DEVELOPING A PREDICTIVE MODEL OF THE AUTECOLOGY OF THE SPRUCE-FIR MOSS SPIDER, *MICROHEXURA MONTIVAGA* CROSBY AND BISHOP 1925 (ARANEAE: DIPLURIDAE).

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ABSTRACT

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The spruce-fir moss spider (*Microhexura montivaga*) is a federally endangered species of spider found only in the high-elevation Southern Appalachian spruce-fir forests on North-facing slopes underneath moss mats. Despite this fact, little is known about some of the basic ecology of the spider, more specifically the characteristics of the habitat found underneath the moss mats. The goals of this project was to determine the temperature and humidity parameters of the microhabitat conditions around known spider locations, catalogue what other species live there, and use predictive mathematical models created in the Maxent software to estimate past and current locations of potential habitats and identify the key environmental factors that drive such a model. iButton temperature and humidity data loggers placed at Mt. Lyn-Lowry, Browning Knob, Whitetop Mountain and Mt. Rogers (a range that encompasses all metapopulations). Lyn-Lowry and Browning Knob are located in the Plott Balsam range in North Carolina. Whitetop Mountain and Mt. Rogers are located in the Mt. Rogers National Recreation Area in Virginia. No statistically significant differences in daily maximum or minimum

temperature between positive and negative presence sites, among metapopulations, or individual sites. A potential set of temperature conversion factors were calculated using percent change for temperature by comparing the collected data, a local weather station, and a U.S. Fish and Wildlife Service deployed HOBO data logger mounted in a tree. Soil samples collected from Blackrock Mountain in the Plott Balsams yielded 2039 individuals comprising 11 orders, with Collembola and Acari being by far the most abundant; this is important as these orders have been hypothesized to be the primary prey items of *M. montivaga*. Maxent models show the current potential range as well as historical models of the last interglacial period and glacial maximum. Maxent models use presence only data and environmental factors to estimate potential habitat. Range during the last glacial maximum was greater than present range while the range during the last interglacial period was less than present range according to the models. They also include potential range expansion and retraction patterns. All models were heavily driven by temperature environmental layers, in particular those dealing with temperature maximums. This research provides a number of potential applications for the conservation and management of *M. montivaga*, such as using collected data to determine conversion factors for temperature data between microhabitat measurements and larger scale measuring methods, such as weather stations. For example, HOBO data loggers mounted in trees measure maximum daily temperature higher by 83.5% compared to microhabitat measurements. This allows for large scale monitoring can be done without having to actually measure the temperatures underneath the moss mats. It is hoped that this research, along with the continuing work of U.S. Fish and Wildlife Service, will contribute to a much more positive outlook for this endangered species.

INTRODUCTION

The endangered and endemic *Microhexura montivaga* is the world's smallest and northernmost member of the family Dipluridae, more commonly known as the funnel web tarantulas. *M. montivaga* range in size from 2.5 mm to 5.6 mm (Coyle 1981) and are restricted to the southern Appalachian Mountains. Although listed as endangered since 1995, little research has been done on the basic ecology of *M. montivaga* (Fridell 1994). The overarching purpose of this project was to define habitat correlates of *M. montivaga* and fill in knowledge gaps that are preventing proper management of this endangered species. The core habitat factors investigated in this research were environmental and community conditions. This information can be used to maintain existing populations and develop predictive models to aid in discovering new populations. Methodology included recording the macro and microhabitat humidity and temperature parameters of known populations, collecting and summarizing preexisting soil and bedrock data, and cataloging other taxa comprising the moss mat community. Further, Maxent software was used for predictive mapping of probability of presence and environmental variable layer analysis. Maxent constructs a predictive map of probability of presence and correlated environmental variables. The Maxent model, soil and bedrock data, and abiotic parameters allow for a better understanding of the spider's microhabitat while the cataloging other taxa allows for potential prey, competitors, and predators to be identified within the microhabitat.

Biology of *Microhexura montivaga*

Diplurids are generally found worldwide within the tropics, with most species found in South and Central America and Australia, although they can also be found in India and Africa. *Microhexura* is the northernmost genera, found in the temperate zone. There are a total of 24 genera with 181 species (Platnick 2008). Raven (1985) describes the three characteristics for the Dipluridae family as the lowered caput and elevated thoracic region, the lateral spinnerets being elongated and composed of three sections, and the sections of the spinnerets being widely separated. The use of *Microhexura* as an informative outgroup to the rest of the diplurids may be possible. However, due to the high level of evolved specialized traits and unique habitat the use of it as an outgroup is debatable (Coyle 1995). The two species of the genus *Microhexura* show a disjunct species distribution. *M. idahoana* is found in conifer forests in the Pacific Northwest of the United States, while *M. montivaga* is found under moss and liverwort mats on north facing slopes in the spruce-fir biome of the Southern Appalachian Mountains (Coyle 1981). While *M. montivaga* is an extreme habitat specialist being found only under the moss and liverwort mats on rock outcrops, *M. idahoana* can be found in duff or moss with webs also commonly being observed under pieces of wood or bark. Less frequently it is found under rocks and decaying logs. Because of this, *M. idahoana* can be seen as a much less specialized species, although high humidity is still a requirement (Coyle 1981).

Identification of *M. montivaga* is based around a specific set of diagnostic characters. The first are the elongated spinnerets, which appear segmented into three parts. The chelicerae are paraxial, roughly parallel and extend forward, protruding from the prosoma. This species, like all mygalomorphs, has two pairs of book lungs. Mature males can be distinguished from females by the presence of a large ventral spur on the first leg and the presence of the palpal organ on the pedipalps (Coyle 1981). Unique to all other diplurids is the longitudinal fovea. Confusing *M. montivaga* with other araneomorph spiders likely to be found in the same microhabitat is extremely unlikely based on the combination of these diagnostic characters.

Webs of *M. montivaga* are found underneath the bryophyte mats and appear as messy tangles of flat tubes and sheets in the interstitial space between the rock substrate and the moss mat. Although their diet has not been confirmed, springtails (Collembola) and mites (Acari) are assumed to play a role due to their great abundance in leaf litter/moss habitats in general (Coyle 1981). To better define the community, and identify potential prey and predators of *M. montivaga*, soil samples from under high elevation bryophyte mats were collected and their biota catalogued.

M. montivaga attains maturity in 2-3 years with females laying eggs in June and spiderlings emerging in September (Coyle 1981). Mating occurs in the fall; once males have completed their last molt they leave their webs in search of females and die that winter (Coyle 1981). Male mating behavior is triggered by the presence of a female's web, which initiates mating behavior (Coyle 1985). Dispersal strategies, which can play a vital role in the biology of this species, are still somewhat debated. *Microhexura idahoana*, the sister species found in the western United States, has been reported from snowfields, giving rise to the idea that ballooning may occur (Coyle 1981). However, because millipedes have also been collected from snowfields, presence does not mean that aerial dispersal is required (Crawford and Edwards 1986). If dispersal is not aerial, the very small size of this animal suggests movement, even across a single mountainside, from one rock outcrop to another, may prove impossible. Genetic flow among and between metapopulations is currently being studied by Dr. Marshall Hedin of San Diego State University. However, previous work with a small sample size suggested that the metapopulations were in fact isolated populations with minimal gene flow (Martens 2005). One of the questions and goals raised by U.S. Fish and Wildlife is to determine the validity of artificially increasing gene flow either in the field or lab, but it is imperative to fully understand the habitat requirements before moving any individuals to a new environment.

Populations and Habitat of *Microhexura montivaga*

Originally collected and described in 1925 by Crosby and Bishop, *M. montivaga* was added to the Federal List of Endangered and Threatened Wildlife and Plants by the U.S. Fish and Wildlife Service in 1995 (Fridell 1994). The reason was two-fold. First was the relatively low abundance of the species. Second was the rapid deterioration of habitat. The known *Microhexura montivaga* population is separated into six metapopulations: Whitetop and Pine Mountains in Virginia, Grandfather Mountain, Roan Mountain, the Black Mountains, the Great Smoky Mountains, and the Plott Balsams of North Carolina (Coyle 2009). The total number of mountain peaks *M. montivaga* is known to inhabit is limited to twenty-two in the Southern Appalachians, resulting in its endemic status. Although past surveys showed possible decreases in abundance (U.S. Fish and Wildlife Service 1998), it appears that all populations outside of Clingman's Dome (Coyle 2009) are currently stable, but the total number of individuals over all populations is unknown.

All metapopulations *M. montivaga* are defined by several shared characteristics. 1.) Populations are restricted to high elevations (5300-6600 ft.) in spruce-fir forests

(Coyle 1981). Spruce-fir forests in this area are dominated by Fraser fir (*Abies fraseri*) and red spruce (*Picea rubens*) (Spira 2011). 2.) Spiders are only known from rock outcrops and boulders that serve as substrate for bryophyte mats. These are generally 1-4 cm. thick and moderately drained; neither dry nor soggy. *M. montivaga*'s sensitivity to desiccation also restricts it to north-facing slopes (Coyle 1981). The bryophyte genera most often encountered include *Bazzania* liverwort, *Dicranodontium* moss, and *Polytrichum* moss (Coyle 2009).

When dealing with such small organisms, it is important to consider the scale of the landscape they experience; for example, habitat can shift from continuous to fragmented as body size shifts from large to small (Borthagaray et al. 2012). Previous research on soil-dwelling spiders has found that soil type, litter composition, temperature, and humidity within the small-scale distribution provided similar spider species and abundance leading to the inference that environmental heterogeneity must be analyzed at all spatial scales (Zieche and Roth 2007). In mite species, for example, it has been shown that particular microhabitats, such as dead wood, significantly increased species diversity on the forest floor (Madej et al. 2011). Although the habitat of *M. montivaga* appears well known, the actual parameters have yet to be documented and this presents one of the primary realized goals of this research.

The importance of microhabitat measurements and predictive mapping is reflected in the goals of the Recovery Plan for the Spruce-fir Moss Spider (U.S. Fish and Wildlife Service 1998). The objectives of the research presented here directly correlate with the goals of this recovery plan. This project contributes to task 1.3, characterization of the species' habitat requirements, by collecting temperature and humidity data, and to task 2, the search for additional populations and/or habitat suitable for reintroduction, by performance of the Maxent mapping software. Description of the natural microhabitat in its community will also assist in developing artificial holding and propagation techniques, which is task 3 of the recovery plan.

Conservation Efforts, Significance, and Loss of Habitat

The endangered status of this endemic spider is one of the driving points of this research. If more is not known and understood, then losing the world's tiniest funnel web tarantula is a real possibility. Highly specific habitat requirements, and loss of that habitat, makes conservation of this endemic spider immediately important. The extensive loss of Fraser fir in the spider's habitat is a direct result of infestation by the balsam woolly adelgid. *Adelges piceae* (Ratzeburg 1844) is an exotic species that was introduced in 1956. After 5-7 years of infection, mature Fraser firs die (White et al. 1993) resulting in loss of the canopy and leading to an increase in heat and light, decrease in moisture, and consequently, desiccation of the moss mats that are vital for *M. montivaga* (Coyle 1997). It is anticipated that decline of the moss mats will lead directly to a decline in the spider population (U.S. Fish and Wildlife Service 1998), and indeed the entire and largely unknown high elevation moss mat community. The loss of Fraser fir is not only detrimental to *M. montivaga*; other endemic arthropod species, such as *Dasycerus bicolor*, a staphylinid beetle, and *Sisicottus montigenus*, a linyphiid spider, have also shown sharp declines with the declines of the fir (Zujiko-Miller 1999, Sharkey 2001). As the populations of Fraser fir continue to disappear due to the woolly adelgid and global warming, it is important to determine as much information on the ecology of *M.*

montivaga and the status of its current populations as possible, to aid in predicting the viability of current and future populations.

