**Title:** Identification of goldenseal (*Hydrastis canadensis* L.) habitat and indicators in Pennsylvania, U.S.A: the influence of climate and site on *in situ* conservation of an edge of range plant species.

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**Authors contributions:** This study was conceived and designed by Eric Burkhart, Grady Zuiderveen, and Ezra Houston. Data collection was conducted by Grady Zuiderveen and Eric Burkhart. Data analysis was conducted by Ezra Houston, Xin Chen, and Grady Zuiderveen. The draft manuscript was written by Ezra Houston with guidance from Eric Burkhart and Xin Chen. All authors contributed to and reviewed the final version.

**Data Accessibility Statement:**

Code used in Maxent modeling, environmental predictor variables, coarse occurrence data, site and soil data, and floristic survey data are available through the link provided here and in Online Resource 5 of the Supporting Information: <https://datadryad.org/stash/share/0TXU6r9E0Zrv2nW_L31dHsKOfVnUoqh_IMfhpfU3MhY>. Goldenseal has a special designation of “vulnerable” under 17 Pa. Code § 45.15. Coordinates were obtained through a data use agreement with the Pennsylvania DCNR, and as such, exact coordinates may not be shared. Provided coordinates have been modified with a random value between -0.1 and 0.1 decimal degrees and rounded to the nearest 0.1 decimal degree.

**<H1> Abstract**

**<H2> Aim**

Goldenseal (Hydrastis canadensis L.) is a perennial herbaceous plant native to eastern North America. Commercial harvesting for the medicinal plant trade and habitat loss have led to international conservation concerns. This study aimed to gain an understanding of habitat predilections for the purpose of guiding *in situ* conservation efforts.

**<H2> Location**

This study was conducted in Pennsylvania, within natural range of the species in the northeastern U.S. The state’s variation in geology and biogeographic location an opportunity to examine the influences of edaphic, topographic, and climatic factors on goldenseal habitat suitability here.

**<H2> Methods**

GIS-based Maximum Entropy (Maxent) modeling using known occurrence points (n=51) was combined with field plot data (n=28) to identify potential factors governing goldenseal’s distribution in PA and identify vegetative indicators of supportive habitat.

**<H2> Results**

Bedrock type and winter temperature were the best predictors of habitat suitability. Suitable bedrock types were base-rich; a trait confirmed in the field by soil test results showing high calcium and pH levels. However, the influence of bedrock is complicated by overlapping land use legacy. Suitability increased with average winter temperature, peaking at 1.0°C toward upper end of winter temperatures in PA. Community analysis identified 159 woody and herbaceous associates, including indicators of the following supportive rich mesic forest types: “Tuliptree-Beech-Maple,” “Red Oak-Mixed hardwood,” and “Central Appalachian Rich Cove”.

**<H2> Main Conclusions**

Model and field results can be used in tandem to assess site suitability, which was found to be greatest within forestlands with slightly acidic to neutral loamy soils underlain by base-rich bedrock types on moist, lower slope positions. Vegetative “indicator” species of these rich-mesic forests including *Liriodendron tulipifera*, *Acer saccharum*, *Lindera benzoin*, *Arisaema triphyllum*, and *Botrypus virginianus* appeared to be useful field indicators of supportive habitat for *in situ* conservation efforts.

**Keywords**

Forest community types, Habitat suitability, *In situ* conservation, Indicator species, Maxent, Species distribution modeling

**<H1> Introduction**

Goldenseal (*Hydrastis canadensis* L., Hydrastidaceae/Ranunculaceae )is a slow-growing herbaceous perennial plant native to eastern North America. It is one of the most important wild harvested medicinal plants in the United States (U.S.)(American Herbal Products Association 2020; Kruger et al. 2020) but is listed as “vulnerable” on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species and is included in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) due to concerns of over-harvesting for commerce and decline in the wild (Oliver 2017; CITES 2024). Goldenseals native range spans from southern Ontario to Kansas, and as far south as Mississippi (Figure 1). Historically, it has been considered most common within its “core range” of Ohio, Indiana, Kentucky, and West Virginia (Lloyd and Lloyd 1884; Sinclair and Catling 2000; NatureServe 2024). The species is less common at the northern edge of its range where it is listed as “Critically Imperiled” (S1) in Vermont, Massachusetts, and Connecticut; and “Imperiled” (S2) in New York and Ontario, Canada (NatureServe 2024).

Goldenseal is most frequently reported from rich mesic hardwood forests (NatureServe 2024), but habitat conditions associated with goldenseal can be broad. Forest types in which it has been documented range from dry-mesic calcareous sites supporting a diverse mix of hardwoods, to cove forests in moist lowland sites (Mueller 2004), oak-hickory forests in the Midwest (Eichenberger and Parker 1976), and sugar maple-basswood forests in New York (Tait 2006). The broad habitat characteristics associated with goldenseal are notable because it is uncommon in parts of its range, and researchers have struggled to identify what factors influence its distribution (McGraw et al. 2003; Sanders 2004; Sanders and McGraw 2005).

Given the long-standing economic and cultural importance of goldenseal, it is probable that the current distribution is heavily influenced by humans (Lloyd and Lloyd 1884; Van Fleet 1914). Records of medicinal use and collection by European settlers date back to the 1700’s, and its medicinal role for the Cherokee, Catawba, and other Native American groups dates back further (Hobbs 1990). It is believed that goldenseal has declined across its native range due to ongoing exploitation by commercial harvesters and loss of forested habitat (Mulligan and Gorchov 2004; Sanders 2004; Predny and Chamberlain 2005; Sanders and McGraw 2005; Albrecht and McCarthy 2006; Oliver 2017; NatureServe 2024). Declines attributed to these combined influences were noted over a century ago (Lloyd and Lloyd 1884), and commercial harvest volumes in recent years remain high, ranging from 11,037 - 56447 lbs. per year between 2011 and 2017 (American Herbal Products Association, 2020). Additionally, forested habitats in the eastern U.S. increasingly face challenges associated with land-use conversion, fragmentation (Riitters and Coulston 2012), non-native insects, and diseases (Herms and McCullough 2014). These changes drive shifts in species composition from native to non-native plants (Harper et al. 2005), which are now pervasive across natural areas in the eastern U.S. and have been found to decrease growth and seed set in native perennial forest herbs (Miller and Gorchov 2004; Miller et al. 2021).

Pennsylvania (PA) is U.S. state within the northeastern range of goldenseal. Here, the species is designated “Apparently Secure” (S4/G3) (NatureServe 2024), with a special designation of “vulnerable” (17 Pa. Code § 45.15.). The species has been documented mostly in the southwestern and southeastern parts of the state, rarely in the southcentral Ridge-and-Valley Province, and is entirely absent from the northern third of the state. Many populations in PA are large and vigorous but are often separated by large distances. Given its seemingly broad habitat requirements, the reason for this distribution in Pennsylvania is poorly understood. Commercial collection of goldenseal has historically focused on “core range states” rather than PA, indicating that overexploitation may not be the primary driver of its low abundance in the state (Zuiderveen 2019). Instead, the legacy of land-use conversion and habitat fragmentation may play a role in limiting its distribution. Many early records of goldenseal were reported in the Piedmont region of southeastern PA (PNHP 2023), but this region contains some of the most fertile soils in the state and has largely been cleared for agriculture (Dewitz 2021). Goldenseal’s distribution is further complicated in PA because it is near the northern end of its range. While it occurs sporadically northwards, it does so mostly in the Hudson River valley and near Lake Ontario (Tait 2006), where winter temperatures are more moderate than in northern PA (Fick and Hijmans 2017). It may be the case that PA represents marginal habitat for goldenseal, and that its rarity in the state is due to cold winter temperatures, especially in northern and high elevation areas.

