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Habitat characteristics of adult frosted elfins (*Callophrys irus*) in sandplain communities of southeastern Massachusetts, USA

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A R T I C L E   I N F O

A B S T R A C T

Changes to land use and disturbance frequency threaten disturbance-dependent Lepidoptera within sandplain habitats of the northeastern United States. The frosted elfin (*Callophrys irus*) is a rare and declining monophagous butterfly that is found in xeric open habitats maintained by disturbance. We surveyed potential habitat for adult frosted elfins at four sites containing frosted elfin populations in southeastern Massachusetts, United States. Based on the survey data, we used kernel density estimation to establish separate adult frosted elfin density classes, and then used regression tree analysis to describe the relationship between density and habitat features. Adult frosted elfin density was greatest when the host plant, wild indigo (*Baptisia tinctoria*), density was >2.6 plants/m^2 and tree canopy cover was <29%. Frosted elfin density was inversely related to tree cover and declined when the density of wild indigo was <2.6 plants/m^2 and shrub cover was $\geqslant$16%. Even small quantities of non-native shrub cover negatively affected elfin densities. This effect was more pronounced when native herbaceous cover was <36%. Our results indicate that management for frosted elfins should aim to increase both wild indigo density and native herbaceous cover and limit native tree and shrub cover in open sandplain habitats. Elimination of non-native shrub cover is also recommended because of the negative effects of even low non-native shrub cover on frosted elfin densities. The maintenance of patches of early successional sandplain habitat with the combination of low tree and shrub cover, high host plant densities, and the absence of non-native shrubs appears essential for frosted elfin persistence, but may also be beneficial for a number of other rare sandplain insects and plant species.

1. Introduction

Sandplain communities of the northeastern United States contain many species of rare Lepidoptera (Schweitzer and Rawinski, 1987; Goldstein, 1997; Wagner et al., 2003). A variety of sandplain plant communities exist in the coastal sandplain, including grassland, heathland, scrub oak (*Quercus ilic-ifolia*) shrubland, pitch pine (*Pinus rigida*) – scrub oak barrens, and pitch pine – oak (*Quercus* sp.) forests (Swain and Kearsley, 2001). These communities form a dynamic mosaic of intergrading habitat patches that rely on disturbance for persistence and spatial extent.

Disturbance-dependent sandplain habitats have decreased in area because of the suppression of disturbances such as

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land clearing and fire (Foster and Motzkin, 1999; Foster et al., 2002; Motzkin et al., 2002; Lorimer and White, 2003), real estate development (Barbour et al., 1998; Breunig, 2003), and invasion by exotic plants (Foster and Motzkin, 1999; Wagner et al., 2003). In Massachusetts, 60–70% of pitch pine-scrub oak barrens have disappeared (Barbour et al., 1998). Sandplain habitats that persist are often small and located in urban and rural landscapes that have been degraded by human activities (Vickery and Dunwiddie, 1997). The conservation of these areas and the rare species that depend on them are a top priority for national, regional and local conservation agencies (The Trustees of Reservations, 1999; MNHESP, 2001; Breunig, 2003).

Despite recent efforts to conserve and maintain disturbance-dependent sandplain habitats, these areas continue to be lost to real estate development and inadequate habitat management. Between 1985 and 1999, southeastern Massachusetts experienced the highest levels of real estate development in the Commonwealth (Breunig, 2003). Modern fire suppression and detection techniques, and region wide declines in burning, mowing and grazing have increased the structural homogeneity of vegetation and changed the plant species composition of disturbance-dependent sandplain habitats as open lands gradually develop into woodlands (Motzkin et al., 2002; Foster and Motzkin, 2003; Lorimer and White, 2003).

Non-native vegetation is replacing native vegetation in both natural communities and anthropogenic landscapes in many parts of North America (Mooney and Hobbs, 2000; Pimentel et al., 2000). The impacts of non-native vegetation on natural communities can be severe, changing among other components, rates of nutrient cycling, hydrologic cycles, and disturbance regimes (Mooney and Hobbs, 2000; Ehrenfeld and Scott, 2001; Evans et al., 2001; Larson et al., 2001). Studies in North American tallgrass prairies have found a positive relationship between native plant species richness and the diversity of phytophagous insects restricted to natural communities (Panzer and Schwartz, 1998). Relative to other biota, butterflies respond quickly to changes in their environment (Thomas et al., 2004) and thus the impacts of non-native species encroachment may be rapid and severe for oligophagous Lepidoptera.

Natural communities associated with pitch pine-scrub oak barrens harbor a large proportion of the rare and uncommon moths and butterflies of the northeastern United States (Wagner et al., 2003; Goldstein et al., 2007). Notably, the federally endangered karner blue butterfly (*Lycaeides mellissa samuelis*) is a well-studied lycaenid butterfly associated with disturbance-dependent sandplain habitat (US Fish and Wildlife Service, 2003). However, in general there is little quantitative data on the basic habitat requirements for the majority of these species of Lepidoptera.

The frosted elfin, (*Callophrys irus*, Godart 1824), is a rare lycaenid butterfly associated with sandplain habitat. While the frosted elfin has a larger global range than the karner blue butterfly, the two species are sympatric in the northern part of their ranges, and where they co-occur, frosted elfins tend to be less abundant (NatureServe, 2005). The distribution of frosted elfin once extended from southern Canada and the northeastern United States, south to Florida, and west to Texas and Wisconsin. The species is now probably extinct

from Canada, Maine and Illinois and is state-listed as endangered, threatened, or of special concern in 11 states in the eastern United States (Packer, 1998; NatureServe, 2005). It has no federal protection and populations receive little to no direct management (NatureServe, 2005). In Massachusetts, it is considered both uncommon and a species of special concern (MNHESP, 2004), however, the state is considered one of the species' last strongholds (Nelson, 2001). The only information on frosted elfin population biology available is from Swengel (1996) who studied the species in Wisconsin, USA during the late 1980s and early 1990s. No studies have been published on frosted elfin populations in the northeastern United States.

