

1 **Growth of male and female *Araucaria araucana* trees respond differently to**
2 **regional mast events, creating sex-specific patterns in their tree-ring chronologies**

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13
14 **Abstract**

15 *Araucaria araucana* is a dioecious evergreen conifer endemic to temperate forests of
16 south Argentina and Chile. It is a long-lived species (maximum age >1000 years), and it
17 presents a high potential for tree-ring based climate reconstructions. However, the
18 species' dioecious habit can result in distinct sex-specific growth patterns, which
19 introduce novel challenges in the interpretation of tree-ring chronology variations. We
20 used a network of 10 tree-ring chronologies from northwest Patagonia (Argentina) to
21 analyze sex-specific growth patterns in *A. araucana* and, for the first time, demonstrate
22 that they result from the contrasting responses of ring width index of male (RWI_{male})
23 and female (RWI_{female}) trees to regional mast events (years with high seed production).
24 During the year of seed maturation and seed dispersal, the growth of females is strongly
25 and significantly reduced, while a growth response of similar magnitude was found in

26 male trees in the previous year, corresponding to the year of pollination. We interpret
27 these growth responses as representing contrasting allocation shifts between growth and
28 reproduction in males and females. The sex-specific growth responses associated with
29 mast events resulted in a particularly strong and distinct signal in a $RWI_{\text{male}}-RWI_{\text{female}}$
30 chronology. Male and female tree-ring chronologies share a strong common signal, and
31 respond similarly (but not exactly) to broad-scale climatic conditions in the growing
32 season. Our results indicate that sex-specific tree-ring chronologies can be used to
33 isolate mast events in *A. araucana* chronologies, providing an opportunity to develop
34 unique multi-century reconstructions of large mast events, and improve dendroclimatic
35 calibration for this species.

36

37 **Keywords:** carbon allocation; dendroecology; trade-off; dendroclimatology; Patagonia.

38

39 **1. Introduction**

40 *Araucaria araucana* (Molina) K. Koch is a long-lived (maximum age >1000 years)
41 dioecious conifer endemic from temperate forests of south Argentina and Chile (Roig
42 and Villalba, 2008; Aguilera-Betti et al., 2017). Its importance for dendroecological and
43 climatic studies is well documented (Mundo et al., 2012; Muñoz et al., 2014; Hadad et
44 al., 2015, 2020; Hadad and Roig, 2016; Rozas et al., 2019), including for climate
45 variability reconstructions (e.g. Villalba et al., 2012; Morales et al., 2020). Furthermore,
46 large-scale atmospheric phenomenon have been detected in *A. araucana* tree rings,
47 evidenced by the link between its growth responses and the sea surface temperature
48 (SST) anomalies of the Niño 3.4 region in the tropical Pacific Ocean, and with the
49 atmospheric pressure differences between the middle and high latitudes (~40°- 65°S) of
50 the Southern Hemisphere, represented by the Southern Annular Mode (SAM) index

51 (Mundo et al., 2012; Villalba et al., 2012; Hadad et al., 2015; Hadad and Roig, 2016;
52 Morales et al., 2020). Analysis of stable carbon isotopes of *A. araucana* tree rings has
53 also provided information on the long-term physiological reaction of this endangered
54 species (International Union for Conservation of Nature, <http://www.iucnredlist.org/>) to
55 recent climate changes, as evidenced by the increase in intrinsic water-use efficiency
56 (iWUE) during recent decades (Arco Molina et al., 2019).

57 Dendroclimatic reconstructions are dependent on a strong and stable relationship
58 between growth and climate (Fritts, 1976). However, the physiological mechanisms
59 linking climate and growth are complex, and include the effects of resource assimilation
60 and allocation, among others, which vary at interannual timescales (Thomas, 2011).
61 This can reflect adaptive responses to stress (Lauder et al., 2019), or result from a
62 potential trade-off or switching of resources in years of high investment in reproduction
63 (Selas et al., 2002; Monks and Kelly, 2006; Hackett-Pain et al., 2018). The effects of
64 dynamic resource allocation is particularly important in masting species, which are
65 characterized by highly variable allocation to reproduction (Kelly, 1994). Years of high
66 investment in reproduction (mast events) represent a major sink of carbon and other
67 resources. For example, Müller-Haubold et al. (2013) showed that in central European
68 beech forests, carbon allocation to reproduction varied between 2-50% of total
69 aboveground Net Primary Production between non-mast and mast events. Negative
70 relationships between growth and reproduction have been reported in many species
71 (Norton and Kelly, 1988; Selas et al., 2002; Hackett-Pain et al., 2018; Lauder et al.,
72 2019), although the nature of this apparent trade-off has been questioned in those cases
73 where carbon resources do not appear to limit tree growth (Mund et al., 2020).
74 Nevertheless, variable allocation of resources to reproduction explains an important

75 component of year-to-year variability in tree growth (Monks and Kelly, 2006; Müller-
76 Haubold et al., 2013, Hackett-Pain et al., 2018).

77 *Araucaria araucana* provides a valuable opportunity to improve understanding of
78 the relationship between reproduction and growth by taking advantage of within-species
79 sex-specific allocation to reproduction (Obeso, 2002). Previous studies in other
80 dioecious species (e.g. *Juniperus communis* subsp. *alpina* (Suter) Celak; *Ilex aquifolium*
81 L.) have indicated that investment in reproduction is higher in female trees, leading to a
82 long-term reduction in female growth relative to males (Obeso, 2002; Ortiz et al., 2002).
83 However, the potential effect of reproduction on interannual growth variation remains
84 largely unexplored. *A. araucana* presents a further advantage as its reproductive cycle
85 crosses multiple years, with pollination and seed maturation occurring in different years
86 (Fig. 1). Consequently, we hypothesize that the costs of reproduction for male and
87 female *A. araucana* trees are concentrated within different years. Costs associated with
88 reproduction in females occur mainly in the year of cone maturation (t), while the costs
89 for males occur mainly in the year of pollination ($t-1$) (Fig. 1). We further hypothesize
90 that these sex-specific costs of reproduction, coupled with a growth-reproduction trade-
91 off (Rozas et al., 2019) and a highly variable reproductive effort between years
92 (Sanguinetti and Kitzberger, 2008; Sanguinetti, 2014), may explain previously reported
93 differences in growth variability between sexes in *Araucaria araucana* (Hadad and
94 Roig, 2016; Rozas et al., 2019). Further, this work aims at testing the relationship
95 between tree-ring chronologies and sea surface temperature to evaluate the climate
96 sensitivity of male and female tree growth.

