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Habitat and Migration Dynamics of North American Tree Species Under Climate Change

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ABSTRACT

Aim: We model and map the climatically suitable habitats and migration potential of 326 tree species by combining forest inventories of the United States, Canada and to a lesser extent, Mexico, with the goal of providing a continental perspective of species ranges and migration potential to facilitate better forest stewardship under a changing climate.

Location: United States, Canada, and Mexico.

Major Taxa Studied: Tree species.

Methods: We use a multi-model ensemble technique to assess climatic habitat suitability under current and future climates, and a migration model to compute colonisation likelihoods to simulate end of century tree species migration. We combine and synthesise these outputs to provide various products relevant to range-wide assessment of tree species.

Results: For 326 tree species, we provide maps of: current habitat suitability, future habitat suitability under SSP2-4.5 and SSP5-8.5 scenarios, and combined habitat suitability and colonisation likelihoods for the end of the current century. In addition, we provide synthesis outputs of (a) climate and topographic statistical range assessments, (b) maps of potential differences in species richness from current to future climates, (c) assessment of model performance, (d) climate-topographic variable-importance groupings and (e) climatic disequilibrium trends across genera.

A continent-wide assessment of both individual and combined species responses showed evidence of climatic disequilibrium for species with smaller ranges, a projected potential reduction in species richness in the middle and lower mid-continental regions, and an increase across the southeastern, northeastern, and northwestern regions of the continent. Also, we found habitat suitability of most eastern species were mainly driven by moisture, while western species showed strong associations with heat and moisture.

Main Conclusions: Our study provides, for the first time, a baseline for understanding the overall continental dynamics of shifting climatic habitats and migration potential of tree species across their entire range, facilitating improved management of North American forested ecosystems.

1 | Introduction

The interaction of climate and topography over many millennia has played a fundamental role in determining continental trajectories of tree species distribution shaped by eco-evolutionary niche dynamics (Williams et al. 2004; Copenhaver-Parry et al. 2017; Cao et al. 2019; Sharma et al. 2022). At a coarse scale, patterns of tree abundance are influenced mainly by climatic drivers, such as temperature, precipitation, and aridity (Cano et al. 2019), while factors such as competition, predation, edaphic conditions, and human interventions are considered to exert finer-scale control (McKenzie et al. 2003; Copenhaver-Parry et al. 2017; Brambilla et al. 2024). While knowledge of the factors driving tree distribution and abundance at a variety of spatial scales is critical for forest management (Palik et al. 2022), our focus in this paper is macroscale mapping of suitable habitats and colonisation potentials for a large number of North American tree species under current and future climates. This coarser scale perspective provides insights on emerging trends across-species ranges which are often masked by finer-scale investigations using truncated ranges (Williams et al. 2004; Davis 2001).

Species distribution models that incorporate broad-scale climate drivers have a played an important role in assessing potential climate change impacts on tree distributions and possible management responses (Guisan et al. 2013). Many previous modelling efforts have been regional in scope, focusing on portions of the continent that are of particular interest or undergoing rapid change (Rotbarth et al. 2023; Foster et al. 2022; Hessburg et al. 2022; Prichard et al. 2021; Iverson et al. 2019). However, given that many tree ranges cross regional and national boundaries, it would be useful to obtain continental-scale distribution and environmental data to provide context and comprehensively assess species' climatic niches. This is an important consideration because incomplete niche specifications under current climate can lead to misleading projections of future climate habitat (Charney et al. 2021).

Studies that have produced continental-scale tree distribution models have typically employed presence/absence (or pseudo absence) data (Shafer et al. 2001; McKenney et al. 2007, 2011). While these studies are useful for estimating species' range limits, they do not shed light on intra-range variation in habitat quality as revealed by abundance-based models (Estrada and Arroyo 2012; Howard et al. 2014). In addition, future habitat changes should incorporate tree migration constraints because not all suitable habitats are likely to get colonised (Prasad et al. 2020; Boisvert-Marsh et al. 2022). Natural tree migration involves the inherently slow process of seed dispersal, seedling establishment, and subsequent maturation to seed production (Viglas et al. 2013). While rare long-distance dispersal events associated with wind events or animal movements can speed up migration rates (Nathan et al. 2002; Hardesty et al. 2006), several studies—covering a range of methodologies—have indicated that trees are unlikely to keep pace with the climate shifts projected for the current century (Sittaro et al. 2017; Prasad et al. 2020; Boisvert-Marsh et al. 2022). Thus, projections of tree distributions should incorporate migration dynamics along with projections of future habitat suitability to better understand both migration limits and management options under climate change.

The current modelling effort is motivated by the Updated Silvics of North America (USNAP, https://www.climatehubs.usda.gov/hubs/southeast/topic/updated-silvics-north-america-project-usnap), a collaborative venture involving three national governments, various academic institutions, and a network of researchers to inform better forest science and silviculture (McNulty 2022). Here we expand the scope of previous distribution modelling efforts (Iverson et al. 2008, 2019; Prasad et al. 2020) and the eastern climate change tree atlas (https://doi.org/10.2737/Climate-Change-Tree-Atlas-v4) to include the entire range of many North American tree species under current and future climates. Our approach employs an ensemble of non-parametric regression-tree-based bagging and boosting methods and simulates end-of-century migration potential by computing colonisation likelihoods based on an average of migration rates from palaeoecological data. The primary goals of our study are to:

a. Model potential suitable habitats of 326 tree species in North America using current relative abundance from forest inventories of the US, Canada, and Mexico, as a function of climate and topography.

b. Project future suitable habitats (denoted as habitat quality—HQ) for two future climate scenarios (the milder SSP2-4.5 and the warmer SSP5-8.5; See IPCC 2023)

c. Compute end of the 21st century colonisation likelihoods (CL) of these projected future habitats based on palaeoecological migration rates, current distribution of HQ and land-use, and

d. Combine HQ and CL classes (HQCL) to assess suitable habitats that could be colonised naturally by the end of the century and distinguish them from those regions that have a lower likelihood of colonisation.

Taken together, these results provide insights into current and future continental trends enabling mapping of species richness and summarising shifts in species richness through time across North American ecoregions (Ecoregions of North America 1997). We summarise model performance measures like R^2 and variable importance across tree species models and assess differences in climatic requirements between eastern and western species. Additionally, we evaluate the degree of climatic disequilibrium across various tree genera. By establishing a continental baseline for both current and potential future distributions, these results can provide a macroscale template from which more regional modelling studies can be formulated by incorporating relevant local factors.

2 | Materials & Methods

2.1 | Forest Inventory Data

Records from the most recently completed inventory cycle of the US Forest Inventory and Analysis (FIA) for each state

were extracted from a total of 979,075 plots across the conterminous US and Alaska sampled from 1998 to 2018 (O'Connell et al. 2017). We combined the Alaska coastal inventory with the limited interior inventory for a total of 16,431 plots across Alaska. We calculated the Relative Importance Value (hear after RIV) index, a measure of relative abundance that accounts for both the number of stems and basal area, as:

$$\mathrm{RIV}(x) = \frac{50 \times \mathrm{BA}(x)}{\sum \mathrm{BA}(\mathrm{AllSpeciesInPlot})} + \frac{50 \times \mathrm{NS}(x)}{\sum \mathrm{NS}(\mathrm{AllSpeciesInPlot})} \quad (1)$$

where x is the species in the plot, BA is the basal area, and NS is the number of stems (summed for overstory and understory trees). In monotypic stands, RIV would reach a maximum of 100%.