The frosted elfin is a univoltine species that over-winters as a pupa. Adults begin to emerge in Massachusetts from late April to early June. The flight period is approximately eight weeks, starting in late April and lasting through mid-June with the peak flight usually occurring in mid-May. Females lay single eggs on host plants, and the larvae develop and remain on the plant for a six-week period, pupating by late July (Nelson, 2002).

The larval host plants of frosted elfins are all legumes (Fabaceae), with most populations feeding on either wild indigo (*Baptisia tinctoria*) or wild lupine (*Lupinus perennis*), but not both (Scott, 1986; Opler and Maliikul, 1992; Schweitzer, 1992; Wagner et al., 2003). These plants are found in xeric, open habitats maintained by natural and anthropogenic disturbances on dry acidic soils (Panzer, 1984; Panzer et al., 1995; Swengel, 1998; Wagner et al., 2003). Wild indigo and wild lupine are characteristic plants of sandplain communities within Massachusetts and their persistence is dependent on disturbance (Swain and Kearsley, 2001).

Like many oligophagous lycaenid butterflies, the decline of frosted elfin appears to be the result of habitat loss, and lack of disturbance in areas where the larval host plant occurs (Shuey et al., 1987; Packer, 1991, 1998; Nelson, 2001, 2002). When host plants are distributed in patches, monophagous insects often live in metapopulations within that landscape (Murphy et al., 1990; Tscharntke and Brandl, 2004). This is probably the case for frosted elfins in the larger tracts of pitch pine – scrub oak communities in southeastern Massachusetts (NatureServe, 2005). Small sub-populations are probably more transient than larger sub-populations, and during our 2-year study, some sub-populations disappeared while others were established.

We surveyed four study sites in southeastern Massachusetts for adult frosted elfin and monitored adult breeding activities to derive an estimate of the breeding adult activity area. We used kernel density estimation to approximate frosted elfin density among our study sites and related 16 habitat variables to seven adult frosted elfin density classes using regression tree analysis (De'ath and Fabricius, 2000).

The aim of our study was to construct a descriptive model that identified which habitat features influence the density of adult frosted elfins at four sites in southeastern Massachusetts. We asked the following questions: (1) Which portions of the total potential habitat area (i.e., early successional grassy open habitats in pitch pine – scrub oak barrens and similar habitats that were anthropogenically produced) within study locations support adult frosted elfins? (2) At what spatial scale do adult frosted elfins conduct breeding

activities? (3) Is there a relationship between adult frosted elfin density and the habitat features we measured?

2. Methods

2.1. Study area

This study was conducted in southeastern Massachusetts, United States, at the Crane Wildlife Management Area (WMA) (Barnstable County), Gavins Pond Municipal Water Authority (MWA) properties (Norfolk County), Myles Standish State Forest (SF) (Plymouth County), and Noquochoke WMA (Bristol County). These areas are on the coastal plain and characterized by xeric sandy soils and relatively flat topography. Due to the large size of Crane WMA and Myles Standish SF, they were partitioned into three and four study locations, respectively. The other two sites were treated as single study locations (Table 1). The study sites were selected based on three criteria: (1) recently documented occurrence records of frosted elfin populations, (2) presence of wild indigo, the host plant of frosted elfins in southeastern Massachusetts, and (3) location within the southeastern portion of Massachusetts, to control for regional variation.

We used Environmental Systems Research Institute's (ESRI) ArcGIS 9.0 (1999–2004) geographic information system (GIS) software to assemble base data layers for each study location that included 1:25000 USGS topographical Quad Images and 0.5 m resolution 1:5000 color digital ortho-images. We delineated all potential frosted elfin habitat within the pitch pine-scrub oak barrens or similar anthropogenic habitats at each study location using the color digital ortho-images, and then verified and refined the mapping with field surveys (Table 1). Wagner et al. (2003, p. 96) defined potential frosted elfin habitat as "xeric and open disturbance-dependent habitats on sandy soil, including openings in pitch pine-scrub oak barrens and similar anthropogenic habitats." Habitat was considered unsuitable for frosted elfin if it did not meet this description, i.e., closed canopy pitch pine-scrub oak barrens.

Common tree species within the potential frosted elfin habitat included eastern white pine (*Pinus strobes*), pitch pine, quaking aspen (*Populus tremuloides*), black locust (*Robinia pseudoacacia*) and several species of oaks. Dominant native shrubs included scrub oak, sweet fern (*Comptonia peregrina*), bearberry (*Arctostaphylos uva-ursi*), blueberries (*Vaccinium* sp.) and the non-native shrubs multiflora rose (*Rosa multiflora*), oriental bittersweet (*Celastrus orbiculata*) autumn olive (*Eleagnus umbellate*) and bush honeysuckles (*Lonicera* sp.). Dominant native herbaceous vegetation included little bluestem (*Schizachyrium scoparium*), poverty oat grass (*Danthonia spicata*), wild indigo, varies species of goldenrods (*Solidago* sp.) and the non-native herbs orchard grass (*Dactylis glomerata*), timothy (*Phleum pretense*), chinese bush-clover (*Lespedeza cuneata*) and several species of clovers (*Trifolium* sp.).

