Improving the temporal transferability of species distribution models under climate change by incorporating historical species-climate relationship

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Abstract

Understanding how species will respond to climate change is one of the current key challenges in ecology and nature conservation. The tempo-spatial variations of climate makes it more challenging to predict species responses to climate change across their entire ranges. Species distribution models have been widely used for identifying how species distributions respond to climatic drivers. Despite the spatial transferability of SDMs has been largely tested, validation of their temporal transferability is still rare. In addition, there is still no consensus regarding how integration of temporally independent data can improve the reliability of model predictions under different time. Here, we modelled the distribution of white oak (*Quercus alba*) across its entire range in the eastern United States for the 1900s and the current. We compared predictive performance, predicted suitability and distributions, and predictor's importance of SDMs accordingly, and quantified climate novelty between the two time periods to assess the temporal transferability and predictive accuracy of SDMs. We found that the SDM fitted with the 1900s climate outperformed that calibrated with the current climate, suggesting its higher transferability from the 1900s to the current. Such difference in transferability between SDMs fitted with the 1900s and current climates may be attributed to the climate novelty and change in limiting factors for white oak distributions during model transfer. Our results demonstrate the temporal transferability of SDMs on predicting temporally independent species distribution across its entire range. With the increased availability of historical species occurrences, incorporating such data into SDMs will increase the reliability of model predictions under future climate change.

Keywords

Species distribution model, temporal transferability, extrapolation, interpolation, climate novelty

Introduction

Climate change has broadly influenced the growth rate, mortality, and geographic distributions of plant species worldwide (e.g. Scheffers et al., 2016), leading to changes in forest composition (Pederson et al., 2015). Underlying this overall pattern, a large amount of variation exists. For example, climate is not changing evenly across space (Prasad et al., 2020), neither over time. In the eastern United States, the last century has witnessed increased mean annual temperatures in the Midwest and Northeast while the Southeast had areas with not only increased but decreased temperature (Zhu et al., 2012). At the same time, climate shifts of more than 100 km across the Northeast and Upper Midwest in terms of spatial velocity have been observed (Loarie et al., 2009). Most of this region experienced growing season temperatures during the 1971 to 2000 period that were cooler than those during the 1911 to 1940 period (McEwan et al., 2011). In addition, changes in climate are not affecting all species equally as species may respond to different climatic drivers across their ranges (Bouchard et al., 2019; Matthews et al., 2019), which leads to a complexity of changes in species climatically suitable habitats (Iverson & McKenzie, 2013). Therefore, the tempo-spatial variations in climate makes it challenging to predict the responses of different species to climate change across space and time.

The influence of climate change on range shifts of plant species has been identified through the rapid development of ecological niche models (ENMs), also termed species distribution models (SDMs) (Davis & Shaw, 2001; Rehfeldt et al., 2006; Iverson et al., 2008; Thuiller et al., 2008; Lavergne et al., 2010). SDMs, basically, build statistical associations between species occurrence and current climate, helping us understand how species respond to a full suite of climatic variables. SDMs are important tools for conservation biology and biogeography and have been used to project species responses under different climate scenarios (Pearson & Dawson, 2003;

Thuiller et al., 2005; Hijmans & Graham, 2006). Reliable predictions of species' response will inform about potential climate-driven shifts in their suitable habitats and aid climate-smart conservation and management plans (Iverson et al., 2008; Iverson & McKenzie, 2013; Peterson et al., 2011; Guisan et al., 2013; Early & Sax, 2014). SDMs usually capture contemporary climate-distribution relationship and then predict current and future species distributions to new climates and geographic space under the assumption of niche conservatism (Peterson & Nyári, 2008; Nogués-Bravo, 2009; Zimmerman et al., 2010; Peterson, 2011; Svenning et al., 2011). When SDMs are transferred across space and/or time to new environmental conditions (Guisan & Thuiller, 2005; Elith & Leathwick, 2009; Peterson et al., 2011), they assume that the suitability of climate conditions for species remains constant across time and space. However, the transferability of SDMs has been considerably discussed and criticized because of the assumption of niche conservatism (Elith & Leathwick, 2009; Wiens et al., 2009; Araújo & Peterson, 2012).

The evaluation of SDM's transferability is one of two main approaches to assess the dynamics of a species' climate niche (Guisan et al., 2014). Some early justifications of conservatism theoretically aim at fundamental niches rather than realized niches (Wiens & Donoghue, 2004; Araújo & Peterson, 2012). Several studies have demonstrated that the fundamental niche, which is primarily determined on environmental conditions (Hutchinson, 1957), can remain unchanged across time and space (Peterson et al., 1999; Wiens & Graham, 2005) while both similarity and differences in estimated realized niches across different regions or times have been reported (Fitzpatrick et al., 2007; Warren et al., 2008; Hof et al., 2010; Medley, 2010). For example, Peterson (2003) found that the potential geographic range of invasive species can be precisely estimated by the realized ecological niche characteristics of their native range. Martínez-Meyer

& Peterson (2006) constructed SDMs for North American plants (mostly trees) based on present-day and the Last Glacial Maximum (LGM) climatological summaries, demonstrating the transferability of SDMs across time by comparing model outputs with the independent occurrence data. Conversely, Broennimann et al. (2007) observed the difference in estimated realized niches between native and non-native ranges of invasive species, which may be evidence of a climate-driven niche shift. Likewise, Boiffin et al. (2017) argued that the niche conservatism is an erroneous assumption when modeling the realized niche because the SDMs calibrated in the native range of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) failed to predict the climate suitability in its introduced range in Europe where non-analogue climates occur. Most recently, a synthesis of 86 studies for 434 invasive species reported that most of the species largely conserve their realized climatic niche across time and space with a tendency to occupy similar climates in both native and introduced ranges even though the assumption of niche conservatism was not satisfied in most studies (Liu et al., 2020a). However, among those studies, the lowest rejection rate of the niche conservatism hypothesis was found when using SDM approaches (Liu et al., 2020a), which suggests that SDMs may be reliable when transferred to new geographic spaces and climates. In addition, Peterson (2011) reported that the characteristics of a species' ecological niche seem to be highly conserved over short-to-moderate time spans.

