Habitat Suitability Modeling: A Tool for Restoring Butternut, Juglans cinerea L., in the Eastern United States

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Abstract

According to the IUCN Red List, the endangered eastern North American tree species, butternut (*Juglans cinerea* L.), has been negatively impacted by an introduced pathogen and declining habitat, hindering conservation efforts. We developed an ensemble model to project spatiotemporal dynamics in suitable habitats for butternut across its native eastern United States (US) range under contrasting emissions scenarios. Our model integrated six algorithms weighted by predictive performance on test data. Predictor variables emphasized temperature, precipitation, topography, and humidity variables influential for butternut based on ecological literature. Across four future periods through the end of the 21st century, the ensemble model projected habitat gains, losses, or stability depending on geographic location and climate model, highlighting variability and uncertainty. While some ensemble projections showed poleward and elevational range shifts per previous climate impact studies, incorporating dispersal limitations in future models could avoid under- or over-estimating shifts. Precipitation seasonality and slope aspect emerged as highly influential variables for projected distribution. Slope gradients may provide local climate refugia amid regional drying. Overall, these results demonstrate complex species-climate interactions across spatiotemporal scales, underscoring the need for adaptive and location-specific conservation strategies attuned to ecological intricacies to ensure biodiversity amid the uncertainties of global change.

1. Introduction

The predicted accelerated climate change in the 21st century is predicted to accelerate and have a significant effect on both the abiotic and biotic components of forest ecosystems, which includes changing habitat suitability and species distribution for various tree species on spatial and temporal scales (Lenoir et al., 2008; Mathys et al., 2017; Kralicek et al., 2022). One notable change is the shift to more favorable conditions for some species, resulting in a range shift for those species through various mechanisms (Kralicek et al., 2022). The resultant negative effect of these changes in climate on species' habitat suitability includes low regeneration success, decline in growth, and increased mortality rate, while the positive effect of the improved habitat condition includes increased growth and regeneration success (Rehfeldt et al., 2014). Globally, various studies have reported the effect of climate change as a proxy for species range shift. The global warming phenomenon is expected to promote species range expansion northward with high elevations and reduction in the southern range with low elevations, especially for North American tree species (Rehfeldt et al., 2014; Monleon and Lintz, 2015; Adeyemo and Granger, 2023).

Butternut *(Juglans cinerea L.)*, a member of the Juglandaceae family, is an early successional species that is native to eastern North America, especially the central and eastern regions of the United States - with its southern extent in northwestern South Carolina, northern Georgia, northern Alabama, northern Mississippi, and Arkansas - and southeastern Canada (Burns & Honkala, 1990; Kartesz, 1994; Morin et al., 2018; NatureServe, 2023). This fast-growing, medium-sized hardwood species has a relatively short lifespan, rarely exceeding 80 years (Rink, 1990). It demonstrates a preference for abundant sunlight and

loamy, moist, yet well-drained soils commonly found in riparian zones. Though it can be found in similar site conditions as eastern black walnut (*Juglans nigra* L.), butternut is reported to be found farther north and at higher elevations, up to 1,500 meters (Rink, 1990; Cogliastro et al., 1997; Morin et al., 2018). Studies by Fernald (1950) and Gleason and Cronquist (1991) also reported that butternut grows well in lower slopes, ravines, and rich mesophytic forests, as well as different bottomland types, such as floodplain forests, creek banks, and terraces. Butternut exhibits intolerance for wet, heavy, clay soils, hence, well-drained soils are crucial for its healthy growth (Cogliastro et al., 1997, 2003). Butternut frequently grows alongside a variety of canopy tree species, including American beech (*Fagus grandifolia* Ehrh.), basswood (*Tilia americana* L.), black cherry (*Prunus serotina* Ehrh.), black walnut (*Juglans nigra* L.), eastern hemlock (*Tsuga canadensis* [L.] Carr.), hickory (*Carya spp.*), and oaks (*Quercus spp.*) (Rink, 1990; Morin et al., 2018). However, it is shade-intolerant and grows best in direct sunlight. While young trees can handle some lateral competition, they cannot withstand overhead shading, and need to be in the canopy by maturity to survive. Only in open fields or stand openings, where shade does not hinder growth, does successful reproduction take place (Skilling, 1993; Ostry et al., 1994; NatureServe 2023).

The rapid decline of butternut is primarily attributed to the pervasive spread of butternut canker disease, caused by the mitosporic fungus, *Ophiognomonia clavigignenti-juglandacearum*, though there is also a hypothesized reduction in suitable habitat due to climate change (Iverson et al., 2008; Ostry et al., 1994; Morin et al., 2018). This destructive disease creates girdling cankers that have been responsible for killing mature butternut trees, young sprouts, and seedlings across the entire range of the species (Ostry et al., 1994). Unfortunately, the disease shows no signs of abating and continues to spread, further exacerbating the downward trend in butternut populations. The future outlook for the species remains concerning, as it has been reported to have lower genetic diversity when compared to similar species such as black walnut (Fjellstrom and Parfitt, 1994; Morin et al., 2000). This low genetic diversity may hinder the species' ability to adapt to the butternut canker and withstand climate change, so understanding the genetic makeup of this species is imperative for its conservation and long-term survival.

The severity of butternut canker disease's impact on butternut populations has been well-established through assessments conducted by the USDA Forest Service Forest Inventory and Analysis (FIA) program and other survey data. From 1966 to 1986, a staggering 77% reduction in individual butternut trees was reported across the species' range, with some states experiencing declines exceeding 80% (Anderson and LaMadeleine, 1978; Ostry et al., 1994). This overall statistic was confirmed by Schlarbaum et al. (1997), who also found that 77% of butternut trees in the southeastern United States died over 30 years. Overall, butternut tree numbers in seven midwestern states have decreased by 23% since 1990 (Ostry and Woeste, 2004). More recently, a FIA assessment in 2015 revealed a steep decline of 58% in the number and volume of butternut trees since the 1980s, with the most significant decreases observed in the Midwest (Morin et al., 2018). In 2019, a comprehensive threat assessment ranked butternuts in the top twenty most severely threatened eastern tree species due to disease. This evaluation combined various threat attributes and species biology to determine the level of risk (Potter et

al., 2019). In Canada, butternut was federally listed under the Species at Risk Act (SARA) in 2005. Three of the Canadian provinces classify the species as critically endangered or imperiled (COSEWIC, 2017). Butternut has "special concern" status in Kentucky, is "exploitably vulnerable" in New Jersey, is "vulnerable" in Tennessee, and is "critically imperiled" in Minnesota (Fig. 1), while not being federally listed and protected under the Endangered Species Act in the United States (NatureServe, 2023). Overall, butternut is considered “vulnerable” by NatureServe, however, it’s generally “Imperiled” in the southeastern U.S. (NatureServe, 2023). According to the IUCN Red List, butternut is endangered, (Stritch and Barstow, 2019). It is classified as either a "sensitive species" or a "species of concern" in 16 National Forests, and several states have taken action to recognize this alarming condition for example the restriction of harvesting healthy butternut on national forests (Ostry *et al.*, 2003; Brosi, 2010; Farlee et al., 2010; Morin et al., 2018). These assessments and designations underline the urgency of addressing butternut's population decline and implementing conservation efforts to safeguard this valuable tree species. The collaboration between various agencies and researchers is crucial to mitigate the impacts of butternut canker disease and preserve butternut's ecological significance in both the United States and Canada.

The need for informed climatic-environmental, science-based decision-making has grown over time as a means to monitor the effects of climate change on habitat suitability and inform assisted migration and restoration efforts to ensure productivity of tree species (Rockström et al., 2009). Uncertainties related to climate change, which result from varying stakeholder objectives, perceptions of future conditions, and developing responses to sporadic and unusual events, increase the difficulty of long-term resource planning (Marchau et al., 2019). These difficulties are intensified with temporal and spatial increases, and expansion in scope of impacts (Smith et al., 2022). Despite significant progress in societally relevant climate research, there is still a persistent gap between the generation of scientific evidence and the practical application of research results by different stakeholders (Kirchhoff et al., 2013). This discrepancy results, in part, from differences in how scientists and decision-makers convey uncertainty, as well as a mismatch between how researchers formulate climate information and how decision-makers view its applicability and credibility (Brugnach et al., 2007; Kloprogge et al., 2007; Lemos et al., 2012; White et al., 2015). Therefore, significant changes in climate research are required to produce results that can be used and successfully support decision-making processes (Kirchhoff et al., 2013; Mayer et al., 2017; Smith et al., 2022). Recently, there has been increased advocacy for the inclusion of species habitat suitability maps, developed from robust modeling techniques, in restoration plans to guide implementation for a successful outcome (Self, 2023).

