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TOWARDS A MORE ECOLOGICAL DENDROECOLOGY

RUBÉN D. MANZANEDO[1,2*] and **NEIL PEDERSON**[2]

[1]Biology Department, University of Washington, Seattle WA98195-1800, USA

[2]Harvard Forest, Harvard University, Petersham, MA 01366, USA

ABSTRACT

The use of tree-ring methods to study ecological processes, known as dendroecology, has been booming over the last decade. We believe that the incredible methodological strides in this subdiscipline over the last half century will be further advanced by purposefully integrating with other ecological subdisciplines and broadening the scope of dendroecology both in terms of methods and theory. Simultaneously, these efforts will greatly benefit a broad range of ecological disciplines through the incorporation of one of the greatest strengths of dendrochronology: highly-resolved ecological data that spans from seasons to centuries. Because these data are still alarmingly scarce in ecology but are crucial to understand the ecology of long-living organisms, we believe better integrating dendroecology and mainstream ecology will benefit both disciplines. We discuss five actions that can be readily embraced by the dendrochronological community to further advance the field while also making it more open for non-dendroecologists. These actions include: (i) promoting diverse or multi-discipline scientific collaborations and partnerships, (ii) diversifying dendroecological data sources, (iii) incorporating inference-based and hierarchical models to the dendroecological toolbox, (iv) improving and updating the global tree-ring databases, and (v) increasing the focus on ecological and evolutionary mechanisms in tree-ring-driven papers. We believe these actions will help facilitate a broad discussion on how to better integrate tree-ring-based ecology within mainstream ecology. We believe this has the potential to trigger major advancements in dendroecology, help resolve long-standing ecological questions and, ultimately, bring a new perspective and scale to ecological theory.

Keywords: tree rings, ecology, ecological theory, macroecology, global change, multidisciplinarity.

ECOLOGICAL DENDROCHRONOLOGY

Dendrochronology has greatly improved our understanding of how trees respond to climate and, more recently, to climate change. As the focus of many studies moves towards studying the ecological consequences of changing climate, dendroecology (*i.e.* the application of dendrochronological methods to address ecological questions) takes on even greater importance. Although dendrochronology and ecology have been linked since their very origins (see the review foreword by Dr. Thomas Swetnam in Amoroso *et al.* 2017), for most of its history dendrochronology has been dominated by climate-oriented research (dendroclimatology). In fact, the first textbook dedicated exclusively to dendroecology was only recently published (Amoroso *et al.* 2017). The use of the term dendroecology itself may have contributed to it being sometimes identified as an exclusively tree-ring science rather than as a true ecological subdiscipline. At the same time, a recent review on the spatial and temporal domains in modern ecology clearly identify highly-resolved, long-term data as one of its most under-represented domains (Estes *et al.* 2018). These are precisely the strengths that dendroecological methods can contribute to ecology. Of the 384 titles reviewed in Estes *et al.* (2018), three included paleoecological data, and an even smaller percentage, perhaps one, likely used tree-ring data, making clear the lack of integration of dendroecology into modern ecology and motivating our call to action.

Dendroecology has a long, rich, and fruitful history of providing insight into the ecology of forests. Methods in detecting and quantifying past canopy disturbances using tree growth releases have been developed and tested over the last 100 years (*e.g.* Marshall 1927; Lorimer 1985; Nowacki and

*Corresponding author: rdmanzanedo@fas.harvard.edu

Abrams 1997; Druckenbrod *et al.* 2013); see the testing of these methods in Trotsiuk *et al.* (2018)). Studies based on these methods have informed the long-term development of forests and landscape dynamics (*e.g.* Heyerdahl *et al.* 2001; D'Amato *et al.* 2008; Bigio *et al.* 2010; Ariya *et al.* 2016), the interactions between disturbance and climate (*e.g.* Swetnam and Betancourt 1990; Villalba and Veblen 1997; Hessl *et al.* 2004; Kajimoto *et al.* 2004; Rodríguez-Catón *et al.* 2015), and species traits (*e.g.* Orwig and Abrams 1994; Stan and Daniels 2010; Nagel *et al.* 2014). Dendroecology has given important insight on the management and conservation of ecosystems (*e.g.* Therrell and Stahle 1998; Spiecker 2002; Copenheaver *et al.* 2006; Altman *et al.* 2013; Rocca *et al.* 2014; Rosa *et al.* 2017). Forest development theory has not been addressed as thoroughly (*e.g.* Baker *et al.* 2005; Pederson *et al.* 2017; Schurman *et al.* 2018). These valuable contributions pave the way for today's work and help push us forward toward the increased application of theory and visibility within ecology.

