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Microhabitat use by larvae and females of a rare barrens butterfly, frosted elfin (*Callophrys irus*)

Gene Albanese · Peter D. Vickery · Paul R. Sievert

Abstract The frosted elfin (*Callophrys irus*) is a localized and declining butterfly found in xeric open habitats maintained by disturbance. We described the effects of woody plant canopy cover, topography and host plant size and density on the quality of microhabitat of wild indigo (*Baptisia tinctoria*) host plants containing late instar frosted elfin larvae at four study sites in southeastern Massachusetts, United States. We also assessed whether females preferentially depositing eggs on host plants within specific microhabitats, therefore conferring greater survivorship to the larvae through the late-instar stage. We found that moderate amounts of canopy cover and large plant size characterized larvae-occupied host plants. In the absence of tree canopy cover, late instar larvae density remained low even when host plant density was high. However, females oviposited on wild indigo plants without regard to any of the vegetative or environmental variables we measured. These results indicate that canopy cover was an important characteristic of microhabitats containing late instar larvae, and late instar larvae occupancy was determined by suitable microhabitat conditions, and not female oviposition selection. Managing for canopy cover and microhabitat heterogeneity within relatively open habitats is recommended for the maintenance of frosted elfin populations.

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Introduction

The potential of a habitat to support a population of butterflies is often characterized in terms of the presence, abundance or density of adults and the types of habitats, and associated plants, adults require for breeding and foraging (Britten and Riley 1994; Smallidge et al. 1996; Grundel et al. 2000; Collinge et al. 2003; among others). However, the resources used by adults may not adequately reflect the requirements of the immature stages, and assessments of habitat quality are usually improved if they include both adult and immature stages (Bergman 1999; Lane and Andow 2003). The larvae of many Lepidoptera are relatively immobile and incapable of moving great distances in search of suitable host plants. Consequently, larvae are usually restricted in terms of microhabitat and food choice to the plant on which they hatched. Thus, the quality of its microhabitat affects the development and survivorship of the occupying larvae. To the extent that microhabitat suitability varies, natural selection should favor larvae on individual plants that have conditions suitable for larval growth and survival.

The restricted distribution of many rare butterflies is the result of factors other than host plant distribution (Quinn et al. 1998; Dennis et al. 2003; Konvicka et al. 2003), and butterfly abundance is often related to the number of host plants growing under specific microhabitat conditions

rather than total host plant abundance (Bourn and Thomas 1993; Bergman 1999; Lane and Andow 2003). Therefore, the conservation of rare and threatened butterfly species not only depends on the identification of adult-habitat associations but also on the determination of the microhabitat conditions suitable for larval development.

Several factors can contribute to the quality of microhabitats for immature Lepidoptera, including: microenvironmental features, climatic conditions, and their interactions (Singer 1972; Ehrlich et al. 1980; Dobkin et al. 1987; Ravenscroft 1994b), the quantity and quality of host plants (Gilbert and Singer 1975; Rausher 1981; Zangerl and Berenbaum 1992; Grundel et al. 1998b), the influence of predators and parasitoids (Sato and Ohsaki 1987; Ohsaki and Sato 1994), and the presence of associating ants (Thomas 1984; Baylis and Pierce 1991; Hochberg et al. 1994; Wagner and Kurina 1997). These factors may be most important for univoltine oligophagous Lepidoptera with restricted host-species options and limited time of larval development.

Our study characterized the microhabitat associations of the immature stages of the frosted elfin (*Callophrys irus*, Godart 1824) in terms of the presence of late-instar larvae on its host plant, wild indigo (*Baptisia tinctoria*). We examined several aspects of the microhabitat associated with host plants occupied by late-instar frosted elfin larvae, and paid particular attention to the effect of woody plant canopy cover, topography and host plant size and density.

The frosted elfin is a non-migratory and oligophagous Lycaenid butterfly that occurs in relatively small, localized populations and produces one brood (generation) per year (Scott 1986; Opler 1998). Populations appear to be monophagous and are limited to xeric sand barrens and savanna habitat with an open vegetation structure, often maintained by anthropogenic activities or natural disturbance (Wagner et al. 2003). The distribution of frosted elfin once extended from southern Ontario and the northeastern United States, south to Florida, and west to Texas and Wisconsin (Opler et al. 1995; Layberry et al. 1998). The species is now likely extinct from Canada, Maine and Illinois and is state-listed as endangered, threatened, or of special concern in eleven states in the eastern United States (Packer 1998; NatureServe 2006).

For some Lepidoptera, preferential host plant selection by ovipositing females may reflect differences in microhabitat quality that maximize larval growth and development (Wiklund 1977; Rausher 1979; Rausher and Papaj 1983; Grundel et al. 1998a). The "preference-performance problem" (Thompson 1988) assumes that host plant preference by ovipositing females has evolved to maximize the success of the immature stages. If females select host plants that increase larval growth and development, this will lead to increased larval survivorship and adult production. This may not be the case for some oligophagous butterflies living in environments where larval survival is primarily explained by differences in the microhabitats of oviposition sites (Weiss et al. 1988). Our study examined this question by comparing the vegetative and environmental variables associated with host plants on which females deposited an egg, to plants that were either occupied or unoccupied by late-instar larvae.

