Trees don't always act their age: size-deterministic tree-ring standardization for long-term trend estimation in shade-tolerant trees

Rachel Dietrich[1], Madhur Anand[1]

[1]School of Environmental Sciences, University of Guelph, Guelph, N1G 2W1, Canada

Correspondence to: Madhur Anand (manand@uoguelph.ca)

Abstract

With increasing awareness of the consequences of climate change for global ecosystems, the focus and application of tree-ring research has shifted to reconstruction of long-term climate-related trends in tree growth. Contemporary methods for estimating and removing biological growth-trends from tree-ring series (standardization) are ill-adapted to shade-tolerant species, leading to biases in the resultant chronologies. Further, many methods, including regional curve standardization (RCS), encounter significant limitations for species in which accurate age estimation is difficult. In this study we present and test two tree-ring standardization models that integrate tree size in the year of ring formation into the estimation of the biological growth-trend. The first method, dubbed size-deterministic standardization (SDS), uses tree diameter as the sole predictor of the growth-trend. The second method includes the combined (COMB) effects of age and diameter. We show that both the SDS and COMB methods reproduce long-term trends in simulated tree-ring data better than conventional methods – this result is consistent across multiple species. Further, when applied to real tree-ring data, the SDS and COMB models reproduce long-term, time-related trends as reliably as traditional RCS and more so than other common standardization methods (i.e. C-method, BAI, conservative detrending). We recommend the inclusion of tree size in the year of ring formation in future tree-ring standardization models, particularly when dealing with shade-tolerant species, as it does not compromise model accuracy and allows for the inclusion of unaged trees.

1 Introduction

Tree-rings have long-served as a record of environmental change in forest ecosystems. Early dendrochronological studies used tree-ring chronologies from climate sensitive species to elucidate the dynamics of growth-climate relationships and reconstruct climate anomalies from

periods before the existence of instrumental records. However, with increasing awareness of the

consequences of climate change for global ecosystems, the focus and application of tree-ring

research has shifted to reconstruction of low-frequency climate related trends in tree growth

(Gedalof and Berg 2010, Boisvenue and Running 2006, Jacoby and D'Arrigo 1997). As it stands,

previous optimism regarding the benefits of carbon fertilization for forest growth (Battipaglia et

al. 2012, Norby et al. 2005) has been quelled by a lack of consistent evidence in real forests.

While many studies have noted increases in long-term growth rates over time in temperate

forests (Gedalof and Berg 2010, Huang et al. 2007, Martinelli 2004) others suggest no change

(Giguère-Croteau et al. 2019, Camarero et al. 2015, Granda et al. 2014, Silva et al. 2010,

Peñuelas et al. 2011). Further, in boreal and drought prone species, growth decline (Chen et al.

2017, Dietrich et al. 2016, Girardin et al. 2012, Silva and Anand 2013) and increased mortality

(Herguido et al. 2016, Liang et al. 2016), in response to climate stress, have been prevalent.

Central to all these studies is the assumption that long-term growth-trends can be accurately and

unbiasedly estimated from tree-ring data.

As it stands, accurate estimation of long-term growth-trends in forests may be limited by poorly

adapted tree-ring standardization (age-trend removal) methods (Briffa et al. 1996) and

inappropriate sampling methods (Nehrbass-Ahles et al. 2014, Brienen et al. 2012). Early

standardization methods (i.e. conservative detrending) were designed to maintain high-frequency

variation in tree-ring series and discard long-term, low-frequency variation. It is accepted that

these methods are inappropriate for estimating long-term, climate related growth-trends (Briffa

1992); however, they are still used in situations where contemporary standardization methods are

not applicable due to restrictive data requirements (e.g. Villalba et al. 2012, Gedalof and Berg

2010, Geoff Wang et al. 2006).

53   Modern standardization methods are designed to estimate biological age/ size-related effects on

54   tree growth independent of time-related variance, thus theoretically, maintaining long-term

55   trends in the final chronologies. Among these, the conversion of tree ring widths to basal area

56   increments (BAI), and the closely related C-method (Biondi and Qeadan 2008), as well as the

57   use of regional curve standardization (RCS), (Briffa et al. 1992), and its many variants (See

58   Helama et al. 2017), have become commonplace (Peters et al. 2015). Traditional RCS relies on

59   the assumption that the species-specific biological growth trend of local trees can be estimated,

60   and thus removed, from a sufficiently large sample of trees using tree age alone. Alternatively,

61   the BAI method assumes that the biological growth trend is sufficiently related to basal area

62   accrued in a given year and, as such, chronologies presented as BAI (instead of raw ring width)

63   contain minimal biological effects. In practice, it is unlikely that this strict relationship accounts

64   for all the variation in ring width that is related to biological size/ age effects. As such, some

65   studies have proposed explicit models of BAI that attempt to include variables related to tree

66   age/ size or environmental conditions (i.e. tree density, soil fertility etc.), (e.g. Linares et al.

67   2008, Nock et al. 2011). Similarly, the C-method (CM) assumes that tree-wise basal area

68   increment (tree ring area) distributed over a growing surface in time is constant and as such,

69   annual deviations from this trend can represent the standardized chronology (free from biological

70   trend), (Biondi and Quadan 2008). Both BAI and CM are best suited to open-growth, shade-

71   intolerant trees where the strict relationship between annual growth and expected BAI is not

72   impeded by early competition for light.

73   However, due to the difficulties in separating climate-related trends that vary on long time scales

74   from those related to biological tree growth and/or succession-related environmental change,

75   none of these methods are likely to produce accurate estimates of external forcing when trees

76   from only a single age or size class are sampled (Brienen et al. 2012, Briffa and Melvin 2011). It

77   follows that studies which only sample even-aged stands or dominant trees are likely to produce

78   biased estimates of long-term growth. While increased awareness of sample biases has led to

79   better prescriptions for study design (see Nehrbass-Ahles et al. 2014, Brienen et al. 2012),

80   systematic tests of the ability of these models to accurately reproduce long-term trends are still

81   limited (e.g. Sullivan et al. 2016, Peters et al. 2015, Esper 2010).

