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Dendroecology

Tree-Ring Analyses Applied to Ecological Studies

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Foreword

The connection between dendrochronology and ecology runs deep. Ecology as a field of study was in great ferment in the American Southwest during the 1910s to 1930s, especially in Tucson, Arizona, where the Carnegie Institute of Washington supported the establishment of the first laboratory in North America dedicated to the study of ecosystems, *and* the first laboratory dedicated to the use of tree rings in the study of climate and archaeology. The ecologists working at the Desert Botanical Laboratory included luminaries such as Daniel T. MacDougal and Frederick E. Clements, and the Laboratory of Tree-Ring Research was established by Andrew E. Douglass. Scientists at the Desert Lab were centrally involved in founding the Ecological Society of America in 1915. The first issue of their flagship journal *Ecology* (Volume 1, Issue 1, January 1920) included an article by Douglass titled "Evidence of Climatic Effects in the Annual Rings of Trees." Although the paper focused mainly on using tree rings as a proxy for rainfall, it also included illustrations of one of Douglass' seminal—and fundamentally ecological—insights regarding the effects of site conditions on climatic "sensitivity" of tree rings. This is a foundational principle of dendrochronology.

The European roots of dendrochronology also grew from tree biology and forest ecology. Bruno Huber, working as a professor of forest botany at the Technical University of Dresden and the University of Munich in Germany in the 1930s, came to tree-ring studies as a tree biologist. Like Douglass, his most famous work involved tree-ring chronology development and applications in archaeological dating, but along the way he laid foundations for subsequent wood anatomy and eco-physiological investigations in dendrochronology.

Throughout the last century dendrochronologists have expanded the applications of tree rings in environmental studies. Dendroclimatology, the application of tree rings in the study of atmospheric processes, has undoubtedly been a driving and overarching endeavor, stimulating and contributing to the myriad other applications, including dendroecology. Indeed, the ready availability of dendroclimatic reconstructions of rainfall, temperature, and drought indices has revolutionized disturbance studies in dendroecology. Fire history and insect outbreak studies, for example, have commonly combined their analyses of disturbance and climate chronologies derived from tree rings, resulting in new insights into climate-disturbance relationships.

Two of the all-time most influential dendrochronologists, Harold C. Fritts and Fritz Schweingruber, published seminal reviews of dendroecology in 1971, 1989, and 1996. Over the past several decades there has been a surge of publications in ecological and forest science journals with dendroecological themes. A Google Scholar search (in March 2017) using the terms "dendroecology" and "dendroclimatology" in the titles returned 5150 and 7080 papers, respectively. Since 1980, the 500 most-cited papers with the term "dendroecology" in the searchable text were cited a total of 14,707 times, while the 500 most-cited papers with the term "dendroclimatology" were cited 13,434 times. Today, many ecological and forest science journals include dendrochronologists on their editorial boards.

Along with the expansion of dendrochronology in ecological studies has been an extension of geographical coverage. In addition to many studies in North and South America, Europe, Asia, Australia, New Zealand and elsewhere, dendroecological studies have followed the example of dendroclimatology in exploiting regional to continental scale networks. Patterns of synchrony and asynchrony of fires, insect outbreaks, forest natality, and mortality, in concert with regional climatic variability, have demonstrated dendroecology as a key tool in macroecology.

One the key reasons that dendroecology has flourished in recent decades is the direct relevance of the insights provided for environmental management. Forest managers especially have embraced the concept that knowledge of past ecological dynamics and structures is valuable for understanding current conditions, and for deciding how to manage for future desired conditions. Recent extreme responses of ecosystems to climate change, including wildfires, insect and pathogen outbreaks, and drought-induced mortality, have been major stimuli for dendroecological investigations.

Given the great fluorescence of interest, publications, and relevance of dendroecology in recent decades, the compilation of a volume of chapters covering broad topical and geographic examples worldwide is most timely and welcome. The editors and authors have here assembled a diverse set of conceptual and methodological reviews, and examples ranging from disturbance ecology, ecophysiology, and forest dynamics to human-environment interactions. The geographical coverage highlights several regions that have benefited most from recent expansion of dendroecology, including South America, Australia, and Asia. Studies in temperate, subtropical, and tropical forests are also included.

