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REGULAR ARTICLE

The policy and ecology of forest-based climate mitigation: challenges, needs, and opportunities

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Abstract Great hope is being placed in the ability of forest ecosystems to contribute to greenhouse gas (GHG) emission reduction targets to limit global warming. Many nations plan to rely on forest-based climate mitigation activities to create additional and long-term carbon sequestration. Here, we take a critical look at the state of the policy and ecology surrounding forest-based natural climate solutions (NCS), with a focus on temperate forests of the United States (US). We first provide a high-level overview of carbon accounting, including key concepts used in the monitoring, reporting and verification of forest-based NCS. Second, we provide a high-level overview of forest carbon dynamics, including pools and fluxes, and drivers of their change. We then identify gaps in the current systems of GHG accounting, and between current ambitions and basic forest ecology. Improved use of data in models provides a path forward to better assessment and anticipation of forest-based climate mitigation. We illustrate this with the creation of a climate-sensitive forestry model, using tree-ring time series data. This climate-sensitive forest simulator will improve planning of site-level climate mitigation activities in the US by providing more realistic expectations of the carbon sequestration potential of forests undergoing climate change. Our review highlights the sobering complexity and uncertainty surrounding forest carbon dynamics, along with the need to improve carbon accounting. If we are to expect forests to play the significant emissions reduction role that is currently planned, we should view immediate emissions reductions as critical to preserve the climate mitigation capacity of forest ecosystems.

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Introduction

To avoid the negative impacts of warming above pre-industrial levels, drastic greenhouse gas (GHG, see Table 1 for a list of acronyms) emission reductions are needed globally. This need is acknowledged with the commitment to limit warming between 1.5°C and 2°C through the United Nations Framework Convention on Climate Change (UNFCCC) Paris Agreement (article 2, 2015). Under this agreement, each Party outlines its planned emissions reductions in its nationally determined contribution (NDC), which together contribute to the global emissions reduction to limit warming. For example, the United States (US) - the world's largest economy, third largest population, and largest cumulative emitter of carbon dioxide (CO_2) from fossil fuels (Boden et al. 2017; Fargione et al. 2018) - has set as its NDC a reduction of net GHG emissions by the year 2030 to 50-52% below its 2005 level of about 6,600 million metric tons (MMT) of CO_2 equivalent (The United States of America Nationally Determined Contribution 2021). Limiting global warming to 2°C is exceedingly challenging, given that global mean temperature has already risen about 1°C over the 20th century and warming lags behind emissions (Hansen et al. 2011). It is unlikely emissions reductions alone will achieve this target, given the rate at which reductions are proceeding (Friedlingstein et al. 2020; Ou et al. 2021). It has thus become apparent that GHG emissions reductions may need to be supplemented with natural climate solutions (NCS), or carbon (C) removal from the atmosphere by natural sinks (National Academies of Sciences 2019). NCS can involve both avoided emissions through protection of sinks, and removal of GHGs from the atmosphere through the creation and/or enhancement of existing C sinks.

Ambition and enthusiasm for NCS is high. For example, a recent analysis from Oxford University's Nature-based Solutions Initiative estimated that global implementation of NCS could contribute the equivalent of 10,000 MMT of reduced CO_2 emissions per year through protecting, restoring and managing sinks. This would entail preventing 270 million hectares (Mha) of deforestation and restoring 678 Mha of ecosystems, in addition to protecting and improving C sinks by improving management on

Table 1 Acronyms, in alphabetical order.

CSP	Carbon storage potential
ESM	Earth System Models
FIA	Forest Inventory and Analysis
FLM	Forest landscape models
FREL	Forest reference emission level
FRL	Forest reference level
FVS	Forest Vegetation Simulator
GHG	Greenhouse gas
HRV	Historical range of variability
IPCC	Intergovernmental Panel on Climate Change
LSM	Land surface model
MMT	Million metric tons
MRV	Monitoring, reporting, and verification
NCS	Natural climate solutions, Nature-based climate solutions
NDC	Nationally determined contribution
NFMS	National forest monitoring system
NGHGI	National greenhouse gas inventory
REDD+	Reducing Emissions from Deforestation and Degradation
SOC	Soil organic carbon
UNFCCC	United Nations Framework Convention on Climate Change

~2.5 billion hectares of land (Girardin et al. 2021). Forests in particular, the largest C sink in the terrestrial biosphere (Pan et al. 2011a), provide a quarter of the total planned emission reductions across all countries' NDCs (Grassi 2017). That is, countries are planning to rely significantly on forests to meet their emission reductions. Focusing on the US (the largest cumulative contributor to the problem), it has the fourth largest forested area in the world and its forests offset approximately 11% of the country's emissions in 2019; the US plans to meet its target partly by enhancing its forest C sink and reducing emissions from forests through protection and management, including investing in activities to increase resilience and restore degraded forest lands (The United States of America Nationally Determined Contribution 2021). Fargione et al. (2018) estimated the maximum climate mitigation potential of US forest-based NCS in 2025 to be over 650 MMT CO_2 equivalent, which is ~10% of the US's 2005-level GHG emissions.

To avoid over-reliance on NCS relative to their potential, enthusiasm for forest-based NCS needs to be tempered in the light of scientific uncertainties that surround the projection of future forest ecosystem C emissions and sinks. The complex interactions between drivers of terrestrial C uptake are poorly characterized, leading to substantial uncertainty in the magnitude and direction of the future terrestrial C sink (Arora et al. 2020; Gatti et al. 2021; Koven et al. 2021). As forest-based NCS initiatives ramp up globally, it is timely to think carefully about how forest C accounting is conducted, the protocols and incentives as they are currently laid out, and how complexities and uncertainties in forest C dynamics can complicate the assessment and anticipation of forest-based climate mitigation.

Here we consider these challenges from both a policy and ecology perspective, with a focus on temperate forests and the US. We begin with an overview of forest-based C accounting, with a focus on key concepts concerning forest C across time and space. We then highlight areas of scientific uncertainty and complexity about forest C stocks and fluxes. We take a first step in bridging these perspectives by identifying the gaps that arise between systems of accounting at different scales, as well as between current ambitions and the scientific uncertainties and complexities of forest C dynamics. We then describe how models and data might be used to set more realistic expectations of forest-based NCS. To do so, we highlight a specific example of a new data source used to improve process representation in an empirical forestry model, which can be used to plan mitigation activities in the US under changing climate. We end by identifying opportunities to improve the estimation and expectation of forest-based climate mitigation.

Carbon accounting - policies, procedures, and concepts

Parties to the UNFCCC are expected to regularly submit economy-wide inventories of GHG emissions and removals, using country-specific systems of monitoring, reporting, and verification (MRV) that follow guidelines set forth by the Intergovernmental Panel on Climate Change (IPCC 2006, 2019a). As a part of this process, C estimation within a national greenhouse gas inventory (NGHGI) assesses trends in emissions and removals from the land sector, often relying on data from a national forest monitoring system (NFMS). For example, in the US, these data are collected and maintained by the USDA Forest Service's Forest Inventory and Analysis (FIA) program (Domke et al. 2021), and the US Environmental Protection Agency is then responsible for GHG reporting to the UNFCCC (U.S. EPA 2021). In addition, global 'stocktakes' are planned (the first of which is taking place 2021-2023), which will assess collective progress toward emissions reductions (Paris Agreement article 2, 2016; Friedlingstein et al. 2020). These will be periodically reported to the UNFCCC to inform new policy, including updating ambitions within NDCs. Independent of UNFCCC reporting are state or provincial (*e.g.,* California Air Resources Board 2021) and entity-level (Eve et al. 2014) estimation and project-level activities which are implemented through regulatory (*e.g.,* California Air Resources Board 2015) or voluntary C offset (*e.g.,* Verra 2021) programs that have independently developed accounting standards.

An additional mechanism under the UNFCCC is known as REDD+ (Reducing Emissions from Deforestation and Degradation, conservation and enhancement of forest C stocks, and sustainable forest management, Paris Agreement Article 5, 2015), through which developing countries can receive results-based payments for forest-based mitigation activities that avoid emissions or remove atmospheric GHG emissions, and contribute to NDCs. Several terms defined under the auspices of REDD+, namely additionality, permanence, reversal, leakage, and safeguards (Voigt and Ferreira 2015), are particularly useful in thinking about forest C accounting across time and space. The REDD+ standard is that GHG mitigation activities should lead to additional C removal beyond a baseline (additionality) that is not counteracted by increased forest-based emissions elsewhere on the landscape (leakage), is stored over a defined time frame (permanence) and not reemitted (reversal), while also protecting communities and biodiversity (safeguards). We describe each of these terms in detail below and illustrate additionality, permanence, reversal, and leakage in Box 1.

Additionality refers to the additional amount of C a project sequesters above or beyond a forest reference emission level (FREL) or forest reference level (FRL). This FRL sets the baseline of C flux for a project area and is often based on data from the recent past, derived from a national monitoring system. The FRL is projected forward in time and compared against results of mitigation activities, to quantify the additional C stored or sequestered or emission reductions (Box 1, Panel 2A). For example, Brazil estimated mean emissions from gross deforestation in the Amazon from 1996-2005 as its FRL, to then calculate emission reductions over the period 2006-2010 (Brazil 2018). Additionality is achieved if mitigation activities result in greater C stock than the expected trajectory (*e.g.,* a decreased rate of deforestation over the project period).

