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Original Article

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Fine-scale drivers of sugar maple (*Acer saccharum*) habitat suitability at its northern range limit

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Abstract

At its northern range limit, climate change is increasing the uncertainty about the persistence of sugar maple (*Acer saccharum*). To inform climate adaptation strategies, we developed a high-resolution species distribution model using a Random Forest algorithm to identify currently suitable habitats, determine their primary environmental drivers, and project future shifts. The model, based on 3664 ground plots and built with fine-scale (20 m) topographic, soil, and climate data, demonstrated high predictive accuracy (76.4%) when tested against a spatially independent dataset (AUC = 0.868). Habitat suitability was found to be co-limited by topographically controlled moisture (topographic wetness index), soil fertility (cation exchange capacity), winter temperature stress (mean coldest month temperature), and wind exposition. Under a near-future climate scenario (SSP3–7.0, 2021–2040), we project a net increase in suitable habitat, with gains (~16%) significantly outweighing losses (~3%). Crucially, these gains are not uniform but form a complex spatial mosaic, highlighting where boreal-dominated landscapes are predicted to become suitable for this key temperate species. This provides a foundational roadmap for land managers to proactively establish climate-resilient forests, offering a significant opportunity to guide actions like assisted migration to the most promising sites.

Keywords spatial analysis, LiDAR-derived terrain metrics, adaptive silviculture, wall-to-wall mapping, airborne laser scanning

Introduction

Climate change is forcing tree species to migrate towards higher latitudes and elevations to track suitable climatic conditions, but natural migration rates are often insufficient to keep pace with the velocity of climate change (Pearson 2006, Aitken et al. 2008). As forests become increasingly vulnerable to multiple stressors such as droughts, fires, and pest outbreaks (Boulanger et al. 2016, Flatley and Fulé 2016, Lecina-Diaz et al. 2021), the implementation of proactive, adaptive management strategies is critical to maintain their health and ecosystem services (Szmyt 2020, Achim et al. 2022). Such strategies, which may include measures like assisted migration, require a detailed understanding of the factors that control a species' habitat suitability.

To support these decisions, species distribution models (SDMs) are powerful tools for estimating habitat suitability across landscapes and under future climate scenarios (Elith and Leathwick 2009). Modern SDM strategies correlate species occurrence records with spatially explicit environmental variables to model the species' response curves, thereby estimating the probability of occurrence (Valavi et al. 2022). However, broad-scale models that rely heavily on climatic variables often overlook the fine-scale biotic and abiotic factors that can ultimately determine whether a species can establish and thrive at a specific site (Araújo and Luoto 2007, Bucharova 2017).

At the operational scale where most silvicultural decisions are made, a more detailed understanding of the processes governing species distributions is crucial. Historically, the refinement of SDM predictions was constrained by structural limitations in predictor resolution, accuracy, and ecological representativeness (Guisan and Zimmermann 2000). This paradigm shifted with the emergence of high-resolution terrain data from airborne laser scanning (ALS), which offers unprecedented capacity to generate ecologically meaningful environmental proxies (Guillaume et al. 2021). Climate variables were typically downscaled from sparse weather stations networks using models calibrated with coarse-resolution digital elevation models (DEM), thereby increasing spatial uncertainty (Chen et al. 2014, Keller et al. 2022). Soil parameters, when included and if available, were frequently derived from limited sampling and interpolated across heterogeneous landscapes, introducing uncertainty given the inherently heterogeneous and discontinuous distribution of edaphic properties (Kravchenko 2003, Shen et al.

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2019). In addition, elevation-derived topographic variables were often computed from low-resolution DEMs, restricting their ability to represent fine-scale terrain-driven ecological processes (Sørensen and Seibert 2007, Camathias et al. 2013). Fine-scale topographic and edaphic gradients regulate tree species' local establishment, growth, and vulnerability to stress (Carteron et al. 2020, Carnicer et al. 2021). Including such variables among predictors in SDMs is therefore essential, as they capture the complex interactions between a species and its local environment (Park and Talbot 2018).

Sugar maple (*Acer saccharum* Marshall), an economically and ecologically important species in North America (Hassegawa et al. 2018, Voyer et al. 2024), is expected to shift its range northwards in response to climate change (McKenney et al. 2007, Iverson et al. 2008). It is a shade-tolerant species that can establish a persistent "seedling bank," i.e. a dense layer of suppressed juvenile trees capable of surviving for decades before rapidly responding to canopy disturbances (Marks and Gardescu 1998). For sugar maple, various earlier studies have shown that topography acts as a mechanistic proxy for various environmental variables including soil moisture redistribution, base cation availability, and disturbance exposure. Within the core of the species' geographic range, upper slope positions and weathered soils depleted in base cations have been associated with the observed decline over the past decades (Horsley et al. 2000, 2002, Boakye et al. 2023). In contrast, mid- to lower-slope positions often provide more favorable conditions, as water flowpaths redistribute weathering products and nutrients toward the rooting zone (Horsley et al. 2000, 2002). Slope orientation and topographic exposure further influence spatial aggregation and the species dominance patterns through microclimatic differences; under highly exposed xeric conditions, more drought-tolerant species such as oaks (*Quercus* L. spp.) tend to dominate, whereas sugar maple is more competitive in mesic and sheltered positions (Nigh et al. 1985, Murphy and McCarthy 2012). Even at the micro-site level, microtopography (e.g. hills versus pits) creates hydrologic refugia that dictate fine-root development and drought resilience in temperate hardwoods (Tauc et al. 2020). Other species exhibit similar topographic dependencies; eastern hemlock (*Tsuga canadensis* (L.) Carrière) shows strong sensitivity to slope gradients and aspects to avoid drought stress (Robin-Abbott and Pardo 2017), while American beech (*Fagus grandifolia* Ehrh) often partitions habitats with sugar maple along fine-scale variations in soil moisture and elevation (Nolet and Kneeshaw 2018, Tourville et al. 2023).

