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Research Article

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Plant–Insect Interactions

The Relationship Between Ants and *Lycaeides melissa samuelis* (Lepidoptera: Lycaenidae) at Concord Pine Barrens, NH, USA

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Abstract

The Karner blue butterfly (*Lycaeides melissa samuelis* Nabokov) (Lepidoptera: Lycaenidae) is a federally listed, endangered species that has experienced dramatic decline over its historic range. In surviving populations, Karner blue butterflies have a facultative mutualism with ants that could be critically important to their survival where their populations are threatened by habitat loss or disturbance. In this study, we investigated the effects of ants, wild blue lupine population status (native or restored), and fire on adult Karner blue butterfly abundance at the Concord Pine Barrens, NH, USA. Ant frequency (the number of times we collected each ant species in our pitfall traps) was higher in restored than native lupine treatments regardless of burn status during both Karner blue butterfly broods, and the trend was statistically significant during the second brood. We observed a positive relationship between adult Karner blue butterfly abundance and ant frequency during the first brood, particularly on native lupine, regardless of burn treatment. During the second brood, adult Karner blue butterfly abundance and ant frequency were not significantly correlated in any treatments or their combinations. Our findings suggest that a combination of native and restored lupine is important for supporting both Karner blue butterflies and ants at the Concord Pine Barrens, and that burning does not affect the mutualism. Thus, scientists and managers at the site may wish to target their habitat management activities to best support both Karner blue butterflies and the particular ant species that provide the greatest benefit to their survival.

Key words: Karner blue butterfly, Lycaenidae, Formicidae, pine barrens, mutualism

Ants (Formicidae) have evolved various complex relationships with other taxa. They function as predators, prey, detritivores, and pollinators, and their various symbioses with plants and animals range from parasitic to mutualistic (Hölldobler and Wilson 1990; Savignano 1994; Schultz and McGlynn 2000; Pierce et al. 2002). One of the many mutualistic relationships between ants and other insects is between ants and larvae of the butterfly family Lycaenidae (Atsatt 1981; Pierce and Mead 1981; Fiedler and Maschwitz 1988; Devries 1991; Savignano 1994; Fiedler 2001). Lycaenid larvae use specialized glands to secrete honeydew that ants collect and ingest, and in return, ants often aggressively defend the larvae from predators and parasitoids (Atsatt 1981; Pierce and Mead 1981; Devries 1991; Savignano 1994; Fiedler 2001). In addition, ant-tended lycaenid larvae have a higher overall survival rate than untended larvae (Pierce and Easteal 1986; Pierce et al. 1987; Savignano 1990).

This complex ant–lycaenid association makes ants important research subjects in the effort to restore endangered lycaenid butterfly species (Pierce et al. 2002; Steiner et al. 2003; James 2006; Saarinen and Daniels 2006; Underwood and Fisher 2006). Since most of these mutualisms are facultative (i.e., not obligatory), ants are not necessarily indispensable to the survival of well-established lycaenid species. However, ants may be critically important to the survival of fragile butterfly populations threatened by habitat loss or disturbance (Cushman and Murphy 1993; Saarinen and Daniels 2006).

Lycaeides melissa samuelis Nabokov (Karner blue butterfly) (Lepidoptera: Lycaenidae) is one such lycaenid species whose survival may benefit from greater understanding of their relationship with ants (Savignano 1990; 1994; Gill 2003). Karner blue butterflies exclusively colonize oak savanna and pine barren habitats with viable populations of the species' sole obligate host plant, *Lupinus perennis* L. (wild blue lupine) (Fabales: Fabaceae) (U.S. Fish and Wildlife Service 2003; Fuller 2008). They once inhabited Ontario and 12 US states extending from Minnesota to Maine (Dirig 1994; U.S. Fish and Wildlife Service 2003), but widespread habitat loss and degradation have caused significant population declines. Today, Karner blue butterflies occur in only seven of those states (IN, MI, MN, NH, NY, OH, WI; U.S. Fish and Wildlife Service 2003). The species is listed as federally endangered (Clough 1992), and US

states with remaining populations maintain ongoing conservation and restoration efforts to protect and increase their populations. Like other lycaenid species, Karner blue butterfly larvae secrete honeydew and are tended by ant partners during their third and fourth instars; thus, conservation and restoration efforts include research into the importance of the relationship between ants and Karner blue butterflies.

