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RESEARCH ARTICLE

Habitat Restoration for Lupine and Specialist Butterflies

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Abstract

The decline of the Frosted elfin butterfly (*Callophrys irus* (Godart)) population in the Rome Sand Plains (RSP) of central New York is directly related to loss of its host plant, Wild blue lupine (*Lupinus perennis* L.), as Eastern white pine (*Pinus strobus* L.) invades the open sandy habitats where lupine grows. A Frosted elfin (New York threatened) population remains where lupine is the densest. We tested the hypotheses that tree canopy hinders lupine performance and restricts elfin behavior. Removal of white pines in experimental plots resulted in dramatic increases in canopy openness. Lupine flowering stems and lupine cover increased significantly in the tree removal plots and remained constant or declined in the control plots. The total number of lupine stems decreased, however, in both control and cleared plots. Observations of butterflies in the experimental plots increased significantly after tree removal, and male elfins, which form mating territories in sandy areas at the edges of lupine patches, established new territories in open patches where trees had been removed. Several new territories have been used each year since tree removal. This rapid response by the butterflies reflects their behavioral preferences for open areas near lupine patches. Selective tree removal at the RSP has benefited individual lupine plants and increased habitat for Frosted elfin butterflies, but more extensive habitat manipulation may be necessary to increase lupine population numbers.

Key words: Frosted elfin butterfly, habitat, lupine, restoration, tree removal.

Introduction

Many Lepidoptera species are threatened by loss of suitable habitat, the causes of which are myriad (New 1991). Maintaining sufficient host plants is fundamental to supporting populations of specialist lepidopterans, and host plant populations can be threatened by habitat fragmentation (Severns 2003), increases in cover by trees (Smallidge et al. 1996; Wagner et al. 2003), and encroachment by weeds and invasive plants (O'Dwyer & Attiwill 2000; Clark & Wilson 2001; Schultz 2001). Some form of vegetative management is needed to maintain populations of many rare butterfly species (New 1991; Swengel 1998). Habitat management often requires disturbance to prevent competitive exclusion of host plants, but it should not facilitate encroachment by weeds. Thus, effective habitat restoration requires an understanding of the ecology of the focal species (Schultz et al. 2003; Wilson et al. 2003) as well as the ecosystem function of their habitat (Potthoff et al. 2005).

Wild blue lupine (*Lupinus perennis* L.) is the larval host for at least four rare species of specialist Lepidoptera in the northeastern United States (Wagner et al. 2003), including Frosted elfin butterfly (*Callophrys irus* (Godart)), which has a remnant population at the Rome Sand Plains (RSP) in central New York, and the federally endangered Karner blue butterfly (*Lycaeides melissa samuelis* Nabokov), for which the RSP are a potential recovery site (U.S. Fish and Wildlife Service 2001). Despite ovipositing on the same plant, *C. irus* uses buds, *L. melissa* uses leaves, and no competition is evident among any lupine-feeding lepidopterans (Shapiro 1974; Swengel 1996). The pine barren habitat in which lupine grows is declining in the eastern United States due to urban encroachment and forest expansion following suppression of fire. Controlled burns can be an effective management tool that favors lupine performance (Grigore & Tramer 1996; Kwilosz & Knutson 1999), but fire is not a preferred option in populated areas; other methods that reduce shading by woody plants such as mechanical harvesting have also been effective (Smallidge et al. 1996; Smith et al. 2002; Forrester et al. 2005) and may be less damaging directly to the butterflies (Swengel & Swengel 2007). Habitat evaluation must be based on the resource requirements of the butterflies (Pullin 1996; Schultz 2001; Dennis & Shreeve 2003), and managed habitat must provide appropriate resources for all aspects of listed species' life histories, including host plants for oviposition and larval feeding, mating locations, and adult food. For Karner blues, for example, habitats with a mix of sun and partial canopy cover appear to provide the best opportunities for oviposition and larval growth (Grundel et al. 1998*a*, 1998*b*).

