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Research article

Integrating genomic data and simulations to evaluate alternative species distribution models and improve predictions of glacial refugia and future responses to climate change

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Climate change poses a threat to biodiversity, and it is unclear whether species can adapt to or tolerate new conditions, or migrate to areas with suitable habitats. Reconstructions of range shifts that occurred in response to environmental changes since the last glacial maximum (LGM) from species distribution models (SDMs) can provide useful data to inform conservation efforts. However, different SDM algorithms and climate reconstructions often produce contrasting patterns, and validation methods typically focus on accuracy in recreating current distributions, limiting their relevance for assessing predictions to the past or future. We modeled historically suitable habitat for the threatened North American tree green ash *Fraxinus pennsylvanica* using 24 SDMs built using two climate models, three calibration regions, and four modeling algorithms. We evaluated the SDMs using contemporary data with spatial block cross-validation and compared the relative support for alternative models using a novel integrative method based on coupled demographic-genetic simulations. We simulated genomic datasets using habitat suitability of each of the 24 SDMs in a spatially-explicit model. Approximate Bayesian computation (ABC) was then used to evaluate the support for alternative SDMs through comparisons to an empirical population genomic dataset. Models had very similar performance when assessed with contemporary occurrences using spatial cross-validation, but ABC model selection analyses consistently supported SDMs based on the CCSM climate model, an intermediate calibration extent, and the generalized linear modeling algorithm. Finally, we projected the future range of green ash under four climate change scenarios. Future projections using the SDMs selected via ABC suggest only minor shifts in suitable habitat for this species, while some of those that were rejected predicted dramatic changes. Our results

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highlight the different inferences that may result from the application of alternative distribution modeling algorithms and provide a novel approach for selecting among a set of competing SDMs with independent data.

Keywords: approximate Bayesian computation, climate change, ecological niche model, extrapolation, last glacial maximum (LGM), model selection

Introduction

Climate change is a major threat to global biodiversity with documented evidence of impacts on individual species, ecosystems, and the services they provide to human populations (IPCC 2001, Parmesan and Yohe 2003, Parmesan 2006, Bellard et al. 2012, Díaz et al. 2019, Weiskopf et al. 2020). It is important to understand the extent to which species' suitable habitats may shift in the future under different climate change scenarios in order to identify vulnerable species and inform conservation efforts. Species distribution models (SDMs) are often used to reconstruct historical, or forecast potential future, range shifts. Historical reconstructions shed light on the locations of glacial refugia (Puschendorf et al. 2009) and the timing and pace of post-glacial expansion (Ordóñez and Williams 2013), while forecasts help to predict species and ecosystem responses to changing environments. The versatility of SDMs makes them a valuable modeling approach, providing insights that underpin contemporary conservation strategies aimed at safeguarding biodiversity in a changing world. However, there are substantial challenges in using SDMs. For instance, successful prediction assumes that the fundamental niche is not only fully occupied but all conditions within it are available to the species (Jackson and Overpeck 2000, Wiens et al. 2009), that species' niches do not evolve over time, and that they do not face dispersal lags or barriers to movement (Corlett and Westcott 2013). Furthermore, different approaches to building SDMs often produce contrasting patterns (Qiao et al. 2015, Steen et al. 2017). The choices made during model construction, such as the selection of modeling algorithms (Qiao et al. 2019), the specific climate models employed for hindcasting or forecasting (Fitzpatrick et al. 2018), and the criteria for selecting background points (Anderson and Raza 2010), can all influence the resulting habitat suitability predictions. Thus, different inferences may be drawn due to the variety of approaches to distribution modeling.

Another challenge is the limited availability of independent data for model validation (Yates et al. 2018). Most evaluations of SDMs rely on contemporary occurrence datasets (presence-absence or presence-background data) for model validation. Since independent data sets are difficult to acquire, quasi-independence can be 'enforced' on the data by using spatial or temporal cross-validation (Araújo et al. 2005, Roberts et al. 2017, Fourcade et al. 2018, Liu et al. 2020). Cross-validation is well-suited for evaluating the accuracy of models focused on present-day distributions, but less useful for comparing hindcasted or forecasted SDMs. This is especially challenging given that conditions in the long past (e.g. the last glacial maximum (LGM)) or future may have

very little overlap with present-day environments (Williams and Jackson 2007). SDM performance declines, sometimes dramatically, under these conditions (Maguire et al. 2016, Fitzpatrick et al. 2018). Thus, there is a need to develop methods to evaluate alternative SDMs to improve confidence in inferred range shifts both in the past and under projected future climate change.

Population genetic data and approximate Bayesian computation (ABC) provide an underexplored alternative to model validation using contemporary or historical occurrence data. ABC is a simulation-based analytical framework that approximates the likelihood function for a complex model through comparisons between simulated and observed data summaries (reviewed by Bertorelle et al. 2010). The framework was originally developed in the field of population genetics (Tavaré 1997, Pritchard et al. 1999) and has since been used to fit and compare demographic models in a wide variety of contexts (e.g. to model the spread of invasive species, Estoup et al. 2010, Ascunce et al. 2011, Sard et al. 2019, or assemblage-level patterns of divergence, Carnaval et al. 2009, Ilves et al. 2010, Smith et al. 2014). Recent studies have incorporated predictions of habitat suitability from hindcasted SDMs to inform demographic simulations in integrated distributional, demographic and coalescent models (iDDC; He et al. 2013, Alvarado-Serrano and Knowles 2014, Massatti and Knowles 2016). These studies often use a single SDM algorithm (possibly selected from a candidate set using occurrence-based SDM validation metrics) in their demographic models (Brown et al. 2016). However, in combination with a suitable genetic dataset and informative summary statistics (Alvarado-Serrano and Hickerson 2016), ABC model selection analyses can also be used to compare the relative fit of alternative SDMs and the many decisions around their implementation (e.g. size of the calibration region, predictor set, etc.). While not the focus of the present manuscript, the posterior probabilities for competing SDMs estimated from ABC could also be used as model weights in ensemble forecasting, allowing researchers to integrate uncertainty in hind- or forecasted species distributions (Araújo and New 2006). Although the potential for using genetic datasets to assess the veracity of SDM outputs has been noted (He et al. 2013, Fordham et al. 2014), actual methodologies and applications remain uncommon.

