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The Prairie State: Using Ecological Niche Modeling to Predict Distributions of Early Land Plants

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The Prairie State: Using Ecological Niche Modeling to Predict Distributions of Early Land Plants

A Thesis

Presented in partial fulfillment of the requirements

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BY

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Scientific Publications

The following manuscripts have been submitted to peer-reviewed open access journals:

Components of Chapter Two and Three have been submitted to the journal *Research Ideas & Outcomes* (RIO) as:

Ryan, Z., Clark, E. K., Cundiff, B., Nichols, J. A., Mahoney, M., Evans, N. M., Campbell, T., & von Konrat, M. (2023). Open-Source Software Integration: A Tutorial on Species Distribution Mapping and Ecological Niche Modelling.

Components of Chapter Three have been submitted to the journal *BioRisk* as:

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Abstract

Bryophytes are environmentally and ecologically significant biological indicators, as their distribution is largely determined by the climate and the land features that shape these factors. Yet it is a challenge to track the ranges of these plants and even more so to predict their future distribution patterns due to their small size and sensitivity to environmental change. This study aims to model the potential distribution of selected bryophyte species in Illinois to investigate the potential impact of global warming and determine what environmental factors affect distribution patterns. Bryophyte occurrences post 1970 of some of the most common epiphytic species and genera were investigated. Over 12,000 georeferenced occurrence records were downloaded from a public biodiversity aggregator, cleaned, and validated. The environmental variables consisted of the WorldClim Bioclim variables and National Land Cover Database land use variables at approximately 1 km^2 resolution. The occurrences and environmental variables were run through a MaxEnt model in R to generate heat maps of potential distribution. Statistical evaluation metrics and validation techniques were used to test model accuracy. Overall, current species models showed a higher level of confidence than the genera models, and all models were primarily reliant on the land use variables over the climate variables. Future models only showed consistent distribution changes across all three climate scenarios, suggesting the selected taxa could be valuable indicators. Attempting to quantify bryophyte-environment relationships and ecological niche modeling potentially provides a means of predicting how bryophytes might respond to environmental changes over time. Using such techniques enables us to test for significant differences in the characterization of niches between taxa. Successful models will represent real world distributions accurately, not only show support for utilizing bryophytes as climate change indicators, but also for this open-source

methodology in the niche modeling for other organisms. Overall, these results will have important implications for species distribution patterns, conservation, land management and our understanding of ecological niche modeling using a poorly studied and overlooked group of plants.

Chapter 1: Introduction

Bryophyte Evolution and Life Cycle

Bryophytes, including mosses, liverworts, and hornworts, are the second largest group of land plants after flowering plants and are pivotal in our understanding of early land plant evolution (Graham et al., 2014; Leebens-Mack et al., 2019; Zhang et al., 2020). Diversification of bryophytes spans at least 400 million years, yet their phylogenetic relationships remain ambiguous due to the lack of fossils, massive early extinctions, late radiations, and conflicting molecular evidence (Y. Liu et al., 2019).

Constructing the evolutionary history of the bryophyte lineages and their relationship with tracheophytes remains controversial despite increasingly advanced molecular techniques over the decades (Donoghue et al., 2021; Leebens-Mack et al., 2019; Nickrent et al., 2000; Puttick et al., 2018; Shaw et al., 2011; Zhang et al., 2020). This is namely because some bryophyte species have traits that are similar or are typically associated with vascular plants, including: water conducting cells, stomata, and leaf-like structures (Donoghue et al., 2021). These traits are found across lineages, making it unclear how the three groups are related to each other and how they are related to the vascular plants.

Most contemporary classifications accepted three independent lineages and divisions, i.e., hornworts (Anthocerotophyta) with approximately 200 to 250 species, the liverworts (Marchantiophyta) with an estimated 8,500 species (Figure 1-1), and the mosses (Bryophyta) (Figure 1-2) with an estimated 13,000 species (Sheffield & Rowntree, 2009; Söderström et al., 2016; Villarreal A. & Cusimano, 2015; von Konrat et al., 2010). However, some recent comparative genomic methods provide evidence indicating bryophytes as a monophyletic group (Figure 1-3) (Bell et al., 2020; Donoghue et al., 2021; Puttick et al., 2018). For example, Puttick et al., 2018 suggests the most likely relationship is Tree A, where bryophytes are in a monophyletic group, yet, Trees B and D are also possible, only differing by the placement of hornworts.

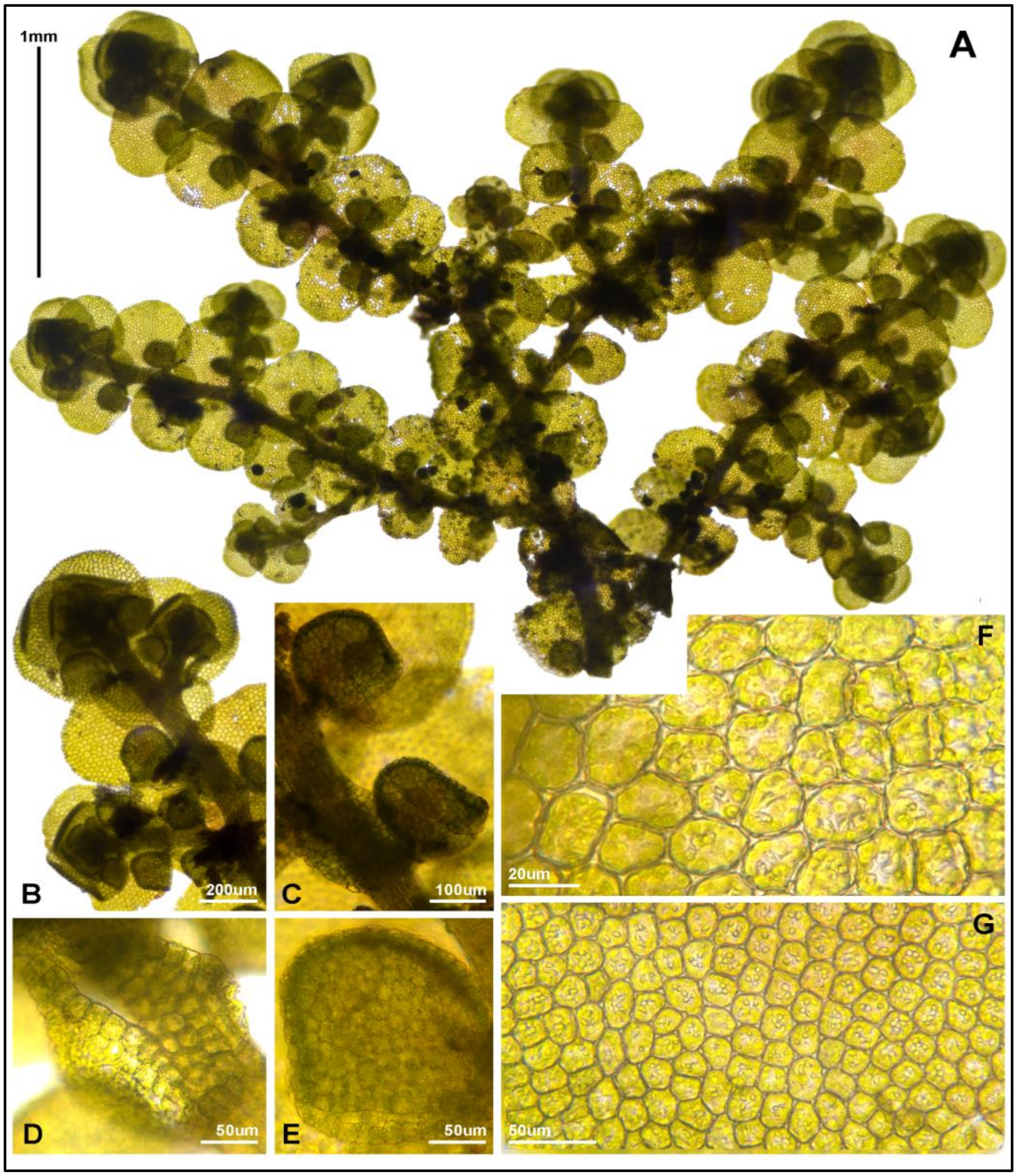

Figure 1-1. The liverwort *Frullania eboracensis* (Lehm.) A: Habitat; B: Stem terminal shoot with inflated sacs or lobules and dorsal leaf lobe; C: Lobules; D: Underleaf; E: Lobule; F & G: Median cells of the leaf lobe.

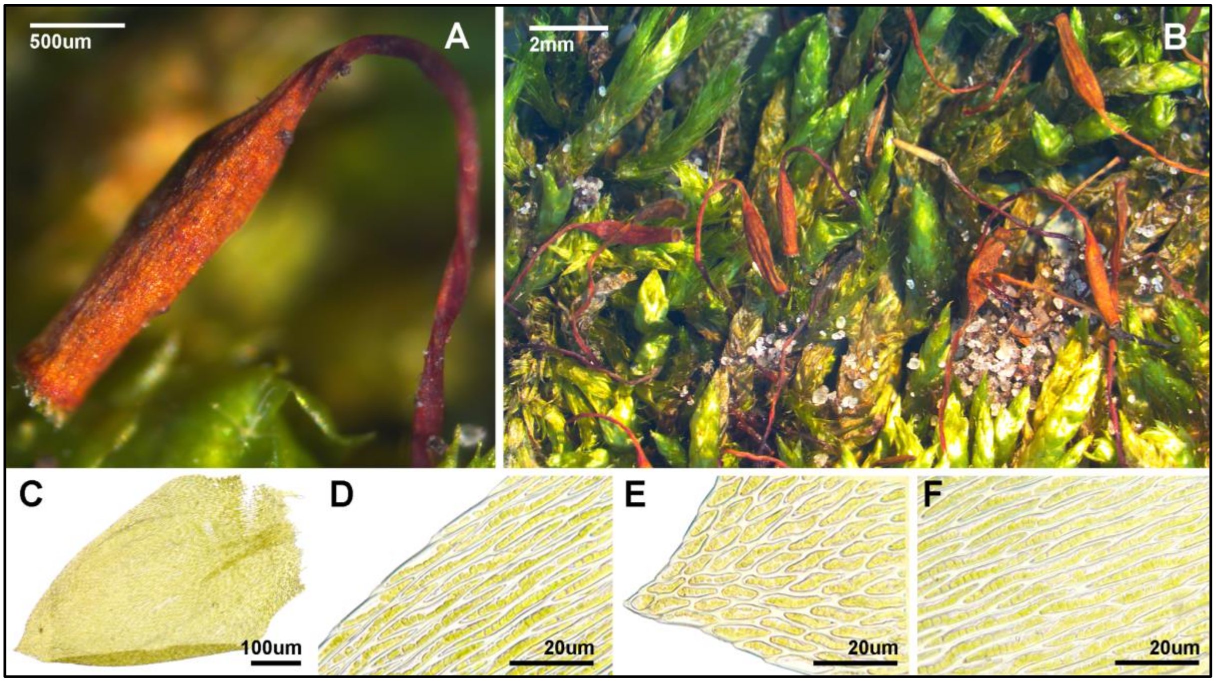

Figure 1-2. The moss *Entodon seductrix* (Hedw.) A: Sporophyte; B: Habitat; C: Leaf; D: Leaf Margin; E: Apex; F: Median Cells.

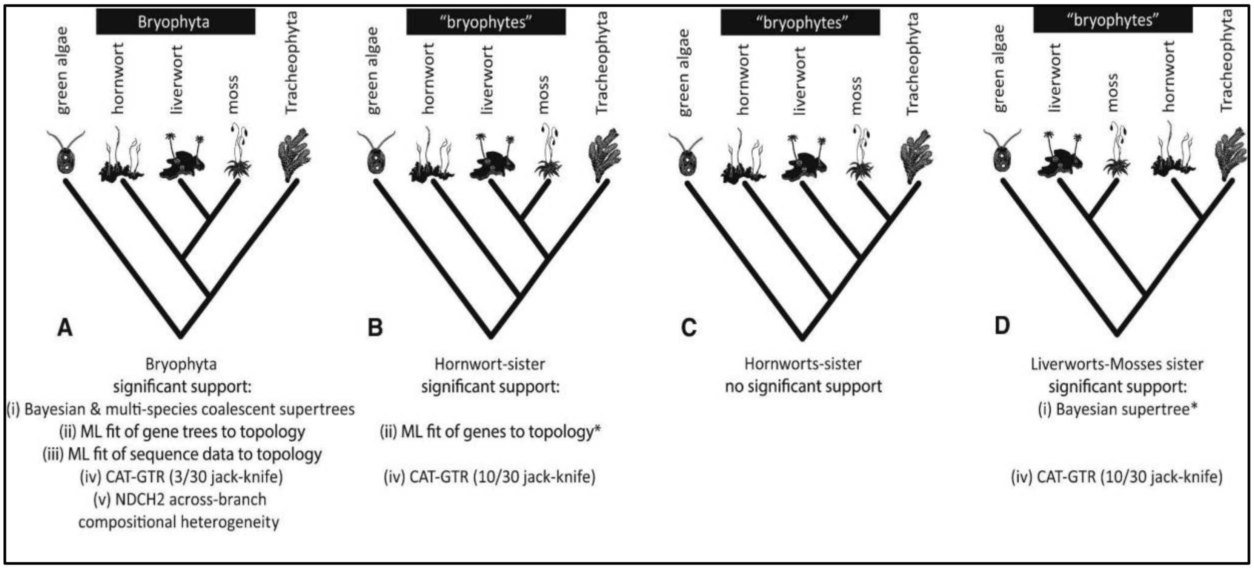

Figure 1-3. Examples of conflicting hypotheses for the evolutionary history of bryophytes and their relationships with other land plants (Puttick et al., 2018).

A key innovation of land plants is a life cycle with an alternation of generations, with both haploid gametophyte and diploid sporophyte generations (Bowman et al., 2019; Qiu et al., 2012). These phases are named for the important product of each stage: the gametophyte creates gametes which come together to make the sporophyte, and the sporophyte undergoes meiosis to produce haploid spores which become the gametophyte (Niklas & Kutschera, 2010). The alternation of generations life cycle strategy is credited with allowing plants to survive through the harsh changes of seasons, as different steps in the cycle thrive in different conditions (Glime, 2017). Bryophytes are unique among land plants in that their haploid gamtetophyte is the dominant, free living generation while the diploid sporophyte is reliant on the gametophyte (Wyatt & Stoneburner, 1984).

Many bryophyte species can live in areas with little moisture due to the capacity of the meiospore stage to survive dry for years (Glime, 2017). The meiospore stage grows into the fully formed gametophyte, the typical “flatter” and green part of the bryophyte reproductive phase. Bryophytes are the only plant group where the sporophyte generation is not dominant: moss and hornwort sporophytes grow for a year at most while liverwort sporophytes last only months or weeks (Shaw et al., 2011).

The generational structure of the bryophyte life cycle makes it difficult to determine individuals, parents, and generation size of a population. Gametophytes can be considered the parents of sporophytes, which are then parents of the next generation of gametophytes, all of which are considered to have higher fitness the more of the next phase they produce (Shaw et al., 2011). However, for matters of population size, it is more appropriate to frame the gametophyte as the individual due to their dominance, with the sporophyte representing a reproductive structure (Shaw et al., 2011).

It is estimated that 50-68% of bryophytes are dioecious, i.e., have gametophytes that are separated by sex (Frey & Kürschner, 2011; Glime 2017), in contrast to only 4-6% of seed plants are dioecious (Glime, 2017). The origin and maintenance of dioecy has been extensively investigated and remains an evolutionary puzzle, but most likely driven by sexual specialization (McDaniel et al., 2013). There are strong arguments that there is an adaptive value of separate sexes beyond the benefits of outbreeding alone based on the observation that dioecy evolves frequently in organisms that depend upon restricted conditions for fertilization (Freeman et al., 1997; McDaniel et al., 2013). Interestingly, female gametophytes can bear upwards of 15 sporophytes with different fathers (Shaw et al., 2011). While it is beneficial for the mother to equally allocate resources to her sporophytes, the father gains reproductive advantage by creating sporophytes that take up as many maternal resources as possible (Shaw et al., 2011). Taxa with a monoicous strategy have the advantage of always being able to breed: populations of dioicous species can be entirely one sex and therefore never produce sporophyte capsules (Glime, 2017). However, these dioecious species often reproduce asexually instead with specialized organs/propagules or by cloning (Frey & Kürschner, 2011).

Bryophyte Physiology

Bryophytes have several morphological and physiological properties that make them ideal as bioindicators or biomonitors. These include their: relatively small size; physiological activity throughout the year; ability to survive in highly polluted or ecologically disturbed areas; lack of roots and process of obtaining nutrients from wet and dry deposition; and resistance to substances that are highly toxic to other organisms (Diaz-Alvarez et al., 2019; Rūta & Paliulis, 2011). These characteristics make bryophytes heavily reliant on environmental factors, while also being distributed around the world. The lack of vascular tissue in bryophytes causes them to be morphologically stunted; they cannot match the vertical growth levels of other plants, yet they have developed complex biochemical adaptations that allow for continued survival in harsh environments (Glime, 2017). In general, bryophytes have a larger occupancy or range compared to vascular plants, but being haploid organisms and highly specialized, they are attached to microhabitats and react easily to minor environmental changes (Sabovljević et al., 2022). These reactions, such as changes in distribution or growth, make bryophytes ideal indicators as these factors can be measured and applied to environmental changes in regions around the world.

Bryophyte Ecology

Bryophytes are integral members of their environmental community as other organisms rely on them for their own survival. For animals such as insects, reindeer, and barnacle geese, bryophytes are a source of food (Alatalo et al., 2020). The matrix structure of bryophytes retains water and provides an insulated home for many forms of microscopic life, for example: tardigrades, mites, rotifers, micro-mollusks, microalgae, microfungi, cyanobacteria, diatoms, single-celled eukaryotes, and numerous groups of invertebrates (Gerson, 1982; Huttunen et al., 2018). Some bryophytes such as *Sphagnum* specifically host nitrogen fixing cyanobacteria which is vital to ecosystem health and plant growth (Cornejo & Scheidegger, 2016; Saxena & Harinder, 2004). Other bryophyte species aid their environment by mineral retention, preventing potassium, calcium, and magnesium from leaching into the soil (Saxena & Harinder, 2004). Therefore, a variety of organisms rely on their interspecific relationships with bryophytes for appropriate shelter and nutrients for the environment as a whole.

At the interspecific level of interaction, there appears to be a low amount of competition between bryophytes (Slack, 1990). Different species tend to grow in groups alongside each other with physically larger species occasionally outcompeting smaller ones (Proctor, 1990; Slack, 1990). Yet competition dynamics are still relevant for determining the community composition of an area, particularly when human intervention causes a change in the environment. Greater diversity and rare species were found alongside a mountain road compared to the untouched areas of the same mountain (Miller & McDaniel, 2004). The building of the road essentially removed existing diversity and community structure, allowing for a blank slate for bryophyte colonization. The areas alongside the road were colonized by rare species only found on lower areas of the mountain, meaning the spore traveled 5 km away from their original propagators (Miller & McDaniel, 2004).

Overall, the physical dispersal ability of bryophytes still requires characterization. Most importantly, the presence or lack of wind appears to have a great effect on the distance a spore travels. European bryophytes with larger spores appear to be more reliant on wind than smaller spores (Zanatta et al., 2020). In areas with low wind speeds such as the Swedish boreal forests, spores reportedly fall close to the original propagator (Hylander, 2009). Even though a large portion of spores will fall close to the propagule, bryophytes have the potential for long distance dispersal due to their environmental resilience. van Zanten and Pócs (1981) document spore survival under conditions typical of high-altitude atmospheric air currents (i.e., desiccation, wetting, and freezing) and provide evidence that bryophyte spores can enter the jet stream and travel great distances. Spores have been shown to withstand desiccation, UV radiation, and extreme temperatures, meaning they can utilize high altitude jet streams to possibly travel at an intercontinental distance (Shaw et al., 2011; Warren et al., 2019). Multiple genetic studies support a long-distance dispersal hypothesis by matching DNA markers in populations worldwide (Shaw et al., 2011; Warren et al., 2019). Even so, it has not been confirmed that wind patterns or jet streams are the cause of these worldwide species, and more complexities are involved in dispersal.

Regardless of dispersal capability, bryophytes can be found in nearly every kind of terrestrial or freshwater environment that lacks permanent ice (Gignac, 2001; Zechmeister et al., 2003). This is due to their lack of true roots; they instead absorb water directly through their surface, and therefore typically are found in moderate or high humidity environments (Gignac, 2001). Bryophyte resilience plays a direct role in their worldwide distribution as well as their differing traits from other plants allow them to occupy a unique niche particulaily where other plants are not found.

Though bryophytes may be widespread, the physical and community characteristics of species are more specific to the environment they are found in than bryophytes collectively. Furthermore, this specificity makes bryophytes sensitive to changes in their environment. Acid rain, pollution, and variations in humidity have been shown to impact bryophyte distribution (Saxena & Harinder, 2004; Wierzcholska et al., 2020). In particular, temperature increases lead to a decrease in net photosynthesis products, bryophyte richness and cover (Alatalo et al., 2020; He et al., 2016). Even minor climatic or land use changes can potentially cause bryophyte distribution in the area to dwindle.

Relevant environmental changes are seen at the level of the microclimate rather than the macroclimate; there is a greater impact on bryophyte diversity and cover of substrate when there is a change in the immediate area a bryophyte grows compared to an ecosystem-wide change

(Gignac, 2001; Táborská et al., 2020). Forests are an environment where microclimate is particularly relevant. The resulting tree cover creates a disparity between ecosystem environmental conditions and conditions underneath the canopy, namely lessening the effects of wind and light (De Frenne et al., 2021; Wierzcholska et al., 2020). Bryophyte distribution is therefore reliant on the microclimate remaining within ranges a species can tolerate. Furthermore, environments like forests have a more established microclimate from their tree cover; a loss of this canopy likely means a foreboding future for the bryophytes beneath. Forest trees commonly act as a substrate for bryophytes, also called epiphytes, meaning that trees are relevant in multiple ways in shaping bryophyte habitats. Bryophyte species often show specific preferences towards the tree species they grow on, forming ecological connections when the tree population is dense (Wierzcholska et al., 2020). Forest continuity therefore has an impact on bryophyte distribution and the fragmentation of forests leads to a lower chance of their survival. Destruction of bryophyte habitats and forest fragmentation is often the result of human development and land use (Cerrejón et al., 2020). Forests in particular are an excellent model for observing microclimate and continuity changes because of the reliance of some bryophyte species on trees.

Objectives and Hypothesis

Predictive species distribution models using presence-only occurrence data have been useful in conservation planning and forecasting climate change impacts for a range of flora and fauna (Lawler et al., 2011). Yet, very limited studies have been applied to modeling bryophyte species distribution, and even fewer studies have forecasted future habitat suitability under various scenarios of global change (Mallen-Cooper et al., 2023). Bryophytes have long been used as bioindicators and combined with their important ecological functional role, unique physiology, as well as broad distribution make them ideal for such studies. Forest bryophytes are of interest due to their dependence on tree-created microclimate and their contribution to diversity. This project aims to test the validity of modeling selected bryophytes, especially epiphytes, of Illinois using species distribution, climate, and land use variables. It is hypothesized that these environmental variables will be significant in shaping bryophyte distribution as a whole. The objectives were as follows: 1) Investigate potential bryophyte species for utilization in ecological niche modeling; 2) Screen and clean presence-occurrence data for selected species for modeling; 3) Generate models at the species and genus level to compare their distribution and niche estimate; 4) Verify models with in situ collections; and 5) Generate models of selected bryophytes and investigate future changes in distribution across climate change scenarios. Furthermore, we have prioritized 1) transparency - by submitting code and raw data with registered online repositories, 2) ease-of use, and 3) open-source software when using and presenting our methods. Significantly, this works towards open science methods, replications and reanalyzes that together benefit science (Allen & Mehler, 2019).

The species and genera selected are those most common within the state for the purpose of creating the most realistic models, as these common groups have more usable occurrence data. If supported by model quality measurements and real-world verification, these models will provide a niche estimate for bryophyte species and genera. Future projections of climate variables will also be utilized to compare the future change in bryophyte distribution within Illinois and provide insight into how climate change is affecting bryophyte populations.

Chapter 2: Predictive mapping of selected bryophytes based on current distribution occurrences

Introduction

Species Distribution Models

The geographic range a plant species exists in is determined by the abiotic and biotic factors of its environment and its capacity for dispersal (Melo-Merino et al., 2020). These three factors are described as the Biotic, Abiotic, and Mobility (BAM) framework (Peterson & Soberón, 2012). Models are built off of one or more of these factors to represent a species niche or distribution (Figure 2-1). The first distribution models were built in the 1980's solely off of abiotic data, when estimated climate conditions became reliably available (Booth et al., 2014). Generally, the more of the BAM framework a model includes, the better it characterizes the distribution of the species.

However, current models still majorly rely on the abiotic portion of the framework because biotic and dispersal elements can be difficult to characterize. Biotic data particularly requires excessive tracking of complex relationships that is left out of a majority of models (Barve et al., 2011). Even if biotic data is lacking, the inclusion of mobility data in a distribution model is relevant in distinguishing between accessible and inaccessible areas for a species (Pecchi et al., 2019). Yet included factors of the framework should be prioritized based on the desired outcome of the distribution model.

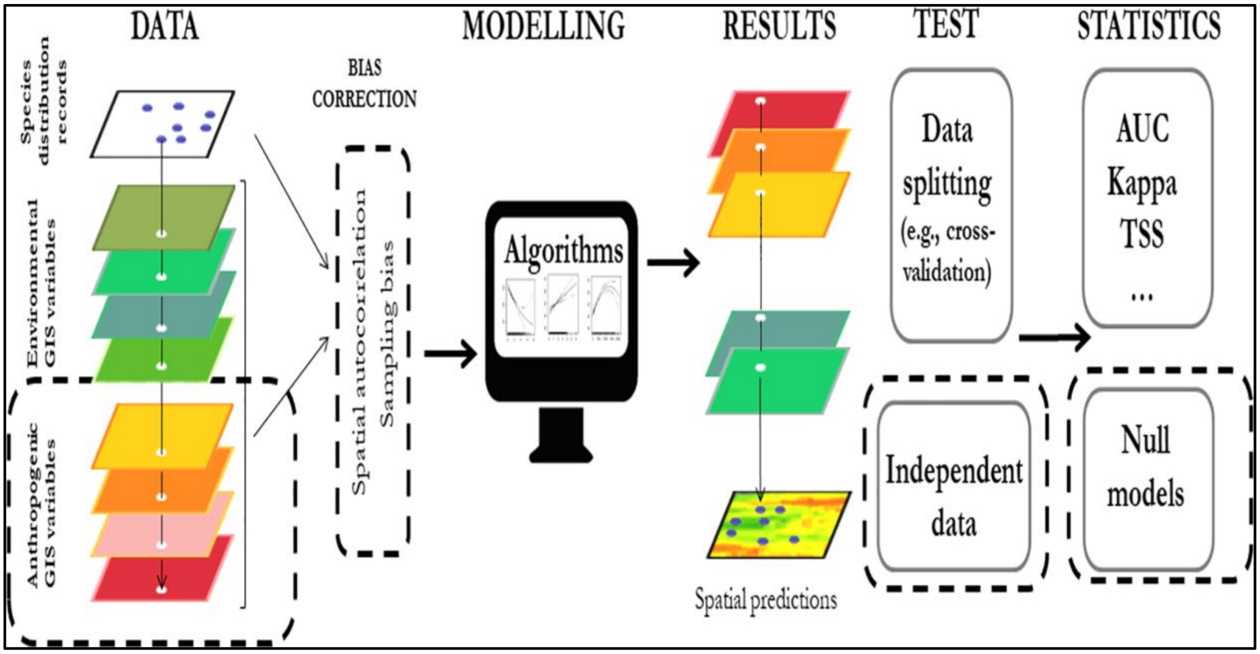

Figure 2-1. The theoretical process of creating a distribution model with a variety of applicable elements. Species distribution data and environmental data are combined to produce a model with projection of potential occurrences. This model is then statistically evaluated for usability (Rodríguez-Rey et al., 2019).

There are two major types of distribution models: ecological niche models (ENMs) for determining potential distributions and species distribution models (SDMs) for estimating actual distributions (Melo-Merino et al., 2020). More specifically, an ENM is for determining a niche, a conceptual idea of distribution, whereas an SDM is grounded in the boundaries of the geographic world (Melo-Merino et al., 2020). These terms are often used interchangeably, but the real distinction lies in the goal of the model: determining a niche or a real distribution. If the goal is to fulfill both roles, then a model can be classified as both an ENM and an SDM.

When constructing a distributional model, different aspects of the BAM framework are prioritized based on the type and therefore purpose of the model. An SDM relies on the mobility to accurately account for geographical barriers, whereas an ENM relies on the abiotic portion to construct a fundamental niche (Barve et al., 2011). The presence or absence of mobility data in a model indicates whether a fundamental or realized niche is being determined. A fundamental niche is a concept rather than a physical geographical space; without the inclusion of geographic barriers, species competition, etc.; the model presents a potential distribution rather than real distribution (Peterson & Soberón, 2012). The ultimate goal(s) of ENMs are to produce a map of probable distribution, determine how suitable an environment is for a species, and identify locations where conservation efforts are needed (Peterson & Anamza, 2015; Srivastava et al., 2019).

Beyond the type of model, SDM or ENM, the mechanisms by which the model is made contribute to what can be determined from the model. Correlational models are the most common method of SDMs and ENMs, using environmental variables and known species distribution to predict the ecology of that species (Melo-Merino et al., 2020). Correlational models therefore imply that the environment directly determines species abundance (Dormann et al., 2012). This is in contrast to mechanistic or forward models which relate the functional traits of species to their ecology, with distribution being an indirect byproduct (Dormann et al., 2012). Just like types of models, hybrid or integrated models can be created using both correlative and mechanistic methodology (Dormann et al., 2012). The distinction on type and method of a constructed model is important for assessing the appropriate method for the desired goal of the research.

Though an SDM may have a specific construction and intention, the quality of the data directly relates to the quality of the model. For example, if occurrences or key environmental parameters are missing from a correlational model, that model is likely unrealistic and worthless (Srivastava et al., 2019). The data used needs to have a reasonable representation of the actual species distribution to be able to model potential distributions. Modeling software assumes that the only species occurrences that exist within the study area are the ones that are input (Booth, 2018). More than just a complete set of occurrences, the inclusion of occurrence absence data can indicate what factors prevent species distribution (Barve et al., 2011; Srivastava et al., 2019). For environmental parameters, only those relevant to the distribution should be included, and parameters should be tested for correlation to prevent overfitting (Srivastava et al., 2019).

Beyond the data source, models should be evaluated statistically and compared to other models; the more iterations run, the better the model will perform (Barve et al., 2011; Srivastava et al., 2019). Finally, grounding the model within a real geographical space by creating a map indicates the relevancy of the model more than a theoretical equation (Srivastava et al., 2019). To construct a useful distribution model the data must be complete and relevant to the methodology of building the model and the information the model is trying to demonstrate.

Modeling Software

Availability of worldwide climate data from databases like WorldClim at the turn of the century caused the boom of distribution modeling research (Pecchi et al., 2019). WorldClim's data was available through the first SDM package BIOCLIM, a collection of 12 climate variables in 1984, which then increased to 35 by 1999 (Booth, 2018; Pecchi et al., 2019). Models created within BIOCLIM describe species occurrences as a range of the climate variables, therefore indicating which variables were the most important in building those models (Booth, 2018).

Since its development, BIOCLIM has been used for modeling environmental distribution, species invasion, rare species occurrences, and site planning for reintroduction of species (Booth, 2018; Booth et al., 2014).

The benefits of BIOCLIM primarily come from its high resolution environmental data and its ease of use: only occurrence data needs to be input to run a model (Booth, 2018). However, BIOCLIM lacks complexity, as it does not include any biotic parameters and can only produce abiotic based models (Booth et al., 2014). Furthermore, though BIOCLIM can produce relevant models for current species extent, it is unable to model future distributions as there are no future climatic data projections (Booth, 2018). The BIOCLIM software was built into the WorldClim database, where the 19 climate parameters are free to download and still see frequent use today for constructing ENMs and SDMs (Booth, 2018; Booth et al., 2014).

The software often used in place of BIOCLIM for presence-only distribution modeling is MaxEnt. MaxEnt stands for “maximum entropy” and works by comparing the randomness of the given occurrence distribution and study area to determine the likelihood of species presence on a scale from 1 to 0 (Pecchi et al., 2019; Phillips et al., 2006; Srivastava et al., 2019). The final model is represented as a heat map of this scale, indicating likelihood of distribution. MaxEnt is primarily a presence-only model, only requiring inputs of occurrence prescenses and environmental variables, but can be modified to include presence and absence data if available (Phillips et al., 2006).

MaxEnt is a generative model, meaning its goal is to learn about the input data and generate new data (Phillips et al., 2006). In contrast, discriminative models like generalized linear or additive models (GLM/GAM) are more common in machine learning; these models can only categorize and create boundaries between dissimilar data (Phillips et al., 2006). Essentially, generative models account for the information at every data point to build their results, rather than building off discriminative groups of data. This plays into the greatest strength of MaxEnt that GLMs and GAMs lack: its ability to create a model with highly predictive accuracy off a small amount of data (Baldwin, 2009; Melo-Merino et al., 2020; Phillips et al., 2006). The lower occurrence requirement allows for models to be created for species distributed in areas inaccessible to survey (Baldwin, 2009). Furthermore, GLMs and GAMs require presence-absence data to correctly run; if absence data is not available, background points are used instead, causing a misleading result (Phillips et al., 2006). MaxEnt will never count dataless areas as occurrence absences, and gives a direct probability distribution of occurrences over the study area rather than just an idea of environmental preference (Phillips et al., 2006).

MaxEnt is also robust against spatial error; specimens with nonspecific locality data can still be used without disrupting the model with locational error (Baldwin, 2009). Penalty functions within the software prevent model overfitting where there is an interaction or correlation between environmental parameters (Srivastava et al., 2019). Compared to other presence-only systems like genetic algorithm for rule set production (GARP) and ecological niche factor analysis (ENFA), MaxEnt produced more confident models and higher resolution maps for its original test and bryophyte species (Phillips et al., 2006; Sérgio et al., 2007). Overall, MaxEnt can model species distribution witch high confidence without a large dataset and excessive variable preparation before modeling.

Maxent models are often validated with area under the curve (AUC) values and a jackknife plots. AUC is the area underneath a receiver operating characteristic curve (ROC) and can be used to determine if random presence sites have an appropriately higher predicted value than random absence sites (Convertino et al., 2012). This value is the measurement used to determine how well the model can discriminate between these sites, indicating the quality of the model (Convertino et al., 2012). The larger the AUC, or area between the curve of the created model and the random reference model, the higher the confidence of the model (Phillips, 2017).

The jackknife plot measures the importance of each environmental parameter by running models dependent on that single variable and models with all variables excluding that one. All of these models are compared to the training gain of the full model to identify which variables make the largest contribution (Convertino et al., 2012). The foundational variables are those with a large determination value in the isolated model and a low value in the removed model (Convertino et al., 2012; Phillips, 2017). Evaluation of AUC and jackknife plots provides an insight into the creation process of the bryophyte models and can be used to estimate generalized and specific niches. The heat maps of the MaxEnt model provide a visualization of bryophyte ranges for sampling and conservation efforts.

Objectives

In Chapter 2 the aim is to construct models of common Illinois bryophytes at the species and genus level. We prioritize data cleaning and thinning for both the occurrence points and the environmental variables to prevent overfitting. The models will be compared based on confidence (AUC), distribution differences, and contribution of environmental variables. This information will allow us to assess the use of MaxEnt for modeling Illinois bryophytes, and will be verified further by collections predicted by the models. It is hypothesized that there will be a difference in distribution and niche determination between the generic level and species level, as the former includes a potential variety of life strategies. Furthermore, as land use and climate variables have been shown to impact bryophyte distribution, it is predicted these models will accurately reflect the real-world distribution of selected bryophytes in Illinois. With quality models, similarities and differences between predicted distributions and niche estimates can be used to assess ecology across bryophyte species and genera.

Methods

Pilot Study

Techniques for distribution mapping of Illinois bryophytes were originally explored in a pilot study (Ryan et al., 2023). The aim of that publication was to offer a detailed introduction to species distribution modeling using open-source software. Exploratory and feasibility studies were performed evaluating the use of bryophytes. The occurrence and climate data were put into QGIS version 3.1.4 to filter and trim to the boundary of Illinois. The cleaned data was input into the MaxEnt Java-based application, creating models of predicted species distribution.

