

REVIEW

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Carbon, climate, and natural disturbance: a review of mechanisms, challenges, and tools for understanding forest carbon stability in an uncertain future

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Abstract

In this review, we discuss current research on forest carbon risk from natural disturbance under climate change for the United States, with emphasis on advancements in analytical mapping and modeling tools that have potential to drive research for managing future long-term stability of forest carbon. As a natural mechanism for carbon storage, forests are a critical component of meeting climate mitigation strategies designed to combat anthropogenic emissions. Forests consist of long-lived organisms (trees) that can store carbon for centuries or more. However, trees have finite lifespans, and disturbances such as wildfire, insect and disease outbreaks, and drought can hasten tree mortality or reduce tree growth, thereby slowing carbon sequestration, driving carbon emissions, and reducing forest carbon storage in stable pools, particularly the live and standing dead portions that are counted in many carbon offset programs. Many forests have natural disturbance regimes, but climate change and human activities disrupt the frequency and severity of disturbances in ways that are likely to have consequences for the long-term stability of forest carbon. To minimize negative effects and maximize resilience of forest carbon, disturbance risks must be accounted for in carbon offset protocols, carbon management practices, and carbon mapping and modeling techniques. This requires detailed mapping and modeling of the quantities and distribution of forest carbon across the United States and hopefully one day globally; the frequency, severity, and timing of disturbances; the mechanisms by which disturbances affect carbon storage; and how climate change may alter each of these elements. Several tools (e.g. fire spread models, imputed forest inventory models, and forest growth simulators) exist to address one or more of the aforementioned items and can help inform management strategies that reduce forest carbon risk, maintain long-term stability of forest carbon, and further explore challenges, uncertainties, and opportunities for evaluating the continued potential of, and threats to, forests as viable mechanisms for forest carbon storage, including carbon offsets. A growing collective body of research and technological improvements have advanced the science, but we highlight and discuss key limitations, uncertainties, and gaps that remain.

Keywords Bark beetles, Carbon risk, Climate change, Disease, Drought, Forest management, Fuels, Future, Insect, Wildfire

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Background

Forests contain a large proportion of Earth's terrestrial surface carbon storage, with continued potential for carbon sequestration over the coming decades to centuries [1, 2]. Forests cover over a third (~310 million ha) of the United States' land area, of which ~58% are privately owned [3]. Maintaining or increasing forest carbon on these lands is a critical component of some nature-based climate solutions, including forest carbon offset projects. Various carbon offset programs have been developed to credit landowners for managing forests to maintain and increase long-term carbon storage, usually focusing on the live tree and standing dead carbon pools because of the potential to broadly manage these portions for long-term carbon stability [4, 5]. Because forests naturally have continual carbon exchanges with the atmosphere, offset programs try to account for these exchanges to achieve carbon stability on the order of decades and up to a century into the future [6].

Forest carbon storage is a critical ecosystem service, and because of this, offset programs can incentivize carbon stability by issuing credits to landowners to create and maintain additional forest carbon [7–9]. Losses of previously credited carbon can sometimes be compensated either by the project owner (for 'intentional' losses) or an insurance buffer pool of credits held by the issuing agency (for 'unintentional' losses). These guarantees against carbon loss from projects may be compromised by events that cause larger than anticipated carbon emissions. These events, called reversals, are expected

to happen periodically as a consequence of natural disturbance regimes endemic to a particular ecosystem [10–13].

Carbon projects exist within a framework wherein there are initial stocks, management that can impact those stocks and the disturbance risks for a finite period of time, and realized disturbances, all which feed back to the initial carbon in the next time step (Fig. 1). Initial carbon stocks represent the carbon before a disturbance or at the start of a year or period of analysis. Potential disturbances, including wildfires, insects and disease outbreaks, and drought, change the composition of initial forest carbon and alter future risk from wildfire [14]. The intensity and likelihood of the disturbances and the susceptibility of forest carbon can be modulated by management actions. Management actions have an immediate, known impact on carbon stocks, and alter the risk of various types of disturbance. Disturbances can be understood through a risk framework, where carbon stocks are impacted based on likelihood of occurrence, the conditional intensity, and conditional severity. More broadly, large enough fluctuations in forest carbon may feedback into climate change, which also impacts disturbance risk.

Wildfire, insect and disease outbreaks, and drought are among the primary natural processes that reduce carbon in forests, but anthropogenic climate change has and will continue to alter the frequency, severity, and timing of disturbances beyond what has occurred historically, affecting carbon stocks at broad spatial and temporal scales (Fig. 1) and challenging carbon storage and policy goals [15–18]. Understanding the evolving

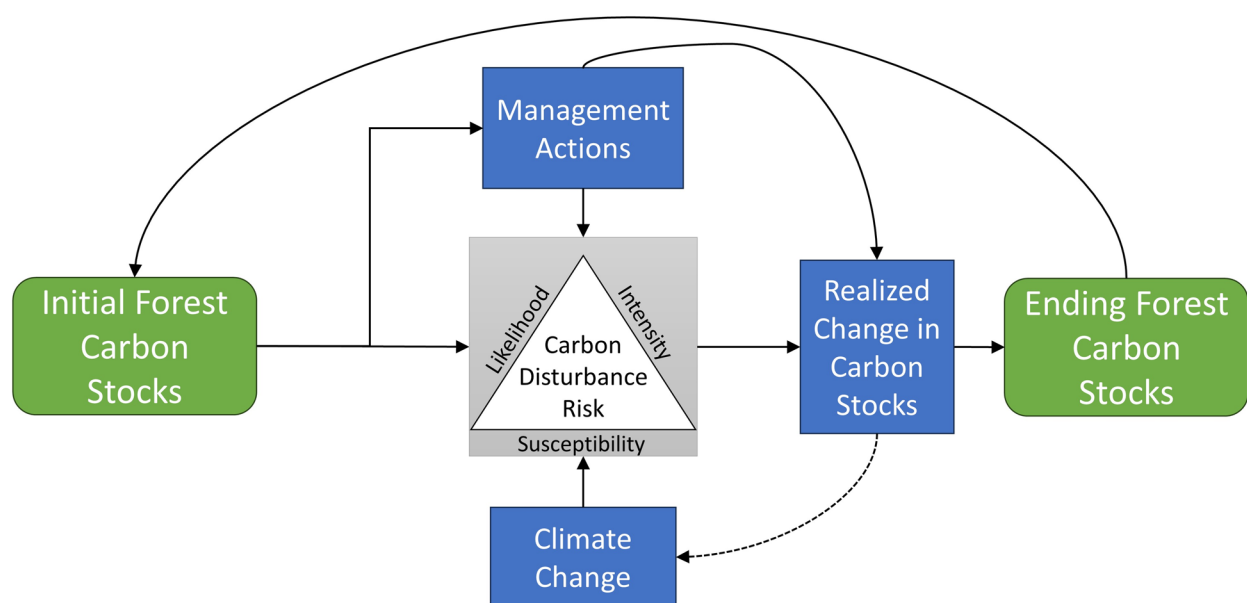


Fig. 1 Conceptual cycle of forest carbon risk as modified by disturbances, management actions, and climate change

Table 1 Natural disturbances and their major effects on forest carbon, expected influences of climate change, and management strategies for carbon risk reduction

	Effects on forest carbon	Climate change effects	Carbon risk reduction
Wildfire	High-severity fire = high tree mortality and carbon loss; low-severity = low tree mortality and carbon loss; long term impacts dependent on severity	Increased fire severity, size, and frequency in many places	Scale, timing, design, and placement of fuel treatments
Insects & disease	Reduced growth and carbon uptake, often leading to tree mortality	Generally, higher susceptibility of hosts to infestation/infection, and for many agents, more favorable environments	Managing for more resistant (increased host defense) and resilient (increased host adaptability) forest structures and compositions
Drought	Reduced growth and carbon uptake, tree mortality when drought is outside a species' adaptive capacity	Higher intensity and frequency	Managing for more resistant (increased drought defense) and resilient (increased drought adaptability) forest structures and compositions; incorporating changes in species envelopes during management
Heat waves	Reduced growth and carbon uptake, and mortality, when heat exceeds a species' adaptive capacity	Warmer temperatures increase likelihood of heat extremes	Managing for more resistant (increased heat defense) and resilient (increased heat adaptability) forest structures and compositions; incorporating changes in species envelopes during management
Wind	Tree mortality via windthrow or breakage	Higher intensity of hurricanes, but no change in frequency; other storm types may become more frequent and/or severe	Alter forest structure to prevent windthrow; reduce forest edges

dynamics of disturbance regimes is critical for maintaining carbon permanence (e.g. ensuring carbon projects are viable over their lifetimes of 20–100 years) because deviations from natural disturbance regimes influence whether forest carbon can in fact remain a viable offset option. However, many offset standards do not incorporate all risks to forest carbon stocks associated with climate change and disturbance events [19, 20]. Climate change has already introduced new uncertainties by rapidly driving ecosystems toward warmer, and in some places drier, futures with greater moisture stress, which likely will include non-stationarity in disturbance regimes that make it more difficult to assess forest carbon risk [17, 21, 22]. With sufficient knowledge of how climate change affects disturbances and forests, preventative management practices or treatments may be implemented to reduce the likelihood of carbon reversals and loss of forest resilience in the future.

