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RESEARCH REVIEW

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Redefining temperate forest responses to climate and disturbance in the eastern United States: New insights at the mesoscale

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Abstract

Aim: Climate and disturbance alter forest dynamics, from individual trees to biomes and from years to millennia, leaving legacies that vary with local, meso- and macro-scales. Motivated by recent insights in temperate forests, we argue that temporal and spatial extents equivalent to that of the underlying drivers are necessary to characterize forest dynamics across scales. We focus specifically on characterizing mesoscale forest dynamics because they bridge fine-scale (local) processes and the continental scale (macrosystems) in ways that are highly relevant for climate change science and ecosystem management. We revisit ecological concepts related to spatial and temporal scales and discuss approaches to gain a better understanding of climate–forest dynamics across scales.

Location: Eastern USA.

Time period: Last century to present.

Major taxa studied: Temperate broadleaf forests.

Methods: We review regional literature of past tree mortality studies associated with climate to identify mesoscale climate-driven disturbance events. Using a dynamic vegetation model, we then simulate how these forests respond to a typical climate-driven disturbance.

Results: By identifying compound disturbance events from both a literature review and simulation modelling, we find that synchronous patterns of drought-driven mortality at mesoscales have been overlooked within these forests.

Main conclusions: As ecologists, land managers and policy-makers consider the intertwined drivers of climate and disturbance, a focus on spatio-temporal scales equivalent to those of the drivers will provide insight into long-term forest change, such as drought impacts. Spatially extensive studies should also have a long temporal scale to provide insight into pathways for forest change, evaluate predictions from dynamic forest models and inform development of global vegetation models. We recommend integrating data collected from spatially well-replicated networks (e.g., archaeological, historical or palaeoecological data), consisting of centuries-long, high-resolution records, with models to characterize better the mesoscale response of forests to climate change in the past and in the future.

KEYWORDS
climate, compound events, disturbance, eastern United States, mesoscale, scale, temperate forests

1 | INTRODUCTION

Quantifying the impact of large, infrequent disturbances across broad spatial and temporal scales represents a major challenge in forest ecology (Asner, 2013). As discrete events, disturbances disrupt the structure and composition of populations or ecosystems and induce changes in their resource or physical conditions (Pickett & White, 1985). Disturbances leading to tree mortality can impact forests for centuries (Foster, Knight, & Franklin, 1998), but less is known about their frequencies and potential synchronization of forest dynamics across scales (Lertzman & Fall, 1998). These interactions can manifest over larger scales in ways that make prediction difficult (Dale, Joyce, McNulty, & Neilson, 2000). When large, infrequent disturbances do occur, they can surprise both forest researchers and managers (Turner, 2010), in part because of the absence of long-term datasets capable of recording past events (Lindenmayer, Likens, Krebs, & Hobbs, 2010).

To address these uncertainties, we begin this review by highlighting progress in studying ecosystems across scales and the challenges that remain. We then focus on the forests of the eastern USA over the last century to investigate whether climate-driven disturbances might synchronize these forests at large scales. Although drought in this region is typically characterized as infrequent, random and occurring only at local scales (Hanson & Weltzin, 2000), we review the possibility of a drought-driven, mesoscale disturbance regime using past literature and model simulations of climate-driven forest mortality. We conclude by affirming the advantages gained from field and modelling investigations conducted at scales equivalent to the underlying disturbance regime (Wu & Li, 2006).

In the temperate, broadleaf forests of the eastern USA, gap dynamics are a common, fine-scale driver of disturbance (Runkle, 1982). These isolated, asynchronous canopy mortality events can approach a steady state over large scales (Bormann & Likens, 1979; Shugart, 1984). Yet, overlooked in this theory are independent observations made since the early 1900s that many eastern U.S. old-growth forests experienced a pronounced period of tree recruitment dating to the late 1600s (Foster, 1988; Gates & Nichols, 1930; Guyette & Spetich, 2003; Haasis, 1923; Henry & Swan, 1974; Hough & Forbes, 1943; Huntington, 1914; Rentch, 2003). In a synthesis that combined these observations and long-term tree-ring data, Pederson et al., (2014) showed that this synchronous recruitment over *c.* 1.4 million km^2 in the 1660s and synchronous tree mortality in the late 1770s covering *c.* 61,000 km^2 resulted from climate-driven disturbance. Less severe disturbances, those ranked 10th–20th in terms of the percentage of trees recording disturbance during an event, had estimated return intervals of 35–75 years (Pederson et al., 2014: fig. A11). These results inform our hypothesis that mesoscale, climate-associated disturbance affect temperate mesic forests, such as those in the eastern USA, through compound events where two or more disturbance drivers occur concurrently and cause greater environmental impact than might be expected because of their rarity (Zscheischler et al., 2018).

This hypothesis builds from the recognition by Wiens (1989) that temporal and spatial scales should be matched appropriately to discern pattern from process in forest dynamics. For example, ecosystem processes vary in a linked manner such that processes over larger areas typically have slower rates (Blöschl & Sivapalan, 1995; O'Neill, 1989; Urban, 2006; Wu, 2013), implying that patterns over larger areas require a longer period of observation to elucidate underlying processes. Evaluating regional or continental forest dynamics for only short time periods (years to decades) increases the likelihood of pseudopredictions (Wiens, 1989) or projections of forest dynamics that are seemingly robust at shorter, smaller scales but are likely to miss the longer temporal characteristics of the underlying drivers. Thus, pseudopredictions do not facilitate the prediction of ecological surprises. Many ecological studies still sample at temporal and spatial scales that are smaller than the underlying processes (Estes et al., 2018), and management of forested landscapes based on short-term observations may result in unanticipated consequences (Millar & Stephenson, 2015). This is especially important in forests where complex interactions between climate, disturbance and ecosystem resilience may cause plant communities to persist in areas where climate has become unsuitable for regeneration over time frames of years to decades (Dullinger et al., 2012; Hobbs, Valentine, Standish, & Jackson, 2017).

These ideas are particularly important at the mesoscale, which is the spatial scale in between forest stands and biomes and the temporal scale in between forest succession and shifts in species ranges. Research at this scale is needed because forests extend across continents and are composed of long-lived tree species, necessitating an assessment of their dynamics from local interactions within canopy gaps to macroscale interactions delimiting continental distributions. Mesoscale dynamics are centred within the most relevant scales for analysis of the response, adaptation to and mitigation against rapid climate change and related human activities affecting forests (Figure 1). Although Delcourt, Delcourt, and Webb (1982) defined the mesoscale with discrete bounds, we adopt the concepts of Roughgarden, Gaines, and Possingham (1988) and Holt (1993), who described it more generally as the scale between community processes at a local study site that can be manipulated through field experimentation and those at larger, biogeographical scales commonly studied in earth sciences. These latter scales are represented today by macrosystems ecology, which focuses on continental scales (Heffernan et al., 2014). Mesoscale forest processes link local, gap

