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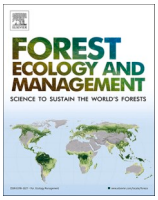

# Integrating disturbance to improve our understanding of range-wide patterns in tree species abundance and demography

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ABSTRACT

Climate and topography have long been recognized as the primary drivers of broad-scale geographic patterns in tree species abundance, demography, and occurrence, but within species ranges, forest disturbance regimes also play a fundamental role by affecting mortality, growth, and recruitment of tree species. Although forests are generally adapted to certain levels of disturbance, the intensification of disturbance regimes over recent decades highlights a pressing need to move beyond a purely climate-based understanding of tree species dynamics and to integrate the role of disturbance into macroscale considerations of forest ecosystems. Here, we review the independent and interactive impacts of four primary disturbance agents — extreme weather events, insect pests and tree diseases, human modification of the landscape, and fire — on North American forests, with considerations for the ongoing and expected effects of changing climate conditions. In particular, we emphasize how contemporary disturbances vary and interact across spatial and temporal scales, as well as how disturbance regimes may shift with future climate change. We show that forests in the eastern and western regions of the USA are largely governed by different sets of dominant disturbances and interactions, such that eastern forests tend to have higher levels of pest incidence and landscape modification by humans, whereas western forests are impacted by greater amounts of areas burned by fire and have experienced greater drought intensity in recent decades. Given this regionalization of disturbance regimes, we discuss how contemporary disturbances can be incorporated into statistical models of tree species abundance and demography to better understand future species trajectories. We summarize the main challenges of modelling disturbances with statistical models but highlight recent advancements and development of new data products that provide opportunities to tackle novel research questions, implement modelling approaches in innovative ways, and generate insights that can be used to inform forest management actions.

## 1. Introduction

Broad-scale geographic patterns of tree species abundance and demography in forest ecosystems have long been recognized to be primarily dictated by climate and topography (Brown, 1984; Copenhaver-Parry et al., 2017; Williams et al., 2004). Within tree species ranges, however, varying disturbance regimes can precipitate substantial deviation in abundance, mortality, growth, and recruitment from expectations derived solely from climate and terrain. Disturbance, defined as any relatively discrete event that disrupts ecosystem structure and changes resource availability or the physical environment (Pickett and White, 1985; Rykiel., 1985), plays an important role in the natural dynamics of forest ecosystems (Pickett and White, 1985; Sousa, 1984). The prevalence, frequency, extent, and severity of forest disturbances can be highly variable, both spatially and temporally (Rogers, 1996; Sommerfeld et al., 2018; Turner, 2010). Disturbance agents can be abiotic (e.g., heat waves, drought, fire, flooding, wind), anthropogenic (e.g., land use change, logging), or biotic (e.g., disease, insects), and they range widely in scale and impact (Rogers, 1996; Seidl et al., 2011), from partial defoliation of a single tree due to moth larvae to mass stand-level mortality caused by a wildfire. Regional disturbance regimes can influence contemporary abundance and demographic patterns irrespective of whether tree species are at their physiological optima, and well-adapted to their local environmental conditions or not (Rehfeldt

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et al., 2018). It is therefore pertinent to move beyond a purely climate-based understanding of tree species abundance and demography by integrating the role of disturbance into macroscale considerations of forest ecosystems.

Forests are generally acclimated to historical levels of disturbance, but shifting disturbance regimes (Cohen et al., 2016; Turner, 2010) due to recent global change can disrupt forest ecosystem processes and challenge our understanding of tree species dynamics (Seidl and Turner, 2022). Across North America, disturbances from extreme weather events (e.g., drought, heat waves), biotic interactions (i.e., insect pests and tree diseases), land use change, and fire are particularly important in modifying macroecological patterns of tree species abundance and demography in forest ecosystems at multiple scales. Specifically, the increasing pace and magnitude of severe weather and climatic extremes (Lenoir and Svenning, 2015), the growing number and severity of non-native insect pests and tree pathogens (Aukema et al., 2010; Gougherty, 2023), the expanding impacts on landscapes by humans (Stanke et al., 2021), and the regional intensification of wildfire activity (Rogers et al., 2020) can drive local and regional processes that result in spatial and temporal deviations from emergent macroscale patterns. The challenge of understanding the shifting nature of these disturbances and concomitant impacts is further complicated by their potential interactions (Seidl and Turner, 2022) — for instance, the amplification of pest damage and fire severity due to recent drought conditions — which can have complex, difficult-to-predict effects on tree species abundance and demography.