The case of *Maculinea arion* L. (large blue butterfly) (Lepidoptera: Lycaenidae) in Britain highlights why understanding this relationship may be critical to the survival of fragile Karner blue butterfly populations (Thomas 1980; Elmes and Thomas 1992; New 1993; Thomas et al. 1998; Als et al. 2004). By the mid-1960s it was apparent that *Maculinea arion* was in sharp decline in its native habitat, and by the early 1970s, conservationists determined they needed to better understand the species' biology in order to save it. Researchers found that larval survival was highly dependent on one species of ant, *Myrmica sabuleti* Meinert (Hymenoptera: Formicidae), which was dependent on intense grazing for survival. Changing land management practices in the 1950s led to more relaxed grazing activity that rendered the habitat unsuitable for *Myrmica sabuleti*. However, the host plant of *Maculinea arion*, *Thymus praecox* Opiz (mother of thyme) (Lamiales: Lamiaceae), still survived under a relaxed grazing regime, so it was not immediately apparent that anything was wrong with the habitat. This understanding of the connection between *Maculinea arion*, *Myrmica sabuleti*, and their shared habitat came too late to save the butterfly species, and it went extinct in Britain in 1979 (Thomas 1980; Elmes and Thomas 1992; New 1993; Thomas et al. 1998; Als et al. 2004). As with this case of *Maculinea arion*, managing to protect their ant partners may prove to be a critical part of Karner blue butterfly conservation efforts as well (Steiner et al. 2003; Saarinen and Daniels 2006; Witek 2008).

In this study, we investigated the relationship between ants and Karner blue butterfly abundance at the Concord Pine Barrens in Concord, NH, USA. On-going conservation efforts at the site are focused on restoring a self-sustaining Karner blue butterfly population by increasing the extent of its native lupine habitat (U.S. Fish and Wildlife Service 2003; Holman and Fuller 2011). The New Hampshire Fish and Game Department (NHFG) work toward this goal by using prescribed burning, periodic mowing, and lupine propagation and planting (Holman and Fuller 2011). New Hampshire Fish and Game managers and scientists also rear Karner blue butterfly larvae, monitor adult populations, and translocate Karner blue larvae between New Hampshire and the closest stable population in New York. However, relatively little is known about the relationship between ants and Karner blue butterflies at the Concord Pine Barrens (but see Savignano 1989; 1990), and greater understanding may enhance conservation efforts.

The goal of our study was to evaluate the relationship between ant frequency (the number of times we collected each ant species in our pitfall traps) and Karner blue butterfly abundance in areas of the Concord Pine Barrens with different wild blue lupine status (native vs. restored) and prescribed burning status (burned vs. unburned). Our specific research questions were: 1) What is the ant community composition at our study site and how does it vary across habitats with different lupine and prescribed burning characteristics?, 2) What effects do these habitat differences have on local Karner blue butterfly population abundance and distribution?, and 3) What trends can we identify in the effects of different habitat characteristics on Karner blue butterflies and ants, and what conclusions can we draw from these trends about the relationship between Karner blue butterflies and ants?

Materials and Methods

Field-Site Description

New Hampshire Fish and Game monitors 24.2 ha of pine barrens habitat in Concord, NH, as a part of their Karner blue butterfly conservation and restoration program. The Concord Pine Barrens is contained within the Concord Municipal Airport, and continues into the adjacent U.S. Fish and Wildlife Service conservation easement and a power line corridor just north of the easement (Fig. 1) . This habitat is divided into 36 GPS-derived monitoring units, each covering ~0.7 ha, in which NHFG conducts their Karner blue butterfly monitoring and identifies the boundaries for prescribed fire. Each unit also contains lupine that is either native or restored by NHFG (Fig. 1). Average annual precipitation at the site is 100 cm, and average summer temperatures range from 10–22°C (National Oceanic and Atmospheric Administration [NOAA] 2013). Pine barren plant communities colonize excessively drained soils, which are drought prone, acidic, and nutrient-poor (Holman and Fuller 2011). Pine barrens are designated as rare community types in New Hampshire, where they are dominated by dense *Quercus ilicifolia* Wangenh (scrub oak) (Fagales: Fagaceae) thickets and heath barrens interspersed with patches of *Pinus rigida* Miller (pitch pine) (Pinales: Pinaceae) and grassy clearings (Holman and Fuller 2011; Sperduto and Kimball 2011). Regular, periodic fires maintain these fire-adapted communities, so managers at this site and throughout the United States use periodic prescribed fires to maintain their unique plant species composition and structure (Sperduto and Kimball 2011).

Karner blue butterflies have been monitored at the Concord Pine Barrens since 1983. The butterflies numbered in the low thousands in the 1980s but declined to fewer than 50 individuals in 1994. The species was believed to be extirpated from the site by 2000 (Helmbolt and Amaral 1994; U.S. Fish and Wildlife Service 2003). New Hampshire Fish and Game began its pine barrens restoration efforts in 2000 and its Karner blue butterfly reintroduction efforts in 2001. By 2010, the local population estimate had peaked at just over 2,400 adult individuals during their second brood flight (Holman and Fuller 2011). In 2013, NHFG mark and recapture data indicated that population numbers exceeded the number of individuals recorded in 2010.