At its northern range limit in Quebec, Canada, sugar maple occupies a distinct environmental niche, typically found on elevated hilltops and well-drained, mesic slopes (Graignic et al. 2018), where topographic controls remain an important factor despite becoming less pronounced toward the species' core range (Drohan et al. 2002, Pitel and Yanai 2014). This preference for elevated sites is thought to be associated with the avoidance of cold air damage and fire (Leithead et al. 2010, Pilon and Payette 2015, Graignic et al. 2018). In contrast, valleys at these latitudes are generally dominated by more cold-adapted boreal conifers (Goldblum and Rigg 2002). Because these ecological constraints operate at such fine spatial scales, accurately representing terrain-driven microclimatic variation becomes essential for modeling habitat suitability (Questad et al. 2014). High-accuracy DEMs allow the extraction of terrain metrics such as slope position, aspect, curvature, topographic wetness indices, and microtopographic variability at spatial resolutions consistent with stand-level ecological processes (Coops et al. 2021, Ahmadi et al. 2023). Integrating these high-resolution terrain proxies into SDM frameworks enables a mechanistic representation of the topographic controls that shape sugar maple distribution at its range limit. In this context, the approach presented here moves beyond climate-dominated models by linking species ecology to fine-scale environmental structure, thereby bridging macroecological projections and operational silviculture.

While previous research has aimed to support the implementation of assisted migration (Etterson et al. 2020, Clark et al. 2022, Palik et al. 2022), comprehensive fine-scale characterizations of sites suitable for prioritizing such interventions remains limited (Wotherspoon et al. 2025). Given the strong terrain dependence of sugar maple at its northern range limit, identifying priority sites requires integrating high-resolution environmental proxies that reflect microclimatic and edaphic constraints. By examining the responses of sugar maple to a range of abiotic factors at a fine spatial resolution, using field-based inventory sample plots (400 m^2) combined with LiDAR-derived terrain metrics, we can gain a better understanding of the species' ecological requirements and propose spatially explicit, climate-informed management strategies. Therefore, this study aimed to: (i) develop and validate a fine-resolution SDM to identify sites currently suitable for sugar maple at its northernmost range limit; (ii) identify the main environmental factors driving this suitability; and (iii) project and analyze climate-induced shifts in habitat to inform conservation and management planning.

Study area

The study was conducted within the Ecological Planning Unit (EPU) 1415 North and Centre North, a 12 466 km^2 region in southern Quebec, Canada (Fig. 1). EPUs are foundational territorial units established for Quebec's forest resource inventory (FRI). They integrate both administrative (e.g. forest region) and ecological boundaries to provide a basis for planning inventory activities and guiding forest management (MRNF 2022).

The selected EPU is situated at the transition between the temperate deciduous and boreal forest biomes and lies within the balsam fir (*Abies balsamea* (L.) Mill.)—yellow birch (*Betula alleghaniensis* Britton) bioclimatic domain (Saucier et al. 2009). It was specifically chosen because it encompasses the northernmost distribution limit of sugar maple, providing a natural laboratory to study the factors constraining its range (Graignic et al. 2014, Sittaro et al. 2017).

The region's geography is characterized by moderately rugged terrain, with elevations generally ranging from 350 to 450 m. The landscape is dominated by surface deposits of thick glacial till and frequent rocky outcrops. The climate is continental, with a mean annual temperature of ~2.5°C and a growing season of 160–170 days. Mean annual precipitation ranges from 1000 to 1100 mm (Saucier et al. 2009).

The vegetation is characteristic of the temperate-boreal ecotone. Mesic sites on well-drained soils are typically dominated by mixed stands of sugar maple, yellow birch, and balsam fir. In contrast, well-exposed hilltops and drier sites often support stands of white birch (*Betula papyrifera* Marshall), balsam fir, or black spruce (*Picea mariana* (Mill.) Britton, Sterns and Poggenb.), while valley bottoms and areas with organic deposits are commonly occupied by conifers mixed with sphagnum moss (*Sphagnum* spp.) and rough alder (*Alnus incana* (L.) Moench) (Saucier et al. 2009).

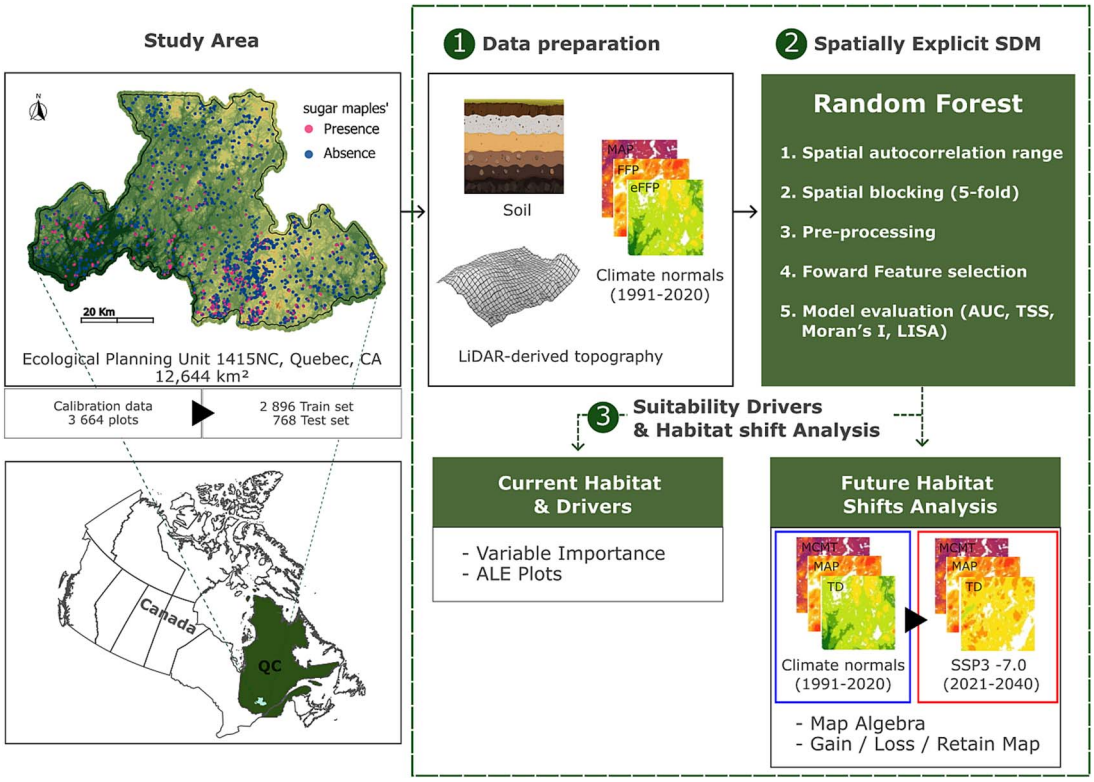

Figure 1 Conceptual diagram of the study area and methodological workflow.

