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Helonias bullata (Swamp Pink) Habitat Characteristics under Different Landscape Settings at Fort A.P. Hill, Virginia

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Abstract - *Helonias bullata* (Swamp Pink) is a federally threatened plant found in many of the wetlands throughout US Army Garrison, Fort A.P. Hill, VA. Wetlands that support Swamp Pink are exposed to periodic occurrences of wildland fire. However, much is not yet known about the relationship between this species and wildland fire. This study examines plant-level characteristics (i.e., number of leaves, rosette size) in relation to habitat-level characteristics through comparison of Swamp Pink under 2 land-management regimes in different military training zones. We evaluated the forest compositional differences based on the presence/absence of wildland fire and military-training zone in wetlands supporting Swamp Pink and in adjacent uplands using non-metric multidimensional scaling (NMS), multi-response permutation procedures (MRPP), indicator-species analysis (ISA), and measures of density, dominance, herbaceous cover, and species richness. Swamp Pink rosettes in wetlands exposed to fire were significantly larger and averaged nearly 1 more leaf per rosette as compared to those surveyed in wetlands that were not exposed to fire. There was significantly less upland tree density in burned sites compared to unburned sites. We found no relationship between training zones and Swamp Pink size and the number of leaves. Additional differences in forest composition were revealed by comparing training zone and the presence/absence of wildland fire in conjunction with one another. Compared to other areas, the training zones with lower fire-frequency and recent evidence of fire featured significantly larger rosettes with more leaves. In uplands, overall community composition was significantly different among plots exposed to different fire-management strategies (MRPP; $P < 0.05$), but no such differences occurred in wetlands ($P > 0.05$). This finding suggests that wetlands limit the effects of fire on community composition. ISA showed that in both wetlands and uplands, different species characterized areas with differing fire influence, suggesting some influence by wildland fire even when such effects were not reflected in overall changes to community composition. The results of this study, the life-history of Swamp Pink, and the distribution of the species in ecosystems characterized by fire (e.g., the New Jersey Pine Barrens) suggest that Swamp Pink is not negatively impacted by fire to a significant degree. The conservation of the Swamp Pink habitat at Fort A.P. Hill may in fact benefit from periodic occurrences of wildland fire. Further research is warranted.

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Introduction

Helonias bullata L. (Swamp Pink) is a rare wetland plant found at US Army Garrison, Fort A.P. Hill, VA, and is one of only 2 monotypic genera representative of the Heloniadaceae family in North America as defined by Weakley et al. (2012). Other taxonomic authorities place Swamp Pink as the sole North American representative of the Heloniadeae tribe within a more widely circumscribed Melanthiaceae family (Stevens 2001, Fuse and Tamura 2000, Kim et al. 2016, Tamura 2016). As such, this species is the most primitive member of the Heloniadeae; its closest taxonomic relatives are native to East Asia (Fuse and Tamura 2016; Kim et al. 2016; Tanaka 1997a, 1997b, 1997c, 1997d, 1997e, 1998; Utech 1978). Low genetic diversity, weak sexual reproductive success, sensitivity to nitrogen, and degradation of wetland habitat have resulted in the listing of Swamp Pink as a federally listed threatened species (Godt et al. 1995, Hernàndez et al. 2016, Laidig et al. 2009, Murdock 1994, Perullo et al. 2015, Punsalan et al. 2016, Sutter 1984, USFWS 1988). Swamp Pink is a Virginia state-listed threatened species with an S2S3 state ranking and a G3 global ranking (NatureServe 2014, Townsend 2016). The geographic range of Swamp Pink encompasses an area from coastal New Jersey and Virginia to the mountains of Virginia, North Carolina, South Carolina, and Georgia (Fig. 1). The availability of suitable habitat appears to be a primary limiting factor for many Swamp Pink populations (Sutter 1984). In its range, Swamp Pink is found in forested wetlands, often rooted in *Sphagnum* (peat moss) hummocks in acidic sandy swamps, bogs, seeps, drainages, and small, meandering streamsides that do not receive prolonged periods of inundation (Godt et al. 1995, Murdock 1994, Weakley et al. 2012).

The US Vegetation Classification (USNVC) community type associated with Swamp Pink at Fort A.P. Hill is best characterized as CEGL006238 *Acer rubrum* (Red Maple)–*Nyssa sylvatica* Marsh. (Black Tupelo)–*Magnolia virginiana* (Sweetbay Magnolia)/*Viburnum nudum* var. *nudum* (Wild Raisin)/ *Osmundastrum cinnamomeum* (L.) C. Presl (Cinnamon Fern)-*Woodwardia areolata* (L.) T. Moore (Netted Chain Fern) Swamp Forest, or equivalently as Coastal Plain/Piedmont Acidic Seepage Swamp (Fleming 2007, Floyd et al. 2015, Hazler and Taverna 2012, Josey et al. 2015).

The comparatively high wildland-fire frequency on military lands, including Fort A.P. Hill, relative to surrounding areas, maintains some of the best examples of non-alluvial wetland seepage communities in the southeastern coastal plain (Fleming 2012, Fleming et al. 2013, Harper et al. 1998, Weakley et al. 2012). Acidic seepage-swamp forest and acidic seepage-bog shrubland—CEGL006499 *Alnus serrulata* (Aiton) Willd. (Smooth Alder)–Sweetbay Magnolia/*Eupatorium pilosum* Walter (Rough Boneset)–*Rhynchospora gracilenta* A. Gray (Slender Beaksedge)-*Xyris torta* Sm. (Twisted Yellow-eyed-Grass) Shrubland—wetland community types are often found intermixed with one another at Fort A.P. Hill (Fleming 2012, Hazler and Taverna 2012, USNVC 2016). Acidic wetlands are composed of intermittent bog habitat where tree cover is more open. Seepage bog habitat is heavily dependent upon fire or mechanical clearing of woody overgrowth that mimics the effects of fire (Fleming 2012). This ecological community has been nearly extirpated from Virginia due to fire suppression, habitat alterations, and destruction (Fleming 2012). Fort A.P. Hill is a regional stronghold for Swamp Pink as well as for rare acidic seepage-bog species such as *Juncus caesarienesis* Coville (New Jersey Rush), a state-listed threatened species in Virginia (VA S2; Josey et al. 2015, Townsend 2016, VanAlstine et al. 2010).

Over half of known Swamp Pink populations range-wide are in New Jersey where the geographic distribution of the species overlaps considerably with the Pine Barrens, an ecosystem known for its dependence on wildland fire (Boyd 1991, PPA 2015). Despite this landscape history of wildland fire in the Pine Barrens, the relationship between Swamp Pink and wildland fire is largely undocumented to date.

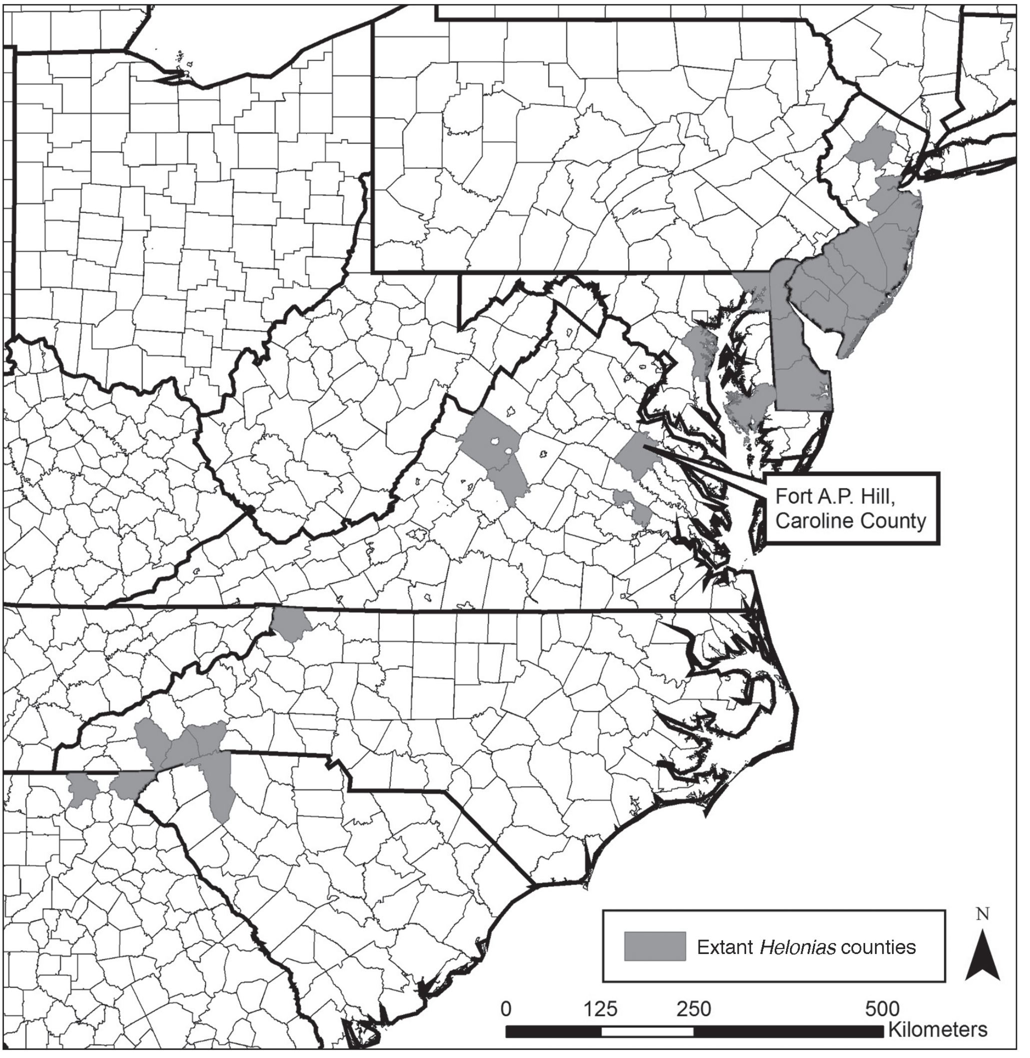

Figure 1. US counties with extant occurrences of Swamp Pink across 7 states: Delaware, Georgia, Maryland, New Jersey, North Carolina, South Carolina, and Virginia (ESRI 2017a, b; USFWS-New Jersey Field Office 2014).