Topography and tree canopy cover can affect vegetation and other environmental patterns within a habitat and, therefore, create microhabitats with different microenvironments (Warren 1987; Weiss et al. 1988; Ravenscroft 1994a; Grundel et al. 1998b). The spatio-temporal extents of these microhabitats are not static, thus the availability and distribution of suitable host plants changes over time. The unpredictability of microhabitats on an annual basis may make adaptive selection of host plants within specific microhabitats less advantageous for univoltine oligophagous butterflies, as in the case of the Bay Checkerspot (*Euphydryas editha bayensis*), where vegetative and other environmental conditions of certain microhabitats favored larval survivorship and adult production during most annual cycles. However, years of unusually wet and cool or drought weather patterns altered the size and location of suitable microhabitats. By distributing eggs across a range of microhabitats, this species was able to ensure at least some successful reproduction during most years (Ehrlich et al. 1980; Dobkin et al. 1987; Weiss et al. 1988).

For some Lepidoptera, the size and/or the local quantity of host plants has been correlated with increased oviposition rates and larval abundance, feeding damage, and successful development (Damman and Feeny 1988; Bourn and Thomas 1993; Zangerl and Berenbaum 1992; Swengel 1995; Grundel et al. 1998b). Among butterflies the relationship between canopy cover and host plant quantity and detectability can also affect both female oviposition behavior (Wiklund 1984; Shreeve 1986; Bergman 1999) and larval survivorship. Rausher (1979) concluded that three species of ovipositing swallowtail butterflies could locate host plants in open conditions more readily than host plants in shade and for two of the species, oviposition rates were greater on non-shaded plants. However, faster larval development and increased survival was associated with shaded host plants for all three species. Similarly, Lane and Andow (2003) found that female Karner blue butterflies (*Lycaeides melissa samuelis*) deposited more eggs in open habitats but that larvae survival was greatest in closed canopy sub-habitats.

Our aim was to construct descriptive models that identified the vegetative and other environmental features associated with frosted elfin host plants. We specifically compared the features of host plants occupied and unoccupied by late-instar larvae. To address how female host

plant selection influenced late-instar host plant occupancy, we compared plants on which females deposited an egg to: (1) plants with late-instar larvae, and (2) host plants that showed no evidence of late-instar larvae. We used classification and regression tree analysis (De'ath and Fabricius 2000) to compare each group and to correlate late-instar larval density with tree canopy cover and host plant density.

Methods

Study area and organisms

We studied the frosted elfin within early successional sandplain communities 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) (Fig. 1, Table 1). These areas are on the coastal plain and characterized by xeric sandy soils and relatively flat topography.

The frosted elfin is a univoltine butterfly species that over-winters as a pupa. The flight period is ~8 weeks, starting in late April and lasting through mid-June with the peak flight usually occurring in mid-May. Adult females deposit single eggs, usually nestled in the apical shoot of a wild indigo plant. Eggs hatch within 1 week of oviposition and early instar larvae feed by skeletonizing young leaves within apical shoots. The larvae remain on the host plant for 5–6 weeks, passing through four larval instars. Late-instar larvae feed on the entire leaves and flower shoots of wild indigo and portions of the main stem's epidermal and cortex tissues (Albanese et al. 2007a). Larvae pupate by late July and remain in pupal diapause until the following spring (Albanese et al. 2007a).

In eastern Massachusetts, frosted elfin larvae feed exclusively on wild indigo. Wild indigo is a characteristic perennial herb of early successional sandplain communities in southeastern Massachusetts (Swain and Kearsley 2001). Wild indigo plants form single or multi-stemmed groups. For the purposes of this study, we defined a wild indigo "plant" as a single or multi-stemmed group of wild indigo with continuous foliage overlap.

Field methods

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 site that included 1:25,000 USGS topographical Quad Images and 0.5 m resolution 1:5,000 color digital ortho-images. We used color digital ortho-images for each study site to delineate all potential frosted elfin habitat within the pitch pine-scrub oak barrens or similar anthropogenic habitats based on Wagner et al.'s (2003 p 96) definition: "xeric and open disturbance-dependent habitats on sandy soil, including openings in pitch pine—scrub oak barrens and similar anthropogenic habitats" (Fig. 2). Habitat was considered unsuitable for frosted elfin if it did not meet this description, i.e., closed canopy pitch pine—scrub oak barrens. We verified and refined the GIS maps with field surveys.

We surveyed each study site for adult frosted elfin aggregations in both 2004 and 2005. We divided the 60-day flight period into three 20-day intervals, and completely surveyed each potential habitat patch once during each interval. To survey each patch systematically, we created field maps using ortho-images marked with incremental 10 m tick marks and 25 m grid lines. We then used the 25 m grid lines as transects and searched all delineated areas while walking along transects at a steady pace (~30 m/min). We counted all adult frosted elfins and recorded their locations on the ortho-image and using a GPS receiver. We were careful not to recount the same individuals twice during a survey. We standardized our sampling effort by searching individual patches for a minimum of 15 min during each visit. All surveys were conducted during weather conditions appropriate for flight (Pollard

Fig. 1 The study area is represented by the cross-hashed section of Massachusetts, US. The locations of each of the four study sites for frosted elfin surveys in 2004–2005 are marked within the enlargement of the study area
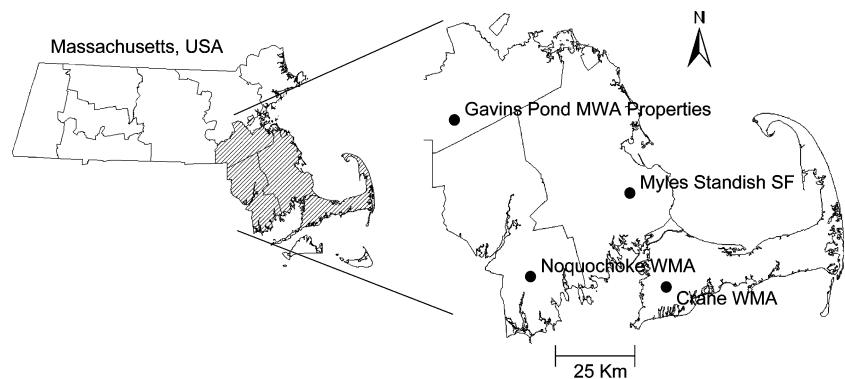
Table 1 The total area of delineated potential frosted elfin habitat surveyed for adult aggregations at four study sites in southeastern, Massachusetts, US, 2004–2005

