

**DERIVING A QUALITATIVE, CONTINENTAL SCALE MODEL OF THE  
SPECIES RICHNESS FOR ECTOMYCORRHIZAL FUNGI IN CANADA AND  
THE UNITED STATES OF AMERICA**

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Brittany Altwasser

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The undersigned certify that they have read, and recommend to the College of Graduate Studies for acceptance, a thesis entitled:

Deriving a Qualitative, Continental Scale Model of Species Richness for Ectomycorrhizal Fungi in Canada and the United States of America

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submitted by Brittany Altwasser in partial fulfillment of the requirements of the degree of Master of Science.

Dr. Jason Pither, UBCO, IKBSAS – Biology and Geography  
**Supervisor, Professor**

Dr. Miranda Hart, UBCO, IKBSAS – Biology  
**Supervisory Committee Member, Professor**

Dr. Melanie Jones, UBCO, IKBSAS – Biology  
**Supervisory Committee Member, Professor**

Dr. Kevin Hanna, UBCO, IKBSAS – Geography  
**University Examiner, Professor**

---

**External Examiner, Professor**

June 19, 2017

**Additional Committee Members include:**

Dr. Brian Pickles, University of Reading

---

## **Abstract**

Understanding the processes that influence richness and diversity patterns across spatial and temporal scales is imperative to ecological research. Our knowledge of how these processes affect ecologically and economically important ectomycorrhizal fungal communities across scales is incomplete. Researchers have begun to explore ectomycorrhizal diversity at larger spatial scales, but have placed little consideration on complex processes and temporal scales. Here, I review the literature on ectomycorrhizal fungal diversity, using the framework of Vellend (2010) in an effort to identify the drivers of ectomycorrhizal fungal diversity, any inconsistencies in the literature, and knowledge gaps. In doing this I am able to hypothesize as to what additional factors might influence ectomycorrhizal diversity. By synthesizing these hypotheses with the predictors identified in the literature, I am able to produce a qualitative predictive model of EMF diversity patterns at the geographic extent of Canada and the USA. This exercise is helpful because it provides a visual representation of all of the factors hypothesized, explicitly or implicitly, to influence the large-scale diversity patterns of EMF. Additionally, this model is used to identify geographic regions that are predicted to harbour high EMF diversity in an effort to increase the sampling efficiency of future projects.

## **Preface**

This study was designed by my supervisor Dr. Jason Pither and me. All of the research was completed by me and the data analyses and methodologies were performed by me with collaboration from Dr. Jason Pither. I wrote this thesis with the guidance of Dr. Jason Pither and it was reviewed by my supervisory committee: Dr. Miranda Hart, Dr. Melanie Jones, and Dr. Brian Pickles.

Selected material from Chapters 2, 3, and 4 of this thesis is being included in a manuscript (in progress) for submission parallel to submission of this thesis. I performed all of the background research, methodology, analyses, and writing for the manuscript with guidance and editing from my co-authors, Dr. Jason Pither and Dr. Brian Pickles. Additionally, selected material from Chapter 2 of this thesis is being included in a manuscript (in progress). I contributed to the intellectual conception of the presented ideas and writing.

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## **List of Abbreviations**

EM – ectomycorrhizal

EMF – ectomycorrhizal fungi

CEC – cation exchange capacity

HSM – habitat suitability model

SI – suitability index

GIS – geographic information system

MAT – mean annual temperature

MAP – mean annual precipitation

## **Glossary**

Geographic information system – A software system that is used to manage and analyze spatial data.

Shapefile – A vector-based geospatial data file specific to the GIS software ArcGIS, and that describes geographic features as points, lines, or polygons.

Data normalization – A method of transforming numerical data from one set of values to another in order to compare data sets with varying scales and units. The data is transformed to a new scale while maintaining the frequency distribution of the input data.

Raster – A data model for geospatial data that uses a series of grid cells to characterize geographic space. Each grid cell is assigned a value representing information or observations within that cell (e.g., temperature).

Spatial resolution – The geographic area covered by each cell in a raster dataset.

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*For my Faja*

## **Chapter 1: Introduction**

Human populations have grown exponentially since the start of the industrial revolution. In order to support our growing needs and demands we have heavily exploited natural resources and expended great amounts of energy. This growth has introduced new stressors to ecosystems and biodiversity. Climate change, habitat loss and fragmentation, pollution, and overharvesting have severely impacted terrestrial ecosystems worldwide. Improving our understanding of how anthropogenic stressors influence organisms and ecosystem functioning is crucial for anticipating and managing their cumulative impacts.

It has been established that ecosystem responses to stressors such as nitrogen deposition and increased atmospheric carbon dioxide are governed in large part by aboveground-belowground interactions or plant-soil feedbacks, particularly between plants and mycorrhizal fungi (van der Putten, 2012; van der Putten et al., 2013, 2016; Wardle et al., 2004). Additionally, it has been demonstrated that these ecosystem services are dependent upon the diversity of the system. Specifically, mycorrhizal fungal (MF) taxa have vast physiological differences which result in high functional diversity among taxonomically diverse communities (Cairney, 1999, 2011; Klironomos, 2000). Functional diversity here refers to the number of MF taxa that provide a unique function, or combination of functions, to their community or ecosystem. The functions provided include, for example, host plant establishment, persistence, and diversity (van der Heijden et al., 1998), nutrient cycling (Fitter, 2005; Koide, Fernandez, & Malcolm, 2014), soil structuring (Rillig & Mummey, 2006). Improved plant diversity can, in turn, enhance nutrient cycling, productivity, stability, and resilience (Tilman et al., 1996). Considering the present and impending anthropogenic stressors on contemporary ecosystems and biodiversity, and given the positive association between MF diversity and ecosystem functioning, it is important that we gain a better understanding of how the diversity of MF varies across geographic space, and what the primary determinants of these patterns are. The over-arching objective of this thesis is to improve our understanding of broad-scale patterns of MF diversity.

Our knowledge of mycorrhizal interactions and the diversity of MF has grown immensely over the past few decades (van der Heijden, Martin, Selosse, & Sanders, 2015) due to increasing interest in the symbiosis and the application of molecular

techniques in their study (Horton & Bruns, 2001; Wang & Qiu, 2006). Nonetheless, research in this area has been predominantly small-scale and reductionist in its approach. Lessons from other areas of research show clear benefits to broadening the spatial and temporal context within which diversity patterns are investigated (Cornell & Harrison, 2014). For example, in plant diversity research, the evolutionary history between plant species richness and soil pH was particularly important in explaining contemporary, geographic patterns of plant richness (Pärtel, 2002). More recently, researchers have begun to consider the implications of biogeographic-scale processes in MF research (Dickie et al., 2014), demonstrating, for example, that climate plays a key role in determining diversity at both small (Bahram et al., 2012; Kernaghan & Harper, 2001) and large scales (Pöhlme et al., 2013; Tedersoo et al., 2012, 2014). Despite the challenges associated with scaling up the findings of local MF research and with adopting a more holistic and broader investigative scope, the benefits that could come from an improved understanding of the biogeographic patterns of MF diversity are potentially significant (Bennett et al., 2017; Dickie et al., 2014; Terrer et al., 2016; Teste et al., 2017). Among the studies that have explored large-scale patterns of MF diversity, the focus has largely been on contemporary factors such as edaphic, biotic, and climatic conditions (Pöhlme et al., 2013; Tedersoo et al., 2012, 2014) as well as some emphasis on dispersal and endemism (Peay et al., 2010, 2012; Pöhlme et al., 2013; Talbot et al., 2014). Studies on MF that simultaneously consider contemporary and historical predictors across local to biogeographic extents are lacking.

My general objective here is to address this shortfall, with the ultimate aim of improving our understanding of the origins of biogeographic scale patterns of MF diversity. I do this focusing on ectomycorrhizal fungi (EMF), which despite associating with a minority of plant species (Brundrett, 2009), have disproportionately large representation in economically and ecologically important boreal and temperate forests (Read, 1991).

I first review the key features of MF and EMF specifically, paying particular attention to topics that are relevant to understanding the origins of EMF diversity patterns. Next, I provide an overview, based on a literature review, of the processes that have been hypothesized to influence EMF biodiversity at various scales. I organize these



hypotheses in relation to scale, and also within Vellend's (2010) framework for community ecology (see sections 2.2 and 2.3), which envisions species assemblages at any scale as being the net outcome of four "high-level" processes: selection, dispersal, speciation, and drift. My thorough (but not exhaustive) review of the literature yielded a list of "low-level" factors (*sensu* Vellend) thought to influence EMF diversity at scales corresponding to a single host plant or stand of trees, up to landscape or regional scales. I then describe how these low-level processes fit within Vellend's framework.

Next, I present hypotheses about additional factors that might influence EMF diversity patterns. To date, most of the studied factors fall under the "selection" heading of Vellend's framework, and the vast majority are "local". I argue that additional, larger-scale selective factors ought to be considered, as well as historical factors that fall under "selection".

Finally, I synthesize the preceding information to produce a qualitative, predictive model of EMF diversity patterns at the geographic extent of Canada and the USA. The purpose of this model is fourfold: (i) to visualize, using a map, how all the factors hypothesized (explicitly or implicitly) influence EMF diversity and interact geographically at continental scales to moderate predicted, broad-scale patterns of EMF diversity; (ii) to explore how the qualitative diversity predictions arising from the models change as one shifts model emphasis, for example, from contemporary to historical predictors; (iii) to evaluate the correspondence between the predicted diversity patterns and available sample data describing local EMF richness, and (iv), to juxtapose existing sampling locations with the predicted diversity patterns in order to identify any key sampling gaps in North America, and to optimize future sampling strategies.

## Chapter 2: Literature Review

### 2.1 Mycorrhizal fungi

Mycorrhizal fungi are a functional group of fungi that form a symbiotic association with plant roots. There are multiple types of mycorrhizal fungi that vary based on morphology and function including ectomycorrhizal fungi (EMF), arbuscular mycorrhizal fungi, ericoid mycorrhizal fungi, and orchid mycorrhizal fungi. EMF are relatively diverse, and thought to include ca. 20,000 taxa that associate with just 2% of plant species (*c.* 6,000), while arbuscular mycorrhizal fungi are comparatively species-poor (*c.* 300-1,600 taxa), but associate with >72% of plant species (*ca.* 200,000) (Brundrett, 2009; van der Heijden et al., 2015).

#### 2.1.1 Structure

As with many other fungi, EMF grow vegetatively as hyphae, which are microscopic chains of cells (Smith & Read, 2008) These hyphae can form macroscopic, ephemeral fruiting bodies known as ‘sporocarps’, or more commonly mushrooms (epigeous sporocarps) or truffles (hypogeous sporocarps) (Smith & Read, 2008). These structures are spore bearing and are important for reproduction. The spore itself is a durable structure that may be adapted for dispersal and/or survival.

Ectomycorrhizae are the structures formed between the ectomycorrhizal fungus and plant root. Almost all ectmycorrhizae share a distinct set of structural characteristics; however, there can be substantial variation in these structures across taxa (Agerer, 2006). The ectomycorrhizal (EM) symbiosis is named for the extent and location of EMF hyphal growth surrounding and within the plant root. Here, the hyphae form two important structures that describe the external (ecto-) nature of the EM symbiosis; (i) the mantle, which wraps around the outside of the host root, and (ii) the Hartig net, which develops within plant cell walls (Smith & Read, 2008). The Hartig net provides an intricate association and acts as the key site of exchange between the EM plant and fungus. The structure and proportion of the fungal mantle varies across EM associations (Agerer, 2006); similarly the degree of root penetration by the Hartig net varies among plant species (Smith & Read, 2008). Any exploratory hyphae that extend outward from the mantle are referred to as extramatrical mycelium; mycelium is a term used to describe a collection of hyphae. These extramatrical mycelia can have different exploration types

that can contribute to varied nutrient acquisition strategies (Agerer, 2001). These exploration types are distinguished by the presence and structure of rhizomorphs (root-like aggregations of hyphae) and the amount and distance covered by the extramatrical mycelia (Agerer, 2001). Additionally, extramatrical mycelia are important sites of exchange between the fungus and the soil as well as a form of connection between the fungal sporocarps and plant root. When the extramatrical mycelia of EMF connect multiple individual plants together they form what are called common mycorrhizal networks (Selosse et al., 2006).

### **2.1.2 Function**

As with all fungi, EMF are heterotrophs and require organic carbon for growth. They can acquire nutrients by absorbing dissolved molecules, typically by secreting various enzymes into their environment. While some EMF are able to acquire carbon with varying degrees of saprotrophy (e.g., via the degradation of lignins and soluble phenolics; Bending & Read, 1997) (Koide et al., 2008), it is unlikely that enough carbon can be sequestered from this method for the growth of sporocarps and subsequently, reproduction (Taylor & Alexander, 2005). Instead, EMF acquire photosynthetic carbon biotrophically from their plant partners, and are considered to be obligate symbionts due to this reliance (Koide et al., 2008). In exchange for carbon, the fungus can provide various nutrients including phosphorus and nitrogen which are often limiting (Koide et al., 2014; Read & Perez-Moreno, 2003), protection from plant pathogens (Marx, 1972) and drought (Parke et al., 1983), and tolerance to heavy metals (Gadd, 2010). Due to the wide range of benefits provided by EMF, many EM plant species are also obligate symbionts in natural systems (Wang & Qiu, 2006). For example, many North American trees have been shown to have inhibited growth in soils that lack native EMF inoculum (Bennett et al., 2017; Teste et al., 2017).

While EMF clearly play an important role in improving host performance directly via their symbiosis, they also have a profound impact on other ecosystem functions and services. They can enhance host establishment and diversity via common mycorrhizal networks (Simard et al., 2012), contribute to carbon and nitrogen cycling (Koide et al 2014), structure the soil (Rillig & Mummey, 2006), and provide food for soil fauna, animals, and humans (Fitter & Garbaye, 1994; Hall, Yun, & Amicucci, 2003).

Importantly, EMF taxa have a variety of physiological differences produced by their structural variation (Agerer, 2006). For example, EMF differ in their abilities to enhance host phosphorus acquisition possibly due to alternate foraging strategies or absorptive abilities (Cairney, 2011). Furthermore, each EMF taxon can provide a unique combination of functions, with varying levels of success, for their host and ecosystem (Cairney, 1999). Therefore, a diverse community of EMF should maintain or promote a larger range of ecosystem functions.

### **2.1.3 Dispersal**

EMF are able to disperse to new habitats by means of hyphal extension and spore release. Hyphal dispersal can occur at short distances belowground, from a millimeter to several decimeters (Agerer, 2001). On the other hand, spore dispersal can be achieved through a variety of mechanisms, and can occur over varied distances. EMF typically produce large amounts of spores, with some wind dispersing species producing trillions annually, in order to enhance the likelihood of dispersing to favourable habitats and establishing once in those habitats (Peay et al., 2012). Wind dispersal occurs in taxa with epigeous sporocarps that have access to air currents above ground. While wind dispersal can cover distances over 5 kilometers (Peay et al., 2012), the majority of spores fall directly beneath or within 1 meter of the mushroom's cap (Galante et al., 2011). Animal vectors have been indicated as the most prominent method of long distance dispersal for EMF (Johnson, 1996). The foraging ranges of mycophagous mammals can vary anywhere from 1 to 100 hectares or more over which spores might be dispersed (Johnson, 1996). This method of dispersal does occur in epigeous sporocarps, but is the primary method of spore dispersal among EMF that form hypogeous sporocarps, as these do not have access to wind.

### **2.1.4 Persistence**

EMF are able to survive unfavorable growing conditions through the formation of resistant propagules such as spores and sclerotia. Sclerotia are aggregations of mycelial tissue and resources that can help the fungus to survive environmental issues like desiccation, freezing, and host absence (Willetts, 1971). These resistant propagules can form a spore bank similar to plant seed banks (Miller, Torres, & McClean, 1994). It is suspected that the spores and sclerotia in these spore banks have varying periods of

viability (Nara, 2009). Recent work has shown that spores can remain viable for at least 4-6 years in multiple taxa (Bruns et al., 2009; Nguyen et al., 2012). Additionally, some spores continued to remain dormant, or inactive, for the first few years which allows the spore bank to maintain propagules in case suitable conditions are temporary (Bruns et al., 2009).

### **2.1.5 Evolution**

EM associations evolved around 150-200 million years ago during rapid angiosperm evolution (Brundrett, 2002; Maherali et al., 2016; Martin et al., 2016). The EM symbiosis is paraphyletic, having evolved independently numerous times in both plants and fungi, causing extensive taxonomic variation (Tedersoo et al., 2010). Co-evolution between EM plants and fungi has probably contributed to this diversification (Hoeksema, 2010).

