



Combining US and Canadian forest inventories to assess habitat suitability and migration potential of 25 tree species under climate change

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Abstract

Aim: To evaluate current and future dynamics of 25 tree species spanning United States and Canada.

Location: United States and Canada.

Methods: We combine, for the first time, the species compositions from relative importance derived from the USA's Forest Inventory Analysis (FIA) with gridded estimates based on Canada's National Forest Inventory (NFI-kNN)-based photo plot data to evaluate future habitats and colonization potentials for 25 tree species. Using 21 climatic variables under RCP 4.5 and RCP 8.5, we model climatic habitat suitability (HQ) within a consensus-based multimodel ensemble regression approach. A migration model is used to assess colonization likelihoods (CL) for ~100 years and combined with HQ to evaluate the various combinations of HQ + CL outcomes for the 25 species.

Results: At a continental scale, many species in the conterminous United States lose suitable climatic habitat (especially under RCP 8.5) while Canada and USA's Alaska gain climate habitat. For most species, even under optimistic migration rates, only a small portion of overall future suitable habitat is projected to be naturally colonized in ~100 years, although considerable variation exists among species.

Main conclusions: For the species examined here, habitat losses were primarily experienced along southern range limits, while habitat gains were associated with northern range limits (especially under RCP 8.5). However, for many species, southern range limits are projected to remain relatively intact, albeit with reduced habitat quality. Our models predict that only a small portion of the climatic habitat generated by climate change will be colonized naturally by the end of the current century—even with optimistic tree migration rates. However, considerable variation among species points to the need for significant management efforts, including assisted migration, for economic or ecological reasons. Our work highlights the need to

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employ range-wide data, evaluate colonization potentials and enhance cross-border collaborations.

KEYWORDS

colonization likelihood, Forest Inventory Analysis, habitat suitability, long-distance migration, multimodel ensemble, National Forest Inventory, random forest, range-wide analysis, stochastic gradient boosting

1 | INTRODUCTION

Climate change has already impacted many natural systems (Scheffers et al., 2016) and is projected to have increasingly serious impacts as the century progresses. Forest ecosystems are of particular concern due to the high levels of biodiversity that they maintain (Aerts & Honnay, 2011) and the slow migration rates of trees (Corlett & Westcott, 2013; Feurdean et al., 2013). Consequently, understanding the response of forests to climate change has been an ongoing focus of scientific research for several decades (see Iverson & Prasad, 1998; Keenan, 2015). A key aspect of this response is the extent to which long-distance tree migration can track the climatic shifts projected for the coming decades (Aitken, Yeaman, Holliday, Wang, & Curtis-McLane, 2008; Iverson, Schwartz, & Prasad, 2004; Prasad, Gardiner, Iverson, Matthews, & Peters, 2013).

Modelling tree migration under climate change is most effective at broad spatial extents which incorporate entire species ranges. One reason for this is that the climate is not changing evenly across the planet. For example, the boreal forest in North America has already experienced more than a 1.5°C increase in mean annual temperature since 1900 (Price et al., 2013), compared to an increase of 0.7°C across the conterminous United States (USGCRP, 2017). These changes, in combination with projections for modest, regionalized changes in precipitation (Gauthier, Bernier, Kuuluvainen, Shvidenko, & Schepaschenko, 2015) indicate that many species could experience different climatic drivers across their range (Bouchard, Aquilué, Périé, & Lambert, 2019; Housset, Girardin, Baconnet, Carcaillet, & Bergeron, 2015; Matthews, Sadler, Kubota, Woodall, & Pugh, 2019). Furthermore, there is a general expectation that populations within a species range will respond differentially to climate change, with trailing populations expected to decline and poleward populations expected to expand (Hampe & Petit, 2005; Pedlar & McKenney, 2017). Indeed, many studies have shown measurable changes in vegetation at the boreal-tundra boundary (Becker-Scarpitta, Vissault, & Vellend, 2019; Chaste, Girardin, Kaplan, Bergeron, & Hély, 2019; Holsinger et al., 2019; Myers-Smith et al., 2019; Sittaro, Paquette, Messier, & Nock, 2017; Truchon-Savard, Jean, & Payette, 2019; Wang et al., 2019; Zhang, Huang, Huang, & He, 2015; Zhang, Liu, et al., 2015).

Efforts to model range shifts of tree species under climate change have evolved through time (Iverson, Peters, Prasad, & Matthews, 2019; Iverson & Prasad, 1998; Iverson, Prasad, Matthews, & Peters, 2008). Early studies tended to focus solely

on climate envelope shifts, identifying suitable climate habitat under current and future conditions (McKenney, Pedlar, Lawrence, Campbell, & Hutchinson, 2007a, 2007b; McKenney, Pedlar, Rood, & Price, 2011; Shafer, Bartlein, & Thompson, 2001; Sykes, Prentice, & Cramer, 1996). Other studies have attempted to generate better predictions by incorporating key drivers of tree suitability, including edaphic variables (Chambers, Périé, Casajus, & de Blois, 2013; Iverson & Prasad, 1998; Iverson et al., 2008; Peters, Iverson, Prasad, & Matthews, 2019), migration constraints (Iverson, Prasad, Peters, & Matthews, 2019; Prasad et al., 2013) and competitive interactions (Araujo & Luoto, 2007). Regardless of the exact approach taken, most efforts incorporate habitat models that relate species abundance or occurrence to a suite of environmental variables. While many studies have employed occurrence data for this step (e.g. Bell & Schlaepfer, 2016; Case & Lawler, 2017), the use of abundance data allows for a more detailed and useful assessment of habitat suitability (Howard, Stephens, Pearce-Higgins, Gregory, & Willis, 2014; Iverson, Peters, et al., 2019; Iverson et al., 2008). However, in North America, seamless coverage of tree abundance data has been challenging to obtain due to national-level differences in data collection methodology and availability in the United States and Canada (see Beaudoin et al., 2014; Forest Inventory Analysis, 2017). Consequently, attempts to model tree migration using abundance-based habitat models have typically been regional in scope (Chambers et al., 2013; Coops & Waring, 2011; Gray & Hamann, 2013), with minimal attempts at cross-border analyses using abundance data owing to several challenges related to the merging of different datasets.

In order to overcome this limitation, we have combined United States' Forest Inventory Analysis (FIA) data (Forest Inventory Analysis, 2017) with spatial datasets derived from Canada's National Forest Inventory (NFI) data (Beaudoin et al., 2014; Beaudoin, Bernier, Villemaire, Guindon, & Guo, 2017) to produce a spatial database of relative abundance for 25 ecologically and commercially important tree species that span the two countries (Table 1). We use this database to model climatic habitat quality (HQ, also referred to as habitat suitability or climatic habitat suitability) under current, and future climate (RCP 4.5 and 8.5 emission scenarios—Moss et al., 2008) using a multimodel ensemble approach (Prasad, 2018). We further employ a migration simulation model (Prasad et al., 2013) to compute colonization likelihoods (CL, also referred to as migration potential) associated with future suitable habitats. Finally, we combine HQ and CL to visualize and assess potential tree shifts under climate change. Specifically, our goals are to a) examine the potential spatial

TABLE 1 Combined R-square values from the random forest and gradient boosting models for the 25 tree species in this study

| Common Name | Scientific Name | Combined R-square |
|----------------------|------------------------------|-------------------|
| American elm | <i>Ulmus americana</i> | 0.27 |
| Balsam fir | <i>Abies balsamea</i> | 0.83 |
| Balsam poplar | <i>Populus balsamifera</i> | 0.42 |
| Bigtooth aspen | <i>Populus grandidentata</i> | 0.36 |
| Bitternut hickory | <i>Carya cordiformis</i> | 0.18 |
| Black cherry | <i>Prunus serotina</i> | 0.44 |
| Black spruce | <i>Picea mariana</i> | 0.88 |
| Black walnut | <i>Juglans nigra</i> | 0.22 |
| Bur oak | <i>Quercus macrocarpa</i> | 0.21 |
| Eastern hemlock | <i>Tsuga canadensis</i> | 0.56 |
| Eastern hophornbeam | <i>Ostrya virginiana</i> | 0.23 |
| Eastern white pine | <i>Pinus strobus</i> | 0.4 |
| Jack pine | <i>Pinus banksiana</i> | 0.73 |
| Northern red oak | <i>Quercus rubra</i> | 0.48 |
| Northern white cedar | <i>Thuja occidentalis</i> | 0.56 |
| Paper birch | <i>Betula papyrifera</i> | 0.78 |
| Quaking aspen | <i>Populus tremuloides</i> | 0.82 |
| Red maple | <i>Acer rubrum</i> | 0.62 |
| Red spruce | <i>Picea rubens</i> | 0.6 |
| Silver maple | <i>Acer saccharinum</i> | 0.11 |
| Sugar maple | <i>Acer saccharum</i> | 0.56 |
| Tamarack | <i>Larix laricina</i> | 0.52 |
| White ash | <i>Fraxinus americana</i> | 0.38 |
| White oak | <i>Quercus alba</i> | 0.53 |
| Yellow birch | <i>Betula alleghaniensis</i> | 0.55 |

distribution of future suitable habitats across the entire range of each species, b) assess the likelihood that newly gained suitable habitats will be colonized in the future, c) evaluate habitats colonized, gained, lost and retained across the two countries and d) provide a template to evaluate current and future management options for important tree species. We use a multistage modelling approach (Prasad, Iverson, Matthews, & Peters, 2016) to minimize the bias and confoundment of the model by modelling HQ as a purely climate response (Matthews et al., 2019; Price, Cooke, Metsaranta, & Kurz, 2015) and allowing for other dependencies, such as land cover and elevation, to be evaluated as optional post-model filters, where appropriate.