Defining such critical habitat parameters as temperature, humidity, bedrock, and soil composition will allow several goals outlined by U.S. Fish and Wildlife (U.S. Fish and Wildlife Service 1998) to be reached. A better understanding of habitat requirements will enhance the effectiveness of captive breeding efforts, which has proven to be problematical. One of the reasons may be that the spiders were being maintained under the wrong conditions. At Lousiville Zoological Park populations were maintained but not well enough for breeding activity to occur (U.S. Fish and Wildlife Service 1998). Knowledge of habitat requirements will also aid in determining possible requirements for establishing new populations, another important goal. If current populations become even more imperiled, it will be important to understand as much as possible prior to any movement of individual spiders to decrease chances of mortality and increases overall success rates of re-establishment.

Species Distribution Modeling

One of the foundations of ecological inquiry is the study of species-environment relationship, and ultimately understanding of the mechanisms accounting for habitat selection and the distribution of a given species (Guisan and Zimmerman 2000). To better determine the range of a given species, spatial modeling can be used. Spatial modeling can also provide important insights into conservation goals (Ferrier 2002). A challenge in evaluating species-environment relationships is the general lack of true absence data (CITE). Maximum entropy (Maxent) spatial modeling (Phillips et al. 2004) can be used to characterize habitat parameters and to predict species occurrence (Phillips et al. 2006) based upon presence-only data. It does this by calculating the probability of distribution of a species by calculating a prediction based on environmental variables (Phillips et al. 2006). Understanding the species' range can also inform on the species-environment relationships and provide paramount information with regards to conservation. The reason for this additional information rests on the fact that spatial modeling allows for individual analysis of environmental variables. Once the most important variables are determined, conservation can then be focused on areas of concern. This tool acts in addition to the micro-scale measurements also done as part of this research. This macro scale approach allows for an analysis of the influence of larger extent factors. One important aspect of the Maxent approach is that it requires only two main parameters: environmental data and presence data for the species (Elith et al. 2011). This is important when considering rare and difficult to locate species which can provide challenges in confirming absence locations (Gu and Swihart 2004). Maxent was chosen because of the software only needing presence data (and not absence data) and the low occurrence of points needed, and the high rate of use with other rare and endangered species.

The objectives of this study were to use Maxent modeling, GIS (geographical information system) environmental layers to: 1) determine the environmental factors most closely associated with *M. montivaga* and 2) predict the potential geographic range of this species using previously established positive presence locations. Such data should be of considerable value to conservation planning of United States Fish and Wildlife Service. Ideally, maps produced from these data would allow future populations to be discovered while also indicating areas where follow up surveys could be productively done. A final application can be found by using known presence locations and the probability of presence to determine how well the known presence locations match environmental layers allowing for inference on the health of populations. A low probability for a positive presence location may be due to a poor match of fundamental niche as determined by Maxent. Previous search efforts for the spider were driven strictly by considering the topography and aspect of the area. Steep, north facing, high elevation areas, the preferred habitat, were determined by simple inspection of topography maps. This study provides more possible locations that can be determined, predicted and explored, hopefully making the status and future of *M. montivaga* more positive.

Literature Review: Soil and Food Web Dynamics

Soil and litter food webs can be immensely important when considering overall ecosystem processes and services. The effects span from simple factors like food production to more complicated contributions to ecosystem properties like climate mitigation and carbon and nitrogen cycling (Trijntje de Vries et al. 2013). Because of the importance of soil organisms, there is a pressing need to map, research, and conserve soil biodiversity (Trijntje de Vries et al. 2013). It can often be difficult to accomplish these goals because higher taxonomic units can be extremely problematic in understanding such systems, as illustrated by research on soil fauna in beech forests dominated by Collembola, Enchytraeidae, and Oribatida (Scheu and Falca 2000). However, the importance of these goals cannot be overstated Increases in the biomass of soil fauna were determined to increase plant productivity by up to 35% (Sackett et al. 2010) while also providing services such as nutrient provision for plants and carbon and nitrogen storage (Trijntje de Vries et al. 2012). The importance of plant productivity in the face of climate change and CO_2 emissions underlies a research emphasis on soil and litter food webs and their related processes. The complexity of the services and processes are compounded by biodiversity of the soil communities, which may ibe greater than the above-ground diversity (Anderson 2009). Loss of biodiversity affects this ecosystem and its functions in a similar manner to others (Eisenhauer et al. 2012). Beyond the services provided to plants, consumption of the microorganisms living in the soil can often be an important contribution to the stability of the overall community (Ladygina et al. 2008). Further, understanding soil food web dynamics as they relate to the time of recovery of food webs is an important area of research. In one study, as long as three years may be needed after an acute physical disturbance for the soil food web to completely return to its previous state (Rygiewicz et al. 2010). Other research has shown that food webs before and after major perturbations may actually reflect two stable states and that the food web may never return to the previous state (Schroder et al. 2012). It should be noted that while this study involved manipulation at the whole-ecosystem level (freshwater lakes), general conclusions may be applicable to soil and litter food webs.

Abiotic dynamics, while not discussed here at length, are also important and should be kept in mind whenever considering soil communities. Mulder and Elser (2009) found that the higher the available phosphorous, the greater the range of faunal biomass sizes; there was a similar response to higher pH. The range of faunal biomass sizes is important, as a wider range of sizes implies a wider range of potential processes. Other research has found that invertebrates are most abundant at micro-sites that were located near the base of slopes due to the increases nutrients and water; all scales were found to be heavily dependent on water (Melguizo-Ruiz et al. 2012). It was also found that limestone sites had higher fauna abundances. As 50% of total animal biomass (Fierer

2009) can be found belowground, there is a scientific obligation to continue to investigate that which is below us. With a range of potential topics related to the dynamics and summarization of soil and litter food webs, the focus of the current literature review is on trophic level dynamics and ecological controls/inputs and dynamics.

Trophic Level Dynamics

Descriptions of trophic levels and trophic level interactions have allowed for a better understanding of many systems. The soil food web is no different, even considering its high diversity (Crotty et al. 2012). Interactions between organisms and functional groups present shifts in chemical and physical properties. The application of stable isotope methodology has allowed an expansion and greater understanding of the complexities occurring in nature from the scale of individual interactions to community interactions (Crotty et al. 2012). One study showed Collembola and oribatid mites had high levels of ^{15}N, which could possibly be related to consumption of certain types of decayed debris and fungal hyphae. However, regulation from the microbial community may also be important, as seen from the observation that fine-scale phosphorous variation had effects on the trophic dynamics of arthropods (Huang et al. 2012). Beyond stable isotope measurements, atomic labeling has also been used. Pollierer et al. (2007), for instance, found that the majority of carbon sequestered by soil microinvertebrates comes from roots. Fatty acid analysis of centipede tissue has been used to determine that maximum prey exploitation occurs during autumn and that most prey items come from the bacteria base chain (as opposed to the fungal base chain) (Ferlian et al. 2012). Current research using isotopes and labeling continue to be important in developing a better understanding of the complex trophic level dynamics occurring in the soil.

A specific debate that has arisen from this work is whether top-down or bottom-up trophic levels control functions in the soil food webs. A strong case for bottom-up control has been made in a number of ecosystems. Eisenhauer et al. (2012) looked to explore the effects of increased CO_2, decreased water availability, and increased nitrogen in grasslands in the United States. Higher CO_2 was found to increase microbial biomass and microarthropod abundance while only increased nitrogen decreased biomass and abundance. The mechanism for the observed relationship was probably a result of beneficial bottom-up effects caused by the increased CO_2, which was enough to counter balance increased nitrogen (Eisenhauer et al. 2012). The authors do warn, however, that the loss in nematodes that occurred could lead to an overall simplification of the soil community long-term. However, this system did not present an argument for only bottom-up controls. Continued analysis of the grasslands found that plant diversity loss may therefore feedback and cause a trophic cascade effect on the soil food webs in regards to long term patterns (Eisenhauer et al. 2012).

Other examples of top-down controls have also been explored and supported by various manipulations. Miyashita and Niwa (2006) removed a web-building spider in a Japanese cedar forest for 1.5 years. Experimentally decreasing spider abundance increased Collembola density, although the overall biomass of the microorganisms in the litter and soil was unchanged. Other studies that removed spiders found more dramatic results. In one study, when spiders were removed from the soil food web, detritivores, specifically Collembola, greatly increased. In some cases, the increase was more than double (Wise 2004). This study focused on the removal of wandering spiders (any spider not relying on webs for prey capture) by fencing off treatments within a deciduous forest for 1.3 years. There was a slight delay in the response, but this was probably due to growth patterns and active size classes of the spiders (Wise 2004).

Of interest is the division in whether trophic cascades may occur in the soil litter at all. Scheu and Setala (2002) presented the idea that cascades would be expected while Warldle (2002) argued the opposite. Wardle's (2002) argument lies in the idea that although bacteria may be regulated in a top-down structure in many ecosystems, fungi are not, leading to an overall lack of a cascade. One meta-study found no evidence for trophic cascades in the soil community as a whole (Sackett 2010), concluding that fungi were not subject to top-down control because of compensatory growth by unpalatable fungi. Scheu and Setala's (2002) argument is centered on the belief that fungi may actually be more susceptible to top-down control due to their slower growth rate in relation to bacteria. Miyashita and Niwa (2006) argue that a more mechanistic approach to the study of trophic interactions may be more appropriate to better understand the dynamics of soil food webs.

One last note regarding trophic dynamics: it is important to not treat the soil food web as an isolated functional group in regard to ecosystem services. Some trophic levels, but not all, show significant responses to manipulation to aboveground interactions. For instance, it may be possible for consumers in the aboveground food web to cause changes in the belowground system; this is important when this concept is coupled with the idea that in aboveground systems predators have been shown to cause large trophic cascades that may trickle all the way down to the soil food web (Wardle et al. 2005).

Ecological Controls and Inputs: Biotic

Inputs and ecological interactions outside of simple trophic level analysis can often be difficult to predict. Part of the reason is that the soil and litter communities can often have contributions from resources that are ancient or produced from slow bedrock processes. For instance, research in wheat and maize fields by Scheunemann et al. (2010) found that “decade old carbon resources form an important component of the soil animal food web, but the [use]… varies with… distribution,” (59). This study utilized tracing C_3 carbon movement in a field converted from one crop type to another. Land use itself can provide other influences as well. Fungal-based food webs in grassland soils were more resistant but less resilient than the bacterial-based food webs found in wheat plantation soils. These fungal-based webs were also more adapted to drought than their wheat plantation counterparts, showing that land use can affect the resilience and resistance of soil food webs; this is of particular concern and deserves recognition in the face of climate change (Trijintje de Vries et al. 2012).

