Using Observational, Experimental, and Focal Species Approaches to Inform the Adaptive Management of Oak Savanna Ecosystems in Western Michigan, USA

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Introduction

Midwestern oak savannas are among the rarest ecosystems in North America (Nuzzo 1986). While these systems were historically fairly common across the Midwestern United States and Canada, a combination of land use change and fire suppression has led to significant habitat loss – it is estimated that less than one percent of the pre-European settlement oak savanna remains on the landscape (Nuzzo 1986, Anderson 2007). As a result, many species associated with oak savanna systems have become threatened or endangered, such as the Karner Blue butterfly (Lepidoptera: *Lycaeides melissa samuelis*), prairie warbler (Passeriformes: *Dendroica discolor*), least shrew (Soricomorpha: *Cryptosis parva*), hill's thistle (*Cirsium pumilum* var. *hillii*), frosted elfin (Lepidoptera: *Callophrys irus*), and Persius duskywing (Lepidoptera: *Erynnis persius*) (BirdLife International 2012, Freeland et al. 2010, MNFI 2007, USFWS 2003). In addition, the removal of fire from the landscape has resulted in the mesophication of many oak-dominated systems and a loss of early-successional oak habitat across the Eastern United States (McCune and Cottam 1985, Nowacki and Abrams 2008, Engber et al. 2011, Arthur et al. 2012, Hanberry et al. 2012). These factors have led to a growing interest in researching, conserving, and restoring oak savanna across the Midwest since the 1990s (Packard 1993, Asbjornsen et al. 2005).

In the context of global climate and environmental change, it is becoming increasingly important to understand the structure and function of rare ecosystems, especially in the context of changing disturbance regimes (Overpeck et al. 1990, Dale 2001, Rosenzweig et al. 2001). In addition, climate change is likely to alter the geographic ranges and distribution of suitable habitat for a number of taxa (Parmesan and

Yohe 2003, Sparks et al. 2007, Kelly and Goulden 2008, Chen et al. 2011). Because resources are often limited in conservation and restoration efforts, effectively identifying the most viable sites for management is critically important, in both the short- and long-term. In this context, the work presented in this dissertation explores the plant community composition of Michigan oak savannas, their response to different management approaches, and the use of the Karner Blue butterfly and other rare species as focal points for site selection at the management-scale, and regionally in the context of climate change.

The first chapter examines the variation in oak savanna plant community composition across a range of disturbance intensities, and the underlying site conditions that may be driving any potential differences. The results of this work suggest that plant community composition can be quantifiably distinct between sites with different disturbance regimes, even though they may be classified as the same community type. Actively managed savanna sites had plant communities distinct from both heavily disturbed sites as well as sites that experience little to no disturbance. These community differences may be driven in part by between-community variation in soil characteristics (especially pH and C:N ratio) and canopy cover. Lastly, several ecological indicator species were identified for these communities, providing a list of species that can help describe site conditions and community differences within the broader oak savanna community type.

The second chapter examines the impact of different mechanical harvesting approaches to savanna restoration in conjunction with prescribed burning on site conditions and the abundance of a variety of different plant cover types. Local oak savanna management goals included maintaining high herbaceous plant cover and low levels of woody regeneration. When used in conjunction with prescribed burning, both masticators and shear cutters (tree shears) were effective at meeting management goals. Herbaceous plant cover was relatively high, while woody and invasive plant growth were low. Without prescribed burning, however, shear cutters were the most effective at meeting management goals -- masticator treatments had high levels of woody regeneration in the absence of fire. The third mechanical approach tested, bulldozing, was largely ineffective at attaining management goals.

The first two chapters largely explore aspects of the “what?” and “how?” questions of Michigan oak savanna management. The third chapter expands the focus to the “where?” by exploring the use of focal species as tools for site selection. The Karner Blue butterfly and its obligate larval host plant, wild lupine (*Lupinus perennis*) are often used as focal species for oak savanna management in the upper Midwest, especially in Michigan, Wisconsin, and (formerly) Indiana (USFWS 2003). In this context, we used species distribution modeling (SDM) to create habitat suitability maps for these two species for the southern Manistee National Forest (MNF). We compared the effectiveness and predictions of seven different SDM approaches and explored the relative importance of different environmental and climatic variables in defining suitable habitat for the Karner Blue and wild lupine. Random forests (RF) and generalized boosted regression models (GBM; sometimes referred to as boosted regression trees) were among the best performing modeling approaches for both species. Elevation, land cover class, and summer precipitation were the most important factors in defining suitable habitat for the Karner Blue, while land cover class, soil drainage class, and mean summer temperature were the most important for wild lupine. While these habitat preferences were largely in line with what other studies have found, the importance of growing season climatic factors was interesting, and leads into the final chapter.

The fourth chapter explores the impact of climate change on the Karner Blue and two other rare savanna associated butterflies: the frosted elfin and Persius duskywing. These three species in particular were chosen because they have historically been associated with oak savanna systems (Packer 1991, Swengel and Swengel 1997, Wagner et al. 2003, USFWS 2003), and they all share the same obligate larval host plant: wild lupine. Different species are likely to have variable responses to climate change (e.g., Williams and Liebhold 2002, Battisti et al. 2005), and Lepidoptera in particular are known to respond to changes in environmental conditions relatively quickly (New 1997, Parmesan 2006). SDMs based on 30-year (1981-2010) climate normals were constructed for all three species across the state of Michigan. These environment × distribution models were projected into the future under two different climate change scenarios: a high-emissions (A1FI) future modeled using the Global Fluid Dynamics Laboratory (GFDL) climate model, and a low-emissions (B1) future model using the Parallel Climate Model (PCM). The results reported in this chapter suggest that by the end of the century, the Karner Blue and frosted elfin will have little suitable habitat available to them in the Lower Peninsula of Michigan, while the Persius duskywing will be largely unaffected by climate change. Furthermore, when incorporating the dispersal abilities of these butterflies, the results of this chapter suggest that without assisted migration, little to none of the suitable habitat remaining for the Karner Blue or frosted elfin will be accessible under a high emissions climate scenario.

As a whole, the results of this work address several knowledge gaps regarding oak savannas, and Michigan oak savannas in particular. This work indicates that even sites categorized under the same oak savanna community type can have quantifiably distinct plant communities as a result of differences in disturbance regimes. The demonstrated importance of disturbance frequency and type is further illustrated in a restoration experiment, where results suggest that shear cutting trees may be the most effective mechanical harvesting approach for meeting local management goals. In addition to site-level characteristics, this work indicates that both landscape-level environmental factors as well as climatic factors are important in defining habitat suitability for the Karner Blue, an important and endangered oak savanna indicator species. Finally, this research suggests that climate change is likely to have variable but significant (in terms of conservation) effects on the distribution and accessibility of suitable habitat for three rare oak savanna butterflies.

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Chapter 1:

An analysis of western Michigan oak savanna plant communities: the community-level impacts of management and disturbance

Introduction

In North America, Midwestern oak savannas are characterized by sparsely distributed mature oak trees and a ground layer dominated by herbaceous vegetation and grasses. This unique ecosystem structure – mature trees coexisting with dense herbaceous vegetation – is thought to have been maintained by a variety of factors, including fire, soil characteristics, and animal grazing (Anderson 2007, Sankaran et al. 2004). These ecosystems were once fairly common throughout the Midwestern United States and Canada (Anderson 2007). Today, less than one percent of the estimated pre-settlement oak savanna remains (Nuzzo 1986). This loss of habitat has largely be attributed to land use change, fragmentation, and fire suppression (Abrams 1992, Scholes and Archer 1997).

There has been a growing effort to maintain remnant and restore additional oak savanna habitat across the Midwestern United States (Asbjornsen et al. 2005). One of the challenges, however, is in actually defining what "good" oak savanna is. Given their heavy herbaceous component and dependence on variable intensity disturbance, these systems can vary significantly across space in terms of community composition and ecosystem structure (Anderson 2007, Asbjornsen et al. 2005). This presents some difficulty in defining desired future conditions for management and restoration efforts – what goals should be set? What metrics should we use to define success? What makes good oak savanna? We can base our goals around our knowledge of savanna remnants (e.g., White 1994, Delong and Hooper 1996), but even those remnants may differ from historical savannas (Anderson 1998, Anderson 2007, Asbjornsen et al. 2005). This task becomes even more challenging when considering the modern anthropogenically-influenced landscape in which restored oak savannas will be managed – in addition to regional variation in savanna communities, we also have to contend with variable amounts of human disturbance and how it can impact community assembly and ecosystem structure. Ideally, oak savanna restoration would follow a "one size fits all" restoration approach, but that is certainly not realistic given this context.

One alternative is to set management goals based on a detailed picture of the regional oak savanna community. Desired future conditions could be defined by targeting certain locally-occurring plant community compositions, creating habitat for focal species, and minimizing risk of invasion by exotics. The first step to this approach, however, is in examining regional or local oak savanna communities. While oak savanna might have a certain ecological or native plant community classification within a region, there are likely several quantitatively distinct plant communities within such classifications as a result of variations in local disturbance (anthropogenic or natural) regimes (e.g., Grimm 1984, Bowles and McBride 1998, Faber-Langendoen and Davis 1995). For example, there are several scattered restored and remnant oak savannas in western Lower Michigan, USA. These systems are largely classified as Oak-Pine Barrens by the Michigan Natural Features Inventory (Kost et al. 2007) despite having relatively wide variability in anthropogenic disturbances and fire regimes.

Using a particular plant community composition as a management goal can make monitoring efforts difficult. Indicator species analysis (ISA) identifies individual or groups of species that act as ecological indicators for a given community (Dufrêne and Legendre 1997). The quality of a species as an ecological indicator is defined by its specificity, the probability of a surveyed species belonging to a particular community, and fidelity, the probability of actually finding the species within each site of a particular community (Dufrêne and Legendre 1997). Managers can use these indicators as focal species to aid in setting management goals and to more easily monitor the success of their efforts (*sensu* Lambeck 1997).

Here, we apply these approaches and examine differences in western Michigan oak savanna plant community composition across a range of disturbance regimes. We quantify changes in community composition, species richness, diversity, and the abundances of individual species of special concern between sites of varying disturbance regimes. We also examine some of the potential disturbance-mediated factors acting as drivers of community assembly across disturbance regimes -- including canopy structure and soil physical and chemical characteristics. We suspect that varying levels of disturbance have a significant impact on plant community composition and species diversity, and that some of these differences will be reflected in ecosystem structure and soil characteristics. If distinct plant communities are identified in this study, we will conduct an indicator species analysis to obtain a list of indicator species for each distinct community.

This study has the potential to be beneficial to land managers working in Michigan oak savannas and, more broadly, Midwestern oak savannas. In addition, this work has the potential to shed light on the relatively poorly-studied and exceedingly rare (Nuzzo 1986) oak savanna plant communities of western Michigan by examining how disturbance (or the lack thereof) ultimately influences community assembly. Furthermore, an analysis of disturbance-mediated environmental factors can help explain these differences, especially in the context of habitat filtering and the regional species pool (Zobel 1997, Díaz et al. 1998).

Methods

Study Site

This study was conducted on the Huron-Manistee National Forests (HMNF) in Lower Michigan, USA. Specifically, our study sites were located on the southern portion of the Manistee, in western Lower Michigan between 43.552º N, 86.093 º W and 43.477 º N, 86.315 º W. Historically, oak savanna systems were fairly common in this region (Nuzzo 1986, Albert and Comer 2008), existing within a matrix of mixed oak-pine forest (Albert and Comer 2008). Today the landscape is dominated by mixed oak forest, red pine (*Pinus resinosa*) plantations, and agriculture. Early successional habitat types like oak savanna, jack pine (*Pinus banksiana*) barrens, and dry sand prairies exist only in small patches.

The oak savanna systems in our study region are typically dominated by white oak (*Quercus alba*) and black oak (*Q. velutina*), with smaller components of red oak (*Q. rubra*), pine (*Pinus* spp.), and cherry (*Prunus* spp.). The ground layers of these ecosystems are often dominated by forbs and grasses, though sedges (*Carex* spp.) can become a nuisance with heavy disturbance. Woody shrubs and tree seedlings are also common. Canopy cover is often heterogeneous, with either single or small groups of trees scattered throughout the site, creating a mix of open and shaded habitat.

Data Collection

Plant community data were collected from a total of 21 sites in 2013 and 2014. Sites ranged in size from 2 to 8 hectares, with sites being < 10 km apart. Within each site, a multiscale random sampling approach was used to collect vegetation data. For herbaceous vegetation, 1-m^2 quadrats were used. We used 4-m^2 quadrats for small woody (i.e., < 2.54 cm diameter) vegetation, and 0.04-ha plots for larger woody vegetation. Within each plot, the identity, number of stems, and estimated cover (%) class was recorded for each plant species. For grasses and sedges, only identity and cover class was recorded. Because sites varied in size, the number of randomly-placed plots within each site was based on total site area such that 5×10^{-4}% of the area was sampled for herbaceous vegetation, 1×10^{-3}% for small woody, and 0.02% was sampled for larger woody vegetation. Using this sampling intensity, a 8 ha site had 40 1-m^2 quadrats, 20 4-m^2 quadrats, and 4 0.04 ha plots.

Forest structure and environmental variables were also recorded for each site. In 2013 and 2014, canopy cover (%) class was estimated using a convex densiometer at all vegetative sampling locations. In 2012, several soil characteristics were recorded at each site, using a transect-based systematic sampling design and the same sampling scheme as our herbaceous vegetation measurements (see above). At each sampling location, the depth of the A horizon was measured using a ruler and samples were collected for the analysis of soil pH and elemental carbon and nitrogen in the laboratory. Soil samples were collected using a 3-cm diameter × 25 cm long hand probe (AMS, Inc.). Soil pH was recorded using an Oakton 2700 benchtop pH meter in a 1:1 soil:water mixture. To determine elemental C and N content, soils were ground to powder using a Retsch RM

100 mortar grinder and analyzed using a Fisons NA1500 elemental analyzer, which uses microcombustion to estimate elemental composition.

The sites used in this study represent a range of disturbance regimes. Of the 21 sites, seven are actively managed as oak savanna, six are heavily disturbed or recently harvested and surveyed as savanna sites, and eight are recently abandoned sites that were formerly managed as oak savanna. Actively managed sites are maintained using hand tools (chainsaws, brushsaws) to control woody vegetation; due to the presence of the federally-endangered Karner Blue butterfly (Lepidoptera: *Lycaeides melissa samuelis* Nabokov), fire is not currently used as a management tool on these particular sites. The heavily disturbed sites represent locations that demonstrate heavy anthropogenic (e.g.., offroad vehicles, heavy machinery) or other disturbance (e.g., high frequency fire) that maintains or creates a savanna-like structure. The abandoned sites in this study were once managed and surveyed for oak savanna species, but have recently (within the last 10 years) been abandoned, and have little to no disturbance regime.

Data Analysis

We used nonmetric multidimensional scaling (NMDS) and permutational multivariate analysis of variance (perMANOVA) to explore community-level differences between sites in species-space. NMDS is a distance-based indirect gradient analysis often used for plant community data (Minchin 1987). Plotting the sites in species-space using NMDS provides a visual interpretation of the differences in plant community composition between sites or groups of sites. We used a Bray-Curtis dissimilarity index (Bray and Curtis 1957) to run the NMDS; all plots were constructed using the 'metaMDS()' command in the R package *vegan* (Oksanen et al. 2015). A dimensionality scree approach was used to determine the appropriate number of dimensions to use in the context of the dimensionality-stress tradeoff. To determine whether our *a priori* site groupings were significantly different from each other in terms of community composition, we analyzed the community data using perMANOVA. The main assumption of this analysis is that multivariate group variances (or dispersions) are homogenous (Anderson and Walsh 2013). To test for this, we used the beta dispersion function ('betadisper()') in the R package *vegan* (Oksanen et al. 2015), which is essentially a multivariate version of Levene's test of equality of variances. If the multivariate group variances were not heterogeneous, perMANOVA was run. perMANOVA analyzes variance by partitioning a distance matrix, in our case a Bray-Curtis dissimilarity matrix, among sources of variation, which were our *a priori* disturbance regimes. A linear model is fit to the distance matrix, and pseudo-F ratios are calculated from a permutation test (Anderson and Walsh 2013, Oksanen et al. 2015). We used 999 permutations without constraint, as our design had no nestedness. perMANOVAs were run using the 'adonis()' command in the R package *vegan* (Oksanen et al. 2015). Because we suspected that herbaceous species would drive community dynamics, we split the dataset into three seperate units: herbaceous-only, woody-only, and all plants. We ran separate NMDS and perMANOVA analyses for each of these datasets. Species observed only once during sampling were excluded from these community analyses to reduce stochastic noise (Cao et al. 2001). This is a conservative approach to excluding rare species, and the debate regarding the exclusion or inclusion of such species is ongoing in the literature (see Poos and Jackson 2012). Rare species were not excluded from any other analyses. Dissimilarity matrices used in these analyses were constructed using percent cover data.

If we found differences between disturbance regimes in terms of plant community composition, we were also interested in identifying ecological indicator species for those distinct communities. Indicator species analysis (ISA), or multilevel pattern analysis, examines the relationship between species occurrence and abundance data and groups of sites (Dufrêne and Legendre 1997). We used the 'multipatt()' function in the R package *indicspecies* (De Caceres and Legendre 2009) to perform ISA for our site groups (i.e., “Managed”, “Disturbed”, “Abandoned”) as well as pairs of site groups (i.e., “Managed” + “Disturbed”, etc.). We also computed potential indicator species-pair combinations – pairs of species that, together, may be a good indicator of a distinct community. This was done using the 'indicators()' function in the R package *indicspecies* (De Caceres and Legendre 2009). We considered plants to be indicator species only when species IndVal scores were above 0.85 ($p < 0.05$). The IndVal score is comprised of specificity, the probability of a surveyed species belonging to a particular site group, and fidelity, defined as the probability of actually finding the species within each site in a group (De Caceres et al. 2010). Separate ISAs were performed on each dataset (herbaceous, woody, and all plants).

To address some of the underlying causes of any potential differences in plant communities between site groups, we examined percent canopy cover, soil pH, soil carbon:nitrogen ratio, and A horizon thickness (cm) across sites. The relationships between these environmental factors and the continuous NMDS ordination axes for each community dataset were explored using separate linear models, with environmental variables as the response and NMDS axes as the predictor variables. We also constructed linear models to look at the relationship between these environmental factors and our categorical *a priori* site groupings (Managed, Disturbed, Abandoned).

Given potential differences in community composition between our site groups, we were also interested in exploring trends in species richness, alpha diversity, and the abundances of species of conservation concern. Differences between site groups in terms of richness and diversity were analyzed using a linear model. Species richness and Simpson's diversity index were computed using the *vegan* package in R (Oksanen et al. 2015). Species accumulation curves, which were used to further investigate biodiversity, were constructed using the *BiodiversityR* package in R (Kindt and Coe 2005). The species of conservation interest considered in these analyses were wild lupine (*Lupinus perennis* L.), butterfly weed (*Asclepias tuberose* L.), spotted knapweed (*Centaurea maculosa* Lam.), and St. John's wort (*Hypericum perforatum* L.). Wild lupine and butterfly weed are uncommon but nonthreatened species that serve as important food sources for several endangered or threatened butterflies (Yarrish 2011, USFWS 2003, Grundel et al. 2000). Spotted knapweed and St. John's wort are non-native invasive (and in the case of spotted knapweed, possibly allelopathic (Bais et al. 2002, Duke et al. 2009)) species becoming more common in early-successional habitats across Michigan, including oak savanna. Area-normalized stem counts, rather than the percent cover values used in the community analyses, were used as the response variable in these analyses. We used linear models to explore between-group differences in the abundance of wild lupine and butterfly weed, and nonparametric Kruskal-Wallis rank sum tests for spotted knapweed and St. John's wort, due to heavy skew in the abundances of those species.

Results

General

Across the 21 sites surveyed, we found a total of 98 plant species, 76 of which were herbaceous and 22 were woody (Table A1.1). The most common species overall was Pennsylvania sedge (*Carex pensylvanica* Lam.), a native sedge that can become a nuisance with frequent disturbance. Big bluestem (*Andropogon gerardi* Vitman) and little bluestem (*Schizachyrium scoparium* Nash) were the most abundant grass species. The most abundant non-grass herbaceous species were sheep sorrel (*Rumex acetosella* L.) and hawkweed (*Hieracium aurantiacum* L.). The most abundant woody species were pin cherry (*Prunus pensylvanica* L.f.) and sand cherry (*Prunus pumila* L.).

Community Analyses

All three NMDS ordinations (herbaceous, woody, all plants) were constructed using two dimensions (Herbaceous 2D stress: 0.139, woody 2D stress: 0.165, all 2D stress: 0.141; stress values < 0.2 are considered suitable (Oksanen et al. 2015, Clarke 1993)). All three datasets also met the multivariate homogeneity of group variances assumption of perMANOVA (Table A1.2). Using perMANOVA, we found differences in herbaceous plant community composition between our *a priori* site groupings (Figure 1a, Table 1). All three site groupings seemed to represent distinct communities, with the largest apparent differences between the Disturbed and Abandoned groups. We did not, however, find any significant differences in woody plant community composition between site groups (Figure 1b, Table 1). Abandoned sites did appear to be marginally different than Managed and Disturbed, but the Disturbed sites were completely indistinguishable from Managed sites in species-space. When considering all plants together, we found significant compositional differences between site groups (Figure 1c, Table 1). Given the previous analyses, it would seem that this is driven primarily by between-group differences in herbaceous, rather than woody, plant communities.

Drivers of Community Composition

For the herbaceous data, canopy cover and soil C:N ratio were positively correlated with NMDS axes 1 and 2 (Table A1.3). Soil pH had a marginally significant negative correlation with both axes (Table A1.3). When considering the entire plant dataset, canopy cover and soil C:N ratio were negatively correlated with NMDS axis 1 and positively correlated with axis 2. In addition, soil pH and A horizon depth (marginally) were negatively correlated with NMDS axis 2 and positively correlated with axis 1 (Table A1.3). The NMDS axes for the woody plant dataset were oriented differently (Figure 1b; Table A1.3b). Canopy cover and soil pH had a strong negative correlation with axis 2, and little correlation with axis 1 (Table A1.3). Soil C:N ratio had a marginally significant ($p = 0.076$, $r^2 = 0.258$) negative correlation with both axes (Table A1.3).

These correlations were reflected when we examined the differences between our *a priori* site groupings. Canopy cover was significantly higher ($p < 0.001$, $F_{2,18} = 17.64$) in Abandoned sites compared with the Managed and Disturbed sites (Figure A1.1), as shrubs and trees have apparently experienced significant recruitment with a lack of disturbance. In terms of soil characteristics, we found differences in the C:N ratio ($p =$

0.024, $F_{2,18} = 4.652$) as well as soil pH between site groups ($p < 0.001$, $F_{2,18} = 11.67$). Soils in Abandoned sites generally had a higher C:N ratio and higher acidity than those in Managed sites (Figure A1.1). We did not, however, found any differences between site groups with respect to the depth of the soil A horizon ($p = 0.249$, $F_{2,18} = 1.501$), suggesting little to no differences between sites in terms of mineral soil disturbance.

Species Contrasts

A number of species demonstrated significant correlations with NMDS axes, illustrating different habitat preferences. Most notably, wild lupine, butterfly weed, and spotted knapweed were associated with lower canopy cover and soil C:N ratios, and higher soil pH (Table A1.4), suggesting a preference for Managed sites. St. John's wort, however, appears to be more associated with Abandoned sites.

These ordination correlations are only partially reflected in our analyses of *a priori* site groupings: we found differences in wild lupine ($p = 0.007$, $F_{2,18} = 6.551$) and butterfly weed ($p = 0.043$, $F_{2,18} = 3.758$) abundance between site groups, with the Managed sites having significantly more lupine stems per square meter than either the Disturbed or Abandoned sites (Figure 4). We did not, however, find any differences between site groups in terms of spotted knapweed abundance ($p = 0.852$, $X^2 = 0.322$) and we found only a marginally significant difference in St. John's wort abundance ($p =$ 0.0.071, $X^2 = 5.303$) between site groups (Figure 5), likely due to the high amount of variability in stem counts across sites.

Species richness varied between site groups for herbaceous ($p = 0.084$, $F_{2,18} =$ 2.857), woody ($p = 0.019$, $F_{2,18} = 4.992$), and full ($p = 0.038$, $F_{2,18}= 3.943$) plant communities. Herbaceous and total plant richness was highest in Managed sites, and lowest in the Disturbed group (Figures 2a and 2c). We found no significant differences between site groups with respect to species diversity for any of the three community datasets (Figure 3).

Indicator Species Analyses

Indicator species analysis of herbaceous community data identified several species for the Managed and Abandoned site groups, and one species, bastard toadflax (*Comandra umbellate* L.), for the Disturbed site group (Table 2). Several species were also identified as indicators for pairs of site groups – Abandoned + Managed and Disturbed + Managed (Table 2). No herbaceous indicator species were identified for the Abandoned + Disturbed pair, perhaps due to the relatively larger differences between plant communities (Figure 1a, Table 1). When considering species pairs, we found a single indicator species pair each for the Abandoned and Disturbed site groups (Table 2). Using only woody plant community data, the only indicator species found were for the Abandoned site group --lowbush blueberry (*Vaccinium augustifolium* Aiton) and wintergreen (*Gaultheria procumbens* L.) (Table 2). No indicator species were identified for site pairings, nor were there any indicator species pairs identified for site groups. When considering all of the plant community data together, the indicator species identified were largely similar to those found for only the herbaceous plant community data (Table 2).

Discussion

In this study, we identified differences in plant community composition between the site groups we classified *a priori* based on disturbance regime. Sites managed using hand tools, more heavily disturbed sites, and abandoned sites all demonstrated significantly different community compositions. These contrasts can be primarily attributed to the herbaceous plant community. Herbaceous plants make up the majority of species in each of these communities, as well as representing the most species turnover between site groups (Figure 1, Table 1). Indeed, there were little to no differences between our site groups with respect to the woody plant community. This contrast between the herbaceous and woody plant communities is not unexpected – broadly, there are more herbaceous than woody plant species (Stevens 2001), so the pool of species on the landscape is generally much larger for herbaceous plants, and as a result there are a wider variety of species available to respond to variations in environmental filtering and competition (Pärtel et al. 1996, Zobel 1997, Díaz and Cabido 2001).

Disturbance regime also had an impact on species richness, with Disturbed sites having lower species counts than either Managed or Abandoned sites (Figures 2a-c). It is important to note, however, that these apparent differences in species richness per unit area were driven by differences in area (Figure 2d) and abundance between site groups; species accumulation curves (Figure 2e) indicate relatively little difference between site groups in terms of richness, but plants were more abundant overall in the Managed sites. Despite having the largest average site area, the Disturbed sites had much lower overall abundance than the Managed sites (Figure 2e). , This trend was also reflected when looking at species diversity: there were no significant between-group differences in species diversity as measured by Simpson's index (Figure 3). These results suggest that while these site groups may differ in terms of community composition, there is little to no difference in biodiversity between groups.

We found a number of differences between site groups when considering the abundance of several species of conservation interest. Wild lupine and butterfly weed were significantly more abundant in Managed sites than either Disturbed or Abandoned (Figure 4). Both of these species are of particular interest in western Michigan oak savanna management due to their importance for butterfly conservation. Wild lupine is the obligate larval food source for three rare and threatened butterflies occurring in scattered pockets around the region: the Karner blue, frosted elfin (*Callophrys irus* Godart), and persius duskywing (*Erynnis persius* Scudder) (USFWS 2003). Butterfly weed is a milkweed primarily pollinated by Hymenoptera and Lepidoptera (Fishbein and Venable 1996), and serves as a preferred nectar source for the adult form of the same three rare and threatened butterflies (Yarrish 2011, Grundel et al. 2000). These two plant species are known to perform well on disturbed sites (Smith et al. 2002, USDA 2015), but these results suggest that the level of disturbance in the Disturbed group is high enough to reduce their abundance. Of the two invasive species of particular concern in these communities, only St. John's wort demonstrated a marginally significant difference in abundance between community type (Figure 5), occurring in more abundance in sites that have been Abandoned. This is not unexpected, given the plant's ability to tolerate higher amounts of shade (USDA 2015). Spotted knapweed, on the other hand, demonstrated no difference in abundance between community types. Though it appeared to be abundant more often in Managed sites, the amount of variation in abundance across all sites for this species was quite high. On sites where spotted knapweed did occur, it was quite abundant: often exceeding densities of 3 plants/m^2.

Indicator species were identified for each distinct community (Table 2). The significant indicators for Managed sites consisted of a list of species frequently associated with oak savanna habitat in the upper Midwestern United States (USFWS 2003, Grundel et al. 2000, Betz and Lamp 1990), especially lanceleaf coreopsis (*Coreopsis lanceolata* L.), butterfly weed, and horsemint (*Monarda punctata* L.). The sole indicator species for Disturbed communities, bastard toadflax (*Comandra umbellata* L.), is a semiparasitic plant often found on sandy, gravelly, or heavily grazed sites (Leicht-Young et al. 2009, Zentz and Jacobi 1989). On Abandoned sites, indicator species consist of plants one would expect to find in both upland forests and semi-open habitats, including false solomon's seal (*Maianthemum racemosum* L.), yellow pimpernel (*Lysimachia nemorum* L.), and canada lettuce (*Lactuca canadensis* L.) (USDA 2015). We also identified indicators for two community groups: Abandoned + Managed and Managed + Disturbed (Table 2). Noteworthy here is the presence of more species traditionally associated with oak savannas in the Managed + Disturbed indicator list, including wild lupine. Finally, we identified a species-pair as indicators for Managed and Disturbed groups; these species pairs represent species, that when found together, act as a significant ecological indicator (Table 2). The types of indicator species identified for each site group in this study reinforces the apparent importance of disturbance, with early successional species associated with Disturbed, and to a lesser extent, Managed sites, while several forest understory species are associated with the less-disturbed Abandoned sites.

The contrasts between communities in this study seem to be driven in part by differences in environmental characteristics (Figures 1 and A1.1, Table A1.3), which in turn are a result of differing disturbance regimes. Indeed, the differences between

Managed and Abandoned sites seems to be driven by a contrast between canopy cover, soil C:N ratio, pH, and A horizon thickness. Canopy cover affects plants by limiting photosynthetic capacity in the understory (Bazzaz 1979). Similarly, the soil C:N ratio affects plants as it is a measure of nitrogen availability (Paul 2007), and along with soil pH and A horizon thickness, also contributes to variation in macronutrient uptake (Paul 2007). These factors, especially canopy cover (Bazzaz 1979), but also soil C:N ratio, pH and A horizon thickness (Reynolds et al. 2003, Ehrenfeld et al. 2005, Dovčiak et al. 2003, Rose et al. 2002), act as filters for the regional species pool, ultimately leading to distinct plant communities (Díaz et al. 1998).

The apparent contrast between the different communities found in this study has the potential to be useful for managers working with oak savanna systems in Michigan, and perhaps more broadly. Managing oak savanna systems can be challenging, particularly the balance of disturbance intensity (Peterson and Reich 2001, Brudvig and Asbjornsen 2007 and 2008). Though the sites in this study are all located on the same soil type (Typic Udipsamments or Entic Haplorthods; NRCS 2015) and surrounded by similar mixed oak forest, differences in disturbance intensity have resulted in quantitatively distinct plant communities. Not unexpectedly, the recently abandoned oak savanna sites have started to undergo succession in the absence of disturbance. In contrast, the difference between managed oak savanna sites and heavily disturbed savanna sites was of note because historically, disturbance was a major component of many savanna ecosystems -- the factor maintaining the coexistence of mature trees and herbaceous vegetation on the site (Anderson 2007, Sankaran et al. 2004). Our results suggest, however, that major disturbances in these systems results in a community with fewer plants overall (Figures 2d and 2e) and lacking in some important savanna associates (e.g., lanceleaf coreopsis, butterfly weed, horsemint), while retaining others (wild lupine, big bluestem, common milkweed; Table 2). This may be due in part to the nature of the disturbance. Historically, the types of disturbances associated with these systems likely included fires, animal grazing, and Native American activities (Anderson 2007). In contrast, the types of heavy disturbance represented in our dataset in the "Disturbed" category included off-road vehicle recreation, heavy equipment use, and high frequency surface fires. This suggests that our actively managed sites more closely reflect historical disturbance regimes than the heavily disturbed sites in this study.

Ultimately, these results suggest that moderate differences in disturbance intensity (or the lack thereof) can significantly alter plant community composition. The results reported here also suggest that if the long-term management goal is to encourage the establishment and maintenance of herbaceous savanna-associated species, it may be more beneficial to (moderately) err on the side of disturbance rather than inaction. This point should be considered in context, however, as different regions may be dealing with different species pools (including invasives) or different abiotic environmental filters. Finally, in terms of indicator species, our actively managed sites are represented by a fair amount of plant species traditionally associated with oak savanna, suggesting that hand-cutting can be effective at meeting management goals when more historically-accurate fire management is not an option.

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Tables and Figures

Table 1. perMANOVA table for herbaceous, woody, and all plants datasets. Effects of *a priori* disturbance groups ("Community Type") for each dataset.

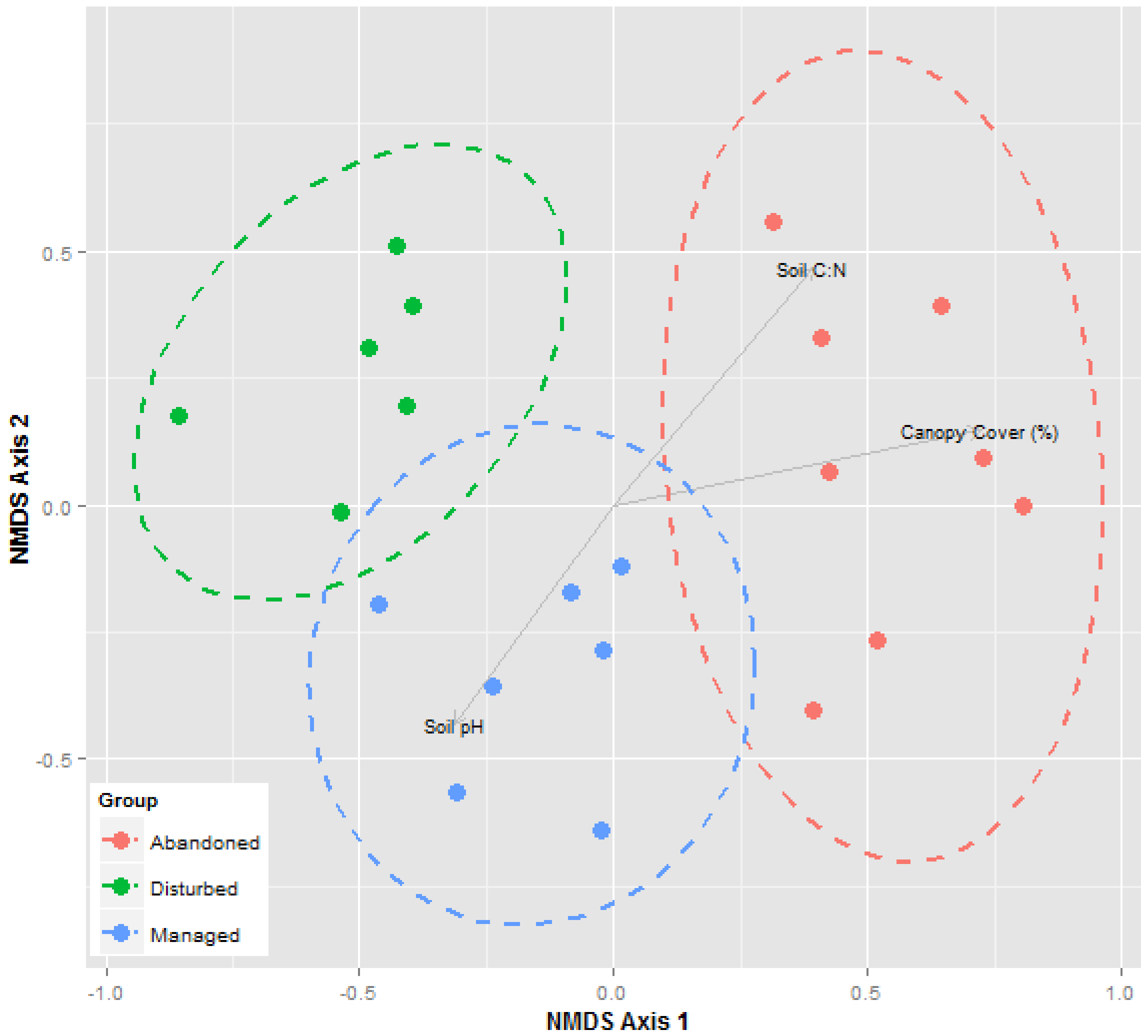
Dataset	Source	df	SS	MSS	F	r^2	Pr(>F)
Herbaceous							
	Community Type	2	1.1619	0.5809	2.7984	0.2372	**0.001**
	Residuals	18	3.737	0.2076		0.7628	
	Total	20	4.8989			1	
Woody							
	Community Type	2	0.7116	0.3558	1.7127	0.1599	0.052
	Residuals	18	3.7391	0.2078		0.8401	
	Total	20	4.4513			1	
All Plants							
	Community Type	2	1.0292	0.5146	2.5936	0.2237	**0.001**
	Residuals	18	3.5712	0.1984		0.7763	
	Total	20	4.6004			1	

Table 2. Indicator species by community type. Statistically significant indicators are listed for each site group (Abandoned, Disturbed, Managed), as well as two group pairs (Abandoned + Managed, Disturbed + Managed). IndVal is the computed indicator value for each species, derived from specificity and fidelity (shown; De Caceres and Legendre 2009). Two species pairs, identified by *, which when found together function as a significant indicator, are also shown.

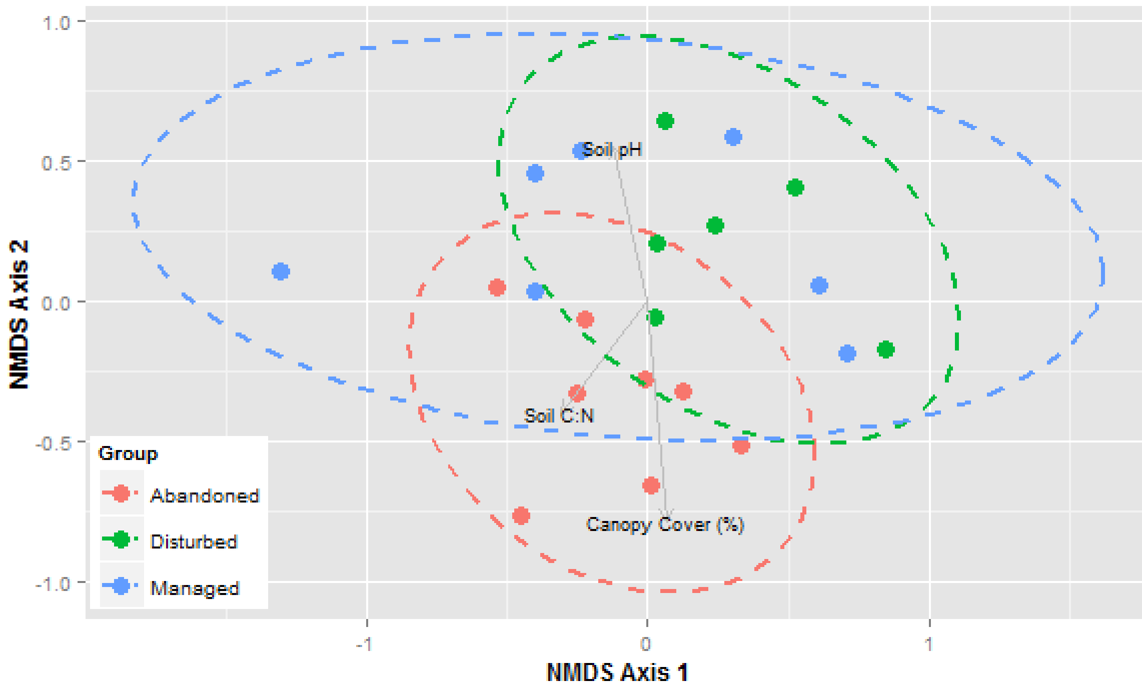
Site Group	Species	Specificity (*A*)	Fidelity (*B*)	IndVal	*p*
Abandoned	False Solomon's Seal	1	1	1	0.001
	Primrose	1	1	1	0.001
	Lowbush Blueberry	1	1	1	0.001
	Yellow Pimpernel	1	1	1	0.001
	Canada Lettuce	0.9852	0.75	0.86	0.003
Disturbed	Bastard Toadflax	1	1	1	0.002
	Common Milkweed + Goat's Rue*	0.8682	1	0.9318	0.007
Managed	Hairy Bedstraw	0.8661	1	0.931	0.006
	Common Spiderwort	1	0.8571	0.926	0.001
	Smooth Aster	0.9576	0.8462	0.9	0.001
	Lanceleaf Coreopsis	0.837	1	0.915	0.005
	Butterfly Weed	0.7597	1	0.872	0.002
	Horsemint	0.8469	0.8571	0.852	0.031
	Big Bluestem + Poverty Grass*	0.8399	1	0.9164	0.005

Group Pair	Species	Specificity (*A*)	Fidelity (*B*)	IndVal	*p*
Abandoned + Managed	Bracken Fern	0.9759	1	0.988	0.002
	Wood Betony	1	0.7333	0.856	0.015
	Cinquefoil	0.9884	0.7333	0.851	0.015
Disturbed + Managed	Wild Lupine	0.8595	1	0.927	0.019
	Big Bluestem	0.8582	1	0.926	0.026
	Little Bluestem	0.9576	0.8462	0.9	0.007
	Common Milkweed	0.949	0.8462	0.896	0.009
	False Dandelion	0.9491	0.7692	0.894	0.025

Figure 1. NMDS plots for each dataset (Herbaceous, Woody, All Plants).
(1a). NMDS plot, plant community composition, for the Herbaceous plants dataset. Site groups are color-coded. Statistically significant environmental variables are displayed as vectors in species-space. 2D stress value: 0.139.



(1b). NMDS plot, plant community composition, for the Woody plants dataset. Site groups are color-coded. Statistically significant environmental variables are displayed as vectors in species-space. 2D stress value: 0.165.



(1c). NMDS plot, plant community composition, for the All Plants dataset. Site groups are color-coded. Statistically significant environmental variables are displayed as vectors in species-space. 2D stress value: 0.141.

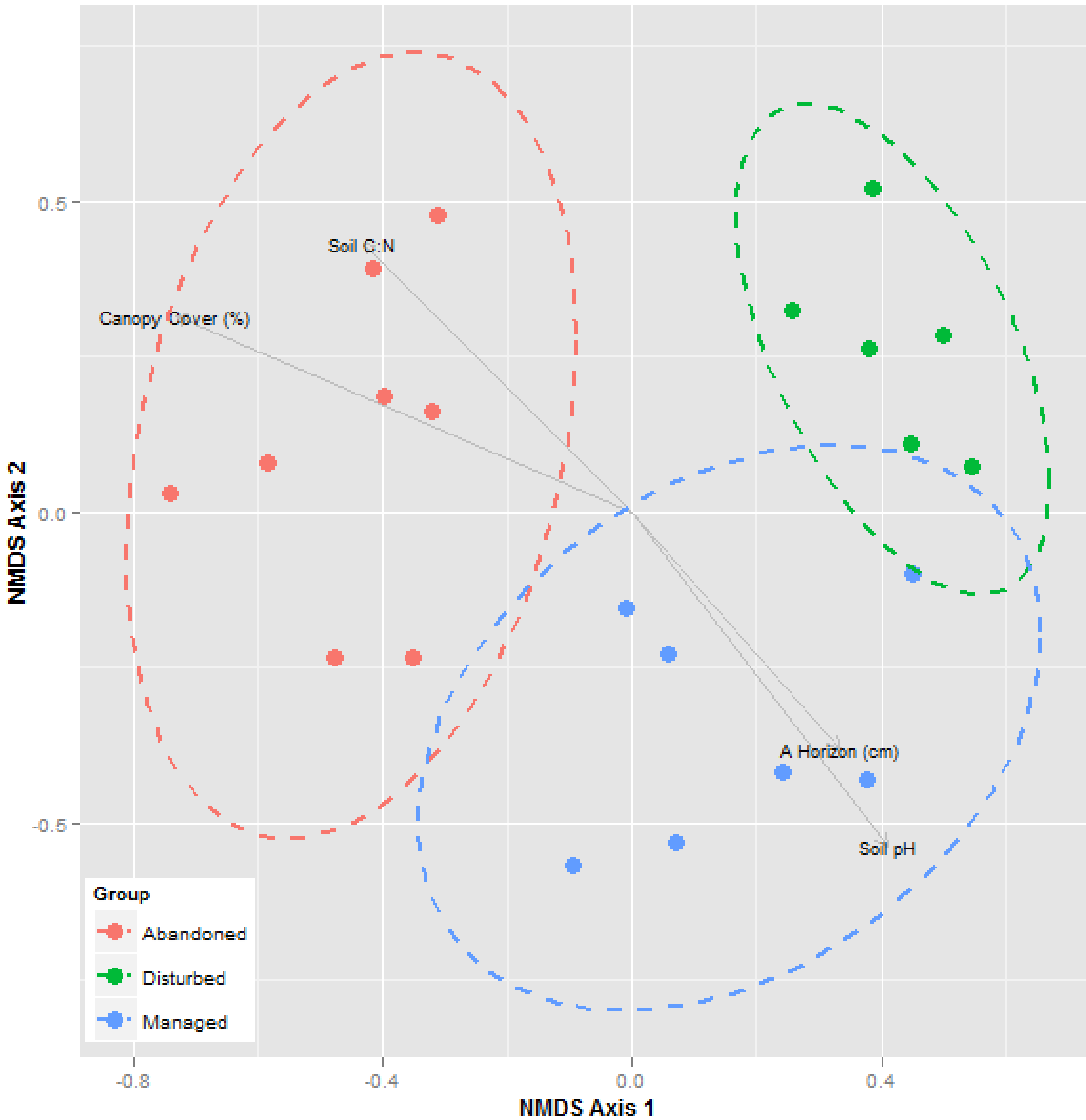


Figure 2a-c. Mean species richness per m² across community types ("site groups") for (a) all plants, (b) herbaceous only, and (c) woody only.

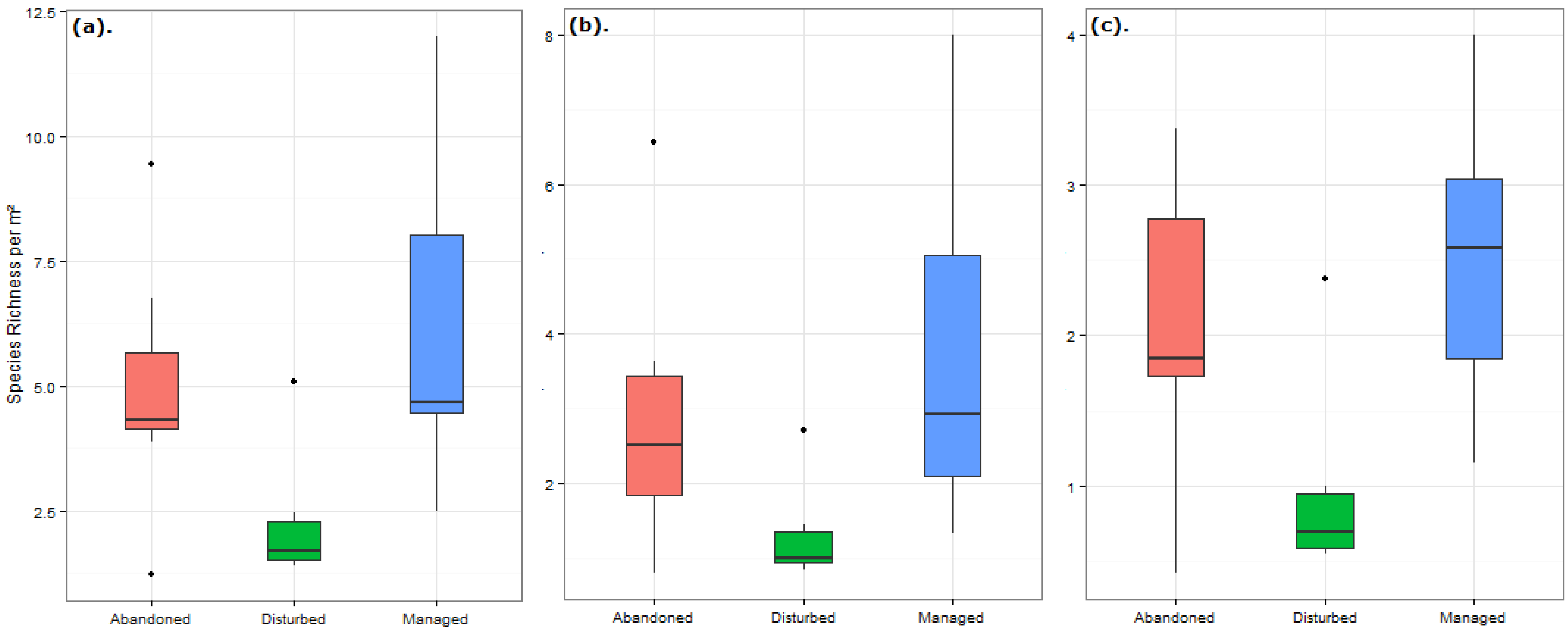


Figure 2d. Mean site area (ha) across site groups.

