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Congruent Long-Term Declines in Carbon and Biodiversity Are a Signature of Forest Degradation

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ABSTRACT

Recent global policy initiatives aimed at reducing forest degradation require practical definitions of degradation that are readily monitored. However, consistent approaches for monitoring forest degradation over the long term and at broad scales are lacking. We quantified the long-term effects of intensive wood harvest on above-ground carbon and biodiversity at fine resolutions ($30\,m^2$) and broad scales (New Brunswick, Canada; $72{,}908\,km^2$). Model predictions for above-ground biomass were highly correlated with independent data ($r=0.77$). After accounting for carbon stored in wood products, net CO_2 emissions from forests for the region from 1985 to 2020 were 141 CO_2e Tg (4.02 TgCO_2e year^{-1}; 32% of all reported emissions). We found strong positive correlations between locations with declines in above-ground carbon and habitats for old-forest bird species, which have lost > 20% habitat over 35 years. High congruence between biodiversity and forest carbon offers potential for policy incentives to conserve both objectives simultaneously and slow rates of forest degradation. These methods could be used to track forest degradation for managed forest regions worldwide.

1 | Introduction

Climate change and biodiversity declines are two of the most pressing issues facing humanity (Ripple et al. 2022). Until recently, the climate and biodiversity crises have been discussed and tackled in discrete, non-unified efforts (Pörtner et al. 2021). Only rarely are long-term trends in carbon and biodiversity jointly examined in forests—which house the majority of Earth's terrestrial biodiversity (Pillay et al. 2022), store an estimated 45% of terrestrial carbon (Bonan 2008), and absorb ~2 gigatonnes of carbon (GtC) annually (Pugh et al. 2019). Understanding the degree to which managed forest landscapes influence carbon stores and biodiversity is crucial for global carbon accounting and biodiversity conservation because these forests occupy 2 billion hectares of the Earth's surface (about 47% of forests globally) (FAO and UNEP 2020). Given an expected increase in global wood demand of up to 54% by 2050 (Betts et al. 2021; Peng et al. 2023) the degree to which managed forest landscapes contribute to carbon and biodiversity conservation stores is particularly important.

Management and conservation of carbon and biodiversity in forests is increasingly a focus of international, national and regional policy attention (Bastin et al. 2019; Pereira et al. 2024). "Natural climate solutions" via tree planting and forest conservation have been repeatedly proposed as a means to combat climate change (Lewis et al. 2019; Luyssaert et al. 2008). International agreements are in place to incentivize carbon storage in forests (West

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et al. 2023). Similarly, in 2022 the United Nations Biodiversity Conference (COP15) developed the Kunming-Montreal Global Biodiversity Framework (GBF) which includes financial incentives for biodiversity conservation ($200 billion per year from public and private sources).

Great potential therefore exists for financial incentives to manage forests for biodiversity–carbon "co-benefits." However, for policy incentives to be effective, methods must be available to quantify the spatial distribution of both outcomes. Although carbon/biodiversity co-benefits have been mapped at broad, global scales (Soto-Navarro et al. 2020), relatively little work has been done at sufficiently fine scales to enable forest management planning, and adherence to policy.

Halting forest degradation, with a particular focus on loss of biodiversity and carbon storage in forests, is a core motivation for the EU policy focused on limiting forest degradation (European Union 2023). But how does one define and quantify forest degradation? Forests are naturally dynamic in both space and time; disturbance—at tree, stand, and landscape scales is typical of forest systems worldwide. Unlike deforestation, which is the relatively unambiguous conversion of forests to non-forest types (e.g., agriculture, urban) understanding degradation requires considering the capacity of a system to reorganize and recover following disturbance (Ghazoul et al. 2015). The key questions are whether local (stand)-scale reductions in biodiversity or carbon are compensated for by regrowth elsewhere in the landscape (resulting in no net landscape-scale loss of biodiversity or carbon) (Betts et al. 2024). Degradation can thus be framed as a continuous recovery function that is a product of both the severity of disturbance and the rate of recovery at landscape scales (Ghazoul et al. 2015); if disturbances are too large or frequent, the system can shift to an alternative state from which it is difficult to return.

The link between biodiversity and forest structural complexity of mature forests is relatively well known (Goetz et al. 2010; MacArthur 1958) and forest bird habitat is strongly associated with forest structural attributes (MacArthur 1964). Indeed, recent work in eastern Canada found that systematic reductions in mature forest due to short timber harvest return intervals has resulted in declining habitat and populations of old-forest associated birds (Betts et al. 2022). This is despite an overall net gain in forest cover for the same region.

Although one might expect declines in mature forest via timber harvest to also be associated with erosion of stored carbon, this point has been heavily debated (Kauppi et al. 2022; Law et al. 2018; Schulze et al. 2022). Mature and old-growth forest in many temperate forest systems is expected to have higher wood volume and above-ground carbon stores than young and intensively managed forests (Gunn, Ducey, and Whitman 2014; Harmon, Ferrell, and Franklin 1990; Sillett et al. 2022), despite the fact that the latter often accumulate carbon at faster rates. Managing for more complex forest structure of mature forests has been demonstrated to increase carbon stocks relative to typical forestry practices (Ford and Keeton 2017). Nevertheless, it is often assumed that a sustained yield approach in managed forests should result in no net carbon loss (Hoxha et al. 2020; Schulze et al. 2022). Life-cycle analyses of wood products often treat uses of wood products as "carbon neutral" under the condition that timber originates from sustainably managed forests. "Sustainable" is often defined as occurring if carbon stocks do not decline at rates greater than annual forest growth (Peng et al. 2023). Thus, temperate managed forests of the world are often considered net carbon sinks in international accounting efforts, and yet Peng et al. (2023), using a time discounting modelling approach, found that wood harvests may result in significant carbon emissions at the global scale. The question of whether current forestry practices result in net gains or losses to above-ground carbon and biodiversity at the landscape scale has yet to be resolved—particularly for forests undergoing shifts from unmanaged to intensively managed harvest regimes.

