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

Running head: Drought impacts on forests

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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 multi-structured 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.

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Introduction

Drought is a departure from the mean climate for a region and represents moisture limitation resulting from below-average precipitation, high temperatures, or both. At the time of this

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writing, drought conditions have continued over much of the continental United States (US) for up to four 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 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 both for management and community ecology, the forest stand (O'Hara and 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.

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

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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.

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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 co-dominant trees in crowded stands (trees with crowns 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

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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 and 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. Their joint distribution of responses can only be predictive if it is observed and estimated as a joint distribution. For example, in contrast to co-dominant 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 Figure 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 both by light and moisture. The large number of positive interactions between light and drought result 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 US

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 and 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

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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 and Day 1939, Cook et al. 2001, Henderson and Grissino-Mayer 2009, Clark et al. 2014b), while growth of many non-oak 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 (Elliot and Swank 1994, Klos et al. 2009, Clark et al. 2011, 2014a, Brzostek et al. 2014), perhaps related to physiology and rooting (Abrams 1990, Abrams and 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 and Mladenoff 2008, Handler et al. 2014).

Opportunistic reports of mortality following drought are common (Hough and 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 and Clark 2002, Anderegg et al. 2013a, b, Berdannier and 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 ten 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 (Dietze and Moorcroft 2011, Lines et al. 2010, Gustafson and 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).

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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 US (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 and 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 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 (Elliot and 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 and 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

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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 US, drought can interact with fire to shape forest dynamics. Over the last century, much of the eastern US has experienced pluvials rather than megadroughts (Stahle et al. 1988, Stahle and 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 and Hessl 2010, Lafon and 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 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 and 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 and Varner 2012, Kreye et al. 2013), although human increases in ignition, alteration of fuels, and active suppression make it difficult to characterize pre-settlement fire regimes (Clark and Royall 1996, Parshall and 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 (McEwan et al. 2011, Belden and Pallardy 2009, Woodall et al. 2009).

Tree growth and mortality patterns in the western US

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

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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 US and adjoining Canada coincides with declining tree growth, often followed by mortality (Allen et al. 2010, Meddens et al. 2012, Williams et al. 2013, Hicke et al. 2013, Joyce et al. 2014, O'Connor 2013, Peters et al. 2014, 2015).

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.S. (Allen et al. 2015). High temperatures can increase drought-induced mortality in piñon (Adams et al. 2009) and are especially challenging for seedlings (Kolb and 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 and 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 and 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 U.S. during the 21st century, particularly for the Southwestern U.S. (Williams et al. 2010, 2013).

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Interactions between drought, fire, climate change, and human fire suppression have altered SSDs in forests throughout the western US (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 and deBenedetti 1979, Dolanc et al. 2013, Lutz et al. 2009) and extensive semi-arid woodlands and ponderosa pine in the Southwest (e.g., Covington and Moore 1994, Brown and Wu 2005, Mast and 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 high-density forests exacerbates moisture stress during drought. High-severity fires now occur in stands that historically supported frequent, low-severity fires (Barton 2002, Savage and Mast 2005, Goforth and Minnich 2008, Savage et al. 2013), and recent high-severity fires are strongly correlated with forest drought stress (e.g., Fig. 5). Projected warming in the 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 non-forest 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. 2000-2013 have resulted in widespread tree mortality from bark beetles (Negrón et al. 2009, Ganey and Vojta 2011, Williams et al. 2010, 2013). Defoliator populations may also benefit from drought-stressed trees, particularly on xeric sites (Weed et al. 2013). However, insect-drought interactions may not be intuitive and resistance to insect herbivory may yield lower drought tolerance and higher mortality rates during subsequent drought events (Sthultz et al. 2009). Early successional species that colonize after bark beetle infestations or wildfire may become more frequent in some areas (Pelz and Smith 2013, Shinneman et al. 2013).

Large diebacks have the potential to change species distributions more rapidly than has occurred in the past (Swetnam and Betancourt 1998, Gray et al. 2006, Millar et al. 2012, Fellows and Goulden 2012). Drought-induced mortality in the 1950s is probably responsible for extensive upslope retreat of ponderosa pine in New Mexico (Allen and Breshears 1998) and *Juniperus deppeana* in southeastern Arizona (Brusca 2013). Recent episodes of drought-induced mortality

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in California extend from high-elevation *Pinus albicaulis* in the Sierra Nevada (Millar et al. 2012) to southern California conifers (Minnich 2007), and a rapid redistribution of coniferous and broadleaf species occurred in southern California mountains during droughts of the early 2000s (Fellows and 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 US 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 (Dobowski 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 (Harper 1977, Grubb 1977, Silvertown 1987, Ibáñez et al. 2007). Susceptibility of juvenile trees may be particularly acute in dry regions where recruitment is already episodic (Brown and 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.

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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_2 (LaDeau and 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 and Adams 2001). Drought-induced increases in fecundity may be followed by reduced seed production up to several years thereafter (Innes et al. 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, e.g., canopy gaps, fires, landslides, ice storms, timber harvesting, and pest outbreaks (e.g., Savage et al. 1996, Brown and Wu 2005, Pederson et al. 2008), and they affect composition, structure, and function for many years (Cooper-Ellis et al. 1999, Dietze and Clark 2008, Kayes and 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 and 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

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(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 and 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).

Post-fire 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 shrub- 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 and 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 (Grossnickle 2005, Nilsson and Örlander 1995) 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 and 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

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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 (Grossirod 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 and 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 and 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, Morin et al.