Management for wild blue lupine at Concord Pine Barrens includes its propagation and planting to supplement the native population (Holman and Fuller 2011); thus, the monitoring units contain a combination of native and restored wild blue lupine (hereafter "native" and "restored," respectively). In addition to restoring lupine host plants, NHFG also periodically burns select units to facilitate lupine regeneration. A subset of monitoring units was burned in 2010 (hereafter "burned"), while other units have not been burned since at least 2001 (hereafter "unburned"). We conducted our study in these monitoring units with their various treatment combinations.

Experimental Design

To characterize ant species composition in the Concord Pine Barrens, we developed a 2×2 full-factorial experiment in which 28 total pitfall traps were placed in 28 of the 36 above-described NHFG monitoring units (one pitfall trap per monitoring unit; Fig. 1) with the following treatment combinations: native lupine and burned ($n = 9$ pitfall traps), native lupine and unburned ($n = 5$ pitfall traps), restored lupine and burned ($n = 5$ pitfall traps), and restored lupine and unburned ($n = 9$ pitfall traps); we set the greatest number of pitfall traps that resource and time constraints permitted. We constructed pitfall traps using plastic pint-sized containers (114 by

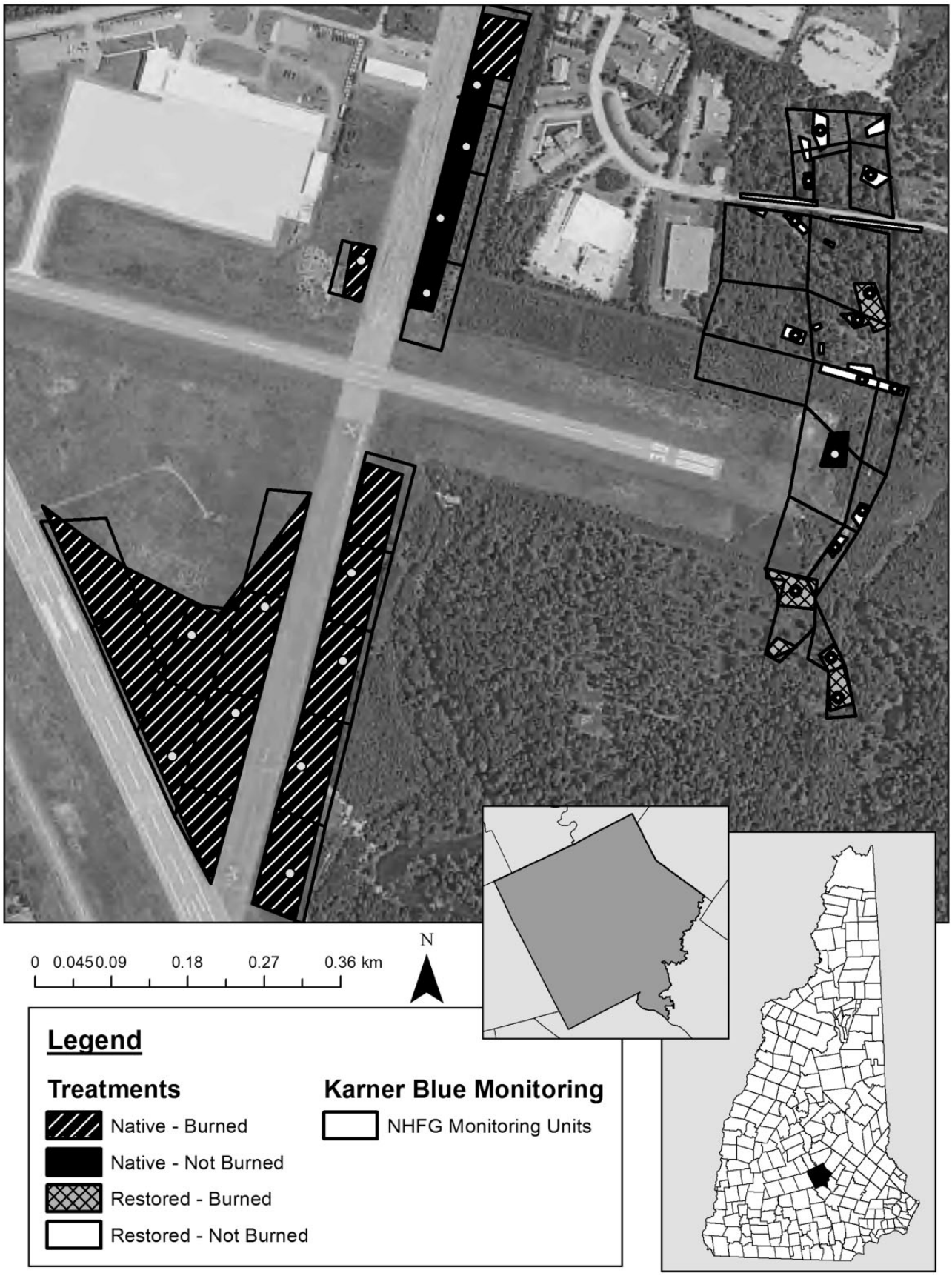

Fig. 1. Aerial map of the Concord Pine Barrens, Concord, NH, highlighting the New Hampshire Fish and Game Karner blue butterfly population monitoring units. Each circle within a monitoring unit represents one of our pitfall traps.

76 mm) with rain guards (lids) made of plastic plates (260 mm diameter) that we secured over the traps with nails. Wild blue lupine is patchily distributed at this site, so we placed each pitfall trap in a discrete lupine patch spaced at least 30 m from another lupine patch within burned and unburned sites.

To characterize ant frequency (defined as the number of times we collected each ant species in our pitfall traps), abundance, and species composition across stages of Karner blue larvae development, after placing our pitfall traps we sampled ants four times between May–June, 2013—twice during each of the Karner blue butterfly broods; hereafter, we refer to these as two "sampling periods" within each brood. We sampled ants during the first butterfly brood in early-mid May, and during the second butterfly brood in early-late June. These sampling periods were chosen based on the documented lag time in development between NHFG's captive-reared butterfly larvae and the wild population larvae.

We used the Ants of the Leaf Litter (ALL) Protocol to determine pitfall trap placement and specimen collection technique (Agosti et al. 2000). To avoid overestimating ant abundance caused by soil disturbance while placing pitfall traps, we covered traps with lids (plastic plates) after placing them in the ground and allowed them settle for a week before starting sampling (Greenslade 1973; Agosti et al. 2000). After one week, we opened pitfall traps and filled them with 50 ml of propylene glycol and one drop of unscented dish detergent to break surface tension. A rain guard (plastic dinner