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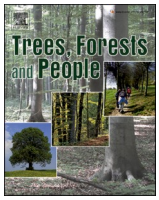

Tree species distributions in the United States and Canada under climate from 20,000 years ago to year 2100

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ABSTRACT

Current locations of species may not be suited to future climate, resulting in ranges that shift to higher latitudes, with potential for range expansion or contraction in extent. To identify potential shifts in distributions of 119 tree species centered in the United States and Canada, I modeled species occurrences under current climate and then predicted to past (20, 10, and 6 thousand years ago) and future climates (six projections during 2071–2100 for North American warming of 4.3 °C to 8.8 °C), with a singular focus on the climate space of tree species, or bioclimatic envelope models. Mean accuracies of withheld samples for models, based on climate of 1900 to 1990, were 0.97, with an average of 6.2 variables per model; annual temperature and temperature of the warmest quarter generally were the most important variables. Based on model predictions under past and future climate, centers of species distributions shifted an average of 565 km latitudinally since climate 20,000 years ago and 440 km to 1065 km shifts were expected in response to end-of-century climates. Overall, 64 tree species may gain more area than lose area that matches current climate space under future climate, whereas 36 species may lose potential climate space, with relative stability for 19 species. Canada and the mountainous western U.S., and National Forests in the mountainous western U.S., were likely to gain climate space appropriate for these species, particularly species of the eastern U.S. Conversely, greatest number of species were predicted to be lost from most of the eastern half of the U.S.; National Forests in the southeastern U.S., particularly in Alabama, Mississippi, and Texas, may lose 25 to 50 of these tree species. Isolation of potential dynamics for tree species already native to northern North America demonstrated that a large pool of diverse species from the southeastern U.S. was predicted to have suitable climate space in Canada and the western U.S. It may be beneficial for managers to become familiar with tree species south or east of their regions, particularly climate-tolerant pine and oak species, to determine which ones are desirable to manage for the future.

1. Introduction

Climate generally is the major factor to determine species ranges, which is a major principle of biogeography (Good , 1931; Turrill , 1939). Species ranges occur in climates where species have tolerances and traits to successfully persist in terms of growth, survival, and reproduction, with additional filtering by non-climate factors (Good , 1931; Turrill , 1939; Hanberry , 2023a). The true physiological tolerances of species to climate are unknown, and limited by competition, disturbance, dispersal barriers, and land use, among other factors (Turrill , 1939; Aitken et al., 2008). Species may expand outside their native range, and climate boundaries, when released into new locations, particularly if cultivated (Early and Sax, 2014). Equally, species may contract in range due to land use changes; for example, in the United States, surface fire-tolerant species of longleaf and shortleaf pines (*Pinus palustris* and *P. echinata*) have contracted in range after disturbance and land use changes associated with Euro-American settlement (Hanberry , 2021a).

With warming climate, poleward range shifts by species are expected (Davis and Shaw, 2001; Williams et al. , 2013). Novel or no-analog communities may develop in time if, for instance, subtropical species shift into areas occupied by circumboreal species, although evidence does not exist for development of these communities based on current climate change (but no-analog communities may have assembled due to land use change; Hanberry and Hansen, 2015; Hanberry , 2021b; Taheri et al. , 2021). Nonetheless, future combinations of southern species with freeze-tolerant northern species are likely to be transient due to little overlap in physiological tolerance to climate, including such cues as chilling requirements and seed stratification (Aitken et al. , 2008). In particular, Morin et al. , (2007), using a model based on phenology for 17 tree species across the United States, found that trees of both

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southern and northern species cannot be productive in the same location because of fruit maturation too late in the year or lack of flowering without chilling to break dormancy at southern range limits and flowering too early to avoid frost damage or too late at northern range limits.

Bioclimatic envelopes are models of the climate space, based on temperature and precipitation, of species, which allow predictions under alternative climates to generate information about possible outcomes of climate change (Williams et al. , 2013). Most projections of future tree ranges are based on statistical relationships between the current distributions of species and climate and other environmental predictor variables (Iverson et al. , 2017). While models of ecological processes incorporate complexity and influences of other factors and may produce better abundance predictions within the bioclimatic distribution, the climate space of species is only known through observations (Dijak et al. , 2017). That is, parameters for species in process-based models use known ranges of temperature, precipitation, or derivatives, which may have been estimated several decades ago, or may simply be grouped into two or three classes of drought tolerance (Dijak et al. , 2017). Indeed, the climate parameter inputs for process-based models may be less accurate than information gained from correlative climate models.

Moreover, some factors are of limited influence and if modeled, may set artificial limits on species distributions. Soils and topography do inform heat accumulation and water balance, but patterns of species associations with soils and topography are fluid (Hanberry , 2023a). This is evidenced by a complete reset of tree abundances and distributions after Euro-American settlement in the eastern U.S., despite relatively stable soils and topography (Hanberry et al. , 2013; Goring and Williams, 2017). Certainly, soil and topography data only are available for recent decades and may not accurately represent soil and topography before tile drainage, altered hydrology, erosion, filling of wetlands, tilling, and flattening of mountains.

Addition of dispersal or competition into models will slow the shifting trajectory of distributions, in effect generating an earlier time step rather than the final time step for the predicted climate interval. Morin et al. , (2008), using a process-based model based on phenology for 16 species across the U.S., showed very mild species shifts when distributions were limited by migration, rather than at equilibrium with climate. A forest landscape change model suggested that hundreds of years are required for climate effects on forest composition to materialize (Wang et al. , 2015). From a human temporal perspective, compositional shifts may be difficult to perceive, particularly in areas where trees are removed less frequently by harvesting and land use. A long transitional interval may occur as southern species and ecosystems replace northern species and ecosystems.

Climate-only correlative models offer transparency by focusing on one influence, providing a useful complement to more complex process-based models that may contain more limited parameter information about climate relationships with species. To my knowledge, continental North American tree distributions for numerous tree species have not been predicted to past and future climates. Here, I isolated dynamics for 119 tree species with ranges centered in northern North America for climate during the 1900s relative to climate 20,000 years ago (ka), 10 ka, 6 ka, and six end-of-century (2071–2100) climate projections under moderate and high emission scenarios. The greatest potential emission scenarios (i.e., SRES A1FI, RCP 8.5, SSP5–8.5), regardless of scenario details, track historical cumulative emissions and provide the best match to mid-century emissions under current and stated policies (Schwalm et al. , 2020); consequently, these emission scenarios encapsulate the risk of worst possible case scenario by the end of century and perhaps beyond that. Nonetheless, variations occur among emission scenarios, general circulation models, and also downscaling methods, while the climate space of tree species may not be captured due to lack of sampling or not filling the entire physiological range. Modeled distributions are of potential climate space based on the model observations; these distributions do not translate to realized ranges, particularly for disjunct locations that may have suitable climate. In addition to supplying species models, my specific questions, to answer by modeling, were focused on providing information about shifts in the tree species predominantly limited to current ranges in the U.S. and Canada:

1) How far may species distributions shift under future climate relative to past climate?
2) Will species potentially expand or contract in distributional area under future climate?
3) How many tree species may be lost and gained over time by national first level administrative divisions (e.g., states or provinces) and National Forests within the U.S., as an example for agencies tasked with forest management?