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2007, Ibanez 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, though 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 and Thomas 2010, Mok et al. 2012, Clark et al. 2014a, Zhu et al. 2014, Vanderwel et al. 2013) 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

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and 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 US (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 US, 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 per yr in the Appalachians to > 2 km per yr on the Piedmont and coastal plain (Schleip et al. 2015). By 2100 mean isotherms 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 and 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 and 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 and Birks 1983). Late Holocene range expansion of three western conifers (Juniperus osteosperma, Pinus edulis, P. ponderosa) may have depended on long-distance dispersal events ranging from 25 to 100 km (Lyford et al. 2003, Gray et al. 2006, Lesser and Jackson 2012, 2013, Norris et al. 2015). Expansion of colonizing populations of *P. ponderosa* may have been slowed by Allee effects (Lesser et al. 2013). However, traditional interpretations

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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 and 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 and D'Amato *in press*). 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 US 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 US (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 and Nowak 2011). Additional evidence of poleward migration could include studies from Woodall et al. (2009), Monleon and Lintz (2015),

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and Delzon et al. (2013). Clearly, the rapid spread (> 10^3 m yr^{-1}) 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 shrub- 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 (e.g., Hollenhorst et al. 1993, Aukema et al. 2011, Kovacs et al. 2011), 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 and Waring 2014).

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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 and Granier 1988, McDowell et al. 2006, Gyenge et al. 2011) also reduces canopy interception of precipitation, thus increasing moisture that reaches the forest floor (Stogsdili Jr 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 non-tree species that can increase beneath open canopies (Nilsen et al. 2001). In dry forests of the western US, such negative effects may be offset by the fire hazard reduction that comes with most management options currently being implemented (e.g., Martinson and Omi 2013, Waltz et al. 2014).

Successful regeneration during drought depends on microsite conditions, including competition from non-preferred species. However, current practices and guidelines for seed transfer may need to be re-considered given the potential for locally maladapted genotypes, as well as the possibility of planting more heat- and drought-tolerant genotypes (Aitken et al., 2008, Joyce and 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 and 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

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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 out-competed by sprouting hardwood species (Haire and 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_2, 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 reources, 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 and Piutti 1998, Martin-Benito et al. 2011), evidence also can be found in stands (D'Amato et al. 2013, Thomas and 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_2 interacts with SSD, because increase in water-use efficiency of individual leaves or

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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 and 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 and 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 US, 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 (Dietze and Moorcroft 2011, Lines et al. 2010), 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 in press). Data sets containing long intervals between censuses can be hard to interpret because they integrate many years of climate variation. Many forest plots are re-sampled at intervals of 4

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to 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., McDowell et al. 2013, Hanson and Weltzin 2000), and few experiments at any scale include extreme drought and heat events (Jentsch et al. 2007) 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 and 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 non-spatial (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_2 (Lenihan et al. 2008, King et al. 2013), establishment mechanisms (Song and Zeng 2014), and patch age structure (Medvigy and Moorcroft 2012). DGVMs are used to predict change in functional types.

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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 and Mladenoff 2008, Loehman et al. 2011), including migration (Lischke et al. 2006, Scheller and Mladenoff 2008, Gustafson and 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^{o}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_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. 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 and Rehfeldt 2013, Rehfeldt et al., 2014).

Related to the third point, there remains a need to develop better model representations of climate-mediated 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. 2008c, Meier et al. 2012). A better understanding of how droughts affect seed production, seed banks, and seedling establishment near range limits, particularly their role

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in local extinctions and re-colonization (Zimmermann et al. 2009, Jackson et al. 2009) might improve characterization of extremes. The limited studies show large variation in fecundity (Clark et al. 2004, Koenig and Knops 2013) and recruitment (Ibanez 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 (Iverson et al. 2004, Prasad et al. 2013, Clark et al. 2003).

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 US, 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 US, 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

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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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Box 1. Forest droughts have increased in recent decades.

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Figure B1.1. Cumulative drought severity index (CDSI) for forested lands from 1987–2013, (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 and Goulden 2012 10. Ganey and 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. Twidwell et al. 2013 22. Williams et al. 2013 23. Worrall et al. 2013.

What changes in drought are in progress now?

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).

Figure B1.2. Drought for forested land of the conterminous United States for two 27–yr periods from 1960 to 2013. For each forest type, drought conditions were summarized as the percentage of months during the 324–month period (27 years) among climate divisions that contained the forested land. (From Peters et al. 2014)

Severe multi-year 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

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forests. Note that the map of cumulative drought over 27 years does not always capture short-term intense drought events.

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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 sub-continental 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 daylength, 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

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., in review).

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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 US, but during the growing season days are long. At this time, moisture is more available in the Northeast than the Upper Midwest.

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.

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 US (black line is drawn at zero difference before and after 1985). (From Clark et al., in review).

Perhaps most important are changes in surpluses and deficits, shown as a different map in Figure B2.2. Despite the fact that deficits dominate in specific regions (the West and Southeast), forests throughout the eastern US 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

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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).

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Figure captions

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Fig. 1. Growth responses to summer drought on mesic sites in Kentucky, from 1796-2005. Average tree growth (orange line with circles) correlates with an independent reconstruction of summer PDSI (Jun, Jul, Aug) (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 ≥ 2) and vice-versa (adapted from Pederson et al. (2012).

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

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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. Photos correspond to populations with size-density conditions that are highly vulnerable to drought impacts.

Figure 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).

Figure 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).

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) Satellite-derived 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).

