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ARTICLE
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Integrating historical observations alters projections of eastern North American spruce–fir habitat under climate change

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Abstract

Spruce–fir (*Picea–Abies*) forests of the North American Acadian Forest Region are at risk of disappearing from the northeastern United States and Canada due to climate change. Species distribution models (SDMs) have been used to predict changes in this critical transitional ecosystem in the past, but none have addressed how seasonal patterns of temperature and precipitation interact to influence tree species abundance. Inferences have also been limited by contemporary inventory data that could not fully characterize species ranges because they either, (1) only sampled species occurrence after large-scale human disturbance and settlement, or (2) did not span critical geopolitical boundaries (e.g., the US–Canadian border) that intersect the focal species' range(s). Here, we built new SDM models to better assess the bioclimatic distribution of four spruce–fir species and to test the importance of seasonal climate interactions. We compiled an extensive database of tree occurrence and abundance from recent (~1955–2012) and historical time periods (1623–1869) to model current species distributions and to predict how these might change under future climate. We found that including historical tree data in our SDMs revealed previously unrecognized suitable habitat along the southern edge of species' contemporary ranges. Random forest models predicted occurrence with high accuracy (area under receiver operator curve >0.98), and the seasonal climate variables that emerged as most important for these cold-adapted species all included interactions that reflected sensitivity to colder temperatures, and preferences for wet weather concentrated in the winter months. Under moderate climate warming (representative concentration pathway 6.0), the northeastern United States retained additional suitable habitat when historical data were included through 2060 for three of the four species: red spruce (*Picea rubens*), black spruce (*Picea mariana*), and balsam fir (*Abies balsamea*), while white spruce (*Picea glauca*) habitat contracted into Canada. In contrast, future predictions from models that used contemporary data alone

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forecast extirpation for all four species from the northeastern United States. Overall, these findings highlight that prediction of species ranges in transitional ecosystems that span geopolitical boundaries and gradients of intense land use are improved when historical data and seasonal climate interactions of both temperature and precipitation variables are incorporated.

KEYWORDS
Abies balsamea, climate change, historical data, occurrence, *Picea glauca*, *Picea mariana*, *Picea rubens*, species distribution models, spruce–fir forest

INTRODUCTION

Tree species distributions are known to correlate with climate, but are also multifaceted and dynamic, depending on other factors including disturbance regimes (Franklin et al., 2016), patterns of resource availability, and human land use (Nowacki & Abrams, 2015). Although changes in any one of these factors can affect species distributions, the effects of climate change merit special attention as it is forcing ecosystems in ways that have no recent analog. To predict how the distribution of tree species will change with climate, we often look to evidence of past migration. Paleological examples indicate increases in temperature can shift species' geographic ranges poleward or upward in altitude (Harsch et al., 2009; Parmesan, 2006), although records also suggest that these dynamics historically played out over hundreds to thousands of years (Schauffler & Jacobson Jr., 2002). Evidence like this creates an expectation that tree species will migrate as the climate changes. Observations of more rapid responses to current global warming, however, have also shown stable or expanding species distributions (Foster & D'Amato, 2015), with some evidence suggesting that tree ranges have stayed stable or shifted on the order of 10s of kilometers in latitude or 10s of meters in altitude over recent decades (Woodall et al., 2018). These variable patterns of contemporary climate response highlight the need to better predict how tree species distributions will continue to shift in the future, the factors that influence these patterns, and possible quantification of underlying uncertainty.

Predicting the impacts of changing climate on trees species' distributions remains difficult, however, due to (1) interactions among climate and the other factors (e.g., disturbance), (2) weaknesses in existing data and models, and (3) trees' sessile growth habit (e.g., dispersal happens slowly across generations). The first two of these challenges can be addressed within the framework of statistical species distribution models (SDMs), also known as ecological niche or bioclimatic envelope models, though SDMs are unsuited to address effects of dispersal or competition associated with (3). Species distribution models are an empirically based approach that correlates the presence of species to climatic variables and assumes the best indicator of a species realized niche is its current distribution (Dyderski et al., 2018; Pearson & Dawson, 2003).

Uncertainty in predictions of species range from SDMs can arise from limitations in climate data, the empirical tree data, or the quantities being predicted. While evidence is growing that tree responses to climate depend on the interactive effects of temperature and precipitation (Foster & D'Amato, 2015; Parmesan, 2006), SDMs do not often consider climate interactions (Peters et al., 2020). In terms of empirical data, potential sources for SDMs vary from historical records from surveyors (Cogbill et al., 2002; Hanberry et al., 2012; Thompson et al., 2013), herbaria, museums, or atlases (Graham et al., 2008) to systematic national plot inventories (Dyderski et al., 2018; Guisan et al., 2007; Iverson et al., 2008; Rogers et al., 2017). Important spatial and temporal limitations can arise from any of these available data, but can be difficult to fully quantify or address. Spatially, national inventory data may be too coarse or have limited capacity to describe species that cross international boundaries (Prasad et al., 2020; Weiskittel et al., 2012). Temporally, intense historic anthropogenic disturbance has altered or reduced the distribution of certain forest species in North America, limiting how well contemporary inventories can describe true bioclimatic niches (Tinner et al., 2013). Once an empirical dataset is chosen, SDMs can be built on either presence/absence occurrence data (Elith et al., 2010; Rogers et al., 2017) or abundance variables (e.g., relative basal area [RBA]; Iverson et al., 2008). This choice of tree variable can affect predictions; abundance may better represent core habitat (Charney et al., 2021), while occurrence models may overpredict suitable habitat (Joyce & Rehfeldt, 2013), which may be a worthwhile risk for the conservation of endangered ecosystems (Ashcroft et al., 2017). How these choices affect models of species that occur at low abundance is not well quantified and reduces our ability to predict future species distributions to an unknown degree.