A most engaging and potentially far reaching development in dendroecology in recent years is a focus on human-environment interactions. This advance is nicely included in chapter examples from Asia, Europe, and North America. These landscape and regional-scale studies demonstrate the broad, multidisciplinary nature of dendrochronology, weaving together and exploiting multiple lines of tree-ring based and other forms of evidence from archaeology, history, paleoecology, and paleoclimatology. In this sense, dendroecology is now embracing the full scope of ecology in its broadest definition: the study of organisms—including humans—and their interactions with the environment. Perhaps dendroecology will continue to develop and evolve as the most synthetic of dendrochronology applications, and if so, this volume will serve as foundational.

Laboratory of Tree-Ring Research
Tucson, AZ, USA
5 March 2017

Thomas W. Swetnam

Preface

Dendroecological studies have fundamentally shaped contemporary views of forest ecology and forest dynamics, particularly in temperate forests. While ecological studies using tree rings have been published for well over a century, the past several decades have seen a rapid acceleration in the rate of publication of dendroecological studies. Most syntheses and reviews of dendrochronology over the past half century have focused on climatology, archaeology, or wood formation (e.g., Fritts 1971, 1976, Eckstein 1984, Cook and Kairiukstis 1989, Schweingruber 1996, Hughes et al. 2001, Vaganov et al. 2006, and to a lesser extent Speer 2010). While dendrochronology has made important contributions in each of these areas, the ecological lessons that dendrochronological research has provided are fundamental to understanding how forested ecosystems will respond to the many threats posed by global environmental change. These threats are not limited to changing climatic conditions, but also include the impacts of invasive species, biodiversity loss, changing disturbance regimes, and the multitude of potential interactions among them. Dendroecology is a significant component of applied research, providing important historical context for adapting existing forest management strategies to mitigate and respond to current and future global environmental change.

The application of tree-ring analyses has emerged as a powerful approach to address complex ecological questions and to quantify environmental change through time. This book presents state-of-the-science reviews and application of tree-ring analyses to ecological problems using examples from tropical, temperate, and boreal forests around the globe. It is organized around four broad topical themes: tree growth and forest dynamics, disturbance regimes, forest decline, and human-environment interactions. Each theme is composed of chapters highlighting recent advances in dendroecology, often illustrated by case studies to demonstrate novel methods and approaches.

Introducing tree growth, Deslauriers et al. (Chap. 2) review the processes of tree-ring formation highlighting novel research on the impacts of resource availability and environmental variation on xylem and phloem growth and ring attributes. Their global perspective contrasts tree growth in boreal through tropical forests, demonstrating how the timing, duration, and rates of cell formation affect wood anatomy and ecophysiology. Deep understanding of these mechanisms and processes provides a strong foundation for the dendroecological interpretations presented in subsequent chapters.

Collectively, the next three chapters highlight advances in dendroecological research of forest dynamics in tropical and temperate forests. Research on more than 200 neotropical tree species has identified a suite of environmental factors that trigger annual ring formation (Schöngart et al., Chap. 3). New knowledge on tree ages and growth trajectories is applied to evaluate and adapt timber harvesting to ensure sustainability of tropical ecosystem functions and services. Similarly, dendroecological advances in seasonal dry tropical forests include the first reconstructions of the historical dynamics of mixed deciduous and seasonal evergreen forests in western Thailand (Baker and Bunyavejchewin, Chap. 4). Tree recruitment and growth releases indicate complex gap dynamics, as well as extensive, synchronous disturbances driven by regional drought. Pederson et al. (Chap. 5) emphasize the importance of multiscale disturbances in temperate mesic forests. Their critical analysis identifies limitations and potential biases inherent to contemporary research, which tends to focus on spatial and temporal scales that are unable to detect large, infrequent disturbances. They present a conceptual model and dendroecological solutions to test alternative hypotheses and address urgent questions on macroecological dynamics of temperate forests.

In their review on altitudinal and latitudinal treelines, the ecotones between forests and tundra, Lloyd et al. (Chap. 6) shed light on the surprisingly complex responses of treeline ecosystems to climate warming. They demonstrate the necessity of integrating dendroecology with spatially explicit measurements of environmental variability, allowing researchers to understand the underlying environmental gradients to which trees are responding. Their integrated research approaches allow us to understand trees not simply as the sum of their rings, but as complex organisms whose overall growth reflects the impact of multiple limiting factors filtered through a number of simultaneously occurring physiological processes.

