

**Analyses of environmental factors for the persistence of
Myrmica rubra (Hymenoptera: Formicidae) in green spaces of
the Greater Toronto Area and applications of ecological
niche/species distribution models**

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A MAJOR PAPER SUBMITTED TO
THE FACULTY OF ENVIRONMENTAL STUDIES
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
MASTER IN ENVIRONMENTAL STUDIES

GRADUATE PROGRAM IN ENVIRONMENTAL STUDIES
YORK UNIVERSITY
TORONTO, ONTARIO

October 2014

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Acknowledgements

I would like to express my gratitude to the following:

Everyone from the Packer Bee Lab for their help and keeping me company. They are my extended family here in Toronto. My special thanks to Scott MacIvor for letting me tag along to his bee nestbox sites and his advice and feedback. Jen Albert for her help and advice in countless ways. She is the one who reasoned with me when things went awry with this project. Thank you. Sheila Dumesh for her help with everything (always very generous with her time), advice, and kindness. I am also so grateful for her help with my fieldwork (driving me to conservation areas and 6 farms regularly for ant surveying). Without her, my fieldwork could not have been possible. Thank you.

Toronto and Region Conservation Authority (TRCA) for letting me study on their lands and loaning me soil analysis instruments.

Rosa Orlandini from the Map Library, York University for her relentless help with geospatial data.

Dr. William Mahaney from the Department of Geography, York University for his help and advice on soil analysis.

Those who contributed to the backyard ant collection project. Thank you for your cooperation: Dr. Clement Kent, Dr. Greg Thiemann, Dr. Lewis Molot, Dr. Martin Bunch, Dr. Felipe Montoya, Dr. Laurence Packer & Dr. Gail Fraser, Nick de Silva, Scott MacIvor, and Sheila Dumesh.

Dr. Gail Fraser who introduced me to wildlife/conservation biology for driving me to conservation areas, purchasing a soil moisture analysis instrument (which contributed to this research project immensely) on my behalf, and her guidance and patience. Thank you, I think I have found my *métier*. She will always be my mentor in biology.

Dr. Laurence Packer for letting me be part of the Packer Bee Lab, his funds for ant processing tools and DNA barcoding, his perspective, guidance, and patience for my research project, invitations to his house parties, and his sense of humour. The best Boss I have had so far. Thank you.

Foreword

Biodiversity is the life support system of Earth. It provides sustenance and the web of life to every organism present regardless of size and biological roles. This life support system is, however, severely compromised by one group of its own members known as invasive species. Invasive species are considered one of the major causes of biodiversity loss.

Taking an initiative to the presence and detrimental effects of the non native invasive ants: European fire ants in the Greater Toronto Area (GTA) was the first step towards this project. Although the transportation of non native species to their introduced ranges is generally anthropogenically done, increased human mobility of late and climate change seem to accelerate the magnitude of propagule.

As the Second Law of thermodynamics clearly states that the degree of chaos in a system has a tendency to increase, including the ecological systems by destabilizing the delicate yet resilient balance of inter and intra species interactions, and this is inevitable as the law is inviolable. After all, the occurrence of invasive species is brought about by humans and that invasive species are survivors in ever changing ecological milieus by quickly adapting to new conditions. It can be seen that the transportation of non native species whether unwittingly or intentionally is self-inflicted damage and that the taxa that are incapable of acclimatizing to new conditions are destined to go extinct. Perhaps the “wars” against invasive species cannot be won and might as well be a lost cause; however, at least some feat must be taken to show that something was done.

This research project is a testament that is meant to shed some light on the direction of the wars and an initial step towards them, for prior to this, no extensive study was conducted in Canada on this non native invasive ant species' ethology and ecological suitability conditions.

My MES Area of Concentration is focused on the mitigation and management of the spread of invasive species in urban green spaces. This Major Paper focuses on non-native European fire ants in the GTA and determining their presence in conservation areas. The key concepts and approaches used in my major paper research will span all four areas of concentration in my POS.

Abstract

The Palearctic native European fire ant *Myrmica rubra* have been sighted frequently across the Greater Toronto Area (GTA) in recent years. Although their populations in the GTA are fragmented, this non native invasive ant species has potential to expand well beyond their current habitats. In order to ascertain the ecological conditions for the persistence of *M. rubra*, an extensive study was conducted at conservation areas across the GTA.

Based on some of the ecological factors required for *M. rubra*, ecological niche models (ENMs)/species distribution models (SDMs) were constructed on 3 different scales using occurrence data for better mitigation and prevention of this invasive species and to predict their future potential geographic distributions in the face of climate change.

From an array of regression analyses, it was found that soil surface moisture level ($p = 0.005$, odds ratio = 1.04), soil surface temperature ($p = 0.001$, Odds ratio = 1.14), and altitude ($p = 0.001$, odds ratio = 0.99) are essential for *M. rubra* to persist. It was also found that *M. rubra* does displace other ant species as well as arthropods, and this is in agreement with the results from other publications. Based on the ENMs/SDMs, this non native invasive species has potential to spread beyond the current distribution range, and susceptible areas should be monitored for future invasion and expansion.

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Chapter One: Introduction

Ants (Hymenoptera: Formicidae) have been omnipresent since the mid Cretaceous period (Keller & Gordon, 2009). Over the past 115 to 135 million years, ants have evolved and diversified into 21 subfamilies, 283 genera, and 15,707 valid species (Keller & Gordon, 2009; Bolton, 2014; Antweb, 2014). Ants are very likely the most successful of all insects, and not only do they outnumber other terrestrial animals in individuals but also nearly outweigh humans (Holldobler & Wilson, 1990; Keller & Gordon, 2009). With an exception of a few parasitic species, ants are eusocial insects displaying characteristics of a reproductive division of labour between members, overlapping generations, and intergenerational cooperation with rearing the brood (Wilson, 1971).

Ants are integral parts of terrestrial ecosystem functioning in seed dispersal, soil turnover/aeration, plant protection, and catabolism of organic matter. (Fisher & Cover, 2007). These ecological roles for ants, however, can be disrupted by their being displaced by abiotic factors as well as biotic ones. Habitat loss and climate change are major abiotic factors for biodiversity loss (Tilman et al., 2001; Bellard et al., 2012); however, introduction of non native species as a biotic factor is more detrimental and often not reversible (Anderson et al., 2004; Didham et al., 2005). Most non native species display ecologically damaging effects (McGinley et al., 2011), and it is conventionally understood that at the stage where the non native population is pervasive and abundant enough to pose ecological or economic damage, it acquires the name “invasive” (Lockwood et al., 2007). The term “invasive species” is defined legally in the USA as “a non native species whose introduction does or is likely to cause economic or environmental harm or harm to human health” (McGinley et al., 2011). Characteristics shown by the species considered invasive include aggressive expansion into both

disturbed and undisturbed habitats and displacement of native species by outcompeting them (McGlynn, 1999). These characteristics also apply to ants; that is, non native invasive ants displace native species of ants as well as other arthropods and vertebrates, disruption of native ant - plant mutualisms, and agricultural losses (Vinson, 1997; Vega & Rust, 2001; Groden et al, 2005; Keller & Gordon, 2009). Amongst the 17 species of invasive invertebrates considered the most damaging pests in the world, five are ants (Keller & Gordon, 2009). *Linepithema humile* (native to central South America), *Solenopsis invicta* (native to tropical and subtropical South America), and *Anoplolepis gracilipes* (native to sub Saharan or India) are a few of the worst invasive ants in their introduced ranges: western US, southern Africa, Australia, Japan, and the pan-Mediterranean region for *L. humile* (Wetterer et al., 2009; Kenis et al., 2008; Lach et al., 2010); southern US, northeastern Mexico, Hawaii, West Indian islands, Taiwan, China, and Australia for *S. invicta* (Wetterer, 2013; Epperson et al., 2010; Kenis et al., 2008; Lach et al., 2010); tropical Asia, Australia, western Mexico, Christmas Island, and the Seychelles for *A. gracilipes* (Wetterer, 2005; Keller & Gordon, 2009; Haines et al., 1994; Kenis et al., 2008; Lach et al., 2010). In addition to these most detrimental invasive ants that are well established in their introduced ranges, there are emerging invasive ants that are gradually expanding their ranges, including *Lasius neglectus* (Seiffert, 2000; Cremer et al., 2008), *Pachycondyla chinensis* (Nelder et al., 2006), and *Myrmica rubra* (Groden et al., 2005; Wetterer et al., 2011). Regardless of the magnitude of the current invasion, with aid of human activities, no continent is immune to invasive ants (Keller & Gordon, 2009).

The European fire ant *Myrmica rubra* (Hymenoptera: Formicidae) is native to the Palearctic region and is never considered as a pest in its native range due to low nest

densities (Grodén et al., 2005). It was accidentally introduced into the USA in the early 1900s as a stowaway hidden in plant material imported from Europe and is now observed in northeastern US, Maritime Canadian provinces, southern Ontario, and the Pacific Northwest (Grodén et al., 2005). *M. rubra*'s first presence in Ontario was recorded in 1975 (Grodén et al., 2005). *M. rubra* displays all the characteristics of invasive species and poses ecological, economic, and societal implications like other invasive species (Ouellette et al., 2010). As a generalist species, *M. rubra* can be found ubiquitously regardless of habitat and soil types, and they are polygynous (multiple queens in one nest) and polydomous (multiple nests in one colony) and displace native ant species (Ouellette et al., 2010; Elmes, 1973; Debout et al., 2007).

As for all invasive species, the most efficient way to combat them is the prevention of accidental transportation, colonization, and spread (Horan et al., 2002; Sumner et al., 2005); however, this is hardly feasible due to the limited availability of resources. Predictive modelling against possible invasion and for mitigation/management if invasive species are already present is a cost effective tool where the practice of prevention is not all feasible (Thuiller, 2007). Predictive modelling such as ecological niche models (ENMs) or species distribution models (SDMs) can predict potential geographical distribution of invasive species based on non random correlations between known occurrences of species and environmental datasets to produce an approximation of the spatial ecological niche (Ward 2007; Peterson, 2003; Guisan & Thuiller, 2005).

The invasion process is extremely complex and entails numerous biotic and abiotic factors (Peterson, 2003); however, ENMs/SDMs can provide reliable information

for potential geographic distribution areas for invasion and increase the likelihood of successful prevention or mitigation of invasive species.

For the construction of ENMs/SDMs, species known occurrence points are georeferenced as presence points, but for invasive species, the availability of true absence/ negative data is often scarce; however, in order to assess models for error rates, absence data are required (Phillips et al., 2006). In order to overcome the unavailability of true absence data, most SDM algorithms use pseudo-absence (randomly chosen non presence points) data points or random background (any location where presence/absence is unmeasured) points (Merow et al., 2013). When species presence points are too close to one another and/or clustered, SDM algorithms tend to overfit predictive outputs, but a remedial process is used to overcome this problem by “relaxing” the cluster using the average value of each sampled variable (the regularization process) for optimum predictive accuracy (Baldwin, 2009; Phillips et al., 2008).

For ENM/SDM algorithms, the output maps use various colours to indicate the degree of predicted probability for habitat suitability, for example, red indicating high suitable conditions for *M. rubra*, green indicating conditions typical of those where the ant is found, and lighter shades of blue indicating low predicted probability of suitable conditions. In order to assess model performances produced by ENMs/SDMs, the receiver operating characteristic (ROC) analysis which evaluates model performance by plotting the proportion of correctly predicted presence points versus that of correctly predicted absence points is used, and model performance of ROC is measured by the area under the curve (AUC), with values ranging from 0 to 1 with values of 1 suggests

optimal performance and 0.5 for model performance no better than a randomly generated one (Phillips et al., 2006). AUC can be interpreted as the probability that a randomly chosen species presence site is ranked above a randomly chosen absence site and it is a measure of how a predictive model is capable of distinguishing between species presence sites and species absence sites (Fielding & Bell, 1997; Elith et al., 2006; Phillips et al., 2006).

In addition to AUC values for model predictive assessment, the omission curve is used to show the magnitude of average omission rate and predicted area. The omission curve measures the predicted probability of occurrence on the x axis and the value of omission error on the y axis. (Phillips et al., 2006). A curve below the predicted omission line indicates good performance of predictive ability and fitness with less omission errors, and the performance increases as the curve moves towards lower right corner of the curve, indicating low omission errors as predicted probability of occurrence increases.

The AUC curve is based upon two variables: specificity and sensitivity. Specificity provides a measure of correctly predicted absence whereas sensitivity represents how well the data correctly predict presence (Baldwin, 2009; Jimenez-Valverde et al., 2009). The curve plots “sensitivity” against “1-specificity” which can be interpreted as the rate of predicted false positives (commission error). A good predictive model shows an AUC curve close to the top left corner of the figure, displaying a high true positive value with less omission.

M. rubra showing typical characteristics of invasive species has potential to expand beyond the currently known regions, and the information obtained from ENMs/SDMs will be an effective tool to combat future invasion of this invasive species.

**Chapter Two: Distribution and abundance of *Myrmica rubra*
(Hymenoptera: Formicidae) in the Greater Toronto Area and its
characteristics with environmental factors.**

Abstract

Distribution, abundance, and environmental factors associated with the presence/absence of the European fire ant *Myrmica rubra* at conservation areas across the Greater Toronto Area were studied. Since an unwitting introduction from its native Palearctic region in early 20th century, *Myrmica rubra* has been keeping a low profile until 1990s. As other non native invasive species, *M. rubra* poses ecological, environmental, economic, and societal threats from displacing native arthropods to being a nuisance pest in urban green spaces. Conditions that were conducive to the persistence of *M. rubra* were investigated by focusing on the presence and number of other arthropods and on environmental factors. From statistical analyses, moderate to high soil surface moisture level, higher ground surface temperature, and low elevation were found to be essential for the presence of *M. rubra*. Also the cause of numerous sightings of this species in recent years was speculated on a phylogenetic basis.

Introduction

One of the major causes of biodiversity loss is the establishment of non-native, invasive species, due to their primarily negative influence on the function and structure of ecosystems in their introduced range and subsequent detrimental impacts (Roura-Pascual et al., 2009). Invasive introduced or non-native species are a significant stressor on ecosystem functions, processes, and structure in terrestrial, freshwater, and marine environments (Ward, 2007; Clinton, 1999; Groden et al., 2005). Even though biotic invasions are neither new nor an exclusively anthropogenic phenomenon, the

number and extent of non-native species becoming invasive is increasing considerably as a consequence of increased human mobility (Roura-Pascual et al., 2006).

Insects are ubiquitous and exist in large numbers. Amongst insects, ants (Hymenoptera: Formicidae) are one of the most successful organisms and can be found anywhere in the world except for Antarctica and Greenland (Wetterer et al., 2011). Ants are an important part of ecological landscapes as scavengers, seed dispersers, and transporters of plant and animal material (Ouellette et al., 2010). There are approximately 15,700 described ant species in the world and about 1,000 species in North America alone (Antweb, 2014; Fisher et al., 2007). Native ant species play essential roles in the proper functioning of nearly all terrestrial ecosystems (Fisher et al., 2007; Christian, 2001), but introduced non-native ants often outcompete native ants for space and resources (Ouellette et al., 2010). Currently over 150 non-native ant species are established outside of their native range (McGlynn, 1999). Not only do non-native ants have negative impacts on native ants via direct competition and predation but also affect them indirectly through disruption of ecological processes such as ant-plant mutualisms (Grodén et al., 2005; Bond and Slingsby, 1984). The threat to ant diversity as a result of invasive species is considered second only to that of habitat destruction (Grodén et al., 2005).

European fire ants *Myrmica rubra* (Linnaeus, 1758) (Hymenoptera: Formicidae) have been reported in the Greater Toronto Area (GTA), Ontario, Canada in the past 10 years (Rudmik, 2011; Grodén et al., 2005). European fire ants are a nuisance by delivering a painful sting: Collingwood (1987) wrote that *Myrmica rubra* “has the most vicious sting of all the British ants” (Wetterer et al., 2011). As an invasive species they

also pose problems environmentally, economically, and societally (Ward, 2007; Groden et al., 2005), however there is a paucity of information on the distribution of species in the GTA. When their nesting and foraging area is disturbed, *M. rubra* congregate to launch an attack on intruders en masse (personal observation). *M. rubra* is considered a nuisance pest on picnic sites and in other urban green spaces (Town of Richmond Hill, 2006) and may reduce property values but also has negative impacts on agriculture as a crop pest by tending aphids and keeping predators of aphids away (Wetterer et al., 2011). In Maine, U.S., *Myrmica rubra* infestations resulted in a significant reduction in native ant densities through competition and predation, and this also applied to the biodiversity of ground dwelling arthropods in general (McPhee et al., 2012; Garnas, 2005). Ouellette et al. (2005) showed that only a few native species can co-exist where *M. rubra* has locally invaded.

The earliest record of *M. rubra*'s presence in North America dates back to 1900 in Massachusetts (Wetterer et al., 2011), and it is purported to have been transported to North America as a stowaway in plant material imported from its native range in northern Europe (Klotz et al., 2008). In its native range in Eurasia, *Myrmica rubra* spreads over 30 degrees of latitude and extends 8,000 km across Europe, ranging from Ireland and the United Kingdom through northern Europe to western Siberia. Their presence has been confirmed as far north as the Arctic Circle and south to the Black Sea (Wetterer et al., 2011; Groden et al., 2005; Agosti and Collingwood, 1987; Elmes et al., 1999). Thus, their tolerance of different habitats is wide. Despite the enormous distribution of *M. rubra* in its native range, this species has spread very little in North America over the past century. Most North American records of *M. rubra* date from the last ten years, indicating that populations in North America are expanding rapidly. Their populations

are fragmented; however, their aggressiveness and adaptability, compounded with their lack of natural enemies in the introduced range (R. Higgins, personal communication, September 3, 2013; Wetterer et al., 2011); i.e., North America, will likely reduce ant species richness and diversity (Grodén et al., 2005; Garnas, 2005; Wittman, 2014).

An Early Detection and Rapid Response Strategy (Tu, 2009) can be used to protect conservation areas and native species from the establishment of invasive species. Depending on the magnitude of invasiveness, three types of actions can be taken: 1) eradication; 2) containment; and 3) control and mitigation (Tu, 2009). However, understanding how invasive species relates to basic environmental variables can help in undertaking these actions.

In this study, I aim to describe how the presence (relative abundance/distribution) of *M. rubra* links to environmental factors in the GTA. Specifically, I characterize local patterns of ant abundance. Results from this study will provide a guideline for prioritizing vulnerable areas of potential future invasion for surveillance and cost effective mitigation/management of already invaded areas in urban green spaces by elucidating the environmental factors associated with successful invasion of *M. rubra*.

Methods

Study sites

In 2011 and 2012, ant and other arthropod samples were collected in 9 and 15 Toronto and Region Conservation Authority (TRCA) properties, respectively across the GTA (Table 2-1) and at 19 other GTA locations (9 residential areas, 2 city parks, 2 open spaces, and 6 farms) across the GTA for visual searching. Sampling sites at each conservation area were pre-selected according to habitat types (forested area, meadow/scrubland, and riparian area), using Google Earth as well as TRCA property maps.

Sampling methods

To estimate relative abundance and the presence/absence of *M. rubra*, pitfall traps were used (Anderson, 1995; Clarke et al., 2008). For pitfall traps, 3 oz. plastic drinking cups (internal diameter of mouth: 51mm, height of the cup: 58 mm) were half filled with saline solution and unscented non hypo allergenic detergent. At each TRCA site, 5 traps were used with minimum disturbance to the surrounding substrate and with the brim of the pitfall trap flush with the ground level. They were placed along a linear transect 5 meters apart, and the location of each trap was recorded on a GPS unit (Garmin etrex Venture HC with accuracy ± 5 meters for 2011; Garmin etrex 10 with accuracy ± 3 meters for 2012). The traps were left open for 48 hours upon arriving at each site with the timing of the trap deployment ranging from 7:30 a.m. to 4:30 p.m., after which the contents were drained and stored in 75% ethanol until identification in the laboratory.

For Tommy Thompson Park in 2011, along a 550 metre linear transect across various habitats on Peninsula C, 12 stations (50 metres apart) were chosen for pitfall

traps. At each station 5 pitfall traps were placed along a linear transect 5 metres apart, perpendicular to the 550 metre transect.

In order to boost sample size, 9 volunteers who reside across the GTA (Richmond Hill [1 site], Thornhill [2 sites], North York [2 sites], Scarborough [1 site], and west/central Toronto [3 sites]) participated in backyard pitfall trapping in mid to late August, 2012. They were given instructions and a questionnaire for pitfall trap set-up and soil samples. When the ant and soil samples were returned, they were stored in a refrigerator until identification.

In 2013, from late May till August, 2 parks in Toronto (G Ross Lord Park and High Park) and 6 farms (1 in Markham, 1 in King City, 2 in Mount Albert, and 2 in Milton) across the GTA were surveyed for the presence/absence of *M. rubra* by visual searching. Each park and farm were visited multiple times for comprehensive coverage and spatial and temporal consistency, and approximately 1 or more hours were spent at each location for visual inspection in search of the fire ants.

Ant identification

Ant samples were visually inspected one by one for identification to the species level under a microscope (Nikon SMZ 1000 with magnification 0.8 – 8x) using key from Fisher et al., (2007), Klotz et al., (2008), Czechowski et al., (2002), Holldobler and Wilson, (1990), Creighton (1950), and websites such as Antweb (Antweb, 2013) and

Ants (Hymenoptera: Formicidae) of Cowling Arboretum and McKnight Prairie (Carleton College, North Field, MN, 2013).

Ants were counted individually for abundance, except for several trap samples (pitfall traps that contained more than 5,000 ants) from Tommy Thompson Park in 2011 whose numbers were estimated as follows. After oven drying for 24 hours at 65 degrees Celsius, 30 randomly chosen ants from each trap sample were weighed, and this was repeated 10 times and averaged in order to estimate the total number of ants in those traps. The weight of each 30 ant sample was consistent amongst the 10 samples, and an average of 30 ant samples was calculated. The total dry ant weight of each trap was divided by this average to estimate the number of units that contain 30 ants. Then the number of ants in each trap was estimated by multiplying the average weight of 30 ants with the number of the 30 ant unit. The accuracy of this method was assessed by following an identical protocol for 10 samples where this biomass method and actual counts were compared. During the course of ant processing, over 170,000 ants were individually identified to the species level.

Soil analysis

In 2012, a small soil core sample (15 mm in diameter, 100 mm in length) was collected from each TRCA site using a corer for soil characteristic analysis and was placed in a Ziploc bag to be analyzed later. Soil compaction was measured (with “Soil Compaction Tester” by Spectrum Technologies, Inc. Plainfield, IL) on site using the probe tip for fine soils provided by the manufacturer. At each pitfall trap location, soil moisture, ground cover surface temperature, and soil surface temperature were

recorded. A level of insolation was determined subjectively due to the amount of direct sunlight reaching the ground (open space: high, approx. 30% of direct sunlight: medium, low: the sun is covered by canopies of trees) and recorded. A vegetation type and its relative density were recorded at each habitat. Soil moisture (by volume) was measured using the ThetaProbe SM300 Soil Moisture Sensor and the HH2 Moisture Meter/Data Logger (Delta T Devices, England, U.K.). The length of the probe is 51.5 mm, which penetrates through the O/A soil horizons where this ground surface nesting species is present. Both ground cover and soil surface temperatures were measured using a Fluke 62 mini Infra Red (IR) thermometer.

The jar test method (Colorado State University Extension (“Using the jar test to determine soil texture”) was used (Swift, 2011) to determine the amount of different soil type contents. Each core sample was placed in a Mason jar with an equal weight of distilled water (United States Department of Agriculture, Natural Resources Conservation Service, 1993). The jar was vigorously shaken for a few minutes with the lid on. An electrode was placed in this suspended mixture to measure pH, and the suspension was subsequently allowed to settle for 24 hours after which, if the supernatant section of the liquid appeared unclear, it was allowed to sit for another 48 hours. If the suspended particles in the supernatant did not settle after 72 hours, the jar was again shaken vigorously and allowed to sit for 24 to 48 hours. Once each soil type had settled into layers, the thickness of each layer was measured against the total thickness to determine the percentage of each soil layer. An overall soil texture type was calculated from the proportion of different soil types (clay, sand, and silt) using the Soil Texture Calculator available from United States Department of Agriculture, Natural Resources Conservation Service (USDA, NRCS, 2013).

Statistical analysis

To elucidate the correlation between the presence/absence of *M. rubra* and other environmental variables, first ordination analysis was conducted using Principal Component Analysis (PCA) and correlation matrix. This multivariate analysis allowed the variables to be grouped according to the type and extent of contribution to the ant presence (Polis et al., 1998). With the outcome of correlation matrix analysis, stepwise regression was performed. In order to ensure the reliability of the regression and to give a different perspective, binary logistic regression (GLM with logit link) was subsequently performed for the environmental predictors to ascertain which factors contribute to the presence /absence of *M. rubra*. PCA, correlation matrix, stepwise regression, and binary logistic regression were performed with Minitab 16 statistical software (Minitab Inc., State College, PA, USA).

Results

Species diversity

During the 2011 and 2012 sampling with pitfall traps, 20 ant species, belonging to 15 genera and 4 subfamilies (Dolichoderinae, Formicinae, Myrmicinae, and Ponerinae) with a total of over 170,000 ants were individually identified. In addition, 5 more species (*Aphaenogaster rudis*, *Lasius neoniger*, *Lasius murphyi*, *Myrmica Americana*, and *Myrmica rugulosa*) were collected during visual surveys in various parks and farmlands in 2013. Excluding the 2011 sampling at Tommy Thompson Park, the

most abundance species, accounting for 99.3 % of individuals collected was *Myrmica rubra*. This species was found in 14 of 15 TRCA conservation areas during this study (Tables 2 – 2 and 2 - 3). The second most abundance species, accounting for 0.21 % of all the ants collected was *Formica subsericea*. This species were found in 11 of the 15 conservation areas (Tables 2 – 2 and 2 - 3).

In 2011, to determine whether there were correlations/associations among the presence of *M. rubra* and other ant species' composition, their relative abundance at a site, and the presence of other organisms, each taxon found in a pitfall trap was examined (Table 2 - 2).

Amongst the 15 TRCA sites, East Duffins Headwaters has the highest species richness (13 species: *M. rubra* relative abundance = 9.4 – 13.7%) whereas Kortright Centre for Conservation appears rather depauperate (1 species: *M. rubra* relative abundance = 100%) (See Tables 2 – 2 and 2 - 3). Non *M. rubra* ant species were found in all habitat types, indicating there is no ant species/habitat type association as is the case for *M. rubra*. Also no apparent correlation between non *M. rubra* ants and other arthropods found during the study was found.

At some sites, higher numbers of collembola and sow bugs were found where the abundance of *M. rubra* was high (Table 2 – 2); however, the correlation between the presence of collembola and sow bugs in abundance and the abundance of *M. rubra* is not statistically significant (Table 2 – 4). Pitfall traps that contain more than 100 *M. rubra* do not include other species of ants; however, when pitfall traps contained less than 100 *M. rubra*, other ant species (if any), up to 17 species of non *Myrmica* ants were found.

Co-existence of *M. rubra* and non *Myrmica* ants is possible only if there are less than 10 or so *M. rubra* are found in a pitfall trap. Pitfall traps without the presence of *M. rubra* often contained *P. imparis*, *A. fulva*, *C. pennsylvanicus*, and *F. subsericea* (Tables 2 – 2 and 2 - 3).

It should be noted that 3 ants collected during visual surveys on a farm in Mount Albert turned out to be *Myrmica rugulosa* from DNA barcoding identification. *M. rugulosa* is native to Europe with no previously reported occurrences in North America.

Soil analyses

Soil samples collected in 2012 show that there are 7 different soil types (clay, loam, sand, sandy loam, silt, silt loam, and silty clay) out of possible 12 soil type combinations. Soil pH ranges from 5.71 to 8.52, and the presence of *M. rubra* was observed at all pH, even at two extreme ends. Soil compaction ranges from 10 to 260 psi, and no correlation was found between soil type and soil compaction as well as between soil type and soil moisture. Silt was found to hold a wide range of soil moisture compared to other soil types (Figure 2 – 1). Soil compaction is not correlated with habitat type.

Habitat

Each conservation area generally contains 3 or more habitat types: 1. Open meadow 2. Forested/woody area 3. Shore or beach area by a brook or a lake 4. Open field with patchy ground cover with variation in size, extent, and uniformity of spatial distribution across a habitat, and the density of ground cover/vegetation varies as well as

soil types at each habitat. *M. rubra* was found in all habitat types, ranging from a very wet sandy brook shore, an open meadow, to a forested area whereas other species are rather habitat type specific such as *Formica exsectoides* and *Lasius umbratus*, which were only found in forested areas (See Tables 2 – 2 and 2 - 3).

Insolation levels varied at each habitat type, and the amount of sun light reaching the soil surface is dependent of the thickness of canopy cover in a forest and/or the density of vegetation and ground cover.

A variety of soil types were found even in the same habitat type. It was also found that soil moisture varied even in the same type of habitat amongst the conservation areas (from 2.3 % by volume to 82.0 %); that is, soil moisture varied from a forested area in one conservation area to another area in another conservation area (Table 2 – 3).

The heaviest infestations by abundance of *M. rubra* were found at Petticoat Creek Conservation Area, Bruce's Mill Conservation Area, Black Creek Pioneer Village, and Tommy Thompson Park. For these four sites, habitat types are a forested area (three out of the four sites) and a marshy meadow area (Petticoat Creek C.A.). Insolation in the forest areas was medium to low whereas the meadow has a high insolation level. The soil moisture level in the forest area at Bruce's Mill Conservation Area was unusually high (59.3 – 82 %) whereas at the other three sites the soil moisture level was much lower and comparable with one another (approx. 15 – 24 %).

Presence/absence of *M. rubra* in relation to environmental factors: Statistical analyses

To determine the relationship between the presence/absence of *M. rubra* and environmental and biotic factors, correlation matrix analysis, stepwise regression, binary logistic regression, and 2 tailed unpaired t-tests were performed. The environmental and biotic factors to be examined were:

1. Habitat type
2. Abundance of *M. rubra* and relative abundance of them in relation to other ant species
3. Presence and abundance of other ant species
4. Soil type
5. Soil pH
6. Soil moisture
7. Soil surface temperature
8. Ground cover/vegetation temperature
9. Type of surrounding areas
10. Soil compaction
11. Insolation
12. altitude

First, correlation matrix analysis was performed to show how and extent of each factor is correlated with other factors. As shown in Table 2 – 5, ground cover/vegetation and soil surface temperatures are correlated with altitude. It also shows that the presence/absence of *M. rubra* is associated with 1. Soil moisture 2. Soil surface temperature 3. Altitude, but the correlation values are relatively low.

Next, in order to confirm the findings with the correlation matrix analysis, a stepwise regression was performed to see whether the results would agree. The stepwise regression completed both forward selection and backward elimination with alpha value set to the default 0.15 to select variables that attribute to the

presence/absence of *M. rubra* at each habitat. The significant but weak (low R^2) outcome agrees with the results obtained by the correlation matrix analysis (See Table 2 - 6).

Another statistical method (binary logistic regression) was used to verify the findings derived from the two aforementioned methods. As expected, the outcome is the same as the previous results, showing that the 3 most influential environmental factors for the presence/absence of *M. rubra* are soil moisture, soil surface temperature, and altitude (See Table 2 – 7). The p-values for each variable are 0.005 (soil moisture), 0.001 (soil surface temperature), and 0.001 (altitude) with corresponding odds ratio values of 1.04, 1.14, and 0.99, respectively. According to the findings with binary logistic regression, 2 tailed unpaired t-tests were performed with the presence and absence (of *M. rubra*) data of each 3 variables to demonstrate that there is a significant difference between two datasets (Figures 2 – 2, Table 2 – 8).