Although some anthropogenic impacts have negatively affected goldenseal (Koffler and Gorby 1957; Lloyd and Lloyd 1884), human involvement in conservation and husbandry practices have the potential to secure the species. One such practice, assisted migration, has been proposed for species in range edge locations or where habitat fragmentation limits dispersal ability. This strategy involves establishing plants outside of their existing range in anticipation of changing environmental conditions (Vitt et al. 2010). Existing goldenseal populations can also be positively impacted through *in situ* conservation efforts. It has been suggested that habitat optimization and population augmentation are required for goldenseal recovery, and altering habitat conditions through natural disturbance simulation has been shown to increase plant size, flowering, and fruit production (Sinclair and Catling 2004; Sinclair and Catling 2005). The agroforestry practice of forest farming is another strategy well suited to goldenseal conservation as it leverages the economic value of the species. Forest farming combines establishment of new patches with habitat optimization to increase yields; potentially accomplishing the same objectives as assisted migration and *in situ* conservation. Forest farming is of interest to landowners in the state (Strong and Jacobson 2006; McLain and Jones 2013) and goldenseal is already cultivated through this practice in PA (Zuiderveen 2019). Successful adoption of forest farming could sustainably meet consumer demand while providing economic livelihood opportunities to those living in forested landscapes (Chittum et al. 2019).

The ability to recognize supportive goldenseal habitat is an important step in these proactive conservation efforts. Habitat modeling through a combination of field and GIS-based approaches can build an understanding of a fundamental niche and guide site selection for establishing new patches. Specifically, identifying “indicator species” (i.e., nearest neighbors and associates) can inform on-the-ground assessments of suitability (Burkhart 2013), since forest vegetation is in part a result of the underlying climatic, topographic, and edaphic factors (Gilliam 2014). However, indicator species are often inadequate predictors of site quality when used alone (Turner and McGraw 2015). For this reason, other field-based data such as edaphic characteristics (pH, soil nutrients) and GIS-based habitat suitability modeling can provide broader guidance. GIS-based habitat suitability modeling can be used to narrow the breadth of potential sites, after which indicators can inform on-the-ground assessments and decision making (Ren et al. 2010).

Goldenseal presence data are limited by land ownership access limitations and lack of botanical surveys across the state; similarly, absence data is complicated by historical and contemporary influences that are difficult to account for. For example, the absence of goldenseal at a site could be the result of previous harvest activities or land use legacies (Bellemare et al. 2002) rather than habitat influences. For this reason, traditional presence/absence modeling is not well suited, and traditional stratified random sampling has limited application (McGraw et al. 2003). Utilizing a modeling approach that requires presence-only data is more suitable. One commonly used method, Maximum entropy (Maxent) (Phillips et al. 2006) outperforms other presence-only, as well as presence/absence modeling techniques such as GLM (Hirzel and Guisan 2002), GAM (Yee and Mitchell 1991), and BIOCLIM (Busby 1991), based on the area under the receiver operating characteristic curve’s (AUC) ability to differentiate between sites where a species is present and sites where it is absent (Elith et al. 2006). This high performance may stem from its ability to fit complex responses and select a relevant set of variables, making it effective when presence data is limited (Anderson et al. 2006; Elith et al. 2006; Hernandez et al. 2006; Wisz et al. 2008; Razgour et al. 2011; Yi et al. 2016).

This study combined Maxent modeling incorporating 51 occurrences with community analysis, soil samples, and topographic data collected in the field at 28 sites to provide an understanding of potential goldenseal habitat in the state, and more broadly the northern edge of range for this species. Given the conservation status of the species in this region, results may aid in population discovery and habitat conservation, and provide guidance for human interventions such as forest farming and assisted migration in northeastern North America. In undertaking this study, we asked the following questions:

1. What abiotic factors are associated with goldenseal occurrences throughout PA?
2. How do factors encountered in the field compare with those identified by the Maxent model?
3. What flora is associated with goldenseal occurrences, and which species might be useful for site selection?

**<H1> Materials and Methods**

**<H2> Study Area**

This study was conducted in PA, within the northeastern U.S. (39°43′-42°16′ N; 74°41′-80°31′ W). The transition from numerous historic and extant goldenseal occurrences in the southern part of the state to no known occurrences in the northern third of the state creates an opportunity to examine the influence of climate on goldenseal occurrence. Further, PA has a variety of physiographic provinces including the Allegheny Plateau, Ridge-and-Valley, and Piedmont (Shultz 1999), providing an opportunity to identify the influence of edaphic and topographic factors on habitat suitability. Finally, there has been more than three centuries of human influence in PA through logging, habitat conversion, and introduction of non-native “invasive” species (DeCoster 1995).

**<H2> GIS-based Methods**

**<***H3> Modeling Habitat Suitability*

Maxent version (3.3.3k) was used to fit the model through the ‘dismo’ package (Hijmans et al. 2017) in R Version 4.2.2 (R Core Team 2022). Maxent samples the landscape -defined by environmental covariates- with a set of occurrence points and a set of randomly produced background points. The resulting probability distributions are compared, outputting a final probability distribution based on the principle of maximum entropy (Elith et al. 2011). Specific to this study, a probability distribution for goldenseal habitat suitability was developed using a set of presence points mapped against 9880 background points randomly distributed across PA. These background points represent the default number of 10000 background points for Maxent with 115 points removed where one or more covariates had missing values due to water features and areas modified by human infrastructure. Predictive performance for Maxent has been shown to be similar across a range of background point levels (Hysen et al. 2022), but the default number of 10000 has been shown to maximize predictive performance for an area the size of PA in some cases (Phillips and Dudík 2008).

**<***H3> Occurrence Data Inclusion Criteria*

Occurrence data for the habitat suitability model included 51 presence points distributed across the known range of goldenseal in PA (Figure 1). Occurrence data was obtained from multiple sources, including field sampling sites (n=28), sites which were found opportunistically in the years following field sampling (n=6), and occurrence points obtained from the Pennsylvania Natural Heritage Program (PNHP) database (n=17). In 2023, the PNHP database included 237 goldenseal occurrences spanning from the 19th century to the present, representing all documented populations in the state. PNHP occurrences were chosen based on a set of selection criteria to ensure consistent data quality between PNHP occurrence data and sites which were visited in the field. First, 163 occurrences which had not been visited since 2012 or were not associated with a named observer were omitted as a proxy to eliminate sites which may have been misidentified or extirpated due to changes in land use or poaching. An additional 35 sites with a location uncertainty distance greater than 100 m were eliminated, ensuring that occurrence points were within or adjacent to raster cells containing the ‘true’ environment data values corresponding to the populations they represented. Lastly, to reduce the effects of spatial autocorrelation, 22 occurrences located within 2.5 km of one another or located outside the extent of environmental variable raster layers were eliminated. Field-visited sites and occurrence points with a lower location uncertainty distance were prioritized for retention during the spatial filtering process.