plate) was installed above each trap to prevent flooding and to deter larger animals from disturbing the traps. During each sampling period, traps remained in the ground for two days before collecting them for specimen removal and identification (Agosti et al. 2000). Each time we collected ants, we also recorded soil temperature, humidity, air temperature, and wind speed using a soil thermometer (model 5976N, Taylor Precision Products Inc., Oak Brook, IL) and a weather meter (Kestrel 4000, Nielsen-Kellerman, Boothwyn, PA). After collection, all ant specimens were pinned and identified to species using *A Field Guide to the Ants of New England* (Ellison et al. 2012).

In addition to ant sampling, we also quantified Karner blue butterfly numbers using both a population survey and larval cage experiment. First, to determine the number and distribution of wild Karner blue butterfly adults in each brood (population survey), we used existing data of Karner blue butterfly abundance collected by NHFG in May–August, 2013, which they collected with their established mark-and-recapture protocol (Gall 1985; Schweitzer 1994) in established Karner blue butterfly monitoring units (Fig. 1). To avoid double-counting individual butterflies and thereby overestimating Karner blue butterfly abundance, we used only initial mark data from the Karner blue population survey and omitted all recapture data. To calculate total Karner blue butterfly abundance in each treatment combination, we calculated abundance within each monitoring unit and summed the abundance totals within each treatment combination. We ensured that we sampled ants in the same sampling units where Karner blue butterfly individuals were documented by locating our ant pitfall traps in these same sampling units (Fig. 1).

Second, we supplemented the Karner blue butterfly adult population survey data with counts of Karner blue butterfly adults that hatched from larvae that may have interacted with ants. To do this, we conducted a larval cage experiment for which we constructed and erected 12 larval cages (each 30.5 by 30.5 by 61 cm^3) in established NHFG monitoring units, in the same 2×2 full-factorial treatment combinations described above ($n = 3$ cages per treatment combination). Each cage was constructed from a wooden frame with the top and sides covered in a fine mesh fabric provided by NHFG. The wooden frame corners and the bottom of the mesh sides were staked into the ground to secure the cage and prevent larvae from escaping. The holes in the mesh fabric were small enough to prevent Karner blue larvae from escaping but did not prevent ants from entering or leaving the cages. We used larvae from the existing NHFG captive rearing program, which includes the ongoing release of captive reared Karner blue butterfly adults into the Concord Pine Barrens. Each set of 10 larvae placed in the larval cages was designated to be released into the specific NHFG monitoring unit where we located each given larval cage. We included the surviving population numbers from the larval cage experiment as location-specific Karner blue butterfly data in our analyses by adding these numbers to those acquired from the population survey for each treatment combination.