2.2. Field methods

During the annual flight period in 2004 and 2005, we surveyed all delineated potential habitat patches within each study location three times. We divided the 60-day flight period into three 20-day intervals, and completely surveyed each potential habitat patch once during each interval. We conducted all surveys during weather conditions appropriate for flight (Pollard, 1988). To standardize sampling effort among potential habitat patches, we searched individual patches for a minimum of 15 min during each visit.

We surveyed each patch systematically. Before field surveys, observers were given ortho-images of each delineated potential habitat patch containing 50 m UTM grid coordinates. The UTM grids on the field maps were marked with incremental 10 m tick marks and 25 m grid lines. The 25 m grid lines were used as transects. The observer searched all delineated areas walking at a steady pace (approx. 30 m/min), proceeding along the transect lines in a linear fashion. When we encountered adult frosted elfins, we counted all individuals. Each individual location was marked on the ortho-image, and the UTM coordinates were recorded using a GPS receiver. We were careful not to recount the same individuals twice during a survey. We surveyed 335 ha of potential frosted elfin habitat in each year of our study.

We then used kernel density estimation to create different density classes among our study locations using the frosted elfin location data. Kernel density estimation is a non-parametric analytical technique that generates a smoothed local density average for data points over a local neighborhood. The parameter *h* governs the size of the local neighborhood used in the local averaging or smoothing. We used a bivariate Gaussian kernel, which has a unimodal normal distribution. The smoothing parameter (*h*) defines the bandwidth of the bivariate normal kernel and is the value in which the mean plus or minus one SD captures 66% of each kernel functions volume. Kernel density estimation is commonly used in ecological research to estimate the home range of a species (Worton, 1987, 1989; Seaman and Powell, 1996).

Our objective was to empirically estimate a bandwidth (*h*) for the bivariate normal kernel scaled to represent observed frosted elfin breeding activity areas. To estimate an adult's breeding activity area, we observed individual adults at our six study locations and mapped their movements. We

Table 1 – Four study sites used for adult frosted elfin surveys, 2004–2005		
Study site	Study location	Total potential habitat area (ha)
Crane WMA	Crane 1	16.7
	Crane 2	95.1
	Crane 3	42.0
Gavins Pond MWA properties	Gavins Pond 1	36.3
Noquochoke WMA	Noquochoke 1	23.5
Myles Standish SF	Myles 1	29.6
	Myles 2	25.4
	Myles 3	56.3
	Myles 4	9.7

Sites were located in southeastern MA, USA, and study locations either were sub-sections within a study site or encompassed the entire site. The area of delineated potential frosted elfin habitat surveyed within each location is listed.

followed each adult continuously, marked each perching location on a map, recorded the perch site with a GPS receiver, and recorded the complete observation time for each individual.

We only used individuals with three or more discrete locations, and for which the sex of the individual could be determined, in this analysis. Frosted elfins were considered to be females when oviposition behavior was observed. Individuals were identified as males when a series of different territorial behaviors were observed, i.e., vertical aerial combat flights and horizontal chasing flights, and no oviposition behavior. The majority of males included in our analysis were encountered early in the flight period; behaviors were predominantly territorial and very few ovipositions were observed during this period suggesting most individuals were male.

We entered each perching location for an individual into the GIS and mapped the breeding activity range using the minimum convex polygon (MCP) method (Mohr, 1947). We then rank-ordered observed MCP areas and identified the 66th percentile; i.e., the MCP area equal to or larger than 66% of the observed MCP areas. Because we used a bivariate Gaussian kernel, the area of the corresponding MCP was converted to the area of a circle. We rounded the radius of this circle to the nearest tenth whole number and used this estimate for the bandwidth (h = 30 m) of the kernel. Using this approach, the bivariate normal kernel accurately represented the distribution of observed activity areas.

We then applied the adult frosted elfin location data from the 2004 and 2005 field seasons to a kernel density estimation program (KERN) (Compton, unpublished program). The program assigned a density estimate to each 10 m^2 cell within the study area. The raster grid output was then displayed as a surface in the GIS. Each raster grid cell in the output was assigned to one of seven adult frosted elfin density classes using the smart quantile classification scheme available in ArcGIS

9.0 (ESRI, 1999–2004). Class boundaries are positioned within large gaps between data values, so groups with similar values were placed in the same class. We preferred this classification scheme over equal and quantile classification options because our data were comprised of many zero density values. We selected seven density classes because density classes 1–6 contained frosted elfin locations and the number of observations present within each density class was within the range of our estimated sample size requirements. Our estimated sample size requirements were calculated using *a priori* power analysis. For the power analysis, we simplified comparisons between density classes to a *t*-test ($\alpha = 0.10$, $1 - \beta = 0.80$) and then estimated the sample size of observations required to detect an effect between frosted elfin density classes for each of the explanatory variables we planned to measure (Table 2). Estimates of variance and effect size for each variable were derived from comparable published data (Niering and Dreyer, 1989; Smallidge et al., 1996; Grundel et al., 1998; Grundel et al., 2000; among others) or identified as plausible based on biological insight. The density classes were displayed in the GIS as a surface with each 10 m^2 cell assigned to a different adult frosted elfin density class (Fig. 1).