**<***H3> Environmental Predictor Variables*

The predictive environment was characterized using 49 environmental variables (Online Resource 1). These variables represent climate, soils, and topography, and have been used in the U.S. Forest Service Tree Atlas (Peters et al. 2020), DISTIB-II (Iverson et al. 2019), and SHIFT (Iverson et al. 2019) to model the distributions of 125 tree species in the eastern U.S. Climatic predictors representing annual trends, seasonality, and extremes of temperature and precipitation from 1970 - 2000 at 1 km resolution were obtained from WorldClim[[1]](#footnote-1) (Fick and Hijmans 2017). Edaphic features representing physical and chemical properties from the topsoil (0- 30 cm in depth) and bedrock geology were derived from the 10 m resolution Gridded Soil Survey Geographic[[2]](#footnote-2) (gSSURGO) dataset using the gSSURGO ArcToolbox in ESRI ArcMap™ 10.8 by aggregating soil characteristics for each 10 m pixel from the corresponding map unit key (MUKEY) (Soil Survey Staff 2014). Soil data was aggregated to a depth of 30 cm to maintain consistency in edaphic representation across soil types with a range in profile depths. The integrated moisture index was developed by Iverson et al. (1997) and other topographic variables including aspect (Beers et al. 1966), roughness (Riley et al. 1999), and topographic position indices (Weiss 2001; Jenness et al. 2013) were derived from a 1 m digital elevation model (DEM) obtained from the PA Department of Conservation and Natural Resources PAMAP program[[3]](#footnote-3) (DCNR 2006). Goldenseal populations often cover areas greater than 1 m or 10 m. To better link edaphic and topographic predictor variables to the range of conditions within the extent of goldenseal populations, variables were resampled to a 90 m resolution. Edaphic predictor variables were resampled by calculating averages over 3x3 10 m pixels using ESRI ArcMap™ 10.8. For topographic variables, the 1 m DEM was first resampled to 90 m resolution, and all topographic variables were calculated from the resulting DEM.

After preliminary analysis, the seven most influential variables were selected for the final model to reduce overfitting and aid in interpretability (Table 1). These variables were selected stepwise based on Pearson correlation coefficient, permutation importance, variable dependency, and biological interpretability (Online Resource 2). First, a Maxent model was fitted using all variables. Pearson correlation coefficients between all variables were computed using the ‘ENMTools’ package in R (Warren et al. 2021). Correlated variables were eliminated based on a threshold of 0.7 or greater (i.e., exhibiting high collinearity), retaining that with the higher permutation importance in the full model. All variables with a permutation importance of 0 were eliminated regardless of correlation. Finally, the variables whose marginal response curves showed dependency upon other variables (i.e., a change in response curve between full model and single variable model) were eliminated to aid in interpretation of biological significance.

**<***H3> Model and Variable Evaluation*

The resulting model was evaluated based on the area under the receiver operating characteristic curve (AUC). AUC is a popular model evaluation metric in the Maxent literature and is interpreted as the probability that a randomly chosen occurrence location is ranked higher than a randomly chosen background point (Merow et al. 2013). The AUC metric ranges from 0 to 1, with values above 0.5 for models with predictive ability better than random (Swets 1979) and with 1.0 for those with perfect predictive ability. AUC values within this range are interpreted along the following scale: excellent AUC > 0.90; good 0.80 > AUC < 0.90; fair 0.70 > AUC < 0.80; poor 0.60 > AUC < 0.70; fail 0.50 > AUC < 0.60 (Araujo et al. 2005). Uncertainty in the AUC metric was evaluated using k-fold cross validation with k=5 subsets. For each subset the model was trained with k-1 subsets and tested on the kth subset (Merow et al. 2013). In effect, the 51 occurrence points were randomly partitioned into 5 subsets, and the model was tested on each subset after using the other subsets to train the model. Assuming an unbiased sample of occurrence points, cross-validation is a useful metric for model performance because it enables comparison between training AUC and testing AUC with independent occurrence data (Araujo et al. 2005).

Variable importance was estimated using a jackknife test by excluding each variable in turn, fitting a model with the remaining variables, and subsequently fitting a model with each variable in isolation (Phillips 2005). Variable importance was then evaluated based on model performance when individual variables were excluded or used in isolation in comparison to the model fitted with the other six variables. The relationship between species presence and each of the seven variables was interpreted based on their response curves. These curves show how the logistic prediction (interpreted as relative habitat suitability on a scale of 0-1) changes across values of each variable.

**<H2> Field Methods**

**<***H3> Goldenseal Population Determination*

During 2015 and 2016, wild occurrences were solicited across PA from botanists, goldenseal diggers, forest landowners, and through examination of herbarium specimens. A focused effort was made to solicit new sites from regions of the state where goldenseal had never been recorded to determine for certain whether the species occurred in these regions but had been missed to date. This was done by sharing news and solicitations via media (including social media) and by having conversations with experienced root diggers and buyers familiar with the plant and the region.

At each study site, up to four sampling plots were established within goldenseal patches. Plots were placed subjectively to capture community edaphic and floristic variation at each site. Goldenseal is a clonal species, spreading through rhizome expansion to form discreet colonies separated by gaps (Sanders 2004; Christensen and Gorchov 2010). Plot spacing and number varied according to population spread and number of discrete patches, with the objective of documenting only vegetation nearest to and interspersed within each goldenseal colony. Populations varied in size from thousands of ramets spread over multiple hectares, to single colonies of approximately 100 ramets. All populations showed evidence of sexual reproduction.

A total of 58 plots were established at 28 field sampling sites for community analysis. Study sites were in the southern two thirds of the state within 19 counties, including two new counties in which goldenseal had not previously been recorded. Eleven sites were located on the Allegheny Plateau, five in the Ridge-and-Valley, and 12 in the Piedmont province (Figure 1).

<*H3*> *Field Site and Community Sampling*

At each site, topographic position, aspect, and a short description were recorded, and populations sizes and areal extents were estimated. Soil samples were collected from the upper 10 cm (A-horizon) in each plot after large coarse organic matter was removed. Samples were sent to the Penn State Agricultural Analytical Services Lab for soil chemistry testing. Results included cation exchange capacity (CEC), water pH, phosphorus, potassium, magnesium, and calcium by the Mehlich-3 (ICP) test. Soil samples were collected from only a subset of the sites (n=19, 65% of sites) due to costs.

Overstory dominant and co-dominant trees were recorded in each plot using the point-centered quarter method (PCQM); the nearest tree species from plot center in each quarter was recorded for a total of four trees per plot. For each tree, distance from plot center and diameter at breast-height (DBH) was recorded. An inventory of understory vegetation—shrubs, ferns, and herbaceous species—was conducted within a circular 0.01-hectare plot. Each plot was visited twice during spring and summer of 2016 and 2017 to capture seasonal changes in associated flora. Voucher specimens of goldenseal were collected from each field site and deposited at the Pennsylvania State University Herbarium (PAC), the Carnegie Museum of Natural History Herbarium (CM), and the Morris Arboretum of the University of Pennsylvania Herbarium (MOAR).

<*H3*> *Statistical Analysis of Field Data*

Descriptive statistics were generated for floristic and edaphic data from each plot. Indicator species analysis (ISA) (McCune et al. 2002) was used to determine differences in associated species based on physiographic province, soil calcium content, and pH. Thresholds for edaphic factors were based on guidelines to maintain a mixed-species woodlot as provided by the Pennsylvania State Soil Analytics Lab. Significance was determined using a Monte Carlo randomization procedure with 4,999 randomizations (McCune et al. 2002). All ISA analysis was performed using PC-ORD (McCune and Mefford 2011). Additionally, importance value percentages were calculated on dominant and co-dominant tree species based on relative frequency, relative density, and relative dominance (Curtis and McIntosh 1951).

<**H1> Results and Discussion**

**<H2> Maxent Model Performance and Variable Importance**

One climatic, four edaphic, and two topographic variables were used to fit the final model and project habitat suitability across PA (Table 1, Figure 2). The resulting model had a training AUC of 0.903 and replicate cross-validation runs had an average testing AUC of 0.873, with a standard deviation of 0.063 (Figure 3). This represents good predictive ability to differentiate between suitable and unsuitable habitat based on a recommended threshold of 0.80 > AUC < 0.90, (Araujo et al. 2005). The two most important predictor variables as measured by percent contribution and permutation importance were bedrock type and mean temperature of the coldest quarter (Table 1). Using the jackknife test, results identified bedrock type as the predictor variable that resulted in the greatest gain when isolated, and the greatest decrease in gain when removed (Figure 4), indicating that it contained the most unique information.

