Forest Ecology and Management 612 (2026) 123708

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Habitat suitability ensembles of genotype and disease resistance for *Juglans cinerea* to assist restoration efforts

Carlisle S. Bascom Jr. [a], Anna O. Conrad [b], Aziz Ebrahimi [c], Douglass F. Jacobs [c], Carrie Fearer [a,*]

[a] Department of Forest Resources and Environmental Conservation, Virginia Tech, Blacksburg, VA, USA
[b] USDA Forest Service, Northern Research Station, Delaware, OH, USA
[c] Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN, USA

ARTICLE INFO

Keywords:
Butternut
Butternut canker disease
Ensemble models
Habitat suitability modeling
Juglans cinerea
Ophiognomonia clavigignenti-juglandacearum
TreeSnap
Global Biodiversity Information Facility
Forest Inventory and Analysis

ABSTRACT

The environmental suitability of a particular organism is often a combination of local climatic factors, resource competition intensity, as well as pathogen and predator pressure. Pathogen pressure, or host resistance, is particularly important in host species severely impacted by disease. Variations in heritable pathogen resistance can lead to differences in apparent habitat suitability of resistant or susceptible subpopulations. In the case of the butternut tree (*Juglans cinerea*), habitat suitability is limited by genetic resistance to the non-native butternut canker disease (BCD) in addition to environmental factors. Further, butternut frequently crosses with the non-native, BCD-resistant, congenic Japanese walnut (*Juglans ailantifolia*) producing fertile hybrids. We sought to develop models of butternut or hybrid genotype and BCD resistance phenotypes that could inform conservation efforts. We combine two regression-based and three machine-learning based composite models to build a series of ensemble habitat suitability models of butternut and hybrid genotype, as well as butternut BCD resistance phenotype. Our ensembles highlight southern Indiana, western Kentucky, western Michigan, and much of New England as climatically suitable for BCD-resistant butternut. Meanwhile, much of the central Midwest and areas south of the Great Lakes are climatically suitable for hybrids. These ensembles can guide conservation efforts seeking to breed BCD-resistant butternut and hybrids by highlighting areas from which to source breeding stock or locate regeneration orchards.

1. Introduction

The suitable habitat of a particular organism is a factor of the fundamental niche, generally considered to be the range of favorable abiotic conditions, and the realized niche, one that is influenced by biotic factors such as competition for resources (Matthiopoulos, 2022; McInerny and Etienne, 2012; Sales et al., 2021). Further, novel pathogens are capable of dramatically changing an organisms' niche upon introduction (Scheele et al., 2025, 2023). The most significant example of such an occurrence in forested landscapes is *Cryphonectria parasitica* (Murrill) Barr., the causal agent of chestnut blight, which reduced the once-dominant American chestnut (*Castanea dentata* (Marsh.) Borkh.) to functional extinction within fifty years (Elliott and Swank, 2008; Paillet, 2002) and shifted chestnut's niche from a canopy to an understory species (Paillet, 1984). Less well understood is how butternut's (*Juglans cinerea* L.) niche has been changed due to butternut canker disease (BCD), caused by the nonnative ascomycete fungus *Ophiognomonia clavigignenti-juglandacearum* (herein "*Oc-j*"; Nair, Kostichka, & Kuntz (Broders and Boland, 2011)). While the exact origin remains enigmatic because *Oc-j* has never been identified outside of North America, the fungus was first detected in southwest Wisconsin circa 1967 (Nair et al., 1979; Renlund, 1971), yet population structure analysis suggests multiple *Oc-j* introductions (Broders et al., 2012).

Butternut is a cold-tolerant, shade-intolerant, short-lived, masting tree that native people prized as a source of food and medicine (Moerman, 1986). It has ecological value as a food source for wildlife and aesthetic value among woodworkers (Meier, 2015). Even though butternut was not historically abundant across the landscape, it is currently listed as "endangered" by the International Union for Conservation of Nature (IUCN) due to BCD (Stritch and Barstow, 2019). In 1995, The U.S. Forest Service estimated that 77% of the butternut population in the southeast had been killed due to BCD and that most of

* Corresponding author.
E-mail address: cfearer@vt.edu (C. Fearer).

https://doi.org/10.1016/j.foreco.2026.123708
Received 14 October 2025; Received in revised form 18 February 2026; Accepted 15 March 2026
Available online 27 March 2026

the surviving trees are so heavily infested with *Oc-j* that they are not reproducing (Forest Service, 1995). Unlike American chestnut, butternuts typically do not produce sprouts after stem death (Schlarbaum et al., 1998). Considering both of these factors, it is conceivable that we have and will continue to lose genetic diversity as distinct butternut populations continue to succumb to *Oc-j* infection, making research on developing host resistance to BCD challenging or impossible.

Another non-native species has had an impact on butternut– the Japanese walnut (*J. ailantifolia* Carr.). Japanese walnut was intentionally introduced to North America in the late 1800s (Zhao and Woeste, 2011) and hybridizes with butternut. Butternut crossed with either Japanese walnut or the 'Heartnut' cultivar (*J. ailantfolia var. cordiformis* (Makino.) Rehder) produces the "buartnut" (*J. x bixbyi* Rehder.) (Bixby, 1919). Butternut and buartnut can be difficult to distinguish morphologically (Bixby, 1919; Farlee et al., 2010; Ross-Davis et al., 2008). Further, buartnut is uniquely fertile among walnut hybrids, yet retains the self-compatibility trait common to walnuts (Farlee et al., 2010). Fertility, as well as the fact that walnuts are wind pollinated, has allowed buartnut to backcross with butternut and Japanese walnut, as well as cross with their hybrids. Resulting complex hybrids compound the difficulty in identifying butternut based on morphology alone, confounding efforts to find non-hybridized butternut germplasm (Ross-Davis et al., 2008). In contrast to butternut, Japanese walnut and their hybrids are generally more resistant to *Oc-j* (Brennan et al., 2020; McKenna et al., 2011). Hybrid resistance to *Oc-j,* combined with the difficulty in morphologically distinguishing butternut from hybrids has impeded breeding efforts utilizing BCD-resistant butternut germplasm (Brennan et al., 2020; Ostry and Moore, 2008). Indeed, complex hybrid proliferation has led to concerns that butternut is suffering a "genetic invasion" (Hoban et al., 2009; Ostry and Woeste, 2004). As such, researchers have identified molecular markers to distinguish butternut from its hybrids (McCleary et al., 2009; Ross-Davis et al., 2008; Zhao and Woeste, 2011). Such work has revealed that hybridization has occurred across butternut's native range (Hoban et al., 2009, 2012a). Since hybrids are more resistant to *Oc-j* and morphologically difficult to distinguish from butternut, hybrids could slowly be replacing native butternut across the landscape, further depleting the butternut gene pool and limiting their ability to persist across the North American landscape (Pike et al., 2020).

While there is some level of BCD resistance among butternut trees (Ostry and Moore, 2008), qualitative resistance (i.e., no symptom progression), remains elusive. Further, many reports have concluded that there is little to no heritable basis for BCD resistance among butternut (LaBonte et al., 2015; McKenna et al., 2011), though recent findings from a range-wide study indicate that some butternut genotypes may be less susceptible to BCD (Conrad et al., 2026). Several *Juglans* species, including Japanese walnut, black walnut (*J. nigra* L.) and Persian or English walnut (*J. regina* L.), are susceptible to *Oc-j* if directly inoculated after wounding (Ostry and Moore, 2007). However, direct inoculations of *Oc-j*, which bypass potential disease resistance mechanisms in the bark, may not reflect realistic host-pathogen interactions (McKenna et al., 2011). Indeed, natural *Oc-j* infections on black walnut are rare (Ostry et al., 1997), suggesting resistance. Given butternut's relatively low quantitative BCD resistance, there has been a focus on utilizing, instead of avoiding, hybrids for BCD resistance breeding (Boraks and Broders, 2014; Brennan et al., 2020; Michler et al., 2006; Pike et al., 2020). This is particularly true in areas where use of butternut alone is not feasible due to disease pressure. For this reason, some states are choosing to propagate and distribute hybrid butternut (e.g., Indiana's Department of Natural Resources).

Butternut has not been successfully crossed with the North American native, *Oc-j* resistant, black walnut (Rink, 1990). Instead, proponents of hybridization have focused on naturalized Japanese walnut hybrids as a source of BCD resistance for butternut breeding, given hybrid fertility and morphological similarity to butternut (Brennan et al., 2020; McKenna et al., 2011). Japanese walnut introgression into butternut populations has the potential to provide BCD resistance, but assessing resistance is complicated by variations in *Oc-j* virulence (Brennan et al., 2020; McKenna et al., 2011), forest type (Morin et al., 2017), and environmental factors (Sambaraju et al., 2018). Therefore, future butternut conservation efforts could be guided by a greater understanding of range-wide variation in BCD resistance and Japanese walnut introgression.

With advancements in computing power and precise remote sensing data, modeling species distributions has become increasingly accessible (Bertelli et al., 2022; Guisan et al., 2013; Hirzel and Lay, 2008). This methodology describes, predicts, and ultimately maps the extent of environmental conditions suitable for a particular species (Franklin, 1995; Guisan and Zimmermann, 2000; Hirzel and Lay, 2008). For brevity, we refer to the product of all such methodologies as habitat suitability models (HSMs). HSMs have been applied to the restoration of both American chestnut (Adeyemo and Granger, 2023; Barnes and Delborne, 2019; Noah et al., 2021) and butternut (Adeyemo et al., 2025). Beyond tree species, HSMs have informed conservation work in other threatened species including Asiatic bears (Su et al., 2021), cetaceans (Hanf et al., 2022) and an endangered Hawaiian alpine plant (Krushelnycky et al., 2023). There are many statistical approaches available to generate HSMs, including machine learning models like random forest (rf) (Breiman, 2001; Cutler et al., 2007; Luan et al., 2020), and maximum entropy (MaxEnt, me) (Elith et al., 2011; Phillips, 2021), as well as regression-based models like generalized linear (glm) and generalized additive (gam) models (Guisan et al., 2002; Li et al., 2017; McCullagh and Nelder, 1989). To avoid systematic biases inherent to any single approach, it is common to develop multiple models and combine them into a single ensemble model (Alaoui and Idri, 2024; Araújo and New, 2007; Georgian et al., 2019; Latif et al., 2013; Rew et al., 2020; Yang et al., 2023).

Recent work developed ensembles to predict changes in butternut suitability across different climate change scenarios (Adeyemo et al., 2025), but did not consider differences within butternut by either BCD resistance phenotype or hybrid genotype. There is evidence that butternut is more cold-tolerant than hybrids (Brennan et al., 2021), suggesting there are at least slight differences in niche suitability. Therefore, we hypothesized that heritable differences in BCD resistance and variance in hybridization rates may be sufficiently predicted by climate, developing gradients of habitat suitability among the broader butternut population. Our research goal was to identify if hotspots of butternut and hybrid genotypes as well as BCD susceptibility and resistance phenotypes exist on the landscape to help guide restoration and management strategies. To address our hypothesis, we utilized a recent dataset of butternut and hybrid families which includes the family origin location, hybrid status, and resistance to BCD (Conrad et al., 2026)

2. Materials and methods

2.1. Data acquisition and pre-processing

Half-sibling family BCD resistance scores and species/hybrid categorizations were obtained as part of ongoing research at the Hardwood Tree Improvement and Regeneration Center at Purdue University (Conrad et al., 2026). Accuracy and precision of family location varied across the dataset, though we lacked trusted metadata on the level of precision for a given family source. Therefore, we elected to aggregate family location data, and all data thereafter, at the county level. Within our study area (see below), aggregation occurred at a minimum across 59.6 km^2 of land for New York County, New York, and at a maximum across 17,278.3 km^2 of land in Aroostook County, Maine. We thusly aggregated the data knowing that doing so would mask important small-scale variations, and potentially inflate predictor autocorrelation, but deemed doing so could still yield informative results. Here, "butternut" refers to genotypes that are unambiguously assigned to the species *Juglans cinerea*. Meanwhile "hybrid" refers to genotypes with

evidence of Japanese walnut introgression. Families were already binned to "butternut" or "hybrid" based on single nucleotide polymorphism-based genotyping and morphology. We binned butternut into *Oc-j* "more resistant" or "less resistant" based on the quantitative BCD resistance phenotype provided by Conrad et al., 2026. For the purposes of this study, "more resistant" families had a breeding value above the mean, while "less resistant" families were below the mean. Given the already limited dataset (~300 families, several of which were binned into single counties), we elected to only bifurcate the phenotype data instead of using quantile or continuous-model approaches. Using the mean breeding value as the threshold between the two subpopulations introduces additional biases, as other methods to assign quantitative resistance, or using alternative thresholds to bin the initial dataset could yield different results. Importantly, "more resistant" trees could still develop symptoms of BCD, although "more resistant" families generally contained trees with less severe disease symptoms. Further, not all families were assigned a BCD resistance phenotype value, for instance, due to an insufficient number of trees within a family, resulting in more "butternut" vs "hybrid" genotype data than "more resistant" and "less resistant" phenotype data. Counties were then split into "butternut", "hybrid", "more resistant" and "less resistant" datasets to build an ensemble of habitat suitability models for each category (Fig. 1). We then split the data into "training" and "test" sets (Fig. 1A). Though there are a range of acceptable data partitioning rations, we sought to balance having sufficient data to train the models but also to accurately test them. As such, for each dataset, counties were subjected to a single, random 70–30 training-test split (Fig. 1A), a common split in model building (Vrigazova, 2021). Other training-test ratios or non-random methods of sample selection (e.g., spatial blocking (Roberts et al., 2017)) were not attempted and doing so may lead to different results. Given the small number of observations, we elected not to perform multiple cross-validated data splits as such efforts would likely only marginally improve the accuracy of our models, or worse, provide misleadingly high performance scores (Vabalas et al., 2019; Varma and Simon, 2006). Previous work has suggested that assigning two pseudo-absences for every one presence datum is appropriate for habitat suitability modeling of rare plant species (Williams et al., 2009). However, recent work modeling butternut suitability specifically used a 1:3.5 presence:pseudoabsence ratio (Adeyemo et al., 2025). Here, we compromised by assigning a 1:3 presence:pseudoabsence ratio for the training data, though we did so without conducting sensitivity analyses. For the test data, the ratio was 1:1 as has been suggested (Allouche et al., 2006). As with any habitat suitability modeling study, altering presence: pseudoabsence ratios can have a profound effect on model accuracy and therefore the conclusions drawn from those models.

