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RESEARCH ARTICLE

Anthromes and forest carbon responses to global change

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Societal Impact Statement

Forest ecosystems absorb and store about 25% of global carbon dioxide emissions annually and are increasingly shaped by human land use and management. Climate change interacts with land use and forest dynamics to influence observed carbon stocks and the strength of the land carbon sink. We show that climate change effects on modeled forest land carbon stocks are strongest in tropical wildlands that have limited human influence. Global forest carbon stocks and carbon sink strength may decline as climate change and anthropogenic influences intensify, with wildland tropical forests, especially in Amazonia, likely being especially vulnerable.

Summary

- Human effects on ecosystems date back thousands of years, and anthropogenic biomes—anthromes—broadly incorporate the effects of human population density and land use on ecosystems. Forests are integral to the global carbon cycle, containing large biomass carbon stocks, yet their responses to land use and climate change are uncertain but critical to informing climate change mitigation strategies, ecosystem management, and Earth system modeling.
- Using an anthromes perspective and the site locations from the Global Forest Carbon (ForC) Database, we compare intensively used, cultured, and wildland forest lands in tropical and extratropical regions. We summarize recent past (1900-present) patterns of land use intensification, and we use a feedback analysis of Earth system models from the Coupled Model Intercomparison Project Phase 6 to estimate the sensitivity of forest carbon stocks to CO_2 and temperature change for different anthromes among regions.
- Modeled global forest carbon stock responses are positive for CO_2 increase but neutral to negative for temperature increase. Across anthromes (intensively used,

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cultured, and wildland forest areas), modeled forest carbon stock responses of temperate and boreal forests are less variable than those of tropical forests. Tropical wildland forest areas appear especially sensitive to CO_2 and temperature change, with the negative temperature response highlighting the potential vulnerability of the globally significant carbon stock in tropical forests.

- The net effect of anthropogenic activities—including land-use intensification and environmental change and their interactions with natural forest dynamics—will shape future forest carbon stock changes. These interactive effects will likely be strongest in tropical wildlands.

KEYWORDS
carbon cycle feedbacks, Coupled Model Intercomparison Project Phase 6, Global Forest Carbon Database (ForC), human-influenced forests, tropical vs. temperate and boreal

1 | INTRODUCTION

Earth's vegetation cover patterns have always been dynamic. Ten thousand years ago, forests covered 57% of Earth's terrestrial surface (about 6 billion [B] ha); today, forests cover about one-third of it (4 Bha; FAO, 2022). Since at least twelve thousand years ago, humans have been influencing the biosphere (Ellis et al., 2021; Fletcher et al., 2021; Stephens et al., 2019). Although the Anthropocene concept (Waters et al., 2016) is contentious and has recently been rejected as a formal geological epoch (Witze, 2024), we are living in a novel era characterized by the unprecedented effects of human activities on the biosphere (Richardson et al., 2023). Human activities, mainly fossil fuel combustion and widespread land use changes, are undeniably responsible for recent climate change trends (e.g., warming) and related Earth system changes (e.g., global ice loss and sea level rise, ocean acidification, widespread biodiversity loss and ecosystem degradation; Elmqvist et al., 2021; Masson-Delmotte et al., 2021; Pimm et al., 2014; Ripple et al., 2017; Steffen et al., 2011). Accordingly, human societies are reshaping the biosphere into increasingly modified anthropogenic biomes (i.e., anthromes; Ellis & Ramankutty, 2008).

The classical terrestrial biome approach defines biogeographical units that support similar potential vegetation types, usually based on climate (Box & Fujiwara, 2013; Whittaker, 1962). Classical biomes—which are widely used in global ecology (e.g., Ramankutty & Foley, 1999)—ignore the variable presence of humans within ecosystems and do not account for human activities in shaping vegetation, which motivated the development of the anthromes concept (Ellis et al., 2021; Ellis & Ramankutty, 2008). The conceptual basis of anthromes is that ecosystem processes in anthropogenic landscapes are produced through interactions among human population density, land use practices, biota, climate, terrain, and geology:

$$ecosystem\ processes = \frac{f(population\ density,\ land\ use,}{biota,\ climate,\ terrain,\ geology)}$$

Integral to the anthrome concept is the idea that human societies shape vegetation and ecosystem processes across landscapes and that population densities and the intensity of land use transformations are generally linked (Boserup, 2013). Nevertheless, population-density-dependent anthropogenic effects on ecosystems beyond land use are not widely incorporated into Earth system models (ESMs) or other predictive methods for modeling future carbon cycle responses to global change.

Nearly all forests of the globe have evidence of human use to varying degrees (Fletcher et al., 2021). For example, Amazonia has evidence of over 4,500 years of polyculture and agroforestry, which have partly influenced forest composition and soil fertility (Levis et al., 2017; Peripato et al., 2023). Many forests have been deforested at some point in the last several centuries, and the practice of forest clearing remains in many tropical countries. Until the 1950s, land use change was the main driver of CO_2 emissions, when it was surpassed by fossil fuel combustion (Friedlingstein et al., 2023). Modern forest transitions (i.e., where lands return to forest from some other land use), have been observed in many post-industrial nations (e.g., the United States, Russia, and Europe) since the 1950s and are projected to occur in many currently industrializing nations (Rudel et al., 2005; Schierhorn et al., 2019). Often, they occur because of rural-to-urban migration during industrialization, resulting in agricultural land-use abandonment and forest regeneration or afforestation (Mather, 1992). Such vegetation cover changes can have noticeable effects on land energy balance and local climate (Burakowski et al., 2016; Li et al., 2020), and have implications for the global carbon cycle (Pan, Birdsey, Phillips, et al., 2011).

Forests have always been of great value to society and the economic valuation of these ecosystems is one way to assess competing drivers for use or conservation. Forests provide wildlife habitat, vital goods, and ecosystem services essential for human well-being, including mitigating climate change (Bonan, 2008; Mooney et al., 2009). Still, forests are being steadily lost or disturbed at a rate of about 4.1 million (M) ha $year^{-1}$; for instance, in 2022, natural disturbance affected 0.59 Mha $year^{-1}$, but 3.5 Mha $year^{-1}$ were lost due to

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deforestation, mostly in the tropics (Global Forest Review, 2023). A recent meta-analysis showed the median economic value of forests to be \$1,837 ha^{-1} $year^{-1}$, with climate regulation being the second most valuable ecosystem service, accounting for 14.4% of their value (Taye et al., 2021). In comparison, the median economic value of arable agricultural land is \$8,350 ha^{-1} $year^{-1}$ with cropland being valued at \$10,920 USD ha^{-1} $year^{-1}$ and pasture being valued at \$3,650 USD ha^{-1} $year^{-1}$ (Griffiths et al., 2023). Consequently, there is a great need to harmonize economic incentives with the land carbon sequestration potential of ecosystems, particularly forests.