The plants involved in the EM symbiosis tend to be woody and include species from a variety of gymnosperm and angiosperm families, including pine, birch, beech, rose, willow, eucalypt, and dipterocarps (Brundrett, 2009). The fungi involved are present in various lineages possibly arising 66 separate times (Tedersoo et al., 2010; Wang & Qiu, 2006).

### **2.1.6 Specificity**

The large ratio of EMF diversity relative to host plant diversity (*c.* 20 000 to 6000 species) implies a generalist habit of hosts towards EMF. Moreover, the paraphyletic origins of the symbiosis should enhance the taxonomic diversity of partners that either the fungus or plant can have. Indeed, almost all species of EM host plants associate with many distantly related EMF taxa. For example, *Pseudotsuga menziesii* (Douglas-fir) potentially associates with thousands of EMF taxa across its geographic range (Trappe, 1977). Similarly, many EMF taxa are able to associate with distantly related host plant species. For instance, a study by Twieg and colleagues (2007) on the EMF communities of Douglas-fir (*Pseudotsuga menziesii*: Pinaceae) and paper birch (*Betula papyrifera*: Betulaceae) found that 42 of 105 EMF taxa identified associated with both hosts. Nevertheless, there is evidence of more specialized associations such as *Alnus* spp. (alders) that engage in extremely specialized associations with comparatively few EMF (Molina, 1981).

### 2.1.7 Identification and sampling

Research on EMF began comparatively recently, as the mycorrhizal symbiosis was itself first described in the 1800's (Frank 1885 as cited by Koide & Mosse, 2004). Moreover, whole EMF communities are challenging to measure, which has made their study more difficult. While EMF sporocarps are often visible and identifiable in the field, they are also ephemeral and can be hidden belowground. Other structures such as propagules and hyphae can be coarsely identified morphologically, but their microscopic size introduces substantial challenges.

Traditionally, EMF diversity was studied above ground by identifying EMF sporocarps (Taylor, 2002). This is problematic because EMF can be active symbionts even when they are not fruiting. This is because symbioses with plants are formed by mycelial growth belowground, and this activity can occur without fungal fruiting. Additionally, fruiting episodes are variable through time (e.g., seasons), and are more sensitive to variations in precipitation and other environmental factors than mycelia (Arora, 1986). Thus, diversity estimates based on fruiting bodies can vary substantially through time and space, and these estimates may not reflect belowground diversity in any systematic way (Gardes & Bruns, 1996).

More recently, sampling strategies have involved removing soil cores and identifying the EMF taxa present on host root tips molecularly, morphologically, or with a combination of both techniques (Taylor, 2002). Problematically, EMF communities are comprised of relatively few abundant species and many rarer species (Horton & Bruns, 2001). Therefore, substantial sampling effort is required to achieve thorough estimates of species richness. The prevalence of rare taxa can also yield substantial variation between spatially proximate samples (Lilleskov et al., 2004). For instance, Lilleskov *et al.* (2004) found that communities were most similar within 3m or less and suggest that cores should be at least 3m apart in order to increase sampling efficiency for stand-level communities. Using rank abundance plots and accumulation curves, researchers can estimate the degree to which increased sampling effort would yield new species (Taylor, 2002).

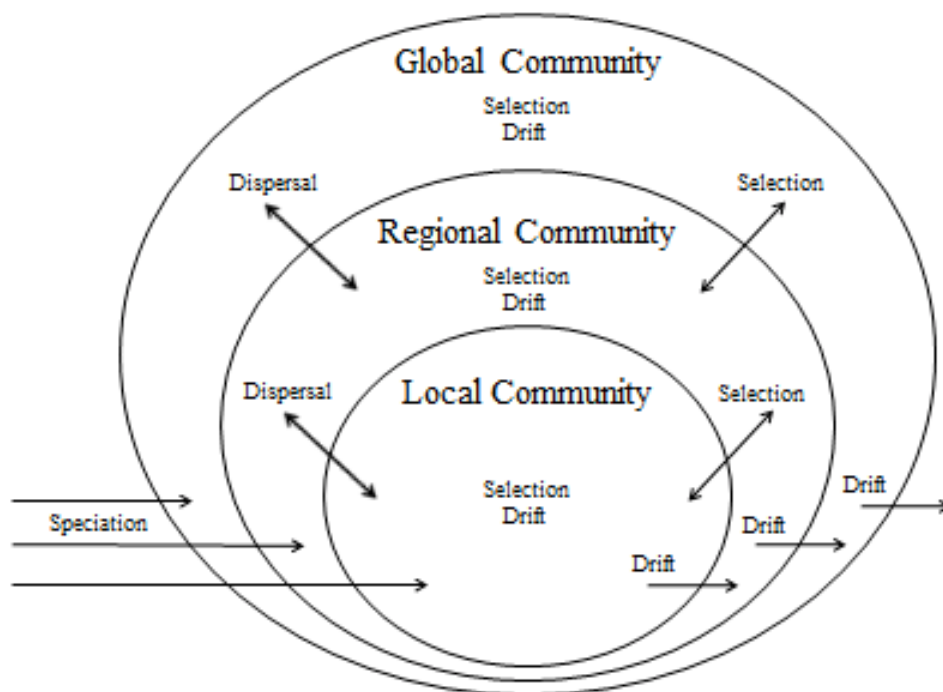
## 2.2 Vellend’s community ecology framework

The processes that generate and maintain EMF richness and/or diversity are the focus of a rapidly expanding literature, and are a matter for debate (Erland & Taylor, 2002; Kernaghan, 2005; Nemergut et al., 2013). Researchers have sought insights from areas including niche theory, island biogeography, and the species pool hypothesis (e.g., Erland & Taylor, 2002; Peay, Bruns, Kennedy, Bergemann, & Garbelotto, 2007; Talbot et al., 2014), but thus far a cohesive framework for investigating and understanding patterns of EMF diversity remains elusive. Below, I use Vellend’s (2010) framework for community ecology for this purpose.

**Table 1 Vellend’s four high-level processes for community assembly.**

Process	Description
selection	deterministic fitness differences between taxa affect abundance
dispersal	the movement of organisms across space introduces new taxa
speciation	the creation of novel species from existing species
drift	stochastic changes in species relative abundances

Vellend uniquely frames the processes that drive community assembly and biodiversity patterns by categorizing them into four “high-level” processes: selection, dispersal, speciation, and drift (Table 1). These processes drive community assembly by introducing new species (dispersal and speciation) and affecting their persistence and relative abundances (selection and drift) through time (Figure 1) (Vellend, 2010). Although this ecological framework wasn’t developed with EMF communities in mind, the same processes should also guide their assembly (Hanson et al., 2012; Nemergut et al., 2013). Under this framework, the different “high-level” processes may vary in their effect on community assembly and diversity depending on location. This makes it essential to understand all of these overarching processes. In the sections that follow, I use this conceptual framework to organize the hypothesized drivers of EMF diversity patterns.



**Figure 1 Vellend’s theory of community ecology.** Depiction of the relationship among “high-level” community assembly processes at various scales. Figure modified from Vellend (2010).

## 2.3 Drivers of EMF diversity under Vellend’s framework

### 2.3.1 Selection

#### 2.3.1.1 Abiotic selection

##### 2.3.1.1.1 Edaphic selection

The soil environment is incredibly important for the growth and diversity of EMF which live almost entirely belowground (Erland & Taylor, 2002). Not only does soil act as a medium for EMF growth, but it also contains important minerals and nutrients, water, plant roots, and other organisms which might affect EMF communities and diversity. Determining the impact of each edaphic (soil related) factor on EMF diversity can be difficult as many are correlated to each other, and/or with other factors such as bedrock type or precipitation.

The EM symbiosis likely evolved as an adaptation in plants to environments that were comparably more seasonal, dryer, and limited in nutrients (Malloch et al., 1980). Given that EMF evolved in response to limited soil nutrients and have been shown to improve host nutrient status in these conditions (Koide et al., 2014; Read & Perez-



Moreno, 2003), it is likely that soil nutrient availability is important in determining EMF community structure and diversity. Indeed, it has been shown that the symbiosis is more likely to occur when the plant is phosphorus or nitrogen limited (Treseder, 2004). Conversely, fertilizing a system has the potential to make the symbiosis unnecessary for EM plants (Johnson, Graham, & Smith, 1997). Due to this reliance, it seems reasonable to expect that EMF will persist at a higher abundance and diversity in low nitrogen or phosphorus soils.

The effect of nitrogen on EMF diversity has been studied in depth (Table 2). The overall consensus is that increasing soil nitrogen, whether natural or by fertilization, causes a change in community composition and has a negative impact on EMF diversity at many scales. Additionally, a meta-analysis by Treseder and colleagues (2004) found decreased colonization across studies under both nitrogen and phosphorus fertilization.

**Table 2 Described effects of nitrogen deposition on belowground EMF communities (modified from Suz et al., 2014).** Short-term fertilization experiments lasted 5 years or fewer. Gradient experiments occurred within one area across a gradient of nitrogen deposition.

Diversity	Community Composition	Study Type	Identification	Geographic Scale	Reference
no change	altered	short-term fertilization	molecular	single stand	Kårén & Nylund, 1997
no change	no change	short-term fertilization	morphological	single stand	Brandrud & Timmermann, 1998
no change	no change	short-term fertilization	molecular	single stand	Jonsson, Anders, & Tor-Erik, 2000
no change	altered	long-term fertilization	morphological	single stand	Fransson, Taylor, & Finlay, 2000
decreased	altered	gradient	morphological	regional to continental	Taylor et al., 2000
no change	altered	short-term fertilization	molecular	single stand	Peter, Ayer, & Egli, 2001
decreased	altered	gradient	molecular	local	Lilleskov et al., 2002
decreased	altered	long-term fertilization	molecular	single stand	Avis et al., 2003
decreased	altered	gradient	morphological	local	Dighton et al., 2004
decreased	altered	long-term fertilization	molecular	single stand	Edwards et al., 2004
decreased	altered	long-term fertilization	molecular	single stand	Parrent, Morris, & Vilgalys, 2006
decreased	altered	long-term fertilization	molecular	local	Avis, Mueller, & Lussenhop, 2008
decreased	altered	gradient	molecular	regional to continental	Cox et al., 2010
decreased	altered	gradient	molecular	single stand	Kjøller et al., 2012
decreased	altered	gradient	molecular	regional to national	Jarvis et al., 2013
decreased	altered	gradient	molecular	continental	Suz et al., 2014

While the effect of nitrogen on EMF diversity is relatively clear, the influence of phosphorus appears more complex. In one study, experimental increases in available phosphorus lead to reduced colonization by EMF as well as a reduced growth response in the associated EM plants (Jones et al., 1990). Similarly, experimental increases in phosphorus elicited reduced colonization by EMF (Aquino & Plassard, 2004). A field study by Erlandson and colleagues (2016) along a moisture and nutritional gradient found that increasing phosphorus was correlated to an increasing richness of EMF; however, plots with high phosphorus availability had nitrate (a form of plant available nitrogen) concentrations which were similar to low EMF richness plots. This suggests that the nitrogen limitation is strong enough, and even enhanced by the alleviated phosphorus limitation, to maintain or enhance the richness of EMF. In another study, the addition of phosphorus was found to decrease both above- and belowground biomass of EMF as well as hyphal length (Pampolina et al., 2002).

The ability of EMF to access nutrients is dependent upon enzyme activity and the production of other compounds (e.g., organic acids; Plassard & Fransson, 2009). In order for EMF to release these compounds, for those compounds to break down complex materials, and for absorption of those products, there needs to be water in the soil. While soil moisture is important for nutrient acquisition, it is also an imperative resource for the growth and survival of EMF. Though maintaining soil moisture is incredibly important for EMF, water saturated soils can cause stress from low oxygen availability (Tedersoo et al., 2012).

While some EMF taxa are able to improve host performance and thrive under drought conditions (Parke et al., 1983), most are generally unable to provide any benefit to, or receive any benefit from, their plant partners under these stressful conditions (Dosskey et al., 1991; Peay et al., 2007). Additionally, EM colonization has been shown to decrease when the plants and/or fungi are drought stressed (Gehring, Mueller, & Whitham, 2006; Swaty et al., 1998; Swaty, Deckert, Whitham, & Gehring, Catherine, 2004) which could lead to reduced diversity. This phenomenon has also been implicated as an important determinant of EMF community composition and diversity for a long time (Worley & HacsKaylo, 1959 as cited by Erland & Taylor, 2002). However, many of these pioneering studies relied on morphological identification of epigeous fungal

sporocarps to determine community structure. Problematically, fruiting generally occurs when soil moisture is high due to these sporocarps being particularly prone to desiccation as compared to belowground structures (Lilleskov et al., 2009). Therefore, aboveground diversity in response to soil moisture changes may be quite different than what is occurring below ground.

Recently, researchers have looked at belowground EMF community structure and diversity in relation to soil moisture (Erlandson et al., 2016; Toljander et al., 2006). Changes in soil moisture have been shown to have a significant impact on EMF community composition and distribution but not on species richness. Additionally, moisture gradients are confounded by productivity and chemical gradients, rendering causal processes difficult to discern. Clearly soil moisture is important in structuring EMF communities, but may play a secondary role to other factors when it comes to influencing species richness patterns.

As with soil moisture, pH can also play an important role in the activity of enzymes and the acquisition of nutrients by EMF. Fluctuations in pH can similarly affect organic compounds that make up EMF, making variation in pH influential. As pH decreases or soil acidity increases there tends to be a shift in the microbial community from bacteria to fungi (Rousk et al., 2009). This change in soil community also reduces bacterial activity causing reductions in nitrate (a form of plant available nitrogen) production (Lucas & Davis, 1961) which can in turn influence EMF diversity. Additionally, the solubility of many important nutrients is directly dependent upon pH. In acidic soils, the availability of many micronutrient cations is increased as hydrogen ions displace them from soil particles, thereby reducing the number of exchangeable cations and decreasing cation exchange capacity (CEC). Nitrogen availability is highest in soils with a pH of about 6-8 but is less sensitive to pH than phosphorus (McKenzie, 2003). Phosphorus availability is highest at a pH of approximately 5.5 or 6 – 7 or 7.5, being bound to calcium at more alkaline pH values or iron and aluminum at more acidic pH values making phosphorus less available (McKenzie, 2003). As discussed previously, an enhanced availability of phosphorus or nitrogen could cause a reduction in the diversity of EMF so pH values which enhance phosphorus and nitrogen availability (e.g., above 5.5/6) could indirectly reduce EMF diversity.

Ectomycorrhizal fungal communities have been found to respond to soil pH changes at the local scale in many studies (Agerer et al., 1998; Andersson & Söderström, 1995; Antibus & Linkins III, 1992; Bakker et al., 2000; Carrino-Kyker et al., 2016; Erland & Söderström, 1991; Fransson et al., 2000; Karén & Nylund, 1996; Qian et al., 1998; Taylor & Finlay, 2003; Wallander et al., 1997); however, across all of these studies just one found that pH had an effect on EMF richness or diversity (Taylor & Finlay, 2003). Taylor and Finlay (2003) found that liming the soil reduced EMF richness from 27 morphotypes in control areas (pH 3.00) to 16 morphotypes in limed areas (pH 2.68). Problematically, this outcome was only found in one study and the pH changes cover just a small range of the pH gradient. Overall, there does not appear to be any clear directional effect of soil pH on EMF richness or diversity. This may be a result of varying pH tolerances among EMF species (Carrino-Kyker et al., 2016; Kluber et al., 2012). Broad-scale studies have implicated pH as being an important predictor of EMF richness and colonization patterns though this is difficult to interpret given the variability of effect at the local scale (de Vries et al., 2012; Soudzilovskaia, Douma, et al., 2015; Suz et al., 2014; Talbot et al., 2014; Tedersoo et al., 2012, 2014).

Heavy metal contamination can be stressful for EMF and their hosts. Despite this, EM plants and EMF are able to occupy habitats contaminated by industrial heavy metal pollution. In fact, EMF are used in bioremediation efforts thanks to their ability to uptake toxic metals (Gadd, 2010; J. L. Hall, 2002). The direct effects that heavy metals have on the richness or diversity of EMF are less well studied, though toxic effects have been found (Dixon & Buschena, 1988). Additionally, studies have shown a reduction in fruiting body production in forests polluted by heavy metals, causing a reduction in EMF species (Rühling & Söderström, 1990). These aboveground effects may, however, not reflect belowground changes in diversity and EM activity. Belowground community compositional differences have been found between heavy metal rich and poor sites but with no differences in diversity (Hui et al., 2011; Op De Beeck et al., 2014; Southworth et al., 2014). Because heavy metals have been shown to have fungal toxic effects, there may still be a link between heavy metal pollution and EMF diversity.