Fortunately, tools are now available to quantify not only current above-ground carbon and biodiversity (via remote sensing) but also to back-cast over the long term to test whether forest management practices have degraded these attributes (Gorelick et al. 2023). We used remotely sensed data (Landsat 5, 7–9) combined with ground-based forest inventory plots to develop spatial models for above-ground biomass and bird habitat (a proxy for biodiversity). We then back-cast these estimates to quantify long-term, regional-scale changes in carbon and habitat over 35 years (1985–2020). Under the hypothesis that older, complex forests house the most carbon and high habitat amounts for mature-forest associated birds we expected spatial congruency in these attributes and their long-term trends. Given that short-rotation intensive forestry in the region preferentially targets structurally complex mature forests, we hypothesized that both bird habitat and carbon would show long-term declines—a signature of forest degradation. Finally, we conducted a life-cycle analysis of harvested wood products to test whether forest management has constituted a net carbon source or sink over the long term (1985–2020).

The methods and maps we present can serve as the basis for long-term monitoring of the effectiveness of different silvicultural regimes for biodiversity and carbon sequestration—two key indicators of forest degradation. These approaches can also facilitate selecting future conservation areas based on habitat and carbon value and evaluating the effectiveness of protected areas and other habitat conservation strategies (Wolf et al. 2021).

2 | Materials and Methods

2.1 | Above-Ground Carbon Modeling

We used forest inventory data from the NB Continuous Land Inventory (CLI; Colpitts 2017; Hennigar and Lamb 2022) to model above-ground biomass across the province of NB (72,908 km^2). The CLI comprises 6049 fixed-area plots established from 2016 to 2020 and trees were identified to species and measured to the nearest 2 cm in diameter at breast height (DBH) within a 400 m^2 circular plot with a nested 50 m^2 plot for small trees (1–7 cm DBH) (Hennigar and Lamb 2022). Plots are remeasured on a 10-year cycle on private land, and a 5–10 year cycle on public (Crown) land. This network of plots represents NB's best unbiased ground inventory of NB forests and is the primary data set used to calibrate and validate remotely sensed forest inventory models (Hennigar and Lamb 2022). We used species-specific form factors and site indices to relate diameter to height and species-level specific gravity to estimate plot-level biomass (Lambert, Ung, and Raulier 2005).

2.2 | Remote-Sensing Data as Predictor Variables in Above-Ground Carbon and Species Distribution Models

Landsat data in the current era (Landsat 5-onward) are available at 30-m pixel resolution and have been collected since 1985 (35 continuous years). We matched the collection date of CLI data to the month and year of Landsat data. July 1 was chosen as the anniversary date for annual mapping. Using Google Earth Engine (GEE), we obtained cloud-free spectral surface reflectance from Landsat collection 1 Tier 1 from 2016 to October 2021 for building and testing our carbon model. We used all cloud-free acquisitions for each pixel, fitting a harmonic function to capture the cyclical reflectance change due to vegetation phenology as well as discontinuities due to disturbance. We used the CCDC (Continuous Change Detection and Classification) algorithm (Zhu and Woodcock 2014), as implemented in the GEE (Cohen et al. 2017) to fit each six Landsat spectral bands in the form of:

$$R_t = A_0 + B_0 t + \sum_{k=1}^{3} \left\{ A_k \cos\left(\frac{2\pi}{T} kt\right) + B_k \sin\left(\frac{2\pi}{T} kt\right) \right\}$$

where R_t is the surface reflectance at time t (represented as day of year) for a spectral band, A_0 is the intercept, B_0 is the inter-annual trend (slope) of surface reflectance, A_k and B_k are the coefficients for intra-annual spectral change; k is the temporal frequency of harmonic components ($k=1$, 2, and 3). T represents the number of days in a year ($T=365.25$). CCDC detects where change occurs in the spectral trajectory. The advantage of this approach is that it capitalizes on (1) within-year changes in reflectance (e.g., differential rates of leaf out across tree species), and (2) among-year changes in reflectance caused by disturbance and regrowth, to add additional forest composition information to raw reflectance bands. The harmonic coefficients (8 coefficients) for each band (6 bands) as well as 6 root-mean-squared error from the harmonic fits were used as environmental variables in the RF (54 variables).

We used Random Forests (RF; Cutler et al. 2007) to model above ground biomass for trees > 3 cm as a function of six Landsat reflectance bands. RFs are a machine-learning approach involving fewer assumptions and often higher prediction accuracy in relation to parametric statistical approaches (e.g., linear regression). We used the RF defaults for continuous response variables, where branches are grown that reduce the sum of squared errors. We evaluated the tuning parameters "numberOfTrees" and "minimum leaf populations"; final models used numberOfTrees = 50 and minimum leaf population = 1. Model error was not sensitive to the number of trees (Figure S1).

Because the relationship between Landsat reflectance and biomass could be spatially nonstationary (i.e., change across geographic space), we used 300, 60 × 60 km randomly selected spatially overlapping modeling zones to build localized biomass models (Figure S2). For each 60-km modeling zone we required a minimum sample of CLI 100 plots. For 19 randomly selected zones, there were less than 100 plots; in these cases, we included additional plots from a 30-km buffer around the 60-km zones as augmented training samples. To ensure that every pixel in the study area had a valid prediction, we built a biomass model for the whole study area using all plots.

The mean from all the local models was used as the final above-ground biomass prediction. The mean out-of-bag error (OOB) from the 301 models was 46.8 with an SD of 5.02. We tested the performance of Random Forest models using a randomly selected hold-out dataset which constituted 20% of our plots ($N=1209$). Finally, we used our final biomass model to predict biomass for each year of available Landsat data (1985–2020) and calculate total biomass change for each 30 m^2 pixel across the study area. We removed the effect of carbon loss due to urbanization by masking our map of carbon change with 2020 Canadian land-use data (Latifovic 2020). All modeling, and backcast predictions were implemented in the GEE.