In this study, we present a novel application of ABC to evaluate the relative support for alternative SDMs and compare these evaluations to model performance metrics estimated from spatially exclusive cross-validation folds, the state-of-the-art method for assessing SDM performance when independent data are unavailable (Anderson and Raza 2010, Valavi et al. 2019). Specifically, we constructed 24 SDMs for green ash

Table 1. Settings used for the 24 distinct SDMs evaluated in this study. BRT: boosted regression tree. GLM: generalized linear model. NS: natural splines.

Climate model	Background extent (km)	SDM algorithm	SDM
CCSM	80	BRT	1
		GLM	2
		Maxent	3
		NS	4
	160	BRT	5
		GLM	6
		Maxent	7
		NS	8
	320	BRT	9
		GLM	10
		Maxent	11
		NS	12
ECBilt	80	BRT	13
		GLM	14
		Maxent	15
		NS	16
	160	BRT	17
		GLM	18
		Maxent	19
		NS	20
	320	BRT	21
		GLM	22
		Maxent	23
		NS	24

Fraxinus pennsylvanica using combinations of different climate models, background extents, and modeling algorithms (Table 1). We then used iDDC modeling (He et al. 2013), a range-wide population genomic dataset for the species, and ABC to evaluate support for alternative SDMs. In our study, iDDC provides a means for selecting the best performing model (i.e. by determining which SDMs lead to simulated genetic datasets with close correspondence to observed data), avoiding limitations associated with the use of contemporary occurrence data for model selection. Finally, we predicted the future range of green ash under each SDM, two alternative global emission scenarios, and two global circulation models to assess the influences of model choice on assessments of vulnerability to climate change and recommended conservation strategies.

Material and methods

Study system

Green ash is a deciduous tree in the family Oleaceae with a current range spanning eastern North America, from Nova Scotia to Alberta and south to Florida and Texas (Fig. 1). The species favors consistently moist and loamy soils that are well-drained and is moderately tolerant to shade (Westwood et al. 2017), making it the most widespread of the ash species. Nonetheless, this species is currently listed as critically endangered on the IUCN Red List, largely due to impacts of the invasive emerald ash borer *Agrilus planipennis* (Klooster et al. 2018, Siegert et al. 2021).

Species distribution modeling

Green ash occurrence data were acquired from the Botanical Information and Ecology Network (BIEN) ver. 4.1.1. (Enquist et al. 2016, Maitner et al. 2018). We excluded geographic outliers and locations with cultivated and naturalized individuals from our occurrence data set. We used 80-, 160- and 320-km buffers around known occurrences to define three different calibration regions from which we drew background sites for modeling. Notably, the largest buffer covers most of the study region save the farthest northern areas (cf. map of occurrences and buffers in Fig. 2). We excluded occurrences and background sites from Kentucky and Louisiana because they were severely undersampled relative to the other parts of the range ($< 0.0001\%$ of all records in each state). To project SDMs to the LGM, we used modeled climate surfaces from Lorenz et al. (2016), based on two paleo earth system models, ECBilt-CLIO (Timm and Timmermann 2007) and CCSM3 (Collins et al. 2006), at 0.5° spatial resolution. After accounting for collinearity, a subset of six environmental variables were retained for SDM construction: mean evapotranspiration ratio, water deficit index, annual precipitation, the coefficient of variation in annual precipitation, and standard deviations of growing degree days and minimum temperature.

We modeled the current and historical distribution of green ash using boosted regression trees (BRTs; Elith et al. 2008), generalized linear models (GLMs; Guisan et al. 2002), MaxEnt ver. 3.3.3k (Phillips et al. 2006, Phillips and Dudik 2008), and natural splines (NS; Mohn et al. 2021) using functions from the 'enmsdmX' R package (Smith et al. 2023). Model calibration (i.e. training and tuning) and evaluation was based on the continuous Boyce index (CBI; Hirzel et al. 2006), calculated from the ratio of predicted and expected frequencies of evaluation points across habitat suitability classes. We used CBI rather than the area under the curve (AUC) or true-skill statistic (TSS), given differences in background area across the 24 models. Both of these metrics are sensitive to, and biased by, differences in background extent (Smith 2013), and would thus be inappropriate for comparing models that differ in the width of buffers used to define background sites. CBI ranges from -1 to 1 and is near zero when the model is no better than a random model and positive for models that are consistent with species presences in evaluation data (Hirzel et al. 2006). Models were calibrated by splitting the occurrence data into three spatially exclusive sets based on subdividing the occurrences into 50 square cells 320 km on a side. Cells were then randomly assigned to three sets, one for training models, the performance of which was assessed against the second set to tune each algorithm's parameters. Once tuned, model accuracy was assessed against the third set, which is the accuracy we report. For the training set we randomly chose 50% of the cells (25), for the calibration set $\sim 20\%$ (9 cells), and the evaluation $\sim 30\%$ (16 cells). We repeated random cell assignments 30 times, for each of which we trained, calibrated, and evaluated models for each combination of climate model, background extent, and