Climate change and warming has been experimentally tested in a number of soil systems. One study tested the effects of warming and nitrogen addition to soil food webs. Nitrogen addition increased microbial biomass and had negative effects on soil nematodes, while warming had less obvious effects and was not as important as the nitrogen cycle effect (Li et al. 2013). This is an important finding because high rates of anthropogenic nitrogen addition are occurring, in particular in developing/agricultural countries and regions. This is different than the results found by Doblas-Miranda et al. (2009), who found temperature and moisture to be important. Doblas-Miranda et al.

(2009) stressed the importance of realizing that abiotic factors affect the soil food webs in a direct and indirect manner because litter acts a food source and a habitat.

Feedback from plants down to the soil community show mixed results. One study found that tree species did not cause different arthropod abundances, while water moisture level increases caused spikes in Collemola abundance. It was hypothesized that, in that system, the plants may primarily just provide structural support (Donoso et al. 2013). However, Franklin et al. (2004) found conflicting results in the Amazonian savanna; there, soil type, vegetation structure, and plant species all determined the composition of the soil communities. They do warn that higher taxonomic resolution is needed to better assess soil food webs, similar to other research reviewed here (Franklin et al. 2004, Scheu and Falca 2000). Change in litter quality, not structure and or the resulting shifts in microclimate, has also been found to be more important than simply structure as Donoso et al. (2013) found. Collembola, when presented with litter in high latitude peat bogs, had a significant shift in diet but their densities did not shift because all species preferred *Betula* leaf litter (Krab et al. 2013). When considering plant interactions, it is also important not to limit analysis to aboveground matter, but also to consider the belowground inputs. This was seen by the strongly reduced effects of drought on most soil trophic groups when plants are present, showing that plant inputs belowground may affect belowground recovery by communities as a whole (Trijintje de Vries 2012).

Although plants may feed the soil community, the feedback return to the plants is also important. Soil fauna have been shown to regulate the aboveground community, although it may vary on the plant functional groups involved. For instance, when soil fauna biomass was increased, coniferous systems showed a significantly larger response than other tree functional groups (Sackett 2010). It may even be possible for soil fauna to regulate ecosystem production when the ecosystem is nutrient-limited (Sackett 2010).

Summary

It is apparent that soil food web structures are extremely complex. Although difficult to predict, knowledge of these systems is paramount for many aspects of applied ecology. Whether focused on restoration efforts, predicting responses to climate change, or conservation of biodiversity, it is clear that consideration and research are needed to better understand the function and dynamics of the soil system. Of particular concern seen in these highly variable responses is a general lack of consistency and predictability at the global scale. Because variation is so high, predictability may be low in some systems. Although some research has shown that bacterial community composition and bacteria:fungi ratios may be predicted from C:N ratios and soil pH (Fierer 2009), it is important to next look for the connection between these measures and the microarthropod and nematode communities.

The need to understand these complex dynamics, both abiotic and biotic, brings about a return to the goals of this research. Both abiotic and biotic interactions are considered in the methods of this project because of their importance in understanding and defining the ecology of a species. In turn, defining the ecology provides the basis for future conservation and management planning. It should be noted that because *M. montivaga* has been on the federal endangered species list for over a decade without an exploration of these dynamics efficient conservation planning and work based on foundational ecology has in turn been minimal.

METHODS

Temperature and Humidity Measurements

Temperature and humidity data loggers were placed at two sites at the farthest known north (Mt. Rogers area, Grayson/Smyth counties, Virginia) and the farthest south (Plott Balsams area, Haywood/Jackson counties, North Carolina) metapopulations. The distributions of these as metapopulations are presumed to be defined by limited dispersal, not only between mountain slopes within a mountain range, but also between appropriate rock structures and bryophyte mats on a single mountain. A positive presence location was chosen within each metapopulation: Whitetop Mountain and Mt. Lyn Lowry, respectively. Negative sites were Mt. Rogers and Browning Knob, respectively.

iButton DS1920 loggers were used for humidity measurements and iBCod50 G loggers were used for temperature data at each site. Three iButton DS1920 and four iBCod50 G loggers were placed at each site and their data averaged. Data loggers were set to record measurements every 30 minutes with a resolution of 0.5 for relative humidity and temperature. Minimum and maximum temperatures as well as the average and difference of minimum and maximum temperate ranges were calculated and reported for each day in all sites for the period of June, 2013 to November, 2013. This encompassed the hottest months experienced by the spider. ANOVA with post-hoc Tukey’s pairwise comparison was done to analyze statistical differences within metapopulations, between metapopulations, presence of spider, and difference between maximum and minimum temperature (isothermality).

Two additional data sets were also incorporated in the final statistical analysis, the Mt. Leconte weather station and a United States Fish and Wildlife Service deployed HOBO data logger placed at Mt. Lyn Lowry. Mt. Leconte is located in the Great Smokey Mountain National Park metapopulations. Data was provided through NOAA and accessed through the National Climatic Data Center for the same period of time as the iButton deployment. The Mt. Lyn Lowry HOBO data logger was mounted in a tree near the iButton site by United States Fish and Wildlife Service during the duration of the iButton deployment as well. These two additional data sets allowed for analysis of the effect of the moss mats on humidity and temperature.

Bedrock and Soil Cataloging

Soil and bedrock data for all sites from the United States Fish and Wildlife Service surveys in 2009 were used to gather and provide predictive power for continued searching for *M. montivaga* populations. Bedrock for all metapopulations was analyzed using data compiled by the United States Geological Society (North Carolina Geology 2013). Specifically, bedrock unit age, primary rock type, and secondary rock type were reported. Soil data were compiled using the same presence sites but utilizing previous data from the United States Department of Agriculture with an area of interest of 1 acre used (The Comparative Soil Survey 2013). Presence sites of the Virginia/Mt. Rogers were omitted as soil survey data were not available. Soil type and percentage is reported for all other presence sites.

Species Distribution Modeling

Previous survey data, specifically 41 presence locations, were used for the Maxent modeling (Coyle 2009). This is more than the 30 locations often recommended

(Wisz et al. 2008). These locations were reported by Dr. Fredrick Coyle during surveys from 2007-2009 that were funded by U.S. Fish and Wildlife Service. Eighty one southern Appalachian sites were examined, both within and outside of the known range of *M. montivaga*; specifically, these were sites characterized by spruce-fir and fir forests and steep north facing slopes. During these surveys two new metapopulations were discovered, expanding the range south to the Plott Balsams and north to Whitetop and Pine Mountains with an overall increase in known mountain peak locations from 9 to 22 (Coyle 2009). Exact GPS points were derived from the handheld GPS unit used by Dr. Coyle and originally reported in UTM. This allowed exact localities to be determined, as opposed to descriptive area ranges, once they were converted to decimal degrees.

ArcMap version 10.1 (ESRI Redlands, CA) was used for all environmental layer management and editing. Environmental layers for solar radiation, aspect, and slope were calculated within the software. Solar radiation in ArcMap is calculated using hemispherical viewshed algorithm first developed by Rich et al. (1994). Slope is calculated by use of the average maximum technique (Burrough and McDonell 1998). Maxent version 3.3.3 was used for the spatial modeling. Maxent is particularly useful for developing models when there are a low number of occurrences. In some cases only five locations are needed to create informative models (Pearson et al. 2007).

Originally 33 environmental layers were used, all at 30 arc seconds resolution. Nineteen of these were taken from the WorldClim database (Hijmens et al. 2005), available online (www.worldclim.org), and included biologically significant forms of temperature and precipitation as rastors. Elevation was also downloaded from WorldClim. Slope, aspect, and solar radiation were calculated within ArcGIS. Other layers were downloaded through the ArcGIS online library within ArcGIS and included deciduous forest cover, quadratic mean diameter, stand density index, U.S. Forest Service fire potential, vegetative percent change, vegetative carbon levels, percent cover and healthy vegetation amounts. The range of the original map included all counties within 0.5 decimal degrees of known locations. Settings for all runs were 20 replicates, bootstrap sampling, random seed, 60 percent training points, and maximum iterations at 10,000, with all other settings set to default. Although regularization is often adjusted to reduce over-fitting by Maxent, simulations have shown that the default values perform in a similar fashion to settings that have been adjusted (Phillips and Dudik 2008). Extract by attribute was used to eliminate low elevation areas and to prevent the final model from being almost completely near-0 probability of presence. 1280 m in elevation was used as the extraction attribute filter. All environmental layers contributing less than 4 percent contribution or 4 percent permutation importance to the original model 33 environmental layer model were removed. Nine of the original layers remained (Table 3). Slope was added despite failing the given percent criteria due to its biological importance; rock outcrops, which are related to slope, and steep terrain are important factors when looking for *M. montivaga* (Coyle 1983). Solar radiation was calculated within ArcGIS using the Spatial Analyst Tool with a time period of 1/1/1980 to 5/1/2012. A correlation matrix was calculated using SPSS to determine statistically significant variable correlations which can have an effect on the percent contribution calculations done by Maxent.

Final model selection was achieved by calculating Akaike information criterion (AIC) values for all model combinations of the remaining environmental layers. The software used for this was Maxent Model Surveyor (Verbruggen 2012). For full description of techniques implemented see Verbruggen et al. 2013. This software runs a Maxent model for every possible combination of the variables selected and reports an AIC value. In this project the 9 variables gave 511 potential models with the highest AIC value being calculated for a 4 environmental layer model. A jackknife test was performed in Maxent on the final model that also gave a ranking of environmental layer importance. P values comparing each individual model to the model with all 4 environmental layers were calculated by using a critical ratio test (Pearce and Ferrier 2000) with modification due to a lack of absence data (see Baldwin and Bender 2008).

The final model's environmental layers were used, along with the projection feature of Maxent, to create a maximum entropy model of the probability of presence for *M. montivaga* during the last glacial maximum (LGM) (~21,000 bp) and the last interglacial period (LIG) (~120,000-140,000 bp). Solar radiation was removed from this model as the data for these time periods were not available.

Soil Community Cataloging

Soil/litter from under appropriate bryophyte mats at Blackrock Mountain, part of the Plott Balsam metapopulation, was collected November 19th, 2012 by the author and Drs. Frederick Coyle and Kefyn Catley. Blackrock Mountain is 1770 m in elevation and has the spruce-fir forest biome. This litter was processed through a Tullgren funnel apparatus to extract the organisms. Removing organisms from attached substrate and initial sorting to morphospecies was done using a high-powered 200x Leica dissecting scope at Highlands Biological Station, NC. Final identification was done at Western Carolina University. Simpson's and Shannon-Wiener diversity indices were calculated to compare to diversity values of other forests. Calculations were done using the number of individuals comprising each order; this being the lowest minimal taxonomic identification level achieved. Cataloging the community of *M. montivaga's* habitat was done to determine potential prey and other predator abundances. Beyond *M. montivaga*, this aspect of the research will provide a greater understanding of the community composition underneath bryophyte mats at high elevation.