Amongst these 3 abiotic factors that are relevant to the presence/absence of *M. rubra*, no correlation was found between soil moisture and altitude as well as between soil moisture and soil surface temperature; however, a correlation was found between soil surface temperature and altitude (See Table 2 – 5).

For habitat type, soil pH, soil type, soil compaction, and insolation, a weak correlation was found between soil moisture and compaction (p-value = 0.075 and Pearson correlation = - 0.324) (See Table 2 – 9); however, no correlations were found for the persistence of *M. rubra* with other variables (p-values \gg 0.05 for these variables) except for soil moisture. A stepwise regression showed that other than those 3 variables mentioned above, soil compaction is relevant for the presence/absence of *M.*

rubra with a p-value = 0.019 and a t-value = 2.50 (Table 2 – 10). A binary logistic regression analysis showed a p-value of 0.036 for soil compaction measured against the presence/absence of the ant with an odds ratio of 1.02 (Table 2 – 11).

Soil moisture and abundance were not correlated (p-value = 0.958, Pearson correlation = -0.010, See Table 2 – 9). Clarke et al. (2008) found no obvious factors that elucidate the variation of the abundance of another invasive species Argentine ant (*Linepithema humile*) in urban parks in San Francisco even though they reported that soil moisture was positively related to general species richness as well as native ant species richness in 24 urban parks in San Francisco.

Both soil surface temperature and ground cover/vegetation temperature were found to be highly correlated (p value = 0.000, Pearson correlation = 0.930, See Table 2 - 5); however, in terms of the extent of attribution to the persistence of *M. rubra*, it was found by stepwise regression that only soil surface temperature is relevant (see Table 2 – 6). Correlation between soil surface temperature and soil moisture was not found (p-value = 0.251, see Table 2 – 5).

Altitude/elevation range for this study spanned 358 metres, ranging from 74.4 metres to 432.3 metres above sea level. No correlation between altitude and soil types (p-value >> 0.05 for all soil types). Also no correlation was found between altitude and soil moisture (p-value = 0.247, see Table 2 – 5). In addition to the attribution of altitude to the persistence of *M. rubra*, it was also found that pH of soil is correlated with altitude (p value = 0.013, Pearson correlation = - 0.436), which this might be due to the tree species prevalent at various elevation levels (Table 2 – 9).

Soil moisture was one of the three most relevant abiotic factors on the presence/absence of *M. rubra*, hence to determine the rate of fluctuation of soil moisture throughout the day, soil moisture measurements as well as soil surface, vegetation cover (only in meadow), and air temperatures were taken every two hours from sunrise (6:46 a.m.) to sunset (7:45 p.m.) on September 6, 2013 in a meadow area and in a forested area (see Figures 2 – 3 and 2 – 4). It was made certain that at least 3 days prior to the experiment, it did not rain and that the condition of soil remained constant and the day of experiment was sunny with no chance of precipitation. During the course of day the soil moisture content varied by only 2.8% (meadow) and 3.0% (forested area) throughout the day (Figures 2 - 3), and it was concluded that the level of soil moisture remained fairly constant throughout the day regardless of habitat types (meadow and forested area).

In addition to all correlation and regression tests, each individual environmental factor was also tested for any correlation with the presence/absence of the ants using binary logistic regression, and the findings were in accord with the aforementioned findings: that is, soil moisture, soil surface temperature, and altitude were the most influential abiotic factors for the persistence of *M. rubra*.

Ant ethology from visual surveys

It is widely accepted that *M. rubra* takes advantages of a wide range of microhabitats for nesting (Grodén et al., 2005). During countless visual surveys in 2011, 2012, and 2013, their nests were found under or within fallen woody debris, under rocks and stones, and even under anthropogenic materials left in a field such as cardboards

and plywood sheets, at the bottom of medium to tall (50 – 150 cm) densely grown marshy plants, and most frequently under leaf litter and under a layer of rather wet straw/dead stem like material whereas the ants were occasionally found foraging on unpaved paths/trails in shady areas but hardly ever sunny areas and rarely on plants. When *M. rubra* were found on plants, the presence of aphids was also checked. According to Seiffert (1988), “*M. rubra* tends aphids more frequently than other members of the genus”. It, however, was hardly observed tending aphids during the field work that spanned 3 years. Only one pitfall trap was found with aphids (100 plus) along with 3 Lepidoptera and 1 Lepidoptera larva on Peninsula C at Tommy Thompson Park in 2011 amongst all the pitfall traps used for this study.

M. rubra is primarily carnivorous (Fisher & Cover, 2007), and under woody debris and rocks on wet soil, they were seen preying on snails and earthworms. At G. Ross Lord Park near York University Keele campus, a single *M. rubra* was seen attacking a small Lepidoptera larva in a dense grassy area.

During the 3 year long visual surveys, *M. rubra* was observed in various microhabitats except for on concrete surfaces. On a sunny summer day, any concrete surface readily exceeds 45 – 50 degrees Celsius, and the low heat tolerance of this species seems to prevent them from foraging on any surface that exceeds 50 degrees Celsius (Brian, 1973; personal observations). If *M. rubra* is exposed to any surface higher than 54 degrees Celsius, it will be killed within 5 – 6 seconds (personal observations), and this may elucidate the absence of infestation south of the service road on Peninsula C at Tommy Thompson Park and their absence in city centres.

***Myrmica rubra* reproductives**

The presence of *M. rubra* larvae was observed in their nests throughout the field season of this study (April through October). During the field work in late August and early September in 2011 and 2012, both alate and dealate queens and males were found in the pitfall traps (Tables 2 – 2 and 2 - 3). Live males were observed en masse in late August, 2012 on tops of fallen logs and a bird observing blind on Peninsula C at Tommy Thompson Park, suggesting that they congregate at higher places than the ground level as observed by Hicks (2012). In mid August (a park near Eglinton Flats, North York) and in early September (Tommy Thompson Park) in 2013, only several *M. rubra* males were found in their nests along with larvae. Every week in late August until early September 2013, male *M. rubra* were sought at various locations at Tommy Thompson Park; however, the abundance in 2013 was much lower than in 2012.

Discussion

Comparisons of ant species diversity and richness, and interaction

Occurrences of *M. rubra* were confirmed at the majority of the sites across the GTA during this study. It is essential to document species composition and other organisms and compare the effects of this non-native invasive ant on the taxa found in each study site as it is widely reported that non-native species often outcompete and displace native species and resources (Holldobler & Wilson, 1990). In addition to understanding biological diversity in the study areas, it is also crucial to elucidate the association of *M. rubra* with biotic and abiotic factors.

The ant species identified in this study is likely to represent the majority of species present in the GTA. The species richness estimate is based on observed captures, and in consideration of the efficacy of pitfall trap capture, which is frequently used for ant surveys (King & Porter, 2005; Ward et al., 2001) and the consistency of species richness found at each conservation area in 2 consecutive years, the estimate of species richness might be considered a reasonable one.

For the pitfall traps with ants present, *M. rubra* were frequently found in those traps. Non *M. rubra* ants were found in the pitfall traps containing more than 100 *M. rubra*; however, a maximum of 17 species of non *M. rubra* ants were found in pitfall traps. This was more apparent when a pitfall trap contained less than 10 or so *M. rubra* ants. Co-existence of non *M. rubra* and *M. rubra* ants seems possible for *P. imparis*, *B. depilis*, *F. subsericea*, and *S. molesta*. The cryptobiotic, hypogeic, small, and inconspicuous nature of *B. depilis* and *S. molesta* reduces competition for food and nesting space with the larger *M. rubra* and allows them to persist in invaded habitats by *M. rubra* (Suarez et al., 1998). Different thermal tolerances of *P. imparis* and *M. rubra* may help avoid displacement by *M. rubra*, for the cold tolerant *P. imparis* is more active in colder months when the activity of *M. rubra* is reduced (Tschinkel, 1987). In addition to these characteristics present in these aforementioned ants, *F. subsericea* and *P. imparis* use their strong repellent chemicals as defence mechanisms (formic acid spray for *F. subsericea* and alkaloidal venom for *P. imparis*) in moderately invaded areas by *M. rubra* (Eaton & Kaufman, 2007; Blum et al., 1980, Sorrells et al., 2011). Probably the physical characteristics and defence mechanisms of these ants allow them to co-exist with a small number of *M. rubra* and to resist displacement by this invasive species.

Whenever *S. molesta* was found, it was nearly always clung to *M. rubra*'s limbs by their mandibles, suggesting aggression between these two species. The aggressiveness of this cryptic ant, in some cases, has been reported with another invasive ant *Solenopsis invicta*, which was unable to colonize areas with high *S. molesta* densities (MacGown: Rao & Vinson, 2004: Vinson & Rao, 2004).

Presence and abundance of ants amongst habitats and infestations

Myrmica rubra was found in all habitat types, suggesting that this invasive species is a generalist in habitat preference and is not limited to a specific habitat (Clarke et al., 2008). Not only is *M. rubra* common to various habitat types but also uses a wide array of microhabitats for nesting and multiple ecosystems ranging from lawns, gardens, recreational parks, scrub-shrub wetlands, and deciduous forests (Grodén et al., 2005). Ouellette et al. (2010) also reported that in Acadia National Park, ME, *M. rubra* occupies habitat types used by most of the entire ant community, predominantly composed of native species.

Although heavy *M. rubra* infestations were observed at 4 conservation areas (Petticoat Creek Conservation Area, Bruce's Mill Conservation Area, Black Creek Pioneer Village, and Tommy Thompson Park), areas of infestation are fragmented for the rest of these lands. Despite the heavy infestation along the transect on Peninsula C at Tommy Thompson Park, the continuous area of infestation ended by a physical barrier such as a road. The infestation of *M. rubra* was fragmented amongst all the conservation areas, parks, and farmlands where this study was conducted; however,

whether the areas where occurrences were not observed represent their early stages of this ant's expansion into these areas or its inability to invade these areas are not known.

Environmental factors relevant to the presence/absence of *M. rubra* from statistical analyses

From an array of statistical methods, it was concluded that soil surface moisture, soil surface temperature, and altitude were the 3 most relevant abiotic factors in the elucidation of the presence/absence of the non-native invasive ant *Myrmica rubra*. Subsequent t-tests showed that for the 3 factors there were significant differences between the data for *M. rubra* present sites and that for absent sites.

As a ground surface nesting species, this cold tolerant Palearctic native species' nests are found under rocks, leaf litter, and fallen woody debris to prevent soil temperature from reaching its lethal limit (Maysov & Kipyatkov, 2011; Brian, 1973). Sufficient amounts of soil moisture will keep soil surface temperature cool during the hot season by way of the heat of evaporation. Also areas with adequate soil moisture will attract prey of this primarily carnivorous ant such as snails and earthworms, and it is beneficial to found a nest in such areas to minimize travel distances for foraging, especially in areas of high nest densities in light of their intraspecific aggression (Garnas et al, 2007). Groden et al.(2005) reported that *M. rubra* populations were associated with "very moist" habitats such as the edges of lakes or ponds, moist forests, and wetlands, and this agrees with the abundant presence of *M. rubra* in the forest area and the low vegetation forest at Bruce's Mill Conservation Area where the soil moisture was exceedingly high (up to 82%). On soil moisture, Wetterer et al. (2011) found that *M.*

rubra was ubiquitous in their native range; however, in the Mediterranean region, it was only found in moist places, confirming the validity of this finding in this study.

Soil moisture has been found to have positive correlations to species richness in parks in San Francisco (Clarke et al., 2008), and for another invasive ant Argentine ant (*Linepithema humile*), their abundance is positively correlated with soil moisture (Holway et al., 2002, 2006).

Mean soil surface temperatures for *M. rubra* presence sites and absence sites are significantly different: $19.0\text{ C}^{\circ} \pm \text{SD } 5.33$ for presence sites and $17.2\text{ C}^{\circ} \pm \text{SD } 4.97$ for absence sites with $p\text{-value} = 0.032$. It was found that minimum soil temperatures were higher for the sites with *M. rubra* present than the absence sites (See Figure 2 - 5), and this must be due to their ectothermic nature and that higher minimum ground temperatures allow them to forage more frequently.

The ratio of deciduous to coniferous trees in general decreases with altitude, and this attributes to increased areas covered by coniferous trees. Groden et al. (2005) did not observe *M. rubra* within a dense spruce-fir coniferous forest habitat along the Maine coast even though the ants were seen at the edge of the spruce-fir forest. In this study, less focus was paid on the species of trees in forest areas in each study area; however, more coniferous trees were observed in the western half of the GTA conservation areas where significantly less numbers of *M. rubra* were collected. In general, conservation areas in the western half are situated at higher altitudes, and as shown in the Results section that altitude and soil surface temperature is correlated, indicating that minimum soil surface temperature at higher altitudes might prevent *M. rubra*'s foraging frequency.

Various studies have shown that for two major non-native invasive ants prevalent in North America, *Solenopsis invicta* (the red imported fire ant) and *Linepithema humile* (the Argentine ant), soil moisture, elevation/altitude, lethal temperatures, seasonal heat accumulation are defining abiotic factors for their distribution within their invaded range (Mallis, 1941: Korzukhin et al., 2001: Porter, 1988: Cokendolpher et al., 1990: Vinson, 1997: Walters et al., 2004: Human et al., 1998), and their findings that show limiting abiotic factors for other invasive ants agree with the findings in this study for *M. rubra*.

As briefly mentioned in the Results section, it was noted that soil compaction was found to have a weak negative correlation with soil moisture level (p-value = 0.075 and Pearson correlation = - 0.324) and that soil compaction is relevant for the presence/absence of *M. rubra* from the binary logistic regression analysis (p-value = 0.036) (See Tables 2 – 9, 2 – 10, and 2 – 11); however, this finding is not comprehensive due to the small number of samples (N = 31) for soil compaction measurements. A t-test for the soil compaction measurements for *M. rubra* presence and absence sites shows that there is no significant difference between the soil compaction of *M. rubra* presence sites and that of the absence sites (P-value = 0.155: mean for presence sites = 142.7 SD = 82.3; mean for absence sites = 105.0 SD = 57.5) (See Table 2 – 12).

Indication of *M. rubra* male swarming for nuptial flights

The emergence of alate *M. rubra* males en masses in late August, 2012 at Tommy Thompson Park and the presence of alate queens observed in pitfall traps suggest a possibility of male only swarming for nuptial flights even though Groden et al.

(2005) reported that throughout their 3 year survey period in Acadia National Park, ME, they observed only two alate queens in numerous infested areas and that no alate males or queens were captured in traps from May through September, and they concluded that they “saw no evidence of a nuptial flight” by the end of August during which alate queens were present (Grodén et al., 2005). The Argentine ant, another non-native invasive ant, is not known to undergo mating flights for dispersal in their introduced range (Suarez et al., 2001). Hicks reported that male only swarming flights in Newfoundland were observed in late September, 2010, also suggesting possibilities of nuptial flights (Hicks, 2012). Based on Hicks’ observations and the mass emergence of male *M. rubra* at Tommy Thompson Park in late August, 2012, nuptial flights do occur in North America even though they may be rare.

A shift towards the increased dependence on colony budding from nuptial flights for dispersal elucidates the locally high nest densities often seen in the introduced range whereas nuptial flights are the major means of dispersal in the native range, resulting in wide range dispersal and subsequently reduced nest densities (Boomsma et al., 1980; Brian, 1956; Elmes, 1974; Elmes, 1975; Grodén et al., 2005; Holldobler et al., 1990).

Persistence, displacement of other ant species, recent emergence, and implications

Albion Hills Conservation Area is the only conservation area amongst 15 TRCA sites where *M. rubra* was not found in pitfall traps. In order to ascertain factors that are not present in other TRCA sites, an ecological niche model with a focus on the most limiting environmental factor amongst 19 combinations of temperature and precipitation

levels and altitude (See Chapter 2) was applied, and the abiotic factor that influences the most for the persistence of *M. rubra* was shown as the wide diurnal temperature range (the mean range of monthly (maximum temperature – minimum temperature)) (See Figure 2 - 6). The wide diurnal temperature range was also the limiting factor at Tommy Thompson Park where the abundance of *M. rubra* was observed; however, t-tests indicated that there was a significant difference between these sites for the 3 most influential factors (i.e. soil surface moisture, soil surface temperature, and altitude) for *M. rubra*'s persistence (Table 2 – 13) in addition to the wide diurnal temperature range.

Other possible explanations for the absence of *M. rubra* at Albion Hills Conservation Area are 1. sample size 2. abundance too low to be detected. An increased number of pitfall traps and more frequent sampling would determine the validity of these possibilities.

Co-existence of *M. rubra* and non *M. rubra* happens as long as the abundance of *M. rubra* in the coexisting habitat is scarce; however, in the pitfall traps where the number of *M. rubra* exceeded 100, no other ant species were found. From these data *Myrmica rubra* appears to displace other ant species. This finding does support the findings by others that exotic ant species negatively impact native ant communities (Ouellette et al., 2010) and that *M. rubra* reduces species richness and diversity and causes the local extirpation of the native ant fauna in Acadia National Park, ME (Garnas, 2005, Groden et al., 2005).

Not only is *M. rubra* characterized as a generalist in habitat preference, it was observed in the centre of a habitat matrix where it is used by most of the overall ant community, and the majority of it are native ants (Ouellette, 2010). This indicates that *M. rubra* is a

superior competitor to native ants for resources and has a great potential for this species to dominate habitats as their populations increase, posing a threat to the current ant community, possibly driving the ecology of the area towards substantial and likely negative changes. Although monogyne forms of ants may have larger dispersal potential, polygyne forms such as *M. rubra* can achieve higher colony densities and consequently place higher impacts on native ants; i.e., complete displacement of native ants by this invasive species (Tschinkel, 2006; Garnas, 2005).

Displacement of native ants by invasive species can be by either interactive or non-interactive processes where non interactive processes as different responses to heterogeneous environmental factors (Wittman, 2014).

In the native range of *M. rubra*, natural enemies such as parasitic *Maculinea* butterfly larvae and co-evolved competitors via habitat displacement keep *M. rubra*'s populations under control (Elmes et al., 1998; Seiffert, 1988); however, in North America, the absence of co-evolved competitors and natural enemies allow this non-native invasive species to multiply and expand to levels of becoming significant pests. Other than the 3 aforementioned abiotic limiting factors, the availability of food resources and surrounding plant community as biotic ecological factors appear to be limiting ones for *M. rubra* in North America (Morrill et al., 1978; Kennedy, 1998) even though the potential roles of these factors on *M. rubra*'s populations in North America are unknown (Grodén et al., 2005).

Despite the broad range of *M. rubra* in the native Palaearctic, this species has a very limited distribution in North America; that is, its occurrence records in the US and Canada come from a very narrow band of latitude. Another astonishing aspect about

M. rubra is how little it has spread over the past 100 years in light of the fact that it has been introduced on multiple occasions (Grodén et al., 2005).

This phenomenon could be elucidated by the following hypotheses: The *M. rubra* populations in North America have a fairly narrow range of climatic tolerances, indicating that the North American populations might have derived from colonists from a limited area or even a single locale and are unable to expand beyond their current latitudinal range in the introduced range even though various *M. rubra* populations in Europe exhibit physiological adaptations to the local climate (Elmes et al., 1999). An array of ecological niche/species distribution models developed as part of this project supports that certain parts of the GTA have very unique micro regional climate that is suitable for *M. rubra* habitat. Perhaps this presumably genetically preselected climate prone nature of *M. rubra* has kept its distribution in North America to a very limited level; in other words, the provenance of the North American populations might have descended from a group(s) which had relatively high cold tolerances, and the range of environmental requirements by this colonizer group as well as its adaptability to local climate conditions contribute to successful establishment within habitable climate zones in its introduced range provided that they are safe from lethal high temperatures of summer (Brian, 1973).

It has been over 100 years since the first recorded occurrence of *M. rubra* was found in Massachusetts, U.S.A. (Ellison et al., 2012); however, *M. rubra* had been keeping its profile low up until 1990s after more than a century of “quiet” presence in North America (Grodén et al., 2005). Reports of *M. rubra* outbreaks are recent, and most records are from the past ten years, indicating that the rate of expansion of the

North American populations is exponential. A feasible and perhaps plausible explanation for this recent explosive emergence of this species might be due to an introduction of a new strain of *M. rubra*. In light of the fact that this species has been introduced to North America on multiple occasions, this speculation seems reasonable. Hicks et al. (2014) reported that there were at least four distinct sources of *M. rubra* in Newfoundland from their mitochondrial DNA and haplotype analyses, supporting this “strain” hypothesis. It was found that based on mitochondrial DNA sequences, Hicks et al. (2014) reported that there were 7 different haplotypes of *M. rubra*, indicating that there are genetic differences amongst North American populations.

In order to control *M. rubra* populations, several biological agents have been tested, ranging from microsporidia, *Pseudacteon* species to fungal pathogens (Higgins, 2013). Target specificity of microsporidia (Microsporidia: Nosematidae) is too broad, and this may infect other arthropods such as honey bees. *Pseudacteon* species (Diptera: Phoridae) have shown very target specific effectiveness to control the red imported fire ant (*Solenopsis invicta*) but not for *M. rubra* (Higgins, 2013). Three types of previously unreported fungal pathogens seem to have some promising effects on *M. rubra* in vitro; however, more work is needed (Evans et al., 2010).

This study provides insight into ecological processes caused by *M. rubra* infestation and environmental conditions in which it thrives, and a fundamental step in understanding the characteristics of this species and the repercussion of *M. rubra* infestation. The results from the data along with the findings from other publications show that it is clear that *M. rubra* does displace native ants and reduces ant species

richness and diversity, and in some cases, this non-native invasive ant causes local extirpation of native ant fauna.

Devoid of co-existing competitors and natural enemies in North America, *M. rubra* is very likely to continue to expand its ranges from coast to coast. It is, therefore, absolutely vital to develop control methods before populations reach peak levels and result in permanent damage to ecological systems. Once an invasive species is established in its introduced range, it is nearly impossible to eradicate it and is very costly if ever possible. The most cost effective way to combat potential threat of invasive species is prevention (Fitzpatrick et al., 2005), and tools often used in invasion biology such as ecological niche/species distribution models should be applied to identify susceptible areas to be vigilant to minimize and prevent possible future damage caused by invasion.

Tables and figures

Conservation area	Location	Dates of sampling
Petticoat Creek Conservation Area	Pickering, ON (43.803° N, 79.106° W)	August 24 & 26, 2011 August 20 & 22, 2012
Glen Rouge Campground	Toronto, ON (43.804° N, 79.145° W)	August 24 & 26, 2011 August 20 & 22, 2012
Rouge Park	Toronto/Pickering, ON (43.814° N, 79.157° W)	August 24 & 26, 2011 August 20 & 22, 2012
Altona Forest	Pickering, ON (43.827° N, 79.140° W)	August 24 & 26, 2011 August 20 & 22, 2012
East Duffins Headwaters	Uxbridge, ON (44.006° N, 79.097° W)	August 24 & 26, 2011 August 20 & 22, 2012
Bruce's Mill Conservation Area	Stouffville, ON (43.944° N, 79.351° W)	August 24 & 26, 2011 August 20 & 22, 2012
Bathurst Glen Golf Course	Richmond Hill, ON (43.927° N, 79.470° W)	August 24 & 26, 2011
Oak Ridges Corridor Nature Reserve	Richmond Hill, ON (43.954° N, 79.429° W)	August 20 & 22, 2012
Boyd Conservation Area	Vaughan, ON (43.814° N, 79.584° W)	August 21 & 23, 2012
Kortright Centre for Conservation	Woodbridge, ON (43.834° N, 79.592° W)	August 21 & 23, 2012
Heart Lake Conservation Area	Brampton, ON (43.740° N, 79.789° W)	August 21 & 23, 2012
Glen Haffy Conservation Area	Caledon, ON (43.938° N, 79.945° W)	August 21 & 23, 2012
Albion Hills Conservation Area	Caledon, ON (43.833° N, 79.926° W)	August 21 & 23, 2012
Black Creek Pioneer Village	Toronto, ON (43.772° N, 79.518° W)	September 14 & 16, 2011 August 29 & 31, 2012
Tommy Thompson Park	Toronto, ON (43.625° N, 79.336° W)	September 9 & 11, 2011 August 28 & 30, 2012

Table 2 - 1: Conservation areas, locations, and dates of sampling for pitfall traps.

Conservation area	Habitat type	<i>M. rubra</i> (% of <i>M. rubra</i> in the trap)	<i>F. subsericea</i>	<i>L. alienus</i>	<i>T. caespitum</i>	<i>C. pennsylvanicus</i>	<i>A. fulva</i>	<i>P. pennsylvanica</i>	<i>T. sessile</i>
Petticoat Creek Conservation Area	Meadow	149 workers 1 dealate queen (100%)	0	0	0	0	0	0	0
	Forested area	30 workers 1 male (86.1%)	0	0	0	5	0	0	0
	By the creek/lake in a light forest area	97 workers 3 males 1 dealate queen 1 alate queen (72.3%)	10	1	0	0	0	0	0
Glen Rouge Campground	Sandy beach/marshy area	1 worker (25%)	0	2	0	0	0	1 alate queen	0
	Forested area	0 (0%)	0	0	0	5	3	1	0
Rouge Park	Non forest vegetation/grassy area by the creek	15 workers (71.4%)	2	4	0	0	0	0	0
	Sandy area by the creek	38 workers (95%)	1	1	0	0	0	0	0
	Meadow, not close to the creek	0 (0%)	0	1	0	0	0	0	0
	Forested area	0 (0%)	0	0	0	1	3	0	0

Table 2 - 2: Ant species and other arthropods sampled at 9 TRCA sites in 2011.

Conservation area	Habitat type	<i>P. imparis</i>	<i>T. ambiguus</i>	<i>C. cerasi</i>	<i>S. molesta</i>	<i>C. novaeboracensis</i>	<i>S. diecki</i>	Collembola	Diptera	harvestmen
Petticoat Creek Conservation Area	Meadow	0	0	0	0	0	0	39	16	8
	Forested area	0	0	0	0	0	0	0	93	7
	By the creek/lake in a light forest area	0	0	0	28	0	0	11	18	2
Glen Rouge Campground	Sandy beach/marshy area	0	0	0	0	0	0	4	28	0
	Forested area	0	0	0	0	0	0	3	24	7
Rouge Park	Non forest vegetation/grassy area by the creek	0	0	0	0	0	0	16	5	3
	Sandy area by the creek	0	0	0	0	0	0	26	15	0
	Meadow, not close to the creek	0	0	0	0	0	0	7	10	0
	Forested area	0	0	0	0	0	0	2	18	0

Table 2 – 2 Continued

Conservation area	Habitat type	sowbugs	wasps	snails	slugs	Hemiptera	spiders	Orthoptera	earthworms
Petticoat Creek Conservation Area	Meadow	16	3	7	7	3	0	1	0
	Forested area	54	1	2	2	0	0	0	3
	By the creek/lake in a light forest area	37	2	3	0	2	2	4	0
Glen Rouge Campground	Sandy beach/marshy area	2	6	1	0	1	3	1	0
	Forested area	16	3	1	2	0	0	0	0
Rouge Park	Non forest vegetation/grassy area by the creek	5	2	0	6	1	1	0	0
	Sandy area by the creek	0	1	1	0	2	3	19	0
	Meadow, not close to the creek	0	5	1	0	1	1	6	0
	Forested area	6	3	0	0	0	0	0	0

Table 2 – 2 Continued

Conservation area	Habitat type	<i>M. rubra</i> (% of <i>M. rubra</i> in the trap)	ticks	Coleoptera	miscellaneous
Petticoat Creek Conservation Area	Meadow	149 workers 1 dealate queen (100%)	0	1	1 earthworm
	Forested area	30 workers 1 male (86.1%)	1	2	0
	By the creek/lake in a light forest area	97 workers 3 males 1 dealate queen 1 alate queen (72.3%)	3	1	2 bees and 1 unidentified insect
Glen Rouge Campground	Sandy beach/marshy area	1 worker (25%)	0	12	0
	Forested area	0 (0%)	0	1	1 chigger
Rouge Park	Non forest vegetation/grassy area by the creek	15 workers (71.4%)	0	2	0
	Sandy area by the creek	38 workers (95%)	0	4	2 Lepidoptera 1 Dermaptera 1 unidentified larva
	Meadow, not close to the creek	0 (0%)	0	8	0
	Forested area	0 (0%)	0	0	0

Table 2 – 2 Continued

Conservation area	Habitat type	<i>M. rubra</i> (% of <i>M. rubra</i> in the trap)	<i>F. subsericea</i>	<i>L. alienus</i>	<i>T. caespitum</i>	<i>C. pennsylvanicus</i>	<i>A. fulva</i>	<i>P. pennsylvanica</i>	<i>T. sessile</i>
Altona Forest	Forested area	4 workers (100%)	0	0	0	0	0	0	0
	By the creek	2 workers (100%)	0	0	0	0	0	0	0
East Duffins Headwaters	Forested area	2 workers (12.5%)	3	0	1	0	6	0	2
	Meadow	3 workers (9.4%)	13	4	2	1	0	0	0
Bruce's Mill Conservation Area	Meadow	6 workers (54.5%)	2 workers 1 alate queen	1	0	0	0	0	0
	Forested area	2565 workers (100%)	0	0	0	0	0	0	0
	Low vegetation meadow	841 workers (100%)	0	0	0	0	0	0	0
Bathurst Glen Golf Course	Meadow	83 workers (95.4%)	1	3	0	0	0	0	0
	Forested area	1 worker (50%)	0	1	0	0	0	0	0

Table 2 – 2 Continued

Conservation area	Habitat type	<i>T. sessile</i>	<i>P. imparis</i>	<i>T. ambiguus</i>	<i>C. cerasi</i>	<i>S. molesta</i>	<i>C. novaeboracensis</i>	<i>S. diecki</i>	Collembola	Diptera
Altona Forest	Forested area	0	0	0	0	0	0	0	5	78
	By the creek	0	0	0	0	0	0	0	1	29
East Duffins Headwaters	Forested area	2	0	0	0	0	1	1	27	99
	Meadow	0	7	0	1	1	0	0	19	107
Bruce's Mill Conservation Area	Meadow	0	0	0	0	0	0	1	0	30
	Forested area	0	0	0	0	0	0	0	6	35
	Low vegetation meadow	0	0	0	0	0	0	0	2	23
Bathurst Glen Golf Course	Meadow	0	0	0	0	0	0	0	3	46
	Forested area	0	0	0	0	0	0	0	2	49

Table 2 – 2 Continued

Conservation area	Habitat type	harvestmen	sowbugs	wasps	snails	slugs	Hemiptera	spiders	Orthoptera
Altona Forest	Forested area	4	172	0	0	3	0	0	0
	By the creek	3	37	1	0	5	1	1	1
East Duffins Headwaters	Forested area	0	22	12	2	2	2	2	0
	Meadow	0	5	17	0	0	24	2	2
Bruce's Mill Conservation Area	Meadow	2	42	1	2	0	11	11	0
	Forested area	1	2	3	0	0	2	0	1
	Low vegetation meadow	0	2	13	5	2	0	0	0
Bathurst Glen Golf Course	Meadow	0	0	4	2	0	22	0	0
	Forested area	0	0	1	1	0	4	1	0