Materials and methods

Our approach involved three main stages. First, we acquired and processed spatial data for sugar maple presence–absence, along with a suite of topographic, soil, and climatic predictor variables for the study area (Section Data Sources and Processing). Second, we used this data to train, validate, and test a Random Forest (RF) classification model to identify currently suitable habitats and their environmental drivers (Section Species Distribution Modeling). Finally, we used the trained model to project habitat suitability under a future climate scenario and analyzed the resulting spatial habitat shifts (Section Predicting and Analyzing Habitat Shifts). All analyses were conducted using R statistical software (version 4.5.0) (R Core Team 2026).

Data sources and processing

Sugar maple presence and absence data

We used sugar maple presence and absence in two stages of the analysis. First, for model calibration, presence–absence data for sugar maple were obtained from the Quebec FRI temporary inventory plots (11.28-m radius) (MRNF 2023), which include all standing trees with a minimum diameter at breast height of 9.1 cm, measured at 1.3 m above ground. A plot was classified as having "presence" of sugar maple when at least one individual was tallied, which equated to an abundance greater than or equal to 25 stems per hectare.

Second, for the analysis of habitat shifts, a presence–absence data raster layer was derived from the Quebec FRI maps (MRNF 2023). These maps are generated using a k-Nearest Neighbors (k-NN) imputation method at a 20-m resolution. High-resolution aerial imagery, satellite data, and LiDAR data are used to derive continuous spectral and structural predictor variables for each grid cell. The k-NN algorithm then imputes detailed dendrometric attributes (e.g. stems per hectare), such as stems per hectare, to each 20-m cell based on the most statistically similar field plots, which are part of the fourth decennial FRI, whose surveys started in 2011. A pixel was classified as having "presence" of sugar maple when abundance was greater than or equal to 25 stems per hectare. Although this layer represents a model-derived output, it serves as a highly robust reference database for sugar maple habitat shifts analysis because it is calibrated and rigorously validated against an extensive network of terrestrial temporary forest inventory sample plots. It should nonetheless be noted that this shared model dependency introduces an additional source of uncertainty in the habitat shift analysis, and results should therefore be interpreted in terms of spatial structure and relative magnitude rather than precise area estimates.

Predictor variables

We compiled a set of 42 potential predictor variables to characterize the environmental conditions of the study area.

Topographic variables

Topographic variables were derived from a 1-m ALS-based DEM (MRNF 2016), resampled to 20-m resolution. We used RSAGA [which runs SAGA GIS software version 9.8.2 (Conrad et al. 2015) directly from R] and *terra* packages in R to derive slope (SLOP), aspect (ASPEC), topographic position index (TPI), topographic wetness index (TWI), and terrain ruggedness index (TRI), among others (see Appendix SA, Table A.1 for a complete list and sources).

Climate

Contemporary (1991–2020) and future (2021–2040) climate data were derived using ClimateNA (Wang et al. 2016), based on an eight-GCM

(general circulation model) ensemble recommended by Mahony et al. (2022) for projections in Canada. This conservative modeling strategy follows the guidance of Dietze et al. (2024) and Pecchi et al. (2019) to minimize uncertainty in mid- to long-term forecasts. Rather than imposing predefined thresholds of temperature or precipitation change, we analyzed the full range of downscaled variables available in ClimateNA, thereby avoiding assumptions about dominant climatic drivers. A selected subset of annual and seasonal predictors, including mean coldest month temperature (MCMT) and mean annual precipitation (MAP), and others was used to characterize site conditions (see Appendix SA, Table A.2 for a complete list).

Projections under SSP3–7.0, a plausible "business-as-usual" scenario that excludes extreme fossil fuel reliance (IPCC 2023, Wotherspoon et al. 2024), suggest a transition to a warmer and wetter climate in the study area. By 2040, MCMT is expected to increase by 1.4–1.7°C, MAP by 78–135 mm, and temperature difference (TD) to decrease slightly (−0.2 to −0.5°C), indicating milder winters, greater water availability, and reduced annual thermal contrast.

Soil parameters

Soil variables were obtained from 100-m resolution digital soil maps (Sylvain et al. 2022) available in "Données Québec" portal, and included physical and chemical properties of the topsoil (0–5 cm), such as cation exchange capacity (CEC), pH, and the proportion of silt, sand, clay, and organic matter (see Appendix SA, Table A.3).

Species distribution modeling

To identify suitable habitats for sugar maple, we developed an SDM using an RF algorithm (Breiman 2001) in classification mode, with sugar maple presence–absence as the response variable. RF aggregates votes across an ensemble of decision trees to produce a class probability, which serves as a continuous index of habitat suitability. This probability surface was then converted into a binary suitability map by applying a threshold selected by maximizing the true skill statistic (TSS) (Allouche et al. 2006). We followed a spatially explicit workflow to (i) quantify the range of spatial dependence in the environmental predictors relative to sugar maple presence–absence, (ii) use this range to create spatially independent training and testing datasets, and (iii) train and evaluate the SDM under spatial blocking.

First, we estimated the spatial autocorrelation range of the predictor set considering the target response, sugar maple presence–absence, and used the resulting distance, 8993 m, to define the spatial block size. This block size was then used to generate spatially independent holdout training (2896 sample plots) and test (768 sample plots) sets (Valavi et al. 2019). The test set was withheld entirely from model development and used solely for final performance evaluation.

Model training was then conducted using *caret* R package (Kuhn 2008) using the training set only, where the same 8993 m spatial block size structured a five-fold spatial cross-validation to tune and select the final model. During each fold, we applied a preprocessing pipeline that (i) removed near-zero variance predictors, (ii) removed correlated predictors when Pearson's correlation >0.9, (iii) applied a Yeo–Johnson transformation, and (iv) centered and scaled predictors. At this stage, 22 predictors were excluded. In addition, within each of the five spatial folds, class imbalance between presences and absences was handled via down-sampling (Valavi et al. 2022).

While the preprocessing pipeline applied within each spatial fold removed predictors with Pearson's correlation >0.9, we additionally performed a global correlation filter, removing one variable from any pair with a Pearson's correlation >0.8 (Kuhn and Johnson 2013); at this step, one more predictor was excluded. Following, we applied Forward Feature Selection to the remaining predictors to remove variables that did not meaningfully improve predictive performance, using Kappa as the optimization criterion (Meyer et al. 2018). Once the parsimonious predictor set was defined, we retrained the final RF model in *caret* using the same preprocessing steps and the same five-fold spatial blocking structure. Model performance metrics were evaluated using predictions generated for the spatially independent test dataset of 768 plots. We then evaluated the model residuals using Moran's I and LISA statistics (Anselin 1995). Finally, the optimal threshold was selected by maximizing the TSS (Allouche et al. 2006). Additional information on the correlation structure among the remaining predictor variables after all selection steps is provided in Appendix SB, Fig. B.3.