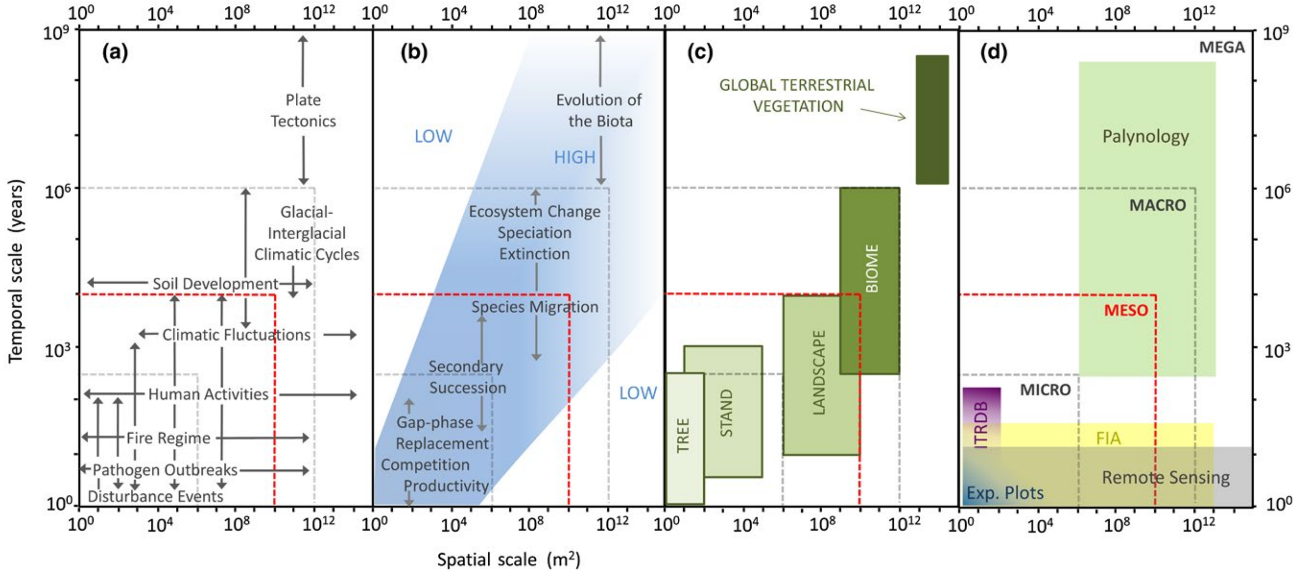

FIGURE 1 (a) Representative environmental disturbance regimes (including climate) across spatial and temporal scales with (b) biotic responses of forests. Disturbance events here include wildfire, wind damage, clear cut, flood and earthquake. The blue shaded area is a region of high predictability (*sensu* Wiens, 1989, reprinted with permission), matching appropriate processes to disturbances at similar scales. (c) Classification of vegetation with scale. Although landscapes may be viewed as scale independent, they are often viewed as a scale larger than stands in practice and encompass scales at which ecosystem processes connect forest mosaics (Lertzman & Fall, 1998). (d) Representative existing forest datasets by scale. Dashed lines divide conceptual scales from local to mega, including mesoscales (in red), which bridge the responses of vegetation, from gaps and forest succession to species migration. ITRDB refers to the International Tree-Ring Data Bank, and FIA refers to the U.S. Forest Service Forest Inventory and Analysis programme. Panels a–c were adapted from the original of Delcourt et al. (1982 and are reprinted with permission). See also Prentice (1992) for a similar analysis to the one in panel d [Colour figure can be viewed at wileyonlinelibrary.com]

dynamics to macroscale species distributions in a hierarchical manner; an example of the triadic structure in scale-dependent systems (O'Neill, 1989; Wu, 2013).

We suggest that conducting more research on the influence of climate on disturbances over broad spatial scales and long timescales would reduce pseudopredictions and the potential for ecological surprises. Although much forest research focuses on either time or space, few studies incorporate both time and space at long temporal scales and wide spatial scales with enough precision and detail (e.g., Falk et al., 2011; Heinselman, 1973). Of these, fewer studies are conducted in forest types where fire is not the dominant disturbance regime (although see Williams, Shuman, Webb, Bartlein, & Leduc, 2004). For example, mesoscale disturbances in the western USA were documented only through the development of centuries-long and spatially extensive tree-ring networks. These networks revealed predictable drivers of fire (La Niña conditions often lead to mesoscale fires; Swetnam & Betancourt, 1990) and enabled analysis on the controls of fires, from tree to regional scales (Falk et al., 2011). No similar network exists in the eastern USA or any other broadleaf-dominated temperate mesic forests. Building upon insights from semi-arid regions, we explore the prevalence of mesoscale disturbances in mesic regions, where various types of disturbances interact at multiple spatial and temporal scales.

Likewise, the representation of climate-driven disturbance is insufficient in most ecosystem models. Process-based modelling studies show that accounting for the interactions of disturbance regimes with climate and land use can significantly affect the outcome of simulated ecosystem responses (Poulter et al., 2010). The development and benchmarking of mesoscale ecosystem model dynamics requires detailed observations across a range of processes and geographical regions, which have been challenging to obtain. Consequently, disturbance and biotic responses remain, in general, inadequately represented as generalized background mortality rates or, at worst, omitted in models used in many carbon cycle and climate change assessments (e.g., Anav et al., 2013).

2 | INSIGHTS FROM CHARACTERIZING FOREST DYNAMICS AT LARGER SCALES

While setting forth a framework for characterizing ecosystems and their dynamics at multiple scales, Tansley (1935) questioned whether ecosystems that appear stable at one scale might be changing slowly at another. Although Tansley's concept of the ecosystem was recognized early (cf. Hutchings et al., 2012; O'Neill, 1989), it was not until the latter half of the 20th century that ecologists began to embrace the importance of scale in ecosystem dynamics (Rose et al., 2017). Delcourt et al. (1982) synthesized a conceptual model of ecological scale that included not only vegetation patterns by time and space (Figure 1), but also how different disturbance regimes affect vegetation patterns at particular scales (see also Delcourt & Delcourt, 1988). This model remains relevant as ecologists continue to appreciate the importance of scale in ecosystem processes (McGill, 2010). Tansley's (1935) call to characterize ecosystems at multiple scales has led to many insights from scaling forest dynamics over larger areas, longer time frames or both simultaneously.

2.1 | Spatial scaling

Although global change affects forests at varying scales, we have learned much from research investigations and data availability at the plot level (Figure 1d). At the smallest spatial scales, for example, studies show that plants fundamentally decrease stomatal conductance in response to the global increase in atmospheric CO_2 concentration; however, only recently have studies begun to characterize how this ecophysiological response affects water-use efficiency at larger scales (Keenan et al., 2013; Norby & Zak, 2011). Free-air CO_2 enrichment (FACE) experiments address several scales, that is, leaf to plot, and provide opportunities for scaling spatial scales with plot diameters extending up to tens of metres, recording responses over decades (Ainsworth & Long, 2005). Yet, results from FACE and other forest experiments have shown the difficulties in maintaining large experiments over longer time-scales (Norby & Zak, 2011). For example, a throughfall displacement experiment with 0.64 ha plots found little impact of reduced precipitation on overstorey tree mortality from 1993 to 2000; however, this experiment occurred during an interval without a severe drought, minimizing its insight for extrapolating the impacts of drought at larger scales (Huston, Todd, & Barlar, 2003).

Spatial scaling issues are also present when studying forest dynamics at the stand level. Tree-ring reconstructions at the stand level reveal disturbance histories but preclude knowledge on whether these events also affected forests regionally. Thus, these spatially limited investigations of disturbance history are likely to support an individualistic perspective on forest dynamics because of their inability to detect larger-scale disturbance events. The few studies that have investigated multiple stands simultaneously have generally reinforced the individualistic stand development perspective (e.g., D'Amato & Orwig, 2008; Rentch, 2003), suggesting that local events are one of the strongest drivers of forest dynamics. In contrast, climatic sensitivity of tree-ring patterns collected at smaller scales generally reflects the climatic sensitivity of trees at larger scales (St. George & Ault, 2014). Furthermore, research conducted across larger spatial scales has recently revealed different perspectives on forest dynamics in systems typically characterized by small-scale dynamics (Jackson & Fahrig, 2015).