Each adult frosted elfin location was assigned to the density class in which it was located. We then randomly selected a subset of adult frosted elfin locations from the pool of all locations within each density class. We based the number of observations chosen within each class on the results of the *a priori* power analysis for sample size. Because the zero density class contained no frosted elfin locations, we chose random UTM points from the entire area of potential habitat that contained no frosted elfins. In addition to meeting the estimated sample size requirement, we based the number of zero density class sampling points selected for each study location on the entire area of delineated and surveyed

Table 2 – Description of the habitat variables measured in the adult frosted elfin study in southeastern Massachusetts, USA, 2004–2005

Variable	Plot size	Description
Wild indigo density	10 m^2	Number of wild indigo plants[a]
Tree cover		% Total woody plant canopy cover greater than 2.5 m in height
Deciduous tree cover		% Total deciduous woody plant canopy cover greater than 2.5 m in height
Coniferous tree cover		% Total coniferous woody plant canopy cover greater than 2.5 m in height
Shrub cover	3.3 m^2	% Total woody plant cover less than 2.5 m in height
Non-native shrub cover[b]		% Total non-native woody plant cover less than 2.5 m in height
Native shrub cover[b]		% Total native woody plant cover less than 2.5 m in height
Herb cover	1 m^2	% Total herbaceous plant cover
Non-native herb cover[b]		% Total non-native herbaceous plant cover
Native herb cover[b]		% Total native herbaceous plant cover
Bare ground cover		% Total exposed soil and rock cover
Litter cover		% Total dead vegetative litter cover
Graminoid cover	1 m^2	% Total graminoid cover
Forb cover		% Total herbaceous plant cover excluding graminoids
Fern cover		% Total *Pteridophyta* cover
Moss cover		% Total *Bryophyta* cover
Year		Year observation collected

Data were collected within vegetation sampling modules at randomly selected frosted elfin locations and points.

a We defined a wild indigo plant as a single or multi-stemmed group of wild indigo with continuous foliage overlap.

b Native and non-native vegetation designations were determined using Sorrie and Somers, 1999.
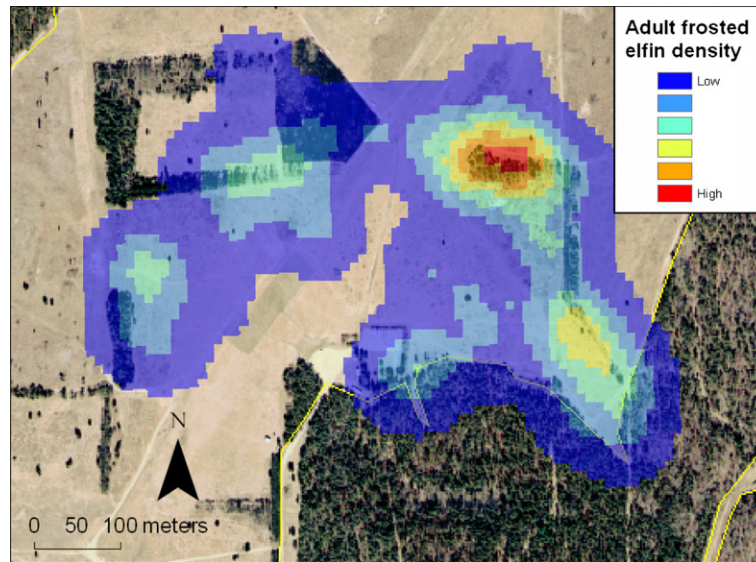
Fig. 1 – A 0.5 m resolution 1:5000 color digital ortho-image of a portion of the Crane WMA in southeastern Massachusetts, USA. Overlaid on the ortho-image is a density surface produced using adult frosted elfin survey locations and kernel density estimation. By monitoring adult frosted elfin breeding activities, we derived an estimate of frosted elfin breeding area and used this for the bandwidth (*h*) of the kernel. We developed different density classes using smart quantile classification in ArcGIS 9.0 (ESRI, 1999–2004). Each color in the density surface represents a different density class range.

potential habitat at the location. We maximized the distance between sample points to prevent sampling points from overlapping and to minimize spatial autocorrelation among observations. We treated density classes as a numeric response variable in the analysis.

We used a module nested plot method to sample vegetation and environmental data at each randomly selected frosted elfin location and point. Each module consisted of four contiguous 10 m^2 plots, and eight 3.3 m^2 and 1 m^2 embedded sub-plots. We measured one density and fifteen cover variables during field studies (Table 2). Cover was estimated using nine cover classes that were converted to midpoints in the analysis. The cover classes and module nested plot methods were adopted from the North Carolina Vegetation survey (Peet et al., 1997), which is a variation of the more traditional, cover class scheme (e.g., Domin, 1928; Braun-Blanquet, 1964; Daubenmire, 1968). These vegetation and environmental data were collected within 155 modules during both 2004 (*n* = 57) and 2005 (*n* = 98).

2.3. Data analysis

We summarized all data with R: A language and environment for statistical computing (2004) and Statistical Analysis System 9.1 (2003) software. We used regression tree analysis to model the variation in adult frosted elfin densities using a set of 16 explanatory habitat variables collected within each density class, along with the variable year (Table 2). Regression tree analysis is a non-parametric technique that is well suited for analyzing complex ecological data. Both the response and the explanatory variables can be count, continuous or categorical, and monotonic transformations of the explanatory variables do not affect the analysis. Regression tree analysis can detect non-linear

responses, explain complex interactions, and it is robust to outliers and missing data values (Breiman et al., 1984; De'ath and Fabricius, 2000).