Despite the spatial transferability of SDMs has been largely tested, validation of their temporal transferability is still rare. The spatial transferability of SDM, the ability of projecting the modelled relationship of SDM to new space, has been well demonstrated (Randin et al., 2006; Peterson et al., 2007; Qiao et al., 2019; Feng et al., 2019). Although less attention has been paid to temporal transferability, the predictive ability of SDMs across time has been supported by several empirical studies (Verela et al., 2009; Dobrowski et al., 2011; Tuanmu et al., 2011; Wogen, 2016). Based on the most recent evidence, whether SDMs are transferrable across time and space may depend on several factors such as climate novelty/dissimilarity (Elith et al., 2010; Fitzpatrick et al., 2018; Feng et al., 2019; Liu et al., 2020b), model calibration (Guevara, Gerstner, & Kass, 2017; Roberts et al., 2017; Norberg et al., 2019; Qiao et al., 2019), and taxonomic groups and species differences (Dobrowski et al., 2011; Liu et al., 2020b). Both simulations (Qiao et al., 2019) and empirical studies (Morán-Ordóñez, 2017) found better transferability of SDMs for areas with similar climate. Likewise, the decrease in predictive skill of SDMs was expected in response to climate novelty (Roberts et al., 2017; Fitzpatrick et al., 2018). Model over-parameterization, fitting complex interactions between climatic variables, may lead to decreased accuracy when models are extrapolated to new space and climates (Roberts et al., 2017; Qiao et al., 2019). One appropriate way of reducing the influence of complexity is including the most likely limiting predictors for species distributions based on expert knowledge and biological justification, which may improve model transferability by producing more ecologically realistic predictions (Guevara, Gerstner, & Kass, 2017; Norberg et al., 2019). Within taxonomic group, species differences exerted great influence on the transferability of SDMs (Dobrowski et al., 2011; Rapacciuolo et al., 2012; Smith et al., 2013). SDMs for species with narrower niches had higher transferability than those with wider niches (Kharouba et al., 2009).

SDMs have been widely used to understand the climatic response of tree species distributions in the eastern US and project potential changes in their suitable habitats under climate change (Iverson & Prasad, 1998; Iverson et al., 2008; Iverson et al., 2019). Most of them related tree species distributions to current climate and predicted potential suitable habitats under future conditions (McKenney et al. 2007a, 2007b; McKenney et al., 2011). Many species distributions may be better calibrated with 20th century (or earlier) climates than those of the most recent decades because of their strong ecological memory (Fitzpatrick et al., 2018). The long-lived trees are likely to be in increasing disequilibrium with the current climate, thus fitting models using current climate may not fully reflect the limiting climatic factors for tree distributions (Goring & Williams, 2017). Although future climate novelty is within the range of values experienced in the past under the most extreme RCP forecast (Charney et al., 2016; Fitzpatrick et al., 2018), SDMs calibrated using climate from each 1,000-year time frame of the past 13,000 years have resulted in different climate suitability predictions for three tree species (Maiorano et al., 2013). Further, Maiorano et al. (2013) found that the predicted climate suitability to both current climate and future climate derived from SDMs fitted to one of the time frames was limited compared to the predictions by SDMs calibrated with data pooled through time. Therefore, without confirming temporal transferability, SDMs merely trained with current species distributions and climate may not reliably project the effects of future climate on tree species distributions.

To overcome this limitation, we test the temporal transferability of SDMs using a temperate hardwood species, the white oak (*Quercus alba*), which is one of ecologically and commercially important species widely distributing across the eastern United States. Its current potential distribution and future suitable habitat has been well studied using SDMs with good model performance (Prasad et al., 2020). To our knowledge, no study has yet been done to test whether the SDM calibrated with its climate-distribution in the past is temporally transferable to current climate predicting suitable habitats of white oak. We propose a new approach for reconstructing the 1900s (i.e.1895-1920, t1) presence localities of white oak using tree cores collected by the U.S. Forest Inventory and Analysis (FIA) program in the eastern United States. We buffer those localities to sample the closest presence localities from the current (i.e. 2000-2016, t2) presence localities to avoid the influence of land use history, biotic interactions, and other non-climatic factors that may impede white oak from occupying its suitable habitats leading to absence across time. We use the presence localities of two different time frames to build SDMs for the 1900s (SDM_{t1}) and the current (SDM_{t2}) distributions of white oak with their contemporaneous climate conditions. Finally, we interpolate and extrapolate SDMs to the withheld test data and to the entire geographic space within and beyond the time fames in which the models are developed, respectively. Our goals are to: 1) investigate how well the SDMs for white oak can be transferred across two different time frames by examining model predictive ability of SDMs and the predicted habitat suitability of white oak between two time frames, the 1900s vs. the current; 2) test if climate novelty could influence temporal transferability of SDMs by comparing the model predictive ability between interpolation and extrapolation; 3) test if incorporating historical species-climate association into SDMs could improve the reliability of SDMs when projecting effects of future climate change onto a species' entire range.

Materials and Methods

Species occurrence

To test the transferability of SDMs across time, we focus on modeling potential distributions across the entire range for white oak at two different time frames: 1900s (t1) and current (t2). Its current distribution and projections of future suitable habitats have been well studied using SDMs with good model performance (Prasad et al., 2020). The localities of white oak for the 1900s were approximated using site tree records in inventory plots from the U.S. Forest Inventory and Analysis (FIA) across the eastern United States. The cores of site trees can estimate tree age and thus indicate the time period the tree has been present in that locality. Cores of site trees have been recently used to understand annual growth and climate relations in states from Maine to Ohio (Canham et al., 2018). With the known age of site trees, we selected all plots with white oak as site trees already present around the 1900s (1895-1920) across its entire range to reconstruct the 1900s presence localities (Figure 1). This sample of presence-only plots was used to construct the SDM_{t1}. To obtain the sample of presences for the SDM_{t2}, we sampled the closest current presence locality to each of the1900s presence point to reduce problems caused by spatial sampling biases (Merow et al., 2013; Boria et al., 2014). This would ensure the same spatial coverage on both datasets and reduce the effects of land-use changes over the years (e.g. Chen & Leites, 2020), changes in biotic interactions due to anthropogenic effects (Liebhold et al., 2017), and the effects of other non-climatic factors. This sampling approach allowed us to focus on the suitable habitats defined by climatic conditions; this is, any potential difference in temporal transferability between SMD_{t1} and SDM_{t2} would be mainly attributed to the changed climatic conditions between the 1900s and the current. Even though this sampling approach ensures that both time periods have the same spatial extent, it may have the drawback of restricting the current climates sampled if a spatial expansion of the white oak range had occurred between the 1900s and the present. However, such possibility is small given the slow or lack of migration in tree species in the last century (Zhu, Woodall, & Clark, 2012). In contrast, the effects of land-use change and other anthropogenic effects leading to the absence of white oak on present distribution are well-documented (Abrams 2003; Foster et al. 2003; Chen & Leites, 2020). To avoid any marginal presences or erroneous records, we removed one locality of white oak in North Dakota that was very far away from the boundary of white oak's range (Little, 1971; black dashed line in Figure 1). A total of 1,765 presence records for both 1900s and current distributions of white oak comprised the final sample (Figure 1).