Study site	Total potential habitat area (ha)	Total number aggregations	Mean (SE) annual aggregation area (ha)	Total occupied host plants	Total unoccupied host plants	Total oviposition host plants [a]
Crane WMA	153.8	1	7.5 (0.02)	55	70	32
Gavins Pond MWA	36.3	4	7.1 (0.08)	109	119	71
Myles Standish SF	121.0	3	2.2 (0.08)	8	14	6
Noquochoke WMA	23.5	2	2.0 (0.04)	35	44	14

The total numbers of aggregations surveyed for late-instar larvae, the mean total annual area of the aggregations and the total number of wild indigo plants in each group sampled are listed for each site. Aggregations were delineated using minimum convex polygons (Fig. 2)

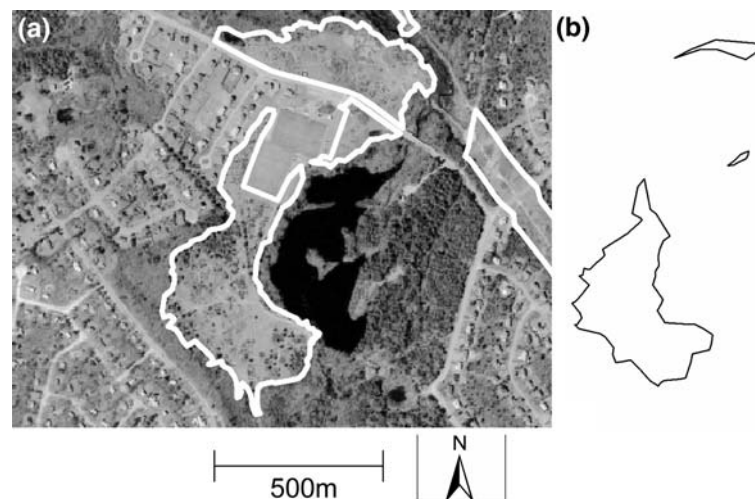[a] Oviposition host plants were only sampled during 2005

Fig. 2 (**a**) A 0.5 m resolution 1:5,000 *gray* scale digital ortho-image of a portion of the Gavins Pond MWA study site in southeastern Massachusetts, US. The white lines outline potential frosted elfin habitat surveyed for adults during the annual flights in 2004–2005. (**b**) The minimum convex polygons (*MCP*) of the adult aggregations within the same area of the Gavins Pond MWA study site. MCPs were delineated using adult frosted elfin locations collected during surveys of the site. We randomly searched wild indigo plants within each MCP for late-instar larvae

1988). We surveyed 335 ha of potential habitat for adults in each year of our study (Table 1).

In 2005, we observed female ovipositioning behavior at each study site and recorded the locations of wild indigo plants on which female frosted elfin deposited an egg. To insure that survey effort per area remained relatively constant across study sites we conducted surveys for oviposition locations systematically and simultaneously with adult surveys. We continuously followed an individual frosted elfin until it deposited an egg. When the female deposited an egg, we uniquely labeled the plant and recorded its location with a GPS receiver. To increase the precision of each recorded location we also marked each plant on a map made from a 0.5 m resolution 1:5,000 color digital ortho-image. When we concluded a set of observations for a particular female we moved ~50 m from the area before observing a new individual.

We then sampled wild indigo plants over a 5-week period from late June to late July, 2004 and 2005 (Table 1). To concentrate and maximize our survey effort during the late-instar larvae surveys, we only searched wild indigo plants in areas that contained aggregations of adults during the corresponding annual flight. We considered a cluster of individual adult locations a discrete aggregation if three or more adult frosted elfin locations were observed within 100 m of each other during an adult survey. We used the 100 m distance threshold because adult locations separated by a distance <100 m were consistently clustered together and adult locations separated by a distance >100 m were always >200 m from the next closest location. Once each adult aggregation was identified, the outermost adult locations within the aggregation were connected within the GIS using the Minimum Convex polygon (MCP) method (Mohr 1947) (Fig. 2). We delineated the MCP areas of nine

adult aggregations across the four study sites in 2004 and of ten aggregations in 2005 (Table 1). While the locations of adult aggregations remained relatively constant between the 2 years of this study, one additional area at the Gavins pond MWA was only detected and surveyed in 2005.

During fieldwork in 2004, we found that late-instar larvae gnawed a distinctive "larval-feeding ring" on the main stems of the host plant they occupied. Based on lab and field tests conducted in 2005, we determined that the larval-feeding ring was a reliable surrogate for detecting late-instar larvae on wild indigo plants (Albanese et al. 2007a). Therefore, in 2005 we included wild indigo plants with only a larval-feeding ring in the late-instar larval occupied group.

In 2004, we systematically surveyed all areas of each MCP for late-instar frosted elfin larvae by proceeding across the length of the area of an aggregation in a linear fashion during which wild indigo plants were haphazardly selected and searched for late-instar frosted elfin larvae. We concentrated our search for larvae on the stems, flowers and young leaves of wild indigo where larvae concentrate resting and feeding activities. When a late-instar larva was detected, we uniquely labeled the plant and recorded its location with a GPS receiver and on a field map. We then measured seven vegetative and other environmental variables (Table 2) at all wild indigo plants containing late-instar larvae within each aggregation ($n = 96$).