Regression trees were grown automatically with the minimum splitting criteria at a node set to ten and the minimum terminal node size set to five. We calculated node impurity from the sums of squares about the group means (De'ath and Fabricius, 2000). We used repeated 10-fold cross validation to select the pruned tree. The data were divided into 10 mutually exclusive subsets of equal size. Each time, we dropped a subset and a new tree was constructed using the remaining subsets. The new tree was then used to predict the response of the remaining subset. From each 10-fold cross validation, we calculated an estimate of average error (±SE) for each tree size (De'ath and Fabricius, 2000). We repeated the 10-fold cross validation 1000 times and used the average and SE of the estimated errors for each tree size to construct a smoothed error curve. We then used the 1 – SE rule to select the pruned tree size (Breiman et al., 1984). From the smoothed error curve we selected the smallest tree size with an estimated error rate within one SE of the tree size with the minimum estimated error. In addition, we derived a *p*-value for the pruned tree using Monte Carlo resampling. We created 1000 trees through random permutation of the data and compared the r^2 of our tree to the distribution of r^2 values for the random trees.

As described in Breiman et al. (1984), we assessed the overall importance of each variable to our final regression tree model regardless of whether the variable occurred in the model. The importance of a variable to a regression tree model may be veiled by other variables that achieve a slightly greater reduction in node impurity at each split. We calculated the relative magnitude of each variable's importance

to our final regression tree model and then normalized and ranked the values. All primary variable splits and possible surrogate splits were included in our assessment.

Because our frosted elfin breeding activity area estimates were based on relatively short total observation times, we were concerned about under-estimating the breeding activity area. We therefore conducted a sensitivity analysis to examine the effect of a larger h estimate on our results. We used the same methods to produce another density surface but with an estimate of 60 m for h. We examined this surface, and reassigned any of the selected frosted elfin sampling locations that changed class assignment. We then constructed separate regression trees and compared the results of these two models. The models were similar and related the same set of explanatory variables to density of adult frosted elfin. Although the splitting rules and predicted values and arrangement of the trees were slightly different, their interpretation and the percent variance each model explained were very similar. Therefore, we used the 30 m estimate of h derived from the breeding activity survey in our final analysis but suggest that the actual value of this parameter probably lies between these two estimates.

In addition, to test the robustness of the final tree model, we performed a fourfold cross validation among the sites included in this study. For this cross validation, we constructed a tree from three of our four study sites and used this model to predict the response at the fourth site. We repeated this process four times, each time excluding one site from the analysis. Splitting and model selection criteria remained constant for all constructed trees and were the same as those previously described. We calculated the total sum of squares explained by each tree and each sites predicted response. We used these results to compare trees to the original model and to each other.

3. Results

Peak frosted elfin flight occurred during the second survey interval in 2004 (May 9–May 29) and the third survey interval in 2005 (May 30–June 18). We recorded 275 adult frosted elfins in 2004 and 304 in 2005 (Table 3). The locations of adult aggregations were largely constant over the two years of this study. Across the study sites, only two small subpopulations ($\leqslant$4 individuals) detected in 2004, had no butterflies in 2005, and a new small sub-population was found in 2005.

Monitoring of the breeding activity area of 38 individuals showed no significant difference between adult males ($n = 18$) and females ($n = 20$) in either the number of seconds observed (two-tailed t-test with equal variances, $t = 1.464$, df = 36, $p = 0.15$), or in the mean MCP for the area of breeding activity (two-tailed t-test with equal variances, $t = -0.915$, df = 36, $p = 0.36$), so observations were pooled for further analysis. The mean MCP area of the pooled observations ($n = 38$) was 1725.5 m^2 (SE = ±403.2). The mean length of time individuals were observed was 612 s (range = 120–1200). However, the size of breeding activity areas was not related to the length of time individuals were observed ($r = -0.14$, $p = 0.38$). When the MCPs of the breeding activity

Table 3 – The number of adult frosted elfins observed during surveys at four study sites in southeastern, Massachusetts, USA, 2004–2005

Study site	Year	Total number of frosted elfin	Peak flight interval
Crane WMA	2004	75	May 9–May 29
	2005	90	May 30–June 18
Gavins Pond MWA properties	2004	161	May 9–May 29
	2005	183	May 30–June 18
Myles Standish SF	2004	29	May 9–May 29
	2005	16	May 30–June 18
Noquochoke WMA	2004	10	May 9–May 29
	2005	15	May 30–June 18

The peak flight interval was defined as the period with the greatest number of adult frosted elfins.

areas were rank-ordered the area of the 66th percentile was 2256.2 m^2.

The habitat features collected within each adult frosted elfin density class, the density range estimates for each class and the number of observations used in our final analysis ($n = 155$) are summarized in Table 4. Greater frosted elfin densities were associated with higher wild indigo density and lower shrub cover. Frosted elfins did not occur (zero density class) in areas with high non-native herb and shrub cover and decreased native herb cover. All of the density classes contained some tree cover, and the lower density classes generally contained greater tree cover than higher density classes. However, the zero density class had the lowest tree cover estimate (mean = 7.1%, SE ± 2.3).

The overall pruned regression tree related density of adult frosted elfins to wild indigo density, tree cover, non-native shrub cover, shrub cover and native herb cover (Fig. 2). The percent of variation explained by the tree model was 77.2%. There was a highly significant difference between the r^2 of our tree to the distribution of r^2 values for the random trees derived from Monte Carlo resampling ($p < 0.001$). The regression tree analysis indicated that wild indigo density was the most important variable for predicting frosted elfin density. The initial partition explained 48.9% of the total sum of squares explained in our model. Frosted elfin density was best modeled by splitting this variable into two groups. Observations with <2.6 wild indigo plants/m^2 formed the left branch and observations with >2.6 wild indigo plants/m^2 appeared in the right branch. The variable tree cover further partitioned the right node. The terminal nodes of this split had a mean class of 2.3 for observations with $\geqslant$29% tree cover and a mean class of 4.7 for observations with <29% tree cover. The mean class of 4.7 was the highest represented in the tree indicating that these two variables were important for high frosted elfin density.