Species distribution modeling (SDM), habitat suitability modeling (HSM), or ecological niche modeling (ENM) (Peterson et al., 2011; Guisan et al., 2017) have been fundamental tools in understanding species habitat ecology and management (Vinagre et al., 2006), improving species restoration and reintroduction efforts (Barnes et al., 2007; Adhikari et al., 2012; Payne and Bro-Jørgensen, 2016; Lentini et al., 2018), and conserving endangered species (Jackson and Robertson, 2011; Stratmann et al., 2016; Hale et al., 2022). These models can be used to assess and predict the probability of species occurrence by analyzing the environmental variables that influence species distribution (Elith et al., 2011). These

models enable the development of insights into species-habitat associations, even in situations where biological datasets are bottlenecks or when predicting potential responses to future climate change and disturbances (Jueterbock et al., 2016; Davis et al., 2021). However, there have been noted variations in the forecasts produced by various modeling techniques that brought about uncertainties in the use of these predictions, which necessitates developing alternative approaches that amplify the signal-to-noise ratio from the prediction output. Ensemble models have demonstrated superior performance compared to individual models, making them a valuable approach to avoid relying solely on one type of model (Araújo and New, 2007; Georgian et al., 2019). By combining the predictions of multiple models, ensemble methods can leverage the strengths of different algorithms, leading to more accurate and robust results (Naimi and Araújo, 2016). This diversity within the ensemble helps mitigate the weaknesses and biases that may be present in any single model, thus enhancing the overall predictive power and reliability of the approach. As a result, ensemble modeling has become increasingly popular, and its effective application in predictive modeling includes modeling species' habitat suitability. For example, Chefaoui et al., 2016 used pseudo-absence data and an ensemble of six models for presence-absence data where the ensembled prediction had the highest predictive accuracy when compared with others. The six presence-absence models were GLM (Generalized Linear Model), GAM (Generalized Additive Model), GBM (Generalized Boosting Model), RF (Random Forest), MARS (Multivariate Adaptive Regression Splines), and FDA (Flexible Discriminant Analysis). However, despite its established improved accuracy by enhancing the ‘signal’ to noise ratio from various model outputs, it still depends on excellent individual predictions to produce better ensembled forecasts (Araújo et al., 2005).

Efforts have been taken to develop disease-resistant variants of butternut and restore the species by adopting various approaches, which include, but are not limited to, backcross breeding with Japanese walnut (*Juglans ailantifolia* Carrière) using the approaches employed for the American chestnut (*Castanea dentata* (Marsh.) Borkh.) (Diskin et al., 2006), identifying resistant butternut, and germplasm collection which has recorded significant progress (Michler et al., 2005; Ostry and Moore, 2008; Woeste et al., 2009; Hoban et al., 2010; Vidal et al., 2017). Though achieving disease-resistant butternut is the first step in its restoration, the ability to reintroduce butternut into North American forest ecosystems requires identifying suitable areas for successful restoration. Considering the advancements made in identifying potentially resistant trees, a thoughtful approach is being taken to choose suitable locations for successful reintroductions (Woeste et al., 2009). While a predictive model was developed to pinpoint potential sites for butternut restoration in Mammoth Cave National Park (Thompson et al., 2006), studies on butternut restoration across its historical range have not been thoroughly investigated. Although Schumacher et al. (2022) attempted to develop a hindcast and modern habitat suitability for butternut and range shifts in relation to its genetic pattern and fossil pollen records using an individual model technique (boosted regression trees, *brt*), no study has attempted to use ensembled models to assess habitat suitability for butternut reintroduction (Araújo and New, 2007; Marmion et al., 2009). Our study focuses on developing an ensembled species distribution model using six refined modeling algorithms to identify and quantify suitable habitats for butternut restoration within its historic range, assess the

range shift in response to climate change, and identify environmental variables contributing significantly to butternut habitat suitability in the eastern United States.

2. Materials and Methods

2.1. Study Design and Data Analysis

The study is limited to the recorded historical range of butternut in the eastern United States, leaving an appropriate buffer for future prediction while considering future climate change based on different prospective climate scenarios. Aggregated occurrence data and pseudoabsence generated background data (response variable) were analyzed in R (R Core Team, 2022) to assess relationships with selected environmental variables (predictor variables). A combination of different regression-based (generalized additive model, "*gam*"; generalized linear models, "*glm*") and machine learning-based (boosted regression tree, "*brt*"; random forest, "*rf*"; support vector machine, "*svm*"; flexible discriminant analysis, "*fda*") techniques were used to develop habitat suitability models by coupling the prediction from these algorithms using the area under the curve (AUC) (Fielding and Bell, 1997) as the weighted criterion for assembly.

2.2. Sourcing Butternut Occurrence Data

The butternut occurrence (presence) data in the eastern United States were obtained from open-access sources, such as the Global Biodiversity Information Facility (GBIF Secretariat, 2023), TreeSnap (Crocker et al., 2020), and iNaturalist (iNaturalist, 2023). The data were verified and filtered for duplicates and outliers using the *CoordinateCleaner* package (Zizka, 2019) in R (R Core Team, 2020). After the cleaning procedure, 300 presence points were retained, which far exceeded the number required for excellent model accuracy, reduced sensitivity to prevalence, and reduced model overfitting as outlined by Merow et al. (2014) and Guisan et al. (2017). Pseudoabsence data were randomly generated from the *sdm* package in R and used to delineate areas in the predefined geographical area where butternut was not present. The recommended ratio of presence-pseudoabsence data for the species distribution model is 1:2; however, to attain a higher level of predictive accuracy, we adopted a ratio of 1:3.5, having randomly selected 1,000 pseudoabsence points using the *bg* argument in the *sdmData* function within the *sdm* package.

2.3. Environmental Predictor Variables

The bioclimatic variables, generated from monthly temperature and precipitation data for biological interpretation purposes in species distribution models, were downloaded from the WorldClim website from 1970 to 2000 at a 30-second arc resolution (Fick and Hijmans, 2017). The soil-based variables and elevation dataset were downloaded from the Soil Survey Geographic Database (SSURGO) (Soil Survey Staff, 2023) and the U.S. Geological Survey National Elevation Dataset (Gesch et al., 2018). The elevation-based variables, such as slope, relative slope position, aspect, and solar insolation, were derived from refereed literature on the environmental requirements for butternut (e.g., van Manen et al.,

2002; Thompson et al., 2006; Morin et al, 2018). According to Booth's (2022) findings, the reliability of certain bioclimatic variables, which involve both temperature and precipitation, in species distribution modeling can vary depending on their proximity to the equator. This is due to discontinuities detected as a result of the interpolation methods, resulting in significant variations over short distances. Nevertheless, it has been established by Bradie and Leung (2017) that these variables still offer valuable information for analyzing species distribution models and should not be excluded unless necessary. The predictor variables were set to the same extent and resolution, after which they were stacked for analysis.

The occurrence data and pseudoabsence (background) points were overlayed on the predictor variables to extract the data from the raster predictors as a dataframe. A point biserial correlation coefficient analysis was conducted, which measures the strength of association between a dichotomous variable (i.e., occurrence = “1” and absence = “0”) and continuous-level variables (predictor variables). Fifteen variables showed a level of association with the response variable and were pre-selected for further analysis. These variables included annual mean temperature (Bio 1), isothermality (Bio 3), temperature seasonality (Bio 4), minimum temperature of the coldest month (Bio 6), temperature annual range (Bio 7), mean temperature of the wettest quarter (Bio 8), mean temperature of the driest quarter (Bio 9), mean temperature of the coldest quarter (Bio 11), annual precipitation (bio 12), precipitation of the driest month (bio 14), precipitation seasonality (bio 15), precipitation of the driest quarter (bio 17), precipitation of the coldest quarter (bio 19), elevation (DEM), and the slope at the respective site.

2.4. Butternut Habitat Suitability Model Development

To address potential multicollinearity issues arising from highly correlated predictor variables, the preselected variables were subjected to testing using the variance inflation factor (VIF). The VIF was implemented within the *usdm* package in R (R Core Team, 2020), following the methodology outlined by Naimi et al. (2014). The VIF approach was chosen for its capability to identify significant variables, while eliminating redundant variables that may not contribute substantially to the response variable. Predictor variables with a VIF value exceeding 10 were systematically eliminated. A sdmData object was constructed using the *sdm* package to develop the habitat suitability model (Naimi and Araújo, 2016). The model structure was defined by specifying the formula, data, replication technique, data partitioning, *sdm* methods, and evaluation metrics. Our analysis included two regression-based techniques (*gam* and *glm*), as well as four machine learning-based algorithms (*brt, rf, svm*, and *fda*) that were selected based on their excellent discriminatory ability. To ensure robustness, a 5-fold cross-validation replication technique was adopted. This process was repeated for 10 runs, resulting in a total of 50 models for each modeling technique and 300 models, in total. The fitted model object was used to predict the suitable habitats for butternut within its range in the eastern U.S., for all the adopted modeling techniques.

To assess the accuracy and predictive performance of our models, each modeling prediction was evaluated based on the two most cited metrics, the area under the receiver operating characteristics curve, *AUC*, and the true skill statistics, TSS, although there has been strong evidence about them being responsive to prevalence (Peirce, 1884; Allouche et al., 2006; Wunderlich et al., 2019). AUC values range

from 0 to 1, where values greater than 0.5 indicate that the model is better at classifying data than random classification and one is perfect classification (Pepe, 2000; Lobo et al., 2008). TSS has a value that ranges from − 1 to + 1, where 1 indicates perfect agreement and values of zero and less indicate a random chance performance. The probability of occurrence predicted by the models was ensembled by using the *AUC* as a weighted criterion for aggregation to produce the final habitat suitability model for butternut. We generated a threshold-based prediction from the AUC-weighted prediction by adopting the sum of the maximum sensitivity and specificity approach (*max*(*se + sp*)) for developing a presence-absence prediction probability (Naimi and Araújo, 2016). The uncertainty analysis was performed to assess the variability among the model replicate predictions by estimating the standard deviation of the butternut habitat suitability prediction. The generated uncertainty analysis map helped identify areas with highly volatile habitat suitability predictions. This study also assesses the relative importance of variables contributing significantly to the distribution of butternut within its range in the eastern United States using the AUC as the weighted criterion.