The decline of the Frosted elfin (New York State threatened) is directly related to loss of its Wild blue

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lupine habitat (Wagner et al. 2003). Frosted elfins are found only in isolated small colonies in early successional habitat and remain in close proximity to their lupine host plants. As a result, they are a species of conservation concern throughout most of their range; the species is conservation listed in 11 different states and extirpated in 2 states and Ontario, their only historic location in Canada (Shepherd 2005). Although southern and coastal populations oviposit on *Baptisia* spp., northern populations are known to use only *L. perennis*. Lupines are decreasing in the RSP, particularly as Eastern white pine (*Pinus strobus* L.) invades the open sandy habitats where lupines grow. *Pinus strobus* is native to the region but is excluded from pine barrens by fire. *Pinus rigida* Mill., on the other hand, is a pine component of barrens communities but does not cast the deeper shade of *P. strobus*. A Frosted elfin population remains at RSP where the lupines are the most dense (Fig. 1). Because of declining openness of this habitat, we began an experiment to examine the hypotheses that a white pine canopy (1) hinders lupine growth and (2) restricts elfin behavior and abundance. Our goal was to examine the effects of tree removal on lupine performance and butterfly behavior.

Methods

Study Site

The RSP comprise approximately 1200 ha of fossilized sand dunes derived from early Holocene glacial lakebed deposits on top of glacial till. Westerly winds sculpted the sand into a parabolic dune system with relief up to 40 m elevation. Due to a high local water table, the swales between dunes maintain saturated soil, whereas the dunes are well-drained sands. As a result, the vegetation consists of a complex mosaic of (1) wetland ericaceous bogs and swamp shrublands and forests; (2) upland oak and pitch pine–dominated barrens with ericaceous understory; and (3) mesic beech, oak, and maple hardwood–dominated forests. The soils are low nutrient, acidic, and fine-grained sands. Aerial photographs from the early and mid 1900s show considerable evidence of anthropogenic disturbance and a landscape much more open than is found currently.

Figure 1. The lupine patch at the RSP, Oneida Co., New York, U.S.A. The inset shows an experimental plot where a white pine had been removed. (Photos by E. Williams.)

Our study was conducted in the most extensive lupine population at a New York state conservation area of the RSP (lat 43.231°N, long 75.581°W). The lupines occur in dense patches in a dune area of less than 1 ha. The lupines are interspersed with trees, including pitch and white pine, white oak, and red maple, as well as extensive areas of open sand with little vegetation and patches of a cryptogamic crust. White pines have increased in abundance and size at this site since the early 1980s (J. Homburger, NYS DEC, Herkimer, NY, personal communication).

Soil cores were collected in September 2005 from seven sample points in dense lupine patches and open sand areas (20 cm depth). Samples were air dried for pH (10 g soil in 10 g H_2O) and nutrient analysis through the Cornell University Nutrient Analysis Laboratory, and these were the replicates for *t*-test comparisons. In June 2006, soil pH was measured on three cores (10 cm depth) taken from each of five 32-m^2 plots in areas of uniform lupine cover, open sand, and mature forest. The plots were replicates for analysis of variance (ANOVA).

Tree Removal Experiment

In May 2002, we identified 18 white pines that appeared to negatively influence the lupine plants underneath. We established octagonal plots (3.5 m radius; total area approximately 33 m^2) composed of eight 4-m^2 wedges around each tree and conducted baseline sampling. We randomly selected 9 of the 18 white pines for removal in January 2003, and the plots were resampled each following June 2003 to 2006. Both before and after tree removal, we counted the number of flowering lupine stems and visually estimated coverage of lupine and ground cover for each sample wedge. All lupine stems were counted in three randomly selected wedges in each plot.

Canopy openness was measured from hemispherical photographs taken after full canopy leaf-out from 2002 to 2005. We took photographs at plant height from four photo points on cardinal directions 2 m from the base of each control or experimental tree. The digital images were analyzed using Gap Light Analyzer (Frazer et al. 2000) to estimate the proportion of the sky not obscured by trees and the potential amount of direct solar radiation on each cardinal quadrat. These quadrats consisted of the two sample wedges on either side of the photo point. In the cleared plots, soil pH (10 g soil in 20 g H_2O) was measured in June 2004 and 2005 on pooled samples from four points (0 to 20 cm depth) within 0.35 m of each photo point.