Table 2 – 2 Continued

Conservation area	Habitat type	earthworms	ticks	Coleoptera	miscellaneous
Altona Forest	Forested area	0	0	0	0
	By the creek	0	0	4	0
East Duffins Headwaters	Forested area	0	0	4	1 centipede 3 unidentified larvae
	Meadow	0	2	2	1 Lepidoptera 2 bees 4 unidentified larvae
Bruce's Mill Conservation Area	Meadow	0	0	14	3 unidentified larvae
	Forested area	0	4	3	1 centipede
	Low vegetation meadow	0	0	14	1 caterpillar 3 unidentified larvae
Bathurst Glen Golf Course	Meadow	0	3	0	5 unidentified larvae
	Forested area	0	0	4	2 frogs

Table 2 – 2 Continued

Conservation area	Habitat type	<i>M. rubra</i> (% of <i>M. rubra</i> in the trap)	<i>F. subsericea</i>	<i>L. alienus</i>	<i>T. caespitum</i>	<i>C. pennsylvanicus</i>	<i>A. fulva</i>	<i>P. pennsylvanica</i>	<i>T. sessile</i>
Black Creek Pioneer Village	Forested area	1 worker (33.3%)	0	0	0	0	0	0	0
	Grassy area	5728 workers (100%)	0	0	0	0	0	0	0
	Near the creek	59 workers (98.3%)	1	0	0	0	0	0	0
Tommy Thompson Park	Dead tree area Station A/1	11 workers (64.7%)	0	0	6	0	0	0	0
	Dead tree area Station B/2	95 workers (100%)	0	0	0	0	0	0	0
	Dead tree area Station C/3	1 worker 1 dealate queen (100%)	0	0	0	0	0	0	0
	Live tree area Station D/4	54 workers 1 dealate queen 4 males (100%)	0	0	0	0	0	0	0

Table 2 – 2 Continued

Conservation area	Habitat type	<i>P. imparis</i>	<i>T. ambiguus</i>	<i>C. cerasi</i>	<i>S. molesta</i>	<i>C. novaeboracensis</i>	<i>S. diecki</i>	Collembola	Diptera	harvestmen
Black Creek Pioneer Village	Forested area	1	1	0	0	0	0	0	5	3
	Grassy area	0	0	0	0	0	0	1	4	1
	Near the creek	0	0	0	0	0	0	0	3	3
Tommy Thompson Park	Dead tree area Station A/1	0	0	0	0	0	0	32	47	1
	Dead tree area Station B/2	0	0	0	0	0	0	3	14	2
	Dead tree area Station C/3	0	0	0	0	0	0	2	38	0
	Live tree area Station D/4	0	0	0	0	0	0	0	8	0

Table 2 – 2 Continued

Conservation area	Habitat type	sowbugs	wasps	snails	slugs	Hemiptera	spiders	Orthoptera	earthworms
Black Creek Pioneer Village	Forested area	3	0	0	0	0	0	0	0
	Grassy area	3	3	1	0	2	2	1	0
	Near the creek	2	1	4	0	0	1	0	1
Tommy Thompson Park	Dead tree area Station A/1	1	6	0	0	6	9	2	0
	Dead tree area Station B/2	1	4	0	0	1	2	0	0
	Dead tree area Station C/3	0	0	0	0	0	3	0	0
	Live tree area Station D/4	0	1	0	0	0	1	1	0

Table 2 – 2 Continued

Conservation area	Habitat type	ticks	Coleoptera	miscellaneous
Black Creek Pioneer Village	Forested area	0	3	0
	Grassy area	1	0	1 Lepidoptera 1 millipede
	Near the creek	0	0	1 chigger
Tommy Thompson Park	Dead tree area Station A/1	0	11	1 Lepidoptera larva 2 bees
	Dead tree area Station B/2	2	4	2 unidentified larvae
	Dead tree area Station C/3	2	4	3 Lepidoptera 1 Lepidoptera larva 100 plus aphids
	Live tree area Station D/4	0	10	0

Table 2 – 2 Continued

Conservation area	Habitat type	<i>M. rubra</i> (% of <i>M. rubra</i> in the trap)	<i>F. subsericea</i>	<i>L. alienus</i>	<i>T. caespitum</i>	<i>C. pennsylvanicus</i>	<i>A. fulva</i>	<i>P. pennsylvanica</i>	<i>T. sessile</i>
Tommy Thompson Park	Live tree area Station E/5	21694 workers 1 alate queen 1 dealate queen 9 males (99.9%)	0	0	0	0	0	0	0
	Live tree area Station F/6	19082 workers 1 <i>Lasius alienus</i> 15 <i>Solenopsis molesta</i> (99.9%)	0	0	0	0	0	0	0
	Live tree area Station G/7	20329 workers 7 dealate queens 25 males (99.9%)	0	0	0	0	0	1	0
	Live tree area Station H/8	21122 workers 1 dealate queen 7 males (100%)	0	0	0	0	0	0	0

Table 2 – 2 Continued

Conservation area	Habitat type	<i>P. imparis</i>	<i>T. ambiguus</i>	<i>C. cerasi</i>	<i>S. molesta</i>	<i>C. novaeboracensis</i>	<i>S. diecki</i>	Collembola	Diptera
Tommy Thompson Park	Live tree area Station E/5	0	0	0	18	0	0	43	36
	Live tree area Station F/6	0	0	0	0	0	0	0	0
	Live tree area Station G/7	0	0	0	5	0	0	0	0
	Live tree area Station H/8	0	0	0	0	0	0	4	11

Table 2 – 2 Continued

Conservation area	Habitat type	harvestmen	sowbugs	wasps	snails	slugs	Hemiptera	spiders	Orthoptera
Tommy Thompson Park	Live tree area Station E/5	4	285	7	2	0	3	3	0
	Live tree area Station F/6	0	500 plus	0	0	0	0	0	0
	Live tree area Station G/7	0	0	0	0	0	0	0	0
	Live tree area Station H/8	32	155	2	4	1	2	3	2

Table 2 – 2 Continued

Conservation area	Habitat type	earthworms	ticks	Coleoptera	miscellaneous
Tommy Thompson Park	Live tree area Station E/5	0	16	26	1 Lepidoptera 1 unidentified larva
	Live tree area Station F/6	0	0	0	<i>Leptothorax ambiguus</i> dealate queen
	Live tree area Station G/7	0	0	0	0
	Live tree area Station H/8	0	0	1	1 unidentified larva

Table 2 – 2 Continued

Conservation area	Habitat type	<i>M. rubra</i> (% of <i>M. rubra</i> in the trap)	<i>F. subsericea</i>	<i>L. alienus</i>	<i>T. caespitum</i>	<i>C. pennsylvanicus</i>	<i>A. fulva</i>	<i>P. pennsylvanica</i>	<i>T. sessile</i>
Tommy Thompson Park	Live tree area Station I/9	15540 workers 6 dealate queens 16 males (99.9%)	1	0	0	0	0	4 workers 1 alate queen	1
	Live tree area Station J/10	2868 workers 8 dealate queens 3 males (99.6%)	0	0	0	0	0	0	0
	Live tree area Station K/11	1 worker (100%)	0	0	0	0	0	0	0

Table 2 – 2 Continued

Conservation area	Habitat type	<i>P. imparis</i>	<i>T. ambiguus</i>	<i>C. cerasi</i>	<i>S. molesta</i>	<i>C. novaeboracensis</i>	<i>S. diecki</i>	Collembola	Diptera
Tommy Thompson Park	Live tree area Station I/9	0	0	0	3	0	0	2	2
	Live tree area Station J/10	0	0	0	11	0	0	1	5
	Live tree area Station K/11	0	0	0	0	0	0	12	9

Table 2 – 2 Continued

Conservation area	Habitat type	<i>M. rubra</i> (% of <i>M. rubra</i> in the trap)	harvestmen	sowbugs	wasps	snails	slugs	Hemiptera	spiders	Orthoptera
Tommy Thompson Park	Live tree area Station I/9	15540 workers 6 dealate queens 16 males (99.9%)	4	38	10	3	0	0	5	19
	Live tree area Station J/10	2868 workers 8 dealate queens 3 males (99.6%)	0	44	77	6	0	2	3	29
	Live tree area Station K/11	1 worker (100%)	0	30	9	1	0	0	4	18

Table 2 – 2 Continued

Conservation area	Habitat type	earthworms	ticks	Coleoptera	miscellaneous
Tommy Thompson Park	Live tree area Station I/9	0	0	1	1 chigger
	Live tree area Station J/10	0	3	5	1 centipede
	Live tree area Station K/11	0	0	1	0

Table 2 – 2 Continued

Conservation area	Habitat type	<i>M. rubra</i> (% of <i>M. rubra</i> in the trap)	Other ants present in the trap	soil type	soil pH	soil surface moisture (% by volume)	ground cover/leaf litter temp or soil surface temp (in °C)	soil surface temp (in °C)
Petticoat Creek Conservation Area	Tall marshy meadow area	19321 workers 2 alate queen 14 dealate queens 1 male (100%)	0	sandy loam	6.85	20.2 16.9 24.2 19.7 15.2	14.2 13.4 14.4 13.6 14.2	15.2 14.6 14.8 15.2 15
	Forested area	30 workers 1 alate queen 1 dealate queen 2 males (94%)	2 <i>Lasius flavus</i>	sandy loam	6.55	22.6 28.6 17.5 19.2	13.6 14.2 14.2 13.8	14.2 14.2 14.4 14.2
Glen Rouge Campground	Sandy beach/marshy area	5 workers (62.5%)	3 <i>Lasius alienus</i>	sand	8.43	12.9 10.2 7 4.4 8	15 10.2 15 15.6 14.8	15 10.2 15 15.8 14.8
	Forested area	2 workers (100%)	0	loam	7.41	10.2 23.2 16.1 16.1 18.8	13.4 13.4 13.8 13.8 13.8	13 13.4 13.4 13.8 13.8

Table 2 – 3: Ant species, soil, and habitat data from the 2012 sampling

Conservation area	Habitat type	ground cover (vegetation)	surrounding area	soil compaction (psi)	insolation
Petticoat Creek Conservation Area	Tall marshy meadow area	dense marsh roots	tall & marshy meadow	200	high
	Forested area		forest	210	medium
Glen Rouge Campground	Sandy beach/marshy area	medium dense marshy	meadowy and marsh growth	80	high
	Forested area		sparsely forested	120	medium

Table 2 – 3 Continued

Conservation area	Habitat type	<i>M. rubra</i> (% of <i>M. rubra</i> in the trap)	Other ants present in the trap	soil type	soil pH	soil surface moisture (% by volume)	ground cover/leaf litter temp or soil surface temp (in °C)	soil surface temp (in °C)
Rouge Park	Non forest vegetation/grassy area by the creek	1 worker (33.3%)	1 <i>Ponera pennsylvanica</i> 1 <i>Crematogaster cerasi</i>	sand	8.23	23 25.7 36.5 25.7 24.1	20.8 20 20.4 20.4 21.8	21.8 20 19.4 19.2 20
	Sandy area by the creek	11 workers (100%)	0	silt	8.08	45.5 57.8 46.6 49.2 42.5	26.2 21.6 23.6 21 21.4	25.2 19.2 23.6 20.2 19.2
	Meadow, not close to the creek	23 workers (95.8%)	1 <i>Aphaenogaster fulva</i>	loam	7.83	18 25.1 26.6 23.8 25.2	15.2 15.2 16.8 16.8 17.8	15.4 15.4 16.2 16.6 17.2
	Forested area	0 workers (0%)	1 alate male <i>Formica subsericea</i> 1 <i>Camponotus pennsylvanicus</i> 1 <i>Aphaenogaster fulva</i>	sandy loam	8.05	17.7 23.2 30.8	15.6 15.6 15.6	15.6 15.6 15.6

Table 2 – 3 Continued

Conservation area	Habitat type	ground cover (vegetation)	surrounding area	soil compaction (psi)	insolation
Rouge Park	Non forest vegetation/grassy area by the creek	medium tall & marshy	open meadow near the creek	120	high
	Sandy area by the creek		by the creek	80	high
	Meadow, not close to the creek	dense	open meadow	200	high
	Forested area	fallen leaves medium, not thick	forest	170	medium

Table 2 – 3 Continued

Conservation area	Habitat type	<i>M. rubra</i> (% of <i>M. rubra</i> in the trap)	Other ants present in the trap	soil type	soil pH	soil surface moisture (% by volume)	ground cover/leaf litter temp or soil surface temp (in °C)	soil surface temp (in °C)
Altona Forest	Forested area	10 workers (71.4%)	1 <i>Formica subsericea</i> 2 <i>Aphaenogaster fulva</i> 1 <i>Camponotus novaeboracensis</i>	silt loam	7.71	26.6 15.7 19.2 12.1 15	15.8 18.8 16.4 17.8 17.2	15.8 16.6 16.4 17.8 17.2
	By the creek	6 workers (66.7%)	1 <i>Lasius flavus</i> 1 <i>Aphaenogaster fulva</i> 1 <i>Stenamma diecki</i>	sandy loam	8.38	12.7 16.4 33.6 29.9	21.2 16.8 16.2 16.8	21.2 16.8 16.2 16.8

Table 2 – 3 Continued

Conservation area	Habitat type	ground cover (vegetation)	surrounding area	soil compaction (psi)	insolation
Altona Forest	Forested area		forest	150	low
	By the creek	no cover	By the creek	90	medium

Table 2 – 3 Continued

Conservation area	Habitat type	<i>M. rubra</i> (% of <i>M. rubra</i> in the trap)	Other ants present in the trap	soil type	soil pH	soil surface moisture (% by volume)	ground cover/leaf litter temp or soil surface temp (in °C)	soil surface temp (in °C)
East Duffins Headwaters	Forested area	0 workers (0%)	3 <i>Aphaenogaster fulva</i> 1 <i>Prenolepis imparis</i>	silt	8	7.9 4 3 6.4 13.1	19.4 18.6 16.2 16.2 16.2	17.4 17.4 16.2 16.2 16.2
	Meadow	7 workers (13.7%)	11 <i>Formica subsericea</i> 10 <i>Lasius alienus</i> 7 <i>Tetramorium caespitum</i> 9 <i>Formica obscuriventris</i> 2 <i>Tapinoma sessile</i> 1 <i>Prenolepis imparis</i> 1 <i>Crematogaster cerasi</i> 3 <i>Solenopsis molesta</i>	loam	8.52	12.7 11.3 18.5 13.3 18	28 31.8 35.8 38.4 28.4	28 31.8 29.8 38.4 31.8

Table 2 – 3 Continued

Conservation area	Habitat type	ground cover (vegetation)	surrounding area	soil compaction (psi)	insolation
East Duffins Headwaters	Forested area	well covered with fallen leaves	forest, slightly elevated	150	low
	Meadow		open field	260	high

Table 2 – 3 Continued

Conservation area	Habitat type	<i>M. rubra</i> (% of <i>M. rubra</i> in the trap)	Other ants present in the trap	soil type	soil pH	soil surface moisture (% by volume)	ground cover/leaf litter temp or soil surface temp (in °C)	soil surface temp (in °C)
Bruce's Mill Conservation Area	Meadow	9 workers (31%)	6 <i>Formica subsericea</i> 11 <i>Formica exsectoides</i> 1 <i>Lasius umbratus</i> 1 <i>Lasius alienus</i> 1 <i>Aphaenogaster fulva</i>	silt	7.54	16.5 16.7 19.1 21 27.7	34.2 30.6 29.8 23.6 21.6	29.6 25.6 23.8 21.2 20.6
	Forested area	8516 workers (100%)	0	silt	7.7	67.9 82 81.3 59.3	15.8 17.2 15.8 15.8	15.4 16.6 15.8 15.8
	Low vegetation meadow	442 workers 1 dealate queen 1 male (100%)	0	silt	7.76	56 61.2 66.3 63.9 61.7	16.4 16.4 16 16.6 16.6	16.4 16.4 16 16.6 16.6
Oak Ridges Corridor Nature Reserve	Meadow	20 workers (74%)	3 <i>Formica subsericea</i> 2 <i>Formica exsectoides</i> 2 <i>Lasius umbratus</i>	silt	7.32	25.4 21.3 13.5 27.3 2.3	23.2 23.6 24.6 20.8 25	19.8 24.4 20.6 18.2 19.2

Table 2 – 3 Continued

Conservation area	Habitat type	ground cover (vegetation)	surrounding area	soil compaction (psi)	insolation
Bruce's Mill Conservation Area	Meadow	thin stemmed grass very dense	meadow in open field	160	high
	Forested area	fallen pine needles	forest	20	low
	Low vegetation meadow	extremely dense ground cover	An open space surrounded by sparsely forested areas	20	open
Oak Ridges Corridor Nature Reserve	Meadow	dense ground cover	meadow in open field	180	high

Table 2 – 3 Continued

Conservation area	Habitat type	<i>M. rubra</i> (% of <i>M. rubra</i> in the trap)	Other ants present in the trap	soil type	soil pH	soil surface moisture (% by volume)	ground cover/leaf litter temp or soil surface temp (in °C)	soil surface temp (in °C)
Boyd Conservation Area	Meadow	1 worker (25%)	2 <i>Lasius alienus</i> 1 <i>Aphaenogaster fulva</i>	sandy loam	7.94	16.7 13.6 18.6 4.5 19.1	12.6 11.8 11.4 11.8 12.4	12.4 11.8 12.4 12.6 12.2
	Creek shore/beach	2 workers (67%)	1 <i>Lasius alienus</i>	loam	7.84	52.1 51.4 45.9 48.1 51.9	11.6 10.8 11.4 10.8 11.4	11.6 10.8 11.4 10.8 11.4
	Forested area	0 (0%)	1 <i>Camponotus pennsylvanicus</i> 1 <i>Aphaenogaster fulva</i>	silt loam	7.05	4.7 15.1 29.8 16.8 12.8	8.6 9.2 8.8 8.4 8.8	8.6 9.4 9.8 10 9.8

Table 2 – 3 Continued

Conservation area	Habitat type	ground cover (vegetation)	surrounding area	soil compaction (psi)	insolation
Boyd Conservation Area	Meadow	very dense forbs (1 metre tall)	meadow near the creek	10	high
	Creek shore/beach	none	creek shore/beach	10	high
	Forested area	well covered with fallen leaves	forest	20	low

Table 2 – 3 Continued

Conservation area	Habitat type	<i>M. rubra</i> (% of <i>M. rubra</i> in the trap)	Other ants present in the trap	soil type	soil pH	soil surface moisture (% by volume)	ground cover/leaf litter temp or soil surface temp (in °C)	soil surface temp (in °C)
Kortright Centre for Conservation	Forested area	0 (0%)	0	sandy loam	6.21	20.1 21.9 33.9 33.9 26.9	13.6 14.4 13.8 13.6 13.6	13.4 14 13.8 13.6 13.6
	Meadow	3 workers (100%)	0	silty clay	7.67	28.7 22.9 23.6 20.5 19	19.6 19.6 21.8 20.8 24.8	14.8 15.4 15.6 15.8 15.8
Heart Lake Conservation Area	Sandy beach	0 (0%)	2 <i>Formica subsericea</i> 1 <i>Lasius alienus</i>	sandy loam	7.8	19.4 13 28.8 27.8 29.1	20.2 19.8 32.2 29.6 19	20.2 19.8 32.2 29.6 19
	Lightly forested area	1 worker (50%)	1 <i>Aphaenogaster fulva</i>	clay	6.77	15 16.6 15.7 23.8 18	19.4 19.6 19.6 19.2 18.8	17.2 16.4 16.2 15.8 16.4

Table 2 – 3 Continued

Conservation area	Habitat type	ground cover (vegetation)	surrounding area	soil compaction (psi)	insolation
Kortright Centre for Conservation	Forested area	fallen pine needles medium coverage	forest	120	low
	Meadow	dense dry grass	meadow in open field	150	high
Heart Lake Conservation Area	Sandy beach	sparse	beach by the lake		high
	Lightly forested area	fallen maple leaves	forest	180	medium

Table 2 – 3 Continued

Conservation area	Habitat type	<i>M. rubra</i> (% of <i>M. rubra</i> in the trap)	Other ants present in the trap	soil type	soil pH	soil surface moisture (% by volume)	ground cover/leaf litter temp or soil surface temp (in °C)	soil surface temp (in °C)
Heart Lake Conservation Area	Forested area	0 (0%)	1 <i>Lasius alienus</i> 2 <i>Aphaenogaster fulva</i>	sandy loam	8.38	13.8 17.2 9 10.2 10.2	18.8 20.8 20.6 19.8 21	17.6 16.6 16.2 17.8 16.6
	Meadow	2 workers (28.6%)	3 <i>Lasius umbratus</i> 1 <i>Lasius flavus</i> 1 <i>Aphaenogaster fulva</i>	silt loam	7.07	13.7 20.1 10.4 12.9 14.1	25.4 30.2 21.8 22 35.4	19.4 23.6 18.6 18.8 26.2
Glen Haffy Conservation Area	Forested area	0 (0%)	0	silt	5.71	15.9 12.3 25.5 19.9	21.4 20.2 19.2 19.4	19.4 16.8 16.8 18.6
	Meadow	3 workers (60%)	2 <i>Aphaenogaster fulva</i>	silt loam	5.74	19.7 19.9 19.8 20 24.6	27.6 30.4 29.6 34.4 26.8	22.6 29.6 27.6 23 21.6

Table 2 – 3 Continued

Conservation area	Habitat type	ground cover (vegetation)	surrounding area	soil compaction (psi)	insolation
Heart Lake Conservation Area	Forested area	fully covered with fallen pine needles	forest steep hill covered with dry pine needles	100	medium
	Meadow	very dense grass cover	meadow in open field	120	high
Glen Haffy Conservation Area	Forested area	well covered with fallen leaves	forest	100	medium
	Meadow	very dense live grass/forbs	meadow	180	high

Table 2 – 3 Continued

Conservation area	Habitat type	<i>M. rubra</i> (% of <i>M. rubra</i> in the trap)	Other ants present in the trap	soil type	soil pH	soil surface moisture (% by volume)	ground cover/leaf litter temp or soil surface temp (in °C)	soil surface temp (in °C)
Albion Hills Conservation Area	sparsely forested area	0 (0%)	1 <i>Camponotus pennsylvanicus</i>	silt	6.5	17.4 14.9	19.6 19.4	17.8 17.2
	Meadow	0 (0%)	1 <i>Formica subsericea</i>	loam	7.87	10.9 13.6 16.5 15.2	27.8 20.6 21.8 24.6	21.4 20 19.8 20.2
Black Creek Pioneer Village	Forested area	17 workers (100%)	0	silt loam	7.7	22.5 19.9 15.3	15.4 15.4 15.6	16 15.4 16
	Grassy area	11985 workers 14 dealate queens (99.9%)	1 <i>Lasius alienus</i> 1 <i>Lasius flavus</i> 1 <i>Solenopsis molesta</i>	silt loam	7.89	24.5 21.5 13.6 18.1	13.4 13.6 12.8 16.2	14.4 15 14.4 16.2
	Near the creek	52 workers 1 dealate queen (100%)	0	silt loam	7.7	22.1	16.2	17.6

Table 2 – 3 Continued

Conservation area	Habitat type	ground cover (vegetation)	surrounding area	soil compaction (psi)	insolation
Albion Hills Conservation Area	sparsely forested area	well covered with fallen leaves	forest hilly & very steep	40	medium
	Meadow	very dense grass cover	meadow	40	high
Black Creek Pioneer Village	Forested area	medium grassy/planty	edge of a meadow, near the creek	230	medium
	Grassy area	very dense grass cover	grassland	230	high
	Near the creek	lightly covered with dry and green grass	lightly forested near a creek	80	medium

Table 2 – 3 Continued

Conservation area	Habitat type	<i>M. rubra</i> (% of <i>M. rubra</i> in the trap)	Other ants present in the trap	soil type	soil pH	soil surface moisture (% by volume)	ground cover/leaf litter temp or soil surface temp (in °C)	soil surface temp (in °C)
Tommy Thompson Park	Live tree area Station K/11 north of the service road	407 workers 4 dealate queens (96.7%)	7 <i>Lasius alienus</i> 1 <i>Ponera pennsylvanica</i> 1 <i>Tapinoma sessile</i> 5 <i>Solenopsis molesta</i>	silt loam	8.01	20.6 20.1 18.4 17.2 26.3	26.2 22.6 22 28.6 32.8	21.8 21.2 21.6 27.2 29
	Meadow, west of Pen C entrance (south side of the road near the 3 way point)	8 workers (88.9%)	1 <i>Formica subsericea</i>	loam	7.92	36.1 30 30.2 27.4	28.8 31 21.4 29.2	21.8 27.8 20.6 27.8
	Meadow south of Pen B entrance south of the road in forested area	16363 workers 2 dealate queens 23 males (100%)	0	sandy loam	7.88	21.4 9.9 14 17.2 14.5	23.2 23.6 24.4 23.6 22.8	22.4 28.6 23.4 21.6 21.2

Table 2 – 3 Continued

Conservation area	Habitat type	ground cover (vegetation)	surrounding area	soil compaction (psi)	insolation
Tommy Thompson Park	Live tree area Station K/11 north of the service road	dense grass	meadowy area, 8 metres north of the service road	100	high
	Meadow, west of Pen C entrance (south side of the road near the 3 way point)	very dense grass/forbs		130	high
	Meadow south of Pen B entrance south of the road in forested area	fallen leaves & medium dense grass	meadow, 5 metres to a forested area to the south	100	medium

Table 2 – 3 Continued

Binary logistic regression	P value
<i>M. rubra</i> presence vs collembola abundance	0.463
<i>M. rubra</i> presence vs sow bug abundance	0.503
Linear regression	R ² and R ² adjusted
<i>M. rubra</i> abundance vs collembola abundance	2.8%, 0.0%
<i>M. rubra</i> abundance vs sow bug abundance	2.5%, 0.0%

Table 2 – 4: Correlation between *M. rubra* presence/abundance vs collembola and sow bug abundance.

Correlation matrix analysis

presence/absence versus 1. soil moisture 2. veg/cover temp 3. soil surface temp 4. altitude

	presence/absence	soil moisture	veg/cover temp
soil moisture	0.226 0.004		
veg/cover temp	0.114 0.157	-0.123 0.124	
soil temp	0.179 0.025	-0.092 0.251	0.930 0.000
altitude	-0.232 0.003	-0.093 0.247	0.366 0.000
	soil temp		
altitude	0.267 0.001		

Cell Contents: Pearson correlation
P-Value

Table 2 – 5: Correlation Matrix for presence/absence against environmental factors.

Stepwise Regression

Presence/absence versus 1. abundance 2. soil moisture, 3. veg/cover temp 4. soil surface temp 5. altitude

Alpha-to-Enter: 0.15 Alpha-to-Remove: 0.15

Response is presence/absence on 5 predictors, with N = 157
N(cases with missing observations) = 1 N(all cases) = 158

Step	1	2	3	4
Constant	0.44933	0.29301	-0.08809	0.04465
abundance	0.00015	0.00014	0.00014	0.00012
T-Value	4.31	4.16	4.31	3.76
P-Value	0.000	0.000	0.000	0.000
soil moisture		0.0068	0.0074	0.0070
T-Value		2.68	2.99	2.89
P-Value		0.008	0.003	0.004
soil temp			0.0201	0.0257
T-Value			2.85	3.60
P-Value			0.005	0.000
altitude				-0.00115
T-Value				-2.98
P-Value				0.003
S	0.476	0.466	0.456	0.445
R-Sq	10.70	14.69	18.99	23.46
R-Sq(adj)	10.13	13.58	17.40	21.45
Mallows Cp	23.2	17.3	10.9	4.0

Table 2 – 6: Stepwise regression for data ordination

Binary Logistic Regression

Presence/absence versus 1. soil moisture 2. soil surface temp 3. altitude (these three factors derived from the stepwise regression).

Response Information

Variable	Value	Count	
presence/absence	1	79	(Event)
	0	78	
	Total	157	

* NOTE * 157 cases were used
 * NOTE * 1 cases contained missing values

Logistic Regression Table

Predictor	Coef	SE Coef	Z	P	Odds Ratio	95% CI Lower	95% CI Upper
Constant	-1.82739	0.763960	-2.39	0.017			
soil moisture	0.0358421	0.0127627	2.81	0.005	1.04	1.01	1.06
soil temp	0.127098	0.0385359	3.30	0.001	1.14	1.05	1.22
altitude	-0.0067938	0.0020274	-3.35	0.001	0.99	0.99	1.00

Log-Likelihood = -94.874

Test that all slopes are zero: G = 27.894, DF = 3, P-Value = 0.000

Goodness-of-Fit Tests

Method	Chi-Square	DF	P
Pearson	162.996	153	0.275
Deviance	189.748	153	0.023
Hosmer-Lemeshow	12.374	8	0.135
Brown:			
General Alternative	7.999	2	0.018
Symmetric Alternative	2.735	1	0.098

Measures of Association:

(Between the Response Variable and Predicted Probabilities)

Pairs	Number	Percent	Summary Measures
Concordant	4571	74.2	Somers' D 0.49
Discordant	1570	25.5	Goodman-Kruskal Gamma 0.49
Ties	21	0.3	Kendall's Tau-a 0.25
Total	6162	100.0	

Table 2 – 7: Binary logistic regression for presence/absence vs the abiotic factors derived by stepwise regression.

	N	Mean	St Dev	SE Mean	T-value	P-value
soil moisture (%): Presence	77	27.0	17.6	2.0		
soil moisture (%): Absence	78	20.1	10.5	1.2		
					2.97	0.004
soil surface temp (deg C): Presence	77	19.0	5.33	0.6		
soil surface temp (deg C): Absence	78	17.2	4.97	0.6		
					2.17	0.032
Altitude (m): Presence	78	168.7	91.8	10.0		
Altitude (m): Absence	78	211.9	99.9	11.0		
					-2.81	0.006

Table 2 – 8: T-test statistics for *M. rubra* presence/absence sites for 3 most limiting abiotic factors.

Correlation matrix analysis for the compact dataset

	presence/absence	abundance_1	soil pH
abundance_1	0.257 0.156		
soil pH	0.001 0.994	-0.115 0.531	
soil moisture	0.349 0.050	-0.010 0.958	0.104 0.572
compaction	0.266 0.148	0.287 0.117	-0.074 0.692
altitude	-0.033 0.858	-0.212 0.245	-0.436 0.013
	soil moisture	soil temp ground	soil temp
soil temp ground	-0.127 0.487		
soil temp	-0.079 0.668	0.940 0.000	
compaction	-0.324 0.075	0.201 0.279	0.273 0.138
altitude	-0.084 0.646	0.508 0.003	0.369 0.038
	compaction		
altitude	0.065 0.730		

Cell Contents: Pearson correlation
P-Value

Table 2 – 9: Correlation matrix for presence/absence in the compact data set.

Stepwise Regression for the compact dataset

Presence/absence versus 1. Abundance 2. Soil pH 3. Soil moisture 4. Soil surface temp 5. Veg/cover temp 6. Compaction 7. altitude

Alpha-to-Enter: 0.15 Alpha-to-Remove: 0.15

Response is presence/absence on 7 predictors, with N = 31
N(cases with missing observations) = 1 N(all cases) = 32

Step	1	2
Constant	0.2078	-0.2689
soil moisture	0.0123	0.0172
T-Value	2.00	2.87
P-Value	0.055	0.008
compaction		0.0030
T-Value		2.50
P-Value		0.019
S	0.484	0.446
R-Sq	12.13	28.15
R-Sq(adj)	9.10	23.02
Mallows Cp	3.8	0.2

Table 2 – 10: Stepwise regression for data ordination with the compact dataset

Binary Logistic Regression for the presence/absence vs factors in the compact dataset

Presence/absence versus soil moisture and compaction (these two factors derived from the stepwise regression).

