

HABITAT MODELING OF A RARE ENDEMIC TRILLIUM SPECIES (*TRILLIUM SIMILE*
GLEASON): A COMPARISON OF THE METHODS MAXENT AND DOMAIN FOR
MODELING RARE SPECIES-RICH HABITAT

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partial fulfillment of the requirements for the degree of Master of Science in Biology

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PREFACE

This thesis is organized in a manuscript format consisting of three chapters. Chapter 1 is an introduction to this project's relevance in the southern Appalachians and contribution to species distribution modeling. Chapter 2 is a summary of scientific literature that explores rare plant species and the growing field of knowledge regarding species distribution modeling. Chapter 3 is the manuscript consisting of an introduction, methods, results, and discussion of the project. Literature Cited lists references from all three chapters.

ABSTRACT

HABITAT MODELING OF A RARE ENDEMIC TRILLIUM SPECIES (*TRILLIUM SIMILE* GLEASON): A COMPARISON OF THE METHODS MAXENT AND DOMAIN FOR MODELING RARE SPECIES-RICH HABITAT

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Many species habitat and distribution models are available that use field habitat observations to identify environmental predictor variables and quantify species-environment relationships. The relative effectiveness in terms of ease of use and accurately predicting habitat is not known for many of the models. The purpose of this study was to compare Maxent (a machine learning probability model) to DOMAIN (a simple GIS statistical profile model) in terms of their habitat prediction. Both models were used to predict habitat for the rare *Trillium simile*, an endemic species of the southern Appalachian Mountains found in the very rich cove environments that also provide critical habitat for other similarly sensitive species. Habitat was characterized by measuring biotic and abiotic variables at 20 sites where the species was found scattered throughout National Forests (Pisgah, Nantahala, Cherokee, and Sumter) in North Carolina and South Carolina, and the Great Smoky Mountains National Park in Tennessee. Digital environmental and climatic data for the known locations were matched to the abiotic and biotic variables measured in the field to create the models. Maxent performed with an AUC of 0.839; a DOMAIN AUC was not available because output was not automatic, and there was insufficient guidance on how to calculate the AUC. Highly suitable, suitable, and unsuitable habitat were identified for *T. simile* using both Maxent and DOMAIN. Model validation was performed by

visiting a total of 12 highly suitable sites predicted by each model, where the original variables were collected for comparison against known occurrence sites. Model predicted data were compared to the known *T. simile* site data using statistical analyses and quantitative assessment. Maxent and DOMAIN models were compared using a method agreement analysis. Univariate ANOVA results, descriptive statistics, and percentages of sites withheld during model testing showed that both models successfully predicted highly suitable habitat for *T. simile* consistent with the characteristics of the known occurrence locations, although predictions were slightly different. Method agreement analysis resulted in a Cohen's kappa of substantial agreement ($\kappa=0.674$) between the methods Maxent and DOMAIN. Specific project objectives coupled with the complexity of understanding and evaluating model performance makes choosing a "best-fit" model a challenge for modeling rare, endemic plant species. Both models were successful at predicting suitable habitat for *T. simile*, and although Maxent proved to work well on a small-scale, DOMAIN was much simpler to use and is thus the recommended method. Additional experience using both models under different project circumstances and informed opinion will further assist modelers in deciding whether to use a complex model like Maxent or a more simple, less flexible model like DOMAIN when modeling habitat distribution for rare plants like *T. simile*.

CHAPTER 1: INTRODUCTION

Rare plant species possess distinct functional traits that significantly contribute to important ecological functions, such as productivity, organic matter degradation, bioerosion, and bioturbation, and their extirpation may alter biogeochemical and dynamic ecosystem processes (Mouillot et al. 2013). Unfortunately, rare species ecosystem functions and the species themselves are vulnerable to extinction as recent trends show a decline in biodiversity and loss of rare species (Mouillot et al. 2013). In the United States over 744 plant species are listed as either threatened or endangered (Farnsworth 2014). The southern Appalachian Mountains of western North Carolina and eastern Tennessee are home to some of the most species-diverse forests, making their conservation and protection a highly desirable goal (Irwin & Andrew 2000). Furthermore, the occurrence of rare species in the herbaceous layer, some of which are categorized as threatened or endangered, contributes to forest ecosystem biodiversity. Because of their specificity of habitat and resources, rare herbaceous plants are useful as indicators of biodiversity (Gilliam 2007).

One rare plant species in the southern Appalachians is sweet white trillium (*Trillium simile* Gleason), which is found in very rich cove sites. These particular cove sites are considered “richer” due to a very high diversity of flora and abundance of endemic species (Loucks et al. 2017). *T. simile* is classified as imperiled in North Carolina and Georgia and critically imperiled in South Carolina, and is endemic to a narrow ecological range in the southern Appalachian Mountains (Pistrang 2016). Most of the extant populations are found in National Forest lands of the three southeastern states North Carolina, South Carolina, and Georgia, as well as the Tennessee side of the Great Smoky Mountains National Park (GRSM). Much more is known about more common trillium species such as *Trillium grandiflorum*

(Michx.) Salisb. compared to knowledge about the ecological importance, specific habitat requirements, and distribution of *T. simile*. There are no peer-reviewed journal articles on these aspects of *T. simile* whose habitat is currently under threat due to factors including land-use conversion, habitat fragmentation, and invasion by non-native shade tolerant weed species (Pistrang 2016).

One way to identify forest habitats where rare plant species are found is through the use of species habitat and distribution models (SDMs) that relate field habitat observations where species are found to environmental predictor variables to quantify species-environment relationships (Guisan & Thuiller 2005). The subsequent models predict potential suitable habitat where certain species are likely to occur based on where we know they already do occur, making the models useful for conservation projects. Maps of potential habitat suitability aid in management of rare, threatened, and endangered species by identifying sites for potential restoration, protection for species introduction, and can lead to discovery of new populations (Hernandez et al. 2006). There is a wide range of methods for modeling species habitat that can be used for rare or common species of plants and animals. Currently, there is growing interest in the use of presence-only data models, which are based on known observations of the species and use no reliable data on where the species is not found (Pearce & Boyce 2006). Presence-only data may be more reliable than presence-absence data because absence data are infrequently available, and even when available may be of questionable value in many situations (Phillips et al. 2006). A 2002 study showed that although presence-absence based methods were often more discriminate than presence-only techniques, they appeared to be less suitable for identifying areas with high conservation concern, which is often the case with rare species (Zaniewski et al. 2002). For instance, if the ultimate goal is to protect endangered or rare species, overestimating

areas of potentially elevated biodiversity might be more preferable than underestimating their existence, thus making presence-only methods quite useful (Zaniewski et al. 2002). A major conclusion of a comparison of several modeling methods also definitively showed that presence-only data are useful for modeling species' distributions (Elith et al. 2006).

In this project, two different types of species habitat modeling programs were used to gain an understanding of *T. simile* habitat requirements: Maximum entropy (Maxent) and DOMAIN. Both Maxent and DOMAIN use presence-only data to predict potential geographic locations of rare species (Philips et al. 2006). Maxent is a general purpose, machine learning probability model that searches for predicted occurrences based on the probability distribution that is most uniform using a set of variables. The DOMAIN model is a simple biophysical envelope that defines the degree of similarity among species-presence sites in terms of their environmental variables (Pearce & Boyce 2006). Strengths and weaknesses and comparisons of various models have been documented, but the relative effectiveness of Maxent versus DOMAIN has not been compared in the southern Appalachian Mountains for a rare herbaceous plant. Therefore, these two models were compared to determine which method might be more useful in terms of accuracy, ease of use, new population discoveries, and other factors in predicting habitat for *T. simile*. With any comparative modeling method exercise, results may differ in a new study area, at a different spatial scale, and with varying qualities of model data, including but not limited to the species of interest and environmental data variables (Hernandez et al. 2006).

The purpose of this research was to compare the advantages and disadvantages of two methods when applied to the same data set in one particular context, which is that of a rare herbaceous plant endemic to the southern Appalachian Mountains. In studies that involve any

kind of species or habitat distribution modeling, choosing the most appropriate method is facilitated by increased publication and access to such comparative papers. Thus, this project can contribute to the growing field of the study of SDM use and effectiveness. The specific objectives of this project were to: 1) characterize the species-rich, diverse habitat of *T. simile*; 2) create and validate habitat models using both Maxent and DOMAIN methods; and 3) evaluate the efficacy and accuracy of the two separate methods for modeling rare species habitat on a small scale for use in the Great Smoky Mountains National Park and the National Forests of the southern Appalachian Mountains.

CHAPTER 2: LITERATURE SUMMARY

Species of Interest: *Trillium simile* (Gleason)

Trillium simile is in the family Melanthiaceae and is commonly known as the “jeweled wakerobin” or “sweet white trillium”. It is also synonymous with *Trillium vaseyi* var. *simile* (Gleason) Barksdale. “Trille” comes from the Latin *trilix* meaning triple, which refers to the plant having parts in threes (Case 2002). *T. simile* is a spring-flowering (late March to early May) perennial herb that is native to the southern Appalachian Mountains in North Carolina, Tennessee, South Carolina, and Georgia. It is endemic to a small area within these four states in the vicinity of the Great Smoky Mountains and southern edge of the Blue Ridge Mountains. Globally, NatureServe lists this species with a G3 rank (21-100 population present) (Pistrang 2016). In North Carolina and Georgia it has a rank of S2 (6-20 populations present), meaning the species is imperiled, and in South Carolina it has a rank of S1 (5 or fewer occurrences) (Pistrang 2016). Because of its narrow range this species is especially vulnerable to land-use conversion and habitat fragmentation (e.g., second home developments), although forest management practices are a low-level threat to this species. These statements by NatureServe are amongst the few notes on threats to this species. There is also a notable lack of studies on the habitat requirements of *T. simile*, although habitat descriptions and publications of other more common *Trillium* species are available. Furthermore, published literature lacks information on the species’ demographics and population dynamics.

T. simile flowers have a sweet, apple-like odor, very unlike the scent of *Trillium erectum* L., which has a fetid odor like wet dog. The petals of *T. simile* are flat, creamy white, spreading and not recurved at the tip. The ovary is dark purple to black, pyramidal at anthesis, very

strongly 6-angled, and 7-12 mm wide. The inflorescence is showy and large, especially compared to other *Trillium* species. The fruits are baccate, purple to black, odorless, orbicular 1-1.5 cm diameter, and fleshy but not juicy (Case 2002). *T. simile* are often found on the edges of forests in very humus-rich soils in rich coves of mature forests over mafic or calcareous rock, often in or near seepages and close to rhododendron (*Rhododendron* L.) thickets (Pistrang 2016). *T. simile* hybridizes with *T. erectum*, giving it the additional common name “confusing trillium”, since identification can be difficult when it is not in its most robust condition and exhibiting the characteristics that distinguish it from *T. erectum* and *Trillium vaseyi* Harbison (Case 2002).

Species Distribution Models

The development of species distribution models (SDMs) is a rapidly developing field in which distributions of plants or wildlife at various spatial scales is applicable in ecology, conservation biology, natural resource management, and several others. Creation of these models is also referred to as environmental niche modeling, ecological niche modeling, predictive habitat distribution modeling, or climate envelope modeling. Regardless of the name, SDMs use computer algorithms to predict species distribution in geographical space. These empirical models relate field observations to environmental predictor variables, and most are based on quantifying species-environment relationships (Guisan & Thuiller 2005; Guisan & Zimmerman 2000). Most of the models do not identify where the species of interest is actually located, but rather identify habitat that is suitable or unsuitable for that particular species based on the input species data and environmental variables.

Most of the common modeling algorithms fall under three techniques: profile, regression-based, and machine learning. Profile techniques use presence-only data and involve simple

statistics that use such variables as environmental distance to known sites. These profile, bioclimatic envelope techniques include DOMAIN and BIOCLIM. Regression-based techniques require both presence and absence data and include generalized linear models (GLM), generalized additive models (GAM), and multivariate adaptive regression splines (MARS). The machine learning techniques include Maximum entropy (Maxent), artificial neural networks (ANN), genetic algorithm for rule set production (GARP), boosted regression trees (BRT), random forest (RF), and support vector machines (SVM). Some of these methods require either presence-only data (e.g., Maxent) or both presence and absence data (e.g., ANN). The result of numerous available modeling algorithms is a growing bank of literature on the suitability, reliability, and advantages and disadvantages of modeling techniques for a certain purpose.

