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Natural forests for a safe climate: Enhancing ecosystem integrity, biodiversity and adaptive capacity for climate mitigation

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Natural forests for a safe climate: Enhancing ecosystem integrity, biodiversity and adaptive capacity for climate mitigation

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Mature and old-growth forests contribute to large-scale conservation targets in the conterminous United States

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Mature and old-growth forests (MOG) of the conterminous United States collectively support exceptional levels of biodiversity but have declined substantially from logging and development. National-scale proposals to protect 30 and 50% of all lands and waters are useful in assessing MOG conservation targets given the precarious status of these forests. We present the first coast to coast spatially explicit MOG assessment based on three structural development measures—canopy height, canopy cover, and above-ground living biomass to assess relative maturity. MOG were displayed by major forest types ($n = 22$), landownerships (federal, state, private, and tribal), and Gap Analysis Project (GAP) management status overlaid on the NatureServe's Red-listed Ecosystems and species, above-ground living biomass, and drinking water source areas. MOG total ~67.2 M ha (35.9%) of all forest structural classes and were scattered across 8 regions with most in western regions. All federal lands combined represented the greatest (35%) concentrations of MOG, ~92% of which is on national forest lands with ~9% on Bureau of Land Management (BLM) and ~3% on national park lands (totals do not sum to 100% due to minor mapping errors in the datasets). MOG on national forest lands supported the highest concentration of conservation values. However, national forests and BLM lands did not meet lower bound (30%) targets with only ~24% of MOG in GAP1,2 (5.9 M ha) protection status. The vast majority (76%, 20.8 M ha) of MOG on federal lands that store 10.64 Gt CO_2 (e) are vulnerable to logging (GAP3). If federal MOG are logged over a decade, and half their carbon stock emitted, there would be an estimated 0.5 ppm increase in atmospheric CO_2 by 2030, which is equivalent to ~9% of United States total annual emissions. We recommend upper bound (100%) protection of federal MOG, including elevating the conservation status of Inventoried Roadless Areas. This would avoid substantial CO_2 emissions while allowing ongoing carbon sequestration to act as natural climate solutions to aid compliance with the Paris Climate Agreement and presidential executive orders on MOG and 30% of all lands and waters in protection by 2030. On non-federal lands, which have fewer MOG, regulatory improvements and conservation incentives are needed.

KEYWORDS

United States, mature forests, biodiversity, carbon, drinking water

Introduction

Forest conservation in the United States has for decades centered on protection and ecological restoration of forests in the later stages of stand structural development because of their irreplaceable biodiversity and ecosystem services (e.g., Davis, 1996; Strittholt et al., 2006). Terms like primary forest, late-successional forest, mature forest, old-growth forest, and ancient forest are routinely used, sometimes interchangeably (Mackey et al., 2014). However, verifiable metrics for national-scale inventory and conservation target setting for these forests are lacking.

Precisely when a forest is considered to be in the later structural development is typically based on several diagnostic features such as the age, height, and diameter-at-breast height (dbh) of the dominant-codominant trees; canopy and understory complexity (vertical and horizontal layering); large standing dead (snags) and down trees (logs); and large trees with broken and highly branched tops. These structural characteristics vary among regions, major forest types, and site conditions (e.g., productive vs. slow growing sites). In particular, gap-phase dynamics, the result of tree death (singular or in cohorts), and blow-down along edges and exposed ridgelines, are important drivers of structural development in later forest development stages. When gaps are formed, the resultant increased light and nutrient levels release suppressed trees to fill the gaps over time (e.g., in the eastern forests, Davis, 1996; Pacific Northwest, Franklin and Van Pelt, 2004; Spies, 2004). The lack of severe stand-level disturbances over extended periods allows trees to acquire impressive stature and old ages associated with increasing biological complexity.

Old-growth forests (the most structurally advanced stage) generally have exceptional levels of biodiversity compared to logged forests (the least structurally advanced) (Luyssaert et al., 2008; Keith et al., 2009; Lindenmayer et al., 2012, 2014; Cannon et al., 2022). However, because of the timber value of older trees they are declining globally (Lindenmayer et al., 2012, 2014; Mackey et al., 2014). The loss of old-growth forests is coupled with changes to the global climate (Lawrence et al., 2022), reducing opportunities for natural climate solutions (Griscom et al., 2017; Moomaw et al., 2019). In the United States, conservation importance of old-growth forests has been recognized in every forested region, including Alaska (DellaSala, 2011; Orians and Schoen, 2012; Vynne et al., 2021; DellaSala et al., 2022), Pacific Northwest (Strittholt et al., 2006; Krankina et al., 2014), West (Rockies, Pacific Southwest, Southwest collectively: Kauffman et al., 1992, 2007), Central (Shifley et al., 1995), Great Lakes (Alverson et al., 1994; Carleton, 2003), Southeast (Hanberry et al., 2018), and Northeast (Davis, 1996; Leak and Yamasaki, 2012; Ducey et al., 2013).

Old-growth forest importance can also be described along a spatial gradient from individual trees within a stand to their context within watersheds and landscapes. At the tree level, the largest trees in old-growth forests may represent just 1% of all stems yet store at least 40% of the above-ground carbon as carbon stock increases with tree size as trees age (Stephenson et al., 2014; Lutz et al., 2018; Mildrexler et al., 2020). At the stand level, old-growth forests store 35 to 70% more carbon, including in the soils, compared to logged stands (Keith et al., 2009; Mackey et al., 2014; Mayer et al., 2020). Old-growth forest stands may also act as a natural buffer against extreme climate conditions (De Frenne et al., 2013; DellaSala et al., 2015; Frey et al., 2016; Betts et al., 2017). At the watershed level, old-growth forests maintain hydrological cycles (Perry and Jones, 2016; Crampe et al., 2021). In the Pacific Northwest, old-growth forests may function as fire refugia in large wildfire complexes (Lesmeister et al., 2021).

Aside from select portions of the West, most old-growth forests in the conterminous United States were eliminated decades-centuries ago as logging and development proceeded from east to west coast. What remains is largely on federal lands where the government has untapped policy options for stepped-up conservation. Some of the remaining old-growth forests on national forest land are within Inventoried Roadless Areas (IRAs) that are at least 2,000 ha. Road building and most forms of logging are prohibited within IRAs but only administratively and not by an act of Congress, meaning protections are not inviolate or permanent (i.e., classified as GAP3 multiple use management). Importantly, significant portions of eastern forests are approaching maturity (100 + years, Gunn et al., 2013). As mature forests with advanced structure recover from historical logging, they could develop old-growth characteristics within just a few decades.

Primary and old-growth forests generally have received increased attention internationally as natural climate solutions (DellaSala et al., 2020; IUCN, 2020; Law et al., 2021), including from policy makers[1] (e.g., March 22, 2022) and conservation non-governmental organizations (NGOs) in the United States[2]; [3] (accessed May 15, 2022). Article 5.1 of the Paris Climate Agreement calls on governments to protect and enhance "carbon sinks and reservoirs," while Article 21 of the UNFCCC COP26 Glasgow Climate Pact emphasizes "the importance of protecting, conserving and restoring nature and ecosystems, including forests... to achieve the long-term global goal of the Convention by acting as sinks and reservoirs of greenhouse gases and protecting biodiversity..." (UNFCCC, 2021). Furthermore, the United States was one of 140 nations at COP26 that pledged to end forest degradation and deforestation by 2030 (United Nations Climate Change, 2021). Also, the Summary for Policy Makers (SPM.D.4) in the Intergovernmental Panel on Climate Change [IPCC] (2022) report mentions safeguarding biodiversity and ecosystem integrity as fundamental to climate resilient developments. Attention to mature and old-growth forests can inform implementation of these policy commitments.

Large-scale conservation proposals for all land and waters have increasingly relied on 30 percent (i.e., 30% protected by 2030 or 30 × 30; Dinerstein et al., 2019; Carroll and Noss, 2021; Carroll and Ray, 2021; Law et al., 2021, 2022; One Earth Global Safety Net[4]; accessed May 28, 2022) and 50 percent (Half Earth) protection targets that involve triage approaches (Noss et al., 2012; Wilson, 2016). Large-scale target setting also has policy relevance, as exemplified by President Joe Biden's January 2021 executive order directing federal agencies to develop 30 × 30 targets for all lands and waters in the United States (White House, 2021). An April 2022 executive order from the President also directed federal agencies to inventory and assess threats to both mature and old-growth forests nationwide for possible protections (White House, 2022). Moreover, regionally specific proposals, such as the 79M ha of proposed protected areas in a five state area (OR, WA, ID, MT, and WY; Bader, 2000), a portion of which includes congressionally proposed wilderness additions in the Northern Rockies Ecosystem Protection Act (S.1276), have not assessed the amount of mature and old-growth forests nor its management status (i.e., how much protection is needed?). In all cases, it is vital that these forests are clearly defined, assessed, and mapped at multiple spatial scales (regional to national) to advise decision makers and NGOs on how best to meet climate and biodiversity policies and conservation targets.

Our objectives are to examine the contribution of mature and old-growth forests in the conterminous United States to: (1) conservation of at-risk forest ecosystems and species based on IUCN Red List criteria (Comer et al., 2022); (2) source catchments for drinking water (Mack et al., 2022); and (3) above-ground living biomass (Harris et al., 2021). We also applied conservation target setting developed for continental scale assessments to determine the contribution these forests could make to 30% (i.e., 30 × 30, Dinerstein et al., 2019) (lower bound), 50% (i.e., Half Earth; Noss et al., 2012; Wilson, 2016) (mid bound), and 100% (upper bound) protections. For our study, we are using estimates of forest structure that correlate with stand development collectively referred to as mature-old growth forests (MOG) to capture both the mature stage that is approaching old growth condition and the most advanced old growth stage as well. We also consider old growth a subset of primary forest defined as any forest stage lacking commercial logging or other industrial-scale developments that impairs ecosystem functions (Mackey et al., 2014). To our knowledge, this is the first comprehensive and spatially explicit assessment of MOG in the conterminous United States.

Materials and methods

Forest structure mapping

We mapped the relative level of forest structural maturity using three published spatial data sets that include forest canopy cover, canopy height, and above-ground living biomass derived from modeled satellite data (**Table 1**). These data were stratified by United States Ecoregions Level III ($n = 28$) (Omernik and Griffith, 2014) and Forest Types Groups ($n = 85$) (Ruefenacht et al., 2008) to account for the influences of variation in life history traits governing tree longevity and local environmental conditions on plant growth and ecosystem processes, as well as differing human and natural disturbance regimes. We used field measurements of canopy height and biomass from the Forest Inventory and Analysis plot database (FIA, 2022) to compare with our modeled forest maturity map and to aid in the interpretation of the map. We used a time series of available spatial data to examine the extent to which forests that were mapped as relatively less structurally advanced coincided with the footprints of severe natural disturbances. Further details on the methodology are provided in the Supplementary.

Expert workshops

A series of regional zoom workshops were conducted from September to November 2021 to consult with ecological and forest conservation experts (Supplementary). In total, 40 experts attended with each workshop focused on a major forested region within their region of interest. Key workshop objectives are listed in the Supplementary, including using participants to provide feedback on the initial modeling results for fine tuning. Expert consensus was that the appropriate level of forest

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[1] https://ktvz.b-cdn.net/2022/02/2022-02-17-DOI-and-USDA-Old-Growth.pdf

[2] https://www.climate-forests.org/

[3] https://forestcarboncoalition.org/

[4] https://www.oneearth.org/the-global-safety-net-a-blueprint-to-save-critical-ecosystems-and-stabilize-the-earths-climate/

ecosystem classification was the 28 Forest Types Groups—which comprise aggregations of more finely defined forest types—spatially modeled from FIA inventory plot data at a 250-m pixel resolution (Ruefenacht et al., 2008) and for Level III ecoregions (Omernik and Griffith, 2014).

Spatial analysis

The three spatial structural data layers of forest cover, canopy height, and above-ground living biomass were made available for the conterminous United States (**Table 1**). Spatial analyses were undertaken using Google Earth Engine (Gorelick et al., 2017). As the three data layers were generated using the Global Land Analysis and Discovery's (GLAD) Landsat Analysis Ready Data (ARD), they shared the same 30-m pixel resolution.

An overview of the workflow to create a seamless conterminous-United States wide spatial data layer of relative forest maturity is provided in **Figure 1**. This included creating a spatial vector file of each Forest Type Group for each Level III Ecoregion. Spatial data layers were generated based on spatial coverage for the Forest Type Groups found in each Level III Ecoregion, resulting in a total of 782 unique combinations. For each pixel, we quantified quartile values for the three structural variables (canopy cover, canopy height, and biomass) within each of the 782 combinations. A score was then calculated for each pixel as follows: (a) the lowest quartile value for each metric was given a score of 0 and the highest a score of 3; then (b) the three metric scores were summed giving a range in possible values from 0 (lowest quartile for the three variables) to 9 (highest quartile for the three variables), representing 10 ordinal forest maturity classes. Based on expert feedback, we then produced a simplified structural class map by classifying pixels with a score of 0 as "indeterminant, those with scores of 1–3 as "Young," scores 4–6 "Intermediate" and scores of 7–9 as "Mature." Using a global spatial data set (Petersen et al., 2016), we analyzed the modeled forest maturity map to identify how much of each maturity class was plantation rather than naturally regenerating forest and excluded plantations from analysis.

Calibration analysis

We used FIA plot data as an independent data source for calibration off the modeled forest maturity structure map. Of the three variables, only canopy height could be used for validation as the input biomass layer used FIA biomass data. The spatial units of analysis (SUA) for comparison with the FIA plot data were generated from the intersection of the map of 85 United States Ecoregion Level III with the maps of the 28 Forest Type Groups. Those SUAs were analyzed for which there were at least 10 FIA plots for each of the three FIA Structural Stage Classification levels (Pole, Mature, Late) ($n = 41$). For each of these 41 SUAs, we calculated aggregate statistics from the quartiles and median values for canopy height and biomass from a random sample of pixels within each of the three modeled structure levels (Young, Intermediate, MOG) with 1.5–5% of pixels sampled. Further details are provided in the Supplementary.

Land ownership and gap analysis project status

The extent and management status of MOG was assessed using spatial data provided by government agencies. We used the forest ownership dataset produced by Sass et al. (2020) for the USDA Forest Service based on 2017 data. Each ownership

TABLE 1 Details for the spatial data layers used in the forest maturity modeling and the attribution and validation analyses.

Layer	Description	Data type and scale/resolution	Calibration data/validation approach	Source
Tree canopy cover	Percent tree canopy cover where trees defined as all vegetation taller than 5 m. forest extent in the year 2000 similarly to Hansen et al., that is, any 30-m Landsat pixel that met a tree canopy threshold of at least 30% with trees taller than 5 m.	Raster (30 m)	Training data to relate to the Landsat metrics were derived from very high resolution image interpretation methods	Hansen et al. (2013) updated to 2010 (GLAD)
Forest height	Forest canopy height	Raster (30 m)	Vegetation structure data collected using airborne lidar instruments (ALS) and GEDI field plots	Potapov et al., 2021
Forest biomass	Modeled estimates of above-ground living biomass	Raster (30 m)	Based on machine learning of satellite band ratios, plot measurements of biomass, and environmental variables	Harris et al., 2021
Ecoregions (Levels III)	Areas of similar ecosystems	vector data layer (at or above 1:24,000 scale)	Field verification trips across 30 United States	Omernik and Griffith, 2014
Forest Type Groups	Aggregation of forest types into 28 categories	Raster (250 m)	Spatial distribution models based on correlations between FIA inventory plot data (2022) and spatial environmental data layers	Ruefenacht et al., 2008

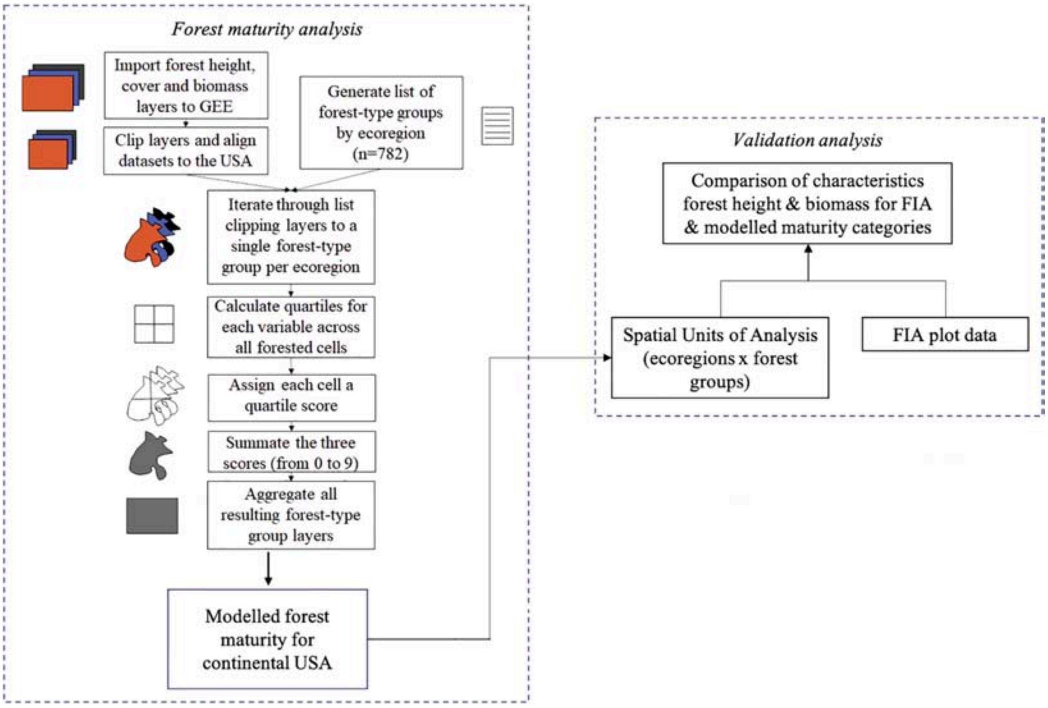

FIGURE 1
Workflow showing main steps in the calculation of the forest maturity structure model for conterminous United States, along with the validation analysis. The three 30-m resolution spatial data sets for forest cover, canopy height, and biomass were analyzed within 872 spatial units of analysis (SUA) defined by the intersection of ecoregions and major forest types. Forest Inventory Analysis (FIA, 2022) plot data were used for a validation analysis. Further details in **Supplementary Information**—Methods.

category was used as a mask to determine the extent of MOG within different tenures across the conterminous United States. The only additional aggregation made was the combination of the two FIA 41 categories, TIMO/REIT and private that were combined into a single masking layer. The Gap Analysis Project (GAP) management status codes (GAP1–4) was applied to MOG using the PAD-US Spatial Analysis Data provided by U.S. Geological Survey [USGS], and Gap Analysis Project [GAP] (2020). GAP 1 (e.g., Wilderness, National Parks) and GAP2 (e.g., National Monuments) were considered protected lands. GAP3 was multiple use management and GAP4 was no protection. The flattened version of the dataset was an important component of the analysis for determining the protected status of MOG. Inventoried roadless areas (IRAs) were filtered from the dataset and classified in our study as GAP2.5—that is—even though IRAs are given GAP3 status in the PAD-US dataset, we gave some credit to IRAs for administrative protections from most forms of logging. To ensure consistency among datasets, we compared the IRA layer to the 2001 Roadless Rule Feature layer provided by the USDA[5] for cross validation. We also assessed additional ownership and management of MOG including National Forests (National Forest System Land Units[6]), National Parks[7] and BLM (Derived from PAD-US[8]). The metadata[9] for landownerships did create some minor overlap problems where IRAs were inadvertently present in the dataset as within other ownerships even though this designation applies only to national forests. Those are recognized in each of the applicable tables as IRA misclassifications. The five western state regional example (79 M ha) that includes the Northern Rockies Ecosystem Protection Act was mapped after Bader (2000).

Biomass calculation

To determine the estimated amount of above-ground living biomass stored within MOG, spatial data produced by Harris et al. (2021) was used as an input layer. Calculating the

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[5] https://data.fs.usda.gov/geodata/edw/datasets.php?xmlKeyword=roadless

[6] https://data.fs.usda.gov/geodata/edw/datasets.php

[7] https://irma.nps.gov/DataStore/Reference/Profile/2224545?lnv=True

[8] https://www.usgs.gov/programs/gap-analysis-project/science/pad-us-data-download

[9] https://www.fs.usda.gov/rds/archive/products/RDS-2020-0044/_metadata_RDS-2020-0044.html

amount of biomass involved firstly warping the dataset to ensure a 30-m pixel size using GDAL and later masking to the extent of determined mature forest. The *R* program exactextractr was then utilized to sum the total amount of biomass within the forests. Due to the discrepancy between the input data being at a 30-m resolution and scaled to Mg/ha, the total value was then converted to produce overall biomass weight in tons.

At risk forest ecosystems and species

The IUCN Red List of Ecosystems (RLE) is an emerging global standard that integrates data and knowledge to document the relative risk status of ecosystem types. RLE criteria were used to assess 655 terrestrial ecosystems in temperate and tropical North America, including 182 forest and woodland ecosystem types in the conterminous United States using the U.S. National Vegetation Classification (Comer et al., 2022). We mapped these ecosystem types nationally using inter-agency LANDFIRE (2016) map products at 30-m pixel resolution with remote sensing data from approximately 2011. The RLE indicators that gauge the probability of range wide ecosystem collapse were measured for each criterion to address: trends in ecosystem extent (A); relative restricted nature of its distribution (B); extent and relative severity of environmental degradation (C); and extent and relative severity of disruption of biotic processes (D). Based on these measures, we categorized ecosystems as Collapsed, Critically Endangered, Endangered, Vulnerable, Near Threatened, Least Concern, Data Deficient, or Not Evaluated. Some 119 (65%) of the 182 United States forest ecosystem types were listed as threatened in some form (i.e., either Critically Endangered (CR) [6.5%], Endangered (EN) [24%], Vulnerable (VU) [24%], or Near Threatened (NT) [10%]).

We also overlaid our MOG map with the modeled distributions of the threatened forest and woodland types to quantify their relative representation within managed and protected lands.

At-risk forest-associated species

We used a database containing an analysis of the habitat requirements for species of conservation concern, including their co-occurrence with standard ecosystem classification units and vegetation structural attributes (Reid et al., 2016). This database includes over 6,000 plant and animal taxa known to occur throughout the conterminous United States. At-risk status was provided using both NatureServe conservation status ranks (Stein et al., 2000) and for listing status under the United States Endangered Species Act (i.e., for species listed as Threatened or Endangered, as well as Candidate or Proposed). We documented relationships through map overlays of species locations with mapped ecosystem type distributions. While incomplete, mapped distributions of forest types provide an initial indication of where MOG may support at-risk forest-associated species.

Drinking water source areas

The USDA Forest to Faucets assessment provides a relative index summarizing the importance of forested land for the provision of surface drinking water based on biophysical and demographic data (Mack et al., 2022). These data were available at the scale of subwatersheds delineated by the USGS, of which there were approximately 100,000 in the United States (USGS et al., 2013). We masked these data by the MOG pixels to provide a spatial layer showing the relative importance of MOG to surface drinking water. We also calculated MOG area for four classes representing each quartile of the relative importance to surface drinking water index and summarized by area for each GAP status and land tenure. Classes ranged from 1 (lowest importance, 0–25% relative importance) to 4 (highest importance, 76–100% relative importance) based on the relative importance to surface water index defined by the USDA Forest Service.

Results

Forest structure classes

Three categories of structural development were identified based on the ten ordinal i.e., ranked categorical classes: young—or least advanced structurally (scores of 1–3)—totaled 41.4 M ha (22.1%); intermediate (scores of 4–6) totaled 78.5 M ha (42.0%); and MOG –most advanced structurally (scores of 7–9)—totaled 67.2 M ha (35.9%) with a grand total of 187.0 M ha of mapped structural classes (**Supplementary Figure 1**). The percentage area of young, intermediate, and MOG within United States Ecoregions Level II is also detailed in **Supplementary Figure 2**. The comparisons of FIA plot based estimates of biomass, canopy height and relative structural maturity are provided in **Supplementary Figure 3** for the 41 spatial units of analysis were there were sufficient plot data.

Mature and old-growth forests spatial extent

The spatial distribution of MOG within the conterminous United States is shown at a national scale (**Figure 2**) and with a zoom-in to eight forested regions where these forests are widely scattered, including the Pacific Northwest (1), Pacific Southwest

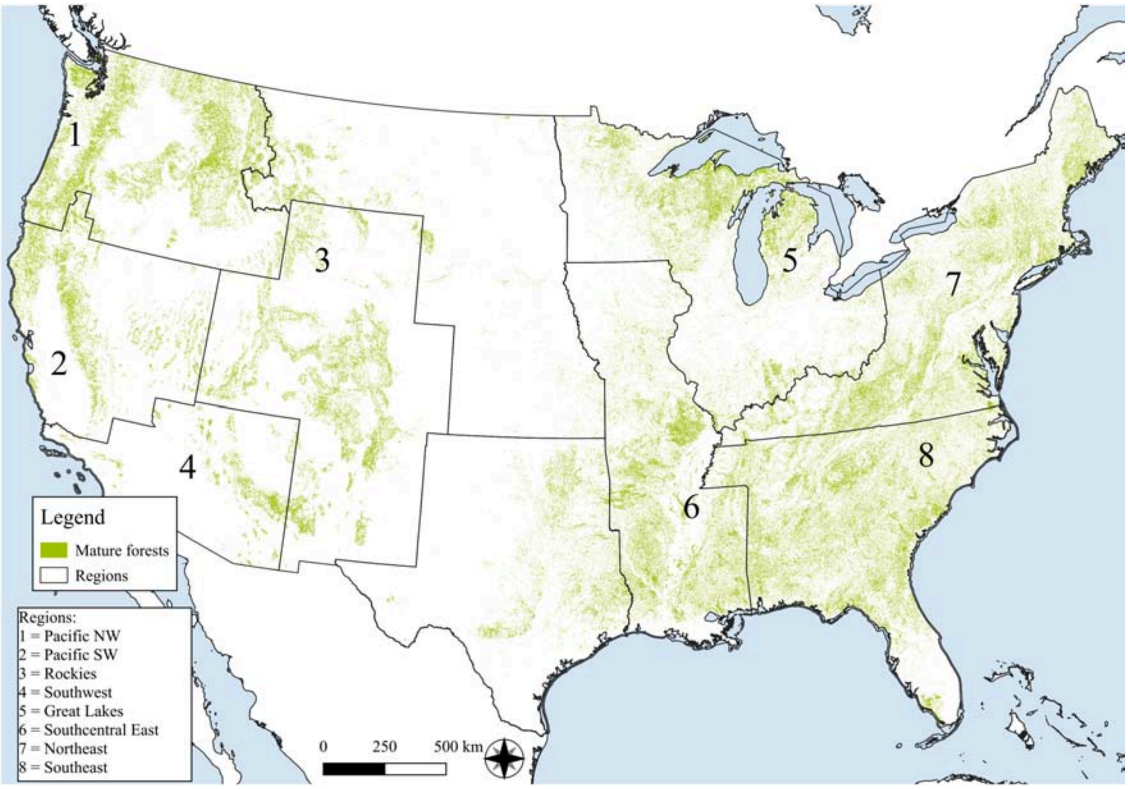

FIGURE 2
Distribution of modeled mature and old-growth forests (MOG) for the conterminous United States. Forest regions with MOG are numbered.

(2), Rockies (3), Southwest (4), Great Lakes (5), South Central (6), Northeast (7), and Southeast (8) (**Figure 3**).

Example photographs of general MOG structural features for major forest types of the conterminous United States illustrate anticipated variability in structural development of these forests (**Figures 4A–F**).

Using the western states regional MOG assessment example, MOG represent ∼7.60 M ha (9.6%) of the 79.1 M ha within the five-state area that includes the Northern Rockies Ecosystem Protection Act under consideration in the United States Congress (**Figure 5**). Only 20% of MOG are in GAP1 and 2 status with 30% in IRAs having intermediate protections (GAP 2.5) (**Table 2**), meaning the vast majority of MOG in this proposal is vulnerable to development pressures.

Mature and old-growth forests major forest types

Mature and old-growth forests were located within 22 forest groups spanning conifer and hardwood types in the conterminous United States (**Table 3**). Nearly all MOG types had their greatest percentages in unprotected status (GAP3, 4; no classifications) with only 14.7% overall in GAP1 and 2 and 7.1% in GAP2.5. Only two forest types, Fir (*Abies* sp.)/Spruce (*Picea* sp.)/Mountain Hemlock (*Tsuga mertensii*) (33.1%) and Other Western Softwoods (41.3%) met the lower bound (30%) target. Percentages would improve for several forest groups if IRAs (GAP2.5 status) received higher protection status. Importantly, FIA major forest classifications inappropriately lump longleaf (*Pinus palustris*) with slash pine (*Pinus elliottii*)-dominated communities as one equivalent forest type, thereby obscuring the imperiled conservation status and biodiversity of longleaf pine wiregrass (*Aristida stricta*) communities. For instance, there are five distinct longleaf pine ecosystem types mapped nationally and assessed under the IUCN Red Listing criteria (Comer et al., 2022), with two listed as Critically Endangered, and three as Endangered that do not show up on the FIA dataset.

Mature and old-growth forests land ownership and GAP analysis project status

Federal lands (36%) have the highest proportion of MOG, of which, National Forests have most (∼92%) of the federal total (**Table 4**). Approximately 24% of MOG on national forest lands

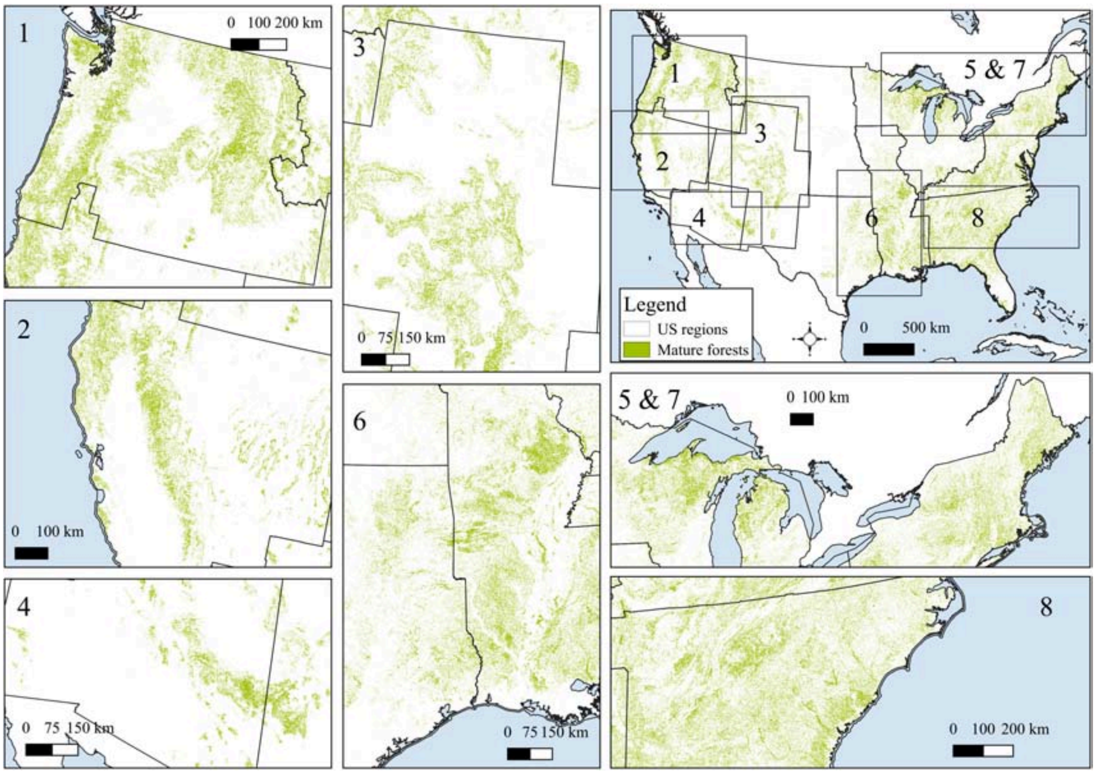

FIGURE 3
Regional zoom-ins of mature and old-growth forests of the conterminous United States. Panels show Pacific Northwest (1), Pacific Southwest (2), Rockies (3), Southwest (4), Great Lakes (5), South Central (6), Northeast (7), and Southeast (8).

are in GAP1 and 2 (**Table 4**). An additional 22% of MOG is within IRAs (GAP2.5). If IRAs received elevated conservation status, that would increase MOG protections in National Forests to 46%, which is within reach of the mid-level 50% target. **Supplementary Table 1** has a breakdown of MOG by GAP status for every national forest.

The rest of MOG on federal lands are held by the National Parks (∼3%) and BLM (∼9%) (categories overlap some due to mapping errors in the datasets). BLM lands in particular are mostly non-forested with some notable exceptions such as in southwest Oregon. However, like National Forests, only ∼24% of MOG on BLM lands have GAP1 and 2 status (**Table 4**). Of non-federal lands, MOG were highest on family private (55%) and lowest on tribal (∼4%). Interestingly, state lands (41%) were the only non-federal category where a lower bound 30% target was met but they did not have much MOG overall. All other non-federal tenures were well below even the lowest 30% target.

Mature and old-growth forests above-ground living biomass

Aggregate above-ground living biomass values in MOG are by far highest on national forests, which contain 45% of the total above-ground living biomass for all ownerships (**Table 5**). For non-federal lands, family private has the most (52%) above-ground living biomass and tribal (4%) the least. The ratio of carbon to above-ground living biomass is typically taken to be 0.5 (i.e., about 50% of the dry weight of biomass is carbon) though globally the ratio can range from 0.4–0.6 (Keith et al., 2010).

Mature and old-growth forests red list of ecosystems

Of the 182 forest and woodland ecosystem types assessed with criteria from the IUCN RLE in the United States, 119 (65%) were categorized from near threatened (NT) to critically endangered (CR); collectively considered here as "threatened" (**Figure 6**). The 102 types categorized as vulnerable (VU) through critically endangered (CR) occurred on 38% of current forest area. Critically endangered and endangered forest ecosystems were concentrated in the eastern states; mostly in areas with the longest and most intensive land use histories. Types found there included Southeastern Interior Longleaf Pine Woodland, Atlantic Coastal Plain Fall-line Sandhills Longleaf Pine Woodland, and West Gulf Coastal Plain Sandhill Oak and

FIGURE 4
Examplary photographs of mature and old-growth forests in the United States. **(A)** Mixed-conifer forest, Sequoia National Park, CA, United States (B. Bryant). **(B)** Mature Eastern Hemlock (*Tsuga canadensis*) stand, Huron Mountain Club Upper Peninsula, MI, United States (B. Boucher). **(C)** Bottomland hardwood forest, Congaree National Park, SC, United States (J. Maloff, Old Growth Network). **(D)** North-Central Interior Dry-Mesic Oak Forest and Woodland (B.S. Slaughter). **(E)** Hardwood hammock forest, Starkey Park, FL, United States (D. DellaSala). **(F)** Top ten largest bald cypress (*Taxodium distichum*) in Florida, Upper Pithlachascotee River Preserve (D. DellaSala). Nearly all old growth cypress was logged in the 1930s.

Shortleaf Pine Forest and Woodland (Supplementary Table 2). Forest type descriptions are maintained for public access on NatureServe Explorer[10] (accessed September 4, 2022).

Large proportions of MOG under GAP1 to GAP 3 status include types categorized by the IUCN RLE as Least Concern (Table 6). About 39.4 M ha (394,000 km^2) of all at-risk (NT-CR) forests and woodlands occurred within area mapped as MOG. While current area of critically endangered forests was quite limited overall, most at-risk forest mapped as MOG was categorized as Near Threatened, Vulnerable, or Endangered. These were commonly located on either federal land, predominately national forests, or family private (Table 6). Importantly, ~12.1 M ha (18%) of MOG with threatened status were located within GAP3 status

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[10] https://explorer.natureserve.org/

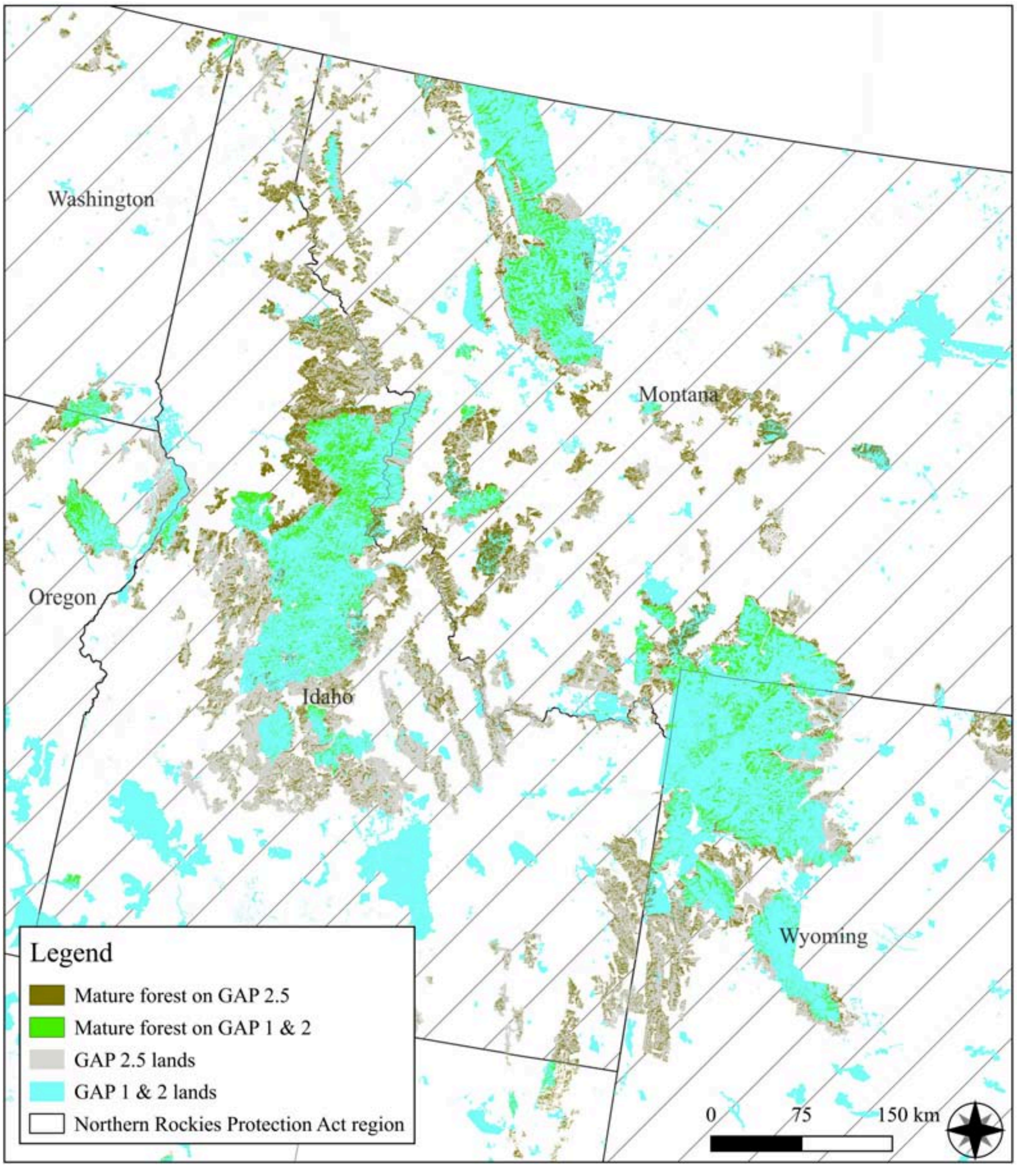

FIGURE 5
Distribution of mature and old-growth forests within the proposed five state protection area (OR, WA, ID, MT, and WY) including the Bader (2000) and Northern Rockies Ecosystem Protection Act (2021) by GAP classifications. GAP2.5 refers to Inventoried Roadless Areas (IRAs) that are not fully protected.

under multiple use management. These were, for example, North Pacific Maritime Mesic-Wet Douglas-fir (*Pseudotsuga menziesii*)-Western Hemlock (*Tsuga heterophylla*) Forest (VU) in the Pacific Northwest, and Southern Rocky Mountain Ponderosa Pine Woodland (VU) in the southern Rocky Mountains (**Figure 6**). The other large proportion of threatened MOG occurred on family private land, mostly throughout the eastern states (**Figure 6**). Examples included Ozark-Ouachita Dry Oak Woodland (EN), Allegheny-Cumberland Dry Oak Forest and Woodland (EN [VU-EN]), or Southern Piedmont Mesic Forest (EN [VU-EN]).

Mature and old-growth forests and at-risk species

Using documented relationships between species of concern and forests, there were 97 mapped forest ecosystem types known to support at-risk species (**Supplementary Table 2**) and the listed species are maintained for public access on the NatureServer Explorer (see text footnote 10; accessed September 5, 2022) under individual forest type summaries. MOG was present in 29.2 M ha of these mapped forest ecosystem types. Species considered "at-risk" within forest types using

TABLE 2 Mature and old-growth forests area (%) within the proposed five state protection area (OR, WA, ID, MT, and WY) that includes Northern Rockies Ecosystem Protection Act by GAP status.

GAP status	Area (ha)	Area (%)
GAP 1	1 174 117	15.4
GAP 2	342 516	4.5
GAP 2.5	2 331 074	30.7
GAP 3	5 033 750	66.2
GAP 4	295 733	3.9
Outside of GAP	755 909	9.9
Total area of mature forest	7 602 025	100
Total project area	79 173 694	–

Outside of GAP are areas with no GAP status, mostly on private lands.

NatureServe conservation status ranks included Vulnerable (G3), Imperiled (G2) or Critically Imperiled (G1) (Stein et al., 2000). From 1 to 64 of these at-risk species were associated with the 97 mapped forest types. Forest types with the most MOG that also included at-risk species were, for example, Laurentian-Acadian Northern Hardwood Forest (37,644 km^2 and 12 at-risk species), South-Central Interior Mesophytic Forest (16,046 km^2 and 50 at-risk species), and Southern Appalachian Oak Forest (10,190 km^2 and 48 at-risk species). Using United States Endangered Species Act (i.e., Threatened or Endangered, as well as Candidate or Proposed) as another measure of at-risk species status, 1 to 15 at-risk species were documented for their association with these 97 forest types. Among those supporting >1 at-risk species and with the extensive area in MOG were, for example, North Pacific Maritime Dry-Mesic Douglas-fir-Western Hemlock Forest (10,370 km^2 and 4 at-risk species), East Gulf Coastal Plain Large River Floodplain Forest (4,295 km^2 and 13 at-risk species), and Atlantic Coastal Plain Blackwater Stream Floodplain Forest (2,417 km^2 and 8 at-risk species).

Of the 97 forest ecosystem types with habitat relationships documented for at-risk species, 70 were considered threatened (IUCN NT, VU, EN, or CR) themselves. Threatened forest types support at-risk species (based here on NatureServe Conservation status ranks) with the most extensive area mapped as MOG in South-Central Interior Mesophytic Forest (EN) (16,046 km^2 and 50 at-risk species), Northeastern Interior Dry-Mesic Oak Forest (EN) (15, 327 km^2 and 12 at-risk species), and Southern Appalachian Oak Forest (VU) (10,190 km^2 and 48 at-risk species) (**Supplementary Table 2**).

TABLE 3 Area (×1000 hectares) and percent (%) of mature and old-growth forest within each Forest Inventory and Analysis (FIA) forest type group.

Forest type group	GAP 1	GAP 2	GAP 2.5	GAP 3	GAP 4	Outside of GAP	Total
Alder/Maple	1.1 (0.7)	5.9 (3.5)	0.8 (0.5)	46.3 (27.6)	7.9 (4.7)	106.4 (63.5)	167.6
Aspen/Birch	84.8 (2.5)	629.5 (18.9)	288.3 (8.7)	864.5 (26)	221.3 (6.6)	1 528.8 (45.9)	3 328.9
California Mixed Conifer	185.7 (13.8)	58.4 (4.3)	139.9 (10.4)	783.9 (58.3)	10.7 (0.8)	304.9 (22.7)	1 343.6
Douglas-fir	654.3 (11.1)	217.6 (3.7)	1 112.9 (18.9)	3 946.9 (67)	235.1 (4)	840 (14.3)	5 893.9
Elm/Ash/Cottonwood	11.7 (1.2)	139.9 (13.8)	1 (0.1)	46.1 (4.6)	75 (7.4)	738.9 (73)	1 011.6
Fir/Spruce/Mountain Hemlock	1 308.2 (29.6)	154.8 (3.5)	1 298.5 (29.4)	2 688.9 (60.8)	86.3 (2)	182.2 (4.1)	4 420.4
Hemlock/Sitka Spruce	127 (26.2)	15.8 (3.3)	55.3 (11.4)	287.6 (59.4)	12.5 (2.6)	41 (8.5)	483.9
Loblolly/Shortleaf Pine	41.5 (0.6)	555.8 (8.1)	9.7 (0.1)	562 (8.2)	229.3 (3.3)	5489 (79.8)	6 877.6
Lodgepole Pine	413.5 (22)	101.4 (5.4)	681.8 (36.3)	1 258.7 (67)	38.3 (2)	67.9 (3.6)	1 879.8
Longleaf/Slash Pine	19.3 (1)	90 (4.8)	3.2 (0.2)	308.7 (16.6)	72.7 (3.9)	1 365.5 (73.6)	1 856.2
Maple/Beech/Birch	65.6 (1.3)	868.6 (16.6)	29.2 (0.6)	523.7 (10)	302 (5.8)	3 484.3 (66.4)	5 244.2
Oak/Gum/Cypress	126.9 (4.1)	398.6 (13)	1.5 (0)	303.1 (9.9)	108.2 (3.5)	2138.7 (69.5)	3 075.5
Oak/Hickory	280.8 (1.6)	1173.9 (6.9)	153.2 (0.9)	1 810.3 (10.6)	1 363.4 (8)	12 421.7 (72.9)	17 050.1
Oak/Pine	23.1 (1.1)	147.6 (7)	7.1 (0.3)	167.6 (7.9)	66.3 (3.1)	1 711 (80.9)	2 115.6
Other Western Hardwoods	28.1 (23.4)	5.2 (4.4)	31.7 (26.4)	61.8 (51.5)	5.5 (4.6)	19.5 (16.2)	120.1
Other Western Softwood	86.9 (35.2)	15 (6.1)	102.1 (41.3)	119.3 (48.3)	16.7 (6.8)	9.1 (3.7)	247
Pinyon/Juniper	405.5 (10.5)	346 (9)	483.6 (12.5)	2 076.4 (53.7)	552.4 (14.3)	485.3 (12.6)	3 865.6
Ponderosa Pine	135.1 (4.2)	103 (3.2)	174.2 (5.4)	1817.3 (56.7)	412.6 (12.9)	738.2 (23)	3 206.2
Redwood	7.2 (9.4)	8.3 (10.9)	0.1 (0.1)	7 (9.2)	11.7 (15.3)	42.1 (55.2)	76.3
Spruce/Fir	31.4 (2)	312.7 (20.1)	16.9 (1.1)	264.5 (17)	153.6 (9.9)	790.9 (50.9)	1 553.1
Tanoak/Laurel	12 (5.9)	17.2 (8.4)	5.7 (2.8)	46.5 (22.6)	23.1 (11.2)	106.6 (51.9)	205.4
Tropical Hardwoods	1 (5)	4.7 (22.3)	0 (0)	7.4 (35.4)	0.3 (1.5)	7.5 (35.9)	20.9
Total	4 212.6	5 632.4	4 751	18 610.1	4 125.5	33 425.3	67 183

GAP2.5 refers to Inventoried Roadless Areas (IRAs). IRAs outside national forests are classification errors in the database. Outside of GAP are areas with no GAP status, mostly on private lands. Percentages are calculated by totaling each forest type group across rows.

TABLE 4 Total area of mature and old-growth forests (×1000 ha) and percent (parenthesis) for the conterminous United States by GAP and ownership.

Ownership and tenure	GAP 1	GAP 2	GAP 2.5	GAP 3	GAP 4	Total per owner
National Parks	822.3 (96.1)	24.5 (2.9)	0.7 (0.1)	3.3 (0.4)	4.4 (0.5)	855.6 (100)
National Forests	2 995.1 (13.7)	2 322.5 (10.6)	4 775.1 (21.9)	14 120.5 (64.7)	137.2 (0.6)	21 834.3 (100)
BLM	161.1 (7.1)	394.5 (17.4)	29.9 (1.3)	1 706.9 (75.4)	0.1 (0)	2262.6 (100)
State	11 5 (2.2)	2 086.3 (39)	4.9 (0.1)	2 054.9 (38.5)	430 (8)	5 343.7 (100)
Federal	4 014.9 (17.1)	2 906.7 (12.4)	4 756.2 (20.2)	15 731.6 (66.9)	402.4 (1.7)	23 514.5 (100)
Corporate private	13.5 (0.1)	215.4 (1.9)	3 (0)	232.4 (2.1)	645.2 (5.7)	11 223.5 (100)
Family private	32.5 (0.1)	296 (1.3)	5.2 (0)	350 (1.6)	1 067.7 (4.8)	22 467 (100)
Tribal	0.4 (0)	13.2 (0.8)	0.2 (0)	7.6 (0.5)	1 481.2 (94.6)	1 566 (100)
Total per GAP	4 239 (6.3)	5 686.8 (8.5)	4 784.2 (7.1)	18 736.3 (27.9)	4 198.1 (6.2)	67 183 (100)

Percentages are calculated across rows. GAP2.5 refers to Inventoried Roadless Areas (IRAs). IRAs outside national forests are classification errors of input datasets.

TABLE 5 Total-above ground living biomass within mature and old-growth forests (×1 M tons) by GAP and ownership.

Ownership and tenure	GAP 1	GAP 2	GAP 2.5	GAP 3	GAP 4	Total per owner
National Parks	281 (94.9)	10 (3.4)	0 (0)	1 (0.3)	3 (1)	296 (100)
National Forests	933 (15.7)	425 (7.1)	1 203 (20.2)	4 095 (68.8)	26 (0.4)	5 956 (100)
BLM	31 (5.3)	64 (11)	7 (1.2)	484 (83.4)	0 (0)	580 (100)
State	17 (1.9)	295 (33.4)	1 (0.1)	397 (45)	74 (8.4)	883 (100)
Federal	1 241 (19.3)	509 (7.9)	1203 (18.7)	4 539 (70.5)	60 (0.9)	6 441 (100)
Corporate private	3 (0.2)	35 (1.8)	0 (0)	42 (2.1)	89 (4.5)	1 970 (100)
Family private	6 (0.2)	47 (1.4)	0 (0)	56 (1.7)	123 (3.7)	3 325 (100)
Tribal	0 (0)	3 (1.1)	0 (0)	1 (0.4)	254 (93.4)	272 (100)
Total per GAP	1 285 (9.6)	920 (6.9)	1 203 (9)	5 091 (38.1)	626 (4.7)	13 351 (100)

Percentages (in brackets) are calculated across rows. GAP2.5 refers to Inventoried Roadless Areas (IRAs). IRAs outside national forests are classification errors of input datasets.

TABLE 6 Area of land (×1000 ha) and percentage area (parentheses) for each of the identified Red Listed Ecosystem (RLE) risk status by GAP and landowner.

	Not evaluated	Data deficient	Least concern	Near threatened	Vulnerable	Endangered	Critically endangered	Total by GAP
GAP status								
GAP 1	1.9 (0)	28.4 (0.5)	3 129.2 (60.3)	1 220.9 (23.5)	623 (12)	181.9 (3.5)	5.1 (0.1)	5 190.4 (100)
GAP 2	1.8 (0)	74.5 (1.5)	1 685.4 (35)	616.6 (12.8)	1 340.4 (27.9)	1 026.4 (21.3)	67.3 (1.4)	4 812.4 (100)
GAP 2.5	0 (0)	0.4 (0.1)	247.1 (81)	46.5 (15.2)	11.2 (3.7)	0 (0)	0 (0)	305.2 (100)
GAP 3	10.4 (0)	139 (0.6)	9 198.4 (42.9)	6 875.9 (32.1)	3 874.3 (18.1)	1 268.1 (5.9)	86.3 (0.4)	21 452.3 (100)
GAP 4	1.4 (0)	76.6 (1.8)	1 040.5 (24.2)	550.5 (12.8)	2 073.2 (48.3)	538.9 (12.5)	13.3 (0.3)	4 294.4 (100)
Landowner								
National Parks	1.5 (0.2)	8.3 (0.8)	558.4 (57.1)	195.2 (19.9)	200.1 (20.4)	15 (1.5)	0 (0)	978.6 (100)
National Forests	12 (0)	93.9 (0.4)	11 963.5 (46.6)	7 327.5 (28.5)	4 359.2 (17)	1 762.5 (6.9)	175.5 (0.7)	25 694 (100)
BLM	0 (0)	5.8 (0.2)	520.3 (19.9)	1 456.9 (55.7)	631.9 (24.1)	2.1 (0.1)	0 (0)	2 617.1 (100)
State	2.8 (0.1)	105.7 (2.6)	1 390.2 (34.4)	326 (8.1)	1 252.2 (30.9)	948.8 (23.5)	20.1 (0.5)	4 045.9 (100)
Federal	11.3 (0)	115 (0.4)	12 454.2 (45.1)	8 369 (30.3)	4 869.4 (17.6)	1 677.8 (6.1)	148.4 (0.5)	27 645.1 (100)
Corporate private	3.6 (0)	419.8 (5.3)	1 618 (20.3)	969.3 (12.1)	2 651.3 (33.2)	2 111.4 (26.4)	213.9 (2.7)	7 987.4 (100)
Family private	15 (0.1)	450.8 (2.7)	2 701.1 (16)	827.7 (4.9)	7 176.4 (42.5)	5 493.9 (32.5)	224.1 (1.3)	16 889 (100)
Tribal	0 (0)	16.4 (1)	738.3 (43.9)	447.1 (26.6)	457.4 (27.2)	21.2 (1.3)	0.2 (0)	1 680.6 (100)
Total by risk status	34.5 (0.1)	1 152.9 (1.9)	19 513.9 (32.4)	11 055 (18.4)	17 009.3 (28.3)	10 762.5 (17.9)	630 (1)	67 183 (100)

Percentages are calculated across rows. GAP2.5 refers to Inventoried Roadless Areas (IRAs). IRAs outside national forests are classification errors of input datasets.

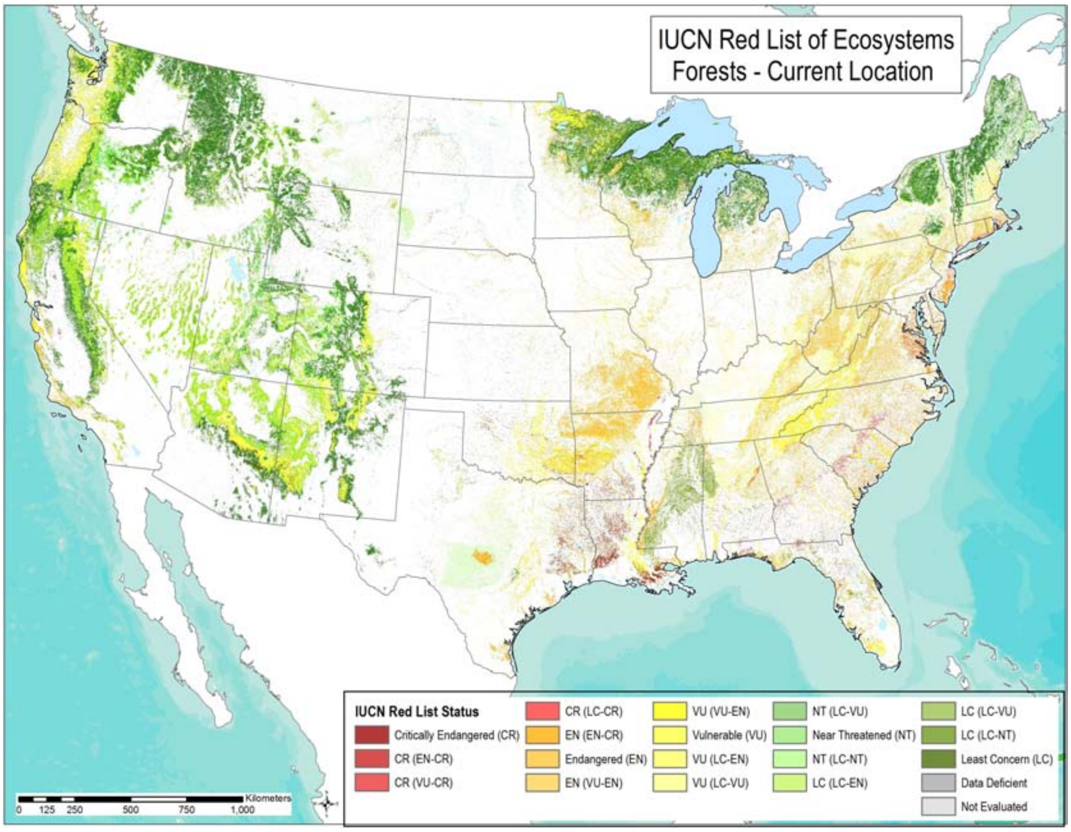

FIGURE 6
Current distribution of 182 forest and woodland ecosystem type categories under the IUCN Red List of Ecosystems (Comer et al., 2022). Nearly all these distributions include mature and old-growth forests (**Supplementary Table 2**).

TABLE 7 Mature forest area (ha) in each relative importance to surface drinking water class by GAP status and land tenure, with percentage of total mature and old-growth forest in the respective GAP/Tenure.

	Class 1 (0–25%)	Class 2 (26–50%)	Class 3 (51–75%)	Class 4 (76–100%)	Total
GAP Status					
GAP 1	1,188,095 (28.2)	1,021,604 (24.2)	1,218,859 (28.9)	790,612 (18.7)	4,219,170 (100)
GAP 2	1,804,722 (31.8)	915,163 (16.1)	1,541,173 (27.2)	1,411,752 (24.9)	5,672,810 (100)
GAP 2.5	1,646,869 (34.4)	1,220,674 (25.5)	1,355,166 (28.3)	561,520 (11.7)	4,784,229 (100)
GAP 3	5,922,561 (31.6)	4,494,644 (24)	4,720,470 (25.2)	3,598,512 (19.2)	18,736,188 (100)
GAP 4	1,178,791 (28.1)	773,969 (18.4)	1,370,386 (32.7)	873,587 (20.8)	4,196,733 (100)
Outside GAP	6,077,230 (20.6)	3,883,699 (13.2)	7,433,106 (25.2)	12,130,797 (41.1)	29,524,833 (100)
Land Tenure					
National Forests	5,713,619 (26.2)	5,498,207 (25.2)	6,119,473 (28)	4,501,227 (20.6)	21,832,525 (100)
National Parks	257,648 (30.1)	145,354 (17)	214,784 (25.1)	237,857 (27.8)	855,644 (100)
Federal Land	7,144,748 (30.4)	5,709,127 (24.3)	6,217,105 (26.5)	4,421,747 (18.8)	23,492,727 (100)
State Lands	1,704,860 (32.0)	803,361 (15.1)	1,360,235 (25.5)	1,463,130 (27.4)	5,331,587 (100)
Family Private Lands	4,381,601 (19.5)	3,208,018 (14.3)	6,200,135 (27.6)	8,666,291 (38.6)	22,456,045 (100)
Corporate Private Lands	3,081,796 (27.5)	1,815,543 (16.2)	2,672,084 (23.8)	3,653,002 (32.6)	11,222,425 (100)
Tribal Lands	611,203 (39)	384,502 (24.6)	517,106 (33)	53,000 (3.4)	1,565,810 (100)
BLM Lands	1,245,174 (55.6)	415,190 (18.5)	358,263 (16)	220,752 (9.9)	2,239,379 (100)
Total	17,818,269	12,309,753	17,639,160	19,366,781	67,133,962

Mature and old-growth forests and drinking water

Based on the USDA drinking water source area dataset, MOG with the highest drinking water value (Class 4) were mostly on Federal lands with surprising large areas on family private and corporate private (**Table 7**). Importantly, a substantial (4.5 M ha, >39%) amount of the highest quality drinking water comes from MOG within GAP3 and 4 status, and much more (12.1 M ha) is outside GAP status all together. Any loss of these forests due to logging and development would potentially impact drinking water supplies.

Discussion

Mature and old-growth forest structure and spatial analysis

Forest age and level of stand development are typically measured through tree ring analysis (e.g., core drill samples from living trees) and diameter distributions of dominant trees but can also be assessed using models based on measurements of forest structure—canopy height, canopy cover, biomass, as in our study. Other forest structural development characteristics indicative of the later stages of forest development include vertical vegetation layering and coarse woody debris (not measured in our study). Differences in the longevity, life history traits and niche requirements of tree species means that in many ecosystem types, the taxonomic composition of the dominant canopy species can reflect stages progressing from early to late seral. Gap-phase dynamics are diagnostic of the most structurally advanced old-growth. Furthermore, environmental factors that regulate plant growth, ecosystem processes rates and site productivity—thermal, moisture, radiation and nutrient regimes—result in variation within the ecosystem type of forest structure classes in terms of tree height, canopy density, and above-ground woody biomass.

Pan et al. (2011) used 2006 FIA plot data and remote sensing data at 1-km resolution to produce an age class distribution map in discrete age intervals of North American forests. Our inventory provides an updated and continuous-based structure map at 30-m resolution for tracking future changes in ecological development and management of MOG that can be updated as new datasets and advancements in monitoring technologies become available. We estimate 67.2 M (~36% of all structural classes) of MOG are scattered across eight geographic regions in the conterminous United States that provide options for stepped up national and regional conservation. With the exception of IRAs, MOG are mostly not large contiguous blocks as they are nested within a highly fragmented matrix that has contributed to edge effects and diminished ecosystem functions (see Heilman et al., 2002).

Federal lands

Combined federal lands represented ~35% of the total MOG structural classes with most (~92%) on national forests and a fraction managed by National Parks (~3%) and BLM (9%) (some overlap in mapping datasets). MOG on federal lands have the highest conservation values reflective of their above-ground living biomass, at-risk ecosystems and species, and drinking water source areas. However, only 24% of MOG on national forest and BLM lands each are fully protected, which is below even the lowest bound 30% target. Our analysis supports 100% of federal MOG for inclusion in protected areas based on their superior climate, water, and biodiversity associated values. We note that adding ~20.8 M ha of unprotected federal MOG to the United States protected areas network would still fall far short of the 30% target for all lands and waters given only 12% of all types are protected nationally. To achieve a near tripling of protections nationally on top of 20.8 M ha of proposed MOG protections would still require another 125 M ha of new protections from all types and landowners (National Geographic, 2021).

An alternative scenario is that the unprotected federal MOG in GAP2.5, 3, and 4 status is logged and then regrown. The consequences of this logging on exacerbating climate change can be assessed in terms of the projected emissions and their effect on the atmospheric CO_2 concentration. A comparison of protected vs. logged federal MOG allows the mitigation benefit of protecting MOG to be further evaluated in terms of carbon emissions avoided. The area of 20.8 M ha at-risk MOG on federal lands currently stores ~5.8 Gt of above-ground living biomass (Federal land GAP 2.5 + 3 + 4; **Table 5**), which is equivalent to 10.64 Gt CO_2. It is assumed that 50% of the carbon that had been stored in the biomass of logged MOG is emitted to the atmosphere due to combustion or decomposition of waste and short-lived wood products (Brown et al., 1997; Keith et al., 2014). This represents a carbon stock loss from the biosphere and a stock gain by the atmosphere. Logging emissions would remain in the atmosphere for decades and are partially removed by sinks. This can be calculated as the fraction of the airborne CO_2 from each pulse of emissions that decreases over time by removals from the natural land and ocean sinks and the regrowth of the forest (Keith et al., 2022). Carbon stock remaining in the atmosphere as the airborne fraction of the emissions was estimated for 2030 (after 8 years) and 2050 (after 28 years) to comply with global emissions reduction targets and for assessing the mitigation potential of full protection. By 2030, 74% of logging emissions would remain in the atmosphere, and by 2050, 54% would remain (Keith et al., 2022). This carbon stock remaining in the atmosphere also can be converted to parts per million by volume (ppm) as the common unit to express atmospheric CO_2 concentration (1 ppm = 7.8 Gt CO_2) (CIDAC, 1990). If 74% of the CO_2 emitted remains in the atmosphere by 2030, then 10.54 Gt CO_2 emissions are required to raise the atmospheric CO_2 concentration by 1 ppm. Logging emissions would consequently result in 0.5 ppm increase in atmospheric CO_2 concentration by 2030 and 0.37 ppm by 2050.

The quantity of logging emissions also can be compared with the total United States emissions that were 5.8 Gt CO_{2e} in 2020[11] (accessed September 5, 2022), which would be 0.532 Gt CO_2 from MOG logging per year, the equivalent to 9.2% of the total annual United States emissions.

We note while such an accelerated increase in logging may be logistically unrealistic due to a number of factors (e.g., clearcut vs. selection logging, congressional appropriations, timber sale economics) not the least of which is accessibility of remaining MOG that becomes increasingly costly as easy to access sites are initially logged. However, the Trump administration issued an executive order in 2019 designed to greatly ramp up logging by 72% on national forests.[12] According to conservation groups, at least some of those sales under the Trump administration are ongoing[13] (accessed September 5, 2022). Additionally, legislation is routinely introduced in Congress to greatly increase federal lands logging at the expense of forest protections[14]. Logging unprotected MOG would also contribute to total United States emissions and make President Biden's stated goal of emissions reduction of 50–52% by 2030 far more difficult to achieve. Conversely, not logging these unprotected MOG would avoid the decadal logging equivalent of ∼0.5 ppm CO_2 (5.32 Gt CO_2) or ∼9% of United States total annual emissions, which would make a meaningful mitigation contribution to the world as natural climate solutions (Griscom et al., 2017; Moomaw et al., 2019; Keith et al., 2022). It is this current decade that is critical for mitigation actions to avoid emissions and not to add to the atmospheric CO_2 concentration, including those from the land-use sector.

The IRA component of MOG represents what remains of intact blocks on national forests. Elevating the conservation status of IRAs to GAP2 would increase MOG protections on national forests to that approaching the mid-bound (50%) target. However, that would take either an act of Congress or administrative changes that remove exemptions for logging and other development projects (e.g., hydroelectric development, mining) along with new regulations making it difficult to overturn roadless protections in general. The national roadless conservation rule has sustained 14 legal challenges upheld in appellate courts, was overturned twice on the Tongass National Forest in Alaska by pro-development administrations (i.e., George W Bush and Donald Trump), and was substantially changed by state petitions to the federal government in Idaho and Colorado. Increasing administrative or congressional IRA protections is key to elevating the conservation status of IRAs so they can be considered GAP2. While there is no comparable roadless policy for BLM lands, MOG could be nominated to the National Landscape Conservation System[15] (accessed May 15, 2022). The BLM oversees 14 M ha of mostly iconic lands and waterways designated by Congress or presidential executive order mainly for conservation purposes that includes national monuments and other protective designations.

Regional

Federal forests in the Eastern region are maturing from logging that eliminated all but a fraction (1–2%) of the old-growth forests over a century ago (Davis, 1996). Most mature forest types in this region lack protections, many are not on federal lands, and most are fragmented especially given that large IRAs are mostly in western regions. Additionally, the USDA Forest Service (2022) revised its 20-year forest management plans for the 416,000 ha Nantahala and Pisgah National Forest in western North Carolina claiming that they needed to log mature forests to create a diversity of seral stages even though classic old-growth forests are still well below historical levels (Davis, 1996). A combination of federal protections, improved forestry practices, and conservation incentives on non-federal lands are needed in this region to meet conservation targets for MOG.

Under the Trump administration, the USDA Forest Service removed protections for large diameter (>50 cm dbh, up to 150 years old) trees on national forests in eastern Oregon and Washington that were in place for over two decades, even though large trees remain below historical levels (Mildrexler et al., 2020). We recommend restoring those protections. The five state western proposal that includes the Northern Rockies Ecosystem Protection Act also contains nearly 11 M ha of MOG with only 20% in GAP1 and 2 status and another 30% in IRAs (GAP2.5). Recent policy and management decisions underscore the importance of increasing MOG protections in this region as well.

Non-federal lands

Family forest owners are a group of nearly 10 million families, trusts, and estates representing the largest landowner category in the United States with one-third of the total forest ownership (vonHedemann and Schultz, 2021). Substantial area of at-risk ecosystems, at-risk species, and drinking water also occur on these lands mostly in the eastern states where federal lands are scarce. Family landowners generally tend to manage their forests for aesthetics, wildlife, conservation, and family ownership legacy providing opportunities for conservation investments (Butler et al., 2016).

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[11] https://www.epa.gov/climate-indicators/climate-change-indicators-us-greenhouse-gas-emissions

[12] https://www.usda.gov/sites/default/files/documents/usda-strategic-plan-2018-2022.pdf

[13] https://www.climate-forests.org/worth-more-standing

[14] https://www.congress.gov/bill/115th-congress/house-bill/2936/text/ih?overview=closed&format=txt

[15] https://www.blm.gov/programs/national-conservation-lands

State lands are under state regulatory authorities and these vary widely in the extent to which they have as either policy or practice the protection of MOG. Aside from state parks, most forested states grant preference to intensive forest management over forest protections. Large corporate landowners manage forests mainly to maximize their return-on-investment by cutting trees when they approach culmination of mean annual increment (just before they reach maturity). MOG therefore are often looked at as a financial liability to be converted into fast growing monocultural plantations on short-timber rotation cycles. Many tribal lands also have timber objectives. In the Great Lakes, however, larger Indian reservations contain more MOG, higher biomass, and better sustain biodiversity than surrounding public lands (Waller and Reo, 2018).

In general, for all non-federal lands, a combination of regulatory improvements and incentives could retain more MOG (Dreiss and Malcolm, 2022). This might include conservation easements, fee-title acquisitions, and carbon offsets that result in verifiable conservation gains over *status quo* management. Our MOG assessment may also provide procurement guidance to the private sector regarding avoiding logging in older forests, as, for example, a recent shareholder resolution at the Home Depot chain to purchase wood not coming from old-growth forests[16] (accessed May 20, 2022).

Data and model limitations

A limitation of our modeled forest structural maturity is that it does not directly provide a measure of forest stand age. Such an effort would need to cross-walk our modeled MOG areas with on-the-ground forest plot metrics derived from the FIA dataset. However, our structural maturity levels (Young, Intermediate, and MOG) overlap well with the FIA Structural Stage Classification levels (Pole, Mature, and Late) and are reasonably indicative of forest age classes.

We assumed that for a given Forest Type Group in a given ecoregion, the level of maturity would be monotonically related to increasing canopy cover, canopy height and biomass. An initial visual inspection of the modeled forest maturity map identified two landscape settings where the forest was likely erroneously assigned a younger structural class. One was forests bordering the alpine zone that naturally have a sparser and shorter canopy and support lower biomass stocks compared to a similar type at a lower elevation. Less obviously, are forests in climatically drier ecoregions on exposed topographic positions that naturally would be sparser, shorter and have less biomass than similar forest types nearby with higher site productivity (McKenney and Pedlar, 2003). The Oak/Hickory Forest Type Group also had some anomalous results with lower-than-expected areas of Young forest. This is likely the result of substantial wildfire suppression in these fragmented forests across their range (Nowacki and Abrams, 2008).

The Forest Type Groups, stratified by United States Ecoregions Level III, were used to represent the major differences in forest ecosystems. However, as these Groups are only intended to indicate broad distribution patterns of forest cover in the United States, modeled with an overall accuracy of 65% (Ruefenacht et al., 2008). They represent a highly generalized level of ecological organization within which resides a rich forest biodiversity that encompasses a range of natural variability in tree growth rates due to local physical environmental conditions that means in some locations there can be a mismatch between stand development and forest structure.

Discretion should be taken when interpreting the MOG water overlay given the differing spatial scale of input datasets. The relative importance to surface drinking water dataset is provided at the scale of subwatersheds, which vary in size and shape as their bounds are largely determined by topographic and hydrologic features of the landscape (USGS et al., 2013). So, while we presented the water importance overlay at 30-m resolution, the masked values are from the coarser dataset, meaning there may be some fine-scale variation missed. There may also be some correlation between MOG area and areas highly valuable for surface drinking water, as the layer incorporates forest metrics including forest cover, forest ownership and insect and disease risk (Mack et al., 2022). Given that the index incorporates many other non-forest variables, the impact of this correlation is likely minimal.

Finally, we did not assess the critical landscape and climate refugia role that larger and more continuous MOG (e.g., IRAs) play in a rapidly changing climate, including enabling species movements (i.e., connectivity up and down elevation, northern latitudinal shifts) and providing minimum critical areas for apex predators and other area and climate sensitive species.

Conservation recommendations

President Biden's Executive Order (White House, 2022) for forests aims to "institutionalize climate-smart management and conservation strategies that address threats to mature and old-growth forests on Federal lands." Mature forests, which include the old-growth forest class, provide superior values compared to logged forests as natural climate solutions (Griscom et al., 2017; Moomaw et al., 2019) in meeting both White House (2021, 2022) executive orders. Moreover, the 30 × 30 executive order includes all lands and waters—and not just federal—that require a combination of conservation measures to achieve this target (e.g., in regions with little federal lands such as the eastern region). However, the current *status quo* management of MOG and low protection levels on all lands presents unacceptable risks at a time when the global community is seeking ways to reduce the rapidly accelerating biodiversity and climate

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[16] https://ir.homedepot.com/~/media/Files/H/HomeDepot-IR/2022/2022%20Proxy%20Statement%20-%20Final.pdf

crises (Ripple et al., 2021). While our analysis presented three target scenarios of 30, 50, and 100% protection, there are climate, biodiversity, and drinking water benefits for choosing the upper bound 100% target for MOG on federal lands with additional measures on non-federal lands to compliment a federal reserve system anchored in MOG. The IRA component of MOG includes remaining relatively intact forest blocks that would benefit from elevating the GAP status of IRAs through enhanced protective measures. One way to do this would be to introduce national rulemaking that protects all remaining federal MOG in and out of IRAs. We note that the White House (2022) also calls for prioritizing the restoration of old-growth forests as "climate-smart forest stewardship." In our view, this can include allowing mature forests to grow into old growth structurally over time as in the Eastern region in order to begin restoring the national and regional deficits in old-growth forests. It can also mean restoring the beneficial role of wildfires in maintaining diverse understories in fire-adapted older forests such as many dry mixed conifer, oak-hickory, and open pine systems (e.g., long-leaf pine wiregrass). Typically, MOG that have experienced severe natural disturbance are logged, including within administrative reserves (such as late-successional reserves under the Northwest Forest Plan in the Pacific Northwest) and even within IRAs. However, we recommend protections extend through post-disturbance successional stages to allow forests to recover carbon stocks (proforestation, Moomaw et al., 2019) and because most carbon in severe disturbances simply transfers from live to dead pools and soils (Law et al., 2021).

A large-scale effort to protect MOG nationwide, including all primary and old-growth forests within the highest end of the mature forest spectrum, would help the United States meet a range of multilateral commitments related to protecting and restoring ecosystem integrity. Ecosystem integrity has long been a bedrock principle in the United Nations, recognized in both the Rio Declaration and Agenda 21, and were agreed to in 1992 at the United Nations Conference on Environment and Development (UNCED) (the 'Earth Summit'). The UNFCCC's Paris Agreement (UNFCCC 1/CP.21), agreed in 2015, carried forward the concept of ecosystem integrity in its preamble, and more recently the Intergovernmental Panel on Climate Change's 6th Assessment Report made numerous references to the fundamental importance of primary forests, ecological restoration and ecosystem integrity (Intergovernmental Panel on Climate Change [IPCC], 2022). Similarly, the Convention on Biological Diversity also recognizes the importance of primary forests and ecosystem integrity *via* decisions 14/5 and 14/30 agreed in 2018 at its 14th Conference of the Parties. The United Nations Strategic Plan for Forests 2030 (ECOSOC Resolution 2017/4), which builds on the 2007 UN Forest Instrument (A/RES/62/98 and A/RES/70/199), emphasizes ending deforestation and preventing forest degradation as key globally priorities. The United Nations global decade on restoration was launched in 2021, following on the 2011 Bonn Challenge, with a target of 350 million ha of restoration, including a pledge of 15 million ha from the United States. The UN Sustainable Development Goals also has a goal of halting and reversing land degradation (United Nations, 2022). Finally, 95 nations, including the United States, recently agreed to support the 30 × 30 initiative as part of their COP15 Convention on Biological Diversity obligations in June 2022. Mature and old-growth forest inventories (White House, 2022) provide a foundation for introducing much needed policies that are based on the upper bound full protection for MOG, which would allow the United States to fulfill its international obligations as a leader in the global effort to end forest degradation and deforestation.

Data availability statement

The datasets presented in this study can be found in online repositories and on matureforests.org; accessed September 9, 2022. The names of the repository/repositories and accession number(s) can be found in the article/**Supplementary material**.

Ethics statement

Written informed consent was obtained from the individual(s) for the publication of any identifiable images or data included in this article.

Author contributions

BR contribute to the development of the article's methods that were added per reviewers request for more on the methodology – the methods were greatly expanded in the article and the online **Supplementary material**. All authors contributed to its completion.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2022.979528/full#supplementary-material

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Using ecosystem integrity to maximize climate mitigation and minimize risk in international forest policy

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Several key international policy frameworks involve forests, including the Paris Agreement on Climate Change and the Convention on Biological Diversity (CBD). However, rules and guidelines that treat forest types equally regardless of their ecosystem integrity and risk profiles in terms of forest and carbon loss limit policy effectiveness and can facilitate forest degradation. Here we assess the potential for using a framework of ecosystem integrity to guide policy goals. We review the theory and present a conceptual framework, compare elements of integrity between primary and human-modified forests, and discuss the policy and management implications. We find that primary forests consistently have higher levels of ecosystem integrity and lower risk profiles than human-modified forests. This underscores the need to protect primary forests, develop consistent large-scale data products to identify high-integrity forests, and operationalize a framework of ecosystem integrity. Doing so will optimize long-term carbon storage and the provision of other ecosystem services, and can help guide evolving forest policy at the nexus of the biodiversity and climate crises.

KEYWORDS

Paris Agreement, primary forest, carbon, forest degradation, deforestation

Introduction

Forest ecosystems are central to international agreements and frameworks that support and set policy agendas, including the United Nations (UN) Framework Convention on Climate Change (UNFCCC), Convention on Biological Diversity (CBD), Sustainable Development Goals (SDGs), and Convention to Combat Desertification (UNCCD). Forests and their ecosystem services provide critical data to inform global environmental assessments such as the Global Forest Resource Assessments (FRAs) of the UN Food and Agriculture Organization (FAO), the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), the System of Environmental Economic Accounting–Ecosystem Accounting (SEEA-EA), and the World Bank's reports on the Changing Wealth of Nations (Lange et al., 2018). The mitigation significance of forests is recognized in Article 5 of the Paris Agreement. Given their mitigation value, updating forest management practices to reduce emissions and increase withdrawals from the atmosphere should be included in many countries' Nationally Determined Contributions (NDCs; Forsell et al., 2016; Grassi et al., 2017; Roe et al., 2019). Forestry practices have the potential to provide a majority fraction of the Agriculture, Forestry, and Other Land Use (AFOLU) sector's contributions to climate mitigation, which may represent up to one-third of net emission reductions needed to limit warming below 1.5–2°C above pre-industrial levels (Federici et al., 2017; Grassi et al., 2017; Griscom et al., 2017; Roe et al., 2019). The current emissions gap between NDCs and what is required to limit warming to 1.5 or 2°C (UNEP, 2019) means that the role of forests may be even greater; for example, forests are referenced heavily in the Intergovernmental Panel on Climate Change (IPCC) special report on 1.5°C in the context of negative emissions (Dooley et al., 2018; IPCC, 2018).

However, given the finite area of available land and the many ecosystem services they provide, there are often conflicting goals for the management of forests in national and international policy contexts, resulting in incoherent policies and policy objectives (Kalaba et al., 2014; Koff et al., 2016; Tegegne et al., 2018; Timko et al., 2018). For example, many of the UN SDGs focused on promoting economic development are at odds with conserving forests and biodiversity (Ibisch et al., 2016). Unclear and inconsistent definitions and accounting rules mean that forest mitigation measures can have a range of results from large-scale protection that preserves carbon storage, sequestration, and ecosystem services, to perverse outcomes with net carbon loss, degraded ecosystems, and negative impacts on other policy goals (Mackey et al., 2013). For example, bioenergy with carbon capture and storage (BECCS) is used in the majority of current global socioeconomic model scenarios to stay below 1.5–2°C of warming (Roe et al., 2019). At these scales, BECCS will require the conversion of vast quantities of native forests into tree plantations or short-rotation forests (Fuss et al., 2014; Creutzig et al., 2015; Smith et al., 2016; IPCC, 2018). Increased bioenergy use is currently resulting in forest degradation and deforestation that will generate net carbon emissions for decades or longer (Birdsey et al., 2018; Booth, 2018; Sterman et al., 2022). Part of the problem is that forest cover and types are largely seen as fungible within the UNFCCC guidelines (UNFCCC, 2002), with no criteria for forest condition or carbon longevity (Ajani et al., 2013; Hansen A. J. et al., 2020; Keith et al., 2021).

From a carbon perspective, "risk of loss" of the stock is of central importance. The risk of loss from disturbances means that some land-based carbon activities will not provide long-term protection of carbon from release into the atmosphere (e.g., Anderegg et al., 2020). This risk is a primary reason that forest-based solutions are often not considered as reliable ways to reduce net emissions and hence are not prioritized as mitigation activities (Grassi et al., 2017). Yet little consideration has been given to differentiating forest types and management schemes based on their "risk of loss" profiles. The Paris Agreement mentions criteria for mitigation that speak to risk, such as equity, sustainability, and integrity, but as of yet there is little guidance on implementation.

The concept of "ecosystem integrity," or related "ecological integrity," has a long history in theoretical and applied ecology (e.g., Kay, 1991; Tierney et al., 2009; Wurtzebach and Schultz, 2016) and is explicitly referenced [e.g., Paris Agreement, CBD post-2020 Global Biodiversity Framework (Convention on Biological Diversity [CBD], 2021), IPCC Working Group II (IPCC, 2022)] or implied in international agreements and national-level legislation and agency directives (e.g., Australian Government, 1999). By providing a holistic view of ecosystem structure, function, composition, and adaptive capacity, the objective of maximizing ecosystem integrity may have the potential to minimize risk of carbon loss and maximize the ecosystem services provided by forests, thereby facilitating greater policy coherence across sectors (Koff et al., 2016; Dooley et al., 2018; Barber et al., 2020). However, the concept is not prioritized in international policy nor operationalized in most national forest policies, thus falling well short of its potential. There are no specific actions or supporting mechanisms for ecosystem integrity in the Paris Agreement, and parties have not articulated how they will identify and protect high-integrity ecosystems. Instead of representing a guiding framework, ecosystem integrity is largely viewed as a potential co-benefit (Bryan et al., 2016; Funk et al., 2019). Particularly important is providing a definition and framework for ecosystem integrity that the CBD (though the Global Biodiversity Framework) and the UNFCCC (through the Global Stocktake) can utilize to achieve their biodiversity and climate mitigation objectives.