We sourced climate data from the Parameter-elevation Regressions on Independent Slopes Model (PRISM) (Daly et al., 1994; PRISM, 2024). We used the thirty year (1980 – 2020) normal at a four-kilometer resolution for all available variables as we did not want to introduce bias with *a priori* assumptions of what climate variables may be important to our models. The temporal range of this dataset closely aligns with the butternut and hybrid family collection, cultivation, and genotype/phenotype assaying (Conrad et al., 2026). This contrasts with the often-used WorldClimv2.1 dataset, which interpolates and derives parameters from 1970 to 2000 (Fick and Hijmans, 2017). As such, we used precipitation, minimum, mean and maximum temperature, minimum and maximum vapor pressure deficit, mean dew point, total solar radiation, clear day solar radiation, and cloud transmittance data. We included both monthly and annual averages. We calculated the climate variable average for every county or county-equivalent in all states east of Minnesota, Iowa, Missouri, Arkansas, and Louisiana, inclusive (Fig. 2A), using R (v4.5.0 (2025–04–11) (Team, 2025, Team, 2025)) via R Studio (v2025.5.0.496, (team, 2025)) with the *tigris* (Walker, 2015), *raster* (Hijmans, 2010), *sf* (Pebesma, 2018; Pebesma and Bivand, 2023), and *dplyr* (Wickham et al., 2023) packages (Fig. 1B). To facilitate the production of parsimonious models, we manually removed variables that had a Pearson's correlation coefficient $|r| < 0.7$ within the training data; a correlation threshold common to HSM studies (Dormann et al., 2013; Krushelnycky et al., 2023; Su et al., 2021; Williams et al., 2024). When possible, we preferentially retained annual over monthly means, as we considered these values more representative of local climate (Fig. 1C). Both the correlation cut off and the preferential retention of annual over monthly means are subjective and alternative methods of predictor selection would likely result in alternative results. Models (described below) are therefore made with a combination of monthly and yearly means, and the variety in temporal resolution may affect model sensitivity. Consistently, temperature variables (T_{min}, T_{mean}, and T_{max}) had strong correlation values and were removed. All predictors used in the final composite models are included in Supplemental Dataset 1.

Organic soil carbon and butternut basal area estimates were derived from the US Department of Agriculture Forest Service Forest Inventory and Analysis program data base (FIADB v2.0.6, (Bechtold and Patterson, 2005)) using SQL queries. We queried the FIADB in R using the *RSQLite* package (Müller et al., 2024). SQL queries that required lengthy computational time utilized the *beepr* package (Bååth, 2024) to inform the user when the query had finished. SQL queries were modified from those provided in the SQL_QUERY_SE column of the REF_POP_ATTRIBUTE table within the FIADB. The queries for organic soil carbon and basal area were based off SQL_QUERY_SE numbers 52 ("Carbon in organic soil, in short tons, on forested land"), and 1004 ("Basal area of live trees (at least 1 in. d.b.h/d.r.c), in square feet, on forested land"), respectively. For soil organic carbon, we restricted our query to only include plots designated by the USDA Forest Service as occurring on accessible forested land ($n = 77{,}360$ plots). For butternut basal area, we restricted our query to include plots from accessible forested land that had live butternut stems ($n = 220$ plots). Estimates were validated with the USDA Forest Service's EVALIDator tool (https://apps.fs.usda.gov/fiadb-api/evalidator) before converting to metric units. Both estimates

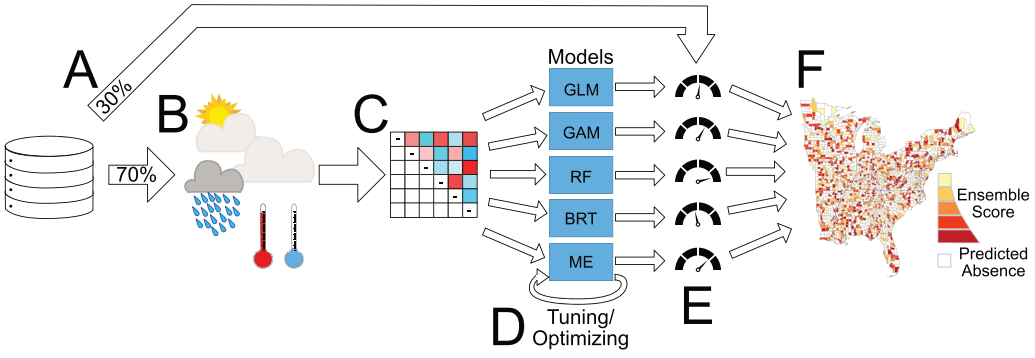

Fig. 1. *Habitat suitability modeling workflow.* A) The data were split, B) climate variables were incorporated and then C) curated to remove multicollinearity, D) models were trained and tuned, E) assessed, and F) combined.

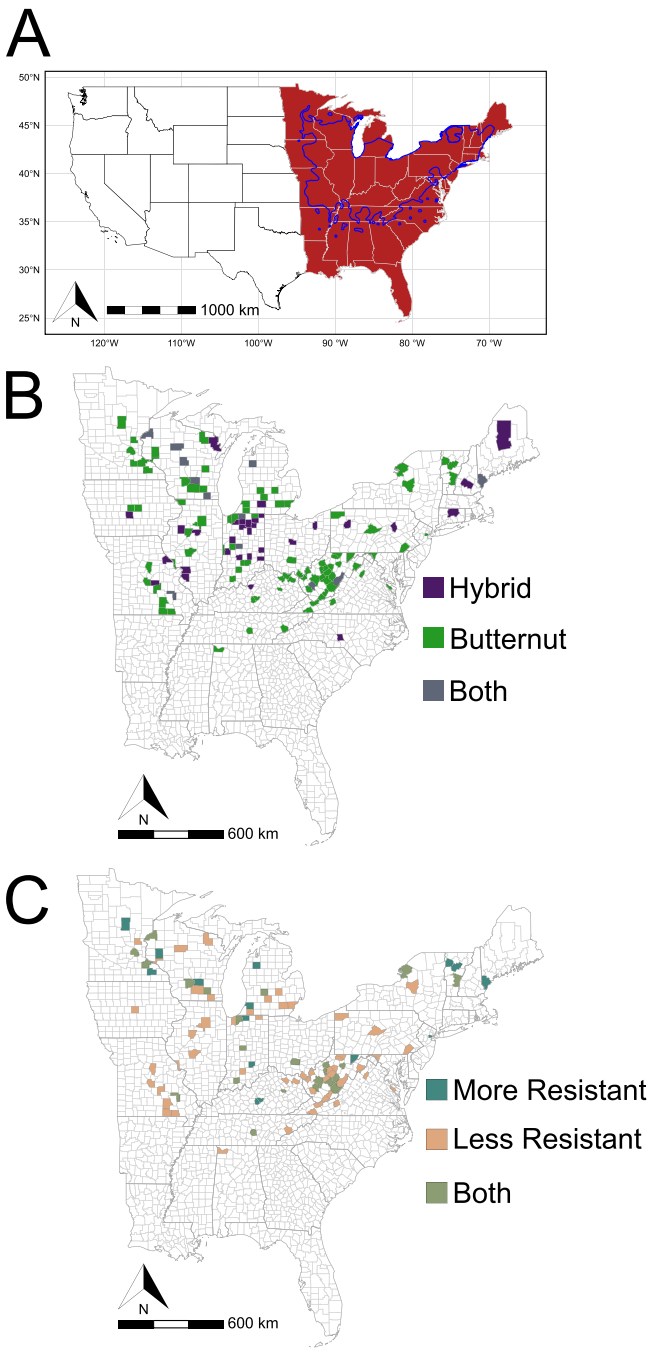

Fig. 2. *Counties of origin of butternut species and hybrid families.* A) Continental United States of America, with the study area highlighted in red. The blue polygon indicates the historic range of butternut within the continental United States. B) Origin of butternut families, hybrid families, or both, aggregated at the county level. C) Origin counties of butternut families, color-coded by BCD resistance, binned as a binary. Counties may have been the origin of more resistant families, less resistant families, or both.

used the data from the 2015 – 2020 evaluation cycle, which temporally aligns with the PRISM (1980 – 2020) and butternut growth (2010 – 2020) data. In 2023, Connecticut overhauled their county system in favor of county-equivalent planning regions with boundaries that differed from previous counties. Averages made from the climate data used the planning region boundaries. Therefore, we assigned the state-wide average of county organic soil carbon value to each planning region to integrate both datasets (Fig S1). Additionally, due to FIA plot sampling intensity and variations in forest cover, several counties lacked an estimate for organic soil carbon. In these instances, we assigned a county an organic soil carbon value calculated from the average of adjacent counties (Fig S1). Ultimately, the number of predictors used to generate each composite model varied from five in the case of the generalized linear model for the butternut genotype data to 17 in the maximum entropy model for less resistant butternut phenotype data.

2.2. Composite and ensemble model generation

We produced five HSMs for each of the four ensembles. Two methods, generalized linear model (glm) and generalized additive model (gam), were regression based. The glm models used base R, while the gams required the *mgcv* package (Wood, 2011). The other three, random forest (rf, from the *randomForest* (Liaw and Wiener, 2002) package), boosted regression trees (brt, from the *gbm* (Ridgeway, 2024) package), and maximum entropy (MaxEnt, me, from the *maxnet* (Phillips, 2021) package), were machine-learning based algorithms. These were chosen as they are commonly used in habitat suitability modeling and are methodologically diverse (Adeyemo et al., 2025; Adeyemo and Granger, 2023; Hanf et al., 2022; Hosseini et al., 2024; Jamali et al., 2024; Latif et al., 2013; Su et al., 2021; Wan et al., 2024; Yang et al., 2023). For the purposes of this study, each of these models is referred to as a "composite model". We prepared an initial composite model from the training data using the complete suite of minimally collinear predictors. We then generated iterative models to improve parsimony and performance by removing minimally influential predictors or tuning in ways unique to each model type (Fig. 1D). For gam, models were uniquely tuned by adjusting the number of basis dimensions, "k", or removing smoothing completely, "s()", where appropriate, largely by trial-and-error. For rf models, the number of trees (ntrees) and variables used at each split (mtry) were manually adjusted to improve the out-of-bag accuracy, a metric often used to assess the accuracy of rf models (Janitza and Hornung, 2018; Shanley et al., 2021). Often, we took a more systematic approach to tuning rf models (via the *caret* (Kuhn, 2008) package) though this rarely improved the out-of-bag accuracy of our composite models. Further, others have suggested that rf HSM models perform better when presence/pseudo-absences are balanced (Valavi et al., 2021). Therefore, we used the "sampsize" option within the random forest function when appropriate to equalize the number of presences and pseudo-absences (ranging from 20:20 in the more-resistant model up to 68:68 in the butternut genotype model). For brt models, we used a "Bernoulli" distribution, a cross-validation fold value of 10, and a shrinkage value of 0.001. In addition to variable omission, subsequent brt models were tuned by adjusting the number of trees (n.trees) parameter. In the "more resistant" brt model, we added a weight in the form of the average BCD-resistance of all the BCD-resistant families in each county. Pseudo-absence counties were assigned a "resistance score" of 0.002. See SI Dataset 1 for complete details on all composite models. Given that composite model tuning was manual, there is potential bias in proceeding with theoretically suboptimal parameter tuning.

In all cases, the strength of each model was evaluated based on the area under the receiver operating characteristics (AUC) score (Hanley, 1989; Pepe, 2000) via the *pROC* (Robin et al., 2011) package. AUC scores range from 0 to 1, with a score above 0.7 being adequate, above 0.8 being good, and above 0.9 being exceptional, though at the risk of over fitting (Çorbacıoğlu and Aksel, 2023; Georgian et al., 2019). Regression models were tuned to reduce their Akaike information criterion (AIC), and deviance. In each case, selecting a final model was a balance between improving AUC without over fitting, and in the case of the regression composite models, reducing AIC and deviance. AUC score can be heavily influenced be sample prevalence (Allouche et al., 2006). Therefore, in addition to AUC score, each composite model was evaluated by its sensitivity (true positive rate), specificity (true negative rate), and True Skill Statistic (TSS = Sensitivity + Specificity – 1). The TSS value ranges from -1–1, with values above 0 indicating a predictive

power better than random. Importantly, TSS is not immune to prevalence biases, and these values only serve as guides to improve model accuracy in relativistic terms, and do not carry any absolute ecological weight.

We further determined the accuracy of each composite model with the withheld test dataset Fig. 1E). Doing so used the MaxKappa statistic, via the *PresenceAbsence* (Freeman and Moisen, 2008) package, to convert the continuous model output to a binary presence/absence (Allouche et al., 2006). Accuracy of the composite models on the withheld test data was calculated by:

$$Accuracy = \frac{\sum P_{true}, N_{true}}{n_{test}} * 100$$

Where P_{true} and N_{true} are the number of correct presence and absence predictions, respectively, and n_{test} is the total number of values in the test dataset.

