

1 **Title:** Climatically controlled reproduction drives inter-annual growth variability in a
2 temperate tree species

3 **Authors:**

4 Andrew J. Hacket-Pain¹, Davide Ascoli², Giorgio Vacchiano³, Franco Biondi⁴, Liam Cavin⁵,
5 Marco Conedera⁶, Igor Drobyshev^{7,8}, Isabel Dorado Liñán⁹, Andrew D. Friend¹⁰, Michael
6 Grabner¹¹, Claudia Hartl¹², Juergen Kreyling¹³, François Lebourgeois¹⁴, Tom Levanič¹⁵,
7 Annette Menzel^{16,17}, Ernst van der Maaten¹⁸, Marieke van der Maaten-Theunissen¹⁸, Lena
8 Muffler¹³, Renzo Motta¹⁹, Catalin-Constantin Roibu²⁰, Ionel Popa²¹, Tobias Scharnweber¹³,
9 Robert Weigel¹³, Martin Wilmking¹³, Christian S. Zang²²

10

- 11 1. Department of Geography and Planning, School of Environmental Sciences, University of Liverpool,
12 Liverpool, UK. Andrew.Hacket-Pain@liverpool.ac.uk
- 13 2. Dipartimento di Agraria, University of Naples Federico II, via Università 100, 80055 Portici (NA), Italy.
14 davide.ascoli@unina.it
- 15 3. DISAA, Università degli Studi di Milano, via Celoria 2, 20123 Milano, Italy. gvacchiano@gmail.com
- 16 4. DendroLab, Department of Natural Resources and Environmental Science, University of Nevada, Reno,
17 NV 89509, USA. fbiondi@unr.edu
- 18 5. Biological and Environmental Sciences, University of Stirling, Stirling, FK9 4LA, UK.
19 Augno1yabas@yahoo.co.uk
- 20 6. Swiss Federal Institute for Forest, Snow, and Landscape Research WSL, a Ramél 18, CH-6953
21 Cadenazzo, Switzerland. marco.conedera@wsl.ch
- 22 7. Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences, P.O. Box 49,
23 230 53, Alnarp, Sweden. Igor.Drobyshev@slu.se
- 24 8. Institut de recherche sur les forêts, Université du Québec en Abitibi-Témiscamingue, 445 boulevard de
25 l'Université, Rouyn-Noranda, QC, J9X 5E4, Canada
- 26 9. Forest Research Centre, (INIA-CIFOR), Ctra. La Coruña km. 7.5, 28040 Madrid, Spain.
27 dorado.isabel@inia.es
- 28 10. Department of Geography, University of Cambridge, Cambridge, UK. Adf10@cam.ac.uk
- 29 11. University of Natural Resources and Life Science – BOKU, Vienna, Austria. michael.grabner@boku.ac.at
- 30 12. Department of Geography, Johannes Gutenberg-University, Johann-Joachim-Becher-Weg 21, 55128
31 Mainz, Germany. C.Hartl-Meier@geo.uni-mainz.de
- 32 13. Institute of Botany and Landscape Ecology, Greifswald University, 17489 Greifswald, Germany.
33 juergen.kreyling@uni-greifswald.de, robert.weigel@uni-greifswald.de, lena.muffler@uni-greifswald.de,
34 wilmking@uni-greifswald.de, tobias.scharnweber@uni-greifswald.de
- 35 14. Université de Lorraine, AgroParisTech, INRA, UMR Silva, 14 rue Girardet, 54000 Nancy, France.
36 francois.lebourgeois@agroparistech.fr
- 37 15. Slovenian Forestry Institute, Večna pot 2, SI-1000 Ljubljana, Slovenia. tom.levanic@gozdis.si
- 38 16. TUM School of Life Sciences, Professorship of Ecoclimatology, Technical University of Munich, Hans-
39 Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany. amenzel@wzw.tum.de
- 40 17. Institute for Advanced Study, Technical University of Munich, Lichtenbergstraße 2 a, 85748 Garching,
41 Germany
- 42 18. Forest Growth and Woody Biomass Production, TU Dresden, Piener Str. 8, 01737 Tharandt, Germany.
43 ernst.vandermaaten@tu-dresden.de, marieke.theunissen@tu-dresden.de
- 44 19. DISAFA, University of Turin, Largo Braccini 2, 10095 Grugliasco (TO), Italy. renzo.motta@unito.it
- 45 20. Forest Biometrics Laboratory, University "Stefan cel Mare" of Suceava. catalinroibu@gmail.com
- 46 21. National Research and Development Institute in Forestry, Marin Drăcea, Calea Bucovinei 73bis,
47 Campulung Moldovenesc, Romania. catalinroibu@gmail.com, popaicas@gmail.com

1 22. TUM School of Life Sciences, Technical University of Munich, Hans-Carl-von-Carlowitz-Platz 2, 85354
2 Freising, Germany, christian.zang@wzw.tum.de
3

4 **Statement of authorship**

5 AJHP conceived and designed the study, conducted analysis, wrote the manuscript. CZ contributed to study
6 design, preliminary analysis and the manuscript preparation. GV and DA helped to conceive the study,
7 prepared datasets and contributed to the manuscript preparation. ADF contributed to the initial
8 development of the study concept. All authors contributed data and contributed to manuscript revision
9 and editing.

10 **Data accessibility statement**

11 Should the manuscript be accepted, the data supporting the results will be archived in an appropriate
12 public repository such as Dryad or Figshare and the data DOI will be included at the end of the article.

13 **Running title:** Climate control of growth via reproduction (45 characters)

14 **Key words:** masting, trade-off, structural equation modelling, SEM, path analysis,
15 dendrochronology, forest growth, drought, European beech, *Fagus sylvatica*

16 **Type of article:** Letter
17

18 **Word counts:** Abstract (136) (133), Main text (4861) (4196)

19

20 **Number of references:** 59

21 **Number of figures, tables, textboxes:** 6

22 **Corresponding author:**

23 Andrew Hacket-Pain
24 Andrew.Hacket-Pain@liverpool.ac.uk
25 Department of Geography and Planning
26 School of Environmental Sciences
27 University of Liverpool
28 Liverpool
29 L69 7ZT, UK
30 +44 (0)151 794 2846

31

1 **Abstract**

2

3 Climatically controlled allocation to reproduction is a key mechanism by which climate influences tree
4 growth and may explain lagged correlations between climate and growth. We used continent-wide
5 datasets of tree-ring chronologies and annual reproductive effort in *Fagus sylvatica* from 1901-2015 to
6 characterise relationships between climate, reproduction and growth. Results highlight that variable
7 allocation to reproduction is a key factor for growth in this species, and that high reproductive effort (“mast
8 years”) is associated with stem growth reduction. Additionally, high reproductive effort is associated with
9 previous summer temperature, creating lagged climate effects on growth. Consequently, understanding
10 growth variability in forest ecosystems requires the incorporation of reproduction, which can be highly
11 variable. Our results suggest that future response of growth dynamics to climate change in this species will
12 be strongly influenced by the response of reproduction.

1 Introduction

2
3 Tree growth and reproduction are key controls on the dynamics of forest ecosystems at a range of
4 timescales, including their response to ongoing climate change. Both growth and reproduction are
5 influenced by climate and resource availability. This makes them related, inducing growth-reproduction
6 trade-offs in many species (Thomas 2011). Growing-season climate influences growth via physiological
7 processes including leaf phenology, photosynthesis, and xylogenesis (e.g. Leuschner *et al.* 2001; Breda *et al.*
8 2006). However, the direction, duration, and timing of climate relationships with growth are not always
9 consistent across space and time, and the processes accounting for the observed relationships are poorly
10 understood, limiting our ability to predict future changes in tree growth (Babst *et al.* 2013; Guillemot *et al.*
11 2017; Peltier *et al.* 2018). A major source of such uncertainty are the processes that cause lagged effects of
12 climate on growth (Piovesan *et al.* 2005; Hackett-Pain *et al.* 2016). However, lagged effects of climate on
13 growth are not well reproduced by vegetation models (Babst *et al.* 2013; Rammig *et al.* 2015). Despite
14 recognition that they can be key drivers of tree growth responses to climate change (“ecological memory”),
15 the processes responsible are poorly understood (Ogle *et al.* 2015; Peltier *et al.* 2018). In some cases,
16 lagged correlations can result from lagged effects within the physical environment (Woodhouse 2003).
17 Alternatively, they have been attributed to “carry-over” or “legacy” impacts within trees after unfavourable
18 years (Anderegg *et al.* 2015). For example, the depletion of internal carbohydrate reserves (Galiano *et al.*
19 2011) may reduce growth the following year (Skomarkova *et al.* 2006), although this has been difficult to
20 demonstrate empirically, in part due to complexities of linking tree-level resources and growth (Mund *et al.*
21 2010; Richardson *et al.* 2013). Additionally, leaf area index, xylem conductivity or fine root dynamic
22 responses to climate may influence growth in subsequent years, creating mechanisms for lagged
23 correlations between climate and growth (e.g. Breda *et al.* 2006; Galiano *et al.* 2011).