Soil texture is another soil property that can affect EMF richness. Finely textured soils have greater water holding capacity, increased nutrient availability, and increased

particulate organic matter, each of which may influence EMF. Particulate organic matter contains nutrients that are unavailable to plants but can be extracted by EMF. The global study by Tedersoo and colleagues (2012) suggests that smaller soil particles, and therefore higher clay or silt content, have a positive effect on EMF richness. A similar pattern was found by de Vries and colleagues (2012); they found that a higher particulate organic carbon and greater fungal biomass were associated with the silt content of soil. A soil that can host a greater amount of fungal biomass has the ability to host a greater number of individuals and species than a habitat that can accommodate less biomass.

Soil characteristics mentioned above, such as texture, moisture, temperature, pH, and nutrient concentrations may vary across soil depths (Fierer et al., 2003). The depth of soil may be an important determinant of EMF diversity because of this increased vertical heterogeneity, increased rooting niche space, and increased soil and nutrient acquisition niche space (Dickie et al., 2002). Dickie and colleagues (2002) found that fungal communities differed between various layers of the soil profile (litter, fermentation, humus, and mineral (B-horizon) layers), suggesting niche differentiation along the vertical gradient. Additional studies have shown compositional shifts in EMF communities across soil horizons (Anderson et al., 2013; Bahram et al., 2014; Genney et al., 2006; Rosling et al., 2003; Tedersoo & Smith, 2013). The spatial partitioning of EMF communities across soil layers and horizons could lead to increased belowground diversity overall. However, sampling effort has been strongly biased towards the top 5-15cm of soil, and consistently so across ecosystems (Pickles & Pither, 2014), despite enormous variation in rooting depth (and thus habitat availability) among ecosystem types (Canadell et al., 1996; Pickles & Pither, 2014; Schenk, 2005; Schenk & Jackson, 2005). Thus, diversity patterns worldwide are poorly known at depths beyond 15cm.

A variety of predictive factors may have an overarching effect on some of the edaphic characteristics mentioned above. Firstly, parent material can influence the texture, nutrient status, and pH of soils. This is because soil is derived from parent material through weathering. If the bedrock is resistant to weathering, and is coarse grained, it will likely give rise to coarsely textured soils. If the parent material is composed of fine, unstable minerals that are readily weathered the resultant soil will likely be finely textured. The composition of the parent material can also impact soil

chemistry and nutrient status when weathered. When cations such as calcium, sodium, potassium, and magnesium are present in parent materials they can easily be liberated and dissolved into water. Limestone is one such material; as it loses these cations it will bind hydrogen ions in the soil and increase pH. Materials such as granite and sandstone that do not liberate these cations tend to produce more acidic soils due to reduced hydrogen binding.

#### **2.3.1.1.2 Climatic selection**

Climatic conditions such as rain and wind may mechanically weather parent material and should affect the processes mentioned above. While precipitation plays an important role in the weathering of parent materials, it also has effects on soil moisture that in turn affects soil properties, EMF, and hosts. A study by Richard and colleagues (2011) experimentally reduced rainfall on soil by 29% for 5 years. They found a significant shift in EMF community composition but no change in richness or diversity. The authors note that frequent climatic fluctuations naturally occur in the study area and might have selected for more drought tolerant EMF taxa. Swaty and colleagues (2004) looked at the long-term effect of drought on EMF and pinyon pine (an EM tree species). In sites where water stress and mortality was highest for hosts, EMF communities had pronounced shifts in composition, reduced species richness, and reduced colonization. While all sites lacked precipitation, the high mortality sites likely had higher air temperatures due to the slope of the site. This could have exacerbated the effects of reduced precipitation. It is likely that temperature and precipitation indirectly affect EMF through their effects on host plants.

Studies along elevation gradients have similarly found community compositional changes and/or higher EMF diversity at lower elevations where precipitation and temperature are moderate or high (Bahram et al., 2012; Jarvis, Woodward, & Taylor, 2015; Kernaghan & Harper, 2001; Miyamoto, Sakai, Hattori, & Nara, 2015; Rincón et al., 2015). Although elevation typically co-varies with temperature and precipitation, it may also co-vary with isolation: higher elevation communities may experience less immigration than lower elevation communities (Bahram et al., 2012; Peay et al., 2007). Thus, disentangling environmental effects from those related to dispersal is challenging.

Temperature has significant biological implications for EMF directly as it affects their enzyme activity and nutrient uptake. Increasing temperatures can indirectly influence EMF diversity through enhanced host plant photosynthesis, belowground carbon allocation, increased decomposition, and soil nutrient availability (Rustad et al., 2001). However, when temperatures become too high it can lead to soil drying, and reduced transpiration and photosynthesis in hosts. Temperature has been implicated as an important determinant of EMF diversity and composition at both small (Clemmensen et al., 2006; Deslippe et al., 2012; Timling et al., 2012) and large scales (Tedersoo et al., 2012, 2014). Deslippe and colleagues (2011) found increased diversity and pronounced compositional changes in EMF communities in a long-term warming experiment in the arctic. Similarly, Timling and colleagues (2014) found decreasing EMF richness with increasing latitude and decreasing temperatures in the arctic.

Among vegetation ecologists, it is widely accepted that the contemporary patterns of plant diversity are linked to historical selective factors in a number of ways. For instance, according to the evolutionary species pool hypothesis (Taylor, Aarssen, & Loehle, 1990) abiotic conditions (e.g., climate and soil conditions) or habitats that were most prevalent throughout the evolutionary history of the relevant lineages should, all else being equal, presently harbour the greatest richness of species. Pärtel (2002) provided evidence in support of this hypothesis: in a global analysis, he showed that the form of relationships between soil pH and plant species richness at local extents was determined by the evolutionary history of the regional flora: floras that evolved in areas where high soil pH was most prevalent exhibited a positive association between local plant richness and pH, whereas floras that evolved in areas of low soil pH exhibited negative associations (richness highest in low-pH conditions). This could be applied to EMF by relating the habitat conditions in their evolutionary history to contemporary relationships.

A separate historical legacy relates to the influences of climate oscillations and associated glaciation events (Dynesius & Jansson, 2000; Petit et al., 2004; Wiens & Donoghue, 2004). For affected regions, glaciation effectively resets diversity to zero for most terrestrial lineages. Thus, extra-tropical regions that have intermittently experienced glaciation are, all else being equal, expected to exhibit lower richness than regions that



have never experienced glaciation (e.g., tropics). Across North America, EMF richness may therefore be expected to increase with increasing time since glaciation, despite their origins in temperate environments. Alternatively, if EMF readily co-evolve in situ (see below), and/or can persist in situ via resistant propagules (such as sclerotia and spores; (Pither & Pickles, in review), then locations that have experienced varied conditions through time could exhibit greater species richness thanks to a “time-integrated” diversity effect (Pither & Pickles, in prep). EMF richness may therefore be expected to increase with increasing habitat heterogeneity in time. This can be viewed in multiple ways, including the velocity of climate change (Loarie et al., 2009; Sandel et al., 2011).

### **2.3.1.2 Biotic selection**

Hosts are arguably the most important determinant of EM fungal presence and diversity. EM fungi rely on their hosts to provide them with photosynthetic carbohydrates that are extremely important for growth and reproduction. Host identity and diversity have been heavily implicated as important predictors of EMF diversity due to their relationship with specificity and preference at the individual and community levels. Ishida and colleagues (2007) demonstrated that taxonomically related host species harbored similar communities of EMF. They also observed a tendency towards higher specificity at the host family level with community dissimilarity being greater between host families than lower taxonomic levels. Therefore, having a greater diversity of hosts (at the family level) had a positive impact on EMF diversity. Gao and colleagues (2013) similarly demonstrated the impact of host specificity on EMF diversity. However, they found a strong correlation between the genus level diversity of hosts and EMF diversity. EM plant species richness also appears to have a positive effect on EMF richness across studies (Dickie, 2007) (Table 3). While EM plant diversity may affect EMF diversity directly through specialization differences, plant diversity can also indirectly affect EMF diversity through impacts on the range of organic substrates entering the soil (Kernaghan et al., 2003). These varying inputs can create more nutritional niche space to host a greater diversity of EMF (Waldrop et al., 2006).

**Table 3 Described effects of increasing host richness on belowground EMF communities.**

Diversity	Community Composition	Study Type	Identification	Geographic Scale	Reference
increased	altered	between forests	morphological	local	Heslin et al., 1992
increased	altered	between forests	morphological	local	Jones et al., 1997
increased	altered	within forest	morphological	local	Kernaghan et al., 2003
not tested	altered	between forests	molecular	local	Ishida et al., 2007
increased	altered	between forests	molecular	local	Peay et al., 2010
increased	altered	within forest	molecular	local	Gao et al., 2013
increased	altered	within forest	molecular	local	Nguyen et al., 2016

Host age and succession may also have an impact on EMF diversity because of their relationship with conditions such as canopy closure, host density, productivity, and nutrient status. Early studies of EMF diversity along forest chronosequences found enhanced richness or diversity of sporocarps with stand age (Kranabetter et al., 2005; Rao et al., 1997; Visser, 1995). However, the gradients reviewed were lacking completeness and could have missed key stand ages in terms of EMF community and diversity changes. These studies focused on stands younger than 17 years only (Rao et al. 1997), older than 20 years only (Kranabetter et al., 2005), or had a large breadth of focus from 6-122 years but with gaps of 35 or more years between some sites (Visser, 1995). Additionally, aboveground sporocarp diversity may not reflect belowground diversity. Palfner *et al.* (2005) and Gebhardt *et al.* (2007) looked at EMF belowground diversity along chronosequences of similar lengths, with no sites greater than 43 years of age. Both found EMF diversity increased with increasing tree age, though Palfner *et al.* found that diversity levelled off in 30 and 40 year old stands. Similarly, Twieg and colleagues (2007) found that EMF belowground diversity increased with stand age and began to level off between 26 and 65 year old stands. They found that the greatest increase in diversity occurred between stands aged 5 and 26 years corresponding to tree canopy closure with only slight increases in diversity as stands got older. Canopy closure occurs because of rapid tree growth rates and increased leaf area. As the trees increase in biomass and productivity belowground systems are enhanced as well with higher root growth and increased carbon allocation to roots and EMF (Twieg et al., 2007). Enhanced

carbon flow to EMF and increased root niche space associated with canopy closure could enhance EMF diversity. Lastly, a study by LeDuc and colleagues (2013) looked at belowground EMF diversity on sites aged 5-56 with no more than 24 years between any two sites. They found rapid increases in diversity between 5 and 19-year-old sites prior to canopy closure with little increase in diversity with subsequent increases in stand age. Additionally, they found that a successional reduction in plant available nitrogen was associated with the community changes in EMF.

Land cover could also play a role in EMF diversity patterns due to changes in host density, host diversity, shifts from ecto- to arbuscular mycorrhizal plants, and urbanization. The various land cover types utilized by the United States Geological Survey (USGS) Land Cover Institute are outlined in Appendix A (Table 9). Mixed forests are a mixture of the evergreen and coniferous forest types that could enhance host diversity and increase EMF richness. Evergreen and coniferous forest types have dominantly woody vegetation with higher percent cover that could support a greater richness of EMF. Closed shrublands and woody savannas have woody vegetation and medium to higher percent cover that could support a high richness of EMF. Open shrublands and savannas have woody vegetation at low percent cover that could support average EMF richness. Cropland/natural vegetation mosaics could include any vegetation types so could support anywhere from low to high EMF richness. Grasslands have mostly herbaceous cover with minimal woody vegetation cover that could support lower EMF richness. Permanent wetlands have some woody vegetation but very high moisture that could likely waterlog soils and cause decreased EMF richness. Croplands do not include any perennial woody crops and are likely dominated by arbuscular mycorrhizal vegetation and probably wouldn't support EMF taxa unless hosts were present. Urban built-up lands, snow and ice, and barren lands are not vegetated and therefore have no EM plants and would support no EMF taxa. Some EMF may be present in these areas where refugia exist at scales smaller than the land cover data sets.

Just as historical abiotic selective processes may impact contemporary EMF richness patterns, so might historic biotic selective processes. As described above, if EMF are able to persist within soils for long periods of time and remain viable (Pither & Pickles, in review), then landscapes that have been historically biotically heterogeneous

should contribute to enhanced contemporary richness. One way I include this is by utilizing climate velocity since the last glacial maximum. Climate velocity is a measure of the local rate that climatic conditions are displaced over geographic space (Loarie et al., 2009; Sandel et al., 2011). This can help to measure climatic heterogeneity through time, which would likely be tied to heterogeneity in other environmental factors. One way to test historical heterogeneity that I was unable to look at, is to evaluate the historic distributions of hosts (Pither & Pickles, in prep), and to integrate host richness through time at each location. Locations that, through time, have hosted a greater number of different host species should exhibit more diverse EMF assemblages.

### **2.3.2 Dispersal**

At small scales dispersal is limited by wind direction and strength (Galante et al., 2011), presence of fauna that eat EMF and disperse spores (Johnson, 1996), and host density (Peay et al., 2010, 2012). Host density may have an impact on EMF richness, particularly because EMF tend to be dispersal limited and thus have a low probability of successfully dispersing among hosts that are far apart (Peay et al., 2010, 2012). Fungal propagules become less likely to reach EM seedlings as distance increases, resulting in reduced EMF species richness and host colonization (Peay et al., 2012; Peay & Bruns, 2014). Similarly, the diversity and abundance of fungivorous animals and the sizes of their ranges could influence the dispersal of EMF but would be much more difficult to quantify.

At larger scales there appears to be a degree of EMF endemism which indicates geographic dispersal barriers (Talbot et al., 2014). Additionally, this endemism may be the result of historic co-dispersal of EMF with their hosts since the last glacial maximum (Pöhlme et al., 2013).

### **2.3.3 Speciation**

The process of speciation is fundamental to understanding the contemporary biogeographic patterning of communities. Unfortunately, our understanding of EMF evolution is limited. We know they have evolved multiple times from saprotrophic ancestors (Hibbett et al., 2000; Kohler et al., 2015; Tedersoo et al., 2010). It also appears that co-evolutionary processes between EM plants and fungi has produced a degree of evolutionary stability in the symbiosis (van der Heijden et al., 2015). However, dormancy

of EMF spore banks could contribute to genetic diversity and richness in space and time. EMF propagules that are able to remain dormant for long periods of time could link historic communities to contemporary communities (Pither & Pickles, in review) and increase local richness estimates regardless of biotic and abiotic conditions.

#### **2.3.4 Drift**

Stochastic changes in the relative abundance of individuals within a community, or ecological drift, is unlikely to be a process of major importance in most places or times but can still be an important contributor to community assembly and diversity (Vellend, 2010). Specifically, drift appears to be of greater importance when selection is weak and the community is small (Vellend, 2010). There are many examples of rare taxa being present in EMF communities, and even being more prevalent (in species richness) than common taxa (Horton & Bruns, 2001). These rare taxa may be susceptible to drift as chance events can more easily result in their extinction or extirpation. The geographic scale at which this occurs is entirely dependent on the scale at which the taxon of interest is rare. If a species is globally rare then drift can elicit the absolute extinction of the taxon across scales, but if the species is only rare locally then it may be extirpated but still present regionally and globally. One caveat is that rare taxa may be present in dormant states that could prevent their extinction.

Additionally, drift should be increasingly important through time, as there are more opportunities for these stochastic events to occur. As time passes some species become extirpated and allow new species to take their place. This may be due to deterministic selective pressures, stochastic drift, or a combination of the two. In EMF communities, this turnover of species can be measured. For example, the entire EMF extramatrical mycelial standing biomass in one forest completely turned over in 10 years (Wallander et al., 2004). Ten years may not have been long enough to see drastic changes in selective pressures which indicates that there is at least some stochasticity or drift involved. In this instance, drift has certainly acted to change the community but may or may not affect richness depending on the species that are present after turnover. This is because other processes, mainly selection combined with dispersal, are acting to combat stochastic extirpation and constantly reintroduce species into communities.

## 2.4 Summary

Upon reviewing the literature for processes that have been hypothesized to influence EMF biodiversity at various scales I was able to uncover distinct gaps in the current knowledge. I was able to do this by organizing these hypotheses in relation to scale and within Vellend's (2010) framework for community. Importantly, many of the hypothesized predictors are local-scale, contemporary, and fall within the process of selection (see section 2.3.1) of Vellend's framework. This indicates that there is a need to consider the effects of more historic and biogeographic factors as well as predictors that fall within the processes of dispersal, speciation, and drift. I attempt to fill some of these gaps by introducing additional factors that might influence EMF diversity across scales. The first factor is climate velocity, which measures the local rate that climate conditions are displaced over geographic space and can help to measure climatic heterogeneity through time. Because climate velocity is related to climatic conditions and can impact other environmental characteristics it fits within the process of selection. The impact that climate velocity has on shifting environments and communities in time and space could also contribute to the process of dispersal. Additionally, because climate velocity looks at change in climate over time, it could impact temporally driven factors that fall within the processes of drift and/or selection. The second factor that I included is glaciation history as it can similarly impact the processes of selection, dispersal, speciation, and drift due to shifting environmental conditions in time and space.