2 | METHODS

Our overall methodology and the data used to model habitat suitability and colonization potentials are illustrated in Figure 1.

2.1 | Combining FIA and NFI-kNN

We use FIA data in the eastern United States to derive relative importance values (RIV, also known as relative abundance) of tree species (Iverson et al., 2008; Peters et al., 2019). This index is calculated as the sum of the (1) abundance (i.e. number of stems) and (2) dominance (i.e. basal area) of each species relative to all trees within the plot (~83K plots in the eastern United States—for details on the FIA plot design please refer to the FIADB user guide available online, and O'Connell et al., 2017). Because the FIA plot locations are unequally sampled across the United States, we aggregated relative importance values over grid cells (20 x 20 km)

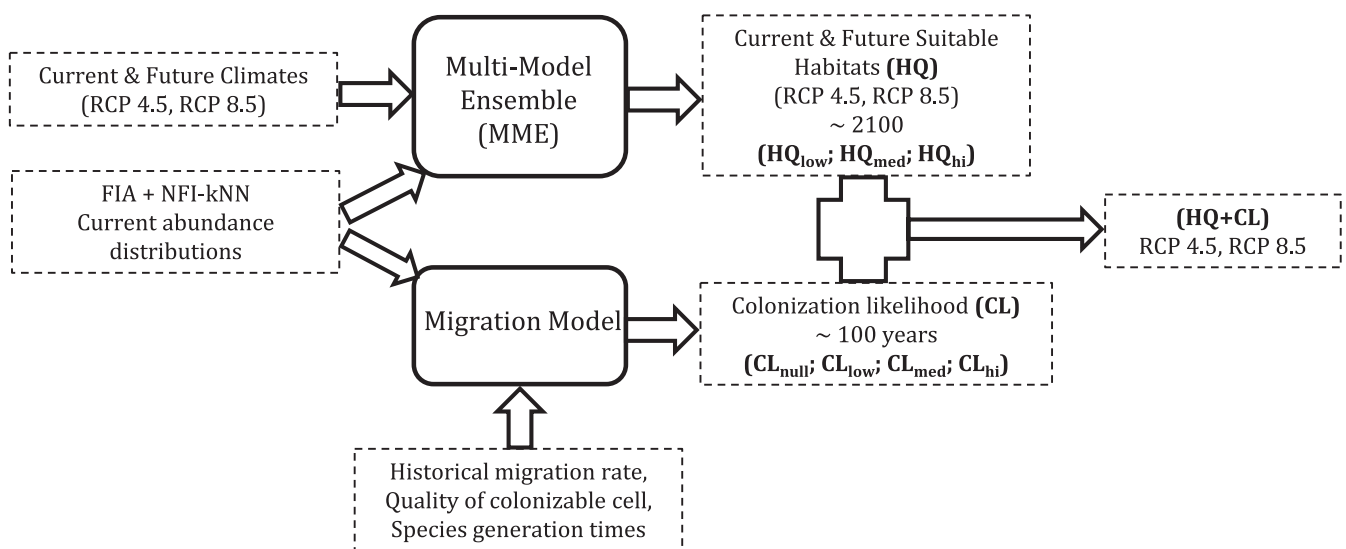


FIGURE 1 Schematic of modelling approach that combines suitable habitats (HQ) predicted by the multimodel ensemble with colonization likelihoods (CL) computed by the migration model into 12 classes of HQCL

that contained at least 2 FIA plots in order to minimize the influence of singletons that can unduly influence the values. The FIA plots in Alaska were not used as they are currently confined to the coastal forests.

Canada's National Forest Inventory (NFI), while different in design from the FIA, includes a field survey component (with 1,116 permanent ground plots) and a remote sensing survey component (Gillis, Boudewyn, Power, & Russo, 2010). The remote sensing component consists of 2 x 2 km sample units located on a systematic national sampling grid of 20 km, with a total of 13,158 sample units in the first current 10-year (2008–2017) re-measurement survey. Recently, Beaudoin et al. (2014), Beaudoin et al. (2017) have produced gridded estimates of forest attributes from the NFI, using a *k*-nearest neighbour (kNN) approach to impute cell values from a combination of NFI photo plot data (Gillis, Omule, & Brierley, 2005), and 26 geospatial data layers including MODIS spectral imagery, climate and topographic variables. One of the products derived from this project was a set of species composition maps that gave estimates of species' relative abundance.

We merged grids of relative abundance from the two data sources (FIA and NFI-kNN) to obtain continuous tree abundance estimates for each tree species. Both indices were scaled from 0 to 100 to indicate the relative per cent composition of each species. One consequence of this merger was that the coarser estimates from the kNN-based approach tended to produce smoother patterns of species relative abundance patterns, likely influenced by the secondary processing. Although admittedly not seamless, the merger provided continuous estimates of relative abundance up to the northern edge of each species range, which was vital for our regression-based ensemble modelling approach. We aggregated the abundance data for the 25 species to a 20 x 20 km resolution that smoothed differences in relative abundance methodologies across the USA–Canada border and allowed a computationally feasible framework for looking at macroscale patterns across the entire range.

Of the 25 species, there were only two (quaking aspen and paper birch) whose ranges extended significantly into the western United States and thus were not fully represented by our abundance data, which was comprised of FIA plots east of the 100th meridian. Additionally, there were some data gaps in the NFI-kNN data for quaking aspen in Ontario, Canada.

2.2 | Climate data

Predictors for the HQ model (described below) were climate normals from the AdaptWest database (AdaptWest Project, 2015; Wang, Hamann, Spittlehouse, & Murdock, 2012) for current (1981–2010) and future (2071–2100) periods. We obtained data for future climate scenarios (Moss et al., 2008), RCP 4.5 (medium emission pathway) and RCP 8.5 (high emission pathway), in order to examine the degree to which habitat projections differed under these alternative pathways (Wang, Hamann, Spittlehouse, & Carroll, 2016). Future climate projections were based on an ensemble of 15 general circulation models (AdaptWest

Project, 2015). The original data, at 1 km resolution, was aggregated to 20 km to match the abundance variables for the HQ model.

2.3 | Multimodel ensemble (MME)

Habitat quality (HQ) for current and future climate scenarios was predicted using a multimodel ensemble (MME) technique (Prasad, 2018) at a cell resolution of 20 x 20 km. The HQ model was developed using current climate values at tree abundance cells and then projected into the future under the RCP 4.5 and 8.5 emissions scenarios. We screened 27 bioclimatic climate variables available in the AdaptWest database using random forest and stochastic gradient boosting (see MME below) to find the best fit for all the 25 species. We selected a subset of 21 climate variables (Table 2) for the final HQ model by examining the variable importance for all 25 tree species that contributed substantially to the overall fit. Highly collinear variables were not selected—but this criterion was relaxed if the variable resulted in a superior fit.

The MME technique involves averaging the consensus predictions of four machine learning techniques: two versions of random forest (RF) and two versions of generalized gradient boosting methods. We used the *ranger* module in R (R Core Team, 2019) with regular and random number of splits for the two versions of RF, and the *gbm* and *Xgboost* modules for the two versions of boosting. The RF approach is a well-known solution to the overfitting problem of individual decision trees by building a forest of decision trees from bootstrapped data and further de-correlating it by randomly choosing a subset of predictors to reduce variance. RF has been used extensively to make reliable predictions with low bias and variance for multidimensional data that are nonlinear and exhibit interactions (Cutler et al., 2007; Prasad, Iverson, & Liaw, 2006). The version of RF with random number of splits, known as extremely randomized forest (ERF), takes this one step further by creating *p* random predictor splits in each node (in contrast with RF, which chooses the 'best' split), independent of the response variable and then the split with the best gain (mean-squared error for regression) is chosen. The rationale is that by randomizing the split the variance is further reduced, but with a slight increase in model bias. To compensate, ERF typically uses the entire learning sample instead of a bootstrapped one to keep the bias low (Geurts, Ernst, & Wehenkel, 2006).

Boosting is a method of iteratively converting weak learners (regressors that are weakly correlated with the true model) to strong ones using decision trees as the base learner by reweighting observations that have higher errors. Stochastic gradient boosting (*gbm* module in R) reduces variance by shrinkage (regularization) and stochasticity in which each newer iteration of the model learns from the previous one by minimizing residuals based on the shrinkage parameter (Friedman, 2002). *Xgboost* is a slightly different approach to boosting which implements an enhanced regularization technique to limit overfitting (Chen & Guestrin, 2016).