2.3 | Species Distribution Models

We used species distribution models (SDMs) developed in Betts et al. (2022) to examine the spatial congruence between areas of high remaining carbon density and areas of high habitat availability. Bird data were collected from 2006 to 2010 at 12,272 sample points distributed across three Canadian provinces: NB, Nova Scotia and Prince Edward Island (Betts et al. 2022). We used presence-only models (Maxent; Phillips et al. 2006) to predict the distributions of 54 bird species as a function of Landsat data that temporally and spatially matched each bird sample point. From these 54 species, we specifically highlight mature-forest associated species according to Birds of the World (Billerman et al. 2020) because habitat and populations of these species are declining at the greatest rates (Betts et al. 2022) and we hypothesized that they would show the highest concordance with distributions and changes in above-ground carbon. Details and model prediction metrics are available in Betts et al. (2022).

2.4 | Biodiversity-Carbon Co-Benefits

We examined the concordance between spatial locations with high carbon and high probabilities of each species' occurrence with Pearson correlations (r) at the 30 m^2 pixel scale for the entire province of NB. Additionally, we tested the degree to which *change* in habitat was associated with change in carbon over the 35-year time period. Under the hypothesis that mature-forest bird species habitat conservation should affect carbon storage, we expected that locations with stable mature-forest bird habitat should show consistent or increasing above-ground carbon. Losses to habitat should be reflected by losses to carbon. We conducted this analysis for 25 km^2 (50 km × 0.5 km) landscapes surrounding long-term Breeding Bird Survey routes distributed across NB ($N=47$).

2.5 | Wood Product Life-Cycle Analysis

Harvested wood products in northeastern North America can be a significant pool of stored carbon depending on the fate of the product and the time period considered (Gunn and Buchholz 2018; Zhao, Wei, and Li 2022). Accounting for this pool is needed to make a complete assessment of the carbon implications of timber harvesting. In addition to the harvested wood fates, a complete quantification also includes estimates of harvest, transport, and manufacturing emissions. To make this assessment, we obtained wood product harvest volume data for 1990–2020 from Canada's National Forestry Database (Canadian Council of Forest Ministers 2022, table 5.1). In the absence of wood product harvest data from 1985 to 1989 to match the entire study period, we extrapolated the 1990–1994 mean volumes for each product category to estimate 1985–1989 volumes. We calculated annual harvest, transport onsite and upstream fossil fuel emissions from 1985 to 2020 based on CO_{2e} emissions per cubic meter harvest volumes using mean factors reported by Cameron et al. (2013, table 3) for harvest operations in NB. We also used mean sawmill and pulp and paper manufacturing emissions factors for NB from Cameron et al. (2013, table 3) to calculate annual forest product manufacturing emissions from 1985 to 2020.

We used a recently published wood product life cycle tool to quantify carbon stored after harvest from 1985 to 2020 (Wei et al. 2023). The Wood Products Carbon Storage Estimator (WPCS Estimator; Wei et al. 2023) estimates carbon stored in wood products over time based on parameters that incorporate combustion efficiency for biofuels, charcoal and landfill decay rates, disposal rates for end-use wood products, recycling rates for recyclable disposed wood materials, and landfill decay rates for waste wood products. (Wei et al. 2023) provide default parameters in a case study for the US state of Maine which borders NB. These parameters are appropriate for NB given that Maine and NB have similar forest species composition and mix of forest products (e.g., pulp, paper, and dimensional lumber) and historically there has been significant cross-border trade in unprocessed wood with ownership of industrial timberland and mills in common on both sides of the border (Irland 2000). The WPCS Estimator reports cumulative wood product carbon pools still in use over time based on annual wood product harvest volume inputs. We calculated the total carbon in use for the period 1985 to 2020.

Our life cycle analysis boundary did not include an attribution of the potential substitution benefits of using wood for energy or the displacement of concrete or steel as building materials. Instead, the results reflect the direct emissions and storage implications of harvested wood products. Depending on the assumptions made about the baseline or reference case uses for energy and buildings, the estimated avoided emissions from making substitution and displacement attributions can be significant (e.g., Gunn and Buchholz 2018) but highly uncertain given the time frame of the study (Brunet-Navarro et al. 2021).

3 | Results

Since 1985, >3 million ha have been clearcut (Figure S3; Betts et al. 2022) with most of this area now occupied by either tree plantations and commercial thinnings, which are dominated by single tree species or a mix of early successional tree species. Despite some ingrowth due to succession, old forest has declined by 39% over the period observed (Figure S3). The pattern of extensive harvest of old forest has the potential to result in "forest degradation" in that these practices simplify forest structure, reduce tree species diversity, and truncate old forest age classes (Hunter 1999). Over the same 35-year time period, forest cover remained relatively stable, increasing by a net 6.5% (Figure 2a, red line; Hermosilla et al. 2022).

Model predictions for above-ground biomass were highly correlated with observed data ($r=0.77$) using only Landsat reflectance data and the CCDC approach (Figure 1). Across the entire region, over the 35-year period observed, we estimate that net above-ground biomass has been reduced by 128.69 Tg. Although areas have gained as much as 150 Mg ha^{-1} over 35 years, others have lost as much as 185 Mg ha^{-1} (Figure 2a,c). Overall, above-ground biomass decline is approximately equivalent to −236.15 Tg of atmospheric CO_2 (CO_2e), using a conversion factor of 1.835, which is conservative given the tree species of NB. Conversion of old forests to younger forests (including plantations) in NB has thus been a significant source of atmospheric carbon. Proportionate declines in above-ground carbon are greatest for private industrial land (−23%) followed by Provincial Crown land (−17%; Table 1). Despite the substantial amount of above-ground biomass on small private woodlots (29.29 million Tg) biomass loss has been relatively low over the 35-year period (−12%; Figure 3b; Table 1).