Measurements from sample wedges and cardinal quadrats were averaged or summed for each plot, and plots became the replicates for statistical analyses. We used repeated-measures ANOVA for analysis, with treatment and year as factors, except for soil pH, for which *t*-test comparisons were made between treatment and control plots for each year. All statistical analysis was done with Statview 5 (SAS Institute, Inc., Cary, NC, U.S.A.).

Butterfly Monitoring

With a single generation per year, Frosted elfins fly from late April into early June in central New York. They depend entirely on *Lupinus perennis* for oviposition and larval feeding, with their eggs placed on buds before flowering has begun. Because butterflies show little, if any, activity on cloudy or cool days, only certain dates during the flight period permitted reliable counting (10–15 days each year). Butterfly abundance was quantified by modified Pollard walks (Pollard & Yates 1993) during each flight season from 2000 to 2006. Using this method, an observer (E.H.W.) walked slowly through the habitat along a standardized route and counted all Frosted elfins seen within 5 m of either side of the path. This route takes 12 minutes for a slow traverse. The Pollard walks give relative comparisons of yearly population sizes rather than absolute estimates. Standardization of Pollard counts by mark–release–recapture was not possible because the behavior of elfins is adversely affected by initial capture for marking (R. Robbins, 2002, Smithsonian Institution, Washington, D.C., personal communication). The location of each butterfly seen during these counts was mapped, as were the territories defended by males.

We tested the influence of canopy on butterfly distribution by comparing observations of adults before (2001–2002) and after (2003–2006) tree removal in the nine control and eight experimental plots (one experimental plot was excluded because it lay outside the standard observation route). The number of butterflies seen within 3 m of the removed and control trees were summed, and the influence of canopy cover on butterfly distribution was evaluated by chi-square analysis with Yates correction.

Results

Physical and Biotic Environment

Surface soils from the RSP were quite acidic in all habitats sampled, but pH was significantly higher in lupine patches than in open sand and forest areas (Table 1). Typical of acidic soils, the Ca levels were very low and Al levels were very high. Higher pH in lupine patches was associated with significantly higher Ca levels.

Removal of white pines resulted in dramatic increases in canopy openness in the experimental plots (Fig. 2). Variation was high in the openness of cut plots because some plots were surrounded by more trees than were others. Soil pH was 0.14 and 0.24 pH units higher in tree removal plots than control plots in 2004 and 2005 samples ($n = 9$; $t = 2.02$, $p = 0.06$; $t = 4.48$, $p < 0.001$, respectively).

An increase in open sand cover in cleared plots and decrease in cryptogram cover in both control and cleared plots (Fig. 3; Table 2) may have resulted from physical disturbance related to repeated visitation during our measurements. Although the litter cover categories have not changed significantly over time (Table 2), with needle litter averaging 50–60% cover and deciduous litter averaging 25–35% cover, the physical nature of the litter has changed in the tree removal plots because little fresh litter has been added and residual litter has gradually decomposed.

Lupine Response

The number of flowering stems and amount of lupine cover have increased in the cleared plots and remained constant or declined in the control plots (Fig. 4; Table 2). The most precise measure of the lupine population comes from individual stem counts conducted in three 4-m^2 wedges in each plot. The total number of individual lupine stems in control wedges declined in 2004 and again in 2005, with a slight recovery in 2006 (Fig. 5), suggesting that continued presence of the pine canopy might be suppressing the lupines. The total number of lupine stems in cleared plots remained constant until a dramatic decline in 2005 and slight recovery in 2006 (Fig. 5). Reduced numbers of lupine stems in 2005 may be a response to annual

Table 1. Soil characteristics (mean ± SE) of the study site: (A) Comparison of lupine patches and bare sand (0–20 cm depth; $n = 7$; September 2005; *t*-test comparisons); (B) pH of lupine patches, bare sand, and mature forest (0–10 cm depth; $n = 5$; June 2006; ANOVA).