Predicting and analyzing habitat shifts

To project changes in habitat suitability, we first generated three key spatial datasets for our study area: (i) the observed presence–absence raster, (ii) the predicted current habitat suitability raster from our model, and (iii) a predicted future habitat suitability raster. The future raster was generated by applying the final model to a suite of predictor variables representing a near-term future climate scenario (SSP3–7.0, 2021–2040), while keeping the soil and topographic variables constant.

Using map algebra, we combined these three raster layers to quantify and categorize habitat shifts. This was done in two ways:

1) **Two-way analysis:** a direct comparison between the predicted current and predicted future suitability maps. This analysis classified the landscape into four categories: "Gain" (unsuitable becomes suitable), "Loss" (suitable becomes unsuitable), "Stable Suitable," and "Stable Unsuitable."
2) **Three-way analysis:** a more detailed analysis that also incorporated the observed presence–absence data. This three-way comparison classified the landscape into eight interpretive categories. For areas where sugar maple is currently absent, the categories were: (i) Stable Unsuitable, where unoccupied habitat is currently unsuitable and is predicted to remain unsuitable; (ii) Habitat Expansion, where unoccupied, currently unsuitable habitat becomes suitable; (iii) Stable Suitable, representing suitable but unoccupied habitat (i.e. potential refugia); and (iv) Loss, where currently suitable but unoccupied habitat becomes unsuitable. For areas where sugar maple is currently present, the categories were: (v) Core Habitat, where suitable habitat is occupied and remains suitable; (vi) Habitat Retraction, where occupied suitable habitat is predicted to be lost; (vii) Advance colonization, where occupied but currently unsuitable sites are predicted to become suitable; and (viii) Stable Unsuitable, representing occupied sites where conditions are predicted as unsuitable both currently and in the future.

To account for dispersal dynamics, we compared current and future predictions under two bounding scenarios: no dispersal, where suitable habitat expansion is constrained to the currently occupied area, and unlimited dispersal, where the species is assumed to be able to access any newly suitable habitat grid cell. These scenarios define

Table 1 Confusion matrix for the RF classification of suitable sugar maple habitats. The evaluation was performed with independent data ($n = 768$).

	Verified presence	Verified absence	Total
Presence prediction	112	166	278
Absence prediction	15	475	490
Total	127	641	768

the range of migration outcomes commonly explored in SDM-based climate projections (McPeek and Holt 1992, Holt and Barfield 2001, Araújo and Luoto 2007). In this study, current habitat was defined at the grid-cell level (20 × 20 m), where each cell predicted as suitable under present climatic conditions, based on the selected probability threshold, was classified as part of the current habitat extent. These scenarios define the upper and lower bounds of potential range expansion under climate change (Cousens et al. 2008).

Results

Current habitat suitability and model performance

The RF model demonstrated high predictive accuracy in identifying currently suitable habitats for sugar maple. When evaluated against an independent test set of 768 inventory plots, the model achieved an area under the receiver operating characteristic curve (AUC) of 0.868, an overall accuracy of 76.4%, a TSS of 0.62, an F1 score of 0.55, and a Kappa of 0.42. The model showed a strong ability to correctly identify presences (sensitivity = 88.2%) and absences (specificity = 74.1%); however, the user's accuracy for presences was considerably lower (40.3%), indicating a tendency toward overprediction consistent with the difference between observed (17%) and predicted (36%) prevalence (Table 1). Internal validation metrics were consistent with these results, with the final model having an Out-of-Bag (OOB) error rate of 18% (see Appendix SB, Fig. B.1 for the receiver operating characteristic (ROC) curve.

Both raw presence–absence data and the model residuals exhibited significant positive spatial autocorrelation. Moran's I for presence–absence was 0.11 ($P < .001$), whereas residuals showed a stronger spatial structure, with Moran's I of 0.19 ($P < .001$). The LISA analysis, performed for the entire dataset (3664 samples), revealed a marked redistribution of spatial cluster types between observed presence and model residuals, with High–High clusters increasing from 10% in the raw data to 35% in the residuals. Low–Low clusters decreased from 29% to 11%, and Low–High clusters declined from 20% to 1%, while Not Significant locations slightly decreased from 40% to 35% (see Table B.1 and Fig. B.2 in Appendix SB for the spatial distribution of LISA clusters both for observed presence and model residuals).

The final map of predicted current habitat suitability is presented in Fig. 2A and B. The model predicted that suitable habitats are predominantly located in the southern portion of the study area, often corresponding to well-drained, elevated terrain, while valleys and the northernmost regions are largely predicted as unsuitable.

Drivers of habitat suitability

Variable importance

The analysis identified a combination of topographic, edaphic, and climatic characteristics as the primary drivers of sugar maple habitat suitability at its northern range limit. Based on the mean decrease in accuracy, the four most influential variables (with relative variable importance higher than 50%) were TWI, CEC, MCMT, and wind exposition (Table 2).

Table 2 Variable importance metrics for the final eight predictors in the RF model, ranked by variable importance.

Variable	Importance (%)	Mean decrease accuracy	Mean decrease Gini
Topographical wetness index (TWI)	100	93.2	158.6
Cation exchange capacity (CEC)	79	79.9	128.1
Mean coldest month temperature (MCMT)	67	67.7	70.8
Wind exposition	59	64.0	78.5
Organic matter	23	33.7	56.4
Mean annual precipitation (MAP)	18	31.1	47.9
Temperature difference (TD) - continentality	9	26.1	23.1
Direct insolation	0	16.4	47.2

Note: Variable importance of environmental and soil predictors: Importance values are scaled to 100% for the most influential predictors. Accuracy decrease represents the reduction in predictive accuracy when a variable is permuted, while Gini decrease indicates the reduction in node impurity (a measure of how mixed the classes are within a node of a decision tree) achieved when the variable is used for splitting in RF trees.

Accumulated local effects of predictor variables

Accumulated local effects (ALEs) plots revealed how each predictor influenced the predicted probability of sugar maple presence–absence, highlighting nonlinear relationships and thresholds-like responses across environmental gradients (Fig. 3). TWI, the most influential predictor, showed a nonlinear effect, with optimal suitability at intermediate values and a sharp decline above 8. Soil fertility was a key driver: cation exchange capacity had a positive effect with values above 2.9 cmolc·kg^{-1}, while organic matter values showed positive effect within the range of 8% and 12%. Climate variables also played a strong role. Mean coldest month temperature showed strong negative response, with increasing negative effect on suitability as temperatures fall below approximately −15°C. Similarly, temperature difference (continentality) had its strongest negative impact below 36.7°C. Wind exposition was positively associated with suitability for values above 1. Direct insolation also showed a nonlinear U-shaped response, with maximum positive effects around 1300 and 1500 MJ·m^{-2}·year^{-1}, and minimum around 1400 MJ·m^{-2}·year^{-1}.