RESULTS

Temperature and Humidity Measurements

Temperature Measurements

Four iBCod50 G data loggers were recovered from Whitetop Mountain, Mt. Lyn Lowry, and Browning Knob for the study period. Three iBCod50 G data loggers were recovered from Mt. Rogers. ANOVA results show maximum daily temperatures were not significantly different for the pairwise comparison of Lyn Lowry-Browning Knob (P=0.82), Whitetop-Lyn Lowry (P=0.19), Whitetop-Mt. Rogers (P=1.00), Mt. Rogers-Browning Knob (P=0.97), and Mt. Rogers-Lyn Lowry (P=0.66); indicating no difference of maximum temperatures within individual sites or within metapopulations. Minimum daily temperatures were not significant for pairwise comparisons of Lyn Lowry-Browning Knob (P=1.00), Mt. Rogers-Browning Knob (P=0.31), Whitetop-Browning Knob (P=0.88), Whitetop-Lyn Lowry (P=0.81), Whitetop-Mt. Rogers (P=0.90) and Mt. Rogers-Lyn Lowry (P=0.14); indicating no difference of minimum temperatures within individual sites or within metapopulations. Average of the minimum and maximum temperatures were also not significant for any pairwise comparison (P>0.90 for all) (Figure 1). The daily maximum, daily minimum, and daily average of minimum and maximum varied by less than 5% within metapopulations (Table 1). Isothermality, the difference between the maximum and minimum temperatures, was significantly different (P<0.02) for all pairs except Mt. Rogers-Whitetop (P=0.26).

Maximum daily temperature was not significantly different between the Mt. Rogers and Plot Balsam sites (P=0.13). Minimum daily temperature was also not significantly different between the Mt Rogers and Plot Balsam sites (*P*=0.10). Average of the minimum and maximum was also not different (*P*=1.00) (Figure 1). Isothermality was significantly different (*P*<0.001) between metapopulations, with 44.65 percent change from the Plott Balsams to the Mt. Rogers/Virginia sites (Table 1).

Daily maximum temperature values did not differ significantly between positive and negative location for *M. montivaga* (*P*=0.52). Daily minimum temperature values did not differ significantly between positive and negative presence sites (*P*=0.98). Average of the minimum and maximum daily temperature was also not different (*P*=0.81) (Figure 1). Isothermality was not significantly different (*P*=0.13) between positive and negative presence sites.

Daily maximum and minimum temperature values differed significantly between data loggers placed under the moss mats, the HOBO logger in the tree, and the Leconte weather station (*P*<0.001). However, the average daily maximum and minimum did not differ significantly between my data loggers across all sites and the HOBO U.S. Fish and Wildlife Service data logger and the Mt. Leconte weather station (*P*=0.08) (Figure 2). Overall, isothermality was, on average, 83.5% lower under moss mats compared to the USFWS logger and 257.8% lower under all moss mats compared to the Leconte weather station (Table 1). Direct comparisons of the iBCod50 G data loggers found at Lyn Lowry to the USFWS data logger in tree showed significant differences in daily maximum temperature and isothermality calculation (*P*<0.001).

Percent change calculations showed low levels of variation for presence/absence of *M. montivaga* and within and between metapopulations for average of daily maximum and minimum, daily minimum, and daily maximum. All of these values showed a less than 5% difference (Table 1). A direct percent change between the Lyn Lowry iButton loggers and the U.S. Fish and Wildlife Service HOBO logger gave a difference in maximum temperature of -14.8%, in minimum temperature of 8.4%, an average of maximum and minimum of -4.2%, and isothermality value of -136.6%.

Humidity Measurements

No loggers were recovered from Browning Knob; they all went missing (assumed stolen). Three were recovered and still operational from Lyn Lowry for the period of June to September, taking a total of 1808 measurements. Three were recovered from Mt. Rogers, one for June-Sept (1808 measurements) and two for June to November (3251 measurements). Three were recovered from Whitetop, two for June to September (1808) and one for June to November (3559 measurements). The U.S. Fish and Wildlife Service HOBO logger recorded from June to November (6427 measurements). Primary cause of failure for recovery was battery failure due to over saturation. Loggers recorded the majority of measurements at greater than 100% RH, so percentage of measurements below 100 was used to calculate differences. Whitetop-USFWS were significantly different (P=0.04); all other pairwise comparisons were non-significant. There was no significant differences between metapopulations (P=0.13) or presence of *M. montivaga* (P=0.98) (Figure 3).

Bedrock and Soil Cataloging

Bedrock age varied from middle to late Proterozoic, although some were identified as simply Precambrian (Table 2). Most common primary rock type was metasedimentary rock while the most common secondary rock type was micha schist.

Both of these were the sole primary and secondary types of the Black Mountains presence locations, which made up 15 of the 43 presence sites.

Soil data varied by location. The Grandfather Mountain soil survey was 100 percent Clingman-Craggey-Rock outcrop complex, windswept, with 15 to 95 percent slopes, and extremely bouldery. Roan Mountain primarily was Wayah-Burton complex, windswept, 30 to 50 percent slopes, and very stony. This contributed 52.3 to 54.3 percent of the soil. Balsam sandy loam, 30 to 50 percent slopes, and extremely bouldery was the second highest contributor with 11.6 to 15.1 percent of the soil. One location in Roan Mountain had, at 5.2 percent of the soil, a Wayah-Burton complex, windswept, 30 to 50 percent slopes, and very stony. The Plott Balsam site was 100 percent Burton-Craggey-Rock outcrop complex, windswept, 8 to 30 percent slopes. The Great Smokey Mountains sites were all of Breakneck-Pullback complex type. 15 to 30 percent slopes and very rocky occurred from 17.6 to 86.8 percent of the soils while 30 to 95 percent slopes were either very rocky or very stony and contributed 13.2 to 100 percent of the soil depending on specific site.

In the Black Mountains, where 21 presence locations were confirmed, Burton-Craggey-Rock outcrop complex, windswept, 30 to 50 percent slopes, and very bouldery was the most common, making up 31.4 to 100 percent of the soil depending on site. The second most common was Burton-Craggey-Rock outcrop complex, windswept, 50 to 95 percent slopes, and very bouldery which made up 1.6 to 66.5 percent of the soil depending on site. Other soil types included Burton-Craggey complex, windswept 15 to 30 percent slopes, rocky (5 to 89.3 percent); Craggey-Rock outcrop-Clingman complex, windswept 50 to 95 percent slopes, rubbly (13.8 to 92.7 percent); and Burton-Craggey complex, windswept, 15 to 30 percent slopes, and rocky (23.4 to 68.5 percent).

Species Distribution Modeling

Based on the given AIC values from the Maxent Model Surveyor, the final model selected was Bio1-Bio10-Slope-Solar. These variables showed statistically significant levels of correlation, with Bio1-Bio10 showing a high correlation value (Table 4). No significance difference ($P<0.05$) was found between partial models and the full model with the exception of Slope-Solar, Slope, and Solar. Area under the curve (AUC) values were greater than 0.9 for all models except the following three models: Slope-Solar, Slope, and Solar (Table 5). An AUC of 0.5 would equate to the null hypothesis, similar to a logistic regression. The four variables selected after calculating AIC values were Slop, Solar, Mean Annual Temperature ("bio1") and Mean Temperature of Warmest Quarter ("bio10") which gave an AIC value of 442.1 for the four variable model and an AUC value of 0.965. Running of Maxent Model Surveyor on these final four values gave similar AIC for all models except the Slope-Solar, Slope, and Solar models. Final percent contribution for bio10 = 80.9, bio1 = 11.6, solar = 4.2, and slope = 3.3 Final permutation importance for bio10 = 82.9, bio1 = 10.9, for solar = 4.8, and for slope = 1.4. Jackknife analysis of the regularized training gain shows the importance of mean temperature of warmest month being the most important and is consistent with the contribution results (Figure 4). Because of the high level of correlation between the two temperature variables (0.949, Table 4) and the lack of statistical difference between the four variable model and the other models, models using only the bio10 may be recommended. Models comparing the Bio1-Bio10-Slope-Solar and Bio10 show similar probabilities of distribution (Figure

5). As seen in Figure 5, populations are most likely to be found in the Black Mountains, Great Smokey Mountains, and Roan Mountain ranges. It should be noted that the model predicts limited populations in the Plott Balsams, which are the southernmost known limit of the spider. Historical potential range based on these models varies greatly, with an extremely limited range during the last interglacial period and a high potential range during the last glacial maximum (Figure 6). Historical models using only bio10 gave uniform probabilities across the entire model range of 0.62 and <0.001 for last glacial maximum and last interglacial period, respectively.

Soil Community Cataloging

Achieving the taxonomic expertise required to identify all individuals in the sample to species was almost impossible because to determine species of some groups scanning electron microscope work or genetic analysis is a requirement, placing it out of the scope of this research. All individuals were identified at least to order. One taxon was identified to order (Geophilomorpha), 2 taxa were identified to suborder, 3 taxa were identified to super family, 16 taxa were identified to family, 6 taxa were identified to genus, and 7 taxa were identified to species, giving a minimum species richness value of 36 not including distinct morphospecies within an identified taxonomic level (Table 6). Total number of individuals counted was 2039 (Table 7). The most prevalent order was Entomobyromorpha (Collembola), with 1203 individuals collected and counted. The subclass Acari (mites, ticks) was the second most prevalent with a total of 656 individuals from 3 orders (Trombidiformes, Sarcoptiformes, and Parasitiformes). Shannon-Weiner diversity index was calculated to a value of 1.17. Simpson's index was calculated to 0.86 (Table 7).

DISCUSSION

Temperature and Humidity Measurements

Previous research shows the role of microclimates to be of great importance in a wide range of taxa. In the spider *Anelosimus studiosus*, temperature in the web can drive the success of solitary or multifemale colonies while also being a key factor in the maturation process (Jones et al. 2007, Jones and Reichert 2008). In aquatic Diptera, emergence time and flight period are influenced by temperature in the Plitvice Lakes. In vertebrate taxa, microhabitats buffer and reduce vulnerability in frogs, and determine growth and size in avian offspring (Dawson et al. 2005, Scheffers et al. 2013). In the Philippines, microclimate habitats have been found to increase in temperature by a range of 0.11-0.66 °C while the macroclimate changes by 1° C (Scheffers et al. 2013). The results of this study also provide evidence that microclimates can buffer and ameliorate the ambient macro level temperature. Although daily maximum, minimums, and average of the maximum and minimum may be staying the same, the difference between the minimum and maximum values remains much more stable under the moss mats in the spruce-fir forest compared to those measurements taken out of the moss mats by the HOBO data logger on Mt. Lyn-Lowry and the Mt. Leconte weather station. This became most apparent when considering data loggers placed underneath the moss mat compared to the logger mounted up in a tree within two meters from the moss loggers. The difference between the Leconte weather station and the moss mat loggers also brought to light the importance of monitored differences between macroclimate monitoring and the microhabitat actually experienced by *M. montivaga*. In creating distribution models of Przeqalski's gazelle, isothermality, the difference between the maximum and minimum temperature, was found to be one of the five most important variables, showing one example of the importance of isothermality from a biological stand point (Hu and Jiang 2010). Indeed temperature stabilization by the moss mats, and especially the reduction of maximum daily temperature, may in fact be two of the defining features of *M. montivaga's* ecologocial requirements.