A	*Lupine*	*Open sand*	*t*	*p*
pH	5.16 ± 0.05	4.70 ± 0.03	7.51	0.0001
Calcium (ppm)	889 ± 65	773 ± 61	3.48	0.0046
Aluminum (ppm)	4857 ± 218	4819 ± 200	0.13	0.90

B	*Lupine*	*Open sand*	*Forest*	*F*	*p*
pH	4.74_a ± 0.09	4.47_b ± 0.03	4.08_c ± 0.07	12.89	0.0002

Different subscripts indicate differences at $p < 0.05$.

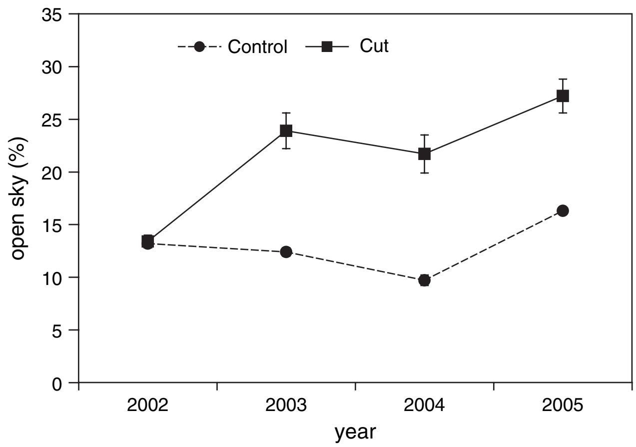

Figure 2. Canopy openness (mean ± SE, $n = 9$) above photo points in control and cleared plots each year since before treatment (2002). Each replicate is an average of four photo points 2.0 m from the plot center on cardinal coordinates.

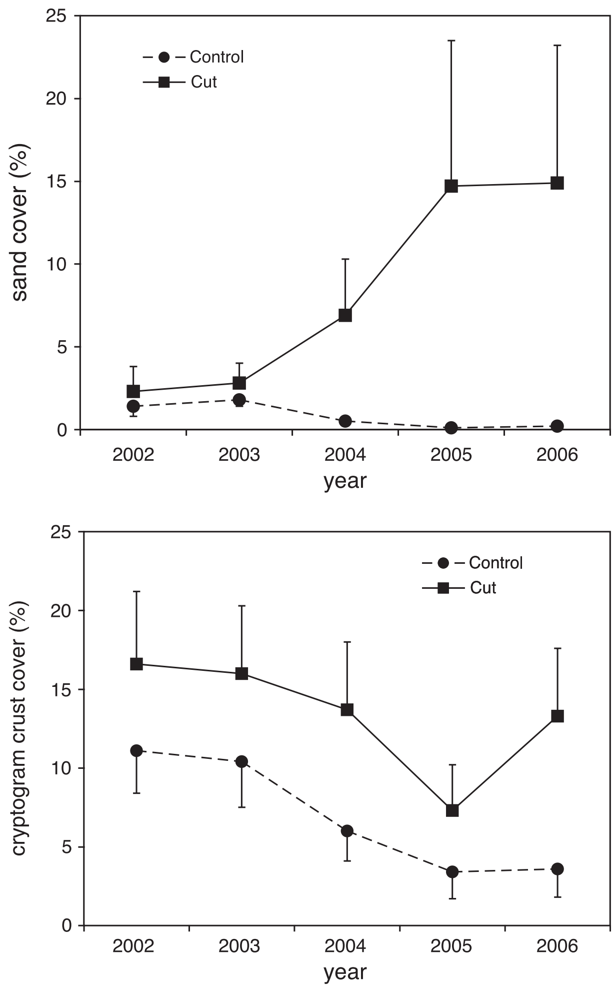

Figure 3. Time course of ground cover variables (above, sand; below, cryptogrammic crust) measured in experimental and control plots from 2002 (before treatment) to 2006 (mean ± SE, $n = 9$). Repeated-measures ANOVA statistics in Table 2.

Table 2. Analysis of lupine performance and ground cover variables measured in control and treatment plots from 2002 (before treatment) to 2006.