Importantly, it is unlikely that any substantial component of this biomass loss is due to natural disturbance (fires, insect outbreak) or heat and drought stress due to climate change. First, we did not observe biomass loss in protected areas that did not experience harvest over 35 years (Figure S4). Second, we found strong correlations between the amount of forest clearcut (reported in Betts et al. 2022) and declines in above-ground biomass over the time period (GLMM: $\widehat{\beta} = -64.54$ [CI −70.56, −58.51], $t=-20.974$, $p<2\times10^{-16}$; Figure S5). Third, the area affected by

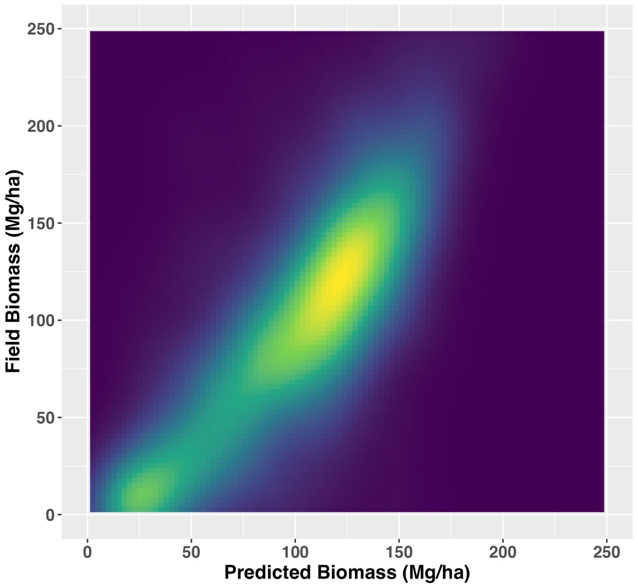

FIGURE 1 | Correlation between the predicted and observed above-ground biomass (Mg/ha) from our Random Forest model. Observed values constitute 20% of data held out as an independent model test set. Note that the relationship between predicted and observed field biomass closely follows a 1:1 (isometric) relationship, indicating low bias in predictions.

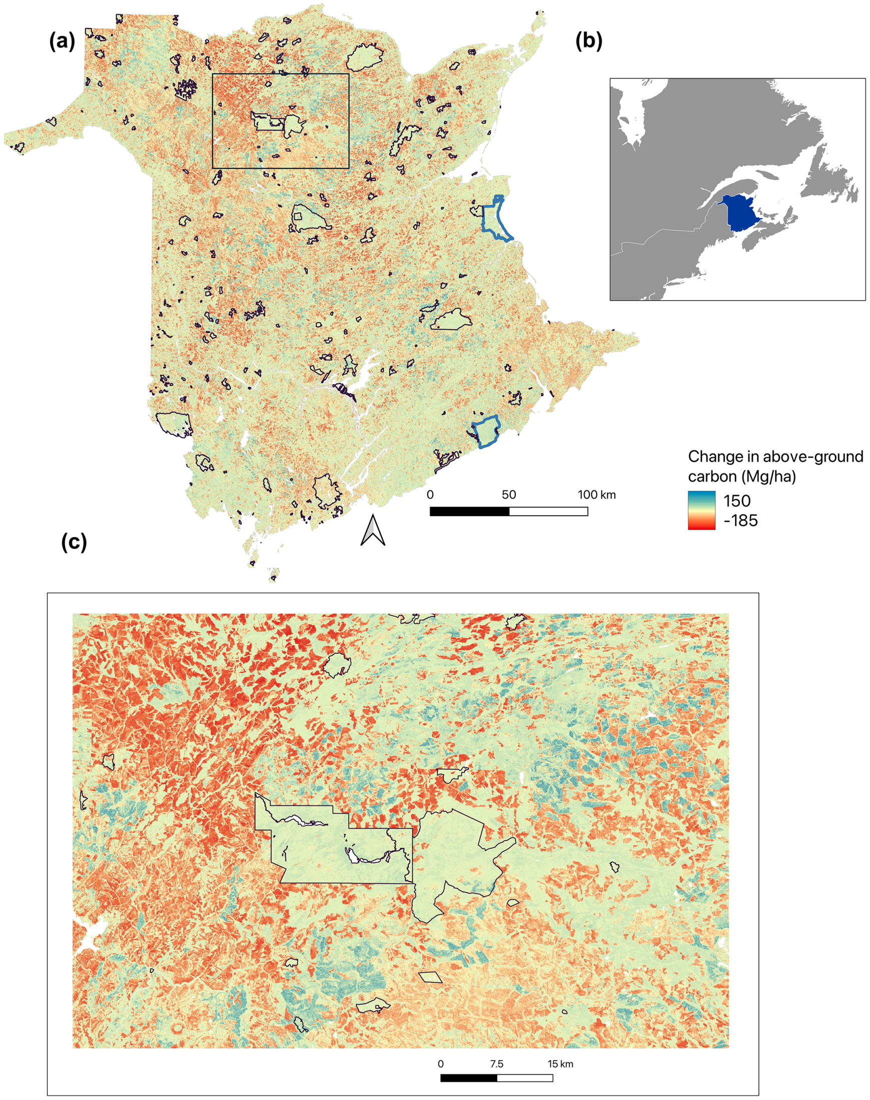

FIGURE 2 | (a) Biomass change across New Brunswick (Mg/ha) from 1985 to 2020 with red indicating areas of high carbon loss and blue as carbon gain. Panel (b) shows eastern North American context for the study region, and (c) is a zoomed-in view of a landscape with high above-ground carbon loss. Provincial protected areas are outlined in black, and Canadian national parks in blue.

TABLE 1 | The above-ground biomass and estimated change for the province of New Brunswick 1985–2020 according to random forest models.

Tenure	Biomass (1985, Tg)	Biomass (2020, Tg)	Change in biomass (Tg)	Biomass change (%)
Federal	18.49	16.68	−1.81	−9.77
Industrial	137.22	105.98	−31.24	−22.76
Provincial	383.91	317.56	−66.36	−17.28
Small ownerships	234.99	205.70	−29.29	−12.46
Total	774.62	645.93	−128.69	−16.61

stand-replacing fire has been exceptionally low; since 2001, the first year of available fire data, on average 0.35% of forest loss each year is due to fire in New Brunswick, with the rest attributable to wood harvest (Global Forest Watch 2024; Figure S6).