Projected shifts in habitat suitability

Under the SSP3–7.0 2021–2040 climate scenario, our model projected a net increase in suitable habitat for sugar maple across the study area (Fig. 2C). The landscape was predicted to undergo dynamic changes, with gains in suitable habitat significantly outweighing losses.

A direct comparison of predicted current and future suitability showed that 15.7% of the study area is projected to become newly suitable (Gain), while only 3.3% of the area is projected to become newly unsuitable (Loss). Most of the landscape was expected to remain stable, with 56.1% remaining unsuitable and 24.9% remaining suitable.

A more detailed analysis incorporating observed species presence provides a nuanced view of these shifts (Fig. 4, see Appendix SB, Table B.2 for representation in a table). The results indicated that the

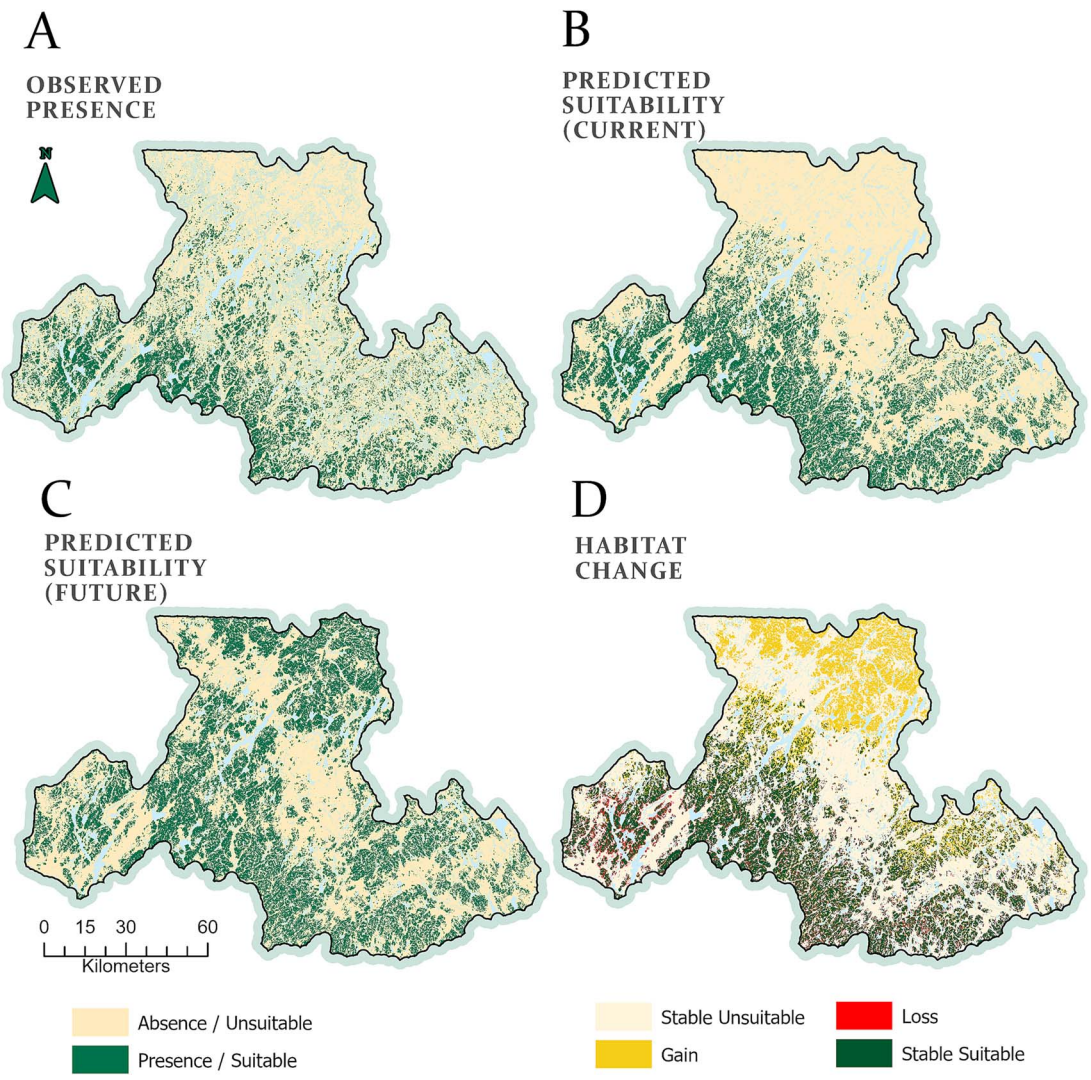

Figure 2 Visual summary of the habitat suitability modeling for sugar maple. Panel (A) shows the observed presence distribution of the species. Panel (B) shows the habitat suitability predicted by the model for current climatic conditions. Panel (C) shows the habitat suitability predicted for the future scenario (SSP3–7.0 2021–2040). Panel (D) synthesizes the projected changes, highlighting areas of habitat gain, loss, and stability.

largest single projected change is Habitat Expansion, where currently unoccupied and unsuitable sites are predicted to become suitable, accounting for 13.7% of the landscape. In contrast, Habitat Retraction, where currently occupied and suitable sites were predicted to become unsuitable, was projected for only 1.7% of the area.

A significant portion of the landscape (14.9%) was classified as stable "Core Habitat" (sites that are currently occupied and predicted to remain suitable). Furthermore, 10.0% of the study area was identified as "Stable Suitable," i.e. suitable under both current and future scenarios but lacks observed species presence. When combined with the 51.1% of Stable Unsuitable sites, these results indicated that ~80% of the landscape remains stable, either as persistently suitable or persistently unsuitable.

Discussion

Current suitable habitat for sugar maple

Our model successfully identified currently suitable habitats for sugar maple with a high degree of accuracy (AUC = 0.868), confirming that a combination of topographic, edaphic, and climatic factors can effectively delineate the species' niche at its northern range limit. The high performance of the model, validated with a spatially independent test set, provides confidence in the subsequent analyses of habitat drivers and future shifts. We observed locations predicted as unsuitable despite isolated presence occurrences in FRI map and, conversely, some locations predicted as suitable where sugar maple was not observed. This suggests that potentially suitable sites may exist beyond current sugar maple presence in the studied landscape, offering opportunities for species introduction or colonization, although this does not necessarily indicate expansion capability due to factors such as dispersal ability, abundance of colonizing species, nature of fragmented landscapes (Iverson et al. 2005), which were beyond the scope of our study. Also, competition with other species may be excluding sugar maple at some sites (Putnam and Reich 2017).