SDMs all use species occurrence data, which come from locations where the species is known to exist and where data are obtained primarily from field sampling although they can also come from natural history collections such as herbariums or online databases. Species data can be presence-only, presence-absence, or abundance data, and various modeling algorithms have been developed for both. Each type of data has pros and cons depending on the aim of the study or project, and many have been shown to outperform others in certain situations. For instance, some studies have shown that the addition of absence data results in better model performance than those studies that just use presence-only data. In fact, some researchers recommend analysis of data in a strictly presence-absence framework whenever possible because fewer assumptions are required and better inferences can be made about occurrence probability (Elith et al. 2006; Yackulic et al. 2013). One study showed that broad-scale models like Maxent and Boosted Regression Tree techniques performed poorly in modeling vulnerable marine ecosystems because absence data was not used. The study suggested such broad-scale models

could improve performance and avoid over-estimation by incorporating true absence data (Anderson et al. 2016). These results suggest using caution when applying and interpreting broad-scale, presence-only models. Also, presence data is not always readily available or reliable because of large, unknown biases due to unsystematic collection schemes, and unlike absence data, occurrence data for most species that come from herbarium collections or that are accessible online have been recorded with an unknown method and intent of collection (Elith et al. 2006; Fithian et al. 2014). Conversely, a 2002 study showed that although presence-absence based methods were more discriminate than presence-only techniques, they appeared to be less suitable to identify areas with high conservation concern (Zaniewski et al. 2002). As a result, presence-only techniques might be more preferable when the species of concern is rare, endangered, or has high conservation priority. Presence-only data has proven useful for habitat modeling, an important finding given the improved accessibility of occurrence records and ever-improving high-resolution environmental data.

Choosing appropriate environmental variables for creating SDMs significantly improves model performance when predictors known to be ecologically relevant to the species of interest are used (Elith & Leathwick 2009). All digital environmental data must be manipulated using a geographical information system (GIS), such as ArcGIS, to prepare them for use by the chosen model (Guisan & Thuiller 2005; Guisan & Zimmermann 2000; Hernandez et al. 2006).

Variables that describe the abiotic environment related to topography (e.g., elevation, slope, aspect), climate, (e.g., precipitation, temperature), land cover, land use, and soil type are amongst the most common digital data variables used because they have been used to help explain vegetation patterns around the world (Guisan & Zimmermann 2000). Topographic data are obtained from the United States Geological Survey (USGS) National Elevation Dataset (NED)

(<http://ned.usgs.gov>; Hernandez et al. 2006; Pearson et al. 2006; Williams et al. 2009). Climate data are typically obtained from WorldClim (<http://www.worldclim.org>) or the National Oceanic and Atmospheric Administration (NOAA) (<http://www.noaa.gov>; Pearson et al. 2006). Even remotely sensed data are used in some modeling programs, although not extensively; the data are typically obtained from USGS Landsat (<http://landsat.usgs.gov>) and provide data from satellite imagery (Williams et al. 2009).

Evaluation of SDMs often focuses on predictive performance of the models and includes statistics such as area under receiver operating characteristic (ROC) curve (AUC), correlation (COR), and Kappa that assess the agreement between presence record data and predictions. AUC measures a model's ability to discriminate between where a species is present and where it is absent, which helps indicate how useful a model is for prioritizing areas as suitable habitat for a particular species. AUC values range from 0 to 1, where 1 is perfect discrimination, 0.5 is discrimination no better than a random guess, and values less than 0.5 are considered failures indicating performance worse than random guessing. Other techniques such as true skill statistic (TSS) were also used. TSS is an alternative measure of model accuracy that works like Kappa but corrects for some of the drawbacks (such as inherent dependence on prevalence) that critics have identified of Kappa while still keeping the advantages (Allouche et al. 2006). Field validation as a method of assessing model performance was nearly nonexistent in published research, despite the fact that ground observation would provide supporting evidence of a model's reliability in predicting suitable habitat. For instance, Maxent modeling was used to predict suitable habitat for a threatened and endangered tree species in New Caledonia and performed at a 91% success rate; however, field validation was notably absent from the study (Kumar & Stohlgren 2009).

Maxent and DOMAIN

The two SDMs of interest in this study were Maxent and DOMAIN. Maxent is a general purpose, machine learning probability model that searches for predicted occurrences based on the probability distribution that is most uniform using a set of variables. Maxent software uses categorical and continuous data and is available for use by both the public and professional organizations. This model is flexible in regard to the variables used and the form of their relationships to species presence (Williams et al. 2009). Studies have shown that Maxent consistently outperforms other traditional linear models (Elith et al. 2006; Phillips et al. 2005) and that it can somewhat compensate for incomplete or small species data sets (as is typical of rare species) and still perform near maximal accuracy level (Hernandez et al. 2006; Kumar & Stohlgren 2009). It should be noted that while Maxent has traditionally been used to model habitat distribution on a large, regional scale, its effectiveness is largely unknown on smaller, ecologically narrow scales (Elith et al. 2011; Phillips et al. 2006).

When using SDMs, creating a balance between complexity and simplicity could benefit model performance, suggesting that researchers should constrain the complexity of their models based on study objective, attributes of the data, and how these interact with the underlying biological processes (Merow et al. 2014). Avoiding very complex or overly simplistic techniques will prevent poorly fit models because ‘over-fit’, complex models run the risk of being superfluous and ascribing significant patterns to noise, whereas ‘under-fit’, simple models could misunderstand the factors that shape species distributions (Merow et al. 2014). Study of the performance of a simple model such as DOMAIN is an opportunity to assess whether a similar technique can still produce reliable habitat predictions. DOMAIN is a simple biophysical envelope that defines the degree of similarity among species-presence sites in terms of their

environmental variables (Pearce & Boyce 2006). The algorithm uses a computerized procedure that calculates a Gower similarity index for each pixel in the study area based upon how closely the environmental values at that point correlate with the environmental values at points of known occurrences. This method also uses fewer biophysical attributes than Maxent and has proven to be more suitable in applications where available records are limited, and thus might be easier to apply at smaller spatial scales (Carpenter et al. 1993; Guisan & Zimmerman 2000). The DOMAIN method uses categorical and continuous data, is available for use by both the public as well as private or government sectors, and its output can be easily integrated into a Geographic Information Systems (GIS). Furthermore, DOMAIN uses continuous similarity function, which gives it increased flexibility as a heuristic tool. In an original early study, DOMAIN, compared to some other alternative models, produced distribution patterns most consistent with species ecology (Carpenter et al. 1993).

Recent and ongoing advancements in GIS allow predictive habitat modeling to significantly improve land managers' abilities to do detailed analyses, inventories, and management practices (Vogiatzakis 2003). The availability and ease of environmental information in digital formats and improvements of GIS-based techniques offer an opportunity to improve and test species distributions mapping (Brotons et al. 2004), which make DOMAIN an attractive method for building SDMs. Also, integrating statistical algorithms and spatial analysis in a GIS makes it possible to rapidly review a species' distribution, even when information is poor or non-existent, and this same integration can be used to predict potential habitat from limited field data (Austin 1998). In general, progress in GIS-based modeling and remote sensing could be a key factor for obtaining more accurate information (e.g., forest structure, vegetation cover, land use) that best represents the habitat of interest (Guisan & Zimmerman 2000). A

number of factors, when collectively taken into consideration, make DOMAIN ideal for study compared to the well-known Maxent technique. These factors include utilization of this technique for rare species by state Heritage Programs in Colorado (Decker et al. 2006) and Wyoming (Beauvais et al. 2004; Beauvais & Smith, 2005); DOMAINs ability to use limited occurrence data (Elith et al., 2006); the availability of DOMAIN for public use; the ability of the method to use categorical data; and the ease by which output can be integrated into a GIS.

Literature that evaluated different models almost always included Maxent, whereas discussion of DOMAIN was more likely to be discussed only if there was a wide range of models being evaluated. BIOCLIM, the other bioclimatic envelope model, was discussed more frequently in detail than DOMAIN. Furthermore, there has traditionally been a lack of comparative studies in which two or more methods have been applied to the exact same dataset. Usually the models are intrinsically evaluated for their performance of various data sets (i.e., multiple species and/or models). Thus, as the number of published comparative papers that show advantages and disadvantages increases, it is more likely that future studies will have the literature to support the choosing of the most appropriate models.

Comparative Model Performance

There are conflicting reports regarding which models have better predictive success and the inconsistency is due to excess amounts of variability that can be introduced into the models. For instance, some studies showed that sample size (i.e., number of occurrences) had no effect on model performance (Elith et al. 2006), whereas other studies showed a negative influence of small sample size (Pearce & Ferrier 2000; Stockwell & Peterson 2002). The difference could be due to the number of adequate localities available for modeling. In a comparative study of four

different models (Bioclim, DOMAIN, GARP, and Maxent) with sample sizes ranging from five to 25 occurrences, method performance was highest for Maxent, although DOMAIN compensated reasonably well and was still a reasonable method for modeling rare species. Useful models have been created with sample sizes as small as five to ten, but increasing sample size had a positive effect on model performance (Hernandez et al. 2006). In addition, decreasing sample size has been shown to negatively affect model accuracy and increase variability across species and between models. However, some algorithms were much less sensitive to sample size, including Maxent, which had amongst the best predictive power across a number of sample sizes. Also, relative to other algorithms, DOMAIN and a genetic algorithm (OM-GARP) had intermediate performance at the largest sample size and among the best performance at the lower sample size (Wisiz et al. 2008). It has also been noted that while sample size is important, failing to consider population status and potential expansion of the species of interest could also negatively affect model performance (McFarland et al. 2015).

Published literature has shown a strong relationship between the type of species distributions being modeled and model performance. A 2015 study assessed performance of three modeling techniques to predict habitat distribution of plant species in the Qom Province rangelands of Iran: logistic regression (LR), Maxent, and artificial neural network (ANN). The species of interest was a flowering plant in the amaranth family with a limited ecological niche like *T. simile*. Results showed that no method was superior in performance and that all performed at good or very good levels, providing yet another indication of the complexities of what is considered an optimal approach to habitat distribution modeling (Sahragard & Chahouki 2015). The results further suggested that several factors must be considered and will have varying effects on model performance: purpose, statistical consideration, data types and

availability, ecological niche, and the range of the species of interest. With all these factors to consider, it is highly likely that the complexities of SDMs will grow as comparative research progresses. Furthermore, this same aforementioned 2015 study is also an example of the various ways in which models can be assessed. Whereas AUC is one method of assessing a model's discriminatory abilities used in several studies, this study introduced the use of true skill statistic (TSS). Comparing models based on different performance assessments serves to make comparative research even more complex.

The nature of the species of interest must also be considered, such as whether it is a specialist or generalist. This influences the spatial extent of the area being evaluated, which could also affect model performance (Guisan & Zimmerman 2000). Although geographic range size and ecological niche breadth may contribute to variation, it is also possible that pixel resolution is inappropriate and some species are simply not suited for climatic modeling (Hernandez et al. 2006). Using higher resolution for some variables could improve broad-scale models like Maxent (Anderson et al. 2016); however, a resolution with large pixels that results in overestimation of suitable habitat might have its advantages. As mentioned previously, studies showed that presence-only techniques appeared to be more suitable for identifying areas of high conservation concern although they were less discriminate than techniques that use absence data. If the ultimate goal is to protect rare or endangered species, overestimating areas of potentially elevated biodiversity might be more preferable than underestimating their existence, thus making presence-only methods quite useful (Zaniewski et al. 2002). Studies have also shown that change in data grain size did not severely affect predictions from SDMs (Guisan et al. 2007). Although the overall trend was towards degradation, the study also noted improvements, and a

change in grain size did not affect models across species types, techniques, or area of study (Guisan et al. 2007).

The debate regarding appropriate scale for SDMs is ongoing, and investigation into what is the best scale has been a complex endeavor that is not straightforward because of the wide array of methods, data types, and diverse research questions (Elith & Graham 2009; Aguirre-Gutiérrez et al. 2013). A recent study investigated the impact of various fine-scale spatial resolutions on modeling 11 rare and endangered species in dry forests of Hawaii. The results showed that for all species of interest, the SDMs had very high AUCs (all greater than or equal to 0.92), showing that regardless of the spatial scale, they were able to reliably discriminate between occupied habitat and background habitat. However, fine scale and coarse scale resolution of certain variables might affect the models and their ability to best capture the environment they are modeling because a finer scale might be necessary to capture the microclimates that are not represented in coarse scale data (Austin & Van Niel 2010; Rovzar et al. 2016). SDMs are thus useful at several spatial scales, but some variables such as temperature and variables that affect the light regime (e.g., aspect, slope, canopy cover) may benefit from finer resolution (Austin & Van Niel 2010).

CHAPTER 3: MANUSCRIPT

HABITAT MODELING OF A RARE ENDEMIC TRILLIUM SPECIES (*TRILLIUM SIMILE* GLEASON): A COMPARISON OF THE METHODS MAXENT AND DOMAIN FOR MODELING RARE SPECIES-RICH HABITAT

Introduction

Sweet white trillium (*Trillium simile* Gleason) is a rare plant species that occurs in the rich mesophytic coves of the southern Appalachian Mountains in counties of western North Carolina, eastern Tennessee, northeastern Georgia and northwestern South Carolina (Figure 1). Extant populations have been documented in the Pisgah, Nantahala, and Cherokee National Forests of NC, the Tennessee side of the Great Smoky Mountains National Park (GRSM), Sumter National Forest in SC, and Chattahoochee National Forest in GA. Globally, it is considered vulnerable with a G3 rank (21-100 known populations) and is endemic to a narrow ecological range in the southern Appalachian Mountains (Pistrang 2016). In North Carolina and Georgia it has a rank of S2 (6-20 known populations), meaning the species is imperiled, and is S1 or critically imperiled (5 occurrence or less) in South Carolina (Pistrang 2016). *T. simile* is a showy, large perennial herb found in very nutrient-, moisture-, and species-rich forested cove sites (Pistrang 2016). The richness of these cove forests refers to the highly fertile soils and presence of more than 25 species of canopy trees and numerous species in the understory, including very diverse herbaceous and shrub layers. These rich cove forests are described as the most diverse forest types in North America (Loucks et al. 2017). As a result, effective conservation and protection of *T. simile* in the National Forests and GRSM of the Southeast depends on identification of these forest habitat types. In addition, these very rich cove

environments where *T. simile* is found could also provide critical habitat for other similarly rare and sensitive species whose survival is threatened (Farnsworth 2014). Effective conservation of these forest types could result in protection of critical habitat for multiple communities of rare plants.

