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The climate sensitivity of carbon, timber, and species richness covaries with forest age in boreal–temperate North America

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Abstract

Climate change threatens the provisioning of forest ecosystem services and biodiversity (ESB). The climate sensitivity of ESB may vary with forest development from young to old-growth conditions as structure and composition shift over time and space. This study addresses knowledge gaps hindering implementation of adaptive forest management strategies to sustain ESB. We focused on a number of ESB indicators to (a) analyze associations among carbon storage, timber growth rate, and species richness along a forest development gradient; (b) test the sensitivity of these associations to climatic changes; and (c) identify hotspots of climate sensitivity across the boreal–temperate forests of eastern North America. From pre-existing databases and literature, we compiled a unique dataset of 18,507 forest plots. We used a full Bayesian framework to quantify responses of nine ESB indicators. The Bayesian models were used to assess the sensitivity of these indicators and their associations to projected increases in temperature and precipitation. We found the strongest association among the investigated ESB indicators in old forests (>170 years). These forests simultaneously support high levels of carbon storage, timber growth, and species richness. Older forests also exhibit low climate sensitivity of associations among ESB indicators as compared to younger forests. While regions with a currently low combined ESB performance benefitted from climate change, regions with a high ESB performance were particularly vulnerable to climate change. In particular, climate sensitivity was highest east and southeast of the Great Lakes, signaling potential priority areas for adaptive management. Our findings suggest that strategies aimed at enhancing the representation of older forest conditions at landscape scales will help sustain ESB in a changing world.

KEYWORDS
adaptive management, biodiversity, boreal–temperate ecotone, carbon, climate change, ecosystem services, forest age, forest growth, species richness, timber production

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William S. Keeton is senior author.

1 | INTRODUCTION

Climate change constitutes one of the greatest threats to forest ecosystem services and biodiversity (ESB) (Sala, 2000; Schröter et al., 2005; Thomas et al., 2004). Broad-scale scenario analyses have predicted negative effects of climate change on a number of services and biodiversity indicators (Sala, 2000; Schröter et al., 2005; Seidl, Schelhaas, Rammer, & Verkerk, 2014; Thomas et al., 2004; Thuiller et al., 2011). Yet, few studies have simultaneously estimated climate change impacts on multiple ESB indicators and quantified their associations (Creutzburg, Scheller, Lucash, LeDuc, & Johnson, 2017; Irauschek, Rammer, & Lexer, 2017). Moreover, the climate sensitivity of ESB may vary with structural and compositional changes induced by forest aging (Boulanger, Taylor, Price, Cyr, & Sainte-Marie, 2018; Pan et al., 2011). For instance, older forests, being more structurally and functionally complex (Becknell & Powers, 2014; Martin, Fenton, & Morin, 2018; Tyrrell & Crow, 1994), are potentially better at buffering against undesired climate change effects on ESB than younger forests of lower complexity (Lindner et al., 2010; Urbano & Keeton, 2017). Large uncertainties about the effects of aging forests on ESB associations and their climate sensitivities hinder the design of the robust adaptive forest management strategies needed to sustain a broad range of species and ecosystem services under a changing climate. Our study addresses these research gaps and, thus, helps guiding forest management to better sustain ESB into the future.

Forest age class distributions, disturbance dynamics, and stand development pathways (i.e., trajectories of structural and compositional development) have been profoundly altered by land-use history and forest management over large portions of the boreal and temperate biomes (Bürgi, Östlund, & Mladenoff, 2017; Collins, Fry, Lydersen, Everett, & Stephens, 2017; Foster et al., 2003; Thom, Rammer, Garstenauer, & Seidl, 2018). For instance, the majority of forests in the US Northeast are still recovering from 19th century clearing and are younger and structurally more simple compared to pre-European settlement conditions (Foster, Motzkin, & Slater, 1998). As forests age, their species composition and structure change (Tyrrell & Crow, 1994; Urbano & Keeton, 2017), which has consequences for ESB (Díaz, Armesto, Reid, Sieving, & Willson, 2005; Fuhr, Bourrier, & Cordonnier, 2015; Seedre, Taylor, Brassard, Chen, & Jõgiste, 2014; Seidl, Rammer, & Spies, 2014). These changes complicate joint management for ESB. Previous studies have quantified the relationships between various indicators of ESB at the end of rotation periods (Lutz et al., 2016; Pukkala, 2016; Triviño et al., 2017), however, stand development likely changes these associations (Bradford & D'Amato, 2012). How associations vary with forest development (i.e., development of complex stand structures and changes in the diversity of plant species) is poorly understood, limiting our ability to optimize the outcome of multiple management objectives, particularly in the face of climate change.

Climate change is a major source of uncertainty when predicting the individual and combined future dynamics of ESB indicators. Boreal–temperate ecotones constitute the transition zone between boreal and temperate biomes and harbor characteristic species of both systems. Ecotones of eastern North America may face exceptionally strong climate forcing in the future (Hayhoe et al., 2017). This may cause severe consequences for ecosystems because ecotones are expected to be particularly sensitive to climate change as many species are currently at the peripheries of their geographic distributions or environmental tolerance ranges (Taylor et al., 2017). Moreover, it is likely that climate change impacts will be spatially heterogeneous and nonlinear due to differences in climate, edaphic conditions, and competitive interactions among other factors (Creutzburg et al., 2017; Frey et al., 2016). The climate sensitivity of ESB may also covary with forest age and development. For instance, older forests might have greater capacity to sustain favorable microclimates for species sensitive to climatic changes than younger forests (Fritz, Niklasson, & Churski, 2009). As a result of spatial heterogeneity, we can expect hotspots in the sensitivity of ESB to climate (Seddon, Macias-Fauria, Long, Benz, & Willis, 2016). The identification of such hotspots would help land managers and policy makers prioritize areas where reallocation of resources for climate adaptation could be concentrated (Thom et al., 2017).