Each composite model was then used to generate a binary HSM for the entire study area. For the purposes of this study, we combined the five composite models made from each dataset into an "ensemble". As such, we ultimately made four ensembles: two based on genotype (butternut or hybrid) and two based on the BCD resistance phenotype among the butternut genotype (more resistant vs. less resistant). To combine composite models into a single ensemble, we weighed each composite model based on either AUC and TSS scores. Pilot analyses demonstrated that the final ensembles, based on weighing composite model scores by ether AUC or TSS, were qualitatively quite similar. Therefore, the ensembles we report here have been weighed by the composite model TSS score using the following equations (Georgian et al., 2019; Oppel et al., 2012):

$$W_z = \frac{TSS_z}{\sum TSS}$$

$$X_e = B_{glm} * W_{glm} + B_{gam} * W_{gam} \ldots$$

Where W_Z is the weight assigned to the composite model, Z, based on that composite model's TSS score divided by the sum of the TSS scores across all composite models. B_{glm} is the binary prediction based on the GLM composite model. The ensemble value for a given county, X_e, is the sum of the products of weights and the binary prediction from each composite model (Fig. 1F). Ultimately, we endeavored to visualize geospatial variation among pairs of ensembles (i.e., more resistant vs. less resistant, butternut vs. hybrid). For the purposes of this study, we combined each pair into what we refer to here as "merged ensembles", one based on phenotype the other on genotype. We merged each ensemble pair by summing the inverse of one ensemble with the other thusly:

$$X_p = X_m + (-1 * X_l)$$

$$X_g = X_b + (-1 * X_h)$$

Where X_p and X_g are the merged ensemble values for the phenotype (more resistant, X_m, vs less resistant, X_l) ensemble and the genotype (butternut, X_b, vs hybrid, X_h) ensemble, respectively. Each county in the merged ensemble has a value between -1 and 1, or NA if not predicted to be suitable by any composite model within the merged ensemble. In the merged phenotype ensemble, a value of 1 means complete agreement across the composite more resistant models, and no overlap with any composite less resistant models. 0 indicates that the more resistant and less resistant ensembles predict the same level of suitability. -1 indicates complete agreement across the composite less resistant models, and no overlap with any composite more resistant model. In the genotype ensemble, a value of 1 is complete agreement across the composite butternut models and no overlap with any composite hybrid model. 0 indicates where the hybrid and butternut ensembles predict the same level of suitability. -1 indicates complete agreement across the composite hybrid models, and no overlap with any composite butternut model. For each merged ensemble, a value between -1 and 1 indicates either overlap from the opposing ensemble or lower confidence among composite models. Because we did not differentiate the cause of intermediate values in the merged ensembles, the interpretation these results should be the relative suitability between ensembles. Suitability scores therein were not independent and had the potential to mask suitability predicted in the independent ensembles.

2.3. Citizen-science resources for ensemble filters and ensemble validation

We utilized two citizen-science databases to filter the merged ensemble models by counties with confirmed sightings of butternut. TreeSnap (https://treesnap.org/) was built specifically to engage the public in efforts to find and record imperiled tree species such as ash (*Fraxinus* spp.), American elm (*Ulmus americana* L.), and American chestnut to assist conservation and breeding efforts (Crocker et al., 2020). TreeSnap data were accessed on June 11th, 2025 and included 289 observations of butternut from October 11th, 2020 through June 1st, 2025. Observations were binned into counties ($n = 98$) which were subsequently used as a filter for the ensembles. The Global Biodiversity Information Facility (GBIF, https://www.gbif.org) is a digital world-wide repository of information with the goal of enhancing interoperability between sources of biodiversity data (Edwards, 2001). GBIF collates data from herbaria and fossil collections through genome sequences and citizen science platforms. GBIF was accessed on June 13th, 2025 and the downloaded data included all mentions of *Juglans cinerea* in North America. The GBIF data were then curated to include only live butternut trees in the United States. The resulting dataset includes 2587 observations from May 2000 through January 2025. 98.15% of observations downloaded from GBIF were categorized as originating from iNaturalist (https://www.inaturalist.org), a nature sharing citizen science social network. Observations from GBIF were then binned into counties ($n = 478$) and those counties were used as a filter for the ensembles. Both the TreeSnap and GBIF citizen-science datasets contain their own spatial biases, as an entry in either database is the result of a tree growing in an accessible area and being witnessed by a person engaging in either reporting system. Further, while there is an "expert validation" protocol for both TreeSnap and iNaturalist, the morphological ambiguity between butternut and Japanese walnut hybrids can add a challenging layer to citizen science field identification.

Butternut basal area estimates from the FIADB include 220 plots across 141 counties inventoried from 2015 through 2020. Counties with both an ensemble score and empirical basal area estimate were then used as an independent assessment of the ensemble. We performed a single-order linear regression of basal area by ensemble score using base R.

2.4. Data visualization

All data were plotted via the *ggplot2* (Wickham, 2016) package and arranged via the *gridExtra* (Auguie, 2017) package. Figures were prepared with Affinity Designer (Serif Europe).

3. Results

3.1. Butternut family data

Previous work genotyped 229 butternut families from 136 counties across the geographic range of butternut (Fig. 2A). Butternut, as opposed to hybrid genotypes, were far more common in this range-wide collection ((Conrad et al., 2026), Fig. 2B, Table 1). Most counties containing butternut genotypes were in West Virginia, while Indiana had the most hybrid families (Fig. 2B, Table 1). Butternut seed solicitation was run out of Purdue University, perhaps resulting in a proximity bias in sample collection (Conrad et al., 2026). Of the 101 counties found to contain

Table 1
Summary of family genotype and phenotype data, as aggregated for this study, delineated by state. Note that not all families that were genotyped were also assessed for BCD resistance phenotype.

Family Genotype				Family Phenotype			
State	n counties, butternut	n counties, hybrid	n counties, overlap	State	n counties, more resistant	n counties, less resistant	n counties, overlap
Alabama	1	0	0	Alabama	0	1	0
Connecticut	0	1	0	Illinois	0	5	0
Illinois	5	4	0	Iowa	0	1	0
Indiana	11	16	2	Kentucky	3	3	1
Iowa	2	1	0	Maine	1	0	0
Kentucky	6	1	0	Maryland	1	1	0
Maine	1	2	1	Michigan	3	6	1
Maryland	2	0	0	Minnesota	4	3	2
Michigan	8	2	1	Missouri	1	7	1
Minnesota	6	0	0	New York	1	2	1
Missouri	7	3	1	Ohio	1	2	1
New Hampshire	0	1	0	Pennsylvania	0	3	0
New Jersey	1	0	0	Tennessee	1	2	1
New York	2	0	0	Vermont	3	1	1
North Carolina	0	1	0	Virginia	0	5	0
Ohio	2	2	0	West Virginia	8	21	8
Pennsylvania	3	2	0	Wisconsin	5	8	3
Tennessee	2	0	0				
Vermont	3	0	0				
Virginia	5	0	0				
West Virginia	21	2	2				
Wisconsin	12	6	5				

butternut, 92 of them were screened for BCD-susceptibility (Fig. 2C, Table 1). Less resistant butternut was more common than more resistant butternut, with only fourteen counties containing only more resistant butternut families (Fig. 2C, Table 1). Most states only had one or two counties with only more resistant families if they had them at all, highlighting the rarity of more resistant BCD butternut on the landscape. Broadly, there was no manifest geographic pattern to the families at this spatial scale (e.g. all hybrids occurring around one city, or BCD resistance being concentrated in New England).

3.2. Composite model performance

How our composite models performed on both training and test data across each dataset is reported in Table 2. Across all composite models and datasets, the mean AUC score ± standard deviation, was 0.86 ± 0.08. Similarly, the TSS was 0.59 ± 0.16 across all composite models and datasets. On withheld test data, the average accuracy of all composite models was 76.99 ± 7.28%. The performance of the composite models varied. For example, on average the glms performed relatively poorly on both the training data (AUC: 0.80 ± 0.06; TSS: 0.47 ± 0.10), as well as the test data (68.88 ± 3.98%). Conversely, the brt composite models performed well on both the training data (AUC: 0.95 ± 0.04; TSS: 0.70 ± 0.12) and the test data (78.98 ± 5.57%). Even though the rf composite models performed the poorest on the training data (AUC: 0.77 ± 0.04; TSS: 0.46 ± 0.14), on average, they performed the best on the test data (85.20 ± 2.85%). The three machine-learning based composite models (rf, brt, and me) marginally outperformed (AUC: 0.87 ± 0.09; TSS: 0.59 ± 0.17; Accuracy: 80.75 ± 6.30%) the two regression-based composite models (AUC: 0.85 ± 0.07; TSS: 0.57 ± 0.15; Accuracy: 71.03 ± 4.83%). The AUC, TSS, and accuracy of composite models, while informative and mathematically interesting, should not be utilized independently given the non-independent distribution of highly aggregated spatial units.

The exact number and type of climatic predictors included in each

Table 2
Composite model performance base on training data and accuracy against previously withheld data.

Dataset	Model	AUC	Sensitivity	Specificity	TSS	Accuracy on Withheld Data
Butternut	glm	0.7408	0.6029	0.7598	0.3627	71.21%
	gam	0.8824	0.6029	0.8824	0.4853	66.67%
	rf	0.7253	0.4706	0.8235	0.2941	83.33%
	brt	0.9295	0.6912	0.951	0.6422	78.79%
	me	0.8507	0.5588	0.8971	0.4559	72.73%
Hybrid	glm	0.8455	0.9259	0.7531	0.679	73.53%
	gam	0.9200	1.0000	0.8025	0.8025	79.41%
	rf	0.8093	0.8148	0.8025	0.6173	82.35%
	brt	0.9703	0.8889	0.9259	0.8148	73.53%
	me	0.9177	0.7407	0.9259	0.6667	76.47%
More	glm	0.8513	0.6522	0.8986	0.5507	64.29%
Resistant	gam	0.9231	0.8696	0.8841	0.7536	73.33%
butternut	rf	0.7719	0.6522	0.8406	0.4928	86.67%
	brt	0.9030	0.6087	0.9420	0.5507	86.67%
	me	0.9512	0.913	0.9130	0.8261	90.00%
Less	glm	0.796	0.7586	0.7414	0.5000	71.15%
Resistant	gam	0.8512	0.6724	0.8678	0.5402	71.15%
butternut	rf	0.7631	0.6379	0.7759	0.4138	88.46%
	brt	0.9778	0.7931	0.9885	0.7816	76.92%
	me	0.8715	0.6379	0.9023	0.5402	73.08%

composite model varied (SI Dataset 1). A given predictor was included in the final composite model if doing so allowed for the highest AUC or TSS score, lowest AIC score, or both, in our non-systematic tuning. Often, this meant including predictors with non-significant p-values (in the case of regression-based algorithms) or low importance scores (in machine learning algorithms), suggesting a subtle but important influence on the model. The inclusion of some predictors were common across several composite models (SI Dataset 1). For instance, the mean precipitation in May contributed to each composite model except for the rf model in the hybrid genotype ensemble. The next most-prevalent predictors were mean annual and October precipitation, which were present in 75% of composite models across all ensembles. Annual minimum vapor pressure deficient contributed to 70% of composite models. Variables related to insolation (SolTotal, SolTrans, and SolClear) contributed to 55 – 65% of all composite models. Organic soil carbon only contributed to 50% of composite models. In the butternut genotype ensemble, spring (April, May) precipitation and annual cloud transmittance were common to each composite model, as were summer (June, July) clear-day insolation and maximum vapor pressure deficit. Common predictors in the more resistant butternut ensemble included

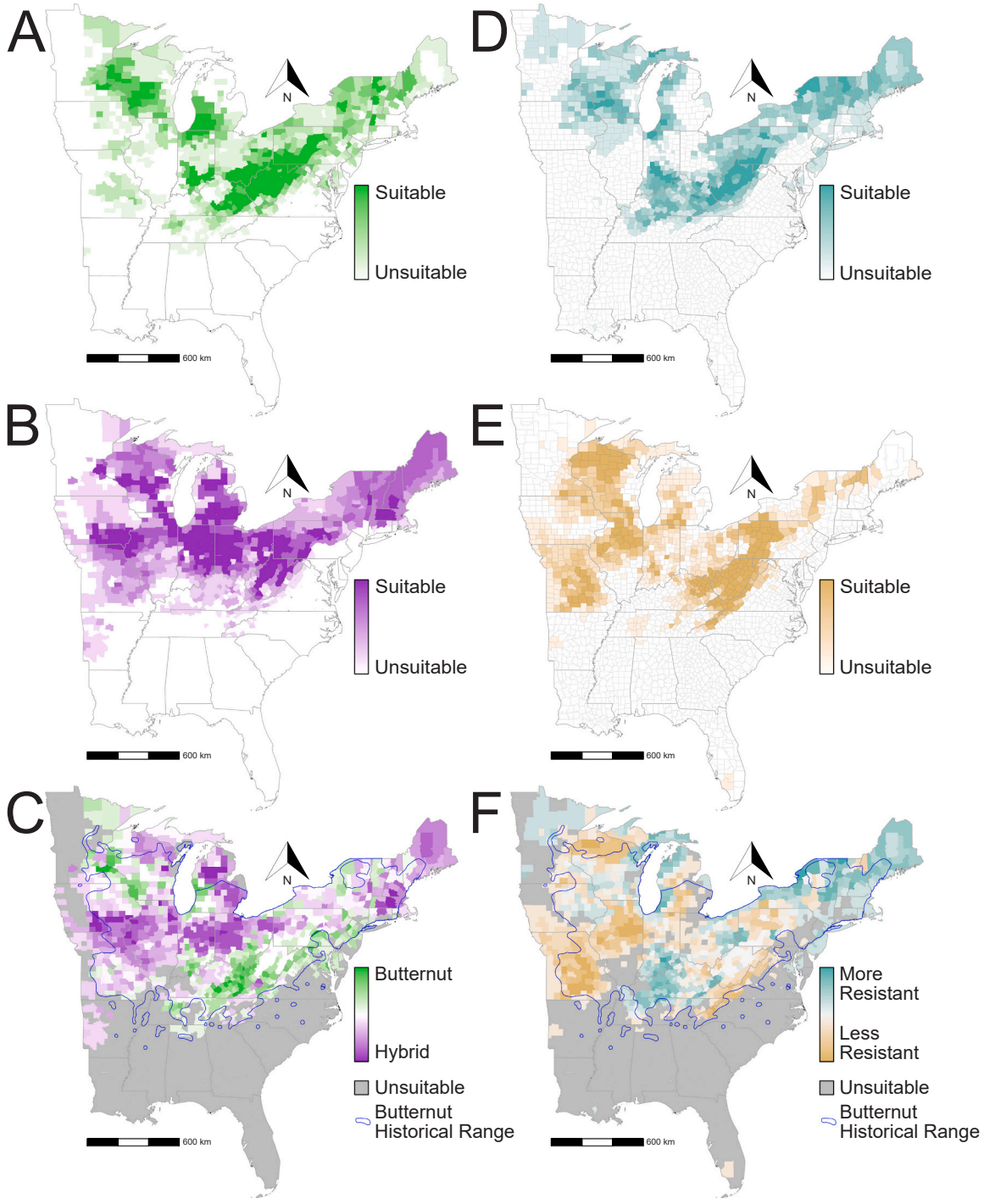

Fig. 3. *Complete range of habitat suitability ensembles* HSM ensembles of A) butternut, B) hybrids and C) merged genotype ensembles. HSM ensemble of D) more resistant butternut, E) less resistant butternut and F) merged phenotype ensembles. In both C and F, white indicates counties in which both ensembles predicted equivalent levels of suitability. Grey indicates counties for which neither ensemble predicted suitability.

