies focused on Norway spruce, a typical masting tree species  
107 (Mencuccini and Piusi, 1995; Selas *et al.*, 2002), but other studies have failed to find evidence to  
108 support the existence of a trade-off between growth and reproduction in this species (Seifert and  
109 Mueller-Starck, 2009). There are various possible explanations for the conflicting reports of this

110 trade-off, including challenges in effectively measuring the cost of reproduction (Obeso, 2002), costs  
111 being offset by the use of reserves (Mund *et al.*, 2010) or compensatory carbon gain via  
112 photosynthesis in the tissues of the developing reproductive organs (Hoch, 2005). Alternatively,  
113 allocation to reproduction and growth may be positively correlated with the same climatic variables,  
114 so that growth and reproduction may be positively rather than negatively correlated (Despland and  
115 Houle, 1997). Additionally, under favourable growing conditions, a reduction in growth associated  
116 with investment in reproduction may be weaker or absent; i.e. the strength of the growth-  
117 reproduction trade-off may depend on stress or resource availability (BarringerKoenig and Knops,  
118 2013; Berdanier and Clark, 2016; Hacket-PainLageard and Thomas, 2017). In these scenarios, a high  
119 investment in reproduction may not translate to a decrease in growth.

120

121 Additionally, allocation to reproduction is known to vary between individuals due to canopy position  
122 and microenvironmental conditions (Davi *et al.*, 2016; Greene *et al.*, 2002; Brooke *et al.*, 2019), tree  
123 age and size (Thomas, 2011; KrouchiDerridj and Lefevre, 2004), genetic control (Seifert and Mueller-  
124 Starck, 2009), or other factors (note that these may not be independent). Consequently, cone  
125 production at the stand scale may be dominated by a subset of “super-producers” (Minor and Kobe,  
126 2017; Brooke *et al.*, 2019). Such intraspecific variation in allocation to reproduction may result in  
127 variation in the cost of reproduction between individuals during population-wide mast years, so that  
128 any growth reductions may be greater in individuals that invest more heavily in reproduction  
129 (Patterson and Knapp, 2018). This would be consistent with numerous studies reporting lower  
130 growth in female individuals in dioecious species (Obeso, 2002). Furthermore, the cost of  
131 reproduction may vary at the individual scale due to differences in stored reserves or access to  
132 belowground resources. Individualistic growth responses to climate have previously been  
133 investigated using tree rings (Carrer, 2011; Buras *et al.*, 2018), but the potential for these to be  
134 driven by individualistic responses to reproduction remains underexplored.

135



136 To investigate how relationships between reproduction, growth and climate vary between  
137 individuals, and their interplay at the tree level, we used data from a Norway spruce population in  
138 the Italian Alps. Population-level data on reproduction was collected for the period 1971-2012, and  
139 13 individual trees were monitored annually for cone production for 29 years (1983-2012, with no  
140 data from 2007). Tree ring samples were collected from these 13 individuals in 2013. We also use a  
141 network of spruce chronologies from the Alps and regional masting records from the MASTREE  
142 database (Ascoli *et al.*, 2017a) to test whether our results can be generalised for Alpine spruce  
143 forests.

144

145 We test the following hypotheses:

146

- 147 1. Seed production is synchronous at the population level, but cone production is dominated  
148 by “super-producers”
- 149
- 150 2. Years of high seed production are associated with reduced growth. The trade-off is stronger  
151 under unfavourable climatic conditions, in this case cool summers
- 152
- 153 3. Growth-reproduction trade-offs are stronger in “super-producers”, resulting in reduced  
154 growth synchronisation in mast years, and growth divergence between “super-producers”  
155 and other trees

156

157

## 158 2. Methods

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159

### 160 2.1 Data collection

161 Analysis focused on Norway spruce (*Picea abies* (L.) Karst.) forests located in the upper Travignolo  
162 Valley (Trento, Italy) at 46.18° N, 11.45° E, between 1500 and 1900 m a.s.l (Paneveggio). The climate  
163 is continental, with mean annual precipitation of 1250-1660 mm·year<sup>-1</sup> and mean annual  
164 temperature of 2.7°C. Spruce seed production has been monitored in Paneveggio since 1962 using  
165 seed traps, although data collected prior to 1971 is considered potentially unreliable and was not  
166 included in our analysis (MencucciniPiusi and Sulli, 1995). Seed traps were deployed in October, and  
167 seeds were collected after snowmelt. Following collection, seeds were sorted and tested in  
168 germination chambers. Counts of viable, predated and damaged seeds were used to quantify annual  
169 reproductive effort.

170

171 In the same forest, long-term monitoring of annual reproductive effort by 13 individual trees was  
172 conducted 1983-2012. All monitored individuals were located within 70 m from one another, and  
173 individual tree reproduction was quantified by an annual cone count during June. Trees were located  
174 at the edge of a gap created in the lower part of the forest (1520 m a.s.l.) for experimental forest  
175 management purposes (Piusi, 1988). The stand was uneven aged, but represented by a single  
176 canopy structure, with small differences in tree height. Cones were counted each year from the  
177 same observation point, providing a consistent indicator of individual and aggregated cone  
178 production. Except for 2007, cones were counted annually until 2013, when some trees were  
179 windthrown (although only data to 2012 was used this analysis, to match the tree ring data – see  
180 below). To extend the stand-level record of reproduction based on the average of the 13 individual  
181 trees, a linear regression between annual mean seed count (across seed traps) and mean cone count  
182 (across trees) for twelve years of overlap (1983-1994,  $R^2 = 0.82$ ,  $p < 0.001$ , Supp. Figure 1) was used to

183 create a 42-year record of population-level reproduction at this site (Figure 1, “cone index”), which  
184 consisted of predicted cone counts for the period 1971-1982 and observed cone counts 1983-2012.

185

186 In 2013, increment cores were extracted from the 13 individual trees that had been monitored for  
187 cone production, by taking two cores per tree at breast height (1.3 m). Cores were mounted and  
188 sanded with progressively finer sandpaper until tree ring boundaries were clearly visible. Tree ring  
189 widths were measured using a binocular microscope and LINTAB measuring devices (Rinntech,  
190 Heidelberg, Germany) to the nearest 0.01 mm. The accuracy of visual cross-dating and  
191 measurements was checked with the COFECHA program (Grissino-Mayer, 2001). Cross-dated series  
192 belonging to the same tree were then averaged. Ring width series were detrended using a double-  
193 detrending protocol, first using a modified negative exponential curve to remove the age- or size-  
194 related trend, and then using a 20-year cubic spline with frequency cut-off of 0.5 to remove trends  
195 associated with disturbance and canopy dynamics (Cook and Peters, 1981). The individual tree ring  
196 series were pre-whitened to reduce temporal autocorrelation by fitting an autoregressive model,  
197 whose optimal order was selected to minimise the Akaike’s Information Criterion (AIC) score. A  
198 stand ring width index (RWI) chronology was created by averaging the detrended series from the 13  
199 trees. Basal area increment (BAI) was calculated for individual trees using the formula:

200

$$201 \quad \text{BAI}_t = \pi(r_t^2 - r_{t-1}^2), \text{ where } r \text{ is the radius of the tree in year } t.$$

202

203 Processing of ring width measurements was conducted using the dplR package in R (Bunn, 2008; R  
204 Development Core Team, 2016). Monthly climate data for Paneveggio was extracted from the  
205 HISTALP dataset at 5’x5’ resolution (Auer *et al.*, 2007), using the histalp package (Zang, 2018).

206

## 207 **2.2 Individual and population-scale analysis**

208 Trends and patterns of seed and cone production were assessed for Paneveggio using population  
209 and individual-tree data (Vacchiano *et al.*, 2018). Synchrony of reproductive effort between  
210 individuals was quantified as the mean Pearson product-moment correlation between pairs of  
211 individual trees, and variability was assessed using the coefficient of variation (CV). Autocorrelation  
212 functions (ACF) were used to test for serial correlation in seed and cone production time-series. We  
213 identified mast events when reproductive effort exceed one standard deviation from the long-term  
214 mean (LaMontagne and Boutin, 2009). We hypothesised that “super-producers” would dominate  
215 overall cone production at the stand scale, either due to larger cone crops in mast years, or more  
216 frequent large cone crops (or both). To test this, we defined individual-level “bumper crops” (the  
217 individual-tree equivalent of a “mast year”) as years when individual tree cone count exceed one  
218 standard deviation from the mean cone count from all 13 individuals over whole the study period.

219

220 Relationships between reproduction and growth, and climate and growth were assessed using  
221 generalised additive models (GAMs). Where GAMs indicated a linear relationship between two  
222 variables (estimated degrees of freedom close to 1), we re-fitted using linear regression models. As  
223 tree ring data (RWI) was detrended, we also removed long-term trends in the climate data using  
224 linear regression. As cone production varied strongly between individuals, analysis was conducted at  
225 the individual level, as well as the population-level. Effects of variable reproduction (between years)  
226 on between-tree growth synchrony was tested by calculating inter-individual growth variability for  
227 each year (using the CV). A higher CV for an individual year indicated greater between-tree growth  
228 variability, representing lower growth synchrony. To test for growth divergence between heavy and  
229 light cone producers, we created a mean RWI chronology of heavy cone producers, and compared  
230 this to a mean RWI chronology of the other trees. We defined heavy cone producers as individual  
231 trees with above average cone counts across the whole study period.