For a forest carbon offset protocol to reasonably account for climate change and disturbance, it is necessary to map and model multiple data layers: the distribution of forest carbon across the country; the frequency, severity, and timing of possible future disturbances; the mechanisms by which disturbances may affect carbon storage; and how climate change may alter each of these elements (Fig. 1). In the United States, there is a growing body of scientific literature, tools, and methods that consider one or more of the aforementioned elements, but rarely all of them, and future climate change effects are often not sufficiently considered.

In this review, we first summarize current literature on the general effects of disturbance on forests and forest carbon in the United States, followed by the general effects of climate change on each disturbance type (Table 1). In ecosystems that have evolved with high-frequency, low-severity disturbance regimes such as wildfire (i.e., fire-adapted forest ecosystems), there are many potential benefits from shifting carbon from ephemeral pools (i.e. duff, litter, and small diameter ladder fuels) into more stable pools (i.e., large aboveground live and dead trees), including reduced temporal variability, reduced wildfire severity, and reduced risk to infrastructure from wildfire. To better understand these interactions, we explore how carbon in different pools affects disturbance risk and carbon stability. Next, we identify and discuss several of the primary tools and datasets that have resulted in significant advances in assessing forest carbon risk to disturbance for the United States. Lastly, we review how data from some of these tools have been utilized to develop management practices for creating ecosystem resilience, with co-benefits of building forest carbon stability to climate change.

Main text

Types of disturbances

Wildfires

How does wildfire affect forest carbon? Wildfires emit existing forest carbon into the atmosphere and affect the capacity to sequester new carbon as well as the rate at which it is sequestered (Fig. 2a). Fire effects on forest carbon may be immediate, through combustion, or may occur over many years through mortality, as dead trees decompose and/or surviving trees exhibit reduced growth rates. This process has occurred for millennia, often tied to human activity [23], and wildfire has been one of the most important contributors to interannual forest carbon variability in North America [10, 24]. Since 1990, wildfire carbon emissions have increased in the United States; however, over the same period, forest growth has offset these emissions, resulting in a net carbon sink in the total forest sector [25]. In Oregon, the 200,000 ha Biscuit Fire in 2002 is estimated to have released 17–22 Mg C ha⁻¹, 16 times the pre-fire annual net ecosystem production (NEP) for this region and negating nearly 50% of the annual total net biome production (NBP) for the entire state [26]. Fire may damage living trees, contributing to delayed mortality from other disturbances [27, 28] or may result in extended periods of post-fire carbon loss due to decomposition of standing or fallen dead trees [29]. By definition, low-severity fires result in less tree mortality than high-severity fires, but still release carbon through combustion of duff, litter, and small trees (e.g. saplings), which are usually not incorporated in carbon accounting protocols but may significantly alter future fire risk and intensity [30].

Large quantities of total aboveground carbon could be lost through combustion and mortality during high-severity wildfire; for example, up to 85% loss was documented following California's 2013 Rim Fire [31]. Additionally, compounding disturbances such as drought, heat, insects, and diseases that result in reduced fuel moisture content or mortality can accelerate carbon loss during subsequent wildfire [32]. During most wildfires, the majority of combustion and carbon loss occurs in smaller trees, brush, shrubs, fine woody debris, litter, and duff, with relatively low percentages of loss in larger tree size classes and coarse woody debris, although these losses increase with fire severity [32, 33] and higher severity fires may be more frequent with climate change [34–37]. For example, the area burned by high-severity wildfires has increased in the western United States by ~8X since 1985 [38], partly due to warmer, drier conditions attributed to climate change. While wildfires themselves are a relatively small proportion of the current total anthropogenic emissions in the United States (between 4–6% during the early 2000s [39]), in

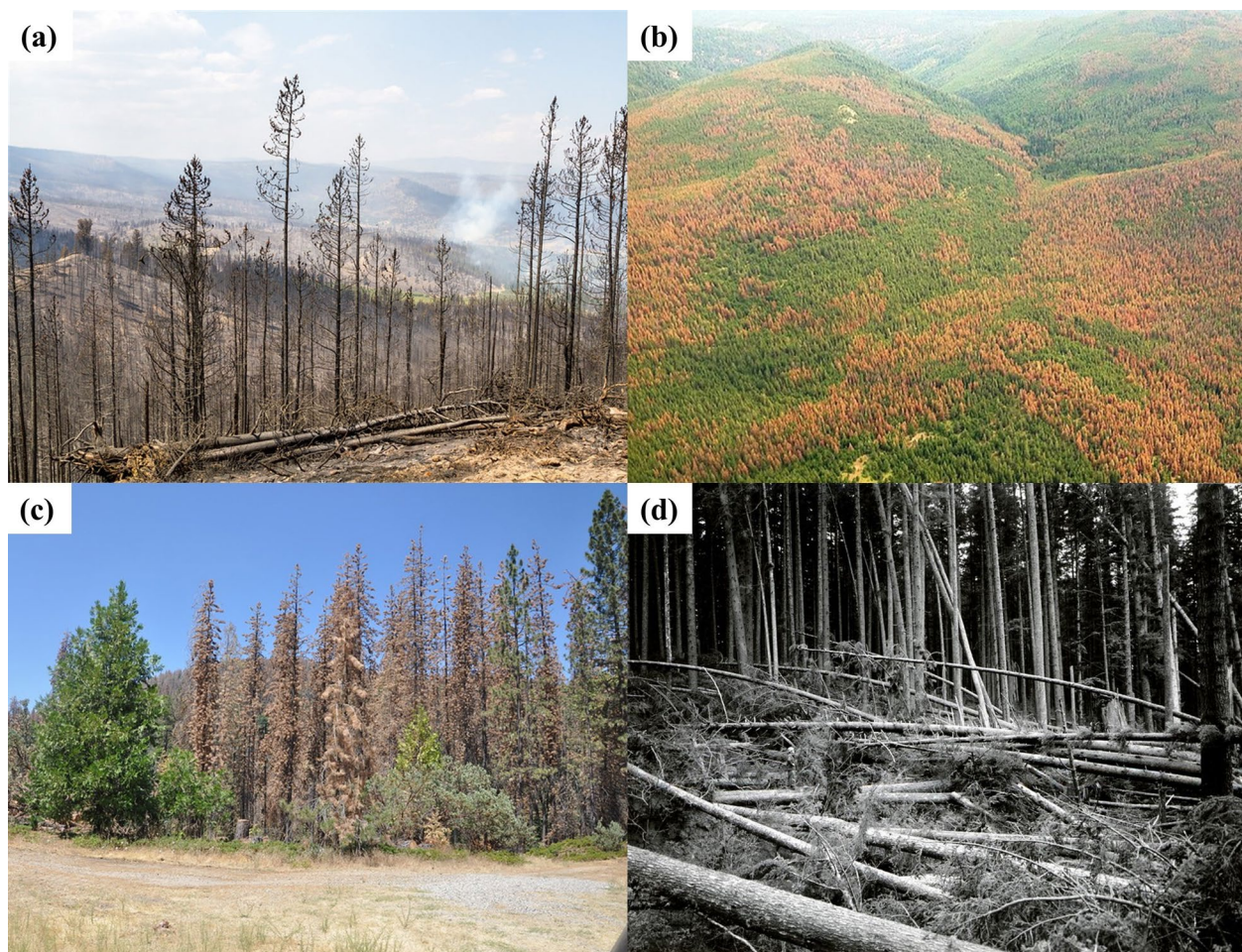


Fig. 2 Examples of four disturbance categories. **a** Wildfire: a post-fire landscape on the Shoshone National Forest, Wyoming [287], **b** insects and disease outbreaks: pine mortality in the Blue Mountains, Oregon [288], **c** drought: dead trees on the Sierra National Forest, California [289], and **d** other localized disturbances, including but not limited to windthrow and hurricanes: windthrow from the 1962 Columbus Day Windstorm in Otis, Oregon [290]

the context of leveraging carbon in forests as a sink, this trend towards increasing high-severity fire is an important piece of the puzzle. In instances with substantial large tree mortality, the remaining dead standing carbon stores of un-consumed large trees take years to decades to decompose and release their carbon, allowing time for partial replacement carbon growth from successional trees in stands where regrowth occurs [40].

Post-fire total carbon recovery generally occurs sooner after low-severity wildfires than high-severity wildfires, but rates vary widely depending on forest type [41–43]. For example, in eastern Oregon, live aboveground carbon lost to high-severity wildfires was over 6X greater than low-severity fires in ponderosa pine (*Pinus ponderosa*) forests, and nearly 3X greater than in mixed-conifer forests [44]. Over the twentieth century, fire suppression policies and other factors have led to increased fuel loads in many fire-adapted forests, increasing susceptibility

to high-severity wildfire and subsequent risks to carbon stability [45]. Across the West, tree mortality and carbon sequestration reductions of surviving trees were significantly higher following wildfires in high-severity/low-frequency fire regimes than in low-severity/high-frequency fire regimes [46]. With climate change, some forests will struggle to regenerate trees post-fire, especially following high-severity fires at large spatial scales and in more arid locations [47].