Due to the prevalence of wildland fire on Fort A.P. Hill and the federal statuary requirements associated with the conservation of a federally listed species on federal lands, an understanding of how wildland fire could impact Swamp Pink is warranted.

To begin to understand the dynamic between this species and wildland fire, we compared rosette size and the number of leaves between rosettes growing in wetlands exposed to recent fire (within 2 y) with rosettes growing in wetlands with no evidence of recent fire. We selected these indicators because larger Swamp Pink rosettes are more likely to flower, produce more flowers and seeds, and have a lower risk of mortality than smaller rosettes (Godt et al. 1995, Peterson 1992). Rosette size has also been shown to be an indicator of health in *Chamaelirium luteum* (L.) Gray (Devil's-bit), the only other North American member of the Heloniadaceae family (Dodds 1996, Meagher and Antonovics 1982, Weakley et al. 2012). Evidence of recent fire in wetlands did not necessarily include any evidence that Swamp Pink individuals were burned, but rather that the surrounding habitat was burned based on burn scars on trees and blackened vegetation. It is unknown how often fires in wetlands directly burned Swamp Pink plants. The plants are frequently surrounded by shallow water and water-saturated peat mosses that interrupt the movement of wildland fires. We also compared the same Swamp Pink plants by grouping them by the military training zone in which each plant was growing—each zone having comparatively different fire frequencies. The effects of fire on Swamp Pink may be secondary or tertiary effects; thus we felt it was important to also characterize the forest compositional differences between Swamp Pink wetlands at Fort A.P. Hill based on the presence/absence of recent fire and military training zone. We also assessed the upland habitats adjacent to each Swamp Pink wetland because wetland communities are influenced by habitat characteristics in adjacent uplands (e.g., the amount of peripheral light penetration).

Field-site Description

US Army Garrison, Fort A.P. Hill occupies 30,673 ha within Caroline (99.8%) and Essex (0.2%) Counties, VA. Fort A.P. Hill is composed of 2 major training zones: the maneuver training areas (MTAs) and the live-fire range complex (RC). The MTAs are used primarily for maneuver and other non-live–fire training exercises. The RC supports a wide spectrum of live-fire operations and is characterized by a much higher fire frequency. Prescribed fires are conducted annually in the RC to reduce fuel accumulation, which increases the effectiveness of established firebreaks and preemptively diminishes the strength of potential wildfire in areas that are likely to ignite during live-fire military training. To meet individual site objectives (e.g., oak regeneration, vegetation control, etc.), areas within the MTAs are burned as needed in one-time events or on a less frequent recurring interval compared to the RCs (Fort A.P. Hill 2015).

Acidic seepage-swamps harboring Swamp Pink are found frequently across Fort A.P. Hill's landscape in the RCs and MTAs (VanAlstine et al. 2010). The installation's wildland fire-management program neither purposefully ignites fires within nor excludes fire from wetlands on the installation, and as a result, low-intensity wildland fires occasionally burn through these wetlands and frequently burn adjacent uplands. Weather permitting, the Fort A.P. Hill Forestry Branch conducts prescribed fires annually from 15 October to 15 April. Ignition typically begins along established roadways or permanent firebreaks, and fire is allowed to burn until the flaming front reaches another firebreak, body of water, or burns out (Fort A.P. Hill 2015). Prescribed fires are not conducted during drought conditions or periods with elevated fire danger, and most occurrences of wildland fire, deliberate or otherwise, are typically low- to moderate-intensity burns due to the prevalence of firebreaks (natural and human-made) and the low fuel accumulation maintained through recurring prescribed fire operations (Fort A.P. Hill 2015).

Methods

Field procedures

We established a total of 36 wetland plots within 29 wetlands where Swamp Pink plants were present; we placed >1 wetland plot in large Swamp Pink wetlands. We also established 69 plots in the uplands adjacent to the Swamp Pink wetlands: 34 along upland mid-slopes and 35 at the hill-top crest above wetlands to account for differences in slope and to create a transect along a topographic gradient (Table 1). We varied the distance between plots depending on topography. We established the mid-slope plot approximately half-way between the wetland plot at the bottom of each hill and the hill-top crest plot at the top. Two of the 36 transects did not include mid-slope plots in order to prevent plot overlap due to an abrupt transition from wetland to hill-top crest. In another case, 2 wetland plots and corresponding mid-slope plots shared a single corresponding hill-top crest plot. To reduce sampling bias in the field, we employed GIS spatial data to pre-determine plot locations and used handheld global navigation satellite system (GNSS) units to navigate to each plot position. We conducted surveys May through September 2014.

We characterized each plot by the presence or absence of fire within the past 2 y; plots with visual evidence of fire (e.g., burn scars, blackened soil, etc.) were characterized as burned. If fire evidence was not present, we characterized the plot as not-burned. We reviewed Fort A.P. Hill Forestry Branch fire records to confirm each characterization. We also noted the location of each plot as within either the MTAs (64 plots) or RC (41 plots)—a designation made to provide a coarse reflection of the long-term fire frequency within the area. It is important to note that although prescribed fires are conducted in the RC annually, this does not necessarily mean

Table 1. Number of plots for each topographic input-factor

	Fire evidence		Training use		
Topographic position	Burned	Unburned	RC	MTA	Total
Crest	21	14	22	13	35
Midslope	22	12	20	14	34
Wetland	13	23	22	14	36
Total	56	49	64	41	105

that the Swamp Pink wetlands and adjacent uplands have recently burned. Fire on Fort A.P. Hill often burns in a mosaic pattern of burned and unburned patches and does not always make contact with the Swamp Pink habitat.

The distribution of Swamp Pink within its habitat is typically non-uniform, so for the sake of practicality and consistency, we collected Swamp Pink rosette data from the first 20 rosettes found closest to the plot center of each wetland plot. We recorded a leaf count for each rosette and 2 measurements of rosette width; width measurements were made roughly perpendicular to each other across the rosettes and used to estimate rosette area using the formula: Area = π (average width/2)^2.

For the purpose of collecting habitat data, each plot consisted of one 0.02-ha circular plot for the collection of tree-stratum species data, a nested 0.0004-ha circular subplot for the collection of shrub-stratum species data, and a nested 1-m^2 rectangular subplot for the collection of herb-stratum species data (Fig. 2). We defined woody plants as having a diameter at breast height (DBH) of at least 5 cm to qualify as a tree-stratum species; species identification and DBH were recorded for each qualifying tree. Shrub-stratum species were woody but did not reach breast height