Globally, terrestrial ecosystems (including forested and non-forested lands) uptake about 30% of annual CO_2 emissions (~3.3 ± 0.8 Gt C yr^{-1} from 2013 to 2022) and thus act as a land carbon sink (Friedlingstein et al., 2023). A large proportion of the land carbon sink resides in forests (Pan, Birdsey, Fang, et al., 2011; Pan, Birdsey, Phillips, et al., 2024; Yang et al., 2023). Hence, forests are mitigating some climate change effects and there is increasing emphasis that forests can be instrumental in slowing the rate of climate change (Cook-Patton et al., 2020; Mo et al., 2023). However, the future strength and magnitude of the land carbon sink remains uncertain, yet highly important for climate change forecasts and policy (Friedlingstein, 2015). Understanding forests as landscapes shaped by both global climate change and local anthropogenic processes is essential to forecasting their future role in the carbon cycle and has implications for human wellbeing.

The land carbon sink has doubled since 1960 (Ruehr et al., 2023), presumably in part due to CO_2 fertilization of forest productivity—a pattern that is captured by most ESMs because of the CO_2 response of photosynthesis. Forests comprise the largest contribution of living plant biomass to the land sink, yet observational evidence for an augmented forest carbon sink is mixed, and there is uncertainty in the CO_2 response of forest biomass or other measures of ecosystem carbon storage (Hogan et al., 2024; Hubau et al., 2020; Walker et al., 2021). CO_2 fertilization is likely to have the greatest effect on ecosystem productivity and carbon stocks in younger, regenerating forests (Walker et al., 2019), to the extent that other factors like drying, warming, or nutrient limitation allow (Anderson-Teixeira & Kannenberg, 2022; Hogan et al., 2024; Terrer et al., 2019). CO_2 fertilization of photosynthesis likely translates to less of an increase in forest carbon storage because of energy loss in the biological processes linking CO_2 assimilation to the production of structural biomass (Hickler et al., 2015; Lloyd & Farquhar, 1996). Methodological difficulties exist in measuring increases in carbon stocks across the range of ecosystem carbon pools (Brown, 2002; Petrokofsky et al., 2012). Yet, global ESMs establish the baseline expectation for the augmentation of the land carbon sink as 16% per 100 ppm atmospheric CO_2 increase (Piao et al., 2013). Satellite, experimental, and field-based observations for a CO_2-driven increase in the land carbon sink vary widely (Walker et al., 2021) but are typically less than those predicted by ESMs (De Kauwe et al., 2016; Terrer et al., 2019). However, there is some evidence that CO_2 fertilization strength is strongest in forests relative to other ecosystems; specifically, using a globally distributed network of eddy-covariance towers, the sensitivity of gross primary productivity (GPP) to CO_2 of evergreen broadleaf forests was measured to be nearly three times greater than that of other ecosystem types (e.g., grasslands or open shrublands; Chen et al., 2022).

Accordingly, the future strength and duration of the land carbon sink are uncertain and will likely depend on the balance of two main drivers and their interaction: 1) human land-use effects, and 2) the sign and strength of climate-carbon cycle feedbacks (Friedlingstein, 2015; Schimel & Carroll, 2024). Here, we aim to estimate how land-use intensification and climate-carbon cycle feedbacks have affected forested anthromes since 1900 by drawing on existing data sources. First, we highlight how human population and land use trends drive patterns of anthrome distribution and their change over time. Although such global land-use trends have been previously described (e.g., Klein Goldewijk et al., 2017), we summarize them here (updated to 2023), emphasizing how population growth and land-use intensification differ in the tropics compared to the rest of the world. Secondly, we use a global sample of forest locations where carbon stocks have been field-measured (from the Global Forest Carbon (ForC) database, Anderson-Teixeira et al., 2018) to categorize forest biomass by anthrome class. These locations provide a global subsample of known forest areas for which we then use a previously published climate-carbon feedback analysis of Coupled Model Intercomparison Project Phase 6 (CMIP6) ESMs (Arora et al., 2020; Koven, 2022) to estimate the sensitivity of forest carbon stocks in different anthromes to increases in atmospheric CO_2 and temperature. A detailed analysis of the mechanisms within individual ESMs leading to different CO_2 and temperature sensitivities among anthromes is beyond the scope of our study, but we speculate on potential causes of variation in these sensitivities in relation to geographic variation in climate and soil type. Our analysis highlights how considering anthrome distribution can augment understanding of the current and future role of forest ecosystems in the global carbon cycle.

2 | MATERIALS AND METHODS

2.1 | Anthrome classification, population trends, and land use patterns by global region

We use the broadest classification of anthromes, which characterizes ecosystems as intensively used, cultured, or wildlands (Figure 1A), based on the intensity and type of direct human interactions with ecosystems (Ellis & Ramankutty, 2008). 'Wildlands' are classified where permanent human populations and intensive land use are not evident; 'cultured anthromes' have permanent human populations, <20% intensive land use (i.e., cities, croplands, and pasturelands) by area, and varying degrees of non-intensive land uses (e.g., foraging, hunting, forestry); and 'intensive anthromes' have dense human populations and >20% intensive land uses by area (Ellis et al., 2021).

It is worth noting that cultured lands may be misclassified as wildlands owing to biases in assessing mobile and low-density human populations and low intensity of land uses (Ellis et al., 2021). For example, nomadic, indigenous populations, such as the Taureg in the

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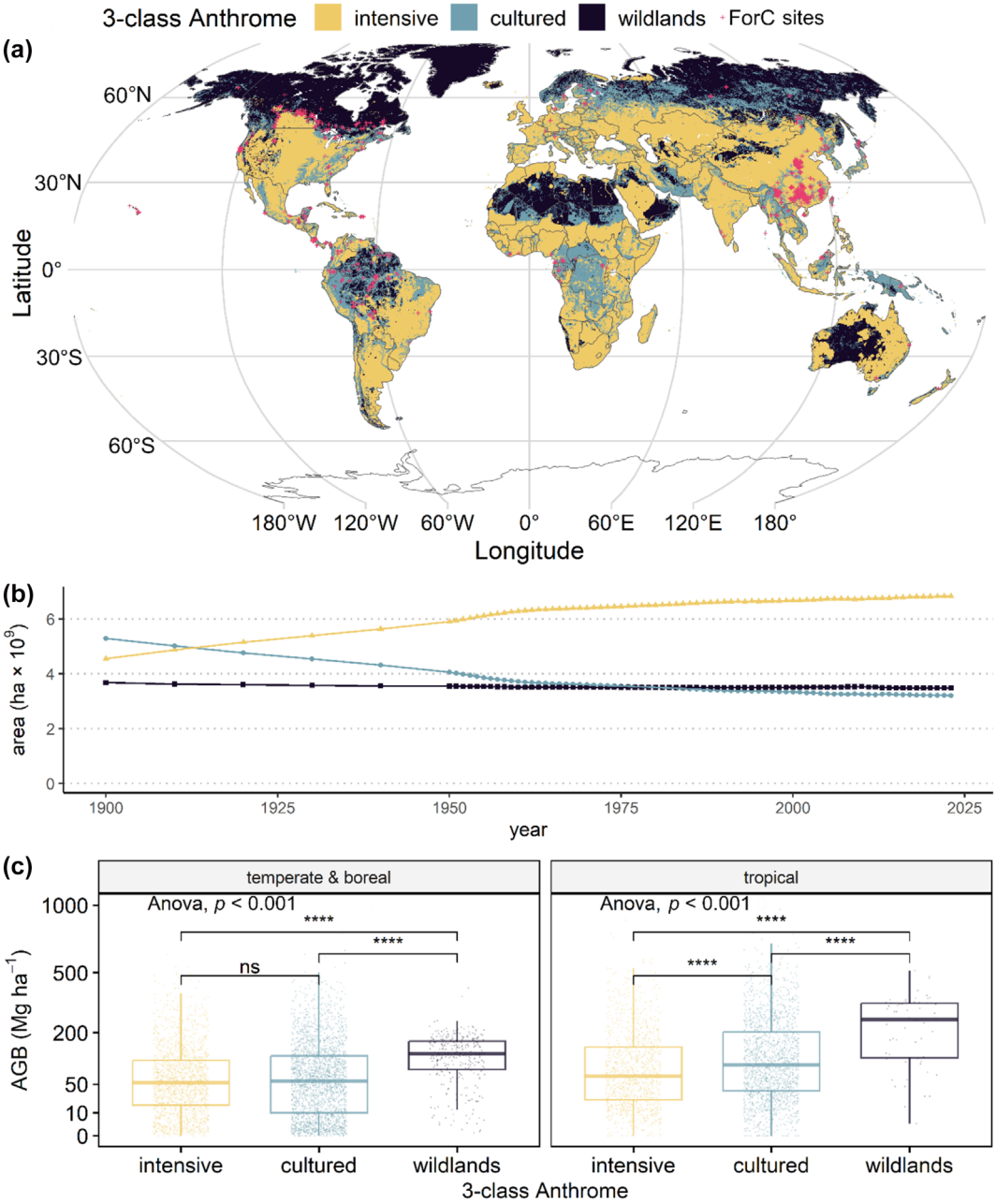