Fig. 6. New recruits to FIA plots are relatively rare for oaks (upper panels) in comparison to 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

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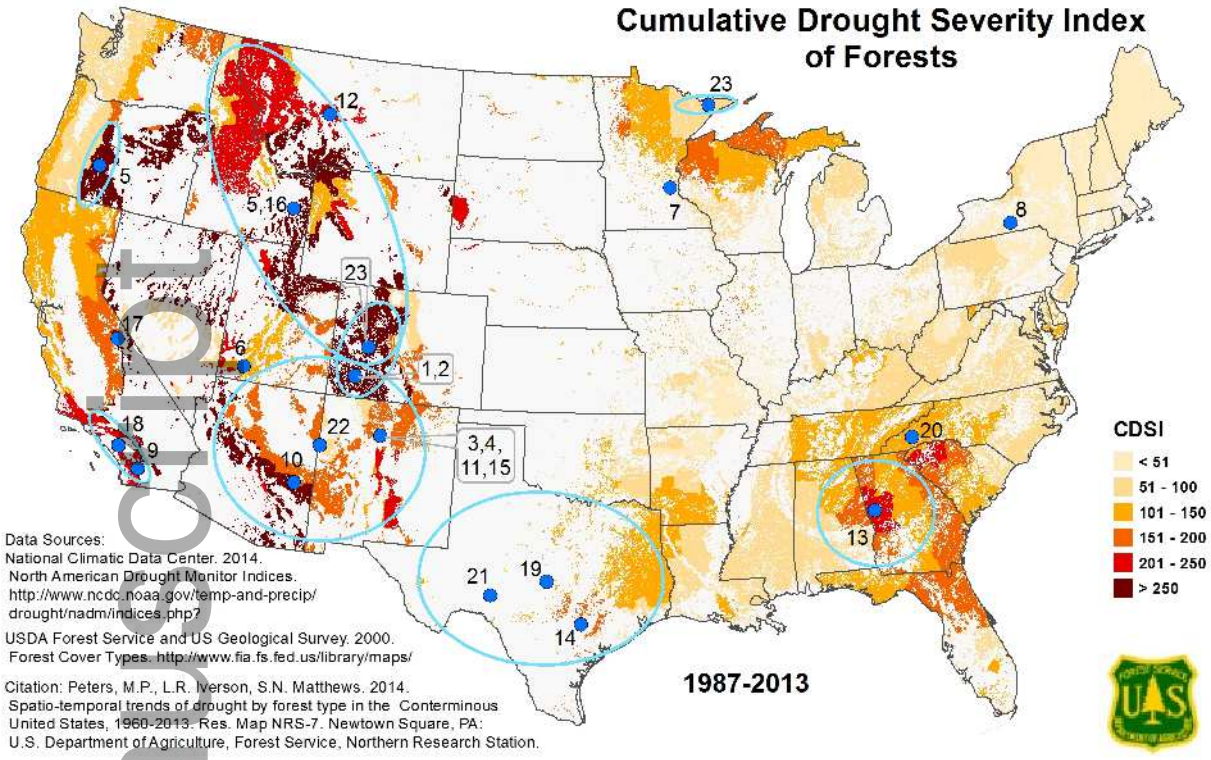
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fact that many models predict increasing oaks. Species are *Quercus alba* (querAlba), *Q. rubrum* (querRubr), *Liquidambar styraciflua* (liquStyr), and *Acer saccharum* (acerSacc). Grey symbols indicate presence of adults. Sizes of red circles are 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*.

Fig. 7. Models of distribution and abundance impose unrealistic relationships on FIA data from the eastern US. 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., in review.

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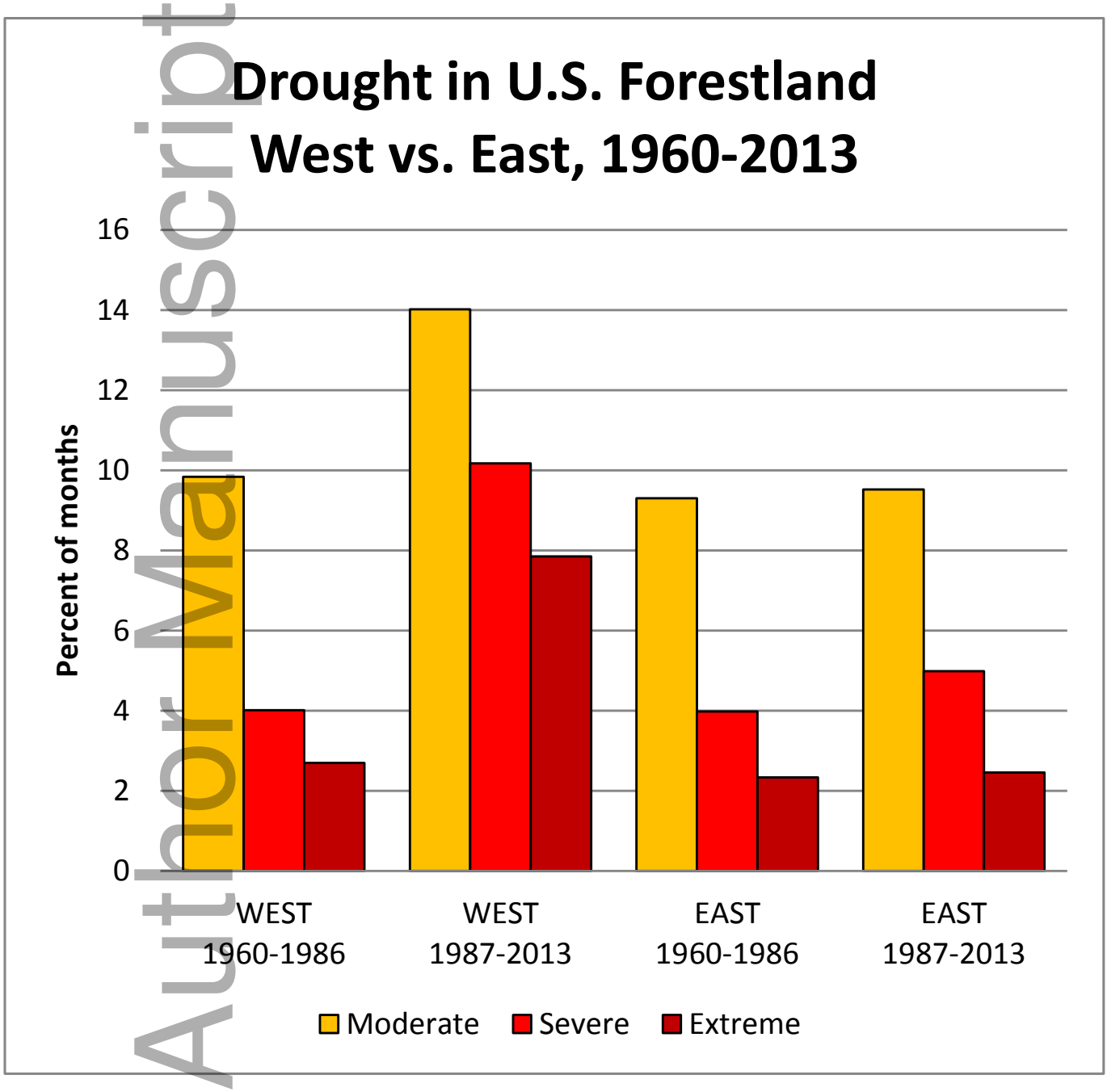


