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### SPECIAL FEATURE

# The impacts of increasing drought on forest dynamics, structure, and biodiversity in the United States

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#### Abstract

We synthesize insights from current understanding of drought impacts at stand-to-biogeographic scales, including management options, and we identify challenges to be addressed with new research. Large stand-level shifts underway in western forests already are showing the importance of interactions involving drought, insects, and fire. Diebacks, changes in composition and structure, and shifting range limits are widely observed. In the eastern US, the effects of increasing drought are becoming better understood at the level of individual trees, but this knowledge cannot yet be confidently translated to predictions of changing structure and diversity of forest stands. While eastern forests have not experienced the types of changes seen in western forests in recent decades, they too are vulnerable to drought and could experience significant changes with increased severity, frequency, or duration in drought. Throughout the continental United States, the combination of projected large climate-induced shifts in suitable habitat from modeling studies and limited potential for the rapid migration of tree populations suggests that changing tree and forest biogeography could substantially lag habitat shifts already underway. Forest management practices can partially ameliorate drought impacts through reductions in stand density, selection of drought-tolerant species and genotypes, artificial regeneration, and the development of multistructured stands. However, silvicultural treatments also could exacerbate drought impacts unless implemented with careful attention to site and stand characteristics. Gaps in our understanding should motivate new research on the effects of interactions involving climate and other species at the stand scale and how interactions and multiple responses are represented in models. This assessment indicates that, without a stronger empirical basis for drought impacts at the stand scale, more complex models may provide limited guidance.

Keywords: climate change, drought, forest dieback, forest management

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#### Introduction

Drought is a departure from the mean climate for a region and represents moisture limitation resulting from

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below-average precipitation, high temperatures, or both. At the time of this writing, drought conditions have continued over much of the continental United States (US) for up to 4 years. Combined warming and variable precipitation have increased forest drought severity in the last two decades, not only in the West, but also the South and the Lake States (Box 1). Prolonged drought affects



Box 1 Forest droughts have increased in recent decades.

**Fig. B1.1.** Cumulative drought severity index (CDSI) for forested lands from 1987 to 2013, (modified from Peters *et al.*, 2014), with selected locations of drought- and heat-induced tree mortality indicated by blue circles (modified from Allen *et al.*, 2010 and Figure 4–7 in IPCC, 2014). Numbers correspond to supporting references. (modified from Peters *et al.*, 2014) (1) Anderegg *et al.* (2012) (2) Anderegg *et al.*, (2013b) (3) Breshears *et al.*, (2005) (4) Breshears *et al.*, (2009) (5) Creeden *et al.* (2014) (6) DeRose and Long (2012) (7) Faber-Langendoen and Tester (1993) (8) Fahey (1998) (9) Fellows & Goulden, (2012) (10) Ganey & Vojta, (2011) (11) Garrity *et al.* (2013) (12) Kaiser *et al.* (2012) (13) Klos *et al.*, (2009) (14) Kukowski *et al.* (2012) (15) Macalady and Bugmann (2014) (16) Meddens *et al.* (2012) (17) Millar *et al.*, (2012) (18) Minnich, (2007) (19) Moore *et al.* (2013) (20) Olano and Palmer (2003) (21) Twid-well *et al.* (2013) (22) Williams *et al.*, (2013) (23) Worrall *et al.*, (2013).

Drought severity and frequency have been especially high during the last few decades in the West, Southeast, and Lake States, at least part of the explanation for tree mortality (Fig. B1.1). The cumulative drought severity index (CDSI) shows the sum of monthly PDSI drought classes (1 – moderate, 2 – severe, 3 – extreme) from 1987 - 2013. Values are aggregated by climate division and shown for the 21 forest cover types defined by the USDA Forest Service (2000). Locations of documented drought-related mortality generally correspond with locations of high CDSI. Compared with the previous 27-year period (1960–1987) the west saw increases in all drought classes and only minor change in the east (Fig. B1.2).

the distributions of species, the biodiversity of landscapes, wildfire, net primary production, and virtually all goods and services provided by forests. Understanding how climatic changes already in progress will affect forests can help us anticipate some of these broader impacts. The synthesis that follows finds that vulnerabilities extend beyond the recent well-publicized forest diebacks in western states to include perhaps all US forests.

Our summary of drought effects emphasizes the fundamental scale for both management and community ecology, the forest stand (O'Hara & Nagel, 2013). We build from what can be learned about climate effects on individual trees, but our principal goal is to anticipate consequences for forest structure and composition, the *size–species distribution* (SSD; Box 2). The SSD is the distribution of trees across species and size classes. The SSD results from interactions of individuals, as each tree responds to local conditions and weather. Competition and climate affect the species and size classes that make up stands in different ways. There is feedback – the structure itself determines how the SSD will respond to drought, through shading and competition for soil moisture. Biogeographic patterns in SSD emerge from these individual responses and interactions with others. Management aims to modify SSDs (e.g., targeted thinning and regeneration) to meet specific resource objectives. However, because SSD responds to climate change as a joint distribution of individuals of many species and size classes, our ability to anticipate impacts and offer solutions to forest managers has been challenged.



Severe multiyear drought episodes in the west are linked to drought-related tree mortality. There are fewer documented examples of recent drought-induced tree mortality in eastern US forests. Note that the map of cumulative drought over 27 years does not always capture short-term intense drought events.

This synthesis of current understanding begins with a summary of the extensive but mostly indirect evidence, from studies of individual trees to forest stands, across landscapes and regions, from short-term observations to the paleoecological record. We consider both the responses to individual drought events and the effects of conditions that could be more arid on average than today. Then, we compare and contrast evidence available at the individual tree and stand scales, including why the latter is more critical, but harder to obtain. This is followed by a summary of what has been learned from that evidence for forest stands and for biogeography and how management practices might adapt to more frequent drought. Finally, we address critical research gaps between our growing knowledge on individual tree responses (in contrast to the stand scale) and where the relevant forecasts are needed. Recommendations include the assembly and parameterization of models based on SSD data capable of predicting at the SSD scale.

## Consequences for forest stands: individual responses translate to abundance and size structure

Not surprisingly, the effects of drought on forest stands are difficult to anticipate due to the novelty of projected new climates and the complexity of interactions across

the SSD, including migration. Furthermore, the additional complexity and nonlinear responses associated with forestry practices and how they influence micro climate are also poorly understood (e.g., Bright et al., 2015). Changing temperatures and precipitation patterns will produce novel combinations of drought frequency, intensity, and seasonality (Wehner et al., 2011; Dai, 2012). Tree populations can disperse and adapt to local climates, including drought stress (Savolainen et al., 2007; Aitken et al., 2008; Montwé et al., 2015). As tree populations arrive in new locations, they interact with existing populations and form new communities. Some will outrun mutualists, competitors, and natural enemies and encounter new ones - processes that are too slow, too small, or too large to observe directly and are therefore difficult to study with experiments. Much of what is known relies on observational data or is inferred from model simulations, both of which provide valuable insights and have inherent limitations.

The most striking result from this review was the large gap between knowledge of drought impacts on individual trees (much) versus responses of forest stands (almost none). To see why individual responses do not readily extrapolate to the SSDs of stands (Box 2), consider how the SSD mediates a climate response. For codominant trees in crowded stands (trees with crowns

#### Box 1 Continued.

Box 2 Moisture and size-species distributions (SSDs)

## How can the effects of drought on forest structure and diversity be quantified? Conversely, what can structure and diversity tell us about past and potential future responses?

Such questions require effective summaries of how temperature, precipitation, and day and season length together influence forest demography – changes in the size–species distribution (SSD) of stands. Annual temperature and precipitation partly explain biodiversity and productivity gradients at subcontinental scales. But their combined effects depend on stand structure and on seasonal timing, more like the hydrothermal surplus and deficit in (Fig. B2.1), the degree hours during months with positive and negative water balance, respectively. Unlike annual values HTS and HTD describe the seasonal convergence of factors that affect competition between size–species classes. They differ from traditional monthly water balance variables (PDSI and Thornthwaite) by including day length, long in the north during the growing season. High temperatures and precipitation contribute to long, warm, wet growing seasons along the Gulf Coast. The resultant high HTS values extend up the moist southern Appalachians, declining to the north and west, but different from either temperature or precipitation alone, in part due to summer deficits. The HTD is especially large in the Piedmont Plateau, Coastal Plain, and western Gulf Coast. The length of the growing season is short in the northern USA, but during the growing season days are long. At this time, moisture is more available in the Northeast than the Upper Midwest.



**Fig. B2.1.** Size–species structure trends with moisture surplus (number of degree hours at positive) and negative (deficit) water balance. Size–species distributions (SSD), shown for four different regions, reflect climate differences and stand history. Dark colors indicate high density of a size–species class, and *vice versa*. Species are in the same order in all graphs. Surplus and deficit both reach maximum values near 3000 degree hours, but in different locations. With sufficient moisture, high temperature (up to a point) increases tree growth and survival. Long days and growing seasons combined with moisture benefit species capable of exploiting these conditions in competition with individuals of other species. Conversely, a large number of degree hours at negative water balance benefits species capable of tolerating drought. In the southeast, surpluses and deficits are both common. The Upper Midwest has much lower precipitation, but also lower temperatures and shorter growing seasons. The Northeast benefits from infrequent deficits, despite lower temperatures. (From Clark *et al.*, 2015).

The hydrothermal surplus and deficit (Fig. B2.1, B2.2) and PDSI (the basis for CDI of Box 1) are two examples of variables used to explain forest properties. Note agreement between CDI (Fig. B1.1) and HTD (Fig. B2.1) in the south, but disagreement in the Upper Midwest. One reason for this difference is the fact that CDI counts every month when PDSI is low, progressively amplifying their effects from month to month, whereas HTD considers the entire growing season as a unit.

#### Box 2 Continued.



**Fig. B2.2.** Deficits commonly develop throughout the eastern US each growing season, particularly in the Midwest and southeast. At left is the difference between surplus and deficit (black isohydrotherm is drawn at -1000 degree hours) from 1970 to 1985. The recent shift to larger deficits is nearly ubiquitous in the eastern USA (black line is drawn at zero difference before and after 1985). (From Clark *et al.*, 2015).

Perhaps most important are changes in surpluses and deficits, shown as a different map in Fig. B2.2. Despite the fact that deficits dominate in specific regions (the west and southeast), forests throughout the eastern USA are exposed to increasing deficits (Fig. B2.2 right).

The size–species distribution (SSD) is a *stand-level variable*, a distribution of species and sizes, related through history, climate, and competition (histograms in Fig. B2.1). Knowledge of the SSD is required for understanding demography, biodiversity, competitive interactions, fuel structure, and response to moisture stress. SSDs are a focus of management practice (Section 5). For a given stand, there is a distribution of stems across species (vertical axes) and size classes (horizontal axes). Disturbance and succession affect the species composition of large and small size classes. Advance regeneration in small classes provides clues to future stand composition. SSDs vary geographically with climate, soils, and over time. For example, species present in the largest size classes can have disproportionate access to light and moisture, thereby suppressing competitors. Crowding affects canopy architecture of individuals, thus influencing their vulnerabilities to drought (e.g., Fig. 7). Thus, different SSDs are expected to respond to drought differently. For this reason, physiology and tree-ring studies of individuals do not directly translate to the forest stand. Thus far, models used to anticipate forest response to drought are based on estimates of how individuals respond to climate. We suggest new efforts to quantify the SSD response (Section 6).

in the main canopy), growth and mortality are dominated by competition. Canopy individuals that otherwise might respond positively to a moist growing season are constrained by competing neighbors that also benefit. At the stand level, mortality can increase as a result of favorable conditions - climate and site conditions that benefit individual tree health can increase stand mortality rates, depending on the SSD (e.g., Clark et al., 2014b). Mechanistically, this positive relationship arises because self-thinning is driven by growth – the faster the growth, the sooner the resource limitations are reached, and the higher the mortality rate (Assmann, 1970). Conversely, drought that depresses growth of individual trees can also decrease crowding pressure by slowing the rate of resource consumption. Unfavorable climate effects could be mitigated by stand characteristics through the active manipulation of stocking (e.g., thinning) or supplementation of limiting resources (e.g., irrigation) (D'Amato *et al.*, 2013; Grant *et al.*, 2013; Erickson & Waring, 2014; Dobrowski *et al.*, 2015).

The knowledge gap between individual trees versus stands is important because ecologists and foresters more often need to understand and predict responses of stands than individual trees. The gap comes from the challenge of observing and estimating whole stand responses, and it helps to explain why models for stands rely on parameters from individual trees. Using individuals to predict stands is an example of 'Simpson's Paradox' or the 'ecological fallacy'. This approach does not permit probabilistic prediction, because individuals within an SSD are interacting with one another.

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Their joint distribution of responses can only be predictive if it is observed and estimated as a joint distribution. For example, in contrast to codominant trees that experience high competition for light, the tallest (dominant) trees with emergent crowns may respond more directly to climate. The rare individuals that make up the right-most diameter extremes (largest trees) in Fig. B2.1 are the focus of many tree-ring studies, but they rarely appear in small (0.0672-ha) Forest Inventory and Analysis (FIA) plots (note that trees are sampled on the larger 0.4-ha plots in Western states). Best represented in plot-based studies are the smallest size classes, which, in crowded stands, can have growth rates that are limited by both light and moisture. The large number of positive interactions between light and drought results from the fact that individuals not severely light-limited can respond most to climate variation (Clark et al., 2014b).

#### Tree growth and mortality patterns in the eastern USA

Despite recent attention to large diebacks in the west, eastern forests are also vulnerable, not only in upland habitats (Abrams, 1990; Graumlich, 1993; Pederson et al., 2012a) but also in bottomlands and coastal wetlands (Stahle & Cleaveland, 1992; Cook et al. 1999). Even where drought does not directly kill trees, the effect of reduced vigor on competitive ability affects forest composition and structure. The question is, which effects will be most severe, how, and on which parts of the landscape? After all, the growth-related drought responses of tree species are diverse (Fig. 1). For example, the drought sensitivity of some pine species is high in the southeastern U.S. region (Schumacher & Day, 1939; Cook et al., 2001; Henderson & Grissino-Mayer, 2009; Clark et al., 2014b), while growth of many nonoak hardwoods shows intermediate drought sensitivity (Klos et al., 2009; Clark et al., 2013; Pederson et al., 2013). Combined high temperatures and low moisture could benefit oaks (Quercus spp.), as drier than normal conditions tend to have less impact on oak growth rates (Elliott & Swank, 1994; Klos et al., 2009; Clark et al., 2011, 2014a; Brzostek et al., 2014), perhaps related to physiology and rooting (Abrams, 1990; Abrams & Kubiske, 1990; Iverson et al., 2008b). Hence, with increasing drought in the Upper Midwest and Lake States, drought-tolerant pines and oaks may replace drought-intolerant quaking aspen (Populus tremuloides), bigtooth aspen (Populus grandidentata), paper birch (Betula papyrifera), and some boreal and lowland conifers (Scheller & Mladenoff, 2008; Handler et al., 2014).

