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Exploring Past and Future Distributions of the Rare Appalachian Oak Fern Using MaxEnt Modeling

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ABSTRACT.—Anthropogenic climate change is projected to have an especially negative impact on the survival of plants that are dependent on limited microclimatic refugia or that already reside at their climatic extreme. Gymnocarpium appalachianum is a narrowly endemic fern restricted to cold mountaintops and algific vents in the central and southern Appalachian region of eastern North America. It is the much rarer of the two documented diploid parents of the circumboreal allotetraploid G. dryopteris-one of the most widespread fern species on the planet. Gymnocarpium appalachianum is a good case study for forecasting how evolutionarily significant, but rare, species might survive on a warming planet. We utilize an ecological niche modeling approach (MaxEnt) to explore the projected distribution of G. appalachianum under past (Last Glacial Maximum) and future climate models. All known verified herbarium records of G. appalachianum were georeferenced, for a total of 70 occurrence points. Nineteen standard bioclimatic variables extracted from WorldClim were used to model near-current climate projections; representative concentration pathways (RCPs 2.6 and 8.5) were used for future climate projections (2070). The temperature annual range, mean temperature of warmest quarter, precipitation of driest month, precipitation of coldest quarter, and mean diurnal range were identified as the key variables for shaping the distribution of *G. appalachianum*. An unanticipated result from our analyses is that *G.* appalachianum has past and current projected habitat suitability in Alaska. Because this overlaps with the current range of G. disjunctum, the other diploid parent of G. dryopteris, it suggests a possible region of origin for this circumboreal tetraploid descendent of G. appalachianum-a research avenue to be pursued in the future. Our study envisions a dire fate for *G. appalachianum*; its survival will likely require an urgent contingency plan that includes human-mediated population relocation to cooler, northern locations. Understanding the long-term sustainability of narrowly endemic plants such as G. appalachianum is critical in decisions about their management and conservation.

Key WORDS.—climate change, ecological niche modeling, endemic species, MaxEnt, oak fern, refugia

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Climate dynamics are a primary determinant of the distribution of living species on Earth (Hewitt, 2004). Although climatic trends vary over time and space, the planet has experienced an overall warming trend since the Last Glacial Maximum (c. 22,000 BP), and the rate of change has significantly accelerated in recent decades due to human activities (Oreskes, 2004). Earth's land and ocean average temperature in 2021 was 0.84°C higher than the preindustrial (1850-1900) average (NOAA, 2022). Globally, the preceding decade was the warmest in human history, with 2016 being the hottest year ever recorded and 2020 the second hottest. According to the Fifth Assessment Report (AR5) of the Intergovernmental Panel on Climate Change (Pachauri *et al.*, 2014), the average temperature on Earth will rise at least another 1°C by 2100. Experts are pessimistic that the current global response to climate change is sufficient to limit warming to only 1.5°C (the goal set forth in the 2015 Paris COP21 agreement) without major upheavals in current political, technological, and sociological norms (Matthews and Wynes, 2022).

Future changes in global temperature are predicted by using representative carbon pathways (RCP) that are modeled on different global reduction scenarios for carbon emissions (van Vuuren *et al.*, 2011). These range from a very stringent RCP of 2.6, which is projected to limit global temperature rise to below 2°C by 2100, to a dire RCP of 8.5 that is estimated to deliver a temperature increase of about 4.3°C relative to pre-industrial temperatures during the same period. Under the "best case" scenario (RCP 2.6), changes in habitable ranges are predicted to drastically modify contemporary biogeographic patterns. Under the "business as usual" scenario (RCP 8.5), precipitous changes in regional climates will dramatically alter the distributions of many species (Abdelaal *et al.*, 2019; Khanum, Mumtaz, and Kumar, 2013; Zhao *et al.*, 2021).

