DISTURBANCE-BASED MANAGEMENT AND PLANT SPECIES CHANGE IN MASSACHUSETTS SANDPLAIN HEATHLANDS OVER THE PAST TWO DECADES

by

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ABSTRACT

Massachusetts sandplain heathlands are habitats of conservation concern, harboring many rare plant species and providing habitat for animals that depend on openlands. These heathlands are threatened by human development, shrub encroachment in the absence of disturbance, and potentially increasing soil nutrient levels. Sandplain heathlands are managed with prescribed fire, in order to maintain their open structure and maintain species diversity. In order to assess how past management was correlated with species change, I used a data set that spanned twenty years from three different heathlands in Massachusetts. I looked for correlations between management and species change. Correlations between species change and prescribed burning were very site, or microsite, specific, indicating that variables such as vegetation type and edaphic characteristics need to be taken into account before management is applied. Prescribed fire was also associated with an increase in ruderal species in one of the sites studied, indicating that there may be undesirable effects of prescribed fire in this system. Species diversity was negatively associated with shrub encroachment, reinforcing the importance of preventing shrubs from encroaching into these heathlands. I also found evidence that burning has not been a successful technique in preventing shrub encroachment in these sites. Lastly, the nitrophilic species *Carex pensylvanica* increased in all three sites, indicating that future studies should investigate the possibility that sandplain heathlands are currently experiencing nitrogen deposition beyond their critical loads.

INTRODUCTION: DISTURBANCE AND HEATHLANDS

Defining Disturbance

Both physical processes, such as fire, and biological processes, such as grazing, act as agents of disturbance (Grime 1977; Sousa 1984). Disturbance is a force that causes partial or total biomass destruction, and in the process creates opportunities for new individuals (or colonies) to become established (Sousa 1984). It is important for the maintenance of many

ecosystems, and many species depend on some form of disturbance for their continued survival (Hobbs & Huenneke 1992).

Disturbance is tightly intertwined with community dynamics and promotes heterogeneity within the landscape (Sousa 1984; Watt 1947; White 1979). It affects species composition and diversity of a site by creating new opportunities for species to become established and by driving the development of organismal life history characteristics (Denslow 1980). Various biotic and abiotic factors change at a site following a disturbance, including the reduction of competition and the increase in resource availability (Noble & Slatyer 1980; Sousa 1984); however these relationships are often complex and difficult to predict. For example, disturbances such as fire may increase some soil nutrients, such as available nitrogen, by combusting organic matter found on the soil surface and increasing nutrient availability (Wan, Hui & Luo 2001). On the other hand, fire often volatizes nutrients such at phosphorus and sulfur and decreases their availability (DeBano 1991). Additionally, the amount of nutrients gained and lost depends not only on the type of nutrient, but also the temperature and duration of the fire (DeBano 1991).

Intensity, frequency, and season of disturbance affect which species will appear following a disturbance (Noble & Slatyer 1980). For example, the season of a prescribed burn is important in determining flowering time and flowering success in many plant species in Florida's pine flatwoods (Platt, Evans & Davis 1988). As the importance of disturbance in maintaining natural communities has become increasingly recognized, the use of disturbance-based management techniques has increased. Disturbance-based management includes techniques such as prescribed fire, mowing, and grazing (Hobbs & Huenneke 1992; Power *et al.* 2001).

Disturbance in Cultural Landscapes

Cultural landscapes are landscapes which were formed by anthropogenic intervention and disturbance; these landscapes reflect a long history of interaction between humans and the nature that surrounds them (Phillips 1998). While North American ecologists have traditionally thought of pristine, untouched, landscapes as their conservation priority, it is increasingly apparent that humans have influenced all systems on earth (Phillips 1998; Vos & Meekes 1999). Cultural

landscapes have been very well studied in Europe, and systems such as European cultural grasslands and heathlands have historically been more highly protected than cultural landscapes in many other parts of the world. It is evident, however, that Europe is not the only part of the world that has long been impacted by human land use; for example tree species present in Belize have been linked to agricultural practices of the Mayans, well over a thousand years ago (Hightower 2012).

One reason that cultural landscapes may be of conservation concern is their societal importance, and the stories that they tell about the history of our interactions with the land (Eberhardt *et al.* 2003; Foster & Motzkin 2003; Phillips 1998). Additionally, many of these landscapes have been recognized as refugia for biodiversity, hosting suites of species that depend on the characteristics of these anthropogenically influenced landscapes for their survival (Foster & Motzkin 2003; Phillips 1998), or that depend on semi-natural landscapes as habitat islands (Duelli & Obrist 2003). For these reasons, many cultural landscapes have been targeted as areas of conservation concern. In 1992 the United Nations Educational, Scientific, and Cultural Organization (UNESCO) began protecting certain cultural landscapes as World Heritage sites, and today protects 82 sites around the world for their value as cultural landscapes (UNESCO 2013).

Many cultural landscapes require continued disturbance in order to maintain their form and function (Foster & Motzkin 2003). In areas where traditional land use is no longer practiced, or where it has become unfeasible, disturbance-based management is often used to manage these landscapes (Dunwiddie & Caljouw 1990; Webb 1998); disturbance-based management may not perfectly mimic the traditional land use that formed the system of interest, and as a result, species composition may change in the managed sites (Webb 1998).

Heathlands

Heathlands are dependent on disturbance to maintain their open structure and function (Specht 1979), as well as to remove nutrients from the system (Power *et al.* 2001). They can be found throughout the world, in tropical, temperate, Mediterranean, and arctic climates (Specht 1979). Although European heathlands are very well studied, literature on heathlands outside of

Europe is more limited. There are both wet and dry heaths; wet heathlands are seasonally waterlogged and dry heathlands occur on well-drained soils (Gimingham 1972; Specht 1979). Factors that unite these heathlands are they: (1) contain vegetation that is evergreen and sclerophyllous; (2) contain, although are not necessarily dominated by, species in the heath families (Ericaceae and the closely related, but less widespread, Diapensiaceae and Grubbiaceae); (3) occur on nutrient poor and acidic soils; and (4) are host to many stress tolerant organisms (Specht 1979).

Edaphic, or soil related, conditions may be one of the most important factors determining the distribution of heathland vegetation (Gimingham 1972). Heathlands often occur in the same areas as grasslands, but heathlands occur on areas with lower nutrient status while grasslands occur in areas with higher nutrients (Aerts *et al.* 1990; Specht 1979). These xeric, nutrient poor conditions reduce competition from ruderal species and limit the establishment of invasive species (Owen & Marrs 2000; Von Holle & Motzkin 2007). In fact, reductions in both soil pH and fertility are standard restoration methods for *Calluna vulgaris* heath in the UK (Owen & Marrs 2000).

The stressful soil conditions in which heathlands thrive are often formed anthropogenically (Motzkin & Foster 2002; Webb 1998), but they may also occur naturally (Specht 1979). Natural heathlands are usually limited to areas that are either seasonally water logged or possess extremely deep and sandy soils (Specht 1979). Anthropogenic heathlands are usually formed by various combinations of traditional agriculture techniques; including grazing, cultivation, turf stripping, and litter removal (Webb 1998). These traditional and harsh agricultural practices amplified stressful site conditions, which prevented the establishment of many species, even after abandonment (Webb 1998).

Sandplain heathlands

Sandplain heathlands are found in a narrow strip along the coast of New England, from Long Island to Cape Cod (Dunwiddie & Caljouw 1990). They occur on dunes or glacial deposits and are characterized by well drained, sandy soils (Massachusetts Division of Fish and Wildlife 1992). Like all heathlands, they are characterized by low-growing vegetation with many

members of the heath family (Ericaceae) and are found on low nutrient, acidic soils (Massachusetts Division of Fish and Wildlife 1992).

The origin of New England heathlands is still being debated, but increasing evidence points to many sandplain heathlands being novel habitats, which did not exist in their present form prior to European settlement (Foster & Motzkin 2003). Evidence, such as pond cores, point to an increase in openlands with European settlement in areas such as Cape Cod (Parshall *et al.* 2003). While the species that make up these assemblages may have existed prior to settlement, the range of current day assemblages was undoubtedly influenced by the traditional agricultural practices of early European settlers (Dunwiddie 1989; Foster & Motzkin 2003). These land use practices included cultivation, tree clearing, and livestock grazing, especially sheep (Motzkin & Foster 2002). In the mid-1800s, agriculture in New England began to be abandoned as people moved further west (Foster 2002; Hall *et al.* 2002); consequently, openlands started to reforest and trees encroached on these areas of New England (Foster 2002). As afforestation occurred, pitch pine and white pine became more dominant than prior to European settlement, replacing trees such as oak, hemlock, and beech (Parshall & Foster 2002).

While the original composition of sandplain heathlands is not completely clear, sandplain heathlands are important for the role that they play in maintaining biodiversity and creating habitat for rare species (Foster and Motzkin 2003). Thus, these habitats are considered a conservation priority and disturbance-based management, such as burning and mowing, is currently used to prevent tree encroachment and to maintain their open structure (Foster 2002).

In addition to tree encroachment, human activities such as urban development have caused a drastic reduction in sandplain heathlands, as the areas where these systems occur are often prime real estate (Dunwiddie & Caljouw 1990).

Statement of objective

The objective of my study was to investigate changes in sandplain heathland species composition over the past two decades as well as how management has affected these changes. In chapter one, I begin by examining how past management is correlated with species composition change at three sites. In chapter two, shrub encroachment over the past two decades

at these sites, as well as how this shrub encroachment may have affected species diversity, is evaluated. Lastly, I turn my focus to the role of soil nutrients in changing species composition, specifically the role of potentially increasing soil nitrogen. I explore the potential for increasing nitrophilic species in these heathlands as well as examine how past management is correlated with these changes.

Overall Study Methods

Study Site

This study was conducted within two sandplain heathlands; one heathland is located on Cape Cod, Massachusetts, within Mass Audubon's Wellfleet Bay Sanctuary. The second heathland is located on Nantucket, an island located approximately 50 km offshore of Cape Cod (Figure 1). Both heathlands are managed by Mass Audubon using primarily prescribed fire, in order to maintain their open heathland structure and promote biodiversity. Additionally, both heathlands contain transects that were established in 1989 by Peter Dunwiddie, in order to monitor the vegetation of these sandplain heathland communities for Mass Audubon.

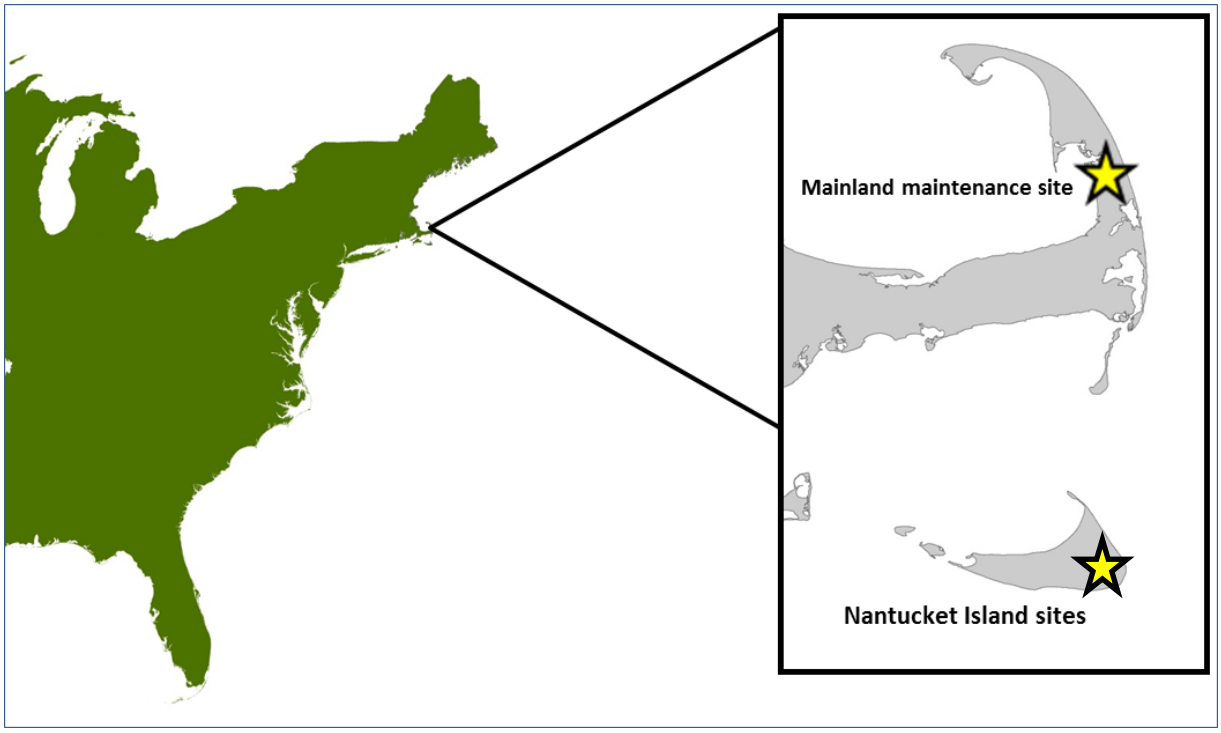

Figure 1: The location of heathland monitoring sites on Cape Cod and Nantucket Island, MA. Both sites are owned and managed by Mass Audubon.

Nantucket

The Nantucket heathland is broken into nine management units (A-I in Figure 2). Management units C and F were not used, due to uncertainty in their management history, thus seven management units at this site were analyzed in this study. There are two sets of transects in this heathland, the 'maintenance transects' (red lines in figure 2) and the 'management transects' (blue lines in figure 2).

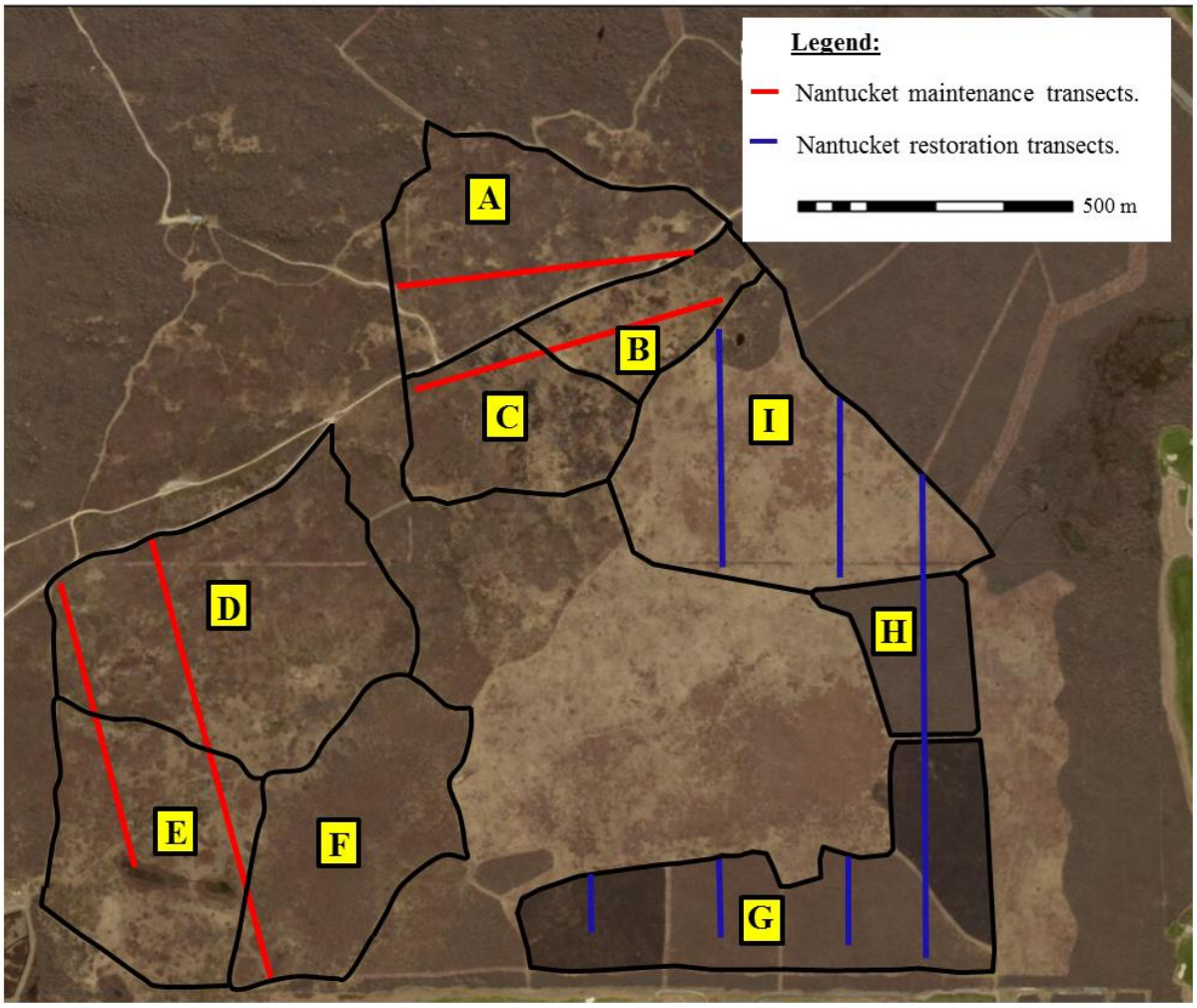

Figure 2: There are nine management units at the Nantucket site: Units A - I, however units C and F were excluded due to unknown management history. Yellow boxes label management units.

The 'maintenance transects' are a set of four transects that were established in 1989/1990 by Peter Dunwiddie (red transects in Figure 2). These transects were established in an existing sandplain heathland that is managed in order to maintain its open structure and sandplain

heathland species composition. After removing any plots with unknown management history, or with missing data, these four transects have 167 plots total. The 1x1m plots are placed every ten meters along the entirety of each maintenance transect.

The ‘restoration transects’ are a set of four transects that were established in 1998/1999 (blue transects in Figure 2). These transects were established in a shrubbier area, where management is applied with the general goal of opening the shrub canopy and promoting the restoration of sandplain heathland structure and species. Plots with unclear management history, or plots that were missing data, were excluded from the analyses. Additionally, I excluded one transect that had particularly high soil nitrogen levels, and which had a species composition that was entirely different from any of the other transects surveyed in this study. This gave us a total of 120 plots at the Nantucket Restoration site. Instead of being placed every ten meters along the entirety of their length, 1x1m permanent plots were placed every 10m along 100m portions of the transects. These portions of transect were chosen randomly by the original surveyors. The management histories for all the plots are known from the time of their establishment, in 1998 or 1999, to the present and are listed in table 1.

All units in the Nantucket site are managed using prescribed burning at various intervals, during the spring or the fall (Table 1). Unit I, within the restoration transects, is also managed using annual mowing and unit H within the restoration transects is an unmanaged control.

Table 1: The management history of all units within the Nantucket heathland site.

Unit	Transect Type	Management history	Total burns	Mowed	Years since burn	Total Plots	Plots with soil data
A	Maintenance	Burned spring 1992, spring 1997 and fall 2004	3	No	6.75	44	10
B	Maintenance	Burned spring 1991, fall 1994, fall 2001, fall 2004, fall 2006 and spring 2010	6	No	1.25	25	10
D	Maintenance	Burned spring 1991, spring 1993, spring 2002, and fall 2006	4	No	3.75	44	10
E	Maintenance	Burned spring 2002 and fall 2009	2	No	0.75	54	10
G	Restoration	Burned spring 2001, spring 2005, and spring 2011	3	No	4.25	50	10
H	Restoration	Untreated Control	0	No	>100	10	10
I	Restoration	Mowed most years since 2002 and burned in spring 2005 and fall 2009	2	Yes	4.25	50	7

Mainland maintenance site

The Mainland maintenance site is located on mainland Cape Cod within a grassy heathland on the Mass Audubon Wildlife Sanctuary. The site has five transects, of varying lengths, within three different management units (Figure 3). All five transects at this site are 'maintenance transects' meaning that the entire site was sandplain heathland at the time of plot establishment and is currently managed to maintain the open structure and species composition of the sandplain heathland. This site is managed with prescribed burning at various intervals (Table 2) and by manually cutting small trees as needed at the beginning of each season. The seasons of the prescribed burns are unknown at this site. After excluding plots with confounded or unknown management history, a total of 57 plots at this site remained.

Table 2: Management history of all units within the Mainland maintenance site.

