Dendroecology is the science that dates tree rings to their exact calendar year of formation to study processes that influence forest ecology (e.g., Speer 2010 [1], Amoroso et al., 2017 [2]). Reconstruction of past fire regimes is a core application of dendroecology, linking fire history to population dynamics and climate effects on tree growth and survivorship. Since the early 20th century when dendrochronologists recognized that tree rings retained fire scars (e.g., Figure 1), and hence a record of past fires, they have conducted studies worldwide to reconstruct [2] the historical range and variability of fire regimes (e.g., frequency, severity, seasonality, spatial extent), [3] the influence of fire regimes on forest structure...
and ecosystem dynamics, and [4] the top-down (e.g., climate) and bottom-up (e.g., fuels, topography) drivers of fire that operate at a range of temporal and spatial scales. As in other scientific fields, continued application of dendrochronological techniques to study fires has shaped new trajectories for the science. Here we highlight some important current directions in the United States (US) and call on our international colleagues to continue the conversation with perspectives from other countries.

**Figure 1.** Demonstration image of a crossdated fire-scarred sample. Image is a *Pseudotsuga menziesii* [(Mirb.) Franco; Douglas-fir] cross section that was sampled for a fire history study in the Salmon-Challis National Forest, Idaho. This crossdated sample spans the period 1427–2001, and each fire scar and season is recorded (e.g., 1835 D, dormant). Sample collection and crossdating conducted by John Sloan and James P. Riser II.

1. **Multiple Lines of Evidence: Stand Age Structure Paired with Fire History**

Fires can affect stand demography and, as a result, alter stand age structure. Other things being equal, low-severity fires tend to thin seedlings and smaller trees, so reproduction occurs episodically in spatial gaps and time periods favorable for recruitment. In contrast, high-severity fires (by definition) kill a high proportion of individuals of all size and age classes, resulting in spatially extensive age cohorts. Intensive and extensive analyses of age structure, both within fire scarred plots and in adjacent stands, continue to yield meaningful insights about the size and severity of past fires (e.g., Brown and Wu 2005 [5]; Heyerdahl et al., 2012, 2014 [6,7]; Lafon et al., 2017 [8]). Expanded age-structure sampling beyond fire-scar sites to intervening stands can enlarge the footprint of fire history information. With sufficient age structure and fire-scar data from multiple locations, geographic patterns of fire extent and severity can emerge (e.g., O’Connor et al., 2017 [9]). Further advances are needed that link fire histories to post-fire forest changes, particularly the vexing issue of the post-fire time period during which tree regeneration, recruitment, and survival occurs. Furthermore, these ecological processes are being altered by climate change and fire-vegetation feedbacks, requiring linking fire history with detailed contemporary post-fire ecology. Recent dendroecological advances into new regions, new communities, and new species (e.g., hardwoods) are documenting the impacts of fire regimes on long-term ecological dynamics that complement influences of soils, topography, or climate in a wide array of environments.
2. Fire Modeling Paired with Fire History

Understanding fire ecology over long time periods is required for managing future forests. Empirical studies and instrumental records are typically short in temporal extent, limiting their utility in forecasting future ecosystem dynamics. Simulation models (e.g., Loehman et al., 2017 [10]) can run for longer modeling periods, but these are typically calibrated against modern records which may not capture long-term variation in climate, recent land use, or some ecosystem processes (Keane et al., 2015 [11]). Tree-ring reconstructions of fire can be used to: calibrate simulation models and determine whether local fire and forest histories might be extrapolated to unsampled areas; assess how and where current fire regimes and forest conditions depart from historical ones; explore the interactions of ancient land management and fire regimes (Swetnam et al., 2016 [12]); and project future fire regimes and forest conditions under changing climate and land management. In addition, fire behavior models (e.g., Hollingsworth et al., 2012 [13]) are being used to help interpret the tree-ring record of past fire (e.g., Heyerdahl et al., 2014 [7]) as well as landscape patterns of fire spread and severity (Conver et al., 2018 [14]).

3. Fire History Networks

A robust network of site-specific fire history reconstructions exists for some parts of the world, but do these fine-scale studies capture variation at landscape or biome scales? New work is testing for effects of spatial scale using [2] spatially-explicit, processed-based models incorporating fire history, climate, and vegetation to model fire histories beyond sites with fire scars (e.g., Swetnam et al., 2016 [12]) and [3] systematic sampling across landscapes and regions (e.g., Heyerdahl et al., 2001 [15]; Farris et al., 2010, 2013 [16,17]; O’Connor et al., 2014 [18]). Such efforts could directly contribute to better understandings of the long-term climatic and human drivers of global change (e.g., Evans et al., 2017 [19]; Loehman et al., 2017 [10]).