24
25 Allocation to reproduction is a key functional trait of plants, and varies both at inter-annual timescales, and
26 across tree lifespan (Thomas 2011; Muller-Haubold *et al.* 2013; Allen *et al.* 2014). Variation in reproductive
27 effort is strongly influenced by climate, especially in species that display “masting”, i.e. highly variable inter-
28 annual seed production synchronised among individuals and populations (Pearse *et al.* 2016; Vacchiano *et*

1 *al.* 2017). Trade-offs between growth and reproduction have been repeatedly observed, and can indirectly
2 affect climate-growth relationships, causing the emergence of lagged climate effects (Piovesan & Schirone
3 2000; Hacket-Pain *et al.* 2015). Additionally, the strength of growth-reproduction trade-offs varies with
4 abiotic stresses such as summer drought (Sletvold & Agren 2015; Hacket-Pain *et al.* 2017), so the
5 magnitude of growth reductions associated with investment in reproduction is also dependent on climate.

6
7 Here, we use a masting tree species (*Fagus sylvatica* L.) to investigate the interplay of climate,
8 reproduction, and tree growth. We hypothesise that climate drives both resource availability and its
9 allocation, including via lagged effects (Fig. 1). This implies that climatically controlled allocation to
10 reproduction may be an important additional mechanism by which climate influences inter-annual
11 variation in tree growth. Testing this hypothesis will improve our ability to understand and predict
12 responses of trees to climate change (Selas *et al.* 2002; Drobyshev *et al.* 2010; Davi *et al.* 2016). We show
13 that temperature and precipitation influence growth in this species both directly, and indirectly through
14 controls on resource allocation to reproduction. Allocation to reproduction is a key driver of growth, and
15 due to its predominant dependence on previous summers' temperature, it is responsible for creating
16 lagged climate effects on growth. Consequently, we argue that including variable resource allocation in
17 models of tree growth will improve their ability to reproduce observed patterns of growth and improve
18 predictions of future tree growth.

1 METHODS

3 Data

4 Tree-ring widths were used to characterise tree growth, with data taken from a tree-ring network covering
5 the whole geographic distribution of *F. sylvatica* (Fig. 2) (Zang *et al.* 2018). The dataset used in this study
6 includes 321 sites, and extends from southern Scandinavia to the Mediterranean Basin, and from western
7 Europe to the Balkans. Sites were selected to represent locally typical closed-canopy *F. sylvatica* forest, and
8 sampling was not designed to specifically target climatically stressed sites or individuals. Each site included
9 a minimum of five trees. As our focus was to understand inter-annual variation in growth, low-frequency
10 ring-width variation was removed using 32-year spline detrending with a frequency cut-off of 0.5 (Cook &
11 Peters 1981), and individual trees were averaged to create mean site chronologies of ring-width indices
12 (*RWI*). Reproductive effort (*RE*) was characterised using a five-class ordinal index of seed production (Ascoli
13 *et al.* 2017a), with seed production chronologies for each NUTS-1 (Nomenclature of Territorial Units for
14 Statistics, see Appendix S1 and S2 in supporting information) region of Europe developed by Vacchiano *et*
15 *al.* (2017). Ordinal data were reclassified to binary, comprising of “mast” (category 4 and 5) and “non-mast”
16 years (category 1, 2 and 3). This approach was designed to maintain linear relationships and reduce the
17 degrees of freedom in the models. *RWI* series from individual sites were further averaged to create regional
18 NUTS-1 growth chronologies (Fig. 2), with correlations between sites in each NUTS-1 checked to ensure
19 growth synchrony within each region (Appendix S3). The number of individual site chronologies
20 contributing to each mean NUTS-1 chronology varied from 3 to 41. Data for monthly mean maximum
21 temperature (*MAX*) and monthly total precipitation (*PRE*) were obtained from the CRU TS 3.23 gridded
22 dataset (Harris *et al.* 2014). Regional climate time-series were calculated by averaging pixel-level climate
23 data across NUTS-1 using the `cruts` package (Taylor & Parida 2016) in R version 3.3.1 (R Development
24 Core Team 2016). Homogeneity of climate within regions was checked by calculating the mean pairwise
25 correlation between all individual grid cells in each region, and we checked that regional climate
26 chronologies represented the climate of the sampled tree-ring sites. Growing season conditions were
27 represented by a three-month window (May-July, MJJ). While the time window corresponding to the
28 strongest relationship with annual growth may vary between populations, previous studies have indicated

1 this window captures the main signal for populations of *F. sylvatica* across Europe (Hacket-Pain *et al.* 2016;
2 Cavin & Jump 2017). Previous summer climate signals (t_{-1} and t_{-2}) were represented using a two-month
3 window (June-July, JJ), which acts as a consistent climate cue of mast years across Europe (Drobyshev *et al.*
4 2010; Muller-Haubold *et al.* 2013; Vacchiano *et al.* 2017).

5

6 **Structural equation modelling (SEM)**

7 We used SEM (path analysis) to examine relationships between climate variables, reproductive effort, and
8 growth (Fig. 1), with analysis conducted at the NUTS-1 regional level. SEM provides a tool to statistically
9 test conceptual models with empirical datasets, including direct and indirect dependency structures (Fig. 1)
10 (Grace 2006). In our initial model, growth was influenced directly by climate conditions in the growing
11 season, which influence physiological processes including phenology, photosynthesis and xylogenesis
12 (Leuschner *et al.* 2001; Breda *et al.* 2006). Links were also included to represent lagged effects of previous
13 summer temperature on growth, which is commonly reported in this species (Piovesan *et al.* 2005).
14 Additional climatic factors such as winter or spring temperature in the year of growth may be important
15 locally, but are not consistently relevant across populations (Lebourgeois *et al.* 2005; Hacket-Pain & Friend
16 2017), and so were not included in this analysis. Links were also included between current growth and
17 annual reproductive effort (Muller-Haubold *et al.* 2013; Hacket-Pain *et al.* 2017), and between current- and
18 prior-year growth. Annual reproductive effort was influenced by previous summers' climate and previous
19 year growth (Drobyshev *et al.* 2010; Vacchiano *et al.* 2017). A full description and justification of our initial
20 model is included in Appendix S4. Aggregated (NUTS-1) data for *RWI*, *RE* and climate variables were tested
21 for multivariate normality and multivariate outliers, using the *MVN* package in R (Korkmaz *et al.* 2014)
22 (Appendix S5), and the linearity of bivariate relationships was checked by graphical plotting (Appendix S6).
23 In SEM, the estimation of parameters aims to minimise the discrepancy between the observed covariance
24 matrix and the covariance matrix implied by the hypothetical model (Grace 2006). SEMs were fitted using
25 diagonally weighted least-squares estimation (DWLS) in the R package *lavaan* (Rosseel 2012) in order to
26 adjust for the categorical endogenous variables included in our data (*RE*). SEMs test the strength, sign and
27 significance of relationships between variables. We used standardised path coefficients to represent these

1 relationships, which can be interpreted as equivalent to partial correlation coefficients. For categorical
2 variables we also plot the raw coefficients to aid interpretation (Grace *et al.* 2005). Indirect effects are
3 estimated by multiplying coefficients along indirect pathways. The raw coefficients and p-values are
4 provided in Appendix S7.

5

6 **Model fitting and validation**

7 Following the recommendation of Kline (2005), we focused the model development and fitting on regions
8 with >100 years of complete data, a threshold met by four regions: two in northern Europe (UKJ and SE2)
9 and two in central Europe (DE1 and DE2) (Fig. 2). Initial analysis of the tree-ring chronologies showed high
10 within-region synchrony between individual *RWI* chronologies in SE2, UKJ and DE1 (see Fig. 2), but lower
11 synchrony in DE2. Cluster analysis revealed a strong dependence of *RWI* to elevation (see Appendix S8),
12 therefore all analyses for DE2 were conducted using two mean chronologies (high and low elevation).

13 Model development and fitting followed the two-stage process recommended by Grace (2006). The first
14 step focused on the concept of goodness-of-fit (GOF) and compared the specified model with the variance-
15 covariance matrix of observed data. This was essentially a test that no important links between variables
16 were omitted. To estimate the GOF we used the χ^2 test (threshold value, $p > 0.05$), the Comparative Fit Index
17 (CIF, threshold value > 0.9), and the Standardized Root Mean Square Residual (SRMSR) and Root Mean
18 Square Error of Approximation (RMSEA) (threshold value < 0.1 and < 0.05 , respectively) (Kline 2005; Grace
19 2006; Rosseel 2012). The second stage of evaluation investigated whether all links included in the model
20 were supported by the data. Insignificant links ($p > 0.05$) were excluded from the model – but only if doing
21 so did not reduce GOF (Grace 2006). As a final check, we compared models with and without the
22 insignificant links using ANOVA. This procedure was used to develop an optimal model for the prediction of
23 *RE* and *RWI* based on climate and prior growth. To estimate confidence intervals around predicted *RWI* we
24 randomly resampled model parameters 1000 times, assuming a normal distribution and using the
25 estimated standard error for each parameter. A 95% confidence interval was based on the distribution of
26 the set of 1000 predicted *RWI* (± 2 sd).