Variable	*Treatment*	*Year*	*Treatment–Year*
Lupine inflorescences	0.225	0.074	0.249
% lupine cover	0.553	<0.0001	0.031
% sand	0.026	0.486	0.003
% cryptogram cover	0.205	<0.0001	0.163
% needle litter	0.194	0.353	0.909
% deciduous litter	0.567	0.317	0.096

Shown are *p* values from repeated-measures ANOVA with arcsine transformation of percentages.

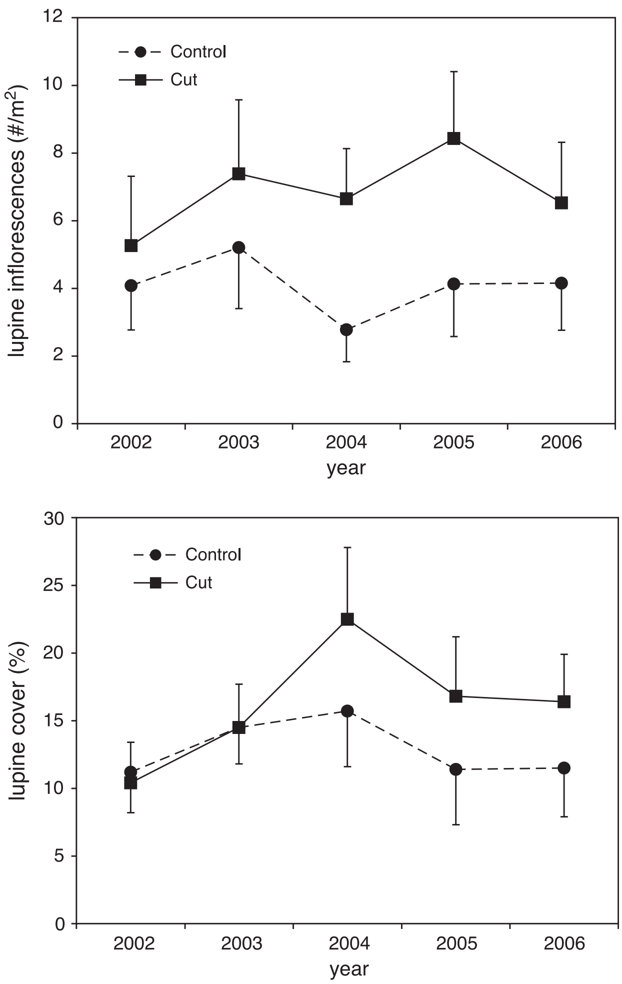

Figure 4. Time course of lupine variables (above, flowering stems; below, cover) measured in experimental and control plots from 2002 (before treatment) to 2006 (mean ± SE, $n = 9$). Repeated-measures ANOVA statistics presented in Table 2.

weather variation; May 2005 was dry and cool after an initial warm week.

Butterfly Response

The abundance of Frosted elfins peaks each year around 10 May within a flight period of late April to early June.

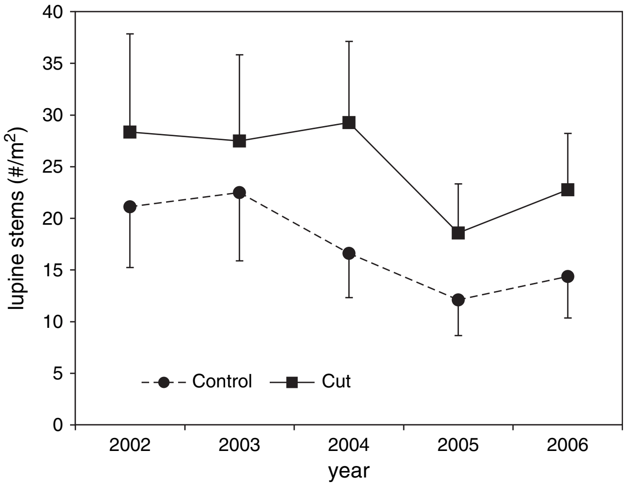

Figure 5. All lupine stems in three demography plots (mean ± SE, $n = 9$) from 2002 (before treatment) to 2006. With repeated-measures ANOVA, the effect of year was significant ($F = 6.236$, $p = 0.0003$), indicating a significant decline in lupine stems over time but the treatment effect and treatment–year interaction were not ($p > 0.39$ and $p > 0.43$).