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100 **2. Materials and Methods**

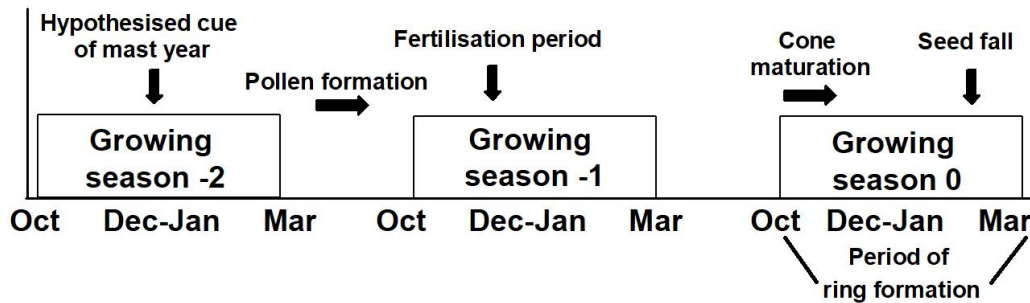
101 **2.1 Timeline of seed production in *A. araucana***

102 *A. araucana* is a masting species, and previous studies have indicated that
103 moderate to large cone and seed crops (“mast events”) occur every 2-5 years (Montaldo,
104 1974; Donoso et al., 2006; Sanguinetti and Kitzberger, 2008). The largest mast events
105 are associated with cone production >2 standard deviations from the long-term mean,
106 and occur synchronously across the restricted geographic distribution of the species
107 (Sanguinetti and Kitzberger, 2008). As the *A. araucana* pollen grain is one of the largest
108 pollen grains (80-100 µm in diameter) among all conifers (Huesser et al., 1988; Owens
109 et al., 1998), synchronization of large-scale flowering may help to alleviate pollen
110 limitation (Pearse et al., 2016).

111 Preliminary observations of *A. araucana* reproductive biology indicate that the
112 primordia of the pollen cones (male) is already formed during the austral fall, while the
113 archesporium is differentiated in winter months, remaining in this stage until mid-
114 October (Del Fueyo et al., 2008). Towards early summer, the pollen grains are mature,
115 and pollination takes place (Del Fueyo et al., 2008; Donoso et al., 2009). Therefore, the
116 microsporangiate strobili or pollen cones (males) can complete their cycle in almost
117 eight months while the megasporangiate strobili or seed cones (females) take more than
118 a year to complete their maturity (Del Fueyo, pers. com.), with seed fall occurring in
119 late summer or early autumn (February-March) of the following year (Fig. 1).

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123 Figure 1: Hypothesised cue of mast years and timeline of *Araucaria araucana* male and
 124 female cone maturation.

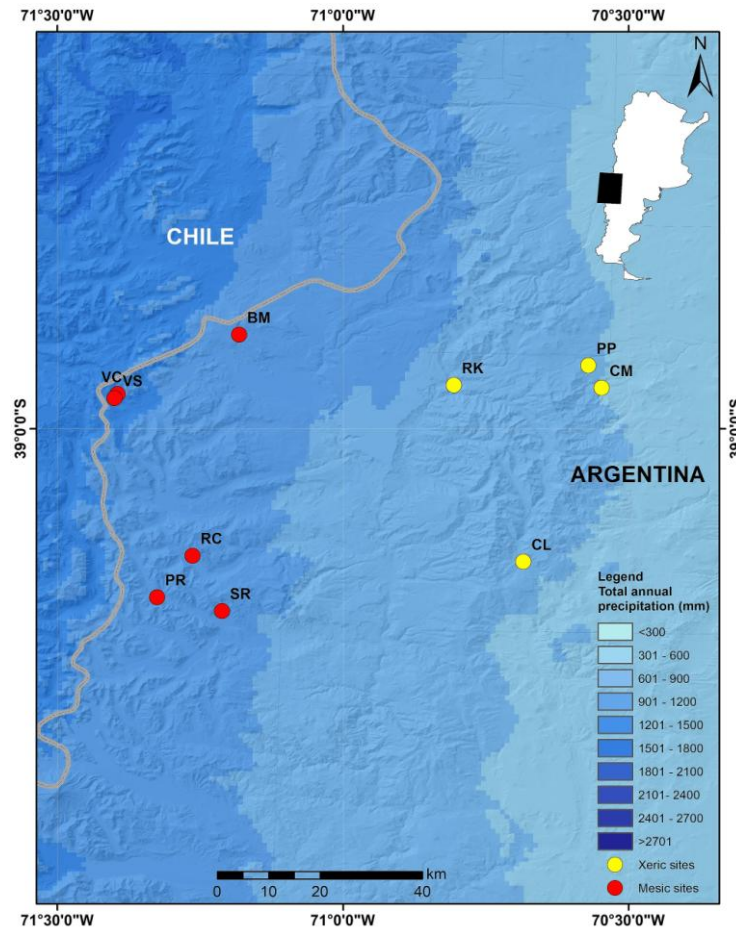
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126 2.2. Study sites

127 Ten stands of *A. araucana* trees (four xeric and six mesic forests) located in
 128 northwestern Patagonia, Argentina, were studied (Fig. 2, Table 1). The region is
 129 characterized by a strong precipitation gradient from west to east, with higher annual
 130 precipitation at the Andes cordillera and lower towards the steppe. The xeric sites are
 131 distributed in an area with a mean annual temperature of 11.1 °C (reference period
 132 1912-2005) and a total annual precipitation around 573 mm (period 1929-2001). Mean
 133 climate at the mesic sites is cooler and wetter, with a mean annual temperature of 8.7 °C
 134 (period 1912-2008) and a total annual precipitation of around 1081 mm (period 1931-
 135 2010) (Hadad et al., 2020).

136 In the field, two or three increment wood cores per tree were taken at breast
 137 height (1.3 m above ground level) with an increment borer of 5 mm diameter for both
 138 female and male *A. araucana* trees. All cores were taken from single-stemmed living
 139 trees and from trunk portions without cracks, branches, reaction wood, or other growth
 140 anomalies that could hinder the tree ring identification and measurement. The sex of the
 141 trees was established by observing with binoculars the presence and type (female/male)

142 of the strobiles (Fig. 3AB). We did not sample trees that could not be unambiguously
143 sexed. A set of 66 (74) female (male) trees were sampled in the xeric forests, while 47
144 (47) female (male) trees were sampled from the mesic sites (Table 1). The sexual ratio
145 of these sites was close to 1:1 (Hadad et al., 2020).
146



147
148 Figure 2: Xeric (yellow dots) and mesic (red dots) study sites from northwestern
149 Patagonia, Argentina (site codes are shown in Table 1). The relative position of the
150 study area is marked as a black rectangle on the inset outline of Argentina. The
151 precipitation gradient from 1970 to 2000 (Fick and Hijmans, 2017) is also shown..