The literature review also indicates inconsistencies regarding some of the factors hypothesized as affecting EMF richness or diversity. Particularly, factors such as soil phosphorus (Aquino & Plassard, 2004; Erlandson et al., 2016; Johnson et al., 1997; Jones et al., 1990; Pampolina et al., 2002; Treseder, 2004) and pH (Agerer et al., 1998; Antibus & Linkins III, 1992; Carrino-Kyker et al., 2016; de Vries et al., 2012; Erland & Taylor, 2002; Kluber et al., 2012; Soudzilovskaia, Douma, et al., 2015; Suz et al., 2014; Talbot et al., 2014; Tedersoo et al., 2014, 2012), which are often described as important in structuring EMF communities, have inconsistent effects on EMF richness or diversity (Table 4) within the literature. Additionally, predictors like rooting depth that have been indicated to have relatively consistent effects on EMF diversity (Table 4) are often overlooked in large-scale studies, particularly when choosing sampling depths. For

example, the global sampling effort by Tedersoo and colleagues (2014) used a sampling depth of 5cm across sampling locations.

**Table 4 The factors hypothesized as driving EMF richness or diversity belowground, the direction of their effect, and consensus within the literature.**

Factor	Putative Direction of Effect	Putative Form of Association	Citations in Agreement
host richness	positive	linear	Gao et al., 2013; Ishida et al., 2007; Jones et al., 1997; Kernaghan et al., 2003; Nguyen et al., 2016; Peay et al., 2010
host age	positive	log-linear	Gebhardt et al., 2007; LeDuc et al., 2013; Palfner et al., 2005; Twieg et al., 2007
host density	positive	linear	Peay et al., 2010, 2012
land cover	depends on cover type	N/A	N/A – related to host richness and density
rooting depth	positive	linear	Anderson et al., 2013; Bahram et al., 2014; Dickie et al., 2002; Genney et al., 2006; Rosling et al., 2003; Tedersoo & Smith, 2013
phosphorus	negative	linear or log-linear	Pampolina et al., 2002
pH	unimodal or negative	unimodal	no clear consensus on the effects on richness or diversity belowground – Taylor & Finlay, 2003
heavy metals	negative	unclear	no described effects on richness or diversity belowground
soil texture	depends on texture	N/A	no clear consensus on the effects on richness or diversity belowground – de Vries et al., 2012; Tedersoo et al., 2012
carbon/nitrogen ratio	positive	linear or log-linear	Avis et al., 2003, 2008; Cox et al., 2010; Dighton et al., 2004; Edwards et al., 2004; Jarvis et al., 2013; Kjølner et al., 2012; Lilleskov et al., 2002; Parrent et al., 2006; Suz et al., 2014; Taylor et al., 2000
moisture	unimodal or positive	unimodal, linear, or logarithmic	no described effects on richness or diversity belowground
CEC	positive	unclear	N/A – related to soil texture
MAT	unimodal or positive	unimodal, linear, or logarithmic	Deslippe et al., 2011; Timling et al., 2014
MAP	unimodal or positive	unimodal, linear, or logarithmic	Swaty et al., 2004 – may be related to hosts
climate velocity	positive	linear	no studies on the effects on EMF
glaciation	positive	linear	no clear consensus on the effects on richness or diversity belowground – Timling et al., 2012



## Chapter 3: Methods

### 3.1 Habitat suitability models

Habitat suitability models (HSMs) are scoring indices used widely for many purposes in conservation, biogeography, and ecology (Elith & Leathwick, 2009). Their uses include quantifying environmental niches, modeling biodiversity, conservation and management planning, and predicting the impacts of climate change and other anthropogenic stressors (Guisan & Thuiller, 2005). HSMs use species-habitat relationships to predict species distributions statistically or theoretically (Guisan & Zimmermann, 2000).

Commonly, empirical, statistical techniques are utilized to estimate habitat suitability based on species presence and absence. This is done by relating local estimates of species richness or occurrence to site specific habitat factors and using statistical techniques such as generalized regression models, ordination, or classification trees to generate a model (Guisan & Zimmermann, 2000). The resulting model is then used to extrapolate presence or richness into unsampled geographic regions. When data are limiting, qualitative literature- or niche-based models can be constructed and can yield valuable information and predictions (e.g., Shafer, Swannack, Saltus, Kaldy, & Davis, 2016). While the accuracy of quantitative models varies depending on a variety of methodological factors, they are usually preferred over qualitative models, data permitting.

Recently researchers describing the broad-scale patterns of EMF richness have utilized statistical techniques to extrapolate local richness or other community estimates across spatial scales (e.g., de Vries et al., 2012; Peay et al., 2015; Roy et al., 2013; Soudzilovskaia, van der Heijden, et al., 2015; Suz et al., 2014; Talbot et al., 2014; Tedersoo et al., 2012, 2014). Because considerable sampling effort is required to achieve thorough estimates of species richness at local scales, a substantially large number of these local studies would be required to understand broad-scale patterns and make predictions about unsampled regions. Here I use a niche-based habitat suitability model (*sensu* U.S. Fish and Wildlife Service, 1981), which is preferred when data is limiting, to make predictions about the richness patterns of EMF in Canada and the United States of America.

### 3.2 GIS data layers

First, I reviewed the literature for papers discussing the effect of various habitat factors on EMF richness (see Chapter 2). Among the articles reviewed, the direction and magnitude of the functional relationship with richness or community composition, geographical scale, and method of identification were compiled. Additionally, promising references in these papers were also reviewed if available. For each predictor, relevant North American or global datasets were acquired from various sources as two dimensional data layers that can be layered or overlapped with one another (see Appendix B). The datasets or layers used in this study included land cover, host species distributions, soil characteristics, climatic variables, and glaciation history. Table 5 describes how each of these datasets relates to the factors reviewed in Chapter 2. Not all factors could be represented in the model, as they lacked sufficient data (e.g., heavy metal pollution) or geographical coverage (e.g., stand age, tree density, and available phosphorus).

**Table 5 The factors included in the habitat suitability model and the hypothesized direction of their effect on EMF diversity or richness.**

<b>Factor</b>	<b>Direction of Effect</b>
host richness	positive
land cover	dependent on cover type
rooting depth	positive
carbon/nitrogen ratio	positive
moisture	positive
CEC	positive
MAT	positive
MAP	positive
climate velocity	positive
glaciation	negative

I obtained digital representations of tree species range maps from the USGS Geosciences and Environmental Change Science Center (1999) as shapefiles. These maps include 679 species of native woody plants defined as ‘trees’ according to Little (1971). The ectomycorrhizal status for each species was determined by first assessing the mycorrhizal associations listed by Brundrett (2009). For remaining uncertainties, other association lists (Phillips et al., 2013; Wang & Qiu, 2006) were consulted followed by a review of the relevant literature. If the mycorrhizal status was not available at the species

level then genus or, occasionally, family level associations were utilized. A total of 241 tree species were designated as EM. The range data for each species was converted to a raster format with a resolution of 5 arc minutes. Each data set was stacked on top of one another to determine the number of species ranges in any given cell. Next, the host richness data was normalized to a scale of 0.01-1 representing a Suitability Index (SI) ranging from least to most suitable for EMF richness (Table 5). Hosts act as a selective force, while host richness can affect the process of dispersal (Table 6).

I then obtained a land cover map from the USGS Land Cover Institute (Broxton et al., 2014) as a raster at a resolution of 15 arc seconds. The raster was then aggregated by a factor of 20 to achieve a resolution of 5 arc minutes. This essentially combines 20 cells into 1 cell. In order to do this, the most common input cell value was given to the output cell to preserve the data format. Land cover suitability was reclassified based on information presented in Chapter 2 (section 2.3.1.2). Values were reclassified on a scale of 0.01-1 representing a SI ranging from least to most suitable for EMF richness. Mixed forests were given a value of 1 being the most suitable for EMF richness; other forest types were given a value of 0.9, closed shrublands and woody savannas were given a value of 0.7, open shrublands and savannas were given a value of 0.5, cropland/natural vegetation mosaics were given a value of 0.3, grasslands were given a value of 0.1, permanent wetlands, croplands, urban built-up lands, snow and ice, and barren lands were given a value of 0.01 being the least suitable for EMF richness. Land cover is related to vegetation so it also acts as a selective force and can affect the process of dispersal (Table 6).

Next, I obtained soil characteristics of carbon-to-nitrogen ratio and CEC for soils at a depth of 0-20cm from the International Soil Reference and Information Centre (Batjes, 2009) as rasters at a resolution of 5 arc minutes. Monthly soil available water capacity from the years 1900-2014 was obtained from the University of Delaware's Center for Climatic Research (Matsuura & Willmott, 2015) as raster data at a resolution of 30 arc minutes. For each year, soil moisture was averaged across months. Then, these yearly averages were averaged together across the 115 years to produce one value of soil moisture for each raster cell. The data was then disaggregated by a factor of 6 to achieve a higher raster resolution of 5 arc minutes. This essentially splits one cell into 6 cells,

each with the same value as the original. Next, each soil characteristic was normalized to a scale of 0.01-1 representing a SI ranging from least to most suitable for EMF richness (Table 5). Soil characteristics act as selective forces (Table 6).

I obtained rooting depth, given as the soil depth (meters) that contains 95% of all roots from International Satellite Land-Surface Climatology Project, Initiative II (Schenk & Jackson, 2009) as a raster at a resolution of 60 arc minutes. The raster was disaggregated by a factor of 12 to achieve a resolution of 5 arc minutes. This essentially divides 1 cell into 12 cells. In order to do this, the input cell value was given to all of the output cells. Next, the rooting depth data was normalized to a scale of 0.01-1 representing a SI ranging from least to most suitable for EMF richness (Table 5). Rooting depth acts as a selective force (Table 6).

Next, I obtained the current mean annual temperature (MAT) and mean annual precipitation (MAP) from WorldClim (Hijmans et al., 2005) as rasters at a resolution of 5 arc minutes. Rasters of the velocity of MAT and MAP change were produced using present and historical values at the last glacial maximum for MAP and MAT from WorldClim using a method from Sandel and colleagues (2011). Next, each climate data set was normalized to a scale of 0.01-1 representing a SI ranging from least to most suitable for EMF richness (Table 5). Temperature and precipitation act as selective forces, while their velocity can measure selection, dispersal, speciation, and drift (Table 6).

Lastly, I obtained information about the glaciation history of North America since the last glacial maximum from the Geological Survey of Canada (Dyke et al., 2003) as shapefiles depicting glacial extent every thousand years since approximately 18,000 years before present. The shapefiles were converted to rasters at a resolution of 5 arc minutes and stacked on top of one another to determine the length of time that any given cell has been glaciated for. Next, the glaciation data was normalized to a scale of 0.01-1 representing a SI ranging from least to most suitable for EMF richness (Table 5). Glaciation history can be a measure of selection, dispersal, speciation, and drift (Table 6).

For all of the mentioned datasets, data were normalized using feature normalization or min-max scaling (Aksoy & Haralick, 2001). For variables hypothesized to have a positive relationship with EMF diversity (e.g., MAT in Table 5), the following

formula was used to directly rescale the range of values to 0.01-1:

$$x' = 0.01 + \frac{(x-x_{\min})(1-0.01)}{x_{\max}-x_{\min}}$$

where  $x$  is the original value and  $x'$  is the normalized value.

This formula ensures that the maximum and minimum values of the original data set are maintained as the maximum and minimum values for the normalized data set. For variables hypothesized to have a negative relationship with EMF diversity (e.g.,

glaciation in Table 5), the following formula was used to inversely rescale the range of

values to 0.01-1:  $x' = 0.01 + \frac{(x_{\max}-x)(1-0.01)}{x_{\max}-x_{\min}}$ . This formula ensures that the minimum

and maximum values of the original dataset become the maximum and minimum values, respectively, of the normalized data set.

**Table 6 The factors included in the habitat suitability model and how they relate to Vellend’s community ecology framework.**

Factor	Selection	Dispersal	Speciation	Drift
host richness	x	x		
land cover	x	x		
rooting depth	x			
carbon/nitrogen ratio	x			
moisture	x			
CEC	x			
MAT	x			
MAP	x			
climate velocity	x	x	x	x
glaciation	x	x	x	x

### 3.3 Representing functional relationships

The suitability of a given area for EMF richness (Habitat Suitability Index) was determined by combining the SI for each factor in a variety of ways. This was done using a multi-criteria approach, first classifying the predictive factors into four distinct categories from the literature review: contemporary biotic, contemporary edaphic, contemporary climatic, and historic (“Categories” in Table 7) (*sensu* Gorsevski, Donevska, Mitrovski, & Frizado, 2012; Hossain & Das, 2010; Miller, Collins, Steiner, & Cook, 1998; Store & Kangas, 2001). By sorting the predictive factors in this way it simplifies the weighting process and the specific categories used ensure that no factor fits under multiple categories as in Vellend’s framework of Table 6. For example, no factor

can be considered as both ‘biotic’ and ‘abiotic’ while a factor can be considered as both ‘selection’ and ‘dispersal’. Within each category the factors were weighted according to the literature consensus on their importance (“Factor Weightings” in Table 7). Next, varied weightings were given to the categories that each variable fell under using four different weighting scenarios (“Category Weightings by Scenario” in Table 7) (*sensu* Svoray, Bar, & Bannet, 2005).

The first scenario weights each category based on the number of factors that it includes (“Even” in Table 7). This way, each factor would get an even weighting in the entire model if it was of equal importance to all other factors in its category. This scenario assumes that no higher-level processes are at work. The next scenario weights each category based on its contribution to the four high-level processes of Vellend’s framework (“Vellend’s Framework” in Tables 5). Each high-level process is given an equal weighting of 0.25. In order to achieve this under the categories in Table 7, the relative contribution of each category to Vellend’s four processes is considered. Firstly, the historic factors of climate velocity and glaciation are the only factors that contribute to speciation (0.25/0.25) and drift (0.25/0.25), half of the factors that contribute to dispersal (0.125/0.25), and 1/5 of the factors that contribute to selection (0.05/0.25). For this reason, they are given an overall weighting of 67.5% (Table 7). The biotic category contributes to 1/2 of dispersal (0.125/0.25) and 3/10 of selection (0.075/0.25), giving an overall weighting of 20% (Table 7). The edaphic category contributes to 3/10 of selection (0.075/0.25), giving an overall weighting of 7.5% (Table 7). Lastly, the climatic category contributes to 1/5 of selection (0.05/0.25), giving an overall contribution of 5% (Table 7). The next scenario weights each category based on its contribution in the EMF literature (“Literature” in Table 7). The last scenario weights each category based on its contribution to broad-scale richness patterns in the vegetation literature; these are the large-scale and historic predictors that are often sidelined in the EMF literature (“Large-scale and Historic” in Table 7).

**Table 7 The weighting of various predictive factors used to determine EMF habitat suitability.** The predictive factors are given individual factor weightings within four distinct categories based on their consensus within the EMF literature, or vegetation literature for the historic category. These four distinct categories are then weighted based on four hypothesized scenarios of EMF community assembly and richness.

Category Weightings by Scenario						
Categories	Even <sup>i</sup>	Vellend's Framework <sup>ii</sup>	Literature <sup>iii</sup>	Large-scale and Historic <sup>iv</sup>	Factors	Factor Weightings
contemporary biotic	0.3	0.2	0.4	0.2	host richness	0.7
					land cover	0.2
					rooting depth	0.1
contemporary edaphic	0.3	0.075	0.4	0.05	C/N	0.8
					moisture	0.1
					CEC	0.1
contemporary climatic	0.2	0.05	0.2	0.375	MAT	0.5
					MAP	0.5
historic	0.2	0.675	0	0.375	climate velocity	0.5
					glaciation	0.5

<sup>i</sup> each “low-level” factor is weighted within broad categories of contemporary biotic, contemporary edaphic, contemporary climatic, and historic only

<sup>ii</sup> each “low-level” factor is weighted within categories and by the number of Vellend’s “high-level” processes they fall under

<sup>iii</sup> each “low-level” factor is weighted within categories and each category is weighted by it’s prevalence within the EMF literature

<sup>iv</sup> each “low-level” factor is weighted within categories and each category is weighted by it’s contribution to broad-scale richness patterns in the vegetation literature

<sup>v</sup> All four scenarios are averaged together

### 3.4 Building the model

Suitability maps were created using map algebra. This involves overlaying the edited, normalized rasters for all predictive variables and applying a cell-by-cell formula that calculates the weighted average of all input rasters. This was done for each pixel to give the average SI of each raster cell. The weighted average was calculated for each of the four scenarios outlined in Table 7 in order to produce four different HSMs. For example,

$$SI_{\text{Even}} = 0.3(0.7(\text{host richness}) + 0.2(\text{land cover}) + 0.1(\text{rooting depth})) + 0.3(0.8(\text{C/N}) + 0.1(\text{moisture}) + 0.1(\text{CEC})) + 0.2(0.5(\text{MAT}) + 0.5(\text{MAP})) + 0.2(0.5(\text{climate velocity}) + 0.5(\text{glaciation})).$$

### 3.5 Testing sensitivity of the model to weighting schemes

The HSMs for each scenario were stacked on top of one another and map algebra was used to calculate the average suitability value across all maps for each cell. The output map represents the average habitat suitability across all models. Next, the same

method was used to calculate the standard deviation of each cell across all maps in order to determine the consistency of predicted richness patterns across models (consistency across models is highest when the standard deviation is low). Lastly, the ratio of the average suitability to the standard deviation was calculated for each cell to determine areas that are consistently predicted to host high richness across models. The log of the ratio of the average suitability to the standard deviation was taken as the values were skewed.

