

Review and synthesis

Forests of the future: Climate change impacts and implications for carbon storage in the Pacific Northwest, USA



Michael J. Case ^{a,*}, Brittany G. Johnson ^b, Kristina J. Bartowitz ^c, Tara W. Hudiburg ^c

^a The Nature Conservancy, 74 Wall Street, Seattle, WA 98126, USA

^b School of Environmental and Forest Sciences, University of Washington, Seattle, WA, USA

^c Department of Forest, Rangeland, and Fire Sciences, University of Idaho, Moscow, ID, USA

ABSTRACT

Rising greenhouse gases are changing the Earth's climate and adversely affecting ecosystems that currently provide a suite of invaluable benefits, from cleaning water to sequestering carbon. Some of the world's most productive forests grow in the Pacific Northwest region of North America, but our understanding of climate change effects on these forests and their carbon is still emerging. Here, we synthesize the current state of research (including empirical, paleo, and modeling studies), discuss the implications on forest growth and carbon storage in Pacific Northwest forests, and identify key knowledge gaps and future research opportunities based on a combination of published studies and expert opinion. Two case studies are presented that illustrate the expected effects of climate change on moist and dry forest ecology and carbon storage. In response to these impacts, we highlight a number of appropriate regional forest restoration and management adaptation strategies. Filling in knowledge gaps will improve the accuracy of forest carbon accounting, a crucial part of the strategy to meet climate mitigation targets and prevent the most severe impacts of climate change.

1. Introduction

Rising greenhouse gases (GHGs) and resulting climate change is already affecting the Earth's terrestrial and aquatic systems (Steffen et al., 2018). Current mitigation efforts are largely aimed at curbing human caused greenhouse gas emissions; however, to keep global temperatures below 1.5 °C and avoid some of the worst impacts of climate change, these strategies must also prevent additional CO₂ from being released from land and sea ecosystems and soak up as much atmospheric CO₂ as possible (IPCC, 2018; USGCRP, 2018). One such removal technology – natural climate solutions – is found within our ability to conserve and restore forests and improve natural resource management practices, which results in increased carbon storage and/or a reduction in GHG emissions (Fargione et al., 2018; Griscom et al., 2017). A critical piece of natural climate solutions is maximizing carbon storage and sequestration, the ability to remove CO₂ from the atmosphere and store it long-term. Natural climate solutions for forests can include afforestation, reforestation, or protecting forest carbon storage and sequestration potential by minimizing impacts (Law et al., 2018; Moomaw et al., 2020; Zomer et al., 2008).

Globally, forests absorb 15–20% of annual human carbon emissions (Le Quéré et al., 2018), most of which is stored either aboveground in tree biomass or belowground as soil carbon. The Pacific Northwest (PNW) region of North America has some of the greatest natural

terrestrial carbon storage potential within North America (Hudiburg et al., 2009; Smithwick et al., 2002). For instance, in the US, live tree aboveground carbon density in PNW moist coastal forests regularly contains more than 80 megagrams (Mg) per hectare (ha) of carbon compared to other regions - forests in Midwest states (40–60 Mg/ha) and forests in Northeast states (60–80 Mg/ha) (Wilson et al., 2013). PNW moist coastal forests are highly productive and have historically stored carbon for long periods of time in part because of their longevity and the high amounts of precipitation they receive, which also manifests in a historically long fire return interval. Further, forests in the West Cascades ecoregion of the PNW are estimated to have more than double the amount of total carbon stored compared to forests in the East Cascades ecoregion (Law et al., 2018). However, there is substantial heterogeneity in PNW forests, and they can differ greatly in response to climate, steep elevation gradients, soils, and complex disturbance and land-use histories (Franklin and Dyrness, 1988). Moreover, there are diverse environments and ecological systems across the PNW that respond differently to a warming climate, changes in disturbance patterns, and natural resource management (Halpern and Spies, 1995).

Broadly, PNW forested systems can be categorized as moist, dry, and subalpine forests. Geographically, moist and dry forest types are generally found on the western and eastern sides of the Cascade Divide, respectively, while subalpine forests are located at high elevations (Fig. 1). Each forest type has a unique set of defining characteristics,

* Corresponding author.

disturbance factors, and responses to a changing climate (Fig. 1). However, many climate mitigation targets that specifically rely on forest carbon storage and sequestration do not incorporate these differences. For example, California's Forest Climate Action Plan (Forest Climate Action Team, 2018), does not account for responses of individual forest types to climate change. Moreover, there are current gaps in our understanding of how climate change will influence forests and how those effects will impact carbon storage and sequestration. These knowledge gaps have the potential to derail the path to current mitigation targets.

In this review, we synthesize how climate change is expected to affect major forest types in the PNW and highlight how carbon storage will likely be impacted. We first summarize the existing literature on the direct and indirect climate change impacts on forests. Second, we identify key climate change impacts on PNW forests and their ability to store carbon. Third, we combine scientific studies and expert opinion to explore some of the critical knowledge gaps of how climate change will impact forests and carbon and offer several actionable strategies in response. These key knowledge gaps form a foundation for future forest carbon research opportunities and, once addressed, will help lead to more accurate projections of climate change impacts on forests and carbon and thus more effective management strategies. To demonstrate this process, we briefly present two case studies that illustrate how climate change is anticipated to affect moist and dry forests and their carbon storage. Finally, we highlight appropriate adaptation strategies that are currently or planned for implementation. This review is intended to be used by regional conservation organizations to better inform their forest restoration and management strategies as well as prepare for an uncertain future.

2. Climate change effects on forests

Climate change impacts forests both directly and indirectly (Bonan, 2008) and can be exacerbated by human effects (Fig. 2). The direct impacts to forests manifest through changes in temperature and precipitation (i.e., climate), whereas indirect effects include changes to the occurrence of disturbances or other factors (e.g., fire, insect outbreaks,

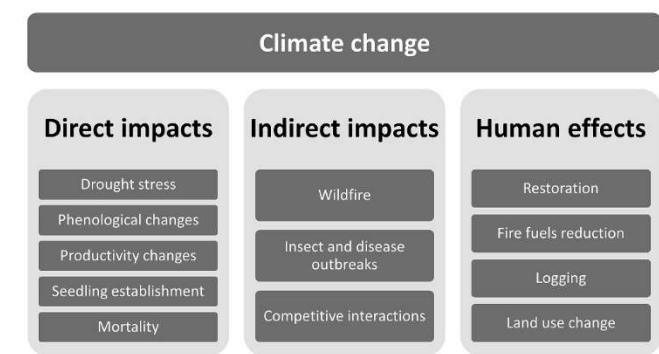


Fig. 2. Direct and indirect impacts of climate change and human impacts on forests in the Pacific Northwest, USA.

pathogens) (Anderson-Teixeira et al., 2013). Some of these disturbances have the power to turn forests from a sink to a source of carbon (Peterson et al., 2014). In the PNW, temperatures have increased 0.86 °C degrees since the first half of the last century (1901–1960) and are projected to warm further, between 2.0 and 2.6 °C by the 2050 s (2036–2065) and 2.8 and 4.7 °C by the 2080 s (2071–2100) (Vose et al., 2017). Projections of future precipitation patterns vary among global climate models but on average show a range of annual average precipitation change from −4.7% to 13.5% (May et al., 2018). Warming temperatures and changing precipitation patterns, particularly during the growing season, will directly and indirectly affect ecosystem productivity and carbon storage, soil moisture availability, wildfire frequency and size, and susceptibility of forests to insect and diseases (Abatzoglou et al., 2017; Hicke et al., 2013; Kolb et al., 2016; Littell et al., 2016; Mildrexler et al., 2016; Ritóková et al., 2016).

2.1. Direct effects

Increasing temperatures and changing precipitation patterns have already affected forests across western North America (USGCRP, 2018).