A key methodological insight was the persistence of significant spatial autocorrelation in model residuals (Moran's I = 0.19, $P < .001$), indicating that broad-scale patterns were largely explained by environmental predictors, yet fine-scale variation remains influenced by

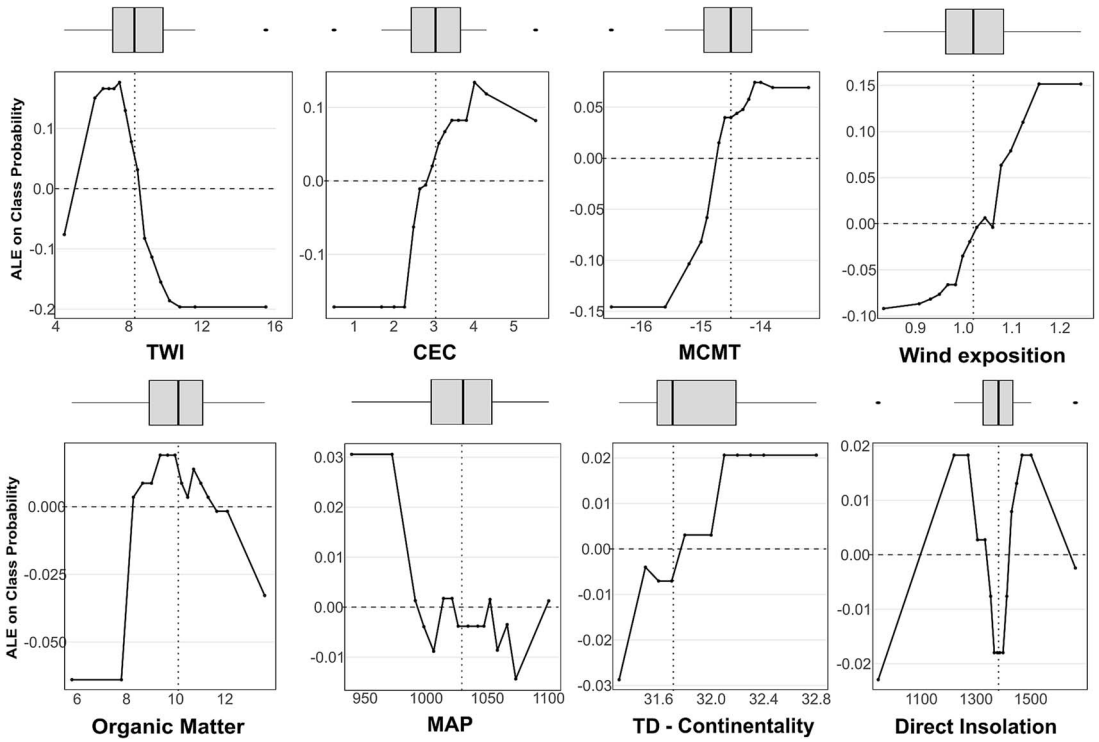

Figure 3 Accumulated local effects plots for the eight predictor variables used in the final RF model. Each plot illustrates the marginal effect of a single variable on the predicted probability of sugar maple presence. The *y*-axis represents the change in the predicted probability from the average prediction. For continuous variables, a box plot of the variable's distribution is shown at the top, and a vertical dashed line indicates the median value. Predictor variables are: TWI (topographic wetness index), CEC (cation exchange capacity *(cmolc·kg*$^{-1}$), MCMT (mean coldest month temperature in °C), wind exposition (index), organic matter (%), MAP (mean annual precipitation), TD (continentality in °C), direct insolation (MJ·m^{-2}·year^{-1}).

unmeasured factors, likely biotic interactions or micro-environmental conditions (Park and Talbot 2018). LISA analysis corroborated this, revealing local clusters of error that highlight the limits of purely abiotic models in capturing species distribution complexity (Carteron et al. 2020). Residual spatial autocorrelation is expected when spatially structured environmental variables or biotic processes are not explicitly modeled, and cannot be entirely removed unless spatial terms as coordinates are included in the model (Legendre and Legendre 2012, Dale and Fortin 2014).

Drivers of habitat suitability at the northern range limit

Our analysis revealed that sugar maple's distribution at its northern limit is not governed by a single dominant factor, but by a complex interplay of climate, topography, and soil. The emergence of MCMT as an important predictor aligns with the established ecological principle that absolute winter minimums are a primary physiological constraint at a species' cold-range edge (Nguyen et al. 2019). However, the influence of temperature extends far beyond broad climatic patterns. The high importance of several topographic variables suggests they act as mediators of the "effective temperature" and moisture conditions experienced by individual trees. This can be best understood along a habitat toposequence from hilltop to valley bottom. More broadly, previous research demonstrates that sugar maple performance is shaped by the interaction of winter climate, soil chemistry, and biotic context. Snowpack insulation, soil base cation availability, and mycorrhizal associations have all been identified as key constraints near the temperate–boreal boundary (Reinmann et al. 2019, Carteron et al. 2020, Tourville et al. 2023). Competitive dynamics with boreal species and American beech can further influence establishment success (St-Jean et al. 2021, Leduc et al. 2024). Our results align with this framework but demonstrate that these constraints are spatially structured along fine-scale terrain gradients.

At the upper end of this toposequence, on ridges and hilltops, the model's preference for sites with high wind exposition and low TWI reflects a critical survival trade-off. High exposure is beneficial because it prevents the pooling of damaging cold air, a major source of mortality in valleys (Fisichelli et al. 2014, Macek et al. 2019). However, this same wind exposure scours away snow. A thin snowpack offers poor insulation against soil freezing but may also reduce damage from subnivean rodents while increasing browsing risk from large herbivores that can more easily access seedlings (Sanders-DeMott et al. 2018). The model's selection of these sites suggests that, at the coldest limits, avoiding lethal air temperatures in frost pockets is a more critical survival filter than the complex pressures of herbivory and soil freezing on exposed ridges.

Moving down to the mid-slopes, the balance of factors shifts. These positions are sheltered enough to accumulate a deeper, more persistent snowpack. This insulating layer is fundamentally important for sugar maple survival, as it protects shallow roots from deep soil freezing, a primary cause of fine root mortality and increased vulnerability to stress (Reinmann et al. 2019). Finally, the model's strong aversion to sites with high TWI reflects the unsuitability of valley bottoms, which suffer from both the accumulation of cold air and poorly drained, physiologically stressful soils.