### **3.6 Evaluating the correspondence between model predictions and empirical data**

Estimates of EMF richness for sites were obtained from recent meta-analyses of EMF at global or continental (North America) scales if available (estimates were only available from Tedersoo et al., 2012, 2014). A total of 32 North American sampling locations and richness estimates were obtained from these two global studies (Appendix A: Table 9). The ranks of the empirical richness estimates were evaluated against the ranks of the model predicted richness values. This was done by using a Spearman rank correlation because the model outputs are ranked, and thus don't conform to Pearson assumptions. A significance level of  $\alpha = 0.05$  was chosen so as to have a low risk (5% chance) of validating my model (correlation between the data sets) when it is not actually valid. If the data sets are correlated then Spearman's rho should be close to 1.

### **3.7 Evaluating geographical gaps in sampling**

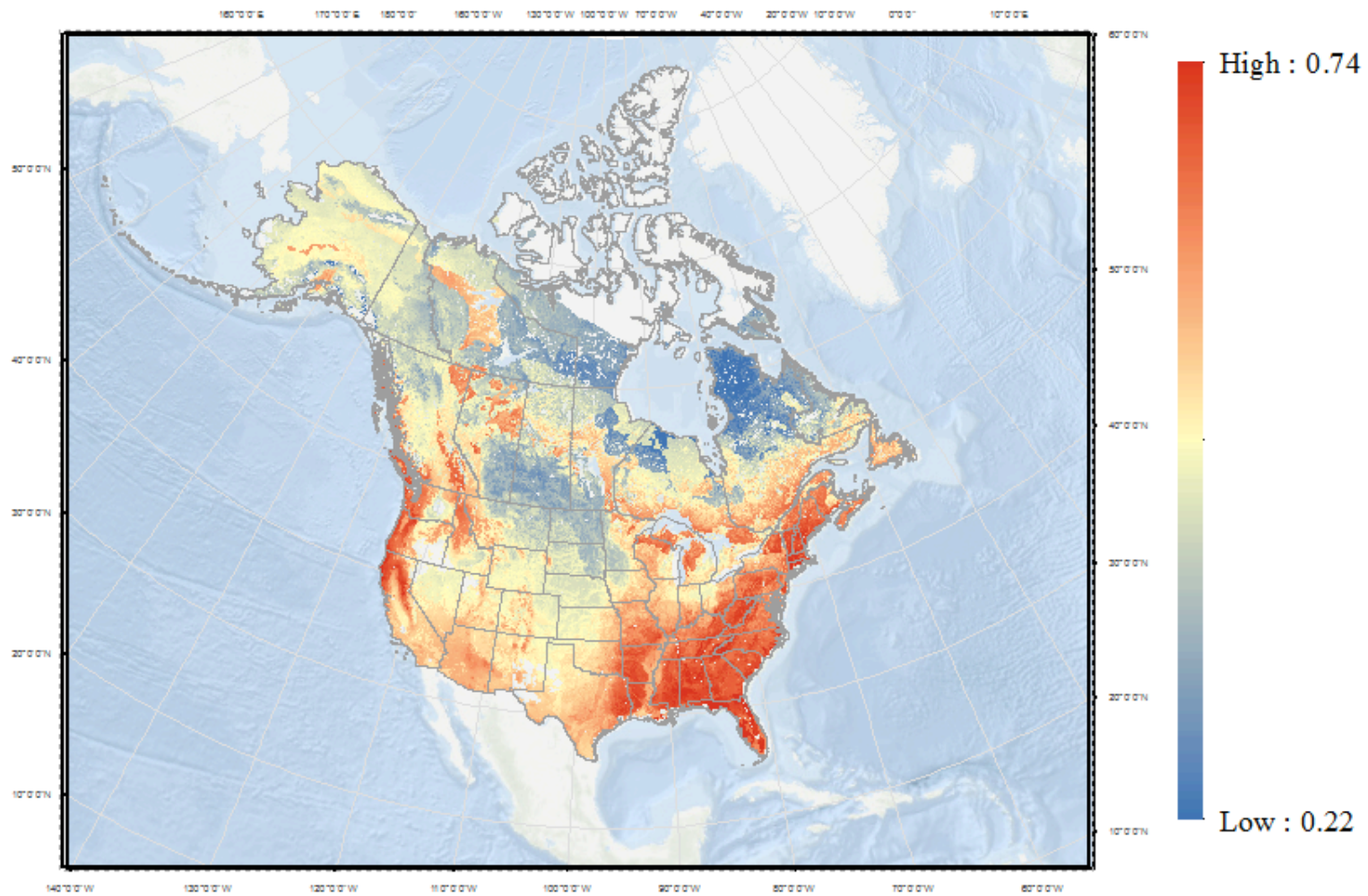
The sampling intensity of recent broad-scale analyses of EMF at global or continental (North America) scales was reviewed. These broad-scale studies were utilized as they contained large amounts of sampling information within one study. Location data could be obtained from other local scale studies with a more intensive, time-consuming review. From the studies reviewed, site location data were obtained. These data were available as latitude and longitude coordinates in decimal degrees from Soudzilovskaia and colleagues (2015) and Tedersoo and colleagues (2012, 2014), and as UTM northing and easting in meters from Talbot and colleagues (2014). All of these data were then overlaid on the averaged HSM and used to compare sampling intensity to predicted patterns of EMF richness. By overlaying sampling locations on the richness suitability map, I can determine if key geographical gaps exist among studies.



## **Chapter 4: Results**

### **4.1 Model outputs**

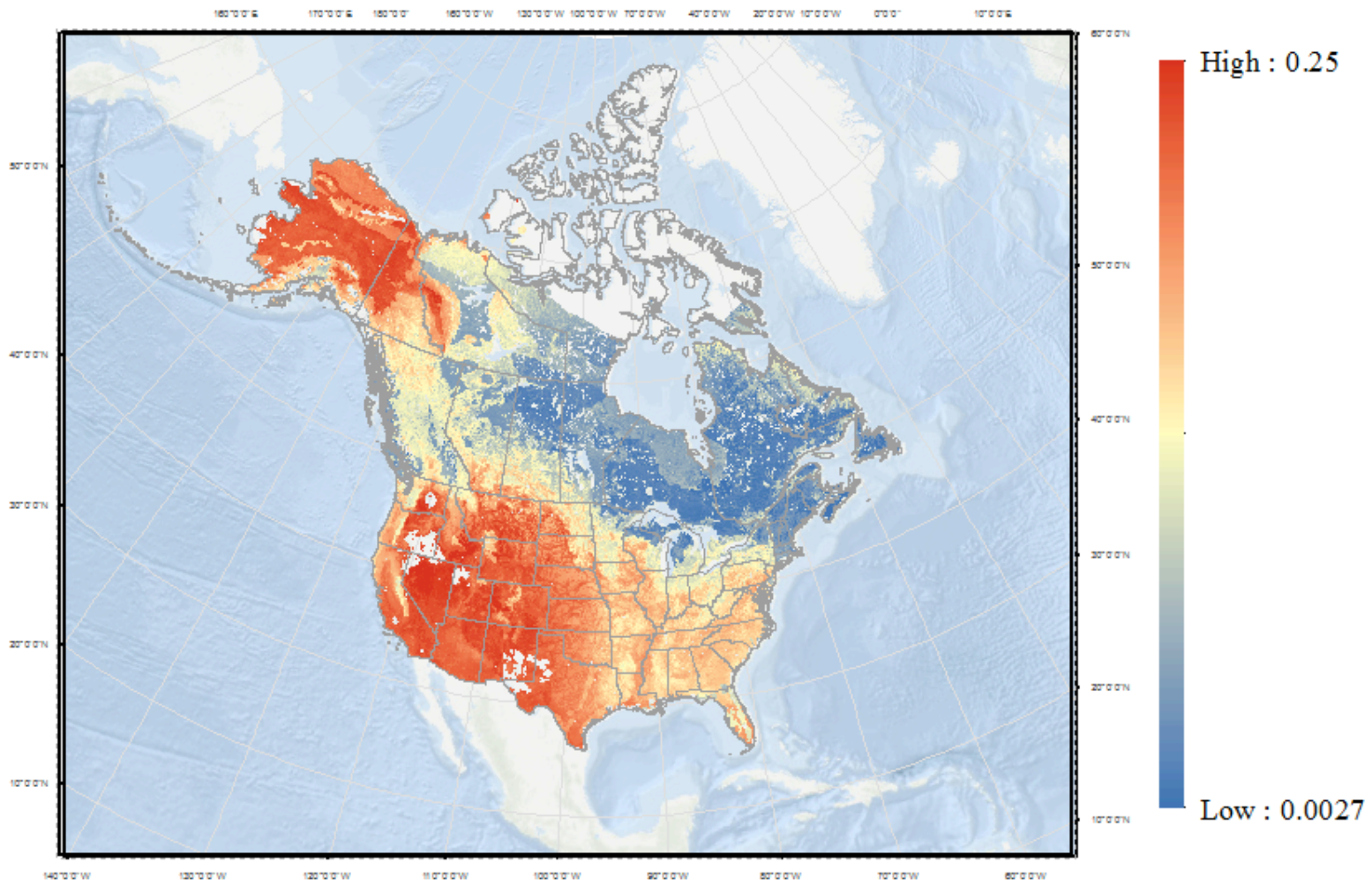
Maps depicting the predictions from each weighting scenario are presented in full within Appendix A (Figures 6-9). Figure 2 below shows the average prediction across scenarios. In this averaged prediction of habitat suitability, approximately 31% of the study area was assigned a predicted richness higher than 0.5 and had average or above-average predicted richness. The highest diversities are predicted within parts of temperate forests across Canada and the USA and parts of the boreal forests in Canada (Figure 2). The factors that correlate significantly with the average habitat suitability map (Figure 2) are climate velocity and hosts (Figure 10).



**Figure 2** The average habitat suitability for the richness of EMF across model types. Values represent the likelihood for hosting EMF richness with possible values of 0.01-1 representing lowest to highest potential richness respectively.

## **4.2 Sensitivity of the model to weighting schemes**

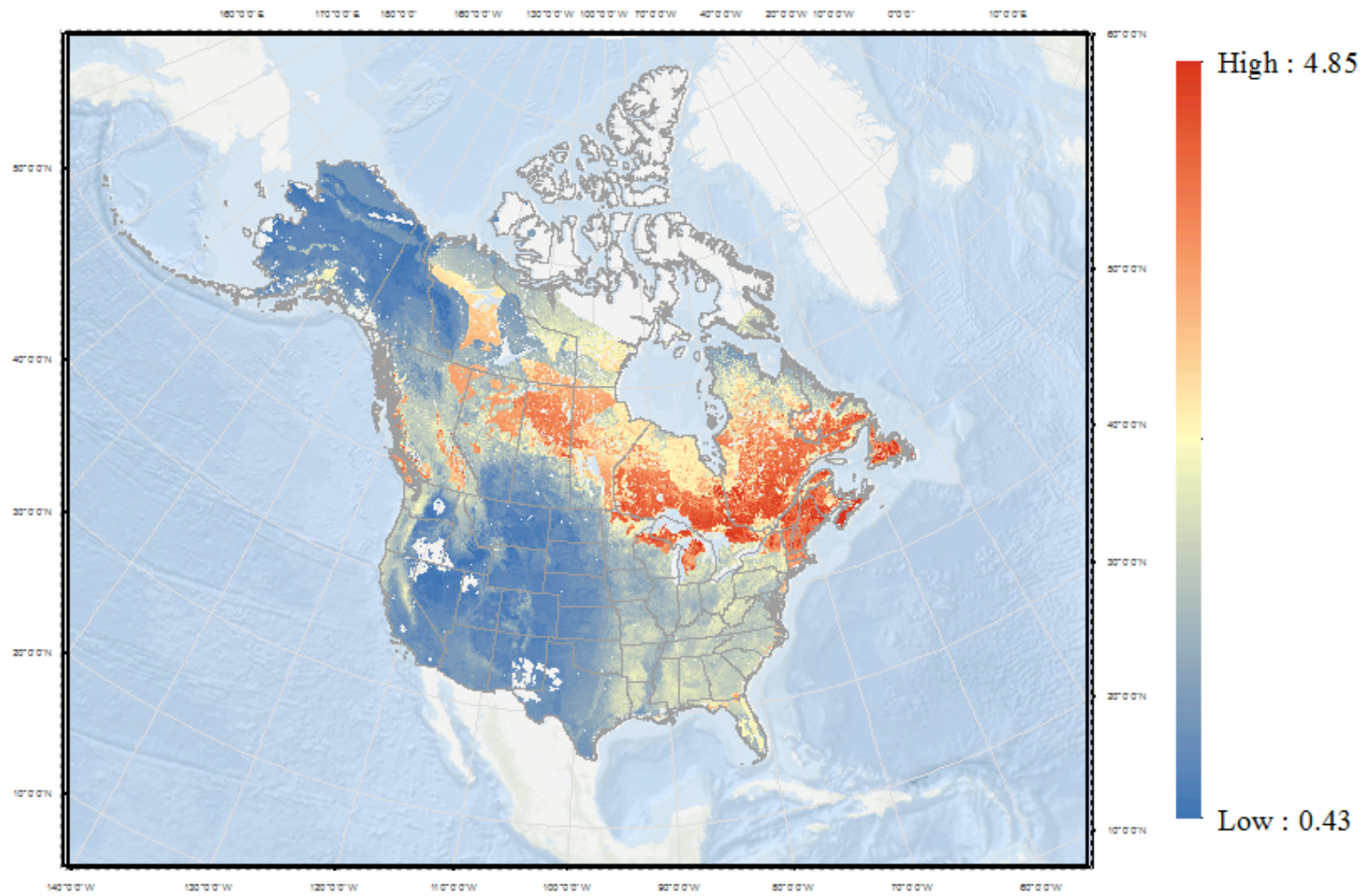
Figure 3 below shows the standard deviation across scenarios. High values represent inconsistencies across models while low values represent consistent rankings. Inconsistent EMF richness suitability occurs most commonly in the desert areas of Western USA and slightly within the tundra of the state of Alaska where EM plant richness is low and historic influences are strong (Figure 3). Consistent EMF richness suitability occurs mainly in boreal and temperate forest areas (Figure 3).



**Figure 3** The standard deviation of habitat suitability for the richness of EMF across model types.

Figure 4 below shows the log ratio of average suitability compared to standard deviation across scenarios. Low values represent habitats that have poor conditions for EMF richness and/or inconsistencies across models. These areas include the tundras in the state of Alaska and desert areas of the conterminous United States (Figures 4). High values represent areas with high consistency and/or high EMF richness suitability. These areas are parts of boreal forests and temperate forests within Canada (Figure 4).





**Figure 4** The log ratio of average habitat suitability compared to standard deviation for the richness of EMF across model types.

### 4.3 Model correspondence to empirical data

None of the weighting schemes or final averaged HSM correlate significantly ( $p > 0.05$ ) to richness estimates from the literature (Table 8).