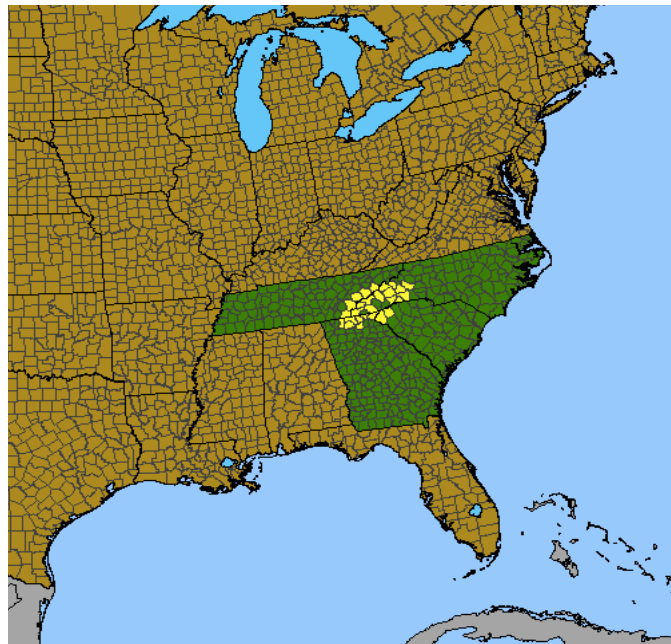


Figure 1. Study area in the southern Appalachian mountain counties of North Carolina, Tennessee, Georgia, and South Carolina where *T. simile* is present and rare (sourced from The Biota of North America Program).

Species habitat and distribution models (SDMs) can be used to identify potential suitable habitat for rare and endangered species, which can aid in location of new populations and identify areas for monitoring or reintroduction of a species. These models use known location occurrences and spatial environmental layers to infer ecological requirements of a species (Hernandez et al. 2006). The habitat modeling program Maximum entropy (Maxent) is one of

the most popular and commonly used habitat modeling programs with over 1,000 published applications since 2006 (Merow et al. 2013) and is just one of a very wide range of SDM options. Maxent and a lesser known and used model called DOMAIN were the two methods used in this project to better understand *T. simile* habitat requirements and to describe potential areas of high habitat suitability. The two SDMs were compared to evaluate their relative usefulness in predicting habitat for *T. simile* in the southern Appalachian Mountains.

Maxent is a general purpose, machine learning probability model that searches for predicted occurrences based on the probability distribution that is most uniform using a set of variables. This model is flexible in regard to the input environmental variables used and the form of their relationships to a species' presence (Williams et al. 2009). Other studies have shown that Maxent consistently outperforms other traditional linear models (Elith et al. 2006). However, while Maxent has been used to model habitat distribution on a large, regional scale, its effectiveness is unknown on smaller, ecologically narrow scales (Elith et al. 2011; Phillips et al. 2006) such as southeastern National Forests or the Tennessee portion of GRSM, which are study areas in this project. The ability to effectively identify suitable habitat in small-scale distributions is important to conservation efforts, protection of rarely-occurring plant species, and searches for additional, previously unknown populations (McCune 2016).

The DOMAIN model is a simple biophysical envelope that defines the degree of similarity among species-presence sites in terms of their environmental variables (Pearce & Boyce 2006). The algorithm uses a computerized procedure that calculates a Gower similarity index for each pixel in the study area based upon how closely the environmental values at that point correlate with the environmental values at points of known species occurrences. This method uses fewer biophysical attributes than Maxent and thus might be easier to apply at

smaller spatial scales (Carpenter et al. 1993). The DOMAIN algorithm has been used effectively by state Heritage Programs in Colorado (Decker et al. 2006) and Wyoming (Beauvais et al. 2004; Beauvais & Smith 2005). The model performs well with limited occurrence data (Elith et al. 2006) and is readily available for public use. DOMAIN can use categorical data and is easily integrated into a Geographic Information System (GIS).

Integration of SDMs into GIS improves the capability of performing detailed analyses, inventories, and management practices (Vogiatzakis 2003). The availability of environmental information in digital formats and progresses in GIS-based techniques offer an opportunity to improve and test species distributions mapping (Brotons et al. 2004), which makes DOMAIN an attractive method. Also, integrating statistical algorithms and spatial analysis in a GIS makes it possible to rapidly review species distribution, even when information is poor or non-existent and can be used to predict potential habitat from limited field data (Austin 1998). Furthermore, DOMAIN uses a continuous similarity function, which gives it increased flexibility as a heuristic tool, meaning a satisfactory solution is possible even when the optimal solution may not be possible. In an early study comparing DOMAIN to other alternative models, distribution patterns were consistent with species' ecology, and DOMAIN was deemed highly appropriate for survey design (Carpenter et al. 1993).

The approach of this study was to identify factors associated with suitable habitat for *T. simile* and to compare the predictive performance on a small scale of Maxent to the simple GIS model DOMAIN. The level of accuracy of the models was estimated given the small geographic range and limited environmental tolerances of rare plant species such as *T. simile* (Hernandez et al. 2006). The results of this project help identify which model might be best to use when modeling species distributions, which can be used to inform the U.S. Forest Service, National

Park Service, and other land managers in their conservation efforts to protect *T. simile* habitat as well as other potentially rare and endemic plant species in the southern Appalachian Mountains. The specific objectives of this project were to: 1) characterize the species-rich, diverse habitat of *T. simile*; 2) create and validate habitat models using both Maxent and DOMAIN methods; and 3) evaluate the efficacy and accuracy of the two separate methods for modeling rare species habitat on a small scale.

Methods

Target Species and Study Area

Location records of extant *Trillium simile* occurrences were obtained from the U.S. Forest Service and Great Smoky Mountains National Park (GRSM). Locations for the species occurrence on federal lands were provided in a GIS format by the NC Natural Heritage Program (NCNHP) botanist. The botanist for GRSM provided general locations *T. simile* has been observed. Occurrences in SC and GA were obtained from internet searches where the species has been observed by wildflower enthusiasts and photographers. Permission to work in the National Forests was granted by the USFS, and a research permit for work in GRSM was obtained.

In GRSM there are approximately six to eight extant occurrence locations, which are located on the Tennessee side of the park only. No occurrences have yet been documented on the North Carolina portion of the park. Maps were used to obtain coordinates or landmarks where the species is thought to occur in the GRSM. Based on the most recent NCNHP element occurrence report for *T. simile* (updated April 6, 2015), there were 45 total species occurrences documented. Of this total, 36 had a current status, meaning they were observed recently, and nine have a historical status (observed during years ranging from 1930 to 1974). Historical

status implies the species has not been found in recent surveys, recently enough to be confident of its occurrence, or that the occurrence is thought to be destroyed. NCNHP also assigned the most recent occurrences a degree of viability ranging from A (excellent) to D (poor), or E (extant, but viability not assessed). The GIS files also assigned accuracy to each species occurrence where accuracy is an estimate of how much of the mapped occurrence is believed to be occupied by the species of interest. The element occurrence report coupled with the GIS shapefiles was used to select locations of high viability (A and B viability) and accuracy. Twenty sites where *T. simile* is documented to have occurred were visited, occurrence was verified wherever possible, and the habitat was characterized. The remaining sites of documented known occurrences were saved for model validation since these sites were expected to be predicted by the models.

Initial Habitat Characterization

Occurrences were characterized by measuring environmental variables at six locations in GRSM and 14 in National Forests in NC, TN, and SC (see Figure 2). The site at each location was characterized using habitat variables that describe the physical and biological environment known to influence herbaceous species occurrence: canopy species, shrub and herbaceous layer, canopy cover, soils, topography, and distances to trails or roads and streams and bodies of water. At each location, a simple count and estimate method was used to assess the size of the population. A systematic walk and count of each individual yielded a population size estimate. In very large areas, a 2 m x 2 m quadrat was used to count individuals and extrapolate out to the entire area.

A *T. simile* individual was chosen at random around which a plot (radius = 5 m) was established. Within the plot, diameter at breast height (DBH) of each tree (≥ 5.1 cm DBH, ≥ 1.4 m tall) was measured, and trees were characterized by canopy class (midstory, overstory, superstory), and mortality class (alive or dead). Shade tolerance of each tree species was identified using the USDA Silvics of North America (Burns & Honkala 1990). Dead trees that could not be identified were recorded as snags. Saplings (single stem < 5.1 cm DBH, ≥ 1.4 m tall) and shrubs (multi-stemmed woody plants < 6 m tall) were identified. Herbaceous plants were identified and classified by degree of ground cover: low ($< 25\%$), moderate (25-49%), high (50-75%), very high ($> 75\%$). Ferns and vines were also accounted for in the same way as herbaceous plants.

Canopy cover was assessed using a camera with a fisheye lens that was placed at plot center approximately half a meter above the ground surface. From the photographs, canopy cover values were quantified using the freely available program ImageJ (<https://imagej.nih.gov/ij/download.html>). From each plot center, a clinometer was used to measure slope steepness (percent), aspect (degrees) was measured using a compass, and topographic position (toeslope, midslope, ridge) was visually assessed. A GPS unit was used to determine elevation (meters). Distances (in meters) to trails, roads or other disturbed areas (e.g., parking lots, picnic areas) were estimated using a measuring tape.

A soil sample was collected from near plot center using a 6-inch core to measure soil pH. The duff layer (leaves, needles, other not decomposed plant material) was cleared away and samples of the O horizon and the topmost mineral horizon (A horizon) were sampled for pH determination following the protocols of the EPA (Mason 1992). Soil samples were placed in a drying oven set at 65°F. They were reweighed until they reached a stable weight (constant dry

weight of soil), after which they were tested. The pH of 10 g of dried soil was measured using the procedure outlined by Hendershot et al. (2007). A ThermoScientific Orion Star A111 benchtop pH meter was used to measure the pH.

Information obtained from the habitat characterization measurements was used to create a profile of the habitat where *T. simile* occurs in the southern Appalachian Mountains. This information was also used to select the types of digital environmental variables to use in the modeling programs, and later in the project to assess the models' predictive performances.

Digital Environmental Variables for Model Development

The environmental variables chosen for the site characterization were considered potential predictors of *T. simile* habitat based on research of other herbaceous species found in southeastern rich cove forests. Choosing the most appropriate input variables is very challenging (Lecours et al. 2016), and this approach was chosen due to the absence of detailed published material on *T. simile* habitat. Studies on SDMs (Velez-Liendo et al. 2013; Lecours et al. 2016; Hijmans & Elith 2017) show that it is important to use variables that are relevant to the ecology of the species rather than what is merely easily accessible, and, ideally, a modeler needs complete understanding of the species prior to modeling (Rodríguez-Castañeda et al. 2012; Porfirio et al. 2014). Ideally, when building an SDM, the modeler should work with species experts to ensure that the input variables agree with the ecological importance of the species (Porfirio et al. 2014).

The measured habitat characteristics from the 20 extant plots were not directly used to develop both the Maxent and DOMAIN models because they were collected at a micro-habitat level of finer spatial resolution. Both models were developed for use at a regional scale of

coarser spatial resolution and thus required regional digital environmental data. A study using Maxent (Bradie & Leung 2016) assessed over 400 distinct environmental variables for nearly 1900 different species. Results showed that Maxent performed with high discriminatory ability due to variables related to temperature and precipitation, which were identified as amongst the most important input variables (Bradie & Leung 2016). Furthermore, terrain attributes such as aspect and slope are highly appropriate, especially in combination with climate and precipitation variables (Lecours et al. 2016), and because light regime is a very necessary component of plant SDMs (Austin & Van Niel 2010). A study by Williams et al. (2009) used four models, including Maxent, to model rare plants using environmental and climate data, and each model yielded reliable predictions of habitat for the rare plant species. In this same study, elevation, canopy cover, and precipitation were identified as the most important variables for strong prediction of occurrence for rare plants of interest (Williams et al. 2009).

In accordance with these findings, the ten digital environmental variables used in this study included USGS National Map National Elevation Data containing elevation, aspect, and slope at 30 m resolution; USDA Geospatial Data Gateway annual average maximum and minimum temperatures, annual average precipitation, and average monthly precipitation for May at highest resolution of 30-arc seconds (~1 km); National Land Cover Database 2011 USFS percent tree cover (canopy cover %) and land cover/land use at 30 m resolution; and soil type from NRCS Soil Data Access. Because rare plant habitats can vary a great deal over small scales, a 30 m x 30 m cell size was preferred and was the best available resolution.