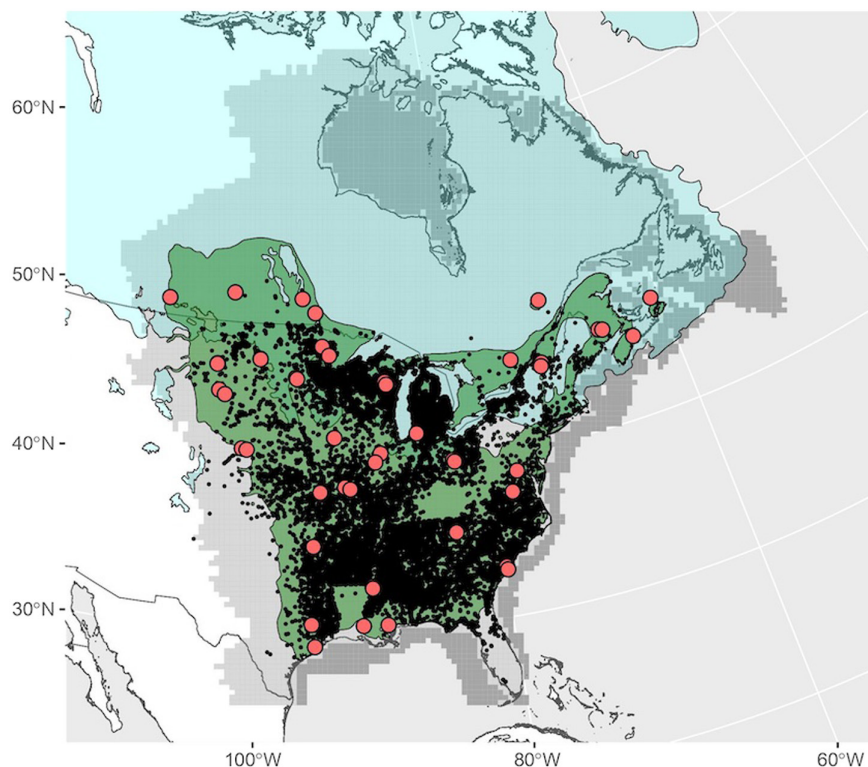


Figure 1. Map of the study region (light gray polygon) in eastern North America. The contemporary green ash range is shown in green (Little 1971), and the maximum extent of glaciation 21 kybp in light blue (Dalton et al. 2020). Occurrence records from the BIEN database are shown with black points, and red points illustrate the location of populations sampled for genetic analysis (by Noakes et al. 2022). The SDM was projected to the gray region (dark gray: 21 kybp, light gray: present). Note the land surface was larger in the past due to changes in sea level. Projection: Albers equal-area conic.

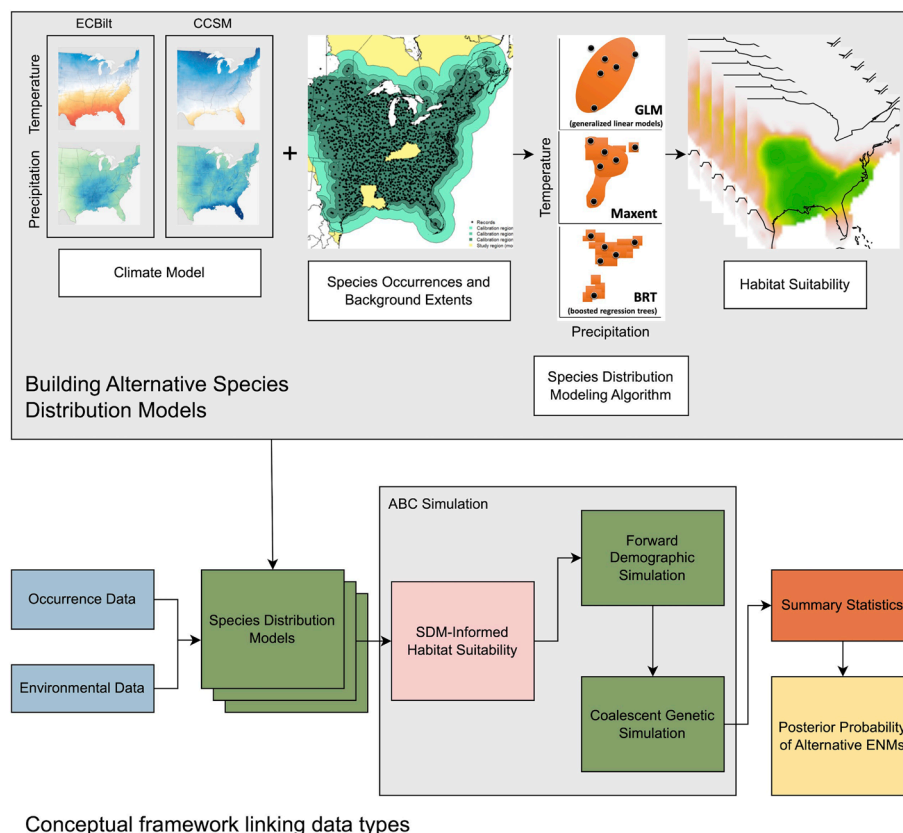
SDM algorithm. We then created an ‘all-sites’ model using all occurrences based on the best parameterization for each algorithm. We projected these all-sites models to the past using climate reconstructions from ECBilt or CCSM climate models using 200-year average climates centered on 500-year intervals (Lorenz et al. 2016), then linearly interpolated habitat suitability in simulation grid cells at 30-year intervals for use in the demographic models described below. We did explore non-linear interpolations (splines, natural splines, basis-splines, etc.), but chose linear interpolation as it did not introduce erratic artifacts. To help assess the degree of similarity among SDM predictions, we implemented a clustering analysis using mean differences between cells in the present and mean differences between cells at 21 kybp as distances between SDMs.

Simulations and approximate Bayesian computation (ABC)

Empirical population genomic data for green ash were collected from samples of fourteen individuals from each of 21 populations across the contemporary species range (a subset of populations from Noakes et al. 2022, Fig. 1). Details of sampling, DNA extraction, restriction-associated DNA sequencing (RAD-seq) library preparation, and bioinformatic

analysis can be found in the Supporting information of Castilla et al. (2024). We filtered the dataset to retain one SNP per RAD locus and remove variable sites where the minor allele frequency was below 0.01. After filtering, the population genomic dataset included 294 green ash individuals and 1000 SNP loci.