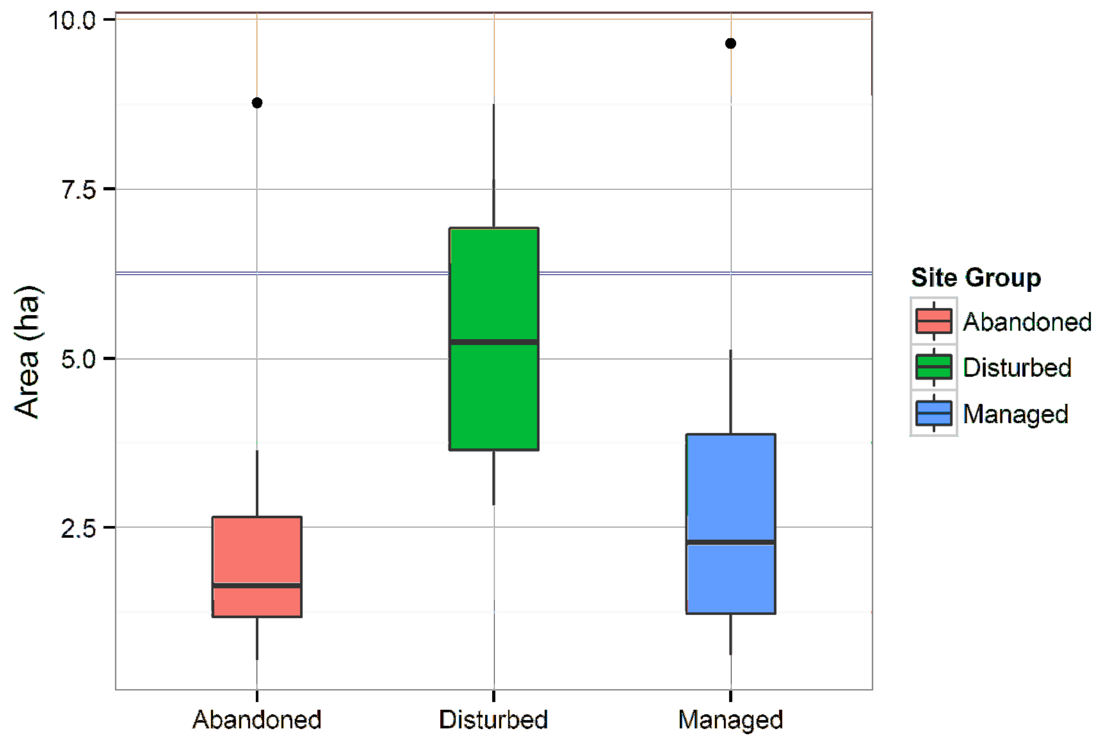


Figure 2e. Species accumulation curves (number of species per individual sampled) for each site group. Mean ±1 SE species from randomized site additions.

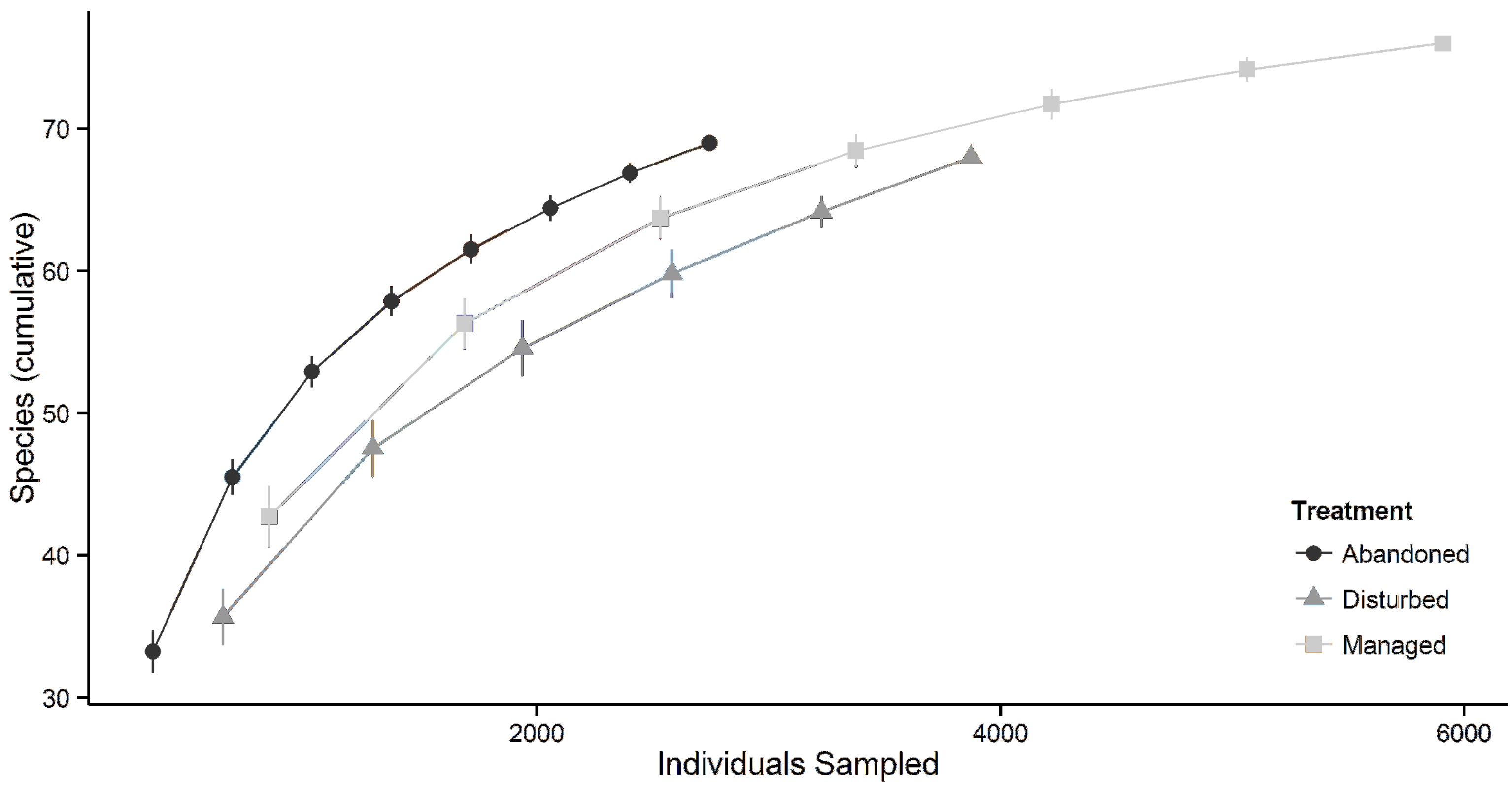


Figure 3. Mean species diversity, as measured by Simpson's diversity index (*D*), across community types ("site groups") for (a) all plants, (b) herbaceous only, and (c) woody only.

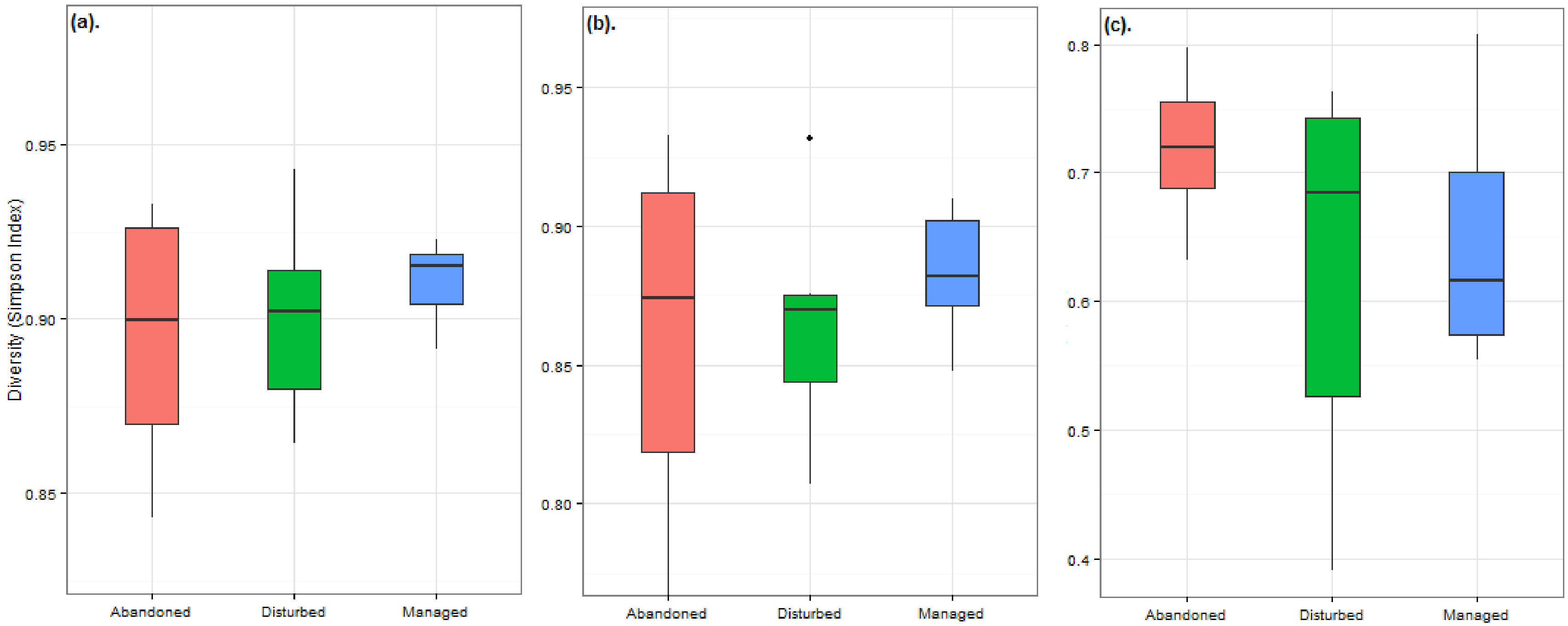


Figure 4. Mean abundance of wild lupine (a) and butterfly weed (b) across community types ("site groups"), which are color-coded. Abundance values are derived from area-normalized stem counts.

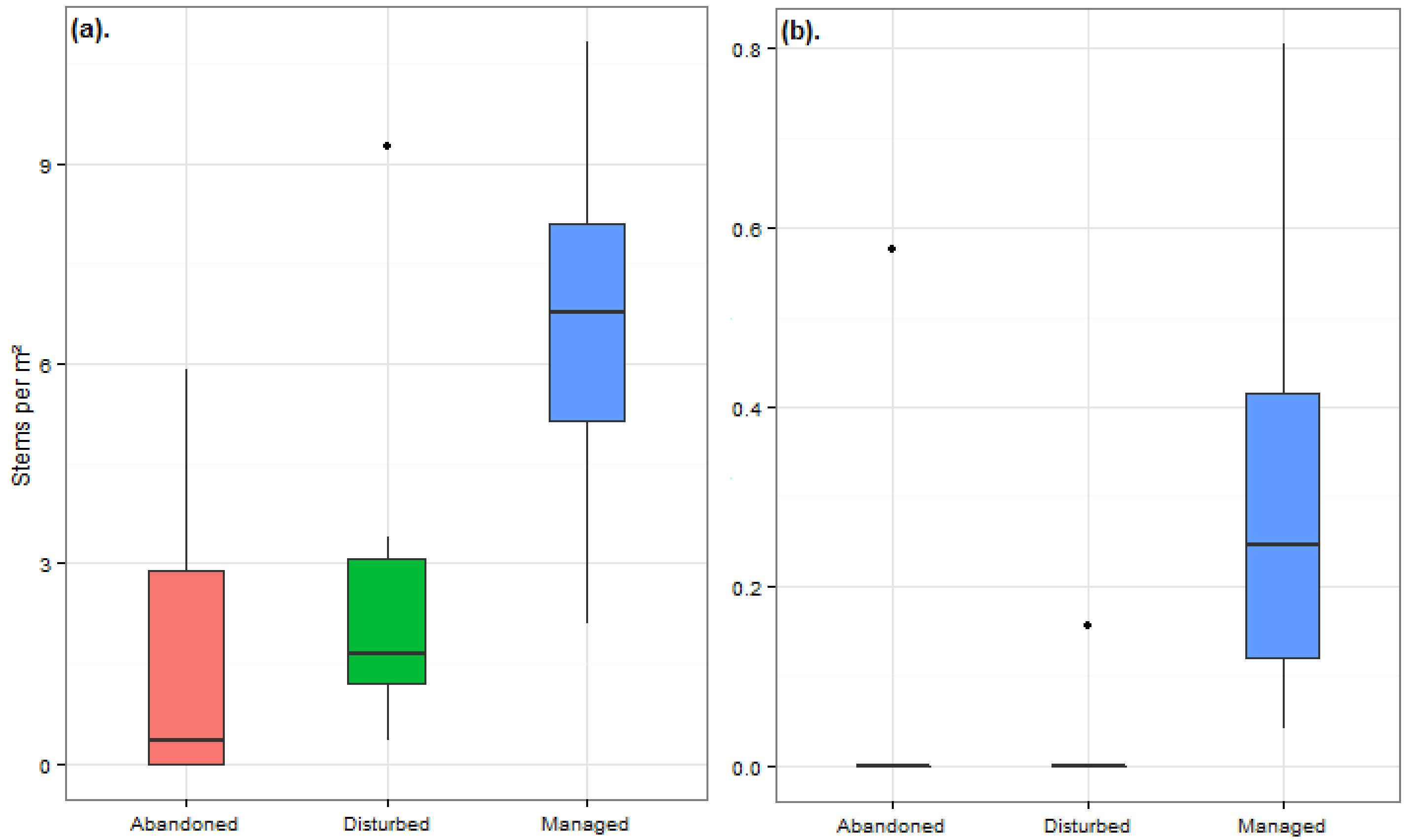
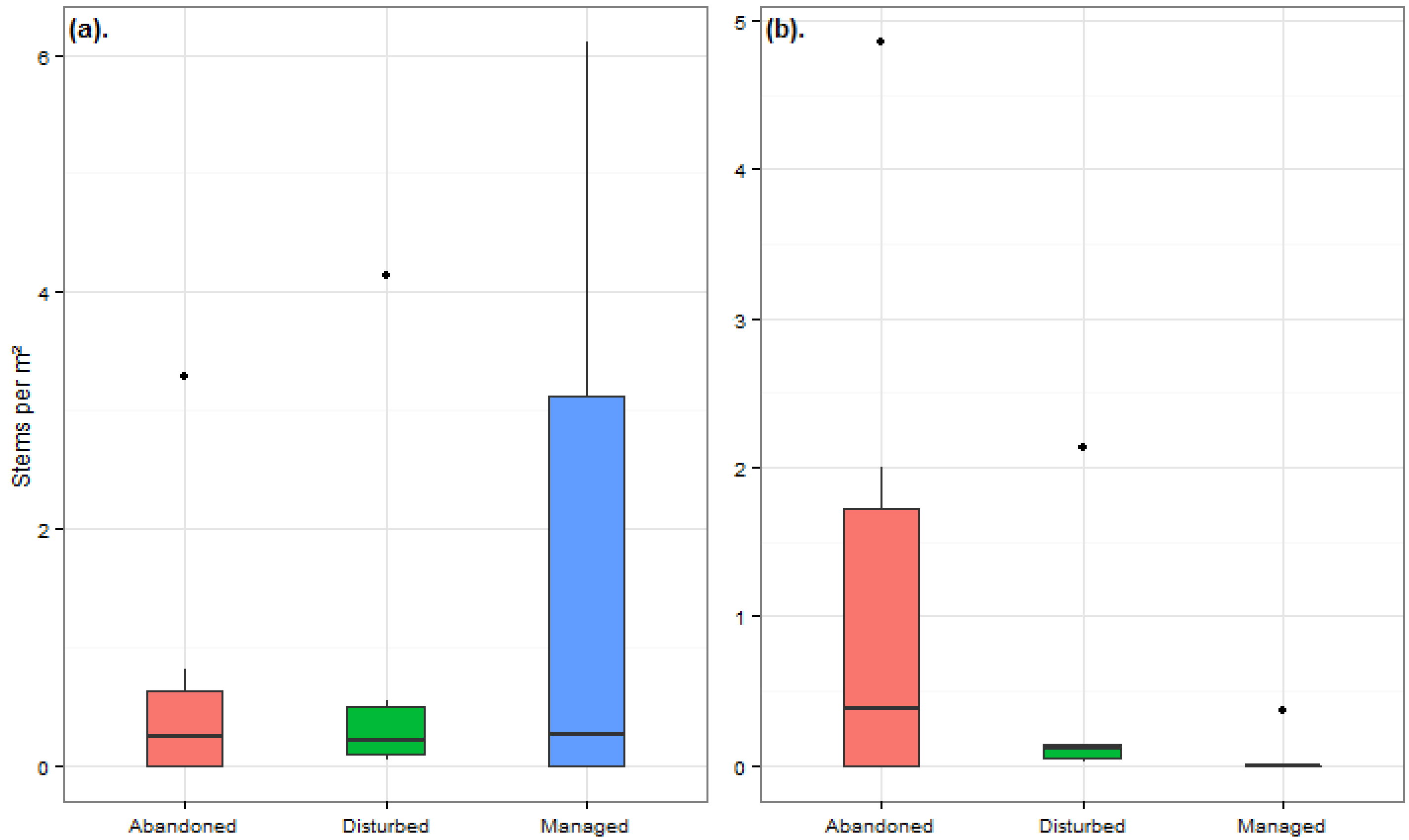


Figure 5. Mean abundance of spotted knapweed (a) and St. John's wort (b) across community types ("site groups"), which are color-coded. Abundance values are derived from area-normalized stem counts.



Chapter 2:

Comparing the effectiveness of three mechanical restoration approaches toward meeting Michigan oak savanna management goals

Introduction

Historically, oak savanna ecosystems were relatively common throughout the Midwestern United States and Canada. These systems existed along the prairie-forest border and within the matrix of mixed oak forests across the region (Anderson 2007). Oak savannas are defined by the coexistence of mature oak trees with a ground layer dominated by herbaceous vegetation and grasses (Anderson 2007). It is thought that the coexistence of mature trees with herbaceous vegetation was maintained by a number of factors, including natural fire regime, poor soils, and animal grazing (Sankaran et al. 2004, Anderson 2007). In addition, research suggests that Native Americans may have intentionally burned many areas for a variety of reasons (e.g., protoagriculture; see Abrams and Nowacki 2008), creating and maintaining oak savannas in the process (Nowacki and Abrams 2008, Abrams and Nowacki 2008, Dorney and Dorney 1989, Cutter and Guyette 1994, see also Denevan 2010).

Today, less than one percent of the pre-European settlement land area of oak savanna remains intact (Nuzzo 1986). This is largely attributed to fire suppression and land use change (Nuzzo 1986, Anderson 2007). This loss and fragmentation of habitat has resulted in a number of savanna-associated species becoming threatened or endangered (Anderson 2007), and the ecosystem itself is considered to be one of the rarest in North America (Nuzzo 1986). For this reason, a concerted effort began in the 1990s (Packard 1993, Asbjornsen et al. 2005) to both research and restore these ecosystems. Restoration efforts and savanna research have taken place in Arkansas (Milks 2005), Missouri (Law et al. 1993, McCarty 1998), Kentucky (Barrioz 2010), Tennessee (Barrioz 2010), Iowa (Asbjornsen et al. 2007), Illinois (Apfelbaum and Haney 1987, Hruska and Ebinger 1995, Brawn 2006), Wisconsin (Leach and Givnish 1999, Brock and Brock 2004), Minnesota (Tester 1989, Peterson and Reich 2001), Indiana (Choi and Pavlovic 1998, Wilcox et al. 2005), Ohio (Abella et al. 2004, Artman et al. 2001), Ontario (Bakowsky and Riley 1992), and Michigan (Lettow et al. 2014).

Research and restoration efforts have focused on a variety of different approaches to oak savanna management (Anderson 2007). A frequently studied topic on the matter is the use of prescribed burning as a management tool. Given its historical association with oak savanna systems, fire has long been considered a tool for oak savanna management. In one of the longest-running prescribed fire experiments, prescribed burns have been used as a savanna management tool at the Cedar Creek Natural History Area in Minnesota since 1964 (White 1983, Tester 1989). Fire is undeniably an important component of savanna ecosystems, and has a demonstrably significant impact on savanna woody plant dynamics (Peterson and Reich 2001), breeding bird communities (Davis et al. 2000), arthropod communities (Siemann et al. 1997), small mammal communities (Tester 1965), and soil biogeochemistry (Dijkstra et al. 2006, Rhoades et al. 2004).

Despite its apparent effectiveness and historical association with oak savannas, fire is not the sole management tool used in these systems. Today, new oak savanna is most often created from mature mixed hardwood forests or degraded oak savannas (e.g., Asbjornsen et al. 2007, Brudvig 2010). This requires a significant thinning of the existing forest stand, and can be achieved using hand-cutting with chainsaws (e.g., Brudvig and Asbjornsen 2007, Nielsen et al. 2003, Abella et al. 2001) or by using machinery and heavy equipment, such as harvesters or bulldozers (e.g., McCarty 1998, Asbjornsen et al. 2007, Brudvig et al. 2011). After thinning, woody regeneration and herbaceous ground cover is often managed using fire, brush saws, or in some cases, herbicides (e.g., Choi and Pavlovic 1998).

Michigan, and central western Michigan in particular, is at the far north-eastern extent of the historical range of Midwestern oak savanna ecosystems (Nuzzo 1986, Anderson 2007). While the majority of Midwest oak savanna systems are dominated by bur oak (*Quercus macrocarpa*), savannas in western Michigan are somewhat unique in that they are dominated by white (*Q. alba*) and black (*Q. velutina*) oak -- bur oak's range extends only into the southern counties of Lower Michigan (Burns and Honkala 1990, Prasad and Iverson 2003). There are a number of actively managed savannas and savanna restoration projects in the region, acting as part of the broader ongoing effort to restore oak savanna. Additional regional management goals include restoring habitat for federally-endangered species such as the Karner Blue butterfly (Lepidoptera: *Lycaiedes melissa samuelis*), and game birds such as the wild turkey (Galliformes: *Meleagris gallopavo*).

In this study, we explore the relative effectiveness of several different savanna restoration approaches at meeting local management goals. We do this using a series of experimental restoration trials established on the Huron-Manistee National Forest in 2008-2009. The experiment is designed to compare the relative effectiveness of three different mechanical thinning approaches in conjunction with prescribed burning: bulldozers, masticators, and shear cutting with tree shears The overall objective of this study is to identify which restoration approach is most effective at promoting herbaceous plant growth, especially wild lupine (*Lupinus perennis*; the obligate larval host plant for the endangered Karner Blue), while minimizing woody plant regeneration and the establishment of invasive species.

Methods

Study Area

This study was conducted on the southwestern Manistee National Forest (MNF), located in western Lower Michigan, USA. Prior to European settlement, this region was historically associated with mixed oak-pine forests and oak savanna systems (Albert and Comer 2008). Today, this region is defined by mixed oak forests, red pine (*Pinus resinosa*) plantations, and agriculture. Oak savannas and other early successional systems exist only in small patches on the landscape. Upland soils in the area are largely glacial outwash in origin, and most are classified as either Typic Udipsamments or Entic Haplorthods (NRCS 2015).

Study Design

Three noncommercial mechanical thinning approaches were compared in this study: bulldozing, masticating, and shear cutting. These methods, while quite different, are all commonly used in forest management. We tested the effectiveness of these methods in creating savanna-like site conditions and in encouraging the growth of desirable cover types using a randomized block experimental design. The study consisted of two distinct management areas: the Pines Point Recreation Area (PPRA), and the Winston Road Management Area (WRMA), approximately 2.5 km apart. Seven experimental blocks were located in the PPRA, while six were located in the WRMA, for a total of 13 blocks. Blocks were 3.24 ha (8 acres) in size, and each consisted of four, 0.81-ha (2 ac) treatments: control, bulldozer, masticator, and shear cutter. Blocks were 50 m apart on average, with a minimum buffer of 25 m of closed-canopy forest between blocks.

Bulldozed treatments were implemented with a bulldozer that removed all ground vegetation and designated mature trees (Figures 1c and 1d). The topsoil of bulldozed treatments was heavily disturbed, and woody debris was pushed into piles. In the masticator treatment, ground vegetation and mature trees were mulched *in situ*; the masticator equipment was limited in its ability to mulch larger diameter mature trees, however, and as a result, more mature trees were left on site (Figures 1a and 1d). Apparent soil disturbance was moderate under the masticator treatment. The shear cutter removed entire trees (whole tree harvest) and created large slash piles. Soil disturbance was minimal. The control experienced no harvesting of mature trees. Harvesting in all treatments and blocks took place in the autumn and winter of 2008 and 2009. In the late summer of 2010, all blocks were subjected to a prescribed burn. Each block was burned as a whole, so each treatment experienced the same relative fire intensity. In late summer 2013 all of the blocks at the PPRA were subjected to a second prescribed burn.

Data Collection

We collected site condition and cover type data for each treatment in each block using a transect-based systematic random sampling design. Transects were set up running across each treatment plot, 20 m apart, for a total of four transects per plot. Four 12.6-m² (2 m radius) vegetation sampling plots were semi-randomly (based on a random number generator) distributed along each transect, at least 20 m apart, for a total of 16 sampling plots per treatment, and 64 per experimental block. Within each sampling plot, percent cover was estimated for the following classes: small (< 60 cm in height) woody vegetation, herbaceous plants, woody plants (flowering/nectar sources), grasses, ferns, invasive plants, Pennsylvania sedge, and wild lupine. The percent cover of bare soil and downed woody debris was also recorded in each plot. Finally, at the center of each sample plot we estimated canopy cover by averaging convex densiometer readings across the four cardinal directions. Data collection began in 2010; grass and Pennsylvania sedge were recorded from 2011 onward.

Data Analysis

To examine the effects of each restoration treatment approach on both site conditions and the relative abundance of different cover types, we used linear mixed effects modeling. Response variables included, separately, all plant cover and habitat characteristic variables sampled within our study sites. Predictors incorporated as fixed effects in the models included treatment, year, and the interaction treatment × year. Potential variation due to location was incorporated into the model by including block as a random effect. Models were fit using restricted maximum likelihood estimation (Bolker *et al*. 2008), and implemented using the R (R Core Team 2015) package *nlme* (Pinheiro et al. 2015). Herbaceous, fern, invasive species, and wild lupine data were log(x+1) transformed to adjust for heavy skew in the data, while small woody, woody flowering, Pennsylvania sedge, grass, woody debris, exposed soil, and canopy cover were square-root transformed to adjust for moderate skew. Marginal and conditional r^2 values were calculated for each model using the methods outlined by Nakagawa and Schielzeth

(2013) and expanded by Johnson (2014). The marginal r^2 reports the amount of variance explained by the fixed factors, while the conditional r^2 reports the amount of variation explained by both the fixed and random factors (Nakagawa and Schielzeth 2013). Least-squares means and contrasts were computed for the treatment and year factors averaged over the interaction term (treatment × year) using the *lsmeans* package in R (Lenth and Hervé 2015). Models were computed separately for the PPRA and WRMA due to differences in prescribed burning (e.g., the 2013 prescribed burn implemented in the PPRA but not WRMA).

To help visualize changes in site conditions over time and across treatments, we computed a detrended correspondence analysis (DCA) using canopy cover, woody debris, exposed soil factors, and management area (as a binary variable). DCA was used due to the need to accommodate a combination of different measurement scales as well as a binary variable, and over concern about the arch effect (Hill and Gauch 1980). The rescaling ('detrending') that DCA implements was not a concern, as visual interpretation was the primary goal; rescaling is less impactful than the arch effect in this respect. DCA plots were constructed for each year individually, and for the mean values of all years together, to visualize the change in site conditions over time. Correlations between cover types and DCA axes were computed for each plot.

Results

Site Conditions

Mechanical treatment had a significant impact on canopy cover, woody debris, and exposed soil in both study sites (Table 1). Canopy cover was significantly higher in the masticator treatment than either of the other two mechanical treatments at PPRA

(Masticator-Shear cutter: $p < 0.001$, $t = 6.501$; Masticator-Bulldozer: $p < 0.001$, $t = 7.13$), while only higher than the bulldozer at the WRMA (Masticator-Bulldozer: $p < 0.001$, $t = 4.742$; Figure 2, Table A2.1). Given limitations of the equipment, it is not surprising that the masticator treatment tended to have higher canopy cover compared with the other two mechanical treatments. The unusually high canopy cover measurements recorded for the shear cutter in 2012 at the WRMA is puzzling, though not entirely out of the margin of variation across all years (Figure 2). Woody debris was highest for the bulldozer and masticator treatments early on in the study, but declined over time (Figure 3). The bulldozer treatment had a strong effect on the amount of exposed soil early on, but that quickly declined as plants colonized the site (Figure 4). The 2013 burn at the PPRA had a significant impact on the amount of exposed soil in 2014 for all of the thinned mechanical treatments (Bulldozer 2013-2014: $p < 0.001$, $t = -6.315$; Masticator: 2013-2014: $p < 0.001$, t -6.519, Shear cutter: 2013-2014: $p = 0.008$, $t = -4.192$), but not the control ($p = 0.975$; Figure 4).

Cover Types

Herbaceous plant cover was significantly affected by mechanical approach at both management areas (Table 2). The shear cutter treatment generally demonstrated the highest levels of herbaceous plant cover, while the control had expectedly low amounts (Figure 5). The masticator and bulldozer treatments were largely indistinguishable in terms of herbaceous cover, especially at the WRMA (Figure 5). Mechanical approach had a significant impact on flowering woody vegetation at the WRMA, but not at PPRA (Table 2). Treatments were largely the same in terms of woody flowering plant cover at PPRA, but the masticator treatment had significantly more cover at WRMA than the other two treatments and the control. The results for all woody (flowering and non-flowering species) vegetation < 60 cm were similar (Table 2). At PPRA, the treatments were largely the same, but there were differences at WRMA (Figure 5). Fire was predictably successful at decreasing woody regeneration in general, as well as flowering woody vegetation specifically. This is illustrated by the stark contrast between the 2013 pre-burn and 2014 post-burn PPRA woody plant cover data (Figure 5).

While the bulldozer treatment had more grass cover early on in the study, there was an overall downward trend in grass cover (Figure 5), especially at the PPRA. Pennsylvania sedge showed different trends between the two management areas, with an overall increase in cover at the WRMA and a slight decrease across treatments at PPRA (Figure 5). While there were significant between-treatment differences in Pennsylvania sedge cover for both management areas (Table 2), this appeared to be statistically driven primarily by relatively low levels in the control (Figure 5, Table A2.2). Treatment also had a significant effect on fern cover, though there was little to no variation over time (Table 2). There were no significant differences between treatments in terms of invasive species cover, but there were changes over time, primarily a general decrease in cover as time progressed (Table 2). Finally, we found a significant treatment effect in the wild lupine cover data (Table 2). This effect was variable across management areas, with the shear cutter and masticator treatments generally having more lupine cover than the bulldozer treatment in the PPRA, and the masticator treatment having more cover than the shear cutter treatment and control at the WRMA (Figure 5, Table A2.2).

Patterns in Site Conditions

The DCAs computed for each year had axes lengths less than 1.75 (Table 3), indicating relatively moderate differentiation between sites (Hill and Gauch 1980). The DCA plot for the 2014 data (Figure 6) illustrates the contrasts between: 1) the controls and treatments, in general, and 2) the (2013) burned (PPRA) and unburned (WMRA) sites. The unburned WMRA sites were distributed more toward the control side of the y-axis, while the burned PPRA sites were distributed along the opposite side. Several key cover types had vectors significantly associated toward the burned direction (> 0 on DCA axis 1 and < 0 on DCA axis 2), including herbaceous plants, wild lupine (% cover and presence/absence), and woody flowering plants (Figure 6, Table A2.3). The DCA plot of mean data by year also illustrates the strong differences between the control and mechanical treatments (Figure 7), as well as the increasing similarity among treatments over time. The fire effects and general differences between management areas are apparent, however, when the management units are plotted separately (Figure A2.2).

Discussion

Different mechanical restoration approaches had impacts on site characteristics (Figures 2, 3, 4; Table 1), which likely influenced the relative abundance of the different vegetative cover types. Bulldozed sites created the most exposed soil early in the study, but these treatments were quickly colonized by plants, and between-treatment differences were minimal. Similarly, masticator treatments (and bulldozer treatments at the PPRA) created the most woody debris, but after a few years the treatments were largely indistinguishable. As expected, all three treatments had significantly lower canopy cover than the control, and the masticator treatment generally had slightly higher cover amounts than either bulldozer or shear cutter due to its tree size limitations. Taken together, these factors had a strong influence on the distribution of sites in environmental space (Figure 6), and likely drove our observed differences in cover type abundances by acting as an environmental sieve for the regional species pool (*sensu* Zobel 1997).

Broadly, the shear cutter treatment was most effective at meeting regional oak savanna management goals, which includes the promotion of herbaceous plant cover while restricting woody regeneration (Figure 5). In addition, by year 5, the shear cutter treatment was more effective than the bulldozer treatments or taking no action (control) at promoting wild lupine establishment and growth at the PPRA (Figure 5), though between-treatment differences are not apparent at the WRMA. While the masticator treatment was also somewhat effective at promoting herbaceous plant growth (including wild lupine), it was ineffective at restricting woody regeneration relative to the other treatments, especially at the WRMA (Figure 5). This difference may be attributed to the relative disturbance intensity of each management approach as applied on-site; shear cutters created a significantly more open canopy than masticators (Figure 2), which were limited in the size of trees that they could remove.

While there were some moderate between-treatment differences in terms of grass cover early in the study, namely bulldozer treatments having somewhat higher abundance, grass generally converged among cover types until it reached around 5% (PPRA) or 10% (WRMA) cover in all treatments (Figure 5). This is likely the result of grass being displaced as other taxa colonize the site and grow in size. Pennsylvania sedge, on the other hand, had variable responses across treatment and time in the two management units. At the PPRA, Pennsylvania sedge generally decreased over time, while maintaining relatively high (but not statistically-significant) cover amounts in the shear cutter and bulldozer treatments. Conversely, cover generally increased over time at the WRMA, with all treatments having significantly more sedge cover than the control (Figure 5). Pennsylvania sedge is often seen as an undesirable species in woodland and forest systems because it tends to form dense mats of vegetation that can make it difficult for other taxa to become established (Abrams et al. 1985, Johnson 1992, Powers and Nagel 2009). For this reason, the jump in cover amount (~15% to 25-45%) from 2012 to 2013 at the WRMA is concerning (Figure 5).

Dense fern cover is undesirable for oak savanna systems for similar reasons as Pennsylvania sedge; the dense shade provided by thick fern cover makes it difficult for other plants to become established (George and Bazzaz 1999). Between our management units, fern cover demonstrated varying responses to mechanical treatment (Figure 5). At the WRMA, control sites had the least cover, while the least cover at the PPRA was observed on the bulldozer treated areas (Figure 5, Table A2.2). While these results are somewhat conflicting, fern cover is highly variable between and within management units, making it difficult to draw major conclusions. Finally, while there were no between treatment differences in invasive species abundance, we did notice a downward trend over time, especially at the PPRA (Figure 5). The gradual decrease at the WRMA is joined by a surprisingly sharp 2012 decrease at the PPRA; this overall trend may be attributable to the sustained 2012 drought (NDMC 2015) and a steady increase in woody plant cover over time (Figure 5).

When comparing herbaceous and woody plant cover types between the two management areas, it appears that the 2013 prescribed burn at the PPRA was quite effective at reducing woody plant cover while promoting herbaceous cover. After the burn, woody plant cover dropped by more than half across treatments, while herbaceous cover more than doubled (Figure 5). Post-fire changes in vegetation can be attributed to a number of factors, especially changes in site conditions (White 1983, Tester 1989, Peterson and Reich 2001). Here, we see that the amount of on-site exposed soil increases dramatically as the ground cover is burned away (Figure 5). Exposed mineral soil, the seed bank, and reduced competition post-fire can all interact to result in an increase in plant diversity (e,g, Brockway and Lewis 1997, DiTomaso et al. 1999).

While the different mechanical treatments used in this study had a clear impact on several site conditions and vegetation cover types, additional inference is limited by design constraints. The data collected in this study is coarse (e.g., "herbaceous plant cover") and prevents any community-level analyses. In addition, no pre-treatment cover type data was collected, which would have allowed us to determine the direct impact of treatment application on different vegetation types, and help identify any potential founder effects.

The results presented here suggest that among mechanical thinning approaches to oak savanna restoration, the shear cutter was the most effective at attaining our desired management goals of high herbaceous plant cover, reduced woody regeneration, and high wild lupine cover. Moreover, post-establishment prescribed burns are effective at furthering these management goals (Figure 5). The masticator approach was only slightly less effective than the shear cutter. Prescribed burning seems to mitigate the masticator's woody regeneration issue (Figure 5), making the two methods competitive. In addition, both of these methods have similar price tags at ~$2,200 per acre (circa 2010 USD; *pers. comm. H. Keough*), which is considerably more expensive than the ineffective bulldozer treatment (~$1,400 per acre). These costs include the 2010 establishment burns. The choice of method, then, ultimately depends on the management strategy being employed. Our results suggest that if the management strategy is to include periodic prescribed burning, either the masticator or shear cutter approach would be effective; if the strategy were restricted in terms of burning, however, using a shear cutter may prove to be more beneficial, as woody regeneration would be lower.

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Tables and Figures

Table 1. Linear mixed effects modeling results for site characteristics at (a) PPRA and (b) WRMA.

(1a). PPRA.

Response Variable	Source	df	*F*	*p*	Marginal r^2	Conditional r^2
Canopy Cover					0.684	0.751
	Treatment	3	120.605	< 0.0001		
	Year	4	3.636	0.0079		
	Treatment × Year	12	0.454	0.9367		
	Source	df	*F*	*p*	Marginal r^2	Conditional r^2
Dead Wood					0.28	0.357
	Treatment	3	2.787	0.0439		
	Year	4	3.967	0.0047		
	Treatment × Year	12	3.017	0.001		
	Source	df	*F*	*p*	Marginal r^2	Conditional r^2
Exposed Soil					0.592	0.687
	Treatment	3	16.272	< 0.0001		
	Year	4	35.131	< 0.0001		
	Treatment × Year	12	6.128	< 0.0001		

(1b). WRMA.

Response Variable	Source	df	*F*	*p*	Marginal r^2	Conditional r^2
Canopy Cover					0.565	0.615
	Treatment	3	53.351	< 0.0001		
	Year	4	2.109	0.0857		
	Treatment × Year	12	0.511	0.9032		
	Source	df	*F*	*p*	Marginal r^2	Conditional r^2
Dead Wood					0.341	0.455
	Treatment	3	9.215	< 0.0001		
	Year	4	7.293	< 0.0001		
	Treatment × Year	12	1.461	0.1527		
	Source	df	*F*	*p*	Marginal r^2	Conditional r^2
Exposed Soil					0.602	0.673
	Treatment	3	11.139	< 0.0001		
	Year	4	30.108	< 0.0001		
	Treatment × Year	12	5.436	< 0.0001		

Table 2. Linear mixed effects modeling results for vegetative cover types at (a) PPRA and (b) WRMA.

(2a). PPRA.

Response Variable	Source	df	F	p	Marginal r^2	Conditional r^2
Herbaceous Veg.					0.291	0.368
	Treatment	3	4.356	0.0061		
	Year	4	11.199	< 0.0001		
	Treatment × Year	12	0.501	0.911		

Response Variable	df	F	p	Marginal r^2	Conditional r^2
Woody Nect. Veg.				0.267	0.355
	3	2.464	0.066		
	4	11.297	< 0.0001		
	12	0.404	< 0.0001		

Response Variable	Source	df	F	p	Marginal r^2	Conditional r^2
All Woody Veg.					0.219	0.312
	Treatment	3	1.313	0.2736		
	Year	4	7.869	< 0.0001		
	Treatment × Year	12	0.7372	0.7125		

	df	F	p	Marginal r^2	Conditional r^2
Pennsylvania Sedge				0.095	0.332
	3	3.817	0.126		
	3	4.794	0.0126		
	9	0.622	0.7755		

Response Variable	Source	df	F	p	Marginal r^2	Conditional r^2
Grass					0.228	0.394
	Treatment	3	4.09	0.009		
	Year	3	12.84	< 0.0001		
	Treatment × Year	9	0.625	0.7733		

	df	F	p	Marginal r^2	Conditional r^2
Wild Lupine				0.192	0.298
	3	6.502	0.0004		
	4	3.09	0.0186		
	12	0.515	0.9016		

Response Variable	Source	df	F	p	Marginal r^2	Conditional r^2
Fern					0.057	0.444
	Treatment	3	3.198	0.0261		
	Year	4	0.706	0.5895		
	Treatment × Year	12	0.151	0.9996		

	df	F	p	Marginal r^2	Conditional r^2
Invasives				0.35	0.359
	3	0.389	0.7511		
	4	15.601	< 0.0001		
	12	1.017	0.4385		

(2b). WRMA.

Response Variable	Source	df	F	p	Marginal r^2	Conditional r^2
Herbaceous Veg.					0.169	0.361
	Treatment	3	7.659	0.0001		
	Year	4	0.825	0.5127		
	Treatment × Year	12	0.435	0.9454		
	Source	df	F	p	Marginal r^2	Conditional r^2
All Woody Veg.					0.282	0.586
	Treatment	3	7.291	0.0002		
	Year	4	13.03	< 0.0001		
	Treatment × Year	12	0.597	0.8396		
	Source	df	F	p	Marginal r^2	Conditional r^2
Grass					0.097	0.213
	Treatment	3	2.579	0.0598		
	Year	3	2.594	0.0588		
	Treatment × Year	9	0.518	0.8567		
	Source	df	F	p	Marginal r^2	Conditional r^2
Fern					0.065	0.541
	Treatment	3	4.311	0.0068		
	Year	4	0.144	0.9653		
	Treatment × Year	12	0.27	0.9925		

Response Variable	df	F	p	Marginal r^2	Conditional r^2
Woody Nect. Veg.				0.299	0.387
	3	6.755	0.0004		
	4	7.933	< 0.0001		
	12	0.515	0.9003		
	df	F	p	Marginal r^2	Conditional r^2
Pennsylvania Sedge				0.379	0.469
	3	6.064	0.0009		
	3	22.762	< 0.0001		
	9	0.618	0.7774		
	df	F	p	Marginal r^2	Conditional r^2
Wild Lupine				0.086	0.406
	3	4.737	0.0186		
	4	0.172	0.9523		
	12	0.186	0.9987		
	df	F	p	Marginal r^2	Conditional r^2
Invasives				0.189	0.189
	3	1.021	0.3869		
	4	4.751	0.0015		
	12	0.471	0.927		

Table 3. Yearly summary table for computed DCA. Eigenvalues, DCA values, and axis lengths are reported for all four axes.

Year		DCA1	DCA2	DCA3	DCA4
2010	Eigenvalues	0.1991	0.0739	0.0732	0.0733
	DCA values	0.1992	0.3802	0.0141	0.0126
	Axis length	1.1679	0.8935	0.8862	0.8868
2011	Eigenvalues	0.1648	0.0686	0.0673	0.0674
	DCA values	0.1652	0.0479	0.0067	0.0052
	Axis length	1.3132	0.9507	0.9418	0.9418
2012	Eigenvalues	0.1899	0.0412	0.0413	0.0414
	DCA values	0.1919	0.0271	0.0050	0.0038
	Axis length	1.7473	0.8137	0.8160	0.8177
2013	Eigenvalues	0.0948	0.0533	0.0531	0.0531
	DCA values	0.0949	0.0366	0.0085	0.0074
	Axis length	1.0777	0.7957	0.7942	0.7941
2014	Eigenvalues	0.2141	0.0561	0.0621	0.0650
	DCA values	0.2169	0.0445	0.0076	0.0061
	Axis length	1.2703	0.8109	0.9065	0.9373

Figure 1. Photographs of mechanical equipment and false color aerial imagery. The masticator (a), shear cutter (b), and bulldozer (c) treatment equipment is shown. A false color aerial photograph (d) illustrates the canopy structural differences between treatments; M: masticator, S: shear cutter, B: bulldozer, C: control.

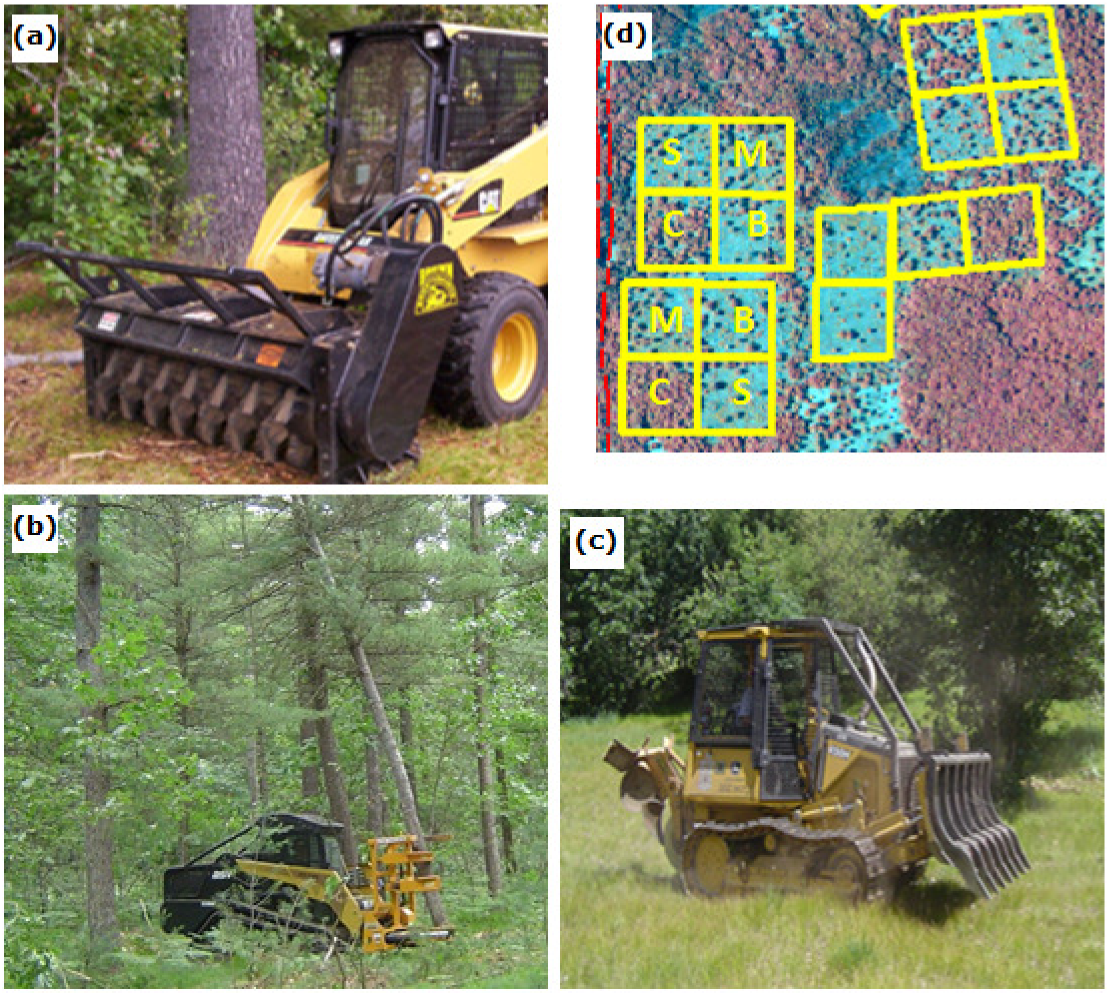


Figure 2. Mean overstory canopy cover (%) ±1 SE across treatments and time both PPRA and WRMA.

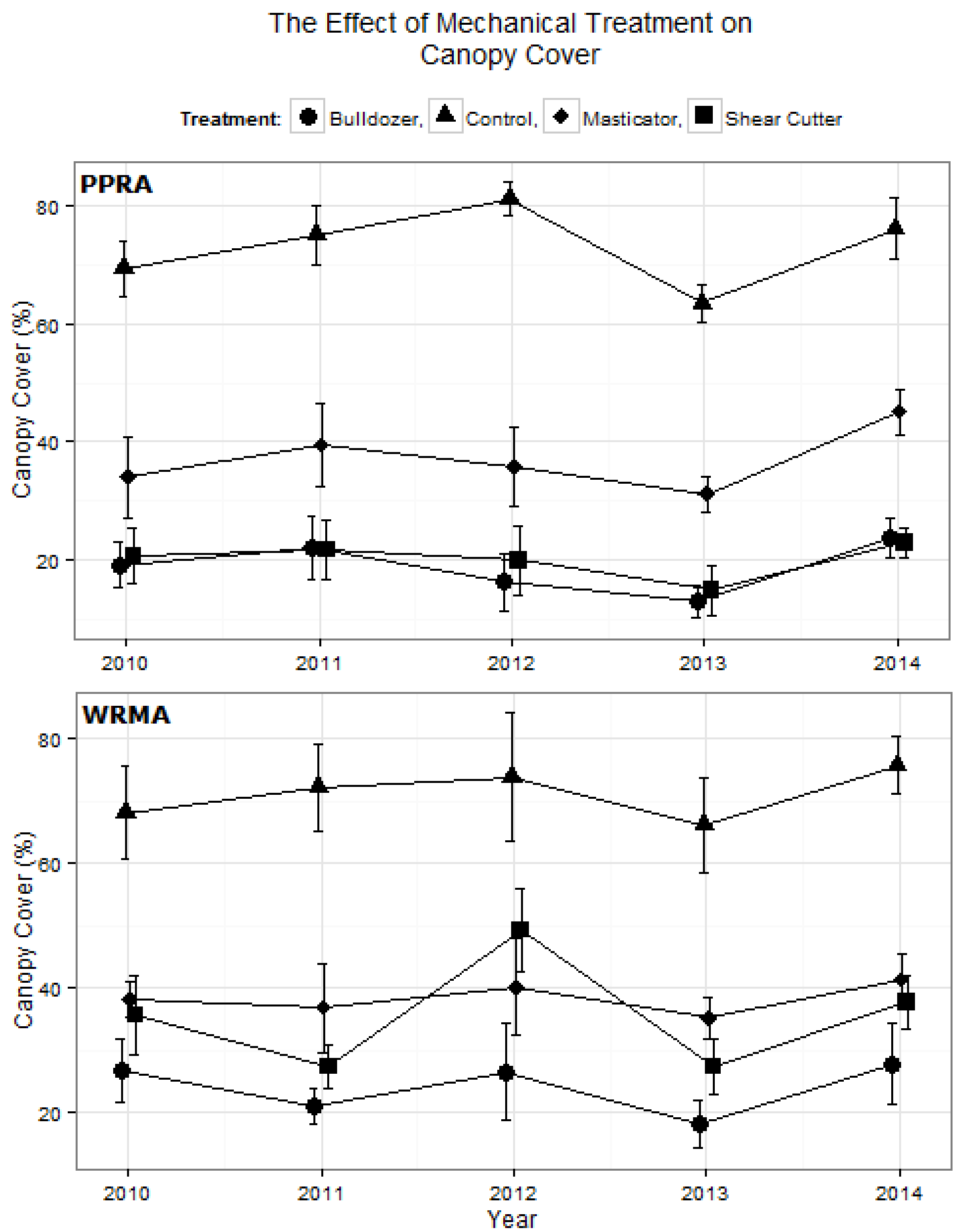


Figure 3. Mean woody debris cover (%) ±1 SE across treatments and time both PPRA and WRMA.