1 We then used independent regions with more limited data availability to validate our models using two
2 approaches. First, we used the multi-modelling approach (Rosseel 2012) to estimate a single model for all
3 discrete regions used in the development of the optimal model structure. Then we ran this multi-group
4 model to predict *RWI* in 26 independent validation regions, based only on climate data, with *RE* predicted
5 using previous summer temperatures. We used this model structure for further validation for eight of these
6 26 regions where we had at least 45 years of complete *RWI*, *RE*, and climate data. Here we used the same
7 optimal model structure, but the parameters were fitted individually in each region, allowing for local
8 differences in sensitivity of growth and masting to climate. As these regions had not been used in model
9 development and fitting, this was a form of model-structure validation, testing the generality of our
10 underlying assumptions of the controls of growth.

1 RESULTS

3 Selection of optimal model linking climate, reproduction, and tree growth

4 Tree growth was significantly correlated with climate and reproductive effort in the five regions used for
5 model development and fitting (Fig. 3 and Appendix S6). These models passed the GOF tests, showing that
6 our proposed model structure linking climate, reproduction and growth was consistent with our datasets
7 (Fig. 1). Growth was reduced in years of high reproductive effort, and was positively correlated with
8 growing season precipitation (Fig. 3). However, not all the linkages in the original models were significant,
9 and comparison of alternative models demonstrated that the effects of MAX_{JJ-1} and MAX_{JJ-2} on RWI could be
10 adequately explained by indirect pathways involving RE (Appendix S9 and S10). In all five regions, a model
11 that included only indirect effects of MAX_{JJ-1} and MAX_{JJ-2} via RE was statistically indistinguishable from a
12 model that included both direct and indirect pathways, and significantly better than a model where
13 previous summers' temperatures could only influence growth directly (Appendix S10). This indicated that
14 the indirect pathway via RE is the dominant (although not necessarily the exclusive) pathway for previous
15 summers' temperature influence on RWI . Consequently, as direct linkages between previous summers'
16 temperature and RWI were not supported by the data they were removed from the optimal model. The
17 linkage between RWI_{-1} and RE was also insignificant, and removing it had no effect on prediction of RE .
18 MAX_{JJ} had no significant influence on growth in any of the five regions in the saturated models (Appendix
19 S9). However, when models were optimised individually for each of the five regions (Appendix S11), MAX_{JJ}
20 was retained in DE2-high, becoming significant when PRE_{MJJ} was removed. We therefore decided to retain
21 the linkage between MAX_{JJ} and RWI in the optimal models (Fig. 3). In conclusion, our optimal model
22 structure predicted RWI on the basis of growing season climate (PRE_{MJJ} and MAX_{JJ}), reproductive effort (RE)
23 and previous year growth (RWI_{-1}), with additional indirect effects of previous summers' temperature as RE
24 was predicted on the basis of previous summers' climate (MAX_{JJ-1} and MAX_{JJ-2}).

25
26 The optimal models explained a higher proportion of observed variance in RWI in northern Europe ($R^2 =$
27 55% and 43% in UKJ and SE2 respectively). Interpretation of coefficients is not straightforward in models
28 with categorical variables (Grace and Bowen, 2005), but in SE2 the raw coefficient for RE , which represents

1 the change in *RWI* in a mast year (i.e. $RE = 1$), was greater than the standardised coefficient for MAX_{JJ} or
2 PRE_{MJJ} , which represents the change in *RWI* for a $\pm 1SD$ change in these climate variables. As a mast year
3 occurred on average every three years in SE2 (Fig. 2), we suggest that RE was the variable with the
4 strongest influence on *RWI* in this region. In UKJ, RE was also an important control on growth, but PRE_{MJJ}
5 had an additional strong influence. In DE1, the model explained 36% of the variance in *RWI*, and PRE_{MJJ} was
6 the strongest influence on growth (RE was insignificant). In DE2-low and DE2-high the models had lower
7 explanatory power, and RE was the only significant linkage with *RWI*. In SE2, UKJ, and DE1, the models
8 reproduced observed patterns of *RWI* successfully, including multi-year growth reductions (Fig. 4).
9 However, fitted models for all regions failed to consistently reproduce the magnitude of growth reductions
10 in years with the narrowest observed rings (Appendix S12). Consequently, the models did not adequately
11 capture an observed increase in inter-annual growth variability during recent decades in UKJ and SE2.

12
13 There were differences in the relative importance of different pathways between regions (pathway
14 coefficients) (Fig. 3). RE had a significant negative impact on growth in all regions except DE1, so that high
15 RE (a mast year) resulted in reduced growth. Generally, summer precipitation (PRE_{MJJ}) had a significant
16 positive influence on growth, but this relationship was weaker in the most northerly region, SE2 and DE2-
17 low, and was insignificant in the high elevation region DE-high. Summer temperature in the year of growth
18 (MAX_{JJ}) had no significant impact on growth in any of the study regions. While always insignificant, it had a
19 weak negative influence on growth in all chronologies except DE2-high, where the relationship was
20 positive.

21
22 Consequently, in SE2 the main climate influence on radial growth was an indirect effect of temperature
23 during the two summers prior to the year of growth, via RE (masting); i.e. the indirect influence of MAX_{JJ-1}
24 and MAX_{JJ-2} were both greater than the direct influence of either PRE_{MJJ} or MAX_{JJ} (Fig. 3). In UKJ the
25 influence of growing season precipitation (PRE_{MJJ}) was stronger than in SE2, but previous summers'
26 temperature, through their influence on masting, also had a strong impact on growth. Radial growth in the
27 previous year had a significant positive influence on growth (i.e. positive autocorrelation) in all five models.

1

2 **Model validation**

3 A multi-group model was fitted using the optimal model structure (Fig. 3), although restricted to UKJ, SE2,
4 and DE2-low. DE2-high was excluded from the multi-group model due to opposite influences of PRE_{MJ} and
5 MAX_{JJ} on RWI , and DE1 was excluded due to the insignificant link between RE and RWI . Including either of
6 these regions in the multi-group resulted in the model failing the GOF tests. The resulting multi-group
7 model was consistent with the results of the individual models (Appendix S13). The model captured the key
8 features of growth in many of the 26 independent validation chronologies from across Europe for the
9 period 1951-2015 (Fig. 6), including individual and multi-year growth depressions, although the magnitude
10 of these growth depressions was not reproduced by the models (Appendix S12 and S14). While correlations
11 were low in some regions, it should be noted that errors in the prediction of RE propagate into the
12 prediction of RWI . Indeed, in several of the regions where the model performed poorly, this was associated
13 with lower model skill at predicting observed RE .

14

15 Then, we fitted the model structure in Fig. 3 individually to eight regions that had not been used in the
16 model development due to smaller sample sizes. The reduced number of linkages in the optimal model
17 allowed model fitting for regions with ≥ 45 years of data (Kline 2005). These individually fitted models (Fig.
18 5) supported the results of the optimal models for the five model development regions (Fig. 3),
19 demonstrating that RE and PRE_{MJ} are major drivers of growth. Seven of the eight models passed the GOF
20 tests (DE8 failed, and was not included further). RE had a significant negative influence on RWI in six of
21 these seven remaining validation models (in addition to the significant negative influence in four of the five
22 original models), and was the largest direct or indirect effect on growth in five regions. PRE_{MJ} had a
23 significant positive influence on growth in one region (DEA), and was positive but insignificant in all other
24 regions except AT3. The influence of MAX_{JJ} was always insignificant, and was negative in all regions except
25 DEB and AT3.

26

1 DISCUSSION

2

3 Across a wide geographical region, a simple model structure with direct influences of summer precipitation
4 and temperature, a negative impact of reproductive effort and an autoregressive term was consistent with
5 observed data (12 of 13 models passed the GOF tests), and explained a high proportion of observed
6 variation in growth in most regions. While the coefficients associated with each linkage showed regional
7 variability (Fig. 3 and 5), our results show that inter-annual variation in growth in *F. sylvatica* can be
8 adequately explained by a framework of direct growing-season climate effects and climatically driven
9 variation in annual allocation to reproduction. Importantly, in eight of twelve individually fitted models
10 (Fig.3 and Fig. 5), the main factor driving inter-annual variation in ring width was allocation to reproduction
11 (*RE*) (Fig. 3 and 5). The influence of climate on growth varied in importance (and direction) between
12 regions, but *RE* had a consistently negative effect on growth; i.e. mast years reduced growth. Importantly,
13 the *RE* influence was consistent across the species' geographic distribution, generalising the results of
14 regionally focused studies (Drobyshev *et al.* 2010; Muller-Haubold *et al.* 2013; Hackett-Pain *et al.* 2017). In
15 our analysis, in seven of the twelve individually fitted models, high *RE* (a mast year) was associated with a
16 larger growth reduction than a dry summer with precipitation one standard deviation below the mean (and
17 in an additional region the coefficients were equal in magnitude). As years of high *RE* usually occur more
18 frequently than dry or warm summers, this implies that *RE* has a greater effect on growth than these
19 climate variables. We note that the window used for growing season climate influences on growth was
20 fixed for all regions, and other climatic influences on growth were not included in our analysis, such as late
21 frost events (Príncipe *et al.* 2017). If the climate window were optimised for individual regions, the relative
22 importance of direct climate influences and *RE* may change and the overall variance explained by the
23 models would increase (Lebourgeois *et al.* 2005; Hartl-Meier *et al.* 2014). Weaker relationships between
24 intra-region *RE* and *RWI* were found in some regions, which may result from variation in the strength of
25 growth-reproduction trade-offs among populations (Sletvold & Agren 2015), perhaps due to differences in
26 non-structural carbohydrate (NSC) storage. However, variation between regions could also be related to
27 the data used to characterise reproductive effort (Ascoli *et al.* 2017a). Intra-regions *RE* correlations were
28 generally high (Fig. 2 and Appendix S2), but fine-scale variations in reproduction effort may not be captured

1 by the data used in this study (Wohlgemuth et al. 2016). Nevertheless, our results provide strong evidence
2 that allocation to reproduction has a consistent negative effect on the growth of *F. sylvatica*, and can
3 explain a substantial part of the observed inter-annual variation in ring width (Drobyshev et al. 2010;
4 Muller-Haubold et al. 2013; Hacket-Pain et al. 2017).