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155 Table 1: Characteristics of the sampled sites and chronology statistics.

Forest type	Site (Code)	Latitude S	Longitude W	Altitude	Sex/N° of trees	Chronology span	Rbar	Start (EPS >0.85)
Xeric	Primeros Pinos (PP)	38° 52'	70° 34'	1628	Female/18	1528-2008	0.309	1705
					Male/16	1277-2008	0.260	1730
	Río Kilca (RK)	38° 53' "	70° 50'	1442	Female/15	1190-2013	0.337	1875
					Male/7	1490-2013	0.270	1875
	Carrerri Malal (CM)	38° 55'	70° 32'	1510	Female/12	1592-2010	0.292	1875
Male/20					1421-2010	0.271	1805	
Catan Lil (CL)	39° 14'	70° 40'	1290	Female/10	1600-2011	0.307	1860	
				Male/25	1631-2011	0.380	1750	
Mesic	Batea Mahuida (BM)	38° 50'	71° 10'	1598	Female/10	1553-2012	0.351	1830
					Male/7	1628-2012	0.350	1780
	Valle El Salvo (VS)	38° 56'	71° 25'	1294	Female/8	1277-2012	0.359	1630
					Male/6	1271-2012	0.335	1705
	Verde Chico (VC)	38° 56'	71° 23'	1267	Female/11	1761-2013	0.346	1895
					Male/10	1716-2013	0.351	1870
	Rucachoroi (RC)	39° 13'	71° 15'	1214	Female/7	1648-2011	0.412	1725
					Male/10	1683-2011	0.401	1865
Pinalada Redonda (PR)	39° 18'	71° 17'	1100	Female/5	1720-2013	0.303	1855	
				Male/7	1626-2013	0.372	1750	
Senda a Rucachoroi (SR)	39° 19'	71° 12'	1507	Female/6	1305-2013	0.401	1885	
				Male/7	1480-2013	0.446	1765	

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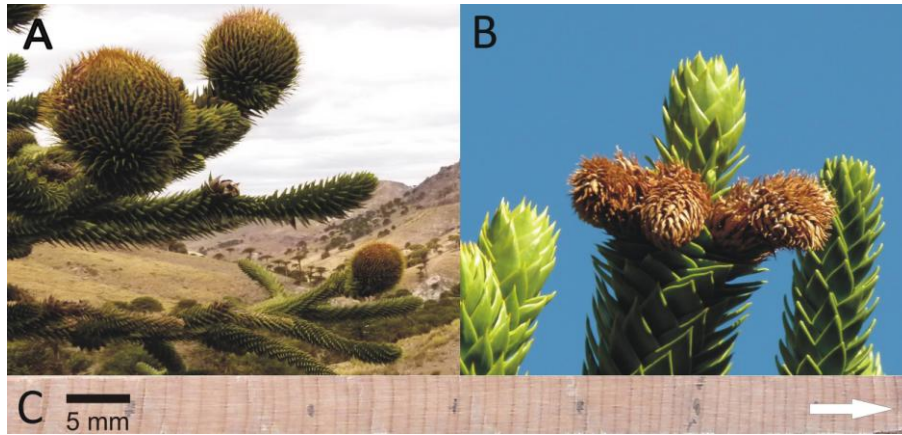
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158 2.2. Laboratory work and chronology development

159 In the laboratory, the core samples were mounted on wooden supports and
 160 polished with progressively finer sandpaper to highlight the tree ring boundary structure
 161 (Stokes and Smiley, 1968, Fig. 3C). Ring widths were measured with a measuring
 162 device (Velmex, USA) , with a precision of 0.001 mm. The quality control of the
 163 measurements of the ring width series was checked with the COFECHA program
 164 (Holmes, 1983).

165

166



167

168 Figure 3: *Araucaria araucana* reproductive and wood features. A) a female tree with
169 large and spherical seed cones; B) a male tree with sub-cylindrical, single, smaller
170 pollen strobili on the tips of the canopy branches; C) a wood sample showing the annual
171 tree ring pattern. The arrow indicates the direction towards the bark.

172

173 Raw ring width chronologies typically contain low-frequency (i.e., decadal and
174 longer) signals associated with changes in tree age and size, canopy position and long-
175 term changes in the environment (Fritts, 1976). In order to evaluate the relationship
176 between annual growth and climate, this low-frequency variance was removed by
177 detrending the raw ring width series using the R package ‘dplr’ (Bunn et al., 2019).
178 Each series was fitted with a 50-year cubic spline with a 50% frequency cut off.
179 Dimensionless ring width indices were created for each series by dividing the observed
180 ring width by the fitted spline. Then, these individual ring width indices were averaged
181 for each tree. Then, all sampled trees at each site were averaged to produce a mean site
182 ring width index (RWI) chronology, and site-specific male and female chronologies
183 using only male and female trees, respectively. We built regional chronologies by
184 averaging the all-tree, male-only and female-only site chronologies. Additionally, we
185 built site-specific and regional chronologies considering the difference between the
186 RWI_{male} and RWI_{female} chronology ($RWI_{\text{male}} - RWI_{\text{female}}$ chronologies). We used spatial

187 correlograms and a Mantel test to investigate the spatial correlation of tree growth
188 across our network of study sites before averaging the individual 10 site chronologies
189 into regional tree-ring chronologies. Mantel tests and correlograms were run with the R
190 package ‘ncf v1.1’ (Bjornstad, 2015). We used Spearman’s rank correlation as the
191 measure of similarity between chronologies for the period between 1980 and the last
192 common year shared by each pair of chronologies (2008-2013).