Permanence requires that the mitigation action leads to long-term (~100 years, Nickerson et al. 2019) storage of additional C or "transformational change", *i.e.*, that drivers of emissions or barriers to enhancement of C stocks are removed (Box 1, Panel 2A; Federici et al. 2018). Permanence is influenced by the residence time of C in pools, which is in turn influenced by management actions and disturbances, among other drivers (Babst et al. 2020; Brienen et al. 2020).

In a reversal, the additional (and potentially baseline) C is removed from the forest system and emitted into the atmosphere, through, for example, disturbances, drought-induced mortality events, release of soil C, etc. (Box 1, Panel 2A). Reversals can be categorized as avoidable or unavoidable in estimating emission reductions or C credits, where drivers are either anthropogenic or natural, respectively. In some cases, local-level projects are not penalized for unavoidable reversals (*e.g.*, fires or insects), but can instead draw from a common buffer pool, which acts as insurance against forest C reversal (Anderegg et al. 2020; Marland et al. 2017).

While permanence and reversal risk protocols concern unwanted or unintended emissions of forest C over time, leakage concerns unwanted or unintended emissions of forest C across space, *e.g.*, activities within the project area leading to forest C emissions outside the project area (Box 1, Panel 1). The ability to assess leakage depends on the scale at which C accounting is occurring. Local-level projects are inherently prone to the failure to account for the influence of large-scale socioeconomic processes (*i.e.*, market drivers), leading to the potential for displaced emissions or double-counting of emission removals at national in addition to local scales. For this reason, C accounting must seek to integrate activities from local to national levels (Lee et al. 2018).

Finally, the REDD+ framework implemented safeguards to attempt to ensure that projects aimed at sustainable C drawdown take action towards the risk of reversal and reduce the displacement of emissions (*i.e.*, leakage) as well as provide co-benefits to local communities (Decision 17/CP.21). These co-benefits are defined in terms of the UN's Sustainable Development Goals, including ending poverty, promoting gender equality, and developing sustainable consumption and production practices. Safeguards are vital to ensure that C drawdown projects take into account the livelihoods and practices of indigenous peoples and local communities and their interdependence on forests, and do not degrade the social and environmental benefits derived from forests.

These standards, most of which are shared across systems of accounting, provide a legal and linguistic framework to evaluate the success or failure of mitigation activities aimed at sequestering C in ecosystems, although the policy for C markets is young and rapidly changing. Indeed, one outcome of the 26th annual Conference of the Parties (COP26) in Glasgow was to finalize regulations surrounding the emerging international C market. As these C accounting systems evolve, it is important to fully consider forest C dynamics, as we describe below, which will

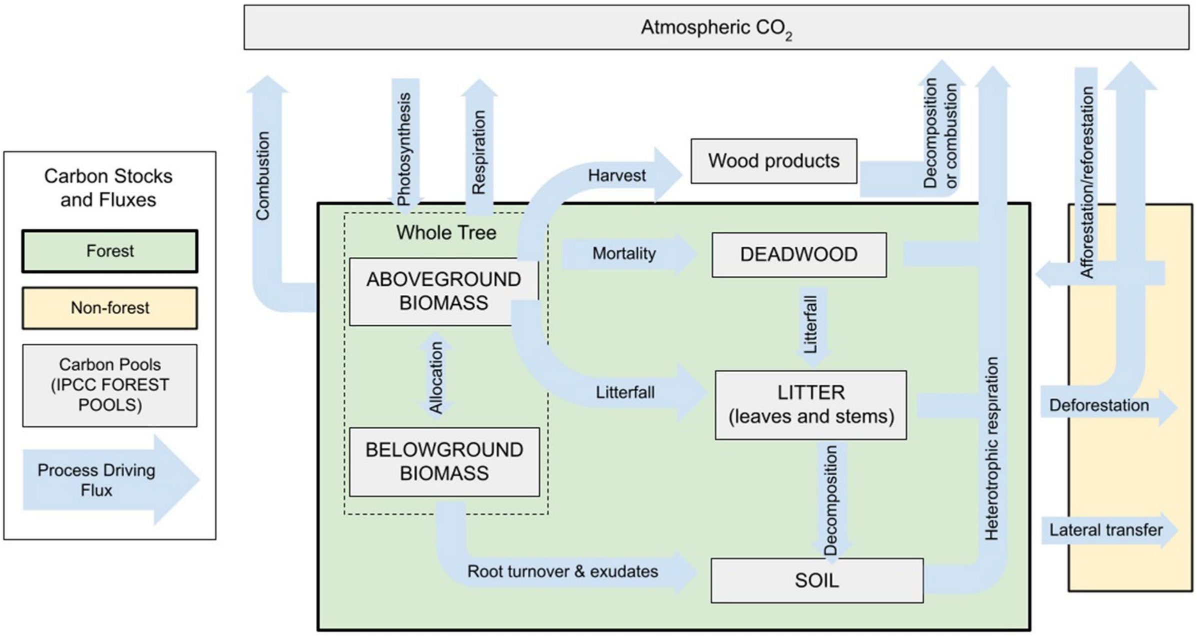


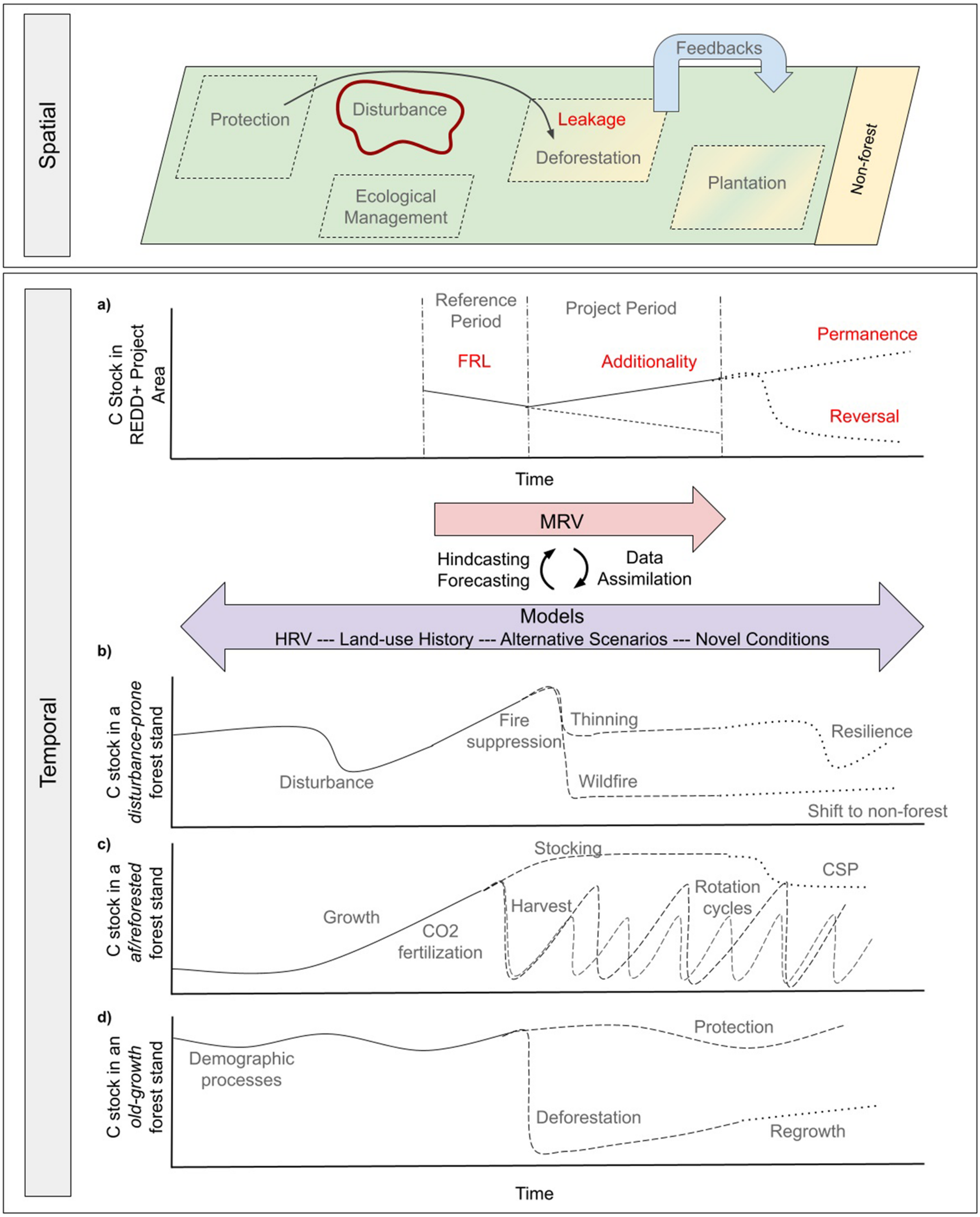
Fig. 1 Forest C cycling. There are C stocks (boxes) and fluxes (blue arrows) within a forest system (green box), including the five IPCC forest C pools (i.e., aboveground biomass, belowground biomass, deadwood, litter, and soil), as well as fluxes between a forest system and other C pools (grey boxes), including wood products, the atmosphere, and non-forested land (yellow box). Uncertainty in the estimation of stocks and the rate of fluxes between C pools can be influenced by disturbance processes, management, and/or changing climate

become increasingly important in validating and verifying these standards.