May, September, and annual precipitation, as well as clear-day insolation in July, total insolation in March, and cloud transmittance in February. Finally, only precipitation predictors (May, September, October and annual) were common in each composite model for the less resistant butternut genotype ensemble. See SI Dataset 1 for a complete list of predictors.

3.3. Ensemble models

All of the ensembles we produced were hypothesis-generating models, suggesting where hybrids genotypes, butternut genotypes, or butternut expressing the more or less resistant phenotypes, could be found. Our butternut genotype ensemble predicted some degree of suitability in 829 counties within our study area, and complete ensemble consensus occurred in 151 (18.22%) counties, representing 2.04×10^5 km^2 of land (Fig. 3A). The ensemble predicted butternut in southern Indiana as well as western Kentucky and portions of western Tennessee. From there, the butternut suitability range extended through southern Ohio, West Virginia, and western Pennsylvania. Additionally, northern New York, Vermont, New Hampshire, and Maine all had some counties that the genotype ensemble predicted as well-suited for butternut. Another hotspot for butternut suitability was predicted in southern Wisconsin and southwest Michigan (Fig. 3A). Our hybrid genotype ensemble predicted suitability in 934 counties, complete agreement occurred in 220 (23.56%) counties, comprising 2.91×10^5 km^2 Fig. 3B). Most of the hybrid suitability extended from southeastern Iowa, across Illinois, and into Indiana, Ohio, and Michigan. West Virginia and western Pennsylvania were also predicted as suitable to hybrids. The range of hybrid suitability extended northward into New York and New England, though with less confidence (Fig. 3B). The merged genotype ensemble predicted suitability for either butternut or hybrids in 1105 counties in our study area (Fig. 3C). Within the merged genotype ensemble, 365 counties (33.03%) had a higher "butternut" than "hybrid" suitability score (Fig. 3C). Our merged genotype ensemble predicted higher suitability for butternut in much of Tennessee, through eastern Kentucky, as well as southern Indiana, southern Ohio, and southern West Virginia. Likewise, there was a region of butternut suitability along the northern Mississippi River, on the border of Iowa, Wisconsin, and southern Minnesota. Upper Minnesota was highlighted predominately by our butternut genotype ensemble. Counties along the eastern coast of Lake Michigan also scored high in our butternut genotype ensemble. Upstate New York and northern Vermont were also predicted to be more suitable for butternut as opposed to hybrids. Finally, southeastern Pennsylvania, New Jersey, and Maryland were also predicted as being suitable for butternuts (Fig. 3C).

Our more resistant butternut phenotype ensemble predicted habitat suitability in 718 counties across the study area, with 65 (9.05%) having complete agreement for habitat suitability across each composite model, encompassing 8.96×10^4 km^2 of land (Fig. 3D). The range of habitat suitability for more resistant butternut ranged from southern Indiana, across much of Kentucky and throughout West Virginia. Most of western Pennsylvania and southern New York were predicted to be at least moderately suitable to more resistant butternut. Upstate New York and much of New England were also predicted as suitable for more resistant butternut. Finally, the ensemble predicted suitability for more resistant butternut through southern Wisconsin and along the eastern coast of Lake Michigan. Our less resistant ensemble predicted suitability in 786 counties, with 157 (20.44%) counties having complete agreement across each composite model, representing 2.47×10^5 km^2 of land (Fig. 3E). Much of Wisconsin and northern Illinois were predicted as suitable for less resistant butternut, as well as most of Missouri. Additionally, a band of less resistant butternut suitability extended from eastern Kentucky, western North Carolina and western Virginia, up through West Virginia and western Pennsylvania. Isolated suitable counties occurred in upstate New York, and northern Vermont and New Hampshire. The merged phenotype ensemble predicted butternut occurring in 1040 counties within the study area (Fig. 3F). Of the 1040 counties, 457 (43.94%) were predicted as more likely to be suitable for more resistant butternut. The merged phenotype ensemble predicted habitat suitable for more resistant butternut to extend from western Tennessee up through western Kentucky and into southern Indiana. Northern Minnesota, as well as portions of Michigan's upper peninsula and down along the eastern coast of Lake Michigan were all predicted as climatically suitable for more resistant butternut. Finally, much of New England and New York, especially the upstate region, were areas that scored high for more resistant butternut (Fig. 3F).

Both the merged genotype and merged phenotype ensembles covered a similar geospatial range (Fig. 3C, F). The two merged ensembles had a slight, yet statistically significant, positive correlation (slope ± standard error: 0.174 ± 0.031; $F_{1930} = 30.4$; $R^2 = 0.03$; $P = 4.64e\text{-}8$; Fig. S2).

3.4. Ensembles filtered through citizen science observations

Both merged ensembles provide hypotheses suggesting where each subpopulation could be found. To assess the spatial distribution hypotheses implied by the ensembles, we filtered each merged ensemble with empirical butternut observations recorded by citizen-science ground observations (Fig. 4). Of the 98 counties within the TreeSnap dataset, 88 (89.80%) were captured within our merged genotype ensemble (Fig. 4A, Table 3). Similarly, 83 counties (84.69%) from the TreeSnap dataset were within our merged phenotype ensemble (Fig. 4B, Table 3). There were observations of butternut within TreeSnap that occurred outside of the predicted range of both ensembles; 10 counties were missed by the merged genotype ensemble and 15 by the merged phenotype ensemble. Most of the TreeSnap counties that were missed by our ensembles were south of our predicted range, as well as occurring in the Atlantic coastal plain. Multiple counties from New York and Kentucky, and individual counties from Wisconsin, Vermont and Indiana, had high genotype, phenotype, or combined ensemble scores (Table 3). The GBIF dataset was larger than the TreeSnap dataset, with observations from 478 counties. 410 (85.77%) counties from the GBIF dataset were captured by our merged genotype (Fig. 4C), and 365 (76.36%) overlapped with our merged phenotype (Fig. 4D) ensembles. As with TreeSnap, most counties that were missed by our ensembles were in the south and east of the Appalachian Mountains. After filtering the ensembles though the GBIF data, several counties from Kentucky and Michigan, as well as neighboring states, had the highest combined ensemble score. The ten counties with the highest combined ensemble scores are presented in Table 3; a complete list of ensemble scores is available in SI Dataset 2.

3.5. Ensembles and butternut abundance

The Forest Inventory and Analysis dataset indicated the presence of butternut in subset of the counties predicted by our ensembles (Fig. 5A, B). Of the 141 counties which contained butternut in the 2015 – 2020 FIA cycle, 121 (85.8%) overlapped with the merged genotype ensemble (Fig. 5A), and 118 (83.7%) overlapped with the merged phenotype ensemble (Fig. 5B). The FIA dataset allowed us to test whether our ensembles are predictive of butternut abundance. Butternut basal area did not significantly vary with the merged genotype ensemble ($F_{1119} = 0.01$; $P = 0.90$; Fig. 5C). However, the merged phenotype ensemble was a statistically significant predictor of butternut basal area ($F_{1116} = 6.2$; $R^2 = 0.05$; $P = 0.014$; Fig. 5D). The phenotype ensemble was positively correlated with butternut basal area, which increased at a rate ± standard error of 0.0035 ± 0.001 m^2/ha per unit increase of ensemble score.

4. Discussion

Habitat suitability modeling (HSM) has become an important tool for species and habitat conservation, an important aspect of forest

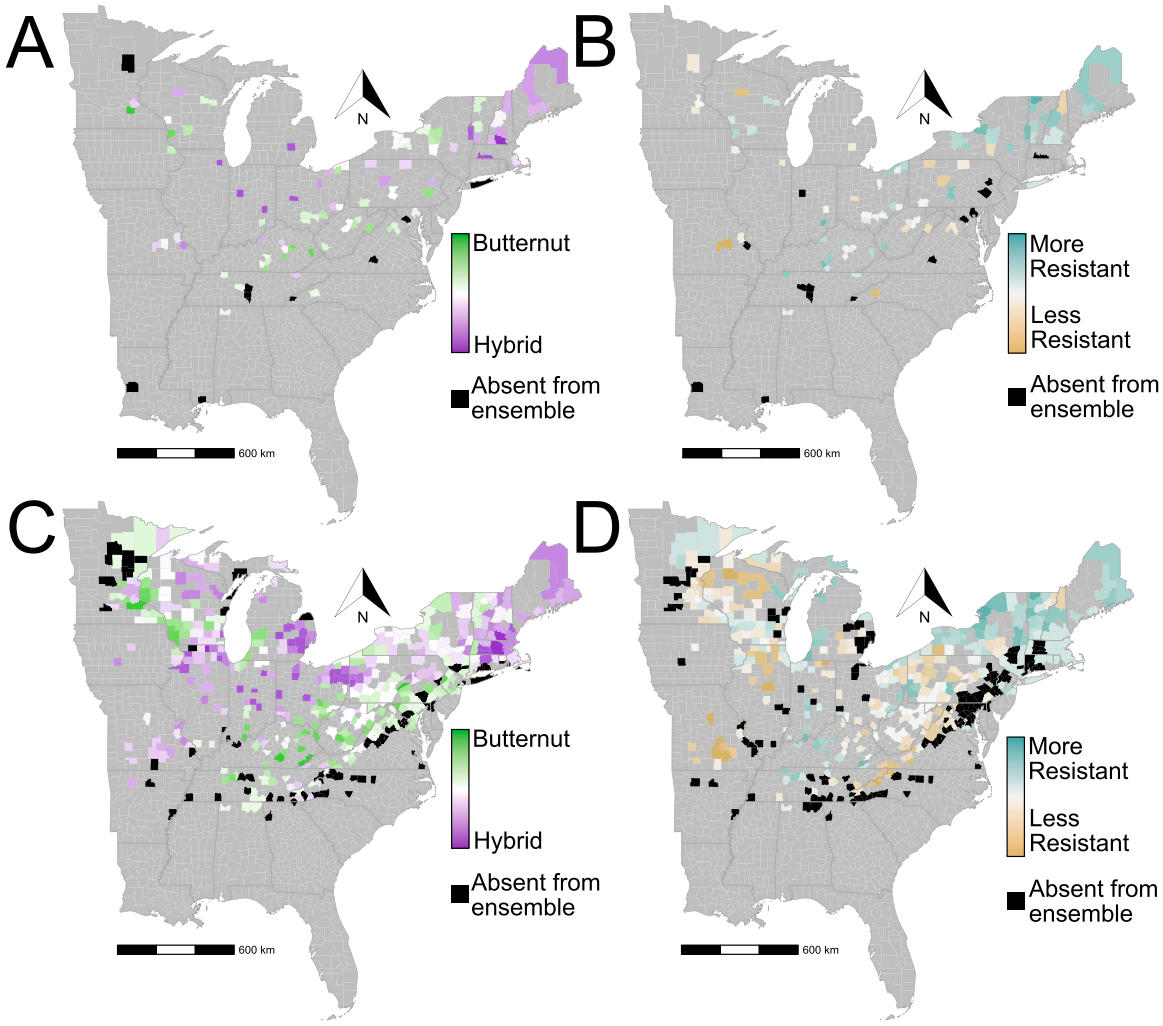

Fig. 4. *HSM ensembles filtered through citizen-science observations.* A) Merged genotype ensemble filtered through TreeSnap citizen-science observations of butternut. B) Merged phenotype ensemble filtered through TreeSnap citizen-science observations of butternut. C) Merged genotype ensemble filtered through GBIF entries for living butternut. D) Merged phenotype ensemble filtered through GBIF entries for living butternut. In each panel, grey counties did not contain butternut observations.

Table 3
Top ten phenotype, genotype, and combined ensemble scores, after filtering through citizen science observation data, arranged by combined ensemble score.