2. Methods

The modeling extent was North America (Fig. 1). For climate, I extracted debiased and downscaled 30-year to 100-year climatologies during 20 ka, 10 ka, 6 ka, 1900–1990, and 2071–2100 (resolution 30 ′onds; CHELSA climate; Karger et al. 2017, 2018, 2020, 2021). Future climate projections included a range of climate for North America from the moderate SSP3–7.0 scenario: GFDL-ESM4 (GFDL; Geophysical Fluid Dynamics Laboratory, USA) that projected an increase of 4.3 °C mean annual temperature, IPSL-CM6A-LR (IPSL; Institut Pierre Simon Laplace, France) with an increase of 6.3 °C mean annual temperature, and UKESM1–0-LL (UKESM1; Met Office Hadley Centre, UK) with an increase of 8.8 °C mean annual temperature. Additionally, I used similar climates from the fossil fuel driven SSP5–8.5 scenario general circulation models GFDL-ESM4 (GFDL; Geophysical Fluid Dynamics Laboratory), MPI-ESM1–2-HR (MPI; Max Planck Institute for Meteorology) and MRI-ESM2–0 (MRI; Meteorological Research Institute), which projected increased temperatures of 5.2 to 5.9 °C in North America. I obtained 13 bioclimatic variables that quantify temperature and precipitation at annual, seasonal, and monthly intervals: mean annual temperature, maximum temperature of the hottest month, minimum temperature of the coldest month, mean temperature of the coldest and hottest three months, mean temperature of the driest and wettest three months, annual precipitation, precipitation during the driest month and driest three months, precipitation during the wettest month, and precipitation during the coldest and warmest three months.

The Global Biodiversity Information Facility (GBIF; Global Biodiversity Information Facility, 2022) is a centralized data repository containing 65,000 datasets of 2 billion species observations, with continual additions. For tree species, I filtered records that were observed since 1990 in North America with coordinate uncertainty less than 1000 m (GBIF occurrence download https://doi.org/10.15468/dl.p748ym accessed on 3 March 2022). To isolate dynamics of native tree species centered in the United States and Canada, I selected common native tree species, with at least 400 records at unique locations, which were uncommon in Mexico (i.e., rarely or not recorded in Mexico; Tellez et al. , 2020; Fig. 1). I extracted climate values at each of the species occurrence coordinates. For pseudoabsences, I used an equal number of random points from the study extent, or background, of North America and Greenland. I likewise extracted climate variables for the absence points.

For modeling of each species, I applied an iterative process to winnow variables for modeling, based on near present climate, and then predicted to each climate interval with application of the random forests classifier, an ensemble nonlinear model (caret package, Kuhn ,2008; R Core Team, 2022; Hanberry , 2024). Many variables contribute minimally to models and can obscure the influence of each variable, although ensemble nonlinear models typically are robust in isolating influence of redundant, highly correlated predictors, such as temperature; a variable reduction process provides some balance between underfitting due to not enough important variables and overfitting due to constraints from numerous variables (Kuhn and Johnson, 2019; Hanberry , 2023b;

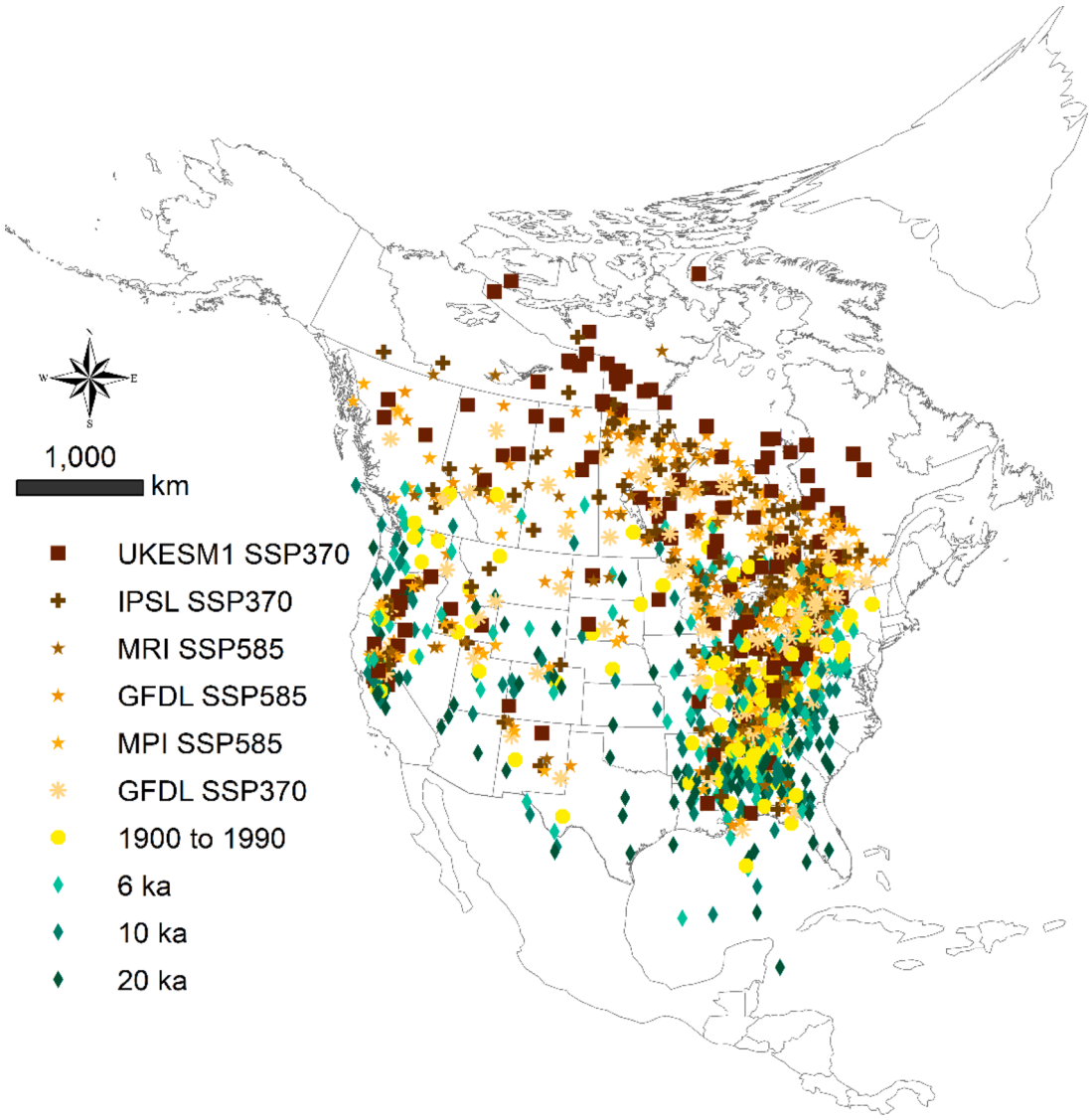

Fig. 1. The centers of tree species distributions changed over time from paleoclimate to current climate to projected future climate for the North American study extent.