FIGURE 1 The global state of anthrome landscapes in relation to forest biomass stocks. (a) Map of Earth's terrestrial anthromes in 2023 (using History Database of the Global Environment (HYDE) 3.3: Klein Goldewijk, 2024). Earth's land surface is classified into three anthrome classes listed in order of decreasing intensity of human influence 1) intensively-used anthromes, which have dense human populations and >20% intensive land uses by area, 2) cultured anthromes, which have low-density human populations and <20% intensive land use and 3) wildlands, without permanent human populations and intensive land use. (b) Recent past (1900–2023) changes in global anthrome extent. Cultured anthrome extent has decreased over time due to the human land use intensification across Earth's ecosystems; wildland area has remained relatively constant. (c) Forest aboveground biomass (AGB) stocks from 7,541 sites in global forest carbon (ForC) database (Anderson-Teixeira et al., 2018, ForC site locations are shown in Figure 1A) by three-class anthrome and global region (tropical vs. temperate and boreal regions). These ForC site locations provide a global subsample of measured forest areas which are used for extraction of coupled model Intercomparison project phase 6 (CMIP6) carbon-cycle feedbacks. See Table S1 for AGB measures of central tendency, and Table S1 for sample sizes and ANOVA statistics. Anova *p*-values and post-hoc comparison of groups using Tukey test are plotted. ****: $p < 0.001$, ns: non-significant.

Sahara Desert, Mushkegowuk in the Hudson Bay region, many Aboriginal peoples of Australia, and likely many other Indigenous groups, tend to be omitted from the population data used in Anthrome classification, leading to potential misclassification of their lands as wildlands, rather than cultured lands. Indeed, the concept of wilderness (or wildlands) can itself be one that excludes people and traditional cultures (Fletcher et al., 2021). Here, we use the term 'wildlands' because of its consistent use in the Anthromes literature, with

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it definitionally representing large landscapes without clear, permanent evidence of human inhabitation or intensive land use. Anthrome classification of land area was based on the History Database of the Global Environment (HYDE) version 3.3 (12 arcsecond or 0.05-degree resolution; Klein Goldewijk, 2024), which is an updated version of HYDE 3.2 (Klein Goldewijk et al., 2017).

About 85% of global land area and 74% (148 of 201) of countries occur in the global tropics—defined here as land between the 35-degree latitudes to include the subtropics. Tropical nations were defined based on IMAGE 3.0 (Stehfest et al., 2014) nation groupings which had most of their land area in the tropics (i.e., IMAGE 3.0 regions for Mexico, Central America, Brazil, Rest of South America, Northern Africa, Western Africa, Eastern Africa, South Africa, Middle East, India, Southeastern Asia, Indonesia Region, Oceania, Rest of Southern Asia, and Rest of Southern Africa). Using data from HYDE 3.3, we compare recent past (1900-present) trends of human population and land use in the tropics vs. the extratropics (temperate and boreal region). Population estimates in HYDE 3.3 are derived from literature prior to 1950 and from the United Nations, Department of Economic and Social Affairs, Population Division (2022) after 1950. Prior to 1960, HYDE 3.3 combines population data with per capita land use estimates to calculate land use areas, whereas data on post-1960 land use come directly from FAO (Klein Goldewijk et al., 2017).

2.2 | Forest biomass by anthromes using the ForC database

The ForC Database (Anderson-Teixeira et al., 2018), which contains forest plot data from 1924 to 2016, was used to assess differences in ecosystem carbon stocks among anthromes. The most prevalent variable in ForC is aboveground biomass (AGB), so we used AGB as the measure of ecosystem carbon stocks to compare across anthromes. Analysis of total ecosystem carbon (including soil carbon) yielded similar patterns (not shown), albeit with much smaller sample sizes. We tested for statistical differences in AGB among anthromes and global regions (i.e., tropical vs. temperate and boreal) using a two-factor ANOVA with a Tukey post-hoc test. Eta squared (η^2) values were computed in the 'effectsize' package (Ben-Shachar et al., 2020) package in R v.4.3.2 (R Core Team, 2023). Although there is likely some potential bias toward well-conserved forests or extensively studied regions (e.g. tropical Africa is underrepresented), ForC sites span the range of stand ages and stand structures representative of forests globally (Table S1).

2.3 | Evaluation of carbon-cycle feedbacks at ForC site locations using from CMIP6 ESMs

Although there are many ways in which forests interact with and influence the Earth's climate system, we focus on sensitivities of forest carbon stocks to changes in CO_2 and temperature using the carbon-concentration (β) and carbon-climate (γ) feedbacks derived from CMIP6 ESM feedback experiments (Arora et al., 2020; Canadell et al., 2021). These feedback parameters were estimated from two experiments per ESM: (1) a 'biogeochemical experiment' in which biogeochemical processes (e.g., photosynthesis) experience rising CO_2 (an increase of 1% year^{-1}, starting from a pre-industrial 285 ppm and quadrupling over 140 years) but the radiative properties of the atmosphere experience a fixed CO_2 concentration of 285 ppm; and (2) a 'fully coupled experiment' in which biogeochemical and radiative processes both experience rising CO_2 (Arora et al., 2020; Canadell et al., 2021). In these experiments, ESMs are initialized with reconstructed 1850 land use (Hurtt et al., 2020), which is held static for the duration of the experiments. The change in land carbon storage (ΔC_L) in this framework is linearized as: $\Delta C_L = \beta_L \Delta CO_2 + \gamma_L \Delta T$, where ΔCO_2 is the CO_2 change, and ΔT is the global mean temperature change (Arora et al., 2013). The carbon-concentration feedback (β; i.e., the land carbon storage response to CO_2 alone; Kg C m^{-2} ppm^{-1}) is estimated from the biogeochemical experiment, and the carbon-climate feedback (γ; i.e., the land carbon storage response to temperature alone; Kg C m^{-2} °C^{-1}) is isolated by comparing the biogeochemical and fully coupled experiments. We analyzed feedback parameters (β and γ) for the nine CMIP6 ESMs included in Figure 5.27 of Canadell et al. (2021) (see table S2); the feedback parameters were harmonized to common spatial resolution (0.5 degree; Koven, 2022). Ensemble mean values (across the nine models) for the entire global land surface averaged +0.89 ± 0.30 (range: 0.37 to 1.36) Gt C ppm^{-1} for β and −33.3 ± 33.8 (model range: −80.1 to −16.0) Gt C °C^{-1} for γ (Arora et al., 2020; Canadell et al., 2021).