Although most research on forest dynamics focuses on live trees, the field of dendroecology is well suited to research on dead trees, including snags and fallen logs, collectively known as woody debris. Dendroecology provides novel methods to estimate dates of tree mortality or fall at an annual level, which are used to calculate decay rates using chronosequences or decay-class transition models. Fraver et al. (Chap. 7) present a case study on three old-growth *Picea rubens* stands in the northeastern USA to demonstrate continuous recruitment of woody debris over the twentieth century, with pulses corresponding to reconstructed gap- and meso-scale disturbances. Given the critical role coarse woody debris plays in forest ecosystems—carbon storage, nutrient cycling, soil development, and maintenance of biodiversity—it is imperative to understand how its abundance changes through time.

The second theme of this book illustrates how dendroecological research has advanced our understanding of disturbance as a vital attribute of forests. Dendroecology also has been instrumental for understanding the drivers of forest decline. Five chapters illustrate how dendroecology allows a unique temporal perspective on disturbance by fire, insects, pathogens, and geomorphic processes. They are followed by two reviews of the intricacies of forest decline in drought-prone climates.

Daniels et al. (Chap. 8) review dendroecological contributions toward understanding of low-, mixed-, and high-severity fire regimes. Four case studies on reconstructions of historical fire frequency, severity, spatial variability, and extent demonstrate the complexity of mixed-severity fire regimes in montane forests in western North America. Similarly, Mundo et al.'s (Chap. 9) dendroecological reconstructions in five different Patagonian forests show diverse and heterogeneous patterns of fire frequency related to climatic variability and human impacts. Collectively these two chapters show how combining dendroecological evidence with independent, corroborating evidence and models of fire extent, behavior, and effects provides a powerful framework for comparing historical and contemporary fire regimes.

Research on insects and pathogens and their effects on forest resilience is an active frontier in dendroecology. Reconstructions of insect outbreaks include millennial length chronologies and research networks facilitating broad-scale spatiotemporal analyses (Speer and Kulakowski, Chap. 10). Moving beyond the reductionist approach of examining only parts of an ecosystem, dendroecologists embrace complexity by studying disturbance interactions and their signals recorded in tree rings. Building on this theme, Lewis et al. (Chap. 11) show how forest ecosystems have evolved to be resilient to native pathogens and insects, but human-induced climate change has contributed to severe epidemics, for example *Dothistroma* needle blight and mountain pine beetle. Concurrently, increasing global trade increases chances of exotic pathogens interacting with native hosts. These human influences interact with other agents often yielding synergistic negative effects.

Stoffel et al. (Chap. 12) review dendroecological analyses of trees affected by earth-surface processes, in which rings preserve valuable archives of past events on timescales of decades to centuries. Their case studies illustrate the breadth and diverse applications of contemporary dendrogeomorphology to understand processes such as flood, soil erosion, debris flows, rockfall, and landslides. Understanding the distribution, timing, and controls of geomorphic processes provides valuable information to assist prediction, mitigation, and defence against these natural hazards and their effects on society.

The instrumental role of dendroecology for understanding forest decline in drought-prone climates around the globe is the third theme of this book. Research on two continents illustrate that forest decline is caused by complex interactions among abiotic and biotic stress factors acting at different spatial and temporal scales. In Spain, drought-triggered forest dieback is predisposed by past forest use and management and increased tree-to-tree competition, which increase vulnerability of individual trees or species to death (Camarero et al., Chap. 13). In these forests, mistletoe and other biotic stressors contribute to drought-induced dieback. Similarly, the decline of native forests in northern Patagonia is complex and driven by multiple factors (Amoroso et al., Chap. 14). Dendroecological analyses of radial-growth patterns show extreme droughts incite immediate growth reductions, followed by persistent growth decline over time. Amoroso et al. (Chap. 14) present a framework for testing alternative hypotheses to a single causal agent, which emphasizes the importance of climatic variability as a key driver of forest decline.