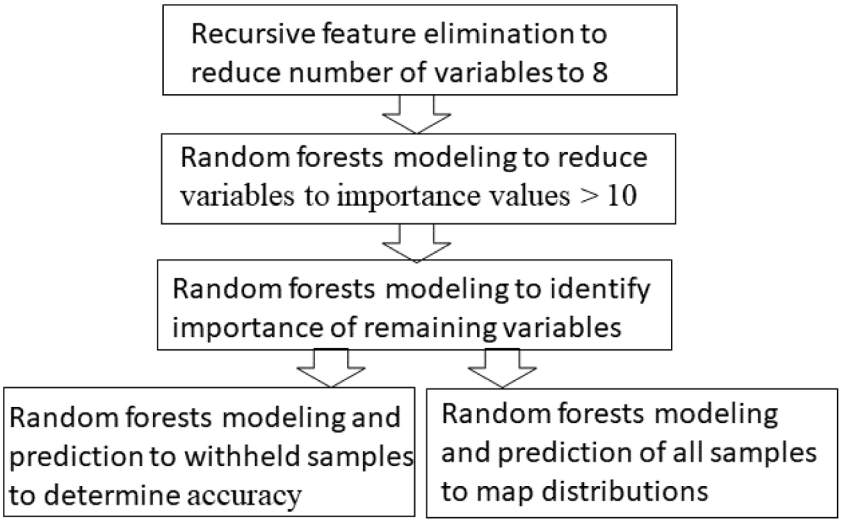

Fig. 2. Steps of the modeling workflow.

Hanberry , 2024). First, with 10-fold cross-validation, repeated three times, I used random forests recursive feature elimination, which builds a model based on all variables, rank-orders variable importance, and removes variables with the least importance based on model evaluation metrics (i.e., accuracy), to reduce to eight variables (Fig. 2). Then, the modeling process is repeated again, retaining only variables that carried an importance value $\geq$ 10 (out of 100 scale; other classifiers will assign weights differently). If a precipitation variable was not included in the final variables, then annual precipitation was added. These remaining variables followed two different modeling pathways. With samples partitioned into training (75 % of samples) and test (25 % of samples), I calculated accuracy metrics. With all the samples, I used models to predict potential distributions under past, near present, and future climates.

For distance and area summaries, layers were projected to the Albers projection (ArcMap version 10.8.2, ESRI, Redlands, California; Snyder , 1987). Species were considered present if predicted probability was $\geq$ 0.50, which is equal to the modeling prevalence and the default probability threshold for binary classification (caret package, Kuhn , 2008). Standard probability thresholds for binary classification hold comparisons among species equal within studies, and as equal as possible among studies, given differences in species samples, predictor variables, and modeling algorithms. I located centers of each distribution by climate and determined shifts in latitudinal distances from distribution centers of near present climate. By species, I calculated ratio of the mean area of future potential climate space to the area of current potential climate space to determine expansion, contraction, or stability. By administrative units, I examined species gains and losses based on predicted climate space under current climate and for agreed predictions of climate space for tree species by five of six future climates. To prevent inclusion of small, disjunct areas of predicted potential climate space, which in general are unlikely to be realized, in administrative units, I removed minor predicted areas using thresholds in area that were larger than the 30 ′ond resolution of prediction units but not larger than the minimum areas of administrative units. The threshold of the area for a species to be counted as present in a first level internal administrative country division (e.g., states or provinces) was $\geq$ 250 km^2, or about 10 % of the smallest unit (i.e., Rhode Island, U.S.). The threshold of area for a species to be counted as present within management units of National Forests of the U.S. was 5 km^2, which represented the minimum size of the management units (i.e., McClellan Creek National Grassland, U.S.) while also being more than one prediction unit (i.e., predictions were based on climate resolution of 30 ′onds).

3. Results

3.1. Accuracy, most important variables, and predicted shifts in distribution centers

Mean accuracies of withheld samples for models based on climate of 1900 to 1990 were 0.97 (sensitivity = 0.98, specificity = 0.96), with an average of 6.2 variables, for 119 species with $\geq$ 400 observations. Mean annual temperature was the most important variable for the greatest number of species (20), but mean temperature of the warmest quarter, precipitation of the driest month, and precipitation of the driest quarter were the most important variables for either 18 or 19 species each. Nonetheless, based on sums of importance values for variables, mean annual temperature was the most important variable overall in models (5869), followed by mean temperature of the warmest quarter (5027) and mean temperature of the coldest quarter (3967) and then the two precipitation variables of dry intervals.

The centers of potential species distributions changed over time, with northern shifts (Fig. 1). Relative to climate of 1900–1990, predicted distribution centers moved an average of 565 km latitudinally since the climate during 20 ka. Three tree species had predicted distribution centers that shifted southwards between 20 ka and 1900–1990 climate due to a warm region of past climate in Alaska, which has support from reconstructions and another past climate dataset (Lorenz et al. 2016). Relative to 1900–1990 climate, predicted distribution centers moved an average of 245 km and 120 km latitudinally since climate during 10 ka and 6 ka, respectively. For end-of-century climates, predicted distribution shifts in latitude were 440 km for GFDL SSP3–7.0, 530 km to 635 km for the three SSP5–8.5 general circulation models, 675 km for IPSL SSP3–7.0, and 1065 km for UKESM1 SSP3–7.0. Nevertheless, six species with relatively restricted ranges (*Abies grandis, Cornus nuttallii, Pinus longaeva, Quercus douglasii, Sequoiadendron giganteum, Umbellularia californica*) in the western U.S. had predicted distribution centers south of current predicted distribution centers under some future climates.

3.2. Species gains and losses in area

Overall, 64 tree species potentially may gain more area that matches current climate space than lose area under future climate in North America, according to the ratio of future predicted mean area for the six end-of-century climates to predicted area for 1900–1990 climate (Table 1). For relative stability, 19 species may maintain in the future 0.90 to < 1.10 of current potential climate space. For losses, 36 species may have future potential climate space equal to 0.07 to 0.89 of current potential climate space; *Pinus palustris* (Fig. 3) and *Abies grandis* were two of the species with greatest predicted losses.

3.3. Gain and loss of tree species by administrative boundaries

For these northern tree species that have greatest number of species predicted in the U.S. and Canada, current climate is predicted to be suitable for some species in southern North America, although these species are uncommon or not recorded as native species (Fig. 4). Based on absolute change in number of species, species loss was predicted to be greatest in most of the eastern half of the U.S., according to number of species gained or lost under five of six end-of-century climates compared to number of species predicted to be present under current climate. The mountainous western half of the U.S. and most of Canada, excluding northeastern Canada, was predicted to gain species. Only one species, *Ulmus thomasii*, was predicted to shift out of the U.S., but this species was concentrated the northern Great Lakes region. Canada was predicted to gain 13 species: *Carya illinoinensis, Ilex decidua, Magnolia grandiflora, Magnolia virginiana, Pinus echinata, Pinus taeda, Quercus falcata, Quercus marilandica, Quercus michauxii, Quercus nigra, Quercus phellos, Quercus stellata, Ulmus alata*.

For U.S. National Forests, similar trends occurred in predicted number of species lost or gained relative to number of these species predicted to be present under current climate (Fig. 5). National Forests in the southeastern-most states may have species losses ranging from 25 to 51 of these tree species, particularly in Alabama, Mississippi, and Texas. National Forests in the western U.S. overall may gain species, with greatest gains of more than 30 species in Colorado, Idaho, and Utah.