Here we review the potential for a framework of ecosystem integrity to minimize risk in forest-based mitigation policies and maximize ecosystem service co-benefits. We first discuss the theory of ecosystem integrity and provide a working conceptual framework. We then compare important elements of ecosystem integrity between primary and human-modified forests, with a focus on elements most relevant for carbon mitigation including risk profiles. Finally, we discuss the policy and management implications of this comparative analysis. By drawing on ecological theory and several sub-disciplines within ecology, we integrate knowledge into a coherent framework of ecosystem integrity (**Figure 1**) that can be used to guide both forest policy at the international level as well as implementation in the form of land use decisions, metrics, and priorities at the national and jurisdictional levels. Our review draws upon decades of evolving forest policy and published literature, including but not limited to peer-reviewed articles, as well as engagement with stakeholders, practitioners, policy makers, and forest ecologists.

Framework for forest ecosystem integrity

Definition

Many definitions of ecosystem integrity exist because ecosystem integrity is not a simple absolute physical property but rather a multidimensional and scale-dependent emergent phenomenon that encompasses important system components and their interactions. The concept has received considerable attention over the past several decades because of the human benefits derived from natural processes and ecosystem states. As noted by Muller et al. (2000), "ecosystem integrity turns out to be the ecological branch of sustainability."

Here we adopt and build upon the general framework originally provided by Kay (1991), whereby ecosystem integrity *integrates different characteristics of an ecosystem that collectively describe its ability to achieve and maintain its optimum operating state, given the prevailing environmental drivers and perturbations, and continue its processes of self-organization and regeneration (i.e., autopoiesis)*. One of the main theoretical divides about ecosystem integrity relates to differentiating compositional (e.g., species richness, genetic diversity, or presence of threatened species), structural (e.g., vegetation density, biomass, food chains, and trophic levels) or functional (e.g., productivity, energy flows, and nutrient cycling) aspects of integrity (De Leo and Levin, 1997; Pimentel et al., 2013; Roche and Campagne, 2017). We suggest these are largely inseparable given the fundamental importance of structural and compositional elements in supporting functional forest ecosystem integrity and the many interdependencies among composition, structure, and function. In practice, available data and resources will determine what can be measured at a particular spatial and temporal scale. Because ecosystem integrity includes the provision of ecosystem services for human benefit, its evaluation typically includes a human dimension (Kay, 1991; De Leo and Levin, 1997; Kay and Regier, 2000; Dorren et al., 2004; Roche and Campagne, 2017).

Components of ecosystem integrity

Based on decades of theoretical and applied studies, we provide a framework for understanding the components of forest ecosystem integrity, their drivers, and their inter-linkages (**Figure 1**). It is important to note that all elements of ecosystem integrity are affected by the prevailing environmental and site characteristics of a given forested location, which must be accounted for when comparing specific locations in space and/or time.

Foundational elements

Forest ecosystem integrity is based on physiological structures that efficiently use and dissipate energy (**Figure 1**). These dissipative structures, or "ecological orientors" (Muller et al., 2000), generate a gradient of energy degradation *via* metabolic reactions that create and maintain themselves (i.e., self-organization). Progressively accumulated exergy (i.e., available energy) becomes stored emergy (i.e., all the energy used to generate a product or service) (Campbell, 2000; Kay and Regier, 2000; Muller et al., 2000). Over the course of evolution, community assembly, and forest succession, this process generates optimized (generally high but not too high; Hengeveld, 1989; May, 2001) ecosystem complexity and distance from thermodynamic equilibrium (Odum, 1969; Kay, 1991; Holling, 1992; Campbell, 2000; Muller et al., 2000), with associated levels of structural complexity, functional diversity, and niche complementarity (Tilman, 1996; Tilman and Lehman, 2001; Thompson et al., 2009). Ecosystem processes that sustain and regulate this self-organizing system, such as productivity, evapotranspiration, reproduction cycles, and nutrient cycling and retention, are optimized in the process (Muller et al., 2000; Dorren et al., 2004; Migliavacca et al., 2021). The resulting forest is a non-linear, self-organizing, holarchic and open system, with reciprocal power relationships between levels (Kay and Regier, 2000).

A critical property of ecosystem integrity that is difficult to assess from structural or compositional elements alone is stability. Following Grimm and Wissel (1997), stability is comprised of resistance (or constancy), resilience, and persistence, which collectively represent an ecosystem's ability to resist or be resilient to change at both short and long time scales (Kay, 1991, 1993; Regier, 1993; Muller, 1998; Kay and Regier, 2000; Andreasen et al., 2001; Parrish et al., 2003). In the case of forest ecosystem integrity, primary drivers of change (exposure) include human land use and other human pressures, and climate change including extreme weather events and increasing disturbances. Resistance indicates a forest's ability to maintain stability *via* dynamic equilibrium within defined ecosystem

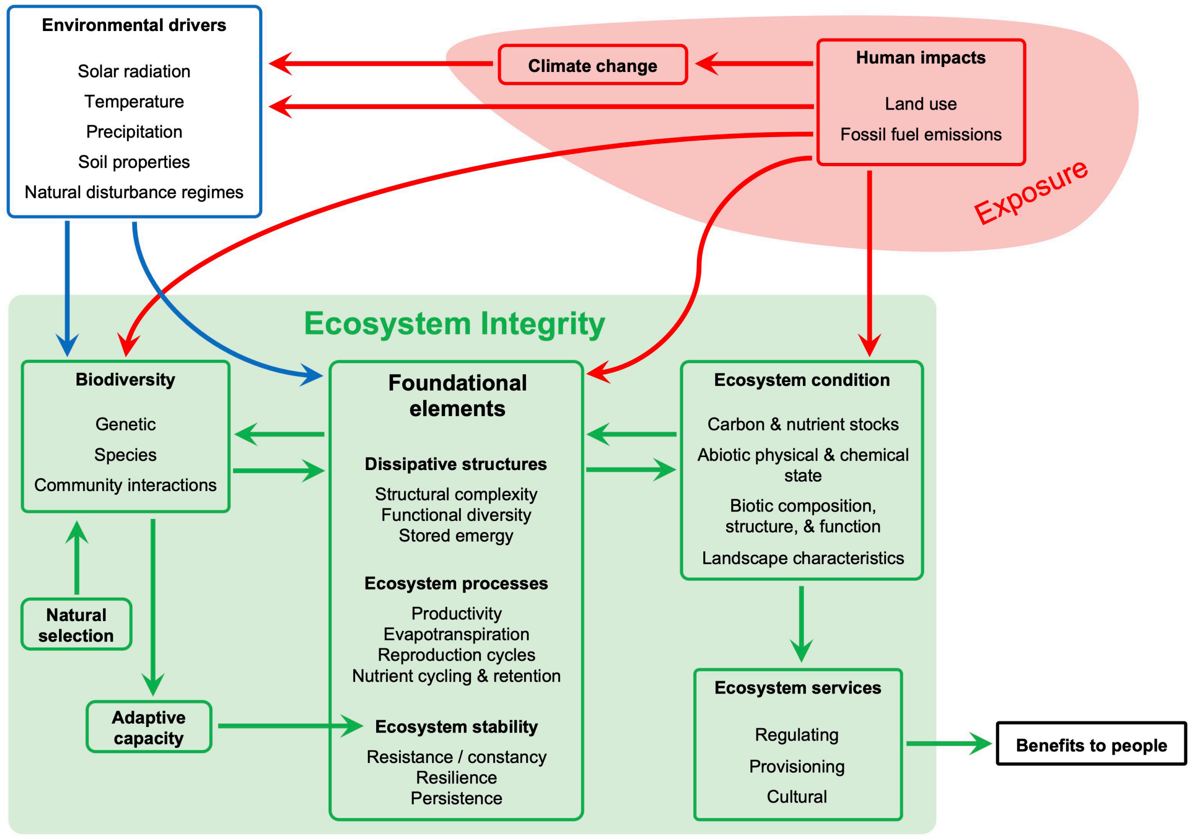

FIGURE 1
Conceptual framework of ecosystem integrity. Integrity is based on foundational elements including dissipative structures, ecosystem processes, and ecosystem stability. These are underpinned by biodiversity, natural selection, and adaptive capacity, and in turn generate a given ecosystem condition and benefits to people. Ecosystem integrity is impacted by environmental drivers and human impacts, including land use and climate change.

bounds (Hughes et al., 2002; Loreau et al., 2002) in response to these drivers. Forest resistance is conferred by negative feedbacks and buffers, for example stable microhabitats in forest interiors and functional redundancy across species. Resilience indicates the ability to return to optimal operating conditions after a state-altering perturbation (Holling, 1973; Kay, 1991; Kay and Regier, 2000; Muller et al., 2000; Thompson et al., 2009). The resulting ecosystem state can be somewhat altered (i.e., "ecological resilience" as opposed to "engineering resilience"), but when viewed over an appropriate time span, a resilient forest is able to maintain its "identity" in terms of taxonomic composition, structure, ecological functions, and process rates–and hence exhibit persistence (Thompson et al., 2009). Forest resilience is generally conferred by regenerative capacity *via* biological legacies (Franklin et al., 2000; Lindenmayer et al., 2019). These components of stability are supported by an ecosystem's adaptive capacity, or the capacity for adaptive change in response to new conditions (Angeler et al., 2019). For example, genetic diversity, species diversity, and phenotypic plasticity allow for varied and time-evolving expression of adaptive traits and species within an ecosystem in response to changing environmental conditions, disturbances, or other pressures (Savolainen et al., 2007; Reed et al., 2011; Rogers et al., 2017). Hence, adaptive capacity is supported by biodiversity (**Figure 1**).

Biodiversity

These foundational elements of integrity are derivatives of the underlying biodiversity of a forest ecosystem, including diversity at the genetic, species, and community levels (**Figure 1**). A wealth of literature provides evidence that biodiversity supports net primary productivity (Chapin et al., 1997; Diaz and Cabido, 2001; Hooper et al., 2005; Thompson et al., 2009; Tilman et al., 2014; Liang et al., 2016; Duffy et al., 2017; de Souza et al., 2019; Matos et al., 2020), adaptation (Steffen et al., 2015; King et al., 2019), resistance (Pimm, 1984; Walker, 1995; Ives et al., 1999; Lehman and Tilman, 2000; McCann, 2000; Loreau et al., 2002; Dorren et al., 2004; Hooper et al., 2005; Thompson et al., 2009; Hautier et al., 2015), resilience (Peterson et al., 1998; Loreau et al., 2001;

Hooper et al., 2005; Drever et al., 2006; Thompson et al., 2009; Ajani et al., 2013; Oliver et al., 2015; King et al., 2019), functional diversity (Cadotte et al., 2011; Levin, 2013; Karadimou et al., 2016), and overall ecosystem functioning (e.g., Lawton, 1997; Tilman, 1997; Hooper et al., 2005; Cardinale et al., 2012; Watson et al., 2018; King et al., 2019). These relationships exist because natural selection yields the characteristic biodiversity and phenotypic plasticity best suited to prevailing environmental conditions, including fluctuating resource inputs, extreme events, periods of stress, and natural disturbances. Specific mechanisms include biotic control of grazing, population density, and nutrient cycling; niche selection and complementarity; biotic and abiotic facilitation; and functional redundancy (i.e., the "insurance hypothesis") (e.g., Naeem et al., 1995; Tilman, 1996; Tilman et al., 1997; Yachi and Loreau, 1999; Loreau, 2000; Tilman and Lehman, 2001; Pretzsch, 2005; Scherer-Lorenzen and Schulze, 2005; Jactel and Brockerhoff, 2007; Thompson et al., 2009; Hantsch et al., 2014; Wright et al., 2017; Liu et al., 2018).

Ecosystem condition

The foundational elements of ecosystem integrity form the basis for assessing ecosystem condition (Keith et al., 2020), specifically in the context of the System of Environmental-Economic Accounting (Committee of Experts on Environmental-Economic Accounting, 2021). Ecosystem condition is defined as "the quality of an ecosystem that may reflect multiple values, measured in terms of its abiotic and biotic characteristics across a range of temporal and spatial scales" (Keith et al., 2020). Ecosystem condition is measured in terms of variables that reflect the state, processes, and changes in the ecosystem, including (i) carbon and nutrient stocks, (ii) abiotic physical and chemical states such as water quantity and quality; (iii) biotic composition, structure, and function; and (iv) landscape diversity and connectivity. Indicators of condition are derived when variables are transformed by assessment against a reference condition. For a given biome and prevailing environmental conditions, these state variables are optimized by the foundational elements of ecosystem integrity and biodiversity (Phillips et al., 1994; Thompson et al., 2009; Roche and Campagne, 2017; Di Marco et al., 2018; Liu et al., 2018).

Ecosystem services

Characteristics of ecosystem condition that relate to the supply of ecosystem services represent an instrumental anthropocentric dimension. Specific ecosystem services can be linked to characteristics of ecosystem condition, and condition indicators can be associated with multiple services (Keith et al., 2020). Ecosystem services can be broadly categorized as regulating, provisioning, and cultural services (Millennium Ecosystem Assessment, 2005; Kandziora et al., 2013; IPBES, 2019; Committee of Experts on Environmental-Economic Accounting, 2021). Regulating services include clean and regulated water flow, air quality, pest and pathogen containment, erosion control, nutrient regulation, resistance and resilience to natural hazards, waste regulation, carbon sequestration and storage, and climate regulation from local to global scales. Provisioning services include the animals, plants, and minerals used for food, medicine, energy, and infrastructure. Cultural services include customary values, ecotourism and nature-based recreation, scientific research, and education.

The concept of ecosystem integrity is useful because it integrates across many properties of forest ecosystems, and thereby optimizes values useful to humans and other organisms. In the words of Koff et al. (2016), "ecosystem integrity is a scientific paradigm that fits the political needs of the present global development agenda focused on complex human-environmental interactions." The concept is holistic and can be adapted to local, national, or international contexts. At jurisdictional levels, the related concepts of "ecological integrity" and "biological integrity" have been used operationally to provide benchmarks for natural resource management (Karr, 1996; Harwell et al., 1999; Campbell, 2000; Muller et al., 2000; Parrish et al., 2003; Tierney et al., 2009; Wurtzebach and Schultz, 2016; Roche and Campagne, 2017). However, as noted above, the international policy community has yet to implement these terms. This is important because ecosystem integrity may be directly linked to forest and carbon risk profiles that, if understood and prioritized, could greatly aid our ability to utilize forests for mitigation and adaptation.

Comparison of ecosystem integrity between forest types

Here, we compare components of ecosystem integrity most relevant for international policy across commonly recognized broad categories of forest types, focusing on primary forests and forests with significant levels of human modification and pressure. We focus on components of ecosystem integrity most pertinent to forest-based climate mitigation, including forest risk profiles as governed by exposure and stability as well as carbon stocks and fluxes. As noted previously, direct comparisons between forest types must account for environmental and site drivers, including the prevailing biome (e.g., tropical, temperate, or boreal) and heterogeneity within as determined by climate, soils, hydrology, and natural disturbance regimes.

Following Kormos et al. (2018), Food and Agriculture Organization of the United Nations [FAO] (2020), and IUCN (2020), primary forests are defined as: (i) largely undisturbed by industrial-scale land uses such as logging, mining, hydroelectric development, and road construction; (ii) established and regenerated by natural biological, ecological, and evolutionary processes; (iii) including the full range of successional stages at a landscape level from pioneer, secondary growth, and old-growth forest stands; and (iv) with the vegetation structure, community networks, and taxonomic composition principally reflecting natural processes including natural disturbance regimes. Primary forests can therefore be distinguished from naturally regenerating forests that are subject to conventional forestry management for commodity production (Puettmann et al., 2015), as well as planted forests, including plantations. For our purposes, primary forest therefore encompasses a range of commonly recognized forest descriptors including intact, virgin, ecologically mature, and old growth forests (Buchwald, 2005; Mackey et al., 2013; DellaSala et al., 2022b).

Foundational elements of ecosystem integrity

Comparison of dissipative structures

In this section we focus on structural complexity because of its importance for carbon stocks. Other components of dissipative structures (**Figure 1**) will be highlighted for their role in supporting ecosystem integrity in following sections (including functional diversity as it relates to biodiversity in the section "Biodiversity," and stored emergy as manifested in biomass and carbon stocks in section "Ecosystem condition"). High-integrity forests that have been allowed time to respond to their emergy signature develop a set of relatively complex ecosystem structures (Campbell, 2000). Canopy structure is particularly influential for other elements of ecosystem integrity such as microclimate, runoff, nutrient cycling, and biodiversity (Hobbie, 1992; Parker, 1995; Didham and Lawton, 1999; Siitonen, 2001; Asner et al., 2010; Goetz et al., 2010; Hansen et al., 2014). Primary tropical forests in particular develop tall, multi-story dense canopies with large variations in plant size and emergent canopy dominants (Kricher, 2011; Hansen A. J. et al., 2020). Temperate forests also develop complex forest canopies as they age, which is associated with high levels of biodiversity and carbon storage (DellaSala et al., 2022b).

Canopy height, in turn, is positively related to aboveground biomass and carbon storage. For example, in Brazil, Democratic Republic of the Congo, and Indonesia, primary forests were 38–59% taller and contained 70–148% more aboveground biomass than other dense tree cover types, including degraded forests, secondary regrowth, and tree plantations (Turubanova et al., 2018). When felling the largest trees or clear-cutting entire stands, logging decreases canopy height, homogenizes forest canopies, and reduces structural complexity (Pfeifer et al., 2016; Rappaport et al., 2018; Bourgoin et al., 2020), which can take centuries to recover. Structural complexity also relates to non-living forest structures, such as dead wood, that provide supporting functions including nutrient cycling, soil formation, and habitat for myriad species (Janisch and Harmon, 2002; Millennium Ecosystem Assessment, 2005; Gamfeldt et al., 2013). When directly compared, primary forests consistently contain a greater volume and diversity of dead wood than forests managed for commodity production (e.g., Guby and Dobbertin, 1996; Siitonen et al., 2000; Siitonen, 2001; Debeljak, 2006).

Comparison of ecosystem processes

Here we focus on ecosystem productivity given its importance for climate mitigation, but note that other ecosystem processes will be highlighted in following sections (evapotranspiration as it relates to drought risk in section "Comparison of risks from drought," reproduction cycles as they relate to regeneration in section "Comparison of regenerative capacity," and nutrient cycling and retention as it relates to nutrient stocks in section "Comparison of ecosystem condition"). Differences in ecosystem productivity and carbon fluxes among forest seral stages have been the subject of much debate. One viewpoint is that forests containing younger trees are more productive, with both higher net primary productivity (NPP, including photosynthesis and autotrophic respiration) and net ecosystem productivity (NEP, also including heterotrophic respiration) than ecologically mature forests (e.g., Ryan et al., 1997; Simard et al., 2007; Goulden et al., 2010). This view has often justified the conversion of primary forests into regrowth forests. While it is true that secondary forests often have higher rates of photosynthesis, this is not always the case, particularly when accounting for the impacts of higher species richness in older primary forests (Liu et al., 2018) and the entire age profile of timber rotations, including times with bare soil and young trees. A wealth of evidence clearly shows that old-growth forests continue to sequester carbon in significant quantities in aboveground biomass, dead wood, litter, and soil organic matter (Phillips et al., 1998; Zhao and Zhou, 2006; Luyssaert et al., 2008; Lewis et al., 2009; Thompson et al., 2013; Gatti et al., 2014; Grace et al., 2014; McGarvey et al., 2015; Schimel et al., 2015; Lacroix et al., 2016; Baccini et al., 2017; Phillips and Brienen, 2017; Qie et al., 2017; Lafleur et al., 2018; Mitchard, 2018). This is why Pugh et al. (2019) found that old-growth forests (defined in that study as >140 years) cover roughly 39% of global forest area and contribute 40% of the current global forest carbon sink, which in turn represents roughly two-thirds of the terrestrial carbon sink (Friedlingstein et al., 2019).

More importantly, when comparing these CO_2 fluxes in the context of mitigation actions, the entire life cycle of management and disturbance must be taken into account. From a carbon balance perspective, converting primary forests into young forests logged for biomass energy, wood supply, or other uses does not offset the original conversion emissions for many decades to centuries (Cherubini et al., 2011; Holtsmark, 2012; Mitchell et al., 2012; Keith et al., 2015; Birdsey et al., 2018; Hudiburg et al., 2019; Malcolm et al., 2020), creating a large carbon debt on policy-relevant timescales (generally years to 1–3 decades). Hence the size, longevity, and stability of accumulated forest carbon stocks, including in the soils, are important mitigation metrics in addition to the rate of annual sequestration (Mackey et al., 2013; Keith et al., 2021).

Stability and risk profiles

Ecosystem stability is comprised of resistance, resilience, and longer-term persistence (**Figure 1**). Combined with exposure to external perturbations, properties of ecosystem stability provide critical information for risk assessments. Risk assessments are undertaken and utilized in a wide variety of scientific and operational contexts (Fussel and Klein, 2006; Glick et al., 2011; Oppenheimer et al., 2014; Rogers et al., 2017), and are critically important to ensure mitigation actions result in long-term carbon storage. Nevertheless, risk assessments are currently either not undertaken or done so in mostly rudimentary and incomplete ways for forest-based carbon mitigation (Mignone et al., 2009; Ajani et al., 2013; Anderegg et al., 2020). Here we focus on the risk of a forest ecosystem experiencing a state-altering disturbance that results in carbon loss to the atmosphere.

Comparison of risks from wildfire

Wildfires are major natural disturbances in temperate and boreal forest ecosystems, although historically rare in tropical wet forests unless caused by humans (Randerson et al., 2012; Archibald et al., 2013; Giglio et al., 2013; Andela et al., 2017). The area burned by wildfire has been increasing in high-canopy cover forests globally over the past 20 years (Andela et al., 2017), and human-caused fires are a major driver of the loss of intact forest landscapes (Potapov et al., 2017). Extreme fire weather conditions have increased in most forests globally over the last half-century (Jolly et al., 2015; Jain et al., 2017; Dowdy, 2018), and wildfires are projected to become more widespread and intense due to climate change (Ward et al., 2012; Flannigan et al., 2013; Abatzoglou et al., 2019; Dowdy et al., 2019; Rogers et al., 2020). Humans have increased forest fire risk by augmenting forest fuels through active management (DellaSala et al., 2022a) and by increasing the number and sources of ignition (Balch et al., 2017). The majority of documented megafires globally have been started by humans under extreme fire weather conditions (Ferreira-Leite et al., 2015; Bowman et al., 2017).

A large body of literature shows that forests managed for commodity production, degraded, or disturbed forests are generally more susceptible to fires because of drier microclimates and fuels, higher land surface temperatures that promote air movement between forests and neighboring open areas, and human ignitions due to access and proximity, particularly in the tropics (e.g., Uhl and Kauffman, 1990; Holdsworth and Uhl, 1997; Cochrane et al., 1999; Laurance and Williamson, 2001; Siegert et al., 2001; Donato et al., 2006; Lindenmayer et al., 2009, 2011; Brando et al., 2014; DellaSala et al., 2022a). Although fires are a natural disturbance agent throughout most boreal forests (Viereck, 1973; Payette, 1992; Gromtsev, 2002; Soja et al., 2007; Rogers et al., 2015), fire frequency in boreal forests increases in proximity to human land use due to fuel drying, human access, and forestry practices such as leaving slash on site, particularly in Siberia (Kovacs et al., 2004; Achard et al., 2008; Ponomarev, 2008; Laflamme, 2020; Terrail et al., 2020; Shvetsov et al., 2021).

In many forest systems, fires in previously logged or managed landscapes can be more intense/severe, emit more carbon to the atmosphere, and take longer to recover than fires in ecologically mature or primary forests due to increased fuel availability, lower fuel moisture, and dense secondary forests that carry crown fires and are susceptible to extensive tree mortality (Odion et al., 2004; Stone et al., 2004; Thompson et al., 2007; Lindenmayer et al., 2009, 2011; Price and Bradstock, 2012; Kukavskaya et al., 2013; Taylor et al., 2014; Bradley et al., 2016; Dieleman et al., 2020; De Faria et al., 2021; Landi et al., 2021). In general, larger and older trees have a greater chance of surviving fires due to thicker bark and lower relative scorch height (Laurance and Williamson, 2001; Lindenmayer et al., 2019). Increased fuel availability in secondary forests can also facilitate fire spread (Lindenmayer et al., 2011). Positive feedbacks between fires and secondary vegetation can lead to permanent forest loss, i.e. "landscape traps," at the warm / dry edge of forest ranges (Payette and Delwaide, 2003; Hirota et al., 2011; Lindenmayer et al., 2011; Staver et al., 2011; Brando et al., 2014; Kukavskaya et al., 2016; Lindenmayer and Sato, 2018). Primary forests are generally more resistant to fire because of higher humidity and fuel moisture, the presence of understory species such as ferns and mosses that limit light penetration to the forest floor and increase water retention, and much less human access (Ough, 2001; Lindenmayer et al., 2009; Taylor et al., 2014; Zylstra, 2018; Funk et al., 2019).

Comparison of risks from drought

Severe droughts represent 60–90% of climate extremes impacting gross primary productivity in the past 30 years (Zscheischler et al., 2014), are a major driver of tree mortality and forest die-off (Allen et al., 2010, 2015; Anderegg et al., 2013; McDowell and Allen, 2015; McDowell et al., 2016; Rogers et al., 2018), and are expected to increase with future climate change (Cook et al., 2014; Trenberth et al., 2014; Yi et al., 2014; Xu et al., 2019; Zhou et al., 2019; De Faria et al., 2021). A large body of literature indicates closed canopy forests are more resistant to drought, particularly in the tropics, due to shading, biophysical microclimate buffering, thicker litter layers, deeper roots, and increased water use efficiency as trees develop (e.g., Briant et al., 2010; von Arx et al., 2013; Frey et al., 2016; Brienen et al., 2017; Qie et al., 2017; Giardina et al., 2018; Caioni et al., 2020; Elias et al., 2020). For a given level of realized drought, some evidence points to larger older trees being more susceptible to drought impacts (Phillips et al., 2010; Girardin et al., 2012; Bennett et al., 2015; McDowell and Allen, 2015; McIntyre et al., 2015; Chen et al., 2016; Clark et al., 2016). Yet there is also contrasting evidence. For example, younger boreal forests can be more susceptible to drought compared to mature forests (Luo and Chen, 2013; Hember et al., 2017) due to competition for space and nutrients and less extensive and shallower root systems. Tree diversity, which is generally higher in primary compared to human-modified forests (see section "Biodiversity"), may increase resistance and resilience to drought *via* adaptive responses and functional redundancy (Jump et al., 2009; Sthultz et al., 2009; Dale et al., 2010; Harter et al., 2015), and intact forest canopies can be relatively resistant and resilient to short-term climate anomalies including drought (Williamson et al., 2000; Saleska et al., 2007). Evidence also suggests that mechanical "thinning," which is frequently proposed and implemented to combat drought, decreases stand-level water use in the short-term but actually increases individual tree water demand *via* higher leaf-to-sapwood ratios and hence drought vulnerability in the long-term (McDowell et al., 2006; Kolb et al., 2007; D'Amato et al., 2013; Clark et al., 2016).

Mature forests transpire large quantities of water from relatively deep in the soil profile, increasing regional cloud cover and precipitation. This acts to increase the proportion of "recycled" water within a given region and thereby decreases the prevalence of regional droughts (Foley et al., 2007; Spracklen et al., 2012; Ellison et al., 2017). For example, air passing over intact tropical forest landscapes can contain twice the moisture content as air over degraded forests or non-forest landscapes (Sheil and Murdiyarso, 2009). Degradation and the loss of intact forest landscapes increases dry and hot days, decreases daily rainfall intensity and levels, and exacerbates regional droughts (Deo et al., 2009; Alkama and Cescatti, 2016).

Comparison of risks from pests and pathogens

Pests and pathogens are an increasing threat to many forests globally, particularly as climate change alters life cycles, potential ranges, and host-pest interactions (Carnicer et al., 2011; Kautz et al., 2017; Seidl et al., 2017; Simler-Williamson et al., 2019). Mature boreal and temperate forests can be more susceptible to pests and pathogens compared to younger forests, in part due to decreases in the resin flow of defense compounds (Christiansen and Horntvedt, 1983; Hansen and Goheen, 2000; Baier et al., 2002; Dymond et al., 2010). Prominent examples include bark beetle and defoliator susceptibility (Kurz et al., 2008; Raffa et al., 2008; Taylor and MacLean, 2009; Krivets et al., 2015; Kautz et al., 2017). Nevertheless, ecologically mature forests tend to be resilient to biotic infestations, as these cyclical events initiate succession and lead to stand- and landscape-level heterogeneity (Holsten et al., 2008; Thompson et al., 2009). Moreover, tree diversity (measured in terms of genetic, species, and age) tends to limit pest and pathogen spread and damage because of resource dilution, host concealment, phenological mismatches, increased predators and parasitoids, alternative hosts, and metapopulation dynamics (Root, 1973; Karieva, 1983; Pimm, 1991; Watt, 1992; Zhang et al., 2001; Jactel et al., 2005; Pautasso et al., 2005; Scherer-Lorenzen and Schulze, 2005; Thompson et al., 2009; Guyot et al., 2016).

In terms of human influence, anthropogenic disturbances such as selective logging can introduce forest pests and diseases (Gilbert and Hubbell, 1996), including non-native, and evidence suggests forest edges and logged forests are more susceptible to beetle attacks due to increases in available host niches and altered moisture conditions (Sakai et al., 2001). Many pests, particularly in temperate and boreal forests, take advantage of weakened tree defenses during drought (Raffa et al., 2008; McDowell et al., 2011; Anderegg and Callaway, 2012; Hicke et al., 2012; Keith et al., 2012; Poyatos et al., 2013; Anderegg et al., 2015). Monocultures, or tree plantations, have been shown to be particularly vulnerable due to a lack of tree diversity, high tree density, and the associated host-pest interactions (Jactel et al., 2005; Macpherson et al., 2017; Lee, 2018).

Comparison of risks from windthrow

Windthrow events can lead to forest mortality and are expected to increase in some regions with climate change (Klaus et al., 2011; Saad et al., 2017). Although these events are somewhat stochastic, they are also influenced by soils, orography, regional climate regimes, and forest composition and structure. Similar to the risks of pests and pathogens, within a given stand there is evidence that older and taller trees are more susceptible to windthrow due to the physics of taller trees and root rot (Lohmander and Helles, 1987; Ruel, 1995). Nevertheless, fragmented or thinned forests experience elevated mortality and collapse of trees from windthrow because of increased exposure (Laurance and Curran, 2008; Reinhardt et al., 2008; Schwartz et al., 2017).

Comparison of risks from species range shifts

Climate regimes have strong influences on the potential and realized ranges of forest tree species, evidenced by the paleoecological record (Overpeck et al., 1991; DeHayes et al., 2000; Davis and Shaw, 2001) and current assemblages (e.g., Neilson, 1995; Foley et al., 2000), and considerable scientific effort is focused on projecting future responses to climate change (e.g., Sitch et al., 2003; Elith and Leathwick, 2009; Rogers et al., 2011, 2017; Ehrlen and Morris, 2015; Prasad et al., 2020). How trees and forest ecosystems will respond is uncertain due to complex interactions between the pace of climate change, physiological tolerances, dispersal and migration rates, phenotypic plasticity and adaptation, the presence of climate refugia, migration of associated species / symbionts, and forest fragmentation, among others (Davis and Shaw, 2001; Iverson et al., 2004; Jump and Penuelas, 2005; Mackey et al., 2008; Nicotra et al., 2010; Prasad, 2015; Rogers et al., 2017). In general, current and projected climate change is expected to degrade biodiversity due to species extinctions and the contraction of realized ranges (Miles et al., 2004; Campbell et al., 2009). Forest and landscape fragmentation in particular is known to hinder resilience and species migration because of the loss of suitable areas for dispersal and limitations on gene flow (Collingham and Huntley, 2000; Loreau et al., 2002; Scheller and Mladenoff, 2008; Thompson et al., 2009). Large areas of primary forests are expected to have higher adaptive capacity and stability compared to forests under human pressure because of their connectivity, biodiversity, and microclimate buffering (Mackey et al., 2015; Watson et al., 2018; Thom et al., 2019; see section "Biodiversity").

Comparison of risks from land use degradation

Human land use pressures on forests generally result in both direct environmental impacts as well as further, often unplanned, degradation or deforestation that accumulates spatially and temporally. This is exemplified by the fact that smaller fragments of primary forest have an elevated likelihood of loss (Hansen M. C. et al., 2020). New roads are the primary driver of further degradation as a result of their construction, use, and continued access (e.g., Trombulak and Frissell, 2000; Wilkie et al., 2000; Laurance et al., 2009; Laurance and Balmford, 2013; Ibisch et al., 2016; Alamgir et al., 2017; Venier et al., 2018; Maxwell et al., 2019). Roads render the surrounding forests much more susceptible to agricultural conversion (Asner et al., 2006; Boakes et al., 2010; Gibbs et al., 2010; Laurance et al., 2014; Kormos et al., 2018), logging (Laurance et al., 2009; Barber et al., 2014), and expanded networks of secondary and tertiary roads (Arima et al., 2008, 2016; Ahmed et al., 2014). Logging and transportation can also lead to severe erosion and nutrient runoff, impacting downstream water quality and quantity (Carignan et al., 2000; Hartanto et al., 2003; Foley et al., 2007), and damage the surrounding forest. For example, in the Amazon, it has been estimated that for every commercial tree removed *via* selective logging, roughly 40 m of roads are created, nearly 30 other trees greater than 10 cm in diameter are damaged, and between 600 and 8,000 m^2 of canopy is opened (Holloway, 1993; Asner et al., 2004). Furthermore, roads reduce animal habitat, are barriers to animal movement and lead to increased animal mortality, including from unregulated hunting, all of which decrease connectivity and genetic exchange (Dyer et al., 2002; Frair et al., 2008; Laurance et al., 2009; Taylor and Goldingay, 2010; Clements et al., 2014). One consequence is a decline in carbon-dense tree species due to overhunting of seed-dispersing animals (Osuri et al., 2016; Maxwell et al., 2019). It is important to note that roughly 95% of deforestation in the Amazon occurs within 5.5 km of a road (Barber et al., 2014), and that illegal logging represents 85–90% of all logging in the tropics (Lawson and MacFaul, 2010; Lawson, 2014; Hoare, 2015) and still roughly one-quarter of logging in Russia (Food and Agriculture Organization of the United Nations [FAO], 2012; Kabanets et al., 2013), which contains the largest areal forest coverage of any country (Food and Agriculture Organization of the United Nations [FAO], 2020). Overall, road building and industrial logging are the largest drivers of initial forest degradation and fragmentation (Hosonuma et al., 2012).

In addition to their direct impacts, roads and land use further degrade forests due to edge effects. Forests at or near an edge can have substantially drier microclimates, increased windshear and movement of dry air into forests, invasive species (dispersed *via* roads and more favorable microclimate conditions for competition), weeds and vines, sun exposure, soil erosion, and fuel loads due to drying and previous logging and fire (Laurance and Williamson, 2001; Mortensen et al., 2009; Brando et al., 2014). This leads to a variety of unfavorable impacts and further risks. Carbon densities tend to be significantly lower near forest edges. For example, biomass is reduced by roughly 50% within 100 m, 25% within 500 m, and 10% within 1.5 km of a forest edge (Laurance et al., 1997; Chaplin-Kramer et al., 2015; Maxwell et al., 2019). Aggregated across the tropics, edge effects are estimated to account for up to one quarter of all carbon loss from tropical deforestation (Putz et al., 2014). Primary productivity is also generally lower near forest edges, and fire susceptibility is higher due to elevated and drier fuel loads and increased human access (Laurance et al., 1998; Cochrane et al., 1999; Nepstad et al., 1999; Laurance and Williamson, 2001; Foley et al., 2007; Adeney et al., 2009; Brando et al., 2014). For example, roads are strong predictors of ignition and wildfire frequency in temperate forests (Hawbaker et al., 2013; Faivre et al., 2016; Parisien et al., 2016; Balch et al., 2017; Ricotta et al., 2018), and road expansion in Siberia has been shown to promote logging and human-caused forest fires (Kovacs et al., 2004). A variety of ecosystem services are degraded due to edge effects, including hydrologic regulation, water quality, modulation of regional climate, and amelioration of infectious diseases (Laurance and Williamson, 2001; Foley et al., 2007). Although the impacts are strongest at a forest edge, the effects can generally be detected up to 2 km from the edge, with higher tree mortality up to 1 km and wind disturbance up to 500 m (Broadbent et al., 2008). Globally, fragmentation is thought to be at a critical threshold, with roughly 70% of the world's forest within 1 km of a human-created forest edge (Haddad et al., 2015; Taubert et al., 2018).

Comparison of regenerative capacity

Ecosystem resilience is underpinned by the natural regenerative capacity of a forest ecosystem, and hence represents a major component of ecosystem stability and integrity (**Figure 1**). Regeneration from major disturbance events requires biological legacies, which are broadly defined as the remaining living and dead structures and organisms that can influence recovery (Franklin et al., 2000; Jogiste et al., 2017). These include living and dead trees, shrubs and other plants, seeds, spores, fungi, eggs, soil communities, and living animals (Franklin et al., 2000; Stahlheber et al., 2015; Lindenmayer et al., 2019). Compared to secondary or human-modified forests, primary forests tend to have the biological legacies (Catterall, 2016; Chazdon and Uriarte, 2016; Lu et al., 2016; Poorter et al., 2016; Lindenmayer et al., 2019) and favorable microclimates (von Arx et al., 2013) required for optimal regeneration. This is evidenced by the fact that secondary forest regeneration is aided by proximity to primary forests (Schwartz et al., 2015; Kukavskaya et al., 2016). Clearcut logging also generates low levels of biological legacies and higher regeneration failures after subsequent fires compared to forests not previously logged (Perrault-Hebert et al., 2017), which is exacerbated by post-fire "salvage" logging (Donato et al., 2006; Lindenmayer et al., 2019). Successive disturbances continue to decrease regenerative capacity, and can lead to permanent forest loss and emergence of non-forest ecosystems (Payette and Delwaide, 2003; Johnstone et al., 2016; Kukavskaya et al., 2016). Compared to degraded or human-modified forests, primary forests with large extents also host a much larger array of seed dispersers and pollinators (Muller-Landau, 2007; Wright et al., 2007; Abernethy et al., 2013; Harrison et al., 2013; Peres et al., 2016).

Comparison of biodiversity

Biodiversity underpins and is affected by the foundational elements of ecosystem integrity (**Figure 1**), but is also a metric of ecosystem condition and can be considered an ecosystem service in its own right. Globally, trees are among the most genetically diverse of all organisms, and forests collectively support the majority (roughly 80%) of terrestrial biodiversity (Hamrick and Godt, 1990; Barlow et al., 2007; Pimm et al., 2014; Federici et al., 2017). There is a substantial body of literature on the effects of disturbance and stand age on biodiversity, with some disagreement among studies depending on context (e.g., Paillet et al., 2010; Edwards et al., 2011; Moreno-Mateos et al., 2017; Kuuluvainen and Gauthier, 2018; Matos et al., 2020). Nevertheless, there are clear and definitive negative impacts of human disturbance and land use on biodiversity (Cairns and Meganck, 1994; Ellison et al., 2005; Barlow et al., 2007, 2016; Gibson et al., 2011; Alroy, 2017; Giam, 2017). Primary and ecologically mature forests typically harbor higher biodiversity than human-modified forests (Lesica et al., 1991; Herbeck and Larsen, 1999; Rey Benayas et al., 2009; Zlonis and Niemi, 2014; Miller et al., 2018; Watson et al., 2018; Lindenmayer et al., 2019; Thom et al., 2019), especially in the understory (e.g., Lafleur et al., 2018). Disturbance generally results in a change in species composition toward early pioneer species (e.g., Bawa and Seidler, 1998; Liebsch et al., 2008; Venier et al., 2014). The effect of human activities on the provision of ecosystem services is evident even if there is little change in the overall forest cover. Degradation in logged forests can be in the form of structural changes such as reduction in old age classes of trees that can cause loss in breeding habitat, particularly for birds (Rosenberg et al., 2019; Betts et al., 2022), and compositional changes such as shifts in tree species abundance that differ in foliar nutrient concentrations that support arboreal folivores (Au et al., 2019). Under less intensive agriculture management, agroforestry can maintain a significant fraction of biodiversity, but it is still considerably lower than in native forests (De Beenhouwer et al., 2013; Vallejo-Ramos et al., 2016).

Biodiversity analyses are also strongly dependent on spatial scale, whereby higher levels of management and disturbance homogenize forest composition and age structure across the landscape, and consequently the biota it supports (e.g., Devictor et al., 2008; de Castro Solar et al., 2015; Tomas Ibarra and Martin, 2015). What can be concluded is that (i) degraded and intensively managed forests tend to harbor lower biological and functional diversity compared to primary forests, which support many as yet unidentified species and act as repositories for species that cannot survive in secondary or degraded forests (Barlow et al., 2007; Gibson et al., 2011), and (ii) natural disturbances are effective at maintaining landscape heterogeneity and the species that depend on disturbed and young forests (Lindenmayer et al., 2019). Global biodiversity loss is currently orders of magnitude higher than background rates and is driven primarily by deforestation and forest degradation (Newbold et al., 2016; Giam, 2017). It is worth noting that although natural tree diversity in boreal forests is typically much lower than in temperate or tropical forests (Thompson et al., 2009; Hill et al., 2019), the biodiversity of other species groups such as bryophytes and lichens can be very high (DellaSala, 2011; Kuuluvainen and Gauthier, 2018), functional diversity in boreal forests is generally high (Esseen et al., 1997; Wirth, 2005), and the broad genetic variability and phenotypic plasticity of boreal trees allows them to tolerate a wide range of environmental conditions (Gordon, 1996; Howe et al., 2003).

Comparison of ecosystem condition

Given our focus on climate mitigation, the primary metric of concern for ecosystem condition is carbon stocks. Primary and ecologically older forests have been consistently found to have the highest carbon stocks compared to secondary, degraded, intensively managed, or plantation forests (e.g., Harmon et al., 1990; Cairns and Meganck, 1994; Nunery and Keeton, 2010; Burrascano et al., 2013; Mackey et al., 2013; Keith et al., 2015, 2017; Federici et al., 2017; Lafleur et al., 2018; Watson et al., 2018). For example, a recent meta-analysis shows that primary tropical forests store on average 35% more carbon than forests affected by conventional management for commodity production (Mackey et al., 2020). Across the tropics, intact forest landscapes cover approximately 20% of total area but store 40% of total aboveground biomass (Potapov et al., 2017; Maxwell et al., 2019). This is fundamentally a function of where carbon is stored in these forests. In wet tropical and some temperate primary forests, roughly half the biomass carbon is stored in the largest 1–3% diameter trees (Stephenson et al., 2014; Lutz et al., 2018; Mildrexler et al., 2020), which have long residence times (Koerner, 2017; van der Sande et al., 2017), and are typically the first to be felled (Cannon et al., 1998; Sist et al., 2014; Gatti et al., 2015; Rutishauser et al., 2016). Agricultural landscapes store comparatively less carbon, but the addition of trees *via* agroforestry has the potential to add up to 9 Pg C globally (Chapman et al., 2020). In boreal forests, especially those that are poorly drained, the majority of forest ecosystem carbon is stored in dead biomass, peat, and soil organic layers that accumulate over the course of forest succession, often protected by permafrost (Deluca and Boisvenue, 2012; Bradshaw and Warkentin, 2015; Lafleur et al., 2018; Walker X J et al., 2020). Boreal forests managed for timber are kept at younger ages, with soils that store significantly less carbon due to mechanical disturbance, tree species conversion, and impacts on litter composition, nutrient cycling, and bryophyte communities (Liski et al., 1998; Jiang et al., 2002; Seedre et al., 2014; Lafleur et al., 2018). Even outside the boreal zone, soil carbon can be a significant fraction of total ecosystem carbon (e.g., Keith et al., 2009), and logging activities generally deplete forest soil carbon due to soil compaction and disturbance, erosion, changes in microclimate that increase respiration rates, reduced leaf litter and root exudates, loss of micorrhizal network carbon, and post-logging "slash" burning (Rab, 2004; Zummo and Friedland, 2011; Buchholz et al., 2014; James and Harrison, 2016; Hume et al., 2018; Mayer et al., 2020). Globally, forests are thought to store only half of their potential carbon stock, with 42–47% of the reduction due to forest management and modification (the remainder being deforestation and land cover changes; Erb et al., 2018). Natural regeneration of forests could in turn restore 123 Pg C, or 27% of the total biomass carbon that has been lost (Erb et al., 2018).

Forest management, degradation, and conversion can also result in the loss of key nutrients such as nitrogen and phosphorous, among others, which are otherwise retained efficiently in undisturbed forests (Likens et al., 1970; Markewitz et al., 2004; Olander et al., 2005; Liu et al., 2019). Nutrients can be artificially added, but heavily managed systems require large inputs to maintain their state and productivity capacity (Noss, 1995; Merino et al., 2005; Pandey et al., 2007). Other elements of ecosystem condition are affected similarly and highlighted elsewhere (landscape connectivity / fragmentation in section "Comparison of risks from land use degradation," biodiversity in section "Comparison of biodiversity," and water quality and quantity in section "Comparison of ecosystem services").

Comparison of ecosystem services

A large body of literature indicates the higher number, quality, and value of ecosystem services provided by primary forests compared to human-modified forests and landscapes. These include regulating services such as water quality and quantity (DellaSala, 2011; Brandt et al., 2014; Keith et al., 2017; Kormos et al., 2018; Taylor et al., 2019; Vardon et al., 2019); carbon storage and sequestration as an ecosystem service of global climate regulation (United Nations [UN], 2021) [discussed above, but see Keith et al. (2019) and Uganda Bureau of Statistics [UBOS] (2020) for examples using Ecosystem Accounts]; local to regional biophysical cooling (Spracklen et al., 2012; Lawrence and Vandecar, 2015); regulation of runoff, sediment retention, erosion control, and flood mitigation (Hornbeck and Federer, 1975; Jayasuriya et al., 1993; Dudley and Stolton, 2003; Furniss et al., 2010; van Haaren et al., 2021); provisioning services such as abundance of game and fish (Gamfeldt et al., 2013; Brandt et al., 2014); cultural services such as landscape aesthetics, recreation, and tourism (Brandt et al., 2014; Brockerhoff et al., 2017); cultural practices and knowledge (Normyle et al., 2022); contributions to physical and psychological health (Stier-Jarmer et al., 2021); and general assessments across a suite of services (e.g., Myers, 1997; Harrison et al., 2014; Shimamoto et al., 2018; Maes et al., 2020).

For example, a detailed assessment of the differences between primary forests and post-logging regrowth forests in terms of their ecosystem condition, the physical supply of a suite of ecosystem services, and their monetary valuation showed the superior aggregated value of the primary forest (Keith et al., 2017). The impacts of mechanical disturbance due to logging, roading, and mining on soil properties reduce the ecosystem services of soil nutrient availability, water holding capacity and erosion prevention (Hamburg et al., 2019). A general assessment of the total economic value of ecosystem services provided by forest ecosystem types showed that primary forests had a higher median value (USD 139 ha^{-1} $year^{-1}$) compared with secondary forests (USD 128 ha^{-1} $year^{-1}$) (Taye et al., 2021). These aggregated values include only the market values for services when known and could not account for non-market values, for example that would be needed to assess biodiversity habitat or many cultural services. The highest reported values for specific ecosystem services were for airflow regulation, water cycle regulation and food for freshwater plants and animals. These services would all have their highest provision from natural ecosystems. In contrast, the value of timber and fiber products is significantly lower.

Lessons from comparative analysis

Taken as a whole and for a given set of environmental conditions, our comparative analysis shows that primary forests have the highest levels of ecosystem integrity compared to human-modified forests, including naturally regenerating forests managed for commodity production, plantations, and previously forested landscapes. One primary set of mechanisms are positive feedbacks whereby forest disturbance tends to beget more disturbance (e.g., Seidl et al., 2017), and degradation begets more degradation (e.g., Venier et al., 2018; Watson et al., 2018). In terms of variables most relevant for mitigation, adaptation, and other international forest policy goals, primary forests store the highest carbon stocks, present the lowest risks of forest and carbon loss reversal, have the highest biodiversity, and provide the largest stocks of ecosystem assets and highest quality flows of ecosystem services, including benefits to the global community, local communities (Vickerman and Kagan, 2014), and Indigenous peoples.

Based on our review, and because human-modified forests can encompass a wide range of management strategies and intensities, we provide further summaries of ecosystem integrity for five main categories of forest types: (A) primary forests; (B) secondary forests; (C) production forests; (D) agro-forests; and (E) plantations (**Figure 2** and **Table 1**). Primary forests have the most developed dissipative structures, the highest levels of ecosystem processes, greater stability and recovery, and thus greater resilience and the lowest risk of loss and damage. As defined here, secondary forests are in recovery from past human impacts especially logging. Although they can transition to primary forests over time, these forests lack some old growth characteristics, are more vulnerable to wildfire and other natural disturbances, and have missing elements of biodiversity. Production forests are a result of conventional forest management for commodity production, and tend to be kept at relatively young ages with associated reductions in dissipative structures, carbon stocks, and resilience. An example of commercial agro-forests is shade coffee where retaining some natural canopy tree cover provides some additional ecosystem service benefits. Subsistence agro-forests are common in many tropical development countries such as Vanuatu where these household and community gardens were, and in many cases still are, the main source of food. Commercial plantations include monocultures of trees species that are essentially tree farms for commodity production (wood, palm oil). Note that there are gradients of human modification, stand age, and ecosystem integrity within these broad categories. For example, mature forests recovering from past human disturbances may not have the full suite of structural, functional, and compositional benefits as primary forests, but they can gain these over time, and generally have higher ecosystem integrity than forests

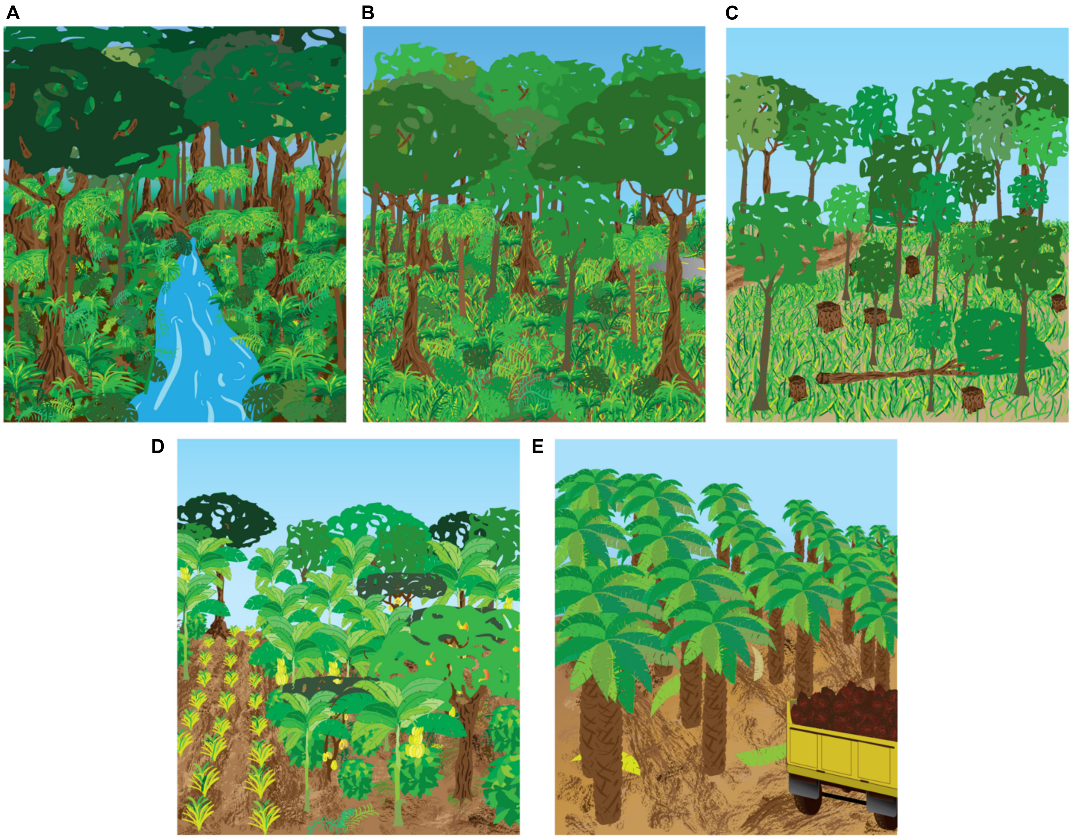

FIGURE 2
Graphical illustrations of five main forest types considered for ecosystem integrity comparisons, including **(A)** primary forests, **(B)** secondary forests, **(C)** production forests, **(D)** agro-forests, and **(E)** plantations. Note this illustration focuses on tropical forests, but the same general differences apply across forest biomes.

TABLE 1 Comparison of ecosystem integrity foundational elements between five main forest types.

Primary forest

- Naturally regenerated forest of native tree species, where there are no clearly visible indications of human activities and the ecological processes are not significantly disturbed
- Likely to have never been commercially logged or intensely managed
- At a landscape level, can comprise early successional (seral) stage following natural disturbances
- More likely to contain full complement of evolved natural biodiversity
- Often the customary territories of Indigenous Peoples

Dissipative structures	*● Ecosystem processes*	*● Stability and risk profiles*	*● Ecosystem integrity level*
● Canopy trees dominated by large, old trees ● In wet tropics, closed canopies ● Dense soil organic stocks ● Typically significant quantities of dead biomass	● Fully self-generating (autopoiesis) ● In temperate and boreal forests, includes seral stages following natural disturbances ● Tight nutrient cycling with minimal leakage and/or erosion ● Clean water supply	● Highly resistant and/or resilient to extreme weather events ● In boreal and temperate biomes, fire-adapted plant species ● Rich biodiversity provides functional and phenotypic adaptive capacity	● High levels for all three factors

Secondary forest

- Natural forests recovering from prior human land use impacts
- Canopies dominated by pioneer and secondary growth tree species
- If not subsequently disturbed by human land use, can continue to develop additional primary forest attributes over time

● Dissipative structures	*● Ecosystem processes*	*● Stability and risk profiles*	*Ecosystem integrity level*
● In wet tropics, canopy closure can occur within 1–2 decades ● Aboveground living significantly less than primary forests ● Some dead biomass may remain	● Fully self-regenerating so long as primary propagules/seed stock are available ● Soil carbon and nutrients stocks can be depleted due to past erosion and biomass removal	● In temperate and boreal forests, increased exposure to wildfire and drought impacts due to more open canopy and drier forest interior ● Reduced biodiversity impairs some key processes (e.g., pollination, top-down tropic control)	● Moderate depending on time since disturbance

Production forest

- The consequence of conventional forest management for commodity production (e.g., timber, pulp)
- Forest predominantly composed of trees established through natural regeneration, but management favors commercially valuable canopy tree species

● Dissipative structures	*● Ecosystem processes*	*● Stability and risk profiles*	*Ecosystem integrity level*
● Logging regimes maintain a predominantly even-aged, younger age structure (∼20–60 years) ● Simplified vertical vegetation structure	● Canopy tree species natural regenerated but some level of assisted regeneration common ● Ongoing soil loss	● More flammable forest conditions ● Greater exposure to invasive species	● Low to moderate depending on intensity of logging regimes and biodiversity loss

Agro-forestry (commercial, subsistence)

- Some level of natural tree species is maintained with subsistence food or commercial crops grown (e.g., shade coffee).
- Swidden subsistence farming commonly used by traditional communities
- Utilizes a mix of natural and assisted regeneration

Dissipative structures	*Ecosystem processes*	*Stability and risk profiles*	*Ecosystem integrity level*
● A curated canopy of trees, often remnant from primary forest or planted from local stock ● Little if any understory ● Ground cover are food crops	● In tradition swidden system, closed nutrient cycle through use of natural regeneration ● Canopy trees buffer food crops from extreme weather and help maintain soil moisture	● Intensive small-scale management and modest level of biodiversity provides assisted resilience and adaptive capacity	● Low to moderate given sufficient management inputs

(Continued)

TABLE 1 (Continued)

Commercial plantation			
• Forest predominantly composed of trees established through planting and/or seeding and intensely managed for commodity production (timber, pulp, plant oil)			
Dissipative structures	***Ecosystem processes***	***Stability and risk profiles***	***Ecosystem integrity level***
• Typically mono-cultures that are harvested at around a young age (~10–20 years)	• Soil water and nutrient retention • Can utilize natural pollinators from neighboring or remnant natural forests	• Exposed to extreme weather events, invasives, pests, and disease • Intensive large-scale management needed	• Low

recovering from more recent human disturbance (DellaSala et al., 2022b).

Implications for policy, management, and future research

Evaluating ecosystem integrity

We have shown that the risk of forest carbon loss can be minimized by prioritizing actions that maintain and enhance forest ecosystem integrity. Ecosystem integrity therefore has the potential to be used as an integrating framework for evaluating forest-based mitigation and adaptation actions. Because ecosystem integrity is an inherently complex concept, the scientific, management, and policy communities need approaches and tools to measure and interpret gradients of integrity consistently across forest types and jurisdictional boundaries (Karr, 1996; Grantham et al., 2020). The metrics and their interpretation should ideally account for the range of spatial and temporal scales involved: small patches of high-integrity forests are valuable, but landscape context is required; snapshots in time are useful, but longer-term dynamics are needed to fully understand integrity.

A complete and exhaustive global representation of forest ecosystem integrity may currently be beyond our reach. Nevertheless, several existing data products represent important elements of ecosystem integrity, each with their own advantages and limitations, and can be used to guide decision making. In the humid tropics, natural and hinterland forests (primary forests and mature secondary growth) have been mapped using multispectral satellite imagery (Turubanova et al., 2018) and spatial statistics (Tyukavina et al., 2016). Canopy structural integrity has recently been mapped using space-based lidar, multispectral imagery, and human pressure indices (Hansen et al., 2019; Hansen A. J. et al., 2020), representing an important step in delineating gradients of integrity. These mapping approaches are inherently more challenging outside the humid tropics where environmental gradients generate a range of potential forest cover and types. Global products therefore tend to rely more on metrics based on the relationships between forest loss/degradation and proximity to human activities, including roadless areas, forest fragmentation, loss of tree cover, and measures of the "human ecological footprint" (Hansen et al., 2013; Haddad et al., 2015; Ibisch et al., 2016; Venter et al., 2016b,a; Beyer et al., 2020; Grantham et al., 2020; Williams et al., 2020). Global Intact Forest Landscapes (Potapov et al., 2008, 2017) have been widely used, but these include patches of non-forest ecosystems and exclude areas of high-integrity forests in patches <50,000 ha. The Food and Agriculture Organization of the United Nations (FAO) has reported on primary forests since 2005 in their global forest assessment reports (Food and Agriculture Organization of the United Nations [FAO], 2020), but a lack of consistency in national-level reporting makes comparisons and trend detection difficult.

Similar to Grantham et al. (2020), we stress the importance of using local data and field observations to further identify and refine estimates of forest ecosystem integrity derived from coarser-scale global mapping products. These may include landscape-level metrics such as frequency distributions of stand age, biomass, coarse woody debris, biodiversity, forest patch sizes and shapes, and forest types and species composition. Individual countries have data archives, collection programs, and often agency directives that either include ecosystem integrity metrics or those with high relevance for integrity assessments (e.g., Muller et al., 2000; Tierney et al., 2009; Wurtzebach and Schultz, 2016). Applying the internationally endorsed SEEA-EA system should also enable a consistent framework for comparisons across spatial and temporal scales. The SEEA-EA standard provides guidance for classifications, definitions, spatially explicit analysis, and temporal consistency. Technical guidance on ecosystem integrity indicators was recently provided by Hansen et al. (2021). Although criteria were provided in the context of CBD's post-2020 Global Biodiversity Framework, many would apply outside this context, including a need for biome to global scale products with spatial resolution sufficient for management ($\leq$ 1 km), temporal re-assessment at intervals of 1–5 years, ability for indicators to be spatially aggregated without bias, credibility through validation and peer review, and accounting for reference states within a given climate, geomorphology, and ecology. Finally, we note the importance of understanding how any given metric of ecosystem integrity connects to the conceptual framework of ecosystem integrity (**Figure 1**).

Implementing ecosystem integrity

Protecting primary forests

Given the superior benefits of primary forests, follows that protecting them would significantly contribute to meeting international climate, biodiversity, and SDGs. Primary forests are disappearing at a rapid rate (e.g., Potapov et al., 2017; Food and Agriculture Organization of the United Nations [FAO], 2020; Hansen M. C. et al., 2020; Silva Junior et al., 2021) and urgently need higher levels of protection to ensure their conservation; only roughly one-fifth of remaining primary forests are found in the International Union for Conservation of Nature (IUCN) Protected Areas Categories I-VI (Mackey et al., 2015). Proven effective mechanisms to protect primary forests include enforcing existing and establishing new reserves and protected area networks, limiting new road construction, payments for ecosystem services, effective governance, and protecting the rights and livelihoods of indigenous peoples and local communities (Mackey et al., 2015; Kormos et al., 2018; Walker W. S et al., 2020). Complementary measures and enabling conditions include supporting legislation and enforcement of protection status, industry re-adjustment to source alternative fuel, food and wood products, and management of weeds, pests, feral animals, and livestock grazing (Mackey et al., 2020).

Protecting primary forests will also be facilitated by changes to current international forest and carbon accounting rules. Existing "net" forest cover accounting rules, such as the IPCC good practice guidelines for national greenhouse gas inventories and the land sector, are problematic because they report net changes and treat all forests equally, regardless of their integrity, thereby incentivizing the conversion of primary forests into commodity production (Mackey et al., 2013, 2015; Peterson and Varela, 2016; Moreno-Mateos et al., 2017; Funk et al., 2019; Skene, 2020). Such changes in forest management can have the perverse effect of accelerating emissions and degrading ecosystems. Similarly, flux-based carbon accounting effectively hides the emissions or lost sequestration potential from logging primary forests (e.g., Skene, 2020) and does not account for the risk profiles of different forest types. Reporting "gross" forest cover changes as well as adopting stock-based accounting (Ajani et al., 2013; Keith et al., 2019, 2021) could more fully leverage an ecosystem integrity framework, and ultimately ensure the maximum mitigation benefits and ecosystem services are secured from Earth's remaining forests.

Management of other forest types

Management of secondary forests for commodity production, along with tree plantations and agroforestry, can contribute to climate mitigation and other SDGs and reduce pressure on primary forests and other natural forests with high levels of ecosystem integrity (Watson et al., 2018; Roe et al., 2019; Chapman et al., 2020). However, the key is to direct these management activities to previously deforested or degraded lands and accompany them with systematic landscape planning and effective governance (Dooley et al., 2018; Kormos et al., 2018; Martin et al., 2020; Morgan et al., 2020). For example, much of the overall timber demand could be harvested from secondary forests, but these are often overlooked as resources by land owners, the timber industry, and governments (Bawa and Seidler, 1998). Globally, intensively managed tree plantations or planted forests supply over 50% of global wood supply (Warman, 2014) yet occupy only 7% of global forest cover (Food and Agriculture Organization of the United Nations [FAO], 2020). It is therefore feasible to meet global wood supply with existing plantations and additional ones established on previously cleared or degraded land. These land uses, however, are decidedly not beneficial for carbon budgets or ecosystem services when undertaken at the cost of clearing or degrading primary forests.

Governments and forest managers can aim to optimize the ecosystem integrity of secondary forests (for example in terms of yield, regenerative capacity, and biodiversity) within the confines of their intended uses (Thompson et al., 2009; Grantham et al., 2020). In tandem with alternative fibers, this will help alleviate pressures on primary forests. A similar argument exists for agricultural productivity (Laurance et al., 2001; Hawbaker et al., 2006; Sabatini et al., 2018). All of these activities can be done with appropriate landscape planning in ways that collectively increase economic yield and ecosystem services, and serve local communities (Bawa and Seidler, 1998; Burton et al., 2006; Mathey et al., 2008; Food and Agriculture Organization of the United Nations [FAO], 2012; Naumov et al., 2016).

Afforestation, forest restoration, and proforestation (i.e., allowing secondary forests to naturally regrow and restore their ecosystem carbon stocks) are also important components of forest-based mitigation and conservation activities (Giam et al., 2011; Griscom et al., 2017; Verdone and Seidl, 2017; Moomaw et al., 2019; Roe et al., 2019; Cook-Patton et al., 2020). Proforestation holds promise for near-term mitigation because the established trees are already on the steepest part of their growth curve (Moomaw et al., 2019; Mackey et al., 2020). However, none of these forest management activities can replace the carbon stocks and ecosystem services of high-integrity primary forests on decadal to century timeframes. It is also generally less expensive to protect primary forests than to reforest or restore forests (Possingham et al., 2015; Griscom et al., 2017). Furthermore, potential "overcrediting" for offset and restoration schemes can result in net harm and carbon emissions, whereas "overcrediting" for primary forest protection only reduces the benefits, but does not lead to net societal and climate damages (Anderegg et al., 2020). We therefore urge that forest restoration should be conducted in concert with protection of primary forests, and not instead.

Finally, we note that selective logging, or so called "reduced impact logging" in tropical forests has been shown many times to be unsustainable (Zimmerman and Kormos, 2012; Kormos et al., 2018), as it results in significant damage to the target forests as well as collateral damages to surrounding forests due to road building, transportation, and further clearing for land uses such as agriculture (Kormos and Zimmerman, 2014; Mackey et al., 2020). Generally, as timber extraction becomes less intensive, the per-tree collateral damages increase exponentially (Gullison and Hardner, 1993; Boot and Gullison, 1995; Bawa and Seidler, 1998; Umunay et al., 2019; Zalman et al., 2019). After the first cut, selective logging is much less economically viable compared to plantations and intensive forestry (Bawa and Seidler, 1998; Naumov et al., 2016). Even measures aimed at reducing emissions *via* collateral damages from selective logging may not generate benefits and merely serve to justify and subsidize the degradation of high-integrity primary forests (Macintosh, 2013; Watkins, 2014; Gatti et al., 2015). Overall, selective logging and its associated degradation may be as much or more harmful than outright deforestation for pan-tropical forests and their carbon stocks (Nepstad et al., 1999; Foley et al., 2007; Baccini et al., 2017; Erb et al., 2018; Bullock et al., 2020; Matricardi et al., 2020).

Relevance for international policy

There has been a recent uptick in the recognition of the importance of ecosystem integrity and primary forests for multiple climate, biodiversity, and SDGs. For example, the preamble to the Paris Agreement notes the importance of ensuring the integrity of all ecosystems, and recent international policy developments point to the importance of maintaining and restoring ecosystem integrity for achieving the goals of the Rio Conventions and all of the SDGs, but in particular SDG 15 (Life on Land). The importance of primary forests for achieving synergistic climate and biodiversity outcomes was also reflected in Working Group II (IPCC, 2022) and III (Nabuurs et al., 2022) of the IPCC's Sixth Assessment Report, as well as key decisions from the CBD 14th Conference of the Parties (14/5 and 14/30) (Convention on Biological Diversity [CBD], 2018).

We strongly recommend an increased focus on integrating climate and biodiversity action, which provides an opportunity to deliver multiple societal goals through ensuring the integrity of ecosystems (Barber et al., 2020). The importance of the nexus between effective action on climate change and biodiversity is reflected in the findings of the first ever joint workshop of the IPCCC and IPBES held in 2021 (Pörtner et al., 2021), which encouraged synergistic climate and biodiversity action and identified priorities for action, in particular the protection and restoration of carbon and species rich natural ecosystems such as forests.

The integrity of ecosystems is also being promoted by civil society as an important factor to consider in the UNFCCC Global Stocktake, a central pillar of the Paris Agreement against which its success or failure will be judged (Climate Action Network, 2022). We suggest that utilizing the UN SEEA-EA to benchmark protection and restoration actions would provide critical information on ecosystem integrity elements for the Global Stocktake to inform high-benefit / low-risk nature-based solutions in evolving NDCs. Successful implementation of the ecosystem provisions of the UNFCCC and the Paris Agreement, including decisions made at COP 25 (1.CP 25 para. 15) calling for integrated action to prevent biodiversity loss and climate change; and COP 26 (CMA/3 para. 21 and 1.CP/26 para. 38) emphasizing "…the importance of protecting, conserving and restoring nature and ecosystems, including forests …," depends upon understanding the significance of ecosystem integrity for stable long term carbon storage and the overall health of the biosphere.

Other recent policies and guiding documents include the Glasgow Leaders' Declaration on Forests and Land Use (United Nations Climate Change, 2021), CBD post-2020 Global Biodiversity Framework (Convention on Biological Diversity [CBD], 2021), IUCN Policy Statement on Primary Forests Including Intact Forest Landscapes (IUCN, 2020), IPBES Global Assessment Report (IPBES, 2019), the New York Declaration on Forests 5-Year Assessment Report (NYDF Assessment Partners, 2019), the European Parliament resolution to protect and restore forests (European Parliament, 2020), and Indonesia's moratorium on converting primary forests and peatlands (Austin et al., 2019).

Nevertheless, there is still much work to be done at national and international levels, with the evolving Paris Rulebook and country NDC's arguably representing the largest opportunity. Translating all these international declarations into coherent national and jurisdictional policies will require an agreed-upon framework of ecosystem integrity, such as provided here, and applicable data products tools for implementation.

Future research directions

Because ecosystem integrity is such an integrative and multidisciplinary concept, research gaps are relatively extensive. We therefore do not offer an exhaustive list, but rather a prioritized assessment of future research directions to improve the understanding, valuation, and operationalization of ecosystem integrity. First and foremost, operationalizing forest ecosystem integrity at scales relevant to policy and planning that span from landscape planning (Morgan et al., 2022) to national strategies (Center for Biological Diversity [CBD], 2022) and international agreements (United Nations [UN], 2021) requires accurate and updated maps of ecosystem integrity and its components. Existing products (described in section "Evaluating ecosystem integrity") touch on aspects of canopy structural integrity, can be used to identify areas of remaining natural forests, and, using time series data, can locate where they have been lost (**Figure 3**). However, their ability to differentiate levels of integrity between forests is limited, and they do not account for the longer-term ecosystem dynamics that comprise functional integrity. It will therefore be helpful to leverage the time series of now decades-long satellite records such as Landsat and the Moderate Resolution Imaging Spectroradiometer (MODIS) to incorporate metrics of stability / resistance, and to capture smaller patches of high-integrity forests, such as in Shestakova et al. (2022). In boreal and temperate forests with naturally occurring stand-replacing disturbances, for example wildfire, it will be critical to accurately separate these from human disturbances, for example by using spatial pattern recognition techniques (e.g., Curtis et al., 2018).

For the purpose of primary forest protection, accurate maps of regularly updated primary forests are needed at sufficient spatial scales and accuracy to support both country-level assessments as well as local decision making. Spatial assessments of forest ecosystem integrity and components, as opposed to categorical maps of forest/no-forest or broad forest types, are particularly needed. In addition to developing countries, this information is needed in the United States, Europe, and other developed countries with little remaining primary forests. In these cases, the most ecologically mature forests for a given ecosystem type (e.g., DellaSala et al., 2022b) likely represent the highest integrity levels rather than primary forests per se (**Table 1** and **Figure 2**) and similarly require both field and remote sensing analysis to be defined and identified (e.g., Federal Register, 2022). Aside from mapping methodologies and data products, we stress the need for continued and new field monitoring programs that evaluate and track ecosystem integrity components as they are impacted by climate and human land use at various scales.

More focused scientific studies on the components of ecosystem integrity as described here (**Figure 1**) are needed to better define, quantify, and monitor integrity in different ecoregions. For example, we know relatively little about how biodiversity and ecosystem composition in many forested regions globally is responding to the combined impacts of climate change, landscape fragmentation, and land use, nor how these will continue to evolve in the future. Such understanding would facilitate management decisions to increase ecosystem integrity or limit its decline, which is particularly important for managing future risks and vulnerability of carbon stocks in the context of carbon markets and offsets (Anderegg et al., 2020). Developing methods for comprehensive yet transferable ecosystem service valuations are particularly important for both scientific understanding as well as conservation mechanisms such as Payments for Ecosystem Services and the UN System of Environmental Ecosystem Accounting.

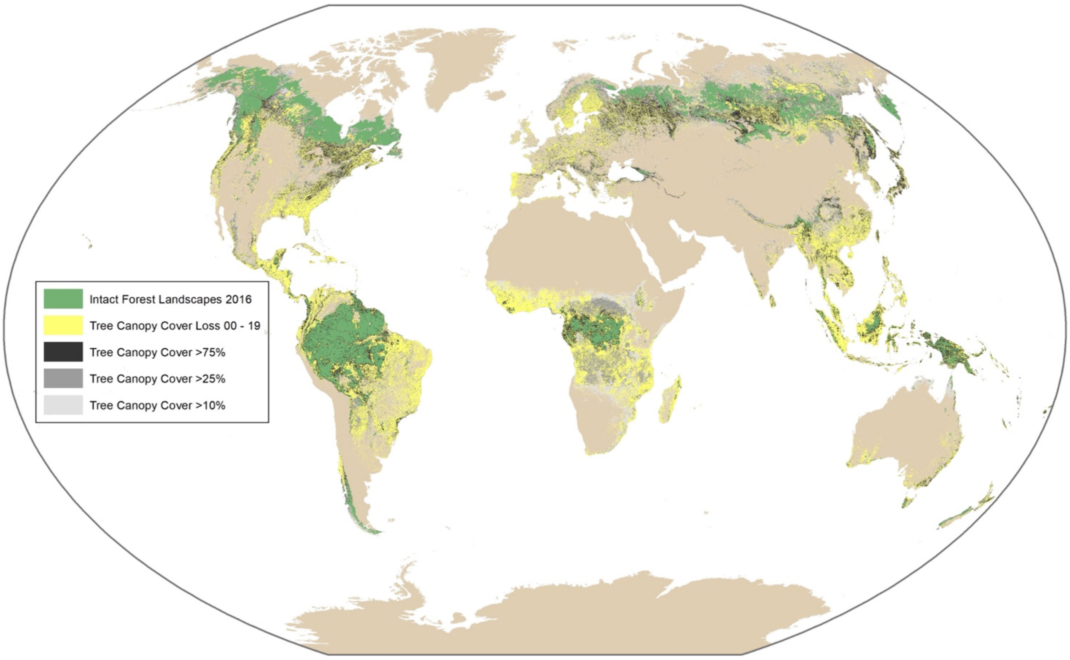

FIGURE 3
Global forest condition as indicated by metrics of Intact Forest Landscapes (IFLs), tree canopy cover, and tree canopy cover loss (from 2000 to 2019). IFLs for the year 2016 are taken from Potapov et al. (2017), and tree cover and tree cover loss outside of IFLs are from Hansen et al. (2013).

Finally, we suggest prioritizing research that optimizes the distribution of secondary forest management, including intensive plantations, to alleviate the pressure on primary and high integrity natural forests worldwide, as well as policy mechanisms needed for incentivization. Such research needs to account for regionally varying economic and equity issues in order to be effective.

Conclusion

In this paper we reviewed the components, importance, and potential for ecosystem integrity to help guide international forest policy and foster greater policy coherence across the climate, biodiversity, and sustainable development sectors. Our operating framework for forest ecosystem integrity encompasses biodiversity, dissipative structures, ecosystem processes, ecosystem stability, and the resulting ecosystem condition and services. A comparative analysis showed that, compared to forests with significant human modification, primary forests generally have higher ecosystem integrity and thus lower risk profiles for climate mitigation.

The scientific and management communities need better tools to accurately forecast the risks associated with different forest ecosystems, particularly those being managed for natural climate solutions and mitigation (Anderegg et al., 2020). Given these tools may be years or more away, we suggest focusing on ecosystem integrity is an optimal solution for categorizing forest-based risks and protecting ecosystem services. Doing so would (i) optimize investment in land carbon stocks and mitigation potential, (ii) identify stocks that provide the best insurance against risk of loss, and (iii) ensure the highest levels of benefits from ecosystem services, thereby optimizing compatibility and synergy between mitigation, adaptation, and SDGs. A number of large-scale data products exist to guide this focus. Nevertheless, there are substantial remaining gaps in terms of understanding, mapping, monitoring, and forecasting forest ecosystem integrity and its components in the midst of increasing human pressure and climate changes. Because primary forests have a higher level of ecosystem integrity than forests managed for commodity production, plantations, or degraded forests, we stress the continuing and increased need for their protection. An effective strategy is to create high carbon density strategic carbon and biodiversity reserves that include primary forests and recovering secondary forests that are quickly accumulating carbon (Law et al., 2022).

Author contributions

BR, BM, VY, and HK conceived the study. BR, BM, and HK led the writing, with contributions from CK, DD, GB, JD, RH, RB, TS, VY, and WM. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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Strategic reserves in Oregon's forests for biodiversity, water, and carbon to mitigate and adapt to climate change

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Creating strategic forest reserves is essential for stemming the loss of biodiversity and contributing to climate mitigation and adaptation. Meeting preservation targets of 30% protection by 2030, and 50% by 2050 would lead to greater protection of animal taxa and tree species habitat, carbon stocks and accumulation, and forests that are important sources of drinking water. Here, we develop a regional framework to specifically identify at a fine resolution (30 m) high priority forestlands for preservation in Oregon, USA. We include a resilience metric that represents connectivity and topographic diversity, and identify areas within each ecoregion that are ranked high priority for carbon, biodiversity, resilience and drinking water. Oregon has less than 10% of its forestlands protected at the highest levels, yet its temperate forests are among those with the highest carbon densities in the world. Reserves for surface drinking water sources and forest habitat for birds, mammals, amphibians, and reptiles could increase to 50–70% protection at the highest levels by 2050. Protected aboveground biomass carbon could triple to 635 teragrams of carbon by 2050. The ownership of the high preservation priority lands for carbon and biodiversity is primarily federal (67% by 2050) followed by private (28% by 2050), with much less in the other ownerships. Forest reserves could be established on federal lands through executive action, regulation and rule-making, while private landowners could be incentivized to store more carbon, limit harvest in certain areas and transfer ownership to land trusts. Protecting mature and old forests on federal lands fulfills an urgent need for protection and provides a low-cost way to simultaneously meet national and international goals. This study provides a flexible, dynamic framework for identifying areas that are high priority to protect for climate mitigation and adaptation at regional and sub-regional scales.

KEYWORDS

forests, carbon, biodiversity, drinking water, resilience, climate mitigation, adaptation

Introduction

Immediate and effective action is essential to address accelerated warming, water shortages and biodiversity losses, which includes animals, plants, and ecosystems (Pörtner et al., 2021). Biodiversity loss, degradation and transformation of ecosystems are already worse than predicted due to past global warming and will continue to escalate with increased warming (IPCC, 2022). Safeguarding biodiversity and ecosystem services depend on effective "conservation of about 30–50% of Earth's land, freshwater and ocean areas, including currently near-natural ecosystems" (IPCC, 2022).

In the conterminous United States, only 6.1% of forestland is protected at the highest level, with 0.2% in strict nature reserves to protect biodiversity, 4.8% in wilderness areas, and 1.1% in National Parks (Nelson et al., 2020). Some of the responsibility for immediate action to halt biodiversity loss, protect human drinking water supplies, and mitigate climate change rests upon the states and requires cross-jurisdictional coordination across complex multi-ownership boundaries.

Over the western US, we previously prioritized forest areas for protection based on their carbon densities and biodiversity of animal taxa and tree species (Law et al., 2021). The study suggests the Pacific Northwest has a large amount of forest area that should be high priority for protection by 2030 and 2050. Yet, Oregon has the lowest percentage (10%) of its forest area permanently protected in the eleven western US states. This shortfall called for a closer examination of available ecological data and policy considerations.

Oregon is positioned to take significant actions to meet the protection targets, as it has more than 12 million hectares of forestland, with some of the highest carbon densities in the world (Hudiburg et al., 2009; Law et al., 2018). Oregon relies on mountain watersheds and rivers for a large portion of the drinking water supply. Identifying important areas for conservation at the local scale may require finer spatial data than our western US study (Law et al., 2021), and consideration of different facets of biodiversity, from species richness to the importance of species with small ranges (Pollock et al., 2017), and consideration of all land ownerships to formulate appropriate policy actions. Here, we refined our regional framework to identify forest areas within Oregon for permanent protections that, if preserved, would stem further biodiversity loss, protect drinking water supplies at their sources, prevent carbon dioxide emissions from forest conversion, and safeguard natural carbon stocks and accumulation. We focus on the following questions:

(1) How much of Oregon's land and forestland is currently protected by ecoregion?
(2) Which forestlands could be strategically preserved under 30 × 30 and 50 × 50 within each ecoregion based on forest carbon, biodiversity and/or climate resilience?
(3) Who owns the high preservation priority forestlands?
(4) How would reaching 30 × 30 or 50 × 50 affect protection of species habitat, current forest carbon stocks and surface drinking water sources?
(5) What are potential social and cultural effects of preservation actions and how could policies address this?

Here we used fine resolution datasets (30 m), and expanded our analysis from using species richness as a biodiversity metric to include a priority class based on landscape characteristics such as connectivity and topographic diversity as a resilience metric (Carroll et al., 2018). Stable land characteristics that increase diversity and resilience are not likely to change with climate change (Lawler et al., 2013). We applied the priority ranking within each ecoregion to address the importance of distributing protections across the diversity of ecoregions (Dinerstein et al., 2017; Law et al., 2021).

Our study demonstrated that Oregon has high carbon density forests that also have high biodiversity and connectivity for species movement. When these characteristics were prioritized within each ecoregion, it identified sufficient forestland to meet both the 30% protection by 2030 and 50% by 2050 targets that are important nationally and internationally. Our study did not consider the effects of livestock grazing, but this topic was recently investigated in Oregon and across the American West (Ripple et al., 2022).