It is now widely acknowledged that Earth is experiencing a sixth mass extinction caused primarily by anthropogenic climate change (Bellard *et al.*, 2012). Current global extinction rates are estimated to be 1000 times higher than the background extinction rate prior to recent human activities (Pimm *et al.*, 2014), and an estimated 16% of global diversity is under direct threat of extinction if we continue along the current trajectory (Urban, 2015). As global temperatures rise, drastic contractions and changes in species ranges are expected. In the southern Appalachian Mountains of eastern North America, a rare plant (*Geum radiatum*) that relies on limited high-elevation cold and wet refugia, is estimated to lose up to 83% of its viable habitat by 2050 (Ulrey *et al.*, 2016).

Anthropogenic climate change is projected to have especially negative impacts on the survival of organisms with limited vagility that are dependent on sporadically distributed microclimatic refugia (Thomas *et al.*, 2004). One such species of immediate conservation concern is the Appalachian oak fern (*Gymnocarpium appalachianum* Pryer & Haufler) in the central and southern Appalachian Mountains of the eastern United States (Fig. 1a). It is restricted to cold mountaintops and algific vents, rare and fragile ecosystems that emit cold air from subterranean ice pockets and often host relict populations not found



FIG. 1. Geographic distributions for the *Gymnocarpium* taxa discussed herein. (a) North American ranges for the diploids *G. appalachianum* in eastern North America (blue circles) and *G. disjunctum* in western North America (orange triangles) based on Pryer and Haufler (1993). Inset on the right of map is an image taken from the holotype specimen of *G. appalachianum* (US 3215838) from Shenandoah National Park in Virginia. (b) Arctic view of global circumboreal distribution of the allotetraploid *G. dryopteris* based on records downloaded from GBIF.org (2022).

elsewhere locally (Cristy and Meyer, 1991). *Gymnocarpium appalachianum* is morphologically cryptic and, prior to the 1990s, was not separated from the widespread circumboreal species *G. dryopteris* (L.) Newman (Fig. 1b; data points obtained from GBIF.org, 2022). The first hint that *G. appalachianum* was a distinct species came from cytogenetic studies by Pryer and Haufler (1993), who reported that *Gymnocarpium* populations in Virginia and West Virginia were diploid with n=40 chromosomes. By contrast, *G. dryopteris sensu stricto* has only been reported as tetraploid with n=80 (Britton, 1953; Gureeva, Mitrenina, and Ulko, 2017; Löve and Löve, 1961, 1976; Löve, Löve, and Bernard, 1980; Manton, 1950; Pellinen, Sarvela, and Uotila, 1999; Sorsa, 1958; Wagner, 1963).

Concurrent isozyme analyses by Pryer and Haufler (1993) revealed that G. appalachianum played a pivotal role in the evolution of its circumboreal tetraploid congener. Gymnocarpium dryopteris was shown to be an allotetraploid hybrid between G. appalachianum and G. disjunctum (Rupr.) Ching. Prior to 1993, G. disjunctum was the only documented diploid (n=40; Löve and Löve, 1976; Sorsa, 1966; Taylor and Mulligan, 1968; Wagner, 1966) Gymnocarpium in North America. The discovery of a second diploid (G. appalachianum) resolved questions regarding the parentage of tetraploid G. dryopteris, but posed an unanticipated biogeographic conundrum. Known populations of the two parental diploids are currently separated by more than 2400 km (Fig. 1a), which leads to the question: how did two such widely disjunct species manage to hybridize to form G. dryopteris (one of the most widespread fern species on the planet)?

Gymnocarpium appalachianum is a rare but evolutionary significant species that is clearly threatened by climate change. Its conservation status is listed as vulnerable (G3) globally, and the species is listed as presumed extirpated (SX) in Ohio, critically imperiled (S1) in Pennsylvania and North Carolina, imperiled (S2) in West Virginia, vulnerable (S3) in Virginia, and its presence and status are under review (SU) in Maryland (NatureServe, 2021). Here, we investigate the likely effects of past and future climate change on the distribution of *G. appalachianum*.