Existing studies and data nonetheless offer opportunities to examine forest dynamics at broader spatial scales. For example, the United States Forest Inventory and Analysis programme, the North American Forest Dynamics network and the Forest Global Earth Observatory (ForestGEO) have the geographical extent to investigate the impacts, distributions and drivers of disturbance that would be difficult to obtain from a small array of plots (e.g., Vanderwel, Coomes, & Purves, 2013). Recent studies using forest inventory data, remotely sensed data, or both have found large-scale evidence for synchronicity in disturbance (Senf & Seidl, 2017) or drought-induced tree mortality (Hu, Wang, Bauerle, & Klos, 2017; Moore et al., 2016). However, because these datasets typically extend only a few decades, they are constrained by recent climatic change and are likely to lack the occurrence of extreme events over the life span of trees that could drive significant changes in a forest (although see Fei et al., 2017). These studies are useful in expanding our perceptions on the extensive spatial impacts of disturbance but might be limited in their ability to represent mesoscale dynamics because of their shorter temporal dimension.

2.2 | Temporal scaling

Long-term ecological studies (> 10 years in duration) have focused on processes that influence forest dynamics through various networks (Lindenmayer et al., 2012). Long-term ecological research networks (e.g., Hobbie, Carpenter, Grimm, Gosz, & Seastedt, 2003) and the global network of flux towers measuring carbon, water and energy exchanges (Ershadi, McCabe, Evans, Chaney, & Wood, 2014) show how mechanisms that drive processes can be investigated over longer time-scales and across several sites. To capture ecosystem processes further over space and time, the National Ecological Observatory Network is composed of sites distributed across the USA (Keller, Schimel, Hargrove, & Hoffman, 2008). This emerging network has been funded for a unique, 30-year period, which will improve ecological forecasting in response to a changing climate but might still not capture mesoscale dynamics fully. The importance of long-duration data has spurred a call for a greater focus on temporal ecology (Wolkovich, Cook, McLauchlan, & Davies, 2014), which requires approaches from both landscape ecology and palaeoecology to discern how ecological systems respond across scales (Gillson, 2009).

Although also imperfect as proxy records, palaeoecological data provide unique insight into current ecosystem conditions by directly recording past events as ecological artefacts (Dey & Guyette, 2000; Sousa, 1984). Covering seasons to years and decades to centuries, networks of tree-ring records, such as those from the International Tree-Ring Data Bank (ITRDB), offer the opportunity to investigate tree, forest and climate interactions at multiple spatio-temporal scales. Many, if not most, of these records were collected from canopy trees to maximize the embedded climate signal by reducing the influence of competition for light from neighbouring or overtopping trees. The disturbance record from canopy trees fades forward in time as their sensitivity to adjacent disturbances decreases in recent decades compared with understorey trees (Nowacki & Abrams, 1997), and thus their theoretical ability to reflect the full disturbance history is also diminished. A test of this idea showed that an ITRDB collection found much less disturbance in the same forest during the 20th century compared with a collection that included smaller trees that were more likely to be in the understorey (McEwan, Dyer, & Pederson, 2011).

Alternatively, the ability of tree-ring collections to record events robustly in the distant past fades because of reduced sample replication going back in time (Bowman, 2007). The accuracy of existing tree-ring networks as rich sources of data to study forest dynamics at multiple temporal and spatial scales may be affected by their sampling designs. Although tree-ring records from old-growth forests may not have been impacted recently by severe disturbance, they can provide a needed archive of longer-term disturbance regimes that may not be apparent currently in younger forests (e.g., Jackson, 2006).

At longer time-scales, Quaternary palynological studies reveal synchronous changes in forest composition from regional to hemispheric scales in response to climatic change (e.g., Gajewski, Viau, Sawada, Atkinson, & Fines, 2006) and suggest that these dynamics are detectable in modern forests if examined at the appropriate scales of investigation. Both temperature and drought have been identified as important drivers of forest composition during the Holocene (e.g., Booth et al., 2012; Peteet, 2000; Shuman, Newby, Huang, & Webb, 2004; Williams et al., 2004). Although they are highly valuable in reconstructing long-term forest dynamics, palynological data have limited ability to discern climate–forest dynamics at highly resolved time-scales (e.g., annual to decadal) because their resolutions are commonly in the range of centuries, but fine-scale analyses are possible occasionally. To increase the resolution and precision of vegetational changes, different techniques (Grimm, Maher Jr, & Nelson, 2009; Peteet et al., 1990) and approaches have been implemented (Williams et al., 2004). For example, McLachlan, Foster, and Menalled, (2000) used pollen, tree rings and archival records to investigate the development of *Tsuga* forests in central New England after anthropogenic and natural disturbance. As a result of the high mobility of pollen, palynological records from lacustrine environments also usually integrate over a large area, decreasing their spatial resolution. Although this varies with topography and other factors (Delcourt & Delcourt, 1988; Prentice, 1985), the fact that these scales are themselves hard to quantify precisely adds additional uncertainty to reconstructions of past vegetation dynamics. In some cases, the taxonomic resolution in palaeoecological reconstructions may extend only to the genus level, although it can be improved using plant macrofossils (Delcourt et al., 1982).

2.3 | Recent studies linking large spatial and temporal scales

Although few mesoscale studies exist in mesic regions at high temporal resolution, recent studies in these and other forested regions have revealed unexpected phenomena. Gravel, Beaudet, and Messier (2010) reported synchronous understorey dynamics across southern Quebec since 1975 and postulated that it might have been triggered by an extreme climate event. Using the largest reported disturbance chronology in Europe (> 11,000 tree cores), Schurman et al. (2018) found that decadal disturbance rates varied unexpectedly for *Picea abies* forests and were likely to be driven by drought extremes. At time-scales approaching a century, past disturbance events in European forests have also led to either an increase (Schurman et al., 2018) or a decrease in the susceptibility of a forest landscape to subsequent disturbance (Thom, Rammer, Garstenauer, & Seidl, 2018). A fire-scar network in the western USA elucidated the first link between Pacific Ocean sea surface temperature variability and wildfire variation caused by drought (Swetnam & Betancourt, 1990). Investigations at multiple scales across this network have since revealed top-down (i.e., climate) and bottom-up (i.e., topography) controls of fire dynamics (Falk et al., 2011). Likewise, reconstructions of insect outbreaks in the western USA revealed evidence contrary to the prevailing so-called stress hypothesis that drought triggered insect outbreaks, showing instead that insect outbreaks were associated with moist June conditions (Swetnam & Betancourt, 1998).

In eastern North America, recent research has shown that large-scale drought does impact forest growth (D'Orangeville et al., 2018; Martin-Benito & Pederson, 2015) and that past severe droughts have led to synchronous, regional-scale forest disturbances (Figure 2) (Pederson et al., 2014). This synchronous, extensive canopy disturbance event was driven by a combination of extreme climatic (compound) events. First, the drought preceding the period with the