Given ubiquitous human impacts and cumulative effects of global environmental change, understanding human-environment relationships is the fourth and final theme. Dendrochronology is at the nexus of archaeology, climatology, and ecology, making it uniquely positioned to study past human-environment interactions. Tree-ring records are ideal for exploring these relationships because they integrate climatic information at temporal and spatial scales relevant to human livelihoods. Hessl et al. (Chap. 15) use a growing network of long tree-ring records from Asia to contextualize human-environment relationships over the last 3000 years. A wide diversity of economic, political, and cultural features in historical Asia filtered, dampened, and amplified the effects of climate on society, suggesting that relationships may not be stable or consistent over time and space. Trouet et al. (Chap. 16) present a long-term perspective, using dendrochronology to quantify Holocene-era land-use changes and forest dynamics in Europe and North America. Their critical analysis highlights limitations when relying on living forests because the majority of lowland forests have been cleared throughout human history so that contemporary tree-ring chronologies might not fully represent past environments. They introduce the concept of "dendro-archeo-ecology" in which ecological information is derived from existing dendroarcheological collections to quantify past land-use changes and their impact on the carbon cycle and Earth's climate.

In the final chapter of this volume we highlight several overarching themes that have emerged from these state-of-the-science reviews, identify areas of substantial progress in dendroecology that have been made in recent decades, and emphasize several pressing questions that dendroecology is well positioned to address.

We envision this book as a waypoint in the science of dendroecology that brings together much of the excellent dendroecological research that has come before us, provides a contemporary overview of the breadth and depth of the existing research, and generates new ideas for the many possible directions that dendroecology might take going forward. We hope that this volume will provide a useful resource for dendrochronologists, ecologists, foresters, and others interested in the conservation and sustainable management of the world's forests.

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Vancouver, BC, Canada — Lori D. Daniels
Melbourne, VIC, Australia — Patrick J. Baker
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Each lead author provided a peer review of another chapter of this book and we are thankful for their thoughtful comments and helpful suggestions.

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Chapter 1
Introduction

Mariano M. Amoroso, Patrick J. Baker, Lori D. Daniels, and J. Julio Camarero

1.1 Introduction to Dendroecology

Forests blanket large areas of the Earth's land masses. They host a large fraction of global biodiversity and terrestrial carbon reserves, and the economic development of most countries has relied directly or indirectly on forests. Forests vary widely in structure and composition—from the low diversity expanses of boreal forest that stretch across the high latitudes of the northern hemisphere to the hyperdiverse tropical rain forests that grow on or near the equator. These differences in structure and composition reflect latitudinal and elevational bioclimatic variation, biogeographic history, and the influence of various historical disturbance regimes. Despite the diversity in physiognomy and its causes, a common feature of all

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forests is the arboreal growth form. The ability of trees to establish a tall canopy through competition for light with their neighbors yields majestic and often crowded woody landscapes. To reach the canopy, trees must grow in height and support large amounts of biomass. Simultaneously, trees draw water and nutrients from the soil up considerable distances into their crowns, which are coupled with the atmosphere through photosynthesis and transpiration. The need to form wood, a tissue with multiple functions (e.g., support, hydraulic conductivity, storage, defense against biotic agents), is a key characteristic of trees and forests. The secondary, or radial, growth processes that drive wood formation are fundamentally the same for all trees. This uniformity of process means that trees and forests should respond in relatively predictable ways to environmental conditions and disturbances. Over the past century, dendrochronology (the study of tree rings) applied to ecological questions has been fundamental in shaping our understanding of how forests function across a broad range of spatial and temporal scales.

Ecology is the study of how organisms interact with one another and their physical environment. At the heart of ecology is the question of how these interactions change over time to influence population and community structure and composition. Dendroecology, which uses precisely dated annual rings of trees and other woody plants to study past changes in ecological systems, has shaped contemporary understanding of forest development and dynamics, forest responses to extreme environmental conditions and disturbances, and, in some cases, long-term interactions between humans and their environments.