2.5. Butternut Distribution Projection

For the projection of butternut habitat suitability within its historical range, three General Circulation Models (GCMs) from the Coupled Model Intercomparison Project 6 (CMIP6) were selected: Australian Community Climate and Earth System Simulator (ACCESS-CM2), Beijing Climate Center Climate System Model (BCC-CSM2-MR), and Hadley Centre Global Environment Model (HadGEM3-GC3.1). Two shared socio-economic pathways, namely stable emission (RCP 4.5) and high emission (RCP 8.5), were utilized across 20-year periods from 2021 to 2100 (i.e., 2021–2040, 2040–2061, 2061–2080, 2081–2100) (Eyring et al., 2016). These GCMs were chosen based on their availability of bioclimatic data and the variability in precipitation projections. ACCESS-CM2 indicates a decrease, HadGEM3-GC3.1 suggests a relatively insignificant decrease, and BCC-CSM2-MR projects a more substantial increase in precipitation (Fig. 2) (Fajardo *et al.*, 2021).

Downscaled future bioclimatic projection data, obtained from the WorldClim website (https://www.worldclim.org/data/cmip6/cmip6climate.html) (Fick and Hijmans, 2017), were utilized for the prediction of butternut habitat suitability under these selected GCMs, RCPs, and periodic years. The data had a spatial resolution of 30 seconds. We quantified the suitable habitat in each of these scenarios as a response to prevailing climatic conditions. RCP 4.5 and 8.5 were denoted henceforth in the write-up as RCP 45 and 85, respectively.

2.6. Effect of Changing Climate on Butternut Range

The study also assesses the shift in the species range as a proxy of prospective climate change by adopting the methodology employed by Iverson et al. (2008) and Adeyemo and Granger (2023). Spatial statistic tools in ArcGIS 10.8.1 were utilized for this analysis. The Mean Center tool was employed to determine the current and future "center of gravity" of butternut distribution. The Mean Center coordinates were used to calculate the distance and direction of potential habitat shifts. Additionally, ellipses representing one standard deviation were created using the Direction Distribution tool for

visualization. We obtained information on potential changes in species' suitable habitats across different scenarios by analyzing mean center distance and direction. The range shift analysis was estimated based on the mean center by calculating the distance (in km) and direction (in degrees) of the future predicted mean center to the historical and predicted suitable habitat mean center.

3. Results

3.1. Variable selection and relative variable importance

The variable preselection process resulted in a reduced set of 15 variables. After excluding correlated variables, eight variables were selected based on their VIF values, while the other seven were eliminated. The minimum correlation was observed between slope and temperature annual range (bio7) with a value of 0.0062, while the maximum correlation was recorded between precipitation seasonality (bio15) and annual precipitation (bio12) with a value of -0.77. Other variables that showed collinearity problems included annual mean temperature (bio1), temperature seasonality (bio4), minimum temperature of the coldest month (bio6), mean temperature of the coldest month (bio11), precipitation of the driest month (bio14), precipitation of the driest quarter (bio17), and precipitation of the coldest quarter (bio19).

For model development, the selected variables were the Digital Elevation Model (DEM), elevation-derived slope (slope), isothermality (bio3), annual temperature range (bio7), average temperature of the wettest quarter (bio8), average temperature of the driest quarter (bio9), annual precipitation (bio12), and precipitation seasonality (bio15) (Fig. 3). Of the eight variables with a VIF < 10, the two most crucial variables influencing butternut distribution were slope and precipitation seasonality (Fig. 4). Slope contributed approximately 20% and precipitation seasonality contributed 18% to butternut distribution (Fig. 4). While there were some variations in the relative importance of variables based on different modeling methods and training or test datasets, the slope consistently demonstrated a higher contribution to butternut habitat suitability in 10 out of 12 modeling techniques and dataset type combinations (Figure S1). The isothermality (bio3) also showed a relative contribution of about 11% to the butternut distribution in the US (Fig. 4). All other variables contributed less than 10% each.

3.2. Model summary and model evaluation

The developed model employed six different model techniques that resulted in 300 model IDs for the butternut habitat suitability model (Table 1). Among the individual models, Random Forest (*rf*) demonstrated the highest predictive performance with an AUC score of 0.94, followed by Boosted Regression Trees (*brt*) with a score of 0.87. The AUC scores for Support Vector Machine (*svm*), Generalized Additive Model (*gam*), Flexible Discriminant Analysis (*fda*), and Generalized Linear Model (*glm*) were 0.88, 0.88, 0.84, and 0.84, respectively (Table 2). With the TSS evaluation, the Random Forest (*rf*), Support Vector Machine (*svm*), Generalized Additive Model (*gam*), and Boosted Regression Trees (brt) emerged as the top four best-performing models, with scores of 0.74, 0.66, 0.65, and 0.62, respectively. The TSS values for Flexible Discriminant Analysis (*fda*) and Generalized Additive Model

(*gam*) were 0.59 and 0.57, respectively (Table 2). The high AUC and TSS values indicate the models' strong predictive ability, and demonstrate that their predictions are better than random chance (Fig. 5).

Table 1
Butternut SDM data and model summary

Class	sdmModels
Name of species	Butternut (*Juglans cinerea* L.)
Number of environmental variables	8
Environmental variables	bio3, bio7, bio8, bio9, bio12, bio15, DEM, Slope
Type	Presence-pseudo-absence
Number of records	1300
Has coordinates?	True
Number of modeling techniques	6
Names of modeling algorithms	*brt, rf, svm, gam, fda, glm*
Data partitioning methods	Cross-validation
Number of replicates	10
Total number of replicates per model	50

Table 2
Butternut HSM evaluation and discrimination metrics

Methods	AUC	COR	TSS	Deviance
brt	0.87	0.58	0.62	0.84
rf	0.94	0.73	0.74	0.54
svm	0.88	0.59	0.66	0.74
gam	0.88	0.60	0.65	0.73
fda	0.84	0.46	0.59	0.87
glm	0.84	0.48	0.57	0.83

3.3. Predicted current habitat suitability and uncertainty analysis for butternut

The ensembled butternut habitat suitability model indicated that the predicted suitable habitat encompassed approximately 131 million hectares for the AUC-weighted threshold-based binary prediction (Fig. 6). However, the agreed predicted suitable habitat from the six model techniques showed

that only about 58 million hectares were suitable for butternut in the US. The uncertainty analysis developed from the standard deviation of the binary-threshold prediction showed a low-level risk associated with the predicted butternut suitable habitat in the eastern US.

3.4. Potential future suitable habitats of butternut based on different climate models

Under the RCP 45 stabilized emission scenario, Fig. 7 illustrates distinct trends in the suitable habitat for butternut. In the ACCESS GCM (Fig. 7A), an initial increase is observed during the first three periods, followed by a subsequent decrease in the final period. Meanwhile, the HADLEY GCM (Fig. 7C) consistently depicts a reduction in suitable habitats throughout the observation period. Conversely, under a high emission scenario (RCP 85), the ACCESS GCM portrays a sustained augmentation in suitable habitats, whereas the HADLEY GCM initially experiences a decline, subsequently followed by a consistent increase during the last three periods. Notably, a transition from stabilized to high emissions scenarios in the ACCESS GCM results in a consistent expansion of suitable habitats across all periods. In contrast, the HADLEY GCM initially witnessed a decline in the first two periods, only to be succeeded by an increase in the last two periods.

However, it is important to note that the BCC GCM projections (Fig. 7B) reveal an overestimation of future suitable habitats for butternut. In this case, nearly all areas are predicted to be suitable, and this overestimation can be attributed to the chosen threshold values for binary classification. The binary classification employed a cutoff point that was exceeded by the probability of an area being suitable for butternut, leading to the overestimation. Furthermore, the rainfall pattern over the years has shown inconsistencies in different parts of the US, as reported by Lindsey (2021).

3.5. Effect of changing climate on butternut range

The butternut range shift analysis was conducted using the ACCESS and HADLEY GCM habitat suitability threshold-based binary predictions because their future habitat suitability prediction obtained was within the ecological interpretation with the exclusion of the BCC GCM. The result showed that the predicted range has a northward range shift from the historical range (the baseline for comparison) with a distance of about 42 km between the two ranges (Fig. 8). This difference in the range between the predicted and the historical range records could be attributed to the effect of the changing climate and unrecorded species occurrence for butternut. Using the historical range and predicted range as a reference point, we projected how this range could shift from 2021 to 2100 under both RCP 4.5 and RCP 8.5, and found that there was a northward range shift for butternut for the two GCMs under both stable and high emissions (Fig. 8). As expected, the high emission scenario showed a greater range shift in distance (km) for butternut habitat in the US for both the GCMs when compared to the stabilized emission scenario. For the ACCESS GCM, the average butternut range shift distance from 2021 to 2100 was 193.45 ± 41.41 km and 253.41 ± 62.98 km for stabilized and high emissions scenarios, respectively (Fig. 9). This translates to about 2.42 ± 0.52 km per year and 3.17 ± 0.79 km per year for stabilized and high emissions scenarios,

respectively (Table S2). The direction of the shift of the predicted range from the historical range was between 280.21° to 289.05° and 267.05° to 288.98° for stabilized and high emissions scenarios, respectively. Similar results were obtained for range shift analysis using the predicted range as the reference point. The average distance was 234.55 ± 40.93 km and 293.31 ± 61.33 km under stabilized and high emissions, respectively, from 2021 to 2100. The direction of shift was between 283.04° to 290.94° and 270.82° to 290.61° for stabilized and high emissions, respectively.