Occurrence Preparation

Bryophyte occurrence data was collected from the Consortium of Bryophyte Herbaria (www.bryophyteportal.org/portal), an online data infrastructure, currently representing over 1.5 million records, that aggregates scientific collection data from over 135 herbaria worldwide. The Bryophyte Portal was selected over GBIF, an international biodiversity database, due to GBIF’s lower number of Illinois bryophyte records. Over 12,000 occurrences were downloaded from the portal that were listed to be in Illinois and included longitude and latitude data (Appendix A).

Records were sorted by number of occurrences per species and genera to determine the most common groups detected in Illinois. The taxonomy and classification of the species and genera, with highest number of occurrences, follows a combination of nomenclatural resources including Goffinet et al. (2008), Goffinet & Buck (2023) and Brinda & Atwood (2023). The following genera selected were determined to be the most detected in the state based on occurrence records: *Anomodon* Hook & Taylor*, Atrichum* P. Beauv.*, Brachythecium* Schimp.*, Bryum* Hedw.*, Dicranum* Hedw.*, Entodon* Müll. Hal.*, Fissidens* Hedw.*, Frullania* Raddi*, Amblystegium* Schimp.*, Hypnum* Hedw.*, Leskea* Hedw.*, Plagiomnium* T.J. Kop., and *Platygyrium* Schimp. The species with the highest number of occurrences were also renamed based on updated taxonomy. The following common epiphytes were selected for modeling: *Amblystegium riparium* (Hedw.) Schimp.*, Amblystegium serpens* (Hedw.) Schimp.*, Amblystegium varium* (Hedw.) Lindb.*, Anomodon attenuatus* (Hedw.) Huebener*, Anomodon rostratus* (Hedw.) Schimp.*, Brachythecium acuminatum* (Hedw.) Austin*, Callicladium haldaneanum* (Gre.) H.A. Crum*, Ceratodon purpureus* (Hedw.) Brid.*, Climacium americanum* Brid.*, Entodon seductrix* (Hedw.) Müll. Hal.*, Leskea gracilescens* Hedw.*, Plagiomnium cuspidatum* (Hedw.) T.J. Kop., and *Platygyrium repens* (Brid.) Schimp. Selected Illinois specimens of taxa used in these studies were randomly verified for correct identification. Those specimens examined all had correct identification.

All genera and species data were filtered to include only occurrences found post 1970, as this is the earliest year included within the climate data. Occurrences were trimmed down to the Illinois boundary in R (v4.2.2; R Core Team, 2022) using the sf package (v1.0.9; Pebsma, 2018) to ensure all records were found within the state (Appendix B). Any occurrences with missing data were removed. Occurrences were further removed using the spThin package (v0.2.0; Aiello-

Lammens et al., 2015) in a process called spatial thinning to only include occurrences 5 km apart from each other at a minimum. This thinning process prevents the overrepresentation of any species or genera and discourages model overfitting. Table 2-1 includes the number of genera occurrences originally downloaded from the Bryophyte Portal and the final number of occurrences used to build the models. Table 2-2 includes the original and final number of occurrences used for the species models.

Table 2-1. Number of occurrence records by genera downloaded and number used for the final models after reclassifying and thinning.

Genus	Total Records	Records Used
Amblystegium	434	169
Anomodon	406	130
Atrichum	359	149
Brachythecium	570	140
Bryum	297	97
Dicranum	211	73
Entodon	401	139
Fissidens	361	119
Frullania	212	68
Hypnum	201	75
Leskea	305	106
Plagiomnium	240	210
Platygyrium	252	85

Table 2-2. Number of occurrence records by species downloaded and number used for the final models after reclassifying and thinning.

Species	**Total Records**	**Records Used**
Amblystegium riparium	155	46
Amblystegium serpens	144	30
Amblystegium varium	194	36
Anomodon attenuatus	164	46
Anomodon rostratus	117	36
Brachythecium acuminatum	259	51
Callicladium haldaneanum	149	29
Ceratodon purpureus	129	34
Climacium americanum	119	29
Entodon seductrix	298	73
Leskea gracilescens	213	56
Plagiomnium cuspidatum	392	70
Platygyrium repens	252	47

Environmental Raster Preparation

Climate data is represented by the Bioclim variables from the WorldClim database (www.worldclim.org/data/bioclim.html). The models are built on the most recent version 2.1 of the data from 1970-2000, at a resolution of approximately 1 km^2. Land use variables are represented by the USA NLCD land cover and tree canopy rasters downloaded from the ArcGIS Online Portal. The layers represent the type of environment and percent coverage by trees respectively as of 2016, the most recent year when both layers were produced.

The raster package (v3.6.11; Hijmans, 2022) in R was used to project the land use variables into WGS84 to match the projection of the Bioclim variables (Appendix B). The land use variables were also resampled, increasing their pixel size to match the 1 km^2 Bioclim variables, as well as reclassified to properly represent their categorical data. All rasters were trimmed down to the extent of IL and stacked together for Spearman correlation analysis. Rasters were removed from the dataset if their correlation coefficient was greater than the absolute value of 0.7 to prevent overfitting of the model. The final raster set included Bioclim 1: Annual Mean Temperature, Bioclim 2: Mean Diurnal Range (Mean of monthly (max temp-min temp)), Bioclim 7: Temperature Annual Range (Bioclim 5-Bioclim 6), Bioclim 13: Precipitation of Wettest Month, Bioclim 18: Precipitation of Warmest Quarter, NLCD Land Cover, and NLCD Tree Canopy Cover.

Model Running and AUC Threshold

Ten thousand random points were selected within Illinois to act as pseudo-absence points to compare to the occurrence, or presence points. Occurrences were randomly split: 75% in the training group to create the model and 25% in the testing group to test model accuracy. Using the dismo package (v1.3.9; Hijmans et al., 2022), preliminary MaxEnt cross-validation models were run with 10 replicates for all species and genera. Cross-validation splits the training data into equivalently sized smaller groups called folds, running the model with all the folds except one, and using the remaining fold for evaluation (Phillips, 2017). This produces an averaged AUC value across the 10 models to give a more accurate representation of model quality. Final models are run with all of the test and training data and produce an AUC value, a jackknife plot, and a heat map of potential distribution. Heat maps were checked for general accuracy based on the Bryophyte Portal occurrences and known Illinois range.

In Situ/Field Validation of Species Distribution Models

A combination of searching for target species in the field combined with non-databased herbarium specimens were used to verify models. The occurrences and heat maps of the five species with the highest AUC were input into ArcGIS Pro to get more precise localities of predicted areas of distribution and presented in approximately 1 km grids. Five selected 1 km^2 areas near Chicago were surveyed for their likelihood of species presence, serving as a real-world verification of the predictive models. Sampling efforts were targeted towards the center of each of these grid areas. Several logistical and practical reasons provided constraints, e.g., access to private backyards, but the observations and collections served as a reasonable proxy for testing predicted occurrences. Voucher specimens collected are deposited at the Field Museum herbarium. Those areas with high likelihood and low likelihood for all five species, without an occurrence present, were targeted for sampling. Collections or observations were also made of bryophytes generally, beyond the targeted five. Bryophyte specimens were also collected from the Nachusa Grasslands, an area with many habitats ranging from rocky outcrops to oak savannah, as part of an ongoing inventory study. Specimens that are part of Field Museum herbarium not included in public repositories that represent regions of Illinois with a predicted high likelihood, such as Lowden Miller State Forest, also served to verify models.

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Results

Genera Models

All AUC values for full (including testing and training data) genera models were above 0.8 aside for *Anomodon*, indicating high confidence in predicting genus distribution. Table 2-3 presents the genera models ranked by AUC value, as well as highlighting the most important environmental variables that contributed most to the model. The single variable models, represented by the dark blue bar on the jackknife plots, were compared on training gain and the two with the highest values were selected as the top and second critical environmental variables. The most unique environmental variable was determined by the lowest training gain of the models that remove a variable, the teal bars on the jackknifes.

Land Cover, Canopy Cover, and Mean Diurnal Range (Bioclim 2) were determined to be the most important variables for model construction. Land Cover produced the highest training gain for all genera aside from *Frullania*, where it was second to Canopy Cover. *Frullania* is the only liverwort representation in this study; all other models, species and genera, are mosses. In addition, *Frullania* species are known for their mostly epiphytic life strategy (e.g., Hentschel et al. 2009), whereas the other genera are more variable. The specific presence and density of trees is therefore more important to *Frullania* distribution than to other genera.

Models are presented in order from highest to lowest AUC value per Table 2-3. All predictive maps represent the likelihood of distribution, with green areas meaning a high likelihood of finding an occurrence of that genus, and gray and light red representing a low likelihood.

Table 2-3. Current genera model quality with most important and unique environmental variables. Any AUC value above 0.8 is considered a confident model.

Genus	**Full Model AUC**	**Top Critical Environmental Variable**	**Second Critical Environmental Variable**	**Most Unique Environmental Variable**
Dicranum	0.94	Land Cover	Canopy Cover	Canopy Cover
Fissidens	0.92	Land Cover	Canopy Cover	Canopy Cover
Platygyrium	0.90	Land Cover	Canopy Cover	Canopy Cover
Plagiomnium	0.87	Land Cover	Canopy Cover	Land Cover
Leskea	0.87	Land Cover	Canopy Cover	Canopy Cover
Brachythecium	0.87	Land Cover	Mean Diurnal Range	Canopy Cover
Bryum	0.86	Land Cover	Mean Diurnal Range	Land Cover
Frullania	0.85	Canopy Cover	Land Cover	Canopy Cover
Atrichum	0.85	Land Cover	Canopy Cover	Canopy Cover
Amblystegium	0.84	Land Cover	Canopy Cover	Canopy Cover
Entodon	0.83	Land Cover	Canopy Cover	Land Cover
Hypnum	0.81	Land Cover	Mean Diurnal Range	Canopy Cover
Anomodon	0.75	Land Cover	Canopy Cover	Land Cover

Notable habitat, substrate, and environmental factors for each genus is shown in Table 2-4. The key areas in the models of the genera that show high likelihood for distribution are also summarized, listed in order of size and highest likelihood values. Genera presented without environmental information lack research in characterization of their specific habitat. Overall, the majority of these genera are primarily found in temperate regions within moist environments, which would suggest that these genera would have the highest likelihood around bodies of water. Though this trend appears, particularly with high likelihood around the Illinois River for most of the models, the Chicagoland area shows a more consistent area of high likelihood. This implies the relevance of factors beyond climate and moist environments, such as forested areas around the Chicago suburbs. This is further supported by the high likelihood in Southern Illinois for a majority of the models.

Table 2-4. Common habitats and high potential distribution areas of the selected genera. Sources: *California Moss EFlora*, 2021; Crum, 1976; *Flora of North America*, 2023; Ludwiczuk & Asakawa, 2021, and Zhu et al., 2023.

Genus	Habitat Characteristics	Areas of High Likelihood
Dicranum	Wood, rock, humus, soil	Chicagoland area, Southern Illinois, Illinois River
Fissidens	Streams; wet and flooded rock, disturbed soil	Chicagoland area, Southern Illinois, Illinois River
Platygyrium	Tree bark, logs, stumps, rock	Chicagoland area, Southern Illinois, Illinois River
Plagiomnium	Shaded stream banks, springs; humus, soil	Chicagoland area, Illinois River, Northwestern Illinois
Leskea	Terrestrial; trees and tree bases, rock, soil	Chicagoland area, Illinois River, Southern Illinois
Brachythecium	Moist areas, not flooded	Chicagoland area, Illinois River, Southern Illinois
Bryum	Wide habitat range, urban environments; sand, concrete and pavement, rock	Chicagoland area, Illinois River
Frullania	Frequently epiphytic; tree bark	Southern Illinois
Atrichum	Moist environments, soil banks, disturbed areas; tree bases	Chicagoland area, Southern Illinois, Illinois River
Amblystegium	Swamps, moist and wet areas; terrestrial	Chicagoland area, Illinois River, Southern Illinois
Entodon	Moist environments; tree bark, rotten wood, soil	Chicagoland area, Illinois River, Southern Illinois
Hypnum	Streams, waterways, moist environments; tree bark, rotten wood, rock, soil	Chicagoland area, Eastern Illinois, Southern Illinois
Anomodon	Tree bases, logs, rocks	Chicagoland area, Southern Illinois, Illinois River, Northwestern Illinois

Dicranum

The full model of *Dicranum* [full AUC = 0.94, replicate AUC = 0.87] has areas of high distribution likelihood in the Chicago suburbs and the forested areas in Southern Illinois (Figure 2-2). In addition, there are a few high likelihood areas scattered mainly around water features in Central Illinois, which stands out against the majority no to low distribution likelihood of this area. As Land Cover is the most important variable for the model, followed by Canopy Cover, the land use and type of habitat is most determinate for *Dicranum* distribution, specifically highlighting forested and water adjacent areas.

Fissidens

The full model of *Fissidens* [full AUC = 0.92, replicate AUC = 0.83] highlights the Chicagoland area, Southern Illinois, and spots around Central Illinois as areas of highest distribution likelihood (Figure 2-3). Though similar to the distribution of *Dicranum*, the model of *Fissidens* predicts a high likelihood of distribution in the city of Chicago as opposed to only the area around it. Overall, the areas of high likelihood between these genera are similar, which is supported by their jackknife plots, with Land Cover and Canopy Cover being the most critical variables. However, *Fissidens* has more red areas of low likelihood where *Dicranum* has more strict no likelihood regions.

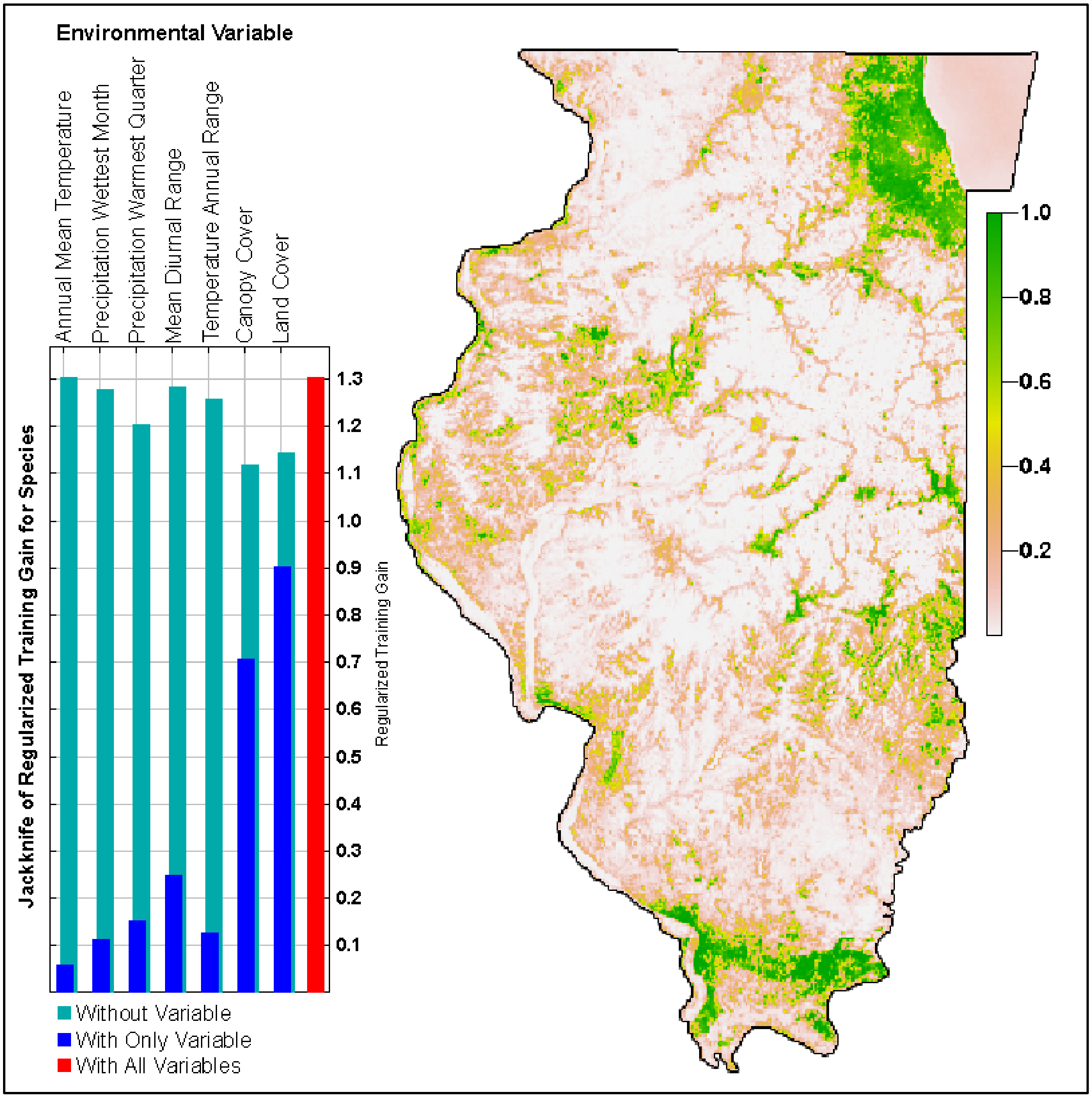

Figure 2-2. Predictive map and jackknife of environmental variables for *Dicranum*.

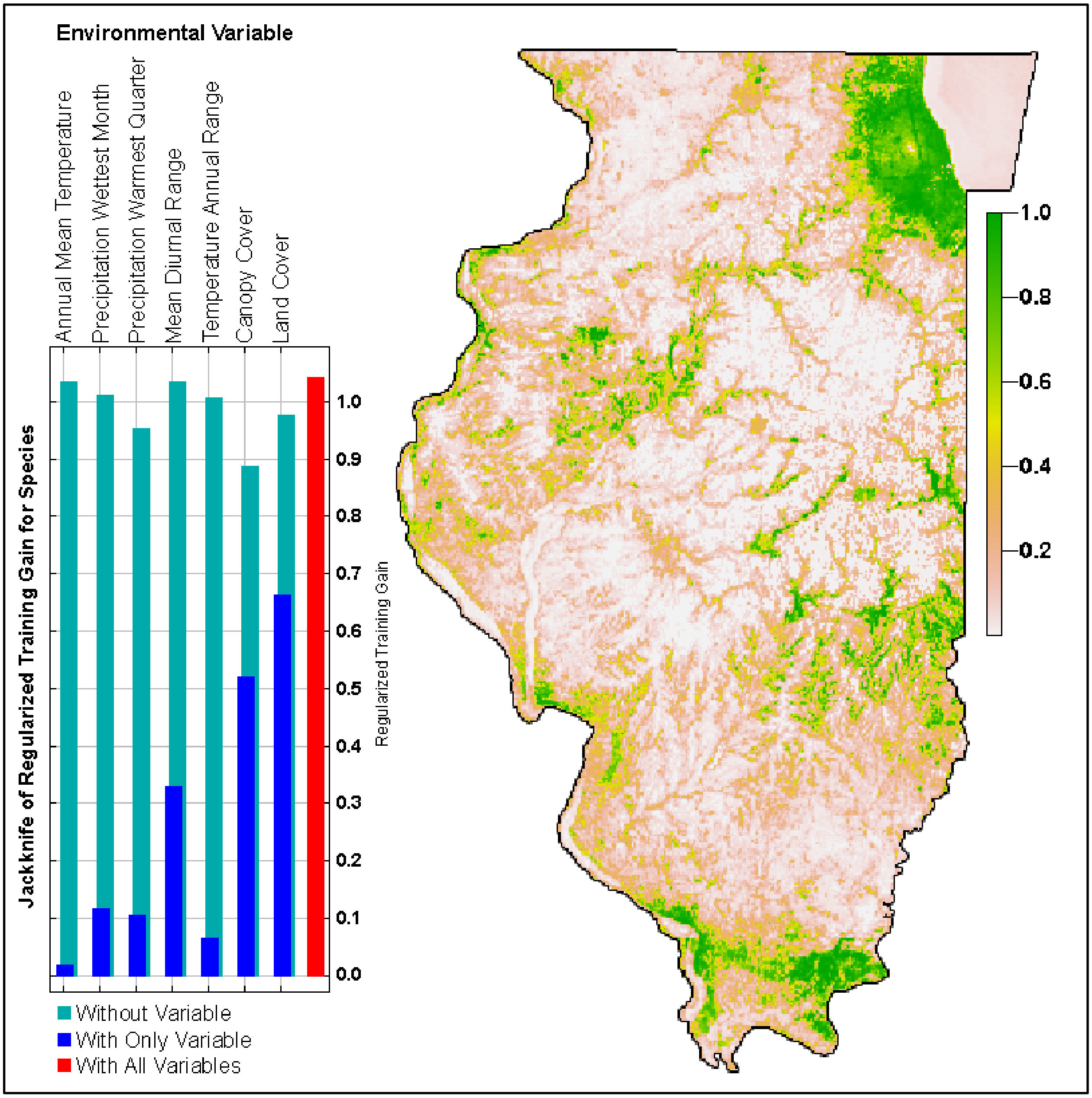

Figure 2-3. Predictive map and jackknife of environmental variables for *Fissidens*.

Platygyrium

The *Platygyrium* model [full AUC = 0.90, replicate AUC =0.86] has a smaller gap in AUC value than the previous two models. The *Platygyrium* distribution map appears very similar to the *Dicranum* map, particularly where both are highly likely to be distributed around, but not in Chicago (Figure 2-4). All areas of high distribution are consistent between the two, aside from *Platygyrium* having increased likelihood around the northwestern border of the state. In terms of variable importance, *Fissidens* and *Platygyrium* are much more similar, with a critical importance from Land Cover and Canopy Cover, as well as relevance of Mean Diurnal Range.

Plagiomnium

The model of *Plagiomnium* [full AUC = 0.87, replicate AUC = 0.83] additionally shows high distribution likelihood around Illinois rivers, even more so than the previous models (Figure 2-5). The emphasis on the habitat here in particular, as the Land Cover is the most important variable by far and supplies the most unique data to the model. The predictive map shows the highest distribution likelihood around the typical Chicagoland area and Southern Illinois forests, but the bodies of water around the state stand out more than any other previous model. The importance of Land Cover to the model also explains the high distribution likelihood in Illinois cities, such as Chicago, Rockford, Peoria, and Decatur.

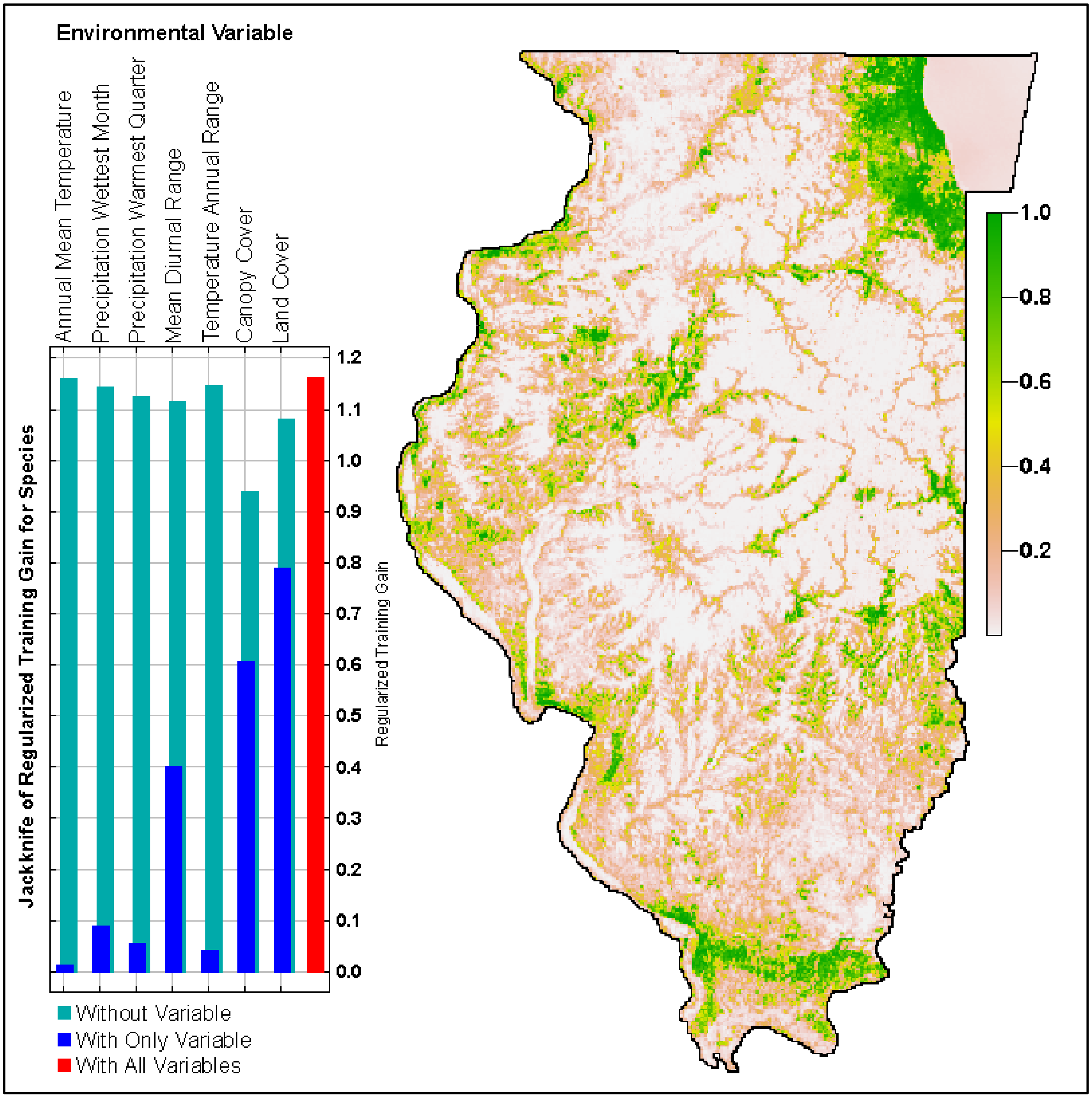

Figure 2-4. Predictive map and jackknife of environmental variables for *Platygyrium.*

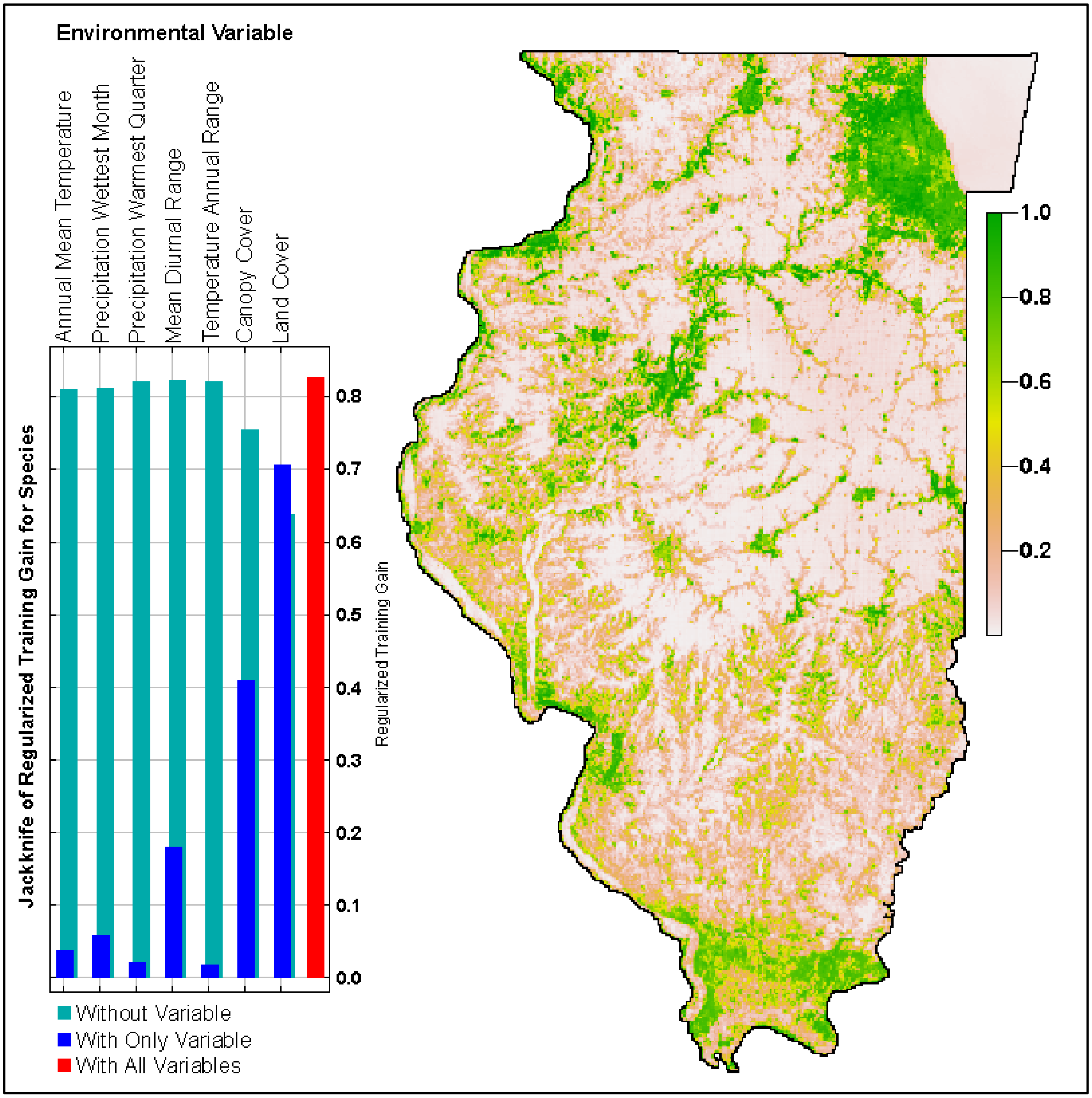

Figure 2-5. Predictive map and jackknife of environmental variables for *Plagiomnium*.

Leskea

Out of the models covered so far, *Leskea* [full AUC = 0.87, replicate AUC = 0.81] has a particularly high distribution likelihood for Chicago and the surrounding suburbs (Figure 2-6). In addition to high distribution in Southern and Eastern Illinois, there is high likelihood scattered around the west of the Illinois River. Overall it appears *Leskea* species are found in urban areas and those near water, which is supported by the prevalence of the Land Cover variable. Some forested areas show high distribution likelihood, but still are nearby to a water source or town; this is the result of Canopy Cover having an important contribution but not overwhelmingly so. It is about as relevant to Mean Diurnal Range, which differs from the models thus far.

Brachythecium

The model of *Brachythecium* [full AUC = 0.87, replicate AUC = 0.82] is similar to the model of *Leskea*, showing the highest distribution around bodies of water and urban areas (Figure 2-7). Furthermore, Land Cover is the most critical variable, with Mean Diurnal Range edging out over Canopy Cover. However, a major difference between these two models is the high likelihood in Northwest Illinois around the Mississippi and Illinois Rivers; the lands near rivers are suggested as a prime habitat for *Brachythecium* species.

Bryum

The model of *Bryum* [full AUC = 0.86, replicate AUC = 0.83] is also similar to the models of *Brachythecium* and *Leskea*, showing the highest distribution around urban areas and rivers throughout the state (Figure 2-8). Yet one key difference from all models of genera thus far is the lack of distribution in the Southern Illinois forests. This is the result of Canopy Cover not being as relevant as Mean Diurnal Range and Land Cover to the model.

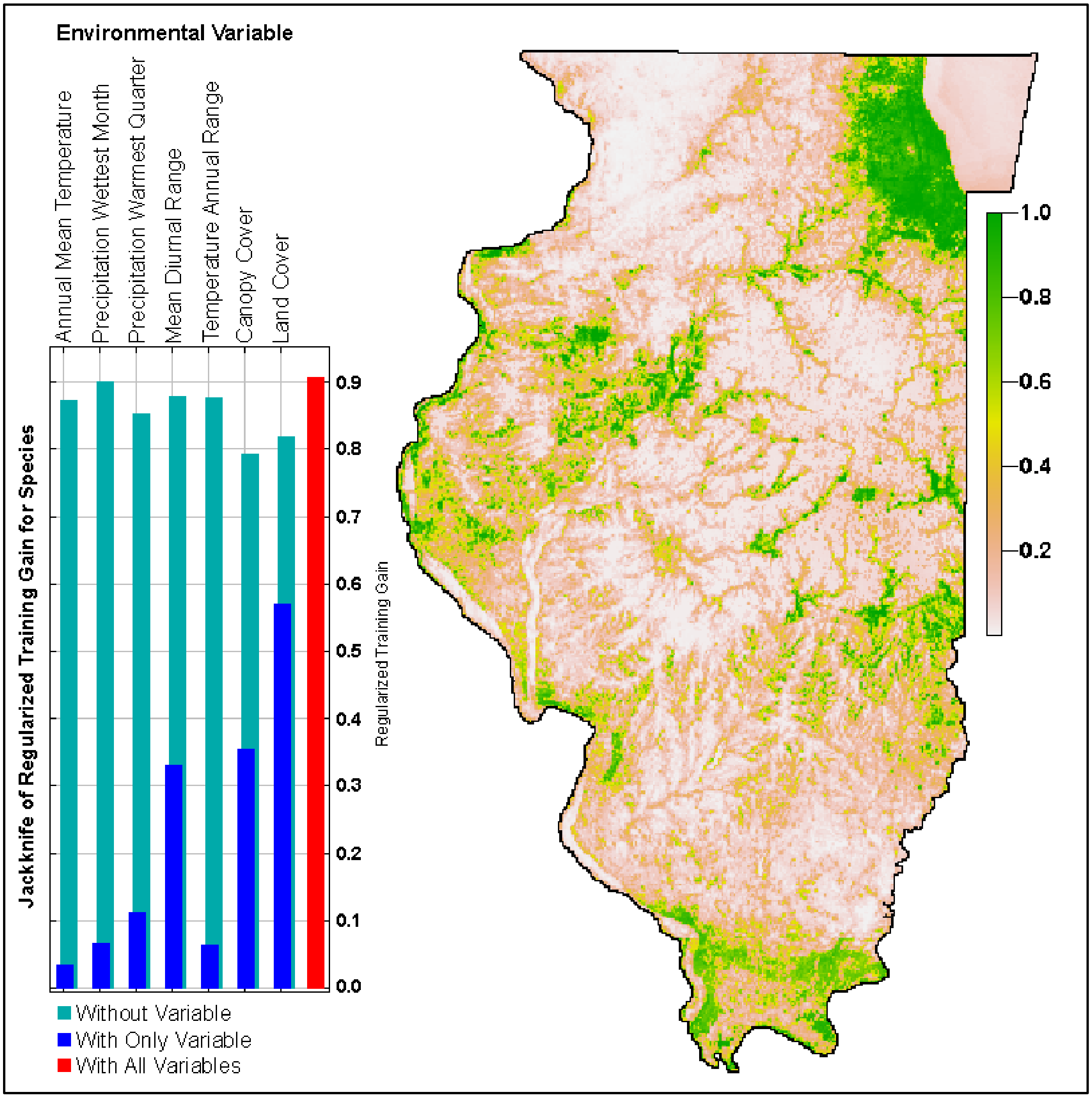

Figure 2-6. Predictive map and jackknife of environmental variables for *Leskea*.