Forest management plans could be more effective if we integrate disturbance into current macroscale analyses of forest ecosystems, particularly as disturbances continue to intensify due to recent global change (Seidl et al., 2017). Here, we lay the groundwork for such efforts by providing an overview of the impacts of four primary disturbance agents on North American forests and discussing how disturbance can be incorporated into statistical models of tree species abundance and demography to better understand future species trajectories. We focus on four sources of disturbance with widespread and systematic impacts on tree species patterns across North America, specifically: (i) extreme weather events, (ii) the occurrence of insect pests and tree diseases, (iii) human modification of the landscape, and (iv) fire. We begin by discussing the role of climate in controlling tree abundance and demography and how future changes in baseline climatic conditions may shift broadscale patterns. Next, we review how each of four disturbances can independently impact tree species abundance and demography, with particular emphasis on how they vary across spatial and temporal scales. We then provide examples of interactions among disturbances and with future climate change that will affect tree species. To demonstrate the importance of considering multiple disturbances we explore the geographic distribution of the four disturbance types and their potential interactions across the conterminous USA, focusing on where the disturbances are most impactful and highlighting unique combinations of threats. Finally, we discuss multiple approaches for integrating disturbance with macroscale models of contemporary and future tree species abundance and demography, and we conclude by identifying remaining challenges and opportunities.

## 2. Setting the stage: climate and future change

Together, temperature, precipitation, and other climate factors mediate processes that impact forests globally, with an influence that touches all levels of ecological organization, from the broadest extent of defining species ranges to the fine-scale regulatory processes of individual tree physiology. Throughout species ranges and across spatial scales, climate forcing exert specific constraints on tree growth and development. For example, at northern latitudes and high elevations, range boundaries are often limited by minimum temperatures (MacArthur, 1972), which impose thresholds where adaptive strategies to overcome freezing conditions and minimize tissue damage and xylem embolisms are key to survival (Wang et al., 2022). Within species ranges, temperature also plays a role in driving patterns of seed production, which can influence recruitment (Clark et al., 2021). The ability of tree species to tolerate moisture deficits and drought by conserving water and limiting stomatal activity also places fundamental limits on species distributions along precipitation gradients (Piedallu et al., 2016).

With the acceleration of climate change over the last 30 years (Dobrowski et al., 2013), there is clear evidence that decadal climatic shifts will fundamentally change the baseline environmental conditions that trees experience, and will affect forest ecosystem function, forest composition, tree distributions, and the growth and vigor of individual trees (Goring and Williams, 2017; Stanke et al., 2021; Zhu et al., 2012). A change in baseline climatic conditions is expected to result in many tree species shifting their distributions northward and upslope, and some shifts in tree abundance have already been documented (Fei et al., 2017). While local population dynamics may be more complex than for species as a whole — for instance, requiring populations to shift in different directions to minimize maladaptation (Gougherty et al., 2021) — they nevertheless indicate that tree distributions and intra-range patterns of abundance and growth will need to shift to maintain their contemporary associations with climate. In the arctic zone, where warming is occurring at higher rates (Overland et al., 2011), shifts in vegetation point to the importance of understanding the impact of novel forest conditions (Gougherty et al., 2024). While some tree species populations may be able to take advantage of newly available habitats that lack interspecific competition, many are likely to struggle to migrate given dispersal limitations, which would necessitate acclimating or adapting to new climates beyond those they have experienced in the recent past.

Climate is also a prominent driver of recent changes in disturbance regimes (Seidl et al., 2011), often increasing the occurrence and severity of disturbances, which in turn affects multiple aspects of forest ecosystems. Based on a global review of studies addressing the climate sensitivity of forest disturbances (Seidl et al., 2017), many of the documented effects of climate on forest disturbance agents are direct, although indirect influences have also been documented through climate-mediated changes in forest structure and composition. Climate also has direct effects on tree diseases (Sturrock et al., 2011) and fire (Williams and Abatzoglou, 2016), and the extent of these effects appear to be increasing throughout species ranges (Bonannella et al., 2024). Looking forward, shifts in disturbances caused by ongoing and future climate change are expected to have profound impacts on forest ecosystems (Lindner et al., 2010), with consequences for macroecological patterns in tree species abundance and demography.

## 3. Extreme weather events

Changes in baseline historical climate conditions are likely to be accompanied by increased frequency, severity, and duration of extreme weather events that will impact tree growth and mortality. Many extreme weather events, such as heat waves, droughts (Peters et al., 2014), extreme precipitation (Jamali et al., 2023), and high winds, have been either documented or predicted to increase with contemporary climate change. These disturbance agents can impact forests at multiple scales — impacts from floods and windthrows may be hyper-localized, while drought and heat waves can occur over entire continents. Long-term repeated extreme events can reduce growth and vigor regionally (Villalba and Veblen, 1997), but larger scale events are more likely to influence tree species at the scale of their geographic ranges. Across western North America, for instance, drought and heat waves have been linked to large-scale mortality events (Allen et al., 2010), and in some cases, moisture deficits so severe that they resulted in a shift in forest conditions (Urli et al., 2015). While some tree species and populations are particularly well-adapted to drought and high temperatures (Niinemets and Valladares, 2006), many could exceed their thermal

and/or hydraulic safety margins (Lancaster and Humphreys, 2020) during heat waves, which can result in reduced photosynthesis, damaged leaf tissue, and stunted growth. Combined with increased annual temperatures and altered precipitation regimes, the impact of extreme weather events are likely to accelerate climate change impacts and exacerbate forest vulnerability to other disturbances, resulting in unique spatial signals across broad geographic domains.