An appropriate model system to test these limitations would capture tree species ranges that span steep climatic gradients, cross geopolitical boundaries, and have a history of land-use change that could have disrupted the expression of realized niches. The Acadian Forest Region (AFR) is an example of a transitional ecosystem in eastern North America that spans the border between the United States and Canada. Projected future changes in climate show some of the most rapidly warming temperatures in the United States and globally (Gonzalez et al., 2018; Karmalkar & Bradley, 2017), including shrinking snow cover, more frequent droughts, and extended periods of low hydrological flows in the summer (Hayhoe et al., 2008). Of particular concern is the fate of the spruce–fir forest type, whose primary tree species, red spruce (*Picea rubens* Sarg.), black spruce (*Picea mariana* [Miller] B.S.P.), white spruce (*Picea glauca* [Moench] Voss), and balsam fir (*Abies balsamea* L.), prefer cooler and moister conditions. Previous SDMs have predicted range contraction of up to 400 km north (Iverson et al., 2008) and reduction of 97%–100% of suitable spruce–fir habitat in the United States in the next 100 years (Hansen et al., 2001). However, these previous efforts often relied on contemporary, US-only inventories that excluded habitat in Canada (Prasad et al., 2020) and may have suffered from obfuscation of past anthropogenic drivers (Foster & D'Amato, 2015; Wason & Dovciak, 2017).

Here, we report models that tested ways to reduce potential uncertainty in predictions of tree species range shifts associated with climate change by addressing the widespread spatial, temporal, and methodological limitations outlined above. For the AFR, we tested how prediction of tree species distributions changed when models were built from a spatially comprehensive dataset that included observations from both the United States and Canada, with and without historical observations, and whether modeling occurrence, likelihood, or abundance variables were comparable. Our specific objectives were to: (1) develop species-specific models of current distributions using contemporary data and climate interactions; (2) compare predictions when both contemporary and historical data were used; (3) evaluate different tree variables of occurrence or abundance; and (4) assess how prediction of future distributions varied based on these choices. Understanding the future dynamics of transitional ecosystems under climate change is critical for prioritizing conservation strategies by identifying future climate refugia (Morelli et al., 2016), as well as where adaptation strategies might mitigate impacts associated with shifts in ecosystem state (Toot et al., 2020).

MATERIALS AND METHODS

Study area

Our analysis focused on the AFR (Figure 1; Appendix S1: Figure S1), a broad ecoregion with diverse topography that spans 7° latitude and experiences correspondingly diverse climates. Much of the region lies at the boundary of the shifting polar front, where warm, wet subtropical systems meet subpolar maritime systems and dry, cold continental air masses. Temperatures ranged on average from −7.4 to 20°C (climate normal 1961–1990) and increased 0.37–0.43°C per decade between 1965 and 2005, with greater increases in the winter (Huntington et al., 2009; Appendix S1: Table S1). Annual precipitation averaged 1111 mm year^{-1}. Soils are mostly derived from glacial deposits that vary with elevation and latitude. We defined our study area by intentionally extending the area of analysis beyond the boundaries of the AFR to include most of the southern and northern extent of the focal species' ranges. We considered several of the most ecologically and economically important conifer species in the AFR; red spruce, black spruce, white spruce, and balsam fir. While the ranges of black spruce, white spruce, and balsam fir extend well into the Canadian taiga, where little tree data have been collected, for the purpose of this analysis, we assumed that characterizing the northern range edge was not necessary to describe species' distributions within the AFR.

Tree data

We gathered observations of tree species occurrence and size (dbh), from agencies in the United States and Canada for the study area. A threshold of 10 cm dbh and greater was used in this analysis since this was the most consistent minimum dbh for the majority of available data. Preliminary analysis performed using smaller dbh thresholds indicated only small changes in predictions of suitable habitat (Andrews, 2016). Specific details about the data protocols used by each organization are available in Andrews (2016) and Andrews et al. (2018). We selected four dependent variables including species occurrence (i.e., presence or absence on a plot) and three measures of relative abundance: relative stem density (RSD; trees ha^{-1}), RBA, and an importance value (IV; 50 × RBA + 50 × RSD), which combines proportional stem density and RBA as defined in Iverson et al. (2011) and scales from 0% to 100%.

Contemporary and historical tree data

We assembled 792,359 species occurrence observations from 248,821 plots to characterize the contemporary

