The Vegetation of Montague Plains Wildlife Management Area, 1993-2016:

Changes over 23 years and Responses to Management

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Summary

Montague Plains Wildlife Management Area (MP WMA) supports extensive pitch pine–scrub oak communities and numerous rare and uncommon species of conservation concern. Active management by MA Division of Fisheries and Wildlife (DFW) since 2000 has attempted to improve habitats for rare and regionally uncommon species while reducing potential wildfire hazard to surrounding communities. The current study was undertaken to document vegetation change over the past two decades, and to evaluate vegetation responses to management activity. A network of permanent plots established in 1993 was re-sampled in 2015-2016; data from both sampling periods were analyzed to document vegetation change and responses to management.

Vegetation in both actively managed and untreated areas has been highly dynamic since 1993. In unharvested plots, white pine (*Pinus strobus*) density increased substantially and grey birch (*Betula populifolia*) decreased. Areas that were harvested since 2000 have substantially reduced overstory density and basal area compared to 1993, including a notable decrease in the density and cover of highly flammable pitch pine (*Pinus rigida*). Species richness is somewhat higher in harvested than in unharvested plots or in scrub oak plots treated with prescribed fire. Some early-successional species (e.g., *Schizachyrium scoparium*) have decreased during the past two decades, and harvested areas now support a few species that were absent or uncommon in 1993. Invasive species remain uncommon at Montague Plain, and there is no indication of a widespread increase of invasive species associated with management activity.

Vegetation has been highly dynamic at Montague Plain over the past century in response to agricultural history and more recent management activity. Recent management strongly influences vegetation composition and structure, though compositional patterns related to earlier agricultural history persist. Some species (e.g., *Gaultheria procumbens*) remain largely restricted to sites that were never plowed, and have not re-colonized former agricultural sites in the century or more since agricultural abandonment. Scrub oak (*Quercus ilicifolia*), which was equally frequent but more abundant on unplowed versus formerly plowed sites in 1993, has increased in abundance on plowed areas that have been harvested since 2000. Black huckleberry (*Gaylussacia baccata*) remains more frequent on unplowed sites, but increased since 1993 on formerly plowed sites, especially those that were unharvested. Thus, current vegetation patterns result from species-specific responses to complex patterns of historical agriculture and more recent management activity.

Management efforts since 2000 have increased habitats for numerous rare species at MP-WMA while reducing wildfire hazard. The long-term success of such efforts will depend on the ability of MA DFW to maintain managed areas in the coming decades. Without such commitment, many harvested areas will revert to dense, forested stands, resulting in decreased habitat for uncommon species and increased wildfire hazard. Protection of remaining undeveloped portions of Montague Plain outside of MP WMA remains a critical conservation priority.

The vegetation of Montague Plain is likely to continue to be highly dynamic in the coming decades in response to disturbance history and changing environmental conditions. Long-term monitoring is needed to provide data for evaluating biotic change and responses to management. Thoughtful planning and increased integration of monitoring and research with management activity are critical components of an adaptive management framework for MP WMA. Such an integrated, long-term approach is needed to enable MA DFW to continue to conserve the remarkable biodiversity of Montague Plain.

Introduction

Montague Plain supports one of the largest remaining inland pitch pine-scrub oak barrens in New England, providing habitats for numerous rare and uncommon species that are priorities for conservation. In 1999, MA Division of Fisheries and Wildlife (DFW) purchased approximately 1400 acres of Montague Plain and adjacent Wills Hill. Combined with the 76-acre Bitzer Tract, DFW now owns and manages much of the undeveloped portion of Montague Plain as the Montague Plains Wildlife Management Area (MP WMA).

MA DFW has established an active management program at MP WMA, with the goal of reducing potential wildfire hazard to surrounding communities while protecting and promoting critical ecological resources, including numerous rare species, uncommon natural communities, and ecological processes (Clark and Patterson 2003; T. Simmons, *pers. comm.*). In developing management objectives and approaches for MP WMA, DFW has utilized considerable information available from prior research at the site (e.g., Motzkin et al. 1996, 1999, 2002; Motzkin 2001; Compton et al. 1998; Fuller et al. 1998; Donohue et al. 2000). Importantly, DFW has also fostered strong ties with academic researchers and regional taxonomic experts to document current ecological conditions at Montague Plain and to evaluate responses to management activities (e.g., Mello 2000; Lindwall and Lombardi 2002; Duveneck 2005; Duveneck and Patterson 2007; Willey 2010; King et al. 2011; Akresh 2012; Milam 2013; Goldstein 2013; Akresh and King 2015). The current project was developed to document vegetation change at MP WMA over the past two decades, and to evaluate vegetation responses to DFW management activities. Results from this study will help to inform future management at MP WMA.

A network of 121 permanent plots was established on Montague Plain in 1993 as part of a study that documented the influence of historical land-use on modern vegetation composition (Motzkin et al. 1996). Eighty-three of these plots were located within MP WMA. In 2015, DFW contracted with G. Motzkin to re-sample permanent plots at MP WMA in order to document vegetation change over the past two decades and to assess vegetation response to management activities. This report summarizes results of vegetation sampling of permanent plots in 2015-2016, and evaluates vegetation change since 1993 in both treated and untreated areas. Recommendations for long-term monitoring to evaluate management activities are discussed, along with opportunities for further integration of research and management efforts at MP WMA.

Specific questions addressed in this study include:

(1) How have vegetation composition and structure changed in areas that were not actively managed (i.e., harvested, mowed, or burned) from 1993 to 2015-2016?

(2) How do the current composition, structure and species richness of harvested areas compare with unharvested areas?

(3) Does the influence of historical land-use on species distributions, as documented by Motzkin et al. (1996), persist in recently managed areas, or has management allowed species that were formerly more common on unplowed sites (e.g., *Gaultheria procumbens*, *Gaylussacia baccata*) to increase in areas that were plowed historically?

(4) Has harvesting and/or mowing resulted in an increase in invasive species?

Methods

Study Site

Montague Plain is an outwash delta of sand and gravel deposited into Glacial Lake Hitchcock, which occupied much of the Connecticut Valley after Wisconsinan glaciation. Drought-prone soils on the plain developed in water-sorted siliceous sand and gravel, with a surface layer of loamy sand resulting from eolian deposition following lake drainage. For detailed information on environmental conditions and site history, see Motzkin et al. (1996). Approximately 1,160 acres (470 ha) of Montague Plain are owned and managed by MA DFW as MP WMA (Fig. 1).

Plot Location and Establishment

Prior to sampling in 2015 and 2016, an attempt was made to re-locate as many of the permanent plots as possible within MP WMA. In 1993, the center of each of 121 plots was marked with a 1-inch diameter, 2' long iron pipe, stamped with the plot number, and hammered ~ 1.5' into the ground. GPS coordinates were not recorded in 1993, but plot locations were carefully mapped using tape and compass, and directions to all plots were permanently archived and provided to MA DFW (Harvard Forest Archives 1993-28; Motzkin 2001). To relocate these plot markers, Brian Hawthorne from MA DFW used the original 1993 plot directions, in conjunction with ortho-photo imagery, to georeference the plot locations in ArcGIS. The resulting datalayer represented the best digital approximation, at the outset of this study, of where the iron pipes were located. Coordinates of the locations of the plot markers from this datalayer were saved as a shapefile and uploaded to a Garmin 60CSx GPS unit for use in field plot re-location. G. Motzkin navigated to these GPS points and conducted searches to find the iron pipes. In several instances, the pipes were readily visible. More often, the pipes were obscured by vegetation or soil litter, and a metal detector was used to locate the pipes. This method worked moderately well in areas that were not recently harvested and in some harvested areas. In numerous other harvested stands, pipes were inadvertently knocked over or buried during harvesting operations, requiring extensive searches to re-locate the pipes. In these instances, tapes were used to establish a grid near the plot location based on the estimated coordinates and information from the original instructions, and the grid was systematically surveyed with a metal detector. Although time consuming, in most cases this method worked remarkably well. If the pipes could not be re-located within ~ 1-1.5 hours of searching, the pipe was recorded as 'not found'. One pipe (Plot 19) punctured a skidder tire during harvesting operations in spring 2015 and was removed from the site at that time (B. Hawthorne, *pers. comm.*). The iron pipe in Plot 121 (outside of MP WMA) could not be re-located by J. Parrott and G Motzkin in the early 2000s. All iron pipes that were re-located were flagged, and GPS co-ordinates were recorded.

Prior to the beginning of this project, B. Hawthorne relocated and flagged five plots in MP WPA. Sixty-four additional permanent markers were re-located during this study, 62 of which are located within MP WMA (Fig. 1). Thus, of 83 permanent plots in MP WMA, 67 (81%) have been relocated since 2015. Attempts to re-locate permanent markers for nine plots in MP WMA were unsuccessful. All but one of these sites had been harvested, mowed, and/or burned by DFW, and the pipes were likely disturbed or obscured by management operations. It is likely that many of these 'missing' pipes could be relocated with additional systematic searches.

At 57 of the re-located permanent markers within MP WMA, and three additional plots where the permanent markers were searched for but not found, 20 x 20 m plots were re-established and vegetation composition and structure sampled following the original sampling protocols. A total of 60 plots were sampled in 2015-2016, representing 72% of the original plots within MP WMA (Fig. 1). For three plots (Plots 22, 40, 42) where the permanent markers could not be re-located despite extensive searches, plots were 're-established' in the general location of the original plots, based on the coordinates generated by B. Hawthorne. These three plots were analyzed as

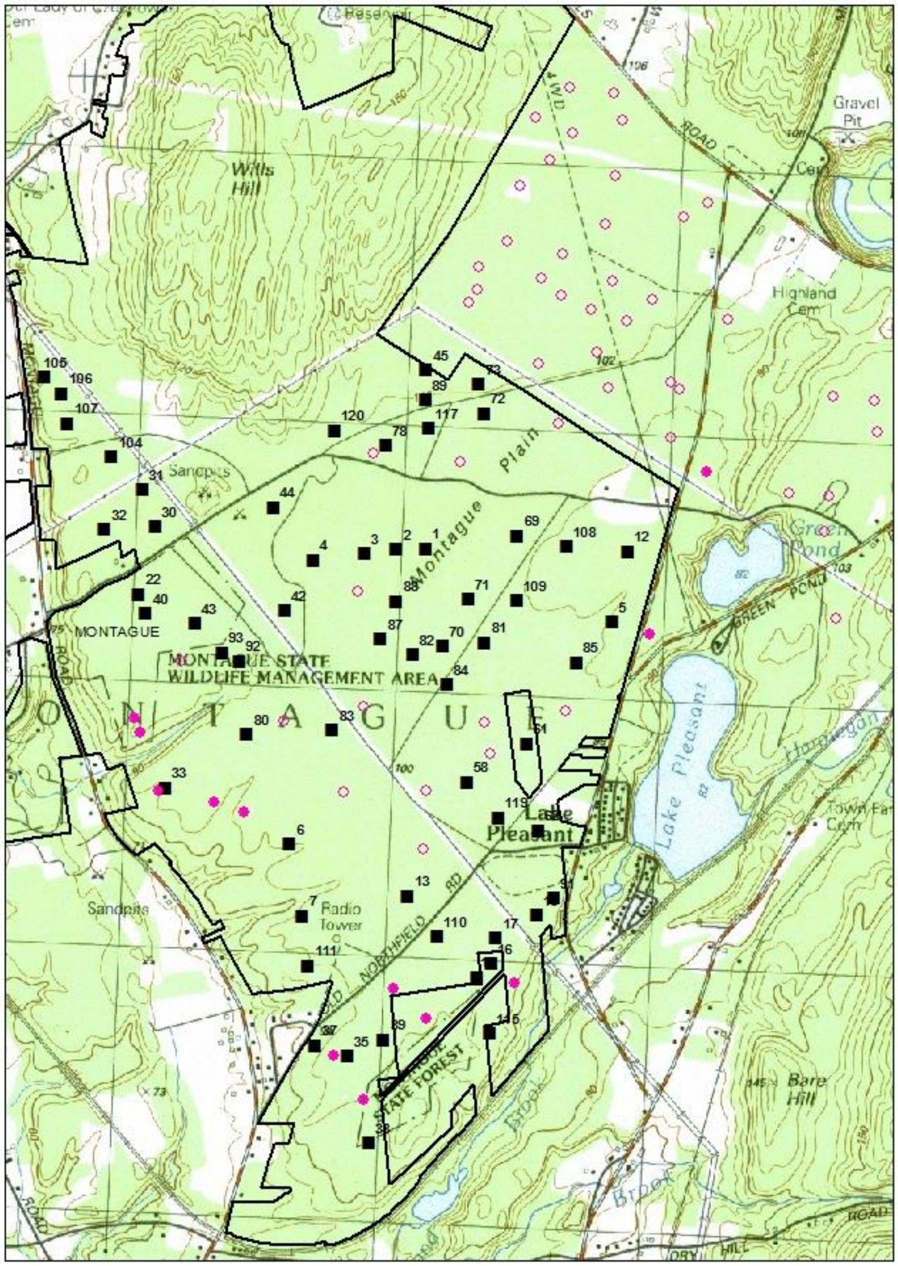


Figure 1. Permanent plots (n=121) established on Montague Plain in 1993 (Motzkin et al. 1996). Filled squares with plot numbers indicate 60 plots that were re-sampled in 2015-2016. Filled circles indicate permanent plot markers that were re-located in 2015-2016 but were not re-sampled. Open circles mark the locations of plots that were not re-located for the current study, most of which are outside of MP WMA (boundaries shown as black lines).

though they had re-sampled the original plots, recognizing that though they were likely near the original plots, they were not in the exact locations.

Plot re-establishment by one field worker using compass and tapes in areas with dense vegetation and limited sight-lines was challenging (!). In order to increase accuracy of plot size and shape, the following field methods were used to establish plot corners. From the permanent marker at the plot center, the diagonal to the NE, NW, SE, or SW corner with the least-obstructed visibility was selected, and a compass and tape used to establish the corner 14.14 m from the plot center. This diagonal with best visibility from the center to the corner was then used as a base line for establishing the other plot corners by carefully measuring distances and right angles. The '3, 4, 5 rule' for right triangles was used to establish the other corners relative to the baseline. For instance, if the best sight-line was to the NE of the plot center, a compass was used to establish the baseline diagonal to the NE corner. It was then necessary to accurately measure 90 degree angles from the plot center on either side of this baseline. To locate the SE corner, a pin was set at 6 m from the plot center along the baseline diagonal, and tapes were pulled from that location and from the plot center to their point of intersection at 8 m SE from the plot center and 10 m from the 6 m point on the baseline diagonal. This location along the SE diagonal was marked and a straight line extended to mark the SE corner at 14.14 m from the plot center through this intersection point. Similar methods were used for the other corners. In cases where sight-lines were unobstructed, corners were marked by extending a diagonal as a straight line towards the 'opposite' corner. The accuracy of these methods was then checked by measuring the length of the four plot sides and both full diagonals (i.e., 28.28 m for a 20 x 20 m square). Results of such checks for numerous plots indicated that these methods worked remarkably well and reduced error from compass use (aside from error associated with locating the first diagonal), allowing substantially greater accuracy in establishing square plots than using a compass and tape to locate all four plot corners (G. Motzkin *pers. observ.*). The center and corners of each plot were marked with bright pink 'survey whiskers', staked flags, and flagging to facilitate plot re-establishment in the future.