## 4. Insect pests and tree diseases

Insect pests and tree diseases (hereafter, pests) can have numerous direct and indirect impacts on tree species abundance and demography, which occur at multiple spatial and temporal scales. Direct impacts include herbivory and necrosis, which can reduce the growth and vigor of affected trees, resulting in excessive host tree mortality (Fei et al., 2019) and altering the demographic trajectory of impacted host populations over time (Gandhi and Herms, 2010). Impacts from native pests can be lessened from the long-term co-evolutionary relationship between pests and hosts when hosts have evolved defenses to limit pest damage. Defenses against non-native pests, however, may be limited (Brockerhoff and Liebhold, 2017), which can allow particularly aggressive pests to devastate host populations and in extreme instances result in localized extirpation. Chestnut blight (*Cryphonectria parasitica*), white pine blister rust (*Cronartium ribicola*), and Dutch elm disease (*Ophiostoma novo-ulmi*) provide historical examples of non-native pests that have profoundly impacted the abundance of their host trees throughout their ranges, while contemporary invasions by sudden oak death (*Phytophthora ramorum*), butternut canker (*Ophiognomonia clavigignenti-juglandacearum*), emerald ash borer (*Agrilus planipennis*), and hemlock woolly adelgid (*Adelges tsugae*) pose similar threats that have not yet been fully realized. Recent estimates suggest that as much as 40 % of aboveground forest biomass in the conterminous USA is at risk from just 15 non-native pest species (Fei et al., 2019) — a percentage that is likely to increase as established non-native pests continue to spread on the landscape and new pest species are introduced.

While host tree species will experience the brunt of direct impacts from pests, non-host trees are also affected. The rapid decline of host species, especially major overstory species, can introduce canopy gaps that facilitate the growth of other species that may be released from competition. For instance, the loss of American chestnut (*Castanea dentata*) as a major overstory tree in the Appalachian Mountains likely facilitated the growth of oak (*Quercus*) and hickory (*Carya*) species throughout the region (McCormick and Platt, 1980). Likewise, maple (*Acer)* and elm (*Ulmus*) species have responded positively to high mortality of ash (*Fraxinus*) species from emerald ash borer in the midwestern USA (Flower et al., 2013). The creation of forest gaps also opens space for the establishment and expansion of non-native understory plants, which may crowd out seedlings of native trees (Eschtruth et al., 2011; Hoven et al., 2017). These same direct and indirect effects on tree abundance are also likely to be evident from lower-impact pests, which do not directly cause tree mortality, but could nevertheless impact local demographic trajectories of host and non-host trees over extended time periods.

## 5. Human impacts on landscape

Compared to pest impacts, the effect of landscape modification by humans on forests may be more systematic. While pests may directly impact specific host tree species, human actions such as urbanization, land clearing for agriculture and cultivated crops, and purposeful plantings of trees for food and cultural uses can have stand-level impacts on tree communities in a variety of ways. In North America, humans have continuously modified the landscape, and Indigenous peoples have a long cultural history of interactions with forests (Williams, 2008), but there was a significant shift in the pace and severity of landscape change post-European colonization. European colonizers engaged in widespread and intensive deforestation efforts, which involved logging, burning, and clearing millions of hectares of forests (Foster, 1992). The effect of these and more contemporary land use disturbances (e.g., fire suppression, forest harvesting, forest replanting, building of infrastructure and travel ways) are evident from reduced diversity and homogenization of forests decades or centuries after an initial shift in land use type or land use intensity (Schulte et al., 2007). Although the trend of large-scale deforestation for agriculture has stabilized in some regions, North America still experiences among the highest levels of forest loss globally — ostensibly due to both natural and human-caused disturbance (Hansen et al., 2010). Even absent large-scale land clearing, more subtle human intervention can impact tree abundance. Preferential planting of desirable or economically important trees, along with removal of undesirable trees, affect local patterns of tree species abundance and composition (Clark and Covey, 2012). Likewise, global trade, urbanization, and habitat degradation have facilitated the introduction of plants from other regions, which can negatively impact native trees, contributing to biotic homogenization and shifts in ecosystem function (Petsch et al., 2022).

Conversion of forests to agriculture, urbanization, and industrialization not only decreases the absolute area available to trees in forest ecosystems but has the secondary effect of fragmenting the landscape and degrading available habitats. Plants in forested landscapes intersected by travel ways (e.g., roads, railroads), agriculture, human infrastructure, and urban development, or in forest patches that occur in matrices of low-quality habitat, could experience significant barriers to seed dispersal and potentially lower migration rates (Dullinger et al., 2015). Lack of connectivity can result in populations becoming isolated and maladapted to local or changing climatic conditions due to disrupted gene-flow and dispersal, especially those species with heavy seeds and shorter dispersal distances. While wind-pollinated and wind-dispersed trees may be less affected by forest fragmentation than animal-dispersed plants (Alados et al., 2010), geographic variation in seed size, dispersal mechanism, and forest fragmentation suggests that tree species will be differentially impacted by human-caused landscape modifications.