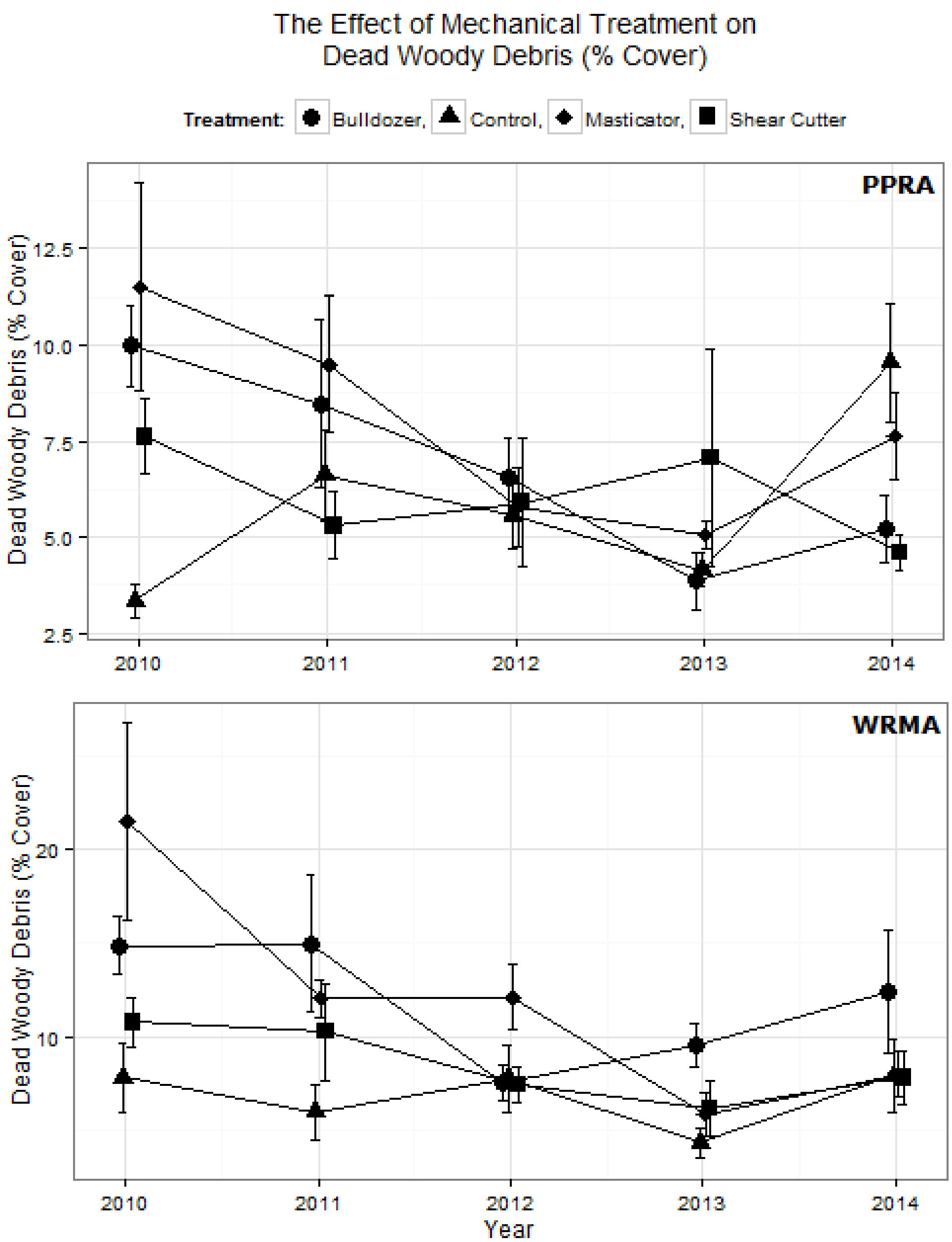


Figure 4. Mean exposed soil cover (%) ±1 SE across treatments and time both PPRA and WRMA.

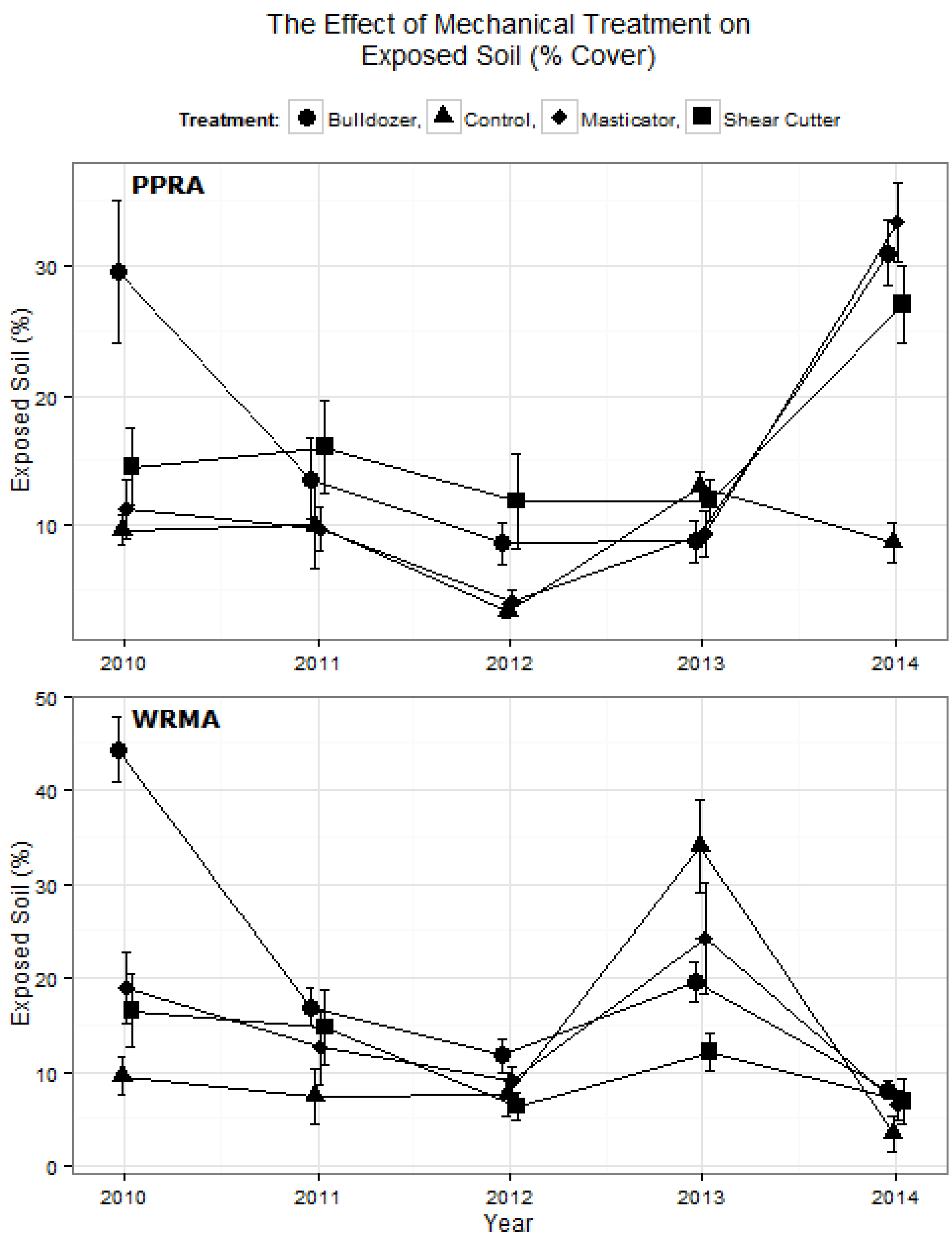


Figure 5. Mean vegetation cover (%) ±1 SE across treatments and time at PPRA (top) and WRMA (bottom).

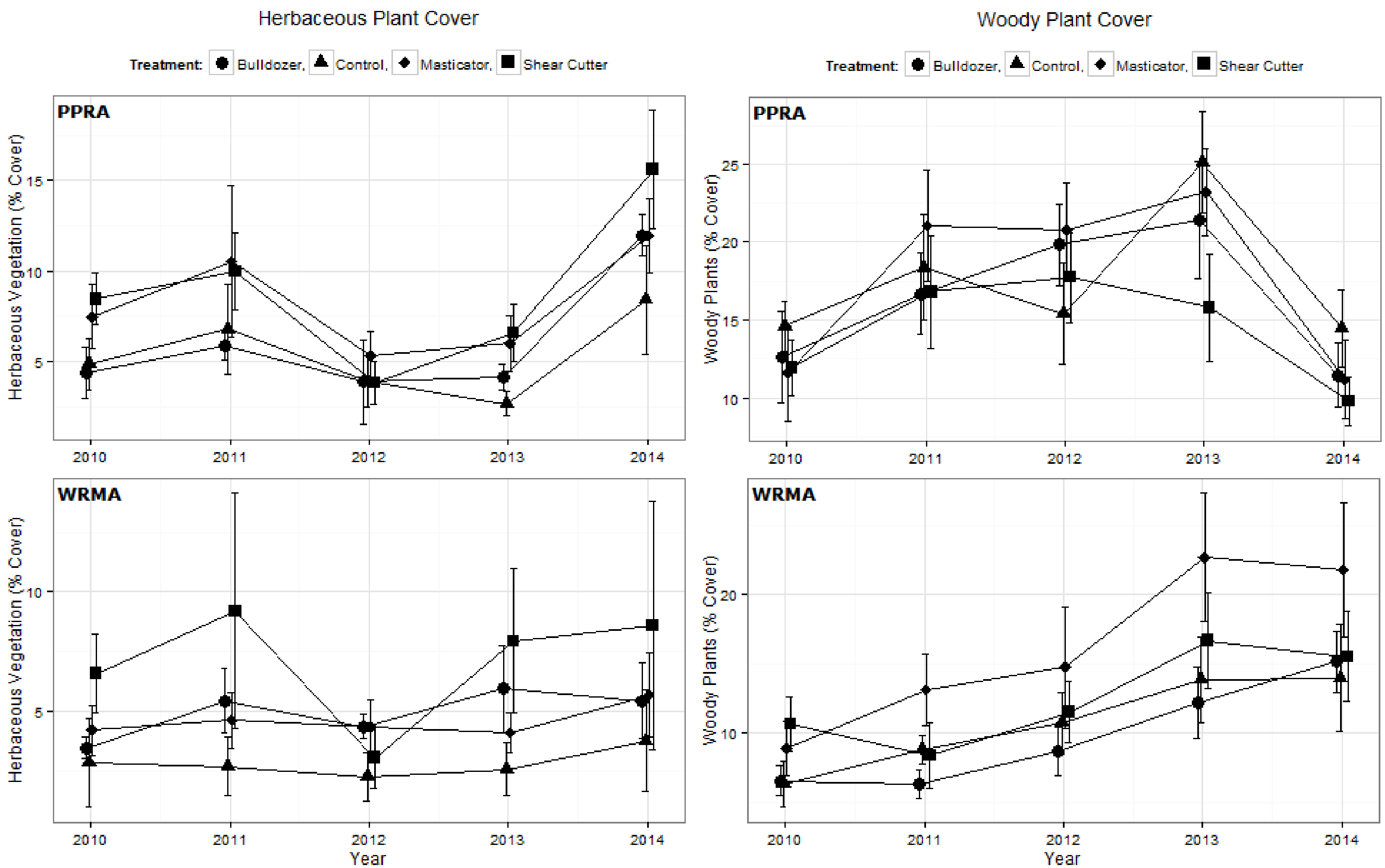


Figure 5 cont'd. Mean vegetation cover (%) ±1 SE across treatments and time at PPRA (top) and WRMA (bottom).

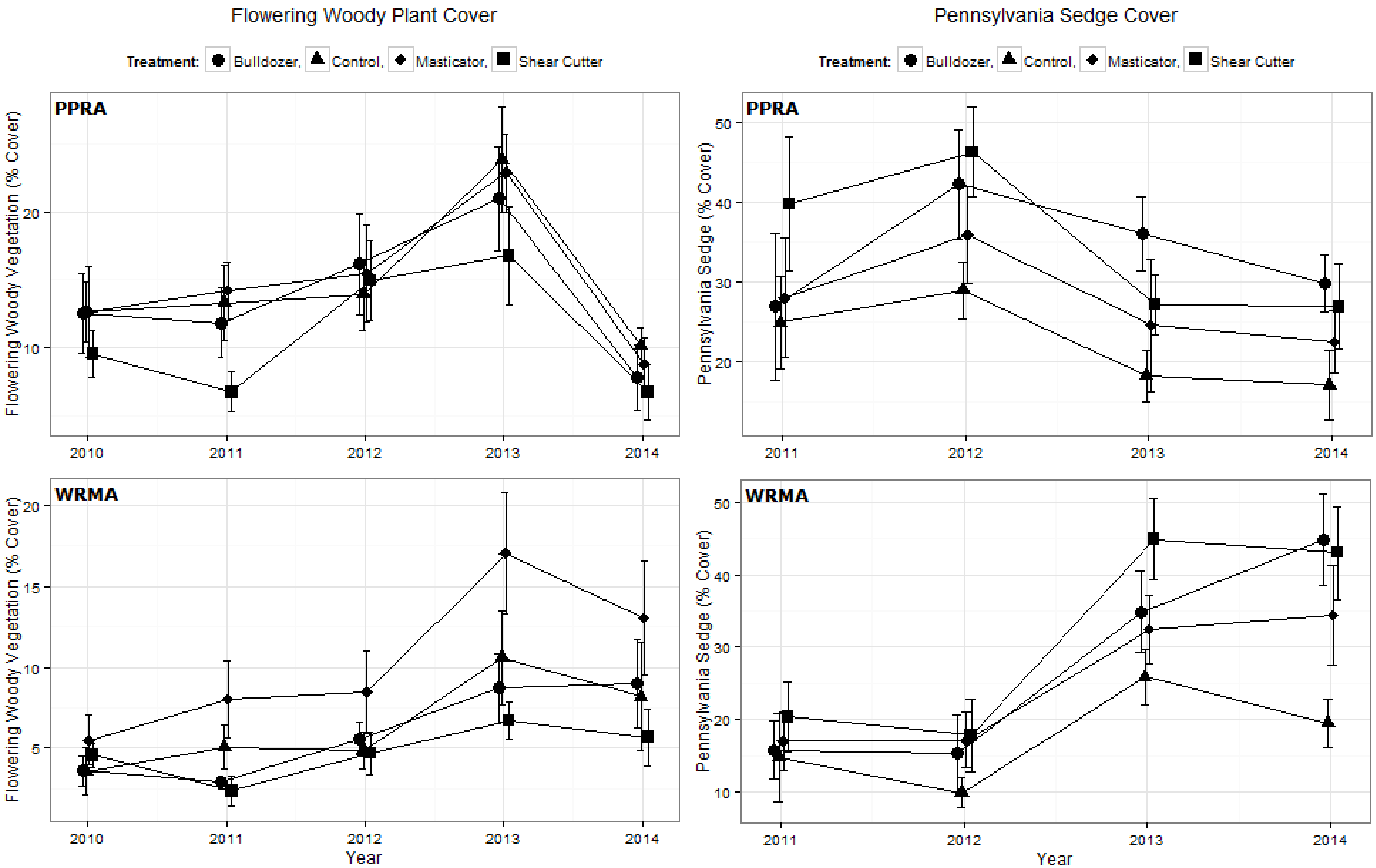


Figure 5 cont'd. Mean vegetation cover (%) ±1 SE across treatments and time at PPRA (top) and WRMA (bottom).

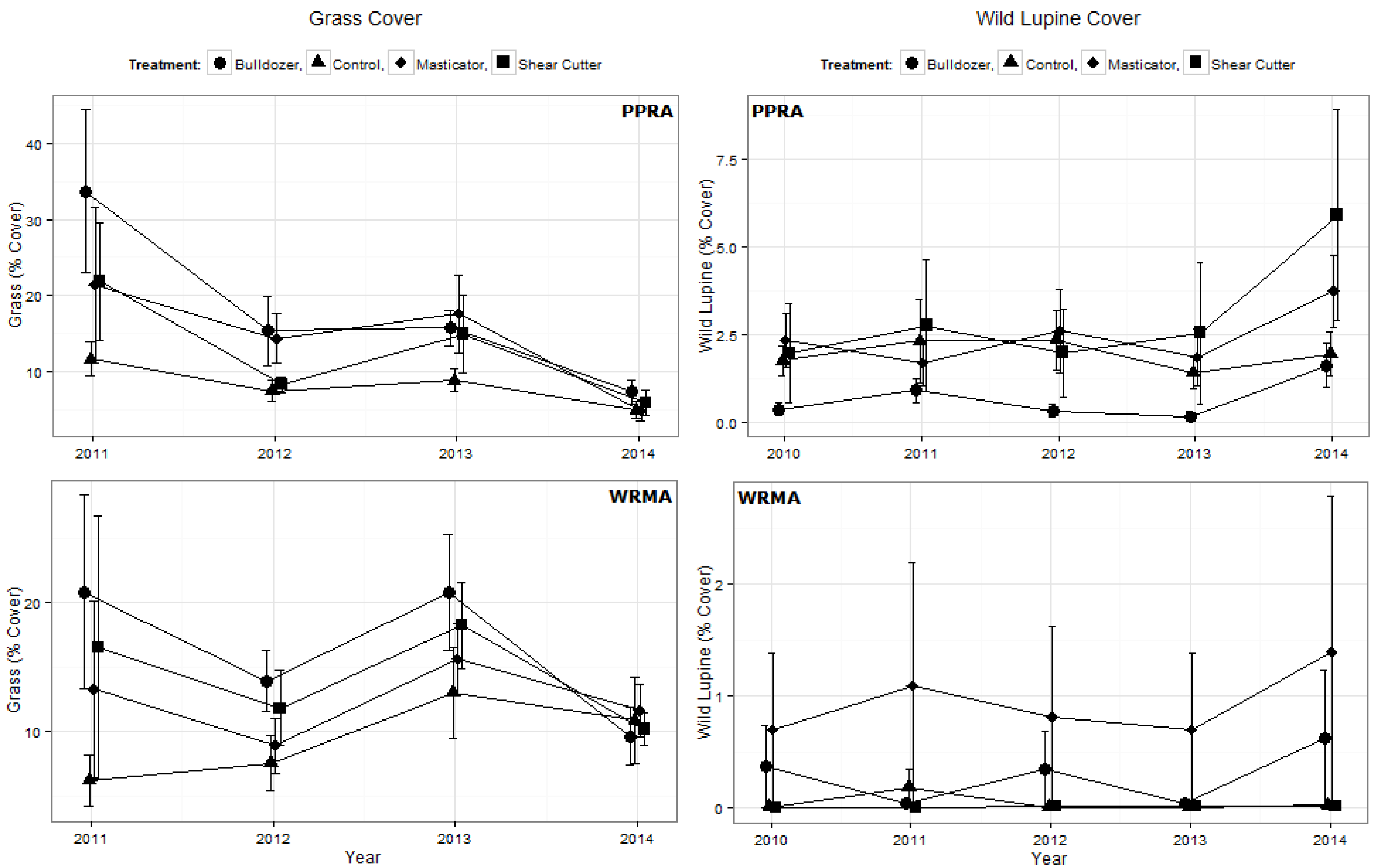


Figure 5 cont'd. Mean vegetation cover (%) ±1 SE across treatments and time at PPRA (top) and WRMA (bottom).

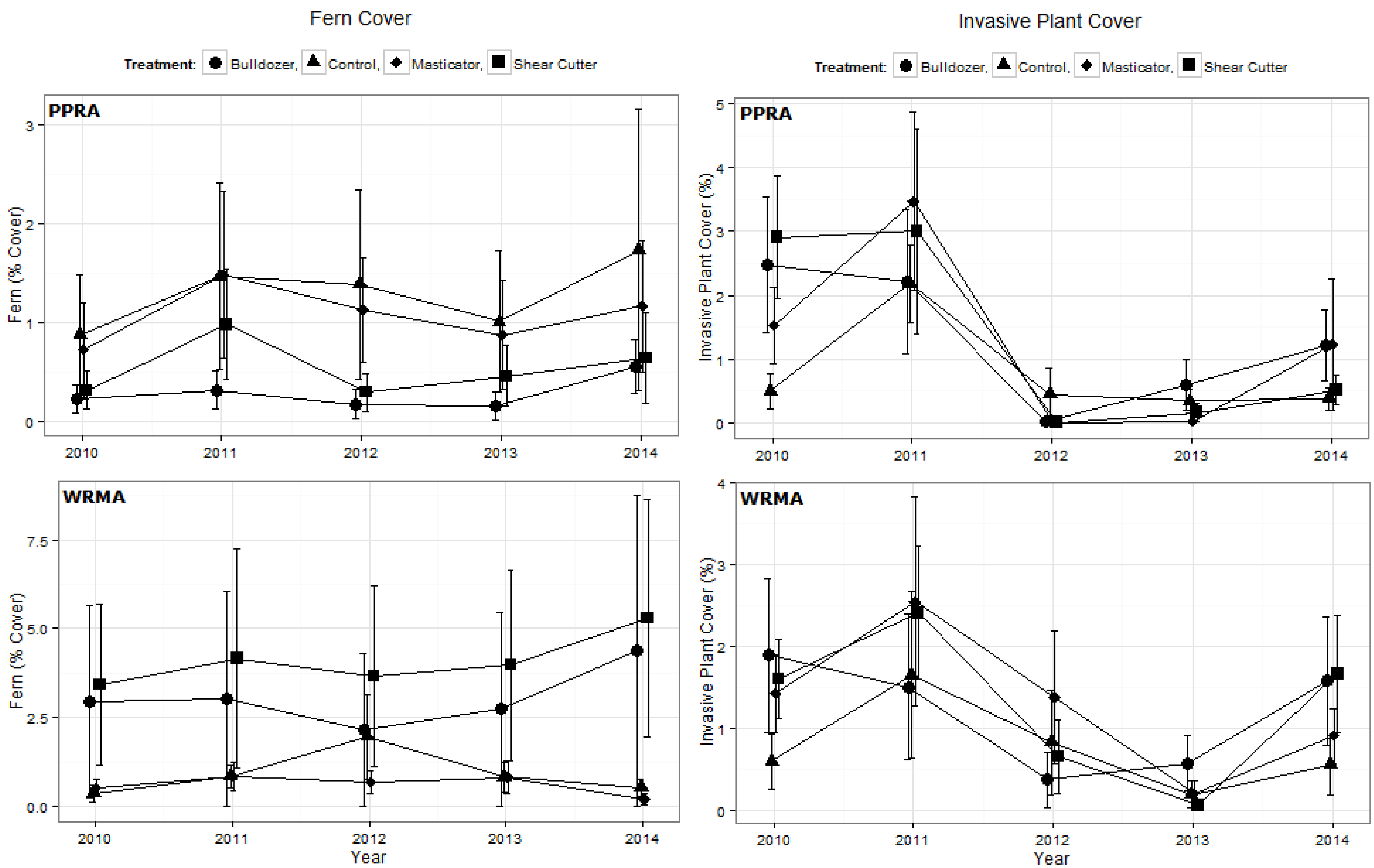


Figure 6. Plot of DCA axes 1 and 2 after five years (2014) of experimental data collection. Shapes and color represent treatments, while shade (light/dark) represents burn status (burned/unburned). The PPRA management area was burned in late summer 2013, while the WRMA was not, leading to difference in site conditions during the 2014 season. Vectors represent significant or marginally-significant ($p < 0.1$) cover type correlations with DCA axes (Table A2.3).

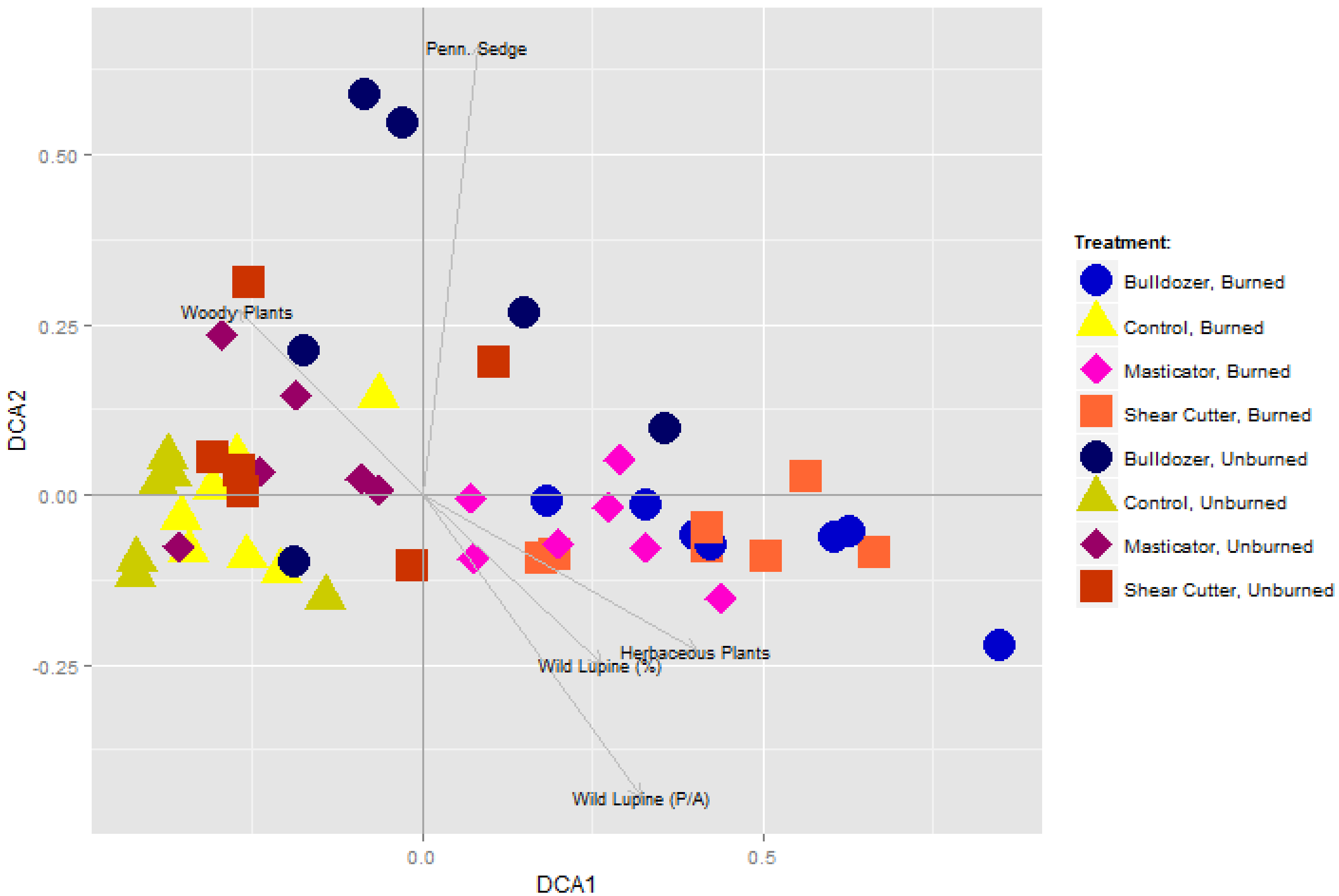
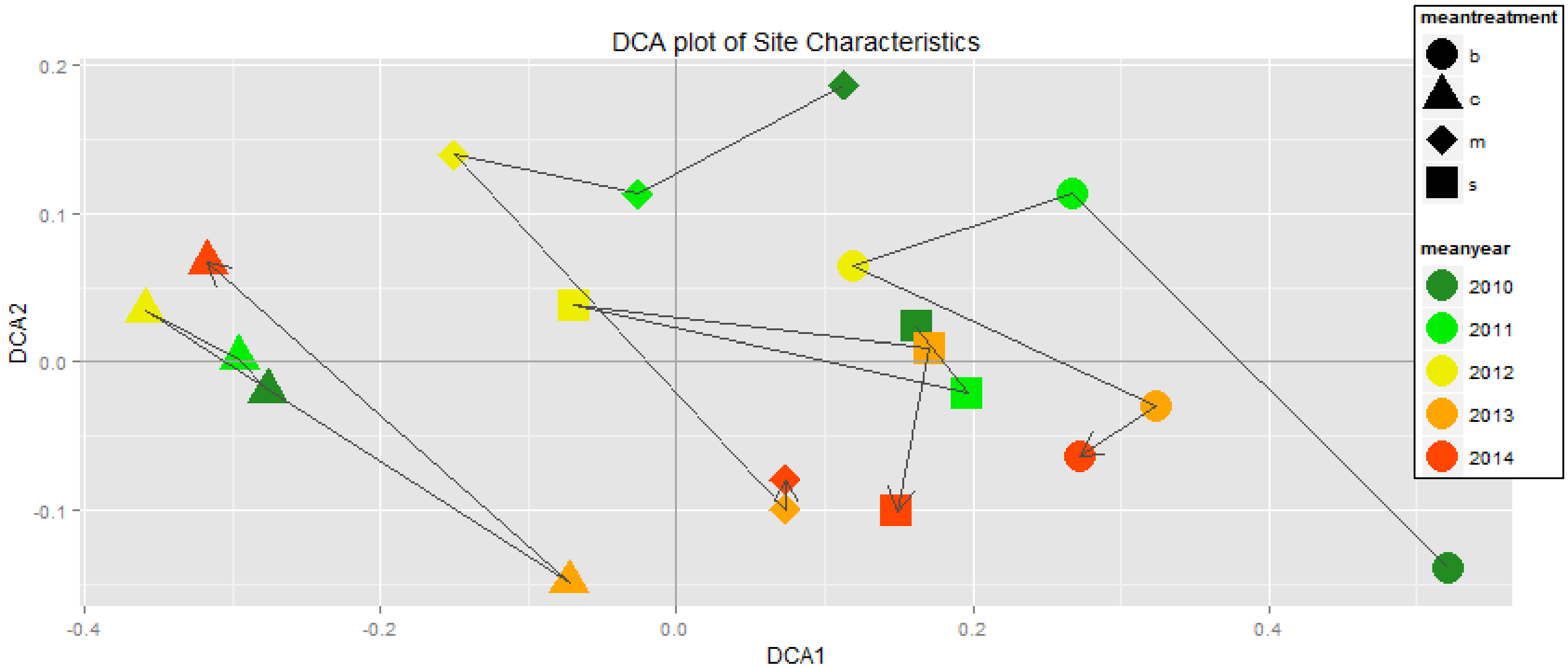


Figure 7. Plot of DCA axes 1 and 2. Mean values for each year are plotted. Shapes represent treatments, while the green-red color gradient represents year. An arrow is drawn through each treatment beginning at 2010 and ending at 2014. The control is located to the far left, while all three treatments are towards the center or right side of the plot. Note that all three treatments begin to converge by 2013, and especially in 2014. This plot includes data from both management units; to see contrasts between management units, see Figure A2.2.



Chapter 3:

Applying and comparing species distribution models at the management scale to inform the conservation of an endangered butterfly and its host plant

Introduction

One of the biggest challenges in the management and conservation of threatened or endangered species is often a lack of resources. Prioritizing land for conservation management or restoration can be difficult and costly, especially when managing a large area, or when relatively little is known about a species' habitat preferences. Species distribution modeling (SDM) offers a relatively low-cost approach that can help land managers develop strategic and effective conservation strategies. SDMs are able to spatially estimate habitat suitability for a given species by modeling relationships between the environment and species occurrence (Franklin 2009, Guisan & Thuiller 2005). Models can also yield important information regarding the relative importance of environmental variables, and estimate how habitat suitability varies with those factors (Elith et al. 2005). However, despite the apparent usefulness of SDM as a tool for management and conservation, there are only a few examples of the technique being used as such in the published literature (Guisan et al. 2013).

Here, we demonstrate management applications of SDM as part of an ongoing effort to identify, maintain, and restore oak savanna habitat for the endangered Karner Blue butterfly (*Lycaeides melissa samuelis* Nabokov) and its obligate larval host plant, wild lupine (Fabaceae: *Lupinus perennis* L.) The Karner Blue is a small Lycaenid butterfly; the adults are generalist nectarivores, while the larvae are specialist herbivores, feeding exclusively on the leaves of wild lupine (Haack 1993). Wild lupine is a perennial plant commonly found on well-drained sandy soils (Meyer 2006). These two species are often used as focal species for the management and restoration of oak savanna ecosystems in the upper Midwestern United States, especially Michigan, Wisconsin, Indiana, and Ohio (USFWS 2003; USFWS 2012).

The Huron-Manistee National Forests (HMNF) are using the Karner Blue and wild lupine as foci for broader oak savanna restoration and management, with a long-term goal of restoring and maintaining over 8,000 ha of oak savanna habitat (USFS 2012). Prioritizing which lands to restore to oak savanna presents a major obstacle to these restoration efforts, especially since management resources are limited and savanna restoration often involves prescribed burning, heavy equipment, or both. Additionally, there have been relatively few studies examining the specific habitat requirements of these two species (Boyonoski 1992, Kelly 1998, Grundel et al. 1998a, Grundel et al. 1998b), further challenging prioritization efforts.

While these challenges offer an opportunity to demonstrate the utility of SDM in a management context, there are additional concerns associated with using SDMs. Indeed, the variety of options available and the perceived complexity of modeling species distributions may contribute to the lack of applied examples of SDMs as tools for conservation (Addison et al. 2013, Guisan et al. 2013).

Broadly, SDM approaches can be categorized into two groups: statistical and algorithmic (or machine learning) models (Franklin 2009). Statistical approaches used in constructing SDMs encompass methods such as generalized linear models (Nicholls 1989), generalized additive models (Yee and Mitchell 1991), regression splines (Elith and Leathwick 2007), and discriminant analysis (Manel et al. 1999). In general, these statistical models have the benefit of being easy to implement and interpret, as many ecologists and managers already have some familiarity with statistical models. In contrast, algorithmic approaches often require a set of extra steps to reach a similar level of interpretability as statistical models (e.g., Elith et al. 2005). Despite the extra effort, however, algorithmic models have been demonstrated to outperform statistical models in a variety of situations (Elith and Graham 2009, Prasad et al. 2006). Algorithmic models commonly used for SDM include artificial neural networks (Manel et al. 1999), classification and regression trees (De'ath and Fabricius 2000), generalized boosted regression trees (Elith et al. 2008), and random forests (Prasad et al. 2006). In addition, the popular maximum entropy approach offered by the MaxEnt software (Phillips et al. 2006) is often grouped as a machine-learning or algorithmic method, though recent work has demonstrated that it is mathematically equivalent to a Poisson regression model (Renner and Warton 2013).

When using SDMs, especially in an applied context where decisions may be made based on model output, it is important to recognize that both model output (i.e., model predictions) and model performance (i.e., model accuracy) can depend heavily on the approach used. Indeed, output and performance can vary significantly between different modeling approaches dependent on a variety of factors ranging from sample size, species prevalence, study scale, and the environmental (i.e., predictor) variables used (Elith and Leathwick 2009, Guisan et al. 2007). There have been several studies comparing the relative performance and accuracy of different SDM approaches (Elith and Graham 2009, Hernandez et al. 2006, Leathwick et al. 2006, Manel et al. 1999, Segurado and Araújo 2004, Wisz et al. 2008), sometimes with conflicting conclusions (e.g., Elith and Graham 2009 and Dormann et al. 2008). For these reasons, the use of multiple modeling approaches is often recommended in any applied context (Araújo and New 2007, Franklin 2009).

Another caveat regarding the use of SDMs is that they define suitable habitat by modeling the relationship between species occurrence data and the environment (i.e., the realized niche) (Kearney 2006). The realized niche of the species of interest is defined not only by the environmental filters on the landscape (*sensu* Zobel et al. 2008), but also by biotic interactions and dispersal limitations (Kearney 2006). In an ideal situation, SDMs would be constructed based on the fundamental niche (Hutchinson 1957), which excludes the impacts of interactions and dispersal on a species' multidimensional niche space. It is for this particular reason that we chose to model the habitat suitability of two closely-interacting species (i.e., a butterfly and its obligate larval host plant). Together, we suspect that these two species are likely to capture important habitat information that may be missed by modeling only one species.

Here, our objective was to demonstrate the conservation application of SDM by constructing and comparing a variety of different SDM approaches at the operational-scale for use in the management and restoration of oak savanna ecosystems for the Karner Blue and wild lupine. More specifically, our goals were to: 1) determine which modeling approaches should be considered for decision-making by comparing model performance across a suite of modeling approaches, 2) evaluate differences in model output (i.e., the distribution of suitable habitat) within and between species, 3) assess the biological basis for these models by analyzing variable importance and response curves, and 4) demonstrate how the SDMs are being used to help inform management decisions.

Methods

Study Area

This study was conducted on the Baldwin-White Cloud Ranger District of the Manistee National Forest (MNF), located in western lower Michigan, USA, between 44º08'N and 43º20'N, 86º25'W and 85º27'W. Historically, this region was dominated by mixed oak-white pine forests, with a variety of early successional systems, such as oak savanna, dry sand prairie, and pine barrens existing within the forest matrix. Today the area is largely dominated by homogeneous mixed oak forests, agriculture, and red pine plantations. Upland soils in the region typically range from sandy loam to sand, and are largely glacial in origin. The study area has a humid continental climate (Köppen climate classification: Dfb; Peel et al. 2007) influenced by nearby Lake Michigan, with average minimum/maximum temperatures of -10.7º/-1.1 º C in January and 13.6 º/28.3º C in July. The area averages 877 mm of total precipitation per year, with a mean of 196 cm of snow per year.

Species Location Data

For the Karner Blue models, we used known locations of populations of butterflies as our response variable. In an effort to determine the presence, relative abundance, and density of the butterfly, the United States Forest Service (USFS) has been conducting surveys on the MNF on a regular basis. A total of 115 sites have been identified as occupied Karner Blue habitat since 2006. These sites range in size from to 2 to 15 ha, with a median size of 6 ha. Butterfly surveys were conducted using the distance sampling technique (see Thomas et al. 2010, Buckland et al. 2001), a common line-transect based approach for sampling populations of Lepidoptera. For wild lupine models, we used the locations of individual plants as the response variable. The geographic locations of 1337 plants were acquired from systematic-random vegetation surveys conducted in 2012, 2013, and 2014, as well as Karner Blue butterfly habitat surveys conducted by the Michigan Natural Features Inventory (MNFI 2013). Individual plant locations were georeferenced using a handheld GPS (Garmin eTrex 30, Kansas, USA) with an accuracy of ± 5 to 10 m.

Environmental and Climatic Data

The environmental predictor variables used in this study were chosen based on previous work relating to the maintenance and restoration of habitat for the Karner Blue and wild lupine (see USFWS 2003) and preliminary analyses. These environmental and climatic data came from a variety of different sources, and are listed in Table 1. Climatic and water table data were resampled to a 30 m spatial resolution using cubic convolution. Given the scale and location of the study area, the main variations in temperature and precipitation are caused by proximity to nearby Lake Michigan, rather than latitude. All other variables were either available or created at a 30 m resolution.

Species Distribution Modeling

To assess variability in model performance and output due to model choice, we used a total of seven different modeling approaches for both species. The approaches used include: generalized linear models (GLM), flexible discriminant analysis (FDA), maximum entropy (MaxEnt), artificial neural networks (ANN), classification and regression tree analysis (CTA/CART), generalized boosted regression models (GBM), and random forests (RF). All models were constructed within the BIOMOD framework (Thuiller et al. 2009) in R version 3.1.0 (R Core Team 2014). GLMs were constructed as quadratic models using a binomial distribution and logit link function; stepwise model selection was performed using AIC. FDA was constructed using three subclasses and five iterations. MaxEnt models were constructed using 200 iterations and the default MaxEnt settings (Phillips et al. 2006); linear, quadratic, product, threshold, and hinge features were enabled. ANN models were constructed using 200 iterations; the size and decay parameters were optimized by cross validation. CTA models were constructed using the default parameters (Therneau et al. 2014). GBM models were constructed using a Bernoulli distribution and 2500 trees. RF models were constructed by randomly sampling 4 variables at each split, using 2500 trees.

Our data came from management and monitoring surveys and did not contain species absence locations. Since most species distribution modeling techniques require both species presence and absence data (see Franklin 2009), we generated pseudo-absences (Elith et al. 2006) following the suggestions of Barbet-Massin et al. (2012). For wild lupine models, a surface range envelope approach (0.05 quantile) was used to generate an equal number of pseudo-absences as presences (n = 1337) for RF, GBM, CTA, FDA, and ANN. Given the smaller sample size (n = 115), we used a disk/buffer approach with a minimum distance of 2.5km to generate (10*presences; n = 1150) pseudo-absences for RF, GBM, CTA, FDA, and ANN for the the Karner Blue models. For both species, a fully random approach was used to generate n = 10,000 pseudo-absences for the GLM and MaxEnt models.

Model Evaluation

All models were evaluated using 10 full runs and 3-fold cross-validation using a 67:33 data split. Model performance was evaluated using the true skill statistic (TSS) and the area under the receiver operating characteristic curve (ROC/AUC) , two commonly-used metrics that assess performance based on the model error matrix (Allouche et al. 2006, Jiménez-Valverde 2012, see also Franklin 2009). While both of these metrics evaluate model performance on a scale from 0 to 1, with higher values indicating better overall performance, the TSS tends to be more conservative. We used one-way analysis of variance to test for differences in model performance for both metrics. Relative variable importance was evaluated for each model by considering each variable independently and shuffling the data. Shuffled data is correlated with the model reference predictions and returns a variable importance score (Thuiller et al. 2009). Variable importance scores were normalized to allow between-model comparisons; scores closer to 1 would indicate a variable has high relative importance in the model, while values closer to 0 would indicate a lower importance. Individual variable response curves were generated using the evaluation strip approach (Elith et al. 2005; Thuiller et al. 2009). Response curves help illustrate the relationship between the range of values of an individual variable and overall model response, where higher model response indicates higher predicted suitability. Response plots were created using the mean and standard deviation of the variable response curves for all 10 model runs. Model outputs between and within species were compared within and between species using Warren's *I*, a statistical measure of niche overlap. Warren's *I* reports niche overlap on a scale from 0, which indicates no overlap, to 1, which indicates perfect overlap (Warren et al. 2008).

Results

Model Performance

Model performance differed between modeling approaches for both species (Table 2); having a significant impact on both TSS (wild lupine: F=1184.7, p<0.001;

Karner Blue: F=35.8, p<0.001) and AUC (wild lupine: F=832.8, p<0.001; Karner Blue: F=26.6, p<0.001). RF performed most effectively for both species, followed by CTA and GBM for wild lupine and GBM and MaxEnt for the the Karner Blue (Table 2). In general, variation in model performance within a given modeling approach was fairly low, suggesting that replicate model runs were consistent in terms of performance. The exceptions were ANN and CTA, which demonstrated the highest variation in within model performance for both species (Table 2).

Variable Importance and Response Curves

Within modeling approaches, there was relatively little variation in variable importance for both species (Table 3), indicating that the replicate model runs were consistent in weighting and selecting environmental variables. There were overall trends in variable importance across modeling approaches. For wild lupine, land cover and mean summer temperatures were among the most important environmental variables for 6 of 7 of the models, and soil drainage was among the most important for 5 of 7 models. Elevation was among the most important variable for 6 of 7 the Karner Blue models, followed by mean summer precipitation and land cover, both of which were among the most important variables for 4 of the 7 models (Table 3).

Response curves for the three most important variables across the three best performing models for each species are illustrated in Figures 1 and 2. For wild lupine, land cover demonstrates a similar trend for the three models illustrated in Figure 1: low model response (i.e., lower likelihood of habitat suitability) for cropland, pastureland, and woody wetlands, and higher model responses (i.e., higher likelihood of habitat suitability) for developed areas, shrublands, grasslands, and deciduous forests. Indeed, variable response demonstrated fairly similar trends across all models; as illustrated in Figures 1 and 2.

Model Predictions

The spatial distribution of within-model predicted suitable habitat was consistent for both species, as illustrated by Warren's *I* values approaching 1 (Table 4). There was, however, some variability exhibited by CTA for wild lupine and ANN for the Karner Blue, indicating some within-model inconsistencies in terms of predicted habitat suitability. Niche overlap was high between the two species for most modeling approaches, especially GBM (Table 4). Visually, the predicted distribution of suitable habitat was similar for both species, though there was significantly more suitable habitat predicted for wild lupine as compared to the Karner Blue (Figure 4).

Discussion

Model Interpretation and Implications

In general, all of the modeling approaches used in this study performed reasonably well. However, performance results did reveal a spectrum in terms of modeling effectiveness; two algorithmic approaches, RF and GBM, demonstrated consistently high performance. In contrast, FDA and GLM were consistently among the poorest-performing approaches, although they still had a TSS > 0.6 for both species (Table 2). The relatively high performance of decision-tree based approaches (RF, GBM, CTA) in this study is in line with other work (e.g., Fukuda et al. 2013, Peters et al. 2007). Since our data is derived largely from monitoring efforts, this may have broader implications for which types of SDM approaches to consider, especially when working with limited datasets generated from ongoing conservation efforts.

The analysis of variable importance and response curves can help construct a biological basis for SDMs. Many of the variable responses in our models were expected and support the results of past research. For example, wild lupine models had the highest responses for grassland, shrubland, and disturbed (developed) areas on moderately-well to excessively-drained soils (Figure 1; see Boyonoski 1992, Pavlovic and Grundel 2009, Smith et al. 2002), and the Karner Blue models exhibited the highest responses for lower elevation non-forested, grassland, shrubland, and disturbed (developed) areas (Figure 2; see Forrester et al. 2005, Grundel et al. 1998a, Grundel et al. 2007, Haack 1993, Kelly 1998, Smith et al. 2002).

Broadly, the between-species Warren's *I* values (Table 4) suggest good predicted niche overlap between the Karner Blue and its obligate host plant. While the Karner Blue certainly has a smaller distribution of suitable habitat across the study area, the relatively high agreement (Table 4, Figure 3) between species is encouraging. Given the close life-history interaction between these two species, the two sets of models presented here, when considered together, likely capture more information regarding habitat preferences than either species independently; especially the rare Karner Blue.

Despite the apparent similarities between species, there were also some unexpected results. The Karner Blue had an apparent preference for areas of lower mean summer precipitation (Figure 2). This was unexpected because while the Karner Blue does require clear (i.e. non-cloudy) weather to mate and reproduce (Swengel and Swengel 1998, USFWS 2003), water-stressed wild lupine plants have been demonstrated to have a negative impact on larval growth (Grundel *et al.* 1998b). This trend may warrant future investigation to determine whether it is biologically important or an artifact of the data.

The approach to constructing and comparing SDMs used in this study can be valuable to conservation efforts in multiple ways. First, comparing a suite of modeling approaches helps address possible variation in model performance due to algorithmic differences. In addition, it allows for the identification and selection of modeling approaches that perform especially well in a particular study area. Secondly, a thorough analysis of variable importance scores and response curves helps identify potential biological explanations for the predictions of the SDMs; completely unexpected results may warrant further investigation. Finally, comparing model output allows the evaluation of consistency of predictions as well as niche overlap between species, which can be especially important when managing specialist species like the Karner Blue.

Management Applications

This study was conducted in association with ongoing conservation efforts for oak savanna ecosystems and the Karner Blue. The SDMs created herein are primarily being leveraged to aid in site selection for habitat restoration and setting up restoration studies. Our general workflow for the use of SDMs as tools for site selection is outlined in Figure 4. The first step is to define the modeling considerations, e.g., What are the species of interest? What is the region of interest? What scale is required? Ideally, the study area should be larger than the region of interest to avoid niche truncation (especially when considering a species on the edge of its fundamental niche; Braunisch et al. 2008, Suárez-Seoane et al. 2014), and the scale considered should be useful for decision-making.

The second step in our workflow is the construction, comparison, and selection of SDMs – which we demonstrate in this paper. The data required for model construction is, in the case of species location data, something that can often be gleaned from ongoing monitoring and surveying efforts, and in the case of many important environmental predictors, publicly available (e.g., satellite imagery, climate data). In this paper, we outline a variety of approaches that can be used to compare model output and performance, including error matrix analyses (e.g., TSS or AUC), plotting variable response curves, and comparing niche overlap. In terms of model selection, we ultimately chose to use the RF and GBM approaches to help inform site selection, based on model performance results for both species (Table 2). Broadly, the model selection choice will vary based on the ecological system and models considered. One could either consider all of the modeling approaches used, create an ensemble model (Araújo and New 2007), or consider only a subset of the best performing models. Given the variety of modeling approaches we used, and concerns regarding automatic model selection in ensemble approaches (see Elith et al. 2010), we chose to consider only the two best performing models from our analysis.

After model construction, an examination of predicted outputs can be used to help inform site selection by both narrowing down the search area and (depending on the scale being considered) identifying individual sites at the management-unit level. For the two models we considered, the mapped predictions (Figure 3) illustrate that habitat suitability was highest for both species in the southern portion of the study area. Predicted suitable habitat for wild lupine was largely located in the southeastern and southwestern lobes of the MNF, and roughly following a developed corridor in the eastern part of the study area

(Figure 3). The predicted suitable habitat for the Karner Blue was largely located in the southwestern lobe of the MNF, with additional patches of suitable habitat in the southeastern, central, and northwestern parts of the study area (Figure 3). We used the mapped prediction output of our models to help inform management in two main ways. First, model predictions were used to prioritize restoration efforts within existing management areas; timber sales and savanna conversions were targeted on the most suitable sites within predefined management areas on the District. Secondly, model predictions were also used to identify several new stand-level sites (4-10 ha in size) across the District as potential candidates for savanna restoration.

Candidate sites selected with the aid of SDMs should be validated with other sources of data whenever possible. In our case, we further examined candidate sites using: 1) USDA Forest Service stand maps, which contained detailed cover information and stand age, and 2) high-resolution aerial photography. These sites were then visited by field crews for a coarse overview, looking mainly for the presence of indicator species, invasive species, and determining the level of on-site disturbance.
Finally, management decisions were made based on: 1) habitat suitability as determined by SDMs, 2) follow-up information (forest stand information, coarse field surveys), and 3) administrative feasibility. Though the conservation efforts for the Karner Blue and oak savanna in general represent an ongoing process for the MNF, over 200 ha of potential habitat have been identified or site-prepped (i.e., overstory harvest, soil scarification) for restoration in two growing seasons (2013-2014) with the help of this SDM-based approach.

Conclusion

Despite its growth as a tool and subject of study in the past decade, there are relatively few examples of the direct applications of SDM to conservation and land management. SDMs represent a valuable tool for conservation efforts, but the lack of examples and their perceived complexity may be hindering their usage and application within the realm of operational management. Here, we demonstrated that by comparing a suite of modeling approaches, analyzing variable response curves, and examining factors such as niche overlap, results of the SDM approach can be of immediate use to managers. Indeed, our general framework for using SDMs as tools to inform site selection for conservation efforts has the potential to be useful in a wide range of conservation contexts.

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Tables and Figures

Table 1. List and brief description of the variables used to train SDMs. All variables were obtained, created, or resampled to a 30 m resolution.