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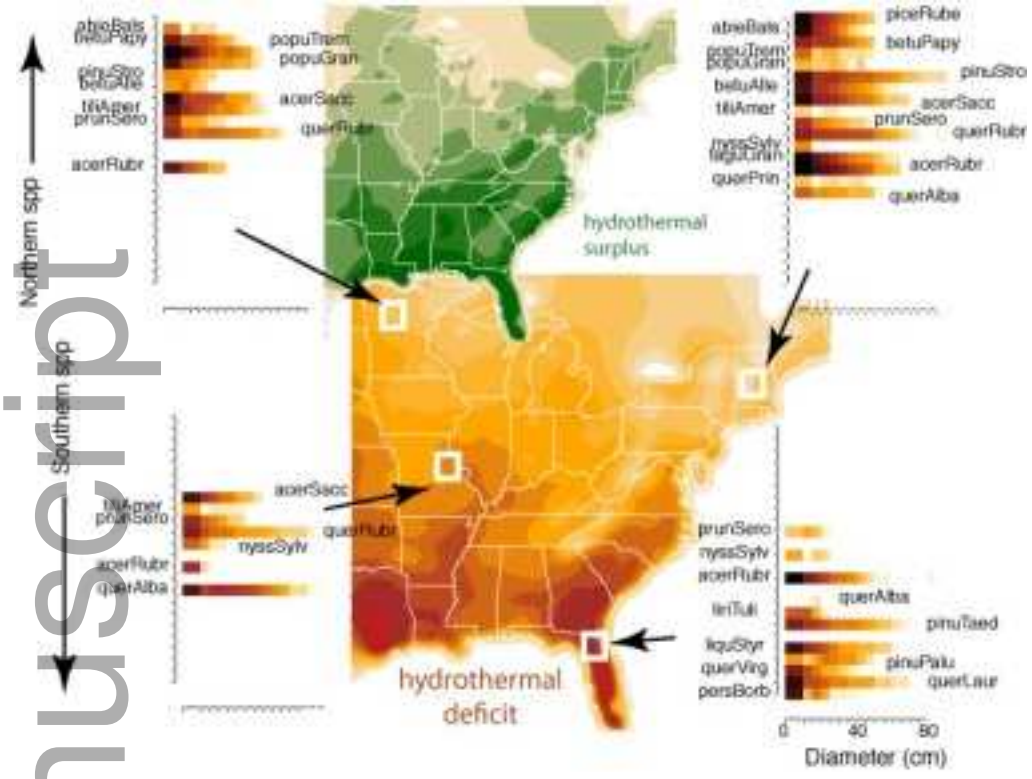
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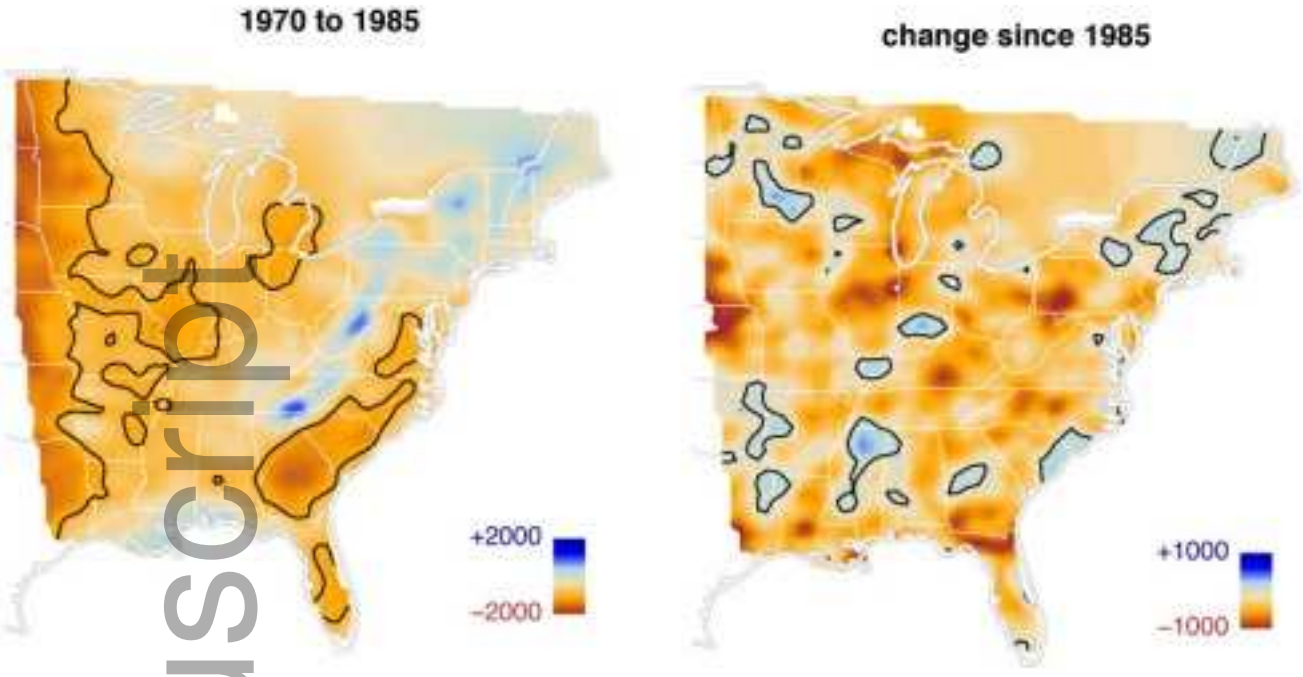