5

6 Furthermore, because *RE* was itself correlated with temperature from previous summers (Figure 3, and see
7 also Vacchiano et al. 2017), an important indirect temperature control on growth was revealed. *RWI* is
8 frequently reported to be negatively correlated with previous summer temperatures (Babst et al. 2013;
9 Hartl-Meier et al. 2014; Hacket-Pain et al. 2016), but comparing alternative models indicated that for our
10 data, the most parsimonious model included only indirect pathways through *RE* (Fig. 3 and 5). In other
11 words, adding direct links between previous summer temperature and growth did not improve the model
12 skill at reproducing *RWI*. We interpret this to suggest that lagged correlations between growth and
13 previous years temperature are largely a consequence of the interplay with reproduction (masting)
14 (Hacket-Pain et al., 2015), rather than resulting from other “carry-over” effects. Further evidence to
15 support this conclusion comes from the consistent direction of the indirect temperature influences. While
16 the coefficients associated with the direct $MAX_{JJ}-RWI$ linkage varied from positive to negative with
17 elevation in central Europe, the influences of previous summers’ temperature through *RE* were consistently
18 negative (Fig. 3 and 5). This indicates that the lagged negative correlations between *RWI* and previous
19 summer temperature (MAX_{JJ-1}) are not primarily driven by “carry-over” effects of hot summers on internal
20 resources levels (e.g. NSC) (Guillemot et al. 2017), as the influence of growing season temperature (and
21 precipitation) on growth switches sign, but the lagged effects do not. Furthermore, regions with weaker *RE-*
22 *RWI* relationships also had weaker bivariate correlations between MAX_{JJ-1} and *RWI* (Fig. 3 and Appendix S6).
23 However, we acknowledge that other mechanisms act over multiple years to create lagged effects on
24 growth, including NSC dynamics, and needle, leaf and root dynamics (e.g. Fritts 1976). These climate-
25 dependent processes are also important controls of growth in *F. Sylvatica*, and may be the main drivers of
26 lagged climate correlations in species that do not exhibit one or more of the key characteristics that
27 underpin the climate-reproduction-growth interplay that we have explored here. Many tree species or

1 populations do not have synchronised and highly variable investment in reproduction (masting) (Herrera *et al.* 1998), show weak relationships between climate and reproductive effort (Vacchiano *et al.* 2017; Patterson & Knapp 2018), or do not exhibit a strong negative relationship between reproductive effort and radial growth (e.g. Lebourgeois *et al.* 2018; Patterson & Knapp 2018). For example, interplay with reproduction seems unlikely to explain the lagged effects of drought on growth in non-masting conifers growing in the southern and western North America (e.g. Anderegg *et al.* 2015; Peltier *et al.* 2018).

7
8 Consequently, the indirect influence of MAX_{JJ-1} on growth (through RE) was an important climatic driver of growth, and in half of the regions (6/12) the total effect of MAX_{JJ-1} on growth was greater than the direct influence of growing season climate (MAX_{JJ} or PRE_{MJJ}). Furthermore, in this study we characterized RE using a binary measure of allocation to reproduction. Higher resolution data may reveal that the variation in RWI explained by reproductive effort is greater than we found here (Hackett-Pain *et al.* 2017). It is also notable that alternative models that only included indirect pathways for the effects of MAX_{JJ-1} and MAX_{JJ-2} through RE captured observed variation in RWI more successfully than when only direct links were included (Appendix S10). This indicates that the ability of MAX_{JJ-1} and MAX_{JJ-2} to predict RWI is improved when they are combined to predict the probability of a year with high RE (i.e. a mast year). In other words, models that included climate effects through RE were better at predicting growth than alternative models that included direct lagged effects on growth (MAX_{JJ-1} and MAX_{JJ-2}) but no influence of RE (Appendix S10).

19
20 Our results imply that adequately explaining observed variation in tree growth requires accounting for flexible allocation of resources, including reproduction, which is a major sink for carbohydrates and nutrients and is highly variable across years (Muller-Haubold *et al.* 2013; Pearse *et al.* 2016). In particular, the effect of reproductive allocation on growth will be an important factor determining the response of growth to future climate changes. Some studies have reported increased investment in reproduction in recent decades (Allen *et al.* 2014), which may have negative effects on forest productivity over short and longer timescales, analogous to the effects of changes in the occurrence of insect outbreaks (Peters *et al.* 2017). Indeed, our results show that a major source of uncertainty in the prediction of future changes in

1 tree growth may originate from uncertainty in the response of tree reproductive effort to climate change
2 (Ascoli *et al.* 2017b; Pearse *et al.* 2017). The proximate drivers of variable seed production in *F. sylvatica* are
3 still uncertain, but the positive correlation between previous summer temperature and seed production
4 has been linked to floral primordia differentiation (Drobyshev *et al.* 2010; Vacchiano *et al.* 2017). The
5 negative correlation with MAX_{JJ-2} may be related to climate effects on resource accumulation (Pearse *et al.*
6 2016; Allen *et al.* 2017; Ascoli *et al.* 2017b).

7
8 Our simple models explain a high proportion of the observed variance in growth. In the twelve regions
9 where models were fitted individually, the combination of growing season precipitation, temperature,
10 previous summer's growth and *RE* could explain $\geq 35\%$ of the observed variance in inter-annual growth in
11 half of the regions ($R^2 \geq 50\%$ in three of the twelve regions) (Fig. 3 and 5). Generally, the lowest tree growth
12 was associated with a combination of high *RE* and dry summers. While these terms were included in the
13 final models, they did not fully reproduce the magnitude of observed growth reductions in years of
14 extreme low growth (e.g. 1976). This may be due to non-linear responses of growth to climate, particularly
15 under climate extremes (Appendix S6), and to interactions, such as between low precipitation and/or high
16 vapour pressure deficit and high temperature, or interactions between low precipitation and reproductive
17 effort. A potential effect of tree age on allocation to reproduction was also not included in our model
18 (Thomas 2011). Other climate factors that we did not include in our models may be important controls on
19 growth locally (Piovesan & Schirone 2000; Skomarkova *et al.* 2006; Drobyshev *et al.* 2010). For example, in
20 mountain and upland regions late spring frost events occurring after leaf-out are associated with narrow
21 tree rings (Dittmar *et al.* 2006; Príncipe *et al.* 2017), and low growth in the DE2-high chronology in 1927,
22 1928, 1953 and 2011 correspond to late frost events reported in the region by Dittmar *et al.* (2006) and
23 Menzel *et al.* (2015).

24
25 Our multi-group model reproduced elements of the independent *RWI* series across the species' geographic
26 distribution, with higher correspondence between observed and predicted *RWI* in Romania, France and the
27 UK (Fig. 6). As expected, the explained variance in these regions was lower than for the individually fitted

1 models (Fig. 3 and 5), as the multi-group model used for predicting *RWI* in the independent datasets did
2 not allow for geographic variation in the sensitivity of *RWI* to growing season climate or *RE*, which was
3 observed in this and previous studies (Piovesan *et al.* 2005; Cavin & Jump 2017). For example, the
4 coefficient associated with summer precipitation was highest in westerly regions (UKJ, DE7, DE1), and was
5 frequently insignificant in eastern regions (AT2, AT3, DE2, PL6). In particular, the model was less successful
6 at predicting *RWI* in the Alpine region (Austria, Switzerland, northern Italy). It should be noted that inter-
7 annual growth synchrony was low in many of these topographically complex regions (Appendix S3),
8 indicating diverse drivers of growth or microclimatic variation in topographically complex regions (Hartl-
9 Meier *et al.* 2014; Hackett-Pain & Friend 2017). Additionally, previous analysis has revealed that while
10 broad-scale climate cues of past years are consistent between populations in *F. sylvatica* (Vacchiano *et al.*
11 2017), there are some differences in the seasonality and nature of cues between populations.
12 Consequently, we would expect the multi-group model to vary in its ability to accurately predict *RE*.