Opportunistic reports of mortality following drought are common (Hough & Forbes, 1943; Parshall, 1995), but connections between drought and tree death are more difficult to quantify than those for tree growth. Extended morbidity can precede death, a legacy of low vigor spanning decades (Wyckoff & Clark, 2002; Anderegg et al., 2013a,b; Berdanier & Clark, 2015), potentially related not only to repeated drought (Pedersen, 1998; Voelker et al., 2008; Pederson et al., 2014), but also to other risk factors that occur during sample intervals, which might be from one to 10 years in many studies. Attribution of death to drought is thus challenging. A synthesis of plot data spanning 50 years, four Midwest states, and 48 000 stems did not find a link between precipitation and mortality, highlighting instead the importance of competition (Yaussy et al., 2013). A number of large studies using FIA data suggest geographic relationships between drought and mortality. Climate variables emerge as weak predictors of mortality at best (Lines et al., 2010; Dietze & Moorcroft, 2011; Gustafson & Sturtevant, 2013), and patterns may be hard to interpret. For example, a tendency toward higher mortality rates in warm climates is expected on the basis of higher productivity in warm climates - partly explained by the fact that high growth is attended by rapid thinning (Assmann, 1970; Clark, 1990). This relationship between temperature and mortality does not necessarily constitute a threat of climate change - geographic variation in mortality rate with average temperature need not indicate vulnerability to high temperature (Zhu et al., 2014).

The interactions involving competition and drought could contribute to habitat shifts. A positive interaction between a drought index such as Palmer Drought Severity Index (PDSI) (low PDSI indicates drought) and local moisture status or light availability means that the largest response to PDSI occurs on moist sites and high light (low competition), respectively. Klos et al.'s (2009) suggestion that dense stands may experience the most severe impacts agrees with the positive interaction between drought and competition found at the stand level in the upper Midwest (Fig. 2) and at the tree scale for many species in the eastern USA (Clark et al., 2011, 2014b). The latter study further found positive interactions between drought and local moisture status for many species (e.g., Fig. 3). The possibility that moist sites will provide refuges if climate becomes more xeric (e.g., Frelich & Reich, 2010) represents a negative interaction, with the largest response to drought on dry sites. The alternative positive interaction could result from competition - the water-demanding species on wet sites fully utilize abundant moisture supply and thus are especially vulnerable when moisture availability declines. Large growth and fecundity responses to drought in southeastern forests could occur initially for

![](_page_6_Figure_1.jpeg)

Fig. 1 Growth responses to summer drought on mesic sites in Kentucky, from 1796 to 2005. Average tree growth (orange line with circles) correlates with an independent reconstruction of summer PDSI (June, July, August) (blue line). The inset demonstrates the relation of annual radial increment of trees on mesic sites to 200 years of estimated hydroclimate (r = 0.545). Chronologies from mesic sites include the following species: *Tsuga canadensis, Liriodendron tulipifera, Quercus muehlenbergii*, and *Fraxinus quadrangulata*. Despite differences in collections and land-use histories, they show a similar change in direction during specific PDSI conditions, positive growth during wet conditions (PDSI  $\geq$  2) and *vice versa* (adapted from Pederson *et al.* (2012a,b).

trees at high moisture levels, where leaf area, and thus, moisture demand is greatest (Fig. 4). Mesic sites might see large transitions due to the fact that they also support sensitive species dependent on abundant moisture (Elliott & Swank, 1994; Clark *et al.*, 2014b). Still another possibility is that sensitivity could be highest on sites of intermediate moisture (e.g., Dormana *et al.*, 2013). Moreover, the sign of the interaction between drought index and local drainage might shift with time, from short-term positive (loss of moisture-demanding species on mesic sites) to negative (eventually the moist sites provide refuges for some species). Sequential drought will have impacts that differ from individual droughts as stands progressively respond (Miao *et al.*, 2009).

Other soil properties can strongly influence the severity of drought. For example, fragipan soils in some pine flatwoods of the West Gulf Coastal Plain restrict root depth and access to deep moisture (Wackerman, 1929; Rahman *et al.*, 2006). Drought may also operate differently in stands of different density and age (Esper *et al.*, 2008). If leaf area decreases during drought, then understory irradiance increases. For trees beyond the seedling stage, Luo & Chen (2013) argue that warming has the greatest impact on mortality of young trees, but there are also reports that old trees show the strongest responses to climate for *Picea glauca* (Wang *et al.*, 2006) and *Quercus robur* (Rozas, 2005). Klos *et al.* (2009) likewise found that the effects of drought on growth and survival might increase with stand age in the southeast. Due to the large sample interval in many climate-mortality studies, evidence is equivocal (see above). The disparate results could also indicate the importance of unobserved variables that covary with density and stand age (D'Amato *et al.*, 2013).

Even in the eastern USA, drought can interact with fire to shape forest dynamics. Over the last century, much of the eastern USA has experienced pluvials rather than megadroughts (Stahle *et al.*, 1988; Stahle & Cleaveland, 1992; Booth *et al.*, 2006, 2012; Cook *et al.*, 2010; McEwan *et al.*, 2011; Pederson *et al.*, 2013), but fires can occur even during brief periods of low precipitation, high temperatures, or both (Clark, 1989; Lynch & Hessl, 2010; Lafon & Quiring, 2012). Excluding fire has long been a management priority of many landowners and agencies. If this history of fire suppression is responsible for reduced oak regeneration in the east, then climate trends otherwise favorable for oak may be offset by fire suppression. However, evidence that temperate forest stands may

![](_page_7_Figure_1.jpeg)

**Fig. 2** Hypothetical zones of drought susceptibility within a size/density management diagram for red pine, where the A line represents conditions approaching the maximum size/density combination for a population and the B line represents the lower limit of full site occupancy by trees. Trees may be susceptible to drought-induced growth declines and mortality in two size/density situations, 1) at high-density conditions approaching the maximum size/density relationship, and 2) at low-density conditions conducive to the development of high levels of leaf area that promote canopy and root architecture that can put individual trees at risk. Photographs correspond to populations with size/density conditions that are highly vulnerable to drought impacts.

see a long-term increase in oaks (Bachelet *et al.*, 2003; Clark et al., 2014b) presents an apparent paradox, in light of the fact that oak recruitment has declined in many regions (Abrams, 2003; Fei et al., 2011). Fire suppression can lead to a 'mesophication' as forest canopies close (Nowacki & Abrams, 2008) and may explain why oak regeneration appears to decline relative to that of red (Acer rubrum) and sugar (Acer saccharum) maples in recent decades (Abrams, 1994, 1998; Hutchinson et al., 2008; Iverson et al., 2008a; Fei et al., 2011; Brose et al., 2013). A decrease in flammability may have followed the loss of American chestnut (Castanea dentata) from eastern forests (Engber & Varner, 2012; Kreye et al., 2013), although human increases in ignition, alteration of fuels, and active suppression make it difficult to characterize presettlement fire regimes (Clark & Royall, 1996; Parshall & Foster, 2003; Guyette et al., 2006).

Taken together, many species are vulnerable to drought in eastern forests. How this vulnerability at the individual scale translates into future forest composition and structure remains uncertain. For instance, the combination of climate, land-use, plant–animal interactions, and fire suppression may have contributed to recent maple recruitment, but this could be reversed by increasing drought (Belden & Pallardy, 2009; Woodall *et al.*, 2009; McEwan *et al.*, 2011).

#### Tree growth and mortality patterns in the western USA

Unlike the east, where drought effects on forest stands are less well documented than the physiological responses of individual trees, the west provides alarming examples of widespread stand replacement, directly or indirectly related to the recent combination of drought and warmer temperatures - 'hotter drought' (Allen et al., 2015). Stand- to region-level consequences of hotter drought and forest dieback in the west are now well documented (e.g., Breshears et al., 2005; van Mantgem et al., 2009; Worrall et al., 2013) (Box 1). Extensive drought across much of the western USA and adjoining Canada coincides with declining tree growth, often followed by mortality (Allen et al., 2010; Williams et al., 2013; Hicke et al., 2013; Joyce et al., 2014; O'Connor, 2013; Peters et al., 2014, 2015).

![](_page_8_Figure_1.jpeg)

**Fig. 3** A joint distribution of three demographic responses is obtained when all responses are fitted simultaneously, as part of the same model. This example shows interactions that control the combined response of *Pinus taeda* to winter temperature (above) and summer PDSI (below) against light availability. Effects differ for growth and fecundity, in juveniles and adults. Amplifying positive interactions (growth) and buffering negative interactions (fecundity) are both evident. In all panels, contours increase from low at lower left to high at upper right (from Clark *et al.*, 2014b).

Increased vulnerability of trees and forests to water stress and mortality risk from warmer droughts is a global phenomenon, well illustrated in the western U.SA. (Allen et al., 2015). High temperatures can increase drought-induced mortality in piñon (Adams et al., 2009) and are especially challenging for seedlings (Kolb & Robberecht, 1996; Chmura et al., 2011). In Arizona and New Mexico, high temperatures combined with droughts coincide with widespread mortality of mesic montane tree species (Mueller et al., 2005; Gitlin et al., 2006; Williams et al., 2010; Ganey & Vojta, 2011) and patchy die-offs in Pinus edulis (Breshears et al., 2005, 2009). Warming is considered most important for seasonal soil water balance due to changes in snowpack dynamics or evapotranspiration (Williams et al., 2013). It contributes to the growth and geographic expansion of insect pest populations (Bentz et al., 2010; Williams et al., 2013; Fig. 5). Varying water deficits appear to be primary drivers of variation in tree recruitment and mortality (Rapacciuolo et al., 2014). A combination of high temperatures during the growing season and low winter-spring precipitation of the previous year can explain much of the variation in conifer growth rates in the southwest (primarily Pinus edulis, Pinus ponderosa, and Pseudotsuga menziesii) (Williams et al., 2013) and northern California (Abies concolor, Abies magnifica, Pinus lambertiana, Pinus ponderosa, and Pseudotsuga menziesii) (Yeh & Wensel, 2000). Similar relationships between moisture, heat, and growth variation are observed for Picea glauca in interior Alaska (Barber *et al.*, 2000), for *Pseudotsuga menziesii* in the central and southwest Rocky Mountains and Mexico (Chen *et al.*, 2010), and for *Populus tremuloides* in western Canada (Hogg *et al.*, 2005). Responses suggest declining growth rates with increasing drought conditions for the western USA during the 21st century, particularly for the southwestern USA (Williams *et al.*, 2010, 2013).

Interactions between drought, fire, climate change, and human fire suppression have altered SSDs in forests throughout the western USA (Westerling et al., 2006; Allen, 2007; Littell et al., 2009; Joyce et al., 2014). Fire suppression has led to increased fuel accumulation and a shift to high-density/small diameter stands, from the foothills to the subalpine zone of the Sierra Nevada (Parsons & DeBenedetti, 1979; Lutz et al., 2009; Dolanc et al., 2013) and extensive semi-arid woodlands and ponderosa pine in the southwest (e.g., Covington & Moore, 1994; Brown & Wu, 2005; Mast & Wolf, 2006; Fulé et al., 2009). Historically low-density forest conditions resulted from the direct and indirect effects of low moisture (McDowell et al., 2006). The modern shift to highdensity forests exacerbates moisture stress during drought. High-severity fires now occur in stands that historically supported frequent, low-severity fires (Barton, 2002; Savage & Mast, 2005; Goforth & Minnich, 2008; Savage et al., 2013), and recent highseverity fires are strongly correlated with forest drought stress (e.g., Fig. 5). Projected warming in the

![](_page_9_Figure_1.jpeg)

**Fig. 4** Drought effects on growth interact with soil moisture. For *Ulmus americana* on the Piedmont Plateau in NC, growth is most sensitive to drought on wet sites at low elevation (see contours), potentially contrary to the intuition that xeric stands are greatest risk of drought. This is a positive moisture index/PDSI interaction – the largest response to PDSI occurs on moist sites (From Clark *et al.*, 2014b).

Yellowstone region could increase fire frequency to the point where lodgepole pine (*Pinus contorta*) stands, historically characterized by infrequent fires, are replaced by woodland or nonforest vegetation (Westerling *et al.*, 2011).

Because drought weakens tree defenses, it also makes trees vulnerable to insect attacks and pathogens (Raffa et al., 2008; Weed et al., 2013). The interaction between recent drought and bark beetle outbreaks is clear in the southwest, where severe drought conditions from ca. 2000 to 2013 have resulted in widespread tree mortality from bark beetles (Negrón et al., 2009; Williams et al., 2010, 2013; Ganey & Vojta, 2011). Defoliator populations may also benefit from drought-stressed trees, particularly on xeric sites (Weed et al., 2013). However, resistance to insect herbivory may reduce drought tolerance and increase mortality during subsequent drought events (Sthultz et al., 2009). Early successional species that colonize after bark beetle infestations or wildfire may increase in some areas (Pelz & Smith, 2013; Shinneman et al., 2013).

![](_page_9_Figure_5.jpeg)

Fig. 5 Forest productivity and mortality and the Forest Drought Severity Index (FDSI) (see text) for the southwest USA (Arizona, New Mexico, and southernmost portions of Utah and Colorado). (a) Annual average late-June to early-August NDVI. (b) Percent standing dead trees in FIA for the three most common southwestern conifer species. (c) Aerial estimates of area having 10 trees per acre killed by bark beetle attack. (d) Satellitederived moderately and severely burned forest and woodland in the SW. Inset shows percent of years within a given FDSI class that were top 10% fire-scar years during AD 1650–1899 (the horizontal line is at the expected frequency of 10%, bins are 0.25 FDSI units wide). Note the inverted axes for FDSI in b–d. (from Williams *et al.*, 2013).

Large diebacks have the potential to change species distributions more rapidly than has occurred in the past (Swetnam & Betancourt, 1998; Gray et al., 2006; Fellows & Goulden, 2012; Millar et al., 2012). Drought-induced mortality in the 1950s is probably responsible for extensive upslope retreat of ponderosa pine in New Mexico (Allen & Breshears, 1998) and Juniperus deppeana in southeastern Arizona (Brusca 2013). Recent episodes of drought-induced mortality in California extend from high-elevation Pinus albicaulis in the Sierra Nevada (Millar et al., 2012) to southern California conifers (Minnich, 2007). Arapid redistribution of coniferous and broadleaf species occurred in southern California mountains during droughts of the early 2000s (Fellows & Goulden, 2012). The extent and severity of drought impacts on western forests raises concern for biodiversity and carbon storage (Gonzalez et al., 2015). The widespread nature of recent drought and its impacts suggest transformations that will have far-reaching consequences.

#### Critical impacts of drought on tree recruitment

The preceding summaries of eastern and western forests focused on growth and mortality responses to drought rather than on recruitment, mostly because the relationship between drought and recruitment is poorly understood. An example of this limited understanding is the recent decline in oak regeneration (Fig. 6) at a time when the eastern USA has experienced higher moisture deficits than the two preceding decades (Fig. B2.2). Recruitment warrants special consideration, both for its central role in decadal-scale responses to drought and because it has been especially difficult to study and predict across multiple scales (Dobrowski et al., 2015). Most empirical research on climate effects on seed production are limited to a few years (or less) and a few small study plots (Clark et al., 1999). Some of the longer studies focus on interannual variation, but few provide evidence for decade-scale effects of increasing drought.