82   Despite these limitations, RCS remains the standard method for estimating long-term growth-

83   trends in tree-ring data (Helama et al. 2017). However, the standard RCS approach encounters

84   large limitations for many species in which accurate age estimation is difficult. Additionally, we

85   suggest the inherent assumption of RCS that biological growth-trends are sufficiently determined

86   by tree age may not be appropriate in all species. More specifically, this assumption is

87   problematic for shade-tolerant trees. Shade-tolerant species exhibit relatively low low-light

88   mortality and thus can persist in forest understories for variable amounts of time before release

89   from overstory light suppression. In these cases, traditional age-deterministic models exhibit

90   high variance, and thus low precision, in the period following tree establishment and leading up

91   to the age when most trees have been released from suppression (Fig. 1). This period of ill-fit

92   means that trees which are released relatively early (or late) from light suppression will exhibit

93   inflated (or deflated) growth relative to the chronology. As a result, the final chronology will

94   show less agreement than would be expected in a shade-intolerant species. Even more

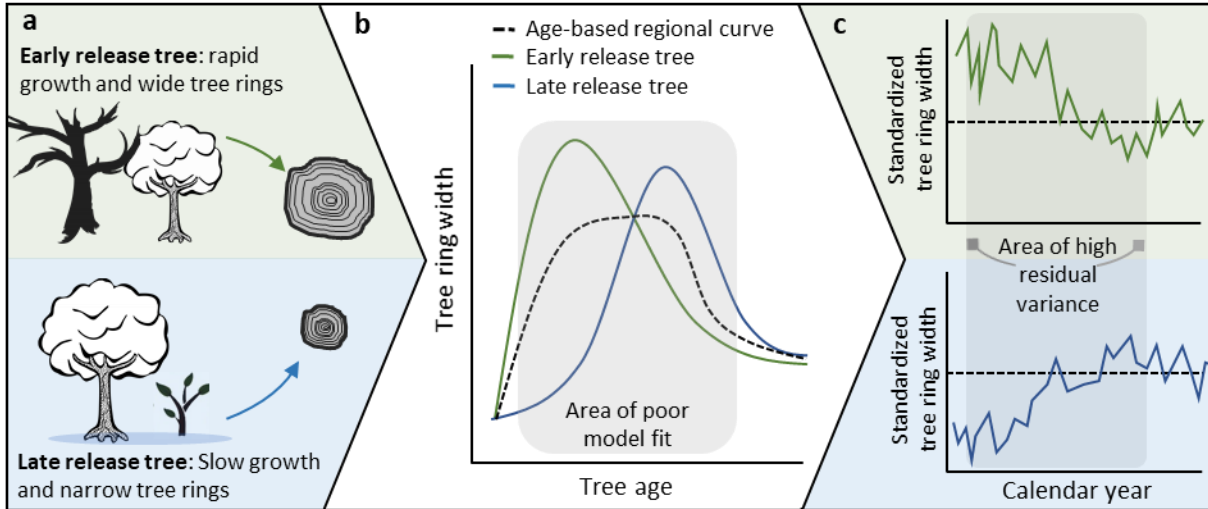
95   problematic, if trees are sampled according to minimum size thresholds, the youngest trees in the

96   chronology are likely to be early-release trees leading to an artificial inflation of modern growth

97   rates in the final chronology. While modifications to traditional RCS that address variance in

98   contemporaneous growth rates and regional environmental conditions have been prevalent in

99   shade-intolerant species (see Helama et al. 2017) there has been little to no focus on the

100 improvement of standardization techniques specific to shade-tolerant tree species.

101 **Figure 1**: (a) In shade-tolerant species young trees are stochastically released from low-light
102 suppression in the understory. (b) Since release from suppression is not strictly related to tree
103 age, widely used communal age-trend models (RCS) poorly model tree growth in the period
104 following establishment and leading up to the age when most trees have been released from
105 suppression. (c) Poor model-fit in this period implies that the biological growth-trend is not
106 entirely removed from individual series and leads to high residual variance when standardized
107 tree-ring series are aligned according to calendar year.
108 Alternatively, in the field of forest growth and yield modelling size-, rather than age-,

109 deterministic predictive growth models are ubiquitous. It is well understood that tree size

110 regulates the capacity for resource acquisition, namely, light (Canham et al. 2004), water and

111 nutrients (Homann et al. 2000), resource allocation (Lehnebach et al. 2018) and metabolic costs

112 (West et al. 2001). As such, the notion of radial growth being deterministic according to size

113 rather than age is logical from both a physiological and ecological perspective. Tree size in a

114 given year is dependent on its previous size and annual growth, so shade-tolerant trees that have

115 yet to be released from overstory light suppression remain small as they grow older. This relaxes

116 the period of 'ill-fit' that would be observed in an age-based model. Accordingly, we propose

117 that a size-deterministic model for tree-ring standardization may be more appropriate than

118   traditional RCS for shade-tolerant tree species. The application of size-deterministic models has

119   been limited, with few examples of tree size in a given year being incorporated into BAI models

120   (e.g. Marqués et al. 2016, Camarero et al. 2015, Nock et al. 2011, Martínez-Vilalta et al. 2008)

121   and even fewer of uniquely size-based tree-ring models (e.g. Bontemps and Esper 2011, Gavin et

122   al. 2008). Further, there have been no systematic evaluations of the ability of size-based models

123   to accurately estimate long-term trends in tree-ring series.

124   We present two tree-ring standardization models that integrate tree size in the year of ring

125   formation into estimation of the biological growth-trend. The first model uses tree diameter as

126   the sole predictor of the communal growth-trend while the second includes the combined effects

127   of both age and diameter. It follows that the objective of this study is to determine the efficacy of

128   both models in estimating long-term growth-trends in their resultant tree-ring chronologies. First,

129   we use modelled tree-ring data from shade-tolerant and intolerant species to make explicit the

130   inappropriateness of age-based models for shade-tolerant trees. Further, we investigate the

131   performance of size-based models relative to contemporary standardization methods in the

132   presence of size thresholds in tree sampling. Last, we apply the developed models to tree-ring

133   data from shade-tolerant temperate species to evaluate model performance relative to

134   contemporary methods on the basis of accurate reconstruction of known long-term, time-related

135   trends in the series.

136   **2 Methods**

137   **2.1 Model formulation**

138   Traditional RCS makes two assumptions about tree growth. First that trees of the same species in

139   a given region exhibit a common growth-trend as they age, and second, that growth of an

140   individual tree in a given year is thus a product of its age and common climatic or environmental

141   forcing in that year (Esper et al. 2003, Briffa et al. 1992). We present a variant of the RCS

142   method that uses tree size, measured by diameter at breast height (DBH), in the year of ring

143   formation as the primary determinant of the common biological growth-trend. As with RCS we

144   assume that the relationship between expected growth and tree size is non-linear and can be

145   approximated for a region from a sufficiently large sample of trees from the species in question.