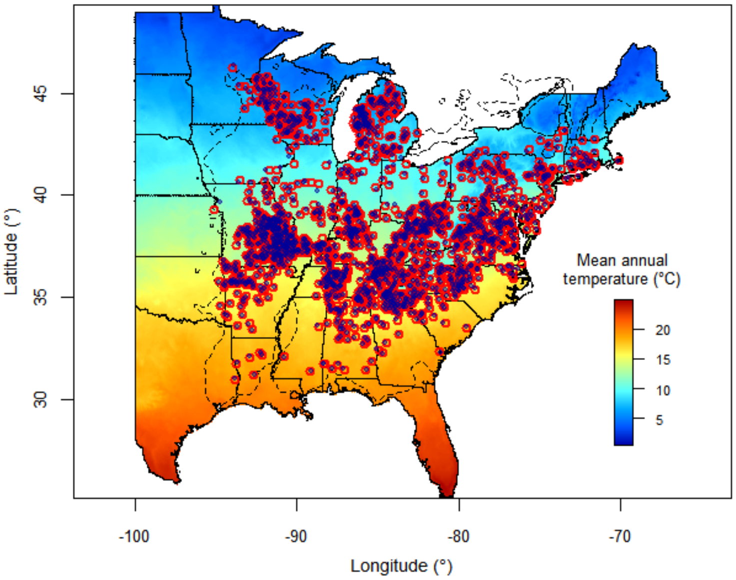

Figure 1 The geographic extent of the study in the United States. The dashed line shows the Little's range for white oak (Little, 1971). A total of 1,765 presence localities of white oak during 1895-1920 (the 1900s, red circles) and 2000-2016 (current, blue dots) are shown with the 30-yr normal of mean annual temperature during 1970-2000 (Wang et al., 2016).

Climate data

We obtained 30-yr climate normals at 1 km resolution from the AdaptWest database (AdaptWest Project, 2015; Wang et al., 2012) for the 1900s (1901-1930) and the current (1981-2010) time frames. A suite of 19 downscaled climatic variables was chosen as predictors for the two different time frames (Table 1). These variables represent four groups reflecting different aspects of climatic conditions for white oak including temperature, precipitation, moisture, and climate extremes.

Table 1 The 19 Climatic variables used to develop the SDMs for white oak in two different time frames.

Acronyms	Variable
	Temperature-related variables
MAT	Mean annual temperature (°C)
MWMT	Mean warmest month temperature (°C)
MCMT	Mean coldest month temperature (°C)
TD	Temperature difference between MWMT and MCMT, as a measure of continentality (°C)
DD<0	Degree-days below 0°C, chilling degree-days
DD>5	Degree-days above 5°C, growing degree-days
DD<18	Degree-days below 18°C, heating degree-days
DD>18	Degree-days above 18°C, cooling degree-days
NFFD	The number of frost-free days
FFP	Frost-free period
bFFP	The day of the year on which FFP begins
eFFP	The day of the year on which FFP ends
	Precipitation-related variables
MAP	Mean annual precipitation (mm)
MSP	May to September precipitation (mm)
PAS	Precipitation as snow (mm). For individual years, it covers the period between august in the previous year and July in the current year
	Moisture-related variables
AHM	Annual heat-moisture index (MAT+10)/(MAP/1000))
SHM	Summer heat-moisture index ((MWMT)/(MSP/1000))
	Temperature extremes
EMT	Extreme minimum temperature over 30 years
EXT	Extreme maximum temperature over 30 years

For more details about the variables, see: Wang et al., 2012; Wang et al., 2016.

Model calibration, performance, and transferability

The overall approach for model calibration and model transfer across time is illustrated in Figure 2. For each time period, we developed a SDM using the MaxEnt algorithm linking the presence-only data with their corresponding 19 climatic variables (SDM_{t1} and SDM_{t2}). MaxEnt uses presence-only data to calibrate SDM, and thus it is suitable for modeling the 1900s distribution of white oak where confirmed absence data was not available. This algorithm estimates species' relative occurrence rates by minimizing the relative entropy between the probability density of species' presence data and the training background (Elith et al., 2010). We randomly selected 10,000 background points (i.e. 'pseudo-absences') from within the geographic region across the eastern United States. All 19 climatic variables were used during model calibration without removing highly correlated variables. However, by default, MaxEnt reduces the number of variables in the final model using regularization to minimize over-parameterization (Phillips & Dudík, 2008; Elith et al., 2011). In addition, one of the most recent studies documented little impact of correlation on model training for MaxEnt algorithm (Feng et al., 2018). We used Maxent with default settings including default feature classes and the regularization multiplier (Elith et al., 2011; Phillips, Anderson, & Schapire, 2006), which have been demonstrated to work well by many empirical studies (Phillips & Dudík, 2008). Therefore, keeping the modelling approach and default settings consistent to develop the SDMs for the 1900s and the current distributions of white oak made model outputs comparable when testing their temporal transferability.

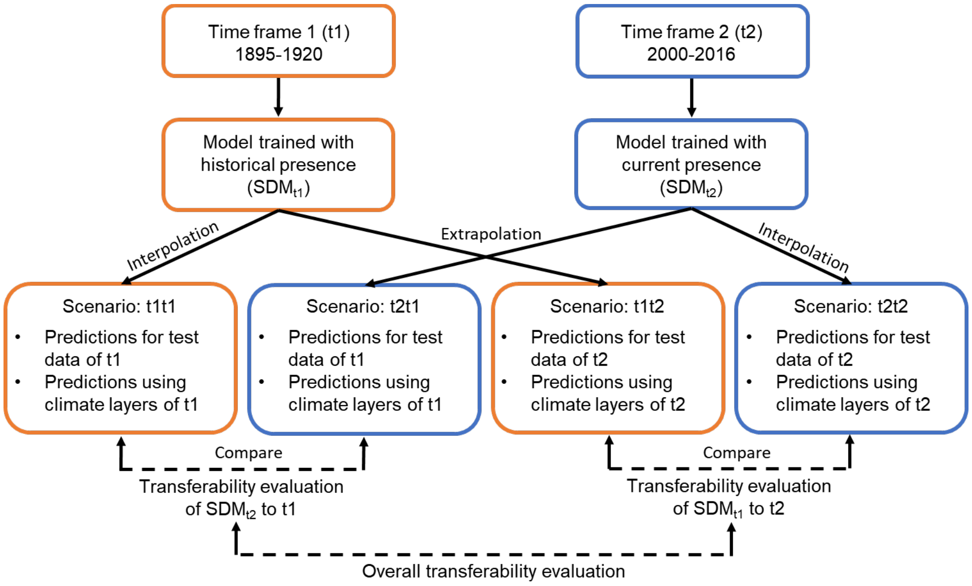

Figure 2 Outline of the analytical design. For each time frame, 75% of the presences and its contemporaneous climate layers were used to build species distribution models (SDM_{t1} and SDM_{t2}, respectively). Each model was used to predict the withheld 25% test data and the entire geographic space of the study within the time frame (e.g. interpolation) and beyond the time frame (e.g., extrapolation) in which the models were developed to predict/hindcast habitat suitability, respectively. The temporal transferability was evaluated by comparing the predictions derived from SDM_{t1} and SDM_{t2} for time frame t1 and t2 separately, leading to four different scenarios.