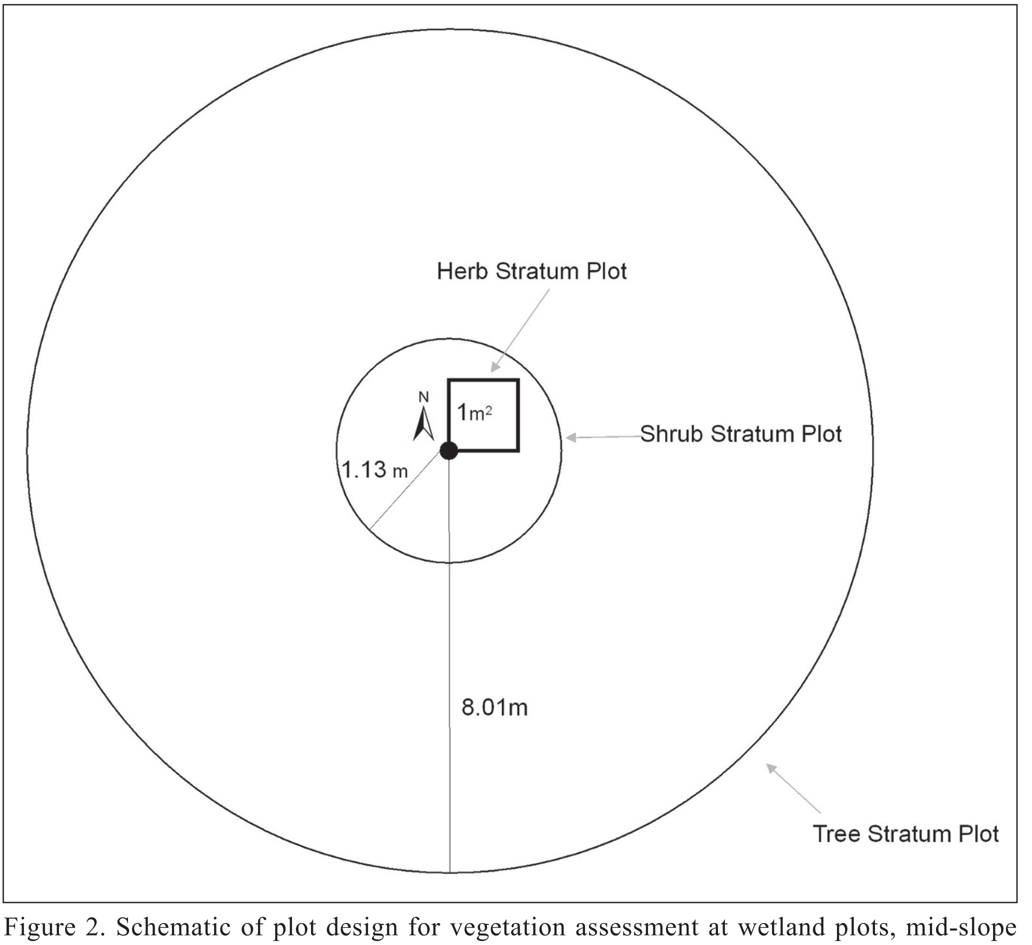

Figure 2. Schematic of plot design for vegetation assessment at wetland plots, mid-slope plots, and hill-top crest plots. Not drawn to scale.

or had a DBH less than 5 cm; we recorded the number of stems present for each shrub species. Herb-stratum species included all non-woody species and woody seedlings; a cover-class value (1–10) was assigned to each species surveyed in the herb stratum in accordance with protocols developed by Peet et al. (1998). We identified vascular plants to species when possible; nomenclature followed Weakley et al. (2012).

Data analysis

We compared Swamp Pink rosette data (number leaves/rosette and rosette area) between burned vs. unburned and RC vs. MTAs plots. We took 2 broad approaches to characterize the habitat differences between wetlands and uplands influenced by fire and training zone: (1) the "irrespective of species" approach focused on the absolute density (stems/plot), dominance (tree basal area/plot and cover class/plot), and species richness (number unique species/plot) in each stratum. This "irrespective of species" analysis intentionally did not differentiate between species within each stratum in favor of looking at the general forest structure (e.g., 1000-cm^2 tree dominance might include measurements from Black Tupelo, Loblolly Pine, and other wetland species). We calculated tree basal area (BA) using the following formula: $BA = \pi(DBH/2)^2$. (2) The "species specific" approach included species composition when comparing different wetland and upland communities using non-metric multidimensional scaling (NMS), multi-response permutation procedures (MRPP), and indicator species analysis (ISA). We conducted NMS, MRPP and ISA using PC-ORD, version 5.10 (McCune and Mefford 2006).

An initial NMS ordination showed strong separation between the species compositions of sites a priori categorized as either upland or wetland based on professional judgment (Fig. 3), indicating that water was a dominant factor in shaping overall community composition. Therefore, we conducted NMS, MRPP, and ISA analyses separately for wetlands and uplands.

We conducted a 2-sample F-test for equal or unequal variances for Swamp Pink rosette area, number of leaves, dominance, density, and species richness. Depending on the F-test results, we performed an unpaired 2-sample t-test assuming either equal or unequal variances. We further categorized the data by the presence/absence of fire and training zone to create 4 different groupings: data collected from plots that were (1) burned within the RC, (2) burned within the MTAs, (3) unburned within RC, and (4) unburned within the MTAs. We performed a single-factor ANOVA to determine significance among groupings. We set a 95% confidence level and an α value of 0.05 for all analyses. If statistically significant values were obtained, we conducted post-hoc t-tests to determine which means were the sources of the resulting differences. We employed a Bonferroni correction to reduce Type I error, decreasing the threshold of significance to 0.0083 during post-hoc t-tests. We conducted statistical analyses in Microsoft Excel 2007.

For species-composition analyses (NMS, MRPP and ISA), we summarized by species vegetation in each stratum. We used relative density and relative basal area to calculate relative importance values for tree species. We calculated density for each shrub-stratum species, and relative cover for each sapling and seedling species. We treated woody species in separate strata as separate species (Carter and Floyd 2013). For the purpose of NMS and MRPP analyses, in both the upland and wetland categories, we assigned plots to one of 3 burn-management classes based on the influence of fire within these areas: (1) low-impact = unburned (i.e., no fire evidence within 2 y) MTAs, (2) intermediate = unburned RC and burned (i.e., fire evidence within 2 y) MTAs, and (3) high-impact = burned RC areas. We based our decision to combine the unburned RC areas and burned MTAs on the small sample size of unburned RC areas, especially in upland plots ($n = 2$), which in itself is a reflection of the high fire-frequency within the RC. We employed NMS ordination to visually evaluate whether community composition differed among the 3 burn-management categories. We used the default parameter-settings of the Slow and Thorough mode in the ordination and employed Varimax rotation to maximize the loadings of among-sample distances along the ordination axes. We conducted MRPPs to determine if differences among burn-management classes were significantly different than expected by chance. The chance-corrected within-group agreement (*A*-value) produced by MRPP describes the effect strength of the groupings in a similar manner to that in which *r*-values describe the strengths of a correlation. *A*-values of 0.30 or greater indicate relatively strong groupings among samples (McCune and Grace 2002). To determine where specific between-class differences occurred, we performed pairwise MRPP analyses with Bonferroni corrections for multiple

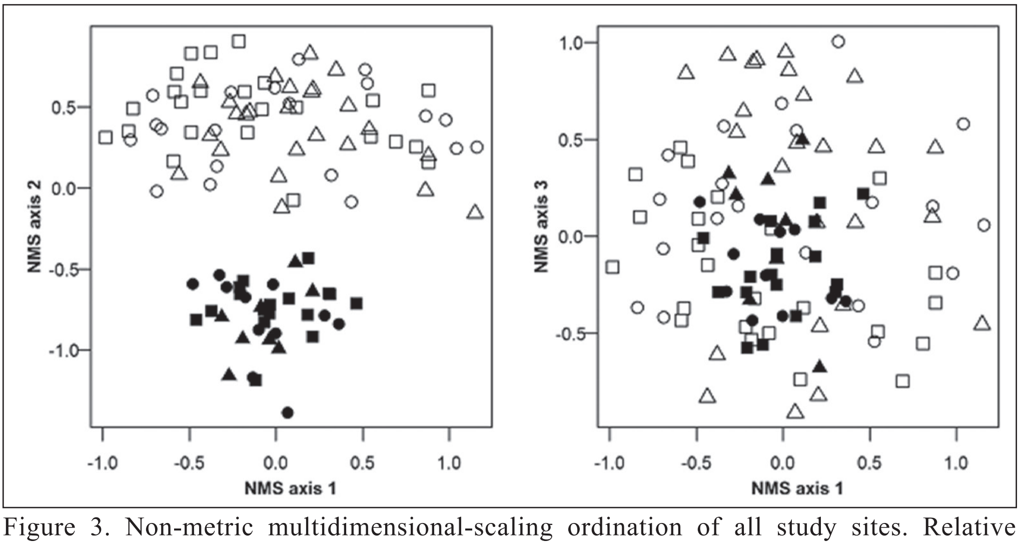

Figure 3. Non-metric multidimensional-scaling ordination of all study sites. Relative density and relative basal area were used to calculate relative importance values for tree species. Relative density was calculated for each shrub-stratum species, and relative cover was calculated for each sapling and seedling species. A strong separation occurred among wetland and upland sites along axis 2 of the ordination. Final stress = 20.3. Open Triangles (∆) = upland, high-impact sites (burned RC plots), open circles (○) = upland, intermediate sites (burned MTA and unburned RC plots), open squares (□) = upland, low-impact sites (unburned MTA plots). Closed Triangles (▲) = wetland, high-impact sites, closed circles (●) = wetland, intermediate sites, and closed squares (■) = wetland, low-impact sites.

comparisons. We conducted both the NMS and MRPP analyses using Sorenson dissimilarities among study sites based on tree relative-importance values, shrub relative-density, and herb relative-cover values.