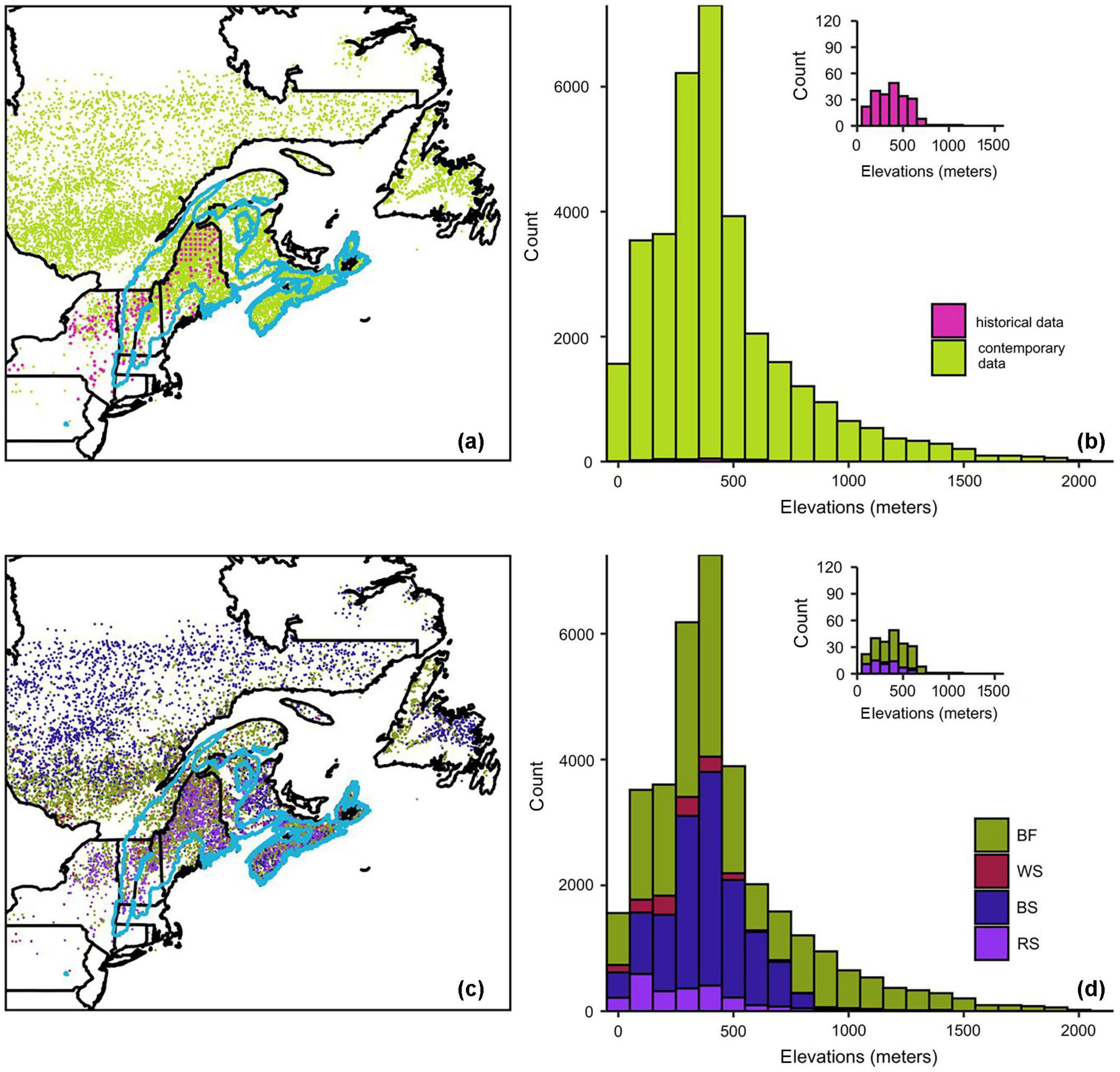

FIGURE 1 Maps and distributions of plots with spruce and fir used in this analysis. Panels (a) and (b) highlight the spatial differences between historical (pink) and contemporary (green) datasets. Panels (c) and (d) highlight species spatial differences. The inset in panel (d) shows the distribution of spruce–fir in the historical dataset, while the larger histogram describes the contemporary data. The histograms are the count of observations by elevation class for the historical and contemporary datasets (panel b) as well as by species (panel d). A more detailed map of the study area is provided in Appendix S1: Figure S1

distribution of species (Appendix S1: Table S2). The data were collected from 1955 to 2012, with the majority collected after 1980 (85%). We also accessed 1342 historical tree observations from 778 plots from a database developed by Cogbill (2000), as well as Thompson and Cogbill (2013), to characterize occurrence prior to widespread disturbance (abundance cannot be determined from these data; Appendix S1: Figure S2). These data were originally collected between 1623 and 1869 and represent tree composition at the time of European settlement in the New England states and New York, although they differ from systematic General Land Office survey data that were collected for areas settled northwest of the Ohio River. The land in our study area was surveyed at the time of division into 40–60 ha lots by proprietors, with the largest tree at the corner of each lot recorded as a demarcation boundary (Cogbill, 2000). Although sampling methods were often poorly documented, Cogbill (2000) considers these data to be representative of township scale (~16 × 16 km) composition at the time of collection (Cogbill et al., 2002). These data provided a unique opportunity to account for habitats and regions that may have historically supported spruce–fir prior to extirpation by land use or other factors.

Climate and topographic data

We used average climate data for 30-year climate normals (1961–1990) from the US Forest Service's Moscow Forest Science Laboratory database to characterize climate coincident with the majority of the plot data (http://charcoal.cnre.vt.edu/climate/future/details.php; Joyce & Rehfeldt, 2013). We considered 33 climatic variables (Appendix S1: Table S1), 16 of which directly measure climate, while the remaining 17 were second-order interactions found useful in prior analyses (Joyce & Rehfeldt, 2013). We also compiled available climate data from Oregon State University's PRISM Climate Group (https://prism.oregonstate.edu/) and computed 30-year climate normals for 1895–1925 to identify any broad-scale climate differences coincident with the historic tree observations. In general, we observed a similar distribution between the contemporary and historical climate normals for the primary variables (Appendix S1: Figure S3), which is likely because of the difficulty of high-resolution climate reconstruction. Consequently, we assumed that the historic tree data could be linked with the contemporary climate variables (Appendix S1: Table S1) alongside the contemporary tree data, which allowed both datasets to consistently inform our models and projections without additional potential uncertainty due to the derivation of climate normals.

We also included topographic variables to capture additional biophysical effects related to soil drainage, exposure, and solar radiation. We determined elevation, slope, and aspect from plot records, or otherwise extracted them from a 30-m digital elevation model (DEM) (NED raster package [Hijmans, 2020] R statistical software [R Core Team, 2019]). We transformed aspect to a measure of northness and eastness using the Beers transformation, which was sin ([aspect + 45] × π/180) + 1 (Beers et al., 1966). We derived five topographic indices using the DEM and the System for Automated Geoscientific Analyses (Brenning, 2008): topographic wetness, convergence, terrain, topographic openness, and site curvature indices.

Species-specific distribution model development

We developed species-specific distribution models for occurrence and the three abundance variables using the random forest package for R (Breimen & Cutler, 2012). Species-specific occurrence models were constructed with and without historical tree data. Random forest models create classification or regression trees with the former being useful for presence/absence occurrence data (Elith et al., 2010; Guisan et al., 2007) and the latter when modeling abundance (e.g., Iverson et al., 2008). The random for- est algorithm relies on equal representation across classes for accurate prediction (Joyce & Rehfeldt, 2013). To accommodate this, we randomly subset absence observations to represent ~50% of data in the occurrence models and 20% in the abundance regression models. Half of the absence data were sampled from areas determined to be climatically similar, and half dissimilar, similar to Joyce and Rehfeldt (2013). In addition, we increased the prevalence of presence or abundance observations by doubling their number as recommended by Pearson and Dawson (2003).