The MME approach is best used where prediction uncertainty needs to be stabilized to yield more robust predictions that reflects

| Climate Abb. | Climate variable |
|--------------|---|
| mat | Mean annual temperature (°C) |
| mwmt | Mean temperature of the warmest month (°C) |
| mcmt | Mean temperature of the coldest month (°C) |
| td | Difference between MCMT and MWMT, as a measure of continentality (°C) |
| map | Mean annual precipitation (mm) |
| mshp | Mean summer (May to Sep) precipitation (mm) |
| ahm | Annual heat moisture index, calculated as (MAT + 10)/(MAP/1000) |
| shm | Summer heat moisture index, calculated as MWMT/(MSP/1000) |
| dd0 | Degree-days below 0°C (chilling degree-days) |
| dd5 | Degree-days above 5°C (growing degree-days) |
| nffd | The number of frost-free days |
| bffp | The Julian date on which the frost-free period begins |
| pas | Precipitation as snow (mm) |
| emt | Extreme minimum temperature over 30 years |
| ext | Extreme maximum temperature over 30 years |
| eref | Hargreaves's reference evaporation ^a |
| cmd | Hargreaves's climatic moisture deficit ^a |
| mar | Mean annual solar radiation (MJ/m ² d ⁻¹) (excludes areas south of US) |
| rh | Mean annual relative humidity (%) |
| tave_sm | Summer (Jun to Aug) mean temperature (°C) |
| ppt_wt | Winter (Dec to Feb) precipitation (mm) |

^aFor more information, see: Wang, T., Hamann, A., Spittlehouse, D. L., & Murdock, T. Q. (2012). ClimateWNA-High-Resolution Spatial Climate Data for Western North America. *Journal of Applied Meteorology and Climatology*, 51(1), 16–29. Hargreaves G., Allen R. (2003). History and Evaluation of Hargreaves Evapotranspiration Equation. *Journal of Irrigation and Drainage Engineering*, 129(1), 53–63.

the consensus (Jones & Cheung, 2015; Martre et al., 2015) by averaging individual model errors (Zhang, Huang, et al., 2015; Zhang, Liu, et al., 2015). It further minimizes bias and variance (Hastie, Tibshirani, & Friedman, 2009) as well as prediction error while extrapolating current prediction to future climates. Only predictions where there was 'consensus' among all models (i.e. where all models predicted nonzero values) were averaged to ensure that the main trends were captured. For the multimodel approach to work well, the models should be based on a similar framework (in our case, decision trees) but should adopt structurally different approaches (the different approaches to random forest and boosting) so that the final ensemble averages these heterogeneous approaches (Tebaldi & Knutti, 2007). The MME also helps mitigate the effects of spurious model artefacts at the low end of the abundance spectrum. Here, the 'consensus' approach averages prediction signals that are present in all four individual models of the ensemble, thus highlighting the dominant patterns of prediction in the ensemble (Prasad, 2018).

2.4 | MME validation

The four models used in the ensemble have built-in validation methods that ensure that the models do not overfit and provide estimates

TABLE 2 The 21 climate variables used as predictors in the HQ (MME) model

of their predictive accuracy. For example, in Random Forest, the training is performed using a bootstrap sample (with replacement), which included 2/3 of the data. At each iteration of the bootstrap sample, the remaining data (called out-of-bag, OOB) are used to measure the predictive accuracy of regression trees grown from the bootstrap sample; these errors are aggregated to obtain the OOB error rate (Svetnik et al., 2003). With large datasets like ours, where the number of observations far exceeds the number of predictors, and with large numbers of decision trees (1,000 in our case), the OOB error rate matches very closely with the cross-validation error rate from separate training and test datasets (Hastie et al., 2009). For boosting, cross-validation was performed (we used 10-fold) to calculate an estimate of the generalization error using 1,000 trees. There was close correspondence between the error rates of Random Forest and stochastic gradient boosting, and we therefore calculated the average R-square to estimate overall model performance (Table 1).

To ensure that we chose the optimal parameters for the random forest and boosting variants in our ensemble, we used a package called *caret* in R which streamlines the model training process for complex regression and classification problems by doing a stratified random split of the data into training and test sets. These two sets are used to evaluate the effect of tuning parameters on model

performance and choose the optimal model across these parameters (Kuhn, 2008).

Finally, our approach to average only the consensus of the four models in the ensemble ensured we chose the most dominant trend across these models, further boosting our confidence in the final result.

2.5 | Estimation of colonization potentials

Colonization likelihoods (CL) were computed for each species using a long-distance migration model that incorporates current abundance, historical migration rates and current habitat fragmentation (Schwartz, 1993). Simulation of long-distance migration was implemented via a fat-tailed inverse power function at a cell resolution of 1 km. The likelihood of an unoccupied cell becoming colonized by a particular species during each generation is a function of that species' abundance in the surrounding cells, the habitat quality of the unoccupied cell (must have at least 10% per cent forest cover, to ensure that it is a habitable cell) and a search window distance function. The colonization likelihood for each unoccupied cell is calculated by summing over all occupied cells at each generation. The stochastic nature of the tail of the long-distance migration is simulated by drawing a random number from an even distribution and comparing it with the calculated likelihood to determine if the cell gets colonized. Simulation using multiple historical migration rates and application to multiple species was made feasible by using convolution and Fast Fourier Transforms to keep the computation time to a minimum (Prasad et al., 2013). For this study, we use an optimistic, but historically defensible migration rate of 50km/century for all species and a generous search window of 500 km (to accommodate stochastic long-distance dispersals) as the limit for migration within each generation. These estimates are generally at the higher end of reported tree migration rates (Davis, 2001; McLachlan & Clark, 2004; McLachlan, Clark, & Manos, 2005; *but see* Snell & Cowling, 2015; Ordonez & Williams, 2013). We deliberately chose not to parameterize individual species migration rates owing to large uncertainties in life histories and dispersal syndromes among the 25 tree species (Iverson et al., 2004).

A recent improvement to this model (cf. Prasad et al., 2013) involved relaxing the requirement for a rigid source–sink boundary along the migration front by allowing it to opportunistically colonize suitable cells throughout the current range of the species. This produces a more realistic migration scenario where colonization can happen within the gaps in the current distribution (infilling or interpolating) as well as at range boundaries (migrating/outfilling). Each species is allowed to migrate based on its current distribution and generation time with no climatic constraints, for approximately 100 years. This ensures that in spite of having a common migration rate, the landscape is colonized based on individualistic species responses. The number of generations (model iterations) required to simulate ~100 years of migration varies

among species depending on their generation time (which varies between 14 and 33 years for the species in this study). For example, for purposes of our models, sugar maple requires ~33 years/generation—that is time to maturity (=3 generations in 100 years), and newly colonized cells can only contribute to colonization in the next generation since the propagules have to mature. For more details on the migration model, see Prasad et al., 2013 and Schwartz, Iverson, & Prasad, 2001. The migration model was implemented in the Julia scientific programming language, to take advantage of its computing capabilities and speed (Bezanson, Edelman, Karpinski, & Shah, 2017).

2.6 | Combining suitable habitats and colonization likelihoods

The habitat quality (HQ) based on relative abundance is estimated by the MME model for the RCP 4.5 and RCP 8.5 scenarios. Outputs are scaled 0 to 100, where 0 represents absence and 100 represents the maximum where the cell contains monotypic stands of that species. These outputs were reclassified into three classes: low (1–5), medium (6–15) and high (16–100). The current distribution of relative abundance based on FIA and NFI (scaled 0–100) was also classified into three classes—low, medium and high—based on the HQ categories described above.

Similarly, the colonization likelihoods (CL) estimated by the migration model (scaled 0 to 100 where 0 represents no colonization and 100 the maximum colonization likelihood) for ~100 years were also reclassified into uncolonized (0), low (1–10), medium (11–50) and high (51–100). These two reclassified rasters were combined to yield 12 combination classes—HQlow/CLnull, HQlow/CLlow, HQlow/CLmed, HQlow/CLhi; HQmed/CLnull, HQmed/CLlow, HQmed/CLmed, HQmed/CLhi; HQhi/CLnull, HQhi/CLlow, HQhi/CLmed, HQhi/CLhi. Note that CLnull refers to the uncolonized class.

The reclassification schemes were based on heuristics after examining the HQ and CL distribution patterns of all 25 tree species. The colour scheme (Figure 1) to depict the combination of HQ and CL classes was chosen to highlight the interplay of HQ and CL as well as the absence of CL (CLnull) in areas where HQ is present. Areas of future predicted HQ, where CL is absent (i.e. where the species cannot migrate, CLnull), are depicted in shades of grey increasing in darkness from HQlow/CLnull, HQmed/CLnull, HQhi/CLnull in that order. If the species is currently present (according to FIA or NFI-kNN estimates), it is depicted as black to distinguish it from future scenarios. The areas where HQ is low (HQlow) and CL increases from low to high (HQlow/CLlow, HQlow/CLmed, HQlow/CLhi) are in progressively darker shades of yellow; areas where HQ is medium (HQmed) and CL increases from low to high (HQmed/CLlow, HQmed/CLmed, HQmed/CLhi) are in progressively darker shades of blue; and where HQ is high (HQhi) and CL increases from low to high (HQhi/CLlow, HQhi/CLmed, HQhi/CLhi) are in progressively darker shades of green. This colour scheme helps distinguish those areas that are modelled to be colonized (coloured) from those that

are suitable, but not colonized (shades of grey), and those that are currently occupied (black).

2.7 | Temporal matching of HQ and CL

As can be expected, combining suitable habitats and colonization likelihoods through time poses a problem because of the approximate temporal periods of the various data and model outputs. The current distribution of the species was based on data that spanned from approximately 2008–2017 from the FIA and NFI-kNN data. The species were allowed to migrate for ~100 years and CL was calculated relative to this current distribution. Because future climatic habitats (HQ) for RCP 4.5 and 8.5 were based on the 2071–2100 equilibrium scenarios, and the current climate spanned 1981–2010, future temporal matching of HQ and CL is approximate. We have therefore assumed that allowing the species to migrate ~100 years with a slight temporal overshoot is justified for combining HQ and CL rather than a premature termination of colonization (Figure 1). Further, we found that this approximation does not alter the outcome of this work to any appreciable degree.