232

233 **2.3 Regional datasets and analysis**

234 To test the generality of our results from Paneveggio, we analysed other spruce tree ring  
235 chronologies from the Alpine region (Italian and Swiss Alps) together with regional records of spruce  
236 mast years. Tree ring chronologies from the International Tree Ring Data Bank (ITRDB) (**insert**  
237 **reference for the chronologies SWIT332, 279, 256 and 329 – I cannot do this at the moment at the**  
238 **ITRDB is unavaible during the US Government shutdown**) were combined with existing and new  
239 tree-ring chronologies from the Italian Alps (Table 2). Detrending and chronology building followed  
240 the protocol used for the Paneveggio site. Regional mastng chronologies were developed for  
241 Switzerland (NUTS-1 region CH0), Slovenia (SI0) and Northwest Italy (ITC) using the MASTREE  
242 database (Ascoli *et al.*, 2017a). In this dataset, annual seed production is summarised in the  
243 database using five ordinal classes. Where multiple records existed in a given year for the same  
244 NUTS-1 region, the modal value was used, following the method of Vacchiano *et al.* (2017). In this  
245 regional-scale analysis, and due to a limited sample size (number of years), ordinal data was then  
246 reclassified to a binary scale, comprising mast years (category 4 and 5) and non-mast years (category  
247 1-3) (Ascoli *et al.*, 2017b). The cruts package (Taylor and Parida, 2016) was used to create NUTS-1  
248 regional climate series from the CRU TS 3.23 gridded dataset (Harris *et al.*, 2014), as region-wide  
249 means of individual-cell monthly values.

250

251

252

253

## 254 3. Results

---

255

### 256 3.1 Seed production: variability between years and individuals

257 Cone production was highly variable at Paneveggio, both between individuals and between years.  
258 Individual tree coefficient of variation ( $CV_i$ ) for cone counts across the period 1983-2012 varied  
259 between 1.11 and 1.97 (mean = 1.39), and the CV of the mean population cone count chronology  
260 (population-level CV,  $CV_p$ ) was 1.19 (1983-2012). The  $CV_p$  for seed trap data 1971-2012 was 1.28.  
261 Cone production and seed counts had significant negative autocorrelation at lag -1 year (Supp.  
262 Figure 2). The extended 1971-2012 cone index, developed using a combination of seed trap data and  
263 mean cone counts, indicated the presence of large mast years in 1976, 1981 and 1995 (cone index  
264  $>2$  standard deviations from the mean), with additional mast years ( $>1$  SD) in 1985 and 1988. The  
265 overall distribution of seed production during the period 1971-2012 was a continuous reserve J-  
266 shaped distribution (Figure 1D and Supp. Figure 3). A Hartigans' dip-test indicated no evidence of  
267 multimodality ( $p \gg 0.05$  for seed count, cone count and combined cone index). In 1997 and 2008 no  
268 cones were counted on any of the 13 individuals, but in every other year cones were observed on at  
269 least one individual. The seed-trap datasets recorded some seed fall in every year – i.e. there were  
270 no years with zero recorded spruce seed production. The full 1971-2012 cone index chronology  
271 showed no long-term linear trend (regression of seed production versus year,  $p > 0.05$ ), and this was  
272 also the case individually for the seed-trap dataset (1971-1994) and the mean cone-count dataset  
273 (1983-2012) (Supp. Figure 4). For the individual tree cone-count series (1983-2012), linear trends  
274 through time were also insignificant for all trees (Supp. Figure 4).

275

276 Cone production varied strongly between the 13 individual trees, and most cones were produced by  
277 a small proportion of individuals (Figure 1). The highest producing individual (ID\_01) produced 26.3%  
278 of all produced cones (1983-2012),  $\times 2.5$  the next highest producer. The lowest producer was  
279 responsible for only 1.7% of total cones. Bumper cone crops associated with individual trees were

280 generally quite rare (Figure 1A). Most tree produced between one and four such bumper crops over  
281 the 29 years of observation, while two individuals failed to produce a single bumper crops. In  
282 contrast, one individual (ID\_01) produced 13 individual bumper crops, equivalent to almost one  
283 every two years on average. Total cone production (1983-2012) was correlated with tree diameter  
284 ( $r= 0.539$ ,  $p=0.057$ , Supp. Figure 5), and there was a significant positive correlation with Basal Area  
285 Increment (BAI) 1983-2012 (Supp. Figure 6). However, with only thirteen trees these relationships  
286 were difficult to quantify, and both relationships were dependent on the inclusion of the highest  
287 producing individual (ID\_01). Correlations were insignificant between total cone production (1983-  
288 2012) and tree age (estimated by counting the total number of measured tree rings).

289  
290 Heavy cone producers remained heavy producers over at least three decades (Figure 1). For  
291 example, excluding the two years when no individuals produced any cones, the highest producing  
292 tree (ID\_01) was the top-ranked producer 19 times ( $19/28 = 67.9\%$ , highest producer in 2/3 of  
293 individual years), and the five individuals with the highest mean rank took 67% of the available  
294 annual top five ranking positions over 28 years. With 13 individual trees, an individual could expect  
295 to be in the top five 38% of all years if ranking was random. In contrast, the lowest ranking tree  
296 (ID\_10) was in the top five on only three occasions, and the five lowest ranking individuals took only  
297 25% of the available top five positions.

298  
299 While highly variable between years and between individuals, cone production was synchronised  
300 between trees (Figure 1). Mean inter-tree correlation was 0.72 (min=0.33, max=0.91, median =  
301 0.73). Cone and seed production at Paneveggio was also strongly synchronised with other Alpine  
302 masting chronologies for spruce. For example, high cone or seed counts were reported from spruce  
303 in 1995 in many of the records contained in the MASTREE database (Ascoli et al. 2017b). Cone index  
304 was positively correlated with neighbouring regional masting chronologies developed for cone and  
305 seed counts for CH0 (Switzerland) ( $\rho= 0.71$ ,  $p<0.001$ ,  $n=30$ ), ITC (NW Italy) ( $\rho=0.44$ ,  $p=0.129$ ,  
306  $n=12$ ) and SIO (Slovenia) ( $\rho=0.13$ ,  $p=0.049$ ,  $n=30$ ).