To determine which environmental predictors were most important, we ran five preliminary random forests consisting of 500 trees for each dataset. We determined the most important variables using the VarImp function; then, we refit final models using the five most important variables in a random forest with 500 trees. For consistency, we used the contemporary climate normals for both the contemporary and historical occurrence observations since preliminary analysis indicated similar model fits (Appendix S1: Table S4) and predictive behavior (Appendix S1: Figures S3 and S4) as models trained using the historical climate normals.

Model evaluation and comparison

We evaluated occurrence models using the area under receiver operator curve (AUC) and out-of-bag (OOB) error. We used mean square error and pseudo-R^2 to evaluate regression models of abundance. In addition, we used kappa values to compare predictions of current distribution against actual distribution (Visser & Nijs, 2006). Kappa values range from −1 to 1, with 1 representing perfect agreement in the distribution of categories between two maps. To calculate kappa, we divided the abundance values into eight equal categories based on the observed data (i.e., quantiles) and compared the resulting categorical maps. We considered the likelihood of occurrence output to see whether it could act as a proxy for abundance by correlating it with predicted basal area using Spearman's nonparametric rank correlation coefficient (ρ).

Predictive mapping

We mapped predicted future distributions for each species using the predict function of the random forest package. Mapped predictions were produced with 0.00833°

(~1 km^2) rasters of the five model-selected climate variables as they varied under future climate scenarios, for the years 2030, 2060, and 2090, although we focus our discussion of results on predictions for 2060 for brevity. Predicted climate rasters were an ensemble mean of each variable generated from various global circulation models (GCMs) under the representative concentration pathway 6.0 (RCP 6.0) scenario (Taylor et al., 2012), which is a moderate forcing scenario. The GCMs used included: (1) Community Earth System Model (CCSM4); (2) Geophysical Fluid Dynamics Laboratory (GFDLCM3); (3) Hadley Meteorological Office (HadGEM2ES); (4) National Center for Atmospheric Research/University Corporation for Atmospheric Research (CESM1BGC); and (5) Centre National de Recherches Météorologiques (CNRMCM5).

RESULTS

Tree data

Balsam fir, black, white, and red spruce occurred in 15%, 9%, 7%, and 4% of plots, respectively (Figure 1). Absence data accounted for 80% of observations and 65% of plots, a majority of which arose from the US Forest Service (USFS) Forest Inventory & Analysis (FIA) data (96%), while most spruce–fir presence data originated from non-FIA sources (97%). The distributions of plot-level RBA, RSD, and IV for white spruce, red spruce, and balsam fir all followed descending monotonic curves. Among plots where it occurred, black spruce RBA exhibited a flat to u-shaped beta distribution with higher concentrations near zero and one, demonstrating a tendency to high dominance and monospecific stands. Relative abundances were higher overall for balsam fir and black spruce, and lower for white and red spruce (Table 1). The addition of historical tree data provided 321, 5, 33, and 544 plots, respectively, to the balsam fir, white spruce, black spruce, and red spruce occurrence data.

Model performance

Random forest classification models were able to predict species occurrence with high accuracy according to AUC values, while also maintaining high sensitivity and specificity (Table 2). All AUC values were greater than or equal to 0.98 (Table 2). Sensitivity, or the percentage of true occurrences that models predicted correctly, ranged from 98.8% (balsam fir) to 99.5% (black spruce) and specificity ranged from 91.0% (black spruce) to 95.2% (red spruce). Occurrence models produced with additional historical data did not differ in accuracy from models built on only contemporary data in regard to OOB error and AUC (Table 2; Appendix S1: Table S4) or kappa statistics (Appendix S1: Table S5). The predictive variables selected remained the same, although their importance rank was altered (Table 2).

For species abundance metrics, random forest regression models that predicted RBA performed slightly better than models of RSD or IV, but all models tended to underpredict absolute abundance values, on average (Appendix S1: Table S5). The average percent difference between the actual and predicted means among abundance variables was 39.5%, 43.6%, and 40.5% for RBA, RSD, and IV, respectively. As often occurs, random forest models were better at detecting mid-range abundance values, but overestimated low abundance and underestimated high abundance.

Current species' distributions predicted from contemporary data

Maps of predicted species occurrence were able to accurately capture recent species presence, with some overprediction (Figure 2a–d). Occurrence maps showed strong spatial agreement between observed and predicted species occurrence (Appendix S1: Figure S6), with kappa

TABLE 1 Statistics of occurrence and abundance (relative basal area [RBA], relative stem density [RSD], and importance value [IV]) by species

	RBA (0–1)		RSD (0–1)		IV (0–100)[a]		
Species	Mean	SD	Mean	SD	Mean	SD	Occurrence (%)[b]
Balsam fir	0.31	0.27	0.39	0.30	33.84	27.09	15.4 (23.4)
White spruce	0.17	0.21	0.17	0.23	16.65	20.39	6.6 (0.36)
Black spruce	0.51	0.37	0.52	0.36	51.47	36.32	9.1 (2.4)
Red spruce	0.21	0.34	0.33	0.22	22.56	22.69	4.1 (39.6)

Note: For abundance measures, the mean and SD across plots where each species occurred, while occurrence is the percentage of plots where the species was observed for both the full and historical (in parentheses) datasets.

[a] Computed as 50 × RBA + 50 × RSD.

[b] Percentage of plots where the species occurred.