Recent advances in dendroecology highlight its promise (Amoroso *et al.* 2017), and as a result, an increasing number of studies incorporate tree-ring methods and data to help in solving long-standing ecological questions. For example, tree-ring methods have recently contributed to the long-discussed relationship between diversity and productivity in forest ecosystems (Jucker *et al.* 2013). They have shown the importance of biotic interactions on the realized niche even in the harshest of environments (Liang *et al.* 2016), and helped understanding the drivers and patterns of genetic differentiation between forest populations (Housset *et al.* 2018). Tree-ring data are one of the few direct data sources that exist to understand both long-term and broad-scale forest dynamics (Pederson *et al.* 2017; Druckenbrod *et al.* 2019), which often go undetected within the commonly used timescales of ecological studies (Buma *et al.* 2018). This is a key contribution of dendrochronology to forest ecology, as tree-ring methods are currently the only methodological approach with the temporal resolution to determine the impacts of extreme events, which can explore ecological patterns in a timescale comparable to that of the lifespan of natural trees. However, a large number of dendroecological studies still use almost exclusively tree-ring data, and many ecological studies do not take advantage of the long-term perspective that tree rings could provide. In a time when climate is changing rapidly and there is a need to describe and understand the long-term ecological consequences of these changes, dendroecology can play a pivotal role to facilitate this integration.

We believe that using more predictive and quantitative approaches that focus on the attribution and testing of drivers, theory development, and a continued integration of more complex modelling like forward modeling can help dendroecology have a greater impact on the field of ecology and the study of global environmental change. Here, we summarize some suggestions that we feel can help to this end.

Increase the Diversity of Collaborations across Disciplines

It is of paramount importance to continue promoting multidisciplinary collaborations that move away from the still common 'tree rings only' approach. Embracing working partnerships with ecologists and with other disciplines greatly enriches dendroecology. Excellent examples of how fruitful these collaborations could be are the highly multidisciplinary PalEON and FunDiv Europe projects. The PalEON project (http://sites.nd.edu/paleonproject/) joins statisticians, vegetation modelers, and tree-ring scientists to work together towards understanding ecological processes and potential climate change impacts on forested systems. The FunDiv Europe project (http://project.fundiveurope.eu/) brought together a highly diverse group of scientists from more than 24 institutions from all branches of ecology (including dendrochronologists) to investigate the functional significance of forest biodiversity. The impressive record of high-profile publications of both projects (44 publications in 7 years in the case of PalEON, 77 in 6 years for FunDiv), bears witness to the benefits of collaborative efforts including paleo- and neo-ecological approaches (discussed also in Buma *et al.* 2018).

We would like to also highlight recent efforts to increase the social diversity within the field, a key challenge for current science (*e.g.* Grogan 2019). One example is the recently established Florence Hawley Ellis Diversity Award (https://www.treeringsociety.org/Awards), which aims at promoting underrepresented groups within dendrochronology by supporting them economically so they can deliver a keynote address in the largest global conference on tree rings, WorldDendro. Actions like this are highly effective in increasing the visibility of excellent science conducted by underrepresented people, benefiting the whole dendrochronological community.

Promote the Use of Complementary and Confirmatory Approaches

Investigating a greater variety of tree species and ecosystems and employing multiple proxies in dendroecological analyses will increase the reliability of measurements and generality of results. Multi-faceted and multi-sourced studies are common in ecology and allow for clever ways to identify and disentangle complex ecological mechanisms. For example, Valladares *et al.* (2014) combined conceptual models, niche-modelling, and observational data to disentangle the effects of plasticity and genetic differentiation. Albert *et al.* (2010) used multiple species and multiple traits within species to reveal the importance of intra- and inter-specific trait variability, and Soliveres *et al.* (2016) considered diversity at many trophic levels simultaneously to understand the importance of diversity on the delivery of multiple ecosystem services at the same time, and the resulting management trade-offs. This is already emerging in certain dendroecological approaches, such as the combination of width metrics with multiple anatomical traits in dendroanatomical studies (*e.g.* Pacheco *et al.* 2018). We believe a multispecies, multifaceted approach will result in a valuable expansion of the methodological toolbox and data available for tree-ring scientists and ecologists.