## 6. Fire

Many tree species in North America are adapted to some level of fire activity, and like other disturbances, fire plays an important role in natural forest function, such as facilitating nutrient cycling and regeneration within many forest ecosystems. However, the growing frequency and heightened severity of fire events, due to a combination of climate change, land use change, and past forest management decisions (e.g., fire suppression), are exposing tree species to megafires (Linley et al., 2022) and fire regimes they have not experienced in recent history, resulting in novel fire-vegetation-climate interactions (Liang and Hurteau, 2023). Increased fire intensity has the potential to shift forest communities away from those that have evolved to accommodate a particular fire regime. In general, immediately following a severe fire, species richness is typically reduced, as is stem density and basal area (Pellegrini et al., 2021), but depending on the geographic location and species composition, forests can begin to recover quickly (Bartels et al., 2016) (but see Celebrezze et al., 2024). Exposure of forest communities to new fire regimes would imply a transition toward more pyrophilic species that can grow and reproduce under the new fire regime. While this has been the case historically, the combined effects of climate change and increased fire severity can result in unexpected consequences, where even fire-adapted species can fail to regenerate following fire (Baltzer et al., 2021).

Pine (*Pinus*) species are a particularly relevant example of a taxonomic group whose abundance and demography are linked to fire (Pausas, 2015), which has played a key historical role in their diversification and evolutionary response to angiosperm competition (Keeley, 2012). Although not all pines tolerate or respond positively to fire (Singh

et al., 2018), the prevalence of fire-adaptive traits (e.g., thick bark, serotinous cones) in many pine species indicates long-term evolutionary associations with direct links to mortality, recruitment, and abundance (Flannigan, 1993; Flannigan and Wotton, 1994). The importance of fire to pine species abundance is also indirectly seen in regions where pines were introduced and their spread was facilitated by human-mediated fire (Franzese and Raffaele, 2017; Richardson and Bond, 1991). Angiosperms can also benefit from fire, which may have contributed to their global spread and diversification over evolutionary time (Bond and Scott, 2010). Certain tree assemblages, such as those in the open oak ecosystems of eastern North America, are dominated by fire-tolerant species and require specific fire regimes to regulate regeneration and maintain forest structure (Hanberry et al., 2018). In addition, the ability of some angiosperms to resprout quickly — a characteristic less common among gymnosperms (Burrows, 2021) — allows some species to respond rapidly after even large and intense fires (Wan et al., 2014). Certain angiosperm species can further resist burning (e.g., due to leaves with relatively high moisture content), driving patchwork patterns of tree species diversity in fire-impacted forests. The complex interplay between fire history and vegetation is important for understanding patterns of abundance and demography for tree species in fire-prone areas which, through human action (Balch et al., 2017) and climate change (Flannigan et al., 2009), are predicted to expand in the future.

## 7. Interactions and geographic patterns of disturbance

The impacts of forest disturbance agents on tree species abundance and demography are not expected to act in isolation, but instead operate interactively, with direct and indirect feedbacks among extreme weather events, pests, land use change, fire, and shifting climate conditions (Seidl et al., 2017). These interactions are complex, frequently non-linear, and compounding over time in ways that preclude straightforward predictions for the outcome of successive disturbances (Kleinman et al., 2019; Sturtevant and Fortin, 2021). For instance, the nature (e.g., extent, intensity) of a specific interaction is determined by a variety of factors (Kane et al., 2017), including the individual disturbance agents and mechanisms, the sequence and arrangement of overlap, the time since previous disturbance, legacy effects, and potential synergy. Despite these complexities, certain impacts of interacting disturbances on tree species are documented in the literature, which provides clarity into the directionality of the marginal effects and interactions (Anderegg et al., 2015; Canelles et al., 2021; de Chazal and Rounsevell, 2009; Dube, 2009). For example, previous research indicates that the majority of recorded interaction effects tend to be positive, such that disturbance is amplified as a result of interacting agents, and links between abiotic and biotic disturbances (where the former influences the latter) seem to be particularly strong (Seidl et al., 2017).

Shifts in temperature and precipitation are occurring at large spatial scales, and thus climate change will have pervasive effects on tree species abundance and demography. Climate change-driven heat waves and droughts have been directly linked to increased tree mortality (Allen et al., 2010), but these extreme weather events can also elevate tree stress (Liu et al., 2024), leaving them vulnerable to bark beetle damage and outbreaks, which can then accelerate tree mortality. High levels of mortality from drought and pests can further result in increased surface fuel loads and tree flammability that exacerbates the severity and extent of forest fires, which can in turn lead to increased tree mortality. While the directional effect of outbreaks on fire behavior and fuel loads will vary (e.g., canopy fires may be reduced immediately following a bark beetle outbreak (Hicke et al., 2012)), it is also possible that mediating forces, such as drought-resistant tree species (Grossiord, 2020), trait diversity (Jactel et al., 2017), and variation in how pests respond to climate change (Jactel et al., 2019), could dampen or reverse these effects in some situations. Nevertheless, this example of how climate shifts, extreme weather events, pests, and fire can interact to cause increasingly higher tree mortality illustrates the interactive and compounding nature of disturbances and how their effects are spatially and temporally dependent.