On the left side of the tree, the partition at $\geqslant$2% non-native shrub cover explained an additional 11% of the total sum of squares. Continuing from this split, the right branch was comprised of observations with <2% non-native shrub cover. These observations were further partitioned by the variable

Density class (class range)	0 (0.0)		1 (0.01–0.05)		2 (0.05–0.13)		3 (0.13–0.24)		4 (0.24–0.37)		5 (0.37–0.54)		6 (0.54–0.85)	
	n = 36		n = 12		n=35		n = 27		n = 19		n = 15		n = 11	
Variable	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Wild indigo density	0.3	0.1	0.9	0.2	1.3	0.2	2.3	0.2	4.2	0.7	6.2	0.7	5.3	0.8
Tree cover	7.1	2.3	25.5	5.2	21.3	2.8	25.0	3.8	16.3	3.2	13.9	6.9	17.3	4.1
Deciduous tree cover	2.0	0.7	7.3	3.4	3.0	0.9	5.6	1.6	4.2	1.6	5.5	1.9	2.6	1.6
Coniferous tree cover	5.8	2.1	18.2	4.8	18.5	2.6	19.9	3.3	11.1	2.6	9.1	1.7	15.5	3.4
Shrub cover	24.4	3.3	32.4	5.0	23.3	2.6	17.8	1.9	9.4	1.9	15.2	3.6	5.2	1.1
Non-native shrub cover	11.4	2.4	5.9	8.1	1.7	0.5	2.7	1.1	0.9	0.5	0.4	0.2	0.0	0.1
Native shrub cover	13.4	2.7	27.2	5.2	21.7	2.7	15.3	2.0	8.5	1.8	15.1	3.6	5.2	1.1
Herb cover	46.4	3.3	51.9	6.2	45.2	3.6	50.2	4.6	55.6	3.6	60.6	4.0	50.2	6.0
Non-native herb cover	27.3	4.6	4.9	0.9	3.9	0.8	5.7	1.6	0.7	0.2	0.9	0.3	1.9	0.8
Native herb cover	20.5	2.2	47.5	6.1	41.8	3.3	44.9	3.9	55.0	3.5	59.7	3.9	48.1	6.0
Bare ground cover	10.6	2.6	8.0	2.4	10.4	2.3	7.5	2.2	5.5	2.0	5.2	2.0	24.2	2.4
Litter cover	29.7	2.5	33.1	5.8	24.3	2.7	22.0	1.8	21.3	2.4	17.6	2.4	5.3	1.9
Graminoid cover	31.4	3.5	38.0	6.7	33.8	3.7	44.7	4.7	42.9	2.8	43.5	3.9	31.2	3.0
Forb cover	15.6	2.0	14.7	2.7	13.3	1.8	7.7	0.7	13.3	2.4	23.1	2.8	20.7	5.1
Fern cover	1.5	0.5	1.1	0.5	0.8	0.4	0.4	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Moss cover	1.8	0.5	6.3	1.5	5.7	1.7	8.6	2.6	7.0	2.6	8.8	3.0	10.2	4.1

Table 4 – Mean and standard error (SE) of the habitat variables collected at four frosted elfin study sites in southeastern Massachusetts, USA, 2004–2005

The adult frosted elfin density class range and the number (n) of observations collected in each class are listed in the coloumn heading.

shrub cover into two terminal nodes. The variable, total shrub cover, included both native and non-native shrubs. However, the splitting rules on the regression tree indicated the observations in the shrub cover terminal nodes contained <2% non-native shrub cover. When shrub cover was <16% the pre-dicted response of frosted elfin density class was 3.4. This indicated that frosted elfin could remain prevalent in areas when wild indigo density is <2.6/m² if shrub cover was <16% and mostly native. When total shrub cover was ⩾16% the predicted response of frosted elfin density dropped to 1.7.
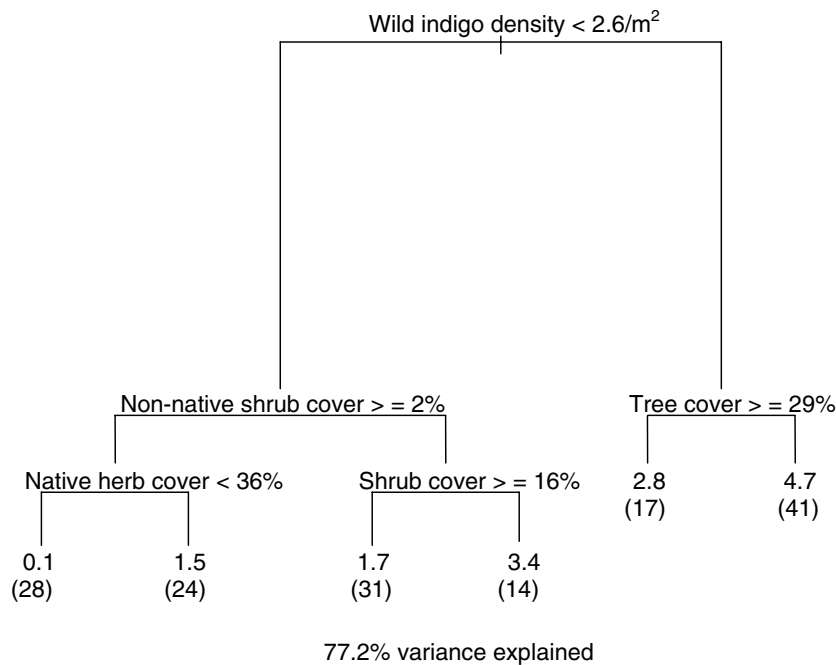