Unit	Management history	Total burns	Years since burn	Plots	Plots with soil data
A	Burned 1989, 1990, 1992	3	10	34	14
B	Burned 1990, 1992, 2011	3	1	7	3
C	Burned 1990, 2011	2	1	16	7

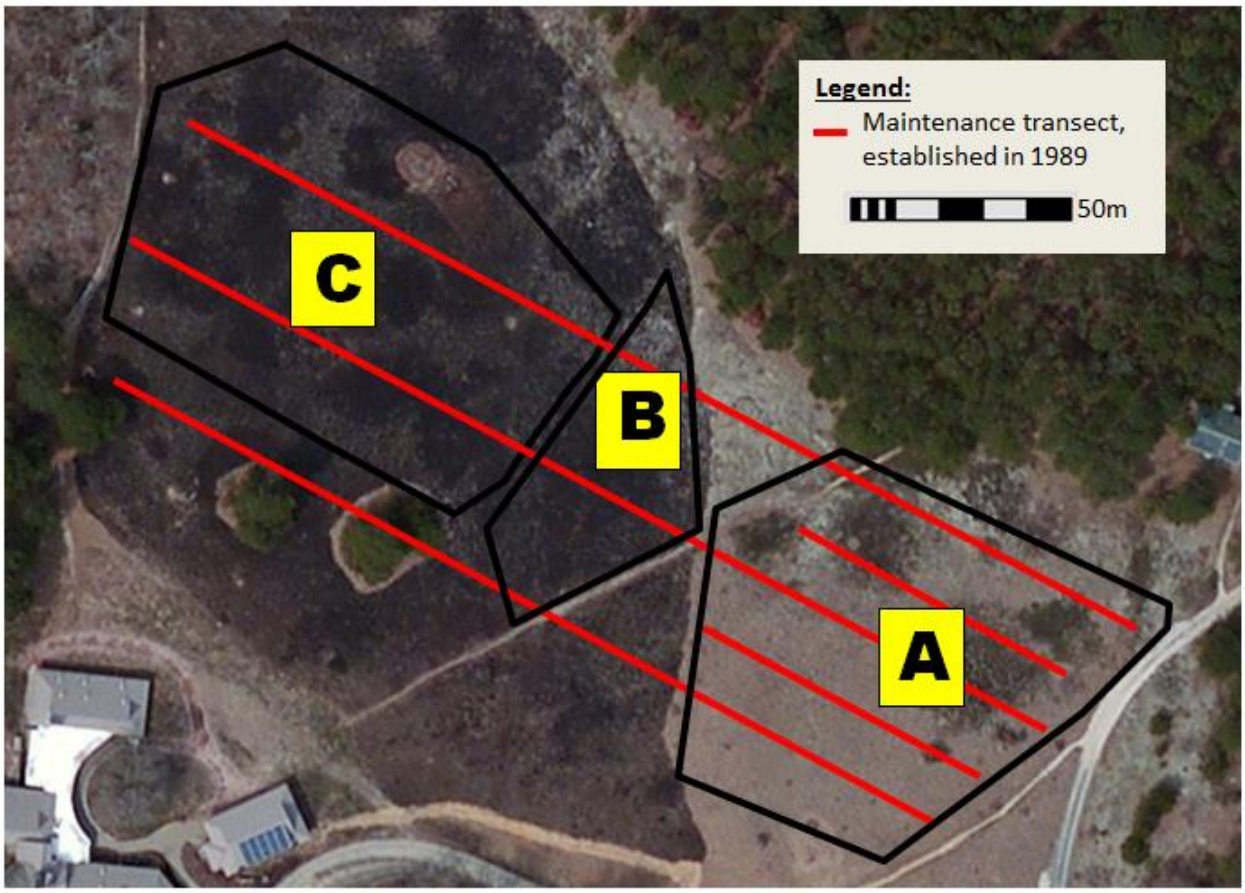

Figure 3: The Mainland maintenance site has three management units (A-C). The site has five transects of varying lengths that were established in 1989. Letters in yellow boxes denote management units.

Survey methods

Permanent monitoring plots were established every 10m along all transects established in 1989 (maintenance transects in the Nantucket site and all transects in the Mainland maintenance site). In the restoration transects on Nantucket, plots were established in groups of ten along

select portions of the transects (Figure 4). Portions of the transects to be surveyed were selected randomly and plots are still 10m apart within these portions of the transects, as in the other sites.

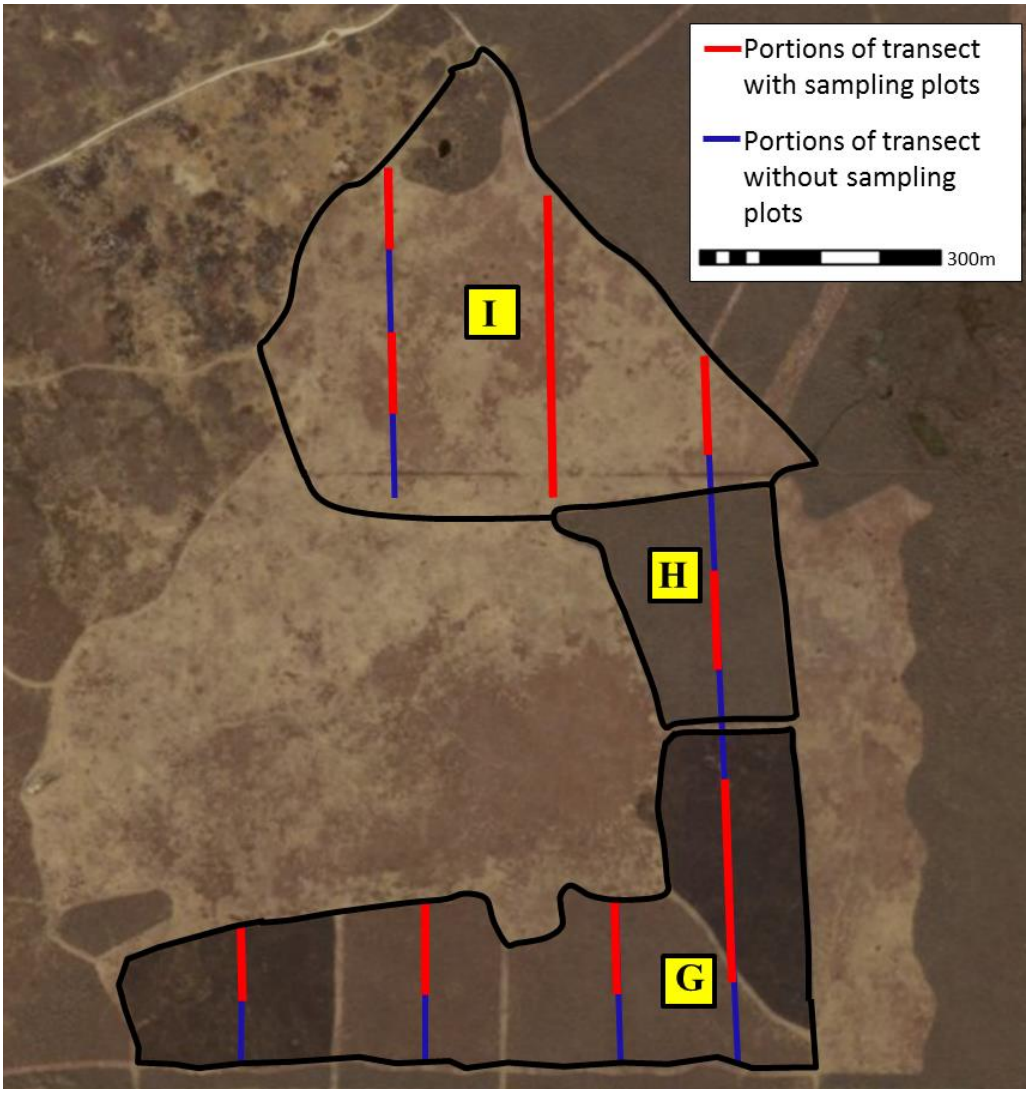

Figure 4: Sampling portions along the Restoration transects in the Nantucket site. 100m portions of transect were chosen randomly and survey plots were established every 10m along these areas of transect.

These plots have been resurveyed at varying intervals using the same survey methods as the original surveyors (Dunwiddie1986). Only the initial and most recent surveys were used in the analyses for this study (dates are shown in Table 3). Presence-absence data were taken within the entire 1x1m plot and vegetation cover classes (<1, 1-5, 6-25, 26-50, 51-75, 76-100) were taken within a strip along the edge of the permanent plot (Figure 5). A 20cm cover class strip

was surveyed in all plots along the maintenance transect, and a 10cm cover class strip was surveyed in the restoration transect (blue transects in Figure 2).

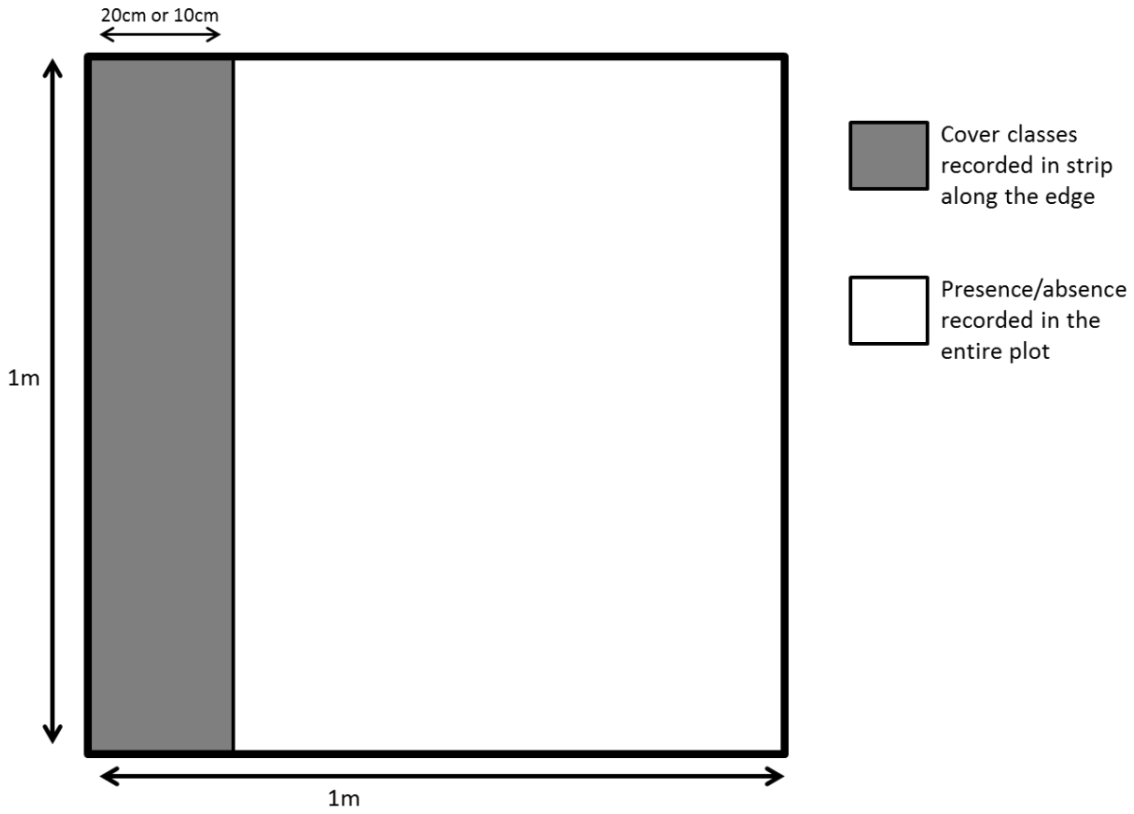

Figure 5: Presence-absence data was taken within the entire 1x1m plot and vegetation cover classes (<1, 1-5, 6-25, 26-50, 51-75, 76-100) were taken within a strip along the edge of the plot. A 20cm cover class strip was used in all plots along the maintenance

Table 3: Survey dates of all surveys of all surveys used in analyses in this study.

Site	Management Type	Unit	Date(s) of initial survey	Date(s) of most recent survey
Nantucket	Maintenance	A	7/12/1990	8/6/2011
		B	7/13/1989	8/6/2011
		D	7/12/1989	7/19/2010
			7/2/1989	7/19/2010
		E	7/12/1989	7/19/2010
			7/2/1989	7/19/2010
	Restoration	G	7/6/1999	7/18/2009
			7/6/1999	7/25/2009
			7/26/1999	7/30/2009
			7/26/1999	7/22/2009
			7/23/1999	7/20/2009
		H	7/12/1999	8/2009
		I	8/11/1998	7/15/2009
			7/15/1999	7/16/2009
			7/15/1999	7/16/2009
			7/16/1999	8/3/2009
			7/8/1999	8/14/2009
Wellfleet Bay	Maintenance	A	7/27/1989	8/3/2012
		B	7/27/1989	8/3/2012
		C	7/28/1989	8/3/2012

CHAPTER 1: DISTURBANCE-BASED MANAGEMENT, EDAPHIC CONDITIONS, AND CHANGE IN SPECIES COMPOSITION IN SANDPLAIN HEATHLANDS

Disturbance-based management and species composition

Different types of management have been used in heathlands worldwide, including litter stripping, turf removal, burning, and mowing. These techniques remove various amounts of

organic matter, and hence differing amounts of nutrients, from the site (Hädtle *et al.* 2006; Härdtle *et al.* 2009; Power *et al.* 2001). Mowing and burning are generally considered less intense techniques, while litter stripping, sod cutting, and turf removal are considered higher intensity techniques and remove more nutrients from the system (Hädtle *et al.* 2006; Härdtle *et al.* 2009). As well has having differing effects on soil nutrients, these techniques have differing effects on species composition (Hädtle *et al.* 2006; Härdtle *et al.* 2009; Power *et al.* 2001). For example, Hädtle et al. (2006) found that the grass family (Poaceae) increased where sod cutting had taken place, whereas dwarf shrubs were promoted by prescribed burning and mowing.

The frequency of disturbance is also important in determining the response of a community to disturbance. For example, Bradstock et al. (1997) saw a reduction in obligate seeders with increased fire frequency in an Australian heathland. This reduction in obligate seeders is predicted by Noble and Slatyer's (1980) vital attribute model. Noble and Slatyer's model predicts that different disturbance frequencies will select for species with different vital attributes, including dispersal modes and age to maturity. For example, species that have not reached reproductive maturity by the time another disturbance disrupts the community may not survive. This suggests short interval times between fires should be avoided if obligate seeders are among the target species (Bradstock, Tozer & Keith 1997).

Although the goal of heathland management is community-based, management actions largely affect individual species (Hobbs and Huenneke 1992). With this in mind, I set out to determine the correlation between different management regimes, soil nutrients, and species composition in sandplain heathlands. The management treatments at these sites primarily allowed me to examine different burning regimes, but the restoration site also contained a mowing treatment and a control.

My primary research question was, how do different management regimes as well as edaphic factors correlate with changes in sandplain heathland community composition over the last two decades?

Methods

Field methods

In the summer of 2012, soil samples were taken from a stratified random subsample of all plots, within all units. The plots were stratified by management unit, except for at the Mainland maintence site where the existence of the smallest management unit (unit B in Figure 3) was not known until after soil samples were collected. Hence, I was not able to stratify within this study unit and only three soil samples were obtained from this unit. Ten soil samples were collected from each management unit on Nantucket and 3 to 14 for each management unit in Mainland maintenance site, for a total of 101 soil samples. Plots with unclear management histories or that were missing any data, were excluded. Additionally, all of transect twelve within unit I of the Nantucket Restoration transects was excluded due to much higher nutrient concentration and a very different species composition from all other transects surveyed. This made for a total of 91 usable soil samples. The breakdown of the usable soil samples can be seen in Table 2 and Table 3.

Soil samples were taken by the field team to a depth of 15cm from each corner of the study plot. We put the cores from all the corners into the same labeled plastic bag, and placed them on ice until returning to the lab. In the lab we sifted soils to 2mm, broke up clumps, and discarded stones roots etc. from the sieve. We extracted ten grams of wet soil using a 2M KCl extraction, which was later analyzed for NH_4^+ and NO_3^-. We froze samples until they were analyzed, using a Lachat Quickchem 8500. The remainder of the sample was air dried and sent to Brookside Laboratories in New Knoxville, OH to be analyzed for Mehlich extractable micro and macronutrients .

Data analyses

All data were analyzed by site, due to very different environmental conditions across sites.

At each site, I compiled species survey data from the original plot survey as well as the last year a plot was surveyed into matrices to be analyzed in PC-ORD (survey dates in Table 3). These data were analyzed using NMS ordinations, run in PC-ORD using autopilot mode (50

iterations with real data and 50 iterations with random data) (Kruskal 1964). I used the Sorenson distance measure, as recommended for community data by McCune and Grace (2002). I correlated axes to species composition in PC-ORD using Kendall's correlations, and tested correlations visually by overlaying species on axes in PC-ORD (McCune, Grace & Urban 2002). Tau correlation values greater than 0.30 are discussed as meaningful (McCune, Grace & Urban 2002).

I ran two sets of ordinations for each analysis: presence-absence data with no, or few, species deleted, and cover class data with rare species deleted. The number of species deleted varied by type of data used (cover class or presence-absence data) and by site, and depended on how many species I had to remove in order to reach a satisfactorily stable and low stress solution. The presence-absence data were collected from the entire 1mx1m plot, and thus contained more rare species than the cover class data. Therefore, in analyzing the presence-absence data I was able to correlate edaphic and management variables with changes in a wider set of species. Cover class data, with rare species deleted, was used to assess changes in dominant species.

Ordination scores were then exported to Microsoft Excel, where the change of each plot along each NMS axis from establishment to the most recent survey, as well as the total length of the vectors, were calculated (McCune, Grace & Urban 2002). Length and direction of vectors were calculated in Microsoft Excel, by taking the position of a plot along one NMS-axis at the end of the survey and subtracting the position of that plot along the same axis at the beginning of the survey; this was done for all axes in the NMS solution. Length was calculated using the Pythagorean Theorem. Therefore, I had developed metrics of how far each plot had moved along all axes in ordination space from the time of plot establishment until the most recent survey.

Due to the non-independence of all environmental predictor variables, environmental predictor variables were ordinated using PCA ordination in PC-ORD, in order to create orthogonal, composite predictor variables (McCune & Mefford 2011; McCune, Grace & Urban 2002). This technique allowed me to examine the correlation between changes in species composition and underlying environmental variables, while recognizing that the environmental variables are complex and co-varying. All soil and management variables were checked for

normality and outliers using histograms and Shapiro-Wilk tests in JMP (SAS Institute Inc. 2010). Data were transformed as necessary, before running PCA ordinations. Variables included in the PCA included relevant management variables (which varied slightly by site), total nitrogen mg/kg, organic matter%, P mg/kg, Ca mg/kg, Mg mg/kg, K mg/kg, Na mg/kg, H%, B mg/kg, Fe mg/kg, Mn mg/kg, Cu mg/kg, Zn mg/kg, Al mg/kg, and S mg/kg. Interpretable axes were selected using the broken stick Eigenvalue: when the actual Eigenvalue is larger than the broken stick value this indicates that these axes represents more of the variation in the data than could be expected due to chance (McCune, Grace & Urban 2002); thus I interpreted these axes. In order to determine which environmental variables were the most strongly correlated with these three axes, Kendall Correlations were run in R 2.11.1 (R Development Core Team, 2010).

To determine which management and edaphic variables were correlated with species composition change, the axes scores of each plot in the environmental-PCA ordinations were used as predictor variables in a multiple regression analysis, and the movement of the plot along each axis in the species-NMS as well as the length of each vector in the species-NMS were used as response variables. I used AICc model selection to select the most informative predictor variables (Hurvich & Tsai 1989). AICc model selection provides a correction for AIC model selection that is better with small sample sizes and prevents over parameterization (Hurvich & Tsai 1989). Regression analyses were run in JMP and interactions were interpreted using JMP factor profiler (SAS Institute Inc. 2010).

Results

Change in species composition and environmental variables

Maintenance Sites:

Nantucket maintenance site

Thirty-nine plots were used for the analyses at this site, due to one plot missing survey data for the original survey. Variables included in the PCA were log(total nitrogen), number of fires, years since last burn, log(organic matter), log(P), log(Ca), log(Mg), log(K), log(Na), H, log(B), log(Fe), log (Mn), log (Cu), log (Zn), Al, S. The broken-stick eigenvalue was smaller

than the actual eigenvalue for the first three axes, thus I interpreted the first three axes of this PCA analysis. The first three axes extracted 60.4% of the variation in the original data (Table 4). Correlations between management and edaphic variables were determined using Kendall's correlations (Table 5).

Table 4: PCA analysis of the management and soil variables for the Nantucket maintenance site. The broken-stick Eigenvalues are smaller than the actual Eigenvalues for the first three axes, therefore I chose to interpret the first three axes.

Axis	Eigenvalue	% of variation extracted by axis	Cumulative % variation	Broken-stick Eigenvalue
1	4.133	24.312	24.312	3.440
2	3.945	23.208	47.520	2.440
3	2.189	12.878	60.398	1.940
4	1.487	8.750	69.148	1.606

Table 5: Kendall Correlations with PCA axes for the Nantucket maintenance site (n=39). Tau values over 0.3 are in bold.