TABLE 2 Results of random forest analyses of occurrence with and without historical data for each species

Species	Prevalence ratio	OOB error	Specificity	Sensitivity	AUC	Top five variables[a]
Occurrence without historical data						
Balsam fir	55:20:25	3.30	94.08	98.84	0.99	PRDD5, MAPMTCM, PRMTCM, MAPDD5, GSPMTCM
White spruce	50:25:25	4.09	92.40	99.41	0.98	PRDD5, PRMTCM, MAPMTCM, MAPDD5, GSPMTCM
Black spruce	55:20:25	4.32	91.01	99.49	0.99	MAPDD5, PRMTCM, PRDD5, GSPMTCM, MAPMTCM
Red spruce	40:40:20	3.15	95.17	99.37	0.99	PRDD5, MAPDD5, PRMTCM, MAPMTCM, GSPMTCM
Occurrence with historical data						
Balsam fir	55:20:25	3.29	94.04	98.89	0.99	PRDD5, MAPMTCM, PRMTCM, GSPMTCM, MAPDD5
White spruce	50:25:25	4.05	92.52	99.38	0.98	PRDD5, MAPMTCM, PRMTCM, MAPDD5, GSPMTCM
Black spruce	55:20:25	4.20	91.26	99.52	0.99	PRMTCM, MAPDD5, PRDD5, MAPMTCM, GSPMTCM
Red spruce	40:40:20	3.32	94.93	99.31	0.99	PRDD5, PRMTCM, MAPMTCM, MAPDD5, GSPMTCM

Note: The prevalence ratio is a ratio of presence to the absence sample from within the hypervolume (HV) to an absence sample from outside the HV. Abbreviations: AUC, area under receiver operator curve; OOB, out-of-bagerror.

[a] GSP = growing season (April–September) precipitation; MAP = mean annual precipitation (mm); DD5 = annual days above 5° C based on mean monthly temperature (days × degree Celsius); MTCM = mean temperature in the coldest month; PRDD5 = PRATIO × DD5; PRATIO = GSP/MAP; MAPMTCM = mean annual precipitation × mean temperature in the coldest month, scaled; PRMTCM = growing season precipitation/mean annual precipitation × mean temperature in the coldest month; MAPDD5 = mean annual precipitation × annual days above 5°C based on mean monthly temperature, scaled; GSPMTCM = growing season precipitation × mean temperature of coldest month, scaled.

values ranging from 0.77 for black spruce models to 0.80–0.83 for red and white spruce and balsam fir (Appendix S1: Table S5). The white spruce model overpredicted presence in interior New Brunswick, but captured populations in northern New England into Canada and along the coast (Figure 2). Despite a lower kappa statistic, the black spruce model captured distinct populations in northern Maine, along the coast, and in the northern Adirondacks. The red spruce model showed a well-defined range that captured extant populations in the Central Appalachians. The balsam fir model was able to capture the wide range of this species. When historical data were included in models based on current climate, small patches of additional habitat were revealed, while the overall habitat distribution remained similar to models built on contemporary data alone. Additional areas included southern New Hampshire and western Massachusetts for balsam fir, eastern New York for white spruce, and southeast Massachusetts and Connecticut for red spruce (Figure 2a–d, in pink).

The maps of predicted abundance tended to underestimate abundance in almost all of the models (Figure 3a–d; Appendix S1: Figures S7 and S8). While exact values were incorrectly estimated, the models were able to capture the cline from lesser to greater abundance, particularly for the RBA and IV models. Black spruce maps presented the most accurate patterns of abundance, representing populations in Québec and along the coasts of eastern New Brunswick, Nova Scotia, and Newfoundland. When likelihood of occurrence was evaluated, spatial similarity for all species was found between current core areas of abundance (i.e., the 75th percentile of predicted RBA, Figure 3a–d) and the likelihood output (Figure 3e–h; Appendix S1: Figure S9).

Future predictions of species' distributions

Maps of species occurrence for the year 2060 show potential shifts of suitable habitat to the north and east, significantly reducing potential habitat for these species in the United States (Figure 2e–l). In 2060, white spruce habitat is projected to disappear completely from the northeastern United States, while persisting in the Canadian AFR in northern New Brunswick, the Gaspe Peninsula, and Cape Breton Island, Nova Scotia. Balsam fir and red spruce habitat persist in patches in Maine, New Hampshire, and the Adirondacks in the United States, as well as the northern and coastal highlands of New Brunswick and Cape Breton Island in Canada. Losses in the United States are met with modest gains to the north for balsam fir and white spruce, and to the northeast for red spruce. Black spruce is likely to occupy regions past the northern extent of the study area used in this analysis. By 2090, balsam fir and white spruce have the greatest area of potential suitable habitat available (Table 3). All species lose area by 2090, however, when compared to current predicted suitable habitat (Appendix S1: Figure S10). Balsam fir (48%) and black spruce (73%) lose the most area, while white and red spruce only experience reductions of 31% and 21% of suitable habitat.