Variable	Description	Source
Aspect	Topographical aspect (˚)	Derived from elevation
Slope	Angle of slope (˚)	Derived from elevation
Elevation	Elevation (meters above sea level)	USGS 30 meter digital elevation model
TWI	Topographic wetness index (Sørensen *et al.* 2006)	Derived from elevation
Soil Drainage	Soil drainage classification	SSURGO; Natural resources conservation service (2014)
Soil Particle Size	Soil particle size classification	SSURGO
Soil Order	Soil taxonomic order	SSURGO
Water Table	Estimated water table depth (meters)	Michigan department of environmental quality (2005)
Land Cover	Land cover type classification	USGS; National land cover dataset (Jin et al. 2013)
Summer Temperature	Mean summer (June-August) temperature (ºC)	PRISM Climate Group (2004), 30-year climate normals
Summer Precipitation	Mean summer (June-August) precip. (cm)	PRISM
Winter Temperature	Mean winter (December-February) temperature (ºC)	PRISM
Winter Precipitation	Mean winter (December-February) precip. (cm)	PRISM

Table 2. Mean model performance (n = 10) ± 1 standard deviation. TSS: True skill statistic, AUC: area under the receiver operating characteristic curve. For both metrics, values closer to 1 represent better performance.

Wild lupine

	TSS	AUC
ANN	0.770 ± 0.02	0.938 ± 0.006
CTA	0.868 ± 0.011	0.963 ± 0.006
FDA	0.763 ± 0.009	0.946 ± 0.003
GBM	0.801 ± 0.008	0.963 ± 0.002
GLM	0.627 ± 0.004	0.889 ± 0.002
MAXENT	0.735 ± 0.006	0.938 ± 0.001
RF	0.990 ± 0.001	0.999 ± 0.001

Karner Blue

	TSS	AUC
ANN	0.846 ± 0.087	0.946 ± 0.024
CTA	0.774 ± 0.068	0.914 ± 0.04
FDA	0.764 ± 0.011	0.946 ± 0.007
GBM	0.906 ± 0.005	0.988 ± 0.001
GLM	0.821 ± 0.019	0.961 ± 0.003
MAXENT	0.869 ± 0.01	0.981 ± 0.001
RF	0.991 ± 0.001	0.999 ± 0.001

Table 3. Mean normalized variable importance for each model (n = 10), ± 1 standard deviation. The three highest values for each model are bolded. Higher values indicate more importance for a particular variable within a model.

Wild lupine							
	ANN	CTA	FDA	GBM	GLM	MAXENT	RF
Aspect	0.016 ± 0.011	0.011 ± 0.007	0.002 ± 0.002	0 ± 0.001	0 ± 0.001	0.001 ± 0.001	0.008 ± 0.003
Slope	0.029 ± 0.008	0.022 ± 0.014	0.01 ± 0.007	0.005 ± 0.003	0.002 ± 0.001	0.001 ± 0.001	0.016 ± 0.003
Elevation	**0.192 ± 0.042**	0.032 ± 0.028	0.098 ± 0.036	0.016 ± 0.007	0.004 ± 0.002	**0.086 ± 0.01**	0.035 ± 0.004
TWI	0.011 ± 0.01	0.012 ± 0.006	0.004 ± 0.003	0.002 ± 0.002	0.001 ± 0.001	0.002 ± 0.001	0.011 ± 0.003
Soil Drainage	**0.133 ± 0.017**	**0.261 ± 0.026**	**0.121 ± 0.032**	**0.303 ± 0.056**	0.045 ± 0.005	0.081 ± 0.008	**0.278 ± 0.03**
Soil Part. Size	0.03 ± 0.013	0.067 ± 0.036	0.014 ± 0.01	0.009 ± 0.006	**0.322 ± 0.003**	0.025 ± 0.008	0.017 ± 0.003
Soil Order	0.037 ± 0.013	0.023 ± 0.032	0.04 ± 0.024	0.01 ± 0.003	0.14 ± 0.002	0.022 ± 0.009	0.055 ± 0.007
Water Table	0.031 ± 0.012	0.019 ± 0.014	0.011 ± 0.008	0.002 ± 0.002	0.004 ± 0	0.001 ± 0.001	0.019 ± 0.006
Land Cover	**0.151 ± 0.026**	**0.147 ± 0.028**	**0.115 ± 0.013**	**0.271 ± 0.044**	0.099 ± 0.003	**0.223 ± 0.01**	**0.144 ± 0.024**
Summer Temp	0.033 ± 0.014	**0.109 ± 0.031**	**0.391 ± 0.058**	**0.284 ± 0.052**	**0.225 ± 0.004**	**0.375 ± 0.018**	**0.208 ± 0.034**
Summer Prcp	0.132 ± 0.03	0.108 ± 0.044	0.084 ± 0.022	0.024 ± 0.008	0.001 ± 0	0.083 ± 0.008	0.083 ± 0.01
Winter Temp	0.077 ± 0.023	0.084 ± 0.018	0.024 ± 0.005	0.023 ± 0.003	0.009 ± 0.001	0.04 ± 0.005	0.046 ± 0.004
Winter Prcp	0.129 ± 0.071	0.105 ± 0.041	0.087 ± 0.033	0.051 ± 0.012	**0.147 ± 0.003**	0.061 ± 0.006	0.08 ± 0.005

Karner Blue							
	ANN	CTA	FDA	GBM	GLM	MAXENT	RF
Aspect	0.088 ± 0.024	0.013 ± 0.027	0.014 ± 0.005	0.014 ± 0.004	0.009 ± 0.002	0.022 ± 0.003	0.008 ± 0.006
Slope	0.063 ± 0.026	0 ± 0	0.007 ± 0.008	0.009 ± 0.004	0.001 ± 0	0.025 ± 0.009	0.006 ± 0.002
Elevation	**0.26 ± 0.042**	**0.166 ± 0.132**	**0.219 ± 0.067**	**0.229 ± 0.05**	0.118 ± 0.017	**0.113 ± 0.011**	**0.363 ± 0.028**
TWI	0.037 ± 0.023	0.002 ± 0.006	0.004 ± 0.005	0.014 ± 0.005	0.015 ± 0.002	0.011 ± 0.007	0.01 ± 0.002
Soil Drainage	0.058 ± 0.018	0.04 ± 0.045	0.006 ± 0.004	0.057 ± 0.025	0.099 ± 0.009	0.088 ± 0.006	0.013 ± 0.009
Soil Part. Size	0.016 ± 0.01	0 ± 0	0 ± 0	0 ± 0	**0.194 ± 0.034**	0 ± 0	0.001 ± 0
Soil Order	0.035 ± 0.013	0.006 ± 0.013	0 ± 0	0.008 ± 0.002	**0.153 ± 0.028**	0.006 ± 0.003	0.006 ± 0.002
Water Table	0.056 ± 0.037	0.005 ± 0.01	0.009 ± 0.006	0.011 ± 0.002	0.011 ± 0.003	0.028 ± 0.008	0.022 ± 0.004
Land Cover	**0.109 ± 0.035**	0.155 ± 0.028	0.06 ± 0.012	**0.242 ± 0.024**	0.086 ± 0.009	**0.1 ± 0.008**	**0.092 ± 0.009**
Summer Temp	0.012 ± 0.009	**0.161 ± 0.065**	0.135 ± 0.035	0.087 ± 0.018	**0.171 ± 0.014**	**0.448 ± 0.018**	0.078 ± 0.015
Summer Prcp	0.078 ± 0.04	**0.306 ± 0.083**	**0.194 ± 0.021**	**0.142 ± 0.042**	0.022 ± 0.005	0.05 ± 0.008	**0.302 ± 0.029**
Winter Temp	0.036 ± 0.02	0.069 ± 0.083	0.087 ± 0.026	0.064 ± 0.023	0.038 ± 0.027	0.037 ± 0.005	0.027 ± 0.003
Winter Prcp	**0.151 ± 0.026**	0.077 ± 0.062	**0.264 ± 0.052**	0.123 ± 0.024	0.085 ± 0.023	0.075 ± 0.01	0.071 ± 0.024

Table 4. Mean niche overlap of model output (Warren's I; n = 45 pairwise combinations for within-species calculations and n = 190 pairwise combinations for between-species calculations) ± 1 standard deviation. A value of 1 signifies perfect niche overlap, while 0 represents no overlap.

	Wild lupine	Karner Blue	Between Species Niche Overlap
ANN	0.934 ± 0.008	0.752 ± 0.041	0.691 ± 0.155
CTA	0.855 ± 0.011	1 ± 0	0.439 ± 0.014
FDA	0.98 ± 0.018	0.978 ± 0.008	0.838 ± 0.005
GBM	0.998 ± 0.001	0.998 ± 0.001	0.924 ± 0.001
GLM	0.999 ± 0.001	0.999 ± 0.001	0.841 ± 0.005
MaxEnt	0.998 ± 0.001	0.983 ± 0.005	0.817 ± 0.006
RF	0.99 ± 0.001	0.983 ± 0.001	0.674 ± 0.008

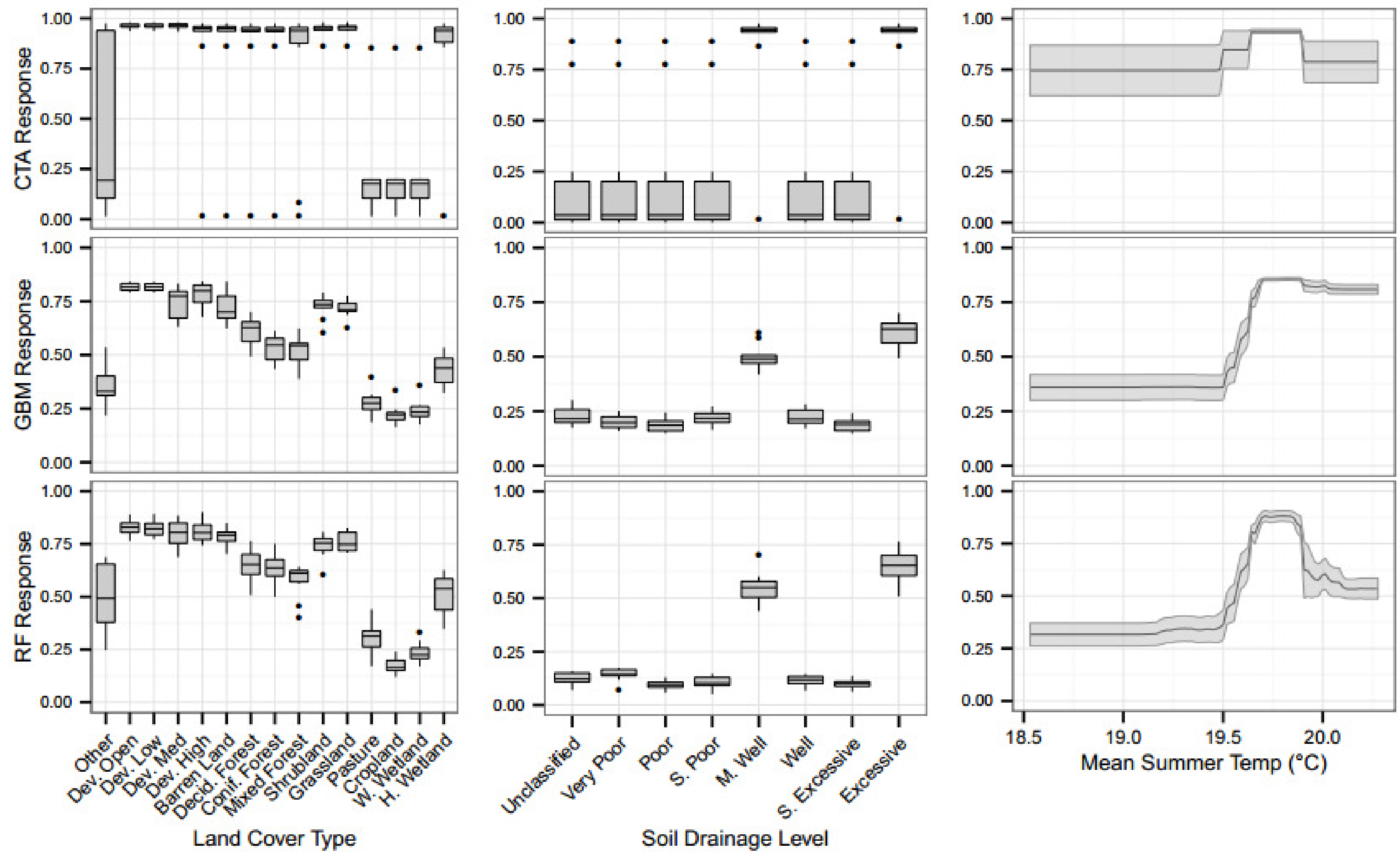

Figure 1. Response plots for land cover type and soil drainage level across the three best-performing wild lupine models: RF, GBM, and CTA (*n* = 10), ±1 standard deviation. The Y axis is a unitless measure of model response, where higher values indicate a higher association with the species of interest. For land cover, "Dev." indicates human development; "W. Wetland" and "H. Wetland" are woody and herbaceous wetlands, respectively. For soil drainage levels, "S." indicates "somewhat", and "M." indicates "moderately".

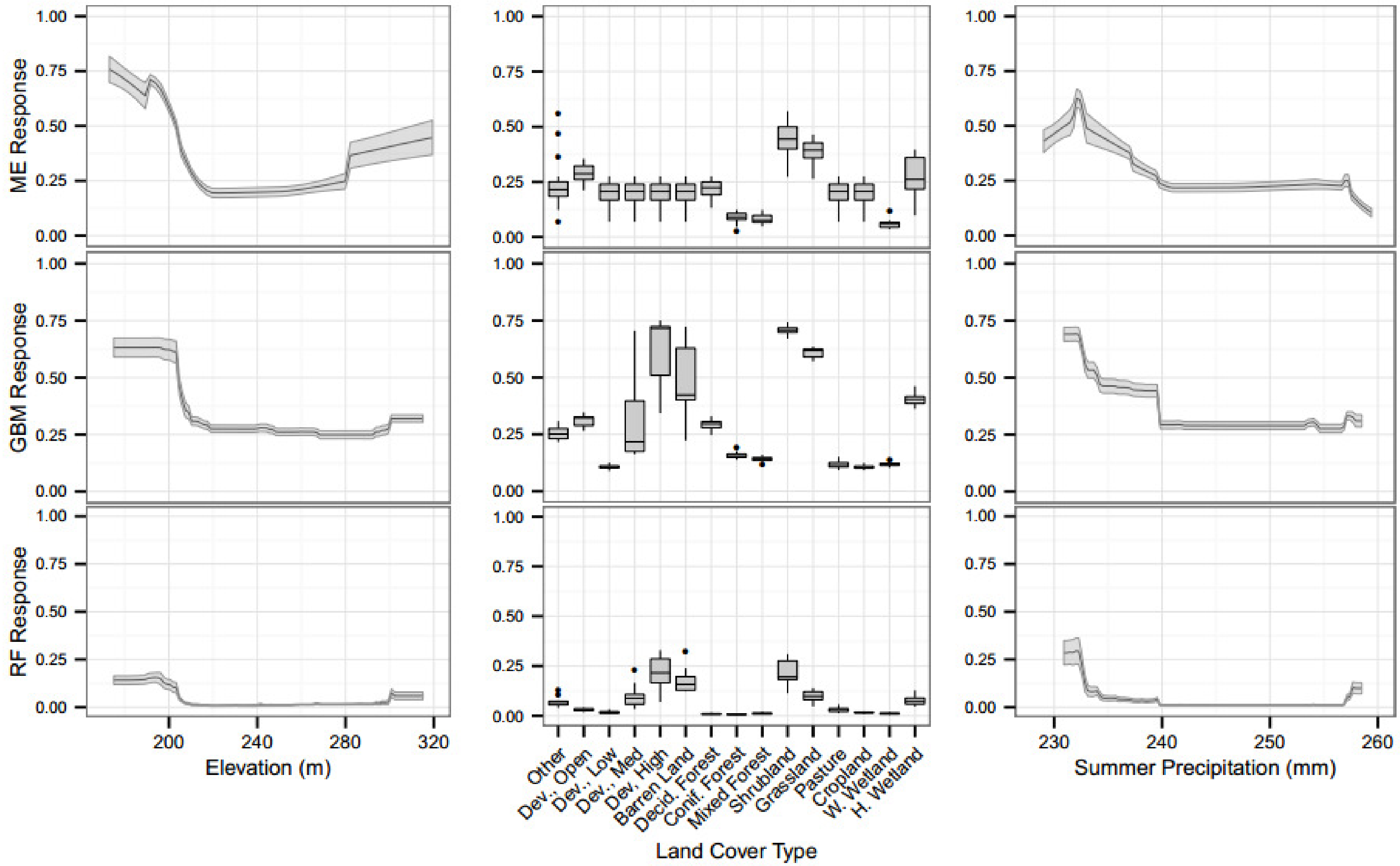

Figure 2. Response plots for elevation and land cover type across the three best-performing the Karner Blue models: RF, GBM, and MaxEnt (ME) (n = 10), ±1 standard deviation. The Y axis is a unitless measure of model response, where higher values indicate a higher association with the species of interest. For land cover, "Dev." indicates human development; "W. Wetland" and "H. Wetland" are woody and herbaceous wetlands, respectively.

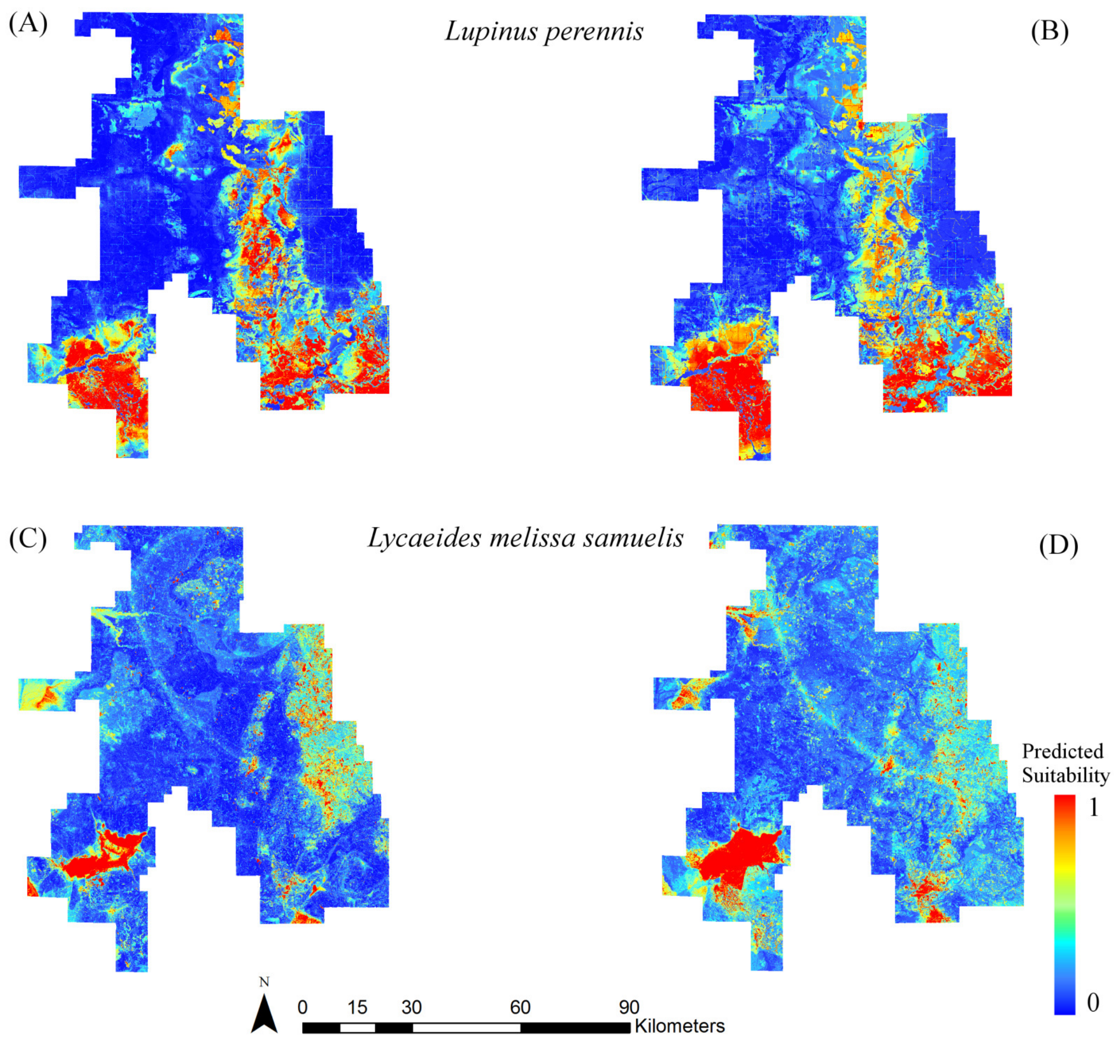

Figure 3. Predicted habitat suitability output of the RF (A, C) and GBM (B, D) models for wild lupine (*Lupinus perennis*) and the Karner Blue (*Lycaeides melissa samuelis*). Habitat suitability is represented by a normalized scale from unsuitable, 0 (dark blue) to highly suitable, 1 (red).

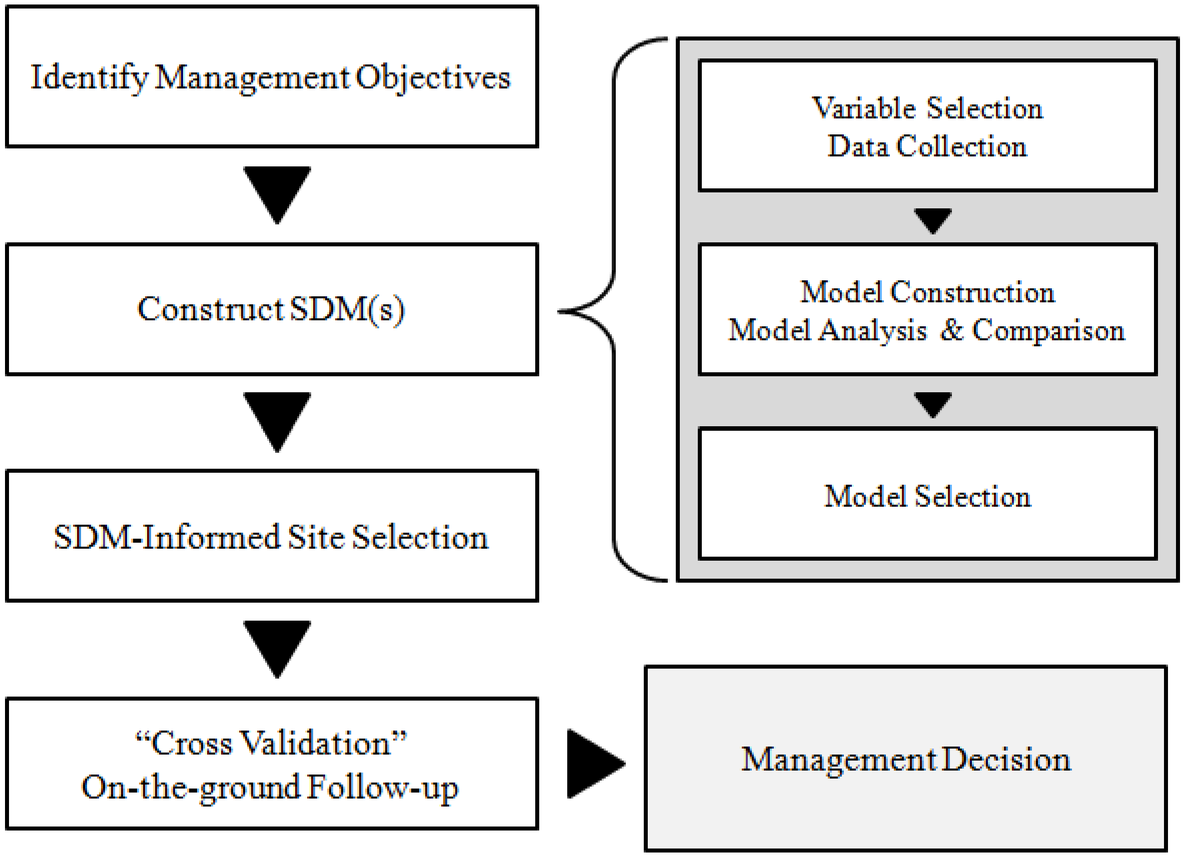

Figure 4. A generalized workflow for SDM-informed restoration site selection.

Chapter 4:

The variable impacts of climate change and simulated assisted migration on the distribution and accessibility of habitat for three rare butterflies in Michigan, USA

Introduction

Insects in general, and Lepidoptera specifically, are expected to have variable responses to climate change (Bale 2002, Parmesan 2006). Changes in climate can induce altered Lepidopteran behavior (Cormont et al. 2011), phenology (Roy and Sparks 2000), and ultimately geographic range (Sparks et al. 2007). Numerous studies have examined possible poleward shifts of butterfly populations (Batalden et al. 2007, Jepsen et al. 2007, Pelini et al. 2009) under climate change. Other studies (Parmesan 2005, Wilson et al. 2005) have revealed that several butterfly populations are climbing in elevation as a response to climate change. Despite these trends, however, different species are likely to have variable responses to climate change, and a few species may even benefit from warmer temperatures (Battisti et al. 2005, Crozier 2004, Williams and Liebhold 2002).

These variable responses to changes in climate conditions make it especially important to investigate the potential impacts of climate change on species that are of particular conservation concern or ecological importance (Hannah et al. 2002). In Michigan, USA, there are three rare butterflies often associated with early successional habitat: the Karner blue (*Lycaeides Melissa samuelis;* Nabokov), frosted elfin (*Callophrys iris;* Godart), and Persius duskywing (*Erynnis Persius;* Scudder). These three species are of conservation interest for both state and private conservation groups; they are all classified as threatened by the state of Michigan (MNFI 2007), and the Karner blue is federally endangered in the United States (USFWS 2003). In addition to its conservation concern, the Karner blue acts as an important indicator species for the management of the exceedingly rare (Nuzzo 1986) oak savanna and oak-pine barren ecosystems in Michigan (USFWS 2003). Here, we examine the potential impact of two different climate change scenarios on the distribution and accessibility of habitat for these three rare butterflies. The potential climate-driven change in the distribution of habitat for these butterflies has important implications for future conservation and management decisions.

SDMs are increasingly being used as tools to aid in planning and management decisions. SDMs model the relationship between species locations in space and environmental variables, producing a model of habitat suitability. This species-environment model can then be applied to geographic space, creating a habitat suitability map (Guisan and Thuiller 2005). These habitat suitability maps are useful in prioritizing conservation efforts or identifying new management areas (Guisan et al. 2013). In addition to computing SDMs, we also incorporated a dispersal model. Virtually all SDM approaches predict habitat suitability for the entire region of interest; in reality, species are often dispersal limited, and much of the potentially suitable habitat may not be realistically available to them in a given timeframe (Araujo and Guisan 2006, Midgley et al. 2007). In the context of conservation planning, then, it is oftentimes more useful to model not only habitat suitability, but also species dispersal over time.

Approaches that model both habitat suitability and species dispersal have the potential to be useful not only in terms of future conservation planning based on natural species response, but also in active management situations. Assisted migration (or managed relocation), the process of manually moving species to new locations (McLachlan et al. 2007), is a management tool currently being considered for a variety of different species in the context of a changing climate. While there is an ongoing and important debate regarding different approaches and the policies surrounding this issue in the literature (Hewitt et al. 2011, McLachlan et al. 2007), the continued existence of many rare or endangered species may depend on assisted migration (Hoegh-Guldberg 2008). Maps of habitat suitability produced by SDMs could be used to identify potential candidate sites for the assisted migration of these rare and endangered species. In addition, models that incorporate both changes in habitat suitability over time and species dispersal ability offer a method to assess the potential effectiveness of different assisted migration sites and strategies.

To examine the potential impact of climate change on the distribution of habitat for these species, we used species distribution models (SDMs) in conjunction with a dispersal model based on cellular automation. We employed this approach with the objective of learning more about the potential impact of climate change on the survival and future distribution of the Karner Blue, frosted elfin, and Persius duskywing. The goals of this study were to: 1) examine the potential impacts of two different climate change scenarios on the distribution of suitable habitat for the three butterfly species of interest, 2) determine the driving factors behind any changes in the distribution of habitat, and 3) investigate the potential effectiveness of assisted migration in increasing the amount of accessible habitat for each of the three species of interest.

Methods

Study System

This study was conducted within the state of Michigan, USA. The state has a mixture of agriculture and urban centers in the south and forest cover in the north. Soils in the state vary widely, with many being glacial in origin; upland soils typically range from sandy loam to sand. The state has a humid continental climate (Köppen climate classification Dfb; Peel et al. 2007), heavily influenced by the Great Lakes.

The three study species, the Karner blue butterfly, frosted elfin, and Persius duskywing, are rare butterflies of conservation concern. The Karner blue is federally-endangered in the US and extirpated from Canada, while the frosted elfin and Persius duskywing are both endangered in the state of Michigan. Broadly, all three species are associated with early-successional habitat, especially the oak savanna and oak-pine barrens that were historically fairly common in southern and western Michigan (Albert and Comer 2008).

Suitability Models

We constructed a series of species distribution models (SDMs) to quantify habitat suitability for the three butterfly species across the landscape. Because predictions can vary between modeling approaches, we used both a random forest (RF) and generalized boosted regression model (GBM) approach to construct the SDMs. Both RF and GBM are known to perform relatively well, especially when true absences are not available (Barbet-Massin et al. 2012). For RF models, the number of variables to test at each split ('mtry') was set to the square root of the number of predictors (Cutler et al. 2007). For both RF and GBM models, 5000 trees were computed in each run. All SDMs were constructed using the BIOMOD framework in R v3.1.0 (Thuiller et al. 2009).

Models were constructed using the centroids of butterfly populations surveyed between 1990 and 2014, with a total of 145 Karner blue populations, 44 frosted elfin populations, and 38 Persius duskywing populations. These locational data were obtained from the US Forest Service (USFS) and the Michigan Natural Features Inventory (MNFI 2014). Our data were obtained largely from monitoring efforts, so species absence data were unavailable. Since SDMs require both presence and absence data, we used a series of pseudo-absences generated according to the suggestions of Barbet-Massin *et al.* (2012): for all three species, we generated 10 separate runs of pseudo-absences using a minimum distance-based approach, creating 100 pseudo-absences for the frosted elfin and Persius duskwing, and an equivalent number of pseudo absences as presences for the Karner blue. Following the suggestions of Barbet-Massin *et al.* (2012), pseudo-absences were generated only in areas at least 15 km away from a known presence location.

Response variables used to construct the models included elevation, soil taxonomic order, soil drainage classification, current land cover, and climate data based on 30-year (1981-2010) normals: mean, maximum, and minimum annual and seasonal temperatures and precipitation. All predictor variables were either obtained at or resampled to an 800-m² spatial resolution (Table A2.1). A preliminary set of models were constructed using all variables. From these preliminary models, the final subset of predictor variables were selected based on their normalized variable importance scores; variables with nonzero normalized importance scores were included in the final models. Ten runs were performed for each set of 10 pseudo absences, for a total of 100 runs per model.

To determine how the distribution and amount of suitable habitat might be impacted by climate change, we projected these SDMs into the future using a series of time points for two climate change models: the Parallel Climate Model (PCM), and the Geophysical Fluid Dynamics Laboratory (GFDL) model. We used PCM in conjunction with the B1 emissions projections (IPCC 2007) as a low-severity climate change scenario and GFDL with the A1FI emissions projections (IPCC 2007) as a high-severity climate change scenario. Given the year-to-year uncertainty inherent in climate models, we used the yearly seasonal means of three multi-decadal periods in our modeling efforts: 2010-2039, 2040-2069, and 2070-2099. Climatic variables considered include mean, maximum, and minimum annual and seasonal temperatures and precipitation. Climate models were downscaled by the US Forest Service Northern Institute of Applied Climate Science (Handler et al. 2014), following Stoner et al. (2013). Mean SDM results were used to make these future projections, and 10 projections were computed for each climate change scenario and time period.

Dispersal Models

Not all of the habitat identified as suitable by SDMs may be accessible by the species of interest. To determine how much of the total predicted suitable habitat is actually accessible by the butterfly species, we used a dispersal model based on cellular automation (Hogeweg 1988). The MigClim package in R (Engler et al. 2012) was used to model the maximum possible area of dispersal for each butterfly species. For these three butterfly species, we used a dispersal kernel and a negative exponential dispersal pattern with an upper limit of 2.4 km dispersal from an occupied or potentially occupied pixel. The average and maximum dispersal distances generated by this function are in line with what others have found in the literature for the two Lycaenid butterflies (King 1995, Knutson et al. 1999), but no published dispersal data exists for the Persius duskywing. Given its similar size and habit, we made the assumption that its dispersal abilities would be roughly similar to the other two species. To standardize predictions, BIOMOD reports predicted habitat suitability on a unitless scale of 0 to 1000 for all modeling approaches. We used a habitat suitability threshold to classify habitat as either suitable or unsuitable. Typically, a value of 500 (or 0.5 on a 0-1 scale) is used to separate suitable from unsuitable habitat (Hirzel et al. 2006). To simulate an optimistic colonization scenario, however, we considered only pixels with a suitability value in the upper two-thirds (> 333) of the suitability range as suitable for colonization. Simulated dispersal events were set to run every year, for a total of 29 dispersal events per set of climate projections (2010-2039, 2040-2069, 2070-2199). This cellular automation-based dispersal simulation represents the maximum possible area physically accessible by the species through time, not the total area the species is projected to occupy. The species are likely to colonize only a few scattered sites, but each of those colonized sites will be able to colonize additional sites further away, and so on -- this is the principle behind the dispersal kernel used by MigClim (Engler et al. 2012). We ran the dispersal model using the species' initial (current) distributions to determine whether the species could persist on the landscape in the face of a changing climate, given an optimal migration/colonization scenario.

This approach was also used to simulate the potential effectiveness of assisted migration in terms of dispersal and habitat accessibility. Two arbitrary hypothetical assisted migration scenarios, 'low' and 'high' effort, were used. Low effort assisted migration involved the creation and establishment of three new butterfly populations in lower Michigan, < 50 km from currently occupied sites, while high effort involved the establishment of three additional populations (six total) across Michigan (including three > 50 km from currently occupied sites). The assisted migration sites were chosen within the specified regions by randomly selecting (ArcGIS 10.1, 'Random Points' function) sites ranked as suitable (suitability values > 333) for both SDMs (RF and GBM) and climate models (GFDL and PCM) in the 2039 time point located on either state or federal land. Separate sets of assisted migration sites were selected for each species. These assisted migration sites were then separately added to the initial distribution of each species. This allowed us to run separate dispersal models to enable the comparison of accessible habitat between models incorporating current distribution, low, and high assisted migration scenarios for each species. Ten runs were performed for each dispersal model.

Analysis

Model performance was evaluated using 10-fold cross validation and two commonly-used model evaluation metrics: the true skill statistic (TSS) and the area under the receiver operating characteristic curve (AUC), both of which are based on the model error matrix (Allouche et al. 2006, Jiménez-Valverde 2012, Franklin 2009). Relative variable importance was evaluated by considering each variable independently and shuffling the data. Shuffled data is correlated with the model reference predictions, and gives a variable importance score (Thuiller et al. 2009). Variable importance scores were normalized to allow between-model comparisons.

To determine the relative effects of different climate change scenarios on the amount of 1) total, and 2) accessible suitable habitat for each species, we performed an analysis of variance on a linear model, with suitable habitat (km^2) as the response variable, and butterfly species, climate scenario, and the interaction between the two as predictors. For both total and accessible habitat, two separate linear models were constructed, one for each SDM approach (RF and GBM). Analysis of variance was also used to evaluate the potential effects of assisted migration on the amount of accessible habitat. Accessible habitat (km^2) was used as the response variable, while species, climate scenario, assisted migration scenario, and their two and three-way interactions were used as predictor variables. Again, separate models were constructed for RF and GBM. All analyses were carried out using R v3.2.1 (R Core Team 2015).

Results

General

The Karner blue and frosted elfin SDMs performed well (mean TSS > 0.85, AUC > 0.9) with low within-model variation, suggesting relatively stable predictions. The Persius duskywing models performed moderately well (mean TSS > 0.65, AUC > 0.8) (Table 1). For the Karner blue and frosted elfin, seven variables were included in the model based on preliminary analyses, while the Persius duskywing used five. Across all three species, average spring precipitation was consistently an important predictor of habitat suitability (Table 2); habitat suitability generally increased across species as spring precipitation increased, especially with amounts over 220 mm (Figure A3.2). In terms of non-climatic variables, both soil order and current land cover were included in all models (Table 2). Entisols were the soil type most consistently associated with suitable habitat for all three species, followed by Inceptisols and Spodosols (Figure A3.2). For the frosted elfin, evergreen and deciduous forest were the most important cover types, while forest, woody wetlands, and open water were associated with suitable habitat for the Persius duskywing (Figure A3.2).

Changes in total suitable habitat

Climate change scenario (GFDL A1FI vs. PCM B1) had a significant effect on the total amount of suitable habitat at the end of the century for each species (RF: $p < 0.001$, $F_{1,54} = 5091.593$; GBM: $p < 0.001$, $F_{1,54} = 583.7$), with the GFDL A1FI projections having more predicted suitable habitat than PCM B1 across species and modeling approaches (Table 3). In addition, each of the three species are projected to respond differently in the context of climate change (RF: $p < 0.001$, $F_{2,54} = 465.688$; GBM: $p < 0.001$, $F_{2,54} = 229.79$) (Table 3, Figure A1). It is important to note, however, that the distribution of suitable habitat varies between climate models. For the Karner blue and frosted elfin, much of the end of century suitable habitat in the GFDL A1FI scenario is located in Michigan's upper peninsula (Table 3, Figure 1), which is quite far (> 200 km) from these species' current distributions, and separated from the lower peninsula by several kilometers of open water.

Changes in accessible habitat

In addition to the total amount of suitable habitat in Michigan, we found significant differences between species in terms of the amount of suitable habitat physically accessible via dispersal (RF: $p < 0.001$, $F_{2,54} = 1.0e4$; GBM: $p < 0.001$, $F_{2,54} = 6909.06$) (Table 4). In the GFDL climate change scenario, the Karner blue and frosted elfin are projected to have little to no accessible habitat by the end of the century (Table 4). The Karner blue is expected to have significantly more accessible habitat under the PCM scenario, though the frosted elfin is still projected to have low amounts of accessible habitat, especially as predicted by the GBM models (Table 4). The Persius duskywing is projected to have a fairly large (> 10,000 km^2) amount of accessible habitat by the end of the century in the GFDL climate scenario, with considerably less under the PCM scenario (Table 4), suggesting that this species may respond somewhat favorably to a warmer climate. Overall, climate change scenario had a significant effect on the amount of accessible habitat for these species under both the GBM models ($p < 0.001$, $F_{1,54} = 917.37$) and the RF models ($p < 0.001$, $F_{1,54} = 1585.01$).

Effect of Assisted Migration on accessibility

Simulated assisted migration scenario had a significant effect (RF: $p > 0.001$, $F_{2,108} = 1.5e4$; GBM: $p > 0.001$, $F_{2,108} = 7038.028$) on the amount of physically accessible habitat available for each species, though the relative effectiveness of assisted migration varied between species and climate change scenarios (species × climate change × assisted migration interaction; RF: $p > 0.001$, $F_{4,108} = 335.58$; GBM: $p > 0.001$, $F_{4,108} = 311.451$) (Table 4). In the RF models, the simulated assisted migration was effective at greatly increasing the amount of accessible habitat for the Karner blue in the GFDL A1FI climate scenario (Table 4). For example, the high effort assisted migration scenario was able to increase the amount of accessible habitat from zero to over 7,000 km^2 in northern Lower Michigan and the Upper Peninsula (Figure 2, Table 4). Low effort assisted migration was only marginally effective in the PCM B1 climate scenario. The frosted elfin simulated assisted migration efforts were effective at increasing the amount of accessible habitat under both climate scenarios (Table 4). For the GBM models, assisted migration was effective at increasing the amount of accessible habitat for the Karner blue and frosted elfin under the GFDL A1FI climate scenario, but was less effective for the PCM B1 scenario (Table 4). For both the RF and GBM models, assisted migration was effective at increasing the amount of accessible habitat for the Persius duskywing, but the species is projected to have relatively high amounts of accessible habitat even without assisted migration (Table 4, Table 3).

Discussion

Parameter results

Climatic variables were significantly more important for the Karner blue than nonclimatic variables, while both climatic and nonclimatic factors seemed to be equally important for both the frosted elfin and Persius duskywing (Table 2). Interestingly, average spring precipitation was by far the most important variable for all three butterfly species (Table 2). This may be due in part to the fact that all three butterfly species share the same obligate larval host plant: wild lupine (*Lupinus perennis* L.). When wild lupine becomes water-stressed, nutritional quality decreases, and this has been demonstrated to have a negative impact on larval growth in Karner blue butterflies (Grundel *et al.* 1998). Additionally, water is an important driver of host plant quality for herbivorous insects in general (Strong et al. 1984, Sagers 1992) and Lepidoptera more specifically (e.g., Scriber 1977). Plant community composition and therefore nectar plant availability and identity for adult butterflies can change along precipitation gradients (Gentry 1988). Fall precipitation was important for all three species as well, though to a much lesser extent (Table 2).

Temperature variables, especially mean summer temperature, were important for the Karner blue and frosted elfin (Table 2). Generally, lower average temperatures (especially < 20 °C) were more associated with suitable habitat (Figure A3.2). This can likely be attributed to the potential for water stress in wild lupine and other herbaceous nectar sources (Grundel et al. 1998), as well as more general changes in plant community composition across the temperature gradient (Gentry 1988, Woodward 1988). The lack of temperature variables in the Persius duskywing models was notable, and may either reflect its broad but fragmented distribution (Shepherd 2005), or the relatively small available sample size of butterfly populations (n=38).

Nonclimatic factors, especially land cover and soil order, were important for the frosted elfin and Persius duskywing (Table 2). Both species were positively associated with evergreen and deciduous forests, as well as more open cover types, especially human development (Figure A3.2). The Persius duskywing also had a positive association with both woody wetlands and open water; this, in conjunction with higher model response for poorly drained soils (Figure A3.2), suggests that it may be able to colonize wetter sites than either of the other two species. The preference of all three species for Entisols, Inceptisols, and Spodosols is unsurprising, given that their shared host plant, wild lupine, is commonly associated with well drained sandy soils (Meyer 2006).

Implications

Climate change scenario had an impact on the total amount of suitable habitat for all three species. The total land area of predicted suitable habitat was higher for the GFDL A1FI scenario than PCM B1 for every species and model (Table 3). However, most of the habitat in the GFDL A1FI climate scenario was distributed in the upper peninsula of Michigan, which is quite far away from the current distribution of these species. Conversely, suitable habitat in the PCM B1 climate scenario was largely distributed in the Lower Peninsula. The GFDL A1FI scenario represents a much larger shift in climate conditions than the PCM B1 scenario, so it is not unexpected to see such a large difference between the two in terms of climatically-suitable habitat distribution. In this context, the low amount of predicted suitable habitat located in the Lower Peninsula for the Karner blue (RF model) and frosted elfin (GBM model) under the GFDL A1FI climate scenario is concerning (Table 3). The only remaining suitable habitat in the Lower Peninsula for these models is located at the very tip, far from the current distributions of these two species (Figures 1 and A1). This suggests a risk of extirpation under a fossil-fuel intensive climate future. Under the PCM B1 climate scenario, however, these two species are projected to do significantly better (Table 3).

In contrast to the frosted elfin and Karner blue, our results suggest that the Persius duskywing is expected to have a relatively large amount of accessible habitat in a warmer climate, especially under the GFDL A1FI scenario. There is, however, a concerningly low amount of predicted suitable habitat for the RF PCM B1 model (< 5000 km²). This may be due to differences in variable weightings (Table 2) and variable responses between the two modeling approaches; the RF models illustrate a stronger model response for high amounts (> 250mm) of spring and fall precipitation, while the GBM models have a stronger response for soil order (Figure A3.2).

While the distribution of suitable habitat for each species is projected to shift along with the climate, the species itself may be restricted in how fast it can respond and how far it can disperse. In the case of the frosted elfin, there was little to no physically accessible habitat available by the end of the century; the exception being 3,586 ± 141 km² (in the Lower Peninsula) under the RF PCM B1 model (Tables 3 and 4, Figure A3.3). According to these results, without management or assisted migration efforts, the frosted elfin has the possibility of being extirpated from Michigan by the end of the century (Figure 2, Table 4). The Karner blue is projected to have marginally more accessible habitat under a low emissions climate future, with over 9,000 km² accessible habitat under both the RF and GBM PCM B1 scenarios. Under the GFDL A1FI scenarios, however, the Karner blue may also be at risk of being extirpated (Table 4, Figure A3.3). The Persius duskywing, in contrast, is predicted to have a relatively large amount of accessible habitat, with over 10,000 km of accessible habitat for every model except RF PCM B1 (Table 4).

The simulated assisted migration efforts had varying levels of effectiveness. For the Karner blue, the high effort assisted migration scenario was able to greatly increase the predicted accessible habitat in the GFDL A1FI climate models (Table 4, Figure 2). If keeping the Karner blue on the landscape into the future is a management goal, assisted migration may be a necessity, given these results. In the case of the frosted elfin, the simulated assisted migration was moderately effective. For both GFDL A1FI models, high effort assisted migration was effective at increasing predicted accessible habitat. Conversely, accessible habitat remained low in the GBM PCM B1 scenario despite our simulated assisted migration efforts (Table 4). The assisted migration simulations were mostly effective for the Persius duskywing, especially for the GFDL A1FI climate models, but may be unnecessary; even without assisted migration, the Persius duskywing is projected to have a relatively large amount of accessible habitat available by the end of the century (Table 4).

The predictions made here, especially the simulated assisted migration results, are very broad. A cellular automation distribution model is broad by definition, and the spatial scale being considered (800 m^2 resolution) precludes the consideration of other factors known to be important to butterfly dispersal and population persistence, such as metapopulation dynamics and fine-scale habitat requirements (e.g., canopy heterogeneity, specific species compositions). Instead, the predictions made here should be taken as a maximum possible dispersal distance under optimal conditions. The actual dispersal distances of these butterflies is likely to be lower without human intervention, especially in the upper peninsula of Michigan where the obligate larval host plant of these three species, wild lupine (*Lupinus perennis* L.), is currently very rare or absent in many locations. In addition, land cover type, one of the more consistent predictors in this study, was held static. In reality, land cover is likely to change significantly over the next century due to forest dynamics and human activity (e.g., urbanization, agriculture). This variability could be built into future modeling exercises.

Conclusions

Based on our results, the Michigan populations of frosted elfin and Karner blue butterflies appear vulnerable to high-emissions (GFDL A1FI) climate change scenarios. In such a climate future, these two species are likely to be extirpated from Michigan without assisted migration efforts or other active management strategies, as we demonstrate here. Under a more tempered climate scenario (PCM B1), however, the Karner blue and frosted elfin are predicted to maintain approximately the same distribution they have today. The Persius duskywing is predicted to be at moderate risk under our RF PCM B1 climate change scenario; in all other climate change scenarios, including high-emissions scenarios, it is expected to perform quite well. In terms of defining and quantifying habitat suitability, average spring precipitation (and to a lesser extent, mean summer temperature) should be an important climatic factor to consider when managing for these three species in the future, given its strong importance in our models.

Finally, in a management context, these types of coarse-scale models can be beneficial in long-term conservation planning and evaluation, but should be followed up with fine-scale models or assessments. Our results, and results from similar modeling efforts, are most useful as broad long-term planning aids, and should be recalculated as newer and better data becomes available.

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Tables and Figures

Table 1. Model evaluation metrics. Mean ± 1 standard deviation (n=10 nested sets of 10). RF: Random Forest, GBM: Generalized Boosted Regression Model. TSS, the true skill statistic, and AUC, the area under the receiver operating characteristic curve, are two common model evaluation metrics based on the model error matrix (Franklin 2009).

	Karner Blue		Frosted Elfin		Persius Duskywing	
	RF	GBM	RF	GBM	RF	GBM
TSS	0.953 ± 0.004	0.950 ± 0.009	0.862 ± 0.009	0.879 ± 0.007	0.670 ± 0.010	0.685 ± 0.008
AUC	0.992 ± 0.002	0.994 ± 0.003	0.948 ± 0.003	0.957 ± 0.001	0.821 ± 0.011	0.844 ± 0.011

Table 2. Mean normalized variable importance scores ± 1 standard deviation (n=10 nested sets of 10). RF: Random Forest, GBM: Generalized Boosted Regression Model.

	Karner Blue		Frosted Elfin		Persius Duskywing	
	RF	GBM	RF	GBM	RF	GBM
Soil Order	0.017 ± 0.002	0.01 ± 0.002	0.089 ± 0.004	0.08 ± 0.003	0.173 ± 0.011	0.239 ± 0.006
Soil Drainage Class	—	—	—	—	0.061 ± 0.003	0.03 ± 0.003
Land Cover Class	0.009 ± 0.001	0.006 ± 0.001	0.128 ± 0.004	0.082 ± 0.003	0.118 ± 0.007	0.146 ± 0.002
Mean Summer Temp.	0.074 ± 0.002	0.058 ± 0.005	0.167 ± 0.004	0.153 ± 0.007	—	—
Mean Spring Temp.	0.04 ± 0.003	0.003 ± 0.001	0.133 ± 0.006	0.015 ± 0.002	—	—
Mean Ann. Daily Max Temp	0.03 ± 0.002	0.001 ± 0.001	—	—	—	—
Mean Winter Prcp.	—	—	0.012 ± 0.001	0.017 ± 0.002	—	—
Mean Spring Prcp.	0.555 ± 0.018	0.885 ± 0.054	0.3 ± 0.004	0.608 ± 0.025	0.442 ± 0.01	0.463 ± 0.001
Mean Fall Prcp.	0.275 ± 0.007	0.037 ± 0.002	0.17 ± 0.011	0.045 ± 0.002	0.205 ± 0.005	0.122 ± 0.001

Table 3. Mean (±1 SD) area of end-of-century (~2100) suitable habitat for each species, across SDM approach and climate model (n=120). RF: Random Forest, GBM: Generalized Boosted Regression Model. The GFDL model represents a high-warming climate future (high emissions [A1FI], high model sensitivity), while the PCM model represents a lower warming future (lower emissions [B1], lower model sensitivity).

	SDM	Climate Model	Total Suitable Habitat (km²)	Suitable Habitat: Lower Peninsula (km²)	Suitable Habtiat: Upper Peninsula (km²)
Karner Blue	RF	GFDL	48961 ± 2749	1438 ± 81	47244 ± 2668
		PCM	15847 ± 785	15496 ± 770	304 ± 15
	GBM	GFDL	68027 ± 5627	13409 ± 1120	53976 ± 4507
		PCM	50940 ± 4355	30248 ± 2702	18497 ± 1653
Frosted Elfin	RF	GFDL	36823 ± 1616	11452 ± 502	25393 ± 1114
		PCM	16434 ± 895	11186 ± 598	5567 ± 297
	GBM	GFDL	46808 ± 5181	5136 ± 533	44798 ± 4648
		PCM	32064 ± 3126	19074 ± 1923	11933 ± 1203
Persius Duskywing	RF	GFDL	63175 ± 3628	30591 ± 1786	31547 ± 1842
		PCM	4261 ± 274	3894 ± 253	320 ± 21
	GBM	GFDL	128782 ± 13786	87283 ± 9121	44636 ± 4665
		PCM	32525 ± 1946	30450 ± 1724	3930 ± 222

Table 4. Mean (±1 SD) area of end-of-century (~2100) accessible habitat for each species, across SDM approach, climate model, and simulated assisted migration scenario (n=120). RF: Random Forest, GBM: Generalized Boosted Regression Model. In the "Low" scenario, three assisted migration sites were selected within 50km of pre-existing populations; in the "High" scenario, the sites in the "Low" scenario were used in combination with three additional sites >50km from pre-existing populations. The GFDL model represents a high-warming climate future (high emissions [A1FI], high model sensitivity), while the PCM model represents a lower warming future (lower emissions [B1], lower model sensitivity).