We also selected random points within each aggregation comparable to the number of plants on which we detected larvae. We located the nearest unoccupied wild indigo plant to the random point. We recorded the seven vegetative and environmental variables in Table 2 at these plants ($n = 102$). During the 2 years of this study, no frosted elfin larvae were located on plants ≤0.15 m² in size because

these were probably seedlings from the same growing season and were not available as oviposition sites for females during the spring adult flight period. Therefore, we excluded unoccupied wild indigo plants ≤0.15 m² from our analysis.

Because we located a large number of late-instar larvae in 2004, we adopted a more systematic sampling protocol to conduct larval surveys in 2005. We overlaid a 5 m² grid on each adult frosted elfin aggregation in the GIS and randomly selected a sample of grid cells. We used photo interpretations of the 0.5 m color ortho-images to stratify the selected grid cells into three groups: grid cells containing no tree canopy cover; <50% tree canopy cover; and >50% tree canopy cover. At each site an equal number of grid cells were selected within each tree canopy cover group. The number of grid cells selected within each aggregation was roughly proportional to the area each aggregation encompassed relative to the total area of delineated aggregations across sites. We located grid cells on the ground using a field map and a GPS receiver. Grid cells without wild indigo were not surveyed. We searched all wild indigo plants within each grid cell for late-instar frosted elfin larvae and/or larval-feeding sign.

We marked all wild indigo plants that contained a late-instar larvae ($n = 75$), or only a larval-feeding ring ($n = 36$), and recorded their locations with a GPS receiver and on a map. At each occupied plant we measured the same seven vegetative and environmental variables as in 2004 (Table 2). A random sample of unoccupied wild indigo plants ($n = 146$) were also selected to compare to the larvae-occupied group. Within grid cells that contained wild indigo plants with no late-instar larvae or larval-feeding rings, we randomly selected unoccupied wild indigo plants. We generated random points within each grid

Table 2 Description of the vegetative and environmental variables measured in the larval frosted elfin study in southeastern Massachusetts, US, 2004–2005

Variable	Definition
Canopy cover	The woody plant canopy cover over the center of the wild indigo plant. The average of four spherical densitometer (Lemmon 1956) readings measured at breast height (1.5 m) in each of the four cardinal directions
Distance to nearest tree	The linear distance (cm) from the nearest edge of the wild indigo plant to the nearest edge of a woody plant >2.5 m in height
Direction of nearest tree	The direction measured in degrees with a compass of the main stem of the nearest woody plant >2.5 m in height
Plant size	The maximum foliar width (cm) of the wild indigo plant multiplied by the maximum height (cm) of the wild indigo plant
Distance to nearest wild indigo plant	The linear distance (cm) from the edge of the wild indigo plant to the edge of the nearest neighboring wild indigo plant
Slope	The steepest slope angle measured in degrees with an optical clinometer from the center of the wild indigo plant
Slope aspect	The direction of the steepest slope angle measured in degrees with a compass from the center of the wild indigo plant

Data were collected in late June and July within frosted elfin aggregations at wild indigo plants occupied by late-instar larvae and randomly selected wild indigo plants unoccupied by late-instar larvae. Wild indigo plants on which adult female frosted elfins were observed ovipositing eggs during the adult flight period were also measured in July of 2005

cell and sampled the nearest unoccupied wild indigo plant with no larval-feeding ring.

To assess the effects of wild indigo density and tree canopy cover on late-instar larval density, we totaled the number of wild indigo plants containing evidence of late-instar frosted elfin larvae within each surveyed grid cell ($n = 93$). We estimated the percent tree canopy cover using nine cover classes (0, 0–≤1%, ≥1–2%, ≥2–5%, ≥5–10%, ≥10–25%, ≥25–50%, ≥50–75%, and ≥75–100%) modified from Braun-Blanquet (1964). Cover classes were converted to midpoints in the analysis. We also recorded the number of discrete wild indigo plants within each 5 m^2 cell.

During the adult surveys, we collected oviposition locations from 87 individual females at the four study sites (Table 1) to assess how female host plant selection influenced late-instar larvae host plant occupancy. We revisited each wild indigo plant on which a female deposited an egg ($n = 123$) during late June and July, and measured the same seven vegetative and environmental variables (Table 2) for comparisons to the late-instar occupied and unoccupied groups. We also examined each plant for late-instar larvae or a larval-feeding ring. Seven of the wild indigo plants in the oviposition group (5.7%) were occupied by late instar larvae and or contained a larval-feeding ring. Therefore, the oviposition group included both plants occupied and unoccupied by late instar larvae but these plants were only included in the oviposition group and each individual plant was only used once in our analysis.

Statistical analysis

All data were analyzed using R: A language and environment for statistical computing (2004) and Statistical Analysis System (SAS) 9.1 (2003) software. We modeled the variation in our response variables using classification and regression tree analysis. We chose this technique because it is well suited for analyzing complex ecological data. Classification and regression tree analysis can detect non-linear responses, explain complex interactions and are robust to outliers. 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 (Breiman et al. 1984; De'ath and Fabricius 2000).

Interpretations of classification and regression trees are straightforward. The two resulting groups of a partition are called nodes. If the groups cannot be further partitioned, they are called terminal nodes. The tree diagram displays the splitting rules used at each partition and each split used to reach a terminal node. The lengths of the vertical lines leading to each node indicate the relative strength of each partition. At each terminal node in a classification tree, the dominant category in each terminal group and the proportion of observations in that category are listed. Trees are interpreted by following the branches to the terminal node.