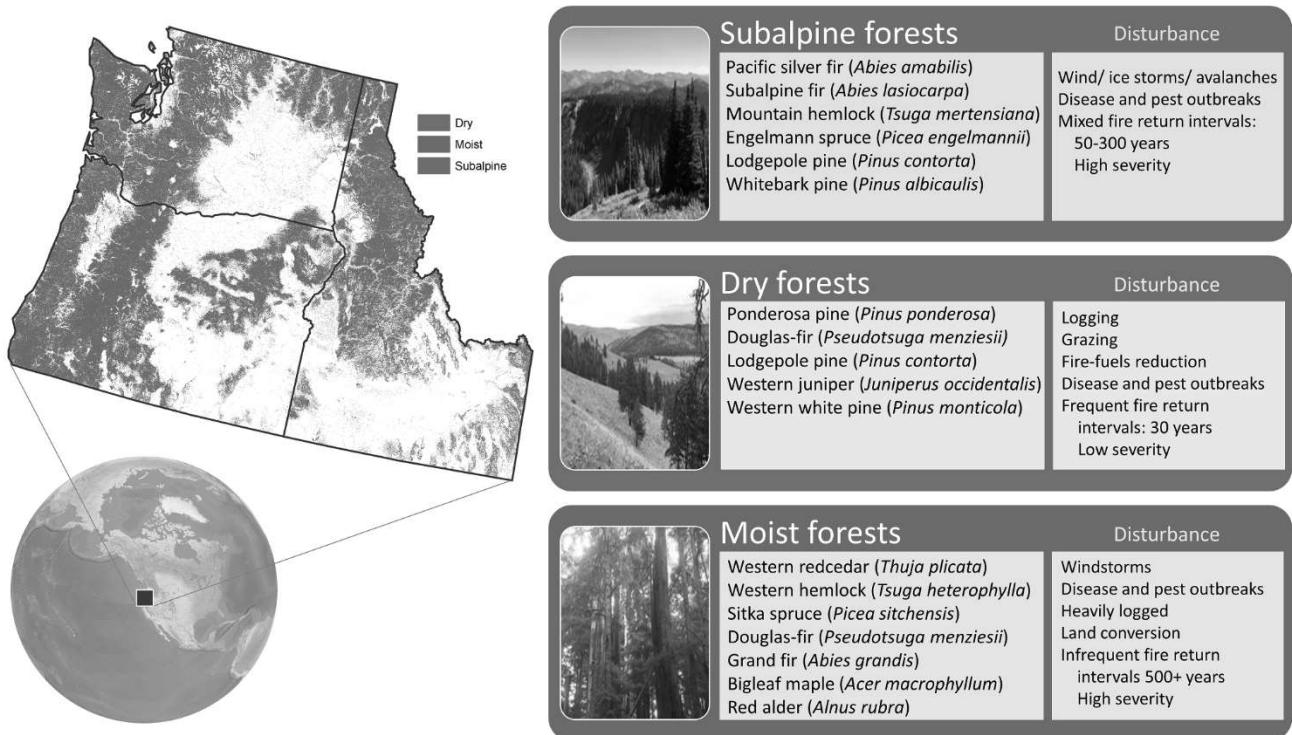


Fig. 1. Forest types of the Pacific Northwest, USA, their dominant tree species, major disturbance factors, and their spatial distributions.

Climate directly affects vegetation growth, reproduction, and survival (Holdridge, 1947; Woodward and Williams, 1987). Examples of the direct effects of climate change include tree mortality (Allen et al., 2010; Anderegg et al., 2013; Berner et al., 2017b; Breshears et al., 2005; Choat et al., 2012; Van Mantgem et al., 2009), changing tree growth rates and phenology (Chmura et al., 2011; Ford et al., 2016; McKenzie et al., 2001; Williams et al., 2010), and altered productivity (Berner et al., 2017a; Boisvenue and Running, 2006; Latta et al., 2010). In addition, modifications in tree population distributions have occurred as species climate envelopes shift in response to both warming temperatures and changes in available moisture (Beckage et al., 2008; Kelly and Goulden, 2008; Monleon and Lintz, 2015). These changes have direct implications on the ability of PNW forests to store and sequester carbon (Wimberly and Liu, 2014).

2.2. Indirect and human effects

Although the direct effects of climate change are expected to have significant impacts on forests of the PNW, it is widely anticipated that the indirect effects of climate change will play an even greater role in large-scale forest processes (Coop et al., 2020; Wimberly and Liu, 2014). Disturbances (e.g., wildfire and insect outbreaks) have increased across the western US (Abatzoglou and Williams, 2016; Cohen et al., 2016; Creeden et al., 2014; Westerling et al., 2006), a trend projected to continue in the future (Cassell et al., 2019; Westerling et al., 2011). This trend is expected to be further exacerbated by continued warming temperatures and a potentially longer and drier summer period (Adams et al., 2009; Allen et al., 2010; Anderegg et al., 2013).

Continued human disturbances, such as harvest, fire fuels reduction, restoration, and land-use changes may decrease carbon storage and adversely affect some ecosystem services (Hudiburg et al., 2019; Law and Waring, 2015). Fire-fuels reduction will mostly likely decrease terrestrial carbon stocks and sequestration potential (Campbell et al., 2012; Hudiburg et al., 2011; Hudiburg et al., 2013a; Mitchell et al., 2009). However, managing for multiple forest management objectives (e.g. economics, fire resilience, and biodiversity) is challenging, and positive outcomes for one objective may negatively impact others (Buotte et al., 2020). There is interest in using management strategies to conserve forest carbon storage in some systems (Krofcheck et al., 2019; Liang et al., 2017), but the efficacy of these strategies is untested and, in

some cases, may lead to forest and carbon losses (Law et al., 2018).

Indirect effects caused by natural and human disturbance will likely increase tree mortality and decrease carbon storage in some forested areas (Bentz et al., 2010; Peterson et al., 2014; Sturrock et al., 2011). As recovery from disturbance may occur in climatic conditions both unsuited to regeneration of historical tree species (Hicke et al., 2006; Jackson et al., 2009; McKenzie et al., 2004) and those generally not ideal for recovering forests (Littlefield, 2019), increased tree mortality may lead to forest species type shifts, an additional confounding factor for effective forest management. Hotter and drier conditions may decrease forest recovery potential (Anderson-Teixeira et al., 2013) as well as increase the potential for short-interval reburns (Buma et al., 2020; Turner et al., 2019). Moreover, the type and magnitude of disturbances will vary by forest type and location (Fig. 3). For example, an increase in the frequency and extent of wildfire is expected in most dry forest ecosystems (e.g., Cansler and McKenzie, 2014; Stavros et al., 2014; Westerling et al., 2011, 2006) and by mid-century, the annual area burned across Washington State is projected to be more than three times higher than it is today (Littell et al., 2009). However, due to historical fire suppression, many of these areas may still be in a fire deficit compared to historic fire regimes (Haugo et al., 2019). Subalpine forests are not exempt from increased wildfire as warming temperatures and less snowpack at high elevations drive more frequent fires and potentially alter forest structure and function significantly (Cansler et al., 2018). More frequent fires in subalpine forests can also reduce tree regeneration and have resulted in the loss of biological legacies, delaying recovery of aboveground carbon (Peterson et al., 2014; Turner et al., 2019). However, the production of pyrogenic carbon, recalcitrant by-products of fire which can be stored for centuries or millennia, could mitigate some of the projected carbon losses in these forests (Jones et al., 2019). The invasion of insects such as mountain pine beetle (*Dendroctonus ponderosae*), which were previously excluded from high elevation forests due to cold temperatures (Bentz et al., 2010), may exacerbate the effects of fire leading to increased mortality and a reduction in subalpine forest carbon stocks (Peterson et al., 2014; Wimberly and Liu, 2014). However, others have found that insect-caused tree mortality does not necessarily increase the likelihood of wildfire across at a large scale (Meigs et al., 2015). The following section explores three major forest types of the PNW and their projected responses to climate change.