This study quantifies the individual and combined performance of multiple ESB indicators in the context of climate sensitivity and forest development within the boreal–temperate transitional forest region of eastern North America. We compiled an extensive and highly unique dataset of indicators related to carbon storage, timber growth rate (i.e., periodic annual increment which indicates potential wood production), and species richness from various sources. Our objectives were to (a) analyze associations between carbon storage, timber growth rate, and species richness along a forest development gradient; (b) test the sensitivity of these associations to increases in annual average temperature and total precipitation; and (c) identify hotspots of climate sensitivity across the study region. Based on previous studies in the temperate and boreal biomes, we expected a logarithmic trend for carbon storage (Keeton, Whitman, Mcgee, & Goodale, 2011; Weng et al., 2012), an early optimum for timber growth rate (Ward, Pothier, & Paré, 2014), and a U-shaped curve for biodiversity (Hilmers et al., 2018) in relation to forest age, which was employed as a proxy for stand development (Franklin et al., 2002; Taylor & Chen, 2011). As mesic temperate and boreal forests age, they develop greater structural complexity in both vertical (e.g., vertically differentiated canopies, range of tree sizes) and horizontal (e.g., patch mosaics, variation in stem densities) dimensions, which may also increase niche availability (Crow, Buckley, Nauertz, & Zasada, 2002; McGee, Leopold, & Nyland, 1999; Urbano & Keeton, 2017). Ultimately, age-related changes are likely to increase both the resistance and resilience of forests to climatic alterations (Lindner et al., 2010), although there remains uncertainty around this question (D'Amato, Bradford, Fraver, & Palik, 2011). We thus expected a lower climate sensitivity of indicator associations with increasing forest age. Moreover, we anticipated distinct variation in climate sensitivity of the indicators across the study region due to nonlinear responses to increases in temperature and precipitation as well as differences in site and stand conditions. In gaining novel insights into ESB associations and their sensitivities to climate, our study highlights opportunities to improve forest management strategies and identifies priority regions for adaptation measures.

2 | METHODS

2.1 | Study area

Our study area spans eastern temperate and northern forests of three ecoregions: "Mixed Wood Shield," "Atlantic Highlands," and "Mixed Wood Plains" (Figure 1; EPA, 2016). These ecoregions roughly encompass the boreal–temperate ecotone of eastern North America. The distinct gradient in environmental conditions and the high competition among species makes ecotones ideal regions to investigate the climate sensitivity of ESB (Boulanger et al., 2017; Evans & Brown, 2017). The forests of these ecoregions span oak-hickory communities in the south over maple-beech-birch to spruce–fir communities in the north.

2.2 | Database and literature review

We performed a database and literature search collecting individual plot records on carbon stocks and timber growth rate (an indicator of wood commodity production), two of the most frequently discussed ecosystem services in forest management and policy (Schwenk, Donovan, Keeton, & Nunery, 2012), and species richness (see Section S1 in the supporting information for more details). We omitted observations with missing values for forest age (i.e., the average age of dominant and codominant overstory trees), conifer share, or geographic coordinates. In total, we collected 74,777 observations from 18,507 plots within the focal ecoregions (Table S1; Figure S1). Most of the plot data were derived from the USDA Forest Inventory and Analysis (FIA) Program. Other sources complemented FIA data, in particular by providing additional information on underrepresented old-growth plots (Anderson-Teixeira et al., 2018; Keeton et al., 2011), rarely measured variables (Kurth, D'Amato, Palik, & Bradford, 2014), or by extending the environmental gradient (e.g., Canada's National Forest Inventory [NFI]). Each observation includes information about carbon pools (aboveground live carbon [ALC]; dead standing carbon [DSC]; dead downed carbon [DDC]; soil organic carbon [SOC]; forest floor carbon [FFC]), timber growth rate (current annual volume increment), or biodiversity within three taxonomic groups (species richness of trees, lichens, or vascular plants). Additionally, for each plot, we collected data on seasonal and annual average temperature and total precipitation (resolution: 1 km; reference period: 1970–2000) (WorldClim, 2016), soil type (resolution: 1 km) (Fischer et al., 2008), management designation/protection status (resolution: 2 km) (CEC, 2010), and elevation (resolution: 1 km) (EROS, 2018).

2.3 | Carbon, growth, and species richness models

We used Bayesian generalized linear models (GLMs) to analyze the performance of carbon storage, timber growth rate, and species richness (described above). To do this, we first scaled and zero-centered all continuous predictor variables. Next, we used a combination of statistical techniques to determine candidate models for each of the nine response variables (ALC, DSC, DDC, SOC, FFC, timber growth rate, and tree, lichen, and vascular plant species richness; see Table S2 for details on statistical methods and variables). For continuous response variables (i.e., carbon storage and timber growth rate indicators), we assumed a Gaussian error distribution. For count response variables (i.e., species richness