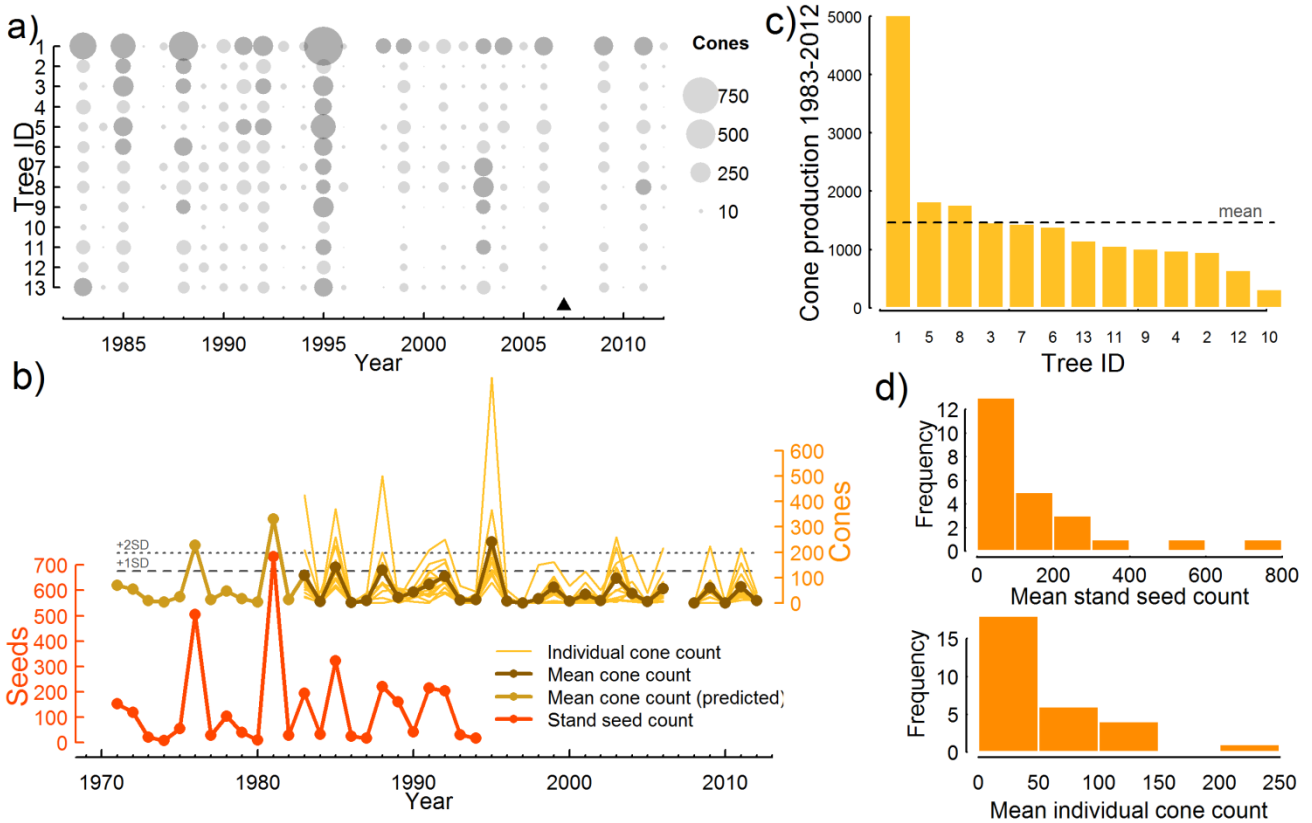




08 **Table 1.** Site and chronologies statistics for all sites. All statistics are reported for residual prewhitened chronology. EPS = Expressed Population Signal, rbar = inter-series  
 09 correlation, SNR = signal-to-noise ratio, AC<sub>1</sub> = first order autocorrelation, MS = mean sensitivity

Site	Lat	Lon	Elev	Period*	Length*	N° trees	EPS	rbar	SNR	Mean (RWI)	SD (RWI)	AC <sub>1</sub> (RWI)	MS
PAN	46.18	11.45	1520	1813-2012	200	13	0.893	0.446	8.34	0.988	0.121	-0.072	0.122
PAN (study period)	46.18	11.45	1520	1971-2012	42	13	0.910	0.436	10.06	0.998	0.075	-0.065	0.085
SWIT332	46.46	9.18	1660	1842-2005	164	10	0.930	0.449	13.34	0.998	0.098	0.050	0.110
SWIT279	46.59	7.98	1850	1689-2011	323	25	0.924	0.455	12.21	0.988	0.121	0.023	0.131
SWIT256	46.30	7.72	900	1882-2005	124	12	0.941	0.527	15.892	0.989	0.218	-0.001	0.260
SWIT329	46.27	7.03	1440	1907-2005	99	16	0.948	0.405	18.239	0.998	0.114	-0.191	0.146
BREP	46.19	10.85	1550	1851-2010	160	20	0.903	0.353	9.341	0.994	0.090	-0.074	0.100
MASP	46.27	9.58	1150	1897-2013	117	31	0.927	0.375	12.693	0.999	0.113	-0.037	0.132
SALP	45.05	6.90	1800	1806-2017	212	25	0.823	0.284	4.649	0.997	0.112	-0.081	0.120
VENP	46.66	10.52	1500	1880-2017	138	10	0.873	0.460	6.868	0.990	0.145	-0.076	0.177
VIEP	45.64	7.27	1500	1842-2016	175	12	0.882	0.405	7.468	0.992	0.100	-0.136	0.117

10 \* Note that period and length are taken from the residual prewhitened chronology, and therefore do not represent the full period of the raw chronology.



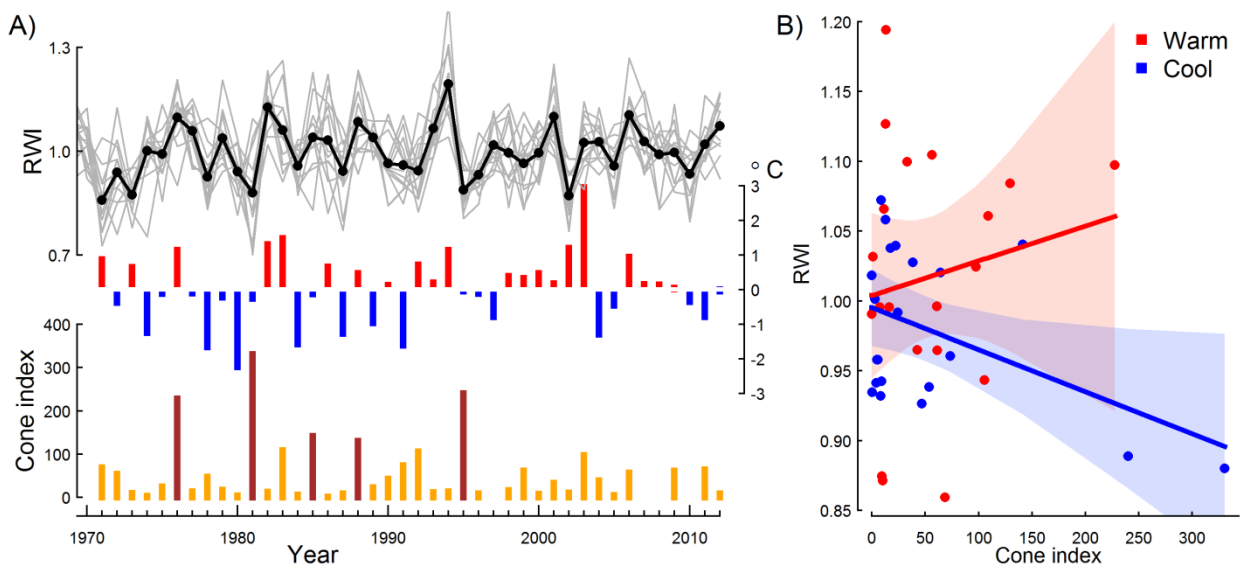
312 **Figure 1.** Cone and seed production at Paneveggio a) Individual tree cone counts 1983-2012. Symbol size is proportional  
 313 to individual cone count, and shading indicates a bumper cone crop (individual cone production greater than the mean  
 314 of all trees across the study period). Triangle indicates year with no data (2007). b) Individual tree cone counts (yellow)  
 315 and the stand mean (dark brown) for the period 1983-2012, and predicted stand mean cone count for the period 1971-  
 316 1982 (light brown). Dashed and dotted lines indicate +1 and +2 standard deviations from the mean, the definitions of  
 317 mast and large mast year respectively. Stand-level seed counts (orange, 1971-1994). Observed and predicted cone  
 318 counts are combined for the period 1971-2012 (“Cone index”), and are used in the rest of the analysis. C) Total cone  
 319 production over the study period for the 13 monitored trees. The dashed line indicates the mean cone production. D)  
 320 Frequency plots for stand-level seed count (1971-1994) and mean individual cone count (1983-2012).  
 321  
 322  
 323

324 **3.2 Stand-scale growth-reproduction trade-offs**

325 The relationship between stand-level ring width index (RWI) (mean of the 13 trees) and the combined stand  
 326 cone index was weak and insignificant ( $r = -0.128$ ,  $p = 0.424$ ). This was consistent when analysed using the

327 seed-count data only (1971-1994,  $r = -0.127$ ,  $p = 0.555$ ), and the cone count data only (1982-2012,  $r = -0.081$ ,  
 328  $p = 0.676$ ). Relationships were also insignificant when tested using GAMs (i.e. allowing for non-linear  
 329 relationships, results not shown). Some mast years were associated with low growth (e.g. 1981, 1995), but  
 330 the large mast year in 1976 was associated with above average growth (Figure 2). Summer temperature  
 331 (mean of May-July) was positively correlated with RWI for the period 1971-2012, ( $r = 0.313$ ,  $p = 0.044$ ; see  
 332 also Figure 3D), and appeared to influence the response of RWI to cone index. In warm summers (summer  
 333 temperature > 1971-2012 mean), there was no significant response to reproduction ( $r = 0.169$ ,  $p = 0.48$ ), but  
 334 in cool summers cone index and RWI were negatively- correlated ( $r = -0.471$ ,  $p = 0.031$ ) (Figure 2). This  
 335 indicated that a growth-reproduction trade-off was restricted to cool summers, where cone index explained  
 336 22% of variation in RWI (but <2% in analysis including all years, Figure 2B). However, with only five mast  
 337 years in the 42-year record, and as the significant relationship in cool summers is dependent on the inclusion  
 338 of the two large mast years in 1981 and 1995, this result should be treated with caution.

339  
340



341

342 **Figure 2.** A) Time series with individual and mean stand RWI chronologies, May-July temperature anomalies and cone  
 343 index. For temperature, red and blue bars indicate positive and negative temperature anomalies respectively. Mast  
 344 years (cone index greater than one standard deviation from the mean) are plotted in dark brown. Note that the  
 345 temperature anomalies are for detrended summer temperature (i.e. the linear trend in temperature is removed). B)

346 The linear regressions for RWI  $\sim$  cone index for cold (blue) and warm (red) summers (1971-2012), including 95%  
347 confidence intervals.

