

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

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37

38 **Highlights**

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

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

42 warming

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

45 temperature)

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

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52 **Abstract**

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

58

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

64

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

69

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

76

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

83 1. Introduction

84

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

98

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

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

119

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

134

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

143

144 We test the following hypotheses:

145

146 1. Seed production is synchronous at the population level, but cone production is dominated
147 by “super-producers”

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149 2. Years of high seed production are associated with reduced growth. The trade-off is stronger
150 under unfavourable climatic conditions, in this case cool summers

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152 3. Growth-reproduction trade-offs are stronger in “super-producers”, resulting in reduced
153 growth synchronisation in mast years, and growth divergence between “super-producers”
154 and other trees

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157 2. Methods

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159 2.1 Data collection

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

169

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

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

184

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

199

$$200 \quad \text{BAI}_t = \pi(r_t^2 - r_{t-1}^2), \text{ where } r \text{ is the radius of the tree in year } t.$$

201

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

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208 **2.2 Individual and population-scale analysis**

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

220

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

233

234 2.3 Regional datasets and analysis

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

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255 3. Results

256

257 3.1 Seed production: variability between years and individuals

258 Cone production was highly variable at Paneveggio, both between individuals and between years.

259 Individual tree coefficient of variation (CV_i) for cone counts across the period 1983-2012 varied

260 between 1.11 and 1.97 (mean = 1.39), and the CV of the mean population cone count chronology

261 (population-level CV, CV_p) was 1.19 (1983-2012). The CV_p for seed trap data 1971-2012 was 1.28.

262 Cone production and seed counts had significant negative autocorrelation at lag -1 year (Supp.

263 Figure 2). The extended 1971-2012 cone index, developed using a combination of seed trap data and

264 mean cone counts, indicated the presence of large mast years in 1976, 1981 and 1995 (cone index

265 >2 standard deviations from the mean), with additional mast years (>1 SD) in 1985 and 1988. The

266 overall distribution of seed production during the period 1971-2012 was a continuous reserve J-

267 shaped distribution (Figure 1D and Supp. Figure 3). A Hartigans' dip-test indicated no evidence of

268 multimodality ($p \gg 0.05$ for seed count, cone count and combined cone index). In 1997 and 2008 no

269 cones were counted on any of the 13 individuals, but in every other year cones were observed on at

270 least one individual. The seed-trap datasets recorded some seed fall in every year – i.e. there were

271 no years with zero recorded spruce seed production. The full 1971-2012 cone index chronology

272 showed no long-term linear trend (regression of seed production versus year, $p > 0.05$), and this was

273 also the case individually for the seed-trap dataset (1971-1994) and the mean cone-count dataset

274 (1983-2012) (Supp. Figure 4). For the individual tree cone-count series (1983-2012), linear trends

275 through time were also insignificant for all trees (Supp. Figure 4).

276

277 Cone production varied strongly between the 13 individual trees, and most cones were produced by

278 a small proportion of individuals (Figure 1). The highest producing individual (ID_01) produced 26.3%

279 of all produced cones (1983-2012), x2.5 the next highest producer. The lowest producer was

280 responsible for only 1.7% of total cones. Bumper cone crops associated with individual trees were

281 generally quite rare (Figure 1A). Most tree produced between one and four such bumper crops over
282 the 29 years of observation, while two individuals failed to produce a single bumper crops. In
283 contrast, one individual (ID_01) produced 13 individual bumper crops, equivalent to almost one
284 every two years on average. Total cone production (1983-2012) was correlated with tree diameter
285 ($r= 0.539$, $p=0.057$, Supp. Figure 5), and there was a significant positive correlation with Basal Area
286 Increment (BAI) 1983-2012 (Supp. Figure 6). However, with only thirteen trees these relationships
287 were difficult to quantify, and both relationships were dependent on the inclusion of the highest
288 producing individual (ID_01). Correlations were insignificant between total cone production (1983-
289 2012) and tree age (estimated by counting the total number of measured tree rings).

290

291 Heavy cone producers remained heavy producers over at least three decades (Figure 1). For
292 example, excluding the two years when no individuals produced any cones, the highest producing
293 tree (ID_01) was the top-ranked producer 19 times ($19/28 = 67.9\%$, highest producer in 2/3 of
294 individual years), and the five individuals with the highest mean rank took 67% of the available
295 annual top five ranking positions over 28 years. With 13 individual trees, an individual could expect
296 to be in the top five 38% of all years if ranking was random. In contrast, the lowest ranking tree
297 (ID_10) was in the top five on only three occasions, and the five lowest ranking individuals took only
298 25% of the available top five positions.