Vegetation Sampling

Vegetation sampling followed the 1993 sampling protocols, with minor modifications. Percent cover of each herb, shrub, and sapling (< 2.5 cm diameter-at-breast-height) species was estimated in eight cover classes (1 = < 1%; 2 = 1-3%; 3 = 4-5%; 4 = 6-15%; 5 = 16-25%; 6 = 26-50%; 7 = 51-75%; 8 = > 75%). Diameter-at-breast-height (dbh) was recorded for all trees (≥ 2.5 cm dbh). Total tree cover and cover of each species were also recorded in 2015-16 for trees ≥ 2.5 cm dbh. Photo-documentation of vegetation composition and structure included four photos taken at the center of each sampled plot at a consistent height above the iron pipe (1.55 m), one photo in each cardinal direction.

In cases where taxa could not consistently be identified to species throughout the growing season, they were recorded by genus or subsequently grouped for analysis (e.g., *Dichanthelium depauperatum* and *D. linearifolium*). Field observations indicate that *Quercus coccinea* is frequently the dominant tree oak at MP WMA, and *Q. velutina* is common. However, in many instances it was not possible to confidently distinguish three oak species: *Q. coccinea*, *Q. velutina*, and *Q. rubra*. This difficulty was pronounced in harvested or mowed areas, where sprouting oaks displayed highly variable leaf shape, leaf pubescence, and bud pubescence, and where acorns were rarely present. In unharvested stands, it was frequently not possible to access oak buds, leaves, or acorns, and bark characteristics were variable. As a result, data on species identification of these three oaks are unreliable. Similar difficulty with oak identification was encountered in 1993, and was further confounded by having field crew members with varying levels of experience conducting vegetation sampling. To address these concerns, data were combined for these species and assigned to '*Quercus* species'. A similar approach was used in 1993 and results reported here should be consistent among the two sampling periods. Nomenclature for the 1993 and 2015-2016 data sets follows Haines (2011).

Management History

Since 2000, MA DFW has conducted diverse management at MP WMA, including prescribed fire, mowing, and forest harvesting, representing active management treatments on ~ 950 acres. Much of the remaining untreated portion of MP WMA on Montague Plain is proposed for management in 2017 (B. Hawthorne, *pers*. *comm*.) Treatments were conducted as part of numerous discrete management events since 2000, with many areas receiving more than one treatment. For instance, most portions of the Bitzer Tract have had prescribed fire, tree cutting, and one or more mowings since 2000 (Fig. 2). Most harvested areas in MP WMA have also been mowed either once or twice. Harvests included a range of silvicultural prescriptions (e.g., shelterwood, thinning, seed tree retention) that retained widely spaced trees in order to substantially reduce the potential for running crown fires and to enhance open habitats for uncommon barrens species (Duveneck and Patterson 2007; Bried et al. 2014).

Figure 2. Aerial images of scrub oak vegetation in the Bitzer Tract (red polygon) in MP WMA in 2000 (left) and 2005 (right). Note fuel breaks that delineated treatment units for prescribed fires. Black squares on the right image show permanent plots re-sampled in 2015-2016, some of which were crossed by fuel breaks. Images from Google Earth (2000) and MassGIS (2005).

In order to evaluate vegetation response to management activities since 2000, it was necessary to group management into simplified categories (Fig. 3). Plots designated as 'Unharvested' were located in areas that, since 2000, were not harvested, mowed, or burned prior to sampling for this study. Some Unharvested plots sampled in 2015 were harvested in 2016; these samples were considered 'Unharvested' for analysis, as they had not been harvested at the time of sampling. Of the 60 plots sampled in this study, 22 were in areas that had not been harvested, mowed, or burned since 2000, and 38 plots were sampled in areas that were harvested, mowed, and/ or burned since 2000 (Appendix 1). Harvested plots were grouped into two time-periods: 'Older' harvests (n=9) include plots that were harvested in 2004-2008, 7-12 years before sampling for the current study; 'Recent' harvests (n=23) were harvested in 2014-2016, 1-3 years before sampling in 2015-2016 (Figs. 3 and 4). In almost all cases, harvested areas were also mowed at or near the time of harvest operations, and nearly all 'Older' plots were also mowed again in 2014-2016. Complex patterns of tree cutting, prescribed fire, and mowing were conducted in dense scrub oak (*Quercus ilicifolia*) stands in the Bitzer Tract at MP WMA beginning in 2000. With few permanent plots

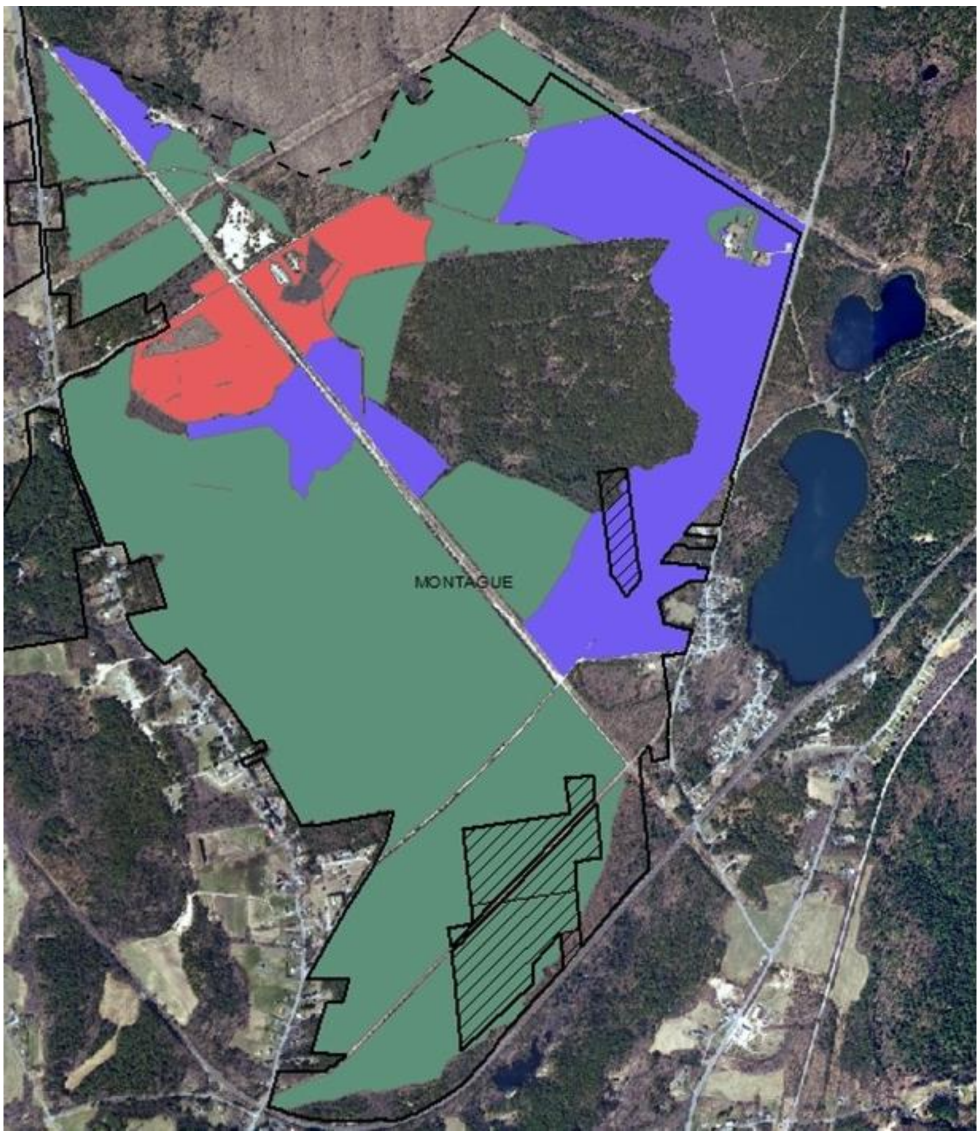


Figure 3. Summary map of management activities on Montague Plain, 2000-2016. Blue indicates areas harvested in 2004-2008; green indicates areas harvested in 2014-2016; red indicates burn/mow/cut treatments since 2000 in the Bitzer Tract. Black lines show MP WMA boundary; cross-hatching shows other ownerships (i.e., MA DCR and Town of Montague). Dashed line indicates the approximate boundary of Montague Plain at the base of Wills Hill. 2005 aerial image from MassGIS.

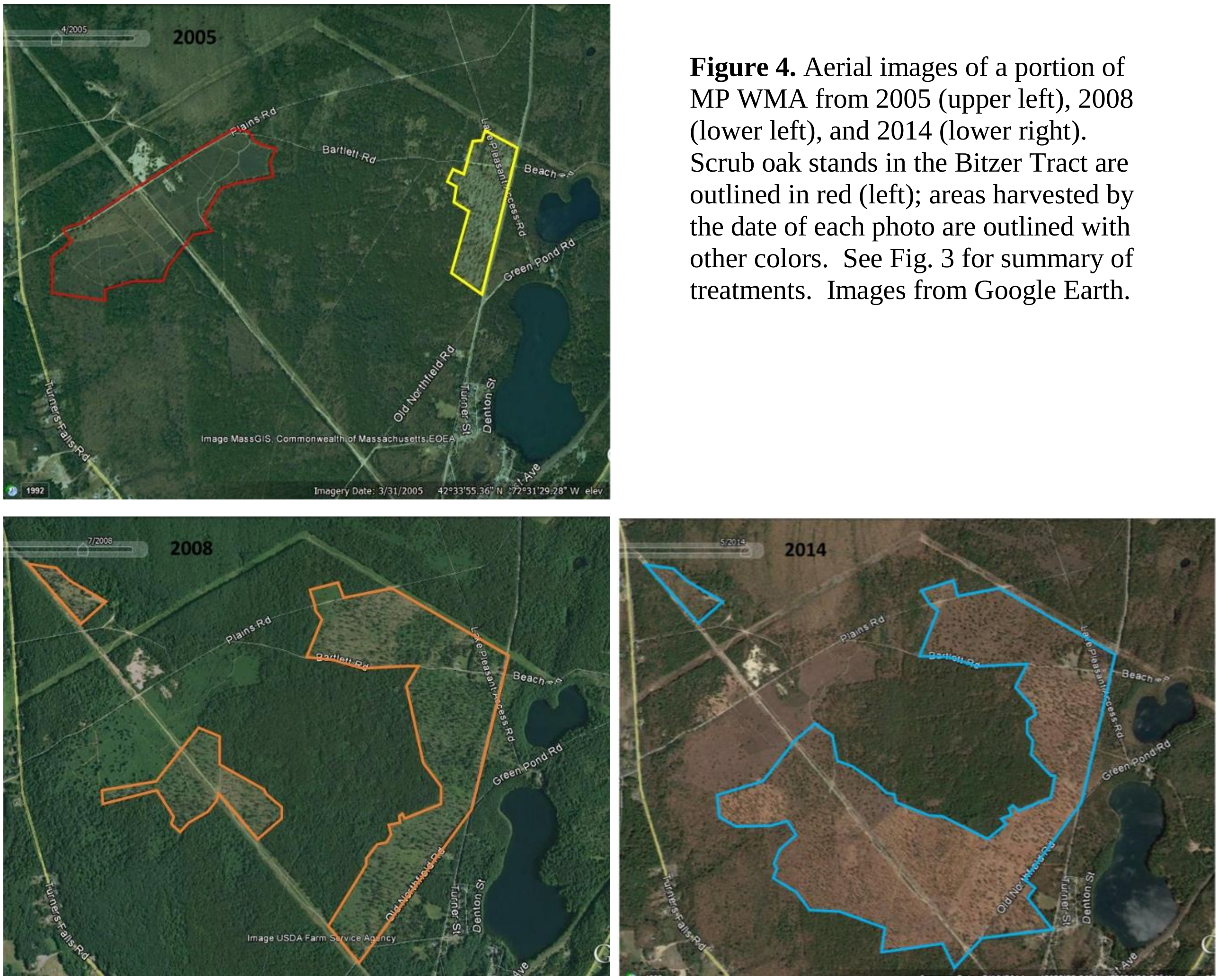


Figure 4. Aerial images of a portion of MP WMA from 2005 (upper left), 2008 (lower left), and 2014 (lower right). Scrub oak stands in the Bitzer Tract are outlined in red (left); areas harvested by the date of each photo are outlined with other colors. See Fig. 3 for summary of treatments. Images from Google Earth.

in this area (n=4) and none that were untreated, statistical analyses were generally precluded. However, data from these plots were included in ordination analyses exploring patterns of vegetation variation. Two plots sampled in 2015-2016 (i.e., Plots 30 and 42) had management histories that differed from all other plots; data from these plots were excluded from most analyses.

Data Analysis

In order to characterize vegetation in 2015-2016, and to assess change in vegetation composition and structure since 1993, summary statistics were calculated for overstory and understory species for all plots combined, and for each of the main management categories (i.e., Unharvested, Older, Recent, Burn). To test whether changes in plot species richness, basal area, and density from 1993 to 2015-2016 differed among Unharvested, Older, and Recent plots, ANOVA was used followed by Tukey's Highly Significant Difference post-hoc tests. In 1993, Motzkin et al. (1996) found that several species were significantly more frequent in areas that were never plowed for agriculture (e.g., *Gaultheria procumbens*, *Gaylussacia baccata*), whereas others were more frequent on formerly plowed sites (e.g., *Polytrichum* spp., *Schizachyrium scoparium*). In order to determine whether current species distributions are similarly associated with agricultural history or whether recent management may have facilitated the spread of some species, Fisher's exact tests were used to compare the frequency of species in 2015-2016 on plowed vs. unplowed sites (Recent and Unharvested plots combined). In cases where results were significant, Fisher's exact tests were then run separately for Unharvested and Recent plots. Older harvested plots were excluded from these analyses because none were on unplowed sites. Burn plots were also excluded, because of small sample size (n=4), all of which were on unplowed sites. Because numerous significance tests were performed, some results may be due to chance. Bonferroni adjustments for multiple tests (Rice 1989) were not performed for these exploratory analyses, accepting that some Type I errors may occur, while most of the conclusions should be sound.

Unconstrained ordination, a form of indirect gradient analysis, was used to characterize modern vegetation variation, and to evaluate relationships between vegetation composition, management history, and patterns of historical land-use. Detrended Correspondence Analysis (DCA) was conducted using PC-ORD 5 (McCune and Mefford 2006), with standard default settings, including downweighting of rare species. Trees ≥ 2.5 cm dbh were treated as separate 'taxa' from individuals of the same species < 2.5 cm dbh. In order to downweight the influence of overstory composition on the ordination results, analyses were based on the cover classes. Species abundances and information on site history were overlaid on the unconstrained plot ordinations to identify variables associated with vegetation variation.

To explore change in vegetation since 1993, separate ordinations were also conducted for: (1) Unharvested plots that have not been actively managed in recent decades; and (2) all harvested plots (Recent plus Older combined). For both sets of analyses, vegetation data from 1993 were analyzed with data from the same plots in 2015-2016 in order to evaluate compositional change. Cover of overstory trees was not recorded in 1993, so the following method was used to estimate tree cover for 1993: the maximum live basal area for a single species in a plot (pitch pine = 45.9 m^2/ha or 200 ft^2/ac) was assigned a value of 100%. Basal area classes corresponding to the eight cover classes were then calculated as a percentage of this maximum (Motzkin et al. 1996). As needed, species were lumped to genus to ensure consistency of data from 1993 and 2015-2016.