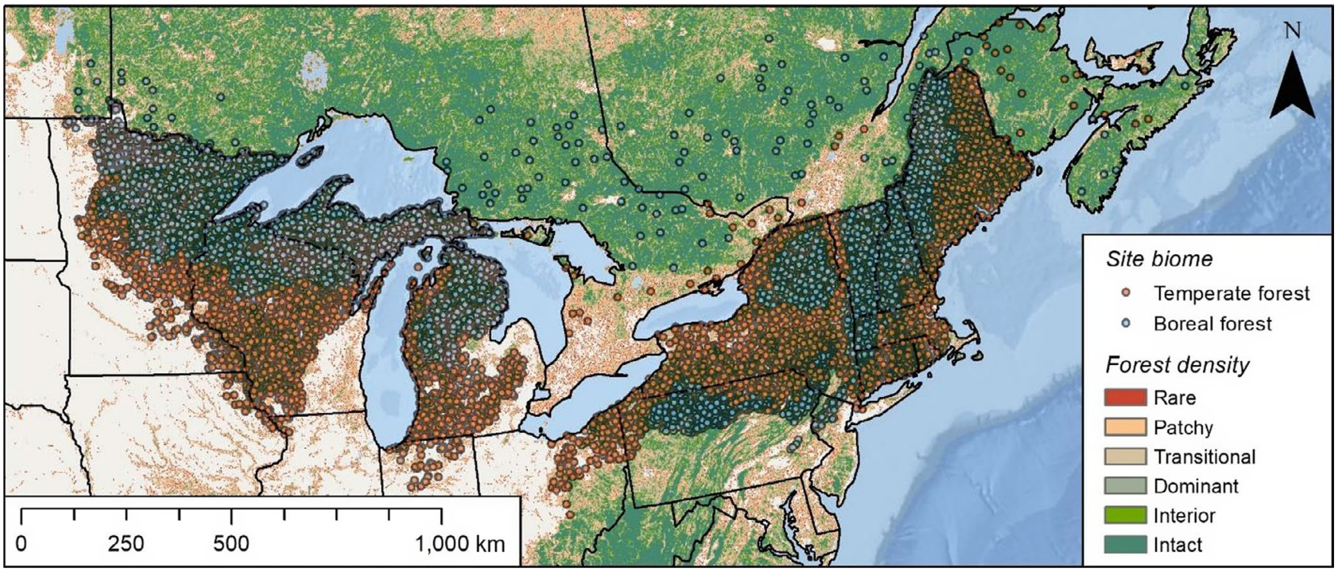

FIGURE 1 Spatial distribution of plots across the study region. We collected 18,507 plots in three ecoregions spanning the eastern temperate and northern forests of the boreal–temperate ecotone in the northeastern United States and southeastern Canada [Colour figure can be viewed at wileyonlinelibrary.com]

indicators), we tested two different error distributions across all candidate models: a negative binomial error distribution and a Gaussian error distribution after log transformation (Ives, 2015). On average, we derived nine candidate models for each response variable, while the number varied between 5 and 14 models depending on interaction terms considered in candidate models and data type (Table S2). A Gaussian field of longitude and latitude was included in all models to control for residual spatial autocorrelation. Based on the partial effect plots derived for all candidate predictor variables using random forest models (Breiman, 2001) and ecological theory (e.g., for the hypothesized covariation of total ecosystem carbon (TEC), timber growth rate, and species richness with forest age), we included smoothing terms for predictors for which we expected nonlinear relationships with the respective response variable.

All models were parametrized within a full Bayesian framework (Bürkner, 2018) at the Vermont Advanced Computing Core (VACC). In a Bayesian framework, all parameters are modeled with uncertainty, and direct probability statements about quantities of interest can be made. We selected the most parsimonious models using the Watanabe–Akaike information criterion (WAIC) (Vehtari, Gelman, & Gabry, 2017). We assessed the predictive accuracy of the final models with posterior predictive checks, and compared the Bayesian R^2, Generalized variance inflation factor (GVIF), partial effects plots, and Moran's I for residual spatial autocorrelation among models. Based on these tests, we maintained the log-transformed count data models, and in four cases (DDC, growth rate, as well as specie richness of trees and lichens), we rejected the model with the lowest WAIC in favor of another model (e.g., if GVIF was >10, see Dormann et al. (2013)). Finally, we used WAIC for backwards elimination of variables with the highest uncertainty in the selected candidate models. The final models (used to predict ESB) performed with moderate rigor, with Bayesian R^2 explaining on average 31.1% of the variance, with the minimum being 8.8% (DSC) and the maximum 66.4% (lichen species richness) (see Table S3 for details). No model showed evidence of strong residual spatial autocorrelation (Moran's I ranged between −0.102 and 0.069).

2.4 | Trends and associations

We used forest age as a proxy for forest stand developmental condition across the study region in a space-for-time substitution approach (Franklin et al., 2002; Taylor & Chen, 2011). Hence, final models were employed to predict the responses of each indicator related to carbon storage, timber growth rate, and species richness to forest age. Specifically, we set all continuous variables except forest age to their mean values and categorical variables to their most frequent levels in the dataset. TEC was derived by summing all carbon pools, whereas total species richness was the sum of individual taxa richness scaled by dividing by the maximum value to ensure their comparability. Subsequently, TEC, timber growth rate, and total species richness were divided by their respective maximums to derive a measure of relative performance as a function of forest age. As our data were limited by a relatively low number of observations for old-growth forests (Figure 2), and as the concept of forest age has limitations in uneven-aged old-growth forests (Keeton et al., 2011), we restricted the interpretation of individual indicators' responses to changes in climate variables to the first 200 years of forest development.

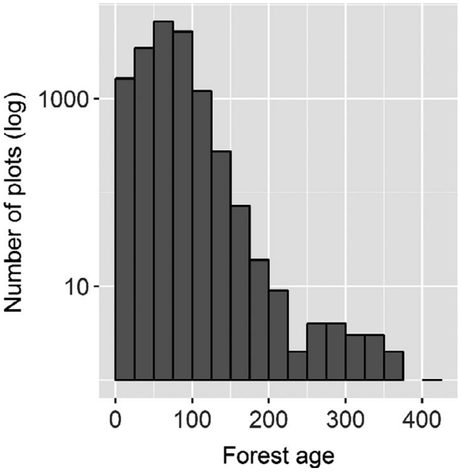

FIGURE 2 Distribution of forest age classes across the 18,507 plots recorded in this study. Forest age is based on the average age of dominant and codominant overstory trees. Note that the *y*-axis is log transformed

Next, we used the Bayesian models to map and identify regional variations in ESB indicators. Using the complete dataset with the original information about stand and site conditions, we predicted the performance of individual response variables for each plot. Subsequently, we derived and mapped TEC and species richness following the same approach as described above. The combined indicator performance was derived by averaging across TEC, timber growth rate, and species richness outcomes. Subsequently, we used inverse distance weighting to derive wall-to-wall (i.e. spatial inter- and extrapolation) estimates for the entire study region.

Central to our analysis was an assessment of similarities in trends (performance change along the entire forest age gradient) and associations (performance at a specific forest age) between TEC, timber growth rate, and species richness. We performed Gleichläufigkeit (GLK) tests (Bunn et al., 2018) for all pairwise combinations of indicators (e.g., TEC and timber growth rate) to assess synchrony in trends within the first 200 years of forest development. A GLK value of 0.5 indicates no mutual pattern of two variables (no covariation), a value of 1 indicates that all values of the variables always increase or decrease in the same years (positive covariation), and a value of 0 means that variables compared pairwise never increase or decrease in the same years (negative covariation). Associations between TEC, timber growth rate, and species richness along the forest development gradient were assessed following the approach described in Bradford and D'Amato (2012). Briefly, we computed the root mean squared error of the performance of two indicators at a given forest age. The resulting curves were averaged to derive the mean divergence (D_{base}) among all indicators.