We conducted ISA using the method of Dufrene and Legendre (1997) in order to determine which plant taxa were most indicative of the different burn-management classes. ISA involves the calculation of an overall indicator value (IV) for each taxon within each class. IV is the product of the relative abundance (RA) and the relative frequency (RF) of a taxon within a given class. RF within a class is the number of sites within that class at which the taxon occurred as a proportion of the total number of sites within the class. RA within a given class is a measure of a taxon's abundance within that class, relative to its abundance across all classes. The relative abundance of taxon 1 within class 1 (RA_{t1c1}) is calculated with the formula:

$$RA_{t1c1} = ra_{t1c1} / \sum_{i=1}^{i} \mathrm{ra}_{t1ci} \times 100,$$

where i is the total number of classes, ra_{t1c1} is the mean proportional abundance of taxon 1 in sites within class 1 and $\sum \mathrm{ra}_{t1ci}$ is the sum of the mean proportional abundances within each class. Final RA values are expressed as percentages. We evaluated the significance of each IV by conducting 999 random permutations of the dataset and taking the P-value as the proportion of the permutations that yielded an IV greater than or equal to the real data.

As was the case for the MRPP and NMS analysis, the abundance of each taxon at each plot was represented by the relative importance for tree species, relative density for shrub species, and relative cover for herb species (all varying on a scale from 0 to 100). A high IV indicates a high propensity of a taxon for a given class, relative to other classes. We conducted a permutation analysis to determine whether each indicator value was significantly higher than expected by chance (999 random permutations of the dataset with recalculation of IV's based on randomized data). Results of this analysis indicate whether each taxon is a significant indicator of a particular management class.

Results

Swamp Pink rosettes in burned wetlands were significantly larger ($P = 0.000$, df = 320, $t = 2.65$) and averaged nearly 1 more leaf per rosette ($P = 0.0085$, df = 563, $t = 4.24$) as compared to Swamp Pink surveyed in unburned wetlands (Table 2). There was significantly less ($P = 0.0408$, df = 37, $t = 2.12$) upland tree density in burned sites compared to unburned sites. All other upland and wetland measures of absolute density, dominance, and species richness were not significantly different between burned and unburned sites (Table 2).

No statistical difference existed between Swamp Pink surveyed in the RC vs. MTAs (Table 3). However, there were statistically fewer trees, less dominance, and lower tree-species richness within the RC wetlands when compared to the MTAs. There was also more upland herbaceous cover in the RC in comparison to the MTAs (Table 3).

The ANOVAs to determine if differences existed between wetland and upland sites that were burned within the RC, burned within the MTAs, unburned within the RC, and unburned in the MTAs identified significant differences between the number of leaves per rosette ($F_{3,561}$ = 5.05, P = 0.0018), rosette area ($F_{3, 561}$ = 11.83 P = <0.001), wetland tree density ($F_{3, 32}$ = 3.61, P = 0.0229), wetland tree dominance ($F_{3,32}$ = 3.64, P = 0.0229), wetland tree species richness ($F_{3,32}$ = 3.20, P = 0.0362), wetland shrub density ($F_{3,32}$ = 0.03, P = 0.0341), upland tree species richness ($F_{3,65}$ = 12.75, P = <0.001), and upland total herb cover ($F_{3,65}$ = 5.01, P= 0.0034) (Table 4).

Table 2. Summary statistics comparing Swamp Pink and associated habitat comparing burned and unburned sites, the asterisks (*) indicate a significant difference (α = 0.05).

	Burned (mean)	Unburned (mean)	t	df	P
Wetland tree density	22.92	27.39	-1.37	34	0.1789
Wetland tree dominance (cm^2)	7898.25	7849.35	0.03	16	0.9732
Wetland tree species richness	5.77	5.26	0.99	34	0.3301
Wetland shrub density	17.77	14.57	-1.26	34	0.2180
Wetland shrub species richness	3.54	3.48	0.13	34	0.9009
Wetland herb total cover	37.92	33.78	1.45	34	0.1564
Wetland herb species richness	8.92	8.17	0.86	34	0.3935
Upland tree density	13.95	19.23	2.12	37	0.0408*
Upland tree dominance (cm^2)	6536.97	6762.77	-0.35	67	0.7248
Upland tree species richness	5.07	5.73	-1.42	67	0.1591
Upland shrub density	25.67	19.42	1.25	67	0.2140
Upland shrub species richness	3.74	3.46	0.63	67	0.5310
Upland herb total cover	7.28	5.15	1.53	67	0.1314
Upland herb species richness	2.56	2.27	-0.80	67	0.4268
Swamp Pink leaves/rosette	8.13	7.29	2.65	563	0.0084*
Swamp Pink rosette area (cm^2)	388.20	292.50	4.24	320	<0.0001*

Table 3. Summary statistics comparing Swamp Pink and associated habitat comparing Range Complex (RC) and Maneuver Training Area (MTA) sites, the asterisks (*) indicate a significant difference (α = 0.05).

	RC (mean)	MTA (mean)	t	df	P
Wetland tree density	20.29	29.27	3.09	34	0.0040*
Wetland tree dominance (cm^2)	5883.40	9129.31	3.05	34	0.0044*
Wetland tree species richness	4.79	5.86	-2.25	34	0.0312*
Wetland shrub density	14.07	16.77	0.94	34	0.3531
Wetland shrub species richness	3.50	3.50	0.00	34	1.0000
Wetland herb total cover	37.64	33.77	1.37	34	0.1795
Wetland herb species richness	8.79	8.23	0.59	20	0.5608
Upland tree density	13.67	17.40	1.87	65	0.0656
Upland tree dominance (cm^2)	6218.63	6881.40	-0.95	67	0.3472
Upland tree species richness	5.00	5.52	-1.13	67	0.2624
Upland shrub density	27.30	20.76	1.32	67	0.1905
Upland shrub species richness	3.81	3.52	0.65	67	0.5159
Upland herb total cover	9.52	4.52	3.60	40	0.0009*
Upland herb species richness	2.81	2.21	1.70	67	0.0935
Swamp Pink leaves/rosette	7.91	7.40	1.62	563	0.1052
Swamp Pink rosette area (cm^2)	321.91	327.83	-0.28	563	0.7790

Post-hoc *t*-tests (Table 5) revealed the mean Swamp Pink rosette area was significantly larger in burned MTAs compared to burned RC sites (P = 0.0021, df = 194, t = -3.11), unburned RC sites (P = 0.0004, df = 162, t = 3.61), and unburned MTAs (P = <0.001, df = 125, t = 4.81). There were also significantly fewer leaves

Table 4. ANOVA results when testing between sites burned within the Range Complex (RC), burned within the Maneuver Training Areas (MTA), unburned within the RC, and unburned in the MTAs, the asterisks (*) indicates a significant difference (α = 0.05).

Variable	df	*F*	*P*
Wetland tree density	3, 32	3.61	0.0229*
Wetland tree dominance (cm^2)	3, 32	3.64	0.0229*
Wetland tree species richness	3, 32	3.20	0.0362*
Wetland shrub density	3, 32	0.03	0.0341*
Wetland shrub species richness	3, 32	2.55	0.0732
Wetland herb total cover	3, 32	1.19	0.3290
Wetland herb species richness	3, 32	1.66	0.1947
Upland tree density	3, 65	2.15	0.1023
Upland tree dominance (cm^2)	3, 65	0.31	0.8127
Upland tree species richness	3, 65	12.75	<0.0001*
Upland shrub density	3, 65	0.83	0.4808
Upland shrub species richness	3, 65	0.29	0.8359
Upland herb total cover	3, 65	5.01	0.0034*
Upland herb species richness	3, 65	0.95	0.4223
Swamp Pinkleaves/rosette	3, 561	5.05	0.0018*
Swamp Pink rosette area (cm^2)	3, 561	11.83	<0.0001*

Table 5. Post-hoc *t*-test results, the asterisks (*) indicate a significant difference (α = 0.0083 using a Bonferroni correction). RC = Range Complex, MTAs = Maneuver Training Areas. [Table continued on following page.]