Response Information

Variable	Value	Count	
presence/absence	1	15	(Event)
	0	16	
	Total	31	

* NOTE * 31 cases were used
 * NOTE * 1 cases contained missing values

Logistic Regression Table

Predictor	Coef	SE Coef	Z	P	Odds Ratio	95% CI Lower	95% CI Upper
Constant	-4.10564	1.65277	-2.48	0.013			
soil moisture	0.0901488	0.0382743	2.36	0.019	1.09	1.02	1.18
compaction	0.0157457	0.0074934	2.10	0.036	1.02	1.00	1.03

Log-Likelihood = -16.499

Test that all slopes are zero: G = 9.944, DF = 2, P-Value = 0.007

Goodness-of-Fit Tests

Method	Chi-Square	DF	P
Pearson	29.0166	28	0.412
Deviance	32.9987	28	0.236
Hosmer-Lemeshow	2.9431	8	0.938
Brown:			
General Alternative	1.1305	2	0.568
Symmetric Alternative	0.3306	1	0.565

Measures of Association:

(Between the Response Variable and Predicted Probabilities)

Pairs	Number	Percent	Summary Measures
Concordant	193	80.4	Somers' D 0.62
Discordant	45	18.8	Goodman-Kruskal Gamma 0.62
Ties	2	0.8	Kendall's Tau-a 0.32
Total	240	100.0	

Table 2 – 11: Binary logistic regression for presence/absence vs soil compaction level

Two sample t-test

		SE		
	N	Mean	StDev	Mean
Compaction(M. rubra: Present)	15	142.7	82.3	21
Compaction(M. rubra: Absent)	16	105.0	57.5	14

Difference = mu (compaction) - mu (compaction_1)
 Estimate for difference: 37.7
 95% CI for difference: (-15.3, 90.6)
 T-Test of difference = 0 (vs not =): T-Value = 1.47 P-Value = 0.155 DF = 24

Table 2 – 12: T-test statistics for *M. rubra* presence/absence sites for soil compaction level.

Two-Sample T-Test and CI: Albion Hills soil moisture, TTP soil moisture

Two-sample T for Albion Hills soil moisture vs TTP soil moisture

	N	Mean	StDev	SE Mean
Albion Hills soil moistu	6	14.75	2.30	0.94
TTP soil moisture	14	21.66	7.38	2.0

Difference = mu (Albion Hills soil moisture) - mu (TTP soil moisture)
 Estimate for difference: -6.91
 95% CI for difference: (-11.52, -2.31)
 T-Test of difference = 0 (vs not =): T-Value = -3.17 P-Value = 0.006 DF = 17

Two-Sample T-Test and CI: Albion Hills soil temp, TTP soil temp

Two-sample T for Albion Hills soil temp vs TTP soil temp

	N	Mean	StDev	SE Mean
Albion Hills soil temp	6	19.40	1.58	0.65
TTP soil temp	14	24.00	3.24	0.87

Difference = mu (Albion Hills soil temp) - mu (TTP soil temp)

Estimate for difference: -4.60
 95% CI for difference: (-6.88, -2.32)
 T-Test of difference = 0 (vs not =): T-Value = -4.25 P-Value = 0.001 DF = 17

Two-Sample T-Test and CI: Albion Hills altitude, TTP altitude

Two-sample T for Albion Hills altitude vs TTP altitude

	N	Mean	StDev	SE Mean
Albion Hills altitude	6	261.85	1.62	0.66
TTP altitude	14	82.07	3.34	0.89

Difference = mu (Albion Hills altitude) - mu (TTP altitude)
 Estimate for difference: 179.78
 95% CI for difference: (177.44, 182.12)
 T-Test of difference = 0 (vs not =): T-Value = 161.91 P-Value = 0.000 DF = 17

Table 2 – 13: T-tests for soil moisture, soil surface temperature, and altitude at Albion Hills Conservation Area and Tommy Thompson Park.

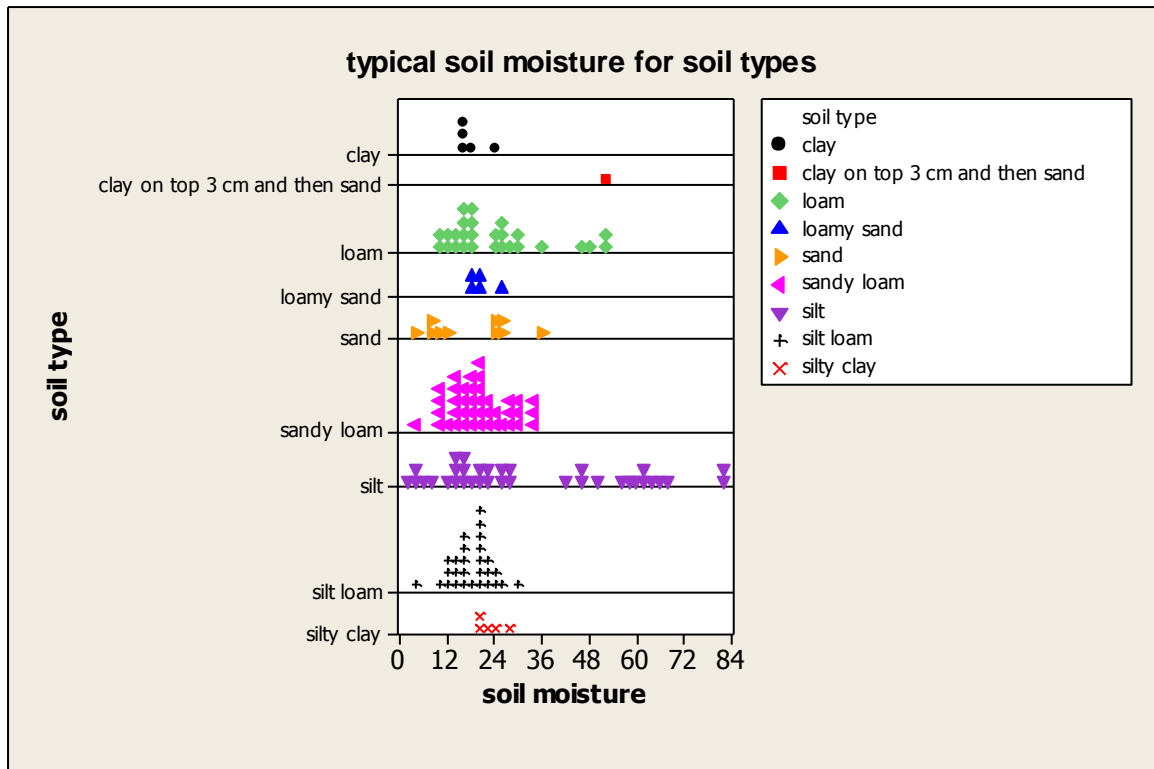


Figure 2 – 1: typical soil moisture level in various soil types

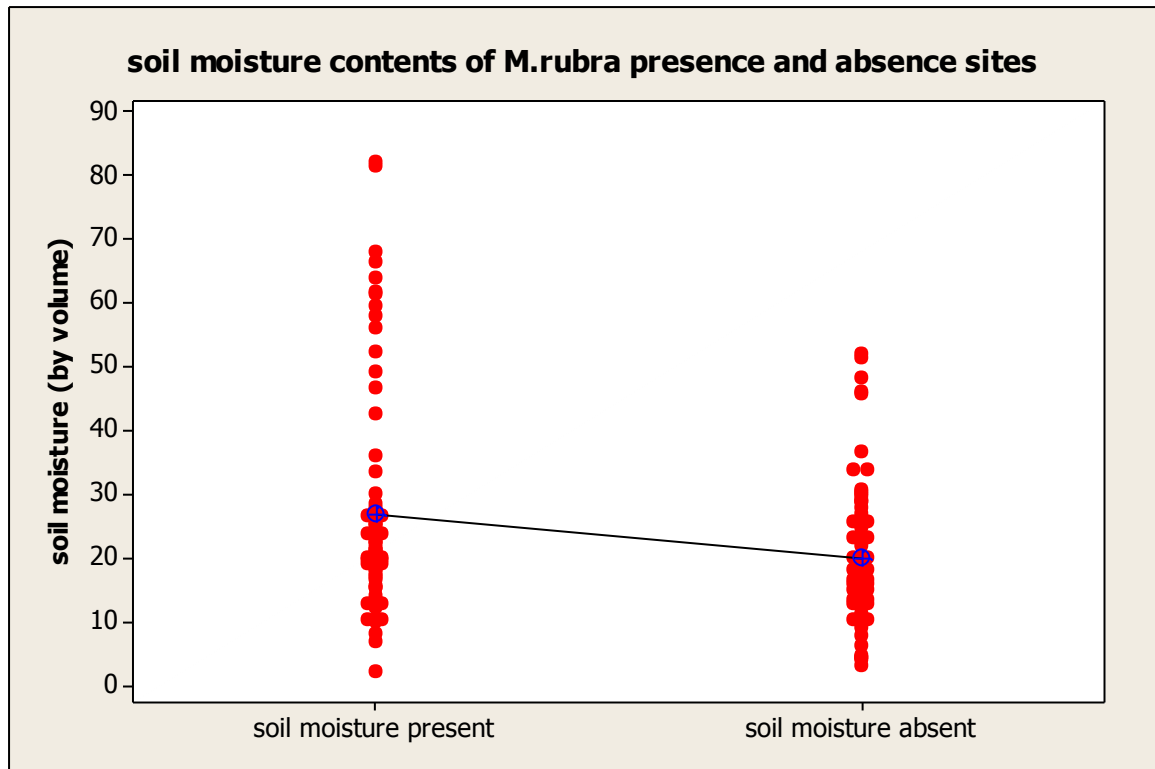


Figure 2 – 2a: Soil moisture levels for the sites with *M. rubra* presence and absence.

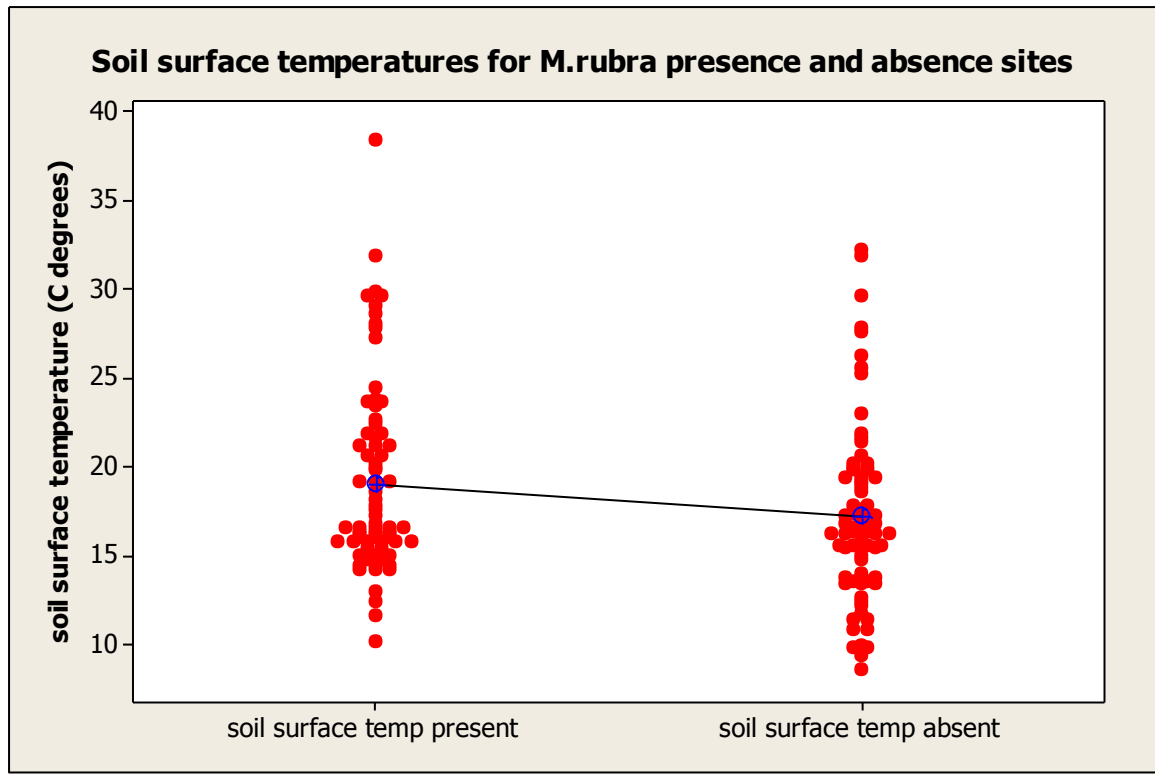


Figure 2 – 2b: Soil surface temperatures for the sites with *M. rubra* presence and absence.

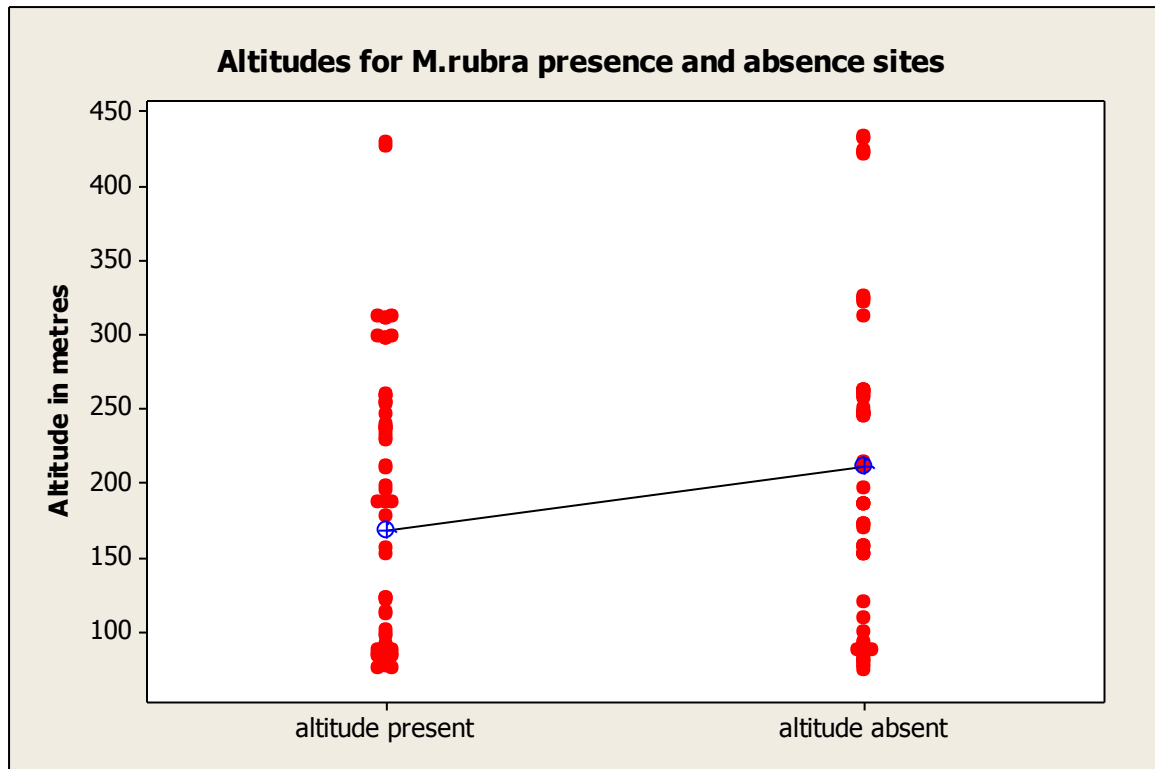


Figure 2 – 2c: Altitude/elevation levels for the sites with *M. rubra* presence and absence.

Figures 2 – 2: Differences between *M. rubra* present and absent sites for 3 most influential abiotic factors.

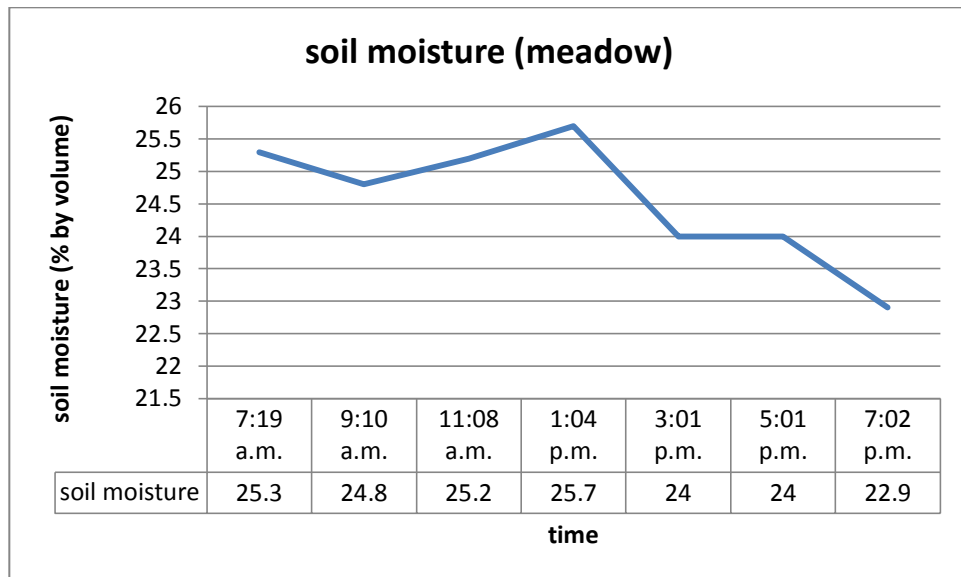


Figure 2 – 3a: At a meadow near Stong Pond on York University campus

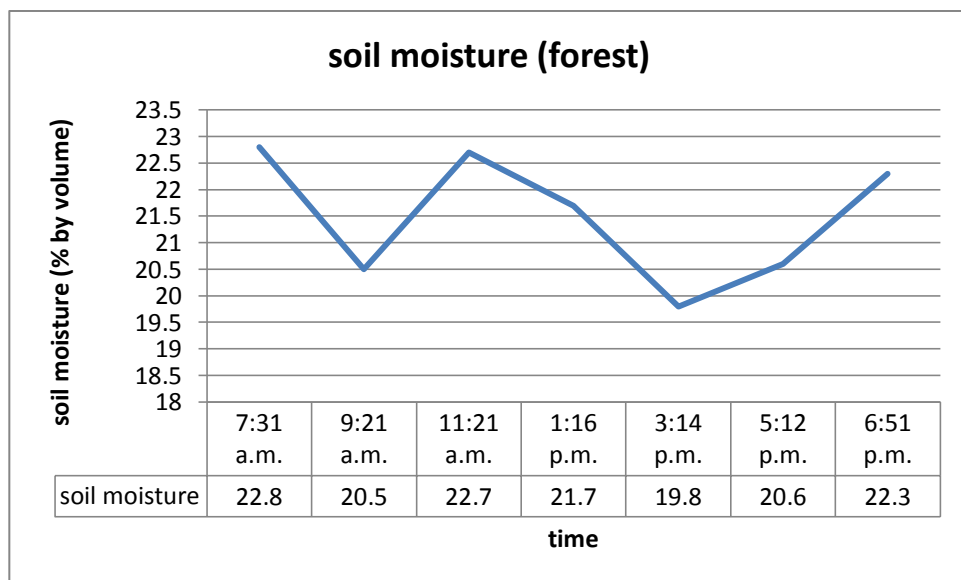


Figure 2 – 3b: In a woodlot on York University campus

Figures 2 – 3: Soil moisture content during the course of day in meadow and forest.

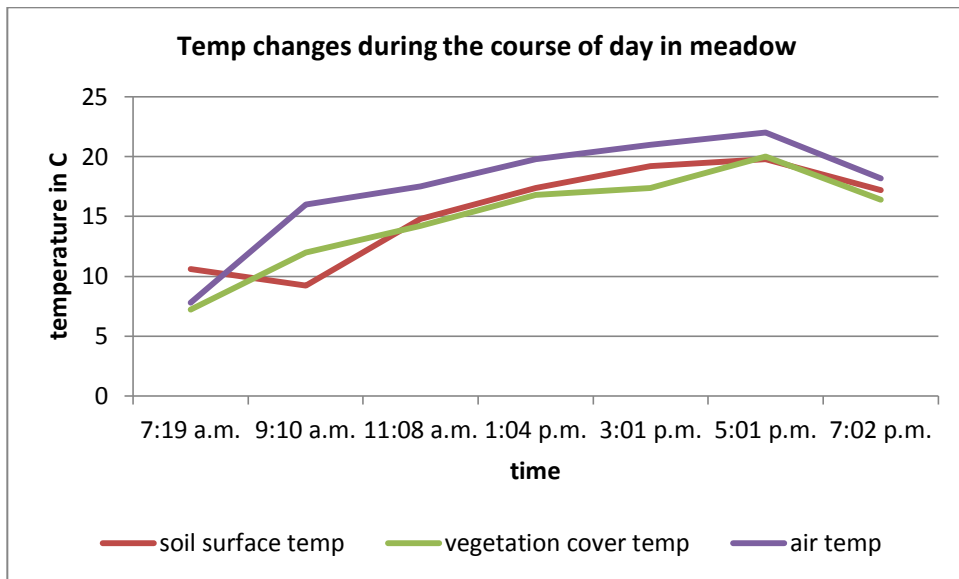


Figure 2 – 4a: Temperature changes in meadow

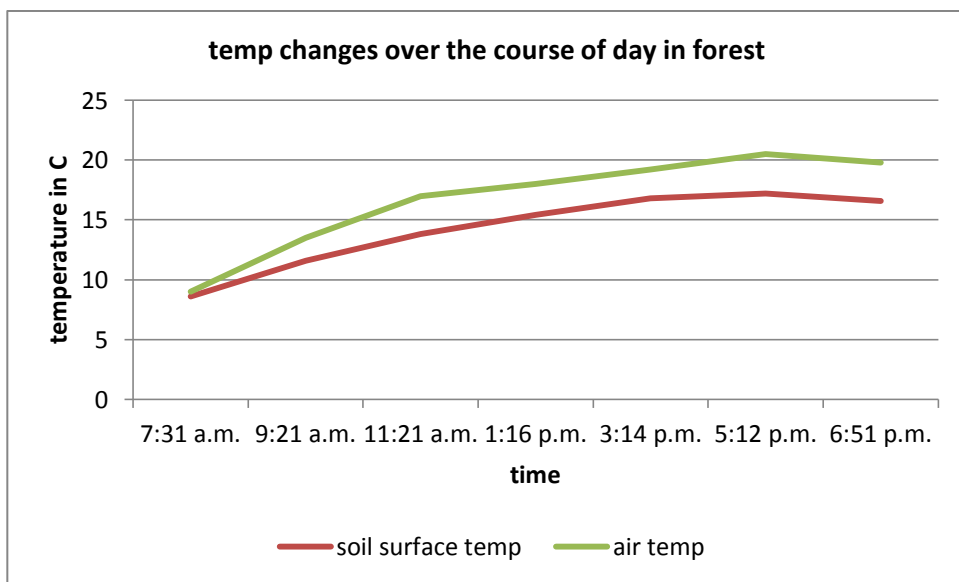


Figure 2 – 4b: Temperature changes in forest

Figures 2 – 4: Soil surface temperature, vegetation cover temperature (only applicable to Figure 2 – 4a), and air temperature during the course of day in meadow and forest.

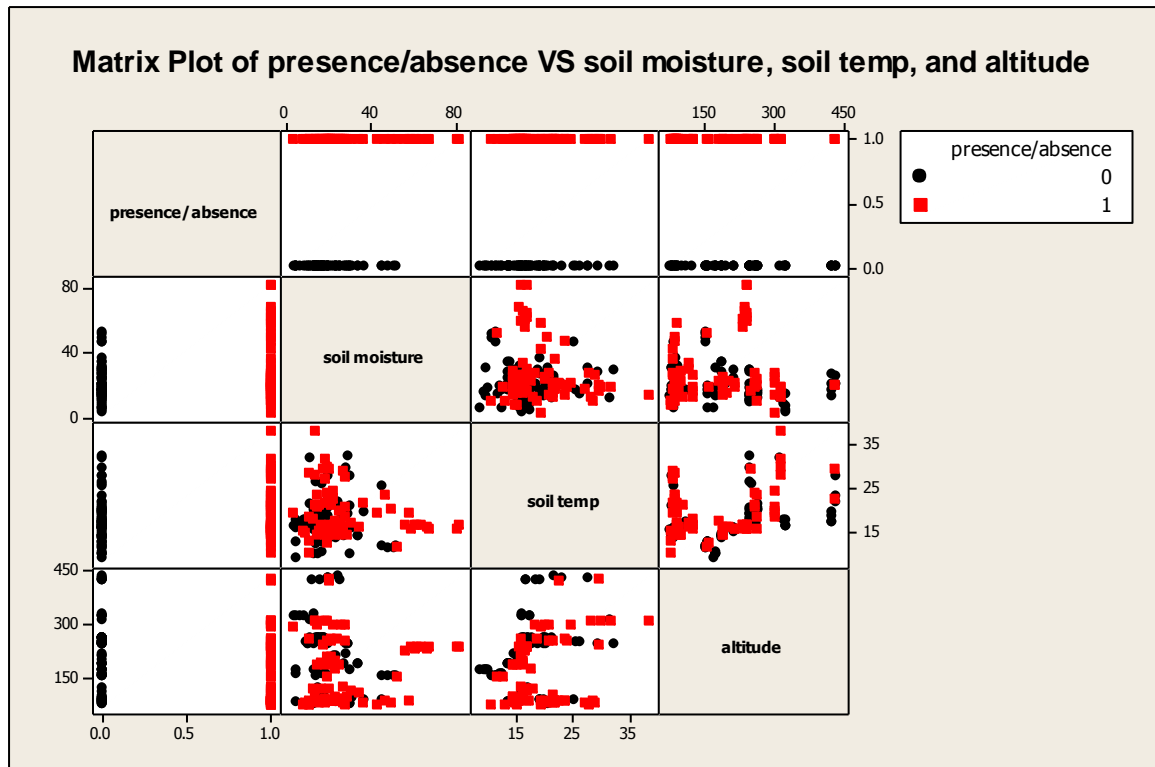


Figure 2 - 5: Matrix plot of presence/absence of *M. rubra* versus soil, moisture, soil surface temperature, and altitude

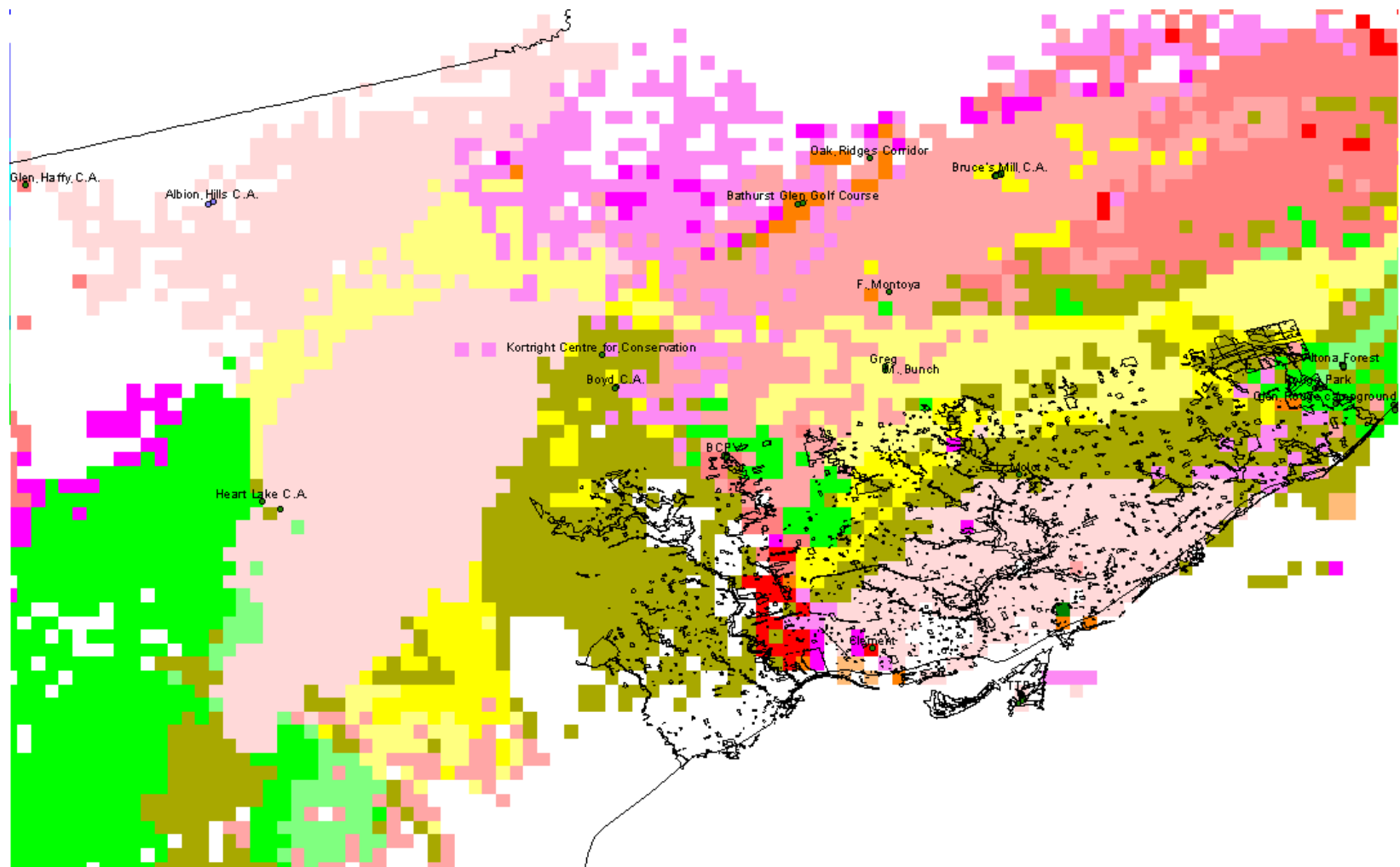


Figure 2 – 6: Ecological niche models showing the most limiting factor for the presence/absence of *M. rubra* in the GTA.

Chapter Three: Potential geographical distribution of *Myrmica rubra* using ecological niche modelling/species distribution modelling on 3 different scales for better mitigation/management.

Abstract

Prevention is the most effective way to combat the expansion of invasive species; however, it is often costly and requires exhaustive efforts. Predicting invasive species' potential geographic distribution is a cost effective way to mitigate and manage invasive species even if they are already present in introduced areas. Species distribution and ecological niche modelling (SDM/ENM) is based on the correlation between the occurrence points of invasive species and their respective environmental factors, and projection onto different areas to predict their potential geographic distributions. In this study, 15 SDM/ENM algorithms were tested, and amongst the 15 algorithms, 4 algorithms with highest resolutions and flexibility were used to predict the non native invasive species *Myrmica rubra*'s distributions on 3 different scales (local/GTA, regional/southern Ontario, and continental/North America) for better prevention and mitigation. In the face of climatic alteration, *M. rubra*'s future geographic distribution was predicted with a possible future scenario, and the possible causes of numerous *M. rubra* sightings in North America in recent years were also considered.

Introduction

One of the major causes of biodiversity loss is the establishment of non-native, invasive species, due to their primarily negative influence on the function and structure of ecosystems in their introduced regions and subsequent detrimental environmental, societal, agricultural, and economic impacts (Roura-Pascual et al., 2006, 2009; Peterson, 2003). Despite the fact that biotic invasions are not exclusively anthropogenic issues, increased human mobility is a vector for negative impacts on ecosystem

functions caused by introduced species (Miravete et al., 2013; Roura-Pascual et al., 2006; Clinton, 2007; Ward, 2007).