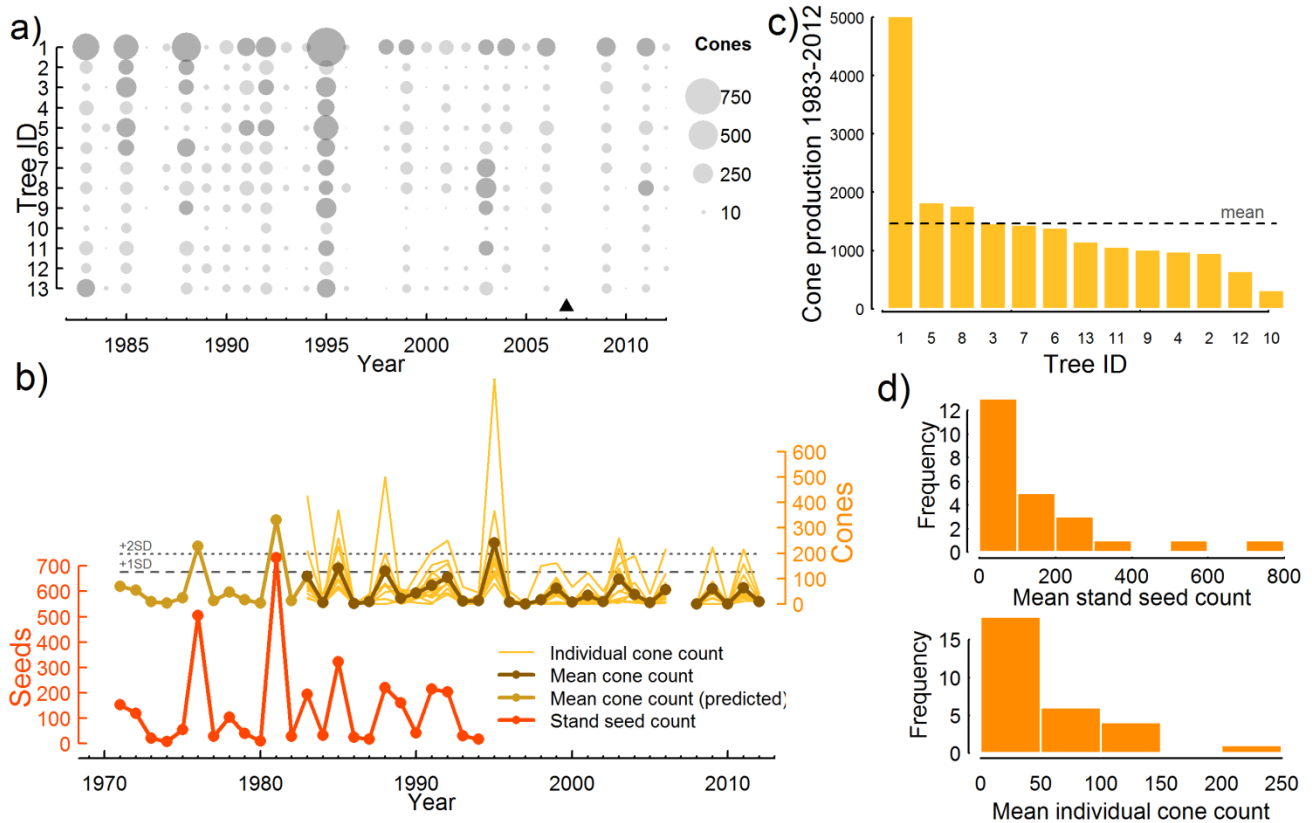
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300 While highly variable between years and between individuals, cone production was synchronised
301 between trees (Figure 1). Mean inter-tree correlation was 0.72 (min=0.33, max=0.91, median =
302 0.73). Cone and seed production at Paneveggio was also strongly synchronised with other Alpine
303 masting chronologies for spruce. For example, high cone or seed counts were reported from spruce
304 in 1995 in many of the records contained in the MASTREE database (Ascoli et al. 2017b). Cone index
305 was positively correlated with neighbouring regional masting chronologies developed for cone and
306 seed counts for CH0 (Switzerland) ($\rho= 0.71$, $p<0.001$, $n=30$), ITC (NW Italy) ($\rho=0.44$, $p=0.129$,
307 $n=12$) and S10 (Slovenia) ($\rho=0.13$, $p=0.049$, $n=30$).

308 **Table 1.** Site and chronologies statistics for all sites. All statistics are reported for residual prewhitened chronology. EPS = Expressed Population Signal, rbar = inter-series
 309 correlation, SNR = signal-to-noise ratio, AC₁ = first order autocorrelation, MS = mean sensitivity

Site	Lat	Lon	Elev	Period*	Length*	N° trees	EPS	rbar	SNR	Mean (RWI)	SD (RWI)	AC ₁ (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

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



311
 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).

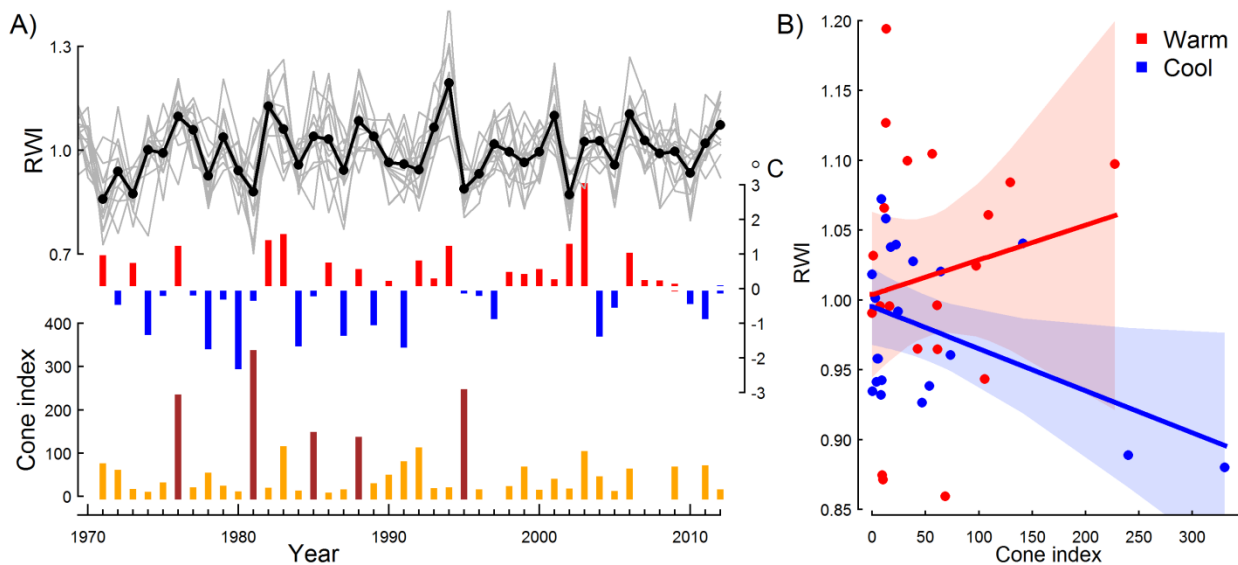
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323 **3.2 Stand-scale growth-reproduction trade-offs**

324 The relationship between stand-level ring width index (RWI) (mean of the 13 trees) and the combined stand
 325 cone index was weak and insignificant ($r = -0.128$, $p = 0.424$). This was consistent when analysed using the
 326 seed-count data only (1971-1994, $r = -0.127$, $p = 0.555$), and the cone count data only (1982-2012, $r = -0.081$,
 327 $p = 0.676$). Relationships were also insignificant when tested using GAMs (i.e. allowing for non-linear

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

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341 **Figure 2.** A) Time series with individual and mean stand RWI chronologies, May-July temperature anomalies and cone
 342 index. For temperature, red and blue bars indicate positive and negative temperature anomalies respectively. Mast
 343 years (cone index greater than one standard deviation from the mean) are plotted in dark brown. Note that the
 344 temperature anomalies are for detrended summer temperature (i.e. the linear trend in temperature is removed). B)
 345 The linear regressions for RWI ~ cone index for cold (blue) and warm (red) summers (1971-2012), including 95%
 346 confidence intervals.