Drought influences tree recruitment (and therefore future forest composition) through numerous mechanisms. For some species, drought severely curtails fecundity, limits seed germination, and increases the mortality of shallow-rooted seedlings. Drought effects on fecundity are further complicated by feedbacks with other factors that drive masting cycles, seed predation, and disturbance regimes that disproportionately impact new germinants. Germination, establishment, and early survival are especially susceptible to environmental variation (Grubb, 1977; Harper, 1977; Silvertown, 1987; Ibáñez *et al.*, 2007). Susceptibility of juvenile trees may be particularly acute in dry regions where recruitment is already episodic (Brown & Wu, 2005; Jackson *et al.*, 2009). High mortality of seedlings suggests a bottleneck on population growth rate, but direct evidence for its effects on fitness of many interacting species is lacking.

The development of moisture limitation over successive years appears especially important for fecundity. In general, female function in trees is often stimulated by resources, including moisture (Perez-Ramos *et al.*, 2010), CO<sub>2</sub> (LaDeau & Clark, 2001), and light availability (Clark *et al.*, 2014b). Seed production of many species shows positive interactions between moisture and light, with trees at high light levels showing the greatest response to moisture availability (Clark *et al.*, 2014b). Warm, dry weather can be beneficial during flower induction the year before seeds ripen (Pucek *et al.*, 1993; Houle 1999), a situation imposed artificially by water restriction in some fruit crops (Owens 1995). This effect may be enhanced if dry conditions follow a wet year (Piovesan & Adams, 2001). Drought-induced

![](_page_10_Figure_6.jpeg)

**Fig. 6** New recruits to FIA plots are relatively rare for oaks (upper panels) in comparison with other species having similar abundances in adult size classes (below). This comes at a time when moisture deficits are becoming more severe throughout the east (Fig. B2.2) and despite the fact that many models predict increasing oaks. Species are *Quercus alba* (querAlba), *Q. rubrum* (querRubr), *Liquidambar styraciflua* (liquStyr), and *Acer saccharum* (acerSacc). Grey symbols indicate presence of adults. Sizes of red circles are in proportion to density of new recruits. When taken as a fraction of sites where adults occur, 98% quantiles for abundances of new recruits on a per-ha basis is zero for *Quercus alba* and *Q. rubrum*, 356 recruits for *Liquidambar styraciflua*, and 23 for *Acer saccharum*.

increases in fecundity may be followed by reduced seed production up to several years thereafter (Innes, 1994; Bréda *et al.*, 2006). Increases in late summer temperatures may negatively affect seed cone initiation, which for piñon pine led to a 40% reduction in seed cone production over the past 30 years (Redmond *et al.*, 2012). Furthermore, year-to-year volatility and high spatial variation that comes with the many feedbacks involving weather, competitors, fungal symbionts, cone and seed insects, and pathogens (e.g., Bell *et al.*, 2014) make this response difficult to quantify.

Interactions involving drought and the biotic environment contribute to recruitment variation following disturbance, for example, canopy gaps, fires, landslides, ice storms, timber harvesting, and pest outbreaks (e.g., Savage *et al.*, 1996; Brown & Wu, 2005; Pederson *et al.*, 2008), and they affect composition, structure, and function for many years (Cooper-Ellis *et al.*, 1999; Dietze & Clark, 2008; Kayes & Tinker, 2012). Examples of the interactions that can occur between disturbance and moisture availability include the increased recruitment near the prairie-forest ecotone in Minnesota during the 1930s drought (Shuman *et al.*, 2009).

Interactions involving moisture availability and pathogen attack are especially important at the recruitment stage. Seedling mortality during the first year can be high due to damping off, often most severe in shaded understories (Hood et al., 2004; Ichihara & Yamaji, 2009). Moist conditions that promote fungal infection (Desprez-Loustau et al., 2006) can also benefit the host plant (Hersh et al., 2012). Combined effects may depend on the pathogen's mode of attack and on the degree of host stress (Desprez-Loustau et al., 2006; Jactel et al., 2012; Oliva et al., 2014). Many pathogens can tolerate a wider range of water stress than the plants they infect, and the combination of pathogen infection and moisture stress on host trees can increase disease severity (Desprez-Loustau et al., 2006). Drought conditions can increase damage from secondary pathogens (those infecting tissue in poor physiological condition), while reducing damage from primary pathogens (those infecting healthy tissue) (Jactel et al., 2012). Long term the SSD may also be impacted by nurse-plant availability to aid persistence of some species. Piñon pine recruitment in the southwest may benefit from high canopy cover following disturbance in areas otherwise predicted to become juniper dominated woodlands (Redmond & Barger, 2013; Kane et al., 2015). Sugar and Jeffrey pine recruitment in western Nevada also benefits from nurse plants and soil water availability (Legras et al., 2010).

Postfire recruitment may be particularly susceptible to drought conditions and lead to recruitment failures or unacceptable reductions in regeneration densities. For example, Feddema et al. (2013) and Savage et al. (2013) predict that ponderosa pine regeneration following high-severity fire will decline on dry sites when fires coincide with drought. Recruitment failures and conversion to shrublands or grasslands are common following recent high-severity fires in the southwest (Roccaforte et al., 2012; Savage et al., 2013). The use of artificial regeneration (planting or direct seeding) offers a potential solution to some of the recruitment failures that have arisen following catastrophic fires and the loss of local seed sources (e.g., Haire & McGarigal, 2008; Zhang et al., 2008; Feddema et al., 2013; Ouzts et al., 2015). However, planting must be done to match seedling genotypes and species for given locations (e.g., Blazier et al., 2004; Will et al., 2010), especially if done in the midst of a long-term or deepening drought. For example, the use of more expensive containerized nursery stock (Nilsson & Örlander, 1995; Grossnickle, 2005) or tree shelters for established seedlings (Taylor et al., 2009) on drought-prone sites may be necessary. If bare-root seedlings are to be planted, those with large root systems (e.g., shoot:root ratios below 2 : 1) should be used (Haase & Rose, 1993; Pinto et al., 2012) to help reduce drought losses.

#### Scale-dependent consequences of drought

Understanding the dynamics of drought and forests at one scale does not mean the results can be directly scaled up or down. Gene flow and conservation efforts that span landscapes or regions can influence species composition over scales that are hard to detect at in stand or individual responses. Likewise, interactions that occur within stands mean that stand-level responses to drought will not necessarily agree with studies of individual growth and survival. Said another way, responses of individual trees at low moisture availability do not tell us how the abundances of different species will change as a result of drought. As an example, the behavior of SSD under drought conditions depends on how individual trees responses translate to population growth rates, each population being an aggregate across individuals of all size classes, competitive environments, and microhabitats (Box 2) and subject to population constraints (e.g., ability to disperse across landscapes) and attributes such as genetic diversity. Species that can tolerate xeric conditions might progressively increase in abundance within stands subjected to frequent or persistent drought and, in turn, make lower transpiration demands. Thus, the moisture for which trees compete depends in part on competition feedback (D'Amato et al., 2013).

Attempts to anticipate the effects of increased drought on local or regional species diversity highlight

the challenges of extrapolating from tree-level studies. For example, Klos *et al.*'s (2009) analysis of FIA data specifically targeting the 1999–2001 drought in the southeast found a weak relationship between stand diversity and drought impacts, suggesting that the partitioning of resources that occurs in diverse stands provides some buffering of drought effects. Relationships between diversity and drought impacts may vary among ecosystems (Grossiord *et al.*, 2014). In western forests, increasing drought could result in loss of some species, especially from warm and dry climates at low elevations, potentially accelerated by dieback (Kelly & Goulden, 2008; Bell *et al.*, 2014).

#### Drought-related biogeographic and biome shifts

Taken together, the evidence for drought effects on forest composition remains mostly indirect. Forests respond to drought not only due to changes in the SSD of trees present in the stand, but also due to immigration and local extinction (Parmesan & Yohe, 2003; Chen et al., 2011). A species' geographic range changes when regeneration is successful beyond the current population frontier or when regeneration fails in a portion of the current range. In some cases, drought will result in relocation of suitable habitats within the geographic region - for instance, at higher or lower elevations or adjacent to wetlands or bodies of water. Migration is more difficult to evaluate, because it occurs at and beyond range limits, where a species is rare and difficult to study. Local heterogeneity in recruitment success (Pitelka et al., 1997; Ibáñez et al., 2007; Morin et al., 2007), low population density, and the potential importance of rare events over broad regions make migration difficult to detect and to quantify (Clark et al., 2003).

Recent reports that some plant species may already be migrating rapidly in response to changing climates make it important to recognize that the term *migration* is not applied consistently. For plants, the term most often refers to accumulated gains and losses in the area occupied by a species, typically at a regional scale. Poleward or upslope expansions in response to a warming climate are examples. A second use of the term refers to latitude- or elevation-weighted change in abundance or performance (Feeley et al., 2011, 2013; Gottfried et al., 2012). Such weighted averages can be calculated for samples where observations are individual organisms, abundances of species on plots, or performance (e.g., growth rate) (Lenoir et al., 2008; Woodall et al., 2009). For example, growth rates of trees can serve as weights to calculate a performance-weighted mean latitude for the species. The mean latitude calculated by this approach can change from one survey to the next, regardless of whether or not the population actually

moves – even if the range is static, the mean will change if individuals in different parts of the range grow faster/slower than before. Such metrics can provide valuable insight into geographic patterns, although they do not represent a change in a species' geographical distribution. Migration is also hard to assess because most studies inform us more about the centers of population ranges than about range limits. Like weighted averages, models fitted to occurrence, abundance, or demographic rates (e.g., Canham & Thomas, 2010; Mok et al., 2012; Vanderwel et al., 2013; Clark et al., 2014a; Zhu et al., 2014) can be dominated by samples where the species is abundant and insensitive to margins. The smooth declines in performance near margins assumed in many models are not widely observed in demographic data (Fig. 7).

Future range shifts are difficult to anticipate, because there is only limited evidence for the combinations of variables that control current range limits. Experimental warming in northern Minnesota showed photosynthesis and growth increases near cold range limits and reductions near warm range limits in planted seedlings (Reich et al., 2015); however, seed germination and establishment were not studied. As documented for decades through forestry provenance trials, trees manifest local adaptation and home site advantage to temperature and moisture conditions (Rehfeldt et al., 1999; Aitken et al., 2008), so that climate change impacts would be expected throughout the range of the species, not just at leading or trailing edges of species ranges (Davis & Shaw, 2001). Potential for rapid adaptation to current changes in climate is not well understood but will depend on the interaction of spatial patterns of genetic variation and modern gene flow (Aitken et al., 2008).

Limited evidence of migration over the last century, a time when the velocity of climate change has been substantial in the northern USA (Zhu et al., 2012), is not in agreement with models that suggest that suitable habitats of many species are shifting faster than are the populations themselves (McKenney et al., 2007, 2011). The combination of large projected habitat shifts with limited evidence for the rapid migration that would be needed to track these suggests that biogeographic patterns could substantially lag behind climate change. Fundamental differences in migration potential for eastern and western forests result because of the importance of topographic relief in the latter. In the eastern USA, with substantial areas of low relief, modest changes in climate can translate to large shifts in locations of suitable habitat (Loarie et al., 2009; IPCC 2014). For the southeast, the rate of recent climate change produces a climate velocity ranging from 0.2 km/yr in the Appalachians to >2 km/yr on the Piedmont and coastal plain (Schliep et al., 2015). By 2100, mean isotherms

![](_page_13_Figure_1.jpeg)

**Fig. 7** Models of distribution and abundance impose unrealistic relationships on FIA data from the eastern USA. The ubiquitous assumption that abundance and performance decline at range boundaries (e.g., a Gaussian model) contrasts with a spline smoothing (dashed red) of data (dots). Example shown here is *Acer barbatum*. From Clark *et al.*, 2015.

could move northeastward from 400 km for a less  $CO_2$ sensitive model (PCM) with high energy-resource efficiency (B1) to 800 km for a more sensitive model (HadleyCM3) with a 'business as usual' scenario (A1F1) (Iverson *et al.*, 2008a). In western forests, increasing drought could result in loss of some species at low elevations, potentially accelerated by dieback (Kelly & Goulden, 2008; Bell *et al.*, 2014), as shifts in climate may be too fast for many populations to adjust by adaptation or migration.

While there is mounting evidence that certain terrestrial and aquatic invertebrates, birds, and herbaceous plants have changed in distribution with warming (Parmesan & Yohe, 2003; Chen et al., 2011), there are only a few examples of rapid contemporary natural tree migrations (e.g., Fastie, 1995; Pitelka et al., 1997). The paleo record provides some examples of rapid spread in response to climate change, such as Corylus expansion into western Europe in the early Holocene (Huntley & Birks, 1983). Late Holocene range expansion of three western conifers (Juniperus osteosperma, Pinus edulis, P. ponderosa) may have depended on longdistance dispersal events ranging from 25 to 100 km (Lyford et al., 2003; Gray et al., 2006; Lesser & Jackson, 2012, 2013). Expansion of colonizing populations of P. ponderosa may have been slowed by Allee effects (Lesser et al., 2013). However, traditional interpretations of the paleo record suggesting that rapid tree migrations were common in the past are hard to reconcile with known dispersal rates and other life-history observations (McLachlan et al., 2005). Paleo evidence can also prove quite ambiguous - for instance, the sporadic occurrence of fossils in lake sediments can mean that a few trees are nearby or that many trees are far away, making it difficult to infer when a population arrives or disappears from a region. Interpretation of Holocene tree migration remains a subject of considerable research.

With their compact moisture and temperature gradients, some of the most effective migrations could be expected in mountainous regions (Jump et al., 2009; Bell et al., 2014). Coops & Waring (2011) predict a distribution shift and reduction in range extent for lodgepole pine in the Pacific Northwest due to late summer drought. Western redcedar (Thuja plicata) and western hemlock (Tsuga heterophylla) may expand, whereas ponderosa pine, lodgepole pine, grand fir (Abies grandis) and noble fir (Abies procera) may contract (Coops et al., 2011). In the Green Mountains of Vermont, some work has indicated northern hardwoods have invaded the lower boundary of boreal forest in several locations over the last half century (Beckage *et al.*, 2008), whereas broader patterns for this region suggest downslope migration of boreal species (Foster & D'Amato, 2015). In this location, the ecotone is sharp, concentrated within 200 m of elevation. Still, even in such topography where dispersal is probably not limiting, tree upslope shifts appear to lag climate change in the Alps (Gehrig-Fasel et al., 2007) and Andes (Feeley et al., 2011).

Although latitudinal migration in response to warming and drought stress could be occurring for some species, evidence of poleward movement of trees is even less obvious than upslope migration. Warming over the last century in the continental USA has been most rapid in the upper Midwest and Northeast, due to the combination of regional climate change and low relief. Poleward migration would be identified by establishment of new recruitment out ahead of established range boundaries, especially in these areas of rapid change. This pattern is not detected in FIA data from the eastern USA (Zhu et al., 2012), but could be occurring at northern limits of several species in Quebec (Boisvert-Marsh et al., 2014). Latitudinal changes might explain some changes in composition at Blackrock Forest of New York (Schuster et al., 2008) and along certain powerline

corridors (Treyger & Nowak, 2011). Additional evidence of poleward migration could include studies from Woodall *et al.* (2009), Monleon & Lintz (2015), and Delzon *et al.* (2013). Clearly, the rapid spread (> $10^3$  m yr<sup>-1</sup>) required to match the pace of shifting habitats is not occurring.