Results

Overstory Composition and Structure

Data on tree composition and structure document substantial changes from 1993 to 2015-2016 in both harvested and unharvested plots. Pitch pine (*Pinus rigida*) density decreased in Unharvested plots from an average of 34 stems per plot in 1993 to 12 stems per plot in 2015-2016 (Fig. 5). During the same time period, pitch pine basal area increased in unharvested stands from 12.7 m^2/ha to 14.1 m^2/ha (55 to 61 ft^2/ac; Fig. 5). Average white pine (*Pinus strobus*) density in Unharvested plots increased from 23 stems in 1993 to 37 stems per plot in 2015-2016. Most of the increase in white pine resulted from a substantial increase in saplings and subcanopy stems < 15 cm dbh compared to 1993 (Fig. 6). Twelve out of 22 Unharvested plots (55%) had no white pine stems ≥ 2.5 cm dbh in 1993, and 68% had fewer than five stems. In 2015-2016, only four Unharvested plots had fewer than 10 white pine stems, and most had considerably higher densities. The highest density of white pines recorded in 2015-2016 occurred in Plot 81, which had 171 live stems ≥ 2.5 cm dbh (4275 stems/ha) compared to only 18 stems in 1993. Grey birch (*Betula populifolia*) density decreased in Unharvested plots over 23 years, from 15 to 7 stems per plot. In 1993, nine out of 22 Unharvested plots (41%) had 10 or more grey birch stems, whereas by 2015-16, only four plots (18%) had 10 or more stems. The density of overstory oaks did not change substantially in Unharvested plots from 1993 to 2015-2016 (Fig. 5).

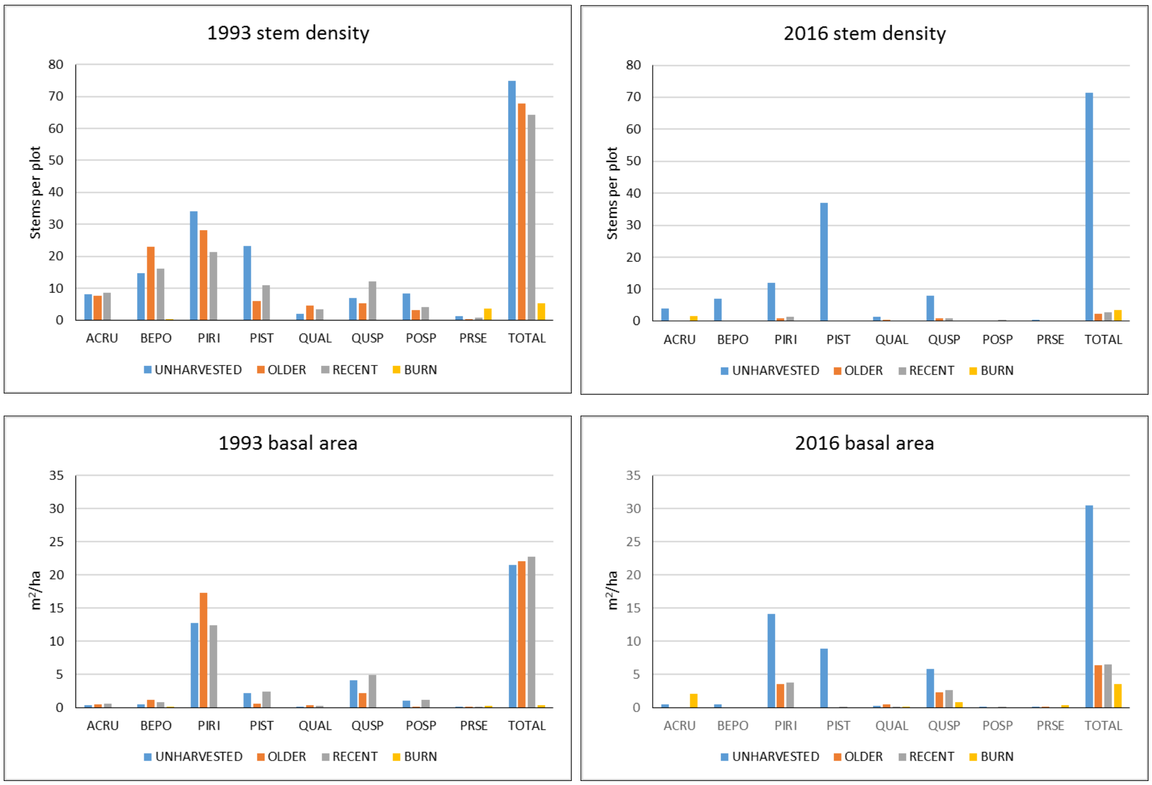


Figure 5. Density and basal area of trees (≥ 2.5 cm dbh) in 1993 and 2015-2016, in Unharvested, Older, Recent, and Burn plots. ACRU = *Acer rubrum*; BEPO = *Betula populifolia*; PIRI = *Pinus rigida*; PIST = *Pinus strobus*; QUAL = *Quercus alba*; QUSP = *Quercus* spp.; POSP = *Populus* spp.; PRSE = *Prunus* serotina (plus one stem of P. pensylvanica); *Quercus* spp. includes *Q. coccinea*, *Q. velutina*, and *Q. rubra*; *Populus* spp. includes *P. grandidentata* and *P. tremuloides*; 'Total' includes species listed plus a small number of stems (< 3%) of other species. Data shown as '2016' were from 2015-2016.

As expected, harvesting dramatically reduced tree density and abundance. Average density of all trees ≥ 2.5 cm dbh in harvested plots was < 3 stems/plot in 2015-2016 for both Recent and Older treatments, and average total basal area was < 7 m^2/ha (30 ft^2/ac). In contrast, average densities in 1993 exceeded 64 stems/plot and average basal area was ~ 22 m^2/ ha (96 ft^2/ac) in plots that were subsequently harvested. Change in density and basal area from 1993 to 2015-2016 did not differ between Older and Recent treatments ($p > 0.94$ for both density and basal area). While most of the decrease in tree density and abundance is directly attributable to harvesting, a small but undocumented amount resulted from storm damage and from mortality of trees after harvesting (G. Motzkin *pers. observ.*). Most Older harvested plots were mowed in both 2004-2009 and in 2014-2016, limiting potential 'in-growth' into the tree layer since 1993. Thus, stem density and basal area in 2015-2016 did not differ substantially between Older and Recent harvests (Fig. 5).

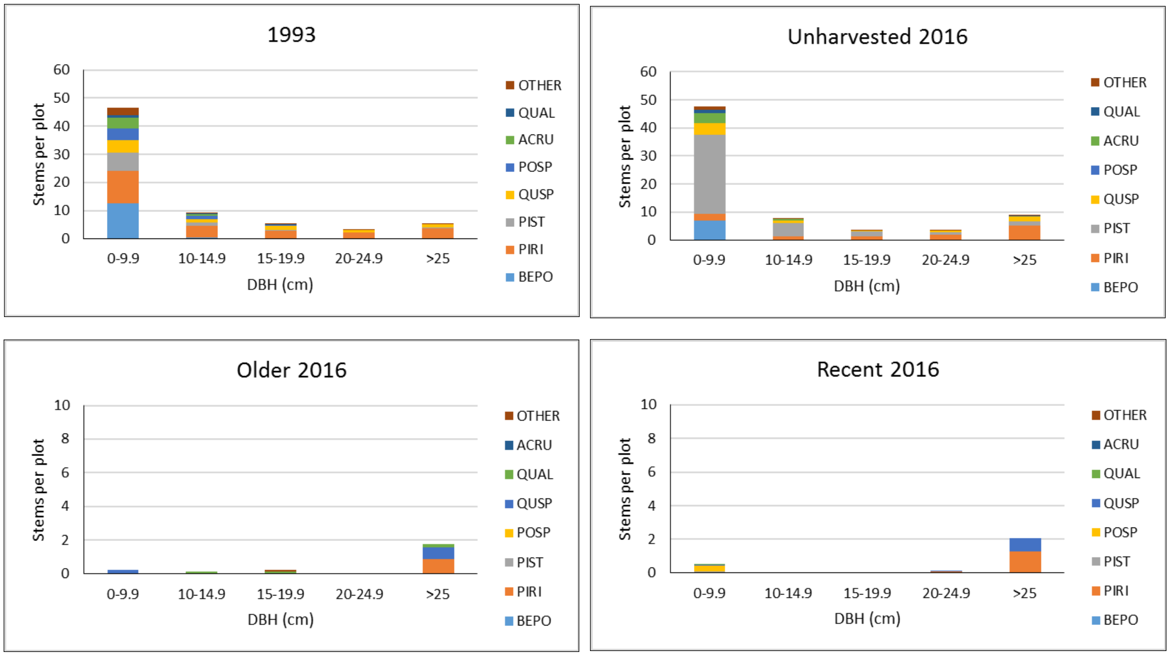


Figure 6. Diameter distributions of trees ≥ 2.5 cm dbh in plots at MP WMA. Data for Unharvested, Older, and Recent plots were from 2015-2016. See Fig. 5 for species abbreviations.

Understory Composition

Species richness in 2015-2016 varied from 11 to 59 species per plot, with most plots supporting 15-30 species (avg. = 24 species). Species richness was higher in Recent and Older harvested plots than in Unharvested or Burn plots (Fig. 7). Several species that are characteristic of recently disturbed sites were more frequent in Recent harvested plots than in Older or Unharvested plots. Some of these species were absent or infrequent in 1993. For instance, sand-sedge (*Bulbostylis capillaris*) was not recorded in 1993 but was present in 2015-2016 in 26% of Recent harvested plots (Table 1). This species did not occur in any Unharvested plots nor in Older harvested plots. Similarly, linear-leaved panic grass (*Dichanthelium depauperatum* and *D. linearifolium*) was not recorded in 1993, but occurred in 24 plots in 2015-2016, including 87% of Recent harvested plots and 33% of Older harvested plots. In contrast, little bluestem (*Schizachyrium scoparium*) was more frequent in 1993 than in 2015-2016, particularly in Unharvested and Recent harvested plots. Little bluestem occurred in 16 Unharvested and 11 Recent harvested plots in 1993, compared to 4 Unharvested and 5 Recent harvested plots in 2015-2016 (Table 1).

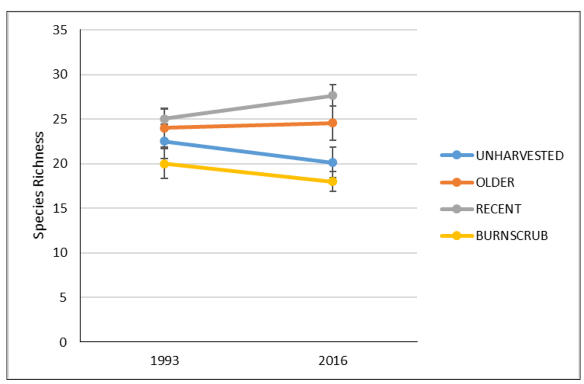


Figure 7. Species richness in 1993 and 2015-2016 in Unharvested, Older, Recent, and Burn plots in MP WMA. Vertical bars are standard errors.

In 2015-2016, wintergreen (*Gaultheria procumbens*) occurred almost exclusively in plots where it was recorded in 1993. Wintergreen occurred in seven Recent harvested plots in 2015-

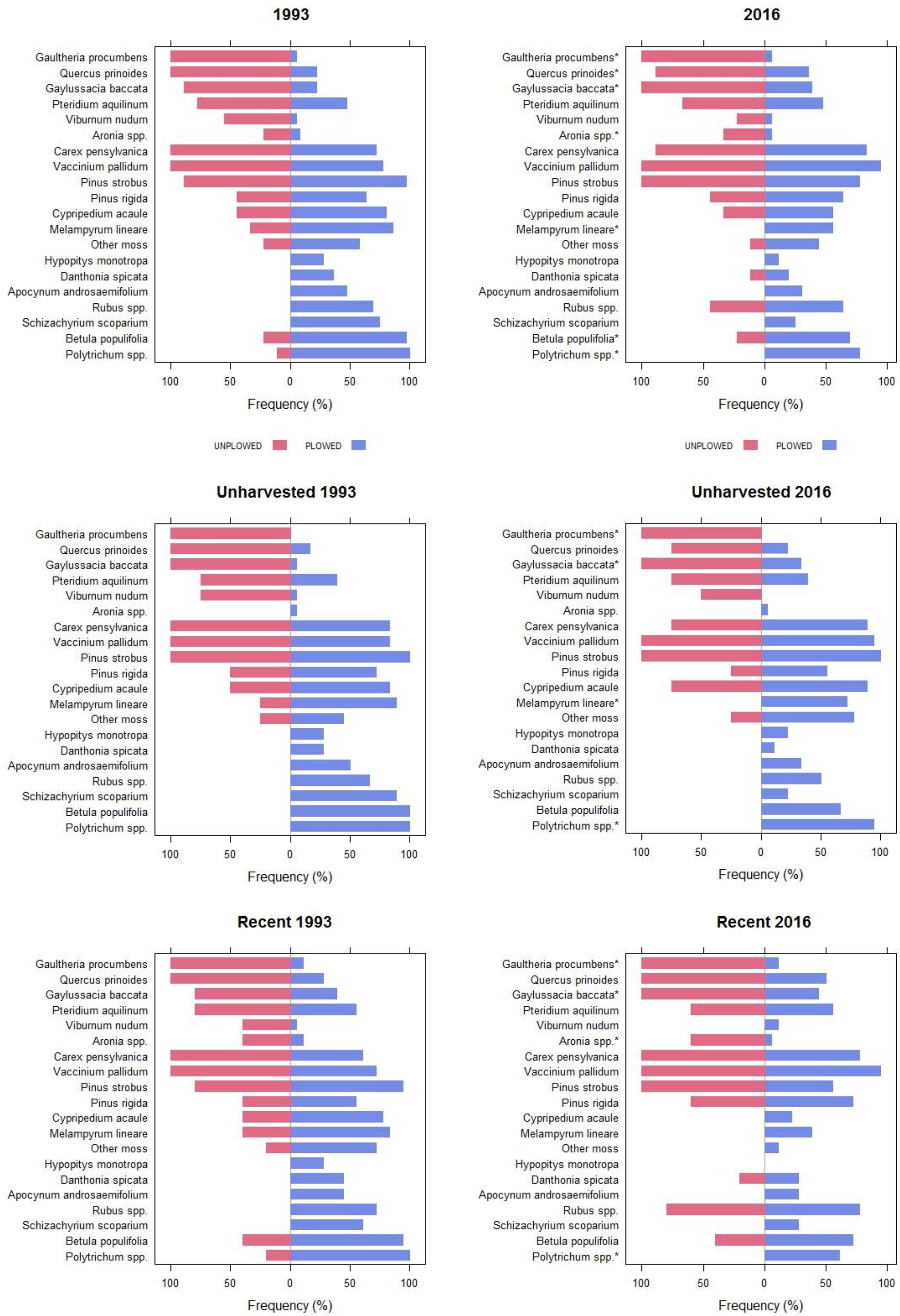


Figure 8. Frequency of occurrence of 20 species associated with unplowed (red) or formerly plowed (blue) sites on Montague Plain in 1993 (Motzkin et al. 1996). Top panels show Unharvested and Recent plots combined (n=45); middle panels: n=22; bottom panels: n=23. 'Recent' plots were harvested and mowed in 2014-2016. Asterisks show Fisher's exact test significant differences ($p < 0.05$) in 2015-2016.

Table 1. Percent frequency of occurrence (%) and mean cover (x̄) of trees and understory species in 1993 and 2015-2016. Species with frequency ≥ 20% in at least one category are shown. Mean cover is based on plots in which the species occurred. Understory species are sorted to highlight differences in frequencies between Unharvested and Recent treatments. *Quercus* spp. includes *Q. coccinea*, *Q. velutina*, and *Q. rubra; Dichanthelium depauperatum* includes *D. linearifolium*; *Dendrolycopodium obscurum* includes *D. hickeyi*; *Potentilla simplex* includes *P. canadensis*.