	Burned w/in RC (mean)	Unburned w/in RC (mean)	*t*	df	*P*
Wetland Tree Density	18.00	23.33	-1.36	12	0.2004
Wetland Tree Dominance (cm^2)	6176.94	5487.05	0.44	12	0.6646
Wetland Tree Species Richness	5.13	4.33	0.99	11	0.3449
Wetland Shrub Density	19.25	7.17	4.52	12	0.0007*
Upland Tree Species Richness	4.92	13.50	-5.53	1	0.1139
Upland Herb Total Cover	9.48	10.00	-0.08	1	0.9462
Swamp Pink Leaves/Rosette	7.78	8.04	-0.53	201	0.5963
Swamp Pink Rosette Area (cm^2)	330.65	313.08	0.57	201	0.5665
	Burned w/in RC (mean)	Burned w/in MTAs (mean)	*t*	df	*P*
Wetland Tree Density	18.00	30.80	-2.32	7	0.0534
Wetland Tree Dominance (cm^2)	6176.94	10,650.25	-1.55	6	0.1710
Wetland Tree Species Richness	5.13	6.80	-1.67	7	0.1388
Wetland Shrub Density	19.25	15.40	1.16	8	0.2809
Upland Tree Species Richness	4.92	5.28	-0.61	41	0.5423
Upland Herb Total Cover	9.48	4.22	3.41	39	0.0015*
Swamp Pink Leaves/Rosette	7.78	8.51	-1.40	194	0.1627
Swamp Pink Rosette Area (cm^2)	330.65	450.65	-3.11	194	0.0021*

per rosette in unburned MTAs compared to burned MTAs (P = 0.0006, df = 171, t = 3.51) and unburned RC sites (P = 0.0077, df = 214, t = 2.69). Wetland shrub density was greater in the sites burned within the RC compared to unburned sites in the RC (P = 0.0007, df = 12, t = 4.52) and greater in unburned MTA sites compared to unburned RC sites (P = 0.0015, df = 21, t = -3.63). Upland herb cover was significantly greater in burned RC sites compared to burned MTAs (P = 0.0015, df = 39, t = 3.41) and unburned MTAs (P = 0.0059, df = 47, t = 2.88). Wetland tree

Table 5, continued

	Burned w/in RC (mean)	Unburned w/in MTAs (mean)	t	df	P
Wetland Tree Density	18.00	28.82	-2.95	15	0.0099
Wetland Tree Dominance (cm^2)	6176.94	8680.44	-2.30	23	0.0310
Wetland Tree Species Richness	5.13	5.59	-0.90	23	0.3764
Wetland Shrub Density	19.25	17.18	0.68	21	0.5050
Upland Tree Species Richness	4.92	5.71	-1.41	47	0.1662
Upland Herb Total Cover	9.48	4.92	2.88	47	0.0059*
Swap Pink Leaves/Rosette	7.78	7.00	1.81	184	0.0727
Swamp Pink Rosette Area (cm^2)	330.65	284.74	1.82	368	0.0699
	Unburned w/in RC (mean)	Burned w/in MTAs (mean)	t	df	P
Wetland tree density	23.33	30.80	1.53	9	0.1602
Wetland tree dominance (cm^2)	5487.05	10650.25	2.00	9	0.0771
Wetland tree species richness	4.33	6.80	2.39	9	0.0405
Wetland shrub density	7.17	15.40	2.81	9	0.0202
Upland tree species richness	13.50	5.28	-5.29	1	0.1189
Upland herb total cover	10.00	4.22	-0.95	1	0.5151
Swamp Pink leaves/rosette	8.04	8.51	0.99	193	0.3239
Swamp Pink rosette area (cm^2)	313.08	450.65	3.61	162	0.0004*
	Unburned w/in RC (mean)	Unburned w/in MTAs (mean)	t	df	P
Wetland tree density	23.33	28.82	-1.76	15	0.0982
Wetland tree dominance (cm^2)	5487.05	8680.44	-3.09	21	0.0056*
Wetland tree species richness	4.33	5.59	-2.23	21	0.0367
Wetland shrub density	7.17	17.18	-3.63	21	0.0015*
Upland tree species richness	13.50	5.71	5.48	24	<0.0001*
Upland herb total cover	10.00	4.92	1.49	24	0.1501
Swamp Pink leaves/rosette	8.04	7.00	2.69	214	0.0077*
Swamp Pink rosette area (cm^2)	313.08	284.74	1.15	183	0.2497
	Burned w/in MTAs (mean)	Unburned w/in MTAs (mean)	t	df	P
Wetland tree density	30.80	28.82	0.42	20	0.6795
Wetland tree dominance (cm^2)	10650.25	8680.44	0.73	4	0.5044
Wetland tree species richness	6.80	5.59	1.86	20	0.0782
Wetland shrub density	15.40	17.18	-0.50	11	0.6236
Upland tree species richness	5.28	5.71	-0.75	40	0.4560
Upland herb total cover	4.22	4.92	-0.56	40	0.5769
Swamp Pink leaves/rosette	8.51	7.00	3.51	171	0.0006*
Swamp Pink rosette area (cm^2)	450.65	284.74	4.81	125	<0.0001*

dominance was significantly greater in unburned MTAs compared to unburned RC sites (P = 0.0056, df = 21, t = -3.09). However, unburned RC sites averaged greater tree species richness compared to unburned MTAs (P = <0.0001, df = 24, t = 5.48) (Table 5).

The NMS ordination including all sites (Fig. 3) produced a 3-dimensional solution that explained 63% of the variation in the original Sorenson dissimilarity matrix (r^2 for correlation of original matrix with NMS axis 1 = 0.10, r^2 for axis 2 = 0.38, and r^2 for axis 3 = 0.15). There was not a clear separation among sites with respect to management class; however, a strong separation occurred among wetland and upland sites along axis 2 of the ordination (Fig. 3:left panel).

The ordination of wetland sites only (Fig. 4) produced a 3-dimensional solution that explained 80% of the variation in the original Sorenson dissimilarity matrix (r^2 for correlation of original matrix with NMS axis 1 = 0.20, r^2 for axis 2 = 0.30, and r^2 for axis 3 = 0.30). As with the ordination of all sites, we observed no clear separations among management classes in the ordination of wetland sites.

The ordination of upland sites only (Fig. 5) produced a 3-dimensional solution that explained 53% of the variation in the original Sorenson dissimilarity matrix (r^2 for correlation of original matrix with NMS axis 1 = 0.12, r^2 for axis 2 = 0.22, and r^2 for axis 3 = 0.19). A weak separation between low-impact and high-impact sites occurred along axis 3 of the ordination plot (note position of triangles and squares along axis 3, right panel of Fig. 5).

MRPP analysis showed overall significant differences among management classes for both upland (A = 0.02, P < 0.01) and wetland sites (A = 0.02, P = 0.04); however,

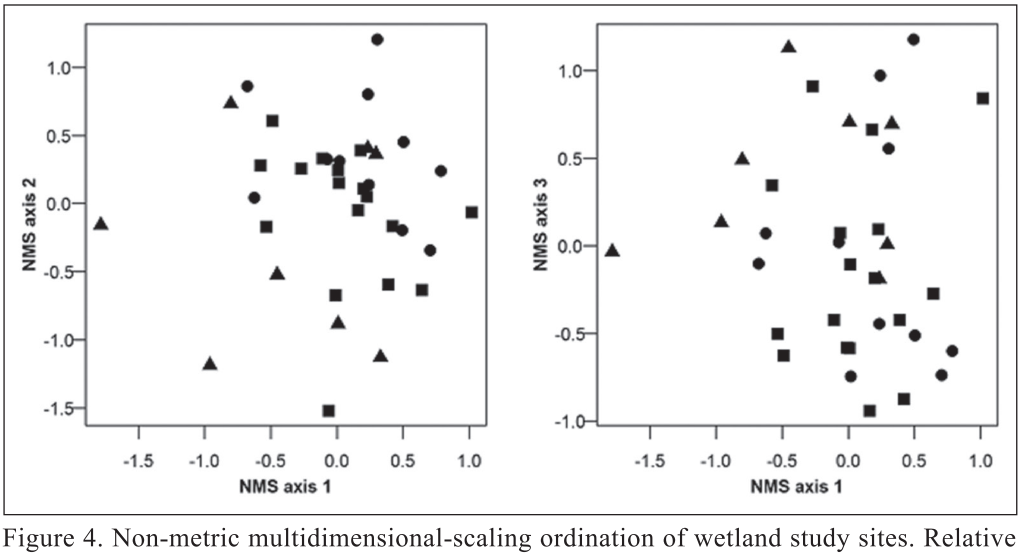

Figure 4. Non-metric multidimensional-scaling ordination of wetland study sites. Relative density was calculated for each shrub-stratum species, and relative cover was calculated for each sapling and seedling species. No clear separations among management classes were observed in the ordination of wetland sites. Final stress = 15.5. Closed Triangles (▲) = wetland, high-impact sites (burned RC plots), closed circles (●) = wetland, intermediate sites (burned MTA and unburned RC plots), and closed squares (■) = wetland, low-impact sites (unburned MTA plots).

pairwise comparisons showed no specific instances of significant differences among the classes for wetland sites ($P > 0.05$ for all 3 comparisons; Table 6). For upland sites, high-impact sites differed significantly from low-impact sites ($P < 0.01$) although the separation among the classes was relatively weak ($A = 0.03$; Table 6).