Changes in fire regime, land cover, and diebacks resulting from combinations of drought, disease, and human action can all contribute to expanding or contracting ranges (Cornwell et al., 2012; Franklin et al., 2013; Jiang et al., 2013), including forest conversion to shrubland and grassland (Lenihan et al., 2008; Man, 2013). Increased fire frequency and/or intensity can rapidly shift composition, structure, and function. The extent to which large diebacks could promote (Linares et al., 2009; Kane et al., 2011), or that forest fragmentation could reduce (Meier et al., 2012), migration capacity may vary widely. Disturbance could accelerate migration for species that would otherwise fail to invade competitive understories (Dukes et al., 2009; Weed et al., 2013). The capacity for drought-induced dieback to accelerate changes to the SSD, including interactions involving fire and insects, suggests that such change could occur at variable rates through time, with periods of slow change punctuated by episodic rapid transitions.

#### Drought and forest management

Drought directly and indirectly affects most of the ecosystem services provided by forests, including timber (Woodall *et al.*, 2013b), carbon storage (Gonzalez *et al.*, 2015), recreational value, and water yield and quality (Brown *et al.*, 2008). Management practices modify the SSD (Box 2) through the manipulation of species, size, and density. While typically done to achieve productivity goals, management can also mitigate or exacerbate effects of drought at tree and stand levels through its influence on local site and climate. For example, in dry western forests, density reduction and prescribed burns to promote timber yield or reduce fire risk also can reduce drought vulnerability (Grant *et al.*, 2013; Thomas and Waring 2014).

Management of established forests for a diversity of species can reduce stand vulnerability to drought. Thinning practices may move from simple reductions in density to stand structural attributes that reduce vulnerability to drought (e.g., Guldin, 2014; Thomas and Waring 2014). For example, the maintenance of uneven-aged stands may spread risks across ages/sizes of different vulnerabilities (e.g., Carter *et al.*, 1984). Forest restoration practices may allow for greater persistence of large, old trees under drought conditions (e.g., Erickson & Waring, 2014). Uncertainty in future climate

can motivate a mix of drought-tolerant species and genotypes. Species composition can be altered directly through selective removal of moisture-demanding species and release of suppressed individuals of more drought-tolerant species. Such replacement occurs naturally following drought-induced dieback in the pinyon-juniper ecosystems (e.g., Floyd et al., 2009). Thinning to reduce crown competition (Aussenac, 2000; McDowell et al., 2006; Gyenge et al., 2011) also reduces canopy interception of precipitation, thus increasing moisture that reaches the forest floor (Stogsdili et al., 1992; Aussenac, 2000) where expanded root systems due to thinning can improve moisture access for individual trees (Dawson, 1996). However, the reduced vulnerability of remaining trees in the short term can increase future vulnerability through changes in tree architecture and physiology. Long-term increases in leaf-to-sapwood area ratios in stands thinned to low densities can increase individual tree water demand (McDowell et al., 2006; Kolb et al., 2007) despite possibly reduced water use by the stand as a whole. Indirect effects can include promoting regeneration (Covington et al. 1997, Moore et al., 1999), also vulnerability to drought (Aussenac, 2000) and competition from nontree species that can increase beneath open canopies (Nilsen et al., 2001). In dry forests of the western USA, such negative effects may be offset by the fire hazard reduction that comes with most management options currently being implemented (e.g., Martinson & Omi, 2013; Waltz et al., 2014).

Successful regeneration during drought depends on microsite conditions, including competition from nonpreferred species. However, current practices and guidelines for seed transfer may need to be reconsidered given the potential for locally maladapted genotypes, as well as the possibility of planting more heatand drought-tolerant genotypes (Aitken et al., 2008; Joyce & Rehfeldt, 2013; Montwé et al., 2015). After all, decades of horticultural practice have clearly shown that growth and reproduction of many species well outside their native ranges is possible, suggesting 'assisted migration' is a viable diversity conservation option (e.g., Schwartz et al., 2012). Management for drought through active involvement in the regeneration process can also prove costly (Nyland, 2007). For species that are especially vulnerable as seedlings (Cavender-Bares & Bazzaz, 2000), steps can be taken to maximize belowground development prior to and immediately after planting (e.g., Burdett, 1990) or to shelter future crop trees (e.g., Aussenac, 2000). Drought may increase reliance on artificial regeneration (i.e., plantings), protection of planted seedlings, and/or seedbed amelioration, such as the manipulation of harvest residues to provide a mulching effect (Roberts et al., 2005; Trottier-Picard

*et al.*, 2014). Artificial regeneration may become especially important for conifers that fail to regenerate or are outcompeted by sprouting hardwood species (Haire & McGarigal, 2008; Zhang *et al.*, 2008; Feddema *et al.*, 2013; Ouzts *et al.*, 2015). Because recruitment depends on local site conditions, knowledge of how different species and genotypes respond on different sites (Blazier *et al.*, 2004; Will *et al.*, 2010; Erickson *et al.*, 2012) should guide management rather than regional climate projections.

#### Knowledge gaps and future directions

#### Challenges/limitations of available data

Efforts to anticipate future forests rely heavily on observational data, which are often unavailable or difficult to extrapolate. For example, droughts are expected to increase in the Northeast (Melillo et al., 2014), a region that has not experienced severe drought since the 1960s, before the regular collection of forest inventory data. Furthermore, many of the variables that affect forests are changing simultaneously, making it difficult to attribute observed changes to rising CO<sub>2</sub>, N deposition, invasive species, or increasing average age of forest stands (McMahon et al., 2010). The interactions that control stand responses to drought remain poorly understood. Our best understanding comes from the study of individual trees (e.g., Fig. 1). As individuals respond, they interact with one another and with natural enemies. Some interactions occur within individuals, such as allocation of carbon resources, with the result that growth, maturation rates, fecundity, and survival can react to drought in different ways (Fig. 3). Other interactions occur between individuals, such as competition in crowded stands. Soil moisture depends not only on climate, but also on redistribution by local drainage, and uptake by competing trees (Fig. 4) (e.g., Loik et al., 2004). Interactions with fungal pathogens and herbivores can impact host individuals differently, depending on species, size, resource availability, and host resistance.

In addition to evidence of climate-competition interactions at the scale of individual trees (Cescatti & Piutti, 1998; Martin-Benito *et al.*, 2011), evidence also can be found in stands (D'Amato *et al.*, 2013; Thomas & Waring, 2015) and across plot networks (Clark *et al.*, 2011, 2014b). Drought effects on SSDs depend on all of these interactions (Box 2). For example, rising CO<sub>2</sub> interacts with SSD, because increase in water-use efficiency of individual leaves or drought tolerance of whole plants varies widely between species and is expected to depend on the light environment and soil moisture (Battipaglia *et al.*, 2013). Likewise, spatial variation of forest response to moisture and temperature gradients can be confounded by land use, management history, soils, and complex hydrology. For example, private landowners in the Pacific Northwest manage some productive lands for timber production, whereas state and federal agencies mostly manage low-productivity and high-elevation forests for diverse objectives (Ohmann & Spies, 1998). In the southeast Piedmont, moisture gradients are confounded by land use and stand age. Typical stands of intermediate moisture status established on former cultivated lands a century ago, whereas xeric sites were grazed, and wet bottomlands were not cultivated and thus tend to support older trees (Oosting, 1942; Quarterman & Keever, 1962). As a consequence, observational data may not yield unambiguous relationships between forest structure and moisture.

Data coverage is also uneven. For example, paleo studies of forest response to past climate come from either tree-ring records or fossil evidence from lake/ bog sediments, which are dispersed unevenly in humid regions. Tree-ring data come primarily from mature trees expected to be most sensitive to climate (Fritts, 1976) and might respond to climate differently from seedlings and saplings. Moreover, open, low-density stand conditions are often preferentially sampled for tree-ring studies to reduce the growth signal resulting from density-dependent interactions.

Data sets that span sufficient temporal variation in climate are limited. Demographic responses to climate change can be estimated from plot data when there are three or more consistent censuses. Thus far, FIA data provide two consistent censuses for most of the eastern USA, but only one census for most of the west. Two censuses provide estimates of mortality rates from numbers of trees that die during the interval (Lines et al., 2010; Dietze & Moorcroft, 2011), of recruitment rates from individuals appearing in a census not present previously (Zhu et al., 2014), and of growth rates from changes in size (Vanderwel et al., 2013). However, the geographic relationships between demography and climate may not represent how demography responds to climate change. Understanding forest change through inventory analysis is further complicated when different designs were implemented between the first and second censuses (Goeking, 2015). Data sets containing long intervals between censuses can be hard to interpret because they integrate many years of climate variation. Many forest plots are resampled at intervals of 4-10 or more years. Intervals this long can include both exceptionally warm, cold, dry, and wet years (e.g., Williams *et al.*, 2013).

Experiments address some of the limitations of observational data by manipulating the environment in a controlled fashion. However, relatively few experiments are available at a scale that provides general insight for climate changes that affect diverse habitats. Because individual trees can be manipulated more readily than forest stands, there is more evidence of drought effects on trees than on stand-level size–species structure. Experiments sufficiently large and long term to determine effects on stand composition and structure are costly; not surprisingly, there are still only a few rainfall exclusion and redistribution experiments on mature temperate forests (e.g., Hanson & Weltzin, 2000; McDowell *et al.*, 2013), and few experiments at any scale include extreme drought and heat events or tree-killing levels of drought stress (cf. Allen *et al.*, 2015).

#### Contributions from models of forest change

Models for forest response to climate change rely heavily on parameters fitted independently to recruitment, growth, and mortality, and primarily from observations on individual trees, rather than stands. Furthermore, interactions complicate prediction efforts (Tinner *et al.*, 2013). To date, much of the research on climate impacts on stand dynamics relies on simulations of several types, three of which are summarized here:

*Species distribution models* (SDMs) are used to map potential future species habitats under climate scenarios (e.g., Guisan & Thuiller, 2005; Franklin, 2010; Matthews *et al.*, 2011; Prasad *et al.*, 2013). Species distributions are calibrated to climate and other environmental variables. The fitted models are then used with climate scenarios generated by GCMs to identify regions of future suitable habitat.

Dynamic global vegetation models (DGVMs) are dynamic and nonspatial (Daly *et al.*, 2000; Sitch *et al.*, 2003; Jiang *et al.*, 2013). Species are aggregated as functional types, such as coniferous, deciduous, and mixed forests, savannas, and woodlands, or grasslands and shrublands (Bachelet *et al.*, 2003). Some incorporate fire, atmospheric CO<sub>2</sub> (Lenihan *et al.*, 2008; King *et al.*, 2013), establishment mechanisms (Song & Zeng, 2014), and patch age structure (Medvigy & Moorcroft, 2012). DGVMs are used to predict change in functional types.

*Forest landscape models* (FLMs) simulate forest demography on landscapes that may include drought, fire, land use, and pathogens. Some FLMs explicitly focus on climate change impacts (Scheller & Mladenoff, 2008; Loehman *et al.*, 2011), including migration (Lischke *et al.*, 2006; Scheller & Mladenoff, 2008; Gustafson & Sturtevant, 2013; Nabel *et al.*, 2013; Snell, 2014). FLMs are used to predict dynamics of forest stands.

Models of climate effects (including drought) continue to improve but are subject to caveats. First is the uncertainty in climate projections – as an example,

three GCMs project climates in 2100 differ by up to 4 °C for mean annual temperature and 60% for precipitation over North America (McKenney et al., 2011). This difference suggests mean latitudes for species' habitats could move northeastward from 400 km for a less CO<sub>2</sub>-sensitive model (PCM) with high energyresource efficiency (B1) to 800 km for a more sensitive model (HadleyCM3) with a 'business as usual' scenario (A1F1) (Iverson et al., 2008b). Second is the uncertainty from heterogeneity not captured in GCM output, from redistribution of precipitation within local drainages - wet and dry sites occupy the same grid cell for regional climate prediction, and from variation in temperature with local topography and vegetation cover. Models of future forest response to future climate begin with this uncertainty in regional and local climate.

Third, all calibration–prediction and simulation approaches incorporate parameters relating drought to recruitment, growth, and survival from separate studies and typically from individual trees, while the interactions that determine drought response depend on the SSD – the interdependence between individuals within the SSD requires that they be considered together (Box 2). Regional or population-level differences in climate relationships are rarely incorporated into these models (e.g., Sork *et al.*, 2010; Joyce & Rehfeldt, 2013; Rehfeldt *et al.*, 2014).

Related to the third point, there remains a need to develop better model representations of climatemediated mortality (McDowell et al., 2011; Allen et al., 2015) and species interactions (Ibanez et al., 2006). Whether or not populations can move to regions of future suitable climate depends on migration, which is poorly understood. For example, potential distributions predicted from SDMs are sometimes bracketed by two extremes - no migration (species lose but do not gain habitat) and unlimited migration (species occupy all suitable habitat) (Thuiller et al., 2005; Iverson et al., 2008b; Meier et al., 2012). A better understanding of how droughts affect seed production, seed banks, and seedling establishment near range limits, particularly their role in local extinctions and recolonization (Jackson et al., 2009; Zimmermann et al., 2009) might improve characterization of extremes. The limited studies show large variation in fecundity (Clark et al., 2004; Koenig & Knops, 2013) and recruitment (Ibáñez et al., 2007). Models that incorporate such estimates predict migration rates that are highly uncertain (Clark et al., 2003). Land cover adds an additional layer of variability, both limiting habitat but often providing recruitment opportunities following disturbance (Clark et al., 2003; Iverson et al., 2004; Prasad et al., 2013).

#### Conclusions

There is broad consensus from modeling studies, increasingly supported by observation that combinations of heat and moisture limitation, and their corresponding indirect effects, will change the health, dynamics, abundance, and distribution of tree species. These changes may accelerate in coming decades. In the eastern USA, drought effects are still primarily observed in responses of individual trees. How species differences, well studied at the individual scale, translate to future stand structure and composition is uncertain. Observations of stand-level responses to evaluate how climate changes interact with changing effects of competitors, mutualists, and natural enemies, which are also responding to climate change, are limited. In the western USA, stand-level forest transformations are in progress now, already highlighting interactions among warming temperatures, drought, insect attacks, and fire. A proactive management strategy for anticipating change can include promoting drought-tolerant species, managed in lower density stands, and potentially drawing on species or genotypes outside their current geographic ranges.