Once data were collected from online sources, they were processed in ArcGIS to be the same format and extent (i.e., cell size, geographic bounds, and projection system). All data were converted to raster format and combined to make a raster mosaic with the same formatting

(Projected Coordinate System NAD 1983 UTM). A previously created mask, or bounding box, of the area of interest was used to clip the raster mosaic so that all layers had the same extent. The raster layers were converted to ASCII files. The editing processes of the digital data were necessary for the files to be able to function in both Maxent and DOMAIN modeling processes.

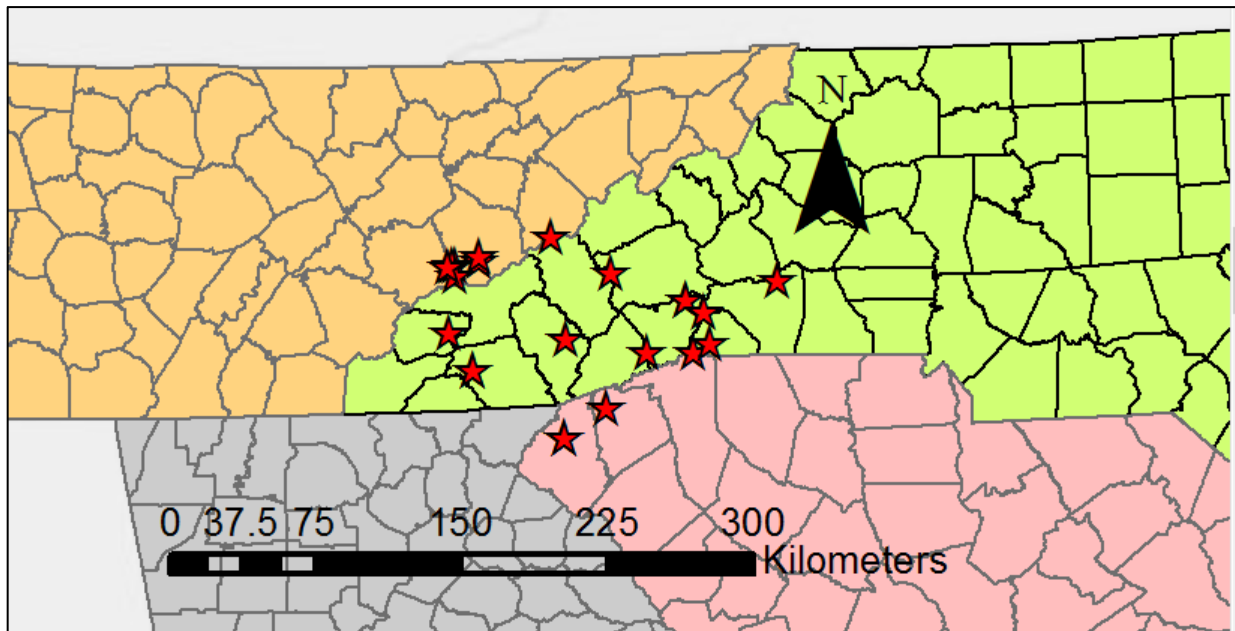


Figure 2. Initial habitat characterization performed at 20 locations in three states (NC, TN, SC) where *T. simile* is documented to have occurred.

DOMAIN Modeling Procedure

The same environmental variables were used in both Maxent and DOMAIN. The modeling procedure was performed in the computer program DIVA-GIS (<http://www.diva-gis.org/>), which was the only platform available to run the DOMAIN procedure. A CSV file of known location coordinates was uploaded. Of the 45 documented known occurrences, 75% (34) were used to build or train the model, and the remaining 25% (11) were used to test the model.

The Gower similarity approach as implemented in DOMAIN uses a metric based upon its proximity in statistical environmental space to the most similar occurrence location. This results in the assignment of a value to a potential site (pixel). The output was a grid where cell values reflect multivariate distance to the nearest known set of conditions where *T. simile* occurs. The highest values (those approaching 1) represented areas most similar to known occurrence conditions and low values were most unlike occurrence locations. The values are not probability estimates, which is what Maxent generates, but rather are interpreted as a measure of classification confidence. Environmental layers and known species location were input into DOMAIN to run the model. The output grid was converted to an ASCII grid. As with Maxent, the value thresholds were user-defined because the statistical surface does not give discrete boundaries for potential habitat. Thresholds were defined into three groups of habitat suitability confidence: unsuitable (<85%), suitable (85-97.4%) and highly suitable (97.5-100%). Value thresholds were chosen based on previous DOMAIN studies (Beauvais et al. 2004; Beauvais and Smith 2005; Decker et al. 2006), which suggested using certain distributions of predicted Gower similarity values.

Maxent Modeling Procedure

Maxent software version 3.3 (<https://www.cs.princeton.edu/~schapire/maxent/>) was freely available for use in this project. Maxent requires only species presence data (not absence) and the environmental variables must be continuous or categorical. Each variable was appropriately assigned as continuous or categorical in the ASCII files. A CSV file of known *T. simile* location occurrences was uploaded. The same numbers of documented occurrences used in DOMAIN were used to build and test the Maxent model: 75% (34) were used to build or train the model, and the remaining 25% (11) were used to test the model. The program generated an estimated probability of presence of the target species ranging from 0 to 1, where 0 is the lowest probability and 1 is the highest. Habitat suitability was categorized into three probability classes that were the same as those defined in DOMAIN: unsuitable (<85%), suitable (>85%) and highly suitable (approaching 100%, generally within 2.5% of the maximum).

Field Validation of Models

Both models were validated in the field by visiting locations predicted by the models and collecting habitat variables and presence data for *T. simile*. Three categories of predicted highly suitable habitat were used: those areas predicted by Maxent only, by DOMAIN only, and those predicted by both models (i.e., overlapping areas that both models predicted as highly suitable). Four sites predicted as highly suitable sites were selected from of each category for a total of 12 field validation sites. Geographical coordinates for the 12 field validation sites were chosen somewhat randomly, but kept near trails or roads for easy access to the site. The same environmental variables collected in the initial habitat characterization were collected at the sites predicted by the models using the same methods. Discovering new occurrences could indicate

success of one model, or both, in correctly predicting suitable habitat. The measured biotic and abiotic variables collected in the field validation sites of each category were compared to the known occurrence location characteristics and between models.

The broad range of suitable habitat as well as the somewhat coarse resolution of the environmental data used to run the models caused potential for an overestimation of amount and distribution of suitable habitat predicted by both models. However, the amount of highly suitable habitat was extremely narrow compared to the unsuitable habitat, and thus sampling unsuitable habitat was deemed unnecessary.

Statistical Analyses and Quantitative Assessment

The predictive performances of both models included statistics such as the area under the receiver operating characteristic (ROC) curve (AUC). AUC measures a model's ability to discriminate between where a species is present and where it is absent. AUC ranges from 0 to 1, where 1 is perfect discrimination, 0.5 is discrimination no better than a random guess, and values <0.5 indicate performance worse than random guessing. The AUC of Maxent was automatically generated as an output, but the AUC for DOMAIN was not. An AUC for the DOMAIN performance was not calculated due to insufficient guidance and output data in the DIVA-GIS program. The goal of the field validation data collection was to observe the models' effectiveness and accuracy at identifying *T. simile* habitat and species rich environments. Ideally, this would help identify which model is most useful on a small scale and has the best ability to predict habitat of *T. simile* and potentially other rare, endemic, rich cove species.

Descriptive statistics of habitat characteristics of known sites versus model predicted sites were calculated in R statistical software (R Core Team 2014). The mean and standard errors for

four abiotic variables (canopy cover, elevation, slope, and soil pH) collected in the 20 known sites and the 12 sites of model prediction were calculated. These descriptive statistics were used to compare variables collected at the sites where *T. simile* is known to occur compares to the means of the characteristics where Maxent and DOMAIN predicted highly suitable habitat.

Univariate ANOVAs were performed in R for the habitat characteristics slope, elevation, canopy cover, and soil pH to see if any of the variables in the sites predicted as highly suitable by Maxent, DOMAIN, and both models were dissimilar to the known *T. simile* sites. For each variable, all possible pair-wise t-tests were also conducted to determine if there were differences in habitat between the following: Maxent highly predicted sites versus known sites, DOMAIN highly predicted sites versus known sites, both models' predicted sites versus known sites, and each of the model predictions versus each other. Due to its circular distribution, a similar approach called a ratio likelihood test, or circular ANOVA, was used for aspect.

During both modeling procedures, 11 sites (25% of the total 45 known sites where *T. simile* is known to occur) were withheld from both models for testing. The percentage of these 11 sites that were correctly predicted as suitable or highly suitable by each model was calculated.

A method agreement analysis as described by Watson and Petrie (2010) was also performed in R. This analysis was used because the two methods being compared, Maxent and DOMAIN, were believed to produce similar results. The analysis calculates a Cohen's kappa value (κ) that describes the degree of agreement between two methods. The value falls within a range of -1 to 1, where -1 is total disagreement between the methods, 0 is no better than random, and 1 is perfect agreement between the methods. A numbered grid was laid over each of the habitat suitability prediction maps by Maxent and DOMAIN. A random number generator was used to randomly generate 50 values, which were identified in the grid overlays. Each value was

placed into one of nine categories in a contingency table. The counts were presented in a two-way contingency table of frequencies with the rows and columns indicating the categories of response for each method. This table was analyzed in R using the method agreement analysis to calculate a Cohen's kappa value.

Results

Habitat Characterization of *T. simile* Known Occurrences

Habitat characteristics (mainly topographical) of the 20 verified extant *T. simile* sites are shown in Table 1. Elevation ranged from 328 m to 1630 m, with an average of 699 m (± 89). Two sites were at much higher elevations than the rest (1609 m and 1630 m), which is not consistent with current descriptions of *T. simile* habitat. Most of the plots (85%) had a northern or northeastern aspect with an average aspect of about 84° and a canopy cover percentage greater than 80%. Percent slope was variable, with half of the sites having slopes greater than or equal to 50%. Soil pH was generally around 6 with more than half the plots having a soil pH greater than 6. The two plots that had the lowest pH levels (5.1 and 5.04) were found at the highest elevations (1609 m and 1630 m, respectively). The majority of the plots (70%) were classified as midslope with the remaining classified as toeslopes, and none of the plots occurred on a ridge.

Table 1. Topographical habitat characteristics of 20 *T. simile* known occurrence locations in NC, TN, and SC. All characteristics were measured for the field validation of both Maxent and DOMAIN models (n=20 for all characteristics except soil pH n=19).

Habitat Characteristic	Mean ± SE	Minimum	Maximum
Elevation (m)	699 ±89	328	1630
Slope (%)	49 ±5	5	85
Canopy cover (%)	83 ±1	71	88
Soil pH	6 ±0.12	5.04	6.78
Aspect (°)	83.6 ±6.8	4	350
Slope position	midslope	--	--

The count of individual *T. simile* stems in known locations revealed a wide range of individuals of a given population. The minimum count was two individuals in a population to over 1000 individuals in a population. The average was 133.5 individuals (SE = 57.1 individuals) in a population.

The forest composition of trees in the 20 extant sites is summarized in Table 2. The most frequently occurring tree was *Liriodendron tulipifera* L. (65% of plots), followed by *Tilia americana* L. (55% of plots), and *Aesculus flava* Aiton and *Betula lenta* L. (both in 40% of plots). *B. lenta* had the highest average tree density (406.4/ha), followed by *Asimina triloba* (L.) Dunal and *A. flava* (390.1 and 292.6/ha, respectively). *L. tulipifera* had the highest basal area (m²/ha) at 20.4%, followed by *B. lenta* and *T. americana* (16.8% and 15%, respectively). *T. americana* was the most frequently occurring sapling amongst the plots (50%), with *Fraxinus spp.* L. and *Carpinus caroliniana* Walter both occurring in 40% of the plots. *Fagus grandifolia* Ehrh. had the highest average sapling density (1170.4/ha), followed by *C. caroliniana* and *Fraxinus spp.* (747.7 and 715.2/ha, respectively).

The proportion of trees in the midstory, overstory and superstory by their shade tolerance (tolerant, intermediate, intolerant) is shown in Figure 3. In the midstory 86.3% of the tree species were shade tolerant, 8.2% were intermediate, and 5.5% were shade intolerant. In the overstory 33.3% of the tree species were shade tolerant, 49% were intermediate, and 17.6% were shade intolerant. The superstory had almost an even proportion of the three different shade tolerances: 34.6% shade tolerant, 30.8% intermediate, and 34.6% shade intolerant.

Shrub species occurred in 17 of the 20 extant *T. simile* sites and at low frequencies. Table 3 lists the 11 shrub species and their frequencies and densities across the 17 sites. *Viburnum cassinoides* L. was the most frequent (41.2% of 17 extant sites), but having a lower mean density (371.5 ± 16.7 clumps/ha) compared to the other shrub species. *Rhododendron maximum* L., and *Rubus spp.* L. were the next most frequent shrub species (35.3%). *Lindera benzoin* (L.) Blume also occurred at 35.3% frequency and had the highest average density (975.3 ± 72.2). *Leucothoe fontanesiana* (Steud.) Sleumer and *Hydrangea radiata* Walter had the highest densities (942.8 ± 138.9 and 715.2 ± 137.9 clumps/ha, respectively) although they occurred at lower average frequencies.