The data collected during this study spanned the hottest months experienced by the spider, and future research can elucidate the buffering potential of the moss mats during the coldest months. It is expected that a similar trend will be seen.

The lack of statistical differences in temperature and humidity between and among the metapopulations sites, and between the positive and negative presence sites, may not be surprising. All sites were previously considered to be within the defined habitat of *M. montivaga*; thus, general characteristics, such as slope, canopy species, and aspect, were similar across all sites. However, this lack of statistical differences may be important in consideration of the U.S. Fish and Wildlife Service stated goals, including identifying potential locations of new populations and sites for future populations. It is hoped that by knowing specific temperature and humidity ranges that success of potential artificial migration events may be more successful. Temperature and humidity are also important in consideration of captive-bred populations. As stated previously, at Lousiville Zoological Park, populations have been maintained successfully, but not well enough for breeding activity to occur (U.S. Fish and Wildlife Service 1998). Hopefully, the abiotic parameters of wild populations provided by this study will aid in the success of potential breeding efforts.

Although collecting data for the southern and northern metapopulations may be a good starting point, future consideration should be given to all metapopulations of *M. montivaga* to fully solidify the knowledge of this spider's ecology. These additional measurements across all metapopulations ould also provide knowledge of the basic biology that is lacking for this endangered species. One fruitful area of research could focus on the differences (both abiotic and biotic) between eastern and western species of *Microhexura*. It should also be noted that a single site was used at each location; therefore, expansion to incorporate multiple rock outcrops at each location would also be helpful. Long term monitoring will also be key to the survival of this species. It may be possible to take the percent change calculations between the Lyn Lowry iButton loggers and the HOBO logger and use it as a conversion factor by multiplying the percent change and non-microclimate measurements, allowing U.S. Fish and Wildlife Service to use the tree-mounted HOBO loggers; this would allow more efficient data collection due to increased storage capacity and durability. Under moss mats, the maximum temperature was lower, the minimum temperature was higher, the average of the minimum-maximum values was lower, and the isothermality was lower. The percentages given in Table 1 should be used when considering the habitat of *M. montivaga* because it would allow for more accurate monitoring by this macro scale conversion factor.

Tying in with these conversion factors is an understanding of the potential effects of global warming, which are of particular concern to the spruce-fir forests (Spira 2011). Global warming may be buffered by certain microhabitats because it appears that microclimates may moderate the macroclimate shifts recorded in forests (De Frenne et al. 2013). Although large scale models are convenient and may enlighten general patterns, microclimates must be considered if proper prediction of the level of imperiled status of a species is to be considered. However, a large scale monitoring goal can be achieved by using the calculated conversion factor to determine more accurate measurements.

Species Distribution Modeling

Maxent modeling is a powerful tool that provides maps and information about which environmental variables are most influential in accounting for species distributions. Environmental layer evaluation from the given model provides a statistical basis for the importance of temperature; specifically, the average temperature of the warmest quarter is the most important in regards to *M. montivaga*. This variable is perhaps a key factor for the species distribution. Positive presence may be related to how much heat the populations are exposed to. As a result, monitoring of population health should be centered on temperature measurements. It may be recommended to focus on collecting microhabitat measurements and large scale measurements at the same time to provide support for the conversion factor calculated in this study. As the necessary conversion factors are refined, monitoring may be done only at the macro scale, driven by GIS datasets. As discussed further in the concluding remarks, these parameters should be monitored using the conversation factor or measuring directly within the moss level due to the temperature differences experienced when underneath the moss matts.

Also of importance is using the model results to inform the possibility of reintroduction and artificial gene flow (Polak and Saltz 2011). This has associated risks, but if individual metapopulations show evidence of inbreeding depression or poor environmental suitability it may be necessary. Furthermore, prior to executing such plans, current accurate species distribution patterns are considered a pre-requisite (Franklin

2009) and maps presented here contribute to the effort of a better understanding of these distribution patterns.

In regards to the potential historical range of *M. montivaga*, it should be noted that Maxent models report on the fundamental niche of a species, not the realized niche (Pearson 2007; Kumar and Stohlgren 2009). This, along with the limited dispersal of non-ballooning mygalomorph spiders, may help explain the geographic isolation as measured by genetic markers between populations. These genetic marker patterns are suggestive of isolating mechanisms that occurred considerably before the last glacial maximum, despite favorable habitat (Hedin 2013). The model of the last glacial maximum shows considerable potential range expansion and supports the hypothesis of large scale favorable habitat. This is not surprising because the temperature environmental layers were calculated to be the most important and the species current range is limited to some of the coldest areas of the models' range. The Maxent model for the last interglacial period was surprising in that it gave a low maximum probability: about 4% maximum probability of presence for any site. This is informative for the historical biogeography of the species. Heavy range expansion and retraction cycles, as seen with the Maxent models, with limited gene flow outside of individual rock outcrops are one possible occurrence and may be informative when considered with the genetic markers. However, these results may simply show that the spider populations are more resilient to the variables tested than originally thought and that although the temperature data are highly correlated with positive presence, those variables may not the best predictor of the realized niche.

The high correlations among several of the environmental variables are not inherently surprising. For example, bio1, mean annual temperature, and bio10, mean temperature of warmest quarter, are by definition related. This correlation may affect the percent contributions of those variables within the model. Although the ratios of importance in the final jackknife analysis may not be perfect due to correlation, the overall selection process and model is still informative of the goals originally outlined. These difficulties may be important from a modeling standpoint, but problems in the application of the final the model are minimized due to the nature of the original goals. In review, the objectives of this study were to use Maxent modeling and GIS environmental layers to: 1) determine the environmental factors most closely associated with *M. montivaga* and 2) predict the potential species range using previously established positive presence locations. The map produced allows a new standard of guidelines to use for future populations to be discovered while also indicating areas where follow up surveys could be productively done. The completion of this research allows for search efforts to move beyond being driven strictly by the topography and aspect of the area.

Overall, it is hoped that the final model will provide base line data for the U.S. Fish and Wildlife Service in the management of this federally endangered spider. By considering the data presented, goals such as better understanding which environmental variables are important and better understanding the distribution (both potential and realized) have taken a large step towards being reached.

Soil Community Cataloging

It should be noted that when calculating diversity index values, the taxonomic identification levels must be the same, limiting calculations to the highest taxonomic level across all individuals collected. One of the limitations of this study, due to time, was identifying all species to the species level. Due to the difficulty of identifying soil Geophilomorpha, calculations done for this research were limited to order as the taxonomic level. The Shannon-Weiner diversity index (1.17) was higher for the same microhabitat in dry evergreen forests, 0.81 (Pragasan 2013) and oak pine forests, 0.96-1.17 (Coleman and Rieske 2006). However, it was lower when compared to Acari-only diversity Pine-oak ridges, Cove Hardwoods (2.485-3.580), Low-elevation oak (2.031-3.065), High-elevation oak (1.965-3.163), and Northern hardwoods (2.124-3.124) of the Southern Appalachians (Lamoncha and Crossley 1998). It should be noted that these Acari-only diversity numbers may or may not make for apt comparisons. Callaham et al. (2006) found a diversity range of about 1.5-2.0 for hardwood forests in South Carolina and 1.0-1.5 for Pine forests which are both higher than the collection from Blackrock Mountain.

In terms of potential interactions with *M. montivaga*, there are a few inferences that may be made. Previous research hypothesized that, given the small size of these predators, the primary diet of the spiders would be Collembola. In this micro-ecosystem, Collembola were the most abundant and diverse group of organisms, and the probability of them serving as prey and being located at the base of the food web would make logical sense. The most common mites, the Sarcoptiformes, also included relatively soft-bodied species that may be suitable as prey. Potential predators of *M. montivaga* were extremely limited; it is an interesting ecosystem to research when it is realized that the largest predator is no more than a few millimeters. Out of more than 2000 individuals collected, a minute percentage was potential predators. The 17 collected spiders were smaller than

M. montivaga and only 3 centipedes were collected. Potential competitors, those species sharing prey, were also limited in regards to the number of total predators to the number of potential prey, such as the 17 spiders to the 1203 Collembola. Based on these observations, *M. montivaga* may be considered the top predator of the microhabitat.

Concluding Remarks

In summary, the data presented here can be expressed as three main points. First, the abiotic conditions of the microhabitat of *M. montivaga* have been defined, including parameters for the warmest months of the year. Second, a catalog of the soil arthropods that share the habitat of *M. montivaga* has been provided and exhibits some interesting patterns. Third, maximum entropy models of highest probability of presence were created to evaluate environmental variables and better understand the past and present biogeography of *M. montivaga*. It is important to note that to take these three points in isolation reduces the explanatory power and usefulness of this research. For example, the maximum entropy models allowed determination that the most important environmental variables were those related to warmest months. The data loggers, in turn, defined exactly what temperature is being experienced by *M. montivaga* during the warmest months. The temperature and humidity measurements should not be viewed as the factors experienced by *M. montivaga,* but rather the abiotic factors experienced by all arthropods in the high elevation moss mat community.

As stated previously, importance of microhabitat measurements, cataloging the soil community, and predictive mapping are all reflected in the goals of the Recovery Plan for the Spruce-fir Moss Spider (U.S. Fish and Wildlife Service 1998). This research directly correlated with these goals by contributing to several conservation tasks. Task

1.3, the characterization of the species' habitat requirements was addressed by collecting the data with the loggers. Task 2, the search for additional populations and/or habitat suitable for reintroduction was completed by the Maxent mapping software. Task 3, development of artificial holding and propagation techniques, was also addressed by measuring the specific habitat of the spider. It should be noted that for both task 1.3 and task 3 that the soil biota catalog also helped address these goals, as an application of this list would allow for better matching ability of the community experienced by the spider.

It is hoped that this research leads to assisting the conservation efforts of *M. montivaga*. Although these new data present a strong baseline for conservation efforts, there is still much work that needs to be done. Multiple positive presence site temperature data from within every metapopulation should be collected. Cataloging soil arthropods would be most informative if identification were done to species and carried out across multiple metapopulations. However, the completed research does have a number of potential applications as it stands. For instance, using the calculated conversion factors for the temperature data, large scale monitoring can be done without having to actually measure the temperatures underneath the moss mats. The feasibility of large scale temperature monitoring with data loggers under the moss mat would be a massive undertaking from a financial and labor stand point. This highlights the importance of the conversion factor; the factor allows for more accurate monitoring while using preexisting infrastructure, such as the Mt. Leconte weather station. Because the Maxent models were driven by temperature, monitoring temperature should be one of the key points of conservation work. The present Maxent model also may be used to potentially locate new populations and identify the most imperiled population from an abiotic perspective. For example, positive presence sites with the lowest probability of presence imply a low abiotic match. These are just two of the potential uses that U.S. Fish and Wildlife Service could implement from the completed research.