Despite many important insights from observational evidence, the foregoing knowledge gaps and future climate change highlight the challenge posed by connecting abundant research on individual tree responses to the scale where predictions are needed - the forest stand. Research priorities should include more attention to effects of drought beyond the individual, for example, to focus on the combined size-species interactions that control diversity and productivity of stands. After the uncertainty in climate itself, the greatest obstacle to understanding impacts of future drought is the limited understanding of drought consequences at stand-to-landscape scales. Models will continue to play an important role, one that depends on improved understanding of stand-level responses and the acquisition of suitable long-term data for detection, parameterization, calibration, and validation. This challenge is related to the need for models that accommodate environmental change and forest response as a coherent joint distribution of species and sizes (the SSD), that responds to drought with adequate feedbacks and interactions. The problem persists despite proliferation of bigger and more complex models, faster processing, and increased computer memory. Without the empirical basis for translating fine-scale to aggregate behavior - in the form of allocation constraints, species interactions, and feedbacks - complex models can provide only limited guidance. These constraints are needed in models when they are fitted to field and experimental data.

Much could be gained from increased efforts focused on the connections from individual to stand, both empirical and modeling. For example, how does decline in individual tree health translate to population structure and abundance of a species, when individuals of all species are responding to climate, often in similar ways? Again, consider the well-known relationship in traditional forestry that the highest mortality rates occur in the most productive stands. Climate changes that place individuals at risk can have unpredictable effects on stands as the individuals within stands respond. At the individual scale, long-term data with regional coverage are needed to infer demographic processes under a range of climates and to detect early signs of change (Breshears et al., 2009). However, predicting changes in stands also requires stand-level inference. The observable physiological responses to temperature and moisture stress must be linked to demographic potential of individuals and to stand attributes, such as size-species distributions. Predicting effects of novel climate on biogeographic patterns would likewise benefit from better understanding of how current biogeography emerges from tree responses to climate. Additional insights might be gained from natural gradients in regions expected to differ in sensitivity to moisture and temperature, with emphasis on connections from individuals to stands. Finally, opportunistic or designed experiments to better understand geographic variation of drought effects still are needed.

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#### References

- Abrams MD (1990) Adaptations and responses to drought in Quercus species of North America. *Tree Physiology*, 7, 227–238.
- Abrams MD (1994) Fire and the development of oak forests. *BioScience*, **42**, 346–353. Abrams MD (1998) The red maple paradox. *BioScience*, **48**, 355–364.
- Abrams MD (2003) Where has all the white oak gone? BioScience, 53, 927–939.
- Abrams MD, Kubiske ME (1990) Leaf structural characteristics of 31 hardwood and conifer tree species in central Wisconsin: influence of light regime and shade tolerance rank. *Forest Ecology and Management*, **31**, 245–253.
- Adams HD, Guardiola-Claramonte M, Barron-Gafford GA et al. (2009) Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. Proceedings of the National Academy of Sciences of the United States of America, 106, 7063–7066.
- Aitken SN, Yeaman S, Holliday JA, Wang T, Curtis-McLane S (2008) Adaptation, migration or extirpation: climate change outcomes for tree populations: climate change outcomes for tree populations. *Evolutionary Applications*, 1, 95–111.
- Allen CD (2007) Interactions across spatial scales among forest dieback, fire, and erosion in northern New Mexico landscapes. *Ecosystems*, 10, 797–808.
- Allen CD, Breshears DD (1998) Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climate variation. Proceedings of the National Academy of Sciences of the United States of America, 95, 14839–14842.

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- Allen CD, Macalady AK, Chenchouni H *et al.* (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, **259**, 660–684.
- Allen CD, Breshears DD, McDowell NG (2015) On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere*, **6**, 129.
- Anderegg WRL, Kane J, Anderegg LDL (2013) Consequences of widespread tree mortality triggered by drought and temperature stress. *Nature Climate Change*, 3, 30– 36.
- Anderegg WRL, Plavcová L, Anderegg LDL, Hacke UG, Berry JA, Fields CB (2013a) Drought's legacy: multiyear hydraulic deterioration underlies widespread aspen forest die-off and portends increased future risk. *Global Change Biology*, **19**, 118–1196.
- Anderegg WRL, Kane JM, Anderegg LDL (2013b) Consequences of widespread tree mortality triggered by drought and temperature stress. *Nature Climate Change*, 3, 30–36.
- Assmann E (1970) The Principles of Forest Yield Study. Oxford, Pergamon.
- Aussenac G (2000) Interactions between forest stands and microclimate: ecophysiological aspects and consequences for silviculture. *Annals of Forest Science*, **57**, 287–301.
- Bachelet D, Neilson RP, Hickler T et al. (2003) Simulating past and future dynamics of natural ecosystems in the United States. Global Biogeochemical Cycles, 17, 1045. DOI:10.1029/2001GB001508.
- Barber VA, Juday BP, Finney BP (2000) Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. *Nature*, 405, 668– 673.
- Barton AM (2002) Intense wildfire in southeastern Arizona: transformation of a Madrean pine-oak forest to oak woodland. Forest Ecology and Management, 165, 205–212.
- Battipaglia G, Saurer M, Cherubini P, Calfapietra C, McCarthy HR, Norby RJ, Cotrufo MF (2013) Elevated CO2 increases tree-level intrinsic water use efficiency: insights from carbon and oxygen isotope analyses in tree rings across three forest FACE sites. *New Phytologist*, **197**, 544–554.
- Beckage B, Osborne B, Pucko C, Gavin DG, Siccama T, Perkins T (2008) An upward shift of a forest ecotone during 40 years of warming in the Green Mountains of Vermont, USA. Proceedings of the National Academy of Sciences of the United States of America, 105, 4197–4202.
- Belden AC, Pallardy SG (2009) Successional trends and apparent Acer saccharum regeneration failure in an oak-hickory forest in central Missouri, USA. *Plant Ecology*, 204, 305–322.
- Bell DM, Bradford JB, Lauenroth WK (2014) Early indicators of change: divergent climate envelopes between tree life stages imply range shifts in the western United States. *Global Ecology and Biogeography*, 23, 168–180.
- Bentz BJ, Régnière J, Fettig CJ et al. (2010) Climate change and bark beetles of the western United States and Canada: direct and indirect effects. BioScience, 60, 602– 613.
- Berdanier A, Clark JS (2015) Multi-year drought-induced morbidity preceding tree death in Southeastern US forests. *Ecological Applications*, in press.
- Blazier MA, Hennessey TC, Lynch TB, Wittwer RF, Payton ME (2004) Productivity, crown architecture, and gas exchange of North Carolina and Oklahoma/Arkansas loblolly pine families growing on a droughty site in southeastern Oklahoma. *Forest Ecology and Management*, **194**, 83–94.
- Boisvert-Marsh L, Périé C, de Blois S (2014) Shifting with climate? Evidence for recent changes in tree species distribution at high latitudes *Ecosphere*, 5, art83.
- Booth RK, Notaro M, Jackson ST, Kutzbach JE (2006) Widespread drought episodes in the western Great Lakes region during the past 2000 years: geographic extent and potential mechanisms. *Earth and Planetary Science Letters*, 242, 415–427.
- Booth RK, Jackson ST, Sousa VA, Sullivan ME, Minckley TA, Clifford M (2012) Multidecadal drought and amplified moisture variability drove rapid forest community change in a humid region. *Ecology*, 93, 219–226.
- Bréda N, Huc R, Granier A, Dreyer E (2006) Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaption processes and long-term consequences. *Annals of Forest Science*, **63**, 625–644.
- Breshears DD, Cobb NS, Rich PM et al. (2005) Regional vegetation die-off in response to global-change-type drought. Proceedings of the National Academy of Sciences of the United States of America, 102, 15144–15148.
- Breshears DD, Myers OB, Meyer CW et al. (2009) Tree die-off in response to global change-type drought: mortality insights from a decade of plant water potential measurements. Frontiers in Ecology and the Environment, 7, 185–189.
- Bright RM, Zhao K, Jackson RB, Cherubini F (2015) Quantifying surface albedo and other direct biogeophysical climate forcings of forestry activities. *Global Change Biology*, 21, 3246–3266.

- Brose PH, Dey DC, Phillips RJ, Waldrop TA (2013) A meta-analysis of the fire-oak hypothesis: does prescribed burning promote oak reproduction in eastern north America? *Forest Science*, 59, 322–334.
- Brown PM, Wu R (2005) Climate and disturbance forcings of episodic tree recruitment in a southwestern ponderosa pine landscape. *Ecology*, 86, 3030–3038.
- Brown TC, Hobbins MT, Ramirez JA (2008) Spatial distribution of water supply in the coterminous United States1. *Journal of the American Water Resources Association*, 44, 1474–1487.
- Brusca RC, Wiens JF, Meyer WM, et al. (2013) Dramatic response to climate change in the Southwest: Robert Whittaker's 1963 Arizona Mountain plant transect revisited. *Ecology and Evolution*, 3, 3307–3319.
- Brzostek ER, Dragoni D, Schmid HP et al. (2014) Chronic water stress reduces tree growth and the carbon sink of deciduous hardwood forests. *Global Change Biology*, 20, 2531–2539.
- Burdett AN (1990) Physiological processes in plantation establishment and the development of specifications for forest planting stock. *Canadian Journal of Forest Research*, 20, 415–427.
- Canham CD, Thomas RQ (2010) Frequency, not relative abundance, of temperate tree species varies along climate gradients in eastern North America. *Ecology*, 91, 3433– 3440.
- Carter GA, Miller JH, Davis DE, Patterson RM (1984) Effective of vegetative competition on the moisture and nutrient status of loblolly pine. *Canadian Journal of Forest Research*, 14, 1–9.
- Cavender-Bares J, Bazzaz FA (2000) Changes in drought response strategies with ontogeny in *Quercus rubra*: implications for scaling from seedlings to mature trees. *Oecologia*, 124, 8–18.
- Cescatti A, Piutti E (1998) Silvicultural alternatives, competition regime and sensitivity to climate in a European beech forest. *Forest Ecology and Management*, **102**, 213– 223.
- Chen PY, Welsh C, Hamann A (2010) Geographic variation in growth response of Douglas-fir to interannual climate variability and projected climate change. *Global Change Biology*, 16, 3374–3385.
- Chen IC, Hill JK, Ohlemüller R, Roy DB, Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming. *Science*, **333**, 1024–1026.
- Chmura DJ, Anderson PD, Howe GT et al. (2011) Forest responses to climate change in the northwestern United States: ecophysiological foundations for adaptive management. Forest Ecology and Management, 261, 1121–1142.
- Clark JS (1989) Water balance and fire occurrence during the last 160 years in northwestern Minnesota. *Journal of Ecology*, 77, 989–1004.
- Clark JS (1990) Integration of ecological levels: individual plant growth, population mortality, and ecosystem dynamics. *Journal of Ecology*, 78, 275–299.
- Clark J, Royall P (1996) Local and regional sediment charcoal evidence for fire regimes in presettlement north-eastern North America. *Journal of Ecology*, 84, 35– 382.
- Clark JS, Beckage B, Camill P et al. (1999) Interpreting recruitment limitation in forests. American Journal of Botany, 86, 1–16.
- Clark JS, Lewis M, McLachlan JS, Hille Ris Lambers J (2003) Estimating population spread: what can we forecast and how well? *Ecology*, 84, 1979–1988.
- Clark JS, LaDeau S, Ibanez I (2004) Fecundity of trees and the colonization-competition hypothesis. *Ecological Monographs*, 74, 415–442.
- Clark JS, Bell DM, Hersh MH, Nichols L (2011) Climate change vulnerability of forest biodiversity: climate and resource tracking of demographic rates. *Global Change Biology*, 17, 1834–1849.
- Clark JS, Bell DM, Kwit M, Powell A, Zhu K (2013) Dynamic inverse prediction and sensitivity analysis with high-dimensional responses: application to climatechange vulnerability of biodiversity. *Journal of Biological, Environmental, and Agricultural Statistics*, 18, 376–404.
- Clark JS, Gelfand AE, Woodall CW, Zhu K (2014a) More than the sum of the parts: forest climate response from joint species distribution models. *Ecological Applications*, 24, 990–999.
- Clark JS, Bell DM, Kwit MC, Zhu K (2014b) Competition-interaction landscapes for the joint response of forests to climate change. *Global Change Biology*, 20, 1979– 1991.
- Clark JS, Iverson L, Woodall CW et al. (2015) The impacts of increasing drought on forest dynamics, structure, diversity, and management. In: Effects of Drought on Forests and Rangelands in the United States: A Comprehensive Science Synthesis. United States Department of Agriculture (eds Vose, JMJS Clark C, Luce H, Patel-Weynand T) Forest Service Gen. Tech. Report WO-93b.
- Covington WW, Fulé PZ, Moore MM (1997) Restoring ecosystem health in ponderosa pine forests of the Southwest. Journal of Forestry, 95, 23–29.

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- Cook ER, Meko DM, Stahle DW, Cleaveland MK (1999) Drought reconstructions for the continental United States. Journal of Climate, 12, 1145–1162.
- Cook ER, Glitzenstein JS, Krusic PJ, Harcombe PA (2001) Identifying functions groups of trees in west Gulf Coast forests (USA): a tree-ring approach. *Ecological Applications*, **11**, 883–903.
- Cook E, Seager R, Heim RRJ, Vose RS, Herweijer C, Woodhouse CA (2010) Megadroughts in North America: placing IPCC projections of hydroclimatic change in a long-term palaeoclimate context. *Journal of Quaternary Science*, 25, 48–61.
- Cooper-Ellis S, Foster DR, Carlton G, Lezberg A (1999) Forest response to catastrophic wind: results from an experimental hurricane. *Ecology*, 80, 2683–2696.
- Coops NC, Waring RH (2011) A process-based approach to estimate lodgepole pine (*Pinus contorta* Dougl.) distribution in the Pacific Northwest under climate change. *Climatic Change*, **105**, 313–328.
- Coops NC, Waring RH, Beier C, Roy-Jauvin R, Wang T (2011) Modeling the occurrence of 15 coniferous tree species throughout the Pacific Northwest of North America using a hybrid approach of a generic process-based growth model and decision tree analysis. *Applied Vegetation Science*, 14, 402–414.
- Cornwell WK, Stuart SA, Ramirez A, Dolanc CR, Thorne JH, Ackerly DA (2012) Climate Change Impacts on California Vegetation: Physiology, Life History, and Ecosystem Change. California Energy Commission, Sacramento, CA.
- Covington WW, Moore MM (1994) Southwestern ponderosa pine forest structure: changes since Euro-American settlement. Journal of Forestry, 92, 39–47.
- Creeden EP, Hicke JA, Buotte PC (2014) Climate, weather, and recent mountain pine beetle outbreaks in the western United States. *Forest Ecology and Management*, **312**, 239–251.
- Dai A (2012) Increasing drought under global warming in observations and models. Nature Climate Change, **3**, 52–58.
- Daly C, Bachelet D, Lenihan JM, Neilson RP, Parton W, Ojima D (2000) Dynamic simulation of tree-grass interactions for global change studies. *Ecological Applications*, 10, 449–469.
- D'Amato AW, Bradford JB, Fraver S, Palik BJ (2013) Effects of thinning on drought vulnerability and climate response in north temperate forest ecosystems. *Ecological Applications*, 23, 1735–1742.
- Davis M, Shaw R (2001) Range shifts and adaptive responses to Quaternary climate change. Science, 292, 673–679.
- Dawson TE (1996) Determining water use by trees and forests from isotopic, energy balance and transpiration analyses: the roles of tree size and hydraulic lift. *Tree Physiology*, **16**, 263–272.
- Delzon S, Urli M, Samalens J-C et al. (2013) Field evidence of colonisation by Holm oak, at the northern margin of its distribution range, during the Anthropocene period. PLoS ONE, 8, e80443.
- DeRose RJ, Long JN (2012) Drought-driven disturbance history characterizes a southern Rocky Mountain subalpine forest. *Canadian Journal of Forest Research*, 42, 1649– 1660.
- Desprez-Loustau ML, Marcais B, Nageleisen LM, Piou D, Vannini A (2006) Interactive effects of drought and pathogens in forest trees. *Annals of Forest Science*, 63, 597–612.
- Dietze M, Clark JS (2008) Rethinking gap dynamics: the impact of damaged trees and sprouts. *Ecological Monographs*, 78, 331347.
- Dietze MC, Moorcroft PR (2011) Tree mortality in the eastern and central United States: patterns and drivers. *Global Change Biology*, 17, 3312–3326.
- Dobrowski SZ, Swanson AK, Abatzoglou JT, Holden ZA, Safford HD, Schwartz MK, Gavin DG (2015) Forest structure and species traits mediate projected recruitment declines in western US tree species. *Global Ecology and Biogeography*, 24, 917–927.
- Dolanc CR, Thorne JH, Safford HD (2013) Widespread shifts in the demographic structure of subalpine forests in the Sierra Nevada, California, 1934 to 2007. Global Ecology and Biogeography, 22, 264–276.
- Dormana M, Svoray T, Perevolotsky A, Sarris D (2013) Forest performance during two consecutive drought periods: diverging long-term trends and short-term responses along a climatic gradient. *Forest Ecology and Management*, **310**, 1–9.
- Dukes JS, Pontius J, Orwig D et al. (2009) Responses of insect pests, pathogens, and invasive plant species to climate change in the forests of northeastern North America: what can we predict? Canadian Journal of Forest Research, 39, 231–248.
- Elliott KJ, Swank WT (1994) Impact of drought on tree mortality and growth in a mixed hardwood forest. *Journal of Vegetation Science*, **5**, 229–236.
- Engber EA, Varner JM (2012) Patterns of flammability of the California oaks: the role of leaf traits. *Canadian Journal of Forest Research*, 42, 1965–1975.
- Erickson CC, Waring KM (2014) Old ponderosa pine growth and mortality responses to restoration treatments at Mt. Trumbull, AZ. *Applied Vegetation Science*, **17**, 97– 108.