77.2% variance explained

Fig. 2 – Pruned regression tree model using seven numeric frosted elfin density classes and 16 habitat variables along with the variable year. Each partition is labeled with the splitting rule and its value. Splitting statements are true to the left and false to the right. Terminal nodes are labeled with the predicted (mean) value of the observations in the terminal group and the number of observations in the group is listed in parentheses. Frosted elfin density was highest when wild indigo density was >2.6/m² and tree cover was ⩽29%. Frosted elfin density was also high in areas with lower wild indigo density when shrub cover was moderate. Frosted elfin density was lowest when wild indigo density was <2.6/m² and non-native shrub cover was ⩾2% and native herbaceous cover was <36%.

Table 5 – The splitting rule value and proportion of the total variance explained by each habitat variable in the pruned regression tree model in Fig. 2

Variable	Splitting rule value	Proportion of total variance explained (%)	Normalized variable importance
Wild indigo density	$2.6/m^2$	48.9	100.0
Non-native shrub cover	2%	10.6	75.1
Native herb cover	36%	4.9	36.5
Non-native herb cover	NA	NA	35.5
Tree cover	29%	7.7	32.8
Shrub cover	16%	5.1	25.1

The importance value of each primary variable included in the final tree and all surrogate splits have been normalized (Breiman et al., 1984). Although non-native herb cover is not included in our final regression tree model, it is included here because of its importance in tree model construction.

The node to the left contained observations with ⩾2% non-native shrub cover. These observations were further divided by the variable native herb cover into two terminal nodes with the lowest mean class frosted elfin density values of the tree. The left terminal node had a mean class of 0.1 indicating that when the left side splitting rules of this tree model were met, frosted elfin density was low to absent when native herbaceous cover was below 36%. The proportion of the total sum of squares explained by each split in the regression tree model and each variable's importance to building the tree are summarized in Table 5. One variable, non-native herb cover did not appear in the tree but was important in tree construction (normalized variable importance = 35.6, variable rank = 4).

All of the regression tree models constructed from three of our four study sites during the fourfold cross validation were comparable and produced r^2 values similar to the all-inclusive final tree model (r^2 = 0.79, 0.79, 0.78, 0.80, respectively). The fourfold cross validation among the sites included in this study yielded an average predicted r^2 value of 0.62. Crane WMA, Gavin's Pond MWA properties, and Noquochoke WMA all had comparable predicted r^2 values (r^2 = 0.76, 0.72, 0.63, respectively). Only when a model was constructed from these three sites and used to predict the response of Myles Standish SF did the predicted r^2 decrease (n = 29, r^2 = 0.38), which suggests that there was a difference between Myles Standish SF and the other sites. Our model may be under sensitive to this difference because we did not include an explanatory variable important to frosted elfin density at Myles Standish SF, e.g., disturbance regime or land use history. In addition, only low density frosted elfin classes were identified at Myles Standish SF. However, the results of the fourfold cross validation indicated that biological differences among frosted elfin classes did not differ substantially among the study sites described by our final tree model.

4.   Discussion

Density of the larval host plant, wild indigo, was the most important explanatory variable in describing adult frosted elfin densities. Because frosted elfin larvae are specialized herbivores and are dependent on wild indigo as a host, their habitats are defined by the occurrence and distribution of the host plant (Tscharntke and Brandl, 2004). Swengel (1996) also concluded that frosted elfins were detected in areas with high host plant density, and host plant abundance was an important predictor of elfin presence. A similar positive relationship between host plant abundance and butterfly numbers has also been found for karner blues (Smallidge et al., 1996; Swengel and Swengel, 1996; US Fish and Wildlife Service, 2003).

We found that adult frosted elfin densities were greatest when host plant density was >2.6/m^2 and tree cover was <29% but that densities decreased when tree canopy cover increased even when host plant density was high (Fig. 2). Greater tree cover may decrease the temperature and have other effects on other microclimate variables. Cooler microclimate temperatures are likely to discourage shade intolerant butterflies that require a minimum threshold temperature for flight (Greatorex-Davies et al., 1993; Lane, 1999).

Our results suggest that optimal adult frosted elfin habitat contained high host plant densities and moderate tree canopy coverage. We found that high-density areas of adult activity were located in open conditions with interspersed tree cover and not in the middle of large open areas (Fig. 1). In a companion study, late instar larvae of frosted elfin were found to be present on host plants close to trees and under partial canopy cover (Albanese, 2006). Partial canopy cover over the host plant may be vital to the successful development of frosted elfin larvae within our study area, though adult frosted elfins are associated with open conditions. This difference in habitat preference between adults and larvae means that this species cannot be simply categorized as either shade tolerant or intolerant; instead this species appears to benefit from canopy heterogeneity. Similarly, the karner blue butterfly is associated with oak savanna habitat, which is also defined by canopy heterogeneity. Karner blue butterflies use areas across a shade gradient with partial canopy areas identified as an important sub-habitat (Grundel et al., 1998; Lane, 1999; US Fish and Wildlife Service, 2003).