			Assisted Migration Scenario: Accessible Habitat (km²)		
	SDM	Climate Model	None	Low	High
Karner Blue	RF	GFDL	0	0	7208 ± 174
		PCM	9213 ± 100	11030 ± 30	11118 ± 24
	GBM	GFDL	1162 ± 9	1719 ± 13	25016 ± 229
		PCM	12408 ± 758	12005 ± 165	11917 ± 161
Frosted Elfin	RF	GFDL	0	20 ± 0	7460 ± 160
		PCM	3586 ± 141	6367 ± 159	6568 ± 29
	GBM	GFDL	3 ± 1	447 ± 95	22129 ± 144
		PCM	6 ± 0	950 ± 307	1929 ± 432
Persius Duskywing	RF	GFDL	11511 ± 149	11623 ± 19	15073 ± 91
		PCM	2157 ± 15	2665 ± 43	2481 ± 251
	GBM	GFDL	42323 ± 534	47023 ± 655	58151 ± 207
		PCM	12910 ± 1235	12286 ± 632	16224 ± 509

Figure 1. Maps (Current and 2039) illustrating the effect of climate change (GFDL, A1FI emissions scenario) on the mean distribution of suitable habitat for the Frosted Elfin. Between model differences (RF vs. GBM) are illustrated. Habitat suitability is reported on a unitless scale ranging from 0 to 1000; gray colors (closer to 0) represent unsuitable habitat, while darker green represents more suitable habitat. In this study, we considered suitability values ≥333 (i.e., the upper 66% of values) to be colonizable by the species. Figure continued on next page. Of particular note here is the loss of suitable habitat in the Lower Peninsula and gain in the Upper Peninsula by the end of the century. (continued on next page)

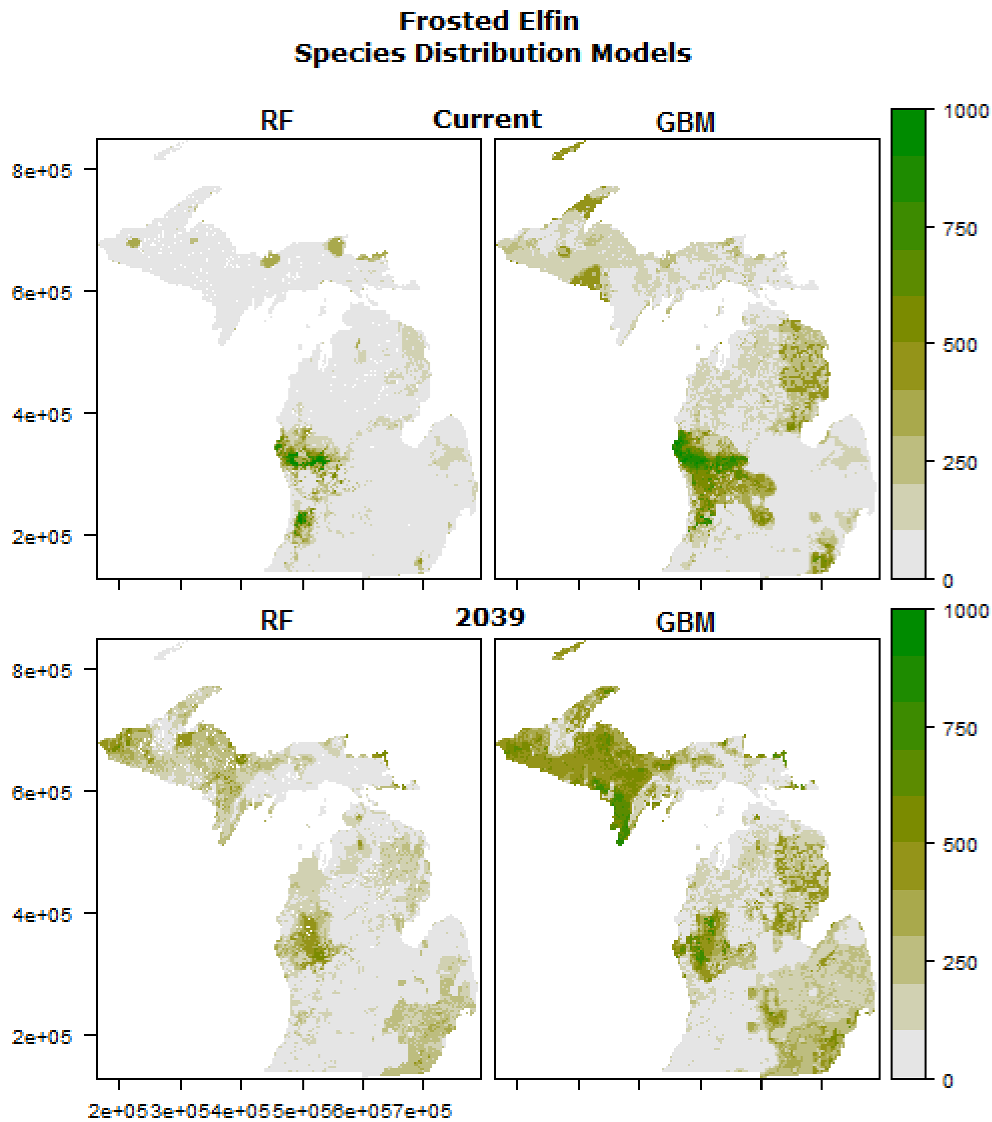


Figure 1 cont'd. 2069 and 2099. Maps illustrating the effect of climate change (GFDL, A1FI emissions scenario) on the distribution of suitable habitat for the Frosted Elfin. Between model differences (RF vs. GBM) are illustrated. Habitat suitability is reported on a unitless scale ranging from 0 to 1000; gray colors (closer to 0) represent unsuitable habitat, while darker green represents more suitable habitat. In this study, we considered suitability values ≥333 (i.e., the upper 66% of values) to be colonizable by the species. Of particular note here is the loss of suitable habitat in the Lower Peninsula and gain in the Upper Peninsula by the end of the century.

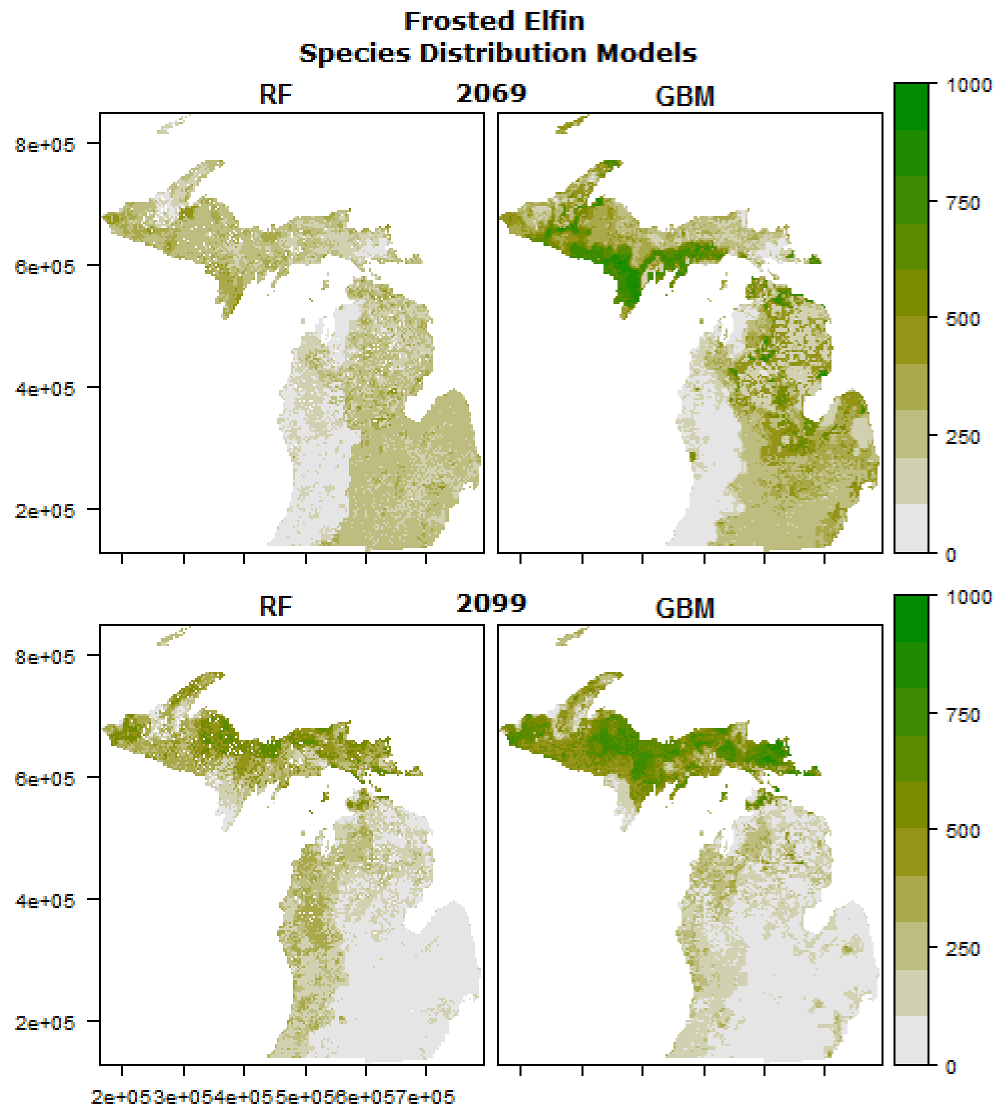
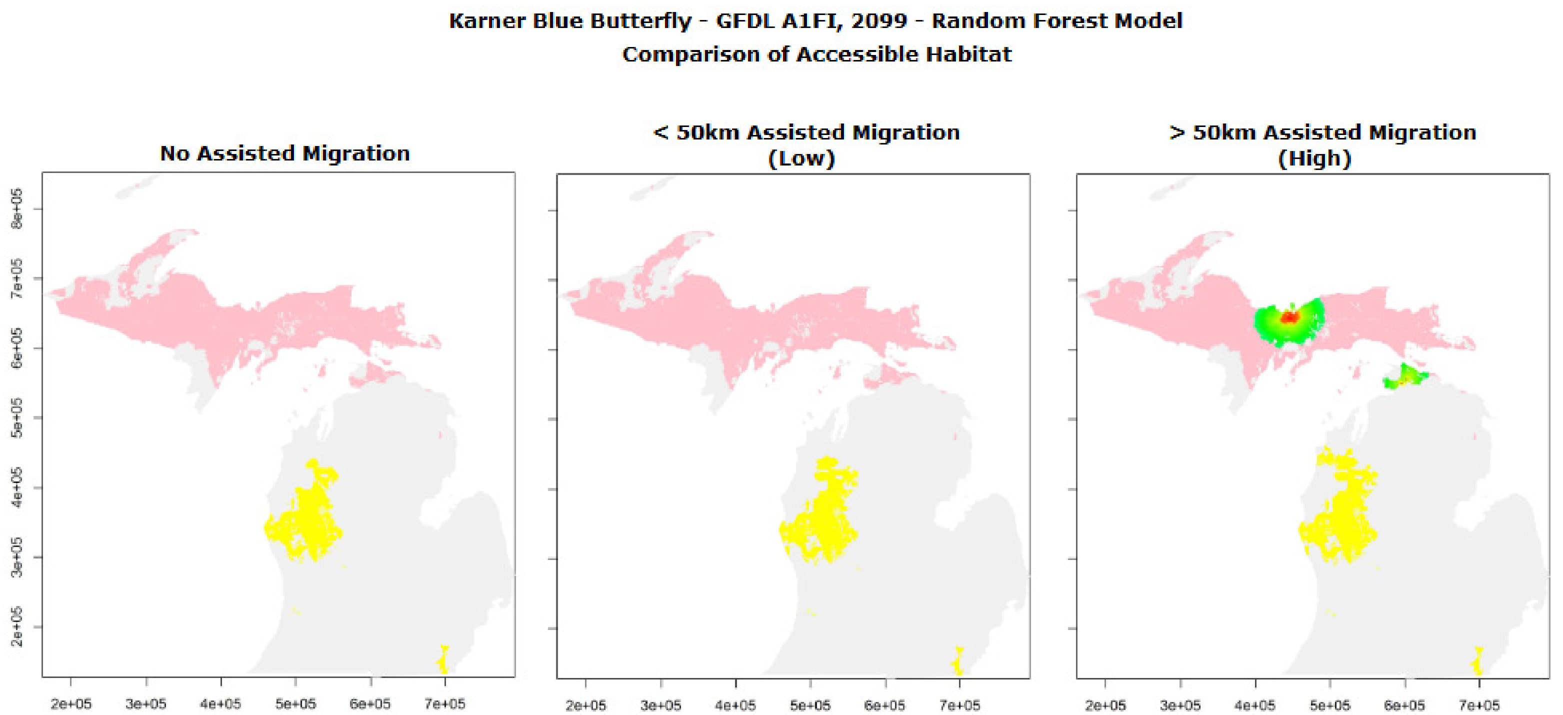


Figure 2. Maps illustrating the mean distribution of predicted suitable habitat that is projected to be physically accessible by the Karner Blue butterfly at the end of the century. The green to red color gradient signifies accessible habitat for the species, with red areas being colonized earlier in the century and green areas being colonized toward the end of the century. Gray represents areas considered unsuitable for colonization (habitat suitability values < 333), pink represents suitable habitat not accessible by the species, and pale yellow represents formerly accessible habitat lost due to changes in habitat suitability over time (i.e., climate change).



CONCLUSIONS

Results, Implications, and Context

Ecological restoration of rare ecosystems like oak savannas can be challenging, especially when there is little historical information to use as a reference (Asbjornsen et al. 2005). The tasks of defining desired future conditions, choosing management strategies, and selecting sites become difficult amid a lack of information. In this context, the main objectives of this work were to: 1) examine the impacts of disturbance intensity and management strategy on oak savanna community composition and structure, 2) identify potential areas for oak savanna restoration and management using the Karner Blue and other rare butterflies as focal species, and 3) given the threatened status and conservation interest in these butterflies, to identify the most important factors in defining suitable habitat for each species, and determine the impact of climate change on the distribution of both suitable and physically accessible butterfly habitat by the end of the century. The results of this work have the potential to be useful for the management of Michigan oak savannas, but also more broadly in oak savanna systems across the Midwestern United States and Canada. Finally, this work underscores areas that demonstrate the need for additional study, particularly in understanding the impact of different management approaches on soil characteristics, indicator species, and oak regeneration, and in further exploring the importance of dispersal in the future management of rare butterfly populations.

Disturbance is known to have a significant impact on plant communities (Denslow 1980, Tilman 1988). The results presented here (in chapters one and two) suggest that disturbance frequency can have a significant impact on oak savanna plant communities, even on sites that are classified as the same community type. Understanding how disturbance can affect Michigan oak savanna communities is important because these systems rely heavily on disturbance to maintain their composition and structure (Sankaran et al. 2004, Anderson 2007). Results from the first chapter indicate that plant community composition is quantifiably different between sites of varying disturbance frequency. Despite these apparent differences in communit composition, however, there were no significant differences in biodiversity as measured by species accumulation curves or Simpson's diversity index between site types.

Results from the second chapter reflect the influence of disturbance on the structure of these communities; there were a number of differences in plant cover types between the different mechanical harvesting approaches and between the burned and unburned management areas. Using either a masticator or shear cutter to harvest sites for savanna restoration was effective at meeting local management goals when used in conjunction with prescribed burning. Without fire, however, the masticator treatment was ineffective at restricting woody plant regeneration, while the shear cutter treatment had relatively low levels of woody plant cover.

Disturbance is important in defining plant communities because it can have both direct (e.g., mortality) and indirect (e.g., altered site conditions) impacts on community composition and structure (Denslow 1980, Tilman 1988, McIntyre et al. 1999). In the second chapter, the difference between the two management areas in the 2014 data illustrates the direct impact of disturbance (in this case, fire) on community structure.

Fire resulted in the direct mortality of a large amount of woody cover (a direct effect), which allowed the establishment of new herbaceous cover (an indirect effect) (Chapter 2). Additional indirect impacts of disturbance can be seen in both chapters one and two, where varying levels of disturbance had an influence on site conditions. In the first chapter, both managed and heavily disturbed sites had higher canopy cover, soil pH, and lower C:N content than recently abandoned sites (Chapter 1). In addition, managed sites had slightly thicker soil A horizons than either abandoned or heavily disturbed sites (Chapter 1). In the second chapter, bulldozed and shear cut treatments had lower canopy cover than the masticator treatment and control (Chapter 2). The amount of exposed soil also differed between treatments, especially near the beginning of the experiment where bulldozed sites had 30-45% bare soil, and between the burned and unburned management areas where fire significantly increased the amount of bare soil at all mechanical treatments in 2014 at the PPRA (Chapter 2).

Ultimately, these direct and indirect impacts of disturbance play a large role in shaping the composition and structure of the plant community. Direct impacts, such as mortality from fire or mechanical harvesting, alter population *in situ* demography and therefore competition dynamics. Indirect impacts, such as an increase in exposed soil, can change how the site acts as an environmental sieve for the regional species pool, ultimately impacting community composition (*sensu* Zobel et al. 1998). Because oak savanna systems are so dependent on disturbance, it is important from a management perspective to recognize the extent to which these factors affect the plant community.

Even moderate differences in management approach (e.g., masticating vs. shear cutting) can have divergent effects on community structure (Chapter 2).

The first two chapters of this dissertation examine aspects of the composition, effects of disturbance, and management approaches for Michigan oak savanna systems. The third chapter explores a potential method of site selection for conservation and restoration efforts. The Karner Blue was used as a focal species not only for its applicability as an ecological indicator, but also because it is federally endangered in the United States (USFWS 2003). Species distribution models (SDMs) constructed for the Karner Blue are therefore useful in two respects: 1). as indicators, or proxies, of oak savanna habitat suitability, and 2). as tools for learning more about this increasingly rare butterfly.

Among the different SDM approaches used to construct models for the Karner Blue and its obligate larval host plant, wild lupine, random forests (RF) and generalized boosted regression trees (GBM) performed consistently well (Chapter 3). The relatively high performance of these two methods is in line with other work based on similar datasets (e.g., Fukuda et al. 2013, Peters et al. 2007). Habitat suitability maps were created based on each SDM approach for both species. Such maps act as a useful tool to assist land managers in identifying or prioritizing potential management areas (Guisan et al. 2013). One potential workflow for this, used on the Manistee National Forest, is outlined in the third chapter.

The results from chapter three also identify several environmental and climatic factors important in defining suitable habitat for the Karner Blue, including elevation, summer precipitation, land cover class, and to a lesser extent, winter precipitation and mean summer temperatures (Chapter 3). These habitat preferences, especially in terms of elevation, land cover, and winter precipitation, support the findings of previous work (Forrester et al. 2005, Grundel et al. 1998, Grundel et al. 2007, Haack 1993, Kelly 1998, Smith et al. 2002, USFWS 2003), though the importance of summer precipitation may warrant further research (Chapter 3).

The third chapter was primarily concerned with the distribution of suitable Karner Blue and wild lupine habitat at the management scale (i.e., a National Forest Ranger District). The fourth chapter expands this concept spatially, by modeling species distributions across the state of Michigan, and temporally, by examining the potential changes in habitat suitability over time across two different climate projections. SDMs were constructed and projected into the future for the Karner Blue, frosted elfin, and Persius duskywing using the RF and GBM approaches, which performed relatively well in the third chapter. This chapter further expanded on the previous by incorporating dispersal into the modeling effort. Dispersal is important to consider, especially in a conservation context, because while SDMs model habitat suitability over the entire area of interest, the organisms being modeled may not actually have the capacity to disperse across the entire area (Araujo and Guisan 2006, Midgley et al. 2007). Results from this chapter indicate that the Karner Blue and frosted elfin may be at risk of extirpation from Michigan under a high-emissions (A1FI) climate scenario, especially as modeled using the Global Fluid Dynamics Laboratory (GFDL) models (Chapter 4). These results also suggest that this extirpation risk could be mitigated by (relatively high effort) assisted migration efforts (Chapter 4). In contrast, the Persius duskywing is expected to perform relatively well under future climate conditions (Chapter 4). While this chapter was primarily concerned with the potential future distribution of suitable habitat for the three rare butterflies, these results also have implications for broader oak savanna management. Lepidoptera are generally considered to be effective indicator species due to their quick responses to environmental change and the fact that they are charismatic and relatively well-studied (New 1997, Parmesan 2006). The loss of these indicators due to climate change could make site selection and long-term planning more challenging.

Limitations and Future Work

The impact of disturbance frequency on community composition is clear given the effect sizes illustrated in the first chapter, but this avenue could be further explored. Analyzing and comparing functional diversity between groups of sites could help explain why the community compositional changes occur, and how oak savanna ecosystem processes respond to disturbance (McGill et al. 2006, Suding et al. 2008, Flynn et al. 2011). This could be further expanded by incorporating phylogenetic community analysis (e.g., Flynn et al. 2011, see Cavender-Bares et al. 2009 and Webb et al 2002). A phylogenetic community approach could provide estimates of niche conservatism, and expansion and colonization abilities, which are becoming increasingly important in the context of global environmental change (Diniz-Filho et al. 2011).

The second chapter was based on an ongoing management trial experiment set up by the MNF. While there are clear differences between mechanical restoration approaches in terms of plant cover types and site conditions, possible inferences from these data are limited due to a lack of specificity. Ideally, complete plant community surveys would be conducted at each experimental block. However, data are collected under broad cover type classifications because monitoring resources on the project are limited and the data are collected by seasonal interns that must be quickly trained. Fortunately, a number of additional cover classes will be recorded beginning in 2015 for the PPRA and WRMA, in addition to a completely new study site established in 2014-2015. The new data being recorded includes genus-level woody cover estimates (e.g., oak, cherry, pine) as well as many of the indicator species outlined in Chapter 1. Also under consideration is the measurement of various soils information, including bulk density.

The SDMs trained and evaluated in the third and fourth chapters were constructed using a variety of datasets, each with their own limitations. Soils data were obtained from the NRCS Soil Survey Geographic Database (SSURGO) (NRCS 2014). These data, while generally accurate, do have a small to moderate amount of uncertainty (e.g., Drohan et al. 2003). The land cover data, obtained from the National Land Cover Dataset (Homer et al. 2015), lacks detail as it is a broad classification (e.g., 'deciduous forest', 'shrubland'). Finally, the climate data, especially the climate change projections used in Chapter 4, have an inherent uncertainty to them. While temperature projections are generally made with relatively high confidence, predictions about changes in precipitation are made with much lower confidence (IPCC 2013). Given the importance of spring precipitation for all three species in Chapter 4, this uncertainty in climate projections suggests that the model predictions should be considered with caution.

In Chapter 4, dispersal was incorporated into the modeling effort using a cellular automation approach, MigClim (Engler et al. 2012); this method is inherently broad. It is important to note that MigClim projects the maximum possible dispersal distance based on the input parameters, and does not try to predict the actual distribution of the species of interest. MigClim works by computing the likelihood of colonization from an occupied cell to nearby accessible (as defined by input parameters) unoccupied cells, and iterating this over a set time frame (Engler et al. 2012). When used at broad spatial scales, it does not incorporate fine-scale site conditions (e.g., canopy cover, herbaceous plant cover), which might further influence the dispersal abilities of the species of interest. Similarly, the metapopulation dynamics important to many butterfly species are not currently modeled by MigClim. Given these limitations, the dispersal predictions made in Chapter 4 should be taken as an estimate of the upper limit of the dispersal ability of the butterfly species, rather than a mean prediction.

Conclusions and Management Implications

Overall, the results illustrate the importance and complexities of disturbance in oak savanna systems and could prove useful to the managers working in these systems. Indeed, the results of Chapter 2 illustrate that even relatively moderate differences in disturbance type (i.e., mechanical restoration approach) can result in quantifiable differences in community structure. The indicator species identified in Chapter 1 are already being utilized on the MNF, and may be of broader use in oak savanna systems across Michigan. Habitat suitability maps constructed from SDMs are broadly useful in site selection and prioritization (Guisan et al. 2013), and the maps made based on the SDMs constructed in Chapter 3 have already been used to help plan the restoration of over 200 ha of oak savanna on the MNF. In general, SDM results in both Chapters 3 and 4 have the potential to be useful to butterfly conservation efforts. A high emissions climate change future may have an adverse impact on habitat suitability for the Karner Blue and frosted elfin, while the Persius duskywing may be largely unaffected. Finally, the environmental and climatic variables most important in defining suitable habitat for these butterflies may help explain their potential climate responses and guide additional research.

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Appendix 1

Table A1.1. Species list with families and scientific names.

Common Name	Family	Scientific Name
Annual Bedstraw	Rubiaceae	*Galium aparine*
Annual False Foxglove	Orobanchaceae	*Aureolaria pedicularia*
Bastard Toadflax	Santalaceae	*Comandra umbellata*
Beaked Hazel	Betulaceae	*Corylus cornuta*
Big Bluestem	Poaceae	*Andropogon gerardii*
Bigtooth Aspen	Salicaceae	*Populus grandidentata*
BirdfootBiolet	Violaceae	*Viola pedata*
Black Cherry	Rosaceae	*Prunus serotina*
Black Medick	Fabaceae	*Medicago lupulina*
Black Oak	Fagaceae	*Quercus velutina*
Black Oatgrass	Poaceae	*Piptochaetium avenaceum*
Black-Eyed Susan	Asteraceae	*Rudbeckia hirta*
Bluebell	Campanulaceae	*Campanula rotundifolia*
Boneset	Asteraceae	*Eupatorium perfoliatum*
Bottlebrush Grass	Poaceae	*Elymus hystrix*
Bracken Fern	Dennstaedtiaceae	*Pteridium aquilinum*
Butterfly Weed	Apocynaceae	*Asclepias tuberosa*
Canada Lettuce	Asteraceae	*Lactuca canadensis*
Canada Wild Rye	Poaceae	*Elymus canadensis*
Cinquefoil	Rosaceae	*Potentilla simplex*
Common Dandelion	Asteraceae	*Taraxacum officinale*
Common Evening Primrose	Onagraceae	*Oenothera biennis*
Common Fleabane	Asteraceae	*Erigeron philadelphicus*
Common Milkweed	Apocynaceae	*Asclepias syriaca*
Common Mountain Mint	Lamiaceae	*Pycnanthemum virginianum*
Common Rockrose	Cistaceae	*Crocanthemum canadensis*
Common Spiderwort	Commelinaceae	*Tradescantia ohiensis*
Daisy Fleabane	Asteraceae	*Erigeron strigosus*
Dwarf Blazing Star	Asteraceae	*Liatris spicata*
Early Goldenrod	Asteraceae	*Solidago juncea*
False Boneset	Asteraceae	*Brickellia eupatorioides*
False Dandelion	Asteraceae	*Krigia virginica*
False Solomon's Seal	Liliaceae	*Maianthemum canadense*
False Spikenard	Liliaceae	*Maianthemum racemosum*
Flowering Spurge	Euphorbiaceae	*Euphorbia corollata*

Frost Aster	Asteraceae	*Symphyotrichum pilosum*
Goat's Rue	Fabaceae	*Tephrosia virginiana*
Hairgrass	Poaceae	*Avenella flexuosa*
Hairy Bedstraw	Rubiaceae	*Galium pilosum*
Hairy Bush Clover	Fabaceae	*Lespedeza hirta*
Hairy Vetch	Fabaceae	*Vicia villosa*
Hawkweed	Asteraceae	*Hieracium aurantiacum*
Hoary Puccoon	Boraginaceae	*Lithospermum canescens*
Horsemint	Lamiaceae	*Monarda punctata*
Junegrass	Poaceae	*Koeleria macrantha*
Lanceleaf Coreopsis	Asteraceae	*Coreopsis lanceolata*
Leafy Spurge	Euphorbiaceae	*Euphorbia virgata*
Little Bluestem	Poaceae	*Schizachyrium scoparium*
Long Leaved Aster	Asteraceae	*Symphyotrichum robynsianum*
Lowbush Blueberry	Ericaceae	*Vaccinium augustifolium*
Multiflora Rose	Rosaceae	*Rosa multiflora*
Paper Birch	Betulaceae	*Betula papyrifera*
Pennsylvania Sedge	Cyperaceae	*Carex pensylvanica*
Perennial Pea	Fabaceae	*Lathyrus latifolius*
Pin Cherry	Rosaceae	*Prunus pensylvanica*
Poke Milkweed	Apocynaceae	*Asclepias exaltata*
Poverty Grass	Poaceae	*Danthonia spicata*
Prairie Heart Leaved Aster	Asteraceae	*Symphyotrichum oolentangiense*
Prairie Ragwort	Asteraceae	*Packera paupercula*
Prairie Willow	Salicaceae	*Salix humilis*
Quaking Aspen	Salicaceae	*Populus tremuloides*
Red Maple	Sapindaceae	*Acer rubrum*
Red Oak	Fagaceae	*Quercus rubra*
Red Pine	Pinaceae	*Pinus resinosa*
Rough Blazing Star	Asteraceae	*Liatris aspera*
Sand Cherry	Rosaceae	*Prunus pumila*
Sassafras	Lauraceae	*Sassafras albidum*
Scots Pine	Pinaceae	*Pinus sylvestris*
Scouring Rush	Equisetaceae	*Equisetum hyemale*
Serviceberry	Rosaceae	*Amelanchier interior*
Sheep Sorrel	Polygonaceae	*Rumex acetosella*
Showy Goldenrod	Asteraceae	*Solidago speciosa*
Showy Tick Trefoil	Fabaceae	*Desmodium canadense*
Silky Dogwood	Cornaceae	*Cornus amomum*
Smooth Aster	Asteraceae	*Symphyotrichum laeve*

Spotted Knapweed	Asteraceae	*Centaurea stoebe*
St. John's Wort	Hypericaceae	*Hypericum perforatum*
Sweetfern	Myricaceae	*Comptonia peregrina*
Switchgrass	Poaceae	*Panicum virgatum*
Thimbleberry	Rosaceae	*Rubus flagellaris*
Thimbleweed	Ranunculaceae	*Anemone virginiana*
Tick Trefoil	Fabaceae	*Desmodium perplexum*
White Oak	Fagaceae	*Quercus alba*
White Pine	Pinaceae	*Pinus strobus*
Wild Bergamot	Lamiaceae	*Monarda fistulosa*
Wild Carrot	Apiaceae	*Daucus carota*
Wild Geranium	Geraniaceae	*Geranium maculatum*
Wild Ginger	Atristolochiaceae	*Asarum canadense*
Wild Lupine	Fabaceae	*Lupinus perennis*
Wild Strawberry	Rosaceae	*Fragaria virginiana*
Wild Wormwood	Asteraceae	*Artemisia campestris*
Wintergreen	Ericaceae	*Gaultheria procumbens*
Wood Betony	Orobanchaceae	*Pedicularis canadensis*
Woodland Sunflower	Asteraceae	*Helianthus divaricatus*
Yellow Flax	Linaceae	*Linum sulcatum*
Yellow Pimpernel	Apiaceae	*Taenidia integerrima*
Grass spp. (other)	Poaceae	Poaceae spp.
Sedge spp. (other)	Cyperaceae	*Carex* spp.

Table A1.2. Beta dispersion table; test of the perMANOVA assumption of homogeneity of group dispersions (group variances). H_0 : group dispersions are equal. The beta dispersion test was performed for each dataset (Herbaceous, Woody, All Plants). If test results were not significant, perMANOVA was performed (Table 1).

	Source	df	SS	MSS	*F*	Pr(>*F*)
Herbaceous						
	Groups	2	0.0311	0.0168	2.4701	0.1081
	Residuals	18	0.1025	0.0063		
Woody						
	Groups	2	0.0315	0.0157	0.837	0.4492
	Residuals	18	0.3382	0.0188		
All Plants						
	Groups	2	0.0206	0.0103	2.3823	0.1208
	Residuals	18	0.0778	0.0043		

Table A1.3. Relationships between measured environmental variables and plant community NMDS axes (Figure 1). Analyses were performed for each dataset: Herbaceous (a), Woody (b), and All Plants (c). Statistically significant values are highlighted in bold, marginally significant in italics.

	Variable	Axis 1	Axis 2	r^2	Pr(>*r*)
Herbaceous	Canopy Cover (%)	0.979	0.203	**0.545**	**0.001**
	O Horizon Thickness	0.619	0.786	0.013	0.882
	A Horizon Thickness	-0.520	-0.854	0.196	0.158
	Soil Elemental C	0.526	-0.851	0.030	0.788
	Soil Elemental N	0.999	0.048	0.067	0.559
	Soil pH	-0.610	-0.792	**0.286**	**0.050**
	Soil C:N Ratio	0.646	0.763	**0.371**	**0.019**
Woody	Canopy Cover (%)	0.060	-0.998	**0.674**	**0.001**
	O Horizon Thickness	0.512	-0.859	0.166	0.205
	A Horizon Thickness	0.519	0.855	0.123	0.299
	Soil Elemental C	0.996	0.086	0.017	0.868
	Soil Elemental N	0.206	-0.979	0.014	0.880
	Soil pH	-0.221	0.975	**0.288**	**0.045**
	Soil C:N Ratio	-0.621	-0.784	*0.258*	*0.076*
All Plants	Canopy Cover (%)	-0.919	0.394	**0.635**	**0.002**
	O Horizon Thickness	-0.522	0.853	0.085	0.437
	A Horizon Thickness	0.659	-0.753	*0.255*	*0.074*
	Soil Elemental C	-0.925	-0.380	0.040	0.694
	Soil Elemental N	-0.964	0.266	0.118	0.313
	Soil pH	0.607	-0.795	**0.455**	**0.005**
	Soil C:N Ratio	-0.707	0.707	**0.374**	**0.022**

Table A1.4. Relationships between individual plant species and plant community NMDS axes (Figure 1). Analyses were performed for each dataset. Statistically significant values are highlighted in bold, marginally significant in italics.

(A1.4a). Herbaceous Dataset

Herbaceous				
Species	Axis 1	Axis 2	r^2	Pr(>*r*)
Annual Bedstraw	0.215	-0.977	0.073	0.503
Annual False Foxglove	-0.949	0.316	0.166	0.200
Bastard Toadflax	-0.803	0.596	**0.508**	**0.001**
Big Bluestem	-0.886	-0.465	0.056	0.672
Birdfood Biolet	0.980	0.201	0.049	0.812
Black Medick	0.430	-0.903	0.121	0.346
Black Oatgrass	-0.922	0.387	*0.185*	*0.052*
Black-Eyed Susan	-0.162	-0.987	0.164	0.198
Bluebell	-0.783	-0.622	0.082	0.568
Boneset	-0.136	-0.991	0.159	0.205
Bottlebrush Grass	-0.717	0.697	0.053	0.811
Bracken Fern	0.990	-0.141	0.190	0.170
Butterfly Weed	-0.124	-0.992	**0.397**	**0.009**
Canada Lettuce	0.918	-0.397	0.230	0.082
Canada Wild Rye	-0.349	-0.937	0.153	0.219
Cinquefoil	0.560	-0.829	*0.272*	*0.074*
Common Dandelion	-0.017	-1.000	0.197	0.129
Common Evening Primrose	0.982	0.188	**0.361**	**0.014**
Common Fleabane	-0.271	-0.963	0.195	0.120
Common Milkweed	-0.898	-0.441	0.077	0.510
Common Mountain Mint	-0.463	-0.887	0.036	0.825
Common Rockrose	0.689	-0.725	0.204	0.125
Common Spiderwort	-0.216	-0.976	*0.268*	*0.060*
Daisy Fleabane	0.797	0.604	**0.570**	**0.001**
Dwarf Blazing Star	0.421	-0.907	0.101	0.454
Early Goldenrod	-0.958	0.286	**0.380**	**0.005**
False Boneset	-0.912	-0.410	*0.239*	*0.085*
False Dandelion	-0.975	-0.223	0.030	0.840
False Solomon's Seal	0.752	0.659	**0.378**	**0.001**
False Spikenard	-0.922	0.387	*0.185*	*0.052*
Flowering Spurge	0.095	-0.995	0.193	0.142
Frost Aster	0.883	0.470	0.086	0.559
Goat's Rue	-0.999	0.053	**0.336**	**0.028**

Hairgrass	0.307	0.952	*0.222*	*0.079*
Hairy Bedstraw	0.021	-1.000	0.016	0.951
Hairy Bush Clover	-0.717	0.697	0.053	0.811
Hairy Vetch	-0.030	-1.000	*0.180*	*0.085*
Hawkweed	-0.097	0.995	0.088	0.482
Hoary Puccoon	-0.325	0.946	0.041	0.715
Horsemint	0.009	-1.000	**0.255**	**0.009**
Junegrass	-0.175	-0.985	*0.255*	*0.054*
Lanceleaf Coreopsis	-0.253	-0.968	0.137	0.312
Leafy Spurge	-0.089	-0.996	*0.185*	*0.062*
Little Bluestem	-0.757	0.653	**0.346**	**0.017**
Long Leaved Aster	-0.889	0.457	0.120	0.361
Multiflora Rose	0.062	-0.998	**0.357**	**0.017**
Pennsylvania Sedge	-0.615	0.789	0.051	0.636
Perennial Pea	-0.148	-0.989	**0.397**	**0.009**
Poke Milkweed	-0.234	-0.972	0.182	0.144
Poverty Grass	-0.657	-0.754	0.167	0.166
Prairie Heart Leaved Aster	0.000	-1.000	0.132	0.255
Prairie Ragwort	-0.423	-0.906	0.241	0.052
Rough Blazing Star	0.461	-0.888	0.106	0.419
Scouring Rush	-0.707	0.707	0.158	0.255
Sheep Sorrel	0.262	-0.965	0.074	0.504
Showy Goldenrod	0.538	0.843	0.118	0.354
Showy Tick Trefoil	0.987	-0.161	*0.240*	*0.080*
Smooth Aster	-0.657	-0.754	0.102	0.453
Spotted Knapweed	-0.304	-0.953	0.245	0.097
St. John's Wort	0.634	-0.774	0.152	0.256
Switchgrass	-0.980	0.198	*0.211*	*0.099*
Thimbleweed	1.000	-0.031	**0.421**	**0.003**
Tick Trefoil	-0.756	0.655	0.071	0.531
Wild Bergamot	0.177	-0.984	*0.232*	*0.053*
Wild Carrot	0.157	-0.988	**0.245**	**0.044**
Wild Geranium	0.127	-0.992	0.149	0.245
Wild Ginger	-0.199	-0.980	0.033	0.826
Wild Lupine	-0.342	-0.940	*0.250*	*0.071*
Wild Strawberry	-0.977	-0.213	**0.316**	**0.026**
Wild Wormwood	-0.347	-0.938	**0.293**	**0.018**
Wood Betony	0.867	-0.499	**0.465**	**0.002**
Woodland Sunflower	0.664	-0.748	0.093	0.542
Yellow Flax	0.524	-0.852	0.199	0.140
Yellow Pimpernel	0.792	0.611	**0.354**	**0.001**

Grass spp.	-0.999	-0.034	0.066	0.783
Sedge spp.	-0.922	0.387	*0.185*	*0.052*

(A1.4b). Woody Dataset.

Woody				
Species	Axis 1	Axis 2	r^2	Pr(>*r*)
Beaked Hazel	-0.703	-0.711	0.150	0.242
Bigtooth Aspen	0.979	0.206	*0.240*	*0.095*
Black Cherry	-0.216	-0.976	0.164	0.194
Black Oak	0.874	-0.486	**0.322**	**0.033**
Lowbush Blueberry	0.014	-1.000	0.204	0.140
Paper Birch	-0.249	0.968	0.109	0.441
Pin Cherry	0.906	-0.423	0.125	0.299
Prairie Willow	0.259	0.966	*0.260*	*0.058*
Quaking Aspen	0.541	0.841	0.138	0.262
Red Maple	-0.781	-0.624	0.046	0.633
Red Oak	-0.044	-0.999	0.027	0.860
Red Pine	-0.560	-0.828	*0.239*	*0.076*
Sand Cherry	-0.398	0.917	0.200	0.112
Sassafras	-0.948	0.317	**0.598**	**0.001**
Scots Pine	0.383	0.924	0.133	0.217
Serviceberry	0.542	-0.840	0.162	0.198
Silky Dogwood	-0.525	-0.851	0.036	0.703
Sweetfern	-0.982	0.190	**0.406**	**0.006**
Thimbleberry	-1.000	0.007	**0.430**	**0.003**
White Oak	-0.673	-0.740	0.112	0.343
White Pine	0.093	0.996	0.103	0.374
Wintergreen	-0.439	-0.899	*0.222*	*0.090*

(A1.4c). All Plants Dataset.

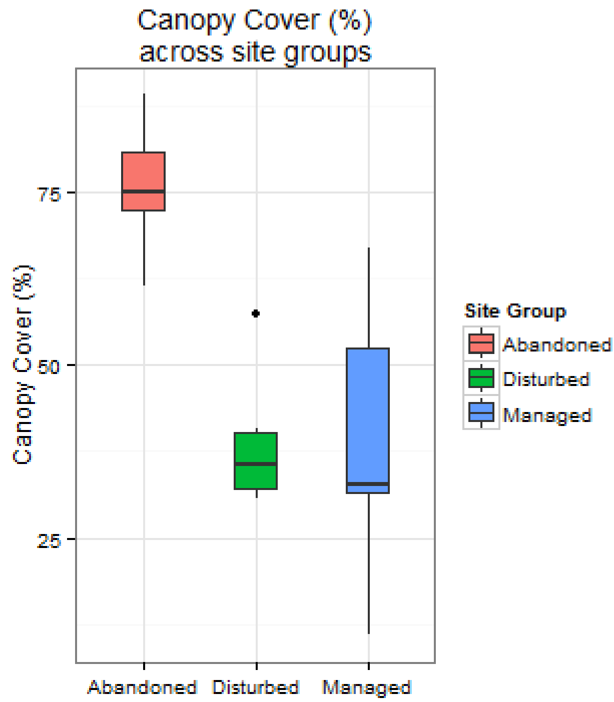
All Plants				
Species	Axis 1	Axis 2	r^2	Pr(>r)
Annual Bedstraw	-0.166	-0.986	0.077	0.494
Annual False Foxglove	0.958	0.288	0.193	0.113
Bastard Toadflax	0.593	0.805	**0.493**	**0.001**
Beaked Hazel	-0.560	-0.829	0.114	0.346
Big Bluestem	0.689	-0.725	0.096	0.463
Bigtooth Aspen	0.950	0.311	0.084	0.513
Birdfood Biolet	-0.840	0.542	0.050	0.867
Black Cherry	-0.416	0.909	**0.301**	**0.050**
Black Medick	-0.662	-0.750	0.075	0.667
Black Oak	-0.343	0.939	0.055	0.595
Black Oatgrass	0.434	0.901	**0.179**	**0.044**
Black-Eyed Susan	0.224	-0.975	0.188	0.146
Bluebell	0.952	-0.305	0.087	0.545
Boneset	0.178	-0.984	0.192	0.146
Bottlebrush Grass	0.936	0.352	0.070	0.699
Bracken Fern	-0.977	-0.213	0.185	0.146
Butterfly Weed	0.131	-0.991	**0.359**	**0.016**
Canada Lettuce	-0.998	-0.070	0.196	0.142
Canada Wild Rye	0.269	-0.963	0.188	0.125
Cinquefoil	-0.553	-0.833	**0.364**	**0.013**
Common Dandelion	-0.060	-0.998	0.196	0.133
Common Evening Primrose	-0.964	0.265	*0.373*	*0.015*
Common Fleabane	0.369	-0.930	*0.235*	*0.060*
Common Milkweed	0.777	-0.630	0.106	0.413
Common Mountain Mint	0.273	-0.962	0.135	0.239
Common Rockrose	-0.733	-0.680	0.179	0.176
Common Spiderwort	0.330	-0.944	**0.287**	**0.047**
Daisy Fleabane	-0.797	0.604	**0.551**	**0.001**
Dwarf Blazing Star	-0.664	-0.748	0.056	0.857
Early Goldenrod	0.738	0.675	**0.299**	**0.011**
False Boneset	0.966	-0.259	*0.333*	*0.023*
False Dandelion	0.993	-0.116	0.024	0.904
False Solomon's Seal	-0.723	0.690	**0.334**	**0.001**
False Spikenard	0.434	0.901	**0.179**	**0.044**
Flowering Spurge	-0.032	-1.000	0.136	0.278
Frost Aster	-0.728	0.685	0.088	0.540
Goat's Rue	0.940	0.341	**0.375**	**0.014**

Hairgrass	-0.229	0.974	0.157	0.200
Hairy Bedstraw	-0.062	-0.998	0.028	0.926
Hairy Bush Clover	0.936	0.352	0.070	0.699
Hairy Vetch	-0.109	-0.994	0.160	0.133
Hawkweed	0.254	0.967	0.079	0.519
Hoary Puccoon	-0.123	0.992	0.114	0.381
Horsemint	-0.103	-0.995	**0.214**	**0.027**
Junegrass	0.371	-0.929	0.171	0.162
Lanceleaf Coreopsis	0.343	-0.939	0.141	0.292
Leafy Spurge	-0.025	-1.000	0.154	0.138
Little Bluestem	0.800	0.600	**0.430**	**0.003**
Long Leaved Aster	1.000	0.012	0.170	0.136
Lowbush Blueberry	-0.747	0.665	**0.363**	**0.008**
Multiflora Rose	-0.072	-0.997	**0.423**	**0.006**
Paper Birch	-0.109	-0.994	0.160	0.133
Pennsylvania Sedge	1.000	-0.031	0.035	0.735
Perennial Pea	0.194	-0.981	**0.332**	**0.024**
Pin Cherry	0.656	-0.755	0.119	0.341
Poke Milkweed	0.232	-0.973	*0.211*	*0.070*
Poverty Grass	0.736	-0.677	0.187	0.154
Prairie Heart Leaved Aster	0.000	-1.000	0.141	0.256
Prairie Ragwort	0.380	-0.925	0.096	0.422
Prairie Willow	0.843	0.538	**0.266**	**0.042**
Quaking Aspen	0.752	0.659	*0.241*	*0.089*
Red Maple	-0.921	0.390	0.037	0.802
Red Oak	-0.569	0.823	0.131	0.335
Red Pine	-0.993	0.116	**0.342**	**0.005**
Rough Blazing Star	-0.701	-0.713	0.065	0.868
Sand Cherry	-0.697	-0.717	0.001	0.995
Sassafras	-0.181	-0.984	*0.224*	*0.095*
Scots Pine	0.956	-0.292	0.076	0.621
Scouring Rush	0.804	0.595	0.149	0.267
Serviceberry	-0.204	0.979	0.067	0.580
Sheep Sorrel	-0.379	-0.925	0.082	0.493
Showy Goldenrod	-0.554	0.832	0.130	0.295
Showy Tick Trefoil	-1.000	0.002	*0.249*	*0.071*
Silky Dogwood	-0.923	0.385	0.047	0.868
Smooth Aster	0.792	-0.610	0.109	0.420
Spotted Knapweed	0.554	-0.833	0.174	0.164
St. John's Wort	-0.845	-0.534	0.098	0.424
Sweetfern	0.088	-0.996	0.143	0.206

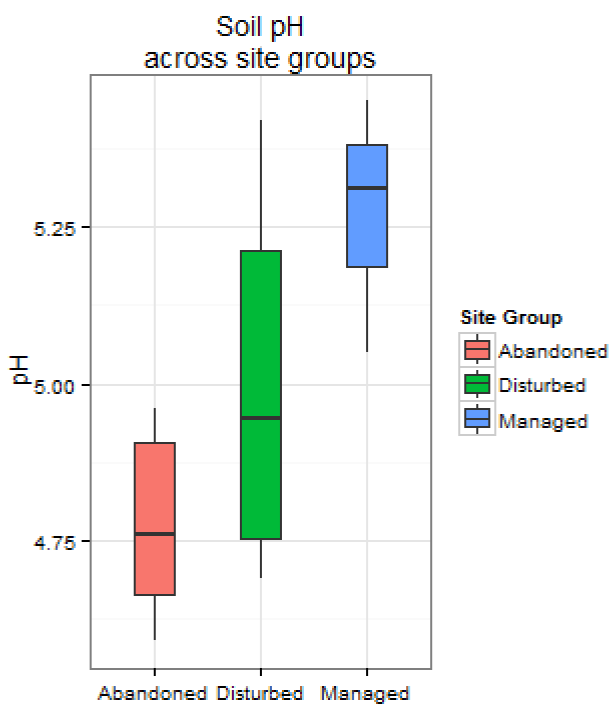
Switchgrass	0.776	0.631	*0.212*	*0.090*
Thimbleberry	-0.112	-0.994	0.111	0.400
Thimbleweed	-1.000	-0.009	**0.427**	**0.003**
Tick Trefoil	0.996	0.088	0.042	0.748
White Oak	-0.724	0.690	**0.304**	**0.049**
White Pine	0.958	0.286	0.007	0.942
Wild Bergamot	-0.323	-0.946	*0.224*	*0.054*
Wild Carrot	-0.295	-0.956	**0.246**	**0.038**
Wild Geranium	-0.043	-0.999	0.065	0.562
Wild Ginger	0.311	-0.950	0.054	0.712
Wild Lupine	0.317	-0.949	**0.357**	**0.028**
Wild Strawberry	0.989	-0.149	**0.349**	**0.017**
Wild Wormwood	0.520	-0.854	**0.276**	**0.024**
Wintergreen	-0.997	0.077	**0.277**	**0.047**
Wood Betony	-0.934	-0.357	**0.445**	**0.003**
Woodland Sunflower	-0.740	-0.673	0.102	0.476
Yellow Flax	-0.564	-0.826	*0.216*	*0.084*
Yellow Pimpernel	-0.774	0.634	**0.300**	**0.001**
Grass spp.	0.979	0.204	0.097	0.581
Sedge spp.	0.434	0.901	**0.179**	**0.044**

Figure A1.1. Between-group differences in environmental variables, including canopy cover (a), soil pH (b), soil carbon to nitrogen (C:N) ratio (c), and soil A horizon thickness (d). Community types are color-coded.