We used the spatially explicit model implemented in the R package ‘holoSimCell’ (<https://github.com/stranda/holoSimCell>) to simulate genomic datasets using habitat suitability projected to the past under each of the 24 SDMs. Briefly, this analytical framework couples forward-time demographic simulations with backward-time coalescent genetic simulations and estimates support for alternative models (i.e. the 24 distinct SDMs) using ABC (Fig. 2). The forward simulation models population growth and dispersal, and is used to establish a colonization history of populations on a spatially-explicit simulated landscape. Parameter values for simulations, including the maximum per-grid cell effective population size (N_e), dispersal parameters (mixture parameter), and parameters related to refugial population size, were drawn from prior distributions (Supporting information) for each simulation. Simulations began at 21 kybp by placing starting populations in areas where predicted habitat suitability in hindcasted SDMs was above a model-specific threshold that maximized the sum of sensitivity and specificity, as evaluated



Conceptual framework linking data types

Figure 2. A conceptual diagram of the iDDC (He et al. 2013) modeling procedure that we use to compare support for alternative SDMs. Occurrence data and environmental data are used to construct multiple SDMs with different climate datasets, background extents, and algorithms, which are then used to constrain population size through space and time in a spatially explicit forward simulation. The colonization history from the forward simulation parameterizes a coalescent simulation, which is used to generate simulated population genomic datasets that are compared to empirical data using ABC.

using contemporary suitability estimates and the range map for green ash (Little 1971). Initial abundances in cells within glacial refugia were scaled linearly by their predicted suitability values. The simulations used habitat suitability layers (in 30-year time steps) from each of our 24 SDMs to set carrying capacity of a cell through time. The colonization history for each replicate simulation was then incorporated into a coalescent simulation in fastsimcoal ver. 2.6 (Excoffier et al. 2013), to efficiently generate simulated population genomic data. Coalescent simulations used the same migration matrix as forward demographic simulations and the recorded sources for newly colonized grid cells at each time step of the forward simulation. We simulated 50 000 replicate datasets for each SDM, resulting in a total of 1 200 000 replicates in our ABC reference table. The reference table included the randomly drawn parameter values used in each simulation and summary statistics characterizing within and among population genetic variation in simulated datasets.

We used ABC to evaluate the support for alternative SDMs by comparing summary statistics from simulations under each SDM to observed summary statistics from our empirical dataset. ABC analyses were conducted using the R packages ‘abc’ (Csilléry et al. 2012) and ‘abcrf’ (Marin et al. 2019). Comparisons between simulated and observed datasets

were based on 473 summary statistics that reflect within- and among-population genetic variation (see the Supporting information for details on summary statistics). We estimated posterior probabilities of each of our 24 SDMs using simple rejection, multinomial logistic regression (Beaumont 2008), neural networks (Blum and François 2010), and random forest (Pudlo et al. 2016) ABC model selection algorithms. Neural networks included 10 networks, 20 units in the hidden layer, and maximum weights set to 50 000. We used 1000 trees to predict the most likely model in our random forest analysis. For multinomial logistic regression and neural networks, we conducted model comparisons using a range of tolerances that accepted between 1200 and 120 000 simulated replicates most closely matching the observed summary statistics (i.e. tolerances between 0.001 and 0.1, respectively). As a post hoc assessment of the ability of our simulation model to produce summary statistics similar to those in the empirical green ash dataset, we compared observed summary statistics to the distribution of summary statistics in the reference table for each model and calculated the frequency of observations smaller than our observed statistics using the ecdf function from the R ‘stats’ package (www.r-project.org).

Given the steep computational requirements of iDDC as a means to evaluate support for alternative SDMs (i.e. together,

simulating 50 000 replicates for all 24 models required the equivalent of ~ 34 years of runtime on a single processor), we conducted additional analyses to assess the sensitivity of model selection results to the total number of simulation replicates considered in the ABC analysis. For these analyses, we subsampled our full reference table (50 000 simulations per SDM, 1.2 million total), retaining from 5000 to 45 000 simulations per model in steps of 5000 simulations, and repeated the neural network model selection analysis with a tolerance of 5% (6000 to 54 000 accepted simulations).

We used leave-one-out cross-validation (neural networks) and out-of-bag (OOB) error rates (random forests) to assess the ability of the ABC model selection analysis to distinguish alternative SDMs (i.e. model identifiability). Leave-one-out cross-validation analyses used 100 replicates per SDM, the neural network model selection algorithm, and a single tolerance value (0.05). All simulations and ABC analyses were performed in R ver. 4.0.3 (www.r-project.org).

Projecting future habitat suitability

Finally, we projected future habitat suitability under each SDM described above using two different future global emission scenarios under the CMIP5 set of climate simulations (RCP4.5 and RCP8.5; [IPCC 2014](#); downscaled projections from [Lorenz et al. 2016](#)) and two global circulation models (GFDL-CM3 and IPSL-CM5-MR; [Griffies et al. 2011](#), [Dufresne et al. 2013](#)). The CCSM and ECBilt-CLIO do not have matching models of contemporary climate in [Lorenz et al. \(2016\)](#). The two models provide contrasting predictions of future precipitation and temperature ranging from hot and dry (IPSL-CM5-MR) to wet and comparatively cool (GFDL-CM3). These four future climate scenarios (2 RCPs $\times$ 2 climate models) were then used to predict suitable habitat for green ash for climate averaged across 2071–2100

(hereafter, '2080'). To assess the degree to which the SDMs must extrapolate to novel climatic conditions in their projections of future suitability and their behavior when projected beyond the range of the training data, we constructed univariate response curves for each predictor while holding the other variables at their means.