193 **2.3. Sex-specific growth patterns**

194 Sex-specific growth variability was assessed by comparing male and female
195 chronologies at the individual, site, and regional level. At the individual-level a
196 Principle Component Gradient Analysis (PCGA) (Buras et al., 2016) was used to
197 characterize within-site growth variability, and to test whether the variability was
198 related to tree sex. PCGA is based on principal component analysis and uses the polar-
199 transformation of the loadings of the first and second principal components to identify
200 population gradients or subpopulations (Buras et al., 2016). Sex-specific growth
201 differences were tested using a Wilcoxon rank test of the angles of the polar coordinates
202 of male and female trees from each site (Gut et al., 2019). Following the
203 recommendation of Buras et al. (2018), tree-ring chronologies used for PCGA were
204 separately detrended using autoregressive models. Detrending was performed using the
205 R package ‘dplr’, with model selection to minimize Akaike’s Information Criterion
206 (the default option in the detrending function) (Bunn et al., 2018). PCGA analysis was
207 conducted for a common overlap period for the trees sampled at each site. A small
208 number of trees were excluded from PCGA at some sites as they were missing some
209 outer tree rings.

210 **2.4. Mast event identification**

211 Mast events occur synchronously in *A. araucana* forests across the study region,
212 and large regional mast events occurred in 1995, 2000, 2007 and 2013 according to
213 Sanguinetti and Kitzberger (2008) and Sanguinetti (2014). As seed fall occurs in March
214 or April, and the tree ring formation starts in October or November of the previous
215 calendar year (Fig. 1), we re-dated the reported mast events to correspond to the
216 calendar year when the rings started forming (e.g. a mast event with seed fall recorded
217 April 1995 and dated to 1995 was re-dated to 1994 to correspond to the equivalent tree
218 ring, which started ring formation in October in 1994, and is consequently dated to
219 1994).

220 **2.5. Relationship between male and female tree-ring width and mast events**

221 Superposed Epoch Analysis (SEA) (Grissino-Mayer, 1995) was used to assess
222 the response of tree growth to mast events. SEA compares the mean growth before,
223 during and after an event with the mean growth of non-event years (Swetnam, 1993).
224 The significance of growth responses was estimated using a bootstrapping procedure
225 with 1,000 simulations (Bunn, 2008). Here, we used SEA to test growth responses of
226 male and female trees to known regional mast events by using the RWI chronologies,
227 testing the growth responses during the mast event and in a three-year window either
228 side of the event. We reported results for the regional RWI chronologies, and we
229 repeated the tests for sex-specific site chronologies (Appendix A). Additionally, we
230 applied SEA to a $RWI_{\text{male}} - RWI_{\text{female}}$ chronology.

231 **2.6. Relationship between sex-specific tree growth and regional climate patterns**

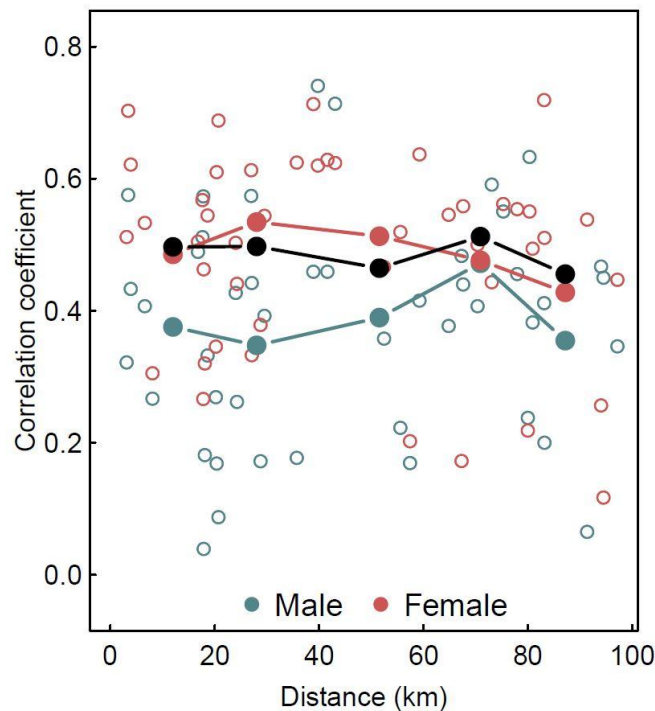
232 To evaluate the spatial relationship between tree growth (female and male) and
233 broad-scale climate patterns, we compared regional RWI chronologies with Pacific sea
234 surface temperature (SST), and land surface temperatures. We used gridded monthly
235 SST and land surface data at a spatial resolution of $0.5^\circ \times 0.5^\circ$ cells for the period 1948-

236 2013 originated from the NCEP re-analysis global dataset (Kalnay et al., 1996). The
237 spatial correlation fields were performed using tools provided on the website of
238 National Oceanic and Atmospheric Administration (NOAA/ESRL Physical Sciences
239 Laboratory, Boulder Colorado, <http://www.esrl.noaa.gov/psd/data/correlation/>).
240 Composite maps were created to evaluate the spatial features of spring-summer (Oct-
241 Mar) SST anomalies in relation with tree growth for two years before the growing
242 season (-2), for the previous growing season (-1) and for the current period of growth
243 (0).

244 **3. Results**

245 **3.1 Growth synchrony**

246 Growth synchrony between sites was high (mean between-site $\rho = 0.49$ male-
247 only chronologies, $\rho = 0.38$; female-only chronologies, $\rho = 0.49$), and did not
248 decline significantly with geographical distance across the study region, including for
249 male- and female-only site chronologies (Mantel correlation = -0.13 , $p = 0.188$; male-
250 only chronologies = 0.08 , $p = 0.339$; female-only chronologies = -0.20 , $p = 0.100$. Fig.
251 4). These analyses indicated that it was appropriate to combine the 10 sites into a
252 regional RWI chronology.



253

254 Figure 4: Spatial variation in the growth synchrony for the sex-specific RWI
 255 chronologies from each site (1987-2013). Each unfilled point shows a pairwise
 256 correlation between male (blue) and female (red) sites, and the filled points show the
 257 Mantel correlogram for male and female chronologies, and for the full site chronologies
 258 including all male and female trees (black).