The range shift analysis result for the HADLEY GCM also showed that the distance of the future predicted butternut range from the historical range and historical range increases with increasing emissions and years, as evident in the analysis output. We found an average of 90.61 ± 59.23 km and 110.70 ± 35.37 km with a corresponding direction of 5.75° to 320.06° and 3.93° to 356.52° for stabilized and high emissions scenarios using the historical range as a reference point. Using the predicted range as a reference point, the average distance of the future butternut species range from the predicted range was 112.23 ± 71.15 km and 131.78 ± 48.23 km with a direction between 315.64° to 355.79° and 21.07° to 351.62° under stabilized and high emission scenarios. Overall, the range shift analysis showed that the changing climate will consistently influence butternut species range shift dynamics in the eastern US with a northward shift and increasing distance as we transition from a stabilized emission to high emission scenario over time.

4. Discussion

In our investigation, we employed an ensemble model that combined the weighted outputs of six distinct algorithms to assess the habitat suitability of butternut within its native range in the eastern US. Our selection of predictor variables was guided by an extensive literature review describing the preferred site and environmental conditions of butternut (e.g., Fernald, 1950; Rink, 1990; Gleason and Cronquist, 1991; Skilling, 1993, Ostry et al., 1994; Thompson et al., 2006; Morin et al., 2018; Pike et al, 2021; Schumacher et al., 2022), specifically focusing on factors with potential significance in shaping the distribution of the butternut tree in the eastern United States. These variables predominantly encompassed climatic parameters, with a pronounced emphasis on temperature and precipitation-related factors. It is worth noting that the global phenomenon of climate change has been unequivocally identified as a primary driver behind the alterations in these critical bioclimatic variables. These alterations are poised to have cascading effects on the distribution patterns and habitat suitability of a multitude of terrestrial organisms, thereby warranting a comprehensive assessment of these effects on ecological dynamics. Climate change is exerting a transformative influence on global biodiversity, inducing shifts in abiotic conditions and the intricate web of biological interactions (Rosenzweig et al., 2008). The compounded consequences of ongoing climatic shifts alongside localized disturbances have begun to surpass the adaptive limits and ecological resilience of numerous species (Blowes et al., 2019). This predicament has given rise to a prevalent and conspicuous phenomenon of observable alterations in the distribution of species across various ecosystems (Chen et al., 2011).

Using the threshold-based, binary predicted butternut suitable habitats as the baseline, our model showed a relative increase in suitable areas with a reduction in annual precipitation. Suitable areas also increased with increasing emissions when compared to the stabilized emissions predictions accompanied with low uncertainty risk described in our results. This implies that butternut species may not grow well in flooded areas as they have been reported to be flood intolerant. This result is corroborated by a study from Crystal and Jacobs (2014) that assessed the drought and flood tolerance of butternut and some naturally occurring individual hybrids and found that butternut showed a negative response to flood treatments. Our model exposes intricate patterns in suitable habitats for butternut, showcasing variability in spatial distribution, temporal changes, and responses to different climate scenarios. This highlights the susceptibility of butternut to alterations in precipitation patterns that are associated with many uncertainties. We recorded contrasting results when quantifying the future suitable area for butternuts in the eastern US as a result of different precipitation predictions from different climate models. There is not enough evidence to conclude that there is a significant decline in the suitable areas for butternut in the US based on our threshold binary model prediction and ACCESS and BCC GCMs. This lack of evidence from the GCMs is supported by the recent discovery of some butternut individuals in the state of Mississippi where our model indicated low habitat suitability which could be attributed to the precipitation projection uncertainties (Granger, 2023, *Unpublished findings*). Though the ACCESS and BCC GCM results were inconclusive, the HADLEY GCM demonstrated a significant reduction in suitable habitat. Although some studies found a decline in suitable habitats for butternut (Iverson et al., 2008; Pike et al., 2021; Schumacher et al., 2022), it is difficult to compare the quantified areas as a result of variations in the unit adopted in these studies. The reduction in the population of butternut has been partly attributed to the butternut canker disease (Morin et al., 2018), and has been largely attributed to the species range shift caused by the increase in global temperature that brought about the shift in suitable habitats to adjacent countries, like Canada (McKenney et al., 2001; Schumacher et al., 2022). For example, though the model's reliability assessment score was low (i.e., 20%), Iverson et al. (2008) reported a reduction of 0.2% and 0.1% in the suitable habitat for butternut with 90.7% of its range within the eastern US and the rest of the range in Canada.

A northward longitudinal range shift has been reported by various researchers for many eastern US tree species, and the results of our predicted butternut range shift analysis agree with this trend (Soja et al., 2007; Iverson et al., 2008; Adeyemo and Granger, 2023). Displaying these results collectively in a polar graph reveals distinct patterns of movement and distance for suitable habitats. Our study reported an increase in the distance and variation of the range shift with increasing emissions for butternut in the eastern US. Various distribution studies provide evidence supporting a northward expansion (e.g., Zhu et al., 2012; Zhu et al., 2014) or movement to higher altitudes (e.g., Peñuelas et al., 2007; Vitasse et al., 2012; Rigling et al., 2013). Simultaneously, some studies indicate a decrease in distribution (e.g., Zhu et al., 2012; Adeyemo and Granger, 2023). Anticipated disparities in exposure and responsiveness to environmental shifts are likely to induce uneven patterns of change across species, space, and time (Antão et al., 2022). Such asymmetries manifest in diverse ways, such as alterations in range and phenological shifts (Burrows et al., 2011; Lenoir et al., 2020; Antão et al., 2022). Our study aligns with this

expectation, revealing that the nature and extent of climate-induced responses significantly hinge on the specific geographic zone and the climatic variables under consideration. These findings underscore the nuanced and zone-dependent nature of ecological responses to environmental changes, emphasizing the need for tailored analyses in understanding the complexities of climate impacts on different species. However, one of the major caveats in predicting species distribution and range shift analysis is that it does not account for the seed dispersal that results in species migration which might bring about the future actual distribution that deviates from predictions of potential distribution (Pearson and Dawson, 2003; Svenning and Skov, 2004; Meier et al., 2012; Zimmermann et al., 2013). Identifying and accounting for species' effective dispersal mechanisms will be integral to predicting future species distribution while eliminating overestimation and underestimation of suitable areas (Neilson et al., 2005; Araújo and Guisan, 2006; Zimmermann et al., 2013). Schumacher et al. (2022) attempted to estimate the butternut dispersal ability using pollen records and reported that the tree squirrel (*Sciurus* spp. L.) is the butternut's primary seed dispersal vector with a dispersal distance of less than 100 m. However, the biotic velocities derived from the pollen records exceeds the possible butternut seed disperser which makes it difficult to integrate into species distribution models.

As climate change intensifies, there is a prevailing notion that high-latitude communities will emerge as focal points of significant transformation, as indicated by previous studies (Venevskaia et al., 2013; Koltz et al., 2018). Our research further illuminates the significance of diverse climatic variables in elucidating butternut species' habitat suitability across both spatial dimensions and temporal dynamics. This distinct understanding contributes to a more comprehensive grasp of the complex interactions between climatic factors, spatial characteristics, and temporal considerations in the context of accelerating climate change. Slope aspect and precipitation seasonality were the two most important variables found to contribute significantly to butternut distribution. Topographic factors, such as elevation, slope, and position, exert a significant influence on vegetation distribution, shaping local environments through alterations in solar radiation reception (Holland and Steyn, 1975; Daws et al., 2002; Moeslund et al., 2013; Sundqvist et al., 2013; Yetemen et al., 2015; Jucker et al., 2018). Particularly, the slope aspect emerges as a crucial determinant impacting microclimates, soil properties, and hydrological processes. Studies by Yang et al. (2020) revealed distinct vegetation variations on different slope aspects, driven by significant differences in soil nutrients. North-facing slopes generally exhibit higher biomass, coverage, height, and species diversity due to increased solar radiation (Holland and Steyn, 1975; Kutiel and Lavee, 1999). Crystal and Jacobs (2014) emphasized that solar radiation, canopy cover, and soil characteristics are influenced by slope aspects, and have pivotal roles in defining suitable habitats for butternut species, known for their shade-intolerant nature. Fungal pathogen dispersal is also affected by stand composition and slope gradients (Tisserat and Kuntz, 1983), as supported by Sambaraju et al. (2018), who found higher trunk canker damage probabilities on butternut trees on flat lands. Romero et al. (2022) established humidity and temperature as key drivers of disease outbreaks, which vary with slope. Recognizing the intricate dynamics of slope gradients in landscapes provides insights for effective butternut restoration management in the eastern US. Pendergrass et al. (2017) projected that seasonal precipitation, especially in regions with high variability, significantly determines the butternut range,

particularly amid changing climates. Our results highlight notable variability, influenced by inconsistencies in future precipitation predictions from various General Circulation Models (GCMs). Barnes and Delborne (2019) stressed that alterations in seasonal precipitation patterns within specific time frames can lead to shifts in suitable areas for species, emphasizing the need for nuanced approaches in managing butternut ecosystems under changing climate conditions.