	PCA Axis 1	PCA Axis 2	PCA Axis 3
Log (Total Nitrogen)	-0.053	-0.204	-0.188
Number of fires	0.189	**-0.380**	**-0.479**
Years since fire	0.279	-0.112	**0.380**
Log (Organic Matter)	**-0.694**	-0.039	0.064
Log (P)	**0.303**	**-0.394**	0.028
Log (Ca)	-0.275	**-0.323**	0.0311
Log(Mg)	**-0.513**	**-0.377**	0.096
Log(K)	**-0.464**	-0.103	-0.178
Log(Na)	**-0.527**	0.028	0.188
H	**-0.317**	-0.152	**0.423**
Log(B)	**-0.54**	0.265	0.064
Log(Fe)	-0.154	**-0.506**	**0.333**
Log(Mn)	-0.104	**-0.651**	-0.295
Log(Cu)	-0.073	**0.375**	0.049
Log(Zn)	-0.260	-0.252	-0.249
Al	-0.274	**0.466**	-0.198
S	-0.192	**0.620**	-0.151

Presence-absence data:

I ran an NMS-ordination on the presence-absence species data from the time of plot establishment (1989/1990) and the data from the most recent survey (2010/2011). A 3-dimensional solution was recommended, using the auto-pilot mode in PC-ORD version 5. This 3-dimensional solution had a stress of 16.24 and a final instability of 0.00. The cumulative correlation coefficient for three dimensions was 0.80 (Table 6). Kendall correlations identified which species were most strongly correlated with each NMS axis (Table 7).

Table 6: Coefficients of determination for the correlations between ordination distances and distances in the original n-dimensional space for NMS ordination on presence-absence data at the Nantucket maintenance site (n=39).

Axis	Increment	Cumulative
1	0.311	0.311
2	0.222	0.533
3	0.268	0.802

Table 7: Kendall Correlations with NMS Ordination on presence-absence data for the Nantucket maintenance site (n=39). Tau values with an absolute value over 0.3 are in bold.

	NMS axis 1	NMS axis 2	NMS axis 3
Agrostis stolonifera	-0.185	**0.490**	0.289
Ammophila breviligulata	-0.086	0.124	-0.142
Arctostaphylos uva-ursi	**0.606**	-0.189	**0.319**
Aster dumosus	0.181	-0.210	0.133
Aster linariifolius	0.242	-0.182	0.022
Aster paternus	**0.536**	-0.233	0.164
Carex pensylvanica	0.121	0.146	0.253
Comptonia peregrina	-0.046	-0.109	0.205
Danthonia spicata	**0.497**	0.001	0.157
Deschampsia flexuosa	0.276	0.165	0.111
Dichanthelium spp	0.263	0.051	0.244
Epigaea repens	0.253	0.028	-0.059
Euthamia tenuifolia	-0.192	**0.421**	0.226
Festuca spp.	-0.023	0.143	0.131
Gaylussacia baccata	-0.291	**-0.310**	**-0.544**
Helianthemum spp	**0.314**	-0.053	0.289
Hieracium sp.	**0.307**	-0.111	0.155
Hudsonia ericoides	**0.419**	-0.055	0.243
Juncus greenei	0.064	**0.390**	0.008
Lechea maritima	0.198	-0.151	0.145
Myrica pensylvanica	-0.002	-0.119	-0.097
Pitysopsis falcata	0.247	0.028	0.028
Potentilla simplex	0.143	0.085	0.135
Quercus ilicifolia	-0.056	-0.094	0.193
Quercus prinoides	0.023	0.206	0.130
Rosa virginiana	0.090	**0.351**	**-0.393**
Rubus flagellaris	0.023	-0.160	0.044
Rubus hispidus	-0.132	-0.054	-0.057
Rumex acetosella	0.040	0.160	-0.064
Schizacrium scoparium	**0.649**	0.091	0.276
Solidago nemoralis	0.225	-0.191	0.055
Solida rugosa	-0.018	0.131	-0.228
Vaccinium angustifolium	0.170	**-0.449**	**0.352**
Viburnum recognitum	-0.102	-0.139	0.156

When I regressed change in NMS axis 1 against the PCA axes, AICc model selection identified the interaction between PCA axis 1 and PCA axis 2 as the most informative variable and the final model had a R square value of 0.22 (Table 8). This interaction was such that at low values of PCA axis 1, PCA axis 2 has a positive slope; while at high values of PCA axis 1, PCA axis 2 has a negative slope. Thus, when there is more organic matter, less P, more Mg, more K, more Na, more B, and the soils are more basic; lower amounts of fire (associated with lower P, Mg, Fe, Mn, and higher Cu, Al, and S) are correlated with increased presence of *Arctostaphylos uva-ursi, Aster paternus, Danthonia spicata, Helianthemum sp, Hieracium sp, Hudsonia ericoides,* and *Schizacrium scoparium*.. On the other hand, when the soil variables were reversed fire, and the associated nutrients, had the opposite association with these species.

Table 8: Multiple regression analysis on change in species presence-absence data. NMS axis 1 vs. environmental PCA axes 1 and 2 plus their interaction term for the Nantucket maintenance site.

Summary of Fit

Rsquare	0.220
Rsquare Adj	0.152
Observations	39

ANOVA Table

Source	**DF**	**SS**	**MS**	**F Ratio**
Model	3	1.722	0.574	3.271
Error	35	6.140	0.175	**Prob>F**
Total	38	7.862		**0.0325***

Parameter Estimates

Term	**Estimate**	**Std Error**	**T Ratio**	**Prob> ⏐t⏐**
Intercept	0.074	0.067	1.10	0.278
PCA axis 1	0.022	0.034	0.65	0.519
PCAaxis 2	-0.011	0.035	-0.31	0.761
PCA axis 1* PCA axis 2	0.064	0.021	3.09	**0.0039***

When performing a regression analysis on change in NMS axis 2 with the PCA environmental axes, AICc model selection identified PCA axis 2 as the most informative predictor variable (Table 9), with a negative relationship between the two variables (Figure 6). Biologically this means that a decreased presence of the ericoid shrubs *Gaylusscacia baccata* and *Vaccinium angustifolium*, as well as an increase in *Agrostis stolinifera, Euthamia tenuifolia,*

Juncus greenei, and *Rosa virginaiana* were correlated with increasing fire, which was associated with more P, Ca, Mg, and Fe as well as less Cu, less Al, and less S.

AICc model selection identified a positive trend between change in NMS axis 3 and PCA axes 1 and 3 (Table 10). This trend was such that *Arctostaphylos uva-ursi* and *Vaccinium angustifolium* increased less in basic soils, with low levels of organic matter, and generally low soil nutrients (with the exception of phosphorus) than they did on more nutrient rich, acidic soils. On the other hand *Rosa virginiana* and *Gaylussacia baccata* exhibited the opposite trend, decreasing in basic soils, with low levels of organic matter, and generally low soil nutrients (with the exception of phosphorus). Looking at the correlation with PCA axis 3, when there were fewer fires and more years since fire (where the soil also tended to be more acidic with higher Fe); there was more of an increase in *A. uva-ursi* and *V. angustifolium* while there was a decrease in *R.virginiana* and *G. baccata.*

There was no correlation found between the length of the vectors and any of the environmental PCA axes.

Table 9 : Results from a regression on change in species NMS axis 2 on presence-absence data vs. environmental PCA axis 2 for Nantucket maintenance site.

Summary of Fit

Rsquare	0.190
Rsquare Adj	0.164
Observations	39

ANOVA Table

Source	**DF**	**SS**	**MS**	**F Ratio**
Model	1	1.070	1.070	8.440
Error	37	4.688	0.127	**Prob > F**
Total	38	5.757		**0.0062***

Parameter Estimates

Term	**Estimate**	**Std Error**	**T Ratio**	**Prob > ltl**
Intercept	-0.072	0.057	-1.27	0.2118
PCA axis 2	-0.083	0.029	-2.90	**0.0062***

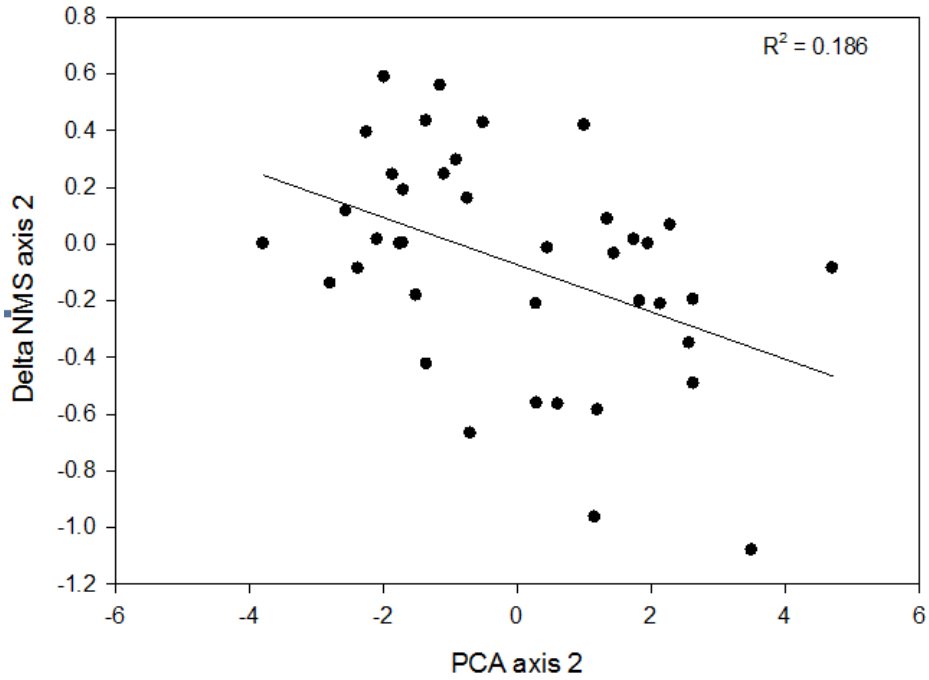

Figure 6: Regression relationship between environmental PCA axis 2 and Change in NMS axis 2 for Nantucket maintenance site (n=39)

Table 10: Relationship between change in NMS axis 3 on cover class data and PCA axes 1 and 3.

Summary of Fit

Rsquare	0.140
Rsquare Adj	0.093
Observations	39

ANOVA Table

Source	**DF**	**SS**	**MS**	**F Ratio**
Model	1	0.807	0.404	2.937
Error	37	4.947	0.137	**Prob > F**
Total	38	5.754		0.066

Parameter Estimates

Term	**Estimate**	**Std Error**	**T Ratio**	**Prob > |t|**
Intercept	-0.012	0.059	-0.20	0.846
PCA axis 1	-0.0497	0.029	1.70	0.097
PCA axis 3	0.069	0.040	1.73	0.093

Cover class data:

I ran an NMS ordination on the cover class data with all rare species (occurring in <5% of plots) removed in order to obtain a stable solution with a satisfactorily low stress. PC-ORD identified a 3-dimensional solution with a stress of 14.63 and instability of 8.2×10^{-4}, as the best solution. Correlations between species and NMS axes were identified using Kendall's tau values (Table 11). The coefficient of determination for the first three axes of this ordination was 0.846 (Table 12).

Table 11: Kendall Correlations with NMS Ordination axes, using cover class data, for the Nantucket maintenance site (n=39). Tau values over 0.3 are in bold.

	NMS axis1	NMS axis 2	NMS axis 3
Arctostaphylos uva-ursi	0.051	**-0.316**	**-0.537**
Epigaea repens	-0.039	-0.119	-0.053
Gaylussacia baccata	**-0.614**	-0.217	**0.504**
Vaccinium angustifolium	-0.056	0.105	**-0.336**
Aster paternus	0.046	**-0.428**	**-0.427**
Euthamia tenuifolia	0.233	**0.356**	0.016
Helianthemum undiff.	0.054	-0.102	-0.13
Hieracium sp.	-0.003	-0.172	-0.231
Agrostis sp.	**0.356**	0.142	0.097
Ammophila breviligulata	0.124	0.219	0.006
Carex pensylvanica	**0.381**	**0.477**	0.083
Danthonia spicata	0.05353	-0.027	-0.273
Deschampsia flexuosa	0.153	0.054	-0.233
Juncus greenei	0.372	0.037	-0.042
Schizacrium scoparium	**0.485**	**-0.339**	**-0.33**
Comptonia peregrina	0.054	0.034	-0.142
Hudsonia ericoides	-0.057	-0.065	-0.275
Myrica pensylvanica	-0.02	0.026	0.114
Quercus ilicifolia	-0.278	**0.306**	-0.226
Rosa carolina/virginiana	-0.059	0.012	0.273
Rubus hispidus	-0.031	0.069	0.008

Table 12: Coefficients of determination for the correlations between ordinations distances and distances in the original n-dimensional space for NMS ordination on cover class data at the Nantucket maintenance site.

Axis	**Increment**	**Cumulative**
1	0.243	0.243

2	0.150	0.394
3	0.453	0.846

Using AICc model selection, the correlation between the movement along NMS axis 1 and PCA axis 2 was significant (Table 13), with a positive relationship between the two variables (Figure 7). Therefore, there has been a decrease in the clonal shrub *Gaylussacia baccata* and an increase in the graminoides *Agrostis sp*, *Carex pensylvanica*, and *Schizacrium scoparium* with fewer fires; which is also associated with less P, Ca, Mg, Fe, Mn, and more Cu, Al, and S.

Table 13: Multiple regression analysis on the change in NMS axis 1 on cover class data and PCA axis 2 for the Nantucket maintenance site.

Summary of Fit

Rsquare	0.146
Rsquare Adj	0.122
Observations	39

ANOVA Table

Source	**DF**	**SS**	**MS**	**F Ratio**
Model	1	1.281	1.282	6.304
Error	37	7.521	0.204	**Prob > F**
Total	38	8.802		**0.0165***

Parameter Estimates

Term	**Estimate**	**Std Error**	**T Ratio**	**Prob > ltl**
Intercept	0.012	0.072	0.17	0.868
PCA axis 2	0.091	0.036	2.51	**0.0165***

Change in NMS axis 2 was found to be correlated with PCA axis 2, PCA axis 3, and the interaction between PCA axis 2 and 3 (Table 14). I determined that at low levels of PCA 2, the relationship with PCA 3 is neutral to slightly positive while at high levels of PCA 2 this relationship changes to one with a strongly negative slope. The association between change in NMS axis 2 and PCA axis 2 can be interpreted such that *Arctostaphylos uva-ursi*, *Aster paternus*, and *Schizacrium scoparium* have all decreased in areas with more fire, which also have higher P, Ca, Na, Fe, Mn, and lower Cu, Al, and S. In these same areas *Euthamia tenuifolia*, *Carex pensylvanica*, and *Quercus ilicifolia* have increased. The relationship between NMS axis 2 and PCA axis 3 shows an increase in *Arctostaphylos uva-ursi*, *Aster paternus*, and *Schizacrium*

scoparium in areas with less fire and more time since fire, which are also more acidic and have higher Fe.

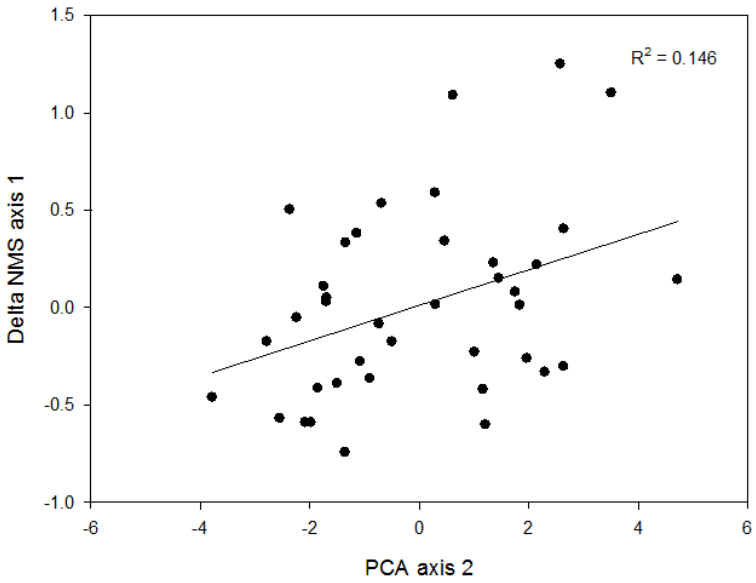

Figure 7: Correlation between Change in NMS axis1 for cover class data at the Nantucket maintenance site and PCA axis 2.

A correlation between change in NMS axis 3 and PCA axis 2 as well as the interaction between PCA axes 1 and 2 were significant (Table 15). At low values of PCA1, PCA2 had a very positive correlation with the change in NMS axis 3. On the other hand, at high values of PCA1, PCA2 had a negative relationship with the response variable. Thus, the interaction was such that when there were low levels of organic matter, Mg, K, Na, and B, as well as high levels of P and basic soils, there was a decrease in *Arctostaphylos uva-ursi*, *Vaccinium angustifolium*, *Aster paternus*, and *Schizacrium scoparium*, and an increase in *Gaylussacia baccata* with increasing fire (associated with more P, Ca, Mg, Fe, Mn, and less Cu, Al, and S).

Table 14: Results from a multiple regression analysis on change in species NMS axis 2 on cover class data vs. environmental PCA axes 2 and 3 plus their interaction term for Nantucket maintenance site.

Summary of Fit	
Rsquare	0.310

Rsquare Adj	0.251
Observations	39

ANOVA Table

Source	**DF**	**SS**	**MS**	**F Ratio**
Model	3	1.582	0.527	5.249
Error	35	3.515	0.100	**Prob>F**
Total	38	5.096		**0.0043***

Parameter Estimates

Term	**Estimate**	**Std Error**	**T Ratio**	**Prob> ⏐t⏐**
Intercept	-0.069	0.051	-1.36	0.181
PCA axis 2	-0.089	0.032	-2.75	**0.0095***
PCA axis 3	-0.160	0.056	-2.88	**0.0068***
PCA axis 2*axis 3	-0.047	0.033	-1.43	0.1625

On the other hand, when there were low levels of PCA 1, or high organic matter, Mg, K, Na, B, and low P and acidic soils; then increasing fire (and associated nutrients) was correlated with an increase in *A. uva-ursi*, *V. angustifolium*, *A. paternus*, and *S. scoparium*, and a decrease in *G. baccata*.. No correlation was found between length of the NMS vectors and any of the PCA axes.

Table 15: Results from a multiple regression analysis on change in species NMS axis 3 on cover class data vs. environmental PCA axes 1 and 2 plus their interaction term for Nantucket maintenance site.

Summary of Fit

Rsquare	0.243
Rsquare Adj	0.178
Observations	39

ANOVA Table

Source	**DF**	**SS**	**MS**	**F Ratio**

Model	3	1.207	0.402	3.743
Error	35	3.515	0.100	**Prob>F**
Total	38	4.970		**0.0197***

Parameter Estimates

Term	**Estimate**	**Std Error**	**T Ratio**	**Prob> ltl**
Intercept	-0.029	0.053	-0.54	0.600
PCA axis 1	0.031	0.026	1.17	**0.251***
PCAaxis 2	0.070	0.027	-2.54	**0.0155***
PCA axis 1*axis 2	-0.033	0.016	-2.05	**0.0476***

Mainland maintenance site:

After removing all plots with an unclear management history, there were 24 plots left for analyses at this site. Additionally, while screening the soil environmental variables, I detected one outlier. Due to the assumptions of normality of PCA, as well as the well-known effect that outliers can have on this analysis, this outlier was removed from the dataset. Variables included in the PCA ordination were log(total Nitrogen), years since last fire, number of fires, log(organic matter), P, Log(Ca), log(Mg), log(K), log(Na), H, log(B), log(Fe), log(Mn), log(cu), log(n), log(Al), and log(S).

The first four axes of the PCA ordination were interpreted (Table 16); these four axes cumulatively represent 72.56% of the variation in the original data (Table 17). Kendall's correlations were used to correlate environmental variables to the PCA axes (Table 17).

Table 16: PCA on environmental variables at Mainland maintenance site. The first four axes were interpreted for this analysis.

Axis	Eigenvalue	Cumulative % of Variance	Broken-stick Eigenvalue
1	5.990	35.237	3.440
2	2.634	50.733	2.440
3	1.991	62.445	1.940
4	1.720	72.562	1.606
5	1.268	80.022	1.356

Table 17: Kendall's correlations between PCA axis scores and environmental variables (n=23). Tau values greater than 0.30 are bold.

	PCA axis 1	PCA axis 2	PCA axis 3	PCA axis 4
Log (Total Nitrogen)	**0.336**	**-0.312**	-0.099	0.296
Years since fire	-0.235	**0.594**	0.280	0.034
Number of fires	-0.224	**0.635**	0.249	-0.162
Log (Organic Matter)	0.020	-0.255	**0.312**	0.271
P	**-0.430**	**-0.406**	0.000	-0.089
Log (Ca)	**-0.369**	-0.064	-0.080	0.088
Log (Mg)	**-0.649**	-0.265	0.045	-0.004
Log (K)	**-0.594**	-0.100	**-0.368**	0.176
Log (Na)	**-0.590**	0.016	0.129	0.121
H	**-0.470**	**-0.311**	0.294	-0.143
Log (B)	**-0.471**	0.194	-0.072	-0.116
Log (Fe)	**-0.372**	-0.008	**-0.309**	-0.127
Log (Mn)	**-0.357**	-0.218	-0.282	**0.411**
Log (Cu)	**-0.565**	-0.016	-0.024	0.056
Log (Zn)	**-0.660**	0.016	-0.087	0.239
Log (Al)	-0.290	**0.432**	**-0.329**	**0.377**
Log (S)	**-0.525**	0.241	-0.016	**0.308**

Presence-absence data:

When I performed an NMS ordination on the presence absence data, PC-ORD recommended a 3-dimensional solution with a final stress of 15.68 and a final instability of $1x10^{-6}$. This solution has a cumulative correlation coefficient of 0.783 with the original data. Kendall's correlations between the three NMS axes and the species present were calculated in R (Table 18). *Carex pensylvanica* is reported as "had zero variance", because all plots surveyed had *C. pensylvanica* present in all surveys.