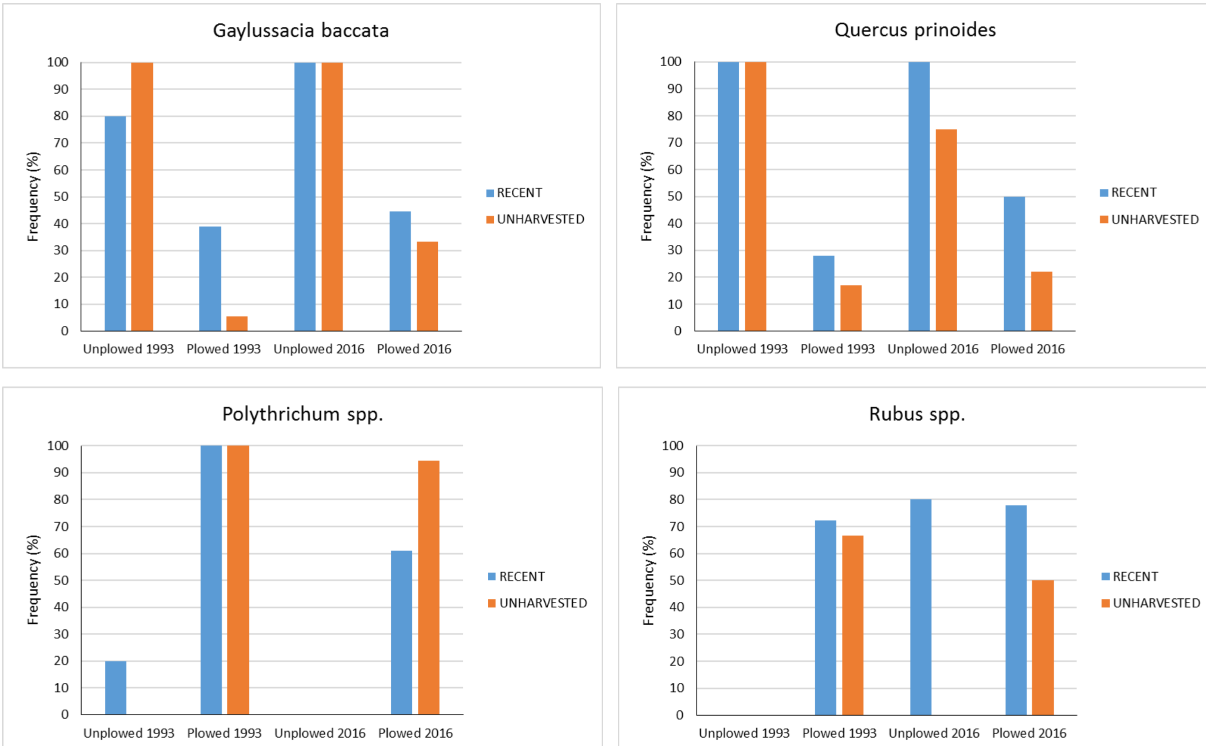
	1993		**2015-2016**									
	All Plots (n=58)		All Plots (n=58)		Unharvested (n=22)		Older (n=9)		Recent (n=23)		Burn (n=4)	
	%	**x̄**	**%**	**x̄**	**%**	**x̄**	**%**	**x̄**	**%**	**x̄**	**%**	**x̄**
Trees (≥ 2.5 cm dbh)												
Acer rubrum	52	3	21	8	50	8	0	0	0	0	25	11
Amelanchier sp.	21	1	12	1	27	1	0	0	0	0	25	2
Betula populifolia	74	2	22	7	59	7	0	0	0	0	0	0
Pinus rigida	83	34	74	19	82	37	78	5	78	6	0	0
Pinus strobus	57	8	40	31	100	33	0	0	4	1	0	0
Populus grandidentata	12	10	7	2	9	1	0	0	9	3	0	0
Populus tremuloides	17	4	5	1	9	1	0	0	4	1	0	0
Prunus serotina	34	1	12	2	23	1	11	1	0	0	25	5
Quercus alba	29	2	19	5	27	7	22	6	9	3	25	2
Quercus spp.	71	12	59	20	86	23	44	22	43	12	25	11
Other												
Herbs, shrubs, saplings (<2.5 cm dbh)												
Prunus pensylvanica	22	3	31	1	0	0	44	1	57	1	25	1
Erechtites hieraciifolius	0	0	17	1	0	0	11	1	39	1	0	0
Carex sp.	0	0	14	1	0	0	0	0	35	1	0	0
Viola sagittata	5	2	14	1	0	0	0	0	35	1	0	0
Ailanthus altissima	0	0	10	1	0	0	0	0	26	1	0	0
Bulbostylis capillaris	0	0	10	1	0	0	0	0	26	1	0	0
Phytolacca americana	0	0	9	1	0	0	0	0	22	1	0	0
Lechea intermedia	0	0	10	1	0	0	11	1	22	1	0	0
Dennstaedtia punctilobula	2	1	9	1	0	0	0	0	22	1	0	0
Vitis sp.	2	1	10	1	0	0	11	1	22	1	0	0
Populus grandidentata	10	4	10	7	0	0	11	1	22	9	0	0
Epigaea repens	5	2	5	1	0	0	0	0	13	1	0	0
Uvularia sessilifolia	2	2	2	1	0	0	0	0	0	0	25	1
Comandra umbellata	3	2	2	1	0	0	0	0	0	0	25	1
Maianthemum racemosum	3	1	2	1	0	0	0	0	0	0	25	1
Piptatherum pungens	3	3	2	1	0	0	0	0	0	0	25	1
Rosa carolina	3	1	2	1	0	0	0	0	0	0	25	1
Prunus susquehanae	14	3	3	1	0	0	0	0	0	0	50	1
Dichanthelium depauperatum	0	0	41	1	5	1	33	1	87	1	0	0
Potentilla simplex	9	3	22	1	5	1	22	1	43	1	0	0
Lespedeza sp.	5	2	12	1	5	1	11	1	22	1	0	0
Aronia sp.	19	7	17	1	5	1	22	1	17	1	75	3
Solidago rugosa	12	3	9	1	5	1	0	0	13	1	25	1
Carex debilis	2	2	9	1	5	1	22	1	9	1	0	0
Lichen spp.	24	2	2	1	5	1	0	0	0	0	0	0
Lysimachia quadrifolia	55	3	50	1	9	1	100	1	70	1	50	1
Populus tremuloides	33	5	21	11	9	1	33	4	30	16	0	0
Danthonia spicata	29	4	22	1	9	1	56	1	26	2	0	0
Castanea dentata	16	2	12	2	9	3	22	3	13	2	0	0
Vaccinium stamineum	10	3	10	1	9	1	22	1	9	1	0	0
Viburnum nudum var. *cassinoides*	22	2	12	1	9	1	0	0	9	1	75	1
Dichanthelium spp.	9	1	55	1	14	1	67	1	100	1	0	0
Diphasiastrum tristachyum	17	4	17	1	14	1	44	1	13	1	0	0
Comptonia peregrina	50	4	33	2	18	1	56	5	35	1	50	1
Gaultheria procumbens	24	6	26	2	18	3	0	0	30	1	100	2

Table 1 cont'd:

	1993		2015-2016									
	All Plots (n=58)		All Plots (n=58)		Unharvested (n=22)		Older (n=9)		Recent (n=23)		Burn (n=4)	
	%	x̄	%	x̄	%	x̄	%	x̄	%	x̄	%	x̄
Schizachyrium scoparium	62	14	29	2	18	1	78	1	22	4	25	1
Kalmia angustifolia	12	3	14	1	18	1	11	1	9	1	25	2
Hypopitys monotropa	24	2	7	1	18	1	0	0	0	0	0	0
Vaccinium corymbosum	14	3	21	1	23	1	22	1	22	1	0	0
Frangula alnus	7	1	17	1	23	1	22	3	13	1	0	0
Chimaphila maculata	12	1	10	1	23	1	0	0	4	1	0	0
Apocynum androsaemifolium	40	2	29	1	27	1	44	1	22	1	50	1
Maianthemum canadense	29	2	21	1	27	1	33	1	13	1	0	0
Quercus prinoides	43	6	53	5	32	1	67	3	61	3	100	25
Dendrolycopodium obscurum	41	3	43	1	36	1	67	1	48	1	0	0
Rubus spp.	55	2	62	2	41	1	89	2	78	2	25	1
Gaylussacia baccata	36	18	48	9	45	14	33	3	57	7	50	2
Pteridium aquilinum	50	9	50	3	45	2	22	3	57	4	100	4
Pinus rigida	59	3	62	2	50	1	100	6	70	1	0	0
Betula populifolia	79	5	64	2	55	2	89	5	65	1	50	1
Melampyrum lineare	81	2	45	1	59	1	67	1	30	1	0	0
Prunus serotina	79	3	78	1	64	1	89	1	83	1	100	1
Other moss	48	2	38	2	68	3	44	1	9	1	25	1
Quercus ilicifolia	97	14	91	17	77	6	100	27	100	9	100	88
Quercus alba	60	3	76	2	77	1	67	4	87	2	25	1
Polytrichum spp.	84	19	64	5	77	7	100	7	48	1	0	0
Amelanchier sp.	71	3	83	1	82	1	67	1	91	1	75	1
Acer rubrum	81	4	88	3	86	2	78	4	91	3	100	1
Carex pensylvanica	83	6	88	2	86	1	100	3	83	3	100	3
Cypripedium acaule	71	2	50	1	86	1	56	1	17	1	25	1
Vaccinium angustifolium	91	13	91	12	91	8	89	16	91	9	100	34
Vaccinium pallidum	84	6	95	4	95	3	89	6	96	3	100	13
Quercus spp.	88	5	95	7	100	6	100	9	100	8	25	1
Pinus strobus	91	4	72	3	100	4	44	1	65	1	25	1

2016, and it was present in each of these same plots in 1993. Black huckleberry (*Gaylussacia baccata*) occurred in three Older harvested plots in 2015-2016, two of which also had this species in 1993. In Recent harvested sites, black huckleberry was present in 11 plots (48%) in 1993, and in 13 plots (57%) in 2015-2016. In Unharvested sites, huckleberry was recorded in 23% of plots in 1993, and in 46% of plots in 2015-2016. Thus, data from 2015-2016 suggest an increase in huckleberry frequency since 1993, with the percentage increase in Unharvested sites greater than that which occurred in harvested sites. Dwarf chinquapin oak (*Quercus prinoides*) occurred in the same number of Burn plots (n=4) and Unharvested plots (n=7) in 1993 and in 2015-2016. However, this species occurred in 14 plots in 1993 that were subsequently harvested (Older and Recent plots combined), compared to 20 harvested plots in 2015-2016, suggesting an increased frequency of occurrence (Table 1).

Analysis of 20 species whose distributions were strongly associated with past land-use in 1993 (Fig. 8 in Motzkin et al. 1996) identified considerable variation in the degree to which current frequencies or abundances correspond with patterns observed in 1993. Wintergreen had similar frequencies in 1993 and 2015-2016 for unplowed versus formerly plowed sites, and remained highly associated with unplowed sites (Fig. 8). Black huckleberry was more frequent on unplowed than plowed sites in both 1993 and 2015-2016, although its frequency on plowed sites has increased since 1993, particularly in Unharvested sites (Fig. 9). In 2015-2016 black huckleberry occurred in



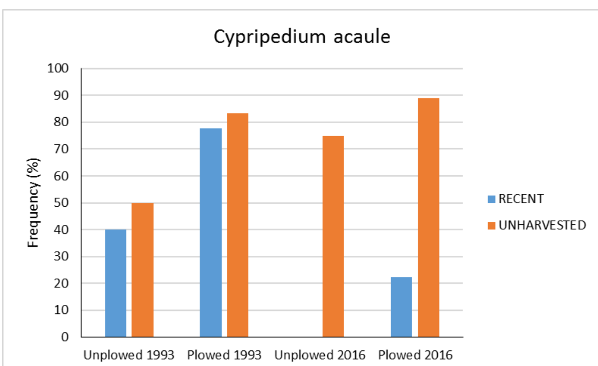


Figure 9. Relationship of agricultural history and recent management to frequency of occurrence of understory species in MP WMA. ‘Recent’ plots were harvested and mowed in 2014-2016.

100% of unplowed Recent and unplowed Unharvested plots, and in 44% and 33% of formerly plowed Recent and Unharvested plots, respectively. In 1993, it occurred in 30% and 6% of Recent and Unharvested, formerly plowed plots (Fig. 9). Little bluestem remained highly restricted to formerly plowed plots, though in 2015-2016 it occurred at much lower overall frequency than it did in 1993. Haircap moss (*Polytrichum* spp.) remained strongly associated with formerly plowed sites, but had lower frequency in Recent harvested areas (Fig. 9), and substantially lower abundance in both Recent and Unharvested plots, in 2015-2016 compared to 1993 (Table 1).

Non-native invasive species are uncommon at Montague Plain, and where present, typically occur in low abundance. Glossy buckthorn (*Frangula alnus*) was found in only 4 plots in 1993 (< 7%), and in 10 plots (16.67%) in 2015-16, including five Unharvested, three Recent harvested, and two Older harvested plots (Table 1). In most of these plots, only one or a few small stems of glossy buckthorn were observed; it was most abundant (4-5% cover) in Plot 108. Tree-of-heaven (*Ailanthus altissima*) seedlings or small saplings were observed in six harvested plots, having not been recorded in any plots in 1993. Multiflora rose (*Rosa multiflora*) was also not observed in the study plots in 1993 and now occurs in low abundance in two Recent harvested plots. Overall, harvesting seems not to have contributed to a substantial increase in non-native invasive species from 1993 to 2015-2016.

Vegetation Ordination and Disturbance History

Detrended Correspondence Analysis was used to characterize vegetation variation among the 60 plots sampled in 2015-2016. Species abundances are overlaid on the resulting plot ordination in Figs. 10 and 11. White pine and red maple (*Acer rubrum*) trees occur almost exclusively in plots with high Axis 1 values. Pitch pine is most abundant in the overstory of plots with high Axis 1 values, but also occurs frequently at lower abundance in plots with low Axis 1 values (Fig. 10). Pitch pine is infrequent or absent from plots with high Axis 2 values. Grey birch is characteristic of plots with high Axis 1 and low Axis 2 values (Fig. 10). Whorled loosestrife (*Lysimachia quadrifolia*) and linear-leaved panic grass are frequent in plots with low to moderate Axis 1 values, and absent from plots with high Axis 1 values. Scrub oak is widespread in the study plots, but most abundant in plots with moderate Axis 1 and high Axis 2 scores (Fig. 10).

Several species are characteristic of plots with low to moderate Axis 2 values, including cow wheat (*Melampyrum lineare*), clubmosses (*Dendrolycopodium* species, not shown), and haircap moss (Fig. 11). In contrast, wintergreen occurs almost exclusively in plots with high Axis 2 values. Black huckleberry and dwarf chinquapin are both more abundant in plots with high Axis 2 scores, and moderately frequent but less abundant in plots with lower Axis 2 values (Fig. 11). Species that are more frequent or abundant in plots with low values for both Axis 1 and 2 include bush clover (*Lespedeza capitata*) and poverty grass (*Danthonia spicata*).

