# 1 When tree rings go global: challenges and opportunities for retro-

# 2 and prospective insight

- 3 Flurin Babst<sup>1,2,\*</sup>, Paul Bodesheim<sup>3</sup>, Noah Charney<sup>4</sup>, Andrew Friend<sup>5</sup>, Martin Girardin<sup>6</sup>, Stefan
- 4 Klesse<sup>7</sup>, David J.P. Moore<sup>8</sup>, Kristina Seftigen<sup>9</sup>, Jesper Björklund<sup>1,10</sup>, Olivier Bouriaud<sup>11</sup>,
- 5 Andria Dawson<sup>8</sup>, R. Justin DeRose<sup>12</sup>, Michael C. Dietze<sup>13</sup>, Annemarie Eckes<sup>5</sup>, Brian
- 6 Enquist<sup>4</sup>, David C. Frank<sup>7</sup>, Miguel D. Mahecha<sup>3</sup>, Benjamin Poulter<sup>14</sup>, Sydne Record<sup>15</sup>,
- 7 Valerie Trouet<sup>7,8</sup>, Rachael Turton<sup>5</sup>, Zhen Zhang<sup>1,16</sup> & Margaret E.K. Evans<sup>7</sup>
- 8 <sup>1</sup>Dendro Sciences Group, Swiss Federal Research Institute WSL, Zürcherstrasse 111, CH-
- 9 8903 Birmensdorf, Switzerland
- 10 <sup>2</sup>W. Szafer Institute of Botany, Polish Academy of Sciences, ul. Lubicz 46, 31-512 Krakow,
- 11 *Poland*
- 12 <sup>3</sup>Max Planck Institute for Biogeochemistry, Jena, Germany
- 13 <sup>4</sup>Department of Ecology and Evolutionary Biology, University of Arizona, Tucson AZ, USA
- 14 <sup>5</sup>Department of Geography, University of Cambridge, Cambridge, England
- 15 <sup>6</sup>Laurentian Forestry Centre, Quebec, Canada
- 16 <sup>7</sup>Laboratory of Tree-Ring Research, University of Arizona, Tucson, USA
- 17 <sup>8</sup>School of Natural Resources and the Environment, University of Arizona, Tucson, USA
- 18 <sup>9</sup>Department of Earth Sciences, University of Gothenburg, Gothenburg, Sweden
- 19 <sup>10</sup>Czech University of Life Sciences, Prague, Czech Republic
- 20 <sup>11</sup>Faculty of Forestry, Stefan cel Mare University of Suceava, Strada Universității 13,
- 21 Suceava 720229, Romania.
- 22 <sup>12</sup>Rocky Mountain Research Station, US Department of Agriculture, Ogden UT, USA
- 23 <sup>13</sup>Earth and Environment, Boston University, USA
- 24 <sup>14</sup>NASA Goddard Space Flight Center, Greenbelt, Maryland 20771, USA
- 25 <sup>15</sup>Department of Biology, Bryn Mawr College, Bryn Mawr, USA
- 26 <sup>16</sup>Department of Geographical Sciences, University of Maryland, College Park, USA
- 27 \*Corresponding author:
- 28 Dr. Flurin Babst
- 29 Swiss Federal Research Institute WSL
- 30 Zürcherstr. 111
- 31 8903 Birmensdorf
- 32 Switzerland
- 33 Email: <u>flurinbabst@gmail.com</u>
- 34 Phone: +48 579 516 164
- 35 Key words:
- 36 Dendrochronology, scaling, data integration, climate change, forest growth, vegetation
- 37 models, xylogenesis, remote sensing, forest inventory, Anthropocene

#### 38 Abstract

39 The demand for large-scale and long-term information on tree growth is increasing rapidly as 40 environmental change research strives to quantify and forecast the impacts of continued 41 warming on forest ecosystems. This demand combined with the now quasi-global availability 42 of tree-ring observations has inspired researchers to compile large tree-ring networks to 43 address continental or even global scale research questions. However, these emergent objectives contrast the paleo-oriented research ideas that have guided the development of 44 45 many existing records. A series of challenges related to how, where, and when samples have been collected is thus complicating the transition of tree rings from a local to a global 46 47 resource on the question of tree growth. Herein, we review possibilities to scale tree-ring data 48 (A) from the sample to the individual, (B) from the individual to the site, and (C) from the 49 site to larger spatial domains. Representative tree-ring sampling supported by creative 50 statistical approaches is thereby key to capture the heterogeneity of climate-growth responses 51 across forested landscapes. We highlight the benefits of combining the temporal information 52 from tree rings with the spatial information offered by forest inventories and earth 53 observations to quantify tree growth and its (a)biotic drivers. In addition, we show how the 54 continued development of mechanistic tree-ring models can help address some of the non-55 linearities and feedbacks that complicate the scaling of tree-ring data. Embracing scaling 56 issues as part of its scope will greatly increase the contribution that dendrochronology can 57 make to assessing climate impacts on forests and supporting the development of adaptation 58 strategies.

## 59 **1. Introduction**

#### 60 1.1. An increasing need to scale tree-ring data

61 Climate change during the Anthropocene is now considered a certainty (Marotzke et al., 62 2017) and environmental research focuses increasingly on quantifying and forecasting the 63 impacts of continued warming on ecosystems and natural resources. Forests are receiving 64 particular attention because they absorb large amounts of excess atmospheric CO<sub>2</sub> from 65 anthropogenic emissions (Le Quéré et al., 2016) and store this carbon in woody biomass for 66 decades to centuries (Körner, 2017). Importantly, rising temperatures can have beneficial or 67 detrimental effects on forests, depending on present climatic limitations (Charney et al., 68 2016). For instance, climate warming in cold-humid areas can stimulate tree growth through 69 a prolonged growing season and more rapid cellular development (Cuny et al., 2014; Rossi et 70 al., 2016). In drier regions, a warming-induced increase in atmospheric water demand 71 triggers physiological changes in trees that lower hydraulic conductivity, reduce the 72 production and allocation of carbohydrates to growth, and ultimately aggravate forest mortality (Adams et al., 2017). This continuum of possible warming effects provides 73 74 incentive to understand forest ecosystem processes and their response to changes in the 75 (a)biotic environment across scales.

76

In principal, measurements of secondary growth patterns in trees, shrubs, and perennial herbs (subsequently called "tree rings") are the primary resource to retrospectively provide tree growth information across large environmental gradients and sub-annual to centennial time scales. Such data are increasingly being accessed to study global change impacts on forest ecosystems. A number of recent studies have compiled large tree-ring networks to hind- and forecast forest growth variability and its climate response (Babst et al., 2013; Charney et al., 2016; Martin - Benito and Pederson, 2015; Restaino et al., 2016; Tei et al., 2017), track the Recovery of growth after extreme events (Anderegg et al., 2015; Wu et al., 2017), relate growth variability to canopy dynamics (Vicente-Serrano et al., 2016), Seftigen et al. in review), or search for signals of CO<sub>2</sub> fertilization (Gedalof and Berg, 2010; Girardin et al., 2016; Peñuelas et al., 2011). In addition, tree-ring data are increasingly used to quantify aboveground biomass increment (Babst et al., 2014b), improve our physiological understanding of xylogenesis (i.e. wood formation; (Rathgeber et al., 2016), and calibrate mechanistic models for climate reconstruction (Guiot et al., 2014).

- 91
- 92 Table 1: Definitions of important terms used in this review (partly inspired by (Scholes,
- 93 2017)

Term	Definition
Scale (noun)	Spatial extent and/or temporal duration.
Scale (verb)	Extrapolation or projection of a result from one scale to another. Linear
	scaling (i.e., proportional or additive scaling) assumes that the driving
	processes are homogeneous over the scale range and that no interactions in
	space or time impose non-linearities. An example is the scaling of forest
	biomass increment from a sample of 0.1-hectare forest plots to a 10,000-
	hectare landscape. If heterogeneities (e.g., in forest type or time-since-
	disturbance) make simple linear scaling inaccurate, power-law scaling can
	capture nonlinearities across scales. For example, the scaling of bole diameter
	to whole-tree biomass involves allometric (power-law) equations, that are
	usually empirically derived, but may be (quasi-)mechanistic.
Downscaling	the process of disaggregation of a result to a smaller scale; i.e., a one-to-many
	problem. Climate system downscaling is a well-known example. The
	aggregated result is known; the challenge is to assign values (along with
	uncertainty) to the underlying subunits, according to some information about
	their heterogeneity.
Upscaling	the process of aggregation to a larger scale; i.e., a many-to-one problem. An
	example is the upscaling of information from many trees at a site to a single
	site-level estimate (e.g. a mean site chronology). Another example is the
	summing of biomass increment estimates from all trees in a forest plot to
D 1.0	reach a stand-level estimate of biomass increment.
Resolution	Also known as "grain", the smallest measurement unit in either space or time.

95 With the exception of parts of the tropics, tree-ring availability is now quasi-global (Babst et

96 al., 2017), inviting the use of existing archives in a variety of research contexts. However, 97 tree rings remain a very local and variable product of tree-internal processes that are 98 modulated by the tree's immediate biotic and abiotic environment (Rathgeber et al., 2016). 99 Making inference and prediction at larger spatial scales based on such local data (involving 100 scaling, interpolation, and projection; Table 1) is challenging and introduces uncertainty that 101 researchers need to be aware of and – to the extent possible – quantify (Figure 1). To that 102 point, inference and prediction at large scales is complicated by heterogeneity (Scholes, 103 2017), for example when a tree-ring network insufficiently represents forest structure, 104 composition, and disturbance regimes across a landscape. Further, fixed statistical 105 relationships often fail to capture non-linearities and feedbacks in environmental systems, 106 calling for mechanistic process representation when modeling tree growth (Section 4). In this 107 light, we find it prudent to quickly pause and examine the potential and challenges associated 108 with scaling tree-ring information. Herein, we address the following three steps:

109

110 (A) From the sample to the whole tree: Tree-ring samples are collected as cross-sections, 111 increment cores, or micro-cores. Regardless of their shape or size, these samples capture 112 growth only at one location along the stem, branch, or root. Multiple samples are often 113 collected from the same individual. After ensuring correct dating of each sample visually 114 and statistically (i.e. "crossdating"; (Black et al., 2016), the measurements of all samples 115 are combined to represent the individual. This first step of upscaling (Table 1) usually 116 uses simple averaging, but can involve more complex approaches such as allometric 117 scaling or structural modeling (Wagner et al., 2017).

(B) From the tree to the site: A "site" is the area that encompasses the sampled individuals.
Upscaling to the site level means combining the measurements from all individuals into
one or multiple time series. This step has typically been approached either by averaging

121 or summing, depending on the tree-ring parameter and the research question: (1) 122 detrending and averaging for total or partial ring width, wood density, and blue intensity; 123 (2) either summing measurements from all individuals within a defined area (Babst et 124 al., 2014b; Dye et al., 2016) or multiplying their average by a known stand density 125 (Alexander et al., 2017) for basal area, volume, and biomass increment; (3) either 126 averaging individual measurements or combining the material from multiple individuals 127 into one measurement ("pooling") for stable isotopes (McCarroll and Loader, 2004); (4) 128 averaging for cell-level measurements, such as cell number, lumen area, or secondary 129 wall thickness (Peters et al., 2018; Rathgeber et al., 2016).

(C) From the site to larger spatial scales: Site records are compiled into tree-ring networks
to cover regions or continents. Depending on the research question, these networks are
either assessed in their entirety, or sites are grouped by species (Zhang et al., 2017),
growth variability (Seim et al., 2015), growth trends (Hellmann et al., 2016), climate
response (Babst et al., 2013; Björklund et al., 2017; Charney et al., 2016; Martin -

Benito and Pederson, 2015), or biogeography (Girardin et al., 2016). At the heart of these spatial assessments are analyses of climate-growth relationships – sometimes combined with clustering techniques, dimension reduction, or embedded in a machine learning framework (see Section 2.2.1). The resulting regional records are assumed to represent the geographic space covered by the underlying tree-ring network, an assumption that will need thorough testing in the future (see Sections 2.1 and 5).





Figure 1: Overview of the propagating uncertainty during the upscaling of tree-ring data.
The primary sources of uncertainty are listed for each scaling step (A-C) at the example
of Norway spruce (*Picea abies*). The sample images are adapted from (Babst et al.,
2014a) and the species distribution map is from lutherie.net/eurospruce.

148 If these upscaling steps are carefully followed and cumulative uncertainties are adequately 149 considered, tree-ring data can theoretically meet the demand for global information on long-150 term forest growth. In practice, however, a series of challenges related to how, where, and 151 when samples have been collected accompanies the transition of tree rings from a local to a 152 global resource.

153

142

- 154
- 155

## 1.2. Challenges associated with scaling tree-ring data

The heterogeneity of environmental systems is best represented if data points are distributed systematically or randomly across the target space. This is not the case for the vast majority of existing tree-ring records because scaling was historically not the goal of dendrochronological sampling. Instead, data collection has been study-specific, for example 160 to date archaeological material, detect disturbance events, or assess the co-variation of tree 161 growth with an environmental variable. More recently, the scope of tree-ring research has 162 broadened to include ecophysiology (Levesque et al., 2017), wood anatomy (von Arx et al., 163 2016), and growth phenology (Cuny et al., 2015). This is fortunate because these emerging 164 fields are considerably advancing our understanding of tree functioning, which will allow 165 non-linearities and feedbacks to be mechanistically modeled and reconstructed (see Section 166 4). Yet, their sampling strategies are also not geared towards scaling and their contribution to 167 representing larger spatial scales with tree-ring observations remains minor. This diverse 168 sampling background complicates upscaling of tree-ring information across all three steps:

169

170 (A) Representing the whole tree: Mature trees are usually sampled along the lower part of 171 the stem, which is oldest and most accessible. How representative stem growth at this 172 location is for the entire tree body depends on the dynamics of resource allocation and 173 biomass formation. Assessing this variability would require sampling an individual at 174 multiple heights, a laborious technique that is readily applied to shrubs (Buchwal et al., 175 2013) but almost never performed on tall trees (but see (van der Maaten-Theunissen and 176 Bouriaud, 2012). In addition, tree boles are never perfect cones and uncertainty from 177 collecting only few samples around the stem needs to be reduced (Bakker, 2005). 178 Another limitation of most existing tree-ring records is that tree dimensions (e.g. 179 diameter and height) at the time of sampling have not been recorded. This hampers the 180 estimation and reconstruction of whole-tree volume or biomass - and thus the 181 representation of growth in absolute terms (Babst et al., 2014b). Aside from physical 182 sampling, our limited understanding of tree-internal processes can bias ecophysiological 183 conclusions drawn from tree-ring data. For instance, tree-ring stable isotope ratios differ 184 from those of freshly produced carbohydrates in leaves because additional isotopic fractionation and mixing occur during transport and transitory storage (Gessler et al.,
2014). These effects are not well understood.