3 | RESULTS

The results demonstrate the importance of migration constraints, where only portions of future suitable habitats (HQ) are predicted to be colonized by 2,100. We modelled, mapped and calculated various statistics for the combinations of HQ and CL for 25 tree species (Table 1) that span the USA–Canada border and used sugar maple (*Acer saccharum*) as an example to illustrate the dynamics of colonization of suitable habitats under future scenarios. Additionally, we illustrate the potential HQ lost, gained and retained and report the per cent colonization of the newly suitable habitats. We also assess the overall trends of HQ and CL for the 25 species. The maps for all 25 species are available in the Data Availability section.

3.1 | HQ Model performance

The combined R-square for the HQ models, based on an average of the random forest and stochastic gradient boosting models, shows that model reliability varied widely among the 25 species (Table 1), averaging 0.49, with a median of 0.52, minimum of 0.11 and maximum of 0.88. Six species had R-square values below 0.3, including silver maple (*Acer saccharinum*; 0.11), bitternut hickory (*Carya cordiformis*; 0.18), bur oak (*Quercus macrocarpa*; 0.21), black walnut (*Juglans nigra*; 0.22), eastern hophornbeam (*Ostrya virginiana*; 0.23) and American elm (*Ulmus americana*; 0.27). Outputs for these species should be used with this caveat in mind. Additionally, these metrics indicate the strength of climatic controls on each species' distribution. The six species with low R-square values, for example,

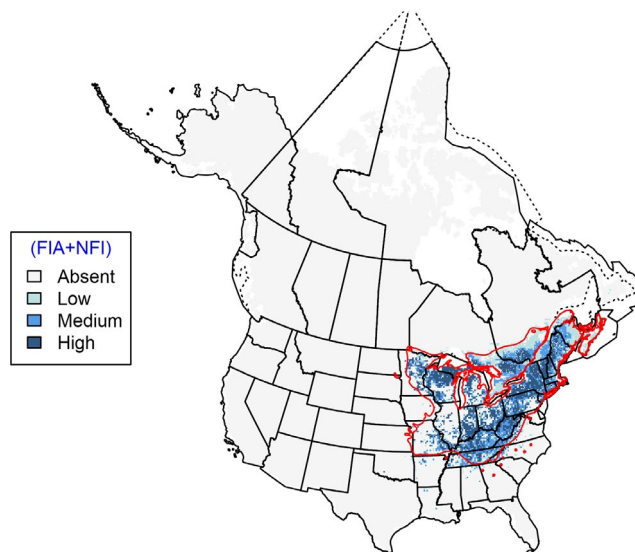


FIGURE 2 Relative abundance (RIV) and current distribution of *Acer saccharum* (sugar maple) based on USA's FIA and Canada's NFI-kNN spatial datasets. The low, medium and high classes are reclassifications of RIV. See Methods section for details on the merger of these two spatial datasets. The red line is the Little's range boundary

exhibit patchy distributions that appear to be weakly correlated with regional climatic patterns.

3.2 | Habitats lost, gained and retained

Sugar maple (*Acer saccharum*) is currently distributed primarily in the eastern United States (Figure 2), but also extends into southern Ontario and Quebec as well as the coastal regions of eastern Canada. Little's range extent (Little, 1971, used extensively for tree species ranges in North America; red line in Figure 2) for this species agrees closely with the current distribution based on the FIA and NFI-kNN abundance estimates. Tracking habitat lost, gained and retained (Figure 3a,b) is useful for gauging how the HQ model is predicting the dynamics of changes in abundance (HQ) under future climates, without considering migration. The amount of habitat lost (shades of red in Figure 3) is much less than that gained (shades of green) or retained (shades of blue), because sugar maple extends its habitat northward under warming climates. The area of habitat lost is greater for RCP 8.5 compared to RCP 4.5, especially in the southern range of the species. The amount of habitat gained in Canada is much greater than the United States, although much of the habitat gained is in the low and medium HQ classes. The majority of new habitat in the United States is found in Alaska, especially under RCP 8.5; though there is little chance that the species would migrate there naturally within the next century as determined by the HQCL analysis in the next section. It should be noted that the habitats retained (shades of blue, Figure 3) show how portions of the area currently occupied are projected to fare based on future predictions by the HQ model. The maps of habitat lost, gained and retained for all 25 species are provided in the Data Availability section.

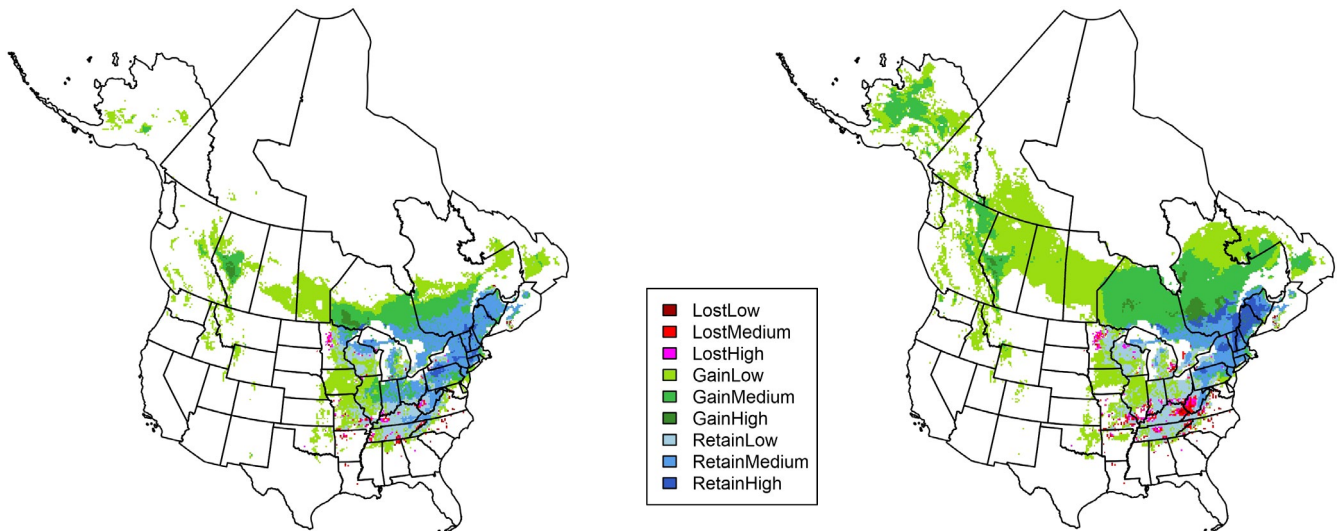


FIGURE 3 *Acer saccharum* (sugar maple) habitats lost, gained and retained by the end of the century under the RCP 4.5 (a, left) and RCP 8.5 (b, right) emissions scenarios. Shades of red (habitat lost), green (habitat gained) and blue (habitat retained) depict three classes of habitat quality (HQ)—low, medium and high—which are reclassifications of raw HQ values. Note that retained habitat cells present predicted, not current, HQ values

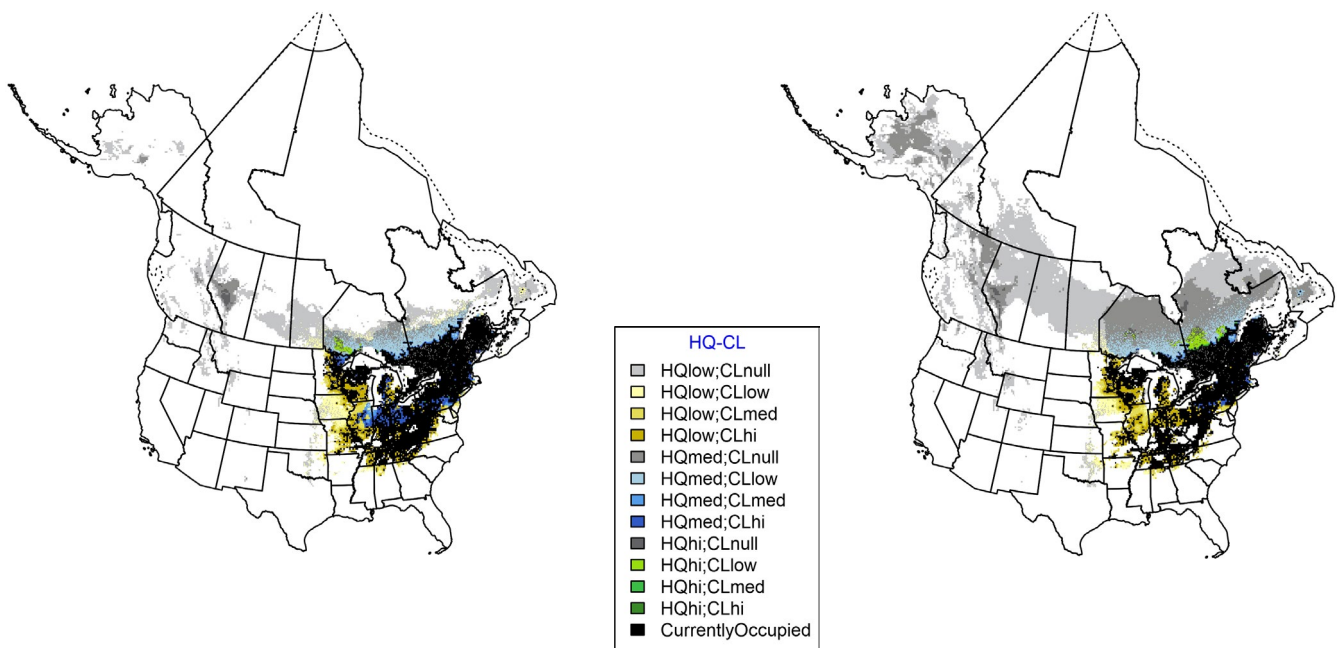


FIGURE 4 *Acer saccharum* (sugar maple) future suitable habitats (HQ) combined with colonization likelihoods (CL) under the RCP 4.5 (a, left) and RCP 8.5 (b, right) emissions scenarios. Currently occupied regions are shown in black. Shades of yellow (HQlow; CLlow; HQlow; CLmed; HQlow; CLhi), blue (HQmed; CLlow; HQmed; CLmed; HQmed; CLhi) and green (HQhi; CLlow; HQhi; CLmed; HQhi; CLhi) depict the three classes of HQ (low, med and hi) and CL (low, med, hi), which are reclassifications of raw HQ and CL values. See section Combining suitable habitats and colonization likelihoods for a description of how the classes were combined