How does climate change affect wildfire? Climate is a primary driver of wildfire activity with cascading consequences for forest carbon [48]. For thousands of years, wildfire has increased in tandem with periods of high temperatures, e.g., during the Medieval Climate Anomaly [49–51]. The role of humans in managing and altering natural fire cycles is compounding the climate change effects [52]. For example, prior to Euro-American coloni-

zation, cultural burning by Native Americans was widespread across the United States, creating fire regimes that were not fully dependent on climate [53–57]. Over the past century, fire suppression policies in the United States have led to a buildup of fuels, priming broad expanses of the landscape to burn under extreme weather conditions when fires cannot be suppressed [58]. Beginning in the late twentieth century, increasing temperature and aridity [23, 59–61] have created more frequent extreme fire-weather conditions, leading to more very large wildfires [62, 63] and area burned at high severity [38, 64], although sufficient fuels are necessary for this pattern to continue.

In the western United States, anthropogenic warming between 1984–2015 has been estimated to explain 45% of total forest area burned [65] and contributed to the increase of very large wildfires [66–68]. Eighteen of the 20 largest wildfires in California history have occurred since 2000, with the five largest occurring since 2018 [69]. Many of the largest wildfires in recent history are linked to climate extremes, including those in the infamous 2020 fire season in the West [70–73]. Over the twentieth century, lengthening of the fire season led to increased wildfire activity [74–76], including increased fire severity [35, 77–80].

Climate change is expected to continue to alter fire regimes into the future. The fire season is projected to increase by as many as 58 days in Southern California by the end of the twenty-first century [81], extending much later into the fall [82–84]. In the Northern Rockies, wildfires are projected to occur more frequently in spring and fall, and intensify in the summer by the mid-twenty-first century [85]. In the Southern Rockies, similar trends are projected, increasing the total annual area burned [86]. In the Northwest, future warming and drying is expected to create more severe fire-weather conditions [87–90], and increase the area burned [91–93], an emerging trend already observed in recent decades. These regional trends are confirmed by multiple national-scale studies [62, 63, 83, 89, 94–96].

In Alaska, area burned in the last half of the twentieth century has been strongly tied to climate [97–99]. These linkages are projected to continue in the future [100, 101]. For example, using a process-based ecosystem model driven with future climate, Balshi et al. [102] reported that by the end of the twenty-first century, wildfire in North American boreal forests could increase carbon emissions from these forests by 4.4X the contemporary rate, and using a dynamic global vegetation model, Bachelet et al. [103] found that increases in wildfire could eventually transition Alaska from a net carbon sink to a net carbon source by the end of the twenty-first century.

In the Southeast, projections for the mid-twenty-first century suggest the fire season will lengthen by 2–3 months, and summertime fire danger, as measured by the Keetch–Byran Drought Index (KBDI), will increase by 40% [104]. Although higher KBDI is primarily driven by increasing temperatures in the Southeast [105], other factors may be important in some subregions [106–108]. For the Upper Midwest and Northeast, Kerr et al. [109] suggested that the maximum period of consecutive days exceeding high-fire danger thresholds (95th percentile Canadian Fire Weather Index) will double by 2100, with the onset of peak fire season beginning in early spring. Some of the highest increases in wildfire probability in the United States are projected to occur in the Upper Midwest and Northeast, doubling by 2100, and are consistent with projections of rising burned areas in parts of the East [94, 95]. Determining the effects of climate change on wildfires has been difficult in areas of the United States where wildfires were historically rare (e.g., Northeast), and where forests represent a small portion of the landscape (e.g., agricultural regions).

For the Hawaiian Islands, wildfire has been a rare occurrence historically, moderated primarily by human activity and secondarily by climate [110, 111]. Recent influxes of non-native vegetation, particularly invasive grasses, have altered the islands' natural fire regimes, increasing fire frequency [112]. Linking climate and wildfire in Hawaii is difficult due to the extreme microclimate gradients in the islands, but lack of precipitation is generally the main climatological driver of wildfire in Hawaii [113, 114]. Resolving these climate connections will be critical to identify wildfire risks to forest carbon in Hawaii [115, 116].

Insects and diseases

How do insects and diseases affect forest carbon? Insects and diseases alter forest function, structure, and composition in complex ways, by regulating primary production, nutrient cycling, stand succession, and the abundance of associated plants and animals [117]. Insects and diseases can also affect other disturbances, such as wildfire. As with wildfire, forest carbon loss occurs due to both tree mortality and sublethal infestation (Fig. 2b; [16]). Defoliation can reduce the capacity of trees to sequester carbon for years after infestation [118–122].

Many insects and diseases pose significant risks to forest carbon in the United States (Table 2). In the West, major tree losses have occurred during the twenty-first century, with affected areas sometimes exceeding burned areas [123, 124]. As much as 15% of total forest cover in the United States is affected annually by insects and diseases [125]. Diseases are often more diffuse than insect outbreaks but affect large areas [126, 127]. During the

Table 2 Examples of forest insects with consequences for forest carbon stability in the United States

Region	Agent	Host tree	References
East	Emerald ash borer (<i>Agrilus planipennis</i>)	<i>Fraxinus</i> spp.	[292]
East	Hemlock woolly adelgid (<i>Adelges tsugae</i>)	<i>Tsuga</i> spp.	[152, 154, 293, 294]
East	Balsam woolly adelgid (<i>Adelges piceae</i>)	<i>Abies</i> spp.	[295]
East	Spruce budworm (<i>Choristoneura</i> spp.)	<i>Picea</i> spp.	[296, 297]
East	Spongy moth (<i>Lymantria dispar dispar</i>)	Most hardwoods	[298]
East	Southern pine beetle (<i>Dendroctonus frontalis</i>)	<i>Pinus</i> spp.	[299, 300]
West	Mountain pine beetle (<i>Dendroctonus ponderosae</i>)	<i>Pinus</i> spp.	[129, 228, 301–303]
West	Spruce beetle (<i>Dendroctonus rufipennis</i>)	<i>Picea</i> spp.	[304]
West	Other bark beetles	Most conifers	[124, 130, 137, 305, 306]
West	Western spruce budworm (<i>Choristoneura occidentalis</i>)	<i>Picea</i> spp.	[120]
West	Douglas-fir tussock moth (<i>Orgyia pseudotsugata</i>)	<i>Pseudotsuga menziesii</i>	[307]
West	Balsam woolly adelgid (<i>Adelges piceae</i>)	<i>Abies</i> spp.	[308, 309]
West	Forest tent caterpillar (<i>Malacosoma disstria</i>)	Most hardwoods	[145]

Region denotes primary area of impact, east or west of the Rocky Mountains

early twenty-first century in western North America, severe outbreaks of mountain pine beetle (*Dendroctonus ponderosae*) [128] caused some forests to switch from carbon sinks to major carbon sources over just 6 years, with multiple decades predicted before full recovery [129]. Since 2000, > 27 million ha have been impacted by mountain pine beetle, partly driven by climate change [128]. Warming allowed mountain pine beetles to erupt at elevations and latitudes where, previously, cold winters killed most brood within host trees [130]. In the West, the amount of carbon in trees killed by bark beetle outbreaks during 1997–2010 was similar to that in trees killed by wildfire, ~ 4.5% of the total carbon in trees in the region [124]. Across the United States, forests recently impacted by insects and diseases sequestered 69% and 28% less total forest carbon, respectively, than did similar unimpacted forests [122]. Using predictive models based on forest inventory data, Anderegg et al. [96] documented that insect-driven mortality risk is highest in the Rocky Mountains, Southwest, and Southeast, and is comparable to observed mortality from wildfires in these regions. Insect-driven forest carbon risk is projected to continue to increase throughout the twenty-first century, particularly in the Rocky Mountains, Sierra Nevada, and the Upper Midwest, but at a much lower rate than wildfire risk, which increases strongly across the entire United States [96].

Disease impacts have also been significant but more difficult to quantify. Beech bark disease has substantially reduced the growth of American beech (*Fagus grandifolia*) in the Northeast, decreasing live tree carbon production by 11% in Maine alone [131]. Root diseases are persistent in the northern Rocky Mountains, reducing

live tree carbon as much as wildfire and more than harvesting or insect outbreaks [132].

The body of literature on the effects of invasive insects and diseases on forest carbon stocks is growing [120]. More than 450 non-native forest insects and pathogens have been introduced into natural areas of the United States, of which > 83 are invasive and cause significant impacts [133]. The rates of new introductions and establishments are high but projecting future impacts is difficult. Under current and projected import patterns, an average of two invasive forest insects are expected to be established in the United States each year, and an economically important forest insect pest is expected to be established every 5–6 years [134]. Historically, impacts of invasive insects and diseases have been much greater in the East than in the West. For example, the chestnut blight and Dutch elm disease are among a few disturbances that have threatened the existence of entire tree genera in the East.