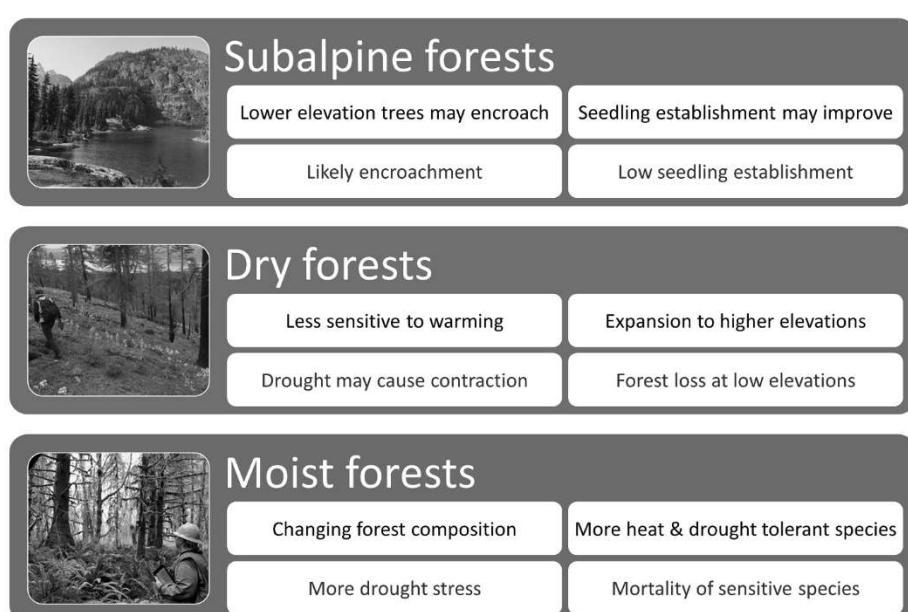


Fig. 3. General forest responses to moderate (black text) and high (red text) levels of climate change. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3. Climate change impacts on PNW forests and carbon storage

There are numerous ways in which climate change will directly and indirectly effect vegetation throughout the PNW (Peterson et al., 2014). As such, we synthesize findings from multiple sources of information including empirical, paleoecological, and modeling studies. Although there are varying degrees of uncertainty associated with future projections, models that simulate changes in climate and vegetation response can provide us insight into these impacts. However, as climate change creates novel conditions, the use of purely correlative models that assume static relationships between vegetation and climate becomes increasingly challenging (Guisan and Thuiller, 2005). Therefore, the use of process-based models (PBMs), which simulate the basic mechanisms that regulate vegetation processes are increasingly used to assess vegetation response to future climate and disturbance regimes (Fisher et al., 2018). PBMs are arguably better able to capture important climate change effects and are increasingly used to simulate vegetation trajectories and to identify key drivers of change (Fisher and Koven, 2020).

A review of PBMs is out of the scope of this paper. Moreover, there are many different types of PBMs and they are diverse in what processes they simulate, how those processes interact with one another, and to what scale PBMs are relevant for. For example, individual-based models can simulate individual organisms and are generally used to address questions about species to species interactions and succession. These models tend to be more complex than other PBMs and therefore usually have a small spatial scope (Fisher et al., 2018). By contrast, big leaf models are relatively simple and represent an entire forest canopy as a single, homogenous layer that simulates photosynthesis and carbon fluxes. Models such as these can be used for a large spatial scope, are computationally efficient, but fail to represent interactions between species or plant functional types. Dynamic Global Vegetation Models (DGVMs) – another type of PBMs – simulate the response of plant functional types to climate change, including plant physiology, biogeography, water relations, and interactions with fire and are relevant when synthesizing potential future changes across a large region and for relatively long time periods. Therefore, for the purposes of this review, we focus on DGVMs, as they are most appropriate for regional simulations and for addressing the effects of disturbances.

Climate modeling of the PNW region projects future increases in temperatures and a substantial reduction of snowpack (Mote and Salathé, 2010). These effects are directly used as inputs to drive PBMs. For instance, global vegetation models, have predicted increases in temperate forest productivity across the PNW with climate change (Kim et al., 2018; Rogers et al., 2011; Shafer et al., 2015). The predictive power of PBMs and climate models can be amplified further through coupling with disturbance models. These combined models predict that gains in productivity and carbon sequestration may only be partially realized or fully lost through natural (fires) and human disturbances, such as harvest (Brodribb et al., 2020). We combine the results from multiple sources of information including, empirical data, modeling projections, and expert knowledge and summarize the expected impacts to forests and carbon for each forest type under generic “moderate” and “high” climate change scenarios (Fig. 4). There is uncertainty associated with each source of information and assumption.

3.1. Moist forests

Moist, coastal PNW forests are some of the most carbon-dense forests in the continental U.S. (Hudiburg et al., 2009). Warming temperatures, increased atmospheric CO₂, and increased growing season precipitation may lead to more growth and productivity in moist forests (Creutzburg et al., 2017; McKenzie et al., 2001, Fig. 4). Carbon storage in old-growth forests might be initially resistant to future changes in temperature and precipitation because of their superior buffering capacity (Seidl et al., 2012). However, even these systems can be limited by low soil water

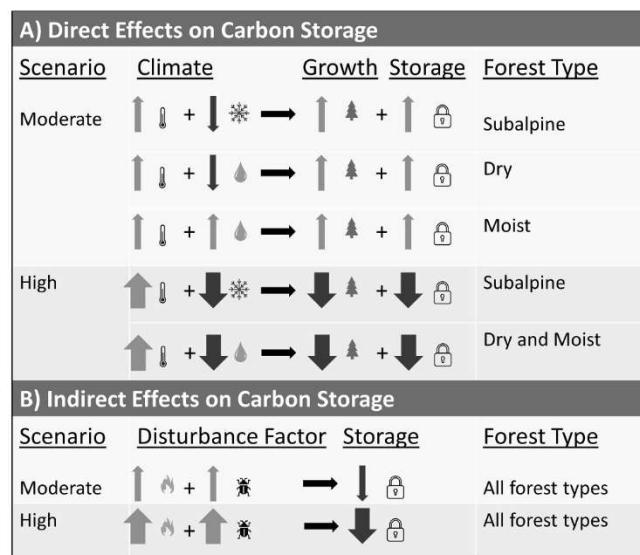


Fig. 4. Projected climate change impacts on forest carbon for moderate and high scenarios for three general forest types of the Pacific Northwest. There are uncertainties associated with each scenario, resulting climate effect, and changes to forest growth and storage. The moderate climate change scenario assumes moderately warmer temperatures, less summer precipitation and more winter precipitation. The high climate change scenario assumes much warmer temperatures, a significant decrease in summer precipitation, and much more winter precipitation. The width of the arrows represents the relative magnitude of change. Carbon storage is represented by the lock symbol.

availability during summer months in some areas and if growing season precipitation or summer precipitation does not increase but temperature does increase, then growth, productivity, and carbon sequestration would decrease (Rogers et al., 2011). Some moist forests are also energy-limited where species-to-species competition and closed canopies reduce light and nutrients for many individuals (Waring and Running, 2007). For example, tree growth in some temperate moist forests in western Washington have been shown to respond positively to warmer temperatures over the recent past (Holman and Peterson, 2006). Therefore, it is plausible that energy-limited forests could transition to more water-limited systems with even drier summer growing periods. This could have serious implications on the amount of carbon that moist forests are able to sequester in live tissue, although there may be temporary carbon storage gains in dead plant material, such as coarse woody debris (Campbell et al., 2019).