Overall, SDMs using Landsat reflectance bands as predictors performed well for most forest bird species when tested on 50% spatially discrete hold-out data ($\bar{x}$ Area Under the Curve (AUC) = 0.73 [range: 0.60–0.90]). SDMs therefore provided reliable estimates of habitat suitability and distributions for most species (for additional details see Betts et al. 2022). We back-cast SDMs to quantify habitat change for forest bird species from 1985 to 2020. Species showing the greatest decreases in habitat were Dark-eyed Junco (*Junco hyemalis*; −41%), Golden-crowned

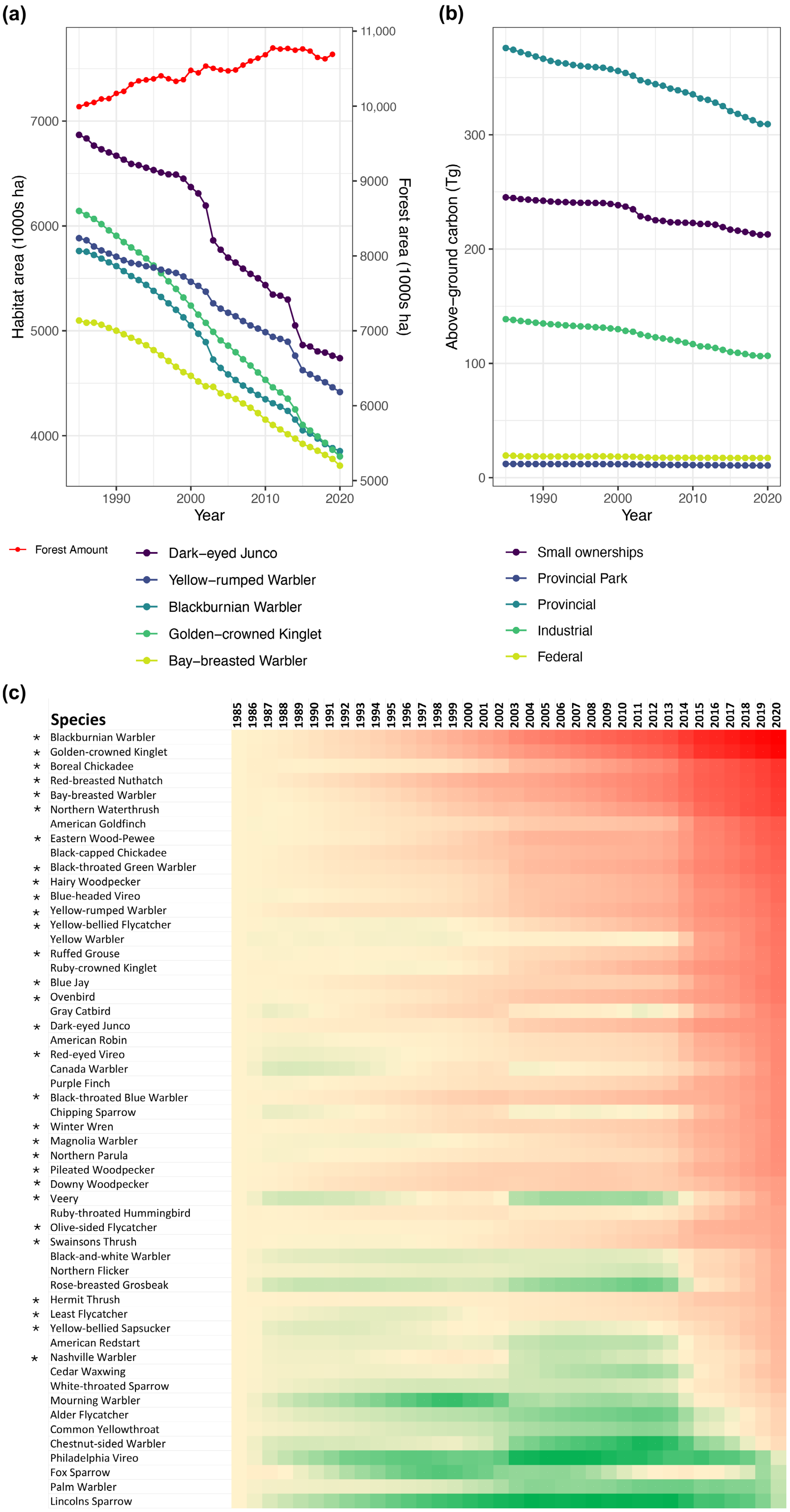

FIGURE 3 | Forest degradation drives long-term declines in forest bird habitat and carbon storage. (a) Habitat trends (1985–2020) for the five bird species exhibiting the greatest declines according to SDMs; all of these species are old forest associated (see Table S2). During the same time interval, total forest cover did not decline (red line, right axis), indicating that habitat loss is a function of forest degradation rather than loss. (b) Above-ground carbon change for five major land tenures in New Brunswick. (c). Habitat change (1985–2020) for 54 species of forest birds according to back-cast species distribution models. Transitions from green, through yellow, to red across cells indicate annual habitat loss. Seventy percent of species show net habitat loss over the full time period, and 95% lost habitat over the past 10 years. Mature-forest associated species are denoted with an asterisk (*).

Kinglet (*Regulus satrapa*; −38%) and Blackburnian Warbler (*Setophaga fusca*; −33%), with seven species showing habitat declines > 25% (Figure 3a,c). In total, 38/54 species (70%) showed habitat declines over the 35-year period in comparison to only 14 species (26%) with habitat increases—all of which are early seral forest associates (Figure 3c). Consistent with our hypotheses, old-forest associated birds showed the greatest rates of habitat declines (Table S1), which is consistent with forest degradation due to harvesting of old forest.