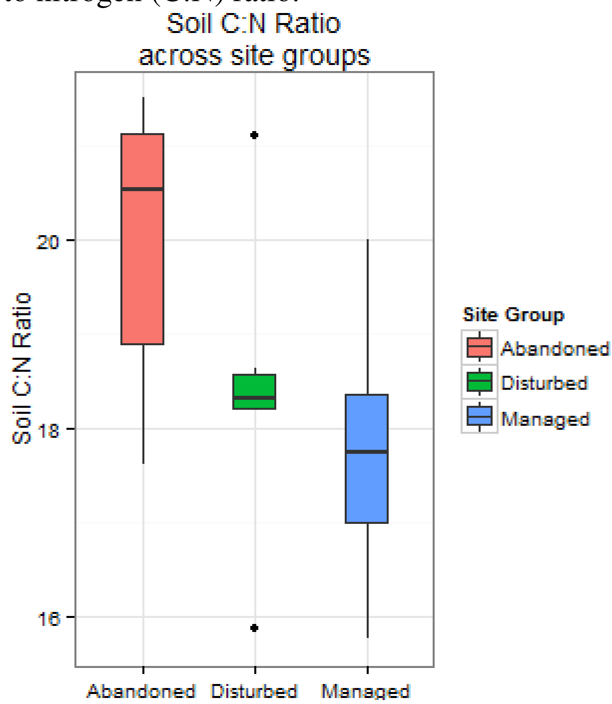
(A1.1a). Canopy Cover.



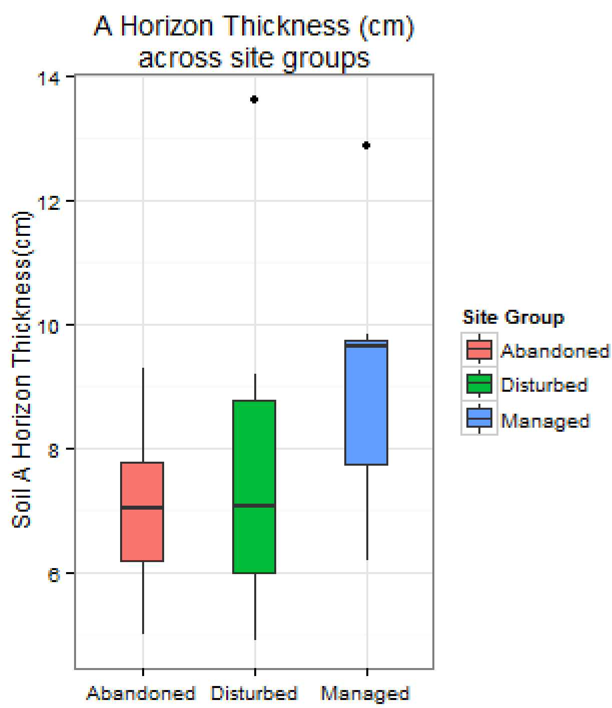
(A1.1b). Soil pH.



(A1.1c). Soil carbon to nitrogen (C:N) ratio.



(A1.1d). Soil A horizon thickness.



Appendix 2

Table A2.1. Least-square means contrasts for site characteristics across treatments, averaged across the interaction term (year) for PPRA (A2.1a) and WRMA (A2.1b).

(A2.1a). PPRA.

Response Variable	(I) Group	(J) Group	Estimate	df	*t*	*p*
Canopy Cover	Control	Bulldozer	4.4414	114	-16.716	< 0.0001
		Masticator	2.5471	114	9.586	< 0.0001
		Shear cutter	4.2743	114	16.087	< 0.0001
	Bulldozer	Masticator	-1.8944	114	-7.13	< 0.0001
		Shear cutter	-0.1672	114	-0.629	0.9225
	Masticator	Shear cutter	1.7272	114	6.501	< 0.0001
Dead Wood	Control	Bulldozer	-0.1603	114	1.091	0.6959
		Masticator	-0.3811	114	-2.594	0.0517
		Shear cutter	-0.0298	114	-0.203	0.997
	Bulldozer	Masticator	-0.2208	114	-1.503	0.4391
		Shear cutter	0.1304	114	0.888	0.8112
	Masticator	Shear cutter	0.3513	114	2.391	0.0846
Exposed Soil	Control	Bulldozer	-1.1839	114	6.329	< 0.0001
		Masticator	-0.5500	114	-2.94	0.0204
		Shear cutter	-1.0283	114	-5.497	< 0.0001
	Bulldozer	Masticator	0.6339	114	3.389	0.0053
		Shear cutter	0.1556	114	0.832	0.8392
	Masticator	Shear cutter	-0.4783	114	-2.557	0.0568

(A2.1b). WRMA.

Response Variable	(I) Group	(J) Group	Estimate	df	*t*	*p*
Canopy Cover	Control	Bulldozer	3.6595	95	-12.322	< 0.0001
		Masticator	2.2511	95	7.579	< 0.0001
		Shear cutter	2.5414	95	8.557	< 0.0001
	Bulldozer	Masticator	-1.4084	95	-4.742	< 0.0001
		Shear cutter	-1.1182	95	-3.765	0.0016
	Masticator	Shear cutter	0.2903	95	0.977	0.7626
Dead Wood	Control	Bulldozer	-0.8461	95	4.526	0.0001
		Masticator	-0.7934	95	-4.244	0.0003
		Shear cutter	-0.3349	95	-1.791	0.2839
	Bulldozer	Masticator	0.0527	95	0.282	0.9921
		Shear cutter	0.5113	95	2.735	0.0368
	Masticator	Shear cutter	0.4586	95	2.453	0.0742
Exposed Soil	Control	Bulldozer	-1.2142	95	5.295	< 0.0001
		Masticator	-0.4728	95	-2.062	0.1732
		Shear cutter	-0.1468	95	-0.64	0.9186
	Bulldozer	Masticator	0.7413	95	3.233	0.009
		Shear cutter	1.0673	95	4.654	0.0001
	Masticator	Shear cutter	0.3260	95	1.422	0.4892

Table A2.2. Least-square means contrasts for cover types across treatments, averaged across the interaction term (year) for PPRA (A2a) and WRMA (A2b).

(A2.2a). PPRA.

Response Variable	(*i*) Group	(*j*) Group	Estimate	df	*t*	*p*
Herbaceous Veg.	Control	Bulldozer	-0.1228	114	0.819	0.8455
		Masticator	-0.4058	114	-2.705	0.0389
		Shear cutter	-0.4602	114	-3.067	0.0142
	Bulldozer	Masticator	-0.2830	114	-1.886	0.2398
		Shear cutter	-0.3374	114	-2.249	0.1166
	Masticator	Shear cutter	-0.0544	114	-0.362	0.9836
Woody Nect. Veg.	Control	Bulldozer	0.2229	114	-0.918	0.7955
		Masticator	0.0426	114	0.175	0.9981
		Shear cutter	0.5920	114	2.437	0.0759
	Bulldozer	Masticator	-0.1803	114	-0.742	0.8798
		Shear cutter	0.3691	114	1.519	0.4293
	Masticator	Shear cutter	0.5494	114	2.262	0.1133
All Woody Veg.	Control	Bulldozer	0.1876	114	-0.829	0.8406
		Masticator	0.0494	114	0.218	0.9963
		Shear cutter	0.4096	114	1.81	0.274
	Bulldozer	Masticator	-0.1381	114	-0.611	0.9285
		Shear cutter	0.2220	114	0.981	0.7605
	Masticator	Shear cutter	0.3601	114	1.592	0.3875
Pennsylvania Sedge	Control	Bulldozer	-1.0256	90	2.625	0.0491
		Masticator	-0.4606	90	-1.179	0.6418
		Shear cutter	-1.1751	90	-3.007	0.0177
	Bulldozer	Masticator	0.5650	90	1.446	0.4744
		Shear cutter	-0.1495	90	-0.383	0.9808
	Masticator	Shear cutter	-0.7145	90	-1.829	0.2668

(A2.2a cont'd). PPRA.

Response Variable	(*i*) Group	(*j*) Group	Estimate	df	*t*	*p*
Grass	Control	Bulldozer	-1.1199	90	3.462	0.0045
		Masticator	-0.6401	90	-1.979	0.2037
		Shear cutter	-0.4690	90	-1.45	0.472
	Bulldozer	Masticator	0.4799	90	1.484	0.4516
		Shear cutter	0.6510	90	2.013	0.1911
	Masticator	Shear cutter	0.1711	90	0.529	0.9519
Wild Lupine	Control	Bulldozer	0.5052	114	-3.316	0.0066
		Masticator	-0.1053	114	-0.691	0.9003
		Shear cutter	-0.0002	114	-0.002	1
	Bulldozer	Masticator	-0.6105	114	-4.007	0.0006
		Shear cutter	-0.5054	114	-3.318	0.0066
	Masticator	Shear cutter	0.1051	114	0.69	0.9008
Fern	Control	Bulldozer	0.2727	114	-2.417	0.0797
		Masticator	-0.0294	114	-0.26	0.9938
		Shear cutter	0.1675	114	1.484	0.4502
	Bulldozer	Masticator	-0.3020	114	-2.677	0.0418
		Shear cutter	-0.1052	114	-0.932	0.7877
	Masticator	Shear cutter	0.1969	114	1.745	0.3056

(A2.2b). WRMA

Response Variable	(*i*) Group	(*j*) Group	Estimate	df	*t*	*p*
Herbaceous Veg.	Control	Bulldozer	-0.6249	95	3.881	0.0011
		Masticator	-0.5447	95	-3.383	0.0057
		Shear cutter	-0.6880	95	-4.272	0.0003
	Bulldozer	Masticator	0.0802	95	0.498	0.9593
		Shear cutter	-0.0630	95	-0.391	0.9795
	Masticator	Shear cutter	-0.1433	95	-0.89	0.8102
Woody Nect. Veg.	Control	Bulldozer	-0.0131	95	0.056	0.9999
		Masticator	-0.7337	95	-3.159	0.0112
		Shear cutter	0.2596	95	1.118	0.6796
	Bulldozer	Masticator	-0.7206	95	-3.103	0.0133
		Shear cutter	0.2726	95	1.174	0.6447
	Masticator	Shear cutter	0.9932	95	4.277	0.0003
All Woody Veg.	Control	Bulldozer	0.0997	95	-0.52	0.9542
		Masticator	-0.7212	95	-3.757	0.0017
		Shear cutter	-0.2539	95	-1.323	0.551
	Bulldozer	Masticator	-0.8209	95	-4.277	0.0003
		Shear cutter	-0.3536	95	-1.842	0.2603
	Masticator	Shear cutter	0.4673	95	2.435	0.0775
Pennsylvania Sedge	Control	Bulldozer	-1.0287	75	2.964	0.0207
		Masticator	-0.8794	75	-2.534	0.0628
		Shear cutter	-1.4340	75	-4.132	0.0005
	Bulldozer	Masticator	0.1493	75	0.43	0.9731
		Shear cutter	-0.4053	75	-1.168	0.6488
	Masticator	Shear cutter	-0.5546	75	-1.598	0.386

(A2.2b cont'd). WRMA

Response Variable	(*i*) Group	(*j*) Group	Estimate	df	*t*	*p*
Grass	Control	Bulldozer	-0.9491	75	2.733	0.0384
		Masticator	-0.4556	75	-1.312	0.5584
		Shear cutter	-0.6146	75	-1.77	0.2959
	Bulldozer	Masticator	0.4935	75	1.421	0.4905
		Shear cutter	0.3345	75	0.963	0.7708
	Masticator	Shear cutter	-0.1590	75	-0.458	0.9679
Wild Lupine	Control	Bulldozer	-0.1108	95	1.213	0.6199
		Masticator	-0.2847	95	-3.119	0.0126
		Shear cutter	0.0231	95	0.253	0.9943
	Bulldozer	Masticator	-0.1740	95	-1.906	0.2325
		Shear cutter	0.1339	95	1.467	0.4617
	Masticator	Shear cutter	0.3078	95	3.372	0.0059
Fern	Control	Bulldozer	-0.0434	95	0.259	0.9939
		Masticator	0.1029	95	0.614	0.9274
		Shear cutter	-0.4565	95	-2.725	0.0377
	Bulldozer	Masticator	0.1463	95	0.873	0.8187
		Shear cutter	-0.4131	95	-2.466	0.0719
	Masticator	Shear cutter	-0.5594	95	-3.339	0.0065

Table A2.3. (A2.3a): DCA summary table for combined-data mean DCA plot. Eigenvalues, DCA values, and axis lengths are reported for all four axes. (A2.3c): Yearly cover type correlations with the first two DCA axes.

(A2.3a).

	DCA1	DCA2	DCA3	DCA4
Eigenvalues	0.1105	0.0185	0.0179	0.0175
DCA values	0.1105	0.0131	0.0015	0.0008
Axis length	0.8798	0.3358	0.3417	0.3486

(A2.3c). Yearly cover type correlations with the first two DCA axes.

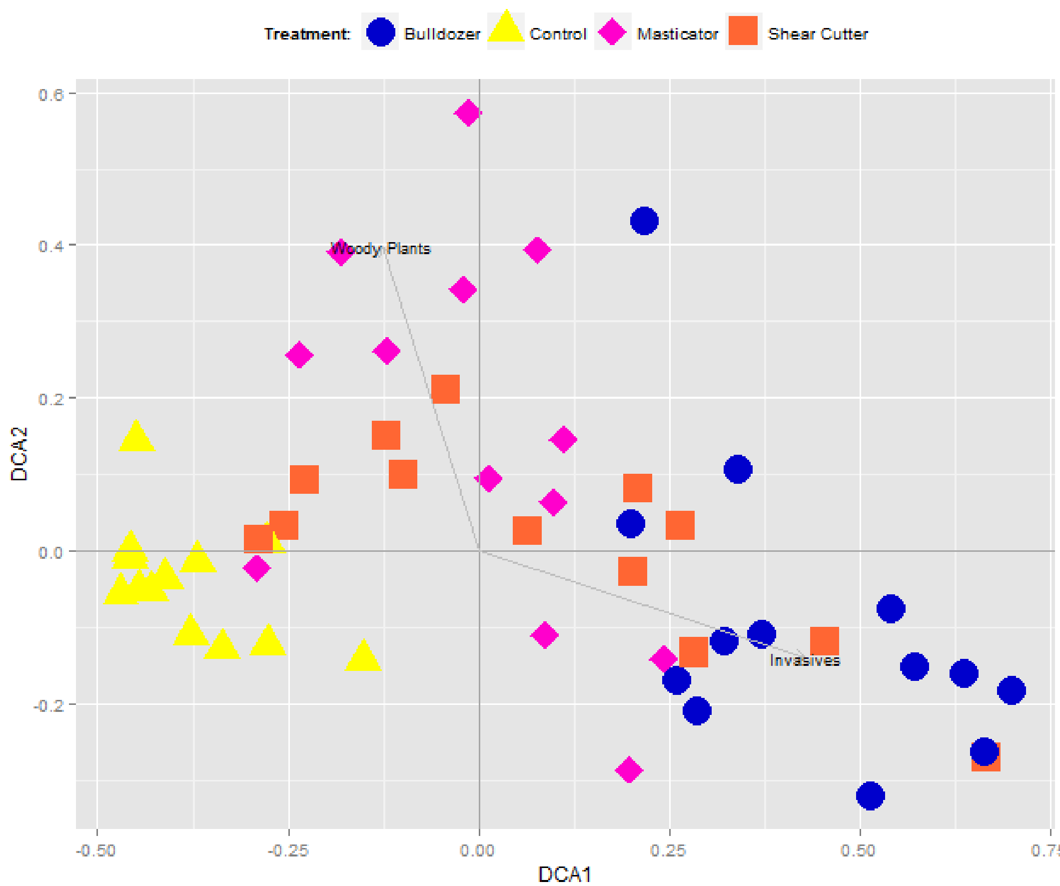
Year	Variable	DCA1	DCA2	r^2	Pr(>*r*)
2010	Wild Lupine (%)	-0.6000	0.8000	0.062	0.224
	Wild Lupine (P/A)	-0.0592	0.9982	0.007	0.864
	Nectar Plants: Herbaceous + Woody	-0.5271	0.8498	0.019	0.657
	Woody Plants	-0.3046	0.9525	**0.175**	**0.008**
	Ferns (%)	0.4020	0.9156	0.004	0.920
	Ferns (P/A)	0.1845	0.9828	0.093	0.117
	Nectar Plants: Woody	-0.4626	0.8866	0.076	0.157
	Nectar Plants: Herbaecous	0.3437	-0.9391	0.022	0.621
	Invasives (%)	0.9502	-0.3115	**0.202**	**0.006**
	Invasives (P/A)	-0.4079	-0.9130	0.085	0.129
2011	Wild Lupine (%)	-0.4818	-0.8763	0.028	0.513
	Wild Lupine (P/A)	-0.7022	-0.7120	0.053	0.278
	Nectar Plants: Herbaceous + Woody	-0.0371	-0.9993	0.014	0.731
	Woody Plants	-0.5581	0.8298	*0.090*	*0.100*
	Ferns (%)	-0.3138	-0.9495	0.027	0.494
	Ferns (P/A)	-0.4544	-0.8908	0.023	0.574
	Grass	0.9707	0.2403	**0.178**	**0.007**
	Nectar Plants: Woody	-0.6421	0.7666	**0.155**	**0.011**
	Nectar Plants: Herbaecous	0.4544	-0.8908	**0.205**	**0.005**
	Invasives (%)	0.6732	-0.7395	0.035	0.427
	Invasives (P/A)	0.9908	-0.1352	0.091	0.111
	Pennsylvania Sedge	0.2601	-0.9656	0.040	0.367
2012	Wild Lupine (%)	-0.5289	0.8487	0.039	0.302
	Wild Lupine (P/A)	-0.6182	-0.7860	0.004	0.886
	Nectar Plants: Herbaceous + Woody	0.1509	0.9885	0.008	0.809
	Woody Plants	0.1278	0.9918	0.031	0.411
	Ferns (%)	-0.1671	-0.9859	0.027	0.424
	Ferns (P/A)	-0.7092	0.7050	0.006	0.858
	Grass	0.2872	0.9579	0.076	0.108
	Nectar Plants: Woody	-0.2057	0.9786	0.008	0.809
	Nectar Plants: Herbaecous	0.9422	-0.3352	0.015	0.652
	Invasives (%)	0.1110	-0.9938	0.011	0.728
	Invasives (P/A)	0.0740	0.9973	0.002	0.946
	Pennsylvania Sedge	0.3212	-0.9470	0.037	0.357

(A2.3c cont'd). Yearly cover type correlations with the first two DCA axes.

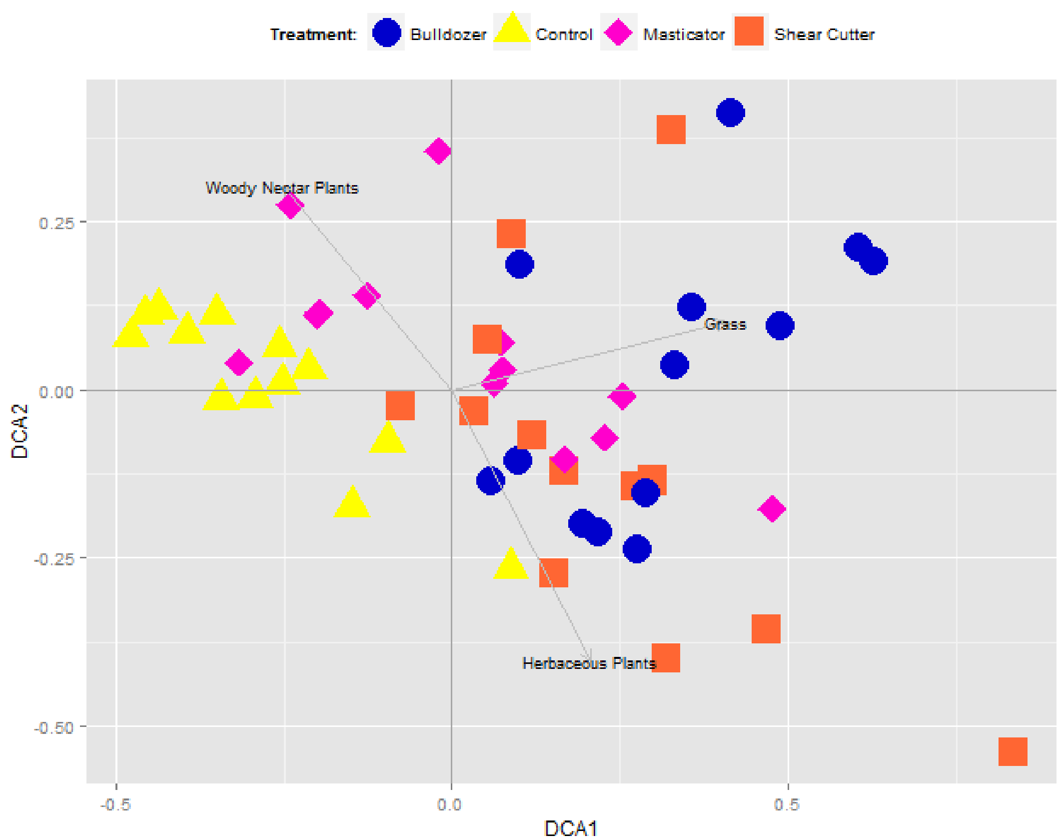
Year	Variable	DCA1	DCA2	r^2	Pr(>*r*)
2013	Wild Lupine (%)	0.3627	0.9319	**0.164**	**0.023**
	Wild Lupine (P/A)	0.1322	0.9912	0.061	0.225
	Nectar Plants: Herbaceous + Woody	-0.2405	0.9707	**0.222**	**0.003**
	Woody Plants	-0.3521	0.9360	**0.364**	**0.001**
	Ferns (%)	-0.3308	0.9437	0.012	0.736
	Ferns (P/A)	-0.3028	0.9530	0.085	0.145
	Grass	0.9824	-0.1867	*0.101*	*0.090*
	Nectar Plants: Woody	-0.4872	0.8733	**0.282**	**0.003**
	Nectar Plants: Herbaecous	0.7887	0.6148	**0.228**	**0.004**
	Invasives (%)	0.9687	-0.2483	0.014	0.727
	Invasives (P/A)	0.4909	-0.8712	0.020	0.665
	Pennsylvania Sedge	0.6837	0.7298	0.101	0.111
2014	Wild Lupine (%)	0.7262	-0.6875	**0.130**	**0.048**
	Wild Lupine (P/A)	0.5856	-0.8106	**0.299**	**0.001**
	Nectar Plants: Herbaceous + Woody	0.7874	-0.6164	**0.143**	**0.026**
	Woody Plants	-0.7042	0.7100	**0.147**	**0.016**
	Ferns (%)	-0.2680	0.9634	0.061	0.172
	Ferns (P/A)	-0.4431	-0.8965	0.002	0.942
	Grass	-0.7019	-0.7123	0.023	0.563
	Nectar Plants: Woody	-0.5070	0.8619	0.064	0.184
	Nectar Plants: Herbaecous	0.8683	-0.4960	**0.214**	**0.006**
	Invasives (%)	0.7563	-0.6542	0.031	0.452
	Invasives (P/A)	0.1889	-0.9820	0.016	0.672
	Pennsylvania Sedge	0.1230	0.9924	**0.444**	**0.001**

Figure A2.1. DCA plots of site conditions computed for each year (A2.1a-e).

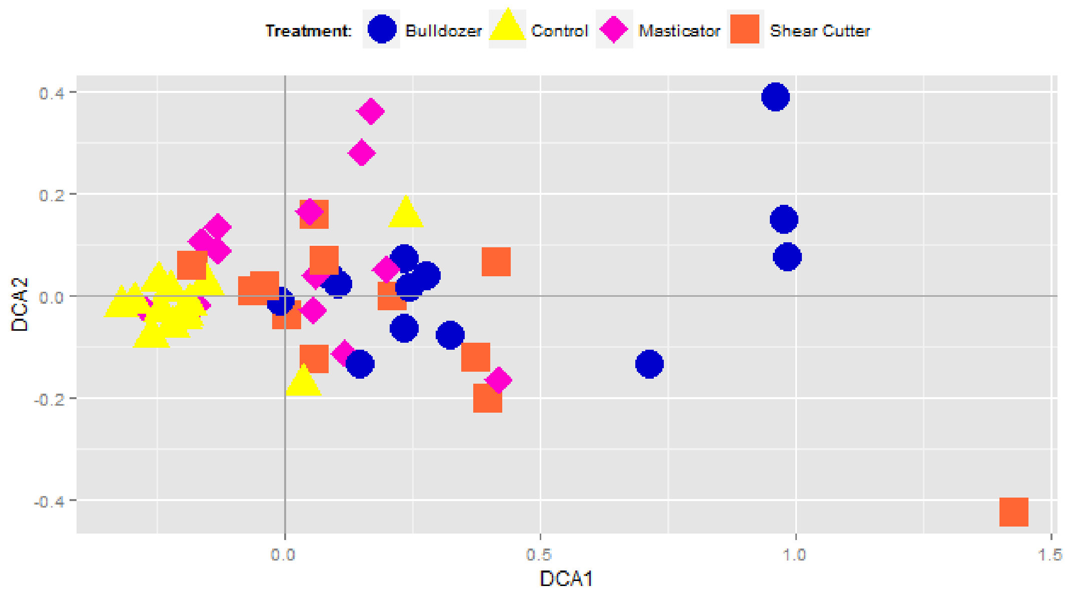
(A2.1a). Plot of DCA axes 1 and 2 at the beginning (2010) of experimental data collection. Shapes and color represent treatments. Vectors represent significant or marginally-significant ($p < 0.1$) cover type correlations with DCA axes (Table A2.3).



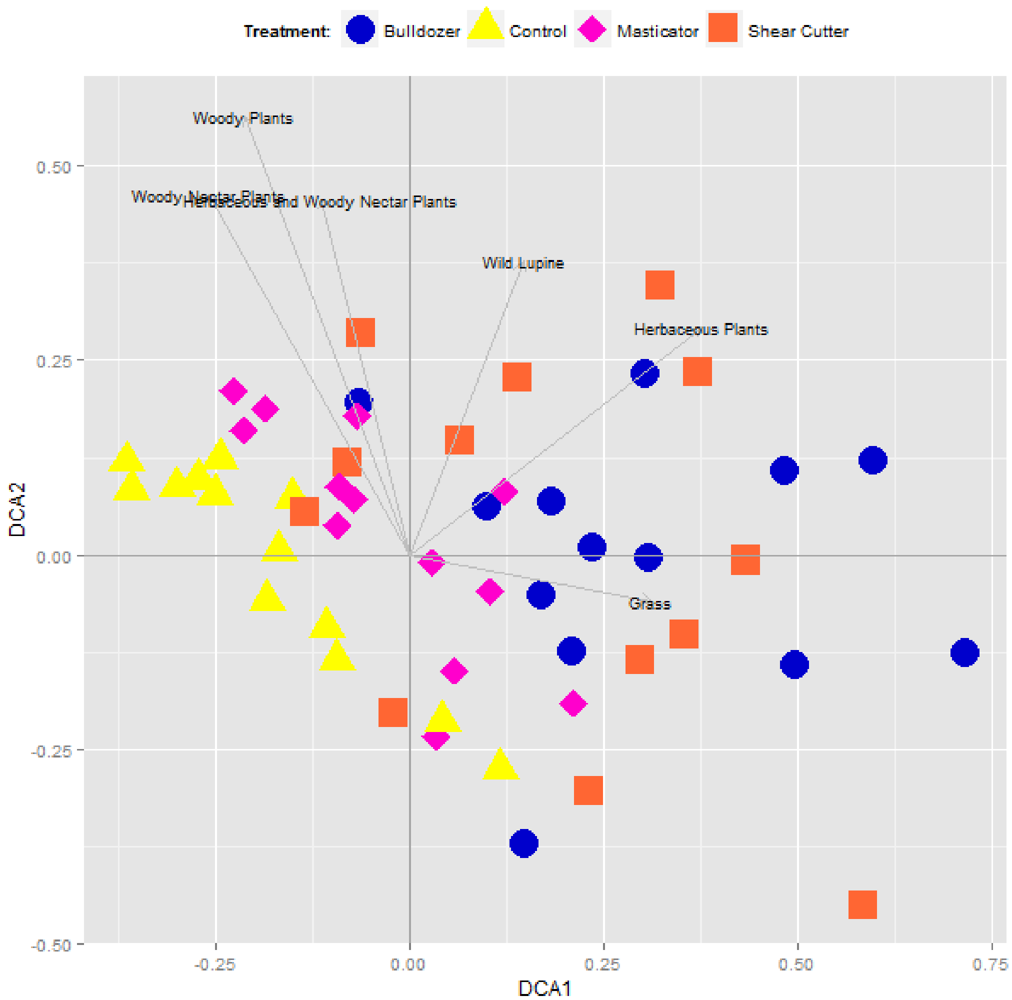
(A2.1b). Plot of DCA axes 1 and 2 after two years (2011) of experimental data collection. Shapes and color represent treatments. Vectors represent significant or marginally-significant ($p < 0.1$) cover type correlations with DCA axes (Table A2.3).



(A2.1c). Plot of DCA axes 1 and 2 after three years (2012) of experimental data collection. Shapes and color represent treatments. There were no significant cover type – axis associations for this year (Table A2.3).



(A2.1d). Plot of DCA axes 1 and 2 after four years (2013) of experimental data collection. Shapes and color represent treatments. Vectors represent significant or marginally-significant ($p < 0.1$) cover type correlations with DCA axes (Table A2.3).



(A2.1e). Plot of DCA axes 1 and 2 after five years (2014) of experimental data collection. Shapes and color represent treatments, while shade (light/dark) represents burn status (burned/unburned). The PPRA management area was burned in late summer 2013, while the WRMA was not, leading to difference in site conditions during the 2014 season. Vectors represent significant or marginally-significant ($p < 0.1$) cover type correlations with DCA axes (Table A2.3).

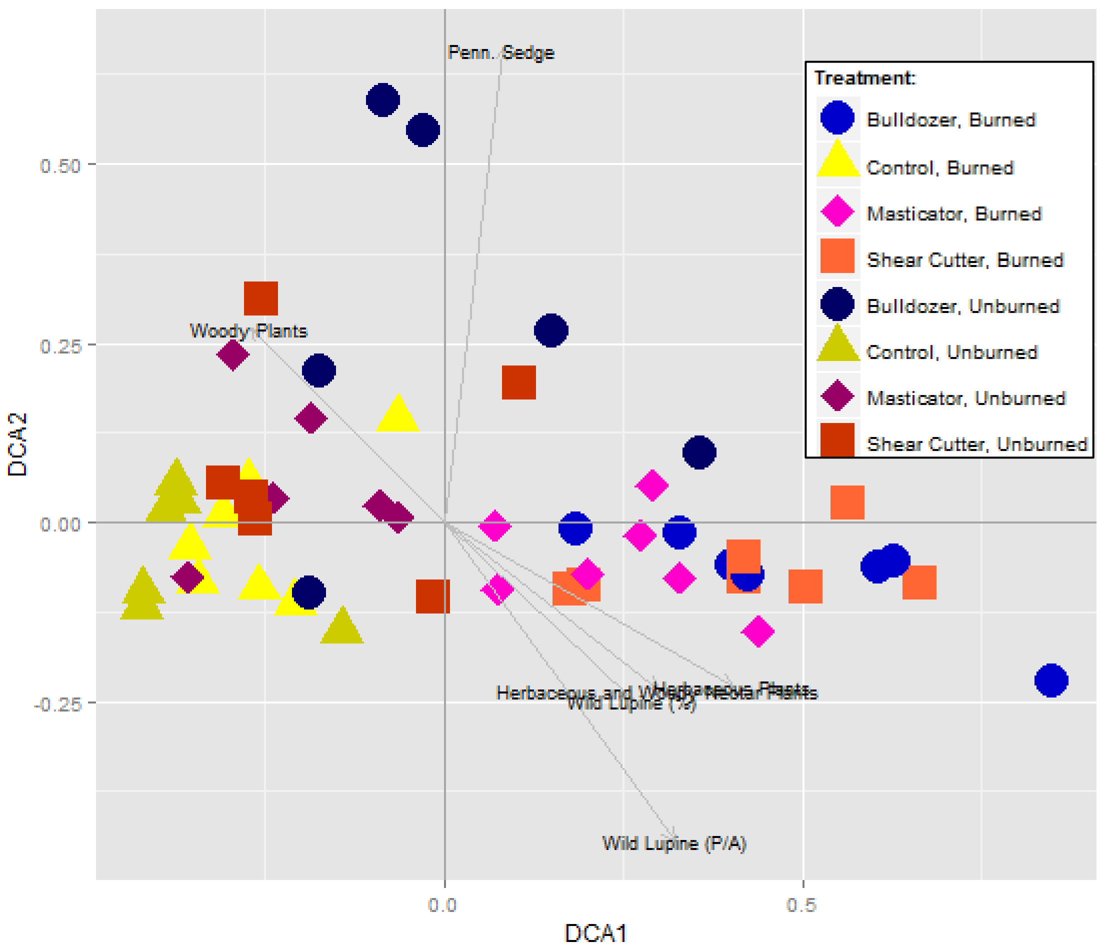
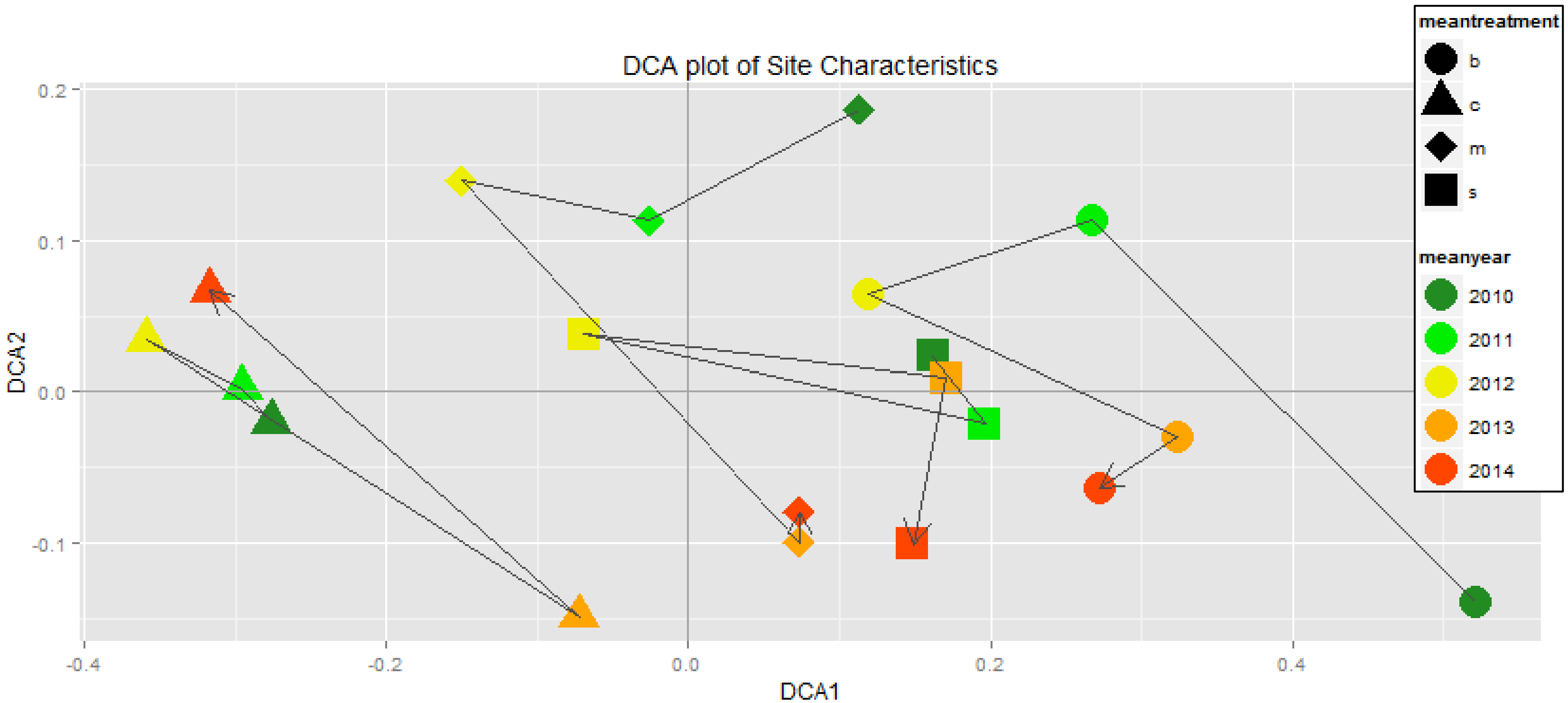
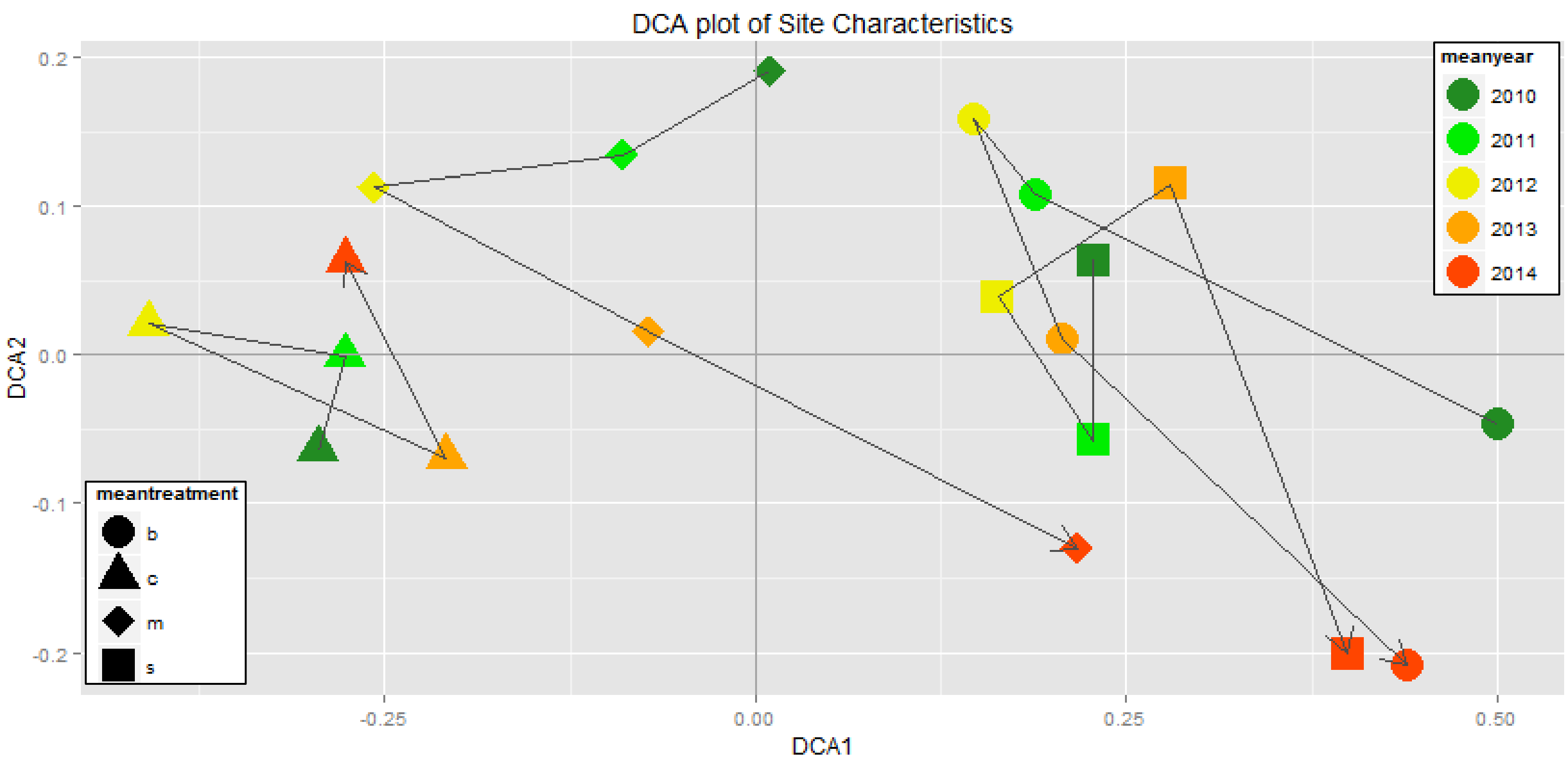


Figure A2.2. Mean yearly DCA plots of site conditions computed with all data (A2a) as well as PPRA (A2b) and WRMA (A2c) separately.

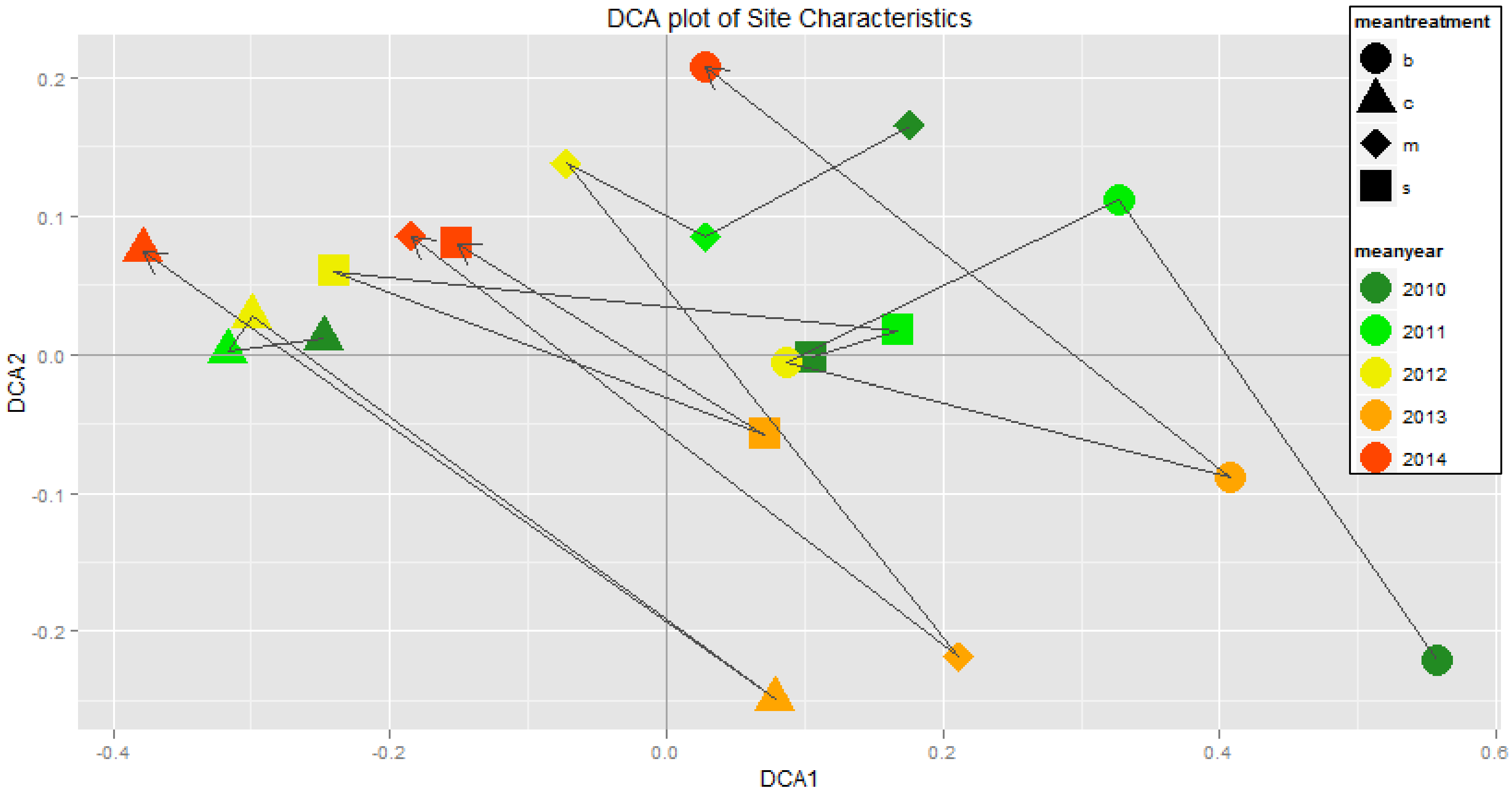
(A2.2a). Plot of DCA axes 1 and 2. Mean values for each year are plotted. Shapes represent treatments, while the green-red color gradient represents year. An arrow is drawn through each treatment beginning at 2010 and ending at 2014. Control plots are located to the far left, while all three treatments are towards the center or right side of the plot. Note that all three treatments begin to converge by 2013, and especially in 2014. **This plot includes data from both management units**.



(A2.2b). Plot of DCA axes 1 and 2. Mean values for each year are plotted. Shapes represent treatments, while the green-red color gradient represents year. An arrow is drawn through each treatment beginning at 2010 and ending at 2014. Control plots are located to the far left, while all three treatments are towards the center or right side of the plot. **This plot only includes data from PPRA**.



(A2.2c). Plot of DCA axes 1 and 2. Mean values for each year are plotted. Shapes represent treatments, while the green-red color gradient represents year. An arrow is drawn through each treatment beginning at 2010 and ending at 2014. Control plots are located to the far left, while all three treatments are towards the center or right side of the plot. **This plot only includes data from WRMA**.



Appendix 3.

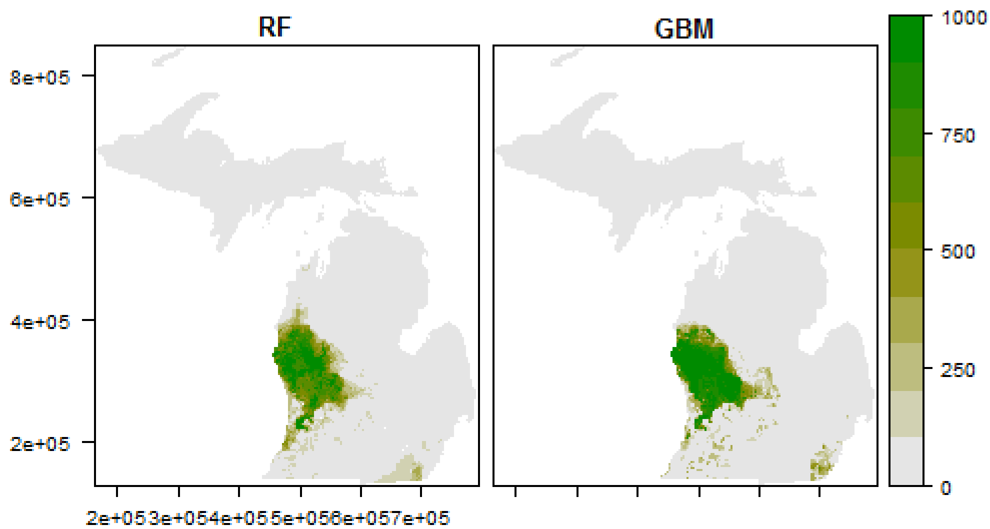
Table A3.1. List of variables considered in preliminary analyses.

Variable	Description	Original Resolution	Resampling or Aggregation Strategy	Source
Elevation	Elevation in meters	30 m	Mean	Gesch et al. 2002
Land Cover	Broad land cover classification (National Land Cover Database, 2011)	30 m	Mode	Homer et al. 2015
Soil Drainage Class	Soil drainage, acquired from the Soil Survey Geographic Database (SSURGO)	Vector	—	NRCS 2015
Soil Order	Soil taxonomic order, acquired from SSURGO	Vector	—	NRCS 2015
Water Table Depth	Depth to water table from surface	30 m	Mean	MIDEQ 2005
Mean Annual Daily Temperature	Average daily temperature mean, across the year	800 m	—	PRISM 2014
Mean Annual Daily Maximum Temperature	Average daily temperature maximum, across the year	800 m	—	PRISM 2014
Mean Annual Daily Minimum Temperature	Average daily temperature minumum, across the year	800 m	—	PRISM 2014
Mean Winter Temperature		800 m	—	PRISM 2014
Mean Spring Temperature		800 m	—	PRISM 2014
Mean Summer Temperature		800 m	—	PRISM 2014
Mean Fall Temperature		800 m	—	PRISM 2014
Mean Maximum Winter Temperature		800 m	—	PRISM 2014
Mean Maximum Spring Temperature		800 m	—	PRISM 2014
Mean Maximum Summer Temperature		800 m	—	PRISM 2014
Mean Maximum Fall Temperature		800 m	—	PRISM 2014
Mean Minumum Winter Temperature		800 m	—	PRISM 2014
Mean Minumum Spring Temperature		800 m	—	PRISM 2014
Mean Minumum Summer Temperature		800 m	—	PRISM 2014

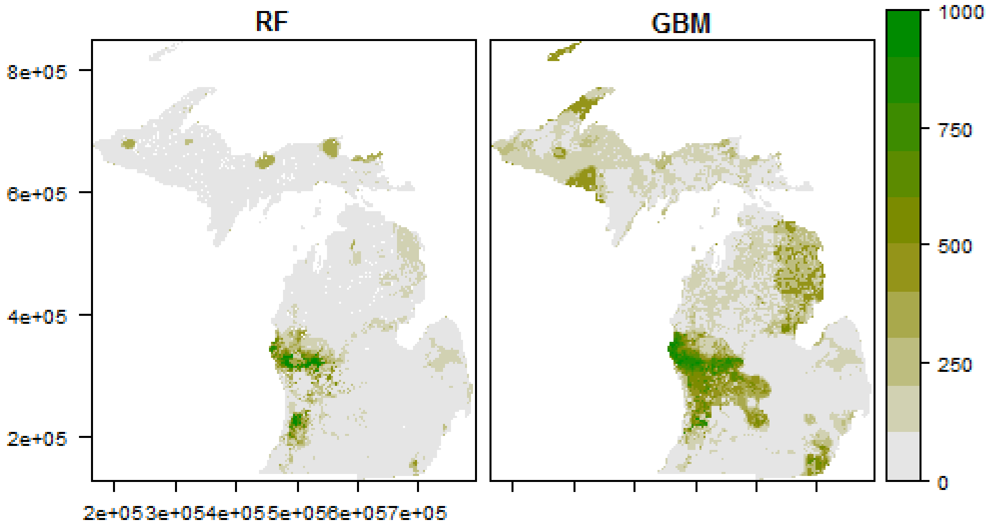
Mean Minumum Fall Temperature		800 m	—	PRISM 2014
Mean Annual Precipitation		800 m	—	PRISM 2014
Mean Winter Precipitation		800 m	—	PRISM 2014
Mean Spring Precipitation		800 m	—	PRISM 2014
Mean Summer Precipitation		800 m	—	PRISM 2014
Mean Fall Precipitation		800 m	—	PRISM 2014
Future Climate Variables	The same 20 climate variables as above, for 2010-2039, 2040-2069, 2070-2099, across two climate change models: GFDL A1FI and PCM B1	12 km	Nearest Neighbor (direct 1:225 conversion)	Stoner et al. 2013

Figure A3.1. (a through u). Maps illustrating the effect of climate change on the mean distribution of suitable habitat for the three butterfly species in this study. Between model differences (RF vs. GBM) are illustrated. Habitat suitability is reported on a unitless scale ranging from 0 to 1000; gray colors (closer to 0) represent unsuitable habitat, while darker green represents more suitable habitat. In this study, we considered suitability values ≥333 (i.e., the upper 66% of values) to be colonizable by the species.