None of the changes along axes were correlated with any of the PCA axes, but total vector length had a negative trend with PCA axis 1 and a positive trend with PCA axis 4, with an R square of 0.26 (Table 19). Plots that had the greatest change in species composition, tended to be correlated with low levels of PCA 1, and thus acidic soils, low levels of total Nitrogen, and high levels of P, Mg, K, Na, B, Fe, Mn, Cu, Zn, S. For PCA axis 4, the plots that with the greatest change in species composition were those that had higher levels of Mn, Al, and S.

Table 18: Kendall's correlations between NMS axes and species presence in Mainland maintenance site, ordination on presence-absence data (n=23). Tau values greater than 0.30 are in bold.

	NMS axis 1	NMS axis 2	NMS axis 3
Ammophila breviligulata	**0.542**	0.009	0.009
Arctostaphylos uva-ursi	-0.274	**-0.54**	0.162
Ionactis linarifolius	0.208	-0.2	**-0.567**
Carex pensylvanica	Had Zero Variance		
Danthonia spicata	0.191	-0.144	0.172
Deschampsia flexuosa	**0.419**	-0.077	**0.423**
Dichanthelium spp.	**-0.332**	-0.257	-0.145
Helianthemum spp.	-0.211	0.154	-0.004
Hieracium sp.	0.036	0.206	-0.008
Hudsonia tomentosa	-0.023	-0.209	0.033
Lechea maritima	**-0.624**	0.031	**-0.427**
Myrica pensylvanica	-0.019	-0.08	0.157
Pinus rigida	0.078	**-0.577**	**0.313**
Pitysopsis falcata	-0.033	-0.2	-0.051
Polygala polygama	-0.294	-0.096	0.197
Prunus maritima	0.29	0.149	0.052
Prunus serotina	0.005	-0.005	0.209
Quercus ilicifolia	**0.333**	**-0.49**	**0.354**
Quercus prinoides	0.098	-0.191	0.07
Quercus velutina	0.107	0.201	0.129
Rumex acetosella	0.125	**0.508**	-0.004
Shizachyrium scoparium	-0.209	-0.209	-0.06
Vaccinium corymbosum	0.116	0.144	0.181

Table 19: Regression relationship between length of NMS axis and PCA axes 1 and 4. Data were from the Mainland maintenance site, using presence-absence data.

Summary of Fit

Rsquare	0.256
Rsquare Adj	0.181
Observations	23

ANOVA Table

Source	**DF**	**SS**	**MS**	**F Ratio**
Model	2	1.337	0.668	3.436
Error	20	3.891	0.195	**Prob>F**
Total	22	5.227		0.0522

Parameter Estimates

Term	**Estimate**	**Std Error**	**T Ratio**	**Prob> ltl**
Intercept	1.302	0.092	14.16	**<.0001***
PCA axis 1	-0.068	0.038	-1.80	0.0866
PCA axis 4	0.134	0.070	1.90	0.0714

Cover class data:

In order to obtain a solution with sufficiently low stress and low instability, when performing an NMS ordination on the cover class data at the Mainland maintenance site, I deleted all species that occurred in less than ten plots, therefore ordinating only the most dominant species. The suggested solution using PC-ORD autopilot mode, was a 3-dimensional solution with a final stress of 13.19 and a final instability 0.00. All NMS axes were correlated to species using Kendall's correlations in R (Table 20).

Change in NMS axis 1 was not correlated with any PCA axes. Change in NMS axis 2 was significantly positively correlated with PCA axis 3 (Table 21; Figure 8). In other words, *Arctostaphylos uva-ursi* decreased and *Lechea maritima* and *Schizachyrium scoparium* increased in soils with high organic matter, and low K, Fe, and Al.

Table 20: Kendall's correlations between NMS axes and species (n=23). Tau values above 0.30 are bold.

	NMS axis 1	NMS axis 2	NMS axis 3
Arctostophylos uva-ursi	-0.066	**-0.553**	**0.547**
Carex pensylvanica	**0.413**	0.233	**-0.61**
Deschampsia flexuosa	**-0.41**	-0.281	0.076
Ionactis linarifolius	**0.346**	0.293	0.267
Lechea maritima	-0.183	**0.462**	0.107
Schizachyrium scoparium	**-0.509**	**0.397**	0.171

Table 21: Linear regression between change in NMS axis 2 and PCA axis 3, using the Cover class data at the Mainland maintenance site.

Summary of Fit

Rsquare	0.188
Rsquare Adj	0.150
Observations	23

ANOVA Table

Source	**DF**	**SS**	**MS**	**F Ratio**
Model	1	2.107	2.107	4.8824
Error	21	9.063	0.432	**Prob>F**
Total	22	11.170		**0.0384***

Parameter Estimates

Term	**Estimate**	**Std Error**	**T Ratio**	**Prob> ⏐t⏐**
Intercept	0.321	0.137	2.35	**0.0288***
PCA axis 3	0.215	0.097	2.221	**0.0384***

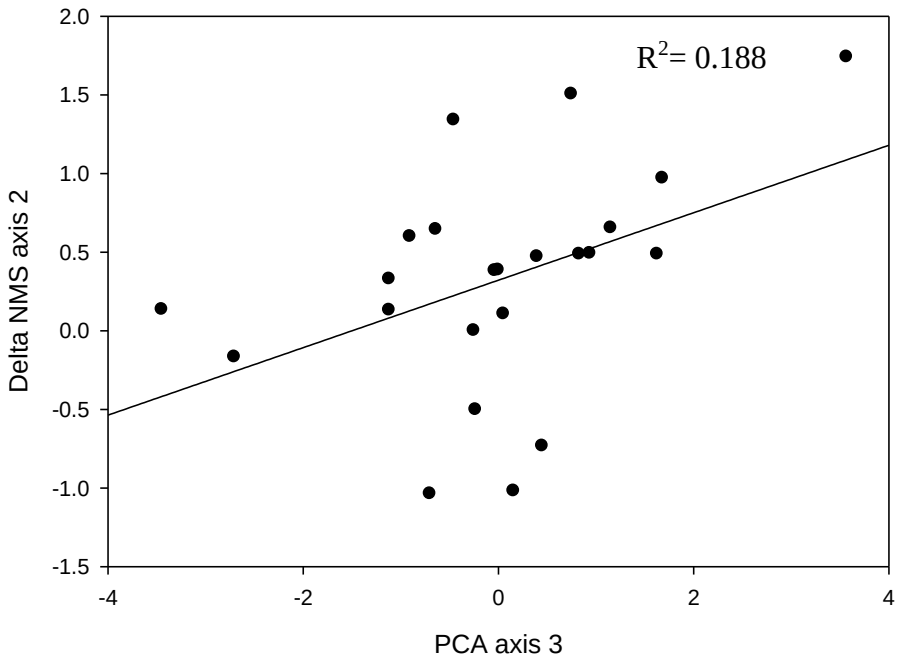

Figure 8: Regression relationship between change in NMS axis 2 and PCA axis 3.

Change in NMS axis 3 from time of plot establishment to the most recent survey was significantly negatively correlated with PCA axis 1 (Table 22). Meaning that where there was more N, less P, fewer micronutrients and the soil was more basic, *Carex pensylvanica* increased and *Arctostaphylos uva-urs* decreased. Change in NMS axis 3 was also negatively correlated with PCA axis 3; so where there was more organic matter, less K, Fe, and Al, there was correlated with and an increase in *C. pensylvanica* and a decrease in *A. uva-ursi*. PCA axis 4 was positively related to the response variable; therefore areas with higher Mn, Al, and S were correlated with increase in *A. uva-ursi* and decreases in *C.pensylvanica.*

Table 22: Multiple linear regression between change in NMS axis 3 and PCA axes. Analysis performed on cover class data in the Mainland maintenance site.

Summary of Fit	
Rsquare	0.700

Rsquare Adj	0.588
Observations	23

ANOVA Table

Source	**DF**	**SS**	**MS**	**F Ratio**
Model	6	14.844	2.474	6.2255
Error	16	6.358	0.397	**Prob>F**
Total	22	21.202		**0.0016***

Parameter Estimates

Term	**Estimate**	**Std Error**	**T Ratio**	**Prob> ltl**
Intercept	-0.074	0.131	-0.56	0.5831
PCA axis 1	-0.169	0.054	-3.13	**0.0065***
PCA axis 2	-0.085	0.088	-0.96	0.3491
PCA axis 3	-0.312	0.103	3.03	**0.0080***
PCA axis 4	0.598	0.208	2.87	**0.0111***
PCA axis 1* axis 2	0.097	0.041	2.35	**0.0321***
PCA axis 2* axis 4	-0.363	0.151	-2.40	**0.0291***

The interaction between PCA axis 1 and PCA axis 2, and the interaction between PCA axis 2 and PCA axis 4 were also significant (Table 22). I determined that for the interaction between PCA1 and PCA2, at low levels of PCA1, PCA 2 has a negative relationship with the response; while at high levels of PCA 1, PCA 2 has a positive relationship. Therefore, when there was little N, more micronutrients, and acidic soils; then less fire and more years since fire, (correlated with higher N, P, lower Al and more acidic soils) were correlated with an increase in *Carex pensylvanica* and a decrease in *Arctostaphylos uva-ursi.* On the other hand, when there was more total nitrogen and fewer micronutrients, the relationship between fire and associated nutrients was reversed- less fire and more years since fire (correlated with higher N, P, lower Al and more acidic soils), were associated with a decrease in *Carex pensylvanica* and an increase in *Arctostaphylos uva-ursi.*

The significant interaction between PCA 2 and PCA 4 shows that at low levels of PCA 2, the relationship between the response (change in NMS axis 3) and PCA 4 is extremely positive. On the other hand, at high levels of PCA 2, the relationship between the response and PCA 4 is mildly negative. Therefore, when there was high nitrogen, fewer years since fire, fewer fires, more P, less Al, and more acidic soils; then areas with more Al, Mn, and S increased in the

species *Arctostaphylos uva-ursi* and decreased in *Carex pensylvanica.* On the other hand, *A. uva-ursi* decreased and *C. pensylvanica* increased with low nitrogen, a high number of years since fire, a large number of fires, low P, high Al, and basic soils.

The length of the NMS vectors between plot establishment and the most recent survey was significantly negatively correlated with PCA axis 1 (Table 23), so where there was more N, more basic soils, and less P, Ca, Mg, K, Na, B, Fe, Mn, Cu, Zn, and S, the vectors had a shorter length.

The length of the vectors were also significantly negatively related to PCA axis 2; where there were more years since fire and more fires (correlated with acidic soils, less N and P, and more Al), the plots did not move as far in ordination space. PCA axis 4 is also negatively correlated with the axis length, such that where there is less Mn, Al, and S, the vectors had a shorter length. There was a significant interaction between PCA axes 2 and 4 (Table 23). It was determined that at low to moderate levels of PCA 2, PCA 4 had a very negative relationship with the response variable, meaning when there was high N and P, fewer years since fire, fewer fires, less Al, and more acidic soils, the plots moved very little in three dimensional space. On the other hand, in a narrow range, at extremely high levels of PCA 2, these soil variables are almost unrelated to length.

Table 23: Multiple regression analysis between vector length and PCA environmental axes.

Summary of Fit

Rsquare	0.659			
Rsquare Adj	0.584			
Observations	23			

ANOVA Table

Source	**DF**	**SS**	**MS**	**F Ratio**
Model	4	7.989	1.998	8.7053
Error	18	4.130	0.229	**Prob>F**
Total	22	12.119		**0.0004***

Parameter Estimates

Term	**Estimate**	**Std Error**	**T Ratio**	**Prob> ltl**
Intercept	1.233	0.010	12.34	**<0.0001***
PCA axis 1	-0.092	0.041	-2.25	**0.0375***
PCA axis 2	-0.282	0.065	-4.32	**0.0004***
PCA axis 4	-0.627	0.144	-4.34	**0.0004***
PCA axis 2*axis 4	-0.344	0.102	3.36	**0.0035***

Nantucket Restoration Site:

Variables included in the PCA were log(total nitrogen), number of fires, mowed or not mowed, H, Al, log(S), log(organic matter), log(P), log(Ca), log(Mg), log(K), log(Na), log(B), log(Fe), log (Mn+1), log(Cu), and log(Zn). Years since last burn and number of burns could not be included separately in this analysis, as the control had zero burns and it had been over 100 years since it had been burned, while all other management units had been burned 4.25 years ago. Therefore we used the number of burns (0, 2, or 3 burns), with the understanding that a plot with zero burns had been "long unburned."

Three outlier plots were detected in the soil data, using box-and-whisker plots in JMP. Due to the assumptions of normality of PCA, as well as the large effect that outliers can have on PCA analyses, these outliers were removed from the dataset. While I recognize that these are likely biologically important points, I opted to remove them for two reasons: 1) in order to meet the assumptions of PCA, and 2) if I included them in the data the PCA would be largely capturing the difference between the majority of the data and these three points, and while this would be interesting, my sample size was not large enough to make such comparisons. Therefore the following analysis focuses on the majority of the edaphic conditions of the Nantucket

restoration site and do not represent the rarer microsites, which may have been excluded from this analysis.

The first four axes of the PCA ordination on environmental variables were interpreted and these axes represent 81.41% of variation in the original data (Table 24). The first four axes were deemed interpretable using the broken-stick Eigenvalue and correlated to environmental variables using Kendall's correlations (Table 25).

Table 24: Eigenvalues for the PCA analysis on environmental variables without outliers at the Nantucket Restoration site (n=25). The first four axes were interpreted.

PCA Axis	**Eigenvalue**	**Cumulative % of variance**	**Broken–stick Eigenvalue**
Axis 1	5.272	31.01	3.440
Axis 2	3.600	52.19	2.440
Axis 3	3.080	70.31	1.940
Axis 4	1.887	81.41	1.606
Axis 5	0.862	86.40	1.356

Table 25: Kendalls correlations between PCA axes and environmental variables (n=25). Tau values above 0.30 are in bold.

	PCA axis 1	PCA axis 2	PCA axis 3	PCA axis 4
Log (Total Nitrogen)	**-0.600**	-0.047	0.147	-0.287
Number of fires	0.004	**0.630**	**-0.389**	-0.028
Mowed or not	**-0.597**	0.175	0.216	**-0.411**
H	0.043	0.012	**0.550**	**0.417**
Al	-0.060	**-0.440**	**-0.487**	0.027
Log (S)	-0.031	**-0.432**	**-0.557**	0.045
Log (Organic Matter)	**-0.498**	**-0.391**	0.157	0.037
Log (P)	**-0.334**	0.057	0.192	-0.114
Log (Ca)	**-0.673**	0.245	-0.124	-0.003
Log(Mg)	**-0.606**	-0.010	0.078	0.118
Log(K)	**-0.665**	-0.081	-0.054	-0.054
Log(Na)	**-0.428**	**-0.366**	0.038	0.191
Log(B)	-0.078	**-0.569**	0.126	-0.003
Log(Fe)	0.020	0.007	**0.498**	**0.357**
Log(Mn+1)	**-0.602**	**0.408**	0.035	-0.229
Log(Cu)	**-0.364**	0.290	**-0.357**	0.284
Log(Zn)	**-0.304**	0.117	**-0.511**	**0.331**

Presence-absence data*:*

In order to obtain a stable solution when running an NMS ordination on the presence-absence data, I removed all species that occurred in five or fewer plots. The best solution was identified as a 4-dimensional solution with a final stress of 9.69 and a final instability of $1x10^{-6}$. The correlation of determination for the first four axes with the original data was 0.895 (Table 26). Kendall tau values between species and NMS axes were calculated (Table 27).

Table 26: Coefficients of determination of distance of plots in ordination space versus distance of plots in original space (n=25).

Axis	Increment	Cumulative
1	0.135	0.135
2	0.294	0.429
3	0.211	0.641
4	0.254	0.895

Table 27: Kendall's correlations between species presence-absence data and NMS axes (n=25). Tau values greater than 0.30 are in bold.

	NMS axis 1	NMS axis 2	NMS axis 3	NMS axis 4
Carex pensylvanica	-0.174	**-0.437**	0.220	**-0.620**
Corylus cornuta	0.124	0.041	**-0.453**	-0.038
Gaultheria procumbens	-0.223	-0.272	**-0.345**	**0.308**
Gaylussacia baccata	0.206	**0.319**	-0.187	0.231
Quercus ilicifolia	0.137	**0.610**	-0.156	**-0.409**
Quercus prinoides	**-0.316**	-0.211	**0.713**	-0.125
Rubus flagellaris	-0.043	**-0.313**	-0.004	-0.285
Rubus hispidus	0.284	-0.292	0.011	-0.192
Vaccinium angustifolium	**-0.607**	0.188	-0.136	**0.402**
Vaccinium pallidum	-0.217	0.125	-0.155	**-0.335**

None of the PCA axes were significantly correlated with change in NMS axis 1. Change in NMS axis 2 was significantly, positively, correlated with PCA axis 2 (Table 28; Figure 9). This relationship means that *Gaylussacia baccata* and *Quercus ilicifolia* presence increased in more plots¸ and *Carex pensylvanica* and *Rubus flagellaris* presence increased in fewer plots in the burned areas of the site, which was also associated with lower Al, S, organic matter, Na, and B and higher Mn.

Table 28: Linear regression between change in NMS axis 2 and PCA axis 2. Regression using the Nantucket Restoration site, presence-absence data without outliers.

Summary of Fit

Rsquare	0.289
Rsquare Adj	0.258
Observations	25

ANOVA Table

Source	**DF**	**SS**	**MS**	**F Ratio**
Model	1	1.152	1.152	9.3647
Error	23	2.829	0.123	**Prob>F**
Total	24	3.981		**0.0055***

Parameter Estimates

Term	**Estimate**	**Std Error**	**T Ratio**	**Prob> ltl**
Intercept	-0.154	0.070	-2.19	**0.0389***
PCA axis 2	0.113	0.037	-3.06	**0.0055***

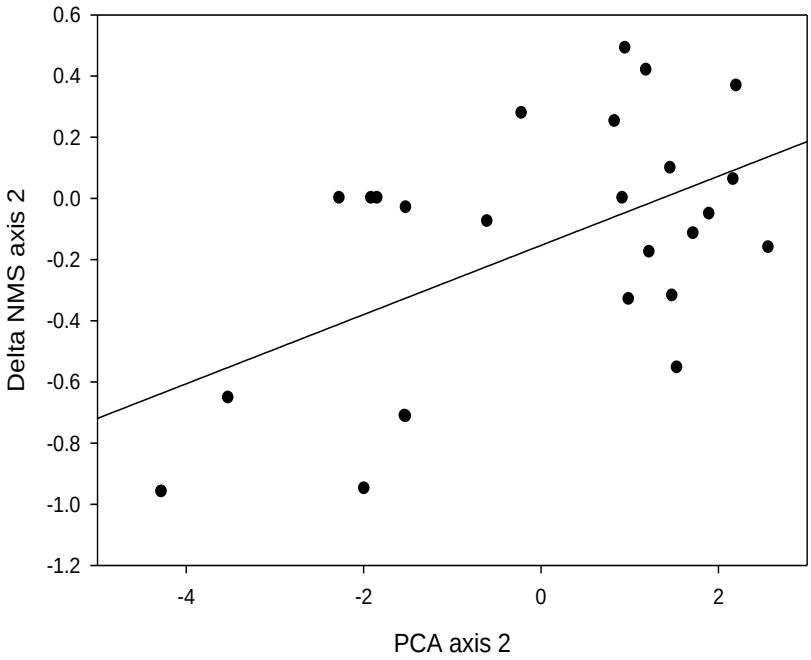

Figure 9: Linear regression between change in NMS axis 2 and PCA axis 2. Analysis on presence-absence data after removing outliers.

AICc model selection identified a negative trend between change in NMS axis 3 and PCA axis 1 (Table 29). This corresponds to an increase in *Quercus prinoides* presence and a decrease in *Corylus cornuta*, and *Gaultheria procumbens* presence in nutrient poor, un-mowed area of the site.

Change in NMS axis 4 was significantly, positively, related to PCA axis 3 (Table 30, Figure 10). *Carex pensylvanica*, *Quercus ilicifolia*, and *Vaccinium pallidum* increased in presence in the burned, more basic soils with more Al, S, Cu, and Zn, and less Fe.

Table 29: Regression between change in NMS axis 3 and PCA axis 1. Analysis on presence-absence data without outliers for the Nantucket Restoration site.