146   Further, we assume that using a sample of trees from a range of size/age classes ensures

147   estimation of the common trend is not confounded by underlying low-frequency climate or

148   environmental forcing in the chronology (Brienen et al. 2012). The size-based regional curve

149   model, hereafter referred to as the **size deterministic standardization (SDS)** model, takes the

150   following form:

151   (1) $E(RW_{y,i}) = B_o + f_1(DBH_{y,i}) + e_{yi}$

152   Where $E(RW_{yi})$ represents the expected ring width of a given tree (i) in year (y), and f_1

153   represents a non-linear function relating DBH of a given tree (i) in year (y) to $E(RW_{yi})$. As in

154   RCS, the communal non-linear relationship is estimated communally for all local trees of

155   interest. In our study we estimate f_1 with a penalized thin plate regression spline in a generalized

156   additive model (GAM), however this relationship could be estimated by a number of different

157   spline-fitting or non-linear regression techniques (i.e. *ffcsaps* function in dplR (Bunn et al. 2018),

158   time-varying splines (Melvin et al. 2007)). Under this paradigm the model residuals (e_{yi})

159   represent individual standardized ring width indices and, by extension, individual tree response

160   to climatic or environmental forcing. Annual model residuals subject to a robust mean, thus,

161   represent the final standardized chronology. This approach differs slightly from traditional RCS,

162   whereby standardized ring width indices are occasionally produced by division of raw

163   measurements by the expected value. Calculation of standardized ring width indices by

164   subtraction from the expected value, as in the case of residuals, is now commonly used as it

165   tends to reduce bias in the resultant chronology (Helama et al. 2004) and eases in the formulation

166   of more complex tree-ring standardization models. However, unlike division methods, the

167   subtraction method does not provide any stabilization of variance in the resulting residuals; as

168   such, it may be necessary to use a stabilization procedure (i.e. log transformation, power

169   transformation) on raw ring width data beforehand.

170   Tree size in a given year can be estimated by outside-in or inside-out techniques. If the pith of a

171   tree is present in the core (or reasonably close to) DBH_y is a simple summation of all previous

172   ring widths since the year of origin, multiplied by two. Alternatively, if the pith is missed, DBH_y

173   can be calculated via subtraction of more modern ring widths (multiplied by two) from the

174   inside-bark diameter. In this case inside-bark diameter is calculated as measured DBH minus

175   bark thickness (multiplied by two), where bark thickness can be directly measured or estimated

176   using species-specific allometric equations (e.g. Stayton and Hoffman 1970).

177   Similar to the model formulation for SDS, RCS models were estimated with GAMs of the

178   following form:

179   (2) $E(RW_{yi}) = B_o + f_1(Age_{yi}) + e_{yi}$

180   Where Age_{yi} is the age of an individual tree in a given year and the resultant standardized tree-

181   ring indices are derived from model residuals (e_{yi}).

182   In addition, a more complex model that integrated independent size and age effects was also

183   evaluated for comparison. This model, hereafter referred to as the **combined model (COMB)**,

184   took the following form:

185   (3) $E(RW_{yi}) = B_o + f_1(Age_{yia}) + f_2(DBH_{yi}) + e_{iy}$

In a large variety of long-lived tree species, accurate age estimation (pith sampling) is difficult or impossible; rendering traditional RCS or combined models inappropriate for all trees sampled. To address this issue, the above model can incorporate unaged trees. Here f_1 represents the non-linear function relating age to expected ring width for the subset of all trees that are aged (ia). In this model, ring widths from unaged trees are assigned arbitrary ages which do not contribute to the linear approximation of the smooth term for Age (i.e. $f_1(\text{Age}_{yia})$ but these trees still contribute to the smooth term for size f_2 (DBH_{yi}). Syntax for missing data in GAMs follows the protocol provided in mgcv (Wood 2011). In this study all GAMs were fit using the mgcv package (Wood 2011) in the R statistical program (v.3.5.0).

In addition to the models presented above we investigated three additional standardization methods; conservative detrending (CD), CM and BAI. Conservative detrending describes functions (i.e. negative exponentials, straight lines) or flexible splines fit to individual tree ring series (see Cook and Kairiukstis 1990). In this study we use spline-fitting techniques rather than modified negative exponentials as they are more appropriate for shade-tolerant tree species. As above, the individual standardized tree ring width indices are derived from model residuals. The C-method estimates tree-specific expected ring widths by assuming constant annual basal area increment (tree ring area) over the life span of the tree (See Biondi and Qeadan 2008). Annual deviations from expected values thus represent standardized ring width indices. For consistency, the standard CM approach in dplR (Bunn et al. 2018) was modified in order to calculate indices via subtraction (residuals) instead of division. Tree ring widths were converted to BAI using the dplR package in R (Bunn et al. 2018). R code for worked examples of all standardization procedures used in this study is available: (https://github.com/Rachel-lynn/SDS-example).

2.2 Simulated tree-ring data

209 We simulated tree-ring data using a well-established gap-phase model. The SORTIE-ND model

210 was chosen over other similar gap-phase models as it better emulates understory light conditions

211 and low-light mortality, both of which are central to the notion of age being an inappropriate

212 determinant of growth in shade-tolerant species. In SORTIE annual radial tree growth is

213 calculated as an asymptotic function of light availability and previous tree diameter. As such, the

214 underlying growth-trend in SORTIE simulated data should be well-approximated by a flexible

215 curve estimated on the basis of tree size (SDS). As such, we use this analysis solely to elucidate

216 the problematic nature of age-based standardization methods for shade-tolerant species not to

217 confirm the efficacy of size-based standardization methods.

218 For simplicity, a 100% sugar maple (*Acer saccharum)* dominated stand was simulated as sugar

219 maple is a model shade-tolerant species that grows in self-replacing stands. All living trees (>5

220 cm dbh), (n=3657) in the final year of the model run were used for further analysis. Additionally,

221 to elucidate our claim that age-deterministic growth estimation is more problematic in shade-

222 tolerant species, we completed a similar SORTIE simulation for the shade-intolerant species

223 white pine (*Pinus strobus*). Again, the stand was 100% white pine, standard model parameters

224 were used, and the simulation was run for 1000 years. All living trees (>5 cm dbh), (n=7362) in

225 the final year of the model run were used for further analysis. Additional details regarding model

226 parameters for the SORTIE simulations are provided in the supplementary materials (S2).

227 To simulate a low-frequency climate-related growth-trend, a logistic trend was added to raw tree-

228 ring width of individual trees produced by both SORTIE simulations. The logistic trend

229 simulated an initial rapid increase in growth and subsequent levelling off that aimed to represent

230 a period of carbon fertilization and eventual acclimation. The logistic model was applied to the

231 last 100 years of growth and took the following form, where RWt_{yi} represents ring widths with

232 the simulated long-term trend and RWr_{yi} are raw ring widths:

233 $$(4) \ RWt_{yi} = RWr_{yi} \left(\frac{k}{1+ae^{-ry}} + 1 \right)$$

234 The logistic trend parameters ($r=0.12, k=0.629, a=20$) were chosen such that increases in

235 individual tree growth averaged approximately 5% per decade. Additionally, we tested the

236 standardization models in their ability to detect simulated negative trends in tree growth as

237 previous studies have noted a failure of contemporary methods to accurately reproduce declining

238 growth trends (Peters et al. 2015). The simulated negative logistic trend took the form of eq (4)

239 with parameters ($r=0.12, k=-0.421, a=20$) chosen such that decreases in growth averaged 5%

240 per decade. For completeness, we also simulated positive and negative linear trends. Results of

241 those analyses are provided in the supplementary materials (S3).