How does climate change affect insects and diseases? Broad generalizations of the effects of climate change on insects and diseases are difficult to make due to the complexity of the life history traits involved among species. Climate change may increase susceptibility to insects and disease by two primary mechanisms: (1) warming driving range expansions in areas historically below temperature thresholds for survival, reducing overwintering mortality, and increasing phenology and voltinism [130, 135–137]; and (2) warming and drought compromising the defense mechanisms of otherwise vigorous trees, leading to higher risks of tree mortality from insects and diseases [16, 138–141]. In the West, warming is expected to expand the range of important insects. For

example, future warming is projected to favor the growth of mountain pine beetle populations at higher latitudes and higher elevations [130, 142] but may be tempered by disrupted seasonality and fractional voltinism, both maladaptive to mountain pine beetle [143]. Furthermore, areas heavily impacted by mountain pine beetle outbreaks during the early twenty-first century are unlikely to experience outbreaks for decades because suitable host trees are depleted. In Alaska, warming and late-summer droughts have been positively correlated with spruce beetle (*Dendroctonus rufipennis*) outbreaks [144], suggesting levels of tree mortality attributed to spruce beetle are likely to increase in the future.

Defoliator responses to warming and drought are variable [139] and include important indirect effects mediated through changes in host tree physiology, primarily leaf chemistry and palatability [139]. Some insect fungal pathogens are important regulators of defoliator populations in the United States and are expected to be negatively affected by drought (e.g., *Entomophaga maimaiga*, which causes extensive epizootics in spongy moth (*Lymantria dispar dispar*) in the East). Hotter and drier conditions have been positively correlated with increased levels of tree mortality from defoliators [145, 146].

Fungal pathogens are sensitive to the timing and quantity of precipitation, ambient temperature, relative humidity, and other factors that influence leaf-surface or soil-moisture content. Some tree diseases that require moist conditions are expected to be negatively affected by climate change [147]. For example, hotter and drier conditions in the Southwest are expected to reduce white pine blister rust infections, but infections may increase where conditions become warmer and wetter [148, 149]. Other tree diseases (e.g., Armillaria root disease) are indirectly affected by climate change through increases in host stress, suggesting warming and drought may increase epizootics [147]. Forest diseases are expected to become more frequent and severe with climate change, but the magnitude of that change is both uncertain and varies by disease and ecosystem. One estimate suggests that by the end of the twenty-first century, the rate of tree mortality due to insects and diseases in the United States will increase by as much as 1.7X, which is a fraction of the 4–14X increase in tree mortality projected due to wildfire [96]. One study projects a 2X (insects) and 3x (diseases) increase in tree mortality rates for the West [150]. In the East, insects will remain one of the most impactful disturbances in the future [151], where summer warming and milder winters are expected to facilitate northward range expansions of some cold-limited insects like the hemlock woolly adelgid (*Adelges tsugae*) and southern pine beetle (*Dendroctonus frontalis*) [148, 152, 153]. However, exact climate change effects will be

complicated by each insect's tolerances of climate and strategies for propagation, insect management practices, and regeneration dynamics in a warmer, drier climate, and natural selection of hosts for resistance to certain insects. For example, Albani et al. [154] projected that expansion of hemlock woolly adelgid would result in a nearly 13% reduction in carbon sequestration in the first third of the twenty-first century, but by end of the twenty-first century these same forests may experience a nearly 20% gain in carbon sequestration due to forest regeneration of climate-adapted tree species. However, this assumes that the insect outbreak's effects do not exceed the carrying capacity of an ecosystem, and that climate change-adapted trees are able to regenerate and replace trees lost to hemlock woolly adelgid.

Overall, climate change likely creates conditions more favorable for many, but not all, insect and disease and pathogen species. Many complex interactions occur among insects and diseases, their host trees, and other community associates that are directly and indirectly influenced by climate, making robust quantitative projections of future carbon risks to insects and diseases difficult [96, 120, 147, 148]. Relevant human activities are particularly multifaceted and difficult to project—including domestic and international trade, global economic markets and commodity pathways, and human population densities and travel—which all influence insect and pathogen introductions and establishments in the United States [155, 156].

Droughts

How does drought affect forest carbon? Drought reduces tree carbon uptake and in some cases results in large tree mortality events (Fig. 2c; [17, 157–163]). Many tree species have some level of adaptive capacity to drought. Some tree species have deep rooting, stomatal control, and leaf shedding that allow them to tolerate drought better than other tree species. Despite this, drought has been identified as the largest disturbance driving primary productivity declines globally [164]. In the United States, the effects of drought on forest carbon are most pronounced in the West, though effects in the East are substantial [165]. The 2011–2015 drought in California killed an estimated 140 million trees, tipping the carbon balance of the state to a net carbon source of -600 Tg CO_2 during 2001–2015 [166]. The projected carbon stocks of California ponderosa pines may not return to levels observed prior to the 2011–2015 drought due to future warming, droughts, and western pine beetle (*Dendroctonus brevicomis*) outbreaks [18], although those prior levels may be inflated due to widespread fire suppression [167]. Similarly, drought and high vapor pressure deficit are strongly correlated with rising tree mortality levels in Alaska [168]. Based on for-

est inventory data, drought and warming are key drivers of the decline of half of the most abundant tree species in the western United States over 2001–2018 [169].

How does climate change affect drought? Climate change is projected to bring more frequent and severe droughts in many regions of the world, and the western United States is frequently identified as a hotspot for increasing droughts [170, 171]. Warming exacerbates drought effects (termed ‘hot droughts’ or ‘climate change-type droughts’; [157, 172]), elevating their lethality to trees and reducing forest carbon stocks. However, projecting changes to forest carbon due to drought remains a major challenge [22, 173]. Ultimately, (1) the effects of drought on forest carbon in the United States during the twenty-first century will be large, and (2) many current models likely underestimate drought stress and associated levels of tree mortality due to drought [22, 96].

Drought impacts on forest carbon stocks in the West are substantial [170, 174–177], and likely to increase in the future. Elevated temperatures increase soil evaporation, thereby reducing soil moisture available to plants, and higher vapor pressure deficit can result in greater transpiration in some plants, where stomatal conductance is a non-linear function of temperature [170, 178]. These climate effects have been widely documented, but the complexity of species-specific plant responses to future climates remain challenging to model. Some experts argue the loss of forests to drought could be substantial across parts of the contiguous United States in the future [22, 96].

Other disturbances—windthrow, heat waves, hurricanes

How do these disturbances affect forest carbon? Forests in the United States also experience many other disturbances that affect carbon stocks, notably hurricanes, severe storms, and heat waves [11]. Particularly for the temperate mixed deciduous forests in the northeast and Midwest, natural cycles of localized disturbances such as ice storms [179] and windthrow [180, 181] are historically more common than wildfire [182], and help create the structural complexity and species/age diversity that are important to maintaining stable carbon storage and sequestration over long time frames [183–185]. While these disturbances cause local and regionwide carbon losses (Fig. 2d), they typically have lower U.S.-wide impacts than wildfire, insect and disease outbreaks, and drought [11, 17, 124]. For example, Hurricane Katrina damaged or killed 385 Tg CO₂ equivalent trees in the Southeast [186]. Over many decades, the net impact of hurricanes to forests in the United States is likely a slight loss of live carbon [187]. Severe storms and windthrow may be important disturbance events, but few compre-

hensive studies document the carbon impacts of these events [11]. One critical recent advancement is a better understanding of how tropical cyclone regimes shape the ecology and evolution of tree species as the intensity and frequency of hurricanes affect forest structure and function [188]. Finally, while heat waves can decrease carbon uptake in forests [189], the most severe consequences occur when heat waves co-occur with severe drought (e.g., ‘hot drought’), as described above. One exception is the heat wave in the Northwest in 2021 in which temperatures of >40 °C caused substantial damage and mortality to trees [190].

How does climate change affect these disturbances? While the overall number of hurricanes is not projected to change substantially with climate change, the intensity of hurricanes is likely to increase [191]. Tree mortality is sensitive to wind speed [187] and more intense hurricanes may increase forest carbon losses, but the overall effect is likely much lower than for wildfire, insect and disease outbreaks, and drought. Of note, a recent meta-analysis found no consistent projected change in wind disturbance in North American forests [16]. A recent review of climate change in the United States indicates that climate change may increase the frequency and/or intensity of multiple storm types that affect forests, including hurricanes, atmospheric rivers, and thunderstorms [192].

Disturbance interactions

While often discussed here and elsewhere as distinct, isolated events, in reality disturbances can have compounding effects. For example, mortality induced by drought, disease, or insect infestation can create elevated quantities of large woody surface fuels with consequences for subsequent wildfire [193, 194]. Fire-induced mortality, which can sometimes be delayed several years post-fire, can affect subsequent fire severity [28] and also increase susceptibility to insect infestation in weakened surviving trees [195]. However, over longer time periods, low severity fires and prescribed fires can reduce tree density and promote resistance to future insect attack [196]. As increased temperatures and aridity widen the opportunity for disturbance-induced mortality at widespread spatial scales, dead trees add surface fuels at rates and quantities that exceed the natural range of variation [197]. Many operational fire behavior models are not yet capable of accurately predicting how these contributions to the large woody surface fuel pool will impact fire behavior [194, 198], but at minimum would likely increase the potential energy release during fires due to an influx of fuels with low fuel moisture content [32], combined with a sharp increase in live-tree density in small size classes as new growth regenerates post-disturbance. In the Sierra

Nevada, areas of higher fire severity and unpredictable fire behavior during the 2022 Creek Fire have been linked to widespread mortality from bark beetles and drought a decade prior [194, 197]. Generalizing disturbance interactions across forest types and conditions is challenging due to uncertainties in the timing, intensity, and spatial scale of mortality [199]. In fire regimes defined by surface fuel spread, mortality may increase fire severity in the short term by creating greater surface loads and fuel continuity [197], whereas in fire regimes defined by spread in canopy fuels, mortality may mimic thinning processes by decreasing the continuity of canopy fuels [199].