187 (B) Representing the site: A traditional focus of tree-ring sampling has been on old and 188 usually dominant individuals of a single species (Cook et al., 1995) that respond to a 189 strong common environmental driver. This approach has served to maximize the 190 common growth variability among trees, which could then be used as a proxy, e.g. for 191 climate reconstruction. Such selective sampling clearly contradicts the objective of 192 quantifying forest growth, because failure to represent the full tree population at a site 193 and over time can severely bias tree-ring estimates of biomass accumulation (Brienen et 194 al., 2017; Nehrbass - Ahles et al., 2014; Peters et al., 2015). In addition, the 195 documentation of most tree-ring records in public archives (e.g. the International Tree 196 Ring Data Bank; ITRDB) is insufficient in terms of site extent, species composition, and 197 forest age or size structure.

198 (C) Representing larger spatial scales: An ideal network of tree-ring sites covers the 199 geographic extent of the study area and reflects, in proportion to the area they occupy, 200 the range of bioclimatic conditions experienced by a given species within this area. This 201 ideal has probably rarely been achieved. Instead, traditional sampling for 202 dendroclimatological purposes has often targeted areas with marginal growth conditions, 203 which only occupy a small fraction of the landscape. We note, however, the difficulty of evaluating the spatial representativeness of existing networks because appropriate 204 205 reference datasets are often lacking (see Section 2.1). If very large amounts of tree-ring 206 data are compiled in mixed-species networks, their coverage can be more readily 207 assessed. For example, a recent evaluation of the ITRDB indicated good coverage of 208 climates with a mean annual temperature below 15 °C, whereas the spatial distribution of 209 sites was strongly biased towards North America and Europe (Babst et al., 2017). Yet,

even across these well-replicated continents, most records are subject to the abovementioned sampling biases and the lack of biometric measurements restricts analyses to
relative (i.e. detrended) growth variability and its climate response (Charney et al., 2016;
St George and Ault, 2014). Going forward, it will be important to develop new tree-ring
networks in more consistent and spatially representative ways (see Sections 2 and 3).

215

216 Uncertainties arising from the above-listed challenges may be more or less relevant in the 217 context of a given study, but they generally propagate through all spatial scales (Figure 1). 218 This does not preclude tree rings from being used in global research, but adds weight to 219 careful data treatment. In the following, we review possibilities to facilitate the scaling of 220 existing and newly collected tree-ring data. In Section 2, we discuss statistical approaches to 221 derive spatial patterns from existing networks, such as the ITRDB. Section 3 highlights 222 possibilities to produce spatially explicit records of forest growth by integrating the temporal 223 information from tree rings with the spatial information from forest inventories and remotely 224 sensed Earth observations. Section 4 describes tree-ring and vegetation models of increasing 225 complexity and scope that can provide a mechanistic understanding of tree growth, which is 226 particularly relevant for predictions into future time frames. In addition to this general 227 review, we provide in each section a practical example related to tree ring-based inference at 228 large scales.

229

## 230 2. Spatial patterns from detrended tree-ring data

## 231 *2.1. On the climate sensitivity bias in global archives*

Thus far, analyses of tree-ring networks have primarily been based on establishing statistical relationships between annual tree-ring records and monthly to seasonal climate. This is because climate is the most important driver of inter-annual tree growth variability around the 235 globe (St George and Ault, 2014) and long-term instrumental records of temperature, 236 precipitation, and derivatives thereof are readily available. However, an important 237 precondition for this approach is that the trees that constitute a tree-ring network actually do 238 respond to changes in one or multiple climate parameters. In other words, the statistical 239 relationships are strongest in areas where climate is most limiting for growth (Fritts, 1976), 240 for example at the cold or dry edge of a species' distribution range. It is exactly these 241 restrictive environments that have frequently been targeted by dendroclimatologists to 242 maximize the co-variation of the tree-ring proxy with the desired climate parameter for 243 reconstruction (e.g. (Wilson et al., 2016). Hence, it seems likely that - even though 244 palaeoclimatology is only one facet of tree-ring research – marginal sites are overrepresented 245 in global tree-ring archives. Depending on the severity of this bias, it may accentuate the 246 derived biogeographic patterns in the climate response of forests (Babst et al., 2013; Charney 247 et al., 2016; St George and Ault, 2014; Zhang et al.) and the networks cannot be considered 248 to be fully representative of forest growth at large scales.

249

250 Quantifying this putative oversensitivity to climate in large tree-ring archives requires the 251 development of new, representative reference networks (see Section 3.1). Initial research in 252 this direction suggests considerable geographic variation in the magnitude of the climate 253 sensitivity bias. For example, Klesse et al (in review a) found that ITRDB tree-ring time series in the US Southwest were 40 to 60% more sensitive to climate variation than 254 255 surrounding samples collected in forest inventory plots. When the two datasets were used to 256 estimate growth trends in response to projected climate change through 2099 in this region, 257 the ITRDB trees implied a 41% greater decline in growth compared to the representative 258 forest inventory sample. By contrast, a Europe-wide comparison of tree-ring data from the 259 ITRDB against a newly collected network of sample plots showed no significant difference in climate sensitivity (Klesse et al. in review b). Hence, a general statement on the magnitude of the climate sensitivity bias in the ITRDB cannot be made at this point and further evaluation efforts – including collating existing data not available through public repositories and/or developing new networks of tree-ring records – will be crucial to increase the representativeness of tree-ring archives for global forest growth.

- 265
- 266

#### 2.2. Statistical projection of relative growth variability

267 Because the collection of tree-ring data worldwide and in near real-time is unrealistic, the 268 goal of upscaling from sites to landscapes (step C) can only be achieved via projection of tree 269 growth across areas where measurements are missing. This is possible based on empirically 270 calibrated relationships between tree growth and its abiotic drivers. For example, networks of 271 detrended tree-ring width data can be used to detect synchronous growth anomalies across 272 sites and help attribute them to the spatial extent of extreme climatic events (Babst et al., 273 2012). One limitation of this approach, however, is the small number of available predictor 274 variables that are spatially resolved and cover sufficiently long time scales. Indeed, the length 275 of most earth observations records does not allow calibrating robust statistical models that 276 could be used to predict tree growth variability. This leaves gridded climate products (e.g. 277 (Harris et al., 2014) as the only option, although these data have some caveats when used in 278 the context of bioclimatic niches (Ols et al., 2017). Climate is an important driver of global 279 tree growth variability, but it is not the only one. The very best calibrations that have been 280 optimized for climate reconstruction explain 50-60% of the variance in the instrumental 281 target (Wilson et al., 2016), whereas seasonal climate-growth relationships that emerge from 282 large networks are much weaker (St George and Ault, 2014). In addition, the seasonality in 283 climate response differs considerably between climatic domains, making it impossible to 284 globally attribute growth variability to climate during a single season. For all these reasons, new and creative statistical approaches are needed to be able to project radial growthvariability at large spatial scales.

- 287
- 288

## 2.2.1 Practical Example 1: Towards gridded tree-ring width anomalies for Europe

289 Here we present and evaluate a machine learning approach to produce gridded tree-ring 290 products at continental scales. We thereby pursue a purely empirical approach (as opposed to 291 mechanistic formulations of biophysical processes; see Section 4) and estimate relative radial 292 growth variability from a set of climatic predictor variables in a regression model. We used 293 random decision forests (RDF; (Breiman, 2001), a well-established technique that provides a 294 flexible framework for learning nonparametric and nonlinear relationships when faced with 295 many and collinear predictors. Our RDF models each contained 100 random decision trees 296 and the final tree-ring width anomalies were predicted by averaging the outputs of each 297 individual decision tree to prevent overfitting. RDF models need to be trained with observed 298 datasets (Figure 2). For this we used European tree-ring width chronologies from the ITRDB 299 (detrended with a 30-year cubic smoothing spline) and climate data from the corresponding 300 CRU TS-3.22 grid cells (Harris et al., 2014), including monthly minimum, mean and 301 maximum temperature, diurnal temperature range, ground frost frequency, precipitation, wet 302 day frequency, vapor pressure, potential evapotranspiration, and cloud cover. Climate data 303 from the preceding and current years (24 months) were entered in the model to account for 304 lag effects frequently observed in tree-ring data (Zhang et al., 2017). The ITRDB contains 305 enough data (~1000 European sites) to train individual RDF models separately for the most 306 frequent tree genera (Table 2), many of which are primarily represented by one species. In 307 addition, we trained a model where sites from all genera were pooled together. To evaluate 308 model performance, we applied a leave-one-site-out cross-validation, under the condition that 309 a specific chronology was only estimated based on other sites of the same genus that do not

	Monthly pro	Monthly predictor variables		Seasonal predictor variables	
Genus	MEF	RMSE	MEF	RMSE	
Abies	0.329	0.146	0.261	0.527	
Fagus	0.313	0.179	0.257	0.512	
Larix	0.158	0.204	0.090	0.302	
Picea	0.310	0.127	0.245	0.515	
Pinus	0.240	0.130	0.173	0.430	
Quercus	0.326	0.136	0.267	0.534	
All sites	0.287	0.145	0.225	0.485	

311

Table 2: Performance of random forest regression models for predicting the growth variability of individual tree genera across Europe, assessed with a leave-one-site-out validation. Seasonal climatic predictors were aggregated for both the previous and current years (March – May; June – August; September – November) and the winter in between (December – February). MEF – Nash-Sutcliffe modeling efficiency; RMSE – root mean square error

318

319 Across the entire European network, approximately 29% of the variance was explained (i.e. a 320 Nash-Sutcliffe modeling efficiency (MEF; (Nash and Sutcliffe, 1970) of about 0.29; Table 2). 321 Importantly, RDF models with monthly predictors yielded stronger predictive accuracy 322 compared to those with seasonally aggregated predictors. This underlines the changing 323 seasonality in climate response across the represented climatic domains (Babst et al., 2013). 324 The RDF models for individual genera performed similarly to the overall model (31-33% 325 explained variance), except for Larix and Pinus where MEF was lower. For Larix, this is 326 likely due to well-documented periodic defoliation by the Larch budmoth (Esper et al., 2007), 327 which negatively affects growth and partly decouples it from its climatic drivers. Excluding 328 known budmoth years is thus a possibility to improve future RDF predictions. For Pinus, the 329 lower RDF performance could simply be related to the large number of *Pinus* species that are 330 represented on the ITRDB, which increases both the distribution range and the diversity in 331 climate response.

333 After the training phase described above, the inferred RDF models were combined with the 334 gridded data products of the CRU TS-3.22 dataset to project radial growth anomalies across 335 Europe, yielding annual raster maps of relative growth variability for each tree genus (Figure 336 S1, Appendix A). Projection excluded those areas falling outside the geographic distribution of a given genus (referencing the 1 km<sup>2</sup> resolution distribution maps in the European Atlas of 337 338 Forest Tree Species; (de Rigo et al., 2016). Accordingly, a CRU TS-3.22 grid cell (0.5° 339 resolution) was included, if it covered at least one smaller grid cell from the distribution maps 340 that reported a presence of the genus at >5%. Encouragingly, our first results show clear 341 differences in spatial growth variability among genera (Appendix A), even for those that 342 belong to the same plant functional type. In addition to attributing these patterns to specific 343 drivers, we are working on improving the RDF performance. This could be achieved by 344 including not only the inter-annual climate variability in the models, but also the long-term 345 mean climatic conditions at each site. This way, the contrasting effects of, e.g., a warm 346 anomaly under cold-humid (expected growth increase) vs. hot-dry (expected growth decrease) 347 conditions can be better accounted for. In addition, we aim to consider non-climatic drivers in 348 the RDF models as suitable spatial data become available.



349

Figure 2: Random decision forest approach to produce gridded projections of radial tree growth variability. This example includes all *Fagus sylvatica* sites that were available from the International Tree-Ring Data Bank as of October 2016.

#### 353 *2.3.* Spatially varying climate responses of radial tree growth

354 The statistical exercise presented in Section 2.2.1 assumes that climate-growth relationships 355 are fixed throughout the domain of interest, whether across all species or in taxonomic groups 356 (genera) – an assumption that we address in the following. It also showed that predicting 357 relative growth variability from climate variability alone leaves a considerable fraction of the 358 variance unexplained. By contrast, changes in the underlying climate-growth relationships 359 should be more straightforward to predict and project because they follow gross 360 biogeographic patterns (Babst et al., 2013; Charney et al., 2016). Indeed, a substantial body 361 of literature has successfully mapped historical climate-growth relationships across space and 362 time (Martin - Benito and Pederson, 2015; Restaino et al., 2016; St George and Ault, 2014). 363 However, if the goal is to interpolate local observations of climate response across the 364 intervening geographic space between unevenly distributed sites, a series of spatial 365 challenges emerges. A first challenge relates to differences in the climate response between 366 species at a given location (Teets et al., 2018). Accounting for this requires high-resolution 367 maps of species composition for the entire target region, which may not exist everywhere 368 and/or lack *in-situ* quality checking (Serra-Diaz et al., 2017). Hence, the influence of species 369 composition on the climate response of forests remains difficult to assess at large scales 370 (Grossiord et al., 2014). A second challenge stems from limited information on micro-371 climate, nutrient availability, hydrology and topography. Such abiotic micro-site conditions 372 can alter the climate response of trees (Nicklen et al., 2016; Salzer et al., 2009), but high-373 resolution data across the scaling area are rarely available. These two challenges are 374 compounded by a third challenge: a shortage of tree-ring data for many species and certain 375 ecoregions, especially in the tropics, that are severely under-represented in public archives

376 (Babst et al., 2017).

378 These spatial challenges force researchers to find a balance between the level of detail that is 379 considered in an analysis and the spatial scale that can be reached with the available data. 380 One relatively coarse option is to construct a single statistical model that describes growth as 381 a function of the climatic niche that encompasses all trees within the scaling region, 382 regardless of species (e.g. the "all sites" RDF model in Section 2.2.1). If we looked at a slice 383 of this growth-climate function along one climate axis of the niche, we would expect it to 384 look unimodal (Figure 3a). However, the underlying function would be multivariate, 385 nonlinear, and relatively data-intensive to parameterize. In addition, this approach assumes 386 that spatial differences in climate response can be solely attributed to gradients in the baseline 387 climate, rather than to differences in species composition, competition, or other co-variates. 388 In other words, site- and species-specific characteristics are averaged out for the sake of 389 generalization, which may be necessary to reach very large spatial domains. In a global 390 context, it may be plausible to subject all species to the same treatment because 391 biogeographic patterns in climate response are generally more pronounced than differences 392 between species (Fritts 1976). In reality, this assumption is violated, because important biotic 393 drivers of tree growth (e.g., pests and pathogens) are observed to be species-specific (Esper et 394 al., 2007).



Figure 3: Idealized growth rate as a function of a single climate variable across the target
niche (a). This function can be approximated by a series of linear segments obtained from
local climate response zones (b).