Moreover, decreased precipitation and increased drought stress during the growing season will likely cause decreased tree growth and productivity for moist forests at the edge of their suitable climatic conditions (Chmura et al., 2011; Luce et al., 2016, Fig. 4). The susceptibility to increased drought stress will vary by species (e.g., the drought tolerant Douglas-fir (*Pseudotsuga menziesii*) compared to the xerophytic western hemlock (*Tsuga heterophylla*) and western redcedar (*Thuja plicata*)). However, even reasonably drought tolerant species, such as Douglas-fir, are sensitive to summer water balance deficits across much of the western U.S. (Littell et al., 2008; Restaino et al., 2016). Therefore, it is possible that forest growth and carbon storage for drought tolerant species may decrease later in the century under more pronounced climate change, with the potential exception at some high-elevation sites (Case and Peterson, 2005; Littell et al., 2010, 2008, Fig. 3).

Paleoecological evidence demonstrates that species move in response to climatic change. For example, western hemlock has been shown to move up in elevation and can displace other species, such as Pacific silver fir (*Abies amabilis*) and mountain hemlock (*Tsuga mertensiana*) during historically warmer (and drier) periods (Dunwiddie, 1986). Paleoecological evidence also shows that during warm and dry

periods, drought tolerant species, such as Douglas-fir and lodgepole pine (*Pinus contorta*), can displace typical moist forest species (Whitlock, 1992). In addition to climate-driven species migration, disturbance regimes (especially fire) could drastically increase in severity and area burned in moist forests during warm and dry periods (Rogers et al., 2011). Increased fire frequency generally promotes more fire adapted and early pioneer species, such as Douglas-fir and lodgepole pine (Cwynar, 1987; Prichard et al., 2009). This evidence suggests that carbon storage and future sequestration rates will be largely dependent on which species survive and thrive in moist forests (Figs. 3 and 4).

Recent vegetation modeling as simulated by some PBM studies indicate that wet, coastal forests and the carbon they store may be relatively stable in the future across multiple climate scenarios (Case et al., 2020; Halofsky et al., 2018a; Shafer et al., 2015). Some of these DGVMs project a potential expansion of low elevation forests across parts of the PNW, which may increase the carbon sequestration potential in some areas (Case et al., 2019; Kim et al., 2018). Leveraging the results of other PBMs, some have advocated for protection of moist carbon-dense forests to ensure both the longevity of the carbon sink potential and the co-benefits they provide for wildlife and salmon habitat (Buotte et al., 2020). Yet others have modeled how forest management and carbon sequestration may change in the future and have advocated for longer harvest cycles to help protect forest carbon storage in moist PNW forests (Law et al., 2018). However, an increase in fire could substantially change carbon storage potential as some DGVM studies project increases in fire across moist forests of western Oregon and Washington and declining forest carbon stocks (Sheehan et al., 2019). For example, a “hot and dry” GCM projection simulated by Rogers et al. (2011), showed an increase of 1200% in area burned for PNW moist forests by the end of the century, resulting in a 24% loss of ecosystem carbon.

3.2. Dry forests

Dry forests in the PNW are projected to experience increased summer temperatures, decreased winter snowpack, and changing spring and fall precipitation patterns (Mote and Salathé, 2010). The growing season in these forests will likely shift to both begin and end earlier in the year due to low snowpack and crippling late-summer droughts. Although the direct impacts of climate change on dry forests will likely be relatively similar to those in moist forests, dry forests have the advantage of a species composition already well-suited to drought. While some projections under increased atmospheric CO₂ scenarios indicate some dry forests may increase their productivity (Hudiburg et al., 2013b; Kim et al., 2018; Rogers et al., 2011), decreased water availability and nutrient limitations may still limit growth, and lead to increased tree mortality (Berner et al., 2017a). Furthermore, potential increases in productivity may be constrained to wet years, and these gains may diminish over prolonged drought periods (Newingham et al., 2013).

Indirect climate effects, such as increased human and ecological disturbances, have and will likely continue to cause large-scale tree stress and potential die-off (Van Mantgem et al., 2009). Human-caused tree mortality from events such as timber harvest and fire-fuels reduction is the largest cause of tree mortality across the western US over the decade (Berner et al., 2017b). Ecological disturbances, such as wildfire, have also played a substantial role in tree mortality. Projected increases in wildfire (Liu et al., 2013) and insect outbreaks (Hicke et al., 2012) due to climate change are expected to further increase tree die-offs and lead to decreases in forest cover (Fig. 4). Both area burned and wildfire severity are also predicted to increase under climate change (Rogers et al., 2011), which may lead to higher tree mortality and fire emissions. For instance, landscape-scale modeling in dry forests of eastern Oregon suggest large shifts in tree species composition, including a decline in subalpine species and increases in lower-elevation species under future climate scenarios (Case et al., 2019; Cassell et al., 2019; Kim et al., 2018).

Climate change also impacts the post-disturbance recovery of dry

forests. Tree seedling establishment is hampered by hotter temperatures and lower snowpack which results in less water availability during the growing season (Davis et al., 2019; Stevens-Rumann et al., 2018). In these conditions, seeds may be unable to germinate and seedlings have increased mortality rates. Moreover, widespread tree mortality from disturbances, such as wildfire, may lead to larger distances to seed sources inhibiting vegetation establishment (Stephens et al., 2018; Tepley et al., 2017). The combination of these factors could lead to the potential conversion from forest area to non-forest following disturbance (Coop et al., 2020; Stevens-Rumann et al., 2018). This is especially concerning in already vulnerable regions like transition and ecotone areas (Albrich et al., 2020).

Future projections for dry forests are somewhat mixed. Fire-fuels reduction, a widely accepted management technique (Halofsky et al., 2020), has been identified as reducing fire severity and potential carbon emissions from fire in dry forest types; however, modeling studies and empirical measurements indicate mixed results (Campbell et al., 2012; Mitchell et al., 2009). Nevertheless, disturbance- and drought-mediated tree mortality, which are likely to increase with continued climate change, can greatly impact long term carbon storage and sequestration potential especially over long (millennial) time scales (Bartowitz et al., 2019; McLauchlan et al., 2013). Other modeling studies indicate that low elevation forest species may expand in some areas, whereas higher elevation forests are simulated to contract (Cassell et al., 2019). However, not all forest types are projected to respond similarly to climate change and PBM fire projections differ substantially. For instance, model simulations in the Blue Mountains of eastern Oregon project a longer growing season, more wildfire events, and a potential contraction of some forest types in dry areas (Kim et al., 2018), a trend supported by more regional and physiologically-based models (e.g., Buotte et al., 2019; Hudiburg et al., 2013a). Interestingly, some drier PNW forests are projected to be small carbon sinks through the year 2100, if fire regimes do not drastically intensify (Rogers et al., 2011).

3.3. Subalpine forests

Subalpine forests are limited by cold temperatures and a short growing season, therefore warmer temperatures and more atmospheric CO₂ may increase tree growth, productivity, and potentially carbon sequestration rates of some species at high elevations (Case and Peterson, 2007; Latta et al., 2010; Peterson and Peterson, 2001, Fig. 4). Climate change would also reduce snowpack depth and increase soil temperatures, two limiting factors for growth at high elevations (Ettl and Peterson, 1995; Peterson et al., 2002; Peterson and Peterson, 2001, 1994; Rochefort et al., 1994), especially for encroaching lower elevation tree species (Franklin et al., 1971; Harsch et al., 2009). However, snowmelt during the dry, summer months is critical for tree growth and seedling establishment at high elevations (Burns and Honkala, 1990) and warming temperatures will intensify summer drought conditions, especially during extreme years (Marshall et al., 2019a,b; Vose et al., 2016). These drought effects may eventually curtail potential gains in carbon sequestration due to warming temperatures and elevated atmospheric CO₂; however, experimental studies in natural systems do not necessarily support this (Brodribb et al., 2020).