The percent of variance in the original vegetation matrix captured by the DCA ordination axes is shown in Table 2. The DCA ordination is strongly correlated with distances in the original vegetation matrix (cumulative R^2=0.621 for Axes 1 and 2). In order to identify factors that may influence vegetation patterns, historical and management variables were overlaid on the unconstrained vegetation ordination (Fig. 12). Axis 1 is strongly associated with the history of recent management; plots that have received no active management since 2000 have moderate to high Axis 1 values, whereas plots that were harvested, mowed and/or burned have lower Axis 1 values. Axis 2 is strongly related to the history of agricultural use; plots that were never plowed have high Axis 2 values, and plots that were plowed for historical agriculture have lower Axis 2 values. Plots that were harvested in 2004-2008 (i.e., ‘Older’ plots) have low to moderate Axis 1 and 2 values in the ordination diagram, similar to many plots that were harvested in 2014-2016 (‘Recent’). Several additional Recent plots have higher Axis 2 values, comparable to the four Burn plots. Combining Axis 1 and 2, plots are separated in the ordination diagram according to two historical variables (Fig. 12): formerly plowed sites that were unharvested when sampled in 2015-2016 are grouped in the lower right portion of the ordination (high Axis 1, low Axis 2), whereas plots that were plowed historically and managed since 2000 are in the lower left (low Axis 1, low Axis 2). Plots that were not plowed historically and have not been actively managed since 2000 are clustered in the upper right of the ordination diagram (high Axis 1 and 2), and plots that were not plowed historically and have been managed recently are in the upper left (low Axis 1, high Axis 2) (Fig. 12).

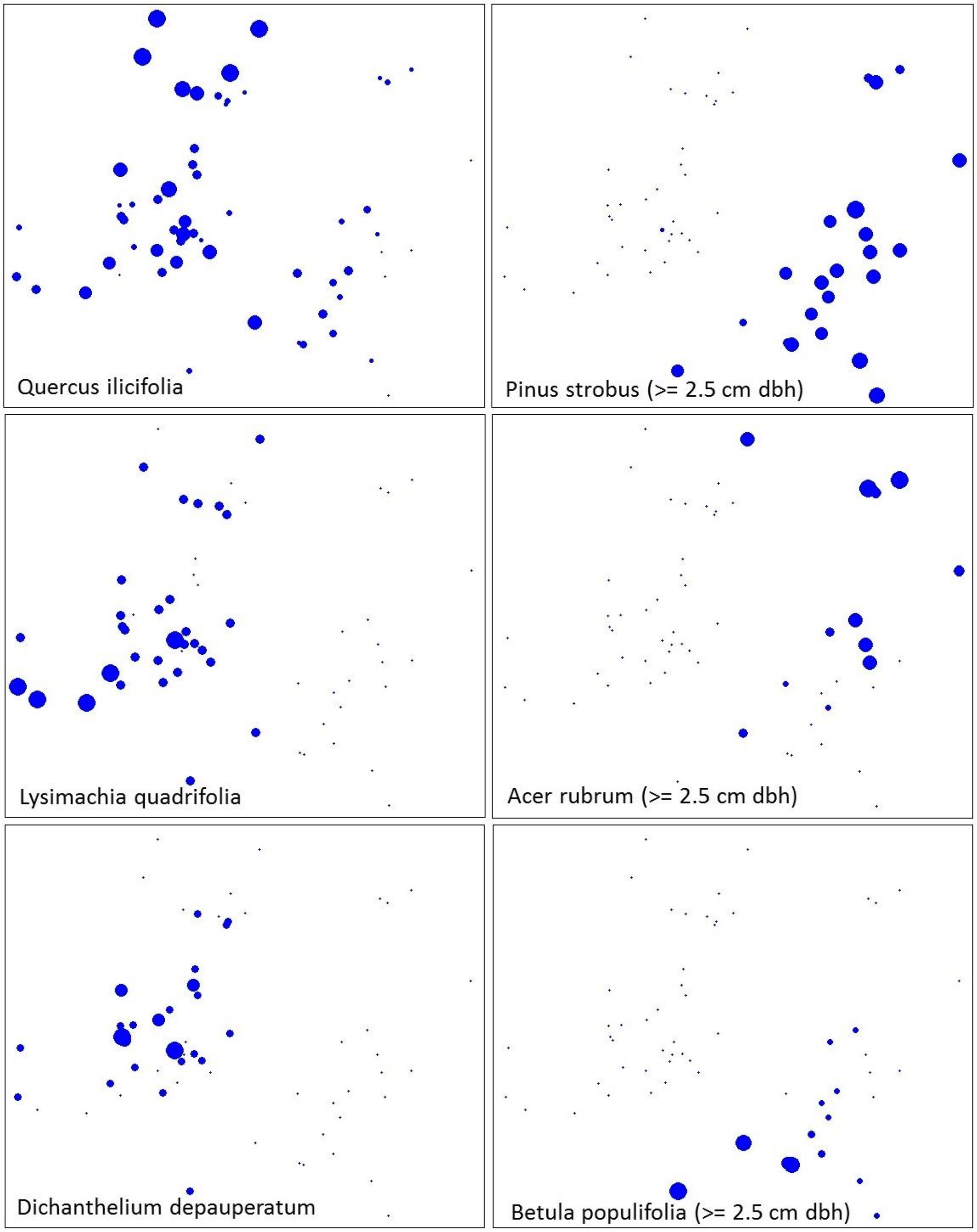


Figure 10. DCA ordination of vegetation data from 2015-2016, with plot ordination overlaid with species abundances. Panels on the left show species that were more frequent or abundant in plots with low Axis 1 (horizontal) values. Panels on the right show species that were more frequent or abundant in plots with high Axis 1 values. The size of the circles is proportional to abundance for each species; small dots indicate plots where the species was absent.

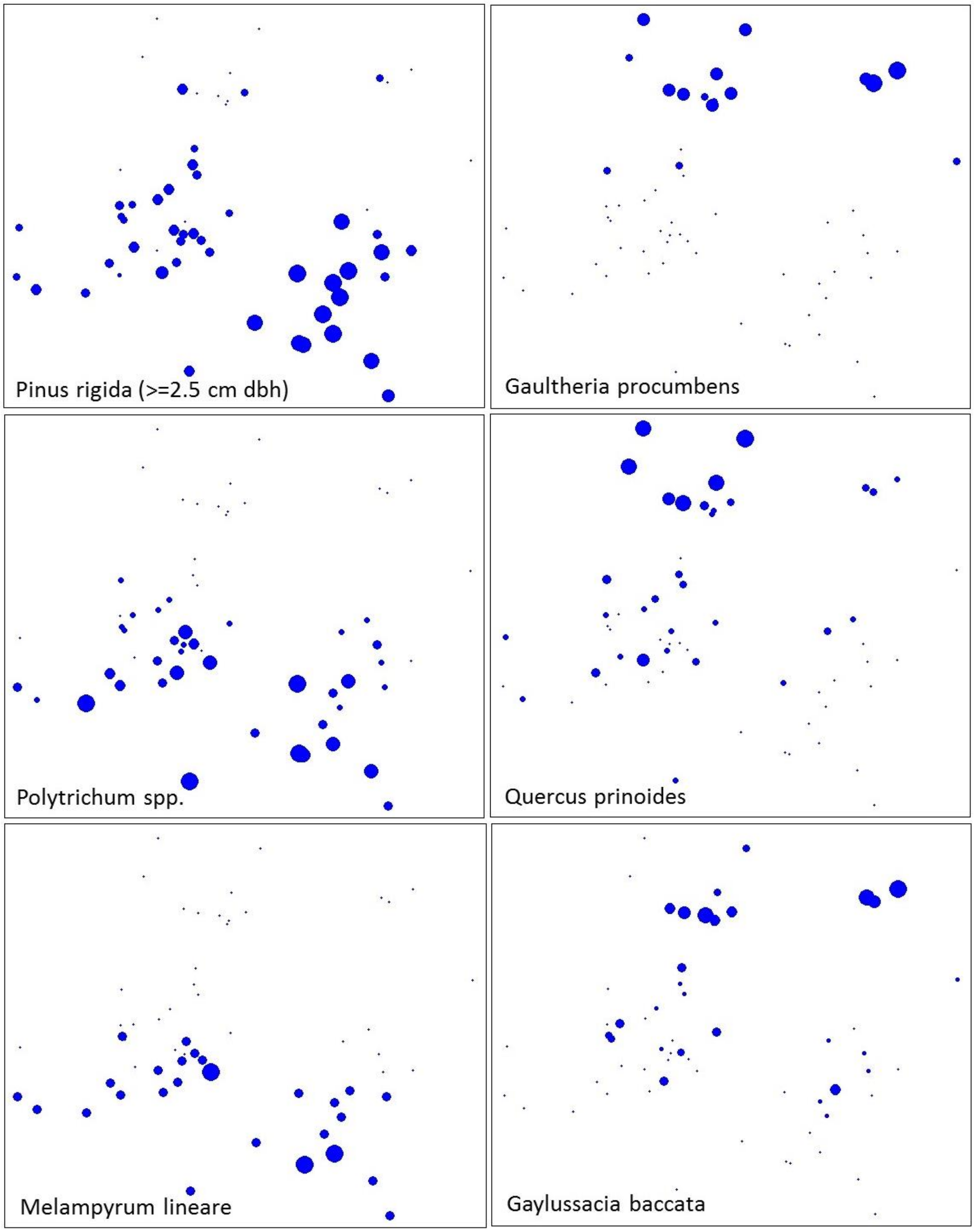


Figure 11. DCA ordination of vegetation data from 2015-2016, with plot ordination overlaid with species abundances. Panels on the left show species that were more frequent or abundant in plots with low Axis 2 (vertical) values. Panels on the right show species that were more frequent or abundant in plots with high Axis 2 values. The size of the circles is proportional to abundance for each species; small dots indicate plots where the species was absent.

Table 2. Coefficients of determination for the correlations between the DCA ordination distances and the distances in the original n-dimensional space of the vegetation matrix. The distance measure used for the original distance was relative Euclidean (McCune and Grace 2002).

Axis	R^2	R^2
	Increment	Cumulative
1	.436	.436
2	.185	.621
3	.051	.672

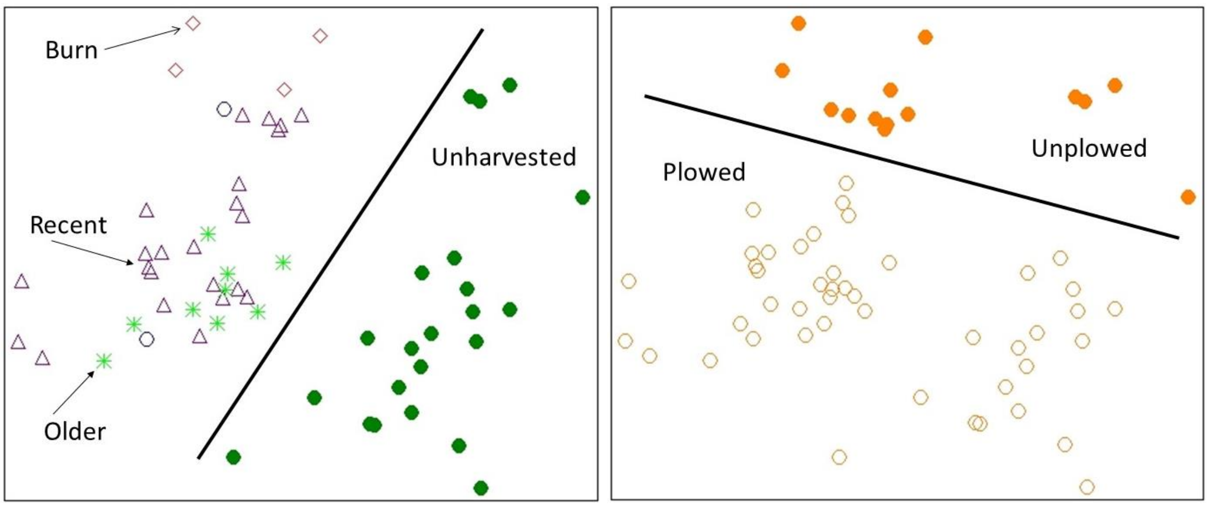


Figure 12. Relationship of the DCA 2015-2016 plot ordination to management since 2000 (left) and agricultural history (right).

DCA ordination of 22 Unharvested plots indicates substantial change in vegetation composition since 1993 (Fig. 13). Vectors connecting individual plots in 1993 to the same plots in 2015-2016 document a consistent shift in vegetation composition, with increased Axis 1 values for all plots. This shift apparently results from a decrease in Unharvested plots of several species that were common in 1993 (e.g., *Schizachyrium scoparium*, *Populus tremuloides*, *Comptonia peregrina*), and an increase in white pine, white oak, and oak species (i.e., scarlet, black, and red oaks combined) in 2015-2016 compared with 1993 (Fig. 13).

Only four out of the 22 Unharvested plots were classified as oak-dominated in 1993 (Motzkin et al. 1996), all of which occurred on unplowed sites (Fig. 13). These four plots had the highest Axis 1 values in the combined 1993-2016 ordination. These plots also changed position in the ordination diagram from 1993 to 2015-2016 less than the other 18 Unharvested plots, which were largely dominated by grey birch and/or pitch pine in 1993 and occurred on formerly plowed sites (Motzkin et al. 1996). A separate ordination of vegetation data from these 18 plots yielded similar results, with less *Schizachyrium scoparium* and *Comptonia peregrina*, and substantial increases in white pine and oaks in 2015-2016 compared to 1993 (data not shown).

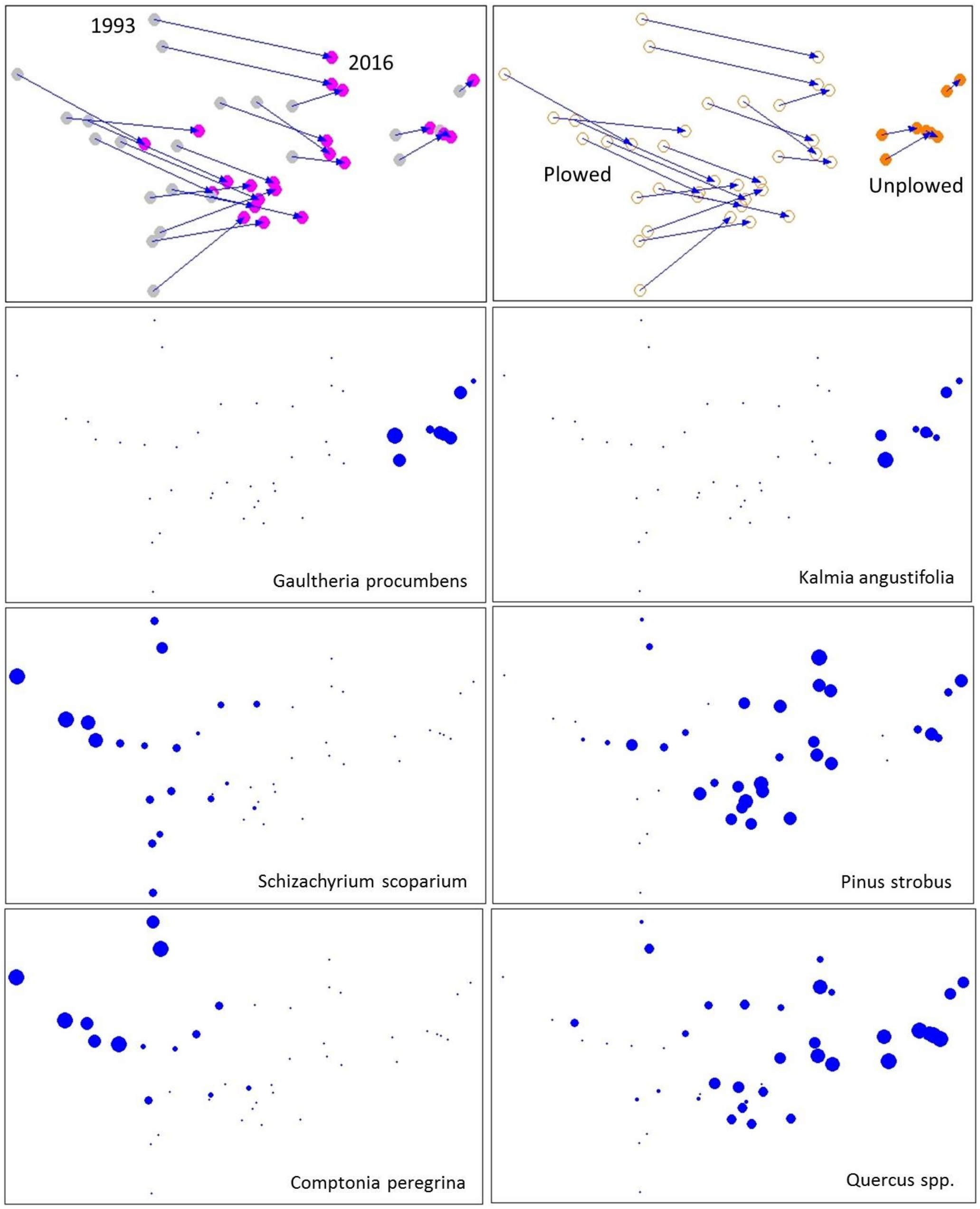


Figure 13. DCA ordination of vegetation data from Unharvested plots in 1993 and 2015-2016. The plot ordination is overlaid with the sampling period (upper left panel) and agricultural history (upper right). Blue arrows connect individual plots from 1993 to 2015-2016. Panels in the 2nd row show species restricted to unplowed sites. Species that were more common in 1993 are shown in the two bottom left panels; species that were more common in 2015-2016 are shown in the two bottom right panels. The size of the circles is proportional to abundance for each species; small dots indicate plots where the species was absent.