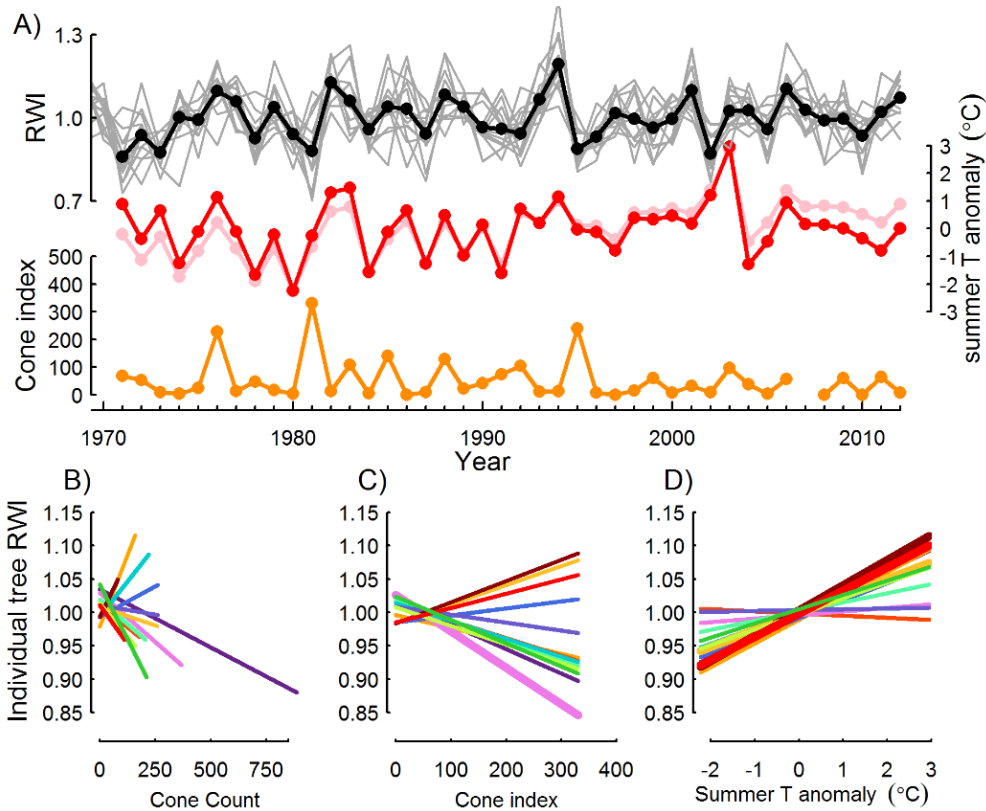
347 To test the generality of these results, growth responses to regional mast years (MASTREE database) were
348 tested for a network of Alpine spruce chronologies. Some sites showed lower growth in regional mast years,
349 particularly those in northwest Italy (ITC: MASP, SALP and VIEP), and also the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

354

355 **3.3 Individualistic growth responses to climate and reproduction**

356 The climate response of individuals showed some variation, but warmer summers were associated with high
357 growth (Figure 3D). However, the growth response of individuals to reproduction showed more variation,
358 both when tested against the corresponding individual tree cone counts (1983-2012, Figure 3B), and when
359 tested against the stand-scale cone index (1971-2012, Figure 3C). However, the relationship was significant
360 in only one individual (note that this was an individual with above-average cone production, but not ID_01,
361 the outstanding super-producer). High investment in cone production (at an individual- and stand-level) was
362 associated with lower growth in the individuals with higher cone productivity (Figure 3). Responses of
363 growth to mast years were close to zero or even positive in individuals with low cone productivity (albeit
364 non-significant). For example, in heavier cone producers, the growth reductions in the heaviest stand-scale
365 mast years were approximately equivalent in magnitude to those associated with coolest summers (Figure
366 3C and 3D). In contrast, the lightest cone producers showed positive growth responses in these years,
367 equivalent in magnitude to the growth increase associated with a warm summer (Figure 3C and 3D).

368



369

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

377

378

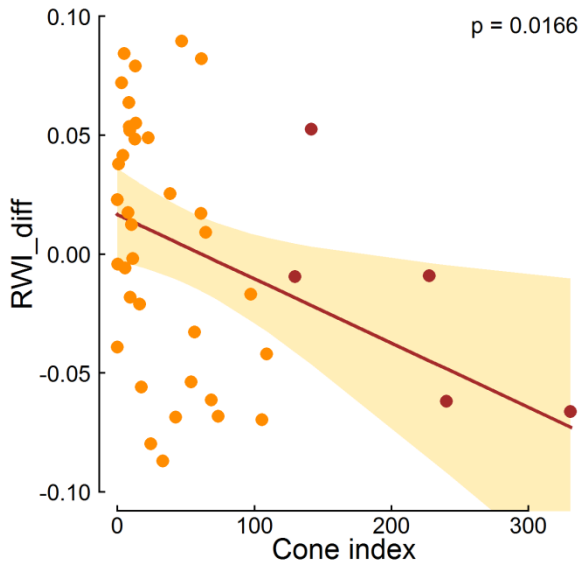
379 Overall, between-tree growth synchrony was high ($r_{bar} = 0.44$, Table 1, and see also Figure 3A), representing
 380 a strong coherence in growth between years. However there were differences in synchrony between years;
 381 in other words, in some years individuals had very similar growth while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

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

392

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

401



402

403 **Figure 4.** Relationship between RWI_{diff} and stand-level cone index (1971-2012), with a 95% confidence interval.