13

14 **Conclusions**

15 We have found that climatically driven variation in reproductive effort is an important control on inter-
16 annual growth variability in *F. sylvatica* and appears to be the dominant factor determining inter-annual
17 radial growth variability in many populations. Additionally, the climatic control of reproductive effort
18 creates indirect climate effects on growth, generating lagged correlations between summer temperature
19 and growth. A similar interplay may be important in explaining antecedent climate effects on growth in
20 other species (Anderegg *et al.* 2015; Peltier *et al.* 2018), but this remains to be fully tested. Importantly, this
21 study also demonstrates that categorical and regional-resolution data on past years can provide useful
22 information to untangle the interplay of climate, reproduction, and tree growth. These results have
23 important implications for models of tree growth, including those that resolve annual ring width or
24 simulate tree growth or NPP. Such models have tended to focus on the direct effects of growing season
25 climate on growth, using approaches that range from phenomenological (e.g. Tolwinski-Ward *et al.* 2011)
26 to physiologically focused process-based models (e.g. Friend & White 2000). Our results demonstrate that
27 climatically controlled variation in allocation to reproduction is an important control on tree growth (at

1 least for beech), and contribute to a growing body of research that indicates that variable resource
2 allocation at a variety of timescales is a key factor influencing tree growth (Drobyshev *et al.* 2010; Thomas
3 2011; Muller-Haubold *et al.* 2013; Hackett-Pain *et al.* 2017). For example, Guillemot *et al.* (2015) suggest
4 that increased investment in reproduction with tree age could explain age-related declines in stem biomass
5 increment (see also Thomas 2011). Decadal variations in reproductive effort (e.g. frequency of “mast
6 years”) (Drobyshev *et al.* 2014; Ascoli *et al.* 2017b) may have effects on growth trends analogous to the
7 influence of cyclic insect outbreaks (Peters *et al.* 2017). Consequently, we argue that including variable
8 resource allocation in models will increase the ability to reproduce observed variability in tree growth and
9 growth-climate relationships. It may also improve predictions of future changes in tree growth, which will
10 at least in part be dependent on the response of reproduction to environmental change.

11

12 **Acknowledgements**

13

14 We are grateful to Wolfram Elling, Christoph Dittmar and ITRDB contributors who provided data, and Janet
15 Maringer who helped to assemble the masting database “MASTREE”. We thank Andrew Tanentzap for
16 advice and guidance on the use of SEM. We are grateful to the three anonymous reviewers whose
17 comments and suggestions improved the manuscript. AJHP acknowledges funding support from the John
18 Fell Oxford University Press (OUP) Research Fund REF161/025. Dataset assembly and preliminary
19 discussions between AJHP, GV and DA occurred with support from the European Union (EU) COST Action
20 PROFOUND (FP1304). AM and CZ acknowledge funding from the European Research Council (FP7/2007-
21 2013) / ERC grant agreement no. 282250. JK, LM, MM-T, RW, MW acknowledge support by the research
22 training group RESPONSE funded by the German Research Council (DFG Fi 846/8-1, DFG GRK2010). FB was
23 supported, in part, by a grant from the Office of Research and Innovation at the University of Nevada, Reno
24 (USA).

25

References

1. Allen, R.B., Hurst, J.M., Portier, J. & Richardson, S.J. (2014). Elevation-dependent responses of tree mast seeding to climate change over 45 years. *Ecology and Evolution*, 4, 3525-3537.
2. Allen, R.B., Millard, P. & Richardson, S.J. (2017). A Resource Centric View of Climate and Mast Seeding in Trees. In: *Progress in Botany* (eds. Cánovas, F, Lüttge, U & Matyssek, R). Springer Cham.
3. Anderegg, W.R.L., Schwalm, C., Biondi, F., Camarero, J.J., Koch, G., Litvak, M. *et al.* (2015). Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. *Science*, 349, 528-532.
4. Ascoli, D., Maringer, J., Hacket-Pain, A., Conedera, M., Drobyshev, I., Motta, R. *et al.* (2017a). Two centuries of masting data for European beech and Norway spruce across the European continent. *Ecology*, 98, 1473.
5. Ascoli, D., Vacchiano, G., Turco, M., Conedera, M., Drobyshev, I., Maringer, J. *et al.* (2017b). Inter-annual and decadal changes in teleconnections drive continental-scale synchronization of tree reproduction. *Nature Communications*, 8.
6. Babst, F., Poulter, B., Trouet, V., Tan, K., Neuwirth, B., Wilson, R. *et al.* (2013). Site- and species-specific responses of forest growth to climate across the European continent. *Global Ecology and Biogeography*, 22, 706-717.
7. Breda, N., Huc, R., Granier, A. & Dreyer, E. (2006). Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science*, 63, 625-644.
8. Cavin, L. & Jump, A.S. (2017). Highest drought sensitivity and lowest resistance to growth suppression are found in the range core of the tree *Fagus sylvatica* L. not the equatorial range edge. *Global Change Biology*, 23, 362-379.
9. Cook, E.R. & Peters, K. (1981). The Smoothing Spline: A New Approach to Standardizing Forest Interior Tree-Ring Width Series for Dendroclimatic Studies. *Tree-Ring Bulletin*, 41, 45-53.
10. Davi, H., Cailleret, M., Restoux, G., Amm, A., Pichot, C. & Fady, B. (2016). Disentangling the factors driving tree reproduction. *Ecosphere*, 7.
11. Dittmar, C., Fricke, W. & Elling, W. (2006). Impact of late frost events on radial growth of common beech (*Fagus sylvatica* L.) in Southern Germany. *European Journal of Forest Research*, 125, 249-259.
12. Drobyshev, I., Niklasson, M., Mazerolle, M.J. & Bergeron, Y. (2014). Reconstruction of a 253-year long mast record of European beech reveals its association with large scale temperature variability and no long-term trend in mast frequencies. *Agricultural and Forest Meteorology*, 192, 9-17.
13. Drobyshev, I., Overgaard, R., Saygin, I., Niklasson, M., Hickler, T., Karlsson, M. *et al.* (2010). Masting behaviour and dendrochronology of European beech (*Fagus sylvatica* L.) in southern Sweden. *Forest Ecology and Management*, 259, 2160-2171.
14. EURFORGEN (2009). Distribution map of Beech (*Fagus sylvatica*). www.euforgen.org. In: www.euforgen.org.
15. Friend, A.D. & White, A. (2000). Evaluation and analysis of a dynamic terrestrial ecosystem model under preindustrial conditions at the global scale. *Global Biogeochemical Cycles*, 14, 1173-1190.
- 16.

1 Fritts, H. (1976). *Tree Rings and Climate*. Academic Publishers, New York.
2 17.
3 Galiano, L., Martinez-Vilalta, J. & Lloret, F. (2011). Carbon reserves and canopy defoliation determine the
4 recovery of Scots pine 4 yr after a drought episode. *New Phytologist*, 190, 750-759.
5 18.
6 Grace, J.B & Bollen, K.A. (2005). Interpreting the results from multiple regression and structural equation
7 models. *Bulletin of the Ecological Society of America*, 86, 283-295.
8 19.
9 Grace, J. (2006). *Structural Equation Modeling and Natural Systems*. Cambridge University Press,
10 Cambridge, UK.
11 20.
12 Guillemot, J., Francois, C., Hmimina, G., Dufrene, E., Martin-StPaul, N.K., Soudani, K. *et al.* (2017).
13 Environmental control of carbon allocation matters for modelling forest growth. *New Phytologist*,
14 214, 180-193.
15 21.
16 Guillemot, J., Martin-StPaul, N.K., Dufrene, E., Francois, C., Soudani, K., Ourcival, J.M. *et al.* (2015). The
17 dynamic of the annual carbon allocation to wood in European tree species is consistent with a
18 combined source-sink limitation of growth: implications for modelling. *Biogeosciences*, 12, 2773-
19 2790.
20 22.
21 Hacket-Pain, A.J., Cavin, L., Friend, A.D. & Jump, A.S. (2016). Consistent limitation of growth by high
22 temperature and low precipitation from range core to southern edge of European beech indicates
23 widespread vulnerability to changing climate. *European Journal of Forest Research*, 135, 897-909.
24 23.
25 Hacket-Pain, A.J. & Friend, A.D. (2017). Increased growth and reduced summer drought limitation at the
26 southern limit of *Fagus sylvatica* L., despite regionally warmer and drier conditions.
27 *Dendrochronologia*, 44, 22-30.
28 24.
29 Hacket-Pain, A.J., Friend, A.D., Lageard, J.G.A. & Thomas, P.A. (2015). The influence of masting
30 phenomenon on growth-climate relationships in trees: explaining the influence of previous
31 summers' climate on ring width. *Tree Physiology*, 35, 319-330.
32 25.
33 Hacket-Pain, A.J., Lageard, J.G.A. & Thomas, P.A. (2017). Drought and reproductive effort interact to control
34 growth of a temperate broadleaved tree species (*Fagus sylvatica*). *Tree Physiology*, 37, 744-754.
35 26.
36 Harris, I., Jones, P.D., Osborn, T.J. & Lister, D.H. (2014). Updated high-resolution grids of monthly climatic
37 observations - the CRU TS3.10 Dataset. *International Journal of Climatology*, 34, 623-642.
38 27.
39 Hartl-Meier, C., Dittmar, C., Zang, C. & Rothe, A. (2014). Mountain forest growth response to climate
40 change in the Northern Limestone Alps. *Trees-Structure and Function*, 28, 819-829.
41 28.
42 Herrera, C.M., Jordano, P., Guitian, J. & Traveset, A. (1998). Annual variability in seed production by woody
43 plants and the masting concept: Reassessment of principles and relationship to pollination and
44 seed dispersal. *American Naturalist*, 152, 576-594.
45 29.
46 Kline, R.B. (2005). *Principles and Practice of Structural Equation Modeling*. Guilford Publications.
47 30.
48 Korkmaz, S., Goksuluk, D. & Zararsiz, G. (2014). MVN: An R Package for Assessing Multivariate Normality. *R*
49 *Journal*, 6, 151-162.
50 31.
51 Lebourgeois, F., Breda, N., Ulrich, E. & Granier, A. (2005). Climate-tree-growth relationships of European
52 beech (*Fagus sylvatica* L.) in the French Permanent Plot Network (RENECOFOR). *Trees-Structure and*
53 *Function*, 19, 385-401.
54 32.