Ordination of vegetation data from plots that were harvested since 2000 (Older and Recent combined) documents a substantial shift in composition from 1993 to 2015-2016, with plots in 1993 having consistently lower Axis 2 values than plots in 2015-2016 (Figs. 14 and 15). Harvested plots in 2015-2016 support several species not observed in 1993, including *Bulbostylis capillaris*, *Erechtites hieraciifolius*, and *Dichanthelium depauperatum/linearifolium*. In contrast, pitch pine, white pine, and pink lady's slipper (*Cypripedium acaule*) were more frequent and/or abundant in 1993 than in 2015-2016, and had lower Axis 2 values. Recent and Older plots overlap substantially in the ordination diagram, although Recent plots were more numerous and more varied. Several Recent plots demonstrated greater change in the ordination diagram from 1993 to 2015-2016 than any Older plots. Although all harvested plots demonstrated substantial shift in the ordination diagram from 1993 to 2015-2016, plots on sites that were never plowed remained distinct, with consistently lower Axis 1 values than plots on sites that were formerly plowed (Fig. 15).

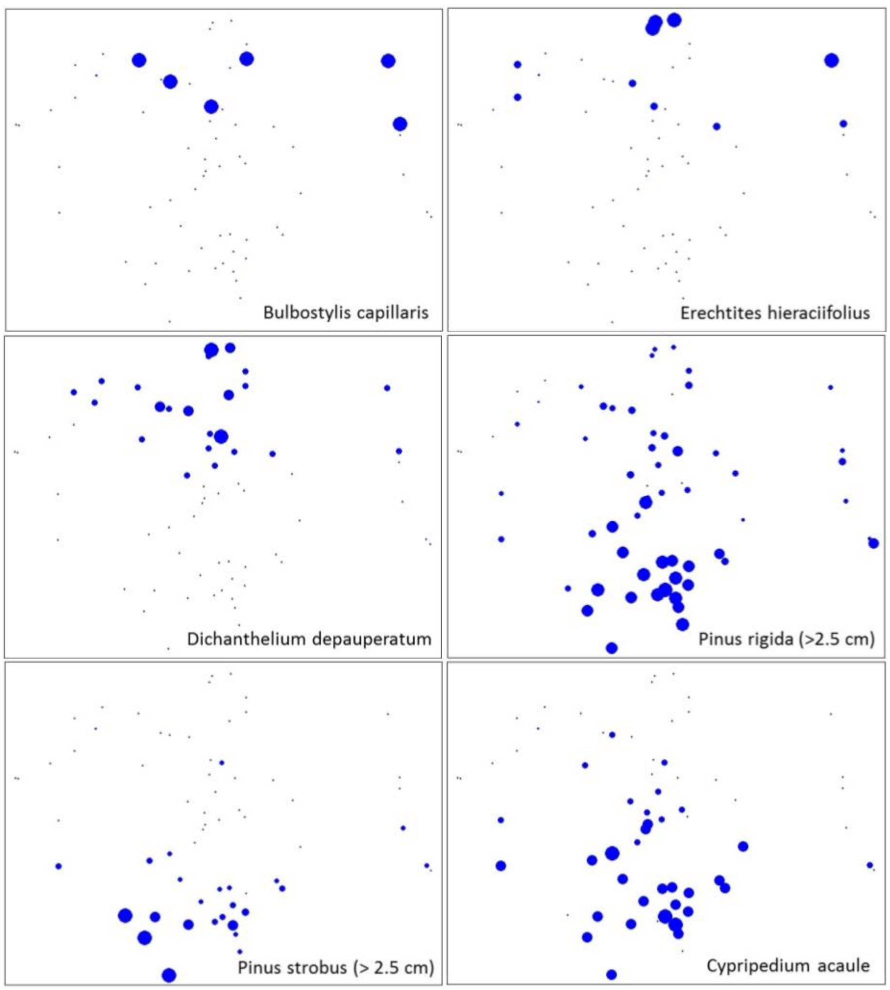


Figure 14. DCA ordination of vegetation data from Older and Recent harvested plots in 1993 and 2015-2016; plot ordination is overlaid with species abundances. The upper two panels and middle left panel show species in harvested sites in 2015-2016 that were absent or uncommon in 1993. The middle right and bottom panels show species that were more frequent or abundant in these plots in 1993, prior to harvesting. The size of the circles is proportional to abundance for each species; small dots indicate plots where the species was absent.

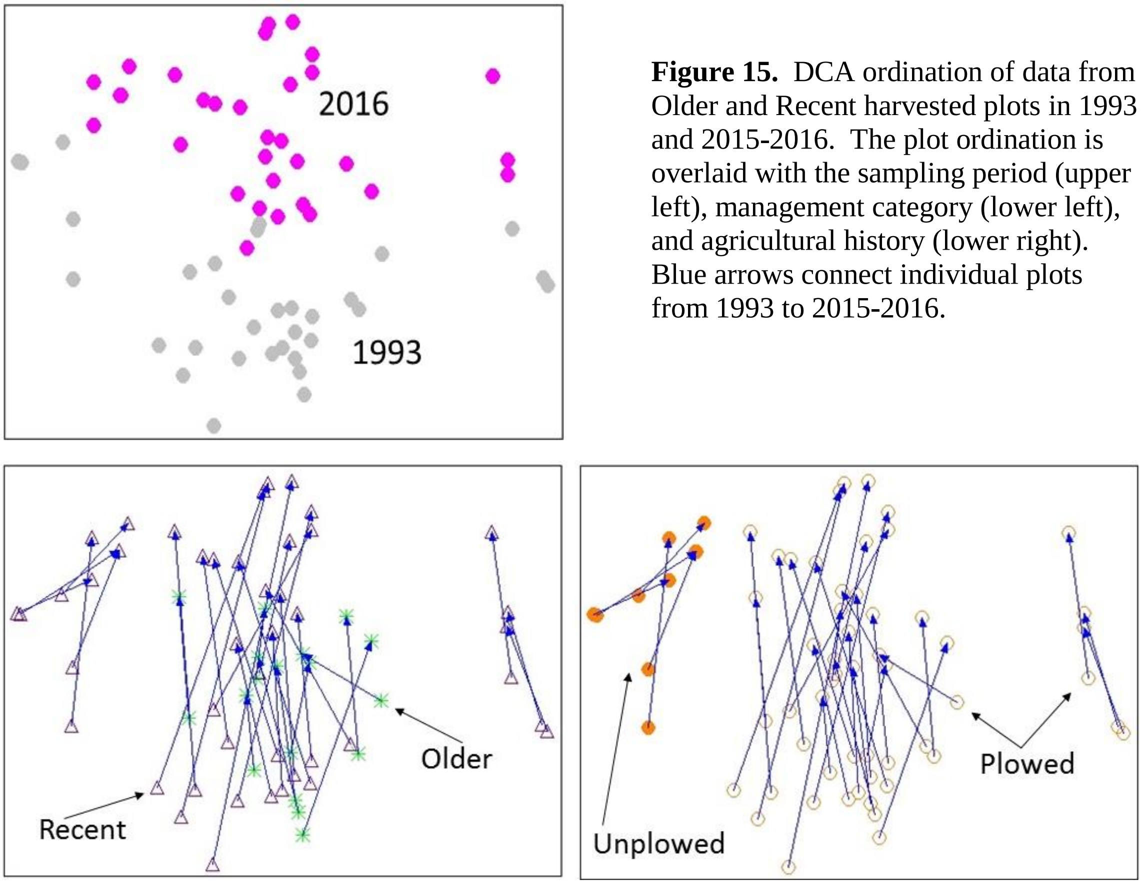


Figure 15. DCA ordination of data from Older and Recent harvested plots in 1993 and 2015-2016. The plot ordination is overlaid with the sampling period (upper left), management category (lower left), and agricultural history (lower right). Blue arrows connect individual plots from 1993 to 2015-2016.

Discussion

Montague Plain supports extensive pitch pine-scrub oak (PPSO) communities that are uncommon, have declined through the historical period, and remain threatened by ongoing development pressure (Motzkin et al. 1999). The establishment of the Montague Plains Wildlife Management Area in 2000 represents a critical milestone in efforts to conserve this ecologically significant site. PPSO communities at MP WMA support numerous rare and uncommon species that are largely restricted to barrens systems characterized by highly flammable fuels, and fire has been an important ecological process at Montague Plain and other PPSO barrens for millennia (Motzkin et al. 1996; Fuller et al. 1998). However, nearby residential, commercial, and industrial development has greatly increased the risk that wildfires could threaten human life or property if fires were to spread from MP WMA. Thus, thoughtful management of MP WMA and other PPSO communities across the Northeast must address both the conservation of uncommon natural communities and numerous rare species, and the critical need to reduce the potential for uncontrolled wildfires to threaten human life or property (Bried et al. 2014).

In order to promote habitats for uncommon species while also reducing wildfire hazard, MA DFW has actively managed approximately 950 acres of MP WMA since 2000, including extensive harvesting, mowing, and use of prescribed fire. Harvesting treatments were used to: (1) substantially reduce the density and cover of pitch pine in forested stands, thereby reducing the likelihood of running crown fires at MP WMA; and (2) promote habitats for numerous rare and uncommon early-successional species. Harvests planned for 2017 will be conducted on much of the remaining portion of MP WMA that occurs on Montague Plain and has not been actively managed since 2000 (B. Hawthorne, *pers*. *comm*.).

Vegetation Composition and Dynamics

Analysis of data collected in 2015-2016 indicates that vegetation variation across MP WMA is related to complex patterns of recent and past human disturbance. Management efforts by MA DFW since 2000, especially extensive harvesting and mowing, have strongly influenced both overstory and understory composition and structure. Importantly, vegetation has also changed substantially since 1993 in unharvested areas; such change largely results from successional dynamics following widespread abandonment of land that was previously cleared for agriculture. Vegetation composition on sites that were never plowed for agriculture differs from vegetation on areas that were plowed and then abandoned in the late 19th and 20th centuries. Such compositional differences have persisted even as vegetation has responded to recent management activities. Thus, current vegetation variation apparently results from species-specific responses to complex patterns of both past agricultural disturbance and more recent management activity.

Relationships between modern vegetation composition and disturbance history are discussed below for the dominant management and vegetation types, along with observations on vegetation change since 1993.

Unharvested Areas

Unharvested areas that have not been actively managed in recent decades were largely dominated by mixed pitch pine-white pine-oak stands in 2015-2016. Only four out of 22 Unharvested plots occurred in areas that were never plowed for historical agriculture. These four plots differed compositionally from plots on post-agricultural sites (Fig. 13). Unharvested plots that were never plowed were largely oak-dominated, and supported several species that were less frequent or less abundant on former agricultural sites, including *Gaultheria procumbens*, *Gaylussacia baccata*, *Kalmia angustifolia*, *Quercus prinoides*, and *Viburnum nudum* var. *cassinoides*. Ordination of data from 1993 and 2015-2016 suggest that Unharvested areas that were never plowed experienced less compositional change since 1993 than plots that were formerly plowed (Fig. 13). In contrast, substantial compositional shifts occurred in most Unharvested plots on former agricultural areas. In 1993, these areas were largely dominated by: (1) relatively open stands of young grey birch, aspen (*Populus* spp.), and/or pitch pine; or (2) dense pitch pine stands. Ongoing tree establishment in the formerly open stands resulted in a substantial decrease in shade-intolerant grey birch, and an increase in pitch pine, white pine, and oaks, since 1993. In Unharvested areas that were pitch pine-dominated in 1993, pitch pine often remains co-dominant, though the density and abundance of white pine saplings and advanced regeneration have increased substantially over the past two decades. Fewer than five white pine stems $\geq$ 2.5 cm dbh were recorded in almost 70% of Unharvested plots in 1993, although white pine seedlings and small saplings were often present in the understory. By 2015-2016, 59% of Unharvested plots supported 20 or more white pine stems $\geq$ 2.5 cm dbh, corresponding to densities of 500 or more stems/ha, and a few plots had more than 70 stems per plot (1775-4275 live stems/ha; Fig. 16). Large white pines observed occasionally in the canopy of these stands presumably provided the seed sources that allowed the substantial increase in white pine by 2015-2016. The increase in white pine was likely also facilitated by the lack of fire during the past few decades, as white pine seedlings and saplings are intolerant of fire and would have been largely eliminated by fires. With available seed sources and the absence of fire or other disturbances, white pine increased dramatically in Unharvested areas over the past few decades. Pitch pine, which generally requires open canopy conditions and exposed mineral soil for establishment, successfully colonized old-fields in the decades following agricultural abandonment, but in recent decades has not established beneath more closed-canopy stands. In the absence of disturbance in Unharvested areas, pitch pines are likely to continue to decrease in relative importance over time as they are overtopped by white pines and oaks, and stand composition is expected to shift increasingly towards mixed white pine and oak.

Figure 16. Unharvested stand with pitch pine overstory, dense white pine saplings, and sparse understory. Photo is looking north from center of Plot 81, June 2016.

Harvested Areas

Much of the Montague Plain portion of MP WMA was harvested by DFW, either in 2004-2008 (i.e., 'Older' harvests) or in 2014-2016 (i.e., 'Recent' harvests), and most harvested areas have also been mowed one or more times (Appendix 1 and 2). As planned, harvests substantially reduced the density and cover of trees, with only 1-4 stems remaining in most harvested plots, compared to initial densities of up to 60-70 stems per plot (Fig. 17). Average basal area of all species combined has also been reduced substantially to ~ 6.5 m^2/ha (28 ft^2/ac) in 2015-2016, representing 30% or less of average basal area in 1993. Pitch pine basal area in harvested plots has been reduced to an average of 3.5–3.8 m^2/ha (15-17 ft^2/ac), or ~ 20-30% of its average 1993 basal area. Duveneck and Patterson (2007) estimated that thinning of dense pitch pine stands to 2.8 m^2/ha (12 ft^2/ac) would substantially increase the wind speeds needed to support running crown fires, and thus substantially reduce the likelihood that such fires will occur. Similarly, Bried et al. (2014) recommended reducing pitch pine cover to ~ 10-30% to reduce wildfire hazard and to promote habitats for early-successional species. Harvesting operations at MP WMA have achieved comparable reductions in pitch pine cover and basal area, substantially reducing the likelihood that running crown fires will develop that could threaten human life or property.