As the plight of the spruce-fir forests continue to worsen, efforts to conserve nation-wide biodiversity will need to be focused on such ecosystems that harbor endemic species. *M. montivaga* may be important to monitoring of the system. As a potential key species within the microhabitat as a top predator, the presence of *M. montivaga* could indicate the health of the moss mats. In turn, these moss mats may be indicators of the overall forest health. As the spruce-fir forest canopy decreases, the moss mats will reflect this. The loss of an entire endemic ecosystem will not just endanger known endemic spiders like *M. montivaga* and *S. montigenus* that reside there, but also any other species that may be adapted for that entire ecosystem. The potential for a complete loss of an entire suite of taxa needs to be seriously contemplated and assessed to encourage intensive conservation and habitat restoration.

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APPENDIX A: TABLE AND FIGURES

Table 1. Percent change comparison of temperature data within metapopulations, between metapopulations, between presence status, and between all sites and USFWS logger on Lyn-Lowry and Leconte weather station.

	Avg Hi	Avg Lo	Avg Temp	Avg Iso
Lyn-Lowry:Browning Knob	-2.75%	0.24%	-1.38%	-18.54%*
Whitetop:Mt. Rogers	0.43%	3.27%	1.67%	-9.17%
Plott Balsam:Virginia	-3.46%	4.99%	0.37%	-44.56%*
Positive:Negative Presence	-1.83%	0.73%	-0.68%	-13.34%*
Lyn Lowry:USFWS	-14.79%*	8.35%*	-4.22%	-136.64%*
All:USFWS	-7.29%*	10.87%	0.83%	-83.53%*
All:Leconte	-25.67%*	29.59%*	-0.98%	-257.65%*

* Correlation is significant at 0.05 level (two-tailed).

Table 2. Summary of bedrock data of positive presence sites from 2009 U.S. Fish and Wildlife Service surveys.

Region	Number of Sites	Unite Age	Primary rock type	Secondary rock type
VA-Mt. Rogers	5	Proterozoic Z	Rhyolite	
G-father Mtn.	3	Late Proterozoic	Metasedimentary rock	Phyllite
Roan Mtn.	3	Middle Proterozoic	Gneiss	Amphibolite
Black Mtns.	21	Late Proterozoic	Metasedimentary rock	Mica schist
Plott Balsams	1	Late Proterozoic	Metasedimentary rock	Slate
Great Smokies	1	Middle Proterozoic	Granitic gneiss	Amphibolite
Great Smokies	4	Late Proterozoic	Metasedimentary rock	Slate
Great Smokies	3	Precambrian	Graywacke	Arkose

Table 3. The 9 layers of the Maxent model for *M. montivaga* prior to AIC calculations and their percent contribution and permutation importance from software output. Slope was added back in to the model after first environmental layer reduction due to biological significance for *M. montivaga*. Bio2 is mean diurnal range, bio3 is isothermality, bio5 is maximum temperature of warmest month, % decid. Canopy is the percentage of deciduous trees in the canopy, bio10 is mean temperature of warmest quarter, and bio1 is annual mean temperature.

Variable	Percent contribution	Permutation importance	Source/Reference
Bio2	16.6	21.6	WorldClim; Hijmans et al. 2005
Bio3	15.2	2.6	WorldClim; Hijmans et al. 2005
Bio5	11	0.4	WorldClim; Hijmans et al. 2005
Elevation	9.8	5.9	WorldClim; Hijmans et al. 2005
% Decid. Canopy	9.6	8.5	ArcGIS Online; NLCD Canopy Cover
Bio10	7.9	13.1	WorldClim; Hijmans et al. 2005
Aspect	4.5	5.3	Generated in GIS
Bio1	3.9	7.6	WorldClim; Hijmans et al. 2005
Solar	1.7	4.8	Generated in GIS
Slope	1.7	2.6	Generated in GIS

Table 4. Correlation matrix of the 9 layers of the Maxent model for *M. montivaga* prior to AIC calculations and their percent contribution and permutation importance from software output.

		slope	aspect	solar	% deciduous	bio10	bio2	bio3	bio5	bio1
slope	Pearson Correlation	1	-.156	-.181	-.235	-.369*	-.129	.209	-.348*	-.278
	Sig. (2-tailed)		.331	.258	.139	.018	.420	.189	.026	.078
aspect	Pearson Correlation	-.156	1	-.357*	-.204	.413**	.331*	.048	.409**	.274
	Sig. (2-tailed)	.331		.022	.200	.007	.034	.767	.008	.083
solar	Pearson Correlation	-.181	-.357*	1	.168	-.482**	-.438**	-.258	-.495**	-.373*
	Sig. (2-tailed)	.258	.022		.294	.001	.004	.104	.001	.016
% deciduous	Pearson Correlation	-.235	-.204	.168	1	.186	-.110	-.059	.033	.282
	Sig. (2-tailed)	.139	.200	.294		.243	.492	.715	.839	.074
bio10	Pearson Correlation	-.369*	.413**	-.482**	.186	1	.741**	.440**	.930**	.949**
	Sig. (2-tailed)	.018	.007	.001	.243		.000	.004	.000	.000
bio2	Pearson Correlation	-.129	.331*	-.438**	-.110	.741**	1	.771**	.908**	.672**
	Sig. (2-tailed)	.420	.034	.004	.492	.000		.000	.000	.000
bio3	Pearson Correlation	.209	.048	-.258	-.059	.440**	.771**	1	.547**	.524**
	Sig. (2-tailed)	.189	.767	.104	.715	.004	.000		.000	.000
bio5	Pearson Correlation	-.348*	.409**	-.495**	.033	.930**	.908**	.547**	1	.836**
	Sig. (2-tailed)	.026	.008	.001	.839	.000	.000	.000		.000
bio1	Pearson Correlation	-.278	.274	-.373*	.282	.949**	.672**	.524**	.836**	1
	Sig. (2-tailed)	.078	.083	.016	.074	.000	.000	.000	.000	

*. Correlation is significant at the 0.05 level (2-tailed).

**. Correlation is significant at the 0.01 level (2-tailed).

Shading indicates statistically significant correlations of variables in final model

N=41

Table 5 .Maximum entropy models for the final subset of environmental layers for the federally endangered spider *M. montivaga*. Range was set to all counties within 0.5 decimal degrees of a known area and at an elevation higher than 1280 m. Reported values are area under curve (AUC), Akaike information criterion (AIC), and P values comparing each model individual model to the model with all 4 environmental layers.

Model	AUC	SE	Z	*P*	AIC
Bio10, Bio1, Slope, Solar	0.965	0.018			442.1
Bio1, Slope, Solar	0.955	0.020	0.347	0.729	451.5
Bio10, Bio1, Slope	0.953	0.020	0.423	0.672	441.1
Bio10, Bio1, Solar	0.965	0.022	-0.030	0.976	438.0
Bio10, Slope, Solar	0.964	0.020	0.014	0.989	440.0
Bio1, Slope	0.946	0.025	0.870	0.384	452.0
Bio1, Solar	0.958	0.021	0.244	0.807	445.7
Bio10, Bio1	0.950	0.020	0.537	0.591	440.4
Bio10, Slope	0.954	0.021	0.349	0.727	439.1
Bio10, Solar	0.961	0.014	0.168	0.866	438.1
Slope, Solar	0.766	0.076	2.731	0.006	592.2
Bio1	0.938	0.026	1.014	0.310	448.3
Bio10	0.946	0.025	0.479	0.632	438.6
Solar	0.658	0.080	3.377	<0.001	597.3
Slope	0.720	0.079	3.069	0.002	587.7

Table 6. Identification of arthropods extracted from the Plott Balsam metapopulation moss mat microhabitat by Tullgren funnel. Sample collected fall of 2012.

Identification Level	Class or Subclass	Order	Identification
Suborder	Acari	Parasitiformes	Mesostigmata
Species	Acari	Sarcoptiformes	*Neanura muscorum*
Family	Acari	Sarcoptiformes	Camisiidae
Family	Acari	Sarcoptiformes	Galumnidae
Family	Acari	Sarcoptiformes	Euphthiracaridae
Superfamily	Acari	Sarcoptiformes	Oripodoidea
Superfamily	Acari	Sarcoptiformes	Eremaeoidea
Family	Acari	Sarcoptiformes	Cepheidae
Superfamily	Acari	Sarcoptiformes	Carabodidae
Suborder	Acari	Trombidiformes	Prostigmata
Family	Arachnida	Araneae	Linyphiidae (2 morphospecies)
Species	Arachnida	Araneae	*Erigone brevidentata*
Genus	Arachnida	Araneae	*Lepthyphantes*
Genus	Arachnida	Araneae	*Baryphyma*
Genus	Arachnida	Araneae	*Neriene*
Genus	Arachnida	Araneae	*Sissicotus*
Order	Chilopoda	Geophilomorpha	
Family	Collembola	Entomobryomorpha	Entomobryidae
Species	Collembola	Entomobryomorpha	*Entomobrya ligata*
Species	Collembola	Entomobryomorpha	*Metisotomoa grandiceps*
Family	Collembola	Poduromorpha	Onychiuridae
Genus	Collembola	Poduromorpha	*Protaphorura*
Family	Collembola	Symphypleona	Sminthuridae (2 morphospecies)
Species	Collembola	Symphypleona	*Sminthurides malmgreni*
Species	Collembola	Symphypleona	*Bourletiella arvalis*
Species	Collembola	Symphypleona	*Sminthurinus hendhawi*
Genus	Insecta	Coleoptera	*Nebria*
Family	Insecta	Coleoptera	Staphylinidae (3 morphs)
Family	Insecta	Coleoptera	Tenebrionidae
Order	Insecta	Coleoptera (larva)	
Family	Insecta	Diptera	Sciaridae
Family	Insecta	Diptera	Anthomyiidae
Family	Insecta	Diptera	Drosophilidae
Family	Insecta	Hymenoptera	Formicidea
Family	Insecta	Hymenoptera	Mymaridae
Family	Insecta	Hymenoptera	Eulophidae

Table 7. Abundance of arthropods extracted from the Plott Balsam metapopulation moss mat microhabitat by Tullgren funnel. Sample collected fall of 2012.