4. Discussion

4.1. Findings for species conservation

Modeling of species in response to climate provides information about potential magnitude of response to future climate, even if species responses are not likely to be faithful to predictions of varied models, due to effects of other factors, primarily land use. Here, I used tree species occurrences to model full ranges of 119 tree species common in the U.S. and southern Canada but generally rare south of the U.S., to examine dynamics of tree species located in northern North America. Mean accuracies were 0.97, for an average of 6.2 variables per model, with annual temperature and temperature of the warmest quarter as the

Table 1
Tree species, predicted areas (km^2; ka = thousand years ago; future mean is mean area predicted for six climates of 2071–2100), and ratios in area between six future climates and 1900–1990 climate.

Species	20 ka	10 ka	6 ka	1900–1990	Future mean	Ratio
Pinus longaeva	69,712	36,605	136,312	386,491	28,724	0.07
Quercus laevis	68,469	240,719	303,262	494,168	108,453	0.22
Pinus palustris	91,735	297,532	495,420	807,947	222,419	0.28
Abies grandis	181,116	305,861	441,980	519,249	163,307	0.31
Quercus douglasii	166,090	158,637	194,064	169,387	64,138	0.38
Acer glabrum	991,974	691,258	1,107,591	1,822,336	739,587	0.41
Pinus sabiniana	207,117	189,508	212,726	209,586	97,847	0.47
Pinus albicaulis	378,539	256,858	544,245	857,062	410,666	0.48
Asimina triloba	573,672	443,838	632,605	1,661,348	842,246	0.51
Juglans cinerea	214,467	294,080	345,566	1,359,959	722,583	0.53
Cercocarpus ledifolius	555,823	657,277	1,110,185	1,412,745	808,110	0.57
Abies lasiocarpa	1,192,897	545,871	1,098,638	1,421,573	875,982	0.62
Quercus kelloggii	336,009	287,573	347,799	317,813	195,962	0.62
Fraxinus nigra	275,353	413,639	883,601	1,739,659	1,118,109	0.64
Pinus monticola	645,222	587,006	727,237	787,444	532,929	0.68
Aesculus californica	177,268	155,320	187,406	165,588	113,742	0.69
Picea engelmannii	1,027,496	649,585	1,003,785	1,695,108	1,174,301	0.69
Picea pungens	1,264,441	1,432,834	2,176,228	2,966,386	2,151,417	0.73
Pinus echinata	284,773	746,441	1,070,139	1,630,646	1,189,993	0.73
Liriodendron tulipifera	477,016	567,518	894,435	1,710,268	1,263,522	0.74
Pinus virginiana	463,988	392,963	514,960	1,183,231	877,800	0.74
Quercus alba	300,884	622,043	1,030,515	2,081,821	1,558,142	0.75
Ilex opaca	235,812	417,767	842,896	1,663,288	1,274,158	0.77
Tsuga canadensis	408,103	449,350	532,566	1,419,242	1,097,417	0.77
Sassafras albidum	537,045	932,447	1,316,705	1,940,671	1,585,544	0.82
Thuja plicata	75,230	304,862	484,366	519,220	425,081	0.82
Cornus florida	495,437	873,090	1,177,371	1,999,190	1,637,869	0.82
Quercus wislizeni	230,902	205,015	233,016	233,502	193,343	0.83
Tsuga heterophylla	263,224	369,458	527,866	567,777	473,871	0.83
Juniperus osteosperma	274,602	814,869	1,093,121	1,562,048	1,305,505	0.84
Quercus garryana	247,592	244,845	259,451	303,963	255,355	0.84
Quercus nigra	232,258	709,363	916,475	1,451,828	1,236,449	0.85
Quercus coccinea	722,573	591,575	691,986	1,568,202	1,342,220	0.86
Fraxinus pennsylvanica	367,577	1,241,217	2,203,917	3,275,987	2,819,431	0.86
Carya tomentosa	729,894	1,347,299	1,664,037	2,005,283	1,734,713	0.87
Pinus elliottii	27,598	310,459	547,460	637,696	568,335	0.89
Picea glauca	351,385	482,152	1,091,920	2,281,023	2,061,076	0.9
Alnus rubra	258,010	228,267	330,737	377,989	345,111	0.91
Aesculus pavia	400,746	1,034,155	1,417,657	1,845,676	1,736,016	0.94
Arbutus menziesii	229,929	357,289	262,841	260,930	248,385	0.95
Ungnadia speciosa	433,002	702,605	832,568	941,239	918,045	0.98
Acer rubrum	566,445	1,116,033	1,721,739	2,424,292	2,365,373	0.98
Juniperus virginiana	786,053	1,188,885	1,797,356	2,738,050	2,708,600	0.99
Quercus geminata	120,604	119,159	184,539	265,773	263,456	0.99
Quercus michauxii	241,265	825,068	1,157,813	1,514,768	1,520,456	1
Populus balsamifera	928,656	1,023,947	2,086,240	3,181,748	3,201,316	1.01
Acer grandidentatum	1,239,165	1,517,315	1,159,670	1,187,201	1,197,182	1.01
Magnolia virginiana	381,110	635,776	1,035,851	1,727,567	1,753,378	1.01
Sequoia sempervirens	100,570	65,181	92,457	159,983	164,090	1.03
Umbellularia californica	173,746	150,453	186,345	230,867	237,200	1.03
Picea mariana	539,807	781,152	1,681,736	2,717,035	2,792,131	1.03
Tsuga mertensiana	1,122,593	627,630	742,301	643,429	666,475	1.04
Quercus falcata	162,711	660,866	982,468	1,407,575	1,478,060	1.05
Quercus bicolor	849,957	987,169	1,152,614	1,706,237	1,794,861	1.05
Pinus taeda	176,622	740,450	1,049,002	1,507,489	1,633,974	1.08
Quercus rubra	812,751	1,240,979	1,241,151	2,125,325	2,335,136	1.1
Quercus montana	650,493	580,681	576,689	1,180,086	1,297,450	1.1
Maclura pomifera	388,984	1,373,899	1,635,345	2,197,452	2,416,113	1.1
Thuja occidentalis	1,366,791	2,038,583	2,556,232	2,767,555	3,068,703	1.11
Quercus phellos	93,516	745,514	1,019,632	1,567,782	1,739,698	1.11
Sabal palmetto	759,180	396,165	576,237	477,503	530,885	1.11
Alnus incana	1,001,279	1,267,304	1,887,378	3,004,119	3,381,326	1.13
Acer macrophyllum	205,804	566,159	379,108	360,567	406,301	1.13
Acer circinatum	1,134,969	674,131	741,653	663,412	753,817	1.14
Juglans nigra	597,251	1,886,075	2,077,570	2,358,783	2,710,497	1.15
Betula papyrifera	364,137	575,275	1,125,806	1,979,556	2,283,959	1.15
Quercus imbricaria	978,566	658,084	985,910	1,524,179	1,759,902	1.15
Cornus drummondii	212,663	1,109,910	1,634,095	1,390,647	1,611,325	1.16
Pinus banksiana	330,746	786,247	1,405,880	2,479,051	2,876,031	1.16
Carya cordiformis	648,113	1,167,881	1,261,487	2,070,147	2,403,632	1.16
Betula lenta	462,351	377,285	389,377	883,608	1,031,484	1.17
Magnolia tripetala	464,856	745,860	1,129,784	1,173,744	1,381,673	1.18
Betula populifolia	567,990	378,010	549,554	959,972	1,132,927	1.18