**Table 8 The Spearman rank correlation coefficient and p-values of comparisons between local richness estimates and various model weighting scenarios.**

	Even <sup>i</sup>	Vellend's Framework <sup>ii</sup>	Literature <sup>iii</sup>	Large-scale and Historic <sup>iv</sup>	Average <sup>v</sup>
<b>Spearman's rho</b>	0.12	0.16	0.13	0.16	0.15
<b>p-value</b>	0.502	0.374	0.490	0.374	0.405

<sup>i</sup> each “low-level” factor is weighted within broad categories of contemporary biotic, contemporary edaphic, contemporary climatic, and historic only

<sup>ii</sup> each “low-level” factor is weighted within categories and by the number of Vellend’s “high-level” processes they fall under

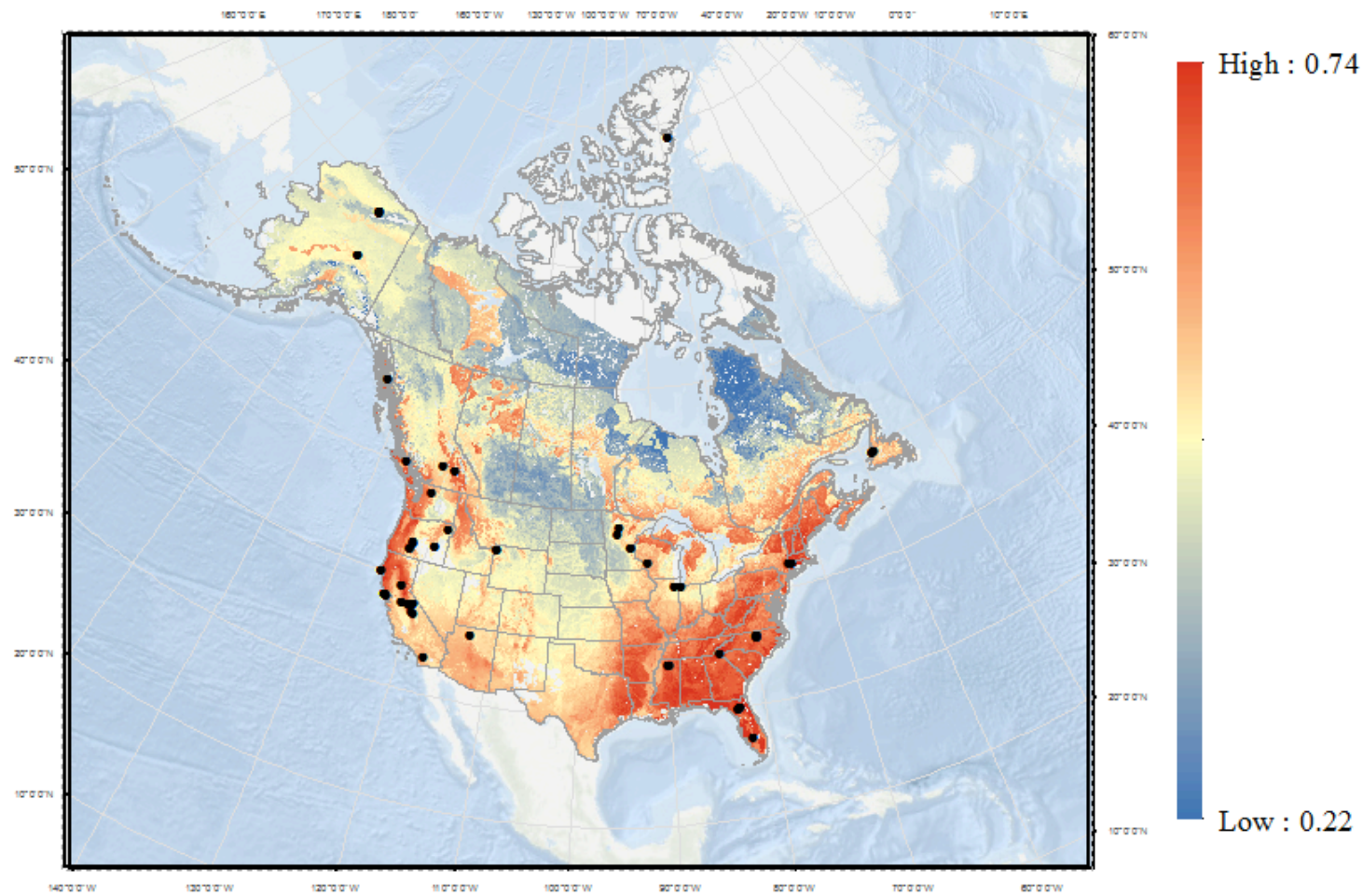
<sup>iii</sup> each “low-level” factor is weighted within categories and each category is weighted by it’s prevalence within the EMF literature

<sup>iv</sup> each “low-level” factor is weighted within categories and each category is weighted by it’s contribution to broad-scale richness patterns in the vegetation literature

<sup>v</sup> All four scenarios are averaged together

### 4.4 Geographical gaps in sampling

A table of sampling locations and richness estimates is given in Appendix A (Table 10). Figure 5 below shows overlaid sampling effort and the average predicted EMF richness across modeling scenarios from section 4.1 above. Richness estimates came from two global studies having a total of 74 (Tedersoo et al., 2012) and 365 (Tedersoo et al., 2014) sampling locations each. Of these sampling locations, just 32 (18 and 14 respectively) were in North America (Table 10). Of the North American sampling locations, only 4 (2 and 2 respectively) were in Canada (Table 10).



**Figure 5** The average habitat suitability for the richness of EMF across model types. Values represent the likelihood for hosting EMF diversity with possible values of 0.01-1 representing lowest to highest potential diversity respectively. Points represent sampling locations.



## **Chapter 5: Discussion and Conclusions**

My overarching goal was to improve the understanding of the origins of biogeographic scale patterns of EMF richness. To this end, I (i) determined key knowledge gaps in the EMF diversity and richness literature, (ii) proposed hypotheses about how this missing information might affect EMF richness patterns at large scales, (iii) combined current ideas from the literature with my own hypotheses to build a qualitative map of predicted EMF richness patterns for Canada and the USA, and (iv) used the resulting maps to highlight geographic regions that are predicted to harbour high EMF richness, and compared this to present sampling strategies in the literature.

### **5.1 Key findings**

In this thesis I synthesized information from the literature regarding processes that have been hypothesized to influence EMF biodiversity at various scales. I organized these hypotheses within the context of scale and within Vellend's (2010) framework for community ecology. By aligning each of the implicated factors with its corresponding "high level" process in Vellend's framework, it became clear that most EMF research pertains to the process of selection, and remarkably little attention has been paid to how drift and speciation influence EMF richness patterns. Moreover, under the branch of selection, most studies have focused on contemporary, local-scale factors. I argue that considering historical and biogeographical processes may yield a more complete understanding of the origins of EMF richness or diversity patterns.

I then constructed a qualitative predictive model of EMF diversity patterns at the geographic extent of Canada and the USA, based on the information gleaned from the literature, and on additional factors such as climate velocity and time since glaciation. To my knowledge, this is the first example of a literature-based habitat suitability model for EMF. The resulting maps provide a powerful visual representation of all of the factors hypothesized, explicitly or implicitly, to influence the large-scale diversity patterns of EMF. Aside from providing substantial material for discussion, they highlight geographic areas that would benefit from targeted sampling in future (see below)

### **5.1.1 Identifying knowledge gaps**

#### **5.1.1.1 Vellend's community ecology framework**

I revealed key knowledge gaps within the present literature by synthesizing the processes that have been hypothesized to influence EMF biodiversity within Vellend's (2010) framework for community ecology. The most prominent knowledge gap identified in this thesis was the almost exclusive review of selective processes over the processes of dispersal, speciation, and drift within the EMF literature. However, there appears to be an overall lack of emphasis on these three factors in the literature more generally (Vellend, 2010).

To date, most of the "high-level" factors that have been implicated as important determinants of EMF community assembly, composition, and diversity have been selective processes with less intensive consideration on dispersal processes (see Chapter 2). It is important to consider all four of these "high-level" processes as they have unique and important impacts on communities across temporal and spatial scales. The process of speciation is the only source of completely new species to communities, drift has stochastic influences on the composition of communities and can possibly lead to extirpation or extinction, dispersal introduces exotic species to communities, and selection has deterministic influences on the composition of communities and can possibly lead to extirpation or extinction.

#### **5.1.1.2 Spatial and temporal scales**

The vast majority of factors that have been implicated as important determinants of EMF community assembly and richness have been local. Challengingly, the "high-level" processes that influence communities vary with spatial scale (Cavender-Bares et al., 2009; Nemergut et al., 2013; Vellend, 2010). Additionally, processes that act at larger spatial scales indirectly influence community assemblages at smaller scales through dispersal and selection (Figure 1).

Selective processes can act at all spatial scales (Vellend, 2010). I found that environmental selection has been recently explored across spatial scales in the EMF literature (see Chapter 2). However, the poorly considered processes of dispersal, speciation, and drift can also act at various scales. The process of drift should be most important at small spatial scales where populations are more likely to be small and prone

to stochastic influences, but should also have more influence when selective processes are weak (Vellend, 2010). Despite acting at small scales, drift has been completely overlooked in the EMF literature. Additionally, the process of speciation is almost negligible compared to the other processes at the local scale but is extremely important at larger spatial scales (Vellend, 2010). This may be because larger geographic regions ought to host larger populations that can experience greater amounts of diversification, particularly when communities are not aggregated. Because the literature has focused mostly on local processes, it is not surprising that speciation has been largely ignored. Lastly, dispersal links communities at various scales and can act to bring taxa between regional communities or between local communities (Figure 1). Geographic barriers to dispersal have been identified as possible influences on regional EMF community composition and assembly (Talbot et al., 2014).

Along with spatial scale, the influence of temporal scale on the process that impact communities has been reviewed (Ricklefs, 1987). Other areas of research have placed increasing amounts of attention on the influence of evolutionary history on present-day communities (Cavender-Bares et al., 2009). Conversely, the factors that have been implicated as important determinants of EMF community assembly and richness have frequently been contemporary with little to no attention on historical factors. While the EMF literature has focused heavily on selective processes, little consideration has been placed on historical selective pressures. The processes of dispersal, speciation, and drift similarly act at various temporal scales. Speciation acts most prominently across long time scales. Historical dispersal or migration patterns might have influenced contemporary communities. Additionally, the effect of drift through time might have shaped contemporary communities.

### **5.1.2 Filling knowledge gaps**

By identifying these key knowledge gaps within the literature, I was able to build hypotheses as to how this missing information might affect EMF richness patterns within Canada and the USA. One factor that was consistently missing from the EMF literature was drift. While drift is extremely important and should be considered when describing the contemporary patterns of richness, it is a difficult process to model. Therefore, while it was not included in the HSM produced in this thesis, I recognize its importance and

predict that it has at least some influence over the contemporary patterns of EMF richness.

Additionally, historical influences and speciation are largely ignored in the EMF literature. These factors were included in the HSM produced in this thesis by considering the time that terrestrial regions have been unglaciated. For regions that have remained unglaciated for longer periods of time, there is more time for speciation or diversification to occur and introduce more species into assemblages. Additionally, time should increase the amount of dispersal that can occur to these areas and increase richness or diversity. Similarly, these regions should have changed ecologically through time as various floral and faunal communities have passed through. This leads to a more heterogeneous habitat through time. This could enhance the number of contemporary taxa due to varied historical selective pressures. Climate velocity is another predictor that was included in this model that could enhance the number of contemporary taxa due to historical heterogeneity.

### **5.1.3 Predicting habitat suitability**

In this thesis I was able to synthesize hypotheses about the processes that influence EMF biodiversity at various scales. By combining the current thoughts with my own hypotheses I was able to build multiple qualitative habitat suitability maps of the predicted EMF richness patterns for Canada and the USA under differing scenarios. I used EMF richness estimates from global studies (Tedersoo et al., 2012, 2014) to compare to the predictions made in the model and all of the weighting scenarios. Importantly, the predictions made should represent the comparative richness between sites. The estimates of EMF richness from these two papers did not correlate significantly with the suitability predictions of any of the scenarios or the main model. While this could reflect missing factors in the model, it may also reflect undersampling at both small and large scales. Problematically, these estimates come from local sampling efforts that can be highly variable. This is because the heterogeneity of local sites can cause large variations from one soil core to another and large amounts of sampling are required to reliably estimate site richness or diversity (Taylor, 2002). In fact, one geographic location was sampled twice with estimates of 35 EMF taxa in one sampling effort and 81 during another (Appendix A: Table 10). This problem is also important to recognize as

the studies mentioned use these variable local estimates of EMF richness to extrapolate to large-scale patterns of richness and diversity. Another issue with comparing to this set of data is that it is quite small (just 32 locations, only 4 of which are in Canada; Table 10) and the sampling is not well distributed throughout the continent (Figure 5).

While the models produced in this thesis are important visual representations of the potential richness of EMF, they also provide key information about which predictors might have the most influence over these patterns. In this model the most important variables for determining EMF richness are the MAT change velocity and hosts (Figure 10). Importantly, both of these factors are biogeographic, historic predictors of richness that have been largely ignored in the EMF diversity and richness literature. This indicates a huge potential to benefit from improved testing of biogeographic and historical predictors on EMF richness. These models are also useful for identifying geographic regions that are predicted to harbour high EMF richness and relaying more efficient sampling efforts.

#### **5.1.4 Richness hotspots and sampling efficiency**

The models used in my thesis indicate that the richness of EMF is predicted to be highest and most consistent in the forested regions of North America, particularly within temperate forests across Canada and the USA and parts of the boreal forests in Canada (Figures 2-4). This makes sense, as EM tree diversities are high in these forested areas. Inconsistent EMF habitat suitability occurs in the Western United States and Alaska where EM plant richness is low and historic influences are strong (Figures 3 and 4). Areas of low consistency and/or low EMF habitat suitability are mainly in Alaska where historical influences are strong but edaphic and biotic predictors are poor (Figures 2-4). Importantly, the model consistently predicts low richness in regions that likely host no, or sporadic, EMF communities (Figures 2-4). These regions include the western and central United States that are mainly plains and deserts. While the model is able to predict low suitability in these areas that likely host little to no EMF richness, it can not be used to predict relative richness in some of the Arctic areas that do host EMF due to lack of host range data.

By visually representing relative EMF richness patterns across North America, and the sampling locations of some large-scale EMF diversity and richness studies, I was

able to vividly show sampling deficiencies. Firstly, many of the sampling locations used in these studies are relatively clustered to one another (Figure 5) considering the geographic extent of Canada and the United States. This isn't surprising as sampling generally occurs at, or near, research station or universities. Additionally, most of the locations sampled by the reviewed broad-scale studies (Soudzilovskaia, van der Heijden, et al., 2015; Talbot et al., 2014; Tedersoo et al., 2012, 2014) are within the United States despite Canada having many suitable EMF habitats and equally high values of predictive richness (Figure 5). The sampled regions tend to be in areas of average to high richness, but miss potential hotspots like north-eastern United States and south-eastern Canada (Figure 5). While sampling higher richness areas is important, it is also valuable to sample areas that are predicted to harbor low richness in order to get a clear picture of EMF richness and diversity. Similarly, sampling pockets of EMF communities in areas like the central United States that may be typically devoid of EM plants and fungi could prove insightful (Figure 5).

## **5.2 Comparisons with previous work**

Recently, statistical habitat suitability models (HSMs) have been utilized in multiple studies for predicting large scale patterns of EMF richness and the habitat factors that might be responsible (e.g., de Vries et al., 2012; Peay et al., 2015; Roy et al., 2013; Soudzilovskaia, van der Heijden, et al., 2015; Suz et al., 2014; Talbot et al., 2014; Tedersoo et al., 2012, 2014). Researchers have done this by producing a single statistical model that relates relatively few local scale estimates of species richness to predominantly local scale abiotic and biotic variables, with some consideration of biogeographic scale factors (e.g., climate). The model is achieved by running the data through programs until richness estimates fit to one or more predictive variables. The resulting model is then used to extrapolate predictions of richness into unsampled geographic regions. Problematically, these studies either ignore or mark as unimportant a variety of factors that are consistently described as important indicators within the literature (e.g. soil texture and CEC, soil nutrients, and soil moisture; Tedersoo et al. 2014). Additionally, estimates of EMF richness or diversity can vary considerably within small distances and large amounts of sampling are required to cover this variation within a site (Taylor, 2002). Because a large number of samples are required to get an idea of

local EMF communities, many of these local studies need to be combined in many ecosystems and across various gradients to make meaningful interpretations about the large-scale drivers of EMF richness or diversity.

Certainly these large-scale sampling efforts are important but may not be able to tell us about large-scale richness patterns for EMF. In order to circumvent this sampling issue and provide a base upon which further studies can compare empirical measure of richness to, I have opted for a literature-based HSM. Given the data availability this modeling technique can be more accurate in describing the large-scale patterns of EMF richness. Importantly, these predictions are based on relationships between richness and environmental factors that have already been described by researchers.

Recently a study was published by Swaty and colleagues (2016) mapping the patterns of mycorrhizal symbioses in the conterminous United States. The distribution of EM symbioses appears to align strongly with the predictions of richness outlined in my model (Figure 2). Interestingly, the areas of my model that are predicted to have higher values of richness seem to align with areas that host strictly EM plants as opposed to various combinations of mycorrhizal types despite this not being one of the factors included in the model (Figure 2). The map from this study is not available as a geospatial dataset so I cannot expressly test how similar my model overlaps with their predictions. However, it is visually clear that there are similar patterns between the two maps.