Results

Species distribution models compared using contemporary occurrences

Assessments of model accuracy based on contemporary occurrences indicated that all 24 SDMs performed well, with median CBI (across 30 evaluation folds) for each model greater than 0.8 ([Fig. 3](#)). Clustering analyses based on mean differences in estimated habitat suitability showed that SDMs based on the same climate model grouped at the LGM, whereas calibration extent was the main grouping factor of contemporary suitability surfaces (Supporting information). Hindcasted SDMs based on both climate models suggest a relatively continuous distribution of the species in what is now the southeastern United States at the LGM (Supporting information). However, SDMs based on the ECBilt climate model tended to infer larger areas of suitable habitat, including areas near glaciated portions of the Midwest, while suitable habitats in SDMs based on the CCSM climate model were restricted to areas along the Gulf and Atlantic coasts at the LGM (Supporting information).

Species distribution models selected using ABC

The rejection, neural network, and random forest algorithms almost always identified SDM 6 (CCSM3 climate model, 160-km background extent, GLM modeling algorithm) as

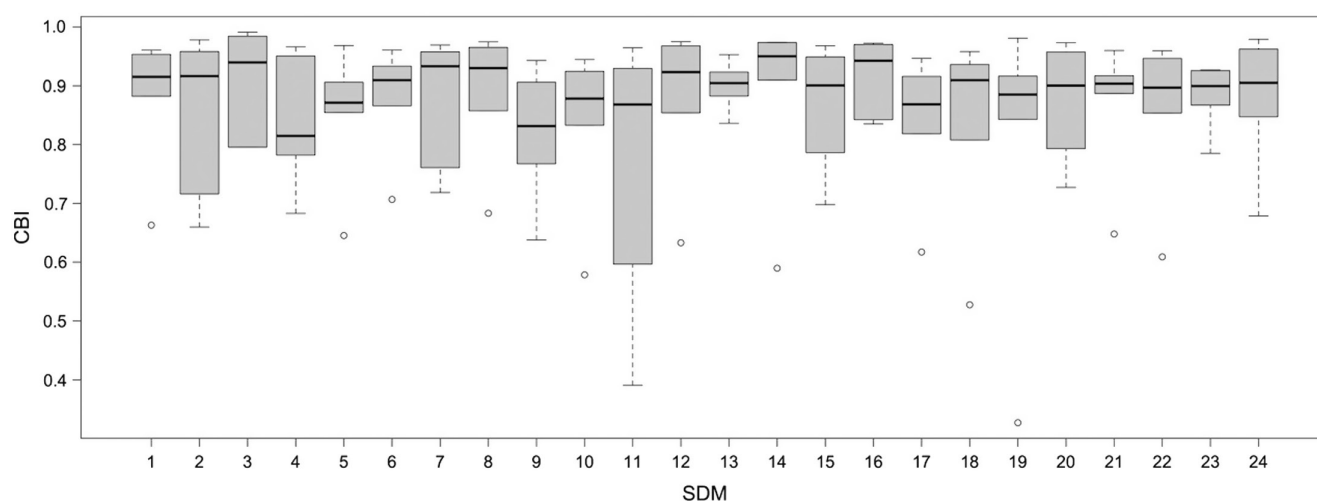


Figure 3. Model accuracy measured using the continuous Boyce index (CBI). Values represent CBI measured against the evaluation folds ($n=30$ repetitions of fold allocations). CBI ranges from -1 to 1 , with values near zero indicating presence predictions that are no better than those from a random model. Boxes show the interquartile range of CBI values for each SDM (Table 1 for SDM settings), with heavy lines showing median CBI and whiskers extending to the range excluding outliers, which are plotted as open circles.

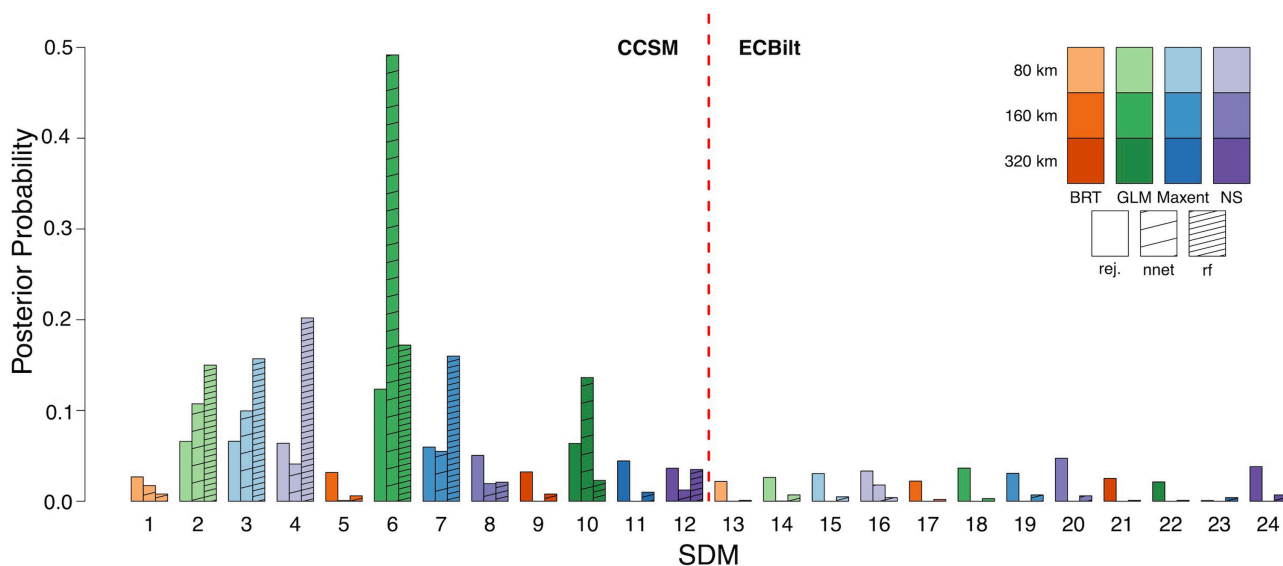


Figure 4. ABC model selection results comparing 24 alternative SDMs. Bar shading illustrates differences in background extent (80-, 160- or 320-km), and SDM algorithm (boosted regression trees, generalized linear models, Maxent, and natural splines). Estimates of posterior support for each model are shown for the rejection (rej., tolerance=0.05), neural network (nnet, tolerance=0.05), and random forest (rf) model selection analyses. *N.b.*, for the random forest, the plot shows the distribution of votes in favor of the different models, rather than estimated posterior probabilities.