1 Lebourgeois, F., Delpierre, N., Dufrêne, E., Cecchini, S., Macé, S., Croisé, L. *et al.* (2018). Assessing the roles
2 of temperature, carbon inputs and airborne pollen as drivers of fructification in European
3 temperate deciduous forests. *European Journal of Forest Research*, 137, 1612-4677.
4 33.

5 Leuschner, C., Backes, K., Hertel, D., Schipka, F., Schmitt, U., Terborg, O. *et al.* (2001). Drought responses at
6 leaf, stem and fine root levels of competitive *Fagus sylvatica* L. and *Quercus petraea* (Matt.) Liebl.
7 trees in dry and wet years. *Forest Ecology and Management*, 149, 33-46.
8 34.

9 Menzel, A., Helm, R. & Zang, C. (2015). Patterns of late spring frost leaf damage and recovery in a European
10 beech (*Fagus sylvatica* L.) stand in south-eastern Germany based on repeated digital photographs.
11 *Frontiers in Plant Science*, 6.
12 35.

13 Muller-Haubold, H., Hertel, D., Seidel, D., Knutzen, F. & Leuschner, C. (2013). Climate Responses of
14 Aboveground Productivity and Allocation in *Fagus sylvatica*: A Transect Study in Mature Forests.
15 *Ecosystems*, 16, 1498-1516.
16 36.

17 Mund, M., Kutsch, W.L., Wirth, C., Kahl, T., Knohl, A., Skomarkova, M.V. *et al.* (2010). The influence of
18 climate and fructification on the inter-annual variability of stem growth and net primary
19 productivity in an old-growth, mixed beech forest. *Tree Physiology*, 30, 689-704.
20 37.

21 Ogle, K., Barber, J.J., Barron-Gafford, G.A., Bentley, L.P., Young, J.M., Huxman, T.E. *et al.* (2015). Quantifying
22 ecological memory in plant and ecosystem processes. *Ecology Letters*, 18, 221-235.
23 38.

24 Patterson, T. & Knapp, P. (2018). Long-leaf pine cone-radial growth relationships in the southeastern USA.
25 *Dendrochronologia*, 50, 134-141.
26 39.

27 Pearse, I.S., Koenig, W.D. & Kelly, D. (2016). Mechanisms of mast seeding: resources, weather, cues, and
28 selection. *New Phytologist*, 212, 546-562.
29 40.

30 Pearse, I.S., LaMontagne, J.M. & Koenig, W.D. (2017). Inter-annual variation in seed production has
31 increased over time (1900-2014). *Proceedings of the Royal Society B-Biological Sciences*, 284.
32 41.

33 Peltier, D.M.P., Barber, J.J. & Ogle, K. (2018). Quantifying antecedent climatic drivers of tree growth in the
34 Southwestern US. *Journal of Ecology*, 106, 613-624.
35 42.

36 Peters, R.L., Klesse, S., Fonti, P. & Frank, D.C. (2017). Contribution of climate vs. larch budmoth outbreaks in
37 regulating biomass accumulation in high-elevation forests. *Forest Ecology and Management*, 401,
38 147-158.
39 43.

40 Piovesan, G., Biondi, F., Bernabei, M., Di Filippo, A. & Schirone, B. (2005). Spatial and altitudinal bioclimatic
41 zones of the Italian peninsula identified from a beech (*Fagus sylvatica* L.) tree-ring network. *Acta*
42 *Oecologica-International Journal of Ecology*, 27, 197-210.
43 44.

44 Piovesan, G. & Schirone, B. (2000). Winter North Atlantic oscillation effects on the tree rings of the Italian
45 beech (*Fagus sylvatica* L.). *International Journal of Biometeorology*, 44, 121-127.
46 45.

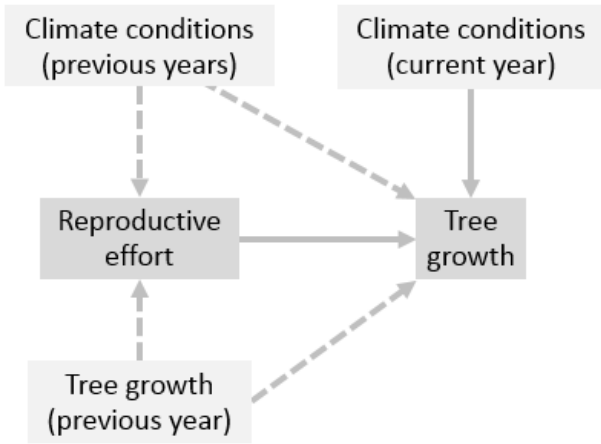
47 Príncipe, A., van der Maaten, E., van der Maaten-Theunissen, M., Struwe, T., Wilmking, M. & Kreyling, J.
48 (2017). Low resistance but high resilience in growth of a major deciduous forest tree (*Fagus*
49 *sylvatica* L.) in response to late spring frost in southern Germany. *Trees*, 31, 743–751.
50 46.

51 R Development Core Team (2016). *R: A language and environment for statistical computing*. 3.3.1 edn. R
52 Foundation for Statistical Computing, Vienna, Austria.
53 47.

1 Rammig, A., Wiedermann, M., Donges, J.F., Babst, F., von Bloh, W., Frank, D. *et al.* (2015). Coincidences of
2 climate extremes and anomalous vegetation responses: comparing tree ring patterns to simulated
3 productivity. *Biogeosciences*, 12, 373-385.
4 48.
5 Richardson, A.D., Carbone, M.S., Keenan, T.F., Czimczik, C.I., Hollinger, D.Y., Murakami, P. *et al.* (2013).
6 Seasonal dynamics and age of stemwood nonstructural carbohydrates in temperate forest trees.
7 *New Phytologist*, 197, 850-861.
8 49.
9 Rosseel, Y. (2012). lavaan: An R Package for Structural Equation Modeling. *Journal of Statistical Software*,
10 48, 1-36.
11 50.
12 Selas, V., Piovesan, G., Adams, J.M. & Bernabei, M. (2002). Climatic factors controlling reproduction and
13 growth of Norway spruce in southern Norway. *Canadian Journal of Forest Research-Revue*
14 *Canadienne De Recherche Forestiere*, 32, 217-225.
15 51.
16 Skomarkova, M.V., Vaganov, E.A., Mund, M., Knohl, A., Linke, P., Boerner, A. *et al.* (2006). Inter-annual and
17 seasonal variability of radial growth, wood density and carbon isotope ratios in tree rings of beech
18 (*Fagus sylvatica*) growing in Germany and Italy. *Trees-Structure and Function*, 20, 571-586.
19 52.
20 Sletvold, N. & Agren, J. (2015). Climate-dependent costs of reproduction: Survival and fecundity costs
21 decline with length of the growing season and summer temperature. *Ecology Letters*, 18, 357-364.
22 53.
23 Taylor, B. & Parida, B. (2016). cruts: Interface to climatic research unit time-series
24 version 3.21 data. <https://CRAN.R-project.org/package=cruts>.
25 54.
26 Thomas, S.C. (2011). Age-Related Changes in Tree Growth and Functional Biology: The Role of
27 Reproduction. In: *Size- and Age-Related Changes in Tree Structure and Function* (eds. Meinzer, F,
28 Lachenbruch, B & Dawson, T). Dordrecht, pp. 33-64.
29 55.
30 Tolwinski-Ward, S.E., Evans, M.N., Hughes, M.K. & Anchukaitis, K.J. (2011). An efficient forward model of
31 the climate controls on interannual variation in tree-ring width. *Climate Dynamics*, 36, 2419-2439.
32 56.
33 Vacchiano, G., Hacket-Pain, A., Turco, M., Motta, R., Maringer, J., Conedera, M. *et al.* (2017). Spatial
34 patterns and broad-scale weather cues of beech mast seeding in Europe. *New Phytologist*, 215,
35 595-608.
36 57.
37 Wohlgemuth, T., Nussbaumer, A., Burkart, A., Moritzi, M., Wasem, U. & Moser, B. (2016). Muster und
38 treibende Kräfte der Samenproduktion bei Waldbäumen. *Schweizerische Zeitschrift für Forstwesen*,
39 167, 316-324.
40 58.
41 Woodhouse, C.A. (2003). A 431-yr reconstruction of western Colorado snowpack from tree rings. *Journal of*
42 *Climate*, 16, 1551-1561.
43 59.
44 Zang, C., Hacket-Pain, A.J., Jump, A.S., Biondi, F., Menzel, A., Buras, A. *et al.* (2018). Climate and drought
45 responses in a continent-wide tree-ring network of European beech (*Fagus sylvatica*). In:
46 *Geophysical Research Abstracts*. EGU, Vol. 20, EGU2018-13454.
47
48