348

349

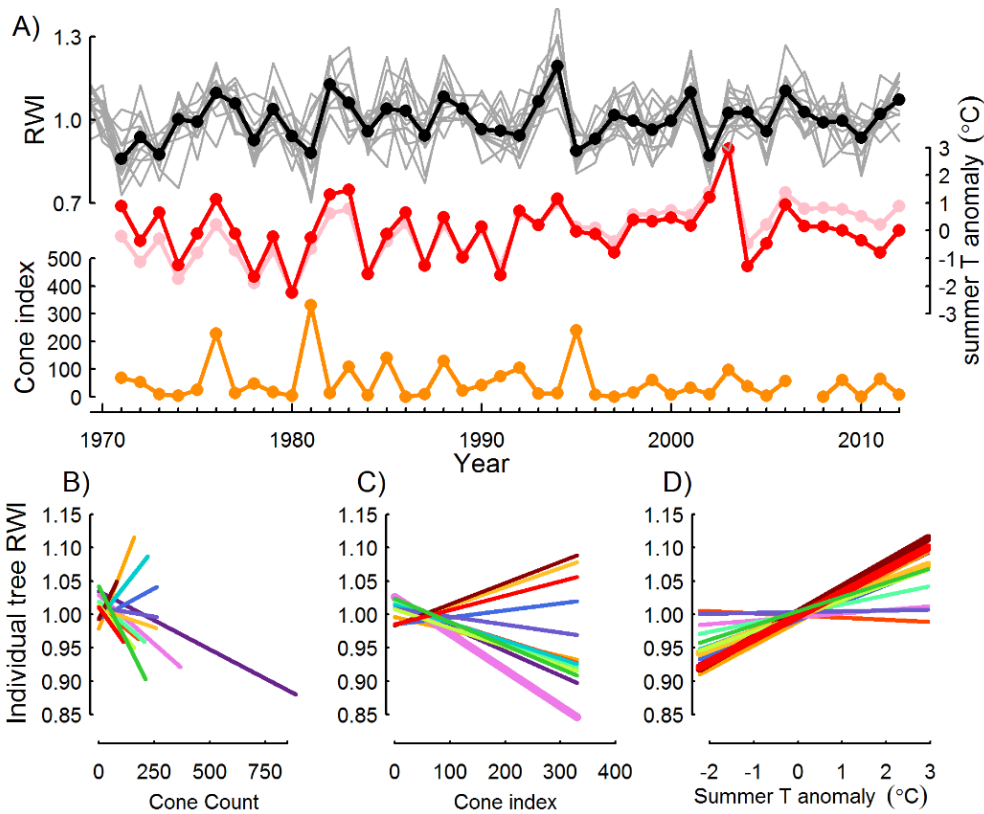
350 To test the generality of these results, growth responses to regional mast years (MASTREE database) were  
351 tested for a network of Alpine spruce chronologies. Some sites showed lower growth in regional mast years,  
352 particularly those in northwest Italy (ITC: MASP, SALP and VIEP), and also the Swiss site SWIT256, but the  
353 growth reduction in mast years were small and marginally significant for only one site (VIEP,  $p=0.048$ ) (Supp.  
354 Figure 7). The lack of a strong and significant relationship between RWI and masting was therefore  
355 consistent with the results from Paneveggio. Short overlapping time series made it difficult to test whether  
356 growth reductions were stronger in colder summers, as found at Paneveggio (Supp. Figure 8).

357

### 358 **3.3 Individualistic growth responses to climate and reproduction**

359 The climate response of individuals showed some variation, but warmer summers were associated with high  
360 growth (Figure 3D). However, the growth response of individuals to reproduction showed more variation,  
361 both when tested against the corresponding individual tree cone counts (1983-2012, Figure 3B), and when  
362 tested against the stand-scale cone index (1971-2012, Figure 3C). However, the relationship was significant  
363 in only one individual (note that this was an individual with above-average cone production, but not ID\_01,  
364 the outstanding super-producer). High investment in cone production (at an individual- and stand-level) was  
365 associated with lower growth in the individuals with higher cone productivity (Figure 3). Responses of  
366 growth to mast years were close to zero or even positive in individuals with low cone productivity (albeit  
367 non-significant). For example, in heavier cone producers, the growth reductions in the heaviest stand-scale  
368 mast years were approximately equivalent in magnitude to those associated with coolest summers (Figure  
369 3C and 3D). In contrast, the lightest cone producers showed positive growth responses in these years,  
370 equivalent in magnitude to the growth increase associated with a warm summer (Figure 3C and 3D).

371



372

373 **Figure 3.** A) Time series with individual (thin lines) and stand-level (thick lines) RWI chronologies, summer temperature  
 374 and cone index. The pink line represents raw summer temperature data, while the red line is linearly detrended data.  
 375 The detrended data is used for the regression analysis. For B-D, only the regression lines are plotted. Each line  
 376 represents the regression between individual tree RWI and B) corresponding individual tree cone counts (1982-2012),  
 377 C) stand-scale cone index (1971-2012) D) summer temperature (detrended anomaly, 1971-2012). Thick lines indicate  
 378 significant models. Line colour represents the individual tree ranking for total 1983-2012 cone count; heavy cone  
 379 producers are purple/blue, and light producers are orange/red.

380

381

382 Overall, between-tree growth synchrony was high ( $r_{bar} = 0.44$ , Table 1, and see also Figure 3A), representing  
 383 a strong coherence in growth between years. However there were differences in synchrony between years;  
 384 in other words, in some years individuals had very similar growth while in other years growth diverged  
 385 between individuals (Figure 3A). The year with the highest stand-scale reproductive effort corresponded to  
 386 the year with the highest between-individual growth CV (lowest growth synchrony) (1981, see Supp. Figure  
 387 9). There was a significant relationship between cone index and growth CV (Supp. Figure 9), suggesting that

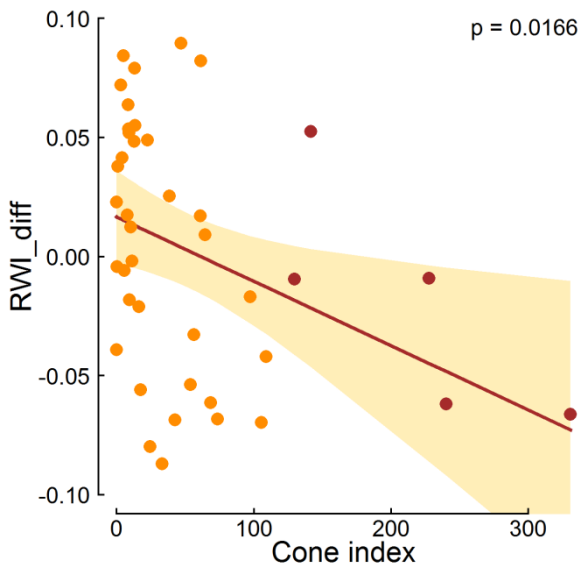
388 high reproductive effort (at the stand scale) was associated with a decline in growth synchrony between  
389 individuals. However, the significance of the relationship was dependent on the inclusion of 1981, the year  
390 with highest cone index and between-tree growth CV. Without 1981, the relationship between-tree growth  
391 CV and cone index became insignificant. A similarly mixed picture emerged from analysis of between-  
392 individual growth CV for other regional chronologies (Supp. Figure 10). Between-tree growth synchrony  
393 decreased in mast years at some sites (e.g. VIEP, SWIT279) although this was never statistically significant  
394 and sample size was always low.

395

396 We also compared the RWI of heavy producers and other trees, to test whether mast years were associated  
397 with a growth divergence ( $RWI_{diff} = RWI_{heavy} - RWI_{light}$ ). Heavy producers were defined as individuals with  
398 greater than average cone production 1983-2012 (Figure 1c). Overall the correlation between RWI  
399 timeseries of heavy and other trees was high ( $r=0.81$ ,  $p<0.001$ ) However,  $RWI_{diff}$  varied according to stand  
400 cone index. The relationship between  $RWI_{diff}$  and cone index appeared to be asymmetric, but in mast years  
401 heavy producers had lower growth relative to light producers (Figure 4). The difference was largest in the  
402 heaviest mast years (Figure 4). The relationship was even stronger if  $RWI_{light}$  was calculated for the  
403 equivalent three lightest producers, rather than for all other trees (results not shown).

404

405



406

407 **Figure 4.** Relationship between RWI<sub>diff</sub> and stand-level cone index (1971-2012), with a 95% confidence interval.

408 Negative values indicate that heavy producing trees had lower growth than other trees. Brown points represent mast  
409 years at the stand scale.