the best or second-best model (Fig. 4, Supporting information). The rejection algorithm favored SDM 6 at every tolerance level except when using the most restrictive threshold (0.001), when SDM 4 (CCSM3 climate model, 80-km background extent, NS modeling algorithm) was favored with a posterior probability of 0.4633. The neural network algorithm also consistently supported SDM 6 at every tolerance except 0.005, where SDM 3 (CCSM3 climate model, 80-km background extent, MaxEnt modeling algorithm) was favored with a posterior probability of 0.4865 (Fig. 4, Supporting information). Notably, neural network-based estimates of cumulative support for models based on the CCSM3 climate model were substantially higher than cumulative support for SDMs based on the ECBilt model in all instances (range 0.82–0.99; Supporting information). The random forest analysis supported SDM 4 as the best model, with a posterior probability of 0.4448 (202/1000 votes) and SDM 6 as the second best model (172/1000 votes; Fig. 4).

Multinomial logistic regression was less consistent, and showed strong support for five different SDMs (posterior probability > 0.75) across the seven tolerances compared. Both climate models, two of the three background extents (80- and 160-km), and all four modeling algorithms were represented among models supported by multinomial logistic regression. The large number of data summaries used in our ABC analyses (473 total summary statistics) may have contributed to the observed instability in model selection results from multinomial logistic regression (i.e. the curse of dimensionality; Pudlo et al. 2016). Given this pattern, and previous observations that ABC algorithms that employ machine learning approaches for dimension reduction are better suited for highly dimensional datasets (Blum and François 2010,

Pudlo et al. 2016), we focus subsequent discussion on results from neural network and random forest ABC analyses, which favored SDMs 3 and 4, but especially SDM 6.

Some observed summary statistics from our empirical green ash dataset fell outside the simulated distributions of these summary statistics under each model. Across the 24 SDMs, between 18 and 89 of the 473 simulated summary statistic distributions did not encompass the empirical values. More frequently, observed summary statistics were in the tails of simulated distributions (e.g. between 109 and 186 observed statistics fell in the 0.1% tails of distributions). Differences between SDMs did not appear to be related to climate model, background extent, or modeling algorithm. Notably, seven of the 210 pairwise F_{ST} values from simulations were consistently higher than the observed pairwise F_{ST} values, regardless of the SDM considered. While this suggests that the simplified recolonization model in our simulations may not accurately represent all aspects of the post-glacial expansion of the species, we did not detect systematic differences in the degree to which simulated summary statistic distributions from the 24 SDMs covered observed values for the 473 summary statistics used in our ABC analyses.

We investigated the minimum number of demographic/coalescent simulations necessary for model selection analysis by reducing the number of simulations per SDM from 50 000 down to 5000 (in increments of 5000). Posterior probabilities from the neural network ABC algorithm varied with no discernable relationship to the total number of simulations included in the analysis. Nonetheless, SDM 6 received the highest support among the competing models in all cases (posterior probability ranging from 0.337 to 0.673; Supporting information).