242 Sixty trees were randomly selected, without replacement, from the simulated tree populations

243 and subject to each of the six standardization methods (SDS, RCS, COMB, CD, BAI, CM).

244 Model residuals (in the case of RCS, SDS, COMB, CD and CM) or transformed (BAI) tree ring

245 widths were compiled into an annual mean chronology using Tukey's biweight robust mean. The

246 resultant chronologies were then tested for significant correlation with the imposed trends using

247 Spearman's rank correlation coefficient. This process was bootstrap resampled (with

248 replacement) 100 times, in order to produce confidence intervals for the resultant mean

249 chronologies and their respective correlation coefficients.

250 To examine the effect of minimum size sampling thresholds on the accuracy of long-term trend

251 reconstruction by each of the standardization methods, we completed the same analysis on trees

252 from the simulated populations that exceeded certain size thresholds. The thresholds employed

253 were 10 cm DBH, which represented a practical minimum size threshold for sampling, and 30

254   and 50 cm DBH which represented thresholds for mature and dominant trees, respectively. The

255   CD method was only applied when size thresholds exceeded 10cm DBH due to the troublesome

256   nature of fitting splines to excessively short timeseries. The mean Spearman's rho for all

257   detrending methods and sampling thresholds were compared using two-way ANOVA and post-

258   hoc tests.

259   **2.3 Real tree-ring data**

260   Additionally, we evaluated the performance of the six standardization methods in real tree-ring

261   data from shade-tolerant species. We collected tree-ring data from seven mature sugar maple

262   dominated stands in Ontario, Canada (Table 1). Further, tree-ring data sets from the shade-

263   tolerant species red spruce (*Picea rubens*) were obtained from the DendroEcological Network

264   database (https://www.uvm.edu/femc/dendro), (Table 1). Red spruce was chosen as it had

265   sufficient replication across studies in the database. Descriptions of the sampling strategies and

266   data processing methods for all sites considered are provided in either the supplementary

267   materials (S4) or in their respective references (i.e. Kosiba 2013, Kosiba 2017). Data was

268   considered suitable for this study if age and DBH estimates were provided and if a minimum 10

269   trees per site and species were sampled and accurately aged. All cores in which pith offset was

270   estimated to be greater than 10 years were considered unaged. To simplify comparisons of the

271   resultant chronologies unaged tree were not included in the models.

272   Prior to model application a time-deterministic thin plate regression spline was applied to all raw

273   ring widths from each site. This ensured there was no underlying time-trend present in the data.

274   Since trees of multiple ages/sizes were sampled in each study we assume the removed time-trend

275   is therefore independent of biological trends in the series. For each site residuals from the

276   regression spline were centred according to the site-wise mean and standard deviation of raw

277   ring widths prior to analysis.

Table 1:
Location, sample size, chronology length and source of tree ring data sets used in this study.

Species	Site (code)	Longitude (°)	Latitude (°)	N. trees total	N. trees aged	Length of chronology	Source
Sugar maple	Toobee Lake (TB)	46.7459	-82.8668	79	67	1750-2015	This study
(*A. saccharum*)	Wolf Mtn. (WM)	46.7390	-82.8467	22	18	1827-2015	…
	Roosevelt Road (RS)	47.2852	-79.7063	20	11	1792-2016	…
	Raven Lake (RL)	45.3309	-78.6339	31	19	1864-2015	…
	Freezy Lake (FR)	45.2998	-78.4329	20	11	1887-2015	…
	Mt. Zion Road (MT)	46.4000	-83.7004	29	15	1777-2015	…
Red spruce	Mt. Mansfield (MTM)	44.3750	-73.8750	111	109	1769-2011	Kosiba et al. (2016)
(*P. rubens*)	Burnt Mtn. (BNT)	44.2068	-72.3515	40	40	1891-2010	Kosiba et al. (2013)
	Mt. Carmel (CAR)	43.7709	-72.9205	41	41	1795-2010	…
	Mt. Ellen (ELL)	44.1656	-72.9221	42	42	1824-2010	…
	Mt. Equinox (EQU)	43.1487	-73.1273	89	89	1857-2010	…
	Mt. Greylock (GRY)	42.6738	-73.1575	44	44	1911-2010	…
	Mt. Ascutney (ASC)	43.4337	-72.4440	20	20	1929-2010	…
	Bristol Cliffs (BRI)	44.1084	-73.0720	19	19	1713-2010	
	Middlebury Gap (MID)	43.9424	-72.9410	14	14	1922-2010	…
	Wolcott Forest (WLC)	44.5965	-72.4215	18	18	1912-2010	…
	Mt. Moosilauke (MOO)	44.0056	-71.8215	54	54	1760-2010	…
	Mad River Glen (MRG)	44.1932	-72.9232	36	36	1927-2010	…

278

279   Again, increasing and decreasing logistic trends (Eq 4) as well as linear trends (Suppl. S3) were

280   added to the (re-centered) tree ring residuals. Trend parameters were chosen such that the

281   increase (or decrease) in tree growth averaged 5% per decade over the last 50 years of growth

282   (*r=0.12, k=0.276, a=20* (positive trend)), (*r=0.12, k=-0.226, a=20* (negative trend)). For each

283   site all trees were subject to each of the six standardization methods (SDS, RCS, COMB, CD,

284   BAI, CM). Model residuals (in the case of RCS, SDS, COMB, CD and CM) or transformed

285   (BAI) tree ring widths were compiled into an annual mean chronology using Tukey's biweight

286   robust mean. The resultant chronologies were then tested for significant correlation with the

287   imposed trends using Spearman's rank correlation coefficient. In both species (sugar maple and

288   red spruce) one-way ANOVA and Tukey post-hoc comparisons were used to test for significant

289   differences in model performance- as estimated by chronology correlation with the imposed

290   trend.

3 Results

3.1 Comparisons of methods in simulated data

In order to evaluate the efficacy of each standardization method we calculated correlations

between chronologies produced by each method and a variety of imposed trends in simulated

sugar maple and white pine tree ring data. Bootstrapped confidence intervals for chronologies

from each of the standardization methods are provided in Figure 2a and 2b for sugar maple and

red pine, respectively. Distributions of the respective spearman's rank correlation coefficients

between the chronologies and the imposed trends are provided in Figure 3a for sugar maple and

3b for white pine.