399

400 A refined version of this approach, while still pooling all species, is to construct separate 401 growth-climate functions for geographic sub-areas ("response zones") of the target domain 402 (Charney et al., 2016). This allows approximating the global response curve with a series of 403 local linear models specific to these response zones (Figure 3b). The zones themselves could 404 be based on existing ecoregions (Omernik and Griffith, 2014) or other (e.g. geological) 405 criteria to account for some of the missing non-climatic co-variates. Alternatively, they can 406 be inferred from the climate responses contained in the tree-ring time series themselves. For 407 instance, Charney et al (2016) defined response zones by first clustering tree-ring sites across 408 North America based on their climate correlation functions and then used an RDF analysis to 409 assign all grid cells on the landscape to one of the clusters according to their baseline 410 climates. This has the significant advantage that, as baseline climates shift in the future, both 411 geographic (i.e. poleward) shifts in the response zones and changes in the climate sensitivity 412 itself can be accounted for. Moving forward, a further refinement could be to capture 413 variation in the local slopes of climate-growth relationships using models that include both 414 long-term climate normals and short-term climate anomalies (and interactions between them) 415 as predictors of growth. In particular, this would capture continuous variation in climate-416 growth responses across climatic gradients.

417

418 Clearly the most precise approach would be to construct the growth-climate function 419 including the effects of individual species. Besides considering species-specific 420 characteristics, this would also account for the fact that populations near the distribution limit 421 are genetically adapted to respond less strongly to variability in limiting climatic drivers 422 (Housset et al., 2018). However, detailed maps of species locations and composition would still be required to represent the actual climate response at a given location (de Rigo et al., 2016; Serra-Diaz et al., 2017) and weight the species-specific responses in a mixed species system. In addition, representative tree-ring data from across the entire distribution range is needed, which is currently not available for most species. Establishing this observational basis through data mining initiatives and the development of new and spatially representative tree-ring networks will be key to enable the projection of species-specific climate responses with precision.

430

431 In contrast to the spatial challenges described above, temporal limitations to empirically 432 forecasting the climate response will not be resolved by extensive and representative 433 sampling. One reason is that the overlap between tree-ring and instrumental data is often 434 limited to a few decades and extrapolation to future time frames is thus based on relatively 435 short-term observations. This is problematic because the climate response is not only 436 determined by how tree growth corresponds to climate on an inter-annual basis. The response 437 can be modified by longer-term climate patterns (Madrigal-González et al., 2017; Mendivelso 438 et al., 2014) that are not captured in short time series. In addition, there may be a 439 compounding effect when "ecological memory" leads to lagged responses after disturbances 440 or climate anomalies (Ogle et al., 2015), or when a recurring climate anomaly alters the 441 growth response itself (Brzostek et al., 2014; Galiano et al., 2012). For example, one hot 442 summer may lead to only a minor decrease in growth rate in a drought-prone region, whereas 443 a sequence of hot summers can cause increasingly dramatic growth declines. By contrast, 444 there can be acclimation, wherein the recurrence of a climate anomaly (e.g. drought) lessens 445 the strength of the growth response (Ainsworth and Long, 2005; Farrior et al., 2015). This is 446 possible because trees are plastic organisms that can shift their resources over time, e.g. by 447 growing more roots, restructuring branches, thickening the bark, or decreasing leaf size. Such 448 physiological changes allow trees to better conserve water and return to normal growth more 449 rapidly after a drought episode. In addition, when we aim to forecast over time periods of 450 generations, we have to consider the possibility of genetic adaptation and species migration 451 (Aitken et al., 2008; Housset et al., 2018). Both of these processes tend to make future 452 generations of trees growing at a location better suited to the new climate than the preceding 453 generations. Finally, the trees of the future are likely to experience different combinations of 454 temperature, precipitation, and atmospheric CO<sub>2</sub> concentrations than those in the past 455 (Ainsworth and Long, 2005). Hence, any attempt to statistically forecast based on stationary 456 observations from the past is always fraught (Gustafson, 2013). For all of these reasons, an 457 advanced mechanistic understanding of tree growth and climate response is needed (Section 458 4).

459

## 460 **3.** Integration of tree rings with other ecological or Earth observations

461 Tree-ring data offer decadal- to centennial-length records of radial tree growth at (sub-462 )annual resolution, allowing growth variability and its drivers to be investigated through time. 463 However, quantifying absolute tree- and site-level growth (steps A and B) from tree rings 464 requires additional information on the dimensions of trees and the characteristics of a forest 465 stand. This kind of information is increasingly available from forest inventories and Earth 466 observations. In turn, tree-ring data can help compensate the coarse temporal resolution of 467 forest inventories (plots are typically revisited once every 3-10 years) and the generally short 468 time series of both data streams. Bringing together the temporal and spatial strengths of these 469 three types of observations opens possibilities to quantify tree growth across a range of 470 scales.

471

#### 472 *3.1. Forest inventories*

Tree rings have been used to assess tree growth in a forestry context since the mid-19<sup>th</sup> 473 474 century, but it is only recently that collections made by forest inventory programs or in other 475 permanent sample plots are being developed into data networks. Examples of these initiatives 476 include Canada (Duchesne et al., 2017), the western United States (DeRose et al., 2017), 477 Romania (Bouriaud et al., 2016), Mexico (G. Gutierez-Garcia, pers. comm.), and parts of the 478 tropics (Brienen et al., 2016). These data are already being used, e.g., to detect signals of CO<sub>2</sub> 479 fertilization (Girardin et al., 2016) or to assess shifts in growth response to climate (Charru et 480 al., 2017; D'Orangeville et al., 2016). Here we lay out opportunities to quantify trends and 481 temporal variability of tree growth that emerge from this novel type of tree-ring network. We 482 also discuss statistical tools for integrating tree-ring with forest inventory data and thereby 483 move beyond the traditional statistical modeling based solely on the principle limiting factors 484 (Fritts, 1976). Finally, we identify some of the challenges that remain for combining tree-ring 485 and forest inventory data into long-term records.

486

487 Collecting tree-ring data in a forest plot context has three major advantages with respect to 488 the scaling and projection of growth or aboveground biomass increment (ABI): 1) sampling 489 is comparatively representative or unbiased, 2) absolute rather than relative tree growth can 490 be quantified, and 3) the inventory offers complementary information on the characteristics 491 of the forest stand in which a tree is growing. Together, these advantages help overcome 492 some of the limitations associated with traditional tree-ring sampling and modeling (see Section 1.2). National forest inventory (NFI) programs are specifically designed to make 493 494 estimates of forest characteristics (area or volume of forest; number and dimensions of trees) 495 at large spatial scales from carefully designed networks of sampling plots (Bechtold and 496 Patterson, 2005). The design may vary from one political entity to another (McRoberts et al., 497 2009), but their spatial representation of forested areas is essentially unparalleled. Within plots, the collection of increment cores in an unbiased manner with respect to tree species and
size or age classes makes sampling more representative of a forest (and overall forest growth)
compared to that designed for dendroclimatological purposes (Nehrbass - Ahles et al., 2014).

Tree-ring data collected in forest plots that are not part of an NFI also make useful contributions to the overarching goal of building representative networks, particularly when the plots are arranged along environmental gradients (e.g., (Buechling et al., 2017; Foster et al., 2016; Rollinson et al., 2016; Sánchez-Salguero et al., 2015). This "representativeness" within forest stands and across landscapes is key to addressing the heterogeneities, nonlinearities, and feedbacks that make scaling a challenge (Scholes, 2017).

507

508 Increment cores collected in forest plots are usually associated with measurements of tree 509 dimensions and stand conditions. A measurement of diameter at breast height (DBH) at the 510 time of sampling makes it possible to reconstruct annual tree diameter (Bakker, 2005), which 511 can then be transformed into absolute estimates of tree growth (Alexander et al., 2017; Babst 512 et al., 2014b). Analyzing absolute growth is key to addressing questions about the role of 513 forests in the terrestrial carbon cycle and integrating tree-ring data with observed or simulated 514 forest productivity (Babst et al., 2014a), Klesse et al. in review b). In this context, metrics 515 like basal area increment (BAI) and ABI are more useful and interpretable than relative 516 growth variability generated by detrending raw tree-level measurements (Cook et al., 1995) 517 to construct a site-level chronology. Besides the associated loss of inter-tree variability, 518 detrending is one of the most subjective and debated aspects of tree-ring research because the 519 choice of method critically affects the environmental information that is preserved in ring-520 width time-series (Sullivan and Csank, 2016).

522 Individual tree growth is also influenced by competition from neighboring trees, and in a 523 carbon accounting context, it becomes critical to quantify, understand, and project such 524 demography-driven changes in forest growth (Chen et al., 2016; Trotsiuk et al., 2016). 525 Capturing the influence of competition on individual tree growth is also key to scaling step B 526 (Figure 4) because individual tree growth both influences and is influenced by forest stand 527 basal area, forming a self-regulating (density-dependent) feedback. Tree-ring data collected 528 in a forest plot context make it possible to model the influence of forest stand conditions 529 explicitly, as exemplified in several recent studies (Buechling et al., 2017; Foster et al., 2016; 530 Rollinson et al., 2016; Sánchez-Salguero et al., 2015). Including such in-situ information in 531 statistical models is expected to produce more realistic predictions of tree growth compared 532 to those based exclusively on climate variability. 533 A В Observations:





Figure 4: Scaling of tree growth from observations of bole diameter and tree-ring width to tree- and site-level aboveground biomass (AGB) involves upscaling steps A and B. Forest plot data provide information on the drivers of tree growth, including site factors such as slope, aspect, and soil conditions, stand-level basal area, and climate.

540 These three characteristics of tree-ring data collected in a forest plot context – 541 representativeness, growth on an absolute scale, and accompanying information on the forest 542 stand – enable the scaling from individual observations of bole diameter and radial 543 increments to stand- and landscape-scale biomass accumulation (Figure 4). Annual 544 reconstructions of DBH can be transformed to whole tree biomass increments using 545 allometric equations (scaling step A; (Forrester et al., 2017). We note that the use of 546 allometric equations is associated with its own set of uncertainties (Alexander et al., 2017; 547 Nickless et al., 2011), some of which can be constrained with additional information derived 548 from tree rings. For example, time series of wood density variation, combined with allometric 549 estimates of tree volume, can improve estimates of whole-tree biomass increment (Bouriaud 550 et al., 2015; Clough et al., 2017). Tree-level biomass increment can then be summed across 551 individuals in the plot and adjusted by a known expansion factor (for either a fixed or 552 variable plot radius design; step B). Subsequently, the plot-level biomass estimates can be 553 scaled to the target population using plot-level expansion factors or pre-determined sample-554 based estimators (Bechtold and Patterson, 2005). Alternatively, plot-level estimates are 555 projected onto some other spatial scale using remote sensing observations (step C; Section 556 3.2; (Jucker et al., 2017).

557

558 Integration of tree-ring and other forest inventory data can also take the form of data 559 assimilation. The two data streams can for example be assimilated using a state-space model 560 (Clark et al., 2007), or a hierarchical Bayesian model with two regressions, one for each type 561 of observation, and a constant of proportionality between corresponding regression 562 coefficients (Evans et al., 2017). Both of these statistical approaches can additionally take 563 advantage of bole diameter re-measurement data for trees with and without increment cores 564 and model the multiple influences on individual tree growth explicitly. Assimilation of these 565 two sources of information on the common process of tree growth should advance our 566 understanding of that process, while refining estimates of both process variability and 567 measurement uncertainty - key elements for improved forecasting of forest ecosystems 568 (Dietze, 2017).

570 An important limitation on long-term reconstructions of NFI plot-level growth arises from 571 temporal changes in stand conditions (e.g., demography and competition). Specifically, the 572 trees that are alive at the time of sampling do not necessarily represent a random subset of the 573 trees that once lived. While random or systematic sampling avoids the biases associated with 574 the tree-selection principle of traditional dendroclimatology, other biases remain (e.g., slow-575 grower survivorship bias, big-tree selection bias, and large tree bias sensu (Brienen et al., 576 2012). These pitfalls highlight the merits of establishing and maintaining permanent NFI 577 remeasurement plots on a multi-decadal scale that can track temporal changes in stand 578 conditions and complement time-series of climatic predictors in statistical models. However, 579 most existing NFIs do not yet offer sufficient temporal depth to account for forest dynamics. 580 One possible solution is to apply the best available empirical models of stand development 581 (i.e., growth-and-yield models, density management diagrams, empirical succession 582 mapping) to reconstruct past stand conditions. Related (Bayesian) approaches may use state 583 data assimilation or a state-space modeling framework to parameterize models of stand 584 development from experimental forests where data do extend for several decades. Addressing 585 the slow-grower survivorship and big-tree selection biases, as well as the competitive 586 influence of trees that are no longer on the landscape will be crucial to fully realizing the 587 research potential of paired tree-ring and forest plot data to reconstruct forest growth in pre-588 inventory times.

589

590 *3.2. Earth observations* 

Remotely sensed Earth observations have long been valued as a tool for broad-scale quantification and monitoring of ecosystem dynamics across space and more recently also time (e.g. (Zhu et al., 2016). The increasing length of continuous satellite records facilitates integration with temporally more coarsely resolved data such as tree rings (Vicente-Serrano et al., 2016). In addition, we emphasize here that the combination of tree-ring data with earth observations is not restricted to large-scale applications, but that it can support and advance all three scaling steps (Figure 5). This is possible because – independent of the spatial scale – all information derived from remote sensing systems is fundamentally based on relating spectral reflectance data to field measurements via empirical models.

600



601

Figure 5: Overview of the spatial scales at which tree-ring and remotely sensed observations
can be integrated to support the three upscaling steps (A-C). dam - decameter

Terrestrial light detection and ranging data (LiDAR; also called terrestrial laser scanning, TLS) are the remotely sensed data most relevant at the individual tree scale. The application of TLS systems to characterize forest stands began about a decade ago (Newnham et al., 2015) and recent methodological advances have included structural modeling of individual trees based on TLS point clouds (Åkerblom et al., 2015). The potential to estimate aboveground (and even below-ground; (Liski et al., 2014) biomass from such data is increasingly 611 explored (Calders et al., 2015), but similar to conventional forest inventory data (Section 612 3.1), TLS does not provide temporal information on tree growth. Hence, the integration of 613 tree-ring and TLS data to reconstruct historical tree dimensions (step A) is promising, 614 because it avoids uncertainties related to the use of allometric functions and may offer a more 615 precise representation of individual tree shapes (Wagner et al., 2017). However, the 616 application of TLS in dense forest stands can be complicated by occlusion effects (e.g. 617 bushes or small trees blocking the view of the scanner), weather conditions (wind, 618 precipitation, or fog), and limitations of the scanning device itself. The latter concern mostly 619 the coarser spatial resolution of distant tree parts (i.e. crowns) compared to that of lower stem 620 parts, as well as the time it takes to scan an entire forest stand from a sufficient number of 621 angles to produce a continuous point cloud. How these challenges affect the integration of 622 TLS data with tree-ring measurements and the quality of the resulting tree volume 623 reconstructions is yet to be explored.