At upland sites, 4 species were significant indicators of high-impact burn management (occurring predominantly at high-impact sites, with indicator values

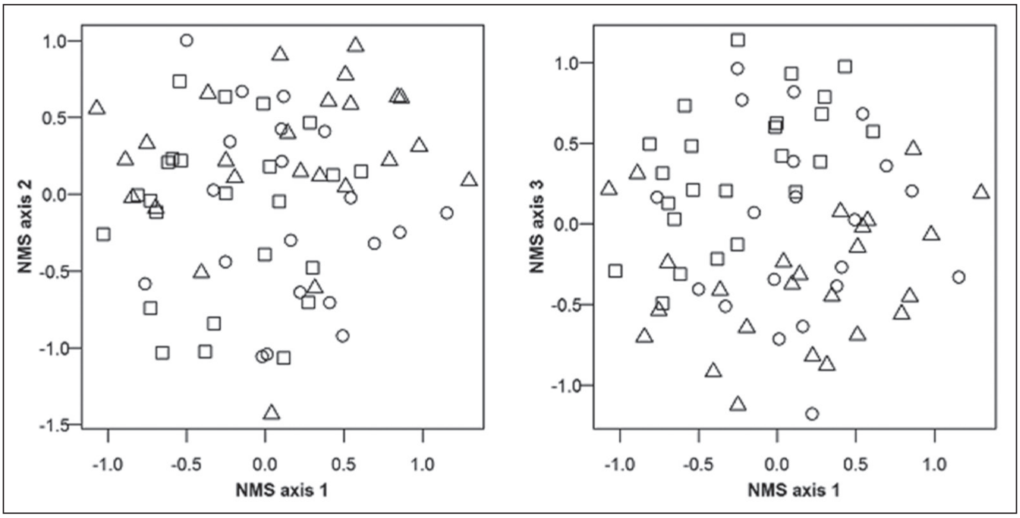

Figure 5. Non-metric multidimensional-scaling ordination of upland study sites. Relative density was calculated for each shrub-stratum species, and relative cover was calculated for each sapling and seedling species. No clear separations among management classes were observed in the ordination of wetland sites. A weak separation between low-impact and high-impact sites occurred along axis 3 of the ordination plot. Final stress = 21.9. Open triangles (Δ) = upland, high-impact sites (burned RC plots); open circles (○) = upland, intermediate sites (unburned RC and burned MTA plots); and open squares (□) = upland, low-impact sites (unburned MTA plots).

Table 6. Multi-response permutation results for comparisons among burn management classes. A = chance-corrected within-group agreement. P = probability of greater Sorenson dissimilarity within groups than expected by chance (permutation test with 999 random permutations, Bonferroni corrections applied for multiple comparisons). Management classes: low-impact = unburned (i.e. no fire evidence within 2 y) maneuver training areas, intermediate = unburned range complex and burned (i.e., fire evidence within 2 y) maneuver training areas, and high-impact: = burned range-complex. ns = not significant ($\alpha = 0.05$).

Management class comparison	*A*	*P*
Upland		
High-impact vs. low-impact	0.03	>0.01
High-impact vs. intermediate	0.01	ns
Intermediate vs. low-impact	0.01	ns
Wetland		
High-impact vs. low-impact	0.02	ns
High-impact vs. intermediate	0.02	ns
Intermediate vs. low-impact	0.00	ns

significant $P < 0.05$ based on permutation analysis). These were: *Quercus montana* (Chestnut Oak) tree, Chestnut Oak sapling, *Kalmia latifolia* (Mountain Laurel) sapling, and Loblolly Pine sapling. Four species were significant indicators of low-impact sites in the uplands: *Ilex opaca* var. *opaca* (American Holly) tree*,* American Holly sapling*, Quercus alba* (White Oak) tree, and *Smilax glauca* (White-leaf Greenbrier) seedling (Table 7). At wetland sites, 2 species were significant indicators of high-impact burn management (*Rhododendron viscosum* [Swamp Azalea]

Table 7. Indicator-species analysis for vegetation taxa in upland plots. Growth-type categories follow Carter and Floyd (2013). Management classes include: high-impact = burned RC plots, intermediate = unburned RC and burned MTA plots, low-impact = unburned MTA plots. Relative abundance (RA) = mean abundance within the management class for which a taxon was most abundant as a percentage of the sum of all mean class abundance. Relative frequency (RF) = percentage of plots within a class upon which the taxon occurred. Indicator value (IV) = product of RA and RF. P = probability that IV is less than or equal to that expected by chance (permutation test with 999 permutations). Management classes: low-impact = unburned (i.e., no fire evidence within 2 y) maneuver training areas, intermediate = unburned range complex and burned (i.e. fire evidence within 2 y) maneuver training areas, and high-impact = burned range complex. ns = not significant (α = 0.05). [Table continued on following page.]

Taxon	Growth type	Management Class	RA	RF	IV	P
Acer rubrum L. (Red Maple)	Sapling	Low-impact	100	4	4	ns
Betula nigra L. (River Birch)	Tree	Intermediate	100	5	5	ns
Carya pallida (Ashe) Engl. & Graebn. (Sand Hickory)	Sapling	High-impact	100	4	4	ns
Carya pallida	Seedling	High-impact	100	4	4	ns
Carya sp. (hickory)	Tree	High-impact	100	4	4	ns
Carya sp.	Sapling	High-impact	100	4	4	ns
Cladonia cristatella Tuck. (British Soldier Lichen)	Herb	High-impact	100	4	4	ns
Cladonia sp.	Herb	High-impact	100	4	4	ns
Clethra alnifolia L. (Sweet Pepperbush)	Seedling	Low-impact	100	4	4	ns
Cornus florida L. (Flowering Dogwood)	Tree	Low-impact	100	13	13	ns
Desmodium sp. (Tick-trefoil)	Herb	Low-impact	100	4	4	ns
Diospyros virginiana L. (American Persimmon)	Tree	Intermediate	100	5	5	ns
Epigaea repens L. (Trailing Arbutus)	Herb	High-impact	100	12	12	ns
Eupatorium capillifolium (Lam.) Small (Dog-fennel)	Herb	Low-impact	100	4	4	ns
Fabaceae sp. (legumes)	Herb	Low-impact	100	4	4	ns
Fagus grandifolia Ehrh. (American Beech)	Sapling	Intermediate	100	5	5	ns
Gaylussacia frondosa (L.) Torr. & Gray ex Torr. (Dangleberry)	Seedling	Low-impact	100	8	8	ns
Ilex opaca Aiton (American Holly)	Tree	Low-impact	72	63	45	<0.01
Ilex opaca	Sapling	Low-impact	83	38	32	0.01
Ipomoea sp. (morning-glory)	Herb	Low-impact	100	4	4	ns
Kalmia latifolia L. (Mountain Laurel)	Sapling	High-impact	95	32	30	<0.01
Kalmia latifolia	Seedling	High-impact	100	4	4	ns
Liquidambar styraciflua L. (Sweetgum)	Sapling	Intermediate	100	5	5	ns
Lycopodiaceae sp. (club moss)	Herb	Intermediate	100	5	5	ns
Lyonia mariana (L.) D. Don (Staggerbush)	Sapling	High-impact	100	4	4	ns
Magnolia virginiana L. (Sweetbay Magnolia)	Tree	Intermediate	100	5	5	ns
Medeola virginiana L. (Indian Cucumber-root)	Herb	Intermediate	100	5	5	ns
Mitchella repens L. (Partridge-berry)	Herb	Intermediate	100	5	5	ns

sapling and Sweetbay Magnolia tree) and 1 species was a significant indicator of low-impact sites (*Vaccinium formosum* Andr. [Southern Highbush Blueberry]) sapling (Table 8). No species were significant indicators of intermediate sites.

Table 7, continued.

Taxon	Growth type	Management Class	RA	RF	IV	P
Nyssa sp. (Black Gum)	Tree	High-impact	100	4	4	ns
Pinus echinata Miller (Shortleaf Pine)	Tree	Intermediate	100	5	5	ns
Pinus sp. (pine)	Sapling	Low-impact	100	8	8	ns
Pinus taeda L. (Loblolly Pine)	Sapling	High-impact	83	20	17	0.05
Pinus taeda	Seedling	High-impact	100	12	12	ns
Poaceae (grass)	Herb	Intermediate	100	5	5	ns
Quercus alba L. (White Oak)	Tree	Low-impact	49	88	43	0.01
Quercus alba	Seedling	Low-impact	100	4	4	ns
Quercus coccinea Muenchh. (Scarlet Oak)	Tree	High-impact	100	12	12	ns
Quercus montana Willd. (Chestnut Oak)	Tree	High-impact	79	56	44	0
Quercus montana	Sapling	High-impact	100	20	20	0.01
Quercus phellos L. (Willow Oak)	Sapling	High-impact	100	4	4	ns
Quercus stellata Wangenh. (Post Oak)	Tree	High-impact	100	4	4	ns
Rhododendron viscosum (L.) Torr. (Swamp Azalea)	Sapling	Intermediate	100	5	5	ns
Rubus sp. (blackberry)	Sapling	Intermediate	100	5	5	ns
Smilax glauca Walt. (White-leaf Greenbrier)	Herb	Low-impact	67	29	19	0.04
Smilax glauca Walt. (White-leaf Greenbrier)	Sapling	Low-impact	100	4	4	ns
Smilax sp. (greenbrier)	Sapling	Intermediate	100	10	10	ns
Toxicodendron pubescens P. Mill. (Poison Oak)	Sapling	High-impact	100	4	4	ns
Vaccinium formosum Andr. (Southern Highbush Blueberry)	Sapling	Low-impact	100	4	4	ns
Vaccinium pallidum Ait. (Hillside Blueberry)	Seedling	High-impact	100	4	4	ns
Vaccinium stamineum L. (Deerberry)	Seedling	Low-impact	100	4	4	ns

Table 8. Indicator-species analysis for vegetation taxa in wetland plots. Growth-type categories follow Carter and Floyd (2013). Management classes include: high-impact = burned RC plots; intermediate = unburned RC and burned MTA plots; low-impact = unburned MTA plots. Relative abundance (RA) = mean abundance within the management class for which a taxon was most abundant as a percentage of the sum of all mean class abundance. Relative frequency (RF) = percentage of plots within a class upon which the taxon occurred. Indicator value (IV) = product of RA and RF. P = probability that IV is less than or equal to that expected by chance (permutation test with 999 permutations). Management classes: low-impact = unburned (i.e. no fire evidence within 2 y) maneuver training areas, intermediate = unburned range complex and burned (i.e. fire evidence within 2 y) maneuver training areas, and high-impact = burned range complex. ns: not significant ($\alpha = 0.05$). [Table continued on following page.]