Mapping and managing forest carbon and forest carbon risk

As outlined in “[Types of disturbances](#)”, disturbances have significant effects on forest carbon. Mapping risk to forest carbon requires two basic components: (1) mapping forest carbon quantities, and (2) mapping disturbance risk via likelihood, frequency, and/or intensity.

Mapping forest carbon on the landscape

Existing forest carbon has been mapped in two primary ways: continental synthesis of inventory data and remote sensing. In this section, we review the foremost methods and datasets that are available to map forest carbon in the United States. Since existing carbon offset programs in the U.S. account for carbon nationally, we focus on datasets that exist for the contiguous United States and/or Alaska and Hawaii and do not include regional datasets and models unless they can be readily scaled to national level.

The USDA Forest Service’s Forest Inventory and Analysis (FIA) program manages the most comprehensive, large-scale measurements of forested plots in the United States. The program includes sites located across ownership boundaries for every state and includes plot measurements repeated every ~10 years. FIA data can be used to explore trends in forest conditions, growth, and disturbance across large areas. FIA divides the United States into 2402.8 ha hexagons [200], and varying numbers of plots within each hexagon are surveyed. FIA records for each tree on each plot include tree species, diameter, height, and status (live or dead). Carbon density can be calculated for each plot and interpolated to obtain estimates of forest carbon stocks (e.g., [201]). FIA has standardized statistical methods for making population estimates from the sparse plot locations in their network. Based on the rich information FIA provides, the Forest Service regularly updates forest carbon stock and flux estimates [25]. In this approach, a system of weights is applied to plot-level data to estimate conditions for the

enclosing hexagon [202]. Another recent dataset used FIA data aggregated at the state level to develop maps of state and regional aboveground forest carbon stocks and carbon sequestration over the course of multiple FIA remeasurements [203].

While FIA is the most comprehensive measurement dataset, it does not provide a spatially contiguous (“wall-to-wall”) map of forest attributes (including carbon) because only a small number of plots are measured within each hexagon. Computational methods have been devised to synthesize contiguous maps from site measurements (e.g., [204]). Although regional data sets are available (e.g., the LEMMA/GNN product for the West Coast [205]), currently TreeMap has the greatest spatial coverage, spanning the conterminous United States. TreeMap uses a machine learning algorithm called random forests to assign the most similar FIA plot to each pixel, producing a seamless tree-level forest model of the conterminous United States (CONUS) at 30 m resolution [206–208]. Because each pixel in TreeMap is linked to an FIA plot visit, each pixel has a list of trees and their measurements that can be used in allometric equations to estimate carbon stocks [209]. TreeMap is available for the western US for 2008 and for CONUS for 2014 and 2016. Currently TreeMap data sets are being created for Alaska and Hawaii.

The second method of measuring forest carbon uses remotely sensed data, which can result in spatially complete coverage and are often combined with FIA data (see [210] for a comprehensive review). The National Aeronautics and Space Administration (NASA) National Forest Carbon Monitoring System (NFCMS) produces carbon estimates through applications of the remote sensing-based Carnegie-Ames-Stanford Approach (CASA) carbon cycle process model [211] and has used FIA data to validate aboveground forest carbon estimates. NFCMS is available for CONUS at decadal intervals (1990, 2000, and 2010) at 30-m pixel resolution [212]. NFCMS builds upon previous mapping work of the National Biomass and Carbon Dataset from NASA and Woods Hole Research Center, which used similar methods to map a static baseline for the year 2000 [213]. NFCMS and FIA have been combined for additional downstream applications, including The Forest Carbon Map sponsored by the Trust for Public Land and American Forests, which provides a simple viewer for existing aboveground carbon storage and sequestration at larger scales (county, state, and/or watershed) for the purposes of conservation and carbon-cost accounting [214].

Mapping carbon risk to disturbance

Numerous methods and models map forest carbon risk to disturbance, and here we highlight noteworthy

datasets that have been created across the United States (Table 3). We selected datasets and tools that are publicly available, peer-reviewed, and have attained widespread use by both the science and forest management communities. While these datasets have significant utility for use in carbon offset programs accounting for climate change, our review is not comprehensive of all tools.

Statistical disturbance models Statistical methods have been used to create future maps of disturbances and carbon stocks while accounting for climate change. For example, Anderegg et al. [96] used statistical models of wildfire, climate stress (primarily drought), and insect disturbance for the contiguous United States from 2000–2100, including the impacts of projected climate change from three different climate scenarios and six earth system models (ESMs). Wildfire effects were based on the Monitoring Trends in Burn Severity (MTBS) dataset [215], which maps burned area based on statistical analyses of observations from 1984–2018 and generally does not include fuel limitations or management effects, and climate stress and insect models of tree mortality from disturbance were constructed from FIA data from 2000–2018 in combination with satellite imagery. The models were cross-

validated and tested against independent datasets. These models capture impacts of climate change, several climate scenarios, and multiple ESMs over the full 2000–2100 period (Fig. 3a). These datasets are publicly available, as is all the underlying code that created them, and a viewer and analysis tool was developed to visualize disturbance risks (<https://carbonplan.org/research/forest-risks>).

Similar to the above models, Wu et al. [22] used several different approaches to project forest carbon stocks across the contiguous United States using multiple ESMs from 2020–2100. Their study examined simplified mechanistic vegetation models, climate niche models of forest biomass by FIA Forest Group, and demographic models of forest growth and climate-sensitive disturbance developed by a previous study [96]. The demographic models showed the strongest agreement with historical biomass and disturbance trends and are expected to provide the most robust information about forest carbon risk. Despite substantial uncertainty and differences across models, there was consistency in some areas with regards to lower or higher climate risk across models [22]. All of these datasets are publicly available (<https://wilkescenter.utah.edu/tools/us-forest-carbon-futures/>).

Table 3 Major datasets and tools available for evaluating forest carbon risk to disturbances in the United States

Datasets and tools	Disturbance	Includes climate change	Ability to project?	Carbon-relevant metrics	Caveats
United States-wide statistical forest carbon models [22]	Fire, insect, drought	✓	✓	Forest carbon stocks 2020–2100; disturbance probabilities and carbon losses from disturbance	Coarse representation of climate-dependent disturbance and regrowth
United States-wide statistical disturbance models [94]	Fire, insect, drought	✓	✓	Burn area, tree mortality from insect and climate stress/drought	Does not model fire behavior or spread
TreeMap and FuelMap	Fire, insect, disease		✓	Tree diameter, height, species, and status	For fuels, relies on FIA transects in a limited subset of plots
Forest Vegetation Simulator (FVS)	Fire, insect, disease		✓	Tree volumes, biomass, density, canopy cover, harvest yields, fire effects	Does not model fire spread
LANDFIRE	Fire, insect, disease			Current state of landscape, disturbance locations	Does not represent full extent of insect and disease-related mortality
National Insect and Disease Risk and Hazard Mapping (NIDRM)	Insect, disease	✓	✓	Insect and disease risk	Uses outdated climate change scenarios; only near-term
USFS Insect and Disease Aerial Survey	Insect, disease			Area infested and carbon affected	Relies on human eyesight/judgment; low accuracy
FSim	Fire	check mark	✓	Burn probability, flame length/fire intensity	Fire spread equations insufficiently model novel fuel structures; does not project vegetation change
Interagency Fuel Treatment Decision Support System (IFTDSS)	Fire		✓	Conditional burn probability under static weather conditions, risk	Static weather; excludes low severity impacts

TreeMap and FuelMap data can be used with Forest Vegetation Simulator (FVS) to project tree growth and carbon storage

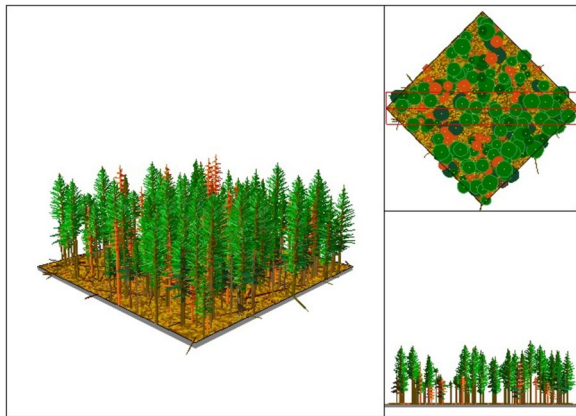


Fig. 3 Modeled visualization of a forest stand from Forest Vegetation Simulator (FVS) using the Stand Visualization Simulator module [217]. FVS is an individual tree growth model for forest stands that can simulate effects of disturbances on tree growth and forest carbon

Forest Vegetation Simulator (FVS) Forest Vegetation Simulator (FVS) is an individual tree growth model for forest stands that began as the growth and yield model Prognosis [216] and has since been expanded to include geographic variants that are specific to every region and many ecologically distinct areas in the continental United States and Alaska [217]. Several model extensions allow users to incorporate economics [218], climate change [219], and disturbances, such as wildfire [220], insects, and disease. The model simulates some stand dynamics (i.e., competition, fire spread, insect and disease spread), but because FVS is designed to be run at the stand level, there are no interactions among stands (Fig. 3).