We estimated the sensitivity of carbon stocks in different forest anthromes to changes in CO_2 and temperature by analyzing the gridded ESM feedback parameters at the same ForC locations used in our other analyses (Figure 1A). Feedback parameters were extracted using the coordinates of the ForC sites using the raster package (Hijmans, 2018) in R v.4.3.2 (R Core Team, 2023). To translate the feedback parameters into carbon stock sensitivities (ΔC) at each ForC location, we used highly accurate records of past global atmospheric CO_2 (Joos & Spahni, 2008) and land surface temperature (Rohde & Hausfather, 2020) trends (Figure S1). Recent past (1900–2021) global mean changes in atmospheric CO_2 (ΔCO_2 of 117.7 ppm), and temperature (ΔT of 1.018°C) were multiplied by ESM β and γ values (individually and for the ensemble mean) to obtain land carbon stock sensitivities. We tested for statistical differences in land carbon stock sensitivities using two-factor analyses of variance (again, individually by ESM and for the ensemble mean) with terms for anthrome class and global region (comparing the tropics to the temperate & boreal extratropics).

2.4 | Potential drivers of forest carbon stock changes to CO2 and temperature in CMIP6 linear feedback analyses

ESMs participating in the linear feedback analysis differ in their model parametrizations (Table S2), but all use an idealized 1% year^{-1} increase in atmospheric CO_2 and static land use (Hurtt et al., 2020).

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Accordingly, there are four potential reasons why ΔC patterns may differ among anthromes. First, differences in temperatures could be driving the pattern. Second, differences in precipitation might be the reason. To assess whether differences in temperature or precipitation match ΔC patters, we use the historical (1850–2014) climate forcing data for the CMIP6 project (Copernicus Climate Change Service, 2021), comparing anthrome classes by global region. Third, differences in the forest cover mark (binary categorization for forest or non-forest) of the static land use forcing data (Hurtt et al., 2020) among selected ESM land areas (chosen based on site coordinates from the ForC database) could lead to differences in the ensemble mean β or γ and, therefore, ΔC. A fourth potential reason is soils, which are represented in the nine CMIP6 ESMs in varying ways (Table S2). Some models use a global soil classification map, such as that of Zobler (1986), which can use either 27 or 106 soil types (at 1-degree resolution) or the Harmonized World Soil Database (Fischer et al., 2008). We examined how changes in the ESM inputs of temperature and precipitation trends (since 1900), forest cover mark, and soil classification vary by three-class anthrome and global region, which we discuss considering ESM ΔC patterns.

3 | RESULTS

3.1 | Forest aboveground biomass differs by anthrome

Forest AGB stocks from 7,541 ForC sites (Figure 1A) ranged from 78 ± 2 Mg ha^{-1} for intensively used land in the temperate and boreal region to 232 ± 17 Mg ha^{-1} for tropical wildlands (Table S1). Statistically significant differences were found by global region ($F_{[1,7,535]} = 352$, $p < 0.001$), anthrome ($F_{[2,7,535]} = 42$, $p < 0.001$), and their interaction ($F_{[2,7,535]} = 19$, $p < 0.001$). The effect size of the global region ($\eta^2 = 0.44$) on forest AGB was about four times stronger than the effect size of anthrome classification ($\eta^2 = 0.11$), and their interaction was relatively weak (Table S3). In the tropics, intensively used forests tend to have less live AGB than cultured forests, with both having substantially less AGB than wildland forests (Figure 1C). Globally, wildland forests have more AGB than cultured or intensively used forests, which were not statistically different (Figure 1C).

3.2 | Global anthrome patterns over time

In 2023, 50.5% (6.83 Bha) of the global land area corresponded to intensively used anthromes, 23.7% (3.21 Bha) to cultured anthromes, and 25.8% (3.48 Bha) to wildlands (Figure 1A). Land use has intensified since 1900, illustrated by an increase in the area of intensively used anthromes with corresponding declines in cultured and wildland anthrome areas (Figure 1B). A finer-scale anthrome classification separates woodlands (defined as land areas capable of supporting trees, using biomes of Prentice et al., 1992) by population density and land-use intensity (Ellis et al., 2020). Wild woodlands can be considered wildland anthromes, while residential, populated, and remote woodlands are cultured anthromes. As of 2023, roughly, 27% of the world's ice-free land area (3.68 B ha) exists in woodland anthromes—with 3.6% (0.48 Bha) corresponding to residential woodlands, 5.5% (0.75 Bha) to populated woodlands, 6.4% (0.87 Bha) to remote woodlands, and 11.6% (1.57 Bha) to wild woodlands (listed in decreasing order of human population density). From 1900 to 2023, residential woodlands increased by 4%, whereas populated woodlands, remote woodlands, and wildland woodlands decreased by 32%, 34%, and 4%, respectively (Figure S2). Meanwhile, there was a collective 50% expansion of intensive land uses (urban, suburban, cropland, pastoral land, and rangeland areas; Figure S2, Ellis et al., 2020). Thus, from 1900 to 2023 there was a net decrease in global woodland anthrome extent of 6.3% (0.09 Bha), most of which occurred from 1900 to 1950 (Figure S2). This pattern is consistent with the global decline in forest cover reported elsewhere (Hansen et al., 2013; Keenan et al., 2015).

3.3 | Drivers of global land use change: comparing tropical to temperate and boreal anthromes

The decline in woodland anthrome extent has occurred due to population growth and increases in land uses which compete with forest conservation (Figure S2, Figure 2). HYDE 3.3. population data show an increase from ~1.67B to 7.89B from 1900 to 2023. Population growth has been slower in the temperate and boreal regions of the world relative to the tropics, with the tropical population surpassing the combined boreal and temperate population in 1979 (Figure 2A). This trend has mostly been driven by an increase in tropical rural population growth relative to rural population growth in temperate and boreal regions (Figure 2A). The global extent of pastureland increased from 2.92 Mha to 7.43 Mha from 1900 to 2023 (Figure 2B) and mirrored temperate and boreal versus tropical rural population patterns (Figure 2A), being roughly stable in the temperate and boreal regions since 1950 but continuing to increase in the tropics. Urban population growth has been somewhat faster in the tropics than in the temperate and boreal regions. However, the extent of built-up land area has increased much faster in the tropics, from 124,238 ha (18% tropical) in 1900 to 831,573 ha (27% tropical) in 2023 (Figure 2B). Additionally, from 1900 to 2023, rangelands nearly doubled in area from 11.2 Mha (54% tropical) to 21.4 Mha (60% tropical) and cropland area increased from 9 Mha (35% tropical) to 16.3 Mha (55% tropical), with increases in rainfed and irrigated land in the tropics outpacing those in the temperate and boreal region (Figure 2B).