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

406

407

408 4. Discussion

409

410 4.1 Characteristics of cone production

411 Cone production at Paneveggio showed characteristics associated with masting. The stand-level CV_p for cone
412 production was almost identical to that reported by Selas *et al.* (2002) for Norway spruce in Norway (1.20),
413 and consistent with other reported values for spruce species and other masting species (Herrera *et al.*, 1998;
414 Koenig and Knops, 2000; Lamontagne and Boutin, 2007). In the heaviest mast years, cone index at the stand
415 scale was six times greater than the long-term mean, representing a substantial resource investment. At the
416 individual tree scale the contrast was even more extreme. In 1995 tree ID_01 produced 18 times more cones
417 that the mean cone production of all trees 1982-2012, and this individual was responsible for 26% of all the
418 cones produced over the study period (by 13 individuals). Various factors may explain such individual
419 variability in reproductive output, including tree age, size, microenvironmental conditions, resource
420 availability, and genetics (Davi *et al.*, 2016; Greene *et al.*, 2002; Seifert and Mueller-Starck, 2009; Thomas,
421 2011; Brooke *et al.*, 2019), although with individual-tree data for only 13 trees, it was not possible to identify
422 the factors controlling long-term cone productivity, or robustly test scaling with tree size. However, our data
423 hinted that high cone production was associated with larger, faster growing trees. Notably, heavy cone
424 producers retained their ranking over three decades. For example, the highest overall cone producer (ID_01)
425 was the heaviest individual producer in two thirds of all years, consistent with the definition of “super-
426 producer” suggested by Minor and Kobe (2017). Previous studies have also indicated that the relative
427 reproductive performance of individual trees can be maintained over multiple years, but have relied on
428 shorter datasets where long-term trends are difficult to identify (Healy, Lewis and Boose, 1999; Krouchi,
429 Derridj and Lefevre, 2004; Linhart and Mitton, 1985).

430

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

434 observed between-tree synchrony in cone counts was higher than that reported by LaMontagne and Boutin
435 (2007) for *Picea glauca*, and represents a highly synchronised variation in resource allocation at the stand
436 scale. Previous studies indicate that this synchronisation is also strong between Alpine spruce stands at local
437 scales (MencucciniPiusi and Sulli, 1995), and under appropriate regional climate conditions, synchronisation
438 between populations can extend over larger spatial scales (Ascoli *et al.*, 2017b). Such synchronisation of
439 cone production can have cascading effects on local communities, starting with the population dynamics of
440 seed predators (Bogdziewicz, Zwolak and Crone, 2016) and extending to pulsed regeneration patterns,
441 interaction with herbivores, and cascading trophic interactions (Ostfeld and Keesing, 2000).

442

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

460

461 **4.2 Growth-reproduction relationships: implications for understanding variation in tree growth**

462 The relationship between reproductive effort and tree growth was variable. At the stand scale, mast years
463 were not consistently associated with reduced growth, and we found similar results in a network of Alpine
464 spruce chronologies. At Paneveggio, this generally low sensitivity of growth to investment in reproduction
465 may be related to the generally favourable growing conditions. Paneveggio is a mesic site for spruce, with
466 relatively high annual increment (typically 8-10 m³ ha⁻¹ y⁻¹). Furthermore, the timing of investment in the
467 maturation of cones (including lignification) is likely timed after the main phase of radial growth in early
468 summer (Deslauriers *et al.*, 2008), which may minimise a direct trade-off for resources between radial
469 growth and reproduction. We found evidence that in climatically unfavourable years (cool summers),
470 investment in reproduction was associated with reduced growth; this can be interpreted as a variation in
471 trade-off strength with climate (Hackett-Pain, Lagueard and Thomas, 2017; Sletvold and Agren, 2015; Villellas
472 and Garcia, 2018), which can explain the generally weak relationships between growth and masting. We
473 suggest that the population-level insensitivity of growth to masting in warm summers observed at
474 Paneveggio may have resulted from increased resource assimilation during these favourable conditions,
475 reducing any trade-off between competing resource sinks. In an earlier study in the same forests,
476 Mencuccini and Piussi (1995) demonstrated that the negative relationship between growth and seed
477 production was stronger at higher elevations (lower temperatures), supporting our findings for variation
478 between years (Figure 2). Consequently, future environmental changes which favour growth may result in
479 relaxation of growth-reproduction trade-offs in high elevation and temperature limited spruce populations,
480 although this remains to be tested.

481

482 **4.3 Synchronisation of growth within populations: influence of climate and reproduction**

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

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

494

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

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

515

516 **4.4 Resource switching and implications for understanding masting**

517 At the population level, we found mixed evidence that increased investment in reproduction resulted in a
518 trade-off with growth; some mast years were associated with reduced growth, but not all. In contrast, Selas
519 et al. (2002) reported stronger effects of seed production on growth in spruce (seed production explained
520 42% of variation in ring width), and Mencuccini and Piuksi (1995) found a negative relationship between ring
521 width and seed production in spruce stands from our study area. In our study, cone index explained 22% of
522 variation in RWI in years with cool summers, but <2% in analysis including all years, Figure 2B). Other studies
523 have also reported a lack of evidence to support a trade-off between tree growth and reproduction (Zywiec
524 and Zielonka, 2013), including in spruce (Seifert and Mueller-Starck, 2009). Monks and Kelly (2006) argue
525 that evidence of resource switching is the most important evidence that masting results from selection for
526 highly variable seed production, and not simply a response to climate (e.g. resource matching) (see also Kelly
527 and Sork, 2002). Our results imply that resource switching was only required during years of unfavourable
528 resource assimilation, but during more favourable conditions growth rate could be maintained even with the
529 additional demands of developing cones. Furthermore, analysis at the individual level demonstrated that
530 cone super-producers did show a reduction in growth in mast years. Consequently, population-level growth
531 chronologies may mask evidence of switching (Patterson and Knapp, 2018), and where possible, evidence of
532 resource-switching should be sought at the individual level (Monks and Kelly, 2006).