The strength of interactions among disturbances will be partially dependent on their degree of spatial overlap, and strong geographic patterns in disturbances implies that some regions, along with their constituent tree species, may be more prone to certain disturbances and specific interactions among disturbances. In an initial exploration of the geographic patterns of the four primary disturbances we assessed (i.e., extreme weather events, pest incidence, human landscape modification, fire), we found distinct patterns of regionalization across the USA, showing that forests in the eastern and western regions are largely governed by different sets of dominant disturbances (Fig. 1) and differing regimes of overlapping high-intensity disturbances (Fig. 2). The eastern USA is dominated by high levels of landscape modification by humans, due primarily to higher population densities (e.g., urban areas), industrialization, and agriculture. There are also relatively high levels of pest incidence in the eastern USA — particularly in the Northeast and Midwest, as well as in the sparser forests of the Great Plains region — and relatively high levels of drought severity in the southeastern states. It is worth noting that areas in the eastern USA with high pest incidence coincide partially with high numbers of non-native pests (Liebhold et al., 2013) — many of which were first introduced in port cities along the eastern coast (Ward et al., 2019) — as well as low-density forests that occur west of the eastern deciduous region (Woodall and Weiskittel, 2021). Meanwhile, the western USA has notably higher levels of drought severity and greater amounts of areas burned by fire. These two disturbance types are likely acting in conjunction with historical fire suppression tactics — an indirect form of landscape modification — that have resulted in increased fuel loads and denser forests (Woodall and Weiskittel, 2021), allowing for larger areas to burn. In addition, human landscape modification is generally less impactful in much of the western USA due in part to lower population density and more rugged terrain, with the exception of isolated instances of highly developed urban areas (e.g., along the Pacific coast). Pest incidence is likewise more sporadic compared to the eastern USA, potentially due to less continuous forests or fewer non-native pests.

Of particular concern for forest health and management are regions where high-intensity disturbances overlap, as trees may need to respond to multiple threats simultaneously. In a simple spatial analysis, we observed several notable regions with multiple high-intensity disturbances (Fig. 2), including California (contending with drought, fire, human footprint, and sporadically pests), the south-central semi-arid prairies of Texas and Oklahoma (contending with fire, pests, and either drought or human footprint), and the southeastern coastal plains of Florida and Georgia (contending with drought, human footprint, and either fire or pests). Although the precise physiographic, environmental, and biotic drivers are unique to each type of disturbance, their cumulative and interactive nature (as discussed above) indicates that trees in these particular regions of the USA could face the greatest adversity from ongoing and intensifying disturbance regimes. The additional influence of temperature and precipitation on disturbances and the potential amplifying effects of future climate change suggest that the total area of forests experiencing high-impact disturbances could expand in the future, with ever-mounting challenges to trees and forest management.

## 8. Modelling considerations

Isolating the individual effects of disturbances and separating them from the baseline roles of climate and topography on tree species abundance and demography is a challenging endeavor in part because disturbances can act independently and interactively on different spatial and temporal scales. Impacts of pest outbreaks and fire, for instance, can be acute in space and time — impacting only a small number of trees for a brief period — while landscape modification may be more systematic and consequential over decades. This potential discrepancy in