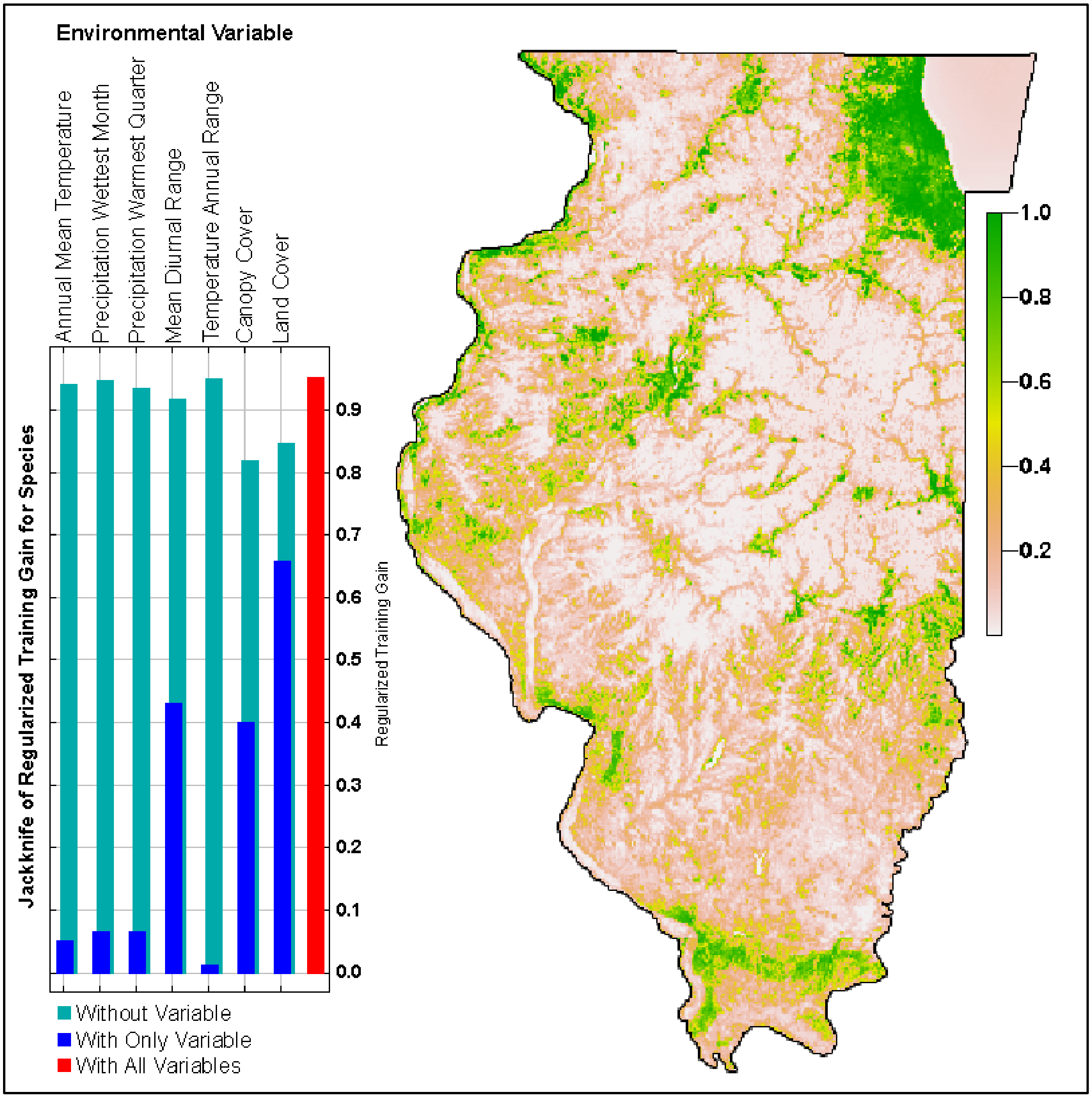

Figure 2-7. Predictive map and jackknife of environmental variables for *Brachythecium*.

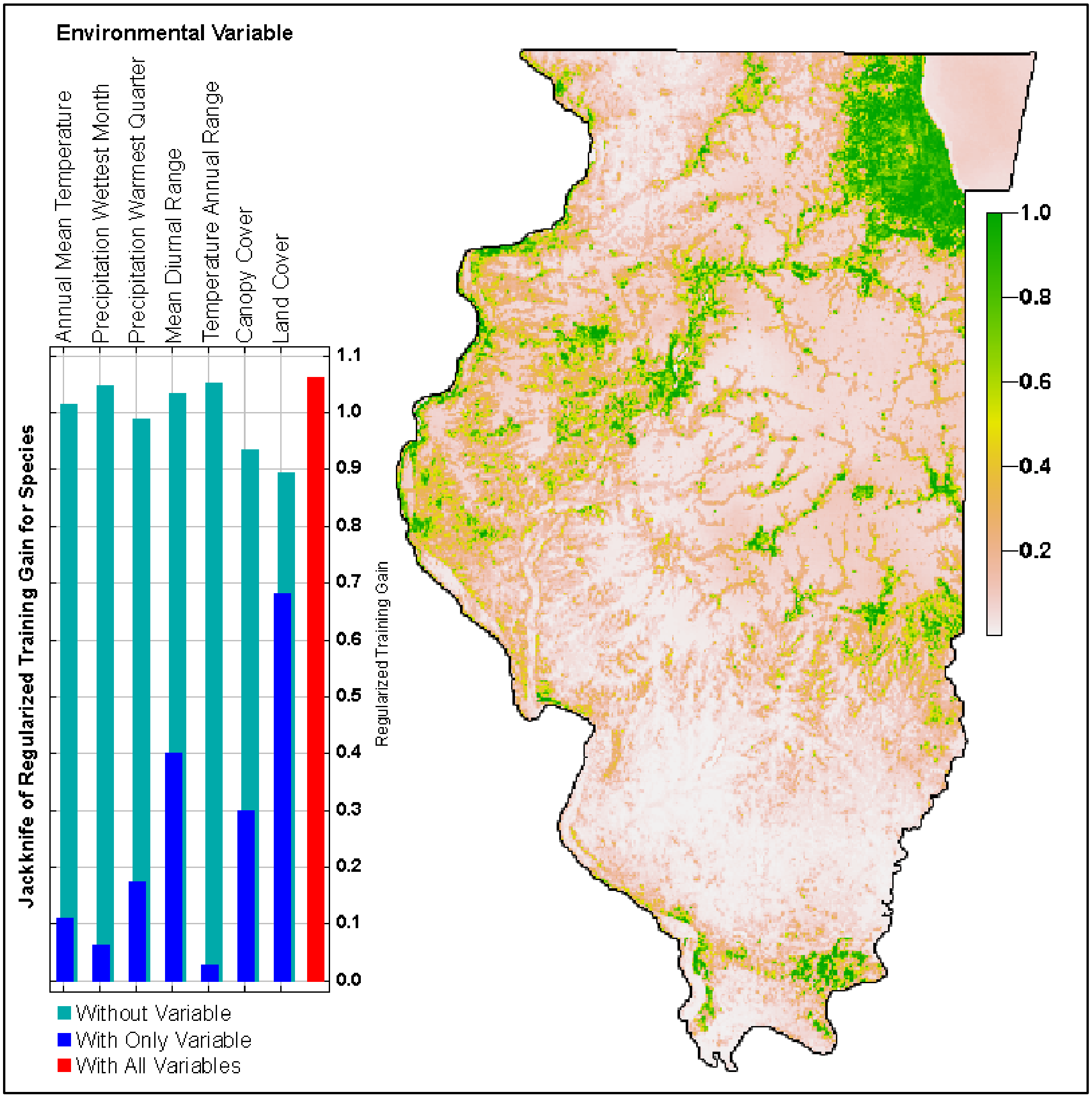

Figure 2-8. Predictive map and jackknife of environmental variables for *Bryum*.

Frullania

As previously discussed, *Frullania* [full AUC = 0.85, replicate AUC = 0.87] stands out from the other genera as the only liverwort and its primarily epiphytic life strategy. Its areas of high distribution differ the most from the other models, with the highest likelihood in the Southern Illinois forests and other forested areas around the state (Figure 2-9). This is supported by the high contribution of Canopy Cover, followed by land use which also incorporates forest presence. The model of *Frullania* is also the only model to show the importance of Annual Mean Temperature and Temperature Annual Range.

Atrichum

The model of *Atrichum* [full AUC = 0.85, replicate AUC = 0.85] is comparable to the model of *Fissidens*, with high distribution likelihood in Chicagoland, Southern Illinois, and around the Mississippi and Illinois Rivers (Figure 2-10). The jackknife is also comparable to *Fissidens* and *Platygyrium*, resulting in the highest gain from Land Cover, followed by Canopy Cover and Mean Diurnal Range.

Amblystegium

The model of *Amblystegium* [full AUC = 0.84, replicate AUC = 0.81] shares the high likelihood areas noted on all the models so far (Figure 2-11). But uniquely, there is a lack of no distribution areas, with most of the state being low distribution. Land Cover remains the most critical variable, but the similar contribution from Canopy Cover and Mean Diurnal Range results in a more generalized distribution.

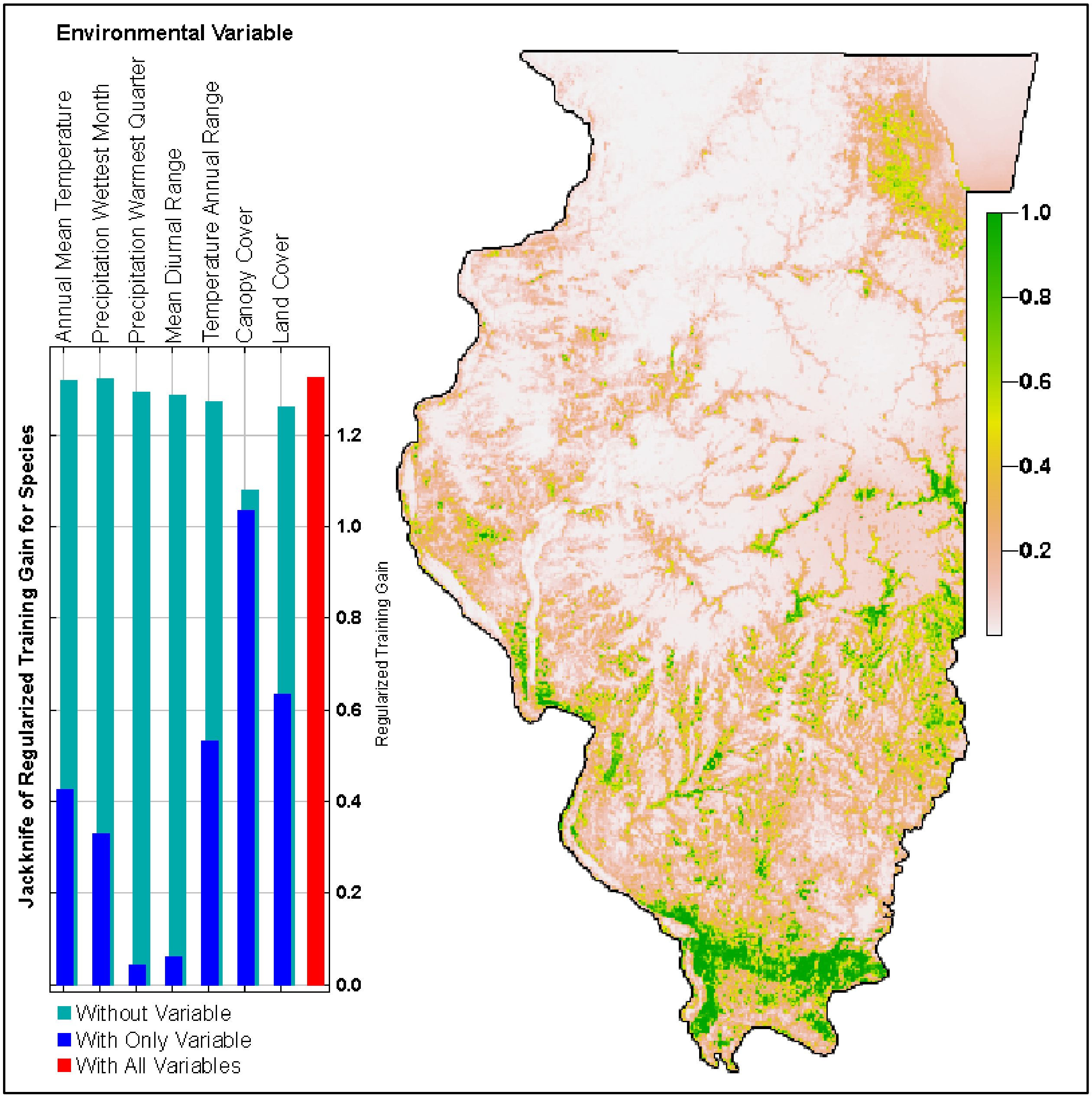

Figure 2-9. Predictive map and jackknife of environmental variables for *Frullania.*

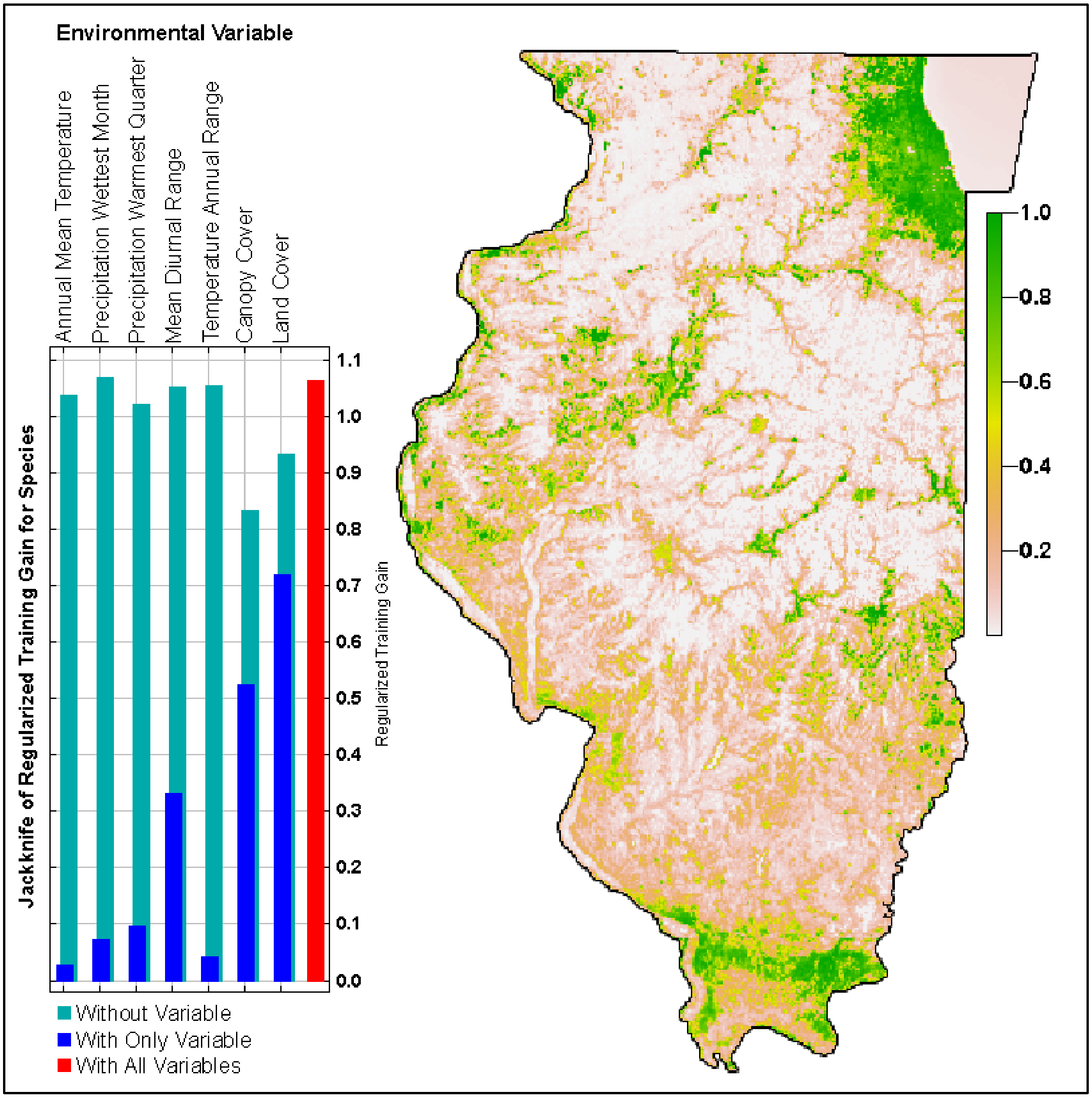

Figure 2-10. Predictive map and jackknife of environmental variables for *Atrichum*.

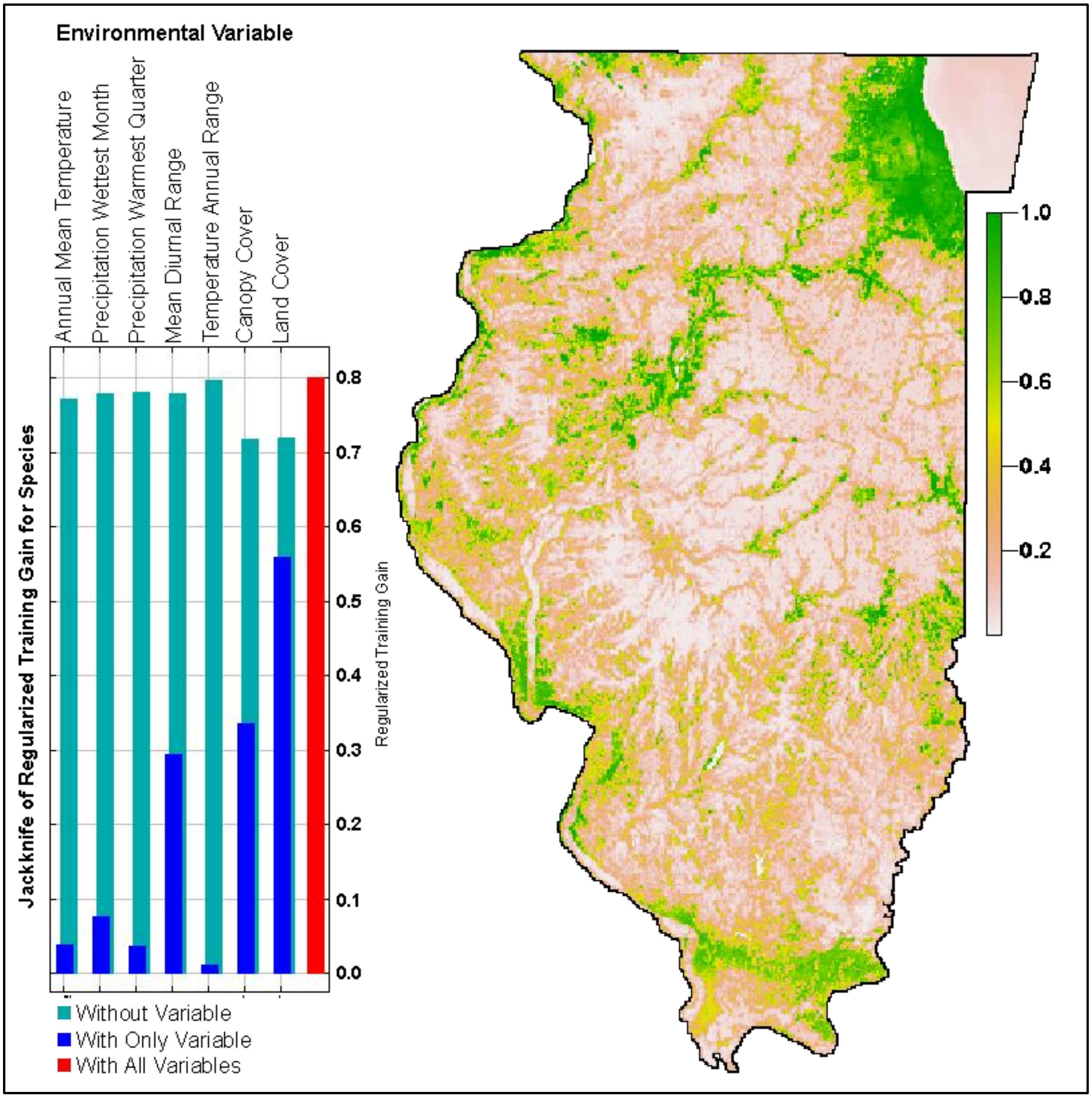

Figure 2-11. Predictive map and jackknife of environmental variables for *Amblystegium*.

Entodon

The model of *Entodon* [full AUC = 0.83, replicate AUC = 0.85] environmental variables are similar to those of the model of *Plagiomnium*: Land Cover being the most critical variable, followed by Canopy Cover, then Mean Diurnal Range (Figure 2-12). The *Entodon* map mirrors the *Plagiomnium* map as well, aside from lower distribution in the South and the central/north region. The distribution likelihood around Southern Illinois is one of the lowest compared to all the models.

Hypnum

The model of *Hypnum* [full AUC = 0.81, replicate AUC = 0.87] has Land Cover as the most critical variable, but Mean Diurnal Range carries more weight in the model than any other (Figure 2-13). This shapes the distribution likelihood, with distinctly high areas scattered around East Illinois. Like other models, there is a high distribution likelihood in the Chicagoland area and Southern Illinois, as well as a few areas around the Illinois River.

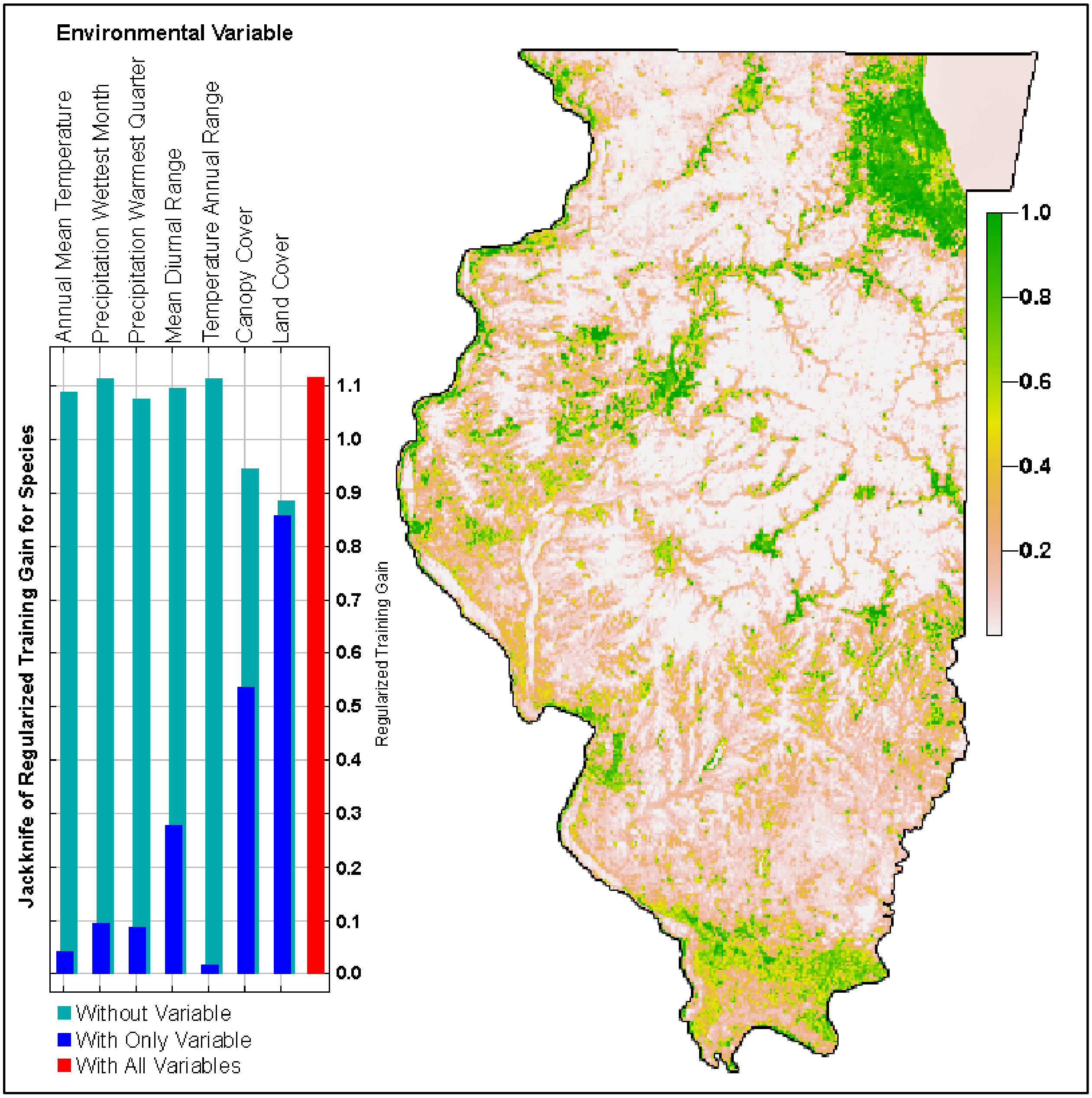

Figure 2-12. Predictive map and jackknife of environmental variables for *Entodon*.

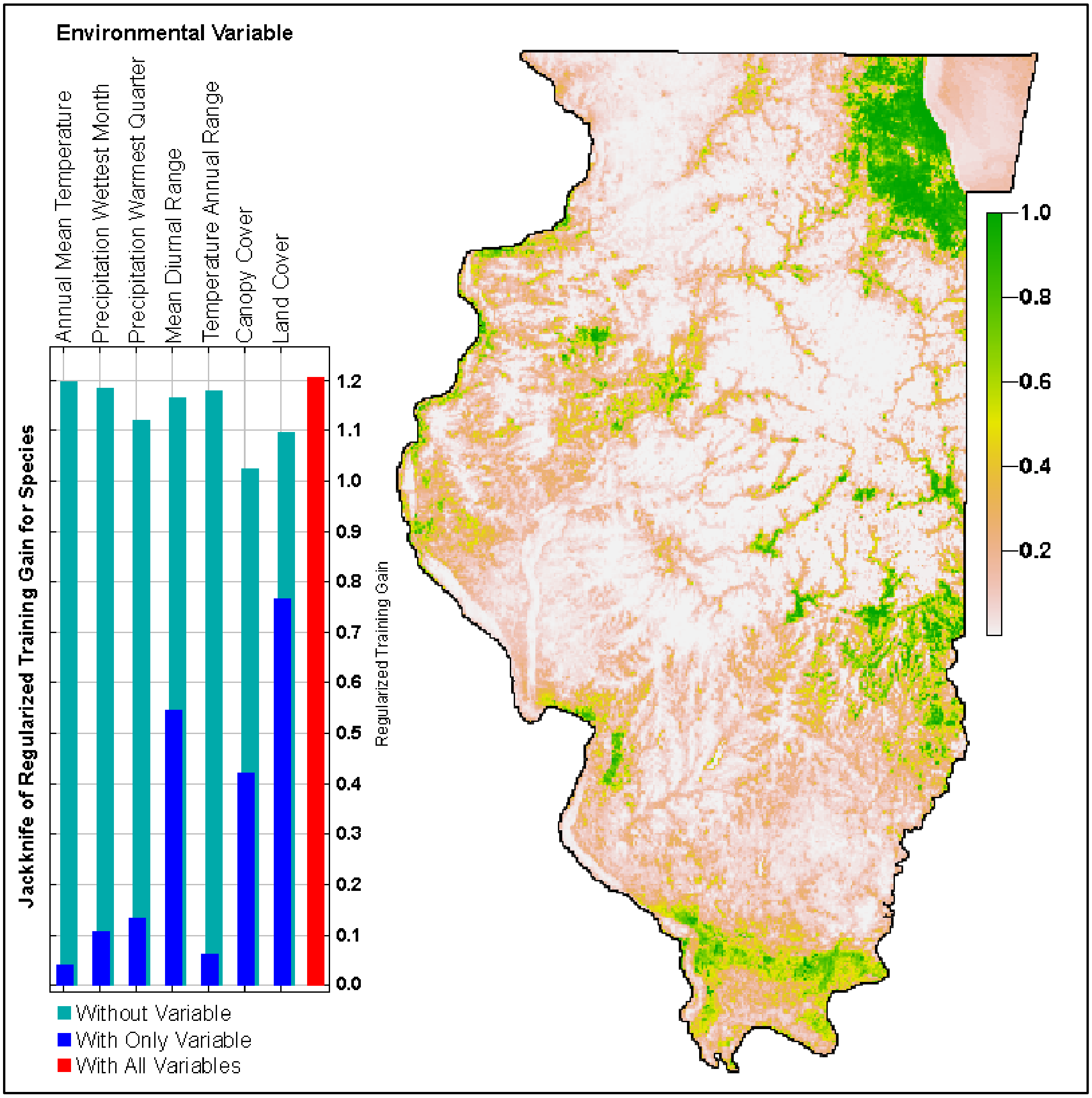

Figure 2-13. Predictive map and jackknife of environmental variables for *Hypnum.*

Anomodon

The model of *Anomodon* [full AUC = 0.75, replicate AUC = 0.82] has a distinctly low full model AUC, despite a higher number of occurrences. The lack of confidence of the model shows in the visible roads represented by red low distribution likelihood lines that are not present in any other model (Figure 2-14). Though the weight of the environmental variables on the model of *Anomodon* are similar to most of the other genera, it is visually apparent how reliant it is on Land Cover. The occurrences themselves do not reflect the high preference towards urbanization (including roads) that the model does. It is possible this genus might have other environmental factors not included in this study that are key in shaping its distribution. This misrepresentation of distribution with the low AUC value opposes the use of the model for real world distribution.

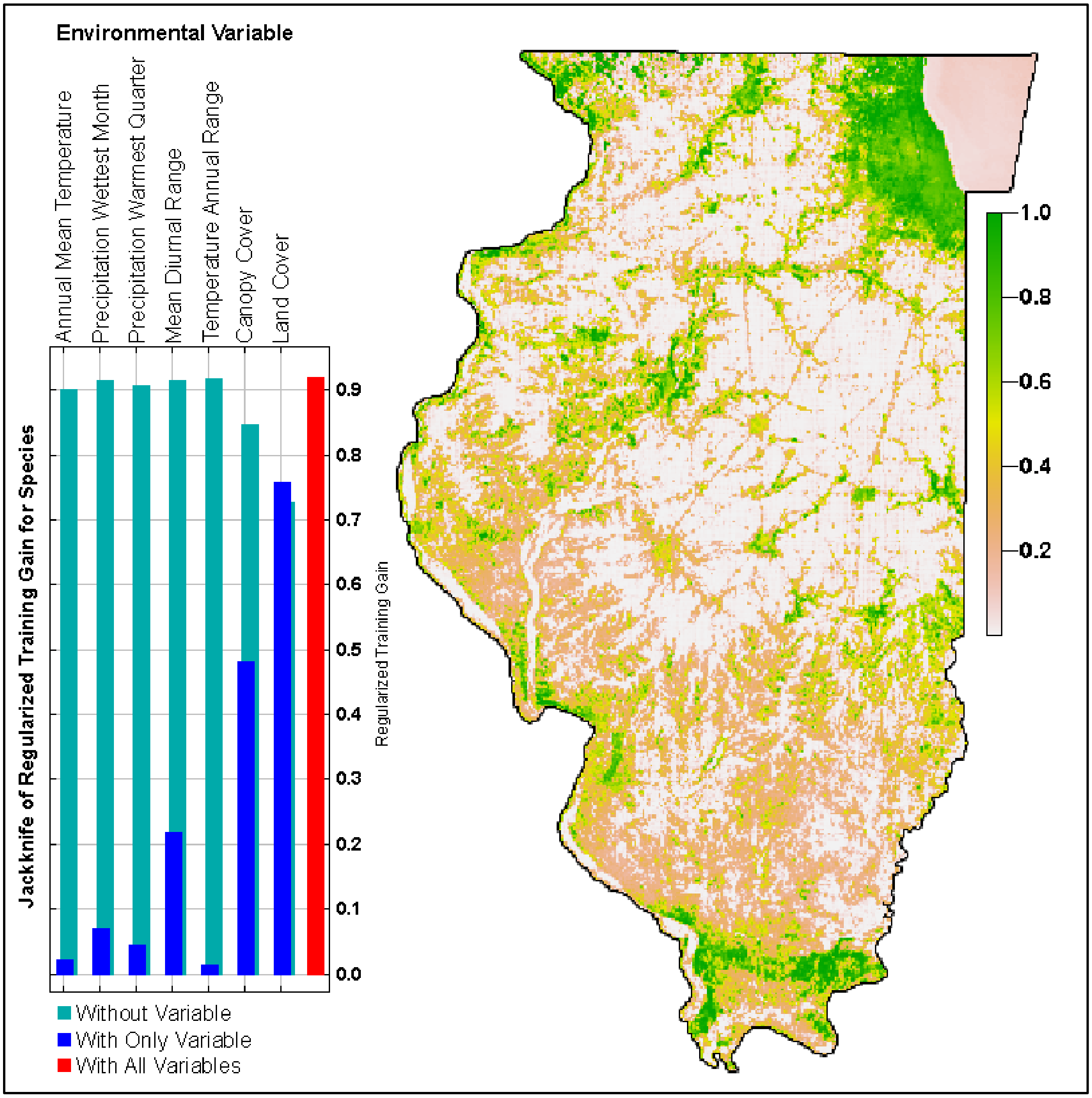

Figure 2-14. Predictive map and jackknife of environmental variables for *Anomodon.*

Species Models

AUC values for all full models of species were over 0.8 aside from *Amblystegium riparium*, indicating high model confidence (Table 2-5). Compared to the AUC of the models of genera, the models of species returned overall higher values.

Table 2-5. Current species model quality with most important and unique environmental variables. Any AUC value above 0.8 is considered a confident model.

Species	**Full Model AUC**	**Top Critical Environmental Variable**	**Second Critical Environmental Variable**	**Most Unique Environmental Variable**
Callicladium haldaneanum	0.98	Mean Diurnal Range	Canopy Cover	Canopy Cover
Amblystegium serpens	0.98	Mean Diurnal Range	Land Cover	Canopy Cover
Entodon seductrix	0.93	Land Cover	Canopy Cover	Canopy Cover
Amblystegium varium	0.93	Mean Diurnal Range	Land Cover	Canopy Cover
Leskea gracilescens	0.92	Mean Diurnal Range	Canopy Cover	Canopy Cover
Platygyrium repens	0.89	Canopy Cover	Mean Diurnal Range	Canopy Cover
Anomodon rostratus	0.89	Canopy Cover	Land Cover	Canopy Cover
Brachythecium acuminatum	0.86	Mean Diurnal Range	Land Cover	Canopy Cover
Plagiomnium cuspidatum	0.81	Canopy Cover	Land Cover	Canopy Cover
Climacium americanum	0.81	Canopy Cover	Land Cover	Canopy Cover
Ceratodon purpureus	0.81	Land Cover	Canopy Cover	Land Cover
Anomodon attenuatus	0.80	Canopy Cover	Land Cover	Canopy Cover
Amblystegium riparium	0.76	Land Cover	Mean Diurnal Range	Land Cover

The most critical environmental variable varies more widely than the genera, where it was dominated by Land Cover. Land Cover is still one of the top two variables in all models except two. Mean Diurnal Range and Canopy Cover are equally the top variable amongst all the models, but Canopy Cover appears more frequently in the second most critical, emphasizing its importance for the species overall.

The preferred habitats of the selected species and the areas of highest likelihood of their models are included in Table 2-6. Species without habitat information are lacking environmental characterization in published works. These habitats overall describe forested and moist environments, suggesting distribution to be limited to these environments. This is overall supported by the high potential likelihood in the forested areas of the Chicago suburbs and Southern Illinois, as well as the stream and lake environments around the Illinois River and Western Illinois. In comparison to the models of the genera, the models of the species show similar habitat characteristics and high likelihood areas but show more diversity between each other than the genera do. This is likely the result of a more particular lifestyle at the species level.

Callicaldium haldaneanum

The model of *Callicladium haldaneanum* [full AUC = 0.98, replicate AUC = 0.88] shows high likelihood areas scattered around the Chicagoland area and a couple spots near the Mississippi and Illinois Rivers (Figure 2-15). The model mainly relies on Mean Diurnal Range, however, Land Cover, Canopy Cover, and Temperature Annual Range share about equal importance to this model.

Table 2-6. Common habitats and high potential distribution areas of the selected species. Sources: Conrad & Redfearn, 1979 *Flora of North America*, 2023; Perdrizet & McKnight, 2012; and Sabovljević et al., 2022.

Species	**Habitat Characteristics**	**Areas of High Likelihood**
Callicladium haldaneanum	Conifer and hardwood forests; bases of trees, logs, stumps, rock, soil	Chicagoland area, Illinois River
Amblystegium serpens	Swamps, moist and moderate environments; tree trunks, rotting wood, rock, soil	Chicagoland area, Western Illinois
Entodon seductrix	Dry hardwood forests; bases of trees, rotting wood, rock, soil	Chicagoland area, Illinois River, Eastern Illinois, Southern Illinois
Amblystegium varium	Shady habitats; bases of trees, logs, rock, humus, soil	Chicagoland area
Leskea gracilescens	Base of and soil around hardwood trees, logs, rock, shingle roof	Chicagoland area, Eastern Illinois, Southern Illinois, Illinois River
Platygyrium repens	Moist forests, shaded areas; bases of trees, logs, stumps, rock, soil	Chicagoland area
Anomodon rostratus	Forests, wetlands; deciduous trees, rock, soil	Eastern Illinois, Chicagoland area, Southern Illinois, Illinois River
Brachythecium acuminatum	Tree trunks and bases of trees	Chicagoland area, Western Illinois
Plagiomnium cuspidatum	Wet meadows and forests, forested peatlands, hardwood forests, cliffs; bases of trees, logs, stumps, rock, soil	Illinois River, Chicagoland area
Climacium americanum	Streams, lakes, swamps, wet to moderate microhabitats; sandy and clay soil	Southern Illinois, Eastern Illinois
Ceratodon purpureus	Habitat variety, urban and disturbed areas; sidewalks, lawns, rock walls	Chicagoland area, Illinois River
Anomodon attenuatus	Trees, rock, soil	Southern Illinois, Eastern Illinois, Chicagoland area
Amblystegium riparium	Streams, rivers, swamps, wet and flooded forests; bases of trees, rock, humus	Chicagoland area, Southern Illinois, Eastern Illinois

Amblystegium serpens

The model of *Amblystegium serpens* [full AUC = 0.98, replicate AUC = 0.92] has similar key environmental variables to the model of *C. haldaneanum*: Mean Diurnal Range is the most critical, and Temperature Annual Range, Land Cover, and Canopy Cover follow behind (Figure 2-16). *A. serpens* shows the highest distribution likelihood also around the Chicagoland area, rivers, and Western Illinois, but covers a larger area than *C. haldaneanum*. The model of the *Amblystegium* genus shares the same high distribution likelihood areas as the model of *A. serpens*, but the former has a much more likely distribution throughout the whole state.