Forest carbon dynamics - pools, fluxes, and drivers

From a forest-centered perspective, the land-atmosphere C flux is determined by stocks and fluxes in and between forest C pools, here described in terms of the five forest C pools delineated by the IPCC (aboveground, belowground, deadwood, litter, soil; IPCC 2006), along with a wood products pool and the C pools of other (non-forest) land use categories (Fig. 1). C in the atmosphere is taken up by living trees through photosynthesis and allocated to primary and secondary metabolism as well as to aboveground (*i.e.*, leaves and stems) and belowground (*i.e.,* roots) biomass. Mortality and turnover of live biomass transfers C to the dead organic matter pools (*i.e.,* deadwood, litter), which decomposes and enters the soil C pool. C also enters the soil pool through exudates from roots, which can be as much as 40-60% of total photosynthate (Silva and Lambers 2021; Simard and Durall 2004), and are in turn consumed by soil microorganisms, passing into the soil food web. C leaves a forest system and returns to the atmosphere through respiration (autotrophic and heterotrophic) or combustion. C can also be removed from a forest through harvest, and thus transferred to a wood products C pool. The rate at which harvested forest C is emitted back into the atmosphere varies tremendously, depending on its fate, for example, as biofuel, building materials, or in a landfill (Fahey et al. 2010). Further, C may leave a forest stand laterally, transported via water (runoff and rivers, Tank et al. 2018). Finally, C in forested systems can be transferred to or from non-forested systems through deforestation vs. afforestation or reforestation, respectively.

A great deal of complexity underlies this simple characterization of forest ecosystem C dynamics and its impact on the atmosphere, as illustrated by three scenarios of change in C stock through time in Box 1. Both natural and anthropogenic drivers influence C pools and fluxes, and it is difficult to disentangle them and attribute emissions or removals to one or the other. Below we detail these natural and



anthropogenic drivers of forest C stocks and fluxes across space and time, then consider how they interact. Lastly, we discuss additional significant scientific uncertainties in forest C dynamics.

◂**Box 1: Key considerations in forest C accounting across space and time** Panel 1 illustrates three key points about forest-based NCS across space. First, REDD+ standards mandate that mitigation activities account for leakage. For example, if emissions from deforestation are avoided through protection of one forest stand, demand for wood products should not be transferred to another forest stand. Second, mitigation activities should account for spatially heterogeneous and contagious disturbance processes that transfer C from the forest to the atmosphere. Third, a diversity of forest-based climate mitigation activities can be employed across space, including forest protection, plantation-style forestry, and ecological forestry. Panel 2 illustrates forest C dynamics through time with implications for forest-based NCS. a) A monitoring, reporting, and verification (MRV) system estimates baseline C storage (*i.e.,* a forest reference level; FRL), which is then projected forward in time and used to assess additionality of a climate mitigation action. In B-D, three scenarios of change in C stock through time are illustrated, with recovery from natural and anthropogenic disturbances (solid lines), and how these legacies interact with alternative management (or no management) scenarios (dashed lines) and novel conditions, such as changing climate (dotted lines). b) Some disturbance-prone forests are at risk of reaching a tipping point under changing climate, but ecological management may help alleviate these vulnerabilities. For example, in the Southwestern US, suppression of fire in forests historically characterized by a high frequency-low severity fire regime has led to overstocked forests. When fire does occur, it can be of uncharacteristically high severity (stand-replacing), leading to a shift to a non-forested state. Thinning treatments have been proposed as a management technique to increase resilience. c) Afforestation or reforestation has been observed with recovery from past land uses (*e.g.*, in the Eastern US) and is proposed as a means to an enhanced forest C sink. We show two contrasting forest management strategies aimed at climate change mitigation, maximizing C stock vs. C flux. In the former, these forests would be allowed to return to a fully stocked state, *i.e.,* reach their carbon storage potential (CSP), although that CSP may decline with changing climate. Alternatively, they could be managed for rapid biomass production with short rotation cycles, *i.e.*, plantation-style forestry, or with longer rotation cycles, *i.e.*, improved forest management. d) Old-growth forest stands, especially in the temperate rainforest zone, have exceptionally high C stocks. These forests could be protected or these stands could be deforested for timber resources, but recovery to CSP would take centuries. Models can supplement MRV systems to broaden the temporal depth by hindcasting to explore HRV and legacy effects, and by forecasting to explore alternative mitigation actions, novel conditions under changing climate, and feedbacks with the climate system. Further, incoming data from MRV systems can be used to improve models.

The magnitude and geographic distribution of forest C fluxes and stocks are shaped by several natural factors, including climate, topography, edaphic features, and eco-evolutionary processes. In the US, for example, the rate of C sequestration (flux) is high in forests of the US southeast, where it is both mesic and warm, and forest C accumulation (stock) is high in (old-growth) forests of the Pacific Northwest, where it is mesic and cool. In 2018, US forests of the South were estimated to have almost 55,000 MMT CO_2 equivalent stock and 316 MMT CO_2 equivalent flux (*i.e.,* net biomass production), while US forests of the Pacific coast were estimated to have almost 69,000 MMT CO_2 equivalent stock and 112 MMT CO_2 equivalent flux (Domke et al. 2022). That is, variation in natural processes, including climate, leads to predictable patterns across space (Nave et al. 2021a; Wiesmeier et al. 2019). Another trend is that with increasing latitude and decreasing temperature, the magnitude of the forest soil C pool increases: forest soil C represents the majority of forest ecosystem C stocks in temperate and boreal systems, making up an estimated 55-60% and 60-85% of the total C stock, respectively (Domke et al. 2017; Kaarakka et al. 2021). Globally, the soils of temperate and boreal forests were estimated to store about 208,000 and 640,000 MMT CO_2 equivalent, respectively (Pan et al. 2011a).

Equilibrium carbon stocks of ecosystems are determined by their productivity and the overall rate of carbon turnover. The carbon turnover time of woody vegetation is dominated by the mortality rate. Tree mortality is often characterized as being the sum of 'background' mortality - the expected mortality rate resulting from the processes of self-thinning during forest succession as well as senescence of large or old trees - and disturbance processes. Natural forest disturbance processes, *i.e.*, tree mortality caused by fires, insect outbreaks, and drought or storm events, influence forest C dynamics across a range of timescales (Axelson et al. 2009; Falk et al. 2007; Kurz et al. 2008; Lynch 2012; Swetnam and Lynch 1993; Zhao et al. 2021). These disturbance processes vary in terms of frequency and severity in a manner that is characteristic of each vegetation type, hence climate, along with influences of topography and soil. That is, forest disturbances occur on return intervals from several years (fire in some ponderosa pine forests of the western US and longleaf pine forests of the US southeast) to several decades (spruce budworm in boreal forests of Canada) to over a millennium (fire in Douglas-fir temperate rainforests), with frequency often inversely related to severity (Keeley et al. 2009; Stephens et al. 2013; Volney and Fleming 2000). Different forest types are thus characterized by disturbances that are expected to occur within a historical range of variability (HRV) in frequency and severity (Jackson 2012; Swetnam et al. 1999). In addition to their effects on aboveground C, natural disturbances may also directly (*e.g.*, consumption of the O horizon during wildfire, Reddy et al. 2015) and indirectly (*e.g.*, microbial soil organic C transformations following wildfire, Knelman et al. 2017) impact forest soil C, with changes often varying with soil depth (Berryman et al. 2020; González-Pérez et al. 2004; Nave et al. 2011; Pellegrini et al. 2018). While fire generally has a negative effect on soil organic carbon (SOC) storage, the magnitude of the effect decreases with increasing soil depth, and at greater depths (*e.g.*, E, B, C horizons) SOC stocks may experience a net increase (Nave et al. 2021b). Recovery from these disturbances can play out over long time scales, from decades to centuries, leaving a spatial signature on forest C stocks and fluxes.

In addition to natural disturbances, human uses of the land have large impacts on forest C dynamics (Fitts et al. 2021). Indeed, agriculture, forestry, and other land use activities contributed ~23% of total global human-caused GHG emissions over the period 2007-2016 (12,000 ± 2,900 MMT CO2 equivalent per year, IPCC 2019b). In the US, forest converted to non-forest has made up the largest source of emissions from forested land since 1990, amounting to 125.3 MMT CO_2 equivalent in 2019, with the greatest cause being loss of forested land to settlements (62.9 MMT CO_2 equivalent in 2019; Domke et al. 2021). At the same time, afforestation across the eastern US, associated with the abandonment of agricultural fields in the wake of the Industrial Revolution, made this region a strong C sink over the last 100 years (Box 1, Panel 2C; Birdsey et al. 2006), contributing to a large US C sink of about 750 MMT CO_2 equivalent per year, though the strength of this sink is thought to have been declining in the later half of the 20th century with forest maturation (Birdsey et al. 2019). Globally, it is estimated that forest regrowth, including from past human uses (*i.e.*, transient recovery to carbon storage potential [CSP], or C carrying capacity), makes up a substantial fraction of the forest C sink (4,767 MMT CO_2 equivalent per year, 2001-2010; Pugh et al. 2019). In addition to this passive forest recovery, active forest management with the goal of sequestering C is recognized as a NCS, *i.e.*, improved forest management (Fargione et al. 2018; Griscom et al. 2017; Kaarakka et al. 2021; Putz et al. 2008). For example, extended rotations in plantation forests (Box 1, Panel 2C) lead to higher accumulated C (Kaarakka et al. 2021) and thinning treatments can lead to more resistant and resilient forest stands in the long-term (Hurteau et al. 2016; Stoddard et al. 2021). The effect of forest management on at- and below-ground C (litter, soil) receives less attention, but a review of 112 studies showed that harvesting activities generally reduce soil C, in a manner that varies considerably with soil depth (James and Harrison 2016). In particular, traditional post-harvest activities associated with site preparation for replanting (clearing and burning residual vegetation) usher C from the land to the atmosphere. In contrast, improved practices with respect to forest soil C can contribute to NCS: the topsoil of lands currently being reforested in the US have the potential to sequester over 7,000 MMT CO_2 equivalent within a century (Nave et al. 2018). Overall, the effect of management on forest soil C depends on the intensity of the management action (*e.g.*, clearcutting vs thinning), the forest type (Nave et al. 2010), and the recovery stage (Zhang et al. 2018).