1.2 An Idiosyncratic History of Dendroecology

The term "dendroecology" is a relatively new term that was originally used in a much narrower sense. Serre-Bachet and Tessier (1989) cite Vins (1963) as the first to use the term in an attempt to expand dendrochronology to include a more direct focus on forest ecology and the many tree species and forest types overlooked in dendroclimatology studies. Within the dendrochronology research community, it took many years to move away from an explicitly climate-focused perspective and internalize the potential and importance of tree rings for ecological studies. For example, in Fritts' (1971) paper entitled "Dendroclimatology and dendroecology," dendroecology received a single paragraph of text in 28 pages and was introduced with the following statement (p. 446): "... some ecological studies dealing with past history of the environment may find useful information in what the dendroclimatologist may regard as 'noise'." For a long period, dendroecology was seen as the reverse side of the dendroclimatology "coin." While dendroclimatology used past tree growth patterns to reconstruct climate, dendroecology focused on how climate and other factors directly and indirectly influenced past tree growth patterns.

Today, "noise" persists when dendroecologists and dendroclimatologists communicate about their respective sides of the dendrochronology coin. For instance, dendroecologists have demonstrated that many characteristics (e.g., size, age, local density) shape the individualistic response of trees to climate variability. To address the idiosyncrasy of individuals, dendroclimatologists either focus on a subset of trees such as large, presumably old, trees growing on resource-limited sites or they compile large datasets that include trees with diverse characteristics but regard the individualistic growth patterns as statistical "noise" in standard tree-ring chronologies, which represent a site- and species-specific climatic "signal." For dendroecologists this "noise" is often the "signal," reflecting one or more of the many potential non-climatic influences on tree growth.

Dendroecology began to enter the mainstream of dendrochronological research in the 1970s and early 1980s due to growing public concerns about the impacts of pollution on forests in North America and Europe. Acid rain and forest decline, in particular, were the subjects of extensive research by teams that included forest ecologists, soil scientists, and dendrochronologists (Le Blanc 1990, Skelly and Innes 1994). In many ways, Fritts and Swetnam's (1989) paper was the catalyst for recognizing dendroecology as an independent subdiscipline of dendrochronology. In their paper, they reviewed the foundational principles of dendrochronology and provided several case studies in which dendrochronology was being applied to pressing environmental issues, such as pollution impacts, regional forest decline, and the impacts of insect outbreaks. Their focus was on the use of tree-ring time series to understand ecological and environmental variability and its impacts on forests. In so doing, they validated the core concepts that define the modern scope of dendroecology. Methodologically, however, their review was limited to ecological and environmental information available from ring-width or ring-density data—that is, they mainly focused on variation in growth patterns and their relationship to environmental patterns. Schweingruber et al. (1990, p. 31) echoed this perspective, stating "the aim of dendroecology is the determination of the year-by-year interplay of relationships among climate, site conditions, and tree growth to assess exogenous and endogenous factors that influence the growth of a plant community." However, many of the early ecological studies using tree rings to understand forest dynamics were more focused on tree establishment dates and ages than on growth patterns.

Many proponents of dendroecology in the 1960–1980s came from a dendroclimatology background and viewed ecology in the context of the ecophysiology of tree growth. They were interested in understanding the drivers of variation in tree growth and were building on centuries of research in forest science that had linked tree growth to environmental conditions. Leonardo da Vinci's fifteenth century observation that tree rings vary between wet and dry years is the earliest documented example of this (Schweingruber 1996). Significant early contributions that are in many ways the foundation of modern dendrochronological thinking were proposed by German and French forest scientists in the eighteenth and nineteenth centuries (e.g., Henri-Louis Duhamel de Monceau; George-Louis Leclerc, Comte de Buffon; Robert Hartig). During the twentieth century, Russian research on tree-ring structure and function (Vaganov et al. 2006) helped bridge the gap between dendroclimatology and dendroecology by explaining the anatomical and physiological bases of tree-ring formation. This bridge facilitated the shift in focus from climate to a forest dynamics perspective. In recent decades, many iconic publications on forest ecology and dynamics have included tree-ring data to advance their arguments for the importance of past disturbances in shaping contemporary forest structure and composition (e.g., Lorimer 1980; West et al. 1981; Pickett and White 1985; Brubaker 1986; Harmon et al. 1986; Fritts and Swetnam 1989; Glenn-Lewin et al. 1992) and provided the basis for modern views of forest stand dynamics (Oliver and Larson 1996; Franklin et al. 2002).