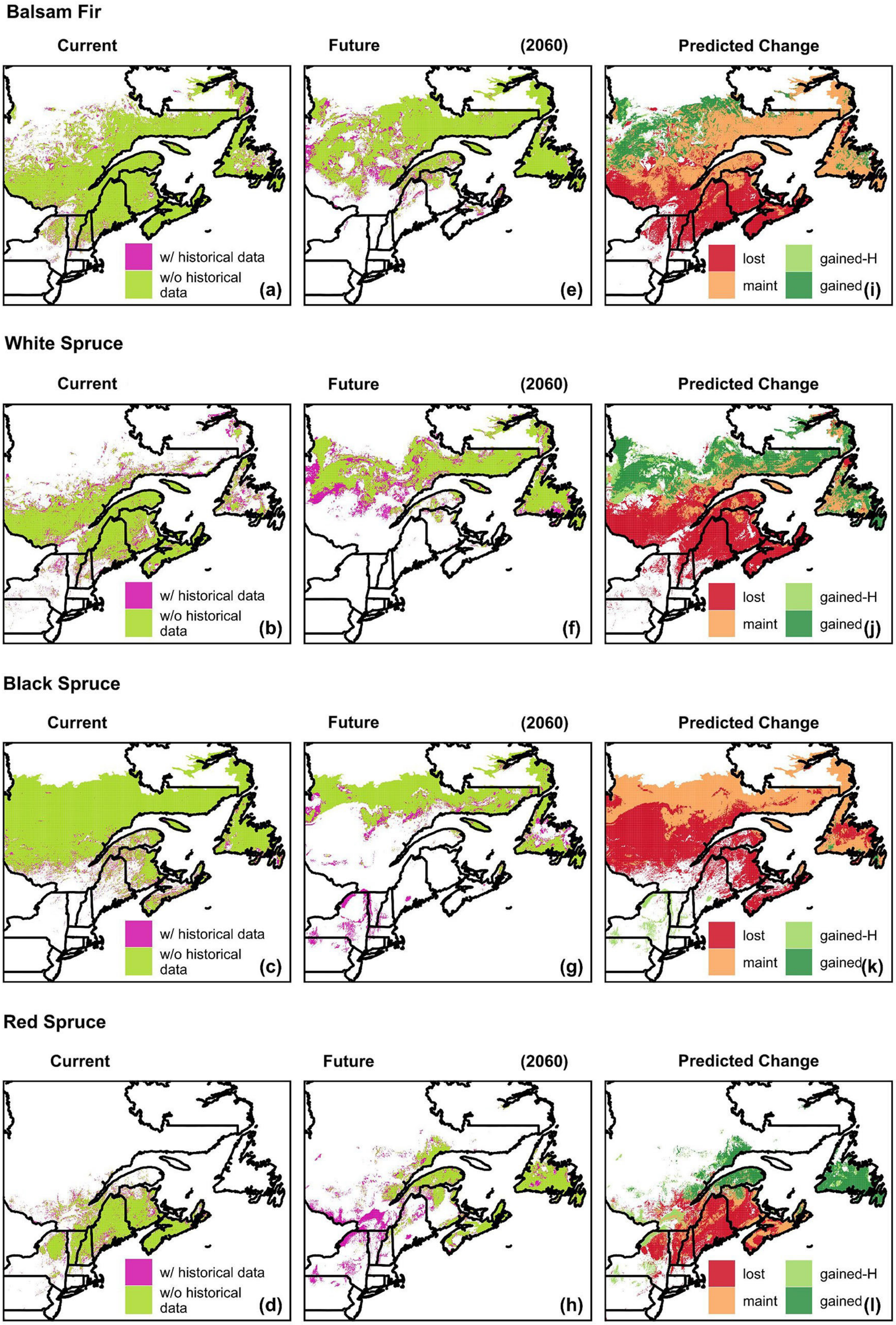

FIGURE 2 Predicted occurrence under current climate normals based on data from 1961 to 1990 (a–d), future occurrence in 2060 (e–h), and change between present and future (i–l) for each species. Occurrence was predicted with and without additional historical data. Additional area predicted as suitable habitat is represented by pink (a–h) and by light green (i–l). "maint" and "gained-H" are suitable habitat maintained or gained with inclusion of historical data (i–l)