A non-native ant, *Myrmica rubra* (Linnaeus, 1758), has been present in North America at least since the early 20th century where it was first recorded in the state of Massachusetts (Grodén et al., 2005; Wetterer et al., 2011). It did not receive much attention until the early 1990s when a dramatic increase in abundance occurred. It is now invading other parts of northeastern U.S.A. as well as in eastern Canada (Grodén et al., 2005; Wittman, 2014). Their populations are fragmented; however, their aggressiveness and adaptability compounded with their lack of natural enemies in the introduced range are factors usually found in dominant invasive ant species (Grodén et al., 2005). Not only is *M. rubra* a nuisance pest on picnic sites and in other urban green spaces (Town of Richmond Hill, 2006) and may reduce property values, but it also has negative impacts on agriculture as a crop pest by tending aphids and keeping predators of aphids away (Wetterer et al., 2011).

Given the negative consequences associated with invasive species, understanding how a species may spread can ultimately prevent their establishment or aid in their control. Predictive modelling using non-random correlations between known occurrences of species and environmental datasets is a central tool in invasion biology (Thuiller, 2007). Predictive models, such as ecological niche models (ENMs) or species distribution models (SDMs), are used to predict areas where environmental conditions are suitable for an invasive species (Ward, 2007; Anderson et al., 2003; Peterson, 2003; Guisan and Thuiller, 2005; Bertelsmeier et al., 2013). “Climate matching” is an approach that predicts the pattern of invasions where ecological niches are a constraint on the

distribution of potential of species (Grinnell, 1917, 1924). Species will be able to establish and maintain populations only in those non-native areas that are equivalent to the ecological conditions to which they are limited in their native range. For both ENMs and SDMs, locality data (geo-referenced coordinates of longitude and latitude from confirmed presence points) and a suite of environmental variables are combined (Ward, 2007). The resulting model is projected onto a GIS map of the area of interest to predict where a species will or will not be able to maintain populations (Peterson et al., 2001). Predictive models can also forecast how distributions may change in the future as a result of global climate change (Menke et al., 2009). Some ENMs/SDMs characterize the distribution of a species in geographic space, modelling its niche in ecological space (e.g. ecological dimensions such as precipitation and temperature), and projecting back into geographic space to predict distributions both in the native and introduced ranges (Ward, 2007).

There are a number of ecological niche modelling algorithms available, depending on their predictive approaches and theoretical assumptions and the types of occurrence data. Some algorithms use pure statistical methods such as generalized linear models (GLMs) and generalized additive models (GAMs) whereas others use approaches based on machine learning techniques (Fitzpatrick et al., 2011; Pearson, 2007). The type and availability of occurrence data (e.g. presence only, presence and background as the environmental space across the study area, presence and absence, and presence and pseudo absence) are factors to consider in algorithm selection.

There is a need for more distribution studies on invasive ants (Ward 2007). In North America, the geographic distributions of two major invasive ants (*Linepithema*

humile and *Solenopsis invicta*) have been modelled and studied with more traditional algorithms such as the Genetic Algorithm for Rule-set Prediction (GARP) (Roura-Pascual et al., 2004, 2006; Sutherst et al., 2005; Peterson et al., 2008). No previously published reports have modelled the potential distribution of *M. rubra* with a focus on North America (Bertelsmeier et al., 2013). In this study, four fundamentally different ecological niche modelling algorithms were used to determine and map the potential geographic distribution of *M. rubra* (Hymenoptera: Formicidae) in urban green spaces across the Greater Toronto Area (GTA), more broadly in southern Ontario and eastern North America as well as in continental North America. Also, the potential geographic distribution of this species was projected into the future using a climate change scenario which simulated an estimation of the climate condition in 2100 with atmospheric carbon dioxide twice the current amount.

Methods

The algorithms used for ENMs are 1) Maxent; 2) BIOCLIM; 3) DOMAIN; and 4) Artificial Neural Network (ANN), and they differ in their theoretical assumptions and modelling approaches (Merow et al., 2013b; Ward, 2007; Peterson et al., 2007) (Appendix 1).

For environmental/climate datasets for EMNs, a collection of different layers containing climate variables with different spatial resolutions were used in keeping with the resolutions commonly used for ENMs (Fitzpatrick et al., 2013; Ward, 2007; Roura-

Pascual et al., 2004; Steiner et al., 2008; Roura-Pascual et al., 2006). In order to evaluate model performances, the threshold independent receiver operating characteristic (ROC) which expresses false negative predictions (omission errors) and false positive predictions (commission errors) was used (Merow et al., 2013a; Phillips et al., 2008). The ROC is measured by the area under the curve (AUC), with values ranging from 0 to 1, with high values indicating good model performance (Phillips et al., 2006). For Maxent, in addition to AUC's, omission curves and sensitivity/specificity curves are used to assess model performances.

ENMs for this project were studied on 3 different scales: 1) the local/GTA level; 2) regional (southern Ontario/eastern North America) level; 3) the continental North America level to help the mitigation/prevention effort against the spread of *Myrmica rubra*. Model building and evaluation were based on cross validation tests between the introduced and native range data as well as within-region data to ensure the reliability of models and to ascertain any difference in niche characteristics between the introduced and native ranges (Herborg et al., 2007; Steiner et al., 2008).

Locality data: Ant samples and sampling sites

Sampling of ants was done on Toronto and Region Conservation Authority (TRCA) properties (9 sites in 2011 and 15 sites in 2012) and at 19 other GTA locations, including residential areas, parks, and farms. Sampling sites contained various habitat types (forested area, meadow, and riparian area) (See Table 2 -1 and Table 3 – 1). A total of 143 occurrence points was used to construct ecological niche models (ENMs)/species distribution models (SDMs) for this project.

Environmental data

Various datasets with a wide array of variables with different spatial resolutions, from 30 arc-second (approximately 1 km x 1 km) to 10 arc-minute (approximately 20 km x 20 km), were obtained from multiple websites (Hijmans et al., 2005; Mitchell et al., 2002). The primary environmental data were obtained from WORLDCLIM (www.worldclim.org) for global coverage. The Worldclim/Bioclim dataset contains 19 climate variables that represent a combination of annual trends, seasonality, and extreme environmental conditions (Ward, 2007; Appendix 2). The climate data were obtained by interpolation of climate station records from 1950 to 2000 (Hijmans et al., 2005).

An additional dataset with coarser resolution (10 arc-minutes “cruCL2” (coverage from 1961 – 1990 (Mitchell et al., 2002)) was obtained from the Tyndall Centre for Climate Change Research (http://www.cru.uea.ac.uk/~timm/grid/CRU_CL_2_0.html). Although these data are older, they include more variables (23) and so were used to compare outcomes with those from the Worldclim/Bioclim dataset.

Ecological niche modelling algorithms

For Maxent, the “Prevalence” mode was set to 0.5 as recommended (Phillips et al., 2006), assuming that typical presence localities have a probability of presence of about 0.5. The maximum number of iterations was set to 500, allowing enough time for convergence whilst cutting down on excess computation time, and the convergence threshold was set to 0.00001: the default setting. Thresholds for favourable habitat

suitability are determined by maximizing sensitivity whilst minimizing specificity (Baldwin, 2009). To estimate the climate variables of importance, a jackknife test was implemented (Phillips et al., 2006), and climate variables that contribute to increase gain for AUC were identified from the output of each run. Numerous runs were attempted with each spatial resolution and the two climatic datasets with reduced numbers of climate variables to determine the significance of each. For each Maxent run, the global environmental space was used as background which obviates the necessity of “absence” occurrence points (Merow et al., 2013; Phillips et al., 2006).

For BIOCLIM and DOMAIN algorithms, runs with various spatial resolutions were made to determine the area coverage differences for species’ potential geographic distributions. Final runs were done with the Worldclim/Bioclim data layers with a 30 arc-second resolution because it gave the highest pixel resolution and AUC values compared to the lower resolution layers.

The ANN algorithm was chosen to map the potential geographic distribution for *M. rubra* for the regional/southern Ontario area because of its high resolution output for the region and its comparable outcome with that of Maxent

Algorithms outputs were exported to ESRI ArcMap 10.0 (Environmental Systems Research Institute (ESRI), Redlands, California, USA) for mapping and further colour enhancement, as necessary.

Modelling approach and evaluation

One hundred and forty-three occurrence points based on the presence of *M. rubra* across the GTA were used to represent the introduced range in North America, and 2,129 occurrence points from its native range (Eurasia) were obtained from the Global Biodiversity Information Facility (GBIF) website (www.gbif.org). Initially over 6,800 occurrence points were obtained from the GBIF native range; however, numerous duplicate and/or replicate occurrence points were deleted to prevent false abundance at a given location.

Separate ecological niche models based on data from the introduced range, the native range, and the combined range were developed to determine model performance as well as the niche characteristics between the introduced and native ranges. To construct ecological niche models that provide a maximum amount of information on potential geographical distribution of *M. rubra*, a three step process was used to ensure the validity as well as accuracy of the models, following Steiner et al. (2008) and Roura-Pascual et al. (2006).

The first step evaluated how accurately the native range occurrence points predicted when projected onto other ranges; i.e., the introduced range in North America. Then, in the same manner, the introduced occurrence points were projected onto the native range. This cross validation analysis was to ensure the reliability and accuracy of the ecological niche models and to ascertain any niche characteristic difference between introduced and native ranges (Herborg et al., 2007; Steiner et al, 2008; Ortega-Huerta et al., 2008). Over 400 predictive models were developed for using the Worldclim and cruCL2 datasets.

The second step was to cross validate within-region (the local/GTA range) predictivity. In order to assess the model performance of the introduced range, the introduced range occurrence points were split into two subsets for training and testing model performance within the introduced range (Roura-Pascual et al., 2006). The subset that includes the occurrence points in the eastern GTA was referred to as the “Eastern” subset whereas the other subset that includes the occurrence points in western GTA is referred to as the “Western” subset (Table 3 - 1, Figures 3 – 1 and 3 - 3). Within-region model predictivity was evaluated using one of the two subsets to predict the other, and vice versa. The crucial point of this “within-region” cross prediction approach is that it tested the ability of the model to predict areas from which no occurrence data were available for training the model (Roura-Pascual et al, 2006). The model performance was assessed with AUC and the predicted area coverage of occurrence points in each subset using occurrence points in the other subset.

The third step was to use the combined occurrence points from the introduced range and the native range to predict the potential geographic distribution range of *M. rubra* on a larger scale. The final ecological niche modelling map on a larger scale was, however, created by superimposing the predicted introduced range onto the basic layer of predictive map developed using the native range occurrence points to obtain enhanced ecological niche predictive maps for maximum information using the Spatial Analysis Tools function from ArcMap after the sensitivity were correctly calibrated for both outputs because each layer of output map has different upper and lower limits of suitability values and needs to be normalized if multiple layers were used.

Validation of the accuracy of the ecological niche model on the GTA/local scale

From late May until August in 2013, 9 locations across the GTA were surveyed for the presence/absence of *Myrmica rubra* by visual searching. The locations used for the validation of the ENM on the local/GTA scale were 3 parks (G Ross Lord Park, High Park, and Rouge Park) in Toronto and 6 farms (1 in Markham, 1 in King City, 2 in Mount Albert, and 2 in Milton). The farms were visited at least twice per week from May through August for comprehensive search coverage as well as spatial and temporal consistency, and at least 1 hour was spent at each location for visual searching for ants at various habitats within a location. To minimize sampling biases for habitat heterogeneity (Clark et al., 2008; McPhee et al., 2012), a focus was placed on forested areas and relatively undisturbed meadows/scrublands on each farm and park for *M. rubra* presence because *M. rubra* tends to avoid areas that are anthropogenically processed such as lawns, parking lots, and pavements.

M. rubra were collected for identification verification, and the geo-coordinates of the location were recorded on a GPS unit. All presence occurrence points were incorporated into the ecological niche model for further evaluative tests.

It should be noted that visual surveys were conducted at randomly selected yet repeatedly visited locales before the predictive models were developed to ensure that visual surveys for ENM accuracy validation was unbiasedly conducted. The geocoordinates of the locales with *M. rubra* present/absent were mapped and measured against the ENMs to assess the performance of the model.

Predicting future distributions due to climate change

To predict potential geographic distributions of *M. rubra* in the future due to global climate change, SDMs developed were projected onto a future climate scenario dataset. The future scenario assumed twice the (current, historical) amount of atmospheric CO₂ concentration and a 4°C average temperature increase. Initially the CCM3 model (x 2 CO₂ concentration) developed by National Center for Atmospheric Research (NCAR), Boulder, CO, USA with a 2.5 arc-minute resolution was used to run a future scenario SDM on Bioclim. The output was subsequently manipulated by raising average global temperature by 4°C, simulating the predicted climate of the 2100s.

Results

Environmental variable dimensionality

For both Worldclim and cruCL2 datasets, the most accurate results were obtained with all 19 and 23 variables, respectively intact rather than with a reduced number of variables for Maxent and ANN. All results had AUC values of >0.99. From the analyses, it was concluded that runs with all the 19 variables produced the most consistent and reliable output, and subsequent runs were performed with the 19 variables for Maxent. To determine the most influential abiotic factors for the persistence of *M. rubra* from the occurrence data obtained during this study (refer to Chapter One), a series of regression analyses concluded that altitude was essential for the

presence/absence of *M. rubra*, and the altitude/elevation dataset was added to the 19 Worldclim global climate datasets to augment the accuracy of the models.

Runs were done with jackknifing manipulation to measure variable importance, and the dimensionality was reduced according to the gain of each variable. Subsequent runs were done with reduced numbers of variables, and the performance of each run was evaluated with the AUC value, the omission error curve plot, and visual inspection of the output map.

For DOMAIN and Bioclim, the reduction of dimensionality of analyses did not differ potential geographic distribution areas substantially; that is, runs with only 10 variables did not differ noticeably from those with all 20 variables. Runs with 16 variables (with mean temperature of warmest quarter, precipitation of wettest month, precipitation of wettest quarter, and maximum temperature of warmest month removed) predicted slightly larger potential *M. rubra* distributions and consistently produced slightly higher AUC's than runs with all 20 variables. With Bioclim, runs with only 10 variables produced additional potential distribution areas in southwestern Ontario compared to those predicted with 20 and 16 variables. Runs with only 10 variables showed lower AUC's than those with 16 variables. These findings were true for the models produced by the DOMAIN algorithms, and as a result, all Bioclim and DOMAIN runs were done with 16 abiotic variables.

ANN runs with reduced variables did not differ substantially from the runs with all 20 variables for potential distributional areas; however, when run with only 10 contributing variables out of the 20, the potential geographic ranges for *M. rubra* were substantially reduced. This reduction of coverage was likely due to the restriction of the

conditions suitable for the persistence of *M. rubra*. Over all, ANN runs with all 20 abiotic variables gave the most consistent and highest AUC values (0.99 – 1.00), and consequently the final ANN model was developed using all the 20 variables.

Spatial resolutions of environmental layers

Larger areas of potential geographic distribution by *M. rubra* were consistently occupied when an environmental dataset with a lower spatial resolution was applied regardless of the algorithms used. An increase in the regularization multiplier in the Maxent settings resulted in larger coverage areas but a reduced AUC value.

“Within region” cross validation/prediction

Figures 3- 1 to 3 - 4 show the results of using the eastern data points to predict the western distribution and vice versa, and the projected occurrence points were compared with the actual occurrence points to evaluate the performance of the models.

Using the occurrence points in the eastern half, 7 locations out of 10 were correctly predicted in the western half locations (AUC = 0.835; Figures 3 - 1 and 3 – 2). Two locations out of 9 were included in the eastern half areas predicted by the western half occurrence points (AUC = 0.833; Figures 3 – 3 and 3 – 4). This might be attributed to the proximity of occurrence sites to one another and higher numbers of occurrence points in the eastern half than the western half, resulting in higher biases placed on the

eastern half for predictability. The AUC values for the cross prediction tests were high despite some discrepancies in predictability between the two subsets.

Forward and backward projection between the native and introduced ranges

Using the occurrence points in the native range of Europe, potential geographic distribution points were projected onto the introduced range. The predicted areas contained some known *M. rubra* occurrences in maritime Canada, the Pacific Northwest, and along the Alaskan coast as well as the actual occurrence points for this study (Figure 3 – 5). The omission curve (the green line) did not deviate from the predicted omission, and the sensitivity/specificity curve was well beyond the random prediction line (AUC = 0.954; Figures 3 – 6 and 3 – 7).

When back-projecting onto the native range with the occurrence points in the introduced range, it was found that some areas of central Europe, central England, eastern Denmark and southern Sweden, areas around the north of the Black and Caspian Seas appeared on the predictive map whereas a substantial part of eastern North America was expected to contain potential distribution areas in the backward projection (Figures 3 – 8a and 3 – 8b). The omission curve slightly augmented in the range of the predicted probability of occurrence between 50 and 75 percent whereas the sensitivity/specificity curve is also well beyond the random prediction line (AUC = 0.999; Figures 3 – 9 and 3 – 10).

ENMs/SDMs on the local/GTA level

Maxent jackknifing did not have a significant influence on better AUC values: precipitation of wettest month and wettest quarter, mean temperature of warmest quarter, and maximum temperature of warmest month. Subsequently runs without these 4 variables were evaluated for AUC values against the runs with all 20 variables intact.

Both Bioclim and DOMAIN were run with the 30 arc-second dataset for maximum resolution. For both algorithms, the predicted coverage areas were comparable; however, with Bioclim areas with low habitat suitability were extended towards southwest of the GTA compared to the outcome with DOMAIN. DOMAIN, however, showed an additional area northwest of the GTA which was not observed with Bioclim (Figures 3 – 11 and 3 – 12). Areas of high habitat suitability predicted by Bioclim were centred around the borders of the city of Toronto, York region, and Durham region.

Noticeable differences between the outputs of the two algorithms, the areas of lower habitat suitability radiated away from the high suitability area for Bioclim whereas as for DOMAIN, generally the gradient of habitat suitability diminished as the distance from an occurrence point increased, and various occurrence points across the GTA made a rather discrete mosaic-like map as opposed to continuous bands of various suitability areas seen in the Bioclim model. The AUC value for Bioclim for the local/GTA level was 0.946 and for DOMAIN it was 0.935 (see Figures 3 – 13 and 3 – 14), and the comparability of the two AUC's indicate the excellent predictive abilities of the models.

ENMs/SDMs on the regional/southern Ontario level

For the Artificial Neural Network (ANN) algorithm, runs with reduced variables by 4 or 5 did not differ substantially from the runs with all 20 variables for potential distributional areas; however, when run with only 10 contributing variables out of the 20, potential geographic areas for *M. rubra* were substantially reduced. Over all, ANN runs with all 20 abiotic variables gave the most consistent and highest AUC values, and consequently the final ANN model was developed using all the 20 variables.

Models were developed with the highest spatial resolution environmental layer (30 arc-seconds) for both Artificial Neural Network (ANN) and Maxent. The same regions (the GTA area and the region east of Lake St. Clair) were predicted by both algorithms for habitat suitability for *M. rubra* yet with different sensitivity (Figures 3 – 15 and 3 – 16). The AUC value for ANN was 1.00, and the percentage of cells predicted present in this environmental layer tile was 0.723 %. For the Maxent model, the AUC was 0.999, and the majority of omission curve was below the predicted omission line, indicating low omission errors for this model (Figures 3 – 17 and 3 – 18).

ENMs/SDMs on the continental/North America level

The results obtained from the cross prediction testing between the native and introduced ranges were used for this model (Refer to the “Forward and backward projection between the native and introduced ranges” on page 109). (see Figures 3 – 19 through 3 – 22). The AUC for the forward projection is 0.954, and the AUC for the backward projection is 0.999.

Figures 3 -19 through 3 – 22 show the predicted areas of high and moderate habitat suitability. The latitudes of predicted areas in the introduced range; i.e., North America, lie between 39.38° N and 61.13° N whereas the native occurrence range falls between 42.50° N and 64.95° N., indicating a similar latitudinal range.

Validation of the accuracy of the ENM on the local/GTA scale

During the field season in 2013, the locales of *M. rubra* collected by visual surveys across the GTA were integrated into the local/GTA level Bioclim algorithm to evaluate the accuracy of the model. *M. rubra* was found on only 1 farm amongst the 6 farms frequently visited during the visual survey period and in 4 parks (Figures 3 – 23 and 3 – 24). In some parts of Rouge Park and Whittamore's Farm, *M. rubra* were found in extreme abundance whereas other areas of those locales appeared devoid of the ants.

The ENM developed with Bioclim on the local/GTA level highly accurately predicted the presence/absence of *M. rubra* when evaluated according to the results by visual surveys which took place in the spring and summer of 2013.

Two parks (High Park and Eglinton Flats) shown in dark orange areas both had moderate numbers of *M. rubra* and nests were intermittently present whereas at G. Ross Lord Park interspersed nest distribution and moderate abundance of *M. rubra* was found in the dark orange areas and high abundance with high nest densities in the areas shown in red, indicating the excellent ability to discriminate the degree of habitat suitability even within a narrow range (Figures 3 – 23 and 3 – 24). Visual surveys

conducted at Rouge Park and Whittamore's Farm where extreme abundance of *M. rubra* was found with very high nest densities matched their corresponding predicted habitat suitability as shown in red, also indicating the validity of this model is high.

Predicting future distributions due to climate change

With the future scenario, the potential distribution of *M. rubra* was slightly reduced in eastern North America whereas a minor increase in suitable areas occurred along the coast of the Gulf of Alaska. In the native range, on the other hand, a major reduction of suitable habitat areas was observed in central Europe with a slight increase in habitat suitability in eastern Fennoscandia (Figure 3 – 25).

Discussion

ENM/SDM maps identify areas where invasive species may be present already (even though they are undetected) and areas where invasive species may occupy in the future. For this study ENMs/SDMs were developed based on occurrence records of non-native invasive *M. rubra* from the introduced range and the native range. Three different scaled SDMs were created to better suit the mitigation/prevention of the potential spread of *M. rubra* (local/GTA level, regional/southern Ontario & eastern North America level, and continental/North America level) with 4 different algorithms. Prioritizing more susceptible areas for invasion using the information obtained from

ENMs/SDMs will increase the prospect of successful management and enable cost effective mitigation/prevention of this invasive ant.

Parameterization of environmental datasets

For Maxent, in order to reduce dimensionality of analyses, a jack knife manipulation was applied, and the performance of each model was evaluated according to the AUC plots and test gains, and the omission error curve plots. Ward (2007) suggested that in some cases, using too few or too many climate variables may produce incorrect predictions. Some variables influence more than others for the accuracy of a model, and numerous models with reduced numbers of variables were tested. Most of them produced reasonable overall AUCs (over 0.85); however, for reduced variables runs with even moderate values of AUCs, they often produced output maps where they showed potential occurrences of *M. rubra* in very unlikely places. Runs with reduced numbers of environmental variables in most cases gave rise to larger areas of potential geographic distribution of *M. rubra* as well. This phenomenon was more pronounced with the cruCL2 datasets, and this may be due to the low spatial resolution of the cruCL2 datasets (10 arc-minutes).

Even with the same number of environmental variables, lower spatial resolution datasets produced larger coverage for potential occurrences than higher counterparts. This finding is in keeping with the SDM results for the Argentine ants conducted by Menke et al. (2009) that coarsening of spatial resolutions produced more widespread predicted occurrence areas. This must be because of the inability of low resolution datasets to detect an absence area between two occurrence points, resulting in one big

blotch rather than showing a space between two occurrence points. For this reason, all ENMs/SDMs were performed with the highest spatial resolution of Worldclim global climate data with 30 arc-seconds which correspond to approximately 1 km x 1 km grids, obviating the use of the cruCL2 datasets. McPherson et al. (2006) and Guisan et al. (2007) mentioned that coarsening the spatial grain of data tends to decrease model performance.

Local/GTA scale ENMs and dimensionality reduction of the dataset

Both Bioclim and DOMAIN runs with all 20 abiotic variables showed high AUC values (above 0.9); however, runs with reduced dimensionality of the data (i.e. with 16 variables) always gave more consistent outcomes and slightly higher AUC's than runs with 20 variables. Average precipitation does not differ significantly from month to month in the GTA throughout the year, and this may attribute to the exclusion of the precipitation related variables.

Regional/southern Ontario & eastern North America scale SDMs

Areas of high suitability for *M. rubra* generated by both Maxent and ANN are very similar, indicating their ability to predict potential distributional areas is high inasmuch as the degree of sensitivity. This discrepancy must be due to their predictive approaches. The AUC values for both algorithms are extremely high and comparable (Maxent = 0.999, ANN = 1.00), suggesting the high performance ability of both models.

The species distribution model generated by Maxent presents a higher resolution for the regional/southern Ontario scale, and it indicates that the central part of the City of Toronto, the southern part of both York and Durham regions as well as the immediate eastern part of Lake St. Clair in southwestern Ontario should be vigilantly monitored for future invasion or further expansions if this invasive species is already present.

Niche difference evaluation by cross projection and on the continental/North America level SDMs

A striking aspect of the forward projection model was its predictive ability to correctly predict the region of the actual occurrence points used to construct SDM models for this study without any North American occurrence points included (Figure 3 – 5). Solely based on the native range occurrence data, the forward projection SDM successfully managed to predict other known *M. rubra* occurrence regions such as Newfoundland, Nova Scotia, and the west coast of Vancouver Island. This finding suggested that ecological niches were spatially conserved from the native range to the introduced range. This high predictability of the geographic dimensions of the process of invasion of the non-native range provides with strong evidence for the ecological niche as a stable limitation on the geographic potential of the species, and this is in agreement with the finding by Peterson (2003). It was also demonstrated by Peterson that ecological niches over evolutionary time were conserved and that the evolution of niche space was not a considerable limitation for species distribution modelling, and this enables climate-based SDMs to be successful in predicting the occurrence of species or

closely related species at previously unsampled localities (Peterson, 2003; Fitzpatrick, 2005).

The backward projection with the occurrence data in the introduced range onto the native range predicted the known hot spots such as central England and Denmark/southern Sweden; however, the potential geographic distribution areas by the backward projection covered less areas than the actual occurrence areas. The following factors are likely to attribute to the distribution differences between the two ranges.

1. Invasion history/equilibrium: *M. rubra* is native to the Palearctic region, and its distribution in the native range is relatively complete; that is, the ant has spent a sufficient time to occupy the suitable areas there. Conversely, an invasion history in the introduced range goes back to as far as early 1900s (Wheeler, 1908), and this non-native invasive species is still expanding to colonize potential suitable habitats in North America, meaning that there must have a sufficient time for the North American *M. rubra* populations to reach its invasion equilibrium and to expand to all available habitats so that the environmental space occupied in the introduced range will be a true representative of the niche. It is likely that *M. rubra* has not been in North America long enough (approximately for 120 years) to portray their current presence areas as a true representation of invaded areas in the introduced range.

2. Unmatched sample sizes: Even though the sample size used to represent the introduced range occurrence data is quite adequate for Maxent (143 occurrence points), the native range occurrence points (2,129 occurrence points) exceed the introduced points by far. This unmatched numbers of occurrence points might have resulted in less

area coverage in the native range when back projected with the introduced range occurrence data.

3. Distribution and proximity of occurrence points: The native range occurrence points extend across central and northern Europe (approximately 2,800 km longitudinally) whereas the introduced range occurrence points span 65 km across the GTA. This discrepancy in spread may attribute to the extent of distribution difference between the two ranges. Also the proximity of the introduced range occurrence points to one another may be a factor to be considered, for some points are as close as 2 km to their neighbouring points whereas the occurrence points in the native range are farther apart from one another. Another possibility is due to the interaction between geographic and environmental space, for the narrow geographic scale at which *M. rubra* occurred in the GTA, spatial autocorrelation in some of the environmental variables used for this model might have resulted in the areas where the clustering of occurrence points occurred, i.e., environmental space. Since the values of the environmental variables sampled at locations in close proximity are not independent from each other, there is some possibility that spatial autocorrelation could happen. This geographical clustering of the introduced occurrence points might have influenced the potential geographic distribution of the native range in the backward projection model.

Despite some discrepancy between the predicted potential distribution areas and the actual areas, the AUC value and the omission error curves show high predictive abilities of the models (Figures 3 – 9 and 3 – 10). The backward projection model also predicted the very susceptible regions for future invasion in the native range where other SDM algorithms also predicted them to be very vulnerable to future invasion.

Based on the high AUC values and omission error curves, both forward and backward projections proved to be able to predict potential geographic distribution of *M. rubra*, and consequently the two output maps were superimposed to give maximum information of *M. rubra*'s potential suitable habitats after the threshold and sensitivity of each output were correctly calibrated (Figures 3 – 19 through 3 – 22).

Differences between forward and backward projections may reveal whether the potential distribution of this species is limited by the same factors that constrain its native distribution, and even considering the aforementioned 3 possible factors that might attribute to the discrepancy between the two ranges, potential geographic distribution areas of *M. rubra* were well predicted with high AUCs.

Predicted areas of high habitat suitability all have annual average precipitation of at least 125 cm, indicating that mesic conditions are a pivotal factor for the persistence of this species. This was in agreement with the findings from Chapter One that one of the 3 most influential factors for the presence/absence of *M. rubra* is high soil surface moisture level which is associated with annual precipitation. Also it was found that soil surface moisture was not correlated with soil type (refer to Chapter One).

For the development of the SDMs for this study, the occurrence points across the GTA were used to represent the introduced range presence points, and any purported occurrence points in North America were not included to ascertain the ability of the models to accurately predict potential geographic distribution areas. The continental/North American level SDM did include the recently reported occurrence points of *M. rubra* in the Maritime Provinces, New England, and Vancouver Island,

strongly indicating that the model's ability to correctly predict potential suitable habitats is high.

The local/GTA scale ENM validation

Due to consistently higher AUC's shown by Bioclim over those by DOMAIN, the ENM for the local/GTA level validation was performed with Bioclim. The local/GTA scale ENM model was thus validated with randomly chosen presence/absence points across the GTA (Figures 3 – 23 and 3 – 24).

The accuracy shown by this validation test suggests that the potential geographical distribution of *M. rubra* in the GTA predicted by the ENM can be reliably applied to monitor susceptible areas that need to be under constant vigilance for future invasion and/or to minimize the expansion of this invasive species for increased likelihood of successful mitigation if they are already present.

Projecting SDMs into the future

Climate change caused by global warming may not affect the persistence of *M. rubra* in North America substantially in this future scenario; however, in the native range the current habitat areas in central Europe may be greatly reduced in the future due to elevated average global temperature, and *M. rubra* is very likely to move to higher latitude areas; i.e., Scandinavia and Fennoscandia (Figure 3 – 25). Bertelsmeier et al.

(2013) showed a similar result for North America; however, their future prediction distribution in the native range did not differ from the current distribution.

This phenomenon for habitats to shift towards higher latitudinal or altitudinal areas was predicted for other invasive species, both for fauna and flora in response to climate change (Lenoir et. al., 2008; Roura-Pascual et. al., 2004; Sutherst et al., 2005). When SDMs were run for a possible future geographic distribution of another invasive ant species Argentine ant (*L. humile*) with Bioclim, the habitat shift towards higher latitude region was also observed (figure not shown) as well as reduction in the current habitats. This analysis represents an initial step towards understanding the influences of climatic alteration in the face of global warming on the potential geographic distribution.

Caveats associated with sampling and environmental data for ENMs/SDMs

The accuracy of models developed for the potential distributions of species depends on sample sizes for model building, type of collected data, the complexity and spatial resolutions of the environmental variables (Menke et al., 2009). For this study, only presence only data were used to construct ENMs/SDMs for the following reasons:

1. absence of species at a given region is difficult to access, especially when dealt with invasive species, and false absences can decrease the reliability of predictive models (Chefaoui et al., 2005).
2. modelling with presence only data determines potential habitat suitability, and inclusion of absence data will restrict habitat suitability disregarding the factors such as

historical restrictions, dispersal limitations, extinction, and biological interactions (Anderson et al., 2003).