The plot level RIV was previously averaged to 20 × 20 km cells by using only plots for which the species was present (Prasad et al. 2020). The choice of 20-km cells helped ensure most forested cells had more than one sample plot and matched the response with the predictors at macroscales, resulting in good regression models (Prasad et al. 2023). While 20-km cells ensured that the RIV could be adequately estimated for most species within cells, when individual species with high RIV occurred in only a few plots within a cell (e.g., < 3 plots), RIV was anomalously high—especially near the edge of species' ranges. To alleviate this problem, we used a 3 × 3 focal mean filter for cells with only 2 or 3 species-present plots and a 5 × 5 focal mean filter if only one species-present plot occurred. For all other cells (with species-present plots > 3), no focal mean filter was applied. The 3 × 3 and 5 × 5 windows were chosen via trial and error to distinguish among sparsely populated cells. This procedure greatly reduced the anomalous peaks of RIV when species occurred in a few plots within a cell, while improving model performance. The same methodology was applied to Alaska's coastal and interior FIA data for the 18 tree species reported in that state. It is noteworthy that the interior Alaska inventory is still in its early stages of sampling and did not cover the whole state.

Canada's National Forest Inventory (NFI) data consists of 2 × 2 km photo plot grids (~10,000) arranged across the country between 2007 and 2017 (Canada's National Forest Inventory 2021; Gillis et al. 2005). Approximately 100 or more stand-level polygons are present within each 2 × 2 km plot. The percent species composition, equivalent to FIA-based relative abundance (RIV), was summarised at the NFI plot level (2 × 2 km) and averaged across 20 × 20 km cells as was done with FIA data.

Canada's NFI data had many gaps related to difficulties in identifying low-density cryptic species in photo plots. We used the nearest-neighbour (focal, moving-window) interpolation approach to fill these gaps and derive a homogeneous response surface amenable to modelling. If the number of plots in a 20-km cell was less than or equal to three, we used a 3 × 3 focal mean, and if greater than three, the original NFI values were used. Also, if the focal 3 × 3 resulted in zeros (usually for regions farther away from the main distribution), the original NFI values were retained. The resulting response surface yielded better-performing models compared to the response surface containing gaps within the main distribution.

The national-level forest inventory program in Mexico (CONAFOR 2004) conducted from 2004 to 2009 contains 26,220 sampling plots, systematically distributed throughout the country, and has a sample density of approximately one plot per 2577 ha of forestland. We chose seven species from the Mexican inventory (Table S1) with good coverage that spanned the border between the US and Mexico (out of 15 for which relative abundance was calculated). The low number of species included for Mexico was due to data limitations stemming mainly from species nomenclature anomalies. The RIV was calculated for these species as per Equation (1) and merged with FIA data.

From an initial list of 340 potential species generated using the US FIA data, the final number was reduced to 326 species (Table S1) based on limitations imposed by combining inventory data and modelling species with very sparse inventories. The final list of 326 included 238 species unique to conterminous US, 7 species that spanned the US-Mexico border, and 81 species that spanned the US-Canada border (including 18 species that spanned the border with Alaska and Canada). The derived RIVs for all three countries were combined to create a response surface that was amenable to distribution modelling.

2.2 | Predictors

Our models incorporated 32 climatic variables and seven elevation and topographic variables (Table 1). We used all possible combinations of predictors because of the large geographic scope of the study, the number of tree species involved, and the reduced importance of collinearity in non-parametric, recursive tree-based models (Ellis et al. 2012; Tomaschek et al. 2018; Chen et al. 2023). Further, certain combinations of predictors are likely relevant for a subset of species in some regions but not in others, making it difficult to ascertain beforehand which variables to include or exclude based on collinearity. The consensus prediction in the multi-model ensemble (MME) scheme (explained in the 'Climatic habitat suitability model' section below), reduced the collinearity related issues. We grouped predictors into five ecologically meaningful categories for comparative purposes (Table 1) – Temperature (Heat); Precipitation (Moisture); growing season (GrowSeason); interactions between temperature and precipitation (HeatMoisture); and elevation and terrain (ElevTerrain).

We obtained climate data from the AdaptWest database (Wang et al. 2016; AdaptWest Project 2021; Mahony et al. 2022) for climate variables for the current (i.e., 1991 to 2020) and projected future (i.e., 2071 to 2100) time periods. We used data for future climate scenarios (CMIP6) associated with shared socioeconomic pathways (SSPs) to examine the degree to which habitat suitability differed under these alternative pathways (O'Neill et al. 2016). We chose the middle-of-the-road warming scenario (i.e., SSP2-4.5) and the fossil-fueled development scenario (i.e., SSP5-8.5) to highlight these alternative outcomes in our analysis. According to IPCC, the end of century temperature increases by 2.7°C for SSP2-4.5 and

TABLE 1 | The 32 climate variables for current climate (1991–2020), CMIP6's SSP2-4.5 and SSP5-8.5 scenarios (2071–2100), and seven terrain variables used as predictors in the habitat quality (HQ) multi-model ensemble (MME) and the five predictor groupings.

Climate Abb.	Climate variables	Predictor grouping
mat	Mean annual temperature (°C)	Heat (Temperature Related)
mwmt	Mean temperature of the warmest month (°C)	Heat (Temperature Related)
mcmt	Mean temperature of the coldest month (°C)	Heat (Temperature Related)
emt	Extreme minimum temperature over 30 years (1991–2020)	Heat (Temperature Related)
ext	Extreme maximum temperature over 30 years (1991–2020)	Heat (Temperature Related)
td	Difference between MCMT and MWMT, as a measure of continentality (°C)	Heat (Temperature Related)
tave_wt	Winter (December to February) mean temperature (°C)	Heat (Temperature Related)
tave_sp	Spring (March to May) mean temperature (°C)	Heat (Temperature Related)
tave_sm	Summer (Jun to Aug) mean temperature (°C)	Heat (Temperature Related)
map	Mean annual precipitation (mm)	Moisture (Precipitation)
msp	Mean summer (May to Sep) precipitation (mm)	Moisture (Precipitation)
pas	Precipitation as snow (mm)	Moisture (Precipitation)
tave_at	Autumn (September to November) precipitation (mm)	Moisture (Precipitation)
ppt_wt	Winter (Dec to Feb) precipitation (mm)	Moisture (Precipitation)
ppt_sp	Spring (March to May) precipitation (mm)	Moisture (Precipitation)
ppt_sm	Summer (June to August) precipitation (mm)	Moisture (Precipitation)
ppt_at	Autumn (september to november) precipitation (mm)	Moisture (Precipitation)
dd0	Degree-days below 0°C (chilling degree-days)	GrowSeason (Growing Season)
dd5	Degree-days above 5°C (growing degree-days)	GrowSeason (Growing Season)
dd_18	Degree-days below 18°C	GrowSeason (Growing Season)
dd18	Degree-days above 18°C	GrowSeason (Growing Season)
nffd	The number of frost-free days	GrowSeason (Growing Season)
bffp	The Julian date on which the frost-free period begins	GrowSeason (Growing Season)
effp	The julian date on which the frost-free period ends	GrowSeason (Growing Season)
dd1040	(10 < DD < 40) degree-days above 10°C and below 40°C	GrowSeason (Growing Season)
eref	Hargreaves's reference evaporation[a]	HeatMoisture (Temperature + Precipitation)
cmd	Hargreaves's climatic moisture deficit[a]	HeatMoisture (Temperature + Precipitation)
mar	Mean annual solar radiation (MJ m-2 d-1) (excludes areas south of US)	HeatMoisture (Temperature + Precipitation)
rh	Mean annual relative humidity (%)	HeatMoisture (Temperature + Precipitation)
cmi	Hogg's climate moisture index (mm)	HeatMoisture (Temperature + Precipitation)
ahm	Annual heat moisture index, calculated as (MAT+10)/(MAP/1000)	HeatMoisture (Temperature + Precipitation)
shm	Summer heat moisture index, calculated as MWMT/(MSP/1000)	HeatMoisture (Temperature + Precipitation)
elv	Elevation, m	ElevTerrain (Elevation & Terrain)
trough	Terrain roughness	ElevTerrain (Elevation & Terrain)