Limited studies have researched the impact of climate change on *Ocj* distribution, the fungal pathogen causing butternut canker, and how it might impact the future distribution of butternut which is not within the scope of this study. Although the exact distribution of *Ocj* has not been extensively mapped, Broders et al. (2015) have described its distribution. Understanding the current range of the pathogen is crucial for predicting its potential impact on butternut in the future. Moore and Ostry (2015) have demonstrated that humidity benefits *Ocj*. This information is essential for hypothesizing how climate change might influence the spread and severity of butternut canker. However, there might be different outcomes under different climate models and future scenarios for example if climate models predict a warmer and more humid future in regions where butternut is present or predicted to occur, we can hypothesize that *Ocj* would thrive under these conditions. Consequently, the pathogen might expand its range, following the predicted future range of butternut. In this scenario, butternut canker could continue to pose a significant threat to the species. Conversely, if climate models indicate a warmer and drier future, we can hypothesize that Ocj might be negatively impacted by these conditions. As a result, the pathogen could become less prevalent or severe, potentially allowing butternut to rebound in its predicted future range. It is essential to note that predicting the future range of *Ocj* is complex and depends on various factors, such as the specific climate models used, the time scale considered, and potential adaptations of both the pathogen and the host species. Additionally, other factors, such as host resistance, management strategies, and ecological interactions, can influence the impact of *Ocj* on butternut populations. While this discussion provides hypotheses on how the distribution of *Ocj* might impact the future distribution of butternut, it is crucial to emphasize that these are speculative scenarios based on available research. Further studies focusing on the distribution and ecology of *Ocj*, as well as the development of more comprehensive climate models, will be necessary to refine these predictions and inform conservation efforts for butternut.

5. Conclusions

In our study, we employed an ensemble model that combined the weighted outputs of six distinct algorithms to assess the habitat suitability of butternut (*J. cinerea*) within its native range in the eastern US. Our ensemble species distribution model reveals complex dynamics in suitable butternut habitats, with variability across space, time, and climate scenarios. This underscores the sensitivity of butternut to shifting precipitation patterns and other climatic factors. These findings have several implications for conservation efforts. Specifically, slope aspect and canopy cover emerge as potential local levers for land managers to create microclimates resilient to regional drying and climate disruption. Targeted planting on north-facing slopes and in mixed stands may mitigate disease spread while supporting

climate-threatened butternut. More broadly, more adaptive and location-specific management will be needed, rather than one-size-fits-all approaches.

For policymakers, dynamic suitable habitat projections highlight the value of emissions mitigation to dampen habitat losses for vulnerable species like butternut. Stabilized emissions scenarios showed more consistent habitat maintenance over time compared to high emissions. Policy incentives promoting biodiversity-friendly forestry and land use practices could also aid conservation. From a research perspective, incorporating dispersal limitations and biotic interactions into future species distribution models is critical to avoid under- or over-estimating range shifts for conservation planning. Identifying effective seed dispersers and their behaviors will enable more accurate predictions. Furthermore, epidemiological research on disease spread and triggers can guide treatment plans.

Ultimately, saving climate-imperiled butternut will necessitate coordinated action across managers, researchers, and policymakers. Our findings illuminate threats but also opportunities to sustain the viability of the eastern butternut tree amid global upheaval if insights are translated into targeted, science-based conservation decisions respecting the ecological intricacies at play. The fate of the butternut tree thus serves as one microcosm of the broader challenges societies face in stemming biodiversity losses from accelerating climate disruption.

Declarations

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Author contributions

Segun M. Adeyemo: conceptualization; data curation; methodology; writing—original draft; writing—review and editing; validation; supervision.

Joshua J. Granger: conceptualization; methodology; writing—review and editing; validation; validation; supervision; funding.

Ashley N. Schulz: writing—review and editing; validation.

Krishna P. Poudel: methodology, writing—review and editing.

Yun Yang: writing— writing—review and editing.

Data availability

All data used in this study are open-source data. Sources of all datasets have been acknowledged in sections 2.2 and 2.3 of this manuscript.

Ethical responsibilities of authors

All authors have read, understood, and have complied with the statement on “Ethical responsibilities of Authors,” as found in the Instructions for Authors. Any opinions, findings, conclusions, or recommendations expressed in this publication are those of the authors and do not necessarily reflect the view of the U.S. Department of Agriculture.

Competing interests

The authors declare no competing interests.

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Figures

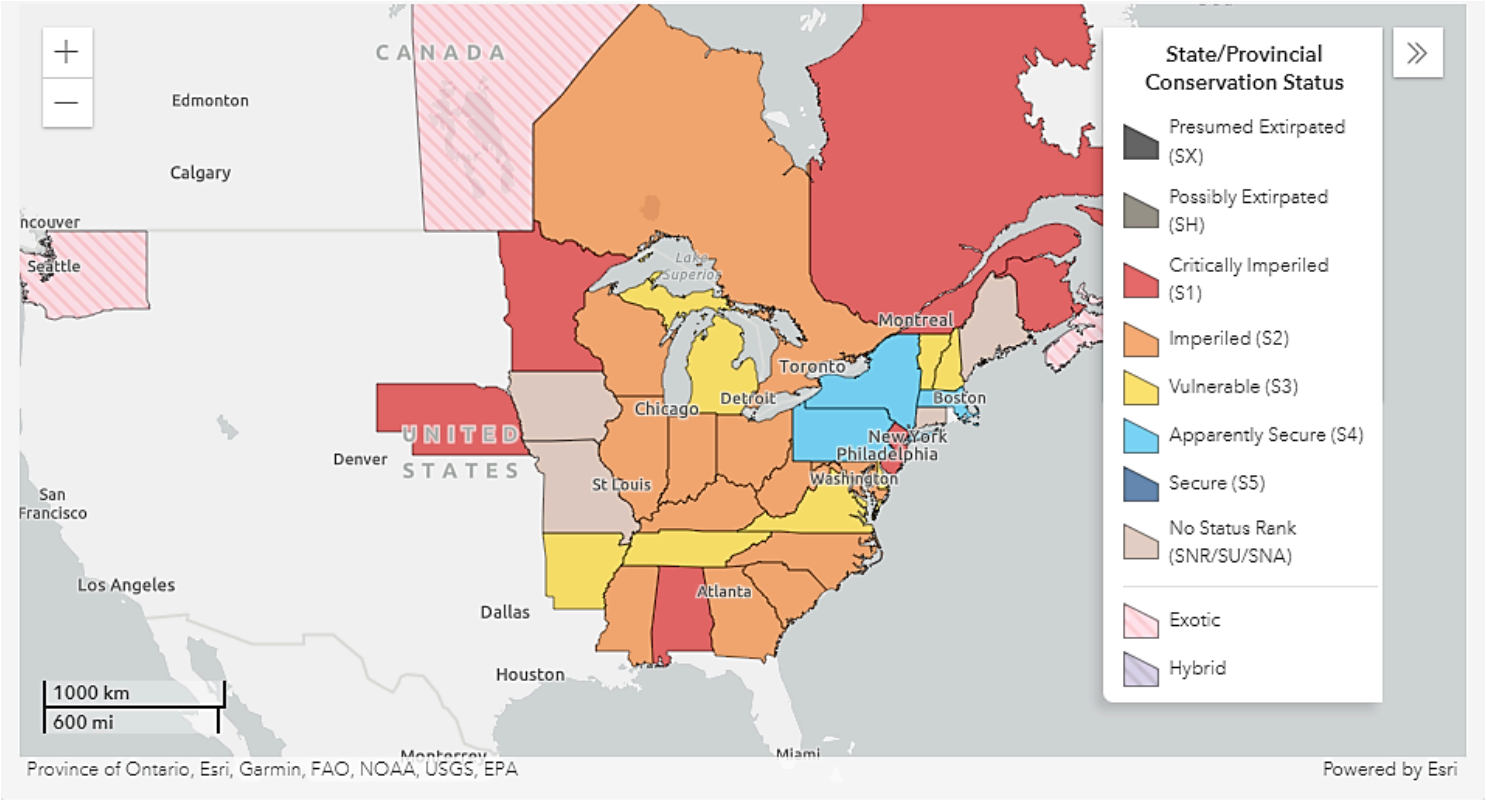

Figure 1

Conservation status of *J. cinerea* in North America (Source: NatureServe, 2023)