Reconstructing fire history from tree rings requires considerable efforts in the field and laboratory, but dendrochronologists recognized many decades ago that broad-scale questions can be addressed by combining publicly-archived data. For example, the International Multiproxy Paleofire Database (IMPD) was established in 2003 and includes 442 (as of 2018-03-30) tree-ring based fire histories across the US. In addition, the Fire and Climate Synthesis (FACS) project is the most complete data set of crossdated fire histories with over 1100 entries (https://www.frames.gov/catalog/24872). Although spatial gaps exist for the eastern US in both the IMPD and FACS, these networks have been critical for analyzing the broad response of fire to variations in climate and vegetation (e.g., Kitzberger et al., 2007 [20]; Swetnam et al., 2016 [12]). Continental and global networks of fire scars and other fire proxies (e.g., ring width or density) are being analyzed to reveal the influence of broad-scale climate patterns on historical fire across multiple spatial scales (Falk et al., 2007, 2011 [21,22]). Fire history analysis software packages like the Fire History Analysis and Exploration System (FHAES; http://www.fhaes.org) and burnr (R system) are freely available and facilitate large meta-analyses and the potential for new creative cross-disciplinary analyses (Brewer et al., 2016 [23]; Malevich et al., 2018 [24]). However, these networks inevitably contain spatial gaps. For example, fire-resistant or fire-rare ecosystems are poorly represented, as are private lands and ecosystems lacking arboreal plants. Spatial fire history networks can facilitate novel, cross-scale, multi-proxy analyses of past fire in areas where land use has destroyed evidence of past fires and in high fire-frequency ecosystems characterized by low-intensity fires. Fire histories have the ability to guide strategies to best adapt fire management protocols in populated, fire-prone landscapes. Hence, scientists should be increasing and improving outreach initiatives, especially to landowners, if we are to fill in spatial gaps within the fire history network.
4. Deciphering Fire and Land-Use Histories

Dendrochronology can elucidate linkages between fire and land-use histories. This science contributes high-resolution chronologies of variables from all three major components of human-fire-climate systems across multiple spatial and temporal scales (e.g., Taylor et al., 2014 [25]). In the US, we tend to separate human influence (via fire) on landscapes into “pre-Euro-American settlement” and “settlement,” yet traditions and cultures blended and varied over hundreds of years (ca. 1500–1800) and across landscapes and regions. This span of time is well represented in the tree-ring record. Collaborations among anthropologists, archeologists, and human geographers to better understand interactions among fire, people, and past landscapes have been limited in most areas with fire history studies. Expansion of multi-disciplinary collaborations will lead to a more coherent picture of linkages between fire and land-use histories (e.g., Swetnam et al., 2016 [12]).

5. Fire Seasonality and Ecology of Scar Formation

Climate-induced changes in fire seasonality are likely to have ecological consequences for forest flora and fauna. The intra-annual position of a fire scar within the annual growth ring contains information about the seasonal timing of past fires (Figure 1), but interpretation of this record is hampered by a lack of knowledge about the seasonal timing of tree-ring growth, viz. cambial phenology, and its drivers. Knowledge of climatic and synoptic weather conditions likely to result in fires can be obtained from intra-annual changes in seasonal climate that produce conditions favorable for fires (e.g., Platt et al., 2015 [26]). Such data can be related to seasonal timing of actual fires recorded in tree-rings (e.g., Rother et al., 2018 [27]). If such studies span long periods of time, human changes in fire-seasonality and effects on trees in natural ecosystems could be elucidated. Combining fire-scar records of seasonality with seasonally-resolved climate reconstructions (e.g., from latewood ring widths) is advancing our understanding of fire-climate relationships (e.g., Margolis et al., 2017 [28]). However, we do not completely understand how fire scars form, or exactly why some trees scar but not others, particularly in regions with a bimodal or year-round fire season. Climate change and local variation in microclimate, as for example along local moisture gradients, complicate our understanding of the timing and triggers of both cambial activity and fire-scar formation.

6. New Fire Proxies within Growth Rings

Exploring and developing new fire proxies within growth rings represent a frontier of dendrochronology. Exciting new advances in anatomical, chemical, and other properties of tree rings, along with phenological studies and experiments, are increasing our knowledge of long-term changes in fire seasonality and perhaps provide a more complete record of fire occurrence at landscape scales, because not all trees exposed to fire form scars (e.g., Arbellay et al., 2014a, 2014b [3,4]). Experimental and observational studies could be combined with fire behavior data to provide insights on scarring or wood anatomical response mechanisms (Smith et al., 2016 [29]). Chemical analysis via Laser Induced Breakdown Spectrometry (LIBS) could provide new insights on whether certain elements act as fire tracers. Analyses of resin ducts are leading to new insights about the interaction of fire and insect outbreaks (Hood et al., 2015 [30]) and might help identify signatures of fire for trees without scars (e.g., Smith et al., 2016 [29]). Another promising frontier is identifying post-fire wood anatomical changes with scanning electron microscopy (e.g., Pearson et al., 2011 [31]).

7. Conclusions

Tree-ring fire histories are powerful tools for understanding fire ecology. Future applications of these tools will deepen our knowledge of fire behavior and fire effects on vegetation across broad spatial and temporal scales. This knowledge is important for delving into past fire regimes, understanding current vegetation and fuel dynamics, and managing them to achieve desired outcomes in the future (e.g., Fulé 2008 [32]). As we continue to apply dendrochronology to study fire, we can also use these
records to address compelling and broad-scale scientific questions related to the carbon cycle and global planetary change. Fire, humans, climate, and vegetation interact in various ways and we need to understand these interactions to develop skillful predictive models. Advancing the fields of fire ecology and science across the country and the globe will become more important as the continents continue to burn and human-induced climate change forces us to pay back the fire deficit.

Acknowledgments: We are grateful to Tom Swetnam for discussions and contributions that improved earlier versions of this manuscript, as well as two anonymous reviewers for comments and suggestions that helped improve the paper. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Author Contributions: GLH, CHB, PMB, DAF, WTF, HDGM, AH, EKH, MWK, CWL, EQM, RSM, ATN, WJP, MTR, TS, RLS, LAS, MCS, EKS, and AHT contributed equally in writing this paper.

Conflicts of Interest: The authors declare no conflict of interest.

References

23. Brewer, P.W.; Velásquez, M.E.; Sutherland, E.K.; Falk, D.A. Fire History Analysis and Exploration System (FHAES) Version 2.0.2; Computer Software; Fire Research and Management Exchange System (FRAMES), 2016. [CrossRef]