(Continues)

TABLE 1 | (Continued)

Climate Abb.	Climate variables	Predictor grouping
tslope	Slope	ElevTerrain (Elevation & Terrain)
taspect	Aspect	ElevTerrain (Elevation & Terrain)
tpi	Topographic position index	ElevTerrain (Elevation & Terrain)
twi	Topographic wetness index	ElevTerrain (Elevation & Terrain)
ttri	Topographic roughness index	ElevTerrain (Elevation & Terrain)

[a]For more information, see: Wang et al. (2012); Hargreaves and Allen (2003).

by 4.4°C for SSP5-8.5 (https://doi.org/10.1017/9781009157896.001). Because current trends reflect SSP5-8.5, we have emphasised this highly plausible pathway (Schwalm et al. 2020). The SSP2-4.5 and SSP5-8.5 projections were based on averaged ensembles of eight general circulation models (Mahony et al. 2022) – ACCESS-ESM1.5, CNRM-ESM2-1, EC-Earth3, GFDL-ESM4, GISS-E2-1-G, MIROC6, MPI-ESM1.2-HR and MRI-ESM2 (CMIP6 AOGCMs– AdaptWest Project 2021). For further details about these eight models, refer to https://wcrp-cmip.github.io/CMIP6_CVs/docs/CMIP6_source_id.html. The original data, at 1 km resolution, were aggregated to 20-km grids to match the response variable. Elevation data (Table 1) were derived from the USGS GMTED2010 digital elevation model (DEM) data at 500 m resolution for the North American continent (Global Multi-resolution Terrain Elevation Data, 2010; Danielson and Gesch 2011). Six terrain variables were derived from the DEM data using R (terrain in terra package: Hijmans 2022; R Core Team 2022) and the topographic wetness index was derived using SAGA GIS (RSAGA package in R; Brenning et al. 2018). The elevation and terrain variables were aggregated (using averaging) to 20-km cells to match the resolution of the response variable (Guisan et al. 2007; Araújo et al. 2019; Wiens et al. 2009).

2.3 | Habitat Quality (HQ) Model

Machine learning approaches, such as random forests and boosted regression trees, have consistently performed well in model intercomparison studies (Elith et al. 2006) and are well suited to modelling continuous response variables. Consequently, we employed a MME approach that features several types of regression-tree-based models (sensu Prasad et al. 2020) to model the relationship between tree abundance and climatic and topographic variables. Specifically, we used three versions of bagging (i.e., ordinary bagging, randomForest, and extremeForests) and two versions of regression-tree boosting (i.e., with and without regularisation). For details on bagging techniques, see Breiman (1996); Breiman (2001); Geurts et al. (2006). For details on boosting, see Friedman (2002); and Chen and Guestrin (2016). For GIS processing we used the terra module (Hijmans 2022), the ranger module for bagging versions (Wright and Ziegler 2017), and the xgboost module (Chen and Guestrin 2016) for boosting in R (R Core Team 2022).

The MME technique employed here involves averaging the consensus predictions of multiple regression models that use similar base-learners. This approach is best suited to situations where prediction uncertainty needs to be stabilised to reflect the dominant trend (Jones and Cheung 2015; Martre et al. 2015) by averaging individual model errors (Zhang et al. 2015). In our approach, only the "consensus" predictions among all models (i.e., where all models predicted nonzero values) are averaged to ensure that the main trends are captured, and the noise minimised.

Built-in validation methods of bootstrap sampling and cross-validation in the five models ensure that the models do not overfit (Svetnik et al. 2003). To ensure that built-in validation was sufficient and optimal model parameters were chosen, we used the package *caret* in R, which creates a stratified random split of the data into training and test sets to evaluate the parameters for best model performance (Kuhn 2008).

2.4 | Migration (CL) Model

We simulated end-of-century natural migration using a lightly parameterised model called SHIFT to calculate future colonisation likelihoods (CL) both inside and beyond the current range based on historical tree migration rates, current abundance of the species (Prasad et al. 2013, 2020) and land cover (NALC 2015). SHIFT simulates long-distance dispersal via a fat-tailed inverse power function under currently fragmented landscapes (Schwartz 1993). Each species is allowed to migrate based on its current distribution and generation time (i.e., the time it takes trees to produce viable propagules) with no climatic constraints and a historically defensible, but generous migration rate of 50 km century^{-1}, and a 500-km search window for stochastic long-distance events. This is done for approximately 75 years (until the end of century) to ensure that despite having a common migration rate, the landscape is colonised to the end of the century to match the future climate (2071 to 2100, SSP2-4.5 and SSP5-8.5) projections from the HQ model. While a migration rate of 50 km century^{-1} is used for all species in this study, the number of generations (model iterations) required to simulate end-of-century migration varies among species depending on their generation time. The newly colonised cells can only contribute to colonisation in the next generation since the propagules have to mature. For a minority of the species for which we could not find generation time in the literature, we assumed a value of three generations, which roughly approximates to 21 to 26 years to reproductive maturity. This is consistent with most of the tree species in the study and matches the end-of-the-century time frame. SHIFT runs at a resolution of 1 km and the

outputs are aggregated to 20 km to match the HQ model (Prasad et al. 2013).

2.5 | Combining HQ & CL (HQCL)

The end-of-century projections of the HQ model were intersected with the CL simulation to depict which suitable habitats could be colonised by the end of the century. To achieve this objective, the HQ outputs, based on relative abundance as modelled by MME, were reclassified into three classes (specifically for combining with CL): low (1–6), medium (7–15) and high (16–100). Similarly, the end-of-century CL computed by the migration model (scaled 0 to 100 where 0 represents no colonisation and 100 the maximum colonisation likelihood) was also reclassified into: uncolonized (0), low (1–10), medium (11–30) and high (31–100).

These classifications (HQ and CL) were combined to yield 12 HQCL combinations by including the null class (i.e., uncolonized suitable habitats at the end of the century). These combinations provide meaningful discrimination among HQCL classes without exceeding the limit for legend interpretability. It should be noted that the HQ and CL reclassification scheme was chosen based on this need for parsimony while generally preserving the structure of the overall distribution for all species. The colour scheme for the legend was carefully chosen to highlight the interplay of HQ and CL classes—especially to distinguish those areas that: (a) have the potential to be colonised; (b) are suitable but not colonised by the end of the century; and (c) are occupied under both current and future climates.

It is noteworthy that the CL model was not able to produce outputs for two species with modelled HQ—which are noted in Table S1. Both these species (*Annona glabra* L. and *Leucaena pulverulenta* (Schltdl.) Benth.) had an R^2 close to zero. The combined HQ and CL output for these two species is therefore absent.

2.6 | Species Richness, Ecoregion Summaries, Variable Importance and Climatic Disequilibrium

We generated species richness maps (across the 326 species) by summing species presence for both current-modelled and future (2071–2100, SSP5-8.5) conditions, allowing us to compare potential shifts in richness over time.