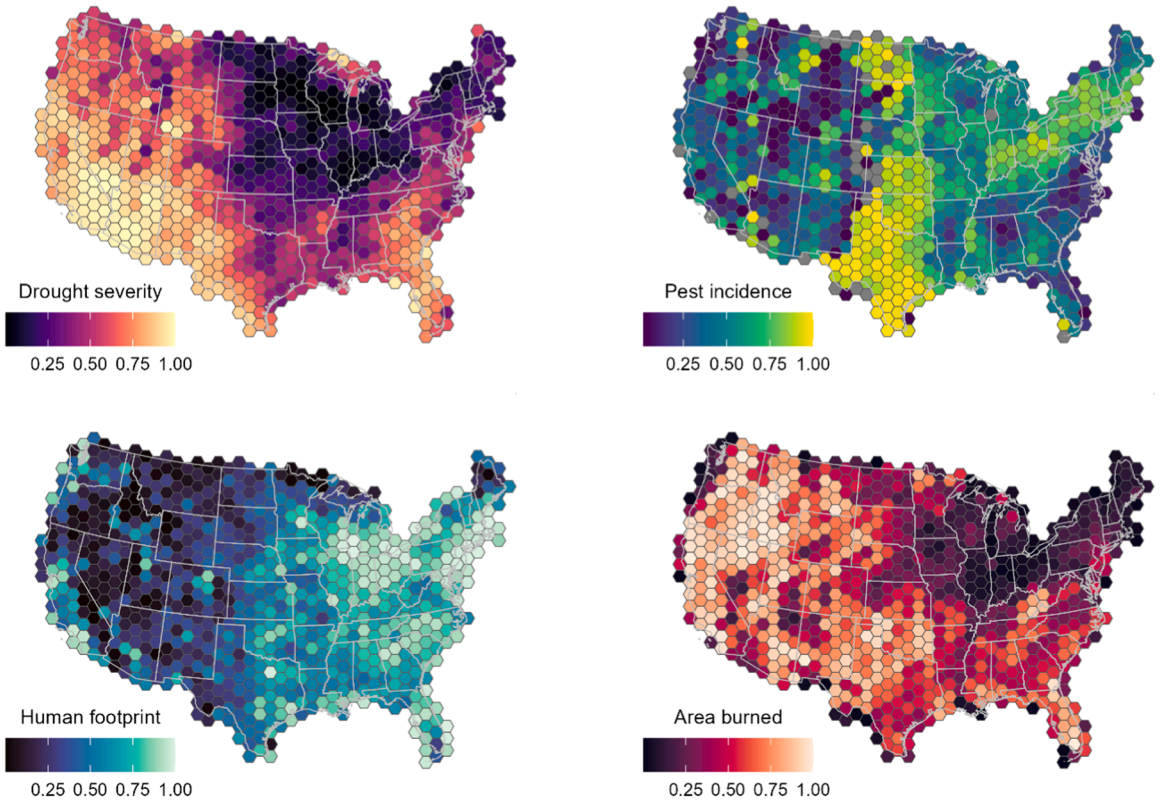


**Fig. 1.** Maps of the relative intensity of cumulative drought severity, forest pest incidence, human footprint, and area burned by fire across the conterminous USA. These four disturbance agents are expected to affect tree species abundance and demography both individually and interactively. Each metric has been scaled to its quantiles to reduce the influence of outliers and facilitate direct comparison between disturbances. In each map, values above 0.5 indicate that the disturbance is greater than the median value for the entire USA. All metrics were aggregated into 11,000 $km^2$ hexagons covering the conterminous USA. See Supplemental Material for a description of how metrics were calculated and mapped.

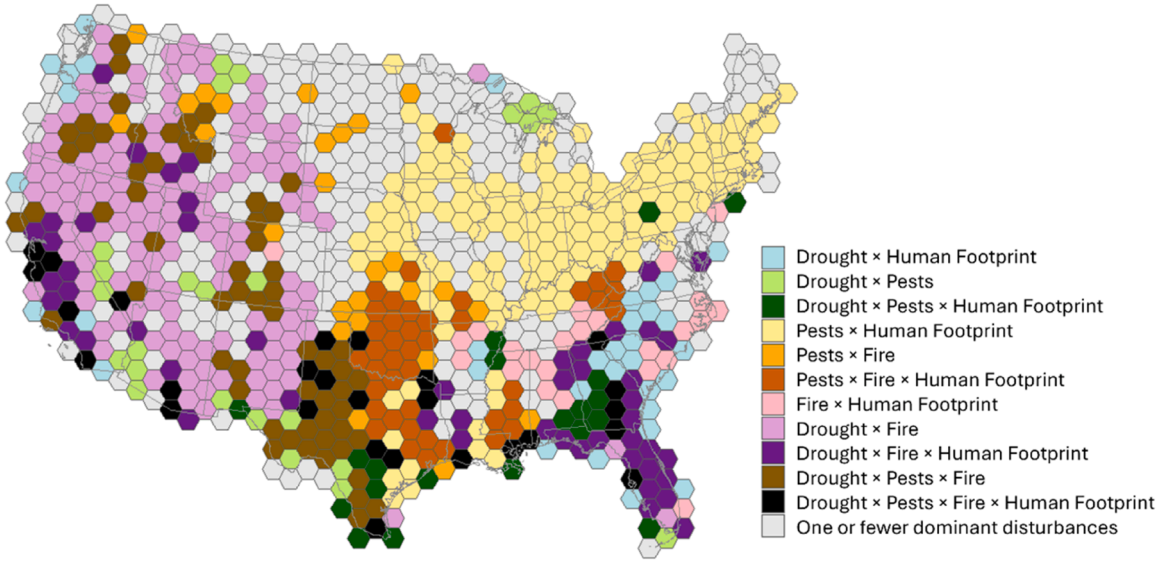


**Fig. 2.** Overlapping high-intensity disturbances in the conterminous USA. Each colored hexagon has above average (i.e., greater than the median value) intensity of at least two of the disturbances shown in Fig. 1. Gray hexagons contained only one or no high-intensity disturbances, or lacked data (i.e., gray hexagons in Fig. 1). Overlapping disturbances may be the most likely to interact to impact tree species abundance and demography.

spatiotemporal scale presents a challenge when our goal is to understand and model range-wide patterns in abundance and demographics, and it raises key questions: Are the effects of finer scale disturbances evident at macroscales? If so, can incorporating the additive and interacting effects of disturbances into macroscale models improve our understanding of tree species abundance and demography? Ultimately, the integration of localized disturbance effects with broader scale impacts of climate, topography, and their combined influence on emergent patterns requires modelling approaches that can account for complex feedback cycles across scales and disturbances.