We conducted the larval cage experiment only on the second Karner blue butterfly brood to ensure that the surviving adults derived directly from the larvae we placed on lupine plants; i.e., during the first brood, we could not ensure that no overwintering eggs remained on lupine plants we placed cages over, so we could not guarantee that surviving larvae were derived from the 10 larvae we added to the larval cages. To ensure that no first brood Karner blue butterfly laid eggs on lupine in the cages, empty cages were placed over randomly selected lupine plants in their respective treatment units before first brood adult flight began, and then checked daily from May 19–June 8, 2013. Adult Karner blue butterflies trapped in the cages were recorded and released. In late June, as second brood larvae developed, we collected 120 larvae raised through NHFG's captive rearing program once they reached their third instar. We placed 10 larvae on the leaves of a single, multiple-stemmed lupine plant in each cage to give them time to develop before pupating; in each cage, the 10 larvae were placed on leaves on 10 different stems of the same lupine plant. We chose these numbers because each Karner blue butterfly larva requires one lupine stem to survive (Lane 1999; U.S. Fish and Wildlife Service 2003); in case this estimate is low, we expressly chose lupine plants with 30 stems or more. Adults that eclosed (average: 16 d later) within cages were then removed, marked, and released. Thus, we determined Karner blue butterfly abundance by combining both wild mark survey data and butterflies that survived to adulthood in our larval cages.

Data Analysis

Ant data were first analyzed separately from Karner blue butterfly data to evaluate the effect of our four treatments on ant frequency, with pitfall traps as the individual sampling units. For analysis we used ant (species) frequency data. We did not compare ant abundance data among treatment groups because observations of the number of individuals found in a given pitfall trap were not likely to be independent (Gotelli et al. 2011). To determine whether our sampling intensity adequately captured species richness, we used ant frequency data to estimate the species richness asymptote using EstimateS (Gotelli et al. 2011; Colwell 2013).

To evaluate the effect of treatments on ant frequency, we conducted a multivariate analysis of variance with covariates using the DISTLM statistical analysis package (Andersen 1991; McArdle and Anderson 2001; Anderson 2004). This analysis allowed us to use an unbalanced design to test both the individual and combined effects of lupine and burn treatments on ant frequency, while also including our environmental measurements (soil temperature, humidity, air temperature, and wind speed) as covariates. Further, DISTLM has the added advantage of making no assumptions about the

underlying data distribution because it relies upon multiple permutations of the data (Andersen 1991; McArdle and Anderson 2001; Anderson 2004); thus, it is robust for comparisons of data sets with small samples sizes (Walters and Coen 2006), as is the case for our ant frequency data. Where DISTLM detected significant differences in ant frequency among treatment groups, we conducted separate pairwise comparisons using Bonferroni-adjusted error rates to reduce the chance of obtaining type I errors due to conducting multiple comparisons on a single data set. Our Bonferroni-adjusted alpha was determined by dividing the standard alpha ($\alpha \leq 0.05$) by the number of pairwise comparisons ($n = 6$), establishing the Bonferroni adjusted alpha at $\alpha \leq 0.008$ (McDonald 2009). We separated our ant frequency data by Karner blue butterfly brood for analysis to determine how ant community composition was different between the two broods. To assess the individual effects of lupine and burn treatments, we included lupine status and burn status as separate explanatory variables. We also added sampling period (i.e., first vs. second sampling period within each brood) as a third explanatory variable in the analysis to evaluate whether the timing of our sampling affected ant frequency and species composition.

Finally, to assess the relationship between ants and Karner blue butterflies, we conducted negative binomial regression analyses (SPSS Statistics v21, IBM, Armonk, NY) to evaluate the relationships between ant frequency and the number of wild Karner blue butterfly adults captured by our adult butterfly survey and larval cage experiments. Negative binomial regression is an appropriate regression analysis for over dispersed count data in which the sample variance exceeds the sample mean (Cameron and Trivedi 1998; Hilbe 2011); our data meet these criteria. To account for the different number of pitfall traps in each treatment combination, we ran separate regression analyses on ant and Karner blue butterfly data within each treatment and treatment combination. For these analyses, we pooled ant frequency data from sample periods 1 and 2, and 3 and 4, for each Karner blue butterfly brood.

Statistical significance for all analyses was determined at $\alpha \leq 0.05$ except where we applied Bonferroni adjustments.