In addition to species richness maps, we also evaluated summary statistics (via boxplots) of species richness differences between current and future (2071–2100, SSP5-8.5) periods for 15 level-1 North American ecoregions (Ecoregions of North America 1997). We chose the SSP5-8.5 pathway because it represents the worst-case future climate and is the most likely future scenario if current trends continue.

To estimate the importance of predictors across species, we used the four most important variables in the randomForest model of the MME to assess the frequency of predictors arising from each of the five climate-terrain groups (Table 1). We used 220 species with $R^2 >= 0.2$ to ensure that predictor importance values were robust (i.e., estimated for species that were not too sparse or scattered in distribution). This analysis was carried out for three species groupings based on the broad geographic regions occupied by each species (i.e., east, west and east–west).

We also tested for evidence of climatic disequilibrium in our distribution models (sensu Seliger et al. 2021), by regressing species' model performance (i.e., R^2 of the MME model) against range size (i.e., log of 20-km cell counts) for each of 15 tree genera. In this analysis, the R^2 values indicate to what extent climatic variables influence the distribution of each species, assuming species at equilibrium are better explained by the included climate variables.

3 | Results

3.1 | Model Performance and Variable Importance

Performance of the habitat quality (HQ) models for the 326 species, as measured using the R^2 metric, differed widely across species (Figure S1)—with sparsely distributed/sampled and/or non-contiguous, scattered species having poor models, and contiguously and densely distributed species with much better performance. Performance also varied somewhat based on geography (Figure S1), with eastern species ($n = 199$; median $R^2 = 0.46$) performing better than western species ($n = 103$; median $R^2 = 0.40$), and the more expansive east–west spanning species the best ($n = 24$; median $R^2 = 0.48$).

Variable importance also varied geographically (Figure S2a–c). Climate variables in the Moisture group were by far the most frequent in the east, followed by the Heat group (see Table 1); Heat–Moisture and Moisture groups were most frequent in the west; and Heat and GrowSeason groups were most frequent for the fewer east–west spanning species. These differences in variable importance shed light on the contrasting drivers of species distribution among the regions. For example, the heightened importance of the heat and moisture variables for western species highlights the key role of these variables in driving species distributions in a region where differences in heat and moisture are influenced by topographically diverse terrain.

3.2 | Current and Modelled Outputs

Among the 326 species modelled, we show outputs for *Populus tremuloides* Michx. (quaking aspen) as an example species because it has a relatively high R^2 of 0.76 and spans a large portion of the continent according to the inventories (Figure 1a) and current-modelled (Figure 1b). Maps, charts and tables for all species are archived in an online database—see Prasad, Peters, et al. (2024). Both future scenarios, SSP2-4.5 and SSP5-8.5 (Figure S3a,b), show some declines in potential suitable habitat in the eastern US, but with northern expansion into the sub-arctic regions, with Alaska seeing a further expansion northwestward. The combination of HQ and CL maps provides details on how migration constraints may affect future range shifts under SSP2-4.5 (Figure 2a) and SPP5-8.5 (Figure 2b). For example, shades of yellow, blue, and pink indicate increasingly suitable habitats that may be colonised by the end of the century.

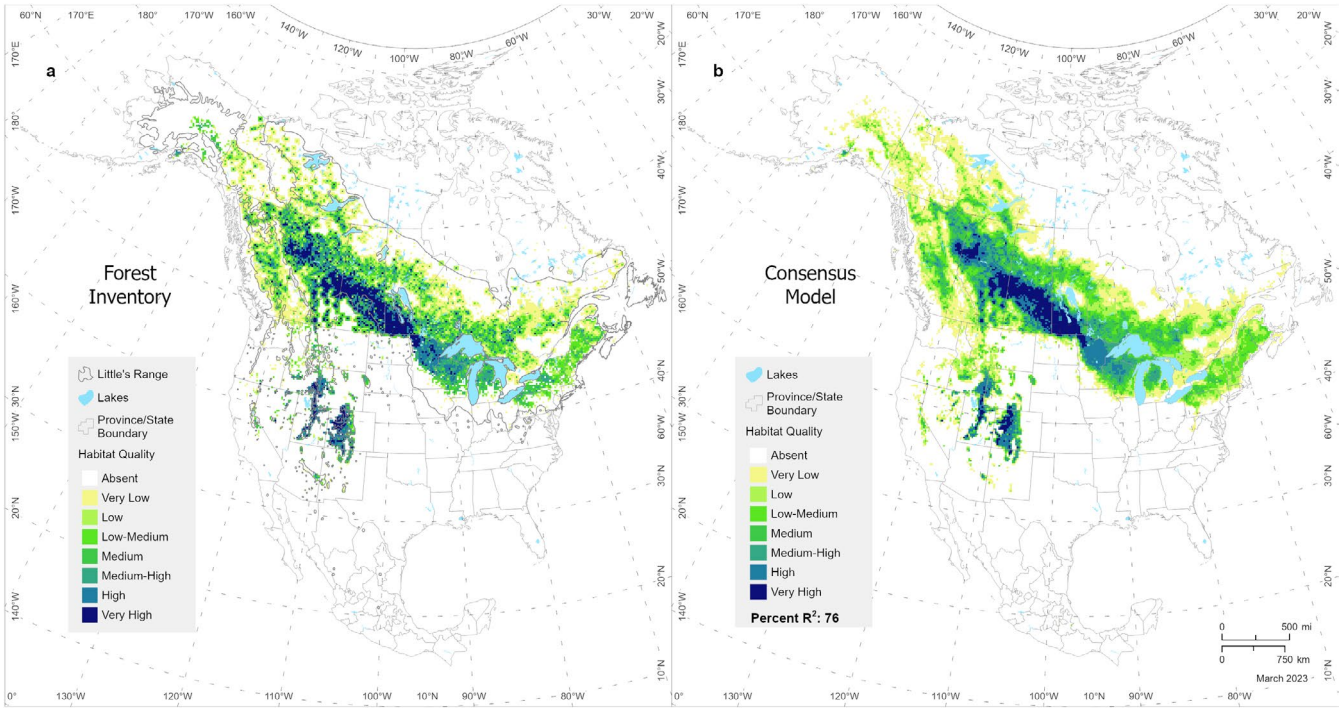

FIGURE 1 | The current distribution (~2018) according to the inventory data (a) and modelled current based on the consensus of models (b) in the multi-model ensemble (MME) of *Populus tremuloides* Michx. (quaking aspen) For details on the mapping techniques and the MME model, see the Methods section. The habitat quality classes (based on reclassifying continuous abundance values) reflect trade-offs among mapping clarity, across-species consistency and parsimony.