All classification trees were developed with the minimum splitting criteria at a node set to ten and the minimum terminal node size set to five. Node impurity was calculated using the Gini index (Breiman et al. 1984). Prior probabilities were set to equal. We used repeated tenfold cross validation to select the pruned tree. The data were divided into ten mutually exclusive subsets of equal size. Each time we dropped a subset, we constructed a new tree using the remaining subsets. The new tree was then used to predict the response of the remaining subset. From each tenfold cross validation, we calculated an estimate of average error and the standard error (SE) of the error estimate for each tree size (De'ath and Fabricius 2000). We repeated the tenfold cross validation 1,000 times and used the average and SE of the estimated errors from 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. Splitting and model selection criteria remained constant for all constructed trees.

To evaluate the overall classification tree performance we calculated the correct classification rate (CCR) and chance-corrected classification accuracy statistic (κ) of each tree. In addition, we derived a p-value for each pruned tree using Monte Carlo resampling. We created 1,000 trees through random permutation of the data. We then compared the (CCR) of our classification trees to the distribution of CCRs.

Each partition in a classification tree yields the greatest reduction in the Gini index (Breiman et al. 1984). Total deviance is a measure of the reduction in the Gini index provided by each partition in a classification tree. To assess the relative importance of each explanatory variable we calculated the percent total reduction in the Gini index associated with each partition in a pruned tree. First, we calculated the total deviance as the difference in the Gini index between the root and the terminal nodes of a pruned classification tree. The proportion of the total deviance explained by each partition in a tree was the percent reduction in the Gini index weighted by the sample size in each daughter node. We defined the percent total reduction in the Gini index associated with each partition in a pruned tree as the partial deviance. We then calculated the partial deviance at each partition and summed each explanatory variables partial deviance across the pruned classification

tree. We expressed the partial deviance as the percentage of the total deviance explained by each variable in the final pruned classification tree.

Wild indigo plants were the sampling units for all classification tree analyses. We used classification tree analysis to model the variation in the categorical response variable late-instar occupied versus unoccupied plants using the set of seven vegetative and environmental variables in Table 2. We first performed separate classification tree analyses on data from 2004 to 2005. We compared the results of these trees to each other to check for possible trends between years. The 2004 and 2005 classification trees related the same set of explanatory variables to the response variable. We then conducted a twofold cross validation using each year's observations to predict the response of the other year. Both classification trees had a CCR of 88%. The average CCR of the observed versus predicted was 87.5%. We therefore pooled both years' observations for the final analysis.

We then performed separate classification tree analyses using the set of seven explanatory variables to model the variation in the categorical response variables adult female oviposition plants versus late-instar larvae occupied plants, and adult female oviposition plants versus late-instar larvae unoccupied plants. Because we only collected data on oviposition plants in 2005, we used only plants measured in 2005 in these analyses.

As part of our final analysis, we performed a fourfold cross validation to assess the potential effects of study sites on each final model. 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 and then predicting the response of the hold out site. We calculated the CCR of each classification tree and each sites' predicted response.

Finally, we used regression tree analysis to model the variation in number of late-instar larval occupied host plants/5 m^2, using wild indigo density and tree canopy cover as the explanatory variables. We used the same splitting and model selection criteria used for the classification tree analysis. Node impurity was calculated using sums of squares about group means (Breiman et al. 1984). We also derived a p-value for the pruned regression tree using Monte Carlo resampling. We compared the r^2 of our regression tree to the distribution of r^2-values of 1,000 randomly permuted trees. The predicted value (mean) of the response variable and the number of observations in each terminal group were listed at each terminal node of the tree. We calculated the total variance explained and the proportion of the total variance explained by each partition in the final pruned tree model.

Results

Larval occupied versus unoccupied wild indigo plants

The classification tree analysis of occupied versus unoccupied wild indigo plants using the set of seven explanatory variables is shown in Fig. 3. The tree model includes only three of the seven explanatory variables. Canopy cover, plant size and distance to nearest tree correctly classified 401 of the 454 observations (CCR = 88%, $\kappa = 0.77$, $p = <0.001$).

Occupied plants were classified as large (>0.6 m^2) with >8% canopy cover or close to trees (≤6 m), or smaller (<0.6 m^2) but under a narrower range of canopy covers (>19% but ≤65%). The greatest numbers of both occupied and unoccupied wild indigo plants were classified by 8% canopy cover and plant size of 0.6 m^2. Canopy cover was the most important variable for describing late-instar larval occupancy on wild indigo plants. Canopy cover initially partitioned the observations into two sub-groups of >8% canopy cover and <8% and further partitioned the observations at 65 and 19% canopy cover (partial deviance = 57%). Plant size was also an important explanatory variable partitioning the observations into two sub-groupings of >0.6 m^2 and <0.6 m^2 (partial deviance = 23%). Distance to nearest tree, split observations with <8% canopy cover and >0.6 m^2 plant size into two terminal groups consisting of observations ≤6 m from the nearest tree and ≥6 m from the nearest tree (partial deviance = 6%).

All of the classification tree models constructed from three of our four study sites during the fourfold cross validation among sites were similar and produced CCRs ranging from 83.7 to 90.0%. The variables canopy cover and plant size consistently defined differences between larvae occupied and unoccupied plants in all of the models. The average CCR for observed versus predicted among the study sites was 79.8% indicating homogeneity among our study sites for the response, occupied versus unoccupied wild indigo plants.