624

625 Airborne remote sensing is showing the most potential for scaling to the site level (step B). 626 LiDAR can provide three-dimensional information about vegetation structure at local to 627 regional scales and structure from motion photogrammetry can provide approximations 628 thereof. This information can be calibrated against *in-situ* data of basal area, canopy height, 629 biomass, stand density, or leaf area to assess spatial variability in these parameters (Jucker et 630 al., 2017). If repeated LiDAR flights are available, it is even possible to monitor temporal 631 dynamics in integrated and height-specific canopy parameters (Griebel et al., 2017), though 632 this is challenging. Temporally resolved LiDAR data are still very rare, but should become 633 more readily available with the increasing use of aircraft (Cunliffe et al., 2016) and drones 634 (Tang and Shao, 2015) in forest monitoring programs. Because of the discontinuous data 635 availability in both space and time, integration of airborne LiDAR with tree-ring records has so far been limited. This link will be strengthened in the future as advances are made on both
sides: tree-ring sampling will become spatially more representative (Section 3.1); airborne
LiDAR will increasingly be used to characterize not only larger forest stands, but also
individual trees (Eysn et al., 2015), which can complement the application of TLS in complex
stands. These efforts are converging towards more precise estimation and reconstruction of
tree- and stand-level biomass or basal area increment.

642

643 While integration of tree-ring data with terrestrial and airborne LiDAR is still in its infancy, 644 their combination with spectral data from polar-orbiting satellites is well established. 645 Examples of environmental research that has used this combination include ecology (D'arrigo 646 et al., 2000; Dorman et al., 2015; Huang et al., 2015), entomology (Çoban et al., 2014; 647 Sangüesa-Barreda et al., 2014) and hydrology (Morales et al., 2015). For example, tree-ring 648 data were used to verify an insect defoliation classification inferred from remote sensing 649 (Çoban et al., 2014), or as a proxy to reconstruct inter-annual fluctuations in lake area 650 observed from Landsat time series (Morales et al., 2015). The satellite-derived parameter 651 most frequently combined with tree rings has been the Normalized Difference Vegetation 652 Index (NDVI), a measure of vegetation greenness. With now over thirty years of repeated 653 observations, global data products such as the Global Inventory for Mapping and Modeling 654 Studies (GIMMS; (Tucker et al., 2005)), have allowed for the comparison of tree-ring and 655 NDVI responses to environmental change across a range of spatial and temporal scales 656 (Coulthard et al., 2017; Vicente-Serrano et al., 2013). The most common approaches have 657 been to either compare the climate signals that are embedded in these two data streams (Del 658 Castillo et al., 2015; Girardin et al., 2014; Pasho and Alla, 2015), or to correlate time series of 659 tree rings and NDVI directly (Beck et al., 2013; Berner et al., 2011; Bunn et al., 2013; 660 Girardin et al., 2016; Poulter et al., 2013; Vicente-Serrano et al., 2016). Generally, these studies have found a positive correlation between inter-annual NDVI variability and annual tree growth, but there are notable exceptions along the North American Arctic treeline (Beck et al., 2013), in Europe (Pasho and Alla, 2015), and in parts of Canada (Girardin et al., 2016) where this correlation is lacking. These exceptions point to two main challenges associated with the integration of tree-ring and satellite observations.

666

667 The first challenge concerns the mismatch in spatial scale between site-level observations of 668 tree rings and raster data from satellite sensors. The latter integrate surface reflectance 669 information at various spatial scales, e.g, 30 m for Landsat, 250 m for MODIS, and 1-8 km 670 for AVHRR. Each pixel integrates a mixture of species, disturbance histories, and land use 671 activities that may affect the spectral information and complicate the comparison with single-672 species tree-ring chronologies. The second challenge emerges from temporal mismatches 673 between the processes of canopy formation, leaf-level photosynthesis, and wood formation in 674 trees. The climate response of photosynthesis is more or less instantaneous, but the time lag 675 between photosynthetic carbon uptake, growth, and biomass increment is well documented 676 (Cuny et al., 2015). Further, it is well known that climate variability can have lagged effects 677 on tree growth via the storage and remobilization of carbohydrate reserves (Richardson et al., 678 2013; Zhang et al., 2017). For all these reasons, tree-ring data and vegetation indices cannot 679 be expected to correspond directly and the dynamics of these temporal lags likely differ 680 between ecosystems, species, and climatic domains.

681

## 682 *3.2.1 Practical Example 2: Comparing tree-ring and NDVI data across Canada*

To illustrate the temporal mismatch of canopy processes and stem growth, we compared treering width, NDVI, and their correlations with monthly CRU TS-3.22 temperature (Harris et al., 2014) from the corresponding grid cells across Canada's boreal forest (Figure 6). We 686 obtained tree-ring width data from 598 plots (19 species) that were established as part of the 687 Canadian NFI program. The tree-ring data were detrended using generalized negative 688 exponential models and whitened (see (Girardin et al., 2016) for details). For each plot, we 689 obtained the corresponding GIMMS-3g NDVI record (Tucker et al., 2005), aggregated into a 690 0.5° regular grid using nearest-neighbor interpolation and subsequently averaged at monthly 691 resolution. Point-wise Pearson correlations were computed between all three datasets over the 692 1982-2002 period. This analysis showed that tree-ring width and NDVI correlate in areas 693 where they are both driven by temperature during the same season (Figure 6). In some areas, 694 however, the seasonality in the climate response differed clearly between NDVI and tree-ring 695 width, which may at least partly explain why some studies report a spatially heterogeneous 696 correlation between the two metrics (Beck et al., 2013; Girardin et al., 2016; Pasho and Alla, 697 2015). From this, we conclude that spatiotemporal patterns in tree-ring data and vegetation 698 indices are not equivalent, and that their differing climatic drivers need to be considered in 699 any comparison.



Figure 6: Pearson correlation coefficients between detrended tree-ring width (TRW), the normalized difference vegetation index (NDVI), and temperature (tmp) over the 1982-2002 period. Panel (a): June-August NDVI *vs.* TRW; Panel (b): NDVI *vs.* tmp; Panel (c) June-August NDVI *vs.* tmp; Panel (d): TRW *vs.* tmp. Please note that sites and grid cells are ordered by increasing latitude in panels (b-d). Dashed lines separate the previous and current year.

707

## 708 4. Mechanistic modeling of tree growth

709 Statistical scaling allows capturing some of the landscape heterogeneity, but the static 710 relationships derived from observations are clearly limited in terms of representing non-711 linearities and feedbacks in ecosystems. Hence, there is need to include more process 712 information when linking wood formation to environmental variability, when reconstructing historical climate (Guiot et al., 2014), and especially when attempting to forecast into a future time frame (Gustafson, 2013). Figure 7 illustrates the current range of tree-ring model complexity, from highly empirical monthly time-step approaches (e.g. (Tolwinski-Ward et al., 2011) to highly physiological simulations of carbon and water flows in whole trees at very fine time steps (De Schepper and Steppe, 2010; Hölttä et al., 2010). A new approach is also shown within this scheme, with the objective of linking specific cambial-growth and whole-tree physiological models for global applications (see Section 4.2.1 for a description).



Figure 7: Models of xylogenesis have been developed at different levels of complexity and
across a range of temporal scales. Efforts are now being made to develop a new and broadly
applicable modeling approach (Section 4.2.1) that will simulate whole tree growth as a
function of environmental influences on physiological processes. Tmp – temperature; prc –
precipitation; lat – latitude; St – photosynthates; Rw – soil moisture

726

## 727 *4.1. Simulating radial growth as a function of climatic controls*

728 (Wilson and Howard, 1968) published the first model of intra-annual xylogenesis, which 729 reproduced the daily cellular development throughout the growing season using "rules" to 730 regulate cellular division, enlargement, wall thickening, and death. Realistic daily xylem 731 development was produced, but no environmental controls were imposed (i.e. the rates of 732 growth processes were model inputs), and so this approach can be considered "descriptive". 733 A handful of models were subsequently published (Howard and Wilson, 1972; Stevens, 734 1975; Wilson, 1973) that still required input parameters that vary in time to produce realistic 735 growth rings. To overcome these limitations, (Fritts et al., 1991) developed a mechanistic 736 model of daily cellular development called TRACH that was driven by temperature, water 737 balance, and day length. This approach was already more general and relatively mechanistic, 738 but it required as input the number of cells produced during the growing season and did not 739 consider the supply of growth substrates (see Section 4.2). Expanding upon some of the ideas 740 in TRACH, the now widely used Vaganov-Shashkin (VS) forward model of tree-ring formation (Vaganov et al., 2006) was developed. The VS model is built around the 741 742 assumption that external multivariate environmental forcing exerts a direct and potentially 743 non-linear influence on secondary tree growth. Accordingly, tree rings and their internal 744 structure (e.g. cell number and size) are simulated based on climatic controls on the kinetics of cell formation (Cuny et al., 2014; Rathgeber et al., 2016). The VS model includes two 745 746 basic conditions for the non-linear dependence of wood formation on the environment: the 747 Principle of Limiting Factor (Fritts, 1976) with respect to daily temperature and soil moisture, and a threshold growth response function to represent the dependence of cell formation onambient temperature and soil moisture (Vaganov et al., 2006).

750

751 The primary output of the VS model consists of synthetically generated standardized tree-752 ring indices that would be expected, if local climate were the only external driver of tree 753 growth. This is similar to empirical approaches (Section 2.2) and the skill of the VS model 754 (unless fine-tuned for specific sites) is roughly comparable to that achieved with statistical 755 transfer function methods that are commonly applied in dendrochronology (Cook and 756 Pederson, 2011; Evans et al., 2006). However, the VS model has significant advantages over 757 purely statistical models in that it provides daily-resolved estimates of integral growth rates 758 throughout the year and attributes them to different climatic drivers (Shishov et al., 2016). 759 This greatly facilitates the interpretation of inter- and intra-annual growth patterns, for 760 instance when capturing a reduction in radial growth rates during summer drought in 761 Mediterranean areas (Touchan et al., 2012). The applicability of the VS model has also been 762 demonstrated for other biomes across Asia and North America (Anchukaitis et al., 2006; 763 Evans et al., 2006; Shi et al., 2008; Zhang et al., 2011). Comparisons between VS-simulated 764 and observed tree-ring chronologies are particularly interesting, as they allow assessing 765 whether temporal non-stationarity in climate-growth relationships arise from climate change 766 alone (Anchukaitis et al., 2006), or from other (a)biotic sources.

767

Problematically, it is impractical to upscale site-level chronologies (step C) using the VS model because the detailed information (more than 40 tunable input parameters) that drives the simulation of cell-level processes in the model is unavailable at large spatial scales. Attempting to facilitate such large-scale application, a numerically more efficient forward tree-ring model, the Vaganov-Shaskin Lite (VSL), has been developed (Tolwinski-Ward et

773 al., 2011). The VSL model excludes the cell-level processes and has thus been reduced to a 774 product of three limiting climatic factors: temperature, soil water balance and solar radiation. 775 Further, it runs on monthly time steps and contains only 12 tunable parameters. A 776 disadvantage of this simplification is that the VSL model cannot resolve sub-monthly growth 777 processes related to, for example, variability in wood density (Björklund et al., 2017) or 778 growth phenology. However, monthly-resolved climatic input data are broadly available from 779 meteorological stations and often contain much fewer gaps than do daily observations. Hence, 780 the VSL model is widely applicable and has been deemed capable of reproducing the 781 variability in tree-ring width chronologies from more than 2000 sites on the ITRDB 782 (Breitenmoser et al., 2014). Moreover, outputs from satellite Earth observations (Section 3.2) 783 and dynamic global vegetation models (DGVMs; Section 4.3) are often provided at monthly 784 resolution, making the VSL model a good candidate for pseudo-proxy experiments (Evans et 785 al., 2013).

786

787 The VS model and its descendent have proven valuable for the study of forest growth 788 responses to climate change, but they still only include climate variables as input parameters 789 and do not consider other internal and external drivers of tree growth. Hence, their ability to 790 forecast tree growth and its climate response does not extend beyond that of empirical models 791 (Section 2). An interesting prospect is to integrate these VS-type models with vegetation 792 models that explicitly simulate relevant biological processes such as photosynthesis, 793 respiration, and resource allocation. For example, (Mina et al., 2016) recently demonstrated 794 that simulations of stand basal area with the ForClim model (Bugmann, 1996) could be 795 improved by implementing the seasonal climate response of synthetic tree-ring chronologies 796 from the VSL model. Such model-model integration approaches appear promising and should be extended to larger scales (e.g. using newly developing NFI networks; Section 3.1) and avariety of DGVMs.

799

# 800

## 4.2. Towards large-scale modeling of whole-tree growth

801 Tree rings are increasingly used to study the impacts of environmental change on forest 802 ecosystems and carbon cycling (Babst et al., 2014a; Babst et al., 2017). For such applications, 803 it is not sufficient to model only direct climate impacts on radial growth (Section 4.1). 804 Models need to additionally account for indirect effects of changing external forcing (climate, 805 CO<sub>2</sub>, etc.) via canopy-level processes (Li et al., 2014). An early example of this is the model 806 of (Deleuze and Houllier, 1998) that – similar to the VS model – was also designed to reduce 807 the parameterization requirements of TRACH and predicts intra-annual wood density profiles 808 of conifer species. In addition to simulating cambial cell division, enlargement, and wall 809 thickening as functions of climate, their model assumes that wall thickening is co-limited by 810 the supply of photosynthates, calculated from temperature and transpiration under the 811 assumption of fixed foliar mass. This model has been successfully used to study intra-annual 812 fluctuations in wood density, in combination with a more comprehensive treatment of plant 813 water and photosynthate transport (Wilkinson et al., 2015). However, the implemented cohort 814 approach to cellular differentiation limits comparisons with observed radial files (von Arx et 815 al., 2016) and does not include scaling of radial-file growth to the whole tree.

816

More recently, (De Schepper and Steppe, 2010) developed a whole-tree model of reversible (diurnal) and irreversible (structural) stem diameter variations, using a very detailed representation of dynamic water and sugar transport between numerous levels in a tree on a time step of less than one second. Irreversible radial growth occurs as a function of local turgor and sugar content, but the focus of the model is on reversible changes. (Hölttä et al.,

822 2010) built on this model by adding cellular-level dynamics and thereby produced a 823 remarkably comprehensive approach to modeling whole-tree growth, albeit omitting 824 hormonal control. Their approach is very promising as a detailed physiological treatment and 825 produces interesting conclusions regarding the effect of tree size on environmental 826 influences. However, photosynthesis and transpiration are computed off-line, rather than as 827 part of the model simulation, and a very large number of empirical parameters are required. 828 Furthermore, the high-resolution time-stepping and consequent computing demands limit its 829 application for large-scale studies of forest-environment interactions. Despite the knowledge 830 of xylogenesis captured by these models, there is to date no generally applicable approach to 831 modeling whole-tree growth at large scales. This would require a broadly applicable model 832 structure with a few key parameter differences between plant functional types (or ideally 833 species), as is currently implemented for photosynthesis in DGVMs (Section 4.3).