Summary of Fit

Rsquare	0.151
Rsquare Adj	0.114
Observations	25

ANOVA Table

Source	**DF**	**SS**	**MS**	**F Ratio**
Model	1	0.460	0.460	4.0752
Error	23	2.599	0.113	**Prob>F**
Total	24	3.059		0.0553

Parameter Estimates

Term	**Estimate**	**Std Error**	**T Ratio**	**Prob> ltl**
Intercept	0.087	0.067	1.30	0.2062
PCA axis 1	-0.059	0.029	-2.02	0.053

Table 30: Regression relationship between change in NMS axis 4 and PCA axis 3. Analysis was run on presence-absence data without outliers.

Summary of Fit

Rsquare	0.217
Rsquare Adj	0.18
Observations	25

ANOVA Table

Source	**DF**	**SS**	**MS**	**F Ratio**
Model	1	1.364	1.364	6.3783
Error	23	4.917	0.234	**Prob>F**
Total	24	6.281		**0.0189***

Parameter Estimates

Term	**Estimate**	**Std Error**	**T Ratio**	**Prob> ltl**
Intercept	-0.198	0.092	-2.14	**0.0431***
PCA axis 3	0.133	0.053	2.53	**0.0189***

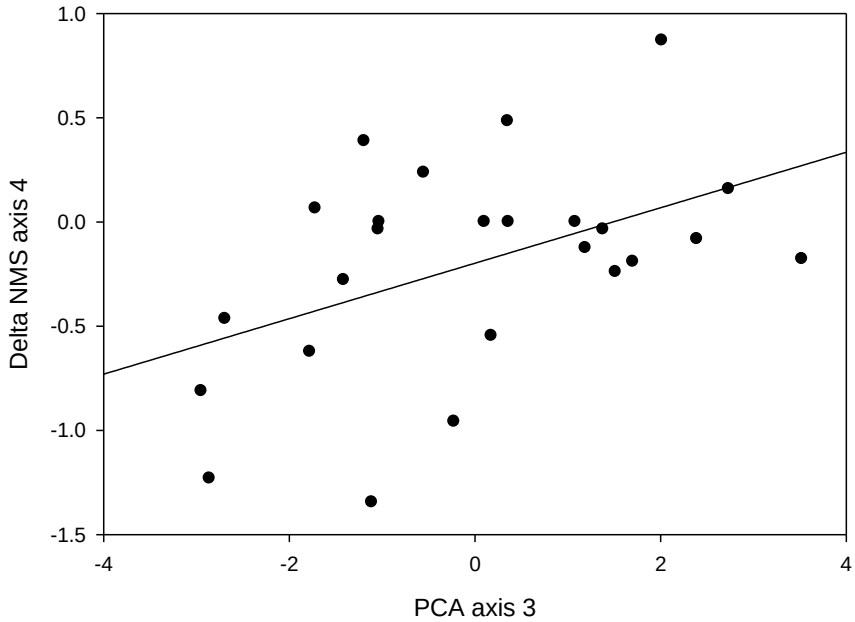

Figure 10: Linear regression between change in NMS axis 4 and PCA axis 3. Regression run on the presence-absence data excluding the outliers at the Nantucket Restoration site.

Cover class data:

In order to obtain a stable solution for this NMS ordination, I removed all species with ten or fewer occurrences. Therefore, this ordination represents the change in cover of only the most dominant plants at this site. This produced a 4-dimensional solution with a stress of 6.73 and a final instability of 0.00. The first four axes have a cumulative correlation coefficient of 0.946 with the original data (Table 31). Correlations between NMS axes and species were assessed using Kendall's correlations (Table 32).

Table 31: Correlation of determination between the first four axes and the original data for four dimensional NMS ordination at Nantucket Restoration site, using cover class data

Axis	Increment	Cumulative
1	0.393	0.393
2	0.169	0.562
3	0.159	0.722
4	0.224	0.946

Table 32: Kendall's correlations between NMS axes and species cover classes for NMS ordination on Cover Class data without outliers at the Nantucket Restoration site (n=25). Tau values >0.30 are in bold. Plants that occured in less than 10 plots were excluded from the ordination.

	NMS axis 1	**NMS axis 2**	**NMS axis 3**	**NMS axis 4**
Carex pensylvanica	**0.677**	-0.064	-0.288	**-0.398**
Gaylussacia baccata	**-0.442**	-0.160	0.019	**0.657**
Quercus ilicifolia	-0.148	**0.460**	**0.382**	**-0.433**
Quercus prinoides	-0.202	0.024	**-0.571**	**-0.427**
Vaccinium angustifolium	-0.113	**-0.556**	0.192	-0.235

Change in NMS axis 1 was significantly related to the interaction between PCA axis 1 and PCA axis 2 (Table 33). The interaction between PCA 1 and PCA 2 was such that at low levels of PCA1, the relationship with PCA2 is highly positive. At high levels of PCA1, the relationship with PCA2 is strongly negative. Therefore, in the mowed areas, where soil nutrients are also higher; fire (which was also associated with reductions in Al, S, organic matter, Na, B, and increased Mn), was negatively correlated with *Gaylussacia baccata* cover and positively correlated with *Carex pensylvanica* cover. On the other hand, in the lower nutrient, un-mowed portions of the site, fire and the associated micronutrients were positively associated with *Gaylussacia baccata* and negatively associated with *Carex pensylvanica.* In other words, in the burned and mowed portions of the site, there has been a decrease in *G. baccata* cover and an increase in *C. pensylvanica* cover, while in the burned-only portions of the site, there has been the opposite trend.

Table 33: Multiple regression analysis between change in NMS axis 1 between 1999 and 2009 and PCA axes 1 and 2 and their interaction tern. Cover class data are from the Nantucket Restoration site, and exclude outliers.

Summary of Fit	
Rsquare	0.408

Rsquare Adj	0.324
Observations	25

ANOVA Table

Source	**DF**	**SS**	**MS**	**F Ratio**
Model	1	1.382	0.461	4.832
Error	21	2.002	0.100	**Prob>F**
Total	24	3.384		**0.0104***

Parameter Estimates

Term	**Estimate**	**Std Error**	**T Ratio**	**Prob> ltl**
Intercept	-0.114	0.062	1.85	0.0783
PCA axis 1	-0.010	0.027	-0.36	0.7246
PCA axis 2	-0.009	0.033	-0.26	0.7940
PCA axis 1* axis 2	-0.059	0.016	-3.79	**0.0011***

Change in NMS axis 2 was significantly related to PCA axis 3, the interaction between PCA axis 1 and PCA axis 4, and the interaction between PCA axis 3 and PCA axis 4. There was also a negative trend with PCA axis 4 without an interaction term (Table 34). The interaction term was such that at low levels of PCA 1, the relationship with PCA 4 was negative, while at high levels of PCA 1, the relationship with PCA 4 was positive. For the interaction between PCA 3 and PCA 4, at low levels of PCA 3, PCA 4 had almost no relationship with the response variable, while at high levels of PCA 3, PCA 4 was negative.

Thus, for the negative relationship with PCA 3, there was an increase in *Vaccinium angustifolium* cover and a decrease in *Quercus ilicifolia* cover where there were fewer fires, associated with acidic soils, more Fe, and less Al, S, Cu, and Zn. For the interaction between PCA 1 and PCA 4, in the mowed, high nutrient site, an increase in *Quercus ilicifolia* and a decrease in *Vaccinium angustifolium* were associated with mowing, more basic soils, less Fe, and increased Zn.

Change in NMS axis 3 was positively related to PCA axis 2. Thus, in areas that experienced more fire (associated with less Al and S), there was an increase in *Quercus ilicifolia* cover and a decrease in *Quercus prinoides* cover. Additionally, there was an interaction between PCA axis 1 and PCA axis 4, and the interaction between PCA axis 2 and PCA axis 4 (Table 35). The interaction was such that when PCA 1 was low, the relationship with PCA 4 was positive.

While when PCA 1 was high, the relationship with PCA 4 was negative. The interaction between PCA 2 and PCA 4 was such that when PCA 2 was low, the relationship with PCA 4 was extremely negative, on the other hand, when PCA was positive, PCA 4 was only mildly negative.

Table 34: Multiple linear regression between change in NMS axis 2 and PCA axes at the Nantucket Restoration site, excluding outliers.

Summary of Fit

Rsquare	0.711
Rsquare Adj	0.635
Observations	25

ANOVA Table

Source	**DF**	**SS**	**MS**	**F Ratio**
Model	5	3.271	0.654	9.3581
Error	19	1.328	0.070	**Prob>F**
Total	24	4.600		**0.0001***

Parameter Estimates

Term	**Estimate**	**Std Error**	**T Ratio**	**Prob> ltl**
Intercept	0.038	0.053	0.72	0.4791
PCA axis 1	0.010	0.026	0.40	0.6926
PCA axis 3	-0.135	0.033	-4.16	**0.0005***
PCA axis 4	-0.070	0.039	-1.80	0.0875
PCA axis 1* axis 4	0.087	0.024	3.56	**0.0021***
PCA axis 3* axis 4	-0.051	0.022	-2.26	**0.0359***

Change in NMS axis 4 had a strong positive trend with PCA axis 1 and a significant negative relationship with PCA axis 4 (Table 36). For the trend with PCA axis 1, in un-mowed areas with lower nitrogen and micronutrients, there has been an increase in *Gaylussacia baccata,* and a decrease in *Carex pensylvanica, Quercus prinoides,* and *Quercus ilicifolia.* For the relationship with PCA 4, in un-mowed areas with more acidic soils, more Fe, and more Zn, there was a decrease in *G. baccata* and an increase in *C. pensylvanica, Q. prinoides,* and *Q. ilicifolia.*

Table 35: Multiple linear regression between Change in NMS axis 3 and PCA axes at the Nantucket Restoration site on Cover Class data, excluding outliers.

Summary of Fit

Rsquare	0.593

Rsquare Adj	0.486
Observations	25

ANOVA Table

Source	**DF**	**SS**	**MS**	**F Ratio**
Model	5	4.492	0.898	5.5412
Error	19	3.081	0.162	**Prob>F**
Total	24	7.573		**0.0026***

Parameter Estimates

Term	**Estimate**	**Std Error**	**T Ratio**	**Prob> ltl**
Intercept	-0.193	0.081	-2.40	**0.0271***
PCA axis 1	0.023	0.039	0.60	0.5564
PCA axis 2	0.145	0.044	3.28	**0.0039***
PCA axis 4	0.091	0.060	1.52	0.1461
PCA axis 1* axis 4	-0.088	0.037	-2.40	**0.0266***
PCA axis 2* axis 4	-0.106	0.033	-3.24	**0.0043***

Table 36: Multiple linear regression between Change in NMS axis 4 and PCA axes 1 and 4. Analysis on Nantucket Restoration site on cover class data with outliers removed.

Summary of Fit

Rsquare	0.384
Rsquare Adj	0.328
Observations	25

ANOVA Table

Source	**DF**	**SS**	**MS**	**F Ratio**
Model	2	2.615	1.307	6.8513
Error	22	4.197	0.191	**Prob>F**
Total	24	6.811		**0.0049***

Parameter Estimates

Term	**Estimate**	**Std Error**	**T Ratio**	**Prob> ltl**
Intercept	-0.159	0.087	-1.82	0.0826
PCA axis 1	0.079	0.038	2.07	0.0505
PCA axis 4	-0.195	0.064	-3.07	**0.0056***

Discussion

Maintenance sites

The correlation between fire and change in the vegetation community was highly affected by soil nutrients, as seen by the fact that my results showed several complex interactions between the two. For example, at the Nantucket maintenance site (NMS axis 1, presence-absence data) in acidic soils with higher overall nutrient levels (except P and B); the presence of fire (associated with low P, Ca, Mg, Fe, Mn, and high Cu, Al, and S), was correlated with an increase in *Arctostapholus uva-ursi*, *Aster paternus*, *Danthonia spicata*, *Heliantemum spp.*, *Hieracium sp.*, *Hudsonia ericoides*, and *Schizacrium scoparium.* On the other hand, in basic soils, with lower soil nutrients, fire was instead associated with a decrease in these species.

Three of the six species most strongly correlated with this axis (*Danthonia spicata Helianthemum spp.* and *Schizacrium scoparium*) were found most frequently in 'High Diversity Native Grasslands' by Dunwiddie et al. (1996). The other three species strongly correlated with this axis, *Arctostapholus. uva-ursi* , *Aster* paternus, and *Hudsonia ericoides*, were found most frequently in 'Broom Crowberry Heathlands', which are characterized by high C:N ratios, and often develop in areas where most of the topsoil has been removed (Dunwiddie et al. 1996).

Broom crowberry heathland is also considered a desirable, native heathland type which is dominated by plants of a smaller stature (Dunwiddie et al. 1996). In the same paper *Hieracium sp.* was classified as weedy. Due to the presence of mostly 'High Diversity Native Grassland' and 'Broom Crowberry heathland' species, I interpreted change in NMS axis 1 as being mostly typical of high diversity, native, sandplain species. Therefore soil nutrient levels were important in determining how fire was associated with changes in typical sandplain heathland species at the Nantucket maintenance site.

Similarly, in the Mainland maintenance site, complicated interactions were seen in NMS cover class axis 3. When in acidic, nitrogen-poor soils that were both phosphorus and potassium-rich, and were high in micronutrients; less fire and more years since fire were correlated with a decrease in *Arctostapholus uva-ursi* and an increase in *Carex pensylvanica*. In this case, fire was associated with soils which tended to be more acidic, higher in nitrogen and phosphorous, and lower in aluminum. On the other hand, when the soil conditions were more basic, with more nitrogen, and fewer micronutrients, this relationship was reversed and fire and the associated micronutrients were correlated with an increase in *A. uva-ursi* and a decrease in *C. pensylvanica.*

Prescribed fire is often applied to these communities with the general goal of preserving sandplain heathland diversity (Harper 1995), but the presence of these interactions underscores the complexity of fire management and demonstrates the necessity of understanding site factors, such as soil nutrients, before applying fire-based management to a site. These interactions may imply that differing underlying soil nutrients are indicative of different habitats, or microhabitats. These habitats may contain different species assemblages from the onset of management and the application of prescribed burning does not appear to be having the same effect on all of these assemblages. Interactions between fire and differing site vegetation have been documented by others. For example, while examining the effects of fire on Mediterranean ecosystems in Spain, Arnan et al. (2007) saw an interaction between vegetation type and burning that was the most important variable examined in determining the response of vegetation composition to fire.

Habitat specialization is likely playing a role in this interaction; habitat specialization influences the life history traits of species present at a site, which influences regeneration following a disturbance (Grime 1977; Noble & Slatyer 1980). For example, the interaction

between fire and microhabitat in Florida scrub was largely due to the number of gap specialists in that system (Menges & Hawkes 1998). Habitat specialization may also play a role in sandplain heathland fire dynamics, but more research on how soil nutrients affect species composition within sandplain heathlands would be necessary in order to better interpret what role habitat specialization is playing in these results.

Nantucket maintenance site

The Nantucket maintenance site had the largest data set of any of the three sites examined. Additionally the vegetation was less confounded with management unit at this site than at the Mainland maintenance site, allowing us to make inferences that were not possible at the other two sites.

The ericoid subshrubs *Arctostapholus uva-ursi* and *Vaccinium angustifolium* tended to decrease in areas that had had more burns and fewer years since fire; these areas also tended to be more basic and have less iron (axis 3, presence-absence data). *Gaylussacia baccata* and *Rosa virginiana* increased under these same conditions. This decrease in subshrubs with fire is similar to what has been reported in the literature, for example in a heathland in England, Ward et al. (2007) saw a decrease in ericoid subshrubs and an increase in graminoids in areas that had been burned for fifty years versus a control. Despite being an ericoid shrub, *Gaylussacia baccata* did not respond the same way to fire as both *Arctostapholus uva-ursi* and *Vaccinium angustifolium*.

Gaylussacia baccata is a management concern in the sandplain heathlands, particularly on Nantucket, because it is an aggressively spreading, clonal, shrub that has been shown to shade out other species and decrease species diversity in these heathlands (Harper 1995). Prescribed burning is currently used as a means of suppressing this undesirable, native species (Dunwiddie & Caljouw 1990; Harper 1995). The success of this management strategy is not clear in these data. For example, looking at NMS axis 2 (presence-absence data), there was an increase in *G. baccata* and a decrease in graminoids associated with parts of the site that had undergone more fire (these areas were also higher in P, Ca, Mg, Fe, and Mn, while being poorer in Cu, Al, and S). The fact that this species is increasing, even in the presence of fire, is unsurprising, given the ease with which it has been shown to regenerate from rhizomes (Matlack 1997). One study even showed enhanced growth of *G. baccata* with both fire and with stem clipping (Matlack, Gibson

& Good 1993). Similarly, an increase in *G. baccata* was seen after a prescribed burn in the Appalachian Mountains (Elliott *et al.* 1999).

Lastly, at this site there appears to be a correlation between increasing ruderal and nitrophilic species with increased fire. NMS axis 2 (presence-absence data) showed an increase in *Agrostis stolinifera, Juncus greenei, Euthamia tenuifolia,* and *Rosa virginiana* with increasing fire (associated with increased P, Ca, Mg, and Fe; as well as decreasing Cu, Al, and S). Both *A. stolinifera* and *J. greenei* grouped the highest with 'weedy' sandplain habitats in a study by Dunwiddie et al. (1996), while *E. tenuifolia* grouped with 'Pennsylvania sedge' grassland type and *R. virginiana* grouped the highest with 'Huckleberry/scrub oak' heathland type (Dunwiddie, Zaremba & Harper 1996), *E. tenuifolia* and *Rosa sp.* have been shown to be significantly associated with the more nitrogen rich areas of this site (Table 37, chapter 2). (Note that *Rosa virginiana* as identified by historical surveyors is likely the same species as *Rosa carolina* as identified in Chapter 2, as these two species are easily confused.) Therefore I interpreted an increase along this axis as an increase in ruderal species and species associated with higher nitrogen. Prescribed fire has been shown to cause a pulse in soil nitrogen in sandplain grasslands (Dudley & Lajtha 1993) and a meta-analysis done by Wan and colleagues (Wan, Hui & Luo 2001), performed a meta-analysis using 87 studies in terrestrial ecosystems and saw a significant increase in both ammonium and nitrates following fire. Therefore a pulse in nitrophilic species following prescribed fire is unsurprising, although it may be concerning due to the naturally low nutrient status of heathlands (Specht 1979) .

One concern with using prescribed fire is potential increases in ruderal and invasive species post-disturbance, which may be due to reduced competition, or the pulse of nutrients that directly follow a fire, or both (Hobbs & Huenneke 1992). This was seen in a California coastal sage scrub, where exotic plant cover was positively correlated with fire frequency (Fleming, Diffendorfer & Zedler 2009).This is obviously an undesirable effect of prescribed fire, and more research is needed to confirm that this is a problem in sandplain heathlands as well as recommend management techniques to reduce this risk. Sandplain heathlands have been shown to harbor fewer non-native, invasive species than other habitats in New England (Von Holle &

Motzkin 2007), although it is conceivable that this trend could change if prescribed fire were to change existing abiotic or biotic conditions.

Nantucket Restoration Site

Vegetation type was more confounded with management unit at this site than in the other two sites, meaning that each management unit had distinct vegetation from the others. Therefore, I am more cautious about interpretations from analyses at this site. The restoration site did not show any clear pattern between species change and burn frequency, or the presence of mowing.

Similar to the maintenance site, fire did not have a predictable correlation with change in the clonal shrub *Gaylussacia baccata.* In the areas that had been burned the most, which were also poorer in Al, Ca, Na, B, and organic matter, while richer in Mn, there was the largest increase in *G. baccata* (as seen in NMS axis 4, presence-absence data). It is also likely that this burn unit had more *G. baccata* at the time of plot establishment. None the less, areas that have only been burned and not mowed (unit G) have had more of an increase in *G. baccata* than the other units, and thus fire does not appear to have been very effective at controlling this species.

Additionally, in areas that were burned and mowed (which are also the areas of the site that are more nutrient rich) there has been less of an increase in *G. baccata.* These are also the areas of the site that are likely to have had the least *G. baccata* to begin with, however mowing may be considered as a management tool for this species in the future. That being said, Matlack et al. (1993) saw an increase in the species after clipping, therefore mowing may not be an appropriate management tool and more study is needed before mowing should be applied as a suppression technique for this species.

This restoration site also shows complex interactions between management and soil variables. For example, in the burned and mowed areas that were higher in organic matter, P, Ca, Mg, K, Mn, Cu, and Zn; there was an increase in *Carex pensylvanica*, *Quercus ilicifolia*, and *Quercus prinoides* cover. While in acidic soils with high Fe, and Zn, mowing correlated with decreased cover in these species.

Conclusion

While prescribed burning has been used as a management technique to prevent shrub encroachment as well as promote native species (eg. Dunwiddie and Caljouw 1990), the correlations between species change and prescribed burning are not completely clear. The effects of burning appear to be very site, or microsite, specific and variables such as the original vegetation and edaphic characteristics need to be taken into account before management is applied. Prescribed burning has also been used to prevent encroachment of the clonal shrub *Gaylussacia baccata*, but this species does not appear to be clearly suppressed by that management technique. In fact, there were instances in this study where *G. baccata* appeared to be increasing disproportionately in areas with increased fire. Furthermore, I found an association between areas with increased ruderal species and areas that had been burned more at the Nantucket maintenance site. This is concerning because a shift towards more nitrophilic, ruderal species, may indicate a species change away from stress tolerant sandplain natives.