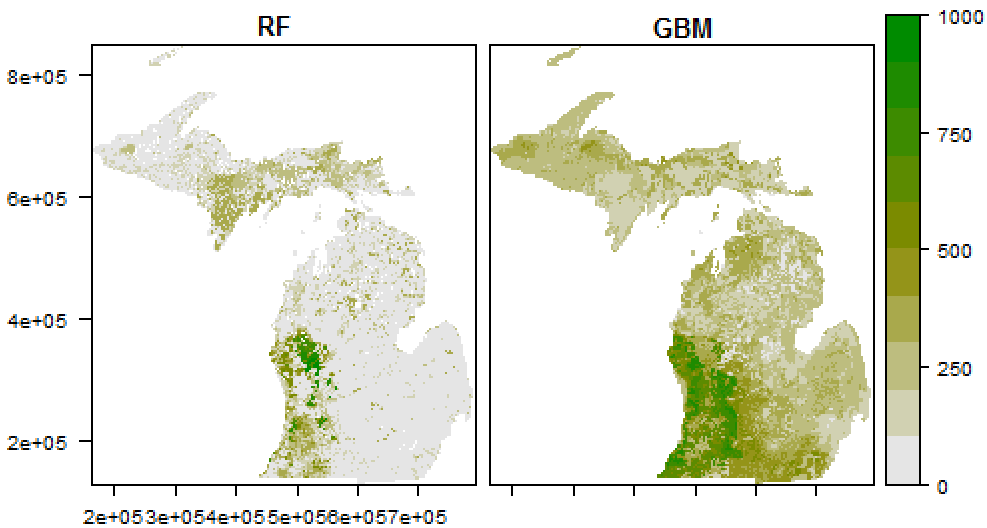
(A3.1a). Karner Blue butterfly species distribution models, current climate conditions. Habitat suitability is represented on a unitless 0-1000 scale.



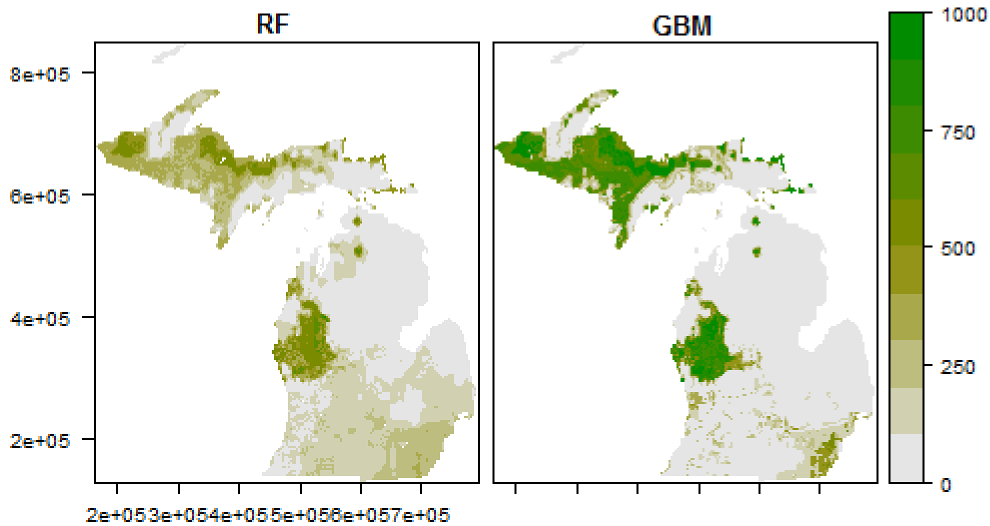
(**A3.1b**). Frosted elfin species distribution models, current climate conditions. Habitat suitability is represented on a unitless 0-1000 scale.



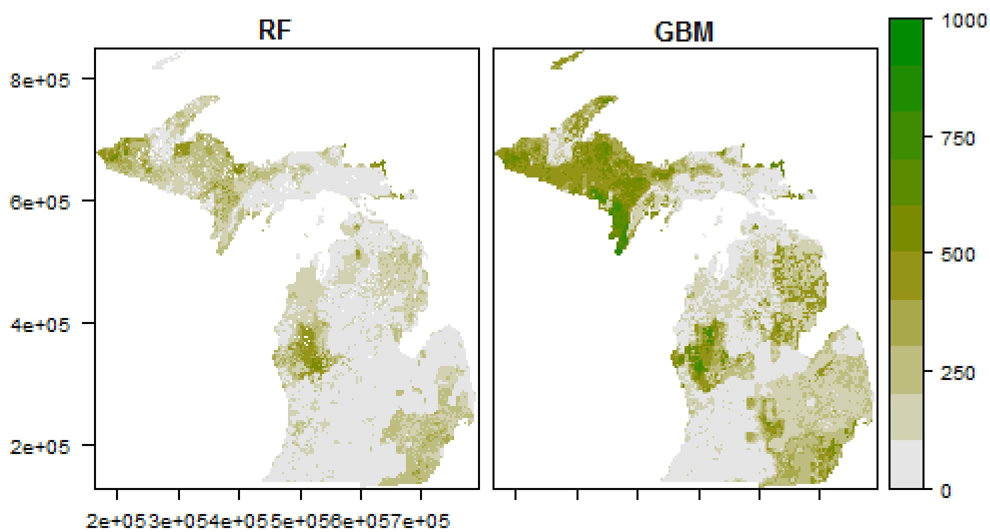
(**A3.1c**). Persius duskywing species distribution models, current climate conditions. Habitat suitability is represented on a unitless 0-1000 scale.



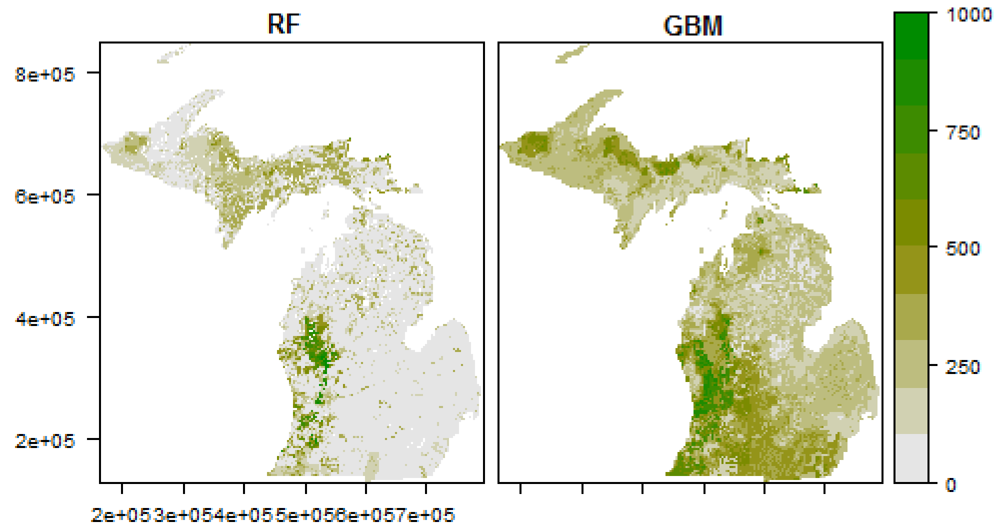
(A3.1d). Karner blue species distribution models, GFDL 2010-2039.



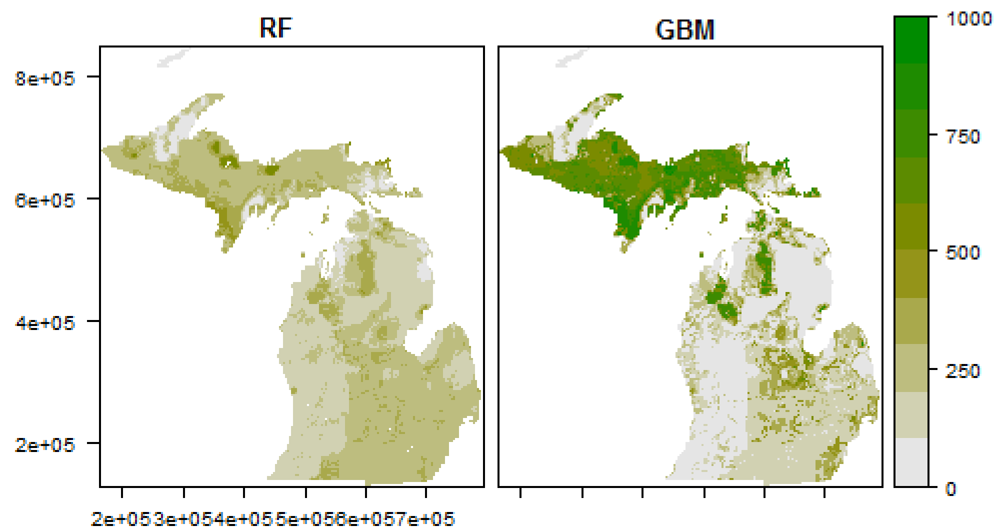
(A3.1e). Frosted elfin species distribution models, GFDL 2010-2039.



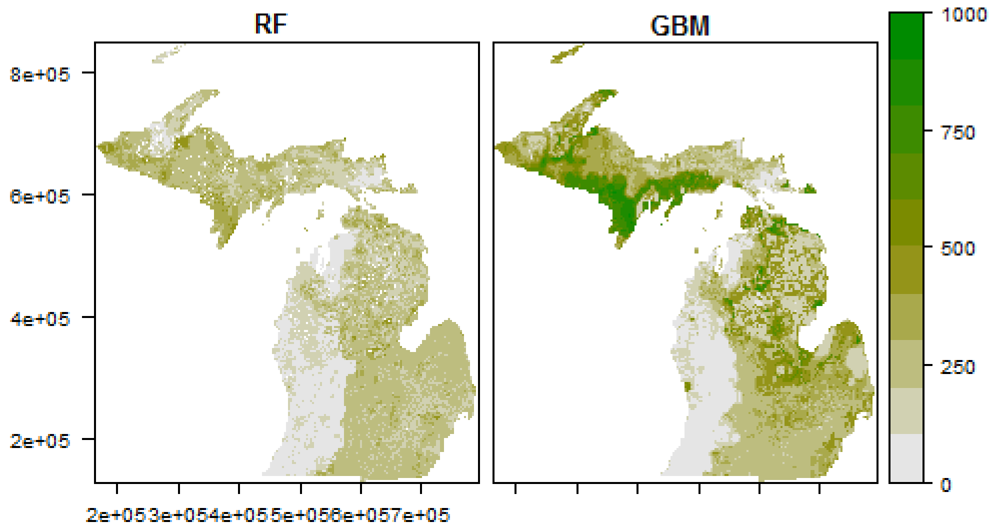
(A3.1f). Persius duskywing species distribution models, GFDL 2010-2039.



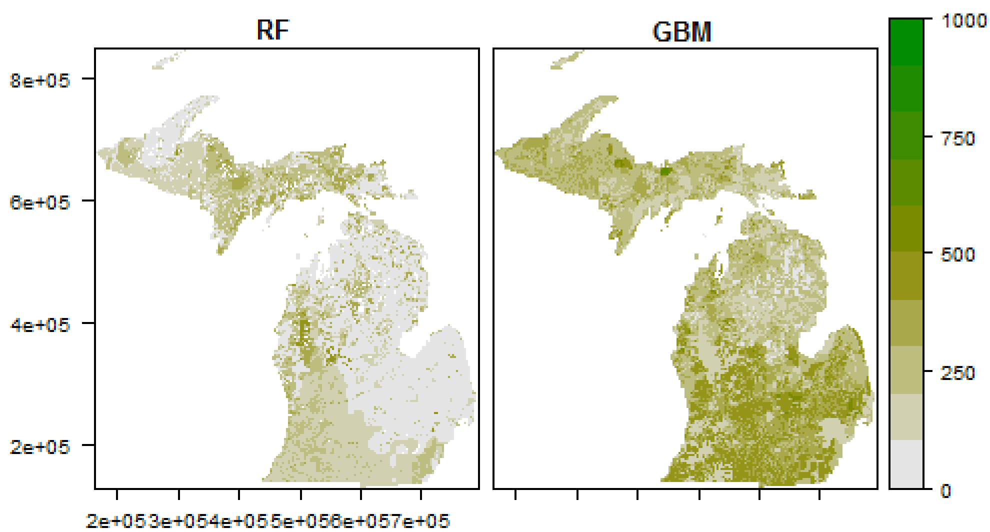
(A3.1g). Karner blue species distribution models, GFDL 2040-2069.



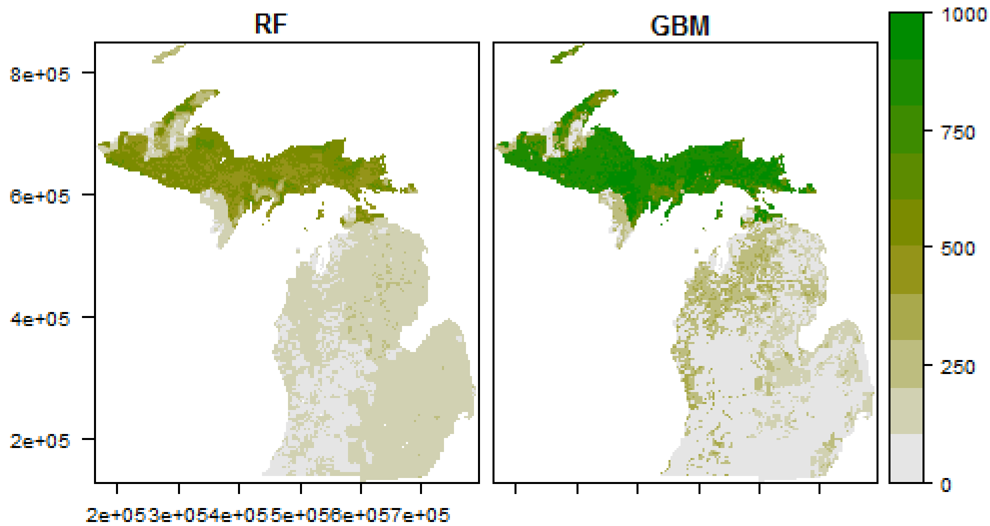
(A3.1h). Frosted elfin species distribution models, GFDL 2040-2069.



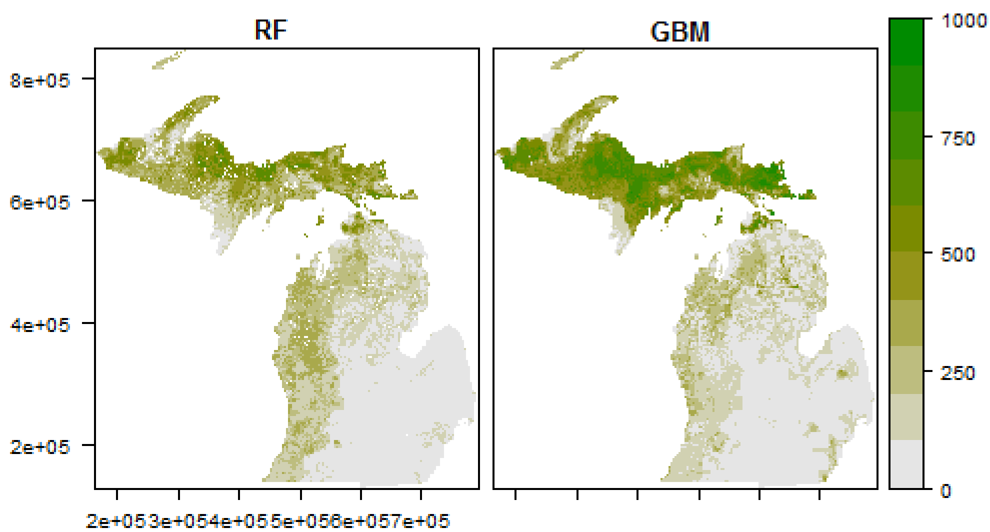
(A3.1i). Persius duskywing species distribution models, GFDL 2040-2069.



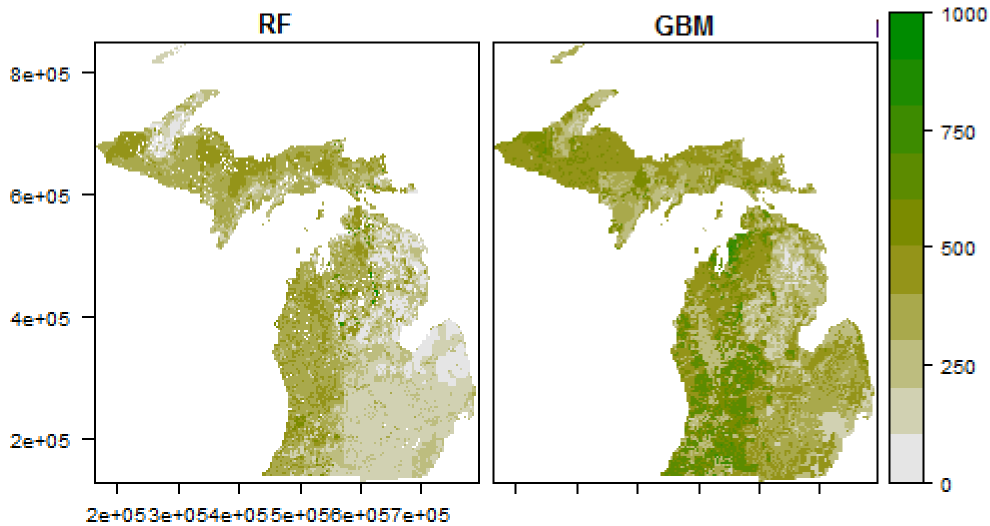
(A3.1j). Karner blue species distribution models, GFDL 2070-2099.



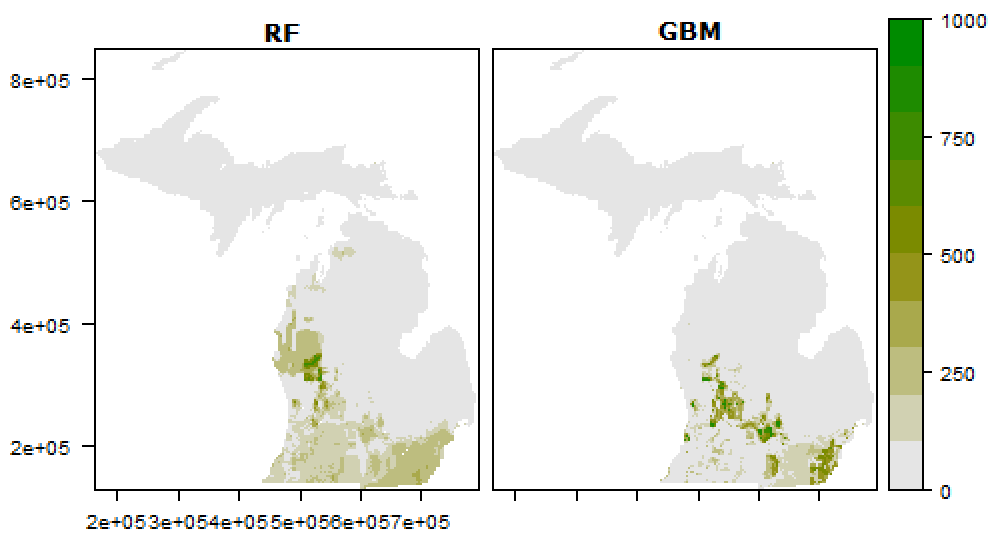
(A3.1k). Frosted elfin species distribution models, GFDL 2070-2099.



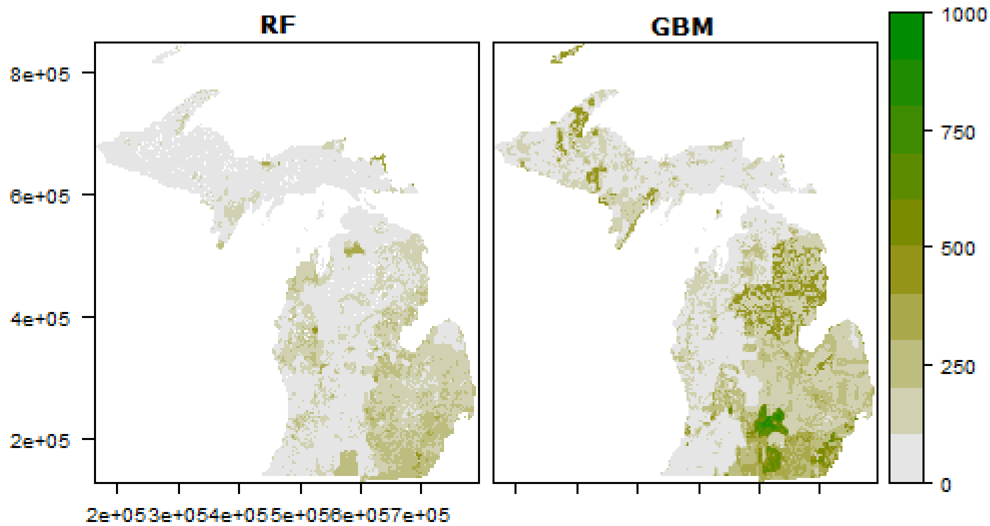
(A3.1l). Persius duskywing species distribution models, GFDL 2070-2099.



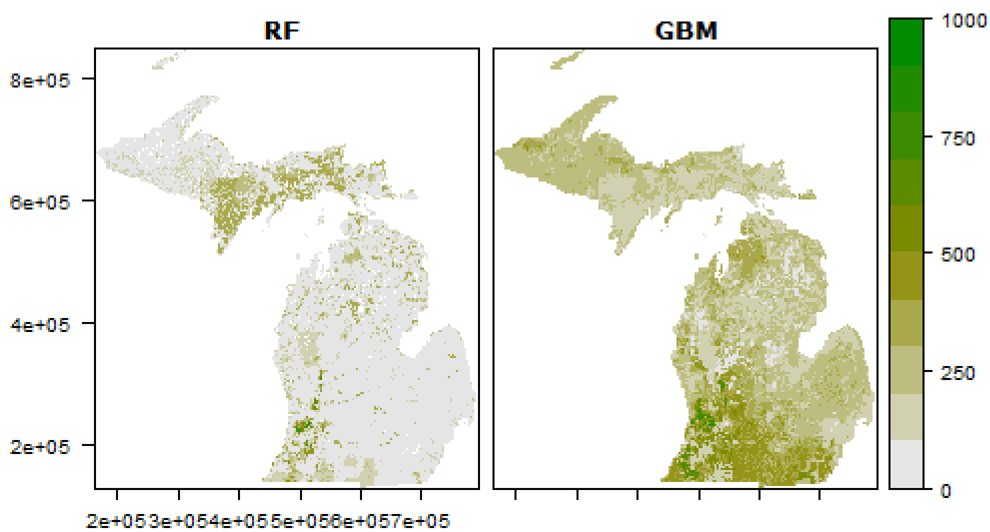
(A3.1m). Karner blue species distribution models, PCM 2010-2039.



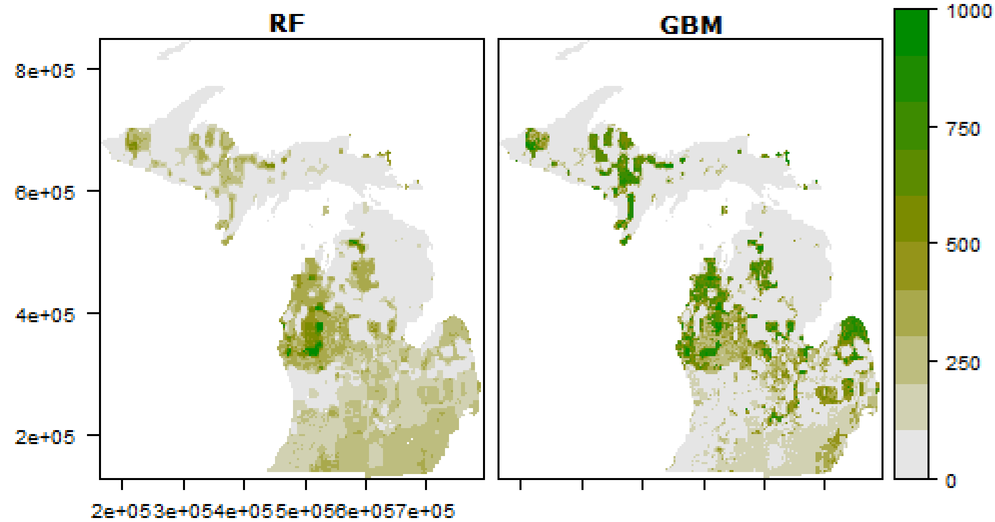
(A3.1n). Frosted elfin species distribution models, PCM 2010-2039.



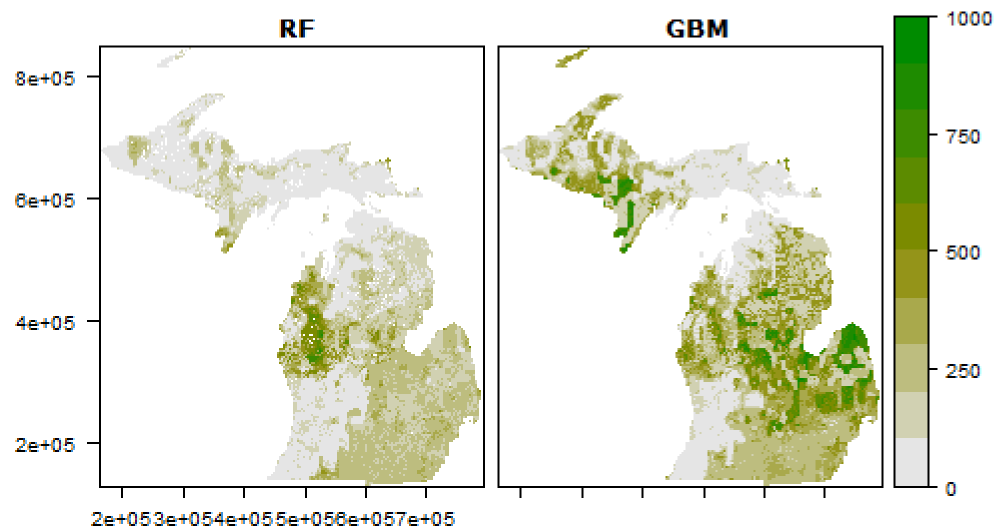
(A3.1o). Persius duskywing species distribution models, PCM 2010-2039.



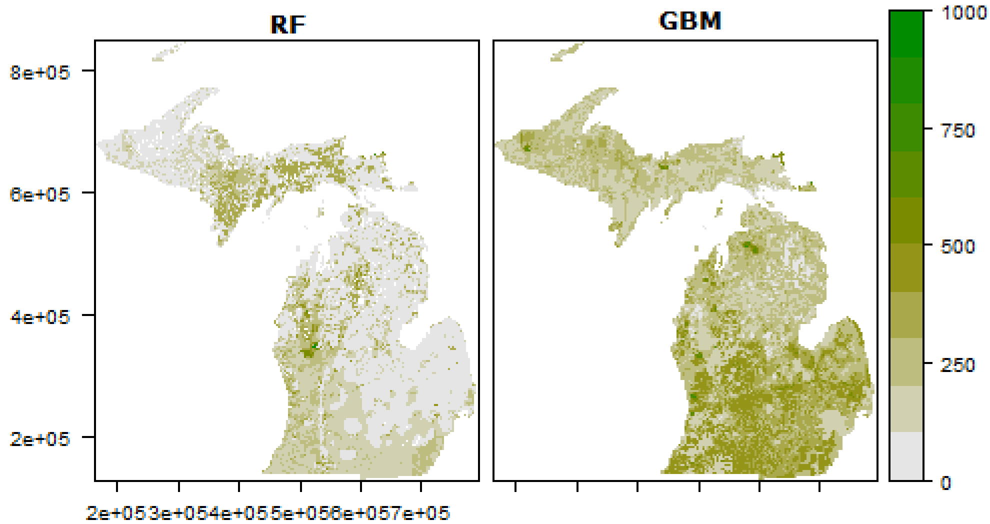
(A3.1p). Karner blue species distribution models, PCM 2040-2069.



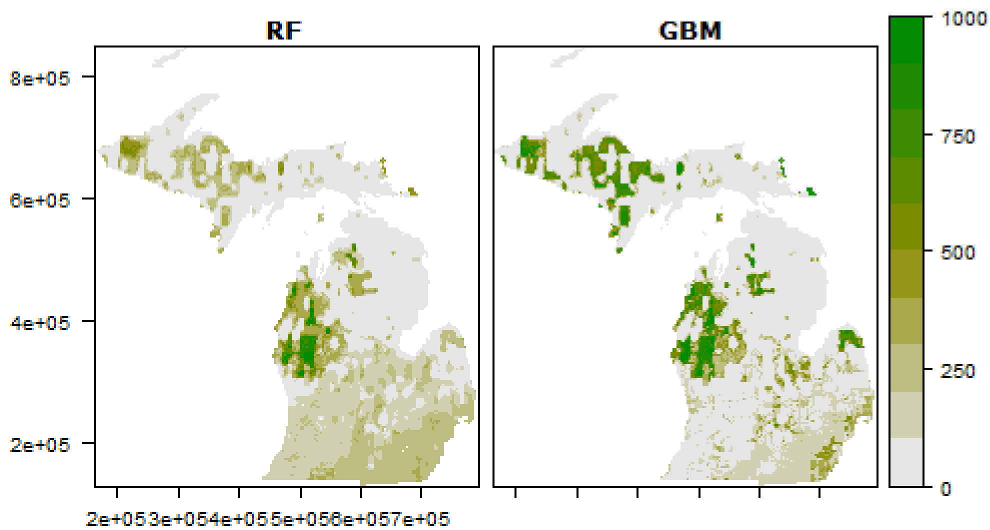
(A3.1q). Frosted elfin species distribution models, PCM 2040-2069.



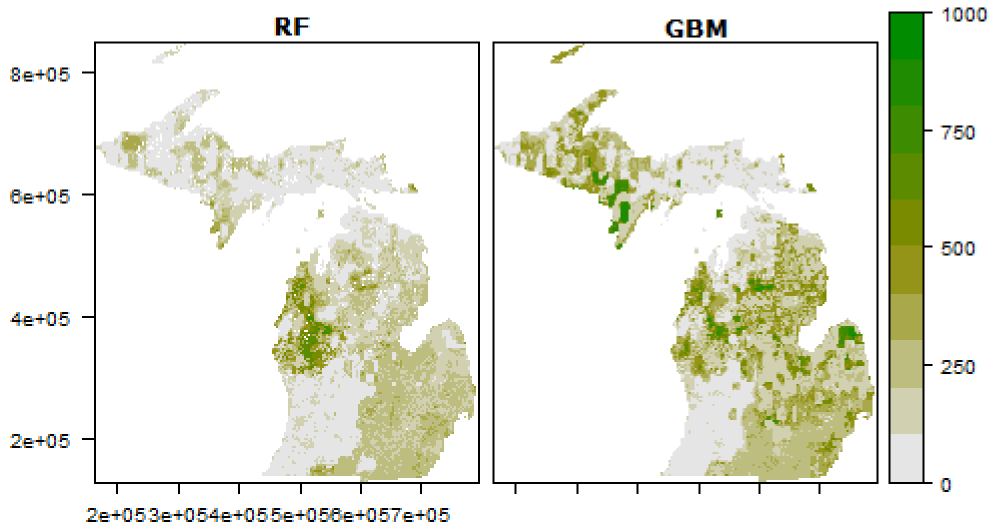
(A3.1r). Persius duskywing species distribution models, PCM 2040-2069.



(A3.1s). Karner blue species distribution models, PCM 2070-2099.



(A3.1t). Frosted elfin species distribution models, PCM 2070-2099.



(A3.1u). Persius duskywing species distribution models, PCM 2070-2099.

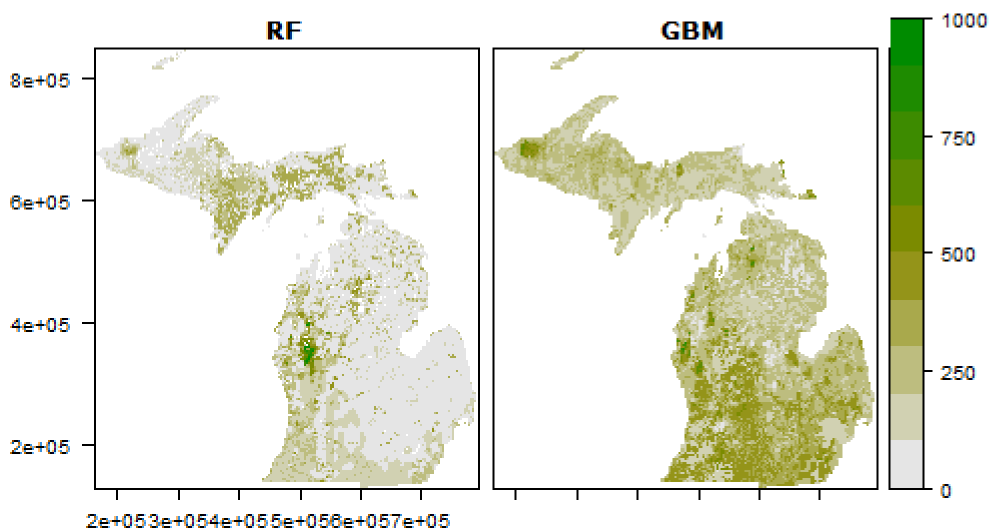


Figure A3.2 index.
Each of the following response plots in figure A3.2 incorporates at least one categorical variable, whose values are labeled with numbers. For soil order (rastert_so), those values are:

Value	Soil Order
1	Unclassified
2	Alfisol
3	Mollisol
4	Entisol
5	Histosol
6	Inceptisol
7	Spodosol

For land cover (rastert_nlcd), those values are:

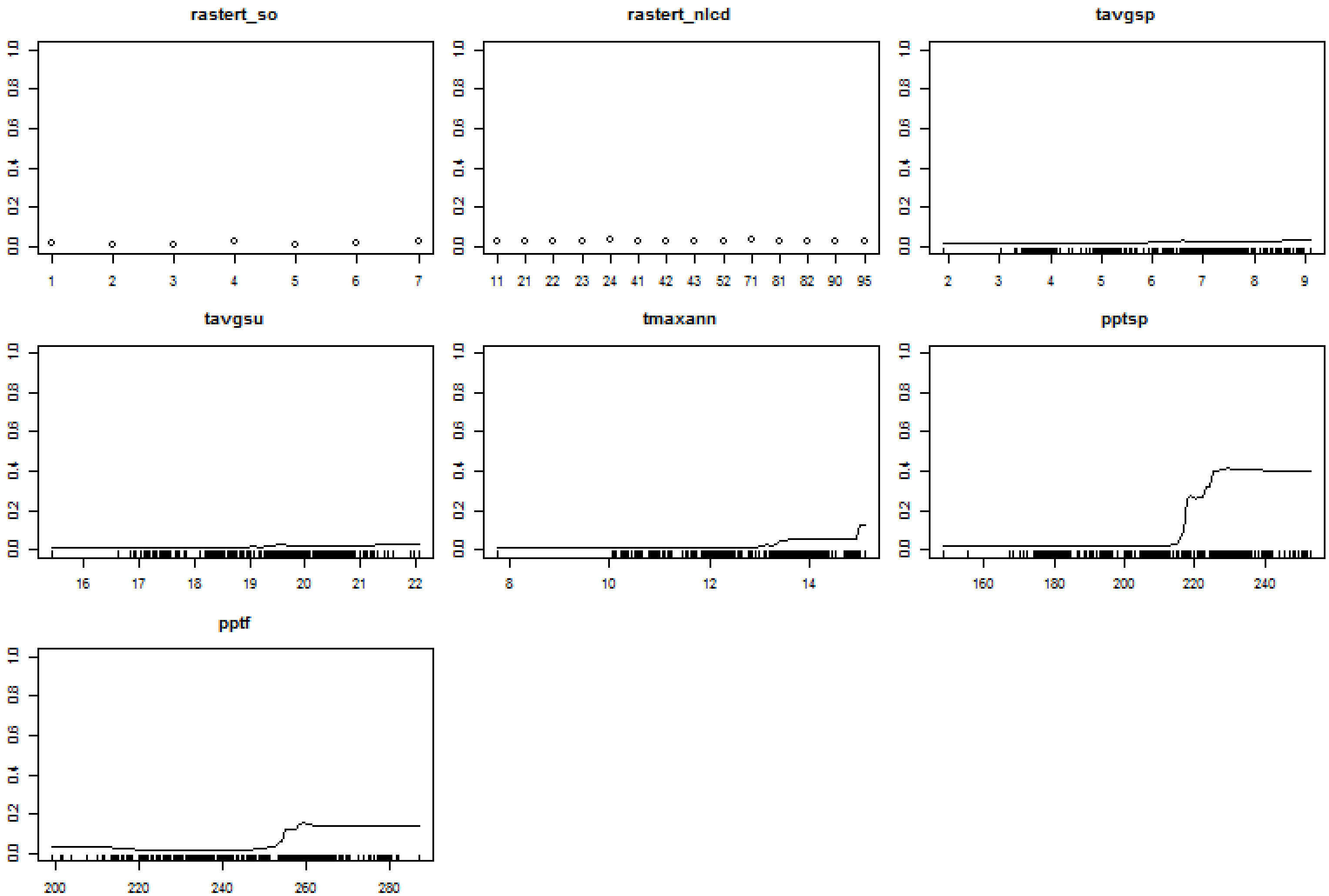
Value	Cover Type
11	Open water
21	Developed land, open
22	Developed land, light
23	Developed land, medium
24	Developed land, heavy
31	Barren land
41	Deciduous forest
42	Evergreen forest
43	Mixed forest
52	Shrubland
71	Herbaceous
81	Hay/pasture
82	Cultivated crops
90	Woody wetlands
95	Herbaceous wetlands

Figure A3.2 index cont'd.

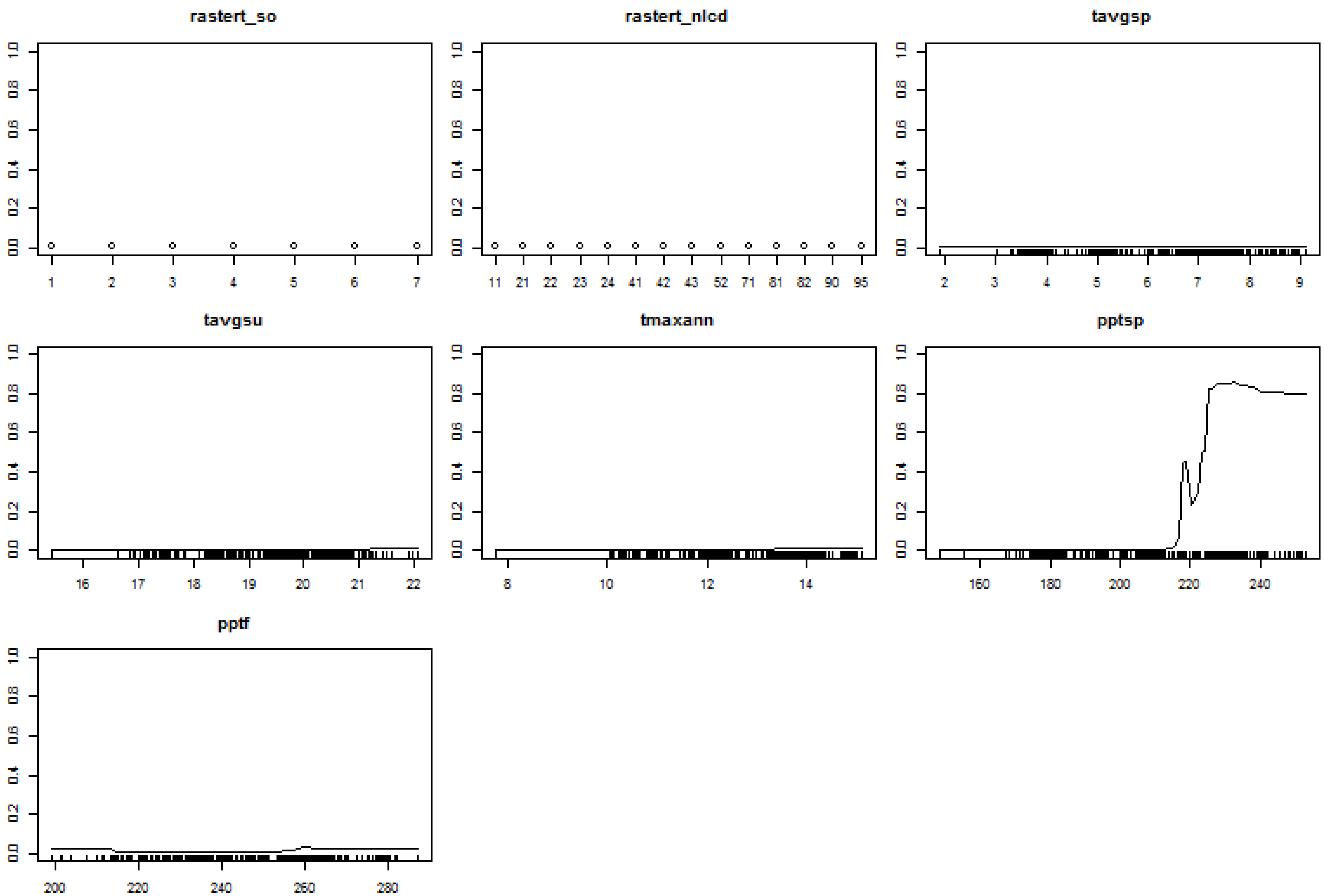
For soil drainage, those values are:

Value	Drainage Class
1	Excessively to poorly drained (variable)
2	Very poorly drained
3	Poorly drained
4	Poorly to very poorly drained (variable)
5	Moderately well drained
6	Well drained
7	Somewhat poorly drained
8	Excessively drained
9	Well to moderately well drained (variable)
10	Somewhat excessively drained
11	Unclassified

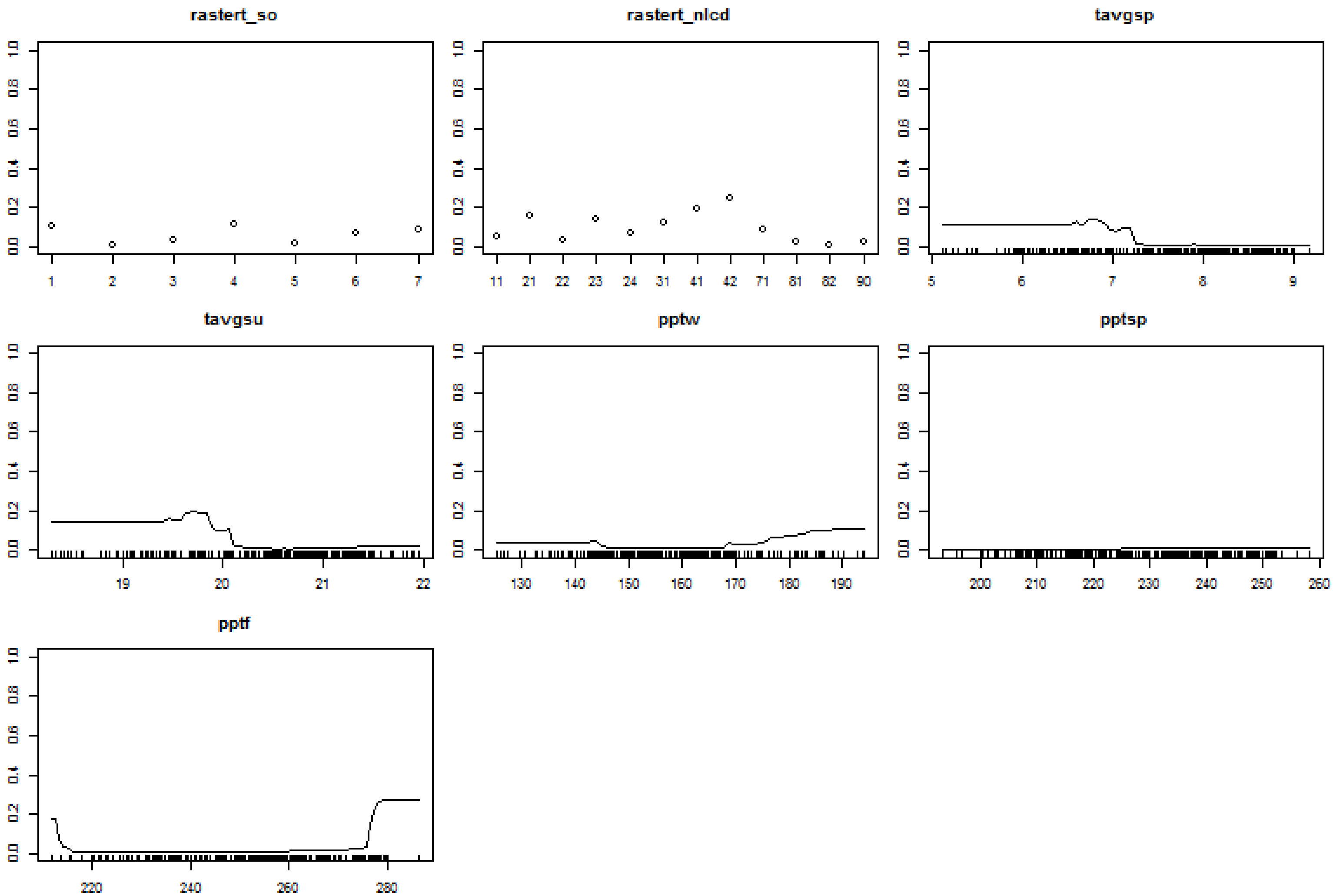
(**A3.2a**). Karner blue, RF. Variable response plots. Mean model response is plotted (y) against each predictor variable (x).



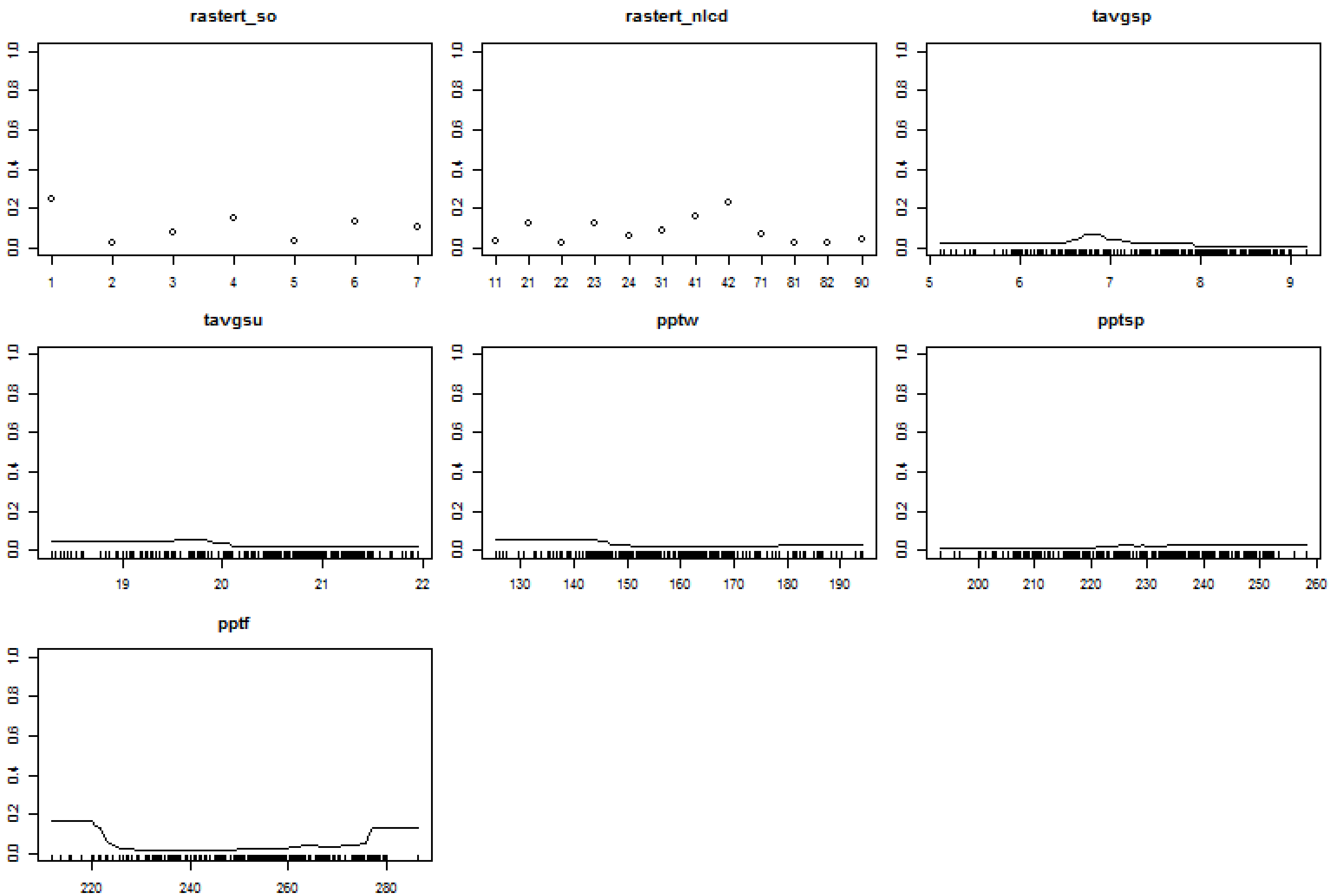
(A3.2b). Karner blue, GBM. Variable response plots. Mean model response is plotted (y) against each predictor variable (x).