### **5.3 Applications**

Being the first qualitative assessment of the distribution and drivers of EMF richness in North America, this work provides researchers and other parties much needed information regarding the potential distribution of EMF richness, including key “hot spots” and sampling strategies. If we know the current EMF richness distributions in North America it will allow us to effectively manage existing populations and preserve richness and/or diversity in the face of many anthropogenic stressors that have already impacted European communities and ecosystem functioning (Arnolds, 1991). Managing EMF communities will in turn aid in EM forest community management, carbon sequestration and conversion, reclaiming heavy metal contaminated sites, etc. Additionally, by predicting the patterns of EMF richness within North America as well as current sampling sites, we are able to see where sampling can be improved. Being able to

inform better sampling efforts can have an array of benefits including: finding previously unknown richness “hot spots”, sampling a larger range of site characteristics in order to improve our knowledge of the factors that influence EMF richness and/or diversity, and improving HSMs.

### **5.3.1 Considering alternate drivers of richness**

My literature review and habitat suitability model have indicated a greater need for the consideration of speciation, drift, and dispersal processes. Additionally, the current efforts to explain broad-scale patterns of richness among EMF, which often focus on contemporary predictors, would benefit from more tests of historical-biogeographical hypotheses. Future studies could look into the historic conditions that EMF evolved in to help explain why certain factors might influence contemporary EMF communities and their richness. This could involve historic climates, edaphic conditions, and host distributions.

### **5.3.2 Strategizing sampling efforts**

A comparison of my habitat suitability model to the large-scale sampling efforts of 4 studies (Soudzilovskaia, van der Heijden, et al., 2015; Talbot et al., 2014; Tedersoo et al., 2012, 2014) has yielded an obvious lack of sampling considering the EM dominated tundra, boreal forests, and temperate forests covering large areas of Canada and the USA. These large-scale sampling efforts miss out on many aspects of the present environmental gradients. Additionally, my thesis displays a lack of sampling within Canada in these studies that are all global or North American. Moreover, there is a need to spread sampling efforts from one another and into areas of very high richness but also areas with mid-level values of richness.

### **5.3.3 Habitat suitability modeling**

Habitat suitability models (HSMs) are useful tools for researchers to assess the comparative habitat suitability of areas, evaluate the effects of future climate change on populations and diversity, and identify management priorities. Future research could look into some of these facets, particularly, the effect of changing climates and anthropogenic inputs on the predicted distributions of EMF richness. Future studies should include better sampling across large-scale gradients to determine their influences on EMF richness across the gradient. This could be particularly useful for predictors like pH and



soil texture that have been debated within the literature. These studies are particularly valuable as the gradient provides a natural transition between varying levels of a predictive factor. Additionally, strategic, intensive large-scale sampling efforts are necessary to validate the model produced in this thesis and to produce more effective statistical HSMs.

## **5.4 Assumptions and limitations**

### **5.4.1 Data**

All of the data utilized has their own inherent assumptions and limitations. For example, the terrestrial water budget data set was produced using potential evapotranspiration and total precipitation time series'. There is an assumption made that soil moisture is simply a reflection of these two variables but it can also depend on soil texture and water losses through run off and drainage. Additionally, this data is limited by the accuracy of the input data sets. Similarly, all data used this thesis is limited in accuracy. Certain data sets like land cover are particularly limited as the value for one 0.5 km pixel is approximated from all of the different land cover types within it. Sometimes, land cover is homogenous across these extents but it can also be heterogeneous. The researchers that produced this data set used MODIS (Moderate Resolution Imaging Spectroradiometer) Land Cover Type data. MODIS is a NASA instrument operated from the Terra and Aqua spacecraft that views 2330km of the Earth's surface every one to two days. They were able to reduce interannual variability of land types by reviewing over time, but still had to assign a land cover type to each pixel based on the most common land type across years. Problematically, many large-scale raster data sets require extrapolations of values from local samples or values to the resolution of the raster pixel. Because of this, many data sets are inherently limited. The host distribution data, which is arguably the most important, is also limited. This is evident in that there are sampling locations in Northern Canada that harbor EM plants and fungi yet are not included in the large dataset of North American trees (Figure 5). This is because many small shrubs and herbaceous plant species that are ectomycorrhizal are not included in this data set. Because of this, the maps produced in this work strictly reflect the potential richness in areas that fall within EM tree distributions.

### **5.4.2 Habitat suitability modeling**

One of the limitations of an HSM for EMF richness is that many variables implicated as being important for determining distributions are directly or indirectly linked to one another. This being the case, many of the variables used are correlated to one another. Despite these correlations, all of the variables have their own unique influence over richness and are still important for modeling patterns of EMF. Another limitation is the lack of useful large-scale data sets. Many data sets are at resolutions that are far too coarse or are patchy with lots of no data raster pixels. Additionally, the literature is lacking for some variables that are thought to be influential for EMF richness. Specifically, many studies indicate that certain abiotic or biotic factors have an influence on community composition but found no effect on richness or diversity. Moreover, many factors appear to be variable in their effects on richness or diversity depending upon the EMF taxa present (e.g., pH; Agerer et al., 1998; Carrino-Kyker et al., 2016; Erland & Taylor, 2002; Kluber et al., 2012). More studies looking at gradients that cover the entire range of values for various predictors are needed to determine the effects on similar communities.

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## Appendices

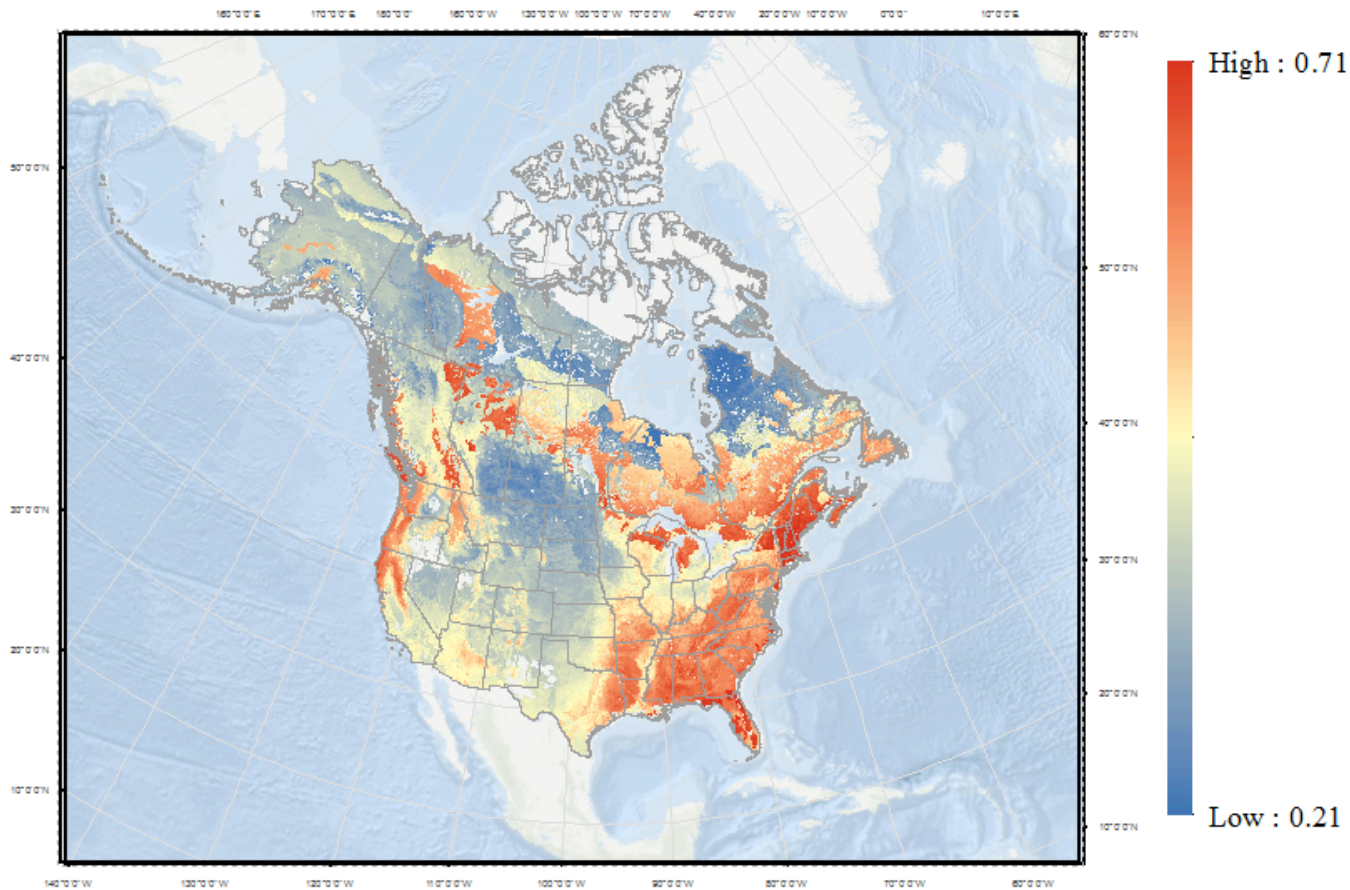
### Appendix A: Supplementary tables and figures

**Table 9 IGBP-DIS land cover classification system.** Cover types and descriptions obtained from Hansen and colleagues (2000).

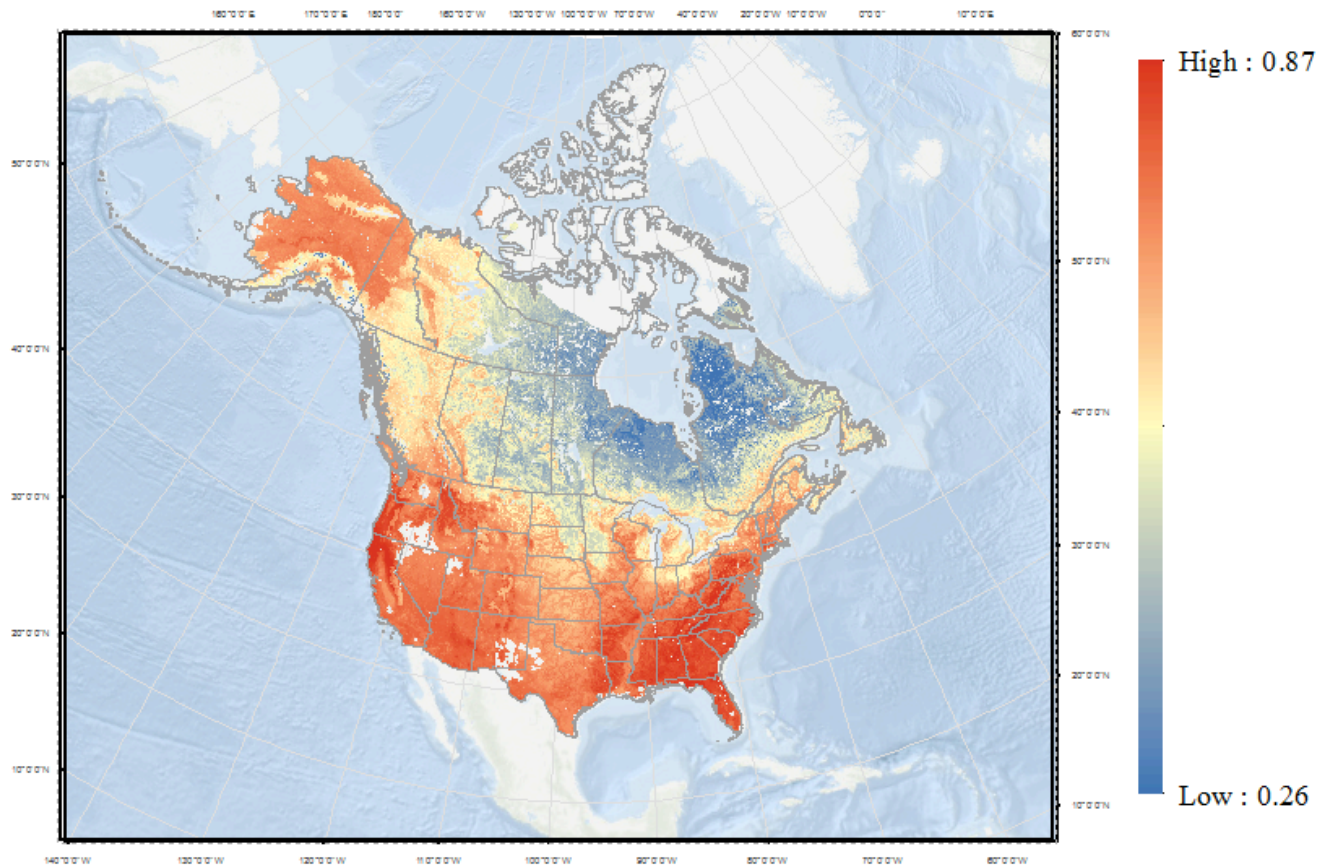
Cover type	Description
evergreen needleleaf forests	lands dominated by trees with a percent canopy cover >60% and height exceeding 2 meters. almost all trees remain green all year. canopy is never without green foliage.
evergreen broadleaf forests	lands dominated by trees with a percent canopy cover >60% and height exceeding 2 meters. almost all trees remain green all year. canopy is never without green foliage.
deciduous needleleaf forests	lands dominated by trees with a percent canopy cover >60% and height exceeding 2 meters. consists of seasonal needleleaf tree communities with an annual cycle of leaf-on and leaf-off periods.
deciduous broadleaf forests	lands dominated by trees with a percent canopy cover >60% and height exceeding 2 meters. consists of seasonal broadleaf tree communities with an annual cycle of leaf-on and leaf-off periods.
mixed forests	lands dominated by trees with a percent canopy cover >60% and height exceeding 2 meters. consists of tree communities with interspersed mixtures or mosaics of the other four forest cover types. none of the forest types exceeds 60% of landscape.
closed shrublands	lands with woody vegetation less than 2 meters tall and with shrub canopy cover is >60%. the shrub foliage can be either evergreen or deciduous.
open shrublands	lands with woody vegetation less than 2 meters tall and with shrub canopy cover is between 10-60%. the shrub foliage can be either evergreen or deciduous.
woody savannas	lands with herbaceous and other understorey systems, and with forest canopy cover between 30-60%.the forest cover height exceeds 2 meters.
savannas	lands with herbaceous and other understorey systems, and with forest canopy cover between 10-30%.the forest cover height exceeds 2 meters.
grasslands	lands with herbaceous types of cover. tree and shrub cover is less than 10%.
permanent wetlands	lands with a permanent mixture of water and herbaceous or woody vegetation that cover extensive areas. the vegetation can be present in either salt, brackish, or fresh water.
cropland	lands covered with temporary crops followed by harvest and a bare soil period (e.g., single and multiple cropping systems. note that perennial woody crops will be classified as the appropriate forest or shrub land cover type.
urban and built-up	land covered by buildings and other man-made structures.
cropland/natural vegetation mosaics	lands with a mosaic of croplands, forest, shrublands, and grasslands in which no one component comprises more than 60% of the landscape.
snow and ice	lands under snow and/or ice cover throughout the year.
barren	lands exposed soil, sand, rocks, or snow and never has more than 10% vegetated cover during any time of the year.
water bodies	oceans, seas, lakes, reservoirs, and rivers. can be either fresh or salt water bodies

**Table 10 Site locations and species richness estimates from 2 global studies used to compare the habitat suitability model to.**

Country	Latitude	Longitude	Species Richness	Study
Canada	50.312	-125.475	56	Tedersoo et al., 2012
Canada	50.7512	-118.57	105	Tedersoo et al., 2012
USA	45.417	-93.167	72	Tedersoo et al., 2012
USA	41.6747	-87.8569	195	Tedersoo et al., 2012
USA	41.6308	-87.0869	201	Tedersoo et al., 2012
USA	40.008	-123.95	79	Tedersoo et al., 2012
USA	37.15	-119.117	80	Tedersoo et al., 2012
USA	45.42	-93.22	123	Tedersoo et al., 2012
USA	44.456	-110.495	81	Tedersoo et al., 2012
USA	44.456	-110.495	35	Tedersoo et al., 2012
USA	36.967	-119.033	101	Tedersoo et al., 2012
USA	37.9	-122.616	57	Tedersoo et al., 2012
USA	43.95	-91.05	46	Tedersoo et al., 2012
USA	35.966	-79.133	134	Tedersoo et al., 2012
USA	43.5	-118.5	140	Tedersoo et al., 2012
USA	45.4	-117.4	117	Tedersoo et al., 2012
USA	39.283	-121.283	182	Tedersoo et al., 2012
USA	35.04	-83.45	58	Tedersoo et al., 2012
Canada	48.948	-57.934	136	Tedersoo et al., 2014
Canada	48.9895	-57.787	136	Tedersoo et al., 2014
USA	68.6228	-149.5968	30	Tedersoo et al., 2014
USA	68.6232	-149.5992	113	Tedersoo et al., 2014
USA	29.74983	-82.21786	89	Tedersoo et al., 2014
USA	37.81383896	-119.8925781	135	Tedersoo et al., 2014
USA	36.01198	-78.97001	146	Tedersoo et al., 2014
USA	37.74811	-119.55345	107	Tedersoo et al., 2014
USA	36.23099	-112.06814	138	Tedersoo et al., 2014
USA	29.73517	-82.44186	101	Tedersoo et al., 2014
USA	37.84895325	-120.5805054	68	Tedersoo et al., 2014
USA	36.0361	-79.0711	141	Tedersoo et al., 2014
USA	35.9794	-79.0928	151	Tedersoo et al., 2014
USA	26.940139	-81.3375	40	Tedersoo et al., 2014