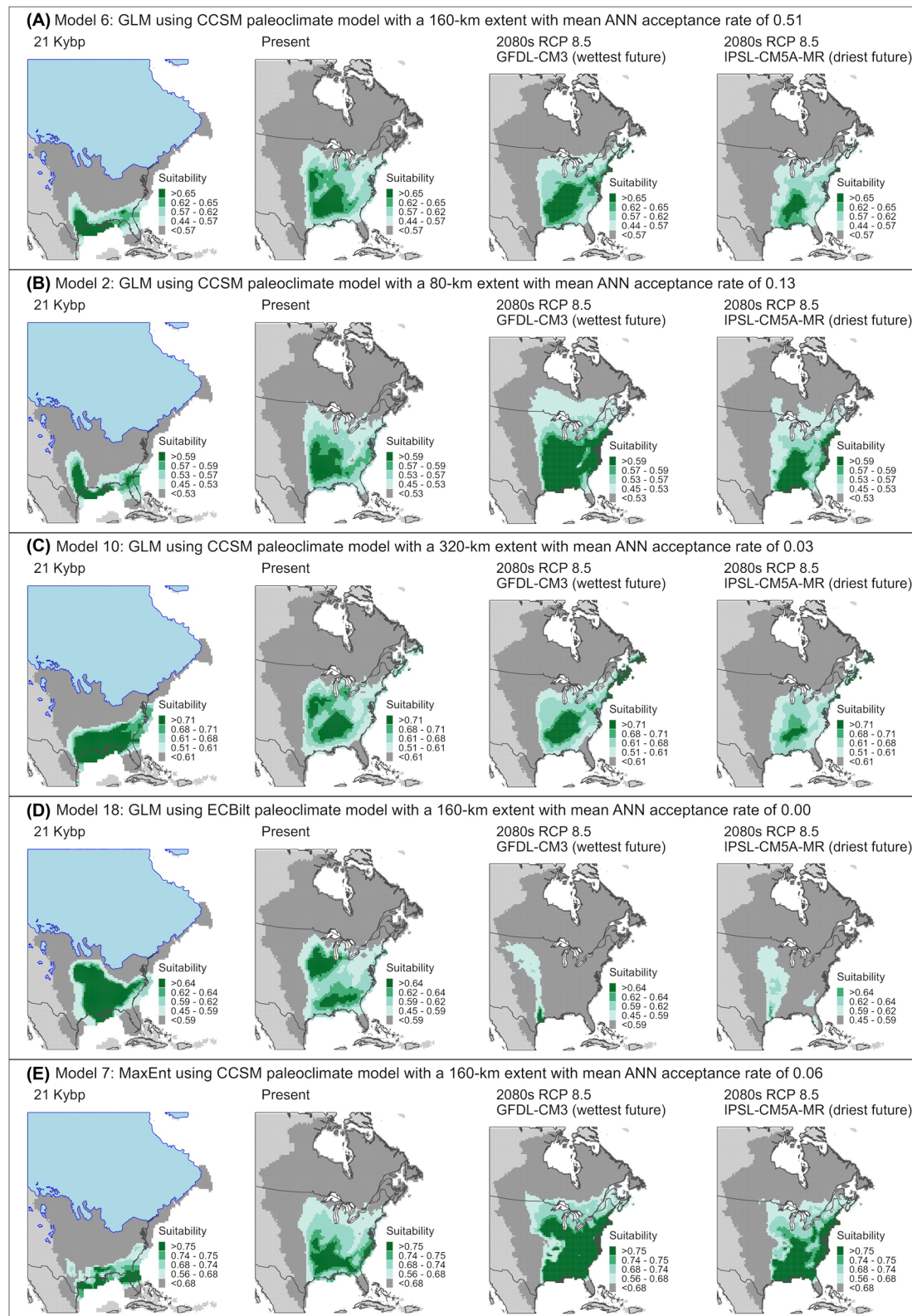


Figure 5. Predictions for select models across time, each row represents predictions from a different model (row 1 is the most supported model, SDM 6). Values for a given model are thresholded using the 70, 80, 90 and 95th quantile values of the raster from 0 kybp. The blue region represents the glacial coverage at 21 kybp (Dalton et al. 2020) and the dark gray and green areas represent the region of inference. To serve as a visual benchmark, we display the modern outline of Canada, the US, and Mexico in each map. Projection: Albers equal-area conic.

ABC cross-validation

Cross-validation using neural networks to select the best SDM showed that, in nearly all cases, the true simulated model produced the highest median posterior probability across 100 cross-validation replicates (Supporting information). Neural network ABC was able to correctly distinguish between hindcasted SDMs based on alternative climate models and SDM algorithms, but less so for background extent. Looking specifically at SDM 6, there was little to no confusion for SDMs constructed with the alternate climate model and very high identifiability within the same climate model (Supporting information). Random forests were able to correctly distinguish between SDMs between 29 and 95% of the time (based on OOB error rates). Identification of individual models was more reliable for SDMs based on CCSM (mean OOB error rate = 22%) than ECBilt (mean OOB error rate = 45%). As seen in the neural network cross-validation analyses, there was little confusion among SDMs based on alternative climate models (OOB error rates between climate models = 0–11%).

Future habitat suitability

Projected habitat suitability for 2080 differed greatly between the alternate climate models and under the two different future climate scenarios (see Fig. 5 for examples and Supporting information for all results). SDMs based on CCSM often suggested a future range that is similar to present day range maps. In contrast, SDMs based on ECBilt predicted a drastic reduction in habitat suitability across the contemporary range by 2080 (Fig. 5D, Supporting information). Within CCSM-based SDMs, future projections showed increased habitat suitability in the northeastern portion of the contemporary range by 2080, especially under the wettest scenario (GFDL-CM3; Fig. 5, Supporting information). Furthermore, SDMs often predicted higher habitat suitability for a given location under this scenario, suggesting that a wetter future may mediate the stressors from climate change for green ash.

Response curves

The responses of each SDM to each predictor varied dramatically inside and outside the range of the training data, with some estimates changing in sign (Supporting information). The three most-frequently selected SDMs (2, 3 and 6) responded most strongly to variability in growing degree days and temperature variability, and to water deficit index.

Discussion

We used simulations and genomic data within an integrated distributional, demographic, and coalescent modeling framework (iDDC; He et al. 2013) to evaluate the relative support for 24 different species distribution models for green ash,

which varied by climate model, background extent, and modeling algorithm. Using iDDC modeling to evaluate SDMs is a novel approach, and it more clearly distinguished particular models than did the state-of-the-art method for model assessment based on geographically distinct cross-validation folds. Specifically, our analyses consistently favored SDMs based on the CCSM climate model over those based on ECBilt. Our model selection analyses, especially those approaches able to deal with multicollinearity and highly dimensional sets of summary statistics (i.e. neural network and random forests), consistently favored SDM 6, utilizing the CCSM climate model, a 160-km background extent, and the GLM modeling algorithm, over alternative models. Projections of past and future locations of suitable habitat differed strikingly across SDMs and future climate scenarios (Fig. 5), illustrating the importance of model evaluations like those conducted here and underscoring recent calls to integrate uncertainty in iDDC modeling studies (Alvarado-Serrano and Knowles 2014, Castilla et al. 2024). By leveraging demographic and coalescent simulations across 21 ka of climate change with summary statistics based on population genomic data collected across the contemporary range, evaluations based on iDDC modeling may improve confidence in the selection of species distribution models and the reliability of projections of habitat suitability under future climates. While the data and computational requirements for ABC-based evaluation of alternative SDMs are steep relative to model validation applications in studies seeking to predict past or future range shifts (Hoban et al. 2019).