3.4 | Modeled changes in recent past land carbon stocks by anthrome

We compare ESM land carbon feedbacks to CO_2 (i.e., the carbon-concentration feedback, β) and warming (i.e., the carbon-climate feedback, γ) for a global subsample of empirically measured forests from various climates, soil conditions, biomass stocks, stand structures, and

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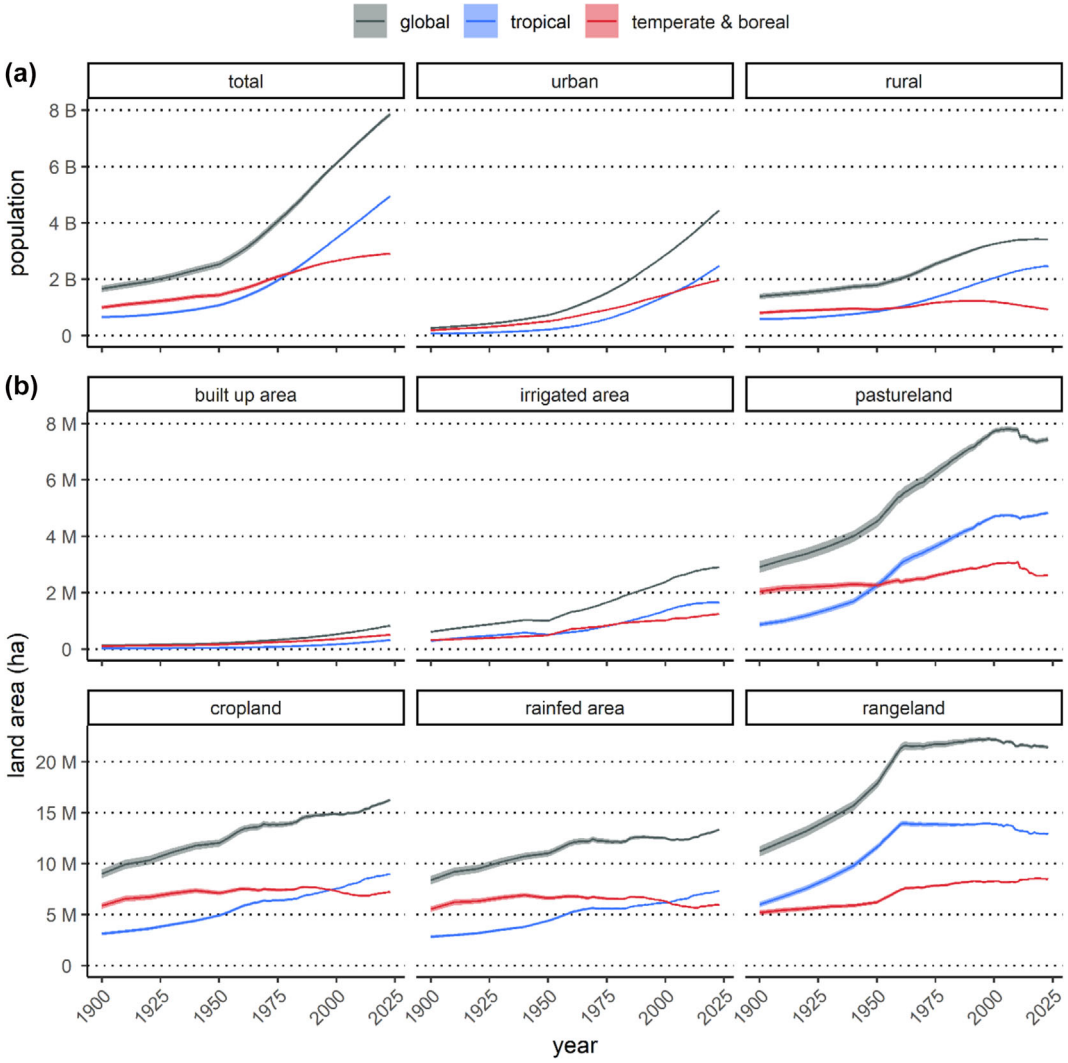

FIGURE 2 Recent past (1900–2023) changes in (a) human population and (b) land use extent for tropical versus temperate and boreal lands. Data are from HYDE 3.3; land cover and population allocation follows Klein Goldewijk et al. (2017). Lines are mean HYDE 3.3 scenario estimates and shaded regions represent 95% confidence intervals.

stand ages (Table S1). Thus, our analyses test whether ESM carbon-cycle feedbacks are distributed uniformly across anthrome land areas (i.e., intensively used, cultured, or wildland landscapes) where forests are known to exist. Although our analyses use CMIP6 ESM ensemble means, β and γ values show similar patterns globally across the nine models used to calculate the ensemble mean (Figure S3, Figure S4). ESM ensemble mean land carbon stock sensitivity (ΔC; 1900–2021) to CO_2 was greater for tropical land (15.4 ± 0.1 Mg C ha^{-1}, n = 2,886) than temperate and boreal land (8.7 ± 0.1 Mg C ha^{-1}, n = 2,334) ($F_{[1,7,534]} = 3{,}824$, $p < 0.001$). Among nine ESMs, this result was consistent for five of them (Figure S5, Table S5). ESM ensemble mean temperature-driven ΔC was more negative for tropical (−5.3 ± 0.1 Mg ha^{-1}) than temperate and boreal land (−1.4 ± 0.1 Mg ha^{-1}) ($F_{[1,7,534]} = 1794$, $p < 0.001$). Seven of the nine ESMs comprising the ensemble mean had a consistent result for temperature-driven ΔC (Figure S6, Table S6). In summary, land carbon sensitivities to both CO_2 and temperature were similar among anthrome classes in temperate and boreal areas, but distinct (i.e., more negative to temperature change and more positive to CO_2 change) for tropical wildlands compared to intensively used or cultured tropical lands (Figure 3, Table S4).