Filter	State	County	Phenotype Enemble	Genotype Ensemble	Combined
TreeSnap	Wisconsin	Crawford	0.43	0.81	1.24
	Vermont	Franklin	1.00	0.23	1.23
	Kentucky	Floyd	0.39	0.83	1.22
	Indiana	Jennings	0.85	0.23	1.08
	New York	Oswego	0.83	0.13	0.96
	Kentucky	Adair	0.65	0.27	0.92
	Kentucky	Metcalfe	0.83	0.07	0.90
	West Virginia	Logan	0.67	0.22	0.89
	New York	Oneida	0.43	0.45	0.89
	Vermont	Chittenden	0.63	0.23	0.86
GBIF	Kentucky	Harlan	0.83	1.00	1.83
	Indiana	Perry	0.83	0.87	1.70
	Michigan	Berrien	0.83	0.62	1.45
	Tennessee	Dickson	0.65	0.71	1.36
	Kentucky	Pulaski	0.32	1.00	1.32
	Indiana	Orange	0.50	0.78	1.27
	Wisconsin	Crawford	0.43	0.81	1.24
	Vermont	Franklin	1.00	0.23	1.23
	Minnesota	Goodhue	0.22	1.00	1.22
	Michigan	Kent	0.57	0.65	1.21

management (Liang and Li, 2024; Moorter et al., 2023; Nayeri et al., 2024). Even from limited observations, researchers can predict habitats of rare species (Breiner et al., 2018). Butternut populations have declined due to past habitat loss, population fragmentation, and poor regeneration due to changes in disturbance regimes (Boraks and Brodders, 2014; Hoban et al., 2012b). Additionally, butternut is affected by two non-native organisms– disease from *Oc-j* and hybridization with Japanese walnut. Understanding how both organisms shape the butternut suitability landscape is critical for conservation, restoration, and management efforts (Pike et al., 2020). Here, we presented HSMs that describe the suitability range of butternut. Further, we utilized a new butternut dataset that included both BCD resistance phenotype and family origin genotype to map habitat suitability for variations in genotype and BCD resistance phenotype. Our intention is for these results to help guide breeding and management efforts aimed at restoring this ecologically and culturally important species by monitoring genetic diversity on the landscape.

4.1. Accuracy and limitations of habitat suitability ensembles

The accuracy of our ensemble models was limited by the number of assumptions we had to make in managing the large and diverse dataset. For example, the coarse spatial resolution of the source family locations

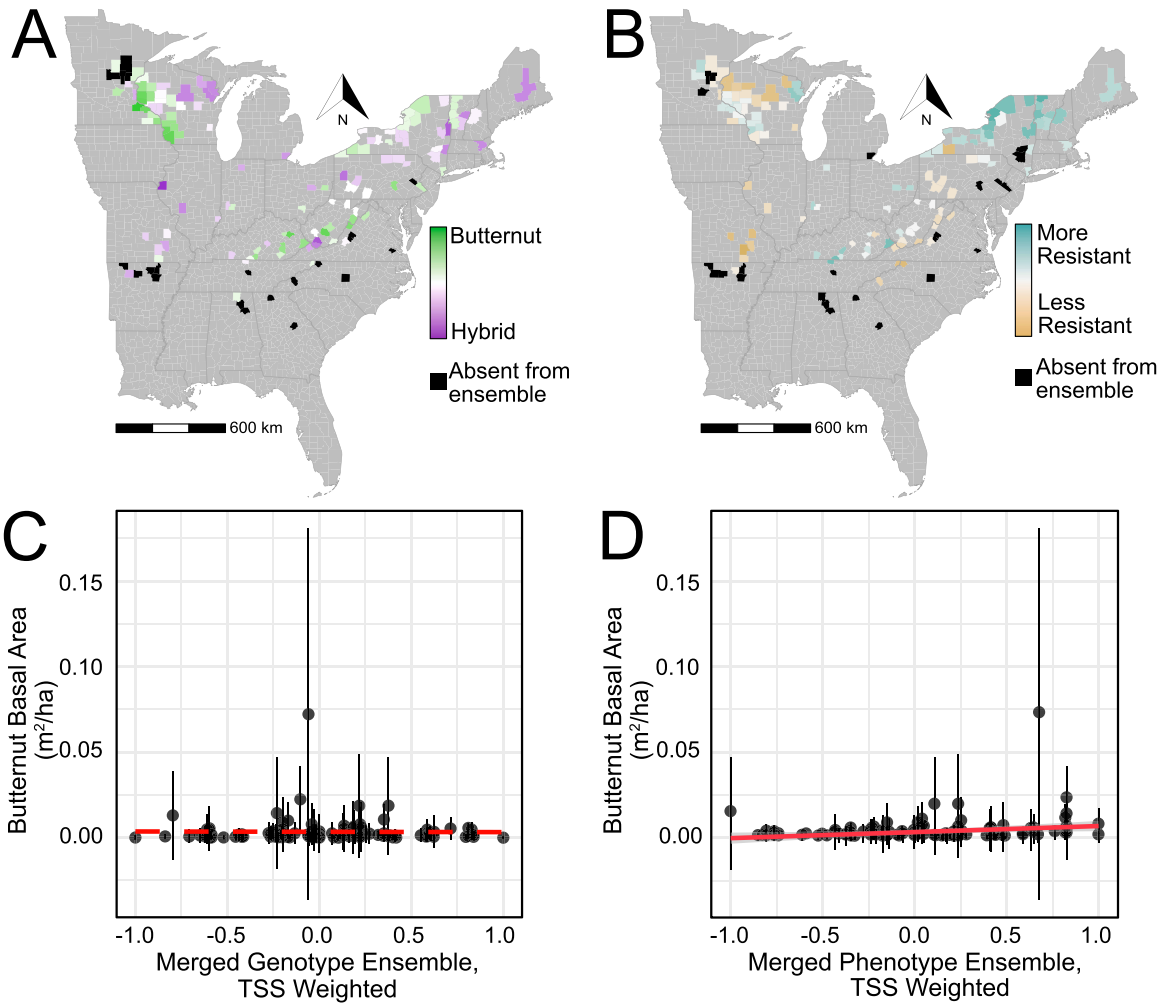

Fig. 5. *Validation of ensemble models with Forest Inventory and Analysis data* A) Merged genotype ensemble filtered by counties in which the FIA detected butternut. B) Merged phenotype ensemble filtered by counties in which the FIA detected butternut. In both panel, grey counties did not contain butternut observations. C) A scatterplot drawn from counties for which there is both a genotype ensemble prediction and basal area estimate. Error bars are derived from the sampling error in the FIA database representing one standard deviation. Dashed red line is a non-significant linear regression model of ensemble score by basal area. D) A scatterplot drawn from counties for which there is both a phenotype ensemble prediction and basal area estimate. Error bars are derived from the sampling error in the FIA database representing one standard deviation. Solid red line is a significant linear regression model of ensemble score by basal area.

which required broad spatial aggregation of climatic data. Further, the location of the butternut and hybrid families was dependent on a previous data set which is not without some spatial bias (Conrad et al., 2026). Likewise, BCD resistance among *Juglans* species and hybrids is a quantitative trait which we made a dichotomy out of based on the score provided by Conrad et al., 2026. BCD resistance is undoubtedly influenced by not only the environment, but also how long local butternut and hybrid populations have been exposed to *Oc-j*. Unfortunately, the spatiotemporal dynamics around *Oc-j's* arrival, or emergence, and spread is not fully understood (Broders et al., 2015, 2012). As such, we cannot confidently factor BCD duration, or point of origin, into our models. Nevertheless, there are variations in BCD resistance among butternut families, and while our brt composite model included a weight for the quantitative score (see Materials and Methods), our ensembles did not account for the uncertainty inherent to a family being classified as "more resistant" or "less resistant". Likewise, Conrad et al., 2026 categorized a family as "butternut" if more than 95% of the single nucleotide polymorphism (SNP) calls were to the butternut genome or based on morphology, if SNP data was unavailable. While fairly conservative, there remains the possibility that trees were misclassified as hybrid or butternut. Additional uncertainty around the genotyping processes, including ambiguity in SNP calls, was similarly not accounted for in our ensembles. Finally, the survey solicitation did not distinguish between wild or planted trees. While planted trees would by necessity need to be in at least a moderately suitable environment to produce the fruit necessary for seed collection (Conrad et al., 2026), their anthropogenic source would undoubtedly confound our models (see Discussion 4.5). Despite these limitations in the source dataset, as our composite models performed within the range of those used in previously published HSMs (Adeyemo et al., 2025; Jamali et al., 2024; Latif et al., 2013; Rew et al., 2020) in terms of composite model AUC and TSS scores as well as accuracy on occurrence data withheld from composite model generation. However, our composite models did not perform as well as others (Georgian et al., 2019). Our ensembles integrated data from multiple sources (PRISM, survey, FIA) each of which has potential bias and uncertainty. Such factors can be technically challenging to incorporate into models such as those presented here. Combined, there are implicit limitations to our models that must be considered when using our HSMs as a potential guide for forest management applications. Together, we conclude that each composite model adequately represented the broad-scale climatic suitability patterns, though underestimates small-scale environmental variations. Indeed, finer scale data could improve composite model accuracy (McGarigal et al., 2016). We assert that these results are to be expected given the relatively low

number of input observations and coarse spatial resolution.

Previous work established that hybrids between butternut and Japanese walnut are generally more resistant to BCD than butternut (Brennan et al., 2020; McKenna et al., 2011). Therefore, one would expect that the habitat suitability of BCD resistance phenotype, inclusive of both butternut and hybrids genotypes, would recapitulate the habitat suitability of highly BCD-resistant Japanese walnut hybrids. As such, when modeling habitat suitability of BCD resistance phenotype and genotype, it is possible that the ensemble models would largely, if not directly, reflect one another. To avoid redundancy in ensemble model predictions, we made our BCD resistance phenotype ensembles using data from only butternut genotypes. Despite this, our two merged ensembles are statistically correlated, though manifestly not directly related in an ecologically relevant sense as evidenced by the low R^2 value. Some correlation is to be expected; areas that are predicted as climatically suitable for BCD resistant butternut would then logically be climatically suitable for butternut genotypes generally. Conversely, this means hybrid suitability negatively scales with BCD susceptibility in butternut. This latter point suggests that Japanese walnut introgression, perhaps, is more likely to be present where butternut is more susceptible to BCD. Presumably, this would only be possible if Japanese walnut or hybrid plantings were particularly prevalent in these areas. However, Japanese walnut was introduced a century before BCD was described and not planted as a replacement to native butternut or in response to BCD. Therefore, the mechanism by which hybrid suitability is negatively correlated with butternut BCD susceptibility depends on additional factors. Indeed, there are myriad potential factors that could underly our observation that hybrid suitability is negatively correlated with butternut BCD susceptibility. For example, perhaps this correlation is due to a higher density of Japanese walnut, or hybrid, plantings in those areas. Higher Japanese walnut, or hybrid, planting could occur perhaps by chance or sociological trends. Further, it is possible that genetic variations in butternut populations lead to locally high levels of BCD susceptibility, perhaps a particularly pathogenic local strain of *Oc-j*, or a combination therein. While these mechanisms remain speculative for now, they would be an interesting subject for future studies.

4.2. The historic range of butternut

Previous work has described butternut as having a broad range across much of northeastern North America (Boraks and Broders, 2014; Farlee et al., 2010; Hoban et al., 2012a, 2009; Little, 1971; Morin et al., 2017; Rink, 1990). The USDA Forest Service's Tree Atlas, which utilizes FIA data, indicated butternut persists sparsely across the native range (Peters et al., 2020). At a minimum, we would expect that an accurate HSM ensemble would recapitulate the native range of butternut. And indeed, both our merged genotype and merged phenotype ensembles comported with the described historic range of butternut. A notable exception is that our ensembles predicted suitability across northern Maine, Michigan, Wisconsin and Minnesota. These regions are beyond butternut's reported northern limit (Little, 1971). However, recent work independently generating butternut HSMs report environmental suitability across similar regions (Adeyemo et al., 2025). That our HSMs predict suitability in these northernly areas was likely due to the training data having butternut and hybrid families from climatically similar areas (e.g., Piscataquis County, Maine). Counties north of butternut's range also appeared in the TreeSnap and GBIF datasets, which were utilized by Adeyemo et al. (2025). While both databases have "expert validation" mechanisms for submissions, the observations are not infallible. Further, butternut is particularly vexing due to morphologically indistinguishable congenic hybrids. Nevertheless, these results at least suggest butternut, hybrids, or both are found beyond the historic northern boundary of butternut specifically in the upper Midwest of the continental United States. Previous work demonstrated that *Oc-j* spores had the poorest germination rates in the coldest temperature trials (4°C) (Moore and Ostry, 2015), suggesting cold intolerance. It is possible that a northern range expansion among butternut would be facilitated by decreased fitness within the pathogen in colder climates. Our results, in combination with citizen science butternut location data, could be early indicators of a northern range expansion, potentially the result of rapid environmental change (Adeyemo et al., 2025; Sittaro et al., 2017), misidentification, or intentional planting. Conversely, most of the counties missed by our ensembles were to the south and southeast of butternut's reported range. This is presumably due to the lack of families collected from this region. To speculate, this likely represents a sample collection bias since these areas are south of butternut's reported range (Little, 1971). Indeed, butternut is typically described as a cold-hardy, heat-intolerant species, especially when compared to black walnut (Rink, 1990). It is therefore reasonable to seek butternut in northerly climates. Recent work into modeling butternut habitat suitability reported favorable environments exist only sparsely in the southeast United States (Adeyemo et al., 2025). However, the TreeSnap, GBIF, and to a lesser extent FIA, datasets suggest that butternut persists to the south of the historical range, which may be an untapped resource in butternut breeding efforts. Indeed, neither TreeSnap nor GBIF are systematic surveys, and it is possible that butternut could be found in areas outside of either filter, but included in our unfiltered merged ensembles. Conversely, observations further south than the historically accepted range could consist of planted trees, which could potentially fair better in hotter climates due to anthropogenic intervention (e.g., supplemental irrigation). These results may be of interest to landowners that may not know the local climate is suitable to butternut, which is an economically valuable ornamental wood crop (Meier, 2015).