3.11 Simulated sugar maple tree ring data

In the simulated sugar maple data, two-way ANOVA suggested a significant effect of both

standardization model (p<0.001) and minimum size sampling threshold (p<0.001) on average

correlation with the positive logistic trend. Alternatively, for the negative logistic trend there was

a significant effect of standardization model (p<0.001) but not of size sampling threshold. For

both positive and negative logistic trends SDS ($\overline{r}_s$=0.974±0.037, $\overline{r}_s$=0.954±0.068, respectively)

and COMB ($\overline{r}_s$=0.965±0.039, $\overline{r}_s$=0.894±0.123, respectively) models produced chronologies with

significantly higher correlations than all other models (p<0.001 for all) but not significantly

different from each other (p=0.998, p=1.000, respectively). For the positive imposed trend BAI

($\overline{r}_s$=0.864±0.236) and RCS ($\overline{r}_s$=0.900±0.162) produced chronologies with correlations

significantly higher than CD ($\overline{r}_s$=-0.503±0.329) and CM ($\overline{r}_s$=0.746±0.306), (p<0.001 for all) but

not significantly different then each other (p=0.996). Notably, correlations exhibited by BAI

chronologies were dependent on size sampling thresholds with BAI chronologies performing

best when size thresholds exceeded 50 cm DBH (Fig 3a). At this threshold BAI chronologies

314 produced significantly higher correlations than when all trees were sampled (p=0.003) and when

315 trees >10 cm DBH were sampled (p<0.001). The CD method produced chronologies that

316 exhibited the lowest average correlation with the imposed positive trend of all models (p<0.001

317 for all).

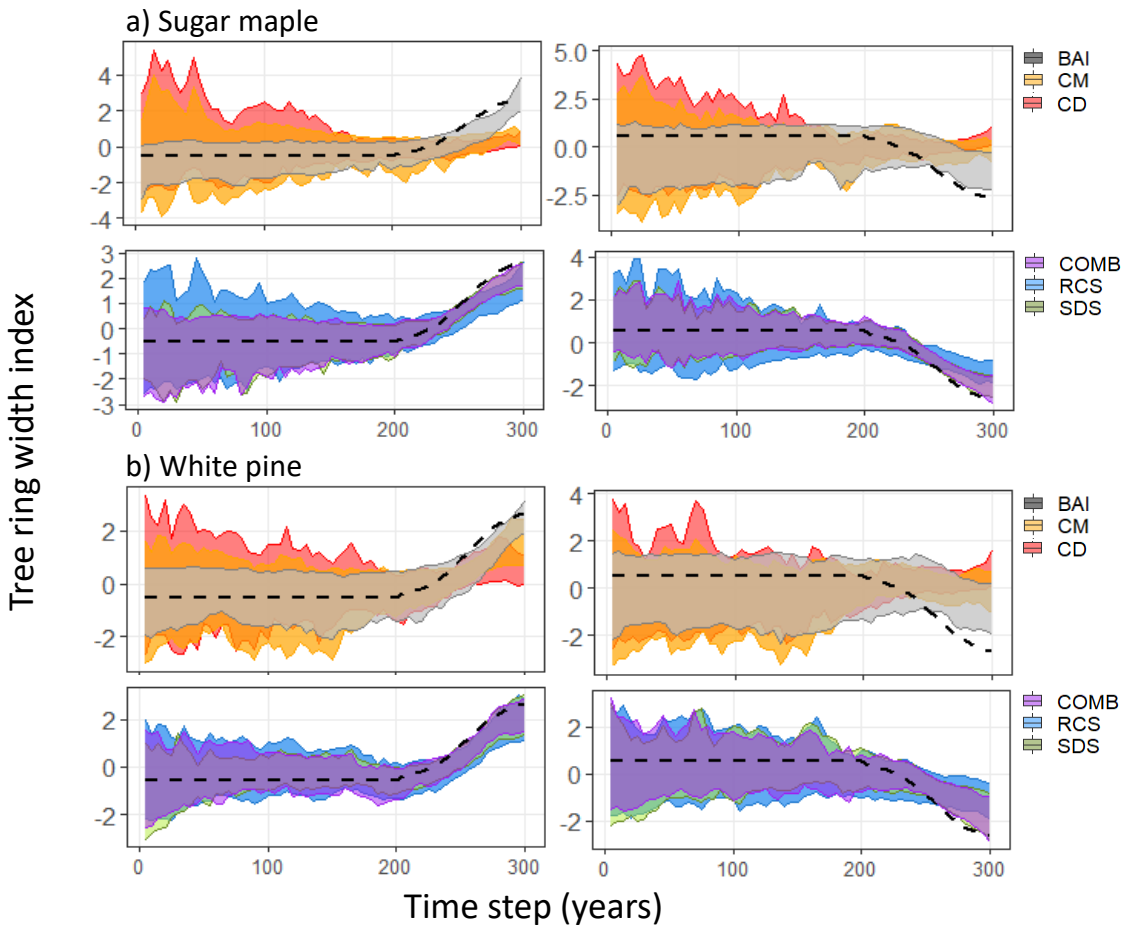



Figure 2: 95% confidence intervals for standardized chronologies produced by each standardization method (legend right side) applied SORTIE simulated sugar maple and white pine tree ring data. Confidence intervals obtained via bootstrap resampling (rep=100) of 60 trees (>10 cm DBH) from the SORTIE simulated populations. Dotted lines indicate the standardized positive (left side) or negative (right side) logistic trend that was added to the raw tree ring data.

318   Alternatively when considering negative imposed trends, BAI ($\bar{r}_s$=0.745±0.426) chronologies

319   performed significantly worse than RCS ($\bar{r}_s$=0.706±0.281, p<0.001) but still better than CD ($\bar{r}_s$=-

320   0.609±0.291) and CM ($\bar{r}_s$=0.666±0.364), (p<0.001 for both). Again, CD chronologies exhibited

321   significantly lower correlations than all other models (p<0.001 for all). Notably, RCS

322   chronologies produced at the 50 cm DBH sampling threshold exhibited significantly lower

323   correlations than all other sampling thresholds (p<0.001), (Fig 3a). All other models exhibited