410

411

## 412 4. Discussion

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413

### 414 4.1 Characteristics of cone production

415 Cone production at Paneveggio showed characteristics associated with masting. The stand-level  $CV_p$  for cone  
416 production was almost identical to that reported by Selas *et al.* (2002) for Norway spruce in Norway (1.20),  
417 and consistent with other reported values for spruce species and other masting species (Herrera *et al.*, 1998;  
418 Koenig and Knops, 2000; Lamontagne and Boutin, 2007). In the heaviest mast years, cone index at the stand  
419 scale was six times greater than the long-term mean, representing a substantial resource investment. At the  
420 individual tree scale the contrast was even more extreme. In 1995 tree ID\_01 produced 18 times more cones  
421 that the mean cone production of all trees 1982-2012, and this individual was responsible for 26% of all the  
422 cones produced over the study period (by 13 individuals). Various factors may explain such individual  
423 variability in reproductive output, including tree age, size, microenvironmental conditions, resource  
424 availability, and genetics (Davi *et al.*, 2016; Greene *et al.*, 2002; Seifert and Mueller-Starck, 2009; Thomas,  
425 2011; Brooke *et al.*, 2019), although with individual-tree data for only 13 trees, it was not possible to identify  
426 the factors controlling long-term cone productivity, or robustly test scaling with tree size. However, our data  
427 hinted that high cone production was associated with larger, faster growing trees. Notably, heavy cone  
428 producers retained their ranking over three decades. For example, the highest overall cone producer (ID\_01)  
429 was the heaviest individual producer in two thirds of all years, consistent with the definition of “super-  
430 producer” suggested by Minor and Kobe (2017). Previous studies have also indicated that the relative  
431 reproductive performance of individual trees can be maintained over multiple years, but have relied on  
432 shorter datasets where long-term trends are difficult to identify (HealyLewis and Boose, 1999; KrouchiDerridj  
433 and Lefevre, 2004; Linhart and Mitton, 1985).

434

435 While variable between years, reproduction was remarkably synchronised between trees ( $r=0.72$ ), with all  
436 trees located within 70 m from one another. Synchrony of seed production declines with distance (Koenig  
437 and Knops, 2000), although not significantly at local scales (Lamontagne and Boutin, 2007). However, the



438 observed between-tree synchrony in cone counts was higher than that reported by LaMontagne and Boutin  
439 (2007) for *Picea glauca*, and represents a highly synchronised variation in resource allocation at the stand  
440 scale. Previous studies indicate that this synchronisation is also strong between Alpine spruce stands at local  
441 scales (MencucciniPiussi and Sulli, 1995), and under appropriate regional climate conditions, synchronisation  
442 between populations can extend over larger spatial scales (Ascoli *et al.*, 2017b). Such synchronisation of  
443 cone production can have cascading effects on local communities, starting with the population dynamics of  
444 seed predators (BogdziewiczZwolak and Crone, 2016) and extending to pulsed regeneration patterns,  
445 interaction with herbivores, and cascading trophic interactions (Ostfeld and Keesing, 2000).

446

447 The long-term response of tree reproduction to climate change will be a key factor determining the  
448 resilience of forest ecosystems (Caignard *et al.*, 2017; Davi *et al.*, 2016), but the response of masting to  
449 ongoing climate change is uncertain (Ascoli *et al.*, 2017b; PearseKoenig and Kelly, 2016; PearseLaMontagne  
450 and Koenig, 2017). Despite their value in addressing how masting will respond to future environmental  
451 change, few long-term records of seed production exist, and have revealed contrasting trends. Allen *et al.*  
452 (2014) found a significant increase in seed production in *Nothofagus*, particularly at high elevations, and  
453 similar increases in seed production have been reported for other genera (Caignard *et al.*, 2017;  
454 OvergaardGemmell and Karlsson, 2007). However, in a large study incorporating over 1000 time-series of  
455 annual seed production, Pearse *et al.* (2017) found an overall decrease in seed production since 1900. In our  
456 study, no significant change in seed production was detected in either a 30-year record of cone production  
457 for individual trees, or a stand-level record of seed production that extended over four decades (1971-2012)  
458 (Supp. Figure 4). Summer temperatures increased significantly over this period. However, our long-term  
459 dataset highlighted the challenges of detecting long-term changes in tree masting. Even with four decades of  
460 data, we observed only three large mast events (1976, 1981, 1995), which together accounted for 34% of all  
461 seed production despite accounting for only 7% of all monitored years. When such rare events dominate  
462 overall seed production, detecting trends in response to climate change is challenging (Vacchiano *et al.*,  
463 2018).

464

## 465 **4.2 Growth-reproduction relationships: implications for understanding variation in tree growth**

466 The relationship between reproductive effort and tree growth was variable. At the stand scale, mast years  
467 were not consistently associated with reduced growth, and we found similar results in a network of Alpine  
468 spruce chronologies. At Paneveggio, this generally low sensitivity of growth to investment in reproduction  
469 may be related to the generally favourable growing conditions. Paneveggio is a mesic site for spruce, with  
470 relatively high annual increment (typically 8-10 m<sup>3</sup> ha<sup>-1</sup> y<sup>-1</sup>). Furthermore, the timing of investment in the  
471 maturation of cones (including lignification) is likely timed after the main phase of radial growth in early  
472 summer (Deslauriers *et al.*, 2008), which may minimise a direct trade-off for resources between radial  
473 growth and reproduction. We found evidence that in climatically unfavourable years (cool summers),  
474 investment in reproduction was associated with reduced growth; this can be interpreted as a variation in  
475 trade-off strength with climate (Hacket-PainLageard and Thomas, 2017; Sletvold and Agren, 2015; Villellas  
476 and Garcia, 2018), which can explain the generally weak relationships between growth and masting. We  
477 suggest that the population-level insensitivity of growth to masting in warm summers observed at  
478 Paneveggio may have resulted from increased resource assimilation during these favourable conditions,  
479 reducing any trade-off between competing resource sinks. In an earlier study in the same forests,  
480 Mencuccini and Piussi (1995) demonstrated that the negative relationship between growth and seed  
481 production was stronger at higher elevations (lower temperatures), supporting our findings for variation  
482 between years (Figure 2). Consequently, future environmental changes which favour growth may result in  
483 relaxation of growth-reproduction trade-offs in high elevation and temperature limited spruce populations,  
484 although this remains to be tested.

485

## 486 **4.3 Synchronisation of growth within populations: influence of climate and reproduction**

487 Summer (May-July) temperature had a positive influence on radial growth in this population, as has  
488 previously been reported from other high elevation spruce stands across the Alps (Castagneri *et al.*, 2014).  
489 The response of growth to temperature was generally positive in all individuals, but with weaker

490 relationships in cone super-producers (Figure 3b). In contrast, the response of growth to reproduction was  
491 not consistent between individuals. Variation in trade-off strength between individuals was partly  
492 dependent on their long-term cone productivity, such that growth reductions in association with high cone  
493 production were generally limited to the heavy cone producers. This is consistent with the findings of  
494 Patterson & Knapp (2018) in longleaf pine forests in southeast U.S.A. Consequently, the individualist growth  
495 response to individual cone production (Figure 3B), and to population-level mast years (Figure 3C), created  
496 increased growth variance in mast years – i.e. less synchronised growth. However, this was not a strong  
497 trend, and we did not find consistent results in the regional network of spruce tree ring chronologies.

498

499 As heavy cone producers tended to exhibit lower growth in mast years relative to light cone producers, mast  
500 years were associated with growth divergences between heavy and light producers (Figure 4). The  
501 divergence increased in strength with increased reproductive effort. This result contrasts with Zywiec and  
502 Zielonka (2013), who reported no difference in growth between high and low producers in *Sorbus aucuparia*  
503 in mast years. However, our results are consistent with numerous reports of growth differences between  
504 male and female individuals in dioecious species (Obeso, 2002), where higher reproductive investment by  
505 females is associated with lower growth rates than in males. As the individual investment in reproduction  
506 was consistent over time (both in absolute cone numbers, and in ranking relative to other individuals), the  
507 growth divergence in mast years between heavy and light cone producers was also consistent and extended  
508 beyond the period of individual tree cone counts (i.e. 1971-1982, the period with stand-level seed counts  
509 only). This indicated that over multiple decades, trees that invested heavily in reproduction showed a  
510 reduction in growth relative to trees with low investment in reproduction in mast years. However, BAI 1983-  
511 2012 was positively correlated with total cone production over this period (Supp. Figure 6), indicating that  
512 long-term high investment in reproduction was not associated with lower growth rates over the study  
513 period. If reproductive output is at least partly controlled by genes, it is still unexplained how poor producers  
514 are maintained in the population over multiple generations, particularly when our results indicate that high  
515 investment in reproduction is not associated with a long-term trade-off with growth. Note that in this study,

516 the 13 trees were growing on a fertile site, on the edge of long-existing canopy gap, and maintained high  
517 growth rates over the study period; light cone producers were not suppressed or growing in marginal  
518 environments.