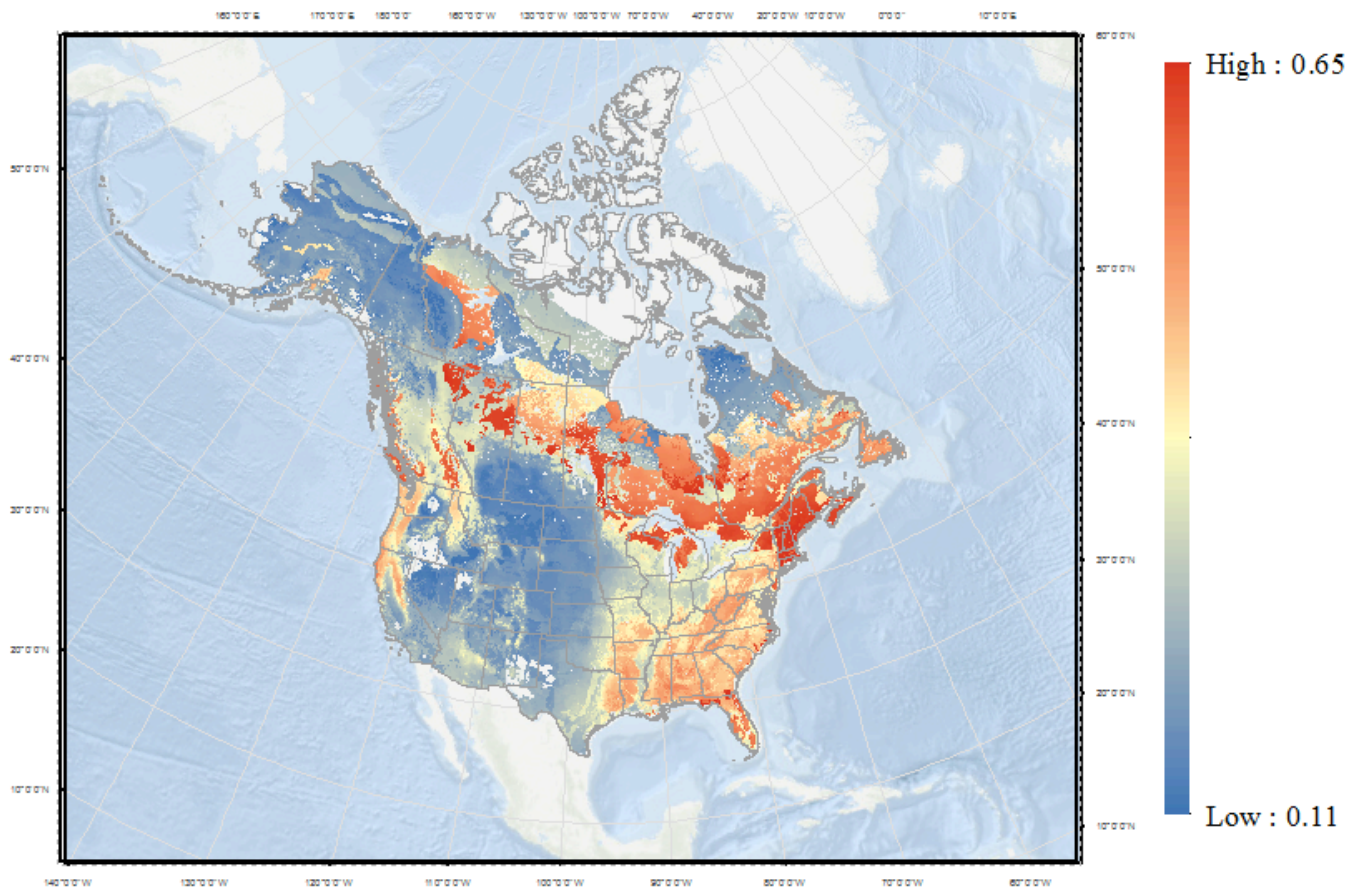


**Figure 6** The predicted patterns of the richness of EMF in the contiguous United States, Alaska, and Canada for the “Even” weighting scenario. Values represent the suitability of habitat for EMF richness. This scenario weights predictive factors within the categories of biotic, edaphic, climatic, or historic based on their presumed importance and studying intensity in the EMF and vegetation literature. The scenario further weights all categories evenly against each other to determine habitat suitability.

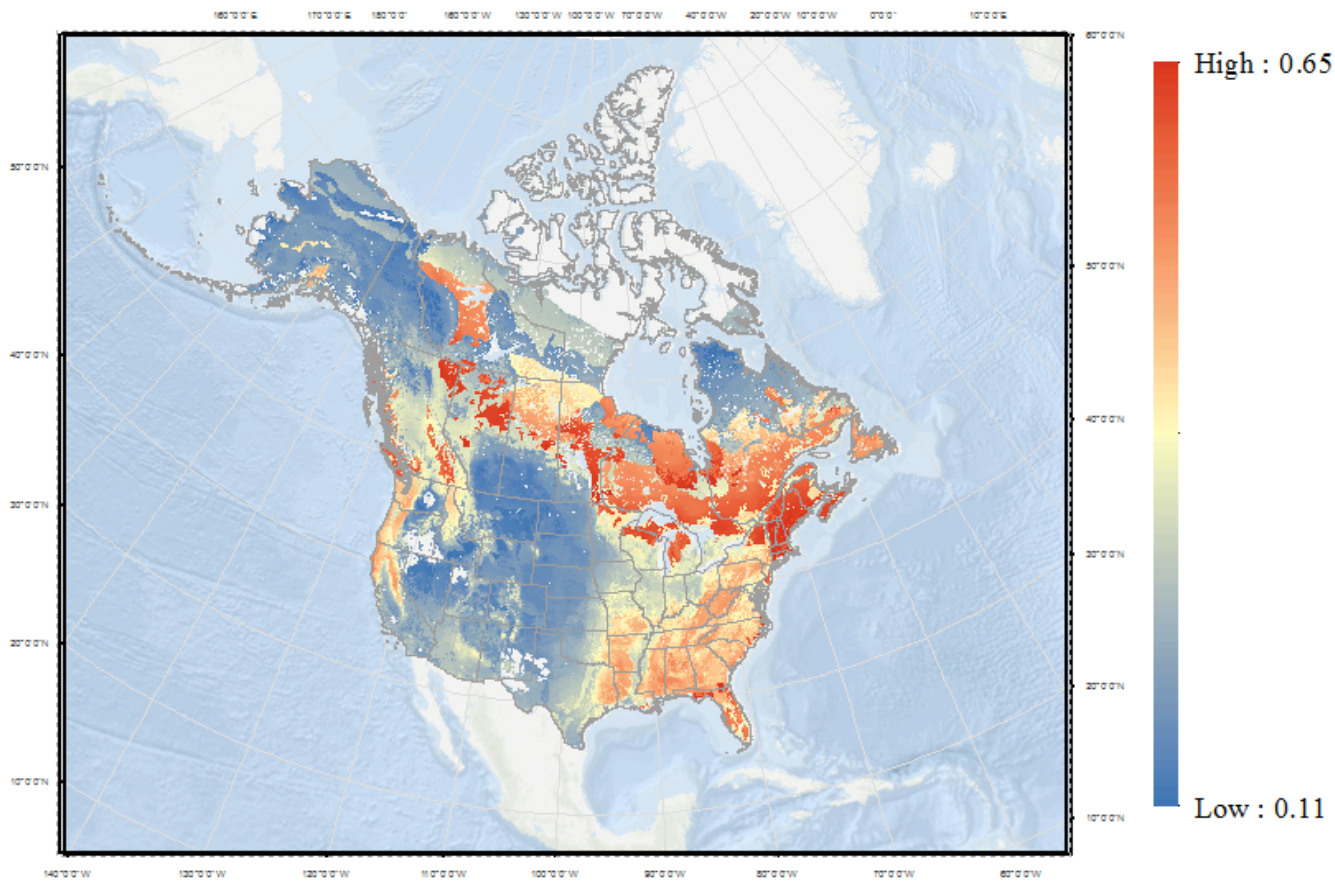


**Figure 7** The predicted patterns of the richness of EMF in the contiguous United States, Alaska, and Canada for the “Vellend’s Framework” weighting scenario. Values represent the suitability of habitat for EMF richness. This scenario weights predictive factors within the categories of biotic, edaphic, climatic, or historic based on their presumed importance and studying intensity in the EMF and vegetation literature. The scenario further weights all categories against each other according to their contribution to Vellend’s 4 high level processes of selection, dispersal, speciation, and drift to determine habitat suitability.

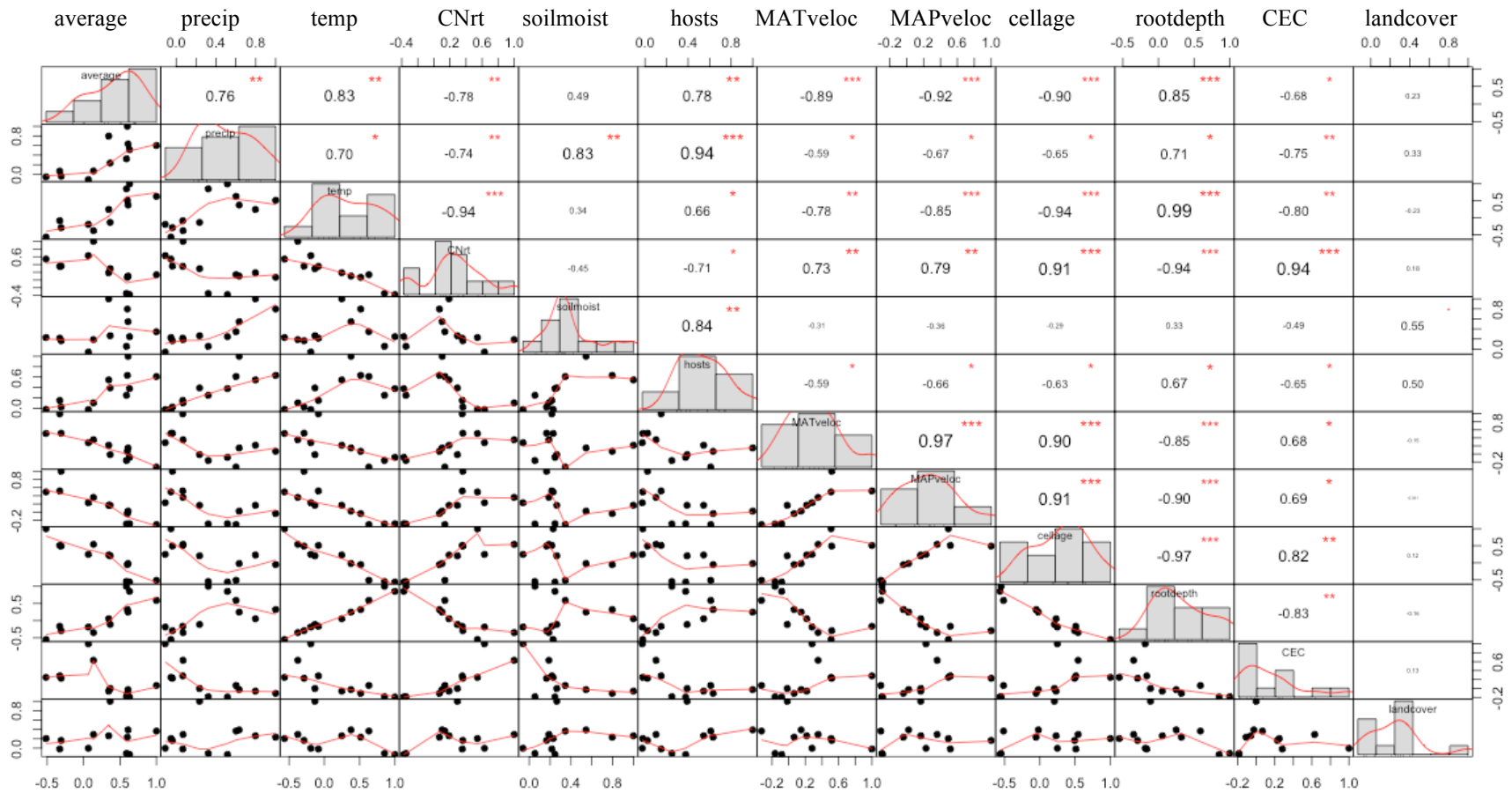




**Figure 8** The predicted patterns of the richness of EMF in the contiguous United States, Alaska, and Canada for the “Literature” weighting scenario. Values represent the suitability of habitat for EMF richness. This scenario weights predictive factors within the categories of biotic, edaphic, climatic, or historic based on their presumed importance and studying intensity in the EMF and vegetation literature. The scenario further weights all categories against each other according to each category’s importance within the EMF literature to determine habitat suitability.



**Figure 9** The predicted patterns of the richness of EMF in the contiguous United States, Alaska, and Canada for the “Large-scale and Historic” weighting scenario. Values represent the suitability of habitat for EMF richness. This scenario weights predictive factors within the categories of biotic, edaphic, climatic, or historic based on their presumed importance and studying intensity in the EMF and vegetation literature. The scenario further weights all categories against each other with enhanced importance on broad-scale and historic factors to determine habitat suitability.



**Figure 10** A correlation matrix of predictor variables and the final EMF diversity ranking. Asterisks represent significance of the correlation and the size and values of numbers represent the strength and direction of the correlation. Average – average ranking across all modeled scenarios, precip – MAP, temp – MAT, CNrt – carbon to nitrogen ratio, soilmoist – soil moisture, hosts – host richness, MAT veloc – velocity of MAT change, MAP veloc – velocity of MAP change, cellage – time since glaciation, rootdepth – rooting depth, CEC – cation exchange capacity, landcov – ranked land cover.

## **Appendix B: Metadata**

### 1. Ectomycorrhizal tree range data

#### General Information

Type: Shape

Source: U.S. Geological Survey (1999)

Title: Digital representation of “Atlas of United States Trees” by Elbert L. Little, Jr.

Last updated: January 2013

Geographic Coordinate System: Datum: NAD 1927, Ellipsoid: Clarke 1866, Units:

Decimal Degrees

Projected Coordinate System: None

Resolution: 0.6 arc minutes

### 2. Land cover data

#### General Information

Type: Raster

Source: USGS Land Cover Institute (Broxton et al., 2014)

Title: 0.5 km MODIS-based Global Land Cover Climatology

Last updated: May 2014

Geographic Coordinate System: WGS 1984

Projected Coordinate System: None

Resolution: 15 arc seconds

### 3. ISRIC-WISE soil data

#### General Information

Type: Raster and MSAccess

Source: ISRIC – World Soil Information (Batjes, 2009)

Title: ISRIC-WISE derived soil properties on a 5 by 5 arc-minutes global grid (version 1.2)

Last updated: January 2012

Geographic Coordinate System:

Projected Coordinate System:

Resolution: 5 arc minutes

#### 4. Soil moisture data

General Information

Type: Raster

Source: The University of Delaware (Matsuura & Willmott, 2015)

Title: Monthly Terrestrial Water Budget Time Series

Last updated: Version 3.01, May 2015

Geographic Coordinate System: Undescribed, most likely WGS 1984 Units: Decimal Degrees

Projected Coordinate System: None

Resolution: 60 arc minutes

#### 5. Rooting depth data

General Information

Type: Raster

Source: International Satellite Land-Surface Climatology Project, Initiative II (Schenk & Jackson, 2009)

Last updated: October 2009

Geographic Coordinate System: WGS 1984

Projected Coordinate System: Geographic

Resolution: 60 arc minutes

#### 6. Climate data

General Information

Type: Raster

Source: WorldClim (Hijmans et al., 2005)

Last updated: Current climate: Version 1.4, January 2006, Past climate: November 2013

Geographic Coordinate System: WGS 1984

Projected Coordinate System: None

Resolution: 5 arc minutes

## 7. Deglaciation data

### General Information

Type: Shape

Source: Geological Survey of Canada (Dyke, Moore, & Robertson, 2003)

Last updated: 2003

Geographic Coordinate System: NAD 1927, Spheroid: Clarke 1866

Projected Coordinate System: Lambert Conic Conformal

Resolution: 5 arc minutes