3. modelling with presence only can successfully predict the fundamental niche of a species, and modelling the fundamental niche is more appropriate for invasive species which are likely to be less limited by biotic interactions (Ward, 2007).

4. Elith et al. (2006) suggested that presence only modelling were sufficiently accurate for potential species distribution modelling.

Defining the species' ecological niche by the extent of each environmental variable is scale dependent, and therefore different degrees of ecological niche can result depending on the spatial resolution of analyses (Roura-Pascual et al., 2006). At different spatial resolutions, the significance of variables differs as climatic factors become more important at coarser resolutions whereas habitat variables become less important, for microhabitats become rather negligible at coarser resolutions. The highest spatial resolution available was used to obtain the maximum sensitivity for both climatic and microhabitat variables in this study to detect any absence regions between two closely spaced presence points.

Potential ecological niche differentiation between the native and introduced ranges due to ecological differences

In general, SDMs cannot integrate biotic influences that restrict the distribution of species such as the presence of natural enemies and competitors (Fitzpatrick et al., 2005); however, as for *M. rubra* in the introduced range of North America, there are no

known natural enemies or competitors present, and therefore only abiotic factors are the main restrictive conditions and that SDMs for *M. rubra* in North America should be able to predict the potential geographic distribution of this non-native invasive species accurately.

For some invasive ant species, introduced populations are ethologically different from native counterparts due to their release from natural enemies, parasites, and competitors present in their native ranges, and this ecological differentiation might give rise to a difference in ecological niche between the two populations (Roura-Pascual et al., 2006).

Another possible explanation for the potential ecological niche difference between the two ranges is that there is very unique microclimate that is very specific to the GTA, and this unique microclimate may be very conducive to the persistence and burgeoning of *M. rubra* in the GTA.

On a molecular/genetic level, *M. rubra* has been around in North America for over a century, and its abundance remained low; however, only in the past 15 years, numerous sighting reports have been made. This “time lag” could be due to 1. possible introductions of new strain(s) of *M. rubra* from the native range 2. time lag for *M. rubra* in North America has taken nearly 100 years before the full potential of expansion began.

It was suggested by Wetterer and Radchenko (2010) that a more recent introduction of a population from a narrow latitudinal range from within Europe might be attributed to this phenomenon that the abundance for the past century remained low yet recent spread is unprecedented. Hicks et al. (2014) found 7 different composite haplotypes using mitochondrial DNA sequences from the cytochromes b and c oxidase genes of *M. rubra*

from 8 locations in North America, suggesting the presence of genetic differences amongst North American populations.

In cases where SDMs show non-overlapping for populations within a species, it could reveal patterns of divergence, and this can be substantiated with molecular data. Also SDMs can be used to validate hypotheses of ecological niche differentiation divergence if molecular data reveal limits to gene flow or other differences based on the behavioural differentiations between the two ranges.

Regarding the “time lag” theory, it was shown by Ward (2007) that it took many decades for invasive ants in New Zealand to spread to a fraction of all areas and that even after 100 years, the occupancy by invasive ants barely reached 50%. This may suggest that *M. rubra* has spent a sufficient time before they unleash their full potential to expand in North America and that there may be enough established populations for further expansion and are ready to invade any regions of suitable habitats.

Anthropogenic factors that interfere with the accuracy of the SDM predictability

An average surface soil moisture level by volume of at least 28% was found to be essential for the persistence of *M. rubra* (Refer to Chapter One). Areas with low surface soil moisture level are considered as non suitable habitats by the SDMs; however, climatically unsuitable habitats can be rendered anthropogenically habitable by means of agricultural as well as recreational irrigation such as in golf courses, urban parks or urban/agricultural run-off. The approaches the SDMs took for the prediction of potential geographic distributions of *M. rubra* do not incorporate such anthropogenic

interferences; therefore, it is possible that the SDM models underestimated areas of potential *M. rubra* distribution in some cases. This is the case for the burgeoning of Argentine ants in California where agricultural and urban run-off contributes to increased soil moisture levels resulting in the persistence of the ants in areas otherwise too xeric (Roura-Pascual et al., 2004).

Conclusion

Prior to this project, no study had been done with a combination of applications of multiple ENM algorithms for the prediction of potential geographic distribution of *M. rubra* on different geographic scales, elucidation of potential niche differences between the native and introduced ranges, and with possible future scenarios in the face of climate change.

Based on the ENM/SDM analyses, *M. rubra* has potential to spread across North America beyond the current distribution range, for they have not reached an invasion equilibrium. High values of AUC's indicated that the ENMs/SDMs constructed in this study were capable of predicting the potential geographic distribution of this non-native invasive ant, and using this information obtained from this predictive modelling, monitoring of susceptible areas for future invasion must be done municipally and provincially for successful prevention and mitigation.

Tables and figures

Locations used for “Western” subset	Locations used for “Eastern” subset
Boyd Conservation Area	Petticoat Creek Conservation Area
Kortright Centre for Conservation	Glen Rouge Campground
Heart Lake Conservation Area	Rouge Park
Glen Haffy Conservation Area	Altona Forest
Black Creek Pioneer Village	East Duffins Headwaters
Bathurst Glen Golf Course	Bruce’s Mill Conservation Area
Residential areas (2) in Thornhill	Oak Ridges Corridor Nature Reserve
Residential area (1) in Richmond Hill	Residential area (1) in North York
Residential area (1) in central/west Toronto	Tommy Thompson Park

Table 3 - 1: subsets for “within-region” cross validation test

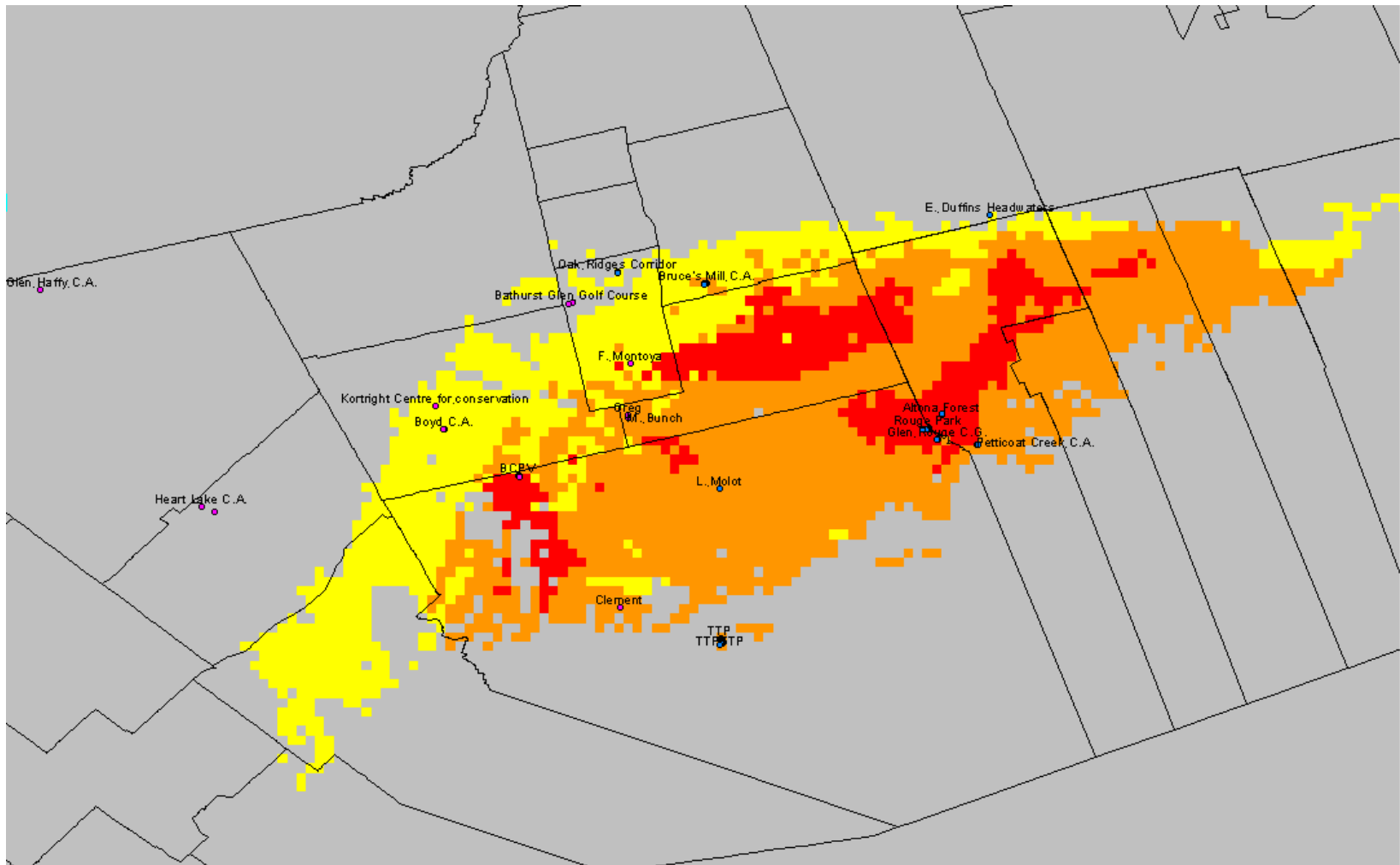


Figure 3 – 1: Cross testing using the eastern half occurrence points to predict the western locations.

Light blue points: locations used for training the model. Purple points: locations to be tested for prediction

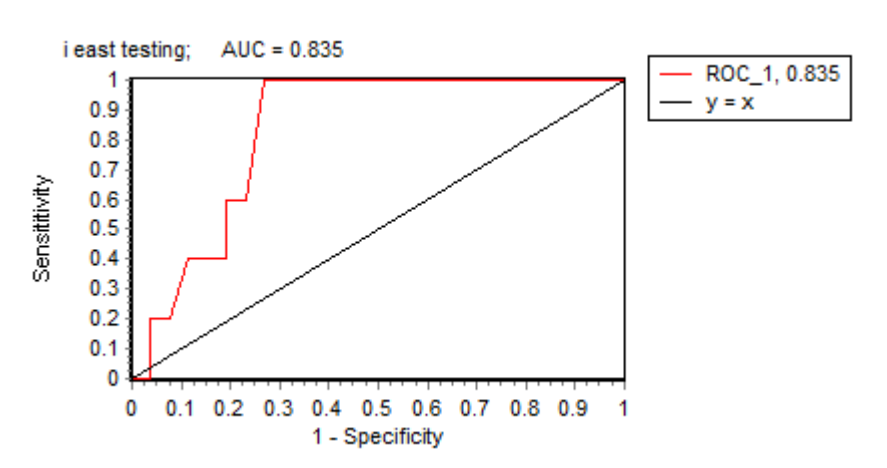


Figure 3 – 2: AUC curve for cross prediction from eastern points to western points

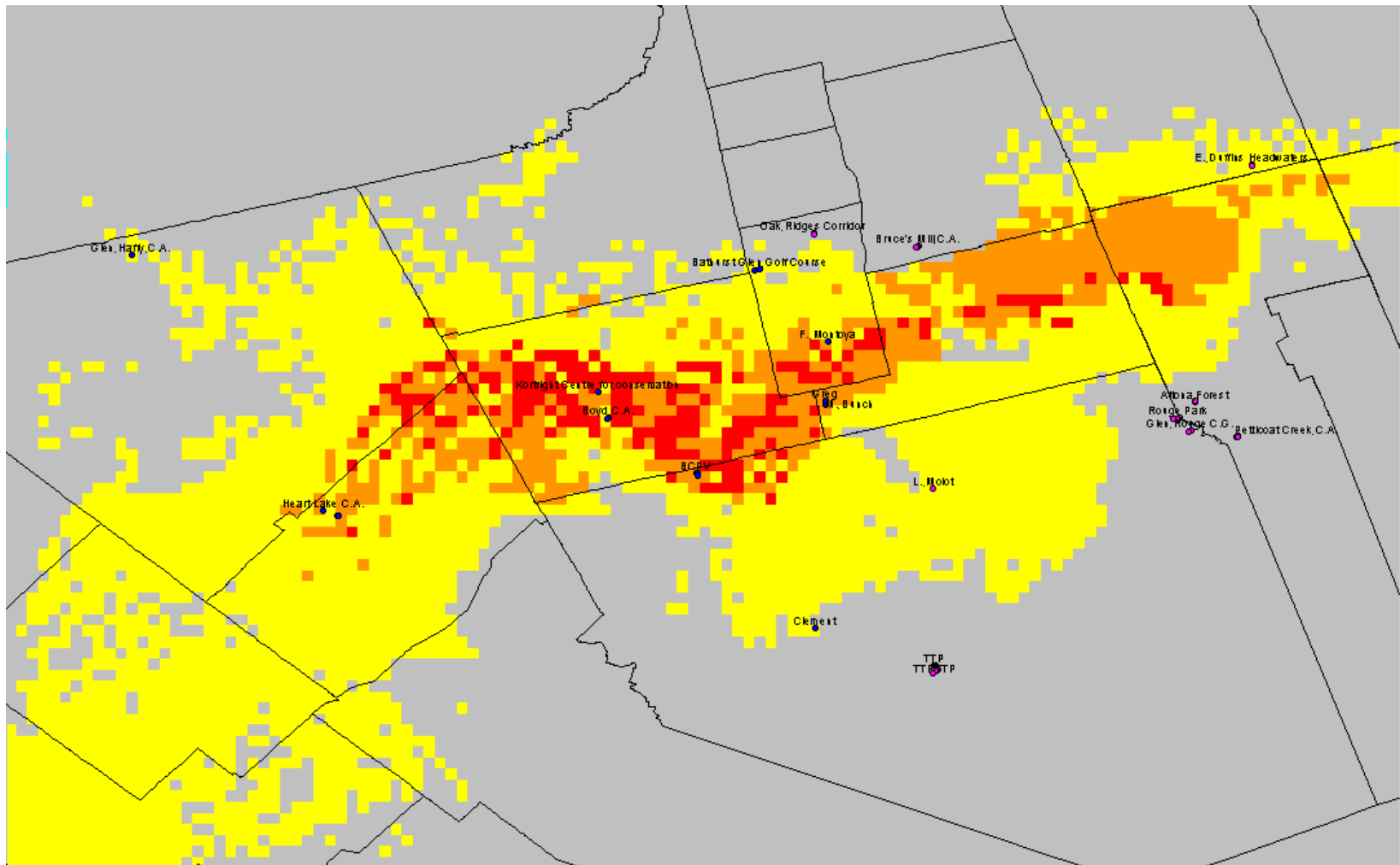


Figure 3 – 3: Cross testing using the western half occurrence points to predict the eastern locations.

Blue points: locations used for training the model. Purple points: locations to be tested for prediction.

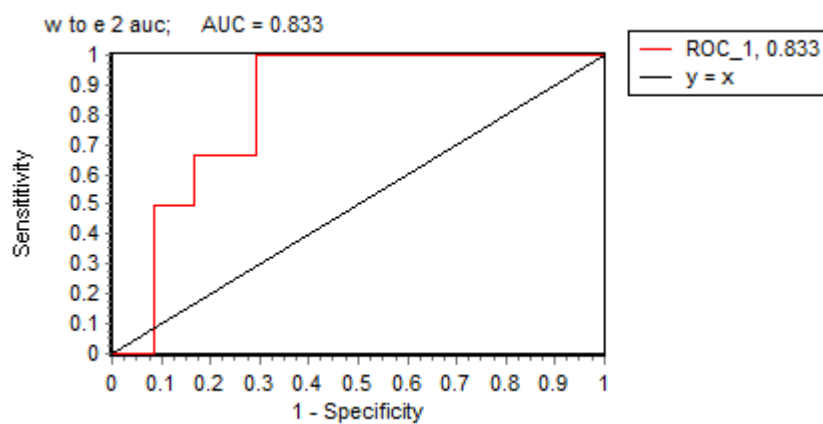


Figure 3 – 4: AUC curve for cross prediction from western points to eastern points

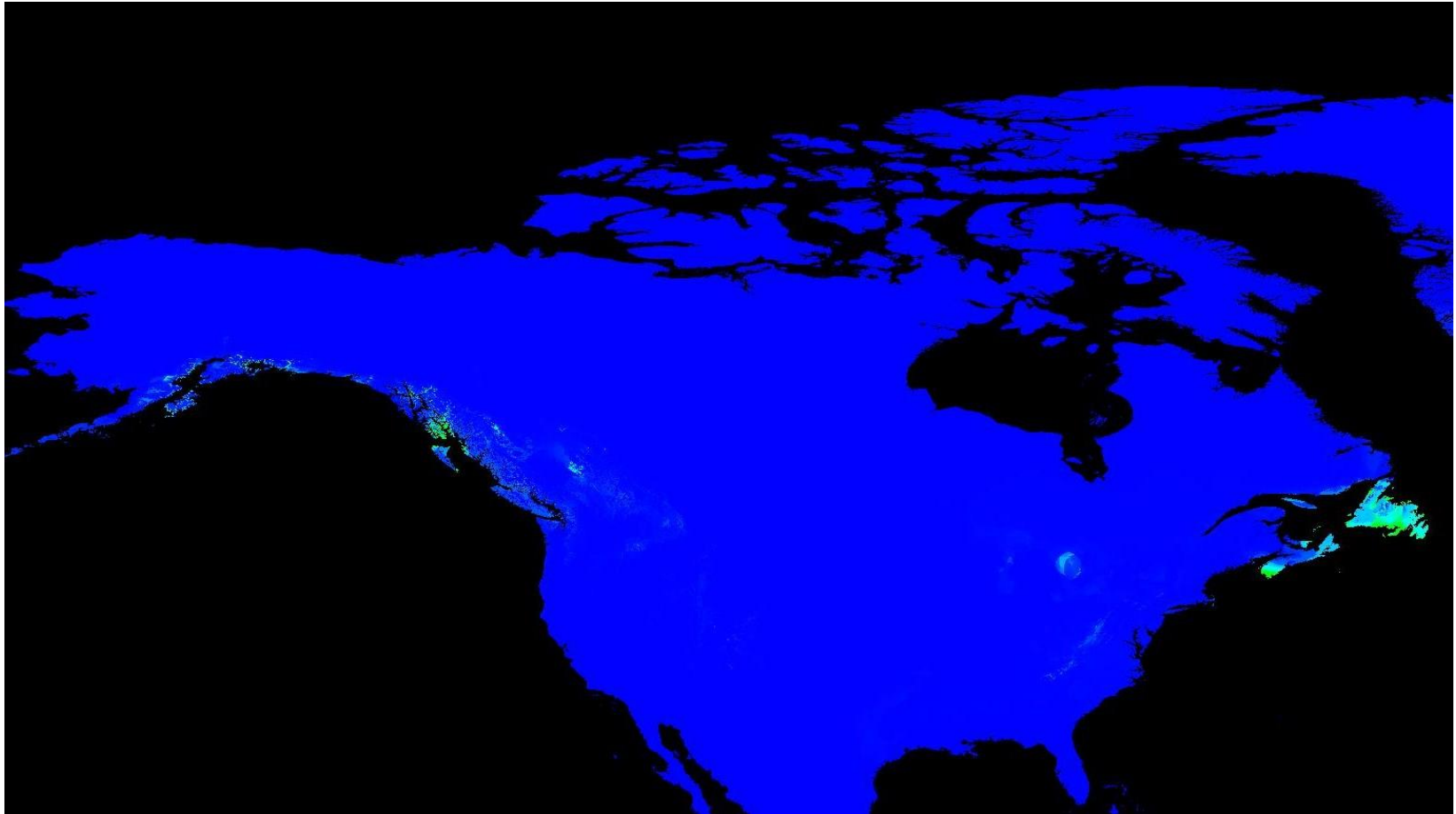


Figure 3 – 5: Forward projection: Native range occurrence points projected onto the introduced range

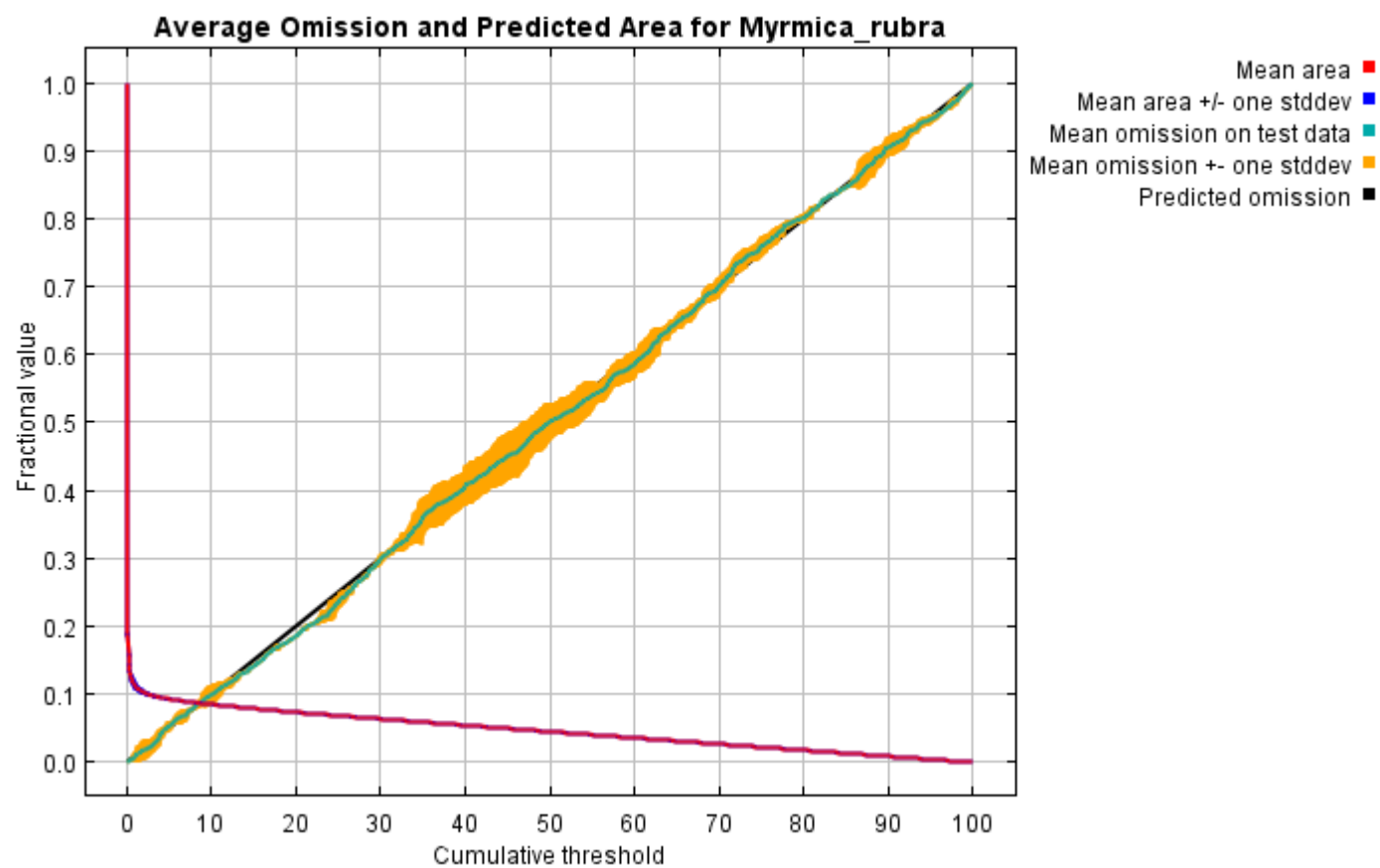


Figure 3 – 6: Omission curve for the predicted introduced range by native occurrence points

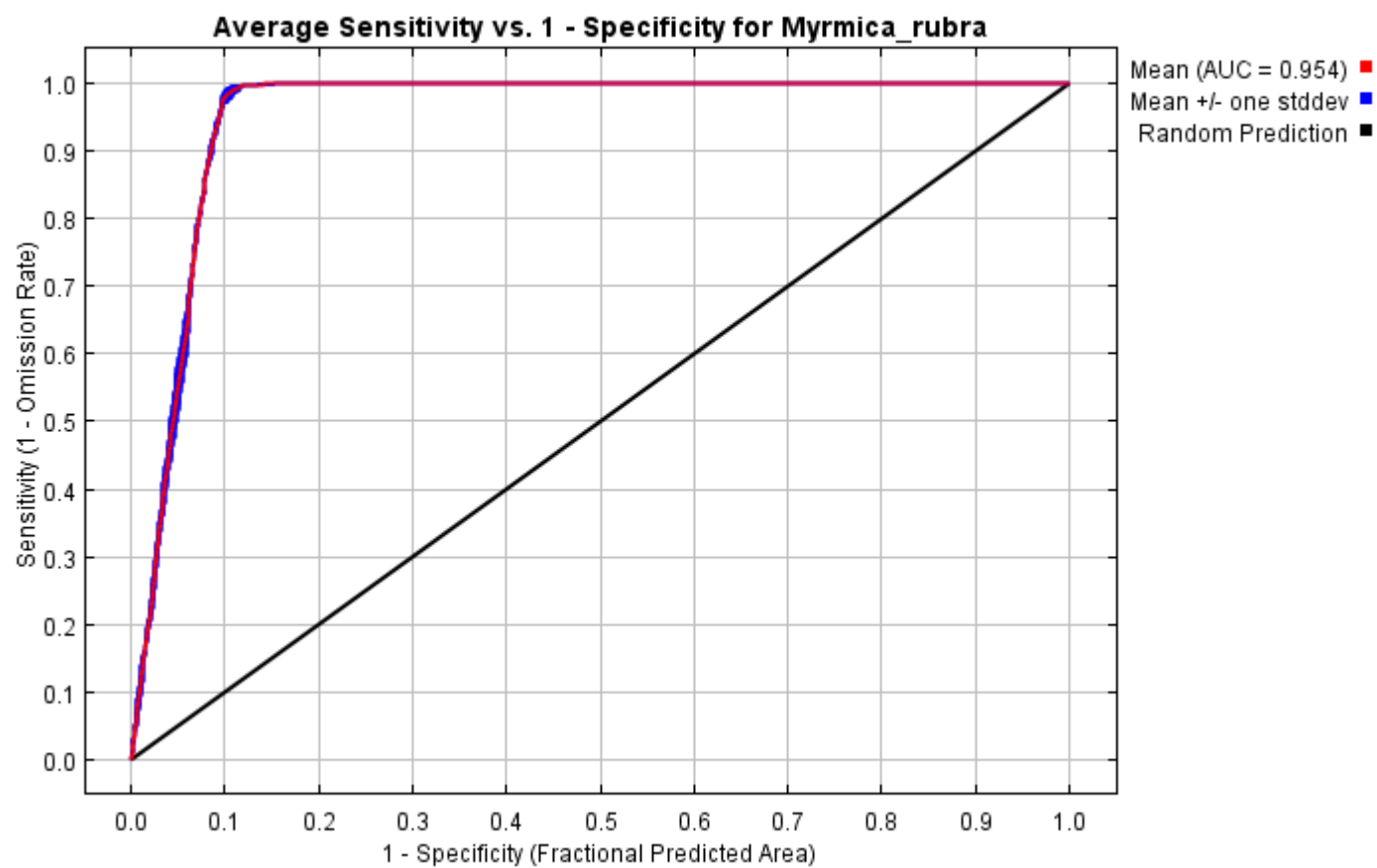


Figure 3 – 7: The AUC value for the predicted introduced range by native occurrence points

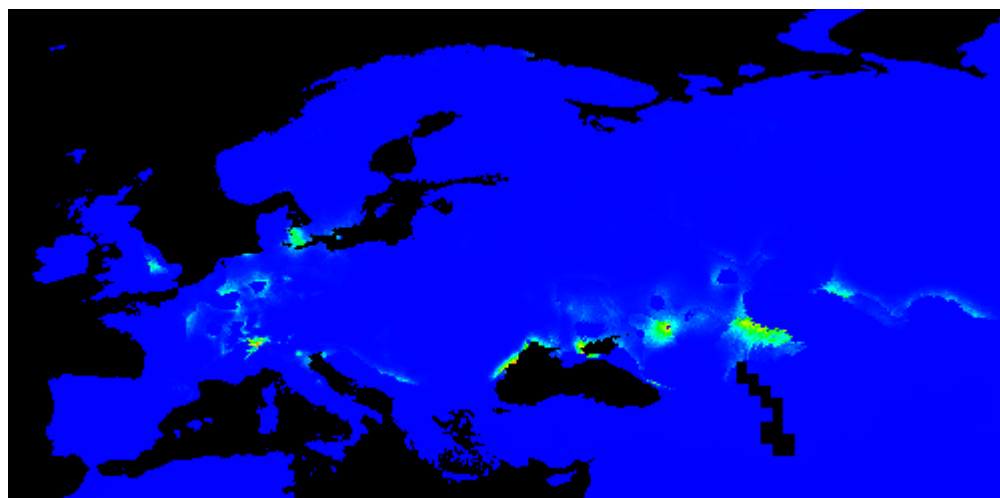


Figure 3 – 8a: Backward projection: Introduced range occurrence points projected onto the native range

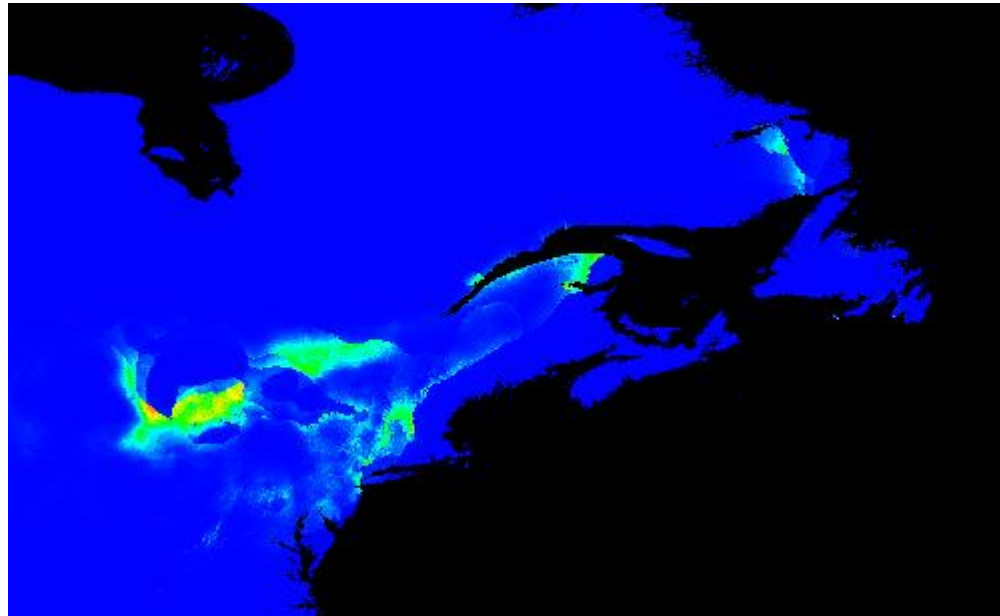


Figure 3 – 8b: Backward projection: projected potential geographic distribution areas in the introduced range using the introduced range occurrence points