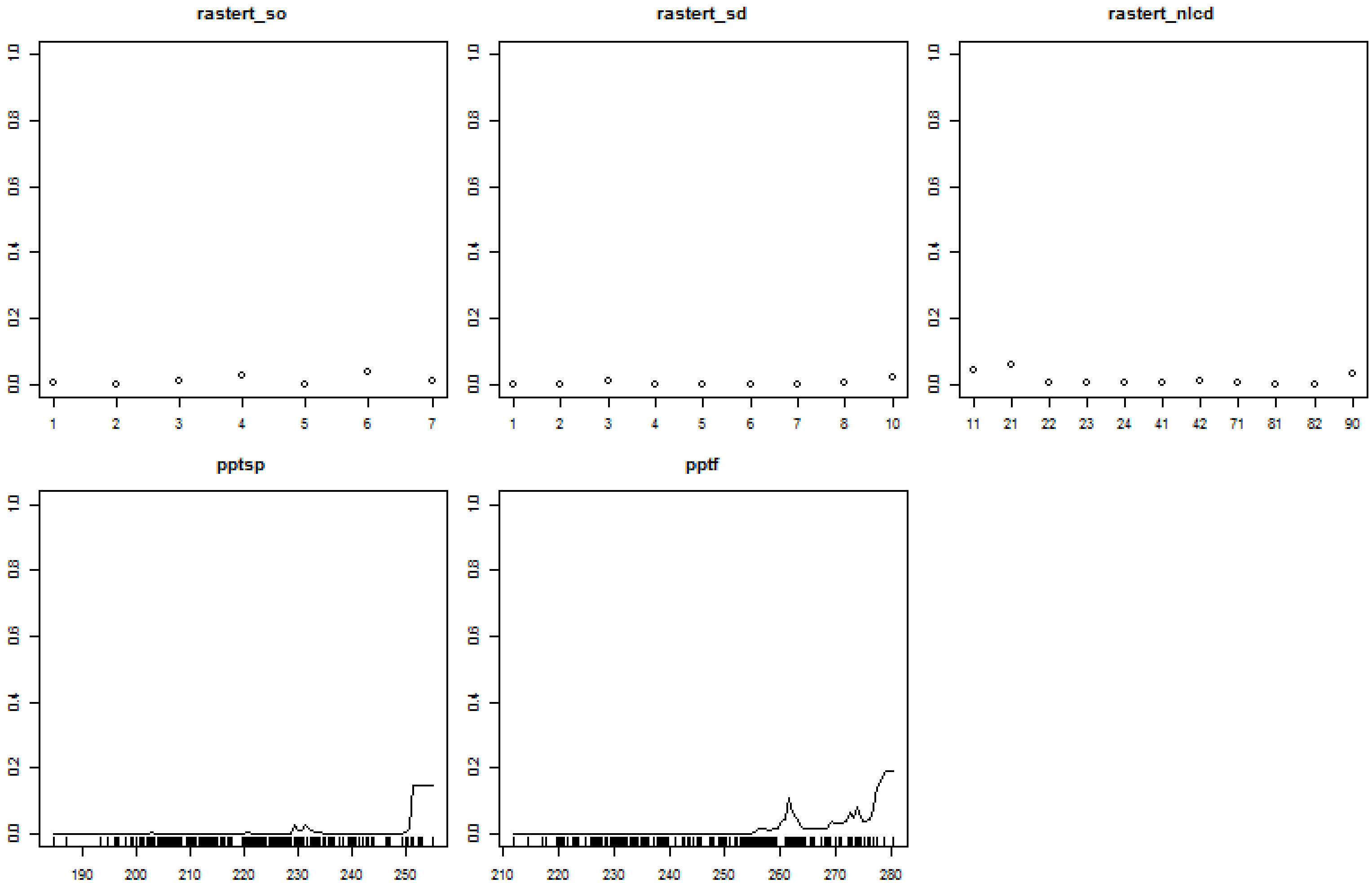
(A2c). Frosted elfin, RF. Variable response plots. Mean model response is plotted (y) against each predictor variable (x).



(A2d). Frosted elfin, GBM. Variable response plots. Mean model response is plotted (y) against each predictor variable (x).



(A2e). Persius duskywing, RF. Variable response plots. Mean model response is plotted (y) against each predictor variable (x).



(A2f). Frosted elfin, GBM. Variable response plots. Mean model response is plotted (y) against each predictor variable (x).

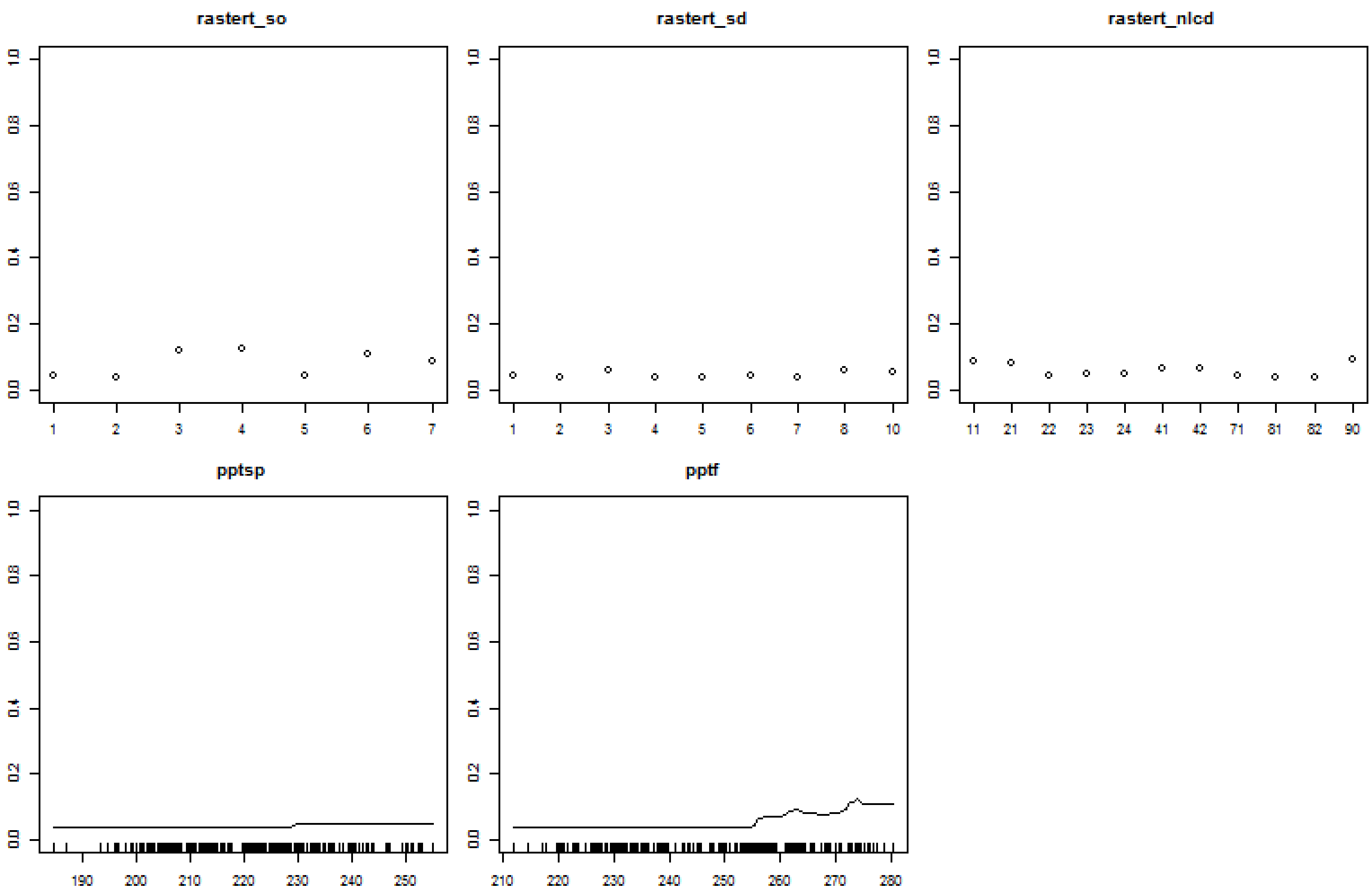
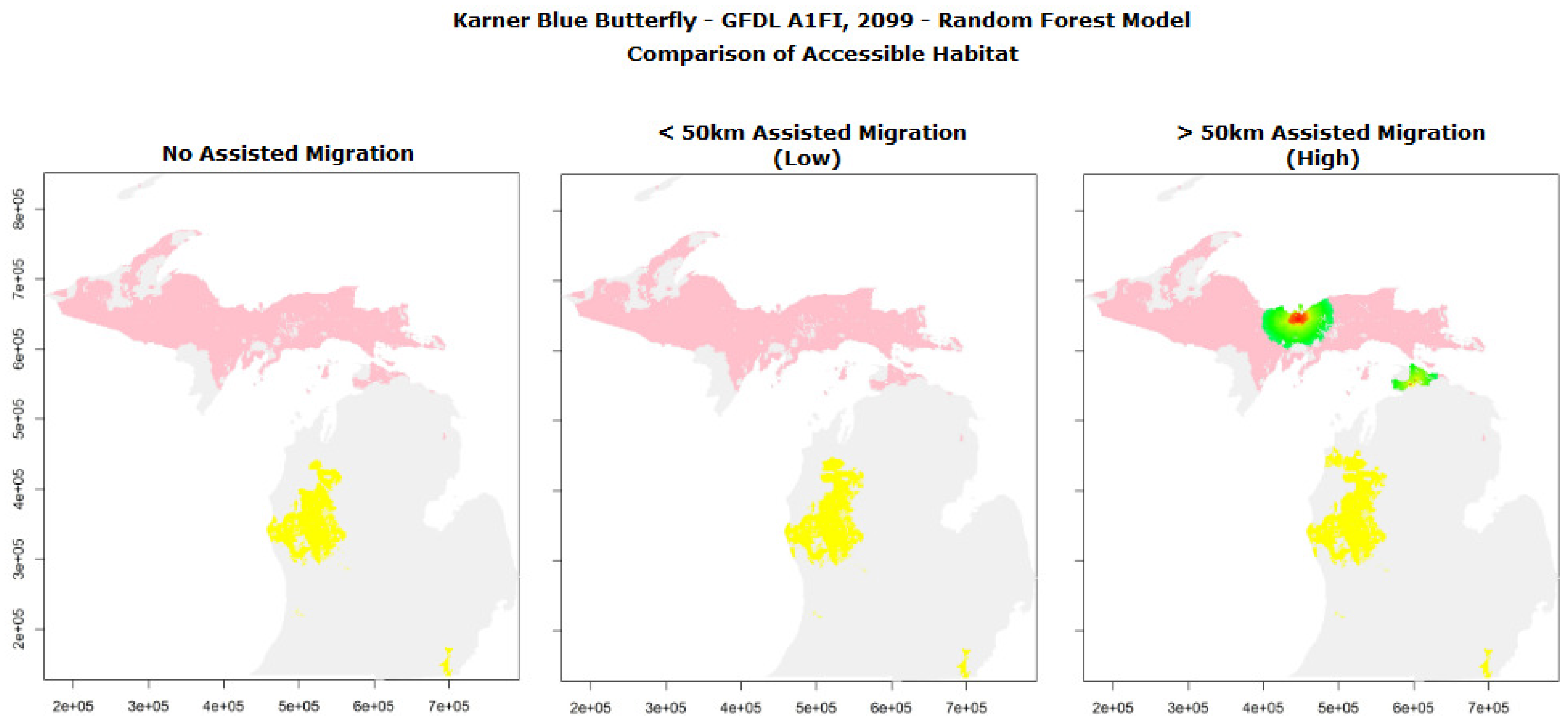
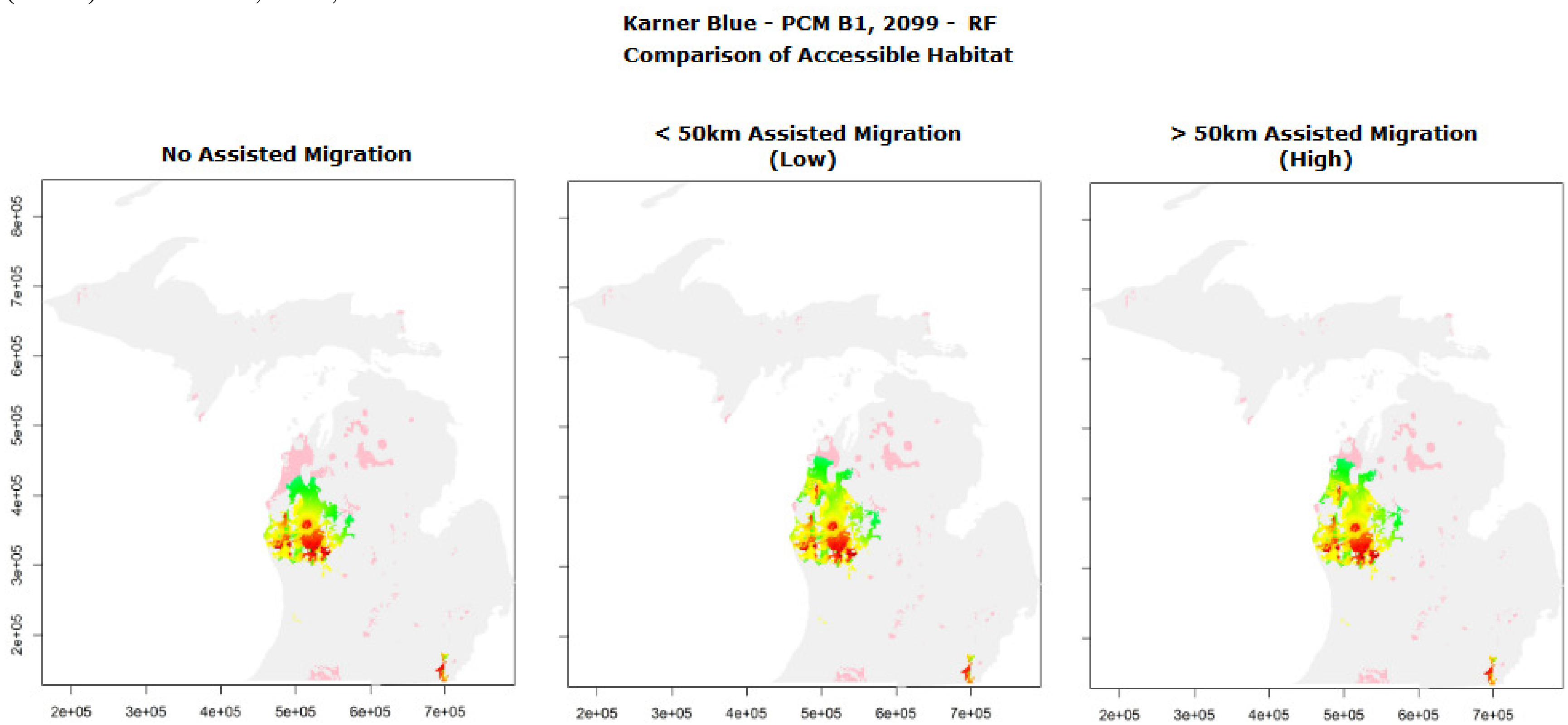


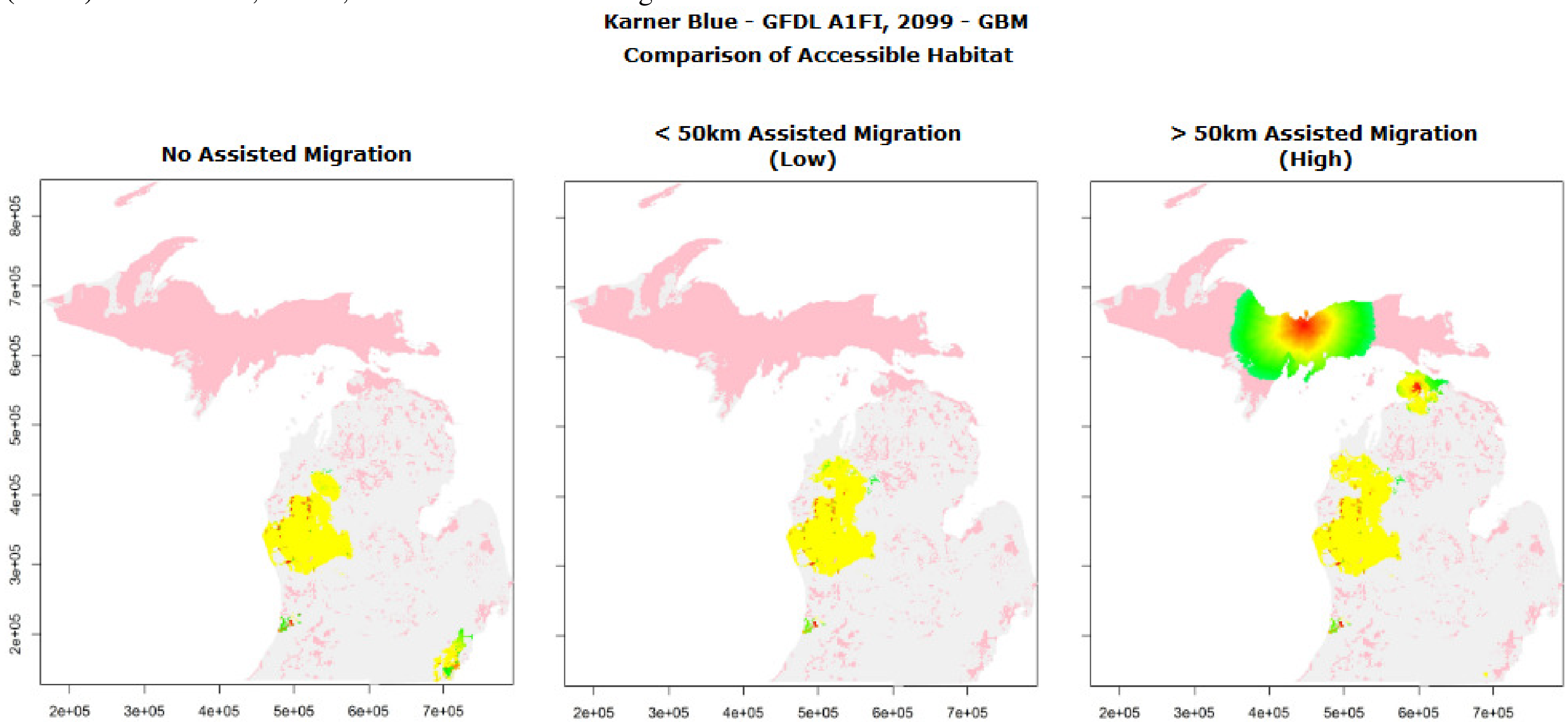
Figure A3.3. Maps illustrating the mean distribution of predicted suitable habitat that is projected to be physically accessible by each butterfly species at the end of the century. The green to red color gradient signifies accessible habitat for the species, with red areas being colonized earlier in the century and green areas being colonized toward the end of the century. Gray represents areas considered unsuitable for colonization (habitat suitability values < 333), pink represents suitable habitat not accessible by the species, and pale yellow represents formerly accessible habitat lost due to changes in habitat suitability over time (i.e., climate change). Maps trios are presented for each species, SDM approach × climate scenario, for a total of 12.
(A3.3a). Karner Blue, GFDL, Random Forest



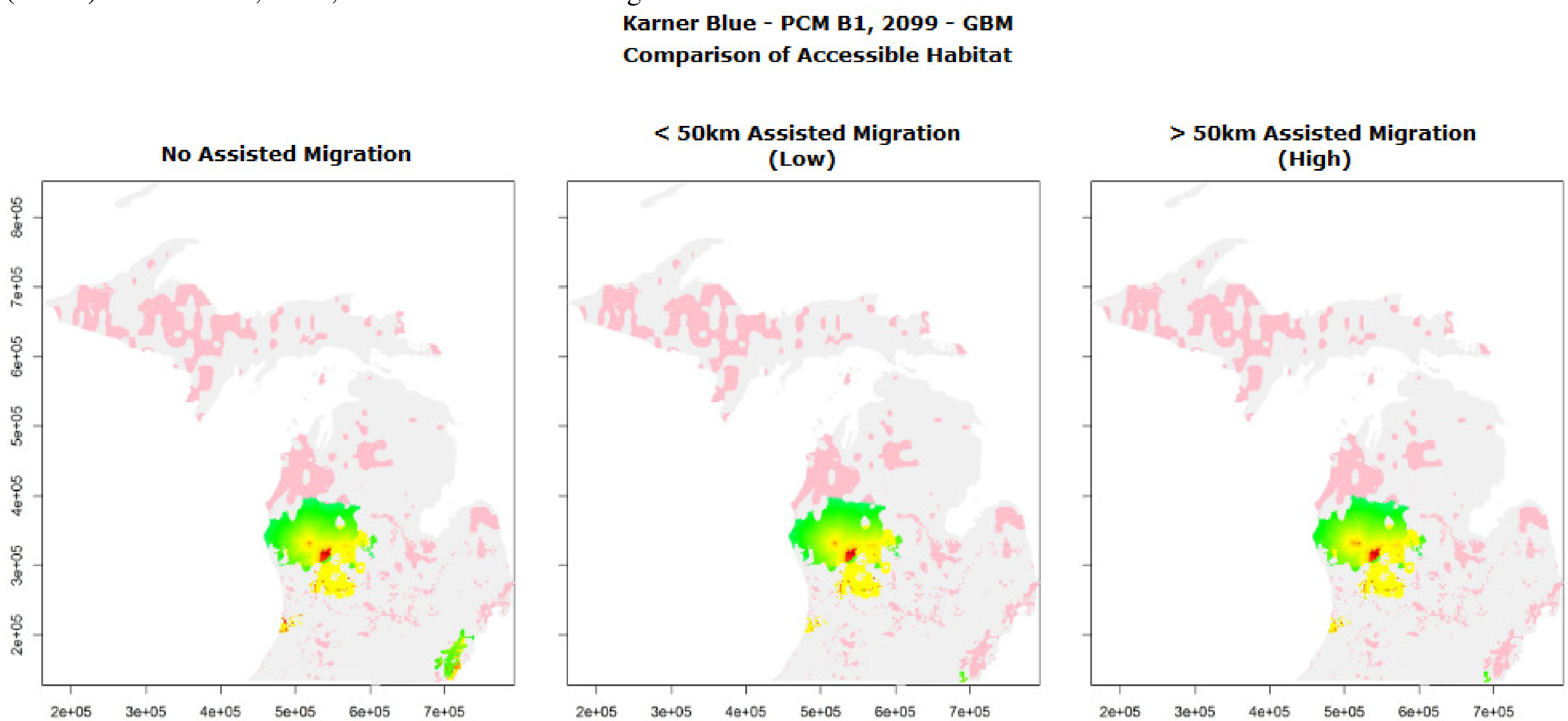
(A3.3b). Karner Blue, PCM, Random Forest



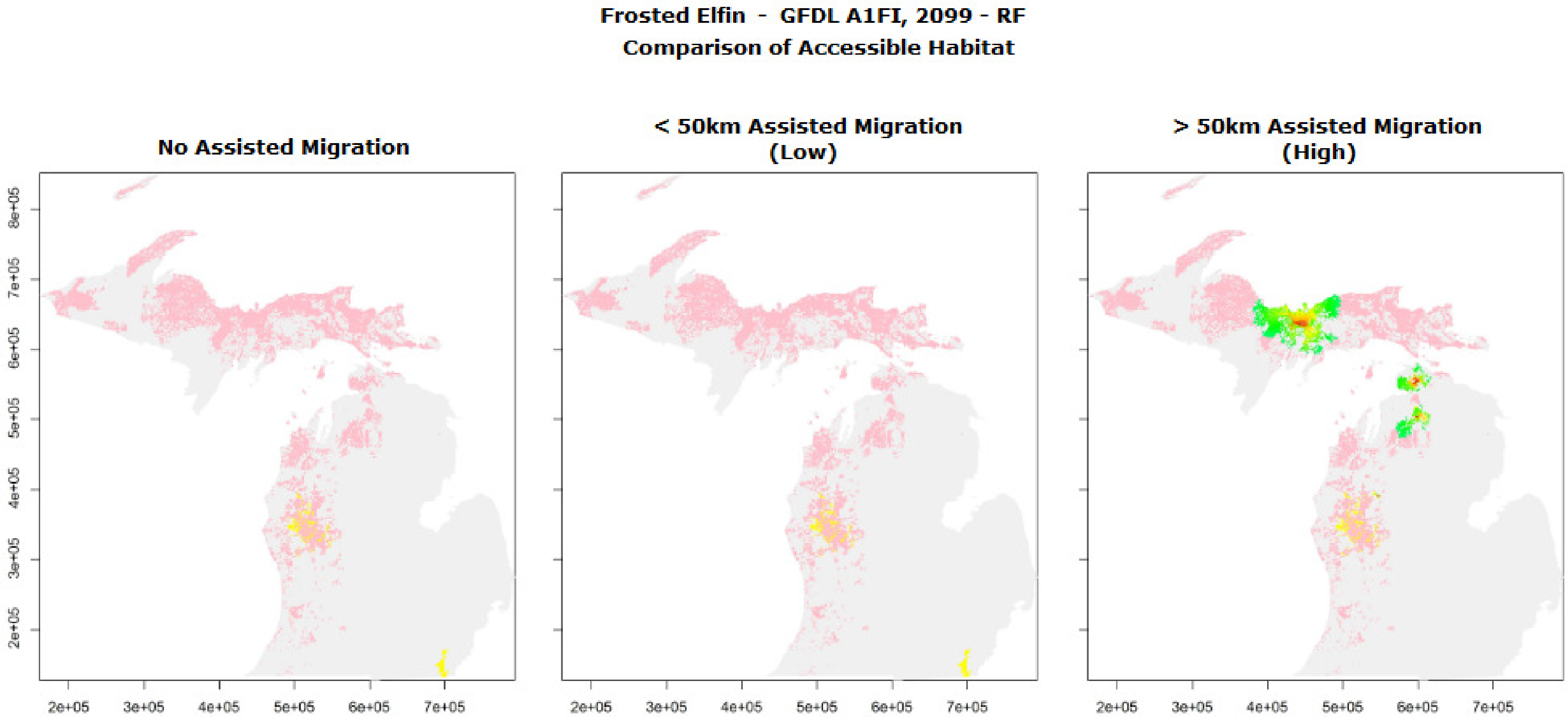
(A3.3c). Karner Blue, GFDL, Generalized Boosted Regression Model



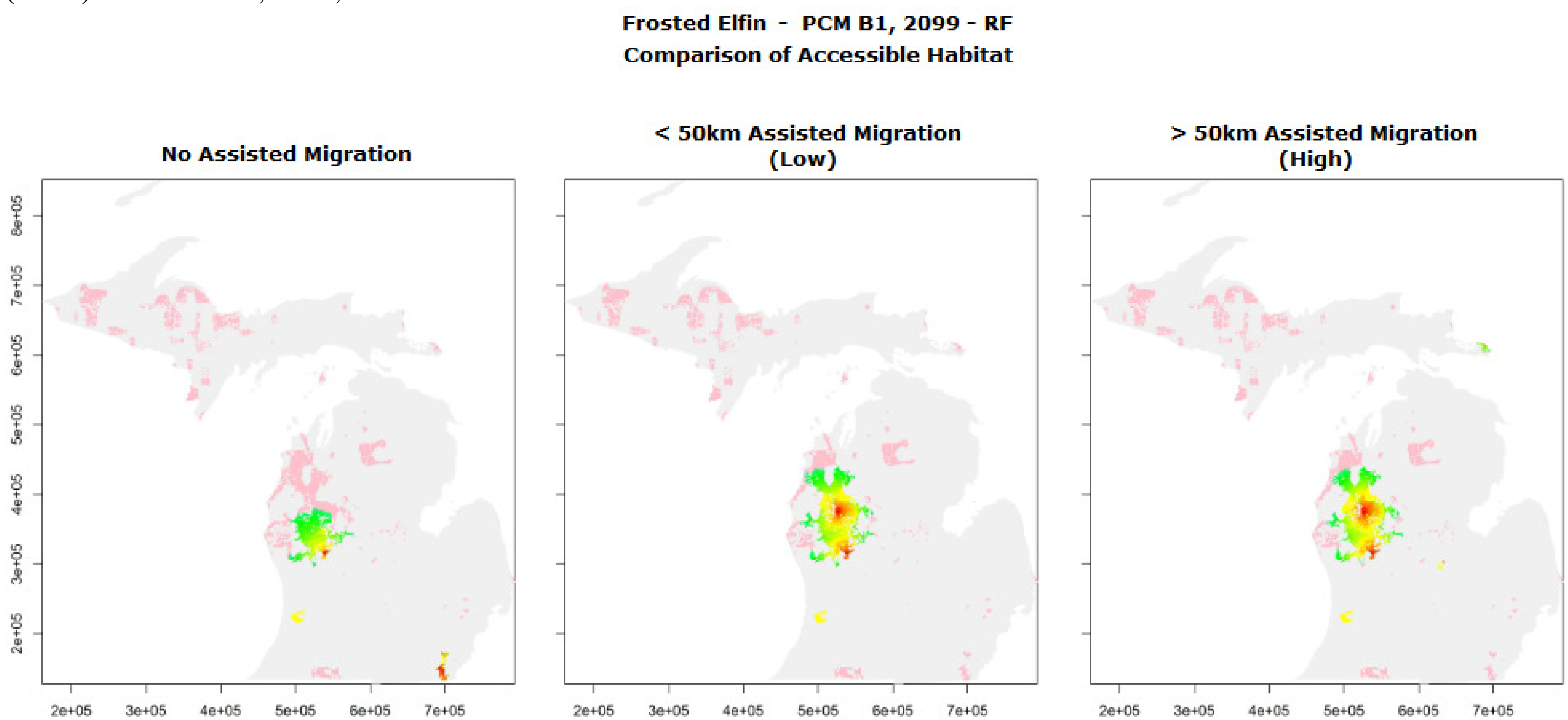
(A3.3d). Karner Blue, PCM, Generalized Boosted Regression Model



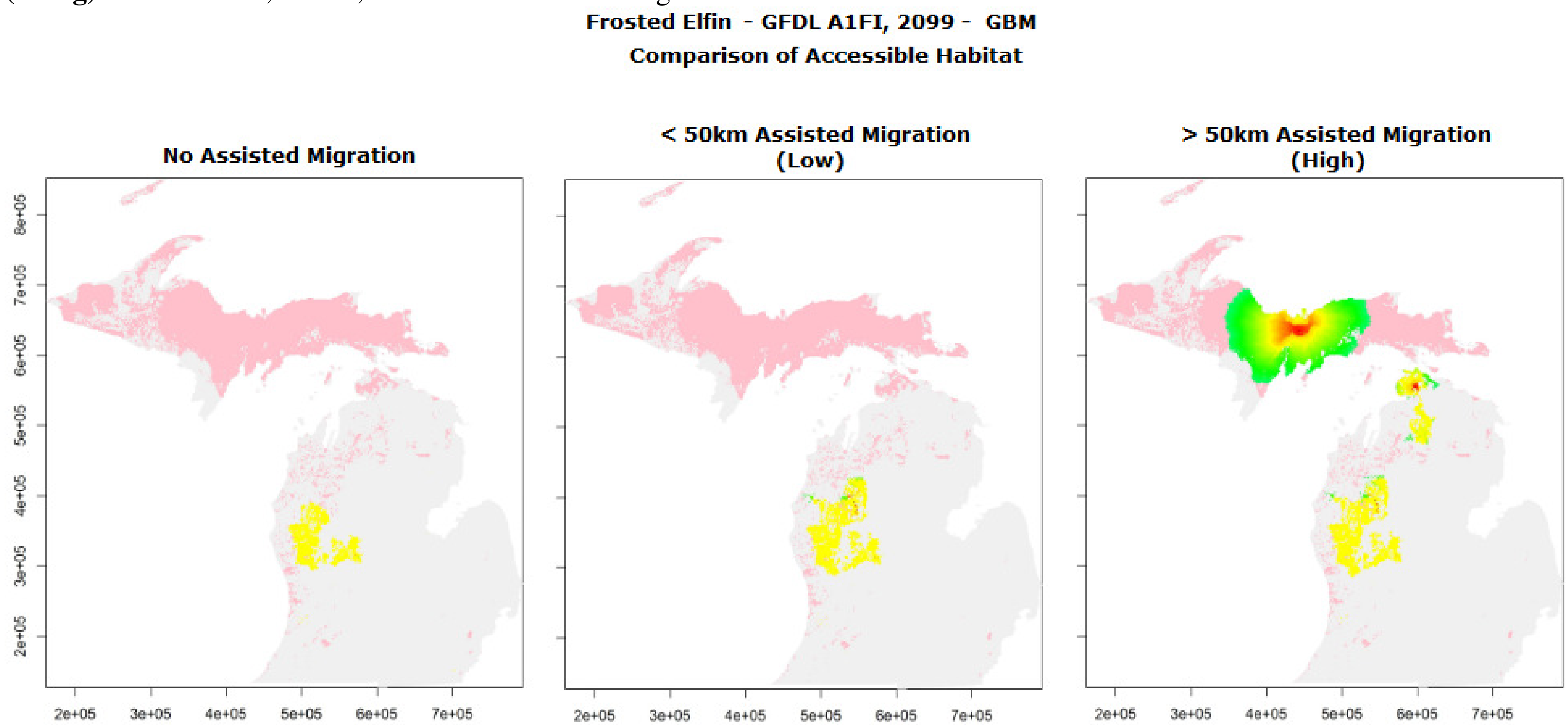
(A3.3e). Frosted Elfin, GFDL, Random Forest



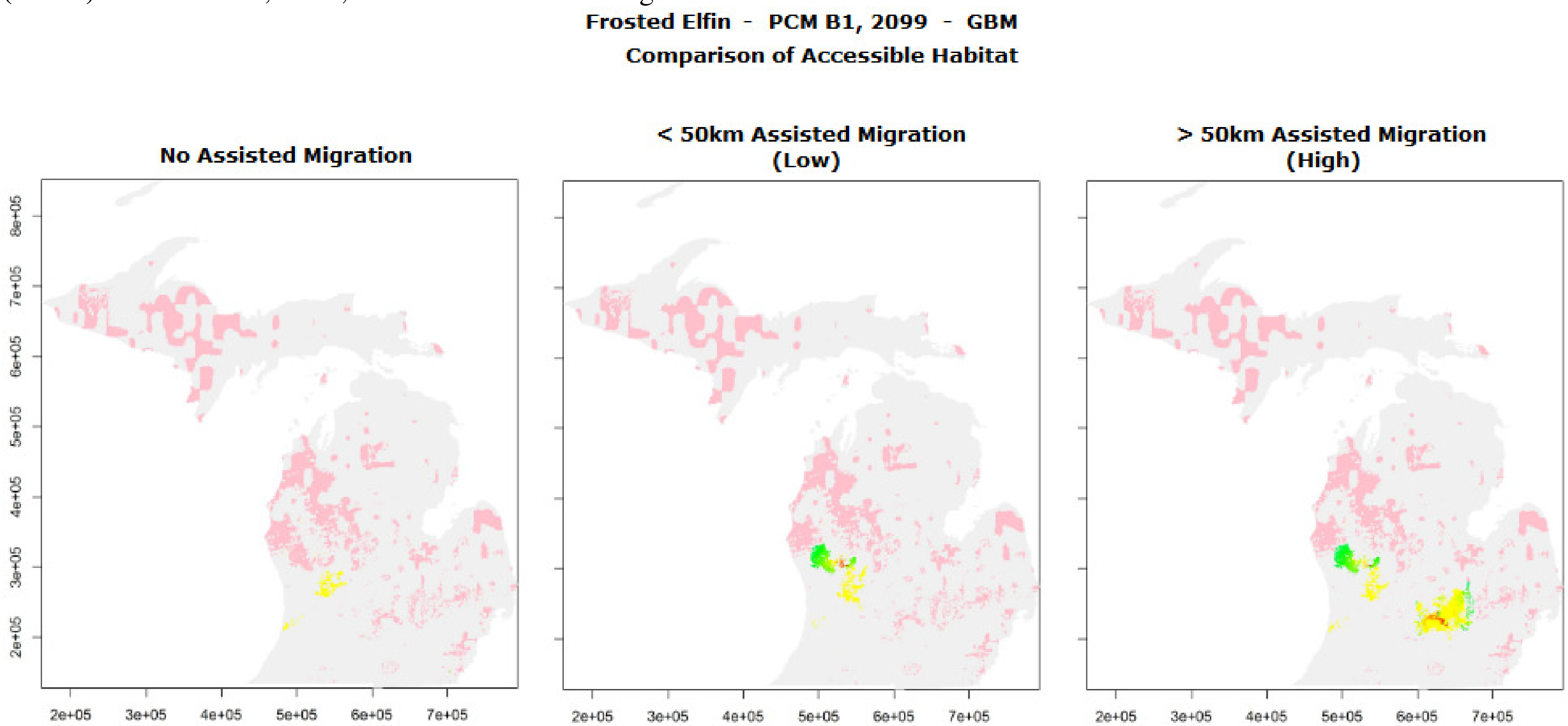
(A3.3f). Frosted Elfin, PCM, Random Forest



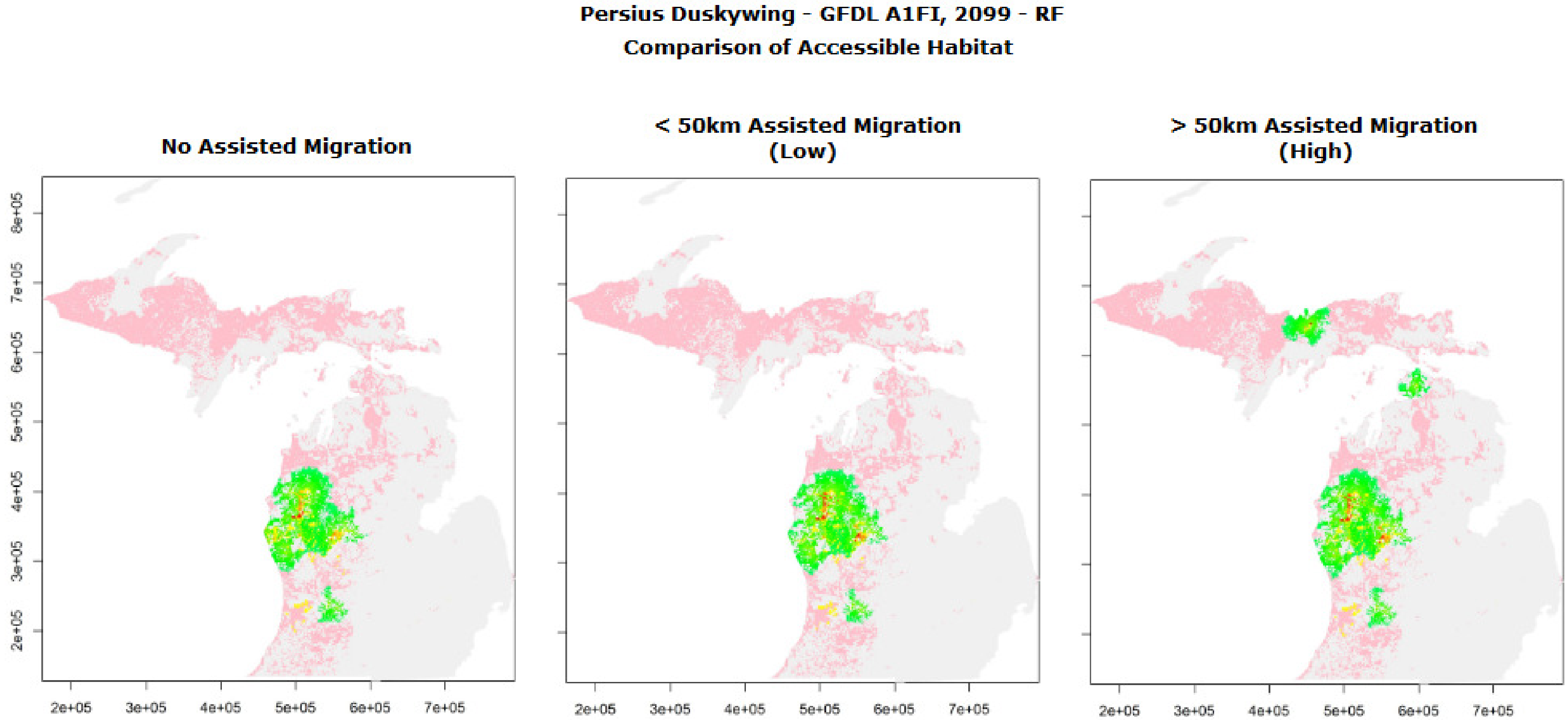
(A3.3g). Frosted Elfin, GFDL, Generalized Boosted Regression Model



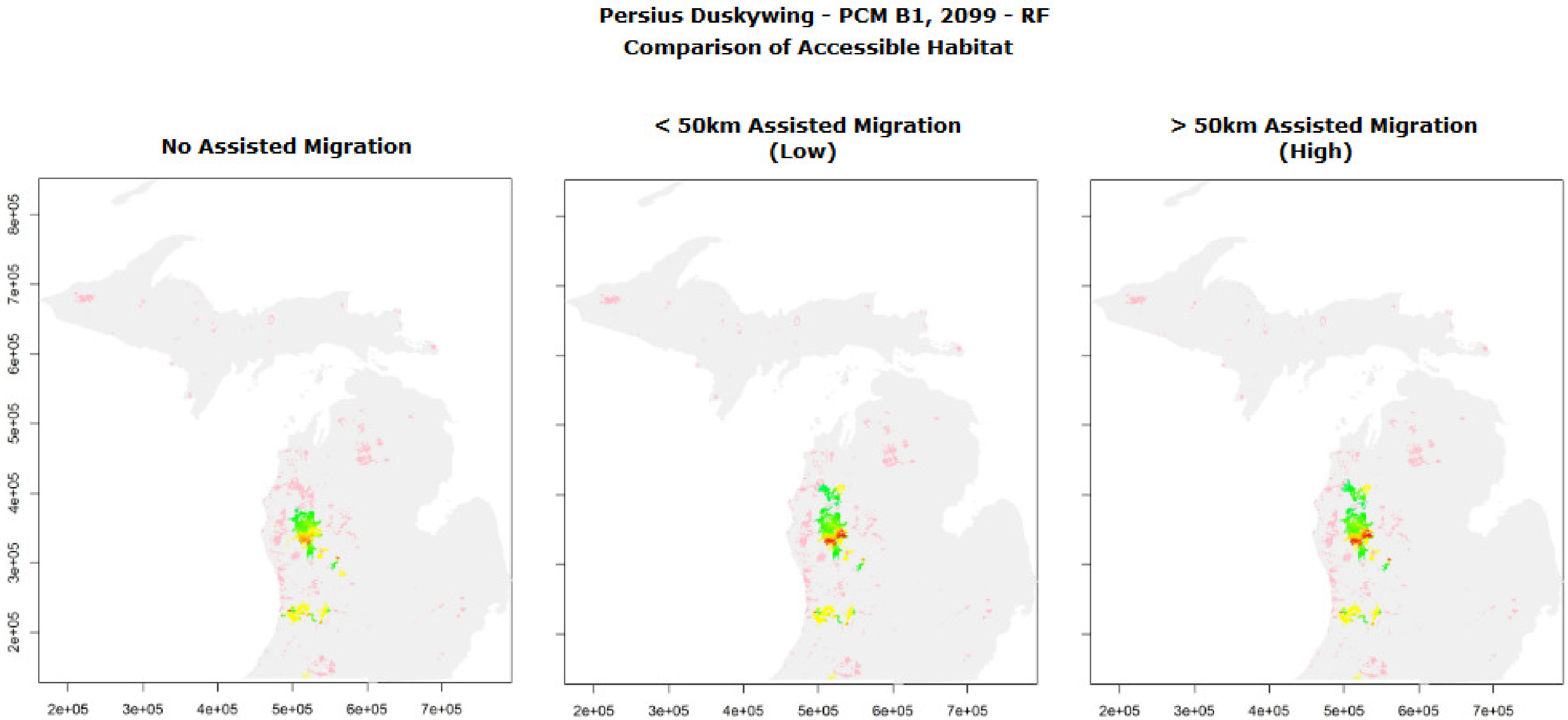
(A3.3h). Frosted Elfin, PCM, Generalized Boosted Regression Model



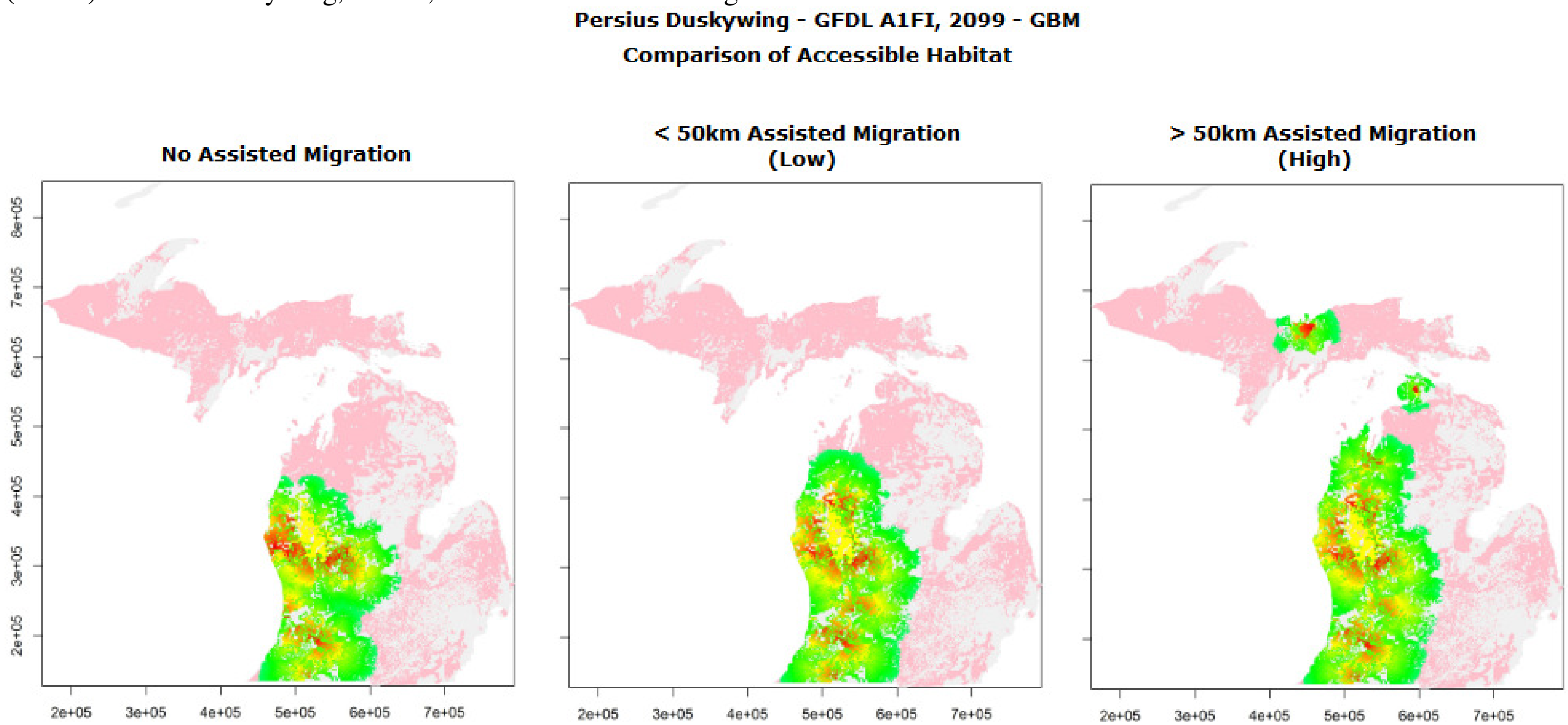
(A3.3i). Persius Duskywing, GFDL, Random Forest



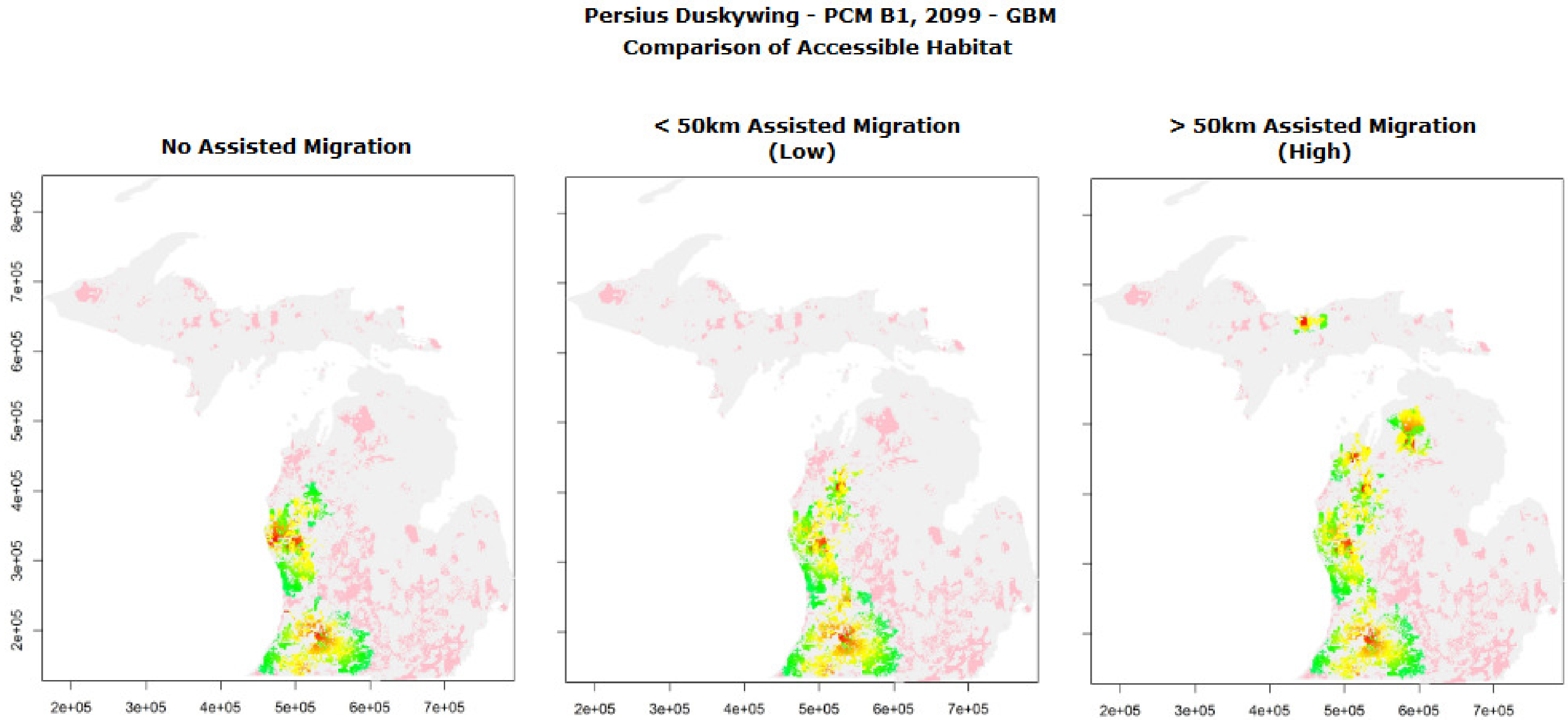
(A3.3j). Persius Duskywing, PCM, Random Forest



(A3.3k). Persius Duskywing, GFDL, Generalized Boosted Regression Model



(A3.3l). Persius Duskywing, PCM, Generalized Boosted Regression Model



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