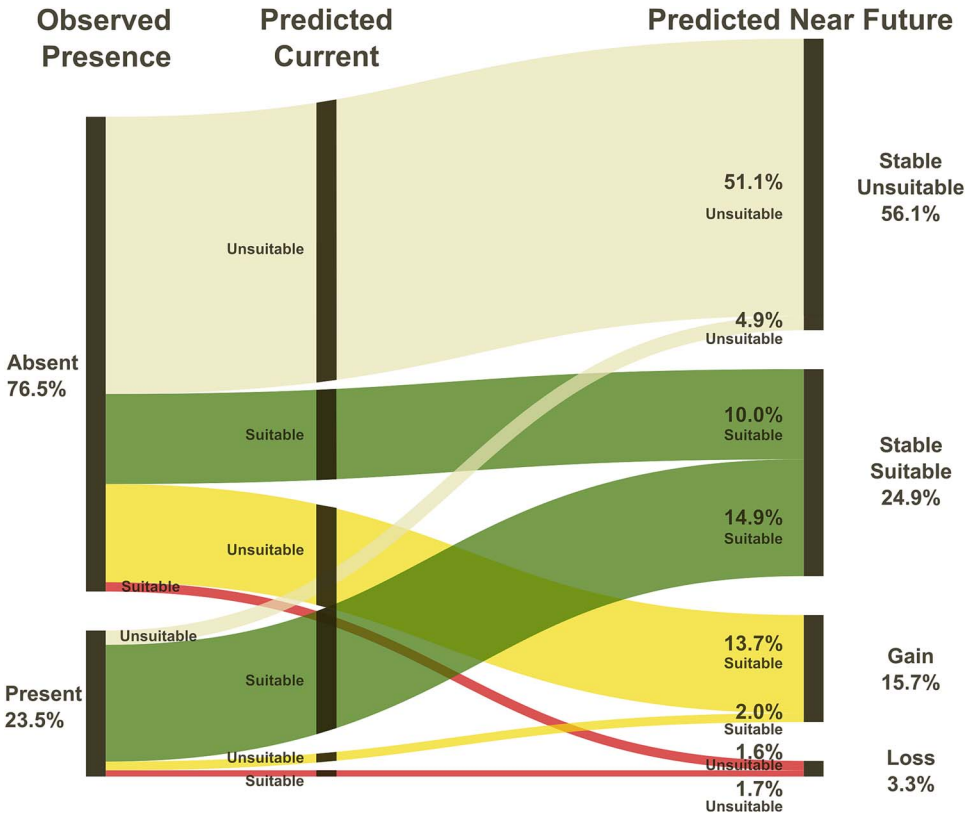

Figure 4 Habitat shifts categorized by the observed presence and absence of sugar maple in the study area located in Quebec, Canada, expressed as a percentage of the study area under the simulation scenario. Habitat shifts are classified into four categories: loss, stable unsuitable (retention), stable suitable (retention), and gain. The observed presence and absence are represented by two vertical axes in the left part of the figure, which are the origin of the 100% of the study area that is further subdivided. Changes in habitat suitability are described in terms of habitats remaining or becoming suitable or unsuitable for both currently occupied and unoccupied sites considering current and near future predictions.

Looking forward, the stability of these topographically defined microhabitats is threatened by the increasing frequency of extreme weather events (Moreau et al. 2020). Warmer winters are projected to lead to more frequent freeze–thaw cycles, which can cause significant damage to fine roots even under an insulating snowpack (Sanders-DeMott et al. 2018). An increase in late spring frosts following an earlier leaf-out could also cause widespread canopy damage. Therefore, even sites that are topographically favorable today may become more vulnerable in the future due to these novel climatic stresses.

Ultimately, this entire system of microclimatic trade-offs is built upon a foundation of soil fertility. The consistent importance of CEC and organic matter demonstrates that even a perfect topographic position is insufficient if the underlying soil is too poor to support the species' growth (St Clair et al. 2008, Bal et al. 2015). While the soil conditions in our study area are generally poorer than those in the species' core range (see Long et al. 2019), this likely reflects a strategy of occupying the best "locally available" sites to withstand the combined pressures of climate and competition. At its northern limit, sugar maple is likely restricted to these locally optimal sites, allowing it to persist in a landscape where it is otherwise at a competitive disadvantage against boreal-adapted species (Collin et al. 2018). The ideal habitat is therefore a site that occupies a specific niche in the toposequence, one that balances the risks of cold air, soil freezing, and herbivory, all while being located on one of the landscape's limited patches of sufficiently fertile soil.

Projected shifts in habitat suitability and management implications

Our final objective was to project habitat shifts under a near-future climate scenario. The model predicted a net increase in suitable habitat of over 14% by 2040, with habitat gains (15.7%) far exceeding losses (3.3%). This finding is consistent with broader continental-scale models that predict a northward expansion of suitable habitat for temperate species (Iverson et al. 2019, Prasad et al. 2020). However, the key contribution of our fine-scale approach is revealing the spatial complexity of this transition. The projected gains do not form a simple, advancing front but rather a heterogeneous mosaic of new suitable patches within the existing boreal landscape (Fig. 2D). This pattern underscores that the projected transition is not a generalized or linear northward shift, but a spatially complex process shaped by changes in climatic conditions and modulated by persistent landscape features such as topography and soil conditions.

The primary climatic driver of habitat gain appears to be the projected increase in winter temperatures (ΔMCMT = +1.7°C), coupled with a substantial increase in precipitation (ΔMAP = +136 mm) in those areas. This combination alleviates the primary cold-stress limitations while providing sufficient moisture to support growth. In contrast, the small pockets of habitat loss (3.3%) are not occurring in the warmest sites, but rather in locations that are currently the driest (MAP <984 mm) and are projected to receive the smallest increase in future precipitation relative to their temperature increase. This

suggests that habitat loss is not driven by excessive heat, but rather by increasing moisture deficits and drought stress (see Appendix SB, Table B.3 for mean climate values by shift category).

This complex pattern of gains and losses presents a significant management opportunity. The dynamics of overlapping boreal and temperate habitats are expected to lead to transitions in forest types, especially after disturbances (Fisichelli et al. 2014, Brice et al. 2020). By identifying precisely where boreal sites are likely to become suitable for sugar maple, our work provides a foundational roadmap for proactive climate adaptation measures in forest management, as proposed by Aquilué et al. (2020) and Fremout et al. (2020). Therefore, managers can use these predictions to guide the establishment of future-adapted, resilient forests that can continue to provide ecosystem services.