2.5 | Climate sensitivity

Finally, we assessed the climate sensitivity of TEC, timber growth rate, and species richness, and their associations by increasing all temperature variables by 4°C, annual precipitation by 200 mm, and seasonal precipitation variables by 50 mm in the statistical prediction. These values roughly correspond with the RCP6.0 emission scenarios projected for the study region by the end of the 21st century (Hayhoe et al, 2017; Nazarenko et al., 2015). The predictions were divided by the respective maximum values under baseline climate to make indicator performance comparable between climate regimes. Relative performances under baseline climate were then subtracted from the relative performance under changed conditions to derive the absolute percent change for each indicator (i.e., the change in percentage points; hereafter "% points").

Following the approach described above, we derived wall-to-wall maps of changes in indicator performance. We also compared the results for GLK under baseline and changed climatic conditions. Moreover, we derived the divergence (D_{cc}) (i.e., the degree of association) between indicators under elevated temperature and precipitation regimes and subtracted the results from the outcome under baseline climate conditions. For example, an increase in divergence indicates a weaker association between TEC, timber growth rate, and species richness at a particular forest age in a warmer and wetter environment. Further, we investigated the sensitivity of all indicators to individual changes in temperature and precipitation. To that end, we predicted the region-wide performance of the nine response variables first toward an increase in all temperature variables of +4°C and subsequently toward an increase in annual precipitation of 200 mm and seasonal precipitation of 50 mm.

All analyses were performed using the R language and statistical computing environment (R Development Core Team, 2018) using the packages dplyr (Wickham, Francois, Henry, & Müller, 2018) and reshape2 (Wickham, 2017) for data organization; foreign (R Development Core Team, 2017) for loading external data sources; pedometrics (Samuel-Rosa, 2015) and randomForest (Liaw & Wiener, 2018) for variable selection of candidate models; brms (Bürkner, 2018) for Bayesian models; usdm (Naimi, 2017) for multicollinearity tests; dplR (Bunn et al., 2018) for GLK tests; fmsb (Nakazawa, 2018) and ggplot2 (Wickham, 2009) for data visualization; and gstat (Pebesma, 2018), raster (Hijmans, 2018), rgdal (Bivand, Keitt, & Rowlingson, 2018), sp (Pebesma & Bivand, 2018), and spdep (Bivand et al., 2019) for spatial analyses.

3 | RESULTS

3.1 | Old forests exhibit highest combined performance of ESB

The combined performance of multiple ecosystem indicators peaked in 200 year old forests as a result of simultaneously high

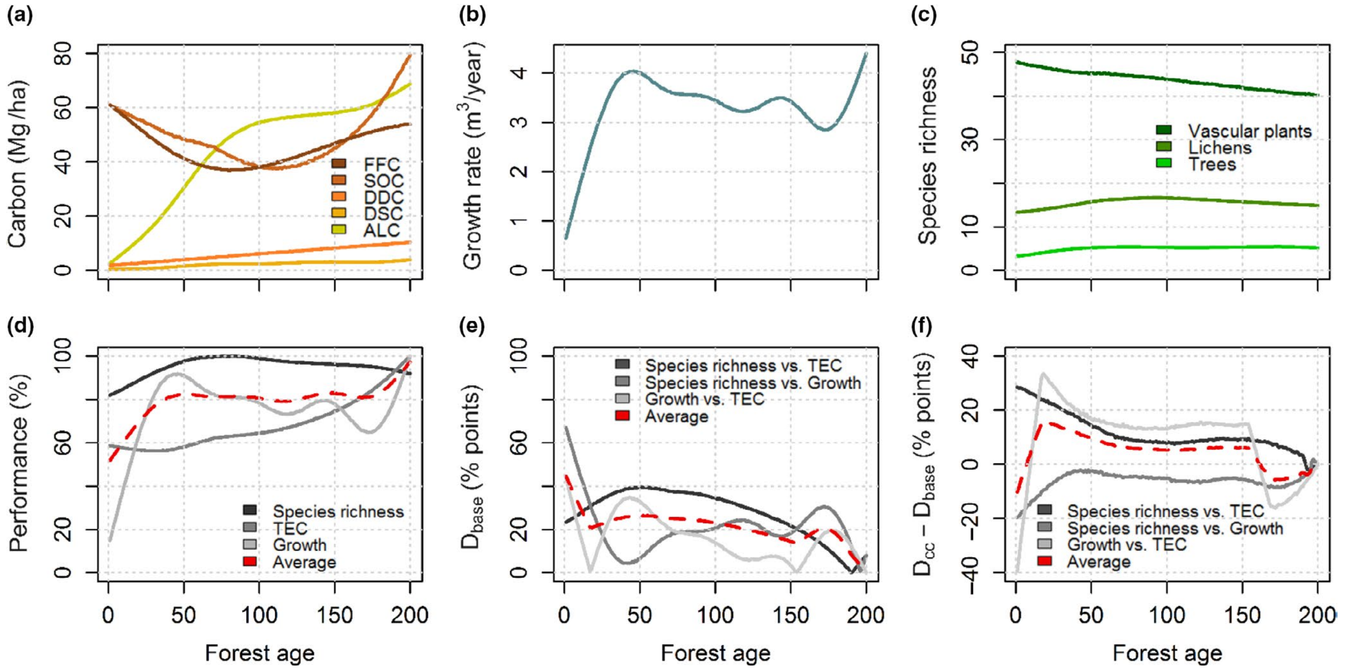

FIGURE 3 Ecosystem services and biodiversity (ESB) performance, associations, and climate sensitivity of associations along a forest age gradient. (a) Carbon pools (aboveground live carbon [ALC]; dead standing carbon [DSC]; dead downed carbon [DDC]; soil organic carbon [SOC]; forest floor carbon [FFC]); (b) timber growth rate; (c) species richness indicators (trees, lichen, and vascular plant species richness); (d) relative combined performance (i.e., ESB outcomes) of total ecosystem carbon (TEC), timber growth rate, and species richness; (e) their associations under baseline climate conditions (i.e., D_{base}, the divergence in performance between indicators); and (f) changes in associations in a warmer and wetter world (i.e., $D_{cc} - D_{base}$, change in the divergence). D_{cc} denotes an increase in temperature by 4°C and precipitation by 200 mm. Note that the *y*-axes in (a)–(c) are in original units, while (d) presents percentages (indicator performance relative to the observed maximum value), and *y*-axes in (e) and (f) are in percentage points (absolute difference of percentages) [Colour figure can be viewed at wileyonlinelibrary.com]