#### 519 520 **4.4 Resource switching and implications for understanding masting**

521 At the population level, we found mixed evidence that increased investment in reproduction resulted in a  
522 trade-off with growth; some mast years were associated with reduced growth, but not all. In contrast, Selas  
523 et al. (2002) reported stronger effects of seed production on growth in spruce (seed production explained  
524 42% of variation in ring width), and Mencuccini and Piussi (1995) found a negative relationship between ring  
525 width and seed production in spruce stands from our study area. In our study, cone index explained 22% of  
526 variation in RWI in years with cool summers, but <2% in analysis including all years, Figure 2B). Other studies  
527 have also reported a lack of evidence to support a trade-off between tree growth and reproduction (Zywiec  
528 and Zielonka, 2013), including in spruce (Seifert and Mueller-Starck, 2009). Monks and Kelly (2006) argue  
529 that evidence of resource switching is the most important evidence that masting results from selection for  
530 highly variable seed production, and not simply a response to climate (e.g. resource matching) (see also Kelly  
531 and Sork, 2002). Our results imply that resource switching was only required during years of unfavourable  
532 resource assimilation, but during more favourable conditions growth rate could be maintained even with the  
533 additional demands of developing cones. Furthermore, analysis at the individual level demonstrated that  
534 cone super-producers did show a reduction in growth in mast years. Consequently, population-level growth  
535 chronologies may mask evidence of switching (Patterson and Knapp, 2018), and where possible, evidence of  
536 resource-switching should be sought at the individual level (Monks and Kelly, 2006).

#### 537 538 **4.5 Implications for reconstructing mast years**

539 Multi-decade records of masting are rare (Ascoli *et al.*, 2017a; Kelly and Sork, 2002; PearseLaMontagne and  
540 Koenig, 2017), but have revealed important insights into the drivers of changes in masting in response to  
541 recent environmental change (Allen *et al.*, 2014; Ascoli *et al.*, 2017b; PearseLaMontagne and Koenig, 2017).

542 Where such long observational records do not exist, reconstructions of mast years using tree ring  
543 chronologies may facilitate improved understanding of the response of masting to long-term environmental  
544 change, and cascading impacts of these changes on forest ecosystems more generally (Ostfeld and Keesing,  
545 2000). For example, Drobyshev (2014) used a multi-century reconstruction of beech mast events in Sweden  
546 to demonstrate that decadal changes in mast frequency were not linked to changes in nitrogen deposition  
547 (as proposed by Overgaard et al. 2007). However, our results indicate that not all mast years are associated  
548 with a reduction in growth (Figure 2), with significant growth reductions limited to years with unfavourable  
549 climate (see Hacket-Pain *et al.* 2017 for similar findings for *Fagus sylvatica*). In this case, negative pointer  
550 years in ring width series may not be enough to identify all mast years, even if combined with historical  
551 climate data for the known climate cues of mast years (the method of Drobyshev *et al.* 2014). A more  
552 complete integration of climate data and tree rings may be required, accounting for factors that influence  
553 the sensitivity of ring width to masting events, but mast years that coincided with climatically favourable  
554 years may ultimately be harder to detect. However, other tree ring parameters may also provide information  
555 on masting. For example, Han *et al.* (2016) reported small differences in  $\delta^{13}\text{C}$  in tree rings associated with  
556 mast years in *Fagus crenata*, and Rodríguez-Ramírez *et al.* (2018) showed potential for mast year  
557 reconstruction based on wood anatomical traits. Additionally, our results indicate that the individualist  
558 responses of trees to masting may also prove useful in identifying mast years using individual tree ring data.  
559 For example, increased between-tree growth variability may be useful for identifying mast years, and  
560 requires no additional information on the sampled trees. This may be a useful source of information to  
561 identify mast years (particularly heavy mast years) (Figure 4), and contribute to a “toolbox” of useful  
562 indicators for tree-ring based reconstruction of mast years.

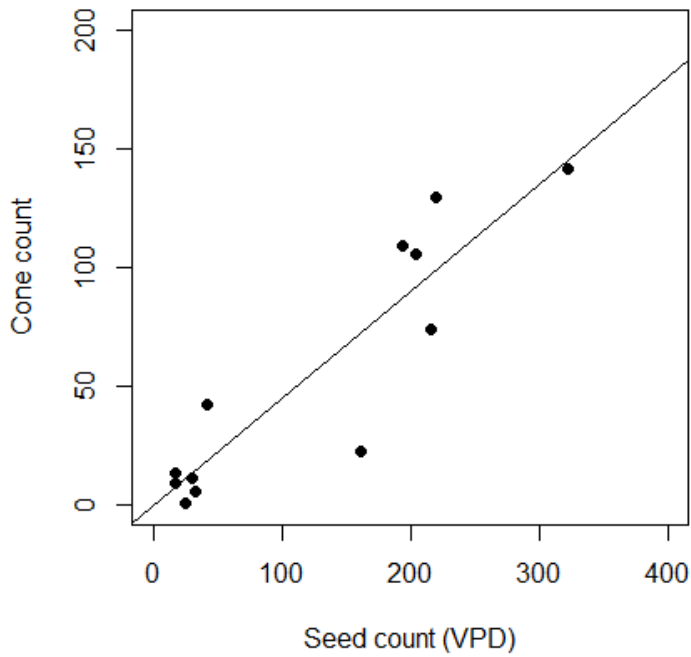
563

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568 were utilised in this study. We thank two anonymous reviewers whose comments substantially improved the  
569 manuscript.

570 **Supplementary Figures**

571

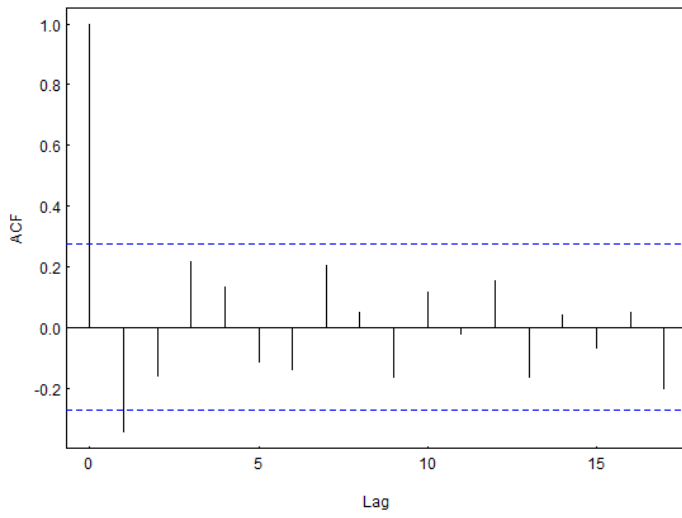


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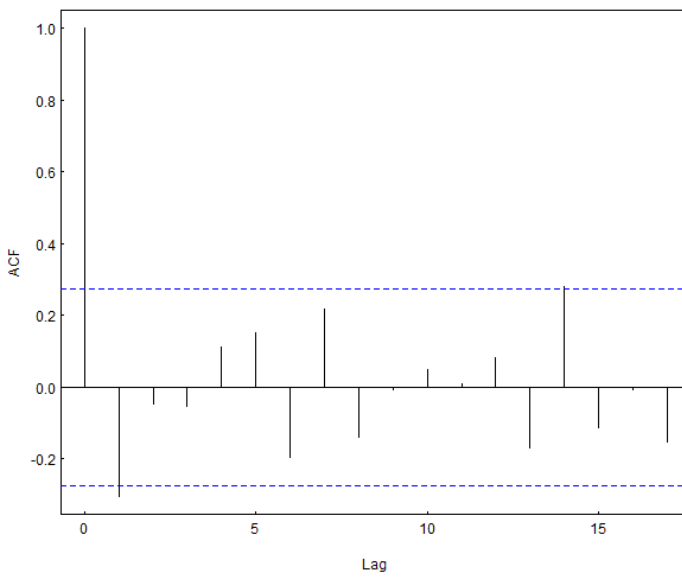
573 **Supp. Figure 1.** Relationship between mean stand cone counts and mean seed count for Paneveggio (VPD,  
574 sum of viable, predated, damaged seeds), 1983-1994.  $R^2 = 0.82$ ,  $p < 0.001$ .