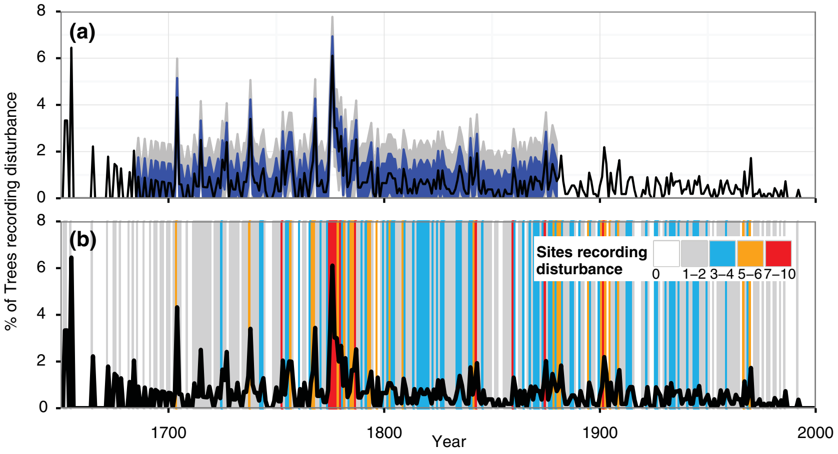

FIGURE 2 Rate and synchrony of inferred canopy disturbance at the mesoscale and extending into the macroscale. (a) Time series of the percentage of trees recording disturbance (thick, black line) across 21 forests in the south-eastern USA. Blue shading represents 1 *SD* from the mean, whereas grey represents 2 *SD*. Shading covers only 1680–1880 owing to presumed increases in uncertainty with the fading record issue discussed in the text. (b) Evidence of synchrony across the 21 forests. The annual mean number of sites recording a disturbance from 1680 to 1880 equalled 2.4 sites (*SD* = 2.0). The mean number of sites recording disturbance during years with elevated rates of disturbance was 4.1 sites, with a range of 2.9–10. Orange and red vertical lines indicate years when the number of sites recorded disturbance > 1 *SD* above the 1680–1880 mean. Adapted from Pederson et al. (2014) [Colour figure can be viewed at wileyonlinelibrary.com]

greatest mortality, beginning in 1775, was partly driven by Pacific Ocean circulation, which is not typically considered a common or consistent driver of moisture in the south-eastern USA (Barlow, Nigam, & Berbery, 2001). Second, tree core samples recorded a severe frost event in May 1774 that historical documents confirm as occurring over *c*. 219,000 km^2 (Pederson et al., 2014). These investigations revealed rare, but important, ecological dynamics in forested ecosystems that were apparent only because equivalent large scales of time and space were used.

3 | A REVIEW OF DOCUMENTED FOREST MORTALITY PROBABLY DRIVEN BY CLIMATE OVER THE PAST CENTURY

To quantify the frequency of mesoscale dynamics in this region, we reviewed published observations by scientists of increased canopy tree mortality in the eastern USA over the last 100 years, in which drought was reported to be one of the several potential mortality agents, and identified 22 such episodes (Table 1). Other mortality agents included insect attack, insect defoliation, frost and fungal disease. Most of these observations were made at the stand or landscape scale, and one-third are found in technical non-peer-reviewed reports. Determining the drivers of tree mortality is challenging (Haavik, Billings, Guldin, & Stephen, 2015). For example, one study minimized drought as a potential factor of tree mortality because the effects of drought were observed to be “roughly equal to those caused by moderate defoliation” and mortality was inconsistent regionally (Nichols, 1968). Given that multiple drivers can be associated with mortality, inconsistent mortality rates across space are not unexpected. The impact of each driver can differ with each event depending on local forest conditions, an uneven or nonlinear spatial intensity of those drivers, or interactions with other factors that vary over space, time or order of impact (see Manion, 1981). For example, insects were observed or noted as factors contributing to tree mortality in seven cases. However, stand inventory (Berdanier & Clark, 2016), dendroecological (Parshall, 1995) and palaeoecological (Booth et al., 2012) studies have reported increased tree mortality during drought. Notwithstanding the difficulties in assigning causation, we use these 22 mortality observations to re-evaluate a hypothesis by Balch (1927), who posited that climate (through drought and late frost) initiated tree mortality in the Southern Appalachians in the early 20th century, weakening the resistance of trees to pathogens. We focus on this hypothesis because it demonstrates how the broader class of climate-driven, compound events may impact mesic forests.

To test whether drought was a significant contributor across all mortality events, we examined, at the location of each event, departures from two climate indices independent of the original mortality observations, using climate records from PRISM Climate Group (2016): mean summer precipitation (June, July, August; JJA) and August standardized precipitation–evapotranspiration index (SPEI) for the same 3-month time-scale (notated as SPEI3). SPEI is a multiscalar drought index that includes the effect of temperature and precipitation and is commonly used to assess the response of forests to climatic variability (Norman, Koch, & Hargrove, 2016). These climate indices show that summer precipitation did, in fact, decrease below ≥ 1 *SE* of the 120-year mean starting 5 years before the observed mortality (Figure 3a). Beginning 2 years before the observed mortality event, mean summer precipitation was > 2 *SE* below the 120-year mean. SPEI3 also reveals this same relationship between drought and mortality (data not shown). Our departure analysis also identified four distinct episodes of increased mortality clustered in space and time between 1930 and 1988 (Figure 3b). Together, our synthesis detects mesoscale drought as a frequent contributor to tree mortality in mesic forests across observers, forest types, time and space, with an average decrease of 26% of summer precipitation departure in the year preceding each event. This finding is particularly relevant because anthropogenic climate change is expected to lead to greater tree mortality from hotter droughts (Allen, Breshears, & McDowell, 2015).

These climate-driven disturbances may greatly influence forest carbon dynamics. Of the studies reporting mortality rates, species-level mortality ranged from 5 to 78%, with 10–20% being the most common percentage reported. Likewise, seven reports noted a loss in basal area of 7–25.3%. In examining reviews on the impact of disturbances on carbon dynamics of eastern U.S. broadleaf forests, there appear to be no examples of the impact of drought as a causal agent in carbon loss (Goetz et al., 2012; Kasischke et al., 2013; Vanderwel et al., 2013). However, many forests in this region are maturing after agricultural abandonment and changes in land use. As they mature, dominant trees increase in size and, potentially, increase in their vulnerability to drought (Bennett, McDowell, Allen, & Anderson-Teixeira, 2015; Kauppi et al., 2015). Thus, there is a need to quantify the impact of extreme climatic events on carbon dynamics in the eastern USA, particularly given that eastern U.S. forests have been sequestering 0.89 MG C/ha/yr (Liu, Loveland, & Kurtz, 2004). Our synthesis suggests the possibility of a substantial decline in carbon sequestration with drought, not only from the mortality of trees, but also with a decline in growth as observed within the south-eastern USA (Clark et al., 2016).

Our analysis of drought-induced mortality events certainly cannot identify all potential climatic drivers; some studies often point to extreme events decades before tree mortality as important factors in tree death (e.g. Berdanier & Clark, 2016; Haavik, Stahle, & Stephen, 2011; Pedersen, 1998). In addition to drought as a climatic agent of mortality, frost and foliage damage also coincided with observed tree mortality, which provides further support to our main hypothesis that extreme climatic events can synchronize disturbance in forests where canopy mortality is frequent, but asynchronous at small scales (Balch, 1927). Given that the 20th century was unusually wet across the eastern USA, our understanding of the synchrony of forest mortality from late 20th century studies is likely to be limited, because prior centuries experienced more frequent and intense droughts across this region (Pederson et al., 2015). Although the eastern USA is projected to

TABLE 1 Summary of observed elevated mortality events in eastern North America since 1913, their duration in years, associated factors and the context of drought in the years preceding each mortality event