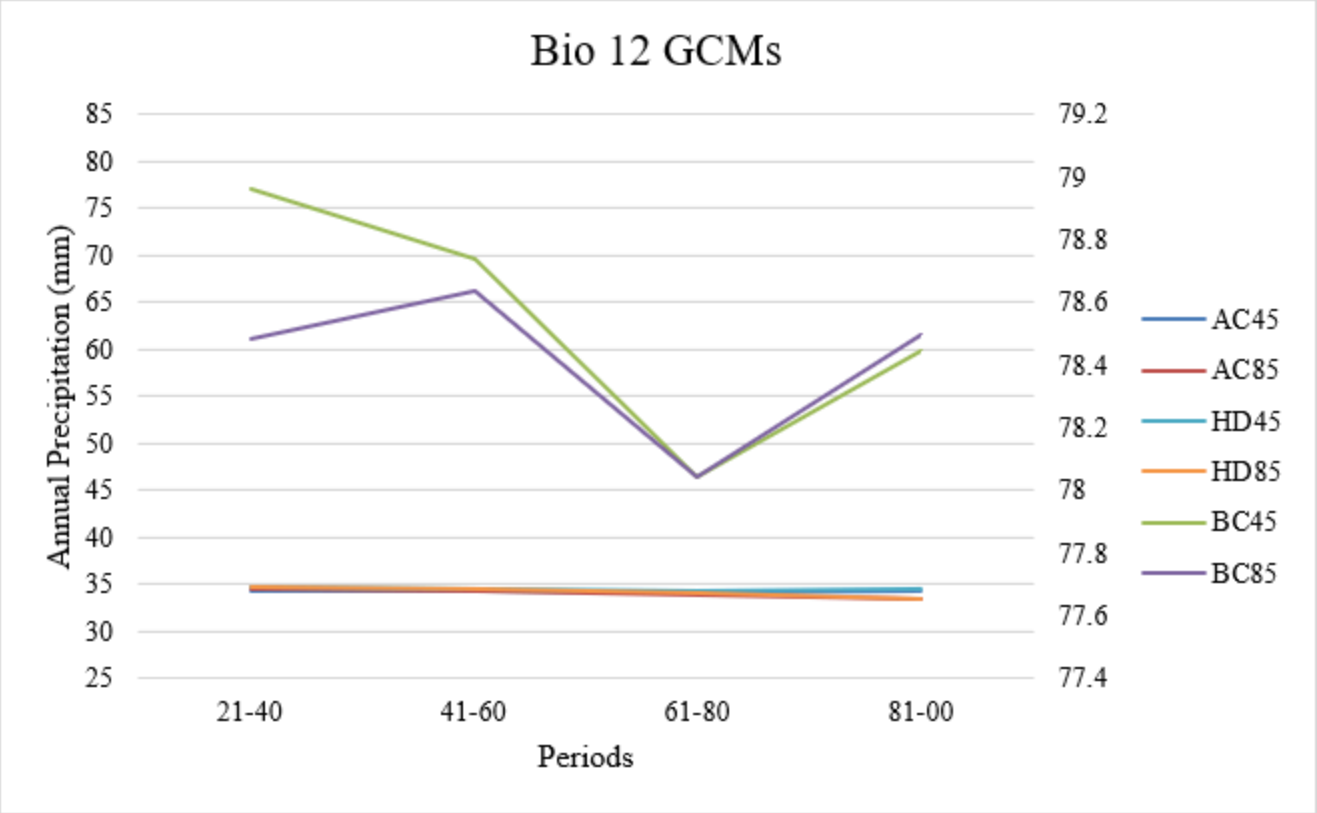

Figure 2

The mean annual precipitation for the GCMs, RCPs, and periods selected for the future habitat suitability model prediction, as obtained from Fick and Hijmans (2017).

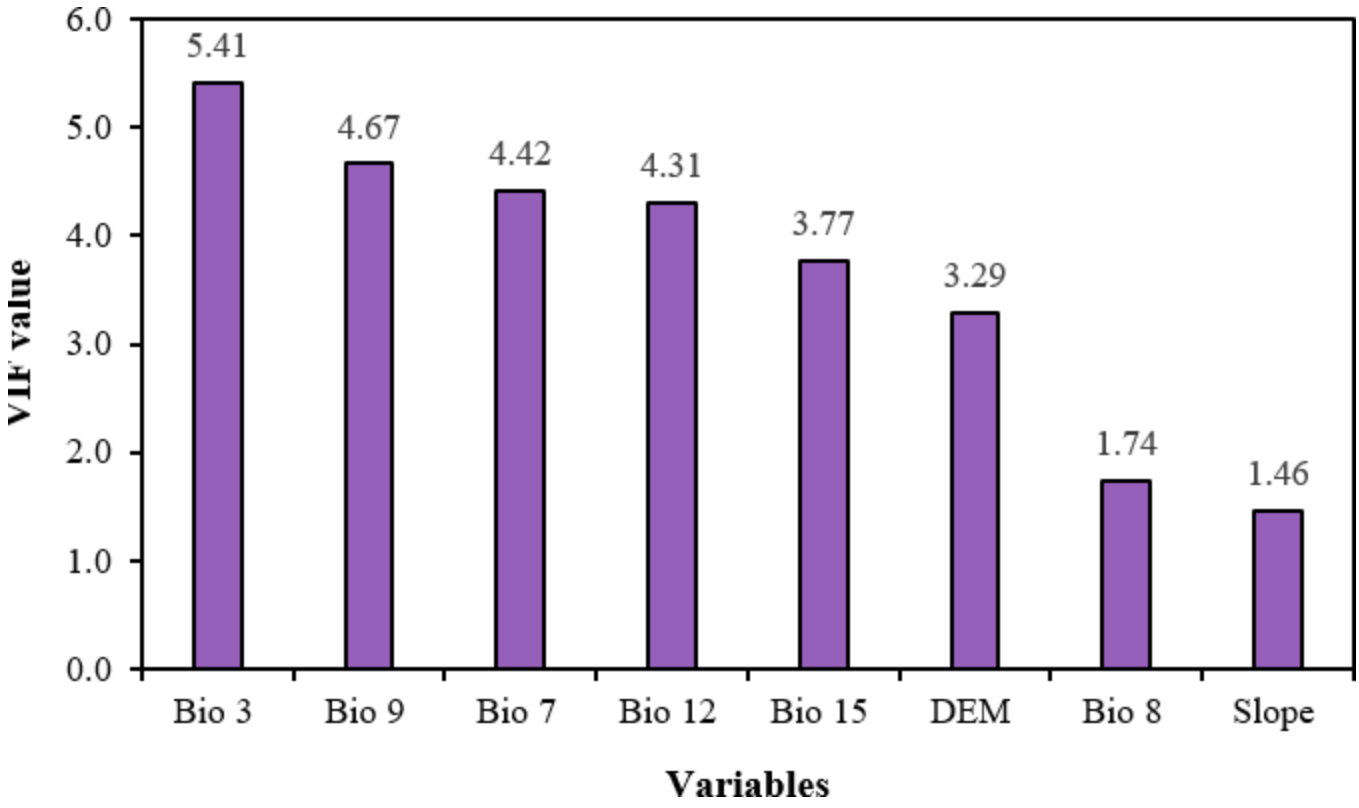

Figure 3

Selected variables with VIF values, excluding collinear variables.

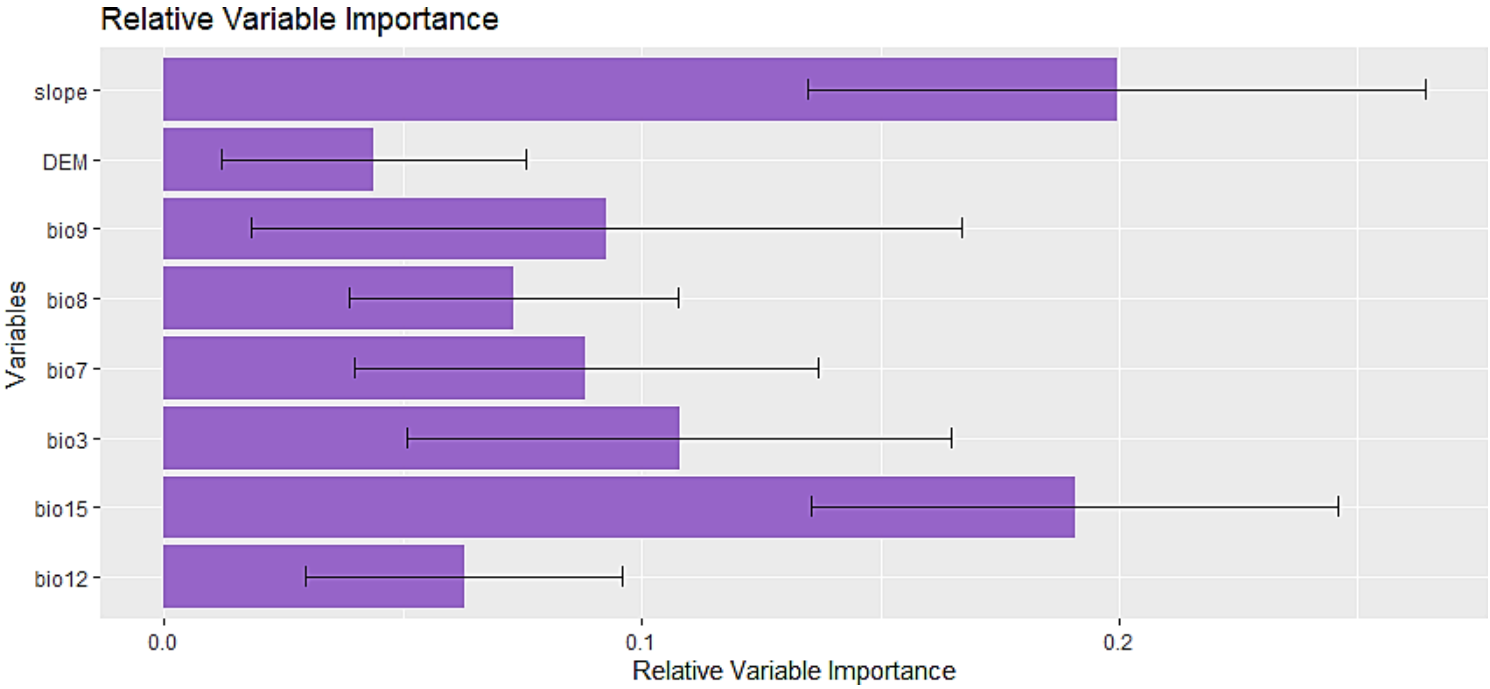

Figure 4

Relative variable importance for the butternut habitat suitability model using AUC as the weighted criterion.