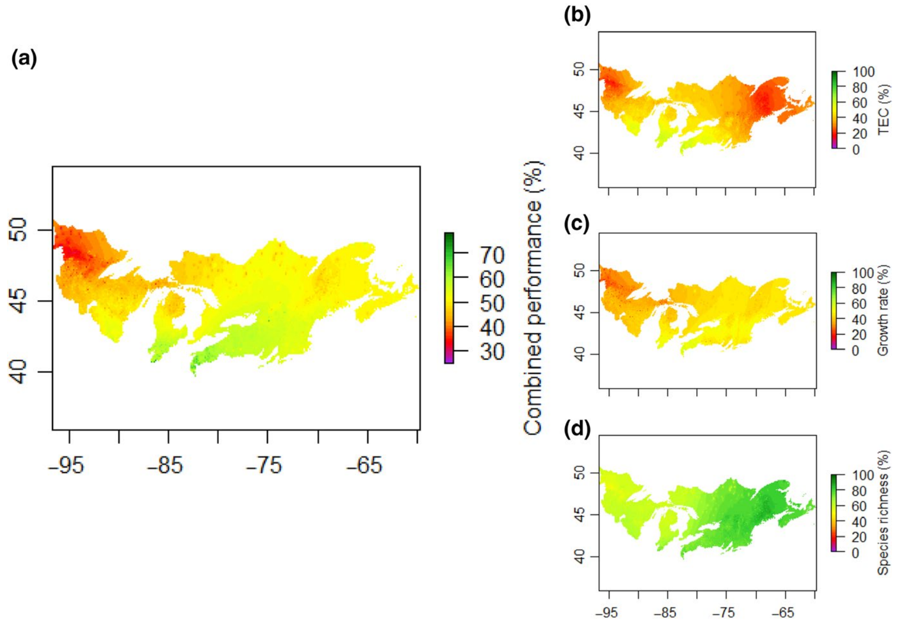

FIGURE 4 Ecosystem services and biodiversity (ESB) performance across the study region. Values were predicted for each inventory plot using final Bayesian generalized linear models, standardized, and spatially interpolated (see text for details). Left panel: (a) Joint average relative combined performance (i.e., ESB outcomes) of total ecosystem carbon (TEC), timber growth rate, and species richness. Right panel: Relative performance of (b) TEC, (c) timber growth rate, and (d) species richness. Note that scales differ between panels [Colour figure can be viewed at wileyonlinelibrary.com]

levels of carbon storage and timber growth rate, coupled with relatively stable species richness along the forest development gradient (Figure 3d). TEC increased with forest age, due to carbon accumulation in all pools (Figure 3a; Figure S2a–e), particularly in forests older than 130 years. SOC and FFC declined during the first 80–120 years, after which both pools increased (Figure 3a; Figure S2d,e). Timber growth rate peaked twice, first between years 40 and 50, and again after year 170 (Figure 3b; Figure S2f). Individual components of species richness were only moderately associated with forest age (Figure 3c; Figure S2g–i). While lichen species richness was highest between years 90 and 100, vascular plant richness slightly decreased with forest age, and tree species richness first increased slightly but leveled off at year 50. As a result, total species richness was quite stable over the 200 years of forest stand development (Figure 3d).

We did not detect common trends in the trajectories of TEC and timber growth rate (GLK = 0.44), timber growth rate and species richness (GLK = 0.56), and TEC and species richness (GLK = 0.44) as related to forest age (Figure 3d). However, ESB associations covaried with forest age. The divergence (D_{base}) among all indicators was highest during the first decade of forest development, constituting on average 37.7% points (Figure 3e). D_{base} decreased with increasing forest age in two distinctive dips within the first and last two decades of the predicted period (ultimately reaching <5% points), indicating the strongest association among TEC, growth rate, and species richness in old forests.

3.2 | Variation in climate sensitivity across boreal–temperate forests

The combined ESB performance varied spatially across the region, being lowest in the northwestern portions (parts of Manitoba, Ontario, and Minnesota) and highest in the central-southern portions (parts of Indiana, Ohio, Michigan, Pennsylvania, and New York) of the region (Figure 4a). The central-south was a hotspot for TEC (Figure 4b) and timber growth rate (Figure 4c), while species richness was positively correlated with proximity to the Atlantic Ocean (Figure 4d).

Ecosystem services and biodiversity indicators were highly sensitive to changes in temperature and precipitation (Figure 5a). On average over the study region, increasing temperature and precipitation together altered the combined indicator performance only marginally (+0.7% points). However, the spatial variability of this effect was high (Figure 5a). The western and northeastern parts of the region, which had low-to-moderate combined indicator performance under current climate conditions (Figure 4a), benefitted from climatic changes. In contrast, large areas in the east and south decreased in performance (Figure 5a). As the decrease in TEC (on average −9.0% points; Figure 5b) and the increase in timber growth rate (on average +13.0% points; Figure 5c) cancelled each other out in many locations, the differences in combined indicator performance were strongly determined by changes in species richness, despite its low magnitude of change on average across the region (−2.1% points; Figure 5d).