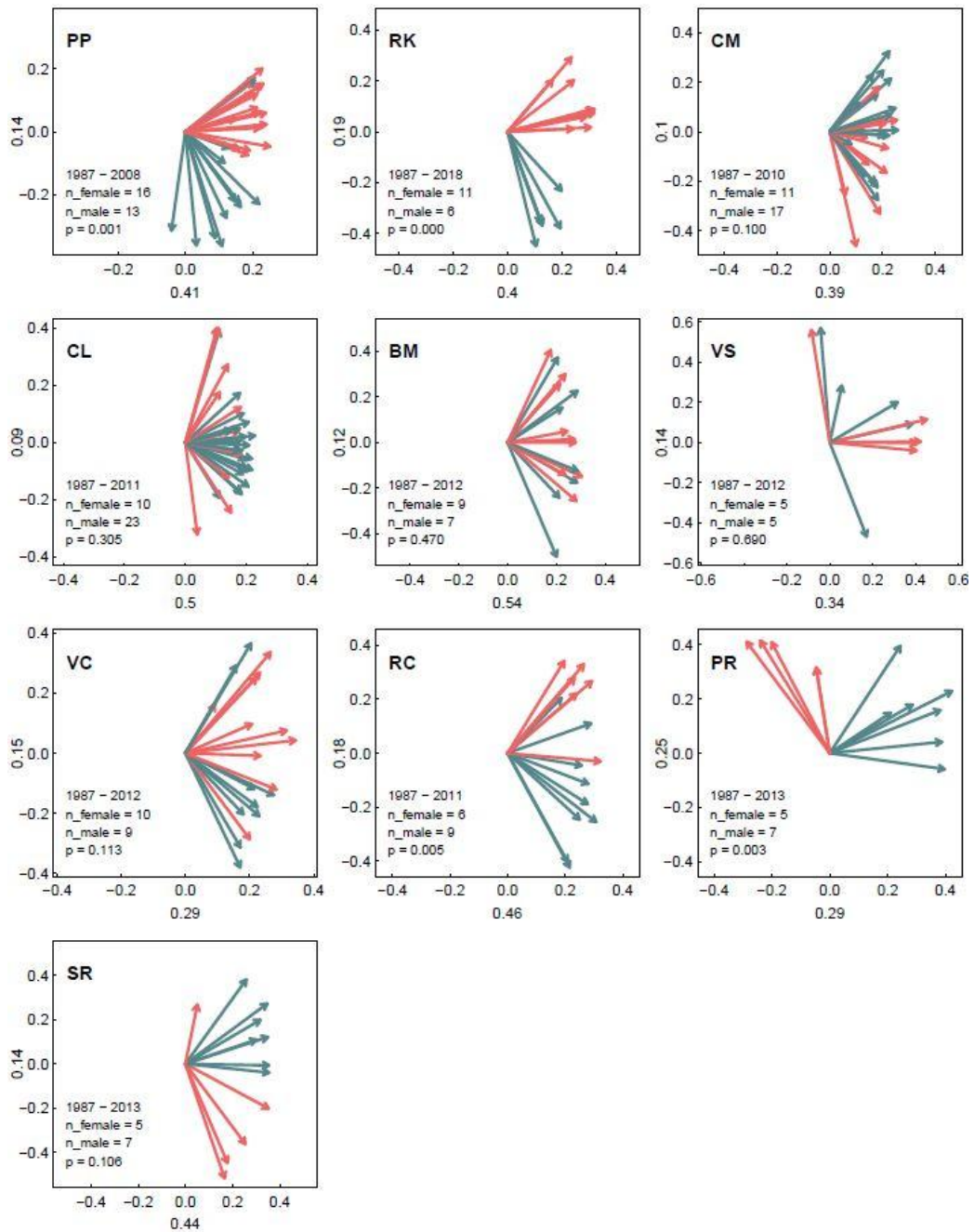
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260 3.2 Sex-specific growth patterns

261 PCGA demonstrated that individual trees within sites shared a strong common
 262 signal (Fig. 5). However, PCGA revealed significant sex-specific high-frequency
 263 growth variability in four sites (PP, RK, RC and PR; Fig. 5), and close-to-significant
 264 differences at further three sites. Sites with significant differences between male and
 265 female high frequency growth variability tended to have lower mean tree age, less
 266 variable growth (coefficient of variation, CV), lower within-site synchrony (\bar{r}) and
 267 higher overall growth (mean ring width), and significant differences between male and
 268 female growth were found in xeric and mesic sites. However, with only ten sample sites

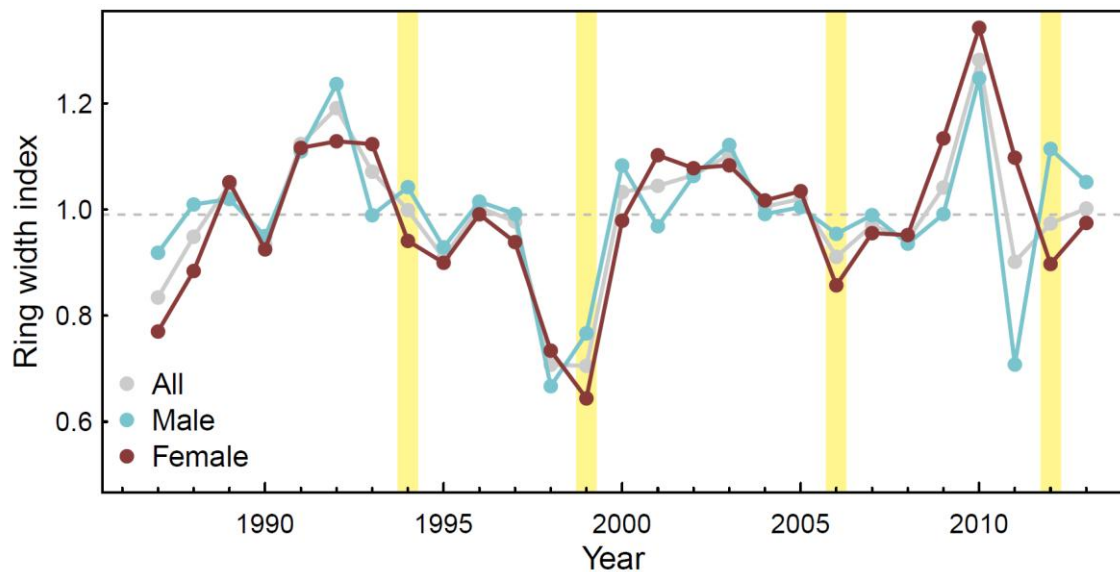
269 it was not possible to robustly test these associations. It was notable however, that the
270 four sites with the strongest sex-specific high frequency growth variability (Fig. 5), also
271 showed the strongest sex-specific growth responses to regional mast events (see
272 Appendix A). Within each site, growth pattern between male and female trees generally
273 showed high synchrony (mean within-site correlation of paired male and female
274 chronologies, $r_{h0} = 0.51$; correlation of the female and male regional chronologies, r_{h0}
275 $= 0.62$, $p = 0.001$, 1987-2013, Fig. 6).