Late-instar larvae density

The regression tree modeling of the number of late-instar larval occupied host plants/5 m^2 against the variables total tree canopy cover/5 m^2 and number of wild indigo/5 m^2 (Fig. 4) further supported the results of the classification tree in Fig. 3. The regression tree analysis of these data produced a tree with three terminal nodes (Fig. 4). The tree suggests that the density of late-instar larvae was best modeled by partitioning wild indigo density at >15/5 m^2 and <15/5 m^2 and total tree canopy cover at >4 and <4%. When wild indigo density was <15/5 m^2, the predicted response of late-instar larvae density was 0.6. Even when
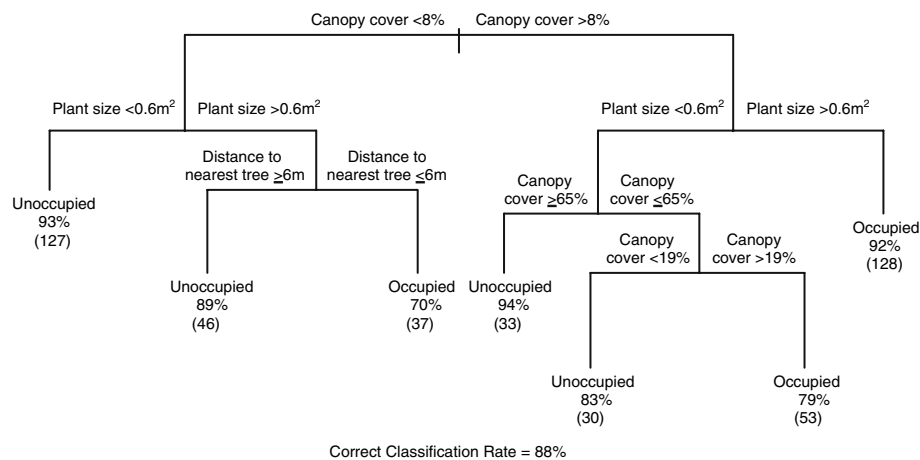
Fig. 3 Pruned classification tree on the categorical response variable late-instar larval occupied versus unoccupied wild indigo plants. The seven explanatory variables used to model the variation in this response are summarized in Table 2. Each of the trees six splits are labeled with the value of the explanatory variable used to determine the split. Trees are interpreted by following the branches to a terminal node. Each terminal node is labeled with the dominant response category of that terminal group, the proportion of observations in the dominant category, and the total number of observations in the group is given in parentheses. The chance correct classification rate statistic (*Kappa*) of the model was 0.77
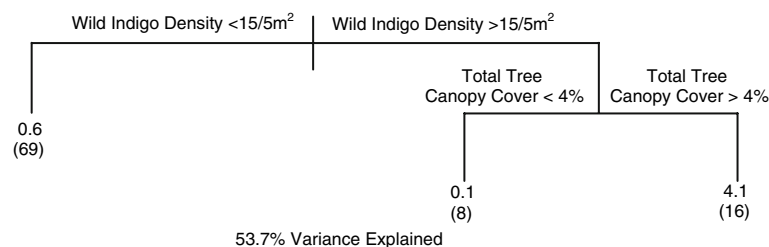

Fig. 4 Pruned regression tree modeling the number of late-instar larval occupied host plants/5 m^2 against the variables total tree canopy cover/5 m^2 and number of wild indigo/5 m^2. Each partition is labeled with the splitting rule and its value. Terminal nodes are labeled with the predicted (mean) value of the observations in the terminal group and the number of observations in the group is listed in parentheses

wild indigo density was high (>15/5 m^2) the predicted response remained low (0.1) when total tree canopy cover was <4%. However, higher wild indigo density in conjunction with >4% total tree canopy cover increased the predicted response to 4.1. The percent of variation explained by the tree model (r^2) was 53.7% ($p = <0.001$). Both partitions explained an equal proportion of the total variance explained by our model ($r^2 = 26.8\%$).

Oppositional versus larval occupied and unoccupied wild indigo plants

The pruned classification tree model of adult female oviposition plants versus late-instar larval occupied plants using seven explanatory variables is shown in Fig. 5. The variables canopy cover and plant size correctly classified 200 of the 234 observations (CCR = 85% κ = 0.71, $p = <0.001$). Canopy cover was the most important variable (partial deviance = 63%) in the model, followed by plant size (partial deviance = 22%).

The interpretation of the classification tree in Fig. 5 was consistent with the interpretation of the larval occupied versus unoccupied wild indigo plant model (Fig. 3). Late-instar larval occupied plants were characterized as large (≥0.6 m^2) and under some tree canopy cover (≥7%) or smaller (≤0.6 m^2) but within a range of tree canopy covers (≥14 but <65%). When canopy cover was ≤7%, larval occupied plants tended to be very large (≤1.9 m^2). In contrast, broader ranges of plant size and canopy cover, when compared to larval occupied plants, characterized oviposition plants. The greatest number of oviposition plants were classified by ≤7% canopy cover and a variety of plant sizes (≤1.9 m^2). Smaller oviposition plants (≤0.6 m^2) tended to have either 7–14% or >65% canopy cover. Similar to larvae unoccupied plants, when oviposition plants measured <0.6 m^2, they tended to be under canopy cover outside the range that characterized late-instar occupied plants.