3.3 | High climate sensitivity of young forests

Climate sensitivity varied markedly among the investigated indicators (Figure 6; Figure S4). Changes in TEC were primarily driven by decreases in SOC (−8.2% and −4.4% points) and FFC (−13.7% and −2.4% points), which were highly sensitive to both increases in temperature and precipitation. DSC and DDC were only moderately sensitive and responded negatively to temperature (−0.1% and −3.3% points) and positively to precipitation (+0.9% and +1.8% points). In congruence with the change in ALC (+9.1% points), an increase in temperature and precipitation improved timber growth rate by 12.9% points, while precipitation had only a small effect on both (+2.4% and −0.4% points, respectively).

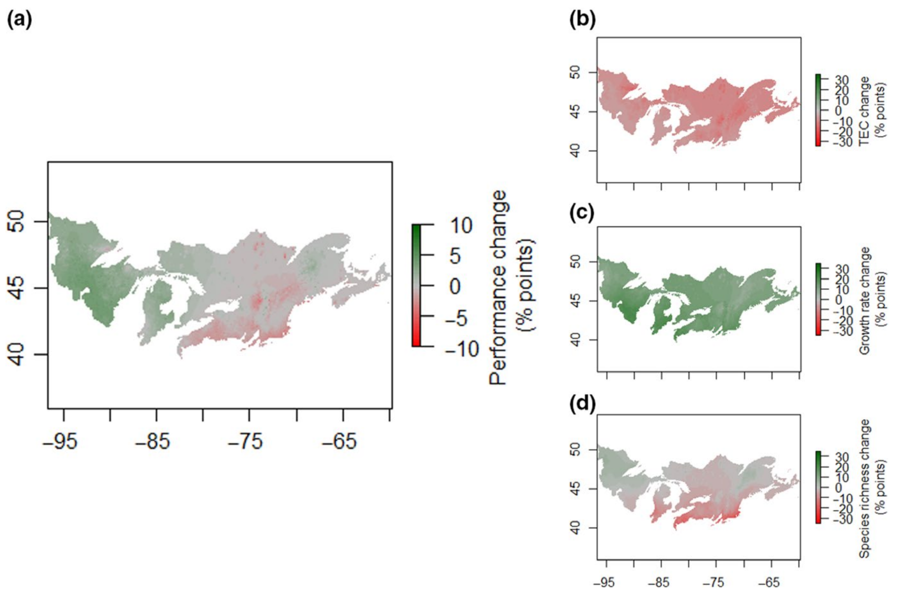

FIGURE 5 Climate-induced changes in ecosystem services and biodiversity (ESB) across the study region. Predictions represent an increase in temperature by 4°C and precipitation by 200 mm. Left panel: (a) Change in the relative combined performance (i.e., ESB outcomes) of total ecosystem carbon (TEC), timber growth rate, and species richness (in % points). Right panel: change in performance (in % points) of (b) TEC, (c) timber growth rate, and (d) species richness. Note that scales differ between panels [Colour figure can be viewed at wileyonlinelibrary.com]

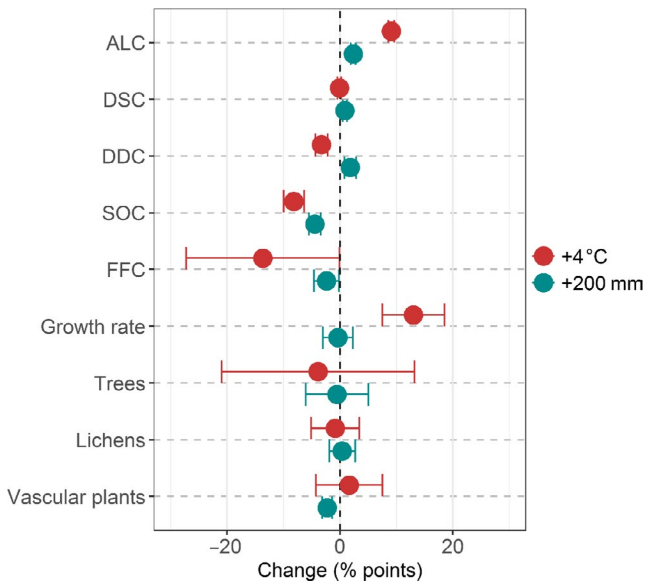

FIGURE 6 Sensitivity of ecosystem services and biodiversity toward increased temperature and precipitation. Presented are mean changes (dots) and confidence intervals (whiskers) for individual carbon storage, timber growth rate, and species richness indicators across the study region. ALC, aboveground live carbon; DSC, dead standing carbon; DDC, dead downed carbon; SOC, soil organic carbon; FFC, forest floor carbon; timber growth rate; trees, lichen and vascular plant species richness [Colour figure can be viewed at wileyonlinelibrary.com]

Changes in species richness components were diverse, of lower magnitude, and exhibited higher uncertainty compared to carbon pools and timber growth rate. Specifically, tree species richness was negatively affected by changes in temperature and precipitation (−3.9% and −0.5% points), lichen species richness showed a weak negative response to altered temperature and a weak positive response to altered precipitation (−0.8% and +0.4% points), and vascular plant species richness was positively affected by changes in temperature and negatively by changes in precipitation (+1.6% and −2.3% points). Spatial variation in climate sensitivity was low for all carbon pools and for timber growth rate (Figure S4). In contrast, species richness components varied in their response to temperature across the region. In particular, tree species richness strongly decreased in the central-southern reaches, while the northwest and northeast of the region benefitted from higher temperatures (Figure S4).

Changes in climate moderately altered the correlation between TEC and growth (GLK = 0.55), between TEC and species richness (GLK = 0.53), and between growth and species richness (GLK = 0.59) along the forest age gradient. Associations between TEC, growth rate, and species richness were more divergent (D_{cc}) than in the baseline scenario (D_{base}) during the first 160 years of forest development (max. increase in divergence: 15.9% points) (Figure 3f). Afterwards, the change in divergence became negative, indicating a stronger ESB association under climate change compared to baseline conditions. Between year 190 and 200, D_{cc} and D_{base} were very similar (on average −1.9% points), demonstrating a stable and strong association among ESB in old forests independent of climatic conditions.