Ecological niche modeling is an important part of analyzing species future ranges and their ability to persist in current sites. MaxEnt is a common modeling algorithm used by conservation practitioners for predicting the distribution of a species from a set of records and environmental predictors (Fourcade *et al.*, 2014). In this study, we use MaxEnt, optimized to reduce overfitting of the model parameters (Radosavljevic and Anderson, 2014), to address the prospects of survival for *G. appalachianum* under near-current predicted climate change models. Our objective is to provide an initial estimate as to the urgency of management and conservation decisions that will need to be focused on this rare and endemic Appalachian fern.

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SPECIES OCCURRENCE RECORDS.—Previous systematics studies of *Gymnocarpium* (*e.g.*, Pryer, 1992; Pryer and Britton, 1983; Pryer, Britton, and McNeill, 1983; Pryer and Haufler, 1993) generated an extensive catalog of expert verified herbarium records for North America. This printed catalog was scanned using

a KIC Bookeye 4 flatbed color scanner and converted into computer readable text with Adobe Acrobat Pro DC (v.15). The PDF file was proofread for fidelity and all data fields (state, county, locality, elevation, latitude, longitude, habitat, collector, collector number, date of collection, and voucher location) for *G. appalachianum* were manually transcribed into an Excel spreadsheet.

GEOREFERENCING SPECIES OCCURRENCE RECORDS.—For each herbarium record with adequate data, Google Earth Pro (Google Earth v.7.3.2.5495, 2018) was used to estimate the latitude and longitude of the collection site. Specimens lacking sufficient information to permit accurate georeferencing were excluded. Geographic coordinates provided on collection labels were checked for accuracy and, if necessary, converted to decimal degrees for analysis. After processing, 182 georeferenced records for *G. appalachianum* representing 70 unique localities were used to model its geographic distribution (Supplementary Appendix A).

SELECTION AND SCREENING OF CLIMATIC VARIABLES.—Climatic data were obtained from WorldClim 1.4 (https://www.worldclim.org/data/v1.4/worldclim14. html) including all 19 bioclimatic variables (Fick and Hijmans, 2017) calculated from averages of global monthly climatic models and data from 1960-1990. Past climate data were also obtained from WorldClim 1.4 originally made available by the Coupled Model Intercomparison Project Phase 5 (CMIP5) (Taylor, Stouffer, and Meehl, 2012). The data were downscaled and calibrated using the Global Climate Models (GCMs) and WorldClim 1.4 as the near-current baseline for each variable. These data project global climate during the Last Glacial Maximum (LGM) around 22,000 years ago. Future climate data predictions were obtained from WorldClim 1.4. The projected climate layers utilize CMIP5 data and the Community Climate System Model 4 (CCSM4; http://www.cesm.ucar.edu) that integrates information from past atmospheric conditions, ocean and land surface temperatures, and sea ice (Gent et al., 2011). Projected climate data for 2070 at RCP 2.6 (best case) and RCP 8.5 (worst case) were employed in model creation. All bioclimatic variables were downloaded at a spatial resolution of 30 arcsecs (\sim 1km, the highest resolution available) and then cropped to the land area of North America and converted into an ASCII format using QGIS 3.2.0 (QGIS.org, 2020). Only those variables corresponding to the ones included in the model were used for projections. Variable selection was performed in R version 4.1.2 (R Core Team, 2021) using package usmd 1.1 (Naimi et al., 2014) to stepwise reduce the number of correlated variables in the dataset while balancing each variable's contribution. Variables were not used in the MaxEnt model if they had a Pearson's correlation coefficient (r) of > 0.9 or < -0.9, and a variance inflation factor (VIF) of over 10 when compared against another variable. Variables that were too closely correlated were removed in a stepwise fashion, until only uncorrelated variables remained in the model. After variable selection, 8 variables remained and only these were utilized for model creation (Table 1).

TABLE 1. The percent contribution and permutation importance of the eight bioclimatic variables used for the *G. appalachianum* species distribution model. Permutation importance measures the variable importance and its effect on predictive model accuracy. Bio07 (Temperature Annual Range) had the most significant contribution and the most information not contained in other variables (largest drop in AUC if excluded).