3.1 | Habitat Amount and Carbon Change

We examined the degree to which each of 54 bird species showed correlations between locations of habitat and above-ground carbon. We found strong positive correlations ($r > 0.5$) for seven species, with 27 species being significantly positively correlated ($r > 0.25$) with high above-ground biomass (Figure 4; Table S2). We also found positive correlations between change in above-ground carbon and change in habitat amount for 33 species (Figure 5; Table S2). Only five species showed statistically significant gains in habitat associated with carbon losses. Unsurprisingly, species showing the strongest correlations between habitat loss and carbon loss were mature-forest associated species (Figure 5; Table S2). Strong positive correlations indicate that conservation of a particular species' habitat should also provide co-benefits in terms of continued carbon storage. Blackburnian Warbler, Black-throated Green Warbler, Black-throated Blue Warbler and Ovenbird exhibited the greatest correlations with forest above-ground carbon and change in above-ground carbon and therefore constitute carbon indicators. Therefore, efforts to conserve these species habitats are consistent with objectives to store above-ground carbon.

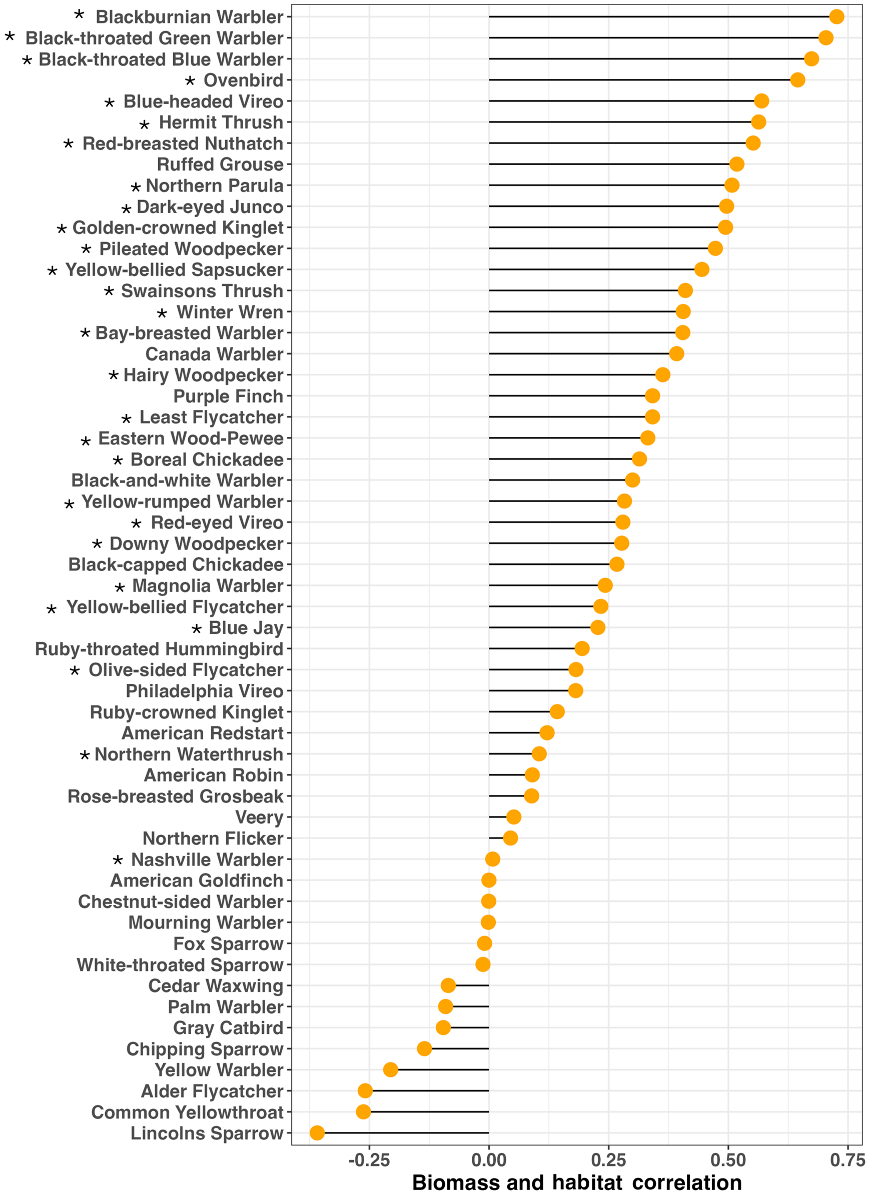

FIGURE 4 | Pearson correlation coefficients (r) for the relationship between bird habitat (from species distribution models) and above-ground biomass (according to above-ground biomass model). Mature-forest species (denoted *) showed strong, positive correlations (e.g., Blackburnian warbler, Black-throated Green Warbler, Black-throated Blue Warbler), and several early seral species (e.g., Lincoln's Sparrow, Common Yellowthroat) show negative correlations.