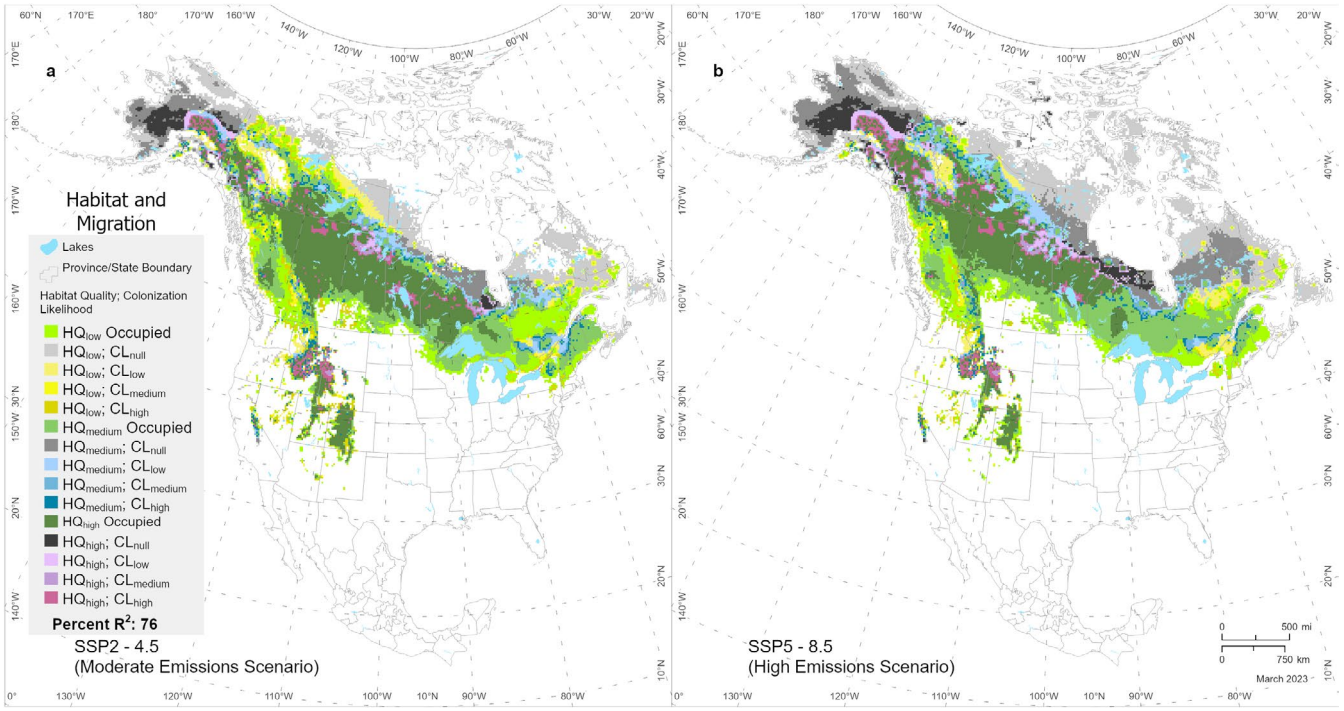

FIGURE 2 | Mapped combination of suitable habitat (HQ—occupied, low, medium, high) and colonisation likelihoods (CL) classes (null, low, medium, and high) of *Populus tremuloides* Michx. (quaking aspen) for the end of century natural migration potential of suitable habitats for (a) SSP2-4.5 and (b) SS5-8.5 scenarios (2071–2100). Shades of green show species habitats that are currently occupied according to the inventory; shades of yellow low HQ class with varying CL classes; shades of blue medium HQ class with varying CL classes; shades of purple high HQ class with varying CL classes; shades of grey are varying HQ classes with no chance of natural migration by the end of century (CL_{null}). For details of HQ and CL models, see the Methods section.

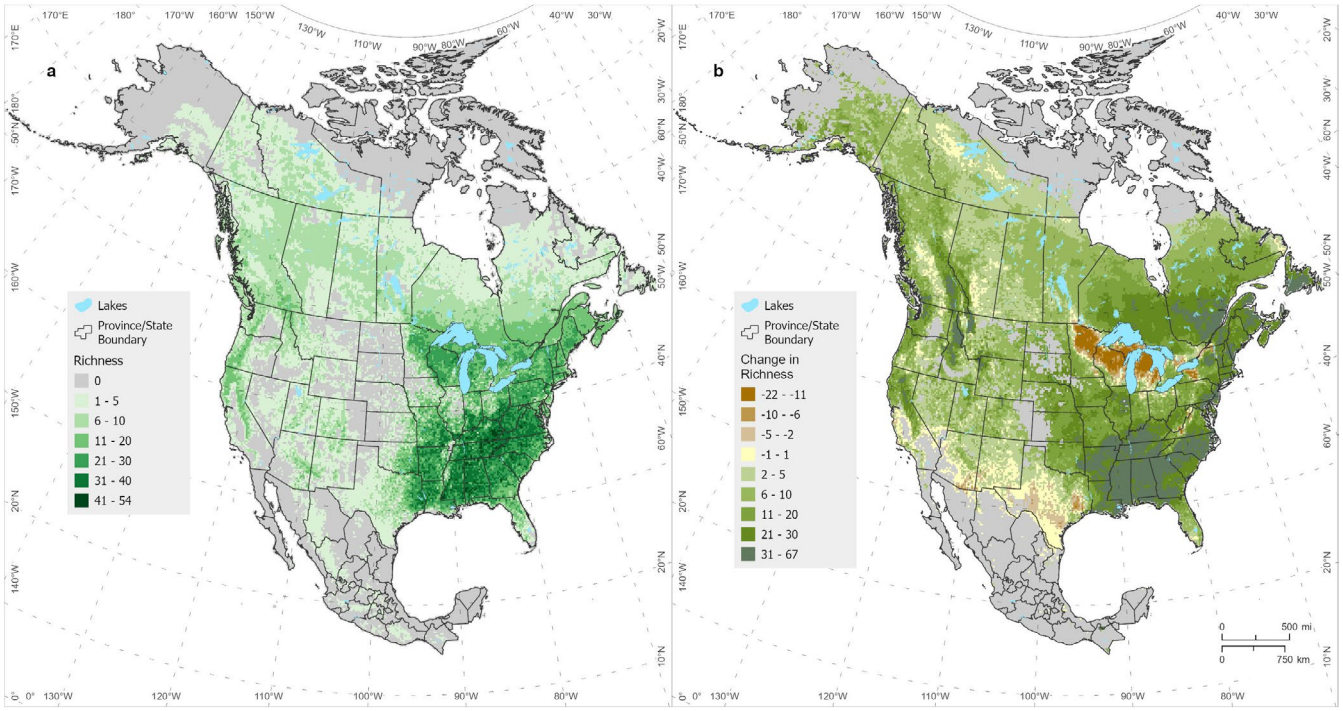

FIGURE 3 | The current species richness map (~2018) of the sum of presence counts of 326 tree species based on the forest inventories (a). Projected species richness difference map between the modelled current and future SSP5-8.5 scenario (2071–2100) (b). The browner regions indicate loss and the greener regions a gain in species richness with yellow showing hardly any change. Because only seven species were used for Mexico due to forest inventory limitations, the change in richness (b) is relevant only for Canada and the US.

The shades of grey indicate areas that are projected to have suitable habitats by the end of the century, but where natural migration is unlikely to occur. These are areas outside the current range which show potential for assisted species migration (Stanturf et al. 2024).

Mean annual temperature and annual precipitation values across current and projected ranges of quaking aspen show expected trends (Figure S4a,b), with temperatures increasing and precipitation becoming much more variable under future scenarios, which implies that predicted habitats occupy a larger range of moisture regimes under future climates.

3.3 | Changes in Species Richness Metrics

Spatial patterns in species richness between the current 326 species according to the inventories (Figure 3a), and the projected future SSP5-8.5 climates (Figure 3b) revealed important variations. Many northern regions of the continent are projected to increase in species richness in the future due to northward habitat shifts projected under climate change. Similarly, the southeastern region of the US shows richness increases (especially in Georgia and Alabama), where more regional increases overwhelm losses. However, several regions are projected to lose more species than they gain. This disparity is the most striking in the northern midwestern regions of the United States (i.e., Minnesota, Wisconsin, and Michigan), and to a lesser degree in the southern, semi-arid states of Texas, and parts of New Mexico and Arizona. This is likely because many northern species with trailing-southern boundaries in the northern midwestern regions lose habitat without a corresponding infill from southern species with leading-northern boundaries (see Discussion for examples). There are also scattered areas in the west, northwest, and in the arctic north that are projected to lose suitable habitats. The areas in Mexico that show current species richness (light green in Figure 3a) are discounted in the projected changes (Figure 3b) because we are using only seven species from the Mexican inventory due to data availability constraints.