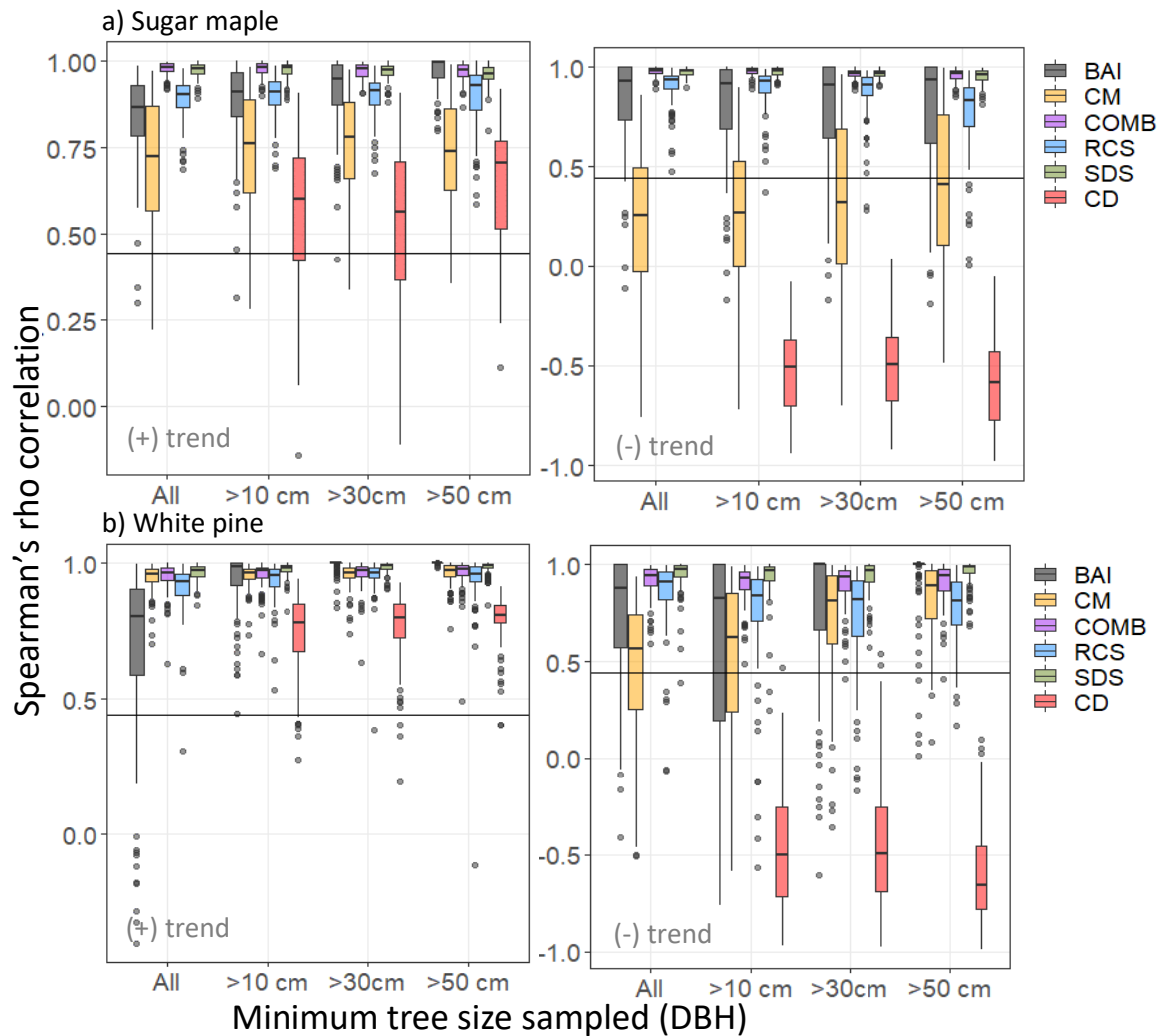



Figure 3: Spearman's correlation between chronologies produced by each of the five standardization methods and the imposed positive (left column) or negative (right column) logistic trend in SORTIE simulated (a) sugar maple and (b) white pine tree-ring data. Correlation distribution created by bootstrap resampling 60 trees (rep=100) from SORTIE simulated tree populations. Horizontal axis denotes minimum tree size (DBH) thresholds for sampling from the population. Horizontal lines indicate threshold for significant Spearman's rho (a=0.05) for correlation between chronologies and the imposed trend.

324   similar correlation distributions across the various size thresholds for sampling.

325   3.12 Simulated white pine tree ring data

326   In simulated white pine data, two-way ANOVA suggested a significant effect of both

327   standardization model (p<0.001) and minimum size sampling threshold (p<0.001) on average

328   correlations for both the positive and negative logistic trend analyses. For the positive trend,

329   chronologies produced by SDS ($\overline{r_s}$=0.977±0.026), RCS ($\overline{r_s}$=0.932±0.091), COMB

330   ($\overline{r_s}$=0.956±0.052) and CM ($\overline{r_s}$=0.953±0.045) produced high correlations across all sampling

331   thresholds with SDS performing significantly better than CM (p=0.006) and RCS (p=0.001). All

332   four models produced significantly higher correlations than those produced by BAI

333   ($\overline{r_s}$=0.899±0.222) or CD ($\overline{r_s}$=0.767±0.126) chronologies, with CD producing the lowest

334   correlations of all models. Contrasts suggested that the significant effect of minimum size

335   threshold was driven by significant differences in correlations from BAI chronologies across

336   sample thresholds, whereby BAI chronologies exhibited significantly lower correlations when no

337   minimum size thresholds (i.e. all trees sampled) were employed (p<0.001 in all cases), (Fig. 3b).

338   When examining negative imposed trends, SDS ($\overline{r_s}$=0.942±0.090) and COMB ($\overline{r_s}$=0.904±0.0.97)

339   models produced chronologies with significantly higher correlations than all the other models,

340   but not significantly different from each other (p=0.594). BAI ($\overline{r_s}$=0.750±0.390) and RCS

341   ($\overline{r_s}$=0.772±0.245) produced chronologies with correlations significantly higher than CD ($\overline{r_s}$=-

342   0.505±0.316) and CM ($\overline{r_s}$=0.623±0.362), (p<0.001 for all) but not significantly different then

343   each other (p=1.00). CD chronologies exhibited significantly lower correlations than all other

344   models (p<0.001 for all). Contrasts suggested that the significant effect of minimum size

345   threshold was driven by significant difference in correlations of chronologies produced by BAI

346   and CM among sampling thresholds. As evident in Figure 3b, BAI chronologies performed

347 significantly better when sampling thresholds exceeded 50 cm DBH and CM chronologies

348 performed best when sampling thresholds exceeded 30 cm DBH.

349 **3.2 Comparisons of methods in real tree-ring data**

350 Standardization methods were evaluated on the basis of correlations between their resultant

351 chronologies and known time-related trends in tree ring series from shade-tolerant species.

352 Confidence intervals surrounding chronologies produced from each of the standardization

353 methods applied to the tree ring series from six sugar maple stands are provided in Figure 4a for

354 both positive and negative logistic trends. The corresponding distributions of Spearman's rank

355 correlation coefficients are provided in Figure 5a with significant differences ($p < 0.05$) being

356 denoted by letters. Chronologies and corresponding correlation coefficients for the identical

357 analysis performed on 12 red spruce stands are provided in Figure 4b and 5b.

358 Regardless of trend direction RCS, COMB and SDS chronologies exhibited comparable and

359 consistent results across both species (Fig. 5). In general chronologies produced by all three

360 methods exhibited conservative, but reliable, estimations of the imposed trends (Fig. 4). SDS

361 produced chronologies with correlations as high or higher (Fig. 5b (negative trend)) than

362 traditional RCS chronologies. Notably, the BAI and CM methods produced strong positive

363 correlations between chronologies and the imposed trend only when the imposed trend was

364 increasing (Fig. 4, 5) but both consistently failed to reproduce negative trends (Fig. 4). Finally,

365 across both species, CD chronologies exhibited low correlations with the imposed trend

366 regardless of direction (Fig. 4,5).