533

534 **4.5 Implications for reconstructing mast years**

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

538 Where such long observational records do not exist, reconstructions of mast years using tree ring
539 chronologies may facilitate improved understanding of the response of masting to long-term environmental
540 change, and cascading impacts of these changes on forest ecosystems more generally (Ostfeld and Keesing,
541 2000). For example, Drobyshev (2014) used a multi-century reconstruction of beech mast events in Sweden
542 to demonstrate that decadal changes in mast frequency were not linked to changes in nitrogen deposition
543 (as proposed by Overgaard et al. 2007). However, our results indicate that not all mast years are associated
544 with a reduction in growth (Figure 2), with significant growth reductions limited to years with unfavourable
545 climate (see Hacket-Pain *et al.* 2017 for similar findings for *Fagus sylvatica*). In this case, negative pointer
546 years in ring width series may not be enough to identify all mast years, even if combined with historical
547 climate data for the known climate cues of mast years (the method of Drobyshev *et al.* 2014). A more
548 complete integration of climate data and tree rings may be required, accounting for factors that influence
549 the sensitivity of ring width to masting events, but mast years that coincided with climatically favourable
550 years may ultimately be harder to detect. However, other tree ring parameters may also provide information
551 on masting. For example, Han *et al.* (2016) reported small differences in $\delta^{13}\text{C}$ in tree rings associated with
552 mast years in *Fagus crenata*, and Rodríguez-Ramírez *et al.* (2018) showed potential for mast year
553 reconstruction based on wood anatomical traits. Additionally, our results indicate that the individualist
554 responses of trees to masting may also prove useful in identifying mast years using individual tree ring data.
555 For example, increased between-tree growth variability may be useful for identifying mast years, and
556 requires no additional information on the sampled trees. This may be a useful source of information to
557 identify mast years (particularly heavy mast years) (Figure 4), and contribute to a “toolbox” of useful
558 indicators for tree-ring based reconstruction of mast years.

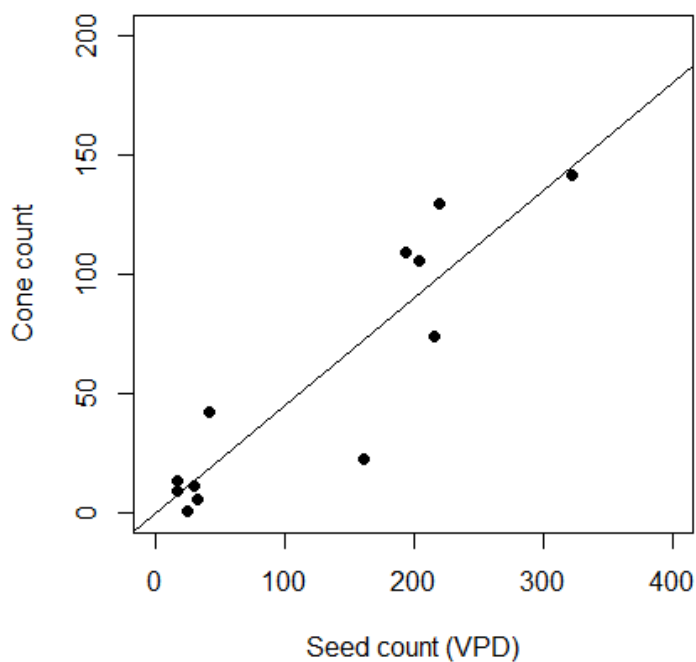
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565 grateful those who contributed ITRDB datasets which were utilised in this study. We thank two anonymous
566 reviewers whose comments substantially improved the manuscript.

567 **Supplementary Figures**

568

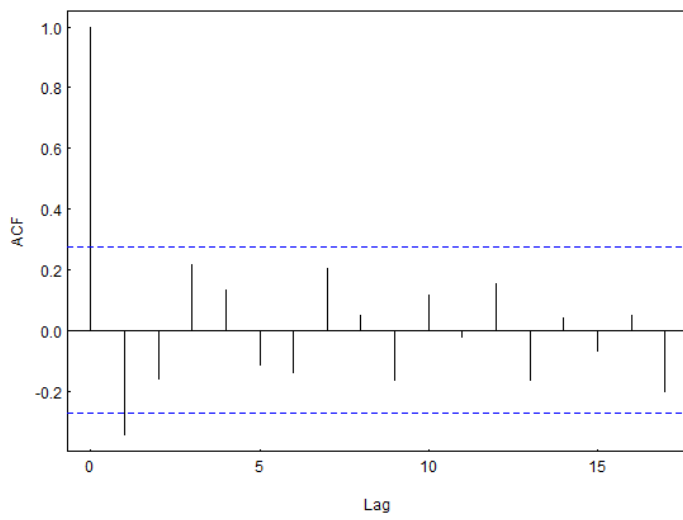


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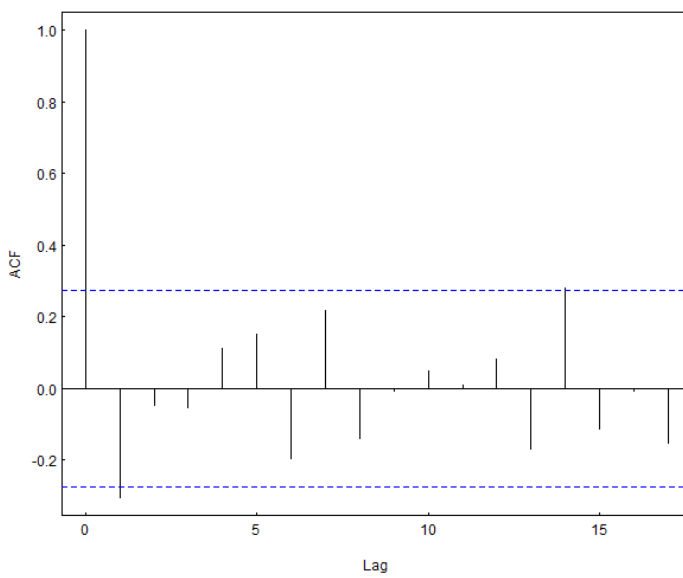
570 **Supp. Figure 1.** Relationship between mean stand cone counts and mean seed count for Paneveggio (VPD,
571 sum of viable, predated, damaged seeds), 1983-1994. $R^2 = 0.82$, $p < 0.001$.