Mortality event no.	Location (source)	Latitude, longitude (°)	Species affected	First year of observed mortality	First year of JJA precipitation departure (duration, % below average)	First year SPEI3 departure (duration, *SD* below mean)	Estimated spatial and temporal grain, along with total extent and duration (ha or km^2; years)	Other contributing factors
1	New Berlin, NY (Long, 1914)	42.6, −75.3	Examined 902 total trees; American chestnut (*Castanea dentata*) (64%) and white and red oak group trees (27%)	1913	1907 (7, 24.0%)	1912 (2, 1.40)	*c.* 16 ha; same season or within a year, possibly (only a single visit after a report of dying trees)	*Armillaria mellea* and other fungal diseases. Frost damage; two sets of leaves lost to frost. *Note*: chestnut blight (*Cryphonectria parasitica*) was not yet observed in this region
2	Bent Creek, NC (Hursh & Haasis, 1931)	35.5, −82.7	Highest mortality among the red oak group [scarlet oak (*Quercus coccinea*), black oak (*Quercus velutina*) and northern red oak (*Quercus rubra*)]; many species with reduced foliage or early shedding of leaves	1925	1922 (6, 17.6%)	1922 (5, 1.12)	Survey of 400 ha (area of the experimental forest station in 1925); 4 years (first observed in August and September 1925 and then again in September 1927 and September 1929)	April 1927, frost killed much new foliage; *Armillaria mellea*, two-lined chestnut borer (*Agrilits biliucatits*) and long-horned beetles (*Prionus* spp.) present. Shallow soils
3	Bland County, VA (Beal, 1926)	37.1, −81.1	"a tract ... which contained approximately three million feet of dead white oak"; presumed 278,709 m^2 of basal area; Oaks, mostly white oaks	1926	1917 (1, 14%) 1915 (1, 15%) 1925 (3, 20%)	1925 (2, 1.90)	"[V]alleys and hollows" within Bland County, VA (*c.* 900 km^2); same season (observed over the summer of 1926)	Severe frosts on 26 and 27 May 1925 in addition to the 1925 drought. No evidence of insects as a cause
4	Tionesta, PA (Hough & Forbes, 1943)	41.5, −79.3	Canopy eastern hemlock (*Tsuga canadensis*) and American beech (*Fagus grandifolia*) mortality	*c.* 1930	1929 (6, 20.6%)	1929 (2, 1.29)	Surveys 109 0.2 ha and ten 0.4 ha plots (*c.* 24 ha); five years (drought-mortality observations in 1929, 1930 and 1934)	
5	Pocahontas County, WV (Tryon & True, 1958)	38.3, −80.0	Scarlet oak	1953	1952 (2, 18.9%) 1955 (1, 9.4%)	1952 (2, 1.17)	"Four plots", size of plots not defined; 3 years, with surveys in August 1954 and September 1956	Sampled for oak wilt, but found no evidence as a mortality agent in 1953; secondary invaders cultured in 1954

(Continues)

TABLE 1 (Continued)

Mortality event no.	Location (source)	Latitude, longitude (°)	Species affected	First year of observed mortality	First year of JJA precipitation departure (duration, % below average)	First year SPEI3 departure (duration, *SD* below mean)	Estimated spatial and temporal grain, along with total extent and duration (ha or km^2; years)	Other contributing factors
6 6 6	North-central and North-east PA (Nichols, 1968; Staley, 1965)	41.5, −77.1	Red oak group, with scarlet oak and then black oak experiencing most mortality. Chestnut oak (*Quercus montana*) experienced mortality in presence of scale. Mortality problem "5 percent or more (commonly 20 to 50 percent) of the oaks in a unit area in a given year". Observed over *c.* 2 × 10^5 acres (1 × 10^5 ha) in north-east PA	1954 1958 1964	1951 (4, 24.1%) 1957 (1, 25.8%) 1962 (5, 34.5%)	1952 (4, 1.33) 1957 (1, 0.51) 1962 (6, 0.62)	"23 plots", size of plots not defined; 2 years (two locations in 1954 and 1955) and 6 years (1956–1961), from Staley (1965); 3–15 0.08 ha plots for each of 70 observation areas embedded in mortality areas of 12–6,000 ha over an area of ≥ 800 km^2; annual observations over 13 years (1953–1966), from Nichols (1968)	Oak leaf roller (*Argyrotoxa semipurpura*) defoliation, root rot, *Agrilus bilineatus* attacks, widespread late spring frost in 1956, 1957 in PA; 1961 frost in WV; *Asterolecanium minus* scale with chestnut oak; no pathogenic fungi cultured; shallow soils
7 and 8	Black Rock Forest, NY (Karnig & Lyford, 1968; Lorimer, 1984)	41.4, −74.0	Basal area of scarlet oak decreased from 35 to 9.7%; 13% of 0.04 ha studied had heavy mortality and losses of 20% basal area; all but one mortality scarlet oak; crown dieback and early leafdrop in shrubs noted	1966	1961 (6, 25.6%)	1961 (6, 1.09)	One 0.09 ha plot surveyed in "early summer 1967" as representative of mortality in scattered locations of southern NY in 1966–1967, from Karnig and Lyford (1968) Two 0.2 ha permanent plots; 4- to 10-year interval between surveys, from Lorimer (1984)	1962 and 1963 outbreaks of canker worms and loopers (*Paleacrita vernata* and *Erannis tiliaria*), near-complete defoliation in area; shallow soils
8	Harvard Forest, MA (Lorimer, 1984)	42.5, −72.2	Highest rates of mortality among white ash (*Fraxinus americana*), pignut hickory (*Carya glabra*), sweet birch (*Betula lenta*) and yellow birch (*Betula alleghaniensis*). Inferred rates of mortality between two censuses	*c.* 1966	1961 (6, 27.5%)	1961 (6, 0.84)	Two permanent plots of 4.02 ha total; 5-year interval between surveys, from Lorimer (1984)	Determining agents of mortality was not the intention of this study
9 and 10	Nantahala Mountains, NC (Biocca et al., 1993; Tainter et al., 1984)	35.2, −83.6	Unspecified northern red oak mortality	1979	1974 (5, 11.3%)	1975 (1, 0.67)	"a meandering transect through each of four areas", area sizes undefined; Retrospective from tree rings collected in February 1980, from Tainter (1984) "two areas in the Wayah Bald area of the Wayah Ranger District were revisited", area sizes undefined; retrospective from tree rings collected in February 1980, from Biocca et al. (1993)	Cold February in 1963, "no significant insect or disease problems which could have contributed to the decline"; "trees were likely weakened during the dry years of 1975–77 with death of a number of trees following a major drought in 1978"

(Continues)

TABLE 1 (Continued)