Taxon	Growth type	Management Class	RA	RF	IV	P
Amelanchier sp. (Serviceberry)	Sapling	Low-impact	100	6	6	ns
Carya sp.	Tree	Intermediate	100	9	9	ns
Chionanthus virginicus L. (Fringetree)	Sapling	Low-impact	100	6	6	ns
Cuscuta sp. (dodder)	Herb	Intermediate	100	9	9	ns

Table 8, continued.

Taxon	Growth type	Management Class	RA	RF	IV	P
Dichanthelium boscii (Poir.) Gould & C.A. Clark (Bosc's Panic Grass)	Herb	Intermediate	100	9	9	ns
Galium aparine L. (Cleavers)	Herb	High-impact	100	13	13	ns
Gaylussacia frondosa	Sapling	Low-impact	100	12	12	ns
Gaylussacia sp. (huckleberry)	Sapling	High-impact	100	13	13	ns
Hypericum sp.	Herb	Low-impact	100	6	6	ns
Ilex decidua	Sapling	High-impact	100	13	13	ns
Ilex decidua Walt. (Possum-haw)	Seedling	High-impact	100	13	13	ns
Ilex verticillata (L.) Gray (Winterberry)	Sapling	Intermediate	100	18	18	ns
Impatiens capensis Meerburg (Orange Jewelweed)	Herb	Low-impact	100	6	6	ns
Juncus effusus L. (Common Rush)	Herb	Intermediate	100	9	9	ns
Juniperus virginiana L. (Eastern Redcedar)	Tree	High-impact	100	13	13	ns
Kalmia latifolia	Seedling	High-impact	100	13	13	ns
Lonicera japonica Thunb. (Japanese Honeysuckle)	Herb	High-impact	100	13	13	ns
Lycopus virginicus L. (Virginia bugleweed)	Herb	High-impact	100	13	13	ns
Lyonia ligustrina (L.) DC. (Maleberry)	Herb	High-impact	100	13	13	ns
Magnolia virginiana	Tree	High-impact	67	63	42	0.04
Mycophycophyta (Lichen)	Herb	Low-impact	100	12	12	ns
Oxydendrum arboreum (L.) DC. (Sourwood)	Sapling	High-impact	100	13	13	ns
Oxypolis rigidior (L.) Raf. (Cowbane)	Herb	Intermediate	100	9	9	ns
Persicaria arifolia (L.) Haraldson (Halberd-leaf Tearthumb)	Herb	Low-impact	100	6	6	ns
Pinus sp.	Sapling	High-impact	100	13	13	ns
Pinus taeda	Seedling	Intermediate	100	18	18	ns
Pinus virginiana Miller (Virginia Pine)	Tree	Low-impact	100	6	6	ns
Platanthera clavellata (Michx.) Luer (Small Green Wood Orchid)	Herb	Low-impact	100	6	6	ns
Pteridophyta (fern)	Herb	Low-impact	100	6	6	ns
Quercus alba	Sapling	Low-impact	100	6	6	ns
Quercus montana	Tree	High-impact	100	13	13	ns
Quercus rubra L. (Northern Red Oak)	Tree	Intermediate	100	9	9	ns
Quercus sp. (oak)	Seedling	Intermediate	100	9	9	ns
Quercus velutina Lam. (Black Oak)	Tree	Intermediate	100	9	9	ns
Rhododendron viscosum	Sapling	High-impact	75	50	38	0.03
Rhododendron viscosum	Tree	High-impact	100	13	13	ns
Rubus flagellaris Willd. (Common Dewberry)	Herb	Intermediate	100	9	9	ns
Rubus sp.	Herb	Intermediate	100	9	9	ns
Smilax rotundifolia L. (Common Greenbrier)	Sapling	Low-impact	100	6	6	ns
Snag (unidentified sp.)	Sapling	Intermediate	100	9	9	ns
Solidago sp. (goldenrod)	Herb	Low-impact	100	6	6	ns
Thalictrum pubescens Pursh (Common Tall Meadow-rue)	Herb	High-impact	100	13	13	ns
Toxicodendron radicans	Herb	Intermediate	100	9	9	ns
Uvularia sp. (bellwort)	Herb	Intermediate	100	9	9	ns
Vaccinium formosum	Sapling	Low-impact	77	59	45	0.01
Viburnum nudum	Seedling	Intermediate	100	9	9	ns

Discussion

Wildland fire effects

The results of this study suggest that wildland fire may have some direct or indirect effect on Swamp Pink growth. Rosettes in burned sites were larger and had more leaves than rosettes in unburned sites when all burned and unburned sites were compared (Table 2).

The significantly lower wetland-tree density, dominance, and tree species richness in the RC compared to the MTAs was unexpected (Table 3), especially because we detected no differences between wetland plots in the MRPP results (Table 6). The history of a higher frequency of fires in the RC resulting from both military training and prescribed fires likely contributes to the forest-composition differences between MTA and RC wetlands. The higher fire-frequency in the RC may also be reflected in the comparison between unburned RC and MTA plots, which revealed a much lower wetland-tree dominance, wetland shrub density, and greater upland-species richness in the RC plots (Table 5). Even though fire had not recently burned through unburned RC plots within the past 2 y, it is reasonable to assume that over longer periods of time fire was still a relatively frequent event in these areas due to the high frequency of military training as well as installation attempts to conduct prescribed fires in the entire RC annually. By comparison, the unburned plots in the MTAs may not have any history of fire disturbance. Even though NMS and MRPP analysis (Table 6) failed to identify a difference between wetlands based on the influence of fire, it was documented that the Swamp Pink rosettes in the unburned plots with the higher fire-frequency (i.e., the unburned RC plots) had more leaves than unburned MTA plots with presumably lower fire-frequencies.

MRPP analysis identified differences between the high-impact and low-impact upland sites, but no difference existed between high-impact and low-impact wetlands (Table 6). The only difference in forest composition in the analysis of habitat conducted irrespective of species was reduced upland-tree density in burned sites compared to unburned sites (Table 2). This finding suggests that the composition of Swamp Pink wetlands is less obviously affected by the low-intensity fires that are typical at Fort A.P. Hill, and that these wetlands may serve as a protective firebreak for the majority of Swamp Pink plants within them (Windisch 1987, 1993). This assertion seems more plausible, considering the high microsite heterogeneity of forested wetlands and the variety of moisture conditions in which Swamp Pink is naturally found (Laidig et al. 2009, Punsalan 2016). Furthermore, fire-intolerant species such as American Holly and *Acer rubrum* L. (Red Maple) were present in every Swamp Pink wetland growing among more fire-adapted species (e.g., *Nyssa biflora* Walt. [Swamp Tupelo] and Cinnamon Fern) irrespective of burn history or training zone (Coladonato 1991, 1992; Tirmenstein 1991a; Walsh 1994). In their fire-frequency study of canebrakes, Gray et al. (2016) found similar results with many of the same fire-intolerant and fire-adapted species growing in wetlands at Fort Benning, Fort Bragg, Fort Jackson, and non-military lands.

ISA detected no significant indicator species at intermediate sites but identified several significant indicator species in the high-impact and low-impact management classes of both wetlands and uplands (Tables 7, 8). Unsurprisingly, the indicator species in the high-impact uplands—Chestnut Oak trees and saplings, Mountain Laurel, and Loblolly Pine are all fairly well adapted to fire (Carey 1992a, b; League 2005). The results of the ISA for low-impact uplands were less easily interpreted. American Holly trees and saplings are fire-intolerant (Coladonato 1991). However, White Oak declines in the mid-Atlantic have been linked to fire suppression (Tirmenstein 1991c). Less is known about the relationship between White-leaf Greenbrier and fire, but other members of the genus *Smilax* tolerate fire fairly well (Carey 1994, Deelen and Timothy 1991, Sullivan 1994). Similarly, there is not a conclusive relationship (positive or negative) between fire and the indicator species identified at high-impact and low-impact wetland sites—Swamp Azalea, Sweetbay Magnolia, and Southern Highbush Blueberry (Gucker 2008, Uchytil 1993). Other species occurred exclusively within a single management class (thus their RA values were 100; Tables 7, 8); however, these taxa were not identified as indicator species because they were not found frequently within that class (i.e., their relative frequencies were low). Further research and a more robust dataset are likely needed to fully investigate the relationships of these species with different burn regimes.