367 **4 Discussion**

368 **4.1 Size- vs. age-deterministic models for long-term trend reconstruction**

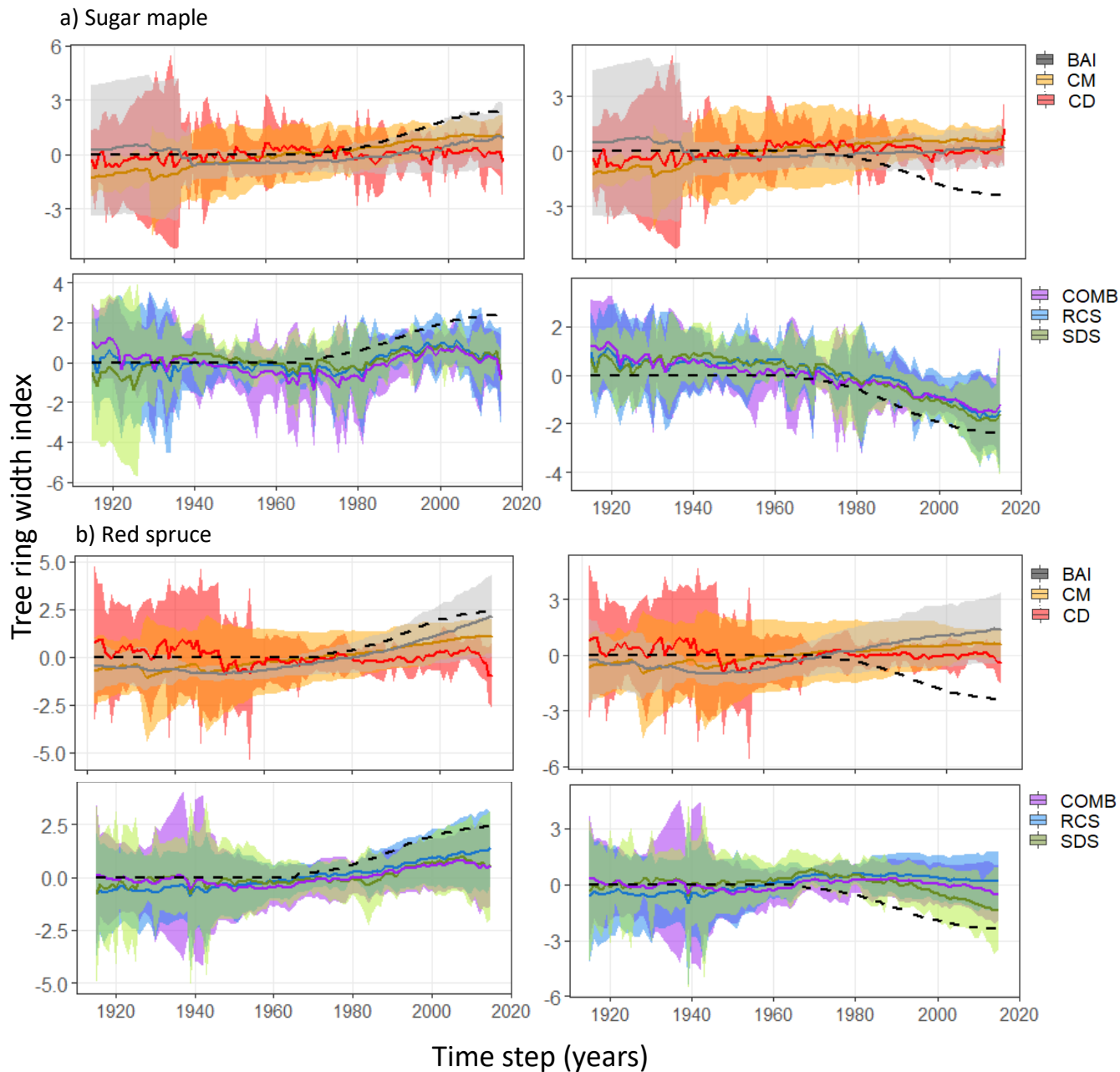



Figure 4: Standardized chronologies produced by each standardization method (legend right side) applied to tree ring series from a) sugar maple (n=6) and b) red spruce (n=12) stands. Solid lines represent the resultant model-wise mean chronologies across all stands considered while ribbons represent respective 95% confidence intervals. Dotted lines indicate the standardized positive (left side) or negative (right side) logistic trend that was added to the raw tree ring data.

369 Using simulated tree-ring data, from the shade-tolerant species sugar maple, we have shown that

370 standardization models which include tree size in the year of ring formation (SDS, COMB)

371 produced chronologies that retain long-term/low-frequency variation better than those produced

372 by models that only included age as a

373 predictor (RCS). Alternatively, in the shade-

374 intolerant species white pine, chronologies

375 produced by the RCS and COMB models

376 showed no significant difference in their

377 estimation of long-term trends, though SDS

378 chronologies slightly outperformed RCS

379 chronologies. As discussed previously, the

380 finding that size-based standardization

381 models perform well in simulated tree-ring

382 data is not surprising given that the SORTIE

383 model calculates annual tree growth as

384 function of tree size. Thus, the underlying

385 growth-trend would be well-approximated by

Figure 5: Spearman's correlation between chronologies produced by each of the five standardization methods and the imposed positive (left column) or negative (right column) logistic trend in tree ring series from (a) sugar maple and (b) red spruce stands. Horizontal lines indicate threshold for significant Spearman's rho (a=0.05) for correlation between chronologies and the imposed trend. Letters indicate significant differences among samples as estimated by Tukey honest significant differences (a=0.05).

386 a flexible curve estimated on the basis of tree size. As such, we use these results solely to

387 elucidate the problematic nature of age-based standardization methods for shade-tolerant species.

388 SORTIE's use of diameter, rather than age, as a determinant of tree growth is not arbitrary; it is

389 well-established that tree metabolic processes are directly related to size (West et al. 2001).

390 Additionally, there is little evidence for a unique effect of age on tree growth that is independent

391 of size (Munné-Bosch 2007 (and within)). With the exception of dendrochronological models,

392 the vast majority of individual tree growth and process models are indeed size-based. It follows

393 that the ubiquitous use of age or calendar year in tree-ring standardization methods (RCS, signal-

394 free standardization, CD, Hugershoff curves) is a practice born out of convenience rather than

395 physiological consideration. As such, we agree with previous accounts that this assumption may

396 be especially problematic in shade-tolerant trees where age and size may not be perfectly

397 correlated (Peters et al. 2015, Bontemps and Esper 2011).

398 Unfortunately, all systematic comparisons of tree-ring standardization methods in real tree-ring

399 data (e.g. Sullivan et al. 2016) are limited by their inability to validate long-term trends estimated

400 by chronologies. In this study we evaluate standardization methods on their ability to reconstruct

401 artificial trends in tree ring data. We show that SDS and COMB models are as reliable as the

402 traditional RCS method in accurately detecting long-term trends in shade-tolerant species.