Table 2. Forest composition of trees (≥ 5.1 cm DBH, ≥ 1.4 m tall) and saplings surround 20 extant *T. simile* populations in NC, TN, and SC. Basal area (m^2/ha) includes only trees.

Species	Frequency (% of plots)		BA % of total	Average Density (#/ha)	
	Tree	Sapling		Tree	Sapling
<i>Liriodendron tulipifera</i> L.	65	25	20.4	185.8	208.1
<i>Tilia americana</i> L.	55	50	15.0	283.7	390.1
<i>Aesculus flava</i> Aiton	40	40	6.1	292.6	357.6
<i>Betula lenta</i> L.	40	20	16.8	406.4	227.6
<i>Fagus grandifolia</i> Ehrh.	25	20	7.7	234.1	1170.4
<i>Fraxinus</i> spp. L.	20	40	2.8	162.5	715.2
<i>Quercus rubra</i> L.	20	25	14.7	130.0	260.1
<i>Halesia tetraptera</i> Ellis	20	20	1.1	260.1	292.6
<i>Carya glabra</i> (Mill.) Sweet	15	20	1.7	130.0	227.6
<i>Acer pensylvanicum</i> L.	15	20	0.1	130.0	520.2
<i>Acer rubrum</i> L.	15	20	1.2	216.7	390.1
<i>Acer saccharum</i> Marshall	15	10	0.7	260.1	325.1
<i>Carpinus caroliniana</i> Walter	10	20	0.6	195.1	747.7
<i>Liquidambar styraciflua</i> L.	10	5	5.0	130.0	130.0
<i>Cornus florida</i> L.	10	0	0.3	195.1	0.0
<i>Tsuga canadensis</i> (L.) Carriere	5	10	0.7	195.1	390.1
<i>Amelanchier</i> spp. Medik.	5	5	0.1	130.0	130.0
<i>Asimina triloba</i> (L.) Dunal	5	5	0.3	390.1	520.2
<i>Betula alleghaniensis</i> Britton	5	0	0.2	130.0	0.0
<i>Cercis canadensis</i> L.	5	0	0.0	130.0	0.0
<i>Magnolia acuminata</i> (L.) L.	5	0	0.0	130.0	0.0
<i>Cornus alternifolia</i> L. f.	0	20	0.0	0.0	227.6
<i>Carya cordiformis</i> (Wangenh.) K. Koch	0	15	0.0	0.0	390.1
<i>Sambucus canadensis</i> L.	0	10	0.0	0.0	260.1
<i>Ulmus rubra</i> Muhl.	0	5	0.0	0.0	520.2
<i>Sassafras albidum</i> (Nutt.) Nees	0	5	0.0	0.0	260.1
<i>Ilex montana</i> Torr. & A. Gray ex A. Gray	0	5	0.0	0.0	390.1
<i>Nyssa sylvatica</i> Marshall	0	5	0.0	0.0	260.1
<i>Ilex opaca</i> Aiton	0	5	0.0	0.0	260.1
<i>Castanea dentata</i> (Marshall) Borkh.	0	5	0.0	0.0	130.0

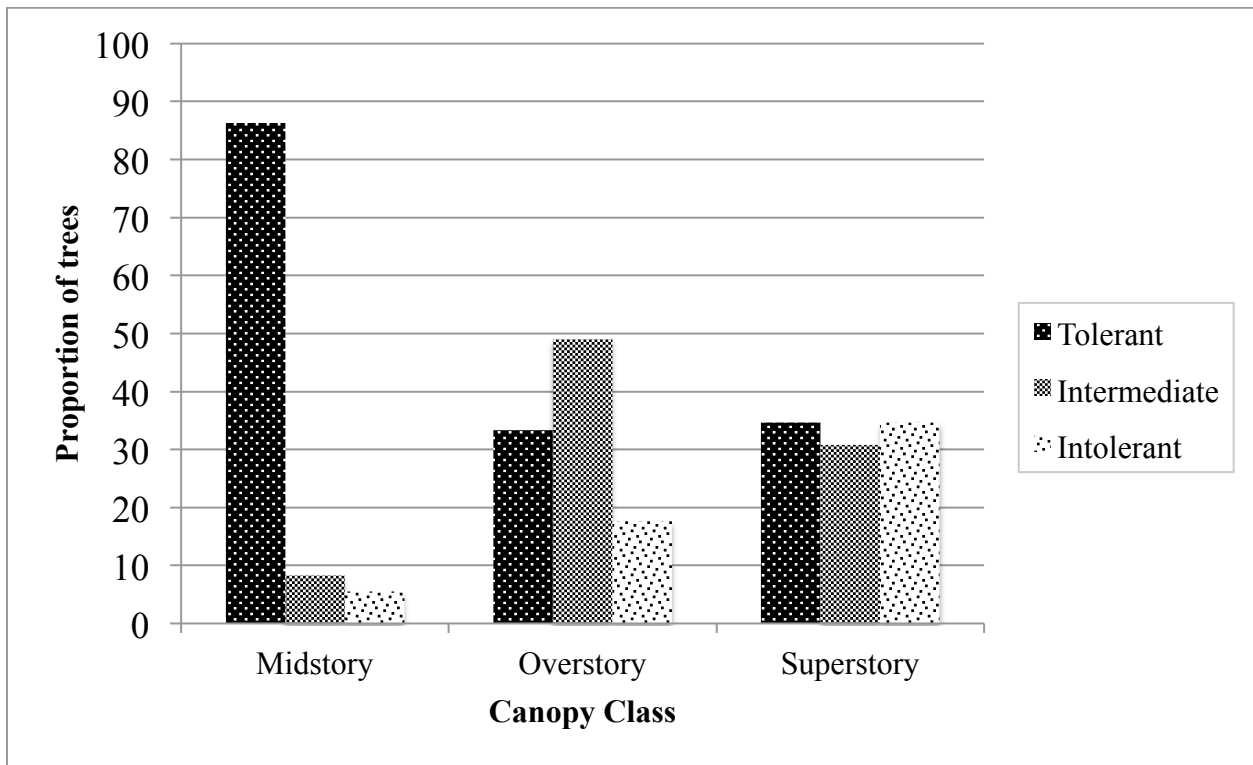


Figure 3. Proportion of trees in the midstory, overstory, and superstory by their shade tolerance across the 20 *T. simile* occurrences sites in NC, TN, and SC.

Table 3. Frequency and density of shrub species identified in 17 of the 20 sites of *T. simile* known occurrence in NC, TN, and SC.

Shrub Species	Frequency (% of plots)	Density Mean \pm SE (clumps/ha)
<i>Viburnum cassinoides</i> L.	41.2	371.5 \pm 16.7
<i>Lindera benzoin</i> (L.) Blume	35.3	975.3 \pm 72.2
<i>Rhododendron maximum</i> L.	35.3	628.5 \pm 25.3
<i>Rubus spp.</i> L.	35.3	671.9 \pm 160.7
<i>Euonymus americanus</i> L.	23.5	292.6 \pm 16.3
<i>Leucothoe fontanesiana</i> (Steud.) Sleumer	23.5	942.8 \pm 138.9
<i>Pyrularia pubera</i> Michx.	17.6	346.8 \pm 90.2
<i>Calycanthus floridus</i> L.	11.8	585.2 \pm 229.9
<i>Hydrangea arborescens</i> L.	11.8	260.1 \pm 92.0
<i>Hydrangea radiata</i> Walter	11.8	715.2 \pm 137.9
<i>Viburnum lantanoides</i> Michx.	5.9	260.1 \pm 0.0

A total of 51 herbaceous species were identified across the 20 extant sites where *T. simile* was verified as being present. The frequencies of these species (including ferns, vines, lycophytes, bryophytes, and grasses) are shown in Table 4. The three most common species across the 20 sites were *Polystichum acrostichoides* (Michx.) Schott (85% frequency), *Actaea racemosa* L. (75%), and *Polygonatum biflorum* (Walter) Elliott (70%). Other common herbaceous plants that occurred at more than half the sites included *Arisaema triphyllum* (L.) Schott (65%), *Tiarella cordifolia* L. (65%), *Veratrum parviflorum* Michx. (55%), and *Viola spp.* L. (55%). Most of the herbaceous species occurred at relatively low (<25% of macroplot) to moderate coverage (25-49%) in all plots where they occurred. Few species tended to occur

frequently at high (50-75%) to very high coverage (>75%); these species included *A. racemosa*, *Laportea canadensis* (L.) Weddell, *Viola spp.*, and *T. cordifolia*.

Nearly all occurrence locations were observed 30 m or less from a trail, service road, major road, or parking lot, and several site edges were within a few feet from a hiking trail. In all six locations in the GRSM, a trail or road was in the immediate vicinity. Also, in greater than 50% of the locations, a water source (seepages, ephemeral streams, creeks, rivers, and waterfalls) was observed within plots or in close proximity.

Table 4. Herbaceous species frequency identified in 20 sites of known occurrence of *T. simile* in NC, TN, and SC.

Herbaceous Species	Frequency (% of plots)
<i>Polystichum acrostichoides</i> (Michx.) Schott	85
<i>Actaea racemosa</i> L.	75
<i>Polygonatum biflorum</i> (Walter) Elliott	70
<i>Arisaema triphyllum</i> (L.) Schott, <i>Tiarella cordifolia</i> L.	65*
<i>Dryopteris campylotera</i> Clarkson	60
<i>Veratrum parviflorum</i> Michx., <i>Viola</i> spp. L.	55*
<i>Laportea canadensis</i> (L.) Weddell, <i>Parthenocissus quinquefolia</i> (L.) Planch., <i>Toxicodendron radicans</i> (L.) Kuntze	45*
<i>Adiantum pedatum</i> L., <i>Ageratina altissima</i> (L.) King & H. Rob., <i>Desmodium nudiflorum</i> (L.) DC., <i>Eurybia chlorolepis</i> (Burgess) Nesom, <i>Hepatica acutiloba</i> DC.	40*
<i>Caulophyllum thalictroides</i> (L.) Michx., <i>Goodyera pubescens</i> (Willd.) R. Br., <i>Prenanthes</i> spp. L., <i>Sanguinaria canadensis</i> L., <i>Maianthemum racemosum</i> (L.) Link	35*
<i>Athyrium asplenoides</i> (Michx.) A. A. Eaton, <i>Collinsonia canadensis</i> L., <i>Geranium maculatum</i> L., <i>Osmorhiza claytonii</i> (Michx.) C. B. Clarke	25*
<i>Impatiens pallida</i> Nutt., <i>Mitchella repens</i> L., <i>Podophyllum peltatum</i> L., <i>Thalictrum clavatum</i> DC., <i>Thelypteris noveboracensis</i> (L.) Nieuwl., <i>Trillium</i> spp. L.	20*
<i>Aristolochia macrophylla</i> Lam., <i>Discorea villosa</i> L., <i>Lysimachia quadrifolia</i> L., <i>Marchantia</i> spp. L., <i>Oclemena acuminata</i> (Michx.) Greene, <i>Polygonum virginianum</i> L., <i>Polypodium virginianum</i> L.	15*
<i>Actaea pachypoda</i> Elliot, <i>Medeola virginia</i> L., <i>Smilax glabra</i> Roxb.	10*
<i>Conopholis americana</i> (L.) Wallr., <i>Disporum lanuginosum</i> (Michx.) G. Nicholson, <i>Hexastylis arifolia</i> (Michx.) Small, <i>Huperzia lucidula</i> (Michx.) Trevis., <i>Hydrophyllum canadense</i> L., <i>Microstegium vimineum</i> (Trin.) A. Camus, <i>Panax quinquefolius</i> L., <i>Smilax rotundifolia</i> L., <i>Vitis rotundifolia</i> Michx., <i>Xanthoriza simplicissima</i> Marshall	5*

*Percentage applies to each herabaceous species in that group

Habitat Distribution Outputs of Maxent and DOMAIN

A side-by-side comparison of the two initial outputs from each of the models shows the similarities and differences in predicting habitat suitability using the two SDM methods (Figure 4). Areas of high suitability (in red) were very fine-scale and had to be magnified for ease of visibility. Figure 4 also depicts areas that were predicted as highly suitable habitat for *T. simile* by both models (circled in white), as well as areas predicted by each model that were not predicted by the opposing model (circled in black). The Maxent distribution output was integrated into ArcGIS and mapped the distribution of highly suitable, suitable, and unsuitable (divided into both unsuitable and highly unsuitable for ease of viewing) habitat throughout the project area (Figure 5a). The average AUC of Maxent was 0.839 (Figure 6). The final DOMAIN habitat distribution map also shows the highly suitable, suitable, and unsuitable habitat distribution (Figure 5b). It did not have to be integrated in ArcGIS since the model ran in its own GIS program DIVA-GIS. An AUC for the DOMAIN map was not an automatic output nor was there sufficient guidance on how to measure the AUC.