1 **FIGURES**

2

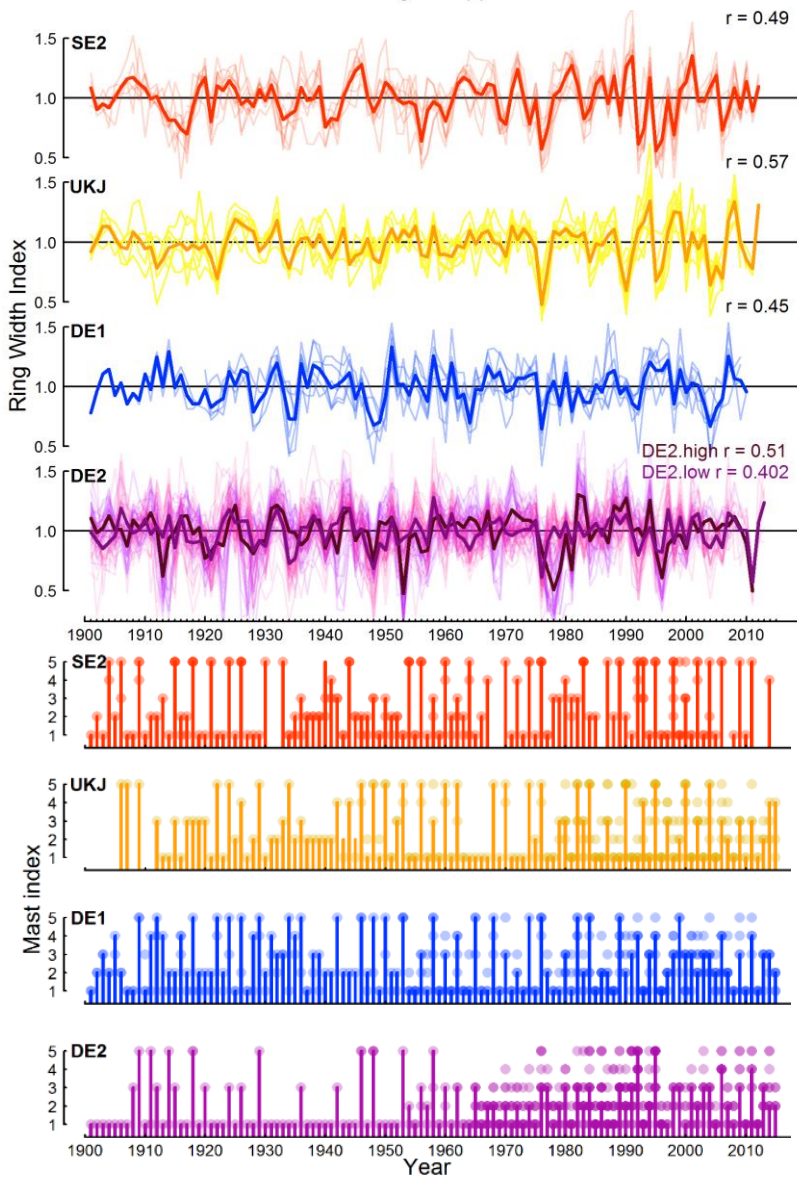
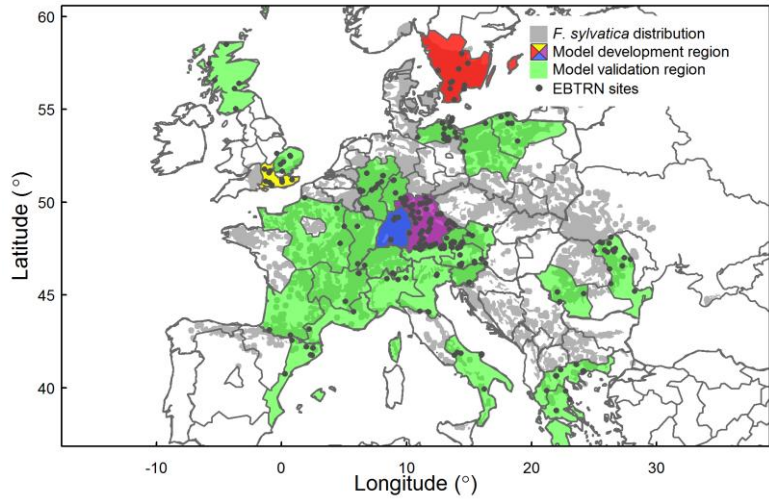


3

4 **Figure 1.** Theoretical model linking climate conditions across multiple years, tree reproductive effort and

5 tree growth. Dashed lines indicate effects operating across years.