**<H2> Climatic Model Results**

Mean temperature of the coldest quarter (i.e., the average winter temperature) was the only climatic variable included in the final model. Suitability increased as average winter temperature increased, peaking at 1.0°C, which represents the upper end of average winter temperatures in PA. Suitability decreased with decreasing winter temperatures down to –5.4°C, near the lower limit of average winter temperatures in the state (Figure 5). PA is near the northern edge of goldenseal’s native range, with only a limited number of isolated populations further north. Many of these northern populations occur in the Great Lakes region and in the Hudson Valley, where the climate is more moderate than in northern PA. Goldenseal has been more commonly reported from southwestern PA, which is contiguous with the “core range” extending south through the Ohio river valley (Lloyd and Lloyd 1884; McGraw et al. 2003; Christensen and Gorchov 2010; NatureServe 2024). ). Climate data used in modeling represents a period ranging from 1970 – 2000. A warming climate in the decades since and the predicted increase in average winter temperatures over the next 50 years (Fan et al. 2015) make exact temperature requirements difficult to determine. It may be the case that goldenseal’s absence in northern PA represents a lag in expansion from previously unsuitable climate conditions due to dispersal or other limitations. A warming climate may be favorable for goldenseal, opening previously unsuitable sites to natural or assisted migration and increasing the viability of forest farming in northern PA and other areas northward. However, model results are only correlative, and no causal mechanism or specific temperature threshold for goldenseal has been established.

**<H2> Edaphic Model and Edaphic Sampling Results**

Bedrock type was the most important modeled predictor variable, with suitable types differing across the state according to physiographic province: Pennsylvanian and Permian formations on the Allegheny plateau, Devonian and Silurian limestone in the Ridge-and-Valley, and Jurassic diabase in the Piedmont. Soil pH and calcium levels were high on average (6.3 and 1778 ppm respectively), but macronutrients varied considerably, with standard deviations commonly half the value of the mean (Table 2). Soil texture also varied but was most commonly classified as loam (Table 2).

The Ridge-and-Valley province is characterized by a series of valleys underlain by limestone, dolomite, or shale, and ridges comprised of sandstone and quartzite (Shultz 1999). Goldenseal is not prevalent in the region, and only five occurrences were available for modeling. Four of these occurred on narrow bands of Devonian and Silurian limestone comprising the lower slopes below erosion resistant sandstone ridges (Berg et al. 1980). The suitability of limestone bedrock is consistent with pH and calcium levels found in soil testing results (Table 2). Although identified by the model as the only suitable bedrock type in the Ridge-and-Valley, it may be that this zone represents the margin of goldenseal’s original habitat in this region, having been extirpated from more fertile limestone and dolomite valley bottom sites through agricultural conversion (Fletcher 1951). Conversely, despite supporting intact forest habitat, the sandstone and quartzite ridges of the region were identified as less suitable. It is likely that the unsuitability of sandstone bedrock types in the Ridge-and-Valley is due to their acidic nature (Blumberg and Cunningham 1982).

The Piedmont region in southeastern PA has some of the most fertile soils in the state and historically supported many goldenseal populations (PNHP 2023). However, most of the forest in this region has been cleared for agriculture. The process of land conversion likely destroyed much of the goldenseal in the Piedmont, as has also been documented in Ohio (Koffler and Gorby 1957). The Gettysburg-Newark lowlands, which are made up of erosion resistant Jurassic diabase, are an exception. Diabase creates rocky outcroppings that prevent farming (Blumberg and Cunningham 1982), and areas underlain by this bedrock support rich, relatively intact forests in an otherwise highly fragmented agricultural landscape. Many of the extant goldenseal populations in this part of the state occur over Jurassic diabase due to this land use legacy. A similar trend has been observed in Virginia, where two goldenseal populations were reported growing on sites underlain by otherwise dissimilar bedrock types sharing the characteristic of being unsuitable for farming (Mueller 2004).

The influence of bedrock on goldenseal habitat in the southwestern part of the state appears to be tied less to land use legacy than in the Ridge-and-Valley or Piedmont, due to the widespread nature of Pennsylvanian and Permian bedrock in this region. Both Pennsylvanian and Permian bedrock are comprised of sequential layers of sandstone, shale, limestone, and coal, and tend to be eroded into steeply sloping hills (Berg et al. 1980). One feature which does stand out as unsuitable for goldenseal habitat is the Mississippian bedrock of the Laurel Highlands. This bedrock is partly composed of erosion resistant acidic sandstone and forms some of the highest mountains in the state. While the acidity of Mississippian bedrock may play a role in decreasing habitat suitability, lower winter temperatures at these high elevations are likely important as well.

Soil suborder was also found to influence habitat suitability. Aquents, soils of recent origin that are usually seasonally or permanently inundated, were the strongest predictors of suitable habitat. These findings are partially supported by previous reports indicating that goldenseal grows well in moist conditions, including wet, predominantly sandy or clay soils. However, contrary to model results, well drained mesic soils are considered optimal (Penskar et al. 2001; Upton 2001; Sinclair and Catling 2001). The high suitability of Aquents may be a misleading result of the 90m resolution of the soil layer capturing occurrences growing on lower slopes adjacent to floodplains, but soil moisture measurements were not collected, pointing to a need for more data.

Udults were also suitable, and as with bedrock results, their suitability may be a function of land-use legacy. Udults are lower in base saturation than other common mesic soil types such as Udalfs, often requiring soil amendments to be used as cropland. They support a high proportion of forested habitat in the state, having escaped land use conversion (Dewitz 2021; Soil Survey Staff 1999). Taken together, soil chemistry and model results indicate that extant populations are disproportionately represented on wet to mesic sites which have escaped land use conversion and are not highly acidic, but otherwise range broadly in fertility. Given the limitations of the NRCS soil data in representing specific soil macronutrient contents and the fact that soil fertility was only sampled at 28 of 51 occurrences used in modeling, more data may be needed to fully interpret these results.

Less influential edaphic variables included organic matter content and permeability rate, both of which relate to soil moisture (Randall and Anderson 2005). Suitability increased with increasing organic matter and decreased in soils with rapid permeability rates, pointing to wetter soils being more suitable (Figure 5). While soil organic matter was not measured in the field, model results are strongly supported by previous literature (Penskar et al. 2001; Upton 2001; Sinclair and Catling 2001; Tait 2006). Modeled suitability of soil permeability rates mostly coincides with textural classes measured in the field, which were predominantly loam. Loam soils have also been reported in previous literature (Penskar et al. 2001) suggesting that goldenseal prefers moderately permeable soils. However, the model also identified impermeable soils to be high in suitability, contradicting both field measurements and the literature (Sinclair and Catling 2001; Tait 2006). This response is potentially due to the coarse resolution of the permeability raster being unable to accurately portray a relationship between soil texture and goldenseal suitability.

**<H2> Topographic Model and Topographic Sampling Results**

The model identified two topographic variables which were influential to goldenseal habitat suitability. Elevation-relief ratio (ERR15), which serves as an indicator of landscape position, was the most influential topographic variable. Calculated as x - xmin/xmax- xmin using a 15-pixel moving window, ERR15 captures elevation relative to the surrounding topography. In the model, lower values of ERR15 (lower slope positions) predicted higher habitat suitability. Integrated Moisture Index (IMI) was also influential, predicting higher suitability at high moisture levels (Figure 5). This index incorporates both soil and topographic features including slope, aspect, cumulative flow of water downslope, landscape curvature, and soil water holding capacity (Iverson et al. 1997).