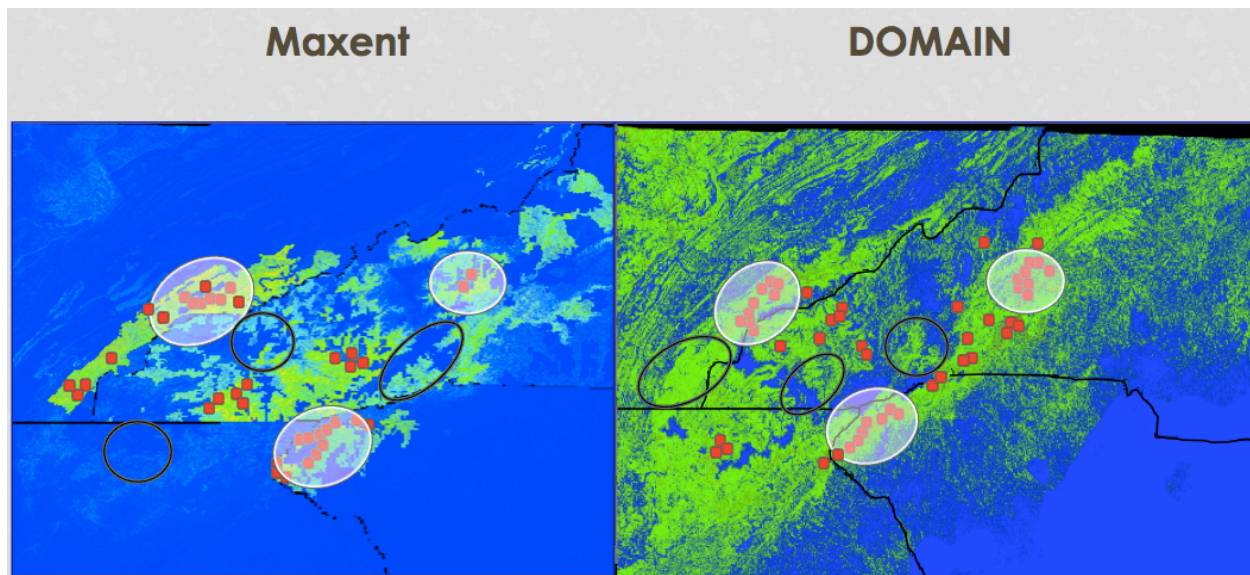


Figure 4. Side-by-side comparison of initial Maxent and DOMAIN model outputs for *T. simile* habitat suitability.

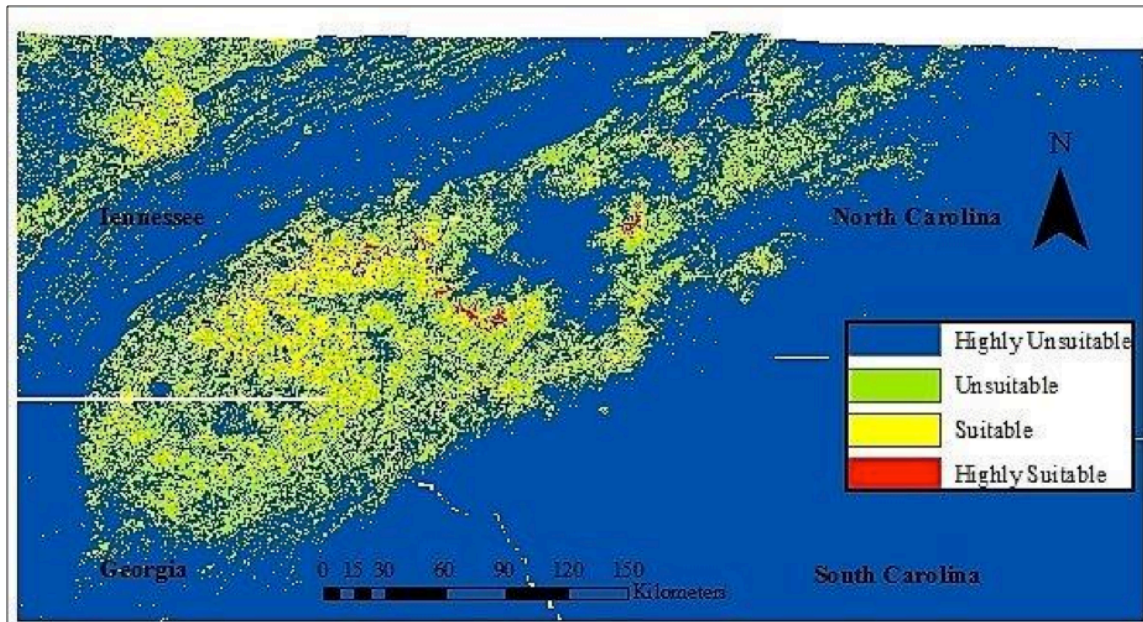


Figure 5a. Maxent predicted habitat for *Trillium simile* across the southern Appalachian mountain region of the southeastern United States, as displayed in ArcGIS.

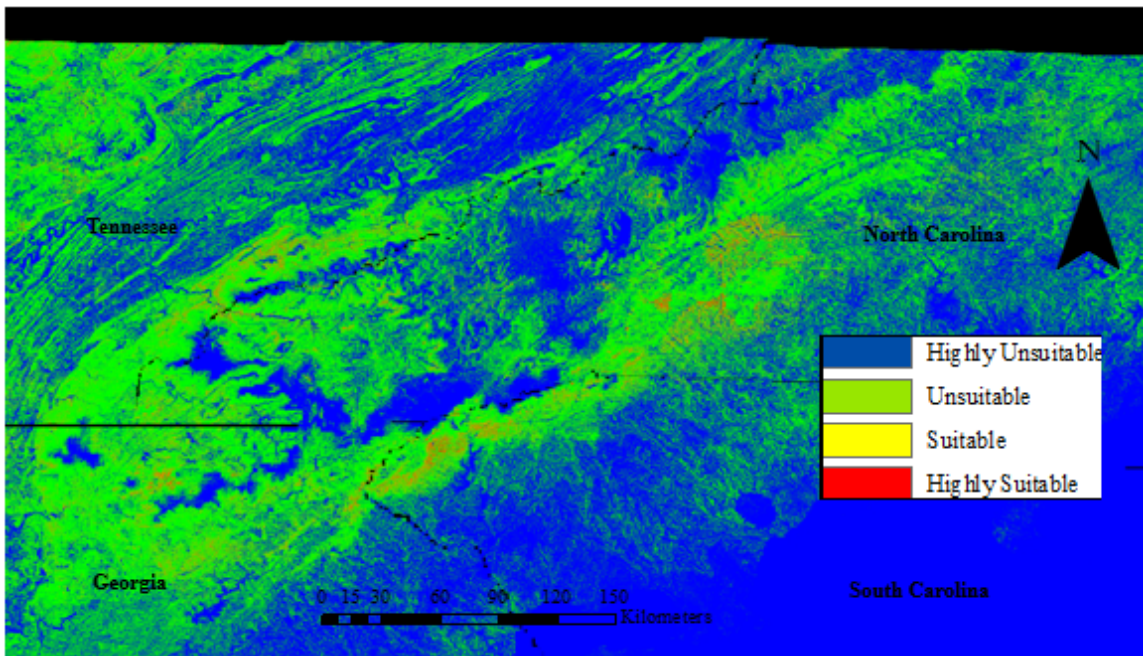


Figure 5b. DOMAIN predicted habitat for *Trillium simile* across the southern Appalachian mountain region of the southeastern United States, as displayed in DIVA-GIS.

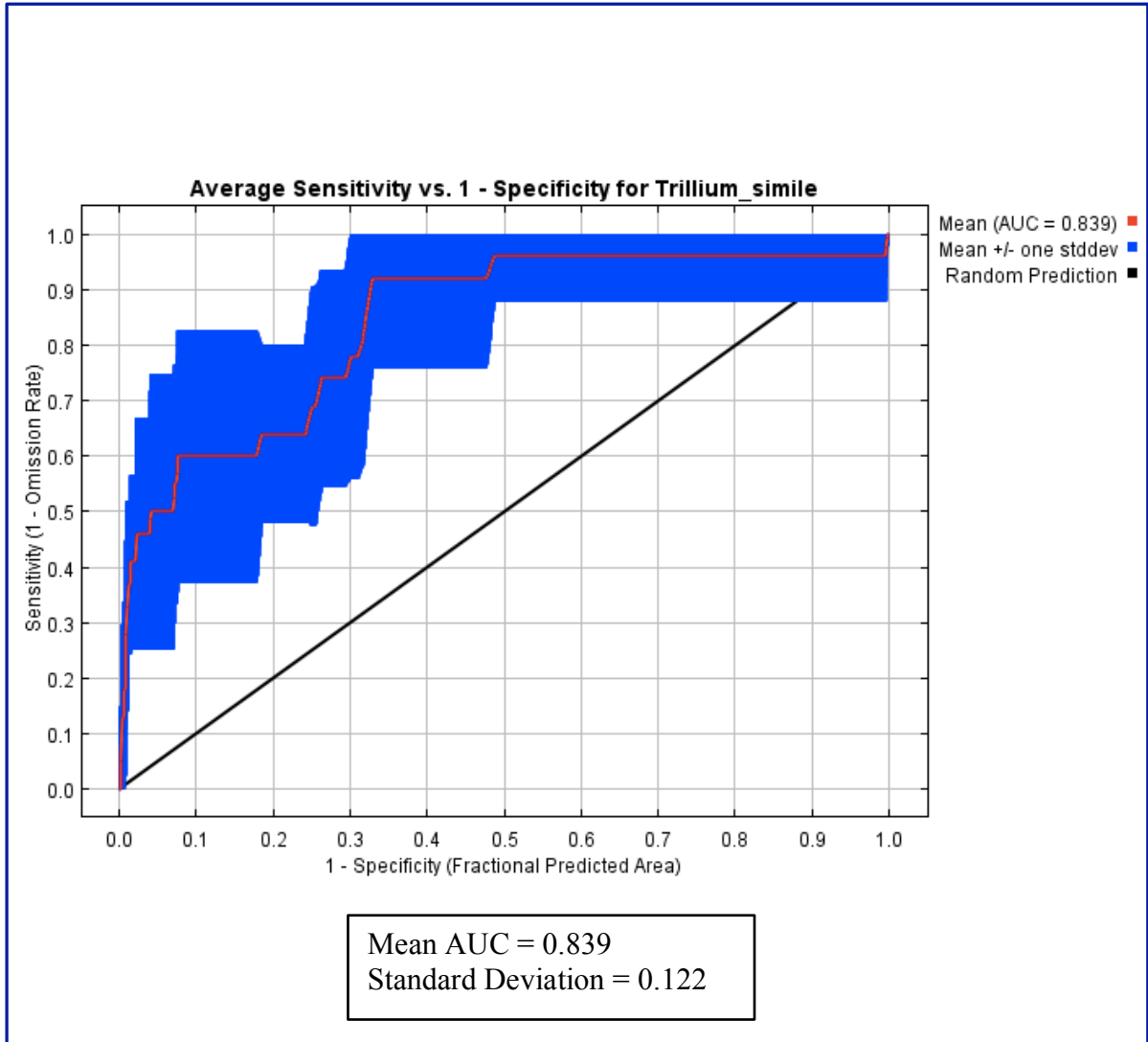


Figure 6. Area under the receiver operating characteristic (ROC) curve (AUC) averaged over the replicated Maxent runs describes the predictive accuracy of the Maxent model performance.

Field Validation of Habitat Distribution Maps

Maxent and DOMAIN both produced maps in which areas of highly suitable, suitable, and unsuitable habitat were defined. With the user-defined cutoffs in place and predicted sites of high suitability chosen, both models successfully predicted sites that were rich cove type forests similar to those observed where *T. simile* is known to occur. This was verified by a statistical, quantitative assessment of the data collected at the sites predicted by the models compared to the data collected at the extant *T. simile* sites. In addition, the appearance of the predicted sites as similar to extant sites is based on familiarity with rich coves forests and the topographic features that characterize them. However, although there was overlap in both maps that were predicted as high suitability, each prediction map also predicted high suitability or suitable areas that the other did not, and these areas were characteristic of the rich cove forests where *T. simile* is known to occur. No new, previously unrecorded *T. simile* populations were discovered during the field validation.

Quantitative Assessment of Maxent and DOMAIN Models

The 20 known *T. simile* sites were compared to the 12 sites predicted as highly suitable by either Maxent, DOMAIN, or both models for the habitat characteristics slope, elevation, canopy cover, and soil pH. The results showing the means and standard errors of the characteristics for the known sites compared to the three types of model prediction are shown in Table 5. The mean slope of the known sites was 49%, and the mean slopes for the Maxent, DOMAIN, and both model predicted sites were slightly lower at 44%, 47%, and 44%, respectively, and all standard error ranges overlapped (Figure 7a). The mean elevation of the known sites was 699 m, whereas the mean elevations for the Maxent, DOMAIN, and both model

predicted sites were much higher at 914 m, 925 m, and 864 m, respectively (Figure 7b). The elevation standard error ranges for the predicted sites all overlapped with each other, but were above the standard error range of the known sites (Figure 7b). For canopy cover, the mean for known sites was 83.2% and the means for the Maxent, DOMAIN, and both model predicted sites were very similar at 81.8%, 80.2%, and 83.0%, respectively, and with overlapping standard error ranges (Figure 7c). The soil pH means for the known sites and the three types of predicted sites slightly more variable, with known site mean soil pH of 6.0, and higher mean soil pH for the Maxent, DOMAIN, and both model predicted sites at 6.3, 6.6, and 6.1, respectively (Figure 7d). Sites that were predicted by both models had a soil pH mean very similar to the mean for known sites, whereas DOMAIN had a mean soil pH higher than the known sites or sites predicted by Maxent.