Results

We collected 1,479 individual ants and 23 species in all our study plots (Table 1). *Lasius neoniger* Emery (Labor Day ant) (Hymenoptera: Formicidae) was the most abundant species and had the greatest species frequency in our pitfall traps, with 545 individuals and 50 observations. *Monomorium emarginatum* DuBois (furrowed Monomorium) (Hymenoptera: Formicidae) and *Myrmica americana* Weber (American ant) (Hymenoptera: Formicidae) followed in abundance with 259 and 151 individuals, respectively, though we observed *Myrmica americana* most frequently. We observed fewer than 100 individuals of the 20 remaining species, and each remaining species was observed fewer than 25 times (Table 1). EstimateS (Colwell 2013) determined our total sampling effort to be 58% (Chao2 = 24.93), indicating that we would need almost twice the number of pitfall traps to capture ant species richness; thus, we may have underestimated ant species richness at this site.

We consistently found more ant species in plots with restored lupine than plots with native lupine during both Karner blue butterfly broods (Table 1). Lupine status (restored vs. native) had no statistically significant effect on ant frequency during the first brood; however, ant frequency was significantly higher on restored lupine during the second brood when soil temperature ($F = 3.62$; df = 1, 25; $P = 0.00$) and wind speed ($F = 2.84$; df = 1, 25; $P = 0.01$) were included in the model as covariables (Table 2). Further, we counted

Table 1. Ant species, abundance, and frequency at the Concord Pine Barrens, Concord, NH, sorted by treatment

Species	Native–Burned		Native–Unburned		Restored–Burned		Restored–Unburned	
	Abundance	Frequency	Abundance	Frequency	Abundance	Frequency	Abundance	Frequency
Aphaenogaster rudis	4	3			19	7	16	10
Camponotus americanus					4	3	3	3
Camponotus novaeboracensis	2	2	1	1	4	3	2	2
Camponotus pennsylvanicus					1	1		
Crematogaster cerasi	1	1						
Dolichoderus taschenbergi	2	1			70	6	16	3
Formica dolosa	18	4	5	1	17	7	12	6
Formica incerta			20	5	10	6	7	4
Formica lasioides	1	1	1	1			1	1
Formica neogagates					1	1	4	1
Formica subsericea					1	1		
Lasius alienus			2	1	8	3	35	4
Lasius claviger					9	2	5	1
Lasius neoniger	150	14	237	12	34	9	124	15
Monomorium emarginatum	98	13	71	8	4	3	86	5
Myrmica AF-can			1	1				
Myrmica AF-smi	5	3			1	1	8	6
Myrmica americana	50	11			36	5	65	17
Nylanderia parvula					16	5	3	2
Polyergus lucidus							1	1
Solenopsis molesta	10	5	3	3	2	1	4	3
Tapinoma sessile	17	4	30	6	6	5	32	6
Tetramorium caespitum	56	6	15	5			12	7
Total	414	68	386	44	243	69	436	97

Numbers are totals for both first and second sampling periods per Karner blue butterfly brood. "Abundance" refers to the number of individuals of each species we counted and "frequency" refers to the number of times we encountered the species in our pitfall traps.

Table 2. Tests for the effects of predictor variables (lupine status, burn status, and sampling period) on ant frequency for each brood at the Concord Pine Barrens, Concord, NH

Covariables	Lupine status				Burn status				Sampling period			
	F	*P*	df	%var	*F*	*P*	df	%var	*F*	*P*	df	%var
1st Brood												
Humidity (%)	1.13	0.36	1, 25	4.19	0.68	0.69	1, 25	2.57	0.36	0.9	1, 53	0.65
Soil temp. (F)	1.68	0.13	1, 25	6.18	0.48	0.83	1, 25	1.85	1.89	0.08	1, 53	3.33
Temperature (F)	0.81	0.59	1, 25	3.02	0.57	0.77	1, 25	2.16	1.79	0.09	1, 53	3.15
Wind speed (mph)	1.73	0.11	1, 25	6.30	0.57	0.76	1, 25	2.18	2.12	0.05*	1, 53	3.69
2nd Brood												
Humidity (%)	1.03	0.41	1, 25	3.44	1.07	0.39	1, 25	3.57	4.53	0.00*	1, 53	7.60
Soil temp. (F)	3.62	0.00*	1, 25	12.16	0.98	0.45	1, 25	3.63	2.24	0.04*	1, 53	3.95
Temperature (F)	0.82	0.56	1, 25	2.71	0.87	0.52	1, 25	2.80	4.41	0.00*	1, 53	7.33
Wind speed (mph)	2.83	0.01*	1, 25	9.37	0.87	0.52	1, 25	3.08	1.48	0.18	1, 53	2.67

We used DISTLM multivariate pseudo-F statistic (McArdle and Anderson 2001; Anderson 2004). For each test the effects of several covariables (humidity, soil temperature, air temperature, and wind speed) were added to the model. *F*-statistics ("F") and *P*-values ("P") were based on Bray-Curtis dissimilarities and obtained using 9999 permutations. Asterisks indicate statistical significance at $P \leq 0.05$. "%var" represents the percentage of the variability in ant frequency explained by each predictor variable.