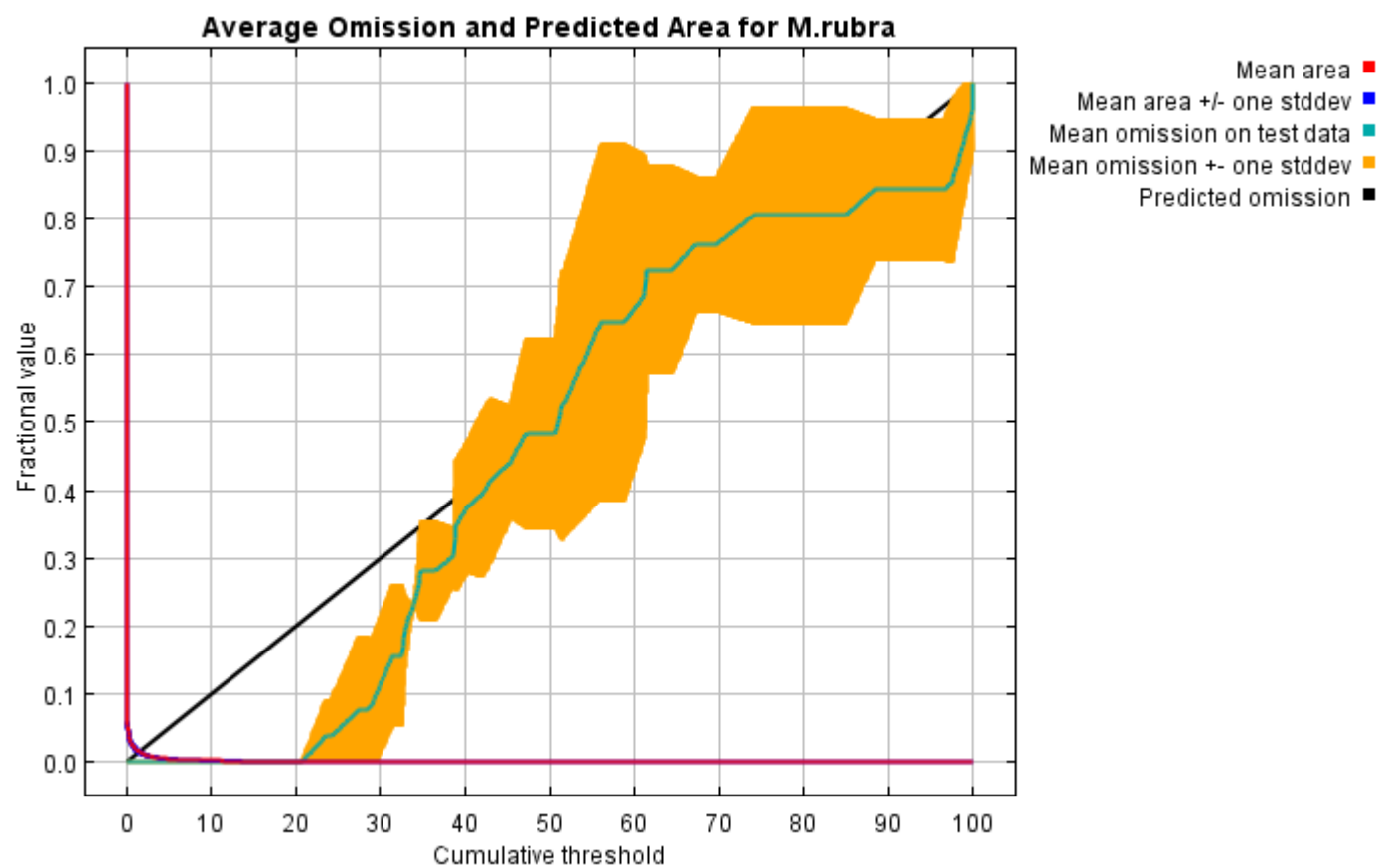


Figure 3 – 9: Omission curve for the predicted native range by introduced range occurrence points

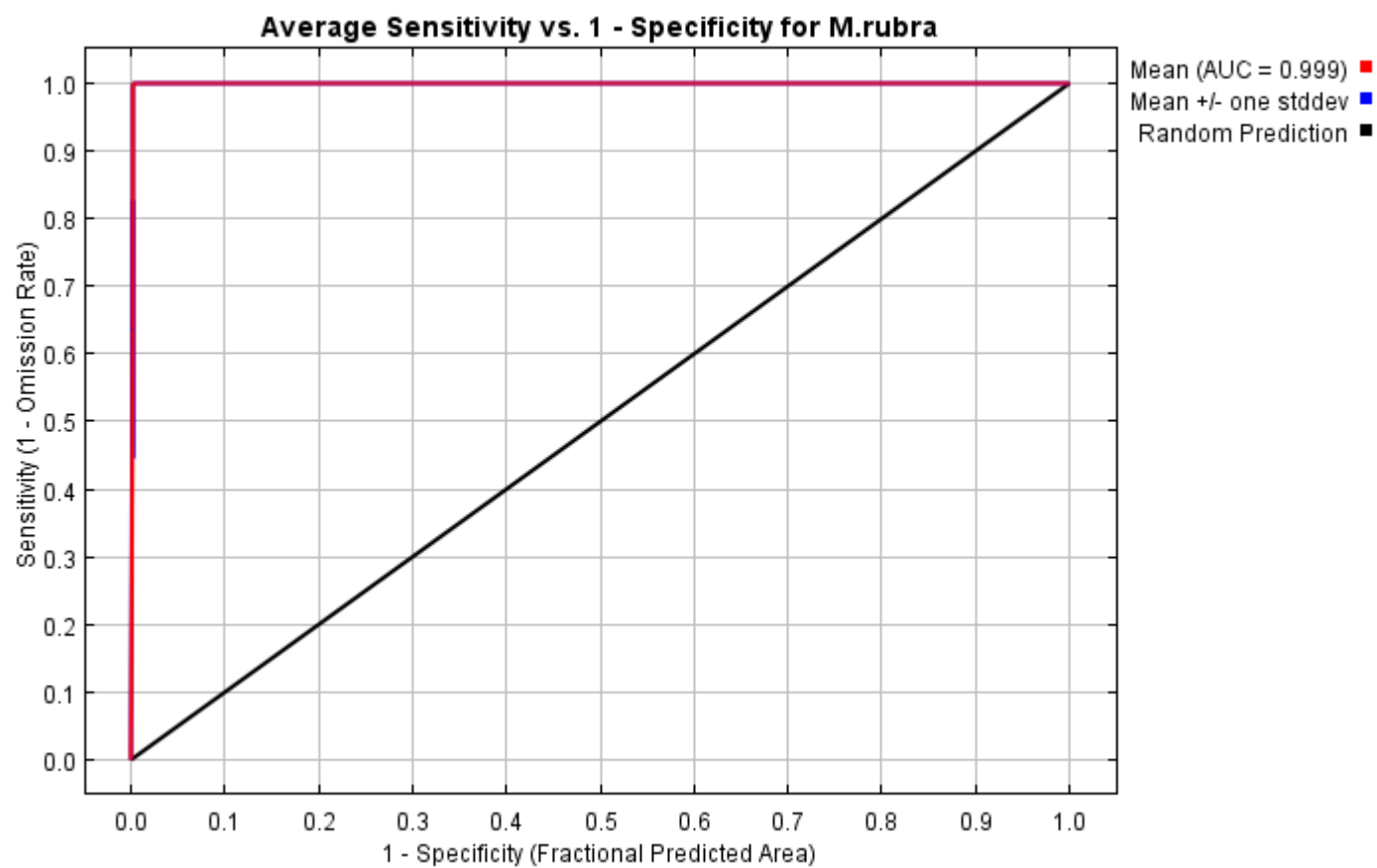


Figure 3 – 10: The AUC value for the predicted native range by introduced range occurrence points

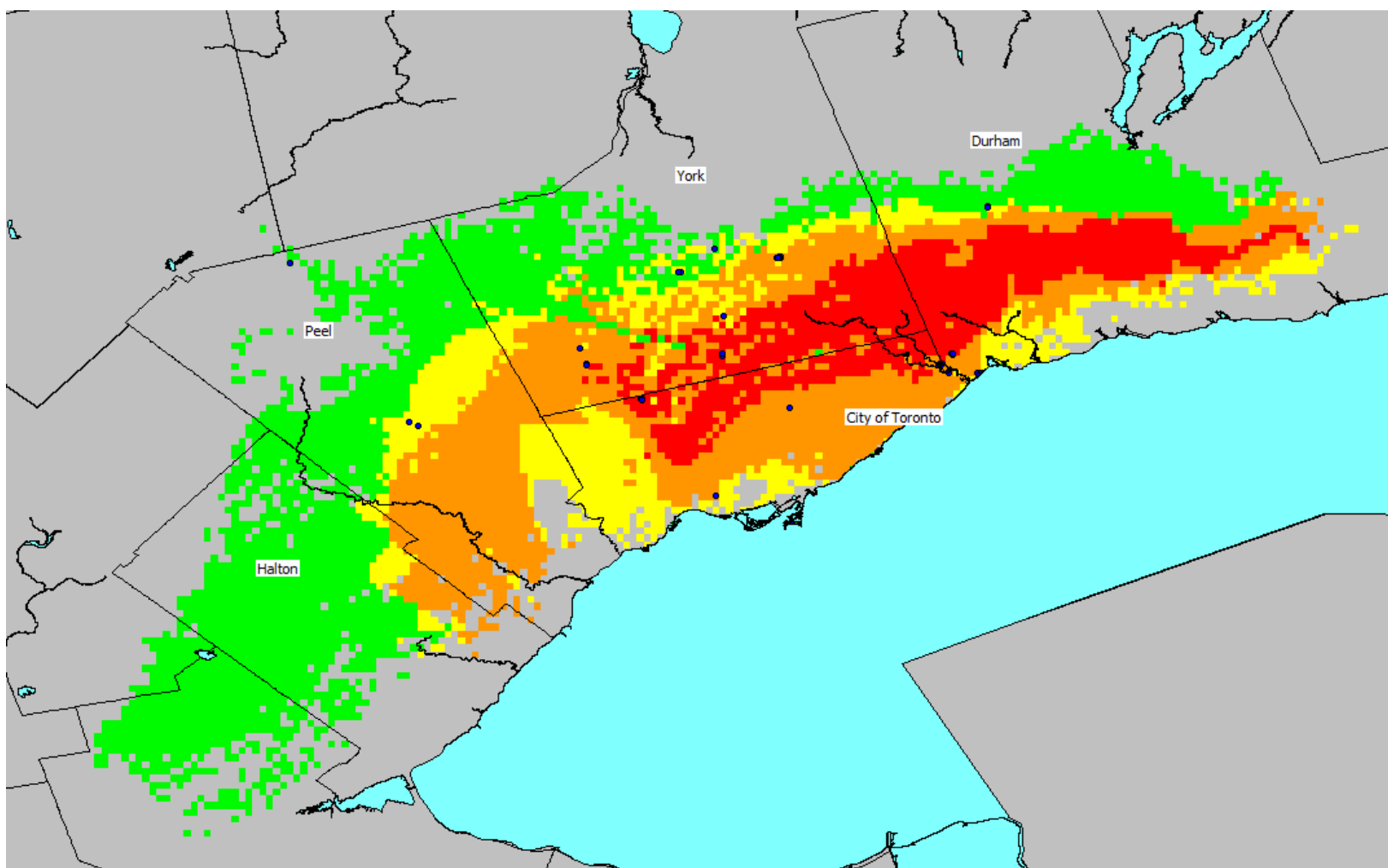


Figure 3 – 11: ENM with Bioclim on the local/GTA level

Red indicating high suitable conditions for *M. rubra*, green indicating conditions typical of those where the ant is found, and lighter shades of blue indicating low predicted probability of suitable conditions. The occurrence points used for training the model shown as blue dots.

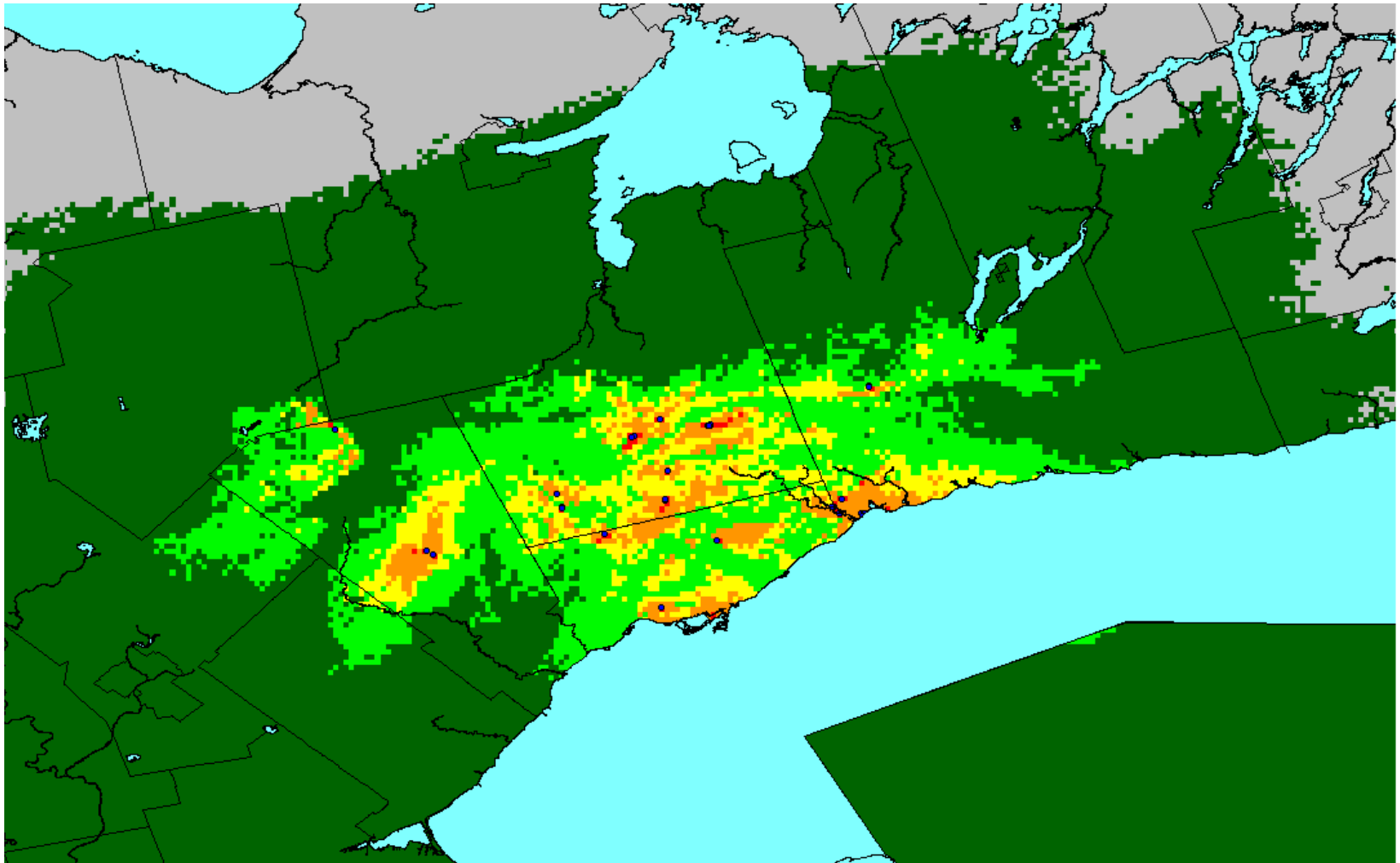


Figure 3 – 12: ENM with DOMAIN on the local/GTA level

The occurrence points used for training the model shown as blue dots

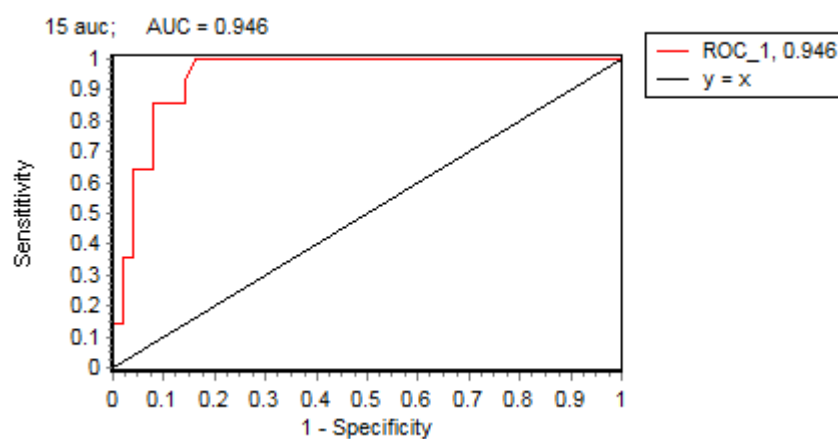


Figure 3 – 13: The AUC curve for Bioclim for the local/GTA level

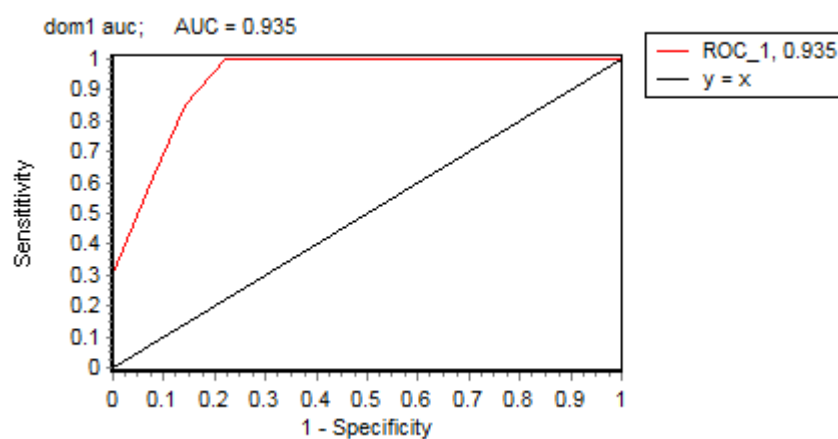


Figure 3 – 14: The AUC curve for DOMAIN for the local/GTA level

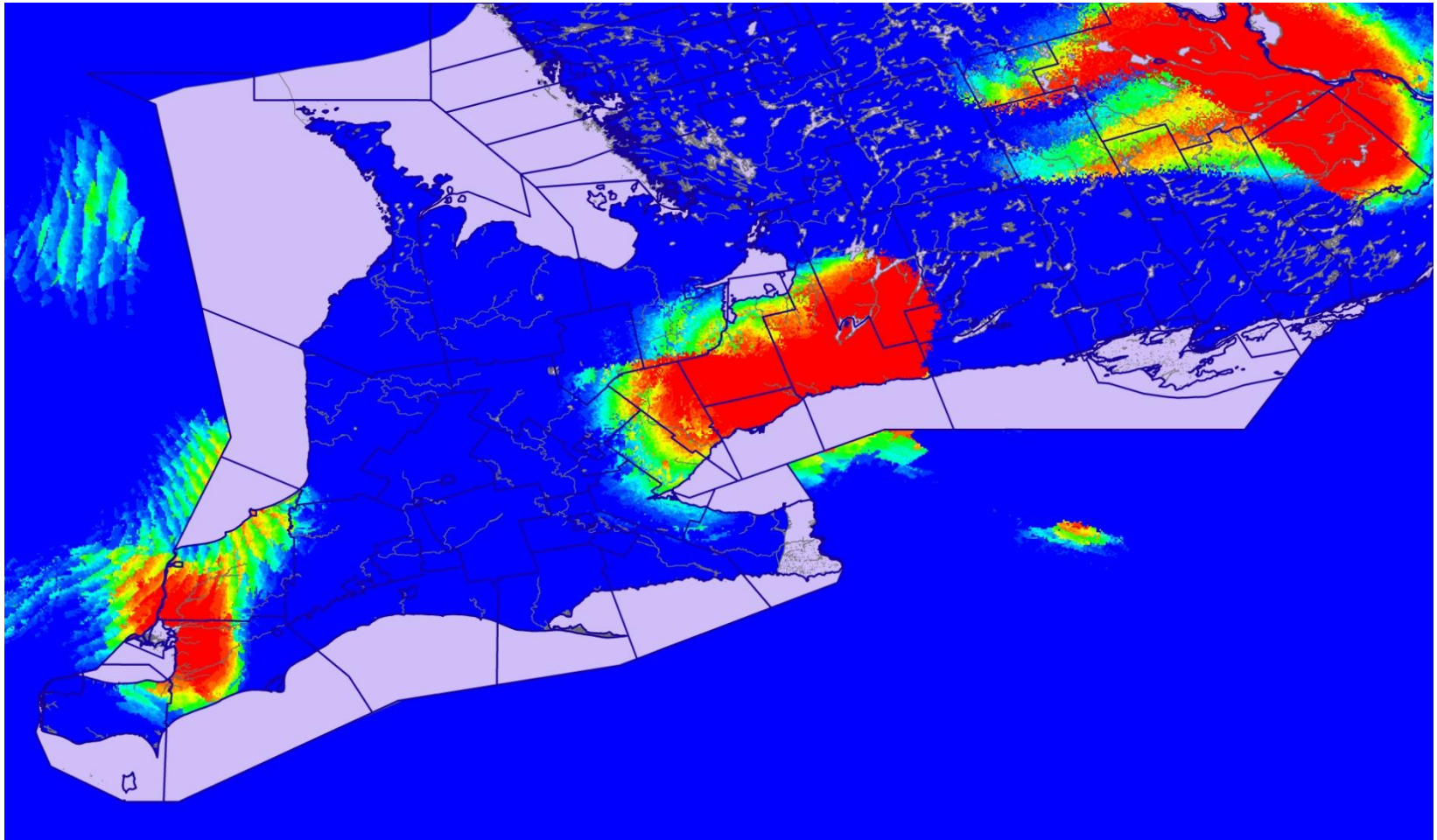


Figure 3 – 15: SDM with Artificial Neural Network (ANN) for the regional/southern Ontario level

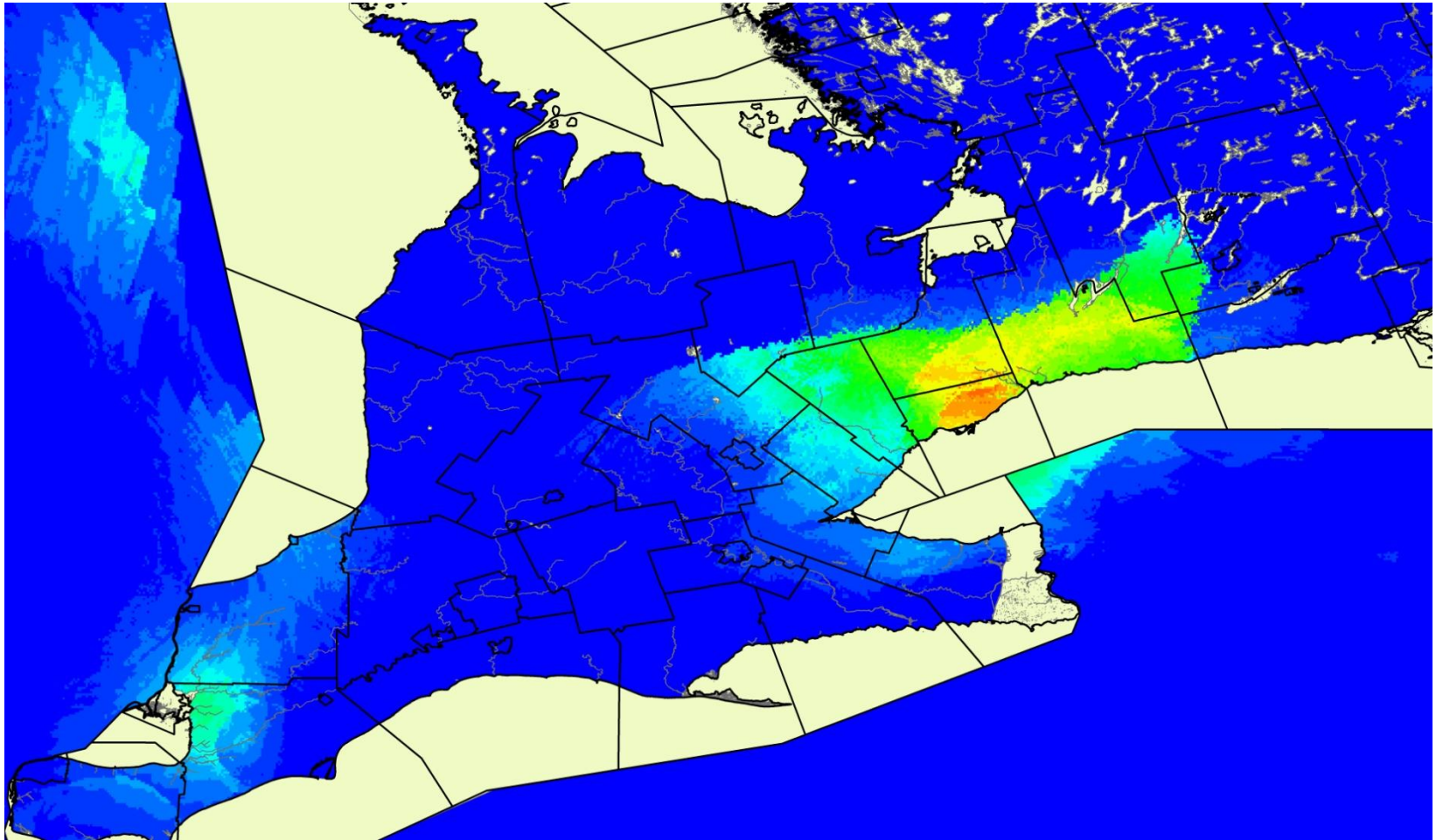


Figure 3 – 16: SDM with Maxent for the regional/southern Ontario level

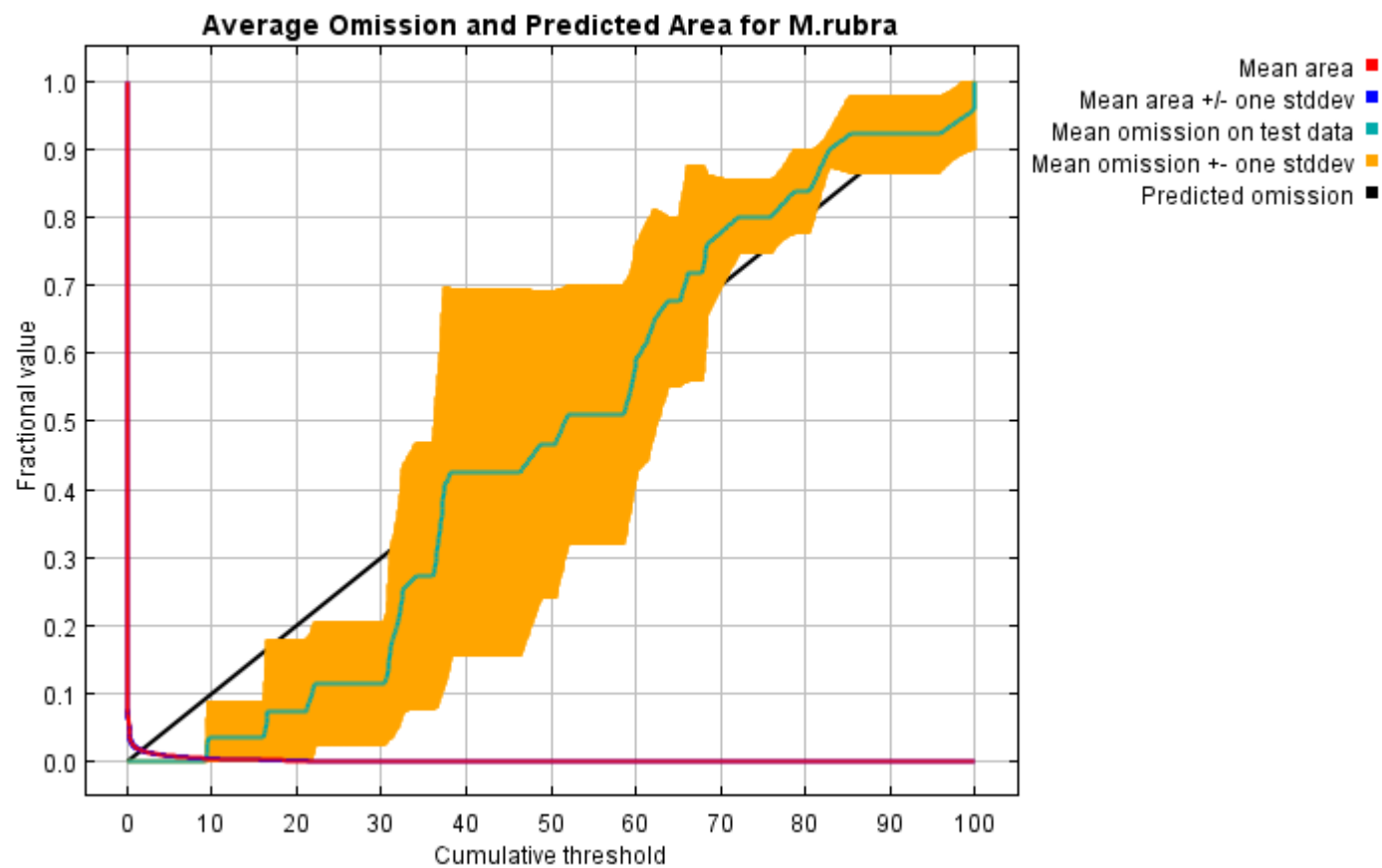


Figure 3 – 17: Omission curve for the SDM with Maxent for the regional/southern Ontario level

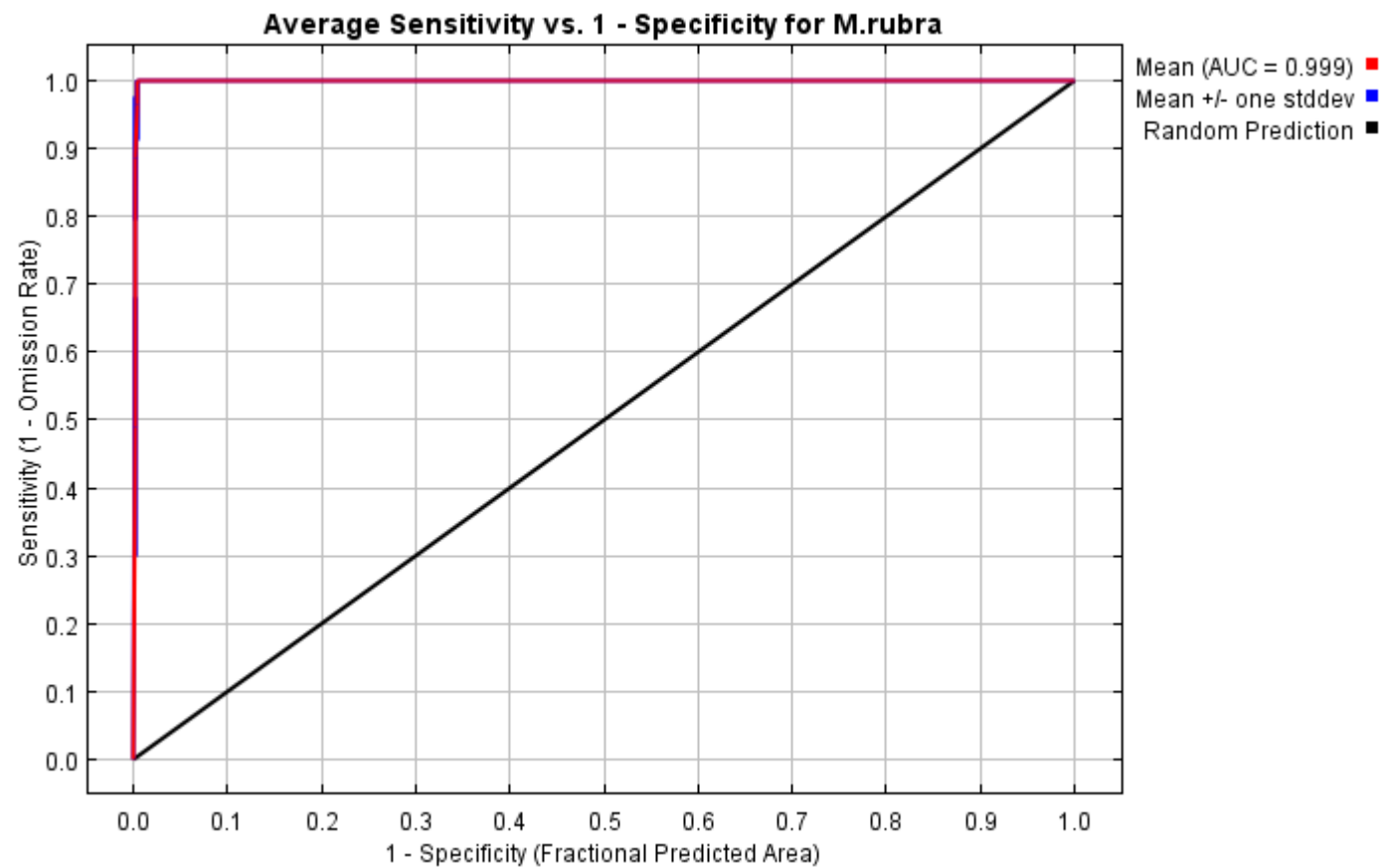


Figure 3 – 18: The AUC curve for the SDM with Maxent for the regional/southern Ontario level