Climate change could lead to an upward migration for some subalpine forests due to a longer growing season and less snowpack (Fonda and Bliss, 1969; Franklin et al., 1971; Heikkinen, 1984; Taylor, 1995; Zald et al., 2012). In addition, these conditions will likely increase the occurrence of fire, which can have a positive impact on treeline migration by reducing shrub and plant density and exposing mineral soil for seedling establishment. However, some empirical data indicates that this trend may not be common or uniform across high-elevation sites (Harsch et al., 2009). Successful regeneration at high-elevation sites depends on multiple factors, including microsite facilitation, and may be limited by unsuitable topographic and edaphic conditions of upslope areas, wind exposure, and patterns of snow distribution (Holtmeier and

Broll, 2012; Macias-Fauria and Johnson, 2013; Smith et al., 2003). The effects of landforms, microtopography, and overstory tree canopies on snow distribution can also influence treeline advance. Further, reduced snowpack, changes in the rain-snow transition zone (Klos et al., 2014), and changes in spring precipitation (Mote and Salathé, 2010) may reduce water availability and increase forest stress at high elevations, with negative implications on carbon storage.

While there is a growing body of literature on mechanistic modeling work relevant to forests, clearly there is an urgent need for regional and landscape scale modeling to better understand vegetation dynamics and carbon implications to climate change (McDowell et al., 2020). These advances will not only allow improved estimates of the carbon sink potential in climate models but will also support more accurate climate mitigation policy and better-informed forest land management plans. Although no model can perfectly represent ecosystem processes or disturbances (ecological or human) (Box, 1976), there is a need to improve PBMs, such as forest structure representation mechanisms (Duarte et al., 2017; Fisher et al., 2018; Stenzel et al., 2019), drought-mortality mechanisms (McDowell et al., 2011), reproduction and dispersal processes (McDowell et al., 2020) and disturbance events (Liu et al., 2011; Thonicke et al., 2001).

3.4. Soil carbon

Soils contain more carbon than plants and the atmosphere combined and can comprise more than half, often nearly three quarters, of total ecosystem carbon (Busse et al., 2019; Schlesinger and Bernhardt, 2013). Unfortunately, this important entity is also one of the least understood pools of carbon on Earth (Zabowski et al., 2011). Soil carbon is notoriously difficult to measure as cycling is complex, has high spatial and temporal variability, and changes significantly with climate, soil, and vegetation characteristics (Prichard et al., 2000). This uncertainty makes it challenging to scale up measurements of soil carbon into Earth Systems Models (Berardi et al., 2020; McNicol et al., 2019) and to predict the effects of a changing climate on one of the most important terrestrial carbon sinks - forests (Birdsey et al., 2006). A large portion of forest soil carbon is stored in the deep layers of soil, but this is often ignored in traditional soils studies (Dietzen et al., 2017; Zabowski et al., 2011). Jobbágy and Jackson (2000) found that including the soil organic carbon (SOC) that occurs between two and three meters deep would increase the global SOC by 56% and that biomes with the most SOC at depth (namely forests, tropical grasslands, and savannas) were vastly underestimated. Management strategies in these regions can have a significant impact on the ability of ecosystems to store carbon; for example, forest harvesting has been found to decrease soil carbon by 25% and most of that loss occurred in the deeper soil layers (20–150 cm) (Gross et al., 2018).

Although land management practices including extended harvest cycles, reforestation, and afforestation can help to keep carbon in high biomass forests (Law et al., 2018), changes in climate will influence soil carbon in ways that are more difficult to anticipate and not generalizable across ecosystems (Bailey et al., 2019). Carbon storage in PNW ecosystems is predicted to be only at half capacity (Homann et al., 2005), but we know very little about how climate might cause the destabilization of existing and added SOC (Bailey et al., 2019). As climate changes, higher temperatures may spur net primary productivity (NPP) through a longer growing season and the input of fresh litter in combination with soil warming may increase decomposition, microbial carbon respiration, and spur a positive “priming” effect which consumes older soil carbon (Bailey et al., 2019; McNicol et al., 2019). The mechanisms behind these interactions are as complex as the processes themselves. The destabilization of SOC can be driven by land use, freeze-thaw cycles, changes in amounts and seasonality of precipitation, reduction-oxidation conditions (perhaps arising from changes in water table levels due to water table fluctuations in response to NPP), and microbial activity, among others (Bailey et al., 2019; Gross et al., 2018; Mayedo, 2018). Due to this

labyrinth of drivers, effects, and indicators, the use of proxies is becoming increasingly common and more accurate as data availability and precision improves (e.g., microbial genome analyses, metabolic quotients, physical fractionation) (Bailey et al., 2018; Schloter et al., 2003). Many of these proxies are particularly valuable for predicting changes in one of the most mysterious and dynamic pools of soil carbon, the microbial community.

The activity of soil microbes is one of the major global carbon pathways and is second only to gross primary productivity (Rustad et al., 2000). Despite the large pool of carbon in soil systems, microbes are generally considered to be carbon-limited (Soong et al., 2020). The soil organic matter, which acts as the primary food source for many soil biota, is low in mineral soil, has a relatively low C:N ratio, and is often chemically or physically protected by the soil mineral matrix (Lehmann and Kleber, 2015; Soong et al., 2020). Microbial interactions, and therefore carbon release, are difficult to quantify or predict as they vary substantially on both temporal and spatial scales (Blagodatskaya and Kuzyakov, 2013). Because of this heterogeneity, as well as creation of “hotspots” or “hot moments” within soil systems due to the input of fresh organic matter, scaling up measurements of soil carbon present a major obstacle to carbon assessments (McNicol et al., 2019). While many studies have focused on the response of the microbial community to a single or few climate change factors (e.g. increased temperature, elevated CO₂, drought), more research is needed to determine the impact of multiple interacting factors and results will likely be unclear and problematic due to the complexity of the overall system (Bardgett et al., 2008). Reducing uncertainty in both measurements and models of soil carbon cycling will be imperative to understanding and predicting the effects of a changing climate (Bradford et al., 2016).

4. Critical knowledge gaps & future directions

Here, we summarize key knowledge gaps in our current understanding of how climate change is expected to affect forest types and their carbon across the PNW. There is a general lack of synthesized information on climate change effects on forests and carbon. In response, we augmented observational and experimental data with expert knowledge, which tends to incorporate information from the published literature, empirical data, unpublished studies, and their experiences (Martin et al., 2012). Our literature review and conversations with regional experts yielded three broad categories of research gaps/opportunities, including: 1) improving our knowledge and ability to measure belowground carbon, 2) monitoring changes in transition zones/ecotones, and 3) improving process-based ecosystem models by advancing predictions for forest carbon cycling (Fig. 5). We also identify a number of action points, where research gaps could be specifically addressed.

4.1. Belowground carbon

Belowground carbon is notoriously difficult to quantify, especially for the entire soil profile. Current research is exploring innovative methods of quantifying this elusive carbon pool. For example, a recent global study utilized climate data and satellite-derived estimates of net primary productivity to develop a relationship between belowground net primary productivity (BNPP) and mean annual precipitation and temperature (Gherardi and Sala, 2020). Studies like this could be valuable when coupled with smaller field-based manipulations to examine the effects of a changing climate on soil BNPP and soil carbon fixation. However, even compiling multiple field studies into statistical approaches (e.g., linear models) of climate-related trends in soil C stocks reveals a large amount of uncertainty when applied over long-time scales. As such, process-based models are arguably the most reliable path forward when attempting to capture these complex dynamics (Crowther et al., 2016). However, the current application of process-based models to belowground processes are limited by the scarceness