- Erickson V, Aubry C, Berrang P et al. (2012) Genetic Resource Management and Climate Change: Genetic Options for Adapting National Forests to Climate Change. USDA Forest Service, Forest Management, Washington, DC.
- Esper J, Niederer R, Bebi P, Frank D (2008) Climate signal age effects—Evidence from young and old trees in the Swiss Engadin. Forest Ecology and Management, 255, 3783–3789.
- Faber-Langendoen D, Tester JR (1993) Oak mortality in sand savannas following drought in east-central Minnesota. Bulletin of the Torrey Botanical Club, 248–256.
- Fahey TJ (1998) Recent changes in an upland forest in south-central New York. Journal of the Torrey Botanical Society, 51–59.
- Fastie CL (1995) Causes and ecosystem consequences of multiple pathways of primary succession at Glacier Bay, Alaska. *Ecology*, 76, 1899–1916.
- Feddema JJ, Mast JN, Savage M (2013) Modeling high-severity fire, drought and climate change impacts on ponderosa pine regeneration. *Ecological Modelling*, 253, 56–69.
- Feeley KJ, Silman MR, Bush M et al. (2011) Upslope migration of Andean trees. Journal of Biogeography, 38, 783–791.
- Feeley KJ, Hurtado J, Saatchi S, Silman M, Clark D (2013) Compositional shifts in Costa Rican forests due to climate-driven species migrations. *Global Change Biol*ogy, 19, 3472–2480.
- Fei S, Kong N, Steiner KC, Moser WK, Steiner EB (2011) Change in oak abundance in the eastern Unites States from 1980 to 2008. *Forest Ecology and Management*, 262, 1370–1377.
- Fellows AW, Goulden ML 2012. Rapid vegetation redistribution in Southern California.
- Floyd ML, Clifford M, Cobb NS, Hanna D, Delph R, Ford P, Turner D (2009) Relationship of stand characteristics to drought-induced mortality in three Southwestern piñon-juniper woodlands. *Ecological Applications*, **19**, 1223–1230.
- Foster JR, D'Amato AW (2015) Montane forest ecotones moved downslope in northeastern US in spite of warming between 1984 and 2011. *Global Change Biology*, 21, 4497–4507.
- Franklin J (2010) Moving beyond static species distribution models in support of conservation biogeography. *Diversity and Distributions*, 16, 321–330.
- Franklin J, Davis FW, Ikagami M, Syphard AD, Flint A, Flint L, Hannah L (2013) Modeling plant species distributions under future climates: how fine-scale do climate models need to be? *Clobal Change Biology*, **19**, 473–483.
- Frelich LE, Reich PB (2010) Will environmental changes reinforce the impact of global warming on the prairie-forest border of central North America? Frontiers in Ecology and the Environment, 8, 371–378.
- Fritts HC (1976) Tree Rings and Climate. Academic Press, New York, NY.
- Fulé PZ, Korb JE, Wu R (2009) Changes in forest structure of a mixed conifer forest, southwestern Colorado, USA. Forest Ecology and Management, 258 1200–1210.
- Ganey JL, Vojta SC (2011) Tree mortality in drought-stressed mixed-conifer and ponderosa pine forests, Arizona, USA. Forest Ecology and Management, 261, 162– 168.
- Garrity SR, Allen CD, Brumby SP, Gangodagamage C, McDowell NG, Cai DM (2013) Quantifying tree mortality in a mixed species woodland using multitemporal high spatial resolution satellite imagery. *Remote Sensing of Environment*, **129**, 54–65.
- Gehrig-Fasel J, Guisan A, Zimmermann NE (2007) Treeline shifts in the Swiss Alps: climate change or land abandonment? *Journal of Vegetation Science*, 18, 571–582.
- Gitlin AR, Sthultz CM, Bowker MA et al. (2006) Mortality gradients within and among dominant plant populations as barometers of ecosystem change during extreme drought. Conservation Biology, 20, 1477–1486.
- Goeking SA (2015) Disentangling forest change from forest inventory change: a case study from the US Interior West. *Journal of Forestry*, **113**, 475–483.
- Goforth BR, Minnich RA (2008) Densification, stand-replacement wildfire, and extirpation of mixed conifer forest in Cuyamaca Rancho State Park, southern California. Forest Ecology and Management, 256, 36–45.
- Gonzalez P, Battles JJ, Collins BM, Robards T, Saah DS (2015) Aboveground live carbon stock changes of California wildland ecosystems, 2001-2010. Forest Ecology and Management, 348, 68–77.
- Gottfried M, Pauli H, Futschik A et al. (2012) Continent-wide response of mountain vegetation to climate change. Nature Climate Change, 2, 111–115.
- Grant GE, Tague CL, Allen CD (2013) Watering the forest for the trees: an emerging priority for managing water in forest landscapes. *Frontiers in Ecology and the Envi*ronment, **11**, 314–321.
- Graumlich L (1993) Response of tree growth to climatic variation in the mixed conifer and deciduous forests of the upper Great Lakes region. *Canadian Journal of Forest Research*, 23, 133–143.
- Gray ST, Betancourt JL, Jackson ST, Eddy RG (2006) Role of multidecadal climatic variability in a range extension of pinyon pine. *Ecology*, **87**, 1124–1130.

- Grossiord C, Granier A, Ratcliffe S *et al.* (2014) Tree diversity does not always improve resistance of forest ecosystems to drought. *Proceedings of the National Academy of Sciences of the United States of America*, **111**, 14812–14815.
- Grossnickle S (2005) Importance of root growth in overcoming planting stress. *New Forests*, **30**, 273–294.
- Grubb PJ (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Review, Cambridge Philosophycal Society*, **52**, 102–145.
- Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, 8, 993–1009.
- Guldin JM (2014) Adapting silviculture to a changing climate in the southern United States. In: Climate Change for Adaptation and Mitigation Management Options: A Guide for Natural Resource Managers in Southern Forest Ecosystems (eds Vose JM, Klepzig KD), pp. 173–192. CRC Press, Boca Raton, FL.
- Gustafson EJ, Sturtevant BR (2013) Modeling forest mortality caused by drought stress: implications for climate change. *Ecosystems*, 16, 60–74.
- Guyette RP, Spetich MA, Stambaugh MC (2006) Historic fire regime dynamics and forcing factors in the Boston Mountains, Arkansas, USA. Forest Ecology and Management, 234, 293–304.
- Gyenge J, Fernández M, Sarasola M, Schlichter T (2011) Stand density and drought interaction on water relations of Nothofagus antarctica: contribution of forest management to climate change adaptability. *Trees - Structure and Function*, 25, 1111–1120.
- Haase DL, Rose R (1993) Soil moisture stress induces transplant shock in stored and unstored 2 + 0 Douglas-fir seedlings of varying root volumes. *Forest Science*, 39, 275–294.
- Haire SI, McGarigal K (2008) Inhabitants of landscape scars: succession of woody plants after large, severe forest fires in Arizona and New Mexico. *The Southwestern Naturalist*, 53, 146–161.
- Handler SD, Matthew J, Iverson L et al. 2014. Minnesota Forest Ecosystem Vulnerability Assessment and Synthesis: A report from the Northwoods Climate Change Response Framework. Gen. Tech. Rep. NRS-133. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA.
- Hanson PJ, Weltzin JF (2000) Drought disturbance from climate change: response of United States forests. Science of the Total Environment, 262, 205–220.
- Harper JL (1977) Polulation Biology of Plants. Academic Press, London.
- Henderson JP, Grissino-Mayer HD (2009) Climate-tree growth relationships of longleaf pine (*Pinus palustris* Mill.) in the Southeastern Coastal Plain, USA. Dendrochronologia, 27, 31–43.
- Hersh MH, Vilgalys R, Clark JS (2012) Evaluating the impacts of multiple generalist fungal pathogens on temperate tree seedling survival. *Ecology*, 93, 511–520.
- Hicke JA, Meddens AJH, Allen CD, Kolden CA (2013) Carbon stocks of trees killed by bark beetles and wildfire in the western United States. *Environmental Research Letters*, 8, 035032.
- Hogg ET, Brandt JP, Kochtubajda B (2005) Factors affecting interannual variation in growth of western Canadian aspen forests during 1951-2000. *Canadian Journal of Forest Research*, 35, 610–622.
- Hood LA, Swaine MD, Mason PA (2004) The influence of spatial patterns of damping-off disease and arbuscular mycorrhizal colonization on tree seedling establishment in Ghanaian tropical forest soil. *Journal of Ecology*, 92, 816–823.
- Hough AF, Forbes RD (1943) The ecology and silvics of forests in the High Plateau of Pennsylvania. *Ecological Monographs*, 13, 299–320.
- Houle G (1999) Mast seeding in *Abies balsamea, Acer saccharum* and *Betula alleghaniensis* in an old growth, cold temperate forest of north-eastern North America. *Journal of Ecology*, 87, 413–422.
- Huntley B, Birks HJB (1983) An atlas of Past and Present Pollen Maps for Europe: 0– 13000 Years Ago. Cambridge University Press, Cambridge, UK.
- Hutchinson T, Long R, Ford R, Sutherland EK (2008) Fire history and the establishment of oaks and maples in second-growth forests. *Canadian Journal of Forestry Research*, 38, 1184–1196.
- Ibanez I, Clark JS, Dietze MC et al. (2006) Predicting biodiversity change: outside the climate envelope, beyond the species-area curve. Ecology, 87, 1896–1906.
- Ibáñez I, Clark JS, LaDeau S, Hille Ris Lambers J (2007) Exploiting temporal variability to understand tree recruitment response to climate change. *Ecological Mono*graphs, 77, 163–177.
- Ichihara Y, Yamaji K (2009) Effect of light conditions on the resistance of current-year Fagus crenata seedlings against fungal pathogens causing damping-off in a natural beech forest: fungus isolation and histological and chemical resistance. Journal of Chemical Ecology, 35, 1077–1085.
- Innes JL (1994) The occurrence of flowering and fruiting on individual trees over 3 years and their effects on subsequent crown condition. *Trees Structure and Function*, 8, 139–150.