With this study, I have begun to elucidate patterns between edaphic factors, fire frequency, and change in sandplain heathland species. Though my results are not conclusive, they do serve as a starting point for further study and propose several interesting new questions that are worth study. This work revealed a complex mosaic of fire and edaphic factors that will require future experimental studies to fully disentangle.

My study suggests that prescribed fire may not be meeting management goals within these sandplain heathlands. First, there is no clear pattern between changes in shrub cover and burn history, with some evidence of increasing shrub cover with increasing burn frequency. Additionally, my study shows evidence of undesirable effects of burning, such as increasing ruderal and nitrophilic species with increasing fire frequency. For these reasons I suggest that alternative management strategies be investigated. I suggest controlled experiments be used in order to research management alternatives to burning, such as mowing, grazing, and turf removal.

CHAPTER 2: CHANGE IN SANDPLAIN HEATHLAND SPECIES COMPOSITION OVER THE LAST TWO DECADES

Changing nutrient status of heathlands

Increasing nitrogen deposition and changing soil nutrient status

Nitrogen is necessary to sustain life on earth, but the vast majority of nitrogen is found in the form of molecular nitrogen (N_2), which is unusable for most living organisms (Galloway *et al.* 2002). Only a few species of microbes and lightning naturally break N_2 into forms of nitrogen that other life forms can use; for this reason nitrogen has historically been a limiting nutrient for many terrestrial ecosystems and many organisms have evolved to live in low nitrogen environments (Galloway *et al.* 2002; Galloway *et al.* 2003; Vitousek *et al.* 1997). Through the cultivation of legumes and other plants that promote bacterial nitrogen fixation, combustion of fossil fuels, and the Haber-Bosch process (used to fix nitrogen, primarily for fertilizer production), humans have drastically increased the amount of available nitrogen on the earth, from approximately 15 teragrams (Tg) N per year created by human activities in 1860 to the astounding rate of approximately 165 Tg N per year created in 2000 (Galloway *et al.* 2002). Today the amount of nitrogen fixed by humans is equal to, or exceeds, the amount fixed by all natural sources combined (Vitousek *et al.* 1997).

In Europe, increasing nitrogen deposition from anthropogenic sources has been implicated in the changing nitrogen status of European heathlands (Bobbink, Hornung & Roelofs 1998). Because heathlands have naturally nitrogen-poor soils, many heathlands are rapidly converting to grasslands with increased nitrogen loads, as grasses outcompete dwarf shrubs and other characteristic heathland species under elevated nitrogen (Aerts & Berendse 1988; Aerts *et al.* 1990; Heil & Diemont 1983). Thus, nitrogen deposition has been identified as a cause of reduced species diversity in European heathlands (Bobbink, Hornung & Roelofs 1998) and as one of the leading threats to heathlands worldwide (Bakker & Berendse 1999; Vitousek *et al.* 1997).

Nitrogen deposition on Cape Cod

Nitrogen deposition has been well documented in the Northeastern United States, with effects recorded on both coastal waters and forest ecosystems (Aber et al. 2003, Driscoll et al. 2003), but there are no published studies on potentially changing nutrient status in sandplain heathlands of New England, despite heathlands being recognized as a nitrogen sensitive system (Achermann & Bobbink 2003).

There are two types of nitrogen deposition, wet deposition and dry deposition. Wet deposition for Cape Cod was recorded at 9.22 kg N ha^{-1} yr^{-1} in 2011 (National Atmospheric Deposition Program (NRSP-3) 2007) and dry deposition data is not available for Cape Cod. Bowen & Valiela (2001) estimated the total rate of nitrogen deposition on Cape Cod as being approximately 11 kg N ha^{-1} yr^{-1} in 2000. The critical load estimated by Achermann and Bobbink (2003) for dry heathland habitat types is between 10 and 20 kg N ha^{-1} yr^{-1} meaning that loads above this may have deleterious effects on dry heathland ecosystems. Thus, Cape Cod is likely experiencing levels of deposition at the lower end of the critical load. While the impacts of elevated nutrient inputs have been well studied in European heathlands, (eg. (Bobbink, Hornung & Roelofs 1998), these effects are less well studied in New World heathland systems.

Other potential causes of changing soil nitrogen

Not all changes in soil nitrogen levels are anthropogenic in origin, soil nutrients may fluctuate due to natural phenomena, such as disturbances. In addition to a change in community structure and species composition, there is a change in resource availability following a disturbance (Sousa 1984; Vitousek, Matson & Cleve 1989). In primary succession, where most of the biomass is removed from the system during the disturbance, one would expect to see an increase in nutrients with time since disturbance; as time since disturbance increases, plant biomass like leaf litter begins to accumulate and the amount of organic matter, and thus the amount of nitrogen mineralization increases (Berendse 1990; Vitousek, Matson & Cleve 1989). For example, in a heathland in the United Kingdom succession resulted in increased ammonium, phosphorus, pH, calcium, and magnesium in soils at later successional stages, even after the

application of canopy clearing management (Mitchell *et al.* 1999). Thus, succession is one possible cause for increasing nitrogen in heathland soils over time.

Fire also changes the nutrient pools of a heathland, often in complex and unpredictable ways (Adams *et al.* 1994). No published studies of the effects of prescribed burning on New England sandplain heathland soil nutrients could be found, but studies in other systems on Cape Cod do exist. Neill and colleagues (2007) looked at the effects of prescribed fire on soil nutrients in an oak-pine forest in New England and found that annual summer burning increased soil pH and reduced the thickness of soil organic matter, but otherwise found negligible effects of burning on soil nutrients in this system (Neill, Patterson III & Crary Jr 2007). On the other hand, Dudley and Lajtha (1993) investigated fire in New England sandplain grasslands and saw an increase in nitrogen availability on the soils surface following a prescribed fire. Soil nitrogen did decrease after rain, due to leaching, but soil nitrogen levels did not return to pre-burn conditions for at least three years following the prescribed burn (Dudley & Lajtha 1993). Additionally, a meta-analysis done by Wan and colleagues (2001), showed a significant increase in both ammonium and nitrates following fires. Nitrogen levels usually returned to pre-fire levels within one year of burning (Wan, Hui & Luo 2001).

While burning may cause an initial spike in available soil nitrogen in heathlands, in the long run consistent fire management generally removes nutrients from heathlands (Adams *et al.* 1994; Power *et al.* 2001). Adams and colleagues (1994) found that heathlands that were never burned had significantly higher levels of soil nitrogen than those that had been repeatedly burned.

Different types and intensities of management affect heathland soil nutrients differently. Powers and colleagues (2001) found that more intensive management treatments, such as high intensity burning or mowing, reduced the rate of litter decomposition, and were thus better at maintaining low nutrient soils in the years immediately following management, than lower intensity fire treatments.

The relationship between grazing and soil nitrogen is also complex, depending on site, soil type, and management regime, among other factors. Grazing involves the removal of nutrients in the system via herbivory but also involves the input of nutrients into the system via

animal excrement. Thus, grazing can both positively and negatively affect soil organic matter, depending on the system, with no consistent trend in one direction or the other (Milchunas & Lauenroth 1993). In addition, grazing introduces a biotic element and therefore the food selection of grazers may have an important influence on plant species composition (Milchunas & Lauenroth 1993). Sheep grazing was a major factor in the formation of these sandplain heathlands, as well as a driver of historical species composition (Dunwiddie 1989; Motzkin & Foster 2002). Stocking rates for sheep in this area were incredibly high, peaking around 20,000 sheep on Nantucket and 17,000 sheep on Cape Cod (Motzkin & Foster 2002). Cattle were also present on both Nantucket and Cape Cod, but stocking rates were much lower (Motzkin & Foster 2002). I could not find any published research on the effect of sheep grazing on soil nutrients or species composition in sandplain heathlands.

Shrub encroachment as a management concern in heathlands

One of the main roles of disturbance in sandplain heathlands is maintaining the open structure of the heathland. In the time of European settlers grazing and traditional agriculture played this role (Motzkin & Foster 2002), and today management aims to prevent encroachment in the same way (Harper 1995). This includes keeping both the abundance and the stature of shrubs and other larger woody species low, and preventing them from outcompeting early successional species. On Nantucket Island, an increase in the clonal shrub, *Gaylussacia baccata* corresponded to a decrease in species richness (Harper 1995). This relationship has been shown in other heathlands as well, for example Specht and Specht (1989) saw a linear decrease in species richness with increasing overstory cover in heath communities throughout Australia.

Statement of objective

In this study I investigated how certain categories of plants increased or decreased in sandplain heathlands over the last two decades and how management and edaphic variables were correlated with these species changes. I had three objectives in this study. (1) To determine if there had been an increase in nitrophilic species in these heathlands over the last two decades, and if management and edaphic variables were correlated with this change. I hypothesized that there had been an increase in nitrophilic species cover. (2) To investigate if there had been a

change in shrub cover at these sites and how past management and edaphic variables were correlated with this change in shrub cover. I hypothesized that there had been an increase in shrub cover. Lastly, (3) to explore changes in species richness within different functional groups and the relationship between these changes and management, edaphic variables, and change in shrub cover.

Methods

As in Chapter 1, all three sites were analyzed separately due to the differences in environmental factors between the mainland site and the Nantucket island sites.

To determine if spatial autocorrelation was a problem for this data set, I conducted a Moran's I test using the 'ape' package, version 2.7-1, in R (Paradis, Claude & Strimmer 2004). This was done for each transect, within each management unit, and was done for the change in indicator species cover, change in shrub cover, and change in species richness of all growth forms. These together make up all the response variables in the multiple regressions that follow.

To investigate if there had been an increase in nitrophilic species in these plots over time, it was first necessary to define what the nitrophilic species in this system were. I ran an indicator species analysis using PC-ORD, which is a test of a non-random distribution of species with respect to a specified environmental variable (Dufrêne & Legendre 1997). The indicator species analysis was run on the subset of plots from which soil data was collected in the summer of 2012, using the vegetation data that was collected the same day as the soil samples. I ran the analysis using the cover class data, using a Monte Carlo test with 4,999 permutations to test for significance. Because this analysis requires a categorical predictor variable, I used Jenks natural breaks to separate the continuous nitrogen values into categorical predictor variables: high, medium, or low levels of total nitrogen (Geiser & Neitlich 2007). For the soil analyses, I tested soils for both ammonium and nitrates, but because nitrates were so limited in these soils (only one quarter of the plots had nitrate values above zero), I summed the data and used total Nitrogen. Hence all indicator species analyses were run for total nitrogen. Once a potential nitrophilic species was identified, I tested for a change in the cover of that species using a paired t-test, with percent cover of the nitrophilic indicator species as the response variable. The paired

t-test was performed using the complete data set from the time of plot establishment versus the most recent survey, and not only for the plots from which there was soil nutrient information.

In addition, I tested which environmental variables were correlated with an increase in this indicator species. I used the environmental PCA axes, developed in Chapter 1 as orthogonal predictor variables that represented both management and edaphic factors at the sites. Variables included in the ordination of environmental variables by site were total nitrogen, years since last burn, number of fires, mowed or not mowed, Organic matter, and the Mehlich extractable ions of P, Ca, Mg, K, Na, H, B, Fe, Mn, Cu, Zn, Al, S, as outlined in Chapter one. I ran a multiple regression analysis for each site, with change in nitrophilic indicator species since plot establishment as the response variable and PCA axes as the predictor variables. I used AICc model selection to identify the most informative models (Hurvich & Tsai 1989).

To test if there had been a change in shrub coverage since plot establishment, I summed the cover classes for all shrub and tree species together within each plot, within each survey interval. I did not include subshrubs into this analysis because the stature of subshrubs is smaller than that of shrubs. Instead my analysis focused on tall shrub encroachment, which would be more likely to shade out native forb species. Additionally, many of the subshrubs in this system are both native and desirable. Species were classified as either shrub or subshrub using the USDA plants database (USDA, NRCS, 2013). With the exception of *Vaccinium angustifolium*¸ all species that were classified as shrub/subshrub in the database were included in the subshrub category. *V. angustifolium* was classified as a shrub due to its larger stature than the other subshrubs. Additionally, species in this genus at this site may be difficult to tell apart and all other species in this genus at this site are considered shrubs in the database.

I used the sum of the shrub cover classes as a response variable in a paired t-test to determine if there had been a change in shrub cover since the time of plot establishment. I predicted that there had been an increase in shrub cover since plot establishment. To determine how management correlated with the change in shrub cover, I used a multiple regression analysis with change in percent shrub cover as the response variable and the PCA axes developed in chapter 1 as the predictor variables, using AICc model selection to select the most informative models.

I assessed the change in species diversity within different growth forms at the sites using the change in species richness of subshrubs, shrubs, forbs, and graminoids. I chose to look at change in species richness within different growth forms, instead of overall species richness, because I felt that looking at changes within different functional groups would provide a better picture of species composition change. Species were separated into different growth forms using the USDA plants database, as described above (USDA, NRCS. 2013). Vines were grouped with subshrubs because there were not enough vines to analyze alone and they are small in stature and often woody, making them most similar to subshrubs in these groupings. In order to assess change in species richness within these groupings, I used paired t-test analyses. I was also interested in how changes in various growth forms were correlated with change in shrub cover so I ran a regression analyses between change in shrub cover and change in subshrub richness, forb richness, and graminoid richness. Finally, in order to assess how change in richness of specific groups were correlated to management and edaphic variables, I used a multiple regression analysis, with change in species richness in a specified growth form as the response variables and the PCA axes developed in chapter 1, as well as their interactions, as predictor variables.

Results

The Moran's I test for spatial autocorrelation was not significant for any of the tests on change in shrub cover or change in the nitrophilic indicator species cover, indicating no spatial autocorrelation was detected for these variables at this spatial scale (plots 10m apart). I found spatial autocorrelation for change in subshrub richness, shrub richness, forb richness, and graminoid richness. I will discuss these findings below.

Nitrophilic indicator species

Nantucket maintenance site

Using Jenks Natural breaks, I separated total nitrogen data (μg/grams dry soil (gds)) into three groups. The low nitrogen group had 14 plots, the medium nitrogen group had 21 plots, and the high nitrogen group had 5 plots, for a total of 40 plots used in this analysis at this site. The indicator species analysis revealed three species that were correlated with the high nitrogen

grouping, *Carex pensylvanica*, *Euthamia tenuifolia*, and *Rosa carolina* (Table 37). I used *C. pensylvanica* in my analyses because it was the strongest indicator and it occurred at all three sites. I verified the relationship between increasing total nitrogen and increasing *C. pensylvanica* using a regression analysis, and total nitrogen was found to be significantly, positively related to *C. pensylvanica* cover ($p<0.0001$) (Figure 11).

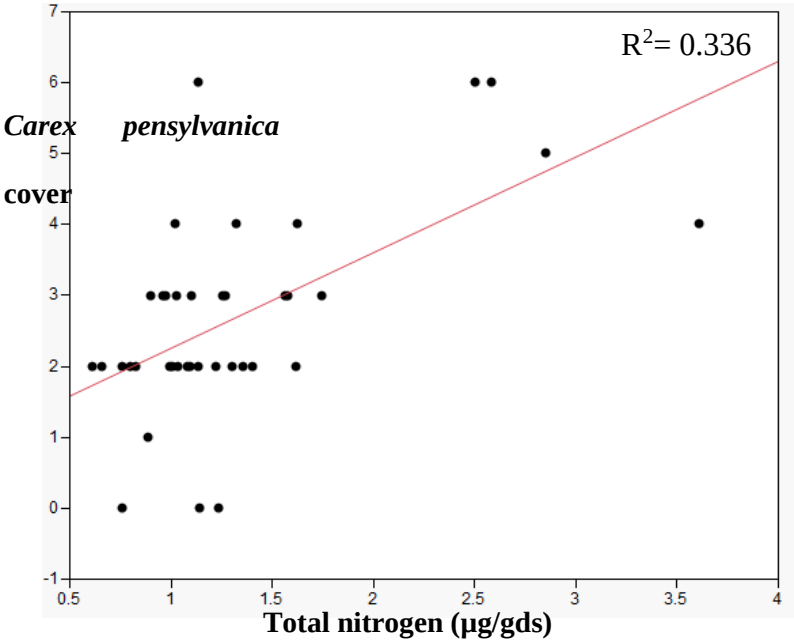

Figure 61: Regression analysis between *C. pensylvanica* cover in 2012 and total nitrogen in the same plot.

Table 37: Indicator species analysis for high, medium, or low total soil nitrogen for the Nantucket maintenance site.

Species	Max group	Observed Indicator Value	Indicator Value from randomized groups		
			Mean	Standard Deviation	*p*
Agrostis stolonifera	high	20	7.4	4.79	0.121
Arctostaphylos uva-ursi	medium	15	14.7	7.75	0.330
Aster dumosus	low	4.8	7.4	4.78	1
Aster paternus	low	20.9	20.3	8.19	0.324
Carex pensylvanica	**high**	**50.5**	**37.1**	**3.44**	**<0.001***
Comptonia peregrina	medium	12.9	14.8	7.8	0.421
Danthonia spicata	high	8.7	16.3	8.22	0.897
Deschampsia flexuosa	high	14.7	13	7.15	0.273
Dichanthelium acuminatum	medium	11.7	11.4	6.09	0.435
Dichanthium depauperatum	low	4.5	11.6	6.37	1
Epigaea repens	medium	14.3	9.6	5.77	0.231
Euthamia tenuifolia	**high**	**45.5**	**18.6**	**8.53**	**0.015 ***
Festuca spp.	high	20	7.6	4.94	0.130
Gaylussacia baccata	low	43.2	33.4	5.72	0.082
Helianthemum spp.	low	4.8	7.6	4.95	1
Hieracium sp.	medium	3.1	9.7	5.83	1
Houstonia caerulea	high	14.7	9.8	5.82	0.232
Hudsonia ericoides	low	17.2	14.2	7.76	0.242
Ionactus linarifolium	medium	4.3	11.3	6.28	1
Juncus greenei	high	16.2	9.8	5.54	0.145
Lechea maritima	low	4.8	7.6	4.95	1
Lilium philadelphicum	low	4.8	7.6	4.9	1
Morella pensylvanica	medium	10.7	11.4	6.1	0.694
Panicum virgatum	medium	7.1	7.6	5.02	0.476
Parthenuccisus virginia	low	4.8	7.6	4.86	1
Pityopsis falcata	low	9.5	9.8	5.94	0.626
Potentilla simplex	medium	3.6	9.8	5.59	1
Quercus ilicifolia	low	27.8	22.4	8.41	0.216
Quercus prinoides	high	12.5	11.4	6.32	0.435
Ranunculus sp.	medium	7.1	7.5	4.82	0.467
Ribes Hirtellum	low	4.8	7.6	4.86	1
Rosa carolina	**high**	**38**	**20.6**	**8.73**	**0.047***
Rubus hispidus	medium	24.4	17.1	8.26	0.144
Rumex acetosella	high	20	7.5	4.79	0.122
Schizachyrium scoparium	high	21.3	30.4	7.04	0.974
Solidago nemoralis	low	4.8	7.5	4.79	1
Vaccinium angustifolim	low	31.1	24.6	8.05	0.147

There was significantly higher cover of *Carex pensylvanica* in this site at the most recent survey (2010/2011) versus the time of plot establishment (1989/1990) (Table 38). Based on AICc model selection, PCA axis 2 (Table 5, Chapter 1) was significantly, positively related to change in *C. pensylvanica* cover (Table 39). Therefore, where there has been less fire (correlated with less P, Ca, Mg, Fe, Mn, and more Cu, Al, and S), there has been the largest increase in *C. pensylvanica*.

Table 38: Paired t t-test between *C. pensylvanica* cover at the time of plot establishment (1989/1990) versus the most recent survey (2010/2011).

C. pensylvanica cover 2010/2011	2.431	t-ratio	2.797
C. pensylvanica cover 1989	2.108	DF	166
Mean difference	0.323	Prob > |t|	**0.0058***
Std. Error	0.116	Prob>t	**0.0029***
Upper 95%	0.552	Prob<t	0.9971
Lower 95%	0.095		
Correlation	0.362		

Table 39: Regression relationship between change in *C.pensylvanica* cover and PCA axis 2 at the Nantucket maintenance site.

Summary of Fit

Rsquare	0.137
Rsquare Adj	0.114
Observations	39

ANOVA Table

Source	**DF**	**SS**	**MS**	**F Ratio**
Model	1	11.246	11.246	5.890
Error	37	70.651	1.910	**Prob>F**
Total	38	81.897		**0.0202***

Parameter Estimates

Term	**Estimate**	**Std Error**	**T Ratio**	**Prob> |t|**
Intercept	0.718	0.221	3.24	**0.0025***
PCA 2	0.273	0.112	2.43	**0.0202***

Mainland maintenance site

Prior to performing Jenks Natural Breaks at the Mainland maintenance site, I omitted one plot from the analysis. This plot was an extreme value of total nitrogen, and when it was included in the analysis, it constituted its own "nitrogen category". This left 30 plots for this

analysis, 8 were classified as low nitrogen, 17 as medium nitrogen, and 5 as high nitrogen. I then performed an indicator species analysis in PC-ORD, which did not identify any significant indicator species (Table 40).