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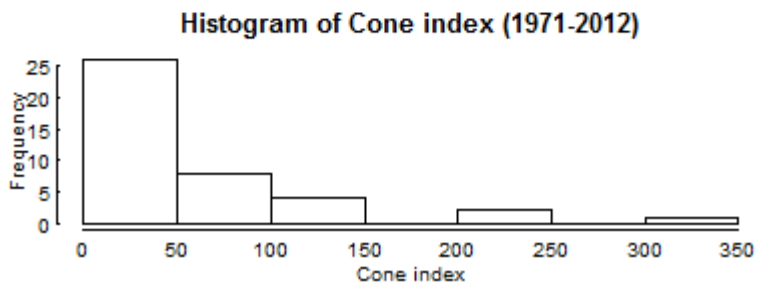
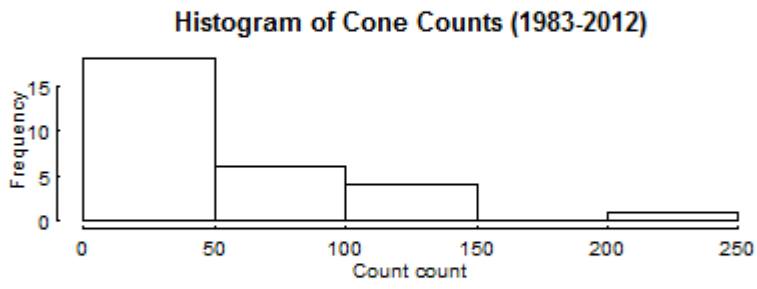
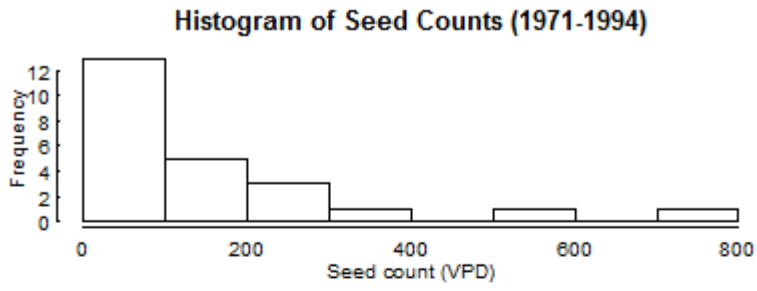
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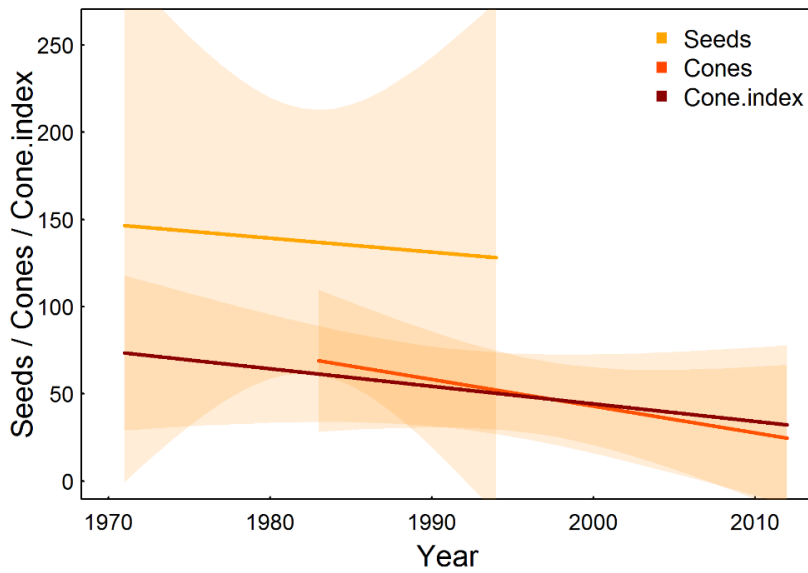
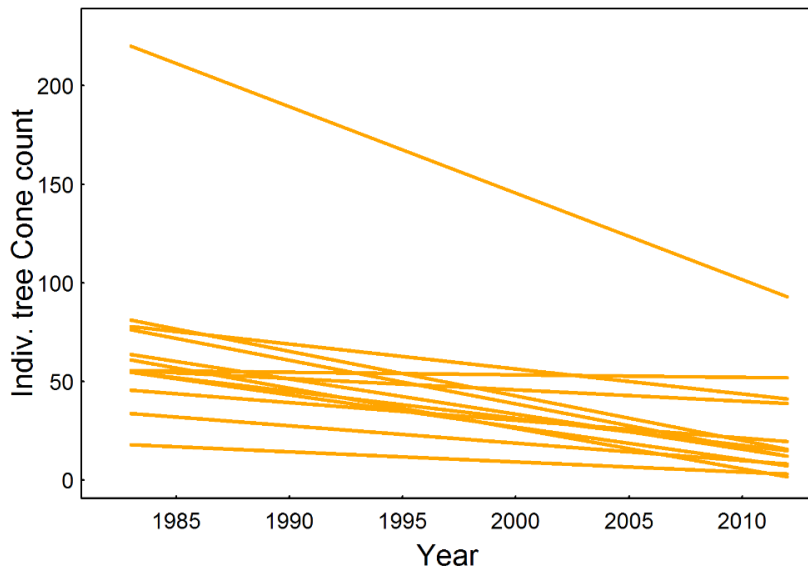
575

576 **Supp. Figure 2.** Autocorrelation functions for cone production (1982-2012) (top panel) and cone index
577 (1971-2012) (bottom panel)

578



579
 580 **Supp. Figure 3.** Distributions of measures of seed and cone production
 581
 582



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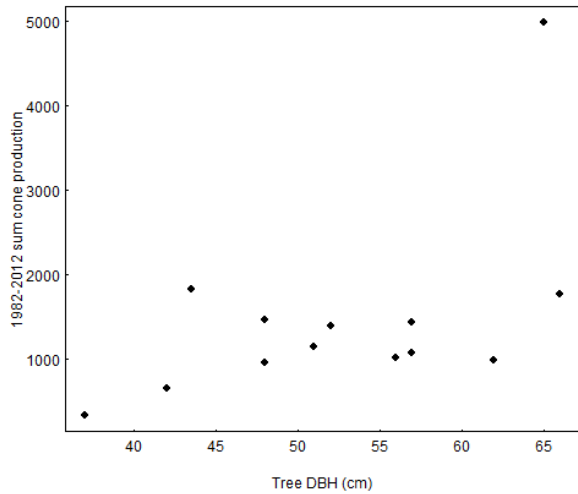
584 **Supp. Figure 4.** Linear trends in cone counts for 13 individual trees. All trends were insignificant at 95%
 585 confidence level (top panel). Linear trends in stand-level measures of seed/cone production. All trends were
 586 insignificant at 95% confidence level (bottom panel).