834

## 4.2.1 Practical example 3: Towards a broadly applicable whole-tree model

836 We have been building on the approaches discussed above to construct a whole-tree model 837 called "Grow Up", that is capable of being parameterized for any species and will be 838 incorporated into a DGVM framework. A tree is assumed to grow as a coordinated whole, led 839 by nutrient uptake and allocation, which promotes cambial activity, resulting in demand for 840 carbon and nutrients from the developing xylem. Cells in one lateral radial file per tree are 841 represented, with the processes of division, enlargement, wall thickening, and death 842 controlled by a range of external and internal factors (Figure 8). The activities of apical 843 meristems are also considered to enable whole-tree growth as described in (Hayat et al., 844 2017), an earlier version of our model. Reserve pools of carbon, nitrogen, and phosphorus 845 enable carry-over effects between years, and the relative activities of the different meristems 846 are controlled by shading, nutrient status, soil water, and phenological signals.

847

848 Three vectors are used to hold the state variables of the cells in the radial file: the cell 849 development stage (i.e. cambial initial, xylem mother, enlarging, thickening, or mature), 850 radial cell diameter, and cell wall thickness. When a cell matures, it is added to the tree stem and not treated further, although heartwood formation occurs in response to canopy die-back. 851 852 The vectors start with the innermost immature cell along the radial file and end at the 853 innermost phloem mother cell, which is a fixed anchor. The vectors are adjusted as cells are 854 added through division or lost through maturation. The primary outputs directly derived from 855 the xylogenetic component of Grow Up are annual width and mass increment of the stem, as 856 well as intra-ring density profiles. More detailed outputs such as the weekly kinetics of 857 cellular development can also be produced for comparison with observations obtained using 858 microcores (e.g. (Cuny et al., 2014). This basic xylogenetic scheme is assumed to be 859 universal in all tree species. However, our understanding of the rules governing cambial 860 activation and dormancy, the rates of cellular division, transitions between cell types, rates of 861 expansion, and rates of cell wall thickening, is currently incomplete and so we are now 862 focused on testing different hypotheses.



Figure 8: New model of cell development in a radial file using a vector approach and rules
for cell differentiation based on internal and external drivers. Tmp – temperature; St photosynthates

867

868 Our initial assumptions for the controls on the development of the radial file assume that the 869 rates of growth of cambial, mother, and enlarging cells are influenced by water supply, 870 temperature, a hormonal signal from the canopy, and the concentration of sugars in the 871 cambium using simple response functions. Cambial cells divide when they reach a critical 872 size, producing mother cells. Mother cells divide if they reach a critical size and transition to 873 (non-dividing) enlarging cells when they reach a certain distance from the phloem. Enlarging 874 cells enter the thickening phase once they reach a critical size, and thickening continues up to 875 a critical limit at which the cell dies and becomes mature and functional xylem (see Figure 8). 876 The critical cell sizes and cell wall thicknesses, as well as the rates of thickening, are 877 currently fixed parameters, with only the rates of cellular growth depending on environmental 878 factors. These assumptions are being tested using microcores collected as components of 879 various field campaigns and experiments (e.g. (Cuny et al., 2014). We are currently working 880 on implementing this scheme within the HYBRID9 DGVM framework, and it is anticipated 881 that this new approach will challenge the predictions of the current generation of DGVMs in 882 fundamental ways, as well as open them up to direct comparison with tree-ring archives.

883

*4.3.* Tree-ring integration with ecophysiological and dynamic global vegetation models
Climate policy relies heavily on predictions from earth system models and the DGVMs that
are part of them (Boucher et al., 2016). Problematically, current DGVMs struggle to simulate
forest growth and its climate response accurately, particularly at annual or longer time scales
(Anderegg et al., 2015; Pappas et al., 2017; Rollinson et al., 2017; Tei et al., 2017; Zhang et
al., 2017). Hence, we see great potential for both tree-ring observations and ecophysiological
models of tree growth to help evaluate and improve DGVMs. A conceptual challenge is

891 thereby to reconcile the carbon source (i.e. photosynthesis) and sink limitations on tree 892 growth (Fatichi et al., 2014; Körner, 2015). Sink limitations (see Section 4.1) and their 893 possible feedbacks on photosynthesis are currently not implemented in DGVMs, which 894 generates uncertainty (Friend et al., 2014) because growth is treated only as a downstream 895 process. Explicitly representing xylogenesis in DGVMs (see Section 4.2.1), or at least 896 evaluating DGVMs at stand and regional scales using ecophysiological models with explicit 897 tree growth modules, could be promising ways to refine projections of forest carbon cycling. 898 Until this approach can be fully implemented and rigorously tested, tree rings should 899 continue to be used in DGVM development by serving as observational references for model-900 data comparisons and model parameterization.

901

902 Past research has revealed a large spread in the ability of different DGVMs to reproduce 903 patterns observed in tree rings. Besides being exceedingly sensitive to climate variability 904 (Rollinson et al., 2017; Zhang et al., 2017); Klesse et al. in review b), modeled NPP tends to 905 recover much quicker after extreme events (Anderegg et al., 2015) and lacks the memory 906 effects that are commonly observed in tree-ring observations also in non-extreme years 907 (Pappas et al., 2017; Zhang et al., 2017). Accordingly, neither the significant correlations 908 with previous year's climate, nor the positive auto-correlation structure of most tree-ring time 909 series are simulated accurately. These findings point to deficits in the carbon allocation 910 schemes that are implemented in current DGVMs (Sitch et al., 2015). Carbon allocation and 911 turnover have been identified as an important source of uncertainty (Bloom et al., 2016; De 912 Kauwe et al., 2014; Friend et al., 2014; Montané et al., 2017) that is compounded by a 913 shortage of long-term observations of root and foliar dynamics.

915	Not surprisingly, an ecophysiological model with a sophisticated carbon allocation scheme -
916	i.e. the MAIDEN model (Misson, 2004) – has shown the highest correlations ( $r > 0.5$ ) with
917	tree-ring chronologies from coniferous and broadleaf species at Mediterranean and boreal
918	sites (Gea-Izquierdo et al., 2015; Gennaretti et al., 2017). MAIDEN uses mechanistic rules
919	for the temporal allocation of photosynthates to four carbon pools (leaves, stem, roots, and
920	non-structural carbohydrates) according to phenological phases. While its large-scale
921	application to estimate tree growth is still limited because certain allocation parameters need
922	to be fitted site-by-site, the integration of the MAIDEN model with tree-ring observations has
923	already been proposed with a view on paleo-applications. For instance, (Guiot et al., 2014)
924	have advocated the use of this and other ecophysiological models in the inverse mode to
925	hindcast climate variability over centuries. In this application, the model parameters are first
926	manually or automatically optimized to represent the observed radial increment. Using
927	model-data-fusion techniques (Peng et al., 2011) the tree-ring data are then assimilated into
928	the model to iteratively constrain the most likely climate conditions (i.e. probability
929	distributions) that produce the observed radial increment in a given year (Boucher et al.,
930	2014). For the pre-instrumental period when only tree-ring data are available, the climate
931	probability distribution of a chosen reference (i.e. average) year is iteratively modified
932	according to the annual tree-ring anomaly from that year (Guiot et al., 2014). This way, a
933	climate probability distribution for each year of the reconstruction is determined. Such
934	climate reconstructions based on mechanistic models have the advantage over purely
935	empirical calibrations that the influence of non-climatic effects that are represented in the
936	model (e.g. CO <sub>2</sub> ) can be assessed.

With a view on DGVM development, model-data-fusion approaches involving tree-ring data(see above) could constrain carbon allocation to stem growth and thereby help evaluate and

940 improve imperfect allocation schemes. In addition, a series of model inter-comparison 941 exercises would be useful to determine, why some models perform better than others in 942 simulating forest growth and its climate response. Such exercises are being conducted for 943 different ecosystem variables (see e.g. the MsTMIP project of the North American Carbon 944 Program; https://nacp.ornl.gov/MsTMIP.shtml) and we are convinced that including tree-ring 945 benchmarks from different ecoregions will be quite fruitful to provide quantitative insight in 946 the representation of critical processes in DGVMs. However, one challenge for comparing 947 multiple models with tree rings will be to generate parameters that are spatially and 948 conceptually comparable. From the tree-ring side, estimates of absolute growth rates (e.g. in g C  $m^{-2}y^{-1}$ ) will be required that optimally account for management, disturbances, and base 949 950 mortality rates (Section 3.1). From the modeling side, the detail of the implemented carbon 951 pools (leaves, branches, stem, coarse and fine roots, non-structural carbohydrates, etc.) and 952 the respective output parameters (or "emergent properties") will need to be examined to 953 determine the best metrics for comparison with tree-ring data.

954

## 955 **5.** Perspectives for tree-ring research

956 Our discussion around the statistical scaling of tree-ring data in sections 2 and 3 has 957 emphasized the need for representative sampling to capture the heterogeneity of forested 958 landscapes. The systematic or random distribution of samples along the body of an 959 individual, of individuals within a site, and of sites across the landscape will allow for more 960 robust projection across the space where observations are sparse or missing. In addition, 961 representative sampling of the area covered by the grid cells of raster data products should 962 reduce the spatial mismatch between tree-ring data and satellite Earth observations or DGVM 963 output. This objective of spatial representativeness is somewhat new to the field of 964 dendrochronology. While other disciplines (e.g. ecosystem ecology or forestry) have a long 965 history of optimizing sampling schemes for spatial or temporal scaling (Scholes, 2017), these 966 ideas have only recently started to enter the scope of tree-ring research and require a certain 967 rethinking of established protocols. For example, if tree-ring sampling should represent a 968 larger population of trees (e.g. a stand), the strength of the common growth variability among 969 trees (traditionally assessed by the mean inter-series correlation or the expressed population 970 signal; (Buras, 2017; Cook and Peters, 1997) cannot serve as the main quality measure of the 971 site-level time series. Hence, new quality criteria and guidelines for tree-ring sampling need 972 to be established that can serve both the needs of individual studies and the overarching goal 973 of scaling. We recommend that this be done within interdisciplinary research initiatives, 974 including dendrochronologists, forest and landscape ecologists, and foresters.

975

976 At present, we have the best control over uncertainties in tree-ring data at the site level. Over 977 the past years, a number of studies have been published that characterized trend biases in 978 time series of tree growth (e.g. (Brienen et al., 2012; Brienen et al., 2017; Peters et al., 2015) 979 or the impact of sampling biases on tree-ring quantification of stand-level above-ground 980 biomass increment (Alexander et al., 2017; Nehrbass - Ahles et al., 2014). These studies will 981 serve as important guidelines in future field campaigns. By contrast, sampling biases at the 982 individual level are insufficiently constrained, in part because the heterogeneity and 983 dynamics of resource allocation to stem growth are not well understood. This could for 984 example be tackled through intense sampling along trees that were commercially felled or 985 uprooted after a storm. If combined with wood anatomical measurements (von Arx et al., 986 2016), such data could additionally serve as an improved test bed for mechanistic models of 987 xylogenesis (Section 4). These models are becoming increasingly important tools to assess, 988 reconstruct, and forecast tree growth responses to a changing environment because – even 989 with the most representative sampling - statistical scaling is limited by non-linearities and feedbacks in ecosystem processes (Scholes, 2017). Finally, uncertainties in tree-ring data will be the most challenging to assess at large spatial scales where individual- and site-level uncertainties cumulate. Yet, as new tree-ring and NFI data with well-quantified uncertainty are made accessible and interoperable across national boundaries, a global network of annually resolved forest biomass reconstructions can emerge. An important application of these data will then be to evaluate the ITRDB and ensure that this legacy of decades of treering research can continue to support Earth system science (Babst et al., 2017).

997

998 When tree rings go global – as is the theme of this review – the goal is to generate knowledge 999 and data that can inform adaptation and mitigation strategies in the face of climate change. 1000 The primary strength of tree-ring records has so far been seen in their temporal depth that 1001 allows placing the current climatic variability and ongoing trends in a millennium-length 1002 context (Wilson et al., 2016). Indeed, it is both important and disturbing to learn that the 1003 severity of recent drought events was unprecedented over the past millennium (Belmecheri et al., 2016; Griffin and Anchukaitis, 2014), that man-made influences on atmospheric 1004 1005 circulation patterns can promote more frequent extreme events (e.g. through Arctic warming; 1006 (Trouet et al., 2018), and that these events are directly linked to forest mortality, disturbances, 1007 and changes in the terrestrial carbon cycle (Schwalm et al., 2012; Williams et al., 2013). 1008 However, anthropogenic climate change is now considered indisputable and there is a need to 1009 transition from temperature reconstructions proving that the Earth is warming at an 1010 unprecedented rate towards tree-ring research that assesses, reconstructs and predicts the 1011 responses and feedbacks of forest ecosystems to climate change. Dendrochronology can 1012 make important contributions at every step of successful scaling (Sections 2 and 3) and 1013 refined process understanding (Section 4). How and how quickly can we expect tree growth and its climate sensitivity to change with continued warming? Will thinning forests mitigate 1014

1015 drought stress? How much carbon would be sequestered by forests under different

1016 management scenarios? By answering these and other relevant questions, tree-ring research

1017 can directly support the development and assessment of climate change adaptation strategies.

1018

## 1019 Acknowledgements

- 1020 F.B. acknowledges funding from the EU-H2020 program (grant 640176, "BACI") and the
- 1021 Swiss National Science Foundation (#P300P2\_154543). S.K. acknowledges the support of
- 1022 the USDA-AFRI grant 2016-67003-24944.