Table 40: Indicator species analysis for total nitrogen at the Mainland maintenance site.

Species	Max group	Observed Indicator Value	Indicator Value from randomized groups		
			Mean	Standard Deviation	*p*
Ammophilia breviligulata	low	12.5	10	5.33	0.432
Arctostaphylos uva-ursi	High	9.1	18.5	9.03	0.925
Carex pensylvanica	High	37.6	37.3	2.3	0.405
Deschampsia flexuosa	High	26.2	28.5	8.85	0.523
Dichanthelium spp.	Medium	9.8	15.8	8.54	0.848
Helianthemum spp.	High	13.9	12.8	5.67	0.322
Hieracium sp.	low	8.5	13.2	6.01	1
Ionactis linarifolius	low	28.5	19.1	9.22	0.122
Lechea Maritima	Medium	27.6	27.5	9.04	0.403
Maianthemum canadense	low	12.5	10	5.27	0.437
Morella pensylvanica	Medium	5.9	10	5.31	1
Polygonella articulata	Medium	17.6	14.1	7.7	0.365
Prunus maritima	High	16.2	14.6	7.64	0.390
Rumex acetosella	low	8.5	13.1	6	1
Schizachachrium scoparium	Medium	42	37.1	3.26	0.068
Vaccinium corymbosum	Medium	5.9	10.1	5.27	1

While there was no clear indicator species for this site, I used *Carex pensylvanica* because it had been shown to be associated with increased nitrogen at the Nantucket maintenance site. Additionally, the relationship between increasing *C. pensylvanica* and increasing total nitrogen appeared to be similar to at the other sites, but the nitrogen levels had lower variation at this site. To demonstrate this, I performed a regression between total nitrogen and cover of *C. pensylvanica* using data from all sites, and the data from this site was in line with the other sites (blue dotes in Figure 12). The regression showed a significant positive relationship between increasing total nitrogen and increasing *C. pensylvanica* at all sites (Table 41).

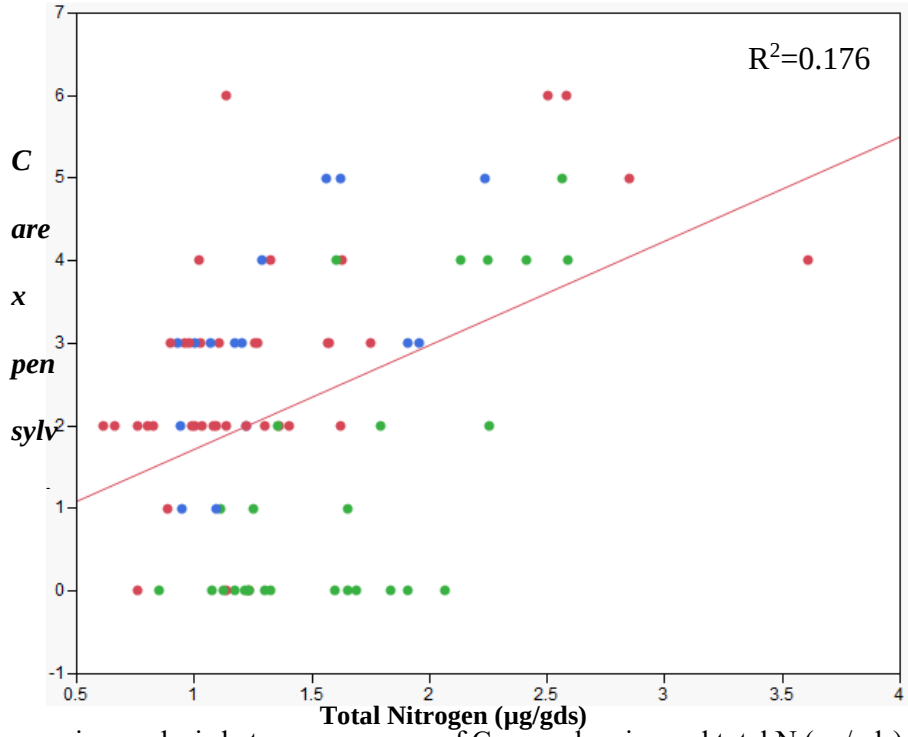

Figure 12: Regression analysis between coverage of C. pensylvanica and total N (µg/gds) for all sites. The green dots are the Nantucket maintenance site, the red dots are the Nantucket Restoration site, and the blue dots are the mainland site.

Table 41: Regression analysis between *C. pensylvanica* cover and total nitrogen at all sites combined.

Summary of Fit

Rsquare	0.176
Rsquare Adj	0.166
Observations	83

ANOVA Table

Source	**DF**	**SS**	**MS**	**F Ratio**
Model	1	40.097	40.097	17.3134
Error	81	187.590	2.316	**Prob>F**
Total	82	227.687		**<0.0001***

Parameter Estimates

Term	**Estimate**	**Std Error**	**T Ratio**	**Prob> ltl**
Intercept	0.460	0.462	0.99	0.3228
Total N	1.261	0.303	4.16	**<0.001**

On average, cover of *Carex pensylvanica* was higher in 2012 than in 1989 at this site (Table 42). Multiple regression analysis of *C.pensylvanica* cover on ordinated environmental

variables identified a significant interaction between PCA 1 and PCA 2 (Table 43). I identified that at low levels of PCA 1, the relationship between change in *C.pensylvanica* and PCA 2 is positive, while at high levels of PCA 1, the relationship with PCA 2 is negative. (Kendall correlations for PCA values at this site can be found in Table 17, Chapter 1). Biologically this indicates that in acidic soils with low total N, high P, Ca, Mg, K, Na, B, Fe, Mn, Cu, Zn, Al and S; *C. pensylvanica* increased more in areas with more fires, and more years since fire (which also tended to be more basic, and low in N and P). In more basic soils, with higher nitrogen, and lower micronutrients; this relationship is reversed and *C. pensylvanica* increased less where there wer more fires and more years since fire.

Table 42: Paired t-test between C.pensylvanica cover in 1989, when the mainland plots were established, and 2012 when they were last surveyed. Cover was higher in the most recent survey.

C. pensylvanica cover 2012	2.667	t-ratio	3.390
C. pensylvanica cover 1989	2.123	DF	56
Mean difference	0.544	Prob > |t|	**0.0013***
Std. Error	0.160	Prob>t	**0.0006***
Upper 95%	0.865	Prob<t	0.9994
Lower 95%	0.223		
Correlation	0.304		

Table 43: Multiple regression between change in *C.pensylvanica* and environmental PCA axes.

Summary of Fit

Rsquare	0.380
Rsquare Adj	0.282
Observations	23

ANOVA Table

Source	**DF**	**SS**	**MS**	**F Ratio**
Model	3	14.226	4.742	3.8749
Error	19	23.252	1.224	**Prob>F**
Total	22	37.478		**<0.0256***

Parameter Estimates

Term	**Estimate**	**Std Error**	**T Ratio**	**Prob> |t|**
Intercept	0.609	0.231	2.64	0.0162*
PCA 1	0.179	0.094	1.90	0.0727
PCA 2	0.142	0.143	1.00	0.3310
PCA 1* PCA2	-0.199	0.070	-2.85	**0.0104***

Nantucket Restoration site

Using Jenks Natural Breaks in R, the low nitrogen group consisted of 8 plots, the medium nitrogen group consisted of 12 plots, and the high nitrogen group consisted of 8 plots. The indicator species analysis, run in PC-ORD identified no significant indicator species, but there was a trend toward *Rubus hispidus* being associated with higher nitrogen (Table 44). However, during past surveys, identification of *R. hispidus* may have been confused by different surveyors (although both have appeared in all years), therefore I chose not to use *R. hispidus* as an indicator species. Rather I chose to continue with *C. pensylvanica* as it grouped with high nitrogen levels in the indicator species analysis, although not significantly, and a regression analysis shows a significant associated between higher nitrogen levels and more *C. pensylvanica* cover at this site ($p<0.0001$) (Figure 13).

Table 44: Indicator species analysis for nitrophilic species at the Nantucket Restoration site.

Species	Max group	Observed Indicator Value	Indicator Value from randomized groups		
			Mean	Standard Deviation	*p*
Carex Pensylvanica	High	35.6	26.7	8.3	0.139
Corylus cornuta	Low	15	15.5	7.6	0.405
Gaylussacia baccata	Low	40.5	35.5	4.4	0.166
Morella pensylvanica	High	17.3	13.3	7.38	0.402
Pteridium aquilinum	High	6.2	11.6	6.57	1
Pyrola rotundifolia	High	9.4	11.7	6.59	0.576
Quercus ilicifolia	Low	38.1	35.3	4.24	0.301
Quercus prinoides	High	28.9	21.6	8.35	0.176
Rosa carolina	High	12.5	10.8	2.06	0.582
Rubus hispidus	High	33.7	15.8	8.18	0.062
Smilax glauca	Medium	12.5	10.7	2.07	0.568
Vaccinium angustifolium	Medium	18.7	18.2	8.07	0.542
Vaccinium vaccilans	Low	23.7	16.9	7.62	0.254

There was a significant increase in *Carex pensylvanica* from 1999, when the plots were established to 2009, when the last complete survey of the plots was conducted (Table 45). Change in *C. pensylvanica* was significantly related to PCA axis 3, PCA axis 4, and the

interaction between the two (Table 46). The interaction was such that at low levels of PCA 3, the relationship between PCA 4 and the response variable was slightly positive, while at high levels of PCA3, the relationship was highly negative. Thus, where there was mowing (associated with more basic soils, and lower levels of Fe and Zn), and fire (associated with basic soils, increased Al, S, Cu, and Zn, and decreased Fe); there has been a slight decrease in *C. pensylvanica* at this site. On the other hand, where there has been mowing (associated with basic soils, and lower levels of Fe and Zn), with less fire (associated with acidic soils, more Fe, and less Al, S, Cu, and Zn), there has been an increase in *C. pensylvanica.* (Kendall correlations for PCA values at this site can be found in Table 25, Chapter 1).

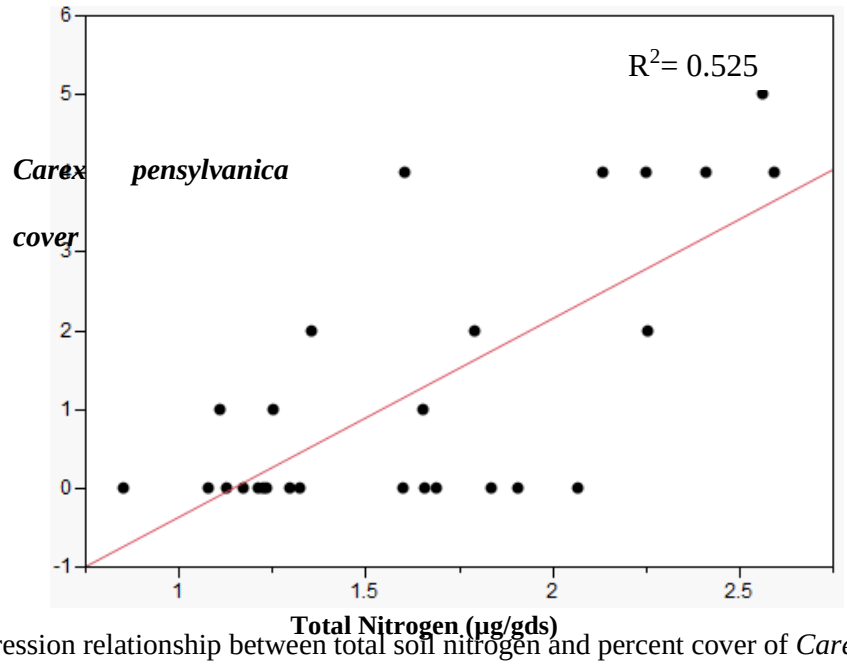

Figure \3: Regression relationship between total soil nitrogen and percent cover of *Carex pensylvanica*

Table 45: A paired t-test on the percent cover of *C. pensylvanica* between 1999 and 2009 at the Nantucket Restoration site shows and increase in the species.

C. pensylvanica cover 2009	1.825	t-ratio	7.493
C. pensylvanica cover 1989	0.842	DF	119
Mean difference	0.983	Prob > |t|	**<0.0001***
Std. Error	0.131	Prob>t	**<0.0001***

Upper 95%	1.243	Prob<t	1.000
Lower 95%	0.723		
Correlation	0.668		

Table 46: Regression relationship between change in *C. pensylvanica* cover and environmental PCA axes at Nantucket Restoration site.

Summary of Fit

Rsquare	0.498
Rsquare Adj	0.426
Observations	25

ANOVA Table

Source	**DF**	**SS**	**MS**	**F Ratio**
Model	3	18.192	6.064	6.933
Error	21	18.368	0.875	**Prob>F**
Total	24	36.560		**0.0020***

Parameter Estimates

Term	**Estimate**	**Std Error**	**T Ratio**	**Prob> ⏐t⏐**
Intercept	0.760	0.187	4.06	**0.0006***
PCA 3	0.306	0.108	2.83	**0.0099***
PCA 4	-0.348	0.136	-2.56	**0.0183***
PCA 3* PCA 4	-0.214	0.074	-2.88	**0.0090***

Change in shrub cover and correlation with management

Nantucket maintenance site

There was an increase in shrub coverage at the Nantucket maintenance site between the final survey (2010/2011) and plot creation (1989/1990) (Table 47). AICc model selection identified a negative trend between the change in shrub cover and PCA axis 2, although with a relatively low R-square value (Table 48), indicating that shrub cover increased where there were more fires. Where there were more fires the soils were also lower in P, Ca, Mg, Fe, and richer in Al and S.

Table 47: Paired t-test between shrub cover at plot establishment and shrub cover at the most recent survey.

Shrub cover 2012	5.623	t-ratio	5.169
Shrub cover 1989	4.341	DF	166
Mean difference	1.281	Prob > ⏐t⏐	**<0.0001***
Std. Error	0.248	Prob>t	**<0.0001***
Upper 95%	1.771	Prob<t	1.000
Lower 95%	0.792		

Correlation	0.653		

Table 48: Regression between PCA axis 2 and change in shrub cover at the Nantucket maintenance site.

Summary of Fit

Rsquare	0.084
Rsquare Adj	0.059
Observations	39

ANOVA Table

Source	**DF**	**SS**	**MS**	**F Ratio**
Model	1	33.483	33.483	3.3731
Error	37	367.286	9.927	**Prob>F**
Total	38	400.769		0.0743

Parameter Estimates

Term	**Estimate**	**Std Error**	**T Ratio**	**Prob> ltl**
Intercept	0.923	0.505	1.83	0.0754
PCA2	-0.471	0.256	-1.84	0.0743

Mainland maintenance site

A paired t-test showed no significant difference in shrub cover between 1989 and 2012 (Table 49) at the Mainland maintenance site. In general the mainland site had very few shrubs, with only 9 out of 57 plots having any shrubs either when the plots were established in 1989 or when they were surveyed in the summer of 2012. AICc model selection did not identify any PCA axes that were correlated with change in shrub cover at this site.

Table 49: Paired t-test between the sum of shrub cover in 1989 and shrub cover in 2012.

Shrub cover 2012	0.316	t-ratio	-0.189
Shrub cover 1989	0.351	DF	56
Mean difference	-0.035	Prob > |t|	0.851
Std. Error	0.186	Prob>t	0.575
Upper 95%	0.337	Prob<t	0.425
Lower 95%	-0.407		
Correlation	0.188		

Nantucket Restoration site

At the Nantucket Restoration site, there was an increase in shrub cover between plot establishment in 1999 and the most recent survey in 2009 (Table 50). AICc model selection identified PCA axis 1, PCA axis 4, and the interaction between PCA axis 2 and PCA axis 4 as significantly correlated with change in shrub cover at the Nantucket Restoration site (Table 51). I identified the interaction as such that at low levels of PCA 2, PCA 4 had almost no slope but at high levels of PCA 2, PCA4 had a positive relationship with the response variable (change in shrubs). For the negative relationship with PCA axis 1, this means that there has been less of an increase in shrubs in areas with low nitrogen, less mowing, and are less rich in micronutrients. For the interaction between PCA 2 and PCA 4, in places that had experienced more fire (which is associated with more P, Ca, Mg, Fe, and Mn, and less Cu, Al, and S); mowing (which is associated with acidic soils, and high Fe, and Zn) was not correlated with a change in shrubs. On the other hand, where there was less fire (associated with less P, Ca, Mg, Fr, Mn, and more Cu, Al, and S); mowing (which is associated with acidic soils, and higher Fe and Zn) was correlated with a decrease in shrub cover. As stated earlier, there was no area of this site that was mowed but not burned.

Table 50: Paired t-test between total shrub cover at plot establishment (1989/1990) and the most recent survey in the Nantucket Restoration site (2010/2011).

Shrub cover 2012	6.758	t-ratio	3.543
Shrub cover 1989	5.617	DF	119
Mean difference	1.142	Prob > |t|	**0.0006***
Std. Error	0.322	Prob>t	**0.0003***
Upper 95%	1.780	Prob<t	0.9997
Lower 95%	0.504		
Correlation	0.456		

Table 51: Multiple regression between change in shrub cover and PCA axes selected by AICc model selection.

Summary of Fit

Rsquare	0.597
Rsquare Adj	0.516
Observations	25

ANOVA Table

Source	**DF**	**SS**	**MS**	**F Ratio**
Model	4	141.484	35.371	7.403
Error	20	95.556	4.778	**Prob>F**
Total	24	237.040		**0.0008***

Parameter Estimates

Term	**Estimate**	**Std Error**	**T Ratio**	**Prob> ltl**
Intercept	1.280	0.437	2.93	**0.0083***
PCA axis 1	-0.509	0.195	-2.62	**0.0166***
PCA axis 2	0.272	0.231	1.18	0.2526
PCA axis 4	1.407	0.319	4.42	**0.0003***
PCA axis 2*4	0.391	0.174	2.24	**0.0363***

Change in species richness over time

Nantucket maintenance site

Change in subshrub richness

Change in subshrubs showed significant autocorrelation in unit A of the Nantucket maintenance site (Moran's I p-value=0.018). This was rectified by removing every other plot, so that no two plots used in the analyses for change in subshrubs were less than 20m apart (Moran's I p-value = 0.801).

A paired t-test, with every other plot removed, showed no difference in subshrub richness between plot establishment and the most recent survey (p= 0.653, n=89). This result was not different if all plots were included in the analysis. There was no relationship between change in subshrub richness and change in shrub cover (p=0.243, n= 89). AICc model selection did not

identify any significant relationship between change in subshrub richness and any of the PCA environmental variables.

Change in shrub richness

A Moran's I showed significant spatial autocorrelation in change in shrub cover in unit B of the Nantucket maintenance site (p=0.026), which was not significantly improved by removing every other plot (p=0.058). I then removed two plots between every plot that was used for the analysis, so that no plot was closer than 30m to any other plot used for the analysis. This reduced the special autocorrelation significantly (p=0.603). There was an increase in shrub richness from 1989/1990 to 2010/2011. This change was significant whether all plots were included, or one third of the plots were deleted to correct for autocorrelation. I have presented the analysis with one third of the plots deleted, in order to be more conservative (Table 52). AICc model selection did not identify any significant relationship between change in shrub richness and any of the PCA environmental variables, this was true using either all the plots or one third of the plots.

Table 52: Paired t-test between shrub richness at plot establishment and the most recent survey

Shrub richness 2010/2011	1.527	t-ratio	2.129
Shrub richness 1989/1990	1.273	DF	54
Mean difference	0.255	Prob > |t|	**0.038***
Std. Error	0.119	Prob>t	**0.019***
Upper 95%	0.494	Prob<t	0.981
Lower 95%	0.015		
Correlation	0.552		

Change in forb richness

A paired t-test, including all plots, showed no difference between forb richness at plot establishment and the most recent survey (p=0.301, n=167). There was no significant relationship between change in forb richness and change in shrub cover, although there was a trend for a decrease in forb richness with more of an increase in shrub cover, with a low R-square value (p=0.061, R^2=0.021, n=167).

AICc model selection identified a significant relationship between change in forb richness and the interaction between PCA1 and PCA2 (Table 53). This interaction was such that at low levels of PCA1, PCA2 had a positive correlation with forb richness. While at high levels

of PCA1, PCA2 had a negative correlation with shrub richness. Thus, where there was more organic matter, less P, more Mg, more K, more Na, more B, and the soils werer more basic; fewer fires (associated with lower P, Mg, Fe, Mn, and higher Cu, Al, and S) were correlated with increased forb richness. Correlations between PCA axes and environmental variables at this site can be found in Chapter 1, table 5.

Table 53: Regression analysis between change in forb richness and PCA environmental axes 1 and 2, as well as their interaction.