Along with edaphic results, the suitability curves for ERR15 and IMI point to goldenseals preference for moist conditions. Although populations sampled in the field occurred across a range of aspects and topographic conditions, most of the populations occupied moist environments in lower slope or bottomland positions (Online Resource 3), supporting model results. Goldenseal’s affinity for lower slope positions is well documented (Meyer and Parker 2003; Tait 2006), and increased soil moisture has been found to increase goldenseal seedling success and growth (Douglas et al. 2002; Albrecht and McCarthy 2006).

**<H2> Community Analysis Results**

A total of 159 species were documented in the study plots: 24 overstory trees; 20 vines, shrubs, and understory trees; 115 herbaceous plants. Of these species, 11% (n=17) were non-native (Online Resource 4). Many of these species have also been documented associating with goldenseal in Michigan (Penskar et al. 2001) and Virginia (Mueller 2004).

The most common trees were tulip-poplar (*Liriodendron tulipifera*) and sugar maple (*Acer saccharum*), occurring in 40% and 38% of plots respectively and having the highest importance value percentages among associated tree species (Table 3, 4). The most common shrub was spicebush (*Lindera benzoin*), which occurred in 83% of the plots (Table 5). The most common herbaceous species was Jack-in-the-pulpit (*Arisaema triphyllum*), which occurred in 79% of the plots. Rattlesnake fern (*Botrypus virginianus*) and marginal wood fern (*Dryopteris marginalis*) were the most common ferns, occurring in 55% of plots.Of the 39 herbs and ferns that were present in more than 20% of plots, 13 differed according to physiographic province, three to calcium levels, and eight to pH (Table 6).

Forest community types where goldenseal was found included “Tuliptree-Beech-Maple,” “Red Oak-Mixed Hardwood,” and “Central Appalachian Rich Cove” (NatureServe 2022; Zimmerman and Hnatkovich 2022; Zimmerman and Fike 2022). Community types were consistent with descriptions of goldenseal habitat in Virginia (Mueller 2004), which tended toward “Central Appalachian Rich Cove”, but somewhat different from New York (Tait 2006), which tended toward “Sugar maple-Basswood.” These forest communities differ by region but are all characterized by high species richness due to their occurrence on deep, mesic, low acidity soils (Fike 1999; Zimmerman and Fike 2022). The most common overstory species, tulip-poplar and sugar maple, are common in rich mesic forests, growing poorly on sites with dry, shallow soils (Burns et al. 1990; Rhoades and Block 2007). Top woody understory and herbaceous associates also indicated site characteristics identified by the model and field sampling; wood ferns are common in a variety of habitats, but spicebush, Jack-in-the-pulpit and rattlesnake fern grow best on nutrient rich mesic slopes and bottomlands (Weakley 2023).

Some associates indicated regional or edaphic site conditions. Indicator species analysis identified tulip-poplar and Jack-in-the-pulpit as indicators in the Piedmont and on sites with pH of 7 or greater. Sugar maple was not associated with a particular region in PA but was an indicator on sites with high calcium and pH between 6 and 7. Rattlesnake fern, which is also a common associate of American ginseng (Burkhart 2013), was an indicator on sites with pH 7 or greater and may serve as a more informative indicator of goldenseal suitability than marginal wood fern due to narrower habitat preferences.

Several non-native species were also present, including 13 taxa classified as moderately to highly invasive in Pennsylvania (Online Resource 4)(PA Department of Agriculture 2023). Of these species, at least one was found in 83% of field plots. The most prevalent non-native taxa were woody shrubs; Japanese barberry (*Berberis thungergii*) and multiflora rose (*Rosa multiflora*) both occurred in over 50% of plots (Table 5). Non-native herbaceous species were also common, with Japanese stilt grass (*Microstegium vimineum*) and garlic mustard (*Alliaria petiolata*) both occurring in over 40% of plots (Table 6). The prevalence of these species in association with goldenseal highlights the widespread shift in plant communities in the northeastern U.S (Miller et al. 2021). As forest composition transitions from native communities to non-native generalist species, the utility of current indicator species for site evaluation may be reduced. Furthermore, non-native species have the potential to negatively impact goldenseal and overall floral diversity (Merriam and Feil 2002; Hamelin et al. 2017) particularly in fragmented landscapes in the urbanized southeastern and southwestern portions of the state where goldenseal is most common (Katz et al. 2003; PNHP 2023). Habitat model results may be necessary to inform site selection efforts where indicator species have been lost, but this analysis provides a potential baseline for restoration of common associates alongside goldenseal itself.

**<H2) Conclusions**

This study suggests that the most important abiotic variables affecting goldenseal habitat suitability are bedrock type and winter temperature, but that bedrock may serve have served as a proxy for land use legacy in the model. Soil suborder, organic matter, integrated moisture index, and permeability affected suitability to a lesser extent. The importance of bedrock type, slope position, and integrated moisture index were confirmed in the field, but other variables identified by the model were not sampled, preventing comparison. Several associates were identified as site indicators, including tulip-poplar and sugar maple in the overstory, and Jack-in-the-pulpit, and rattlesnake fern in the understory. Non-native shrubs were common in the understory and pose a potential risk to wild goldenseal populations by competitive exclusion and habitat modification, particularly in proximity to urban areas in the southeast and southwest of the state.

*In situ* conservation has a role to play in maintaining habitat integrity in the face of non-native exotics, while other techniques such as forest farming and assisted migration can be used to increase the number of populations on suitable sites. Model and field results can be used in tandem to guide site selection for both forest farming and assisted migration. Modeled suitability can first narrow down the range of potential sites, namely, forestlands underlain by base-rich bedrock types on moist, lower slope positions in the southern half of the state. These sites can then be evaluated in the field based on the presence of indicator species such as tulip-poplar, sugar maple, spicebush, Jack-in-the-pulpit, and rattlesnake fern. Finally, soil testing can be used to confirm suitability, which is favored in loamy soils with slightly acidic to neutral pH.

The influences of land use legacy and climate on goldenseal habitat in PA require further investigation. Planting studies on reverted agricultural sites could be used to determine whether their absence from these forest stands is due to a lack of dispersal or a phase shift impeding recolonization, while models incorporating land-use may better predict goldenseals distribution throughout the state. Likewise, planting studies to determine specific temperature tolerance and models incorporating projected future winter temperatures could assess the degree to which goldenseal habitat may expand in PA, and to identify potential areas for forest farming and assisted migration in northern parts of the state.

<**H1> References**

Albrecht MA, McCarthy BC (2006) Comparative Analysis of Goldenseal (*Hydrastis canadensis* L.) Population Re-growth Following Human Harvest: Implications for Conservation. Am. Midl. Nat. 156(2): 229–236. [doi: 10.1674/0003-0031(2006)156[229:CAOGHC]2.0.CO;2.](doi:%2010.1674/0003-0031(2006)156%5b229:CAOGHC%5d2.0.CO;2.)

American Herbal Products Association (2020) Tonnage Surveys of Select North American WildHarvested Plants, 20011–2017. Silver Spring (MD): American Herbal Products Association; 2020. <https://www.ahpa.org/article_content.asp?edition=2&section=4&article=33> Accessed 22 Janurary 2024

Araujo MB, Pearson RG, Thuiller W, Erhard M (2005) Validation of species–climate impact models under climate change. Global change biology, 11(9): 1504-1513. <https://doi.org/10.1111/j.1365-2486.2005.01000.x>

Beers T, Dress P, Wensel L (1966) Notes and observations: aspect transformation in site productivity research. J For 64(10):691–692

Bellemare J, Motzkin G, Foster DR (2002) Legacies of the agricultural past in the forested present: an assessment of historical land‐use effects on rich mesic forests. J. Biogeogr. 29(10‐11): 1401–1420. <https://doi.org/10.1046/j.1365-2699.2002.00762.x>

Blumberg B, Cunningham R (1982) An Introduction to Soils of Pennsylvania. College of Agricultural Sciences, The Pennsylvania State University.