## 1023 References

- Adams, H.D., Zeppel, M.J., Anderegg, W.R., Hartmann, H., Landhäusser, S.M., Tissue, D.T.,
  Huxman, T.E., Hudson, P.J., Franz, T.E., Allen, C.D., 2017. A multi-species synthesis of
  physiological mechanisms in drought-induced tree mortality. Nature ecology &
  evolution 1, 1285.
- 1028 Ainsworth, E.A., Long, S.P., 2005. What have we learned from 15 years of free air CO2
- enrichment (FACE)? A meta analytic review of the responses of photosynthesis,
  canopy properties and plant production to rising CO2. New Phytologist 165, 351-372.
- 1031 Aitken, S.N., Yeaman, S., Holliday, J.A., Wang, T., Curtis McLane, S., 2008. Adaptation,
- 1032 migration or extirpation: climate change outcomes for tree populations. Evolutionary1033 Applications 1, 95-111.
- 1034 Åkerblom, M., Raumonen, P., Kaasalainen, M., Casella, E., 2015. Analysis of geometric
- 1035 primitives in quantitative structure models of tree stems. Remote Sensing 7, 4581-4603.
- 1036 Alexander, M.R., Rollinson, C.R., Babst, F., Trouet, V., Moore, D.J., 2017. Relative
- 1037 influences of multiple sources of uncertainty on cumulative and incremental tree-ring-
- 1038 derived aboveground biomass estimates. Trees, 1-12.
- 1039 Anchukaitis, K.J., Evans, M.N., Kaplan, A., Vaganov, E.A., Hughes, M.K., Grissino-Mayer,
- 1040 H.D., Cane, M.A., 2006. Forward modeling of regional scale tree-ring patterns in the 1041 southeastern United States and the recent influence of summer drought. Geophysical
- 1042 Research Letters 33.
- 1043 Anderegg, W.R.L., Schwalm, C., Biondi, F., Camarero, J.J., Koch, G., Litvak, M., Ogle, K.,
- 1044 Shaw, J.D., Shevliakova, E., Williams, A.P., Wolf, A., Ziaco, E., Pacala, S., 2015. Pervasive
- 1045 drought legacies in forest ecosystems and their implications for carbon cycle models.
- 1046 Science 349, 528-532.
- 1047 Babst, F., Alexander, M.R., Szejner, P., Bouriaud, O., Klesse, S., Roden, J., Ciais, P., Poulter,
- B., Frank, D., Moore, D.J., 2014a. A tree-ring perspective on the terrestrial carbon cycle.0ecologia 176, 307-322.

- Babst, F., Bouriaud, O., Alexander, R., Trouet, V., Frank, D., 2014b. Toward consistent
  measurements of carbon accumulation: A multi-site assessment of biomass and basal
  area increment across Europe. Dendrochronologia 32, 153-161.
- Babst, F., Carrer, M., Poulter, B., Urbinati, C., Neuwirth, B., Frank, D., 2012. 500 years of
  regional forest growth variability and links to climatic extreme events in Europe.
  Environmental Research Letters 7, 045705.
- 1056 Babst, F., Poulter, B., Bodesheim, P., Mahecha, M.D., Frank, D.C., 2017. Improved tree-1057 ring archives will support earth-system science. Nature Ecology & Evolution 1, 0008.
- 1058 Babst, F., Poulter, B., Trouet, V., Tan, K., Neuwirth, B., Wilson, R., Carrer, M., Grabner, M.,
- 1059 Tegel, W., Levanic, T., 2013. Site and species specific responses of forest growth to
- 1060 climate across the European continent. Global Ecology and Biogeography 22, 706-717.
- Bakker, J.D., 2005. A new, proportional method for reconstructing historical tree
  diameters. Canadian Journal of Forest Research-Revue Canadienne De Recherche
  Forestiere 35, 2515-2520.
- 1064 Bechtold, W.A., Patterson, P.L., 2005. The enhanced forest inventory and analysis
- 1065 program-national sampling design and estimation procedures. Gen. Tech. Rep. SRS-80.
- Asheville, NC: US Department of Agriculture, Forest Service, Southern Research Station.85 p. 80.
- 1068 Beck, P.S., Andreu-Hayles, L., D'Arrigo, R., Anchukaitis, K.J., Tucker, C.J., Pinzón, J.E.,
- 1069 Goetz, S.J., 2013. A large-scale coherent signal of canopy status in maximum latewood 1070 density of tree rings at arctic treeline in North America. Global and planetary change
- 1071 100, 109-118.
- 1072 Belmecheri, S., Babst, F., Wahl, E.R., Stahle, D.W., Trouet, V., 2016. Multi-century 1073 evaluation of Sierra Nevada snowpack. Nature Climate Change 6, 2-3.
- 1074 Berner, L.T., Beck, P.S., Bunn, A.G., Lloyd, A.H., Goetz, S.J., 2011. High latitude tree 1075 growth and satellite vegetation indices: Correlations and trends in Russia and Canada 1076 (1982–2008). Journal of Geophysical Research: Biogeosciences 116.
- Björklund, J., Seftigen, K., Schweingruber, F., Fonti, P., Arx, G., Bryukhanova, M.V., Cuny,
  H.E., Carrer, M., Castagneri, D., Frank, D.C., 2017. Cell size and wall dimensions drive
  distinct variability of earlywood and latewood density in Northern Hemisphere
  conifers. New Phytologist 216, 728-740.
- 1081 Black, B.A., Griffin, D., Sleen, P., Wanamaker, A.D., Speer, J.H., Frank, D.C., Stahle, D.W., 1082 Pederson, N., Copenheaver, C.A., Trouet, V., 2016. The value of crossdating to retain
- high frequency variability, climate signals, and extreme events in environmental
  proxies. Global change biology 22, 2582-2595.
- 1085 Bloom, A.A., Exbrayat, J.-F., van der Velde, I.R., Feng, L., Williams, M., 2016. The decadal
- 1086 state of the terrestrial carbon cycle: Global retrievals of terrestrial carbon allocation, 1087 pools, and residence times. Proceedings of the National Academy of Sciences 113, 1285-
- 1088 1290.
- Boucher, É., Guiot, J., Hatté, C., Daux, V., Danis, P.-A., Dussouillez, P., 2014. An inverse
  modeling approach for tree-ring-based climate reconstructions under changing
  atmospheric CO2 concentrations. Biogeosciences 11, 3245.
- 1092 Boucher, O., Bellassen, V., Benveniste, H., Ciais, P., Criqui, P., Guivarch, C., Le Treut, H.,
- 1093 Mathy, S., Séférian, R., 2016. Opinion: In the wake of Paris Agreement, scientists must
- 1094 embrace new directions for climate change research. Proceedings of the National
- 1095 Academy of Sciences 113, 7287-7290.

- Bouriaud, O., Marin, G., Bouriaud, L., Hessenmöller, D., Schulze, E.-D., 2016. Romanian
  legal management rules limit wood production in Norway spruce and beech forests.
- 1098 Forest Ecosystems 3, 20.
- 1099 Bouriaud, O., Teodosiu, M., Kirdyanov, A., Wirth, C., 2015. Influence of wood density in
- 1100 tree-ring based annual productivity assessments and its errors in Norway spruce.
- 1101 Breiman, L., 2001. Random Forest, 45, 5-32. Examples.
- 1102 Breitenmoser, P., Brönnimann, S., Frank, D., 2014. Forward modelling of tree-ring width
- and comparison with a global network of tree-ring chronologies. Climate of the Past 10,437-449.
- 1105 Brienen, R.J., Gloor, E., Zuidema, P.A., 2012. Detecting evidence for CO2 fertilization from
- 1106 tree ring studies: The potential role of sampling biases. Global Biogeochemical Cycles
- 1107 26.
- 1108 Brienen, R.J., Gloor, M., Ziv, G., 2017. Tree demography dominates long term growth 1109 trends inferred from tree rings. Global change biology 23, 474-484.
- 1110 Brienen, R.J., Schöngart, J., Zuidema, P.A., 2016. Tree rings in the tropics: insights into 1111 the ecology and climate sensitivity of tropical trees, Tropical Tree Physiology. Springer,
- 1112 pp. 439-461.
- 1113 Brzostek, E.R., Dragoni, D., Schmid, H.P., Rahman, A.F., Sims, D., Wayson, C.A., Johnson,
- 1114 D.J., Phillips, R.P., 2014. Chronic water stress reduces tree growth and the carbon sink of 1115 deciduous hardwood forests. Global Change Biology 20, 2531-2539.
- 1116 Buchwal, A., Rachlewicz, G., Fonti, P., Cherubini, P., Gärtner, H., 2013. Temperature
- 1117 modulates intra-plant growth of Salix polaris from a high Arctic site (Svalbard). Polar1118 Biology 36, 1305-1318.
- Buechling, A., Martin, P.H., Canham, C.D., 2017. Climate and competition effects on treegrowth in Rocky Mountain forests. Journal of Ecology.
- 1121 Bugmann, H.K., 1996. A simplified forest model to study species composition along 1122 climate gradients. Ecology 77, 2055-2074.
- 1123 Bunn, A.G., Hughes, M.K., Kirdyanov, A.V., Losleben, M., Shishov, V.V., Berner, L.T.,
- 1124 Oltchev, A., Vaganov, E.A., 2013. Comparing forest measurements from tree rings and a
- space-based index of vegetation activity in Siberia. Environmental Research Letters 8,035034.
- Buras, A., 2017. A comment on the expressed population signal. Dendrochronologia 44, 130-132.
- 1129 Calders, K., Newnham, G., Burt, A., Murphy, S., Raumonen, P., Herold, M., Culvenor, D.,
- 1130 Avitabile, V., Disney, M., Armston, J., 2015. Nondestructive estimates of above ground
- 1131 biomass using terrestrial laser scanning. Methods in Ecology and Evolution 6, 198-208.
- 1132 Charney, N.D., Babst, F., Poulter, B., Record, S., Trouet, V.M., Frank, D., Enquist, B.J.,
- Evans, M.E., 2016. Observed forest sensitivity to climate implies large changes in 21st century North American forest growth. Ecology letters 19, 1119-1128.
- 1135 Charru, M., Seynave, I., Hervé, J.-C., Bertrand, R., Bontemps, J.-D., 2017. Recent growth 1136 changes in Western European forests are driven by climate warming and structured 1137 across tree species climatic habitats. Annals of Forest Science 74, 33.
- 1138 Chen, H.Y., Luo, Y., Reich, P.B., Searle, E.B., Biswas, S.R., 2016. Climate change -
- associated trends in net biomass change are age dependent in western boreal forests ofCanada. Ecology letters 19, 1150-1158.
- 1141 Clark, J.S., Wolosin, M., Dietze, M., IbáÑez, I., LaDeau, S., Welsh, M., Kloeppel, B., 2007.
- 1142 Tree growth inference and prediction from diameter censuses and ring widths.
- 1143 Ecological Applications 17, 1942-1953.

- 1144 Clough, B.J., Curzon, M.T., Domke, G.M., Russell, M.B., Woodall, C.W., 2017. Climate -
- driven trends in stem wood density of tree species in the eastern United States:
  Ecological impact and implications for national forest carbon assessments. Global
  Ecology and Biogeography 26, 1153-1164.
- 1148 Çoban, H.O., Özçelik, R., Avci, M., 2014. Monitoring of damage from cedar shoot moth
- 1149 Dichelia cedricola Diakonoff (Lep.: Tortricidae) by multi-temporal Landsat imagery. 1150 iForest-Biogeosciences and Forestry 7, 126.
- 1151 Cook, E.R., Briffa, K.R., Meko, D.M., Graybill, D.A., Funkhouser, G., 1995. THE SEGMENT 1152 LENGTH CURSE IN LONG TREE-RING CHRONOLOGY DEVELOPMENT FOR 1153 PALEOCLIMATIC STUDIES. Holocene 5, 229-237.
- 1154 Cook, E.R., Pederson, N., 2011. Uncertainty, emergence, and statistics in 1155 dendrochronology, Dendroclimatology. Springer, pp. 77-112.
- 1156 Cook, E.R., Peters, K., 1997. Calculating unbiased tree-ring indices for the study of climatic and environmental change. Holocene 7, 361-370.
- Coulthard, B.L., Touchan, R., Anchukaitis, K.J., Meko, D.M., Sivrikaya, F., 2017. Tree
  growth and vegetation activity at the ecosystem-scale in the eastern Mediterranean.
  Environmental Research Letters 12, 084008.
- 1161 Cunliffe, A.M., Brazier, R.E., Anderson, K., 2016. Ultra-fine grain landscape-scale 1162 quantification of dryland vegetation structure with drone-acquired structure-from-1163 motion photogrammetry. Remote Sensing of Environment 183, 129-143.
- 1164 Cuny, H.E., Rathgeber, C.B., Frank, D., Fonti, P., Fournier, M., 2014. Kinetics of tracheid
- development explain conifer tree ring structure. New Phytologist 203, 1231-1241.
- 1166 Cuny, H.E., Rathgeber, C.B.K., Frank, D., Fonti, P., Mäkinen, H., Prislan, P., Rossi, S., del
- 1167 Castillo, E.M., Campelo, F., Vavrčík, H., Camarero, J.J., Bryukhanova, M.V., Jyske, T., Gričar,
- J., Gryc, V., De Luis, M., Vieira, J., Čufar, K., Kirdyanov, A.V., Oberhuber, W., Treml, V.,
  Huang, J.-G., Li, X., Swidrak, I., Deslauriers, A., Liang, E., Nöjd, P., Gruber, A., Nabais, C.,
  Morin, H., Krause, C., King, G., Fournier, M., 2015. Woody biomass production lags stem-
- 1171 girth increase by over one month in coniferous forests. 1, 15160.
- 1172 D'arrigo, R., Malmstrom, C., Jacoby, G., Los, S., Bunker, D., 2000. Correlation between 1173 maximum latewood density of annual tree rings and NDVI based estimates of forest 1174 productivity. International Journal of Remote Sensing 21, 2329-2336.
- D'Orangeville, L., Duchesne, L., Houle, D., Kneeshaw, D., Côté, B., Pederson, N., 2016.
  Northeastern North America as a potential refugium for boreal forests in a warming
  climate. Science 352, 1452-1455.
- 1178 De Kauwe, M.G., Medlyn, B.E., Zaehle, S., Walker, A.P., Dietze, M.C., Wang, Y.P., Luo, Y.,
- 1179 Jain, A.K., El Masri, B., Hickler, T., 2014. Where does the carbon go? A model-data
- 1180 intercomparison of vegetation carbon allocation and turnover processes at two
- temperate forest free air CO2 enrichment sites. New Phytologist 203, 883-899.
- de Rigo, D., Caudullo, G., Houston Durrant, T., San-Miguel-Ayanz, J., 2016. The European
  Atlas of Forest Tree Species: modelling, data and information on forest tree species.
  European Atlas of Forest Tree Species. Publ. Off. EU, Luxembourg, pp. e01aa69+
  https://w3id. org/mtv/FISE-Comm/v01/e01aa69 (Cited on pages 3, 11, and 28).
- 1186 De Schepper, V., Steppe, K., 2010. Development and verification of a water and sugar
- 1187 transport model using measured stem diameter variations. Journal of Experimental
- 1188 Botany 61, 2083-2099.