SDM_{t1} and SDM_{t2} were calibrated using 75% of the presence localities randomly split and their contemporaneous 19 climate variables. The remaining 25% of presence localities were withheld as test data for model evaluation and transfer. Each model was used to predict the withheld 25% test data and the entire geographic space of the study within the time frame (e.g. interpolation) and beyond the time frame (e.g., extrapolation) in which the models were developed. This approach resulted in two interpolative (hereafter 't1t1' and 't2t2') and two extrapolative scenarios (hereafter 't2t1' and 't1t2') (Figure 2): a) t1t1, 1900s interpolation for 1900s climate, using SDM_{t1} to predict suitability for the test data withheld when building SDM_{t1}; b) t2t1, current extrapolation, using SDM_{t1} to hindcast suitability for the test data withheld when building SDM_{t1}; c) t1t2, 1900s extrapolation, using SDM_{t1} to predict suitability for the test data withheld when building SDM_{t2}; d) t2t2, current interpolation, using SDM_{t2} to predict suitability for the test data withheld when building SDM_{t2}.

To evaluate model fit based on 75% training data, we used one threshold-independent evaluation metric - the area under the receiver operating characteristic curve (AUC), and two threshold-dependent indices - minimum training presence omission rate (OR_{MTP}) and 10% training omission rate (OR_{10}). The OR_{MTP} indicates the proportion of test data presences with predicted probability values lower than the threshold associated with the zero omission rates in the training data. The OR_{10} indicates the proportion of test data presences with predicted probability values lower than the threshold that arises from the training data and is equal to the probability value that leaves 10% of the training presences with the lowest predicted suitability below itself. OR_{MTP} values > 0 or OR_{10} values > 10% indicates overfitting (Muscarella et al., 2014). We used both of OR_{MTP} and OR_{10} because an over-fitted SDM could have an OR_{MTP} of 0 but > 10% OR_{10} when the predicted suitability had a long tail among the low predicted values for withheld test data. We also calculated the difference between AUC_{TRAIN} and AUC_{TEST}, with values > 0 indicating over-parameterization.

To quantify model accuracy, the ability to predict potential species distributions within the time frame in which the model was developed, we calculated commonly used performance metrics such as AUC, true skill statistics (TSS), and sensitivity (proportion of correctly predicted presences; 0-1 values) on 25% withheld test data. The probabilities predicted by the SDMs were converted to presence/absence using the 10% omission rate threshold used for calculating OR_{10}. AUC values range from 0 to 1 with values > 0.8 indicating good discriminative ability (Swets, 1979); TSS values can range from -1 to 1, with values above 0 indicating models better than random (Allouche et al., 2006).

To evaluate the temporal transferability of the SDMs, i.e. their ability to predict potential species distributions in a different time frame, we calculated single-direction (TI_{t1t2} and TI_{t2t1}) and overall transferability indices ($TI_{overall}$) based on AUC scores (Tuanmu et al., 2011) as:

$$TI_{t1\rightarrow t2}=1-\frac{|AUC_{t1t1}-AUC_{t1t2}|}{0.5} \tag{1}$$

$$TI_{t2\rightarrow t1}=1-\frac{|AUC_{t2t2}-AUC_{t2t1}|}{0.5} \tag{2}$$

$$TI_{overall}=1-\frac{0.5\times(TI_{t1\rightarrow t2}+TI_{t2\rightarrow t1})}{1+|TI_{t1\rightarrow t2}-TI_{t2\rightarrow t1}|} \tag{3}$$

where AUC_{t1t1} and AUC_{t2t2} are AUC values for interpolation of t1 and t2, respectively. And AUC_{t1t2} and AUC_{t2t1} are AUC values for extrapolation of t1 and t2, respectively. Their values range from 0 to 1, with values close to 1 indicating good transferability. In addition, we calculated Schoener's *D* statistic, the most common measure of niche overlap (Schoener 1970; Broennimann et al., 2012), to test temporal transferability of the SDMs across the geographic space. Using scenario t1t2 as an example, the SDM_{t1} was extrapolated to map suitability under current climate. This extrapolated suitability map was compared with the interpolative suitability map generated by SDM_{t2} to calculate Schoener's *D* statistic. Therefore, the Schoener's *D* statistic evaluates the pairwise similarity between the extrapolation of SDM_{t1} and interpolation of SDM_{t2}, reflecting the model transferability across the geographic space. The value ranges from 0 (no overlap) to 1 (identical predictions). Finally, we converted the predicted habitat suitability (probabilities) maps into binary species presence/absence maps based on the 10% omission rate threshold used for calculating OR_{10}. A high level of agreement in predicted presence/absence between the two models indicates good transferability for a time frame.

Quantification of climate novelty and limiting factors

Climate novelty may lead to decreased predictive skill of the SDMs when the models are transferred across time (Fitzpatrick et al., 2018). We quantified climate novelty between the training sample and its interpolative and extrapolative regions by calculating multivariate environmental similarity surfaces (Elith et al., 2010). This measure of similarity calculates, for each climate variable, the closeness of any given point in the interpolative or extrapolative regions to the probability distribution of the climate variables of the reference points (i.e. the points used to fit the model) (for more details about the method, see Appendix S3 in Elith et al. 2010). We related the pattern of climate novelty to predicted suitability across geographic space for the four scenarios illustrated in Figure 2, and between climate novelty and transferability. When the SDMs are transferred beyond the time frame where the model was developed, the predicted suitability of areas with high level of climate novelty/dissimilarity should be interpreted with caution. To quantify whether the climate factors driving habitat suitability have changed across time frames, we generated maps showing the limiting factors for habitat suitability for SDM_{t1} and SDM_{t2}. The limiting factor was defined as the most influential variable for the predicted suitability at each pixel based on the modeled response curves between the fitted functions and each predictor variable for SDM_{t1} and SDM_{t2} derived from the MaxEnt algorithm (Elith et al., 2010).