Variable	Code	Percent Contribution	Permutation Importance
Temperature Annual Range	Bio07	33.8	43.3
Mean Temperature of Warmest Quarter	Bio10	28.1	21.8
Precipitation of Driest Month	Bio14	26.0	19.1
Precipitation of Coldest Quarter	Bio19	5.6	11.9
Mean Diurnal Range	Bio02	5.3	3.4
Precipitation Seasonality	Bio15	1.0	0.0
Mean Temperature of Wettest Quarter	Bio08	0.3	0.5
Precipitation of Warmest Quarter	Bio18	0.1	0.0

MODEL OPTIMIZATION.-To optimize the MaxEnt model's complexity, but to prevent overfitting, we utilized the ENMeval 2.0 package (Kass et al., 2021) in R version 4.1.2 (R Core Team, 2021). ENMeval was used to partition the data using the block method by dividing all locations, both *G. appalachianum* and background locations, into four equal geographically contiguous groups. This was done to reduce artificial spatial bias by limiting the spatial autocorrelation between locations that were used in training versus testing, a possible side effect of the limited range of G. appalachianum (Peterson, Cobos, and Jiménez-García, 2018; Radosavljevic and Anderson, 2014). Of these groups, three were used for training and the fourth for testing. In utilizing ENMeval to find the optimal model parameters, the regularization multiplier (RM) was tested between 0.5–6, increasing by an interval of 0.5 for a total of 12 RM parameters. The feature combination (FC) parameters were tested with six different combinations of the five different parameters included in MaxEnt: linear (L), quadratic (Q), hinge (H), product (P), and threshold (T). The six feature combinations used were L, LQ, H, LHQ, LQHP, and LQHPT. The ENMeval package was used to test the above 72 parameter combinations. The model permutation with the lowest average omission rate and the highest average validation area under the curve (AUC) was chosen as optimal for the final MaxEnt model to balance complexity with accuracy (Kass et al., 2020; Velasco and González-Salaza, 2019).

MODEL SIMULATION.—To model the predicted near-current geographic distribution of *G. appalachianum* we utilized MaxEnt 3.4.4 (Phillips, Anderson, and Schapire, 2006). The 70 georeferenced unique localities in eastern North America (Supplementary Appendix A) were used as 'present' locations, while 10,000 random points confined to within 7 arc degrees of known *G. appalachianum* records were used as background locations for model construction. During model construction, five occurrence localities were excluded that occupied the same grid cell as another sample. Jackknife tests were performed to measure the contribution of each of the bioclimatic

variables for the model. MaxEnt was run with a maximum of 5,000,000 iterations or until the convergence threshold of 0.00001 was achieved. All other parameters were left as default. The model was run as 10 replicates, and all results are reported as an average of those. Habitat suitability probabilities in the model ranged from 0.0 (no suitability) to 1.0 (optimal suitability). A habitat was considered as suitable for *G. appalachianum* if the likely occurrence values were over 0.5 and optimal over 0.9.

MODEL AND CLIMATIC VARIABLE EVALUATION.—The model was evaluated for accuracy from the receiver operator characteristic curves (ROC). The importance of each of the climatic variables to the MaxEnt model was assessed by the variable percent contribution, permutation importance, and the variable importance interpreted from a Jackknife test.

MAP AND FIGURE GENERATION.—Vector shapefiles of North American states and provinces were obtained from Natural Earth Data (https://www.naturalearthdata.com/). All distribution maps were visualized using QGIS 3.2.0 (QGIS.org, 2020). The area in km² of predicted suitability was calculated in QGIS 3.2.0 using the GRASS 7.2 (GRASS Development Team, 2017) function r.report.