Counts fluctuate because of changes in temperature and cloud cover. With analysis restricted to the middle of the flight period (4–20 May), a significant positive correlation exists between daily maximum temperatures and the number of butterflies counted ($r^2 = 0.277$, $p = 0.0099$). Considerable variation exists among years in the maximum number of elfins observed, with 2001, 2005, and 2006 having substantially higher counts than other years (Fig. 6). Differences in weather patterns help explain the variation. Since 2000, years 2001 and 2006 have had the fewest days in March with maximum temperatures above freezing; these conditions could enhance survival by reducing the probability of premature emergence and exposure to harsh weather or pathogens. In addition, 2001 and 2006 have had more sunny days during the first half of May,

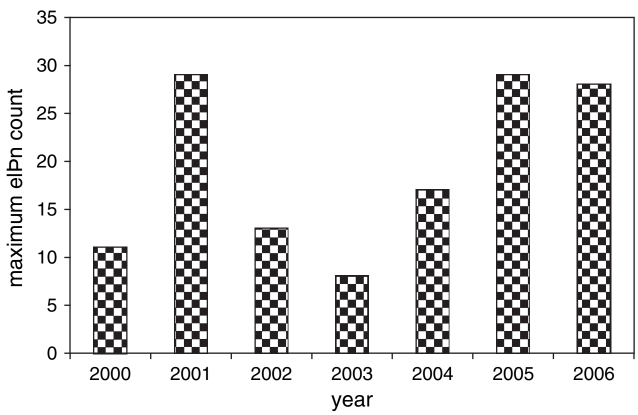

Figure 6. A comparison of the maximum single-day counts each year since 2000 of Frosted elfins in the RSP.

conditions that result in synchronous maturation and are ideal for mating and oviposition.

Tree removal clearly altered butterfly usage of the habitat (Fig. 7). Based on a total of 735 observations of butterflies, there was a significant increase in usage of experimental plots (chi-square $= 11.12$, $df = 1$, $p < 0.001$) from 2003 on but no difference in the usage of control plots (chi-square $= 2.62$, $df = 1$, n.s.). The frequency of observation more than doubled in two experimental plots that were part of larger areas at least twice the size of the experimental plots (3-m radius circle), but the rate of observation remained low in three experimental plots that were partially covered by branches from adjacent trees.

Each year, male Frosted elfins established territories within open patches next to concentrations of lupines (Fig. 8). The areas in which males landed repeatedly were located along open trails through the study site and

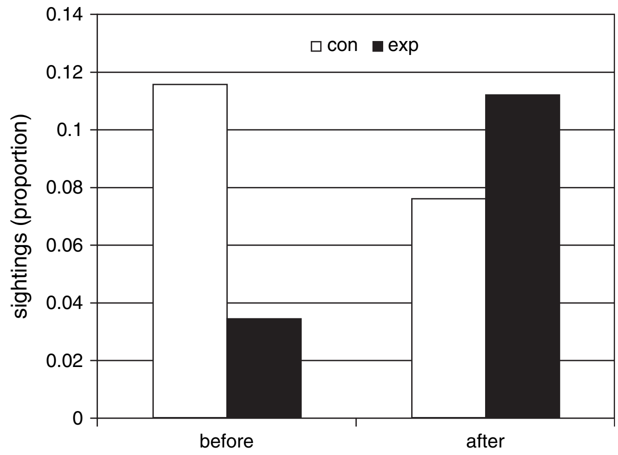

Figure 7. The proportion of sightings of Frosted elfins observed in the experimental and control plots before (2001–2002) and after (2003–2006) tree removal.