4 | DISCUSSION

4.1 | Variation of carbon, growth, and species richness across forest age

Ecosystem services and biodiversity change over time as boreal–temperate forests undergo processes of stand development. Although there were no common trends in the trajectories of TEC, timber growth, and species richness in relation to forest age, their combined performance was highest in older forests. Our results only partly support the expected response curves relating these indicators to forest age (Figure 3d). Specifically, TEC continued to increase in older forests and did not follow a logarithmic curve to an asymptote as predicted. This increase was driven by both above- and belowground carbon pools. As forests develop toward late-seral stages, mortality of canopy trees increases through both density-dependent and density-independent processes (Franklin et al., 2002), leading to dead tree recruitment and deadwood accumulation (Garbarino, Marzano, Shaw, & Long, 2015) (Figure 3a). However, our data suggest that the increase in deadwood occurs concurrently with increases in ALC (Figure 3a), which is a much larger carbon pool than deadwood in our study system (e.g., up to an order of magnitude larger in 200 year old forests). Temporal dynamics of ALC are likely due to increases in the structural complexity of temperate and boreal forests (Lorimer & Halpin, 2014), which has been related to carbon accumulation in previous studies (McGarvey, Thompson, Epstein, & Shugart, 2015; Thom & Keeton, 2019; Urbano & Keeton, 2017) (see also discussion about growth rate below). Although decomposition gradually releases carbon to the atmosphere via respiration, the large accumulations of deadwood and litter in old forests also contribute to organic matter and free carbon incorporation into the humus layer and soil profile, thereby increasing belowground carbon pools (Manzoni & Porporato, 2009) (Figure 3a). The initial decrease of FFC and SOC in young forests is likely a legacy of carbon carried over from predisturbance stands, which slowly releases from redeveloping stands through decomposition (Franklin et al., 2000; Harmon, 2001).

Timber growth rate peaked after the first four to five decades in our study (Figure 3b). This finding is consistent with previous models in which growth rate was highest in relatively young and even-aged, secondary forests (Bormann & Likens, 1979; Halpin & Lorimer, 2016). However, we did not anticipate an acceleration of the growth rate after forests reached about 170 years in age. Uncertainty clearly increased, as indicated by the credibility interval in our results (Figure S2f), which reflects variability in the sample size across ages. However, the variance in the credibility intervals was not sufficient to override the general trend. In addition, we only calculated timber growth rate from the FIA data, thereby avoiding any confounding age-related trends that otherwise might have been attributed to multiple data sources. Thus, our finding of an acceleration in timber growth rate in older forests appears robust. This acceleration might be explained by tree growth releases at multiple canopy positions as forests age, experience gap dynamics, and interact with partial disturbances that free up growing space and increase light availability for mixtures of shade-tolerant and shade-intolerant species (Gough, Curtis, Hardiman, Scheuermann, & Bond-Lamberty, 2016; Hanson & Lorimer, 2007; Hardiman, Bohrer, Gough, Vogel, & Curtis, 2011). This inference is partially supported by previous research showing that renewed growth and physiological function in mature and old forests sometimes leads to an increase in growth rate (Keeton, 2018). Further research is needed to resolve whether and why the growth rate increases late in forest stand development.

Total species richness was insensitive to forest age overall but followed a unimodal hump-shaped curve instead of the expected U-shaped curve (Figure 3d). The pattern was driven by the increase in the number of tree and lichen species during the first decades, while vascular plant species richness decreased with forest age (Figure 3c). On the one hand, this finding supports the notion that biodiversity change during forest development strongly depends on the species or taxonomic groups studied (Thom et al., 2017; Thorn et al., 2017). For instance, rare lichen species are often associated with old-growth forest conditions (Selva, 1994) and are used as indicators of forest health (McCune, 2000). The overall species richness derived here may thus represent only one aspect of biodiversity within forest landscapes and conservation strategies. Moreover, a mix of different age classes implying various seral habitat conditions is needed to support a high beta-diversity on forest landscapes (Franklin, 1993). On the other hand, our analysis might exclude some important variables to estimate the effects of forest structure on species richness. In particular, the R^2 of vascular plant species was low (0.112, see Table S3). A more detailed analysis incorporating a higher number of variables related to forest structure and composition represents an important area for future research building on our analyses (see e.g., Zilliox & Gosselin, 2014). For instance, we used conifer share as key variable to describe forest vegetation. While this simplification limits details, for instance, on the dominant species in each plot, it increased computational efficiency (computational time of the Bayesian models was several weeks on the VACC) and data availability.

4.2 | Carbon, timber growth, and species richness associations are sensitive to climate

Our study has shown that associations between TEC, timber growth, and species richness vary with forest age and are sensitive to climatic changes. However, TEC, timber growth rate, and species richness did not follow similar trajectories with forest age based on the results of the GLK tests. Rather, we found strong variations in divergence and congruence between the investigated indicators throughout the 200 year forest development gradient. Despite this variation, their combined performance peaked and the deviance in performance of the investigated indicators was lowest in old forests. This indicates neither a trade-off nor a synergistic behavior among these indicators; rather, forest age and associated stand development drive each indicator's performance independently.

While the strong association between indicators was stable in old forests, our findings suggest that the mix of ESB provided in younger forests may shift into the future as a result of climate change. For example, our analysis suggests a decrease in TEC while, congruent with changes in ALC, timber growth rate increases. However, we acknowledge that the responses to climate change are likely more complex and will be influenced by multiple interacting factors, including stressors such as drought frequency, spread of invasive pests and pathogens, altered disturbance dynamics, and airborne pollutants (Ollinger, Aber, Reich, & Freuder, 2002; Seidl et al., 2017). As tree species migration is unlikely to keep pace with climate change (Thom et al., 2017; Thom, Rammer, & Seidl, 2017a), ecosystems may become increasingly maladapted with negative consequences for ESB. For instance, an increase in water shortage caused by higher evapotranspiration and longer dry periods in the study region (Allen et al., 2010) will likely reduce the growth rate and cause mortality of tree species with low drought tolerance (Eilmann & Rigling, 2012). Species currently predominating on dry sites may have to migrate long distances to occupy similar newly available niches under climate change. Mechanistic models enable the simulation of natural processes and emergence from interactions among vegetation, climate change, other anthropogenic stressors, and natural disturbances, and can thus improve the simultaneous predictions of future ESB outcomes in the study region (Boulanger et al., 2017).

