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Invited review

When tree rings go global: Challenges and opportunities for retro- and prospective insight



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ABSTRACT

The demand for large-scale and long-term information on tree growth is increasing rapidly as environmental change research strives to quantify and forecast the impacts of continued warming on forest ecosystems. This demand, combined with the now quasi-global availability of tree-ring observations, has inspired researchers to compile large tree-ring networks to address continental or even global-scale research questions. However, these emergent spatial objectives contrast with paleo-oriented research ideas that have guided the development of many existing records. A series of challenges related to how, where, and when samples have been collected is complicating the transition of tree rings from a local to a global resource on the question of tree growth. Herein, we review possibilities to scale tree-ring data (A) from the sample to the whole tree, (B) from the tree to the site, and (C) from the site to larger spatial domains. Representative tree-ring sampling supported by creative statistical approaches is thereby key to robustly capture the heterogeneity of climate-growth responses across forested landscapes. We highlight the benefits of combining the temporal information embedded in tree rings with the spatial information offered by forest inventories and earth observations to quantify tree growth and its drivers. In addition, we show how the continued development of mechanistic tree-ring models can help address some of the non-linearities and feedbacks that complicate making inference from tree-ring data. By

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embracing scaling issues, the discipline of dendrochronology will greatly increase its contributions to assessing climate impacts on forests and support the development of adaptation strategies.

1. Introduction

1.1. An increasing need to scale tree-ring data

Climate change during the Anthropocene is now considered a certainty (Marotzke et al., 2017) and environmental research focuses increasingly on quantifying and forecasting the impacts of continued warming on ecosystems and natural resources. Forests receive particular attention because they absorb large amounts of excess atmospheric CO₂ generated by human activities (Le Quéré et al., 2016) and store this carbon in woody biomass for decades to centuries (Körner, 2017). Importantly, rising temperatures can have either beneficial or detrimental effects on forests, depending on their present climatic limitations (Babst et al., 2013; Charney et al., 2016; St George and Ault, 2014). For instance, climate warming in cold-humid areas can stimulate tree growth through a prolonged growing season and more rapid cellular development (Cunv et al., 2014; Rossi et al., 2016). In drier regions, a warminginduced increase in atmospheric water demand triggers physiological responses in trees that lower hydraulic conductivity, reduce the production and allocation of carbohydrates to structural growth, and ultimately increase tree mortality (Adams et al., 2017). This continuum of possible consequences from warming provides an incentive to understand how changes in the biotic and abiotic environment affect forest ecosystem processes across a range of spatial and temporal scales.

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 at sub-annual to multicentennial time scales. Such data are increasingly used to study the impacts of global change on forest ecosystems. A number of recent studies have compiled large tree-ring networks to hind- and forecast forest growth variability in response to climate (Babst et al., 2013; Charney et al., 2016; Martin-Benito and Pederson, 2015; Restaino et al., 2016; St George and Ault, 2014; 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 press), or search for signals of CO₂ fertilization (Frank et al., 2015; 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 wood formation (Rathgeber et al., 2016), and calibrate mechanistic models for climate reconstruction (Guiot et al., 2014).

Tree-ring records are available on all forested continents (Babst et al., 2017; Brienen et al., 2016), inviting the use of existing and the development of new tree-ring archives for a variety of research contexts. However, tree rings remain a very local and variable product of tree-internal processes that are modulated by a tree's immediate biotic and abiotic environment (Rathgeber et al., 2016). Inference and prediction at large spatial scales based on such local data (involving scaling, interpolation, and projection; Table 1) is challenging and introduces uncertainty that researchers need to be aware of and – to the extent possible – quantify (Fig. 1). Scaling is complicated by heterogeneity (Scholes, 2017), for example when a

tree-ring collection insufficiently represents forest structure, composition, and disturbance regimes across a landscape. Dendrochronologists often counteract heterogeneity by increasing the number of collected samples per tree, site, or region. This approach can indeed reduce uncertainties around the mean record for the desired scale (e.g. a site or regional chronology), but its success for improving spatial representation of tree growth critically depends on the underlying sampling strategy (see below). Another challenge for scaling is that fixed statistical relationships derived from a given dataset may not capture the high dimensionality in driver and response variables, their couplings, non-linear processes and feedbacks. This calls for a better understanding of the true variability in the system and ideally for mechanistic process representation to model tree growth (see Section 4). Given the above context, we find it prudent to briefly pause and examine the potential and challenges associated with scaling tree-ring information before making large-scale inference. Herein, we address the following three upscaling steps:

- (A) From the sample to the whole tree: Tree-ring samples are collected as cross-sections, increment cores, or micro-cores. Regardless of the shape or size of samples, individual measurements capture growth only at one position along/around the stem, branch, or root. Multiple samples are thus often collected from the same individual to better capture its growth variability. After visually and statistically ensuring correct dating of each annual growth ring (i.e. "crossdating"; Black et al., 2016; Stokes and Smiley, 1968), the measurements of all samples are generally combined to represent the radial growth of the individual. This first step of upscaling (Table 1) usually involves averaging or pooling, but the representation of tree-level change may be with raw measurements, detrended and/or standardized tree-ring indices, conversion to basal area increment, or other forms of allometric scaling or structural modeling.
- (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 that are usually referred to as "chronologies". An underlying assumption is thereby that the site is a subsample of a population of trees and the derived chronology is typically regarded as the best estimate of this population's growth variability (Wigley et al., 1984). The criteria for sampling trees within a site vary according to the aims of a given study. For example, old and dominant individuals are selectively sampled for dendroclimatic reconstructions; plot designs, stratified or random samplings are often preferred for dendroecological studies; and trees with specific characteristics (e.g. scars) are targeted to assess the natural disturbance history of a site. Researchers are also interested in within-site variability that is driven by microsite conditions (e.g. topography Salzer et al., 2014) and may contain relevant ecological information that is otherwise averaged out when only a mean site chronology is calculated (Buras et al., 2016; Peters et al., 1981).
- (C) From the site to larger spatial scales: Site records are compiled into tree-ring networks to cover regions or

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