Table 3. Mean (±SE) ant frequency and pairwise comparisons of the combined effects of treatment category on ant frequency by brood at the Concord Pine Barrens, Concord, NH

Treatment Combinations	First brood					Second brood				
	Mean ant frequency (± SE)	*F*	*P*	df	%var	Mean ant frequency (± SE)	*F*	*P*	df	%var
Native–Burned	2.06 (0.32)	1.66	0.08	1, 26	5.99	1.72 (0.32)	1.59	0.15	1, 26	5.78
Native–Unburned	1.70 (0.34)					2.70 (0.30)				
Native–Burned	2.06 (0.32)	1.62	0.09	1, 26	5.86	1.72 (0.32)	2.88	0.00*	1, 26	9.96
Restored–Burned	3.30 (0.79)					3.70 (0.60)				
Native–Burned	2.06 (0.32)	0.35	0.88	1, 34	1.03	1.72 (0.32)	3.32	0.00*	1, 34	8.89
Restored–Unburned	2.17 (0.31)					3.22 (0.33)				
Native–Unburned	1.70 (0.34)	0.82	0.56	1, 18	4.36	2.70 (0.30)	4.64	0.00*	1. 18	20.48
Restored–Burned	3.30 (0.79)					3.70 (0.60)				
Native–Unburned	1.70 (0.34)	1.29	0.21	1, 26	4.74	2.70 (0.30)	3.97	0.00*	1, 26	13.25
Restored–Unburned	2.17 (0.31)					3.22 (0.33)				
Restored–Burned	3.30 (0.79)	0.89	0.44	1, 26	3.32	3.70 (0.60)	0.73	0.56	1, 26	2.74
Restored–Unburned	2.17 (0.31)					3.22 (0.33)				

Pairwise comparisons were conducted using the multivariate F-statistic ("F") and Bonferroni adjustments for multiple comparisons. Asterisks indicate statistical significance at Bonferroni-adjusted $P \leq 0.008$. "%Var" represents the percentage of the variability in ant frequency explained by each comparison.

a greater number of ant species in burned plots during the first butterfly brood, as well as more ant species in unburned plots during the second brood; however, the effect of burn status on ant frequency was not statistically significant during either brood (Table 2).

Sampling period had significant effects on ant frequency during both broods, and ant species counts differed between broods depending upon the timing of sampling (Table 2). We counted a greater number of ant species during the first sampling period of the first brood, as well as during the second sampling period of the second brood. Sampling period during the first brood significantly affected ant frequency when we included wind speed in the model as a covariate ($F = 2.12$; df = 1, 53; $P = 0.05$). Similarly, sampling period significantly affected ant frequency during the second brood when humidity ($F = 4.53$; df = 1, 53; $P = 0.00$), air temperature ($F = 4.41$; df = 1, 53; $P = 0.00$), and soil temperature ($F = 2.24$; df = 1, 53; $P = 0.04$) were included as covariates (Table 2).

Pairwise comparisons indicated that the combined effects of lupine and burn status on ant frequency differed by butterfly brood. None of the six comparisons had any significant influence on ant frequency during the first brood, but four comparisons were statistically significant during the second brood (Table 3). Specifically, we encountered significantly more ant species in restored burned than native burned plots, and significantly more ant species in restored unburned than native burned plots. Restored burned plots had significantly more ant species than native unburned plots, and restored unburned plots had significantly more ant species than native unburned plots. The only pairwise comparisons of ant frequency that were not statistically significant during the second brood were native burned vs. native unburned and restored burned vs. restored unburned (Table 3), indicating that during the second brood ant frequency was influenced by lupine status but not by burn status.

Karner blue butterfly population surveys and the larval cage experiment yielded data for 430 adult butterflies. We observed strong positive relationships between ant frequency and Karner blue butterfly abundance during the first brood, regardless of burn treatment (Table 4). Specifically, the relationship between ant frequency and Karner blue butterflies was significant during the first brood in all

Table 4. Model significance of negative binomial regressions to test the relationship between ant frequency and Karner blue butterfly abundance by brood at the Concord Pine Barrens, Concord, NH