Figure 17. Recently harvested area with open canopy of residual pitch pines and a sparse understory. Cover of sprouts is expected to increase rapidly in the next few years. Photo is looking north from Plot 6, at the end of the first growing season after harvest and mowing in spring 2015.

Long-term reduction of wildfire hazard requires that dense pitch pine forests comparable to those that occurred prior to harvesting not become re-established. Field observations of harvested areas in 2015-2016 indicated considerable variability in the extent to which pitch pine seedlings and sprouts were common in Recent and Older harvested areas. Overall, pitch pine seedlings or sprouts were more frequent in harvested sites than white pine, and appeared to be increasing in some areas, consistent with the ability of pitch pine to both sprout and to establish from seed on sites with open canopy conditions and exposed mineral soil. In areas where dense pitch pine has become established in the understory of harvested stands, periodic mowing or other treatments will be needed to prevent the re-establishment of dense pitch pine stands comparable to those that occurred prior to harvesting. Trembling aspen and big-tooth aspen have also sprouted prolifically or established from seed in some harvested areas (Fig. 18).

Figure 18. Dense aspen stems in a stand that was harvested and mowed in 2015. Photo was taken in August 2015, looking east from center of Plot 73.

While most aspen stems were too small to be recorded as ‘trees’ in 2015-2016, rapid growth and high stem densities suggest that aspens are likely to dominate some harvested areas in the near future, in the absence of mowing or other treatments. Similarly, grey birch sprouts are abundant in some harvested stands and are likely to increase in importance in the absence of additional management (Fig. 19).

Figure 19. Sprouting of grey birch (bright green) in the understory of an area that was recently harvested and mowed, May 2016. The open overstory has widely spaced pitch pines and scarlet oaks.

In the 8-12 years since ‘Older’ plots were harvested and initially mowed, sprouts and tree seedlings were largely prevented from reaching the ‘tree’ size class (i.e., $\geq$ 2.5 cm dbh) by additional mowing in 2014-2016. This has presumably contributed to the substantial compositional overlap between Older and Recent harvested plots indicated by ordination analyses (Fig. 15). A few early-successional species were observed more frequently on disturbed soils in Recent harvested plots than in Older plots (e.g., *Bulbostylis capillaris*, *Erechtites hieraciifolius*), suggesting that these species establish soon after disturbance but may not persist for more than a few years.

Ordination results demonstrate considerable compositional change in harvested plots, while also highlighting persistent compositional differences related to earlier land-use history (Fig. 15). Such compositional differences largely result from a set of species characteristic of unplowed sites that have not successfully colonized former agricultural fields during the past century (Motzkin et al. 1996; Donohue et al. 2000). Additionally, several species occur preferentially in formerly plowed areas and were infrequent or less abundant in unplowed areas (Motzkin et al. 1996). The relationships of individual species distributions to patterns of past land-use and recent management activity are highly variable; several species of ecological and conservation interest are discussed below.

Scrub oak provides critical habitat for rare moth species and is also characterized by extremely flammable fuels. In 1993, scrub oak was equally frequent on unplowed and plowed sites at Montague Plain, though it was most abundant in unplowed scrub oak stands (Motzkin et al. 1996). In contrast, scrub oak was both more abundant and more frequent on unplowed sites in PPSO communities throughout the Connecticut Valley of Massachusetts (Motzkin et al. 1999). Data from Montague Plain in 2015-2016 suggest that scrub oak abundance has been influenced by harvesting activity. While scrub oak continues to dominate scrub oak thickets on unplowed sites in the Bitzer Tract, it is now more abundant in harvested areas on formerly plowed sites than in unharvested areas with similar agricultural histories or in unharvested stands on unplowed sites (Fig. 10). This result is consistent with the observation that scrub oak is relatively shade-intolerant. Although scrub oak occurred in 1993 at low abundance in many forested stands on former agricultural sites at Montague Plain, it has apparently increased in abundance since that time on formerly plowed sites that have been harvested. As a result, scrub oak is now abundant at MP-WMA both in scrub oak thickets and in many harvested plots, and occurs with lower frequency and abundance in Unharvested plots (Table 1). Dwarf chinquapin oak is not as widely distributed as scrub oak at Montague Plain; it is most frequent and abundant in scrub oak stands on sites that were never plowed, and more frequent on formerly-plowed areas that were harvested versus unharvested. Like scrub oak, dwarf chinquapin oak shows a trend towards increased abundance in harvested sites.

Wintergreen remains highly restricted to unplowed sites on Montague Plain (Motzkin et al. 1996, Donohue et al. 2000). Wintergreen occurred in only two formerly plowed plots in 2015-2016, and it was recorded from these same two plots in 1993. There is no indication from data from 2015-2016 of increased frequency of wintergreen in response to recent management activity. Because wintergreen typically occurs in low abundance (i.e., < 5% cover), additional data are needed to determine whether the abundance of wintergreen has changed locally in response to management.

Black huckleberry is of particular management interest because it has highly flammable fuels and, where abundant, strongly influences fire behavior (Patterson et al. 1983). Huckleberry is more frequent and abundant on unplowed sites at Montague Plain than on sites that were plowed for historical agriculture. Huckleberry is, however, less restricted to unplowed sites than wintergreen.

In 2015-2016, black huckleberry occurred with moderate frequency and abundance on formerly plowed areas that had been harvested. Additional data are needed to evaluate huckleberry response to harvesting, and to assess the relative importance of sexual reproduction versus asexual spread in former agricultural areas.

Lowbush blueberry (*Vaccinium angustifolium*) had similar frequencies on formerly plowed vs. unplowed sites at Montague Plain in 1993, whereas *V. pallidum* was more frequent on unplowed sites (Motzkin et al. 1996). These species remain widespread on plowed and unplowed sites, and in harvested, unharvested, and burned sites across MP WMA. Interestingly, both species appeared to be somewhat more abundant in Older harvested sites in 2015-2016 than in unharvested or Recent harvested sites (Table 1). These data are consistent with field observations of high abundance of lowbush blueberries (and extremely high fruit production in 2015!), in areas west of Lake Pleasant Rd. that were harvested in 2004-2008. Additional work is needed to confirm this pattern and to determine the extent to which any increased abundance in harvested sites is influenced by sexual reproduction versus vegetative spread.

Burn Treatments

Only four plots were sampled in 2015-2016 in the Bitzer Tract scrub oak stand, all of which received one or more burn/cut/mow treatments since 2000. Mowed fuel breaks traverse portions of at least two of these plots (Fig. 20). Permanent plot markers were not re-located for two plots, so data from 2015-2016 were not from the exact locations as in 1993. As a result of small sample size and lack of untreated scrub oak plots for comparison, quantitative assessment of vegetation change in response to burn treatments was not possible. Field observations and plot data suggest that vegetation composition in 2015-2016 was similar to 1993, although vegetation structure and fuel loads varied considerably in response to the time since mow or burn treatments. *Piptatherum pungens*, a regionally uncommon grass that was observed in scrub oak thickets in the Bitzer Tract in 1993, was also noted there in a few locations in 2015-2016.

Figure 20. Dense scrub oak stand in the Bitzer Tract, with 4-5 m wide mowed fuel break. The fuel break crosses the northeastern portion of Plot 44. Scrub oak was ~ 2-3 m in height in September 2016, except in the fuel break where it was ~ 1 m tall. Management of this plot included tree cutting in 2008, prescribed fire in 2009, and mowing in 2012. The fuel break was mowed at least three times since 2000, most recently in 2015.

Other Disturbances

In addition to recent management activity, Montague Plain continues to experience occasional wildfires, storms, and other disturbances that influence vegetation composition and structure. An example from one plot (Plot 45) that was visited regularly between 1993 and 2015-

2016 illustrates the complex disturbance history and highly dynamic conditions that have occurred over the past few decades. When Plot 45 was first sampled in July 1993, it supported a pitch pine stand that had established in a former agricultural field, with oaks and white pine recorded in the subcanopy and understory. Two weeks later, the plot was burned in an ~ 12-acre wildfire that eliminated most of the understory white pines and caused substantial sprouting of oaks and some pitch pine seedling establishment over the next 2-3 years (G. Motzkin *pers. observ*.). In 1996-1997, this stand was damaged in winter storms that caused substantial snapping and mortality of overstory pitch pines (Lavelle 1998; G. Motzkin *pers. observ*.). In 2006, another wildfire burned Plot 45, along with Plots 89 and 73 in a nearby aspen stand, again causing sprouting of hardwoods. In 2015, Plot 45 was heavily thinned and the understory mowed. Thus, in 22 years, this plot experienced two wildfires, winter storm damage, harvesting, and mowing. The density of trees ≥ 2.5 cm in this plot decreased from 118 stems in 1993 to one residual pitch pine in September 2016, though pitch pine seedlings and sprouting oaks are now common and likely to increase in the coming years. Although this plot is somewhat unusual in having experienced two wildfires in recent decades, it is otherwise similar to much of Montague Plain in its complex and highly dynamic disturbance history. Several additional storm events have caused canopy damage in portions of MP WMA since 1993 (G. Motzkin *pers. observ*.). In addition, southern pine beetle (*Dendroctonus frontalis*), which was first documented at Montague Plain in 2015, is likely to cause pitch pine mortality in the coming years.

Management Approach

In order to reduce potential wildfire hazard while promoting early-successional habitats for uncommon species, a combination of mechanical treatments (i.e., cutting and mowing) and prescribed fire is recommended for PPSO communities throughout the Northeast (Bried et al. 2014). Several studies at MP WMA have demonstrated that this management approach has been successful in providing habitats for regionally uncommon wildlife, including shrubland birds, native bees, and hognose snakes, all of which were more common in managed versus untreated areas (King et al. 2011; Milam 2013; Akresh and King 2015; Akresh et al. 2015; King et al. 2016). A 2013 survey also documented the persistence of a diverse Lepidoptera assemblage at MP WMA, including several rare species, in areas that have been intensively managed (Goldstein 2013). Although much is unknown about the biology and requirements of rare moth species, several species are thought to be specific to a few common plant species at Montague Plain, especially scrub oak, lowbush blueberries (*Vaccinium pallidum* and *V. angustifolium*), and pitch pine (Wagner et al. 2003; Goldstein 2013). Vegetation data from monitoring of permanent plots, in combination with recent inventories of Lepidoptera, are useful for evaluating the likely influence of management activities on uncommon moth species. Although the density of pitch pines was substantially reduced in harvested areas, Montague Plain continued to support a diverse assemblage of pitch pine-specialist moths, including the state-listed *Zanclognatha martha*, which was the most abundant rare species documented in surveys conducted in 2000 and 2013 (Mello 2000; Goldstein 2013). It appears that harvesting of pitch pines to reduce wildfire hazard has not negatively impacted rare moths or other pitch pine-specialist moths at MP WMA (Goldstein 2013), although the effects of extensive harvests since 2014 have not been evaluated. Data from the current study suggest that management efforts since 2000 have resulted in an increase in abundance of scrub oak and possibly lowbush blueberries in harvested sites. Such increases are likely to benefit the diverse assemblage of scrub oak and lowbush blueberry moth specialists at Montague Plain, including several rare species.

In cases where host-plant species are rare in the existing network of permanent plots, additional data are needed to assess management effects on both host-plants and associated insect species. For instance, New Jersey tea (*Ceanothus americanus*), which is known to support the rare moth *Apodrepanulatrix liberaria*, is infrequent in permanent plots at Montague Plain. Similarly, *Lupinus perennis*, which supports the rare butterfly frosted elfin (*Callophrys irus*), has not been recorded in permanent plots in MP WMA, although it occurs in several locations at Montague Plain. Monitoring protocols should be developed to assess management effects on populations of these and other host-plant species (Goldstein 2013). In addition, because much remains unknown about the biology of many of the rare insect species characteristic of PPSO communities, efforts to minimize potential negative impacts of management on conservation targets are warranted. In particular, the approach implemented in the Bitzer Tract of diversified management of small treatment units may help to minimize potential negative impacts of individual treatments on rare species. Although harvesting, mowing, and/or burn treatments may result in mortality of some individuals of rare or uncommon species (Fig. 21; Erb and Jones 2011), diversified treatment of small units, and protocols that incorporate species phenology into the timing of management, may help to minimize negative population effects and allow potential source populations to persist.

Figure 21. Broken box (?) turtle shell at the southwest corner of Plot 45, September 2016, in an area that was harvested and mowed in 2015. The cause of mortality is unknown.

Recommendations for Research, Monitoring, and Management

Since 2000, MA DFW has conducted extensive management to reduce wildfire hazard while maintaining and expanding habitats for numerous uncommon species characteristic of pitch pine-scrub oak communities. In order to evaluate management within an adaptive framework, long-term monitoring and research should be closely integrated with management efforts. DFW has sponsored or facilitated a wide range of research at MP WMA, including several studies that have explicitly evaluated the effect of management activities on plant and animal composition. The following recommendations are intended to help further integrate research and monitoring with management efforts at MP WMA:

(1) *Maintain Network of Permanent Plots.* In order to maintain the existing network of permanent plots within MP WMA, a plan is needed to facilitate plot relocation, along with guidelines for re-marking, maintenance, and periodic re-sampling of permanent plots. Re-sampling of permanent plots is recommended every 10-20 years. Although many permanent plots within MP WMA were re-located for this study, permanent markers in areas that had been harvested were extremely difficult and time-consuming to re-locate. Many of the permanent markers were damaged, knocked over, or buried by management operations, and several iron markers searched for in harvested areas could not be re-located (Fig. 22). A rigorous system of plot marking and re-location is critical to help limit the loss of additional permanent plots, and to greatly facilitate long-term monitoring efforts. Several possibilities for improved marking of permanent plots should be considered, including: (1) use of a survey-quality GPS device to determine coordinates of iron pipes marking the center of permanent plots with sub-meter accuracy; (2) marking of two or more trees near

Figure 22. Permanent plot markers (1" diameter iron pipes) damaged by harvest or mowing operations in Plots 64 (left) and 73 (right). Many permanent markers were also knocked over and buried, making re-location difficult.

plot centers with numbered tree tags, and recording distances and bearings to the plot center from tagged trees; (3) placement near plot centers of pieces of heavy marine plywood or other materials (e.g., 2' x 2' cement pavers) that are likely to remain intact and visible and are not likely to be removed or destroyed during harvesting and mowing operations. In several instances, plywood coverboards from past wildlife studies at MP WMA remained in place near plot centers and were instrumental in re-locating permanent plot markers. Importantly, coverboards persisted even in areas that had been harvested and/or mowed in recent years; (4) re-locating and re-marking of permanent plot centers *before* management operations, followed by re-marking of plots immediately *after* management.

(2) *Coordinate Research and Management*. Where harvesting or other mechanized treatments are planned, thoughtful coordination of research and management efforts is critical to accommodate long-term studies that provide important data on biotic responses to management. Such coordinated efforts would have helped to prevent the elimination of some long-term study sites by harvesting and mowing in 2014-2016, with only minor modification of management activity. To facilitate rigorous assessment of management effects, designation of representative untreated areas is also recommended (see below). In some cases, it may be necessary to augment the existing network of permanent plots to enable adequate sampling of management treatments (i.e., burn/mow treatments in scrub oak stands in the Bitzer Tract). If, through management agreement or acquisition, MA DFW develops management plans for those portions of Montague Plain that are currently outside of MP WMA, it is critical that research and management be well-coordinated prior to any active management. Periodic meetings between resource managers and researchers at MP WMA are recommended to coordinate activity and to improve information transfer in advance of management activities.