3.5 | Explaining modeled changes in recent past land carbon stocks

Of the possible drivers of modeled forest carbon stock changes that we evaluated, we found that historical (1850–2014) temperature and precipitation patterns and forest cover were mostly well-represented in ESMs, but that soils differed among anthromes. Precipitation patterns were not starkly different in intensively used, cultured, and wildland ESM land areas in either global region (Figure S7A). Tropical wildland areas had more variable historical precipitation and less variable historical temperature ranges compared to intensively used or cultured tropical lands (Figure S7A and S7B). The percentage of model

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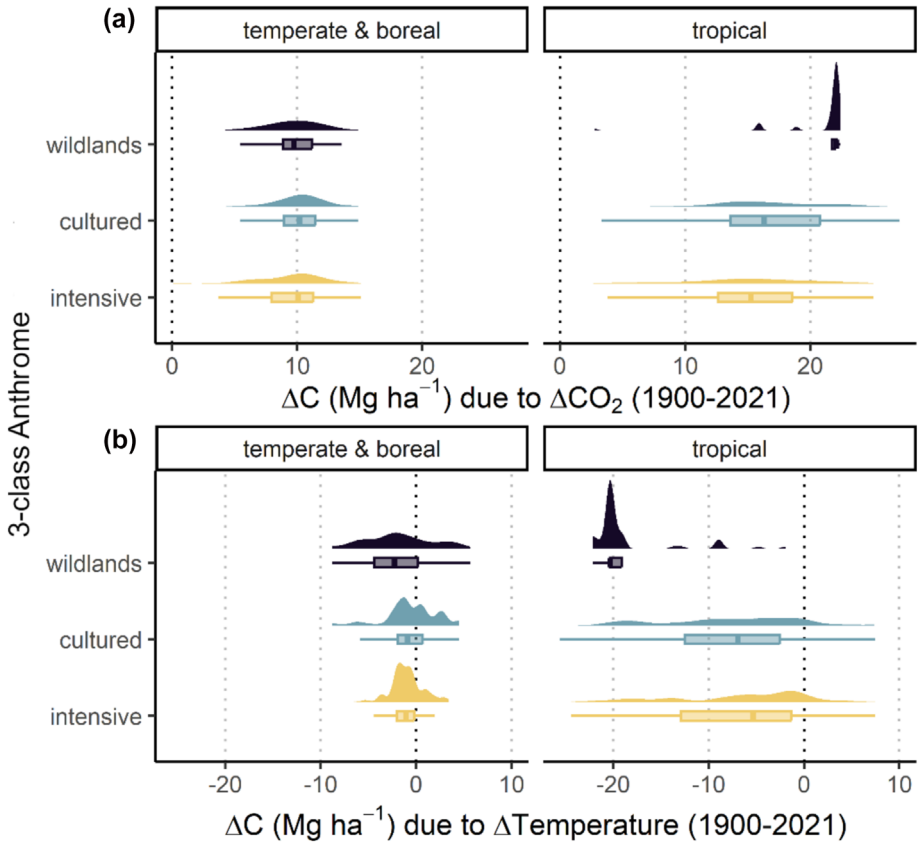

FIGURE 3 Sensitivity of land carbon stocks (ΔC, Mg ha^{-1}) to (a) CO_2 and (b) temperature increase for a global sample of forested land areas by anthrome classification and global region from 1900 to 2021. Values are derived from Coupled Model Intercomparison Project Phase 6 (CMIP6) earth system model (ESM) ensemble mean carbon-cycle feedbacks at ForC site locations (see methods), with positive values meaning land carbon accumulation and negative values meaning land carbon loss. Land carbon stock sensitivities among CMIP6 ESMs were consistent with these results from ensemble mean for five of nine models for ΔCO$_2$ (figure S5) and seven of nine models for ΔTemperature (figure S6).

land areas classified as forest in the CMIP6 static land cover data (based on the LUH2v2 forest, non-forest mark, Hurtt et al., 2020) differed among anthromes. In the temperate and boreal global regions, 49% of intensively used lands, 65% of cultured lands, and 83% of wildlands (corresponding to 0.5-degree global grids where ForC sites were located) were forested. In the tropics, differences were less apparent, with 87% of intensively used lands, 71% of cultured lands, and 99% of wildlands being forested (Figure S7C). Thus, regarding the global sample of known forest areas used in this study (based on ForC sites), input forest cover for the ESMs participating in the linear-feedback analyses better captures actual forest cover in the tropical anthromes than in temperate and boreal anthromes (Figure S7C). Lastly, differences in soil classification were evident using the Zobler (1999) data (Figure S7D) and the Harmonized World Soil Database (v.1.2., Fischer et al., 2008, Figure S8), both of which are used to some capacity in the models contributed to the CMIP6 linear feedback experiments (see Table S2). Tropical soils are distinct from temperate soils, and differences exist among anthromes, with wildlands being distinctly different from intensively used or cultured lands. Such differences were more pronounced in the tropics than in the temperate & boreal regions (Figures S7D and S8).

4 | DISCUSSION

Recent past land use patterns and ESM land carbon stock sensitivities among anthromes for a global subsample of forests (Figure 1A) show differing patterns between tropical to temperate and boreal regions of the world (Figure 3). These results have implications for the global carbon cycle. Anthrome intensification will occur as the global population growth continues, and patterns from the recent past (Figure 2) can help inform hypotheses about their future responses to global change drivers (e.g., CO_2, warming, and competing land uses).

4.1 | Anthromes, land use change, and the global carbon cycle – comparing the tropics to the rest of the world

Land use intensity is a key component of anthrome classification. Forest AGB stocks on intensively used and cultured lands are lower than those of wildlands (Figure 1C). Forests with more intensive land use can have less biomass if they are in more arable or accessible lands (e.g., closer to human settlements or roads). These forests are typically younger because agriculture has lasted longer, are more likely to be logged or fragmented, and are more vulnerable to fire, wind damage, or other disturbances (Asner et al., 2010; Helmer et al., 2008; Hu et al., 2017). Land use change (e.g., forest conversion to agriculture) is a significant net carbon source to the atmosphere and occurs primarily in the tropics (Friedlingstein et al., 2023). Three countries (Brazil, Indonesia, and the Democratic Republic of the Congo) account for 55% of the annual CO_2 flux due to land-use change (Friedlingstein et al., 2023; Obermeier et al., 2024). The net carbon source of tropical forest land-use change is 11% of total annual anthropogenic

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emissions (or 1.3±0.7 Gt C yr^{-1} from 2013 to 2022); this source is the sum of emissions due to deforestation or other land-use change and removals due to afforestation and forest restoration, and its uncertainty is large (Friedlingstein et al., 2023).

Although the magnitude of tropical forest land-use change as a net carbon source may be slowing (Baccini et al., 2017; Friedlingstein et al., 2023; Hubau et al., 2020), recent trends in emissions from land-use change in tropical anthromes likely reflect an intensification of smallholder agriculture and other land-uses, which lead to forest degradation, plus forest carbon loss from tropical montane forests (Feng et al., 2022; Lapola et al., 2023). Land-use intensification, which characterizes anthrome conversions, can have knock-on effects on other geophysical processes. For example, the annual land carbon losses due to land-use change may be increased by up to 5.1% in Amazonia and 3.8% in Congo due to deforestation-induced rainfall decline and warming (Li et al., 2022). On the other hand, forest regrowth following disturbance and degradation (e.g., clearing, fire, or logging) is a significant carbon sink driven by conversion among anthromes. For example, from 1999 to 2019, Pan, Birdsey, Phillips, et al. (2024) reported a tropical regrowth forest carbon sink of 1.46 Gt C $year^{-1}$, which is substantially larger than the estimate for temperate and boreal intact forests of 1.04 Gt C $year^{-1}$. Moreover, a recent analysis showed that the recovering tropical forests had sequestered between 0.9 and 1.3 Gt C $year^{-1}$ from 1984 to 2018, with great potential to continue to act as carbon sinks if allowed to mature, especially in the Asian tropics where recovering forests are more prevalent (Heinrich et al., 2021). Thus, the strength of the tropical regrowth forest carbon sink has been increasing over the last several decades, whereas the strength of the temperate and boreal intact forest carbon sink has been decreasing (Pan, Birdsey, Fang, et al., 2011; Pan, Birdsey, Phillips, et al., 2024).