(*continued on next page*)

Table 1 (*continued*)

Species	20 ka	10 ka	6 ka	1900–1990	Future mean	Ratio
Castanea dentata	405,269	474,801	459,048	1,017,172	1,205,840	1.19
Ulmus thomasii	58,396	391,210	504,580	495,501	590,376	1.19
Prunus virginiana	1,548,285	2,397,605	3,107,730	3,444,608	4,120,011	1.2
Diospyros virginiana	683,471	1,213,388	1,718,779	2,190,106	2,651,709	1.21
Cornus nuttallii	308,495	684,801	503,589	410,354	501,436	1.22
Betula nigra	654,816	1,291,758	2,172,079	2,515,881	3,097,286	1.23
Quercus ilicifolia	175,528	384,381	446,705	612,920	757,877	1.24
Acer spicatum	328,517	552,409	909,834	1,712,905	2,132,937	1.25
Populus grandidentata	512,656	641,162	885,472	1,758,305	2,190,090	1.25
Oxydendrum arboreum	264,628	494,908	916,523	1,433,557	1,811,237	1.26
Quercus palustris	735,499	1,234,054	1,359,742	1,797,580	2,278,229	1.27
Carya glabra	1,051,327	1,405,829	1,749,521	2,374,978	3,018,545	1.27
Prunus pensylvanica	488,979	822,021	1,455,843	2,619,116	3,338,752	1.27
Ulmus rubra	945,050	2,617,642	3,283,547	2,907,121	3,721,928	1.28
Magnolia grandiflora	378,427	581,635	963,822	1,480,714	1,907,769	1.29
Quercus shumardii	649,779	1,981,602	2,233,742	2,028,751	2,628,419	1.3
Quercus velutina	887,280	1,472,944	1,884,419	2,164,401	2,804,683	1.3
Acer pensylvanicum	374,377	449,734	617,680	1,083,936	1,405,666	1.3
Celtis occidentalis	1,069,530	2,092,313	2,700,094	2,166,328	2,823,053	1.3
Prunus caroliniana	99,269	506,586	784,645	1,196,801	1,576,239	1.32
Quercus stellata	720,705	1,412,008	1,685,490	2,018,759	2,701,377	1.34
Acer nigrum	958,789	1,205,643	1,391,509	1,542,345	2,073,244	1.34
Robinia pseudoacacia	656,549	1,247,864	1,520,112	2,419,694	3,268,830	1.35
Quercus virginiana	185,700	366,134	583,813	898,509	1,223,496	1.36
Pinus rigida	191,642	340,251	328,864	599,680	817,591	1.36
Larix laricina	260,329	447,790	1,005,502	1,805,999	2,473,445	1.37
Pinus resinosa	387,647	667,912	845,927	1,735,740	2,394,265	1.38
Fraxinus americana	725,171	1,586,309	2,019,354	2,394,254	3,305,582	1.38
Morus rubra	1,288,638	2,610,060	2,919,598	2,883,864	4,053,519	1.41
Ulmus americana	743,046	1,705,662	2,407,784	2,586,367	3,656,935	1.41
Catalpa speciosa	1,068,307	1,810,223	2,083,281	2,600,413	3,693,839	1.42
Cornus alternifolia	761,802	728,235	1,016,210	1,860,650	2,646,500	1.42
Quercus marilandica	583,005	1,251,562	1,484,289	1,817,985	2,616,595	1.44
Abies balsamea	281,550	348,311	675,466	1,274,924	1,848,616	1.45
Quercus macrocarpa	676,461	1,964,747	2,641,868	2,163,592	3,151,920	1.46
Acer saccharinum	838,714	2,179,821	2,580,168	2,558,232	3,778,312	1.48
Aesculus glabra	1,075,733	2,659,467	3,458,491	2,181,830	3,254,517	1.49
Carya illinoinensis	782,115	1,672,215	1,997,410	2,115,534	3,175,772	1.5
Ilex mucronata	364,372	546,578	786,132	1,309,996	1,987,880	1.52
Corylus americana	1,324,841	1,594,851	2,493,158	2,153,256	3,299,202	1.53
Ulmus alata	186,965	1,108,900	1,502,400	1,665,128	2,570,807	1.54
Betula alleghaniensis	371,640	569,944	787,647	1,296,298	2,046,835	1.58
Sorbus americana	516,045	663,595	1,106,055	1,513,196	2,417,951	1.6
Sequoiadendron giganteum	375,966	322,435	511,159	400,245	667,651	1.67
Picea rubens	591,471	541,629	573,170	792,592	1,391,748	1.76
Ilex decidua	62,536	1,080,446	1,420,239	1,359,770	2,509,382	1.85

most important variables. Summer temperatures are important predictors of tree species models in North America, even for marginally comparable studies, such as composition of pollen samples from eastern North America during the past 21,000 years (Blois et al. , 2013; Hanberry , 2023a). Relative to climate of 1900–1990, predicted centers of distributions shifted about 440 km to 635 km northwards according to five of six end-of-century climate models, which is similar to the distance tree distributions have moved since climate during 20 ka (Dyke et al. , 2005; Delcourt and Delcourt, 1987), but less than mean distribution shifts of 1065 km northwards predicted by the climate for the UKESM1 general circulation model under the moderate SSP3–7.0 scenario. Likely due to greater land area of the northern part of the continent, more than half of the tree species potentially may gain more area than lose area that matches current climate space under future climate. A key finding was the potential replacement of western tree species with eastern tree species under future climate change, a predicted outcome that may interact synergistically with western expansion of eastern tree species due to land use change (Hanberry , 2021b).

Movement of distribution centers from climate of 20 ka to climate 1900–1990 was comparable to movement from climate of 1900–1990 to 2071–2100, given temperature change $\leq$ 6.3 °C, suggesting that dispersal rates may be too slow for tree species to remain in a climate similar to their current climate space during an interval that is less than the longevity of many tree species. Since deglaciation, boreal tree species of *Picea mariana, Picea glauca, Abies balsamea, Larix laricina, Populus balsamifera, Populus tremuloides, Betula papyrifera*, and *Pinus banksiana* moved 1490 km with maximum rates reaching 200 m per year and 14 km per century (Dyke et al. , 2005; Delcourt and Delcourt, 1987). Established trees of course cannot unroot and many individuals have the potential to be in the same location a century from now. Trees are long-lived and overall most vulnerable to climate during early development before root systems develop, although heat waves, prolonged heat, and drought may cause die-offs of established trees, particularly depending on factors such as site conditions (e.g., moisture related to soils and topography), stand conditions (e.g., stocking rates), and tree species tolerances to drought and heat (Keane et al. , 2018). Plant migration occurs through incremental changes in population dynamics of differential survival after propagule dispersal.