Materials and methods

Study region

The study region is Oregon, USA, with a total land area of about 25.06 Mha, of which 12.45 Mha (~49.7%) is forested (**Figure 1**). Oregon has strong climatic gradients from the Pacific coast to the inland high desert, and multiple mountain ranges that have their own climatic gradients associated with aspect and elevation. Because of this variation, we chose to identify areas with relative potential for protection within each ecoregion. Oregon has nine Environmental Protection Agency (EPA) level 3 ecoregions (Omernik and Griffith, 2014) ranging from temperate mesic forests in the Coast Range and West Cascades ecoregions to semi-arid East Cascades and high biodiversity forests of the Klamath Mountains to interior mixed-conifer forests of the Blue Mountains. Ecoregions are defined by seasonal temperature, precipitation, soil properties, and vegetation types. Three of the eleven ecoregions have little to no forest, including the Columbia Plateau, Northern Basin and Range, and Snake River Plain. Soils range from the high nitrogen and high soil water holding capacity of the Coast Range ecoregion to volcanic soils in the semi-arid East Cascades,

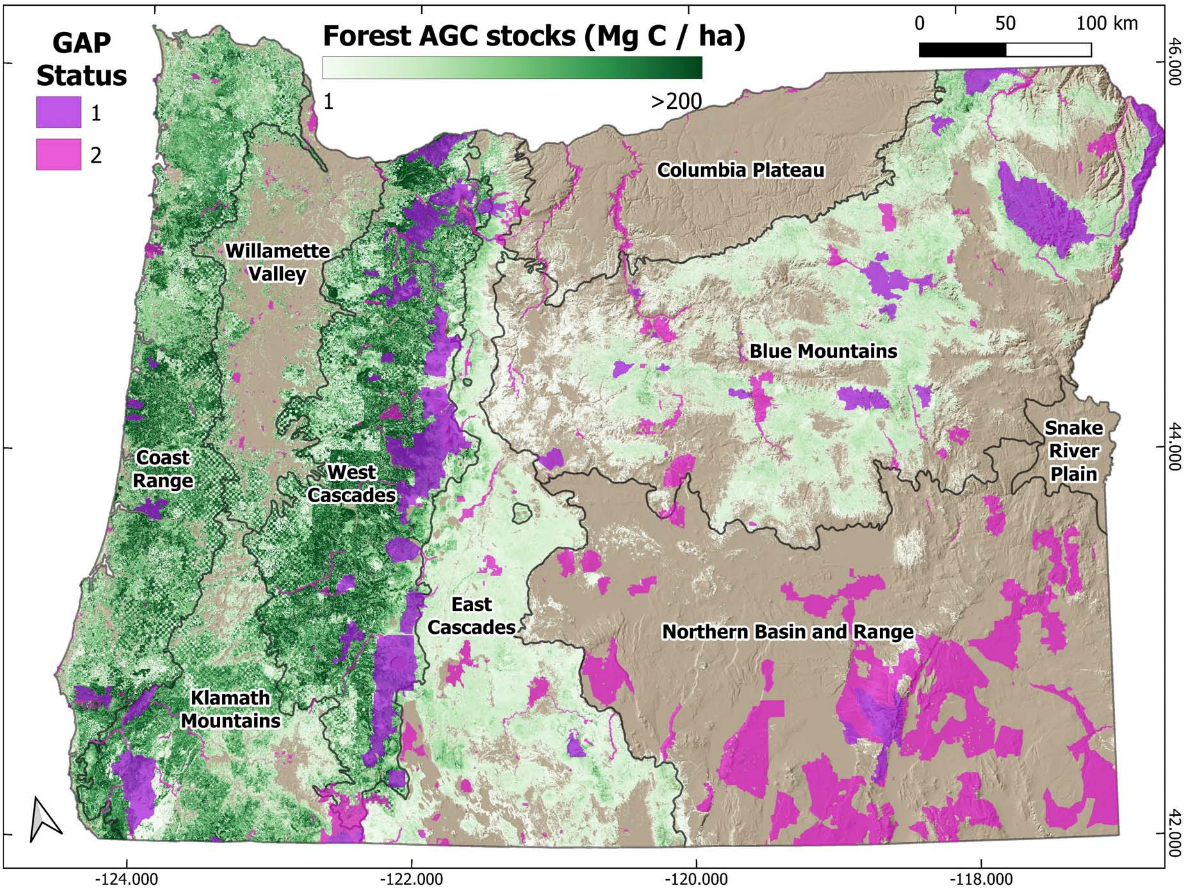

FIGURE 1

Current protected lands and forest aboveground carbon stocks across Oregon. Protected lands depicted here are assigned GAP Analysis Project (GAP) Status 1 or 2 by the Protected Areas Database of the United States (PAD-US v. 2.1) (USGS GAP, 2020) and include both forestlands and non-forestlands. These statuses characterize areas with permanent protection from anthropogenic conversion of natural land cover. Forest aboveground carbon stocks (Mg C ha^{-1}) in 2017 were spatially modeled from inventory measurements, satellite remote sensing, and environmental data (Landscape Ecology Modeling Mapping and Analysis (Lemma) Team, 2020).

affecting productivity. The study region provides a range of conditions that might be expected at much larger scales.

The forests in the region experienced intensive harvesting across public and private lands from the early 1900s through the late 1980s. Implementation of the Northwest Forest Plan (NWFP) in the wetter western portion of Oregon, Washington, and Northern California to protect sensitive aquatic and terrestrial species and habitat in old-growth forests resulted in an 82% decrease in timber harvest on public forestlands. These protections also benefited other ecosystem services like watershed protection (Frissell, 2013) and increased forest carbon accumulation on public lands. Prior to implementation of the NWFP, both public and private forests were about equal net carbon sources (Turner et al., 2011). Between 1990 and 2007, net carbon accumulation on public lands, even after accounting for fires and harvest, was 8 times that on private lands where intensive harvest of young tree plantations continued (Turner et al., 2011; Law et al., 2022). This demonstrates how forest carbon increases when harvest on public lands is limited for biodiversity and water protection. In the drier eastern forests, a set of rules were adopted around the same time to protect sensitive species, older trees and aquatic life, but these rules were rolled back by the US Forest Servic (2021).

Data processing

We analyzed the current extent, future opportunities, and benefits of forest preservation across Oregon using existing spatial datasets related to live tree aboveground carbon stocks, biodiversity, climate resilience, disturbance, and other factors. These spatial datasets were mapped at 30 m to 90 m spatial resolution and thus well suited to inform local to regional forest management decisions (Hansen et al., 2013; USGS GAP, 2018). Therefore, we conducted our spatial analysis at moderately high (30 m) spatial resolution using a common grid in an Albers

Equal Area projection. We analyzed and visualized data using the open-source software R (version 4.0) (R Core Team, 2021) with the libraries *terra* (Hijmans, 2022), *raster* (Hijmans, 2019), *sf* (Pebesma, 2018), *data.table* (Dowle and Srinivasan, 2021), and *ggplot2* (Wickham, 2016). We created the maps using open-source software QGIS (v3.20; R Core Team, 2021).

Current and additional protection to meet targets

We determined the current extent of protected lands across Oregon using the Protected Areas Database of the United States (PAD-US version 2.1) that is the official national inventory of protected areas. The PAD-US is a geospatial database created by the United States Geological Survey (USGS) GAP Analysis Project (GAP) that includes information on the spatial extent and protective status of public and private lands across the nation (USGS GAP, 2020). Protective status is characterized by GAP status codes that describe management intent to preserve biodiversity following guidelines from the International Union for the Conservation of Nature (IUCN). The highest protective statuses are GAP 1 and 2, which are for lands that have management plans to maintain the natural state of ecosystems and include permanent protection from human activities that cause land cover conversion. GAP 1 typically aligns with IUCN Categories Ia, Ib, and II, whereas GAP 2 aligns with IUCN Categories III through VI. We clipped the PAD-US shapefile to the boundaries of Oregon and then gridded the GAP status codes at 30 m resolution. Lands can have multiple GAP status codes when under multiple forms of management, in which case we used the lowest GAP status code. We then computed the total land and forest area with permanent protection (GAP 1 or 2) in each ecoregion, as well as how much additional area would be required to protect 30 and 50% of total land and forest area in each ecoregion.

Prioritizing forest protection using preservation targets

To strategically meet the 30 × 30 and 50 × 50 preservation targets in each of Oregon's ecoregions, we jointly and singularly prioritized forestlands for protection using carbon, biodiversity, and climate resilience metrics (*sensu* Law et al., 2021). For each prioritization metric, we computed the percentile rank (0–100%) of every grid cell compared to all other grid cells in the ecoregion. We then computed each grid cell's overall forest preservation priority rank by reranking the sum of its live tree aboveground carbon stocks, biodiversity, and climate resilience ranks. We identified the highest ranked currently unprotected forestlands that could be strategically protected (GAP 1 or 2) to meet each preservation target with the prioritization metrics.

For the carbon priority ranking, we focused on live tree aboveground carbon stocks (AGC). Tree AGC stocks in Oregon's forests typically account for 41 to 55% of total ecosystem carbon and are a focus for climate change mitigation because of their sensitivity to forest management activities. Tree AGC stocks have been mapped across Oregon's forestlands for the year 2017 using forest inventory, satellite, and environmental datasets (Landscape Ecology Modeling Mapping and Analysis (Lemma) Team, 2020). Specifically, tree AGC stocks were mapped for all live trees $\geq$2.5 cm diameter at breast height that occurred in areas that had or could potentially have at least 10% tree cover (Landscape Ecology Modeling Mapping and Analysis (Lemma) Team, 2020). To account for impacts of recent stand-replacing disturbances (e.g., wildfires, logging), we identified areas where forest loss occurred from 2017 to 2020 using the most recently available Global Forest Change dataset derived from 30 m resolution Landsat satellite data (Hansen et al., 2013). We set tree AGC stocks to zero in any grid cell where forest loss was observed during this period, and assumed the disturbances did not cause a permanent transition to non-forest.

For the biodiversity priority ranking, we used terrestrial vertebrate species (hereafter animal) richness by taxa and tree species richness. Current potential habitat distribution of 1,718 animal species was mapped by the USGS at 30 m resolution across the contiguous U.S. using geospatial predictors (USGS GAP, 2018). This included potential habitat for amphibian, bird, mammal, and reptile species found in the region. These habitat maps do not include stopover habitats for migratory species. Furthermore, we characterized the current potential habitat distribution of 89 tree species across Oregon based on the presence or absence of live tree basal area mapped state-wide at 30 m resolution using forest inventory, satellite, and environmental datasets (Landscape Ecology Modeling Mapping and Analysis (Lemma) Team, 2020). For each species that occurred in Oregon, we masked out habitat on non-forestlands, which resulted in our analysis including 544 animal species and 89 tree species. We then estimated species richness for each taxon by counting the number of species with habitat in each forested grid cell. For each grid cell, we (1) derived an animal priority rank based on the ranked sum of the four animal taxa ranks and then (2) derived the biodiversity rank by reranking the sum of the animal and tree priority rank.

For the climate resilience ranking, we used a metric of terrestrial landscape resilience that incorporated geophysical and topo-climatic diversity and landscape permeability (Buttrick et al., 2015). Landscape resilience refers to the capacity of a landscape or ecoregion to maintain biological diversity and ecological function despite climate change. As the climate continues to warm, biodiversity and ecological function are more likely to be maintained in landscapes that are topographically complex and permeable to movement of animals and plants. Complex topography provides corridors and microsites where species can move in response to climate change while a landscape free of barriers (i.e., highly permeable) allows species to take advantage of different microclimates. We used the terrestrial landscape resilience dataset (90 m resolution) produced for the Pacific Northwest USA by The Nature Conservancy (Buttrick et al., 2015). The topo-climatic diversity metric incorporated a heat-load index computed from a digital elevation model and topographic index as a metric of relative variation in water availability. Permeability is a measure of the hardness of barriers, connectedness of natural cover, and arrangement of land uses. More details are in Buttrick et al. (2015).

To select areas with the highest priority for preservation that could meet the 30 × 30 and 50 × 50 targets, forestlands within each ecoregion were ranked by carbon, biodiversity, and/or climate resilience metrics. We used pixel by pixel prioritization ranking rather than neighborhood average for adding spatial structure to the prioritization. The highest ranked forests were then combined with areas currently protected at GAP 1 or 2 until each preservation target was reached. We then assessed who owns these high-preservation priority forestlands, as well as potential effects of increased forest preservation for carbon, biodiversity, and drinking water.

Ownership of high preservation priority forests

Forestland ownership across the state was assessed using the Oregon Department of Forestry (ODF) data representing forest ownership conditions in 2015. The ownership classes in this spatial dataset include Federal, Tribal, State, Local, Private, and Industrial. We examined current ownership of forestlands, as well as ownership of forestlands that we identified as high priority for preservation.

Assessing effects of forest preservation on carbon, biodiversity, and water

We assessed current protection of forest carbon, biodiversity, and surface drinking water across Oregon, as well as potential protection of these ecosystem services if each preservation target was met. To help Oregon's public water systems and communities, the Department of Environmental Quality identified and mapped public surface drinking water source areas across the state, including rivers, streams and lakes (Oregon Department of Environmental Quality [DEQ], 2019). We used these data in our analysis. First, we quantified the amount of tree AGC stocks, animal and tree species' habitat, and surface drinking water source areas that are currently protected (GAP 1 or 2) across forestlands in Oregon. Next, we quantified potential protection of these ecosystem services if the 30 × 30 and 50 × 50 preservation targets were met. We focused particularly on forestlands that could be jointly prioritized for preservation using carbon, biodiversity, and climate resilience metrics. Given the importance of protecting the habitat that sustains threatened and endangered (T&E) species, we summarized current and potential habitat protection for animal species that are currently listed by Oregon and/or the federal government. A list of current T&E species is maintained by the Oregon Department of Fish and Wildlife (2021). We excluded from analysis (1) T&E fish, sea turtles, shore birds, and marine mammals; (2) animal species with only distinct population segments listed as T&E [e.g., Pacific marten (*Martes caurina*)]; and (3) the streaked horned lark (*Eremophila alpestris strigata*) because habitat data were not available.

Results

Current protected forests

Oregon has 12.45 Mha of forestland of which 1.23 Mha is protected at GAP 1 or 2 levels, less than 10% of the forested area (**Figure 1** and **Table 1**). The largest protected forest area is in the mesic West Cascades (0.55 Mha) followed by the Blue Mountains in eastern Oregon (0.32 Mha) and Klamath Mountains in southwestern Oregon (0.13 Mha). Oregon's portion of the Coast Range with its heavily forested temperate rainforests is primarily in industrial ownership and managed as tree plantations and, therefore, it holds the smallest portion of forestland that is permanently protected (3%, 0.06 Mha). When the Washington to California portions of the Coast Range are included, it increases to 10%. Similarly, the full Blue Mountains ecoregion that extends into southeast Washington has 10% of its forestland permanently protected (0.48 Mha) (Law et al., 2021).

High priority areas for preservation of carbon and/or biodiversity

The forest preservation rankings for carbon and/or biodiversity at GAP 1 or 2 status levels are widely distributed across the forested ecoregions (**Figures 2B,C**; **Supplementary Figures 1–6**). However, the climate resilience rank highlights large areas within the ecoregions with larger landscape features that are important for resilience (**Figure 2D**), such as the topography of mountain ranges in southwest Oregon, the Coast Range, Cascades, and Blue Mountains in the northeast.

To reach 30% protection in each forested ecoregion by 2030, an additional 2.5 Mha (20.1% of forest area) would need to be protected in less than 10 years (**Table 1**). To reach the 50% target, a total of 5 Mha (40.1%) would need to be protected by 2050, most of which is in the Blue Mountains, followed by East and West Cascades and the Coast Range (**Figure 3**).

TABLE 1 Current extent of all forestlands, protected forestlands, and additional forestlands needed to meet preservation targets for each ecoregion in Oregon.

								Additions needed to meet preservation targets							
								All lands				Forest			
	All lands	Protected lands		All forest		Protected forest		30% target		50% target		30% target		50% target	
Ecoregion	Mha	Mha	%	Mha	%	Mha	%	Mha	%	Mha	%	Mha	%	Mha	%
Blue Mountains	6.20	0.55	8.9	3.42	55.2	0.32	9.4	1.3	21.1	2.5	41.1	0.7	20.6	1.4	40.6
West Cascades	2.90	0.61	21	2.72	93.8	0.55	20.2	0.3	9.0	0.8	29.0	0.3	9.8	0.8	29.8
Coast Range	2.34	0.06	2.6	2.01	85.9	0.06	3.0	0.6	27.4	1.1	47.4	0.5	27.0	0.9	47.0
Columbia Plateau	1.75	0.04	2.3	0.09	5.1	0.00	0.0	0.5	27.7	0.8	47.7	0.0	30.0	0.0	50.0
East Cascades	2.73	0.14	5.1	2.13	78.0	0.09	4.2	0.7	24.9	1.2	44.9	0.5	25.8	1.0	45.8
Klamath Mountains	1.56	0.14	9.0	1.34	85.9	0.13	9.7	0.3	21.0	0.6	41.0	0.3	20.3	0.5	40.3
N. Basin and Range	5.95	1.34	22.5	0.25	4.2	0.08	32.0	0.4	7.5	1.6	27.5	0.0	−2.0	0.0	18.0
Snake River Plain	0.26	0.00	0.0	0.00	0.0	0.00	0.0	0.1	30.0	0.1	50.0	0.0	30.0	0.0	50.0
Willamette Valley	1.37	0.03	2.2	0.49	35.8	0.01	2.0	0.4	27.8	0.7	47.8	0.1	28.0	0.2	48.0
Oregon	25.06	2.91	11.6	12.45	49.7	1.23	9.9	4.6	18.4	9.6	38.4	2.5	20.1	5	40.1

Forestlands are considered currently protected if GAP 1 or 2 (IUCN categories Ia-VI).

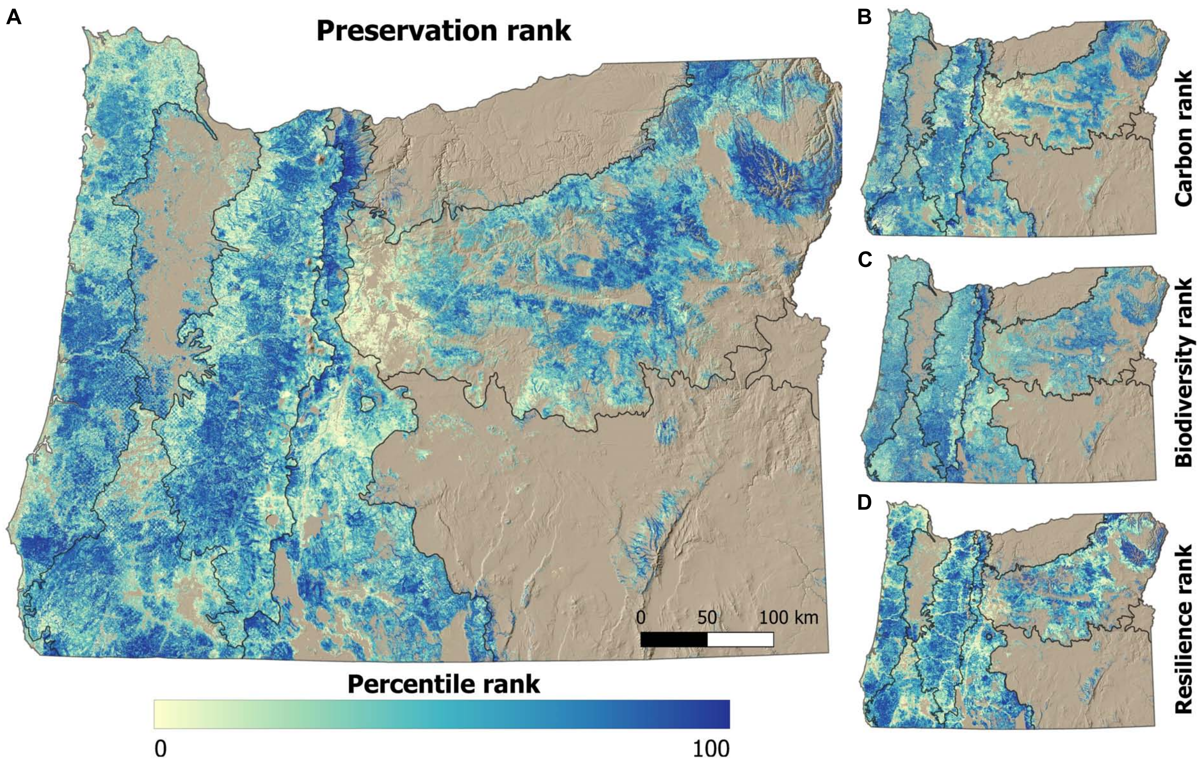

FIGURE 2

Oregon forest preservation, carbon, biodiversity, and climate resilience priority rankings. **(A)** Forest preservation priority ranks were derived from **(B)** carbon, **(C)** biodiversity, and **(D)** climate resilience priority ranks within each ecoregion. Forest carbon ranks were based on tree aboveground carbon stocks (AGC) stocks. Forest biodiversity ranks incorporate species richness of amphibians, birds, mammals, reptiles, and trees. Climate resilience priority ranks incorporated topoclimatic diversity and landscape connectivity.

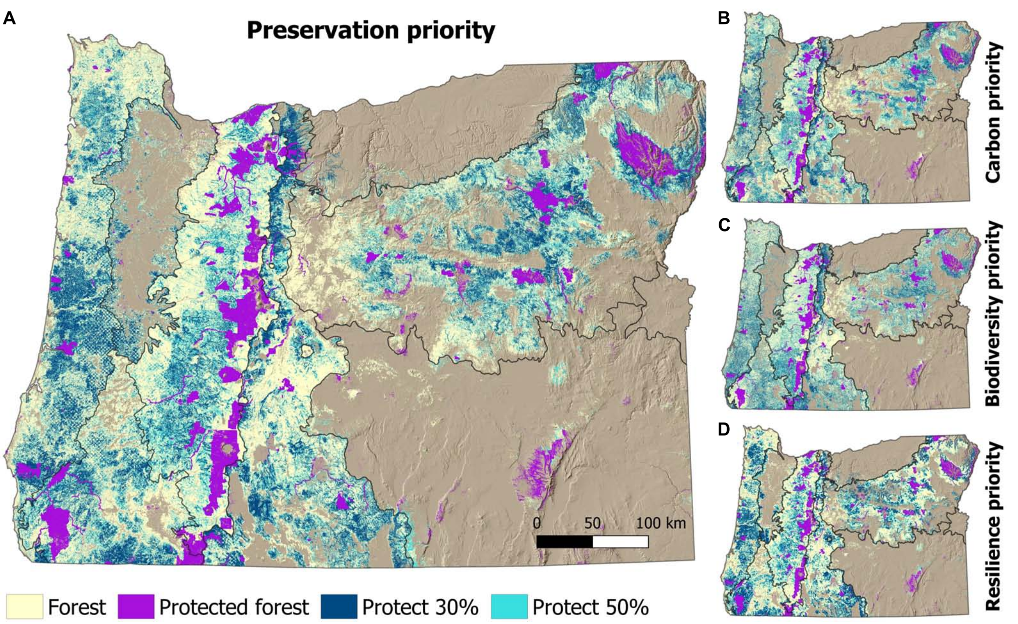

FIGURE 3
Forestlands prioritized to meet preservation targets across Oregon. Preservation targets include protecting 30 and 50% of each ecoregion's forestlands. To identify preservation targets, the current extent of forest protection was determined for each ecoregion and then the highest ranked unprotected forestlands were sequentially added to the protected area network until each preservation target was met. **(A)** Forest preservation priority targets are shown, as are the **(B)** carbon, **(C)** biodiversity, and **(D)** climate resilience priority targets.

We chose four areas for closer examination as examples of potential co-benefits and synergies with existing public lands (**Figure 4**).

The Coast Range ecoregion stretches along the coasts of Washington, Oregon, and northern California. The low elevation mountains (~1000 m) generally have deep soils with high soil water holding capacity and frequent fog that keeps vapor pressure deficits relatively low, resulting in a longer period of photosynthesis. The Coast Range contains two of the tallest conifer species in the world–Coast Douglas-fir (*Pseudotsuga menziesii var. menziesii*) and Sitka spruce (*Picea sitchensis*). These cool, temperate, moist forests can achieve higher biomass carbon density than tropical forests (Law et al., 2018). It is also the most intensively logged ecoregion. Within the areas we identified as high priority for both carbon and biodiversity are the Devil's Staircase Wilderness and the 32,375 ha Elliott State Research Forest (**Figure 4**). Both areas have a large portion of mature and old forests. Together, the ESRF reserves in Conservation Research Watersheds and adjacent Devil's Staircase Wilderness Area represent 26,404 ha of protected reserve (3.8% of Coast Range forestland), the largest in the Oregon Coast Range. The Devil's Staircase Wilderness was designated in 2019, and could be expanded to a larger area with connectivity corridors on BLM and State forestlands. The 83,000-acre Elliott State Forest was established as Oregon's first state forest in 1930. By 2020, half of it had been clearcut and planted. In 2020, the Elliott State Research Forest (ESRF) was established following an attempt to privatize the area for industrial management. The Research Forest has strong public support for conservation values including protection of mature and older forests, and threatened and endangered species (northern spotted owl, marbled murrelet, and Oregon Coast coho). Approximately 61% of the Elliott is identified as a reserve to meet state conservation goals, including 13,759 contiguous hectares, and another 5,870 ha of reserves located in harvest areas "protecting older trees and critical species habitat" (Oregon Division of State Lands, 2021; College of Forestry, 2022). To meet IUCN rules and national goals, at least 75% of the ESRF needs to be protected as strict reserves (IUCN, 2013).

The Klamath Mountains ecoregion is very diverse in climate, topography and plant and animal species. This area extends from southwestern Oregon into northern California where high priority forestlands provide connectivity between several large protected Wilderness Areas (Law et al., 2021). The most diverse forest flora in western North America (Whittaker, 1960) is found here, with more than 3,500 plant species, partly due to its steep climatic and topo-edaphic gradients. Plant communities range from temperate rain forests to moist inland forests, oak forests and savannas, and high elevation forests. The Kalmiopsis and Wild Rogue Wilderness Areas are in the Klamath Mountains, and each one presents potential for expansion (**Figure 4**). The Kalmiopsis was designated an Area of Global Botanical Significance by the IUCN, one of only seven in the United States. The area experienced the large Biscuit Fire

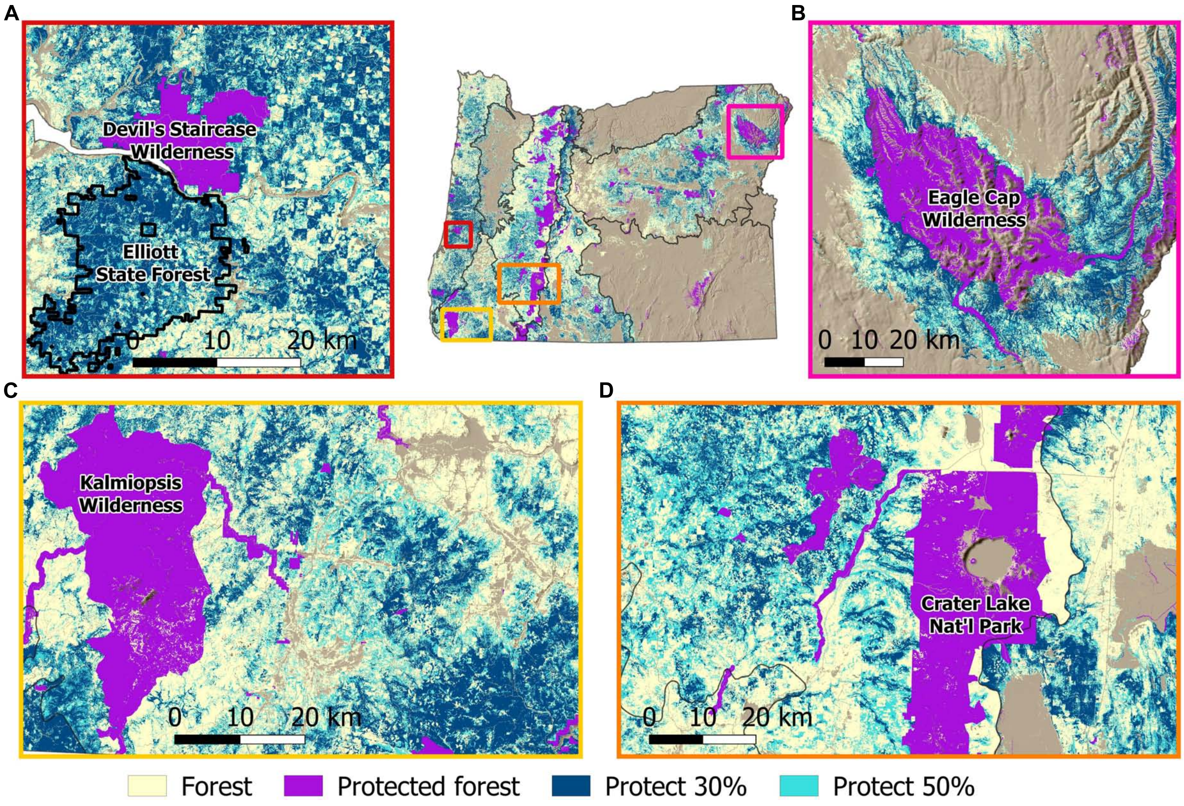

FIGURE 4
Close-up examples of forestlands prioritized to meet preservation targets in Oregon. Examples include forestlands around the **(A)** Devil's Staircase Wilderness and Elliot State Forest in the Coast Range, **(B)** Eagle Cap Wilderness in the Blue Mountains, **(C)** Kalmiopsis Wilderness in the Klamath Mountains, and **(D)** Crater Lake National Park in the Cascade Mountains. In these examples, forestlands were jointly prioritized using carbon, biodiversity, and climate resilience metrics.

in 2002, but has been slowly recovering its carbon stocks as conifer regeneration continued and woody biomass increased in the 10 years after the fire (Donato et al., 2015). The proposed Wild Rogue Wilderness would protect the Zane Grey Roadless Area, the largest forested BLM roadless area in southern Oregon and northern California.

The West Cascades ecoregion has a moist temperate climate that supports high productivity coniferous forests that are also intensively managed for logging. High-elevation forests along the Cascades Crest have received more protection including Crater Lake National Park, Oregon's only National Park (**Figure 4**). Crater Lake and surrounding forestlands include significant expansion opportunities of its protected area boundaries to include multiple rivers and elevating the protection of species (GAP 1 or 2) to become part of the strategic reserves system. The Crater Lake Wilderness Proposal would designate 219,744 hectares (2,197 km^2) of intact roadless forestlands as Wilderness on National Forest and National Park lands in a conservation area.

The Blue Mountains ecoregion contains a complex of mountain ranges interspersed with valleys stretching from the Cascades in the west to the Rocky Mountains in the east. This is the largest ecoregion in Oregon and has the largest Wilderness area in the state. The area supports diverse and abundant native fish and wildlife populations and has a significant portion of the region's remaining road-free wildlands. The forest types have fire-adaptive traits related to the wildfire regimes in this ecoregion, with ponderosa pine dominated forests in the south and a greater mix of dry, moist and cold forest types in the north due to receiving more moisture through the Columbia River Gorge. The Eagle Cap Wilderness (**Figure 4**) is surrounded by roadless areas and presents expansion opportunities that would help secure connectivity in a crucial wildlife corridor with large Wilderness areas in the Rocky Mountains.

Land ownership of high priority areas

In 2015, Oregon forestlands were primarily owned by the federal government (59%), private entities (31%), and industry (7%), whereas little was owned by state, local, or tribal governments (0–3%; **Table 2**). However, forest ownership widely varied among ecoregions. The federal government owned 66–77% of forestlands in the Blue Mountains, East and West Cascades, and Northern Basin, with these four ecoregions together accounting for 80% of federal forestlands statewide. Conversely, private or industrial owners held 57–92% of forestlands in the Coast Range, Columbia Plateau, Snake River Plain, and Willamette Valley, though these ecoregions together made up only 35% of private and industrial forestlands statewide because, with the exception of the Coast Range, these ecoregions are minimally forested. In terms of total forest area, private ownership was concentrated in the Blue Mountains and Coast Range, which respectively, accounted for 30 and 20% of private forestlands statewide. Similarly, industrial ownership was concentrated in the Coast Range and West Cascades, which respectively, accounted for 46 and 36% of all industrial forestlands statewide. The notable checkerboard pattern of forest carbon stocks and preservation priorities in the Coast Range (Figures 1–3) reflects differences in forest management between public and private ownership.

The ownership of the high preservation priority forestlands for carbon and biodiversity is primarily federal (72% by 2030, 67% by 2050) followed by private (20% by 2030 and 25% by 2050), with much less in the other ownerships (Figure 5). The additional federal lands needed to meet the high preservation priority targets adds up to 1.75 Mha by 2030 and 3.3 Mha by 2050 (Table 1 and Figure 5). Prioritizing biodiversity increases the percentages on private lands (Figure 5, right frame).

There are large differences among ecoregions in the ownership of high priority forestlands (Figure 6). For example, 80 to >90% of high priority forestlands are federally owned in the Cascade, Klamath, and Blue Mountains, whereas about 80% are privately owned in the Willamette Valley. In ecoregions with very little forestlands (Willamette Valley, Snake River, and Columbia Plateau), most high priority areas are privately owned. The highest population density is in the Willamette Valley and the other two ecoregions are drier. In the Coast Range, 60% of high priority forestlands are on federal lands, and 15% are on Tribally owned lands, the highest in the State.

Forest habitat, carbon, and drinking water if protected

Meeting the forest preservation targets would substantially increase protection of tree carbon stocks, animal and tree species' habitat, and surface drinking water source areas. Tree AGC stocks in all of Oregon's forests is 905 Tg C (Table 3). Currently, only 12% of Oregon's tree AGC stocks (104 Tg C) are in protected areas, mostly in the West Cascades (65 Tg C), followed by the Blue Mountains (13.5 Tg C) and Coast Range (10.9 Tg C). If the 30 and 50% forest preservation targets were met, then protected tree AGC stocks would total 405 and 635 Tg C (Table 3). The West Cascades and Coast Range would account for about 60% of the additional protected carbon stocks.

For most of the considered animal taxa and tree species, only a small percentage of their forest habitat is currently protected. Merely 6 and 14% of animal and tree species have at least 30% of their forest habitat currently protected. Moreover, the median percentage of forest habitat currently protected ranges from 8 to 12% among amphibian, bird, mammal, and reptile species and is 10% among tree species (Figure 7A). If the 30 and 50% forest preservation targets were met, then the median amount of forest habitat protected would be 27–42 and 45–63% among animal taxa, respectively, and reach 41 and 67% among tree species (Figure 7B).

Meeting these forest preservation targets would substantially increase forest habitat protection for threatened and endangered (T&E) species and other species of interest (Table 4). For example, only 8% of marbled murrelet (*Brachyramphus marmoratus*) and spotted owl (*Strix occidentalis*) forest habitat is currently protected, yet 36–44% would be protected if the 30% forest preservation target was met. Similarly, forest habitat protection for Canada lynx (*Lynx canadensis*) would increase from 12 to 40%, while it would increase from 34 to 55% for wolverines (*Gulo gulo*). Important non-T&E species such as wolves (*Canis lupus*) and beavers (*Castor canadensis*) would see forest habitat protection increase from 35 to 59% and from 10 to 40%, respectively, if this preservation target was met. These wolf and beaver habitat targets would help fulfill a recent proposal for rewilding the American West (Ripple et al., 2022). The additional habitat that could be protected by 2030 and 2050 increases dramatically for most of these species when forestlands are jointly prioritized based on carbon, biodiversity and climate resilience, which includes connectivity for animal movement.

Forestlands account for 78% (4.14 Mha) of the 5.3 Mha of surface drinking water source areas across Oregon, yet only 9% (0.37 Mha) of these forestlands are currently protected at GAP 1 or 2 levels (Table 5). This would increase to 27% by 2030 and 48% by 2050 if the high priority areas for carbon, biodiversity and resilience are protected (GAP 1 or 2). Most of the currently protected surface water source areas and the areas suitable for potential increases in protection are in the West Cascades, though protection of surface water sources areas would also increase notably in the Blue Mountains, Klamath Mountains, and Coast Range (Figure 8).

Discussion

Regional considerations for protecting carbon, biodiversity, and water

The IPCC AR6 (2022) states that "maintaining the resilience of biodiversity and ecosystem services at a global scale depends on effective and equitable conservation of approximately 30–50% of Earth's land, freshwater and ocean

TABLE 2 Current forestland ownership and management within each ecoregion and overall for Oregon.

Ecoregion	Ownership land management					
	Federal	State	Tribal	Local	Private	Industrial
Blue Mountains	2.26 (66%)	0.02 (1%)	0.02 (0%)	0.00 (0%)	1.14 (33%)	0.00 (0%)
West Cascades	2.11 (77%)	0.03 (1%)	0.00 (0%)	0.01 (0%)	0.30 (11%)	0.30 (11%)
Coast Range	0.61 (29%)	0.26 (13%)	0.01 (0%)	0.02 (1%)	0.79 (38%)	0.39 (19%)
Columbia Plateau	0.01 (14%)	0.00 (1%)	0.00 (1%)	0.00 (0%)	0.08 (84%)	0.00 (0%)
East Cascades	1.42 (67%)	0.05 (2%)	0.00 (0%)	0.01 (0%)	0.61 (28%)	0.04 (2%)
Klamath Mountains	0.79 (58%)	0.01 (1%)	0.00 (0%)	0.00 (0%)	0.55 (41%)	0.00 (0%)
Northern Basin and Range	0.18 (71%)	0.01 (4%)	0.00 (0%)	0.00 (0%)	0.06 (25%)	0.00 (0%)
Snake River Plain	0.00 (6%)	0.00 (1%)	0.00 (0%)	0.00 (0%)	0.00 (92%)	0.00 (0%)
Willamette Valley	0.04 (8%)	0.01 (2%)	0.00 (0%)	0.01 (1%)	0.33 (66%)	0.11 (22%)
Oregon	7.43 (59%)	0.40 (3%)	0.03 (0%)	0.05 (0%)	3.86 (31%)	0.84 (7%)

The extent of forestland in each category is given in million hectares (Mha) and as a percentage of total forestland within each ecoregion. Ownership land management data from the Oregon Department of Forestry (2015).

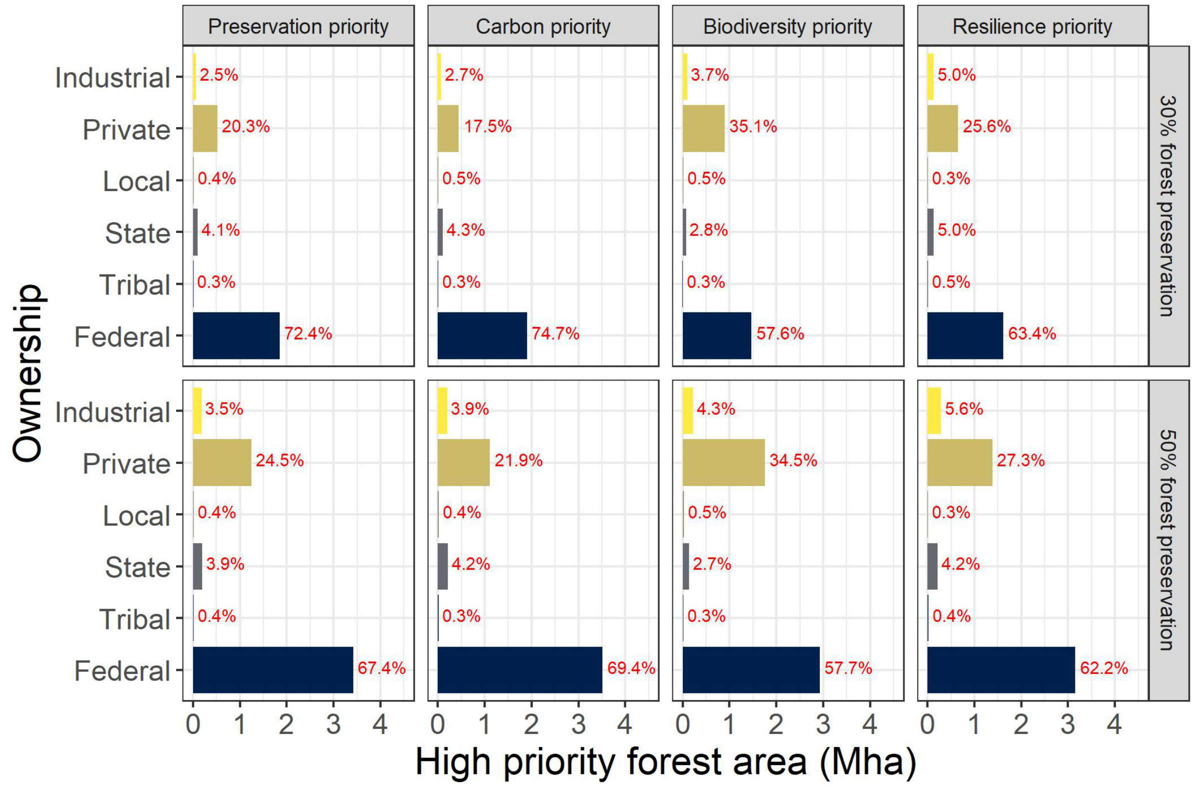

FIGURE 5
Land ownership of high priority forest areas to protect in Oregon to meet preservation targets. Ownership is summarized for each preservation target (rows) and priority (columns). Land ownership data from Oregon Department of Forestry (2015).

areas, including currently near-natural ecosystems." This acknowledges the multiple lines of evidence that maintaining ecological integrity of biodiversity is essential for addressing climate change effectively.

Accordingly, our analysis prioritizes areas within ecoregions to ensure biodiversity losses are reduced, or even enhanced in some areas through natural recovery of species and reintroductions, across the range of ecosystems. This approach also benefits carbon for climate mitigation, protects water availability and increases other ecosystem services.

A global application of the ecoregion approach found that temperate broadleaf, mixed, and conifer forests could achieve

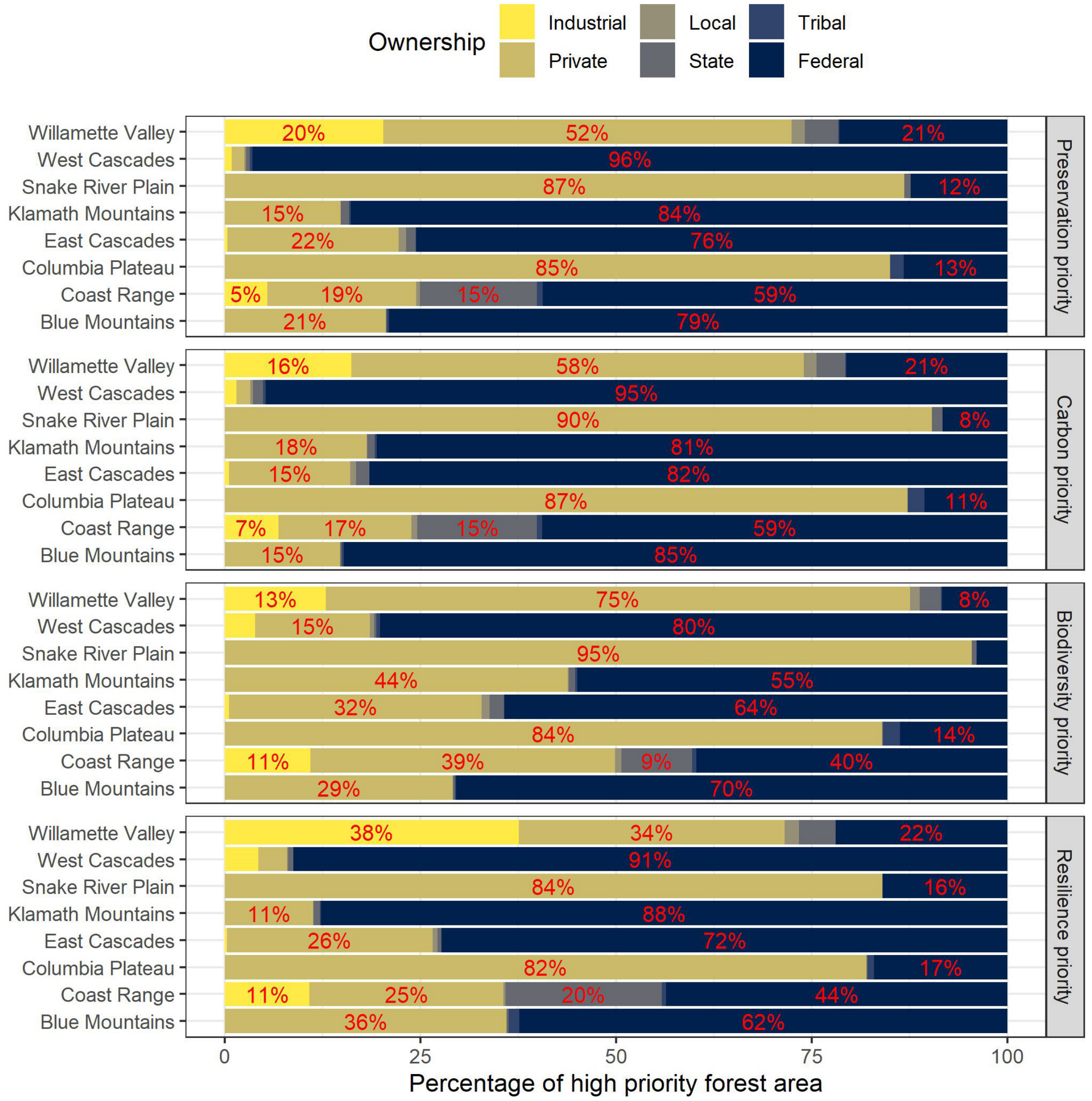

FIGURE 6
Land ownership of high priority forest areas to protect to reach 30% preservation for each ecoregion in Oregon. Ownership is summarized for each preservation priority **(rows)**. Land ownership data from Oregon Department of Forestry (2015).

protection of half of the global forest area, and the majority of the ecoregions are categorized as “imperiled” or “could recover” (Dinerstein et al., 2017). This emphasizes the need for protection.

Here, we found that the current 1.3 Mha protected as GAP 1 or GAP 2 status would increase to 2.5 Mha by 2030 and 5 Mha by 2050 to meet the preservation targets. Federal lands account for the majority of the protected area needed, which would provide more permanence. Protecting high carbon priority forests from timber harvest (GAP 1) is critical to dampen the accelerating anthropogenic carbon dioxide emissions.

Mitigation strategies need to explicitly protect existing old-growth forests, and allow mature secondary forests to regrow to their carbon capacity. For climate mitigation using natural climate solutions, effectiveness is based on the time that a unit of biomass carbon is resident in a forest ecosystem stock and thus kept out of the atmosphere (Körner, 2017; Mackey et al., 2020). Oregon’s wet coastal forests have among the highest carbon residence times of any forests in the western USA (Berner et al., 2017). The large and old trees dominate forest carbon in temperate and tropical forests, and can maintain large carbon stocks and accumulation for centuries (Luyssaert et al., 2008; Hudiburg et al., 2009).

TABLE 3 Current tree aboveground carbon (AGC) stocks in each ecoregion's forests, protected forests, and forests that would be protected by meeting preservation targets using joint prioritization.

	All forest	Unprotected forest		Protected forest		Forestland preservation target			
						30% protection		50% protection	
Ecoregion	Tg C	Tg C	%	Tg C	%	Tg C	%	Tg C	%
Blue Mountains	110.8	97.2	88	13.5	12	53.0	48	79.1	71
West Cascades	323.6	258.6	80	65	20	125.7	39	220.7	68
Coast Range	240.3	229.4	95	10.9	5	117.9	49	171.9	72
Columbia Plateau	1.5	1.5	94	0.1	6	0.9	58	1.2	79
East Cascades	73.8	69.4	94	4.4	6	35.8	48	50.1	68
Klamath Mountains	112.9	103.5	92	9.4	8	50.6	45	80.7	71
N. Basin and Range*	1.7	1.3	75	0.4	25	–	–	1.0	60
Snake River Plain	< 0.1	< 0.1	99	< 0.1	1	< 0.1	36	< 0.1	56
Willamette Valley	40.3	39.7	98	0.7	2	20.7	51	30	75
Oregon	904.9	800.5	88	104.4	12	405.1	45	634.8	70

*32% of forestlands in the Northern Basin and Range ecoregion are currently protected, thus summaries of tree AGC stock protection were not computed for the 30% forest preservation target. Each category includes tree AGC stocks in teragrams (10^{12} g or million metric tons) of carbon and as the percentage of the ecoregion's total tree AGC stocks. Tree AGC stocks protected by meeting each preservation target include the stocks in current protected forests. Tree AGC stocks are considered currently protected if they occur on forestlands as GAP 1 or 2 status.

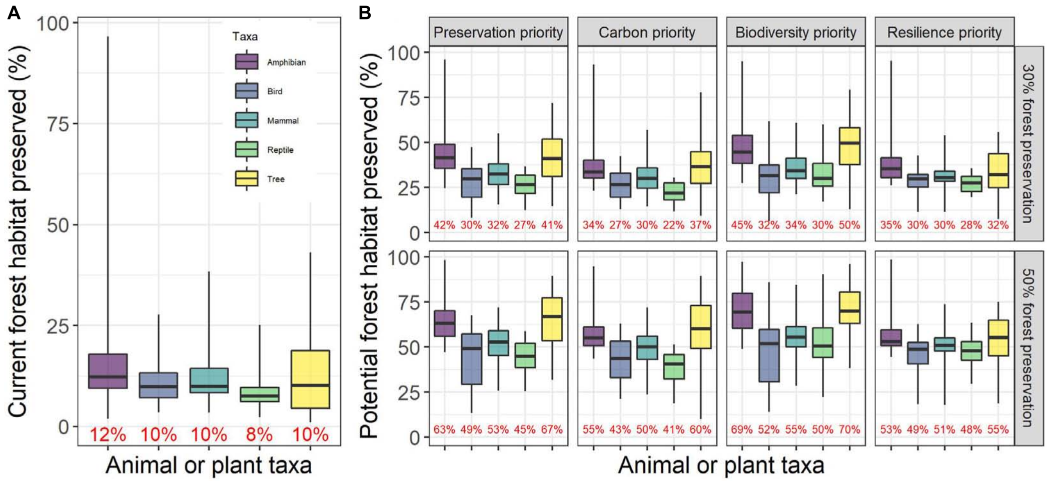

FIGURE 7
Current and potential protection of animal taxa and tree species forest habitat across Oregon. The percentage of each species' forest habitat that **(A)** is currently protected and **(B)** would be protected by meeting preservation targets based on each priority. The median percentage of current and potential protected species habitat is provided for each taxon (red text). Boxplots depict medians (intra-box lines), 25th–75th percentiles (box edges), and 5th to 95th percentiles (whiskers). Animal and tree species habitat data were from the USGS GAP (2018) and Landscape Ecology Modeling Mapping and Analysis (Lemma) Team (2020), respectively.

Oregon inventory data show that stand ages reach beyond 1,000 years, and public lands have far more stands older than 200 years than private lands do (Hudiburg et al., 2009). Mean and maximum live biomass are also higher on public lands. The maximum mean trend of biomass within each ecoregion occurred by the age of 300 years in the Coast Range to 430 years in the West Cascades and 600+years in the Klamath Mountains, and biomass continued to increase beyond these ages (Hudiburg et al., 2009). Ecoregions with the highest ecosystem carbon density in vegetation and soils are the Coast Range, West Cascades, and Klamath Mountains (330, 318 and 316 Mg C ha^{-1}, respectively), with 55% of it in live tree carbon (180, 175, 173 Mg C ha^{-1}) (Law et al., 2018). Oregon's forest carbon stocks could almost double in the absence of disturbance (Hudiburg et al., 2009). These trends are influenced by harvest intensities, particularly in the Coast Range where the temperate rainforests have so little forestland protected, yet they are among the highest carbon dense forests in the world (**Table 1**).

TABLE 4 Current and potential habitat protection for animal species listed as threatened (T) or endangered (E) by the state of Oregon.

				Forest habitat protected (%)		
Common name	**Scientific name**	**State (Federal) status**	**Forest habitat (km^2)**	**Current**	**30% protected**	**50% protected**
Oregon spotted frog	*Rana pretiosa*	T	507	17	42	65
Marbled murrelet	*Brachyramphus marmoratus*	E (T)	14,913	8	44	65
Northern spotted owl	*Strix occidentalis caurina*	T (T)	39,379	8	36	59
Canada lynx	*Lynx canadensis*	T	16,211	12	40	62
Kit fox	*Vulpes macrotis*	T	295	25	26	32
Washington ground squirrel	*Urocitellus washingtoni*	E	1	4	27	41
Wolverine	*Gulo gulo*	T	791	34	55	71

Several of these species are also listed by the federal government. Each species includes the amount of forest habitat that is currently protected (GAP 1 or 2), as well as how much would be protected by reaching the 30 and 50% preservation targets when jointly prioritizing forestlands based on carbon, biodiversity, and climate resilience metrics. Information on listing status was from the Oregon Department of Fish and Wildlife as revised October 2021.

TABLE 5 Surface drinking water source areas for public water systems in each ecoregion's forests, protected forests, and forests that would be protected by meeting preservation targets using joint prioritization.

						Preservation target			
	All lands	**All forest**		**Protected forest**		**30% protection**		**50% protection**	
Ecoregion	**Mha**	**Mha**	**%**	**Mha**	**%**	**Mha**	**%**	**Mha**	**%**
Blue Mountains	0.26	0.18	70	0.02	12	0.09	48	0.13	70
Coast Range	0.77	0.7	91	0.00	1	0.18	26	0.32	46
Columbia Plateau	0.13	0.01	6	0.00	1	0.00	48	0.00	64
East Cascades	0.01	0.01	92	0.00	7	0.01	68	0.01	81
Klamath Mountains	0.81	0.65	80	0.02	2	0.12	19	0.25	38
N. Basin and Range	0.00	0.00	0	0.00	0	0.00	0	0.00	0
Snake River Plain	0.02	0.00	0	0.00	0	0.00	27	0.00	55
West Cascades	2.28	2.2	97	0.33	15	0.59	27	1.09	50
Willamette Valley	1.03	0.39	38	0.01	1	0.12	30	0.20	50
Oregon	5.30	4.14	78	0.37	9	1.11	27	2.00	48

Joint prioritization was based on forest carbon, biodiversity, and climate resilience metrics. Surface drinking water source areas are considered currently protected if they occur on forestlands as GAP 1 or 2 status. Surface drinking water source areas were mapped by the Oregon Department of Environmental Quality (DEQ) (updated 2019).

Although we did not simulate changes in forest carbon and accumulation under future climate, our previous studies showed that preserving 50% of high priority forests by 2050 would triple the amount of carbon accumulation compared to current levels over the western United States (Law et al., 2021), accounting for projected climate effects including CO_2 enhancement of photosynthesis constrained by nitrogen and carbon losses from forest fires. Because we prioritized relatively high carbon density within each forested ecoregion in our current study, the carbon accumulation is probably lower than if priorities were only in the ecoregions with the highest net accumulation (average of 1.4 compared to 4 to 8 Mg C ha^{-1} yr^{-1}; Law et al., 2013).

A global study assumed an average accumulation rate of 0.14 MgC ha^{-1} yr^{-1} for boreal and temperate forests over the next decades (Griscom et al., 2017). Our estimate for natural forest management in Oregon is almost ten times the global value. We also found that limiting harvest to half of current levels on public lands and doubling harvest cycles to 80 years on private lands was three times more effective as a land use strategy than replanting and reforestation after cutting within current forest boundaries in Oregon (Law et al., 2018). The global study presents different results, highlighting the need for consistent approaches for national, regional and state-level analysis to refine estimates of forest carbon benefits.

There is concern that protecting areas that are vulnerable to increased drought and fire will be ineffective, however, species diversity, and threatened and endangered species still need habitat, refugia and connectivity with other protected areas. Wildfires tend to be patchy, and a majority of trees survive low to mixed-severity fires (Halofsky et al., 2011) that can be critical habitat, and burned forests still retain the vast majority of their carbon (Hudiburg et al., 2009; Law et al., 2018). When very few populations of a given species exist, the potential to recolonize areas with strong site fidelity is needed.

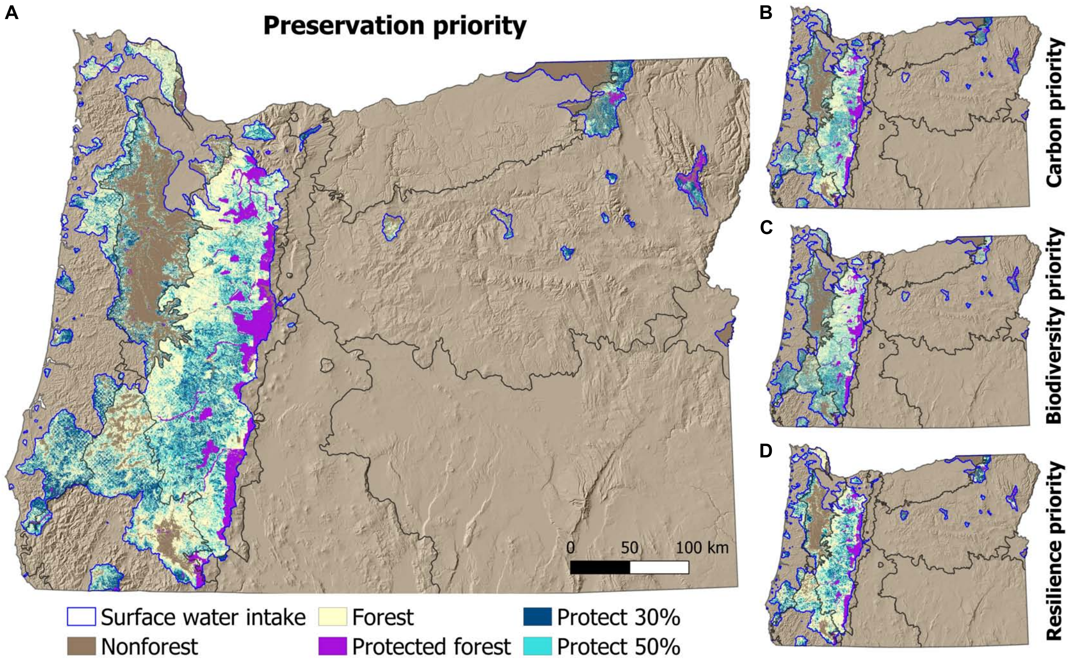

FIGURE 8
Current and potential protection of surface drinking water source areas in forestlands across Oregon. Potential protection is shown for the **(A)** forest preservation priority targets, as well as for **(B)** carbon, **(C)** biodiversity, and **(D)** climate resilience priority targets. Surface drinking water source area data were from the Oregon Department of Environmental Quality (Oregon Department of Environmental Quality [DEQ], 2019).

The conservation of habitat suitability is necessary even if it is currently unoccupied by those populations (Merkle et al., 2022). Moreover, transboundary assessment of priority areas for preservation and connectivity is essential, as well as collaborative development of implementation plans that transcend political boundaries (Noss et al., 2012; Law et al., 2021).

Across the western U.S., federal forestlands are the dominant source of clean drinking water, and private forestlands are the most likely to experience land use change and impacts on water supplies (Liu et al., 2021). In western Oregon, where human population is concentrated and projected to continue growing rapidly, communities depend on drinking water from both private and federal forestlands. While there is concern about the impacts of wildfire on drinking water sources, forestlands tend to be adapted to these periodic disturbances and recover with minimal interventions. However, repeated harvesting, road networks and application of pesticides can expose aquatic systems to chronic stressors that continuously reduce water quantity and degrade water quality (e.g., soil erosion, sediment load, higher stream temperature) (Rieman et al., 2003; Karr et al., 2004).

As warming increases, mountain snowpack is expected to melt earlier in spring, which reduces drinking water supplies (Evan and Eisenman, 2021). The Cascade Mountains are expected to be among the most vulnerable mountain ranges because of their mild climate where even small temperature increases will result in precipitation falling as rain rather than snow, further reducing snowpack accumulation and increasing melt. This ecoregion is the largest area currently protecting forest drinking water sources at GAP 1 or 2 status and it is critical for additional preservation area for protection of habitat, biodiversity, and carbon. Protecting clean drinking water sources from extractions (mining, logging) is cost effective and essential, as loss of forest cover or conversion to plantations has been shown to reduce water supplies by up to 50% as compared to mature forests (Segura et al., 2020). Logging is still occurring in Oregon watersheds that feed surface water and replenish groundwater sources of drinking water.

In the drier Klamath and Blue Mountains ecoregions, dependence of water supplies on sufficient accumulated winter snowpack is amplified due to less rainfall. The mountains serve as crucial water collection sources for these areas. Mountains receive far more moisture than the lower elevation valleys and canyons that they eventually supply with water. As snow melts, it recharges soil water to support ecosystems through seasonally dry summers. The slow transfer of water sustains water supplies and maintains summer stream flows that in turn support high levels of biodiversity in aquatic and riparian systems. Mountain water is also of major importance to agriculture. In these seasonally dry forests, protecting forested watersheds will be crucial to the long-term water security of the region.

Older forests in Oregon's watersheds exhibit greater water retention and improved late summer stream flows compared to managed plantations (Segura et al., 2020). Intact forests also tend to harbor more large and old trees, bolstering carbon stores and biodiversity services that large trees provide (Lutz et al., 2018; Plumtre et al., 2021). As warming increases, protecting the integrity of these intact forested watersheds would help sustain valuable ecosystem services, including a clean, reliable supply of water. Oregon's largest protected area, the Eagle Cap Wilderness, demonstrates the tremendous value of a largely protected forested mountain range for providing a reliable source of clean water to the ecosystems and communities of northeast Oregon.

Some ecoregions will see declines and even biome shifts as warming continues, but this is somewhat counteracted by the positive effect of atmospheric CO_2 on photosynthesis and lengthened growing seasons in the wetter ecoregions. The effects of increasing atmospheric CO_2 will continue in spite of reaching greenhouse gas reduction targets because surface temperatures will not immediately return to previous levels and may persist for a millennium or more (Solomon et al., 2009). While strategic forest reserves for climate mitigation and adaptation by plants and animals may face near-term challenges, the urgency and benefits of protecting landscapes for community and ecosystem values is nonetheless very high as the world moves to transition away from fossil fuel pollution.

The diversity of ecoregions and forest communities within Oregon also suggests that systems will respond differently to warming across the region. Even within forest types, individual species have unique adaptations and vulnerability thresholds. In Oregon's Coast Range, conversion of diverse conifer systems to Douglas-fir plantations has increased vulnerability to Swiss Needle Cast disease (Shaw et al., 2021), and climatic change may further exacerbate this vulnerability (Mildrexler et al., 2019). Moreover, young industrial plantations show a higher incidence of high severity fires, almost twice as many as on public lands (Levine et al., 2022). In other ecosystems, disturbance-induced shifts may facilitate changes in species composition, including shifts toward communities better adapted to changing climatic conditions. Taken as a whole, Oregon's exceptional ecosystem diversity will help buffer its forests against large-scale shifts in ecosystems.

Improving measurement, reporting and verification

To initiate strategic reserves, consistent guidelines, definitions, and accounting rules need to be established. Similar to international requirements for monitoring, reporting and verification (MRV; Ellis and Moarif, 2015), there is a need to upgrade our measurement systems as recommended in national and international reports (e.g., Law et al., 2008; Ciais et al., 2014). Consistent, current metrics will help refine locations for reserves, establish baseline conditions, and monitor changes in plant and animal species, forest carbon and other metrics of condition. Updated metrics will also ensure reliability in protection agreements.

An executive order issued by President Biden in 2022 recognized the importance of mature and old-growth forests in limiting climate change and makes their conservation a national policy.[1] The land management agencies are tasked with defining mature and old. Carbon per unit area ground (carbon density) is an essential climate variable for mitigation, and can be used to distinguish mature from young forests. Carbon density is computed from tree diameter and height and can be used to identify the inflection point at which the increase following stand-replacing disturbance begins to slow for a tree community within ecoregion. In addition, tree diameter and height are useful to infer site fertility and could be used to scale forest carbon potential in different environments. When assessing the mitigation potential of forests in a region, we must consider that carbon density and removal rates are strongly variable with edaphoclimatic conditions, even within the same forest type. Young forests have low carbon density compared to mature and old (Hudiburg et al., 2009). Age alone is not a good metric because it is not measured well in most regions or is approximated from tree diameter. Furthermore, age is a good indicator of the time since the last stand-replacing disturbance only in early successional stands with pioneer tree species. In late-successional stands with shade-tolerant trees (i.e., long suppression phases), maximum tree age is not necessarily related to disturbance. Long-term repeated measurements of ecosystems across the landscape/ecoregion provide a much more precise picture of carbon dynamics, like the repeated direct measurements of diameter and height in federal inventories (Forest Inventory and Analysis [FIA], 2014). In addition, these measurements are used to produce a metric of structural diversity that is important for biodiversity.

Coordination among federal, state and international programs are needed for consistency of repeated measurements, reporting, and verification. To inform strategic assessments and decision making, spatial datasets must represent environmental conditions consistently across the country at moderate to high spatial resolution (30–250 m) and must be updated at least every 5-year (e.g., for the federally mandated National Climate Assessment produced every 4 years), and include:

- ○ Processed inventory data that use height and dbh in improved algorithms for estimating aboveground biomass carbon.

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[1] https://www.federalregister.gov/documents/2022/04/27/2022-09138/strengthening-the-nations-forests-communities-and-local-economies

- More frequent maps of forest area, forest type, forest carbon stocks, forest age (young, mature, and old) and spatial estimates of uncertainty for each product.
- Consistent and repeated measurements of plant and animal species richness and habitat quality in a measurement system that is co-located or coincides with the forest inventory, and data reporting to a central database.
- Habitat connectivity data products.
- Ecosystem model projections of future forest carbon dynamics and vulnerabilities to drought, fire, and insects under various climate scenarios (transition model projection from research oriented to operational oriented analysis).

Socioeconomic and policy challenges and solutions

To some extent, forest management priorities on national forests have changed from timber harvest and maximizing wood production to conservation and adaptation to climate change (USDA Forest Service, 2022). These changes are well aligned with strategic forest reserves that can serve as focal areas of ecological integrity and genetic diversity that benefit adjacent areas (Greater Protected Areas). As our western US and Oregon analyses show, achieving protected area targets is a practical goal and does not require all federal forestlands. Many areas will remain outside protected areas, but these forests will experience long-term benefits from increased proximity to protected landscapes.

Forest ownership by public real estate investment trusts (REITs) and timber investment management organizations (TIMOs) have the goal of maximizing return on investment. In Canada and the United States, 60% of the timberland area owned by the top ten entities was in REITs in 2015. Over the past 40 years, as much as 304,000 hectares of Oregon's non-industrial forest ownership has transferred to forest industries by buyouts and mergers, now dominated by a few industrial owners in each county (Willer, 2021). As of 2020, at least 40% of private forest lands are owned by investment companies as public or private REITs whose forestland portfolio is managed by TIMOs. The industry consists of investors or owners and corporate management that serves them, and it often subcontracts harvest, transport, reforestation and pesticide chemical application. Forest operations are compartmentalized. While REITs and TIMOs seek to monetize the value of timber harvest, they also have been involved in projects that monetize ecosystem services, carbon sequestration, and, in some cases, a land use change from forestry to development. Integrated forest companies own forestland and mills and they, on the other hand, depend on a consistent, predictable supply of wood. They view limits on harvest for ecosystem values as an encumbrance that impacts the bottom line. REITs, TIMOs and integrated forest product companies own the bulk of private forests in Oregon, but there are approximately 1.49 million hectares of family owned non-industrial forests that are enjoyed for privacy, wildlife, scenic values, water and, to a far lesser extent, harvest.

Currently, there is little incentive to manage private forestlands for ecosystem resilience to climate change impacts, biodiversity or carbon storage, and industrial management has resulted in significant losses of habitat and biodiversity and carbon stocks, and degraded water systems. Oregon's private forests laws have lagged behind those in California and Washington for decades, and recent changes adopted in 2022 focus primarily on changes for threatened and endangered fish species, not climate mitigation, terrestrial biodiversity or drinking water supplies.

Land trusts have played a role in protecting Oregon's private forestlands, yet their coverage area is growing but not yet substantial. With significant funding, land trusts could play a greater and important role in securing high-priority private forest lands from development and harvest. Land trusts typically use conservation easements to protect key private lands from extractive management and to protect certain values in perpetuity. This analysis provides a framework to spatially examine the value of private forestlands and prioritize efforts for the greatest climate mitigation and biodiversity protection benefits.

To sustainably achieve climate and conservation goals, projects must not lead to more emissions from deforestation and forest degradation (Nolan et al., 2021). To do so and be included in meeting preservation targets, lands should be protected at GAP 1 or GAP 2 status (IUCN 1a to VI). Roadless areas that are not currently inventoried should be inventoried to determine if they qualify.

Projects have to demonstrate permanence of protected forest carbon, and account for leakage and additionality. Regular assessment of permanence, leakage and additionality is essential for forest offsets programs to ensure there is not over-crediting (Anderegg et al., 2020). Moreover, carbon accounting among projects is needed to understand their contributions to meeting climate goals. Permanence can be addressed by requiring a portion of the credits (e.g., 20%) be set aside as a buffer in case natural disturbances occur in the project area (wildfire, beetle kill; Anderson et al., 2017). Leakage means that protecting one area of forest could result in cutting elsewhere, even in another country, and currently there is no international program to track it. Leakage could be addressed by assuming leakage exists and providing only partial credit for projects. Although a regulatory pathway is the typical approach to constraining what qualifies for meeting the intended goal with a minimum of unintended consequences, the requirement of additionality can hinder success in protecting private and indigenous forestlands. Additionality means one has to demonstrate that the climate benefits of preserving forests would not have occurred without the project. An option is to have science-based verification of proposed projects before they are approved, and if a proposed project cannot protect the whole area, then provide partial credit for the areas that are most likely to be protected with permanence. Accounting and incentives could be applied to ensure the protection targets are met at local to national scales. Offsets are just one of a number of ways (and not the best way from a climate mitigation perspective) in which forest ecosystem carbon removals from the atmosphere and accumulated carbon stocks can be used, accounted for, and forest stewards rewarded.

Conclusion

The most important action Oregon can take to mitigate climate change, reduce biodiversity losses, and protect watersheds for drinking water is to set aside existing forests. Reforestation or afforestation can be done too, but it takes decades for young trees to mature into net carbon sinks. Planting young trees will not result in much additional storage within the time forest carbon stocks need to increase in order to contribute to emission reduction and global warming targets.

The approach developed by Law et al. (2021) demonstrated the value of coupling forest carbon and biodiversity metrics into a spatially continuous prioritization framework that can be applied across large, diverse forested regions. Here, we improved the approach by adding a resilience metric that represents connectivity and topographic diversity, and used finer resolution (30 m) and more recent data to better resolve within-state variability in carbon, drinking water sources, and biodiversity and resilience metrics. An ecoregion-based approach along with resilience-based metrics will ensure species and habitat are protected and connected so that species can move to areas where they can survive and thrive as climate change intensifies.

The analysis identifies the potential for a well distributed forest reserve network within Oregon that captures unique ecological facets by ecoregion to achieve targets for protecting 30% of forests by 2030 and 50% by 2050. Protecting forest carbon, watersheds, and biodiversity are universally important priorities regionally, nationally and globally, and our framework could be applied in other regions for mitigation and adaptation to climate change.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: The forest prioritization dataset generated for this study will be publicly archived with PANGAEA (https://www.pangaea.de/). Further, the following existing dataset were analyzed for this study. Forest structure and composition data were from the Landscape Ecology Modeling Mapping and Analysis (Lemma) Team (https://lemma.forestry.oregonstate.edu/data). Forest disturbance data were from University of Maryland's Global Forest Change dataset (https://earthengine.google.com/). Protected Area data were from the United States Geological Survey GAP Analysis program (https://doi.org/10.5066/P92QM3NT), as were species habitat maps (https://doi.org/10.5066/F7V122T2). Forest land management data were from the Oregon Department of Forestry (https://spatialdata.oregonexplorer.info/). Surface drinking water source data were from the Oregon Department of Environmental Quality (https://www.oregon.gov/deq/wq/programs/Pages/DWP-Maps.aspx).

Author contributions

BL: conceptualization the project. BL and LB: investigation and writing – original draft preparation. LB: data analysis and visualization. BL, LB, DM, WR, and RB: writing – review and editing. All authors have read and agreed to the published version of the manuscript.

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Conflict of interest

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2022.1028401/full#supplementary-material

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Ecosystemic resilience of a temperate post-fire forest under extreme weather conditions

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Introduction: The effects of climate change are exacerbating the fire risk in forests worldwide. Conifer plantations in particular are especially vulnerable to fire outbreaks. At the end of the extraordinarily hot and dry summer of 2018, a forest pine plantation burned in Brandenburg, NE Germany. Different forestry interventions were carried out after the fire, while one area of the damaged plantation remained untouched.

Methods: We investigated the resilience of the forest ecosystem and the effectiveness of different active and passive forest restoration measures during the subsequent relatively warm and dry years 2019–2021.

Results: One year after the fire, *Populus tremula* showed strong spontaneous colonization at all sites. In contrast, the majority of planted *Pinus sylvestris* plantlets died on the plots that had been salvage-logged after the fire. Three years after the fire, *Populus tremula* successfully established itself as the dominant tree species on all plots, with the highest abundance on the plot where the overstorey of the dead pines was left. *Betula pendula*, *Salix caprea,* and *Pinus sylvestris* showed lower abundance, with their proportion increasing with decreasing cover by dead trees. The distribution of regrowing trees is very heterogeneous across the different treatments and plots. In the clear-cut plots, the extreme microclimatic conditions expose the young trees to additional heat and drought, while the retention of deadwood measurably buffers the temperature and water stress.

Discussion: The resilience and adaptability of naturally regenerating forests that develop into ecosystems that are more diverse seem more promising than restoration through intervention. Apart from hampering restoration under extreme weather conditions, post-fire salvage logging contributes to soil degradation and loss of organic carbon.

KEYWORDS

restoration, rejuvenation, microclimate, temperature, VPD, salvage logging, deadwood retention

Introduction

Landscape fires are a substantial and inherent component of many ecosystems around the World (Pausas and Keeley, 2019). Between 2001 and 2010, a global average of approximately 464 Mha burned every year, with a relatively low share in forest biomes (Randerson et al., 2012). In many regions of the world, fires have become larger, more frequent, and more widespread (Iglesias et al., 2022). For instance, in southern boreal forests of Western Siberia, the current fire regime is unprecedented for the last five millennia (Feurdean et al., 2020). In general, Earth seems to enter an age of fire, the Pyrocene (Pyne, 2020). Fires are increasingly perceived as a challenge, and fire suppression management has been implemented (Doerr and Santín, 2016). In Europe, between 1986 and 2016, an average of approximately 140,000 ha of fire-related disturbances was recorded per year, accounting for 0.06% of the total forested area (Senf and Seidl, 2021). The frequency and impact of forest fires depend on the region, climate, vegetation composition, and human land use (Lavorel et al., 2007). By emitting greenhouse gases and aerosols as well as modifying surface properties, fires can affect not only vegetation but also climate (Lavorel et al., 2007). As an effect of ongoing climate change, the increasing frequency of fire weather, the expanding length of the fire season, the area burned and the occurrence of fires will become all the more important in the future (Bowman et al., 2020). Apart from climate change, the forests' structural, physiological and mechanical characteristics are other decisive factors affecting forest vulnerability and these can be controlled by forest management (Forzieri et al., 2021).

In Central Europe, only 0.5% of fires are of natural origin, while ca. 39% are negligently and 56% deliberately ignited due to arson (Ganteaume et al., 2013). In Germany, the average area burned since 1991–2018 was around 447 ha per year and only 283 ha between 2009 and 2018 with around 0.5 ha burned per fire, while the state of Brandenburg represents the area that burned the most (Fernandez-Anez et al., 2021). Most fires in Germany (65%) were recorded in coniferous forests (Gnilke and Sanders, 2021). The dominant forest type in the region of Brandenburg are Scots pine (*Pinus sylvestris*) monocultures on sandy soils that have replaced many of the previous and less-flammable broadleaved forest (Dietze et al., 2019).

As summarized by Dimitrakopoulos et al. (2011), the ignitability or flammability of plants is related to the time and temperature of ignition (Anderson, 1970; Martin et al., 1994) as well as the chemical fuel properties (Rundel, 1981). This relates to the heat and ash contents, as high heat content increases fuel combustibility and fire intensity (Shafizadeh et al., 1977) and high ash content reduces fuel flammability (Philpot, 1970). *Pinus sylvestris* takes 28.063 s to ignite at 248.25°C ignition temperature, and has a relatively high heat and low ash content compared to other coniferous species (Dimitrakopoulos et al., 2011). The flammability of cones and needle litter is another important component that contributes to the fire properties of pine forests (Fonda, 2001; Fonda and Varner, 2004). Especially the moisture content was reported to be a relevant factor due to increasing ignition times and lower ignition frequency (Popović et al., 2021). A moisture content of the surface material of less than 30–35% increases the fire ignition probability (Tanskanen et al., 2005). Besides that, organic metabolites such as cellulose, tannins, terpenes, and alkane wax contents are crucial chemical components (Ormeño et al., 2020). Canopy depth and leaf area index are forest stand characteristics negatively correlated with ignitability, while clearcuts of former Scots pine stands showed the highest ignition probability; also the frequency of ignitions was lower for sites with higher canopy cover and leaf area index (Tanskanen, 2007). The flammability of pine stands was shown to be higher in stands that have burned previously considering flame height and residence, shoot flammability as well as time to ignition or higher combustibility (Romero and Ganteaume, 2021).

Although fire prevention, early detection, and documentation have improved, there is less agreement on how forest owners should manage their forests after fire disturbance, especially in areas where there have been far fewer fires in the past.

As the frequency of fire events is expected to increase in Central European forests (San-Miguel-Ayanz et al., 2019), an appropriate post-fire management approach is needed to support effective forest restoration while safeguarding the provision of ecosystem services and reducing the risk of future fire events (Ascoli et al., 2013). Many strategies focus on fire prevention and increased suppression through the development of detection technologies, and less effort is expended in forest management measures such as improving forest structures and species composition and converting timber plantations into more natural and climate-resilient forests that are less prone to fire (FAO, 2007). Regardless of international scientific evidence, the conventional response to calamities is mostly the immediate clearing of sites and artificial reforestation (Moreira et al., 2012a). This is often also promoted legally and financially by policy makers in the European Union (Vallejo et al., 2012b). However, this is not always the most cost-effective approach and ignores the natural properties of the ecosystem that can facilitate the restoration processes (Moreira et al., 2012b). Soil protection and water regulation, management of trees, habitats, and biodiversity are to be considered as restoration objectives (Robichaud, 2009; Vallejo et al., 2012a). In the worst case, fires and forest management can increase the risk of regeneration failure. In Siberia, it was found that dry pine stands and repeatedly disturbed forests were the most vulnerable to experience a biome shift during regeneration toward steppe vegetation (Kukavskaya et al., 2016).

In this study, we investigate the post-fire succession of a forest fire area that burned in summer 2018 and the effectiveness of different silvicultural treatments on forest regeneration and microclimate regulation. In particular, sites that had been cleared, thinned, or not managed were investigated in both one and two vegetation periods after a forest fire (e.g., after one growing season in December 2019 and after two growing seasons in May 2021) in a Scots pine plantation in north-eastern Germany. Measurements of temperature and relative humidity accompanied the recording of succession.

Materials and methods

Study sites

The study sites are located in a forest fire area that burned in late August 2018 in the south of Brandenburg, Germany, approximately 60 km south of the Berlin city border. The fire affected about 400 ha of Scots pine monocultures that were established for timber production in different years after World War II. Most of the pine trees died immediately or in the following weeks after the forest fire. After the fire, different forest owners chose a variety of restoration interventions, while some of the areas remained unmanaged. After the first investigations started already in 2019, an ecosystemic research project was initiated in May 2020 with comprehensive ecological monitoring.[1] Some plots sampled in the present study are part of the PYROPHOB research project. The project is based on the collaboration of eight institutions that investigate the effects of forest fire and different post-fire management approaches on ecosystemic development to formulate strategies for developing more pyrophobic and climate-resilient forests in burned areas.

The study area is characterized by relatively low annual precipitation of 500–550 mm on average and a negative ecoclimatic water balance of –220 to –170 mm per year and therefore represents one of the driest regions in Germany (Schulze et al., 2013). It is also characterized by relatively high temperatures in summer and cold winters, so that the annual fluctuations are relatively large. The average annual temperature is 8.5°C with an annual variation of 18.5 and 19.0°C (Gauer and Aldinger, 2005). The postglacial landscape has an average altitude between approximately 95 m and 110 m above sea level. The soil was formed from deposits of meltwater sands and periglacial and fluviatile sands and gravels.

The years 2018–2021 were exceptionally warm (DWD, 2022) and dry with severe impacts on soil water availability and drought stress (Marx et al., 2016) across Germany.

Tree rejuvenation and microclimate were sampled in the years 2019 and 2021. However, the location of both sampled indicators does not always coincide with each other (**Figure 1**). Some sites were surveyed before and after forestry interventions had been carried out and therefore had to be attributed to different treatments for the two sampling periods (**Table 1**).

The study sites are located in the flat lowlands of Brandenburg on poor sandy soils. Due to the proximity of sampling plots and the absence of significant topographic structures, other factors such as elevation, slope, exposition, and soil were not considered in this analysis.

Rejuvenation

Tree rejuvenation was surveyed in December 2019, the first growing season after the fire and in May 2021, when the third growing season started. In 2019, two clearcut sites (CC_1, CC_2) and two unmanaged sites (UM_1, UM_2) were investigated on two sample plots each. In 2021, one clearcut (CC), one thinned (TH), and one unmanaged (UM) site were surveyed on two sample plots each.

Before the surveys started in 2019, a north-oriented 50 m to 50 m grid with a centered point in each grid was created within the forest fire polygon using ArcMap (Version 10.7.1). Within homogeneous forest sections, centric points were selected as study plots but leaving out forest roads and skidding trails. The points were located with a GPS device with an accuracy of 5–10 m. There, sample plots of 10 m radius were established, every rejuvenating tree individual was recorded and taxonomically determined. For each tree also the vitality status was documented, differentiating apex, side shoot, and leaf damages. In addition, dead individuals were counted in 2019. In 2021, combined damages were registered, which were not encountered in 2019. Dead trees were not recorded in 2021 due to bad identifiability. The number of trees counted on the sampling plots was interpolated to one hectare.

Microclimate

Microclimate data were collected during summer 2019 and 2021. In 2019, two sample plots per site with two data-loggers each were mounted on a wooden pole into a white box facing north in order to protect them from direct sunlight (Blumröder et al., 2021). One data-logger measuring temperature was located at 1.3 m on the pole, another one measuring temperature and relative humidity was at 0.1 m above ground on the same pole. Data-loggers were installed on May 10, 2019, and records were taken starting from May 11, 2019 in 30-min intervals. Before demounting the data-loggers on September 13, data were downloaded twice and all records of installation and demounting days were excluded as samples. From the remaining 123 days in the sampling period, the hottest days were selected, being defined as days with a daily mean temperature over all samples above 23.22°C, which represents the upper 25% quantile. From the resulting 31 days, the five maximum values per day were extracted and averaged as the daily maximum temperature (T_{max}) for each data-logger. The driest days were

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[1] www.pyrophob.de

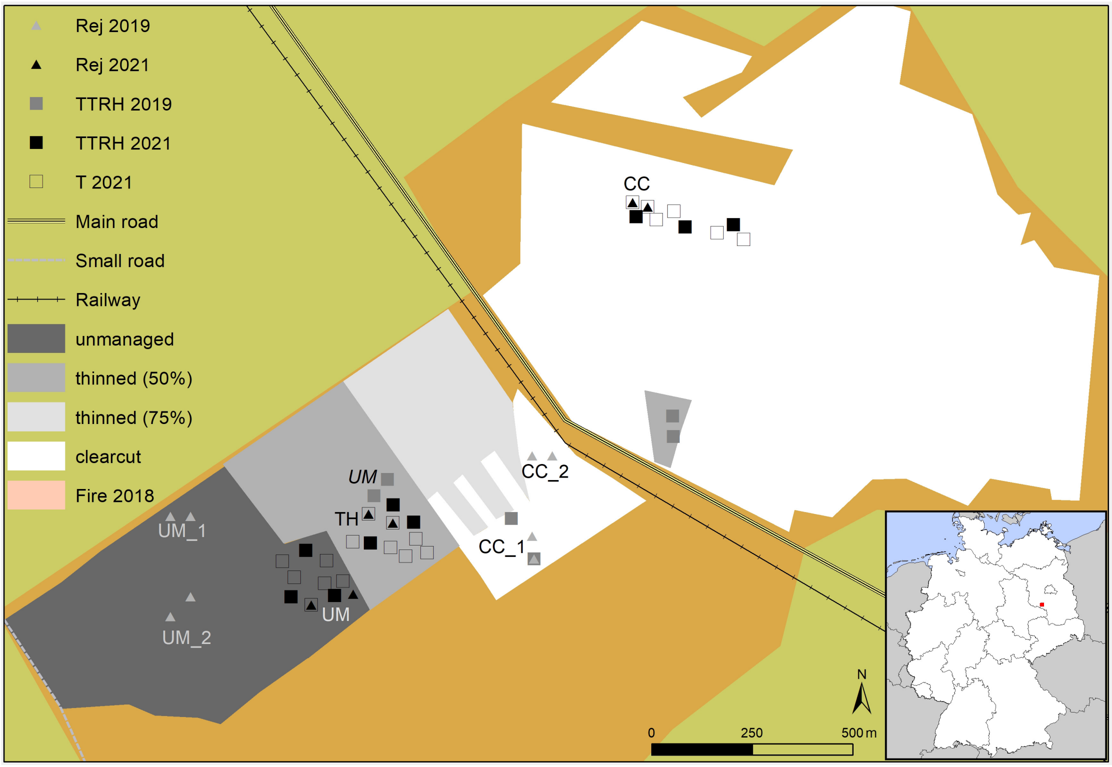

FIGURE 1
Overview of study sites in the south of Brandenburg, Germany, and respective treatments and sample plots (Rej, location of the rejuvenation assessment and the corresponding year; TTRH, location of temperature data-loggers at 1.3 m above ground together with data-loggers measuring temperature and relative humidity at 0.1 m above ground in the corresponding year; T 2021, temperature data-logger at 1.3 m above ground in the year 2021).