4.3. Butternut canker disease resistance

Factoring into butternut habitat suitability is *Oc-j* habitat suitability. Environments particularly favorable to *Oc-j* could be deleterious to all but the most resistant butternuts. Conversely, an environment unsuitable to butternut may weaken the tree and put it at a disadvantage when infected by *Oc-j*. Whether and how the environment factors into BCD severity is a combination of how suitable the environment is to both pathogen and host, also known as the disease triangle (Leveau, 2024). To this point, early work failed to find strong evidence of BCD resistance heritability among butternut populations, and BCD severity was thought to be fully determined by the environmental suitability of the pathogen and host. McKenna et al. (2011) found direct inoculation of *Oc-j* to progeny of disease-free butternut trees readily developed BCD, though results about heritability among naturally occurring infections in a common garden experiment were inconclusive. LaBonte et al. (2015) did not find evidence of heritability of BCD resistance within a single stand near Whitewater, Wisconsin. Instead, environmental conditions, specifically drier upland sites, were a stronger predictor of disease progression. Likewise, researchers using the FIADB to assess range-wide patterns in butternut decline concluded that ecoregion (a proxy for similar environmental conditions), forest type and stand maturity were the strongest predictors of the rate of butternut decline (Morin et al., 2017). There, the authors found that butternut was most prevalent in mature maple/beech/birch stands in southern Wisconsin and central Minnesota, while butternut populations have remained the most stable in western and upstate New York and northern Vermont. In our ensembles, these same regions were highlighted as areas climatically suitable to more resistant butternut. More recently, long-term common garden experiments monitoring natural BCD infections have provided evidence that BCD resistance is indeed heritable (Conrad et al., 2026), though only detectable when disease incidence and severity is high. Those results conform to models whereby disease resistance is variable across scales (Laine et al., 2011). Heritable BCD resistance necessitates that observed BCD severity is not solely due to local environmental factors, though environmental factors, such as precipitation (Sambaraju et al., 2018) and proximity to riparian zones (LaBonte et al., 2015), are manifestly involved in disease expression. Indeed, while environmental

factors undoubtedly have a prominent role in determining BCD severity, there is evidence that there is some heritable BCD resistance among the butternut genotype (Conrad et al., 2026).

Previous work has identified that isolates of *Oc-j* have different levels of virulence (Brennan et al., 2020; McKenna et al., 2011), and therefore it can be challenging to uncouple local host resistance from local pathogen virulence. Conrad et al. (2026) addressed this via a long-term common garden natural infection experiment. Presumably, the test trees were infected by a single local strain of *Oc-j*, or at least strains of similar virulence, under similar environmental conditions. Therefore, variation in BCD resistance is at least partially a function of genetics. The spatial variation in *Oc-j* virulence has likely played a role in selecting for BCD resistance among native butternut populations (Schlarbaum et al., 1998). More virulent strains of *Oc-j* could cause mortality events so complete, and if butternut disease resistance is merely slight, there is limited opportunity for natural selection. Meanwhile, relatively low-virulence strains of *Oc-j* could allow for a chance for mild BCD resistance to be selected for. For example, while *Oc-j* is generally accepted to have arisen or arrived in southwest Wisconsin in the late 1960's, genomic structure analysis suggests at least three emergence or introduction events (Broders et al., 2012). One population cluster occurs in New England, where some have suggested that observed butternut dieback in the early 20th century was erroneous attributed to *Melanconis juglandis* Ellis & Everhart Grave (Graves, 1923, 1919). Instead, some suggest, these butternut mortality events were potentially low-virulence strain of *Oc-j* (Broders et al., 2015, 2012). It was only when a more virulent strain arrived or emerged in the late 1960's in southwest Wisconsin did forest pathologists take note. In our merged phenotype ensemble, New England and upstate New York are broadly more suitable to the more resistant phenotype. These observations support a hypothesis that *Oc-j* resistance has been selected for in the northeast region of the United States for at least a century. Given the relatively short life span of butternut, it is possible that we can detect the adult progeny of those trees that had enough heritable BCD resistance to reproduce after an early wave of mortality. Similarly, recent work compared BCD resistance among butternut and hybrids with two isolates of *Oc-j* and found that the isolate from southern Indiana was far less pathogenic than the one from northern Indiana (Brennan 2020). Our merged phenotype ensemble predicts southern Indiana to be more suitable for more resistant butternut. Butternut families from southern Indiana would have been exposed to a potentially less virulent strain of *Oc-j*. Therefore, seed collected for Conrad et al. (2026) from wild populations could be the first or potentially second generation of butternut resultant from relatively mild selective pressure for disease resistance.

Demonstrating BCD-resistance heritability opens the possibility of finding BCD-resistant breeding stock. The ensembles presented here are tools that are directly applicable for forest management efforts focused on finding and preserving BCD-resistant butternut germplasm as well as areas that are climatically suitable for restoration planting.

4.4. Japanese walnut introgression

Hybridization between butternut and Japanese walnut has occurred across much of butternut's range (Hoban et al., 2009). Introgression is prevalent in areas closer to human settlements (Hoban et al., 2012a), presumably due to Japanese walnut's use as an ornamental and orchard tree (Zhao and Woeste, 2011). We did not include forest type or human population density in our analysis, yet our genotype ensembles largely support results from range-wide Japanese walnut introgression studies. For example, Vermont has relatively low levels of Japanese walnut introgression (Hoban et al., 2012a, 2009), and our ensemble indicates much of Vermont as being suitable for butternut. Conversely, there has been prevalent Japanese walnut introgression in Connecticut (Hoban et al., 2009), with butternut absent from continuous forest in that state (Hoban et al., 2012a). Our merged genotype ensemble models broadly predicted Connecticut to be more suitable to hybrids than butternut. Previous work found evidence of prevalent Japanese walnut introgression in western North Carolina (Hoban et al., 2009), though only in "anthropogenic landscapes" (Hoban et al., 2012a). Our merged genotype ensembles predicted higher hybrid suitability in western North Carolina. In addition to Connecticut and North Carolina, Hoban et al. (2012) found extensive Japanese walnut introgression in the fragmented forests and anthropogenic landscapes of Massachusetts. Our merged genotype ensemble similarly predicted hybrid suitability in Massachusetts. Previous work sampling butternut from New York, Vermont, New Hampshire, and Maine found that 13% of trees were F_1 hybrids with maternal Japanese walnut (Boraks and Broders, 2014). In support of this, much of New Hampshire and Maine were predicted as more suitable to hybrids in our merged genotype ensemble. Outside of the northeast, there are other regions highlighted as areas of interest our ensembles predicted as suitable to more resistant butternut with low suitability to hybrids: southern Indiana, western Michigan, southern Kentucky, and northern Tennessee. There was little Japanese walnut introgression within continuous forests of southern Indiana (Hoban et al., 2012a), but the BCD resistance of butternut in that area are understudied. Similarly, to our knowledge, no work has investigated butternut from western Michigan. This work expands on Conrad et al. (2026), which found BCD-resistant butternut in southern Indiana and western Michigan. However, independent studies will need to investigate BCD resistance and rates of hybridization in these areas.

In our merged genotype ensemble, hybrid suitability extended contiguously from eastern Michigan, through western Ohio, northern Indiana, much of Illinois and Missouri, and extended into southern Iowa. Japanese walnut introgression is relatively understudied in these areas, though there is evidence of prevalent introgression occurring in northern Indiana (Hoban et al., 2012a). Therefore, conservationists looking to capitalize on the BCD resistance found among hybrids for breeding stock, the western portion of the Great Lakes region may be an area of particular interest.

4.5. Butternut abundance

We utilized both the TreeSnap and GBIF datasets as observation-based filters to our ensembles. However, they are not estimates of abundance. In contrast, FIADB basal area estimates allows us to assess butternut abundance as a function of our ensembles. Hypothetically, butternut should be more abundant if the local populations have heritable resistance to BCD. This is complicated by the morphological ambiguity of congenic hybrids, which are both more resistant to BCD than butternut, and may be mistaken for the species genotype in the field. Nevertheless, butternut basal area is slightly, but significantly, positively correlated with our merged BCD-resistance phenotype ensemble. Such validation of our ensemble with an external dataset strengthens our confidence in the ensemble's prediction power. However, given the low R^2 value (0.05) of the relationship between our merged phenotype ensemble and butternut basal area, there are clearly other drivers of butternut basal area. For example, known factors influencing butternut abundance include stand type and soil moisture levels (Morin et al., 2017), neither of which was explicitly included in our models. Further, there is inherit sampling error associated with every FIA estimate, based in part on the number of plots used to derive one's estimate (Bechtold and Patterson, 2005). Given the low density across its range, butternut is particularly difficult to derive accurate estimates. Finally, models built on finer spatial resolution may be more correlated with plot-level FIA estimates and could be studied in a systematic fashion, including across other tree species. In contrast to the relationship of butternut basal area to our merged phenotype ensemble, our merged genotype ensemble is not a significant linear predictor of butternut basal area. This is somewhat counter-intuitive, given that hybrids are more resistant to BCD than butternut (Brennan et al., 2020; McKenna et al., 2011; Pike et al., 2020). In addition to the aforementioned caveats, which are likewise true for the merged genotype ensemble, a potentially vital addition is

that Japanese walnut introgression is more common in anthropogenic landscapes (Hoban et al., 2012a). While the FIA program was designed to be a systematic and unbiases survey, complications arise if a plot is on inaccessible private land, which would be more common in urban landscapes. Combined, there is a clear gap in assessing the abundance, as measured by basal area, of hybrids. Recently, the USDA Forest Service began building an inventory of urban forests (Edgar et al., 2020). As the urban FIA program builds a robust database of North American urban landscapes, it is possible that butternut (and misidentified hybrids) abundance maps predict the suitability range of Japanese walnut introgression genotypes as described here. Previous studies have identified that hybrids have a larger diameter, and therefore basal area, than butternuts across northern New England and New York (Boraks and Broders, 2014). Exploring the extent of Japanese walnut introgression, and thereby probing the question of hybrid fitness and local habitat suitability, would require broader studies like those of Boraks and Broders (2014), but conducted across the range of butternut.

5. Conclusion

Ensembles of species habitat suitability are typically based on occurrence data from a single species. The ensembles presented here advance the field of habitat suitability modeling by mapping ensembles made of subpopulations of a single species (by genotype and phenotype). Our ensembles suggested that southern Indiana, much of Kentucky, northern Tennessee, the eastern coast of Lake Michigan, and portions of Upstate New York and Vermont as all suitable for putatively disease resistant butternut. Further, much of Missouri, northern Illinois and Indiana, as well as western Ohio and eastern Michigan are more suitable to hybrids than butternut. While our ensembles performed adequately, the climate variables included only capture a small part of the explanatory power necessary to strongly predict local abundance. Nevertheless, it is our expectation that these ensembles will help guide breeding and conservation efforts by identifying areas of interest for future field-based evaluations. This work could inform forest managers on areas where butternut conservation should be prioritized. Our work highlights areas where it is feasible to preserve an endangered species and protect important genetics on the landscape. Importantly, this work is but the first piece of a larger conservation puzzle; work must be done focusing on the climatically suitable areas we highlight to identify areas locally suitable by land use history, stand type, soil moisture regiments, and policies around forest management.

CRediT authorship contribution statement

Bascom Jr Carlisle: Writing – original draft, Visualization, Software, Methodology, Formal analysis. **Anna O. Conrad:** Writing – review & editing, Conceptualization. **Aziz Ebrahimi:** Writing – review & editing. **Douglass F. Jacobs:** Writing – review & editing. **Carrie Fearer:** Writing – review & editing, Supervision, Methodology, Conceptualization.

Funding

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Declaration of Competing Interest

The findings and conclusions in this publication are those of the authors and should not be construed to represent any official USDA or U. S. Government determination or policy. The authors declare no conflicts of interest.

Acknowledgement

We would like to thank Andrew Gaugherty and Carrie Pike, USDA Forest Service, for their feedback on an earlier version of this manuscript. Additionally, we would like to thank the two anonymous reviewers for their help improving this manuscript, and for their commitment to improving research in this field.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.123708.

Data availability

Data will be made available on request.

References

Adeyemo, S.M., Granger, J.J., 2023. Habitat suitability model and range shift analysis for American chestnut (*Castanea dentata*) in the United States. Trees For. People 11, 100360. https://doi.org/10.1016/j.tfp.2022.100360.

Adeyemo, S.M., Granger, J.J., Schulz, A.N., Poudel, K.P., Yang, Y., Zhou, Q., 2025. Habitat Suitability Modeling: a tool for restoring butternut, *Juglans cinerea L.*, in the eastern United States. J. For. 1–29. https://doi.org/10.1007/s44392-025-00057-6.

Alaoui, O.E., Idri, A., 2024. An empirical evaluation of ensemble strategies in habitat suitability modeling. SN Comput. Sci. 5, 501. https://doi.org/10.1007/s42979-024-02828-y.

Allouche, O., Tsoar, A., Kadmon, R., 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). J. Appl. Ecol. 43, 1223–1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x.

Araújo, M.B., New, M., 2007. Ensemble forecasting of species distributions. Trends Ecol. Evol. 22, 42–47. https://doi.org/10.1016/j.tree.2006.09.010.

Auguie, B., 2017. gridExtra: Miscellaneous functions for "grid" graphics.

Bååth, R., 2024. beepr: Easily play notification sounds on any platform.

Barnes, J.C., Delborne, J.A., 2019. Rethinking restoration targets for American chestnut using species distribution modeling. Biodivers. Conserv. 28, 3199–3220. https://doi.org/10.1007/s10531-019-01814-8.