Mortality event no.	Location (source)	Latitude, longitude (°)	Species affected	First year of observed mortality	First year of JJA precipitation departure (duration, % below average)	First year SPEI3 departure (duration, *SD* below mean)	Estimated spatial and temporal grain, along with total extent and duration (ha or km^2; years)	Other contributing factors
11	Thumping Dick Cove, TN (McGee, 1984)	35.3, −85.9	"During an 8 year period, 26 percent of the hickory (*Carya* spp) and 18 percent of white oak (*Quercus alba*) and northern red oak (*Q. rubra*) >17 inches DBH have died". Hickories specified were *Carya ovata* and *Carya cordiformis*. Mortality to have occurred 3–4 years before 1982	1981	1980 (1, 37.6%)	1980 (2, 1.03)	"a general cruise of the study area" (40 ha area); 1 year (surveyed in spring 1982)	Defoliating insects in 1979 and 1980: spring canker-worm (*Paleacrita vernata*), linden looper (*Euranis tiliaria*) and the half-winger geometer (*Philigia titea*). Blowdown said to be another factor
12	Robinson Forest, KY (Stringer et al., 1989)	37.5, −83.2	Mortality of several species, primarily red oak group (scarlet and black oak most common), followed by hickories, white and chestnut oak. Some stands with mortality ≥ 10%	c. 1985	1983 (2, 28.1%) 1986 (3, 27.4%)	1983 (2, 1.55) 1986 (3, 1.13)	303 ha; 3 and then 2 years (drawn from the difference in photographs from a 1985 aerial survey from a fire tower and a field survey completed in 1982; aerial survey repeated in 1987 for mortality in 1987)	Mortality heavier on mid to upper xeric slopes. Two-lined borer galleries noted on all dead or declining oaks. No sign of infection or mycelia
13	Coweeta, NC (Clinton et al., 1993)	35.1, −83.5	Scarlet oak formed 44% of all gaps, followed by northern red (16%), black oak (11%) and then hickory (11%). Estimated a 293% increase in gap formation; turnover rate prior = 526 years, after = 66 years	*c*. 1987	1986 (3, 34.6%)	1986 (3, 1.32)	Nine 0.081 ha transects set 201 m apart for a real extent of 0.73 ha; 1 year (surveyed in 1988)	*Armillaria mellea* also seen throughout the study area
14	Pioneer Forest, MO (Jenkins & Pallardy, 1995)	37.3, −91.3	78.3% scarlet oak and 52.6% black oak	*c*. 1985	1983 (2, 41.8%)	1983 (2, 1.24)	62, 0.1 ha (¼ acre) plots in across three forest areas, totalling an area of 6,728 km^2; retrospective from tree rings collected in 1990 and 1991	Extreme temperatures and early spring frosts noted. Scarlet oak mortality more common in restricted rooting zones and on south- and west-facing slopes
14	Fristoe, MO (Jenkins & Pallardy, 1995)	36.9, −90.3		*c*. 1985	1983 (2, 40.6%)	1983 (4, 0.73)		
14	University Forest, MO (Jenkins & Pallardy, 1995)	36.9, −90.3		*c*. 1985	1983 (4, 35.8%)	1983 (2, 1.26)		
15	Walker Cove, NC (Olano & Palmer, 2003)	35.7, −82.3	Decline in basal area from 32.95 to 32.91 m^2/ha and density from 548 to 533 stems/ha between 1984 and 1989. "Mortality was higher during drought". *Tilia Americana* and *Fagus grandifolia* had a notable increase in rate of mortality	*c*. 1987	1986 (3, 32.8%)	1986 (3, 1.28)	19, 0.1 ha plots in a 21.5 ha forest; permanent plots re-surveyed every 5 years from 1979 to 1994	Determining agents of mortality was not the intention of this study

(Continues)

TABLE 1 (Continued)

Mortality event no.	Location (source)	Latitude, longitude (°)	Species affected	First year of observed mortality	First year of JJA precipitation departure (duration, % below average)	First year SPEI3 departure (duration, *SD* below mean)	Estimated spatial and temporal grain, along with total extent and duration (ha or km^2; years)	Other contributing factors
16	Pleasant Hill Ranger District, AR in 2000; Boston Mountain, Pleasant Hill, Bayou, and Buffalo Ranger Districts, AR in 2002 (Starkey et al., 2004)	36.1, −94.4	Red oak most severely affected in 2000. "Comparing species groups, red oaks were more severely affected across all strata than white oaks or other species—22 percent of basal area per acre with moderate to severe dieback or dead compared to 8 and 7 percent, respectively"	1999	1998 (2, 22.8%)	1998 (2, 0.68)	Seventeen stands over three districts using five basal area prism plots separated by ≥ 46 m (over *c.* 478 km^2) and a broad aerial survey of *c.* 2,428 km^2; ranging from same year to 2 years (surveys from 1999 to 2002)	Red oak borer (ROB; *Enaphalodes rufulus*) present. "ROB attacks (both old and new) were noted only on red oak species—54 percent of basal area per acre had 1 or more old attacks and 45 percent had 1 or more new attacks"
16	Potosi and Salem Ranger Districts, MO (Starkey et al., 2004)	37.7, −91.1	By 2000, "20 percent of scarlet and black oak basal area per acre dead, and 11 percent with moderate to severe decline"	1999	1999 (1, 38.3%)	1999 (1, 0.63)		"almost 45 percent of basal area per acre had over 10 attacks", with these attacks being red oak borer
17	Boston Mountains, AR (Spetich, 2004)	35.7, −93.1	Many species died, but "northern red oak snags per ha more than doubled, increasing from 23 trees per ha to 51 trees per ha respectively" 2000–2002 survey period, "red oak mortality increased 7–20 percent while white oak and other species increases were only 2–7 percent and 2–8 percent"	2001	2001 (1, 36.4%)	1998 (5, 0.66)	24, 0.3 ha plots across an area of 32 ha; 1 year (plots established in winter 2000 and re-surveyed in November and December 2001)	Largest increase in ROB attacks in moderately/severe and dead crown condition classes in the 1–10 and 11–20 attacks on trees
18	Okmulgee Wildlife, OK (Bendixsen et al., 2015)	35.6, −96.0	"Sudden and unexplained near total canopy mortality was observed over several tens of hectares of xeric oak forests in east-central Oklahoma in late summer 2008" in forests dominated by post-oak (*Quercus stellata*) and blackjack oak (*Quercus marilandica*)	2008	2006 (1, 1.4%)	2005 (3, 0.48)	53,435 random points analysed by remote sensing within 3,700 ha; 1–2 years after potential events triggering mortality	Low (closer to water), steeper, north-east to south-east slopes most common locations for mortality. Frost in 2007: "warmest March on record in 2007 followed by severe cold in early April". Opportunistic or weak pathogens isolated from some trees, *Botryosphaeria obtusa* (nine trees), *Biscogniauxia mediterranea* (six trees) and *Discula quercina* (three trees)

Note. Unless otherwise noted, mortality of affected species is reported as the percentage of trees lost. Events are numbered by first year of observed mortality and correspond to the labels in Figure 3b. JJA refers to June, July and August. SPEI3 refers to the standardized precipitation–evapotranspiration index for 3 months estimated in August (i.e., considering precipitation and temperature for JJA). A list of the data sources is given in the Appendix.