3.3 | Quantifying Habitat Quality and Colonization Likelihood

The combination of HQ & CL (Figure 4a,b) allows for the evaluation of future suitable habitats, both where there is virtually no chance of natural colonization (HQCL combinations with CL_{null}—shades of grey), and where colonization is more likely (coloured HQCL

combinations—shades of yellow, blue and green). The black areas show the current distribution (FIA + NFI-kNN) of sugar maple to contrast it from those that show HQ and CL combinations under future climates. Under future climate, substantial amounts of uncolonized suitable habitat appear to the north and northwest of the current sugar maple distribution (Figure 4, shades of grey). This is particularly true for the warmer RCP 8.5, which projects suitable habitat

as far north and west as Alaska. Of the HQ that shows colonization, areas of 'infilling' migration are apparent in the mid-western United States (Figure 4, shades of yellow denoting lower HQ), where apparent gaps in the current distribution become colonized, in addition to some westward migration. Central Ontario and Quebec in Canada show higher combinations of HQ and CL (Figure 4, shades of blue and green) denoting 'outfilling' migration at the edge of the species range. Maps of HQCL combinations for all 25 species are provided in the Data Availability section.

3.4 | Habitat dynamics, all 25 species

In addition to the species-specific maps and graphs, assessing all 25 species together provides insights into general patterns in habitat and colonization dynamics. This analysis also allows comparison of the HQ gained and lost for the two climate scenarios (RCP 4.5 and RCP 8.5) separately for the United States and Canada (Figure 5, 6, 7 & 8), as well as the per cent colonized in all the newly gained habitats (Figure 9).

For the United States, the trends in suitable habitats gained (Figure 5a,b) do not change dramatically between the two climate scenarios, except for generally more widespread habitat gains under the RCP 8.5 scenario for many species. For Canada (Figure 6a,b), there are much larger increases in habitat gained under the RCP 8.5 scenario compared to the RCP 4.5 scenario. This is consistent with the greater warming, and consequently larger northward shifts, associated with RCP 8.5 scenario. However, the degree to which species exhibited differential responses to the two emissions scenarios appear tied to current range location, with boreal species (e.g. black

spruce) that are already close to the northern boundaries of the continent showing less change between scenarios, while more southerly positioned species (e.g. sugar maple) exhibiting much greater gains under RCP 8.5. Additionally, it is primarily the low and medium HQ classes that increase in both countries (blue and orange), much less of the high HQ (grey) changes except for a few species. For example, bur oak (*Quercus macrocarpa*) gains nearly a million square km of high HQ habitat under RCP 8.5 in Canada. For species that show large gains in suitable habitat, a major portion of the gain for the United States is due to the expansion of habitats into Alaska.

Generally, there is a greater amount of habitat lost in the conterminous United States (under RCP 8.5 as compared to RCP 4.5 - Figure 7a,b). As noted above, our study did not include FIA plots in Alaska (due to limited spatial coverage)—so, current habitats are absent, but future habitats are present due to HQ model predictions. The quality of habitat lost varies across species; however, balsam fir (*Abies balsamea*; under RCP 8.5), tamarack (*Larix laricina*), black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), eastern white pine (*Pinus strobus*), northern white cedar (*Thuja occidentalis*), eastern hemlock (*Tsuga canadensis*), quaking aspen (*Populus tremuloides*) and white oak (*Quercus alba*) all lost considerably more high-quality habitat than either of the other HQ classes. The amount of habitat lost was generally lower in Canada (Figure 8a,b) because most species expand their habitats northward under climate warming. However, significant habitat losses were projected for primarily northern species such as black spruce (*Picea mariana*; especially under RCP 8.5, for which a sizeable amount of high-quality habitat is lost), jack pine (*Pinus banksiana*; especially under RCP 4.5 for which a sizeable amount of low-quality habitat

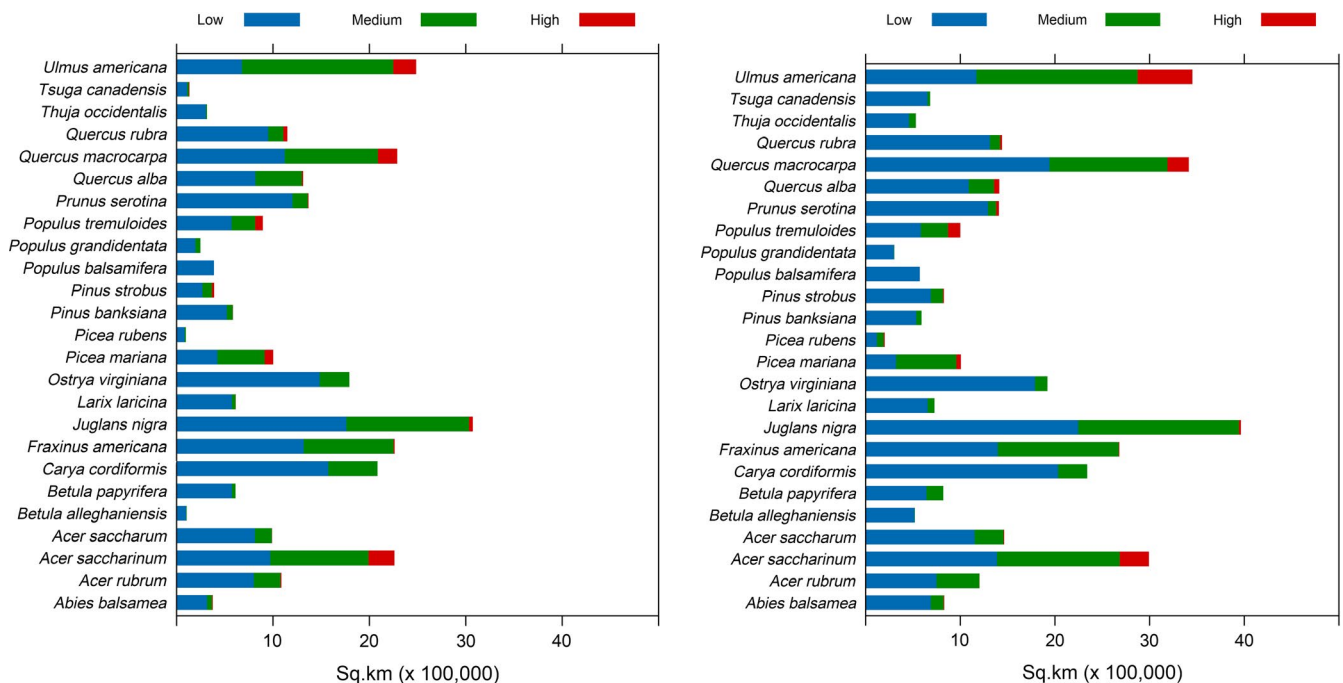


FIGURE 5 Area of low-, medium- and high-quality habitat gained by 25 tree species in the United States by the end of the current century under RCP 4.5 (a, left) and RCP 8.5 (b, right). The low, medium and high classes are reclassifications of predicted suitable habitats