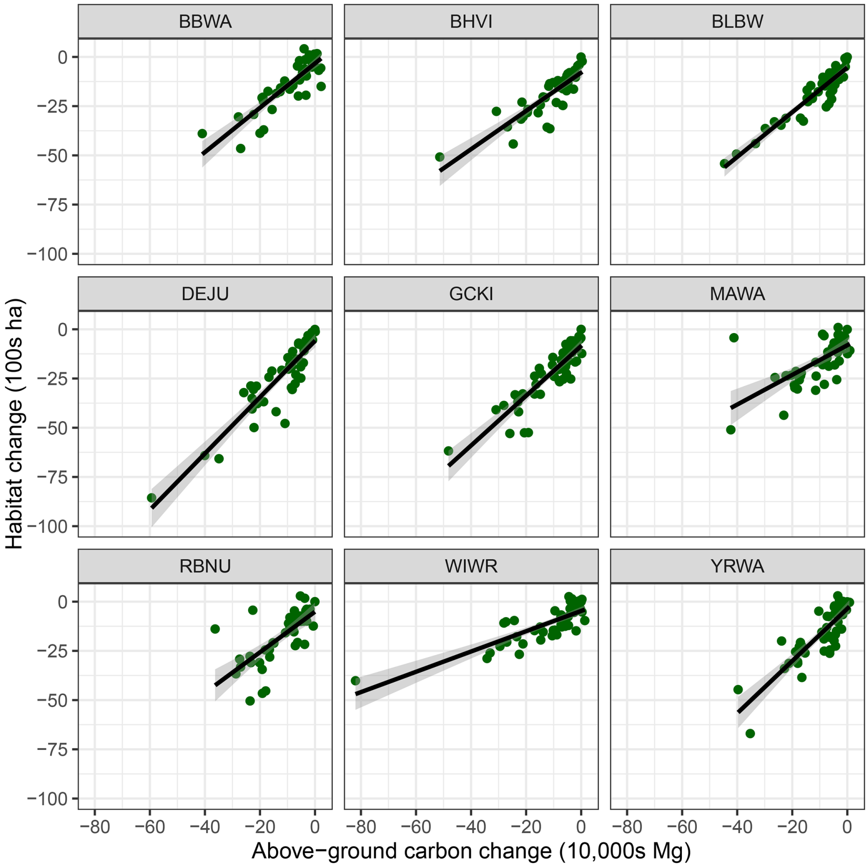

FIGURE 5 | The relationship between change in above-ground carbon occurring from 1985 to 2020 and habitat change within a 200 m-diameter buffer surrounding BBS routes ($N=47$) for nine mature forest-associated species with the greatest rates of habitat decline. Black lines are regression lines and grey bands are 95% confidence intervals (regression estimates in Table S2). As expected, above-ground biomass loss is strongly associated with habitat loss, which indicates that potential for conservation synergies between biodiversity and carbon. Bay-breasted Warbler (BBWA), Blue-headed Vireo (BHVI), Blackburnian Warbler (BLBW), Dark-eyed Junco (DEJU), Golden-crowned Kinglet (GCKI), Magnolia Warbler (MAWA), Red-breasted Nuthatch (RBNU), Winter Wren (WIWR), Yellow-rumped Warbler (YRWA).

3.2 | Life Cycle Analyses

Life cycle analyses revealed that the above-ground biomass losses are compensated to some extent by carbon storage in wood and paper products. Forests of NB have lost a net 236 Tg CO_2e since 1985, but 99 Tg CO_2e of that is stored, at least temporarily, in wood or the waste stream. These storage pools have not balanced total losses from timber harvest, and we estimate net emissions to be 141 Tg CO_2e since 1985. Wood products storing the most carbon include building materials (lumber) and home applications (e.g., furniture and flooring). Transport of wood products and manufacturing contributed to carbon emissions, but these sources were dwarfed in comparison to emissions from forest harvest (and consequent biomass reductions; Figure 6). Of note is that pulp and paper is the least durable product for carbon storage and amounts to 44% of the production volume from NB forests from 1985 to 2020.

4 | Discussion

Forest degradation is a pervasive global problem, which has recently prompted international agreements and policies focused on reducing or eliminating wood sourced from degraded forests (European Union 2023). The challenge is how to best define forest degradation and monitor it over the long term. It is tempting to simplify the issue by pointing to stand-level forest practices drivers of degradation (e.g., selective harvesting, clearcutting, planting). However, whether or not degradation is occurring depends on the rate at which ecosystem processes and services recover from disturbance across entire landscapes (Betts et al. 2024; Ghazoul et al. 2015; Ghazoul and Chazdon 2017). Thus, monitoring degradation requires long-term data, and information on trends in the forest elements of interest. Here, we present an example of methods for detecting degradation across a major wood producing region of Canada where forest harvest dominates. We used two broadly recognized indicators—biodiversity and forest carbon—that are readily quantified using remote sensing.

According to our forest-inventory plot-derived model, above-ground biomass in NB forests has declined by a total 246 Tg CO_2e, which is 141 Tg CO_2e (4.02 Tg year^{-1}) after accounting for lifecycle carbon. This is equivalent to 32% of the province's total annual emissions (12.4 Tg in 2020), and greater than all annual oil and gas emissions combined (3.3 Tg year^{-1}) (Government of Canada 2023). Note that these results may be seen as conservative, given that we did not calculate the counterfactual of no wood harvest over 35 years; we do not provide estimates of the