Results

MODEL OPTIMIZATION AND ACCURACY EVALUATION.-Recent studies have demonstrated that tuning and optimizing ecological niche models is necessary to maximize both model fit and generalizability (Elith and Graham, 2009; Kass et al., 2021; Merow et al., 2014; Warren and Siefert, 2011; Zhao et al., 2021). Ecological niche models can be particularly sensitive to different combinations of model parameters (Hallgren et al., 2019) that can lead to weak projectability into past and future conditions (Guevara et al., 2017). Model optimization and tuning with the ENMeval package were used here to evaluate which of the 72 different parameter combinations best fit *G. appalachianum*. The parameter set with the lowest average omission rate (Supplementary Fig. 1a) was selected for use in the final model. Because the lowest average omission rate was shared across several regularization multiplier (RM) values (2.5-5.5) for the hinge (H) feature, the combination of the lowest average omission rate with highest average validation area under the curve (AUC) was used to pick which RM value to use in the final model. The set of parameters used in the final model had a RM of 2.5 and a hinge feature. Our selected model parameters had the lowest average omission rate of 0.0625 (Supplementary Fig. 1a) and the highest average AUC of 0.9549 (Supplementary Fig. 1b). We chose not to select our parameters solely based on the lowest difference in Akaike information criterion (delta AICc) because this method has been shown in simulation to give overly simplistic results with no correlation between AIC and predictive accuracy (Velasco and González-Salazar, 2019). The parameters for the lowest delta AICc, and therefore the lowest complexity, for our data are linear and quadratic features with a RM of 0.5 (Supplementary Fig. 1c).

Our *G. appalachianum* species distribution model receiver operator characteristic (ROC) curves showed high predictive strength with AUC values of 0.961 for the training data and 0.988 \pm 0.002 for the test data. The ROC is the false positive rate of a model prediction plotted against the true positive rate of the model. This is measured by the area under the curve (AUC), the area that is enclosed by the ROC. The AUC is the probability that any random location will have a higher suitability than any random background point; therefore the higher the value of the AUC the more accurate the model prediction result (Phillips and Dudík, 2008).

The importance of each of the climatic variables to the MaxEnt model was assessed by the variable percent contribution, permutation importance, and the variable importance interpreted from a Jackknife test. The permutation importance measures the decrease in AUC from randomly permuting the values of the climatic variable (Phillips, Anderson, and Schapire, 2006). The Jackknife test measures the amount of useful information in each variable. It does this by calculating the gain and AUC of each variable by itself and by excluding the variable from the model (Elith, Kearney, and Phillips, 2010).

The percent contribution and permutation importance of each bioclimatic variable to model the geographic distribution are shown in Table 1. Temperature annual range (Bio07) shows the most significant contribution at 33.8%, followed by mean temperature of warmest quarter (Bio10), precipitation of driest month (Bio14), precipitation of coldest quarter (Bio19), and mean diurnal range (Bio02), at 28.1%, 26%, 5.6%, and 5.3%, respectively. The three other variables (precipitation seasonality [Bio15], mean temperature of wettest quarter [Bio08], and precipitation of the warmest quarter [Bio18]) each had \leq 1% contribution to the model. The permutation importance of the temperature annual range (Bio07), the mean temperature of the warmest quarter (Bio10), precipitation of the driest month (Bio14), and the precipitation of the coldest quarter (Bio19) were 43.3%, 21.8%, 19.1%, and 11.9%, respectively. These four variables contain a cumulative permutation importance of 96.1% while only having a cumulative percent contribution of 93.5%.

EVALUATION OF IMPORTANT CLIMATIC VARIABLES.—The response curves indicating the presence probability of suitable habitat for *G. appalachianum* for the five most important bioclimatic variables used in the model are shown in Figure 3. Figure 3a shows that habitat suitability (>0.5) rapidly decreases as temperature annual range (Bio07) increases beyond 35°C and was optimal (>0.9) between 23.1–34.04°C. Habitat suitability also decreases as mean temperature of the warmest quarter (Bio10) increases beyond 22.77°C, where the optimal mean temperature was between 12–21.29°C (Fig. 2b). The presence probability of *G. appalachianum* is positively correlated with the amount of precipitation in the driest month (Bio14), with suitable habitat above 62.11 mm and optimal precipitation for habitat suitability above 72.26 mm (Fig. 2c). Suitability is negatively correlated with the amount of precipitation in the coldest quarter

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Fig. 2. Variable response curves of probability for the five most important bioclimatic variables used in generating the MaxEnt model. All response curves are an average of ten replicates. Values > 0.5 are considered suitable for presence of *G. appalachianum*; values > 0.9 are considered optimal.