TABLE 1 Overview of time and kind of intervention on the study sites in relation to the collected data.

	Site	Data collection	Intervention
Rejuvenation (2019)	UM_1	Dez 2019	None
	UM_2	Dez 2019	None
	CC_1	Dez 2019	Clearcut: Winter 2018/2019; Pine planted: March 2019
	CC_2	Dez 2019	Clearcut: Winter 2018/2019; Red oak planted: Autumn 2019
Microclimate (2019)	Clearcut	Summer 2019	Clearcut: February 2019
	Thinned	Summer 2019	Thinned: Spring 2019
	Unmanaged	Summer 2019	None
Rejuvenation and microclimate (2021)	CC (clearcut)	Rejuvenation: May 2021; microclimate: Summer 2021	Clearcut: Winter 2018/2019
	TH (thinned)		Thinned: Beginning of 2020
	UM (unmanaged)		None

filtered as days with a daily mean vapor pressure deficit (VPD) over all samples above 1.22 kPa, which represents the upper 25% quantile. From the resulting 31 days, the five maximum values were extracted and averaged as daily maximum VPD (VPD_{max}) for each data-logger.

Data-loggers were installed again on May 18, 2021, but in a slightly different setting. In the frame of the PYROPHOB project, ten sampling plots per treatment were established. On each sampling location, a wooden pole with a white box facing north containing one data-logger measuring temperature at 1.3 m above ground was installed. On three plots per treatment, a second data-logger measuring temperature and relative humidity was installed at 0.1 m above ground. Records were taken starting from May 19, 2021 in 10-min intervals until August 25, 2021. After excluding days with incomplete samples, out of the remaining 86 days the hottest days were selected as days with a daily mean temperature over all samples above 22.52°C, which represents the upper 25% quantile. From these resulting 22 days, the five maximum values were extracted and averaged as daily maximum temperature (T_{max}) for each data-logger. The driest days were filtered as days with a daily mean VPD over all samples above 1.19 kPa, which represents the upper 25% quantile. From the resulting 22 days, the five maximum values were extracted and averaged as daily maximum VPD (VPD_{max}) for each data-logger.

Non-parametric tests (Kruskal–Wallis rank-sum test) were conducted to test for differences among the treatments as normality distribution could not be confirmed according to Shapiro–Wilk normality test with Pairwise Wilcoxon Rank Sum Tests (p-values adjusted using Bonferroni corrections) for pairwise comparisons among treatments. The treatments comprise clearcuts (e.g., post-fire salvage-logged where all trees have been removed using harvesters and skidders), thinned (e.g., about half of the trees have been removed using harvesters and skidders), and unmanaged (none of the trees have been removed after the fire). All data processing, analyses, and figures were computed using R (R Studio Version 1.3.1093).

Results

In 2019, one growing season after the forest fire, the passively restored sites, where no intervention was carried out after the fire, showed the highest number of rejuvenating trees (mean = 39,248 trees per hectare; standard deviation = 15,181; $n = 4$). On actively restored sites, where trees were planted after clearcutting, fewer trees were recorded (mean = 33,709 trees per hectare; standard deviation = 12,392; $n = 4$). In 2021, two growing seasons after the fire, fewer trees were recorded. Sites where all timber remained on site after the forest fire showed the highest number of living young trees (mean = 21,740 trees per hectare; standard deviation = 22,328; $n = 2$) followed by the clearcut sites (mean = 19,752 trees per hectare; standard deviation = 2,814; $n = 2$) and sites where burnt trees were partially removed (mean = 13,226 trees per hectare; standard deviation = 1,598; $n = 2$). *Populus tremula* was the dominant rejuvenating tree species across all sites and years (**Figures 2**, **3**).

Except for *Pinus sylvestris*, after the first growing season, the majority of saplings were alive (**Figure 2**). Few individuals of *Populus tremula* showed signs of damages at the apex and side shoots. After two growing seasons, the proportion of damaged trees increased. In addition, multiple damages on the same tree individuals were recorded for some trees (**Figure 3**). Pine trees showed the highest mortality. In particular, planted seedlings mostly died (23–40% survived) approximately 1 year after planting while naturally rejuvenating pine trees mostly survived (91–100% survived) (**Table 2**).

On the actively restored plots, the total number of surviving pine trees was higher for pines that were established naturally compared to the planted ones. On the unmanaged sites, where no pine trees were artificially planted, the number of living pines varied between 2,928 and 16,202 trees per hectare (**Figure 4**).

Species richness varied between four to five species on the clearcuts, including sites where *Pinus sylvestris* and *Quercus rubra* were planted. *Quercus rubra*, representing a non-native species in the region, was the only tree species that did not rejuvenate naturally. On the unmanaged sites, two to five species were recorded, and five on the thinned sites. In the first sampling season, unmanaged sites showed a slightly higher Shannon Diversity Index value compared to the post-fire salvage logged sites (**Figure 5A**). After the second vegetation season, the increasing dominance of *Populus tremula* and the lower abundance of other species in the plots resulted in a lower Shannon Diversity Index value (**Figure 5B**). At this time, the value was highest in the clearcut and lowest in the unmanaged site though this was substantially influenced by planted non-native trees in the clearcuts.

In both sampling years, T_{max} of the warmest days and VPD_{max} during the driest days differed between the treatments ($p < 0.01$). In 2019, T_{max} at 1.3 m was significantly higher on the clearcuts compared to thinned ($p = 0.04$) or unmanaged ($p = 0.013$) sites, while thinned and unmanaged sites did not significantly differ from each other ($p = 1$) (**Figure 6A**, top). At 0.1 m, compared to unmanaged sites T_{max} was significantly higher on the clearcuts ($p < 0.001$) and thinned sites ($p < 0.001$), while T_{max} did not differ between the clearcut and the thinned sites ($p = 0.65$) (**Figure 6A**, bottom). Maximum VPD was highest on the clearcut and significantly lower on the thinned sites ($p = 0.024$). The unmanaged stand showed the lowest VPD_{max}. It was significantly lower compared to the thinned ($p = 0.011$) and the clearcut sites ($p < 0.001$) (**Figure 6B**).

In 2021, T_{max} at 1.3 m was highest on the clearcut and significantly lower on unmanaged sites ($p = 0.0025$). There was no significant difference between the clearcut and the thinned sites (**Figure 7A**, top). At 0.1 m, T_{max} was highest on the clearcuts and thinned sites, which did not significantly differ from each other. Unmanaged sites were significantly cooler than thinned ($p = 0.00028$) and clearcut ($p = 0.0045$) sites (**Figure 7A**, bottom). Maximum VPD was lowest on unmanaged sites and significantly higher on thinned and clearcut sites ($p < 0.001$), which did not differ from each other (**Figure 7B**).

Discussion

Natural succession

The results of this study show that 1 year after a forest fire, the pioneer tree species *Populus tremula* showed strong spontaneous colonization at all sites. In contrast, the majority

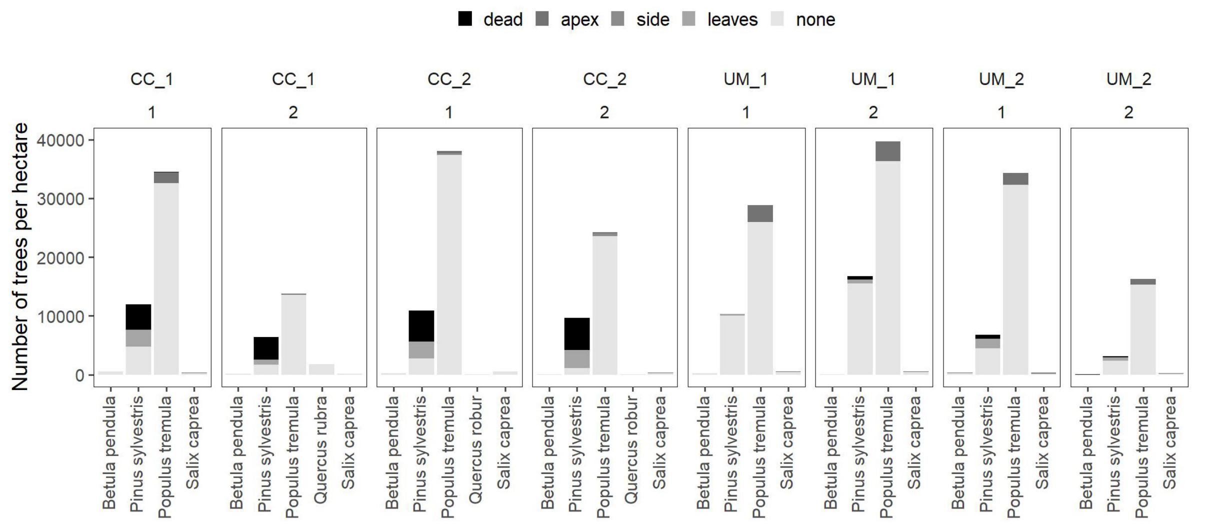

FIGURE 2
Distribution of vitality and damages for tree species occuring per treatment (CC, clearcut; UM, unmanaged) and plot (two plots per treatment represented by the number below the treatment name) recorded in the year 2019. Colors of the stacked bars indicate the damage recorded on each tree individual.

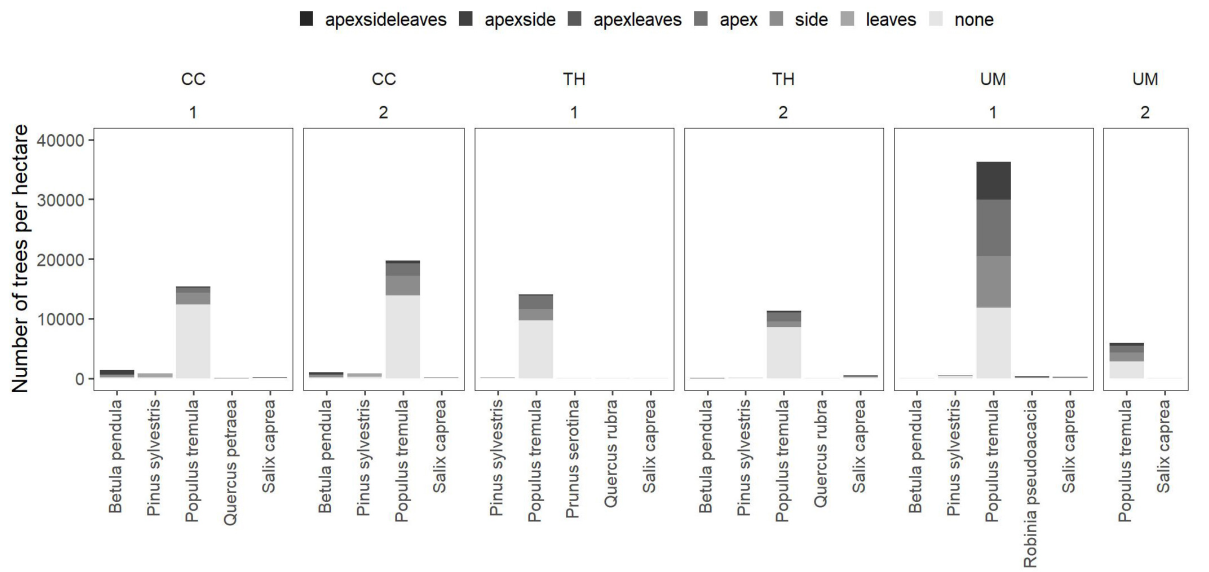

FIGURE 3
Distribution of vitality and damages for tree species occuring per treatment (CC, clearcut; TH, thinned; UM, unmanaged) and plot (two plots per treatment represented by the number below the treatment name) recorded in the year 2021. Colors indicate the damage recorded on each tree individual.

of planted *Pinus sylvestris* seedlings had died on the actively restored sites. In the clear-cut plots, the extreme microclimatic conditions exposed the young trees to additional heat and drought stress, while the retention of deadwood buffered both temperature and vapor pressure deficit. Three years after the fire, *Populus tremula* was the dominant tree species on all plots, with the highest abundance where the dead or dying overstorey was not removed. *Betula pendula*, *Salix caprea,* and *Pinus sylvestris* were also present, but with lower abundance. Strong regeneration of *Populus tremula*, *Salix caprea*, *Betula pendula,* and *Pinus sylvestris*, and less frequently also *Larix decidua* in the first 6 years after the fire was also found in burned pine forests in the Czech Republic (Adámek et al., 2018). There, the number of individuals of *Populus tremula* and *Salix caprea* decreased in

TABLE 2 Proportion of surviving individuals of *Pinus sylvestris* in the clearcut (site = CC) and the unmanaged (site = UM) sites comprising naturally established (type = nat) and artificially planted (type = pla) trees, and total number of surviving *Pinus sylvestris*.

Site	**CC_1**				**CC_2**				**UM_1**		**UM_2**	
Plot	**1**		**2**		**1**		**2**		**1**	**2**	**1**	**2**
Type	**nat**	**pla**	**nat**	**pla**	**nat**	**pla**	**nat**	**pla**	**nat**	**nat**	**nat**	**nat**
% surviving	100	40	100	23	100	27	98	31	100	97	91	94
Total surviving	4,775	2,865	1,432	1,114	3,724	1,942	1,751	2,419	10,313	16,202	6,143	2,928

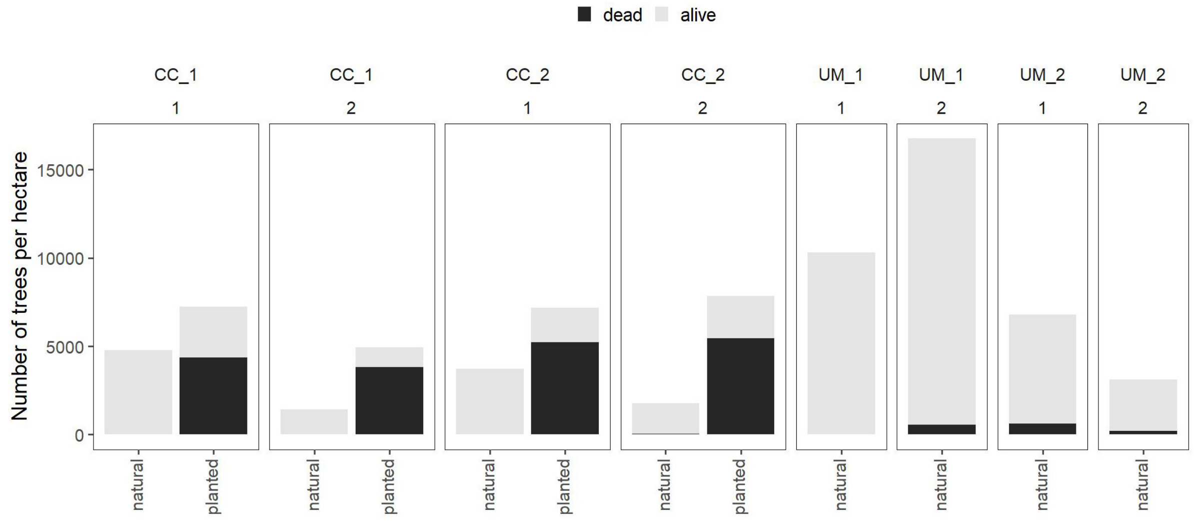

FIGURE 4
Number of individuals of actively planted and naturally rejuvenating *Pinus sylvestris* counted per treatment (CC, clearcut; UM, unmanaged) and plot (two plots per treatment represented by the number below the treatment name) recorded in the year 2019 stacked as dead (black) and living (gray) trees.

later stages, probably due to unfavorable habitat conditions. The establishment of pioneer tree species is not only relevant for the reforestation of the forest after a fire, but especially the ability of aspen to resprout after disturbance can contribute to a faster regeneration after future disturbances such as subsequent forest fires (Porter et al., 2022).

Although additional trees have been planted on the clearcut sites studied in 2019, the total abundance of naturally established trees clearly exceeded the trees counted on the post-fire salvage logged and actively restored sites (a total of 11,682 individuals that established naturally were counted compared to 8,340 planted trees).

Fire causes the combustion of organic layers covering the soil and can change the soil structure and chemical properties (Ne'eman et al., 1997; Úbeda and Outeiro, 2009). As fire temperatures rise, soil microorganisms, invertebrates, and seeds existing in the upper soil layer are more severely affected (Ne'eman et al., 1997). This might possibly result in a reduction in soil productivity and the survival chances of rejuvenating plants as well as an increase in carbon emissions from soil. The loss of organic matter and the destruction of soil structures can therefore be the cause of a decreased soil water retention capacity after fire (Úbeda and Outeiro, 2009; Pereira et al., 2018). Hence, whether for economic or for ecological reasons, a main goal in the management of the post-fire rejuvenation is a rapid reestablishment of soil cover (Mauri and Pons, 2019).

Active restoration

Reforestation by seeding or planting is commonly applied in post-fire forest restoration projects (Mazza, 2007; Moreira et al., 2009; Beghin et al., 2010; Morat, 2019), especially in forests where timber production is a main management objective (Franklin and Agee, 2003; Sessions et al., 2004; Ürker et al., 2018). In many countries, forest owners are obliged by law to reforest burned forests by replanting which can be subsidized by institutional funding programs (Mavsar et al., 2012; Ryu et al., 2017). Artificial reforestation is generally recommended in stands where the existing species are not

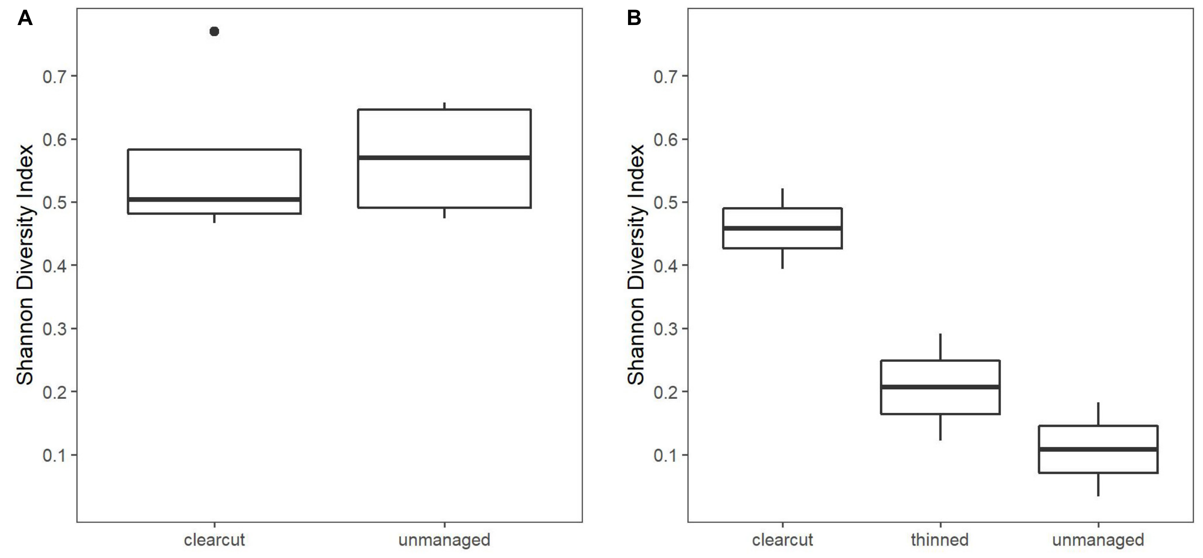

FIGURE 5
Shannon diversity index for tree rejuvenation: **(A)** one growing season; **(B)** two growing seasons after the fire.

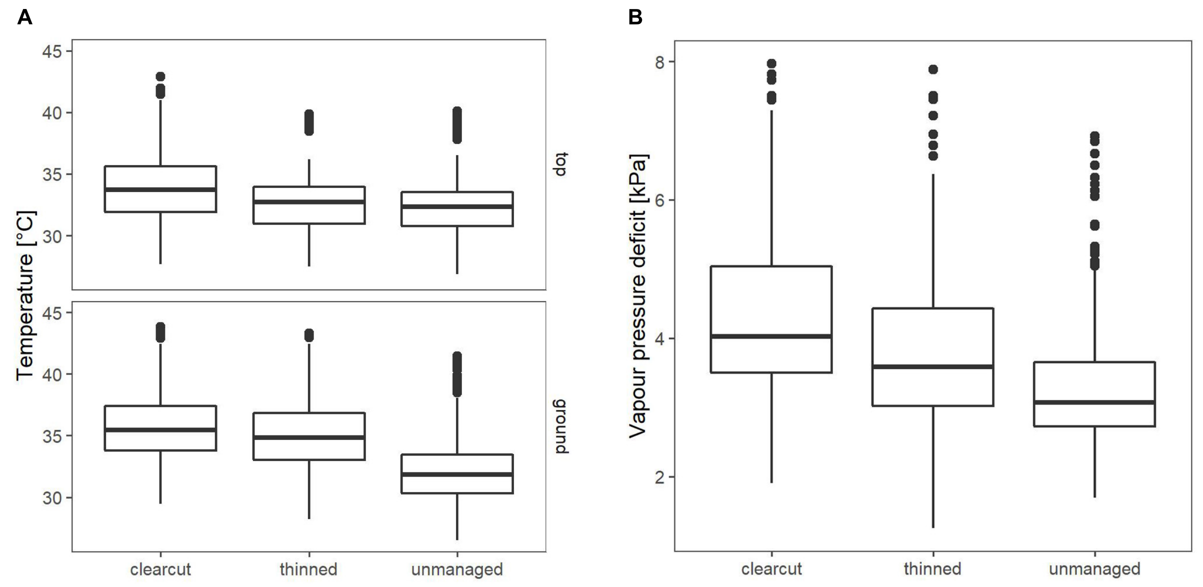

FIGURE 6
(A) Mean maximum temperature on hottest days (*n* = 31 days) in 2019 (top = 1.3 m; ground = 0.1 m). **(B)** Mean VPD on driest days (*n* = 31 days) in 2019, measured 0.1 m above ground.

fire-adapted, where no reproductive material has survived the fire and natural regeneration is not expected, or when forest species conversion is planned (Ne'eman et al., 1997; Beschta et al., 2004; Moreira et al., 2012b; Vallejo et al., 2012b; Ryu et al., 2017; Morat, 2019). The common perception is that planting on degraded areas is essential in order to ensure sufficient post-fire regeneration (Moreira et al., 2009; Vallejo et al., 2012a; Tinya et al., 2020). It is claimed that natural regeneration is unsuccessful, where post-fire salvage logging was applied and that artificial regeneration on these stands might be indispensable but as shown in the Italien Alps natural restoration is an effective alternative (Beghin et al., 2010). It is also argued that in ecosystems that have been modified by human interventions over a long time, natural succession is not sufficient to ensure site regeneration and might therefore not comply with the restoration objectives (Ne'eman et al., 1997;

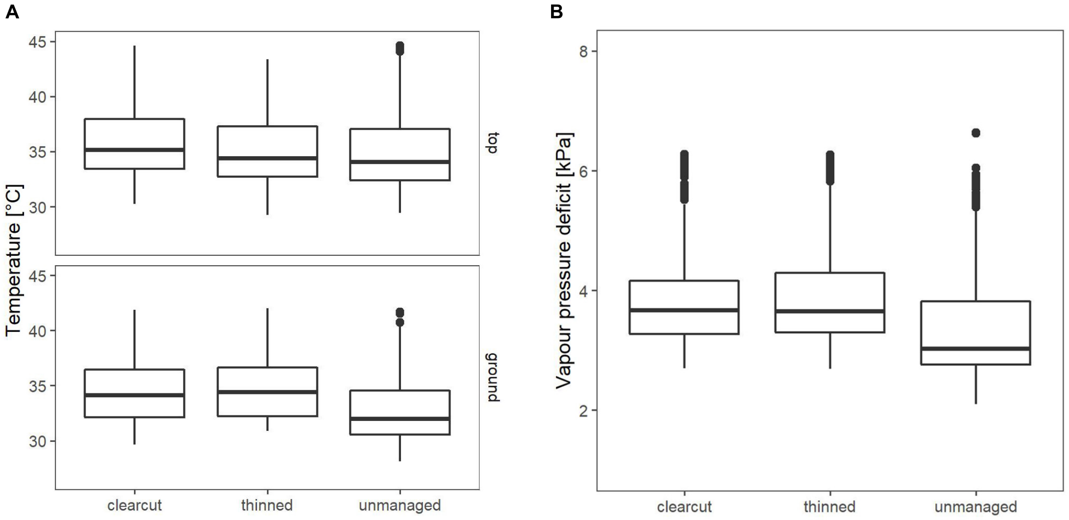

FIGURE 7
(A) Mean maximum temperature on hottest days (n = 22 days) in 2021 (top = 1.3 m; ground = 0.1 m). **(B)** Mean VPD on driest days (n = 22 days) in 2021, measured 0.1 m above ground.

Pausas et al., 2004). However, on sites where sufficient natural regeneration is expected, artificial reforestation measures are generally not recommended (Ne'eman et al., 1997; Beschta et al., 2004; Donato et al., 2006; Mavsar et al., 2012; Ibisch, 2019).

Nevertheless, reforestation is often applied before the ecosystem was given the chance to regenerate by itself, even when natural regeneration would suffice (Moreira et al., 2009). This also happened at the clearcut and replanted sites investigated in the frame of this study and the PYROPHOB project. Human intervention, such as post-fire salvage logging, aiming to speed up reforestation might impair natural regeneration processes, negatively impact biodiversity of usually slowly regenerating forests, promote exotic alien species or simply recreate the fire-prone stand condition prevailing before the forest fire (Franklin and Agee, 2003; Lindenmayer and Noss, 2006). Our findings show, that in the studied area, sufficient natural regeneration is taking place, even on clearcuts despite the lower abundance compared to the unmanaged sites. There is no need for active restoration in the study area, and the secondary site degradation due to post-fire salvage logging on the cleared and thinned sites could have been prevented by allowing natural regeneration.

Planting is usually conducted using saplings that were grown in tree nurseries, giving them a developmental advantage over seedlings germinating on the site. Due to this advantage, planted trees are claimed to have higher survival chances than natural regeneration, especially given the harsh post-disturbance conditions (Pausas et al., 2004; Newton et al., 2006). However, Alanís-Rodríguez et al. (2015) have observed a survival rate of 35% of the planted individuals even after costly replacement of dead seedlings over the first years after planting. In our case, the survival rate of pine was even lower. Nevertheless, pine saplings were planted repeatedly after the fire and subsequent clearcutting, from 2019 to 2021. While Scots pine plantations have always been established and favored as economically viable tree species by many forest owners in Brandenburg, the growing conditions seem to have become unsuitable in the climatically extreme years 2019–2021, which might represent a new average within a few years. Based on our findings, we cannot recommend establishing or replanting Scots pine stands. This type of forest plantation has already been described as "neither environmental-friendly nor climate smart, given their enhancement of climate-warming, low climate change mitigation potential, and negative effect on groundwater recharge" (Leuschner et al., 2022).

In a study conducted by Moreira et al. (2009) in the first regeneration phase after a forest fire in central Portugal, survival and growth rates of naturally regenerating oak (*Quercus faginea*) and ash (*Fraxinus angustifolia*) resprouters were higher than when the same species were planted. Tinya et al. (2020) obtained similar results with naturally regenerating seedlings (*Quercus petraea*, *Carpinus betulus,* and *Fraxinus ornus*) in a mountain forest in Hungary. In a study conducted by Donato et al. (2006) in regenerating Douglas-fir (*Pseudotsuga menziesii*) stands in Oregon, USA, natural conifer regeneration on sites was generally abundant and sufficient for the reestablishment of the stand according to regional standards, implying that active reforestation may not be necessary while post-fire salvage logging killed 71% of the natural regeneration and increased fine fuels on the site that added to greater subsequent fire risks. Ne'eman et al. (1997) made similar observations on regenerating *Pinus halepensis* stands in the first year after a forest fire on Mount Carmel in Israel. In a post-fire remote sensing-based study conducted by Vlassova and Pérez-Cabello (2016) in Northeast Spain, various regeneration mechanisms of the naturally regenerating species were sufficient to ensure the recovery of the future forest stand regardless of the applied treatment method. Additionally, it was argued that planting might have undesired effects on the stands' native biodiversity and genetic composition (Ne'eman et al., 1997; Mavsar et al., 2012). In a study by Schmidt and Wichmann (2000), both the mean number of species and diversity in the tree and herb layers were lower in the planted plots than on the naturally rejuvenated plots. Although Ürker et al. (2018) measured a more successful establishment of planted saplings over natural regeneration, they also acknowledged the negative effects of pine plantations on various ecosystem services like habitat provision and biodiversity maintenance and concluded that seeding or natural regeneration should be preferred over plantations in post-fire restoration.

In many countries, reforestation by planting after site preparation is considered as the most successful reforestation technique and is often preferred over seeding (Espelta et al., 2003; Pausas et al., 2004; Ginzburg and Steinberger, 2012; Alanís-Rodríguez et al., 2015). This could not be confirmed by our study. However, it is important to ensure that sufficient seed trees are available, especially pioneer tree species that can recolonize degraded forests rapidly. It is therefore advisable to conserve and promote these species in regions with large monocultures that are, or can become, calamity prone areas. In addition, they play an important role in conversion of monocultures to far less flammable forests.

Direct seeding is another possible reforestation strategy used in active restoration. It is cheaper and considered to have a lower environmental impact than planting. Broadcast seeding can also be conducted from the air, representing an option for the restoration of remote areas (Lamb and Gilmour, 2003; Pausas et al., 2004; Mansourian et al., 2005; Vallejo et al., 2009). Pausas et al. (2004) reported research performed after a wildfire in Catalonia where a relatively successful germination rate (circa 5%) was obtained from an aerial seeding. It is also argued that seedlings which directly regenerated from seeds and were exposed to the stands' conditions in their early development, will be better acclimatized and less susceptible to stand conditions than nursery-grown and transplanted seedlings (Vallejo et al., 2009). However, establishment rates of seeds are often lower comparing to planted seedlings, whether due to unsuitable site conditions for germination, extreme weather events, competition through fast growing ground vegetation or due to seed predation by birds and rodents (Espelta et al., 2003; Lamb and Gilmour, 2003; Pausas et al., 2004; Mansourian et al., 2005). Espelta et al. (2003) reported higher seedling establishment rates on planted plots in comparison to plots where seeding was conducted. In a research project by Pausas et al. (2004) after a wildfire in eastern Spain, predation rates of pine (*Pinus halepensis*) seeds applied by aerial seeding were high with more than 80% predated during the first 6 months after seeding. Restoration by seeding has eventually failed, as germination was not observed in any of the examined plots. In a burned pine (*Pinus halepensis*) forest in Greece, Spanos et al. (2010) observed the same woody species composition but a lower seedling establishment on the seeded plots compared to the non-seeded, naturally regenerating control. Thus, natural regeneration following fires, without intervention, may be preferable.

Post-fire salvage logging

Post-fire salvage logging is the most common post-fire activity, and often the first measure applied after fire in various forest types around the world (Ne'eman et al., 1997; McIver and Starr, 2001; Beschta et al., 2004; Lindenmayer and Noss, 2006; Peterson et al., 2009; Vallejo et al., 2012b; Ascoli et al., 2013; Leverkus et al., 2014). This strategy seems to be especially attractive for private forest owners dependent on the revenues from charred wood and on the subsidies often granted by the state for post-fire salvage logging operations (Vallauri, 2005; Vallejo et al., 2012b). However, the harvested charred logs have often only very little economic value, sometimes not even covering the operation costs (Ibisch, 2019). This was the case in post-fire studies conducted in Mediterranean forests in Italy and Spain, where the high costs for post-fire logging resulted in no economic benefits (Beghin et al., 2010; Leverkus et al., 2012). Nevertheless, economic output will depend on the level of damage caused to the trees, harvesting technologies, and market conditions (Pereira et al., 2018). Further arguments in favor of post-fire salvage logging are fuel reduction on the forest floor reducing the risk of future fires, the prevention of pest outbreaks, the safety of forest visitors, and the facilitation of further restoration measures (like planting) planned for the stand (Ne'eman et al., 1997; McIver and Starr, 2001; Lindenmayer and Noss, 2006; Beghin et al., 2010; Castro et al., 2011; Leverkus et al., 2012; Ascoli et al., 2013). Additionally, for certain tree species (e.g., pines, oaks, beeches), the exposure of the mineral soil, soil scarification through the logging operations and the improvement in light conditions through tree removal can support a more successful germination and seedling establishment (McIver and Starr, 2001; Sessions et al., 2004; Beghin et al., 2010; Ascoli et al., 2013).

On the other hand, salvage logging might cause more disturbance to the ecosystem than the fire itself (Lindenmayer and Noss, 2006). Arguments against salvage logging include the risk of soil compaction and erosion through logging operations and additional road building, an increase in runoff and sediment loads, the damage to ground vegetation and especially natural rejuvenation, the modification of hydrological cycles, the removal of biological legacies responsible for the improvement of microclimatic conditions and habitat provision for regenerating organisms and hence, the reduction in structural and species diversity (McIver and Starr, 2001; Beschta et al., 2004; DellaSala et al., 2006; Lindenmayer and Noss, 2006; Lindenmayer et al., 2008; Robichaud et al., 2011; Ibisch, 2019). In studies conducted in coniferous mountain forests in the USA and Canada, logging operations have generated soil compaction, reduced infiltration, and increased runoff rates and sedimentation in recently burned areas. Logged areas also experienced a slower recovery rate of regenerating vegetation compared to the unlogged control (Donato et al., 2006; Robichaud et al., 2011; Wagenbrenner et al., 2016). Beghin et al. (2010) showed that even when logging was conducted 4 years after the fire, it contributed to a prolonged soil disturbance. Other post-fire research projects have obtained similar results of increased soil compaction and erosion and a decrease in seedling recruitment and soil cover following post-fire logging operations (Inbar et al., 1997; Martínez-Sánchez et al., 1999; Spanos et al., 2010; de las Heras et al., 2012; Marañón-Jiménez et al., 2013; Moya et al., 2015; Malvar et al., 2017; Urretavizcaya and Defossé, 2019). Further studies have observed an increased fire risk due to fine woody debris left on the site after logging (Ne'eman et al., 1997; Donato et al., 2006), a reduction in soil nutrients (Merino et al., 2005), a decrease in seedling height growth (Martínez-Sánchez et al., 1999), and a decrease in species richness and diversity (Leverkus et al., 2014). In a study comparing different treatment methods in a mountain forest in Hungary, large cleared areas also experienced a limited seed dispersal, apparently due to the lack of seed sources on the stand as well as the lack of habitat for seed-dispersing animals (Tinya et al., 2020). The microclimatic conditions induced by salvage logging, such as decreased soil moisture and increased surface and soil temperature, have been commonly observed as unfavorable for woody species regeneration (Castro et al., 2011; Ginzburg and Steinberger, 2012; Marcolin et al., 2019; Tinya et al., 2020) but favorable for competing ground vegetation (Sessions et al., 2004; Beghin et al., 2010). In combination, this can result in seedling dehydration and mortality.

A major motivation for forest owners to clear the site early after the fire is the risk of losing timber revenues for rotten timber (Moreira and Vallejo, 2009; Robichaud et al., 2011; Vallejo et al., 2012b; Pereira et al., 2018). Sessions et al. (2004) estimated a volume loss of 22% of the still merchantable logs due to wood deterioration in the first years after a large forest fire in Oregon. Nevertheless, when applied immediately after the fire, logging operations might have a greater negative effect on the exposed vulnerable soil compared to a later implementation (Ne'eman et al., 1997; Mazza, 2007; Peterson et al., 2009; Wagenbrenner et al., 2016). Although soil degradation can be reduced or even avoided by certain harvesting techniques (e.g., cable systems, skyline yarding, helicopter), these are usually more expensive and their cost-effectiveness is dependent on the timber price (McIver and Starr, 2001; Vallejo et al., 2012b; Leverkus et al., 2018; Marcolin et al., 2019). On the other hand, the later post-fire logging takes place, the higher is the potential damage to tree rejuvenation already established on the stand (Martínez-Sánchez et al., 1999; McIver and Starr, 2001; Lindenmayer and Noss, 2006; Castro et al., 2011; Fischer and Fischer, 2012). According to Franklin and Agee (2003), post-fire logging generally does not facilitate ecological ecosystem recovery and is therefore often inappropriate for post-fire forest restoration.

Deadwood retention

Passive restoration favors natural succession and prescribes no artificial intervention in the natural processes of the ecosystem. Apart from natural rejuvenation, this also includes leaving burned residual wood on site, regardless of its state, size, or position. Organic materials remaining from the pre-disturbed stand are also called biological legacies, defined by Franklin et al. (2000) as "…the organisms, organic materials, and organically generated environmental patterns that persist through a disturbance and are incorporated into the recovering ecosystem." In burned forests, they are represented by surviving living trees, standing charred trees, standing dead snags as well as lying deadwood in different sizes and degrees of combustion (Franklin and Agee, 2003; Noss et al., 2006). Post-fire ecosystems are rich in biological legacies that are considered essential for post-fire recovery processes, especially in the initial regeneration phase (Franklin and Agee, 2003; Beschta et al., 2004; Noss et al., 2006; Leverkus et al., 2014). Many researchers have described the positive effects of biological legacies on regenerating ecosystems (DellaSala and Hanson, 2015). One major benefit provided through the sheltering effect of both standing and lying residual deadwood is the amelioration of the stands' microclimatic conditions—keeping temperatures stable, protecting the soil and vegetation from direct solar radiation, and retaining soil moisture levels more favorable for germination and for the establishment of natural regeneration (Martínez-Sánchez et al., 1999; Pausas et al., 2004; Moreira and Vallejo, 2009; Peterson et al., 2009; Beghin et al., 2010; Castro et al., 2011; Marañón-Jiménez et al., 2013; Moya et al., 2015; Ibisch, 2019; Marcolin et al., 2019).

Our findings show that the retention of the dead trees provides shade and reduces both surface and ambient temperature. In turn, the vapor pressure deficit is reduced, lowering additional water losses through evapotranspiration and desiccation of plants. As water presents one of the most limiting resources for tree growth in the study region and these conditions are likely to worsen in the future, it is becoming ever more important to prevent additional water loss. Our data confirm the microclimatic benefits provided by deadwood left on site. Apart from contributions to cooling and moisture retention in the vegetation period, it can also be beneficial under winter conditions, as it absorbs heat radiation and promotes snow melting, providing adequate growth conditions for the seedlings in its proximity (Castro et al., 2011). Surviving charred vegetation with undamaged root system supports soil stabilization while coarse and fine woody debris protect the soil from compaction and erosion (Marañón-Jiménez et al., 2013; Leverkus et al., 2014; Vlassova and Pérez-Cabello, 2016; Marcolin et al., 2019). Surviving living trees also act as seed sources providing reproductive material for the regeneration onsite, while both living trees and dead snags can be used as perches for seed-dispersing species and thereby help accelerate natural succession (Franklin and Agee, 2003; Whisenant, 2005; Moreira and Vallejo, 2009; Marzano et al., 2013). Additionally, coarse woody debris and snags provide habitat for many post-disturbance specialized species, like cavity-living birds or wood decomposing insects, thereby increasing species diversity and often forming regional diversity hotspots. Increased species diversity is also promoted by increased structural diversity and heterogeneous light conditions on uncleared stands (Beschta et al., 2004; Mazza, 2007; Beghin et al., 2010; Marzano et al., 2013; Leverkus et al., 2014; Marcolin et al., 2019). Another benefit is the retention of nutrients stored in the wood and their later provision through decomposition onsite (Peterson et al., 2009; Gustafsson et al., 2012; Marañón-Jiménez et al., 2013; Leverkus et al., 2014; Vlassova and Pérez-Cabello, 2016). Uncleared stands also act as carbon pools (Gustafsson et al., 2012; Leverkus et al., 2018). Finally, it is argued that burned trees left on site do not increase future fire risk, as the snags slowly decay and are gradually integrated back into the soil in comparison to logging treatments where large amounts of flammable slash are often left on the ground (Donato et al., 2006).

Various study projects investigating the effects of different post-fire treatments have measured higher rates of vegetation recovery, natural seedlings emergence and abundance (Beghin et al., 2010; Castro et al., 2011; Marañón-Jiménez et al., 2013; Marzano et al., 2013; Chen et al., 2014; Leverkus et al., 2014; Moya et al., 2015; Vlassova and Pérez-Cabello, 2016), growth rates (Martínez-Sánchez et al., 1999; Marañón-Jiménez et al., 2013; Moya et al., 2015), species richness and diversity (Marzano et al., 2013; Leverkus et al., 2014), soil moisture, and soil microbial activity (Ginzburg and Steinberger, 2012), as well as increased structural diversity (Beghin et al., 2010), when deadwood remained on the regenerating stand in comparison to cleared stands. These positive effects were attributed to the ecological functions of deadwood residuals. Besides the protective effects of deadwood on plant desiccation by providing more favorable site conditions for tree growth, deadwood significantly reduces herbivorous browsing through increased surface roughness (Marangon et al., 2022).

Beschta et al. (2004) conducted a literature review investigating the ecological effects of common post-fire treatments and concluded that post-fire forest restoration aiming to maintain the stands' ecological functions should include the retention of large, living or dead, standing or lying trees. Regarding the concern that deadwood could increase stand flammability, they argue that woody debris is principally not responsible for carrying wildland fire but rather for the finer fuel sources such as grasses and tree foliage. Although Castro et al. (2011) measured no difference in seedling density between logged and unlogged stands, they concluded that the passive method should be preferred since the "no-intervention" plots seemed to enjoy an improvement in microclimatic conditions without suffering the disturbing effects of logging related heavy machinery observed on the logged plots. In addition to the better height growth and seedling recruitment rates, Moya et al. (2015) also observed the emergence of other tree species only in the "no-intervention" plots in a Mediterranean region, generating a higher species diversity in those stands. In a study conducted by Marzano et al. (2013), coniferous species (*Pinus sylvestris* and *Larix decidua*) considered as pioneers did not benefit from the exposed conditions on the salvaged areas and performed better in the proximity of deadwood. They concluded that there is a higher probability for seedling survival and establishment in the presence of at least one deadwood element within one meter from the regeneration. Once biological legacies have been removed from the stand, it takes a long time until they are replaced and their functions are recovered (Franklin and Agee, 2003).

Logging operations also increase the risk of further soil degradation as well as potentially damaging surviving or emerging natural regeneration (Lindenmayer and Noss, 2006; Marzano et al., 2013; Moya et al., 2015; Vlassova and Pérez-Cabello, 2016; Marcolin et al., 2019). In a study conducted in a burned pine stand (*Pinus halepensis*) in Spain, wood removal was shown to generate high seedling mortality while decreasing seedling growth due to mechanical damage and the exposed site conditions created by the logging operations (Martínez-Sánchez et al., 1999). Besides the physical damage, negative effects include the alteration of soil properties, water, carbon, and nutrient cycles, the facilitation of stand colonization by invasive species, the reduction in connectivity between non-burned forest areas, the homogenization of the forest structure, and the loss of structural diversity as well as a change in the stands' plant and animal species composition (Beschta et al., 2004; Lindenmayer and Noss, 2006; Lindenmayer et al., 2008 Peterson et al., 2009; Vlassova and Pérez-Cabello, 2016). Beghin et al. (2010) reported that while the passive strategy applied in their study was successful, the active measures traditionally prescribed by regional authorities were shown to alter the natural forest structure and slow down its regeneration. Others claim that the removal of biological legacies, especially of the surviving, still living trees, could potentially decrease the natural regeneration capacity of the stand and slow down the recovery of ecosystem functions and service provision (Ne'eman et al., 1997; Beschta et al., 2004; Beghin et al., 2010; Fischer and Fischer, 2012; DellaSala, 2020).

Conclusion

Questions about how to manage forests after such an event become more pressing, especially with an increasing fire risk under climate change. Catastrophic events and disturbances in timber plantations such as forest fires in artificial Scots pine monocultures can also help forests to develop into more structurally diverse, broad-leaved or mixed stands compared to actively restored sites where dead trees are removed and economically targeted trees are planted simultaneously. Even in planted Scots pine monocultures that were affected by a forest fire, there is a potential for natural succession, which supports the development into more broad-leaved stands. At the same time, the conditions for the reestablishment of coniferous plantations are becoming ever more severe, and effective active restoration becomes more difficult than in the past. Maintaining and developing a sufficient seed tree abundance, especially of pioneer tree species, can contribute to the forest resilience and help reestablish and maintain ecological functions and services after disturbance. In addition, the ability of certain tree species to resprout adds to the resilience of ecosystems and promotes their recovery from stress and disturbances. The development of the forest ecosystem under unfavorable growing conditions during extreme years with exceptionally hot temperatures and ongoing water deficits shows that the temperate forests of Central Europe still hold a certain inherent adaptive capacity that might be helpful in coping with the upcoming impacts of climate change. This does not mean, of course, that drastic changes in vegetation can be ruled out if the climate crisis continues to intensify as unchecked as it does at present.

Data availability statement

The datasets presented in this study can be found in online repositories. The name of the repository: Zenodo; https://zenodo.org/record/7371511#.Y4SRd32ZOUk.

Author contributions

JB did the conceptualization of the study and collected the microclimatic data, computed all data analyses, and wrote the first manuscript draft. FS, AG, and SG collected the rejuvenation data in the field in the frame of their bachelor thesis. PI was responsible for the conceptualization and supervision of the study. All authors contributed to finalizing the manuscript.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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Assessing carbon stocks and accumulation potential of mature forests and larger trees in U.S. federal lands

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Mature and old-growth forests (collectively "mature") and larger trees are important carbon sinks that are declining worldwide. Information on the carbon value of mature forests and larger trees in the United States has policy relevance for complying with President Joe Biden's Executive Order 14072 directing federal agencies to define and conduct an inventory of them for conservation purposes. Specific metrics related to maturity can help land managers define and maintain present and future carbon stocks at the tree and forest stand level, while making an important contribution to the nation's goal of net-zero greenhouse gas emissions by 2050. We present a systematic method to define and assess the status of mature forests and larger trees on federal lands in the United States that if protected from logging could maintain substantial carbon stocks and accumulation potential, along with myriad climate and ecological co-benefits. We based the onset of forest maturity on the age at which a forest stand achieves peak net primary productivity. We based our definition of larger trees on the median tree diameter associated with the tree age that defines the beginning of stand maturity to provide a practical way for managers to identify larger trees that could be protected in different forest ecosystems. The average age of peak net primary productivity ranged from 35 to 75 years, with some specific forest types extending this range. Typical diameter thresholds that separate smaller from larger trees ranged from 4 to 18 inches (10–46 cm) among individual forest types, with larger diameter thresholds found in the Western forests. In assessing these maturity metrics, we found that the unprotected carbon stock in larger trees in mature stands ranged from 36 to 68% of the total carbon in all trees in a representative selection of 11 National Forests. The unprotected annual carbon accumulation in live above-ground biomass of larger trees in mature stands ranged from 12 to 60% of the total accumulation in all trees. The potential impact of avoiding emissions from harvesting large trees in mature forests is thus significant and would require a policy shift to include protection of carbon stocks and future carbon accumulation as an additional land management objective on federal forest lands.

KEYWORDS

carbon stock, climate change, large trees, mature forests, national forest lands

1. Introduction

Nature-based climate solutions are needed to meet anticipated national targets associated with the Paris Climate Agreement which establishes a global framework to avoid dangerous climate change by limiting warming to less than 2°C (United Nations, 2015). In the United States, the Biden administration announced a "roadmap" for nature-based solutions during the COP27 climate summit (White House, 2022a). Reducing carbon dioxide (CO_2) emissions and increasing CO_2 removals from the atmosphere using forests are considered to be the most significant of terrestrial natural climate solutions globally and in the U.S. (Griscom et al., 2017; Fargione et al., 2018).

Protecting mature forests to achieve their potential to reduce greenhouse gases is controversial in part because it restricts logging (Law and Harmon, 2011; Moomaw et al., 2020). Forests in the later stages of seral development (mature and old-growth, DellaSala et al., 2022a) and the large trees within them (Stephenson et al., 2014; Mildrexler et al., 2020) play an outsized role in the accumulation and long-term storage of atmospheric carbon, and consequently enabling their protection where lacking has been recognized as an effective nature-based climate solution (Griscom et al., 2017). Notably, President Joe Biden issued an executive order (White House, 2022b) recognizing the climate value of mature and old-growth forests and directed federal officials to define and inventory them on Federal lands and develop policies for their conservation. Thus, providing techniques for defining when forests qualify as mature and quantifying their relative carbon content and storage potential has high policy relevance.

This undertaking supports the nation's goal of achieving net-zero greenhouse gas emissions by 2050 and to conserve 30% of the nation's land by 2030 (White House, 2021). Protecting older, larger trees and mature forests would also help reverse the global degradation of older forests that have diverse ecological values (Lindenmayer et al., 2012), and facilitate the continued growth of mid-sized trees toward maturity (Moomaw et al., 2019). Mature forests provide refugia for many imperiled species (Buotte et al., 2020; DellaSala et al., 2022a), store disproportionate amounts of above-ground carbon in forests (Stephenson et al., 2014; Lutz et al., 2018; Mildrexler et al., 2020), and historically constitute a large volume of valuable timber (Johnson and Swanson, 2009). These values often conflict with one another resulting in contentious policy debates about land management objectives and best practices, particularly on federal lands in the U.S. where much of the remaining mature forest area resides according to national forest inventory data (Bolsinger and Waddell, 1993; DellaSala et al., 2022a). Recent studies of land values reveal that the importance of mature forests for ecosystem integrity and non-timber ecosystem services far exceeds their value for timber products (Watson et al., 2018; Gilhen-Baker et al., 2022).

Some researchers argue that it is necessary to log larger trees in fire-suppressed forests in the western U.S. to restore fire regimes, reduce biomass, and minimize emissions from wildfires (Kirschbaum, 2003; Hessburg et al., 2020; Johnston et al., 2021). However, these assertions have been challenged (Stephenson et al., 2014; Lutz et al., 2018; Mildrexler et al., 2020; DellaSala et al., 2022b) in part because removing larger trees from forests having high carbon stocks creates a significant "carbon debt" that can take decades or centuries to repay (Moomaw et al., 2019; Law et al., 2022).

It follows that our objectives are to (1) present an approach to defining larger trees and mature forests on federal lands; (2) estimate the current carbon stock and annual carbon accumulation in larger trees in mature forests across a representative selection of national forests, and (3) estimate the carbon stock and accumulation left unprotected by current binding designations.

We do not identify the proportion of mature forest area and carbon stocks that could be classified more specifically as "old growth." Defining old-growth in a consistent way across the diversity of temperate forests is challenging since existing definitions are based on structural, successional, and biogeochemical factors that are unique for individual forest types and researcher's interests (Wirth et al., 2009). Our characterization of mature forests has ecological and policy relevance for restoring old-growth characteristics over time, pursuant to the presidential executive order as well (DellaSala et al., 2022a). Thus, we determined that this paper would be more broadly focused on mature forests rather than old-growth forests.

2. Materials and methods

2.1. Approach

Our approach requires addressing two components: (1) individual trees referred to as the "larger" trees in a forest; and (2) mature forest stand development represented by stand age. This method for identifying larger trees in mature stands—and the related assessment of above-ground live carbon stocks and annual carbon accumulation—is intended to be broadly applicable and readily implementable independent of how mature stands are defined. We settled on defining stand maturity with respect to the age of maximum Net Primary Productivity (NPP), which is estimated as the annual net quantity of carbon removed from the atmosphere and stored in biomass (see section 2.2 for definitions of key terms). NPP was calculated by combining 4 terms: Annual accumulation of live biomass, annual mortality of above-ground and below-ground biomass, foliage turnover to soil, and fine root turnover in soil (He et al., 2012). Live biomass and annual mortality were estimated from the Forest Inventory and Analysis (FIA) database. Foliage and fine root turnover were estimated using maps of leaf area index (LAI) and forest age to derive LAI-age relationships for different forest types. These relationships were then used to derive foliage and fine root turnover estimates using species-specific trait data (He et al., 2012).

This is a particularly appropriate approach to maturity in the context of how forests help temper climate change. Our integrating method of associating the median tree diameter with age is intended to be applicable to other definitions of stand maturity, including simple ones applied across the landscape without regard to specific stand characteristics, for example a uniform age cutoff.

2.2. Key definitions and data source

Net Primary Productivity (NPP)—The difference between the amount of carbon produced through photosynthesis and the amount of energy that is used for respiration. Estimate is based on the net increment of tree and understory biomass, leaf production, and fine root turnover (He et al., 2012).

Biomass—The carbon stored in live trees greater than 1 inch (2.54 cm) diameter at breast height (dbh), including stump, bole, bark, branches, and foliage.

Carbon stock—The carbon stored in live biomass at a point in time, unless otherwise defined to include additional ecosystem components, in units of megagrams (Mg) or teragrams (Tg) of carbon (C).

Carbon accumulation—The net change in carbon stock of live tree biomass over a period of time, in units of megagrams (Mg) or teragrams (Tg) of carbon (C), per hectare (ha^{-1}) and/or or per year (yr^{-1}).

Metric ton—In the literature, the term metric ton (Mt or tonne) is often used instead of megagram.

Definitions of other terms commonly used in this paper are included in the **supplementary material**.

To apply our method to each national forest, recent FIA data collected by the U.S. Forest Service were queried using the EVALIDator online query system (USDA Forest Service, 2022). The sampling approach and estimation methods of forest inventory variables in the FIA database follow documented procedures (**Supplementary material**; Bechtold and Patterson, 2005). Our analysis is focused on above-ground carbon in live-trees, though some representative data are also presented about all ecosystem C pools to show the full potential of protecting carbon stocks on selected national forests.

2.3. Study area

The study area includes 11 individual national forests or small groups of national forests in the conterminous U.S. (**Table 1** and **Figure 1**), selected to represent the geographic diversity of U.S. forests and to have at least one forest in each USFS region. Forests with similar characteristics within a region were grouped if preliminary analysis determined that there were insufficient sample data to develop the biomass distributions for a single forest by main forest types.

2.4. Defining larger trees and mature forests

We combine two key indicators—stand age and tree diameter—in a way that could be used by land managers to assess maturity for informing management practices, in contrast to basing maturity and management on either tree diameter or stand age alone as in some previous studies (Mildrexler et al., 2020; Johnston et al., 2021). Mature forests are defined as stands with ages exceeding that at which accumulation of carbon in biomass peaks as indicated by NPP. We considered FIA sample plots to represent stands of relatively uniform condition. The sampled areas and trees are partitioned into uniform domains during field sampling and data processing if more than one stand condition falls within the sampling area. For this study, a new term "Culmination of Net Primary Productivity" (CNPP) is used to describe the age at which NPP reaches a maximum carbon accumulation rate. Physiologically, peak productivity occurs approximately at the age when the growing space in the

TABLE 1 National Forests, sampling dates, and number of sample plots used in our study.

National Forest	FIA sampling dates	Number of sample plots
Gifford Pinchot, WA	2008–2019	626
Malheur, OR	2011–2019	758
Black Hills, SD	2013–2019	348
Chequamegon-Nicolet, WI	2013–2019	559
Green Mountain, VT and White Mountain, NH	2013–2019	580
Appalachian National Forests[1]	2013–2020	982
White River, CO	2010–2019	291
Flathead, MT	2010–2019	341
Arizona National Forests[2]	2010–2019	849
Central California National Forests[3]	2011–2019	410
Arkansas National Forests[4]	2017–2021	427

[1] Pisgah (NC), Nantahala (NC), Cherokee (TN), Monongahela (WV), Jefferson (VA), George Washington (VA).

[2] Coconino, Prescott, Tonto, Sitgreaves, AZ.

[3] Eldorado, Stanislaus, and Sierra, CA.

[4] Oachita, Ozark-St. Francis, AR.

ecosystem is fully covered by leaf area—i.e., tree canopy closure reaches 100%. After this age, NPP either stays constant or declines gradually, depending on tree species composition, and other environmental factors such as nutrient availability (Kutsch et al., 2009; He et al., 2012). Previous analyses of FIA data indicate that peak NPP occurs at a relatively young stage of stand succession, roughly 25—50 years following stand establishment (**Figure 2**; He et al., 2012; Dugan et al., 2017; Birdsey et al., 2019). Foresters have a similar metric, referred to as the "culmination of mean annual increment" (CMAI), that is based on estimated net volume increment (i.e., volume growth minus mortality) as a function of age, rather than net productivity as a function of age, which is more relevant to assessing forests potential to reduce greenhouse gases. CMAI is calculated in the same way as CNPP, except that the mean annual increment variable is net volume increment instead of net primary productivity.

Larger trees are then defined as having a diameter at breast height (dbh) that is equal to or greater than the median diameter in forest stands at or near the age of stand-level CNPP. A range of ages around the age of CNPP, taken to be the CNPP age plus or minus one age class (30-year bin size), was used in order to have sufficient FIA sampling plots (generally 100 or more) to develop a tree diameter distribution for individual forest types. Then the median diameter of the distribution is used as the lower diameter threshold of maturity for the population of trees in the CNPP age class.

Our approach involves clustering (post-stratifying) sample plots by forest type and stand age class, and individual sample trees by tree diameter class, and then calculating estimates for the clusters (populations) as groups. Because most clusters include a wide distribution of tree diameters, there can be larger trees present in stands having ages below CNPP age, and *vice versa*, stands with ages above CNPP age can have trees with diameters below the lower diameter limit. The definitions of mature stands and associated larger trees in this study is conceptually consistent with stages of maturity derived from classifying FIA sample plots (Stanke et al., 2020; USDA Forest Service, 2022) and from an approach involving spatial data (DellaSala et al., 2022a). **Table 2** compares the terminology and approaches of each.

To estimate the area of mature stands based on sample plot characterization, we used the FIA stand-size variable coded as "large diameter" (column 2 of **Table 2**) because our method is not based on stand-scale variables alone but rather a crosswalk

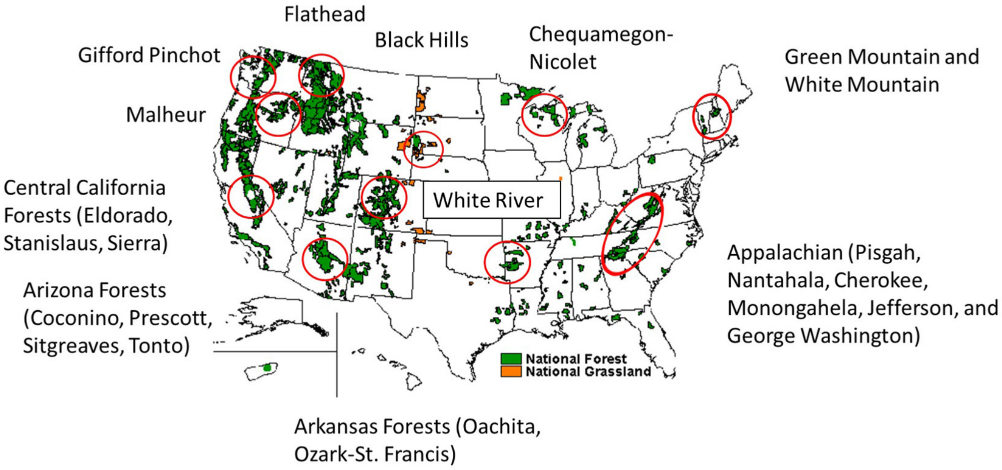

FIGURE 1
Approximate locations of 11 National Forests in our study area.

of stand and tree population variables. Large diameter stands are defined by FIA as those with more than 50 percent of the stocking in medium and large diameter trees, and with the stocking of large diameter trees equal to or greater than the stocking of medium and small diameter trees.

2.5. Estimation of carbon stock and accumulation in living biomass

We used the age-to-diameter crosswalk to estimate live above-ground carbon stocks and annual carbon accumulation for larger trees in forests above the CNPP threshold. We focused on live above-ground biomass since it is typically the largest of the C pools (except for soil in some cases) and is the most dynamic in terms of how carbon stocks and accumulation change with age or tree size (Domke et al., 2021). The estimated carbon in biomass of trees or stands is taken directly from the FIA database and is based on measurements of dbh and height. The current standard FIA approach to estimating biomass from tree measurements uses the component ratio method (Woodall et al., 2011). Unless stated otherwise, we use the term "carbon" to refer to carbon in live-tree biomass, not the carbon in all ecosystem carbon pools. Live-tree biomass includes the main stem or bole of the tree, rough or rotten sections of the bole, tree bark, branches, and leaves.

Estimation of the carbon accumulation rate is based on remeasurement of the same grid of sample points and trees at intervals ranging from 5 to 10 years depending on the state, with generally shorter remeasurement cycles in the eastern U.S. compared with the western U.S. (**Table 1**). Carbon in live-tree biomass was estimated at the beginning and end of the time period, and carbon accumulation was calculated as change in carbon over the period divided by the number of years.

The uncertainty of estimates of carbon stock and carbon accumulation was taken directly from the FIA data retrieval system that reports sampling error with 67% confidence, which we multiplied by 1.96 to report estimates with 95% confidence. These uncertainty estimates do not include the uncertainty of using biomass equations to estimate

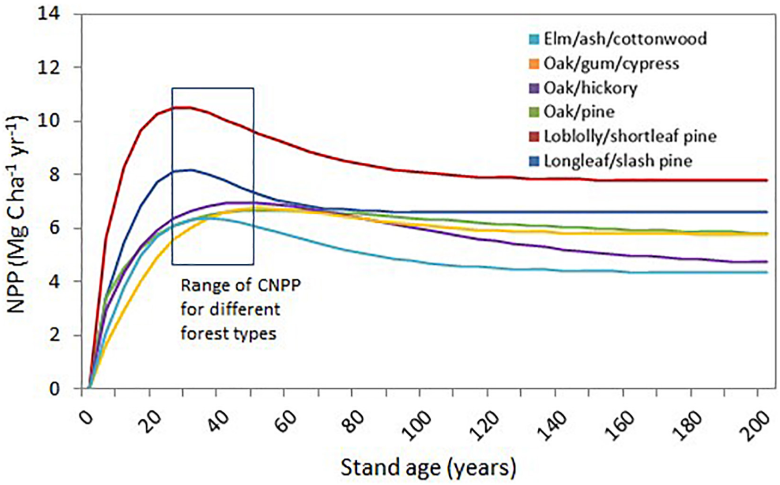

FIGURE 2
Net primary productivity (NPP) for selected forest types in the South (He et al., 2012). Culmination of NPP (CNPP) occurs at the stand age having the greatest annual increment rate, typically at or just after the tree canopy closes. Younger stands are those with ages less than CNPP. Older stands have ages greater than CNPP. CNPP is highly variable among forest types and geographic regions—in this example, from ages 23 to 45. The He et al. (2012) paper includes detailed uncertainty analyses of these and other NPP curves.

TABLE 2 Successional stages of forest maturity or stand structure as defined by several studies.

Maturity or structural stage	FIA stand-size[1]	Stanke et al. (2020)[1]	DellaSala et al. (2022a)[2]	This study[3]
1	Small diameter	Pole	Young	Young
2	Medium diameter	Mature	Intermediate	Mature
3	Large diameter	Late	Mature/Old-growth	

Classifications across the rows are similar but not identical.

[1] Stand structural stage is classified based on the relative basal area of canopy stems in various size classes.

[2] Forest maturity model based on three spatial data layers of forest cover, height, and above-ground living biomass for all landownerships.

[3] Based on culmination of net primary productivity (CNPP) and median stand diameter at CNPP. Late succession or old-growth not distinguished from mature.

tree carbon from diameter and height measurements or from wood density.

2.6. Domains and filters

We filtered the data to include only sample plots that were classified in the database as belonging to the national forest or group of forests being analyzed. For estimating CNPP, we screened out sample plots if they showed evidence of logging or natural disturbance. The remaining "undisturbed" stands, however, could still include some tree mortality and loss of live biomass associated with aging and succession, or small-scale disturbances. All plots including those disturbed or harvested were included in final estimates of the carbon stock and accumulation for the whole forest or for reserved and unreserved areas within the National Forest. Reserved and unreserved areas were defined by the FIA database variable "reserved class." The classification of reserved is not the same as land defined as "protected" by the USGS GAP analysis project (USGS, 2019). Reserved land is withdrawn by law(s) prohibiting the management of land for the production of wood products, though tree harvesting may occur to support other management objectives. We use the classification "unreserved" as a proxy for forest areas that are lacking protection from timber harvest, while acknowledging that this definition of unreserved land may not be consistent with other definitions of unprotected land.

2.7. Model outputs

Estimates of carbon stock and accumulation are presented separately for reserved and unreserved forest areas since the target for future management policies may focus on carbon stocks of older forests in areas that could be logged in the future. Some additional details regarding definitions and calculation protocols are available in the **Supplementary material**.

3. Results

3.1. National forest characteristics

Individual forests and groups of forests range in forest area from about 0.4 to 2.0 million hectares (M ha), and the total area of all forests analyzed is about 8.9 M ha (**Table 3**). The carbon stock in above-ground biomass ranges from 9 to 113 million megagrams (Mg). There is a wide range of average C density, with the lowest amount of 21 Mg ha^{-1} in Arizona National Forests, and the highest amount of 166 Mg ha^{-1} in the Gifford Pinchot National Forest in Washington. The total carbon in the forest ecosystems, which includes above- and below-ground biomass, dead wood, litter, and soil, is from 2 to 5 times the amount of carbon in above-ground biomass alone (Domke et al., 2021). All but one of the national forests studied (the Black Hills National Forest in South Dakota) experienced an increase in above-ground carbon over the

TABLE 3 Biomass carbon stock and accumulation for all live-trees greater than 1 inch (2.54 cm), for each National Forest or group of forests studied.

National Forest	Total forest area (ha)	Total biomass C stock (Mg)	Total biomass C accumulation[1] (Mg yr^{-1})	Average C density (Mg ha^{-1})	Average C accumulation[2] (Mg ha^{-1}yr^{-1})
Gifford Pinchot	508,502	84,233,113	878,348	166	1.73
Malheur	584,951	23,566,550	234,124	40	0.40
Black Hills	394,508	9,130,825	−32,622	23	−0.08
Chequamegon-Nicolet	583,050	30,777,312	607,023	53	1.04
Green and White Mountains	478,285	35,572,874	299,164	74	0.63
Appalachian Forests	1,216,520	112,798,380	1,122,302	93	0.92
White River	685,869	30,887,524	N/D	45	N/D
Flathead	906,902	39,688,676	N/D	44	N/D
Arizona Forests	2,083,049	43,194,094	N/D	21	N/D
Central California Forests	996,197	86,238,281	125,730	87	0.13
Arkansas Forests	454,986	64,714,071	1,498,668	142	3.29
Total	8,892,819	560,801,700	4,732,737	63	0.91

[1] Change in carbon stock over approximately the last 10 years.

[2] Average of national forests with available growth data from FIA database.

"N/D" means data were not available.

remeasurement period, ranging from 0.13 (Central California) to 3.29 (Arkansas) Mg $ha^{-1}yr^{-1}$. All of the national forests were affected by disturbances—the most common being fire, insects and logging—though the areas and mix of disturbance types that occurred and the areas undisturbed are highly variable among the forests (**Supplementary Table 1**). Natural disturbances can result in significant tree mortality and transfer of carbon from live to dead trees, and gradual net emissions over several decades especially if the disturbances are of high severity (Birdsey et al., 2019). In the case of logging disturbances, emissions are significant both in the near term and over time, even when accounting for the amount of carbon in the harvested live trees that is initially transferred to the long-term harvested wood product pool (Hudiburg et al., 2019).

3.2. Culmination of net primary productivity and diameter limits

The estimated CNPP ages range from 35 to 75 years among the 11 National Forests with an average age of 50 years (**Table 4**) and are highly variable by forest type within each forest (**Supplementary Table 2**). Productivity at CNPP ranges from <1.0 to about 4.0 MgC $ha^{-1}yr^{-1}$, which is higher than the average productivity among all age classes since it represents the peak value. Typically, the productivity values after CNPP age decline at a variable rate by region and forest type (**Figure 2**). The estimates of CNPP age may be affected by sparse data points for some age classes, different stand disturbance histories, and other factors that influence tree growth rates over time such as climate and topography. In this study, the age at CNPP is used to define the lower age threshold for mature forests.

Determining the age threshold associated with CNPP involves examining the distribution of biomass by diameter (dbh) class for the stand-age class window around the age of CNPP. In most cases, there is a clearly defined peak of biomass at the median diameter of the distribution (**Supplementary Figure 1**). Because of the diversity of stand conditions associated with CNPP across the landscape, as well as uneven aged stand conditions, there are rather wide distributions of tree sizes associated with any particular CNPP (**Supplementary Figure 1**). Since the FIA stand-age data we used were compiled into diameter classes of 2 inches (5 cm), we used the upper end of the range to define the diameter threshold. Typically, there is more carbon stored in the population of trees with diameters at and near the diameter at CNPP, though these trees can grow to much larger sizes as indicated by the upper end of the diameter distributions. For the national forests in this study, the diameter limits ranged from a low of 4 inches (10 cm) for Douglas-fir in the Flathead National Forest to a high of 18 inches (46 cm) for two forest types in the Central California National Forests (**Supplementary Table 2**). Combining CNPP with median diameter in a cross-tabulation results in identifying the carbon stocks in larger trees in mature forests for each national forest, highlighted in yellow in the example table (**Supplementary Table 3**).

TABLE 4 Average age and tree diameter at culmination of net primary production (CNPP), all forest types combined on 11 National Forests in our study area.

National Forest	Average CNPP age (Years)	Diameter threshold (Inches/cm)
Gifford Pinchot	45	13/33
Malheur	45	12/30
Black Hills	75	14/36
Chequamegon-Nicolet	45	9/23
Green and White Mountains	35	12/30
Appalachian Forests	35	11/28
White River	55	6/15
Flathead	45	8/20
Arizona Forests	75	12/30
Central California Forests	50	16/41
Arkansas Forests	40	10/25
Average of all Forests	50	11/28

Tree diameters represent the lower age bound of mature forests (i.e., age at CNPP). Detailed ages and tree diameters by forest type are shown in supplementary Table 2.

3.3. Comparison of CNPP and CMAI

Evaluation of forest inventory data indicated that CNPP and CMAI occur at about the same age (**Supplementary Figure 2**). Some older studies based on different data, mainly from volume growth and yield studies, associate CMAI with a greater age (e.g., McArdle, 1930). This difference is likely caused by several factors such as management intensity, temporal changes in productivity from environmental changes, and sampling protocols.

3.4. Carbon stocks and accumulation of larger trees in mature stands

The total C stock and C accumulation of larger trees in stands older than age at CNPP compared with all trees and stands is highly variable among the different forests analyzed (**Table 5**). Likewise, sampling errors are highly variable, reflecting the total areas classified as mature and therefore the number of FIA sample plots therein. Sampling errors for C accumulation estimates are significantly higher than for C stocks, mainly because the variability of accumulation rates among sample plots is higher than the variability of stock estimates.

TABLE 5 Estimated area, carbon stock, carbon accumulation, and sampling errors for larger trees in mature stands within individual National Forests based on most recent forest inventory data (Table 1).

National Forest	Area (ha)	C Stock (Mg)	C stock sampling error[1] (%)	Net C accumulation (Mg yr^{-1})	Net C accumulation sampling error[1] (%)	C stock[2] (% of total NF)	Net C accumulation[2] (% of total NF)
Gifford Pinchot	440,005	68,148,420	5.5	380,998	22.7	80.9	43.4
Malheur	471,439	16,886,265	7.1	165,949	19.1	71.7	70.9
Black Hills	215,379	3,711,144	14.6	−15,167	82.2	40.6	−46.5
Chequamegon-Nicolet	303,176	20,625,499	6.9	281,034	11.9	67.0	46.3
Green and White Mountains	301,884	15,786,690	7.9	60,593	141.7	44.4	20.3
Appalachian	1,033,833	83,571,980	6.2	675,970	15.3	74.1	60.2
White River	390,370	26,038,059	13.1	N/D	N/D	84.3	N/D
Flathead	507,053	27,841,625	13.6	N/D	N/D	70.2	N/D
Arizona National Forests	1,738,672	36,254,717	11.2	N/D	N/D	83.9	N/D
Central California National Forests	821,991	65,973,313	8.8	−66,370	52.2	76.5	−52.8
Arkansas National Forests	384,972	41,808,132	6.3	619,759	13.5	64.6	41.4
Total/mean	6,608,774	406,645,844		2,102,766		72.5	44.4

[1] With 95% confidence.

[2] Calculated by dividing values by those in Table 3. The percentages of carbon stocks and accumulation of larger trees in mature stands compared with all forests are also shown (last 2 columns). Larger trees in mature stands are the subset of the forest population composed of trees greater than the median dbh associated with CNPP in stands greater than CNPP age (Figure 2). Areas of mature forests estimated by a proxy variable "stand-size class" from FIA (see methods).

"N/D" means data were not available.

Of the 11 forests, the C stock of larger trees in mature stands ranged from 41 to 84 percent of the total C stock of the forests, whereas C accumulation ranged from −53 to 71 percent of the total C accumulation. This difference between changes in C stock and C accumulation reflects several underlying causes: (1) younger forests can have higher NPP rates than mature forests as illustrated in **Figure 2**; (2) increasing mortality as forests grow older because some trees die from overcrowding or insects and diseases; and (3) disturbances such as severe wildfire that kill significant numbers of trees can reduce NPP, in some cases to a negative number.

3.5. Carbon stocks and accumulation in mature stands and larger trees in unreserved forest areas

The methodology described above can be further refined to separate out unreserved areas that could be designated for protection of carbon stocks and accumulation on national forest lands. In the 11 forests analyzed, unreserved C stocks of larger trees from all tree species in mature stands ranged from 36 to 69 percent of total C stocks (**Table 6** and **Supplementary Table 4**). Unreserved C accumulation of such trees in mature forests ranged from 12 to 60 percent of total C accumulation, not including the Black Hills national forest where the unreserved C accumulation was negative because of logging and natural disturbances (primarily insects). Typically, one or a few species comprise the main part of unprotected stocks and accumulation. Generally, the percentage of unreserved C accumulation is less than the percentage of unreserved C stock because the growth rates of mature forests are somewhat lower than younger forests.

3.6. Potential protected carbon stocks with variable diameter and age limits

The final stage of the analysis estimated the amount of C in unreserved areas above variable diameter and age limits for logging (**Supplementary Table 5**). These data further illustrate the functionality and flexibility of the age to diameter association that we developed for policy makers and land managers. The impact of selecting either the diameter limit or the age limit, or both, is highly dependent on the distribution of the estimated C stocks by these factors. For example, the diameter limit for Gifford Pinchot at a stand age of 80 years (20 inches; 51 cm dbh) would protect 57% of the total above-ground C, and the age limit of 80 years would protect 79% of the total above-ground C. In contrast, the diameter limit for Chequamegon–Nicolet at a stand age of 80 years (13 inches; 33 cm dbh) would protect only 27% of the total above-ground C, and the age limit of 80 years would protect only 48% of the total above-ground C. Each of the studied forests has a unique pattern of unreserved C based on diameter or age limits.

4. Discussion

4.1. Summary of results

The average age of maximum carbon accumulation (CNPP) ranged from 35 to 75 years for all forest types combined (**Table 4**), and the ranges were wider for individual forest types (**Supplementary Table 2**). Many factors contribute to determining the CNPP age (e.g., tree species, competition, site productivity, and climate). The lowest CNPP ages were estimated for the eastern forests in the southern and northern Appalachian regions, while the highest CNPP ages were found in the West. Typical diameter thresholds that separate smaller from larger trees (based on CNPP age) ranged from 6 to 16 inches (15–41 cm), with larger diameter thresholds found in the Western forests. The unprotected carbon stock of larger trees in mature stands ranged from 4 to 74 million MgC (**Table 6**), representing between 36.0 and 68.3 percent of the total carbon in the forest biomass. Forests with the highest percentage of unprotected carbon stock in larger trees in mature forest stands included Gifford Pinchot, Malheur, Chequamegon–Nicolet, and Appalachian National Forests. The unprotected carbon accumulation of larger trees in mature stands ranged widely from 11.5 to 60.2 percent of the total carbon accumulation in biomass, with one forest (Black Hills) showing a reduction in biomass.

4.2. Diameter and age thresholds

Our approach to establishing mature forest definitions and diameter thresholds for larger trees is rooted in a crosswalk of stand age and tree diameter that integrates two variables used to describe mature forests and trees. Both tree diameter and stand age have been used independently in the past to identify the lower bounds of maturity and provide guidance for on-the-ground tree and forest management decision rules (Mildrexler et al., 2020; Johnston et al., 2021). The two variables complement each other because although age is a good indicator of stand maturity, it can sometimes be difficult to determine a precise stand age in the field especially for stands of multi-aged trees, whereas tree diameter is an easily and accurately measured variable in any forestry operation. While our approach lacks complexity, it can form the foundation for more detailed analyses needed to guide on-the-ground management decisions.

Our approach is based on the application of FIA data, a standard source of detailed field inventory data for all forests of the U.S. that is readily available to the public and continuously updated. There are sufficient sample plots to evaluate most

TABLE 6 Carbon stocks and accumulation in larger trees in mature stands in unreserved forest areas, all forest types, within 11 National Forests in our study.

National Forest	Unreserved C stock		Unreserved C increment	
	Mg	% of total C[1]	Mg yr^{-1}	% of total C increment[1]
Gifford Pinchot	57,074,409	67.8	378,553	43.1
Malheur	16,103,923	68.3	108,878	53.7
Black Hills	3,625,966	39.7	−22,597	−69.3
Chequamegon-Nicolet	19,949,333	64.8	271,540	44.7
Green and White Mountains	12,794,081	36.0	60,821	20.3
Appalachian	74,359,965	65.9	675,969	60.2
White River	17,767,821	57.5	N/D	N/D
Flathead	18,383,736	46.3	N/D	N/D
Arizona National Forests	23,540,573	54.5	N/D	N/D
Central California National Forests	51,225,061	59.4	14,483	11.5
Arkansas National Forests	40,184,951	62.1	747,726	49.9
Total	335,009,819	59.7	2,235,373	47.2

[1] Calculated by dividing values by those in Table 3. Percentages of total forest C stock and accumulation are included. Detailed estimates by forest type are in supplementary Table 4.

National Forests individually or in groups, and different forests or regions can be compared or aggregated using consistent and high-quality data. Furthermore, FIA data have become a standard for many other forest analysis tools and greenhouse gas registries (Hoover et al., 2014), so consistency across platforms is also feasible. Finally, there are developments underway to integrate FIA-based ground data analysis with other approaches based on remote sensing and mapping to support policy and land management (Dugan et al., 2017; Harris et al., 2021; Hurtt et al., 2022), which is the objective of future research building directly on this study and related work (DellaSala et al., 2022a).

Moreover, using CNPP as the threshold for stand maturity is an extension of and a refinement on prior work. The concept of CNPP is closely related to CMAI, which has been used for many decades to describe the point at which tree volume increment is greatest in the maturation of a forest stand for assessing return on investment in forestry operations (e.g., Assmann, 1970; Curtis, 1994) but more recently has been proposed as a way to identify the minimum age of ecosystem maturity for protection efforts (Kerr, 2020). Published CMAI estimates are often derived from managed forests and plantations, which limits their applicability to low-intensity management regimes. Also, CNPP is more closely related than volume to the carbon variables of interest (C and CO_2) for analyses of climate mitigation potential by the forest sector to reduce emissions or remove atmospheric CO_2. Considering the uncertainties of establishing the exact age for forests that did not originate as tree plantations, CNPP and CMAI often occur at similar ages in the life of forests, that is, at or very near the age of crown closure and the onset of tree physiological maturity (Burns and Honkala, 1990; Groover, 2017).

4.3. Uncertainty and data limitations

Most forests or groups of forests studied had sufficient sample plots to keep uncertainty of carbon estimates (described in methods) within 15% of the estimated values (**Tables 1**, **5**). In contrast, the uncertainties of carbon accumulation estimates were significantly larger and more variable, ranging from 13 to 142% of the estimated values (**Table 5**). Although the same number of sample plots were available for both estimates, the variability of C accumulation estimates was much higher in some cases, most likely because C accumulation has higher interannual variability if affected by natural disturbances, tree mortality, and tree growth rates that can vary from year to year. Although the reported uncertainty is related to sample size and variability of the tree populations studied, there is additional uncertainty associated with the biomass models used to estimate above-ground biomass carbon. The error of biomass models typically ranges from about 10–15% for large forest areas, with 95% confidence (US Environmental Protection Agency, 2021).

Our ecosystem C estimates only include above-ground live biomass in trees greater than one-inch (2.4 cm) dbh. C pools in standing and down dead wood, understory vegetation including tree seedlings, litter on the forest floor, and soil C account for significantly more C that could double or quadruple the amount of estimated C stock depending on the geographic location of the forest and other land characteristics such as physiography and soil depth (Domke et al., 2021; US Environmental Protection Agency, 2021). Above-ground live biomass is typically the most dynamic of the C pools in forests, though in some cases, particularly related to logging and natural disturbance, the dead wood and litter C pools may change significantly over short periods of time (Domke et al., 2021).

Forest age is an important variable used to estimate when NPP reaches a maximum value (CNPP) above which forests are considered mature. However, forest age (or time since disturbance) can be difficult to determine especially for uneven- or multi-aged forests and is based on coring trees and counting tree rings from just a few sample trees on a sample plot in the FIA sampling protocol. It is likely that the sample trees that are cored do not represent the population of larger and older trees on a sample plot, meaning that the assigned age could be biased to younger ages (Stevens et al., 2016). In some cases, the NPP curve is rather flat at and around the age of CNPP, making it difficult to identify the precise age associated with CNPP. Despite these issues, age is an easily understood metric that is closely related to forest maturity, and the approach of identifying the median diameter associated with CNPP using a 30-year window of age classes helps to mask the uncertainty of using age as a critical step in the methodology.