The suitability of various modelling approaches will be dependent on the purpose of the study and the scale of the desired spatial and temporal inference (see Box 1 for an overview). Data-driven non-parametric approaches, for instance, are particularly useful for exploring non-linearities and complex interactions among predictor variables, whereas linear, parametric to semi-parametric approaches are useful for hypothesis testing and identifying directional relationships (Tredennick et al., 2021). In the former case, data-driven non-parametric models have frequently been used to understand macroscale dynamics, where broader emergent patterns are the focus of interest, and where a lack of finer scale data and computational bottlenecks prevent a more distributional approach. At continental scales, regression tree-based bagging methods have proven useful for modelling macroscale dynamics of species abundance (Peters et al., 2019; Prasad et al., 2023), which respond non-linearly and interactively with climate and other environmental variables (Iverson and Prasad, 1998; Moore et al., 1991). Ensembles that capture the consensus among multiple algorithms can quantify overall habitat suitability, colonization likelihood patterns, and conditions under current and future climates (Prasad et al., 2025). While these macroscale models are useful for delineating boundary conditions for wide-ranging species, a different approach may be needed to understand more local-scale species responses. For example, semi-parametric models that predict the full conditional distribution of the response (i.e., location, scale, and shape of the response in addition to the mean) may be suited for this purpose (Rigby and Stasinopoulos, 2005). Boosted generalized additive models (GAMs), which allow specification of linear, smooth, spatial, and spatiotemporal effects from a wide range of continuous, discrete, and mixed discrete-continuous distributions, provide one such approach (Hofner et al., 2016; Hothorn et al., 2011; März, 2019). Likewise, Bayesian approaches that integrate prior knowledge of interacting spatio-temporal disturbances on trees are useful for understanding different demographic responses (Perret et al., 2025), that act across hierarchical scales (Li and Yang, 2025). Probabilistic prediction intervals and quantiles can be assessed to provide a better grasp on uncertainty, although as noted earlier, more nuanced hybrid approaches may be needed when the scales overlap or the assumption of stationarity is violated (e.g., Bar-Massada and Belmaker, 2017; Kupfer and Farris, 2007).

The relative merits of process-based mechanistic models and statistical models have been discussed in the literature quite extensively (e.g., Baker et al., 2018; Connolly et al., 2017; Kearney and Porter, 2009; Kearney et al., 2010). Process-based models are highly relevant when incorporating basic mechanisms that shape vegetation dynamics utilizing first principles. Generally, it is better to have parameters derived from causal processes to simulate real-world phenomena because of their superior ability to extrapolate to new situations. In contexts where scaled parameters from such experiments are available, it would be a viable alternative to statistical approaches. However, in addition to the difficulty in obtaining these parameters, dynamic models must causally derive multiple parameters that are sensitive to perturbation in multivariate settings. This is especially true with tree species which have wide tolerances and typically exhibit gene × environment reaction norms resulting in variable response - hence making them more amenable to non-parametric statistical analysis (Prasad et al., 2024). Dynamic process-based models, however, can be useful for forecasting processes with specific biophysical requirements, and for simulating migration, growth, and competition of tree species across landscape scales. For example, we have used a historically based migration model to simulate future colonization likelihoods of tree species (Iverson et al., 2004; Prasad et al., 2013). Dynamic Global Vegetation Models, such as MC2 has advanced our understanding of plant functional transitions (Kim et al., 2017). Fine scale interactions in ecosystem models captured at the species levels allow processes to be simulated under novel conditions (Zhou et al., 2018) and integrated into landscape simulation models (e.g. LANDIS-II Landis Pro (Gustafson et al., 2023). Comparing results of statistical and process-based models can be useful in some contexts for arriving at a consensus, or opening further avenues of research (Iverson et al., 2017). Ultimately, there are many directions and promising avenues to model the effects of disturbance on tree species abundance and demography at various scales, including advances in multivariate analyses, joint distribution modelling, and trait-based techniques that can allow for novel insights into interactions and mechanisms shaping forest composition (Clark et al., 2021).

## 9. Challenges and opportunities

Integrating disturbances into macroecological models of tree species abundance and demography will present numerous challenges that require thoughtful reflection and intentional planning. Among the most important considerations will be selecting the appropriate spatial, temporal, and taxonomic scales of analyses to detect the impacts of disturbances. For instance, the timing of disturbances, and in particular their sequence, will be important for isolating their impacts, as disturbance events can be hyper-localized and follow one another relatively quickly (e.g., pests outbreaks facilitating fire, or vice versa (Canelles et al., 2021; Kane et al., 2017)). Parsing these interactive effects will likely require time series of high-precision data. While this sort of data may not be available for all disturbances in all regions, some disturbances (e.g., land use change, human footprint, fire) are generally well-mapped at global scales (Andela et al., 2019; Winkler et al., 2021).