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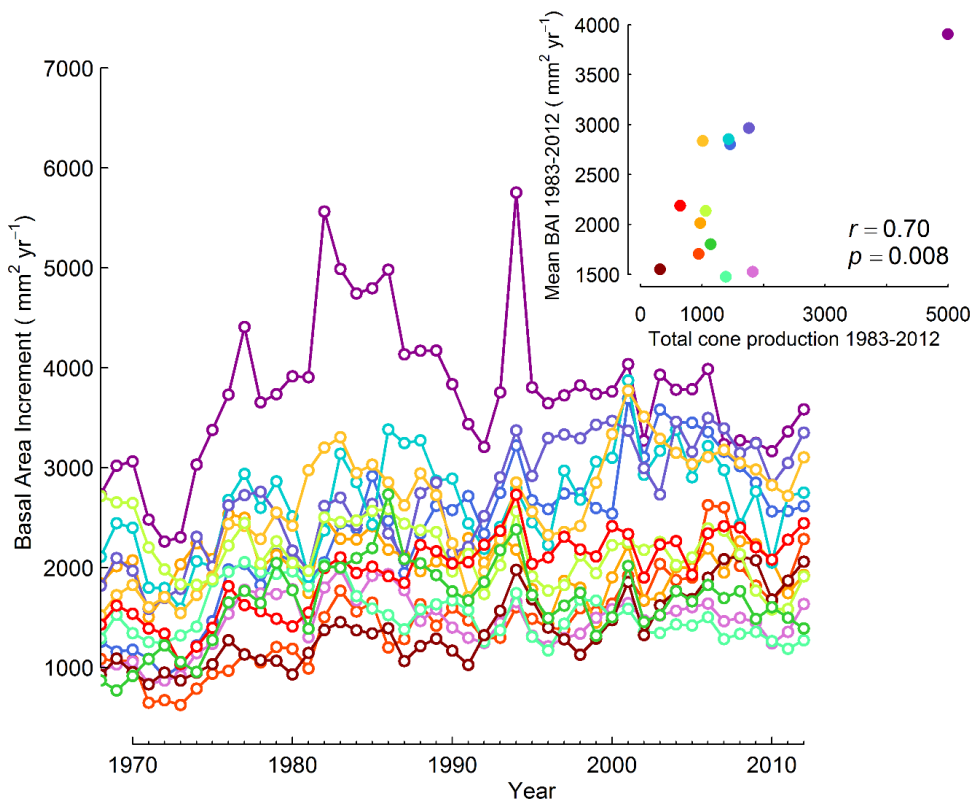
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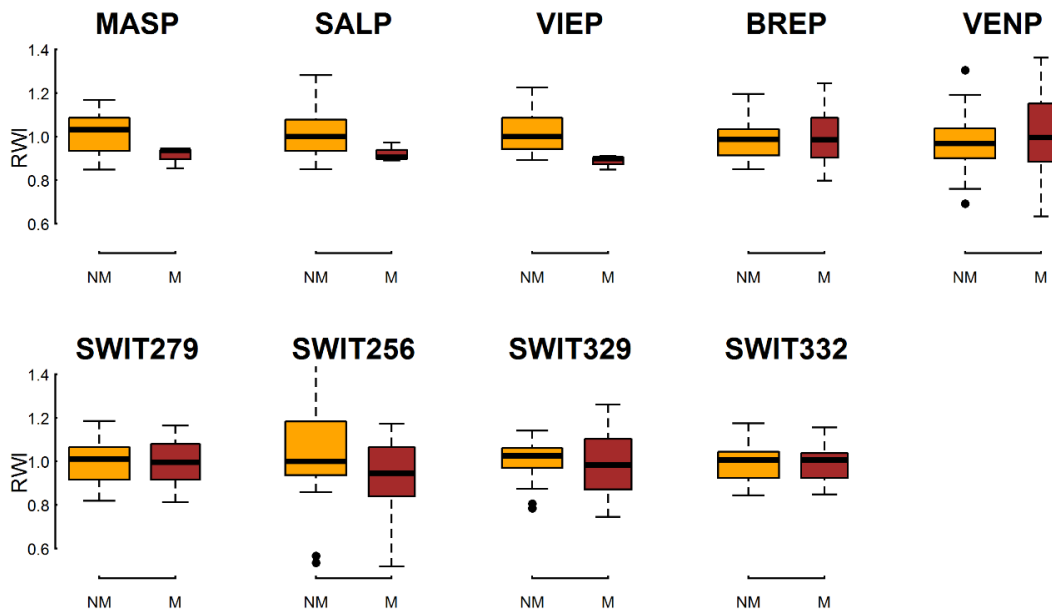
592 **Supp. Figure 5.** Relationship between tree diameter at breast height (DBH) and total cone production (1983-
 593 2012)