Climate change itself, along with its root cause, the increased concentration of CO_2 in the atmosphere, are anthropogenic drivers of change in forest ecosystem C dynamics. Decades of research have generated several relatively robust high-level predictions about their effects on ecosystem C dynamics, including 1), that increased atmospheric CO_2 leads to increased rates of C sequestration in some forest ecosystems (Walker et al. 2020); 2) but that the fertilizing effect of increased atmospheric CO_2 on terrestrial C storage is likely limited by nutrient availability (Davies-Barnard et al. 2020; de Vries et al. 2014; Finzi et al. 2006; Hungate et al. 2003; Norby et al. 2005) or drought stress (Allen et al. 2015; Williams et al. 2013; Xu et al. 2019); 3) and that changes in climate will likely lead to increased rates of tree mortality that will reduce C turnover times (Anderegg et al. 2020; McDowell et al. 2016; McDowell and Allen 2015; Williams et al. 2013); 4) and finally that the growing weight of evidence documents the sensitivity of SOC to global change drivers (Karhu et al. 2010; Knorr et al. 2005; Wang et al. 2019), particularly in the northern circumpolar region where a substantial proportion of the global SOC is stored (Jackson et al. 2017), with higher rates of soil microbial activity, including decomposition and respiration, with warming temperatures (Koven et al. 2017; Wu et al. 2018). The overall future C balance of the terrestrial biosphere is generally therefore considered to be a balance between the opposing forces of the first against the latter three (Arora et al. 2020; Friedlingstein et al. 2014; Koven et al. 2020).

Natural drivers can interact with direct anthropogenic drivers, such as land use or land management, as well as indirect anthropogenic drivers, such as changing climate, in important ways (Earles et al. 2014). For example, in the western US, a combination of increased fire risk with climate change (drier fuels, longer fire season, and more extreme conditions; Abatzoglou and Williams 2016; Anderegg et al. 2020; Goodwin et al. 2020; Westerling 2016; Williams et al. 2013), and long-term fire suppression (Box 1, panel 2B; Brookes et al. 2021, Steel et al. 2015) have caused certain regions to switch from a C sink to a C source in the last two decades: the southwestern US became a source of 114 MMT CO_2 equivalent over the period 1990-2011, mostly because of fire (Birdsey et al. 2019). And though the area burned across the western US has been increasing over the last few decades (Domke et al. 2021), a large fire "debt" still exists (Barrett et al. 1997; Goodwin et al. 2020; Hagmann et al. 2021; Murphy et al. 2018; Stephens et al. 2007), perpetuating the fuel build-up problem. Climate change is expected to increase the frequency, severity, and extent of natural forest disturbance processes (Becknell et al. 2015; Koontz et al. 2021; Krawchuk et al. 2009; Millar and Stephenson 2015; Seidl et al. 2017; Sommerfeld et al. 2018), but exactly how much and how is not well understood (Merganičová et al. 2019). Forests could reach a tipping point, where large-scale degradation (*i.e.*, mortality and loss of resilience) caused by uncharacteristic disturbances (*e.g.*, drought, fire, bark beetles) could potentially lead to a permanent shift to non-forest (Box 1, panel 2B; Barton and Poulos 2018; Falk 2013; Millar and Stephenson 2015; Miller et al. 2018; Serra-Diaz et al. 2018). Thinning, prescribed burns, and other adaptive management strategies can help to avoid or moderate the effects of tipping points that result in catastrophic loss of C from forests (Box 1, panel 2B; Agee and Skinner 2005; Hessburg et al. 2021; McDowell et al. 2016; North et al. 2015; Walker et al. 2018). Indigenous communities have been managing these ecosystems for millenia through, for example, intentional burning practices (Crawford et al. 2015; Trauernicht et al. 2015), providing a historical perspective to guide contemporary management (Roos et al. 2021). While uncertainties remain about what and how much management is needed to reduce the risk of uncharacteristic disturbance under a changing climate and where management efforts should be prioritized, combining western science and Indigenous knowledge systems is key to filling this gap (Jessen et al. 2021; Levis et al. 2020; Prichard et al. 2021).

In the tropics, deforestation, large-scale fire disturbances, and climate changes are also thought to be ongoing threats that could push forests past a tipping point, destabilizing the hydroclimatic feedbacks that maintain Amazon rainforest and other tropical forest areas (Lovejoy and Nobre 2018; Staal et al. 2018). By some estimates, deforestation of the Amazon basin has reached 17% of the original forested area (Lovejoy and Nobre 2019), and these land-use changes combined with climate change have altered regional climate (Sampaio et al. 2007), potentially slowing forest regrowth in secondary forests (Elias et al. 2020) and making the Amazon region a net source of C to the atmosphere (Brando et al. 2020; Gatti et al. 2021).

Finally, complex feedbacks between the biosphere and the climate system may lead to surprising outcomes. Experiments with coupled atmospheric and Earth system models (ESM) have suggested that increases in forest cover, intended to mitigate climate change, can lead to counterproductive responses of the climate system (Bonan 2008). These can be mediated via changes in albedo (Mykleby et al. 2017; Swann et al. 2010), in surface energy balance (Luyssaert et al. 2018), and cloud feedbacks (Laguë et al. 2021). 'Teleconnections', where land cover changes in one region affect climate patterns in another, are also commonly predicted by models, suggesting another means through which intended climate mitigation from increased forest cover might be negated (Koch et al. 2021; Swann et al. 2012). These complex effects, effectively a form of "leakage," are highly relevant as humanity considers forest-based NCS on a massive scale. However, these model-predicted effects are difficult to distengle in standard ESM simulations, making it challenging to attribute such teleconnections to specific land use changes (Laguë et al. 2019). Simulations aimed at illustrating the impacts of a particular land use change have typically been very idealized (Duveiller et al. 2018; Koch et al. 2021), or have been implementations of global land use reconstructions that modify many components of the land surface simultaneously (Lawrence et al. 2016; Pongratz et al. 2010; Tebaldi et al. 2021). In sum, there are persistent and systemic difficulties in robustly projecting the future dynamics of the numerous interlinked systems - hydrological, energetic, biogeochemical, ecological - that determine ecosystem C balance under a non-stationary climate.

Mind the gap (between policy and ecology)

Successful forest-based climate mitigation will require both better systems of C accounting and policies that are cognizant of fundamental trade-offs in forest ecosystem C dynamics and the provisioning of other forest ecosystem services. Here we first highlight some of the gaps in our current system(s) of C accounting, followed by a second set of gaps between our scientific understanding of forest ecosystems vs. the policy surrounding forest-based climate mitigation.

Gaps in accounting

Forest-based NCS are employed at different scales (global, national, local) with associated standards for accounting (estimation of emission reductions and removals), leading to inconsistencies between them. For example, the global stocktake and NGHGIs each have different mandates with respect to estimating anthropogenic land flux and assessing the impact of changes in policy or management on C storage. As a result, the magnitude of the difference between the estimates produced by these two procedures is substantial: ~10% of total anthropogenic emissions (Grassi et al. 2018a, 2021). The global stocktake is expected to use a top-down process similar to the Global Carbon Budget approach (Friedlingstein et al. 2020), which attempts to balance estimated emissions from the land and energy sectors with observations of atmospheric CO_2 as well as modeled estimates of the ocean and land sinks. This global accounting process includes emissions and removals from all lands - in effect, what the atmosphere "sees". In contrast, NGHGIs, which are compiled following IPCC guidelines (IPCC 2006, 2019a) for UNFCCC reporting, assess the anthropogenic land flux by estimating emissions and removals only on managed lands - those directly influenced by human activities (*e.g.,* harvesting, oil and gas prospecting, fire management). Hence emissions from unmanaged lands, such as fires in boreal forests, do not enter in NGHGI estimates. Further, because it is so difficult to disentangle natural from anthropogenic drivers of forest productivity, current IPCC guidelines allow natural removals (*e.g.,* due to baseline forest C sequestration) from managed forested lands to be counted towards net emissions in NGHGIs (though some countries have applied methods for disentangling natural and anthropogenic effects on managed lands; Kurz et al. 2018). In other words, the standard of additionality applied to REDD+ projects is not applied to national-scale C accounting. In addition, the area of land considered managed, and hence included in a NGHGI can change, resulting in substantial changes in the estimates of emissions and removals. In the US, the managed forested land area increased by 24.5 M ha in interior Alaska as of 2019 (US EPA 2019), resulting in an increase both in the estimated US forest land C stocks (31,548 MMT CO_2 equivalent, primarily from soil C) and in the interannual variability in C stock changes (primarily due to wildfire). There is some concern that without transparent reporting (*i.e.*, why more area is included) it is possible to make apparent progress towards targets by classifying more forested land as managed.