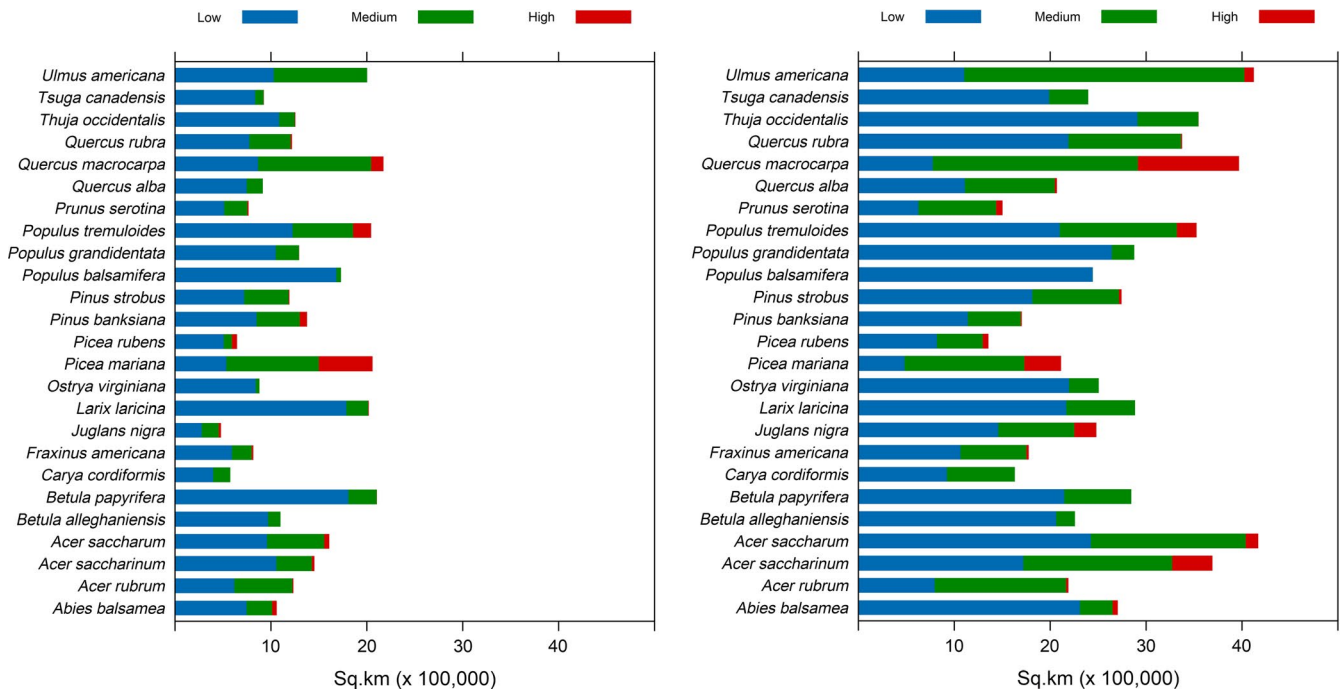


FIGURE 6 Area of low-, medium- and high-quality habitat gained by 25 tree species in Canada by the end of the current century under RCP 4.5 (a, left) and RCP 8.5 (b, right). The low, medium and high classes are reclassifications of predicted suitable habitats.

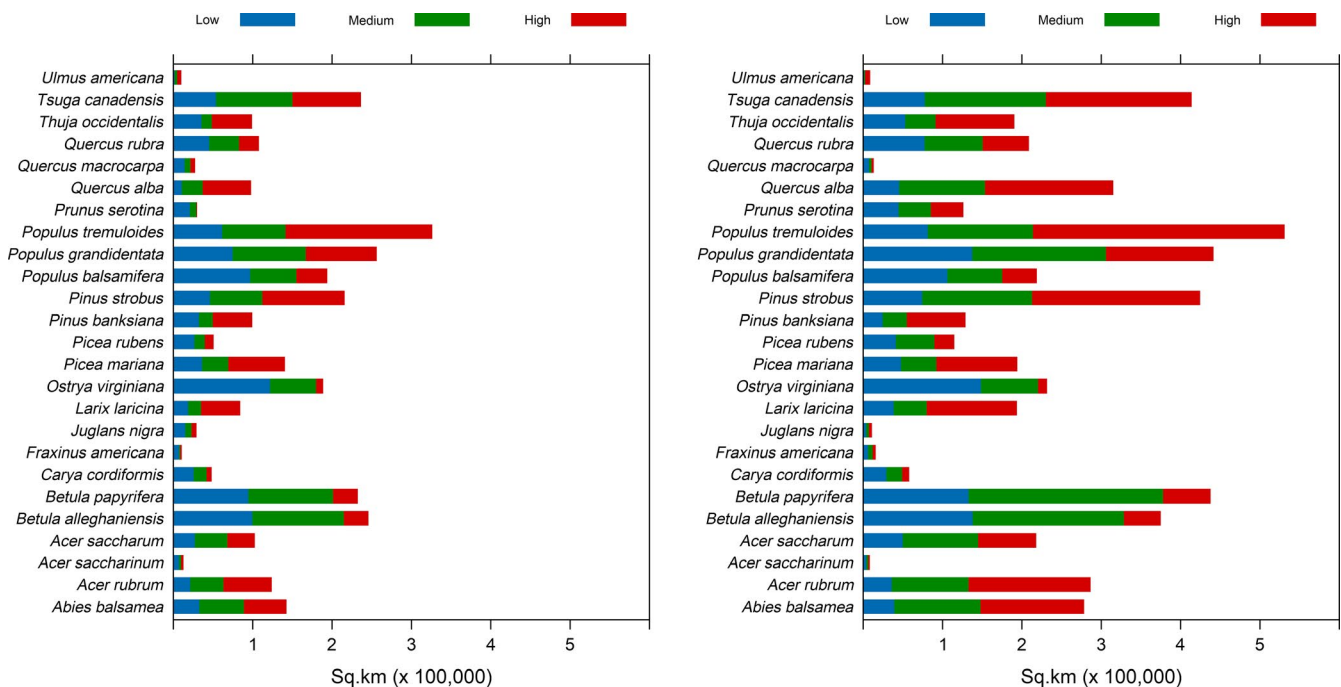


FIGURE 7 Area of low-, medium- and high-quality habitat lost by 25 tree species in the United States by the end of the current century under RCP 4.5 (a, left) and RCP 8.5 (b, right). The low, medium and high classes are reclassifications of predicted suitable habitats.

is lost) and balsam poplar (*Populus balsamifera*). Conversely, temperate hardwood species, such as white oak (*Quercus alba*) and black cherry (*Prunus serotina*), had most of their habitat losses in the United States. Note that the amount of habitat gained (Figures 5 and 6) is often an order of magnitude larger compared to habitat lost (Figures 7 and 8).

3.5 | Colonization likelihood of gained habitats

While climatically suitable habitats generally increase for most species in the future, a relevant consideration is the likelihood of these habitats being naturally colonized in a similar time frame. Areas with positive combinations of both HQ and CL

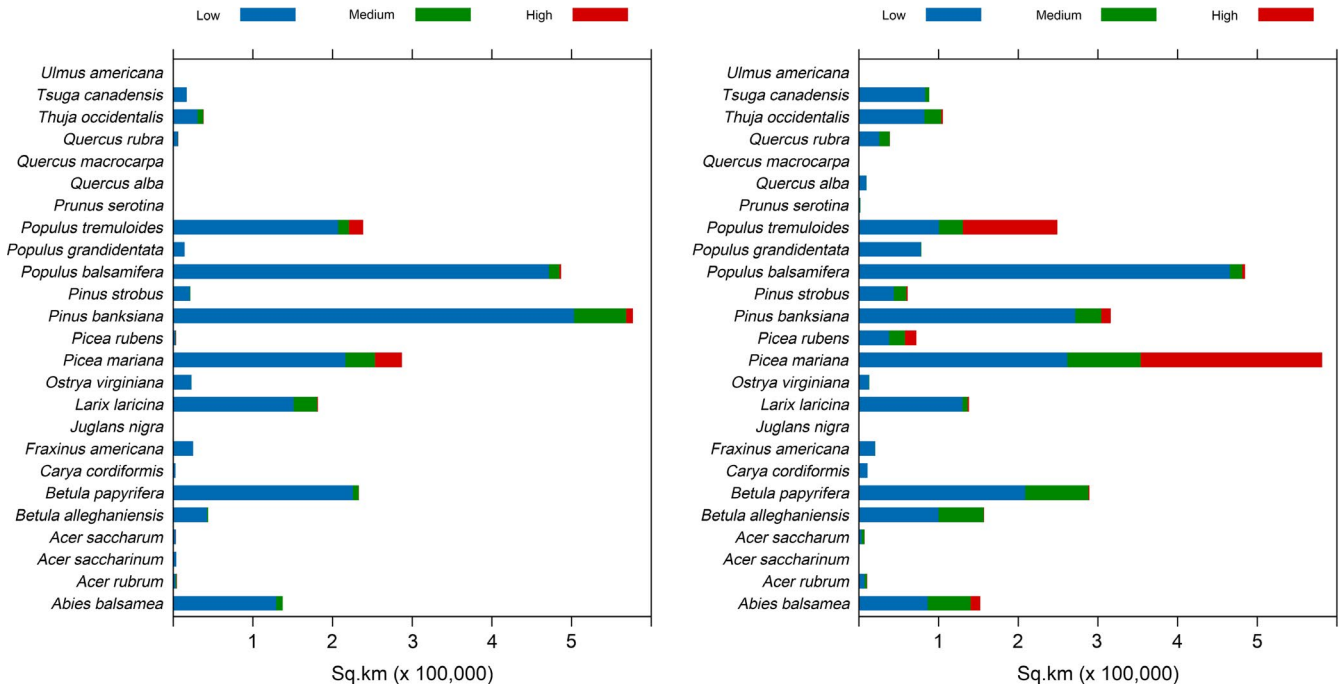


FIGURE 8 Area of low-, medium- and high-quality habitat lost by 25 tree species in Canada by the end of the current century under RCP 4.5 (a, left) and RCP 8.5 (b, right). The low, medium and high classes are reclassifications of predicted suitable habitats