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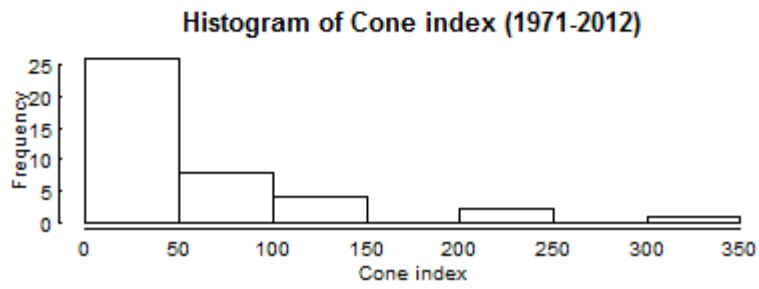
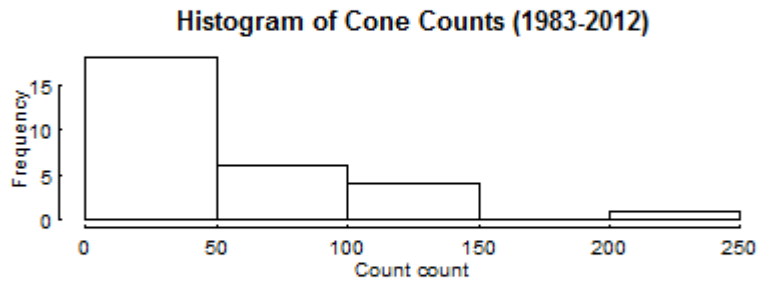
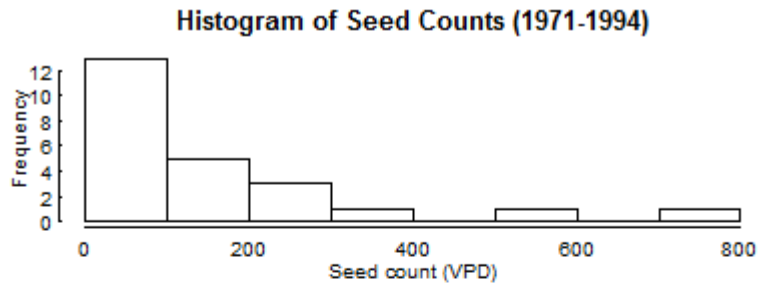
578

579 **Supp. Figure 2.** Autocorrelation functions for cone production (1982-2012) (top panel) and cone index

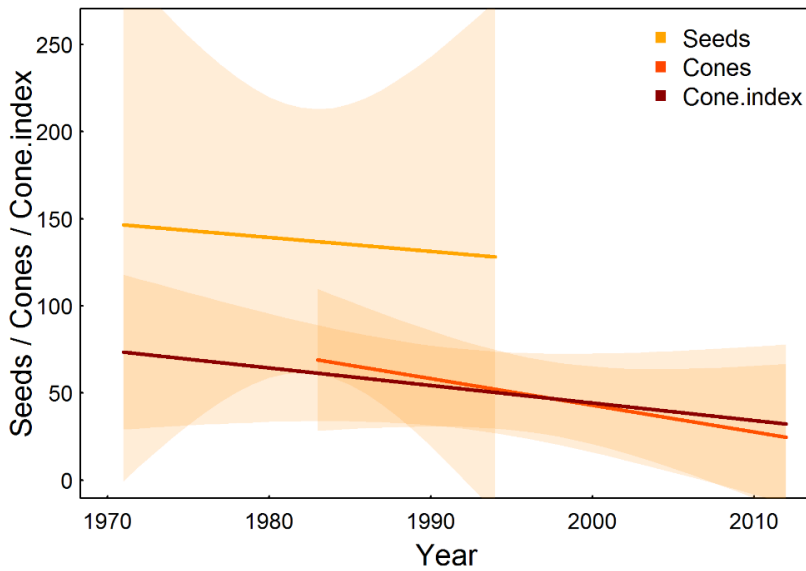
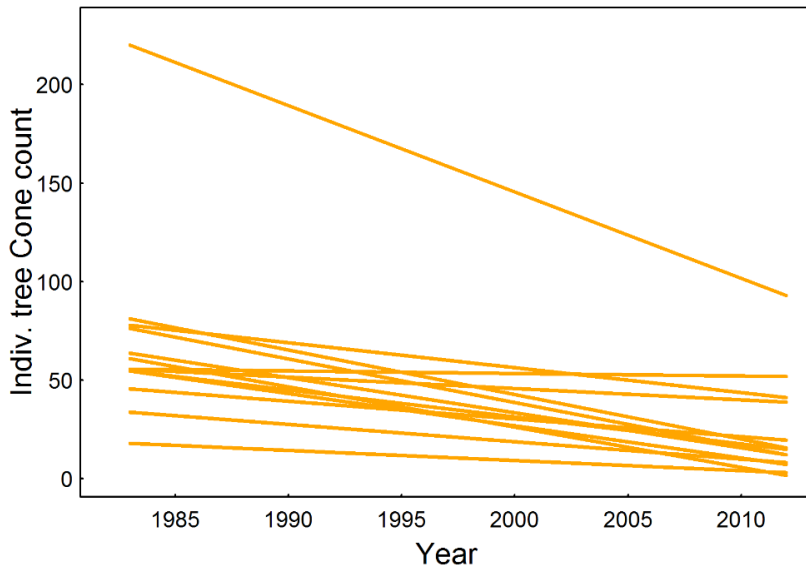
580 (1971-2012) (bottom panel)

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582  
 583 **Supp. Figure 3.** Distributions of measures of seed and cone production  
 584  
 585



586

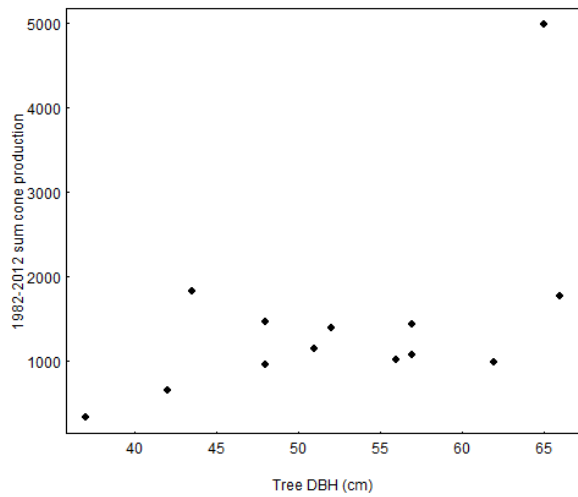
587 **Supp. Figure 4.** Linear trends in cone counts for 13 individual trees. All trends were insignificant at 95%  
 588 confidence level (top panel). Linear trends in stand-level measures of seed/cone production. All trends were  
 589 insignificant at 95% confidence level (bottom panel).

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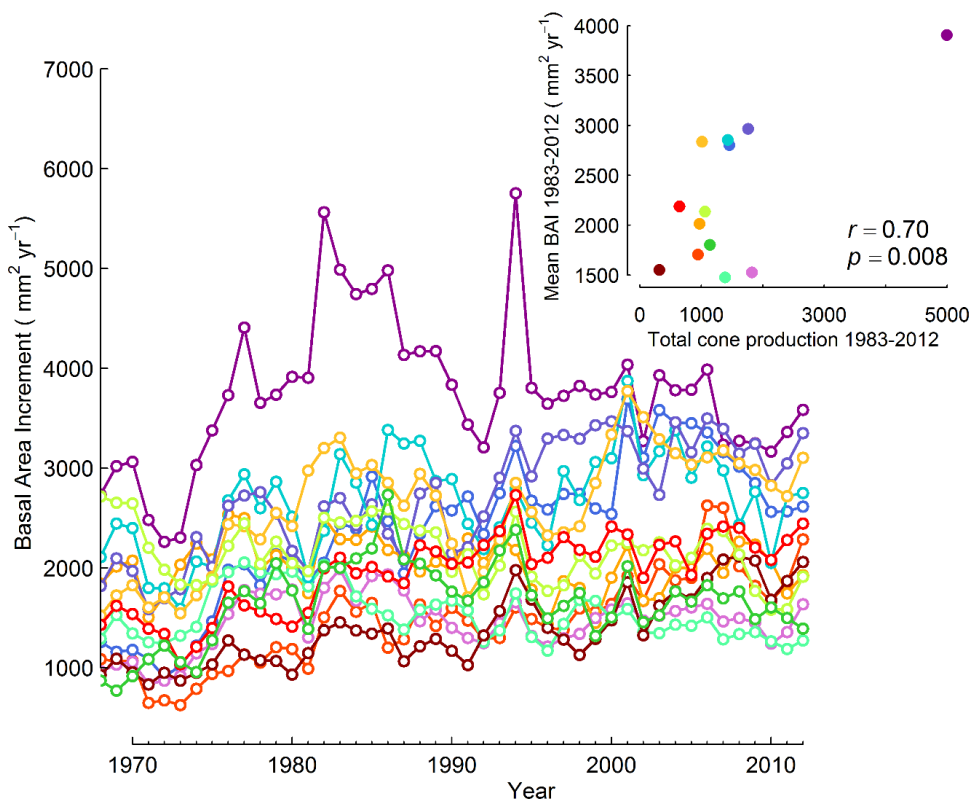
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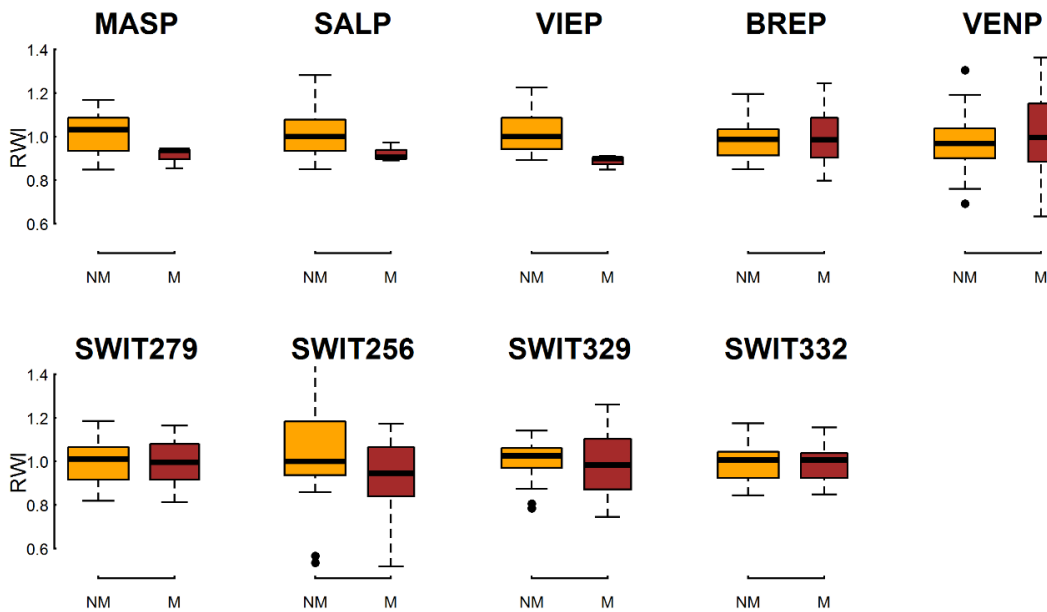
595 **Supp. Figure 5.** Relationship between tree diameter at breast height (DBH) and total cone production (1983-  
 596 2012)