Accounting is also often incomplete with respect to important components of the C cycle, in particular, soil C. At local scales, accounting of all five IPCC forest C pools is often required by voluntary market standards, and estimates are easier to generate at a small scale. However, at national scales, certain pools can be excluded if they are considered not important (Decision 12/CP.17), so most countries do not quantify belowground forest C pools (FAO 2019; Yanai et al. 2020). This is problematic because the soil C pool is in fact the largest terrestrial organic C pool on Earth (Jackson et al. 2017), at the same time that it is poorly quantified or constrained, both because of a lack of data, especially at greater soil depths (Gross and Harrison 2019; James and Harrison 2016), and a poor understanding of the mechanisms driving its flux (Terrer et al. 2021; Todd-Brown et al. 2014). Recent efforts to better quantify US forest soil C adjusted the estimate upwards over 4,000 MMT CO_2 equivalent, or an increase from 44% to 56% of total forest ecosystem C (Domke et al. 2017). To avoid climatically important discrepancies between the intended and actual impacts of NCS, accounting should be complete.

Another issue concerning systems of C accounting is the timeframe and spatial scale used to determine baselines of forest C storage, or FRL. For example, if the FRL is 1990, but this follows ~100 years of fire interruption in a forest system characterized by a high frequency-low severity fire regime, then (overstocked) forest structure and composition in 1990 is by no means a good 'baseline' to compare against (Box 1, panel 2B). In addition, MRV systems typically have shallow temporal depth and hence may miss natural long-term processes, such as species succession and disturbance regimes, when setting baselines of C stock and flux, leading to poor assessment of additionality. There are also problems associated with establishing a FRL at very small and very large spatial scales. A local-level estimate of FRL may miss heterogeneous landscape processes (Seidl et al. 2020), whereas a national or large regional estimate may average this heterogeneity, making it difficult to attribute baseline C flux to, for example, land-use change vs. demography (Hoover and Smith 2021). Forest disturbance processes in particular make it necessary to think about the establishment of a FRL across both space and time. At large spatial extents, stand-replacing disturbance processes should generate a distribution of forest age class (Turner et al. 2001; Windmuller-Campione et al. 2021). Young, recently disturbed forest stands grow into older forest stands, which become increasingly susceptible to large disturbances (*e.g.,* wildfire or insect outbreaks) that will return them to the young forest side of the age distribution. Using this distribution of forest age class, or more generally a metric of stand structure, for forests characterized by stand-replacing disturbance processes would improve the assessment of what is attainable, in terms of expected forest C storage (Pan et al. 2011b). Indeed, the expected forest age class distribution could be used to estimate how much of a buffer is needed. Finally, current protocols to estimate a FRL operate in the absence of any consideration of how ecosystem and global C balance will be affected by direct, indirect, or interaction effects of changing climate and/or atmospheric CO_2 concentrations (Friedlingstein et al. 2014; Seidl et al. 2017).

To better anticipate the potential for forest-based climate mitigation and make progress towards targets, estimates of baseline C storage must incorporate scientific understanding of forest C dynamics over space and time, including the impacts of disturbance processes, legacy effects of human land uses, and their interaction with changing climate (Anderegg et al. 2020; Grassi et al. 2018b). This is not to say that forest-based climate mitigation activities should only be performed when accurate baselines are achieved; instead, in planning, policymakers and practitioners need to be cognizant of the implications of the timeframe and spatial scale used in estimating the FRL.

Uncertainty surrounding baseline forest C storage is also caused by the process of estimation or scaling from observations. Measurements of trees are scaled to whole-tree biomass using allometric equations, then summed across trees to estimate plot-level biomass, and then scaled up to national biomass estimates. Uncertainty or variation in these allometric equations is often underestimated, and because they are power-law relationships, a small amount of error can generate an enormous amount of uncertainty surrounding biomass estimates at landscape and national scales (Alexander et al. 2018; Chave et al. 2004). Inconsistencies between satellite data, ground-level measurements, and biomass estimates, generated by uncertainties in data and/or allometric scaling are ignored in C accounting for many projects (Yanai et al. 2020), leading to overconfidence in the estimates of removals or additionality. Thus, there is a key gap between the role of uncertainty in scientific understanding, and the treatment of uncertainty in forest climate mitigation policies. Adopting policies that incentivise reporting, including fully characterizing sources of uncertainties, while advancing ways to reduce uncertainties would help address this gap.

Gaps between policy and forest ecosystem science

A second set of issues surrounding forest-based climate mitigation concern the gap between current ambitions and fundamental trade-offs in forest ecosystem C dynamics. Many assessments of the potential for forests to mitigate climate change depend upon forests reaching their maximum CSP (Hurtt et al. 2019). A recent estimate indicates that fully stocking productive forests of the US has the potential to sequester an additional 187.7 ± 9.1

MMT CO_2 equivalent per year (Domke et al. 2020). However, managing towards maximum stock carries with it an increasing risk of reversal in certain disturbance-prone forest types. Indeed, there is a temporal trade-off between the short-term C consequences of management (*i.e.*, biological emissions/removals and/or combustion emissions) vs. the long-term C consequences of disturbance in an unmanaged forest (Hurteau et al. 2008). In addition, there is a trade-off between managing for maximum C stock vs. maximum C flux. Flux is greatest in young, fast-growing forests and C stock is greatest in old forests. This suggests that forest-based climate mitigation activities can lead to additionality by two contrasting paths: protecting forests that already have high C stock or promoting fast-growing forests with high C flux (Box 1, panel 2C, D). Fahey et al. (2010) argued that the latter approach, plantation forestry, combined with the use of harvested wood for products that return to the atmosphere slowly - essentially, treating the forest system as a biological pump - is the best way to remove CO_2 from the atmosphere. In practice, this is an optimization problem that requires substantial future research (Oliver et al. 2014). Prioritizing intensive plantation-style forestry over high accumulated C in an old growth forest system is counterproductive if the harvested wood is used in a way that returns the C to the atmosphere faster than it would have from the forest itself, *i.e.*, for products that have a short lifespan, and/or it leads to reduced stock of overall ecosystem C (including negative impacts of forest harvest on litter and soil C pools; Mayer et al. 2020; Terrer et al. 2021). Clearly, improved accounting of all forest C pools, the wood products pool, and the full C consequences of forest harvest and disturbance processes is required to make robust judgements about this optimization problem (Geng et al. 2017; Gunn and Buchholz 2018).

A final gap in forest NCS policy is neglect of environmental and social safeguards, which aim to preserve co-benefits derived from forest ecosystems (Pörtner et al. 2021). Some climate mitigation projects - the creation of forest monoculture plantations, for example - have been actively harmful to biodiversity and other environmental objectives (Brundu and Richardson 2016). Generally speaking, biodiversity increases ecosystem function (Cardinale et al. 2012), including productivity (Hua et al. 2016; Mori et al. 2021) and resilience against forest threats, from drought to pest outbreaks (Chapin et al. 2009; Folke et al. 2004; Rist and Moen 2013). Other environmental safeguards should include stronger provisions for soil and water conservation; many NCS policies only require minimizing impacts, without explicit policies to conserve soil or water.

Social safeguards and co-benefits are also necessary for forest and community resilience as climate changes (Hajjar et al. 2021), and are not necessarily enforced under carbon-centered verification schemes. These safeguards include land and labor rights, the inclusion of vulnerable or underrepresented populations in decision-making from an early stage, and free, prior, and informed consent by the local community and/or indigenous groups. In fact, in the US, agricultural and rangeland management practices on tribal lands have been shown to conserve carbon stocks more than parallel practices on non-indigenous lands (Teasdale et al. 2007; Wall and Masayesva 2004; West and Post 2002). Sustainable and equitable US carbon programs could benefit from the work of established coalitions of indigenous communities such as the National Indian Carbon Coalition (https://www.indiancarbon.org/). Partnership between Indigenous and non-indigenous communities and governance entities, for example California's partnership with the Yurok Tribe (Manning and Reed 2019), would help ensure that NCS projects adhere to these social safeguards (McCarthy et al. 2018; Johnson et al. 2021). Poor implementation of forest NCS has already been detrimental to ecosystem C storage, water balance, and food security of local communities (Abreu et al. 2017; Fuss et al. 2018; Holl and Brancalion 2020; Pörtner et al. 2021; Veldman et al. 2015). However, voluntary and private programs have been developing standards to verify that these safeguards are implemented, as well as linking measurable co-benefits to C credits through, for example, Verra's Climate, Community, and Biodiversity Program (Verra 2021).

Across scales of accounting, transparent, credible and complete estimation of emissions and removals is needed to more accurately assess progress; this requires attributing drivers of C storage in order to better anticipate consequences of mitigation actions. While complexities in forest C uptake contribute to the uncertainty in the additionality, permanence, reversal, leakage, and co-benefits of forest-based mitigation activities, process-based forest simulation models are one useful tool to quantify and reduce uncertainty in forest C counting over space and time.