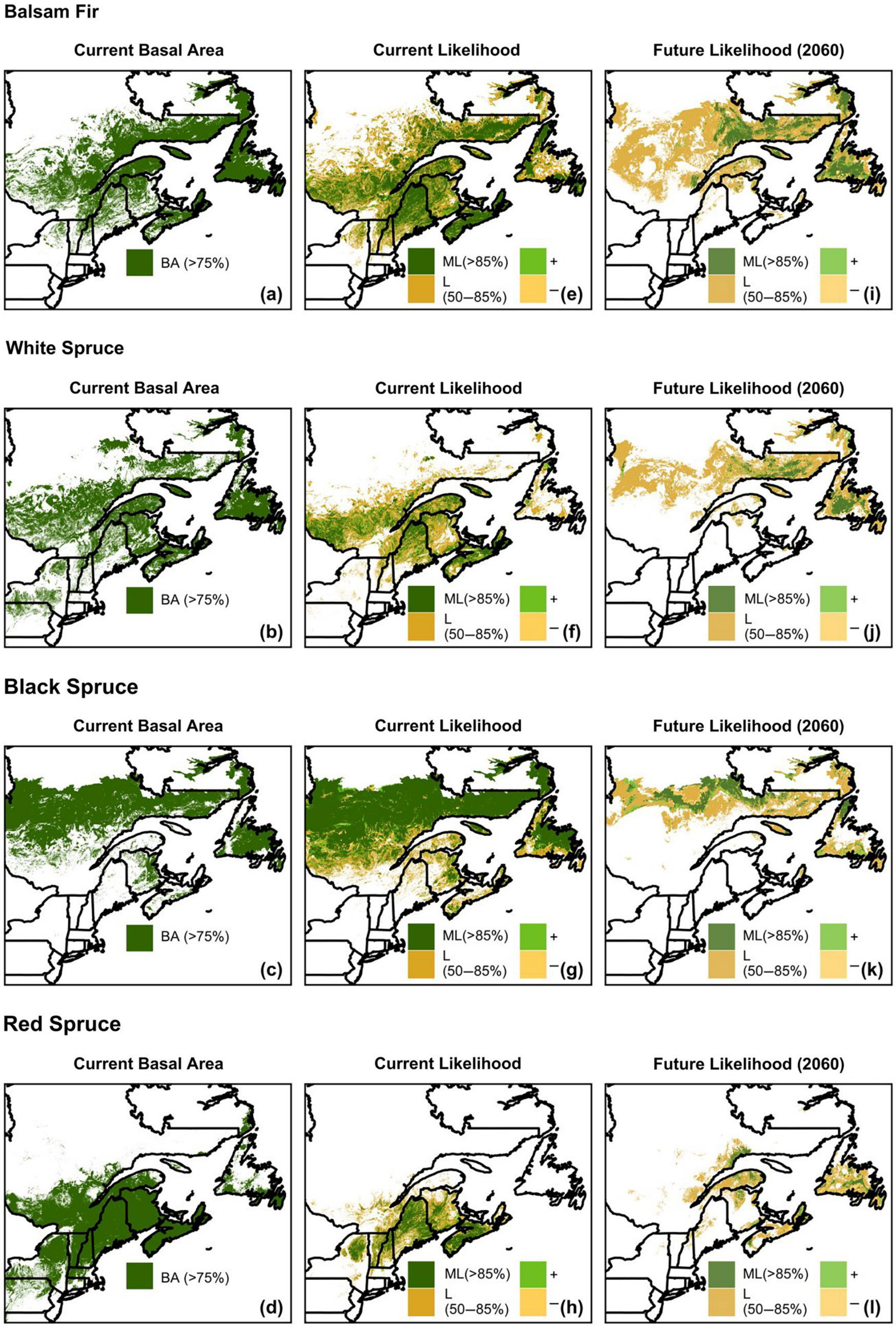

FIGURE 3 Predicted current basal area (BA; a–d), likelihood (e–h), and future likelihood (i–l) for spruce and fir species. Only current predicted basal area greater than the relative 75th quantile is shown to highlight core areas of abundance. For the likelihood figures (e–l), areas that are "most likely" (ML, >85% of votes) are shown in dark green and "likely" (L, between 50% and 85% of votes) in yellow. Light green (+) indicates that with the inclusion of historical data, areas switched from likely to most likely. Light yellow (−) indicates a switch from most likely to likely

TABLE 3 Area (thousands of km²) potentially occupied by each species under the presence/absence models with and without the historical data (percentage change from current area indicated by values in parentheses)

	Occurrence model with only contemporary data				Occurrence model with contemporary and historical data			
Species	Current	2030	2060	2090	Current	2030	2060	2090
Balsam fir	1521	1302 (−14.4)	1142 (−24.9)	791 (−48.0)	1523	1370 (−10.1)	1220 (−19.9)	870 (−42.9)
White spruce	971	941 (−3.1)	815 (−16.1)	668 (−31.2)	950	946 (−0.4)	867 (−8.7)	713 (−24.9)
Black spruce	1604	1005 (−37.3)	753 (−53.1)	434 (−72.9)	1617	1033 (−36.1)	817 (−49.5)	506 (−68.7)
Red spruce	495	469 (−5.3)	401 (−19.0)	391 (−21.0)	504	525 (4.2)	518 (2.8)	578 (14.7)

Models that included historical tree data produced significant differences in predicted future habitat for all four species, (Figure 2e–l, Table 3; Appendix S1: Figure S5), identifying 198,557 and 236,446 km² of additional suitable habitat for red and black spruce, respectively. Without the addition of historical data, these species were predicted to be extirpated from the United States by 2060. Additional habitat was also identified in Québec for balsam fir and white spruce when historical data were included. In addition, red spruce showed a positive increase in suitable habitat of 4.2%, 2.8%, and 14.7% for 2030, 2060, and 2090, respectively, unlike predictions for the three other species.

Future likelihood of occurrence

The likelihood of future occurrence was mapped from the random forest models with and without the historical data for each species (Figure 3i–l; Appendix S1: Figure S11). These predictions were similar to future presence/absence maps, but highlight potential core areas of suitable habitat. No locations with a likelihood greater than 85% were predicted to be within the United States for any of the four species by 2060. "Likely" habitat was identified in the United States for balsam fir and red spruce with hotspots including Cape Breton Island and the Côte-Nord area along the Gulf of St. Lawrence within Québec. The addition of historical data made no impact on habitat area with a likelihood of 50%–85% (i.e., "likely" habitat). For example, additional habitat identified in the United States in 2060 using historical data (Figure 2f) was nevertheless not considered likely (Figure 3j). However, historical data did increase the rating of some areas from "likely" to "most likely" (i.e., black spruce habitat deemed "most likely," with likelihood >85%, increased by 5089 km²).

DISCUSSION

Species distribution models based on current bioclimatic niches are commonly used to assess vulnerability of a species or ecosystem to future changes in climate (Dyderski et al., 2018; Rogers et al., 2017), yet our findings illustrate that projected distributions are sensitive to the abundance variables used (Charney et al., 2021), the geographic extent of the underlying training data (Appendix S1: Figure S12), and to whether or not historical occurrence data are included. The most important predictor variables varied by species and allow additional inference based on life history characteristics. All occurrence models predicted species observations with high accuracy but the area occupied by each species varied when historical data were included and when alternative abundance metrics were used, while they were less sensitive to the temporal alignment of the climate normals with the period of observation (contemporary vs. historic; Appendix S1: Figures S4 and S5). The addition of historical data identified both persistent and additional suitable habitats by 2060 on the southern edge of species' ranges for ensemble climate change projections (RCP 6.0), which gives a more promising picture for the continuation of current forest composition than models based on contemporary occurrence alone.

In particular, we found that the likelihood metric from occurrence models and abundance models were more suitable for assessing the landscape for habitat refugia hotspots. The likelihood metric can be derived from more available occurrence data such as historical observations; thus, information from a variety of inventories can be combined into a single, inclusive dataset for SDMs. When we used thresholds to refine the species ranges from model likelihood (Figure 3), it generally showed that additional habitat gained from the inclusion of historical data had relatively low likelihood for the occurrence of spruce–fir species. Predictions from SDMs that rely solely on current inventory data should be reconsidered in light of our results that show predicted ranges are sensitive to the inclusion or exclusion of historically accurate data (Appendix S1: Figure S10).

Models predicted species abundance best for species whose distribution correlated strongly with biophysical gradients and exhibited higher dominance where they occurred, while models were weaker for those species with wider geographic distributions, but lower prevalence and dominance within plots. For example, black spruce observations were concentrated at the northern extent of the study area where dominance indicated by RBA and RSD could reach 100%. Abundance modeling may have performed the best for black spruce because its abundance varied so strongly across a latitudinal and climatic gradient. In comparison, abundance models for white spruce performed the worst. This species occurs at low local abundance (mean RBA 17%) across its very large range. As a result, abundance models likely captured a larger portion of white spruce's fundamental niche, but could not differentiate its realized niche given the region's disturbance history. In contrast, red spruce models were conservative and tended to underpredict its abundance. More conservative prediction of red spruce abundance was a result of the species' tendency to occur in mixtures with moderate to low dominance (mean RBA ~21%) and its limited range, which reflects both its narrow ecological niche and historic selective logging of this species from lower elevation mixed-wood stands in the 19th and early 20th centuries (Foster & D'Amato, 2015; Kelty & D'Amato, 2006).