- Intergovernmental Panel on Climate Change. 2014. Climate Change 2014: Impacts, Adaptation, and Vulnerability. Working Group II Contribution to the IPCC 5th Assessment Report Intergovernmental Panel on Climate Change, Stanford, CA.
- Iverson LR, Schwartz MW, Prasad AM (2004) How fast and far might tree species migrate in the eastern United States due to climate change? *Global Ecology and Bio*geography, 13, 209–219.
- Iverson LR, Hutchinson TF, Prasad AM, Peters MP (2008a) Thinning, fire, and oak regeneration across a heterogeneous landscape in the eastern U.S.: 7-year results. *Forest Ecology and Management*, 255, 3035–3050.
- Iverson LR, Prasad AM, Matthews SN, Peters M (2008b) Estimating potential habitat for 134 eastern US tree species under six climate scenarios. *Forest Ecology and Man*agement, 254, 390–406.
- Jackson ST, Betancourt JL, Booth RK, Gray ST (2009) Ecology and the ratchet of events: climate variability, niche dimensions, and species distributions. Proceedings of the National Academy of Sciences of the United States of America, 106, 19685–19692.
- Jactel H, Petit J, Desprez-Loustau ML, Delzon S, Piou D, Battisti A, Koricheva J (2012) Drought effects on damage by forest insects and pathogens: a meta-analysis. *Global Change Biology*, 18, 267–276.
- Jiang X, Rauscher SA, Ringler TD et al. (2013) Projected future changes in vegetation in western North America in the twenty-first century. Journal of Climate, 26, 3671– 3687.
- Joyce DG, Rehfeldt GE (2013) Climatic niche, ecological genetics, and impact of climate change on eastern white pine (*Pinus strobus* L.): guidelines for land managers. *Forest Ecology and Management*, **295**, 173–192.
- Joyce LA, Running SW, Breshears DD et al. 2014. Ch. 7: Forests. Climate change impacts in the United States: the third national climate assessment. In: U.S. Global Change Research Program (eds Melillo JM, Terese TC, Richmond TC, Yohe GW), pp. 175–194. National Climate Assessment, U.S. Global Change Research Program, Washington, DC. doi:10.7930/J0Z60KZC.
- Jump AS, Matyas C, Penuelas J (2009) The altitude-for-latitude disparity in the range retractions of woody species. *Trends in Ecology & Evolution*, **24**, 694–701.
- Kaiser KE, McGlynn BL, Emanuel RE (2012) Ecohydrology of an outbreak: mountain pine beetle impacts trees in drier landscape positions first. *Ecohydrology*, 6, 444– 454.
- Kane JM, Meinhardt KA, Chang T, Cardall BL, Michalet R, Whitman TG (2011) Drought-induced mortality of a foundation species (*Juniperus monosperma*) promotes positive afterlife effects in understory vegetation. *Plant Ecology*, **212**, 733–741.
- Kane JM, Dugi FL, Kolb TE (2015) Establishment and growth of piñon pine regeneration vary by nurse type along a soil substrate age gradient in northern Arizona. *Journal of Arid Environments*, **115**, 113–119.
- Kayes LJ, Tinker DB (2012) Forest structure and regeneration following a mountain pine beetle epidemic in southeastern Wyoming. *Forest Ecology and Management*, 263, 57–66.
- Kelly AE, Goulden ML (2008) Rapid shifts in plant distribution with recent climate change. Proceedings of the National Academy of Sciences of the United States of America, 105, 11823–11826.
- King DA, Bachelet DM, Symstad AJ (2013) Climate change and fire effects on a prairie–woodland ecotone: projecting species range shifts with a dynamic global vegetation model. *Ecology and Evolution*, 3, 5076–5097.
- Klos RJ, Wang GG, Bauerle WL, Rieck JR (2009) Drought impact on forest growth and mortality in the southeast USA: an analysis using Forest Health and Monitoring data. *Ecological Applications*, 19, 699–708.
- Koenig WD, Knops JMH (2013) Large-scale spatial synchrony and cross-synchrony in acorn production by two California oaks. *Ecology*, 94, 83–93.
- Kolb PF, Robberecht R (1996) High temperature and drought stress effects on survival of *Pinus ponderosa* seedlings. *Tree Physiology*, **16**, 665–672.
- Kolb TE, Agee JK, Fule PZ, McDowell NG, Pearson K, Sala A, Waring RH (2007) Perpetuating old ponderosa pine. *Forest Ecology and Management*, 249, 141–157.
- Kreye JK, Varner JM, Hiers JK, Mola J (2013) Toward a mechanism for eastern North American forest mesophication: differential litter drying across 17 species. Ecological Applications: A Publication of the Ecological Society of America, 23, 1976–1986.
- Kukowski KR, Schwinning S, Schwartz BF (2012) Hydraulic responses to extreme drought conditions in three co-dominant tree species in shallow soil over bedrock. *Oecologia*. doi:10.1007/s00442-012-2466.
- LaDeau SL, Clark JS (2001) Rising CO2 levels and the fecundity of forest trees. *Science*, **292**, 95–98.
- Lafon CW, Quiring SM (2012) Relationships of fire and precipitation regimes in temperate torests of the Eastern United States. *Earth Interactions*, **16**, 1–15.

#### 2350 J. S. CLARK et al.

- Legras EC, Vander Wall SB, Board DI (2010) The role of germination microsite in the establishment of sugar pine and Jeffrey pine seedlings. *Forest Ecology and Manage*ment, 260, 806–813.
- Lenihan JM, Bachelet D, Neilson RP, Drapek R (2008) Response of vegetation distribution, ecosystem productivity, and fire to climate change scenarios for California. *Climatic Change*, 87, 215–230.
- Lenoir J, Gégout JC, Marquet PA, de Ruffray P, Brisse H (2008) A significant upward shift in plant species optimum elevation during the 20th century. *Science*, 320, 1768–1771.
- Lesser MR, Jackson ST (2012) Making a stand: five centuries of population growth in colonizing stands of Pinus ponderosa. *Ecology*, 93, 1071–1081.
- Lesser MR, Jackson ST (2013) Contributions of long-distance dispersal to population growth in colonizing Pinus ponderosa populations. *Ecology Letters*, 16, 380–389.
- Lesser MR, Parchman TL, Jackson ST (2013) Development of genetic diversity, differentiation and structure over 500 years in four ponderosa pine populations. *Molecular Ecology*, 22, 2640–2652.
- Linares CJ, Camarero J, Carreira A (2009) Interacting effects of changes in climate and forest cover on mortality and growth of the southernmost European fir forests. *Global Ecology and Biogeography*, 18, 485–497.
- Lines ER, Coomes DA, Purves DW (2010) Influences of forest structure, climate and species composition on tree mortality across the eastern US. *PLoS ONE*, **5**, e13212.
- Lischke H, Zimmermann NE, Bolliger J, Rickebusch S, Loffler TJ (2006) TreeMig: a forest-landscape model for simulating spatio-temporal patterns from stand to landscape scale. *Ecological Modelling*, **199**, 409–420.
- Littell JS, McKenzie D, Peterson DL, Westerling AL (2009) Climate and wildfire area burned in western US ecoprovinces, 1916-2003. Ecological Applications, 19, 1003–1021.
- Loarie SR, Duffy PB, Hamilton H, Asner GP, Field CB, Ackerly DD (2009) The velocity of climate change. *Nature*, 462, 1052–1055.
- Loehman RA, Corrow A, Keane RE (2011) Modeling climate changes and wildfire interactions: effects on whitebark pine (*Pinus albicaulis*) and implications for restoration, Glacier National Park, Montana, USA. Forests, 2, 832–860.
- Loik ME, Breshears DD, Lauenroth WK, Belnap J (2004) A multi-scale perspective of water pulses in dryland ecosystems: climatology and ecohydrology of the western USA. Oecologia, 14, 269–281.
- Luo Y, Chen HYH (2013) Observations from old forests underestimate climate change effects on tree mortality. *Nature Communications*, **4**, 1655.
- Lutz JA, van Wagtendonk JW, Franklin JF (2009) Twentieth-century decline of largediameter trees in Yosemite National Park, California, USA. Forest Ecology and Management, 257, 2296–2307.
- Lyford ME, Jackson ST, Betancourt JL, Gray ST (2003) Influence of landscape structure and climate variability on a late Holocene plant migration. *Ecological Mono*graphs, 73, 567–583.
- Lynch C, Hessl A (2010) Climatic controls on historical wildfires in West Virginia, 1939–2008. Physical Geography, 31, 254–269.
- Macalady AK, Bugmann H (2014) Growth-mortality relationships in Pinus edulis reveal shifting mortality thresholds and climate sensitivity across warmer and cooler droughts. *PLoS ONE*. doi:10.1371/iournal.pone.0092770.
- Man G (2013) Major Forest Insect and Disease Conditions in the United States: 2012. US Forest Service, Washington, DC.
- van Mantgem PJ, Stephenson NL, Byrne JC et al. (2009) Widespread increase of tree mortality rates in the western United States. Proceedings of the National Academy of Sciences of the United States of America, 323, 521–524.
- Martin-Benito D, Kint V, del Río M, Muys B, Cañellas I (2011) Growth responses of West-Mediterranean *Pinus nigra* to climate change are modulated by competition and productivity: past trends and future perspectives. *Forest Ecology and Management*, 262, 1030–1040.

Martinson EJ, Omi PN 2013. Fuel Treatments and Fire Severity: A Metaanalysis. Res. Pap. RMRS-RP-103WWW. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO.

Mast JN, Wolf J (2006) Spatial patch patterns and altered forest structure in middle elevation versus upper ecotonal mixed-conifer forests, Grand Canyon National Park, Arizona, USA. Forest Ecology and Management, 236, 241–250.

- Matthews SN, Iverson LR, Prasad AM, Peters MP, Rodewald PG (2011) Modifying climate change habitat models using tree species-specific assessments of model uncertainty and life history-factors. *Forest Ecology and Management*, 262, 1460–1472.
- McDowell NG, Adams HD, Bailey JD, Hess M, Kolb TE (2006) Homeostatic maintenance of ponderosa pine gas exchange in response to stand density changes. *Ecological Applications*, 16, 1164–1182.
- McDowell NG, Beerling DJ, Breshears DD, Fisher RA, Raffa KF, Stitt M (2011) The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends in Ecology and Evolution*, 26, 523–532.

- McDowell NG, Fisher RA, Xu C et al. (2013) Evaluating theories of drought-induced vegetation mortality using a multimodel-experiment framework. New Phytologist, 200, 304–321.
- McEwan RW, Dyer JM, Pederson N (2011) Multiple interacting ecosystem drivers: toward an encompassing hypothesis of oak forest dynamics across eastern North America. *Ecography*, 34, 244–256.
- McKenney DW, Pedlar JH, Lawrence K, Campbell K, Hutchison MF (2007) Potential impacts of climate change on distribution of North American trees. *BioScience*, 57, 939–948.
- McKenney DW, Pedlar JH, Rood RB, Price D (2011) Revisiting projected shifts in the climate envelopes of North American trees using updated general circulation models. *Global Change Biology*, **17**, 2720–2730.
- McLachlan J, Clark JS, Manos PS (2005) Molecular indicators of tree migration capacity under rapid climate change. *Ecology*, 86, 2088–2098.
- McMahon SM, Parker GC, Miller DR (2010) Evidence for a recent increase in forest growth. Proceedings of the National Academy of Sciences of the United States of America, 107, 3611–3615.
- Medvigy D, Moorcroft PR (2012) Predicting ecosystem dynamics at regional scales: an evaluation of a terrestrial biosphere model for the forests of northeastern North America. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 367, 222–235.
- Meddens AJH, Hicke JA, Ferguson CA (2012) Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the western United States. *Ecological Applications*, 22, 1876–1891.
- Meier ES, Lischke H, Schmatz DR, Zimmermann NE (2012) Climate, competition and connectivity affect future migration and ranges of European trees. *Global Ecology* and Biogeography, 21, 164–178.
- Melillo JM, Richmond TC, Yohe GW Eds. 2014: Climate Change Impacts in the United States: The Third National Climate Assessment. U.S. Global Change Research Program. doi:10.7930/J0Z31WJ2.
- Miao S, Zou CB, Breshears DD (2009) Vegetation responses to extreme hydrological events: sequence matters. *The American Naturalist*, **173**, 113–118.
- Millar CI, Westfall RD, Delany DL, Bokach MJ, Flint AL, Flint LE (2012) Forest mortality in high-elevation whitebark pine (*Pinus albicaulis*) forests of eastern California, USA; influence of environmental context, bark beetles, climatic water deficit, and warming. *Canadian Journal of Forest Research*, **42**, 749–765.
- Minnich RA 2007. Southern California coniferous forest. In: Terrestrial vegetation of California, 3rd edn (eds Barbour MG, Keeler-Wolf T, Schoenherr AS), pp. 339–336. Chapter 18. University of California Press, Berkeley and Los Angeles, CA.
- Mok HF, Arndt SK, Nitschke CR (2012) Modelling the potential impact of climate variability on species regeneration potential in SE Australia. *Global Change Biology*, 18, 1053–1072.
- Monleon VJ, Lintz HE (2015) Evidence of tree species' range shifts in a complex landscape. PLoS ONE, 10, e0118069.
- Montwé D, Spiecker H, Hamann A (2015) Five decades of growth in a genetic field trial of Douglas-fir reveal trade-offs between productivity and drought tolerance. *Tree Genetics & Genomes*, **11**, **29**.
- Moore MM, Covington WW, Fulé PZ, Parsons DJ, Swetnam TW, Christensen NL (1999) References conditions and ecological restoration: a southwestern ponderosa pine perspective. *Ecological Applications*, 9, 1266–1277.
- Moore GW, Edgar C, Vogel JG, Washington-Allen RA, March R, Zehnder R (2013) Widespread Tree Mortality from the 2011 Texas Drought: Consequences for Forest Structure and Carbon Stocks. AGU Fall Meeting Abstracts, p.599.
- Morin X, Augspurger C, Chuine I (2007) Process-based modeling of species' distributions: what limits temperate tree species' range boundaries. *Ecology*, 88, 2280–2291.
- Mueller RC, Scudder CM, Porter ME, Talbot Trotter R, Gehring CA, Whitham TG (2005) Differential tree mortality in response to severe drought: evidence for longterm vegetation shifts. *Journal of Ecology*, 93, 1085–1093.
- Nabel J, Zurbriggen N, Lischke H (2013) Interannual climate variability and population density thresholds can have a substantial impact on simulated tree species' migration. *Ecological Modelling*, 257, 88–100.
- Negrón JoseF, McMillin JoelD, Anhold John A, Coulson Dave (2009) Bark beetlecaused mortality in a drought-affected ponderosa pine landscape in Arizona, USA. Forest Ecology and Management, 257, 1353–1362.
- Nilsen ET, Clinton BD, Lei TT, Miller OK, Semones SW, Walker JF (2001) Does Rhododendron maximum L. (Ericaceae) Reduce the Availability of Resources above and Belowground for Canopy Tree Seedlings? American Midland Naturalist, 145, 325– 343.
- Nilsson U, Örlander G (1995) Effects of regeneration methods on drought damage to newly planted Norway spruce seedlings. *Canadian Journal of Forest Research*, 25, 790–802.

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- Nowacki GJ, Abrams MD (2008) The demise of fire and "mesophication" of forests in the eastern United States. *BioScience*, **58**, 123–138.
- Nyland RD (2007) Silviculture: Concepts and Applications. Waveland Press, Long Grove, IL.
- O'Connor CD 2013. Spatial and temporal dynamics of disturbance interactions along an ecological gradient. Ph.D. Dissertation, University of Arizona, Tucson, AZ.
- O'Hara KL, Nagel LM (2013) The stand: revisiting a central concept in forestry. *Journal of Forestry*, **111**, 335–340.
- Ohmann JL, Spies TA (1998) Regional gradient analysis and spatial pattern of woody plant communities of Oregon forests. *Ecological Monographs*, 68, 151–182.
- Olano JM, Palmer MW (2003) Stand dynamics of an Appalachian old-growth forest during a severe drought episode. *Forest Ecology and Management*, **174**, 139–148.
- Oliva J, Stenlid J, Martínez-Vilalta J (2014) The effect of fungal pathogens on the water and carbon economy of trees: implications for drought-induced mortality. *New Phytologist*, 203, 1028–1035.
- Oosting HJ (1942) An Ecological analysis of the plant communities of Piedmont, North Carolina. American Midland Naturalist, 28, 1–126.
- Ouzts J, Kolb T, Huffman D, Sánchez-Meador A (2015) Post-fire ponderosa pine regeneration with and without planting in Arizona and New Mexico. Forest Ecology and Management, 354, 281–290.
- Owens JN (1995) Constraints to seed production: temperate and tropical forest trees. *Tree Physiology*, **15**, 477–484.
- Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, 37–42.
- Parshall T (1995) Canopy mortality and stand-scale change in a northern hemlockhardwood forest, Canadian. Journal of Forestry Research, 25, 1466–1478 ISI.
- Parshall T, Foster D (2003) Fire on the New England landscape: regional and temporal variation, cultural and environmental controls. *Journal of Biogeography*, 29, 1305–1317.
- Parsons DJ, DeBenedetti SH (1979) Impact of fire suppression on a mixed-conifer forest. Forest Ecology and Management, 2, 21–33.
- Pedersen B (1998) The role of stress in the mortality of midwestern oaks as indicated by growth prior to death. *Ecology*, **79**, 79–93.
- Pederson N, Varner JM III, Palik BJ (2008) Canopy disturbance and tree recruitment over two centuries in a managed longleaf pine landscape. *Forest Ecology and Man*agement, 254, 85–95.
- Pederson N, Bell AR, Knight TA et al. (2012a) Long-term perspective on a modern drought in the American Southeast. Environmental Research Letters, 7, 014034, doi:10.1088/1748-9326/7/1/014034.
- Pederson N, Tackett K, McEwan RW et al. (2012b) Long-term drought sensitivity of trees in second-growth forests in a humid region. Canadian Journal of Forest Research, 42, 1837–1850.
- Pederson N, Bell AR, Cook ER et al. (2013) Is an epic pluvial masking the water insecurity of the greater New York City region? Journal of Climate, 26, 1339–1354.
- Pederson N, Dyer JM, McEwan RW et al. (2014) The legacy of episodic climatic events in shaping broadleaf-dominated forests. *Ecological Monographs*, 84, 599– 620.
- Pelz KA, Smith FW (2013) How will aspen respond to mountain pine beetle? A review of literature and discussion of knowledge gaps. Forest Ecology and Management, 299, 60–69.
- Perez-Ramos IM, Ourcival JM, Limousin JM, Rambal S (2010) Mast seeding under increasing drought: results from a long-term data set and from a rainfall exclusion experiment. *Ecology*, 91, 3057–3068.
- Peters MP, Iverson LR, Matthews SN 2014. Spatio-temporal trends of drought by forest type in the conterminous United States, 1960–2013. Res. Map NRS-7. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA. [scale 1:12,000,000].
- Peters MP, Iverson LR, Matthews SN (2015) Long-term droughtiness and drought tolerance of eastern US forests over five decades. *Forest Ecology and Management*, 345, 56–64.
- Pinto JR, Marshall JD, Dumroese RK, Davis AS, Cobos DR (2012) Photosynthetic response, carbon isotopic composition, survival, and growth of three stock types under water stress enhanced by vegetative competition. *Canadian Journal of Forest Research*, 42, 333–344.
- Piovesan G, Adams JM (2001) Masting behaviour in beech: linking reproduction and climatic variation. *Canadian Journal of Botany*, **79**, 1039–1047.
- Pitelka LF, Gardner RH, Ash J et al. (1997) Plant migration and climate change. American Scientist, 85, 464–473.
- Prasad AM, Gardiner J, Iverson L, Matthews S, Peters M (2013) Exploring tree species colonization potentials using a spatially explicit simulation model: implications for four oaks under climate change. *Global Change Biology*, **19**, 2196–2208.