276



277

278 Figure 5: Sex-specific differences in growth variability according to PCGA (PC1 and
 279 PC2). Red arrows indicate female individuals and blue arrows indicate male individuals.
 280 For each site, PCGA was conducted on individuals for the post-1987 period of the
 281 chronology. Individuals that did not reach the end of the chronology were excluded, as
 282 PCGA requires all individuals to have complete data over the entire testing period. *p*-
 283 values are based on Wilcoxon rank tests.



284

285 Figure 6: Ring width index of female, male and regional chronologies for the period
 286 1987-2013. Shading indicates regional mast events.

287

288 3.3 Sex-specific growth-mast event relationships

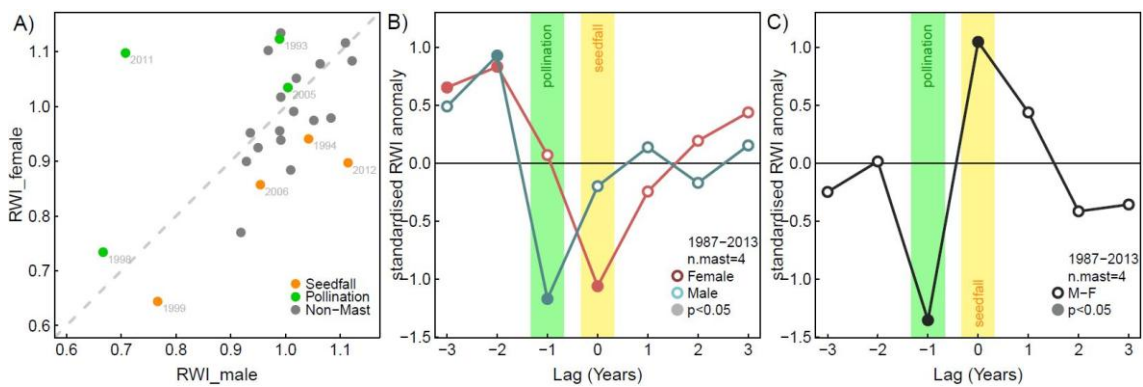
289 The narrowest tree ring of the full regional chronology (including all male and
 290 female trees) was associated with the mast events in 1999, but overall, growth of the
 291 combined male and female chronology was not significantly lower in mast years than
 292 non-mast events ($t = -1.547, p = 0.200$). Indeed, in the mast events of 1994 and 2012,
 293 growth was close to the long-term average.

294 In female trees, a mast event was associated with significantly lower growth (-
 295 15.42% compared to the 1987-2013 mean, significance estimated by bootstrapped
 296 resampling, Fig. 7B). This growth reduction was restricted to a single year, with close-
 297 to-normal growth in the years before and after seedfall. In males, a similar growth
 298 response was observed (-15.38%), but shifted by one year, with the significant growth
 299 anomaly associated with the year of pollination immediately prior to a mast event (Fig.
 300 7B). Growth of male trees returned to close-to-normal levels the following year (the
 301 year of seedfall, associated with low growth in females). In both males and females,

302 growth was higher one and two years prior to a mast event, respectively, coinciding
 303 with the years immediately prior to pollination and flowering. The sex-specific growth
 304 responses in association with mast events resulted in a particularly strong and distinct
 305 signal in a $RWI_{\text{male}}-RWI_{\text{female}}$ chronology (Fig. 7C). Mast events were associated with a
 306 highly distinctive sequence of a significantly negative anomaly followed by a
 307 significantly positive anomaly in the $RWI_{\text{male}}-RWI_{\text{female}}$ chronology (Fig. 7C).

308 As our dataset included only four mast events and could be sensitive to the effect
 309 of individual cases of a randomly associated mast event and low growth, we re-ran all
 310 analysis excluding one mast event each time, and found consistent results. Figure 7A
 311 also supports the robustness of our results, demonstrating variation in the strength of the
 312 male-female differences between mast events, but also demonstrating that all four
 313 observed mast events (seedfall) are associated with reduced female growth relative to
 314 males, and vice-versa for the associated year of pollination.

315



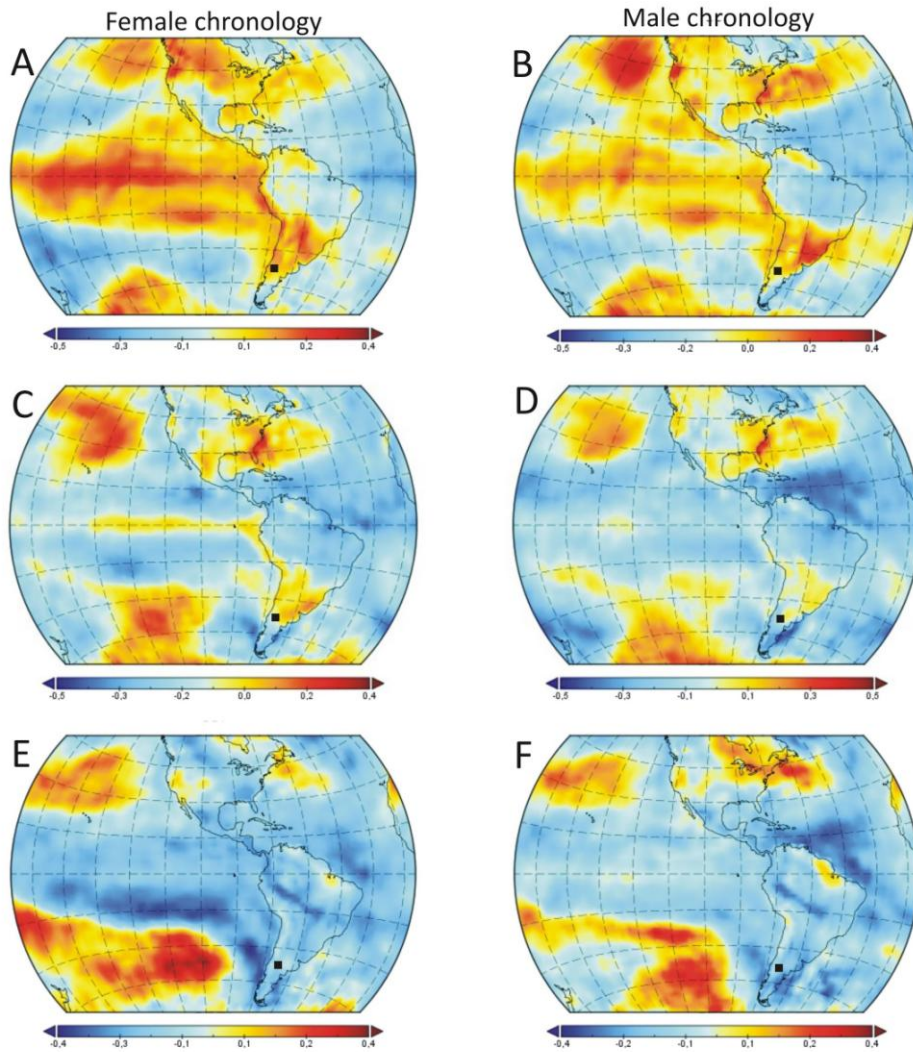
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317 Figure 7: Regional sex-specific growth patterns associated with masting (for each site
 318 see Appendix A). A) Relationship between male and female RWI (1987-2013)
 319 according to reproductive state (pollination and seedfall years, corresponding to the four
 320 large regional masting events). B) Superimposed epoch analysis showing the response
 321 of male (blue) and female (red) RWI to mast events during the period 1987-2013. Lag =
 322 0 is the year of seedfall, and lag = -1 is the year of pollination. Filled circles indicate