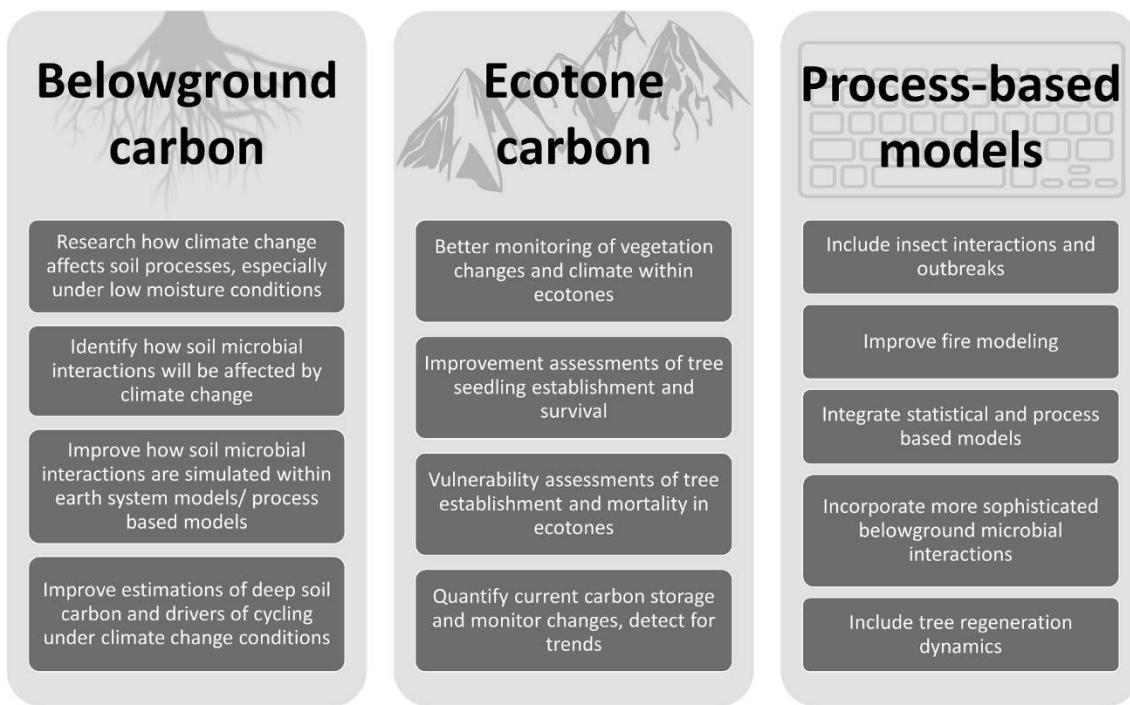


Fig. 5. Three key research gaps and/or opportunities that will advance scientific understanding of how climate change will impact forests and their carbon.

of data on microbial and deep soil carbon (Crowther et al., 2016). Quantifying these pools through isotopic analysis (Paterson et al., 2009), predictive collaboration between satellite imagery and digital soil mapping (Minasny and McBratney, 2016), or intensive field sampling with repeat soil surveys, long-term experiments, and space-for-time substitution methods (Smith et al., 2020) is necessary to better represent these pools of carbon in PBMs.

The majority of current studies focus on soil organic carbon despite the fact that inorganic carbon (SIC) comprises 30–40% of global soil carbon stocks and up to 90% in arid and semi-arid regions (Lal, 2004). Although SIC can have high spatial variation, there has been recent success developing predictive models utilizing existing soil survey data (Filippi et al., 2020). Incorporating more data regarding inorganic carbon pools, especially in arid and semi-arid regions, into modelling efforts will improve their accuracy. Overall, predicting the responses of soil carbon to future changes in climate will rely on real field data from experimental treatments across the world and collaborative model development.

4.2. Transition Zones/Ecotones

Transition zones, also referred to as ecotones, are defined as areas where spatial changes in vegetation structure or processes are more rapid than in adjoining plant communities (Levin et al., 2012). Ecotones typically span the intersection between two or more biomes or ecosystems and are crucial in landscape ecology due to their impact on the movement of animals and nutrient cycling, as well as being indicators of climate change (Risser, 1995). For instance, small changes in climate can lead to competitive interactions between plant species, leading to changes in vegetation composition and structure. This process is well established in paleoecological studies that document climate-induced vegetation shifts in the PNW (e.g., Blinnikov et al., 2002; Whitlock, 1992; Whitlock and Bartlein, 1997).

We have summarized how climate change impacts vary by forest type (Fig. 3) and are anticipated to impact forest carbon (Fig. 4); however, we recognize that some of the largest changes are expected to occur in ecotones. Some vegetation in these areas may already be stressed from competitive interactions, insects, and/or diseases.

Moreover, ecotones are also likely to be areas of new colonization, such as at upper and lower treelines, forest-grassland ecotones, and more generally at the climatic limits of species distributions (Allen and Breshears, 1998; Brubaker, 1986; Thuiller et al., 2008; Williams et al., 2010). For instance, warmer temperatures and longer growing seasons have led to increased tree growth and productivity, and new colonization into areas that were not previously occupied by trees at high-elevation sites (Peterson et al., 2002; Peterson and Peterson, 2001, 1994; Zald et al., 2012). By contrast, warming temperatures and decreasing soil water availability can lead to declining tree growth and seedling establishment at lower treelines, where forests and woodlands transition to shrublands and grasslands (Davis et al., 2019; Harvey et al., 2016; Luce et al., 2016; Restaino et al., 2016; Stevens-Rumann et al., 2018). Conversion to non-forested vegetation will likely lead to less productive ecosystems and less carbon sequestration (Coop et al., 2020).

Vegetation modeling studies generally support the notion that ecotones will be areas of greater change of vegetation in the future (Case et al., 2020; Rogers et al., 2011; Shafer et al., 2015). These studies demonstrate that some of the largest shifts of vegetation types are projected to occur at the margins of forest types and at lower and upper treelines. In response to these trends, we advocate that new monitoring and modeling efforts be targeted within ecotones given their likelihood of overlapping stressors and potential for ecosystem change. Increased monitoring of vegetation changes – such as changes in vegetation growth rates, percent cover, carbon sequestration and fluxes, vegetation mortality and tree establishment. These data could then be combined with climatic data to identify corresponding climatic drivers, which could greatly inform and improve future modeling projections. For instance, establishing long-term monitoring plots that measure tree growth and collecting climate data could be used to parameterize more site-specific PBMs. More general modeling studies could also directly incorporate climate vulnerability assessments of tree establishment and mortality within ecotones (e.g., Case and Lawler, 2016). Climate and vegetation modeling studies also indicate that disturbances, such as wildfire, will likely be key drivers of those changes, as illustrated by the critical role that wildfire plays in the simulated dynamics between forests, woodlands, and grasslands (King et al., 2013; Laflower et al., 2016).

There are a few modeling studies that specifically examine carbon

dynamics within PNW ecotones (see Bachelet et al., 2018, 2015; Hudiburg et al., 2013a; Hudiburg et al., 2009; Rogers et al., 2011; Sheehan et al., 2019). In general, future projections for some of these modeling studies show potential carbon gains east of the Cascade Crest, largely due to increased productivity during non-summer months and at high elevations, most likely driven by warming temperatures and a longer growing season, a trend supported by vegetation modeling studies (Case et al., 2019; Rogers et al., 2011; Shafer et al., 2015). Regional modeling studies also generally agree that summer drought and increased fire occurrence on the west side of the Cascades could lead to end of century carbon losses across the distribution of some moist forests (Rogers et al., 2011; Sheehan et al., 2019). This latter trend has implications for long-term carbon sequestration and future harvest potential in some of the largest biomass producing counties in the region (Graves et al., 2020), but few are actively examining these potential impacts. Although there are large uncertainties with these projections, they illustrate some large-scale trends that can be used when prioritizing where to monitor ecosystem transitions. Establishing and collecting baseline data within some of these areas before they burn again could provide critical validation data for models greatly improve our ability to simulate future projections.

4.3. Process-Based modeling improvements

Ecosystem PBM is an important tool for predicting future forest carbon storage and fluxes in forests (Fisher et al., 2018). There has been substantial progress made on the representation of forest and disturbance processes in PBMs over the last two decades. For example, the representation of trees has increased in both resolution and structure in DGVMs (Koven et al., 2019; Lawrence et al., 2019) and fire processes are improving (Lasslop et al., 2014). Nevertheless, there are still significant challenges in PBMs, especially when modeling changes in forests and carbon at regional scales (Fisher and Koven, 2020). In light of these challenges, we discuss a few opportunities in mechanistic modeling which are specific to the PNW region that could improve projections of forests and forest carbon cycling.