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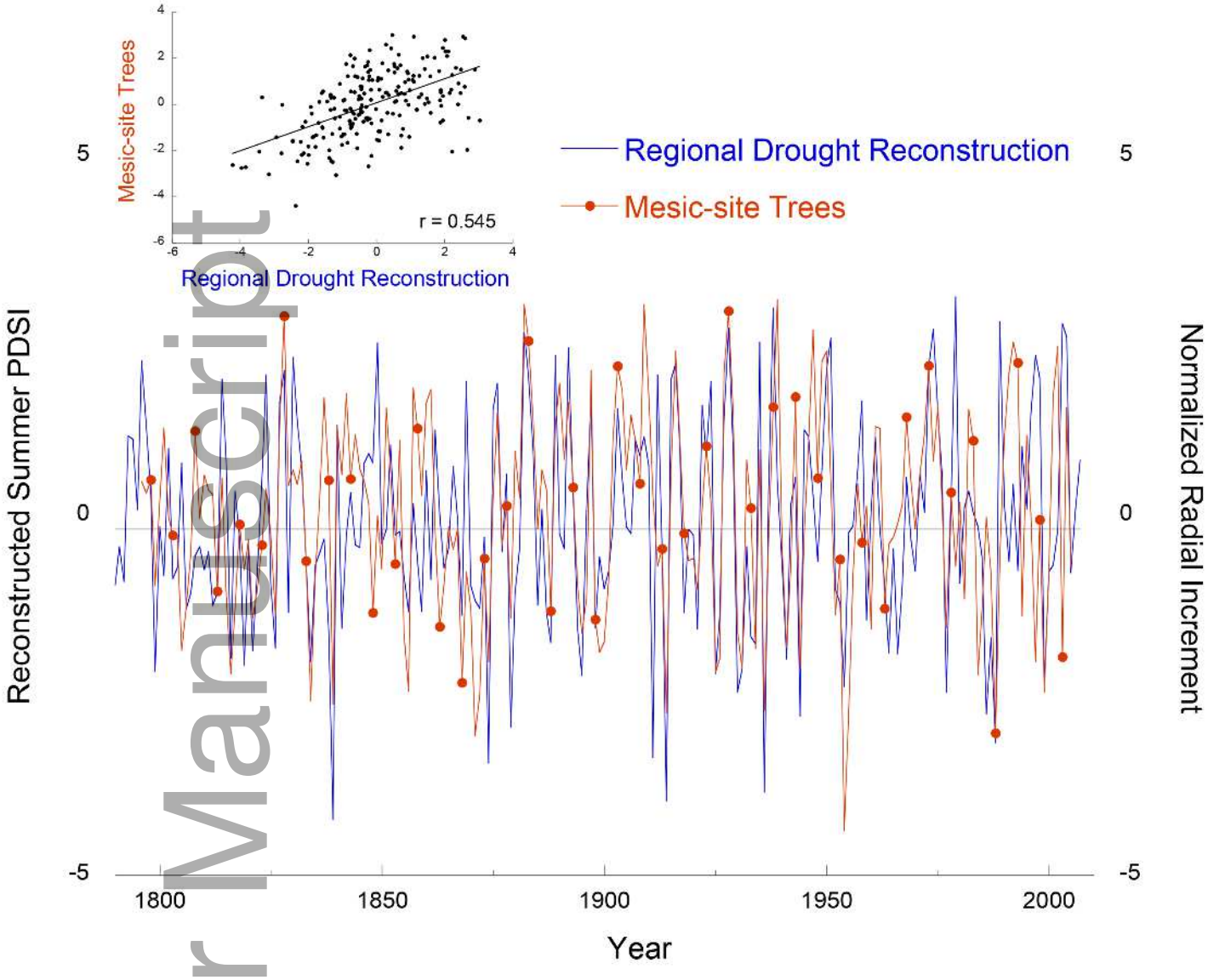
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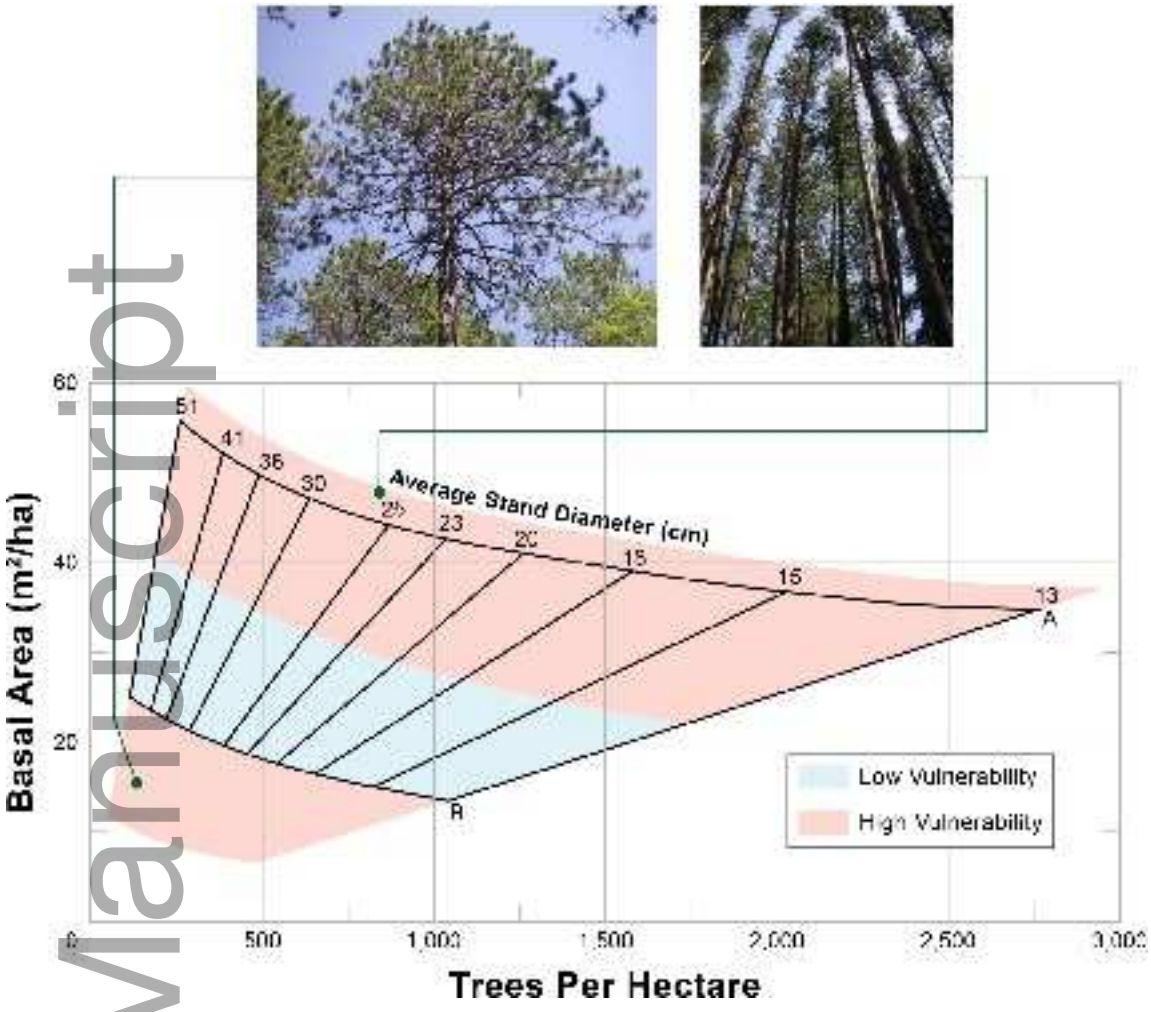