If species remain in place, conditions eventually will become unsuitable for success of the species. In this study, the species-rich subtropical southeastern U.S. was predicted to lose the greatest number of species. Conversely, the mountainous western U.S. was predicted to gain the greatest number of species, as temperature will become ideal for species adapted to warmer conditions. Even if increased temperatures may be beneficial to some species in energy-limited forests, warmer temperatures allow invasion and competition by species with optimal success in warmer temperatures, due to a trade-off between traits for growth and traits for cold tolerance (Aitken et al. , 2008). That is,

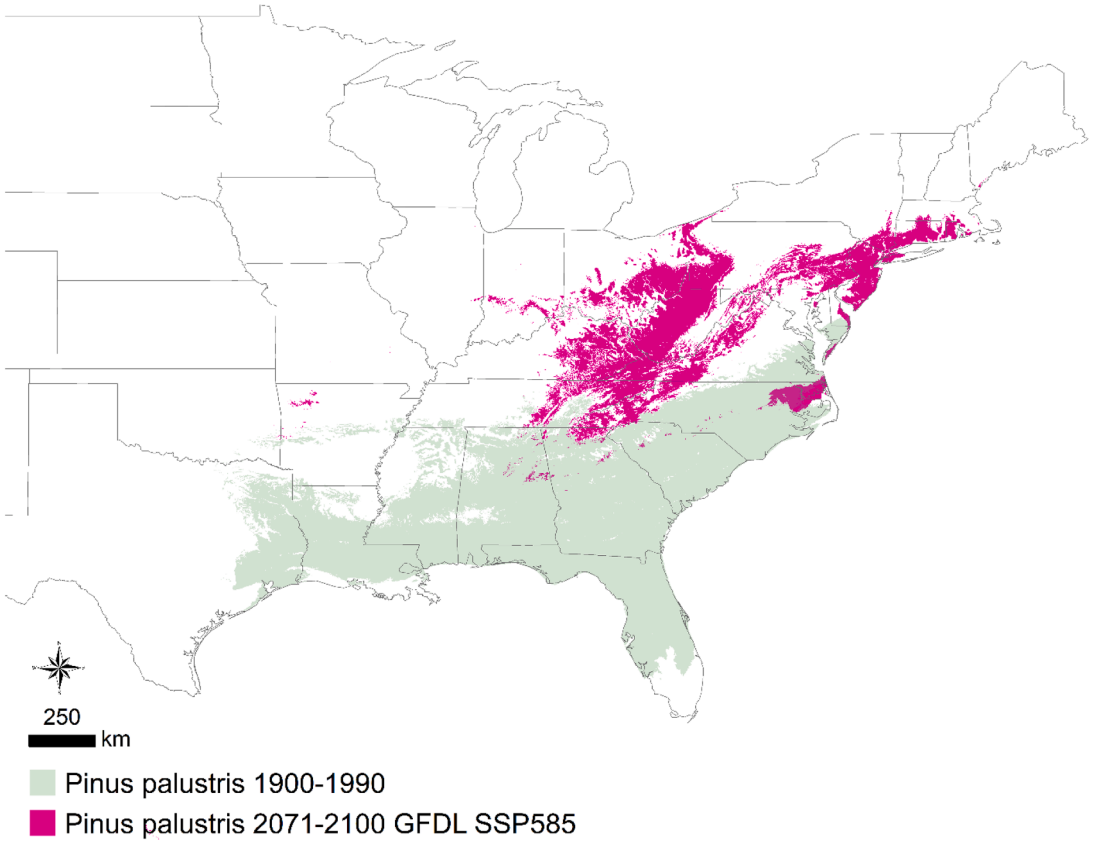

Fig. 3. *Pinus palustris* lost potential climate space in the future, illustrated with one example of predicted future distribution, compared to current potential climate space.

focusing on climate change effects on species present in a given location, as a closed ecosystem, will neglect the effects of interactions with new, competitive species shifting within the same country.

These models do not provide an expected rate of change. Climate, which typically expresses at least three decades of conditions as opposed to shorter term weather, may require decades to manifest an influence on tree records. Although climate has warmed since the end of the Little Ice Age, no cohesive pattern of tree species shifting poleward is yet apparent in the U.S. (Hanberry and Hansen, 2015; Taheri et al. , 2021). Therefore, a long lag period may occur between when climate changes and when climate appears to influence recorded trees. Lag times of tree response to changing climate in the past typically were clustered around 100 years (Williams et al. , 2002).

Rate, direction, and magnitude of change will depend on a variety of factors, including resistance by species that already occupy the growing space and human influences. Many tree species distributions are not in equilibrium due to Euro-American settlement and land use (Hanberry et al. , 2013; Goring and Williams, 2017; IPBES , 2019). This will add complexity to relatively straightforward range shifts that occurred under past climate change, although human activities influenced tree distributions in the past (Schweger et al. , 2011). The competing influence of land use may drive tree species in the opposite direction expected by climate change, that is, to drier and warmer conditions. Land use change, rather than climate change, was associated with expansion of eastern tree species westward into the central North American grasslands, in a drier direction rather than shifts to track temperature (Hanberry , 2021b). Indirect effects of climate change through disturbances, which have been altered by land use, also may affect direction and rate of change. Severe fires likely will increase due to land use, from accumulation of tree fuels after exclusion of frequent surface fires after Euro-American settlement, combined with increased temperatures that will dry coarse tree fuels and extend the fire season (Keane et al. , 2018). In conjunction with availability of trees at greater densities than in historical forests, native and non-native insects that damage trees likely will benefit from longer growing seasons and increased over-winter survival (Aitken et al. , 2008).

Future distributions for about half of the modeled tree species increased in predicted area, likely reflecting greater area in the northern North American continent, including Canada. Due to greater area of the North American continent at higher latitudes, northern shifts in tree species distributions may be more likely to lead to expanded climate space than contractions. Boreal species particularly have expanded in absolute area with poleward advancement over time (Hanberry , 2023b). While loss of circumboreal tree species (e.g., *Picea*) is of concern in the U.S., loss may not pose a concern at continental scales, according to these models. Moreover, Canada was predicted to gain 13 tree species, including tree species of the southeastern U.S, such as the primary pine plantation species of *Pinus taeda*. Some species of the central eastern U.S. already are naturalized in Canada. Any gains in southern species may mean that the tree species or ecosystem type, such as tundra, that currently occupy the area may lose range (Jackson et al. , 2000). Indeed, forests occurred in the Arctic when atmospheric carbon dioxide concentration was 420 parts per million about 4 million years ago (Brigham-Grette , 2013; Jimenez-Moreno et al. , 2019).