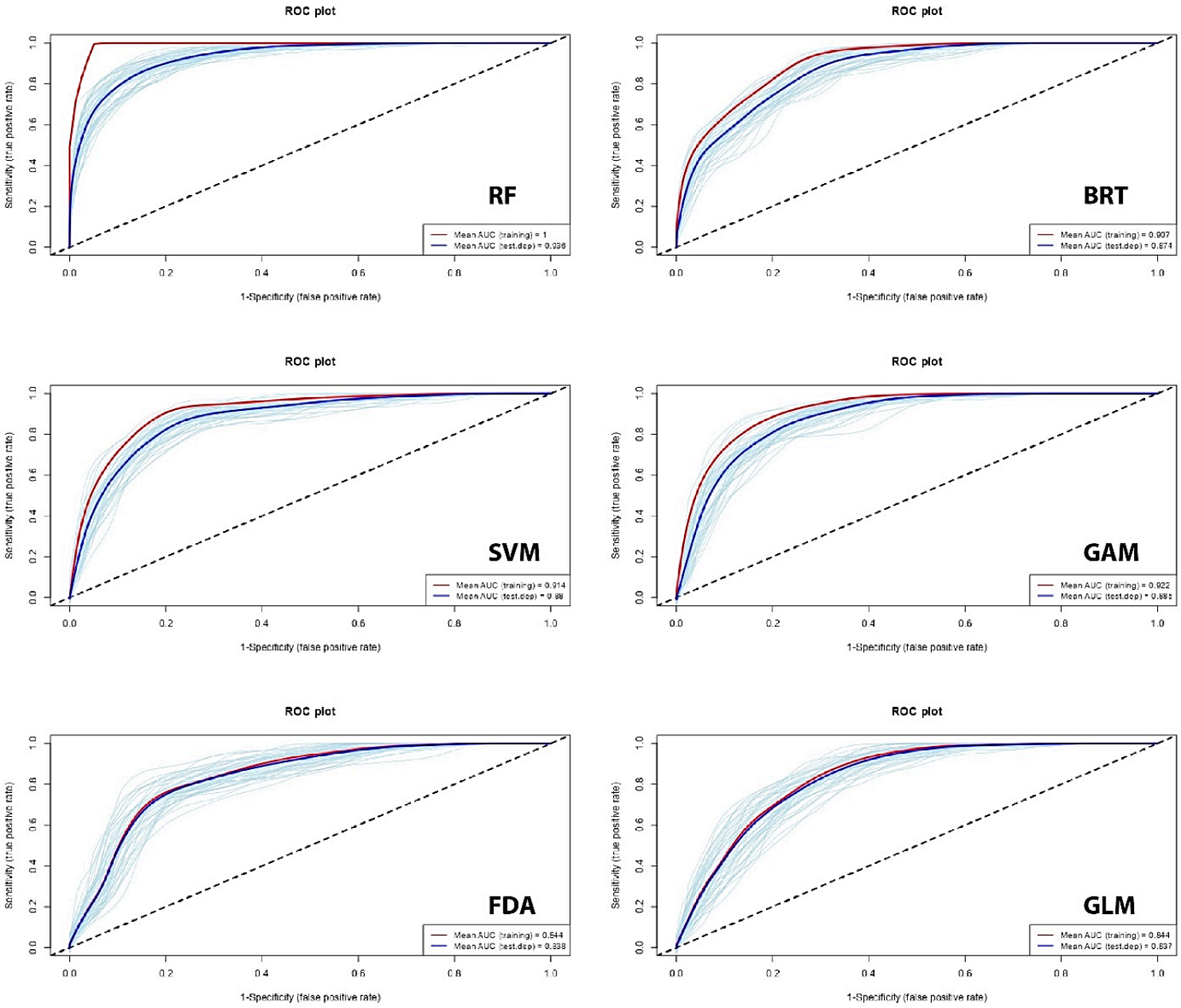

Figure 5

Receiver Operating Characteristic plots with area under the curve (AUC) statistics to illustrate the performance of our model regarding the training and testing datasets. The curves are consistently positioned well above the dotted random reference line (AUC = 0.5), demonstrating the meticulous selection of both training and testing datasets, the model's proficiency in discriminating between suitable and unsuitable habitats for butternut, and a low mean misclassification error rate.

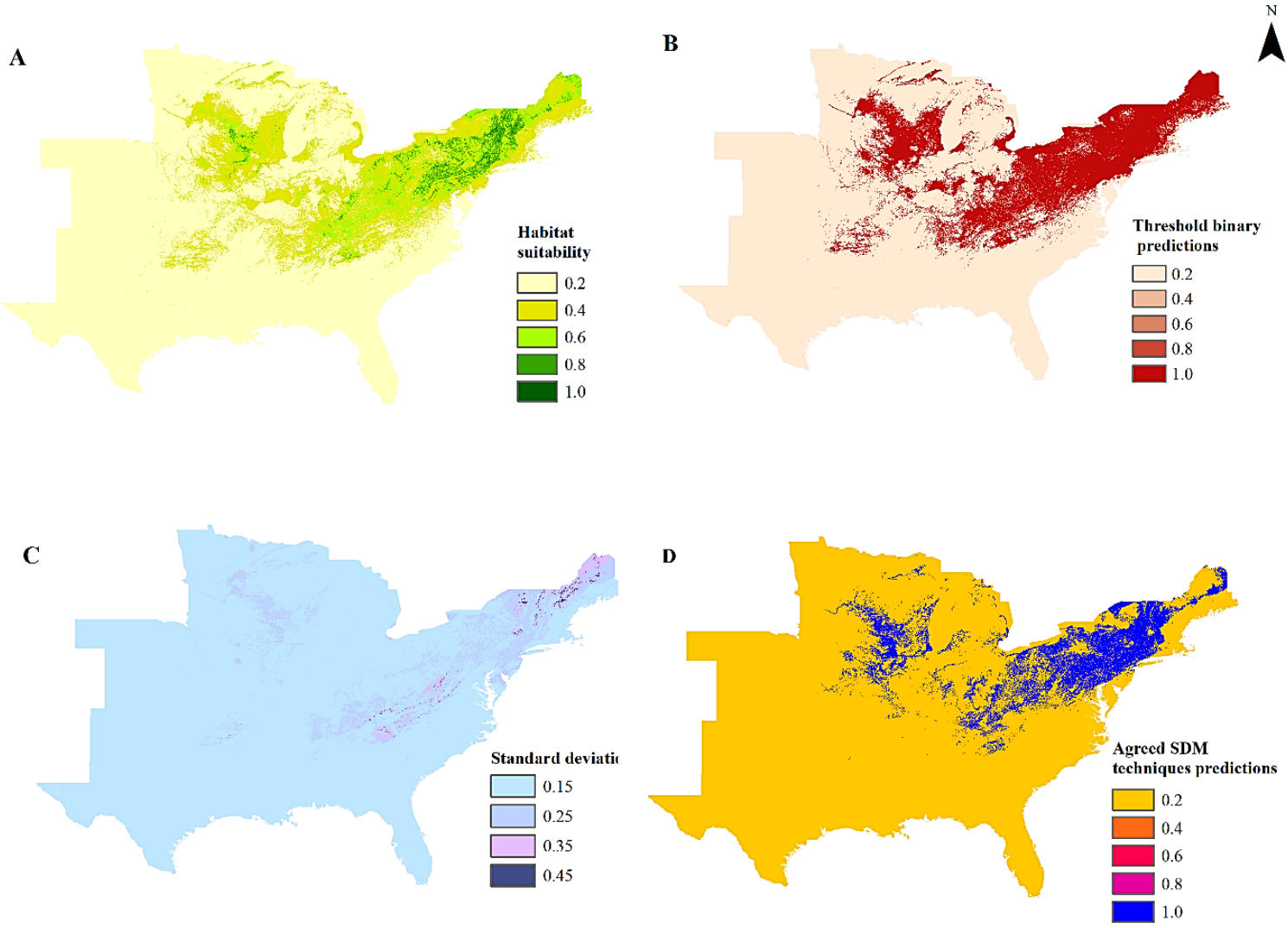

Figure 6

Predicted suitable habitats for butternut (*J. cinerea*) in the US, where (A) is the probability of habitat suitability for butternut, (B) is the AUC-weighted threshold-binary classification, (C) is the uncertainty analysis from the binary classification, and (D) is the agreed suitable habitat for butternut.