Panel 1 illustrates three key points about forest-based NCS across space. First, REDD+ standards mandate that mitigation activities account for leakage. For example, if emissions from deforestation are avoided through protection of one forest stand, demand for wood products should not be transferred to another forest stand. Second, mitigation activities should account for spatially heterogeneous and contagious disturbance processes that transfer C from the forest to the atmosphere. Third, a diversity of forest-based climate mitigation activities can be employed across space, including forest protection, plantation-style forestry, and ecological forestry. Panel 2 illustrates forest C dynamics through time with implications for forest-based NCS. a) A monitoring, reporting, and verification (MRV) system estimates baseline C storage (*i.e.,* a forest reference level; FRL), which is then projected forward in time and used to assess additionality of a climate mitigation action. In B-D, three scenarios of change in C stock through time are illustrated, with recovery from natural and anthropogenic disturbances (solid lines), and how these legacies interact with alternative management (or no management) scenarios (dashed lines) and novel conditions, such as changing climate (dotted lines). b) Some disturbance-prone forests are at risk of reaching a tipping point under changing climate, but ecological management may help alleviate these vulnerabilities. For example, in the Southwestern US, suppression of fire in forests historically characterized by a high frequency-low severity fire regime has led to overstocked forests. When fire does occur, it can be of uncharacteristically high severity (stand-replacing), leading to a shift to a non-forested state. Thinning treatments have been proposed as a management technique to increase resilience. c) Afforestation or reforestation has been observed with recovery from past land uses (*e.g.,* in the Eastern US) and is proposed as a means to an enhanced forest C sink. We show two contrasting forest management strategies aimed at climate change mitigation, maximizing C stock vs. C flux. In the former, these forests would be allowed to return to a fully stocked state, *i.e.*, reach their carbon storage potential (CSP), although that CSP may decline with changing climate. Alternatively, they could be managed for rapid biomass production with short rotation cycles, *i.e.,* plantation-style forestry, or with longer rotation cycles, *i.e.,* improved forest management. d) Old-growth forest stands, especially in the temperate rainforest zone, have exceptionally high C stocks. These forests could be protected or these stands could be deforested for timber resources, but recovery to CSP would take centuries. Models can supplement MRV systems to broaden the temporal depth by hindcasting to explore HRV and legacy effects, and by forecasting to explore alternative mitigation actions, novel conditions under changing climate, and feedbacks with the climate system. Further, incoming data from MRV systems can be used to improve models.

Opportunities: using models and data to fill gaps

Models

Because climate has such pervasive effects on forests, and the climate system is changing, forest dynamics, including C sequestration and storage, are expected to change. Simulation of forest dynamics is at present the only plausible means of anticipating the future ecosystem services provided by forests, *i.e.*, to plan climate mitigation, at both large (global) and small (site-specific management) scales. Models are also key to reconstructing past forest dynamics (*e.g.,* improving estimates of baseline forest C dynamics, Keane et al. 2018), assessing progress towards goals (*i.e.*, MRV; Box 1, Panel 2), and attributing change to different drivers (Thom et al. 2018), so that progress can be more accurately portrayed and anticipated. For all these reasons, forest models have a key role to play in guiding and improving forest-based NCS.

There is a great diversity of models that simulate forest systems (Albrich et al. 2020), including gap models (Bugmann 2001; Shugart et al. 2018), growth and yield models (Peng 2000; Porté and Bartelink 2002; Weiskittel et al. 2011), forest landscape models (Shifley et al. 2017), and dynamic global vegetation models (Fisher et al. 2018). No one model is ideal for the NCS problem, since the problem spans many scales and processes. Broadly speaking, forest models range from process-based, including land surface and forest landscape models, to empirical, *i.e.*, forest stand-scale models used by foresters. Each have key capabilities, or explicit representation of key processes, needed to address scientific uncertainties or fill gaps, as well as specific areas for improvement. Land surface models, for example, will likely play a key role in the global stocktake process (Grassi et al. 2021); a major source of uncertainty in their projections of the future forest C sink concerns the strength of the CO_2 fertilization effect - *i.e.*, to what degree it may not be realized because other factors become limiting to plant growth (nutrients, soil moisture). Forest landscape models excel at the explicit representation of spatially contagious forest processes, such as fire and insect outbreaks, which cause reversal of forest C stocks. The science of assessing reversal risk would be advanced with better representation of the influence of forest stand structure on fire risk and fire behavior in FLMs, which would help better navigate the trade-off between forest stocking and reversal risk that is inherent in some forests. We detail these two classes of process-based forest models further in Box 2.

The strength of empirical forestry models is their long history of development and use for site-specific forest management, and more recently, their use to estimate forest C stock, including life cycle analysis of C in wood products. That is, they form the basis for forest C calculators (reviewed by Zald et al. 2016). Historically, they have undergone extensive parameterization and validation to satisfactorily represent the stand-level competition-driven self-thinning process characteristic of closed-canopy forest stand development (Shifley et al. 2017; Weiskittel et al. 2011), hence they are the simulation tool of choice used by silviculturists to make forward projections of natural forest stand dynamics. They are the only modeling approach to directly simulate the effect of alternative silvicultural treatments on C stocking and other desired outcomes (Moore et al. 2012; Puhlick et al. 2020). And while stand-level forestry models are inherently limited in representing fire contagion compared to forest landscape models, they do have the capacity to estimate fire risk as a function of current fuels profile, fuel loading, and stand conditions (sensu Reinhardt and Crookston 2003). Grounded in local observations (statistically parameterized and initiated with regional forest inventory data) they have great potential to guide local-level forest management activities aimed at climate mitigation. However, they lack representation of the direct influence of climate on tree growth (*i.e.*, C flux) and hence should be expected to extrapolate poorly to novel climate conditions (Evans 2012).

Box 2: Process-based forest models Land surface models (LSMs) simulate the energy, water, C, and nutrient dynamics of the terrestrial biosphere in terms of coupled biophysical, hydrological and biogeochemical processes (Fisher and Koven 2020). LSMs scale from detailed physiological models of plant processes (*e.g.,* subhourly radiative transfer, photosynthesis and gas exchange, soil moisture dynamics), through plant growth and soil biogeochemistry processes, up to vegetation dynamics and changes in long-term C storage. The representation of vegetation structure within LSMs varies along a continuum of heterogeneity and realism from, at the coarsest end of the spectrum, "big-leaf" models, where vegetation is modeled as a homogeneous surface, to cohort models, which track the average individual in a group, such as a species and age class (Moorcroft et al. 2001), to individual tree models, as in spatially explicit individual-based models (Sato et al. 2007), which use forest gap models or individual-based models to simulate forest dynamics (Christoffersen et al. 2016; Friend et al. 1993; Maréchaux and Chave 2017; Sakschewski et al. 2016). The key strength of LSMs is their process-based linkage of surface energy balance, hydrology, plant physiology, biogeochemistry and nutrient cycling, and ecological dynamics (competition, demographics, fire, plant mortality, land management, etc.) into a single framework. They are most commonly used as components of Earth system models (ESM) to explore the coupled interaction of these processes, including the role of the land in influencing climate, the potential impacts of climate change (including fires, floods, vegetation mortality, crop productivity), and the impacts of changing land use and management (Lawrence et al. 2016; Luyssaert et al. 2018). LSMs are the tool of choice to estimate emissions and removals from the land sector for the global C budget (Friedlingstein et al. 2020), but the persistently wide spread of LSM projections (Koven et al. 2021) is due in part to their high process complexity. Newer approaches to managing the complexity of LSMs via isolation of individual sets of processes (Chitra-Tarak et al. 2021; Fisher and Koven

2020; Needham et al. 2020) as well as data assimilation either to calibrate models parameters (Fer et al. 2018; Thomas et al. 2017) or to update predicted model states with existing data (Fox et al. 2018; Raiho et al. 2020; Smith et al. 2020a) may allow future generations of LSMs to be more closely constrained by data and provide guidance on management at finer resolution. In particular, LSMs can in principle generate estimates of the 'risk of reversal' due to certain classes of climate hazard (fires, droughts, heatwaves, chronic warming) which might be applied to estimate the size of buffers necessary to mitigate against such risks (Buotte et al. 2019). More needs to be done to make LSMs or ecosystem models usable at a site-specific scale. One step in that direction is the PEcAn project (Predictive Ecosystem Analyzer, https://pecanproject.github.io/), a freely-available set of tools and reproducible workflows to incorporate multiple data streams into state-of-the-art ecosystem models at a user-specified location.