Table 5. Means and standard error ranges for habitat characteristics associated with 20 known *T. simile* sites and sites predicted as highly suitable by Maxent, DOMAIN, or both models.

	Mean \pm SE			
	Slope (%)	Elevation (m)	Canopy Cover (%)	Soil pH
Known	49 \pm 5	699 \pm 89	83.2 \pm 1.0	6.0 \pm 0.12
Maxent	44 \pm 4	914 \pm 29	81.8 \pm 1.2	6.3 \pm 0.16
DOMAIN	47 \pm 8	925 \pm 48	80.2 \pm 2.8	6.6 \pm 0.15
Both	44 \pm 9	864 \pm 74	83.0 \pm 3.2	6.1 \pm 0.16

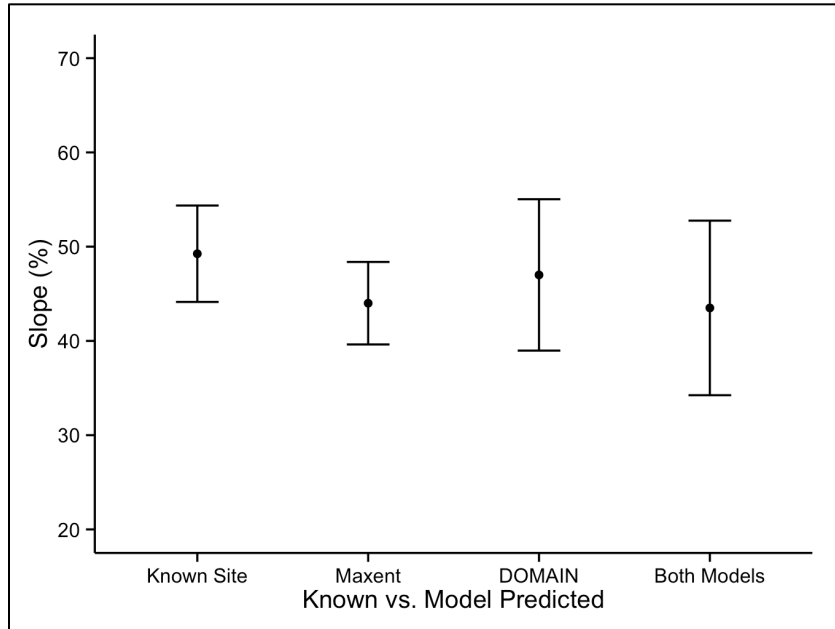


Figure 7a. Mean slope with standard error bars at 20 known sites compared to sites predicted as highly suitable by Maxent, DOMAIN, and both models.

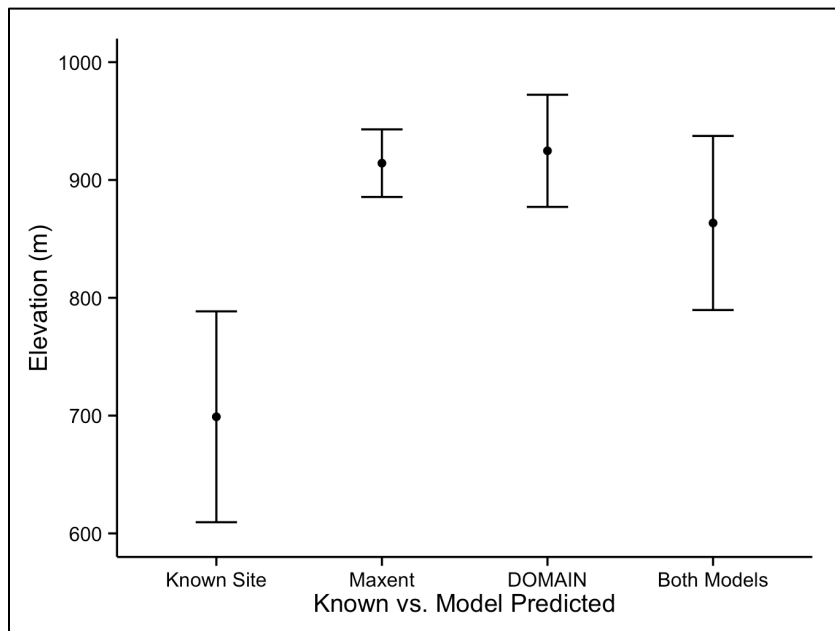


Figure 7b. Mean elevation with standard error bars at 20 known sites compared to sites predicted as highly suitable by Maxent, DOMAIN, and both models.

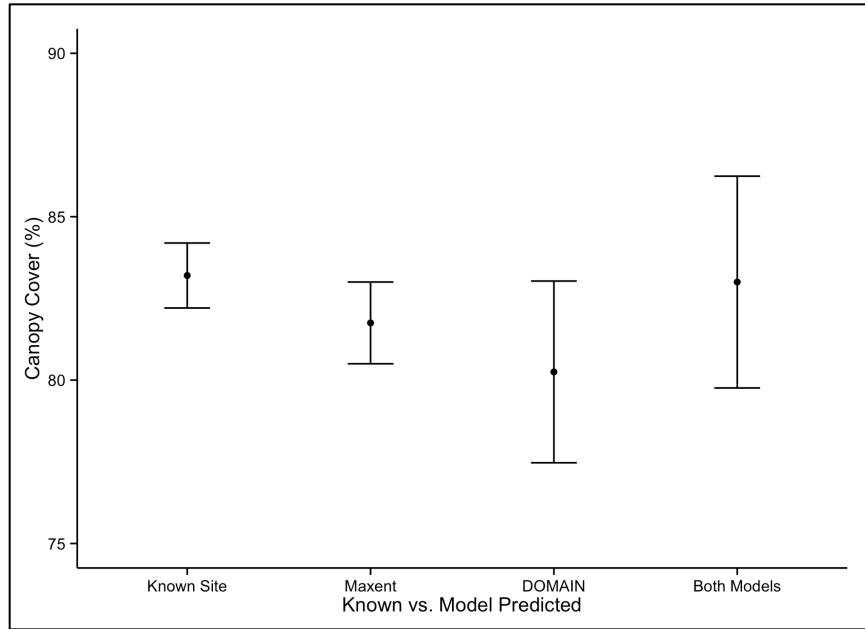


Figure 7c. Mean canopy cover with standard error bars at 20 known sites compared to sites predicted as highly suitable by Maxent, DOMAIN, and both models.

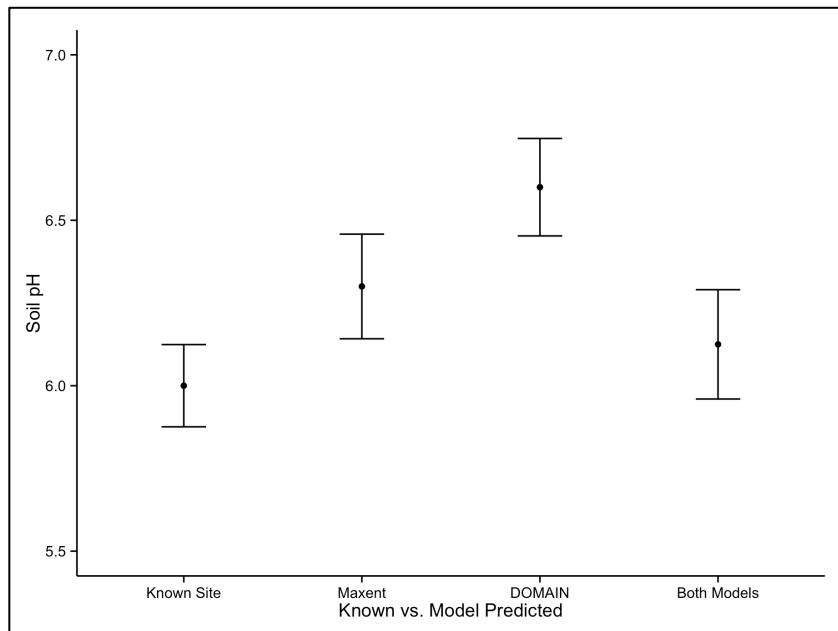


Figure 7d. Mean soil pH with standard error bars at 20 known sites compared to sites predicted as highly suitable by Maxent, DOMAIN, and both models.

The univariate ANOVA for slope, elevation, canopy cover, and soil pH, and the circular ANOVA for aspect for all possible pair-wise t-tests yielded p-values that were not significant. From this information, it can be concluded that there is no significant difference between the known *T. simile* sites and those predicted by the models Maxent and DOMAIN. Table 6 provides a summary of the univariate ANOVA results, including p-values, for slope, elevation, canopy cover, and soil pH. The results of the circular ANOVA for aspect showed no significant difference between known sites and predicted sites (p=0.4517).

Table 6. Summary univariate ANOVA results of habitat characteristics for the known *T. simile* sites and sites predicted as highly suitable by Maxent and DOMAIN.

Habitat Characteristic	Numerator Degrees of Freedom	Denominator Degrees of Freedom	Mean Square	Mean Square Error	F-value	p-value
Slope (%)	3	28	58.3	427.7	0.1364	0.9375
Elevation (m)	3	28	104703	112345	0.932	0.4383
Canopy Cover (%)	3	28	10.93	21.88	0.4996	0.6856
Soil pH	3	27	0.44	0.23	1.927	0.1491

Out of the documented 45 sites of known *T. simile* occurrence, 11 sites were withheld from the model building and used for model training. Of these 11 sites Maxent correctly predicted 8 sites (73%) as either highly suitable or suitable, whereas DOMAIN correctly predicted 9 sites (82%). Overall, out of the 45 known sites used to both build and test the model, Maxent successfully predicted 93% of the sites as suitable or highly suitable, and DOMAIN successfully predicted 95% of the sites as suitable or highly suitable. It should be noted that the

45 sites do not include the other unofficial occurrences where *T. simile* has been sited, only those that are officially documented. In addition, Maxent failed to identify a known location, not officially documented, in Chatahoochee National Forest of Georgia where *T. simile* was verified in the field validation.

The results of the count from the grid overlay for the method agreement analysis were presented in a two-way contingency table of frequencies with the rows and columns indicating the categories of response for each method Maxent and DOMAIN (Table 7). The frequencies of the agreement between the two methods are shown along the right downward diagonal. The method agreement analysis calculated a Cohen's kappa value of 0.674 from the contingency table of frequencies, which suggests that there was substantial agreement between the Maxent and DOMAIN methods. Although there is no formal scale for categorizing the kappa value, according to Watson and Petrie (2010) this value falls within the range of substantial agreement, where method agreement is substantial if $0.61 < \kappa < 0.80$.

Table 7. Method agreement analysis contingency table of frequencies showing the comparison of sites predicted by Maxent and sites predicted by DOMAIN for evaluating the degree of model agreement.

		Maxent		
		Unsuitable	Suitable	Highly Suitable
DOMAIN	Unsuitable	28	1	1
	Suitable	3	5	0
	Highly Suitable	0	4	8

Discussion

The environmental variables chosen for the initial site characterization were considered potential predictors of *T. simile* habitat based on research of other herbaceous species typically found in southeastern rich cove forests. This approach was chosen due to the absence of detailed published material on *T. simile* habitat. The herbaceous layer in eastern forests constitutes a small fraction of the entire vegetative biomass, but is very important for ecosystem function and diversity because of its contribution to productivity, organic matter degradation, bioerosion, bioturbation, and other biogeochemical and dynamic ecosystem processes (Mouillot et al. 2013). A significant relationship has been found between herbaceous community composition and overstory tree species, both locally and at a forest stand scale (McEwan & Muller 2011). The greater proportion of tolerant tree species in the uppermost canopy classes indicates movement toward later successional forests, which is consistent with reports that *T. simile* is typically found in more mature forests (Pistrang 2016). The 20 extant *T. simile* sites were characteristic of southern Appalachian rich cove forests where several species of herbaceous plants as well as upper canopy tree species flourish and are strong indicators of a rich cove forest (Elliott et al. 2014).

In addition to tree species composition in the canopy, both basal area and percent canopy cover are characteristics related to herb species richness, evenness, and diversity (Ford et al. 2000). Although not explicitly used in building the models, identification and abundance (as a percent cover) of the herbaceous layer species that are found with *T. simile* are also important variables for characterizing habitat of this species. The percent canopy cover is important for assessing the amount of light available for the herbaceous layer (Elliot et al. 2014; Ford et al. 2000; McEwan & Muller 2011; Thiemann et al. 2009). Canopy cover in the extant *T. simile* sites

averaged 83%, indicating that it thrived in low light conditions. Woodland herbs respond to light condition changes, and the quality and quantity of light associated with gaps generates the greatest response in understory herb species because most are light-limited (Whigham 2004). The average elevation range was consistent with what is reported as typical for *T. simile* (500-700 m) (Pistrang 2016), with some exceptions falling outside of this range at lower and higher elevations.