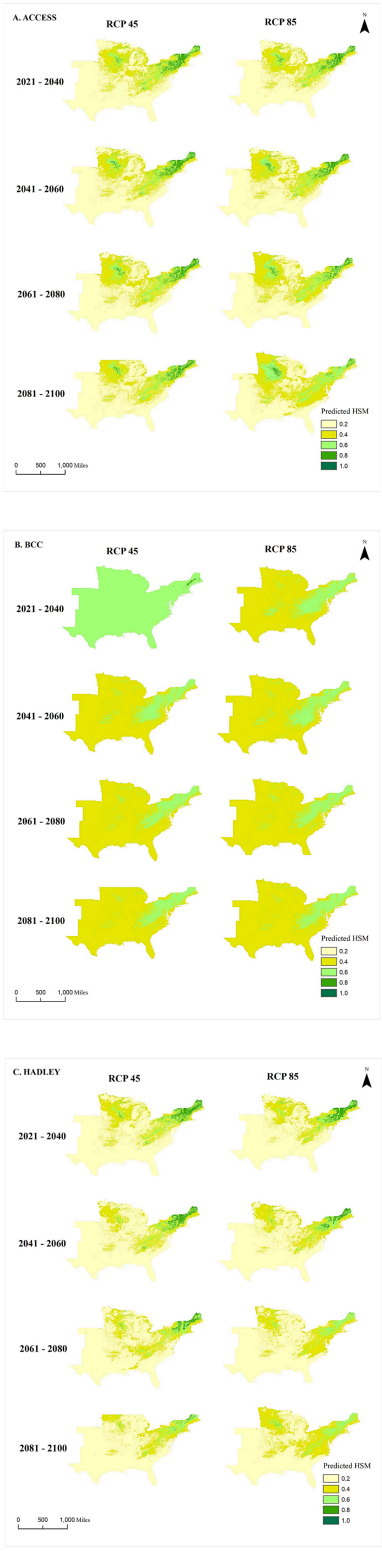

Figure 7

Future butternut habitat suitability predictions using 3 GCMs (A. ACCESS, B. BCC, C. HADLEY), 2 RCPs (RCP 4.5 and RCP 8.5), and 4-time intervals (2021-2040, 2041-2060, 2061-2080, 2081-2100).

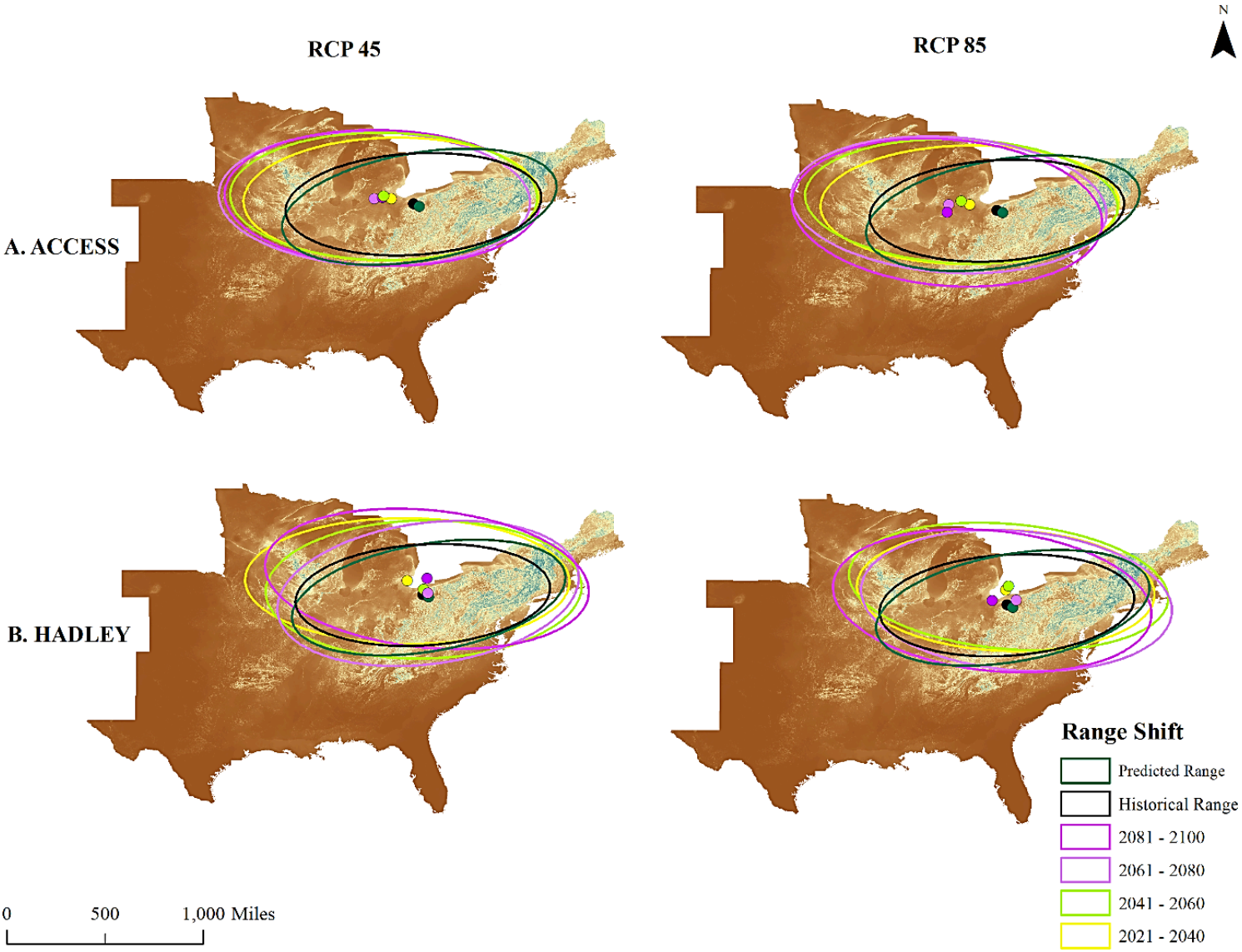

Figure 8

Distance (km) and direction (degrees) of the butternut range shift using the historical range as the baseline.

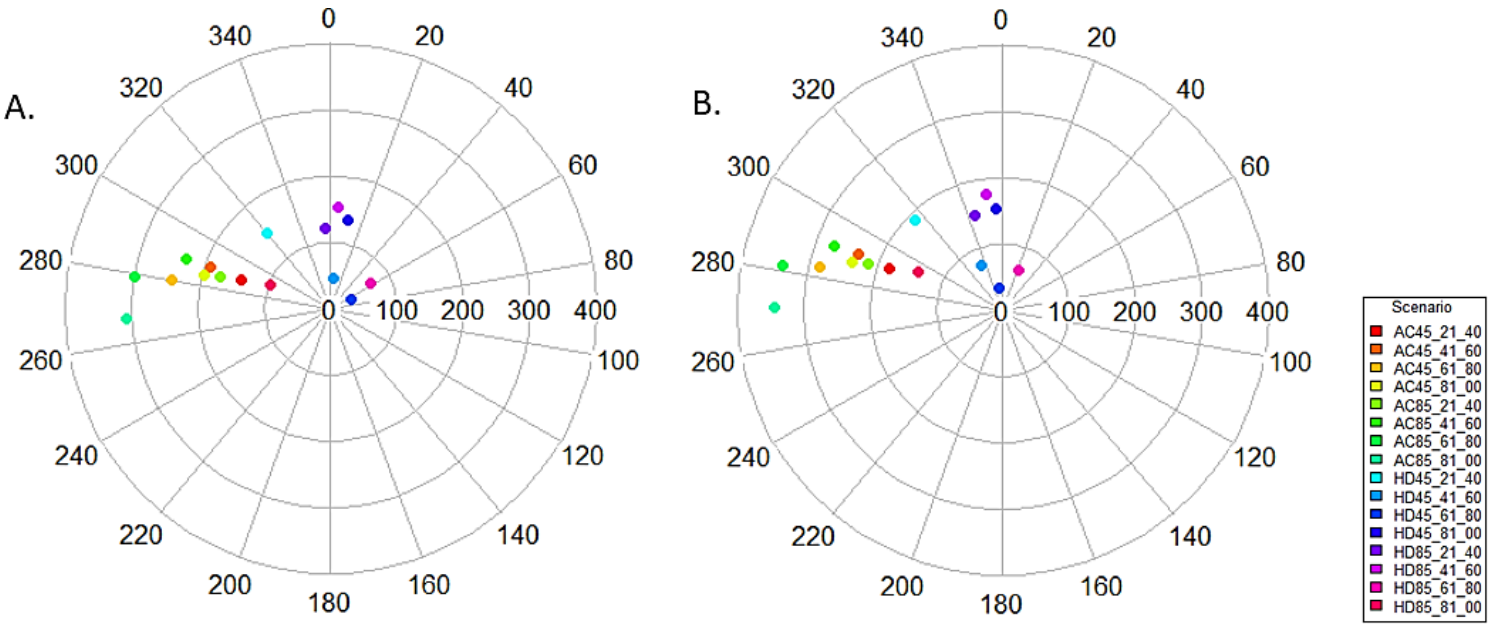

Figure 9

Visualizing the distance (km) and direction (degrees) of the predicted butternut range shift under different GCMs (ACCESS and HADLEY), periods (2021 – 2040, 2041 – 2060, 2061 – 2080, and 2081 – 2100), and representative concentration pathway (RCP 4.5 and RCP 8.5) where A is the range shift from the historical range while B is the range shift from predicted range.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- SupplementaryMaterials.docx