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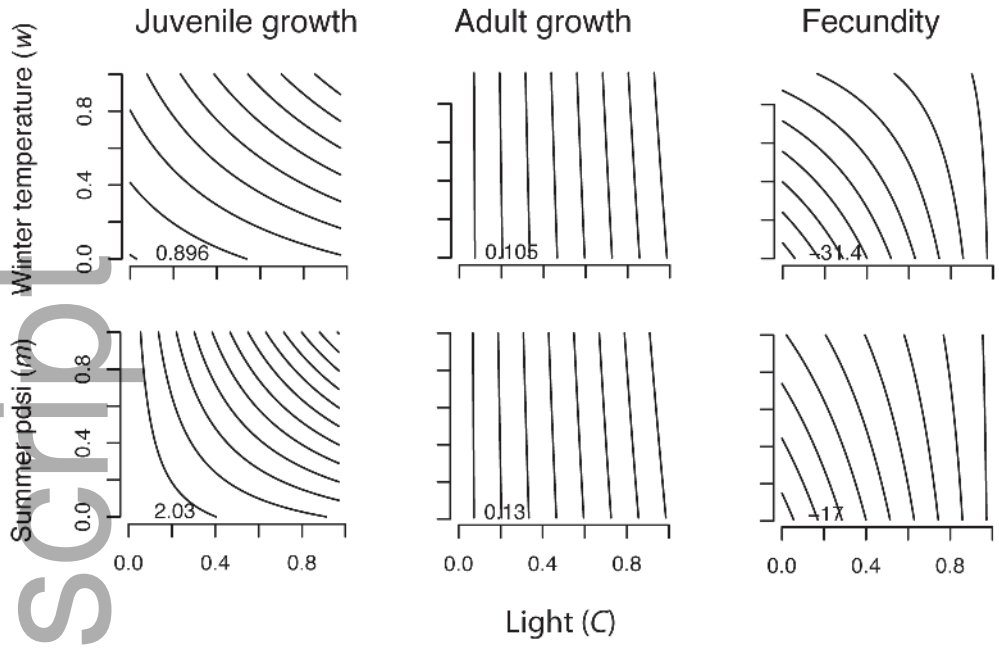
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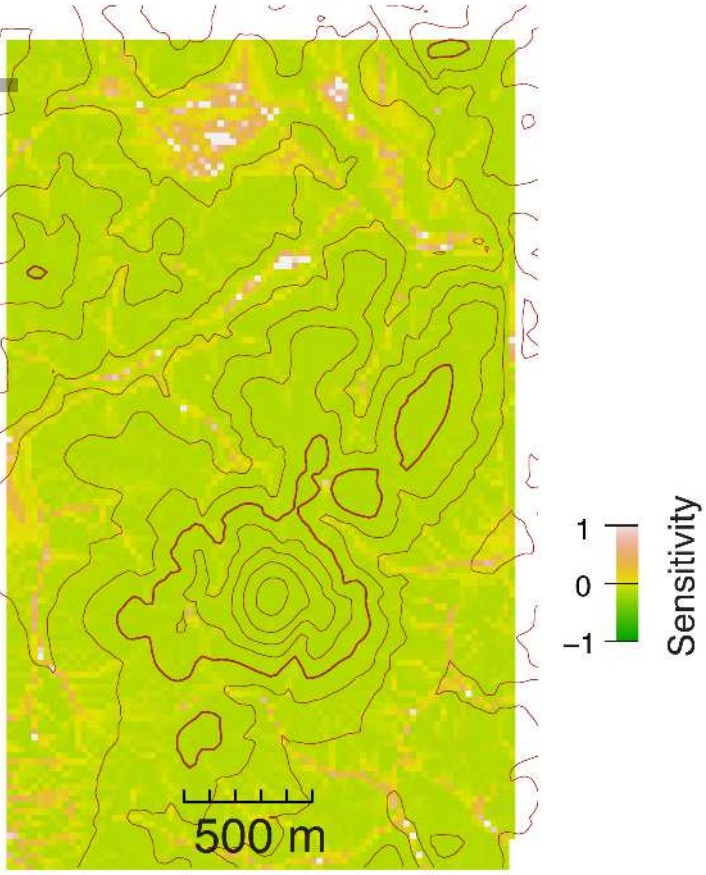