4.4. Policy and management implications

Recent policy goals target "net zero" emissions for all sectors by 2050 to arrest the global climate emergency. Since net zero cannot be achieved by reducing fossil fuel emissions alone (United Nations, 2015; Griscom et al., 2017), the potential of nature-based climate solutions to contribute to this larger goal is the subject of legislation and executive orders in the U.S. The approach and methodology developed here are designed to inform policy makers about federally managed mature forests and their large and vulnerable C stocks and high rates of accumulation of carbon from the atmosphere. Some recent legislation and executive orders specifically call for increased analysis of the current and potential role of mature forests and large trees (White House, 2021, 2022b; U.S. Congress, 2022). The approach and methods presented here provide options for policy makers to consider as the specific land management rules are implemented by agencies for national forest lands.

Our study further corroborates that large areas of mature federal forests are significant carbon sinks that lack protection. Results indicate that 10 of the 11 forests analyzed were carbon sinks over the last decade or so, with the largest sinks occurring in the Eastern U.S. Forests with less disturbance and/or younger age-class distributions had greater increases in above-ground carbon per area than forests with higher rates of disturbance and/or older age-class distributions. These observations reflect multiple factors: the past history of management, trends in incidence and severity of recent natural disturbances and logging, and the inherent age at which the productivity of different forest types begins to level-off or decline. We also note an important distinction that rates of carbon accumulation tend to be higher in younger forests while the largest amounts of stored carbon are found in mature forests. Protecting these carbon sinks and avoiding losses of carbon from logging would require a policy shift to focus more on the potential role of federal forests in climate mitigation (DellaSala et al., 2022a). Such a shift requires considering how both natural disturbances (exacerbated by climate change) and harvesting are emitting carbon stored in larger trees across federal forest lands. In this context, it is notable that national and regional estimates of emissions from logging (direct plus lifecycle emissions) are 5–10 times greater than direct emissions from natural disturbances (wildfire, insects, and wind combined) (Harris et al., 2016; Law et al., 2018).

For operational land management practices, it is often easier to apply a diameter limit in timber operations by species than an age limit by forest type, because as noted previously it can be challenging to determine a precise stand age, whereas measuring tree diameter is simple and accurate [although see DellaSala et al. (2022a) for an alternate approach to stand maturity without age or dbh determinations]. The diameter limits derived here are based on stand age at CNPP and so have that element of maturity embedded in their determination. And, as noted, this approach can be used regardless of the age selected. For some forest types, stand level characterization is obscured by their frequent association with selective logging and/or natural disturbances like wildfire, making larger trees the more appropriate component for defining maturity.

The results presented here by region and forest type reveal that there is a wide variation in CNPP age and associated tree diameters reflecting variation in forest type/composition, climate, competition for resources and soil moisture, disturbance dynamics, site productivity, and geographic region. This variability needs to be considered in developing policies and management practices. It is also important to consider risks of loss to stored C from natural disturbances, and other values of forests that are tied to land management objectives, which may or may not be compatible with increasing C stocks and accumulation.

We developed an approach to assess mature forests and their current carbon stock and accumulation benefits, and applied the methods to 11 different case studies of individual or groups of National Forests that can inform implementing the president's executive order. This method can be applied regardless of how mature stands are defined (e.g., it is readily applicable to age thresholds above CNPP). And this ground-based estimation approach can be linked with remote sensing and mapping approaches (e.g., DellaSala et al., 2022a) to provide a geographic view of forest maturity as well as protected status beyond the reserved/unreserved designation available in the FIA database.

This work can also be extended to more clearly identify that subset of mature forests that are truly old-growth, and estimate the associated carbon stocks and accumulation. As forests get older, they tend to have very large and increasing carbon stocks, making them especially valuable as carbon reserves (DellaSala et al., 2022a; Law et al., 2022). Even when threatened by natural disturbances or climate change, there is substantial evidence that old-growth forests can continue to maintain or increase carbon stocks (Stephenson et al., 2014; Law et al., 2018; Lesmeister et al., 2021; Begović et al., 2022). Building upon our definition of mature forests, future research could further inform management decisions by more clearly and consistently identifying those mature forests that are truly old-growth or that potentially could become old-growth, and estimating their carbon stocks and accumulation.

5. Conclusion

Our study presents a framework for in-depth analysis and management of larger trees and mature forests on federal lands. The integration of basic data about stand age, tree diameter, biomass carbon dynamics, and reserved status comprises the main elements of the methodology. After applying the methods to 11 national forests, we found that the unprotected carbon stock in larger trees in mature stands ranged from 36 to 68% of the total carbon in tree biomass. The unprotected annual carbon accumulation in tree biomass of larger trees in mature stands ranged from 12 to 60% of the total accumulation in all trees. The potential climate impact of avoiding emissions from logging larger trees and mature forests is thus significant. Key discussion points focused on uncertainty, policy implications, and land management practices. This work is highly relevant to emerging policies regarding climate change, nature-based climate solutions, and mature forests including the role of larger trees.

Data availability statement

Publicly available datasets were analyzed in this study. This data can be found here: https://www.fia.fs.usda.gov/tools-data/.

Author contributions

RB led the research along with GR and DD. All authors contributed to the writing.

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Conflict of interest

GR and CR were employed by Natural Resources Defense Council, Inc.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2022.1074508/full#supplementary-material

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Forest-clearing to create early-successional habitats: Questionable benefits, significant costs

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A campaign is underway to clear established forests and expand early-successional habitats—also called young forest, pre-forest, early seral, or open habitats—with the intention of benefitting specific species. Coordinated by federal and state wildlife agencies, and funded with public money, public land managers work closely with hunting and forestry interests, conservation organizations, land trusts, and private landowners toward this goal. While forest-clearing has become a major focus in the Northeast and Upper Great Lakes regions of the U.S., far less attention is given to protecting and recovering old-forest ecosystems, the dominant land cover in these regions before European settlement. Herein we provide a discussion of early-successional habitat programs and policies in terms of their origins, in the context of historical baselines, with respect to species' ranges and abundance, and as they relate to carbon accumulation and ecosystem integrity. Taken together, and in the face of urgent global crises in climate, biodiversity, and human health, we conclude that public land forest and wildlife management programs must be reevaluated to balance the prioritization and funding of early-successional habitat with strong and lasting protection for old-growth and mature forests, and, going forward, must ensure far more robust, unbiased, and ongoing monitoring and evaluation.

KEYWORDS

natural climate solutions, forest carbon, old-growth forests, young forest, clearcutting, biodiversity, ecosystem services, wildlands

1. Introduction

In this paper we conduct a wide-ranging and integrated assessment of the campaign to expand early-successional forest habitats in two regions of the United States: (1) the Northeast, i.e., New England states (Connecticut, Maine, Massachusetts, New Hampshire, Rhode Island, Vermont) and mid-Atlantic states (New York, Pennsylvania, New Jersey, Maryland, Delaware); and (2) the Upper Great Lakes areas of Michigan, Wisconsin, and Minnesota north and east of the prairie-forest border [see Cochrane and Iltis (2000), Frelich and Reich (2010), Anderson et al. (2018)]. We review the history of forest disturbance and biodiversity research, the genesis of the forest-clearing campaign and the conservation rationales, the contrasts between natural old-growth forests and intensively managed forests, the impacts of forest-clearing projects, and the current balance of activity between forest management and protection. We conclude that instead of intensive and costly management to create additional early-successional habitats, a new "natural" alternative should be considered which would protect and allow the dynamic growth of established aggrading, mature, and old-growth forests alongside maintaining existing early-successional habitats, where appropriate, for targeted species and cultural values. Although the focus of our analysis is two regions, we believe it offers useful lessons for many other parts of the U.S. and world experiencing similar situations (DellaSala et al., 2022b).

1.1. History of forest development and disturbance

Every place on Earth has a dynamic ecological trajectory based on temperature, rainfall, soils, natural disturbances, and other conditions. In the Northeast and Upper Great Lakes regions of the United States the predominant ecological trajectory of the landscape in the absence of intensive human activity is toward "old-growth" forests: a resilient, diverse, carbon-dense, and self-sustaining "shifting mosaic" of tree ages, microhabitats, and native species above and below ground (Pelley, 2009; Thom et al., 2019; Raiho et al., 2022).

For thousands of years before European settlement, vast "primary" forests were inhabited by a thriving Native human population and harbored many exceptionally large trees, and ecosystems that would be characterized as "old-growth" today (Lorimer, 1977; Whitney, 1994; Lorimer and White, 2003). Up to 90% of the Northeast was covered by such forests, and dominated by shade-tolerant and moderately shade-tolerant species (Foster, 1995; Cogbill, 2000; Cogbill et al., 2002; Shuman et al., 2004; Thompson et al., 2013; Foster et al., 2017; Oswald et al., 2020b). Approximately 50–60% of the Upper Great Lakes landscape, and 40–50% of the Southern Great Lakes landscape, consisted of old-growth forests (Cottam and Loucks, 1965; Frelich, 2002). These percentages in the Great Lakes regions pertain to older even-aged and multi-aged forests (generally more than 120 years old). Old-growth forests in the East include sites with trees more than 380 years old, established in the 1640s and earlier (Lorimer, 1980; McCarthy and Bailey, 1996; Abrams et al., 1998; Abrams and Copenheaver, 1999; Pederson, 2013; Heeter et al., 2019), and studies of remnant old-growth stands indicate they are adapted to long-intervals between catastrophic disturbances. Young trees of late-successional species (e.g., sugar maple, hemlock, beech) released from suppression combined with new seedlings of mid-tolerant tree species (e.g., white pine, yellow birch, American basswood, black cherry, white ash, northern red oak) after windstorms, and high intensity fires in conifer forests or blown down hardwood forests are followed by early-successional shade-intolerant species (e.g., paper birch, quaking, and bigtooth aspen) with some mid-tolerant species as listed above.

The terms "primary forest," "old-growth forest," and "mature forest," are not standardized (Leverett, 1996; Buchwald, 2005; Mackey et al., 2014; DellaSala et al., 2022a). For this analysis, we use the following definitions:

- Primary forest. A forest composed of native species that has never been logged and has developed following natural disturbances and under natural processes, regardless of its age (Kormos et al., 2018; FAO, 2020).
- Old-growth forest. A forest affected primarily by the forces of nature, with dominant canopy tree species at or beyond half their lifespan, and with structural characteristics such as canopy gaps, pit and mounds, large snags, gnarled tree crowns, a thick duff layer, and accumulated large coarse woody debris (Martin, 1992; Frelich, 1995; Dunwiddie and Leverett, 1996; Mosseler et al., 2003b; D'Amato et al., 2006; Mackey et al., 2014; USDA Forest Service and Bureau of Land Management, 2022).
- Mature forest. A forest with trees of intermediate age and lower levels of old-growth structural characteristics, but from which old-growth conditions are likely to develop over time if allowed to continue to grow (Spies and Franklin, 1991, Frelich, 1995; Strittholt et al., 2006; Keeton et al., 2011).

Old-growth forests not only have a high degree of structural diversity, but also contain a wide variety of tree species, herbaceous plants, insects, mosses and fungi, and deep, carbon-rich soil with an associated soil microbiome (Frelich, 1995; Davis, 1996; Lapin, 2005; D'Amato et al., 2009; Maloof, 2023). Permanent and semi-permanent large openings are rare in old-growth forests of these regions, associated mainly with cliffs and scree slopes, ridge tops, wetlands, peat bogs, serpentine barrens, avalanche tracks, river margins, pond and lake margins, and coastal shrublands and bluffs (Whitney, 1994; Foster and Motzkin, 2003; Fraver et al., 2009). Old-growth forests contain natural gaps of different sizes, which can be location-specific (wet, rocky, sandy) or part of a dynamic ecological trajectory due to disturbances, such as fire, windstorms, beaver activity, and insect outbreaks (Whitney, 1994; Boose et al., 2001; Frelich, 2002; Seymour et al., 2002; D'Amato et al., 2017). As a result the forest ecosystem remains intact and resilient, supporting widespread re-sprouting and recovery of trees.

Openland and early-successional habitats were not common before the arrival of Europeans in the Northeast or Upper Great Lakes (Cooper-Ellis et al., 1999; Foster et al., 2002; Faison et al., 2006; Anderson et al., 2018; Oswald et al., 2020b; Frelich et al., 2021). Early-successional habitats characterized about 1–4.5% of the Northeast, with greater amounts in coastal pine barren communities of Cape Cod, Long Island, and New Jersey (Lorimer and White, 2003). About 32% of the entire states of Minnesota, Wisconsin, and Michigan was represented by early-successional habitats, mostly in the savannas and prairies in the southern and western parts of the region. To the north, early-successional habitats were found in tens of thousands of patches of shorelines, marshes, sloughs, bogs, cliffs, and fire-prone sand plains (Veatch, 1928; Curtis, 1959; Marschner, 1975). Thus, the region had both dense forests and permanently open habitats maintained by the physiography of the landscape, including prairies and savannas maintained before European settlement by frequent fires—now almost absent due to agricultural conversion of the land. It is important to note that these open habitats were not early-successional stages for forests.

Native people living in the Great Lakes and the Northeast practiced subsistence hunting, fishing, and plant gathering, as well as burning and small-scale farming. Their population was less than 1% of the current population and largely centered along the coast and in major river valleys, with localized and modest impacts across most of the region (Whitney, 1994; Lorimer and White, 2003; Milner and Chaplin, 2010; Oswald et al., 2020b; Frelich et al., 2021; Tulowiecki et al., 2022).

The arrival of Europeans generated a radical landscape transformation. Upland areas, densely forested for thousands of years, were cleared for agriculture and kept open by crop cultivation, cattle and sheep grazing, increased burning of (dry) cleared land, and intensive use of remaining woodlands (Foster and Motzkin, 2003; Faison et al., 2006; Rhemtulla and Mladenoff, 2007; Scheller et al., 2008; Curtis and Gough, 2018; Oswald et al., 2020b). By the height of deforestation from 1850 to 80, 30% of northern New England and 40–50% of southern New England had been cleared (Foster et al., 2017), and by 1920 more than 90% of the Upper Great Lakes region was cutover (Greeley, 1925; Frelich, 1995).

Widespread deforestation caused a major shift in vegetation from long-lived and interior forest species to generalist and early-successional species (Thompson et al., 2013; Foster et al., 2017). Many of the latter species had been uncommon before European settlement, others migrated to the region, and some plants that had previously grown only on extreme and rare sites expanded their distribution and became common "old field" species (Marks, 1983). Early naturalists recognized that populations of some wildlife species had increased greatly due to this abundance of human-created early-successional habitats (Peabody, 1839). By the late 19th century, New England agriculture was declining, leaving countless abandoned and overgrown fields, grasslands, heathlands, and shrublands, as well as old-field white pine forests, and dense sprout woodlands. By the mid–20th century, significant areas of cutover forests were acquired by the public and allowed to begin growing back on state and federal lands (Titus, 1945; Jones, 2011; Knowlton, 2017). Today, millions of acres of forest are a globally significant example of ecological recovery, and the extent of early-successional habitats has declined accordingly (McKibben, 1995; Foster et al., 2002; Litvaitis, 2003; Foster et al., 2017). Consequently, species that depend on early-successional habitats have been returning to more historic levels, including the Bobolink *(Dolichonyx oryzivorus),* Eastern Meadowlark *(Sturnella magna),* Golden-winged Warbler (*Vermivora chrysoptera*), Yellow-breasted Chat (*Icteria virens*), and New England Cottontail (*Sylvilagus transitionalis*) (**Figure 1**; Litvaitis, 1993; Foster, 2002; Askins, 2011; Foster, 2017).

Although old-growth forests were the predominant ecological condition before European settlement, they are extremely rare today (Frelich, 1995; Dunwiddie et al., 1996; Davis, 2003; D'Amato et al., 2006; DellaSala et al., 2022b), much less common than younger habitats (**Figure 2**). A few relatively large tracts of old-growth and protected recovering forests survive in New York, Michigan, and Minnesota, but just small fragments remain across vast regions including all of New England. However, many mature forests are poised to transition to old-growth, and some are undergoing this transition (Ducey et al., 2013; Gunn et al., 2014). This can occur through a straightforward process of forest development and maturation.

In the Northeast, forests older than 150 years of age cover only about 0.3% of New England and 0.2% of the Mid-Atlantic region (USDA Forest Service, 2022b). Old-growth forests cover a scant 0.06% of Connecticut (Ruddat, 2022). A Massachusetts survey found a mere 1,100 acres of old-growth forest in 33 small stands, comprising just 0.02% of the land base (D'Amato et al., 2006). Most of the old-growth forest in the Northeast is found in the Adirondack and Catskill parks in New York (Dunwiddie et al., 1996; Davis, 2003; Keeton et al., 2011; New York Department of Environmental Conservation, 2021). In the Upper Great Lakes region, only about 1.9% of the currently forested area remains as primary forest that was never logged. Including secondary forests, approximately 5.5% of the northern hardwood forest type is older than 120 years of age, compared to 89% in the presettlement forest; for red-white pine this is 2.5% versus 55%. For all forest types, about 5.2%

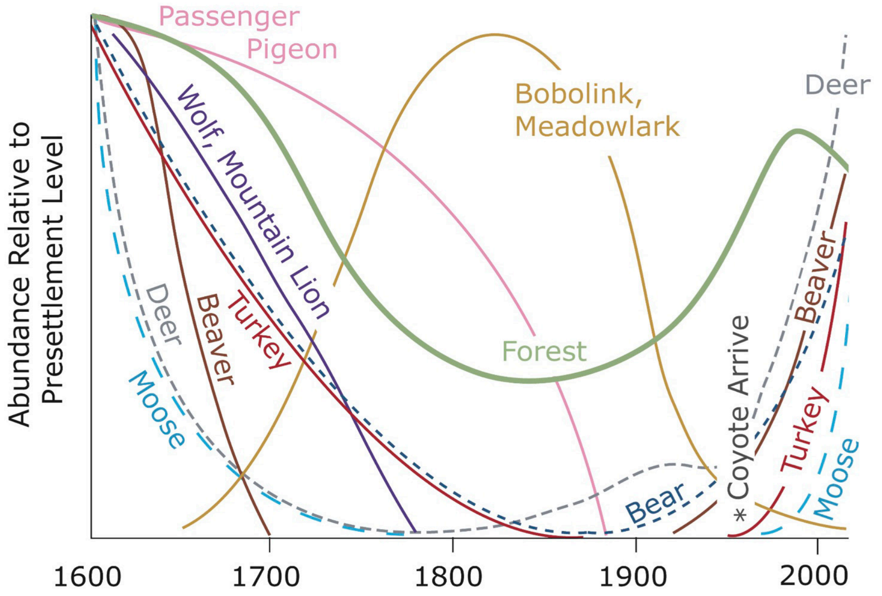

FIGURE 1
Changes in land cover and wildlife dynamics in New England from ~1600–2000. The green line shows the abundance, decline and then recovery of forest in New England, which paralleled the population changes in moose, beaver, and deer. The inverse trend is found in openland (early-successional) species, typified by bobolink and meadowlark. The inverted U shows the low population densities of these and other early-successional species before European settlement, increasing populations of these species as forests were cleared, and a return to lower populations as the forests have grown back. *The coyote is not native to New England. Adapted from Foster et al. (2002); also see **Figure 2**.

is old-growth compared with 68% before European settlement (Frelich, 1995).

1.2. Genesis and rationales of the early-successional habitat campaign

1.2.1. Genesis of the campaign and the "Young Forest Initiative"

A concerted campaign is working to slow and reverse the natural decline in early-successional habitat and species that accompanied the regional reduction in deforestation, intensive forestry, and agriculture. This campaign is promoting early-successional habitat through multiple activities: clearcutting, "group selection," and other forms of patch clearfelling in established forests; intensive "mechanical treatments" such as brushhogging and mowing; and herbicide application and prescribed fire in successional habitats and younger forests, which are often accompanied by other mechanical treatments (DeGraaf and Yamasaki, 2003; Oehler et al., 2006; American Bird Conservancy, 2007; Schlossberg and King, 2007; King et al., 2011; Yamasaki et al., 2014).

These intensive management activities have long been advocated to benefit popular game species that favor early-successional habitats, such as the American Woodcock (*Scolopax minor*), Ruffed Grouse (*Bonasa umbellus*), and White-tailed Deer (*Odocoileus virginianus*) (Lenarz, 1987; Caron, 2009; Derosier et al., 2015). In the last decade, an expanded management campaign has included popular non-game species that also use these habitats (see Section "1.2.2 Rationale for forest-clearing: halt the decline of specific wildlife species" below). This campaign involves an increasing number and diversity of agencies and organizations, and captures rising amounts of public money from state and federal sources. The goal is to maintain the recent historical and degraded condition of the natural forests of the region.

A key milestone in the genesis of this campaign was the 2008 American Woodcock Conservation Plan (AWCP; see **Table 1** for Abbreviations), published by the Wildlife Management Institute (WMI) in collaboration with game management agencies and sportsmen's organizations (Kelley et al., 2008). The goal is to increase American Woodcock populations to early 1970s levels by clearcutting 11.2 million acres of forest in the Northeast and Upper Great Lakes regions—an area larger than the state of Maryland. WMI also launched the Upper Great Lakes Woodcock and Young Forest Initiative (YFI) to gain public support for the creation of early-successional habitats in Michigan, Minnesota, and Wisconsin (Wildlife Management Institute, 2009, 2010).

Wildlife Management Institute (WMI) soon began expanding the YFI to a national campaign (Gassett, 2018; Weber and Cooper, 2019). Recognizing the controversial nature of such widespread forest-clearing, the organization hired a marketing firm to "shape an overall communications

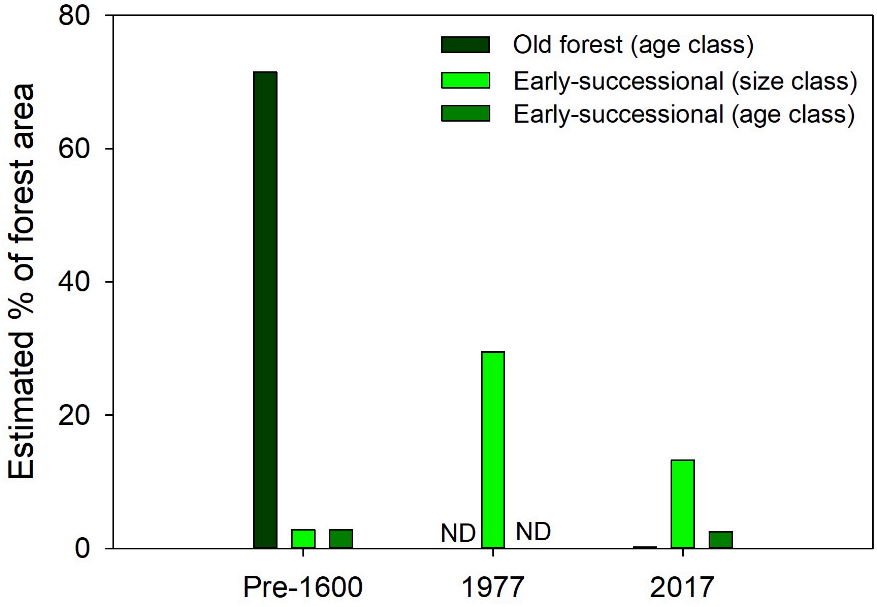

FIGURE 2
Estimated change in average % of early-successional and old forest habitat from pre-European settlement to current times in the Northeast US as extracted from multiple sources. Old forest is defined > 150 years old. The 1600 estimate for early successional forest is based on "seedling-sapling (1–15 years)" age class (Lorimer and White, 2003). The 1977 estimate is based only on "seedling-sapling" size class as reported in Oswalt et al. (2019); age class data were unavailable (ND = no data). Current estimates (2017) reflect two sources: Oswalt et al. (2019) and USDA Forest Service (2022b) wherein early successional forest (size class) reflects "seedling-sapling," the smallest class defined by the USDA Forest Service; and early successional forest (age class) reflects the 1–15 year age class. Note that while early-successional forest declined since 1977, it is similar and perhaps multiple times higher than pre-settlement values; and recent accounting is likely an underestimate: it does not include areas such as highway medians, small patches, or corridors (< 0.4 ha or < 36.5 m wide) that may be found on properties such as golf courses, farms, public and private institutions, and private yards. In contrast, old forest habitat has decreased dramatically (old forest data are barely visible in 2017 on this scale).

strategy" (Seng and Case, 2019). This firm administered opinion surveys and focus groups that showed most forest landowners value beauty, scenery, nature, and biodiversity far more than logging or financial return. A plan was then devised to promote early-successional habitats through an extensive network of partnerships. Terms which focus group participants found unappealing, such as clearcutting, early-successional habitats, shrub, and scrub, were replaced with the more appealing "young forests." Simple and positive language emphasized forest "health," wildlife, habitat diversity, and scientific-sounding outcomes. A pseudo-historical pitch was crafted to emphasize the decline of once common and familiar species without acknowledging the highly artificial and historically anomalous nature of their former abundance (see **Table 2** for more details). Numerous publications were produced, such as, "Talking About Young Forests," to help "natural resource professionals. . .effectively advocate for creating and managing young forest habitat on public and private lands" (Oehler et al., 2013).

In 2012, YFI inaugurated the "youngforest.org" website, aimed at persuading target audiences to support the campaign (Young Forest Project, 2012). Within a decade, the YFI had recruited more than 100 "partners" (**Supplementary material 1**, Young Forest Project, 2022a). These are primarily traditional forestry and game species management interests, such as timber companies (Lyme Timber Company, 2017; Weyerhaeuser Company, 2020), federal and state forestry agencies (New York Department of Environmental Conservation, 2015; USDA Forest Service, 2018), federal and state wildlife agencies (U.S. Fish and Wildlife Service, 2015c; Connecticut Department of Energy and Environmental Protection, 2021b), and sportsmen's organizations (Russell, 2017; Weber and Cooper, 2019). All of these partners benefit from forest-clearing through increased profits from timber sales, larger agency budgets, more staff, direct payments for creating young forest habitat, or elevated populations of desired game species (see **Supplementary material 1** for state-by-state examples of forest-clearing).

The YFI has attracted generous financial support from a wide range of public agencies, private organizations, and large corporations such as Richard King Mellon Foundation, U.S. Forest Service, U.S. Fish and Wildlife Service, American Forest Foundation, and Shell Oil Company [see Connecticut Department of Energy and Environmental Protection (2018); New Jersey Audubon (2018);

TABLE 1 Abbreviations.

AWCP	American Woodcock Conservation Plan.
BBS	North American Breeding Bird Survey.
GAP 1	Gap Analysis Project Status 1. An area permanently protected from conversion of natural land cover, where ecosystems are allowed to function and develop predominantly under the influence of natural processes. Examples include National Parks, Wilderness Areas [see U.S. Geological Survey (2022b)].
GAP 2	Gap Analysis Project Status 2. An area permanently protected from conversion of natural land cover, but which may allow management practices that degrade the quality of existing natural communities. Examples include National Wildlife Refuges, State Parks, and Nature Conservancy preserves [see U.S. Geological Survey (2022b)].
GAP 3	Gap Analysis Project Status 3. An area predominantly protected from conversion of natural land cover, but subject to extractive uses. Examples include National Forests, Bureau of Land Management lands, most State Forests, and some State Parks [see U.S. Geological Survey (2022b)].
GAP 4	Gap Analysis Project Status 4. Lands with no mandates to prevent conversion of natural habitat types to unnatural land cover. Examples include agricultural and developed lands [see U.S. Geological Survey (2022b)].
IUCN	International Union for the Conservation of Nature.
SGCN	Species of Greatest Conservation Need.
SWAP	State Wildlife Action Plan.
WMI	Wildlife Management Institute.
YFI	Young Forest Initiative.

National Fish and Wildlife Foundation (2022b)]. In addition to activities on public lands, money is directed to land trusts (New England Cottontail, 2021) and private landowners (Natural Resources Conservation Service, 2018) through numerous state and federal sources. Much of this activity, supported by the significant money available for forest-clearing for early successional habitats (American Bird Conservancy, 2015; Natural Resources Conservation Service, 2019; Ruffed Grouse Society, 2022), engages broad support by well-intentioned landowners and conservationists by portraying this clearing as "restoration" to retain or save declining species (Smith, 2017; Weidensaul, 2018). There is little acknowledgment that, although these species are truly declining, they were artificially elevated in their abundance by colonial and relatively modern land-use practices that were abandoned in 19th and especially the 20th century.

Currently, every state in the Northeast receives substantial funding for early-successional habitat projects, either through direct federal programs or shared stewardship agreements (Fergus, 2014; USDA Forest Service, 2021b, 2022e; National Fish and Wildlife Foundation, 2022a; Sharon, 2022; Young Forest Project, 2022b). Even as forests are naturally recovering and helping to mitigate climate change in the absence of intensive logging, the momentum and money to clear forests and create open habitats is growing. For instance, the Infrastructure Investment and Jobs Act (2021) authorizes billions of dollars to increase logging for "wildfire risk reduction," "ecosystem restoration," and production of "mass timber" buildings (Parajuli, 2022; USDA Forest Service, 2022a). These massive programs will significantly increase early-successional forest habitats across the country, including in the Northeast and Upper Great Lakes regions. In contrast, there appear to be few resources devoted to protecting and expanding mature and old-growth forests.

Meanwhile, forest and wildlife managers–and a surprisingly large number of scientists—contend that the campaign to artificially expand early-successional habitats is vital because: (1) numerous wildlife species that depend on these habitats are declining and potentially endangered (Fergus, 2014), (2) the "restoration" of such habitats is needed to halt and reverse this decline (Young Forest Project, 2022c), and (3) the history of the region includes significant disturbance and presence of early successional habitats (Oehler et al., 2006). However, as noted previously, targeted population increases in specific species are mismatched generally with longer historical trends (**Figure 1**). Below is a more specific review of the rationales for these

TABLE 2 Marketing and communication strategies used by Young Forest Initiative.

Strategies	Recommendations	Actions and outcomes
Identify public values	Mobilize opinion surveys and host focus groups of landowners and the public to identify values. Set up regional pilot campaigns.	Recognize that forest owners and the public value beauty, scenery, nature, and biodiversity more than logging or financial return. Promote these values as enhanced by young forests.
Change language	Avoid terms with negative or unclear or connotations, i.e., "clearcutting," "early successional," "scrub," or "shrub."	Refocus language to emphasize "young forest" and emphasize that "a diversity of wildlife requires a diversity of habitats."
Create websites	Focus on target audiences such as private landowners, conservation professionals, residents of forested communities, and hunters.	Establish the Young Forest Project website as a central information hub that emphasizes benefits and collaboration to promote campaign goals.
Recruit partners	Identify partners with an interest in "young forest" species (i.e., deer, Ruffed Grouse, Wild Turkey, and Golden-winged Warbler).	Use the Young Forest Project website to build an extensive network of "partners" and include links to their websites (see **Supplementary 2**).
Persuade the public	Promote timber harvesting and active management to create young forests as a benefit to plants and wildlife.	Avoid and diminish negative impacts of clearcutting and focus on how "ugly [clearcuts] grow quickly into beautiful [habitats]."

assertions, along with questions and concerns that have been raised in response.

1.2.2. Rationale for forest-clearing: Halt the decline of specific wildlife species

The primary justification cited for forest-clearing is that populations of many species needing early-successional habitats are declining (King et al., 2001; King and Schlossberg, 2014; Yamasaki et al., 2014; North American Bird Conservation Initiative, 2019; Rosenberg et al., 2019). Monitoring populations of species and preventing decline is a legitimate concern. Failure to take action in the past has allowed many species to become endangered or go extinct. Therefore, if these assertions are true, if losing species is a possibility, and if there are no plausible alternative explanations, a reasonable conclusion is that some species may need additional early-successional habitat to survive and thrive and would therefore justify habitat experiments and intensive habitat management programs to protect these species.

It is important to recognize that documentation of the decline of early-successional species is almost invariably based on a very recent baseline, generally dating to the 1960s or later (DeGraaf and Yamasaki, 2003; Massachusetts Audubon Society, 2013; North American Bird Conservation Initiative, 2014; Rosenberg et al., 2016, 2017, 2019; Connecticut Department of Energy and Environmental Protection, 2019; Sauer et al., 2020; Littlefield and D'Amato, 2022). This time period is a convenient benchmark because it falls within the lived experience of many of today's wildlife and forest managers and the landowners and public that they are trying to reach. It also coincides with the first annual North American Breeding Bird Survey (BBS), which took place in 1966 (Sauer et al., 2013). Prior to this time there was little reliable quantitative information on most bird populations (Foster, 1995; Foster et al., 2002; Dunn et al., 2005).

Although useful in many ways, the BBS is flawed as a truly long-term baseline for bird population trends. An ongoing deficiency is that the BBS is not a representative sampling of the broader landscape: it surveys habitats primarily near secondary roads and leaves out a wide range of habitats (Dunn et al., 2000; Dunn et al., 2005; Sauer et al., 2017). Furthermore, the quality of the data is inconsistent because volunteer observers have varying abilities (Dunn et al., 2000), including age-related declines in bird detection abilities and mobility (Farmer et al., 2014).

Beyond these problems, using a mid–1960s baseline for wildlife populations is fundamentally misguided. Every history of the region shows that at the time of the first BBS the Northeast and Upper Great Lakes regions were (and still are) in transition—with unnaturally high amounts of early-successional habitat such as abandoned farmland and forests recovering from intensive clearing and historically anomalous levels of fire, grazing and other human disturbances (Whitney, 1994; Foster et al., 2002; Mladenoff et al., 2008; Mladenoff and Forrester, 2018). As a result, the 1960s populations of wildlife species that occupied and thrived on such habitats were likely inflated well beyond what they would be in natural forests before European settlement (Litvaitis, 1993). This set the stage for a decades-long dramatic downward population trend due to recovering landscapes that are not yet within their true ecological trajectories (Massachusetts Audubon Society, 2013; Connecticut Department of Energy and Environmental Protection, 2019; Rosenberg et al., 2019).

Wildlife population trends since the 1960s need to be viewed in the context of a much longer timeframe (Schulte et al., 2005a,b), as has been provided by many superb studies of changes in major tree species for the region (Mladenoff et al., 2008; Thompson et al., 2016). For examples, **Figure 1** spans the period from 1600 to today, displaying dual juxtaposed bell curves—one with forests (and some forest-associated species) steadily declining until the mid–1800s and then recovering through present day, and the other an inverse curve showing early-successional species populations increasing and then declining during that period (Foster et al., 2002). The recovery of the forested landscape may be causing previously inflated early-successional populations to restabilize closer to their natural baseline prior to the arrival of Europeans and under the conditions in which these species evolved.

Despite these caveats, State Wildlife Action Plans (SWAPs) rely heavily on the erroneous 1960s baseline for gauging the status of early-successional species. A SWAP must be filed with the U.S. Fish and Wildlife Service by each state to qualify for a number of major federal grants (The Wildlife Society, 2017). SWAPs include a list of Species of Greatest Conservation Need (SGCN), encompassing species that appear on federal or state lists as threatened or endangered, as well as those which are deemed rare, declining, or vulnerable to decline within that state (Minnesota Department of Natural Resources, 2016). SWAPs are useful sources of information for wildlife managers, but they are limited in scope, focusing on individual species within one state, rather than regional and national biodiversity (Pellerito and Wisch, 2002; Paskus et al., 2015).

With their mid–1900s baseline, SWAPs skew state-level biodiversity policies and programs toward management for conditions of that era. As noted, this is comfortable for wildlife and land managers who grew up during and recently after that time and appeals to many members of the public. However, this has created a false sense of endangerment for early-successional species that: (1) are common and of "least concern" based on International Union for the Conservation of Nature (IUCN) criteria (IUCN, 2012); (2) were historically uncommon (i.e., naturally rare, and at a natural population level); or (3) are non-native (i.e., did not occur in that state prior to European settlement and contribute to under-estimating populations of mature and old-growth forest species). The supposedly grave state of these species is reinforced further by the YFI. For example, its handbook for wildlife managers includes a list of "89 species of wildlife classified as [SGCN] that require young forest habitat to survive and breed" (Oehler et al., 2013).

Although these species use early-successional habitats, only a small number of them are listed under the federal Endangered Species Act (U.S. Fish and Wildlife Service, 2022b), and many of them fall into the following categories:

- They are at the edge of their range in a particular state and were temporarily increased in numbers by past forest-clearing, but are now abundant and widely distributed across their range, such as the Yellow-breasted Chat (*Icteria virens*) in Connecticut or the Prairie Warbler in Massachusetts (Nolan, 1978; Southwell, 2001);
- They were probably rare in, or not native to, a particular state before the arrival of Europeans and moved in as a result of the widespread forest clearing in the 19th century, such as Golden-winged Warbler (Askins, 2011) and Chestnut-sided Warbler (Litvaitis, 1993; Foster et al., 2002) in New England;
- They have declined in population and distribution since the 1960s, but had a limited distribution in the landscape before European settlement, such as the New England Cottontail (*Sylvilagus transitionalis*) (**Figure 3**; U.S. Fish and Wildlife Service, 2015a);
- They have declined from past unnaturally high mid–20th century populations, but continue to be abundant and widely distributed, such as the American Woodcock (Seamans and Rau, 2018), Northern Bobwhite (*Colinus virginianus*) (Giocomo et al., 2017), Whip-poor-will (*Caprimulgus vociferus*), Bobcat (*Lynx rufus*), Smooth Green Snake *Opheodrys vernalis*), Eastern Buck Moth (*Hemileuca maia*), and Wild Lupine (*Lupinus perennis*) (NatureServe, 2022);
- Their declines can be attributed to other causes besides lack of habitat, such as the impact of West Nile virus on Ruffed Grouse populations (Stauffer et al., 2018);
- They benefit from limited, scientifically-backed habitat management, not forest-clearing, as with restoration of Wild Lupine (*Lupinus perennis*) for the protection of specialist butterflies (Pavlovic and Grundel, 2009; Plenzler and Michaels, 2015).

Including species of questionable "conservation need" on state SGCN lists has helped to validate and encourage forest-clearing and other intensive management to expand early-successional habitats. For instance, a major goal of the Connecticut SWAP is to "keep common species common" (Connecticut Department of Energy and Environmental Protection, 2015), which has been translated into an intensive focus on forest-clearing (Neff, 2017) and is promulgated in agency publications such as "The Clear Cut Advantage" (Connecticut Department of Energy and Environmental Protection, 2013). Many federal and state agencies have goals for significantly expanding early-successional habitats from current levels (USDA Forest Service, 2018; Massachusetts Division of Fisheries and Wildlife, 2022b) without clear plans for monitoring and maintaining the habitat they are creating.

A further problem is that forest-clearing advocates exaggerate the number of species that "require" or "need" early-successional habitat. For instance, the YFI website asserts, without evidence, that, "if we fail to actively create and renew young forest. . .[m]any songbirds will rarely be seen or heard [and] the New England Cottontail and Appalachian Cottontail could. . .go extinct (Young Forest Project, 2022c). Another YFI publication claims that, "more than 40. . .kinds of birds need young forest. . ." (Fergus, 2014), yet only 12 species of birds in the Northeast are actually considered early-successional forest specialists (Askins, 1993).

Among the species most commonly cited to justify large-scale forest-clearing are the American Woodcock, Ruffed Grouse, Golden-winged Warbler, and New England Cottontail. As discussed in detail in **Supplementary 3**, whether this strategy is necessary or desirable is open to question for each of these species. For example, the woodcock (Seamans and Rau, 2018), grouse (Wiggins, 2006), and cottontail (Fuller and Tur, 2012) are game species subject to being killed by hunters while the cause and potential solutions to warbler declines are uncertain (Streby et al., 2016).

There is a contention that forest-clearing not only "restores" early-successional species, but also benefits many interior species (Chandler et al., 2012; Stoleson, 2013; King and Schlossberg, 2014; Yamasaki et al., 2014; Schlossberg et al., 2018; New Jersey Department of Environmental Protection, 2018). Yet, these claims are based on a few studies that are limited in their targeted species, timeframe, and geographic scope, and rarely examine alternative hypotheses. For instance, although interior forest bird species may use available early-successional habitats to some extent, there is little evidence that such habitats are favored or necessary for their survival (Vega Rivera et al., 1998; Marshall et al., 2003; Dorazio et al., 2015).

Aside from questions regarding its necessity, long-term effectiveness, and unintended consequences, the intense focus on creating and restoring early-successional habitats diverts resources from exploring strategies to address other factors that are known to impact wildlife populations. These factors include food availability, over-hunting, disease, climate change, environmental toxins, and myriad other reasons that are not connected simply to the areal extent of early-successional habitat.

1.2.3. Rationale for forest-clearing: Halt decline of early-successional habitats

Before European settlement, countless small patches of early-successional habitats were created in the forests of the Northeast and Upper Great Lakes regions on a continuing basis, including by wind and ice storms, insect infestations and disease, drought, floods, fire, and to a lesser extent grazing by large mammals (Runkle, 1982; Peterken, 1996). Contemporary

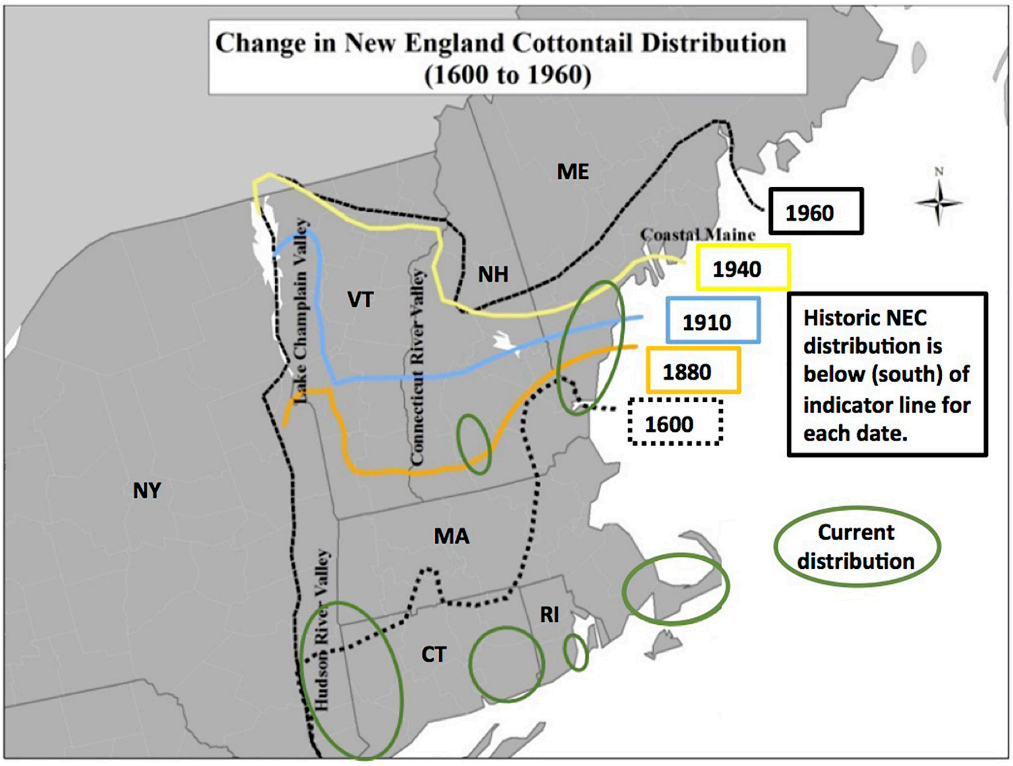

FIGURE 3
Changes in New England Cottontail (NEC) distribution over time. The estimated range of New England Cottontails (NEC) documented circa ~1600 (below the dashed line) included primarily Connecticut (CT) and Rhode Island (RI), and part of Massachusetts (MA). The distribution expanded dramatically northward following European settlement and land use (~1620–1960) to include Vermont (VT), Maine (ME), New Hampshire (NH), and into New York (NY; Hudson River Valley and Lake Champlain Valley). This dramatic expansion was followed by range contraction (~1960–2022) with forest regrowth and urban and suburban development. Green ovals represent the current documented distribution of NEC. Note that parts of current range still extend outside of pre-European settlement bounds, particularly in ME. NEC distribution map adapted from U.S. Fish and Wildlife Service (2015a,b).

studies of old-growth forests in the eastern U.S. suggest such small gaps are less than 0.1 acre in size. Larger openings were created by beaver impoundments and at intervals of hundreds of years by catastrophic windstorms and tornados. While uncommon in the Northeast outside of coastal pine barren communities, fire occurred every few decades and sometimes created large openings in the Upper Great Lakes region (Frelich, 1995; Lorimer and White, 2003). Native people generally caused minimal forest disturbances except around settlements scattered along coasts and river corridors (Motzkin and Foster, 2002; Parshall and Foster, 2002; Munoz and Gajewski, 2010; Oswald et al., 2020b; Frelich et al., 2021).

Advocates of clearing forests for early-successional habitats assert that natural and pre-European disturbances have been greatly attenuated and, therefore, managers must step in to create them (DeGraaf and Yamasaki, 2003; Oehler et al., 2006; Fergus, 2014; King and Schlossberg, 2014; Littlefield and D'Amato, 2022). While these habitats are reduced from their zenith in the 1800s and early 1900s (Foster et al., 2002; Litvaitis, 2003; Lorimer and White, 2003), extensive early-successional habitats still exist and are continuously produced, naturally and by widespread human activity. Natural disturbances such as storms, insect infestations and disease (including many novel non-native types that were not present when Europeans arrived), floods, and beaver impoundments, continue to create forest openings (Whitney, 1994; Askins, 2000; Frelich, 2002; Zlonis and Niemi, 2014; Wilson et al., 2019). Many types of human disturbances including farming, forest harvesting, and the expansion of electrical transmission lines provide additional extensive areas of early-successional habitats.

About 13% of forest area in the Northeastern United States is currently in the smallest (seedling-sapling) size class (Oswalt et al., 2019), a decline of more than 50% over the past 40 years, but several times higher than estimated presettlement values (Lorimer and White, 2003; **Figure 2**). Early-successional habitats in the Upper Great Lakes regions today are more difficult to quantify, because much of the southern and western portions of the three states are covered by savannas, prairies, and agricultural land. However, a study found that 4.4% of the area of Michigan north of the prairie-hardwood transition is characterized by forests less than 20 years old (Tavernia et al., 2016), and forests less than 20 years old are estimated to cover 12% of all forested lands in Wisconsin and Minnesota, respectively (Kilgore and Ek, 2013; Wisconsin Department of Natural Resources, 2020; USDA Forest Service, 2022b).

Approximately 65% of timber removals in the Northeast detected in U.S. Forest Service Inventory Data (FIA) are commercial clearcuts, shelterwood, high-grade, group selection, or pre-commercial thinning treatments (Belair and Ducey, 2018)—all major sources of early-successional habitats. In the Northeast and Upper Great Lakes, tens of thousands of acres of these habitats are created each year by the clearcutting of public and private timberlands—more than 10,000 acres in the national forests alone (USDA Forest Service, 2003; USDA Forest Service, 2017). Among the nine Northeast states, almost 19 million acres (16%) are farmland, most of which was formerly forested (U.S. Department of Agriculture, 2020), and about one-third of agricultural lands provide a mosaic of early-successional habitats such as grassland, woodland, wetland, and other open habitats (Brady, 2007; Jeswiet and Hermsen, 2015).

Expansive early-successional habitats are also the byproduct of urban and industrial developments. Examples include pipeline and powerline corridors (King et al., 2009; Askins et al., 2012), highway rights of way (Huijser and Clevenger, 2006; Amaral et al., 2016), golf courses (Tanner and Gange, 2005), greenways (Mason et al., 2007), wind and solar power arrays (South Carolina Department of Natural Resources, 2020; Zaplata and Dullau, 2022), military bases (Young Forest Project, 2022d), airports (Cousineau, 2017), and reclaimed strip mines (Bulluck and Buehler, 2006). Most of these development categories are not included in current inventories of early-successional habitats.

Additional factors are expected to increase the inventory of early-successional habitats. The forests of New England, for example, are rated as "above average" in health, but climate change is projected to have widespread impacts that will expand early-successional habitats (Janowiak et al., 2018; USGCRP, 2018). These impacts include major disturbances from storms (Miller-Weeks et al., 1999; Koches, 2019; Seitz, 2019), increased precipitation and flooding (National Wildlife Federation, 2009; Connecticut Department of Energy and Environmental Protection, 2020; Moustakis et al., 2021), periods of extreme heat and drought (Baca et al., 2018), insect and disease outbreaks (Paradis et al., 2008; Massachusetts Department of Conservation and Recreation, 2018), the introduction of new invasive species (Seidl et al., 2017), and shifts of vegetation and habitats northward (Chen et al., 2011; Toot et al., 2020). SWAPs and the YFI do not take into account such climate impacts.

Another potential source of early-successional habitats is the use of intensive forest management to increase climate "adaptation" and "resilience" of forests, which includes clearcutting, thinning, prescribed burning, and "assisted migration" through tree plantings (Foster and Orwig, 2006; USDA Forest Service, 2021a, 2022c; Climate Change Response Network, 2022a,b, Massachusetts Department of Conservation and Recreation, 2022; Northern Institute of Applied Climate Science, 2022; USDA Forest Service, 2022c). Such intensive forest interventions are, to date, mostly conceptual and experimental (Millar et al., 2007, D'Amato et al., 2011; Sheikh, 2011; Schwartz et al., 2012; Park and Talbot, 2018; Aquilué et al., 2020; Palik et al., 2022). Many questions remain regarding their economic, ecological, and legal and administrative feasibility (Handler et al., 2018). A prudent course would be to move cautiously with such novel strategies while expanding protection for mature and old-growth forests, which have a high degree of ecosystem integrity, genetic diversity, and adaptive capacity (Mosseler et al., 2003a; Thompson et al., 2009; Rogers et al., 2022).

An increasingly common rationale for forest-clearing is that it is necessary to recreate the way that Native people lived in relationship with the land. This is based on the extensively criticized hypothesis that long before European settlement, humans were deliberately managing most of the Northeast and Upper Great Lakes landscape using forest burning and clearing to improve habitat for favored plants and animals (Day, 1953; Mann, 2005; Abrams and Nowacki, 2008; Poulos and Roy, 2015). Some accounts take the idea even further, contending that by 1600, North America was "a humanized landscape almost everywhere" (Denevan, 1992), managed by Native people as a "garden" (Pyne, 2000), with virtually no "natural" plant communities (Williams, 2002). According to this view, the cessation of widespread and frequent pre-European burning and the reforestation of large parts of the region (which had been cleared after European settlement) have resulted in a massive loss of early-successional habitats and species, seriously threatened major plant communities, and reduced native biodiversity (Brose et al., 2001; Poulos and Roy, 2015; Abrams and Nowacki, 2020). The assumed loss of management by Native people is also cited as a major cause of the transition now underway of many oak forests to forests dominated by shade-tolerant species (Abrams, 1992; Brose et al., 2001; Abrams, 2005; Nowacki and Abrams, 2008).

Native burning and other subsistence practices, such as hunting, fishing, plant gathering, and small-scale farming had notable ecological impacts in the immediate vicinity of native encampments and settlements in the Northeast and Upper Great Lakes regions (Whitney, 1994; Lorimer and White, 2003; Oswald et al., 2020b; Frelich et al., 2021; Tulowiecki et al., 2022). However, modern land managers seem to be inappropriately misinterpreting a set of novel landscape conditions created by European land use over the last few centuries as having pre-European origins (Chilton, 2002; Oswald et al., 2020b; Cachat-Schilling, 2021). Extrapolating this misinterpretation to a regional scale has led to claims of widespread and intensive Native manipulation for millennia before European settlement. Unfortunately, these sweeping assumptions are being used to justify large-scale clearing and prescribed burning of established and recovering forests (Pyne, 2000; Brose et al., 2001; Williams, 2002; Oehler et al., 2006; Poulos and Roy, 2015; Abrams and Nowacki, 2020). In 2019 alone, 365,306 acres of forest—an area larger than Rocky Mountain National Park—were burned through prescribed fire in the Northeast and Upper Great Lakes, according to state forestry agencies (Melvin, 2020). Examples of major prescribed fire projects are found in Connecticut (Connecticut Department of Energy and Environmental Protection, 2021a), Massachusetts (Clark and Patterson, 2003), Michigan (Michigan Department of Natural Resources, 2022), and Vermont (USDA Forest Service, 2022d). This is in addition to the significant expanses of forest that are cleared under the premise of creating early-successional habitat.

Beyond the greater risks from mechanized modern forest management, there is significant controversy regarding the hypothesis of intensive and extensive management of the pre-European landscape by Native people (cf., Cachat-Schilling, 2021). For example:

- The presumption that the presettlement landscape was dominated by agriculturally based Native people who regularly burned large areas relies primarily on written or oral accounts by European explorers, travelers, and colonists. The vast majority of these narratives were not objective descriptions, but were vague, subjective, biased, or even meant to promote profit-making enterprises (Russell, 1981; Forman and Russell, 1983; Russell, 1983; Vale, 1998; Vale, 2002; Barrett et al., 2005; Munoz et al., 2014; Foster, 2017).
- Maintenance of the envisioned anthropocentric landscape would have required Native communities to move every 10–20 years, thereby creating extensive early-successional habitat and a wide variety of even-aged forest patches. This scenario is not supported by archeological studies of pollen and charcoal (Chilton, 2002; Oswald et al., 2020b).
- Localized burning and other land use did commonly occur in some population centers along the New England coast where maize agriculture had developed, the estuaries of New York, New Jersey, Delaware, and Maryland, around the eastern Great Lakes, and along major rivers (Russell, 1981; Motzkin and Foster, 2002; Milner and Chaplin, 2010; Munoz and Gajewski, 2010). However, throughout much of the rest of the Northeast and Upper Great Lakes regions, there is no evidence of significant land clearing or agriculture (Chilton, 2002; Parshall and Foster, 2002; Lorimer and White, 2003; Faison et al., 2006; Matlack, 2013; Oswald et al., 2020b). Rather, pollen and charcoal studies show that the vast interior of these regions had a dispersed, low-density population that was seasonally mobile and utilized native resources, not agriculture (Milner and Chaplin, 2010; Foster, 2017; Oswald et al., 2020b; Frelich et al., 2021). Archeological evidence indicates that many Native settlements in these regions are a relatively recent phenomenon—for example, Iroquois settlement began during the last millennium (Warrick, 2000; Bruchac, 2004; Jordan, 2013) and New England coastal settlement was likely encouraged by trade with Europeans (Foster, 2017).
- Pollen and charcoal studies as well as fire records indicate that fire activity before the arrival of Europeans tracked climate and vegetation at broad scales, rather than changes in the size of Native populations (Oswald et al., 2020b; Frelich et al., 2021). Indeed, the period of greatest Native population, shortly before the time of European colonization, was one of relatively low fire activity. At smaller spatial scales, particularly near the coast, some pollen records do show relatively high fire activity just prior to European settlement in areas of higher human population densities (Stevens, 1996; Lorimer and White, 2003; Parshall et al., 2003). Sites on steep slopes in the Appalachians have both a pre-history and a historic pattern of frequent crown and ground fires (Delcourt and Delcourt, 1998; Shumway et al., 2001; Buckley, 2010). Overall fire activity spiked after forest-clearing by European settlers created dry and flammable early-successional habitats, spiked again in the late 19th and early 20th centuries with the expansion of fire-prone abandoned farmlands and cutover forests, and has dramatically declined in the last century (Irland, 2013, 2014; Frelich et al., 2021).
- Long before the first colonization of North America 15,000–18,000 years ago, Northeast and Upper Great Lakes ecosystems had evolved and were maintained by climate and natural disturbances (Foster et al., 2002; McEwan et al., 2011; Noss et al., 2014; Pederson et al., 2014; Oswald et al., 2020b). Historical data and pollen studies indicate that before European settlement, forests were mainly characterized by long-lived shade tolerant and moderately shade tolerant species, not fast growing, early-successional and weedy species that would indicate widespread Native burning (Russell, 1983; Foster et al., 2002; Motzkin and Foster, 2002; Parshall and Foster, 2002; Parshall et al., 2003; Faison et al., 2006; Shuman et al., 2019; Oswald et al., 2020b). Oak savannahs along the prairie-forest border in the Upper Great Lakes region were far more widespread than today and likely maintained at least in part by greater frequencies of fire, including burning by Native people (Whitney, 1994; Frelich et al., 2021; Paciorek et al., 2021). However, the current shift of some forests from disturbance-tolerant species to shade-tolerant species can be explained by changes in climate and other factors rather than a lack of human-caused fires (Foster et al., 2002; McEwan et al., 2011; Noss et al., 2014; Pederson et al., 2014; Oswald et al., 2020b).
- Fire-prone ecosystems occupy about 25% of the forested landscapes of northern Minnesota, Wisconsin, and Michigan (Heinselman, 1973; Frelich, 1995;

Frelich and Reich, 1995). However, even with the high occurrence of fires, there was still a much higher proportion of old-growth prior to European settlement than today (Frelich, 1995). Approximately 55% of forests were old growth within the 25% of the landscape that is fire prone (pine and oak forests with some aspen birch and spruce). These areas had 100–250 year return times for severe fires, so that only 55% of the stands would reach an age of 120 years or more. There were both natural and human understory burns, which helped maintain the old multi-aged condition in some stands. Elsewhere, for example in northern hardwood forests, where fires were much less common, the proportion of old-growth was much higher and wind storms were the primary disturbance. Severe fires that set succession back to birch and aspen were quite rare in these areas and were confined largely to blowdown areas. Only small proportions of fire-prone forest landscapes in the Boundary Waters Canoe Area Wilderness and Voyageurs National Park had a long history of regular understory burns (Johnson and Kipfmueller, 2016; Kipfmueller et al., 2017).

- In the Northeast, only limited areas are susceptible to fire, such as coastal pine barrens of Massachusetts, New York, and New Jersey, as well as scattered pavement barrens and sandplain communities in upstate New York and the Connecticut Valley (Forman and Boerner, 1981; Motzkin et al., 1999). Climate change and European land use have been the most important agents of change on these landscapes (Motzkin et al., 1999; Parshall et al., 2003).

In summary, current understanding of the role of fire and other disturbances in the Northeast and Upper Great Lakes regions before the arrival of Europeans is based on uneven, area-specific, and often-inconclusive information (Oswald et al., 2020a; Frelich et al., 2021). Available evidence does not support the hypothesis of widespread, intensive, ongoing burning and other land management over millennia by Native people (Cachat-Schilling, 2021). Instead, the evidence points to human use before European colonization limited to areas near settlements and ultimately constrained by a regional human population that is estimated to be less than 1% of the present population (Milner and Chaplin, 2010).

1.2.4. Rationale for forest-clearing: Reduce the prevalence of "mature" forests

Forest-clearing advocates assert that, in parallel with the presumed lack of "young" forests, there is an overabundance of "mature," and "even-aged" forests across the landscape. They contend that these forests do not provide an adequate diversity of habitats, and that "active management" can "restore" forest diversity and resiliency by "mimicking" natural forest disturbances and conditions (National Commission on Science for Sustainable Forestry, 2007; Fergus, 2014; King and Schlossberg, 2014; New Jersey Department of Environmental Protection, 2018; Rohrbaugh et al., 2020; Littlefield and D'Amato, 2022). Prior to evaluating this rationale it is important to note that a forest termed "even-aged" can include ages that vary by about 20% of the dominant age, and may also include young trees/advance regeneration, dead trees, and a mosaic of habitats (for example, due to insect damage or storms). "Even-aged" does not mean "even-sized" and tree growth is highly influenced by local site conditions for that species. The term "even-aged" can evoke images of a tree farm or a plantation, but natural forests do not have such a uniform structure, particularly those older than 60–80 years. Although 60–80 year old trees may be termed "mature," or almost "overmature," they are at far less than half their natural lifespan and likely at far less than 20% of their potential carbon accumulation (Thompson et al., 2009; Leverett et al., 2021). Most important, forests that are relatively even-aged will transition on naturally toward old-growth and uneven-aged condition if simply left alone (Gunn et al., 2014; Catanzaro and D'Amato, 2019).

With these caveats in mind, it is important to determine if and when removing mature or "even-aged" forests has net benefits. In terms of risks, there is considerable evidence that human-created or -maintained habitats do not provide the complexity, resilience, and diversity over long periods of time that are provided by natural forest ecosystems (Nitschke, 2005; North and Keeton, 2008; Thompson et al., 2009; Lindenmayer and Laurance, 2012; Belair and Ducey, 2018; Thom and Keeton, 2020). Moreover, countless interconnected and long-term ecological variables and processes are not well understood or are still simply unknown—and therefore cannot be "replicated" by human intervention with any confidence.

Taken together, long-term monitoring and further research on these issues should be a top priority. After a natural disturbance a forest can be a chaotic jumble of dead and damaged trees, downed wood, and tip-ups—many involving immense old trees and their associated biodiversity above and below ground (Lain et al., 2008; Santoro and D'Amato, 2019). In a natural forest, snags and downed logs and uproot mounds and pits are large and enduring for 100 years or more, there are no large areas of bare ground or scarified soil, and downed wood and vegetation remains on site (Foster et al., 2003). After an extreme event, such as a hurricane, there may be abundant advance regeneration, understory vegetation, and a mix of damaged and undamaged trees. These building blocks help the forest recover and resist the intrusion of invasive species (Plotkin et al., 2013, D'Amato et al., 2017). Even forests with almost no advance regeneration can regenerate rapidly after a major disturbance (Faison et al., 2016).

To summarize, current programs that create new early-successional forest habitats involve clearing established forested areas. These human-made habitats are dramatically different from the old-growth forest habitats with a mosaic of natural disturbances that dominated the landscape of the Northeast and most of the Upper Great Lakes before European settlement. Early-successional habitats have declined since their peak in the 19th and early 20th centuries but they are still widely represented, actively created by natural and human disturbances, likely undercounted, and expected to increase in the future. In light of the concerns discussed above, there is a compelling argument for re-evaluating the assertion that creating more early-successional habitat is essential for the survival and health of ecosystems, habitats, or species.

2. Impacts of forest clearing projects

2.1. Impacts on biodiversity

Advocates contend that widespread and increased forest-clearing will not have significant negative environmental impacts and can even benefit species associated with mature and old-growth forests (Chandler et al., 2012; Schlossberg et al., 2018; Nareff et al., 2019). Yet, there is ample evidence that this will result in the loss of mature forests and future old-growth habitats, reduced connectivity, an increase in edge habitats, the spread of invasive species, and deleterious effects due to mechanical disruption and species isolation (Wilcove et al., 1986; Small and Hunter, 1988; Franklin, 1989; Askins, 1992; Faaborg et al., 1993).

Meanwhile, and perhaps most important, we have insufficient data on many classes of organisms, and vast numbers of species are still undiscovered (Mora et al., 2011). Numerous moss species need older trees with thicker moisture-holding bark to survive droughts (Zhao et al., 2020). Native snails and insects are more abundant in older forests (Jordan and Black, 2012; Maloof, 2023). These forests host vast networks of plant roots and mycorrhizae, which may link trees to each other and allow the transfer of resources between mature trees (Simard et al., 2012). There is evidence that millions of species of fungi and bacteria swap nutrients between soil and the roots of trees in an interconnected "wood-wide web" of organisms (Steidinger et al., 2019). As scientific methodology evolves, so does our ability to detect tiny organisms and new molecules, including those of critical importance for medicine. In 2018, 16 new species were discovered in a teaspoonful of soil in Massachusetts (Schulz et al., 2018). A study of enchytraeids (a type of annelid worms) in maple forests of northern Minnesota found 9 species new to science (Schlaghamerský et al., 2014). Forest maturity increases the presence of groundwater macroinvertebrates and, in particular, uncommon species (Burch et al., 2022).

Unfortunately, few forests are surveyed for all types of life-forms before clearing to create early-successional habitats. "Resetting" a forest to age "zero" by clearing it reduces ecological complexity immediately because it prevents the full expression of structural and ecological diversity as well as myriad ecosystem services. Recovery is uncertain. Although southeastern U.S. forests are some of the most frequently logged forests in the world (Hansen et al., 2013)—resulting in ample early successional habitat—the region has experienced dramatic long-term declines in early-successional birds (Hanberry and Thompson, 2019). Even less-intensive logging activity can diminish or eliminate disturbance-sensitive and slowly dispersing plant and animal species, with recovery potentially taking many decades, if at all (Duffy and Meier, 1992; Petranka et al., 1994; Hocking et al., 2013).

It is instructive to contrast previously cleared forests that are designated as parks or preserves, where forest ecosystems have been allowed to function and develop predominantly under the influence of natural processes (i.e., GAP 1 areas) with forests subject to clearing of established forests to create early-successional habitats (i.e., some GAP 2 areas) or to commercial logging (i.e., GAP 3 or GAP 4 areas). For more detail on GAP classifications, see **Table 1** and U.S. Geological Survey (2022b). Forests that are allowed to recover naturally and develop past the stem-exclusion phase steadily gain structural complexity and biodiversity, in part from ongoing low-to-moderate severity disturbances (Zlonis and Niemi, 2014; Miller et al., 2016; Hilmers et al., 2018). Indeed, the accumulated legacy of a mosaic of natural disturbances is greatest in unmanaged old-growth forests (Oliver and Larson, 1996; Askins, 2000; Lorimer and White, 2003). For instance, the 1-million-acre Boundary Waters Canoe Area Wilderness in Minnesota has taller tree canopies, greater tree species richness, and a larger number of bird species than adjacent managed national forest lands (Zlonis and Niemi, 2014). This wilderness also hosts a similar richness of bird species that favor young forests, such as the Chestnut-sided Warbler (Zlonis and Niemi, 2014). In Maine's "forever wild" Baxter State Park, natural insect outbreaks create open habitats that benefit early-successional species (Oliveri, 1993). A survey of Michigan habitats concluded that designated wilderness areas had considerable early-successional habitats, even though they were not open to logging or habitat management (Taverna et al., 2016). As discussed below, findings were similar in New York's "forever wild" Adirondack and Catskill forest preserves (Widmann et al., 2015).

Numerous rare, threatened, and endangered wildlife species depend upon mature and old-growth forests and their ecosystem services. These species include migratory birds such as the Cerulean Warbler (*Setophaga cerulean*) (U.S. Fish and Wildlife Service, 2006; Dawson et al., 2012) and Wood Thrush (*Hylocichla mustelina*) (Bertin, 1977; Hoover et al., 1995; Rosenberg et al., 2003). They include mammals such as the Eastern Spotted Skunk (*Spilogale putorius interrupta*) (Lombardi et al., 2017; Hassler et al., 2021; Pearce et al., 2021), Appalachian Cottontail (*Sylvilagus obscurus*) (Chapman et al., 1992), Northern Long-eared Bat (*Myotis septentrionalis*) (U.S. Fish and Wildlife Service, 2022a), and Allegheny Woodrat (*Neotoma magister*) (Balcom and Yahner, 1996; Lombardi et al., 2017). They include plants such as Butternut (*Juglans cinerea*), (Schultz, 2003), Canada Yew (*Taxus canadensis*) (Dunwiddie et al., 1996; Windels and Flaspohler, 2011), Frasier Sedge (*Cymophyllus fraserianus*) (Godt et al., 2004), and American Ginseng (*Panax quinquefolius*) (McGraw et al., 2013). Some species reach their highest densities in old-growth forests, including southern and northern flying squirrels, forest interior birds, and spring ephemeral wildflowers.

The fragmentation of forests, particularly with roads and other human intrusion, can result in the decline of forest interior species. This can have significant impacts on the abundance, species richness, and community dynamics of migratory birds (Small and Hunter, 1988; Askins, 1992; Hagan et al., 1996; Zuckerberg and Porter, 2010; Askins, 2015; Betts et al., 2022). Apex predators can be lost, leading to further biodiversity loss as well as altered dynamics of disease, carbon accumulation, invasive species, and biogeochemical cycles (Terborgh et al., 1999; Anderson et al., 2004; Estes et al., 2011; Terborgh, 2015). Even common forest species are subject to major declines due to loss of natural forest habitats. A global report shows a 69% decrease in monitored wildlife populations between 1970 and 2018, in large part due to habitat fragmentation and degradation (WWF, 2022). Fragmentation can increase prevalence of wildlife diseases including Raccoon Roundworm (*Baylisascaris procyonis*) (Wolfkill et al., 2021) and may be a factor in oak decline and loss of ecosystem services (Tallamy, 2021) as well as reduced underground biodiversity—a concern that is less explored in the Northeast and Upper Great Lakes than in western forests (Simard, 2021).

Figure 1 reflects biodiversity impacts of habitat changes and hunting over several hundred years. Habitat loss was a factor in the decline of deer, moose, beaver, turkey, wolf, mountain lion, and bear, but intensive hunting and trapping probably had the greatest impact (Foster et al., 2002). Coyotes migrated eastward following wolf extirpation, interbred with wolves, and partially filled the vacant niche left by wolf extirpation. Deer can thrive in disturbed landscapes, which explains their recovery once hunting pressure was relieved (Michigan Department of Natural Resources, 2016). Forest-clearing is widely used today to boost populations of deer and other game species (Lashley et al., 2011; Dechen Quinn et al., 2013; Michigan Department of Natural Resources, 2017). However, high deer population densities can have significant negative effects on forest regeneration, native herbaceous plants—especially charismatic floristic groups such as orchids—and songbirds and their habitats (Alverson et al., 1988; deCalesta, 1994; Rooney and Waller, 2003; Knapp and Wiegand, 2014; Jirinec et al., 2017). Clearing established forests can also introduce and spread invasive and non-native species that ultimately reduce biodiversity (McDonald et al., 2008; Eschtruth and Battles, 2009; LeDoux and Martin, 2013; Coyle et al., 2017). Managed forests have been found to have as much as three times more invasives than fully protected national parks or wilderness (Riitters et al., 2018). Invasive plants can have a negative impact on native animal populations, including birds, mammals and other vertebrates (Fletcher et al., 2019). Invasive earthworms are a serious concern, particularly the new threat of jumping worms (*Amynthas spp.*) that destroy forest soil very rapidly (Frelich et al., 2019).

2.2. Impacts on the atmosphere

Forests influence water cycles, reduce local and global temperatures, and sequester and accumulate carbon. While carbon receives the most attention, multiple biophysical processes are crucial and interactive (Makarieva et al., 2020; Lawrence et al., 2022). Proponents of forest-clearing assert that carbon emissions are offset by increased sequestration rates of younger forests, by converting trees to wood products, by burning logging "waste" for bioenergy, and by forest carbon accumulation elsewhere—or that the amount of forest removal is so small as to be inconsequential (Hawthorne, 2020; Jenkins and Kroeger, 2020; USDA Forest Service, 2021a). On the contrary, these activities have significant climate costs, including the release of greenhouse gases from the cutting, processing, and transporting of trees for wood products; the disposal of waste and wood products; the release of methane from each log landing; the release of carbon from disturbed soils; and the loss of carbon uptake and accumulation by standing trees (Smith et al., 2006; Nunery and Keeton, 2010; Ingerson, 2011; Mika and Keeton, 2013; Catanzaro and D'Amato, 2019; Cook-Patton et al., 2020; Leturcq, 2020; Vantellingen and Thomas, 2021).

Some studies suggest that younger forests between 30 and 70 years (Catanzaro and D'Amato, 2019) or 40–80 years (Leverett et al., 2021) can sequester carbon at a faster rate than mature or old-growth forests. Other analyses indicate that lands reserved from logging in the Northeast have net carbon sequestration rates that are roughly 33% higher than in logged forests and are projected to sequester more carbon over the next 150 years (Brown et al., 2018). Nevertheless, the climate mitigation value of forest carbon lies not in the sequestration rate but in the total amount that is accumulated and kept out of the atmosphere (Mackey et al., 2013). The power of forests in this process is unparalleled and far greater in old forests than in young forests, both above and below ground; carbon continues to accumulate for centuries (Zhou et al., 2006; Luyssaert et al., 2008; Keeton et al., 2011; Curtis and Gough, 2018; Leverett et al., 2021; Law et al., 2022).

The amount of carbon lost when cutting a mature or old-growth forest is not recovered by fast-growing young forests for many decades to well over a century (Harmon et al., 1990; Aalde et al., 2006; Krebs et al., 2017). One study found almost no net carbon accumulation for 15 years after clearcutting—currently a critical time window for reining in global greenhouse gas emissions (Hamburg et al., 2019). In some cases, older forests are accumulating more carbon as the climate warms (Finzi et al., 2020), they are better able to withstand physiological stress, and they are also more resistant to the stress of climate change than younger forests, particularly regarding carbon storage, timber growth rate, and species richness (Thom et al., 2019). Soil accounts for approximately 50% of total ecosystem carbon storage in the Northeast, with mineral soils comprising the majority (Fahey et al., 2005; Petrenko and Friedland, 2015). Forest-clearing can mobilize and release soil carbon for decades (Nave et al., 2010; Petrenko and Friedland, 2015; Lacroix et al., 2016). It can take from 60 to 100 years for soils on a site to recover from clearcut logging (James and Harrison, 2016).

It is crucial to note that forest carbon stocks in the U.S. are already depleted by about 60% due to past logging and clearing (McKinley et al., 2011) and ongoing timber removals (Gunn et al., 2019). Logging accounts for about 86% of the carbon emitted by U.S. forests each year—far greater than insects, storm damage, fire, development and other uses combined (Harris et al., 2016; Duveneck and Thompson, 2019). Although a small percentage of the carbon in trees that are cut is stored in durable wood products, in the U.S. about 76% of carbon in trees cut for timber is released into the atmosphere each year (Domke et al., 2018), with most of it emitted quickly in processing, waste, and short-lived products (Harmon et al., 1996; Ingerson, 2011; Harmon, 2019; Leturcq, 2020). A logged mature forest stores less than half of the carbon of an uncut mature forest, even if carbon stored in wood products is included in the carbon storage total of the logged areas (Nunery and Keeton, 2010; Law et al., 2022). Impacts are similar for forest-clearing to produce wood bioenergy, which advocates claim is "carbon neutral" (Collins et al., 2015). However, cutting and burning trees releases large amounts of carbon immediately that would take many decades to be recover–if the forest grows back. In addition to other disrupted biophysical processes, this is time we cannot afford in light of the urgent climate crisis (Schulze et al., 2012; Law et al., 2018; Sterman et al., 2022). In short, clearing forests—whether for early-successional habitat or bioenergy—results in serious impacts to the atmosphere. In terms of maximizing carbon accumulation, allowing forests to regrow and remain standing—termed proforestation—is demonstrably preferable to cutting them (Buotte et al., 2019; Moomaw et al., 2019; Mackey et al., 2020; Rogers et al., 2022).

Despite widespread past clearing, the forests of the Northeast and Upper Great Lakes have recovered to the point that they are among the most intact and carbon-dense in the eastern U.S. (Zheng et al., 2008; Zheng et al., 2010; Foster et al., 2017). In addition, because these forests grow vigorously, decay slowly, and are, on average, less than 100 years old, they have centuries of growth ahead and enormous capacity for additional carbon storage (Pan et al., 2011; Williams et al., 2012) and climate stabilization. If allowed to continue growing, these forests can potentially increase *in situ* carbon storage by a factor of 2.3 to 4.2 (Keeton et al., 2011) and perform crucial ecosystem services (Meyer et al., 2022). For these reasons, the New England Acadian region was identified as a Tier 1 stabilization area in the Global Safety Net (Dinerstein et al., 2020). The potential in the Upper Great Lakes region is also significant, where continued forest recovery in existing forests could add substantial amounts of carbon storage (Rhemtulla et al., 2009).

2.3. Impacts on human health and well-being

With more than 50 million acres of U.S. forests projected to be developed over the next 50 years (Thompson, 2006), forest-clearing for early-successional habitats risks further loss of vital natural green space and threatens the stability of regional temperature and water cycles. All of these have impacts on communities. There is an increasing recognition that natural ecosystems offer the public numerous benefits to physical, mental, and spiritual health, as well as social well-being (Karjalainen et al., 2010; Berman et al., 2012; Buttke et al., 2014; Newman and Cragg, 2016; Hansen et al., 2017; Watson et al., 2018; Connecticut Department of Energy and Environmental Protection, 2020). Adolescents may benefit more from natural woodlands than other types of green space in terms of cognitive development and reduced emotional and behavioral problems (Maes et al., 2021). Natural areas are important places to avoid human-related noise and listen to sounds of the natural world, which can decrease pain, lower stress, improve mood, and enhance cognitive performance (Bratman et al., 2015; Buxton et al., 2021).

Protecting intact habitats as refuges for people—even small areas—aligns with the principles of "harm reduction"—practical strategies and ideas aimed at reducing negative consequences. Increasing the well-being of a community, and avoiding or minimizing negative consequences of heat stress, acute physical and mental stress, and a long-term sense of loss can prevent a more serious or chronic condition, particularly in vulnerable populations such as adolescents, pregnant women, seniors, veterans, and those in recovery (Wang et al., 2019; Tiako et al., 2021). The positive impacts of nature on the promotion of mental health has enormous economic benefits (Bratman et al., 2019) and as does preventing mental illness (The Lancet Global Health, 2020).

In addition to social well-being, nature-based outdoor recreation can be an important factor in diversifying and stabilizing local economies (Power, 1996; Power, 2001; Haefele et al., 2016). Studies have shown that recreationists prefer spending time in forests and other landscapes that are natural and free of human manipulation (Vining and Tyler, 1999; Dwyer, 2003; Eriksson et al., 2012). The positive economic effects of robust ecotourism and increased property values can benefit an entire community (Morton, 1998; Lorah and Southwick, 2003; Holmes and Hecox, 2004; Phillips, 2004; Rasker et al., 2013; Fernandez et al., 2018; Cullinane et al., 2022).

In contrast, clearing forests to expand early-successional habitat can threaten human health. For example, it provides optimal habitat for White-tailed Deer and White-footed Mouse

(*Peromyscus leucopus*)—the most competent hosts for the vector of Lyme disease, the Eastern Blacklegged Tick (*Ixodes scapularis*) (Allan et al., 2003; LoGiudice et al., 2003; Levi et al., 2012; Telford, 2017; DellaSala et al., 2018; Robertson et al., 2019). There were 185 deaths from auto collisions with animals in 2019 and an estimated 2.1 million animal collision insurance claims in 2020–21, up 7.2 percent from the previous year, with most collisions involving deer (Insurance Information Institute, 2021).

3. Options and alternatives

As discussed above, forest-clearing projects across the Northeast and Upper Great Lakes are proceeding without well-founded consideration of conditions before European settlement, long-term plans for experimental controls and monitoring, or baseline ecological inventories. Assessments made of potential harm to non-target species are cursory, incomplete, or outdated. Quantifiable negative impacts—such as the spread of invasive species, elevated temperatures, increased fire and flood risk, destabilized and decreased climate mitigation and adaptation, degradation of healthy public green spaces, and ongoing expenditures of time and resources—are frequently overlooked. Meanwhile, potentially imperiled interior and old-growth forest species often do not receive adequate attention. Such chronic knowledge gaps render scientific assessment of the impacts of early-successional habitat projects difficult or impossible. Major interdisciplinary reports (Connecticut Department of Energy and Environmental Protection, 2020) offer a strong rationale for addressing these gaps by devoting significant funding to balancing these priorities, to monitoring, comprehensive ecological inventories, and to strengthening management standards and guidelines.

Reassessing the current forest-clearing campaign is an urgent priority: negative impacts are immediate, and once a forest has been cleared or fragmented it takes a century or more to begin to recover a mature or old-growth condition. This is far too late to address the biodiversity, climate, and public health crises that we face in the next critical decades. There are multiple compelling arguments for a new approach that greatly expands wildland preserves while maintaining needed amounts of early-successional habitats and timber production.

3.1. The importance of parks and preserves

There is growing international recognition that the preservation of mature and old-growth forests is essential to address the dual global crises of biodiversity loss and climate change, as well as to promote public health and well-being (Zhou et al., 2006; Luyssaert et al., 2008; Gilhen-Baker et al., 2022; Law et al., 2022). However, in their drive to expand early-successional habitats, land managers have relegated the recovery and protection of old-growth forests to a tiny fraction of their pre-European extent (New Jersey Department of Environmental Protection, 2017; Massachusetts Division of Fisheries and Wildlife, 2022b). The U.S. Forest Service and Bureau of Land Management together administer the largest remaining tracts of mature and old-growth forests in the U.S., yet they are only now beginning a process to inventory these forests (The White House, 2022). Nationally, only about 24% of these forests are protected from logging (DellaSala et al., 2022a).

An extensive system of large, diverse, and connected parks and preserves can help address this challenge (Noss, 1983; Noss et al., 1999; Wuerthner et al., 2015). Studies show that eastern national parks tend to have larger trees, older forests, and more standing deadwood than surrounding managed forests (Miller et al., 2016). They also have greater tree species richness and a higher percentage of rare tree species (Miller et al., 2018). Cool interior forests such as those in parks and other preserves provide shelter for species that are most sensitive to temperature increases (Betts et al., 2017; Betts et al., 2022; Kim et al., 2022; Xu et al., 2022). Protected forests provide important climate benefits in accumulated carbon and avoided greenhouse gas emissions, and the potential to significantly increase carbon storage (Depro et al., 2008; Keeton et al., 2011; Zheng et al., 2013; McGarvey et al., 2015; Brown et al., 2018; Williams et al., 2021; Law et al., 2022). In addition, parks and preserves directly benefit people by producing clean air and water, reducing flooding, preventing soil erosion, cooling surrounding areas, and buffering damage from sea level rise (Luedke, 2019).

Climate scientists and conservation biologists around the world agree that a major expansion of nature preserves is necessary to address the threats of species extinctions and climate change (Di Marco et al., 2019; Yeo et al., 2019; Barber et al., 2020; FAO and UNEP, 2020; Bradshaw et al., 2021). There is a broad consensus that this requires the permanent protection of at least 30% of the Earth by 2030 (Noss et al., 2012; Dinerstein et al., 2019; Rosa and Malcom, 2020; Thompson and Walls, 2021). The U.S. falls far short of meeting this goal. Only about 8% of the U.S. land base now has protection from resource extraction and development equivalent to the U.S. Geological Survey's GAP 1 level and less than 5% meets GAP 2 standards; the vast majority of these lands are in Alaska and the West (Scott et al., 2001; Aycrigg et al., 2013; Jenkins et al., 2015; Lee-Ashley, 2019; Rosa and Malcom, 2020; Thompson and Walls, 2021; U.S. Geological Survey, 2022a,b). As noted previously, most old-growth forests in the U.S. have no formal protection, even on many GAP 2 public lands, leaving their future uncertain (DellaSala et al., 2022b).

The Northeast and Upper Great Lakes regions are deficient in natural area protection (Scott et al., 2001; Anderson and Olivero Sheldon, 2011; Foster et al., 2023). There are a few notable exceptions, such as the Boundary Waters Canoe Area Wilderness, Isle Royale National Park, Adirondack Forest Preserve, and Baxter State Park, which meet GAP 1 standards (U.S. Geological Survey, 2022a,b). However, less than 1% of the Northeast and Upper Great Lakes regions is estimated to meet this strict level of protection U.S. Geological Survey (2022a). This percentage could be greatly increased through an expanded network of parks and preserves on large tracts of federal and state public lands, and could include key undeveloped private lands acquired from willing sellers (Foster et al., 2017; Meyer et al., 2022; Office of Senator Angus King, 2022). This would have numerous outsized benefits; for example, one study estimated that protected forests cover about 5% of the Northeast (including Virginia) yet store 30% of the aboveground carbon in the region (Lu et al., 2013). New wildland preserves would promote the recovery of mature and old-growth forest ecosystems and provide habitats for wide-ranging imperiled wildlife such as the Gray Wolf (*Canis lupus*) and Canada Lynx (*Lynx Canadensis*). They would also offer natural green space to tens of millions of people in major urban communities, reducing pressure on the few existing protected areas (Rhode Island Division of Statewide Planning and Rhode Island Department of Environmental Management, 2019; Reynolds, 2021).