Although the representation of disturbance, including wildfire and insect outbreaks, in ecosystem PBMs continues to improve, model parameters and assumptions for these disturbances remain simplistic and underdeveloped (Liu et al., 2011). Disturbances can have substantial impacts on forest carbon storage and sequestration (Coop et al., 2020; Kurz et al., 2008; Turetsky et al., 2011) and therefore, improving our ability to simulate disturbances is crucial for understanding how carbon and carbon cycling will be impacted by climate change. For instance, many ecosystem PBMs do not simulate insect outbreaks or the effect of climate change on insect outbreaks. This lack of an important disturbance factor offers an opportunity to not only include insect outbreaks in ecosystem PBMs but also to include a mechanism that would prescribe insect occurrence and simulate prognostic modules for future insect outbreak prediction in ecosystem models (Edburg et al., 2011). Fortunately, there are empirical data of insect outbreaks in the PNW for model evaluation and validation (Hicke et al., 2012). There is also the prospect of developing predictive models of beetle population dynamics for multiple beetle species, including host tree status (Buotte et al., 2019). Future data collection and monitoring should be designed with the intent of specifically using the data to drive PBMs. The ecosystem modeling community also needs an improved understanding of mortality by insect and host species condition. Similar to the effects of fire, insect outbreaks can be very heterogeneous in tree mortality and our understanding as to why trees may survive or die can be greatly improved. Historically, modelers have oversimplified these issues, such as mortality, but some have developed a clear path forward and offer conceptual advances (Harmon and Bell, 2020). There are also opportunities to improve our knowledge on the basic life history of insects and how they are affected by changes in climate.

There are several possibilities to improve fire simulations in

ecosystem PBMs by advancing simulations of ignition sources, area burned, and fire severity (Hantson et al., 2016; McLauchlan et al., 2020; Thonicke et al., 2010). Lightning strikes are the main source of wildfires in PNW forests (Rorig and Ferguson, 1999) and most ecosystem PBMs do not simulate this important factor. Moreover, it has been suggested that climate change may increase the occurrence of lightning strikes (Romps et al., 2014), and therefore future model simulations could incorporate climate-induced fire ignitions and spread. However, simulating future lightning strikes could be computationally challenging for many modeling efforts. Nevertheless, there have been improvements on fire spread within modeling grid cells (e.g., see Conklin et al., 2016), although few models simulate grid-to-grid fire spread (e.g., Bachelet et al., 2001; Kim et al., 2018; Rogers et al., 2011; Sheehan et al., 2019). Integrating fire weather models with PBMs could lead to more collaborations and better parameterization with weather and climate modelers. For example, DGVMs used to simulate vegetation across the PNW currently use thresholds for rain and snow from outside of the PNW region and could be easily updated to represent more regionally relevant thresholds (e.g., see Dai, 2008; Kienzle, 2008). Information on fire fuel moisture content is also rapidly developing in fire science and could be integrated from publicly available databases, such as the National Fuel Moisture Database (NFMD), which enables users to view sampled and measured live- and dead-fuel moisture information. Databases such as this could be integrated into PBMs and would represent more accurate conditions when simulating wildfire for shorter timeframes; however, more sophisticated advancements would be needed to capture live fuel moisture in dynamic vegetation models.

There are also opportunities to incorporate current vegetation, structure, disturbances, and belowground carbon dynamics into PBMs (Trugman et al., 2019). For instance, many land surface models that simulate forest structure do so at a very coarse level and do not necessarily represent what is actually found on or in the ground, much less individual tree structures (Or, 2020). There are also opportunities to leverage existing data sources, such as forest inventory data to aid in model initiation and parameterization. There has been some progress on incorporating aboveground structure into models, for example simple forest structure algorithms have been integrated into cohort or age-based models; however, many of these models are at the stand scale and not at a regional scale (Lu et al., 2017). Therefore, future efforts could improve forest age-cohort representations in process-based models and to run those models at scales appropriate for landscape planning. Belowground microbial interactions, more thoroughly described above, are typically characterized by overly simplistic microbial processes in PBMs leading to large inaccuracies in model projections (Soong et al., 2020; Wieder et al., 2015). Many PBMs, such as DGVMs, do not even simulate these simple microbial processes. Subsequently, there are multiple opportunities to incorporate these and other key processes, such as tree regeneration, into a suite of PBMs.

Generally, there is a lack of species and site-specific data that is available for process-based model parameterization and validation (Hudiburg et al., 2013a). This data gap can lead to inaccurate model simulations and can influence the decisions made about a range of conditions and future possibilities. Basic life history information, that is, the timing and magnitude of growth, reproduction, and mortality of a species, greatly impacts model output and ultimately defines how realistic future simulations may be. For instance, some DGVMs use allometric information from only two representative species; one for all evergreen tree species and one for all deciduous tree species (Bachelet et al., 2001). Additional research could identify allometric information, such as average and maximum tree diameter, height, and leaf area for more species that are representative for additional plant functional types. This data can be used to improve interactions between plant types, estimations of biomass and carbon, and to improve fire modeling simulations and ultimately carbon dynamics. Basic information on species' life histories is of the upmost importance when trying to model any future scenario and its relevance should not be underestimated

(Tewksbury et al., 2014). Moreover, empirical data collection could be implemented with model use in mind, this approach has potential to remove uncertainty and improve the reality of model output (Hudiburg et al., 2017; Kelly et al., 2016). For instance, paleo-data is a useful source of information for model validation of future simulations; however, there are few studies that apply paleo-data into modeling efforts within the PNW region (Buma et al., 2019).

5. Case studies

To demonstrate how this review can be used to better inform current forest restoration and management strategies, we briefly present two case studies that detail how 1) climate change is expected to affect two very different forest types and their stored carbon and 2) management is being applied to build climate change resilience and preserve long-term carbon storage.

5.1. Ellsworth Creek Preserve – Context & impacts

The first case study is located at Ellsworth Creek Preserve (Ellsworth), a young, moist forest in southwestern Washington dominated by conifers (Fig. 6). Having been logged multiple times during the past, Ellsworth is now being restored to old-growth conditions and is managed for multiple objectives, including timber production, long-term carbon storage, salmon habitat, wildlife diversity, and climate change resilience (Churchill et al., 2007). Across this region of southwestern Washington State, climate change is expected to result in warmer temperatures and less precipitation during the already dry growing season, which could lead to a spread of insects and diseases and potentially more fires, as illustrated by the 2015 Paradise Fire in the nearby Olympic National Park. Although there is strong agreement among climate projections that temperatures are expected to warm across southwestern Washington, there is significant uncertainty associated with precipitation projections (Hudec et al., 2019). Nevertheless, it is anticipated that climate impacts may significantly alter the composition, structure, and ecological function of moist forest systems and could lead to substantial carbon storage losses across the region

(Fig. 4). For instance, increased fire occurrence has the potential to shift forest structure from mature or late-successional (i.e., old-growth) forest types to early seral stages of forest development, changing the landscape, amount of carbon stored in woody biomass, and the abundance of species that rely on mature forests (Halofsky et al., 2018a). A hotter, drier climate may also facilitate the establishment and competitive advantage of more southern ranging plant species, a trend supported by some regional modeling studies (Rogers et al., 2011; Shafer et al., 2015). However, empirical data supporting these trends are sparse and paleo-ecological analogs are not necessarily representative of future climate change.