323 significant values at $p < 0.05$. C) Superimposed epoch analysis (SEA) showing the
324 response of the $RWI_{\text{male}}-RWI_{\text{female}}$ chronology to mast events during the period 1987-
325 2013. Lag = 0 is the year of seedfall, and lag = -1 is the year of pollination. Filled
326 circles indicate significant values at $p < 0.05$. (SEAs of each site are shown in Appendix
327 A).

328 **3.4 Large-scale climate controls on growth**

329 Both female and male chronologies showed positive and significant spatial
330 correlations with the growing season tropical SSTs ($p < 0.05$) over two years before (-2)
331 the tree growth. Correlations were higher for female trees (Fig. 8A) than for male trees
332 (Fig. 8B). Male and female RWI were weakly correlated with SST in the previous
333 growing season (-1). However, female chronology showed a slightly positive, but not
334 significant correlation with SST for the El Niño 3.4 region. In contrast, growth was
335 generally negatively and significantly ($p < 0.05$) correlated with tropical and subtropical
336 SSTs in the year of growth for female trees, with the highest correlations towards
337 sectors of the sub-equatorial Pacific and near the mid latitude coast of the South
338 American continent in the current period (Fig. 8 E-F). The correlation fields for male
339 and female chronologies showed broadly similar patterns, but correlations with SST
340 were stronger for the female chronology. Positive correlations were evident towards
341 higher latitudes of the Pacific, with an apparent spatial coherence of this pattern for both
342 female and male trees.



343

344 Figure 8: Spatial correlation coefficient fields (Pearson's correlation) between female
 345 (left panel) and male (right panel) regional RWI chronologies and Pacific Sea Surface
 346 Temperature (SST) and land surface temperature. A-B) correlations with the two
 347 previous growing season (Oct-Mar) SSTs, C-D) correlations with the previous growing
 348 season (Oct-Mar) SSTs, and E-F) correlations with the current growing season SST.
 349 Correlations were calculated for the period 1948-2013. Black squares indicate the study
 350 region. Significance intervals for $p < 0.05$ are < -0.242 and > 0.242 , respectively. Maps
 351 were created using the spatial correlation tools provided by the NOAA/ESRL Physical
 352 Sciences Laboratory, Boulder Colorado from its website at
 353 <http://www.esrl.noaa.gov/psd/data/correlation/>.

354 **4. Discussion**

355 **4.1. Sex-specific growth patterns and growth-mast event relationships**

356 Beyond the broad spatial similarity observed between different sex chronologies,
357 our study identified distinct sex-specific growth patterns at individual, site and regional
358 level. This is consistent with previous studies performed with *A. araucana* (Hadad and
359 Roig, 2016; Rozas et al., 2019), and other dioecious tree species (*Juniperus thurifera* L.;
360 Rozas et al., 2009). We showed, for the first time, that these sex-specific growth
361 patterns were linked to differences in the growth response of male and female trees in
362 relation to mast events. In association with a mast event, growth was significantly
363 reduced in female trees (which bear the seed cone), while growth was significantly
364 reduced in male trees in the year prior to a mast event, in association with high male
365 investment in pollen cones (the reproductive cycle of *A. araucana* occurs over two
366 years). We interpreted these growth reductions as representing resource switching or a
367 trade-off between growth and reproduction (Monks and Kelly, 2006; Müller-Haubold et
368 al., 2013). However, we noted that while growth was always reduced during mast
369 events compared to the previous years of growth, albeit offset by one year in males,
370 (Fig. 6 and Fig. 7B), not all narrow tree rings were associated with mast events, and
371 growth reductions associated with mast events varied substantially in magnitude (Fig.
372 6). This may have resulted from interactions between mast events and growing
373 conditions during the ring formation (Hackett-Pain et al., 2017, 2019), or the status of
374 internal reserves which may buffer any trade-off between growth and reproduction
375 (Mund et al., 2020). In our regional RWI chronology, the absolute growth response to
376 mast event was variable between the four mast events, however the response of male
377 and female trees relative to each other was notably consistent. In the pollination year
378 prior to a mast event, the growth of males was always lower than females, even when

379 the absolute growth rate was close to normal (e.g., the mast event in 1994). In the
380 following mast year, the relative growth performance of males and females was always
381 reversed, such that female growth was lower than males, again even when absolute
382 growth was close to normal. This “natural experiment” in a dioecious species where the
383 main costs of reproduction occur in different years for males and females, as in *A.*
384 *araucana*, provides a powerful tool to disentangle the effects of mast events and
385 coincident climate variability (Drobyshev et al., 2014). In our study this is shown by the
386 distinct response of a $RWI_{\text{male}}-RWI_{\text{female}}$ chronology (Fig. 7C).

387 On the other hand, we noted that while we found strong results in regional
388 chronologies, some sites showed stronger sex-specific growth patterns than others (Fig.
389 4). Expansion of our tree-ring network and analysis of intra-annual growth features (e.g.
390 wood density, early/latewood proportions) of male and female trees may help to explain
391 why some sites did not show the strong sex-specific growth and mast responses that
392 were clear in the regional tree-ring chronology (Fig. 5, Appendix A). These mast event-
393 insensitive chronologies tended to be from sites with older trees, and presented lower
394 and more synchronised growth with higher interannual variability, perhaps indicating
395 greater effects of growth limiting factors.