There is ample evidence that expanded wildland preserves governed by natural disturbance regimes would provide early-successional habitats at least equivalent to the natural conditions in which native species evolved. For example, "On reserved forest land in New York [i.e., primarily the "forever wild" Adirondack and Catskill Preserves]... 3 percent [of forest area is] in seedling/sapling and non-stocked stands" (Widmann et al., 2015). Consistent with this, it is estimated that the proportion of the landscape before European settlement "in seedling–sapling forest habitat ranged from 1 to 3% in northern hardwood forests [i.e., beech–birch–maple–hemlock] of the interior upland" (Lorimer and White, 2003).

3.2. Protecting and restoring natural forest ecosystems

The most common strategy for creating early-successional habitats is to clear established forest tracts, purportedly to simulate the continually "shifting mosaic" of patches across a natural landscape (Schlossberg and King, 2007; Smith, 2017; Massachusetts Division of Fisheries and Wildlife, 2022a). However, as discussed above, forest-clearing is not equivalent to natural disturbances; it has significant costs in biodiversity, carbon accumulation, and other ecosystem services; and reduces the possibility of recovering old-growth forest ecosystems dramatically. Moreover, unlike the conservation of mature and old-growth forests, creating and/or maintaining (every 10–12 years) early-successional habitats requires a permanent, resource-consuming commitment of intensive management to replace openings lost to forest succession (DeGraaf and Yamasaki, 2003; Askins, 2011; Bakermans et al., 2011; Yamasaki et al., 2014). This does not take into consideration the mitigation and remediation of unintended environmental side effects: such artificially created "restoration" areas are expensive to maintain (Oehler, 2003; Schlossberg and King, 2007) and there is no assurance that adequate funding will continue to be available. These are serious disadvantages that argue against the current forest-clearing of established natural forest ecosystems.

Among these different perspectives, there is a more balanced alternative: protect and recover mature and old-growth forests wherever possible, quantify the true extent of early-successional habitat and focus maintenance on ecologically suitable lands, including private lands, and encourage efforts to increase protection the full range of natural ecosystems on private lands. At this time there is no indication that this approach is receiving serious consideration from land managers. Yet the likelihood of significant benefits and greatly reduced costs are a compelling argument for such consideration.

4. Discussion

We evaluated peer-reviewed papers, published research, agency reports, and other materials related to a campaign that is focused on expanding early-successional habitats in the Northeast and Upper Great Lakes regions. Each year, this campaign is clearing thousands of acres of established forests. Conversely, the protection of old-growth forests and unmanaged mature forests is currently relegated to a tiny fraction of the land base.

Overall, the forest-clearing campaign is based on two main rationales, which are both open to serious questions and alternative hypotheses:

The primary rationale is that the decline of a number of early-successional species is a pervasive and potentially existential threat. Yet, the baseline for measuring this decline almost invariably begins in the late 1960s, when populations had begun to decrease from abnormally high levels as forests recovered from past clearing. Relying on an artificial baseline that reaches back only 60 years, in an ecosystem where most tree species live for hundreds of years, and during a regional recovery from widespread and intensive land clearing, is fraught with problems. Moreover, it is questionable that any species in these regions needs artificial expansion of early-successional forest habitats to survive and thrive across its multi-state range. Other than limited surveys of birds, game species, and endangered species, there is no reliable information on wildlife populations before the arrival of Europeans, no comprehensive census of forest species even today, and no long-term analysis that systematically estimates wildlife population trends over the last several hundred years.

A second major rationale is that early-successional habitats have dwindled dangerously, have already fallen below the levels that existed before European settlement, and are not being adequately replenished—thereby endangering native biodiversity. However, there is ample evidence that these habitats remain plentiful across these regions (and are likely more prevalent than is accounted for currently), are considerably more abundant than presettlement, and continue to be created by natural and human disturbances—including by mounting climate change impacts. Although early-successional habitats were maintained to some extent by Native people before the arrival of Europeans, these were limited to areas of high population densities near settlements.

Despite its wide-ranging and long-term implications, the campaign for early-successional forest clearing was formulated by a small number of agency, academic, and special interest professionals, with little comprehensive research and analysis, controlled experimentation, strategic planning, monitoring and evaluation, or public involvement and accountability. This organized and aggressive campaign has confused the public and made it challenging for a range of scientists to engage in an open dialogue about an optimal and balanced approach that prioritizes climate stability, ecosystem integrity and public health. Yet, public awareness has grown regarding the evident impacts of forest-clearing projects on biodiversity, climate change, and natural green spaces and, in turn, so has public opposition to these projects (Ketcham, 2022; Potter, 2022; Whitcomb, 2022).

The Gap Analysis Project (GAP) of the U.S. Geological Survey (2022b) can provide the foundation for a balanced alternative to the current costly, intrusive and controversial approach that prioritizes protecting and sustaining natural systems and processes to the greatest extent possible. We suggest the following.

- Establish a significantly expanded system of public parks, wildland preserves, and connecting corridors across the Northeast and Upper Great Lakes with permanent protection under GAP 1 standards. This would preserve old-growth, mature, and recovering forests and allow them to reach their natural maximum ecological potential. Openlands that were deforested in the past, such as grassy areas and farm fields, would be allowed to recover unimpaired, which would provide ample young forest habitats over the next decade. In parallel, new areas of successional habitat would be created by natural disturbance regimes now, and in the future.
- End the clearing of established forests to create early-successional habitats on lands, such as wildlife refuges, under GAP 2 classification. Instead, focus on conserving grassland, shrubland, and savanna habitats where the landform and soil naturally supports their ecological function and species. Examples include coastal landscapes of southern New England and New York, and the Upper Great Lakes prairie-forest transition zone. Re-establish natural disturbance regimes to the extent possible, but allow targeted forest management where appropriate.
- Strengthen the protection of GAP 3 "multiple-use" public lands such as national forests, to maintain natural ecosystems, carbon storage, and public access to green spaces to the extent possible. This includes avoiding intensive resource extraction that destroys or permanently impairs the integrity and productivity of natural systems.
- Regarding public and private lands with no formal protection (GAP 4), encourage the conservation of natural ecosystems and species to the extent possible. This includes agricultural lands and other open space with considerable potential to conserve early-successional habitats. These landowners would continue to determine how they manage their lands, but they would be provided with complete and accurate information on the benefits and costs of habitat management alternatives.

Implementing this "natural" alternative would be prudent, cautious, and low cost, and would permanently sustain the full range of native ecosystems. Allowing deforested lands to recover would accumulate much more carbon and avoid the steep carbon loss associated with cutting established forests (Smith et al., 2006; Cook-Patton et al., 2020).

In the face of many challenges, the people of the Northeast, Upper Great Lakes, and beyond are looking to public lands as a major solution to the loss of biodiversity, the threat of climate change, and the need for healthy public green spaces. We can realize this potential by rebalancing the vision for these lands to ensure the recovery and preservation of the full range of native habitats and the wildlife that depend on them—without ongoing intensive human intervention. There has never been a more appropriate time to make such a transition.

Author contributions

MK, JM, and SM developed the original concept and contributed research, writing, and editing of the manuscript. LF, EF, SB, and DF contributed research, writing, and editing of the manuscript. All authors contributed to its completion and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

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Does fragmentation contribute to the forest crisis in Germany?

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Intact forests contribute to the ecosystem functionality of landscapes by storing and sequestering carbon, buffering and cooling the microclimate, and providing a range of related ecosystem functions. Forest fragmentation not only poses a threat to many organisms but also reduces the resistance and resilience of the ecosystem, which is especially relevant to the ongoing climate crisis. The effects of recent extreme heat years on forests in Germany have not been studied in detail for the influence of fragmentation. We investigate the relation of forest fragmentation with temperature and vitality in Germany per ecoregion at the canopy level using satellite imagery at 1-km and 30-m resolution. We compiled and correlated forest maps for connectivity based on Thiessen polygons, canopy temperatures on the hottest days based on land surface temperature, and forest vitality based on the maximum normalized difference vegetation index per growing season. We differentiated between ecoregions and main forest types. In 2022, larger intact tree-covered areas that are less fragmented have relatively low temperatures on hot days and higher overall vitality. Nearly 98% of the almost 1.95 million forest fragments at 30-m resolution in Germany are smaller than 1 km^2, which cover nearly 30% of the total forest area. To counteract the forest crisis, forest and landscape management should aim to reduce fragmentation and maintain tree biomass and forest cover in the landscape. Increasing the size of continuous forest fragments contributes to ecosystem-based adaptation to climate change.

KEYWORDS

land surface temperature (LST), normalized difference vegetation index (NDVI), Thiessen connectivity, forest fragmentation, forest cover

1. Introduction

Land use and infrastructure increasingly fragment naturally continuous ecosystems into several smaller fragments more or less isolated from each other (Riitters, 2007; Ibisch et al., 2016). While large unfragmented forest landscapes are considered some of the most vital ecosystems in the world that provide crucial benefits to numerous species (Minnemeyer and Potapov, 2017), fragmentation is a key driver for the loss of ecosystem integrity (Rogers et al., 2022). Large intact forests are the greatest sinks of atmospheric carbon and store disproportionately higher amounts of carbon than fragmented forests, making them an important natural solution in any climate change mitigation and adaptation solution (Potapov et al., 2017; Moomaw et al., 2019). In addition, risks of diminished biodiversity and local extinctions are higher with increasing fragmentation of intact forest landscapes (Betts et al., 2017). Forest fragmentation results in the expansion of forest edges, exposing the forest fragments to higher anthropogenic disturbances (Vieilledent et al., 2018). Higher fragmented and more isolated forest fragments tend to advance changes in local climatic conditions, leading to drier, hotter, and increasingly volatile microclimate (Laurance et al., 2002; Briant et al., 2010; Tuff et al., 2016). Nevertheless, small forest fragments and green canopy cover adjacent to the highly modified anthropogenic landscape also provide substantial benefits for regulating the microclimate (Aalto et al., 2022). However, such effects are more pronounced in large intact forests (Gohr et al., 2021).

The long-term history of forest fragmentation in Central Europe has led to a mosaicked landscape that consists of agricultural lands with scattered fragments of temperate forests. In Central Europe, nearly 40% of the current forested area is located closer than 100-m from the forest edge including the largest continuous mountain forests (Estreguil et al., 2013). Penetration of drought stress and wind into a forest can be measured until several hundred meters from the forest edge, leading to alterations in the forest microclimate and an increase in tree mortality (Laurance et al., 2011). Forest microclimatic changes have been reported at tens to hundreds of meters from the forest edge (Harper et al., 2005; Tuff et al., 2016). This could possibly be one reason for the increased damage due to forest fires every year (Armenteras et al., 2013; Driscoll et al., 2021). The carbon loss that is associated with the edge effects caused by forest fragmentation is another recently recognized factor associated with fragmentation (Silva Junior et al., 2020).

This study refers to all the forest patches as forest fragments irrespective of their size. Smaller forest fragments are largely influenced by the effects of their surrounding edges, and only larger forest fragments with a substantial proportion of interior area can buffer from environmental and biotic changes associated with the edge. The forest edge effect is the outcome of many interacting environmental effects. There are both physio-chemical and biotic impacts from the surroundings on the forest ecosystem. Microclimatic and mesoclimatic impacts are of special relevance for forest vitality as heat and drought stresses have increased over the past decades and are expected to rise substantially in the near future (Jacob et al., 2018). Extreme heat events are more likely to occur with ongoing climate change and contribute to water stress and drought, especially for forest ecosystems (Fisher et al., 2017). In Germany, we speak of a forest crisis based on the severe forest damage in recent years due to droughts, heat waves, pests (especially the bark beetle outbreak in 2018), and mismanagement (Lindner et al., 2014; Schuldt et al., 2020; Blumröder et al., 2021; Ibisch, 2022; Thonfeld et al., 2022). Healthy forests can contribute to landscape cooling, especially on hot days and during heat waves (Gohr et al., 2021).

Although there is a wealth of knowledge on how fragmentation affects temperature and forest vitality in tropical forests (Taubert et al., 2018; Silva Junior et al., 2020), very little research has linked the patterns of fragmentation with temperature and forest vitality altogether in temperate forests, such as forests in Germany. The characteristic features of temperate and tropical forests are inherently different; hence, it is important to understand these linkages specific to temperate forests to develop region or biome-specific forest management strategies. Therefore, it is imperative to understand these effects in temperate forests also. This study aims to expand the current knowledge about the relationship between forest fragments, their sizes, and the associated variations in temperature and forest vitality in Germany. In particular, we addressed the following questions:

(1) Is forest fragmentation associated with spatial variations in landscape temperature and forest vitality?
(2) Are the thermal gradients and variations in forest vitality inside forest fragments influenced by the size and degree of isolation of the forest fragments?

The information obtained in this study provides input to both forest management and landscape planning striving for ecosystem resilience and an ecosystem-based adaptation to climate change. Existing monitoring apps such as the European Forest Condition Monitor (Buras et al., 2021) or the Waldmonitor (Welle et al., 2022) focus on vegetation vitality. Extending this monitoring with analyses of forest fragmentation can contribute to the understanding of forest vulnerability. This study provides evidence-based arguments for reducing forest fragmentation in intensively managed landscapes.

2. Materials and methods

We quantified the relation of forest fragmentation with land surface temperature and forest vitality in Germany per ecoregion at the canopy level using a four-step methodological approach: (i) compilation of annual national forest cover for the year 2022 as well as temperature and vegetation vitality data; (ii) preliminary treatment of all datasets, including standardization of spatial resolution and calculation of annual averages of the hottest days and the maximum vitality within the growing season; (iii) conversion of the forest dataset into a presence–absence forest cover map and calculation of the degree of fragmentation; and (iv) analysis of the relation between forest fragmentation, temperature, and forest vitality using zonal statistics and bivariate choropleth mapping per ecoregion and per forest type. Dataset preprocessing was performed in the code editor of the Google Earth Engine. Post-processing and visualizations were prepared with ArcGIS 10.7 and RStudio version 4.0.3.

2.1. Ecoregions of Germany

To account for the influence of regional characteristics, such as altitude and plant communities, we based our analysis on nine defined ecoregions in Germany (Olson et al., 2001; Bundesamt für Naturschutz [BfN], 2017; **Figure 1**). The justification of ecoregions as a conglomerate of similar geographical and biological characteristics in terms of the assemblage of species is considered proven (Smith J. R. et al., 2018). The influence of altitudinal effects is represented in the segmentation of the ecoregions in Germany. Hence, we consider the investigation of fragmentation patterns within the ecoregion borders appropriate. Since the two northernmost ecoregions in Germany, the Baltic Sea ecoregion and the North Sea ecoregion, exhibit little forest cover, they were excluded from the analysis.

2.2. Forest cover and forest types

We created a forest cover map of Germany at a 30-m resolution for 2022 from the Global Tree Cover 2000 dataset, using a canopy cover threshold of 50%, by subtracting the tree cover loss from 2001 to 2021 (Hansen et al., 2013). We did not account for forest cover gain since no reliable data are available to date. The dataset is derived from the Landsat 7ETM + data, and forest cover is characterized as any vegetation taller than 5 m in height (Hansen et al., 2013).

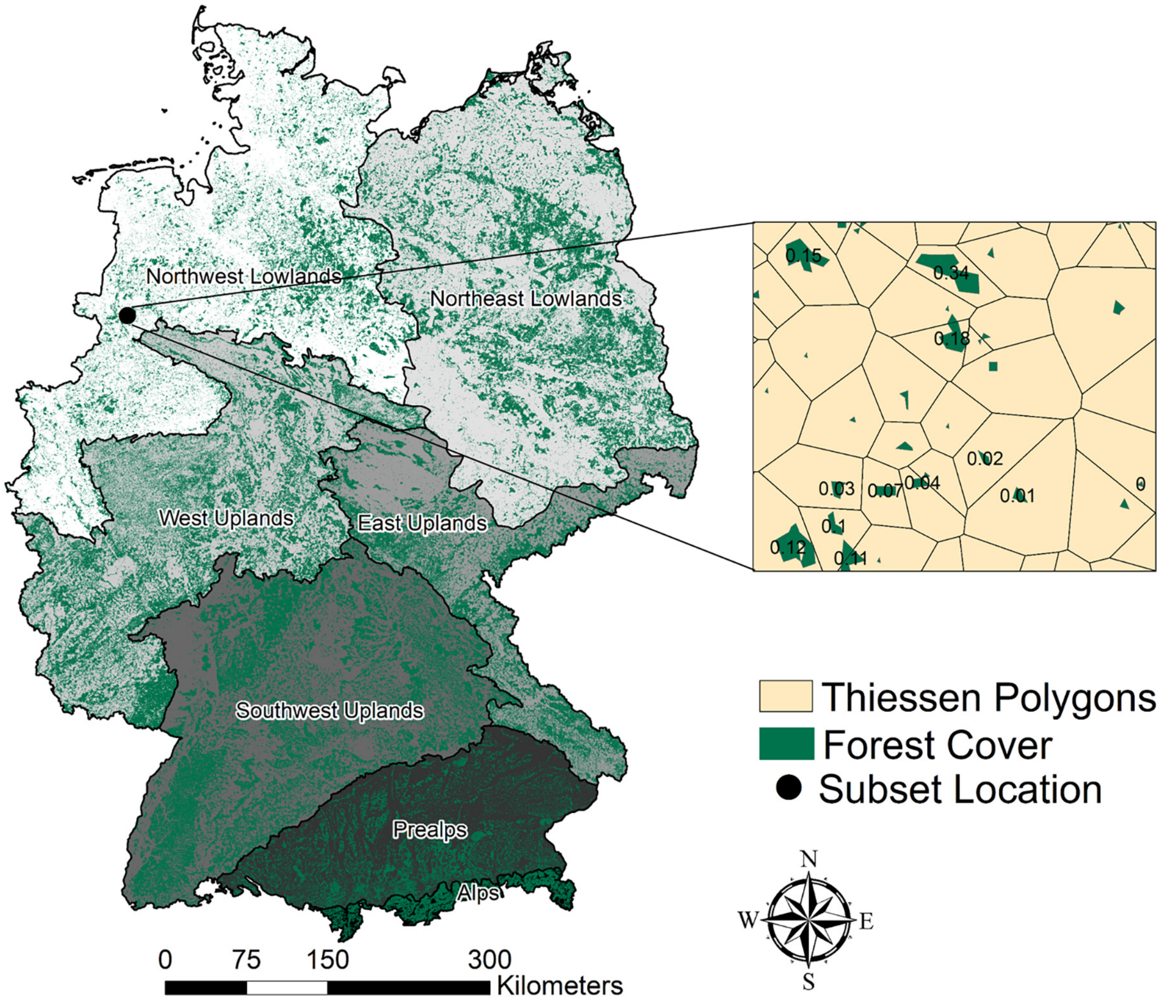

FIGURE 1

Map of Germany categorized by seven ecoregions (left, Bundesamt für Naturschutz [BfN], 2017). The Baltic Sea and North Sea with low forest cover shares are excluded from the original dataset. Forest cover (green) is based on the Global Forest Change dataset (Hansen et al., 2013) with forest areas of 2021 (defined per pixel as more than 50% forest coverage based on Hansen et al., 2013). An example region of a forest-covered area with corresponding Thiessen polygons and corresponding connectivity values in the range of 0–1 is shown on the right.

This threshold is based on the ability to distinguish tall woody vegetation in multispectral imagery, particularly those present in global-scale earth observation systems such as Landsat and MODIS (Hansen et al., 2010). Despite being criticized for not differentiating native and planted forests, these high-resolution maps are suitable for capturing biophysical features that depend on forest cover across the globe (Tropek et al., 2014). The resulting forest coverage of 27.9% for Germany in 2022 (**Supplementary Table 1**) differs from the official statistics. The official statistics, with a forest coverage for 2021 of 31.9% (Bundesministerium für Ernährung und Landwirtschaft [BMBL], 2022), include "legal forest" areas without actual tree cover and do not include some woodlands or tree coverage in urban areas. In comparison, in this study, only forest with measurable tree cover is considered and the relatively small forest patches on small islands and at the coastline of the Baltic Sea and the North Sea ecoregions are omitted, which leads to the smaller area of total forest coverage.

We created a forest type map of Germany at 30-m resolution from the latest available CORINE Land Cover product of 2018 at 100-m by first reclassifying the dataset into three forest type classes, namely, broad-leaved, coniferous, and other forests, and secondly reprojecting, resampling (to 30-m), and masking the dataset to the compiled forest cover map at 30-m resolution.

2.3. Forest fragmentation

Thiessen polygon connectivity (refer to, e.g., Ibisch et al., 2016; Mehdipour et al., 2019; Wu et al., 2019) of the forest fragments was used as a proxy to estimate forest fragmentation. The measure combines both fragment size and isolatedness from other forest fragments and is a unitless value ranging between 0 (high fragmentation) and 1 (low fragmentation). It is defined as the ratio between the size of a forest fragment and its surrounding Thiessen polygon. A Thiessen (or Voronoi) polygon describes the area around a sample point/area where any position taken from inside the polygon is closer to the sample point/area than to any of the other sample points/areas. The greater the value of Thiessen connectivity, the closer the neighboring forest fragments are and hence the lower the fragmentation.

The forest cover raster dataset of Germany for 2022 was converted to forest polygons using the centroid method, and one point per forest polygon was generated. Thereafter, Thiessen polygons were created, and Thiessen polygon connectivity values were computed per forest polygon (refer to **Figure 1**). Using these connectivity values based on the forest cover of Germany for 2022, we generated a forest fragmentation map at 30-m resolution.

2.4. Forest temperature

Extreme heat events are more likely to occur with ongoing climate change and contribute to water stress and drought, especially for forest ecosystems (Fisher et al., 2017). In the temperate biome, healthy forests can contribute to landscape cooling (Gohr et al., 2021). At the same time, the forests are heavily impacted by natural and anthropogenic disturbances. The radiative skin temperature of the land surface is the driving force in the exchange of long-wave radiation and turbulent heat fluxes at the surface–atmosphere interface (Li et al., 2013) and has presented valuable results in several sensible heat flux models (Zhan et al., 1996). Land surface temperature closely resembles air temperature trends when analyzing the effects of forest cover on local temperature even at different latitudinal zones (Li et al., 2016) as even with the heat effect of land surface during the day, there is a heat exchange between air and land surfaces (Jin and Dickinson, 2010; Mildrexler et al., 2011). Therefore, the land surface temperature dataset of Germany qualifies for the assessments of forest canopy temperature and is based on the MODIS Aqua MYD11A1 dataset at 1-km spatial resolution, captured every day at ∼1.30 pm Central European Time (CET). The temperature is measured from the radiation intensity in the infrared range (bands 31 and 32 with 10.8–12.3 μm) (Wan et al., 2015). To create a dataset with the per pixel mean temperature of the hottest days in 2022 from January until October, each day was signatured with the mean temperature of Germany and subsequently the resulting 124 days that exceed 30°C were selected (**Supplementary Table 1**, refer to Gohr et al., 2021). This way, we generated a map of the mean temperature on the hottest days in German forests for 2022, the warmest year since records began (Deutscher Wetterdienst [DWD], 2022; together with 2019, the summer of 2022 was the third warmest summer since 1881; Imbery et al., 2022). The same procedure was applied to generate means of the temperature on the hottest days for the years 2013–2022 in respect to ecoregions (**Supplementary Figure 1**).

2.5. Forest vitality

The normalized difference vegetation index (NDVI) is a measure of photosynthetic activity and is commonly used as a proxy for vegetation stress and water balance and therefore indicates vegetation vitality (Lambert et al., 2013; Chakraborty et al., 2022). Furthermore, the NDVI can serve as an explanatory variable for the effects of temperature changes on forest cover (Weng et al., 2004; Deng et al., 2018). The NDVI dataset of Germany is based on the MODIS Aqua MYD13A2 dataset of 16-day composites at 1-km spatial resolution. The composite is preprocessed from MODIS imagery using the near-infrared and visible spectra, is captured every day at ∼1.30 pm CET, and is completed by selecting the best pixel with low clouds, a low view angle, and the highest NDVI (Didan, 2015). For the growing season from May to September, this results in 10 images covering Germany in 2022. We created a map of forest vitality for Germany in 2022 using the maximum value of the growing season. The maximum value per pixel was selected to acknowledge different peaks of "greenness" for different vegetation for the tree-covered areas in 2022. The minimum value was not considered since the influence of fragmentation on healthy forests was the main objective. Minimum values have a diverse range of potential reasons such as outbreaks of pests and diseases, water stress, or other environmental factors. If only the maximum values are taken into account, the loss of vitality may be somewhat underestimated, but this error does not affect the regional assessment of spatial patterns (or temporal changes) substantially. The same procedure was applied to generate means of the greenest NDVI for the years 2013–2022 with respect to forest types and ecoregions (**Supplementary Figures 2**, **3**).

2.6. Analysis

We reclassified the forest fragments into three different categories based on fragment size, that is, small (below 1 km^2), medium (between 1 and 5 km^2), and large (larger than 5 km^2). We resampled the preprocessed temperature and NDVI datasets to 30-m spatial resolution. We extracted the raster datasets using the forest cover mask to prepare temperature, NDVI, Thiessen connectivity, and forest type data for forest cover in Germany. In order to study the spatial relationship between fragmentation, temperature, and forest vitality across different ecoregions in Germany, we prepared bivariate choropleth maps that spatially represent the variation in one variable with respect to another. In addition, we computed statistical information per forest fragment size per ecoregion for Thiessen connectivity, temperature, and vitality, respectively, using the zonal statistics tool in ArcMap 10.7. For a time series of changes in maximum vitality per growing season and changes in the mean temperature on the hottest days, we used a similar approach. For each year from 2013 to 2022 and each ecoregion, we extracted the mean and standard deviation of the temperature and vitality dataset in the corresponding forested areas (by subtracting forest loss of previous years).

3. Results

Conditions regarding fragmentation, temperature, and vitality in the tree-covered areas vary widely across Germany. Larger intact tree-covered areas that are less fragmented (e.g., parts of the Black Forest in the Southwest, **Figure 2A**) exhibit relatively low temperatures on hot days (**Figure 2B**) and higher vitality (**Figure 2C**). Populated areas with low forest coverage and higher fragmentation (e.g., parts of Northwest Germany) feature higher temperatures on hot days and lower vitality in the often very small forest fragments.

3.1. Fragmentation, temperature, and vitality

The current forest distribution in Germany is the result of a long history of anthropogenic land use (Kaplan et al., 2009). The current forest cover in Germany accounts for approximately 9.9 million

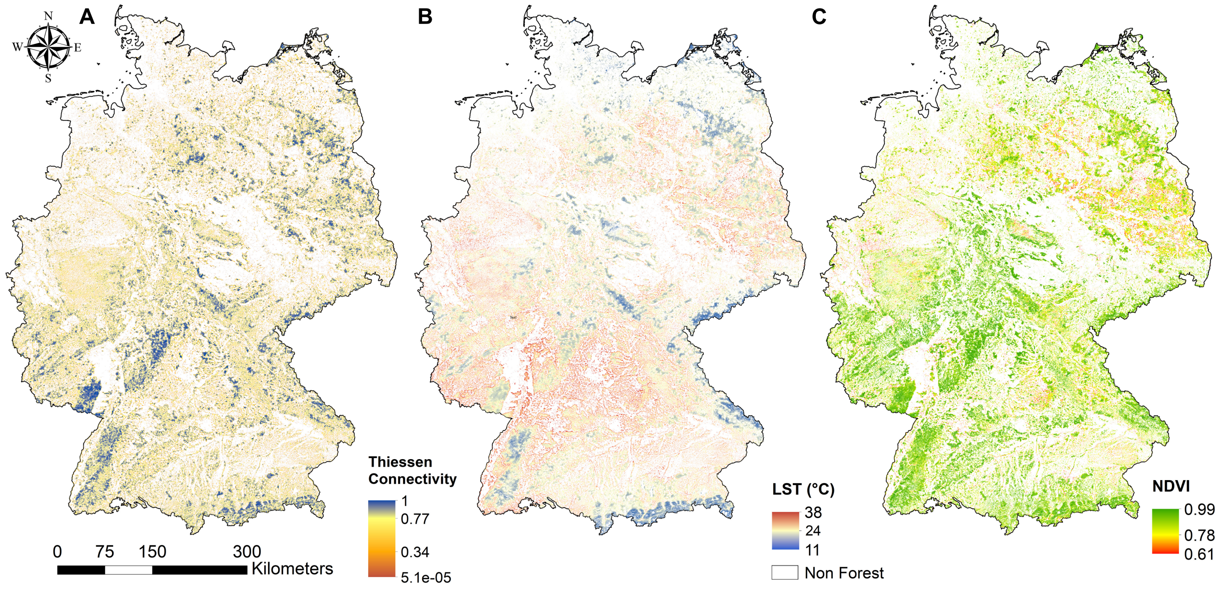

FIGURE 2
Characteristics of tree-covered areas in Germany 2022 across the terrestrial ecoregions in terms of **(A)** forest fragmentation (Thiessen connectivity), **(B)** land surface temperature [land surface temperature (LST); MODIS Aqua MYD11A1] indicated as the per pixel mean of hot days (≥30°C) in 2022, and **(C)** forest vitality (NDVI; MODIS Aqua MYD13A2) indicated as the maximum value of the growing season May–September.

hectares with our study approach [official statistics state 11.4 million hectares (Bundesministerium für Ernährung und Landwirtschaft [BMBL], 2022)] and, at a 30-m resolution, is fragmented into nearly 1.95 million small forest fragments out of which 1.92 million are smaller than 1 km^2 and only around 2,000 forest fragments are larger than 5 km^2 with a maximum size of 3,800 km^2.

With respect to distribution within different ecoregions, 68% (Alps) to 16% (Northwest Lowlands) of Germany is covered by forest (**Supplementary Table 1**). In terms of total area covered by forests, the West Uplands have the highest forest share of 21,960 km^2. A higher value of Thiessen connectivity (closer to 1) indicates higher connectedness of forest fragments and hence less fragmentation. We analyzed the median of Thiessen connectivity values over all the forest fragments in different size classes, and the results indicate that large forest fragments have higher values of Thiessen connectivity in all the ecoregions ranging from 0.75 to 0.87 (**Supplementary Table 2**), while this range is only 0.58–0.70 in medium-sized forest fragments and 0.31–0.51 in the small-sized forest fragments. When comparing Thiessen connectivity across different ecoregions, forest fragments in all the size classes have the highest values in the Alps. Thiessen connectivity across different forest sizes in all the ecoregions is higher in the large-sized forest fragments than small-sized forests by a magnitude of 0.35–0.49, while this value for large- to medium- and medium- to small-sized fragment comparison lies in the range of 0.13–0.27. The median of Thiessen connectivity values across the ecoregions is high when grouping the values per fragment size.

The 2022 hottest day median temperatures of forests with large fragments were lower compared to small fragments in all the ecoregions by 1.29°C in the Alps to as large as 3.28°C in the Southwest Uplands (**Supplementary Table 2**). When comparing medium-sized forest fragments with large fragments within these two ecoregions, this difference is between 0.8 and 2.46°C. When comparing small- and medium-sized forest fragments, the difference in temperature ranges between 0.46 and 0.82°C. The highest variation in temperatures between the different-sized forest fragments was found in the Southwest Uplands. The effect of decreasing temperatures with higher elevation is depicted by the ecoregions since the elevation is one classification variable of ecoregions. This pattern was validated on a pixel basis throughout Germany (refer to **Supplementary Figure 4**). The total of hot days in 2022 varied per ecoregion. In the Alps, 24 days above 30°C were registered, in comparison with the Southwest Highlands 107 days above 30°C in 2022 (full list refer to **Supplementary Table 1**).

The median vitality values, compiled as medians of the maximum NDVI of the growing season in 2022 in Germany, are generally lower in smaller forest fragments and higher in larger forest fragments (**Figure 3** and **Supplementary Table 2**). Since the areas are not discriminated by forest type (**Supplementary Figures 3**, **5**, **6**), a more generalized pattern can be observed. The highest vitality is found in the largest fragments of the Alps, the Western Uplands, and the Southwest Uplands. Vitality values below 0.8 are only observed in the smallest fragments of the Southwest Uplands, and the Northeast and Northwest Lowlands.

Small forest fragments correspond to low connectivity, low vitality, and higher temperatures throughout all ecoregions and their respective altitudinal ranges when looking at the scaled medians across Germany in 2022 (**Figure 3** and **Supplementary Table 2**). The uncertainty (under- or overestimation due to mixed pixel effect) of values in small fragments below 1 km is high since the temperature and forest vitality are originally captured at 1-km spatial resolution. Nevertheless, there are regional specifics for the temperature and forest vitality. The highest temperatures were observed in the small fragments of the Southwest Uplands, and the lowest temperatures could be found in the largest fragments of the Alps. In the small fragments of the Northeast and Northwest Lowlands, the lowest vitality was observed. The highest vitality was registered in the largest fragments of the Alps and the Western Uplands.

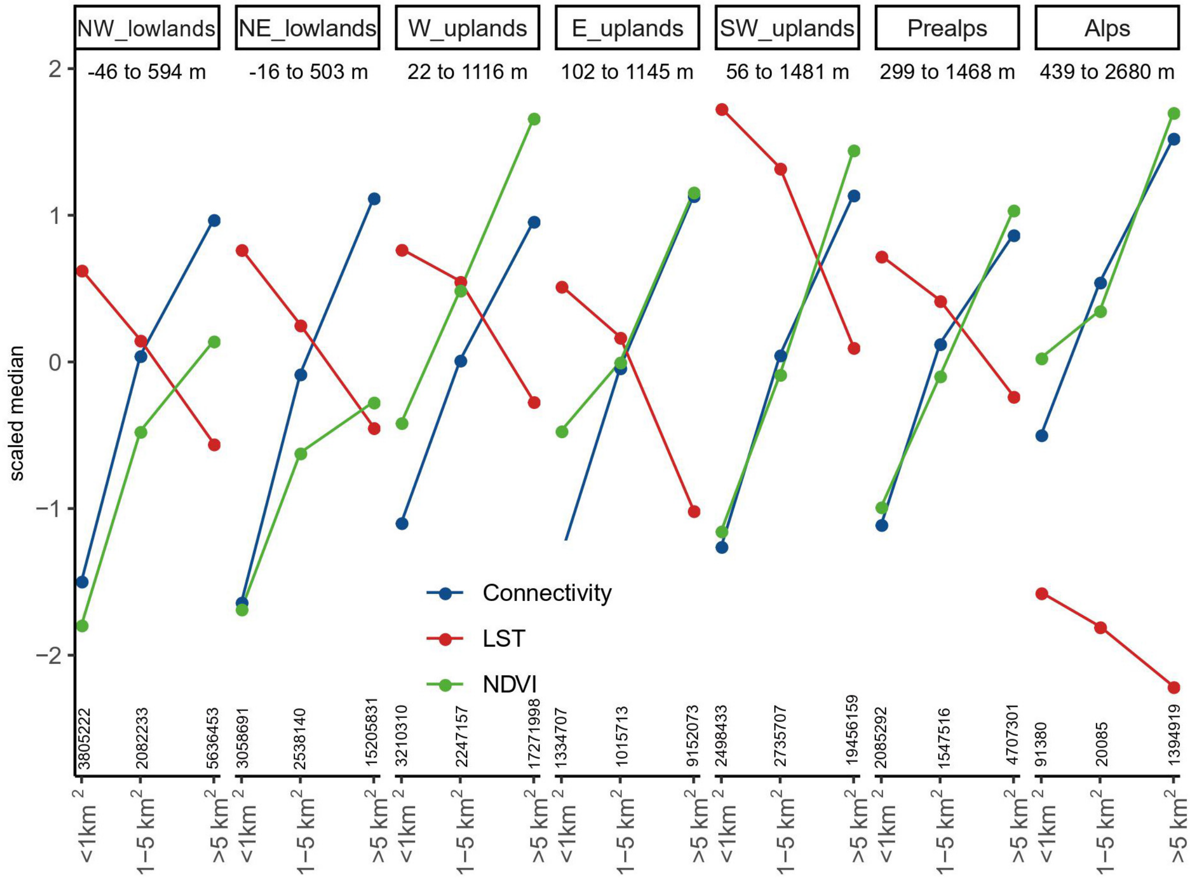

FIGURE 3

Scaled median (median per indicator for tree-covered areas in Germany 2022 divided by the standard deviation) per ecoregion with respect to different forest fragment sizes (<1 km^2, 1–5 km^2, and >5 km^2). The indicators are Thiessen connectivity for forest-covered areas in Germany in 2022 (blue), land surface temperature [land surface temperature (LST); MODIS Aqua MYD11A1] based on the mean of the hottest days in 2022 (red), and the NDVI (MODIS Aqua MYD13A2) based on the maximum value of the growing season 2022 (green). Altitudinal ranges per ecoregion are depicted below the headings. The coverage of each fragment size group is depicted above the *X*-axis in km^2.

3.2. Spatial variations in fragmentation, temperature, and forest vitality

The bivariate choropleth maps between Thiessen connectivity and land surface temperature (**Figure 4A**) and Thiessen connectivity and forest vitality (NDVI) (**Figure 4B**) depict how the studied proxy indicators vary in geographical space with respect to each other. Cyan and magenta color tones on the map indicate a positive association between the two variables, while blue and red color tones indicate a negative association. For instance, the spatial variation between the high connectivity of tree-covered areas in Germany in 2022 and respective low temperatures can be observed in larger, better-connected forest areas (**Figure 4A**, blue areas). This relationship is not only true for large forest landscapes (e.g., part of the Black Forest or the Alps) but can also be found in areas with smaller forest fragments (e.g., Schorfheide in the Northeast Lowlands). Similar patterns can be found between the high connectivity of tree-covered areas and a high vitality (**Figure 4B**, magenta areas). However, the spatial pattern is more scattered. Especially the Northeast Lowlands show higher connectivity with a lower vitality signal. In the higher altitudes (e.g., the Alps), temperatures are low when the connectivity is high, but only some areas show a high vitality with high connectivity, while other areas show reduced connectivity and vitality (**Figure 4B**, Alps ecoregion magenta and green areas). When comparing the bivariate choropleth maps for broad-leaved and coniferous forest types (**Supplementary Figures 5**, **6**), there is a clear indication that broad-leaved forests in Northern and Eastern Germany, representing the natural vegetation, have been severely degraded and fragmented in the past. Coniferous plantations seem to benefit from larger forest blocks and higher connectivity, having a higher NDVI such as the northern Black Forest in the Southwest of Germany.

The range of variations taking into account all the forest fragments per ecoregion can be observed in the scaled data ranges of the connectivity in tree-covered areas in their relation to hot day temperatures and maximum vitality (**Figure 5**). Forest in the Alps is relatively less fragmented than in other ecoregions, is cooler, and has the highest forest vitality. The Lowlands show the lowest median connectivity and lowest vitality, while having similar median temperatures as the Uplands. The highest median temperature is recorded in the Southwest Uplands. In the Western and Eastern Uplands and the Prealps, slightly higher connectivity is accompanied by lower temperatures and higher vitality. When investigating the distribution of Thiessen connectivity per ecoregion regardless of fragment groups, the connectivity is much lower (**Figure 5**), the reason being that all the ecoregions are dominated by the presence

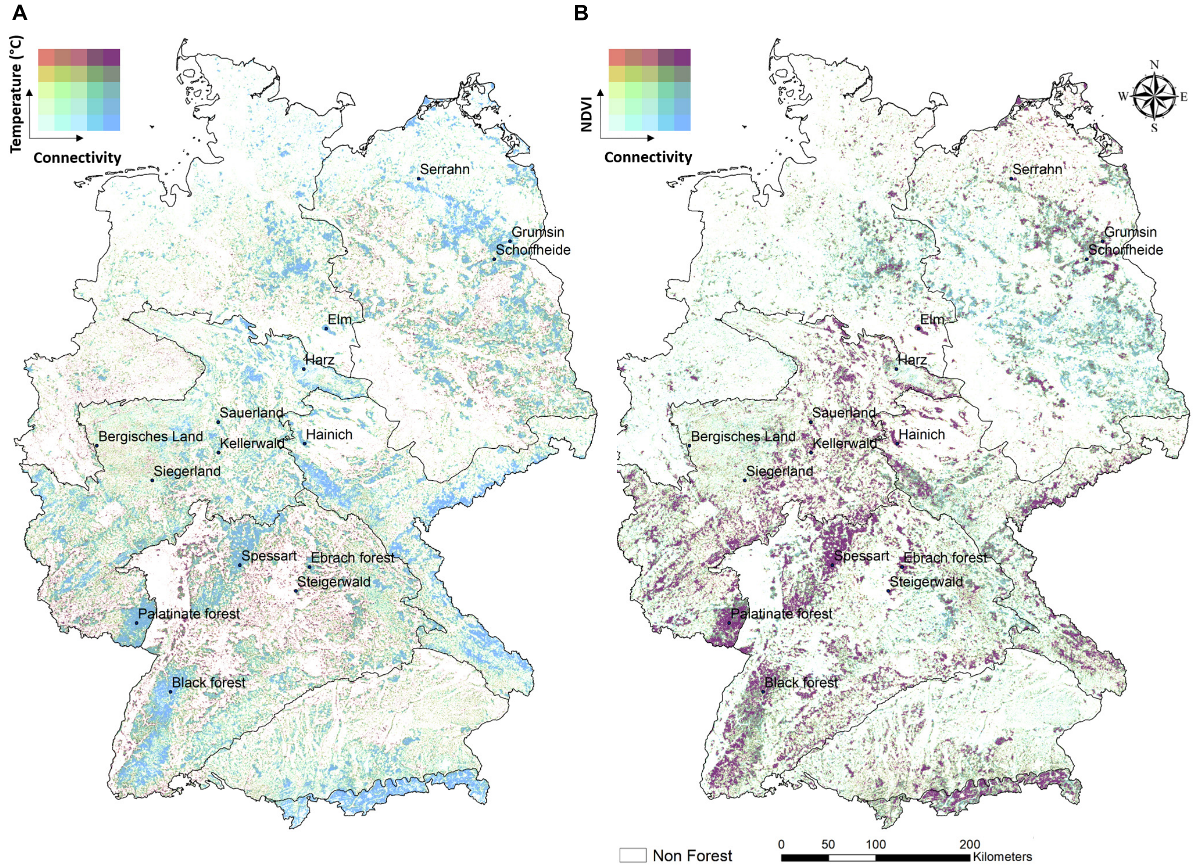

FIGURE 4
Bivariate maps of tree-covered areas in Germany in 2022 and the relation between the degree of fragmentation with temperatures and vegetation vitality. **(A)** Thiessen connectivity and land surface temperature of hot days in 2022. **(B)** Thiessen connectivity and the maximum NDVI per growing season in 2022.

of forest fragments smaller than 1 km^2. Hence, lower overall connectivity values are evident.

4. Discussion

In the studied year 2022, forest fragmentation clearly impacted local temperatures on hot days and forest vitality. Here, we show that these effects vary by ecoregion and we discuss implications for landscape and forest management.

4.1. Regional implications of fragmentation on forest temperature and vitality

Independent of the ecoregion, larger fragments of tree-covered areas show the highest connectivity, the lowest temperatures, and the highest vitality. Lower values of Thiessen connectivity in all ecoregions result from the dominance of small-sized forest fragments indicating a great degree of fragmentation. The area with the least fragmented forest in Germany are the Alps (highest Thiessen connectivity with a median of 0.38 as compared to the maximum value of 1). In comparison with the other ecoregions, this area is less urbanized due to its topography, and therefore, the effects of fragmentation through infrastructure (Ibisch et al., 2016) or cities are less severe. The overall high forest vitality in the Alps ecoregion is congruent with other studies that measured a growing biomass stock and an expanding forest-covered area, despite intensified natural and human-induced disturbances (Bebi et al., 2017). The Alps are the smallest of all ecoregions with 7,796 data points of the tree-covered areas observed. The high elevation and terrain with steep slopes are most likely a reason for the diverse range of temperature values from low to high. Even though fewer hot days in the year 2022 for the Alps ecoregion were detected, the Alps are also threatened by climate change and more frequent temperature extremes (Seidl et al., 2011; Gobiet et al., 2014). A larger forest cover in mountainous regions can help retain permanent snow cover longer than non-tree-covered areas (Hesslerová et al., 2018).

The Prealps are characterized by the highest altitudinal range of all ecoregions from 299- to 1,468-m elevation (refer to **Figure 3**). As a consequence of more intensive land use, the tree-covered areas in the Prealps are less connected and less vital as compared to the Alps, and the land surface temperature median is ca. 5°C higher than in the Alps. The foothills of the Alps are also impacted by climate change (e.g., Thrippleton et al., 2020).

The Southwest Uplands are the ecoregion in Germany with the highest measured temperatures of forest canopies in 2022. Therefore, the forest is rarely connected (Thiessen connectivity median 0.18) with a medium vitality (median NDVI 0.79) and high temperatures

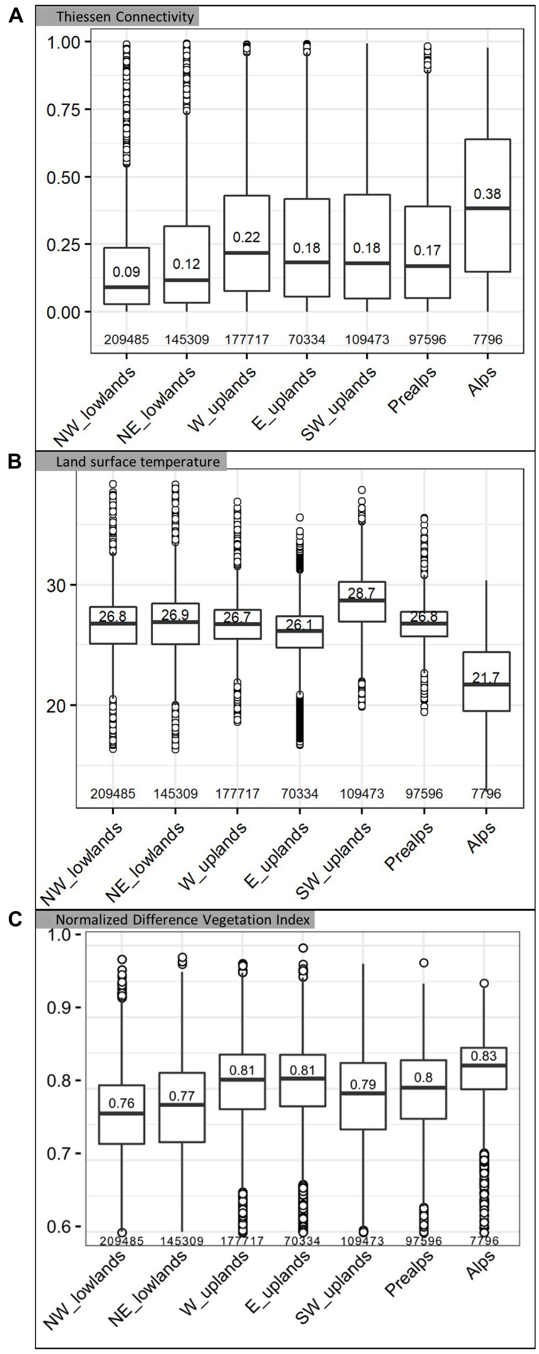

FIGURE 5
Boxplots of connectivity, temperature, and vitality for tree-covered areas in Germany 2022 per ecoregion including all values regardless of the size of a fragment. The median of each dataset per boxplot is depicted as a bold horizontal line, the line above represents the upper quartile of which 75% of the values fall below and the line below the median represents the lower quartile with 25% of the values below. **(A)** Thiessen connectivity for forest-covered areas in Germany as of 2022. **(B)** Land surface temperature (LST) based on the mean of the hottest days in 2022. **(C)** Vitality (NDVI) based on the maximum value of the growing season in 2022 (for better readability, outliers below 0.6 are not depicted). The count of data points per ecoregion is depicted above the *X*-axis.

(median of 28.7°C is 7°C hotter than in the Alps). It is in fact the hottest region in Germany in terms of regional climate and is highly populated. In this ecoregion, there are a few highly connected forests such as the Black Forest in the south-westernmost part but mostly areas with low connectivity and smaller forest fragments. A small-scale study in the area, investigating Scots pine forest edges using dendroecological investigations and close-range remote sensing, found that these forest edges are more vulnerable to drought, showing increased mortality rates and lower tree vitality (Buras et al., 2018). A study conducted in Switzerland using thermal imaging found that the resilience to the drought of broad-leaved forests varies by species (Scherrer et al., 2011). Lower vitality values with a median of 0.71 for the year 2022 can be related to the spruce forest dieback, which is the dominant tree type in the ecoregion. Still, coniferous forests in dense stands seem to benefit from higher connectivity and show higher vitality, especially in the Black Forest (**Supplementary Figures 3**, **5**, **6**). Larger broad-leaved dominated forest areas in the northern part of the ecoregion, such as the Spessart, Steigerwald, or Ebrach forests, show relatively high vitality (**Supplementary Figure 5**).

The Eastern Uplands share a similar value of low connectivity (median 0.18) as the Southwest Uplands but a higher vitality (median 0.81) and 2°C lower temperatures. A strong temperature decline, vitality, and connectivity increase from medium to large forest fragments and can be associated with less intensively managed forests. In the Bavarian forest region, the mainly coniferous forest is relatively vital and connected (**Figure 4**). However, the vegetation is under stress due to climate-related bark beetle outbreaks of spruce before 2012 (Lausch et al., 2013a,b). The same is true for the Erzgebirge with deforestation due to a recent bark beetle outbreak (Gdulová et al., 2021). The Thuringian Forest still can be recognized as a relatively well-connected area with relatively low temperatures and higher vitality, despite Norway spruce being the main tree species (Thiel et al., 2006). But for some years, it already suffers from heavy storms and bark beetle outbreaks, and it is most likely, that in this area, the effects of climate change will become more frequent, such as a rise in temperatures, more frequent temperature extremes, and a decreased water supply during the growing season (Frischbier et al., 2014).

The Western Uplands are characterized by slightly higher overall connectivity than the Eastern and Southwest Uplands but show higher temperatures and not notably higher vitality (**Figure 5A**). A high connectivity and high vitality are visible in the Palatinate Forest (Pfälzerwald), on the southern edge of the ecoregion. In general, the vitality is higher than in the other Uplands, especially, because of the relatively high share of broad-leaf forests with a higher vitality range *per se* (**Supplementary Figure 3**). At the same time, the ecoregion is dominated by large coniferous plantations and experienced strong Norway spruce dieback in the last years. The Western Uplands are one of the formerly largest forest regions in Western Germany, including the Sauerland, Bergisches Land, Siegerland, and Harz mountains. After years of massive dieback and salvage logging, the remaining forests are in relatively poor condition, fragmented, and with reduced vitality (Popkin, 2021).

In the Northeast Lowlands and the Northwest Lowlands, the small size forest fragments show the lowest connectivity. Even in larger forest fragments with higher connectivity detected, the vitality values are low. This is due to a large number of coniferous plantations in both ecoregions (**Supplementary Figure 6**). Many Scots pine plantations do not seem to benefit from the generally somewhat lower temperatures in the north. They are often well-connected, but this does not translate into a better vitality signature. In general, there seems to be a gradient toward higher vitality in the north, possibly due to the buffering impact of the sea with its maritime climate, a higher precipitation potential, and a lower drought potential than in the south of Germany (Zink et al., 2016). This effect of continentality is reflected to some extent by the ecoregions. The median connectivity of 0.09 and median vitality of 0.76 are the lowest of all ecoregions in the Northwest Lowlands and therefore can be attested to the less connected forest cover of all ecoregions. The fragmented landscape leads to low connectivity and higher temperatures, and the coniferous plantations (according to ground-truthing) have low vitality. These effects are repercussions, especially of the extreme years from 2018 onward, and consequent bark beetle outbreaks (refer to **Supplementary Figure 2**). Interestingly, the largest beech forest in Northern Germany, the Elm, lies within the Northwest Lowlands and shows relatively high Thiessen connectivity values with high vitality and low temperatures (refer to **Supplementary Figures 5**, **7**).

4.2. Effects of fragmentation

Independent of the ecoregion, larger fragments of tree-covered areas show the highest connectivity, the lowest temperatures, and the highest vitality (**Figure 3**). The cooling functions of forest fragments increase with higher connectivity. This cooling effect was also observed in a study on reforestation (Huang et al., 2022). Our results regarding the correlation between high connectivity and increasing forest vitality, based on the NDVI in the temperate forest realm, correspond to other studies with similar results. Others used the NDVI, and for connectivity "vegetation continuous fields," and found that higher connectivity in protected areas correlates to high NDVI values (Sun et al., 2021). Other factors influencing the NDVI that are not covered in this study would be local and regional characteristics such as climate, soil moisture, dominant tree species, and the degree of disturbance.

This study focuses on regional assessments and could not scrutinize the effects of fragmentation through skidding trails and small-scale edge effects. These patterns potentially increase the fragmentation impacts and most likely have additional effects on the local forest temperature and vitality (Buckley et al., 2003; Sufo Kankeu et al., 2016; Shirvani et al., 2020). The characteristics of native and planted forests in Germany were not covered in this study. To date, no comprehensive and explicit spatial information on the native and planted forests is available, neither for the globe (Grantham et al., 2020) nor for Germany. It is also important to note that in some areas, the NDVI and Thiessen connectivity are not necessarily positively correlated. There are definitely other relevant effects such as the type of forests. For example, in the Scots pine forests of northeastern Germany, relatively low vitality is observed despite high connectivity. However, especially these forests represent mostly planted even-aged monocultures with low structural diversity, relatively open canopies, and many timber extraction roads and trails. Our analysis could not take into account that there is also internal forest fragmentation, which contributes to the vulnerability of the ecosystem in the form of forest roads and skid trails as there are currently no data available. The situation in Germany is currently worsening because the infrastructure for the expansion of renewable energy production is pushing into the forest. Here, wide permanent access roads and openings for wind turbines increase the forest edges and the edge effects in the midst of the forest.

To promote the protection of remaining old-growth broad-leaved forests, UNESCO recognized some old temperate forests in Europe as natural heritage, which are component parts of the serial UNESCO transnational property "Ancient and Primeval Beech Forests of the Carpathians and Other Regions of Europe" (Voloscuk et al., 2013; Ibisch et al., 2017; Jovanović et al., 2019; UNESCO, 2022). In Germany, the Hainich National Park, Kellerwald-Edersee National Park, Serrahn Forest, and the Grumsin Forest are part of this property and show relatively high connectivity, especially in the core zones, despite being of relatively small size. These areas are highly important not only in terms of being a heritage site but also as a cooling factor in the landscape, a remnant habitat, and are of recreational value for humans.

4.3. Recommendations for landscape and forest management

Forest vitality and functionality are not only impacted by climate change and natural disturbances but also by silvicultural management. The management attempts of the last decades to protect forests in Europe did not mitigate climate warming (Naudts et al., 2016) but even led to increased temperatures within forests (Blumröder et al., 2021). Effective ecosystem management must allow ecosystems to mature through the growth of biomass, information, and network and to maintain or enhance working capacity in the best possible way. The production and storage of biomass and biogenic free energy in the ecosystem—including dead wood, humus, or organic molecules in mineral soil—are the physical basis of all possible natural ecological processes in the ecosystem. Linking to the development of biophysical capacity is also an increase in the ecohydrological capacity of forest ecosystems. The conservation of "green water" stored and mobilized by ecosystems (Ellison et al., 2017; Sheil, 2018; Te Wierik et al., 2021) and microclimatic regulation (Blumröder et al., 2021, 2022) deserve the highest priority in management (Ibisch, 2022). To mitigate hot temperature extremes in European forests, the increase in the broad-leaved tree fraction is a necessary measure (Schwaab et al., 2020). German forests are already highly fragmented. In some forest-poor regions, it is recommended to increase tree and forest cover to buffer temperatures and contribute to forest vitality (Gohr et al., 2021). The regulating function of connected forests within the water, energy, and carbon cycles is more needed than ever (Ellison et al., 2017) since highly fragmented forests with more forest edges provoke more carbon loss (Smith et al., 2018).

Remote sensing and especially new datasets like the dominant tree species of German forests (Welle et al., 2022) will support monitoring fragmentation as seen in other countries (Kupfer, 2006). It is an urgent task for the state rapporteurs of the federal states and the federal ministries responsible for forests to ensure that forest fragmentation is included in the forest status reports and the corresponding analyses of forest health.

Fragmentation is caused by infrastructure expansion and land use changes but also by (past) forest management: When plantations collapse by massive tree dieback, they are often salvage-logged. The regeneration capacity decreases under climate change and potentially these areas are then converted into open lands. It is inevitable that forest fragmentation in the near future will further increase due to large-scale tree dieback in monocultures. The ban on salvage logging and clearcutting seems to be a necessary step in forest management. The existing smaller forest fragments have the potential to be transformed into larger core forest areas for enhanced ecosystem development. This can be achieved by the abandonment of timber extraction, implementing reforestation measures such as assisted restoration, planting native trees, natural regrowth, agroforestry solutions, and commercial plantations.

5. Conclusion

The study reflects that the forests in Germany are highly fragmented, which weakens their ecosystem functionality. This study provides observational evidence to show that highly fragmented forests exhibit higher temperatures and less forest vitality. Thereby, the fragmentation in Germany as of 2022 substantially contributes to the current and ongoing forest crises. The existing small forest fragments have immense potential to be transformed into larger core areas for better ecosystem functioning. With increasing forest fires and extreme climatic events in Germany and worldwide in general, there is an urgent need to advance forest management and restoration efforts that can safeguard the benefits of functional forests as much and as long as possible. Reducing the fragmentation of forests is a crucial contribution to ecosystem-based adaptation to climate change.

Data availability statement

The original contributions presented in this study are included in the article/**Supplementary material**, further inquiries can be directed to the corresponding author.

Author contributions

PI, DM, and CG designed the research. DM and CG performed the analysis, visualization, and wrote the original draft. PI and JB provided comprehensive support in the assessment and interpretation of the results. All authors contributed to the interpretation of the results and the subsequent revisions of the manuscript.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2023.1099460/full#supplementary-material

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Strict forest protection: A meaningful contribution to Climate-Smart Forestry? An evaluation of temporal trends in the carbon balance of unmanaged forests in Germany

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The role of unmanaged forests is discussed controversially in the context of climate change. One of the key questions is, whether they can contribute to the mitigation of climate change as a carbon sink and storage. However, carbon dynamics of forests after the cessation of management are not well understood. We analyzed a set of 64 forest sites, covering wide gradients of time since abandonment (0–68 years) and stand age (65–261 years) in even-aged, unmanaged beech forests. Five sites that were unmanaged for >100 years complemented the main dataset. We compiled site-specific carbon balances, distinguishing six carbon-compartments: Carbon in aboveground living and dead biomass, carbon in belowground living and dead biomass, and carbon in the organic layer and the mineral topsoil (0–30 cm). We found positive effects of increasing TSA on the carbon stock in living biomass and aboveground dead biomass for up to 50 years after management ceased. The average increase of the total carbon stock over 50 years of TSA was ≈ 80 Mg C ha^{-1}. The effect of stand age on aboveground living biomass showed a convex relation. Aboveground dead biomass increased logistically with TSA, while belowground dead biomass decreased. On average, the five sites unmanaged for >100 years held lower total carbon stocks compared to the observed biomass peak around 50 years of TSA. However, they contained considerably higher amounts of deadwood. Carbon in the mineral soil did neither change with TSA nor with stand age and was driven by pH. Carbon stocks in newly unmanaged forests increased almost linearly for approximately 50 years after cessation of management. Subsequently, a stabilization or medium-term decrease in carbon stock was observed, likely due to the initiating transition from even-aged to multi-aged structures. We conclude that, besides their value for biodiversity and ecosystem functions, the potential of naturally developing forests as a medium-term carbon sink and long-term stable carbon storage should be considered as a valuable contribution to Climate-Smart Forestry.

KEYWORDS

Climate-Smart Forestry, time since abandonment, unmanaged forest reserves, carbon storage, carbon sink, climate change, strict forest reserves, soil organic carbon

1. Introduction

The high complexity of policies devised to mitigate climate change requires a sound understanding of natural carbon cycles in different ecosystems (Pan, 2011; IPCC, 2021). In this respect, forests are of particular interest, as they constitute a large terrestrial carbon sink and storage (Carey et al., 2001; Luyssaert et al., 2008; Pan et al., 2013; Pugh et al., 2019), even in intensively managed regions of the world. The type and intensity of management has a strong impact on the level and persistence of forest carbon stocks (Mikoláš et al., 2021; Mackey et al., 2022). In Central Europe, most forests are managed with varying intensity. In Germany, there are no true primeval or virgin forests (Sabatini et al., 2018; see Buchwald, 2005 for context), but an increasing proportion of forest area is being set aside from active management (Meyer et al., 2022).

Deforestation and forest use has caused large carbon debts from European forest ecosystems in the past (Naudts et al., 2016, but see discussion in related eLetters). In recent decades, however, the growing stock, and thus carbon storage, of European forests has increased considerably (Spiecker et al., 1996; Spiecker, 2001; Pan, 2011; Pretzsch et al., 2014). Currently it is, sometimes heatedly, debated whether the mitigation of climate change is better served by the abandonment of forest managment or the intensification of management and utilization of wood (Schulze et al., 2020; but see: Kun et al., 2020; Welle et al., 2020; Ameray et al., 2021; Luick et al., 2021; Schulze et al., 2021, 2022). Already, the scientific debate has advanced towards lobby work and political decision making (Raven, 2021; Irslinger, 2022). Climate change, together with the diverse demands of society on forests and forest management, sets the challenge for Climate-Smart Forestry (CSF) (Bowditch et al., 2020; Verkerk et al., 2020). One important goal of CSF is to optimize carbon uptake and storage in forests and wood products and the substitution of fossil fuels and materials with a large carbon footprint. However, CSF should not be mislabeled as "carbon forestry", as it also incorporates resilience of forests to climate change, biodiversity and other ecosystem functions and aims to create synergies in forest management (Nabuurs et al., 2018). It is important that Climate-Smart Forestry management decisions are based on scientific evidence.

Naturally developing forests are an important element of the EU Biodiversity Strategy (European Commission, 2020) and the German National Biodiversity Strategy (BMU, 2007). Germany aims at allocating 5% of the national forest area to natural development. Several other European countries are also withdrawing large forest areas from management, in order to conserve and restore the native biodiversity and to mitigate climate change. This has further sparked the debate about the effects of forest management and abandonment on climate change mitigation, as is the case for most approaches of nature-based solutions to climate change (Seddon et al., 2020).

The argument whether to increase biomass harvest or to increase carbon stocks by ceasing management is complex and subject to uncertainty (Ciais et al., 2008; Bellassen and Luyssaert, 2014; Pukkala, 2018). It is crucial to develop a better understanding of carbon dynamics in unmanaged forests, not least in view of the economic trade-offs that go along with abandoning productive forest sites. Empirical data to evaluate the potential mid- and long-term effects of ceasing management are scarce, restricting a factual debate. Better data and understanding should also help to improve strategic planning and the selection of forest stands for strict protection, based on their characteristics and the targeted objectives.

The state of knowledge on aboveground growing stocks and dynamics over the time period of a production cycle is well-established in temperate Europe (Pretzsch, 2010; see **Figure 1**) Regarding forests where management has ceased and that grow beyond the extent of the typical production cycle (approx. 160 – 180 years), there is uncertainty about future stand development and related ecosystem functions. Strict forest reserves (SFR; bindingly set aside for natural forest development; see Parviainen et al., 2000) have been studied to an extent, but the results are as yet inconclusive. So far, they have only reached the initial phase of transition toward old-growth structures and dynamics, a long process that likely takes centuries. Old forests, abandoned for more than a century, are generally rare and thus not well studied. Even these forests often bear legacies of former management to the present day. It is generally assumed that, if left undisturbed and in the long-run, a forest ecosystem will naturally evolve toward an ecological "steady state" or dynamic equilibrium (Bormann and Likens, 1994; Franklin et al., 2002). This status is believed to resemble the structure of primeval forests. In Europe, there are only few remnants of primeval forest left (Sabatini et al., 2018). Recently, records on wood volume and biomass stocks in primeval beech (*Fagus sylvatica*) forests of Eastern Europe were published (Hobi et al., 2015; Glatthorn et al., 2018; Stillhard et al., 2022) and several classical studies are available (e.g., Leibundgut, 1978; Korpel', 1995). Meyer et al. (2021) rated the respective evidence for European primeval forest as "established but incomplete", i.e., there are only few studies but their findings are similar. Concerning the carbon balance of old forests, opinions differ. Several studies demonstrated a persistent carbon sink in old-growth forests (Janisch and Harmon, 2002; Knohl et al., 2003;

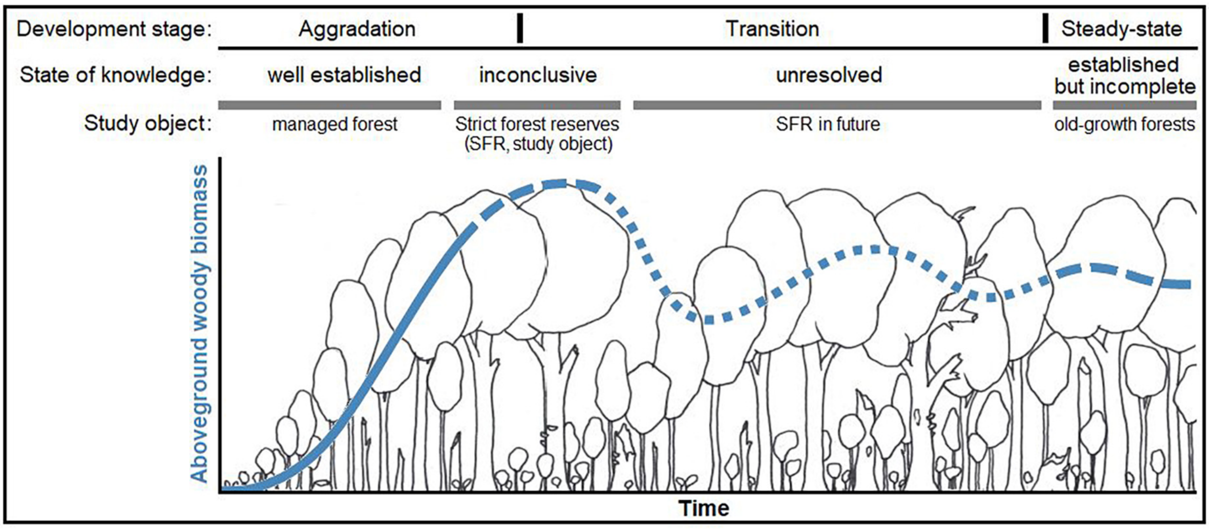

FIGURE 1
Qualitative representation of our conceptual model [modified graphical abstract from Meyer et al. (2021)*] on the state of knowledge and the hypothesized development of formerly managed forests toward old-growth forests. The figure exemplary represents aboveground woody biomass, as it is the most investigated and reported compartment, however with distinct ambiguity about its long-term development in strict forest reserves. We hypothesized that, after abandonment, carbon stored in aboveground woody biomass increases over time, however approaching an upper limit ("carbon carrying capacity," defined by environmental conditions, etc.) within an unknown period of time. Structural changes and other processes may induce fluctuations around this capacity over time, however a stable steady-state is approached in the long run. *The referenced article is an open access article under the terms of the Creative Commons Attribution-Non-Commercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.© 2021 The Authors. Journal of Ecology published by John Wiley & Sons Ltd on behalf of British Ecological Society.

Hessenmöller et al., 2008; Luyssaert et al., 2008; Heiri, 2009; Brang et al., 2011), while studies based on modeling approaches assumed steady-state or negative carbon balances (Hasenauer, 2011; Köhl et al., 2011).

The largest deficiency in the understanding of forest carbon dynamics concerns strictly protected or re-wilded forests, i.e., formerly managed stands that now develop naturally. Although data on SFR are increasingly available, time-series over longer periods are scarce and not representative (Meyer, 2020). Thus, the medium-term development (i.e. several decades) of formerly managed forests and their transition toward primeval forest structures are not well understood. This is critical, as setting aside forests is regarded as a contribution to the mitigation of climate change in Europe (BMU, 2007; European Commission, 2020). Moreover, across all forest types the state of knowledge regarding the belowground carbon stocks and dynamics is rather poor (Fahey et al., 2010; Ameray et al., 2021).

Against this backdrop we asked how carbon stocks change after the abandonment of managed forests. We hypothesized that the carbon stock would increase with time since abandonment (TSA), eventually reaching a saturation point or carrying capacity (Gupta and Rao, 1994; Keith et al., 2009). Furthermore, we hypothesized that the effect of stand age on carbon stocks would be a convex function. We expected the growth of living biomass and deadwood accumulation to be the main contributors to an increasing carbon stock. We further hypothesized that, similar to the findings of Meyer et al. (2021), a saturation of the carbon sink could become apparent, however only after several decades of TSA. We expected no effects of TSA and stand age on carbon stocks in the mineral soil and organic layer, as partial harvest practices are reported to have only little effect on these compartments (Lal, 2005; Mayer et al., 2020) and we assume these effects of moderate canopy opening to be comparable to natural disturbances.

2. Materials and methods

To test our hypotheses, we collected data from 100 strict forest reserves (SFR) throughout Germany (**Figure 2A**), covering a large geographical range of Central European temperate forest. As time-series data are rare, especially for the higher range of TSA, we followed a space-for-time substitution approach (Likens, 1989), resulting in a chronosequence (Walker et al., 2010) of sites with differing TSA and stand ages.

2.1. Site selection

Suitable candidate sites were screened from the database of German SFR (Münch, 2007) based on forest type, TSA and stand age. The majority of the candidate site pool was made up of even-aged beech stands, followed by oak (*Quercus* spp.) dominated stands (**Table 1**). This reflects that natural forest communities in Germany are dominated by beech and oak forest types (83%) (Schmitz, 2014).

To account for environmental gradients, we stratified the candidate sites of beech and oak dominated stands into sub-groups. Based on soil and site characteristics from the SFR database, beech stands were divided into nutrient poor and nutrient rich

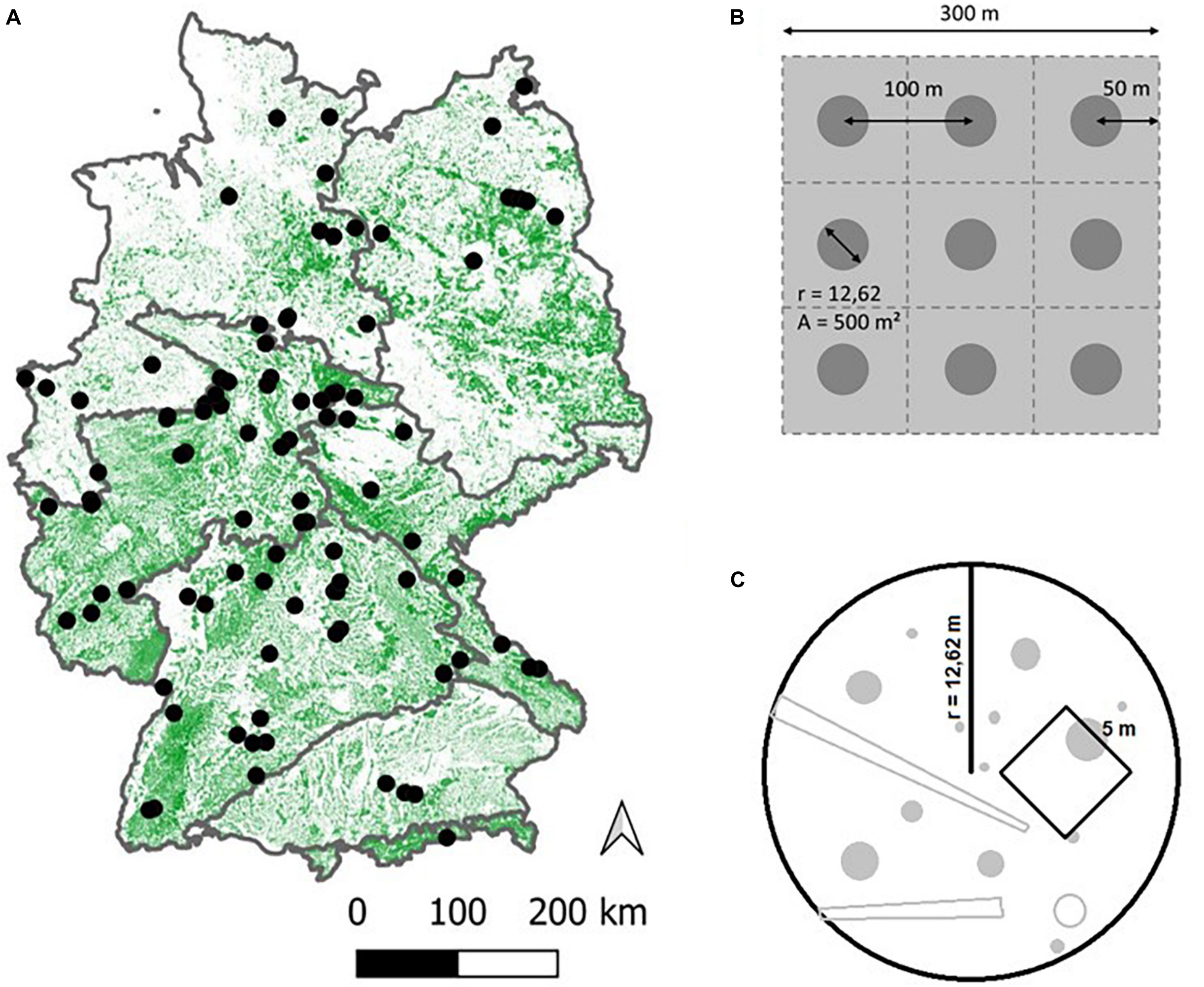

FIGURE 2
Overview of the 100 site locations across Germany **(A)**. The map depicts forest cover, the boundaries shown encompass the major natural regions of Germany (Meynen et al., 1953). Nine circular plots per site were laid out in a 3 × 3 grid whenever possible **(B)**, covering an area of 9 ha. Distance between plot centers was 100 m and distance from the outer plot centers to the stand boundaries was 50 m. The plot area was 500 m^2 (r = 12.62 m) on which all inventory objects were sampled. A sub-area of 5*5 m was laid out to record tree regeneration **(C)**.

sites, as well as the planar to colline, submontane and montane altitudinal range, resulting in six sub-groups of even aged beech forest (**Table 1**). Mixed oak forest candidate sites were divided into two sub-groups of wet-favorable and dry site conditions. In some cases, beech-forests were managed in group selection systems and thus, a uniform stand age cannot be determined. Therefore, an additional sub-group "multi-aged" stands was added for beech sites.

For the selection of beech and oak sites, we applied an orthogonal site selection procedure to cover the ranges of both TSA and stand age independently, resulting in a two-dimensional chronosequence with multiple combinations of TSA and stand age. For each forest type and sub-group, candidate sites were assigned to classes of TSA (class-width 15 yr.; e.g., 0-15 yr., 16-30 yr., etc.) and stand age (class-width 40 yr.; e.g., 80-120 yr., 121-160 yr., etc.). For each forest type one data point from each occupied class was randomly selected. We applied a weighted random sampling approach (Efraimidis and Spirakis, 2016) to promote underrepresented major natural regions of Germany (Meynen et al., 1953; **Figure 2A**). Sites located in these regions were assigned with higher selection probabilities. This allowed us to improve the spatial coverage and evenness of selected set of sites, as otherwise over-represented natural regions would dominate the dataset.

Multi-aged beech sites were selected to represent a gradient of TSA only, and we incorporated nutrient conditions as well as the colline and submontane altitudinal range.

SFR representing other forest types (**Table 1**) are currently not available in sufficient quantity to compile a reasonable selection and thus gather statistically useful data. Hence, only individual sites were selected within similar ranges of TSA and stand age.

Lastly, five beech forest sites that have been unmanaged for more than 100 years completed our set of selected sites. Forests unmanaged for that long are rare in Germany and the best natural reference available for the temporal development of SFR.

Following the site selection process, on-site inspections were conducted, to determine whether the selected sites met the selection

TABLE 1 Overview over the number of selected sites (N) per forest type and sub-group (nutrient supply, altitudinal range) and the ranges of TSA [y] and stand age [y] (reference year: 2020). Multi-aged sites that were selected, are noted in brackets.

Forest type	Nutrient supply	Altitudinal range	N: age-class, (multi-aged)	Range: TSA, (stand age) [yr.]
Beech	Poor	colline	13, (2)	4 – 65, (91 – 202)
Beech	Poor	submontane	9, (3)	13 – 55, (140 – 20)
Beech	Poor	montane	6	0 – 74, (155 – 261)
Beech	rich	colline	23, (2)	6 – 68, (65 – 222)
Beech	rich	submontane	10, (4)	10 – 59, (98 – 173)
Beech	rich	montane	5	22 – 48, (160 – 232)
Beech (TSA $>$ 100 yr.)	–	–	5	106 – 400 + , (200 – 465)
Oak-Hornbeam	–	–	11	13 – 67, (120 – 220)
Oak-Hornbeam	–	–	3	20 – 50, (143 – 182)
Alder-Elm	–	–	1	70, (176)
Spruce	–	montane	1	43, (215)
Beech	–	–	1	48, (194)
Pine	–	–	1	34, (158)

Beech = *Fagus sylvatica*; Oak = *Quercus* spp.; Hornbeam = *Carpinus betulus*; Alder = *Alnus* spp.; Elm = *Ulmus* spp.; Spruce = *Picea abies*; Pine = *Pinus sylvestris*.

criteria and that stands of suitable size were present. We followed a standardized protocol on all sites, assessing forest type and structure, management legacy, deadwood, tree species composition and terrain. Exclusion criteria were, for example, wrong forest type, unsuitable species composition based on pre-established thresholds, management legacy did not fit designated TSA or unfavorable terrain. Excluded sites were replaced by a repeated random pick from the respective TSA/stand-age class and were inspected accordingly.

2.2. Data collection

Nine circular plots (each with $r = 12.62$ m, $A = 500$ m^2; Figure 2C) were established on each site. Generally, these plots were set up in a 3 × 3 grid, with 100 m distance between plot centers and 50 m internal buffer from the stand boundaries (Figure 2B). In cases where this grid could not be laid out, due to restrictions in the shape of the stand or difficult terrain, the most compact configuration feasible was chosen, to ensure spatial coherence of the plots.

Field data was collected between December 2020 and June 2021. All standing trees with $\geq$ 7 cm diameter at breast height (DBH) were registered. For each object, DBH, species, object class, position within the plot and individual slope at the base were recorded. Heights were measured for three trees of each species occurring on the plot. Lying objects (longitudinal axis $\leq$ 10 gon (gradian) to terrain surface) were recorded when their DBH or lower diameter was $\geq$ 20 cm for dead objects and $\geq$ 7 cm for living objects. Species, degree of decomposition (five stages), object class, length and their position on the plot were noted. The object class consisted of the life class (living, dead), position class (e.g., upright or hanging) and the compartment class (complete, stem only, etc.). Regeneration was recorded on a 5 × 5 m subsection of the plot, differentiating between species, height class and whether they were browsed. Additionally, the average slope of the plot, as well as exposition and topography were determined.

2.3. Dataset

We revised the initially available site information by contacting the site managers, asking for information on the last management activity and exact stand age. If managers were able to supply detailed information, we adjusted our data accordingly. TSA is generally counted from the year the site became an SFR legally, but the last management activity might date back several years before that. If no information was available we assumed that interventions are usually executed in 10-year cycles and increased TSA by five years, as the average time since the last management activity. We obtained site specific climate data on average annual temperature, annual precipitation and the climatic water balance of a recent drought period (Kaspar et al., 2013; DWD Climate Data Center (CDC), resolution 1 × 1 km, reference period 1991 - 2020, dry years 2018-2020). Site specific data on usable field capacity (uFC) in the upper 30 cm of the soil were calculated based on the soil sample characteristics. Plot specific elevation was acquired from digital elevation models (resolution 25 m, and 1 m if available).

Field data was checked for plausibility and recording errors. Species- and site-specific height curves were fitted using the height measurements taken in the field. They were used to estimate the height of all standing objects without height measurement.

2.4. Carbon content of biomass

Species specific volumetric functions were applied to calculate individual object volume (R-package "nwcalc", unpublished). These functions yield similar results to the standard calculations used in the German national forest inventory (Riedel and Kändler, 2017; Riedel et al., 2017), however the latter do not allow to consider incomplete objects (i.e., broken trees) or deadwood. Extrapolation factors were applied to account for unmeasured objects below the DBH threshold in the lying deadwood compartment and we further compensated for decay stage (see Supplement in Meyer et al., 2001). Object biomass was derived from the computed and extrapolated volumes by multiplying with species specific wood densities from the global wood density database (Zanne et al., 2009). Regeneration biomass was calculated following Annighöfer et al. (2016). Root biomass was modeled based on DBH, applying the species specific functions from Forrester et al. (2017).

The carbon content was calculated by multiplying biomass with a factor of 0.488 for broadleaved species and 0.508 for conifer species (Thomas and Martin, 2012). Subsequently, all numbers given refer to carbon content (Mg ha^{-1}).

2.5. Soil organic carbon

Volumetric soil samples were taken on a subset of three plots per site. On each of those plots samples were taken at three systematically distributed satellite locations (10 m from the plot center, 0°, 120° and 240° azimuth). Generally, samples were taken with a root auger. It was driven into the soil until a total sample depth of 30 cm in the mineral soil was realized. The sample was divided into four compartments: the organic layer and three depth-classes of the mineral soil (0 – 5 cm, 5 – 10 cm and 10 – 30 cm). On the plot level the samples of each compartment were combined into mixed samples. If the soil conditions were not appropriate for the use of the root auger the organic layer was sampled with a humus pot. Sample rings were used to take samples from the mineral soil accordingly. If the full sampling depth to 30 cm could not be achieved, this was noted and considered in the quantification of the soils carbon content. Detailed information on the soil bulk density and chemical analysis can be found in the **Supplementary material 1**.

In eight forest stands the root auger method and the sample ring method were applied simultaneously to standardize the comparison of the produced results. As yet, only the latter method is widely accepted. Comparative analysis showed the two methods to deliver similar results. Models for soil organic carbon were built from a data subset of beech age-class stands containing only the sampled plots.

2.6. Data analysis

We distinguished six carbon compartments for our analysis. Separately for above- and belowground, we differentiated living and dead biomass as individual carbon compartments. The other compartments were carbon in the mineral soil (0-30 cm), hence termed "mineral topsoil", and carbon in the organic layer.

The data were clustered into subsets based on forest type. Age-class beech sites made up the largest subset with n = 64 sites. Previously, one site was excluded from the analysis ("An den zwei Steinen", ID = 07-005). Here, intense grazing pressure from red deer has led to an open stand structure with a degraded canopy and lack of regeneration or understory development. We assessed this stand development to be very unique. Due to its position at the end of the (continuous) TSA gradient (TSA = 74 yr.) the site significantly reduced model adequacy.

For data analysis, the categorization of forest types by distinguishing between nutrient rich or poor sites, as well as the three altitudinal ranges was replaced by continuous variables. Allowing us to analyze the six different beech forest types collectively. We used the pH values obtained from soil analysis as a proxy for nutrient availability. Abiotic conditions were described by average annual temperature and annual precipitation, average plot slope, topography and exposition. Elevation was significantly correlated to temperature and precipitation and therefore excluded. Additionally, usable field capacity was used to model carbon in living biomass, while the climatic water balance of the recent drought period (years 2018-2020) was used to model carbon in dead biomass. Stand characteristics included were TSA, stand age and the share of beech.