Class or Subclass	Order	Number
Acari	Parasitiformes	52
Acari	Sarcoptiformes	583
Acari	Trombidiformes	21
Arachnida	Araneae	17
Chilopoda	Geophilomorpha	3
Collembola	Entomobryomorpha	1203
Collembola	Poduromorpha	53
Collembola	Symphypleona	56
Insecta	Coleoptera	30
Insecta	Diptera	17
Insecta	Hymenoptera	4
	Total Number	2039
	Shannon Index	1.17
	Simpson Index	0.86

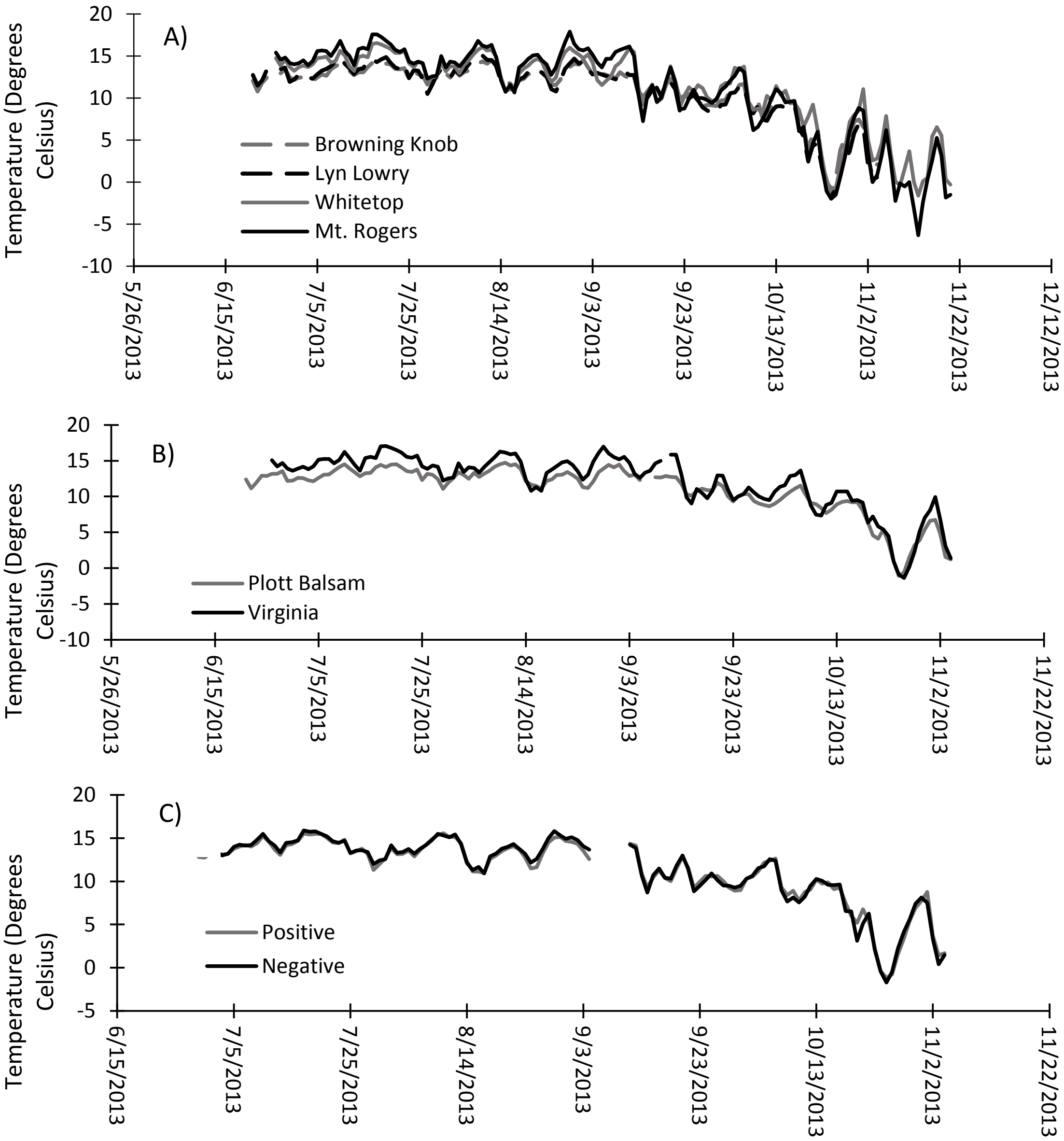

Figure 1. Temperature data logger summary A) Average of daily maximum and minimum temperature for Browning Knob, Lyn Lowry, Whitetop, and Mt. Rogers. Tukey's pairwise comparison shows no significant differences between any of the pairs (P>0.05). B) Average of daily maximum and minimum temperature for the two metapopulations studied, in the Plot Balsams and Virginia (Mt. Roger's area), which showed no significant difference (P=1.00). C) Average of daily maximum and minimum temperature for positive versus negative presence sites. Positive presence sites were Lyn Lowry and Whitetop, while negative sites were Mt. Rogers and Browning Knob. Presence was not significant (P=0.81).

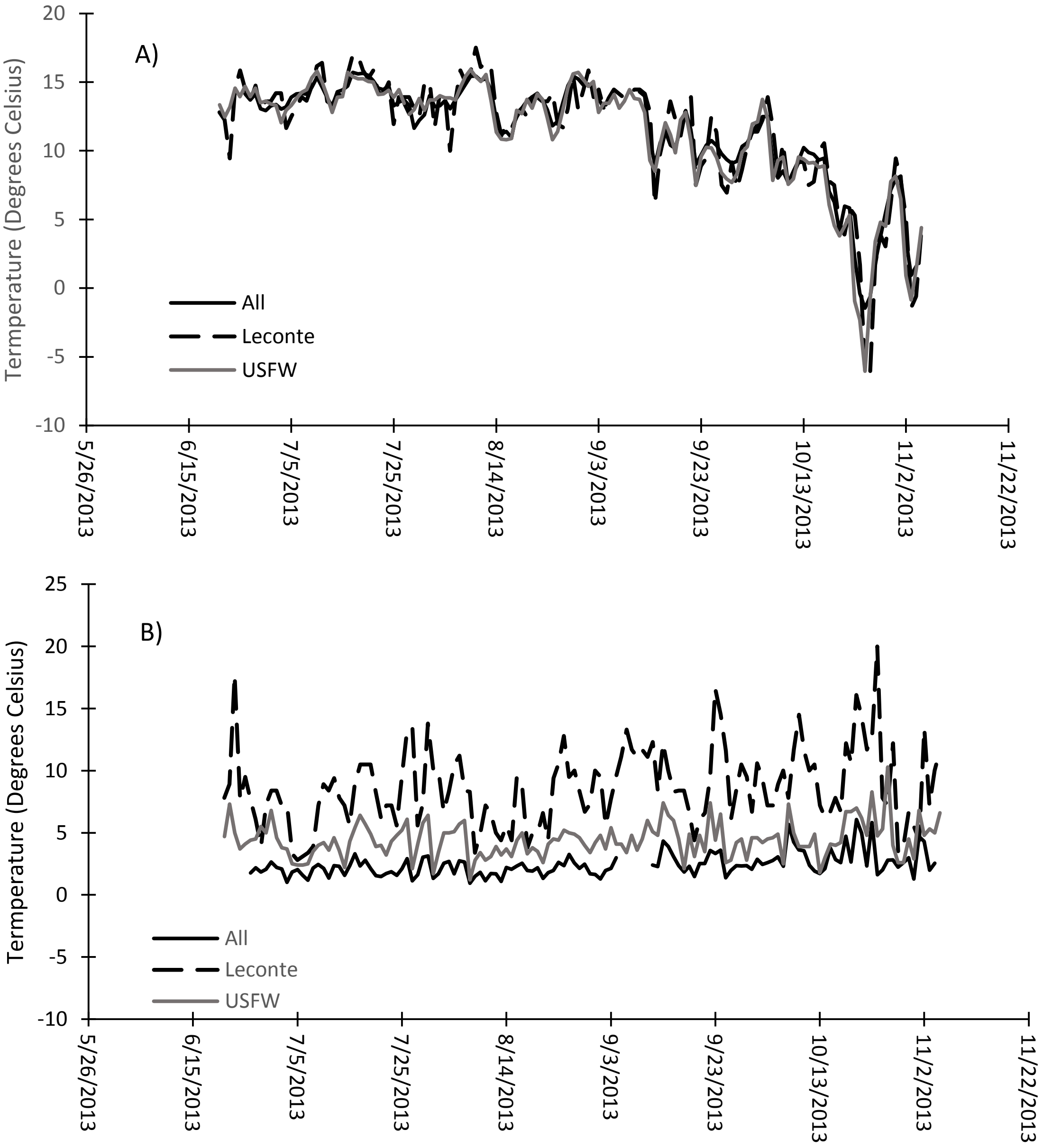

Figure 2. Comparisons with HOBO and weather station data A) Average of the daily maximum and minimum temperature values from all iBCod50 G data loggers placed under moss mats at Mt. Rogers, Whitetop, Lyn Lowry, and Browning Knob (“All”) compared to the values for the Lecont weather station and the USFWS HOBO logger mounted in a tree near the Ly Lowry iBCod50 G loggers. There was no statistical difference (P=0.08). B) Difference of the daily maximum and minimum temperature values for the same scenarios as (A) were significantly different (P<0.001).

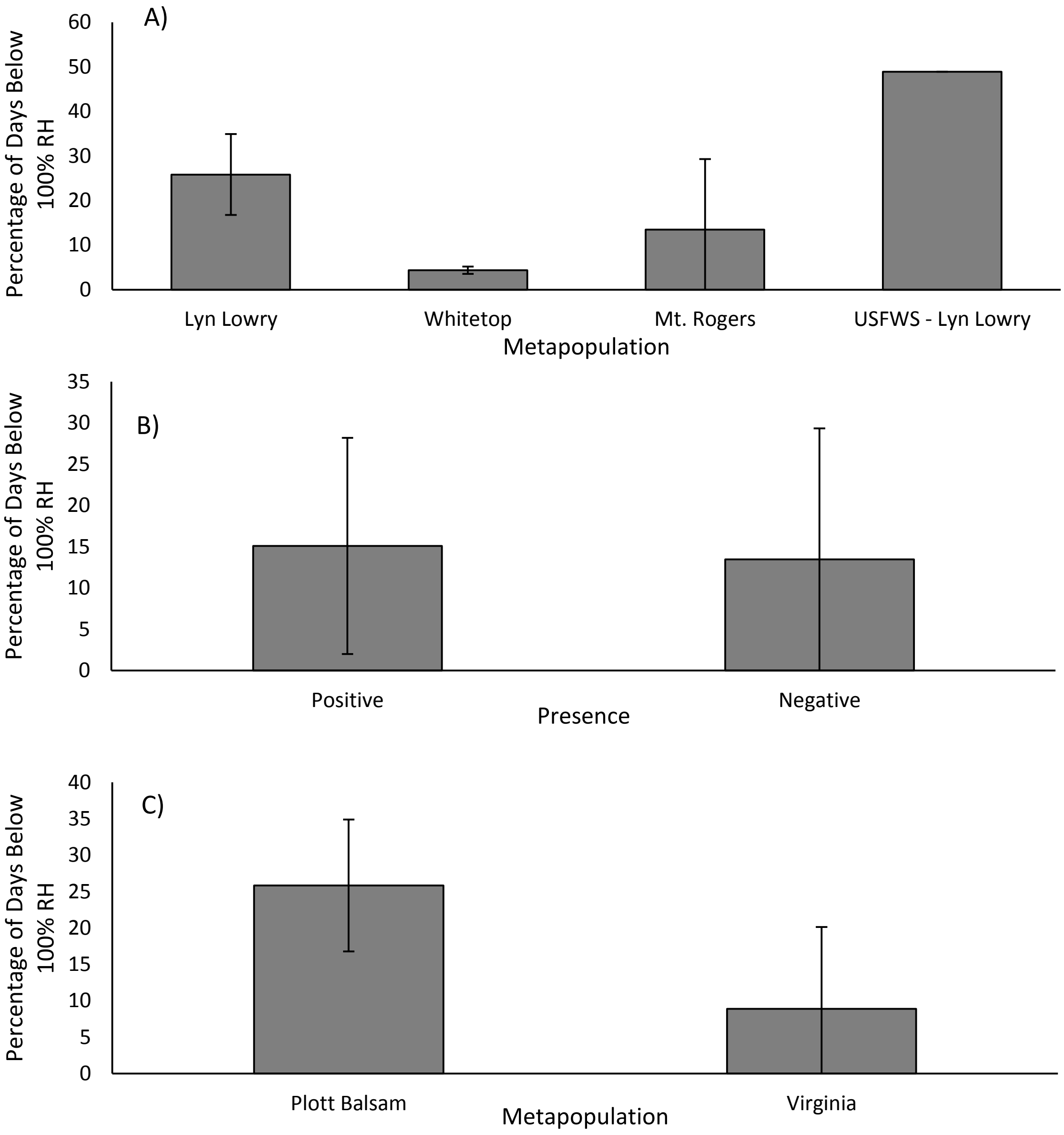

Figure 3. Humidity data logger summary. A) Percentage of days measured below 100% RH for each site. Tukey's pairwise comparison showed that Whitetop-USFWS were significantly different (P=0.04) but all other pairwise comparisons were insignificant (P>0.05). USFWS logger was mounted in tree compared to all other sites which where iButton DS 1920 loggers placed down near moss mats. B) There was no significant differences between metapopulations (P=0.13) or C) presence of *M. montivaga* (P=0.98) (Figure 3). Bars are standard deviation. The USFWS logger was not included in the metapopulations and presence analysis.