Using the ecological fire-effects categorization in Frost (1998), Swamp Pink wetlands at Fort A.P. Hill might best be described as oligopyric sites that do not burn under normal conditions due to wetness and a lack of fuel continuity attributed to variations in vegetation. Conversely, the ecological fire effects of adjacent uplands at Fort A.P. Hill seem to fit the description of very light understory-thinning fires, only removing shrub and sapling stems and occasionally burning hot enough to remove large subcanopy trees. Light understory-thinning fires, which are frequent in the RC, form a community with bi-layered stands consisting of a tree canopy and rich herb layer (Frost 1998).

Reduced upland-tree density in burned areas, compared to unburned uplands, could positively influence Swamp Pink size and leaf production, possibly due to increased light penetration, but further study is needed. However, if lower tree-density in burned uplands had a definitive positive effect on Swamp Pink, larger rosettes with more leaves would have been expected in the wetlands downhill from burned uplands in both the MTAs and RC compared to those occurring in wetlands downhill from unburned uplands, but this was not the case. Although Swamp Pink rosettes in burned MTAs were larger with more leaves when compared with unburned MTAs (Table 5), there were no other significant differences in forest composition in the "irrespective of species" analysis we conducted (Table 5). There were only 2 unburned upland sites available for study in the RC; thus, it is difficult to draw any conclusions from the comparison of burned vs. unburned RC sites.

Several observations suggest that Swamp Pink may be adapted to withstand periodic wildland fire. As previously discussed, our results suggest that wetlands supporting Swamp Pink at Fort A.P. Hill are less obviously affected by wildland fires compared with uplands, presumably burning on a less frequent interval and at a lower intensity than plants in adjacent uplands. Swamp Pink has been well documented in other coastal plain populations growing with species characterized by their dependence on fire. For example, *Pinus rigida* Miller (Pitch Pine), a serotinous species frequently associated with Swamp Pink in the New Jersey Pine Barrens, requires fire to facilitate reproduction (Gucker 2007, USFWS 2014). At least 9 different Pine Barrens community types are described as having some level of fire dependence (Eastern Ecology Group 1997; Neid 2007, 2011; Neid and Sneddon 2005; Sneddon 2005, 2006; Sneddon and Windisch 1998; Strakosch-Walz 2004; Walz 2013). Of these communities, 1 is even described as being "maintained by active ordinance explosion and burning on a military range" (Sneddon and Windisch 1998). *Chamaecyparis thyoides* (L.) BSP (Atlantic White Cedar) is another dominant canopy species frequently associated with Swamp Pink (Gordon 2016, Laidig et al. 2009, Windisch 1993). This species is readily killed by fire, but successful seedling establishment is largely dependent on fires of moderate severity at relatively short intervals (25–100 y), and in many areas, increased fire suppression has led to its decline (Frost 1998, Tirmenstein 1991b).

Weakley and Schafale (1994) indicated that most "coastal plain fire species" are not necessarily fire-dependent, but rather are adapted to moist-to-wet, acid, peaty or sandy situations. The habitat preference of Swamp Pink seems to fit this description. In the coastal plain, this habitat type is largely maintained by fire—as is the case at Fort A.P. Hill (Fleming 2012, Fleming et al. 2013, Weakley and Schafale 1994, Weakley et al. 2012). Weakley and Schafale (1994) pointed out that analogous habitat also exists in the mountains of the Southern Blue Ridge of North Carolina when alluvial wetlands occurring over felsic rocks yield acidic, nutrient-poor soils even in the absence of fire. This fact may in part explain the non-contiguous distribution of Swamp Pink in Virginia, occurring in the ridge and valley and the coastal plain physiographic provinces (Virginia Botanical Associates 2016, Weakley and Schafale 1994).

The life history and morphology of Swamp Pink also suggest some possible adaptations to fire. Swamp Pink possesses a thick, stout rhizome that contains much of the plant's biomass (Godfrey and Wooten 1979, Weakley et al. 2012, Utech 1978). In the event of a surface fire, Swamp Pink rosettes may lose leaves; however, the rhizomes in many cases should remain unharmed and capable of regenerating new rosettes. A comparable behavior has been documented in *Sarracenia* spp. (pitcher plants), which are similarly adapted to low-nutrient wetlands, can reproduce via rhizomes, and are adapted to frequent fires. Research has indicated that reducing competing vegetation by physical removal or by fire has the ability to increase pitcher plant foliage (Barker and Williamson 1988, Brewer 1999). Although Swamp Pink produces relatively few flowering rosettes, and Maddox (1990) found that the seeds sown immediately after collection lost viability by 4 weeks, these life-history characteristics may be of some benefit to the species because Swamp Pink is not largely reliant on seeds and/or flowers that could be destroyed during a wildland fire event (Godt et al. 1995, Murdock 1994, Sutter 1984).

Management and conservation implications

The results presented here and those by Dodds (1996) and Windisch (1993) suggest that Swamp Pink is not negatively impacted by non-catastrophic fire and that greater conservation threats can be attributed to habitat loss from competition, changes to hydrology, and development (Laidig et al. 2009, USFWS 2014, Windham and Breden 2000). In the coastal plain, fire may also be an effective means to manage Swamp Pink acidic seepage-swamp habitat. Harper et al. (1998) recommended managing herbaceous seeps for endangered species with a fire regime that simulates natural fire occurrence, preferably in spring to match the time when uplands are most frequently burned (Komarek 1964). Windisch (1993) also warned that Swamp Pink populations were occasionally reduced by fires during drought conditions in the past. The threat of fires during drought conditions further justifies wildfire-prevention programs which aim to reduce fuel accumulation to preemptively diminish the severity of wildfires—especially during drought conditions—that are ignited by incendiary munitions or other means (Fort A.P. Hill 2015). Indeed, even the US Fish and Wildlife Service and the Georgia Department of Natural Resources recommend occasional fire to reduce woody competition as part of the conservation and management of Swamp Pink (Chafin 2010, USFWS 2015). Good anecdotal evidence has been put forward by the Georgia Plant Conservation Alliance Safeguarding Program that mountain bogs in Georgia, including those harboring Swamp Pink, have benefited from fire as a management tool (Moffett and Radcliffe 2016).

Military training and land-management practices have often been found to facilitate the restoration of rare habitat types, and the comparatively high biodiversity and presence of threatened and endangered species on military land is well documented (Aycrigg et al. 2015, Gray et al. 2016, Lee Jenni et al. 2012, Orth and Warren 2006, Stein et al. 2008, Zentelis and Lindenmayer 2015). Recent literature suggests that management based on historical averages does not produce enough local variation over space and time to replicate the heterogeneous landscapes tied to evolutionary feedback mechanisms between pyrogenic vegetation and fire (Fill et al. 2015). In contrast, military training and land management designed to support training produce spatially and temporally distributed disturbances of many types, sizes, frequencies, periodicities, and severities that often mimic heterogeneous disturbance patterns that were once more prevalent but have been suppressed over time (Beaty et al. 2003, Stein et al. 2008, Warren et al. 2007). Military lands managed by prescribed fire, in tandem with fires ignited by military training often possess a fire-return interval less than 3 y (Gray et al. 2016), and some of the most exceptional examples of fire-dependent ecosystems in the southeastern US are found on military bases in and adjacent to artillery ranges where frequent fires are a certainty and unexploded ordnance prevents development (Peet and Allard 1993). One well-chronicled example of this dynamic between military training and endangered species in fire-dependent systems is found in the *Pinus palustris* Mill. (Longleaf Pine–*Aristida* spp. (wiregrass) forests at Fort Bragg, NC, which are preferred habitat for the federally endangered *Picoides borealis* Vieillot (Red-cockaded Woodpecker) and are ideal for Army training (Beaty et al. 2003, Stein et al. 2008).

Future considerations

In spite of mounting conditional evidence advocating fire, the use of fire as a management tool for Swamp Pink is still not universally accepted, largely due to the lack of accepted science on the subject. Studies on Swamp Pink are hampered by challenges in determining the actual number of individual plants because a single rhizome often gives rise to multiple rosettes, making accurate counts difficult and often impossible without destructive sub-surface sampling. Additionally, Swamp Pink rosettes can move as much as 5 cm in a 2-y period, and seeds often fall short distances from their parent plants, resulting in several plants growing together in 1 clump (Godt et al. 1995, Sutter 1984, USFWS 1991). Dodds (1996) found that light levels had profound effects on Swamp Pink, and future Swamp Pink research should consider variables related to light penetration (e.g., canopy-gap analysis, topographic effect, etc.). Furthermore, in the absence of an experimental study that specifically monitors the short- and long-term effects of prescribed fire on Swamp Pink, scientists are limited in what conclusions can be drawn as to the relationship between this species and fire.

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