The classification trees constructed from three of the four study sites during the fourfold cross validation among

Fig. 5 Pruned classification tree on the categorical response variable late-instar larval occupied wild indigo plants versus wild indigo plants on which frosted elfins were observed depositing an egg. This analysis was performed using the same set of explanatory variables used to construct the tree in Fig. 3 (Table 2). The chance correct classification statistic (*Kappa*) of the model was 0.71
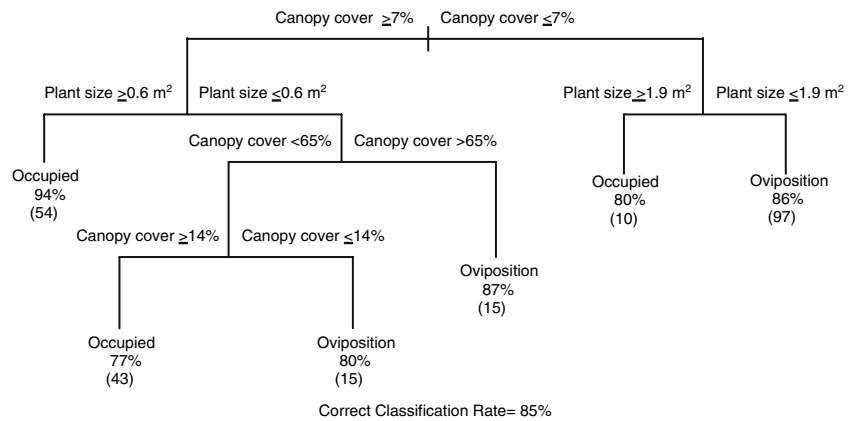
sites had an average CCR of 80.5%. When the response of each site was predicted using these models the average CCR for the observed versus predicted was 74.6%. While our sampling effort was consistent across study sites, the number of adult females varied among sites. This resulted in considerably fewer oviposition plants sampled at Noquochoke WMA and Myles Standish SF ($n = 14$ and 6, respectively), than at Gavins Pond MWA and Crane WMA ($n = 71$ and 32, respectively). When either Noquochoke WMA or Myles Standish SF was removed from the analysis, the splitting rules, arrangement of the trees, and CCRs of the models remained the same (85%). The CCR for observed versus predicted was high for both sites (86.5 and 92.3%, respectively). These sites had little influence on the final model but were accurately predicted by the models constructed from Crane WMA and Gavins Pond MWA, suggesting that the variables and splitting rules used to classify the response variable were similar for these sites. In contrast, when either Crane WMA or Gavins Pond MWA was excluded from the model, the CCR of the trees constructed from the three remaining sites declined (77 and 75%, respectively). When the responses of these sites were predicted using these models, the CCR for the observed versus predicted also decreased (65 and 54.8%, respectively). This implies that these two sites heavily influenced the final model. However, we included all of the sites in the final model because we sampled each site sufficiently, all of the models included the same variables and had relatively high CCRs, and both Noquochoke WMA and Myles Standish SF were accurately predicted in the fourfold cross validations.

The results of our comparison between oviposition plants and larval unoccupied plants suggest that there was no difference between these two groups, based on the variables we measured. The CCR (63%) was only 9% greater than the percentage of unoccupied observations (54%) included in the analysis. The κ statistic was only 0.23. We were unable to construct any trees from three of

the four study sites for the fourfold cross validation among sites, further suggesting that this model was weak. However, based on the results of the fourfold cross validation among sites performed on oviposition versus late-instar larvae occupied plants, we suggest that some correlation probably exists among the study sites included in this analysis.

Discussion

In this study we compared the vegetative and environmental features associated with wild indigo plants that were occupied, with those that were not occupied by late-instar frosted elfin larvae. Our analysis revealed that tree canopy cover and host plant size strongly influenced occupancy by late-instar larvae. We also investigated patterns in oviposition to determine if adult females were selecting host plants and microhabitats that conferred greater survivorship through larval development to the late-instar stage. Our results indicate that females appear to indiscriminately deposit eggs with regard to wild indigo microhabitat. Therefore, the presence of late-instar larvae on wild indigo was a function of differing rates of larval survivorship among microhabitats, and not the result of oviposition selection.

Canopy cover was the most important discriminating variable between occupied and unoccupied host plants. Canopy cover influenced both the occupancy of wild indigo and the density of late-instar larvae. Few larvae were found in the absence of tree canopy cover despite high wild indigo density (Fig. 4). In a companion study, we found that the highest densities of adult frosted elfin were in areas with <29% tree canopy cover or <16% shrub cover (Albanese et al. 2007b). Our study demonstrates the importance of tree canopy cover over host plants for development of frosted elfin larvae. Several other studies have shown a similar relationship between canopy cover and increased

numbers of butterfly larvae (Grundel et al. 1998b; Bergman 1999; Lane and Andow 2003).

Shade provided by canopy cover may have improved host plant quality by affecting the balance of nutrients and the concentrations of defensive chemicals within wild indigo plants. Proteins, carbohydrates, water and other nutrients are often limiting factors during Lepidopteron larval development (Simpson and Simpson 1990; Slansky 1993). When water levels decrease in insect foods, larvae digestive efficiency and growth rates generally decline (Slansky and Scriber 1985). Elevated protein content in plant foods can increase the survivorship of Lepidoptera larvae (Cates et al. 1987; Taylor 1988). Temperature and water stresses may be exacerbated in the xeric and open habitat of wild indigo, which could reduce protein and water available to feeding larvae, and increase the concentrations of alkaloids and other secondary compounds in the plants (Mattson 1980). Shade provided by canopy cover moderates daytime temperature extremes and water stress for plants and larvae. Grundel et al. (1998a) found that Karner blue butterfly larvae, fed shade-grown leaves from their host plant wild lupine (*Lupinus perennis*), had significantly higher growth rates.

The effect of host plant size on late-instar occupancy varied with tree canopy cover. Larger (>0.6 m^2) host plants were occupied by larvae when tree canopy cover was >8%. Smaller plants (<0.6 m^2) were occupied by larvae under more canopy cover (>19%, ≤≤5%). Only larger (>0.6 m^2) host plants were consistently occupied by larvae when tree canopy cover was <8%. However, these plants were in close proximity to trees (≤6 m) and were likely influenced by canopy shade (Fig. 3). The effects of canopy cover and host plant size may not have been mutually exclusive because relatively large host plants may have provided some supplemental cover for larvae.