We also evaluated how projected shifts in suitable habitats are reflected in level-1 ecoregions of North America (Ecoregions of North America 1997). Figure 4a shows the number of species lost or gained for 13 level-1 ecoregions (Figure 4b), with the grey box showing the range of the mean and median. Most of the ecoregions' mean/median ranges are positive, indicating a net gain in future habitats (the exception being *Southern Semiarid Highlands*). Interestingly, the regions showing high losses (i.e., Minnesota, Wisconsin, and Michigan, in Figure 3) are subsumed under the *Northern Forests* and *Eastern Temperate Forests* ecoregions (with currently 33 and 54 species), both of which show a net increase in the mean/median range, although the min/max ranges indicate that losses and gains are also steep (i.e., below −20 and above 30—see Figure 3). The *Northwestern Forested Mountains*, the *Hudson Plain*, the *Taiga*, and the *Tundra* ecosystems also show net increases in the mean/median range, indicating increased availability of suitable habitats in these northern ecoregions with future warming. Southern ecoregions mainly encompassing Mexico do not show significant changes due to the limited number of species with primarily Mexican distributions in this study (i.e., only seven). However, it is important to note that gains in suitable habitats for most species do not necessarily translate into a species successfully colonising

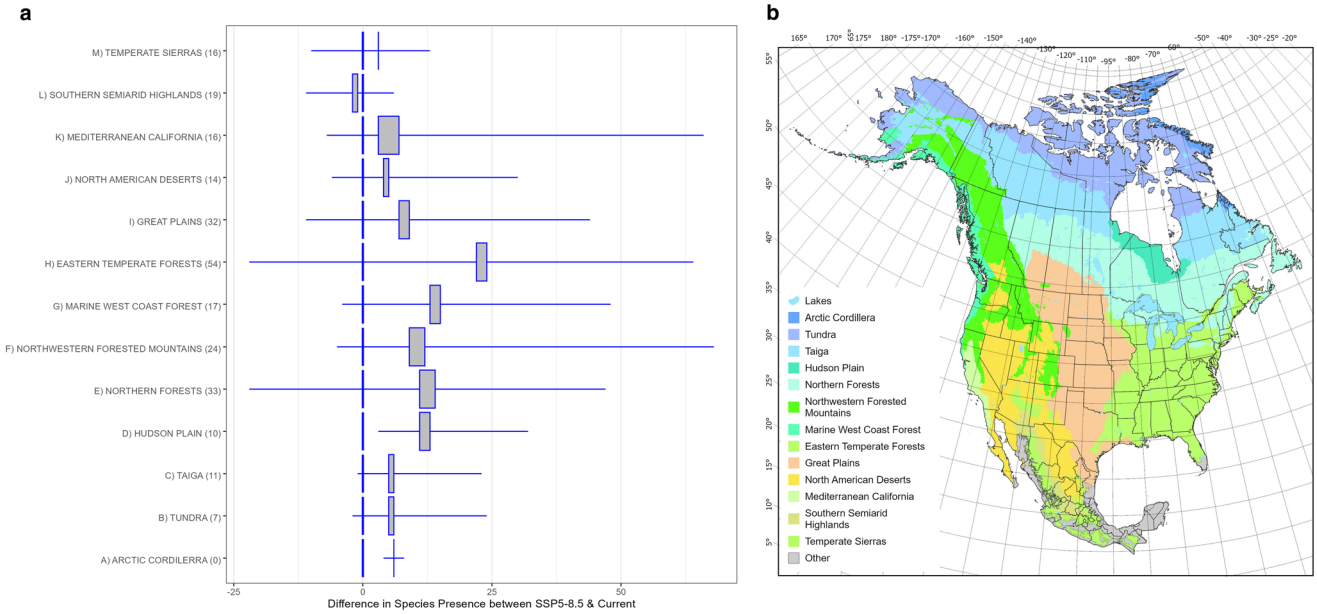

FIGURE 4 | Boxplot statistics (a) of species richness differences (presence counts of 326 tree species) between future (SSP5-8.5, 2071–2100) and current scenarios for level-1 ecoregions of North America (b). The grey box in (a) indicates the range of mean and median values. The numbers in parentheses after the ecoregion names denote the current number of species found in that ecoregion. Because only seven species were used for Mexico due to forest inventory limitations, mainly Mexican ecoregions are not represented fully (greyed out in b).

these habitats by the end of the century, as explained previously for quaking aspen (See Figure 2).

3.4 | Climatic Disequilibrium

Graphs for 14 major genera and one for all other genera combined (OTHERS) (Figure 5) show a positive relationship between the suitable habitat area (log of 20-km cell count) and model performance (i.e., R^2)—indicating that climate can better explain the pattern of abundance of large-ranged species compared to smaller-ranged species. The general reduced role of climate for small-ranged species is consistent with (Seliger et al. 2021) who noted these species tended not to be at equilibrium with climate. This suitable area-model performance signal we detected was consistent for most tree genera, but it is worth noting that statistical significance was lower for genera with fewer observations (e.g., magnolia (*Magnolia* L.) and spruce (*Picea* A. Dietr.)), although only birch shows statistical non-significance at the 0.05 level.

4 | Discussion

Motivated by the ongoing effort to update the Silvics of North America (USNAP, McNulty 2022), this analysis of 326 tree species models across the three North American countries is an ambitious undertaking. Our main objective with this effort is to highlight variations in *macroscale* patterns of habitat and colonisation potentials across a broad range of tree species spanning the entire continent.

Despite some challenges which we list below, we believe this is the first time that this type of multi-species, continental-scale effort has been undertaken in North America (for a similar effort in Europe, see Mauri et al. 2022), setting the stage for further comparisons as data quality and modelling techniques improve (Prasad, Pedlar, et al. 2024). Even though we could use only seven Mexican species that spanned the border with the US due to inventory data limitations, Mexico is a biodiversity hotspot (Mora 2022) with at least 2885 native tree species, represented in 612 genera and 128 families (Tellez et al. 2020). Integrating data from the Mexican inventory therefore is particularly informative and we hope that future collaborative initiatives and cross-border cooperation will continue to build on the work presented here.

4.1 | Species Responses

For many wide-ranging species, integrating forest inventories across countries allowed assessment of potential expansions into colder northern regions, along with declines in the warmer southern regions of species' ranges (Rotbarth et al. 2023). For many of these species—for example, *Abies balsamea (L.) Mill.* (balsam fir), *Picea mariana* (Mill.) Britton, Sterns & Poggenb. (black spruce), *P. glauca* (Moench) Voss (white spruce), and *Pinus strobus L.* (eastern white pine), the decrease in climatic HQ in southern regions can be contrasted with increasing shifts into northern and northwestern Canada and Alaska, especially for the SSP5-8.5 scenario (see the online archived database—Prasad, Peters, et al. 2024). However, natural colonisation is highly unlikely to occur in regions far away from the current boundary. For western species, however, this loss in southern habitats is far less pronounced for similar wide-ranging species (e.g., *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr. (white fir), *A. grandis* (Douglas ex D. Don) Lindl. (grand fir), *Pinus contorta* Douglas ex