Results

Model accuracy and transferability

Both SDM_{t1} and SDM_{t2} performed well for interpolation based on the threshold-independent and threshold-dependent metrics (Table 2). The negative AUC_{DIFF} values, 0 OR_{MTP}, and $OR_{10} < 0.1$ suggest that both SDM_{t1} and SDM_{t2} were not over-parameterized. The AUC_{TRAIN} scores were both > 0.8 for SDM_{t1} and SDM_{t2}. The AUC_{TEST} values of two SDMs were both > 0.85 with sensitivity > 0.9 and TSS > 0.5, indicating a good discrimination ability in the test data within the respective time frames in which the SDMs were developed.

Table 2 Evaluation metrics of MAXENT SDMs for white oak in two different time frames.

Model	Scenarios	AUC_{TEST}	AUC_{TRAIN}	AUC_{DIFF}	OR_{MTP}	OR_{10}	Sensitivity	TSS
SDM_{t1}	t1t1	0.869	0.822	-0.046	0.000	0.091	0.909	0.576
SDM_{t2}	t2t2	0.863	0.817	-0.046	0.000	0.057	0.943	0.570

SDM_{t1}– SDM fitted with 1900s presence and climate. SDM_{t2}– SDM for current presence and climate. Metrics were calculated using the 25% withheld test data. AUC_{TEST}– AUC based on predicted values in the test data. AUC_{TRAIN} - AUC based on predicted values in the training data. AUC_{DIFF}– AUC_{TRAIN} - AUC_{TEST}. OR_{MTP}– minimum training presence omission rate. OR_{10}– 10% training omission rate. TSS– true skill statistic.

Both SDMs developed for time frames t1 and t2 showed good temporal transferability when projecting across time frames (Table 3). The AUC values for scenario t1t2 and t2t1 were > 0.85, sensitivity values > 0.92, and TSS values > 0.56. However, there is a slight difference between the AUC, sensitivity, and TSS values for the two SDMs when transferring them across time frames. TI for t1t2 was slightly higher than that for t1t2. This suggests that SDM_{t1} was slightly more transferable than SDM_{t2}. Likewise, Schoener's *D* statistics indicates that SDM_{t1} predictions resulted in more similar habitat suitability maps across geographic space than SDM_{t2} when the two SDMs were transferred to different time frames. Nevertheless, the overall transferability of two SDMs across time frames was still good ($TI_{overall}$ = 0.969), and so were two single-direction TI's for SDMt1 and SDMt2, 0.933 and 0.926, respectively. Therefore, SDMs were transferable beyond the time frame in which the models were developed for predicting species occurrences in withheld test data of each time frame.

Table 3 Evaluation metrics of model temporal transferability for white oak between two frames.

Scenarios	AUC	Sensitivity	TSS	TI	Schoener's *D* statistic	$TI_{overall}$
t1t2	0.854	0.925	0.567	0.987	0.933	0.969
t2t1	0.856	0.921	0.569	0.972	0.926	

Metrics were calculated based on the suitability values predicted by the model developed for time frame t1 (SDM_{t1}) for test data in time frame t2 (scenario t1t2) and *vice versa* (scenario t2t1).

Habitat suitability across the white oak geographic range

In general, SDM_{t1} and SDM_{t2} had good ability for predicting white oak suitable habitats under their contemporaneous climate (i.e., the 1900s climate and current climate, respectively) across the geographic space. All high suitability areas were predicted within Little's (1971) white oak range whereas relatively lower predicted suitability was outside of the species range (on-diagonal Figure 3a). Comparing the suitability maps between scenario t1t1 and t2t2, we found that the interpolative prediction for the 1900s and current climate were similar, suggesting that the distribution of white oak suitable habitats did not substantially shift across time frames (on-diagonal Figure 3a). However, the models point to areas where suitability may have changed, particularly around the northern range of white oak and the lower mid-Atlantic region, with relatively higher suitability predicted by SDM_{t2} and lower suitability predicted by SDM_{t1}.

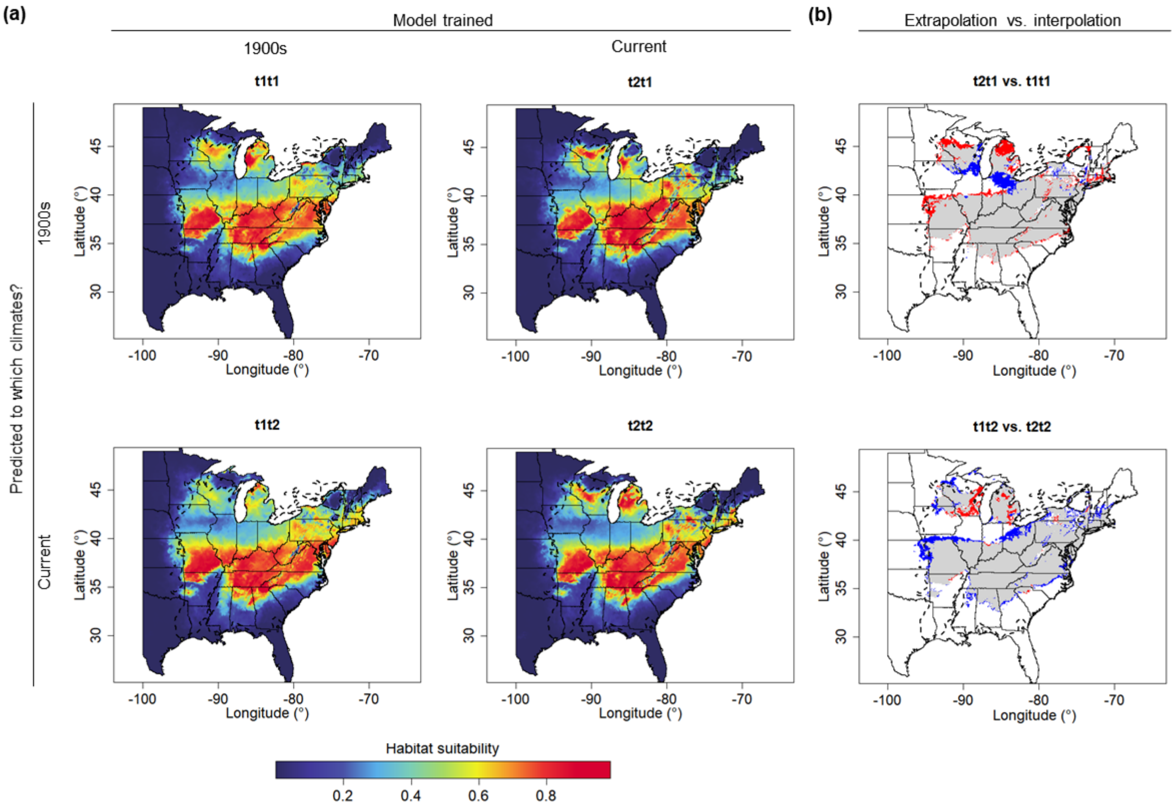

Figure 3 Distribution of habitat suitability and predicted presence/absence of white oak in geographic space by SDM$_{t1}$ and SDM$_{t2}$. The black dashed line indicates Little's range for white oak (Little, 1971). (a) Distribution of habitat suitability maps for each scenario: t1t1, t2t1, t2t2, and t1t2. (b) Spatial comparison of presence/absence predictions between two SDMs: gray = areas modeled as presence by the two models, red = presence only predicted by the ENM$_{t1}$, blue = presence only predicted by the ENM$_{t2}$, and white = absence.