The Fire and Fuels Extension to the Forest Vegetation Simulator (FFE-FVS) estimates potential fire behaviors and simulates fire behavior and effects at a stand under specific weather, wind, and moisture conditions. FFE-FVS does not model landscape fire spread but can be combined with landscape spread models to estimate conditional wildfire effects. FFE-FVS can be used to estimate conditional fire behaviors without causing any impacts to the stand, which may be useful in exploring short-term changes in fire behavior due to treatments. FFE-FVS can also simulate the effect of fires on tree mortality and growth, carbon pools, and produce smoke and carbon emissions estimates. A submodel within FFE-FVS tracks carbon in seven pools: aboveground live trees, belowground live, belowground dead, standing dead, forest dead and downed wood, forest floor (duff and litter), and herbs and shrubs. It also calculates carbon emissions for simulated fires. Long-term carbon emissions from dying and dead trees are computed for subsequent cycles as well. The carbon submodel also tracks carbon stored in harvested wood products, including leakage.

In addition, FVS has nine insect and disease extensions, in which each extension affects tree growth and stand development [217]. Recent software updates have created compatibility problems, so only the dwarf mistletoe and root disease extensions are available today. Updates for the extensions for blister rust, bark beetle, Douglas-fir tussock moth, and western spruce budworm are underway.

FSim (Large Fire Simulator) FSim is a stochastic, spatially explicit fire behavior model that estimates the likelihood and intensity of wildfires across large regions. Representing the landscape as a grid, FSim simulates probability of ignition, fire spread, and behavior using thousands of hypothetical fire seasons (Fig. 4; [221]). FSim results for the United States at 270-m resolution for landscape conditions circa 2014 and 2020 are publicly available [222, 223]. Simulations have been used to evaluate the effects of climate change on wildfire [84, 85, 90] and the effects of an invasive species (annual grass) on wildfire behavior [224], among other applications. FSim can also be used for risk assessment using the Highly Valued Resources and Assets (HVRAs) concept, which combines the probability and intensity of burning with the susceptibility of the valued resource, such as forest carbon, to burn probability and intensity gradients [225]. The effects of fire can be positive or negative depending on the types of HVRAs and their response to different intensity levels (e.g., quantifying the effect on post-fire carbon due to low-, medium-, or high-severity fires). This risk assessment method can be applied at any spatial extent (e.g., national forest, counties, watersheds) by aggregating the relative importance of each HVRA within the area. However, modeled fire behavior in FSim, and other models based on the Rothermel fire spread equation [226], are insufficient to model novel fuel structures that may become more common with climate change. In particular, these models cannot simulate fire behavior under conditions where compounding disturbances create large quantities of dead large woody debris [194], nor under mass fire conditions where fires can generate unique local weather systems [198]. Models to capture these types of spread conditions are an active area of research. However, FSim is calibrated until fire spread produces a number of large fires and mean fire size within targets based on recently observed fires. In this way, despite the above limitation, model results are within observed parameters. FSim also does not project changes in vegetation due to climate change, a major area of uncertainty.

FuelMap FuelMap is a dataset that was built by imputing FIA measurements of litter, duff, and downed woody material (DWM) to a contiguous grid across the contigu-

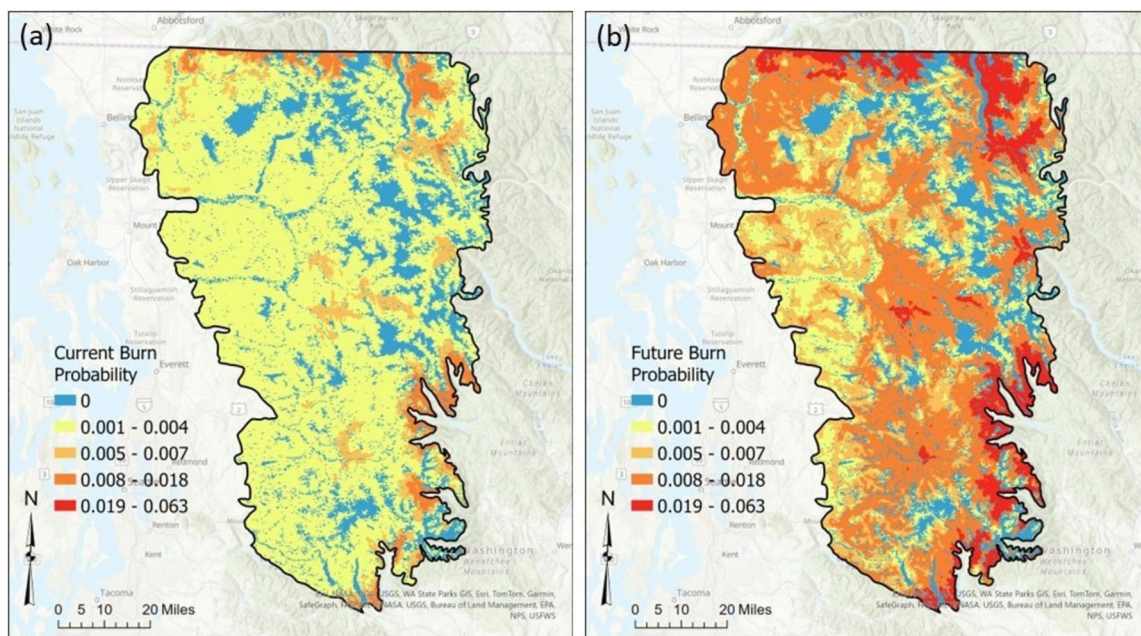


Fig. 4 The FSim Large Fire Simulator can project how future climate change may alter spatial fire probability patterns, which can then affect forest carbon. The two maps show contemporary, 1992–2020 (a) and mid-twenty-first century, 2035–2064 (b) annual burn probability at 270-m resolution for a landscape in Cascade Mountains of northern Washington State, United States, simulated by FSim [291]

ous United States [227]. FuelMap and TreeMap (“[Mapping forest carbon on the landscape](#)”) are consistent with each other, both by input data and methods. Forest carbon response functions to fire have been successfully mapped across the contiguous United States at 30-m resolution using FuelMap and Tree Map (see “[Mapping forest carbon on the landscape](#)” above). In other words, the amount of carbon retained onsite and emitted during fire have been calculated in FVS across a set of six fire intensities for each FIA plot in FuelMap and TreeMap, meaning that these can now be mapped spatially across CONUS. These functions can be combined with the probability of fire at each of these six intensities that FSim outputs to estimate the risk of levels of tree mortality and carbon emissions (Fig. 5). FuelMap is reliant on FIA transects in a limited number of plots. This method can miss the impact of spatial heterogeneity of fuels on the landscape, so the resolution at which FuelMap should be used is still under investigation.

USFS Insect and Disease Survey The USDA Forest Service Insect and Disease Survey maps insect and disease activity annually across the United States. Surveyors in airplanes record damage to trees in polygons across forests, noting the disturbance agent, host tree species, and damage type and severity. Nationally consistent geospatial data sets are available back to 1997, and data sets for individual regions are available for earlier years. This dataset

has been used to map bark beetle-caused tree mortality in the western United States [228] and associated carbon loss [121]. The accuracy of snag counts in this dataset was found to be 3–44% in two recent studies [229, 230].

National Insect and Disease Risk Map (NIDRM) NIDRM is a comprehensive nationwide assessment and database created by the USDA Forest Service of the potential hazard for tree mortality due to major forest insects and diseases. It summarizes landscape-level patterns of potential insect and disease activity and offers a science-based administrative planning tool for allocating pest-management resources. To capture spatial variations in forest health, NIDRM utilizes 186 insect and disease hazard models. The NIDRM products, compiled at a resolution of 240 m, support forest planning and enable forest-health hazard assessments at regional and national scales. These products can be used to identify the potential impacts of insects and pathogens on forests in the United States. The latest version of NIDRM (available at <https://usfs.maps.arcgis.com/apps/MapTour/index.html?appid=ade657567ff445d5bb3aaa7d898d9fb9>) was completed in 2018 for a 15-year assessment period (2013–2027) [231].