4.3 | Climate sensitivity of boreal–temperate forests

Our results indicate differences in the climate sensitivity across indicators and among geographic regions arising from the heterogeneity in climate, soil, and forest conditions within the boreal–temperate transition zone (Figure 5; Figure S4). While TEC and timber growth rate was highly sensitive to changes in climatic conditions across the entire study region, the sensitivity of species richness was less pronounced overall yet varied spatially more strongly. TEC decreases were mainly driven by reductions in SOC and FFC (Figure 6; Figure S4d–n). Elevated temperature and precipitation increase decomposition rates of organic material stored in soils and on the forest floor, which leads to release of carbon into the atmosphere (Barraclough, Smith, Worrall, Black, & Bhogal, 2015; Jansson & Berg, 1985). However, it has to be noted that the comparably low number of observations for SOC and FFC (119 and 130) in our analysis induced a wide credibility interval (Figure 2e,f), and temperature extrapolations of our models were outside the observed value range for most parts across the study region (Figures S4a–r). Uncertainty about the effects of future changes in plant and soil communities ultimately altering SOC and FFC warrants further investigation (Rouifed, Handa, David, & Hättenschwiler, 2010).

The predicted increase in timber growth with temperature is congruent with other studies reporting enhanced productivity in a warmer world (Boisvenue & Running, 2006; D'Orangeville et al., 2018). However, recent research has shown that reduced winter snowpack and increased soil freezing are negatively affecting the growth rate of sugar maple (*Acer saccharum*), one of the study region's most important tree species (Reinmann, Susser, Demaria, & Templer, 2019). This example demonstrates the high degree of uncertainty in overly general predictions regarding growth responses due to the potential for complex interactions and process feedbacks. Moreover, negative effects from altered disturbances regimes (Kang, Kimball, & Running, 2006), other stressors like invasive species and airborne pollution (Dukes et al., 2009; Ollinger et al., 2002), and changes in tree species composition (Morin et al., 2018) may neutralize the positive direct effects of climate change on timber growth. Thermal conditions in parts of the northern reaches of the study region may become more suitable to support species from temperate biomes (Hamann & Wang, 2006). In contrast, the southern reaches will likely lose boreal species, which face strong competition from temperate species even under current climatic conditions (Murray et al., 2017). As changes in the mix of species and ecosystem services are likely to be nonuniform across the region, challenges will vary for forest management intended to maintain high levels of multiple ESB outcomes simultaneously.

4.4 | Managing forests in the face of climate change

Although our analysis suggests that old forests exhibit the highest combined ESB performance, less than 0.2% of the investigated sites are currently occupied by forests older than 200 years (Figure 2). This suggests a large potential to improve joint ESB outcomes in temperate and boreal forests of eastern North America by enhancing the representation of late-successional and older forest stand structures. For example, our results suggest that increased application of longer rotations as a component of multifunctional forest management would help achieve a broader range of ESB objectives.

Climate change is predicted to have overall negative impacts on the future provisioning of ecosystem services (D'Orangeville et al., 2018; Schröter et al., 2005; Thom et al., 2017; Thom, Rammer, & Seidl, 2017b) and biodiversity (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012; Thomas et al., 2004; Thuiller, Lavorel, Araujo, Sykes, & Prentice, 2005). The slow adaptation process of forests implies that adaptive forest management strategies require long lead-in times (Maciver & Wheaton, 2005). Our study indicates that management aimed at increasing representation of older stand structures on forest landscapes could partly offset the negative effects of climate change on carbon storage (Figure 3f). Moreover, our study indicates how such adaptive efforts could be concentrated in areas most sensitive to climate effects on ESB. In particular, regions east and southeast of the Great Lakes constitute priority areas for adaptive measures as these were identified as potential hotspots of decreasing ESB outcomes under increasing temperature and precipitation regimes (Figure 5a). However, we recognize that our results are dependent on the specific response variables, which do not represent the full spectrum of ESB attributes of forests in the region. Nevertheless, the available variables are directly applicable to key objectives of contemporary forest management.

The slow development of forests on the one hand and the worldwide increasing demand for timber on the other hand (FAO, 2016) creates a challenge for forest managers that is further heightened by the impacts of climate change. Altering age-class distributions at the landscape scale is one strategy to mitigate climate change impacts that would specifically address currently overrepresented mature forests in the study region (Figure 2), while a mix of all development stages needs to be retained to support ESB indicators associated with different forest conditions (see e.g., Swanson et al., 2011). Moreover, increasing the relative abundance of older forests may result in less harvested timber in the transition phase until the desired development stage is reached. However, this initial decrease may be mitigated in the intermediate to long term as the mean annual increment increases in older forests (Figure 3b). This transition phase could be shortened through the use of silvicultural practices designed to increase rates of late-successional forest development and structural complexity in managed forests (Fahey et al., 2018; Felipe-Lucia et al., 2018; Keeton, 2006,2018). Case studies in mixed-northern hardwood conifer forests have demonstrated positive impacts of these measures on carbon storage (Ford & Keeton, 2017; Urbano & Keeton, 2017), timber growth rate (Arseneault, Saunders, Seymour, & Wagner, 2011; Schuler, 2004), and late-successional biodiversity (Kern, Montgomery, Reich, & Strong, 2014; McKenny, Keeton, & Donovan, 2006; Smith, Keeton, Twery, & Tobi, 2008). Field experiments coupled with mechanistic modeling may improve our understanding of the underlying processes determining the dynamics of ESB across forest development stages. In particular, a better understanding of the variation in nutrient and water cycling, photosynthesis rates, and habitat structures supporting high species diversity along forest development gradients may help to optimize landscape-oriented management strategies. Addressing these processes in adaptive forest management frameworks will help sustain ecosystem services and multiple elements of biodiversity in a rapidly changing world.

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SUPPORTING INFORMATION

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