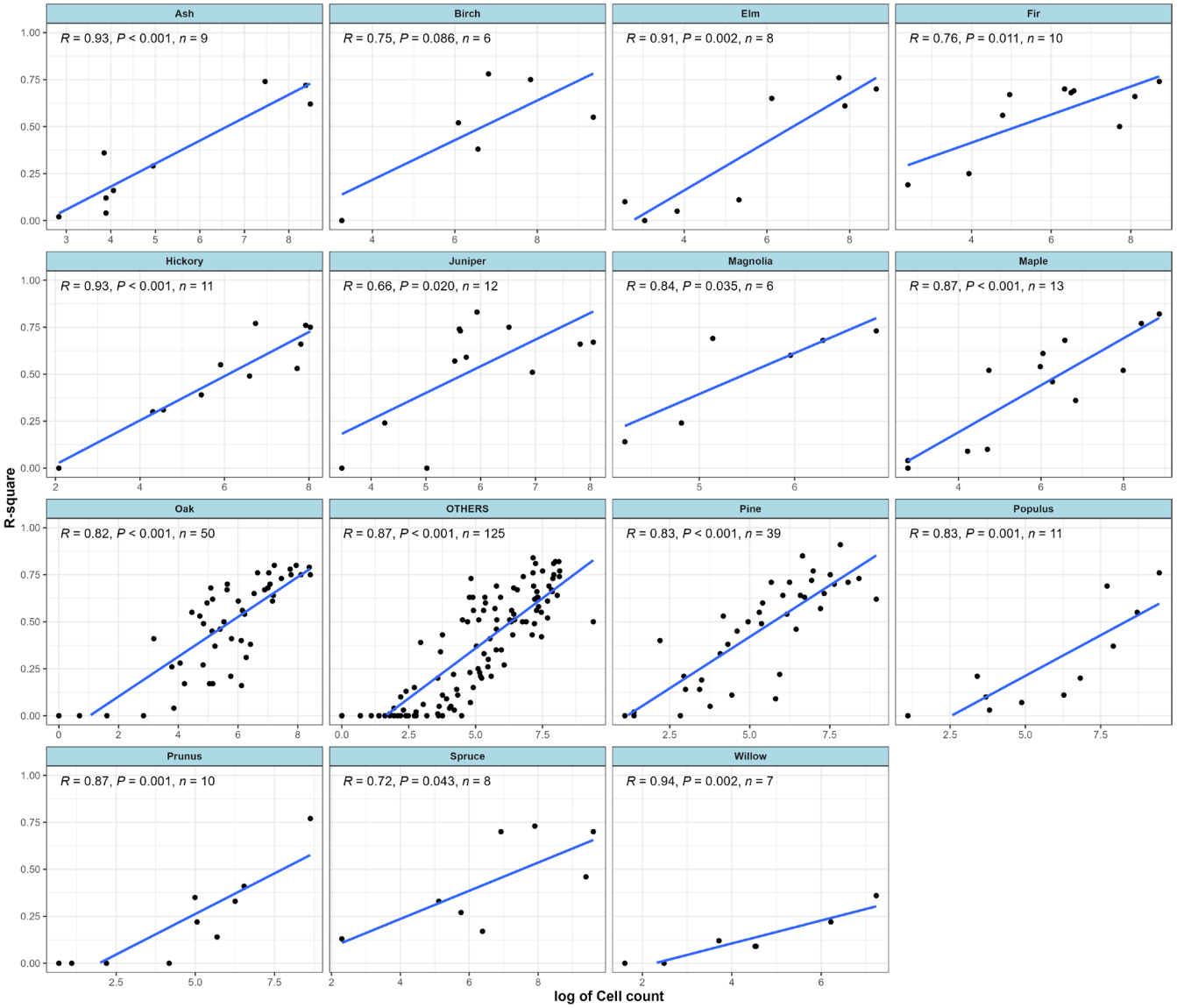

FIGURE 5 | Relationship of model performance (*R*-square) with species range size (log of 20 km cell count). For the 14 major genera and the rest of the genera (OTHERS), the slope is positive, indicating that climate explains more of the variation for species with larger coverages. Only Birch shows statistical non-significance at the 0.05 level (Pearson correlation coefficient).

Loudon (lodgepole pine), *Picea engelmannii* Parry ex Engelm. (Engelmann spruce), *Pseudotsuga menziesii* Carrière (Douglas fir)). Many southwestern species (e.g., *Neltuma glandulosa* Torr. (honey mesquite) (formerly of genus *Prosopis*), *Juniperus ashei* J. Buchholz (Ashe Juniper), *Pinus edulis* Engelm. (common pine), *J. pinchotii* Sudw. (Pinchot juniper), *J. osteosperma* (Torr.) Little (Utah juniper), *J. monosperma* (Engelm.) Sarg. (oneseed juniper), etc.) have contiguous (although not wide-ranging) distributions with good model performance, with predicted spread to the northwest. For the more southern species in the group (e.g., honey mesquite and Ashe Juniper), the future HQCL combinations spread north towards the upper Midwest as well as the eastern US. For *Quercus grisea* Liebm. (grey oak), which spans the US-Mexico border, future HQCL projections point to both expansions of habitat north into the US as well as to the south into Mexico—however, most of the northern habitats in the US are not colonisable by the end of century.

4.2 | Species Richness Changes

Modelling multiple species across their entire range enables assessment of potential continent-wide diversity changes, allowing insights not possible with individual species and/or countries. For example, while we see an end-of-century reduction in species richness across the middle and lower portions of the continent (especially in Minnesota, Wisconsin, Michigan, and Texas in the US—see Figure 3), we see an increase in richness in many other regions in the north and also in the southeastern regions, a pattern that is difficult to gauge from individual species models. The northern states of Minnesota, Wisconsin, and Michigan show large reductions in species richness because they represent a region of flux where many species lose suitable habitats under SSP5-8.5 (for e.g., white spruce, black spruce, quaking aspen, *Pinus resinosa Aiton* (red pine), *P. banksiana Lamb.* (jack pine), *Tsuga canadensis (L.) Carrière* (eastern hemlock), *Acer rubrum L.* (red maple), *A. saccharum Marshall* (sugar maple), *Betula*

papyrifera Marshall (paper birch), *Fraxinus nigra Marshall* (black ash), *Quercus rubra L.* (northern red oak), *Q. alba L.* (white oak), etc.)—but, losses are not compensated by southern species habitats moving into that region (Prasad, Pedlar, et al. 2024).

Changes in species richness among level-1 ecoregions of North America varied, although many showed net increases, particularly the *Northern Forests*, *Eastern Temperate Forests*, *Northwestern Forested Mountains*, *Hudson Plain* and the *Taiga* ecoregions (Figure 4). While our analyses provide a coarse continental picture of how species richness of dominant tree species may change in future climates, a more detailed analysis integrating traits or phylogenetic relationships would help identify areas where contemporary forest assemblages may be most threatened (Gougherty et al. 2024; Wieczynski et al. 2019).

4.3 | Species Ranges and Climatic Disequilibrium

Understanding differences in variable importance across predictor groupings in the eastern and western regions offers insights into the main drivers across all studied tree species. The fact that the HeatMoisture predictor groups are more prominent in the west (Figure S2) points to the greater role of heat- and moisture-related constraints, including drought (Allen et al. 2015) in that region (see Table 1 for explanation of the predictor groupings). While species are influenced by broader aspects of climate-topo interactions at wider ranges, for species with smaller ranges, this may not be true. Narrowly distributed species are strongly influenced by specialised niche requirements due to factors such as historically contingent eco-evolutionary dynamics, interspecific competition, and dispersal limitations, which could have impeded adaptation and migration (Morin and Lechowicz 2013). For these species, microclimate and local disturbance dynamics, including fire, may play a more prominent role in defining their niches. It has been documented that climatic disequilibrium is more common for tree species with small ranges due to the predominance of finer-scale biotic and abiotic drivers (Seliger et al. 2021). Our study supports this pattern as we found that climate did not strongly explain the distributions of smaller-ranged species, and this signal was evident among most of the major tree genera we assessed (Figure 5—only *birch* genus showed statistical non-significance at 0.05 level). Identifying the drivers of these species' ranges will be challenging, yet necessary, as small-ranged species may be at the greatest risk of extirpation from future climate or land-use change.