We used the statistics software R (R Core Team, 2016) to apply general additive models (mgcv::gam; GAM) with a "log" link-function from the package "*mgcv*" (Wood, 2011). Site identity was accounted for as a random effect. Carbon content in the above- and belowground compartments of dead biomass was log-transformed.

Lastly, we combined the GAM models of the six carbon compartments into a predictor function of carbon stock, sensitive to the predictor variables used in the GAMs. Dummy data based on the average environmental conditions were used, with six levels of TSA (10 – 60 yr.) and four levels of stand age (80, 120, 160, and 200 yr.).

It was not possible to fit robust models to the data subsets of multi-aged beech and oak forests due to low sample size. Uniquely represented forest types as well as the five beech reference sites (TSA > 100 y) were included comparatively.

3. Results

3.1. Carbon storage and variability

Across the 100 sites, the site averages of total carbon storage ranged between 186.5 and 493.0 ($\bar{x}$ = 315.6) Mg C ha^{-1}. Out of the ten sites with the highest total carbon storage, seven were nutrient rich beech stands. Carbon stored in the aboveground living biomass alone varied between 59.0 and 261.9 ($\bar{x}$ = 151.6) Mg C ha^{-1}, while it was 15.2 – 47.7 ($\bar{x}$ = 29.7) Mg C ha^{-1} belowground. Aboveground dead biomass contained between 1.3 and 61.0 ($\bar{x}$ = 14.1) Mg C ha^{-1} and carbon in belowground dead biomass ranged from 1.5 to 28.2 ($\bar{x}$ = 7.7) Mg C ha^{-1}. The soil organic layer held 0.5 to 65.3 ($\bar{x}$ = 13.5) Mg C ha^{-1}, while the mineral soil had a carbon stock of between 31.9 and 304.8 ($\bar{x}$ = 97.4) Mg C ha^{-1}.

For even-aged beech stands, the average amount of carbon stored in aboveground living and dead biomass increased for approximately 50 years of TSA as well as with increasing stand age (**Table 2**). Average values were lower for both high stand age (201 – 240 yr.) and TSA (61 – 75 yr.). The five sites with TSA > 100 yr. had the highest average value. With either increasing TSA or stand age the standard deviation between site average values increased.

TABLE 2 Mean and standard deviation of aboveground carbon (Mg ha^{-1}) in dead and living biomass for even-aged beech forests in pooled groups of TSA and stand age (reference year: 2020).

TSA [yr.]	Carbon: $\bar{x}$ (Mg ha^{-1})	Carbon: σ (Mg ha^{-1})	
0 - 15	142.7	51.6	
16 - 30	150.6	58.5	
31 - 45	174.6	62.4	
46 - 60	186.6	61.1	
61 - 75	152.5	72.9	
> 100	190.7	97.7	
Stand age [yr.]			**German forest inventory: $\bar{x}$ (Mg ha^{-1})**
41 – 80	86.0	17.4	110.9*
81 - 120	189.7	60.2	144.8*
121 - 160	172.2	57.3	150.6*
161 - 200	170.0	63.2	148.6*
201 - 240	145.2	62.1	*NA*
240	175.9	97.4	*NA*

Mean and standard deviation from multiple samples were computed with combinevar() in the R-package "fishmethods" (Nelson, 2022). For comparison with managed forests, we converted the publically available volumes per age class from the German Forest Inventory (Schmitz, 2014; https://bwi.info/) to Mg C ha^{-1}. Managed stand with stand age > 160 yr. are recorded as one group in the German inventory. *As aboveground deadwood is reported independent of stand age, we added the average amount of 21 m^3 ha^{-1} to these values.

3.2. Carbon in living biomass

The 64 age-class beech forest sites stored 80.5 – 261.9 ($\bar{x}$ = 162.5) Mg C ha^{-1} in aboveground living biomass. Increasing TSA had a positive effect on carbon stored in the living biomass (Table 3 and Figure 3; see also Supplementary materials 2, 3). While the relationship was linear for approximately 0 – 45 years after abandonment, it subsequently leveled out to 180 – 200 Mg C ha^{-1} (Table 2 and Figure 3), showing a decreasing effect at higher values of TSA. Over 50 years of TSA, the average increment was 70–80 Mg C ha^{-1}. Stand age showed a convex relationship with carbon content in the living biomass, peaking at 150 yr. The effect of stand age was greatest in the aboveground compartment, while it was not a powerful predictor in the belowground compartment (Supplementary material 3). A higher share of beech trees was associated with higher carbon stocks aboveground, whereas no effect of species mixture was detected belowground. The strongest environmental predictor was annual precipitation, displaying a negative linear relationship with carbon stock. Soil pH (0-5 cm) had a convex relationship to carbon in living biomass, with an optimum around pH = 5.5.

3.3. Carbon in dead biomass

The 64 age-class beech forest sites stored 1.3 – 46.3 ($\bar{x}$ = 11.7) Mg C ha^{-1} in aboveground dead biomass. Model fits were weaker for carbon in dead biomass, compared to living biomass (Table 3). Increasing TSA had a positive effect on carbon in the aboveground deadwood compartment, leveling out around TSA = 50 yr. (Figure 4C; Supplementary material 4). Belowground, TSA correlated negatively with the carbon stock in dead biomass (Supplementary material 5). It was further indicated that higher amounts of precipitation correlated positive with higher amounts of deadwood. Increasing average annual temperature showed a weak positive influence on carbon stock.

3.4. Carbon in the soil

The 64 age-class beech forest sites stored 1.2–65.3 ($\bar{x}$ = 14.1) Mg C ha^{-1} in the organic layer and 40.9–266.2 ($\bar{x}$ = 92.1) Mg C ha^{-1} in the mineral soil. Carbon in the organic top layer and the mineral soil were most notably dependent on soil pH (Table 3; see also Supplementary material 6, 7). While pH > 5 did not influence the amount of carbon stored in the organic layer, pH values below pH = 5 correlated strongly to increasing amounts of

TABLE 3 A separate GAM model was built for each carbon compartment and total carbon stock (Supplementary materials 2–9).

	Aboveground		Belowground		Organic layer	Mineral topsoil	Total
	Living	Dead	Living	Dead			
TSA	/	/	/	\	∩	–	/
Stand age	∩	–	–	–	–	–	∩
Share beech (Vol.) *	/	\	–	–	\ *	–	/
Plot slope	–	–	/	–	–	–	–
Precipitation	\	∪	\	–	–	–	–
Temperature	–	–	–	/	–	\	–
pH	∩	–	–	–	\	/	/
uFC	–	NA	–	NA	NA	NA	–
Cwb	NA	–	NA	–	NA	NA	NA

The indicated trends per predictor variable are simplified main trends. For the exact fitted spline consult the respective GAM panels (Supplementary materials 2–9). Clear evidence for a relationship is highlighted in dark-gray, weaker evidence in light-gray. Altough the variables may have contributed to the respective GAM, the evidence of their relationship with the carbon compartment is weak. uFC (usable field capacity) was used in models for living biomass, cwb (climatic water balance for dry years 2018–2020) was used in models for dead biomass. *We used the share of non-beech and non-oak tree species in the GAM for the organic layer, to better reflect the higher turnover rate of admixed deciduous species (see discussion in "4.3. Soil."). (no evidence: –; positive relationship: /; negative relationship: \; convex relationship: ∩; concave relationship: ∪; predictor not used in models of these carbon compartments: NA).

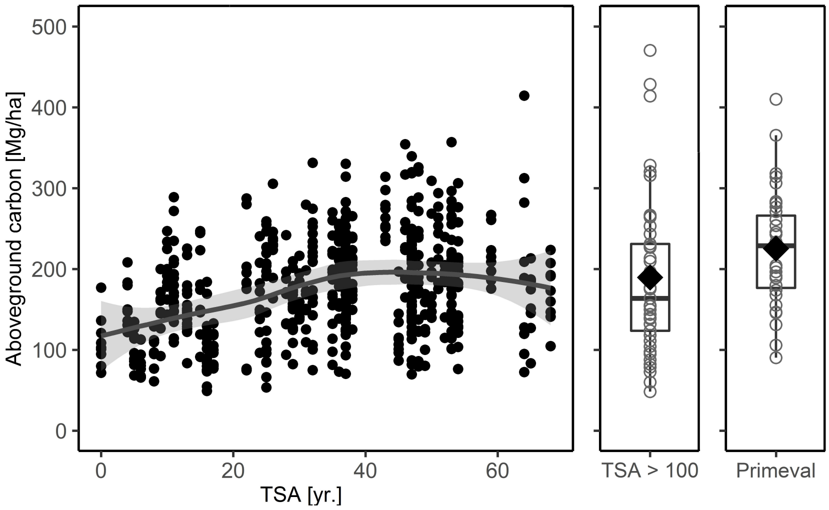

FIGURE 3
Total carbon in aboveground biomass (living + dead) for the age-class beech forest plots used in the main analysis, the five study sites in forests with TSA > 100 years and the primeval beech forest reference. The latter are plot values from three Slovakian primeval forests (Glatthorn et al., 2018). The solid line depicts a loess smoothing function (aboveground total carbon ~ TSA + stand age), the gray shaded area is the 95% confidence interval. For forests with TSA > 100 years and the primeval forest we used boxplots, with median (thick black line), 25-and 75-percentiles and the whiskers not exceeding the 1.5-fold of the interquartile range. The mean value is indicated by a diamond.

stored carbon. Conversely, the mineral topsoil showed increasing carbon stocks with pH values rising above pH = 5. Carbon storage in the mineral topsoil was additionally affected by a negative linear correlation with average annual temperature. An increasing share of admixed tree species (i.e., broadleaved tree species others than beech and oak) correlated to decreasing amounts of carbon stored in the organic layer. TSA did not affect carbon stock in the mineral topsoil, while a weak convex relationship was found for carbon stock in the organic top layer. However, when only accounting for carbon stock in the topmost layer of the mineral soil (0-5 cm) there was a concave relationship with increasing TSA (**Supplementary material 8**).

3.5. Beech stands with TSA > 100 yr.

The five beech forest sites with TSA > 100 yr. had a total carbon storage between 266.6–407.2 ($\bar{x}$ = 327.5) Mg C ha^{-1}. The average total carbon stock was slightly higher in the old beech forest sites than in the age class beech sites (**Figures 4**, **5**). Carbon stored in aboveground deadwood was highest in old beech forest sites 24.6 – 61.0 ($\bar{x}$ = 39.6) Mg C ha^{-1}.

3.6. Other forest types

Total carbon stock in multi-aged beech forest ranged between 264.8 and 495.0 ($\bar{x}$ = 343.0) Mg C ha^{-1} (**Supplementary material 10**), the latter value being the highest total carbon stock of all sites. Wet-favorable mixed-oak stands varied between 232 – 326.4 ($\bar{x}$ = 278.4) Mg C ha^{-1} of total carbon stock (**Supplementary material 11**). The additional forest types had a total carbon storage between 210 – 395.8 Mg C ha^{-1} (**Supplementary material 12**). Both multi-aged beech stands and wet favorable oak stands did not show an apparent trend in carbon storage with increasing TSA. We presented these sites in S 10-12 and compared their aboveground carbon storage levels with values obtained from our age-class beech forest prediction model.

3.7. Total carbon & carbon prediction model

The 64 age-class beech forest sites stored 208.1 – 444.5 ($\bar{x}$ = 319.1) Mg C ha^{-1} in total. The majority of the total carbon pool was made up of the living biomass stock and the carbon stored in the mineral soil (**Figures 5**, **6**). Increasing TSA was a positive driver of the total carbon stock for 50 years, with a decreasing effect at high values of TSA (+ 50 yr.) (**Supplementary material 9**). Additionally, increasing pH in the mineral soil showed a positive relationship with total carbon stock.

We illustrated the modeled changes of total carbon stock per carbon compartment across TSA and with varying stand age (**Figure 6**). The highest level of carbon storage was found at a stand age of 160 yr. and TSA = 50 yr. Generally, a stand age of 160 yr. held the highest levels of carbon storage compared to other stand ages at all respective levels of TSA. The major contribution to increasing carbon stocks were the above- and belowground living biomass compartments, followed by aboveground dead biomass.

4. Discussion

4.1. Living biomass

We found independent effects for both TSA and stand age on carbon storage in even-aged, beech dominated stands. The

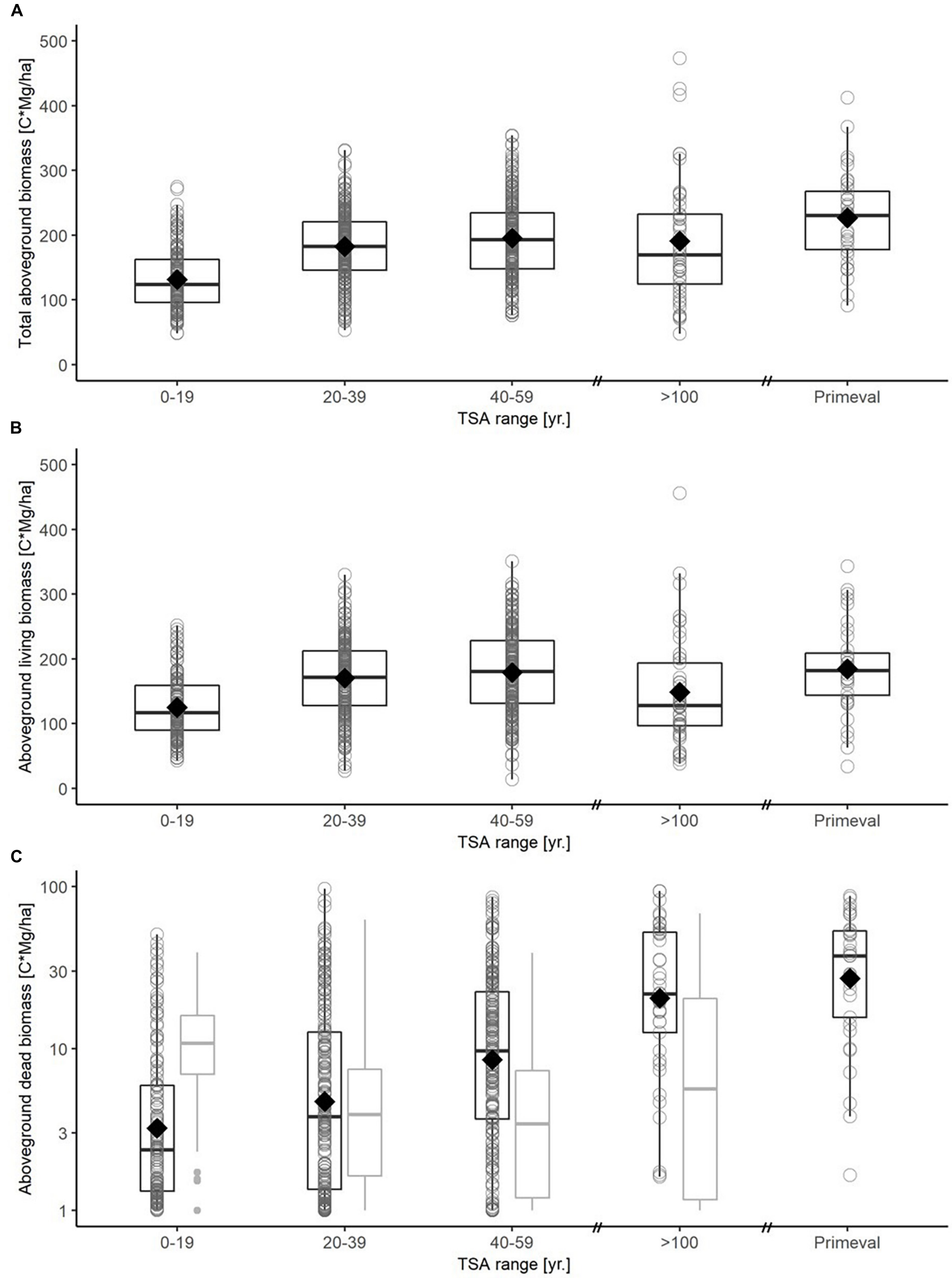

FIGURE 4
Boxplots for carbon in total aboveground biomass **(A)**, aboveground living biomass **(B)** and dead biomass **(C)** for different TSA classes (0-19 yr., 20-39 yr., 40-59 yr., > 100 yr., primeval forest). A boxplot is drawn for each TSA class based on plot-level data, with median (thick black line), 25-and 75-percentiles (box) and whiskers not exceeding the 1.5-fold of the interquartile range. The mean value is indicated with a diamond. Note that carbon in dead biomass is shown on a logarithmic scale. Dead biomass **(C)** is differentiated between aboveground (black boxplots) and belowground (gray boxplots) carbon stock. The virgin forest reference is based on plot level data from three Slovakian virgin forests (Glatthorn et al., 2018), here data on belowground dead biomass was not available.

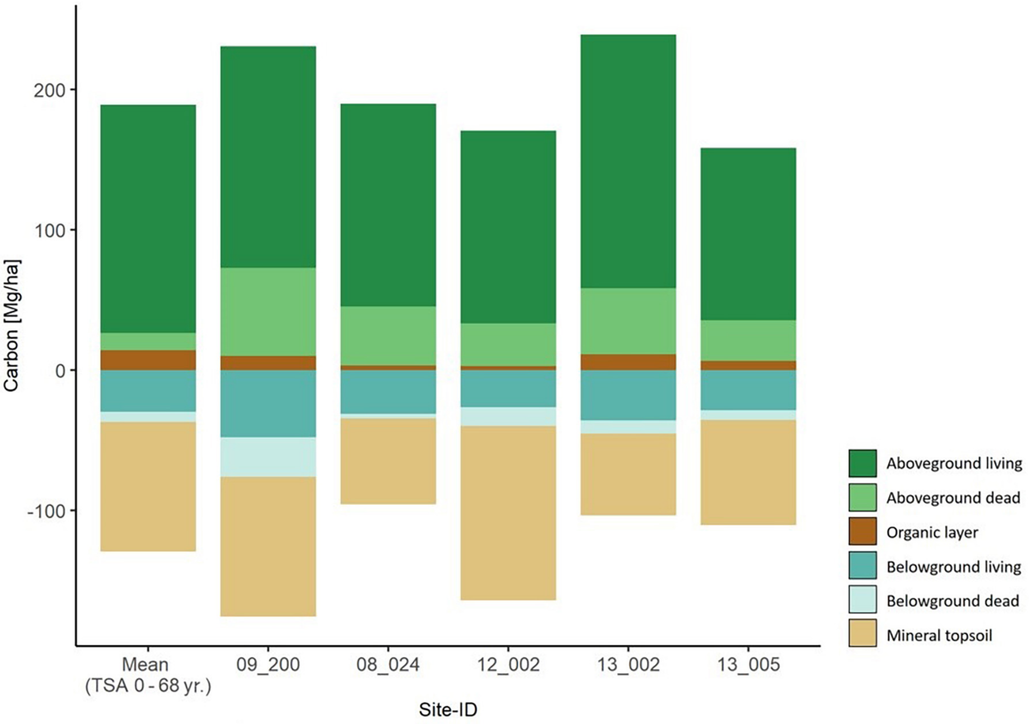

FIGURE 5
Carbon storage in all six carbon compartments for the five old beech forest sites with TSA > 100 years. They are sorted by ascending TSA from left to right. The mean values per carbon compartment of the main sites (TSA 0 – 68 yr.) are depicted in the left-most column.

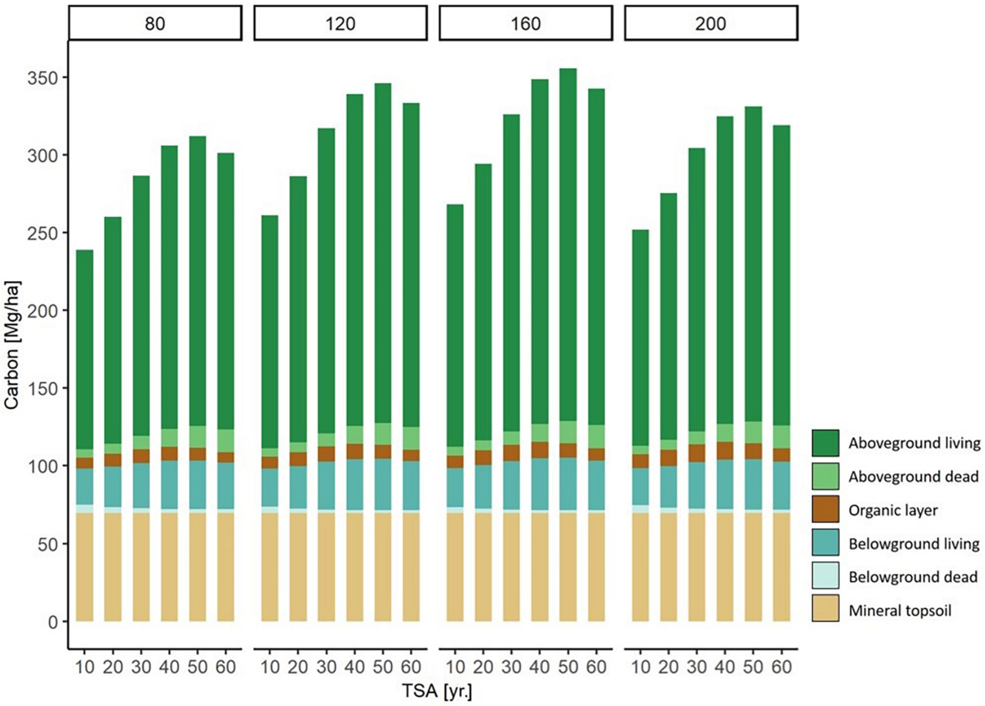

FIGURE 6
Modeled carbon storage in each carbon compartment for forest stands of different stand age (80, 120, 160, and 200 yr.) along a TSA gradient (10 - 60 yr.). For example, on the left there are six 80 year old beech stands, with a TSA of 10, 20, 30, 40, 50, and 60 years, respectively. The values are modeled based on a fictional stand, under average environmental conditions. Through the separation of stand age and TSA, the effects of the two variables can are expressed simultaneously.

positive linear relationship of TSA on carbon storage for the first 50 years after the end of forest management is consistent with results based on real time series (Meyer et al., 2021). Beside the effects of site conditions and other abiotic factors, reflecting the physiological requirements and constraints of beech (Leuschner and Ellenberg, 2017), stand growth is determined by stand age (Pretzsch, 2010). We observed a peak of living biomass around a stand age of 150 years. Klein et al. (2013) found a maximum for living biomass in unmanaged beech sites at the age of 160 years. On the basis of inventory data from Spain, a maximum carbon stock was found in undisturbed mature stands but not in older stands (Molina-Valero et al., 2021).

The negative influence of young stand age on aboveground living biomass can be explained by the still maturing stand, that is not yet filling its potential growing space. The observed negative effect of high stand age is more complicated to interpret. The textbook opinion is that volume increment in beech stands levels out gradually with stand age (> 150 yr.; Pretzsch, 2010), but this does not explain decreasing stocks of living biomass that we found for TSA > 50 yr. An increase of age-related mortality was not observed, as there was no effect of stand age on the aboveground dead biomass carbon stock. A possible explanation could be found in the management history of the stands. According to our observations in the field, most of the old stands were at least partly harvested before abandonment, resulting in a reduced level of biomass. Brown et al. (1997) showed that forest stands that were harvested in the past had a significant potential to increase aboveground biomass, compared to old-growth forest biomass levels, because they lack large diameter trees (diameter > 70 cm).

However, we want to stress that the observed decrease of carbon stock in living biomass for TSA > 50 yr. and the negative effect of high stand age could be an artefact caused by the space-for-time substitution, lower number of sites with TSA > 50 yr., lack of information on management legacy or inaccuracy of the reported stand age. Correspondingly, time series data from German SFR do not show a negative effect of stand age on biomass stock or increment in unmanaged beech and oak forests (Meyer et al., 2021).

The positive effect of an increasing share of beech on carbon storage in living biomass is in line with findings by Meyer et al. (2021), where pure beech stands reached higher levels of biomass as well as higher net increment in biomass than mixed forest types. This contradicts the consistent reports of a positive biodiversity-productivity relationship in forests (Liang et al., 2016). However, the seemingly emerging trend of higher productivity in pure beech stands would have to be studied in more detail to draw deeper conclusions. It must be stressed that the negative diversity-productivity relationship we found refers solely to the influence of tree species diversity on biomass production in beech forests and does not apply to other important metrics, such as biodiversity or ecosystem resilience.

4.2. Dead biomass

Regarding the opposing effects of TSA on above- and belowground dead biomass, we found that the negative relationship of belowground deadwood with TSA was largely driven by tree stumps. Management induces high frequencies of stumps that, with increasing TSA, successively decrease in frequency and biomass due to decomposition (**Figure 4C**). For better comparison with the existing literature, we use aboveground deadwood volumes in the following list of values. Across all of our 100 sites inventoried, we found average aboveground deadwood volumes of 4 – 450 ($\bar{x} = 63$ m^3 ha^{-1}). The 64 age-class beech stands with TSA $\leq$ 68 yr. had 4 – 180 ($\bar{x} = 51$) m^3 ha^{-1} of aboveground deadwood. The five old beech sites (TSA > 100 yr.) had distinctly higher amounts of aboveground deadwood volume with 128 – 450 ($\bar{x} = 206$) m^3 ha^{-1}. The latter was mostly driven by one particular site, that had an average of 450 m^3 ha^{-1} due to high deadwood input from large silver fir (*Abies alba*). Excluding this outlier, the remaining four sites had 128 – 161 ($\bar{x} = 145$) m^3 ha^{-1} of aboveground deadwood. Siemonsmeier et al. (2020) measured an average of 121 m^3 ha^{-1} in eight German strict forests reserves based on seven sites with TSA = 40 yr. and one site with TSA = 29 yr. For comparison, managed forests in Germany hold an average of 21 m^3 ha^{-1} of deadwood (Schmitz, 2014)[1]. The primeval beech forest remnants in the Carpathians hold average deadwood volumes of 111 – 177 m^3 ha^{-1} (Commarmot et al., 2005; Feldmann et al., 2018; Stillhard et al., 2022).

An increase in deadwood volumes after cessation of management is a common trend in SFR (Christensen et al., 2005; Vandekerkhove et al., 2009; Meyer and Schmidt, 2011). Deadwood stocks accumulate over time, as the decay of beech deadwood can take up to 50 years (Přívětivý et al., 2016). Based on our data, an exponential increase of aboveground dead biomass can be expected for the first fifty years after abandonment. Later on, the rate of increment likely slows, so that altogether the increase of deadwood follows a logistic course, eventually approaching values similar to primeval beech forests. Meyer and Schmidt (2011) found a mean net increase of 1 m^3 ha^{-1} year^{-1} in northwestern German SFR with up to 28 years of TSA. However, deadwood formation is largely subject to stochastic events (i.e., natural disturbances) and therefore difficult to predict, especially on the small spatial scale of typical German SFR.

4.3. Soil

The range and distribution of carbon stocks in the organic layer and the mineral top soil we found correspond well to the range reported in the German forest soil inventory (Grüneberg et al., 2019). The carbon stock in the organic layer showed a convex relationship with TSA (**Supplementary material 6**) and our initial hypothesis had to be rejected (but see below). This pattern might be explained by an inverse relationship of canopy openness (i.e., a driver for mineralization) and TSA, indicated by the rapid decrease in belowground dead tree carbon (i.e., decaying stumps, see section "4.2. Dead biomass") and the exponential increase in aboveground dead tree carbon (**Figure 4C**). The share of admixed tree species also had an effect on carbon in the organic layer. An increasing share of other broadleaved tree species caused a decrease in organic layer carbon stocks, which can be explained by a higher turnover rates for most broadleaved species litter compared to beech litter (Vesterdal et al., 2008). However, the strongest predictor for organic layer carbon stock was soil pH, with higher stocks under more acidic conditions. A dominant opposing

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[1] https://bwi.info/

trend regarding soil pH (i.e., smaller stocks under more acidic conditions) was found for carbon stocks in the mineral topsoil (0–30 cm). This is similar to findings by Grüneberg et al. (2019) and can partly be explained by the positive effect of increasing soil pH on the soil biological activity and bioturbation (i.e., relocation of organic carbon from the organic layer to the mineral topsoil). However, regarding the carbon stock potential in the mineral soil, a characterization based solely on pH seems insufficient. The effect of soil texture (i.e., clay content), was found to have a pronounced effect on carbon storage in the mineral soil (Grüneberg et al., 2019), however these criteria were not determined for our samples. A strong influence of soil type on carbon storage was also documented for primeval beech forests (Pichler et al., 2021).

The negative effect of increasing temperature found for carbon stocks in the mineral topsoil could be explained by the general temperature-induced acceleration of biological and chemical processes causing an increase of the mineralization rate.

In line with our hypothesis, TSA and stand age had no visible effect on carbon stocks in the mineral topsoil. However, there was a concave effect of TSA on carbon stock in the topmost layer (0-5 cm; **Supplementary material 8**). This effect was inverse compared to the convex effect of TSA on carbon stock in the organic layer, indicating a dynamic tradeoff between these compartments. A similar zero-sum situation was described for artificial canopy gaps in acidic beech forests by Bauhus et al. (2004). Our results suggest that the tradeoff exists in both directions and continues over the course of progressing TSA. In other words, the relatively open canopy conditions after harvest promote mineralization in the organic layer and a shift of carbon to the topmost mineral soil layer. After abandonment, the canopy closes and the mineralization rate decreases, due to lower surface temperatures. In turn, the storage in the organic layer increases, but the input to the mineral soil is reduced and its carbon stock decreases, due to continuing mineralization and carbon leaching. After several decades, disturbances cause canopy openings and mineralization of the organic layer increases again, and so does the input to the topmost mineral soil layer. Further, this tradeoff seems to apply for beech forests across different site conditions. In consequence, the mineral topsoil in total might remain largely unaffected by stand age and TSA, as long as canopy disturbance (in the past, present and future) does not exceed a moderate level.

Other reasons why there were no visible effects of TSA on mineral topsoil in total could be that some important factors were missing, or that our sampling depth was not deep enough. Observed temporal changes in topsoil carbon stocks in German forests in general, differing with soil type and region (mean = 0.75 Mg ha^{-1} year^{-1}, range = -0.71 – 1.35 Mg ha^{-1} year^{-1}; Grüneberg et al., 2019), further complicate the interpretation of data from space-for-time approaches. As the site conditions are very individual, it would be appropriate to make direct comparisons on the same site (Gleixner et al., 2009) regarding subtle differences in stand age and TSA. However, in paired plot studies (i.e., forest reserve vs. adjacent managed forest) no significant differences regarding carbon storage in the topsoil were found between managed and lately unmanaged (TSA > 40; Mund, 2004; Krueger et al., 2017; Nord-Larsen et al., 2019) or even primeval beech forests (Leuschner et al., 2022). The latter, however, had a higher carbon storage in the upper subsoil (30-60 cm), confirming that in the neighboring managed stands clear cuts in the past (80-100 years ago) had long-term effects on the carbon stock in the upper subsoil. According to Gleixner et al. (2009), broadleaved forests tend to store a higher fraction of carbon in deeper layers. Nevertheless, this is only an indication toward negative effects from forest management, but not for a persistant carbon sink in the soil of unmanaged forests. According to Wirth et al. (2009), the dynamics of the soil carbon pool are still unclear, as there are no chronosequential studies on deep soil horizons and approaches are blind to the continuous export of dissolved organic carbon.

4.4. Other forest types

Due to the low number of oak and multi-aged beech forest sites it was not possible to conduct a robust statistical exploration of the data. Therefore, the set of sites for our main analysis had to be restricted to age-class beech stands. Furthermore, an unclear management history of the multi-aged beech stands compromised their classification as multi-aged. In fact, some of these sites were formerly managed as even-aged stands but information on stand age was lost or no longer applicable. Initially, the single sites of additional forest types were selected within similar ranges of TSA and stand age to be comparable among themselves. Unfortunately, over the course of our study, several corrections had to be made to the basic attributes and a comparison within a singular range of TSA was not possible.

While the modeled values for age-class beech followed the modeled course with increasing values of TSA, multi-aged beech and wet-favorable oak sites did not appear to display a pattern along the gradient of TSA (**Supplementary material 10**, **11**). Modeled values corresponded well with the values measured in other forest types (**Supplementary material 12**) that were dominated by broadleaved species. Site typical conifer stands reach lower levels compared to modeled beech stands.

4.5. Carbon storage over time

We found that aboveground carbon storage increased significantly over time for approximately 50 years. This matches the expectations from our hypothesis and the findings of other studies (Halpin and Lorimer, 2016; Meyer et al., 2021). Compared to the values reported for German managed forests (**Table 2**), SFR had a stronger increment with stand age, while managed forests had stable aboveground volumes for stand ages > 100 (Schmitz, 2014; See text footnote 1), SFR peaked at younger stand ages and maintained high volume levels with further increasing stand age.

Through the combined effect of TSA and stand age, carbon stocks of medium aged stands profited most from abandonment, which is reflected in our prediction model. To test this, we ran a GAM, replacing current stand age with "age at abandonment" (AAA). This model also showed a convex relation between stand age and carbon stored in living biomass, with a peak of AAA at a stand age of 120 years. We interpret this finding as the combination of high annual volume increment and already high levels of biomass stock of medium aged stands, because the main harvest had not been initiated at the time of abandonment. This suggests, that the observed effect of stand age could indeed be an effect of management (see also 4.1). Nevertheless, the age-independent, positive effect of TSA on aboveground living biomass suggests that all stands profit from the cessation of management, independent of stand age.

Halpin and Lorimer (2016) found that aboveground living biomass in unmanaged forests declined when stands transitioned from even-aged to multi-aged structures. The descending aboveground carbon storage with high stand age (**Table 2**; age class 201 – 240 yr.) and the high standard deviation in old stands (stand age + 240 yr.) may indicate the onset of the terminal phase and overmaturing trees, with the associated structural changes. Our models also show a negative effect of high stand age and decreasing levels of living biomass for TSA > 50 yr. However, DBH-density distributions on our sites suggest that the transition to multi-aged, "old-growth" structures is not very advanced yet. Given the findings of Halpin and Lorimer (2016), it is conceivable that living biomass levels will decrease with further increasing TSA, as our models predict.

A moderate decrease of aboveground living carbon stock (about -15%) is also indicated by the mean value in the five beech forest sites that were unmanaged for > 100 years. In total, the accumulating aboveground deadwood compensated the lower carbon stock in living biomass to an extent (**Figure 4**). The mean value of carbon in aboveground living biomass on these five sites was similar to the stocks reported for an old forest reserve in Denmark (Nord-Larsen et al., 2019) and top values documented for the Hainich National Park in Germany (Mund, 2004). Past management of these sites may still affect carbon storage and stand structure to the present day. For example, management legacies are still present in the form of old wood pasture oaks, or the underrepresentation of distinct tree cohorts (i.e., dbh 40-70 cm), likely due to unfavorable conditions for regeneration under an even-aged managed stand in the past.

SFR at the peak around 50 years of TSA had similar carbon stocks in living biomass as primeval beech forests in Slovakia (Glatthorn et al., 2018; **Figure 4B**). This suggests that, in the long run, carbon stocks in living biomass may rise again when tree demography has progressed towards old-growth structures. Considering that the aboveground deadwood carbon stock in primeval forests is even larger than that in our long unmanaged stands (**Figure 4**), the total aboveground carbon stocks might well exceed those of SFR with TSA around 50 years by then. We want to remark that stock and deadwood volumes in the three Slovakian primeval forests (**Figures 3**, **4**; see also Feldmann et al., 2018) are not exceptionally high but average, compared to other primeval beech forests in this region (Korpel', 1995; Kucbel et al., 2012; Petritan et al., 2012; Stillhard et al., 2022). Overall, when comparing carbon storage levels of our sites, including the old beech sites, to data from primeval forests it seems reasonable to assume that, after fast initial growth, the carbon stock stabilizes already at early stages of natural forest development (Molina-Valero et al., 2021), at a level relatively close to the site-specific carbon carrying capacity (Gupta and Rao, 1994; Keith et al., 2009).

4.6. Total carbon storage

Our finding that the total carbon stock was mostly driven by TSA and soil pH (**Supplementary material 9**) highlights that the total carbon pool of a forest stand is dominated by living biomass, and the carbon stock in the mineral soil. Accordingly, the highest total carbon stocks are to be expected on fertile sites with high soil pH and a forest stand that has accumulated biomass for several decades, set aside at a stand age around 120 yr. or younger. It is up to future studies with extended datasets, to further assess the development of the carbon stock in stands with TSA > 50 years.

4.7. Sources of uncertainty

It was noticeable, that our GAMs were not able to predict the extreme levels of carbon storage we measured. This may be due to a lack of information on certain abiotic parameters or management legacies related to productivity and biomass stock in our data. Due to a reduced density of data points, the development of carbon stock beyond 50 years of TSA could not be reliably predicted. SFR with TSA > 50 years are rare and thus, the confidence intervals of our models widen at the high range of TSA. For this reason, we limited our carbon prediction model to 10 – 60 years of TSA (**Figure 6**) and emphasize the reduced reliability for the highest values of TSA.

As discussed previously, stand age and management legacy were additional sources of uncertainty. Stand age was based solely on silvicultural records, that do not necessarily reflect the true age structure of the stand. For example, two stands may have the same age in the records, but differ greatly in the field as one was harvested intensively before being set aside while the second stand experienced low levels of management intervention.

It is apparent that space-for-time substitution is inferior to time-series data. Better data on management history and stand structure are required to obtain more reliable estimates of carbon stock dynamics and the effects of TSA and stand age.

5. Conclusion

After abandonment, forests increase their carbon stock to notably higher values compared to still managed stands. The central compartment of that increase is the living biomass. Several studies have found that the carbon stock in unmanaged forest can increase over long periods of time (Carey et al., 2001; Knohl et al., 2003; Luyssaert et al., 2008; Klein et al., 2013; Herbst et al., 2015; Gustavsson et al., 2017; Pukkala, 2017; Curtis and Gough, 2018). Within the observed gradient of TSA, our study supports these findings. We found a linear increase of the carbon storage over the first 50 years after abandonment. However, our data remain inconclusive on the expected development of the carbon stock past 50 years of TSA.

In the light of the efforts to mitigate climate change and the heated discussion about whether to set aside forest to natural development or not, it is important to consider that how we manage forests is not only relevant to climate change, but also to biodiversity, ecosystem functions and cultural values (Watson et al., 2018). It is important to continue the observation and collection of data in order to better understand naturally developing forests. Our study shows that long-term time-series data are essential to reliably disentangle specific effects, such as the influence of stand age or soil characteristics.

The coming decades are critical for climate change mitigation. According to the current state of knowledge, unmanaged forests can reliably sequester and store carbon from the atmosphere within a limited timeframe and the constraints of their natural carrying capacity (Keith et al., 2009). Our results suggest, that this timeframe is at least 50 years long. Over time, the sink function diminishes and naturally developing forests become a passive, but stable carbon storage (Nord-Larsen et al., 2019; Stillhard et al., 2022). Half a century of predictable carbon uptake may be utilized in climate-smart forest management planning. This timeframe is well within the range of climate goals formulated by the IPCC (2021). We feel that in some cases the term "Climate-Smart Forestry" is being constrained within the context of bioenergy production and product substitution. However, it is a concept aiming to integrate and optimize multiple forest functions (Nabuurs et al., 2018). We encourage that the potential of naturally developing forests to sequester and store carbon, as well as for biodiversity and other ecosystem functions should be addressed in devising Climate-Smart Forestry (Nabuurs et al., 2018; Bowditch et al., 2020; Verkerk et al., 2020).

Data availability statement

The dataset used in this study, R-code to reproduce our analysis and metadata are archived in a Figshare data repository (https://doi.org/10.6084/m9.figshare.21967052). Tables with attributes on the object-, plot- and site-level are included.

Author contributions

RN, PM, and EF contributed to the conception and design of the study. RN organized the database, performed the statistical analysis, and drafted the manuscript. EF wrote sections of the manuscript, revised, contributed references, and provided supervision. MB and PM acquired funding, revised the manuscript, and contributed references. All authors contributed to manuscript revision, read, and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2023.1099558/full#supplementary-material

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Re-appraisal of the global climatic role of natural forests for improved climate projections and policies

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Along with the accumulation of atmospheric greenhouse gases, particularly carbon dioxide, the loss of primary forests and other natural ecosystems is a major disruption of the Earth's system and is causing global concern. Quantifying planetary warming from carbon emissions, global climate models highlight natural forests' high carbon storage potential supporting conservation policies. However, some model outcomes effectively deprioritize conservation of boreal and temperate forests by suggesting that increased albedo upon deforestation could cool the planet. A potential conflict of global cooling vs. regional forest conservation could harm environmental policies. Here we present theoretical and observational evidence to demonstrate that, compared to the carbon-related warming, modeling skills for assessing climatic impacts of deforestation is low. We argue that estimates for deforestation-induced global cooling result from the models' limited capacity to account for the global effect of cooling from evapotranspiration of intact forests. Specifically, transpiration of trees can change the greenhouse effect via small modifications of the vertical temperature profile. However, due to their convective parameterization (which postulates a certain critical temperature profile), global climate models do not properly capture this effect. This may lead to an underestimation of warming from the loss of forest evapotranspiration in both high and low latitudes. As a result, conclusions about deforestation-induced global cooling are not robust and could result in action that immediately worsened global warming. To avoid deepening the environmental crisis, these conclusions should not inform policies of vegetation cover management, especially as studies from multiple fields are accumulating that better quantify the stabilizing impact of natural ecosystems evolved to maintain environmental homeostasis. Given the critical state and our limited understanding of both climate and ecosystems, an optimal policy with immediate benefits would be a global moratorium on the exploitation of all natural forests.

KEYWORDS

ecosystem stability, climate stability, primary forests, precipitation, evapotranspiration, convective parameterization

1. Introduction

The Earth is suffering from climate destabilization and ecosystem degradation (Figure 1), and humanity seeks to stop both (IPBES, 2019; IPCC, 2021). Policies for global climate stabilization focus on decarbonization and are informed by the outcomes of global climate models that formalize our evolving understanding of the Earth's system—currently, by the model simulations from the 6th Coupled Model Intercomparison (CMIP6) for the 6th Assessment Report of the Intergovernmental Panel on Climate Change (IPCC, 2021). With the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) formed 24 years later than IPCC, the ecosystem preservation narrative is less formally developed (Wilhere, 2021). Proponents of ecosystem preservation often borrow from the decarbonization argumentation and invoke the carbon storage potential of natural forests as a major illustration of their climatic importance. For example, the ground-breaking proforestation initiative in the United States emphasizes how much carbon unexploited natural forests can remove from the atmosphere if allowed to develop to their full ecological potential (Moomaw et al., 2019; Faison et al., 2023).

At the same time, the carbon-storage argument for temperate and boreal forests is undermined by the fact that global climate models suggest that deforestation in these regions could cool the planet. Based on these models, increased albedo is estimated to overcome the warming caused by deforestation-induced carbon emissions (Jia et al., 2022, Figure 2.17) even if the latter can be underestimated (Schepaschenko et al., 2021). These model outcomes have been known for quite a while (e.g., Snyder et al., 2004), but recently these ideas clearly gained prominence and are even approaching implementation. A recent *Science* commentary warned that regrowing boreal forests would not make the Earth cooler (Pearce, 2022), a conclusion that is derived purely from global climate model simulations (e.g., De Hertog et al., 2022). The World Resources Institute's report "Not just carbon" noted that the increased albedo from deforestation would cool the Earth and emphasized that the positive climate role of boreal forests is only a local effect (Seymour et al., 2022a,b). Aligned with these modeling studies, a recent study in *Nature Ecology and Evolution* did not include primary boreal forests into Nature's critical assets (Chaplin-Kramer, 2023). One of the criteria for an ecoregion to be classified as a critical asset was its proximity to people—and primary boreal forests are often distant from any human settlements (which is a major reason for why they are still primary). Together, these models and mainstream messages not only de-emphasize the preservation of natural boreal and, to a lesser degree, temperate forests, but they implicitly prescribe and incentivize their destruction.

In this Perspective, we would like to ring an alarm bell by showing that this potentially biased picture of the role of natural forests, in particular boreal forests, for stabilizing Earth's climate is based on a few model assumptions that rule out important evapotranspiration feedbacks and can result in policies deepening rather than mitigating the climate crisis. We also outline a clear and possible path forward.

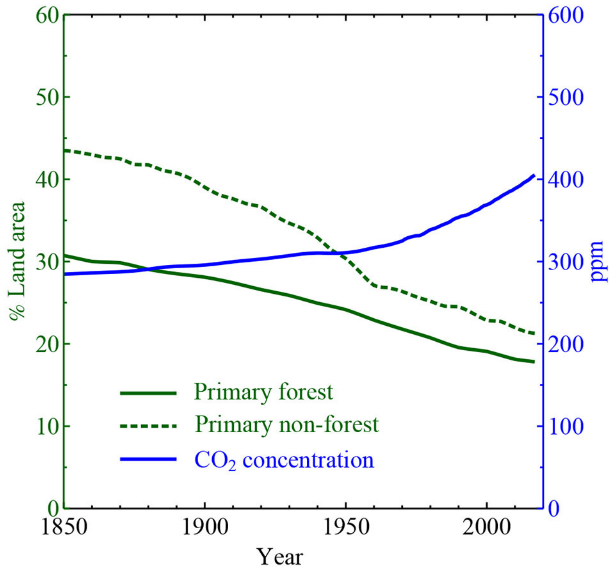

FIGURE 1
Decline of primary forest and non-forest ecosystems (left axis, data from Hurtt et al., 2020, their Figure 7) and increase of atmospheric CO_2 (right axis, data downloaded from https://www.eea.europa.eu/data-and-maps/daviz/atmospheric-concentration-of-carbon-dioxide-5). During the industrial era, primary ecosystems have declined, and CO_2 concentration has grown, by approximately one half.

2. Global cooling from plant transpiration

2.1. Local vs. global cooling

We argue that the conclusion of a cooler Earth upon the loss of boreal forests stems from the limited capacity of global climate models to quantify another forest-related effect acting in the opposite direction: global cooling from forest transpiration. The ability of transpiring plants to provide local cooling is well-known (e.g., Alkama and Cescatti, 2016; Huryna and Pokorný, 2016; Bright et al., 2017; Ellison et al., 2017; Hesslerová et al., 2018, and see Figure 2). Instead of converting to heat, some of the absorbed solar energy is spent on breaking the intermolecular (hydrogen) bonds between the water molecules during evapotranspiration. As a result, the evaporating surface cools.

When more sunlight is reflected back to space, the planet receives less energy and it is intuitively clear that it must cool. In comparison, evaporation cools locally, but the captured energy does not disappear: it is released upon condensation elsewhere in the Earth's system. The methodology of explaining why the planet warms with increasing CO_2 is well-developed (e.g., Benestad, 2017, and references therein). In contrast, how and whether loss of plant transpiration could warm or cool the planet remains conceptually unclear. While the IPCC reports recognize that global cooling from plant transpiration exists (Jia et al., 2022, Figure 2.17), its physical mechanism is not to be found in literature. Nevertheless, the environmental science is inherently transdisciplinary, and understanding this effect is important for the broader community of ecosystem researchers and conservationists, as it will enable a

FIGURE 2
Local cooling from plant transpiration. With incoming solar radiation of about 1 kW m^{-2}, dry area on the deforested plot **(left)** has temperature of 55.3°C. Young transpiring trees **(right)** lower the surface temperature by almost 30°C. Distance between the two spots is 1 m. Measurements and photo credit Jan Pokorný.

critical assessment of model outputs offered to guide large-scale vegetation management.

2.2. Methods

To illustrate the global thermal effect of transpiration, we will use a simple model of energy transfer (Figure 3). The greenhouse substances are represented by discrete layers that absorb all incoming thermal radiation and radiate all absorbed energy equally up and down. All the imaginary planets shown in Figure 3 are in a steady state: none is warming or cooling. In the absence of absorbers, the Earth's surface emits as much thermal radiation as it absorbs solar radiation (Figure 3A). Each layer of the greenhouse substances redirects part of the thermal radiation back to the Earth's surface. As a result, the planetary surface is warmer according to the greater the amount of absorbers (cf. Figures 3B, C).

When a certain part of the incoming solar radiation is absorbed in the upper atmosphere (for example, by aerosols or clouds), it escapes interaction with the absorbers beneath. Accordingly, in such a case the planetary surface is colder by an amount by which the absorbers would multiply this escaping part if it dissipated to thermal radiation at the surface (cf. Figures 3C, D). Figures 3C, D show that, with unchanged amount of greenhouse gases (e.g., carbon dioxide) and unchanged total flux q of absorbed solar energy, the planetary surface temperature depends on *where* solar energy dissipates to thermal radiation.

Similarly, in the presence of the non-radiative fluxes of sensible and latent heat, the amount of solar energy converted to thermal radiation at the surface diminishes—and so does the amount of thermal radiation redirected by the absorbers back to the surface. Thus, surface thermal radiation and temperature are smaller (cf. Figures 3D–F). The non-radiative fluxes "hide" a certain part of absorbed solar energy from the greenhouse substances easing its ultimate release to space. Convection, condensation and precipitation "deposit the latent heat removed from the surface above the level of the main water vapor absorbers, whence it is radiated to space" (Bates, 2003). This energy escaping partially from interaction with the absorbers is the physical mechanism behind global cooling from plant transpiration.

A related process is the atmospheric transport of heat from the equator to higher latitudes, where the water vapor concentration in the colder atmosphere is smaller. This transport likewise "hides" a certain part of solar energy absorbed at the equator from the abundant greenhouse substances (water vapor) in the warm tropical atmosphere. As a result, despite the amount of absorbers does not change, the globally averaged greenhouse effect diminishes and the planetary surface cools (Bates, 1999; Caballero, 2001). The potential of this effect was illustrated by Marvel et al. (2013), who modeled an idealized atmosphere with two strong circulation cells connecting the equator and the poles. With such a circulation, the Earth's surface became eleven degrees Kelvin cooler than the modern Earth (Marvel et al., 2013, their Figure 1e and Figure 3 bottom).

An increase in the non-radiative flux F_L (from $F_L = 0$ in Figure 3D to $F_L \simeq 0.4q > 0$ in Figures 3E, F) decreases surface thermal radiation F_s by a magnitude proportional to the flux change ΔF_L and to the number $\Delta\tau$ of absorbing layers beneath the height where this flux dissipates to thermal radiation ($\Delta\tau = 1$ in Figure 3E and $\Delta\tau = 2$ in Figure 3F). Historical deforestation affected about 13% of land area $S_l = 1.5 \times 10^8$ km^2 (or 3.8% of planetary surface $S_E = 5.1 \times 10^8$ km^2) (Figure 1). With the global mean latent flux of $F_L = 80$ W m^{-2}, if deforestation has reduced this flux by thirty per cent ($\Delta F_L \sim -0.3F_L$), this could increase the surface radiation by $-0.038\Delta F_L \Delta\tau \sim 0.9$ W m^{-2} (cf. Figures 3D, E, $\Delta\tau = 1$) or twice that number (cf. Figures 3D, F, $\Delta\tau = 2$), Table 1. Given an equilibrium climate sensitivity $\varepsilon \sim 1$ K/(W m^{-2}) (Zelinka et al., 2020), the latter case corresponds to a warming of about two degrees Kelvin (Table 1). If the optical thickness of the atmosphere,

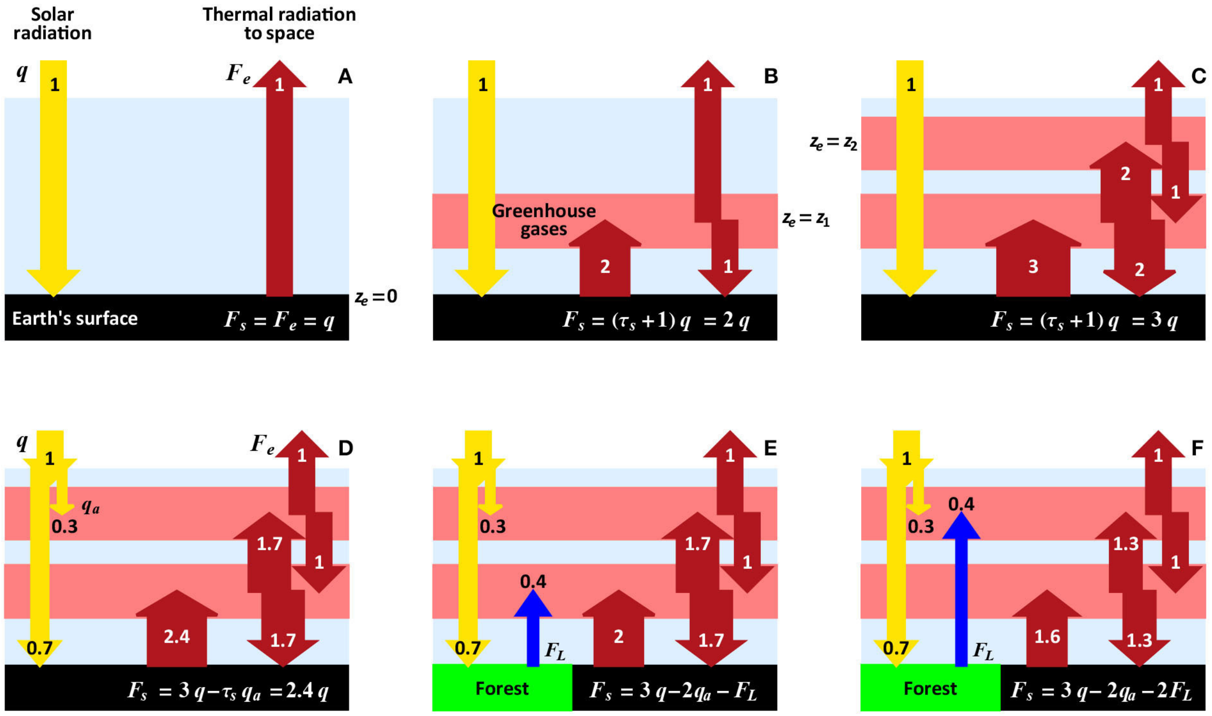

FIGURE 3
Scheme to illustrate the dependence of the planetary surface temperature on the amount of greenhouse substances **(A–C)** and on the magnitude and spatial distribution of the non-radiative energy fluxes **(D–F)**. Thickness of each layer of the greenhouse substances corresponds to unit optical depth $\tau = 1$ (one free path of thermal photons—the mean distance between two consecutive acts of absorption and re-emission by the absorber molecules); τ_s is the total number of layers: $\tau_s = 0$ in **(A)**, 1 in **(B)**, and 2 in **(C–F)**. A "gray" atmosphere is assumed, where absorption of thermal radiation is the same for all wavelengths (Ramanathan and Coakley, 1978; Makarieva and Gorshkov, 2001; Gorshkov et al., 2002). Thermal radiation of the planetary surface $F_s = \sigma T_s^4$ (W m^{-2}) and of the upper radiative layer to space $F_e = \sigma T_e^4$ are related to surface temperature T_s and temperature of the upper radiative layer T_e by Stefan–Boltzmann law, where $\sigma = 5.7 \times 10^{-8}$ W m^{-2} K^{-4} is the Stefan–Boltzmann constant. All energy fluxes are shown in the units of absorbed solar radiation q, which is in the steady state equal to thermal radiation emitted by the planet ($F_e = q$); in **(D–F)**, $q_a = 0.3q$ is solar energy absorbed by the atmosphere (not to be confused with the reflected solar radiation (albedo), which is assumed to be constant and not shown); in **(E, F)**, F_L is the non-radiative heat flux accounting for both sensible and latent heat. Thermal radiation is emitted to space from mean height z_e with temperature T_e: $z_e = 0$ in **(A)**, $z_e = z_1 > 0$ in **(B)**, and $z_e = z_2 > z_1$ in **(C–F)**.

and, accordingly, the magnitude of $\Delta\tau$, is greater, the cooling can be proportionally larger.

In a steady state with the unchanged amount of greenhouse substances, temperature T_e and height z_e of the upper radiative layer remain constant (e.g., Figures 3C–F). Therefore, surface warming caused by loss of plant transpiration should be manifested as an increase in the temperature difference between the surface and the upper radiative layer, i.e., the mean temperature lapse rate[1] $\overline{\Gamma} = (T_s - T_e)/z_e$ should grow (see discussion and Figure 5 in Section 2.4).

2.3. Dependence of global transpirational cooling on atmospheric circulation

The higher up in the air column that convection transports heat, the more pronounced global cooling it exerts. This is because the energy is radiated more directly to space from the upper atmospheric layer (cf. Figures 3E, F). In addition to the altitude, it matters how rapidly the cooled air descends. When the air rises and increases its potential energy in the gravitational field, its internal energy accordingly declines, and it cools. While evaporation cools the evaporating surface, the release of latent heat during condensation in the rising air partially offsets this decline of the internal energy of air molecules, making the rising air warmer than it would be without condensation. Radiating this extra thermal energy to space takes time. The more time spent by the air warmed by latent heat release in the upper atmosphere (above the main absorbers), the more energy is radiated unimpeded to space and the stronger the global transpirational cooling. With the characteristic radiative cooling rate of the order of 2 K day^{-1}, it takes about 15–30 days to radiate the latent heat released by tropical moist convection (Goody, 2003).

Therefore, long-distance moisture transport (including the biotic pump run by forests, Makarieva and Gorshkov, 2007) enhances global transpirational cooling: moist air travels for many days, and thousands of kilometers from the ocean to land, where it ascends and latent heat is released. The dry air warmed by latent heat makes the same long way back in the upper atmosphere, thereby radiating energy to space (Figure 4). If, on the contrary, the

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[1] Temperature lapse rate Γ is the absolute magnitude of the vertical temperature gradient, $\Gamma \equiv -\partial T/\partial z$.

TABLE 1 Estimates of global warming from the loss of tree transpiration associated with deforestation; ΔF_L (% of the global mean value F_L) is the local reduction of latent heat on the deforested area ΔS (% of land area S_l); ΔT is the change of *global* surface temperature upon deforestation.

References	Area affected	ΔS (%)	ΔF_L (%)	ΔT (K)
Snyder et al. (2004)	Tropical*	16	−30	0.24
Davin and de Noblet-Ducoudré (2010)	Global**	90		0.55
This work (Figures 3D, F)	Historical***	13	−30	2

*Tropical forests replaced by deserts in a coupled atmosphere-biosphere model.

**Deforestation of a fully forested planet without changing the albedo; ΔT is the sum of two effects, change in roughness and change in evapotranspiration efficiency as shown in Table 1 of Davin and de Noblet-Ducoudré (2010).

***Estimated as $\Delta T \sim -(\Delta S/S_l)(S_l/S_E)\Delta F_L \Delta\tau\varepsilon$, assuming that deforestation reduces latent heat flux by 30% of $F_L = 80$ W m^{-2} (Trenberth et al., 2009) on area $\Delta S \sim 13\%$ of land (the area affected by historical deforestation (Figure 1), $S_l/S_E = 0.29$ is the relative global land area) with $\Delta\tau = \tau_s = 2$ as optical depth of the atmosphere (Figures 3D, F); $\varepsilon \sim 1$ K/(W m^{-2}) is the assumed equilibrium climate sensitivity to radiative forcing. Note that with $q = 239$ W m^{-2}, the idealized planet with $\tau_s = 2$ shown in Figure 3F approximately corresponds to the modern Earth with $q_a = 78$ W m^{-2} $\simeq 0.3q$, $F_s = 390$ W m^{-2} $\simeq 1.6q$, $F_L = 97$ W m^{-2} $\simeq 0.4q$ (Trenberth et al., 2009).

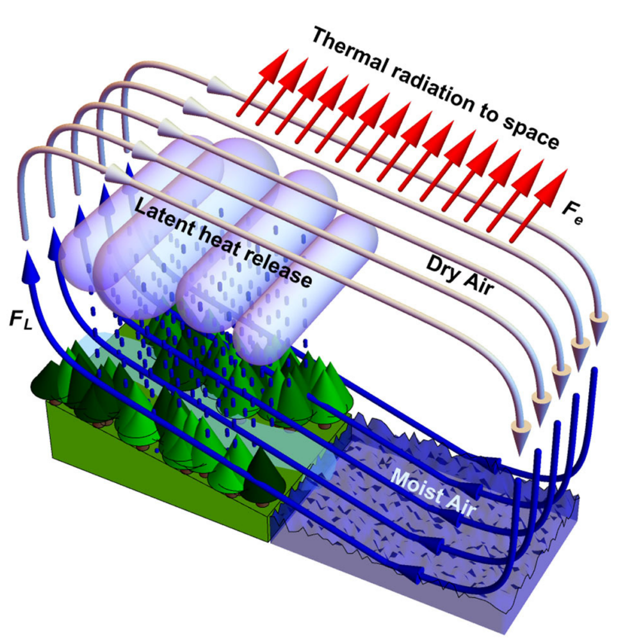

FIGURE 4
Visualization of the link between transpirational cooling and air circulation. After latent heat is released upon condensation, this energy can be radiated to space while the air travels back to the ocean in the upper troposphere.

warmed air descends rapidly and locally, then most heat is brought back to the surface before it is radiated, and the global power of the net cooling effect can be nullified. Therefore, disruptions in the long-distance moisture transport (e.g., by deforestation) and violent local rains should warm the Earth. In smaller convective clouds up to a quarter of ascending air descends locally at a relatively high vertical velocity (Heus and Jonker, 2008; Katzwinkel et al., 2014). These effects are not taken into account when assessing the temperature effects of land cover changes (e.g., Bright et al., 2017).

Current global climate models do not correctly reproduce either the long-distance ocean-to-land moisture transport or the moisture transport over the ocean (Sohail et al., 2022). For example, the Amazon streamflow is underestimated by up to 50% (Marengo, 2006; Hagemann et al., 2011, their Figure 5). This corresponds to a 10% error in the global continental streamflow, the latter being of the same order as global continental evaporation. Similarly, global climate models do not correctly reproduce how the local diurnal cycle of convection changes upon deforestation by producing extreme low and high temperatures (Lejeune et al., 2017, their Figure 7). These are indirect indications of the models' limited capacity to reproduce global transpirational cooling. We will now discuss the cause of this limited capacity.

2.4. Global transpirational cooling in global climate models

We have seen that, for a given amount of absorbers, surface temperature is determined by the vertical distribution of the non-radiative heat fluxes (Figures 3D–F). But these fluxes themselves depend on the vertical temperature gradient: if the air temperature declines with height faster than a certain critical lapse rate of air temperature, the atmosphere is unstable to convection. The non-radiative heat fluxes originate proportional to the difference between the actual and the critical temperature lapse rates (Ramanathan and Coakley, 1978).

Therefore, *strictly* speaking, it is not justified to freely vary where and how the non-radiative heat fluxes dissipate to thermal radiation, not paying attention to whether the resulting vertical temperature profile is physically consistent with the convective fluxes specified *a priori*. However, since the non-radiative (convective) and net radiative energy fluxes in the Earth's atmosphere are of the same order of magnitude (100 and 60 W m^{-2}, respectively, Trenberth et al., 2009), a *rough* estimate of global transpirational cooling can be obtained from considering the radiative transfer alone as done in Figures 3D–F. (This would not be possible if the convective fluxes were an order of magnitude higher than the radiative flux). We emphasize that our goal here is not to obtain an accurate estimate of global transpirational cooling, but simply to present plausible arguments showing that it is overlooked and it can be large.

An exact estimate of what happens when the evapotranspiration and the latent heat flux are suppressed on a certain part of land area requires solving the problem simultaneously for the radiative-convective transfer and the temperature profile. This problem is too complicated for modern global climate models to address, therefore they apply the so-called *convective parameterization*. Convective parameterization in climate models postulates the (generally unknown) value of a critical temperature lapse rate instead of solving for it. While the numerical simulation is run, *"whenever the radiative equilibrium lapse rate is greater than the critical lapse rate, the lapse rate is set equal to the critical lapse rate"* (Ramanathan and Coakley, 1978). Therefore, by construction, global climate models cannot provide any independent information about the climatic effect of evapotranspirational cooling—that should be manifested as the change in the global mean lapse rate—besides what was fed into them *a priori* via convective parameterization.

The reason for this artificial constraint on the impact of evapotranspirational cooling is that global climate models have been built with a major goal of assessing radiative forcing from changing carbon dioxide concentrations. Accordingly, they do have this capacity: this forcing can be approximately estimated assuming an unchanged atmospheric temperature profile. It is under this assumption that Arrhenius (1896) obtained the first ever estimate of global warming from CO_2 doubling[2]. But radiative forcing caused by the suppression of evapotranspiration is a conceptually different problem for which convective parameterization precludes a solution that would be non-zero in the first order. Therefore, in the models, global warming resulting from the loss of transpirational cooling is, for the same deforested area, at least one order of magnitude smaller than our estimate (Table 1). For example, according to global climate models, tropical deforestation on 16% of land area would produce a global warming of 0.2 K (Snyder et al., 2004), while converting about 90% of global land area from forest to grassland (with unchanged albedo) would warm the Earth by about half a degree Kelvin (Davin and de Noblet-Ducoudré, 2010), see Table 1.

As a further illustration of the lack of conceptual clarity with regard to global transpirational cooling, one can refer to the conclusion of Davin and de Noblet-Ducoudré (2010, their Table 1) that modeled global warming due to the loss of evapotranspiration is a "non-radiative" forcing. This conclusion is reached by noting that loss of evapotranspiration practically does not change the radiation balance at the top of the atmosphere: $\Delta F_e \to 0$ such that $\Delta T/\Delta F_e \gg \varepsilon$. However, using this logic, CO_2 increase would not be a radiative forcing either, because, once the planetary temperature equilibrates, CO_2 increase *per se* (feedbacks absent) does not change the outgoing radiation at the top of the atmosphere. Indeed, Figure 3 illustrates how the steady-state planetary temperature changes due to the radiative forcing from an increased amount of greenhouse substances (Figures 3A–C) and due to the radiative forcing from changing non-radiative fluxes (Figures 3D–F). The incoming solar and outgoing longwave radiation remain the same in all cases ($F_e = q$ and $\Delta F_e = 0$).

In current models, it is assumed that as the planet warms, the temperature lapse rate should slightly diminish following moist adiabat (the so-called lapse rate feedback, Sejas et al., 2021). While robust across models, this feature is not, however, supported by observations that indicate an increase in the lapse rate (Figure 5). The temperature difference between the surface and the upper radiative layer z_e (located between 500 and 400 mb, Benestad, 2017) grows at approximately the same rate as the surface temperature itself. This effect is especially pronounced over land (Figures 5C, F) and is consistent with a radiative forcing imposed by changing non-radiative fluxes, including those due to the land cover change (Figures 3D–F). In addition to transpiration losses, the non-radiative fluxes of both latent and sensible heat are additionally reduced due to a decrease in surface roughness as the tree cover is removed during deforestation (Bright et al., 2017; Winckler et al., 2019).

3. Discussion and conclusions

Recognizing that for the ecological audience it could be difficult to assess the credibility of our quantitative estimates, we would like to emphasize two of the more unequivocal points. First, global climate models do indicate that the regional loss of forest evapotranspiration leads to global warming. Although the global effect is small (Table 1), it is of the opposite sign compared to the albedo-related cooling from deforestation that is invoked to argue that certain forests (boreal in particular) are not globally beneficial in the climate change context. Despite this obvious importance for policy-relevant model outcomes, a conceptual description of how evapotranspiration cools the Earth, and how its loss would lead to global warming, is absent from the meteorological literature. If and when conceptual understanding is lacking, how can one independently assess whether the models get the effect right?

Second, we have discussed that, from the first principles, we can expect global warming resulting from the loss of evapotranspiration to manifest itself as an increase in the vertical lapse rate of air temperature. Due to the convective parameterization, global climate models keep this lapse rate roughly constant as the planet warms (Held and Soden, 2006; Jeevanjee et al., 2022). However, this model feature does not agree with observations that accommodate a considerable increase in the temperature difference between the surface and the upper radiative layer (Figure 5).

Land and energy policies based on the model outcomes that we have criticized are being shaped right now and an evaluation/reevaluation that avoids harm is paramount. While the above arguments continue to percolate in the meteorological literature, readers from all disciplines should be interested in evaluating and discussing these concerns and can approach their colleagues in the field of meteorology to see how they respond to the above two challenges, thus getting an indirect confirmation (or disproval) of our argumentation.

At the most basic level, our results highlight the importance of a *valid concept* at the core of a model. The assumption of an *a priori* specified critical lapse rate in the convective parameterization yields a negligible global transpirational cooling, which translates into de-emphasizing the preservation of boreal forests. Concepts are powerful; incorrect concepts can be destructive. This brings us to the question, is there a *concept* that ecology could offer to put at the core of a global climate model, to adequately represent the biosphere?

From our perspective, it is the concept of environmental homeostasis, which is the capacity of natural ecosystems to compensate for environmental disturbances and stabilize a favorable for life environment and climate (Lovelock and Margulis, 1974; Gorshkov, 1995). Recent studies discuss how biotic control can be evident in the observed dynamics of the Earth's temperature (Leggett and Ball, 2020, 2021; Arnscheidt and Rothman, 2022).

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[2] If the lapse rate Γ is known, an alternative way to calculate how surface temperature rises with increasing concentration of greenhouse substances is to calculate the change of radiative height $\Delta z_e = z_2 - z_1$ (cf. Figures 3B, C) using the hydrostatic equilibrium; then use $\Delta T_s = \Gamma \Delta z_e$.

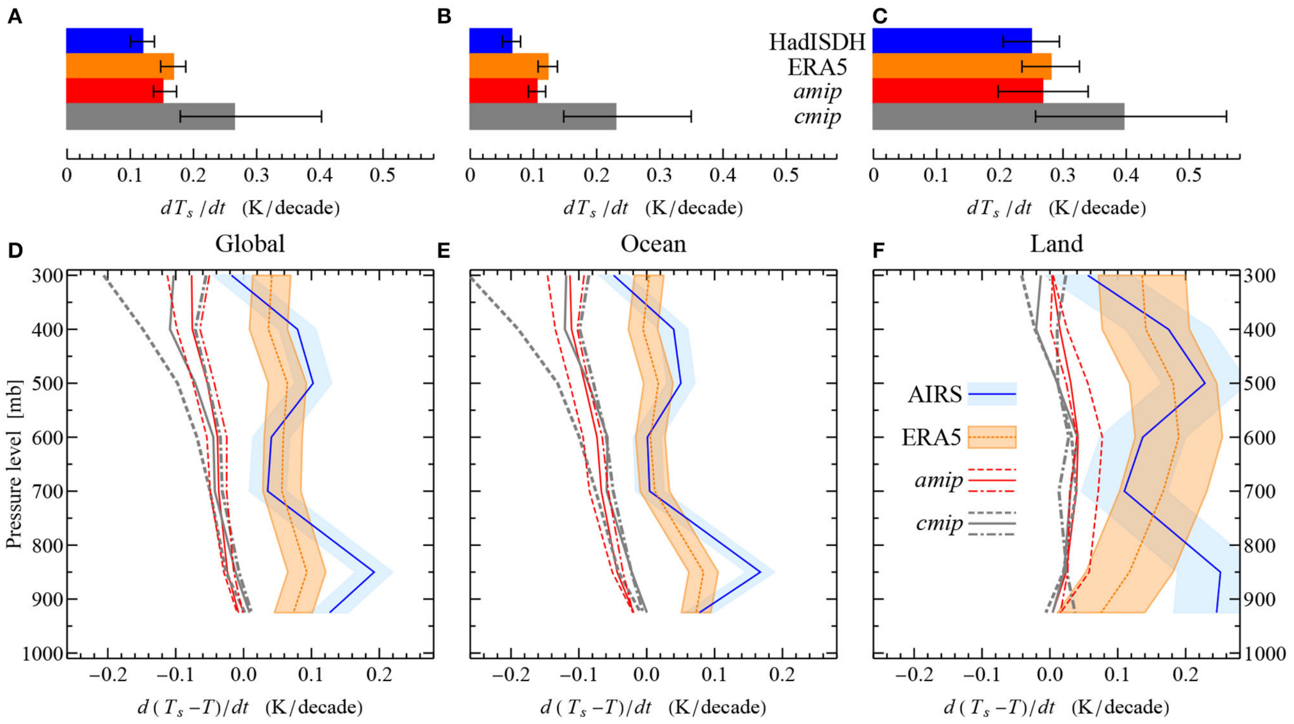

FIGURE 5
Mean trends of the surface temperature T_s **(A–C)** and of the temperature difference $(T_s - T)$ between the surface and atmospheric pressure levels **(D–F)** for the planet as a whole **(A, D)**, ocean **(B, E)**, and land **(C, F)** over 1988–2014 in models (*amip*, *cmip*) vs. observations (AIRS, HadISDH, ERA5). In **(A–C)**, whiskers for HadISDH and ERA5 indicate ± one standard deviation, for *amip* and *cmip*—the maximum and minimum values. Shading in **(D–F)** indicates ± one standard deviation. Dashed, solid and dash-dotted model curves in **(D–F)** were obtained, respectively, by using the maximum, median and minimum values of dT_s/dt and dT/dt in the model ensembles (*amip* and *cmip*). Data from Supplementary Figure S4 of Allan et al. (2022): AIRS, Atmospheric Infrared Sounder satellite data (Tian et al., 2019); HadISDH, The Met Office Hadley Centre homogenized and quality controlled, integrated sub-daily data set (Willett et al., 2014); ERA5, the fifth generation European Center for Medium-range Weather Forecasts global reanalysis (Hersbach et al., 2020); *amip*, Atmospheric Model Intercomparison Project, atmosphere-only simulations (without the ocean-atmosphere feedbacks in the climate system) (Gates et al., 1999); *cmip*, Phase 6 of the Coupled Model Intercomparison Project (includes *amip* simulations as an integral part) (Eyring et al., 2016). See Allan et al. (2022) for further details. In **(D–F)**, $d(T_s - T)/dt$ for AIRS is calculated using HadISDH dT_s/dt. Note that altitude $z(p)$ of a given pressure level p increases slightly as the surface temperature grows, but for $p < 300$ mb it is a minor effect compared to the increase of the temperature difference $T_s - T(p)$.

When the information about how the natural ecosystem influences environment is lacking, the best guess could be to assume that they provide a stabilizing feedback to the disturbance.

There was already a predicament in climate science that could have been facilitated by such an approach. It was the *missing sink* problem: when the rates of carbon accumulation in the atmosphere and the ocean became known with sufficient accuracy, it turned out that a significant part of fossil fuel emissions could not be accounted for. The enigmatic missing sink was later assigned to the terrestrial biota (Popkin, 2015). While now it is commonly referred to as plant *CO_2 fertilization*, this is a response at the level of the ecological community as a whole: for there to be a net sink, as the plants synthesize more organic matter, heterotrophs must refrain from decomposing it at a higher rate under the warming conditions (cf. Wieder et al., 2013). Surprisingly, while the idea that *ecological succession proceeds in the direction of the ecosystem attaining increased control of the environment and maximum protection from environmental perturbations* was dominant in ecology (Odum, 1969), a community's stabilizing response to the CO_2 disturbance was not predicted but rather opposed by ecologists on the basis that undisturbed ecosystems should have a closed matter cycle[3] (Hampicke, 1980; Amthor, 1995). However, based on the premises of the biotic regulation concept (Gorshkov, 1995; Gorshkov et al., 2000), and long before the missing sink was assigned to the terrestrial biota, Gorshkov (1986, p. 946) predicted that the undisturbed ecosystems should perform a compensatory response to rising atmospheric CO_2 by elevating synthesis of carbohydrates.

Today, climate science faces a new challenge. Global climate models with an improved representation of clouds display a higher sensitivity of the Earth's climate to CO_2 doubling than models with a poorer representation of clouds (Zelinka et al., 2020; Kuma et al., 2023). This implies more dire projections for future climate

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[3] This represents what can be called Odum's paradox, who thought that ecological succession culminates in ecosystem's maximum control of the environment (Odum, 1969). But if the ecosystem functions on the basis of closed matter cycles, its environmental impact (and, hence, environmental control) is zero by definition. The biotic regulation concept introduced the notion of *directed openness* of the matter cycles to compensate for environmental disturbances (Gorshkov, 1995).

change, but also poses the problem of how to account for the past temperature changes that are not affected by the model improvements and have been satisfactorily explained assuming a lower climate sensitivity. The concept of the environmental homeostasis and the biotic regulation of the environment provide a possible solution: the climate sensitivity may have been increasing with time—reflecting the decline of natural ecosystems and their global stabilizing impact (Figure 1).

Currently, climate model uncertainties are assessed by comparing outputs from models developed by different research centers (Zelinka et al., 2020). This provides a minimal uncertainty estimate, as the model development may follow universal principles sharing both progress and errors. A distinct approach would be to attempt building a model that departs significantly from the others in its core concept and see if such a model can be plausibly tuned to competitively describe observations. Success of such a model would force the range of model uncertainties to be extended. As global climate models are currently being used to elaborate strategies for the survival of humanity as a whole, such a stress test on their performance would not be superfluous.

Such an endeavor requires a plausible alternative concept, and we propose that a global climate model built around the stabilizing impact of natural ecosystems can become such an alternative. This will require an interdisciplinary effort and an account of global transpirational cooling, the role of natural ecosystems in the long-distance moisture transport (Makarieva and Gorshkov, 2007; van der Ent et al., 2010; Ellison et al., 2012; Poveda et al., 2014; Molina et al., 2019; Makarieva et al., 2023) and water cycle stabilization (Zemp et al., 2017; Baudena et al., 2021; O'Connor et al., 2021) and the distinct impact of ecosystems at different stages of ecological succession on the surface temperature and fire regime (e.g., Aleinikov, 2019; Baker and Spracklen, 2019; Lindenmayer et al., 2022) and the cloud cover (Cerasoli et al., 2021; Duveiller et al., 2021). Living systems function on the basis of solar energy that under terrestrial conditions can be converted to useful work with a near 100% efficiency. What processes are enacted with use of this energy, is determined by the genetic programs of all the organisms composing the ecological community. Randomly changing the species composition and morphological status of living organisms in the community—for example, by converting to developed land (removing natural elements altogether), replacing natural forest with a plantation, clearing large expanses for farmland, or forcing areas of forest to remain in an early successional or degraded state—disturbs the flow of environmental information and disrupts the ecosystem's capacity to respond to environmental disturbances (Makarieva et al., 2020; Kellett et al., 2023). We need a better understanding of this fundamental regulation and its tipping points.

While fundamental science is being advanced, the precautionary principle should be strictly applied. Any control system increases its feedback as the perturbation grows. Therefore, as the climate destabilization deepens, the remaining natural ecosystems should be exerting an ever increasing compensatory impact per unit area. In other words, the global climate price of losing a hectare of natural forest grows as the climate situation worsens. We call for an urgent global moratorium on the exploitation of the remaining natural ecosystems and a broad application of the proforestation strategy to allow them to restore to their full ecological and climate-regulating potential.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

Author contributions

AM wrote the first draft of the manuscript. All authors contributed to conception and design of the study. All authors contributed to manuscript revision, read, and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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Using essential biodiversity variables to assess forest ecosystem integrity

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Introduction: An unprecedented amount of Earth Observations and in-situ data has become available in recent decades, opening up the possibility of developing scalable and practical solutions to assess and monitor ecosystems across the globe. Essential Biodiversity Variables are an example of the integration between Earth Observations and *in-situ* data for monitoring biodiversity and ecosystem integrity, with applicability to assess and monitor ecosystem structure, function, and composition. However, studies have yet to explore how such metrics can be organized in an effective workflow to create a composite Ecosystem Integrity Index and differentiate between local plots at the global scale.

Methods: Using available Essential Biodiversity Variables, we present and test a framework to assess and monitor forest ecosystem integrity at the global scale. We first defined the theoretical framework used to develop the workflow. We then measured ecosystem integrity across 333 forest plots of 5 km^2. We classified the plots across the globe using two main categories of ecosystem integrity (Top and Down) defined using different Essential Biodiversity Variables.

Results and discussion: We found that ecosystem integrity was significantly higher in forest plots located in more intact areas than in forest plots with higher disturbance. On average, intact forests had an Ecosystem Integrity Index score of 5.88 (CI: 5.53–6.23), whereas higher disturbance lowered the average to 4.97 (CI: 4.67–5.26). Knowing the state and changes in forest ecosystem integrity may help to deliver funding to priority areas that would benefit from mitigation strategies targeting climate change and biodiversity loss. This study may further provide decision- and policymakers with relevant information about the effectiveness of forest management and policies concerning forests. Our proposed method provides a flexible and scalable solution that facilitates the integration of essential biodiversity variables to monitor forest ecosystems.

KEYWORDS

ecosystem monitoring, species diversity, tropical forests, ecosystem structure, kunming-montreal global biodiversity framework (GBF), earth observations, biodiversity conservation

1. Introduction

Forests are complex ecosystems, and their physical, biological, and functional components interact with each other (Hansen et al., 2021), which is fundamental to maintaining ecosystem resilience and the capacity to provide ecosystem services (Watson et al., 2018). However, anthropogenic drivers such as land-use change threaten forests and exacerbate climate change and biodiversity loss (Díaz et al., 2019). Additionally, biodiversity loss may not be effectively reverted, focusing only on forest cover loss without considering other components of ecosystem functioning. For instance, fragmentation may lead to reduced habitat for animal species and significant degradation of the forest ecosystem (Morris, 2010), resulting in reduced functioning of the systems on which humans and other organisms depend (Grantham et al., 2020). Therefore, projects related to climate mitigation and biodiversity loss focus not only on one specific ecosystem service but also include the components of ecosystem integrity to deliver long-term benefits for people and the environment.

The protection of forests and the assessment and monitoring of ecosystem integrity across scales are some of the key targets of international frameworks such as the Post-2020 Global Biodiversity Framework and the United Nations 2030 Agenda (CBD/SBSTTA/24/3/Add.2, 2021). Ecosystem integrity has been defined as "*a measure of ecosystem structure, function and composition relative to the reference state of these components being predominantly determined by the extant climatic–geophysical environment*" (Hansen et al., 2021). It describes how complete, healthy, and resilient an ecosystem is to both natural and human perturbations (Seddon et al., 2021). The structure of the forest encompasses the three-dimensional architecture of individual plants and the connection of their attributes (Hansen et al., 2021), while the function characterizes the movement or storage of energy or matter within an ecosystem (Bellwood et al., 2019). The composition describes how a forest's natural features are distributed within the ecosystem (genetic diversity, species richness, and community assemblages).

In recent decades the number of open-source satellite image collections has increased tremendously, which resulted in a growing number of high-quality biological remote-sensing products (de Paula et al., 2019). One well-known example is the Global Forest Cover Change map by Hansen et al. (2013). These remote sensing products are also known as Earth Observations (EO) and are particularly useful due to their global coverage and high temporal resolution (Skidmore and Pettorelli, 2015). The potential of EOs to measure and monitor biological products globally has not gone unnoticed. In 2013, the Group on Earth Observations Biodiversity Observation Network (GEO BON) set up a new framework to develop Essential Biodiversity Variables (EBVs) (Pereira et al., 2013). EBVs can be a combination of *in-situ* and remotely sensed data, or they can be derived from either (Giuliani et al., 2017; Schmeller et al., 2017; Kissling et al., 2018). There are currently 20 EBVs in six classes, including genetic composition, species populations, species traits, community composition, ecosystem function and structure (Hansen et al., 2021). Since the introduction of this concept, global political frameworks have proposed EBVs as the basis for monitoring advancements towards biological targets (Geijzendorffer et al., 2016). However, researchers have emphasized the importance of continuous testing of the application of EBVs across different scales and ecosystems (Pereira et al., 2013).