Forest landscape models (FLMs) are used to explore forest dynamics in response to processes that propagate spatially across landscapes, especially disturbances (Dobor et al. 2018; Scheller and Mladenoff 2007; Shifley et al. 2017), and therefore the 'reversibility' of C sinks. Explicit simulation of the spread of fire and the movement of insects and seeds is an important element of anticipating forest CSP. FLMs are both spatially explicit and spatially interactive, including representation of subgrid land cover heterogeneity and interaction between adjacent units, making possible the simulation of lateral processes. Landscapes are gridded into sites, and within each site, forest stand demographics are modeled, for example, using forest gap models. Trees can be represented in cohorts (Mladenoff 2004; Schumacher et al. 2004) or as individuals (Seidl et al. 2012). Some FLMs integrate physiological models (de Bruijn et al. 2014; Dijak et al. 2017), and hence can be used to explore the interacting effects of climate and multiple disturbance processes (*e.g.*, wind and insects, Seidl and Rammer 2016; fire, insects, pathogens, Loehman et al. 2016), as well as management (Schumacher and Bugmann 2006). Outputs of forest features from FLMs can be coupled with a C model (Dymond et al. 2016) and used to quantify the interacting effects of species composition, climate change, disturbance, and management on CSP (Loudermilk et al. 2017). Some FLMs can further account for emissions from wood products. FLMs are useful for both hindcasting (Colombaroli et al. 2010; Henne et al. 2011) and forecasting (Elkin et al. 2013; Temperli et al. 2013), hence the attribution of natural and anthropogenic disturbance processes (Keane et al. 2018). Like LSMs, there is a need to make FLMs more user-friendly, *i.e.*, create interfaces that make it possible for foresters and planners to better take advantage of their capabilities. Shifley et al. (2017) identifies avenues for future development and broader applications for FLMs so that they can further contribute to management and policy decisions regarding forest-based NCS.

Data

Key to improving models, and filling some of the gaps identified above, is the use of data, and in particular, combining data with information at complementary spatial and temporal scales (extent and resolution; Babst et al. 2018; Bustamante et al. 2016; Dietze et al. 2018). Forest inventory data form the basis for empirical forestry models. In the US, the permanent sample plot network of the FIA program provides on-the-ground data designed to be representative of the range of forest conditions in each state (Burrill et al. 2018). However, these field measurements are time-consuming and expensive to collect, so plots are revisited on 5- to 10-year intervals. This multi-year temporal resolution makes inventory data less than ideal for detecting the influence of climate variability on tree growth. A complementary source of data with annual resolution, available for many important tree species in boreal and temperate forests, are ring-width data, generated from increment cores. The increment borer was invented by foresters in the 1800's to measure tree growth. Surprisingly then, their use in forestry models has been limited. Instead, tree-ring data have been used by foresters primarily to age forest stands and hence estimate site productivity, by ecologists to reconstruct forest disturbance regimes (Brookes et al. 2021; Swetnam et al. 1999; Swetnam and Lynch 1993) and understand responses to climate variations (Pederson et al. 2014), and by climatologists to reconstruct past climate and hydrologic variation (Cook et al. 2004; Fritts 1976; Woodhouse and Pederson 2018). Though annual growth rings are most reliably formed in extra-tropical realms, hence their utility is limited in tropical forests (Silva and Lambers 2021), tree-ring data collected in the context of a forest inventory or other statistically designed sampling program provide an unbiased way to parse multiple drivers of tree growth, allowing for the attribution of natural or anthropogenic drivers (Clark et al. 2007; Evans et al. 2017; Evans et al. 2022; Dye et al. 2016; Heilman et al. 2022; Klesse et al. 2018, 2020).

Combining data sources to make a climate-sensitive forestry model

Here we illustrate the approach of combining data sources to improve an empirical forestry model in a manner critical for site-specific forest-based NCS purposes. In particular, by adding tree-ring to forest inventory data in the parameterization of a stand-level forest growth and yield model, the Forest Vegetation Simulator (FVS), this model has been updated to explicitly represent the direct effects of climate variation on tree growth, hence C sequestration (Giebink 2021). FVS is the forest growth and yield model most widely used in the United States (Dixon 2002). Its 22 regional variants are normally parameterized with regional, historical inventory data alone. Users then provide site-specific tree and plot inventory data to initialize forest stand conditions to simulate growth, mortality, and forest response to any number of management actions, including silvicultural treatments (Crookston and Dixon 2005). FVS forms the basis for multiple C calculators (Fahey et al. 2010; Zald et al. 2016). Indeed, FVS has been used in the US to guide local-level management decisions aimed at creating additional C sequestration and storage over long time scales (Moore et al. 2012; Puhlick et al. 2020), and is used by some entities in the US voluntary C market for calculating emissions and removals (*e.g.*, Climate Action Reserve Inventory Tool for FVS, CARIT-FVS).

Relatively recently, it became possible to explore potential climate change impacts in FVS with the Climate-FVS extension (Crookston et al. 2010). However, these modifications are coarse. Climate-FVS uses estimates of climatic suitability from species-level environmental envelopes, based on species occurrence data (*e.g.*, Rehfeldt et al. 2006), to modify forest dynamics, including tree-level growth. Tree growth can also be modified at the population level using data on the average growth response to average climate from a very limited number of provenance trails (*e.g.*, Leites et al. 2012). Expected growth is modified in Climate-FVS by whichever--either the species- or population-level response to changing climate--is most limiting.

An alternative is to use tree rings sampled at a broad spatial scale to quantify intraspecific (population-level) heterogeneity in average growth rate and the sensitivity of growth to interannual climate variability (Canham et al. 2018; Klesse et al. 2020; McCullough et al. 2017). Increment cores sampled in FIA's network of permanent sample plots throughout the interior western United States before 2000 were recently discovered and compiled into a tree-ring data network (DeRose et al. 2017). This unbiased FIA tree-ring data set (Klesse et al. 2018) presented a unique opportunity to use the rich information on climate effects recorded in annual growth rings, complemented by inventory data from their associated forest plots, to parameterize FVS growth models. Using these FIA data for dominant tree species in the US semiarid state of Utah, including ponderosa pine (*Pinus ponderosa*) and Engelmann spruce (*Picea engelmannii*), Giebink (2021) parameterized a climate-sensitive version of the large-tree diameter growth model used in FVS. With the addition of tree-ring data, this model captures heterogeneity in climate response beyond what is provided by the current FVS growth model and at higher temporal resolution than Climate-FVS. Four results of this effort to make FVS climate-sensitive are relevant. First, parameterization with tree rings yielded more accurate predictions of growth, in an out-of-sample validation exercise spanning just 10 years (Giebink 2021).

A second result is that the addition of climate sensitivity typically reduces projected future basal area compared to FVS projections (Fig. 2 and Supplemental Fig. 1), which follows logically, given the negative temperature sensitivity of tree growth across Utah. By failing to account for the climate sensitivity of tree growth, the FVS model overestimates the rate of C sequestration of most forest stands.

A third point is that incorporating the direct effect of climate on tree growth made it possible to model how climate might interact with other drivers of variation in absolute tree growth, such as competition. That is, multiple regression modeling enabled by the combination of tree ring and other forest inventory

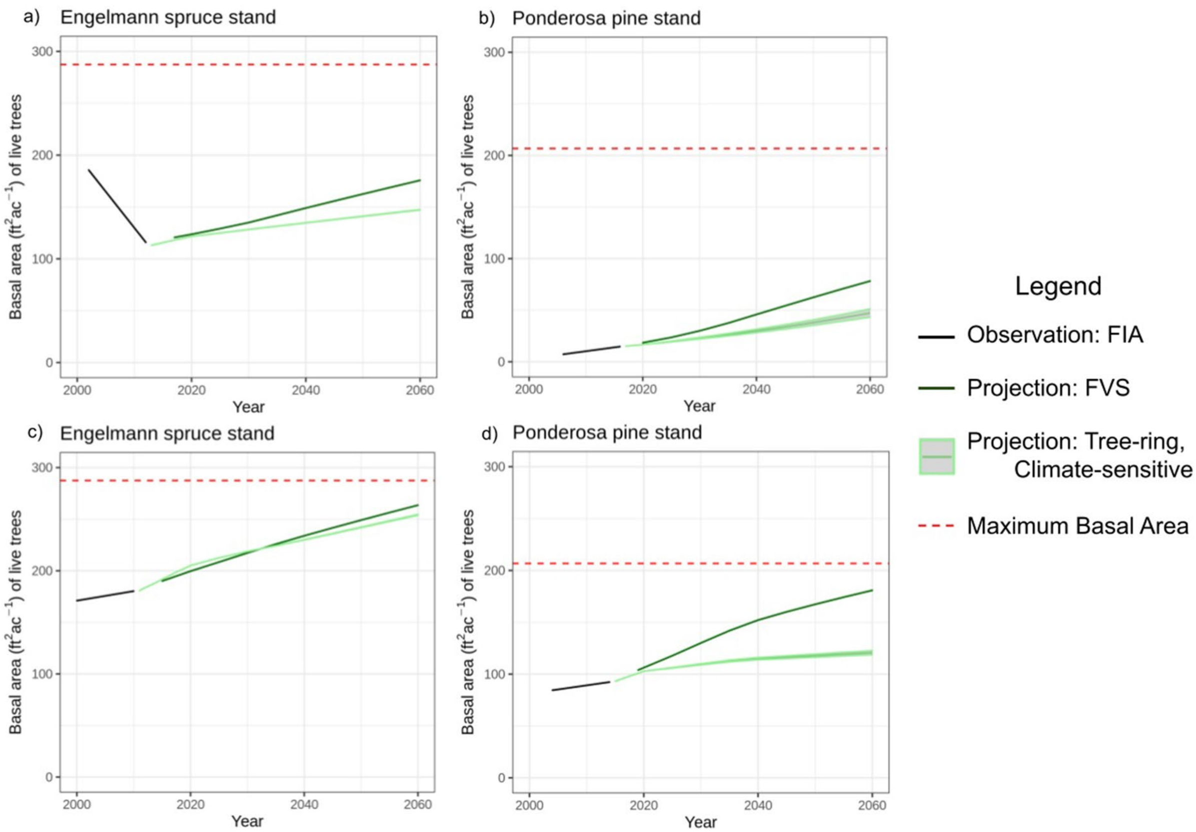


Fig. 2 Observed and projected C storage with and without the effect of climate. Total basal area of live trees in pure Engelmann spruce or ponderosa pine stands in semiarid Utah as observed by the Forest Inventory and Analysis (FIA) program (black line), modeled without the effect of climate by the Forest Vegetation Simulator (FVS; dark green line), or modeled with the effect of climate by a tree-ring-informed model based on FVS (light green line) with species-specific maximum basal area (dashed red line; Keyser and Dixon 2019). The FVS projection cycle was set to 5 years, so the basal area of live trees is calculated every 5 years. Basal area of live trees is calculated annually with outputs from the climate-sensitive, tree-ring informed model. PRISM climate data were used for years before 2020 (Daly et al. 2008), whereas beginning with the year 2020 (and after), downscaled projections under the representative concentration pathway (RCP) 8.5, were used (Supplemental Table 1, Reclamation 2014). Therefore, the climate-sensitive, tree-ring informed projection is an average with standard deviation between outputs from an ensemble of 32 climate models