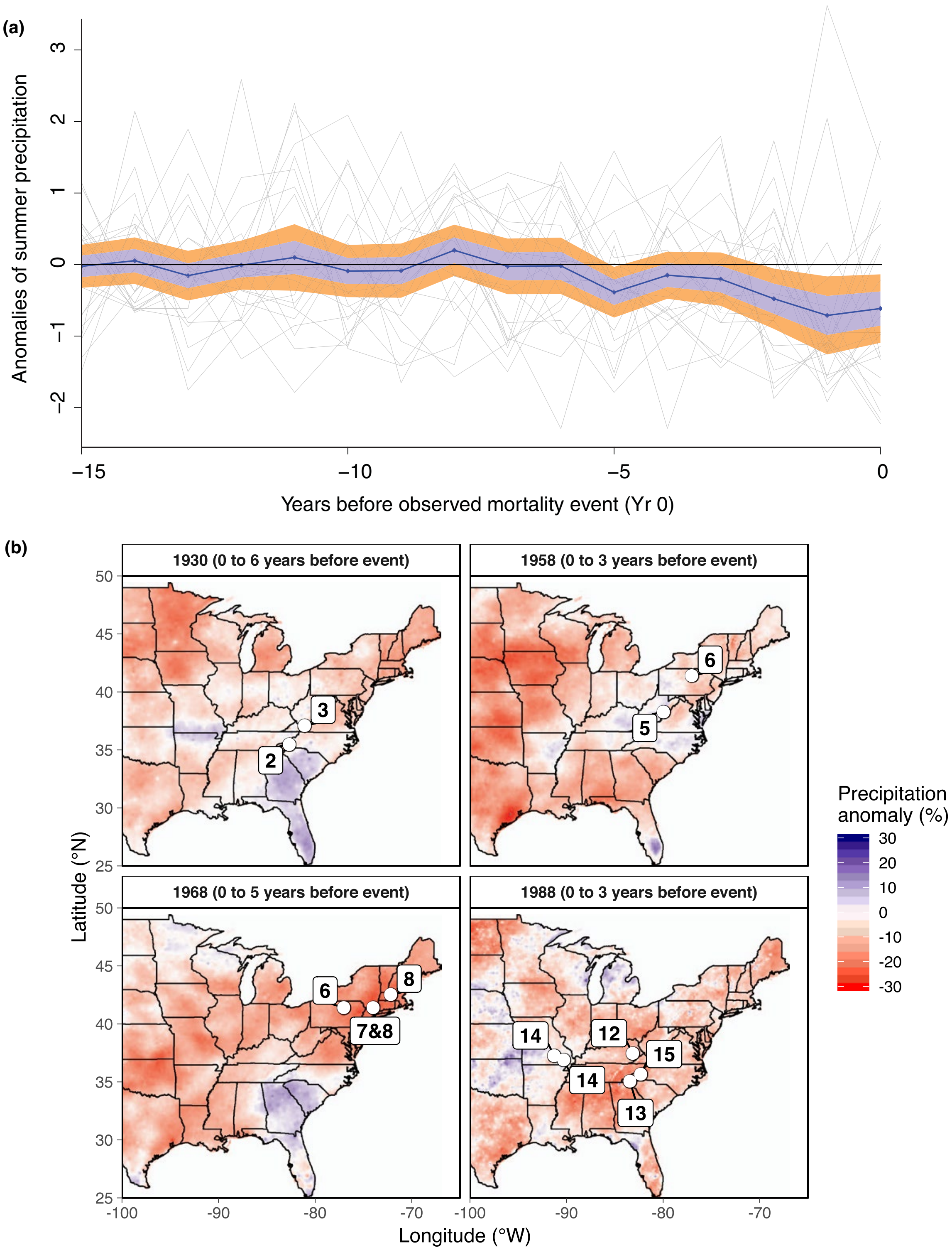

FIGURE 3 (a) Fifteen years of summer precipitation departures before the year of observed elevated mortality. Precipitation from at or near each observation was normalized to compare relative differences between regions. The blue line equals the mean departure of precipitation during and before the year of observed mortality. Blue shading represents 1 *SEM*, and orange shading represents 2 *SEM*. Each individual contributing series is shown in the background in light grey. References for each mortality event, descriptions of observed mortality, and the duration, severity and intensity of moisture conditions before and during each mortality event are summarized in Table 1. (b) Observations of elevated regional tree mortality events across eastern North America grouped by years of observed mortality. Numbers show the location of the mortality event linked to the reference in Table 1 of the Appendix. Colour layer shows the relative deviation (as a percentage) from cumulative annual precipitation for a number of years within the period before the mortality event (year 0) shown in each panel (from 0 to between 3 and 6 years). Negative values (red shades) depict droughts, and blue shades depict wet periods [Colour figure can be viewed at wileyonlinelibrary.com]

become wetter, it is also likely to experience more consecutive dry days in summer (Luce et al., 2016) that could increase the impacts of drought, imparting long-term legacies on forests. Drought has been shown to alter the rate of forest succession (Dovčak, Frelich, & Reich, 2005) and create colonization windows that affect species establishment (Bartha, Meiners, Pickett, & Cadenasso, 2003). What emerges here is the considerable insight into forest dynamics by scaling high-resolution ecological studies simultaneously across larger spatial scales and longer time-scales.

4 | UNANSWERED QUESTIONS CONCERNING THE MODELLING OF MESOSCALE FOREST PROCESSES

Similar to observational and experimental studies, the scaling of processes that influence forests is one of the most vexing challenges in developing dynamic vegetation models (Bugmann & Solomon, 2000). At the mesoscale, forest dynamics involve the birth, growth and death of trees, as drivers for either stand development or compositional change. Most individual- or cohort-based forest models implement interacting submodules to simulate tree demography through deterministic and stochastic processes (Moorcroft, Hurtt, & Pacala, 2001; Shugart, 1984; Shugart et al., 2018). These submodules are dynamically linked to simulate forest patch development processes. However, patches at different successional stages are averaged to simulate forest development at larger scales, which could mask or lead to unlikely emergent phenomena. Averaging patches presents a scaling issue that might be a shortfall in understanding potential complexities in forested ecosystems (Bugmann & Solomon, 2000; Smith & Urban, 1988).

Individual-based forest models suggest that disturbances might alter the distribution of biomass across a landscape to produce a quasi-equilibrium mosaic; however, disturbances that create large patches relative to the size of the landscape might also result in unpredictable or non-equilibrium forest dynamics (Shugart, 1984). These dynamics could involve hysteresis and other complex non-linear behaviours in transitions to alternative states (e.g., Hirota, Holmgren, Van Nes, & Scheffer, 2011). Simulations also show that species composition is altered more rapidly when these models include interactions between disturbance regimes and climate (Overpeck, Rind, & Goldberg, 1990).

To illustrate this interaction between patch stochasticity and mesoscale disturbance, we also tested the hypothesis of Balch (1927) by simulating potential natural forest vegetation for the north-eastern USA (0.5° × 0.5° grid cells extending over 2.5×10^9 m^2) using the dynamic vegetation model LPJ-GUESS (Smith, Prentice, & Sykes, 2001). The model simulates stand (i.e., grid cell) structure with gap-sized patches (1,000 m^2) and vertical structure at the cohort-level within a specified number of patches in each stand. At the patch level, stochastic processes include establishment, background mortality and a generic, patch-destroying disturbance with a return frequency of 100 years exclusive of climate factors. We ran three scenarios (1, 10 and 100 patches per stand) to examine whether climate can synchronize mesoscale dynamics in forests normally regulated by stochastic gap dynamics. Each scenario was initialized with a 1,000-year spin-up using detrended climate drivers and pre-industrial CO_2, followed by a 114-year simulation driven by observed climate data (Harris, Jones, Osborn, & Lister, 2014) and observed CO_2 concentrations from Sitch et al. (2015) for the years 1901–2014. Beginning in the year 2015, we imposed a 5-year extreme drought, with a 30% reduction in monthly precipitation relative to the 2005–2014 climatology, with a subsequent frost defoliation event, in which trees lost 70% of their leaves in 2020. The magnitude of this simulated drought and frost approximates a typical severe drought as observed from our review of tree-mortality literature along with a second predisposing climate factor providing an example of an uncommon, but realistic, climate-driven compound event in eastern U.S. forests.

The patch-level disturbance had a much larger impact on inter-annual- to decadal-scale stand dynamics in the one patch per stand simulation than the 10 or 100 patches per stand because of high stochasticity in establishment and mortality. For the entire simulation period, the one patch per stand simulation results in less stability at the landscape scale, as seen by higher variability in biomass and other variables (Figure 4). During the extreme drought scenario, simulated biomass does not vary substantially during the first 4 years of drought, showing the resilience of these forests to drought alone as a climate forcing. With the addition of frost as a subsequent climate forcing, a realistic severe drought does cause a large collapse in biomass at the mesoscale regardless of the number of patches per stand. Without this subsequent frost event, a reduction in precipitation of 75%, much greater than that found in the literature review, was necessary to reduce stand biomass across 1, 10 or 100 patches per stand. Thus, our model results clearly illustrate how compound climate extremes (Zscheischler et al., 2018) may synchronize small-scale forest gap dynamics to converge across landscapes at the mesoscale and support the hypothesis of Balch (1927).