**Box 1**

| Considerations | Parametric models | Non-parametric / Machine-learning |
|---|---|---|
| Assumptions | Frequently assume errors are independent and identically distributed; predictors have a causal association with response | Minimal; frequently are robust to correlated variables |
| Data distribution | Defined by probability distributions; sensitive to outliers | No distributional assumptions; less sensitive to outliers |
| Hypothesis testing and inference | Straightforward comparisons to null models and null distributions | Less direct, but possible via simulation and response curves; mostly black-box and used mainly for prediction |
| Interactions | Specified *a priori* | Tree-based base-learners incorporate interactions |
| Types of Models | Generalized linear models; Generalized additive models (semi-parametric); Linear mixed effects models; Bayesian hierarchical models | Random Forest; Boosted regression trees; Maxent; Neural networks |

Another important consideration will be whether climate-driven disturbances (e.g., drought, pest outbreaks, fire) can be separated from the direct role of climate on tree species abundance and demography. Work integrating fire in statistical models of *Proteaceae* abundance and presence in the Cape Floristic Region of South Africa showed that fire variables, including fire frequency and area, can improve model fit, and can offer greater inference than climate-only models (Tucker et al., 2012), and similar results have been shown in other fire-prone systems (Kelly et al., 2017). However, in some regions, climate can be more accurately mapped than disturbances, leaving little variability for disturbance to explain. This issue was highlighted by Crimmins et al. (2014), who showed that including fire information in distribution models of California plant species added little to the accuracy or inference of the models — despite fire being the primary disturbance in California — partially because the effects of fires were already being captured by direct climate effects. Modelling approaches that can account for direct and indirect effects of disturbance on tree species abundance and demography, as well as effects among predictor variables (e.g., structural equation models), could be useful for examining interrelated predictors. Likewise, models capable of "scaling up" the effects of disturbance – spatially, temporally, or taxonomically – or being capable of hierarchical partitioning could offer insights into the scales where the effect of disturbances are most impactful or measurable. Taxonomic partitioning could be particularly informative as, in the same way tree populations are adapted to local environmental conditions, populations are likely adapted to different levels of disturbance, based on their ecological memory of historic disturbance regimes (Banks et al., 2013).

Despite these potential challenges, recent advancements in methodologies and development of new data products provide opportunities to tackle novel research questions and implement modelling approaches in innovative ways. For instance, to address intraspecific sensitivity to disturbance, new approaches for integrating adaptive genomic information into broad-scale models have become available that could improve our understanding of tree species responses to environmental change and disturbance (Lachmuth et al., 2024). To more efficiently characterize and quantify disturbance events, remotely sensed satellite data with high revisit frequency could be particularly useful for mapping disturbances that occur over short time periods, such as insect defoliation and small-scale fires. Likewise, near-real-time disturbance detection (Ye et al., 2021) could offer forest managers valuable data to conserve tree species that are particularly vulnerable to certain disturbance agents or events. While not all types of disturbance can be detected equivalently with satellite data (Stahl et al., 2023), advances in algorithms may improve accuracy and transferability over time. Data quality is also an important consideration, as some disturbances like fire and landscape modification are more easily mapped than species-specific pest damage that only impact particular host species. Future disturbance predictions will be equally valuable for anticipating future tree dynamics (Gao et al., 2021; Wang et al., 2017; Zhang et al., 2023), especially if contemporary dynamics can be well-characterized. Looking forward, we anticipate that technology and techniques will continue to evolve and produce new or improved streams of data that can be utilized in ongoing and future efforts to analyze the impacts of disturbance at varying scales.

Ultimately, integrating disturbance into models of macroecological patterns in tree species abundance and demography will provide added inference and potentially new insights into the factors driving those patterns. Improved understanding of how disturbance influences tree species dynamics can then be used to inform management actions and conservation efforts. For example, assessing the relative importance of various disturbance agents at local and regional scales can aid forest managers in strategizing how to anticipate and mitigate shifts in disturbance regimes, as well as prioritizing and implementing site-specific and landscape-level initiatives. The ability to identify and effectively model potential threats and risks associated with disturbance could be particularly relevant for guiding management plans intended to promote and preserve specialized stand conditions, such as old-growth forest, and could help managers decide whether resisting, accepting, or directing future change is the most effective strategy (i.e., RAD decision framework (Schuurman et al., 2022)). Looking to the future, the modelling approaches discussed in this review can be used to project how disturbance will change and interact to influence tree species abundance and demography at varying spatiotemporal scales. Forest managers could use these predictions to consider adaptive and/or mitigative actions that enhance the ability of forest ecosystems to resist future change or remain resilient in the face of intensifying disturbance. For instance, future models that highlight the need for increased resources (e.g., finances, labor) or specific management actions (e.g., pest control, prescribed fire) to maintain or promote desired forest traits. Alternatively, in cases where models of future disturbance regimes strongly imply an imminent transition in forest conditions (e.g., to a significantly altered state), forest managers could plan ahead and start making intentional, directed changes that promote tree species or genotypes that are best adapted to the future expected conditions (e.g., pyrophilic or drought-tolerant) (Muller et al., 2019). Regardless of the exact scenario, we anticipate many opportunities to incorporate and apply the knowledge gained by integrating disturbance into macroscale models of tree species abundance and demography.

## CRediT authorship contribution statement

**Andrew V. Gougherty:** Conceptualization, Visualization, Writing – Original Draft. **Hannah L. Clipp:** Conceptualization, Visualization, Writing – Original Draft. **Anantha M.** Prasad: Conceptualization, Writing – Original Draft. **Matthew P. Peters:** Conceptualization, Visualization, Writing – Original Draft. **Stephen N. Matthews:** Conceptualization, Writing – Original Draft.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper

## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.122875.

## Data availability

No data was used for the research described in the article.

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