(3) *Reconnaissance Surveys*. A plan should be developed to augment periodic sampling of permanent plots with systematic observations and data collection across MP WMA to document significant disturbances that are not adequately represented in the permanent plots. In particular, because of the low density of plots in some areas (e.g., Bitzer scrub oak

stands), and of residual trees within plots in harvested areas, the existing network of permanent plots is not adequate for documenting many wind, ice, fire, insect, or other events that cause damage to residual trees after management operations. For instance, storm damage in the western portion of MP WMA resulted in substantial snapping and some blowdown of residual canopy trees after harvest operations in 2015 (Fig. 23).

Figure 23. Storm damage to residual trees in stands that were harvested in spring 2014. Note blow-down and snapped tree (left photo) and leaning stems (right). Photos were taken near Plot 107 (left) and looking south from center of Plot 104 (right) in September 2016.

Such damage was not well-documented in this study because few permanent plots occurred in the damaged area, and those that did had low overstory densities resulting from recent harvests. Adequately assessing such events may require sampling across larger areas than the existing 400 m^2 sample plots. The importance of such events is highlighted by monitoring that was conducted after winter storms in 1996-1997, which documented species-specific damage patterns, including 9% snapping of overstory pitch pines in 37 plots (Lavelle 1998). Tree blowdown from several additional small wind-disturbances that have occurred at Montague Plain since the early 1990s have not been documented (G. Motzkin *pers. observ.*). It is recommended that systematic reconnaissance surveys be conducted annually across MP WMA to identify localized disturbances that warrant documentation, followed by mapping, sampling, or other documentation at scales appropriate to each event. Such reconnaissance may also help to facilitate early detection of pests or pathogens, including southern pine beetle (*Dendroctonus frontalis*) which was documented at Montague Plain in 2015 and is likely to cause pitch pine mortality in the coming years.

(4) *Characterize Fuels*. Protocols should be developed for long-term monitoring of fuel conditions in major stand types at MP WMA, and for assessing management effects on fuels and fire behavior.

(5) *Biological Inventories and Monitoring*. Inventories of moths, bees, and birds have provided critical information on the biodiversity significance of MP WMA (Mello 2000; King et al. 2011; Goldstein 2013; Milam 2013). These studies should be augmented with inventories of other taxa to establish baseline conditions for evaluating biotic change over time. In particular, an inventory of the complete flora of Montague Plain is recommended, as

numerous plant species observed at MP WMA are not represented in the network of permanent plots. Documentation of the flora will provide critical data for assessing response to management efforts and changing conditions over time. Comparable inventories should be repeated at approximately 10-year intervals to assess biotic change.

(6) *Monitoring of Rare Species*. Specific monitoring protocols should be developed to assess management effects on populations of rare and uncommon plant and animal species, as well as host-plant species for rare or uncommon insects that are not well-represented in the network of permanent plots. Target species for host-plant studies include *Ceanothus americanus* and *Lupinus perennis* (Goldstein 2013). For species that have been the focus of populations studies in recent years (e.g., whip-poor-will, prairie warbler, hognose snake, etc.; King et al. 2016), monitoring and periodic re-assessment of population status and responses to management are recommended. Population studies of the responses of rare moths to management treatments would be particularly valuable.

(7) *Designation of Untreated Reserves*. A system of representative areas within MP WMA should be designated as small reserves that will not be actively managed, and will serve as long-term 'controls' for evaluating management effects. Such small reserves should include representative examples of characteristic vegetation types and historical land-use patterns, increasing habitat diversity at MP WMA and facilitating long-term studies of vegetation response to past land-use and active management. In time, such reserves will also provide insight into the structure and dynamics of older forests that, though rare today, were likely more common historically on sand plains in the Connecticut Valley (Motzkin et al. 1999).

(8) *Plan for Long-term Management*. The ecological and conservation value of management efforts at Montague Plain will ultimately depend on the extent to which MA DFW is successful in implementing long-term management, including maintenance of treated areas. Because harvesting often creates favorable conditions for pitch pine to become established, long-term commitment to follow-up mowing or other treatments is needed to prevent the re-establishment of dense stands that could once again reduce habitat value for uncommon barrens species and increase wildfire hazard. After harvesting, regular mowing represents a practical approach to maintain extensive areas of early-successional habitats with diminished wildfire hazard, along with prescribed fire when possible.

Conclusions

Montague Plain has long been recognized as a high conservation priority due to its uncommon natural communities, numerous rare species, and underlying, high-quality aquifer. Approximately half of Montague Plain was developed in the 20th century for residential, commercial and industrial uses (Motzkin et al. 1999), and numerous proposals over the past 50 years have promoted intensive industrial development of remaining areas. Several hundred acres abutting MP WMA remain unprotected and threatened by industrial development. If such development were to occur, it would not only eliminate important rare species habitats and uncommon communities in the developed area, but would also likely alter the dynamics and viability of rare species populations within MP WMA. Thus, long-term protection of undeveloped portions of Montague Plain remains a critical conservation priority.

The establishment of the Montague Plains Wildlife Management Area in 2000 represents an important milestone in efforts to conserve this ecologically significant site. In order to conserve uncommon pitch pine-scrub oak communities and numerous rare species while reducing the risk that wildfires may cause damage to human life and property, MA DFW initiated an ambitious program of fuels reduction and habitat management across most of MP WMA. Several studies have confirmed that such an approach has increased habitats for numerous rare and regionally uncommon early-successional species. The long-term success of such management efforts will ultimately depend on the degree to which MA DFW maintains the actively managed areas in the coming decades with mowing, prescribed fire, or other treatments. A strong commitment to long-term monitoring is also needed to facilitate periodic re-assessment of management objectives and approaches at MP WMA. Such a commitment will benefit from increased coordination and integration of research and management efforts at MP WMA.

The vegetation of Montague Plain has been highly dynamic over the past century in response to widespread abandonment of agricultural land, occasional wildfires, storms, and more recent management activity. Approximately 80% of undeveloped portions of Montague Plain was cleared and plowed for historical agriculture, and then allowed to re-forest naturally following abandonment of agricultural land in the late 19th and early 20th centuries. Since 2000, much of MP-WMA has been actively managed, including substantial reduction in canopy cover and basal area on > 850 acres that have been harvested. Both actively managed and untreated areas have changed substantially over the past few decades, and current vegetation patterns result from species-specific responses to complex patterns of historical agriculture and more recent management activity.

The vegetation of MP WMA is likely to continue to be highly dynamic in the future in response to ongoing management, other disturbances, and changing environmental conditions. Montague Plain thus provides an unusual opportunity to document biotic response to varied disturbance history and changing environmental conditions, and to incorporate such an understanding into long-term management efforts to conserve the remarkable natural communities, rare species and other ecological resources of this dynamic landscape.

Literature Cited

Akresh, M. E. 2012. Prairie warbler nest-site selection, nest survival, and demographic response to management in a pitch pine-scrub oak barren. MS Thesis, Univ. of Massachusetts, Amherst.

Akresh, M. E., and D. I. King. 2015. Eastern whip-poor-will breeding ecology in relation to habitat management in a pitch pine–scrub oak barren. Wildlife Society Bulletin DOI: 10.1002/wsb.621

Akresh, M. E., D. I. King, and R. T. Brooks. 2015. Demographic response of a shrubland bird to habitat creation, succession, and disturbance in a dynamic landscape. Forest Ecology and Management 336: 72-80.

Bried, J. T., W. A. Patterson III, and N. A. Gifford. 2014. Why pine barrens restoration should favor barrens over pine. Restoration Ecology 22: 442-446.

Clark, K. H. and W. A. Patterson III. 2003. Fire management plan for Montague Plain Wildlife Management Area. University of Massachusetts, Amherst, MA.

Compton, J. E., R. D. Boone, G. Motzkin, and D. R. Foster. 1998. Soil carbon and nitrogen in a pine-oak sand plain in central Massachusetts: role of vegetation and land-use history. Oecologia 116: 536-542.

Donohue, K., D. R. Foster, and G. Motzkin. 2000. Effects of past and present on species distribution: land-use history and demography of wintergreen. Journal of Ecology 88: 303-316.

Duveneck, M. J. 2005. Characterizing canopy fuels as they affect fire behavior in pitch pine (*Pinus rigida*) P. Mill. MS Thesis, Dept. of Natural Resources Conservation, Univ. of Mass., Amherst.

Duveneck, M. J. and W. A. Patterson III. 2007. Characterizing canopy fuels to predict fire behavior in pitch pine stands. Northern Journal of Applied Forestry 24: 65-70.

Erb, L. and M. T. Jones. 2011. Can turtle mortality be reduced in managed fields? Northeastern Naturalist 18: 489-496.

Fuller, J. L., D. R. Foster, J. S. McLachlan, and N. Drake. 1998. Impact of human activity on regional forest composition and dynamics in central New England. Ecosystems 1: 76-95.

Goldstein, P. Z. 2013. Lepidoptera sampling at Montague Wildlife Management Area – 2013. Final report to MA Natural Heritage and Endangered Species Program, Westborough, MA.

Haines, A. 2011. *Flora Novae Angliae*. Yale University Press, New Haven, CT.

Harvard Forest Archives 1993-28. Montague Plain Study 1993: Historical Maps, Plot Locations, Species Maps. Harvard Forest, Petersham, MA.

King, D. I., S. Schlossberg, R. T. Brooks, and M. E. Akresh. 2011. Effects of fuel reduction on birds in pitch pine–scrub oak barrens of the United States. For. Ecol. and Management 261: 10-18.

King, D. I., J. C. Milam, and M. E. Akresh. 2016. Fauna and fire at the Montague Plains Wildlife Management Area. Webinar presentation for the North Atlantic Fire Science Exchange, May 19, 2016. http://www.firesciencenorthatlantic.org/events-webinars-source/

Lavelle, N. 1998. Effects of 1996-1997 winter storms on pine and mixed hardwoods on the Montague Sand Plain in central Massachusetts. BA thesis, Mt. Holyoke College, South Hadley, MA. Harvard Forest Archives HF 1998-09.

Lindwall, B. and R. Lombardi. 2002. The Montague Plains Wildlife Management Area – a botanical survey of power line rights-of-way. Report to MA Natural Heritage and Endangered Species Program, Westborough, MA.

McCune, B. and J. B. Grace. 2002. *Analysis of Ecological Communities*. MjM Software Design, Gleneden Beach, Oregon.

McCune, B. and M. J. Mefford. 2006. *PC-ORD. Multivariate Analysis of Ecological Data. Version 5*. MjM Software, Gleneden Beach, OR.

Mello, M. J. 2000. Inventory for state-listed Lepidoptera and *Cicindela* at Montague Plain Barrens in and adjacent to Montague State Wildlife Management Area. Report to MA Division of Fisheries and Wildlife, Westborough, MA.

Milam, J. 2013. Effects of fuel reduction and habitat restoration on native bee communities in Massachusetts pitch pine–scrub oak barrens. Unpublished data.

Motzkin, G. 2001. Montague Plain: a resource manual of historical and ecological information gathered by Harvard Forest. Ecological Restoration Program, MA Biodiversity Initiative, Massachusetts Natural Heritage and Endangered Species Program, Westborough, MA.

Motzkin, G., D. Foster, A. Allen, J. Harrod, and R. Boone. 1996. Controlling site to evaluate history: vegetation patterns of a New England sand plain. Ecological Monographs 66: 345-365.

Motzkin, G., S. C. Ciccarello and D. R. Foster. 2002. Frost pockets on a level sand plain: Does variation in microclimate help maintain persistent vegetation patterns? Journal of the Torrey Botanical Society 129: 154-163.

Motzkin, G., W. A. Patterson III, and D. R. Foster. 1999. A historical perspective on pitch pine-scrub oak communities in the Connecticut Valley of Massachusetts. Ecosystems 2: 255-273.

Patterson, W. A. III, K. E. Saunders, and L. J. Horton. 1983. *Fire Regimes of Cape Cod National Seashore*. U.S. Department of Interior, National Park Service, North Atlantic Region, Office of Scientific Studies, OSS 83-1.

Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution 43: 223-225.

Wagner, D. L., M. W. Nelson, and D. F. Schweitzer. 2003. Shrubland Lepidoptera of southern New England and southeastern New York: ecology, conservation, and management. Forest Ecology and Management 185: 95–112.

Willey, L. 2010. *Spatial Ecology of Eastern Box Turtles (*Terrapene carolina carolina*) in Central Massachusetts*. PhD Dissertation. University of Massachusetts, Amherst.

Appendix 1. Permanent plots sampled in 2015-2016 in MP WMA. 'Unharvested' plots had not been harvested or mowed at the time of sampling. 'Recent' plots were harvested and mowed in 2014-2016. 'Older' plots were harvested and mowed in 2004-2009, and re-mowed in 2014-2016. 'Burn' plots were treated with prescribe fire, mowing, and cutting, beginning in 2000.

Plot	Plowed	Sampled	Management	Notes
1	Y	2016	Unharvested	
2	Y	2016	Unharvested	
3	Y	2016	Unharvested	
4	Y	2016	Recent	
5	Y	2015	Older	
6	Y	2015	Recent	
7	Y	2015	Recent	
12	Y	2016	Older	
13	Y	2015	Recent	harvested but not mowed in 2014
15	N	2015	Recent	
16	Y	2015	Unharvested	
17	N	2015	Recent	
18	N	2016	Unharvested	
22	N	2016	Burn	
30	N	2016	Exclude	included in some ordinations
31	Y	2016	Recent	
32	Y	2016	Recent	
33	N	2015	Unharvested	
35	Y	2015	Unharvested	
37	N	2015	Unharvested	
38	Y	2015	Unharvested	
39	Y	2015	Unharvested	
40	N	2016	Burn	
42	Y	2016	Exclude	included in some ordinations
43	N	2016	Burn	
44	N	2016	Burn	
45	Y	2016	Recent	
58	Y	2015	Recent	
61	Y	2016	Older	
62	Y	2015	Older	
69	Y	2016	Unharvested	
70	Y	2016	Unharvested	
71	Y	2016	Unharvested	
72	Y	2015	Older	
73	Y	2015	Recent	
78	Y	2016	Recent	
80	N	2015	Recent	
81	Y	2016	Unharvested	
82	Y	2016	Unharvested	
83	N	2016	Recent	
84	Y	2015	Unharvested	
85	Y	2015	Unharvested	
87	Y	2016	Unharvested	
88	Y	2016	Unharvested	
89	Y	2016	Recent	
91	N	2016	Unharvested	
92	Y	2016	Older	
93	Y	2016	Older	also burned in 2008
104	Y	2016	Recent	
105	N	2016	Recent	
106	Y	2016	Recent	
107	Y	2016	Recent	
108	Y	2016	Older	
109	Y	2015	Unharvested	
110	Y	2015	Recent	
111	Y	2015	Recent	
115	Y	2015	Unharvested	
117	Y	2016	Recent	
119	Y	2015	Older	
120	Y	2015	Recent	

Appendix 2. Photos of harvesting operations at MP WMA, 2015-2016. Top and middle photos: harvesting equipment, and processing and landing areas, on Old Northfield Rd., April 2016. Open stands of pitch pines (middle right) and oaks (bottom left) had dramatically increased sight-lines soon after harvest and mowing treatments. Bottom right photo shows the view east up the delta slope from the intersection of Turners Falls Rd. (visible in photo) and Hatchery Rd., May 2016.