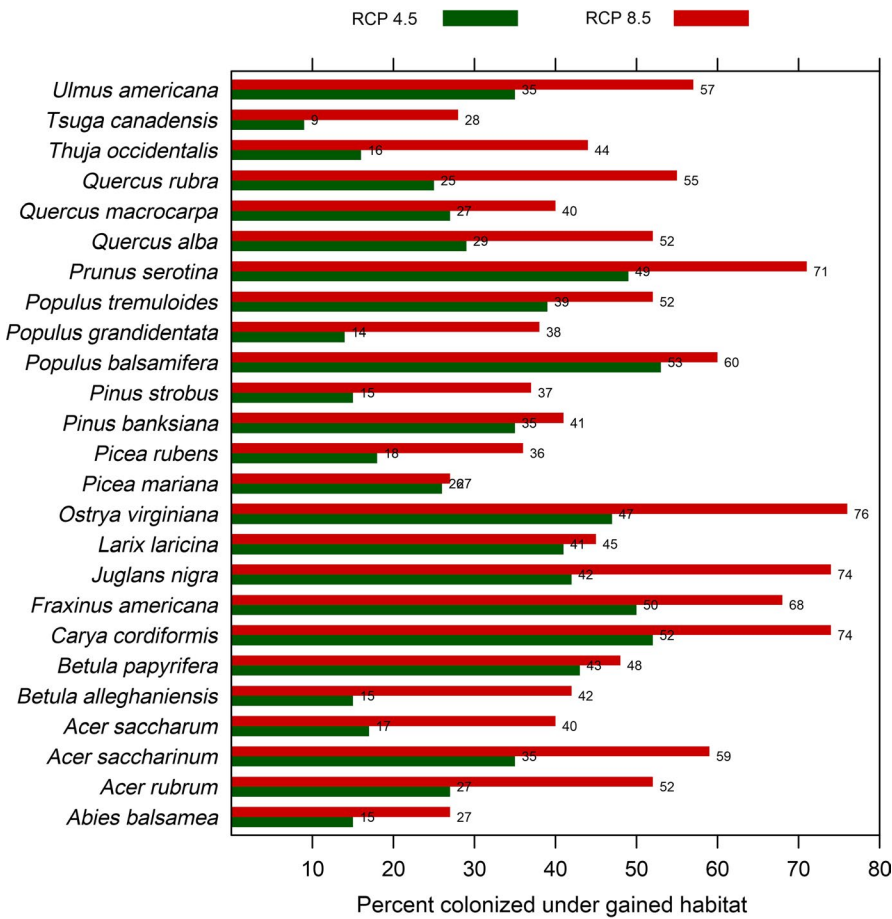


FIGURE 9 The percentage of newly gained habitat that was projected to be colonized by the end of the current century for 25 tree species under RCP 4.5 and RCP 8.5 emissions scenarios

were projected to have some probability of colonization within ~100 years under future climates (e.g. coloured cells in Figure 4), as compared to cells that had essentially no chance of colonization (grey cells in Figure 4). For each species and emissions scenario, we calculated the percentage of new habitats (depicted as shades of green—GainLow, GainMedium and GainHigh, in Figure 3) that have the potential to be colonized (Figure 9). In general, the proportion of habitats colonized is much higher under RCP 4.5 than for RCP 8.5, reflecting the greater amount—and more northerly distribution—of habitat gained under RCP 8.5. For example, for sugar maple, only 17 per cent of the habitat gained under RCP 8.5 has any potential to be colonized ($CL > 0$), compared to 40 per cent under RCP 4.5. For some species the per cent colonized, especially under RCP 8.5, is rather low (e.g. eastern hemlock—*Tsuga canadensis*, eastern white pine—*Pinus strobus*) and may require special attention from managers. Species that currently occupy widespread northern habitats (e.g. black spruce—*Picea mariana*, tamarack—*Larix laricina*, jack pine—*Pinus banksiana*) do not show appreciable difference between RCP 4.5 and RCP 8.5 scenarios.

4 | DISCUSSION

To our knowledge, this is the first attempt to combine the forest inventories of the United States and Canada to model range-wide habitat suitability, using a continuous response variable of relative abundance in combination with potential tree migration under climate change. In the following sections, we first discuss species dynamics by evaluating changes in suitable habitats (HQ) and then focus on how colonization likelihood (CL) computed by the migration model supports a more realistic picture of HQCL dynamics.

4.1 | Changes in suitable habitats and management implications

Changes in climatically suitable habitats provide useful metrics to understand how habitat expansion under future climates can impact the United States differently compared to Canada. The future habitat projections also provide a visual map of the altered climatic landscapes in which these species will exist in the future. Many species that are currently in the eastern United States are projected to gain suitable habitat in Canada. The maps of habitats gained, lost and retained (Figure 3, and Data Availability section), and the multispecies summaries for each country separately (Figures 6 to 9), show how these dynamics play out for individual species, which is useful for forest managers in both countries. Species whose current range is primarily in the United States (red maple—*Acer rubrum*, silver maple—*Acer saccharinum*, sugar maple—*Acer saccharum*, white ash—*Fraxinus americana*, bigtooth aspen—*Populus grandidentata*, northern red oak—*Quercus rubra*) and especially those that just reach the southern edge of Canada (bitternut hickory—*Carya cordiformis*, black walnut—*Juglans nigra*,

eastern hophornbeam—*Ostrya virginiana*, black cherry—*Prunus serotina*, white oak—*Quercus alba*, bur oak—*Quercus macrocarpa*, American elm—*Ulmus americana*) are expected to gain habitat in Canada in the future under both RCP 4.5 and RCP 8.5 scenarios and lose habitat in the United States (Figures 6 to 9).

All 25 species gained more habitat than they lost under future warming scenarios, often by an order of magnitude (Figures 6, 7 versus Figures 8, 9). The species that are projected to have the highest gains in the United States include silver maple (*Acer saccharinum*), black walnut (*Juglans nigra*), bur oak (*Quercus macrocarpa*) and American elm (*Ulmus americana*)—these species have relatively low R-square values (Table 1), so these outcomes should be interpreted cautiously. The species projected to suffer the greatest losses in habitat quantity and/or quality within the United States include quaking aspen (*Populus tremuloides*), bigtooth aspen (*Populus grandidentata*), paper birch (*Betula papyrifera*), yellow birch (*Betula alleghaniensis*), eastern hemlock (*Tsuga canadensis*), white pine (*Pinus strobus*), white oak (*Quercus alba*) and red maple (*Acer rubrum*)—the latter three of which are of major commercial importance, followed by aspen and birch. White pine (*Pinus strobus*), white oak (*Quercus alba*) and red maple (*Acer rubrum*) are also projected to increase their habitats elsewhere within the United States, but the bulk of the newly gained habitat is in the lowest HQ class. Our models do not show an overall major threat for the sugar maple industry currently or in the future in the northeast (Figure 3), although habitat losses are projected for locations where the industry is currently not prominent, primarily in the southern states of the United States. In Canada, most species gained habitat along the northern edge of their ranges, including species that are currently limited to the far southern portion of the country such as black walnut (*Juglans nigra*) and bitternut hickory (*Carya cordiformis*). Most habitat loss was associated with the southern range limits of boreal species such as black spruce (*Picea mariana*), jack pine (*Pinus banksiana*) and quaking aspen (*Populus tremuloides*). These are all major commercial species and such losses could have important implications for forest industry in the longer run (Pedlar & McKenney, 2017).

In the United States, almost all species lost more habitats under the harsher RCP 8.5 scenario compared to RCP 4.5 (Figure 7). In Canada, this trend is reversed, with the notable exception of black spruce (*Picea mariana*; Figure 8). This pattern is consistent with the notion that habitats will shift further northward under more extreme warming scenarios. For many species in our study, this translates into habitat gains in Canada, though northern species that already extend to nearly the northern land limits of the continent (e.g. black spruce - *Picea mariana*) would be expected to gain little habitat from such shifts.

The loss of the high HQ class is greater relative to low and medium HQ (Figure 7) for the United States, which is cause for concern. The extent of this trend varies among species, but should be factored into management protocols. More focused management in areas where the models are depicting this trend may be warranted. In Canada, although the amount of habitat lost is lower compared to

the United States, black spruce, balsam poplar and quaking aspen all lose sizeable amounts of habitat. In fact, quaking aspen (*Populus tremuloides*) loses a significant amount of high-quality habitat in both the United States and Canada. While these losses in habitat are cause for concern, species like black spruce (*Picea mariana*) are also quite opportunistic and can colonize relatively rapidly under changing conditions (Joyce & Rehfeldt, 2017; Truchon-Savard et al., 2019).

The magnitude of the habitat losses reported here is relatively small compared to those reported in some earlier studies. For example, McKenney, Pedlar, Lawrence, Campbell, and Hutchinson (2007b) reported that over half of the tree species in their study were projected to have smaller climatic niches in the future (compared to none in the current study)—with the majority of losses happening at species' southern range limits. One reason for these different findings may be the use of abundance (as opposed to occurrence) data in the current study, which allows for a more detailed (and nuanced) delineation of suitable habitat. In fact, for many of the species examined here, southern range limits are projected to remain relatively intact, albeit with reduced habitat quality. Thus, while leading-edge habitats are projected to expand rapidly due to greater warming at these latitudes, trailing-edge populations may remain viable, but subject to greater climatic stress. Findings such as this illustrate the value of the range-wide abundance data employed here.

For the United States, the state of Alaska is poised to gain climatically suitable habitat for many of the 25 species according to our HQ model under both RCP 4.5 and RCP 8.5, but with the latter resulting in greater gains of high-quality habitat (Figure 3—see Appendix for maps of habitats lost, gained and retained for all 25 species). This finding reflects the rapid rate of warming projected for the north-western region of North America (Bintanja, 2018; Coumou, Di Capua, Vavrus, Wang, & Wang, 2018; Goosse et al., 2018). This gain in HQ via Alaska signals future potential possibilities for the United States, but, as indicated by our colonization models, many species would have essentially no chance of reaching this region by means of natural migration by the end of the century, as discussed in the next section.