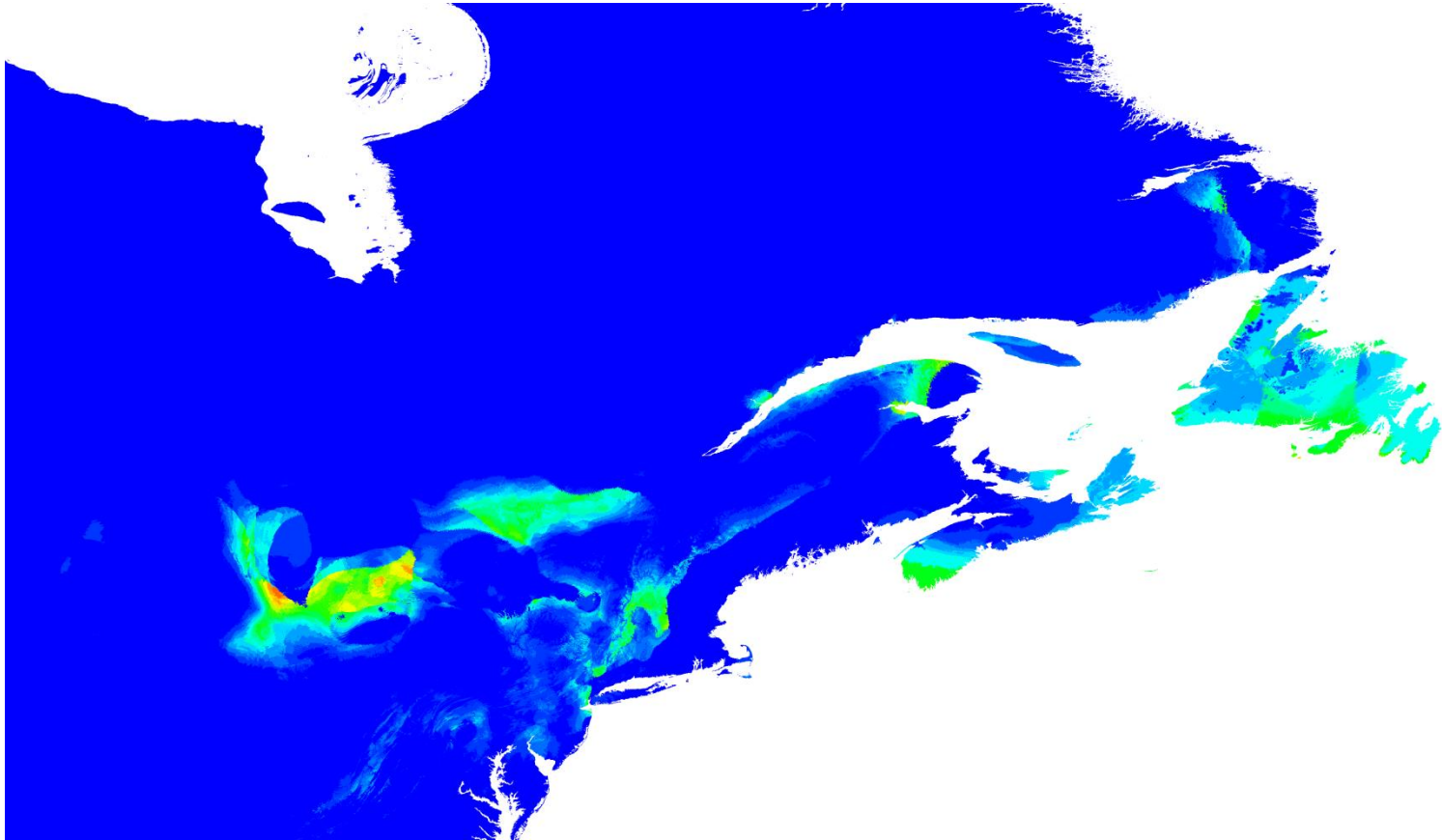


Figure 3 – 19: Predicted distribution of *M. rubra* in eastern North America

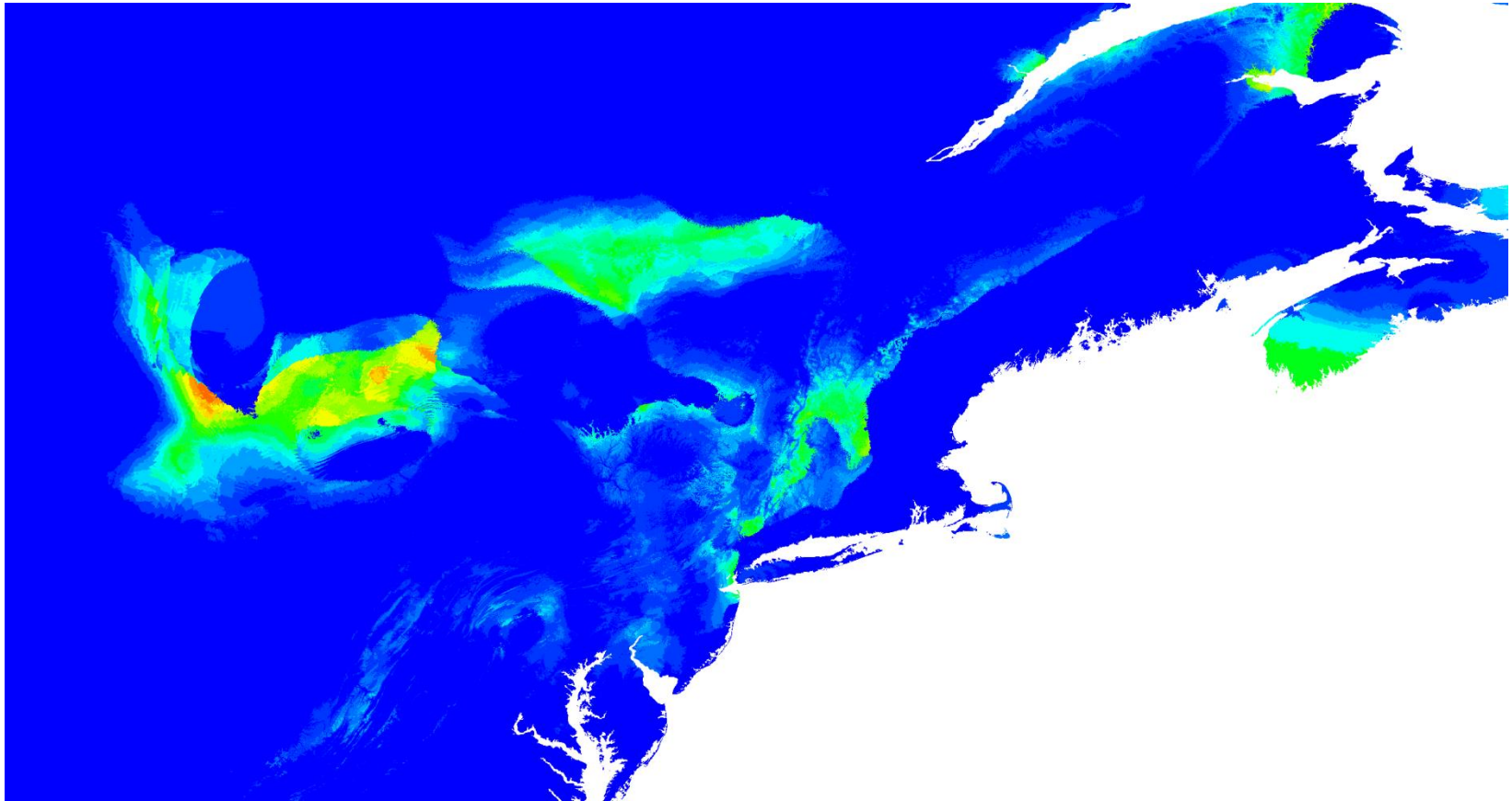


Figure 3 – 20: A close-up of the predicted distribution of *M. rubra* in eastern North America

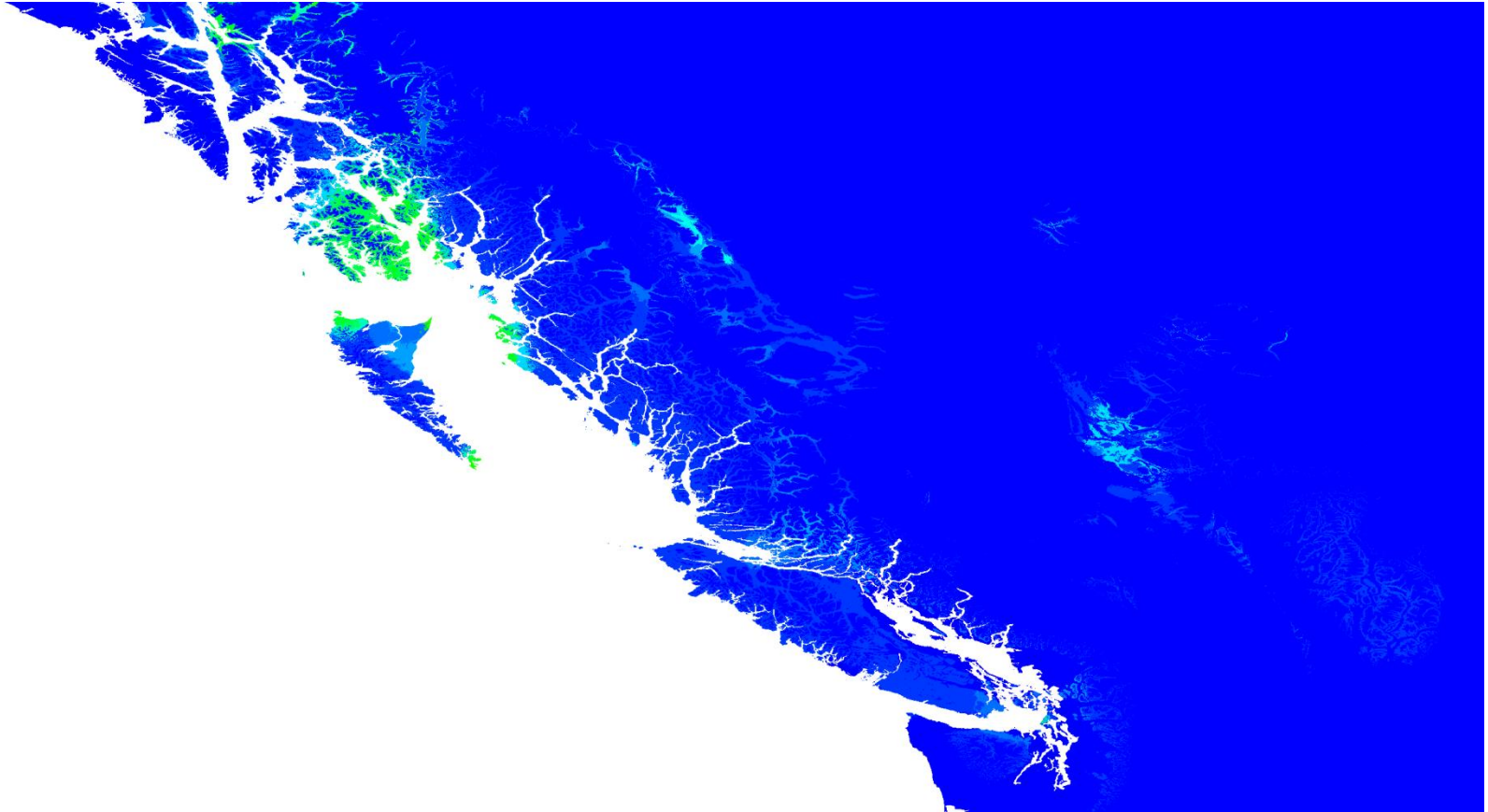


Figure 3 – 21: Predicted distribution of *M. rubra* in Pacific Northwest and along the Gulf of Alaska

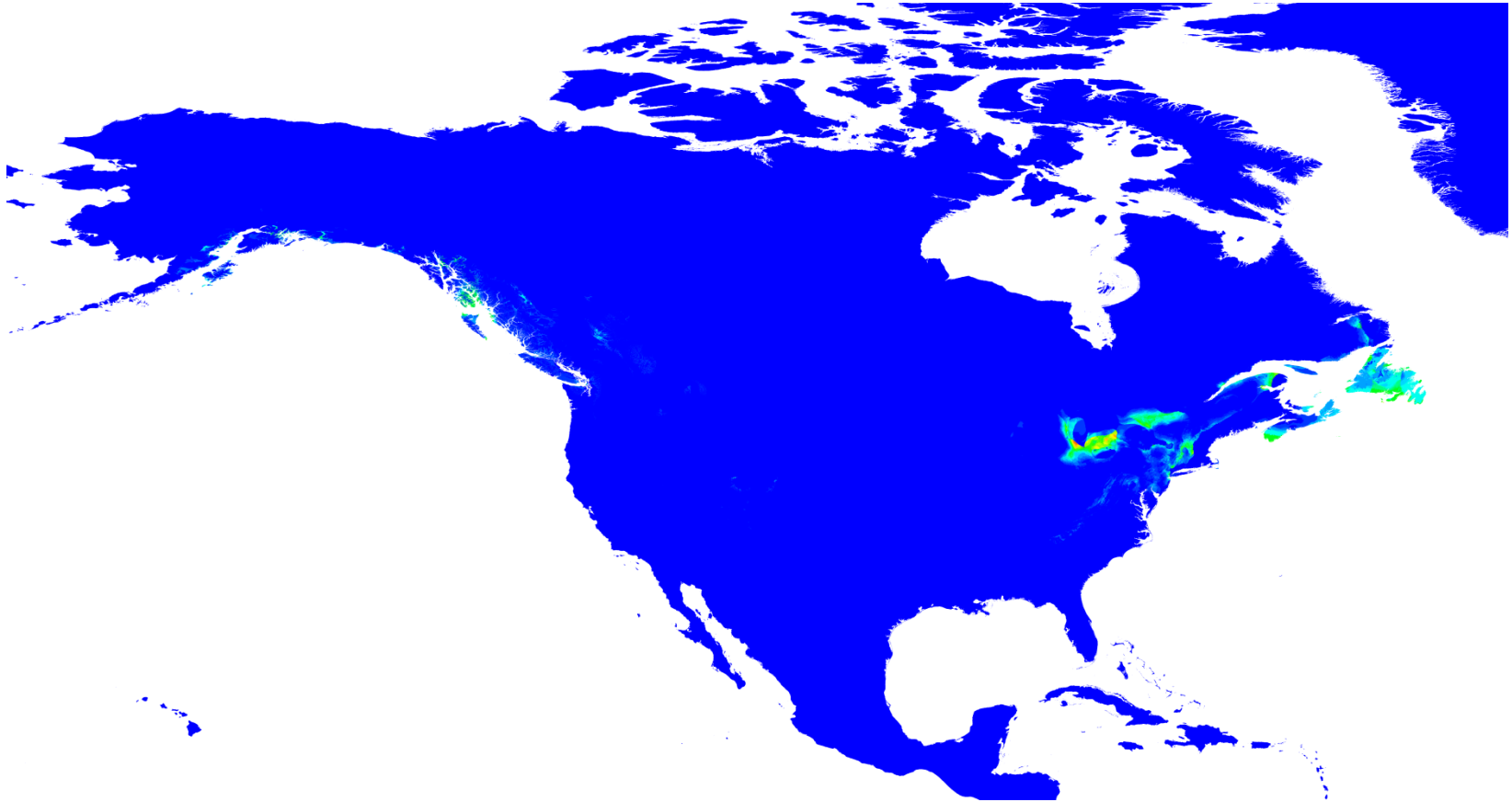


Figure 3 – 22: Predicted distribution of *M. rubra* in North America

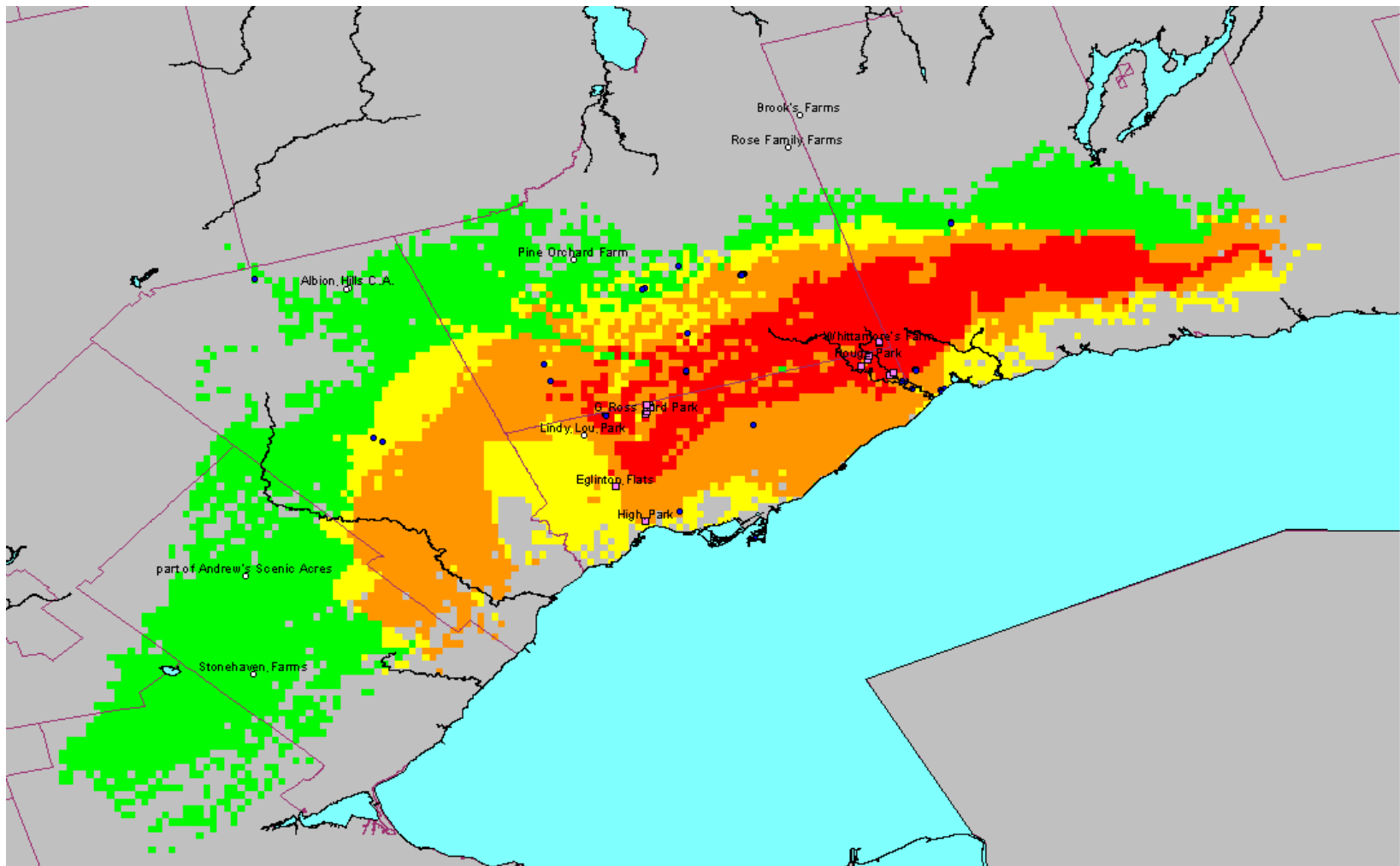


Figure 3 – 23: Validation of the accuracy of the ENM by randomly chosen actual occurrence points

M. rubra occurrence points for constructing the model shown as blue dots, actual *M. rubra* presence locales shown as purple dots, and *M. rubra* absence locales shown as white dots

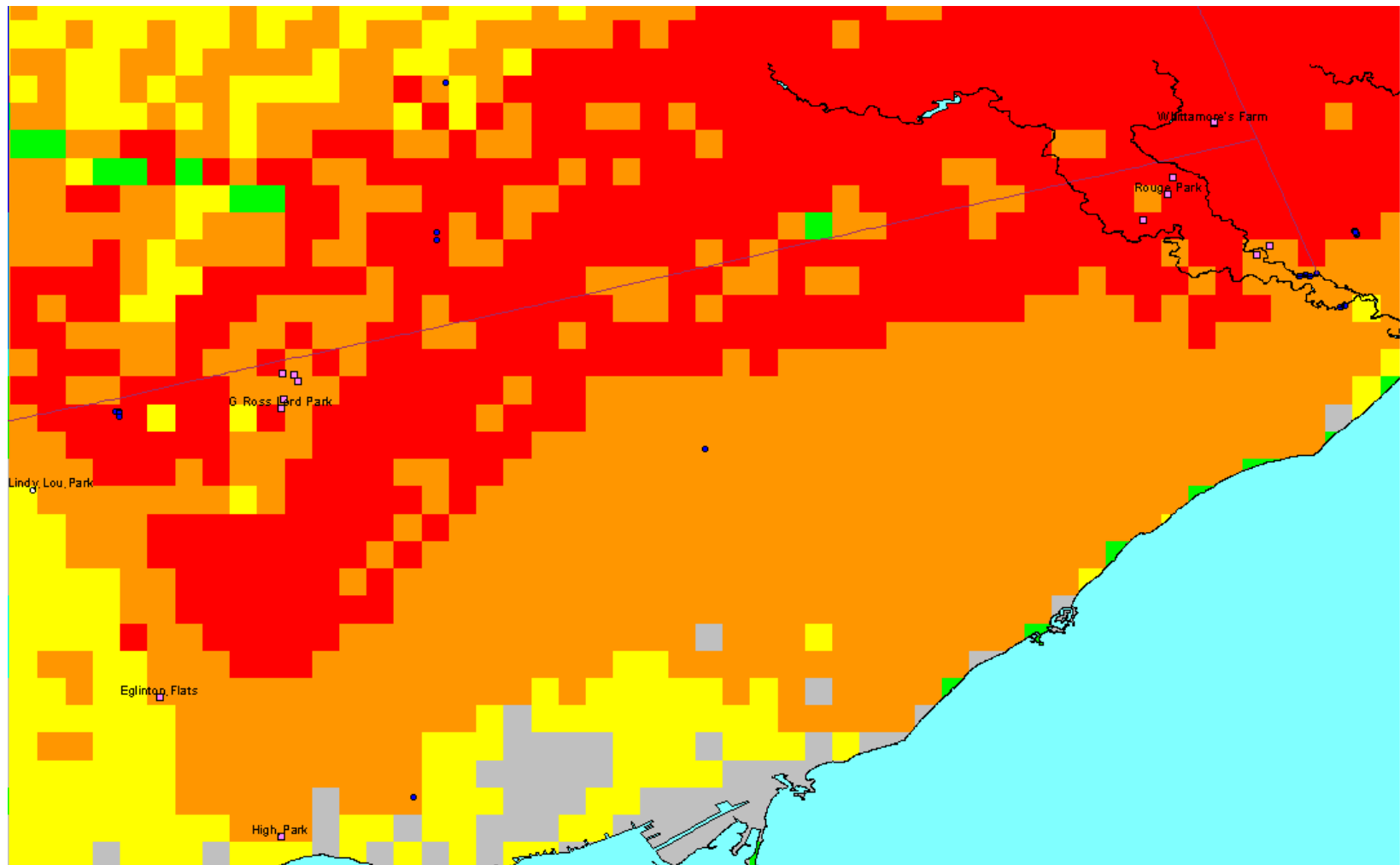
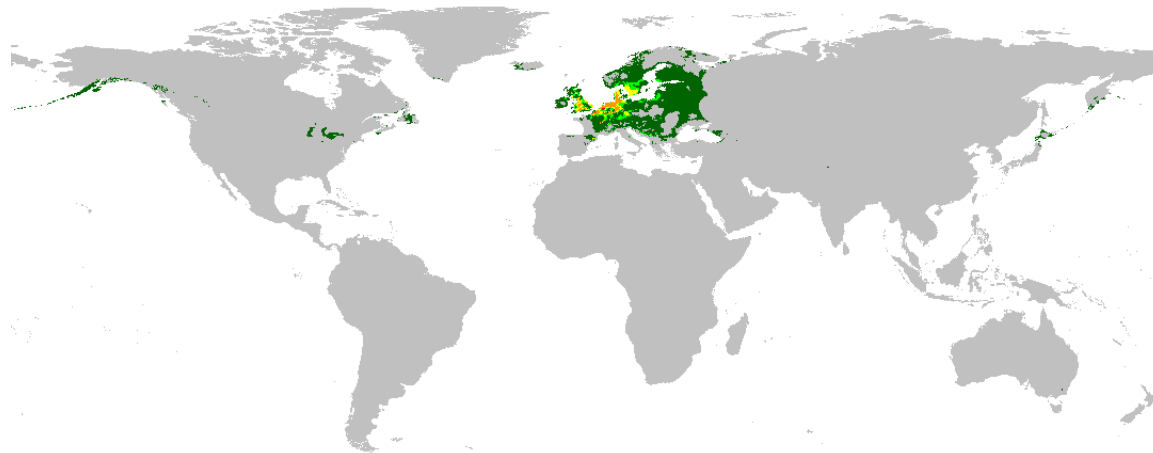
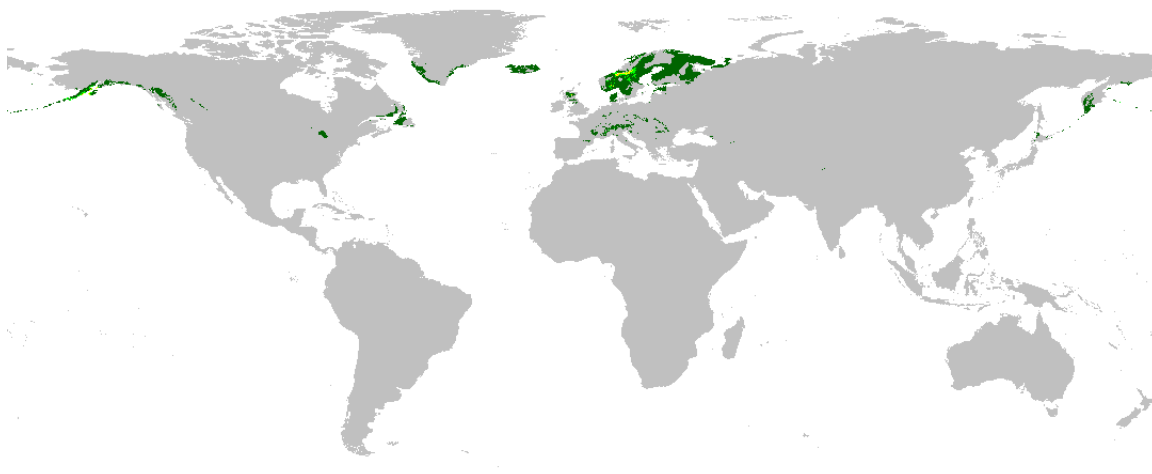


Figure 3 – 24: Close-up view of Figure 3 – 23 for occurrence points in accordance with the predicted areas

M. rubra occurrence points for constructing the model shown as blue dots, actual *M. rubra* presence locales shown as purple dots, and *M. rubra* absence locales shown as white dots



Current



With a 2100 scenario (x2 CO₂ and a 4 degree average temperature increase)

Figure 3 – 25: current and future scenario SDMs for *M. rubra*

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Appendices

Appendix 1

Maxent (Phillips et al., 2006) is based on a maximum entropy algorithm to predict potential geographic distributions of species and has been shown to outperform other algorithms traditionally used for ENMs such as the Genetic Algorithm for Rule set Prediction (GARP) (Elith et al., 2006; Hernandez et al., 2006). Maxent uses general purpose machine learning methods (Phillips et al., 2004). The modelling approach of Maxent is to estimate the target probability distribution by seeking the probability distribution of maximum entropy; i.e., the closest to uniform (Ward, 2007). Maxent is capable of handling small sample sizes (as few as 10 samples) and uses presence only records along with their background and always converges to a unique and optimal probability distribution (Phillips et al., 2006).

BIOCLIM (Nix, 1986; Busby, 1991) uses a bioclimate envelope (a rectilinear volume in environmental space) to summarize the climate at occurrence points (Ward, 2007), and its predictive process is based on the extent of the climate variables that appropriately fit within the extreme values determined by the set of occurrence points (Ward, 2007). This algorithm relies entirely on presence records, and prediction is made without any reference to other samples from the study area (Pearson, 2007).

DOMAIN (Carpenter et al., 1993) is based on the Gower metric, a distance-based method to evaluate the suitability of new sites by correlating their environmental similarity to known presence occurrence points; that is, a predicted suitability index is

obtained by calculating the minimum distance in environmental space to any presence record (Phillips et al., 2006). Like BIOCLIM, DOMAIN uses presence only records.

Artificial Neural Network (ANN) uses machine learning techniques (Pearson, 2007).

ANNs are computer systems created to emulate the structure and operation of the brain that have the capability to learn output data from sets of input patterns (Pearson et al., 2002). Three advantages of ANN over other ENM algorithms are 1) categorical environmental data can be used, 2) ANN does not assume a normal distribution of the data and 3) it can be used to predict sparse/patchy distributions (Pearson et al., 2002).

Appendix 2

1. Annual mean temperature
2. Mean monthly diurnal temperature range
3. Isothermality
4. Temperature seasonality
5. Maximum temperature of warmest month
6. Minimum temperature of coldest month
7. Temperature annual range
8. Mean temperature of wettest quarter
9. Mean temperature of driest quarter
10. Mean temperature of warmest quarter
11. Mean temperature of coldest quarter
12. Annual precipitation
13. Precipitation of wettest month
14. Precipitation of driest month
15. Precipitation seasonality
16. Precipitation of wettest quarter
17. Precipitation of driest quarter
18. Precipitation of warmest quarter
19. Precipitation of coldest quarter

Appendix 3

Several of *Myrmica* ants were collected on 2 farms in Mount Albert where the local/GTA level ENM model predicted as unsuitable for *M. rubra*. The *Myrmica* ants from the 2 farms were extremely difficult to identify to the species (nearly indistinguishable from *M. rubra*) and were subsequently sent for DNA barcoding. The DNA barcoding results showed that these ants were *Myrmica rugulosa*; however, no previous records of *M. rugulosa* occurrences in North America exist.