Uniquely in the future, greater intermixing of tree species from the eastern and western U.S. may occur over time as eastern species potentially shift into the western U.S. and Canada. In response to past climate change, tree species shifted in distributions, which produced emerging and disbanding associations and biomes (Davis and Shaw, 2001; Williams et al. ,2004). However, past changing associations occurred through latitudinal mixing of boreal and temperate species because during the past 10,000 years, the central North American

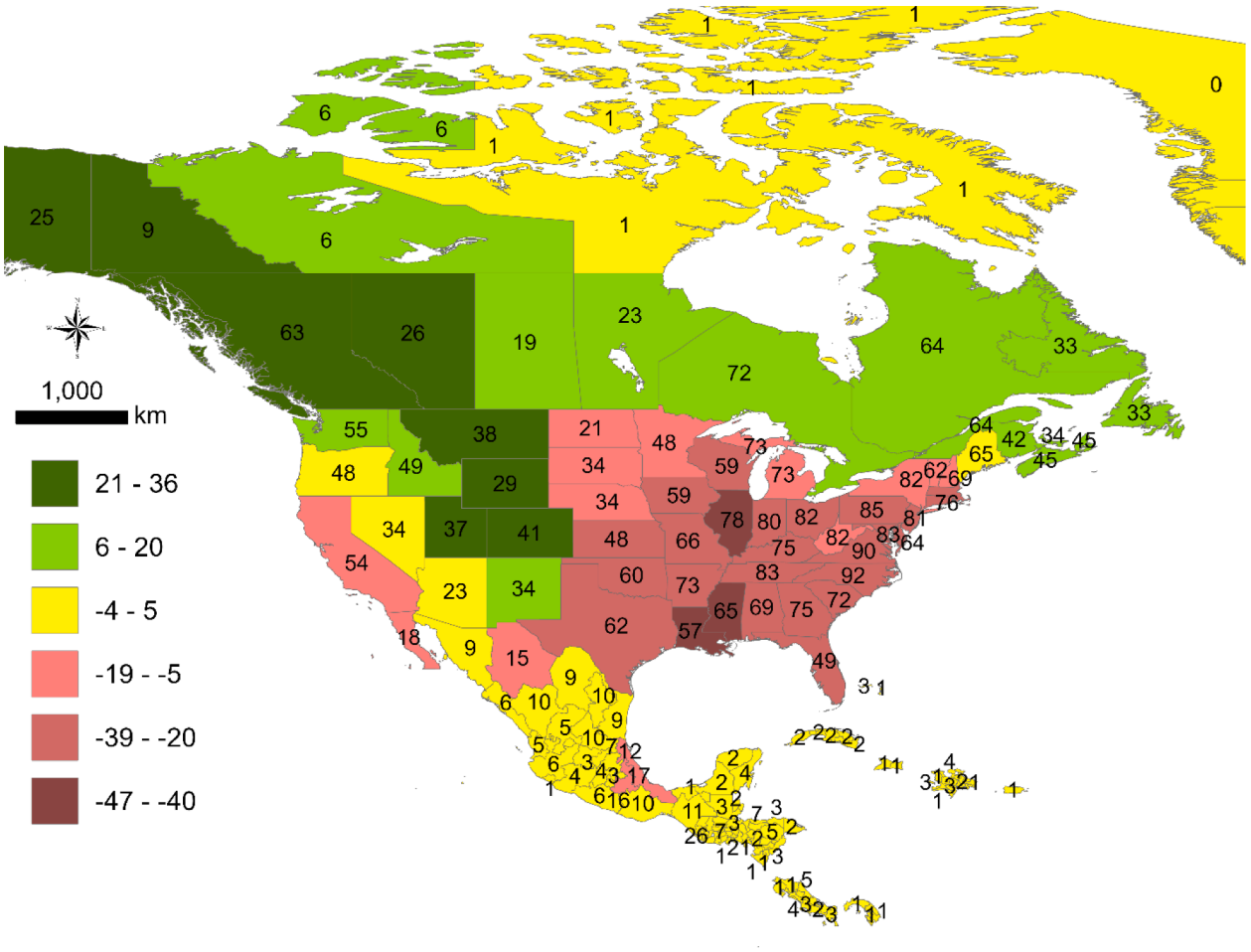

Fig. 4. Absolute difference between future number of predicted species compared to current number of predicted species, with current predicted number of species listed for the internal administrative country division, for tree species established in northern North America.

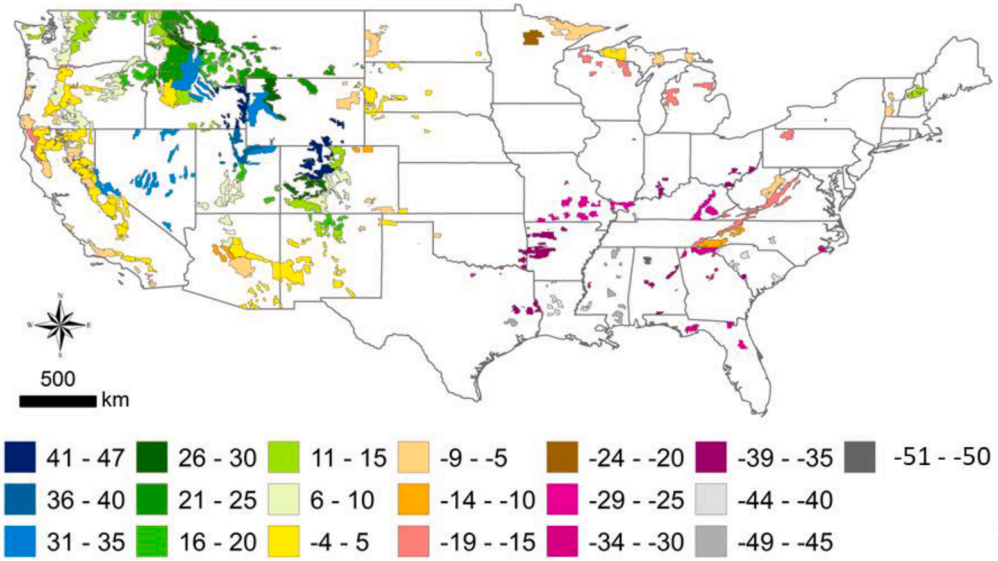

Fig. 5. Potential future turnover in species number for U.S. National Forests, for tree species established in northern North America.

grasslands separated eastern and western tree species. Nonetheless, low levels of eastern tree species occur in the central North American Great Plains grasslands and the Rocky Mountains that border the western side of the grasslands, with documented increases in tree densities since Euro-American settlement (Hanberry , 2021b). Land use change, resulting in frequent surface fire exclusion, but not climate change, has allowed increased tree entry into the Great Plains grasslands region (Hanberry , 2021b; Hanberry , 2022). However, in the future, a

synergistic interaction between land use and climate change is likely to strengthen the pattern of westward expansion by eastern tree species. According to these models, gains in the mountainous western U.S., including for example 47 tree species predicted for the White River National Forest in Colorado, are primarily from the diverse pool of tree species of the eastern U.S. Nonetheless, predicted climate space is not the same as realized ranges, even though potential climate space is based on where trees are recorded to occur (Early and Sax, 2014). Some potential locations are disjunct and likely were not realized in the past and will not be realized in the future (Hanberry , 2023b). Comparisons in changes are between suitable climate space both now and in the future, which do not translate directly to achieving and maintaining that area, due to various constraints that are not related to climate, including dispersal barriers and land use.

In administrative units that are predicted to lose native tree species and gain southern species, managers may be in the position to determine which endemic species or shifting species, native to more southern regions, to support under the stress of climate change. Desired tree characteristics may include tolerance to climate change, fires, and insects, while supporting biodiversity and other ecosystem services, such as forest products. Tree species of the eastern U.S. were present as minor constituents of western forests before Euro-American settlement (e.g., *Acer negundo, Celtis occidentalis, Fraxinus pennsylvanica, Ulmus americana*; Tatina and Hanberry, 2022), resulting in native status for some of these species. But eastern tree species may support eastern plants and animals, creating consequences for native species of the west (Livezey , 2009). Tree species from Mexico may be more compatible with western ecosystems and better options to consider than tree species from the eastern U.S.