BONAP, the Biota of North America Program (2014) *Hydrastis canadensis*. Bonap North American Plant Atlas. <https://bonap.net/MapGallery/County/Hydrastis%20canadensis.png>. Accessed 22 January 2024

Berg TM, Edmunds WE, Geyer AR, Glover AD, Hoskins DM, et al (1980) Geologic map of Pennsylvania 2nd ed. 1:250,000. Pennsylvania Geological Survey. [https://ngmdb.usgs.gov/Prodesc/proddesc\_34341.htm. Accessed 22 January 2024](https://ngmdb.usgs.gov/Prodesc/proddesc_34341.htm.%20Accessed%2022%20January%202024)

Burkhart E (2013) American ginseng (*Panax quinquefolius* L.) floristic associations in Pennsylvania: Guidance for identifying calcium rich forest farming sites. Agroforestry Systems 87(5). <http://dx.doi.org/10.1007/s10457-013-9627-8>

Burns RM, Honkala BH, Coordinators T (1990) Silvics of North America: Volume 2. Hardwoods. United States Department of Agriculture (USDA), Forest Service. Agriculture Handbook, 654, 1990.

Busby JR, (1991) BIOCLIM - a bioclimate analysis and prediction system. Plant Prot. Q. Aust. <https://caws.org.nz/PPQ567/PPQ%2006-1%20pp008-9%20Busby.pdf>. Accessed 22 January 2024

Chittum HK, Burkhart EP, Munsell JF, Kruger SD (2019) Investing in forests and communities: a pathway to sustainable supply of forest farmed herbs. Herbalgram 124 (Nov-Jan): 60-77. [http://cms.herbalgram.org/herbalgram/issue124/files/HG124-forestfarmingFEAT2.pdf. Accessed 25 January 2024](http://cms.herbalgram.org/herbalgram/issue124/files/HG124-forestfarmingFEAT2.pdf.%20Accessed%2025%20January%202024)

Christensen DL, Gorchov DL (2010) Population dynamics of goldenseal (*Hydrastis canadensis*) in the core of its historical range. Plant Ecology 210(2): 195–211. <https://doi.org/10.1007/s11258-010-9749-2>

CITES (2024) Appendices I, II, and III. [https://cites.org/eng/app/appendices.php. Accessed 22 January 2024](https://cites.org/eng/app/appendices.php.%20Accessed%2022%20January%202024)

Curtis J, McIntosh R (1951) An Upland Forest Continuum in the Prairie-Forest Border Region of Wisconsin. Ecology 32: 476-496. <https://doi.org/10.2307/1931725>

DeCoster LA (1995) The legacy of Penn's Woods: a history of the Pennsylvania Bureau of Forestry. Pennsylvania Historical and Museum Commission for Department of Conservation and Natural Resources, Bureau of Forestry.

Dewitz J (2021) National Land Cover Database (NLCD) 2019 Products [Data set]. U.S. Geological Survey. <https://doi.org/10.5066/P9KZCM54>

Douglas JA, Follett JM, Parmenter GA, Walle JE (2002) Effect of shade, fertiliser and irrigation on the production of goldenseal (*Hydrastis canadensis* L.). Proc Agronomy Soc NZ, 32, 27-34. [https://www.agronomysociety.org.nz/uploads/94803/files/2002\_4.\_Goldenseal\_production.pdf Accessed 25 January 2024](https://www.agronomysociety.org.nz/uploads/94803/files/2002_4._Goldenseal_production.pdf%20Accessed%2025%20January%202024)

Eichenberger MD, Parker GR (1976) Goldenseal (*Hydrastis canadensis* L.) distribution, phenology and biomass in an oak-hickory forest. <http://hdl.handle.net/1811/22395>

Elith J, Graham H, Anderson CP, et al (2006). Novel methods improve prediction of species’ distributions from occurrence data. Ecography, *29*(2), 129-151. <https://doi.org/10.1111/j.2006.0906-7590.04596.x>

Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ (2011) A statistical explanation of MaxEnt for ecologists. Diversity and distributions, 17(1), 43-57. <https://doi.org/10.1111/j.1472-4642.2010.00725.x>

Fan F, Bradley RS, Rawlins MA (2015) Climate change in the northeast United States: An analysis of the NARCCAP multimodel simulations. Journal of Geophysical Research: Atmospheres, 120(20), 10-569. <https://doi.org/10.1002/2015JD023073>

Fick SE, Hijmans RJ (2017) WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37 (12): 4302-4315. <https://doi.org/10.1002/joc.5086>

Fike J (1999) Terrestrial & palustrine plant communities of Pennsylvania. Bureau of Forestry, PA. Department of Conservation and Natural Resources.

Fletcher SW (1951) the Expansion of the Agricultural Frontier. Pennsylvania History: A Journal of Mid-Atlantic Studies, 18(2), 119-129. <https://www.jstor.org/stable/27769196>

Gilliam F (Ed) (2014) The herbaceous layer in forests of eastern North America. Oxford University Press.

Hamelin C, Gagnon D, Truax B (2017) Exotic invasive shrub glossy buckthorn reduces restoration potential for native forest herbs. Sustainability, 9(2), 249. <https://doi.org/10.3390/su9020249>

Harper KA, Macdonald SE, Burton PJ, et al (2005) Edge influence on forest structure and composition in fragmented landscapes. Conservation biology, 19(3), 768-782. <http://dx.doi.org/10.1111/j.1523-1739.2005.00045.x>

Herms DA, McCullough DG (2014) Emerald ash borer invasion of North America: history, biology, ecology, impacts, and management. Annual review of entomology, 59, 13-30. <https://doi.org/10.1146/annurev-ento-011613-162051>

Hernandez PA, Graham CH, Master LL, Albert DL (2006) The effect of sample size and species characteristics on performance of different species distribution modeling methods. Ecography 29(5): 773–785. <https://doi.org/10.1111/j.0906-7590.2006.04700.x>

Hirzel A, Guisan A (2002) Which is the optimal sampling strategy for habitat suitability modelling. Ecol. Model. 157(2–3): 331–341. <http://dx.doi.org/10.1016/S0304-3800(02)00203-X>

Hijmans RJ, Phillips S, Leathwick J, Elith J, Hijmans MR J (2017) Package ‘dismo’. Circles, 9(1), 1-68.