(Bio19), which is suitable between 47.2 and 314.2 mm and optimal between 47.2 and 265.85 mm (Fig. 2d). Finally, the model predicts a rapid increase in presence probability for *G. appalachianum* as mean diurnal range increases (Bio02), with suitability highest above 7.68°C and optimal above 8.47°C (Fig. 2e).

Potential suitable habitat for G. Appalachianum under near-current climate conditions.—The species distribution model predicts that habitat suitability is



Fig. 3. Projections of species distribution models for *G. appalachianum* based on an average of ten replicates in MaxEnt. The near-current modeled habitat for *G. appalachianum* in eastern North America (a), and the southern coast of Alaska (b). Projections of *G. appalachianum* at the LGM in eastern North America (c), and the Pacific Northwest coast (d). Future climate projections utilizing the CCSM4 model for RCP 2.6 in 2070 (e), and RCP 8.5 in 2070 (d). Near-current, past, and future projected suitable habitats for *G. appalachianum* are displayed only when probability of presence is > 0.5.

concentrated in the east-central United States, particularly within the central Appalachian Mountains (Fig. 3a), which mostly covers the known distribution range of our 70 documented occurrence records. Surprisingly, the model also suggests that some areas of suitability may exist in the southern coast of Alaska (Fig. 3b), within the current range of *G. dryopteris* and *G. disjunctum* (Fig. 1). The total area within North America considered suitable for *G. appalachianum* by the model (with at least 0.5 presence probability) is 47,457 km²; highly suitable habitats (with at least 0.9 presence probability) occupy 12,284 km².

POTENTIAL SUITABLE HABITAT FOR G. APPALACHIANUM UNDER PAST AND FUTURE CLIMATE CONDITIONS.—Our species distribution model's prediction for *G. appalachianum*

during the Last Glacial Maximum (LGM) greatly exceeds its current documented range (Fig. 3). From the central Appalachians, the region of high suitability forms a band paralleling the southern edge of the Laurentide Ice Sheet as far west as southeastern Missouri (Fig. 3c). In addition, the LGM model projects a large area of suitable habitat for *G. appalachianum* paralleling the Pacific coast from the northern Cascades Range of Washington to the south coast of Alaska (Fig. 3d). Future projections for the distribution of *G. appalachianum* in 2070 (Fig. 3e-f) show a dramatic increase in the total area of suitable habitat (with at least 0.5 presence probability) of 112,070 km² for RCP 2.6 and of 151,596 km² for RCP 8.5 as compared to 47,457 km² for the near-current, but significant displacement to the northeast compared to its near-current distribution (Fig. 3a, b). The projected distribution of *G. appalachianum* for RCP 2.6 in 2070 is concentrated in southern New England but extends as far south as the northern and central Appalachian Mountains (Fig. 3e). The RCP 8.5 projections for 2070 show an additional shift north in New England, and the loss of all the potential G. appalachianum habitat (Fig. 3f). In both future predictions, all suitable habitat for *G. appalachianum* in Alaska disappears.