Entodon seductrix

The model of *Entodon seductrix* [full AUC = 0.93, replicate AUC = 0.83] notably has over twice the amount of occurrences included as the previous two. Both the model of *E. seductrix* and model of *Entodon* are the most reliant on Land Cover and Canopy Cover, as well as having similar areas of high distribution likelihood (Figure 2-17).

Amblystegium varium

The model of *Amblystegium varium* [full AUC = 0.93, replicate AUC = 0.95] shows great confidence due to the consistency of AUC values, despite the lower number of occurrences used. The areas of likelihood are also more consistent between the models of *A. varium* and *Amblystegium* than with *A. serpens* (Figure 2-18).

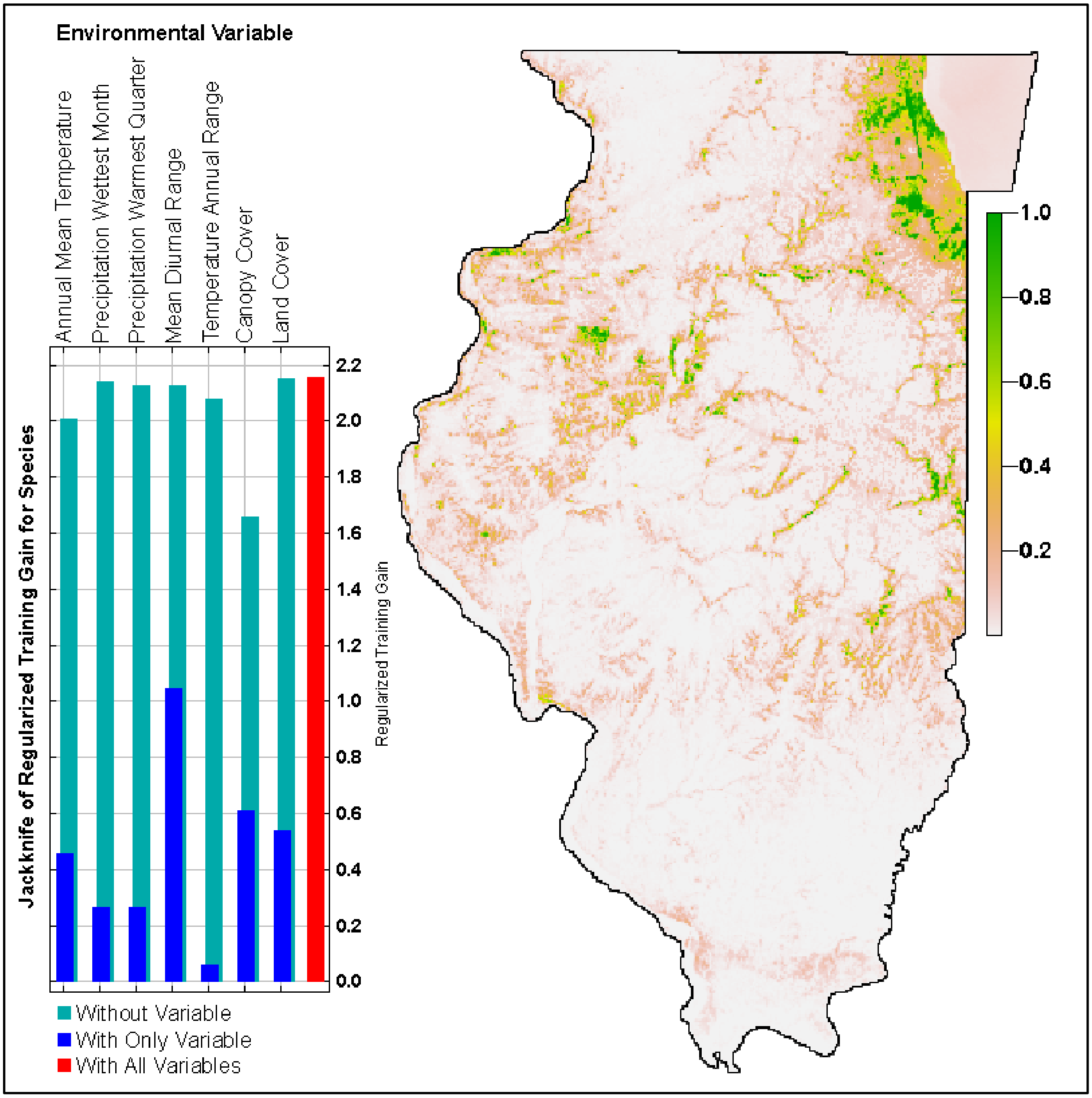

Figure 2-15. Predictive map and jackknife of environmental variables for *Callicladium haldaneanum.*

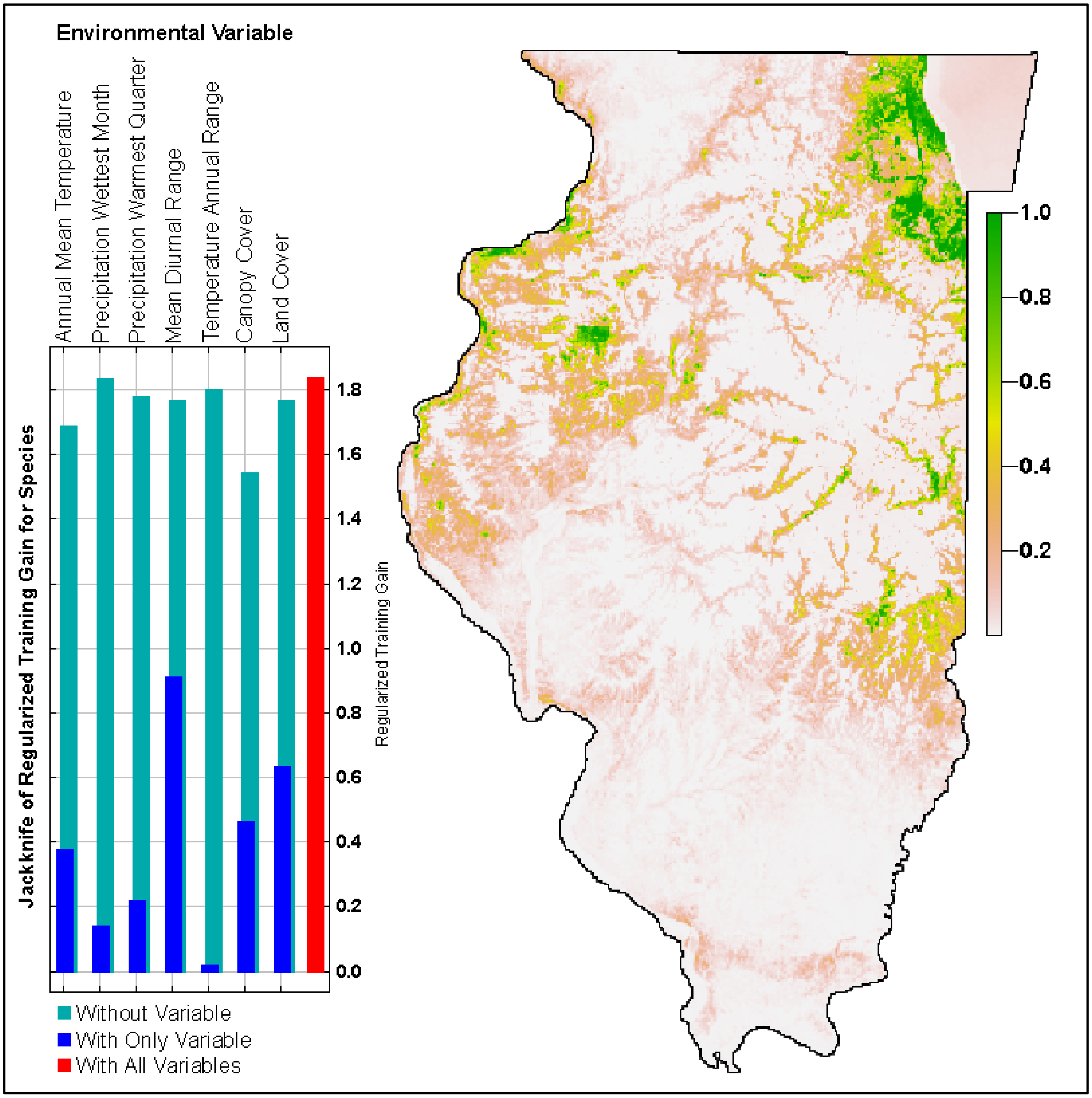

Figure 2-16. Predictive map and jackknife of environmental variables for *Amblystegium serpens.*

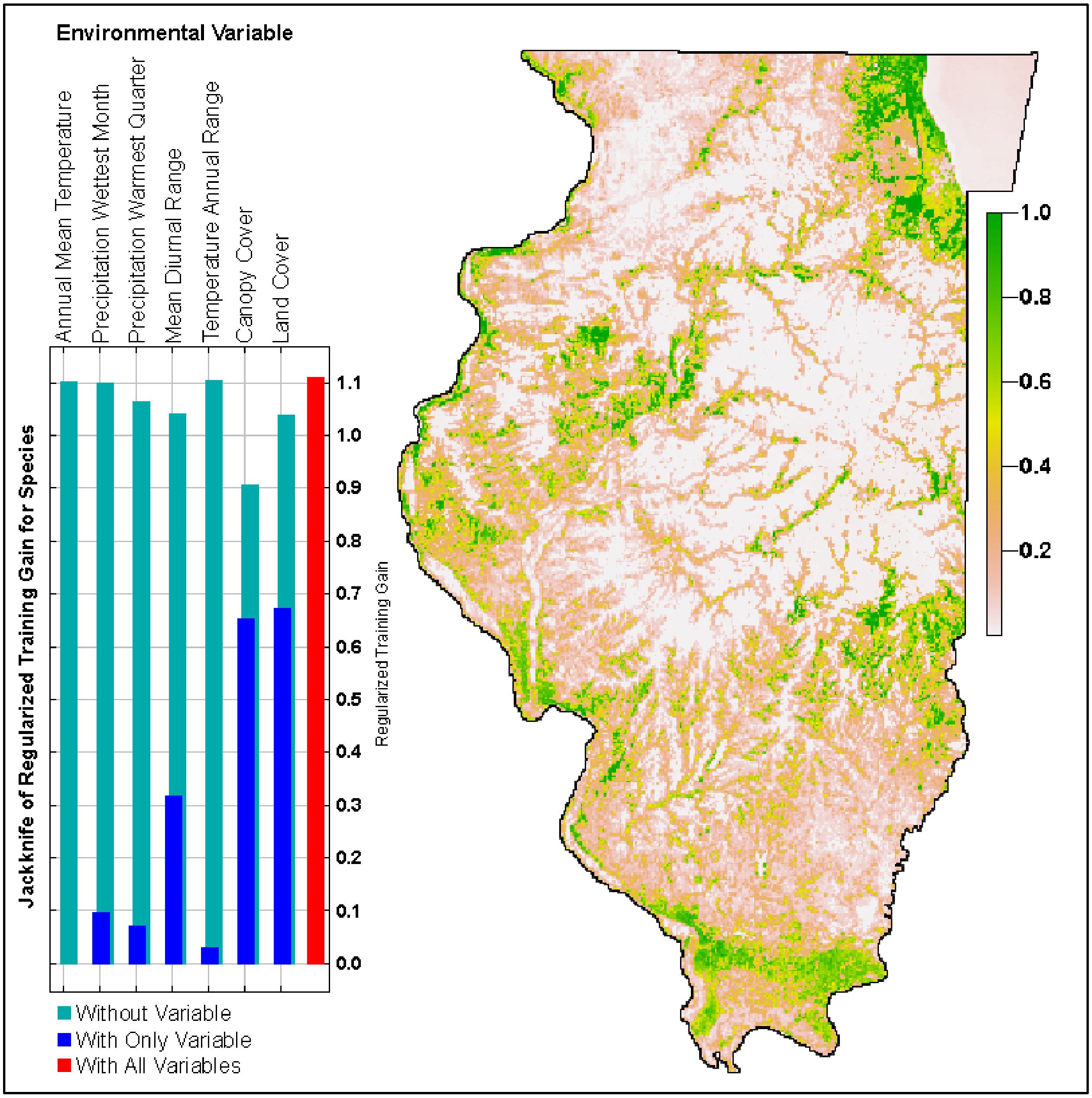

Figure 2-17. Predictive map and jackknife of environmental variables for *Entodon seductrix*.

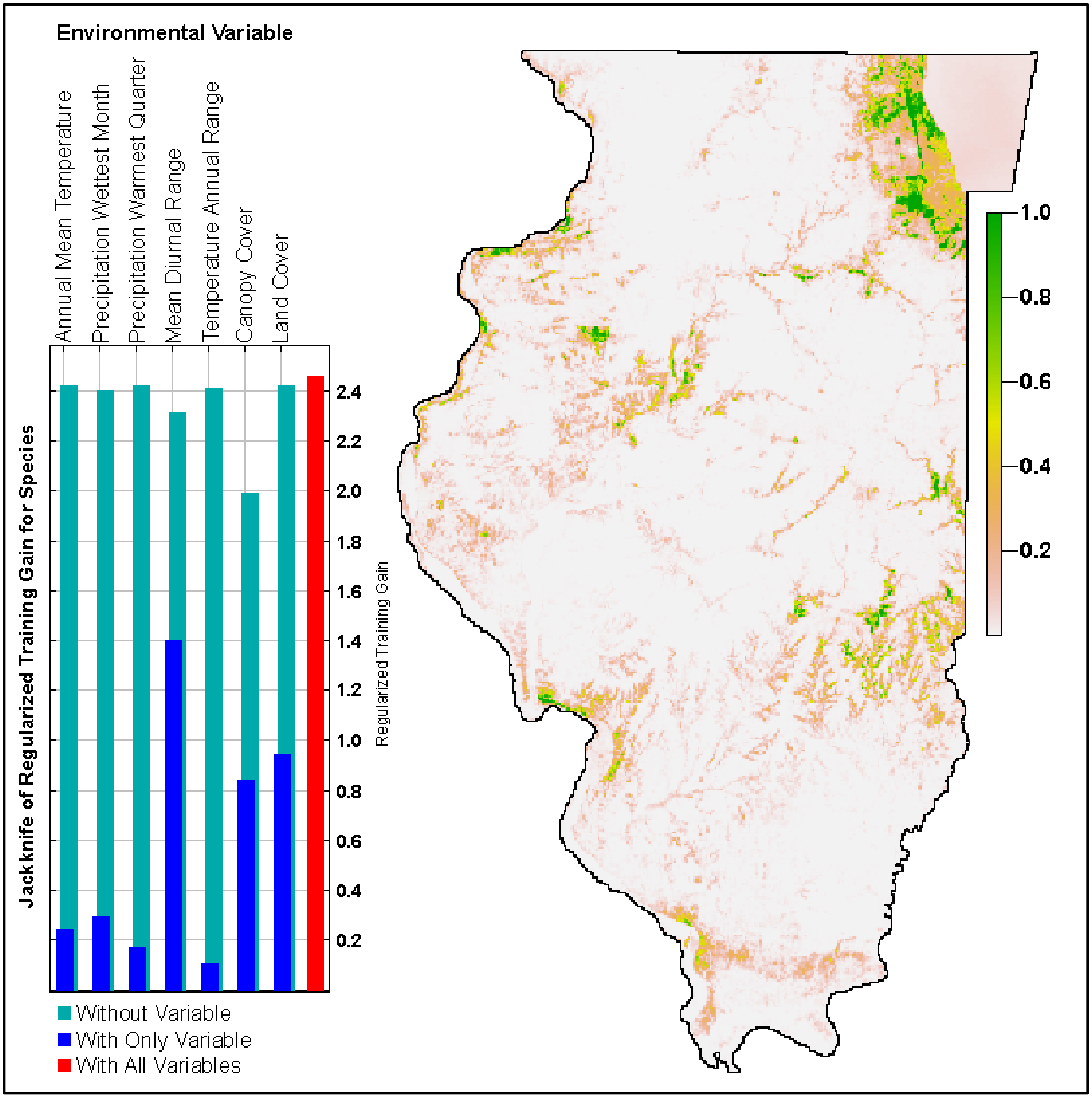

Figure 2-18. Predictive map and jackknife of environmental variables for *Amblystegium varium.*

Leskea gracilescens

The model of *Leskea gracilescens* [full AUC = 0.92, replicate AUC = 0.84] is built off the Mean Diurnal Range, Canopy Cover, and Land Cover variables in almost equal amounts (Figure 2-19). Compared to the model of the *Leskea* genus, the former two environmental variables have increased in their contribution where Land Cover remains the same. These increases account for the major distribution differences between the two models: there are decreases in distribution likelihood of the model of *L. gracilescens* in the western Chicago suburbs and in the western part of the state due to the lower Canopy Cover values.

Platygyrium repens

The model of *Platygryium repens* [full AUC = 0.89, replicate AUC = 0.88] also is equally built off the Land Cover, Canopy Cover, and Mean Diurnal Range like the model of *L. gracilescens* (Figure 2-20). Furthermore, Land Cover provides consistent support between the models of *Platygyrium* and *P. repens*, just like the models of *Leskea* and *L. gracilescens*. The distribution likelihood of *P. repens* also looks similar to the *L. gracilescens* map, as well as the *Platygyrium* map with fewer high distribution areas.

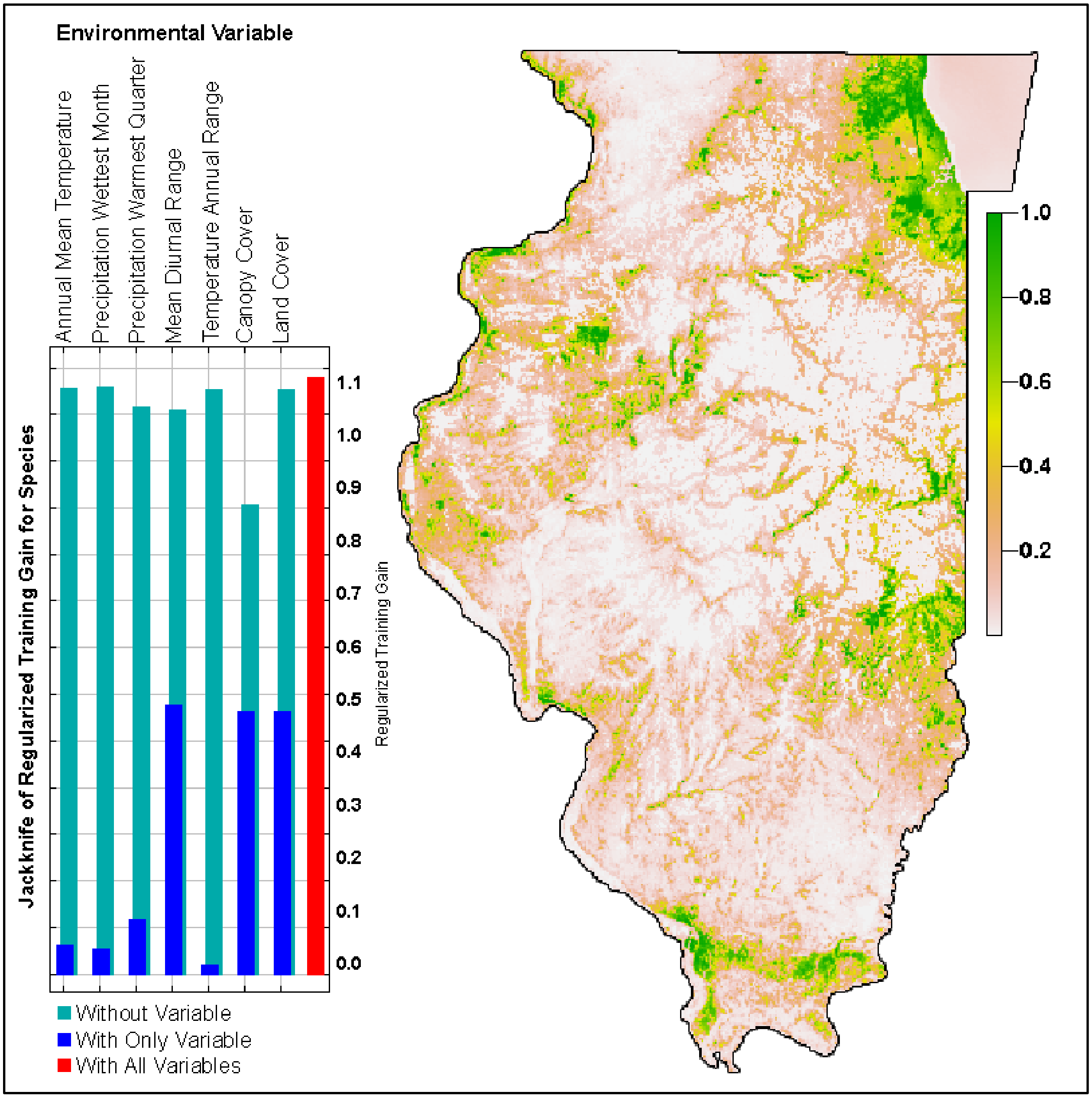

Figure 2-19. Predictive map and jackknife of environmental variables for *Leskea gracilescens*.

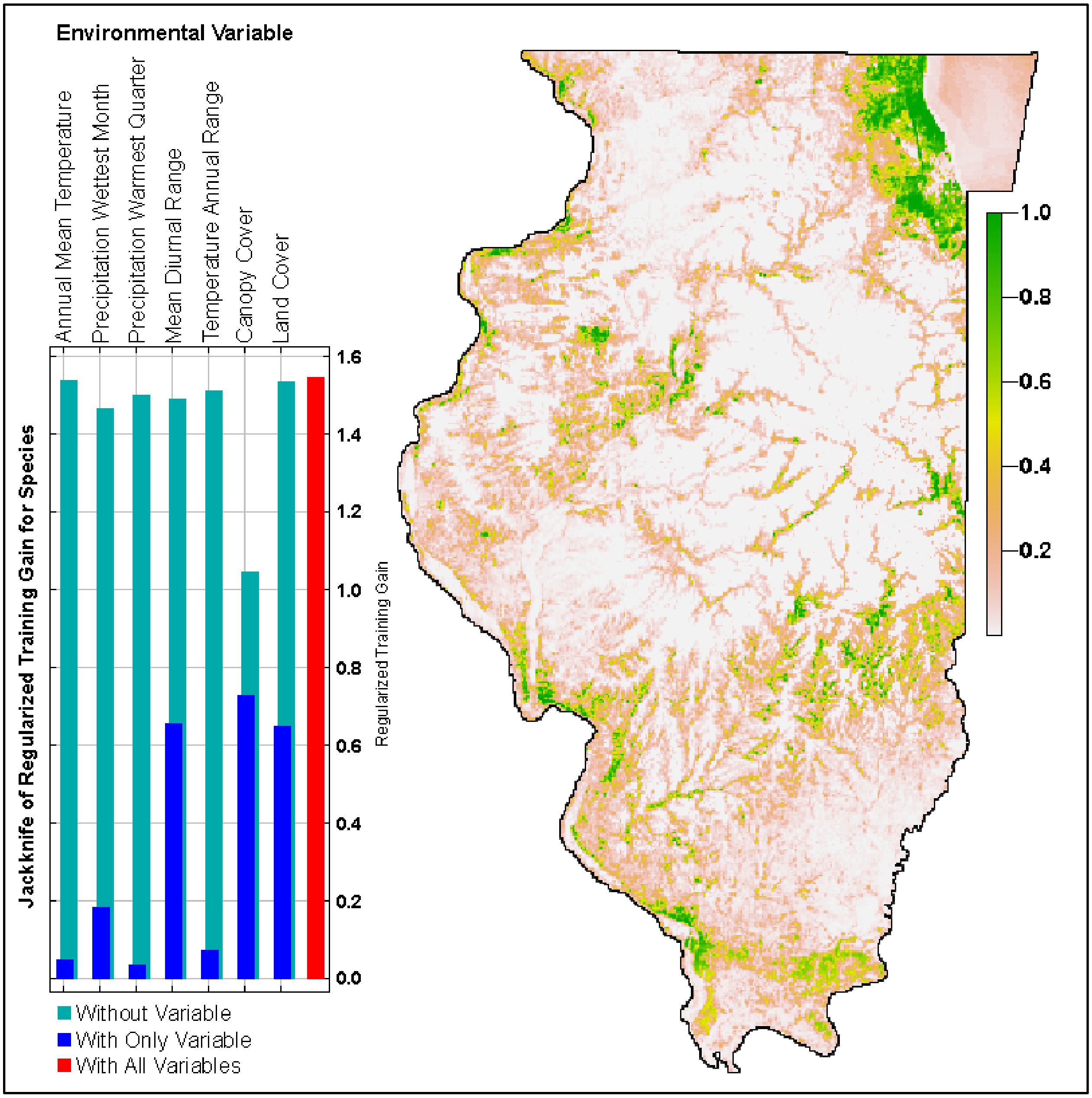

Figure 2-20. Predictive map and jackknife of environmental variables for *Platygryium repens.*

Anomodon rostratus

The model of *Anomodon rostratus* [full AUC = 0.89, replicate AUC = 0.90] has similar AUC values, but should also be considered with caution due to its lower occurrence values. The model of *A. rostratus* differs greatly from the model of *Anomodon*, as Canopy Cover is much more critical to the species model (Figure 2-21). This is evident in their different distribution likelihoods as well, as *A. rostratus* follows the pattern of forests supplied by Canopy Cover much more closely. Land Cover must also be recognized as a critical variable, similarly to the model of *Anomodon.*

Brachythecium acuminatum

The model of *Brachythecium acuminatum* [full AUC = 0.86, replicate AUC = 0.92] is built off a reasonable number of occurrences and has Mean Diurnal Range as its most critical variable unlike the previous models (Figure 2-22). The model of *Brachythecium* is built off Land Cover; Mean Diurnal Range is not nearly as relevant. The model of the species is more limited in its distribution likelihood than the full genus, a result of the basis on Mean Diurnal Range.

Plagiomnium cuspidatum

The model of *Plagiomnium cuspidatum* [full AUC = 0.81, replicate AUC = 0.88] shows a drop in AUC compared to the other species. *Plagiomnium cuspidatum* shares the same pattern of high likelihood areas as the model of *Plagiomnium* but with more generalized areas of no likelihood. The key difference between the two models is the much greater importance of Canopy Cover to *P. cuspidatum,* on the same level as Land Cover (Figure 2-23). Despite this increased importance of Canopy Cover, there is still low likelihood predicted for the species in the Southern Illinois forests.

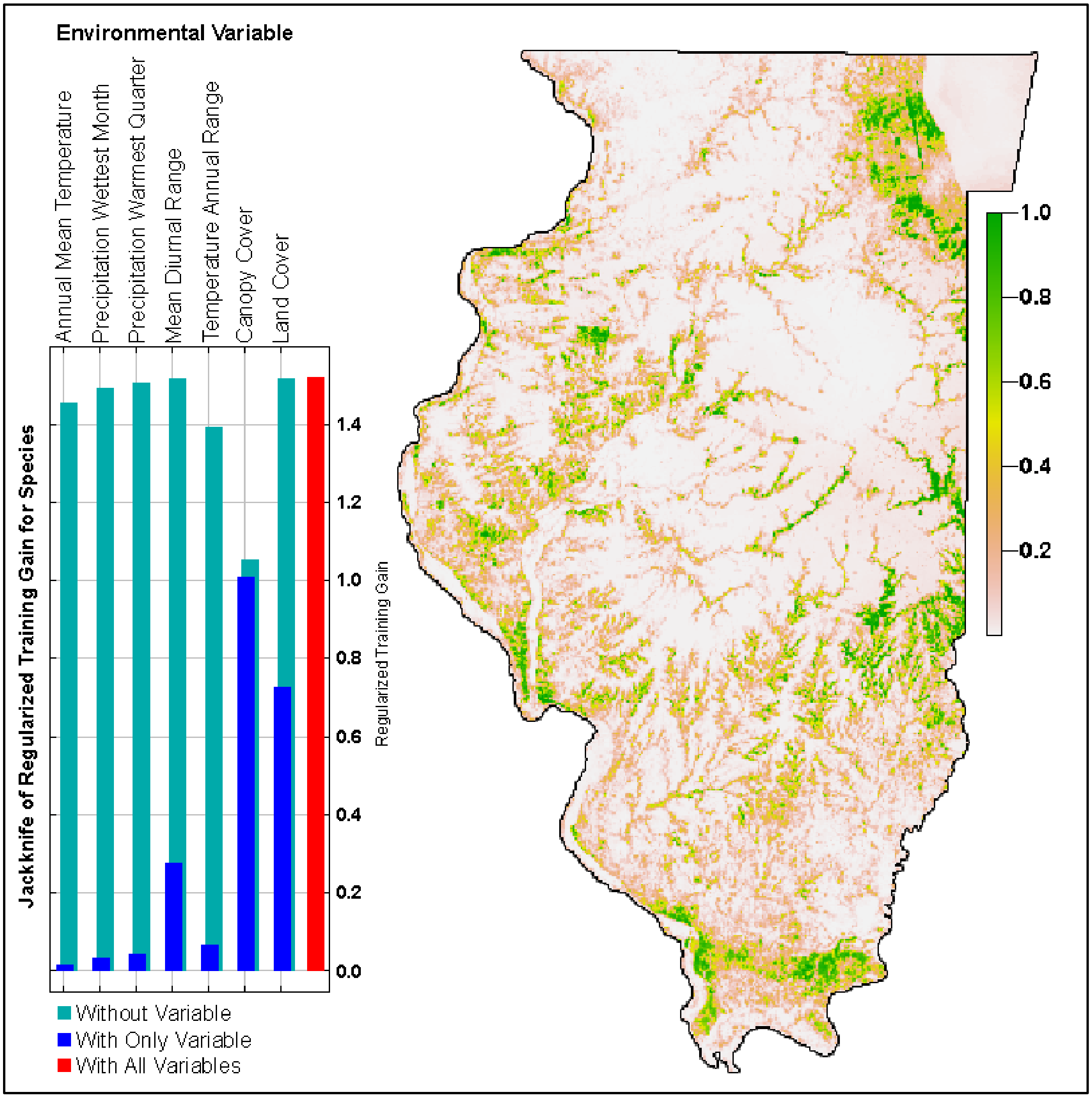

Figure 2-21. Predictive map and jackknife of environmental variables for *Anomodon rostratus*.

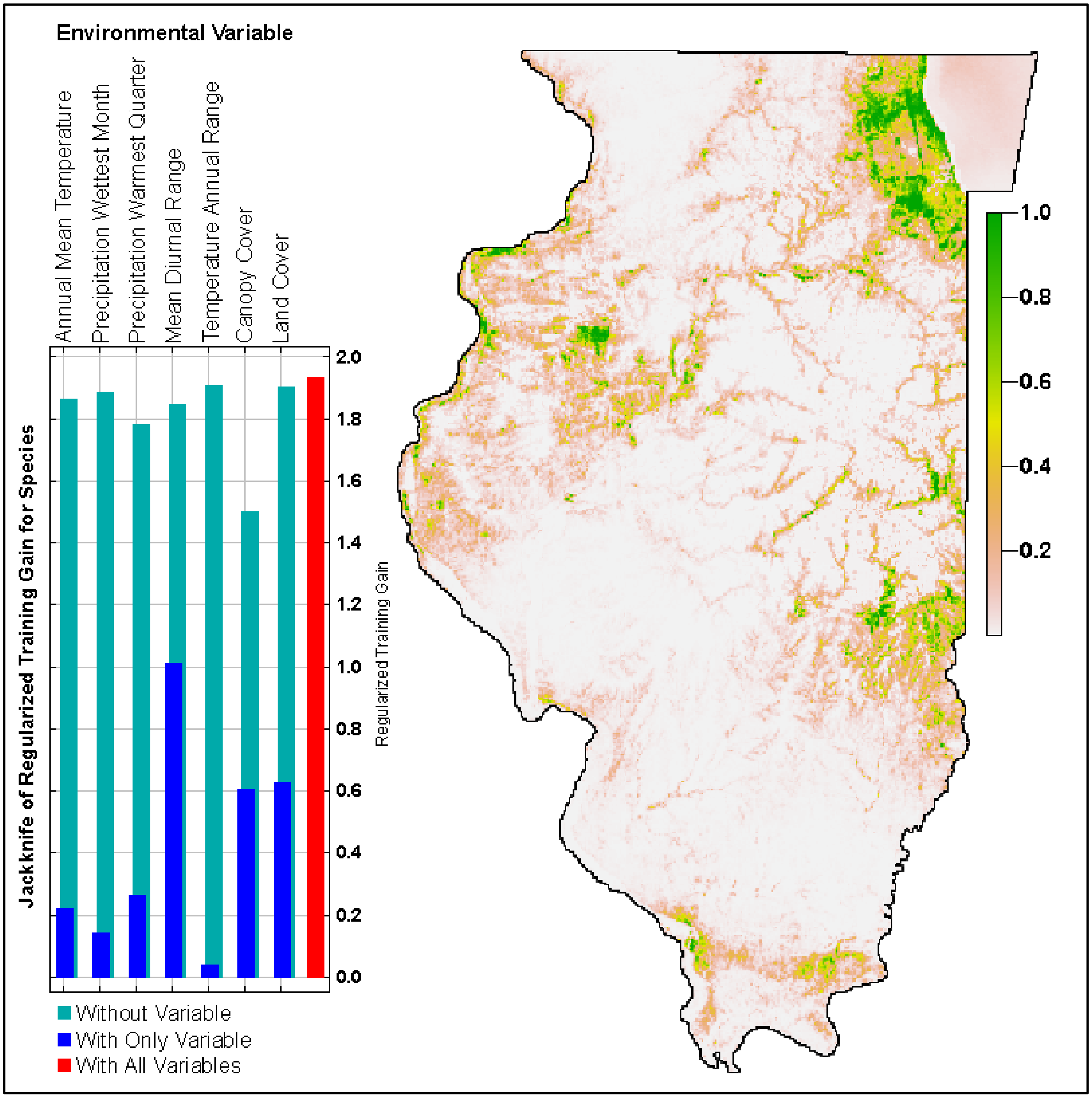

Figure 2-22. Predictive map and jackknife of environmental variables for *Brachythecium acuminatum.*

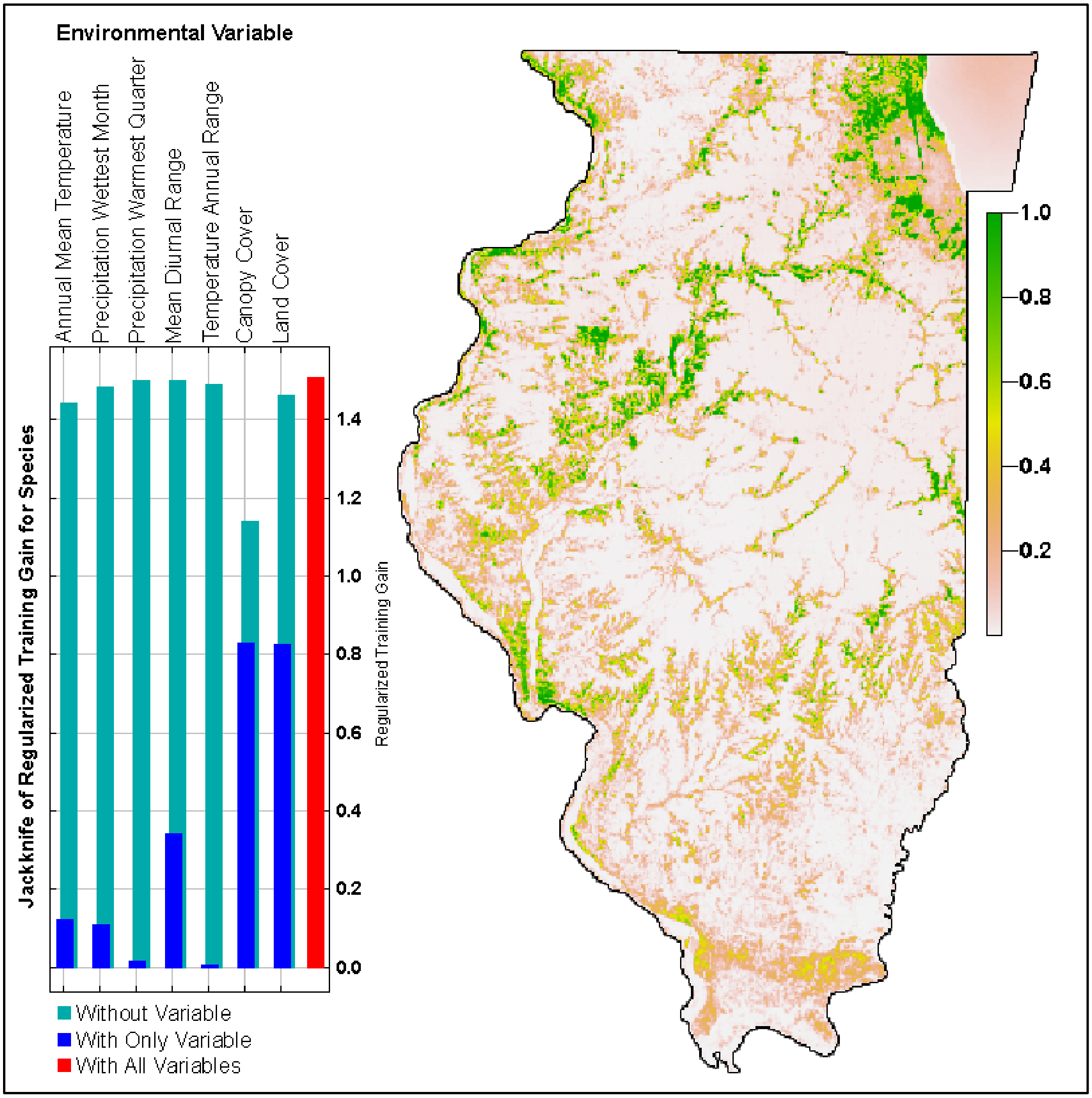

Figure 2-23. Predictive map and jackknife of environmental variables for *Plagiomnium cuspidatum.*

Climacium americanum

The model of *Climacium americanum* [full AUC = 0.81, replicate AUC = 0.93] is built off a small number of occurrences but appears to have a very consistent life strategy. Canopy Cover is very critical to this model, which is further emphasized by its very sparse distribution likelihood: Southern Illinois forests and scattered woods in the Chicago suburbs and along the east (Figure 2-24). This is further emphasized by the contribution of Temperature Annual Range to the model, only highlighting distribution in the south of the state.