5.2. Ellsworth Creek Preserve – Adaptation response

In response to projected climate impacts, the Nature Conservancy (TNC), who owns and manages Ellsworth Creek Preserve, is focused on building the resiliency of this moist forest. Syntheses such as this review, which identify potential impacts, can help facilitate decision-making when there is uncertainty (Millar et al., 2007). TNC is now implementing a number of adaptation strategies to increase forest resilience, such as actively thinning overly dense forested areas to reduce the number of trees and lower tree-to-tree competition. These strategies are aimed at improving the growing conditions for the remaining trees, generating revenue, and accelerating late-successional characteristics, such as increasing structural diversity of the forest (Halofsky et al., 2018b). TNC is also using forest thinning and planting to promote species diversity, especially of broadleaf species, a climate resilience strategy (Halofsky et al., 2018b). Increasing species diversity can also help mitigate some of the uncertainty associated with managing for more resilient species in the face of contrasting future precipitation projections. Although fire has historically occurred on long time scales in this wet, maritime region (Agee, 1996), it is currently actively suppressed due to the danger of very high fuel loads, which could lead to severe, stand-replacing fires and aboveground carbon losses. TNC is also in the early stages of testing the experimental planting of more drought tolerant genotypes and species at Ellsworth. This resilience-building adaptation strategy will help inform future management and could

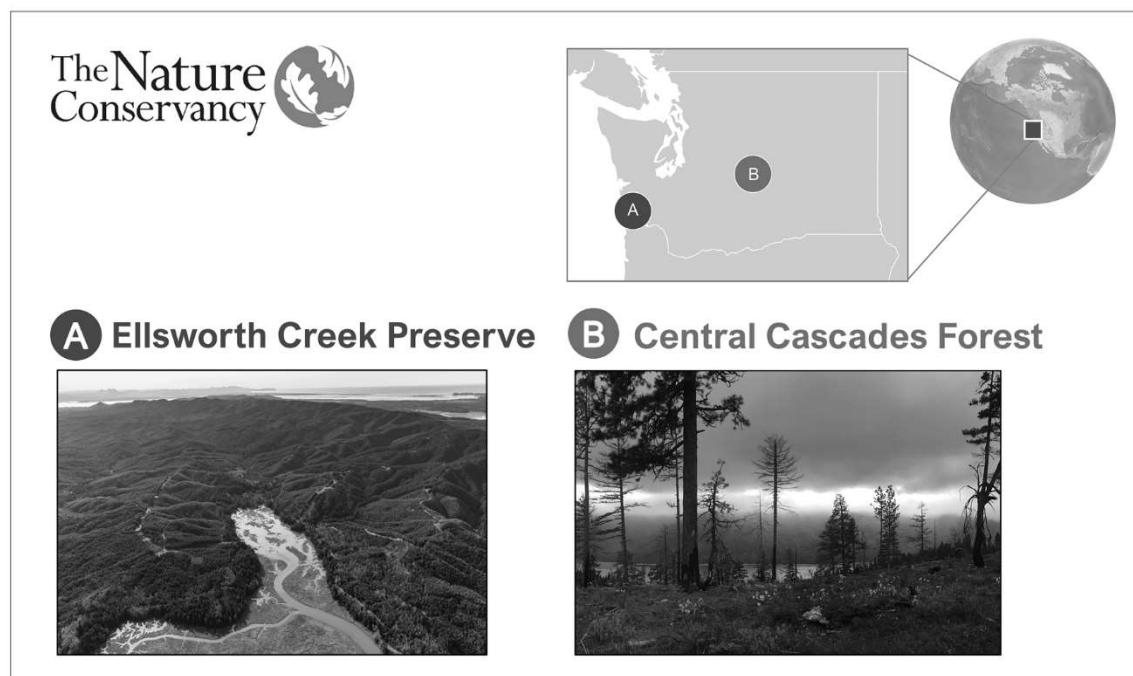


Fig. 6. Approximate location of the two case study examples in Washington State, USA; Ellsworth Creek Preserve, a moist forest, and Central Cascades Forest, a dry forest.

have long-term carbon benefits (Spittlehouse and Stewart, 2003).

5.3. Central Cascades forest – Context & impacts

The second case study is the Central Cascades Forest, situated on the east slopes of the Cascade Mountains in central Washington (Fig. 6). This is a dry, conifer-dominated forest and represents a mix of stand ages and structures characterized by large seasonal differences in temperatures and limited precipitation amounts. The Central Cascades Forest is largely defined by past harvest history and historically more frequent but less severe fire regime (Agee, 1996). However, decades of fire suppression and highly selective harvesting has left much of these forests overcrowded and not very resilient to future impacts (Hessburg et al., 2005). TNC currently manages the Central Cascades Forest for water quality, wildlife habitat, recreation, and fire risk reduction objectives (Rolph et al., 2015). However, climate change is expected to result in warmer temperatures (especially during the summer months), less snowpack, and a longer, drier summer period (Mote and Salathé, 2010). The projected warming may also manifest in negative feedbacks – for example, reduced snowpack may accelerate warming in winter and lead to even lower soil moisture (Raymond et al., 2014). Precipitation projections for this region are more uncertain than temperature, but indicate that winter and spring may become wetter, whereas summer may get drier (Raymond et al., 2014). Nevertheless, these climate effects will likely result in more drought, larger and more frequent fires, possible tree regeneration failure, and decreased forest productivity and carbon sequestration (Fig. 4).

5.4. Central Cascades forest – Adaptation response

To combat warmer temperatures and a longer, drier summer period, TNC is implementing active thinning in overly dense stands and controlled burning to reduce the number of trees and understory fuels, well recognized adaptation strategies in dry forests (Hessburg et al., 2015; Sohn et al., 2016). The goal is to reduce competition and fire risk and increase the overall resilience and help preserve the long-term carbon storage of the remaining forest. Although forest thinning has been identified as decreasing the likelihood of tree mortality during drought (e.g., Bradford and Bell, 2017), the combination of thinning and prescribed burning has been shown to reduce fire spread and severity (Prichard et al., 2020). TNC is testing this assumption across the Central Cascades Forest and monitors annually to evaluate the effectiveness of thinning and burning for forest resiliency. Selective forest thinning and planting are being used to promote more species diversity, especially of broadleaf species, an adaptation strategy that increases ecological resilience of dry forests (Dymond et al., 2016). TNC will also be implementing the experimental planting of more drought tolerant seed sources and species in the Central Cascades Forest in hopes of building a more resilient forest. The effects of management actions, such as thinning and burning, combined with the results from experimental plantings are aimed at decreasing the uncertainty associated with climate change and to better inform adaptive management.

6. Conclusion

We have reviewed some of the key ways in which climate change is expected to affect PNW forests and the carbon they store. For instance, under a high warming scenario, a longer summer dry period may lead to drought stress and decreased growth, productivity and a potential decrease in the ability of moist forests to sequester carbon. Although many tree species in moist forests are very long-lived, an increase in wildfire occurrence could also facilitate the establishment of more southern species in some areas. Dry forests will likely experience hotter and drier summers, less snowpack, and an increase in wildfire extent and a longer fire season. Carbon storage will likely decrease due to these impacts and there may even be areas that shift from forests to non-forest

vegetation. Subalpine forests are expected to experience some of the largest changes in climate and subsequently carbon storage will be affected. Although moderate warming may increase growth, productivity, and carbon storage, a high degree of warming and subsequent loss of snow pack could lead to decreases. However, it is important to note that subalpine forests may also experience a shift in species composition, with species from lower elevations moving up and out-competing subalpine species. This could have a positive effect on carbon storage and sequestration rates.

Through this review, we have identified some critical knowledge gaps of climate change impacts on forests and their carbon. We anticipate that these key knowledge gaps will provide a sounding board for future research opportunities in the PNW. We also anticipate that filling these knowledge gaps will help lead to more accurate projections of climate change impacts on forest carbon and will help regional conservation organizations, such as TNC, better inform their current forest restoration and management strategies. To demonstrate this process, we briefly presented two case studies that illustrate how climate change is anticipated to affect two forest types and their carbon. Although others have more thoroughly reviewed and summarized forest adaptation strategies (e.g., Halofsky and Peterson, 2016), we demonstrate how climate impacts can be identified and leveraged to tailor adaptation strategies for safeguarding forest carbon. This approach provides an example of how science and management practitioners can apply this review and better prepare for an uncertain future in the PNW.

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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.

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