The use of tree rings to understand forest dynamics also has its origins in the eighteenth and nineteenth centuries, but primarily from the perspective of forest growth and yield. European scientists and foresters had long recognized the utility of annual growth rings for estimating growth rates. For example, Varennes de Fenille (1791, p. 48) described the influence of annual "accidents" (e.g., hot and dry summer, insect infestation, spring frost) on individual growth rings, growth releases due to competition, and releases following the death of neighboring trees. He highlighted the differences between high- and low-frequency variability in tree-ring series *versus* the age-related decline in ring width as trees grew. However, the use of tree rings to understand the ecology and dynamics of unmanaged forests and forested landscapes did not emerge until the late nineteenth and early twentieth centuries. In the 1850s, Sir Dietrich Brandis, then Superintendent of the teak (*Tectona grandis* L.) forests of Pegu, Burma (now Myanmar), and future Inspector-General of Indian Forests for the British Empire, described regional variation in teak growth patterns across parts of Southeast Asia. Using data on growth rates and tree ages derived from tree rings, Brandis (1956) established a quantitative basis for the management of teak forests in southern Burma. The principles that he established for stand- and landscape-scale management of these teak forests served as the basis for forest management practices across the tropics for the next century.

As Gifford Pinchot and John Muir established the foundations of modern forest management and conservation practices in western North America in the early twentieth century, ecologists were beginning to use tree rings to address questions regarding the underlying nature of forests. For example, Cooper (1913) used tree rings to characterize the age structure of the "climax" forest of Isle Royale in Lake Superior, Michigan. He found most trees were relatively young, despite the perception that these forests were untouched by humans. Similarly, Haasis (1923) used tree rings sampled in 1915–1916 to demonstrate that a large proportion of trees in the "many-aged virgin hardwood stands" of southeastern Kentucky were 250–255 years old. He attributed the origin of this distinct age class to an extreme drought in 1662 that led to fires burning through these forests and creating a discrete pulse of post-fire regeneration. Some surviving larger oaks showed reduced growth in the two decades preceding 1662. Marshall (1928) used tree rings to identify the years in which fires occurred in western white pine forests in northeastern Washington and the Idaho panhandle. The oldest fires burned in 1610, the year that "Oliver Cromwell was celebrating the close of the Thirty Years War" and "the infant Louis XIV was starting his long and infamous reign in France" (Marshall 1928, p. 48).

From a modern dendrochronological perspective, early studies of forest growth and ecological dynamics using tree rings were limited because they were largely based on ring counts. Crossdating was still in its infancy and was being used primarily by dendroclimatologists and dendroarchaeologists (Douglass 1909; 1929;

1937). However, it ultimately paved the way for more quantitative analyses of tree-ring data (Glock 1937). Perhaps the first "true" dendroecological study belongs to Bailey (1925), one of the great wood anatomists of the twentieth century. In his 1925 paper on the "spruce budworm biocoenose," he recognized that spruce budworm defoliation had the potential to create missing rings, which would compromise the ability of ring counts to accurately date outbreaks. To address this problem, he identified distinct frost rings in the tree-ring series and used those as marker years to correctly date the rings and determine the years of spruce budworm outbreaks over the preceding two centuries.

1.3 Dendroecology and Shifting Paradigms on Forest Dynamics

Dendroecological studies have been central to the shifting ideas about forest development and responses to disturbances over the past century. In the first half of the twentieth century, Clements' (1916, 1936) ideas on succession and climax dominated ecological thought on plant community composition, structure, and dynamics. However, a growing body of dendroecological studies was revealing the role of contingency in forest dynamics and the potential for multiple developmental pathways in the wake of unpredictable disturbances. These studies provided much of the empirical basis for challenging, and eventually overturning, the Clementsian notion of succession and climax. Cooper's (1923) research used tree rings to describe the stochastic patterns of disturbance and post-disturbance forest development that followed glaciation in Glacier Bay, Alaska. This built on his earlier work studying forest responses to fire on Isle Royale, Michigan (Cooper 1913) and avalanches and rock slides at Robson Pass, British Columbia, Canada (Cooper 1916). In a "virgin" forest in the northeastern US, Hough and Forbes (1940) demonstrated how individual stands in the landscape had been subjected to a complex series of interacting disturbances over the past 300 years and how these idiosyncratic, site-specific disturbance histories interacted with edaphic conditions to generate a variety of forest stand structures.