Model comparisons using iDDC provide an alternative to more traditional methods that rely on contemporary occurrences to select the ‘best’ model. Previous studies have illustrated that model performance declines when SDMs are projected to novel conditions (Yates et al. 2018, Qiao et al. 2019, Liu et al. 2020). This is a major concern for studies that attempt to predict the species range in the past or future. Information from fossils can address some of these limitations (e.g. through the use of fossil occurrences to validate models; Martínez-Meyer et al. 2004, Waltari and Guralnick 2009, Roberts and Hamann 2012, Poli et al. 2022), but the fossil record is sparse for many taxa. The signatures of past demographic events are retained in population genetic datasets; therefore, integrating these data in SDM evaluation provides more robust inference. In our analysis, response curves show very different behavior for models projected to novel environments particular to the LGM or 2080 (especially water deficit, variability in precipitation and growing degree days; Supporting information). Contemporary occurrences, which cannot, by definition, sample conditions different from the present, are limited in their ability to assess model performance for cases that involve temporal transfer. The iDDC approach can thus help to improve both the reconstruction of Quaternary range shifts and the prediction of climate-driven range shifts of the future.

iDDC can also be used to identify broad key ‘features’ that pose decision-points in the modeling process. These decision

points often have the potential to affect model predictions dramatically, and yet a priori, it is difficult to make an argument for or against them. For example, best practices state that the extent of the calibration region should reflect the area that is accessible to the species via dispersal (Barve et al. 2011, Araújo et al. 2019). However, limited knowledge of dispersal makes defining this area exceedingly difficult. In our case, models using 80- and 160-km buffers to describe this region were strongly supported (mean selection probability across all methods 0.41 and 0.47, respectively), in contrast to the 320-km buffer (mean support 0.08). We also found differences between modeling algorithms. Support for GLMs was highest (mean across all methods 0.37), compared to MaxEnt (0.29), NS (0.18), and BRTs (0.12). Our work thus confirms that for robust model transfer, simpler models may be better (Merow et al. 2014, Bell and Schlaepfer 2016). Finally, regardless of the SDM algorithm or background extent, we found strong support for SDMs based on the CCSM over the ECBilt paleoclimate model. Compared to ECBilt, CCSM incorporates a more sophisticated set of processes (e.g. varying sea level height and meltwater pulses; Lorenz et al. 2016). However, it is crucial to acknowledge that we are still far from comprehending the full extent of the biological implications arising from the differences in climate models employed.

Conservationists and ecosystem managers aim to pinpoint species in need of interventions like assisted migration. To effectively discern these species, accurate predictions of future ranges are essential (Beaumont et al. 2019). In this context, our results highlight that the SDMs achieving the highest support for correspondence with past range shifts are models that predict a relatively small reduction in the species' range in the future (Fig. 5). Notably, our ABC model selection clearly favored one model (SDM 6 – CCSM3 climate model, 160-km background extent, GLM modeling algorithm; Fig. 4–5), which forecasted green ash distributions at 2080 that resemble the current range, albeit with significant habitat loss in the northwestern region. However, our overall results suggest that climate change may have a limited impact on green ash this century, making it a lower priority for assisted migration. This aligns with a previous assessment that ranked the species 109 out of 419 priority US tree species due to its low climate sensitivity and high adaptive capacity (Potter et al. 2019). Nonetheless, we do identify a pressing concern for green ash conservation in the northwestern region where the most loss is expected. The non-native emerald ash borer, *Agrilus planipennis*, remains the foremost threat to this species, leading to the tree's Critically Endangered classification (Westwood et al. 2017). The northwestern populations form a distinct genetic group that displays valuable traits for pest resistance (Steiner et al. 2019). Despite their limited geographic extent, the loss of northwestern populations could thus substantially diminish the adaptive potential of green ash.

There are notable limitations associated with the approach for SDM evaluation taken in our study. In particular, selection of the optimal SDM may be influenced by a number of assumptions made during modeling, many of which are inherent in other uses of SDMs to hind- and forecast ranges.

For instance, we assume negligible evolutionary change in the fundamental niche of the species since the LGM. While this assumption is contentious (Jackson and Overpeck 2000, Colwell and Rangel 2009, Nogués-Bravo 2009), it seems more likely to hold in species with lengthy generation times (e.g. trees). We further assume linear changes in habitat suitability over time (i.e. suitability was linearly interpolated on 30-year intervals for our simulations) and a proportional relationship between estimated habitat suitability and population size. Notably, the latter assumption could be relaxed, by modeling alternative functional forms for the relationship between suitability and population carrying capacity (Brown and Knowles 2012, Brown et al. 2016), though such a comparison would multiply the computational demands of the analysis by a factor of two for each additional alternative. The data requirements of the method described here may also be limiting in some cases due to the need for a genetic dataset and substantial computational resources. That being said, high-throughput sequencing technologies (Baird et al. 2008, Ali et al. 2016) have made population genomic data far more accessible and datasets in online repositories (e.g. GenBank's Sequence Read Archive) are rapidly accumulating, meaning this approach could be performed on dozens of existing and free-to-use datasets. Furthermore, our sensitivity analyses suggest that it may be possible to obtain reliable inferences using far fewer simulations than conducted here (possibly as few as 5000 simulations per model), easing the computational burden of iDDC simulations.

To our knowledge, our study is the first to use iDDC modeling to evaluate alternative SDMs. In green ash, we found consistent support for distribution models based on the CCSM climate model (Lorenz et al. 2016), which predicted a relatively large refuge across the southeastern US at the LGM. The best-supported model also included an intermediate background extent (160-km) and the GLM SDM algorithm, although we expect that the particular combination of settings that lead to optimal SDM performance will differ among species. Predictions of future range shifts under this model identified a set of climate-vulnerable populations that may also be resistant to invasive pests and worthy of consideration in future conservation efforts, although alternative SDMs did not unequivocally identify these same populations as needing special attention (Fig. 5, Supporting information). While using iDDC to select among a set of competing SDMs requires computational resources for simulations and a population genetic or genomic dataset for the species, it provides a useful alternative to model evaluations based on contemporary occurrence data alone. Furthermore, posterior probabilities estimated from ABC could be used as weights in ensemble forecasting, which avoids the need to identify a 'best' model by combining predictions across SDMs (Araújo and New 2006). In our study, ABC was able to distinguish among competing SDMs, despite similar performance among models when assessed using contemporary occurrence data. We expect that integrating information in population genetic datasets will improve both reconstructions of past range dynamics and confidence in projections of future range shifts.

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Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.s7h44j1fx> (Robinson et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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