The overprediction of low values exhibited in the abundance maps does not discount these models as a useful conservation tool. Areas that predict low abundance of an at-risk species are not likely to be chosen for the conservation of critical habitat (Guisan et al., 2013; Ashcroft et al., 2017). Although abundance models underestimated actual observed values, they were able to detect variation in abundance and maintained patterns of relative density across the landscape. The likelihood output from occurrence-only models also displayed parallel landscape patterns. Although the abundance of rarer species (e.g., white spruce) was not predicted as accurately, the relative results could still highlight the most suitable habitat. In sum, likelihood maps from occurrence models had similar utility to those developed from abundance data and have the potential for wider application due to the greater availability of occurrence data from both contemporary and historical time periods.

The variables selected as most important were surprisingly consistent across all 20 models and concentrated primarily on weather during winter months. Five climate variables were often selected (i.e., PRDD5, MAPDD5, PRMTCM, MAPMTCM, and GSPMTCM) from the 41 variables considered and all were climate interactions, showing that both precipitation and temperature help determine species' habitats (Appendix S1: Figure S13). In particular, temperature variables reflected a preference or tolerance for colder climates for all four species, while precipitation variables indicated preferences for wet weather concentrated in the winter months. Previous studies have emphasized the importance of summer temperature as an indicator of species occurrence and growth (Duveneck et al., 2014) and have examined the correlation between mean July temperature and the tree line (Cogbill et al., 1997). Alternatively, recent biogeographical studies suggest that tolerance to climate extremes, particularly freezing temperatures, accounts for 80% of variation in range size (Mathews & Bonser, 2005). In this analysis, mean temperature of the warmest month was not as important as cold weather variables (Wason & Dovciak, 2017).

While our models predict that potential spruce–fir habitat will decrease in the United States and throughout much of the AFR, they also suggest that extensive areas of suitable habitat will persist in Canada. Hotspots include the Gaspé Peninsula and other high elevation areas along the Gulf of St. Lawrence, Anticosti Island, and interior and northern regions in Newfoundland. Small populations along the Appalachian Mountains in Maine and New Hampshire will also be important locations for refugia in the United States. These predicted refugia agree with similar analyses for the "boreal conifer forest" under future climate (Tang & Beckage, 2010). While coastal habitats did not emerge as important persistent habitats in our projections, with the exception of red spruce in Nova Scotia, past persistence of white and black spruce in coastal New England during a period of warming between 6000 and 5000 years suggests that cool and foggy marine conditions may not be adequately represented in our modeling framework and these areas could continue to act as refugia in the near future (Schauffler & Jacobson Jr., 2002). In addition, our model for red spruce using both contemporary and historical data indicated a potential increase in habitat, particularly in Newfoundland. The species may be responding to area with potentially higher temperature and precipitation, as has been observed in other studies (e.g., Kosiba et al., 2018).

Potential and important model limitations should be considered in conjunction with our species-specific findings. Underlying differences in the spatial resolution, sampling methods, and minimum threshold dbh (Appendix S1: Figures S14–S17) add uncertainty to the contemporary data. The historic dataset may also suffer from possible limitations related to the unknown reliability of species identification, the general representativeness of the observations, the accuracy of location information, and the changes in historic climate over the subsequent 100–200 years prior to our models (Cogbill, 2000). The latter limitation might be particularly important given that the period of our historical observations (1623–1869) overlapped with the Little Ice Age (~1300–1860), which may explain why inclusion of these observations extended the "refugia potential" of each species further south under warming climatic trends. Consequently, it is possible that climate change is already influencing species occurrence trends and altering what might be considered suitable habitat.

For example, substantial changes in species composition and spruce habitat are known to have occurred with a 0.55°C change in temperature, though over millennia, (Gajewski, 1988) and temperatures in the northeast United States have risen approximately 1°C in the last century with greater increase along the shoreline from New Jersey to New Hampshire (Hayhoe et al., 2007), though effects of coincident changes in precipitation remain unexplored. In addition, changes in land use have been reported to have a greater effect on species composition shifts in the United States than climate change (Nowacki & Abrams, 2015). Finally, our models did not account for changes in soil conditions, potential variation in snowpack, or the complex spatiotemporal varying effects of disturbance agents like spruce budworm (*Choristoneura fumiferana*; e.g., Chen et al., 2021) on suitable habitat. Overall, we highlight that developing suitable SDMs can be complex, particularly for transitional ecosystems that span geopolitical boundaries (e.g., Prasad et al., 2020; Weiskittel et al., 2012) and species whose current distributions may be truncated due to historic land use or other complex factors.

By building SDMs using the fullest representation of a species' range, we identified areas of potential species persistence and refugia that would otherwise be missed. Our models add notable contributions over previous efforts in that they show (1) that distributions of spruce–fir species are particularly sensitive to interactions of temperature and precipitation patterns during the winter; (2) how the inclusion of historical, presettlement data expands predictions of future habitat under climate change with no loss in general model accuracy; and (3) that likelihood from more widely available occurrence-only models can predict potential refugia with efficacy that is equivalent to models of relative abundance. Our results clearly support the need for extensive regional and representative datasets, particularly for ecotonal tree species like the ones studied here, while the combination of occurrence likelihood and inclusion of key historical data were critical in ensuring reliable predictions of potential future conditions.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The contemporary field and climate data used in the analysis (Weiskittel, 2022a) are available from Figshare: https://doi.org/10.6084/m9.figshare.18480848. The historical climate normals (Weiskittel, 2022b) are available from Figshare: https://doi.org/10.6084/m9.figshare.18480854. The derived current and future spatial rasters by species (Weiskittel, 2022c) are available from Figshare: https://doi.org/10.6084/m9.figshare.18480860.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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