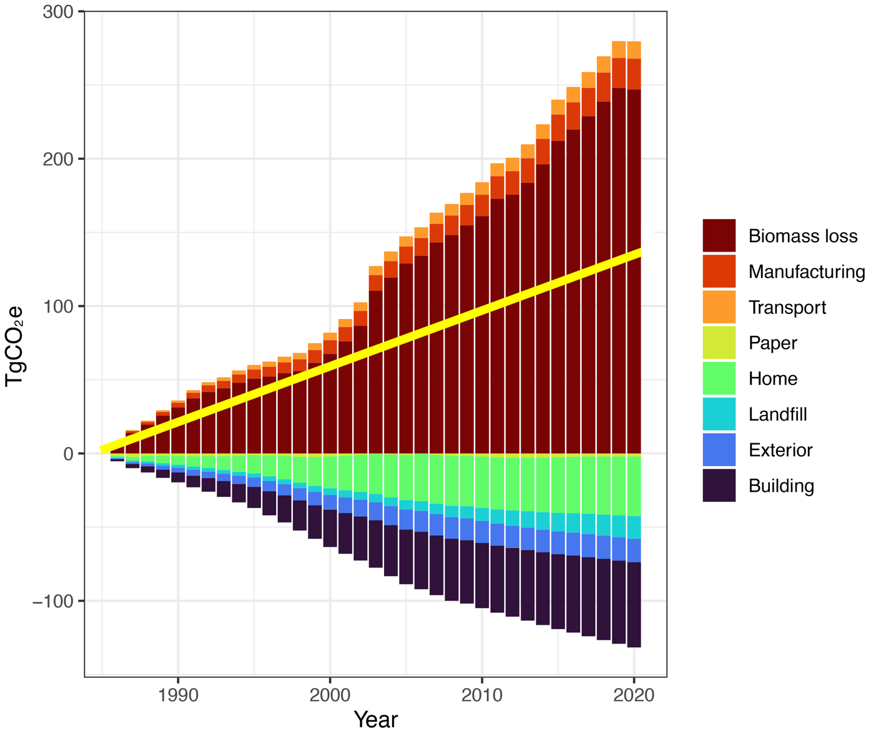

FIGURE 6 | Results from life-cycle analysis showing cumulative net carbon emissions from NB forests of 141 Tg CO$_2$e from 1985 to 2020. The yellow solid line indicates net emissions over time. Harvested wood product pools reflect Wei et al. (2023) categories. "Building" includes products used in construction. "Exterior" products include railroad ties and other exterior uses. "Landfill" includes disposed wood waste. "Home" includes wood product applications such as flooring and furniture. "Paper" incorporates four paper product categories with differing service lives (newspaper, graphic paper, packing paper, and household paper). "Transport" emissions include both harvest and transport from the forest to the mill. "Manufacturing" emissions are associated with processing of wood to final products. Biomass loss is primarily due to forest harvest.

carbon that could have been stored if mature forest stands were not harvested and instead accumulated carbon over time.

Although our results might have been predictable given the relatively high harvest rates and short harvest rotations in NB forests (typically about 50 years) they stand in contrast to most predictions in the literature about the carbon storage role of managed forests (Hennigar, MacLean, and Amos-Binks 2008; Cameron et al. 2013). Cameron et al. (2013) showed that it is the emissions from harvest, transport and processing that contributed the most to a positive carbon emissions budget, and that tree growth in managed forests constituted a net carbon sink. A reason for the discrepancy between our historical approach and the results of forest landscape harvest modeling is that the latter assumes a "regulated" forest in which future harvest rotations are not shorter than the age of current stands on the landscape. Our findings, based on long-term empirical data, support the findings of Peng et al.'s (2023) projection model-based approach showing that regrowth in young forests will not offset emissions from harvesting old forest.

Similar to carbon declines, and as we have reported elsewhere (Betts et al. 2022), old-forest bird habitat has exhibited precipitous declines, with species declining at rates of 38% (1.1% year^{-1}). Habitat loss is linked to population declines for the majority of old-forest species (Betts et al. 2022). We expect similar patterns for other biodiversity elements that are poorly monitored, have strong associations with old Acadian (Wabanaki) forest, and are likely more sensitive to harvest than birds (e.g., lichens; Whitman and Hagan 2007), flying squirrels (Smith, Forbes, and Betts 2013), herbaceous plants (Roberts 2002).

The systematic declines in both above-ground carbon and habitat for old-forest birds is consistent with the signature of forest degradation. However, there is cause for optimism. Strong correlations between habitat for old-forest birds and current locations with high above-ground carbon indicate an opportunity to incentivize carbon-biodiversity co-benefits for both small and large forest landowners in NB. International and national carbon markets could potentially be harnessed to offset the financial opportunity cost to landowners of reducing harvest rates in NB forests. International policies precluding forest degradation could also provide incentive for changes to forest practices to increase habitat and carbon.

Methods for slowing loss of standing carbon in eastern Canadian forests include strict reserves, but also lengthening harvest rotations. Many tree species in the region can live > 300 years, and old-growth forests can continue to store carbon long after maximum growth rates (i.e., the peak of mean annual increment) have been achieved. "Improved forest management" more in-line with the mostly gap-driven natural disturbances in the region (Lorimer 1977) (i.e., single-tree or group selection harvest) shows promise as a way of maintaining carbon (Gunn and Buchholz 2018) and old-forest bird habitat (Pohlman et al. 2023). A future challenge will be restoring forests that have already been degraded via short-rotation harvests. Naturally regenerated forests following clearcutting in this region tend to be comprised of shade-intolerant, short-lived tree species (e.g., *Betula papyrifera*, *Populus tremuloides*) or short-lived climate vulnerable species (*Abies balsamea*). Unless seed sources for trees in the pre-harvest forest (e.g., *Acer saccharum*, *Betula alleghaniensis*, *Picea rubra*) are within dispersal distance, or unless active restoration takes place, there is some risk that these forests could remain in an alternative stable state for hundreds of years.

Importantly, the methods we present here could be used to estimate the status quo rate of long-term above-ground carbon decline, and subsequently test the degree to which carbon-offset programs function (i.e., the "additionality" of incentive programs) and whether policies limiting degradation are effective. The requirements for these models are inventory ground plots (which are available in many forestry jurisdictions) and Landsat data (freely available globally). In particular, as "dynamic baseline" approaches to quantifying carbon additionality become more mainstream in offset methodologies, developing techniques to confidently quantify forest carbon stock changes remotely will continue to be imperative. Similarly, our open-source GEE code can be used in long-term monitoring of habitat change for any species with sufficient locational data to determine if changes to current policies are achieving intended conservation effects. Together, we suggest that the remote-sensing-derived models for carbon and biodiversity that we present here could be applied across entire regions of the globe to assess the landscape-level trajectory of forest degradation.

Author Contributions

Matthew G. Betts: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration. **Zhiqiang Yang:** conceptualization, data curation, formal analysis, investigation, methodology, writing – review and editing. **John S. Gunn:** formal analysis, methodology, writing – review and editing. **Sean P. Healey:** conceptualization, methodology, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data used in the analyses are available at https://doi.org/10.6084/m9.figshare.27055528.v1. Raw data from the MBBA are available at: https://www.birdscanada.org/naturecounts/default/searchquery.jsp. Original, unprocessed Landsat images are available from Google Earth Engine: https://developers.google.com/earthengine/datasets/catalog/landsat. Unprocessed images are too large (>2 TB each) to provide on an open access server; we provide Python code on Figshare to enable download of relevant files. All data and code used in bird distribution models are available here: https://figshare.com/articles/journal_contribution/Breeding_Bird_Survey_Data_with_Habitat_Variables_for_Eastern_Canada_and_Modeling_Scripts/14522322.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.