Hobbs C (1990) Goldenseal in early American medical botany. Pharmacy in history, 32(2), 79-82. <https://www.jstor.org/stable/41111308>

Hysen, L., Nayeri, D., Cushman, S., & Wan, H. Y. (2022). Background sampling for multi-scale ensemble habitat selection modeling: Does the number of points matter?. Ecological Informatics, 72, 101914. <https://doi.org/10.1016/j.ecoinf.2022.101914>

Iverson LR, Dale ME, Scott CT, Prasad A (1997) A GIS-derived integrated moisture index to predict forest composition and productivity of Ohio forests (USA). Landscape Ecology, 12, 331-348. <https://doi.org/10.1023/A:1007989813501>

Iverson LR, Peters MP, Prasad AM, Matthews SN (2019) Analysis of Climate Change Impacts on Tree Species of the Eastern US: Results of DISTRIB-II Modeling. Forests, 10(4), 302. <https://www.fs.usda.gov/treesearch/pubs/57857>

Iverson LR., Prasad AM, Peters MP, Matthews SN. (2019) Facilitating adaptive forest management under climate change: A spatially specific synthesis of 125 species for habitat changes and assisted migration over the eastern United States. Forests, 10(11), 989. <https://doi.org/10.3390/f10110989>

Jenness J, Majka D, Beier P (2013) Corridor Designer Evaluation Tools. <https://corridordesign.org>. Accessed 17 March 2024

Koffler A, Gorby M (1957) Contributions to the History of *Hydrastis canadensis* (Goldenseal) in Ohio. Ohio J. Sci. 57(3): 169–170. [https://kb.osu.edu/server/api/core/bitstreams/4936c3fd-a206-5cc2-b6fd-854655217d21/content Accessed 22 January 2024](https://kb.osu.edu/server/api/core/bitstreams/4936c3fd-a206-5cc2-b6fd-854655217d21/content%20Accessed%2022%20January%202024)

Kruger SD, Munsell JF, Chamberlain JL, Davis JM, Huish RD (2020) Describing medicinal non-timber forest product trade in eastern deciduous forests of the United States. Forests, 11(4), 435. <https://doi.org/10.3390/f11040435>

Lloyd JU, Lloyd CJ (1884) *Hydrastis canadensis*. J. U. & C. G. Lloyd.

McCune B, Grace JB, Urban DL (2002) Analysis of ecological communities. MjM software design Gleneden Beach, OR. <http://dx.doi.org/10.1016/S0022-0981(03)00091-1>

McCune B, Mefford MJ (2011) PC-ORD, Multivariate analysis of ecological data, Version 6. Gleneden Beach: MjM Software Design

McGraw JB, Sanders SM, der Voort MV (2003) Distribution and Abundance of *Hydrastis canadensis* L. (Ranunculaceae) and *Panax quinquefolius* L. (Araliaceae) in the Central Appalachian Region. J. Torrey Bot. Soc. 130(2): 62. <http://dx.doi.org/10.2307/3557530>

McLain RJ, Jones ET (2013) Characteristics of Non-Industrial Private Forest Owners Interested in Managing Their Land for Nontimber Forest Products. J. Ext. 51(5): 11. <http://dx.doi.org/10.34068/joe.51.05.07>

Merow C, Smith MJ, Silander JA J (2013) A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. Ecography, 36(10), 1058-1069. <https://doi.org/10.1111/j.1600-0587.2013.07872.x>

Merriam RW, Feil E (2002) The potential impact of an introduced shrub on native plant diversity and forest regeneration. Biological Invasions, 4, 369-373. <https://doi.org/10.1023/A:1023668101805>

Meyer SP, Parker GR (2003) Distribution and Habitat Classification of Goldenseal (*Hydrastis canadensis* L.) in the Hoosier National Forest, Indiana, USA. Natural Areas Journal, 23(4), 332-340.

Miller KE, Gorchov DL (2004) The invasive shrub, *Lonicera maackii*, reduces growth and fecundity of perennial forest herbs. Oecologia, 139, 359-375. <https://www.jstor.org/stable/40005554>

Miller KM, McGill BJ, Weed AS et al (2021) Long‐term trends indicate that invasive plants are pervasive and increasing in eastern national parks. Ecological Applications, 31(2), e02239. <https://doi.org/10.1002/eap.2239>

Mueller R (2004) *Hydrastis canadensis* L. - Two Appalachian Occurrences. [http://www.asecular.com/forests/hydrastis.htm. Accessed 22 January 2024](http://www.asecular.com/forests/hydrastis.htm.%20Accessed%2022%20January%202024).

Mulligan MR, Gorchov DL (2004) Population Loss of Goldenseal, *Hydrastis canadensis* L. (Ranunculaceae), in Ohio. J. Torrey Bot. Soc. 131(4): 305–310. <https://doi.org/10.2307/4126936>

NatureServe (2022) Central Appalachian Rich Cove Forest [web application]. NatureServe, Arlington, Virginia. Available [https://explorer.natureserve.org/](https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.687966/Acer_saccharum_-_Fraxinus_americana_-_Tilia_americana_-_Liriodendron_tulipifera_-_Actaea_racemosa_Forest). Accessed 22 January 2024

NatureServe (2024) NatureServe Explorer: An online encyclopedia of life [web application]. Compr. Rep. Species – Hydrastis canadensis. <https://explorer.natureserve.org/> Accessed 22 January 2024

Oliver L (2017) Hydrastis canadensis. IUCN Red List Threat. Species 2017 ET44340011A44340071. <https://dx.doi.org/10.2305/IUCN.UK.2017-2.RLTS.T44340011A44340071.en>

P Anderson R, Dudík M, Ferrier S et al (2006) Novel methods improve prediction of species' distributions from occurrence data. Ecography, 29(2), 129-151. <https://doi.org/10.1111/j.2006.0906-7590.04596.x>

Penskar MR, Choberka EG, Higman PJ (2001) Special plant abstract for *Hydrastis canadensis* (goldenseal). Michigan Natural Features Inventory: 1–3. <https://mnfi.anr.msu.edu/abstracts/botany/Hydrastis_canadensis.pdf> Accessed 22 January 2024

Pennsylvania Department of Conservation and Natural Resources (2001) Bedrock Geology of Pennsylvania. <https://www.dcnr.pa.gov/Geology/PublicationsAnddata/Pages/default.aspx>. Accessed 22 January 2024

Pennsylvania Department of Conservation and Natural Resources (2006) PAMAP Program 3.2 ft Digital Elevation Model of Pennsylvania. <https://www.pasda.psu.edu/uci/DataSummary.aspx?dataset=1247>. Accessed 22 January 2024

Pennsylvania Natural Heritage Program (2023) PA Department of Conservation and Natural Resources, Harrisburg, PA. Element Occurrence Digital Data Set.

Peters MP, Prasad AM, Matthews SN, Iverson LR (2020) Climate change tree atlas, Version 4. U.S. Forest Service, Northern Research Station and Northern Institute of Applied Climate Science, Delaware, OH. <https://www.nrs.fs.fed.us/atlas>. Accessed 17 March 2024

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecol. Model. 190(3–4): 231–259. <http://dx.doi.org/10.1016/j.ecolmodel.2005.03.026>

Phillips SJ, Dudík M (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31(2): 161–175. <https://doi.org/10.1111/j.0906-7590.2008.5203.x>

Predny ML, Chamberlain JL (2005) Goldenseal (*Hydrastis canadensis*): an annotated bibliography. <http://www.srs.fs.fed.us/pubs/21009>. Accessed 22 January 2024

Randall JS, Anderson S (2005) Soils Genesis and Geomorphology. Cambridge University Press, UK, ISBN, 521812011, 832.

Razgour O, Hanmer J, Jones G (2011) Using multi-scale modelling to predict habitat suitability for species of conservation concern: The grey long-eared bat as a case study. Biol. Conserv. 144(12): 2922–2930. <http://dx.doi.org/10.1016/j.biocon.2011.08.010>

R Core Team (2022) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, R version 4.2. 2.