Bechtold, W.A., Patterson, P.L., 2005. The Enhanced Forest Inventory and Analysis Program - National Sampling Design and Estimation Procedures85For. Serv., South. Res. StnNC: US Dep. Agric08010.2737/srs-gtr-80.

Bertelli, C.M., Stokes, H.J., Bull, J.C., Unsworth, R.K.F., 2022. The use of habitat suitability modelling for seagrass: a review. Front. Mar. Sci. 9, 997831. https://doi.org/10.3389/fmars.2022.997831.

Bixby, W.G., 1919. The butternut and the Japanese walnut. Am. Nuts J. 10, 76–83.

Boraks, A., Broders, K.D., 2014. Butternut (*Juglans cinerea*) health, hybridization, and recruitment in the northeastern United States. Can. J. For. Res. 44, 1244–1252. https://doi.org/10.1139/cjfr-2014-0166.

Breiman, L., 2001. Random forests. Mach. Learn 45, 5–32. https://doi.org/10.1023/a:1010933404324.

Breiner, F.T., Nobis, M.P., Bergamini, A., Guisan, A., 2018. Optimizing ensembles of small models for predicting the distribution of species with few occurrences. Methods Ecol. Evol. 9, 802–808. https://doi.org/10.1111/2041-210x.12957.

Brennan, A.N., McKenna, J.R., Hoban, S.M., Jacobs, D.F., 2020. Hybrid breeding for restoration of threatened forest trees: evidence for incorporating disease tolerance in *Juglans cinerea*. Front. Plant Sci. 11, 580693. https://doi.org/10.3389/fpls.2020.580693.

Brennan, A.N., Uscola, M., Joly, R.J., Jacobs, D.F., 2021. Cold and heat tolerances of hybrids for restoration of the endangered *Juglans cinerea* L. Ann. For. Sci. 78, 36. https://doi.org/10.1007/s13595-021-01053-4.

Broders, K.D., Boland, G.J., 2011. Reclassification of the butternut canker fungus, *Sirococcus clavigignenti-juglandacearum*, into the genus *Ophiognomonia*. Fungal Biol. 115, 70–79. https://doi.org/10.1016/j.funbio.2010.10.007.

Broders, K., Boraks, A., Barbison, L., Brown, J., Boland, G.J., 2015. Recent insights into the pandemic disease butternut canker caused by the invasive pathogen *Ophiognomonia clavigignenti-juglandacearum*. For. Pathol. 45, 1–8. https://doi.org/10.1111/efp.12161.

Broders, K.D., Boraks, A., Sanchez, A.M., Boland, G.J., 2012. Population structure of the butternut canker fungus, *Ophiognomonia clavigignenti-juglandacearum*, in North American forests. Ecol. Evol. 2, 2114–2127. https://doi.org/10.1002/ece3.332.

Conrad, A., Ebrahimi, A., Warren, J., Fetter, K., Pike, C.C., Kell, C., Mckenna, J., Williams, M., Faradonbeh, M.Z., Jacobs, D.F., 2026. Susceptibility to butternut canker disease in field trials is influenced by disease level and hybridization. Can. J. For. Res. 0. https://doi.org/10.1139/cjfr-2025-0234.

Çorbacıoğlu, Ş.K., Aksel, G., 2023. Receiver operating characteristic curve analysis in diagnostic accuracy studies: A guide to interpreting the area under the curve value. Turk. J. Emerg. Med. 23, 195–198. https://doi.org/10.4103/tjem.tjem_182_23.

Crocker, E., Condon, B., Almsaeed, A., Jarret, B., Nelson, C.D., Abbott, A.G., Main, D., Staton, M., 2020. TreeSnap: a citizen science app connecting tree enthusiasts and forest scientists. Plants People Planet 2, 47–52. https://doi.org/10.1002/ppp3.41.

Cutler, D.R., Edwards, T.C., Beard, K.H., Cutler, A., Hess, K.T., Gibson, J., Lawler, J.J., 2007. Random forests for classification in ecology. Ecology 88, 2783–2792. https://doi.org/10.1890/07-0539.1.

Daly, C., Neilson, R.P., Phillips, D.L., 1994. A statistical-topographic model for mapping climatological precipitation over mountainous terrain. J. Appl. Meteor. 33, 140–158. https://doi.org/10.1175/1520-0450(1994)033<0140:astmfm>2.0.co;2.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D., Lautenbach, S., 2013. Collinearity:a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36, 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x.

Edgar, C.B., Nowak, D.J., Majewsky, M.A., Lister, T.W., Westfall, J.A., Sonti, N.F., 2020. Strategic national urban forest inventory for the United States. J. For. 119, 86–95. https://doi.org/10.1093/jofore/fvaa047.

Edwards, J.L., 2001. The global biodiversity information facility: an international network of interoperable biodiversity databases. Joho Chishiki Gakkaishi 10, 58–61. https://doi.org/10.2964/jsik_kj00001039357.

Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E., Yates, C.J., 2011. A statistical explanation of MaxEnt for ecologists. Divers. Distrib. 17, 43–57. https://doi.org/10.1111/j.1472-4642.2010.00725.x.

Elliott, K.J., Swank, W.T., 2008. Long-term changes in forest composition and diversity following early logging (1919–1923) and the decline of American chestnut (*Castanea dentata*). Plant Ecol. 197, 155–172. https://doi.org/10.1007/s11258-007-9352-3.

Farlee, L., Woeste, K., Ostry, M., McKenna, J., Weeks, S., 2010. Identification of butternuts and butternut hybrids, 11. FNR-420-W. Purdue University Cooperative Extension Service.

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Clim. 37, 4302–4315. https://doi.org/10.1002/joc.5086.

Forest Service, 1995. Forest insect and Disease Conditions in The United States 1994. USDA-Forest Service, Forest Pest Management, Washington D.C.

Franklin, J., 1995. Predictive vegetation mapping: geographic modelling of biospatial patterns in relation to environmental gradients. Prog. Phys. Geogr.: Earth Environ. 19 (4), 474–499. https://doi.org/10.1177/030913339501900403.

Freeman, E.A., Moisen, G., 2008. PresenceAbsence: an R package for presence-absence model analysis. J. Stat. Softw. 23, 1–31. https://doi.org/10.18637/jss.v023.i11.

Georgian, S.E., Anderson, O.F., Rowden, A.A., 2019. Ensemble habitat suitability modeling of vulnerable marine ecosystem indicator taxa to inform deep-sea fisheries management in the South Pacific Ocean. Fish. Res. 211, 256–274. https://doi.org/10.1016/j.fishres.2018.11.020.

Graves, A.R., 1919. Some diseases in greater New York. Mycologia 111–124.

Graves, A.R., 1923. The Melanconis disease of the butternut (*Juglans cinerea* L.). Phytopathology 411, 434.

Guisan, A., Edwards, T.C., Hastie, T., 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecol. Model 157, 89–100. https://doi.org/10.1016/s0304-3800(02)00204-1.

Guisan, A., Tingley, R., Baumgartner, J.B., Naujokaitis-Lewis, I., Sutcliffe, P.R., Tulloch, A.I.T., Regan, T.J., Brotons, L., McDonald-Madden, E., Mantyka-Pringle, C., Martin, T.G., Rhodes, J.R., Maggini, R., Setterfield, S.A., Elith, J., Schwartz, M.W., Wintle, B.A., Broennimann, O., Austin, M., Ferrier, S., Kearney, M.R., Possingham, H. P., Buckley, Y.M., 2013. Predicting species distributions for conservation decisions. Ecol. Lett. 16, 1424–1435. https://doi.org/10.1111/ele.12189.

Guisan, A., Zimmermann, N., 2000. Predictive habitat distribution models in ecology. Ecol. Model. 135 (2–3), 147–186. https://doi.org/10.1016/s0304-3800(00)00354-9.

Hanf, D., Hodgson, A.J., Kobryn, H., Bejder, L., Smith, J.N., 2022. Dolphin distribution and habitat suitability in North Western Australia: applications and implications of a broad-scale, non-targeted dataset. Front. Mar. Sci. 8. https://doi.org/10.3389/fmars.2021.733841.

Hanley, J.A., 1989. Receiver operating characteristic (ROC) methodology: the state of the art. Crit. Rev. Diagn. Imaging 29, 307–335.

Hijmans, R.J., 2010. raster: geographic data analysis and modeling. CRAN Contrib. Packag. https://doi.org/10.32614/cran.package.raster.

Hirzel, A.H., Lay, G.L., 2008. Habitat suitability modelling and niche theory. J. Appl. Ecol. 45, 1372–1381. https://doi.org/10.1111/j.1365-2664.2008.01524.x.

Hoban, S.M., McCleary, T.S., Schlarbaum, S.E., Romero-Severson, J., 2009. Geographically extensive hybridization between the forest trees American butternut and Japanese walnut. Biol. Lett. 5, 324–327. https://doi.org/10.1098/rsbl.2009.0031.

Hoban, S.M., McCleary, T.S., Schlarbaum, S.E., Anagnostakis, S.L., Romero-Severson, J., 2012a. Human-impacted landscapes facilitate hybridization between a native and an introduced tree. Evol. Appl. 5, 720–731. https://doi.org/10.1111/j.1752-4571.2012.00250.x.

Hoban, S.M., Schlarbaum, S.E., Brosi, S.L., Romero-Severson, J., 2012b. A rare case of natural regeneration in butternut, a threatened forest tree, is parent and space limited. Conserv. Genet 13, 1447–1457. https://doi.org/10.1007/s10592-012-0386-2.

Hosseini, N., Ghorbanpour, M., Mostafavi, H., 2024. Habitat potential modelling and the effect of climate change on the current and future distribution of three *Thymus* species in Iran using MaxEnt. Sci. Rep. 14, 3641. https://doi.org/10.1038/s41598-024-53405-5.

Jamali, F., Amininasab, S.M., Taleshi, H., Madadi, H., 2024. Using an ensemble modeling to predict the potential distribution and habitat suitability of caracal (*Caracal caracal*) in southwestern Iran. Glob. Ecol. Conserv. 52, e02968. https://doi.org/10.1016/j.gecco.2024.e02968.

Janitza, S., Hornung, R., 2018. On the overestimation of random forest's out-of-bag error. PLoS ONE 13, e0201904. https://doi.org/10.1371/journal.pone.0201904.

Krushelnycky, P.D., Fortini, L.B., Mallinson, J., Felts, J.M., 2023. Empirical estimation of habitat suitability for rare plant restoration in an era of ongoing climatic shifts. Sci. Rep. 13, 19257. https://doi.org/10.1038/s41598-023-46793-7.

Kuhn, M., 2008. Building predictive models in R using the caret package. J. Stat. Softw. 28. https://doi.org/10.18637/jss.v028.i05.

LaBonte, N.R., Ostry, M.E., Ross-Davis, A., Woeste, K.E., 2015. Estimating heritability of disease resistance and factors that contribute to long-term survival in butternut (*Juglans cinerea* L.). Tree Genet. Genomes 11, 63. https://doi.org/10.1007/s11295-015-0884-8.

Laine, A., Burdon, J.J., Dodds, P.N., Thrall, P.H., 2011. Spatial variation in disease resistance: from molecules to metapopulations. J. Ecol. 99, 96–112. https://doi.org/10.1111/j.1365-2745.2010.01738.x.

Latif, Q.S., Saab, V.A., Dudley, J.G., Hollenbeck, J.P., 2013. Ensemble modeling to predict habitat suitability for a large-scale disturbance specialist. Ecol. Evol. 3, 4348–4364. https://doi.org/10.1002/ece3.790.

Leveau, J.H.J., 2024. Re-envisioning the plant disease triangle: full integration of the host microbiota and a focal pivot to health outcomes. Annu. Rev. Phytopathol. 62, 31–47. https://doi.org/10.1146/annurev-phyto-121423-042021.

Li, M., Zhang, C., Xu, B., Xue, Y., Ren, Y., 2017. Evaluating the approaches of habitat suitability modelling for whitespotted conger (*Conger myriaster*). Fish. Res. 195, 230–237. https://doi.org/10.1016/j.fishres.2017.07.024.

Liang, D., Li, C., 2024. Habitat suitability, distribution modelling and GAP analysis of Przewalski's gazelle conservation. Animals 14, 149. https://doi.org/10.3390/ani14010149.

Liaw, A., Wiener, M., 2002. Classification and regression by randomForest. R. News 2, 18–22.

Little, E.L., 1971. Atlas of United States trees. Conifers Important Hardwoods U. S. Dep. Agric. Misc. Publ. 1146 Wash. D. C. 1.

Luan, J., Zhang, C., Xu, B., Xue, Y., Ren, Y., 2020. The predictive performances of random forest models with limited sample size and different species traits. Fish. Res. 227, 105534. https://doi.org/10.1016/j.fishres.2020.105534.

Matthiopoulos, J., 2022. Defining, estimating, and understanding the fundamental niches of complex animals in heterogeneous environments. Ecol. Monogr. 92. https://doi.org/10.1002/ecm.1545.

McCleary, T.S., Robinchaud, R.L., Nuanes, S., Anagnostakis, S.L., S.Schlarbaum, S., Romero-Severson, J., 2009. Four cleaved amplified polymorphic sequence (CAPS) markers for the detection of the *Juglans ailantifolia* chloroplast in putatively native *J. cinerea* populations. Mol. Ecol. Resour. 9, 525–527. https://doi.org/10.1111/j.1755-0998.2008.02465.x.

McCullagh, P., Nelder, J.A., 1989. Gen. Linear Models10.1007/978-1-4899-3242-6.