- 1189 Del Castillo, J., Voltas, J., Ferrio, J.P., 2015. Carbon isotope discrimination, radial growth,
- and NDVI share spatiotemporal responses to precipitation in Aleppo pine. Trees 29, 223-233.
- 1192 Deleuze, C., Houllier, F., 1998. A simple process-based xylem growth model for
- describing wood microdensitometric profiles. Journal of Theoretical Biology 193, 99-1194 113.
- 1195 DeRose, R.J., Shaw, J.D., Long, J.N., 2017. Building the forest inventory and analysis tree-1196 ring data set. Journal of Forestry 115, 283-291.
- 1197 Dietze, M.C., 2017. Prediction in ecology: a first principles framework. Ecological 1198 Applications.
- 1199 Dorman, M., Svoray, T., Perevolotsky, A., Moshe, Y., Sarris, D., 2015. What determines
- tree mortality in dry environments? a multi perspective approach. EcologicalApplications 25, 1054-1071.
- 1202 Duchesne, L., D'Orangeville, L., Ouimet, R., Houle, D., Kneeshaw, D., 2017. Extracting
- 1203 coherent tree-ring climatic signals across spatial scales from extensive forest inventory
- 1204 data. PloS one 12, e0189444.
- 1205 Dye, A., Barker Plotkin, A., Bishop, D., Pederson, N., Poulter, B., Hessl, A., 2016.
- 1206 Comparing tree ring and permanent plot estimates of aboveground net primary1207 production in three eastern US forests. Ecosphere 7.
- 1208 Esper, J., Buntgen, U., Frank, D.C., Nievergelt, D., Liebhold, A., 2007. 1200 years of regular
- outbreaks in alpine insects. Proceedings of the Royal Society B-Biological Sciences 274,671-679.
- 1211 Evans, M.E., Falk, D.A., Arizpe, A., Swetnam, T.L., Babst, F., Holsinger, K.E., 2017. Fusing
- 1212 tree ring and forest inventory data to infer influences on tree growth. Ecosphere 8.
- Evans, M.N., Reichert, B.K., Kaplan, A., Anchukaitis, K.J., Vaganov, E.A., Hughes, M.K.,
  Cane, M.A., 2006. A forward modeling approach to paleoclimatic interpretation of treering data. Journal of Geophysical Research-Biogeosciences 111.
- 1216 Evans, M.N., Tolwinski-Ward, S.E., Thompson, D.M., Anchukaitis, K.J., 2013. Applications
- 1217 of proxy system modeling in high resolution paleoclimatology. Quaternary Science 1218 Reviews 76, 16-28.
- 1219 Eysn, L., Hollaus, M., Lindberg, E., Berger, F., Monnet, J.-M., Dalponte, M., Kobal, M.,
- Pellegrini, M., Lingua, E., Mongus, D., 2015. A benchmark of lidar-based single tree detection methods using heterogeneous forest data from the alpine space. Forests 6, 1721-1747.
- Farrior, C.E., Rodriguez-Iturbe, I., Dybzinski, R., Levin, S.A., Pacala, S.W., 2015. Decreased
  water limitation under elevated CO2 amplifies potential for forest carbon sinks.
  Proceedings of the National Academy of Sciences 112, 7213-7218.
- 1226 Fatichi, S., Leuzinger, S., Körner, C., 2014. Moving beyond photosynthesis: from carbon
- source to sink driven vegetation modeling. New Phytologist 201, 1086-1095.
- 1228 Forrester, D.I., Tachauer, I., Annighoefer, P., Barbeito, I., Pretzsch, H., Ruiz-Peinado, R.,
- 1229 Stark, H., Vacchiano, G., Zlatanov, T., Chakraborty, T., 2017. Generalized biomass and leaf
- 1230 area allometric equations for European tree species incorporating stand structure, tree
- age and climate. Forest Ecology and Management 396, 160-175.
- 1232 Foster, J.R., Finley, A.O., D'amato, A.W., Bradford, J.B., Banerjee, S., 2016. Predicting tree
- 1233 biomass growth in the temperate-boreal ecotone: Is tree size, age, competition, or
- 1234 climate response most important? Global change biology 22, 2138-2151.

- Friend, A.D., Lucht, W., Rademacher, T.T., Keribin, R., Betts, R., Cadule, P., Ciais, P., Clark,D.B., Dankers, R., Falloon, P.D., 2014. Carbon residence time dominates uncertainty in
- terrestrial vegetation responses to future climate and atmospheric CO2. Proceedings ofthe National Academy of Sciences 111, 3280-3285.
- 1239 Fritts, H.C., Vaganov, E.A., Sviderskaya, I.V., Shashkin, A.V., 1991. Climatic variation and
- 1240 tree-ring structure in conifers: empirical and mechanistic models of tree-ring width,
- 1241 number of cells, cell size, cell-wall thickness and wood density. Climate Research, 97-1242 116.
- Galiano, L., Martínez-Vilalta, J., Sabaté, S., Lloret, F., 2012. Determinants of drought
  effects on crown condition and their relationship with depletion of carbon reserves in a
  Mediterranean holm oak forest. Tree physiology 32, 478-489.
- Gea-Izquierdo, G., Guibal, F., Joffre, R., Ourcival, J., Simioni, G., Guiot, J., 2015. Modelling
  the climatic drivers determining photosynthesis and carbon allocation in evergreen
  Mediterranean forests using multiproxy long time series. Biogeosciences 12, 36953712.
- 1250 Gedalof, Z.e., Berg, A.A., 2010. Tree ring evidence for limited direct CO2 fertilization of 1251 forests over the 20th century. Global Biogeochemical Cycles 24.
- 1252 Gennaretti, F., Gea-Izquierdo, G., Boucher, E., Berninger, F., Arseneault, D., Guiot, J., 2017.
- 1253 Ecophysiological modeling of photosynthesis and carbon allocation to the tree stem in1254 the boreal forest. Biogeosciences 14, 4851.
- Gessler, A., Ferrio, J.P., Hommel, R., Treydte, K., Werner, R.A., Monson, R.K., 2014. Stable
  isotopes in tree rings: towards a mechanistic understanding of isotope fractionation and
  mixing processes from the leaves to the wood. Tree physiology 34, 796-818.
- Girardin, M.P., Bouriaud, O., Hogg, E.H., Kurz, W., Zimmermann, N.E., Metsaranta, J.M., de
  Jong, R., Frank, D.C., Esper, J., Büntgen, U., Guo, X.J., Bhatti, J., 2016. No growth
  stimulation of Canada's boreal forest under half-century of combined warming and CO2
- 1261 fertilization. Proceedings of the National Academy of Sciences.
- Girardin, M.P., Guo, X.J., De Jong, R., Kinnard, C., Bernier, P., Raulier, F., 2014. Unusual
  forest growth decline in boreal North America covaries with the retreat of Arctic sea ice.
  Global change biology 20, 851-866.
- 1265 Griebel, A., Bennett, L.T., Arndt, S.K., 2017. Evergreen and ever growing–Stem and 1266 canopy growth dynamics of a temperate eucalypt forest. Forest Ecology and 1267 Management 389, 417-426.
- Griffin, D., Anchukaitis, K.J., 2014. How unusual is the 2012–2014 California drought?Geophysical Research Letters 41, 9017-9023.
- 1270 Grossiord, C., Granier, A., Ratcliffe, S., Bouriaud, O., Bruelheide, H., Chećko, E., Forrester,
- 1271 D.I., Dawud, S.M., Finér, L., Pollastrini, M., 2014. Tree diversity does not always improve
- resistance of forest ecosystems to drought. Proceedings of the National Academy ofSciences 111, 14812-14815.
- 1274 Guiot, J., Boucher, E., Gea-Izquierdo, G., 2014. Process models and model-data fusion in 1275 dendroecology. Frontiers in Ecology and Evolution 2, 52.
- 1276 Gustafson, E.J., 2013. When relationships estimated in the past cannot be used to predict
- 1277 the future: using mechanistic models to predict landscape ecological dynamics in a
- 1278 changing world. Landscape ecology 28, 1429-1437.
- 1279 Harris, I., Jones, P., Osborn, T., Lister, D., 2014. Updated high resolution grids of
- 1280 monthly climatic observations-the CRU TS3. 10 Dataset. International Journal of
- 1281 Climatology 34, 623-642.

- Hayat, A., Hacket-Pain, A.J., Pretzsch, H., Rademacher, T.T., Friend, A.D., 2017. Modeling
  Tree Growth Taking into Account Carbon Source and Sink Limitations. Frontiers in plant
- 1284 science 8.
- 1285 Hellmann, L., Agafonov, L., Ljungqvist, F.C., Churakova, O., Düthorn, E., Esper, J.,
- 1286 Hülsmann, L., Kirdyanov, A.V., Moiseev, P., Myglan, V.S., 2016. Diverse growth trends
- and climate responses across Eurasia's boreal forest. Environmental Research Letters11, 074021.
- Hölttä, T., Mäkinen, H., Nöjd, P., Mäkelä, A., Nikinmaa, E., 2010. A physiological model of
  softwood cambial growth. Tree Physiology 30, 1235-1252.
- 1291 Housset, J.M., Nadeau, S., Isabel, N., Depardieu, C., Duchesne, I., Lenz, P., Girardin, M.P.,
- 2018. Tree rings provide a new class of phenotypes for genetic associations that fosterinsights into adaptation of conifers to climate change. New Phytologist.
- Howard, R., Wilson, B., 1972. A stochastic model for cambial activity. Botanical Gazette133, 410-414.
- 1296 Huang, K., Yi, C., Wu, D., Zhou, T., Zhao, X., Blanford, W.J., Wei, S., Wu, H., Ling, D., Li, Z.,
- 1297 2015. Tipping point of a conifer forest ecosystem under severe drought. Environmental1298 Research Letters 10, 024011.
- Jucker, T., Caspersen, J., Chave, J., Antin, C., Barbier, N., Bongers, F., Dalponte, M., Ewijk,
  K.Y., Forrester, D.I., Haeni, M., 2017. Allometric equations for integrating remote sensing
  imagery into forest monitoring programmes. Global change biology 23, 177-190.
- 1202 Körner C 2015 Deredigm shift in plant growth control Current Opinion in
- 1302 Körner, C., 2015. Paradigm shift in plant growth control. Current Opinion in Plant1303 Biology 25, 107-114.
- 1304 Körner, C., 2017. A matter of tree longevity. Science 355, 130-131.
- 1305 Le Quéré, C., Andrew, R.M., Canadell, J.G., Sitch, S., Korsbakken, J.I., Peters, G.P., Manning,
- A.C., Boden, T.A., Tans, P.P., Houghton, R.A., 2016. Global carbon budget 2016. EarthSystem Science Data 8, 605-649.
- Levesque, M., Andreu-Hayles, L., Pederson, N., 2017. Water availability drives gas
  exchange and growth of trees in northeastern US, not elevated CO2 and reduced acid
  deposition. Scientific Reports 7.
- 1311 Li, G., Harrison, S., Prentice, I., Falster, D., 2014. Simulation of tree-ring widths with a 1312 model for primary production, carbon allocation, and growth.
- 1313 Liski, J., Kaasalainen, S., Raumonen, P., Akujärvi, A., Krooks, A., Repo, A., Kaasalainen, M.,
- 1314 2014. Indirect emissions of forest bioenergy: detailed modeling of stump root
  1315 systems. Gcb Bioenergy 6, 777-784.
- 1316 Madrigal-González, J., Ballesteros-Cánovas, J.A., Herrero, A., Ruiz-Benito, P., Stoffel, M.,
- 1317 Lucas-Borja, M.E., Andivia, E., Sancho-García, C., Zavala, M.A., 2017. Forest productivity
- 1318 in southwestern Europe is controlled by coupled North Atlantic and Atlantic
   1319 Multidecadal Oscillations. Nature communications 8, 2222.
- 1320 Marotzke, J., Jakob, C., Bony, S., Dirmeyer, P.A., O'Gorman, P.A., Hawkins, E., Perkins-
- Kirkpatrick, S., Le Quéré, C., Nowicki, S., Paulavets, K., 2017. Climate research must
  sharpen its view. Nature Climate Change 7, 89.
- 1323 Martin Benito, D., Pederson, N., 2015. Convergence in drought stress, but a divergence
- 1324 of climatic drivers across a latitudinal gradient in a temperate broadleaf forest. Journal
- 1325 of Biogeography 42, 925-937.
- 1326 McCarroll, D., Loader, N.J., 2004. Stable isotopes in tree rings. Quaternary Science 1327 Reviews 23, 771-801.

- McRoberts, R.E., Tomppo, E., Schadauer, K., Vidal, C., Ståhl, G., Chirici, G., Lanz, A.,
  Cienciala, E., Winter, S., Smith, W.B., 2009. Harmonizing national forest inventories.
  Journal of Forestry 107, 179-187.
- 1331 Mendivelso, H.A., Camarero, J.J., Gutiérrez, E., Zuidema, P.A., 2014. Time-dependent
- 1332 effects of climate and drought on tree growth in a Neotropical dry forest: Short-term
- tolerance vs. long-term sensitivity. Agricultural and Forest Meteorology 188, 13-23.
- 1334 Mina, M., Martin-Benito, D., Bugmann, H., Cailleret, M., 2016. Forward modeling of tree-1335 ring width improves simulation of forest growth responses to drought. Agricultural and
- 1336 Forest Meteorology 221, 13-33.
- Misson, L., 2004. MAIDEN: a model for analyzing ecosystem processes in dendroecology.
  Canadian Journal of Forest Research 34, 874-887.
- 1339 Montané, F., Fox, A.M., Arellano, A.F., MacBean, N., Alexander, M.R., Dye, A., Bishop, D.A.,
- 1340 Trouet, V., Babst, F., Hessl, A.E., 2017. Evaluating the effect of alternative carbon 1341 allocation schemes in a land surface model (CLM4. 5) on carbon fluxes, pools, and 1342 turnover in temperate forests. Geoscientific Model Development 10, 3499.
- Morales, M., Carilla, J., Grau, H., Villalba, R., 2015. Multi-century lake area changes in the
  Southern Altiplano: a tree-ring-based reconstruction. Climate of the Past 11, 1139.
- Nash, J.E., Sutcliffe, J.V., 1970. River flow forecasting through conceptual models part I—
  A discussion of principles. Journal of hydrology 10, 282-290.
- 1347 Nehrbass Ahles, C., Babst, F., Klesse, S., Nötzli, M., Bouriaud, O., Neukom, R., Dobbertin,
- 1348 M., Frank, D., 2014. The influence of sampling design on tree ring based 1349 quantification of forest growth. Global change biology 20, 2867-2885.
- 1350 Newnham, G.J., Armston, J.D., Calders, K., Disney, M.I., Lovell, J.L., Schaaf, C.B., Strahler,
- A.H., Danson, F.M., 2015. Terrestrial laser scanning for plot-scale forest measurement.
  Current Forestry Reports 1, 239-251.
- 1353 Nicklen, E.F., Roland, C.A., Ruess, R.W., Schmidt, J.H., Lloyd, A.H., 2016. Local site 1354 conditions drive climate–growth responses of Picea mariana and Picea glauca in 1355 interior Alaska. Ecosphere 7.
- Nickless, A., Scholes, R.J., Archibald, S., 2011. A method for calculating the variance and
  confidence intervals for tree biomass estimates obtained from allometric equations.
  South African Journal of Science 107, 1-10.
- 1359 Ogle, K., Barber, J.J., Barron Gafford, G.A., Bentley, L.P., Young, J.M., Huxman, T.E., Loik,
- 1360 M.E., Tissue, D.T., 2015. Quantifying ecological memory in plant and ecosystem 1361 processes. Ecology letters 18, 221-235.
- Ols, C., Girardin, M.P., Hofgaard, A., Bergeron, Y., Drobyshev, I., 2017. Monitoring climate
  sensitivity shifts in tree-rings of eastern boreal North America using model-data
  comparison. Ecosystems, 1-16.
- 1365 Omernik, J.M., Griffith, G.E., 2014. Ecoregions of the conterminous United States:
  1366 evolution of a hierarchical spatial framework. Environmental management 54, 12491367 1266.
- Pappas, C., Mahecha, M.D., Frank, D.C., Babst, F., Koutsoyiannis, D., 2017. Ecosystem
  functioning is enveloped by hydrometeorological variability. Nature ecology & evolution
- 1370 1, 1263.
- 1371 Pasho, E., Alla, A.Q., 2015. Climate impacts on radial growth and vegetation activity of
- 1371 Tasho, E., Ana, A.Q., 2013. Chinate impacts on radial growth and vegetation activity of 1372 two co-existing Mediterranean pine species. Canadian Journal of Forest Research 45, 1373 1749 1756
- 1373 1748-1756.