LANDFIRE disturbance layers LANDFIRE (LF) tracks annual landscape changes resulting from natural disturbances starting in 1999 and provides spatial vegetation and fuels layers for FSim, FuelMap, and FVS at 30-m res-

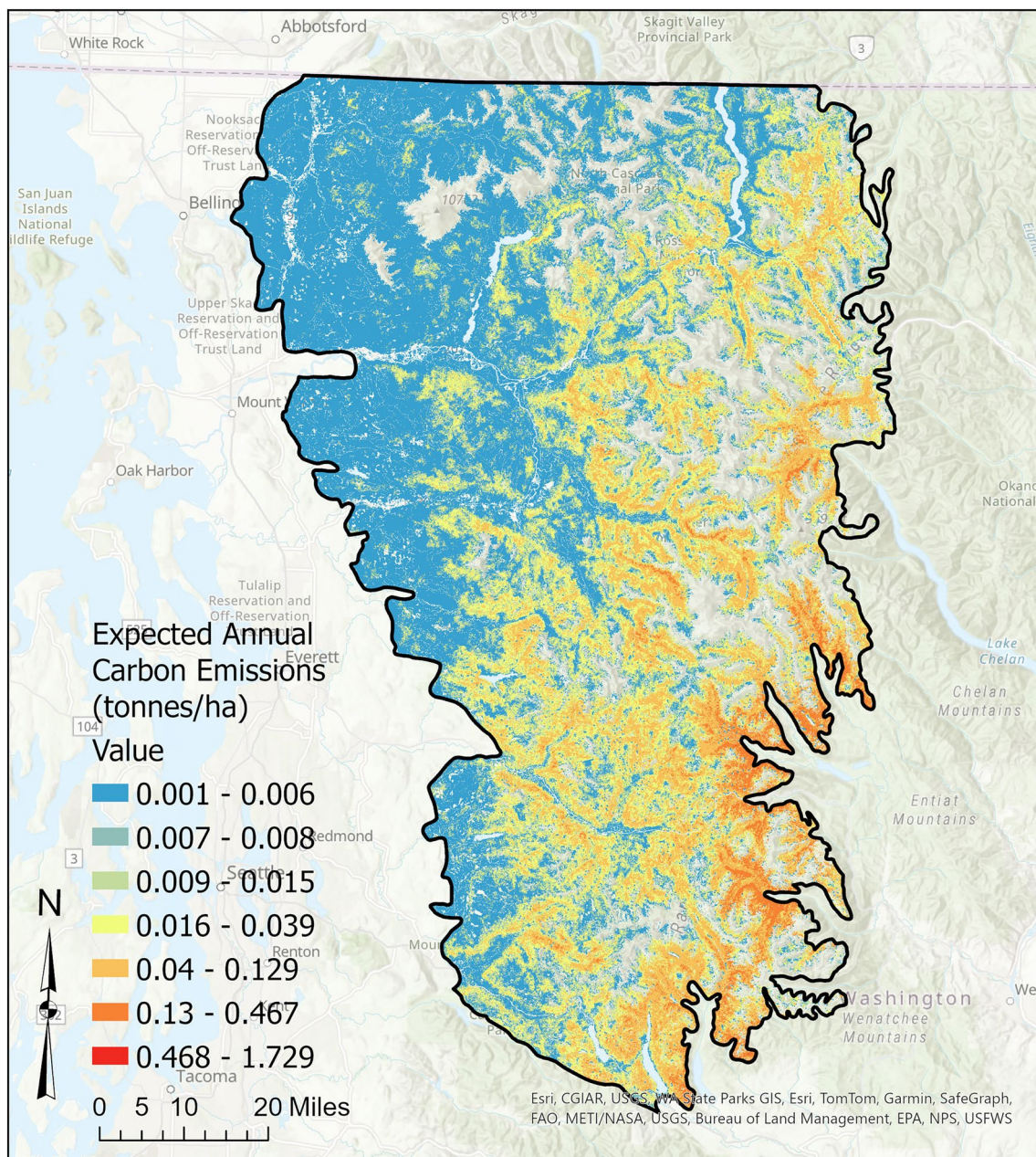


Fig. 5 A risk map derived from integrating TreeMap and FuelMap data with the Fire and Fuels Extension to the Forest Vegetation Simulator (FFE-FVS) (e.g. Fig. 3) and FSim simulations (Fig. 4) for a landscape in the Cascade Mountains of northern Washington, United States [R. Houtman, unpublished data]

olution. The initial version of the dataset identified disturbances using diverse geospatial datasets to detect and categorize changes in vegetation cover, supplemented by Landsat-based composite images to assign disturbance severity between time steps using the Difference Normalized Burn Ratio (dNBR) [232]. In the second generation of the dataset (LF ReMap, or LF 2.0 [233]), multiple teams enhanced the accuracy of disturbance representa-

tion by incorporating Monitoring Trends in Burn Severity (MTBS) and the Rapid Assessment of Vegetation Condition after Wildfire (RAVG) datasets to identify burned areas. The disturbance dataset tracks wildfires >1000 acres (404.7 ha) in the West and 500 acres (202.3 ha) in the East and can be used to monitor tree mortality from insects, diseases, and drought. Prior to 2020, the dataset incorporated only polygons reported through national

datasets such as the USDA Forest Service Activity Tracking System (FACTS) database. The 2020 release of LANDFIRE [234] includes polygons reported by Insects and Disease Detection Survey (IDS), which may not capture the full extent of insect and disease-related tree mortality and are coarse resolution with low accuracy.

Interagency Fuel Treatment Decision Support System (IFTDSS) IFTDSS combines fire behavior and spread simulation models with an approachable user interface. IFTDSS models simple fire behavior and landscape burn probability under static weather from a set of random ignitions, and the expected fire spread from a user-defined ignition set. Treatments like thinning, mastication, and prescribed fire are simulated by altering input files representing the fuel model [235], canopy cover, canopy height, crown base height, and/or crown bulk density based on the intended effects of the treatment. The user then specifies a set of static weather and fuel moisture conditions to simulate fires, allowing for exploration of various scenarios. The primary purpose of IFTDSS is to aid land managers in fuel treatment planning by simulating the effects of fuel treatments on the landscape. This led to some simplifications of the model framework to make problems tractable. Because IFTDSS models fire spread under static weather, the risk model excludes impacts from lower severity fires. Fire model outputs are conditional based on the specified weather scenario. The same fire spread caveats apply to IFTDSS as to FSim due to the utilization of the same underlying Rothermel equations. In order to explore impacts to carbon, IFTDSS outputs would need to be combined with a tree-level carbon map such as TreeMap and FuelMap.

Strategies to manage forest carbon

In forests adapted to low- to moderate-severity wildfire, fuel reduction treatments are effective at reducing the intensity and severity of wildfire [236–240]. Fire intensity affects severity, which in turn affects the amount of carbon emitted during the fire (through combustion) and afterward (through decomposition), as well as the rate of carbon sequestration after wildfire [10]. If fuel treatments spatially coincide with a future wildfire, carbon emissions from the fire are often reduced [241]. However, the benefits of individual fuel treatments are uncertain because it is impossible to predict the specific locations of future wildfires. Furthermore, the effects of fuel treatments diminish over time, typically lasting 5–15 years in forest fuels. In one study, ~7% of the area treated was subsequently intersected by a wildfire during the effective life of the fuel treatment [242]. Also, potential reductions in carbon emissions must be balanced with initial losses occurring during fuel treatments, including carbon

emissions by machinery and vehicles, and long-term effects on forest carbon fluxes. The choice of treatment type—mechanical, prescribed fire, or a combination of the two—significantly affects how much carbon is initially lost and how much is sequestered after treatment, as well as fire behavior in the event that a fire occurs [243, 244]. Treatments can be strategically applied in some forests, for example where high-severity wildfires may cause type-conversions to shrublands or grasslands, which have lower carbon storage capacities.

In the near-term (< 50 years) following landscape-level fuel reduction treatments, total forest carbon stocks are diminished, even when accounting for avoided carbon losses from subsequent wildfires [239, 245–248]. Rather than tracking just total carbon, an alternative approach tracks carbon stored in large aboveground live trees as the dominant stable carbon pool in the forest [249–251]. In mixed conifer forests in the Sierra Nevada, live tree carbon in both untreated and recently treated stands was substantially lower than that estimated for stands in a historical (1865) landscape, which had frequent fires [249]. Prescribed fire released 14.8 Mg C ha⁻¹, with pre-fire thinning increasing the average release by 70% and contributing 21.9–37.5 Mg C ha⁻¹ in milling waste. All fuel treatments increased fire resistance, but treatments that included prescribed fire had lower torching and crowning potentials. Hurteau et al. [250] reported similar findings in ponderosa pine forests in the Southwest. While aboveground carbon was greater under the baseline fire-excluded treatment scenarios, higher potential for torching and crowning in untreated stands exposed the carbon stocks to greater risk.

Management regimes that reduce forest stand density and favor large, fire-resistant trees may increase the amount of stable carbon on the landscape. This equates to a potential risk reduction that can be quantified, or at least qualitatively categorized, by some of the mapping frameworks discussed in “Mapping carbon risk to disturbance”. For example, using the LSim model to explore the effects of different treatment and wildfire management approaches over 60 years, Young and Ager [251] found that increasing the treatment area 5X over current treatment rates produced the most stable forest carbon on the landscape over time. Similarly, fuel treatment effects simulated over a 90-year period using LANDIS-II found that the no-treatment scenario has significantly greater overall carbon loss than treatment scenarios in frequent-fire forest types in the Sierra Nevada [252]. Specific ecosystems may attain a net benefit from treatments over decades to centuries. In another study, long-range carbon dynamics were modeled in conjunction with fuel treatments in the Pacific Northwest. The authors concluded that due to the low consumption of the majority of fuels

and the limited duration of the effectiveness of fuel treatments, long-term carbon storage potential was reduced, even where high wildfire risk existed [253]. Balancing demands for carbon storage with demands for reducing wildfire severity would require fuel treatments to be implemented strategically throughout landscapes, rather than indiscriminately treating all stands [237].