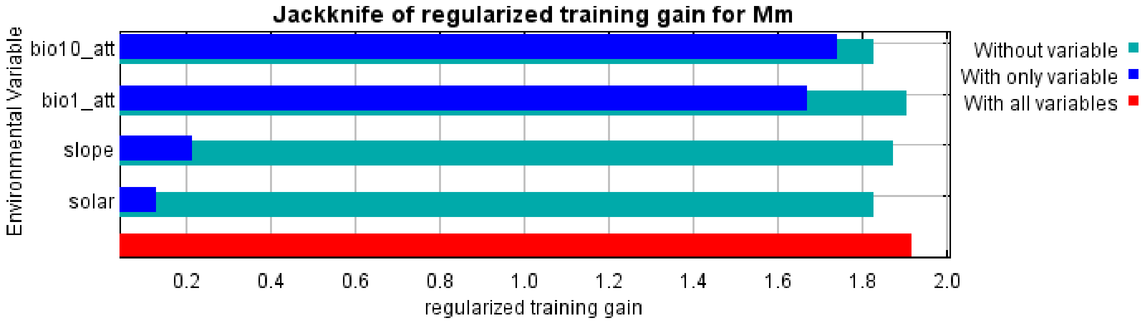

Figure 4: Results of jackknife evaluations of predictor variables for the Maxent model for *M. montivaga*. "bio10" is mean temperature of warmest quarter, "bio1" is mean annual temperature. In the final model, bio10 had the highest percent contribution (80.9) and highest permutation importance (82.9).

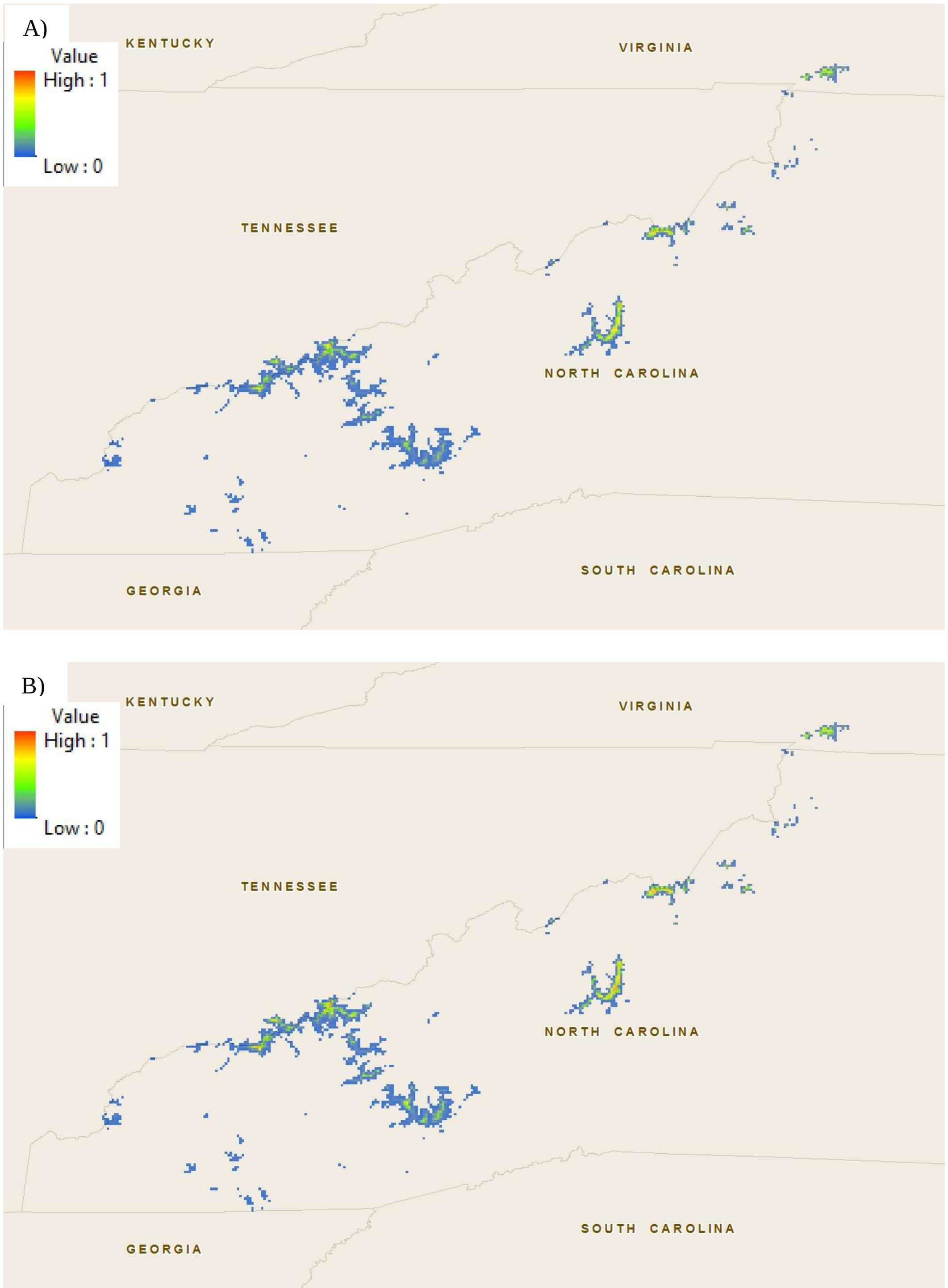

Figure 5: Map predicting probability of *M. montivaga* presence in the present. Probability values range from 0 to 1. A) Variables used include mean temperature of warmest quarter, mean annual temperature, solar radiation, and slope. B) Mean temperature of warmest quarter only. Range was set at 1280 m and within 0.5 decimal degrees of known location.

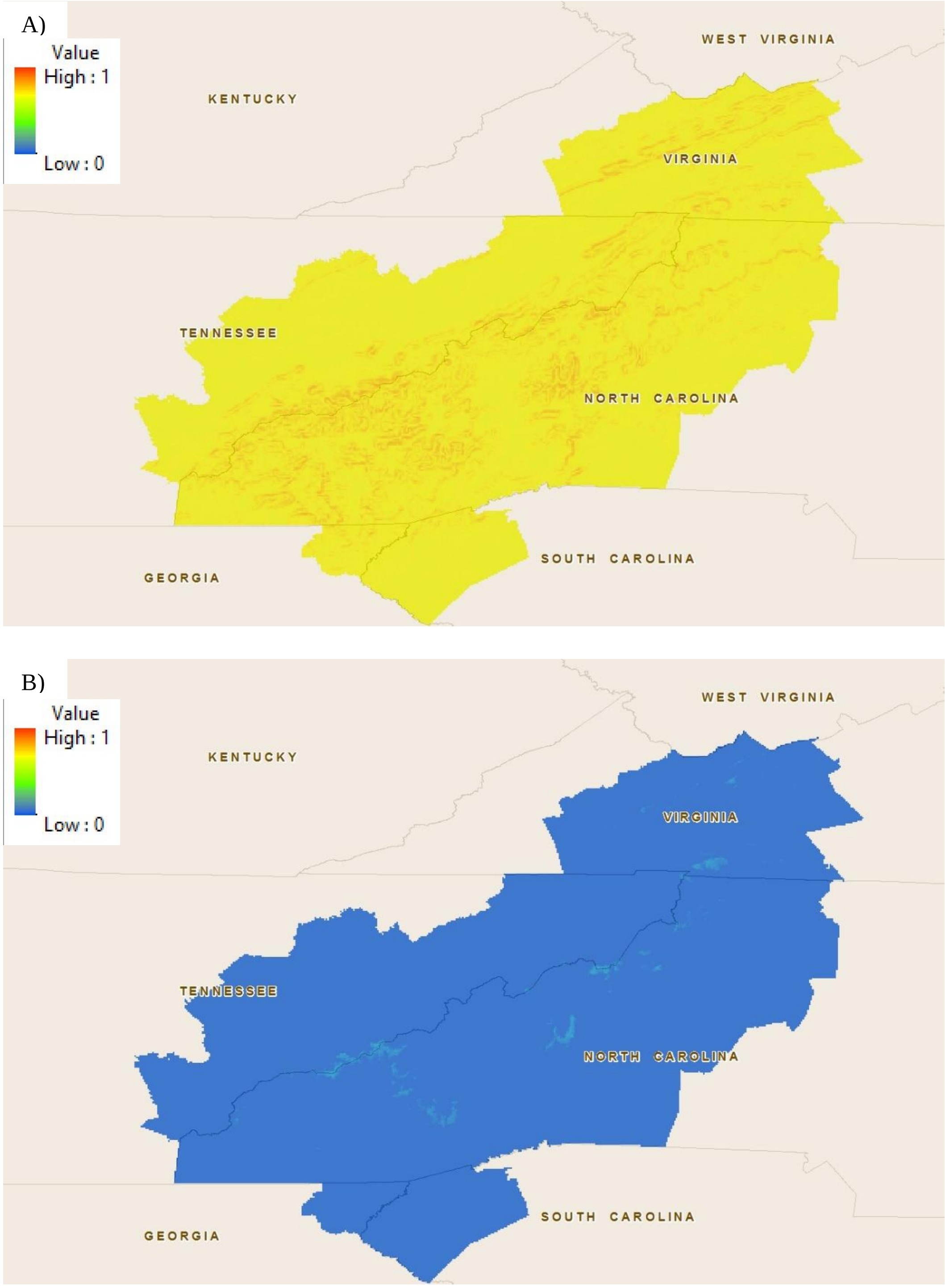

Figure 6: Maps predicting probability of *M. montivaga* presence for A) last interglacial period B) last glacial maximum. Variables used include mean temperature of warmest quarter, mean annual temperature, and slope. Range was set to all counties within 0.5 decimal degrees of positive presence locations.