- Pucek Z, Jedrzejewski W, Jedrzejewska B, Pucek M (1993) Rodent population dynamics in a primeval deciduous forest (Bialowieza National Park) in relation to weather, seed crop, and predation. Acta Theriologica, 38, 199–232.
- Quarterman E, Keever C (1962) Southern mixed hardwood forest: climax in the Southeastern Coastal Plain, U.S.A. *Ecological Monographs*, 32, 167–185.
- Raffa KF, Aukema BH, Bentz BJ, Carroll AL, Hicke JA, Turner MG, Romme WH (2008) Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *BioScience*, 58, 501–517.
- Rahman MS, Messina MG, Fisher RF (2006) Intensive forest management affects loblolly pine (*Pinus taeda* L.) growth and survival on poorly drained sites in southern Arkansas. *Southern Journal of Applied Forestry*, **30**, 79–85.
- Rapacciuolo G, Maher SP, Schneider AC et al. (2014) Beyond a warming fingerprint: individualistic biogeographic responses to heterogeneous climate change in California. Global Change Biology, 20, 2841–2855.
- Redmond MD, Barger NN (2013) Tree regeneration following drought- and insectinduced mortality in pinon-juniper woodlands. New Phytologist, 200, 402–412.
- Redmond MD, Forcella F, Barger NN (2012) Declines in pinyon pine cone production associated with regional warming. *Ecosphere*, 3, 120.
- Rehfeldt GE, Ying CC, Spittlehouse DL, Hamilton DA (1999) Genetic responses to climate in *Pinus contorta*: Niche breadth, climate change, and reforestation. *Ecological Monographs*, 69, 375–407.
- Rehfeldt GE, Leites LP, Bradley St Clair J, Jaquish BC, Sáenz-Romero C, López-Upton J, Joyce DG (2014) Comparative genetic responses to climate in the varieties of *Pinus ponderosa* and *Pseudotsuga menziesii*: clines in growth potential. *Forest Ecology* and Management, **324**, 138–146.
- Reich PB, Sendall KM, Rice K, Rich RL, Stefanski A, Hobbie SE, Montgomery RA (2015) Geographic range predicts photosynthetic and growth response to warming in co-occurring tree species. *Nature Climate Change*, 5, 148–152.
- Roberts SD, Harrington CA, Terry TA (2005) Harvest residue and competing vegetation affect soil moisture, soil temperature, N availability, and Douglas-fir seedling growth. Forest Ecology and Management, 205, 333–350.
- Roccaforte JP, Fulé PZ, Chancellor WW, Laughlin DC (2012) Woody debris and tree regeneration dynamics following severe wildfires in Arizona ponderosa pine forests. *Canadian Journal of Forest Research*, 42, 593–604.
- Rozas V (2005) Dendrochronology of pedunculate oak (*Quercus robur* L.) in an oldgrowth pollarded woodland in northern Spain: tree-ring growth responses to climate. *Annals of Forest Science*, 62, 209–218.
- Savage M, Mast JN (2005) How resilient are southwestern ponderosa pine forests after crown fires? Canadian Journal of Forest Research, 35, 967–977.
- Savage M, Brown PM, Feddema J (1996) The role of climate in a pine forest regeneration pulse in the southwestern United States. *Ecoscience*, 3, 310–318.
- Savage M, Mast JN, Feddema JJ (2013) Double whammy: high-severity fire and drought in ponderosa pine forests of the Southwest. *Canadian Journal of Forest Research*, 43, 570–583.
- Savolainen O, Pyhäjärvi T, Knürr T (2007) Gene flow and local adaptation in trees. Annual Review of Ecology, Evolution, and Systematics, 38, 595–619.
- Scheller RM, Mladenoff DJ (2008) Simulated effects of climate change, fragmentation, and inter-specific competition on tree species migration in northern Wisconsin, USA. Climate Research, 36, 191–202.
- Schliep EM, Gelfand AE, Clark JS (2015) Stochastic modeling for velocity of climate change. Journal of Agricultural, Biological, and Environmental Statistics, 20, 323– 342.
- Schumacher FX, Day BB (1939) The influence of precipitation upon the width of annual rings of certain timber trees. *Ecological Monographs*, 9, 387–429.
- Schuster WSL, Griffin KL, Roth H, Turnbull MH, Whitehead D, Tissue DT (2008) Changes in composition, structure and aboveground biomass over seventy-six years (1930-2006) in the Black Rock Forest, Hudson Highlands, southeastern New York State. *Tree Physiology*, 28, 537–549.
- Schwartz MW, Hellmann JJ, Jason MM et al. (2012) Managed relocation: integrating the scientific, regulatory, and ethical challenges. *BioScience*, 62, 732–743.
- Shinneman DJ, Baker WL, Rogers PC, Kulakowski D (2013) Fire regimes of quaking aspen in the Mountain West. Forest Ecology and Management, 299, 22– 34.
- Shuman B, Henderson AK, Plank C, Stefanova I, Ziegler SS (2009) Woodland-to-forest transition during prolonged drought in Minnesota after ca. AD 1300. *Ecology*, 90, 2792–2807.
- Silvertown JW (1987) Introduction to Plant Population Ecology. Longman, White Plains, NY.
- Sitch S, Smith B, Prentice IC et al. (2003) Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. Global Change Biology, 9, 161–185.

#### 2352 J. S. CLARK et al.

- Snell RS (2014) Simulating long-distance seed dispersal in a dynamic vegetation model. *Global Ecology and Biogeography*, 23, 89–98.
- Song X, Zeng X (2014) Investigation of uncertainties of establishment schemes in dynamic global vegetation models. Advances in Atmospheric Sciences, 31, 85–94.
- Sork VL, Davis FW, Westfall R, Flint A, Ikegami M, Wang H, Grivet D (2010) Gene movement and genetic association with regional climate gradients in California valley oak (*Quercus lobata* Nee) in the face of climate change. *Molecular Ecology*, 19, 3806–3823.
- Stahle DW, Cleaveland MK (1992) Reconstruction and analysis of spring rainfall over the southeastern US for the past 1000 years. Bulletin of the American Meteorological Society, 73, 1947–1961.
- Stahle DW, Cleaveland MK, Hehr J (1988) North Carolina climate changes reconstructed from tree rings: AD 372 to 1985. *Science*, 240, 1517–1519.
- Sthultz CM, Gehring CA, Whitham TG (2009) Deadly combination of genes and drought: increased mortality of herbivore-resistant trees in a foundation species. *Global Change Biology*, 15, 949–961.
- Stogsdili WR Jr, Wittwer RF, Hennessey TC, Dougherty PM (1992) Water use in thinned loblolly pine plantations. Forest Ecology and Management, 50, 233–245.
- Swetnam TW, Betancourt JL (1998) Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. *Journal of Climate*, 11, 3128–3147.
- Taylor M, Haase DL, Rose RL (2009) Fall planting and tree shelters for reforestation in the east Washington cascades. Western Journal of Applied Forestry, 24, 173–179.
- Thomas Z, Waring KM (2015) Enhancing resiliency and restoring ecological attributes in second-growth ponderosa pine stands in northern New Mexico, USA. Forest Science, 60, 13–085.
- Thuiller W, Lavorel S, Araujo MB, Sykes MT, Prentice IC (2005) Climate change threats to plant diversity in Europe. Proceedings of the National Academy of Sciences of the United States of America, 102, 8245–8250.
- Tinner W, Colombaroli D, Heiri O et al. (2013) The past ecology of Abies alba provides new perspectives on future responses of silver fir forests to global warming. Ecological Monographs, 83, 419–439.
- Treyger AL, Nowak CA (2011) Changes in tree sapling composition within powerline corridors appear to be consistent with climatic changes in New York State. *Global Change Biology*, **17**, 3439–3452.
- Trottier-Picard A, Thiffault E, DesRochers A, Paré D, Thiffault N, Messier C (2014) Amounts of logging residues affect planting microsites: a manipulative study across northern forest ecosystems. *Forest Ecology and Management*, **312**, 203–215.
- Twidwell D, Wonkka CL, Taylor CA Jr, Zou CB, Twidwell JJ, Rogers WE (2013) Drought-induced woody plant mortality in an encroached semi-arid savanna depends on topoedaphic factors and land management. *Applied Vegetation Science*. doi: 10.1111/avsc.
- USDA Forest Service and US Geological Survey. 2000. Forest Cover Types. http://www.fia.fs.fed.us/library/maps/.
- Vanderwel MC, Lyutsarev VS, Purves DW (2013) Climate-related variation in mortality and recruitment determine regional forest-type distributions. *Global Ecology and Biogeography*, 22, 1192–1203.
- Voelker S, Muzika R, Guyette R (2008) Individual tree and stand level influences on the growth, vigor, and decline of red oaks in the Ozarks. Forest Science, 54, 8–20.
- Wackerman AE (1929) Why prairies in Arkansas and Louisiana? Journal of Forestry, 27, 726–734.
- Waltz AEM, Stoddard MT, Kalies EL, Springer JD, Huffman DW, Sánchez-Meador A (2014) Effectiveness of fuel reduction treatments: Assessing metrics of forest resi-

liency and wildfire severity after the Wallow Fire, AZ. Forest Ecology and Management, 334, 43-52.

- Wang GG, Chhin S, Bauerle WL (2006) Effect of natural atmospheric CO2 fertilization suggested by open-grown white spruce in a dry environment. *Global Change Biology*, 12, 601–610.
- Weed AS, Ayres MP, Hicke JA (2013) Consequences of climate change for biotic disturbances in North American forests. *Ecological Monographs*, 83, 441–470.
- Wehner M, Easterling DR, Lawrimore JH, Heim RR, Vose RS, Santer BD (2011) Projections of future drought in the continental United States and Mexico. *Journal of Hydrometeorology*, **12** (6), 1359–1377.
- Westerling AL, Hidalgo HG, Cayan DR, Swetnam TW (2006) Warming and earlier spring increase western US forest wildfire activity. *Science*, 313, 940–943.
- Westerling AL, Turner MG, Smithwick EAH, Romme WH, Ryan MG (2011) Continued warming could transform Greater Yellowstone fire regimes by mid-21st century. Proceedings of the National Academy of Sciences of the United States of America, 108, 13165–13170.
- Will R, Hennessey T, Lynch T, Holeman R, Heinemann R (2010) Effects of planting density and seed source on loblolly pine stands in southeastern Oklahoma. *Forest Science*, 56, 437–443.
- Williams AP, Allen CD, Swetnam TW, Millar CI, Michaelsen J, Still CJ, Leavitt SW (2010) Forest responses to increasing aridity and warmth in southwestern North America. Proceedings of the National Academy of Sciences of the United States of America, 107, 21289–21294.
- Williams AP, Allen CD, Macalady AK et al. (2013) Temperature as a potent driver of regional forest drought stress and tree mortality. Nature Climate Change, 3, 292– 297.
- Woodall C, Oswalt CM, Westfall JA, Perry CH, Nelson MD, Finley AO (2009) An indicator of tree migration in forests of the eastern United States. *Forest Ecology and Management*, 257, 1434–1444.
- Woodall CW, Domke GM, Riley K, Oswalt CM, Crocker SJ, Yohe GW (2013b) Developing a framework for assessing global change risks to forest carbon stocks. PLoS ONE, 8, e73222.
- Worrall JJ, Rehfeldt GE, Hamann A, Hogg EH, Marchetti SB, Michaelian M, Gray LK (2013) Recent declines of *Populus tremuloides* in North America linked to climate. *Forest Ecology and Management*, 299, 35–51.
- Wyckoff PH, Clark JS (2002) The relationship between growth and mortality for seven co-occurring tree species in the southern Appalachian Mountains. *Journal of Ecol*ogy, 90, 604–615.
- Yaussy DA, Iverson LR, Matthews SN (2013) Competition and climate affects US hardwood-forest tree mortality. *Forest Science*, 59, 416–430.
- Yeh HY, Wensel LC (2000) The relationship between tree diameter growth and climate for coniferous species in northern California. *Canadian Journal of Forest Research*, 30, 1463–1471.
- Zhang J, Webster J, Powers RF, Mills J (2008) Reforestation after the Fountain Fire in northern California: an untold success story. *Journal of Forestry*, **106**, 425–430.
- Zhu K, Woodall CW, Clark JS (2012) Failure to migrate: lack of tree range expansion in response to climate change. *Global Change Biology*, **18**, 1042–1052.
- Zhu K, Woodall CW, Ghosh S, Gelfand AE, Clark JS (2014) Dual impacts of climate change: forest migration and turnover through life history. *Global Change Biology*, 20, 251–264.
- Zimmermann NE, Yoccoz NG, Edwards TC et al. (2009) Climatic extremes improve predictions of spatial patterns of tree species. Proceedings of the National Academy of Sciences of the United States of America, 106, 19723–19728.