We found that when wild indigo densities decreased, adult butterfly densities remained relatively high if shrub cover was primarily native and was below 16%. The effects of increased shrub cover on frosted elfins are probably similar to the effects of tree cover. Additionally, wild indigo was absent from vast areas of closed canopy, scrub oak shrubland (Albanese, personal observation).

The invasion and or establishment of non-native plant species on sandplains was detrimental to frosted elfin populations. Even low amounts of non-native shrub cover (⩽2.1%) reduced adult frosted elfin densities. This effect was more pronounced when native herbaceous cover was also below 36% (Fig. 2). Although, non-native herbaceous cover was not included in our final model, it was an important explanatory variable in the tree construction (Table 5). Importantly,

most of the potential habitat surveyed during this study contained some non-native vegetation.

The relationship between non-native vegetation and low frosted elfin densities at our study sites suggests that non-native vegetation may affect frosted elfin populations more dramatically than the normal succession of open habitat. Non-native vegetation encroachment may alter soil characteristics at these sites and change the xeric nutrient poor conditions characteristic of wild indigo habitat. The effect of low non-native shrub cover on frosted elfin densities may suggest that other factors that correlate with exotic shrub cover such as management regime and site history are important. The vegetation and the disturbance history in many of our sites were consistent with the findings of Neill et al. (2007), who found that high cover of non-native vegetation distinguished recent agricultural grasslands from other land cover categories within the coastal sandplain of Martha's Vineyard, Massachusetts. Many of the openings in the pitch pine-scrub oak barrens of Myles Standish SF and Crane WMA have been cleared, fertilized and planted with non-native species by state management agencies (Simmons, 1999; Epsilon Associates Inc., 2001). Some of these species are invasive non-native shrubs and non-native mat-forming grasses and forbs (e.g., multiflora rose, autumn olive, bush honeysuckles, orchard grass, timothy and clovers). Other non-native species have colonized these areas independently (e.g., oriental bittersweet) (Simmons, 1999; Epsilon Associates Inc., 2001; Simmons, personal communication). Areas surrounding potential frosted elfin habitat in the Noquochoke WMA, and portions of all of the utility rights-of-way included in this study, contained substantial non-native shrub and herb cover. Semi-annual mechanical brush cutting and mowing, without biomass removal, during late summer and autumn are the only modes of disturbance in many of these locations (Simmons, 1999; Epsilon Associates Inc., 2001; Simmons, personal communication). These methods leave vegetative debris and increase above ground biomass, thus raising nutrient inputs, retaining soil moisture, and inhibiting nitrogen leaching. When aggressive non-native vegetation is established, these conditions favor woody species and aggressive grasses (Maron and Jefferies, 2001)

More mesic, high nutrient, soil conditions resulting from non-native species cover and current and/or past management practices may favor non-native plant communities at the expense of native vegetation characteristic of xeric nutrient depleted soils. Invasive non-native species often out-compete plants of nutrient poor conditions (Huenneke et al., 1990; Hobbs and Huenneke, 1992; Wedin and Tilman, 1990; Maron and Jefferies, 1999; Stohlgren et al., 1999). Wild indigo and other plants of low nutrient, open soils are particularly vulnerable to increased soil nutrients (Aerts and Berendse, 1988; Bobbink and Roelofs, 1995; Power et al., 1995; Weiss, 1999; Ockinger et al., 2006). Weiss (1999) suggested that the extirpation of the oligophagous bay checkerspot butterfly (*Euphydryas editha bayensis*) from nutrient poor serpentine grasslands in the area of San Francisco, CA, during the 1990s was caused by increased nutrient levels that resulted in an invasion of introduced grasses. In eastern Great Britain, a long-term study reported declines in the number of non-grass feeding Lepidoptera relative to other sites in the region,

as coarse grass cover increased and became the dominate cover. The grass species and growth conditions described are comparable to the non-native grasses encountered on our study sites (Pollard et al., 1998). Similarly, a long-term study of calcareous grasslands in Germany, Wenzel et al. (2006) reported substantial declines in monophagous butterflies dependent on nutrient-poor grassland plants, and increases in butterfly species associated with host plants common in nutrient rich grasslands.

Our study is the first to quantify habitat variation for populations of adult frosted elfins and one of only a few studies to directly address the habitat requirements of rare Lepidoptera associated with disturbance-dependent sandplain habitats in the northeastern United States. The high densities of frosted elfin in open habitats containing moderate native shrub cover and low tree canopy cover demonstrated that frosted elfin habitat in our study area is comprised of a mosaic of open sandplain habitats, including grasslands with isolated trees, heathland, and thickets of closed pitch pine-scrub oak barrens. Conservation management of the frosted elfin should aim to provide areas of high wild indigo density in open landscapes with native tree and shrub canopy heterogeneity. Management should attempt to reduce non-native shrub and herbaceous cover and to increase native herbaceous cover. Both Farnsworth (2007) and Clarke and Patterson (2007) reported that rare sandplain plant species had a stronger affinity to open early successional sandplain habitats than common species. Management for frosted elfin should benefit and maintain both the suite of rare insects that thrive in shrublands (Goldstein, 1997; Wagner et al., 2003), and the rare plants associated with more open sandplain habitats with lower tree and shrub densities. We recommend comparable research be conducted in other portions of the frosted elfin's range to aid in the refinement of these management recommendations. Our results highlight the need for research focusing on the effects of non-native species establishment on Lepidoptera associated with xeric nutrient poor habitats.

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