Over the ensuing decades dendroecological studies of forests enhanced understanding of the importance of unpredictable historical events and disturbances in shaping present-day forest structure and composition. The ubiquitous effects of natural disturbances on forests emerged from tree-ring studies conducted in the 1940–1950s in the USA with signal contributions from Buell (Buell and Cain 1943; Buell and Catlon 1951; Buell and Catlon 1950; Isaak et al. 1959), Spurr (1954), and Stephens (1955). In the 1970–1980s, the number of dendroecological publications increased dramatically, describing research on forest dynamics driven by wind (e.g., Estes 1970; Henry and Swan 1974; Oliver and Stephens 1977; Lorimer 1980), insects (Brubaker and Greene 1979), and fire (e.g., Heinselmann

1973; Dietrich and Swetnam 1984). Simultaneously, studies conducted in other parts of the world reinforced the global importance of disturbance and stochastic events as drivers of forest dynamics (e.g., Kassas 1951 in the United Kingdom; Blais 1962 and Payette and Gagnon 1979 in Canada; Veblen et al. 1977 in south-central Chile; Veblen and Steward 1980 in New Zealand; Morrow and LaMarche 1978 in Australia; and Engelmark 1984 in Sweden). These foundational dendroecological studies contributed to a paradigm shift in forest ecology that arose in the 1970–1980s emphasizing nonequilibrium dynamics, multiscale dynamics, and the importance of humans as agents of disturbance and drivers of forest dynamics.

1.4 The Geography of Dendroecology

The expansion of dendroecological research to represent all forests around the globe has been uneven (Worbes 2002, 2004). As the examples cited above suggest, dendroecological studies have heavily emphasized temperate and high-latitude forests, particularly in the Northern Hemisphere. Southern Hemisphere forests have received less attention, although important contributions from Argentina, Chile, and New Zealand have highlighted common patterns in forest dynamics across hemispheric boundaries. In contrast, dendroecological studies have only recently penetrated tropical forests. Encyclopedic assessments of wood quality and the properties of regional tree floras in the late nineteenth and early twentieth centuries indicated the presence of annual growth rings in many tropical tree species, particularly in tropical areas subjected to certain seasonality (e.g., flooding, drought) from Africa and southern America (Mariaux 1967) and monsoon-influenced regions such as South and Southeast Asia (e.g., Gamble 1904, Chowdhury 1939). However, the lack of distinct temperature seasonality, poorly understood phenological patterns, complex wood anatomies, and often challenging logistical issues have greatly limited the potential for dendrochronological studies of tropical tree species (Bormann and Berlyn 1980). Nevertheless, significant advances have been made over the past two decades to identify hundreds of tropical tree species in South America, Africa, and South and Southeast Asia (Worbes 2002; 2004) that possess annual growth rings. This has provided the necessary foundation for dendroecological methods to address long-standing questions regarding the dynamics of species-rich tropical forests and expands the geographical reach of dendroecology into all of the major forest biomes of the world.

1.5 Contemporary Applications of Dendroecology

Dendroecological studies have fundamentally shaped contemporary views of forest ecology and forest dynamics. While ecological studies using tree rings have been published for well over a century, the past several decades have seen a rapid acceleration in the rate of publication of dendroecological studies. Most syntheses and reviews of dendrochronology over the past half century have focused on climatology, archaeology, or wood formation (e.g., Fritts 1971, 1976, Eckstein 1984, Cook and Kairiukstis 1989, Schweingruber 1996, Hughes et al. 2001, Vaganov et al. 2006, and to a lesser extent Speer 2010). While dendrochronology has made important contributions in each of these areas, the ecological lessons that dendrochronological research has provided are fundamental to understanding how forested ecosystems will respond to the many threats posed by global environmental change. These threats are not limited to changing climatic conditions; they include the impacts of invasive species, biodiversity loss, changing disturbance regimes, and their myriad potential interactions. Dendroecology is a significant component of applied ecological research, providing important historical context for adapting existing forest management strategies to mitigate and respond to current and future global environmental change.

We envision this book as a waypoint in the science of dendroecology that brings together much of the excellent dendroecological research that has come before us, provides a contemporary overview of the breadth and depth of the existing research, and generates new ideas for the many possible directions that dendroecology might take going forward. We hope that this volume will provide a useful resource for dendrochronologists, ecologists, foresters, and others interested in the conservation and sustainable management of the world's forests.

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