measurements made it possible to statistically parse and attribute variation in tree growth to multiple drivers. We found competition within the stand increases climate sensitivities, suggesting that forests can be managed (thinned) to mitigate the stress associated with warming temperatures (Keen et al. 2021).

Fourth, an increase in stocking over time directly corresponds to increasing risk of stand-replacing fire - an inherent risk in forests of the intermountain western US. During the simulation of forest stand development in FVS, fire hazard can be described by the Fire and Fuels Extension (Rebain et al. 2021) under moderate or severe weather conditions (*e.g.,* temperature, fuel moisture, and wind speed). Potential fire behavior is strongly influenced by the stage of stand development, stand structure (*i.e.,* even-aged vs uneven-aged), surface fuel loading (down and dead fuel), and ladder fuels (*i.e.,* saplings and understory vegetation). Management actions that alter the composition or structure of overstory trees, as well as the redistribution of the fuels profile (*e.g.,* removing snags, masticating surface fuels, etc.) can influence fire hazard, and can be simulated artificially in FVS to evaluate possible outcomes (including C stocks). Thus, FVS allows for scenario planning of potential mitigation activities at a scale relevant to the management of forest stands. These results become important as managers seek to anticipate appropriate stocking levels, navigating between targets for increased carbon stocking vs. the risk of forest C reversal.

With locally sourced tree-ring time series data and this climate-sensitive version of FVS, managers can better characterize climate vulnerability and expected climate impacts specific to their management unit, at least in temperate and boreal forest systems. In extra-tropical forest systems, tree rings can contribute to a better estimate of baseline C sequestration under changing climate (*i.e.,* FRL). An important next step, in terms of combining data sources to improve forest carbon modeling, would be to link these ground-based, point observations (forest inventory and tree-ring data) with remotely sensed observations. Remotely sensed vegetation biomass or carbon stocks based on spectral, microwave or lidar measurement can be used to monitor changes in carbon stocks caused by changes in land use, management, and disturbance (*e.g.,* Li et al. 2018; Wang et al. 2021), and they already play an important role in national carbon monitoring programs (*e.g.,* Roswintiarti et al. 2013; Shvidenko et al. 2011; Waterworth and Richards 2008). Remotely sensed surface energy balance measured by reflectance or thermal infrared techniques can be used to monitor warming or cooling potential of the land surface depending on land use (Smith et al. 2020b; Stavros et al. 2017). These methods are arguably the most appropriate source of continuous data for spatial monitoring of these key ecosystem-climate feedbacks (Kustas et al. 1994; Sellers et al. 2018; Yang et al. 2013) - above-ground carbon stocks and land-atmosphere energy balance - as well as the effect of management on aboveground ecosystem processes.

Conclusion

At this juncture in the climate crisis, it has become necessary to view human activities - how energy is generated and used, how land is used, how forests are managed - as part of a larger whole of interconnected hydrological, energetic, biogeochemical, ecological, and climate systems. From this perspective arises both the opportunity and challenge of managing forests to mitigate climate change. We conclude with three points about this opportunity and challenge in terms of what needs to be done.

First, it is critical that the enthusiasm surrounding forest-based NCS be tempered in the light of serious scientific uncertainties surrounding forest C dynamics in a non-stationary climate, including the risk of climate-driven forest loss. Put another way, NCS are designed to impact the global C cycle, hence their structures should broadly reflect known risks to the viability of long-term C storage. Specifically, gridded 'climate risk' maps that indicate locations where forest persistence is in doubt, should be routinely appended to estimates of C sink persistence and estimates of necessary buffers in forest-based NCS planning. Further, estimates of land-climate feedbacks, involving changes in C, water and energy balance brought about by large scale forest management, should also be an integral part of forest-based NCS planning, to avoid unintended consequences. The climate benefits of forest-based NCS can be overestimated if these uncertainties and complexities, among others, are not accounted for. In fact, changes in the climate system have advanced so much already that maintaining historical levels of C sequestration by the land sector may be the best we can hope to achieve, let alone additional C sink behavior, above that baseline.

Following closely on the first point is a second: that the success of forest-based NCS depends critically upon improved forest C accounting. This includes improvements in data, in accounting practices and procedures, and in attribution of C dynamics, facilitated by data and models, though we note also that investment in data and models must also consider the C consequences of data collection as well as model development and simulations (Lannelongue et al. 2021). An evidence-based path to success clearly requires data on the most significant C cycle pools and fluxes, of which forest soil C and the causes of its loss are the most neglected. C accounting across scales currently have different objectives and standards with respect to estimating storage and flux, making it very difficult to scale from project-based management actions to global atmospheric consequences. While C accounting procedures do not need to look exactly the same at all scales (not all ecological processes are important at all scales), greater continuity across scales would facilitate the kind of adaptive management that is urgently needed.

At all scales, improved attribution of C stocks and fluxes to natural and anthropogenic causes is necessary to estimate and anticipate how much forest-based NCS can realistically contribute to climate mitigation. Models provide a way to parse drivers of C storage and flux, and greater investment in model development, including the addition of new data sources, would improve process understanding and attribution. We have provided one example: a tree-ring-informed, climate-sensitive version of FVS makes it possible to provide climate driver input to a stand-level decision support tool to evaluate boreal and temperate forest management tactics explicitly in terms of C stock and flux projections. A further improvement would be to better capture in empirical forestry models the non-linear response of tree growth to multiple, interacting environmental drivers (increased atmospheric CO_2, increased evaporative demand, N availability, etc.), *i.e.*, reflecting underlying physiological processes.

A third point on forest-based climate mitigation is that it is important to be cognizant of fundamental trade-offs in forest ecosystem functioning, and between climate regulation vs. other ecosystem services provided by forests, to avoid perverse outcomes. It is not possible to maximize the C stock and C flux of a forest system at one time and spatial location, as illustrated in Box 1. Plantation-style forestry with short rotations will maximize land C flux, whereas maintaining mature forests that have accumulated (and continue to accumulate) C will maximize land C stock. Consideration of other important goals besides C such as ecosystem resilience, biodiversity, water, etc., will likely require striking a balance between maximizing C flux vs C stocks in forest management planning. This multiple use perspective, which uses natural processes to guide management approaches, has been referred to as ecological forestry (Franklin et al. 2018; Kohm and Franklin 1997). In practice, some mix of these three basic strategies at scales of the landscape or larger, is most likely to maximize multiple goals (Box 1, panel 1; and see Seymour and Hunter Jr. 1992). Indeed, the co-benefits of forest management aimed at climate mitigation, including the maintenance of biodiversity, tend to be underestimated or undervalued. An important priority is to not neglect these co-benefits or other safeguards, as there are many ways that forest preservation, restoration, re/afforestation, and improved forest management can contribute to addressing the climate crisis. Moving forward, national-scale programs may take inspiration from the progress made by voluntary programs, such as Verra's Climate, Community, and Biodiversity Program, to better account for the co-benefits of NCS management that are brought about by coupled conservation or multi-use approaches.

These priorities provide a path forward for realistically assessing forest-based mitigation potential so that progress towards national and global emission targets can be made, including updates to reduction ambitions. Rather than viewing the emissions reduction potential of forests as permission to continue to produce GHGs, a more realistic perspective might be to view emissions reductions as critical to preserve the climate mitigation capacity of forest ecosystems.

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Data Availability Forest inventory data were accessed from the Forest Inventory and Analysis (FIA) database (https://apps.fs.usda.gov/fia/datamart/datamart_sqlite.html). The tree-ring dataset analysed are not publicly available, but are available from the corresponding author on reasonable request (DeRose et al. 2017). Climate data were accessed from PRISM Climate Group (Daly et al. 2008) and climate projections were accessed from the online archive of Downscaled CMIP3 and CMIP5

Climate and Hydrology Projections (https://gdo-dcp.ucllnl.org/downscaled_cmip_projections).

Code Availability All code can be accessed from https://github.com/clgiebink/UT_FVS.

Declarations

Competing interests The authors have no conflicts of interest to declare that are relevant to the content of this article.

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