396 **4.2. Sex-specific growth responses to climate**

397 Our results showed broadly similar responses of male and female chronologies to
398 variation in Pacific SSTs during the growing season months. We found that growth of
399 males and females was positively correlated with SSTs two years prior to growth, with
400 slightly stronger correlations for female trees. This lag in the effect of the climate on
401 tree growth is commonly observed in many species (Fritts, 1976). The climate
402 conditions in northern Patagonia are strongly coupled with the El Niño–Southern
403 Oscillation (ENSO) (Garreaud et al., 2009). The occurrence of warm (El Niño) events in

404 the tropical Pacific is associated with a decrease (increase) temperature (precipitation)
405 during austral spring months (September to November) and an increase (decrease)
406 temperature (precipitation) during the summer months (December to February) in north
407 Patagonia (Montecinos and Aceituno, 2003; Garreaud et al., 2009). Generally opposite
408 conditions are observed during La Niña events (Garreaud et al., 2009). Therefore, the
409 positive correlation observed between tree growth and SSTs could indicate a positive
410 relationship between *A. araucana* growth and spring precipitation two years prior to the
411 current growth period, indicating a possible interaction of growth with El Niño
412 conditions in the tropical Pacific. Furthermore, we found weak correlations between
413 growth and SST in the previous year, consistent with Mundo et al. (2012) who also
414 reported a weak negative correlation between *A. araucana* tree regional growth and sea
415 surface temperature in the El Niño Southern Oscillation (ENSO) 3.4 region in the
416 previous growing season, although they did not test this for males and females
417 separately. Our results showed that female trees had a slightly positive, but not
418 significant correlation with equatorial SST in the previous year, a response not detected
419 in the male chronology. In contrast, cold SSTs, that are linked to La Niña events, during
420 the current growing season were associated with lower growth in both male and female
421 trees, although the correlation was stronger for females (Fig. 8). This negative
422 correlation observed between *A. araucana* growth and tropical SSTs could be associated
423 with high temperatures during spring and lower precipitations during summer months
424 for the current period. Thus, growth responses to broad-scale climate controls appeared
425 to be sex-specific, as was also reported by Rozas et al. (2019) for *A. araucana* forests
426 growing on the windward side of the Andes. Other studies also reported differences in
427 growth-climate relationships in dioecious species (*J. thurifera*; Rozas et al., 2009). In
428 this sense, male trees are frequently reported to have higher drought tolerance than

429 female ones (Montesinos et al., 2012, Rozas et al., 2009). This is consistent with our
430 results where females were more strongly negatively correlated with SSTs during the
431 period of ring formation. This may result from higher water use efficiency in males
432 (Montesinos et al., 2012). Although not tested in our current analyses, we propose that
433 differences in growth sensitivity to climate between male and female trees may also
434 partly result from the interplay of climate, mast events and sex-specific costs of
435 reproduction, either where climate acts as a cue for mast years (Hackett-Pain et al.,
436 2018), or where growing season climate interacts with coincident reproductive
437 investment to influence tree growth (Hackett-Pain et al., 2017). Indeed, gender
438 differences in growth are often increased under stressful conditions (Verdu et al., 2004).

439 **4.3 Implications for mast events and climate reconstructions**

440 Long observation records of mast events rarely exceed several decades in length,
441 but such datasets provide the key to identifying long-term changes in mast events and
442 the drivers of such changes (Pearse et al., 2017; Ascoli et al., 2019). Several attempts
443 have been made to extend observational mast events records using tree-rings (Speer,
444 2001; Drobyshev et al., 2014), but these efforts have been hampered by weak mast
445 event signals in chronologies (Speer, 2001; Hackett-Pain et al., 2019, Koenig et al.,
446 2020), or difficulties in distinguishing between the signature of mast events and climate
447 (Drobyshev et al., 2014). Our results indicate that sex-specific responses to mast events
448 in dioecious *A. araucana* tree species offer a potential methodology for tree-ring-based
449 mast reconstructions, which could be extended over multiple centuries. Particularly, the
450 distinct difference of relative growth between male and female trees in the year of
451 pollination and seed fall may provide a method to distinguish mast years from other
452 non-mast growth decreases (Drobyshev et al., 2014). Although our results are regionally
453 consistent, we note that important uncertainties remain to be solved, including

454 understanding the observed between-site growth sensitivity to mast events, and the
455 potential effect of changes in tree age and/or size on the masting signal (Hadad et al.,
456 2015; Hadad and Roig, 2016; Rozas et al., 2019; Bogdziewicz et al., 2020). This
457 method would only be applicable to dioecious species, but important masting species
458 could be also studied including species of the genus *Juniperus* and the masting
459 dioecious podocarps of New Zealand such as *Dacrydium cupressinum* (Norton and
460 Kelly, 1988).

461 **5. Conclusions**

462 Male and female *A. araucana* tree-ring chronologies share a strong common
463 signal and are strongly regionally correlated. Nevertheless, we have demonstrated that
464 contrasting growth responses of male and female trees to regional mast years are
465 responsible for distinct sex-specific growth variability in this dioecious species. Growth
466 of male and female trees is reduced in response to mast events, but in different years.
467 Complementary studies are now required to establish whether sex-specific climate-
468 growth relationships in this species result from an interplay with mast events, requiring
469 the identification of the climatic cues that act to synchronise *Araucaria* mast events at a
470 regional scale. Furthermore, our results provide a framework for future work to
471 reconstruct *A. araucana* mast events over multiple decades or centuries. This would
472 improve understanding of the regeneration dynamics of this endangered species.
473 Furthermore, we argue that the ability to isolate mast events signals in tree-ring
474 chronologies can provide the basis for improving dendroclimatic calibration in *A.*
475 *araucana* trees.

476 **Author contribution statement**

477 Martín A. Hadad: Conceptualization, Methodology design, Provision of data,
478 Investigation, Data analysis, Writing - original draft, review & editing. Andrew Hackett-

479 Pain: Conceptualization, Methodology design, Investigation, Data analysis, Writing -
480 original draft, review & editing. Fidel A. Roig: Conceptualization, Supervision, Writing
481 - original draft, review & editing. Julieta G. Arco Molina: Provision of data, Writing -
482 review & editing.

483 **Disclosure statement**

484 No potential conflict of interest was reported by the authors.

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501 **Appendix A. Supplementary data**

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