Phylogenetic niche conservation (Pyron et al. 2015)—the tendency for closely related species to have similar niches—could also shed light on variables driving species ranges. However, even though species came from 41 plant families (Table S2), with over a third in Pinaceae ($n = 65$) or Fagaceae ($n = 57$), model performance was not taxonomically biased. While we may have expected model performance of species-rich genera to cluster together, because range size and climatic tolerances may be phylogenetically conserved, performance consistently increased with range size across all genera assessed (Figure 5).

4.4 | Migration Considerations

It is expected that some tree species may not be able to adapt or naturally migrate sufficiently to keep pace with projected climate change (Aitken et al. 2008). In addition, climatic non-equilibrium, interspecific exclusions, and phenotypic plasticity can result in species occupying non-optimal niches and niches beyond their current distribution (Namkoong 2001; Thomson and Parker 2008; Pedlar and McKenney 2017; Rehfeldt et al. 2018; Sáenz-Romero et al. 2020). For example, many North American tree species have much wider climatic tolerance (Figure S4a,b) than the current distribution implies (McKenney et al. 2011; Booth 2017). While this could theoretically allow opportunistic migration under future climates, there are many constraints that limit this possibility, including barriers to migration, interspecific competition, and edaphic preferences. The combined HQ and CL (HQCL) maps we provide facilitate continental assessment of assisted migration opportunities by projecting future habitats that can be colonised naturally by the end of the century. For quaking aspen (Figure 2), areal coverage of colonised (shades of yellow, blue, and pink) and uncolonised (shades of grey) habitat is much smaller than that of currently occupied habitat (shades of green). Also, most of the colonisation tends to be "outfilling" (i.e., beyond the current range). This pattern can be observed for many wide-ranging species with somewhat dense and continuous distributions because there is less area for "infilling" migration (colonisation "within" the species distribution). Conversely, for species with spotty and scattered distributions, the area colonised by "infilling" migration can be quite large, wherein gaps within the current distribution are colonised. For example, *Pinus ponderosa* Lawson & C. Lawson (ponderosa pine) has an arc-shaped distribution, being abundant in both the Rockies and the Sierra Nevada—the internal gaps of the arc are filled by infilling migration while the northern regions beyond the current boundaries in Canada are filled by outfilling migration (see online archived database—Prasad, Peters, et al. 2024). For vulnerable species with potential for "infilling" migration, assisted migration efforts can focus on facilitating within-range migration (Stanturf et al. 2024). For example, for *Magnolia macrophylla* Michx. (bigleaf magnolia), a narrowly distributed species in the southern US which ranks high in overall vulnerability (see table 3 in Potter et al. 2017), there is significant potential for infilling migration (see online archived database—Prasad, Peters, et al. 2024).

Selecting genotypes which are climatically suitable for within-range movements (infilling migration) provides a low-risk type of assisted migration. Similarly, those with potential for more "outfilling" migration can potentially be assisted with range expansion efforts, although such movements are more controversial (Aubin et al. 2011; Ste-Marie et al. 2011; Pedlar et al. 2012, 2021). While such broad-scale assessments (infilling and outfilling) are facilitated by the HQCL maps, localised efforts will require more detailed information on site conditions, such as microclimate, seed-zones, soils, land-cover/land-use change, species-interactions, and disturbance (e.g., pests, fire risk).

4.5 | Inventory and Modelling Challenges

The macroscale nature of the analysis introduces some challenges owing to the diverse types of species and the

heterogeneous nature of inventories across the countries. While the focal averaging procedure resolved some of the artefacts due to differences in inventories among the countries, there were still some that could not be resolved. For example, the sparsity of FIA plots and Canadian and Mexican NFI survey limitations for some regions were harder to overcome. This is evident in eastern Montana and western North Dakota and in southern Quebec, which reveal large gaps in sampling for quaking aspen (Figure 1a). As expected, for many tree species (especially those with sparse and/or scattered distributions), the model performance was poor (Figure S1). This feature revealed which species were ill explained by climate-topo interactions and hence could be in climatic disequilibrium.

We employed climate-topographic interactions to model broad patterns of tree habitats under current and future climates because of the diversity of ecosystems, and heuristics based on expert knowledge and distributional statistics to reclassify outputs. We recognise that some precision may be sacrificed with this approach—however, we subscribe to the view that generality, realism, and precision cannot be optimised simultaneously given the stochastic nature of ecosystems and the pervasive human influence on these systems (Levins 1966, 1993; Mahnken et al. 2022). Our study deliberately did not include non-climatic variables, which have a higher degree of uncertainty at continental scales and are generally more relevant at regional and local scales (Williams et al. 2004). However, we recognise that historical macroscale trends were not simply confined to climate-topo interactions for all genera. Pines, especially, have co-evolved with fire (as avoiders, tolerators, and preferers) since the Cretaceous (145 mya) (Keeley 2012; Badik et al. 2018; Singh et al. 2018).

It should be noted that the migration rate of 50 km century^{-1} and a 500 km search window for rare long-distance migration were applied uniformly to all species (i.e., no difference in migration rates between animal and wind dispersed species) to avoid over-parameterising and fine-tuning the migration model for individual species. These numbers roughly represent observed historical trends—i.e., the migration of tree species since the Last Glacial Maximum (Davis 1981; Portnoy and Willson 1993; King et al. 1997—but see McLachlan et al. 2005; Napier et al. 2019, and as counter point, Tzedakis et al. 2013; Edwards et al. 2014; Fernandez et al. 2021). The use of a generalised migration rate may introduce inaccuracies for some species that are predominantly animal dispersed as well as some rare/sparse species. However, tweaking migration rates for individual species based on highly uncertain and difficult to obtain migration parameters can also lead to widespread inconsistencies among species especially because of the large number of species considered in this study. It is worth noting that more realistic migration simulations are possible when targeting species for which empirically determined migration rates are available (Mendes et al. 2024; Fricke et al. 2022).

5 | Conclusions

This effort provides, for the first time, continent-wide models of distribution and abundance for 326 tree species based on national forest inventory data from the United States, Mexico, and Canada, and will be featured in the upcoming update to the Silvics of North America series. These products, made possible by the collaborative sharing of national data in combination with local information, can facilitate management for maintaining healthy and productive forests across North America.

Author Contributions

Anantha Prasad conceived and designed the research, did data analysis and interpretation, and wrote the manuscript. Matt Peters was responsible for figures and providing crucial support. John Pedlar was responsible for providing major support related to Canadian inventory and editorial refinements. Andy Gougherty was responsible for providing additional support and interpretation of phylogenetic aspects of the analysis. Franz Mora provided relative abundance data derived from the Mexican forest inventory. Dan McKenney, Steve Matthews, Steve McNulty and Lauro López-Mata provided additional support to complete the manuscript. All authors contributed to and reviewed the drafts and gave final approval for publication.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in USDA Forest Service Research Data Archive at https://doi.org/10.2737/RDS-2024-0020, reference number RDS-2024-0020.

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Supporting Information

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