Many scaling assumptions are also implemented in ecosystem models that compromise real-world complexity for data limitations, theoretical knowledge (or lack thereof) or computational constraints. The current generation of dynamic global vegetation models (DGVMs) simulates ecosystem dynamics across millennia and continental scales by implementing "big-leaf" canopy photosynthesis routines and "mean individual" to aggregate population dynamics for landscapes (e.g., Prentice et al., 2007). However, as we demonstrate, landscape heterogeneity is an important component of characterizing forest responses to disturbance, and the big-leaf approach may lead to a misdiagnosis of the sensitivity of ecosystems to climate extremes. An emerging group of landscape simulation models incorporates multiple scales and pulse disturbance regimes without reaching an equilibrium state (e.g., Scheller et al., 2007), also recognized by DGVM models as a key component for addressing the impacts of climate change. Mesoscale investigations can provide relevant information to improve the scaling assumptions in ecosystem models and evaluate model projections. For example, because small disturbances are frequently observed over short research periods, upscaling them over time may lead to incorrect

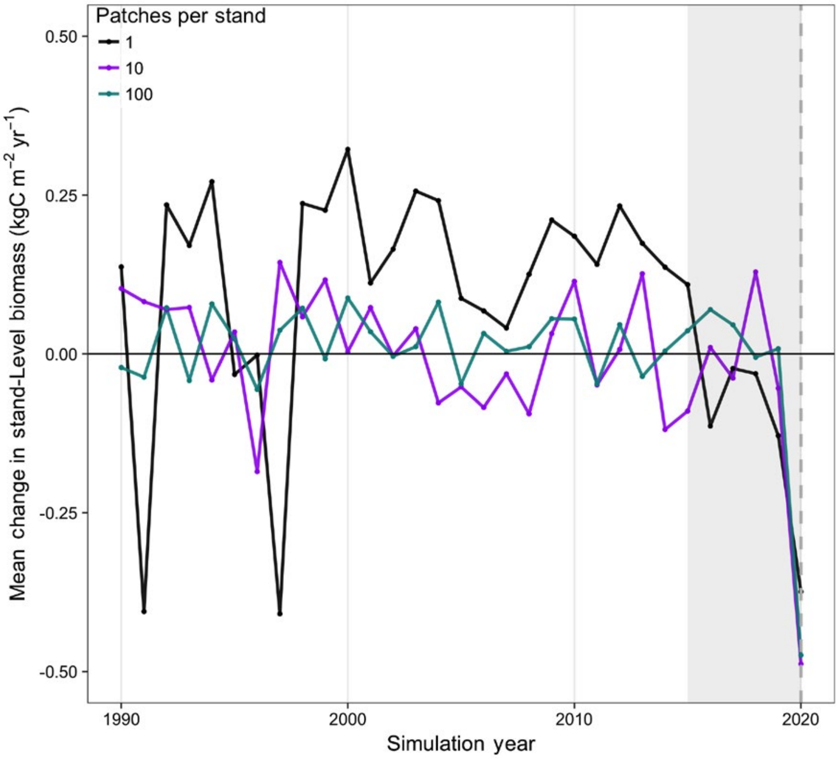

FIGURE 4 Simulation of potential forest vegetation for the north-eastern USA using the dynamic vegetation model LPJ-GUESS. A 5-year drought with a 30% reduction in precipitation was imposed, beginning in 2015 (grey shading), followed by a frost defoliation event, where trees lost 70% of their leaves in 2020 (dashed grey line) [Colour figure can be viewed at wileyonlinelibrary.com]

conclusions on the drivers of forest development (Wiens, 1989), particularly if the system and processes are non-stationary (Wolkovich et al., 2014). Different sizes and scales of disturbance would also impose different lags onto future disturbance and forest development. Likewise, Anderegg et al. (2015) reported that the duration of drought legacies simulated by models underestimated the duration estimated from tree-ring data. Upscaling from the plot scale can result in large uncertainties and have larger influences in nonlinear and somewhat chaotic systems with large variances (Ruel & Ayres, 1999). Mesoscale studies of disturbances would bridge between micro- and macroecology and assist in quantifying uncertainties associated with upscaling ecological data.

5 | CONCLUSION: OPPORTUNITIES FOR REVEALING FOREST DYNAMICS AT MESOSCALES

We have highlighted the potential for drought to affect forest dynamics at the mesoscale using observational data and simulations from the past century, insights that were not evident at smaller spatial and shorter temporal scales. These data show that large, infrequent disturbances may synchronize gap dynamics in temperate mesic forests at larger scales, a finding that was also recently documented in European forests (Senf & Seidl, 2017). We believe that even greater insight is possible from combining multi-century, site-based studies across broad geographical regions with modelling to span spatial and temporal scales further. Relatively untapped sources include historical documentary data (Mock, Mojzisek, McWaters, Chenoweth, & Stahle, 2007), historical structures (de Graauw, 2017; Trouet, Domínguez-Delmás, Pearson, Pederson, & Rubino, 2017), archaeological data (Scharf, 2014; Trouet et al., 2017), fine-scale pollen analysis (Fuller, Foster, McLachlan, & Drake, 1998) and the continued development of tree-ring networks (Babst, Poulter, Bodesheim, Mahecha, & Frank, 2017; Pederson, Young, Stan, Ariya, & Martin-Benito, 2017) along with simulation modelling (Bond-Lamberty et al., 2015).

Although determining mesoscale forest dynamics and the scales of their underlying drivers is not trivial, frameworks exist for attributing disturbance regimes to the resulting forest dynamics at various scales. Where disturbance drivers have already been characterized, researchers can infer connections from the disturbance event to the forest response using the characteristics of those disturbance regimes, including their frequency, rotation period, size and severity (Turner, 2010). For example, Vanderwel et al. (2013) used data about specific disturbance regimes in a forest inventory database in attributing regional tree mortality within the eastern USA. For environments where the drivers are less known or not as obvious, Wiens (1989) suggests an exploratory, multi-scale approach by systematically varying scales, grains and extents. Wimberly and Ohmann (2004) provide an example of this approach by statistically identifying disturbance processes that account for specific scales of forest land-cover change. Our review is limited in that we can only identify instances of drought-driven mortality post hoc from the literature, potentially underestimating the impacts of drought in these forests; nonetheless, these observations still enable the identification of mesoscale mortality patterns linked to underlying climate disturbance events using systematic drought data across the eastern USA over the past century.

Tansley (1935) postulated that vegetation might always be undergoing a state of change. More than 80 years later, ecologists are still appreciating the extent and complexity of these changes and how they vary with scale. Nowhere is this challenge greater than at the mesoscale, the nexus where local-scale field experiments and macroscale ecological observations seldom intersect. New data at these scales will inform modelling efforts on the likelihood of simulated phenomena. Characterizing these broad-scale dynamics will be important as climate change and disturbance increase impacts on ecosystems at regional to continental spatial scales (Heffernan et al., 2014). Given that climate change has the potential to create disturbances with long-lasting consequences, we need to understand the response of forests at these scales in order to adapt or mitigate their consequences (Guerrero, McAllister, Corcoran, & Wilson, 2013) in a manner that considers the linkages between spatial extent and temporal duration in forest dynamics.

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DATA ACCESSIBILITY

Data used in the results shown in Figures 2–4 are available from the Harvard Forest Data Archive at http://harvardforest.fas.harvard.edu/harvard-forest-data-archive

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BIOSKETCH

The expertise of the authors includes forest simulation modelling (individual based to dynamic global vegetation models), repeated forest surveys and dendrochronology. The authors have studied forests from individual stands to the terrestrial biosphere and have examined interconnections with climate, disturbance and the carbon cycle. These approaches have led to a common recognition of both the challenges in investigating forests at the mesoscale and the potential insights from considering forest dynamics at these longer temporal and spatial scales.

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APPENDIX REFERENCES DOCUMENTING EPISODES OF ELEVATED MORTALITY AND NUMBERED CHRONOLOGICALLY AS IN TABLE 1

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