These findings have direct implications for guiding strategies like assisted migration. The "Gain, Unoccupied" zones (13.7%) and the "Stable Suitable, Unoccupied" zones (10.0%) together represent over 24% of the study area. These are the primary areas where management actions can be targeted to accelerate the establishment of sugar maple, a species well adapted to the prevailing temperate conditions at these sites. Such a strategy may help prevent a potential "maladaptation lag," a process that typically unfolds over longer temporal scales, whereby boreal species are no longer suited to the climate, but their temperate successors have not yet colonized (Fisichelli et al. 2014, Brice et al. 2020). However, as maladaptation and species turnover operate over decadal timescales, proactive interventions such as assisted migration also require careful monitoring, as future climatic trajectories and biotic interactions may influence long-term outcomes.

Our abiotic map may be seen as necessary first step towards overcoming non-climatic barriers to sugar maple's occurrence in the studied landscape. These include limited genetic variability in northern populations, which can increase vulnerability to late frosts and pests (Graignic et al. 2018, Gunter et al. 2000; Nolet and Kneeshaw 2018); the strong dependence on specific mycorrhizal associations (Lankau et al. 2015); biotic resistance from established boreal communities (Carteron et al. 2020); and seed predation (Brown and Vellend 2014). Therefore, our work opens the door for the next phase of research: field trials and soil analyses within these predicted suitable zones to understand and overcome these biotic constraints. Understanding how sugar maple naturally expands (or fails to expand) within these areas will also help clarify whether natural regeneration alone is sufficient, or if silvicultural interventions are essential to match the pace of habitat creation (Brown and Vellend 2014, Carteron et al. 2020).

Methodological considerations and model limitations

While our approach provides a robust assessment of sugar maple habitat, it is important to acknowledge the limitations inherent in the data and modeling process. The model's tendency toward overprediction, reflected in the lower user's accuracy for presences (40.3%) and the gap between observed (17%) and predicted (36%) prevalence, is an expected outcome of two compounding methodological factors. First, the down-sampling strategy applied within each spatial fold calibrates the model toward equal class prevalence during training, which is known to inflate predicted prevalence when applied to imbalanced real-world distributions (Valavi et al. 2022). Second, TSS-based threshold optimization is mathematically equivalent to the sensitivity–specificity sum maximizer criterion, which inherently prioritizes sensitivity over precision, a behavior that is amplified under low prevalence conditions (Jiménez-Valverde and Lobo 2007). While this results in a higher rate of false positives, it minimizes omission errors, which in conservation and management contexts carry higher ecological costs than commission errors: failing to identify a suitable site represents a missed opportunity for intervention, whereas a false positive simply warrants field verification (Fielding and Bell 1997, Jiménez-Valverde and Lobo 2007). In a context where the primary goal is to identify candidate sites for assisted migration, this tradeoff is therefore considered acceptable and methodologically defensible.

Beyond the modeling strategy itself, the quality of the input data also introduces uncertainty. The soil and climate predictor variables were not direct measurements at every site but were derived from models. The soil maps are based on spatial interpolations from field surveys, and the climate data are downscaled from models of weather station data. Therefore, the relationships identified by our model, particularly for soil properties, should be interpreted as strong ecological trends rather than precise quantitative thresholds (Walthert and Meier 2017). In contrast, a key strength of our study is that the topographic variables were derived from high-resolution LiDAR data, providing a fine-scale, accurate measurement of the landscape features that strongly influence microclimate.

A central challenge in this study was addressing spatial autocorrelation. Although environmental predictors explained most of the spatial variance, significant residual spatial clustering persisted in the model's residuals. In ecological systems, such residual structure is expected, as not all spatially structured drivers or biotic processes can be measured or included (Legendre and Legendre 2012, Dale and Fortin 2014). We addressed this by implementing spatial blocking to ensure independence between training and testing data, thereby reducing inflation of model performance metrics. Residual spatial autocorrelation should, therefore, be interpreted as reflecting unmeasured fine-scale processes rather than a methodological flaw.

Finally, our model is correlative and does not explicitly simulate key ecological processes. This is particularly relevant to interpreting the observed mismatch between predicted suitable habitat and species presence. Biotic interactions (Dormann et al. 2018), such as competition from established boreal species or the presence of specific mycorrhizal partners, were not included but are known to be critical for establishment (Carteron et al. 2020, Chamard et al. 2024). The model also does not account for dispersal dynamics, meaning it predicts where habitat is suitable, not whether the species can reach it. Lastly, the model is calibrated for the environmental conditions at the northern range limit; the identified relationships may not be directly transferable to the core of the species' range where different factors may be limiting. Despite these limitations, the model provides a robust and spatially explicit assessment of abiotic habitat suitability, which is a first step for guiding targeted management decisions and framing the next generation of research questions on biotic interactions.

Conclusion

In this study, we successfully modeled and mapped suitable habitat for sugar maple at its northern range limit, identifying the key climatic, edaphic, and topographic factors that govern its distribution. The local expansion of sugar maple habitat appears to follow a topographic gradient, with suitability highest on hilltops and gradually decreasing toward valleys. Our findings reveal that habitat suitability is co-limited by winter temperature, soil fertility, and topographically mediated moisture. Projections indicate that climate change will create a

significant amount of new suitable habitat, not as a uniform wave, but as a complex spatial mosaic within the boreal landscape. This fine-scale prediction of where temperate species may persist or expand presents a clear opportunity for proactive management. Our work provides a spatially explicit tool for practitioners to guide the establishment of climate-resilient forests through targeted actions such as assisted migration, while highlighting the critical need for further research into the biotic factors that will mediate these transitions.

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Author contributions

João Paulo C. de Liz (Conceptualization, Formal analysis, Methodology, Writing—original draft), Nelson Thiffault (Supervision, Writing—review & editing), Nicholas C Coops (Supervision, Writing—review & editing), Alexandre Morin-Bernard (Writing—review & editing), and Alexis Achim (Conceptualization, Funding acquisition, Project administration, Supervision, Writing—review & editing).

Supplementary material

Supplementary material is available at *Forestry: An International Journal of Forest Research* online.

Conflicts of interest

None declared.

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Declaration of competing interest

The authors state that they have no financial interests or personal relationships that could have influenced the work presented in this paper.

Data availability

Raw data and R scripts are available at "https://github.com/metafor-ulaval/Fine-Scale_Drivers_of_Sugar_Maple"

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