- 1374 Peng, C., Guiot, J., Wu, H., Jiang, H., Luo, Y., 2011. Integrating models with data in ecology
- 1375 and palaeoecology: advances towards a model-data fusion approach. Ecology Letters1376 14, 522-536.
- 1377 Peñuelas, J., Canadell, J.G., Ogaya, R., 2011. Increased water use efficiency during the
- 1378 20th century did not translate into enhanced tree growth. Global Ecology and 1379 Biogeography 20, 597-608.
- 1380 Peters, R.L., Balanzategui, D., Hurley, A.G., von Arx, G., Prendin, A.L., Cuny, H.E.,
- 1381 Björklund, J., Frank, D.C., Fonti, P., 2018. RAPTOR: Row and position tracheid organizer
- 1382 in R. Dendrochronologia 47, 10-16.
- Peters, R.L., Groenendijk, P., Vlam, M., Zuidema, P.A., 2015. Detecting long term growth
  trends using tree rings: a critical evaluation of methods. Global change biology 21, 20402054.
- 1386 Poulter, B., Pederson, N., Liu, H., Zhu, Z., D'Arrigo, R., Ciais, P., Davi, N., Frank, D., Leland,
- 1387 C., Myneni, R., Piao, S., Wang, T., 2013. Recent trends in Inner Asian forest dynamics to
- 1388 temperature and precipitation indicate high sensitivity to climate change. Agricultural
- 1389 and Forest Meteorology 178-179, 31-45.
- Rathgeber, C.B., Cuny, H.E., Fonti, P., 2016. Biological basis of tree-ring formation: acrash course. Frontiers in plant science 7.
- 1392 Restaino, C.M., Peterson, D.L., Littell, J., 2016. Increased water deficit decreases Douglas
- 1393 fir growth throughout western US forests. Proceedings of the National Academy of 1394 Sciences 113, 9557-9562.
- 1395 Richardson, A.D., Carbone, M.S., Keenan, T.F., Czimczik, C.I., Hollinger, D.Y., Murakami, P.,
- Schaberg, P.G., Xu, X., 2013. Seasonal dynamics and age of stemwood nonstructural carbohydrates in temperate forest trees. New Phytologist 197, 850-861.
- Rollinson, C.R., Kaye, M.W., Canham, C.D., 2016. Interspecific variation in growth
  responses to climate and competition of five eastern tree species. Ecology 97, 10031011.
- 1401 Rollinson, C.R., Liu, Y., Raiho, A., Moore, D.J., McLachlan, J., Bishop, D.A., Dye, A., Matthes,
- J.H., Hessl, A., Hickler, T., 2017. Emergent climate and CO2 sensitivities of net primary
  productivity in ecosystem models do not agree with empirical data in temperate forests
  of eastern North America. Global change biology.
- Rossi, S., Anfodillo, T., Čufar, K., Cuny, H.E., Deslauriers, A., Fonti, P., Frank, D., Gričar, J.,
  Gruber, A., Huang, J.G., 2016. Pattern of xylem phenology in conifers of cold ecosystems
  at the Northern Hemisphere. Global change biology 22, 3804-3813.
- Salzer, M.W., Hughes, M.K., Bunn, A.G., Kipfmueller, K.F., 2009. Recent unprecedented
  tree-ring growth in bristlecone pine at the highest elevations and possible causes.
  Proceedings of the National Academy of Sciences 106, 20348-20353.
- 1411 Sánchez-Salguero, R., Linares, J.C., Camarero, J.J., Madrigal-González, J., Hevia, A.,
- 1412 Sánchez-Miranda, Á., Ballesteros-Cánovas, J.A., Alfaro-Sánchez, R., García-Cervigón, A.I.,
- 1413 Bigler, C., 2015. Disentangling the effects of competition and climate on individual tree
- 1414 growth: a retrospective and dynamic approach in Scots pine. Forest Ecology and 1415 Management 358, 12-25.
- 1416 Sangüesa-Barreda, G., Camarero, J.J., García-Martín, A., Hernández, R., de la Riva, J., 2014.
- 1417 Remote-sensing and tree-ring based characterization of forest defoliation and growth
- 1418 loss due to the Mediterranean pine processionary moth. Forest Ecology and
- 1419 Management 320, 171-181.
- 1420 Scholes, R.J., 2017. Taking the mumbo out of the jumbo: progress towards a robust basis
- 1421 for ecological scaling. Ecosystems 20, 4-13.

- 1422 Schwalm, C.R., Williams, C.A., Schaefer, K., Baldocchi, D., Black, T.A., Goldstein, A.H., Law,
- 1423 B.E., Oechel, W.C., Scott, R.L., 2012. Reduction in carbon uptake during turn of the 1424 century drought in western North America. Nature Geoscience 5, 551-556.
- 1425 Seim, A., Treydte, K., Trouet, V., Frank, D., Fonti, P., Tegel, W., Panayotov, M.,
- 1426 Fernández Donado, L., Krusic, P., Büntgen, U., 2015. Climate sensitivity of
- 1427 Mediterranean pine growth reveals distinct east-west dipole. International journal of 1428 climatology 35, 2503-2513.
- 1429 Serra-Diaz, J.M., Enquist, B.J., Maitner, B., Merow, C., Svenning, J.-C., 2017. Big data of tree 1430 species distributions: how big and how good? Forest Ecosystems 4, 30.
- 1431 Shi, J., Liu, Y., Vaganov, E.A., Li, J., Cai, Q., 2008. Statistical and process based modeling
- 1432 analyses of tree growth response to climate in semi arid area of north central China: A
- 1433 case study of Pinus tabulaeformis. Journal of Geophysical Research: Biogeosciences 113.
- 1434 Shishov, V.V., Tychkov, I.I., Popkova, M.I., Ilyin, V.A., Bryukhanova, M.V., Kirdyanov, A.V.,
- 1435 2016. VS-oscilloscope: A new tool to parameterize tree radial growth based on climate conditions. Dendrochronologia 39, 42-50.
- 1437 Sitch, S., Friedlingstein, P., Gruber, N., Jones, S., Murray-Tortarolo, G., Ahlström, A.,
- 1438 Doney, S.C., Graven, H., Heinze, C., Huntingford, C., 2015. Recent trends and drivers of
  1439 regional sources and sinks of carbon dioxide. Biogeosciences 12, 653-679.
- 1440 St George, S., Ault, T.R., 2014. The imprint of climate within Northern Hemisphere trees.
- 1441 Quaternary Science Reviews 89, 1-4.
- 1442 Stevens, D.W., 1975. A computer program for simulating cambial activity and ring 1443 growth. Tree-Ring Bulletin.
- Sullivan, P.F., Csank, A.Z., 2016. Contrasting sampling designs among archived datasets:
  implications for synthesis efforts. Tree physiology 36, 1057-1059.
- Tang, L., Shao, G., 2015. Drone remote sensing for forestry research and practices.Journal of Forestry Research 26, 791-797.
- 1448 Teets, A., Fraver, S., Weiskittel, A.R., Hollinger, D.Y., 2018. Quantifying climate–growth
- relationships at the stand level in a mature mixed species conifer forest. Global changebiology.
- 1451 Tei, S., Sugimoto, A., Yonenobu, H., Matsuura, Y., Osawa, A., Sato, H., Fujinuma, J., 1452 Maximov, T., 2017. Tree - ring analysis and modeling approaches yield contrary
- 1453 response of circumboreal forest productivity to climate change. Global Change Biology.
- 1454 Tolwinski-Ward, S., Evans, M.N., Hughes, M.K., Anchukaitis, K.J., 2011. An efficient
- 1455 forward model of the climate controls on interannual variation in tree-ring width. 1456 Climate Dynamics 36, 2419-2439.
- Touchan, R., Shishov, V., Meko, D., Nouiri, I., Grachev, A., 2012. Process based model
  sheds light on climate sensitivity of Mediterranean tree-ring width. Biogeosciences 9,
  965.
- 1460 Trotsiuk, V., Svoboda, M., Weber, P., Pederson, N., Klesse, S., Janda, P., Martin-Benito, D.,
- 1461 Mikolas, M., Seedre, M., Bace, R., 2016. The legacy of disturbance on individual tree and
- stand-level aboveground biomass accumulation and stocks in primary mountain Piceaabies forests. Forest Ecology and Management 373, 108-115.
- 1464 Trouet, V., Babst, F., Meko, M., 2018. Recent enhanced high-summer North Atlantic Jet
- 1465 variability emerges from three-century context. Nature Communications 9, 180.
- 1466 Tucker, C.J., Pinzon, J.E., Brown, M.E., Slayback, D.A., Pak, E.W., Mahoney, R., Vermote,
- 1467 E.F., El Saleous, N., 2005. An extended AVHRR 8 km NDVI dataset compatible with

- MODIS and SPOT vegetation NDVI data. International Journal of Remote Sensing 26,4485-4498.
- 1470 Vaganov, E.A., Hughes, M.K., Shashkin, A.V., 2006. Growth Dynamics of Conifer Tree1471 Rings: Images of Past and Future Environments Springer, New York.
- 1472 van der Maaten-Theunissen, M., Bouriaud, O., 2012. Climate-growth relationships at
- 1473 different stem heights in silver fir and Norway spruce. Canadian Journal of Forest
- 1474 Research 42, 958-969.
- 1475 Vicente-Serrano, S.M., Camarero, J.J., Olano, J.M., Martín-Hernández, N., Peña-Gallardo,
- M., Tomás-Burguera, M., Gazol, A., Azorin-Molina, C., Bhuyan, U., El Kenawy, A., 2016.
  Diverse relationships between forest growth and the Normalized Difference Vegetation
  Index at a global scale. Remote Sensing of Environment 187, 14-29.
- 1479 Vicente-Serrano, S.M., Gouveia, C., Camarero, J.J., Beguería, S., Trigo, R., López-Moreno,
- J.I., Azorín-Molina, C., Pasho, E., Lorenzo-Lacruz, J., Revuelto, J., 2013. Response of
  vegetation to drought time-scales across global land biomes. Proceedings of the
  National Academy of Sciences 110, 52-57.
- von Arx, G., Crivellaro, A., Prendin, A.L., Čufar, K., Carrer, M., 2016. Quantitative wood
  anatomy—practical guidelines. Frontiers in plant science 7.
- Wagner, B., Ginzler, C., Bürgi, A., Santini, S., Gärtner, H., 2017. An annually-resolved stemgrowth tool based on 3D laser scans and 2D tree-ring data. Trees, 1-12.
- Wilkinson, S., Ogée, J., Domec, J.-C., Rayment, M., Wingate, L., 2015. Biophysical
  modelling of intra-ring variations in tracheid features and wood density of Pinus
  pinaster trees exposed to seasonal droughts. Tree physiology 35, 305-318.
- 1490 Williams, A.P., Allen, C.D., Macalady, A.K., Griffin, D., Woodhouse, C.A., Meko, D.M.,
- 1491 Swetnam, T.W., Rauscher, S.A., Seager, R., Grissino-Mayer, H.D., 2013. Temperature as a
- 1492 potent driver of regional forest drought stress and tree mortality. Nature Climate 1493 Change 3, 292-297.
- Wilson, B., 1973. A diffusion model for tracheid production and enlargement in conifers.Botanical Gazette 134, 189-196.
- 1496 Wilson, B.F., Howard, R.A., 1968. A computer model for cambial activity. Forest Science1497 14, 77-90.
- 1498 Wilson, R., Anchukaitis, K., Briffa, K.R., Büntgen, U., Cook, E., D'arrigo, R., Davi, N., Esper,
- J., Frank, D., Gunnarson, B., 2016. Last millennium northern hemisphere summer
  temperatures from tree rings: Part I: The long term context. Quaternary Science
  Reviews 134, 1-18.
- 1502 Wu, X., Liu, H., Li, X., Ciais, P., Babst, F., Guo, W., Zhang, C., Magliulo, V., Pavelka, M., Liu, S.,
- 1503 2017. Differentiating drought legacy effects on vegetation growth over the temperate1504 Northern Hemisphere. Global change biology.
- Zhang, Y., Shao, X., Xu, Y., Wilmking, M., 2011. Process-based modeling analyses of
  Sabina przewalskii growth response to climate factors around the northeastern Qaidam
  Basin. Chinese Science Bulletin 56, 1518-1525.
- Zhang, Z., Babst, F., Bellassen, V., Frank, D., Launois, T., Tan, K., Ciais, P., Poulter, B.,
  Converging Climate Sensitivities of European Forests Between Observed Radial Tree
  Growth and Vegetation Models. Ecosystems, 1-16.
- 1511 Zhang, Z., Babst, F., Bellassen, V., Frank, D., Launois, T., Tan, K., Ciais, P., Poulter, B., 2017.
- 1512 Converging Climate Sensitivities of European Forests Between Observed Radial Tree 1513 Growth and Vegetation Models. Ecosystems.
- 1514 Zhu, Z., Piao, S., Myneni, R.B., Huang, M., Zeng, Z., Canadell, J.G., Ciais, P., Sitch, S.,
- 1515 Friedlingstein, P., Arneth, A., 2016. Greening of the Earth and its drivers. Nature climate
- 1516 change 6, 791-795.

1518 Appendix A: Supplementary figure







Figure S1: Gridded tree-ring width anomalies (increment) between 2006-2010 for the six
most represented tree genera on the International Tree Ring Data Bank. The maps have been
produced using the random decision forest approach presented in Figure 2 of the main
manuscript.