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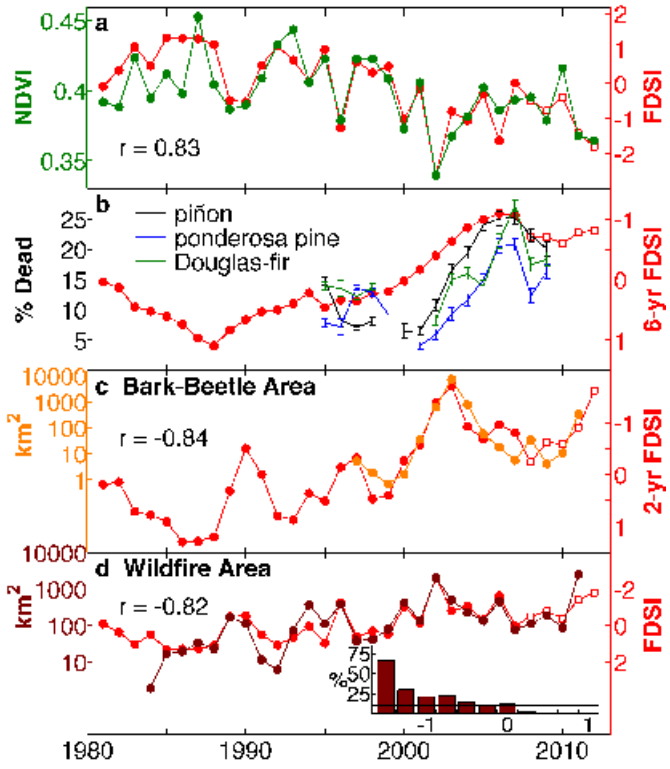
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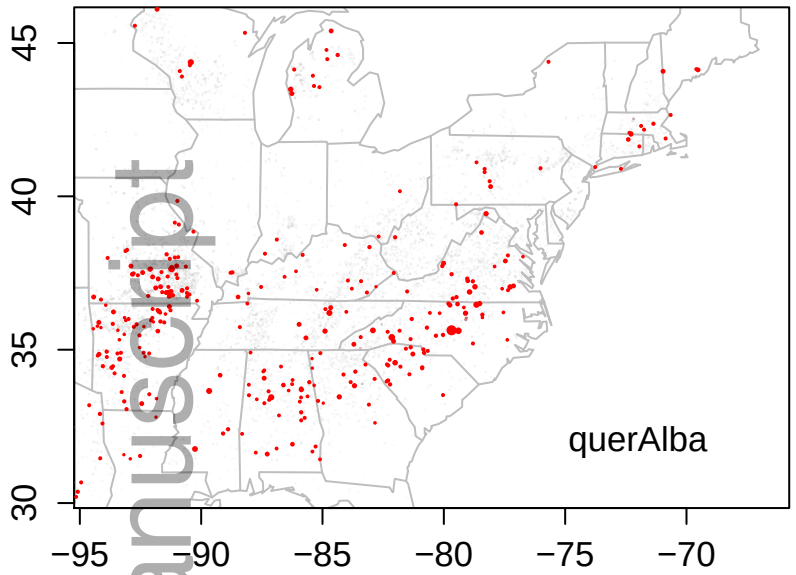
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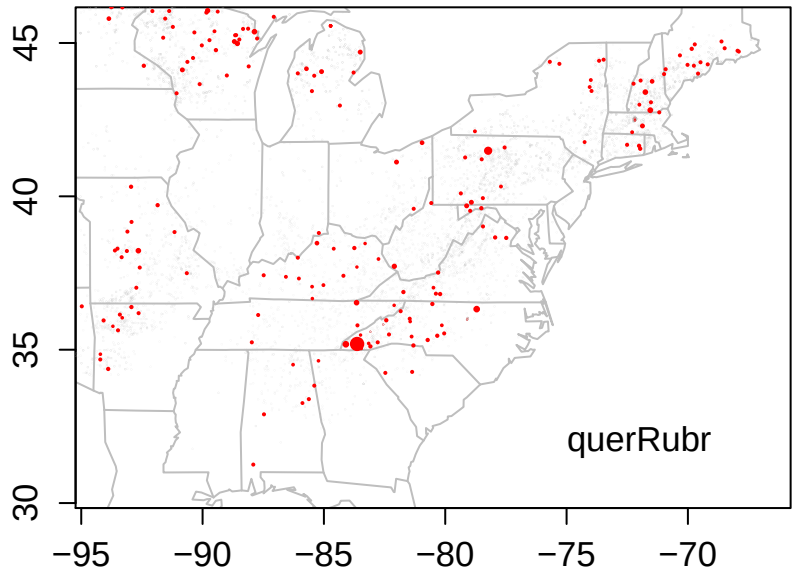
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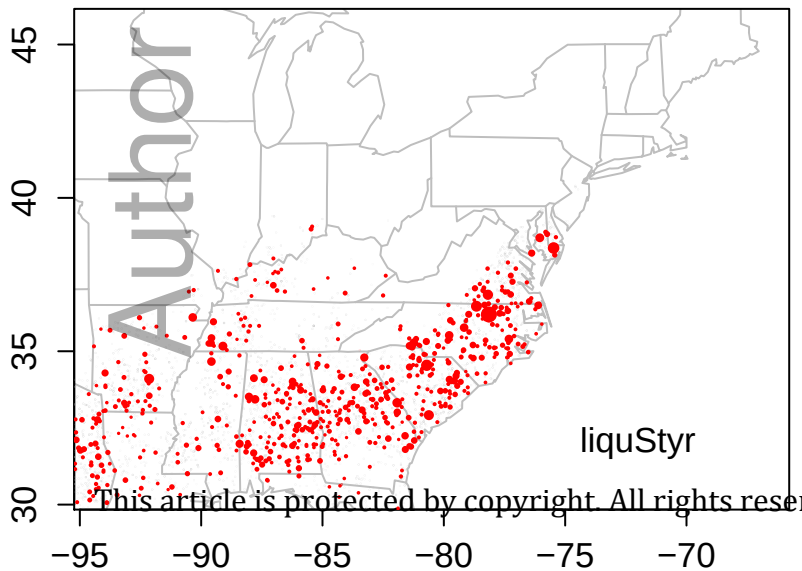
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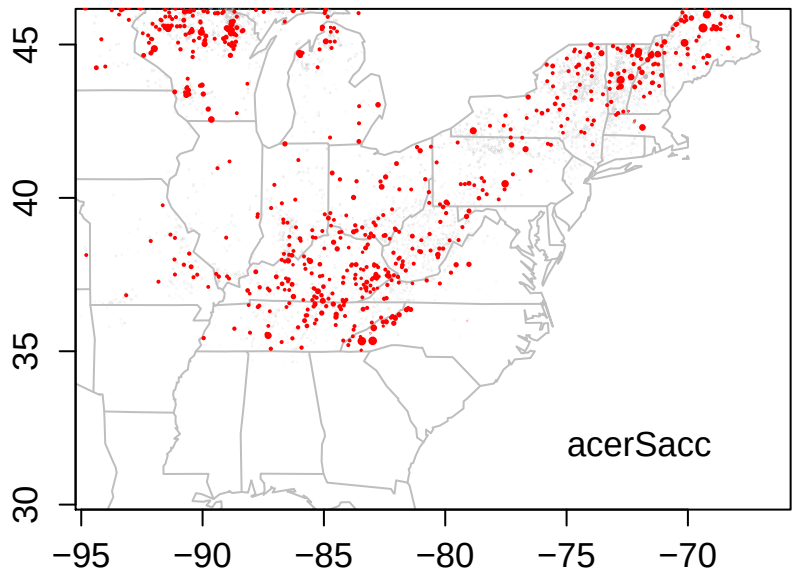