Ceratodon purpureus

The model of *Ceratodon purpureus* [full AUC = 0.81, replicate AUC = 0.79] has lower AUC values and a lower number of occurrences, yet the distribution map on the Bryophyte Portal appears relatively consistent with known distribution. The model mainly relies on Land Cover, and areas of high distribution are all in the northern side of the state, mainly along the Illinois River and Chicago suburbs (Figure 2-25). This model does not explain the lack of distribution in Southern Illinois but does show that it is not due to climate, as none of the climate variables were highly relevant to the model. This is notable as the climate variables such as Annual Mean Temperature show clearly different values between Northern and Southern Illinois, implying a correlation between *C. purpureus* distribution and temperature.

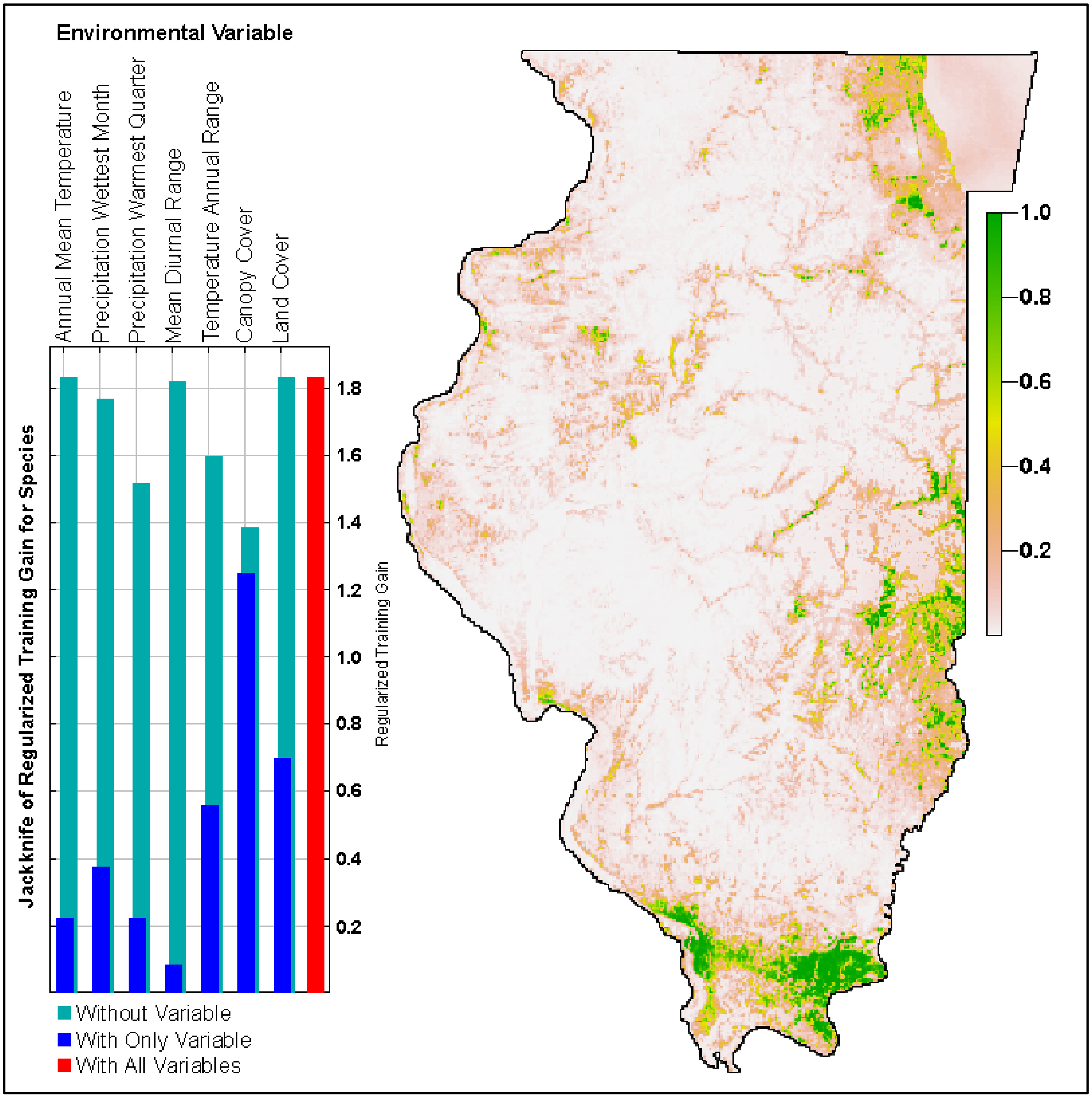

Figure 2-24. Predictive map and jackknife of environmental variables for *Climacium americanum.*

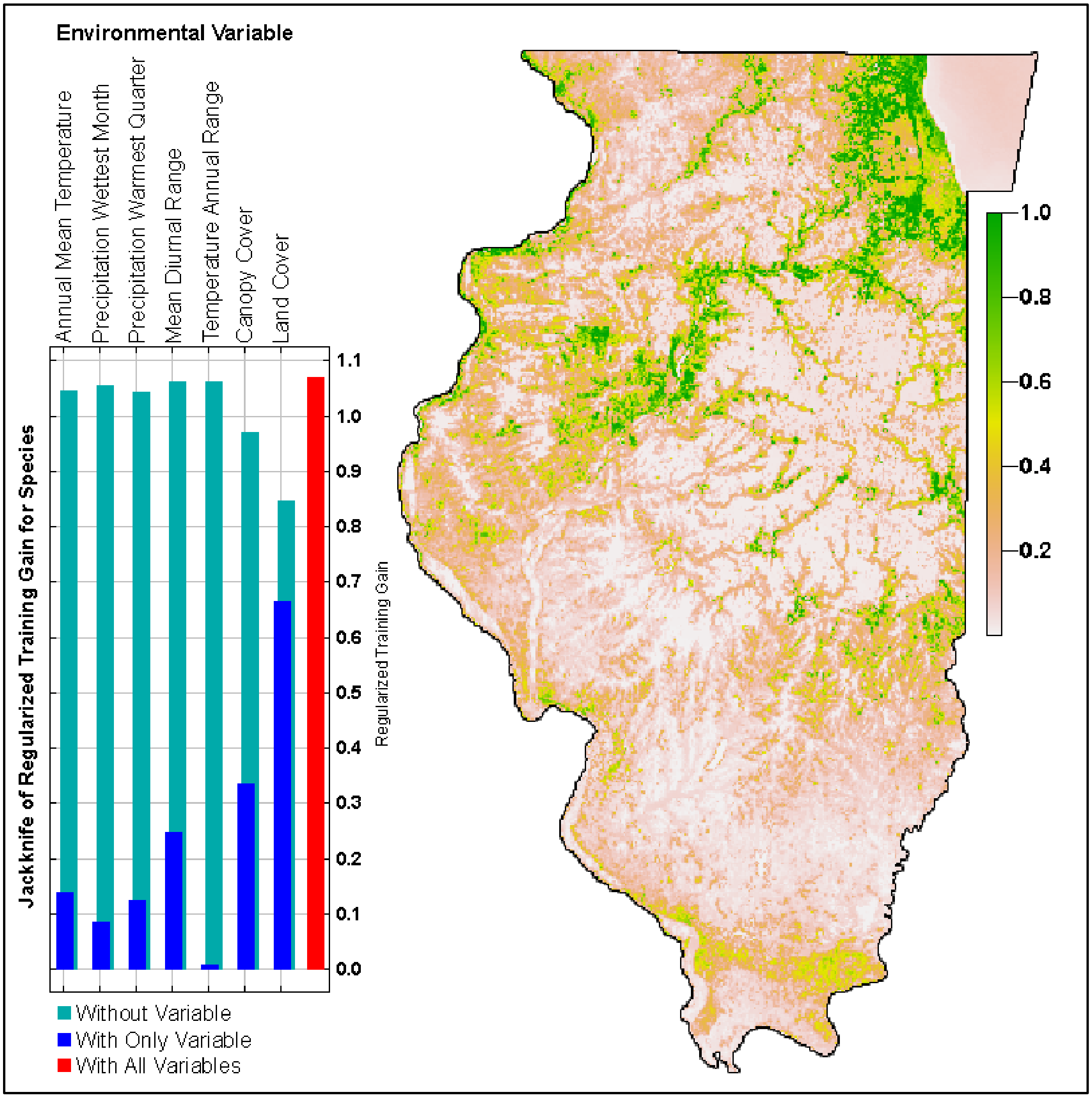

Figure 2-25. Predictive map and jackknife of environmental variables for *Ceratodon purpureus.*

Anomodon attenuatus

The model of *Anomodon attenuatus* [full AUC = 0.80, replicate AUC = 0.91] is almost identical to the model of *A. rostratus* : both relying on Canopy Cover and secondarily Land Cover (Figure 2-26). Their areas of distribution likelihood mirror each other as well, with *A. attenuatus* having a slightly higher likelihood in Southern Illinois and slightly lower around the mouth of the Illinois River.

Amblystegium riparium

The model of *Amblystegium riparium* [full AUC = 0.76, replicate AUC = 0.79] is built more like the model of the *Amblystegium* genus than either of the other models of the species, prioritizing Land Cover over Canopy Cover (Figure 2-27). Even so, the high likelihood areas differ between the two, with *A. riparium* having areas in the west and south and lacking distribution around the Illinois River. This model of the species also looks much different than *A. varium* and *A. serpens*, particularly due to its statewide cover in low likelihood. The lack of distribution around bodies of water is a concern as *A. riparium* is often found along banks and other wet areas. The low AUC value of this model along with its questionable heat map is a sign that this model should be given low weight and is likely not as realistic as the other models of the *Amblystegium* genus and species.

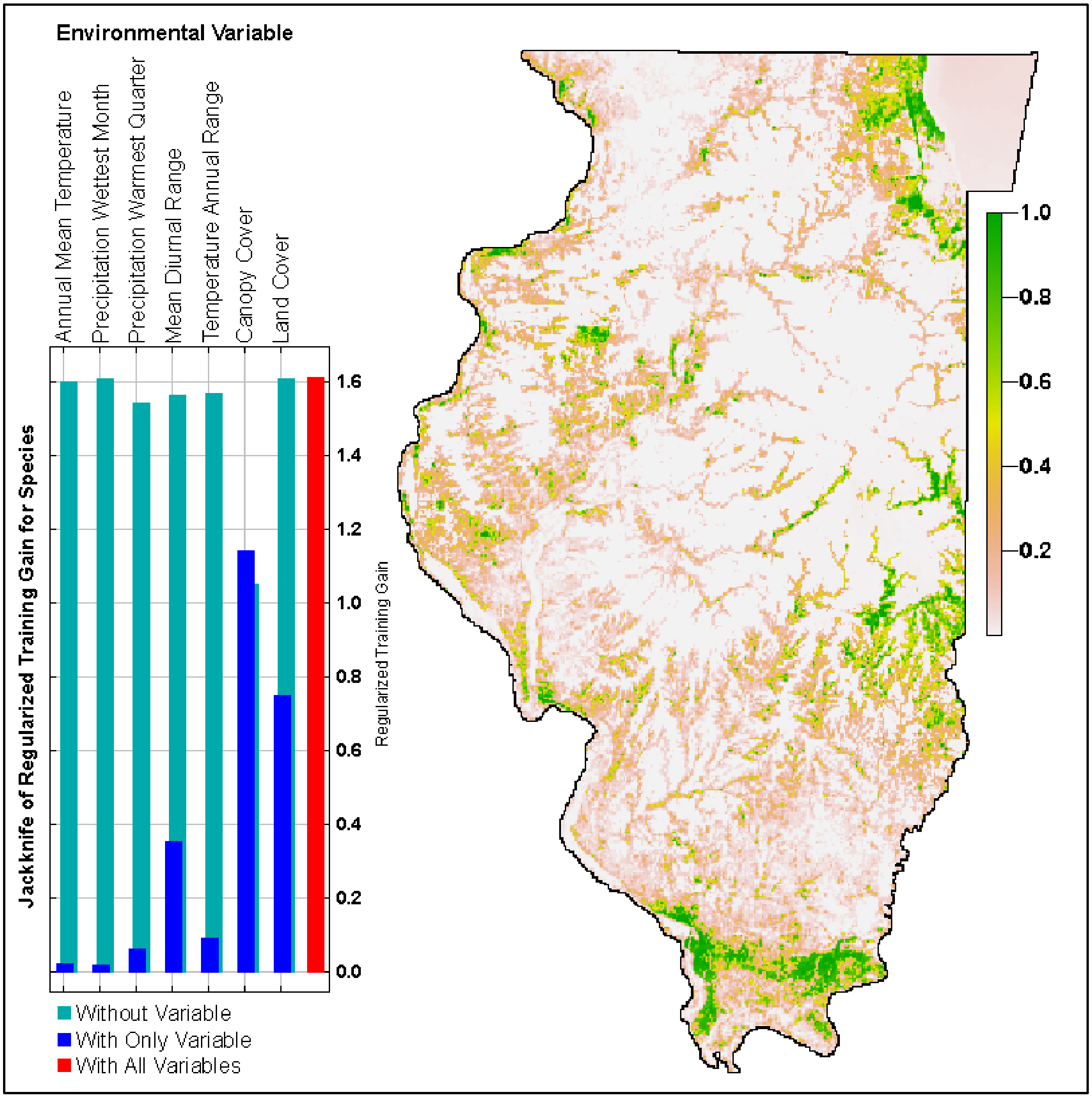

Figure 2-26. Predictive map and jackknife of environmental variables for *Anomodon attenuatus.*

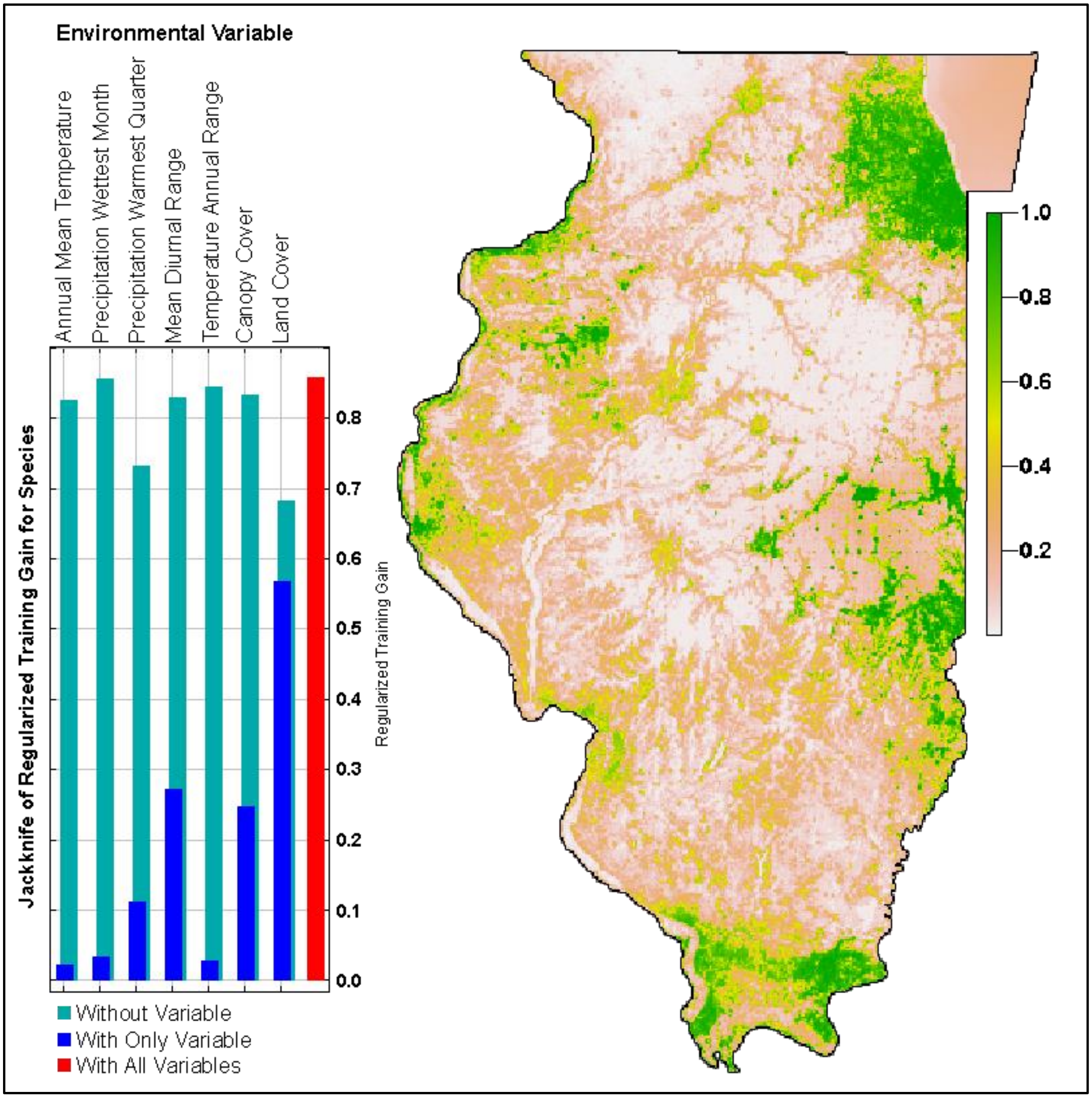

Figure 2-27. Predictive map and jackknife of environmental variables for *Amblystegium riparium.*

Distribution Verification

The species selected for verification around the Chicagoland area represented those with highest model AUC values. These included *Amblystegium riparium, Amblystegium serpens, Callicladium haldaneanum, Entodon seductrix,* and *Leskea gracilescens.* Figure 2-28 depicts selected regions in the vicinity of Glenview, Evanston, Skokie, Morton Grove and Winnetka that were divided into approximately 1 km grid sectors. It was predicted that a majority or all of the species would be found at areas of high likelihood, where none or one would be found at low likelihood areas. For example, at Crow Island Woods, a high likelihood area predicting that all five species could possibly be growing there, *C. haldaneanum*, *E. seductrix*, and *L. gracilescens* were all found, in addition to unidentified *Amblystegium* species. In contrast, in low likelihood grid sectors, such as light industry or heavy residential areas near Skokie and Morton Grove, only one target species was found, or none at all. As discussed previously there were several logistical problems including accessibility of private residents' backyards and sampling strategy, but these surveys did offer a proxy for verification. Overall, the models intuitively reflected the type of habitats available for bryophytes reflecting the high, moderate, and low likelihood regions (Figure 2-29).

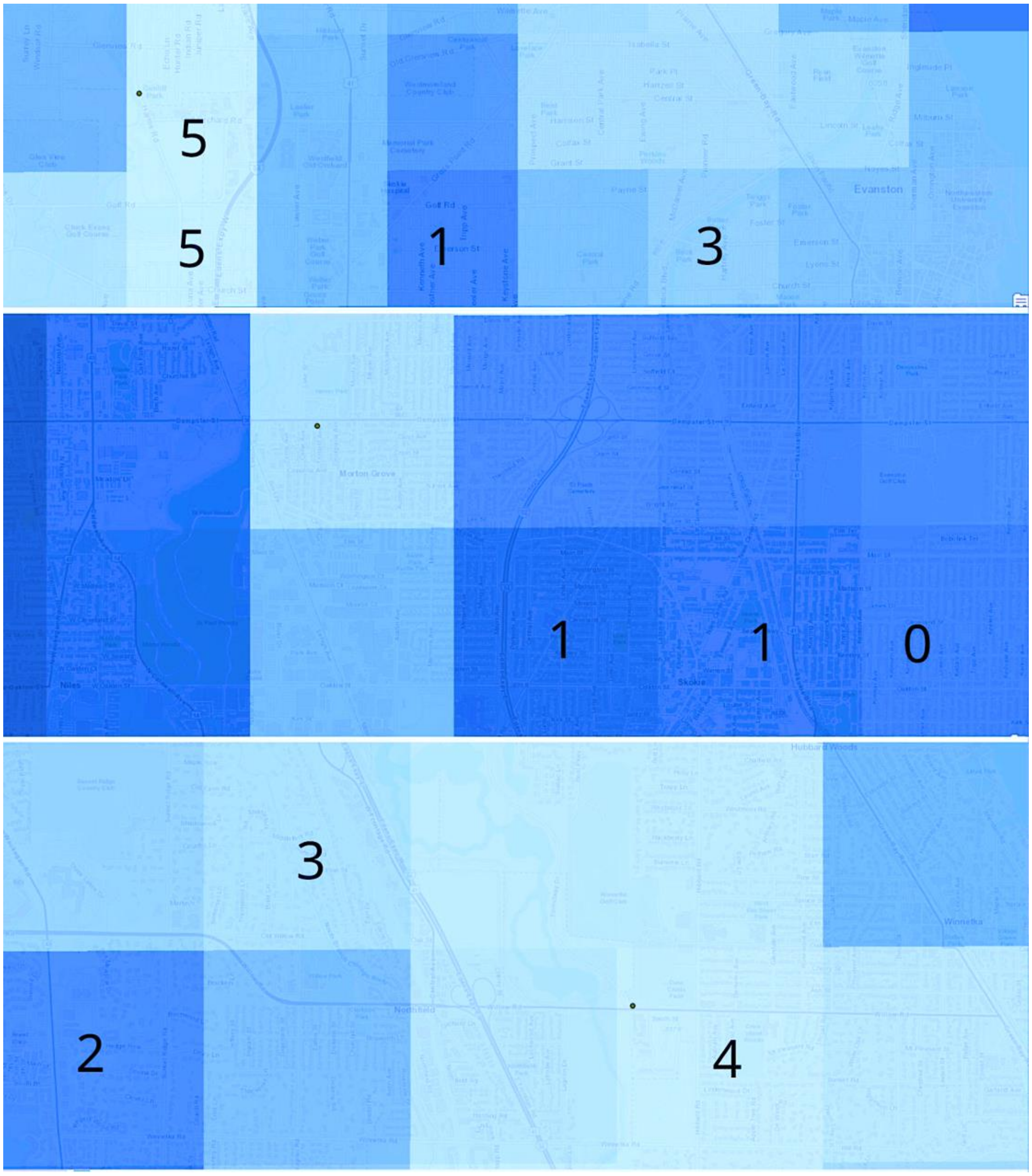

Figure 2-28. Chicagoland areas (Top: Glenview and Evanston; Middle: Morton Grove and Skokie; Bottom: Winnetka) selected for occurrence surveying of the five species models with the highest AUC values. The heat maps of the models have been stacked, indicating that a light blue area represents a high distribution likelihood for all species and a dark blue area represents a low likelihood for all species. Each square is a ~1 km² area, and numbers on the grids indicate how many target species were found at that location.

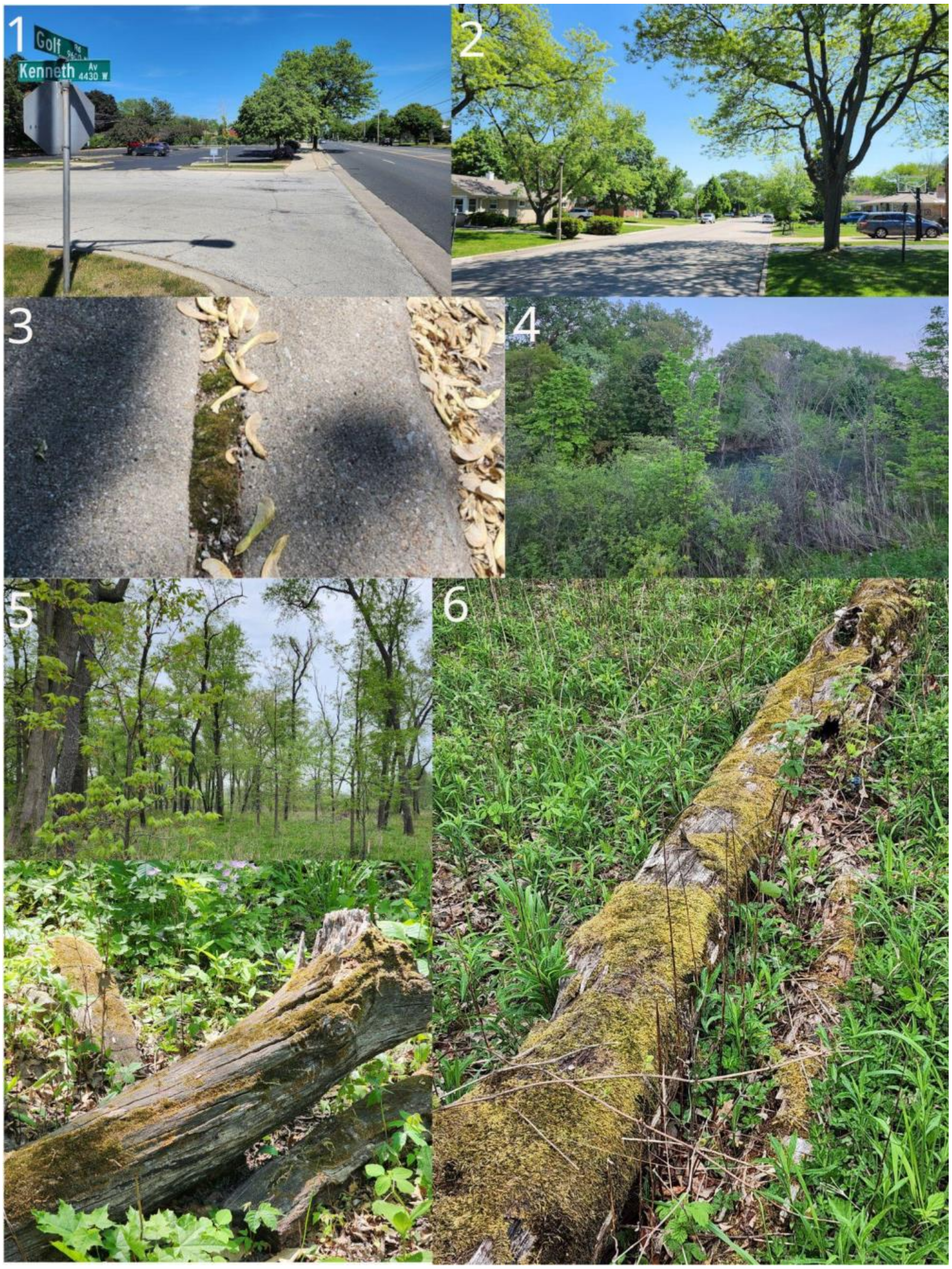

Figure 2-29. Environments and habitats of sampled Chicagoland areas ranging from highly residential, light industry, and small to moderate natural reserves. 1-3: Low likelihood suburban area near Glenview and Evanston, only one target species found; 4: Butler Park, medium likelihood area, three target species found; 5: Harms Woods, high likelihood area, five target species found; 6: Crow Island Woods, high likelihood area, four target species found.

Discussion

In this study, it is evident that species and genera distribution maps, derived from models, have the potential to be an effective tool for determining real world distribution patterns and characterizing ecological niches. The relevant environmental variables in these models can begin to describe the niches, while high likelihood areas can be targeted for field collections and observations of habitat. Known species and genera habitats can be used to test model validity. There was an overall pattern of high likelihood in three major areas for the generic-level models: i) forests in the Chicago suburbs ii) and Southern Illinois, as well as iii) the Illinois River. These areas also showed high likelihood for species-level models, but in general these models had more limited areas of high likelihood. This is a result of their more specific habitat restraints, rather than the broader habitats that define the genera.

Ultimately, there is a correlation between forested areas and areas of high likelihood in the models, which fits with the known habitat characteristics of the species investigated (Table 2-6). All these descriptions include a mention of forest environments or trees as substrate, aside from *Climacium americanum*. Forest bryophyte species studied previously have been shown to be reliant not only on the microhabitat created by canopy cover, but also the availability of substrates like dead wood (Evans et al., 2012; Löbel et al., 2018). In turn, these bryophytes contribute substantial diversity to these forest environments without heavy competition from other plant species (Cerrejón et al., 2022; Evans et al., 2012; Raabe et al., 2010). The models of the species not only support the understood prevalence of bryophytes in forested areas, but also can be used as a tool for extending the known distribution in unsurveyed forests. This was exhibited in the Northern Chicago field work, as managed forest and park areas were identified by high likelihood predictions. Furthermore, *Entodon seductrix* was located at these tree covered areas on decaying wood, where it is commonly known to be found (Buck, 1980). The models of the species particularly support their known habitat ranges, making them a useful tool for finding occurrences and describing the niche of bryophyte groups. For species and genera where the general habitat is unknown, these models can particularly provide insight.

Model Quality

AUC is the most popular metric of fit for MaxEnt models, a measure of model quality built by how well a model can discriminate between presence and absence sites (Convertino et al., 2012; C. Liu et al., 2011). The larger the area between the curve of the experimental model and the random model, the larger the AUC value and the higher the model confidence (Phillips, 2017). All models of species and genera aside from the models of *Anomodon* and *Amblystegium riparium* had AUC values of over 0.8, suggesting that these occurrences were well described by the set of environmental variables and that there is high confidence in their predicted distribution. However, models built on lower occurrence numbers and those that vary greatly from their replicate AUC value may not be so realistic. The largest gaps in AUC values are seen in the models of *Fissidens, C. haldaneanum, E. seductrix, C. americanum*, and *A. attenuatus.* As most of these models represent the species level rather than the genus level, it is apparent that lower occurrence numbers are related to AUC discrepancies. The models of *C. haldaneanum* and *C. americanum* in particular were based on only 29 occurrences, so in the 10-fold replicate models, only 2 occurrences are used for testing the constructed model; any outliers in environmental variable preference would therefore cause a large skew. Though MaxEnt is known for its ability to work with low occurrence numbers, the main concern with a small dataset is the weight of outliers on the model, which is one of the greatest weaknesses of the program (Phillips et al., 2006). There is also the concern of correct longitude and latitude data, as some specimens were provided generalized coordinates because they lacked specific locality data. This is a pitfall for all SDMs, as inaccurate geodata lead the models to interpret the environmental variables incorrectly (Naimi et al., 2014).

Even more detrimental would be outliers of misidentified or reclassified species due to the larger discrepancy in life strategy. This is a particular concern for all species models, as bryophytes are notoriously difficult to identify at the species level. Qualifying occurrences at the genus level provides more assurance models are built off correctly identified specimens, and allows for a larger data set to be utilized. Yet species models can still be appropriately built with a stronger effort to survey equally across the study area. As all of these genera and species are common within Illinois, it is possible that collections groups passed them over in favor of rarer species. Additionally, thorough review of the species taxonomy on the Bryophyte Portal can provide more confirmed occurrences to the dataset without drastic sampling efforts. There is also the consideration that the final occurrences used were cut down too far: more data could be added without surveys by using older occurrences and by thinning them out by a shorter distance. A thinning distance of 5 km may be too cautious, since bryophytes are shown to be reliant on microclimate of the area (Gignac, 2001; Táborská et al., 2020), which can vary greatly in a matter of kilometers. If land use and climate stays consistent within an area, there is no detriment to including older occurrences. Models of bryophytes built in the future should explore these possibilities, but be wary of potential overfitting or inaccurate distribution prediction.

Concerning the models of *Fissidens, E. seductrix,* and *A. attenuatus*, all are built from a moderate if not large amount of occurrence data. Occurrences for these models may therefore show discrepancies in environmental variable preference due to a broader presence of life strategies. Particularly comparing the genera to species models, the former had lower AUC values overall likely due to the combination of different species with different strategies being modeled as one. Naturally, species can also be widely tolerant such as *E. seductrix* and *A. attenuatus*, but modeling at the species level can provide more specific insight into unique niche characteristics. Furthermore, species level models can be more useful regarding locating occurrences and specific conservation efforts. Incomplete collections, particularly those of epiphytic species, are not just relevant for Illinois but a worldwide concern (Wierzcholska et al., 2020). Rather than extensive field studies, collecting environmental data by remote sensing saves time and reaches inaccessible areas; particularly this method has been shown to work with bryophyte distribution and richness models (Asner, 2013; Cerrejón et al., 2020; Skowronek et al., 2017). It may be worth considering an umbrella species approach to determining distribution and for conservation purposes, where one prevalent species with a similar ecology to others (typically in the same genus) can be used as a target to project the distribution of all the similar species (Roberge & Angelstam, 2004). Overall, while models of bryophyte genera are generally more reliable due to data availability, models of species can provide more precise and applicable data if there is a greater effort to collect and identify species occurrences.

Environmental Variable Importance

The models constructed across the bryophyte species and genera were mainly reliant on the Land Cover and Canopy Cover variables, with Mean Diurnal Range to a lesser extent. This is similar to other bryophyte MaxEnt distribution models that showed overwhelming importance of forest continuity (Wierzcholska et al., 2020) and Mean Diurnal Range specifically (Cihal et al., 2017; Silva et al., 2014) in other continents. The consistency of environmental contribution across models of Illinois bryophytes and models of bryophytes around the world supports the idea of a generalized bryophyte niche. Furthermore, this consistency and the confidence of these models provides support for locating taxa in Illinois with relative accuracy. Naturally, forests are the most likely target area for this assumption, as a majority of the models show a high likelihood of distribution around the Southern Illinois forests and include the presence of Canopy Cover. Distribution around bodies of water, particularly the Illinois River stick out as well, though this is not as prevalent as forest distribution. This reflects the habitat characteristics of the chosen taxa, as they are frequently present in forested and/or moist environments (*California Moss EFlora*, 2021; Conrad & Redfearn, 1979; *Flora of North America*, 2023; Ludwiczuk & Asakawa, 2021; Perdrizet & McKnight, 2012; Sabovljević et al., 2022; Zhu et al., 2010).

Research on comparing distribution models between taxonomic levels is limited, and this study is one of the first to explore such differences with bryophytes. The generalized niche provides some use for determining bryophyte distribution, it misses the intricacies between the genera and species that can be used to better target specific distributions. Most notably the model of *Frullania*, the only liverwort genus studied, shares the same critical environmental variables with the moss genera but shows a much higher prevalence of Canopy Cover in the jackknife. This importance of Canopy Cover is supported by primarily epiphytic life strategy of Frullania (Conrad & Redfearn, 1989; Crum, 1976; Heylen & Hermy, 2008). Furthermore, the higher importance of Annual Mean Temperature and Temperature Annual Range align with the findings in Cerrejón et al., that lower temperature days had a much larger impact on liverworts than mosses (2020). Even the distribution of *Frullania* is distinctly different, with a noticeable lack of distribution throughout Northern and Central Illinois. It is apparent that even just from representation of one liverwort that the niche estimate of mosses and liverworts should be considered separately, particularly for determining distribution. The moss genera share much more consistent predicted distribution and importance of environmental variables.