Several researchers have acknowledged the importance of soil characteristics and fertility in the herbaceous community, specifically soil pH (Elliot et al. 2014; Gilliam & Dick 2010; McEwan & Muller 2011; Small & McCarthy 2002). The results of the soil pH are consistent with known rich cove soils that generally have "sweet" soils with pH greater than 6. Also, the pH range of the most frequent herbaceous plants found in the plots matches the range of pH that is typical and expected. For instance, *A. racemosa*, *P. biflorum*, and *A. triphyllum*, the most frequently observed herbaceous plants in the *T. simile* sites, are all typically found in rich soils and are indicators of southern Appalachian rich cove forests (Elliott et al. 2014).

Conservation of woodland herbs, both abundant and threatened, must continue to be addressed, and future research needs to focus on restoration and maintenance of herbaceous plant in areas that are directly influenced by human activities (e.g., activities resulting in forest fragmentation) (Whigham 2004). Most of the extant sites were 30 m away or less from either a trail, service road, major road, or parking lot, and several site edges were only a few feet away from a hiking trail. It is debatable whether *T. simile* is an edge species or it is found near roads and trails because they happen to be visible from those locations. Patch size was also highly variable from site to site, ranging from two individuals in one population to over a thousand in another population, both of which were not far from a road or trail. Hernandez et al. (2006)

argue that reasonable models can be developed for rare species even if they have varying population sizes and small geographical ranges. Fragmentation and disturbance variables have also been cited as important influences on herbaceous composition (Elliot et al. 2014; Thiemann et al. 2009; Whigham 2004). Because the majority of the 20 sites were so close to a road or trail, there is potential for threat of increased takeover by exotic invasives, removal of plants by people using the trails, accidental destruction when people deviate from trails or parking areas, destruction by vehicles, and even expansion of parking areas and road pull-offs.

Both models produced outputs maps that predicted highly suitable habitat in overlapping areas, however, there were also locations predicted as highly suitable by one that was not predicted by the other. This could be because the models weigh the input variables differently and thus “view” their environments differently. Certain digital environmental variables and even the nature of a species and its habitat could have an affect on the distributions of individual models. It is possible that each method modeled the rich cove habitat of this rare species differently because there are several attributes (e.g., competition, resource partitioning, dispersal ability, predation tolerance, and interaction with soil microbes) that contribute to relative abundance and rarity of plant species (Klironomos 2002). Furthermore, rare plant species have complex relationships with their environments (Miller-Struttman 2013), which could affect SDM distribution output. SDMs are incomplete approximations in that distributions are always influenced by unknown factors, potentially related to rarity attributes, which interact spatially in an unknown way (Lobo et al. 2007) and could account for variations in distribution predictions. Studies discuss how two models can effectively model habitat distribution with good predictive performance (i.e., better than random prediction), even if they have different spatial output distributions (Velez-Liendo et al. 2013; Lecours et al. 2016). Instead of relying on a single,

‘best’ model, many studies suggest model averaging or using multiple SDM maps that use a combination of environmental variables to get the overall best representation of an area and a more robust performance (Thuiller 2003; Lecours et al. 2016; Hijmans & Elith 2017; Pacifici et al. 2017). Other researchers argue that while it is important to compare model performance and predictive capabilities, more research is needed on why these differences occur on the statistical level of various SDM algorithms, even before they can be effectively compared (Elith & Graham 2009).

There are ways the models could be improved. Studies on SDMs show that it is important to use variables that are relevant to the ecology of the species rather than what is merely easily accessible (Velez-Liendo et al. 2013; Lecours et al. 2016; Hijmans & Elith 2017). Thus, it is potentially very useful to develop new, more ecologically relevant predictor variables from the easily accessible existing data using a statistical program such as R (Hijmans & Elith 2017). Furthermore, SDMs typically rely completely or partially on climatic variables as predictors (as was done in this project using precipitation and temperature values), when in fact these variables could be associated with uncertainties from interpolation between sparse data stations (Deblauwe et al. 2016). Satellite-based climatic predictor data (i.e., remotely sensed data) of temperature and precipitation could potentially improve models because they might be a more effective alternative to climatic variables collected from stations on the ground, particularly where stations are sparse across a particular landscape (Deblauwe et al. 2016). The nature of *T. simile* is such that a microclimate may have an impact on where it will grow, and the data used in this study were coarse (~1km) and unable to capture microclimate. Satellite-derived data might be better able to capture the microclimates that influence habitat for rare plant species (Williams et al. 2009; Deblauwe et al. 2016; Dymytriva et al. 2016). Forest-structure data such as canopy

height and other predictors have also been shown to significantly improve models for rare and threatened lichens (Dymytrva et al. 2016), especially when the species have particular microhabitat requirements. This may be the case with *T. simile* and other rare plants for which habitat distributions warrant further research into their microhabitat requirements. Furthermore, both Maxent and DOMAIN outputs could have been improved had selected input data been different from what was actually chosen. For Maxent in particular, there is wide variety of settings in the software package to build the model from these data, including background data, regularization, sampling bias, model output, and model evaluation (Merow et al. 2013). As a result, model predictions could be different given alternative data input and settings rather than using the default settings.

Maxent had a “good” performance with an AUC of 0.839, considering a random prediction is 0.5 and a value approaching 1 is considered a perfect prediction. To understand the AUC obtained in a study and give a rating, one has to rely on previous work done in similar studies. Yang et al. (2013) used Maxent to predict the potential distribution of a rare medicinal plant, and the predictive performance was very high (AUC=0.923). The AUC of the Maxent model performance for *T. simile* distribution (0.839) could be classified as “good” compared to this study’s performance. Unfortunately, an AUC for DOMAIN to compare to the Maxent AUC was not obtained. The DIVA-GIS program and the scant literature on guidelines for DOMAIN did not have guidance on how to properly calculate an AUC or similar predictive performance value. The drawback of this was an inability to compare DOMAIN to Maxent in terms of AUC. Although AUC is currently considered the standard method to assess the accuracy of predictive distribution models, some studies raise concerns about its extensive use because its meaning and use could be misleading, biased, and not appropriate for directly comparing models (Lobo et al.

2007; Peterson et al. 2007; Elith & Hijmans). Khatchikian et al. (2011) found that DOMAIN had a very low prediction performance AUC, the lowest out of five compared models, including Maxent, which had the second highest. However, DOMAIN presented with the highest level of robustness (>96%), whereas Maxent scored among the lowest in robustness, where robustness of a model refers to its ability to effectively perform while its variables or assumptions are altered. Even though AUC might be high, model performance robustness can tell an opposing story and a high AUC score does not necessarily imply suitability accuracy (Lobo et al. 2007). While an AUC value is one important way to assess model performance, it should not be the only means of comparing model performance and should be used in conjunction with other methods such as statistical analysis of field validation data.

Field validation, which is an especially critical step in assessing the predictive performance of rare species habitat models (Jiménez-Valverde et al. 2008; Lobo et al. 2008; Rebelo & Jones 2010) revealed similarities between habitat characteristics at predicted high suitability sites compared to extant *T. simile* populations visited during the initial habitat characterization. This indicates that both Maxent and DOMAIN predicted suitable habitat for *T. simile* accurately. The descriptive statistics of the habitat characteristics slope, elevation, canopy cover, and soil pH showed that the means of the abiotic variables were close to those of the known sites. Furthermore, the univariate ANOVA results for these same habitat characteristics and a circular ANOVA for aspect revealed that all pair-wise t-tests had p-values that were not significant. From this it could be concluded that there was no statistical difference between known *T. simile* sites and sites predicted as highly suitable by Maxent, DOMAIN, and areas where both predicted highly suitable habitat.

Both models had high, comparable predictive performance in terms of the sites that were withheld for model testing, although DOMAIN performed slightly better. Of the 11 sites withheld for model testing, Maxent correctly predicted 8 sites (73%) as either highly suitable or suitable, whereas DOMAIN correctly predicted 9 sites (82%). Overall, out of the 45 documented known sites used to both build and test the model, Maxent successfully predicted 93% of the sites as suitable or highly suitable, and DOMAIN successfully predicted 95% of the sites as suitable or highly suitable, both of which were very high predictions. These results further support the fact that both models performed comparably well, and were not significantly different in their predictions.

Taking into consideration the results of the quantitative assessments of the data, Hijmans & Elith (2017) discuss how it is much easier to create a model and make predictions on species and habitat distributions and much more difficult to assess how good the model actually is. However, they propose model agreement analysis (Watson & Petrie 2010) as appropriate method for comparing models, which was used in this study. The method agreement analysis showed that both models Maxent and DOMAIN had substantial agreement ($\kappa=0.674$) and were both suitable for modeling *T. simile* habitat, further supporting the quantitative assessments.

In terms of qualitative assessment, Maxent was a more complicated model to use than DOMAIN. Pre-processing the data involved several time-consuming steps. The Maxent program itself has several settings that can be adjusted prior to running the model with the processed data, making it difficult to understand under what parameters to properly run the model. The Maxent program's output varies in response to different settings and what the user does affects the output because alternatives to the default settings may be more appropriate (Merow et al. 2013). Settings that affect the modeling options include choice of background

samples and accounting for environmentally biased sampling, which can both lead to different interpretations of various model outputs and challenges for model validation.

Experimenting and working with Maxent on different scales, with different species, and with various project objectives, would be beneficial to understanding how to best to operate the program. Because of the popularity of Maxent for habitat suitability modeling, several resources exist to serve as guidelines (e.g., how to format data, suggestions for settings). Although this was extremely helpful in modeling *T. simile* habitat, the steep learning curve creates a limited amount of time to learn about possible issues that could affect model performance or how to make informed decisions to help it perform better. Another aspect of Maxent that could be seen as an advantage is the automatic generation of the environmental variable response curves that show how environmental predictor variables affect model prediction. The AUC is also an automatic output in the Maxent program.

Many of the user qualities of DOMAIN were opposite those of Maxent. For example, the user interface of DOMAIN was very simple. Because the data for both models was processed the same way and the same variables were used, once pre-processing was complete, running the model with DOMAIN was very simple and straightforward. The settings for DOMAIN as used in DIVA-GIS were minimal, only calling for settings necessary to make the model operate. Although the simplicity was an advantage, there is also the potential disadvantage associated making few adjustments. Also, the DIVA-GIS system was the only workable format for running the DOMAIN model; it is a simple platform that requires no licenses, but lacks the versatility and flexibility of a proprietary program like ArcGIS. Furthermore, because of the simplicity of the model and the lack of published material in which DOMAIN was used, there was very minimal guidance. The guidance was limited to how to input data and at the very least obtain a

visual output. DOMAIN also appears in very few published articles compared to Maxent, causing a lack of information and suggestions from others who have used the model. Unlike Maxent, however, DOMAIN does not provide environmental predictor variables response curves, and the AUC is not immediately generated but rather is a separate process, which is not presented in this research.

As mentioned, pre-processing of the digital environmental variables prior to input was the same for both Maxent and DOMAIN. Both models ran quickly once initiated, and both allowed user-defined cutoffs for habitat suitability. Also, the range of either probability of suitable habitat (Maxent) or confidence of suitable habitat (DOMAIN) was 0-1 for both models. Because of the user-defined cutoffs, suitability ranges of both, and use of the same environmental variables, the two model outputs were directly comparable. The image outputs of habitat suitability across the area of interest were also easily integrated into ArcGIS (Maxent) or kept in DIVA-GIS (DOMAIN), where modifications of the images were possible for clarity and use as *T. simile* habitat maps or maps of particular types of species-rich rich cove forests.

Differences in the levels of simplicity or complexity have been explored in the literature with various SDMs. Jiménez-Valverde et al. (2008) suggests that more complex models, such as Maxent, might be better suited to modeling realized habitat distributions, whereas simpler models, like DOMAIN, may be more appropriate for modeling potential habitat distributions. Therefore, DOMAIN might be the preferred method for species that are candidates for conservation prioritization and propagation, like *T. simile* and other rare and endemic plant species. ‘Under-fit’ models like DOMAIN might be too simple and have insufficient flexibility and thus misunderstand the factors that shape species distributions flexibility. On the contrary, ‘over-fit’ models, like Maxent, could have excessive flexibility, which runs the risk of being

superfluous and ascribing significant patterns to noise (Merow et al. 2014). Both extremes in model capabilities make model selection challenging, and there are differences in opinion that favor simpler or more complex SDMs (Merow et al. 2014).

In conclusion, with limited time, a simpler, less flexible model like DOMAIN might be more beneficial to use, whereas a more complex model like Maxent could be better if the user has plenty of experience and a working knowledge of the program and its settings. In this project, Maxent proved to work well on a small scale although it has been used primarily for species on larger scales (Elith et al. 2011; Phillips et al. 2006); however, DOMAIN performed equally as well and was a simpler process. While both Maxent and DOMAIN modeling method provided a useful and successful tool for predicting suitable habitat for *T. simile* in the southern Appalachian Mountains region, this study recommends DOMAIN because of its ability to predict highly suitable habitat for *T. simile* using a simpler, GIS-based method. Further experience with each model under various conditions is recommended and essential to truly understanding how SDMs perform and which might be preferred.

LITERATURE CITED

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