A great deal of agreement was found in the predictions of habitat suitability by SDM$_{t1}$ and SDM$_{t2}$ across the geographic space when the models predicted across time frames, indicating good overall transferability of SDMs across time frames (off-diagonal in Figure 3a). Accordingly, suitable habitats predicted by the two SDMs were consistent in most of regions in the southern U.S.

However, the predicted suitability around the leading edge of white oak showed different patterns between the two models (upper panel of Figure 3a for t1, and lower panel of Figure 3a for t2). The mapped agreement and disagreement in predictions of presence/absence for the four scenarios is presented in Figure 3b. Relatively higher disagreement between the two SDMs was found when hindcasting presence/absence onto the 1900s climate with SDM$_{t2}$, as compared with predicting onto current climate with SDM$_{t1}$ (Figure 3b), specifically in the northwest edge of the distribution in the 1900s where SDM$_{t1}$ predicted presence while SDM$_{t2}$ failed to do so. However, SDM$_{t2}$ predicted more species presence in the lower bound of the Midwest. In addition, as can also be seen in Figure 4, SDM$_{t2}$ predicted significantly smaller values of habitat suitability than SDM$_{t1}$ for both t1 (paired t-test, $t = 7.15$ and $p< 0.01$) and t2 (paired t-test, $t =2.63$ and $p< 0.01$). Even though these differences were small in terms of predicted probability values, they may result in a great amount of difference in the binary prediction of presence/absence with a given threshold for thousands of pixels in the geographic space. Differences in habitat suitability values suggest that the climatic associations captured by two SDMs from their respective time frames were different.

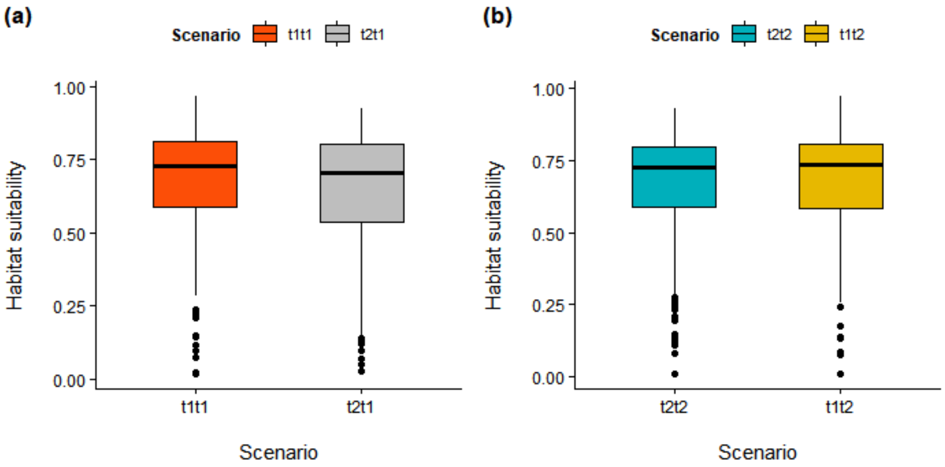

Figure 4 Box plot of predicted habitat suitability from two SDMs for the same withheld test data in two different scenarios: (a) t1t1 versus t2t1, comparison of predicted suitability between SDM$_{t1}$ and SDM$_{t2}$ for withheld test data of time fame t1, (b) t2t2 versus t12, predicted suitability between SDM$_{t1}$ and SDM$_{t2}$ for withheld test data of time fame t2.

Climate conditions and limiting factors

Comparing the climate conditions between training data and interpolative projected regions for SDM_{t1} and SDM_{t2} (Figure 5a and 5d), we found that the climate conditions were not considerably different across the entire range of white oak. The most similar climate conditions were found in the focal part of white oak range for both interpolative scenarios t1t1 and t2t2.

However, the climate conditions between training data and extrapolative projected region (t1t2 and t2t1) was slightly less similar than the interpolative projected region (Figure 5b and 5c). This pattern confirmed the slightly lower predicted ability by the two models beyond the time frames where the models were developed (Figure 3a). When projecting onto the different time frame, the climate similarity for SDM_{t1} was generally higher than that for SDM_{t2} specifically in the northern range of white oak. This pattern was consistent with the slightly higher transferability of SDM_{t1} (Table 3). A notable difference existed in the predicted presence for white oak when SDM_{t2} was projected to the 1900s climate in the very upper corner of Midwest, which could be attributed to the dissimilarity of climate conditions (Figure 3b and Figure 5b).