For this set of relatively northern species, greatest number of species were predicted to be lost in most of the eastern half of the U.S. In terms of species loss, the William B. Bankhead National Forest in Alabama may lose up to 51 species of this set of tree species. However, species information is not available to correctly calculate southern limits of optimal conditions for many southern species because native tree species have current ranges restricted by the Atlantic Ocean. These species might persist under hotter conditions where there is a limited pool of competitors, as in Florida, even if some of Mexico's 3000 native tree species may replace tree species of the eastern U.S.

Operational drivers can create resistance or acceleration of compositional changes. Tree migration has received assistance from dispersal by animals for millions of years and humans for millennia (Tulowiecki and Larsen, 2015; Jara-Guerrero et al. , 2018). Forest management practices such as selective cutting and planting may prevent compositional change. A variety of tree ages occur in the U.S., but most forests are several decades old (Pan et al. , 2011). With limited overstory tree removal, long-lived, drought- and heat-tolerant native tree species may be able to hold growing space against faster-growing species that do not contain traits to tolerate climate change. In the U.S., management for pine and oak species currently helps maintain these species against competition by fire-sensitive species now that historical fire regimes are no longer in place (Bragg et al. , 2020). Humans can accelerate tree migration though planting and tree removal, while slowing forest transition through forest management and restoration.

4.2. Modeling limitations and uncertainty

The essential purpose of displaying the magnitude of climate change effects on species distributions is fulfilled by modeling, but uncertainty in modeling arises from multiple sources, in addition to the effects of non-climate factors on distributions. I modeled six future climates from five general circulation models and two emission scenarios. Five of the six climates had gains of 4.3 °C to 6.3 °C for North America by 2071–2100, but the UKESM1 general circulation model for the moderate SSP3–7.0 scenario projected an even hotter end-of-century future with an 8.8 °C gain for the continent. This latter general circulation model may be considered a later time step in warming and species response trajectories. While changing precipitation patterns also are important components of climate data, the primary range shifts occur in a northward direction dominated by temperature patterns. Downscaling of climate can create different outcomes, particularly for extreme events (Lopez-Cantu et al. , 2020). However, these downscaled climate variables may be the only ones available for the latest CMIP6 models and North America with application of a statistical method, rather than simple interpolation. Additionally, while variation occurs among climate data, the general magnitude and details of change remain similar at the continental scale.

Modeling approaches may influence models. A variety of classifiers are available, but random forests is very commonly applied due to accuracy and in any event, generally ensemble nonlinear classifiers find comparable solutions to maximize accuracy, despite different algorithms (Hanberry , 2023b). Selection of candidate climate variables also may affect models, even though these bioclimate variables are standard representations of temperature and precipitation for months, quarters, and years for species distribution modeling. Subsequent methods for reduction of variables also can produce different models, but recursive feature elimination is an approach to increase accuracy, albeit slightly; reduction to one temperature variable to avoid correlation likely will result in bias (Hanberry , 2023b).

Although about 30 % of the modeled tree species were predicted to lose climate space in the future, only 11 species were predicted to lose climate space in the future that was < 0.6 of current climate space, with no apparent bias resulting from the modeling process and variable selection. Commonalities did not occur in models with decreasing distributions due to important variables, with eight different most important variables, although these species distributions varied in being influenced by the coldest month and coldest quarter and precipitation of the warmest quarter, more than the overall influence by annual temperature, temperature of the warmest quarter, and precipitation during dry intervals. Also, no locations or range areas were shared, as two of these species occurred with restricted ranges in California (*Pinus sabiniana, Quercus douglasii*) or a restricted range in California and the southwestern U.S. (*Pinus longaeva*) or had increasing wide ranges from California and the Pacific Northwest (*Abies grandis*) to the mountainous western U.S. (*Acer glabrum*). *Cercocarpus ledifolius* and *Pinus albicaulis* were intermediate in range area but occurring at different elevations, whereas two species occurred in the southeastern U.S. (*Quercus laevis, Pinus palustris*), and two species were wide-ranging in the eastern U.S. (*Asimina triloba, Juglans cinerea*).

While models appeared to exhibit no particular biases due to constraints from one variable, some climate models fit species distributions better than others. For example, six species with relatively restricted ranges (*Abies grandis, Cornus nuttallii, Pinus longaeva, Quercus douglasii, Sequoiadendron giganteum, Umbellularia californica*) in the western U.S. had predicted distribution centers south of current predicted distribution centers under some future climates. Predicted current climate space did not match well with the observed ranges from samples for these species, even though species with similar observed ranges had predicted current climate space that resembled observed ranges. Models of climate space are not equivalent to realized ranges, although realized ranges are contained within models of climate space.

Models of climate space may change as recorded observations and observed ranges change. Observations may be incomplete due to limited sampling throughout the entire climate range of some species, particularly rare species or species with imbalanced distributions. For this study, one uncommon species, *Ulmus thomasii*, was predicted to shift out of the U.S., but samples did not extend to very rare southern populations. *Ulmus thomasii* is concentrated yet uncommon in the Great Lakes region, of Minnesota, Wisconsin, and Michigan in the U.S. and Ontario and Quebec in Canada, with even more rare records extending to Arkansas and Tennessee (Scholz , 1957; Kartesz , 2015; University of Guelph Arboretum. , 2021; iNaturalist , 2024). Therefore, the model

captured the majority of the population and not the outliers. Indeed, models will more accurately predict concentrated observations over dispersed observations so that models for rare species with imbalanced distributions will be less useful than for more abundant species or rare species with more balanced distributions. Observations also may be inadequate because species ranges are in transition since Euro-American settlement, due to land use and disturbance changes that affect historical balances (Hanberry , 2021a). Some historically-dominant species, such as *Pinus palustris,* have contracted ranges that do not contain the climate space of the species, although it is possible that loss of genotypes or subspecies may have resulted in actual loss of climate tolerances. If species observations do not capture the full climate range, then models will not be accurate depictions of potential tolerance. Additionally, geographic restrictions, such as the Gulf Coast, may prevent observations of the full potential climate space of a species.

5. Conclusions

Temperature warming beyond the normal range of variation is likely to have negative effects on survival, growth, and reproduction of species. While potential climate space is not the same as realized ranges, modeling of species distributions allows determination of potential magnitude of change in response to climate. Movement of predicted distribution centers from 20 ka to 1900–1990 demonstrated that tree species will need to cover more ground than may be possible by 2071–2100 to remain in climate similar to their current climate space. For these 119 tree species abundant in northern North America, predictions are for increased climate space in the future for most tree species, likely because the North American land mass has greater area at higher latitudes compared to lower latitudes, but with greatest loss of tree species in the eastern U.S. Eastern and western tree species may increase intermixing in time, based on predictions under future climate change in synergy with realized outcomes from land use change; in particular, eastern tree species may replace high-elevation western species. Although generally not native to the western U.S. and Canada, southeastern U.S. tree species are a source of future tree species and land managers may consider evaluating these species for desired characteristics that are tolerant of climate change and can support species and other ecosystem services.

CRediT authorship contribution statement

Brice B. Hanberry: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization.

Declaration of competing interest

The author declares no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Model predictions are posted at Forest Service Research Data Archive: https://www.fs.usda.gov/rds/archive/catalog/RDS-2023-0057.

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