Even so, lumping together species into their genera still excludes variable life strategies present within the genera. Though across the board the models of species share similar high likelihood areas (Chicago, Southern Illinois, the Illinois River) there is a visible difference in distribution from species to genera, and from species to species. For example, the model of *Amblystegium* shows distribution throughout the state but primarily around Chicago and the Illinois River. The model of *A. riparium* shares this statewide and Chicago likelihood pattern but has low likelihood directly around the Illinois River. Furthermore, the model of *A. serpens* has a much more limited likelihood than the other two models, with no likelihood throughout the state and less high likelihood around Chicago. The *Amblystegium* genus is known to have a cosmopolitan distribution, whereas *A. riparium* and *A. serpens* show a specific preference towards moist environments, with the later sometimes being found in forests (Conrad & Redfearn, 1989; Crum, 1976; *Flora of North America*, 2023). This more particular habitat seen in the species supports that there would be less potential distribution compared to the generic level. Even considering the low confidence of the model of *A. riparium*, this pattern of more particular likelihood at the species level is present in almost all of the genera/species paired modeled: *Anomodon, A. rostratus* and *A. attenuatus; Brachythecium* and *B. acuminatum; Leskea* and *L. gracilescens; Platygyrium* and *P. repens;* and *Plagiomnium* and *P. cuspidatum*. The only pair that does not fit this pattern is *Entodon* and *E. seductrix*, which share more similar areas of high likelihood. Describing the critical environmental variables, and therefore the niche, at the species level provides more precise and accurate data than generalizing bryophyte distribution.

Furthermore, the models of the bryophyte species are more variable than the models of the genera in what environmental variables contribute most to their model. The models of *A. serpens, A. varium, B. acuminatum, C. haldaneanum* and *L. gracilescens* have Mean Diurnal Range as their most critical environmental variable, and the models of *P. repens* and *A. riparium* include it as the second most critical. A similar MaxEnt study of bryophytes in the Brazilian Atlantic Forest also identified the high relevance of Mean Diurnal Range (Silva et al., 2014). Though this variable was relevant in the models of the genera, it never contributed as much as the land use variables. This is a further testament to the differing life strategies between the species: those listed may be more susceptible to climate patterns than other bryophytes, which is important considering how climate change may alter bryophyte distribution as a whole.

The models of *A. attenuatus, A. rostratus, C. americanum*, *P. cuspidatum,* and *P. repens* have Canopy Cover as their most critical variable. One explanation for the prevalence of Canopy Cover throughout the models of the species is the partial epiphytic lifestyle that all of the species' exhibit. The species that are more reliant on Canopy Cover could exhibit this lifestyle more than others and tend to be distributed around forests. Alternatively, the cover from the trees provides a habitat beneficial to these species, one that differs from the climate outside the tree cover (De Frenne et al., 2021; Wierzcholska et al., 2020). If this is the case, this is evidence for the importance of microclimate over macroclimate for bryophyte distribution. The Bioclim variables included within the models of the species and even genera could be too large of a scale to be relevant to bryophyte distribution. Canopy Cover therefore functions as a microclimate proxy within the models of the bryophytes. The models of species that have Land Cover as the primary variable, *A. riparium, E. seductrix,* and *C. purpureus* likely are less reliant on microclimate and even macroclimate than others. Though these species can exhibit an epiphytic lifestyle, they may prefer other substrates and habitats, such as near bodies of water or generally in the open air.

An alternative method to using environmental variables is to collect the information by remote sensing, using satellites to image and read more precise data. Remote sensed climate data has outperformed climate variable estimations in species distribution models (Cord et al., 2014). Particularly because of the higher resolution, the success of these models could better represent microclimate factors that bryophytes are more reliant on (Casas et al., 2021; Deneu et al., 2022; Mehmood et al., 2022; Sun et al., 2023).

Model Verification

Assessing the accuracy of species distribution models (SDMs) is critical for both conservation planning and ecological forecasting (Lawler et al., 2011). Yet, although SDMs are widely used in ecology, testing predictions from SDMs against independent assessments of occurrence are lacking (Lee-Yaw et al., 2022). As discussed, there are a number of challenges to surveying predicted distributed patterns inferred by the models, notwithstanding the lack of a systematic sampling or transect routine for large one km^2 grids. However, these challenges were somewhat mitigated because the targeted species selected here largely have specialized habitats, such as growing at the base of tree trunks, and surveys could focus on those habitats. Despite these challenges in situ observation largely supported the predicted distribution patterns as inferred by the models. All occurrences of the five species used to construct these models around the northern Chicagoland area were collected in the year 1989. This illustrates that occurrence data from over three decades ago remains effective for predicting species distribution patterns inferred by modeling.

Chapter 3: Predictive mapping of selected bryophytes across climate change scenarios

Introduction

Bryophytes as Climate Change Indicators

Bryophytes have a number of characteristics and features, such as their physiological reliance on the environment, small size, broad distribution, and sensitivity to the environment that make them potentially good biological indicators. Gignac (2001) proposed over two decades ago that bryophytes might have potential climate change indicators. Recently, there have been a growing number of studies using bryophytes to investigate changes in species distribution and future habitat suitability in a changing climate (e.g., Hespanhol et al. 2022; Mallen-Cooper et al. 2022; Zanatta et al., 2020). More specifically, monitoring the growth or distribution of bryophytes can provide insight into the effects of a changing climate. For example, monitoring the growth and distribution of the bryophytes that only tolerate a small pH range can provide insight into the soil pH of the study area over time (Saxena & Harinder, 2004). Any specific environmental factor relevant to bryophyte niches can be tracked this way. Habitable environments will still show occurrences of bryophytes, whereas areas no longer habitable to specific species will lack occurrences (Cerrejón et al., 2020). This method of distribution tracking over time can show directionality and patterns in climate change on a broader scope. Furthermore, this tracking also provides insight into what environmental factors are the most important to determining bryophyte distribution.

SSP Scenarios and Bioclim Projections

Future predictions of what climate variables might look like are classified into Shared Socioeconomic Pathway scenarios (SSPs) (Böttinger & Kasang, 2021). The SSPs improve on the older climate projections, Representative Concentration Pathways (RCPs), by accommodating for the increased greenhouse gas effect and including various societal approaches to climate change while remaining comparable to these originals (Böttinger & Kasang, 2021). SSP 126 represents the most sustainable and “green” response, SSP 245 a “middle of the road” continuation of current policies, and SSP 585 where corporations dominate and fossil fuels are heavily exploited (Böttinger & Kasang, 2021). All five SSP scenarios are integrated into the future Bioclim variables for creating models from 2021-2040 to 2081-2100. Bryophyte models based off these SSP and RCP scenarios have shown a general loss in habitable areas available as the scenarios get more severe, across genera and environment (Kou et al., 2020; Mallen-Cooper et al., 2023; Patiño et al., 2016). Extreme habitat loss has predicted to result in a 62-87% decrease of 35 endemic island species of bryophytes, will result in their Red Listing or extinction (Patiño et al., 2016). For alpine environments, temperature appears to be the limiting factor in bryophyte distribution, predicting that the range of these species will shift northward with global warming patterns (Kou et al., 2020; Mallen-Cooper et al., 2023). *Didymodon* in particular has an overall gain of habitable territory in Tibet, indicating that this genera is a suitable climate change indicator for the country (Kou et al., 2020). Modeling of future bryophyte distribution patterns therefore reveal what species and genera need to be targeted for conservation and those that are robust enough to track climate change patterns.

Objectives

In Chapter 3 the aim is to create models of the same bryophyte species and genera seen in Chapter 2 using projections of the Bioclim variables to assess how distributions will change with different societal responses. By identifying species and/or genera sensitive to these changes, these bryophytes can be further explored as climate change indicators, to assess environmental changes indirectly and at a smaller scale. It is hypothesized that bryophyte distribution will change over time across three different climate change scenarios based on societal responses. It is expected that the species level will be more informative climate change indicators than the generic level due to ecological and physiological factors.

Methods

Models of future bryophyte distribution are based off the NASA Goddard Institute for Space Studies Model (GISS-E2-1-G) of the Bioclim variables. This GCM was selected for its use in one of the few North American focused bryophyte modeling studies (Oke & Hager, 2017). Data was downloaded from the WorldClim database for the years 2040-2060 and the SSP scenarios SSP 126, SSP 245, and SSP 585. For consistency and to support comparison between current and future models, the same five Bioclim variables were used for all models, as well as the 2016 Land Cover and Canopy Cover variables. The same occurrences for species and genera were used and the same procedure for generating the current models was followed (see Chapter 2 Methods).

Results

Genera Models

The full model area under the curve AUC values are overall slightly lower than the current genera models, but still remain consistently over 0.80 (Table 3-1). The values are also generally consistent across the SSP scenarios, as well as with their replicate value, aside from *Bryum*. This is likely the result of the wider variety of life strategies within the large genus, as well as a lower number of replicates included in the model. The most critical environmental variable for the future genera models is consistent with the current models: all primarily were built from the Land Cover data aside from *Frullania* where Canopy Cover was more important. This is reasonable as these are the only two environmental variables representing recorded data rather than modeled data. For consistency, models are presented in the order as seen with the Chapter 2 models of genera.

Table 3-1. Future genera model quality for the complete data set and replicate fold averages. Any AUC value above 0.8 is considered a confident model.

Genus	SSP 126 AUC		SSP 245 AUC		SSP 585 AUC	
	Full	**Replicate**	**Full**	**Replicate**	**Full**	**Replicate**
Dicranum	0.91	0.89	0.84	0.91	0.89	0.89
Fissidens	0.87	0.85	0.85	0.86	0.90	0.85
Platygyrium	0.88	0.85	0.91	0.83	0.80	0.89
Plagiomnium	0.89	0.83	0.87	0.84	0.86	0.84
Leskea	0.81	0.84	0.83	0.82	0.78	0.83
Brachythecium	0.84	0.84	0.87	0.83	0.82	0.84
Bryum	0.84	0.84	0.90	0.81	0.71	0.88
Frullania	0.88	0.87	0.86	0.88	0.90	0.88
Atrichum	0.82	0.86	0.88	0.84	0.82	0.86
Amblystegium	0.84	0.80	0.81	0.82	0.80	0.82
Entodon	0.85	0.85	0.85	0.85	0.85	0.85
Hypnum	0.89	0.84	0.89	0.84	0.89	0.85
Anomodon	0.81	0.81	0.88	0.79	0.81	0.82

Dicranum

Though the current and future models of *Dicranum* are primarily built on the Land Cover and Canopy Cover variables, the future models show increased importance of the Bioclim variables. All the future scenarios show an increase in gain from Mean Diurnal Range, particularly the SSP 245 model (Figure 3-1). This model also has a small, but noticeable amount of gain from the precipitation variables: Precipitation of Wettest Month and of Warmest Quarter. The *Dicranum* SSP 126 model also shows an increase in importance of Precipitation of Warmest Quarter, and the SSP 585 shows a small gain from Temperature Annual Range. The presence of these variables is likely due to the smaller occurrence size, with the models picking up on smaller patterns within the data. Distribution wise, there are no substantial differences between the future models; all show a decrease in likelihood from the current model of *Dicranum*. The SSP 245 contrasts with the other models of genera for this scenario by showing the lowest distribution throughout the state. The SSP 126 model is relatively similar to the SSP 585 model with the inclusion of more high likelihood areas around the western border of the state.

Fissidens

The key difference between the current model of *Fissidens* and the future models of *Fissidens* is the importance of Mean Diurnal Range in the latter. All four models still have Land Cover and Canopy Cover as the key variables, but there is a noticeable increase in gain from Mean Diurnal Range from the current to the future models (Figure 3-2). Of the three future models, SSP 585 has the lowest increase in Mean Diurnal Range, and also has the most similar distribution prediction to the current model of *Fissidens*. The SSP 126 model sees a decrease in likely distribution areas mainly around the Illinois River and western border, and SSP 245 showing even more of a decrease around the river, but a small increase around the Chicago suburbs.

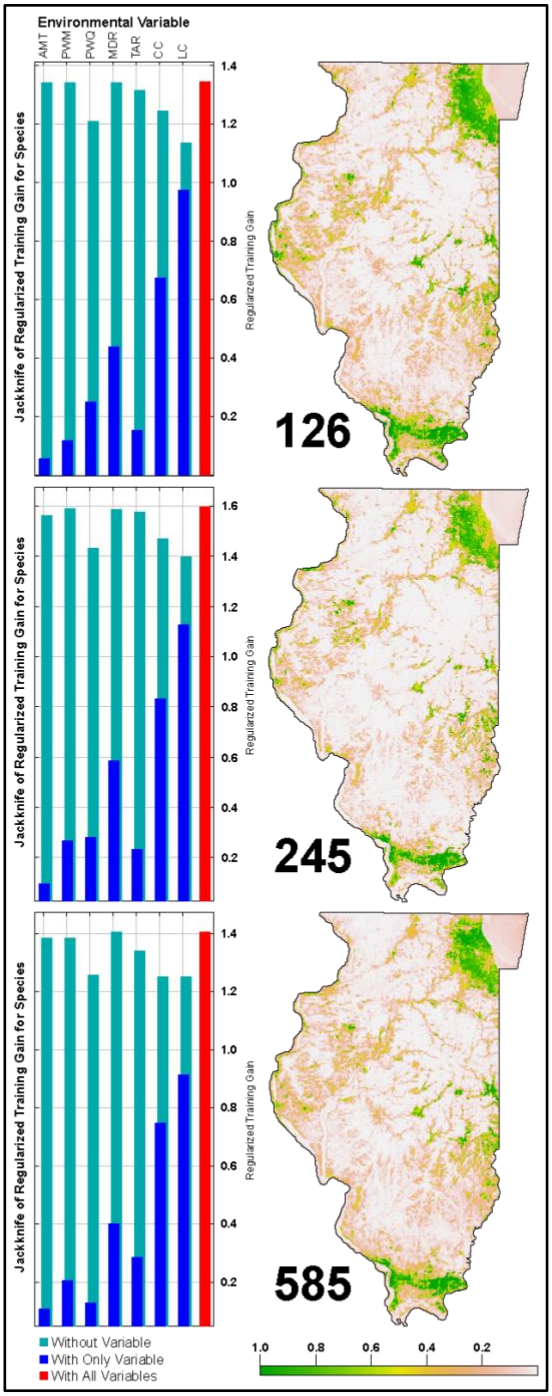

Figure 3-1. Predictive maps and jackknifes of environmental variables for *Dicranum* 2041-2060 climate scenarios.

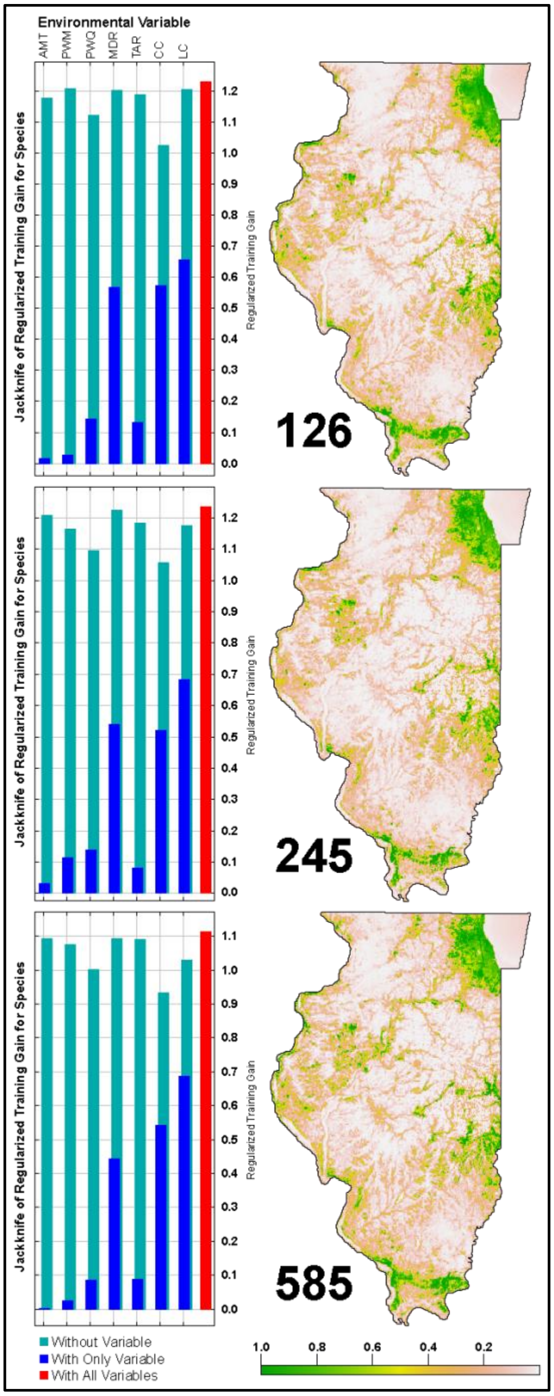

Figure 3-2. Predictive maps and jackknifes of environmental variables for *Fissidens* 2041-2060 climate scenarios.

Platygyrium

The models of *Platygyrium* show a clear pattern of distribution loss along the Southern Illinois forest: the current model has a high likelihood across the area, but the future models show a decrease in likelihood on the east side of the forest from the best (SSP 126) to worst (SSP 585) climate response (Figure 3-3). Aside from this area, the SSP 126 and SSP 245 models are fairly similar, with the later having some more low likelihood areas in the north and west. The SSP 585 model of *Platygyrium* shares the high distribution areas with the rest of the models but shows the greatest loss of distribution with more no likelihood areas throughout the state. The future models all see an increase in the importance of Mean Diurnal Range, which is on par with the contribution of Canopy Cover.

Plagiomnium

The future models of *Plagiomnium* share a consistent distribution with the current model. The SSP 126 model sees a slight loss in distribution likelihood around the Illinois River, but an increase in the southern and northern edges of the state, particularly the Southern Illinois forest (Figure 3-4). The SSP 245 and SSP 585 models are very similar to each other, showing slight distribution loss throughout the state but a similar pattern to the current model in the Southern Illinois Forest. The models of *Plagiomnium* are consistently built off of Land Cover and Canopy Cover, showing an increase in the importance of Mean Diurnal Range in the future models.

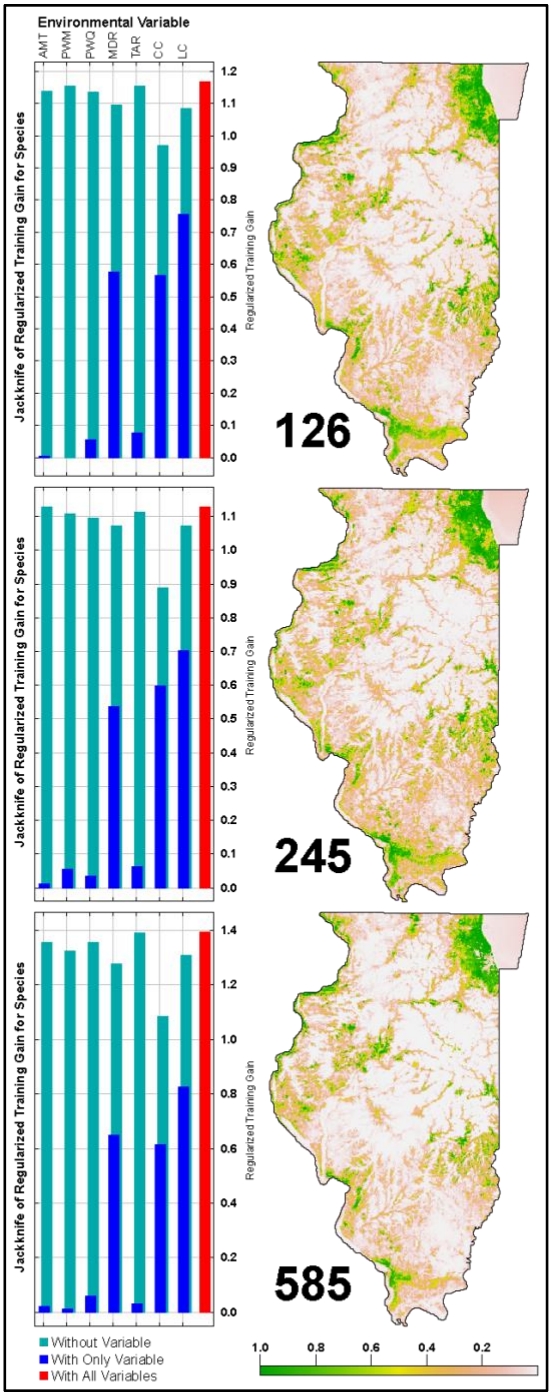

Figure 3-3. Predictive maps and jackknifes of environmental variables for *Platygyrium* 2041-2060 climate scenarios.

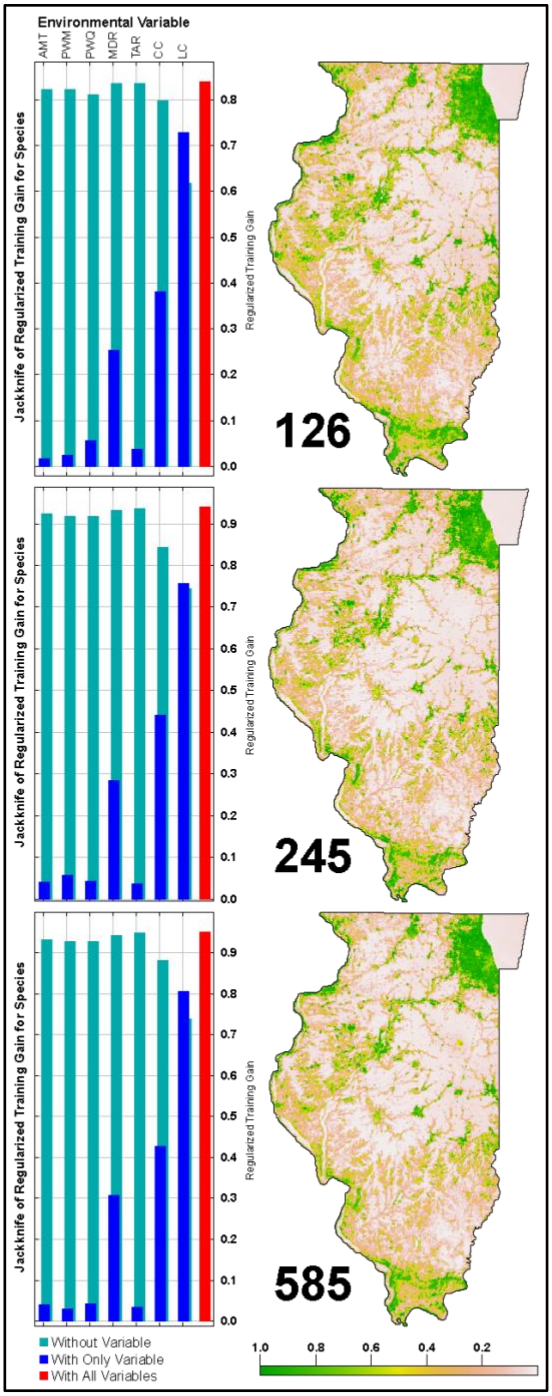

Figure 3-4. Predictive maps and jackknifes of environmental variables for *Plagiomnium* 2041-2060 climate scenarios.

Leskea

The current model of *Leskea* shares the most consistent distribution with the SSP 245 model. The latter shows a minor increase in distribution likelihood around the northern Mississippi river (Figure 3-5). The SSP 126 and SSP 585 models of *Leskea* show a slight decrease in distribution, particularly in more no likelihood areas throughout the state and in the Southern Illinois forests. The environmental variables are consistent between all the models, built off of Land Cover, Canopy Cover, and Mean Diurnal Range. The future models of *Leskea* show a slight increase in the importance of Mean Diurnal Range, which likely accounts for the small change in distribution likelihood. The *Leskea* distribution shows fairly high resilience to climate change throughout the future models.

Brachythecium

The future *Brachythecium* models show similar information to the other future models so far: the SSP 245 scenario shows the most distribution gain with increases around high likelihood areas and in Southern Illinois (Figure 3-6). All four *Brachythecium* models are based on the same representation of the environmental variables, with Land Cover as the most critical and Canopy Cover and Mean Diurnal Range showing equal importance. Overall, all future models show a loss in distribution likelihood compared to the current model somewhere within the state. But the Southern Illinois forests are of particular interest, as the high likelihood pattern of the current model is most similar to the SSP 585 model; both the SSP 126 and SSP 245 models show a lower likelihood in this area.

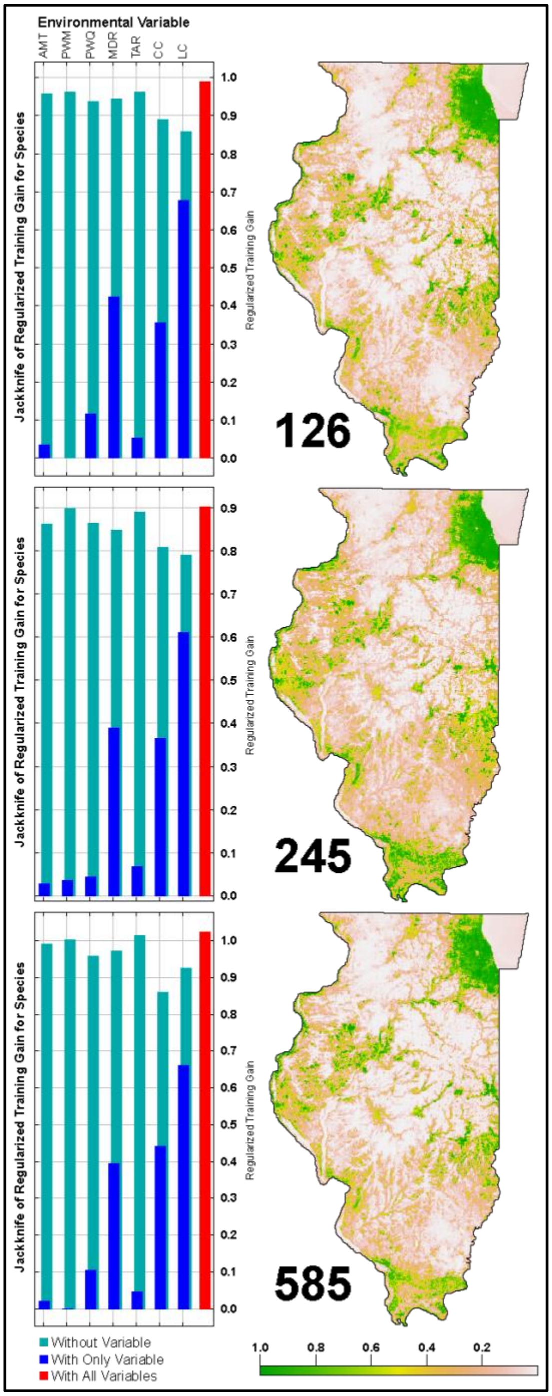

Figure 3-5. Predictive maps and jackknifes of environmental variables for *Leskea* 2041-2060 climate scenarios.

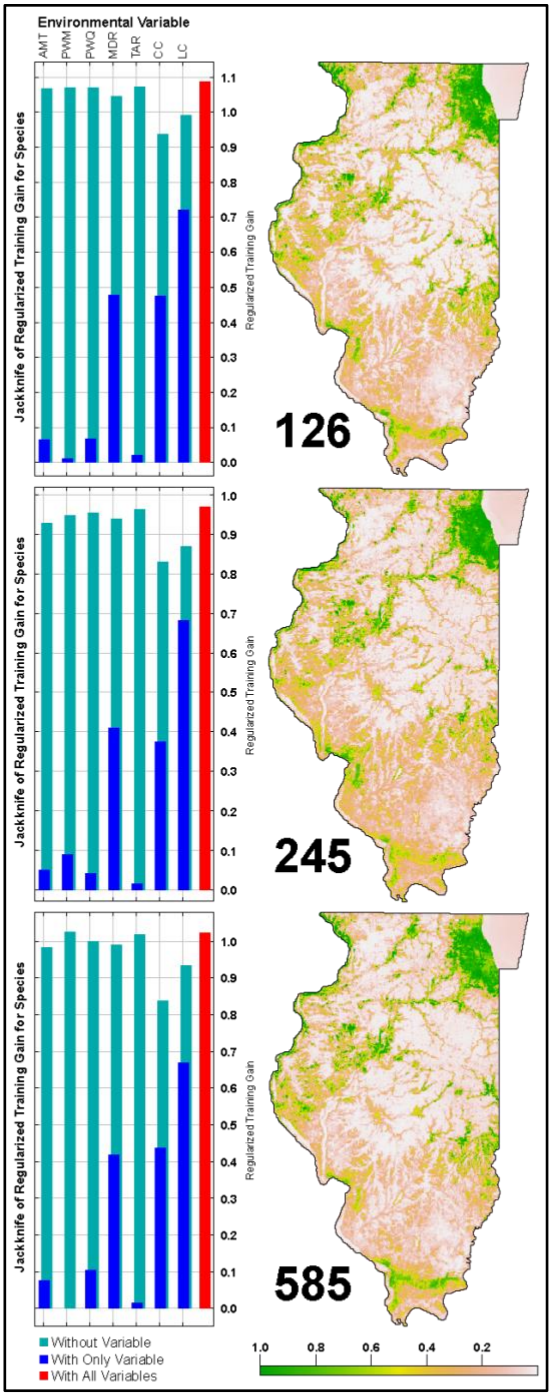

Figure 3-6. Predictive maps and jackknifes of environmental variables for *Brachythecium* 2041-2060 climate scenarios.

Bryum

Despite the variable AUC values of the future models of *Bryum*, their predictive distributions follow a reasonable pattern. All of the future and current models are based on the same environmental variables: mainly Land Cover, with secondary importance from Canopy Cover and Mean Diurnal Range (Figure 3-7). The current model of *Bryum* is most similar to the distribution of the SSP 126 future model, with the latter having slightly more areas of likelihood. The SSP 245 model of *Bryum* shows the highest distribution likelihood, particularly around the Mississippi River and western border. The SSP 585 model shows a substantial decrease in distribution likelihood, with a majority of the state showing no likelihood for *Bryum*.

Frullania

The future model of *Frullania* all show an increase in predictive distribution compared to the current model. This is particularly apparent in the increased distribution in the Chicagoland area for all future models (Figure 3-8). The SSP 126 model of *Frullania* shows the most gain in distribution, mostly noticeable in the likely distribution areas around the Illinois River. The SSP 585 shares the same likely areas as the SSP 126 model, while the SSP 245 model is missing likelihood around the river. All of the future models have an increase of importance in Mean Diurnal Gain that the current model of *Frullania* lacks, and a slight decrease of importance for Temperature Annual Range; these two factors likely explain the distribution increase for the future projections. Canopy Cover followed by Land Cover remain the most critical environmental variables for all four of the models of *Frullania*. The SSP 585 model differs from the rest by relying more on Annual Mean Temperature and Precipitation of Wettest Month, making the Bioclim variables of balanced importance.

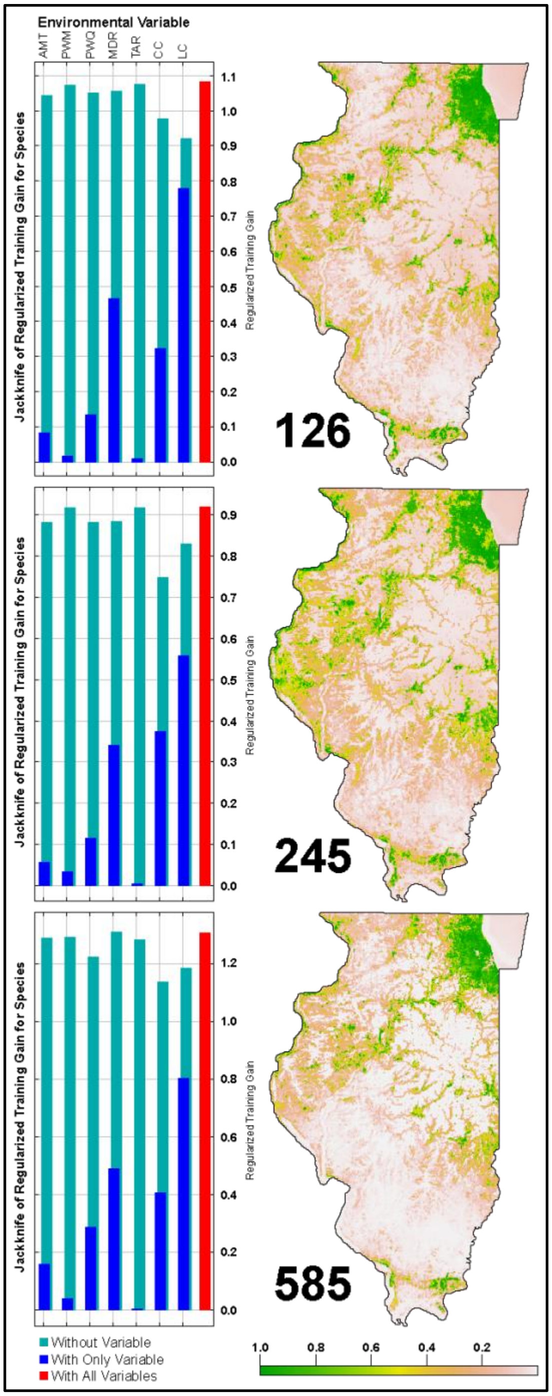

Figure 3-7. Predictive maps and jackknifes of environmental variables for *Bryum* 2041-2060 climate scenarios.

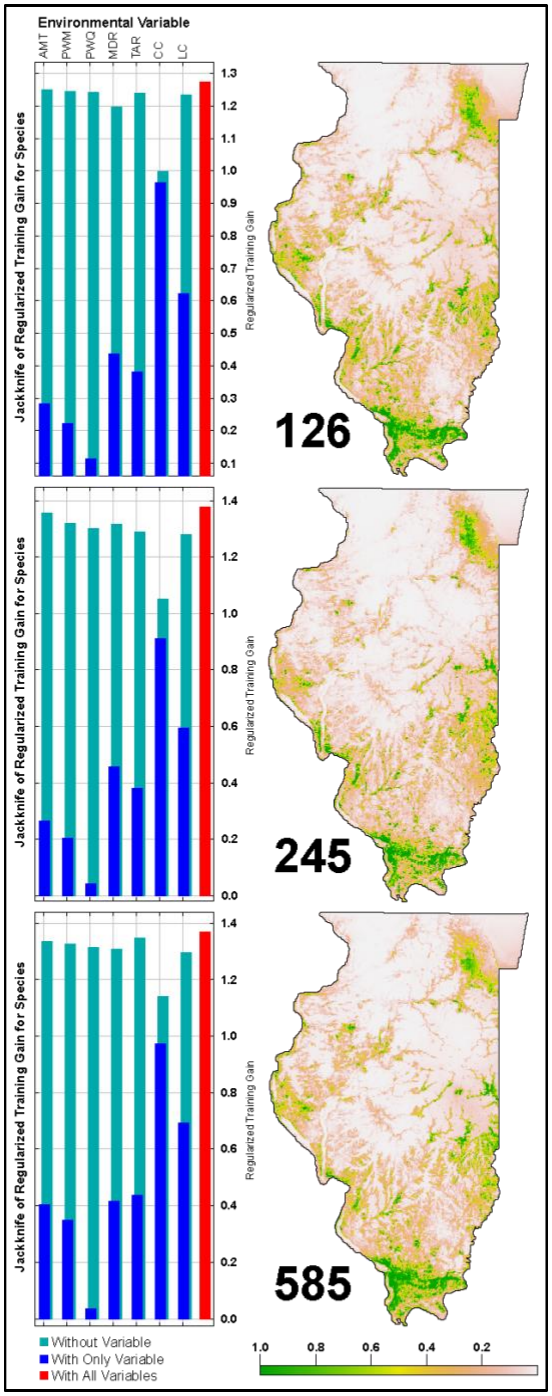

Figure 3-8. Predictive maps and jackknifes of environmental variables for *Frullania* 2041-2060 climate scenarios.

Atrichum

The future scenario models all show a slight loss in distribution compared to the current model of *Atrichum*, particularly around the southern central region (Figure 3-9). Similarly to the previous two models, the future model of *Atrichum* with the widest distribution is the SSP 245 scenario with expanded high likelihood areas and more low likelihood areas than no likelihood. Respective to the other environmental variables, this is also where Mean Diurnal Range shows more importance to the model. The jackknifes between all four models are similar as well, relying on Land Cover and Canopy Cover primarily. The SSP 126 and SSP 585 models of *Atrichum* have a more similar distribution to each other, but the latter has slightly more areas of high likelihood. Even though SSP 126 has more low likelihood areas than SSP 585, these models show a small pattern towards distribution increase as the climate change response worsens.