Ren H, Zhang Q, Wang Z, Guo Q et al (2010) Conservation and possible reintroduction of an endangered plant based on an analysis of community ecology: a case study of *Primulina tabacum* Hance in China. Plant Species Biol. 25(1): 43–50. <http://dx.doi.org/10.1111/j.1442-1984.2009.00261.x>

Riley SJ, DeGloria SD, Elliot R (1999) Index that quantifies topographic heterogeneity. Intermt J Sci 5(1–4):23–27

Riitters KH, Coulston JW, Wickham JD (2012) Fragmentation of forest communities in the eastern United States. Forest Ecology and Management, 263, 85-93. <http://dx.doi.org/10.1016/j.foreco.2011.09.022>

Sanders S (2004.) Does Breeding System Contribute to Rarity of Goldenseal (*Hydrastis canadensis*)? Am. Midl. Nat. 152(1): 37–42. <https://www.jstor.org/stable/3566642>

Sanders S, McGraw JB (2005) *Hydrastis Canadensis* L. (Ranunculaceae) Distribution does not Reflect Response to Microclimate Gradients across a Mesophytic Forest Cove. Plant Ecol. 181(2): 279–288. <https://doi.org/10.1007/s11258-005-7222-4>

Shultz, CH (Ed) (1999) The geology of Pennsylvania. Harrisburg: Pennsylvania Geological Survey.

Sinclair A, Catling PM (2000) Status of Goldenseal, *Hydrastis canadensis* (Ranunculaceae), in Canada. The Canadian Field Naturalist 114(1): 111-120.

Sinclair A, Catling PM (2001) Cultivating the increasingly popular medicinal plant, goldenseal: Review and update. Am. J. Altern. Agric. 16(03): 131–140. <http://dx.doi.org/10.1017/S088918930000905X>

Sinclair A, Nantel P, Catling P (2005) Dynamics of threatened goldenseal populations and implications for recovery. Biological Conservation, 123(3), 355-360. <http://dx.doi.org/10.1016/j.biocon.2004.12.004>

Soil Survey Staff (1999) Soil Taxonomy: A Basic System of Soil Classification for Making and Interpreting Soil Surveys. 2nd ed. USDA NRCS. <https://www.nrcs.usda.gov/sites/default/files/2022-06/Soil%20Taxonomy.pdf> Accessed 23 January 2024

Soil Survey Staff (2014) Gridded Soil Survey Geographic (gSSURGO) Database for Pennsylvania. United States Department of Agriculture, Natural Resources Conservation Service. [https://gdg.sc.egov.usda.gov](https://gdg.sc.egov.usda.gov/) Accessed 23 January 2024

Strong N, Jacobson MG (2006) A case for consumer-driven extension programming: agroforestry adoption potential in Pennsylvania. Agrofor. Syst. 68(1): 43–52. <http://dx.doi.org/10.1007/s10457-006-0002-x>

Swets JA (1979) ROC analysis applied to the evaluation of medical imaging techniques. Investigative Radiology, 14, 109–121.

Tait CR (2006) Spatial distribution and habitat preference of goldenseal (*Hydrastis canadensis*) in New York. Dissertation, State University of New York College of Environmental Science and Forestry.

Turner JB, McGraw JB (2015) Can putative indicator species predict habitat quality for American ginseng? Ecol. Indic. 57: 110–117. <https://doi.org/10.1016/j.ecolind.2015.04.010>

Upton R, editor (2001) Goldenseal root: *Hydrastis canadensis*; standards of analysis, quality control, and therapeutics. American Herbal Pharmacopoeia, Santa Cruz, Calif.

Van Fleet W (1914) Farmers’ Bulletin 613: Goldenseal Under Cultivation. USDA Farmer’s Bulletin.

Vitt P, Havens K, Kramer AT, Sollenberger D, Yates E (2010) Assisted migration of plants: changes in latitudes, changes in attitudes. Biological conservation, 143(1), 18-27. <https://doi.org/10.1016/j.biocon.2009.08.015>

Warren DL, Matzke NJ, Cardillo M, et al (2021) ENMTools 1.0: An R package for comparative ecological biogeography. Ecography, 44(4), 504-511. <https://doi.org/10.1111/ecog.05485>

Weakley AS (2023) Flora of the southeastern United States: Pennsylvania. University of North Carolina Herbarium, North Carolina Botanical Garden. [Available as a download via link]

Weiss AD (2001) Topographic position and landforms analysis (Poster). San Diego, CA: ESRI User Conference. <https://www.jennessent.com/downloads/TPI-poster-TNC_18x22.pdf> Accessed 17 March 2024

Wisz MS, Hijmans RJ, Li J et al (2008) Effects of sample size on the performance of species distribution models. Divers. Distrib. 14(5): 763–773. <https://doi.org/10.1111/j.1472-4642.2008.00482.x>

Yee TW, Mitchell ND (1991) Generalized additive models in plant ecology. J. Veg. Sci. 2(5): 587–602. <https://doi.org/10.2307/3236170>

Yi Y, Cheng X, Yang ZF, Zhang SH (2016) Maxent modeling for predicting the potential distribution of endangered medicinal plant (*H. riparia* Lour) in Yunnan, China. Ecol. Eng. 92: 260–269. <http://dx.doi.org/10.1016/j.ecoleng.2016.04.010>

Zimmerman E (2022) Pennsylvania Natural Heritage Program. Sugar Maple – Mixed Hardwood Floodplain Forest Factsheet. Available from: <https://www.naturalheritage.state.pa.us/Community.aspx?=30017>. Accessed 22 January 2024

Zimmerman E, Fike J (2022) Pennsylvania Natural Heritage Program. Tuliptree – Beech – Maple Forest. Available from: <https://www.naturalheritage.state.pa.us/Community.aspx?=16065>. Accessed 22 January 2024

Zimmerman, E, Hnatkovich A (2022) Pennsylvania Natural Heritage Program. Red Oak - Mixed Hardwood Forest Factsheet. Available from: <https://www.naturalheritage.state.pa.us/Community.aspx?=16061>. Accessed 22 January 2024

Zuiderveen GH (2019) Goldenseal (*Hydrastis canadensis* L.) Phytochemistry, Trade, and Habitat: Implications for Conservation and Forest Based Cultivation. Dissertation, The Pennsylvania State University.

**Fig. 1** Goldensealsampling sites and occurrences added for GIS-based analysis across Pennsylvania

**Fig. 2** The Maxent model projected onto the environmental variables with occurrence points. Warmer colors show areas with a higher predicted suitability forgoldenseal

**Fig. 3** Habitat suitability model test AUC curve forgoldenseal. Specificity is established using predicted area, rather than true commission due to having presence presence-only data

**Fig. 4** Jackknife test for variable importance in predicting goldenseal habitat suitability. Regularized training gain represents how much better the model fits the presence data when compared with a normal distribution. The teal color represents model performance lost when a given variable was removed from the model, while blue represents model performance with that variable alone. Red represents model performance with all variables combined

**Fig. 5** Marginal Response curves for the 7 predictor variables included in the final goldensealhabitat suitability model. An explanation of each variable can be found in Table 1

**Table 1**. Descriptions, contributions, and sources of predictor variables used to develop the goldenseal habitat suitability model in Maxent

**Table 2.** Soils summary data from goldenseal populations in Pennsylvania

**Table 3.** Relative abundances and importance value percentages (IV %) for dominant or co-dominant overstory tree species associated with goldenseal in Pennsylvania

**Table 4.** Dominant and co-dominant trees associated with goldenseal in Pennsylvania along with indicator species analysis (ISA) results

**Table 5.** Shrubs and vines associated with goldenseal in Pennsylvania along with indicator species analysis (ISA) results

**Table 6.** Herbaceous species associated with goldenseal in Pennsylvania along with indicator species analysis (ISA) results

1. <https://www.worldclim.org/data/bioclim.html> [↑](#footnote-ref-1)
2. <https://www.nrcs.usda.gov/resources/data-and-reports/gridded-soil-survey-geographic-gssurgo-database> [↑](#footnote-ref-2)
3. <https://www.pasda.psu.edu/uci/DataSummary.aspx?dataset=1247> [↑](#footnote-ref-3)