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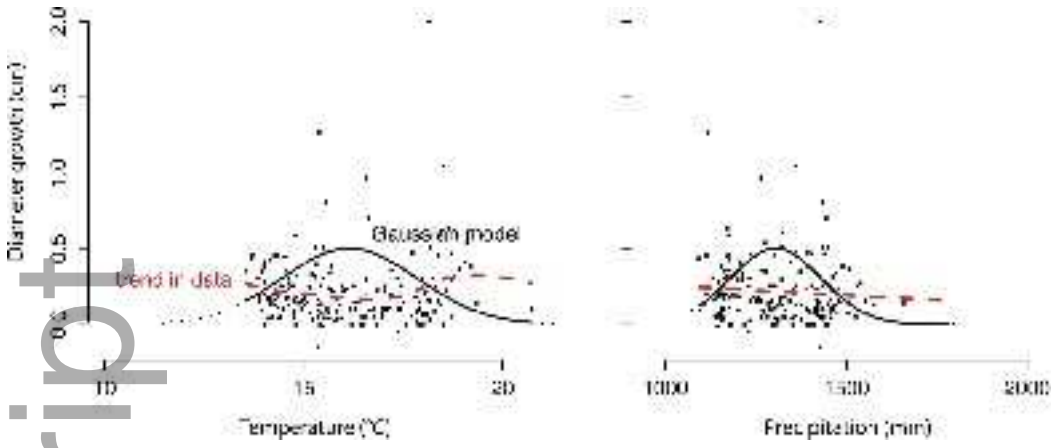






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