Incorporate Inference-Based and Hierarchical Methods to Ecological Tree-Ring Data Analysis

One of the main barriers that has limited the integration of dendroecology into ecological studies is methodological. Dendrochronology's close links to geography and climatology have resulted in methods that focus on the challenges and particularities of climate reconstructions and climate-tree growth relationships (*e.g.* Douglass 1919; Hawley *et al.* 1941; Schweingruber 1996). Although robust dendroclimatological methods were developed in the mid-20th Century (*e.g.* Fritts 1958), dendroecological methods have been somewhat slower to advance (but see Amoroso *et al.* (2017) and references therein). Outside of tree-ring reconstructions of fire history, there is still little consensus on sampling strategies or data analyses for tree-ring studies examining stand- to landscape-level ecology despite recent efforts (Nehrbass-Ahles *et al.* 2014; Carrer *et al.* 2018). In addition, there are very few dendroecological studies conducted at regional to global scales, which are crucial to understand the large impacts of climate change (but see Charney *et al.* (2016), D'Orangeville *et al.* (2018), Klesse *et al.* (2018a)). Another example of the legacy of dendroclimatic approaches on some dendroecological studies is that of understory trees, which are still commonly not sampled. Understory trees are important ecological players in determining ecosystem structure, resilience, development, and stability, and so including them strengthens our ability to understand forest dynamics. The response of understory trees to climate and climate change, and their ecological function, may differ from that of dominant trees (Orwig and Abrams 1997). As a result, tree-ring studies that focus only on dominant trees are limited in capturing the broad array of forest ecosystem responses to changing climate (Klesse *et al.* 2018b). A recent study highlighted the need for and benefits of studying forest ecology at meso- to macro-ecological scales (Druckenbrod *et al.* 2019). In addition, increasing emphasis should be placed on expanding the number of measured covariables, standardizing sampling strategies, using more complex and nuanced analytical methods, and considering the effect of a wider range of factors on tree performance. Factors such as microhabitat characteristics, spatial relationships, and intra- or inter-specific competition are of critical importance for tree growth (*e.g.* Canham *et al.* 1988; Benavides *et al.* 2016), yet are rarely included in dendroecological studies. It seems increasingly clear that a serious discussion on the dendrochronological and dendroecological sampling methods and their influence on data interpretation is needed (Briffa and Melvin 2011; Nehrbass-Ahless *et al.* 2014; Sullivan and Csank 2016; Brienen *et al.* 2017; Carrer *et al.* 2018).

Most dendroecological papers examining tree growth relationships to climate have used a common subset of analyses, namely (i) correlations with monthly climatic variables, (ii) trend analyses, (iii) simple or multiple variable correlations, (iv) moving correlation analyses, (v) frequency analyses, and (vi) spectral analyses. These analyses have been useful in understanding species responses to climate, but are limited in addressing complex ecological interactions. Incorporating new methodological developments that are increasingly used in ecology provide a way to achieve a clearer understanding of the mechanisms behind tree-ring patterns while controlling for co-occurring variables that may potentially bias our results. In particular, incorporating hierarchical modeling, such as mixed model regression to control for variable interaction and covariation (*e.g.* Manzanedo *et al.* 2018), and structural equation models to account for the causal relationship between variables (*e.g.* Elliott *et al.* 2015) hold great potential to advance dendroecological studies. These methods are well developed and integrated in commonly used statistical software (*e.g.* R software), and have been successfully used in multiple dendroecological papers. They can also complement the current developments within dendroecology, such as ecosystem modelling using Bayesian approaches (Itter *et al.* 2017) or physiological models of tree growth (*e.g.* Tolwinski-Ward *et al.* 2011; Hayat *et al.* 2017).