In contrast to tropical forests, land-use changes in temperate and boreal forests contribute less to ecosystem carbon dynamics or the global carbon cycle overall. Land use processes resulting in carbon sinks in temperate and boreal regions include forest establishment on previously unforested land areas via woody encroachment (Stevens et al., 2017) and forest maturation (Pugh et al., 2019). Although a consensus is lacking and there is substantial year-to-year variation, recent evidence contends that the temperate and boreal forest carbon sinks may be stronger than the tropical forest carbon sink, and that the temperate and boreal forest carbon sink strength is related to the growth of young trees in existing forests and the regrowth of forests on deforested land (Yang et al., 2023). Specifically, using synthetic aperture radar imagery to assess trends in forest carbon stocks, Yang et al. (2023) found that from 2010 to 2019 live biomass carbon stocks increased by 0.50 ± 0.20 Gt C $year^{-1}$ globally and that boreal (+0.37 ± 0.12 Gt C $year^{-1}$) and temperate (+0.13 ± 0.9 Gt C $year^{-1}$) forests were the main contributors (with tropical forest showing a small loss). Hence, the tropical forest regrowth sink may be waning, with implications for the strength of the global land carbon sink (Hubau et al., 2020, but see Heinrich et al., 2021). Although land-use change is still the main driver in the tropics, forest maturation and natural disturbance dynamics of temperate and boreal forests are increasingly important to the global land carbon balance.

Over half of the primary forests are in boreal regions of the Northern Hemisphere, which sequester about 1.3 ± 0.5 Gt C yr^{-1} (Luyssaert et al., 2008). Depending on how emissions and removals are calculated for national greenhouse gas inventories (NGHGIs), large swaths of primary forests can be excluded because the UN IPCC Good Practice Guidance does not require nations to report emissions from unmanaged lands (IPCC, 2006, 2010). The current IPCC definition of managed lands includes areas 'where human interventions and practices have been applied to perform production, ecological or social functions' (IPCC, 2006, p.4.76). Regarding wildland anthromes, the classification of managed vs. unmanaged lands is the subject of considerable definitional debate which increases uncertainty surrounding our understanding of land carbon balance (Nabuurs et al., 2023). Accordingly, a large gap exists (1.8 Gt C yr^{-1}) in estimated land CO_2 fluxes between NGHGIs and the ensemble mean bookkeeping model, most of which likely lies in temperate and boreal forests (Dorgeist et al., 2024; Grassi et al., 2021, 2023). However, employing an anthromes perspective reveals that only 26% of the global land surface is wildlands (Figure 1) and even these lands do not entirely lack human influence (Ellis et al., 2021; Fletcher et al., 2021). Moreover, given recent land-use trends (Figure 2), even the choice to leave forests as forests is a management decision; thus, in the modern Anthropocene, all lands are managed to some degree.

Representing all forests in NGHGIs and global carbon budgets by applying a holistic approach that classifies forests across their range in human population density (i.e., from intensively-used to cultured to wildland forests) will be important for accurately documenting their role in the global carbon cycle (Houghton, 2020). Additionally, there is high uncertainty in the magnitude and sign of the future tropical forest carbon balance because of the uncertain ecophysiological response of tropical forests to climate change (Chen et al., 2022; Hubau et al., 2020; Lloyd & Farquhar, 1996) and because it is unclear if deforestation rates will continue to decline in the coming years to decades (FAO, 2022; Feng et al., 2022). Accountability for land management in the tropics is imperative not only at national governance levels (Obermeier et al., 2024), but also among individual landholders, consortiums, and communities (Furumo et al., 2024). Communities manage at least 22% of tropical forest land carbon stocks and occupy about 50% of tropical terrestrial lands, owning up to 11% of it; thus, carbon storage and sequestration goals will rely on the participation of local land stewards (Frechette et al., 2018).

4.2 | Wildland tropical forests are uniquely vulnerable to climate change

Modeled land carbon stock sensitivity to warming and CO_2 across anthromes were similar in temperate and boreal forests, but different for tropical wildlands compared to intensively used or cultured tropical lands (Figures 3, S5, S6). Modeled tropical wildland carbon stocks are particularly sensitive to warming, illustrating the potential vulnerability of wildland tropical forests to climate change (Doughty et al., 2023; Hubau et al., 2020; Nobre et al., 2016). Notably, the Amazon region is

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disproportionately represented in our sample of tropical wildland areas, which was based on ForC AGB measurements (Figure 1A), so our results regarding wildland tropical forests should be understood in that context. We infer patterns of land carbon stock sensitivity in relation to past climate trends, model input forest cover (from 1850 static land use), and soil classification. Although there is some variation in the magnitude of carbon-climate feedback strength among the nine ESMs used to calculate the ensemble mean (Figures S3 and S4), variability in ΔC among models (represented as standard error) is homoscedastic across anthromes in the tropics and the temperate and boreal zone (Figure S7). Moreover, the expected effect of any mismatches (or errors) in the environmental data we use (CO_2, temperature, or soil class) is to weaken the estimated relationships between response (ΔC) and explanatory (environmental) variables (Lichstein et al., 2014). The differences in modeled land carbon stock sensitivity to CO_2 increase and warming among tropical anthromes in ESMs (Figure 3) do not appear to be related to historical trends in precipitation or temperature (Figure S8). These land carbon stock sensitivities also appear unrelated to patterns of static forest cover (from 1850 to 2,100) represented in ESM feedback experiments (i.e., by LUH2v2 forest/non-forest mark from Hurtt et al., 2020) because each anthrome had approximately ≥50% forest cover in ESM land areas (Figure S8).

Although there are differences in how the land carbon cycle represented in the CMIP6 models contributed to the linear feedback analysis, the most likely explanation for the observed differences is how soils affect land carbon (i.e., productivity) responses to CO_2 and temperature increase. One explanation may be a rudimentary representation of biogeochemical constraints on land carbon uptake in ESMs, which are only included in some of the models contributing to the CMIP6 linear feedback experiments (Table S2) and are notoriously difficult to represent in large ESMs (Knox et al., 2024). Some models contributed to the CMIP6 linear feedback analysis have nitrogen dynamics, but only one has phosphorus dynamics (ACCESS-ESM 1.5, Arora et al., 2020, Table S2), which are integral to modeling tropical forest land carbon dynamics, especially in high-biomass wildland tropical forests subject to nutrient limitation (Fleischer & Terrer, 2022; Gier et al., 2024; Yang et al., 2014). A second explanation may be the ability of ESMs to capture the range of soil variability present in wildland tropical forests, and its effect on water and carbon flux from the soil and plants to the atmosphere. Both datasets used in ESMs that have spatial soil classification show tropical wildlands to be distinct from intensively used or cultured tropical lands (Figures S8 and S9). In a previous version of the UK ESM (HadCM3LC), the positive land carbon-cycle feedback was associated with drought-induced forest dieback in the Amazon and significant carbon loss from soils due to elevated soil respiration (Cox et al., 2000, 2004). Changing the soil parameterization from a single-layer to a four-layers confirmed the robustness of the positive feedback, but diminished its magnitude and extended its timescale (Jones et al., 2005). This example illustrates how tropical forest carbon-cycle feedbacks are depended on the number and properties of the soil layers included in ESMs being particularly sensitive to water and carbon fluxes from the soil to the atmosphere, which are mediated by complex plant-water processes that are especially difficult to model and empirically validate (Knox et al., 2024).