403 Further, SDS appears to provide more reliable reconstructions when the underlying trend is

404 negative. To our knowledge, only one other study has evaluated size-deterministic models on the

405 basis of long-term trend reconstruction in chronologies. Bontemps and Esper (2011) compared

406 RCS and SDS chronologies in common beech (*Fagus sylvatica* L.)) and conclude that both

407 exhibit similar variations, with the magnitude of difference varying between 3-7%. However,

408 other studies have examined the influence tree size in explicit models of BAI. In tropical tree

409 species of varying shade-tolerance Nock et al. (2011) note that linear mixed models of BAI that

410 included tree diameter had more support than those that included age. This result is corroborated

411 by analyses of mixed models of BAI in Mediterranean pine species which suggest that the effect

412 of DBH on BAI is more important than the effect of tree age (Marqués et al. 2016). In line with

413 discussion above, Nock et al. (2011) attribute this finding to size being a more important

414 determinant of light capture as it relates to tree height and crown size (King et al. 2005).

415 The resultant chronologies are indeed more likely to be influenced by the sample of the

416 underlying tree population than by choice of standardization model. Tree age can be difficult or

417 impossible to accurately estimate for some trees. In contrast, annual tree size can be reliability

418   estimated from DBH and tree-ring measurements more ubiquitously. We note that in this study

419   only 66% of sugar maple trees could be accurately aged. Since unaged trees are likely to be the

420   oldest trees in the chronology, it follows that RCS chronologies may exhibit poor sample

421   replication (especially in early years) and may be significantly shorter than those typically

422   produced by SDS or COMB models. This has obvious implications for data quality and

423   suitability. Considerably problematic is the "segment length curse" whereby, almost all

424   standardization methods are ill-equipped to estimate long-term trends on time scales greater than

425   or equal to the length of the chronology itself (Cook et al. 2005). Excessively short RCS

426   chronologies are therefore limited in their application. A large advantage of SDS and COMB

427   models is that they can incorporate otherwise inadmissible tree-ring data.

428   This study does not explicitly test the efficacy of COMB models relative to SDS in the presence

429   of unaged trees. Nor have we provided evidence to suggest that the added complexity of COMB

430   models relative to SDS is beneficial to accurate reconstruction of trends in the resultant

431   chronologies. Given, the merit the of size-deterministic models presented here, we suggest future

432   research explore the implications of the trade-off between model information and complexity in

433   the presence of unaged trees.

434   **4.2 BAI, CM and CD methods for long-term trend reconstruction**

435   The finding that CD did not produce accurate long-term trends in simulated tree-ring data is

436   consistent with our expectations (Peters et al. 2015, Briffa et al. 1992). We maintain CD should

437   be avoided if the goal is long-term reconstruction from tree-ring data. More interestingly, we

438   have shown that CM and BAI, although designed for shade-intolerant open growth trees, do not

439   reliably reconstruct negative long-term trends in simulated white pine tree ring data. Further, our

440   analysis suggests BAI is less reliable when small/young trees are sampled. This result is

441 corroborated in our study by a failure of both methods to reconstruct negative trends in shade-

442 tolerant, sugar maple and red spruce, tree ring data. Further, this finding is in line with Peters et

443 al. (2015) who note low reliability of BAI and that BAI is likely to produce erroneous trends

444 when the underlying trend is of low signal, as would be the case for young/small trees that have

445 low BAI rates and low climate sensitivity.

446 Both BAI and CM impart a strict relationship between tree size and growth. It has been

447 suggested that this relationship may not account for the entire biological growth-trend, leading to

448 the maintenance of erroneous long-term trends in the resultant chronologies (Peters et al. 2015).

449 Erroneous increasing trends are indeed noted in both sugar maple (Fig 4a) and red spruce (Fig

450 4b) chronologies produced by BAI and CM in our study. Accordingly, we caution future studies

451 in their interpretation of BAI and CM trends in low-signal tree-ring series. Other studies have

452 explicitly modelled size and/or age effects on BAI using a mixed-effect modelling approach (e.g.

453 Marqués et al. 2016, Camarero et al. 2015, Nock et al. 2011, Martínez-Vilalta et al. 2008). We

454 suggest this approach may better account for species- and site-specific factors that influence

455 expected growth rates, leading to more accurate estimates of long-term trends in the resultant

456 chronology. While our findings regarding the importance of inclusion of size in tree-ring

457 standardization models are presented in the context of raw tree-ring width models, they are also

458 directly relevant to explicit models of BAI. A more thorough discussion of the limitations of CD,

459 BAI and CM method as relevant to reconstruction of long-term trends is beyond the scope of this

460 study. The interested reader is directed to Peters et al. (2015).

461 **4.3 Other considerations and future research**

462 It is important to note that the goal of this study was not to explicitly test the effect of sample

463 biases (i.e. modern sample bias, selection bias, etc.) on trend reconstruction, but instead to assess

464   reliability across different underlying sampling distributions. Accordingly, our results do not

465   suggest that any of the discussed standardization methods are immune to sample biases (i.e. big

466   tree selection bias, slow grower survivorship bias) as our study is not designed to detect, and

467   isolate, the effects of contemporaneous differences in growth among trees that produce these

468   biases. There is now substantial evidence to suggest that the long-standing practice of sampling

469   only dominant trees or trees exceeding a minimum size threshold within a stand leads to

470   considerable bias in the resultant chronology (Nehrbass-Ahles et al. 2014, Brienen et al. 2012,

471   Briffa and Melvin 2011). This bias is consistent across standardization methods (Duchesne et al.

472   2019, Nehrbass-Ahles et al. 2014). We maintain that in cases of long-term trend reconstruction,

473   stands should be sampled according to the underlying stand age/size distribution, either through

474   use of fixed-plots or random tree selection, regardless of the standardization procedure used.

475   Given the underlying physiological justification of the models presented here, we have no reason

476   to suggest they are not broadly applicable to species of all shade-tolerance levels. We

477   recommend future studies investigate the applicability of SDS and COMB models to both tree-

478   ring width and BAI data in wider range of species. That said, shade-tolerant and broadleaf

479   species, and their applicable standardization procedures, are underrepresented in

480   dendrochronological studies (Zhao et al. 2019). Further, the applicability of enhanced tree ring

481   standardization models (including traditional RCS and BAI) to global tree ring data sets are

482   limited by widely unavailable metadata (i.e. tree age and DBH) in tree ring databases.

483   Accordingly, we recommend more stringent requirements on the inclusion of applicable

484   metadata in global databases in order to accommodate more complicated standardization models.

485   We advocate for continued refinement of tree-ring standardization procedures that are relevant to

486   the ecological questions they aim to address.

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