597



598

599 **Supp. Figure 6.** Basal Area Increment (BAI) chronologies for each individual. Line colour represents the  
 600 individual tree ranking for total 1983-2012 cone count; heavy cone producers are purple/blue, and light  
 601 producers are orange/red. Inset plot shows the relationship between total cone production (1983-2012) and  
 602 individual tree BAI over the same time period.



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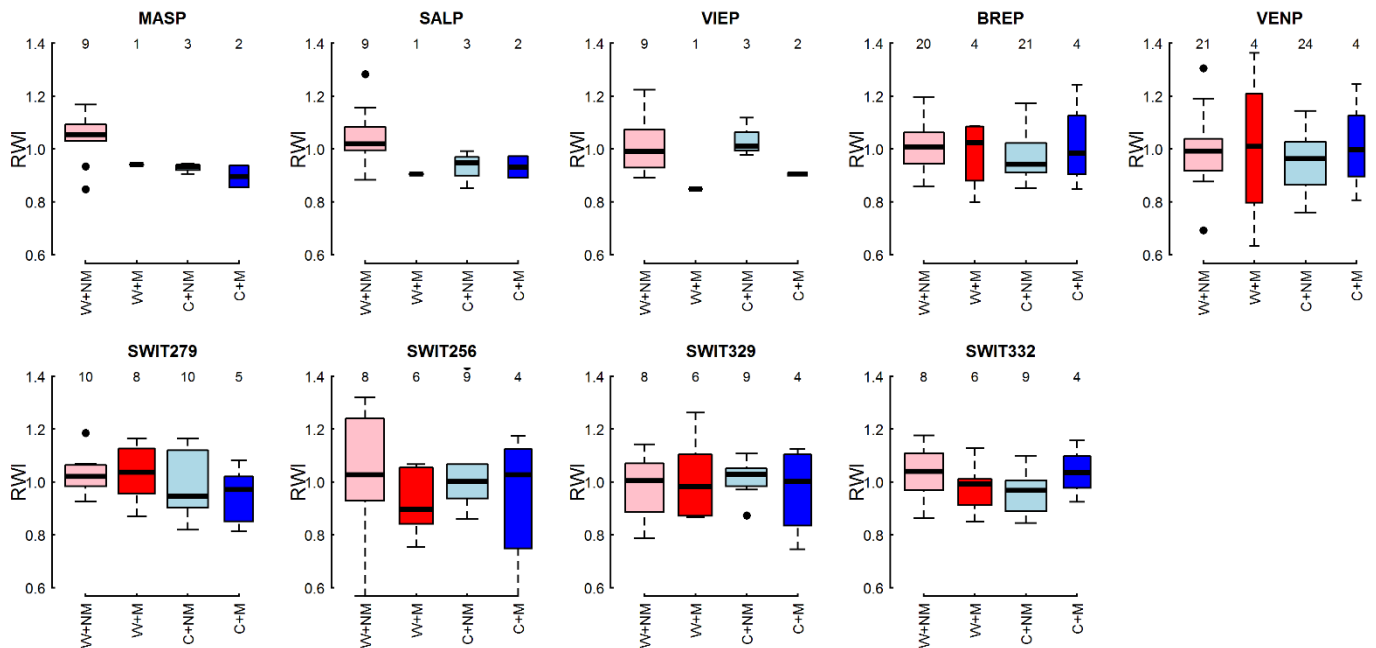
604 **Supp. Figure 7.** Boxplots of RWI according to regional masting category (mast years taken from the MASTREE

605 database for ITC, ITH and CH0). Orange = non-mast year, brown = mast year.

606 Difference in RWI between NM and M years marginally significant for VIEP ( $p=0.0484$ , Wilcoxon test)

607

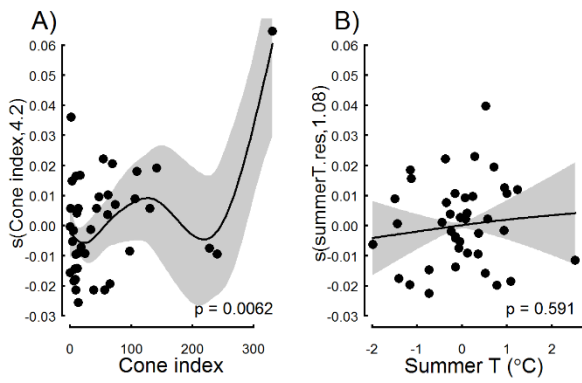
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610 **Sup. Figure 8.** Boxplots of RWI according to summer temperature and masting. Red = warm summers (W),

611 Blue = cool summer (C). Pale = non-mast (NM), bright = mast (M) year.



612

613 **Supp. Figure 9.** GAM models with 95% confidence intervals for between-tree growth CV and A) cone index,  
 614 B) summer temperature. The smoother for Cone Index is significant, showing an increase in growth CV (a  
 615 decline in synchrony) in years of high seed production at the stand level, but not significant relationship with  
 616 summer temperature (May-July).

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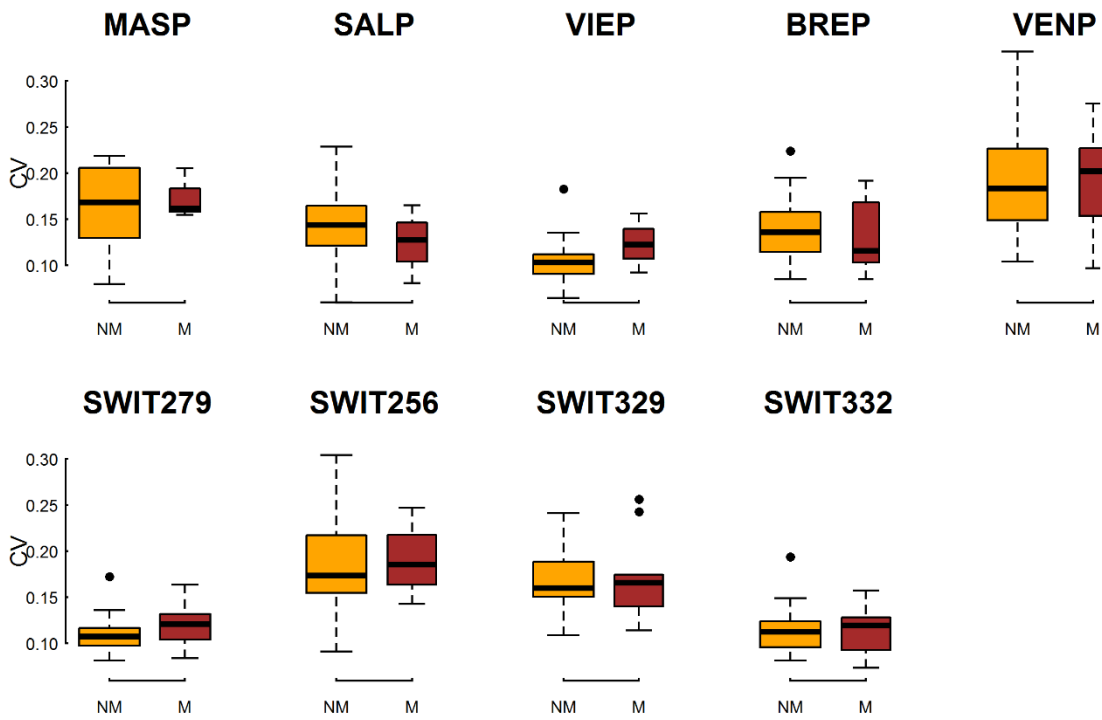
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624 **Supp. Figure 10.** Boxplots of  $CV_{RWI}$  according to masting status in Alpine spruce tree ring chronologies. No

625 differences were statistically significant (Wilcoxon tests). Orange = non-mast year, brown = mast year

626

627

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