Summary of Fit

Rsquare	0.279
Rsquare Adj	0.217
Observations	39

ANOVA Table

Source	**DF**	**SS**	**MS**	**F Ratio**
Model	3	12.286	4.095	4.520
Error	35	31.714	0.906	**Prob>F**
Total	38	44.000		**0.009***

Parameter Estimates

Term	**Estimate**	**Std Error**	**T Ratio**	**Prob> ⏐t⏐**
Intercept	$-3.718e^{-7}$	0.152	-0.00	1.000
PCA axis 1	0.097	0.078	1.25	0.220
PCA axis 2	-0.081	0.079	-1.01	0.318
PCA axis 1*2	-0.139	0.044	-3.20	**0.003***

Change in graminoid richness

A paired t-test, including all plots, showed a decrease in graminoid richness at the Nantucket maintenance site from the time of plot establishment to the most recent survey (Table 54). Change in graminoids was significantly, negatively related to change in shrub cover (Table 55). There was no significant correlation between change in graminoid richness and any of the PCA environmental axes, tested using AICc model selection.

Table 54: Paired t-test of graminoid richness in 1989/1990 and graminoid richness in 2010/2011.

Graminoid richness 2010/2011	2.311	t-ratio	-4.213
Graminoid richness 1989/1990	2.707	DF	166
Mean difference	-0.395	Prob > |t|	**<0.0001***
Std. Error	0.094	Prob>t	1.000
Upper 95%	-0.21	Prob<t	**<0.0001***
Lower 95%	-0.580		
Correlation	0.641		

Table 55: Regression analysis between change in graminoid richness and change in shrub cover from 1989/1990 to 2010/2011

Summary of Fit

Rsquare	0.145
Rsquare Adj	0.140
Observations	167

ANOVA Table

Source	**DF**	**SS**	**MS**	**F Ratio**
Model	1	35.353	35.353	27.969
Error	165	208.563	1.264	**Prob>F**
Total	166	243.916		**<0.0001***

Parameter Estimates

Term	**Estimate**	**Std Error**	**T Ratio**	**Prob> |t|**
Intercept	-0.211	0.094	-2.25	**0.026***
Change in shrub cover	-0.144	0.027	-5.29	**<0.0001***

Mainland maintenance site:

Change in subshrub richness

Using a paired t-test, there was no change in subshrub richness in this site from 1989 to 2012 (p=0.290, n=57). Using a regression analysis, there was no relationship identified between change in subshrub richness and change in shrub cover from 1989 to 2012 (p=0.870, n=57), nor were any correlations between change in subshrub richness and the PCA environmental axes identified, using AICc model selection.

Change in shrub richness

Using a paired t-test, shrub richness decreased at the Mainland maintenance site from 1989 to 2012 (Table 55). Correlations between change in shrub richness and any PCA environmental axes were not identified using AICc model selection.

Table 56: Paired t-test of shrub richness in 1989 and shrub richness in 2012

Shrub richness 2012	0.211	t-ratio	-8.039
Shrub richness 1989	1.386	DF	56
Mean difference	-1.175	Prob > |t|	**<0.0001***
Std. Error	0.146	Prob>t	1.000
Upper 95%	-0.883	Prob<t	**<0.0001***
Lower 95%	-1.468		
Correlation	0.211		

Change in forb richness

Forb richness at the Mainland maintenance site was greater in the 2012 survey than it was in the 1989 survey (Table 57). There was no correlation between change in forb richness and change in shrub cover (p=0.198, n=57), although there were very few shrubs at this site. Change in forb richness was significantly, positively related to PCA axis 2 (Table 58). Therefore areas that had less total nitrogen, more years since fire, more total fires, less P, less H, and more Al have experienced a larger increase in forb richness. (Correlations between PCA axes and management and environmental variables can be found in chapter 1, table 17.)

Table 57: Paired t-test of difference between forb richness in 1989 and forb richness in 201.

Forb richness 2012	1.579	t-ratio	3.480
Forb richness 1989	1.070	DF	56
Mean difference	0.509	Prob > |t|	**0.0010***
Std. Error	0.146	Prob>t	**0.0005***
Upper 95%	0.802	Prob<t	0.9995
Lower 95%	0.216		
Correlation	0.383		

Table 58: Regression analysis between change in forb richness and PCA axis 2.

Summary of Fit	
Rsquare	0.241
Rsquare Adj	0.205
Observations	23

ANOVA Table

Source	**DF**	**SS**	**MS**	**F Ratio**
Model	1	7.443	7.443	6.672
Error	21	23.426	1.116	**Prob>F**
Total	22	30.870		**0.0173***

Parameter Estimates

Term	**Estimate**	**Std Error**	**T Ratio**	**Prob> ⏐t⏐**
Intercept	0.696	0.220	3.13	**0.005***
PCA 2	0.350	0.136	2.58	**0.017***

Change in graminoid richness

Graminoid richness was lower at the Mainland maintenance site in 2012 than it was in 1989 (Table 59). Change in graminoid richness was not significantly related to shrub cover (p=0.929, n=57), although there were not many shrubs at this site. There was a positive trend between change in graminoid richness and PCA axis 2 and a negative trend with PCA axis 3 (Table 60). Therefore areas that had less total nitrogen, more years since fire, had experienced a larger number of fires, less P, less H, and more Al, tended to have an increase in graminoid richness at this site. While areas with more organic matter, less K, less Fe, and less Al, were more likely to decline in graminoid richness. (Correlations between PCA axes and management and environmental variables can be found in chapter 1, table 17.)

Table 59: Paired t-test of graminoid richness in 1989 vs. graminoid richness in 2012

Graminoid richness 2012	2.895	t-ratio	-4.576
Graminoid richness 1989	3.456	DF	56
Mean difference	-0.561	Prob > |t|	**<0.0001***
Std. Error	0.123	Prob>t	1.000
Upper 95%	-0.316	Prob<t	**<0.0001***
Lower 95%	-0.807		
Correlation	0.244		

Table 60: Multiple regression between change in graminoid richness and PCA axis 2 and PCA axis 3.

Summary of Fit

Rsquare	0.244
Rsquare Adj	0.168
Observations	23

ANOVA Table

Source	**DF**	**SS**	**MS**	**F Ratio**
Model	2	4.328	2.164	3.2269
Error	20	13.411	0.671	**Prob>F**

Total	22	17.739		0.0610

Parameter Estimates

Term	**Estimate**	**Std Error**	**T Ratio**	**Prob> ltl**
Intercept	-0.478	0.171	-2.80	**0.011***
PCA axis 2	0.189	0.105	1.80	0.087
PCA axis 3	-0.217	0.121	-1.79	0.088

Nantucket restoration site:

Change in subshrub richness

At the Nantucket restoration site, subshrub richness was higher in 2009 than it was in 1999 (Table 61). Using a regression analysis, change in subshrub richness was not related to change in shrub cover (p=0.904, n=110). AICc model selection identified a negative trend between change in subshrub richness and PCA axis 1 (Table 62). PCA Axis 1 is negatively correlated with total nitrogen, mowing, organic matter, P, Ca, Mg, Na, Mn, Cu, and Zn (Chapter 1, Table 25).

Table 61: Paired t-test between graminoid richness at plot establishment and graminoid richness at the most recent survey.

Graminoid richness 2009	0.536	t-ratio	2.156
Graminoid richness 1999	0.472	DF	109
Mean difference	0.109	Prob > |t|	**0.033***
Std. Error	0.051	Prob>t	**0.017***
Upper 95%	0.209	Prob<t	0.9834
Lower 95%	0.001		
Correlation	0.777		

Table 62: Regression analysis between change in subshrub richness and PCA axis 1.

Summary of Fit

Rsquare	0.149
Rsquare Adj	0.112
Observations	25

ANOVA Table

Source	**DF**	**SS**	**MS**	**F Ratio**
Model	1	1.194	1.193	4.032
Error	23	6.807	0.296	**Prob>F**
Total	24	8.000		0.057

Parameter Estimates

Term	**Estimate**	**Std Error**	**T Ratio**	**Prob> ⏐t⏐**
Intercept	$-3.47e^{-18}$	0.109	-0.00	1.000
PCA axis 1	-0.095	0.047	-2.01	0.057

Change in shrub richness

Significant autocorrelation was detected in unit G for the change in shrub richness (p=0.050). This was corrected for by removing every other plot from the analysis (p=0.995). The results presented here are using every other plot. There was a trend for average shrub richness to be higher in the 2009 survey than in 1999 (Table 63). If all plots are included, average shrub richness is significantly higher in 2009 than in 1999 (p=0.0004). Using AICc model selection, I identified no significant correlations between change in shrub richness and change in any of the PCA environmental axes.

Table 63: Paired t-test between shrub richness at the most recent survey and shrub richness at the time of plot establishment.

Shrub richness 2009	3.164	t-ratio	1.861
Grub richness 1999	2.927	DF	54
Mean difference	0.236	Prob > |t|	0.068
Std. Error	0.127	Prob>t	**0.0341***
Upper 95%	0.491	Prob<t	0.9998
Lower 95%	-0.018		
Correlation	0.710		

Change in forb richness

Autocorrelation for change in forb richness was found in unit I (p=<0.0001). This autocorrelation could not be corrected by removing every other plot, so I removed two plots between every plot used and autocorrelation was not detected using a Moran's I (p=0.947). When running a paired t-test on every three plots, average forb richness was not different in the most recent survey from forb richness at the initial survey (p=0.286, n=33). This did not change if all plots were included in the analysis (p=0.207, n=110). Using one in three plots in a regression analysis, change in forb richness was not significantly related to change in shrub cover (p=0.829, n=33). This did not change if all plots were included in the analysis (p=0.413, n=110). No significant correlations between change in forb richness and the PCA axes representing soil and management variables were identified using AICc model selection.

Change in gramidnoid richness

Graminoid richness was higher in the most recent survey than at plot establishment (Table 64). Change in graminoid richness was not significantly related to change in shrub cover (p=0.4972, n=110). No significant correlations between change in graminoid richness and PCA axes were identified using AICc model selection.

Table 64: Paired t-test between graminoid richness at plot establishment and graminoid richness at the most recent survey.

Graminoid richness 2009	0.061	t-ratio	.861
Graminoid richness 1999	0.427	DF	54
Mean difference	0.182	Prob > |t|	0.068
Std. Error	0.045	Prob>t	**0.0341***
Upper 95%	0.271	Prob<t	0.9998
Lower 95%	0.092		
Correlation	0.657		

Discussion

Change in Carex pensylvanica

I identified *Carex pensylvanica* as a potential nitrophilic indicator species in this system. This is not the first study to associate this species with high nitrogen levels. For example, in New Jersey Pine barrens, Gray et. al. (2012) determined that graminoid cover, which at their site was almost exclusively *C. pensylvanica,* was positively related to increasing ammonium levels in the soil. Most of the nitrogen in this study was ammonium, with less than one quarter of the plots having nitrate values above zero. Therefore in developing an indicator for high total nitrogen, this was mostly an indicator for high ammonium. Similarly, in a study by Abrams and Dickmann (1983), the authors wished to identify the mechanisms that caused *C. pensylvanica* to increase after disturbance, and found that growth of the species was increased by both fertilization and clear cutting.

I saw an increase in *C. pensylvanica* cover in all three sites from the time of plot establishment to the most recent study. It is possible that this increase is due to increasing nitrogen concentrations in this system. This increasing nitrogen could be caused by multiple factors including succession (Vitousek, Matson & Cleve 1989), increased nitrogen availability following fire (Dudley & Lajtha 1993), or anthropogenic deposition (Galloway *et al.* 2002). No matter the source, increasing nitrogen status in these systems is of conservation concern, as heathlands are nitrogen sensitive systems (Achermann & Bobbink 2003) and changes in soil nitrogen have been implicated in species change (Aerts *et al.* 1990) and the loss of diversity (Bobbink, Hornung & Roelofs 1998) in heathlands in Europe.

When examining the correlation between changing *Carex pensylvanica* cover and management and edaphic factors at these sites, patterns were not very clear. At the Nantucket

maintenance site I saw an increase in *C. pensylvanica* cover in areas with less fire (which were also lower in Ca, Mg, Fe, Mn, and higher in Cu, Al, and S). This is surprising, as others (eg. Abrams and Dickmann, 1983) have associated *C. pensylvanica* with disturbances, such as fire. On the other hand, Matlack et al. (1993) saw a decline in this species in a New Jersey pin barren, even in sites where shrub clipping, removal of litter, and fertilization had been applied. In the study by Matlack and colleagues (1993), disturbed areas also saw an increase in the shrub *Gaylussacia baccata*, as did the burned areas at this site. It is possible that increases in the *G. baccata* overstory suppressed the sedge, *C. pensylvanica*, as solar radiation has been shown to be important in the growth of *C. pensyvlvanica* (Abrams & Dickmann 1983).

At the Mainland maintenance site, a complicated interaction between soil nutrients and fire was observed. In areas with more acidic soils, less nitrogen, and fewer micronutrients; more fires (associated with more years since fire, basic soils, and soils that are poorer in nitrogen and phosphorus) were associated with an increase in *C. pensylvanica*. On the other hand, in basic soils, with more nitrogen and fewer micronutrients, more fires, more years since fire and associated soil conditions were associated with a decrease in the species. This may be because areas that are lower in nitrogen were less likely to have had *C. pensylvanica* to begin with, and thus they would have been more likely to see an increase in the species with a pulse of nitrogen following a fire. On the other hand, areas that were higher in nitrogen may have already had the species present and hence there was less opportunity for an increase in *C. pensylvanica* cover.

In the Nantucket restoration site, *C. pensylvanica* increased less in areas that were both burned (associated with basic soils, increased Al, S, Cu, and Zn, and decreased Fe) and mowed (associated with basic soils, and lower levels of Fe and Zn). On the other hand, where mowing has occurred, and there were fewer fires, there was an increase in *Carex pensylvanica* cover. This may have been due to the opening of the canopy in the unit that was burned and mowed, while the burn only unit experienced more encroachment by shrub species such as *Gaylussacia baccata.* Opening of the canopy is likely important for the growth of *C.pensylvanica*, allowing increased solar radiation (Abrams & Dickmann 1983) as well as potentially increasing the amount of ammonium in the soil (Pietikäinen & Fritze 1995).

It is clear that even though the presence of *Carex pensylvanica* is correlated with higher levels of soil nitrogen, increased soil nitrogen is not necessarily the cause of the observed increase in the species. More experimental studies must be done in order to determine if this species is in fact an adequate indicator for increasing soil nitrogen in this system. This species has been documented to respond to disturbance (Abrams & Dickmann 1983) and it is possible that increases in this species were caused by another factor, such as fire, or the pulse in soil nitrogen that may occur following a fire (Dudley & Lajtha 1993). That being said, this study does provide evidence for potentially increasing soil nitrogen concentrations in these Massachusetts sandplain heathlands. I suggest nitrogen addition studies in order to better understand the effect of increasing soil nitrogen on sandplain heathland vegetation.

Change in Shrub Cover

An increase in shrub cover was seen in both the Nantucket maintenance site and the Nantucket Restoration site. Not enough shrubs were present to assess shrub cover at the Mainland maintenance site. The increase in shrubs at the Nantucket sites is concerning, as preventing shrub encroachment, and maintaining an open structure in these sandplain heathlands, is often stated as a management goal (eg. Dunwiddie and Caljouw 1990). Additionally, shrub encroachment has been implicated in the loss of diversity in Nantucket heathlands (Harper 1995) as well as Australian heathlands (Specht & Specht 1989).

In order to inform management, I aimed to find correlations between areas with less shrub encroachment and management regimes. I found that at the Nantucket maintenance site, an increase in shrubs was positively correlated with areas that had more fires (which were also poorer in P, Ca, Mg, Fe, and richer in Al and S). This is discouraging, as prescribed fire is the main management technique that has been used to prevent shrub encroachment at this site, as well as in other sandplain heathlands (Dunwiddie & Caljouw 1990; Harper 1995). This association may be due to the fact that one of the dominant shrubs, *Gaylussacia baccata*, is a clonal shrub that has been shown in other studies to be stimulated by disturbances such as fire and stem clipping (Matlack, Gibson & Good 1993).

In the restoration site, a smaller increase in shrubs was correlated with mowing (which was associated with areas that were also lower in nitrogen and higher in micronutrients). This suggests the potential utility of mowing as a management technique for preventing shrubs from encroaching in the system. This technique has been promising in other semi-natural grasslands, for example, in Sweden a mowing treatment was successful in preventing shrub encroachment and maintaining species diversity (Hansson & Fogelfors 2000). Mowing was also successful at preventing shrub encroachment in a tallgrass prairie in Iowa (Van Dyke *et al.* 2004). Although the success of managing *Gaylussacia baccata* with mowing has not been documented and may be more difficult, due to the potential of disturbance such as clipping, promoting the species (Matlack, Gibson & Good 1993). Additionally, due to vegetation type and management regime being confounded at the Nantucket Restoration site, it is possible that shrubs had a greater increase with burning because there were more shrubs in the burned areas to begin with.

Change in Species Richness

All three sites showed differing trends in changing species richness, with no consistent pattern in changing species richness for any particular growth form across sites. For example, graminoids decreased in richness in both the Nantucket maintenance and mainland maintenance site, but increased in richness in the Nantucket restoration site. It is not clear why change in graminoids richness differed between the sites, and while it is tempting to believe that restoration may be opening the shrub canopy at the Nantucket restoration site, and hence allowing grass establishment, this is not supported by my our data. First, I saw an increase in shrub cover at the Nantucket maintenance site, and second because no correlation between changing shrub cover and change in graminoid richness was observed at the restoration site. It is also important to note that changes in graminoid richness must be viewed cautiously because our surveys are just a snapshot in time and herbaceous species, such as graminoids, may show particularly high levels of seasonal and interannual fluctuations (Knapp & Smith 2001).

At the Nantucket maintenance site, change in graminoid richness was negatively associated with change in shrub cover, meaning that where shrubs had increased the most, graminoid richness had decreased the most. This negative correlation between change in

graminoid richness and change in shrub cover has been seen with shrub encroachment in grassland habitats worldwide. For example increased shrub cover has been correlated with decreasing graminoid richness in a tallgrass prairie in the central United States (Briggs, Hoch & Johnson 2002). Although restoration techniques may have some success in dealing with this decrease in diversity, for example in semi-natural calcareous grasslands in France, shrub clearing was successful at increasing species diversity over the course of a six year study (Barbaro, Dutoit & Cozic 2001).

At the Nantucket maintenance site, change in forb richness did not differ significantly over time, but change in forb richness was associated with the interaction between PCA axis 1 and PCA axis 2. This is the same interaction that was important in the change in typical sandplain heathland species, seen in Chapter 1 (NMS axis 1- presence-absence data). In this interaction, in areas with more organic matter, less P, more Mg, more K, more Na, more B, and more basic soils; fire (associated with less P, Mg, Fe, Mn, and more Cu, Al, and S) is correlated with an increase in forb richness. The importance of this interaction underscores the complexity of fire management in this system, fire does not always have the same correlation with changing vegetation, but rather depends on edaphic variables, and likely the original vegetation, of the area to which it is applied. At this site fire was correlated with an increase in forb richness in one set of environmental conditions, and a decrease in forb richness when those conditions were not met.

In the Mainland maintenance sire, forb richness increased over time and was also positively associated with PCA axis 2. Thus, at this site, the increase in forb richness was correlated with increasing years since fire and increasing number of fires (which was correlated with less total nitrogen, less phosphorus, and more aluminum). More study is necessary to disentangle time since fire and number of fires at this site, but it seems likely that the most recently burned areas at this site had not yet reached maximum forb diversity, as they were burned only one year prior to the most recent survey. Heathland vegetation in a sandplain heathland in Australia reached maximum species diversity three to five years following a burn (Bell & Koch 1980). On the other hand, the half of this site that had been burned less recently was burned ten years ago, which is much longer than three to five years ago. More study is needed to determine at what point in succession sandplain heathlands reach maximum forb

diversity. Many of the target sandplain species, such as species in the genus *Helianthemum*, are forbs and thus managing for forb diversity may be a management goal. Until further study produces more concrete management suggestions, I suggest a rotating schedule of burning in order to maintain a patchwork of sites that have experiences different times since fire. A patchwork type management has been suggested in rangelands grazed by livestock in the Great Planes of the Unites States, in order to promote heterogeneity and hence increase diversity within that system (Fuhlendorf & Engle 2001).

Conclusion

In this study I identified the species *Carex pensylvanica* as a potentially nitrophilic species. This species increased in cover in all of the plots over time. While this is in no way conclusive, it does provide evidence for increasing nitrogen status in these heathlands over time and warrants further study, specifically with experimental work, such as nitrogen addition studies.

An increase in shrub cover was seen in both of the Nantucket sites. As increases in shrub cover have been shown to reduce species richness in heathlands (Harper 1995; Specht & Specht 1989), preventing shrub encroachment should be a management goal. Prescribed fire appeared to have little effect on encroaching vegetation and managers should investigate alternatives to burning, such as mowing. Changes in species richness within various growth forms showed complex associations with management and edaphic variables and further study is necessary in order to develop management regimes to preserve diversity at these sites.

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