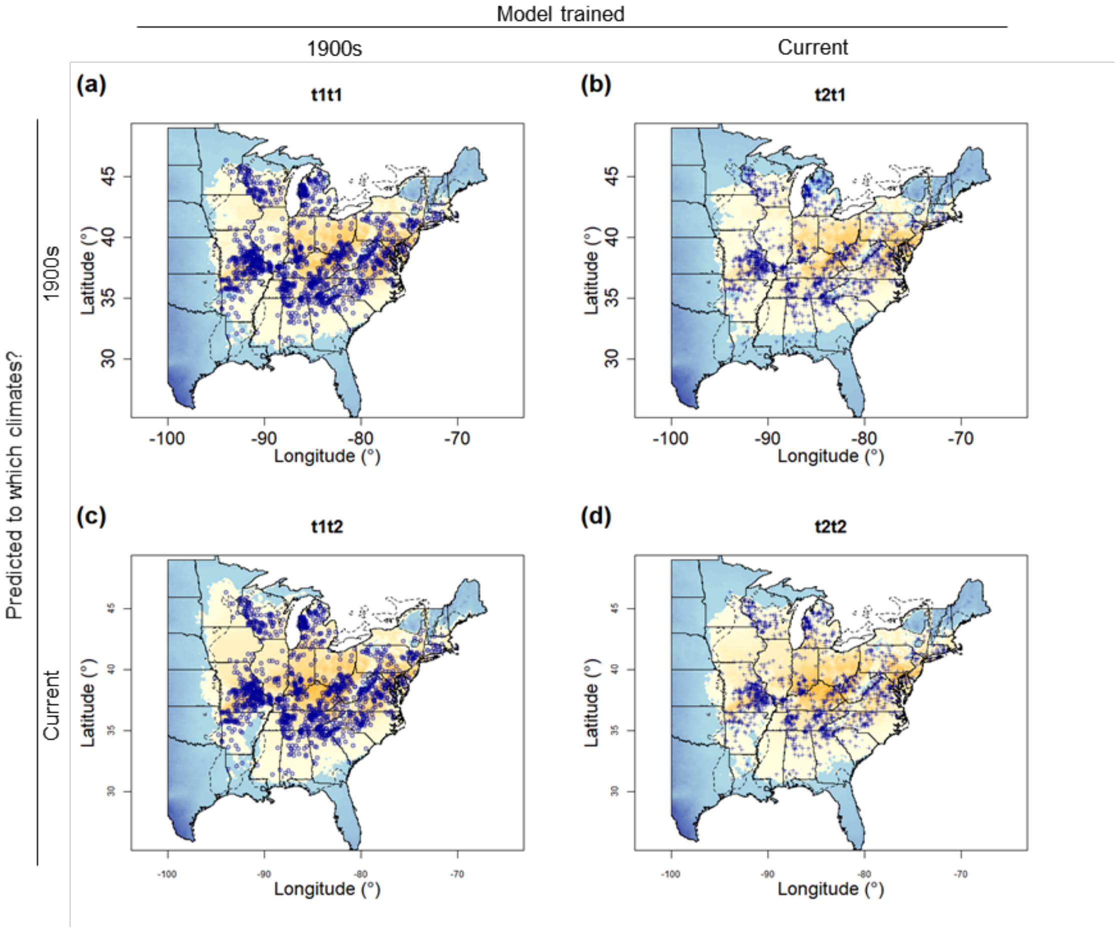

Figure 5 Comparison of climate conditions between training data and projected regions using all variables and the multivariate environmental similarity surface (MESS) methods for four different scenarios: (a) t1t1, (b) t2t1, (c) t1t2, and (d) t2t2 overlaid with blue circles denoting the 1900s (t1) presence localities and blue stars denoting the current (t2) presence localities. Shading colors indicate values of MESS coded from blue (negative) to orange (positive) with more intense colors denoting higher absolute values. Negative values represent climate dissimilarity while positive values indicate climate similarity (Elith et al., 2010). The black dashed line indicates Little's range for white oak (Little, 1971).

To further look at what drove the habitat suitability at any given locality across the range of white oak, we generated the maps showing the limiting factors for each SDM (Figure 6). The spatial patterns of limiting factors for each model substantially varied between two the SDMs across the entire range, which suggests that the climate association captured by SDMs varied across space and time. As expected, high summer temperatures (MTWM, Figure 6), likely associated with moisture balance limitations, appeared limiting the southern part of the range for both time periods. In the northern range, however, PAS (precipitation as snow), reflecting coldness/moisture in winter, appears limiting in the 1900s while heat/moisture balance (SHM) appears limiting for current climates, indicating a shift as climate warms. Comparing the maps for both time periods, it is noticeable that the geographic extent where MTWM is likely limiting, increased northward from the 1900s to the current climate period.

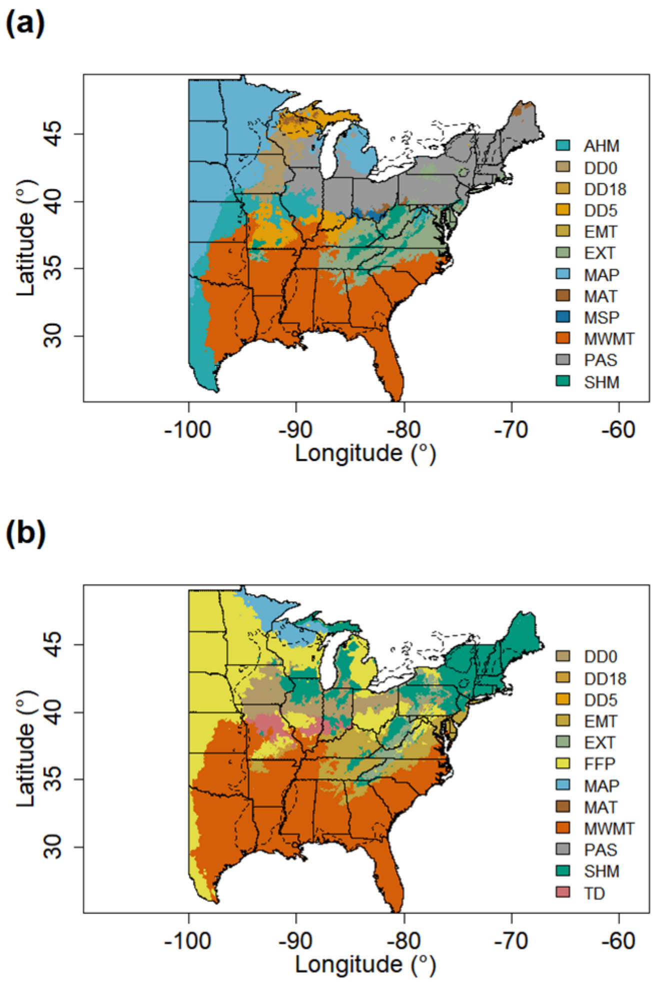

Figure 6 Limiting factors of the predicted habitat suitability at every single pixel across the study area based on the underlying model and fitted functions for (a) SDM$_{t1}$ and (b) SDM$_{t2}$. The limiting factor was defined as the variable that most influenced the model prediction (for more details, see Elith et al. 2010). The climatic variables appeared in both (a) and (b) were coded with the same color. The black dashed line indicates Little's range for white oak (Little 1971). See Table 1 for the acronyms of each variable and more details.

Discussion

This study demonstrates the temporal transferability of SDMs for white oak across a 100-year scale for white oak. Both SDMs fitted with their contemporaneous climate layers were able to accurately predict habitat suitability and species presence/absence when projected onto the 1900s and current climate. Nonetheless, the accuracy of the interpolative projection was slightly higher than that of the extrapolative projection for both ENMs (Table 2 and 3). Of both models, SDM_{t1} and SDM_{t2}, SDM_{t1} had higher predicted skill when used to predict onto current climate (Table 3). SDM_{t2} tended to produce a narrower range of habitat suitability values than SDM_{t1} regardless of the time frame onto which the model was transferred (Figure 4), and this may lead to considerable disagreement between SDM_{t2} and SDM_{t1} in predicting presence/absence over geographic space. One possible explanation to this pattern is that the multivariate climate conditions between the training data and projected regions were more similar for SDM_{t1} than SDM_{t2} (Figure 5). The latter likely extrapolated outside of climate conditions in the training data (current climate) when it was transferred to the 1900s climate. Overall, the spatial extent and distribution of suitable habitats for white oak did not change much with only a slight difference in the predicted values of habitat suitability across its geographic range over the last century (Figure 6).