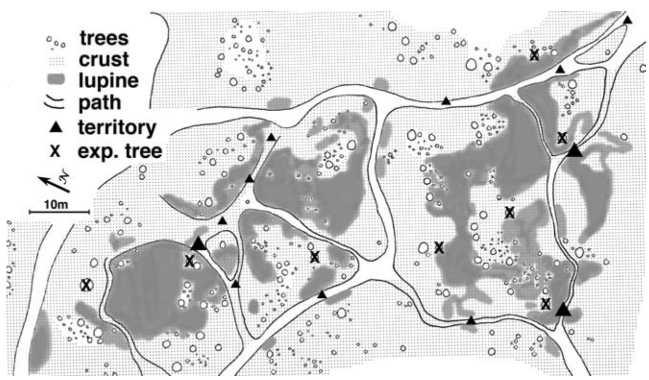

Figure 8. A map of the study site in the RSP. Each X marks an experimental white pine that was removed during the winter of 2002–2003 (a ninth tree was removed in a satellite area). Triangles designate the sites of male territories, whereas the three larger triangles mark territories that were added after tree removal from experimental plots.

covered less than 10 m^2 each. A number of such sites were in use during the 7 years of the study; most were used repeatedly on different days and in different years, with several in use every year. A noticeable change was that, in the first year after tree removal, males added territories in three newly opened sand patches where experimental trees had been removed. Each of these sites was within 1.5 m of the stumps of the removed pines (Fig. 8, larger triangles). The three new territories have been used every flight season since tree removal (2003–2006). The addition of new territory sites has been conspicuous.

Discussion

The experimental removal of white pines did improve lupine flowering and expand habitat for the Frosted elfin population. Increased sunlight and decreased soil acidity favor the growth of larger and more abundant flowering stems, and more lupine inflorescences represent an increased oviposition resource for Frosted elfin females. In addition, the experimental clearings have created open spaces for additional territories for Frosted elfin males, which may reduce male–male competition and result in increased reproductive success of the population. The sites for territories are proximate to the lupine patches where females lay eggs. This rapid and sustained response by the butterflies reflects their behavioral preferences for open areas.

It is tempting to consider the increase in elfin abundance since the 2002–2003 tree removal as evidence for an expanding Frosted elfin population, but more years of observation are needed to confirm such a numerical response. Weather conditions produce enough variation in day-to-day counts that a larger sample is needed to make that evaluation (the temperature dependence of total counts of Frosted elfins has been noted elsewhere as well; Swengel & Swengel 2000). Furthermore, the actual size of the population remains uncertain because the count results are relative rather than absolute and the influence of habitat alteration on natural enemies remains unknown (the larvae are cryptic and pupate in the leaf litter). All these factors may influence measures of elfin abundance.

Despite limitations in determining its actual size, the population at the RSP is large for this species. Frosted elfins are never abundant. The counts reported here (maximum count near 30) are from 12-minute Pollard walks, with more butterflies observable during extended searches. In contrast, Shapiro (1974) reported never finding more than 30 Frosted elfins at one time, and from 18 counts within New York state from 2003–2005, only two counts reached a high of 30 individuals (Fiore & Wallstrom 2003–2005). Thus, habitat management at RSP has a real effect on Frosted elfin distribution and abundance.

Our results suggest that individual lupine stems have benefited from the increased light and soil pH levels in tree removal plots as shown in increased stem size and lupine cover. We have not seen evidence of an accompanying recruitment in the number of stems, however. Lupine reproduces vegetatively as well as by seed. Many of the stems that we counted are undoubtedly branches of individual plants rooted deep in the sandy soil, and the lack of additional stems over time suggests that additional branching or vegetative propagation has not occurred. Furthermore, the apparent lack of seedling recruitment in experimental plots is in accord with repeated observations of lupine seedling failure in the broader RSP lupine population despite abundant natural seed germination. Attempts to expand lupine coverage by direct seeding has attained limited success. Taken together, these observations suggest that a soil factor may be limiting the ability of the lupine population to expand. Summer drought is an obvious potential limitation to seedling establishment, but there are others, including the availability of rhizobial bacteria for the establishment of nitrogen fixing symbiosis, as well as a soil environment conducive to the establishment of that symbiosis (Parker 2001).