Improve Tree-Ring Databases to Accommodate Ecological Data

A main factor hindering the implementation of nuanced modelling approaches in dendroecology (such as the mentioned mixed and structural equation modelling) is that they require a large number of covariables and a good prior understanding of the ecological mechanisms in play (see next section). By contrast, many dendrochronological collections often record limited metadata at the tree level, mainly average elevation and geographical coordinates at the plot level, and tree diameter. This is reflected in the information available within the most comprehensive tree-ring database, the International Tree-Ring Data Bank (ITRDB). The ITRDB does not currently support the systematic inclusion of tree-level or even plot-level variables other than elevation and area coordinates. Plot characteristics can be uploaded to the ITRDB as an annex to each file, but very few sites include this information, and in its current format, this information could not be systematically downloaded or processed. Consequently, the apparent wealth of tree-ring data in the ITRDB contrasts with a very limited number of studies using it for ecological purposes (discussed in Zhao *et al.* (2018), but see *e.g.* Charney *et al.* (2016)). For ecologists and dendrochronologists to effectively use large tree-ring databases to tackle complex ecological questions, databases need to be improved so they can accommodate this extra information. In addition, classic dendrochronological sampling would benefit tremendously by including more information like plot and site variables (above- and belowground), such as the new DendroEcological Network database (https://www.uvm.edu/femc/dendro), multiple species and traits, and information on the spatial structure of the forest (both horizontally and vertically). This will allow large tree-ring collections to be used to assess major macroecological questions with the rigor and complex modelling that they require (*e.g.* Davis *et al.* 2009; Nehrbass-Ahles *et al.* 2014).

Another limitation in much of dendroecological research is the still prevalent use of only macroclimate variables (Foster *et al.* 2016) or calendar-based climatic variables rather than seasonally-meaningful variables like monthly or seasonally-averaged values of precipitation, temperatures, etc. (Kim and Siccama 1986). Trees are likely to be strongly influenced by their local microclimate as much as by their historical macroclimate (Leimu and Fischer 2008) and thus the use of macroclimate records from ‘nearby’ climate stations or gridded interpolated datasets (*e.g.* Climate Research Unit by the University of East Anglia) often do not capture site-specific microhabitat, topographical, or biotic interactions (Foster *et al.* 2016). Incorporating local climate data and topographical conditions (Bunn *et al.* 2011; Lloyd *et al.* 2017) help tease apart the relative importance of multiple variables and their interactions. Likewise, refinements in using meteorological variables that match physiological processes provide greater insights into the growth of trees (Carrer *et al.* 2016). Collaborating closely with climatologists is key in this sense, because their reconstruction methods have greatly improved and now provide much more detailed results that can be complemented with *in situ* measurements. This approach is being developed by the physiological and growth modelling community, which is rapidly improving our understanding of how and when trees grow (*e.g.* Hayat *et al.* 2017), and commonly include a large array of *in situ* environmental measurements. Promoting and integrating this new and exciting avenue of research will pay great dividends to the whole ecological community.

Focus on Ecological and Evolutionary Mechanisms and Theory

Dendroclimatology has been very successful in reconstructing and modelling the climatic mechanisms linked to tree-ring growth (reviewed in Hughes *et al.* 2010). Bringing this mechanistic scope into dendroecology would improve the soundness of dendroecological results and contribute to building a more mechanistic theory of tree growth that explains the ecological and evolutionary drivers behind the changes in growth trends and responses to climate and other environmental factors like air pollution (*e.g.* Bishop *et al.* 2015), differences in correlation strength or timeframes (*e.g.* Carrer and Urbinati 2006), or disturbance recurrence (*e.g.* D'Amato and Orwig 2008). Recent developments in understanding the physiological processes influencing wood formation (*e.g.* Deslauriers 2017) can certainly contribute to this goal and set the biochemical processes being selected for or against. Using ecological and evolutionary theory to interpret dendroecological results would greatly enhance dendroecology. Well-established ecological hypotheses or mechanisms, such as conspecific negative density dependence (Janzen 1970; Connell 1971), coevolution (Ehrlich and Raven 1964), niche partitioning (Maynard-Smith 1966), Hubbel neutral theory (Hubbel 2001), WBE model of allometric scaling (West *et al.* 1997), or local adaptation (Kawecki and Ebert 2004) need to be more frequently incorporated into the analysis and interpretation of tree-ring results. This will help generalize the ecological mechanisms affecting our systems and will facilitate the exchange of ideas and results with other ecological disciplines. To fully integrate within ecology, dendroecology needs to build upon and contribute to the general body of knowledge of ecology.

In conclusion, we call for a broad discussion on the current challenges and future of dendroecology as a discipline. We hope the ideas we propose here help make dendroecology more effective and better integrated with other ecological studies. We acknowledge that these recommendations entail a large effort by the tree-ring community, but feel that if implemented, they can greatly benefit both the dendroecological and ecological scientific communities. Given the pervasive shortage of long-term and highly-resolved data in most ecological studies, and the importance of having ecological data with a timescale and resolution comparable of that of the longest-living organisms in our ecosystems, tree rings can play a pivotal role in helping advance ecology, by bringing new perspectives and scales that help resolve long-standing ecological questions.

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