Several researchers have documented increased abundance of butterfly larvae on larger host plants (Bourn and Thomas 1993; Ravenscroft 1994a; Grundel et al. 1998b). Female frosted elfins deposit their eggs in the apical shoots of wild indigo plants and early instar larvae feed on the young leaves in these shoots (Albanese et al. 2007a). Young leaves are a high quality food for larvae because protein and water levels are highest in young leaves, and defensive plant compounds and digestibility reducing defenses increase with leaf age (Mattson 1980; Scriber and Slansky 1981; Slansky 1993). Because of their greater size, large wild indigo plants have a greater number of apical shoots and more abundant young foliage for developing larvae. As a larva develops, it typically defoliates the initial shoot on which it hatched. The larva then moves to other shoots on the host plant and concentrates feeding on young foliage (Albanese et al. 2007a). Anthes et al. (2003), also noted a similar association between larvae of the marsh

fritillary butterfly (*Euphydryas aurina*) and large host plants. They suggested that this strategy eliminated the risks of predation and exposure to adverse weather conditions associated with moving to another host plant. In our study, distance to nearest wild indigo plant was not a significant explanatory variable, and thus was not included in the occupied versus unoccupied wild indigo plants model (Fig 3.). This further suggests that frosted elfin larvae are restricted to the host plant on which they hatch. Large host plants may provide sufficient food for developing frosted elfin larvae to survive until pupation enabling them to avert the dangers of moving among neighboring plants.

The architecture of a plant, and the surrounding vegetation, can also affect the apparency of a host plant and thus the susceptibility of the occupying larvae to predation and parasitism. Sato and Ohsaki (1987) found that the most important difference in the survivorship of larvae among suitable host plants for three species of swallowtail butterfly was the inability of braconid parasitoids to locate larvae on host plants growing in overshadowing vegetation. Therefore, a butterfly species may use a host plant of nutritionally lower quality because the pressures of predation and parasitism are lower (Ohsaki and Sato 1994). The strong association of late-instar frosted elfin larvae with large shaded host plants may be the result of higher larval mortality within smaller and/or non-shaded plants because of the superior search efficiency of parasitoids and predators under open conditions. In addition, frosted elfin larvae have a loose facultative relationship with ants (Albanese et al. 2007a). The abundance of associating ants varies among open and shaded microhabitats and can increase with increased host plant quality (Baylis and Pierce 1991; Lane 1999). Selecting microhabitats that enhance the opportunity to attract a "standing guard" of ants can decrease predation and parasitism rates and increase the growth rates and survivorship of some larvae (Cushman et al. 1994; Grundel et al. 1998a; Pierce et al. 2002).

We did not detect an oviposition preference for larger plants or shaded microhabitats. Our findings imply females lay eggs indiscriminately without respect to any of the vegetative and environmental features measured. In this study, females were wild indigo specialists and only laid eggs in the apical shoots of the host plant. However, further adaptive specialization to fine scale microhabitat conditions may not exist because of significant variation in macro-environmental conditions over longer temporal scales than the scope of this study. Within xeric, disturbance-dependent habitats, the spatio-temporal extent of suitable microhabitats for frosted elfin larvae are likely not static. Highly selective oviposition preference may not be a successful strategy for this univoltine butterfly because of the stochastic nature of disturbance and the variability of climate. Similar to the conclusions of Weiss et al. (1988),

distributing eggs across a range of microhabitats may help insure successful reproduction during atypical annual cycles. Our conclusions on oviposition preference should be interpreted with caution because of the small sample size of ovipositing females at two sites and the fact that we studied oviposition behavior for only 1 year. We recommend further research be conducted on the oviposition behavior of this species over several years and among several large populations. Further applications of our findings should consider possible differences among sites and annual differences in behavior.

Ecological studies that identify essential habitat and resources are a requirement for successful Lepidoptera conservation (Murphy et al. 1990; Dennis 2006), yet these key variables are largely unknown for most species of Lepidoptera restricted to pitch pine-scrub oak barrens in the northeastern United States (Wagner et al. 2003). Resolution of this conservation problem is only possible through the acquisition of autecological data for the rare and declining Lepidoptera of this unique ecosystem (Goldstein 1999; Wagner et al. 2003; New 2007). Our study is the first to quantify the previously unidentified habitat requirements of populations of immature frosted elfin. Results from our analyses indicate the importance of canopy heterogeneity in maintaining appropriate larval habitats. Providing host plants with a diverse range of microhabitats has been suggested to be vital to the long-term persistence of some rare butterfly species (Weiss et al. 1988; Lane and Andow 2003). Our conclusions, however, are based on a static analysis of microhabitat and would be improved by research that incorporates significant variability in environmental conditions. Such research could then identify the effects of changing availability and distribution of suitable larval host plants among several generations.

We recommend that further research be conducted on the effects of shaded microhabitat on host plant quality and the parasitism and predation rates of frosted elfins and other rare Lepidoptera restricted to pitch pine-scrub oak barrens, and similar habitats. Also, studies are needed to determine how different management practices affect frosted elfin populations. Conservation and management of frosted elfins should aim to provide areas with 0–65% canopy cover containing wild indigo and thus provide adequate host plants along a gradient of open and shaded microhabitats. Management should recognize the potential importance of canopy cover to the different life stages of open habitat associated Lepidoptera and attempt to include isolated trees and partial and closed canopy tree and scrub thickets within open habitats.

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