4.2 | Colonization of suitable habitats—HQCL combinations

While our HQ models provide valuable insights into future habitat shifts, it is well understood that only a portion of future suitable habitats will be naturally colonized by the end of the century. Therefore, the combination of HQ with CL allows for a more realistic assessment of the future habitat occupancy by incorporating colonization likelihoods of future suitable habitats based on an optimistic historical migration rate of ~50 km/century (Figure 4, online maps). As might be expected, the area of HQ colonized is much smaller than that uncolonized for most species (grey shades dominate over coloured ones in Figure 4, especially under RCP 8.5). However, for species with scattered, spotty distributions (e.g. bitternut hickory—*Carya cordiformis*, black cherry—*Pinus serotina*, black walnut—*Juglans*

nigra, white ash—*Fraxinus americana*, silver maple—*Acer saccharinum*, eastern hophornbeam—*Ostrya virginiana*), the per cent colonized is quite high because there is a lot of infilling migration wherein gaps in the current distribution are colonized. For the remaining species, that are more continuous in distribution (e.g. balsam fir—*Abies balsamea*, sugar maple—*Acer saccharum*, yellow birch—*Betula alleghaniensis*, black spruce—*Picea mariana* and bur oak—*Quercus macrocarpa*), the per cent colonized is much lower because the majority of colonization tends to be 'outfilling' at the range borders. These species also tend to have larger future habitat envelopes that extend far beyond current range limits, which further contributes to their low colonization percentages. It should be noted that these are optimistic results because we consider all suitable habitats, and any likelihood of colonization—including rare events. However, this approach is useful for comparison purposes as it should not alter the relative variation among the 25 species.

These findings (Figure 9, Figure 4 and rest of the maps in Data Availability section) can help to identify suitable conservation strategies for the various tree species examined here. For example, for the species listed above with considerable potential for infilling migration, efforts could focus on facilitating within-range movements, while for those species relying primarily on migration at range edges, efforts aimed at assisted range expansion may be appropriate. Our results suggest that differing approaches could be featured in the two countries—for example, a focus on within-range conservation in the United States and range expansion in Canada. These contrasting situations require different approaches, but a common paradigm of international cooperation to combat the consequences of rapid climate change.

4.3 | Role of assisted migration

As outlined above, this study identifies a number of situations in which various forms of assisted migration could be considered as potential tools for promoting forest conservation and adaptation under climate change (Pedlar et al., 2012). Within-range movements of climatically suitable genotypes represent a relatively low-risk form of assisted migration that could help better align population-level climate preferences with projected future climate (Ste. Marie, A. Nelson, Dabros, & Bonneau, 2011). Such movements would be particularly useful for encouraging within-range colonization (i.e. infilling migration), which was identified as a potential source of habitat gain for many species in the current study. For example, the infilling migration could focus on encouraging species to establish in more mesic landscape positions, to combat the forecasts of increasing drought, or simply to manage for increasing the species abundance in their current positions for enhanced potential for local expansion. Near-range movements, which aim to assist range expansion at northern/upslope boundaries (Ste. Marie et al., 2011), are another form of assisted migration that could be employed to promote forest conservation under climate change. In this case, HQCL maps such as those presented here, by highlighting both 'infilling' and

'outfilling' migration, could be used to identify general planting locations that aim to mimic natural migration patterns. For example, the focus could be in assessing regions just beyond the colonized areas (the coloured regions in Figure 4) for assisted migration. Such efforts may be required in the event that migration rates are slowed due to human-made and/or natural barriers. Finally, assisted migration efforts that involve long-distance movements well beyond current range limits (Ste-Marie et al., 2011) may be of interest for certain species and regions. As noted above, Alaska is projected to gain suitable habitat for nearly every species in this study. However, for temperate tree species that are currently limited to the eastern United States and south-eastern Canada (i.e. 15 of the 25 species examined here), translocation to Alaska would involve movement distances on the scale of thousands of kilometres and the creation of highly novel species assemblages. Such movements have been the source of ongoing ethical and ecological debate (Aubin et al., 2011) and would require careful assessments before being undertaken.

Proactive efforts to elucidate climate responses by trees, including carefully designed provenance trials in regions of interest, could have concrete benefits in the future. HQ and HQCL maps, such as those presented here, can be very helpful in evaluating the suitability of test sites, along with post-model filters to censor areas that are unsuitable in terms of land cover, elevation or edaphic factors. Regardless of the exact approach taken, efforts to conserve forest habitats across United States (including Alaska) and Canada will call for close cooperation between the two countries, not only for mitigating ill effects, but also for realizing the opportunities these changes offer.

4.4 | Post-model filter

Even though a sizeable portion of the gained climatic habitats are colonized according to our models (Figure 9), these are estimates under a full climatic response and optimistic historical migration rate (50 km/century). While these 'first-stage' estimates give us reasonably good approximations for how the species are likely to respond under future climates, they do not consider ground realities like land cover, topography and soils that can modify the outcomes for species. This was intentional, given that we wanted to focus on climate and not confound the HQ model with extraneous considerations. While we cannot accurately predict how land cover will change in the future, current land use patterns can help determine where management activities, such as assisted migration efforts, could be implemented. To explore the use of post-model filters, we used the North American land cover map (NALC, 2010, a 30-metre Landsat-based dataset that distinguishes 19 land cover classes and vegetation types) to mask certain land cover classes from our sugar maple HQ map. Specifically, we filtered cells where current land cover would preclude forest establishment (i.e. cells classified as water, permafrost, barren land, cropland, urban/built-up land and wetlands). According to our HQ model, under the RCP 8.5 scenario (Figure 3, right), approximately 4.31 million km² of HQ-low, 2.5 million km² of

HQ-medium and 0.38 million km² of HQ-high become available by the end of the current century. These amounts, with the land cover mask overlaid, shrink by 35% for HQ-low; 20% for HQ-medium; and 9% for HQ-high. Additionally, in line with our multistage scheme, regions where topography, soil depth or type (Carteron et al., 2020) are major modifiers can be further filtered or modelled by more accurate regional databases, depending on the interest/expertise of the manager, to produce locally relevant maps.

4.5 | Limitations and strengths of the FIA + NFI approach

One of the novel aspects of this study is the combination of relative importance data (derived from the USA's FIA dataset) with per cent composition data (derived from Canada's NFI-based data product), which allowed us to model the entire range of almost all the species considered here. Though there are differences between the two data sources, and the merger of FIA and NFI data while not optimal, can be justified in terms of 'information gain' derived from our MME approach for predicting HQ. Additionally, because FIA data were not available for interior Alaska that area could not contribute to the MME; however, these data would have included only a few species, such as black spruce and quaking aspen, and not changed our overall conclusions.

One of the consequences of post-processing of the NFI data (via MODIS and k-nearest neighbour approach) is that the relative abundance is smoothed (because it tends to eliminate the tails of the distribution) compared to the FIA plot-based data. This may have resulted in more conservative migration potentials, but our optimistic assumption of the migration rate of 50 km/century should compensate for this deficiency (Davis, 2001; McLachlan & Clark, 2004; McLachlan et al., 2005; *but see* Snell & Cowling, 2015; Ordóñez & Williams, 2013).

4.6 | Future directions

An important consideration with respect to tree responses to climate change is that populations may be adapted to climate in only a portion of the range (i.e. local adaptation). This means that, for widespread species, populations may respond differently to climate across the species' range (Leites, Rehfeldt, & Steiner, 2019; Peterson, Doak, & Morris, 2019). In addition, natural populations tend to occur in climates colder than where they grow the best—that is, populations occur in climates suboptimal for their growth and productivity—this discrepancy increases with the degree of winter cold of the provenance (Rehfeldt, Leites, Joyce, & Weiskittel, 2018). However, capturing this variability across the entire species' range via habitat suitability models is not possible without data from provenance studies and/or genetic analysis, which tend to be sparse or non-existent for many species. One way to approximately assess this variability in the absence of these

data is to split the range into three regions based on plant hardiness zones (PHZ): leading cold-adapted, a trailing warm-adapted and the 'optimal' middle (Prasad, 2015). We are in the process of using this approach for the 25 species studied here to evaluate intraspecific variability in conjunction with the range-wide analysis to understand how the leading-edge and trailing-edge responses can be different. Our current multistage approach, when combined with the analysis of intraspecific variability, will have direct relevance to future climatic changes because the leading and trailing regions can be under greater climatic stress, although they may possess genotypes better adapted to extreme climates (Hampe & Petit, 2005; Isaac-Renton et al., 2018; Rehm, Olivas, Stroud, & Feeley, 2015).

In conclusion, our study underscores the importance of evaluating range-wide habitat suitability and colonization potential of tree species when examining climate change impacts on future tree distributions. For the species examined here, habitat losses were primarily experienced along southern range limits, while habitat gains were associated with northern range limits—though there was also a significant amount of infilling migration within the ranges of species with discontinuous distributions. However, even with optimistic tree migration rates, our models predict that, for most of the species examined here, only a small portion of the climatic habitat generated by climate change will be colonized naturally by the end of the current century. Significant management efforts, including assisted migration of populations and species, may need to be considered in order to conserve and promote tree species that are deemed important for economic or ecological reasons. Our work highlights the need for increased cross-border cooperation as management demands can differ between the United States and Canada owing to the differing species-specific objectives and responses under future climates.

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CONFLICT OF INTERESTS

We have no competing interests.

DATA AVAILABILITY STATEMENT

Can be accessed via: <https://doi.org/10.5061/dryad.qz612jmbn> (36 MB). 1) Unzip the downloaded file to a folder, 2) go to the 'Data' folder and 3) open file index.html. This will allow rapid visualization of three sets of maps for the 25 species: 1) abundance distribution; 2) habitats lost, gained and retained (RCP 4.5 and RCP 8.5); 3) combined maps of HQ and CL (RCP 4.5 and RCP 8.5).

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