6

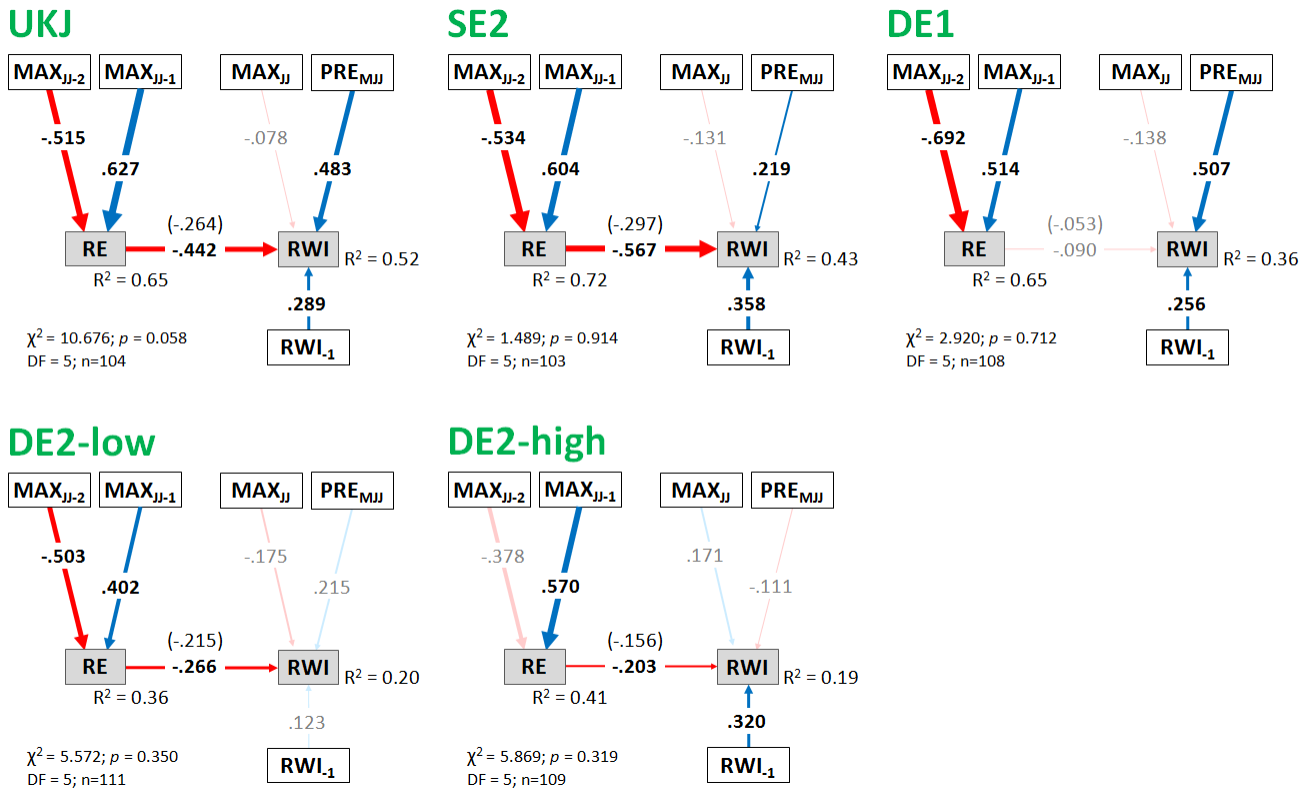


20

21

22

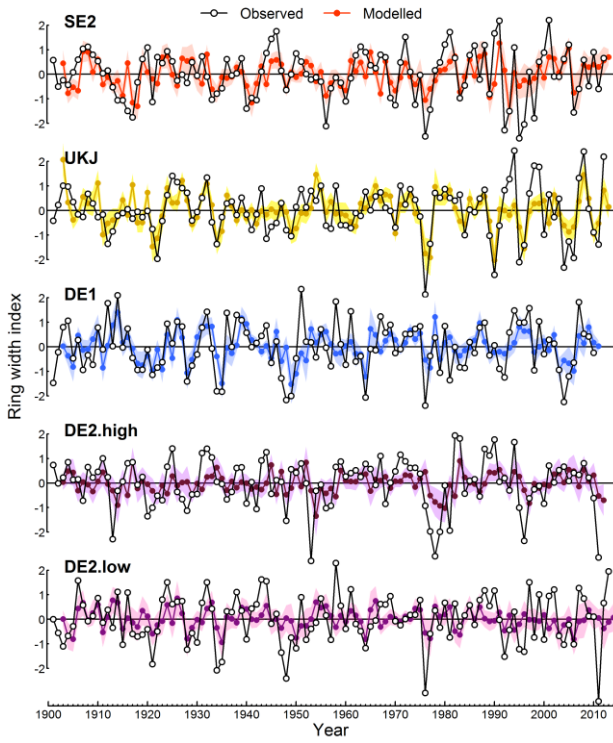
1 **Figure 2.** Study location and summary of data. A) Study regions (NUTS-1) including the geographic
2 distribution of *Fagus sylvatica* (EURFORGEN 2009) , and locations of individual RWI chronologies. B) Ring-
3 width index chronologies for each region. Individual chronologies plotted in pale colours, and the mean
4 regional chronology in dark colours. r represents the mean correlation between sites in each regional
5 chronology. For DE2, cluster analysis revealed two distinct groups of chronologies, which correspond to
6 high (paler purple) and low (darker purple) elevation (see Appendix B) C) Annual reproductive effort (RE) (1-
7 2-3 = non mast year; 4-5 = mast year) of *F. sylvatica* in each region. Individual records are plotted as points
8 (colour intensity represents the number of records in a class), with the modal values plotted as bars.
9



1
2
3
4
5
6
7
8
9
10
11

Figure 3: Structural Equation Models for model development and fitting regions, representing the effects of temperature and precipitation on radial growth, with indirect pathways involving the effects of allocation to reproduction (*RE*). Following mediation analysis, direct pathways from MAX_{JJ-1} and MAX_{JJ-2} to *RWI*, and from RWI_{-1} to *RE*, have been removed. Blue and red arrows indicate positive and negative relationships respectively. Numbers on the arrows indicate the standardized path coefficients, with arrow thickness proportional to the coefficient strength. Coefficients in parenthesis refer to raw coefficients. Pale colours indicate non-significant pathways ($p < 0.05$). The proportion of explained variance (R^2) for each endogenous variable is also shown.

1



2

3 **Figure 4.** Comparison of observed and predicted *RWI* for model development regions (models described in
4 Figure 3). Shading represents 95% confidence interval for model predictions. Note that *RWI* is modelled as
5 a function of PRE_{MJJ} , MAX_{JJ} , and RWI_{-1} , and predicted *RE* (predicted from MAX_{JJ-1} and MAX_{JJ-2}) – i.e.,
6 observed *RE* is not used to predict *RWI*.

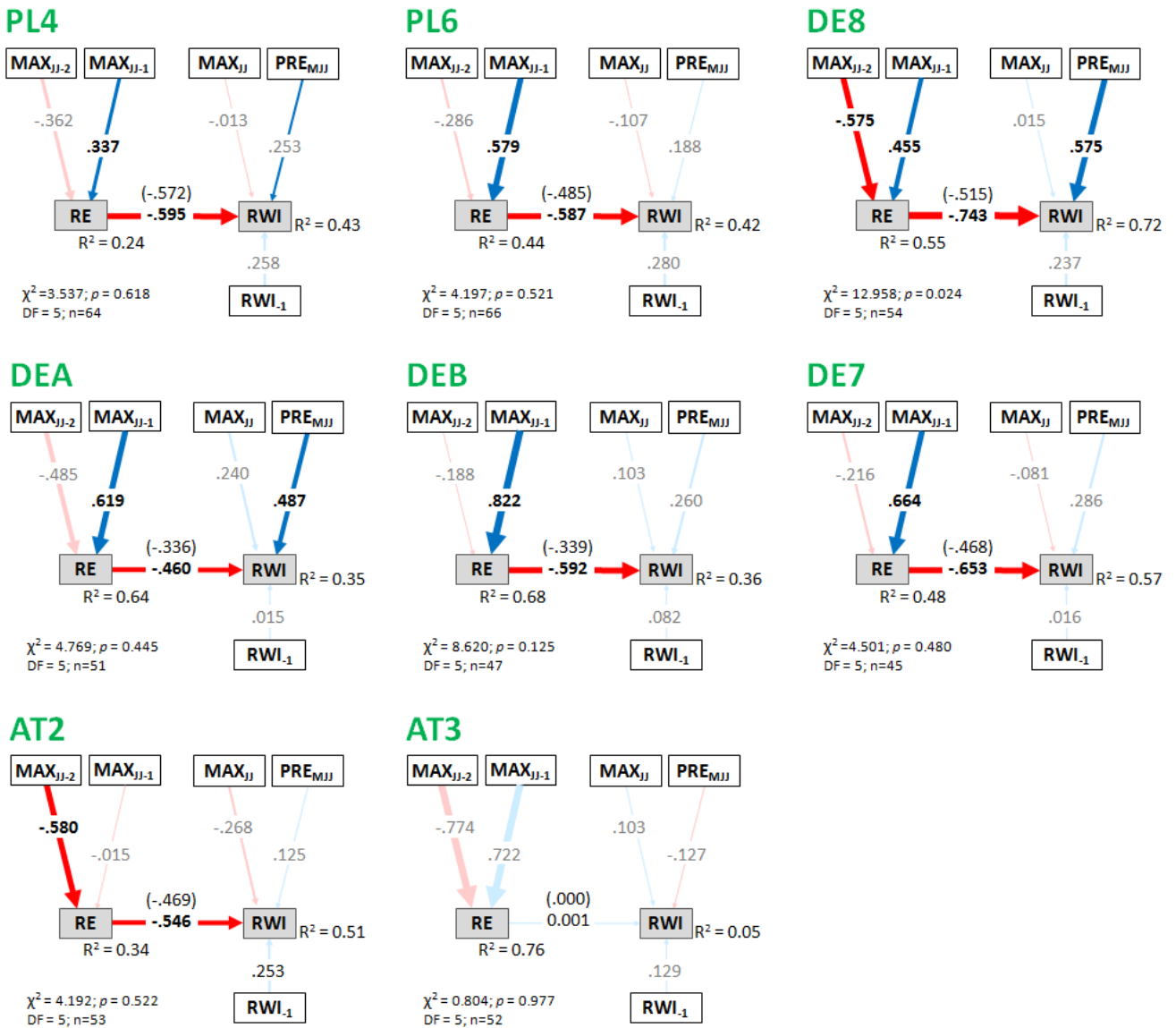
7

8

1

2

3



4

5

6 **Figure 5:** Model in Figure 3 fitted individually to each of an additional eight validation regions with >= 45

7 complete observations. Blue and red arrows indicate positive and negative relationships respectively.

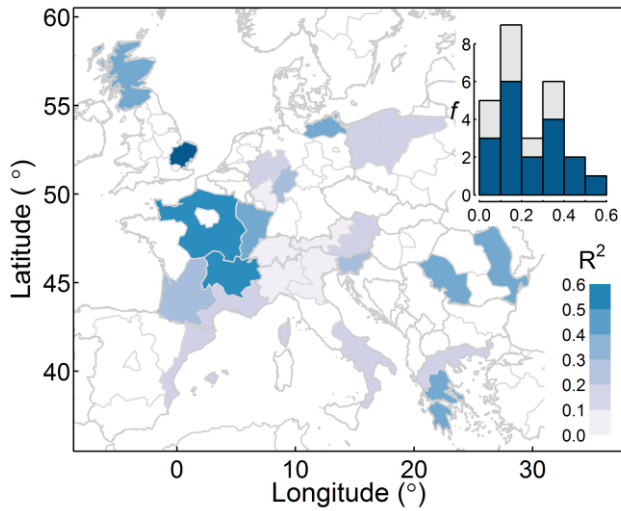
8 Numbers on the arrows indicate the standardized path coefficients, with arrow thickness proportional to

9 the coefficient strength. Coefficients in parenthesis refer to raw coefficients. Pale colours indicate non-

10 significant pathways (p<0.05). The proportion of explained variance (R²) for each endogenous variable is

11 also shown.

12



1

2 **Figure 6.** Comparison of predicted and observed tree ring chronologies from independent validation
 3 regions. *RWI* was predicted for each region using the multi-group model. Note that in these models, *RE* was
 4 predicted using climate data, and predicted *RE* is then used in the model predicting *RWI*. The inset
 5 frequency plot shows the distribution of R^2 , with light grey bars indicating regions where the regional *RWI*
 6 chronology shows low intra-region synchrony (mean correlation between sites < 0.3, see Appendix S3).

7