Temporal transferability of SDMs is increasingly studied when projecting modelled relationships to past or future climates to look at potential effects of climate change on species distributions (Guisan & Thuiller, 2005; Elith et al., 2006; Elith & Leathwick, 2009; Peterson et al., 2011). Our results support the findings of previous studies that tested the temporal transferability of SDMs across different time scales (Tingley et al., 2009; Varela et al., 2009; Rapacciuolo et al., 2012), and found evidence for the temporal transferability of SDMs within a century (Smith et al., 2013;

Yates et al., 2018). Our findings also indicate that the accuracy of interpolative projections was slightly higher than that of extrapolative projections for two SDMs (Table 2 and 3). This pattern is consistent with recent studies demonstrating the declined performance of SDMs when they were transferred to different time (Kharouba et al., 2009; Dobroski et al., 2011; Rubidge et al., 2011; Rapacciuolo et al., 2012).

The good temporal transferability of SDMs demonstrated in this study could be possibly attributed to the low level of climate novelty found in both the interpolative and extrapolative regions (Figure 3). The models should transfer well when they are projected to highly similar analogous environments (Wenger & Olden, 2012; Wogan, 2016). When projecting SDM_{t1} onto the 1900s and current climates, we found high level of climate similarity between its training data and the projected regions across the entire range of white oak (Figure 5a and 5c), suggesting that current climate was within the range of values experienced by the 1900s white oak distribution.

The notable mismatch in the upper corner of Midwest between the 1900s interpolation and current extrapolation (upper-right panel Figure 3a and upper panel Figure 3b) we found could be explained by climate novelty or non-analogue climate in that region (Figure 5b). We found that Schoener's *D* statistic for scenario t2t1 was less than that for scenario t1t2, suggesting that SDM_{t2} could not project suitable habitats as well as SDM_{t1} onto the 1900s climates because of the dissimilar climate conditions in the upper corner of Midwest were not captured by the SDM_{t2} (Figure 5b). This trend in decreased transferability caused by climate novelty was also illustrated by Thuiller et al. (2004) and Fitzpatrick et al. (2018). Apart from the primary difference between model projections around the leading edge of white oak, we found regions with disagreement between SDM_{t1} and SDM_{t2} in predicted presence across the focal range of white oak (on-diagonal Figure 3a). This pattern could be induced by the novel combinations of climatic variables in extrapolative regions that were not captured by the models. Another possible explanation could be that the associations between species presence/absence and climate were different, which could be demonstrated by the spatially varying associations between climate limiting factors and habitat suitability for the two SDMs (Figure 6).

Without doubt, high temporal transferability is likely to increase our confidence using SDMs to project habitat suitability into the future. However, it is notable that SDM_{t2} is less transferable than SDM_{t1} and hints to a potential increase in mismatch as climate continues to change. Our findings show that the 1900s climate captured by SDM_{t1} was more similar to the current climate (Figure 5). The less temporal transferability of SDM_{t2} was attributed to the dissimilarity between the training sample and predicted regions, suggesting that the multivariate climate surfaces instead of one single climate variable in the 1900s were outside of the range of those captured by SDM_{t1}. As the dissimilarity between current and future climate is predicted to increase (Fitzpatrick et al., 2018), the transferability of SDM_{t2} is likely to further decrease. To project reliable habitat suitability under future climate, it would be better to pool the 1900s and current presences to increase the breadth of multivariate climate spaces captured by SDMs (Nogués-Bravo et al., 2016).

In the context of climate change, climate factors limiting habitat suitability could shift across geographic space, and this may lead to changes in habitat suitability for a given location across time. A variable might be important to species distributions at one time whilst not as important in a different time period (Broennimann et al., 2007; Monahan & Hijmans, 2008). Our results support this and suggest that the limiting factors for the white oak distribution were different between the 1900s and current (Figure 6), leading to difference in habitat suitability between

1990s and current climates across the range of white oak (Figure 3). Further, we found that the southern range of white oak was more determined by MWMT across periods while the limiting factors for its northern range shifted from variables reflecting the coldness of winter and moisture regime (PAS and DD0) to SHM and FFP reflecting summer moisture and length of growing seasons (Figure 6). Although the range-wide analysis that usually considers species distribution as homogenous across its entire range may not reflect variability in the response of different populations (Prasad et al., 2020), our results of the limiting factors for white oak range under current climate suggest that summer temperatures may be important drivers for the populations in the southern range while variables related to growing season length may determine its northern populations (Figure 6). This spatially varying pattern of climatic drivers for white oak distribution aligns with the fact that the response of different populations for widespread species to climate may vary across their ranges (Leites, Rehfeldt, & Steiner, 2019; Peterson, Doak, & Morris, 2019).

Although we modeled the 1900s and current suitable habitats for white oak with all climatic variables using Maxent default settings, we did not observe over-fitting for SDM_{t1} and SDM_{t2} (Table 2). Feng et al. (2019) found that Maxent can handle redundant variables in model training and removing correlated variables has little impact in Maxent model performance. However, reduced model complexity may contribute to improved model transferability (Norberg et al., 2019). Tuning parameters in Maxent setting through different combinations of feature classes and regularization multipliers (Muscarella et al., 2014), and selecting predictor variables based on expert knowledge and biological plausibility may further improve the transferability of ENM to produce more ecologically realistic predictions of species distributions across time (Guevara, Gerstner, & Kass, 2017).

Conclusion

In conclusion, with the reconstructed the 1900s presence localities of white oak inferred from tree ring data, we offered a new approach for testing the temporal transferability of SDM by projecting models onto different climates and examining the change in species-climate response across its range. By doing so, we pooled species presence localities from two time periods to better encompass the climatic niche of white oak experienced in the 1900s and current. We demonstrated the temporal transferability of SDM for white oak across its entire range in the eastern United States and found that the SDM fitted with the 1900s climates were more transferable to the current because it encompassed most of climate conditions experienced by the current species presences. The difference in transferability between SDMs fitted with the 1900s and current climates may be attributed to the climate novelty and change in limiting factors for white oak distributions. One of the main reasons for the growth of studies testing the temporal transferability of SDMs is the increase in the availability of historical distributions of species (Kharouba et al., 2009; Dobroski et al., 2011). Improved methods to project SDMs onto different time frames (past and future) are of great importance to better understanding the response of species distributions across time in the face of climate change.

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Data and code availability statement

The species occurrence data for the 1900s and the current as well as all resulting species distributions will be made publicly available on Zenodo upon publication of this study. All code underlying the analysis will be publicly accessiable through GitHub.

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