DISCUSSION

CLIMATIC VARIABLES MOST PERTINENT TO PREDICTING HABITAT SUITABILITY.—Our species distribution model identified the most important bioclimatic variables for predicting G. appalachianum habitat suitability (>0.5) as: 1) annual temperature range (Bio07) less than 35.87°C, 2) mean temperature of the warmest quarter (Bio10) below 22.77°C, and 3) precipitation of the driest month (Bio14) above 62.11 mm (Table 1, Fig. 2a-c). These predictions are consistent with the cool, moist montane microclimates where G. appalachianum is currently found (Prver and Haufler, 1993). It is notable that the strongest area of suitability for G. appalachianum is in northwest North Carolina and northeast Tennessee, slightly south of its current range. In theory, this area seems suitable, as it is cool and wet, though G. appalachianum is mysteriously absent except for one population in the far northwestern corner of North Carolina. However, unlike the current range of *G. appalachianum*, this area was entirely unglaciated during the last glacial period (Clark et al., 2009). The past projection (Fig. 3b, c) of *G. appalachianum* and its current association with algific cold air seepage suggest it may have an affinity for glaciers. The current range of G. appalachianum in West Virginia and Pennsylvania is dominated by forested, low-elevation parallel ridges that run southwest to northeast forming narrow valleys that have been deforested for agricultural production. This deforestation represents a two-fold threat to the continued survival of G. appalachianum in the area, contributing to localized temperature increases while simultaneously creating barriers to range expansion. The response curves shown in Figure 2 predict that it will be difficult for G. appalachianum to persist as global temperatures continue to rise and there are more extreme heat events in North America. Increasing

annual temperature ranges and mean summer temperatures coupled with increased frequency of drought (Urban, 2015) is likely to drastically decrease overall habitat suitability and lessen the buffering effects of microclimate refugia.

ANALYSIS OF NEAR-CURRENT SUITABLE HABITAT FOR G. APPALACHIANUM.—Our species distribution model affirms that the most suitable habitat for *G. appalachianum* is a narrow band in the central Appalachian Mountains in eastern North America (Fig. 3a). As expected, there is extensive overlap between known populations and areas that the model suggests are of high suitability. This narrow band comprises a region of mountains that are cooler and taller than areas further to the north. The geography and climate conditions that circumscribe the current range of *G. appalachianum* are likely to limit its northern migration as local temperatures rise, possibly trapping the species in less suitable habitat. The notable absence of the species from the southern end of the projected modern range might be explained by previous periods of warming since the last ice age, or perhaps by the lack of cold air drainage microsites because North Carolina and Tennessee were never glaciated. Further studies are needed to explore these hypotheses.

Our model also identifies potential habitat suitability along the southern coast of Alaska and the Pacific Coast of British Columbia (Fig. 3b), over 5,000 km from the nearest known population of *G. appalachianum*. This intriguing possibility may be crucial for resolving the origin of the circumboreal allotetraploid species G. dryopteris. The two hypothesized parents of this hybrid (G. appalachianum and G. disjunctum) are currently separated by about 2,400 km of unsuitable habitat (Figs. 1a, b). Because of the enormous distance separating the current ranges of the diploid parents, it has been impossible to identify a possible region of sympatry where they might have hybridized to form G. dryopteris. By projecting climate suitability of G. appalachianum into the past (Fig. 3c, d), we see a substantial increase of habitat suitability in the Pacific Northwest, closely matching the current range of *G. disjunctum* (Fig. 1a). Our preliminary analysis of habitat suitability of *G.* disjunctum into the past also coincides with this region (data not shown). Perhaps this area may have been the point of contact between the two diploids that formed tetraploid *G. dryopteris*?

HYPOTHESIZED PAST AND FUTURE DISTRIBUTIONS FOR G. APPALACHIANUM.—During the LGM (ca. 22,000 BP), eastern North America was dominated by massive ice sheets that extended as far south as West Virginia and Kentucky (Clark *et al.*, 2009), covering a significant part of the current range of *G. appalachianum* (Fig. 3a). Our model predicts the existence of glacial refugia for *G. appalachianum* in the central and southern Appalachian Mountains that may have extended west paralleling the southern edge of the Laurentide Ice Sheet as far as southeastern Missouri (Fig. 3c). This region is thought to have been dominated by cool mixed forests at the lower elevations with taiga and alpine regions at the higher elevations (Cogbill, White, and Wiser, 1997; Jackson *et al.*, 2000). This is in line with the current affinity of *G.*