All of the disturbance risks discussed here are also being impacted by climate change (Fig. 1). In that context, climate change is not only a driver for management designed to sequester carbon in light of disturbances, but also contributes to the design of silviculture treatments to mitigate direct impacts on specific forests. Managing for site-specific stand structures that include features such as high overstory compositional diversity [184], age diversity [254], spatial complexity [255], and trait diversity [256] are strategies that can increase forest resilience in the face of climate change, ideally while also continuing to maintain stable carbon stocks [185]. Treatments can be implemented that create climate-resilient forest structure traits while simultaneously maximizing carbon sequestration rates that create long-term stability. These strategies may also reduce the initial carbon stored onsite [257], demonstrating the value of understanding how treatments impact multiple overlapping priorities.

Although some fuel treatments may catalyze net carbon uptake over a long period, Wiechmann et al. [244] reported three of five types of fuel treatments resulted in a net loss in forest carbon 10 years after treatment in the Sierra Nevada. The two treatment types that recovered carbon over 10 years were a burn-only and understory thin-only. Conversely, over the long run, a combination of prescribed fire and mechanical thinning is most effective at reducing potential fire severity where it has been studied [238, 257]. Across 10 locations in the United States, Boerner et al. [243] found that mechanical treatments do reduce forest carbon significantly more than prescribed fire, although there was a greater increase in carbon sequestration after mechanical treatments.

Spatial relationships of fuel treatments and wildfires are important to consider. At the landscape level, effects from different treatment scenarios can be highly dependent on the spatial configuration of treatments and the percent of the landscape that is treated. Finney [258] and Ager et al. [259] reported that treating 10% of a forest landscape reduces expected losses of large trees by 70%. Treatments strategically placed in relation to how fire spreads are an effective technique for reducing fire exposure beyond the treatment area, including transmission to valued natural and cultural resources [260]. However, the dynamics of fire spread vary widely by forest type, and the design and implementation of fuel treatments that are sensitive to the ecology of an individual forest

could help achieve desired objectives in forest resilience [45]. For example, Agee and Skinner [236] outlined both a methodology for restoration of fire-excluded dry forests (thin from below, reduce surface fuels, and retain the largest, oldest trees) and the characteristics of the ecosystem that determine the forests in which the application of these techniques should be prioritized (historically fire-frequent, low-severity, low-density forests). Management of longleaf pine (*Pinus palustris*) forests in the Southeast using the Stoddard-Neel method, a holistic management approach that was derived in the first half of the twentieth century, may require greater initial fuel reductions prior to the reintroduction of repeated prescribed fires [253]. Alternatively, in order to return forests to within the range of natural variation prior to fire suppression, management of forests that tend to burn at high intensity and high severity, such as jack pine (*Pinus banksiana*) and lodgepole pine (*Pinus contorta*) forests, could benefit from a patchy fuel landscape that allows for some amount of self-limiting high-severity fire. Eastern hardwoods may require an entirely different approach, with mechanical thinning being the primary activity used to meet restoration goals [261].

Management practices that lead to an unintended increased risk of high-severity wildfire (e.g., fire suppression and reductions in harvesting) have also led to an increased risk of insect and disease-induced tree mortality in certain forests [262]. Greater homogeneity can decrease overall resistance and resilience of a forest to biotic disturbances, while higher tree densities increase the number of available hosts for transmission of insects and diseases. Because of this, many of the same strategies that have been proposed for preserving forest carbon in the face of wildfire are also proposed for reducing levels of tree mortality attributed to some types of insects and diseases. In the Northern Rockies, Hood et al. [263] reported there was up to 50% host tree mortality after a mountain pine beetle infestation in dense, untreated stands; 39% mortality in stands that had been treated with prescribed fire; and almost no mortality in stands that were treated with mechanical thinning and prescribed fire. Low-severity fire has been shown to induce trees to fortify their resin ducts, thereby increasing resistance to future mountain pine beetle infestation [264]. In addition, thinning is widely regarded as an effective means for increasing resistance and resilience to several notable bark beetles, likely due to reductions in tree competition, increases in tree vigor, increases in tree spacing, and changes in microclimate that disrupt aggregation pheromone plumes [265–268]. The efficacy of thinning to reduce levels of bark beetle-induced tree mortality has even been demonstrated under extreme drought conditions (e.g., [269]). Although sanitation harvesting

of infested trees has been proposed to alleviate tree mortality [270], these strategies are not as effective for reducing forest carbon risk since they run counter to the natural disturbance cycle of many forest types [271]. In eastern hemlock (*Tsuga canadensis*) forests, simulations show that allowing hemlock wooly adelgid to progress naturally through a stand (versus salvage scenarios) may result in the least impact to long-term carbon sequestration and net forest carbon [272].

As with fuel treatments for wildfire, forest thinning can sometimes serve as an effective strategy to reduce forest carbon risk from drought, bolstering forest resistance (the ability to sustain growth during drought) and resilience (the capacity to recover growth after drought) [273–277]. This is achieved by reducing tree densities, which is the primary driver of resource competition at the stand level [277], and by enhancing available growing space [278]. While the potential of thinning to reduce drought effects is widely acknowledged, its effectiveness varies substantially by context and ecosystem, and is influenced by various factors. Stands with lower tree densities, achieved through more substantial thinning practices, generally exhibit heightened resistance and resilience [279–281]. Results from a recent meta-analysis of stand density and tree mortality relationships in yellow pine (ponderosa pine and Jeffrey pine, *Pinus jeffreyi*) forests suggest that substantially lower stand densities are required to maintain adequate levels of resistance to bark beetles in contemporary forests compared to recent historic forests, due to the effects of warming and drought on forest structure and composition, including transitions from low-density, open and park-like forests to dense, second-growth forests [268]. Maintaining stands at such low densities may be required to promote high levels of resistance to drought and bark beetles in the future and represents a substantial change from current management prescriptions, of which the carbon consequences over time are largely unknown.

The benefits of thinning on carbon risk reduction, through reduced future disturbances, diminish with time since last treatment [281, 282]. Notably, the effects of thinning differ between broadleaves and conifers, although additional studies are needed [283]. Furthermore, the specific thinning method employed can yield contrasting outcomes. Thinning from above (involving removal of dominant and co-dominant trees) has the potential to minimize drought-induced growth reductions by reducing tree diameter, fostering a more intricate vertical structure that stratifies competition, while thinning from below (involving the removal of smaller diameter trees in lower canopy positions) may result in larger diameters and a monolayered structure, intensifying competition [284]. The type of thinning may also

result in either complementary or opposing effects on different disturbances [285]. For example, thinning from below is often used in fuels reduction resulting in forests of large, older trees, which are typically more susceptible to bark beetles (e.g., [231]). Conversely, thinning from above can reduce susceptibility to bark beetles but may increase surface fuels resulting from harvest residuals.

Overall, our understanding of relationships between forest carbon risks and treatments that reduce tree damage and mortality from insects, diseases, and drought has some critical limitations, uncertainties, and gaps. These include: (1) a complete accounting of carbon emissions during treatments, (2) the likelihood of a tree mortality event (e.g., bark beetle outbreak) occurring during the period of time when treatments are effective, recognizing that efficacy declines with time since treatment, (3) the amount of landscape that needs to be treated to impart desired effects, and (4) the post-treatment rate of carbon uptake.

Conclusions

Forest carbon storage is a critical ecosystem service that is facing heightened risks as climate change facilitates larger and more severe wildfires, widespread insect and disease outbreaks, and more intense droughts in many forests of the United States [286]. To minimize negative effects and maximize resilience of forest carbon, these risks must be accounted for in carbon offset protocols, carbon management practices, and carbon mapping and modeling techniques. Many of the example tools discussed in “Mapping carbon risk to disturbance” demonstrate the significant conceptual challenges of combining all the interacting land surface, climate, and ecological processes that are needed to analyze forest carbon risk, a task that becomes increasingly complicated with climate change and over temporal trajectories. Additional challenges lie in scaling up modeling efforts and management techniques across the United States, and it is noteworthy that all the studies on managing forest carbon risk discussed in “Conclusions” have been executed on a local project or regional scale, not at a national scale. The latter requires consistent accounting across variations in forest types, disturbance trajectories, and resource availabilities. However, with the continuous advancement in scientific understanding and computational capabilities, the foundation now exists to scale up analyses that were previously only possible on a local scale. This represents the next critical step towards elevating forest carbon risk science to a level that can facilitate a better understanding of forest carbon risk from climate change and disturbance across the entire United States and create opportunities for strategic forest management directed at reducing those risks.

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Author contributions

AD, RH, and PG designed, conducted, wrote, and performed final editing on the manuscript. WA, CF, JH, JK, KR, CS, and KY contributed intellectual material to the manuscript and assisted with review and editing throughout the process.

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Declarations

Competing interests

The authors declare no competing interests.

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