McGarigal, K., Wan, H.Y., Zeller, K.A., Timm, B.C., Cushman, S.A., 2016. Multi-scale habitat selection modeling: a review and outlook. Landsc. Ecol. 31, 1161–1175. https://doi.org/10.1007/s10980-016-0374-x.

McInerny, G.J., Etienne, R.S., 2012. Ditch the niche – is the niche a useful concept in ecology or species distribution modelling? J. Biogeogr. 39, 2096–2102. https://doi.org/10.1111/jbi.12033.

McKenna, J.R., Ostry, M.E., Woeste, K., 2011. Screening butternut and butternut hybrids for resistance to butternut canker. Proceedings of the 17th Central Hardwood Forest Conference. USDA Forest Service. Northern Research Station, Newtown Square, PA.

Meier, E., 2015. Wood! identifying and using hundreds of woods worldwide, 1st ed. Wood Database.

Michler, C.H., Pijut, P.M., Jacobs, D.F., Meilan, R., Woeste, K.E., Ostry, M.E., 2006. Improving disease resistance of butternut (*Juglans cinerea*), a threatened fine hardwood: a case for single-tree selection through genetic improvement and deployment. Tree Physiol. 26, 121–128. https://doi.org/10.1093/treephys/26.1.121.

Moerman, D.E., 1986. Medicinal Plants of Native America, Vols. 1 and 2. The University of Michigan Press. https://doi.org/10.3998/mpub.11394575.

Moore, M.J., Ostry, M.E., 2015. Influence of temperature and humidity on the viability of *Ophiognomonia clavigignenti-juglandacearum* Conidia. Plant Dis. 99, 1841–1846. https://doi.org/10.1094/pdis-09-14-0976-re.

Moorter, B.V., Kivimäki, I., Panzacchi, M., Saura, S., Niebuhr, B.B., Strand, O., Saerens, M., 2023. Habitat functionality: integrating environmental and geographic space in niche modeling for conservation planning. Ecology 104, e4105. https://doi.org/10.1002/ecy.4105.

Morin, R.S., Gottschalk, K.W., Ostry, M.E., Liebhold, A.M., 2017. Regional patterns of declining butternut (*Juglans cinerea* L.) suggest site characteristics for restoration. Ecol. Evol. 8, 546–559. https://doi.org/10.1002/ece3.3641.

Müller, K., Wickham, H., James, D.A., Falcon, S., 2024. RSQLite: SQLite interface for R.

Nair, V.M.G., Kostichka, C.J., Kuntz, J.E., 1979. *Sirococcus clavigignenti-juglandacearum*: an undescribed species causing canker on butternut. Mycologia 71, 641–646. https://doi.org/10.1080/00275514.1979.12021049.

Nayeri, D., Cushman, S., Ganey, J., Hysen, L., Gunther, M.S., Willey, D., Wan, H.Y., 2024. Multiscale habitat suitability modeling for a threatened raptor offers insight into ecological model transferability. Ecol. Model 496, 110845. https://doi.org/10.1016/j.ecolmodel.2024.110845.

Noah, P.H., Cagle, N.L., Westbrook, J.W., Fitzsimmons, S.F., 2021. Identifying resilient restoration targets: Mapping and forecasting habitat suitability for *Castanea dentata* in eastern USA under different climate-change scenarios. Clim. Chang. Ecol. 2, 100037. https://doi.org/10.1016/j.ecochg.2021.100037.

Oppel, S., Meirinho, A., Ramírez, I., Gardner, B., O'Connell, A.F., Miller, P.I., Louzao, M., 2012. Comparison of five modelling techniques to predict the spatial distribution and abundance of seabirds. Biol. Conserv. 156, 94–104. https://doi.org/10.1016/j.biocon.2011.11.013.

Ostry, M.E., Katovich, S., Anderson, R.L., 1997. First report of *Sirococcus clavigignenti-juglandacearum* on black walnut. Plant Dis. 81, 830. https://doi.org/10.1094/pdis.1997.81.7.830d.

Ostry, M.E., Moore, M., 2007. Natural and experimental host range of *Sirococcus clavigignenti-juglandacearum*. Plant Dis. 91, 581–584. https://doi.org/10.1094/pdis-91-5-0581.

Ostry, M.E., Moore, M., 2008. Response of butternut selections to inoculation with *Sirococcus clavigignenti-juglandacearum*. Plant Dis. 92, 1336–1338. https://doi.org/10.1094/pdis-92-9-1336.

Ostry, M.E., Woeste, K.E., 2004. Spread of butternut canker in North America, host range, evidence of resistance within butternut populations and conservation genetics, Black walnut in a new century. Proceedings of the 6th Walnut Council Research Symposium. U.S.D.A. Forest Service, North Central Research Station, St. Paul, MN, Lafayette, IN.

Paillet, F.L., 1984. Growth-form and ecology of American chestnut sprout clones in northeastern Massachusetts. Bull. Torre Bot. Club 111, 316. https://doi.org/10.2307/2995913.

Paillet, F.L., 2002. Chestnut: history and ecology of a transformed species. J. Biogeogr. 29, 1517–1530. https://doi.org/10.1046/j.1365-2699.2002.00767.x.

Pebesma, E., 2018. Simple features for R: standardized support for spatial vector data. R. J. 10, 439. https://doi.org/10.32614/rj-2018-009.

Pebesma, E., Bivand, R., 2023. with applications in R. CRC Press, United States. Spat. data Sci. https://doi.org/10.1201/9780429459016-3.

Pepe, M.S., 2000. Receiver operating characteristic methodology. J. Am. Stat. Assoc. 95, 308. https://doi.org/10.2307/2669554.

Peters, M.P., Prasad, A.M., Matthews, S.N., Iverson, L.R., 2020. Climate Change Tree Atlas, Version 4Northern Research Station and Northern Institute of Applied Climate ScienceU.S. Forest Service(accessed 7.17.25), ⟨URL https://www.nrs.fs.fed.us/atlas⟩.

Phillips, S., 2021. maxnet: fittingMaxent" Species Distrib. Models "glmnet.

Pike, C.C., Williams, M., Brennan, A., Woeste, K., Jacobs, J., Hoban, S., Moore, M., Romero-Severson, J., 2020. Save our species: a blueprint for restoring butternut (*Juglans cinerea*) across eastern North America. J. For. 119, 196–206. https://doi.org/10.1093/jofore/fvaa053.

PRISM, G., 2024. PRISM [WWW Document]. ⟨URL https://prism.oregonstate.edu⟩, (accessed 4.16.25).

Renlund, D.W., 1971. Forest Pest Conditions in Wisconsin, Annual Report. Wisconsin Department of Natural Resources, Madison, WI.

Rew, J., Cho, Y., Moon, J., Hwang, E., 2020. Habitat suitability estimation using a two-stage ensemble approach. Remote Sens. 12, 1475. https://doi.org/10.3390/rs12091475.

Ridgeway, G., 2024. gbm Gen. Boost. Regres. Models.

Rink, G., 1990. Juglans cinerea L. butternut, silvics of North America, 654. USDA Forest ServiceAgricultural Handbook, Washington DC.

Roberts, D.R., Bahn, V., Ciuti, S., Boyce, M.S., Elith, J., Guillera-Arroita, G., Hauenstein, S., Lahoz-Monfort, J.J., Schröder, B., Thuiller, W., Warton, D.I., Wintle, B.A., Hartig, F., Dormann, C.F., 2017. Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. Ecography 40, 913–929. https://doi.org/10.1111/ecog.02881.

Robin, X., Turck, N., Hainard, A., Tiberti, N., Lisacek, F., Sanchez, J.-C., Müller, M., 2011. pROC: An open-source package for R and S+ to analyze and compare ROC curves. BMC Bioinform 12, 77. https://doi.org/10.1186/1471-2105-12-77.

Ross-Davis, A., Huang, Z., McKenna, J., Ostry, M., Woeste, K., 2008. Morphological and molecular methods to identify butternut (*Juglans cinerea*) and butternut hybrids: relevance to butternut conservation. Tree Physiol. 28, 1127–1133. https://doi.org/10.1093/treephys/28.7.1127.

Sales, L.P., Hayward, M.W., Loyola, R., 2021. What do you mean by "niche"? Modern ecological theories are not coherent on rhetoric about the niche concept. Acta Oecologica 110, 103701. https://doi.org/10.1016/j.actao.2020.103701.

Sambaraju, K.R., DesRochers, P., Rioux, D., 2018. Factors influencing the regional dynamics of butternut canker. Plant Dis. 102, 743–752. https://doi.org/10.1094/pdis-08-17-1149-re.

Scheele, B.C., Heard, G.W., Cardillo, M., Duncan, R.P., Gillespie, G.R., Hoskin, C.J., Mahony, M., Newell, D., Rowley, J.J.L., Sopniewski, J., 2023. An invasive pathogen drives directional niche contractions in amphibians. Nat. Ecol. Evol. 7, 1682–1692. https://doi.org/10.1038/s41559-023-02155-0.

Scheele, B.C., Heard, G.W., Duncan, R.P., Clulow, S., Sopniewski, J., 2025. An invasive pathogen generally contracts species to their niche cores, not margins. Ecography 2025. https://doi.org/10.1111/ecog.07612.

Schlarbaum, S.E., Hebard, F., Spaine, P.C., Kamalay, J., 1998. Three American tragedies: chestnut blight, butternut canker, and Dutch elm disease, 1997 April 8. In: Britton, K. O. (Ed.), Exotic Pests of Eastern Forests Conference Proceedings, 10. U.S. Forest Service and Tennessee Exotic Pest Plant Council, Nashville, TN, pp. 45–54, 1997 April 8.

Shanley, C.S., Eacker, D.R., Reynolds, C.P., Bennetsen, B.M.B., Gilbert, S.L., 2021. Using LiDAR and random forest to improve deer habitat models in a managed forest landscape. For. Ecol. Manag. 499, 119580. https://doi.org/10.1016/j.foreco.2021.119580.

Sittaro, F., Paquette, A., Messier, C., Nock, C.A., 2017. Tree range expansion in eastern North America fails to keep pace with climate warming at northern range limits. Glob. Chang. Biol. 23, 3292–3301. https://doi.org/10.1111/gcb.13622.

Stritch, L., Barstow, M., 2019. Juglans cinerea Butter IUCN Red. List Threat. Species 2019.10.2305/iucn.uk.2019-1.rlts.t62019689a62019696.en.

Su, H., Bista, M., Li, M., 2021. Mapping habitat suitability for Asiatic black bear and red panda in Makalu Barun National Park of Nepal from Maxent and GARP models. Sci. Rep. 11, 14135. https://doi.org/10.1038/s41598-021-93540-x.

team, P., 2025. RStudio: integrated development environment for R. Posit Software. PBC, Boston, MA.

Team, R.C., 2025. R: A language and environment for statistical computing. R. Found. Stat. Comput. https://doi.org/10.32614/r.manuals.

Vabalas, A., Gowen, E., Poliakoff, E., Casson, A.J., 2019. Machine learning algorithm validation with a limited sample size. PLoS ONE 14, e0224365. https://doi.org/10.1371/journal.pone.0224365.

Valavi, R., Elith, J., Lahoz-Monfort, J.J., Guillera-Arroita, G., 2021. Modelling species presence-only data with random forests. Ecography 44, 1731–1742. https://doi.org/10.1111/ecog.05615.

Varma, S., Simon, R., 2006. Bias in error estimation when using cross-validation for model selection. BMC Bioinform. 7, 91. https://doi.org/10.1186/1471-2105-7-91.

Vrigazova, B., 2021. The proportion for splitting data into training and test set for the bootstrap in classification problems. Bus. Syst. Res. J. 12, 228–242. https://doi.org/10.2478/bsrj-2021-0015.

Walker, K., 2015. tigris: load census TIGER/Line shapefiles. CRAN Contrib. Packag. https://doi.org/10.32614/cran.package.tigris.

Wan, G.-Z., Li, Q.-Q., Jin, L., Chen, J., 2024. Integrated approach to predicting habitat suitability and evaluating quality variations of *Notopterygium franchetii* under climate change. Sci. Rep. 14, 26927. https://doi.org/10.1038/s41598-024-77824-6.

Wickham, H., 2016. ggplot2: elegant graphics for data analysisSpringer-Verlag New York.

Wickham, H., François, R., Henry, L., Müller, K., Vaughan, D., 2023. dplyr: A grammar of data manipulation.

Williams, J.N., Seo, C., Thorne, J., Nelson, J.K., Erwin, S., O'Brien, J.M., Schwartz, M.W., 2009. Using species distribution models to predict new occurrences for rare plants. Divers. Distrib. 15, 565–576. https://doi.org/10.1111/j.1472-4642.2009.00567.x.

Williams, D.A., Shadwell, K.S., Pearse, I.S., Prevéy, J.S., Engelstad, P., Henderson, G.C., Jarnevich, C.S., 2024. Predictor importance in habitat suitability models for invasive terrestrial plants. Divers. Distrib. 30. https://doi.org/10.1111/ddi.13906.

Wood, S.N., 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. J. R. Stat. Soc. Ser. B (Stat. Method. 73, 3–36. https://doi.org/10.1111/j.1467-9868.2010.00749.x.

Yang, X., Zhang, X., Zhang, P., Bidegain, G., Dong, J., Hu, C., Li, M., Zhang, Z., Guo, H., 2023. Ensemble habitat suitability modeling for predicting optimal sites for eelgrass (*Zostera marina*) in the tidal lagoon ecosystem: Implications for restoration and conservation. J. Environ. Manag. 330, 117108. https://doi.org/10.1016/j.jenvman.2022.117108.

Zhao, P., Woeste, K.E., 2011. DNA markers identify hybrids between butternut (*Juglans cinerea* L.) and Japanese walnut (*Juglans ailantifolia* Carr.). Tree Genet. Genomes 7, 511–533. https://doi.org/10.1007/s11295-010-0352-4.