appalachianum for cooler temperatures, north-facing slopes, and cold air seepage zones. Along the Pacific coast from Washington State to Alaska, our LGM model predicts substantial habitat suitability for *G. appalachianum* through the ice-free corridor extending from the U.S./Canadian border to Beringia (Fig. 3d). It is important to note, however, that our study did not take into account past sea level models, which could open up some additional potential habitat along the coast of northwest North America from Washington State to Beringia. This distribution is largely congruent with the current range of *G. disjunctum*, suggesting a possible time frame for the hybridogenesis of *G. dryopteris*. However, to explore this possibility would require a separate full analysis that includes estimating past distributions for both *G. disjunctum* and *G. dryopteris*.

There is no doubt that global temperatures will continue to rise between now and 2070; the only question is how much (Pachauri et al., 2014). Under the "best case" model for predicted climate change (RCP 2.6), most of the appropriate habitat of *G. appalachianum* moves from the central Appalachian Mountains to the Atlantic coast of New England (Fig. 3e). Much of the current range becomes unsuitable or suboptimal, and all the potential habitat for it in western North America disappears. The buffering effects of microclimate refugia, which G. appalachianum currently relies on at many sites, may not be sufficient in preventing habitat loss in the face of global climate change. Although many ferns are thought to have greater vagility than seed plants because they disperse by means of tiny spores (Wolf, Schneider, and Ranker, 2002), the prevailing winds and the distances involved make successful colonization tenuous. Under the "worst case" 2070 scenario (RCP 8.5), suitable habitats for *G. appalachianum* move even farther north and east (Fig. 3f), incrementally reducing the probability of successful migration. Without a meaningful reduction in global carbon emissions, the long-term prognosis for G. appalachianum is bleak, as it is for other narrowly endemic, climatically constrained species.

CONCLUSIONS

The current range of *G. appalachianum* is defined by a narrow band of cool, moderate temperatures and abundant precipitation in the central Appalachian Mountains. Annual temperature range, temperature maximums, and minimum precipitation are modeled to be the most important variables for predicting habitat suitability. Both the "best case" model for projected climate change (RCP 2.6) and the "worst case" 2070 scenario (RCP 8.5) predict that human-caused climate change will dramatically impact these variables. *Gymnocarpium appalachianum* is one of many north temperate species that will be pushed to the limits of its environmental tolerance (Broennimann *et al.*, 2006; Dullinger *et al.*, 2012), with few options other than migrating to higher elevations and higher latitudes (Feeley *et al.*, 2013; Kelly and Goulden, 2008). For *G. appalachianum*, which is already largely confined to the higher peaks of the central Appalachians, the opportunity for localized movement to higher

elevations is negligible. To avoid extinction, the species will need to undergo long distance migration to New England. However, it seems unlikely that *G. appalachianum* will be able to transition in 50 years through one of the most urbanized and disturbed regions of North America and reach new suitable habitats. If climate change is left unchecked and *G. appalachianum* is unable to move rapidly northward, the long-term outlook for this species is grim.

Author contributions

KMP and MDW conceived of the project, NMH oversaw all data analyses, and KMP and NMH led manuscript production. JVA and VC were Duke undergraduate student participants who assisted NMH in data collection and analyses. All authors participated in scientific discussions and read the final manuscript.

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APPENDIX A. SUPPLEMENTARY DATA

Supplementary data to this article can be found online at: https://docs. google.com/spreadsheets/d/1_ItqYK3UNF8ivGjubjdHxovkLMnlMzyn/edit? usp=sharing&ouid=101727712945149346428&rtpof=true&sd=true

SUPPLEMENTARY MATERIAL

SUPP. FIG. 1. Graphs displaying the effect on model performance of different model features at regularization multiplier (RM) values from 0.5–6 as tested in the R package ENMeval (Kass *et al.*, 2021). Features included are linear (L), quadratic (Q), hinge (H), product (P), and threshold (T). The six feature combinations used were L, LQ, H, LHQ, LQHP, and LQHPT. The graphs display the average omission rate (a), average validation AUC (b), and delta AICc (c).