594



595

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



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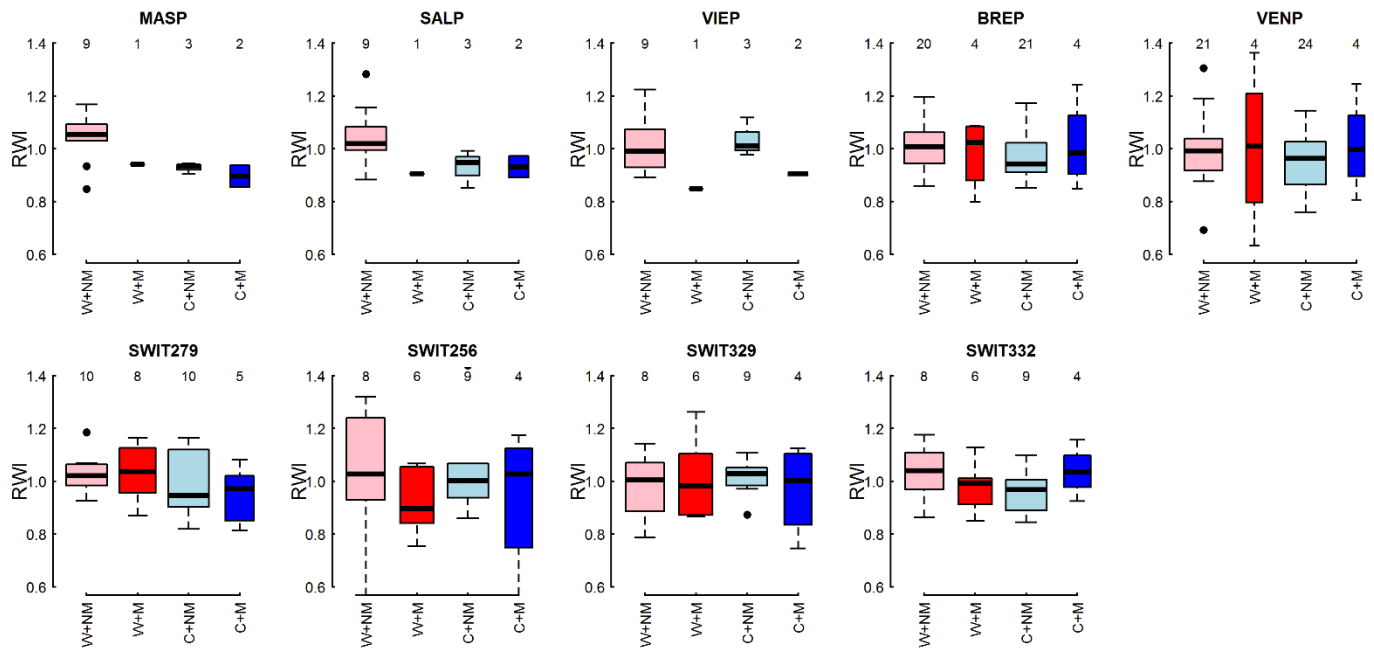
601 **Supp. Figure 7.** Boxplots of RWI according to regional masting category (mast years taken from the MASTREE

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

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

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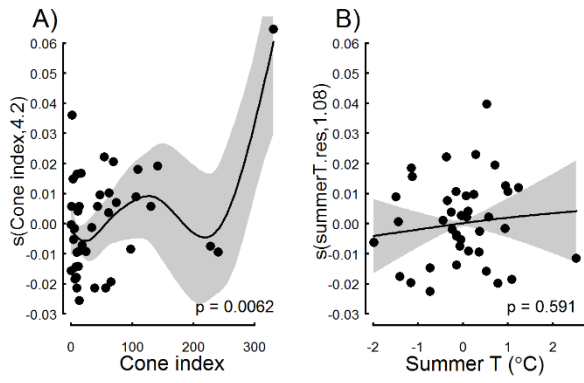
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607 **Sup. Figure 8.** Boxplots of RWI according to summer temperature and masting. Red = warm summers (W),

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



609

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

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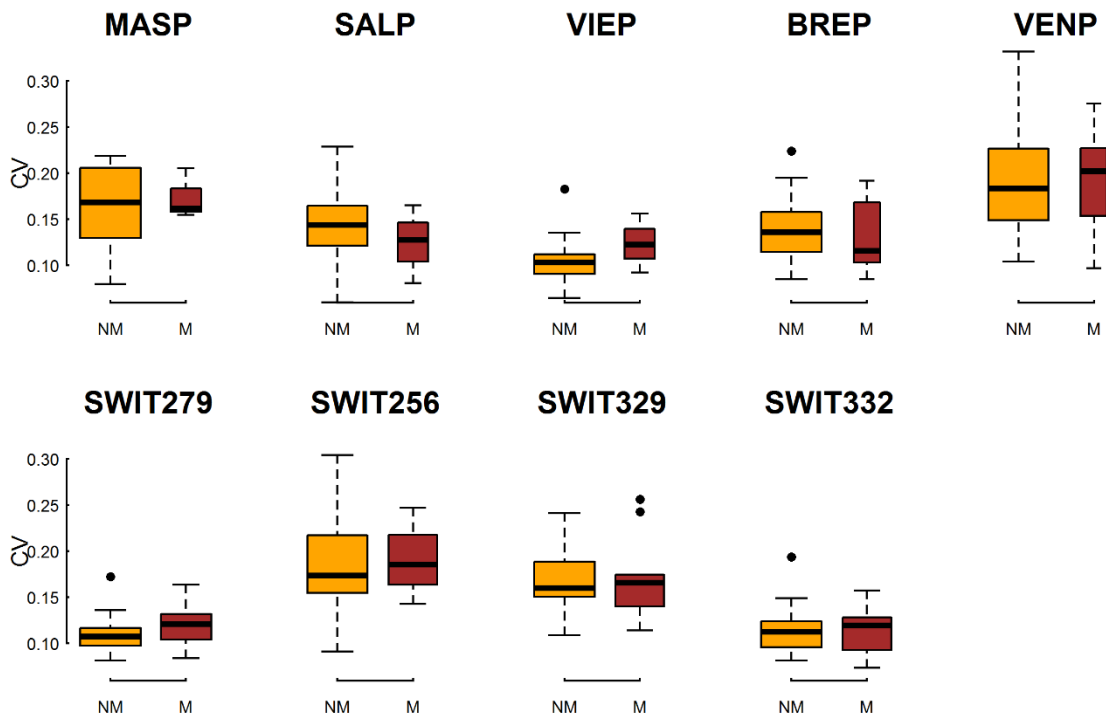
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621 **Supp. Figure 10.** Boxplots of CV_{RWI} according to masting status in Alpine spruce tree ring chronologies. No

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

623

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