Soil at RSP is quite acidic, averaging pH 4.0 to 5.2 and is 0.3 to 0.5 pH units higher in unshaded lupine populations than in open sand or forest areas. Various interactions at low pH may influence the ability of legumes to establish symbiotic associations with nitrogen-fixing bacteria; the solubility of acidifying iron and aluminum ions increases dramatically below pH 5.5 and the solubility of nonacidifying nutrients decreases (including the essential nutrient molybdenum) (Brady & Weil 2002). In preliminary studies, laboratory measurements of *Bradyrhizobium* cultured from RSP lupines have confirmed the general observations that rhizobial growth is inhibited strongly below pH 7 and that growth is increased by added molybdenum (unpublished data). Aluminum toxicity is known to be a problem when soil acidity is below pH 5.5 and calcium:aluminum ratios are less than 1 (Brady & Weil 2002), conditions that are certainly prevalent at RSP. Dirig (1994) has also observed the requirement by lupine for soil calcium, and other lupines are reported to be constrained to narrow pH ranges (O'Leary 1982). The lack of new stems in our experimental plots suggests that natural recruitment of lupines at RSP may occur slowly or only in occasional years.

As is true with other restoration efforts in pine barrens (Grigore & Tramer 1996; Kwilosz & Knutson 1999; Swengel 2001), maintenance of open barrens habitat at RSP may require disturbance that sets back the natural succession toward northern hardwood forest. The existence of pitch pine populations and evidence from a single pollen core (Russell 1996) suggest that fire played a role in RSP ecosystems in the past. Fire does more than simply open up a forest canopy; it volatilizes nitrogen, deposits wood ash that provides a source of mineral nutrients, and raises soil pH through ashes' buffering capacity (Lynham et al. 1998). All these factors are favorable for enhancing nitrogen fixation by legumes. Although fire may reduce seed and seedling survival, burning has substantially increased *Lupinus perennis* seedling and adult performance elsewhere (Grigore & Tramer 1996). Fire management may be more effective at RSP than physical tree removal for the natural expansion of lupine populations that could sustain increased populations of lupine specialist butterflies. Fire usage must be tempered by the need to reduce harm to the focal butterflies (Swengel 1996, 1998; Swengel & Swengel 2007), however, suggesting that a mix of management strategies may be the best solution. Herbicide usage as well as mechanical cutting can help retard succession (Smallidge et al. 1996; Forrester et al. 2005).

In addition to Frosted elfins, the federally endangered Karner blue butterfly could flourish at RSP, given enough expanded lupine coverage. Frosted elfins and Karner blues commonly co-occur yet do not affect one another negatively (Shapiro 1974; Swengel 1996). Studies with Karner blues (Grundel et al. 1998*a*, 1998*b*) have found that dappled shade increases lupine growth and butterfly usage, so even though encroachment by trees through succession must be retarded, broad clear-cuts are not optimal. Continued habitat management by logging and burning is warranted, however, to expand habitat for these listed species.

Conclusions

In this experiment, cutting selected trees expanded the open habitat favorable to lupine flowering and Frosted elfin reproduction. Removal of canopy allows more sunlight to reach the ground and spurs increased flowering of existing *Lupinus perennis*. Adding to the population size of lupines, however, requires attention to other factors; additional light is necessary but insufficient for a numerical response by the plants. In contrast to plants, butterflies of interest can respond to canopy removal within a single year, as Frosted elfins did in this study. Newly open areas where trees had been removed expanded the habitat used by the butterflies and gave room for additional defended male territories, potentially increasing reproductive rates. The benefits of canopy reduction have been conspicuous for restoring the open sand habitat needed by lupines and Frosted elfins at the RSP.

Implications for Practice

- In sand barrens habitats, canopy removal can spur greater growth of existing early succession plants but may be insufficient to increase their numbers.
- Butterfly species of concern respond quickly to canopy removal and make use of the newly opened areas, potentially increasing their population sizes more rapidly than the vegetation can respond to habitat modification.
- Canopy removal is an important component of restoration of sand plains communities.

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