Amblystegium

For the model of *Amblystegium*, there are only minor changes in distribution likelihood between the three scenarios, with the SSP 126 differing the most from the other two (Figure 3-10). In this scenario, there is more of a low likelihood rather than no likelihood throughout the state, particularly in the north, similar to the current model of *Amblystegium*. The SSP 126 and current models have very similar areas of high likelihood distribution, aside from a greater likelihood in the Southern Illinois forests and lower likelihood along the northern Illinois River in the SSP 126 model. The SSP 245 and SSP 585 models are almost identical in their distribution likelihood, indicating an unlikely distribution change for *Amblystegium* without a “green” response. Even in this case, *Amblystegium* distribution will remain relatively consistent.

The jackknives for the future and current models are similar as well, with Land Cover being the most critical for all models and Canopy Cover and Mean Diurnal Range at a similar amount of importance. The only difference is the minor increase in importance of Canopy Cover and decrease of Mean Diurnal Range in the SSP 245 model, likely because the diurnal range is slightly more variable in the SSP 245 data than in the other scenarios.

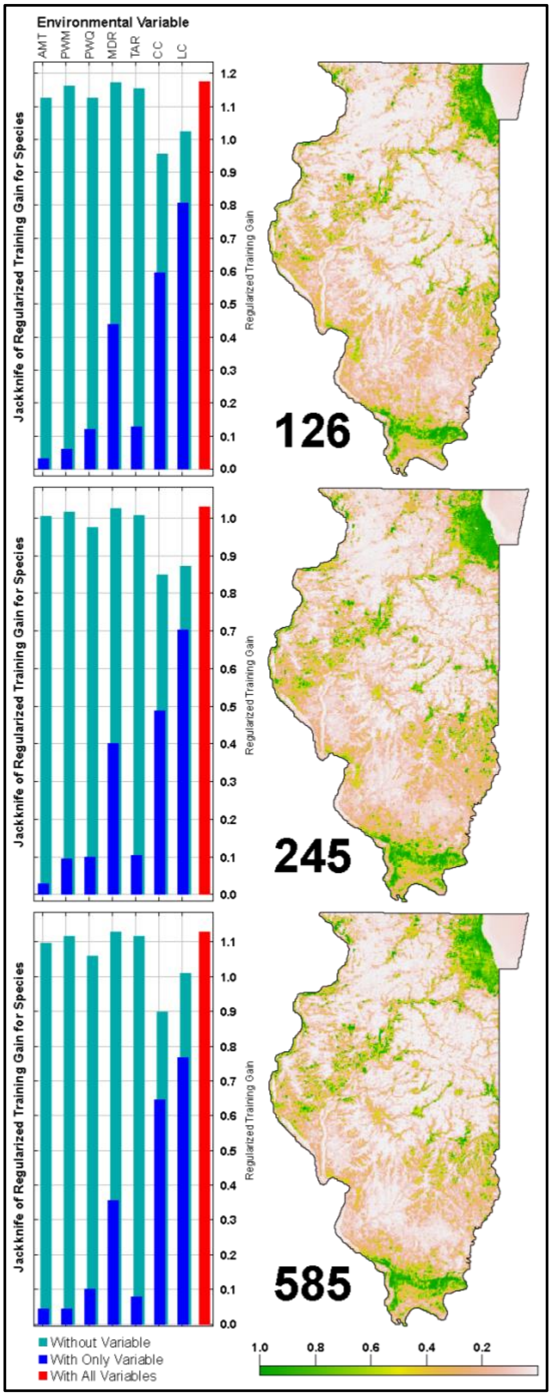

Figure 3-9. Predictive maps and jackknifes of environmental variables for *Atrichum* 2041-2060 climate scenarios.

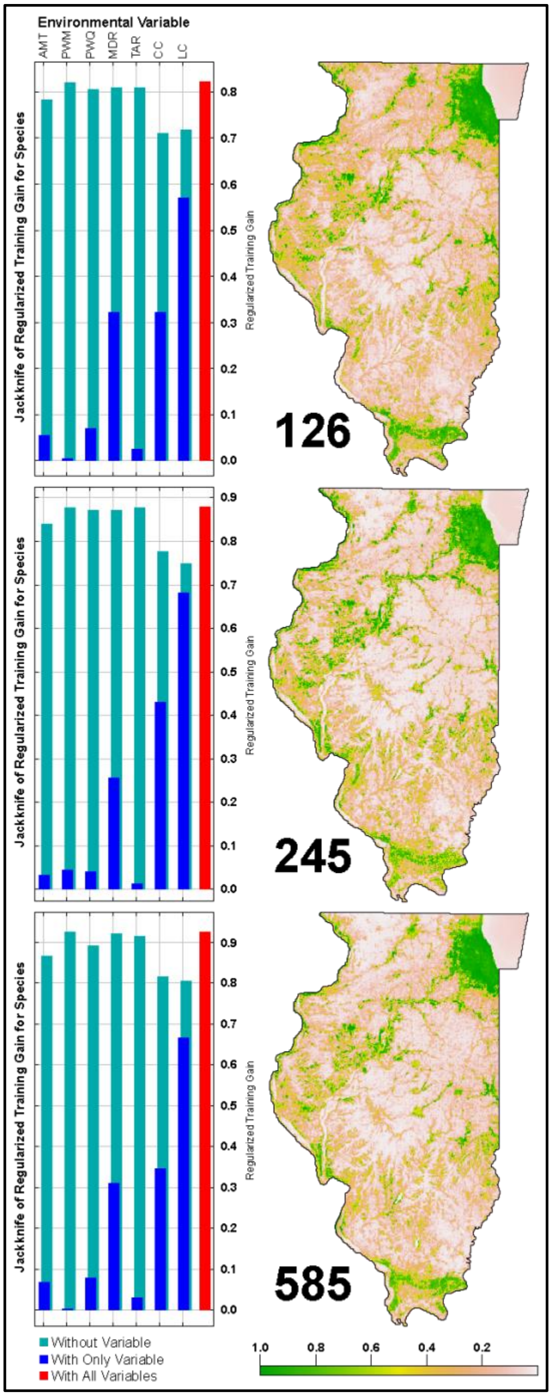

Figure 3-10. Predictive maps and jackknifes of environmental variables for *Amblystegium* 2041-2060 climate scenarios.

Entodon

The *Entodon* distribution stays pretty consistent between the current model and the SSP 245 model, with some minor loss in the SSP 585 model (Figure 3-11). In the SSP 126 model, there is a distinctly smaller distribution from the rest, particularly around the rivers. The SSP 126 model is also the only future model of *Entodon* where Mean Diurnal Range shows an increase in gain. Beyond this, the future models are consistent with the current model, built off of Land Cover and Canopy Cover. The connection between Mean Diurnal Range and the lower distribution likelihood in the SSP 126 model shows a sensitivity to climate factors unseen in other models. Though land use may be the primary factor across all models, climate still plays a role in shaping bryophyte distribution.

Hypnum

The future models of *Hypnum* see an increase in likely distribution compared to the current model. All three scenarios show more likelihood around the Illinois River and western border, with the SSP 245 and SSP 585 scenarios showing an increase in Southern Illinois as well (Figure 3-12). There are no distinct differences between any of the environmental variables of importance, all models are built off of Land Cover, Mean Diurnal Range, and Canopy Cover to a lesser degree.

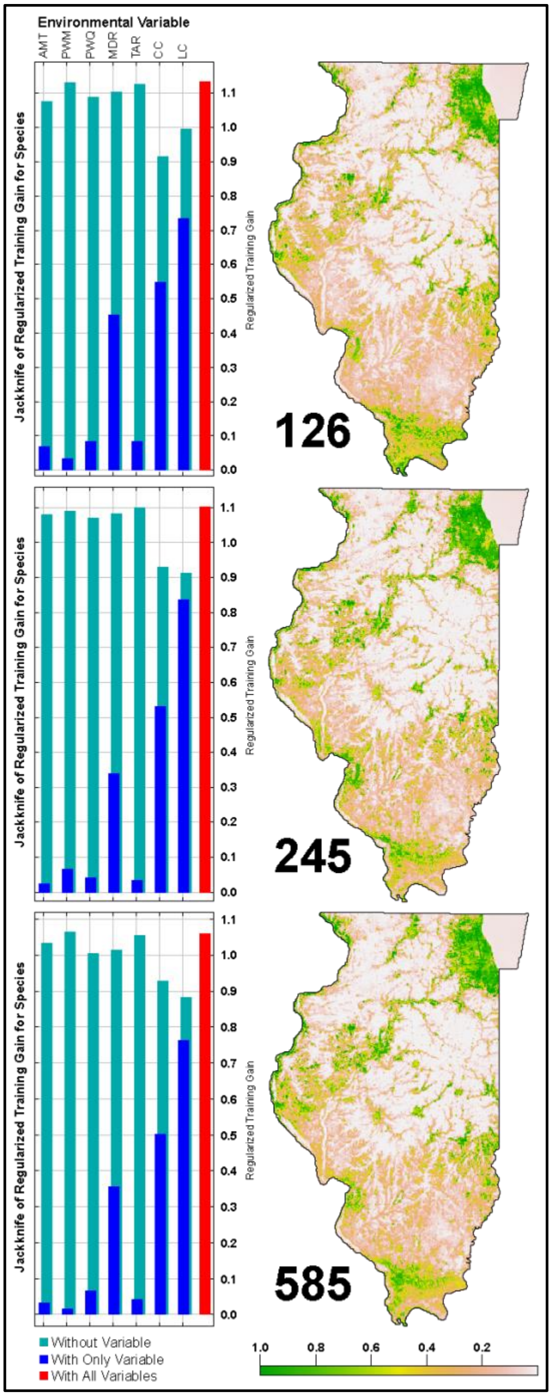

Figure 3-11. Predictive maps and jackknifes of environmental variables for *Entodon* 2041-2060 climate scenarios.

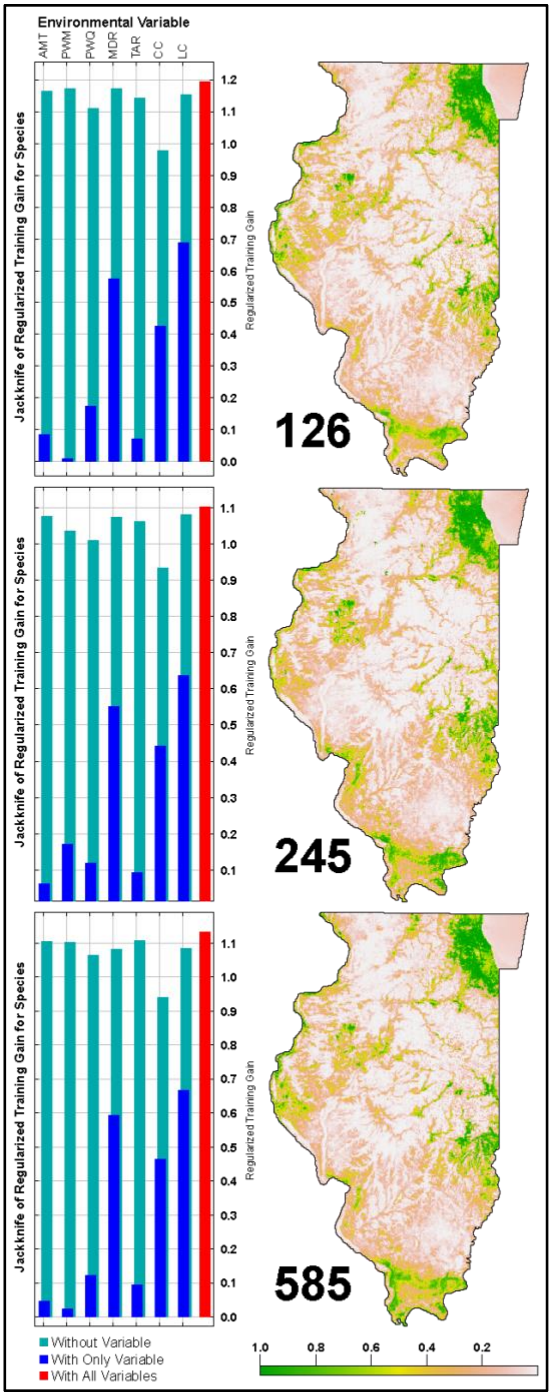

Figure 3-12. Predictive maps and jackknifes of environmental variables for *Hypnum* 2041-2060 climate scenarios.

Anomodon

The models of *Anomodon* are even more consistent with each other: the current and three future models all have Land Cover followed by Canopy Cover as the most critical variables (Figure 3-13). Mean Diurnal Range is the only relevant climate variable within the model. For distribution, all future scenarios imply there will be a more generalized distribution throughout the state, with more low likelihood areas than no likelihood areas like in the current model. The SSP 126 and SSP 585 models have a similar pattern of distribution, with SSP 245 showing a slight increase in high likelihood areas. These are mainly along the central/southern region and along other consistent high areas. The higher AUC values of the SSP 245 compared to the other two scenarios might explain this, suggesting the climate projections on the world's current path will produce the highest distribution for *Anomodon*.

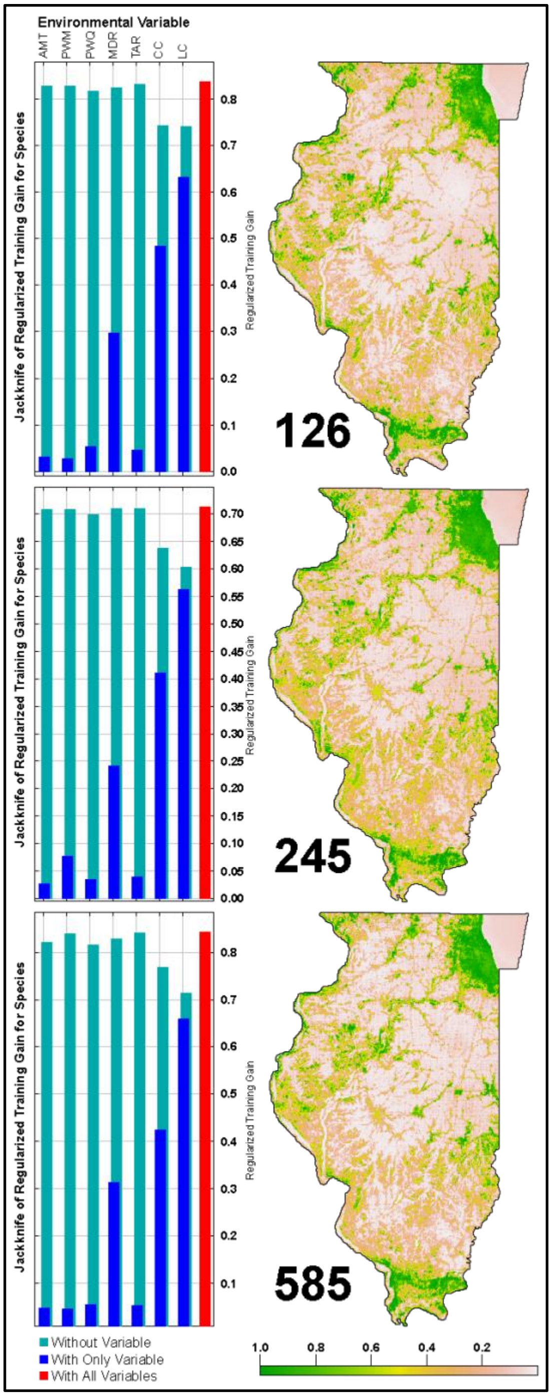

Figure 3-13. Predictive maps and jackknifes of environmental variables for *Anomodon* 2041-2060 climate scenarios.

Species Models

The AUC values for the species future models are mostly on par with their respective current models, but the two sets are more variable than the current and future genera models (Table 3-2). Notably the future models for *Anomodon attenuatus, Climacium americanum,* and *Plagiomnium cuspidatum* have higher AUC values than their current day models; these models all had relatively low values for their current models. The most critical environmental variables are consistent between the current and all future model scenarios, aside from *Entodon seductrix, Plagiomnium cuspidatum, and Platygyrium repens*. In the case of all these species, the primary variable from the current model only has a slightly lower amount of training gain. Overall, these measures attest to the consistency of the model structure between the current and future species models.

Callicladium haldaneanum

The current model of *C. haldaneanum* current is almost indistinguishable from the SSP 126 model, with a slight increase in high distribution north of Chicago (Figure 3-14). The SSP 585 model is also very similar, with a larger low likelihood area in the north than the current model. The SSP 245 model is the only one that shows significant decrease in distribution, with Central Illinois becoming a no distribution area almost completely. The environmental variables remain consistent across the models, aside from the decrease of importance of Mean Diurnal Range in the SSP 126 model, and its increase of importance in the SSP 245 and SSP 585 models.

Table 3-2. Future species model quality for the complete data set and replicate fold averages and the most important environmental variable to the model. Any AUC value above 0.8 is considered a confident model.

Species	**Top Critical Environmental Variable**	**SSP 126 AUC**		**SSP 245 AUC**		**SSP 585 AUC**	
		Full	**Replicate**	**Full**	**Replicate**	**Full**	**Replicate**
Callicladium haldaneanum	Mean Diurnal Range	0.99	0.88	0.85	0.94	0.97	0.88
Amblystegium serpens	Mean Diurnal Range	0.87	0.95	0.91	0.96	0.97	0.93
Entodon seductrix	Canopy Cover	0.87	0.84	0.91	0.84	0.89	0.84
Amblystegium varium	Mean Diurnal Range	0.89	0.95	0.91	0.96	0.95	0.93
Leskea gracilescens	Mean Diurnal Range	0.90	0.86	0.82	0.88	0.82	0.87
Platygyrium repens	Mean Diurnal Range*	0.91	0.87	0.87	0.91	0.78	0.92
Anomodon rostratus	Canopy Cover	0.89	0.89	0.95	0.88	0.94	0.87
Brachythecium acuminatum	Mean Diurnal Range	0.96	0.89	0.97	0.90	0.82	0.91
Plagiomnium cuspidatum	Land Cover	0.92	0.86	0.88	0.86	0.89	0.88
Climacium americanum	Canopy Cover	0.95	0.89	0.92	0.92	0.86	0.92
Ceratodon purpureus	Land Cover	0.81	0.83	0.85	0.81	0.90	0.83
Anomodon attenuatus	Canopy Cover	0.94	0.84	0.89	0.86	0.90	0.85
Amblystegium riparium	Land Cover	0.77	0.78	0.74	0.85	0.88	0.76

* The *Platygyrium repens* SSP 245 model has a slightly higher gain from Land Cover than Mean Diurnal Range

Amblystegium serpens

The future models of *A. serpens* future models all see a decrease in distribution from the current model. The SSP 126 and SSP 245 models show the largest distribution loss and appear similar to each other, aside from SSP 126 having low distribution likelihood in the north and SSP 245 in the central region (Figure 3-15). The SSP 585 model of *A. serpens* shows the highest distribution likelihood of the future models, with more distribution in the Chicagoland area and along the western border. This model also has the most similar build to the current model, with the main difference between the increase in Land Cover importance in the SSP 585 model. In the SSP 126 model, Land Cover and Canopy Cover have an equal level of importance, and in the SSP 245 model, these two variables and the Mean Diurnal Range are near equivalent, despite being dominant in every other model of *A. serpens*.

Entodon seductrix

The future models of *E. seductrix* future have a similar distribution to the current model, with the SSP 585 model showing only a loss of distribution in low likelihood areas (Figure 3-16). The SSP 126 model also shows a loss of low likelihood areas, but to a larger extent throughout the state. The SSP 245 model is the only future model that shows a loss of high distribution areas, around Central and Southern Illinois. All the models have a similar build, relying on Land Cover and Canopy Cover. The only minor difference is the increase of the importance of Mean Diurnal Range in the SSP 126 and SSP 245 models. It is apparent *E. seductrix* is resilient to changes in climate change, or at least much more reliant on land use than climate factors.

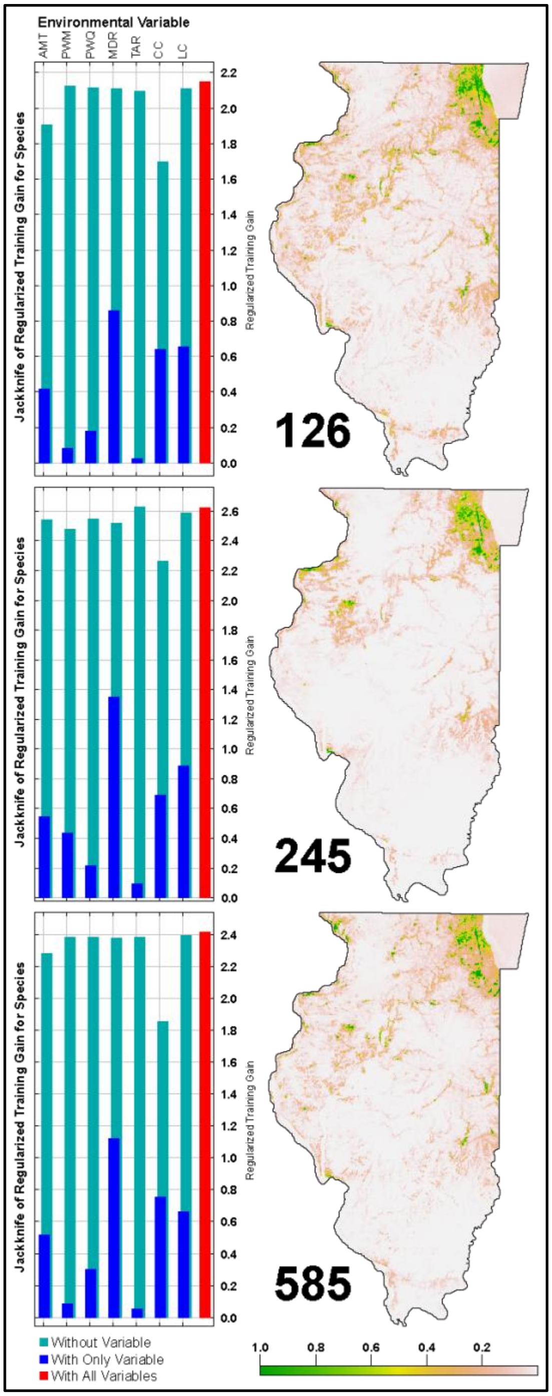

Figure 3-14. Predictive maps and jackknifes of environmental variables for *Callicladium haldaneanum* 2041-2060 climate scenarios.

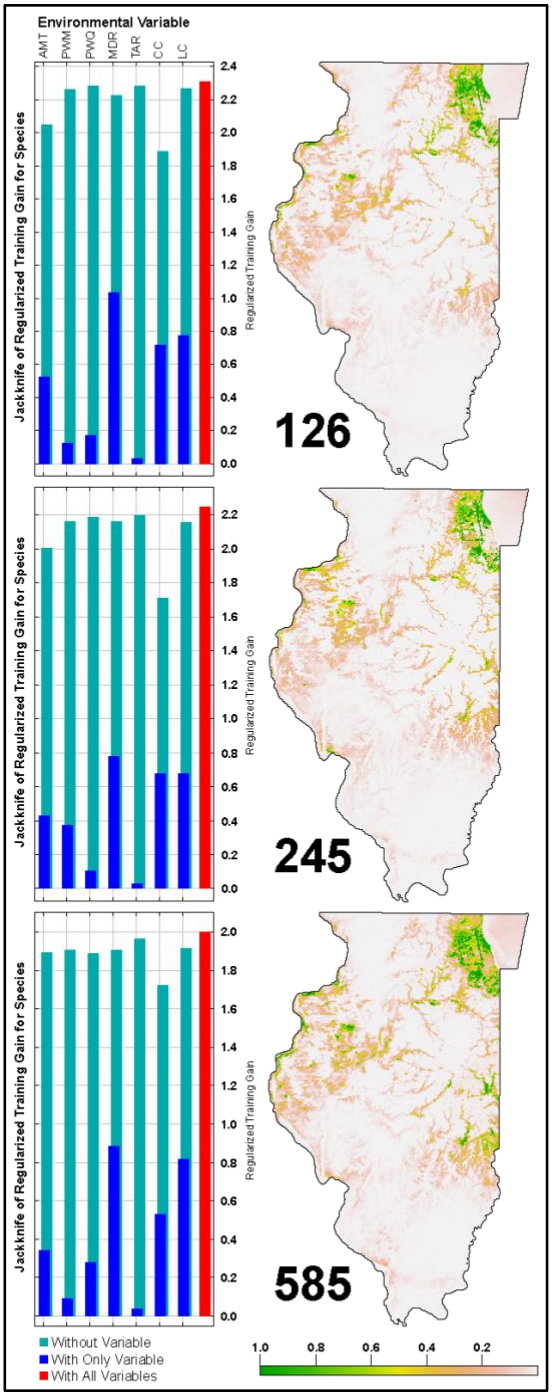

Figure 3-15. Predictive maps and jackknifes of environmental variables for *Amblystegium serpens* 2041-2060 climate scenarios.

Amblystegium varium

The distribution difference between the future models of *A. varium* future is similar to the pattern seen in the models of *A. serpens*. There is an overall loss in distribution from the current to the future models, with the SSP 126 and SSP 245 models showing the greatest loss (Figure 3-17). The SSP 585 model shows arguably gain compared to the current model of *A. varium*, losing distribution in the east but gaining low likelihood areas in the west. For the importance of environmental variables, the current model is most similar to the SSP 126 model, dominated by Mean Diurnal Range and the two land use variables showing equal importance. The SSP 245 model shows a notable increase in the importance of Land Cover, where the SSP 585 model shows a decrease in Mean Diurnal Range relative to the current model of *A. varium*.

Leskea gracilescens

The future models of *L. gracilescens* show a loss in predicted distribution from the current model. The SSP 126 and SSP 585 models show similar distribution, with a loss in likelihood in Chicago, Southern Illinois, and along the Illinois River (Figure 3-18). The SSP 245 model differs from the rest with an extreme loss of distribution in Northern Illinois and a slight gain along the eastern border. This is the result of the importance of Temperature Annual Range to the model and the decreased importance of Land Cover. The rest of the environmental variables are consistent across the models, with a small increase in Mean Diurnal Range in the SSP 126 and SSP 585 models from the current model of *L. gracilescens*.

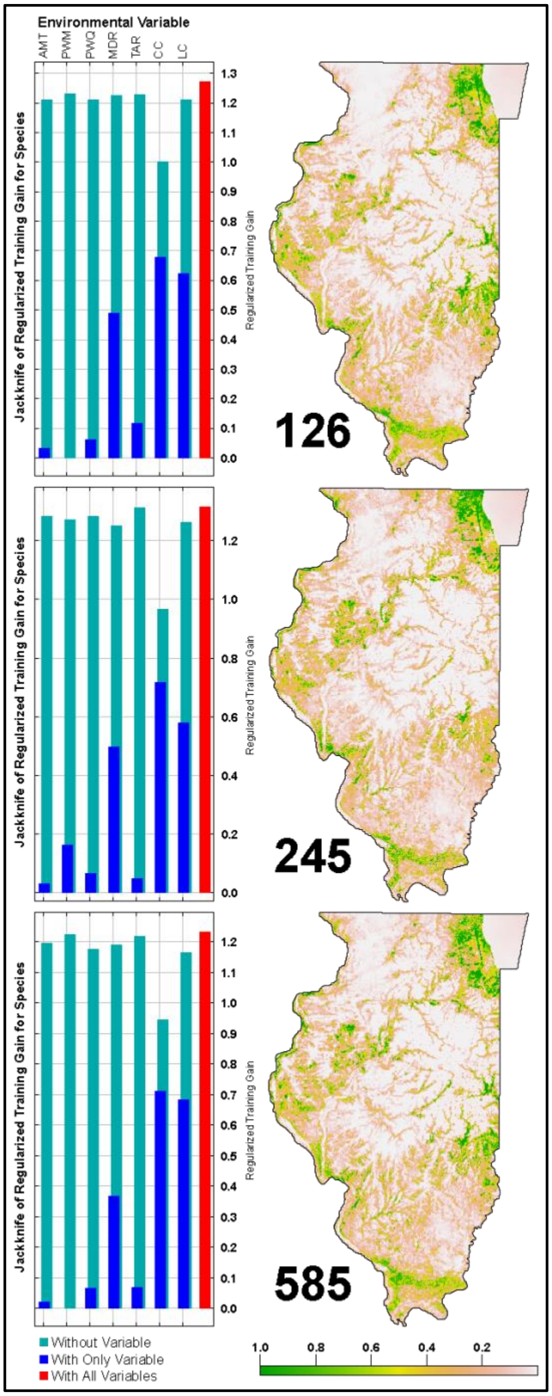

Figure 3-16. Predictive maps and jackknifes of environmental variables for *Entodon seductrix* 2041-2060 climate scenarios.

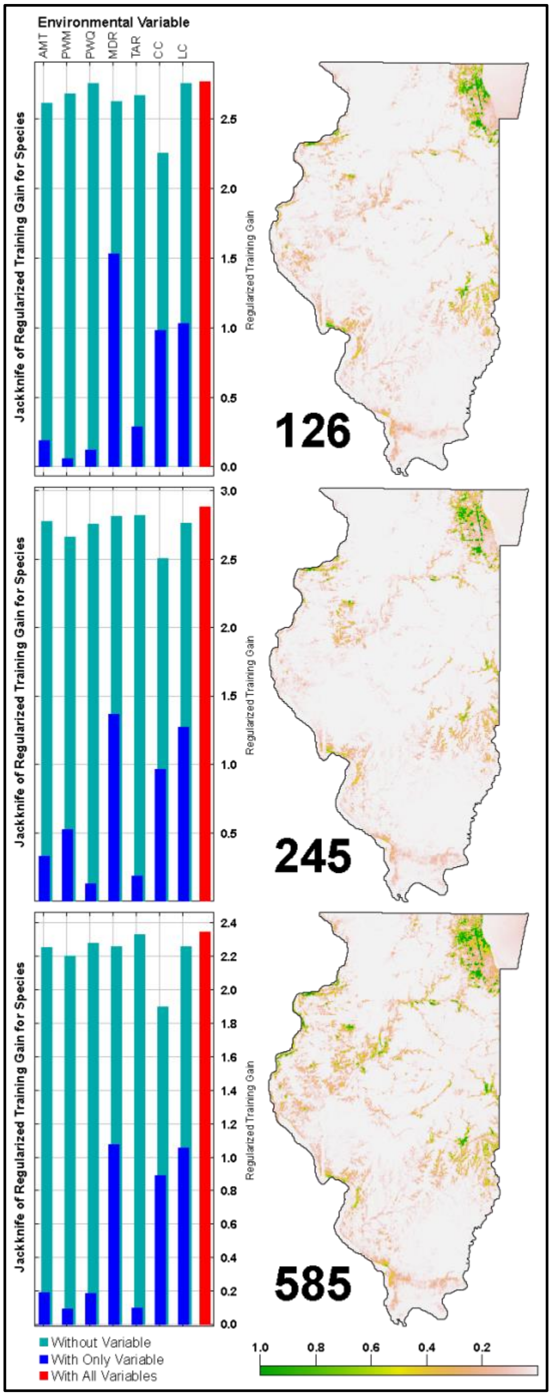

Figure 3-17. Predictive maps and jackknifes of environmental variables for *Amblystegium varium* 2041-2060 climate scenarios.

Platygyrium repens

The future models of *P. repens* show a pattern of distribution loss as the climate response worsens. The SSP 126 distribution matches the current distribution, with some small areas of gain and loss along the Illinois River and western border (Figure 3-19). The SSP 245 model shows more loss, particularly around Western and Southern Illinois. The SSP 585 includes this loss as well as additional loss around the Illinois River and Northern Illinois. The future models all show an increase of importance of the top three variables in the current model of *P. repens*: Land Cover, Canopy Cover, and Mean Diurnal Range. There is also a minor presence of Temperature Annual Range in the models, particularly in the SSP 585 model.

Anomodon rostratus

The current model of *A. rostratus* is relatively indistinguishable from the SSP 126 species model. The other two future models show distribution increase in different areas: the SSP 245 has an increase around Chicago and the northern Illinois River, while the SSP 585 model shows an increase around the southern Illinois River and Southern Illinois (Figure 3-20). The contribution of environmental variables is fairly consistent across the four models, aside from the small decrease in Mean Diurnal Range in the SSP 126 and SSP 245 models.

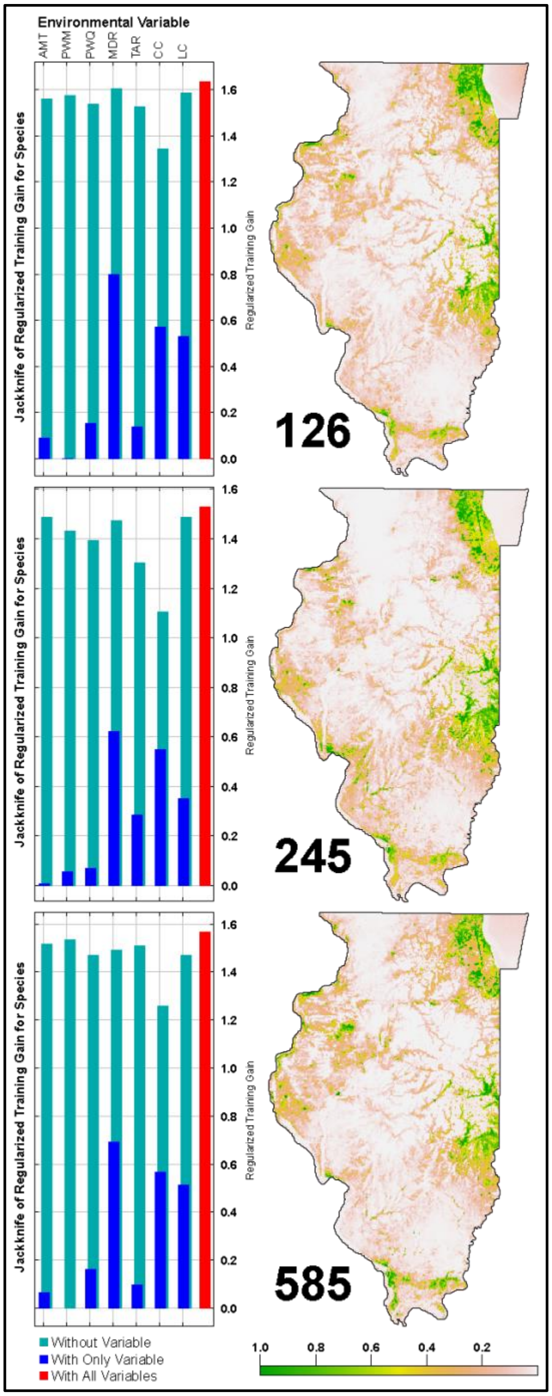

Figure 3-18. Predictive maps and jackknifes of environmental variables for *Leskea gracilescens* 2041-2060 climate scenarios.

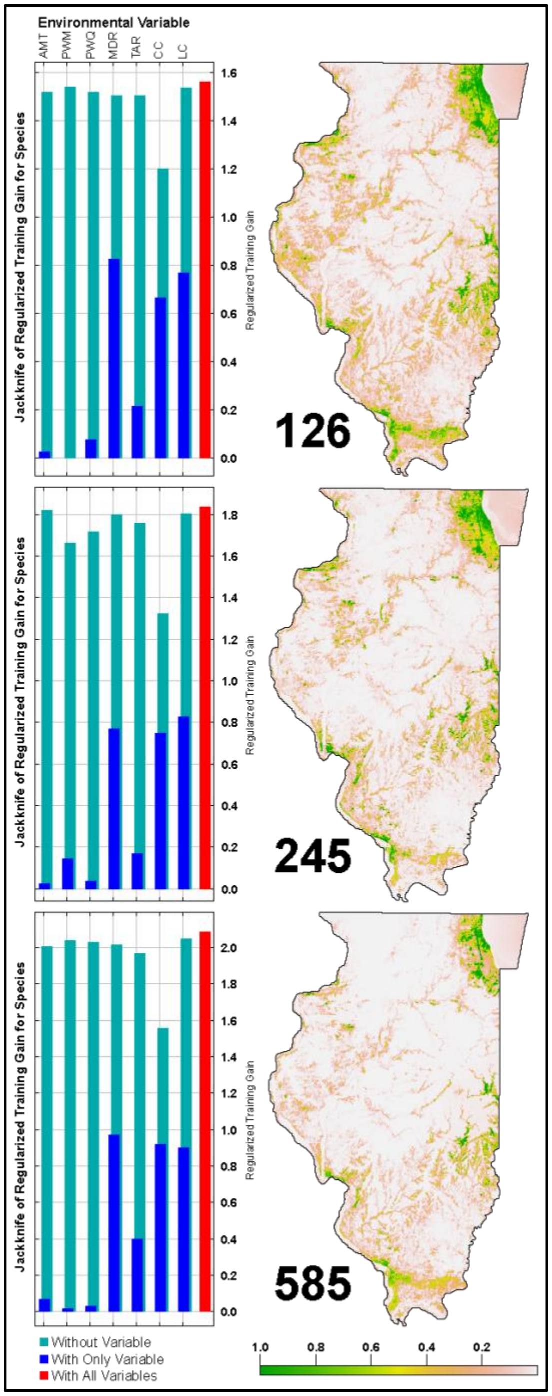

Figure 3-19. Predictive maps and jackknifes of environmental variables for *Platygyrium repens* 2041-2060 climate scenarios.