Reliable and consistent monitoring of forest ecosystem integrity is crucial to mitigating climate change and biodiversity loss (Keenan et al., 2015). Integrating different EBVs to monitor ecosystems globally may enable the development of a more consistent, accurate and scalable framework for sustainable management and global collaboration (Reddy, 2021). Although scientists have attempted to quantify ecosystem integrity, few studies have explored how EBVs can be organized in an effective workflow to create a composite index describing forest ecosystem integrity and differentiate between plots at the local and global scale (Hansen et al., 2021). Here, we build on previous studies defining forest ecosystem integrity by using available EBVs to present and test a framework which assesses forest ecosystem integrity of plots at the global scale. Using readily available EBVs to assess and monitor ecosystem integrity will help scientists and policymakers to acquire comparable information more easily on the state of ecosystems. Ultimately, knowing where ecosystem integrity is high or low may also help land managers and conservationists prioritize areas of high importance.

2. Materials and methods

2.1. Measuring ecosystem integrity

To assess forest ecosystem integrity, we developed an Ecosystem Integrity Index score (EII_{score}) for forested plots based on the aggregation of spatially explicit EBVs representing structure, function, and composition, the three components defining ecological integrity. Our framework is consistent with previous definitions of ecosystem integrity, such as the one provided by Hansen et al. (2021). We focused on forested ecosystems across the globe (Hansen et al., 2013), as EBVs of forested ecosystems are the most readily available compared to other ecosystems.

The first component of ecosystem integrity, structure, is designed to capture aspects of ecosystems related to vegetation structure and spatial configuration, including fragmentation. The second component, function, captures the amount of specific ecosystem function variables such as energy flow and nutrient cycling. The third component captures ecosystem composition, which accounts for species abundance and community composition.

Here we used the following indicators to characterize the elements of ecosystem integrity: the Biodiversity Intactness Index (BII, Newbold et al., 2016) representing the element composition, Net Primary Productivity (NPP, Running and Zhao, 2019) describing the element function, and Loss in Forest Connectivity (LFC, Grantham et al., 2020) representing the element structure (Table 1). Each EBV was selected according the following criteria: ability to describe of the ecosystem integrity components, resolution, open access and publication date.

The BII is defined as the average richness- and area-weighted impact of a set of activities on the populations of a given group of organisms in a specific area (Scholes and Biggs, 2005; Newbold et al., 2016) based on the Projecting Responses of Ecological Diversity In Changing Terrestrial Systems (PREDICTS) database (Hudson et al., 2017) with the most recent update occurring in October 2021 (Phillips et al., 2021). Newbold et al. (2016) developed hierarchical mixed-effects models that considered four human-pressure variables, including land use, land-use intensity, human population density and

TABLE 1 Datasets used to calculate the EII_{score} with their respective resolution, a brief description of what the data entails and the reference.

Dataset	Spatial resolution	Details	Data link	Reference
Net Primary Production (NPP)	~500 m^2	MODIS MOD17A3HGF Version 6 product on annual Net Primary Production (NPP) at 500-meter (m) pixel resolution.	Google Earth Engine	Running and Zhao (2019)
Biodiversity Intactness Index (BII)	~1 km^2	Extent and spatial patterns of changes in local biodiversity based on modeled responses to land-use and related pressures.	Natural History Museum	Newbold et al. (2016)
Loss of Forest Connectivity (LFC)	300 m	Average connectivity of forest lost around a pixel.	Adapted from Grantham et al. (2020)	Grantham et al. (2020)
Human Modification Index (HMI)	~1 km^2	Cumulative measure of human modification of terrestrial lands based on modeling the physical extents of 13 anthropogenic stressors and their estimated impacts in 2016.	Google Earth Engine	Kennedy et al. (2019)
Global Forest Cover Change	~30 m	Global Landsat data characterizing forest extent, loss, and gain from 2000 to 2012.	Google Earth Engine	Hansen et al. (2013)
Plantations	Polygons	Global map of the world's planted forests and tree crops.	ArcGIS	Harris et al. (2019)

Rows highlighted in gray indicate datasets used to derive the EIIscore, while rows without highlighting indicate the datasets used to filter the plots used to validate the EIIscore.

distance to the nearest road to explain differences in local biodiversity among sites. Biodiversity is measured as sampled species richness and abundance based on the PREDICTS database. Further details are provided in Newbold et al. (2016). The resolution of the BII is 1 km^2.

NPP is a well-known representation of the net input of carbon to vegetation impacted inter-alia by climate (e.g., solar inputs, precipitation), soil quality, and nutrient status (Walker et al., 2021), with a well-known relationship to biomass production (Vicca et al., 2012) and carbon-use efficiency (DeLucia et al., 2007).

LFC represents the average connectivity of a forest around a pixel and was estimated following Grantham et al. (2020). The method compares currently observed forest extent with potential forest extent given human modification to the landscape to ensure that areas with naturally low connectivity are not penalized. The final estimate ranges from 0 to 1, so low values represent the least loss and high values represent the greatest loss.

As both NPP and LFC have different resolutions (1 km^2) from the BII, we used a bilinear method (Gorelick et al., 2017) to resample the pixel size of NPP and LFC to 1 km^2. This step was necessary to enable us to perform zonal statistics and derive the EII. Our EII has therefore a pixel size of 1 km^2.

The EII_{score} of any given forested land can be calculated using three EBVs, e.g., BII, NPP and LFC. First, (i) we calculate the global 90th percentile values for each of the three EBVs considering only the global intact forest area (Hansen et al., 2013) that has a Global Human Footprint Index value (Kennedy et al., 2019) of less than 0.4 and which is outside plantations mapped by Harris et al. (2019). Then, (ii) for each pixel, we calculate the relative value of each EBV by dividing the pixel value by the corresponding global 90th percentile value (Figure 1), with pixels with value above 90th percentile were given the value of 1. Subsequently, (iii) we calculate the EII value for each pixel in the study forest plots by taking the mean of the relative BII, NPP and LFC values. Note, using this methodology, EII values should only be calculated for forested areas where the BII, NPP and LFC values are known. Finally, (iv) the EII_{score} of the plot is found by taking the sum of all EII pixels in that given plot (Figure 1). Throughout this paper, we use two different notations: EII and EII_{score}. With EII, we refer to the index at the pixel level and with EII_{score} to the index at the plot level.

2.2. Extracting validation plots

To validate the EII_{score}, we first extracted 333 plots (polygons) of 5 km^2 through stratified sampling. We hypothesized that different forest conditions could affect ecosystem integrity (Potapov et al., 2011). The plots were selected in two categories; 166 plots were assigned the "Top" category with high-quality forests, and 167 lower-quality forests were assigned the "Down" category. The high-quality forest plots were selected so that they would contain forest cover classified with no forest conversion or degradation by Potapov et al. (2011), while lower-quality forest plots were selected to have forests classified by Potapov et al. (2011) that have not experienced loss and have at least 30% forest cover by Hansen et al. (2013), however, are classified as deforested or partially deforested by Potapov et al. (2011).

All plots were extracted outside of plantations (Harris et al., 2019), protected areas (UNEP-WCMC and IUCN, 2022) and islands (Sayre et al., 2019), were located below 1,000 m altitude (Sayre et al., 2019) and not located in Antarctica. Each plot was extracted by hand through Google Earth Engine, was automatically assessed for suitability and manually assessed through visual confirmation (Supplementary Figure 1). Suitability was acknowledged when more

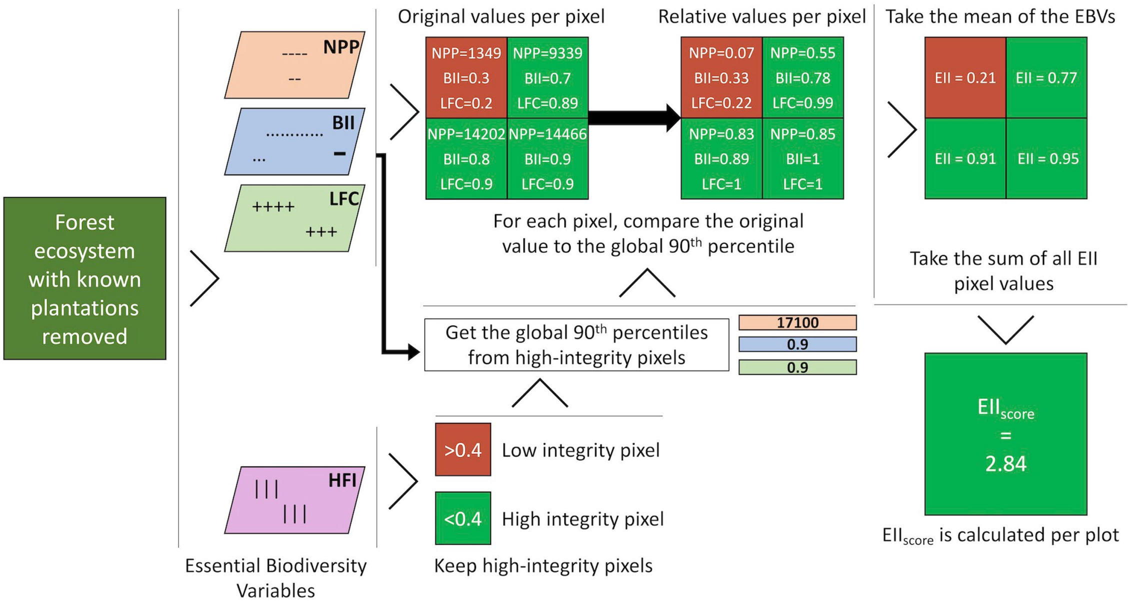

FIGURE 1
Visual representation of the workflow used to calculate the $\mathrm{EII}_{\mathrm{score}}$ for forested plots. NPP is the Net Primary Product, BII is the Biodiversity Intactness Index, LFC is the Loss of Forest Connectivity, and HFI is the Human Footprint Index. EII is the ecosystem integrity index. The EIIscore, NPP, BII, LFC, and HFI all have a pixel size of 1 km^2. Note values shown are for this example only and are not real values from the sampled lands in this study.

than 90% of the plot was covered with intact forest (Hansen et al., 2013).

For each of the plots, the mean biomass density according to Global Ecosystem Dynamics Investigation (GEDI) L4B product (Dubayah et al., 2022) and the mean canopy height (Potapov et al., 2021) were recorded to compare the relationship between the $\mathrm{EII}_{\mathrm{score}}$ and these variables.

2.3. Statistical analyses

Using the 333 plots mentioned above, we tested for significant differences between areas of high integrity ("Top") and low integrity ("Down"). After testing for normality of the data through a Shapiro–Wilk test and visual assessment of the Q-Q plots and histograms, we determined that the data were non-normally distributed, despite transformations and removal of outliers. Thus, we moved on with a nonparametric Kruskal Wallis test using R (package stats v4.1.1) to test if the response variable ($\mathrm{EII}_{\mathrm{score}}$) could be explained by the explanatory variable (Categories: 'Top', 'Down').

2.4. Sensitivity and validation analyses

We performed a sensitivity analysis to assess to what extent the results for the $\mathrm{EII}_{\mathrm{score}}$ are sensitive to the weight used to define the importance of the different indicators making up the EII. To assess the sensitivity of $\mathrm{EII}_{\mathrm{score}}$ to weight, we compared the degree of concordance between plot ranking estimated by the $\mathrm{EII}_{\mathrm{score}}$ considering BII, NPP and LFC having the same weight to the median plot ranking estimated by considering the following weight possibilities: BII has weight 0, BII has weight ½, LFC has weight 0, LFC has weight ½, NPP has weight 0, and NPP has weight ½. The benefit of the $\mathrm{EII}_{\mathrm{score}}$ is that it provides a single and simple measure that can be used to monitor progress and inform management planning without having to measure the full array of metrics related to forest integrity. Such benefit of an ecosystem integrity composite index and exercise of validation considering the correlation with other metrics has been previously used for other ecosystem integrity indices, such as the forest landscape integrity index (Duncanson et al., 2022). Here, we present an example of a validation exercise demonstrating how $\mathrm{EII}_{\mathrm{score}}$ is correlated with field measurements related to forest conditions, specifically canopy height and biomass. All these analyses were done considering each of our 333 plots.

Using a Kendall Tau correlation test (R package stats v4.1.1), we estimated if there was a significant correlation between our $\mathrm{EII}_{\mathrm{score}}$ and the validation datasets of biomass and canopy height. All data were tested for normality with a Shapiro–Wilk test (R package stats v4.1.1). A visual analysis of the residual distribution was done before moving on to a parametric or non-parametric test.

We also validated our EII against the forest landscape integrity index from Grantham et al. (2020), which is a well-validated index of forest modification, and therefore, forest integrity. We extracted the average values of our index (EII) and the average values of the forest landscape integrity index (FLII) from Grantham et al. (2020) by forested biomes. We extracted only values of both indices that overlapped with the map of intact forest landscapes (Potapov et al., 2017). With this analysis, we provide a better representation of our index across biomes. As our EII includes an indicator, the LFC, which is also included in the FLII, we performed a sensitivity analysis to prevent a potential similarity between EII and FLII due to the influence of LFC. We calculated global maps of the EII considering the absolute relative change for each indicator (BII, LFC, and NPP), highlighting which has the lowest deviation from the EII at every geographical point. This approach captures the magnitude of deviation without bias towards its direction. By analyzing the geographical distribution of these deviations, we can discern if a particular indicator consistently dominates or if the influence is balanced among all three.

3. Results

Model results from our plots ($n = 333$) revealed that the $\mathrm{EII}_{\mathrm{score}}$ strongly related to the categories of forest condition (Down: $n = 167$, Top: $n = 166$). Furthermore, the $\mathrm{EII}_{\mathrm{score}}$ was not sensitive to weight but was sensitive to plot size. Forest condition metrics, including biomass and canopy height, were correlated with the $\mathrm{EII}_{\mathrm{score}}$. Forests with high ecosystem integrity are located particularly in the Boreal forests and in the tropical rain forests in South America, Africa and Asia (Figure 2).

3.1. Assessment of ecosystem integrity index

Our results showed a significant difference between $\mathrm{EII}_{\mathrm{score}}$ in the forest condition categories 'Top' and 'Down' ($\chi 2 = 19.193$, $df = 1$, $p < 0.001$). We found that Top category has significantly higher values of the $\mathrm{EII}_{\mathrm{score}}$, with a mean of 5.88 (CI: 5.53–6.23), whereas the Down category has a mean of 4.97 (CI: 4.67–5.26) (Figure 3).

3.2. Assessment of sensitivity and validation

We used the Kendall concordance coefficient to verify if the median rank of all plots across the six different weight possibilities (y-axis in Figures 4A,B) changed, considering the situation where all indicators have the same weight ($\mathrm{EII}_{\mathrm{score}}$ reference weight x-axis in Figures 4A,B). Considering Top category, we did not find a significant change in the rank of the plots when using different weights for the indicators (Kendall coefficient = 0.93, P ~ 0). Similarly, we did not find a significant change in the rank of the plots when using different weights for the indicators considering the Down category (Kendall coefficient = 0.92, P ~ 0) (Figure 4).

Metrics related to field measurements of forest conditions, like biomass and canopy height, can be described by the $\mathrm{EII}_{\mathrm{score}}$ in the 333 plots. The positive term of biomass ($z = 2.859$, $p = 0.004$) and the Kendall concordance coefficient ($\tau = 0.194$) illustrate the weak but significant correlation with the $\mathrm{EII}_{\mathrm{score}}$ (Figure 5A). Confidence intervals around the trend are smaller in areas with lower biomass; thus, the $\mathrm{EII}_{\mathrm{score}}$ is more likely to give accurate results in areas with biomass up to 200 $\mathrm{Mg\,ha^{-1}}$. Canopy height, like biomass, was positively correlated ($z = 3.610$, $p < 0.001$) with the $\mathrm{EII}_{\mathrm{score}}$ in the plots and the Kendall concordance coefficient ($\tau = 0.245$) showed a weak correlation, too (Figure 5B). The confidence intervals around the trend for the $\mathrm{EII}_{\mathrm{score}}$ compared to canopy height are relatively small, particularly between the 10–20 m height range.

We found a strong agreement between the average values of our EII across forested biomes with the FLII (Figure 6). Our results also confirmed that the concordance between the EII and the LFII is not driven by any single indicator (Supplementary Figure S4).

3.3. Uncertainty

The individual components of the $\mathrm{EII}_{\mathrm{score}}$ (i.e., BII, NPP, and LFC) all contain inherent uncertainty and variability derived from measurement errors associated with spatial and temporal scales across datasets. In addition, each of the underlying components were developed for other purposes. Thus, qualitative uncertainty is also associated with combining and applying these individual components in different contexts and answering different questions. Underlying uncertainties associated with each individual component apply equally to the $\mathrm{EII}_{\mathrm{score}}$.

The 333 plots were assessed for differences between the "Top" and "Down" classifications. A significant difference between the two categories was apparent but came with inherent uncertainty. Confidence intervals for the $\mathrm{EII}_{\mathrm{score}}$, which were developed graphically using the R package ggplot2 (v. 3.3.6), represent the confidence that the total sum of $\mathrm{EII}_{\mathrm{score}}$ values of all the pixels in a "Top" or "Down" category land falls within a certain range. The results showed us that

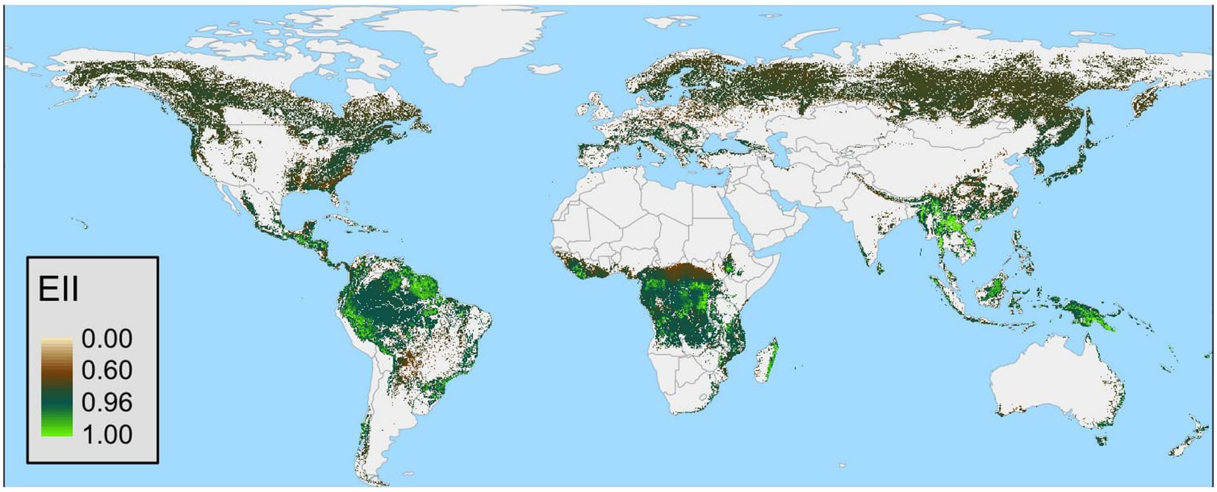

FIGURE 2
Global map of the ecosystem integrity index. The map is not in the original resolution of $1\mathrm{km}^2$ for representation proposal.

there was a 95 percent chance that our output was correct and that the $\text{EII}_{\text{score}}$ was significantly different in the "Top" category compared to the "Down" category. Despite this certainty, the underlying variables increased the uncertainty of our results.

The primary uncertainty associated with the BII is that the species population sampling is not comprehensive. In practical terms, species may or may not be observed at any given sampling location for reasons other than that they were not actually present. Related to species absence/presence is species misidentification. Another uncertainty is that the data in the PREDICTS database (Hudson et al., 2017) are for individual species and, by definition, do not address the impacts of human activities on species interactions or the importance of trophic relationships. Finally, these data are designed to be used in localized contexts, while the $\text{EII}_{\text{score}}$ is used to make global-level inferences.

The loss in forest connectivity is calculated as the ratio between the current forest configuration around each pixel to the potential forest configuration (Grantham et al., 2020). As the current forest configuration is represented by the forest cover maps from Hansen et al. (2013), likely, uncertainties associated with the estimation of forest cover maps (e.g., cloud cover, edge effects, changing land use at differing spatial and temporal scales) are introduced when estimating the loss in forest connectivity.

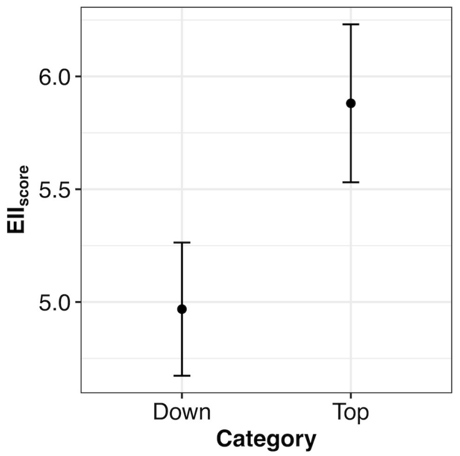

FIGURE 3
Mean (± 95% confidence intervals) of the $\text{EII}_{\text{score}}$ for the 227 plots by forest condition category type (levels: Down, Top). A lower $\text{EII}_{\text{score}}$ indicates that the structure, function, and composition were lower, whereas a higher $\text{EII}_{\text{score}}$ means those predictors were higher. Confidence intervals are of similar size. EII is the ecosystem integrity index.

4. Discussion

The $\text{EII}_{\text{score}}$ provides an indication of how forest ecosystems across the world perform, considering ecological integrity. Our index is built on the efforts to operationalize the concept of ecosystem integrity across scales using satellite-based EOs and essential EBVs (Hansen et al., 2021). However, our approach differs from previous studies as we not only produced a global map of $\text{EII}_{\text{score}}$, but we also developed a scalable workflow that estimates $\text{EII}_{\text{score}}$ at local scales but can easily be applied at larger scales. Our index showed an important property: it is insensitive to the weight used for the indicators of ecosystem integrity (structure, function, and composition). Overall, our results suggest that our index provides a reliable picture of the plots' performance that is not driven by the importance (weight) assigned to the $\text{EII}_{\text{score}}$ indicators. However, it can be used to identify the importance of area-based conservation efforts. Both characteristics are important in the context of ongoing efforts to support the monitoring and reporting of progress within the Post-2020 Global Biodiversity Framework.

The $\text{EII}_{\text{score}}$ differentiated pristine from degraded forests globally, indicating that the combination of EBVs used in this study can capture

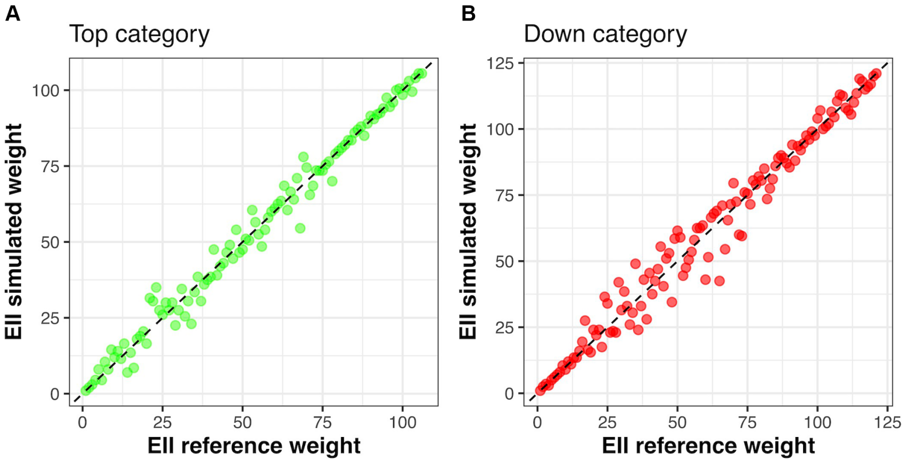

FIGURE 4
The relationship among the median rank of each plot with a given category compared to the reference estimation of $\text{EII}_{\text{score}}$ where the three indicators have the same value. **(A)** shows the relationship considering plots within the category top and **(B)** plots within the category down. Note that most points in both figures align with a 1:1 dashed line, which indicates that plots did not change their original rank ($\text{EII}_{\text{score}}$ reference weight – all indicators have the same weight) in relation to the median across a plot rank considering six possibilities of weights ($\text{EII}_{\text{score}}$ simulated rank) as explained in the text. EII is the ecosystem integrity index.

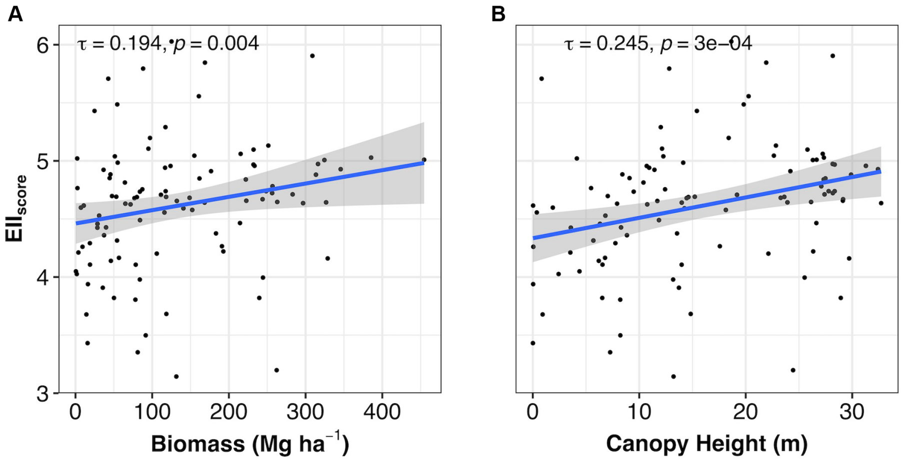

FIGURE 5
Relationship of the EII_{score} with **(A)** biomass and **(B)** canopy height for the 227 plots. The raw values (as jitter) and the effects with their respective confidence intervals (95%) are shown. Additionally, the Kendall Tau coefficient and the respective value of *p* are given. A lower EII_{score} indicates the structure, function and composition were lower, whereas a higher EII_{score} means those predictors were higher. EII is the ecosystem integrity index.

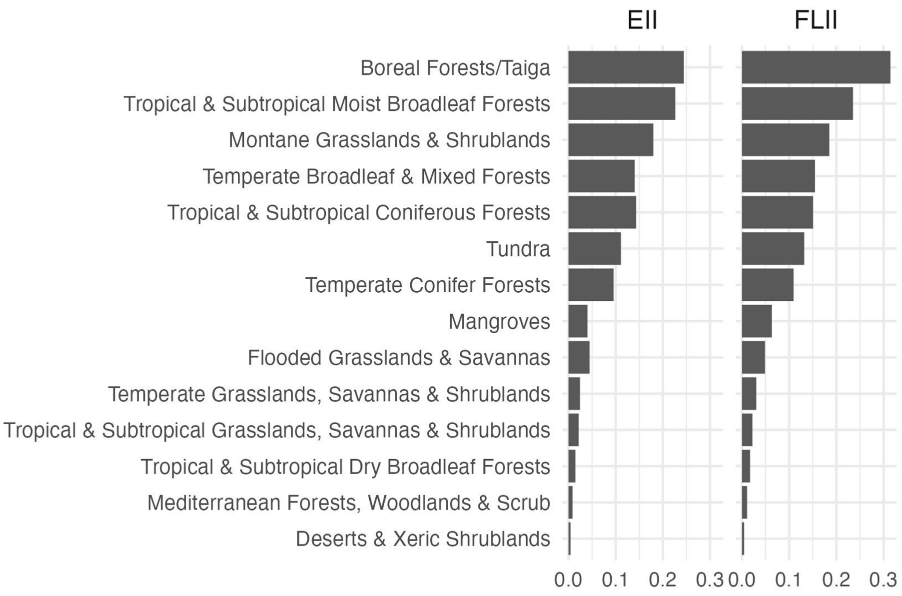

FIGURE 6
Average values of the ecosystem integrity index (EII) and the forest landscape integrity index (FLII) from Grantham et al. (2020). Note that the average values per biome are almost the same for both indices.

different aspects of ecosystem integrity. Previous studies have emphasized the need to reconnect forested habitats to protect threatened species (e.g., Newmark et al., 2017) and thus highlight the need for an index that can measure and monitor multiple interdependent ecosystem characteristics. This study focused on differences in ecosystem integrity among plots on the global scale. Based on such an assessment, policymakers and institutions facilitating monetary incentives to conserve forested lands can make key policy decisions related to the conservation of ecosystems. However, we recognize that measuring the EII_{score} at other scales (e.g., global, biome, political region, ecoregion) is fundamental to halting forest integrity reduction (Keenan et al., 2015). For example, local forest management strategies will need to calculate the EII_{score} over much smaller scales to facilitate comparisons across forests with similar characteristics. Our EII_{score} has a resolution of 1 km^2, which is why we recommend using the EII_{score} only over large, forested areas to increase the variety of pixels. Additionally, this coarse resolution has resulted in some regions being assigned forest pixels even though no forest exists. This results from edge effects, which occur on the edges of plots. Edge effects are a result of pixels being square and the size of their resolution. Pixels can not be split or cut off, so sometimes the edge of a pixel falls inside or outside a plot of interest. In this example, some areas have forests, but on the edge of the forests, there is some overlap of forest pixels into areas without forests. When more detailed

EBVs regarding biodiversity become available, we will be able to improve the quality of the resolution and thus reduce the edge effects.

Weights may have an impact on the value of a composite index, as weighting is strongly related to how the information conveyed by the different dimensions is aggregated into a composite index. Here we used only one indicator to represent each of the components of ecosystem integrity and considered our main underlying objective that each indicator has the same importance to ecosystem integrity. Indeed, we did not find a significant difference between the median $\text{EII}_{\text{score}}$ using equal weight compared to the six possibilities of assigning different weights to the $\text{EII}_{\text{score}}$ indicators. It is likely that we could have found a different result if we had used more indicators that are interrelated or if we had used more possibilities of weight distribution among the indicators than the six we used here. Note that when one indicator has weight 0, the other two indicators have weight ½, and when one indicator has weight ½, the other two indicators have weight ¼. Additionally, we tested for linearity of the $\text{EII}_{\text{score}}$ with plot size (Supplementary Methods). Finally, we acknowledge that the $\text{EII}_{\text{score}}$ may correlate with a broad range of metrics related to forest integrity and anthropogenic pressures. Examples of these metrics include measures related to forest condition (e.g., canopy height, biomass, structural complexity), forest ecosystem state (e.g., species diversity and abundance), and the intensity of anthropogenic pressures (e.g., land conversion). However, independently of the method used to assign a weight, weighting implies a 'subjective' evaluation. Like the choice for weight, we also chose to sum the pixel values to get a plot's $\text{EII}_{\text{score}}$. As expected, we thus also found a linear relationship between the $\text{EII}_{\text{score}}$ and plot size (Supplementary Figure 2). Therefore, we encourage future studies to use other indicators to assess ecosystem integrity and use different weighting distributions among those indicators. This will improve our knowledge about casual relationships among ecosystem integrity indicators and their application in different contexts.

We found that the $\text{EII}_{\text{score}}$ was consistent with positive forest condition trends, including biomass and canopy height. This result thus supports the idea that our $\text{EII}_{\text{score}}$ can distinguish between a healthy, thriving forest and a degraded forest (Shapiro et al., 2021). Forest degradation is often a product of human modification through, for example, land-use change, leading to forest fragmentation and resulting in reduced functioning with biodiversity loss and decreased ecosystem services (Potapov et al., 2012; Chaplin-Kramer et al., 2015; Haddad et al., 2015; Betts et al., 2019). Monitoring forests using EOs will help scientists and policymakers to identify degradation patterns and act upon them to halt or even reverse the trend. Although the results are consistent, the confidence intervals in plots with high biomass are still large making the $\text{EII}_{\text{score}}$ less trustworthy in such areas. The high variation may be because the indicators we chose are not necessarily the best ones to capture this specific dimension of the ecosystem. Previous literature has found that old-growth forests could generate relatively lower values of NPP (Wang et al., 2011), while these forests have been used as indicators of high ecological integrity (DellaSala et al., 2022). Biomass, like NPP, is related to forest age (Wang et al., 2011), so this could have influenced our results.

As originally calculated (Scholes and Biggs, 2005) for one specific region (Africa), the BII provided confidence intervals consistently within 10% of the reported best estimate. Subsequently, Hui et al. (2008) conducted a more detailed analysis to disaggregate the uncertainty across taxonomic groups and biomes and found similar overall uncertainty but were able to identify mammals as the taxonomic group with the highest uncertainty as well as degraded areas and savannas.

Globally, large climatic and water availability gradients result in two orders of magnitude variation in field-measured NPP for any vegetation type on an annual scale (Running et al., 2004; Running and Zhao, 2019). Interannual variability in vegetation response to precipitation and temperature variation is estimated at 20–30% (Running et al., 2004). Validation studies show that MODIS data can largely duplicate field observations and capture observed variability in field data. Unquantifiable sources of error in MODIS data include the effects of poor weather station coverage (Zhao et al., 2006), extreme weather events, and cloud contamination, which has been estimated to differ across ecoregions.

A future next step in the development of the approach presented here is to include optimization algorithms to classify areas of high integrity within ecoregions. Our approach was based on the overlap across different global layers and EBVs to extract averaged values per pixel. Using optimization algorithms would make it possible to directly maximize the search for high-integrity pixels and simultaneously other ecosystem services or species richness. Further work should consider how businesses can use the $\text{EII}_{\text{score}}$ to account for the risks and impacts of their operations on biodiversity and ecosystem services. These may include assessing the risks across a business portfolio, considering the implementation of certain projects, or producing a business counterfactual for $\text{EII}_{\text{score}}$ so that the company can compare its nature and biodiversity impact against a standard baseline. From conservation and management perspectives, the $\text{EII}_{\text{score}}$ can be a valuable metric to assess how different project interventions can deliver the best results considering nature conservation and social benefits for the local populations directly related to those projects.

Finally, in our study, we have used EBVs which have global coverage, but it is important to consider that there are still global biases in the availability of EBVs (Peterson and Soberón, 2018). Therefore, it is important that future studies using EBVs to account for ecosystem integrity consider carefully spatial and temporal resolutions of EBVs in order to continue improving their use to support efforts to monitor nature state such as the recently agreed Kuming-Montreal Global Biodiversity Framework. This also brings the opportunity for collaboration among countries and initiatives such as the GEOBON (The Group on Earth Observations Biodiversity Observatory Network) and fosters data availability and training capacity necessary at the global scale.

5. Conclusion

This study relied on integrating global EBVs to develop and test a framework to assess and monitor forest ecosystem integrity and health from local to global scales. Data availability, scalability, and functionality will be essential in the new Post-2020 Global Biodiversity Framework context. Therefore, the proposed methodology and EII are easily implementable and can be applied across multiple scales. The EIIscore can be used as a valuable metric for countries and businesses to quantify the impact of their actions on biodiversity and forest health monitoring. Still, further research is needed to improve methodology limitations and understand underlying dataset uncertainties. We expect that our study adds to the ongoing efforts to provide a solid ground for decision-making questions impacting the climate and biodiversity in the context of the recently agreed Kunming-Montreal Global Biodiversity Framework.

Data availability statement

Publicly available datasets were analyzed in this study. The data and the code used in this study can be found at: https://github.com/single-earth/ecosystem-integrity-index.

Author contributions

AD and KV designed the study, analyzed the data, and wrote the article. KM produced the dataset and contributed to the writing of the article. M-LB, LB, KG, DK, ML, and KV contributed to the writing of the article.

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Conflict of interest

Publisher's note

Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2023.1098901/full#supplementary-material

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Site-specific additionality in aboveground carbon sequestration in set-aside forests in Flanders (northern Belgium)

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Introduction: *In situ* carbon sequestration in forests is important in the context of climate change mitigation, and setting aside managed forests has been proposed as an option for increased carbon sequestration. Comparing set-aside and managed forests may provide insights and rules of thumb on the potential for additional *in situ* carbon sequestration in set-aside forest.

Methods: In an observational study, we compared re-inventory data from the network of set-aside forest reserves in Flanders, which have been unmanaged for 17–66 years (2 surveys with a 10 years interval), with re-inventory data from the regional forest inventory, representing the overall forest area in Flanders (2 surveys with a 15 years interval).

Results: The aboveground carbon pools and sequestration rates were higher in the set-aside forests compared to the average forest in Flanders. In the average Flemish forest, the aboveground carbon pool increased from 64.7 to 85.1 tC ha^{-1}, over a period of 15years. In the set-aside forests, the mean pool was higher at the first measurement and further increased from 84.8 to 102.4 tC ha^{-1}, over a period of 10years. The mean aboveground annual carbon sequestration rate was 1.3 tC ha^{-1} year^{-1} in the average forest in Flanders and 1.8 tC ha^{-1} year^{-1} in the set-aside forests. The stocks and fluxes depended on the soil conditions and were higher in set-aside forests on silt and sandy silt sites compared to wet and sand sites. The set-aside forests on dry sites showed additionality in *in situ* aboveground carbon sequestration. We saw no indication of approaching a culmination point in the first decades following set-aside: plots with high carbon pools did not show lower carbon sequestration. In conclusion, set-aside forests can combine high carbon pools with high sequestration rates on suitable sites. Under the current management policy, we expect Flemish forests—regular and set-aside—to further increase their carbon pools in the coming decades.

KEYWORDS

carbon storage, aboveground biomass, dead wood, forest inventory, forest reserve

1 Introduction

The Fit for 55 package of the European Union set ambitious net carbon removal targets in the land use, land use change and forestry (LULUCF) sector, i.e., minimum 310 Mt. CO_2 equivalent by 2030. The European Union primarily relies on its forests to reach this target. Forests represent important carbon stocks (Luyssaert et al., 2008), providing carbon sequestration *in situ*, both above- and belowground (Pregitzer and Euskirchen, 2004). As such, forests can be used as carbon offsets to reach carbon neutrality, and carbon sequestration has become an important forest management objective. However, the impact of forest management and the potential of forests as carbon sinks is not yet fully understood (Hoover et al., 2012; Ameray et al., 2021), and carbon stocks and sequestration do differ between forest types and regions (Hoover and Smith, 2021; Matuszkiewicz et al., 2021).

In their concept of proforestation, Moomaw et al. (2019) advocated setting aside existing forests to further develop as unmanaged ecosystems as a low-cost approach with immediate effect to increase sequestration of atmospheric carbon. Yet, the role of set-aside forests in carbon removal is debated. The capacity for carbon sequestration in biomass, combining storage *in situ* and *ex situ*, has been argued to be higher under intensive forest management, in the short term (Ameray et al., 2021), and old unmanaged forests have long been considered carbon neutral, containing a large carbon stock but providing little or no significant carbon sink (Seedre et al., 2015; Nord-Larsen et al., 2019; Meyer et al., 2021). However, carbon stocks have been found to increase with forest stand age in all biomes (Pregitzer and Euskirchen, 2004), and even unmanaged primary forests have been demonstrated to still steadily accumulate carbon for centuries (Luyssaert et al., 2008). In the debate on the role of managed vs. unmanaged forests in climate change mitigation, a forest's potential to accumulate or sequester carbon and its capacity to store carbon in carbon stocks are complementary and should be assessed separately. Aboveground carbon stocks in unmanaged compared to managed forest stands have been found to be either larger (Mund, 2004; Nunery and Keeton, 2010; Burton et al., 2013; Keith et al., 2014; Ford and Keeton, 2017; Glatthorn et al., 2018; Matuszkiewicz et al., 2021) or similar (Mund, 2004; Ford and Keeton, 2017; Schaedel et al., 2017; Glatthorn et al., 2018; Bouriaud et al., 2019), depending on the silvicultural management studied. Ameray et al. (2021), in their review of forest carbon management, found extensive forest management to be an intermediate compromise between the high short-term carbon sequestration of intensive forest management and the greater carbon stocks in conservation forests.

In regions with a long history of intensive forest management and no remaining primary forests (e.g., north-western or central Europe), the aboveground carbon stock in forests is expected to be distinctively lower than the natural ecosystem carbon carrying capacity (Keith et al., 2009; Moomaw et al., 2019; Nagel et al., 2023). Forests in these regions thus represent a high potential for carbon storage. Carbon sequestration will only slow down, with the carbon stocks reaching a dynamic steady state (Bormann and Likens, 1994), when the carrying capacity is approached (Nord-Larsen et al., 2019; Stillhard et al., 2022). In the absence of primary forest reference sites, however, we have no clear indication of the forests' ecosystem carbon carrying capacity. Forests set aside from active management may gradually provide an estimate of the carbon sink potential of forests at specific site conditions (Hoover et al., 2012; Meyer et al., 2021; Nagel et al., 2023).

The comparison of carbon stocks and fluxes in managed vs. set-aside forests is relevant in the context of carbon removal certification regulations. A carbon removal project may be eligible for certification if the carbon stocks and sequestration rates are significantly higher than the baseline value of business as usual, i.e., if the project provides "additionality" in carbon removal. In this observational study, we focused on Flanders (northern Belgium), an area heavily altered by human activity with no remaining primary forest and in which forests are currently extensively managed after a long history of intensive harvesting. We aimed to establish whether the set-aside forests in Flanders provide additional *in situ* aboveground carbon sequestration compared to the average Flemish forest. For this purpose, we quantified mean aboveground carbon stocks and carbon stock change rates for a number of set-aside forests and the overall forest in Flanders. To take into account the local site conditions that determine forest productivity and dynamics, we distinguished five site types. The site-specific comparison of carbon stocks will provide guideline values for the carbon sink potential of forests in Flanders.

2 Materials and methods

Flanders is a densely populated lowland area with a mild Atlantic climate: mean annual temperature 9°C–11°C, mean annual precipitation 600–900 mm. Forests cover approximately 140,000 ha of Flanders, i.e., 10% of the total area, spanning a range in forest and soil types from nutrient poor oak-pine forests on sandy soils to ash-alder forests on moist loamy soils. Only 16% of the forest is considered ancient woodland, and more than 50% of the forest is the result of reafforestations from the 20th century (De Keersmaeker et al., 2015). All forests have been intensively managed in the past, mainly for wood production. As recreation and nature conservation have become more prominent forest functions, forest management and harvests have become more extensive over the past decades (Vandekerkhove, 2013). The current wood harvest ratio is relatively low. In forests managed by the Flemish government, for instance, about 30% of the annual increment is harvested (Govaere and Leyman, 2020). Since 1995, specific forest areas have been legally protected and officially set aside in a network of strict, i.e., non-intervention forest reserves, covering the different forest types present in Flanders. In this study, we compare aboveground carbon stocks and carbon stock change rates of set-aside forests with the average Flemish forest, which represents managed stands as well as some unmanaged forests, based on data from the monitoring program of the forest reserves and the regional forest inventory.

2.1 Inventory data

The regional forest inventory of Flanders is based on a systematic sampling on a geo-referenced grid of 1 km × 0.5 km, with nested circular inventory plots on the grid intersections that are located in forest. The first inventory (further called NFI1) was performed in a short measuring campaign in 1997–1999. The second inventory (NFI2), in 2009–2018, was a continuous monitoring with 10% of the grid intersections visited per year. NFI1 consisted of 2,423 plots, NFI2 of 2,479 plots. During NFI1, the position of the plot center was determined using descriptive maps and marked underground in the field. As no accurate GPS was used during NFI1, location of the plots during NFI2 was challenging and retracing a plot center strongly relied on the position of remaining large trees in the plot. Only 841 of the original plots could be paired in NFI2, and the paired plots are biased towards older stands with large trees. In order to represent the average Flemish forest, we used the full datasets of NFI1 and NFI2, i.e., including both paired and unpaired plots. The strict forest reserves in Flanders are monitored using circular nested plots similar to the NFI, but located on a tight systematic grid of 50 m × 50 m within the forest reserve, with plots on alternately selected grid intersections. In forests that are hard to access, e.g., swamp forests, only a core area is monitored. For this study, we used circular plot data from 11 strict forest reserves ($n = 607$ circular plots) and core area data from two waterlogged forest reserves ($n = 3$ core areas), which had been monitored two times with a mean monitoring interval of 10 years in the period 2000–2017. At the time of the first monitoring, the forests had been left unmanaged for 7–56 years (see Supplementary Table S1). Dendrometric data on standing live trees and standing and lying dead wood are collected in a similar way in the forest inventory and in the forest reserves (see Supplementary Table S2 for details).

To account for the impact of different site conditions, we applied the typology of the Potential Natural Vegetation map of Flanders of De Keersmaeker et al. (2013), which is a site classification based on the Belgian soil map that recognizes seven Potential Natural Vegetation site types for forests in Flanders. We assigned a site type to each plot of the forest inventory and forest reserve datasets. The five site types used in this study are waterlogged soils, wet alluvial soils, moist and dry silt or sandy silt soils, and sand soils (see Supplementary Table S3 for details). The two other site types of De Keersmaeker et al. (2013), i.e., spring and outer dike habitats, have a limited share in the forest area of Flanders and any plots on these site types were included in the site type “waterlogged soil” in our study. In a region with a long history of forest management, such as Flanders, the actual tree species composition may differ quite considerably from the potential natural vegetation at a site. The mean tree species composition of the forests on each site type in the forest inventory and forest reserve datasets is shown in Supplementary Table S4. We did not consider the effect of stand age in our study, although relevant for carbon stocks (cf. Pregitzer and Euskirchen, 2004), as no data on stand age is included in the NFI and several set-aside and NFI forest stands are multi-aged.

2.2 Carbon stocks

First, we determined the aboveground carbon stock in living tree biomass for each plot following the method described in the national forestry accounting plan of Belgium (Perin et al., 2019):

$$C_{stock\_LT} = \sum_{plot} \left(V_{stem} \times VEF + V_{stump} \right) \times WD \times CF$$

with $C_{\text{stock\_LT}}$ the total aboveground carbon stock of the living trees in a plot in tC ha^{-1}; V_{stem} the volume of the merchantable stem of a tree, i.e., the part of the stem with diameter >7 cm, in m^3 ha^{-1}; VEF a species-specific volume expansion factor to expand merchantable volume to total aboveground tree volume; V_{stump} the volume of the bottom part of the stem, which is not included in the merchantable timber, in m^3 ha^{-1}; WD a species-specific wood density value (t m^{-3}); and CF the carbon fraction of dry matter in tC per t dry biomass. We calculated the merchantable stem volume—V_{stem}—for each tree based on its diameter and height using species-specific two-entry tariffs (see Supplementary Table S2) and used volume expansion factors—VEF—modeled as a function of diameter, height and species according to Longuetaud et al. (2013). We calculated the stump volume—V_{stump}—as a cylinder with height 10 cm and radius derived from the tree's diameter and height using taper functions of Dagnelie et al. (2013). We used the species-specific wood density values—WD—from the national forestry accounting plan of Belgium (Perin et al., 2019; Supplementary Table S5) and the default carbon fraction—CF—of 0.5 as in Penman et al. (2003). As we focus on aboveground carbon stocks only, we did not use a root-to-shoot ratio (i.e., factor R in Eq. 3.2.3 of the IPCC Good Practice Guidance for LULUCF; Penman et al., 2003) to derive the belowground volume of living trees from the aboveground volumes.

Then, we calculated the aboveground dead wood carbon stock for each plot as the sum of the carbon stocks of standing dead trees, snags and logs:

$$C_{stock\_DW} = \sum_{plot} \left(V_{trees} + V_{snags} + V_{logs} \right) \times CC$$

with C_{stock_WD} the total aboveground carbon stock of dead wood in a plot in tC ha^{-1}; V_{trees} the volume of the standing dead trees in the plot in m^3 ha^{-1}; V_{snags} the volume of the snags in m^3 ha^{-1}; V_{logs} the volume of the lying dead wood in m^3 ha^{-1}; and CC the carbon content in tC m^{-3}. The volumes of the different dead wood categories—V_{trees}, V_{snags}, V_{logs}—were calculated slightly differently, depending on the available dead wood data for the two forest inventories and the forest reserves (for details see Supplementary Table S2). We multiplied the total aboveground volume of dead wood in each plot with a site-specific factor of carbon content per wood volume—CC, based on the main tree species composition per site type and species-specific dead wood density and carbon content values for mid-stage decayed wood from Stakėnas et al. (2020) and Přívětivý and Šamonil (2021) (see Supplementary Tables S6, S7).

Thereafter, to assess the total aboveground carbon stock in each plot, we summed the plot-level aboveground carbon stocks of living trees and dead wood. We then calculated the mean of the plot-level total aboveground carbon stocks for each site type and for each inventory. We used the 95% confidence intervals of these means to evaluate whether the mean carbon stock significantly differed between the set-aside and average forests, i.e., using the dataset of the forest reserves and the dataset of the NFI, and between the five site types, i.e., comparing the different site types within each of the two datasets. We considered the mean carbon stock to differ significantly between two groups, i.e., between the two forest types or between two of the site types, when the confidence intervals of the two means under consideration did not overlap.

Finally, to determine an aboveground carbon stock representative for either the average or the set-aside forests in Flanders, we calculated the overall mean carbon stocks of NFI1 and NFI2, which represent a systematic sampling across Flanders, and weighted mean carbon stocks for the first and second forest reserve monitoring, weighting the plot-level carbon stocks of each site type by the site type's relative share in the forest area of Flanders, i.e., the number of plots of each site type in the regional forest inventory, using the functions *weighted.mean* from the *stats* library and *wtd*.var. from the *Hmisc* library. We inspected the 95% confidence intervals of the means and considered the mean carbon stocks to differ significantly between the set-aside forests and the average Flemish forest when the confidence intervals of the means did not overlap.

2.3 Carbon stock change rates

We calculated the annual change in aboveground carbon stock as the difference between the stock at the second and first inventory or monitoring, divided by the time interval between both:

$$C_{stockchangerate} = \frac{C_{stock_{t2}} - C_{stock_{t1}}}{t2 - t1}$$

For the forest inventory data, which contain both paired and unpaired plots in the two inventories, we assessed carbon stock change rate at the site type level, using the mean stock at the first and second inventory for each site type and the mean time interval of 15 years between both inventories. For the permanent plots of the forest reserve monitoring, we first calculated carbon stock change rate at plot level, using the plot-level carbon stock of each survey and the reserve-specific time interval between the two monitoring campaigns, and then calculated the mean carbon stock change rate for each of the five site types using the plot-level stock change rates. We used the 95% confidence intervals of the means to evaluate whether the mean annual carbon stock change rates significantly differed between site types and between set-aside forests and the average forest in Flanders. For the forest inventory data, we derived the confidence intervals based on the approach of Derrick et al. (2017) for comparing samples that contain both paired and independent observations.

Similar to the carbon stocks, we determined a carbon stock change rate of an average or set-aside forest representative for the whole of Flanders. For the forest inventory data, we calculated the overall stock change rate as the difference between the mean stocks of the entire first and second inventory divided by the mean time interval of 15 years between both inventories. For the forest reserves data, we weighted the plot-level carbon stock change rates of each site type by the site type's relative share in the forest area of Flanders, i.e., the number of plots of each site type in the regional forest inventory. We used the 95% confidence intervals of the overall carbon stock change rates to evaluate whether the mean annual carbon stock change rate significantly differed between the set-aside forests and the average Flemish forest.

To check whether the set-aside forests were approaching their ecosystem carbon carrying capacity, we plotted the annual carbon stock change rate in relation to the stock at the first survey. All calculations were done in R version 4.2.1 (R Core Team, 2022); graphs were made with ggplot2 (Wickham, 2016).

3 Results

Our calculations showed that the aboveground carbon stocks—for living trees, dead wood and the total aboveground biomass—increased between the first and second survey, differed between the average Flemish forest and the set-aside forests, and varied among the five site types (Figure 1 and Table 1; more details in Supplementary Tables S8, S9). The annual carbon stock change rates also differed between regular and set-aside forests and among the site types (Figure 2 and Table 1; details in Supplementary Tables S8, S9).

3.1 Carbon stocks

3.1.1 Set-aside vs. average forests

Overall, the aboveground carbon stocks were significantly higher in the set-aside forests than in the average forest in Flanders (see the asterisks in Figure 1 and Table 1). The mean total aboveground carbon stock significantly increased from 64.7 to 85.1 tC ha^{-1} over a 15 years period for the average Flemish forest, and from 84.8 to 102.4 tC ha^{-1} over a 10 years period in the set-aside forests. The carbon stock in living tree biomass significantly increased from 62.2 to 81.4 tC ha^{-1} for the average Flemish forest, and from 80.2 to 95.8 tC ha^{-1} in set-aside forests; the carbon stock in dead wood significantly increased from 2.0 to 3.7 tC ha^{-1} for the average Flemish forest and from 4.6 to 6.6 tC ha^{-1} in the set-aside forests.

3.1.2 Site type effect

The carbon stocks significantly differed among the site types in both the average Flemish forest and the set-aside forests, except for dead wood at the first inventory (see the grey italic letters in Table 1). The total aboveground carbon stock and the aboveground carbon stock in living trees were highest on the silt soils, followed by the sandy silt soils, and then the sand, wet alluvial and waterlogged sites. The aboveground carbon stock in dead wood was highest on wet alluvial sites and lowest on sand sites, for both the average Flemish forests and the set-aside forests at the second inventory. For the set-aside forests at the second inventory, dead wood carbon stocks were also significantly higher on sandy silt soils than on waterlogged and silt soils. The total aboveground carbon stock significantly increased between inventories in all site types except the waterlogged sites, in both the set-aside forests and the average Flemish forest (Figure 1; see the arrows in Table 1). The carbon stock in living trees significantly increased on the dry sites for both the set-aside and average forests and on the wet sites for the average Flemish forests only. The dead wood carbon stocks showed a different pattern for the set-aside and average forests, with significant increases over time on silt sites for the set-aside forest and on wet alluvial, sandy silt and sand sites for the average forest.

3.1.3 Set-aside vs. average forests within site types

The total aboveground carbon stocks were significantly higher in the set-aside forests than in the average forests on all site types and for both inventories (asterisks in Figure 1 and Table 1). The carbon stocks in living trees were higher in set-aside forests on all site types except on the wet alluvial sites at the second inventory, and the carbon stocks in dead wood were significantly higher in set-aside forests on wet alluvial, sandy silt and sand sites (asterisks in Table 1).

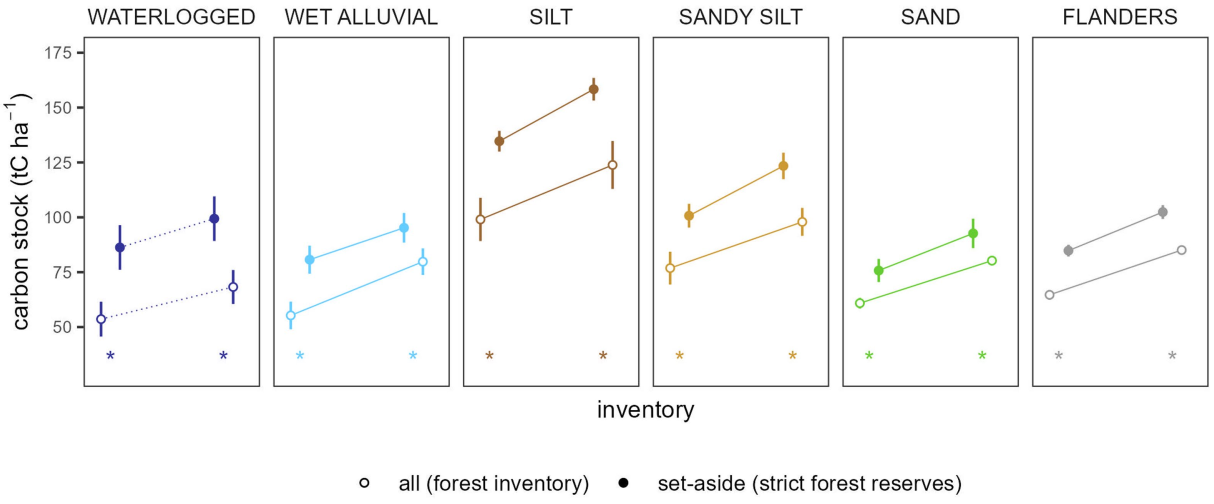

FIGURE 1
The aboveground carbon stocks (tC ha^{-1}) at the first and second inventory in the average Flemish forest and the set-aside forests, for each of the five site types and for the whole of Flanders (mean and 95% confidence interval). The mean interval between the first and second inventory was 15 years for the regional forest inventories and 10 years for the forest reserves. Solid lines indicate a significant increase over time; asterisks indicate a significant difference between the average and set-aside forests per inventory. See Supplementary Table S3 for more details on the site types.

3.2 Carbon stock change rates

3.2.1 Set-aside vs. average forests

The overall stock change rates were significantly higher in the set-aside forests than in the average Flemish forest (asterisks in Figure 2 and Table 1). The mean annual change rate of total aboveground carbon in Flanders was 1.3 tC ha^{-1} year^{-1} for the average Flemish forest and 1.8 tC ha^{-1} year^{-1} in the set-aside forests. For the living trees, the mean annual aboveground carbon stock change rates were 1.2 tC ha^{-1} year^{-1} for the average Flemish forest and 1.6 tC ha^{-1} year^{-1} in the set-aside forests; for dead wood, the values were 0.1 tC ha^{-1} year^{-1} for the average Flemish forest and 0.2 tC ha^{-1} year^{-1} in the set-aside forests.

3.2.2 Site type effect

The carbon stock change rates differed between the site types in the set-aside forests, except for dead wood (see the grey italic letters in Table 1). For total aboveground carbon and aboveground carbon in living trees, the stock change rates were significantly higher on the silt and sandy silt sites compared to the sand, wet alluvial and waterlogged sites.

3.2.3 Set-aside vs. average forests within site types

The total aboveground carbon stock change rates were significantly higher in the set-aside forests compared to the average forests on sandy silt and sand soils (asterisks in Figure 2 and Table 1) and the aboveground carbon stock change rates in living trees were significantly higher in the set-aside forests on silt and sandy silt sites (asterisks in Table 1).

3.2.4 Effect of initial carbon stock

For the studied plots in the set-aside forests, the annual carbon stock change rates were mostly positive and independent of the initial aboveground carbon stock (Figure 3). We saw no slow-down in carbon sequestration for plots with high initial carbon stock levels.

4 Discussion

We used datasets originating from two monitoring networks, i.e., the regional forest inventory and the strict forest reserve monitoring, to calculate and compare statistics on aboveground carbon stocks for the average and set-aside forests in Flanders. We acknowledge that caution is needed when comparing carbon stocks among studies and countries because of differences in definitions and calculation approach, e.g., with regard to diameter thresholds (Cienciala et al., 2008), stem volume estimates (Gschwantner et al., 2019, 2022), allometric biomass functions or biomass expansion factors (Neumann et al., 2016), wood density and carbon content (Vande Walle et al., 2005; Weggler et al., 2012). For our comparison, we applied the same wood volume tariffs, volume expansion factors, wood density values, and carbon content to convert the inventory data to carbon stocks. Despite small differences in the data collection protocols (see Supplementary Table S2), we consider our dataset suitable for reliable assessment and comparison of aboveground carbon stocks and carbon stock change rates. Besides providing an overall mean representative for either the average forest or the set-aside forests in the whole of Flanders, we also looked at the effect of the local soil conditions by distinguishing five site types. Below, we consider differences in management history, stand composition, and stand age in discussing our results.

4.1 Carbon stocks

The mean overall aboveground carbon stock for the average forest in Flanders was 64.7 tC ha^{-1}, with 95% confidence interval 62.4–66.9 tC

TABLE 1 The aboveground carbon stock (mean m and standard deviation sd, tC ha^{-1}) at the first and second inventory and the annual carbon stock change between both inventories (with standard deviation sd, tC ha^{-1} year^{-1}) in average and set-aside forest in Flanders, specified for the five site types in this study and for the whole of Flanders.

		All forests									Set-aside												
		Stock$_{t1}$			Stock$_{t2}$				Stock change		Stock$_{t1}$				Stock$_{t2}$					Stock change			
		(tC ha^{-1})			(tC ha^{-1})				(tC ha^{-1} year^{-1})		(tC ha^{-1})				(tC ha^{-1})					(tC ha^{-1} year^{-1})			
Pool	Site type	m	sd		m	sd			Δ^{A}		m	sd			m	sd				m^{B}	sd		
Living trees	Waterlogged	48.4	39.7	*d*	64.7	45.4	*d*	↗	1.1	*a*	83.4	34.6	*b*	*	94.3	35.2	*c*	*		1.2	1.5	*b*	
	Wet alluvial	55.7	42.4	*cd*	75.3	55.5	*cd*	↗	1.3	*a*	75.0	31.9	*b*	*	85.9	33.0	*c*			1.1	1.7	*b*	
	Silt	98.5	55.3	*a*	119.8	72.1	*a*	↗	1.4	*a*	130.9	36.9	*a*	*	152.7	39.9	*a*	*	↗	2.2	1.5	*a*	*
	Sandy silt	73.5	44.7	*b*	93.8	54.7	*b*	↗	1.3	*a*	92.4	33.0	*b*	*	112.8	37.7	*b*	*	↗	2.0	1.3	*a*	*
	Sand	58.1	30.7	*c*	76.9	39.7	*c*	↗	1.2	*a*	71.9	27.5	*b*	*	87.4	34.6	*c*	*	↗	1.6	1.4	*b*	
	Flanders^{C}	62.2	39.2		81.4	49.5		↗	1.3		80.2	34.1		*	95.8	39.6		*	↗	1.6	1.5		*
Dead wood	Waterlogged	1.6	5.3	*a*	3.6	7.7	*ab*		0.1	*a*	2.8	2.9	*a*		5.0	4.9	*b*			0.2	0.4	*a*	
	Wet alluvial	2.0	5.3	*a*	4.5	8.2	*a*	↗	0.2	*a*	5.7	11.1	*a*	*	9.5	12.1	*a*	*		0.4	0.9	*a*	
	Silt	2.9	8.2	*a*	4.4	10.8	*ab*		0.1	*a*	3.9	5.5	*a*		5.8	6.3	*b*		↗	0.2	0.6	*a*	
	Sandy silt	2.0	5.5	*a*	4.2	8.2	*ab*	↗	0.1	*a*	8.6	11.9	*a*	*	10.9	12.2	*a*	*		0.2	0.7	*a*	
	Sand	2.0	5.2	*a*	3.3	5.5	*b*	↗	0.1	*a*	3.9	4.3	*a*	*	5.3	5.0	*b*	*		0.2	0.4	*a*	
	Flanders	2.0	5.5		3.7	7.0		↗	0.1		4.6	7.1		*	6.6	7.9		*	↗	0.2	0.6		*
Total	Waterlogged	53.6	33.7	*c*	68.3	46.4	*d*		1.0	*a*	86.2	34.8	*b*	*	99.3	34.8	*c*	*		1.4	1.4	*b*	
	Wet alluvial	55.3	42.4	*c*	79.8	56.9	*cd*	↗	1.6	*a*	80.8	31.4	*b*	*	95.4	33.2	*c*	*	↗	1.5	1.5	*b*	
	Silt	99.0	50.0	*a*	123.8	74.5	*a*	↗	1.6	*a*	134.8	37.0	*a*	*	158.5	40.4	*a*	*	↗	2.4	1.4	*a*	
	Sandy silt	76.9	46.1	*b*	97.9	56.1	*b*	↗	1.4	*a*	101.0	31.9	*b*	*	123.7	35.5	*b*	*	↗	2.3	1.3	*a*	*
	Sand	60.9	33.3	*c*	80.3	40.8	*c*	↗	1.3	*a*	75.8	27.2	*b*	*	92.7	34.5	*c*	*	↗	1.7	1.4	*b*	*
	Flanders	64.7	39.8		85.1	50.7		↗	1.3		84.8	33.9		*	102.4	39.6		*	↗	1.8	0.4		*

The italic letters in grey indicate whether site types significantly differed in carbon stock or carbon stock change rate; the arrows indicate whether the carbon stocks significantly increased between inventories; and the asterisks indicate whether the carbon stocks and stock change rates significantly differed when comparing the average and set-aside forests (significances based on the 95% confidence interval limits in Supplementary Tables S8, S9).

[A] Difference between the mean stocks of each site type (or the full dataset for Flanders) at the first and second inventory, divided by the mean 15 years interval between inventories. No standard deviation.

[B] For each site type: mean of the plot-level annual stock change rates between the first and second monitoring.

[C] The values for Flanders are the mean and standard deviation of all plot-level values for the regional forest inventory data (systematic sampling) and the weighted mean and standard deviation for the set-aside forests, i.e., taking into account the prevalence of each site type in the forest area of Flanders (see Methods for details).

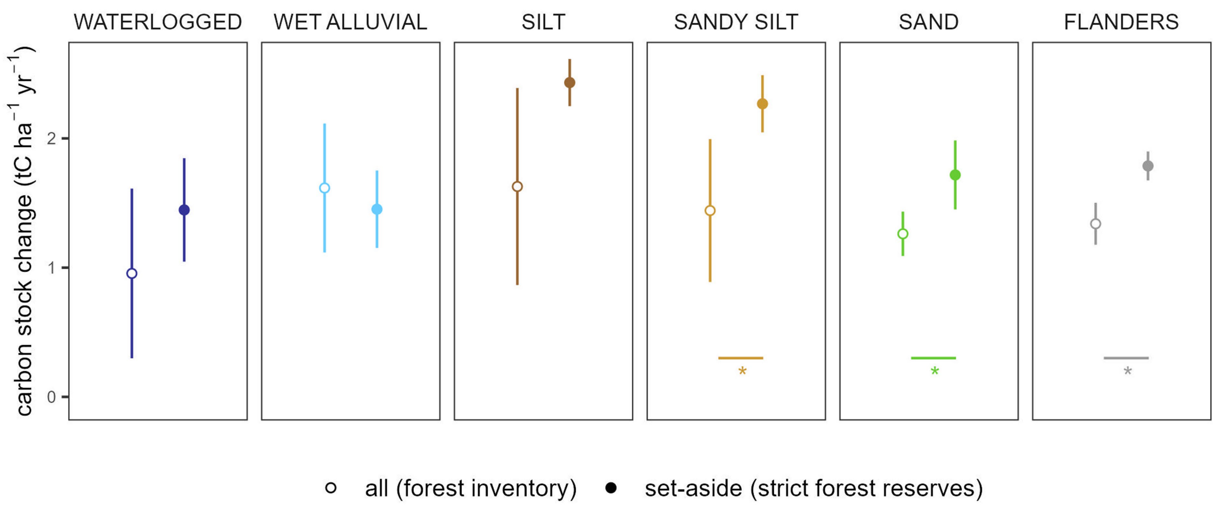

FIGURE 2
The annual carbon stock change (tC ha^{-1} year^{-1}) between the two inventories in the average Flemish forest and the set-aside forests, for each of the five site types and for Flanders as a whole (mean and 95% confidence interval). Asterisks indicate a significant difference between the average and set-aside forests. See Supplementary Table S3 for more details on the site types.

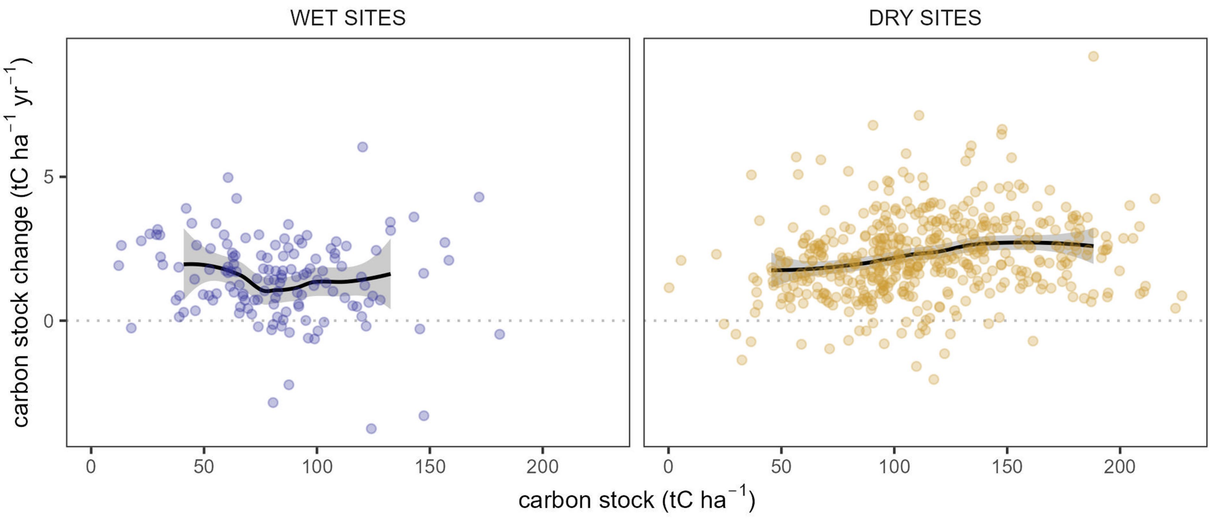

FIGURE 3
The annual aboveground carbon stock change rate (tC ha^{-1} year^{-1}) plotted against the aboveground carbon stock at the first monitoring (tC ha^{-1}) for the set-aside forests on wet and dry sites. The lines represent LOESS smoothing functions and the ribbons 95% confidence intervals.

ha^{-1}, in the first survey between 1997–1999 and 85.1 tC ha^{-1}, with 95% confidence interval 83.0–87.1 tC ha^{-1}, in the recent inventory between 2009–2018. Recent forest inventories in neighboring countries showed slightly lower (69 tC ha^{-1}, France, IGN, 2023), similar (85 tC ha^{-1}, the Netherlands, Arets and Schelhaas, 2019) or higher (101 tC ha^{-1}, Germany, 2017 Carbon Inventory: bwi.info) total aboveground carbon stocks. In other countries in western and central Europe, the total aboveground carbon stock in 2020 ranged from 71–75 tC ha^{-1} (United Kingdom, Ireland), over 84 tC ha^{-1} (Austria, Czech Republic) to 105 tC ha^{-1} (Switzerland) (Forest Europe, 2020: Annex 8, Table 13). For the carbon stock in living aboveground biomass, integrated figures for forests in central-west Europe (75 tC ha^{-1} in Korhonen et al., 2020; 85 tC ha^{-1} - converted from biomass by multiplying by 0.5—in Avitabile et al., 2023) are similar to our value for Flanders (79–83 tC ha^{-1}). In sum, the aboveground carbon stock for the average forest in Flanders was comparable to the stocks in other temperate European forests. The relatively large increase between the first and second inventory indicates that the forest carbon stocks in Flanders are catching up or keeping pace with other countries in temperate Europe (see section 4.2). This is remarkable as most forests in Flanders are quite young, i.e., 77% of the forests are afforestations of heathland and grassland that originated after 1850 (De Keersmaeker et al., 2015), and older forests have a long history of intensive management, often as coppice (Vandekerkhove et al., 2009, 2011). The gradual buildup of the stock levels is probably the combined result of the transformation of coppice to high forest since the 1950s, the loss of a sales market for pine timber, and the shift towards close-to-nature selective harvest systems during the last decades because of the decline in the economic function of forests in favor of recreation and conservation (Vandekerkhove et al., 2009; Vandekerkhove, 2013). The aboveground carbon stocks differed among the site types in our study. Forests on the fertile, silt and sandy silt sites generally showed higher aboveground carbon stocks, because of their higher productivity and a high share of well-preserved older forest stands, i.e., former hunting grounds. Forests on wet and sand sites had lower stocks. On the wet sites, the lower stocks were probably due to a more recent history of coppice management and high mortality combined with fast dead wood decay in poplar stands. For the sand soils, the lower stocks can be related to low site productivity and a high share of relatively young pine stands.

The set-aside forests in Flanders showed significantly higher mean overall aboveground carbon stocks than the average Flemish forest at both inventories, i.e., 84.8 tC ha^{-1}, with 95% confidence interval 82.1–87.5 tC ha^{-1}, at the first survey between 2000–2007 and 102.4 tC ha^{-1}, with 95% confidence interval 99.3–105.6 tC ha^{-1}, at the recent monitoring between 2010–2017. Most set-aside forests in our study originated from structure-rich mature forests with a rather high aboveground standing wood volume at the moment they were set aside as forest reserves. The higher initial stock in the set-aside forests, combined with a higher stock change rate (see section 4.2), resulted in an amplified difference in final stocks. The higher stocks in set-aside forests are in line with other studies that also found higher aboveground carbon stocks in set-aside vs. managed stands, e.g., in German beech forest (Mund, 2004) and the Białowieża biosphere reserve (Matuszkiewicz et al., 2021). Similar to the average Flemish forests, the aboveground carbon stocks in our set-aside forests were highest on fertile silt and sandy silt sites.

The dead wood carbon stocks in the studied set-aside forests were larger than in the average Flemish forests (Supplementary Table S9), particularly in the forests on wet alluvial soils, with a dead wood share of 10%, and the forests on sandy silt soils, with a dead wood share of 9%. These high dead wood shares may be because of a high dieback of *Populus* in the forests on wet alluvial soils and of light-demanding tree species in the beech forests on sandy silt soils. The overall share of dead wood in the aboveground carbon stocks of the average and set-aside forests in our study was similar to the share of dead wood in other studies in managed (Mund, 2004; Glatthorn et al., 2018) and set-aside (Mund, 2004; Den Ouden et al., 2020; Förster et al., 2021; Meyer et al., 2021) stands in western and central Europe. The mean dead wood volumes in the studied set-aside forests on the dry site types (i.e., 27–54 m^3 ha^{-1}, Supplementary Table S11) were also in line with the median values reported for set-aside beech and oak forests in northwestern and central Europe (53 m^3 ha^{-1}; Vandekerkhove et al., 2009).

4.2 Carbon stock change rates

The mean overall aboveground carbon stock change rate for the average forest in Flanders was 1.3 tC ha^{-1} year^{-1}, with 95% confidence interval 1.2–1.5 tC ha^{-1} year^{-1}, similar to recent forest inventory values in the Netherlands (1.2 tC ha^{-1} year^{-1}, Arets and Schelhaas, 2019) and Germany (1.1 tC ha^{-1} year^{-1}, 2017 Carbon Inventory: bwi.info), above the range reported in the 2019 National Inventory Reports for countries in central-west Europe (−1.4 to 1.0 tC ha^{-1} year^{-1}, Günther and Gniffke, 2022), and much higher than recent figures for France (0.5 tC ha^{-1} year^{-1}, IGN, 2023). Korhonen et al. (2020) reported a steady increase in carbon stocks in forest biomass in the European Union between 1990 and 2020, with forest growth exceeding cutting and mortality. In central-west Europe, the total living forest biomass showed an annual increase of 1.2% between 1990 and 2020 (Korhonen et al., 2020). In Flanders, the increase in living tree biomass reached more than 25% over a mean interval of 15 years, or more than 1.5% per year between 1998 and 2014. The relatively low overall harvest ratio in forests in Flanders (Govaere and Leyman, 2020), the high potential for additional carbon storage (see section 4.3), and the absence of large-scale stand-replacing disturbances, such as bark beetle outbreaks, lead to the relatively high carbon stock change rates for Flanders.

In set-aside forests in Flanders, the mean annual carbon stock change rate ranged from 1.4 to 2.4 tC ha^{-1} year^{-1} for the different site types, with an overall mean for Flanders of 1.8 tC ha^{-1} year^{-1} and the 95% confidence interval between 1.7 and 1.9 tC ha^{-1} year^{-1}. The carbon stock change rates in set-aside forests in Flanders were hence similar to or larger than the global values for primary forests (0.8–1.4 tC ha^{-1} year^{-1}, Luyssaert et al., 2008). In general, the carbon stock change rates in the studied set-aside forests were also significantly higher than for the average Flemish forest, which was expected: no biomass is removed in set-aside forests and the studied set-aside forests have not yet reached their carbon carrying capacity (see section 4.3). Ford and Keeton (2017) also found higher aboveground carbon fluxes in unmanaged set-aside compared to managed northern hardwood-conifer forests. On the wet alluvial sites, however, we saw similar carbon stock change rates in the set-aside and average Flemish forests, which may be related to high dieback and fast dead wood decay of poplar in the set-aside forests. Moreover, forests on wet alluvial sites are often left unmanaged also outside official set-aside areas as harvesting wood on wet sites is difficult or restricted by legal constraints. When looking at the carbon stock change rates for specific site conditions, our values for set-aside forests on sand soils (1.7 tC ha^{-1} year^{-1}) were comparable to set-aside pine forests on poor soils in the Netherlands (1.4 tC ha^{-1} year^{-1}; Den Ouden et al., 2020), and our values for set-aside forests on silt and sandy silt soils (2.4 and 2.3 tC ha^{-1} year^{-1}) were in line with set-aside forests on relatively fertile soils in Germany (mixed oak: 0.9–2.3 tC ha^{-1} year^{-1}; beech and mixed beech: 1.1–3.4 tC ha^{-1} year^{-1}; converted from biomass by multiplying by 0.5; Meyer et al., 2021) but lower than set-aside beech forests on loamy soils in the Netherlands (3.2 tC ha^{-1} year^{-1}; Den Ouden et al., 2020).

The mean accumulation of dead wood in the set-aside forests was 1.1 m^3 ha^{-1} year^{-1}, similar to the mean volume change rate in set-aside beech forests in Germany (1.1 m^3 ha^{-1} year^{-1}, Meyer and Schmidt, 2011) but lower than the median accumulation rate in set-aside oak and beech forests across Europe (1.64 m^3 ha^{-1} year^{-1}, Vandekerkhove et al., 2009).

4.3 Potential for additional carbon storage

In the average Flemish forest on fertile sites, we found total aboveground carbon stocks of 97.9 tC ha^{-1} for the sandy silt sites and 123.8 tC ha^{-1} for the silt sites, much lower than the values reported for well-stocked managed beech forests in Slovakia (170 tC ha^{-1}, Glatthorn et al., 2018), Germany (178 tC ha^{-1}, Mund, 2004), or France (209 and 220 tC ha^{-1}, Lecointe et al., 2006). In the set-aside forests on fertile sites, the observed total aboveground carbon stocks, i.e., 123.7 tC ha^{-1} on sandy silt and 158.5 tC ha^{-1} on silt, were higher than in the average

Flemish forest, but also still lower than in reference set-aside beech forests in Germany (174 tC ha^{-1}, Nagel et al., 2023; 238 tC ha^{-1}, Meyer et al., 2021; 247 tC ha^{-1}, Mund, 2004) or the Netherlands (252 tC ha^{-1}, Den Ouden et al., 2020) or in set-aside mixed broadleaved forests in Germany (166 and 216 tC ha^{-1}, Meyer et al., 2021) and Denmark (244 tC ha^{-1}, Nord-Larsen et al., 2019). The total aboveground carbon stocks observed in the set-aside forests on sand soils, i.e., 92.7 tC ha^{-1}, were also lower than in oak and beech forests in northern Germany (117 tC ha^{-1} and 158 tC ha^{-1}, Förster et al., 2021). Aboveground volumes in old unmanaged oak and beech forests on rich and poor sites in central and northwestern Europe (Vandekerkhove et al., 2009) are generally 1.1–1.8 times higher than in the set-aside forests on silt, sandy silt and sand in Flanders. In the set-aside forests on waterlogged and wet alluvial sites, the carbon stocks, i.e., 99 and 95 tC ha^{-1}, or aboveground volumes, i.e., 353 and 369 m^3 ha^{-1} (Supplementary Table S11), were also well below the potential carbon stock of 165 tC ha^{-1} observed for alder forests in the Białowieża Biosphere Reserve (Matuszkiewicz et al., 2021) or the 690 m^3 ha^{-1} in primary alluvial forest in the Czech Republic (Janik et al., 2008).

4.4 Additionality of set-aside forests

The significantly higher carbon stocks and carbon stock change rates in set-aside forests indicate the additionality for *in situ* carbon sequestration of the measure of setting aside forests in the framework of carbon removal. This additionality may last for several decades. The studied set-aside forests appeared to be still below the ecosystem's carbon carrying capacity: the carbon stock change rates were not lower for plots with high initial carbon stocks (no clear trend in Figure 3), indicating that the carbon accumulation did not yet slow down and the carbon stock continued to increase in forests that already built up a large carbon stock over time. Studies in German set-aside forests indeed indicated that the *in situ* carbon sequestration—and hence additionality of setting aside forests—remains high during at least the first 50 years after set aside, before they approach their ecological carrying capacity and related dynamic steady-state level (Meyer et al., 2021; Nagel et al., 2023).

The share of set-aside forests in the overall forest area is and will remain relatively small. To reach the carbon removal targets of the Fit for 55 package of the European Union, it will be essential to complement setting aside forests with sustainable management in the remaining forest area, combining biodiversity, wood production and recreation goals with a gradual increase of the forests' carbon stocks (cf. Nunery and Keeton, 2010; Triviño et al., 2015; Law et al., 2018).

5 Conclusion

In the average forest in Flanders, owing to a relatively low harvest intensity, the aboveground carbon accumulation was similar to neighboring countries such as Germany and the Netherlands and high compared to several other European countries. In the set-aside forests in Flanders, the initial stocks and the carbon accumulation were significantly higher than in the average Flemish forest and similar to set-aside and previously managed forests in neighboring countries. The additionality in aboveground carbon depended on the soil conditions, with *in situ* aboveground carbon sequestration similar in set-aside and average forests on wet sites and higher in the set-aside than in the average forests on dry sites. Furthermore, there was no indication that the carbon stocks approached the carbon carrying capacity of the set-aside forests in the first decades following set-aside. Considering the relatively low aboveground carbon stocks in Flemish forests compared to reference forests elsewhere in Europe, the potential for additional *in situ* carbon sequestration in Flemish forests, managed and set-aside, remains high.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

LK and KV contributed to the conception and design of the study. AL and LG organized the databases and performed the calculations. MV wrote the first draft of the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2024.1236203/full#supplementary-material

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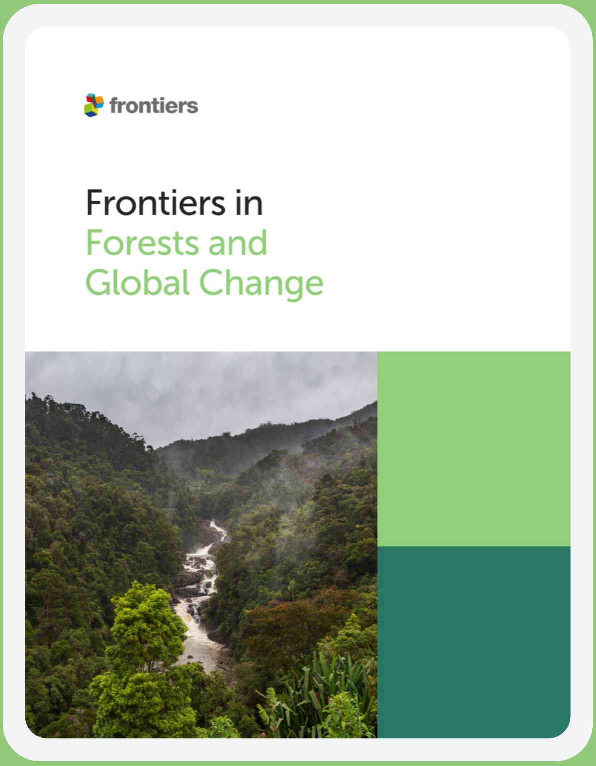

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