Accordingly, there is a known bias for ESMs in the linear feedback experiments to overestimate tropical biomass production and underestimate biomass production in the temperate and boreal regions (especially the southern hemisphere; Gier et al., 2024); yet, the ESM carbon-concentration and carbon-climate feedback ensemble means are robust and represent our best model-based understanding of how land carbon stocks have responded to CO_2 and climate since 1900 (Arora et al., 2020; Canadell et al., 2021; Friedlingstein, 2015). The ensemble means show a pattern of greater land carbon stock sensitivity to both CO_2 and temperature for tropical wildlands relative to other anthromes, which has implications for how tropical wildlands are managed regarding natural resource demands considering the Rio conventions on reduced degradation and deforestation of tropical

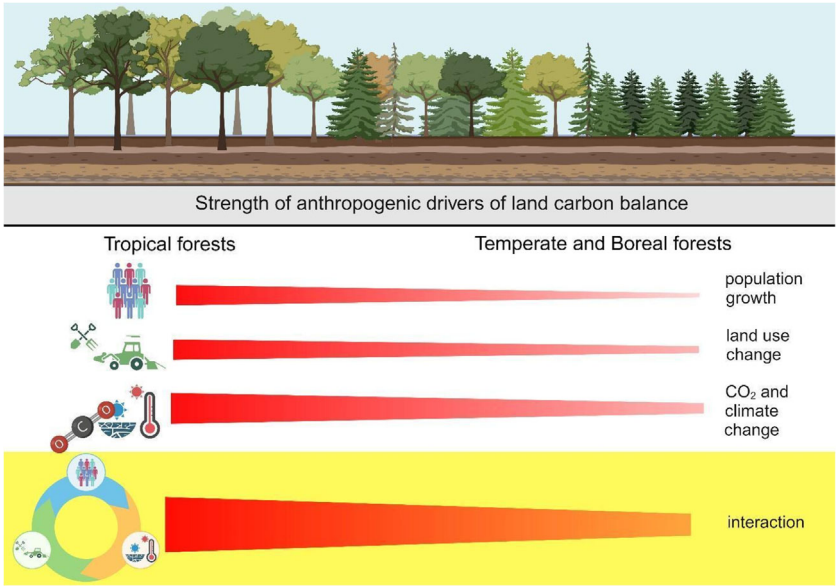

FIGURE 4 The strength of the three important anthropogenic drivers of ecosystem carbon stock sensitivity for tropical (left) versus temperate and boreal forests (right). Population growth and land use change since 1900, but especially since 1950, have affected tropical land areas more than temperate and boreal land areas (Figure 2). Recent past climate change (since 1900) is affecting all forests but is affecting modeled tropical forest carbon stocks to a greater degree, especially wildlands (both more positively to CO_2 increase and more negatively to warming) (Figure 3). The interaction between population growth, land use change, and future climate change (yellow) will determine future forest carbon stocks across the range of human land use intensities and ultimately their contribution to the global land carbon sink; such interactions are likely stronger in the tropics where population growth and resource demand are highest.

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lands. Major challenges persist regarding tropical forest conservation, yet they will be instrumental in the role of these ecosystems in the future of the global carbon cycle. Allowing for tropical forest regrowth and restoration is imperative to providing tropical trees the best chance at adapting to change.

5 | CONCLUSION

Earth's forests are widely affected by human activities and continue to be dynamic in their responses to land use and climate change (Figure 4). Aboveground biomass stocks vary among anthromes with tropical wildland forests having the largest stocks (Figure 1; Anderson-Teixeira et al., 2018); the vulnerability of these forest carbon stocks to climate and land-use change will determine future global land carbon balance. Although impacts vary, land use changes are most dynamic in the tropics (Figure 2). According to ESMs, climate change is affecting all forests, with CO_2 increase leading to a positive response of forest carbon stocks globally, with the strongest responses in wildland tropical forests (Figure 3). Modeled results show that recent past temperature increase has led to slight declines in temperate and boreal forest carbon stocks, but greater and more variable declines in tropical forest carbon stocks, with wildland tropical forests being particularly sensitive (Doughty et al., 2023). The stronger climate and carbon feedbacks of tropical wildlands compared to tropical cultured or intensively used lands in ESMs appears to be related to soil type differences of these ecosystems (Figure S8, Figure S9); the mechanisms linking soil variation and its effect on modeled carbon and climate feedbacks of terrestrial land carbon stocks is unclear, likely varies for each of the ESMs included the CMIP6 linear feedback experiments (Table S2) and warrants further model development and investigation. Ecosystem processes that govern carbon-cycle feedback to temperature and CO_2 are complex, and although there is substantial uncertainty about how carbon-cycle feedbacks will affect future forest functioning (i.e., carbon sinks), forest responses will depend on future land-use change, economic and political drivers of human behavior, and natural forest dynamics (Figure 4). These drivers will determine future anthrome forest structure, biomass carbon stocks, and their contribution to the global carbon cycle (Gatti et al., 2021; Nobre et al., 2016); the realistic expectation is future weakening of the land carbon sink (Schimel & Carroll, 2024).

AUTHOR CONTRIBUTIONS

JAH conceived of the presented idea under the guidance of APW, JWL, ECE, and EHH. JAH conducted the analyses. CK processed and contributed CMIP6 carbon cycle feedback data. JAH, MEC, EF, VH, CDK, SAK, DML, YL, YM, JQ, SR, CT, EV, APW, and ECE attended the *New Phytologist* symposium "Anthromes, CO_2, and Terrestrial Carbon: From the deep past to net-zero" in March 2023. JAH, JWL, EHH, MEC, EF, VH, CDK, SAK, KKW, DML, YL, YM, JQ, SR, CT, EV, APW, KZ, and ECE participated in virtual discussions and commented on and revised manuscript drafts.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All data used have already been publicly archived. The ForC database (Anderson-Teixeira et al., 2018) is available at: https://github.com/forc-db CMIP6 carbon cycle feedback data were processed from models contributed to CMIP6 linear feedback experiments by Charlie Koven and are available at: https://github.com/ckoven/cmip6_beta_gamma_maps/.

Additional datasets which were used (e.g., CMIP6 historical climate, historical CO_2 data, and Berkeley Earth surface temperature data) are cited.

Analyses (including R code) are documented at: https://github.com/hoganhaben/P3_Anthromes_ForestCarbon

SUPPORTING INFORMATION

This paper contains a supporting information file with six supporting tables and nine supporting figures.

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