Brachythecium acuminatum

The models of *B. acuminatum* display a pattern of distribution shifting southward as the societal climate response worsens. The SSP 126 model is comparable to the current species model, with increased likelihood around Chicago and Western Illinois (Figure 3-21). The SSP 245 model shows the first southward shift, losing low likelihood regions in the north but gaining them in the south; the future model also shows increased distribution around the consistent areas of high likelihood. The decrease in distribution in the SSP 585 model compared to the other models is apparent, but also shows a greater likelihood in the Southern Illinois forests compared to the current model. The major difference between the jackknife plots is the importance of Mean Diurnal Range: the SSP 126 and the SSP 245 models show a decrease from the current *B. acuminatum* model, but the SSP 585 model shows an increase. *Brachythecium acuminatum* stands out from the other species models as it is particularly reliant on Mean Diurnal Range.

Plagiomnium cuspidatum

The future models of *P. cuspidatum* all show an increase in areas of distribution across the state. The SSP 126 model gains more high likelihood distribution areas throughout Central Illinois (Figure 3-22). The SSP 245 and SSP 585 models show a pattern of increase towards Northern Illinois, with the latter showing a loss in Central Illinois and gain along the northern Mississippi. There is no substantial difference between all of the environmental variables, all four models of *P. cuspidatum* are built off the land use variables primarily, followed by Mean Diurnal Range.

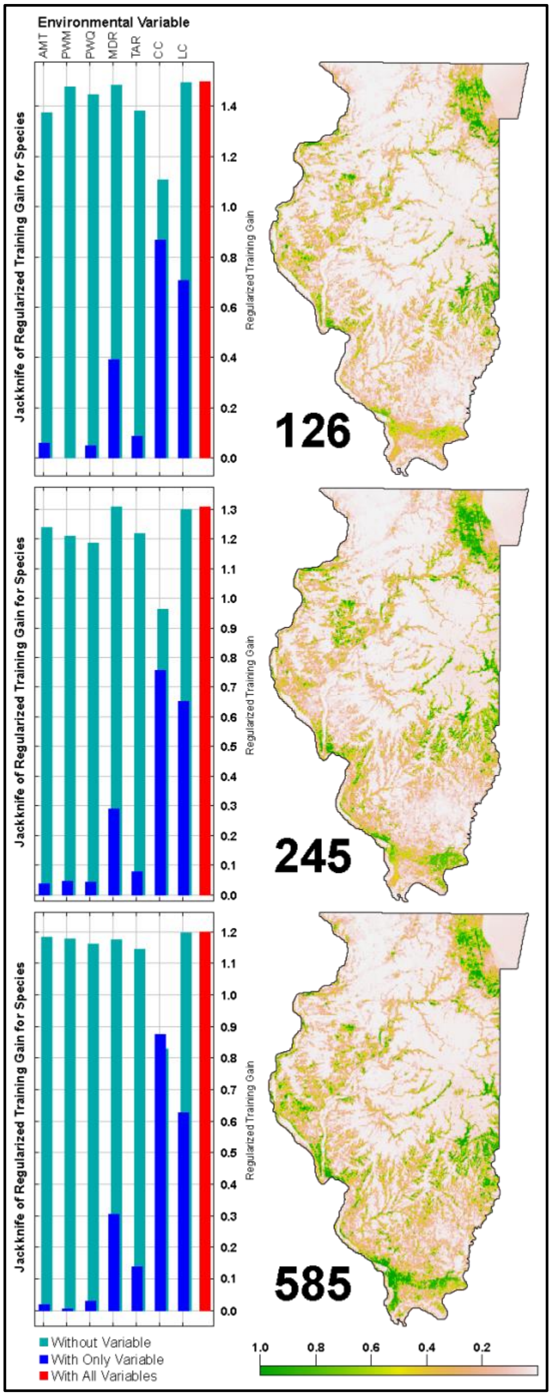

Figure 3-20. Predictive maps and jackknifes of environmental variables for *Anomodon rostratus* 2041-2060 climate scenarios.

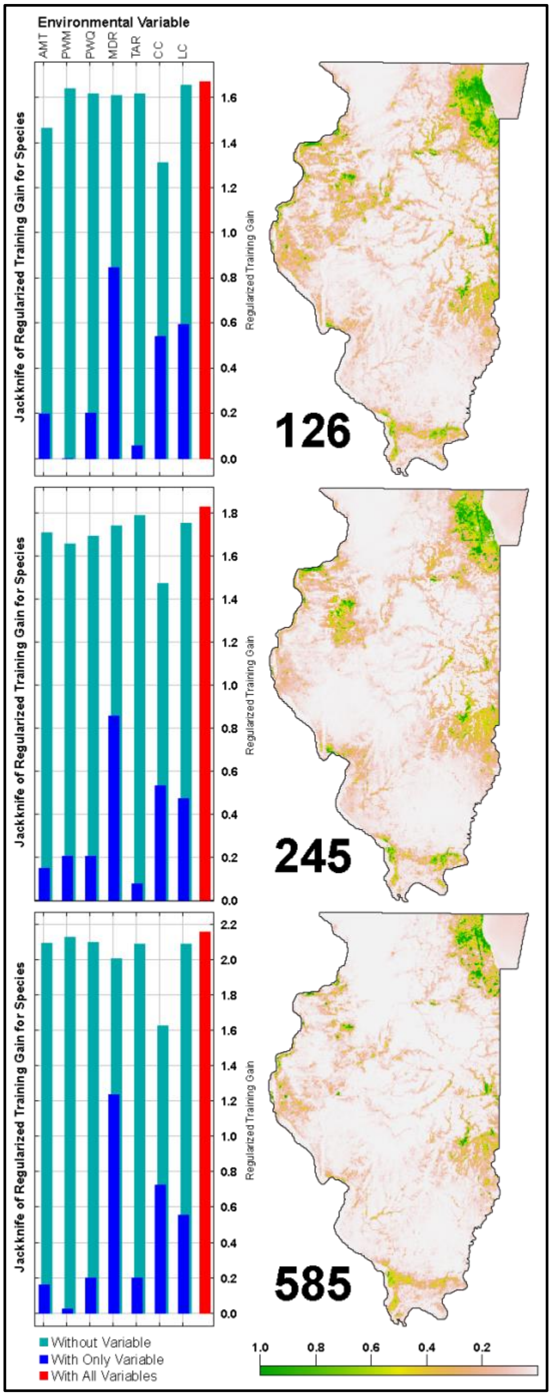

Figure 3-21. Predictive maps and jackknifes of environmental variables for *Brachythecium acuminatum* 2041-2060 climate scenarios.

Climacium americanum

The future models of *C. americanum* remain consistent with the current model, only losing some high distribution likelihood along the eastern border as the climate change response worsens, and a smaller increase in distribution likelihood in Southern Illinois (Figure 3-23). Beyond these areas, the model distribution only differs in its low likelihood and no likelihood areas. This is the result of the consistent importance of Canopy Cover, which even shows a slight increase in the SSP 245 and SSP 585 models. These two models also see a slight increase in the importance of Land Cover. The reliance of *C. americanum* on more of the climate variables, such as the consistency of Temperature Annual Range suggests that this species might be useful as a climate change indicator.

Ceratodon purpureus

All of the future models of *C. purpureus* differ from the current model by showing a high distribution likelihood throughout Chicagoland, as opposed to just the suburbs (Figure 3-24). Aside from this, the SSP 126 model has a fairly similar distribution to the current model. The SSP 245 model shows an increase in high likelihood areas along the western and eastern borders of the state and the SSP 585 model shows this increase along the eastern border and in Southern Illinois. The environmental variable contribution is consistent throughout the four models, with a small decrease in Canopy cover in the SSP 245 and SSP 585 models, and a small increase of Land Cover in the SSP 245 model.

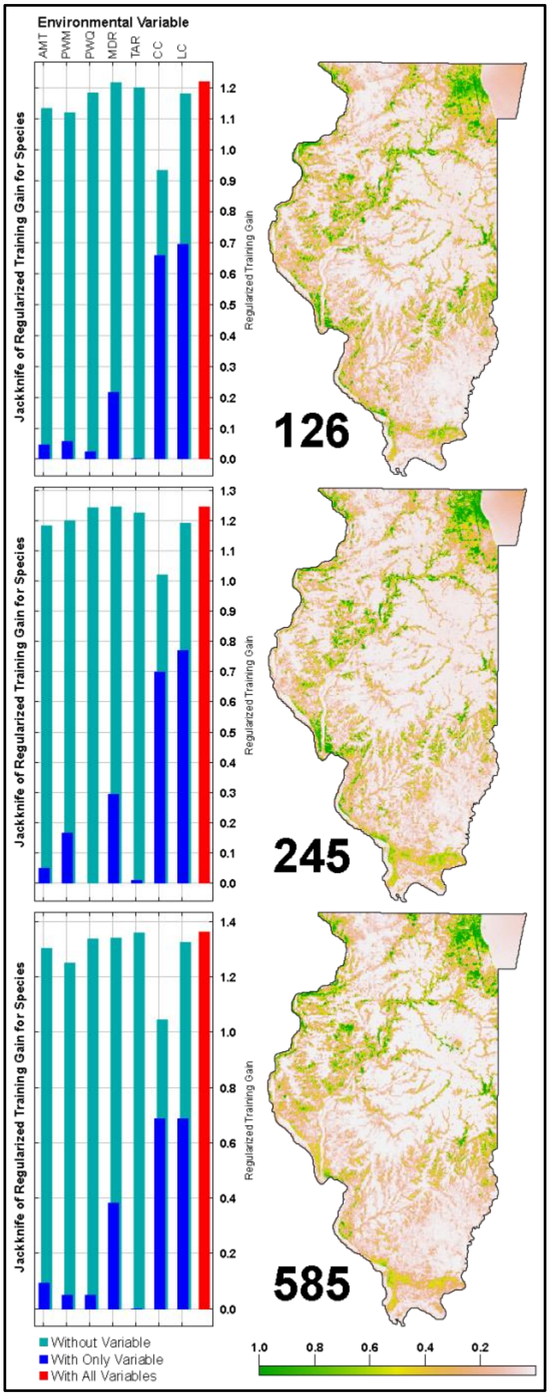

Figure 3-22. Predictive maps and jackknifes of environmental variables for *Plagiomnium cuspidatum* 2041-2060 climate scenarios.

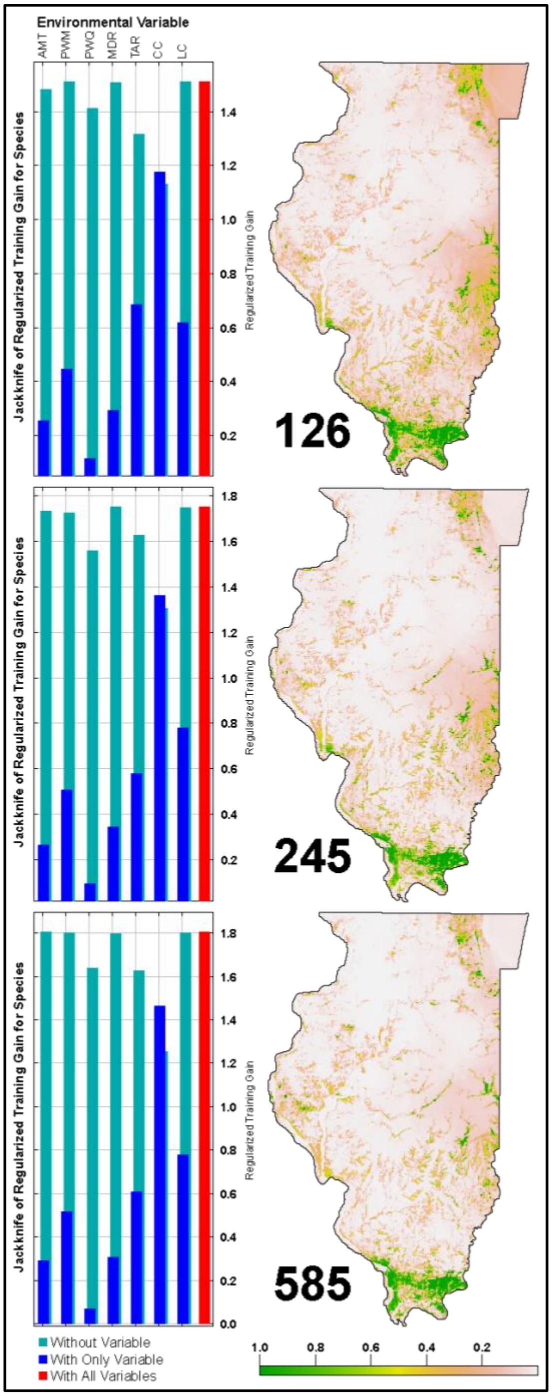

Figure 3-23. Predictive maps and jackknifes of environmental variables for *Climacium americanum* 2041-2060 climate scenarios.

Anomodon attenuatus

All of the future models of *A. attenuatus* show an increase in distribution likelihood compared to the current model. The SSP 126 model shows the largest increase, with more high likelihood areas around Chicago, western border, and the rivers (Figure 3-25). Between the SSP 126 and the SSP 245 model, distribution is lost around the Illinois River but Chicago and the western border still show more distribution than the current model of *A. attenuatus*. The SSP 585 model is the most similar to the current model, losing distribution from the other future models but still showing a slight increase from the current model around the high likelihood areas. The jackknife plots also show a similar relationship of important variables between the current and SSP 585 model, with a decrease in Canopy Cover in the latter. Canopy Cover also shows a decrease of importance in the SSP 126 and SSP 245 models, along with a large increase from Mean Diurnal Range.

Amblystegium riparium

All of the future models of *A. riparium* differ in predictive distribution from the current model and between each other. Compared to the current model, the SSP 126 model shows a decrease of distribution likelihood in the south, but an increase in the north (Figure 3-26). The SSP 245 model sees a slight increase in distribution likelihood in the Chicagoland area, but an overall decrease everywhere else. The SSP 585 model shows a high increase in distribution throughout the state and high likelihood areas, but particularly in the north; this model also differs in the decrease of importance from Land Cover compared to the current model of *A. riparium*. The other two future models mainly differ from the increase in gain from Mean Diurnal Range.

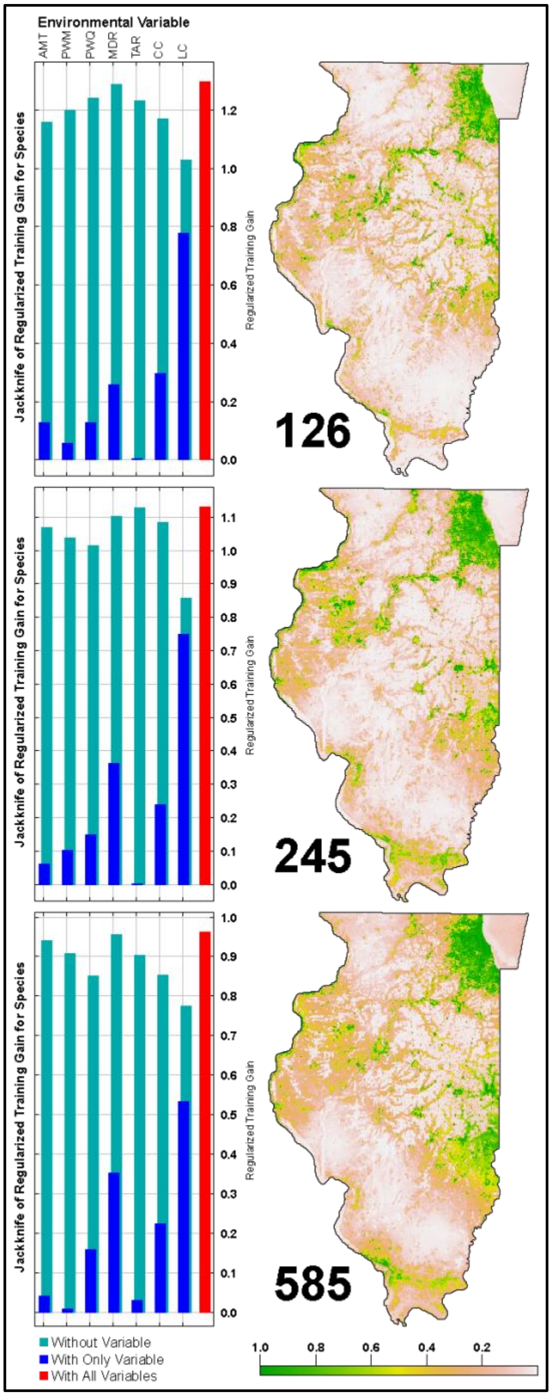

Figure 3-24. Predictive maps and jackknifes of environmental variables for *Ceratodon purpureus* 2041-2060 climate scenarios.

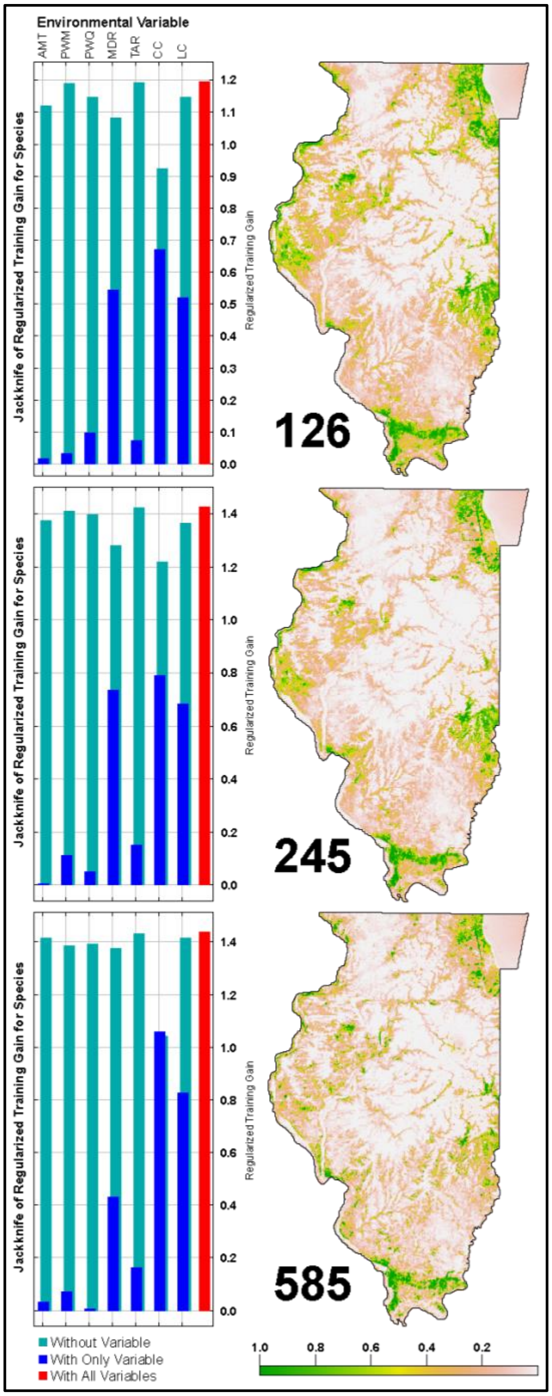

Figure 3-25. Predictive maps and jackknifes of environmental variables for *Anomodon attenuatus* 2041-2060 climate scenarios.

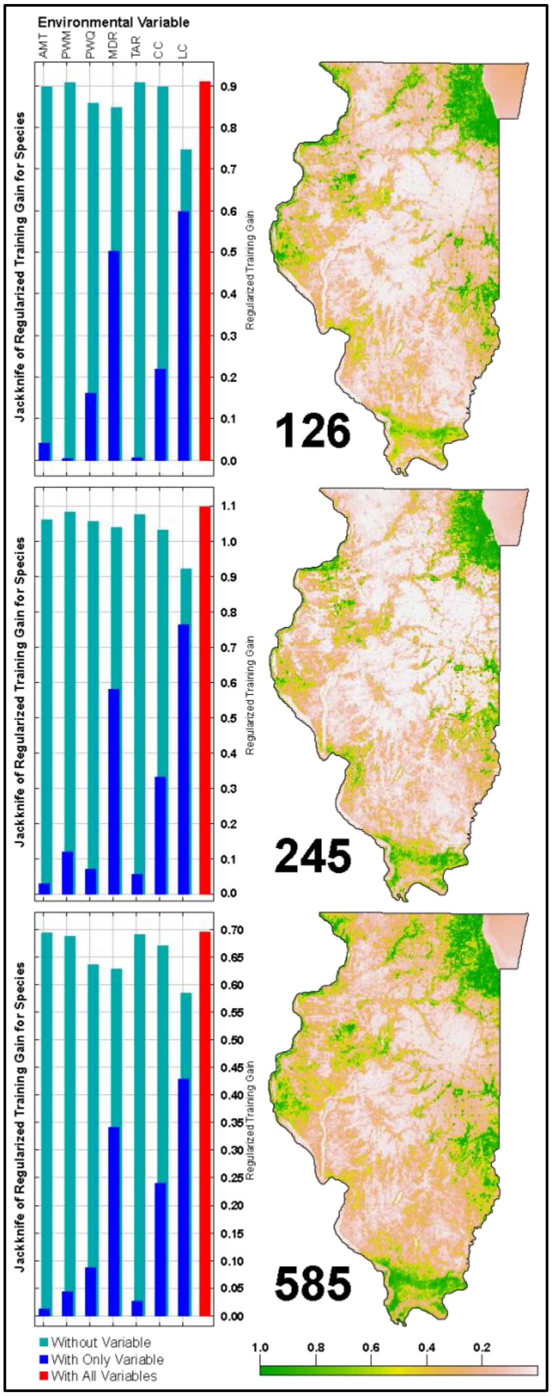

Figure 3-26. Predictive maps and jackknifes of environmental variables for *Amblystegium riparium* 2041-2060 climate scenarios.

Of the 26 models, the top ten bryophyte taxa that showed the greatest change in distribution are listed as potential climate change indicators (Table 3-3). The models of *Anomodon* and *Amblystegium riparium* were excluded from consideration due to their low AUC values. The models ranked represent those with the most substantial changes in high likelihood areas across the SSP scenarios, as the largest changes in distribution provide more information on how environments are being shaped by climate change. Symbols in Table 3-3 represent an overall increase, decrease, or no net change in distribution area for each scenario compared to the current model throughout Illinois.

Table 3-3. Models of potentially useful species and genera for climate change indication showing distinct distribution changes across SSP scenarios

Species or Genus	**SSP 126**	**SSP 245**	**SSP 585**
Leskea gracilescens	↓	↓	↓
Ceratodon purpureus	↑	↑	↑
Platygyrium	↓	↓	↓
Amblystegium serpens	↓	↓	↓
Bryum	↑	↑	↓
Frullania	↑	↑	↑
Amblystegium varium	↓	↓	↓
Dicranum	↓	↓	↓
Brachythecium acuminatum	↑	—	↓
Fissidens	↓	↓	—

Discussion

Climate change is one of the largest growing global threats to biodiversity and ecosystems affecting individual species and the way they interact with their habitats (Weiskokf et al. 2020). The persistence of bryophytes from their first ancestors 450 million years ago is evidence these species lineages are continually responding and adapting to change, and therefore have potential as climate change indicators (Ruklani et al., 2021; Villarreal et al., 2016). Using the GISS-E2.1 model for changes climate, it is predicted that the annual temperature will increase throughout the world, while in Illinois the precipitation will increase; these increases are present in all three SSP scenarios, but the change is more substantial as the climate response worsens (Nazarenko et al., 2022). Therefore, the changes in bryophyte distribution are inferred to be reacting to these higher temperature and precipitation values. This is supported by the reliance of bryophyte physiology on temperature and precipitation for metabolic processes and reproduction (Di Nuzzo et al., 2021). The overall change in predicted distribution across many models of species and genera is likely a result of bryophytes being sensitive to these climate changes. Most models indicate a reduction in distribution range that could be attributed to loss of suitable habitats or environmental changes impacting their dispersal.

There is a strong pattern of consistency across the climate scenario models: for most models, all scenarios either show a decrease or an increase together. This is the result of only minor climate alterations at the time of these models, as they only go as far as 2041-2060. Additionally, this is possibly a testament to the life strategy of these specific genera and species: *Frullania* and *P. cuspidatum,* for example, both show overall distribution increases and likely will be benefited by increased temperature and precipitation. Five taxa did not show any substantial distribution change across the SSP scenarios: *Plagiomnium, Amblystegium,* *Anomodon, Entodon seductrix,* and *Climacium americanum*. All other taxa had distinguishable distribution change across their models, providing support for these bryophytes as potentially useful indicators of climate change.

However, it is important to recognize that as climate change alters environments in a variety of ways, it might be these alterations that impact the changing bryophyte distribution. For example, soil chemistry has been shown to affect distributions of species such as *Anomodon attenuatus, Calicladium haldaneanum, Amblystegium varium, Platygyrium repens, Amblystegium riparium,* and *Leskea gracilescens* to the point where they can be grouped based on effects such as high or low calcium in the soil (Ab Lah et al., 2021; Perdrizet & McKnight, 2012). Soil is extensively altered by effects of climate change, especially in the way organic matter in the soil is altered by temperature changes (Prasad & Pietrzykowski, 2020). Another example is air pollution, which has shown to correlated with abundance and diversity of bryophytes in London (Larsen et al., 2007). Air pollution and climate change go hand in hand, as both primarily come from emissions of CO_2 (Bytnerowicz et al., 2007). Furthermore, the effects of pollution are not limited to cities: forest environments as well have seen negative impacts from air pollution such as a decrease in tree health and nutrient availability (Bytnerowicz et al., 2007). Soil chemistry, air pollution and other environmental factors that are a result of or linked to climate change may be the real distribution drivers of these bryophyte species, and these variables could account for variation between model distribution and real world.

Model Quality

The AUC values of the future models were consistently above 0.8, with some of the future models having higher values than their respective current model. The only full model values with an AUC below 0.8 were the SSP 585 model of *Bryum* and the SSP 126 and SSP 245 models of *A. riparium*. For the future models, the AUC value is interpreted as confidence in the distribution heat map created. Assessments of model quality are difficult and model realism impossible when supplying projected data from 2041-2060 on previously collected occurrences.

Environmental Variables

The predictive power of niche models allows for niche estimates at a large scale and show patterns of correlation between distribution and factors such as climate (Fuchs et al., 2018). The relationship between climate variables and distribution is important for predicting changes in distribution as the environment is altered. Like the current models, Land Cover and Canopy Cover were the most critical environmental variables overall for the future models. As these are the two variables that represent past rather than projected data, and that land use was overall very important for the future models, it is expected for them to be so prevalent. This is not the case for all future bryophyte distribution models, as it was seen in Tibet that the importance of forest presence was outweighed by elevation, as climate factors vary at different elevation levels (Kou et al., 2020). Additionally, precipitation measures were shown to be of more importance for select moss species worldwide (Mallen-Cooper et al., 2023). As one of the major weaknesses of MaxEnt is implying distribution and environmental importance to areas outside of the study boundary, larger scale or more specific models need to be created to evaluate the fully realistic importance of land use and climate variables (Phillips et al., 2006).

The land use variables were included in the models for more realistic predictions of distribution, assuming that land use does not change drastically in the next few decades. However, the inclusion of these variables means the contribution of the projected Bioclim variables is more difficult to visualize on the heat maps, and therefore it is harder to visualize the potential impact of climate change. This study supports that the majority of these taxa are more reliant on land use variables than climate variables, meaning that these taxa will be less susceptible to climate changes than climate defined species (Ab Lah et al., 2021; Zhang et al., 2023). Models created in other studies may want to explore climate change models with land use removed, but the prevalence of land use to these models provides a more realistic prediction of distribution that can be compared across the scenarios. Yet Ferretto et al., (in press) attests to the importance of including land use and habitat variables in future models, as these provide more useful information for conservation and land management efforts.

The same species that had Mean Diurnal Range as their most critical variable in the current models also had them in their future models. The prevalence of a climate variable might imply that these species would be more susceptible to climate change compared to the other species and genera, and therefore would make quality indicators. However, the function of an indicator is to “track” climate change by a change in distribution. Visualizing or quantifying how many areas of high likelihood are lost and gained provides the tangible distribution change that factors of climate change can be inferred from (Kou et al., 2020). Even if Mean Diurnal Range or any climate variable is important to a model or predicted distribution, if there is not a difference in distribution, that species or genus cannot be a quality indicator.

Indicator Quality

Creating species distribution models for climate change scenarios is useful for determining how habitats are changing in the onset of this change (Parveen et al., 2022). This can be done by selecting a climate change indicator species or genus to track this habitat and environmental change. The most important factor in determining a quality indicator is distribution difference from the current model to the future models. More specifically, alterations in high likelihood are the more reliable patterns to follow. The best distribution changes include gain as well as loss of high likelihood areas, but general gain and loss can make for quality indicators too. The taxa of interest must therefore be able to adapt to the new environmental conditions in a new habitat even if the old one if lost: the alternative being smaller populations and a risk of extinction, which does not make for a useful indicator (Culshaw et al., 2021). Following this criteria, the best indicators explored in this study are *C. purpureus* and *L. gracilescens*. The future models of *C. purpureus* show substantial visual differences throughout the state, indicating it is not only sensitive enough to change distribution but to change more specifically based on the type of climate scenario. However, it is concerning that the AUC values of the current and future models are towards the lower end of the threshold, and that the models are based on a lower number of occurrences. Similar concerns arise with the models of *A. attenuatus* and *A. riparium*: substantial distribution change, but lower AUC values. The models of *L. gracilescens* show a smaller overall distribution change than the models of *C. purpureus* but are more reliable for their higher AUC values and occurrence number. As all of these models are built off of species data, this would suggest that indicators should be used at the species level rather than the genus level. Genera typically have a wider range of lifestyle strategies than species, meaning only some of their species could be affected by climate change: this makes distribution tracking much more difficult. However, the models of *Frullania*, *Fissidens*, *Dicranum* show substantial differences around more specific areas: Chicagoland for the former and the Illinois River for the latter two. This supports the idea of using indicators at a more localized area rather than statewide. The benefit of being able to use genera as indicators means occurrences will be easier to find and identify. At local levels where genera models show clear differences, they might be more useful than species.

There was overall more variation between the models of the different scenarios than between the current and future models. Furthermore, these models also saw changes at more local levels, rather than throughout the state. Notably, the models of *Platygyrium*, *P. repens*, and *A. rostratus* all saw visible distribution changes around Southern Illinois, with *Platygyrium* showing a drastic change. The model of *P. repens* also saw visible changes around Chicagoland as well as the model of *C. haldaneanum*. Though none of these models were built on a substantial number of occurrences, their visible change in distribution suggests enough sensitivity to be used as an indicator. For models of bryophytes built in the future, quantifying distribution changes in areas lost and gained such as with SDMtoolkit in GIS can provide more statistical support to selected indicators (Brown, 2014; Kou et al., 2020).

Though there were distribution differences between the current and future models, it is possible that rarer species may show more drastic changes and therefore be useful climate change indicators. While common species and genera are easier to find and create a larger sample, it is likely that these groups are common because they can tolerate the range of climate and habitats Illinois has to offer. Rarer species can then be precisely selected based on their local ecology as support for their relevance as an indicator (Wierzcholska et al., 2020). Though rarer species may not be prevalent enough to track distribution changes, they likely are more sensitive to climate and land use changes and would therefore be useful indicators. Future studies should explore distribution changes with these rarer species. Furthermore, climate projections of different time periods rather than different climate scenarios may show more visual distribution change and provide more evidence to use of certain species and genera as climate change indicators.

Chapter 4: Conclusion

Overall, the majority of the models of common Illinois species and genera showed a high level of confidence, indicating a realistic distribution prediction and relevance of included environmental variables to the bryophyte niche. This realism is further supported by the Chicago field collections which were correlated in presence likelihood. However, a few these included models showed some inaccuracies in other parts of the state because of lacking data. These models are only constructed off available data, and with incomplete sampling they might produce less than realistic results. Furthermore, it is important to note that this model relies only on climate and land use data, the exclusion of relevant factors makes the results and interpretations imperfect. For example, the exclusion of dispersal capability means likelihood areas are probably lower than predicted; without dispersal the predicted distribution is more of a niche estimate than a real world distribution (Mallen-Cooper et al., 2023; Wierzcholska et al., 2020). Furthermore, even though the MaxEnt models have shown to be relatively successful here, utilizing other distribution modeling applications may provide additional insight. Exploring other SDM methods could reveal superior distribution models for the Illinois study area; such comparisons can be easily done with versatile tools like BIOMOD (Hao et al., 2019; Kaky et al., 2020).

The current models of both species and genera suggest that bryophyte distribution is primarily shaped by the Land Cover and Canopy Cover Factors. More specifically, bryophyte distribution is limited more by the lack of forest cover, farmland, and to a lesser extent, urban areas. Similarities in the importance of land use between the models of species and genera suggest that Illinois bryophytes can be described by a general level niche. However, such a generalization ignores the preferences of the specific groups, such as the increased importance of

Canopy Cover in *Frullania* or the prevalence of Mean Diurnal Range in select species. These differences are relevant particularly for purposes of land management and conservation projects, as different species or even groups of bryophytes show their own environmental preferences. Future bryophyte distribution models should consider modeling at the species level to recognize these intricacies; using MaxEnt for an area the size of Illinois, the study results suggest at least 40-50 occurrence points for a well-founded model based on the species models of this study. As far as climate factors, Mean Diurnal Range was the most relevant to the models, but still second to land use. This is potentially the result of Canopy Cover providing a specific microclimate that is more distribution determinant than macroclimate. Future studies should prioritize collection on microclimate data (such as local temperature, humidity, light, etc.) to explore its relevance more directly to bryophyte distribution. One potential avenue to collecting more resolute data without extensive measurements is through remote sensing, e.g., collecting images of the study area via satellite to serve as environmental data. Remote sensing has been shown to be effective in creating SDMs, as its high resolution provides a more accurate representation of the environment and creates a more realistic model useful for land management and intervention (Casas et al., 2021; Deneu et al., 2022; Mehmood et al., 2022; Sun et al., 2023).

The future models of bryophyte species and genera generally showed a high degree of confidence, and were similar to the current models, in that they were reliant on land use variables. Overall, the models of species showed more pronounced distribution changes between the climate change scenarios, likely as a result of their more consistent ecological strategies. The models of the genera, though they include more occurrences, encompass the life strategies of all their species which leads to a more generalized result. More relevant than level of taxonomy is the ecology of the bryophytes, as species or even genera with similar ecology are likely to distribute in similar patterns. Further research into the ecological strategies and similarities of Illinois species can be useful for selecting an appropriate indicator. Additionally, the future models in this study explored only the distribution of species and genera common to Illinois from 2041-2060. Building models with rarer species and with more time frames of climate projections could produce more pronounced distribution changes, which would further aid in indicator selection. Though the future models of this study do not show an abundance of drastic distribution changes, the differences between the climate change scenarios still support the use of bryophytes as climate change indicators. However, it cannot be ignored that pollution, air pollution in particular, is shaping bryophyte distribution patterns. With the passing of the Clean Air Act in 1970, bryophytes and lichens have begun growing in places that previously had no occurrences and heavy air pollution (e.g., Hutsemékers et al., 2023). Therefore, the sensitivity of bryophytes to pollution suggests that they can be quality indicators for this change as well; it has already been observed in the Chicagoland area that bryophytes assimilate heavy metals (Maari et al., 2023).

Utilizing macroclimate and land use data, predicting potential distribution of common Illinois bryophytes has shown promising signs of success for determining distribution and the niches of these plants. The high model confidence and similarity to known habitats attests to the realism of the models. In addition, this method is open-source and quickly run method that can be utilized for study areas around the world. Knowledge of bryophyte distribution as well as the environmental factors that shape them allows for targeted conservation and land management projects without excessive field study, as well as a measurement of how climate change is shaping the environment before any drastic changes arise.

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Appendix A: Occurrence data table

All raw and edited bryophyte occurrence data can be accessed here: https://doi.org/10.5281/zenodo.7978094. There are three data tables including all of the Illinois bryophyte occurrences with geodata downloaded from the Bryophyte Portal, and the thinned occurrence data used to build the genera and species models.

Appendix B: R code

Code developed in R for this project can be accessed here: https://github.com/Zryanne/maxent-R. This repository includes two files: “Raster Prep Code” and “Occurence Thinning and MaxEnt Modeling Code.” More detailed steps walking through the code are included in the description of the files.