Treatments	First brood	Second brood
Overall Model	$\chi^2 = 2.39$, $P = 0.12$	$\chi^2 = 0.93$, $P = 0.34$
Native	$\chi^2 = 5.36$, $P = 0.02$*	$\chi^2 = 0.16$, $P = 0.69$
Restored	$\chi^2 = 0.00$, $P = 0.99$	$\chi^2 = 2.61$, $P = 0.11$
Burned	$\chi^2 = 5.30$, $P = 0.02$*	$\chi^2 = 0.40$, $P = 0.53$
Unburned	$\chi^2 = 6.31$, $P = 0.01$*	$\chi^2 = 2.87$, $P = 0.09$
Native × Burned	$\chi^2 = 1.58$, $P = 0.21$	$\chi^2 = 0.31$, $P = 0.58$
Native × Unburned	$\chi^2 = 35.40$, $P = 0.00$*	$\chi^2 = 12.00$, $P = 0.73$
Restored × Burned	$\chi^2 = 10.13$, $P = 0.00$*	$\chi^2 = 2.00$, $P = 0.16$
Restored × Unburned	$\chi^2 = 0.29$, $P = 0.59$	$\chi^2 = 3.30$, $P = 0.07$

Asterisk indicates statistical significance, determined at $\alpha \leq 0.05$.

lupine and burn treatments and their combinations except in restored, native burned, and restored unburned plots. During the second brood, ant frequency was not significantly correlated with Karner blue butterflies in any treatments or their combinations (Table 4).

Discussion

Native and restored wild blue lupine had differing effects on ant community composition and on the strength of the relationship between Karner blue butterflies and ants at our study site. We observed a significant relationship between Karner blue butterflies and ants only in study plots with native lupine during the first Karner blue butterfly brood. This significant relationship occurred regardless of burn status, which suggests that native lupine may play an important role in the relationship, especially during the first brood. We collected significantly more ant species from study plots with restored lupine than with native lupine during the second brood, and this was also a trend during the first brood, which suggests that restored lupine attracts more ants during both broods.

The difference between where we observed a stronger relationship between Karner blue butterflies and ants and where we observed higher ant frequency may be due to the natural distribution of Karner blue butterflies in relation to ant distribution and foraging activity. Ants are patchily distributed throughout a given landscape, and varying microclimate conditions (e.g., temperature and moisture) attract different species of ants (Levings 1983; Savignano 1990; Agosti et al. 2000). At our site, the microclimate climate conditions during the first brood in plots with native lupine may attract those ant species most likely to interact with Karner blue butterflies, thereby increasing the chance of their interaction during that brood. This possible effect, coupled with high Karner blue butterfly abundance in native lupine plots and the limited dispersal of adult Karner blue butterflies at our site (Holman and Fuller 2011), strengthens the chance of observing this positive relationship during the first brood. Karner blue butterflies disperse short distances (<100 to 200 m) within their natal habitat and may also disperse from their natal patch to other habitat patches 0.5–2 km away, depending upon surrounding habitat structure (U.S. Fish and Wildlife Service 2003). At the Concord Pine Barrens, Karner blue butterflies are more likely to remain in their natal habitat (i.e., lupine populations at the site) than to emigrate to nearby lupine populations (Holman and Fuller 2011) because the surrounding landscape is heavily developed. Combined, these factors increase the likelihood that ants will interact with Karner blue butterfly larvae in the plots with native lupine where Karner blue butterflies are so abundant during the first brood.

Microclimate conditions may also help explain the higher ant frequency we observed in study plots with restored lupine. At the Concord Pine Barrens, plots with restored vs. native lupine occur in separate locations that differ in sun exposure, with restored lupine occurring in the moderately shaded areas of the conservation easement and native lupine occurring on the sun-exposed municipal airport grounds. Differences in sun exposure affect microclimate conditions of ants' nests and foraging grounds, as ants operate within a specific temperature and humidity range (Hölldobler and Wilson 1990; Agosti et al. 2000). Low humidity coupled with extreme temperatures can cause desiccation, but too much moisture can cause physical barriers to movement and wash away their chemical trails (Agosti et al. 2000). Thus, the moderately shaded areas of the conservation easement with restored lupine at our study site may create more favorable temperature and humidity conditions for ant activity. We observed that microclimate variables were significant covariates in our model, despite having collected environmental data only during ant collection; thus, future studies should collect environmental data continuously throughout the growing season to better evaluate the effects of microclimate on ant frequency.

It is possible that sun exposure is partially responsible for the lack of a strong relationship between ants and Karner blue butterflies during the second brood. The amount of sun exposure affects the rate of lupine senescence during late summer (Dirig 1994; U.S. Fish and Wildlife Service 2003); early senescence is more likely to occur in areas with high sun exposure than areas with moderate shade (canopy cover) (Maxwell 1998). The timing of lupine senescence is important for second brood Karner blue butterflies because they must fully develop and pupate before senescence occurs (Grundel et al. 1998; Lane 1999); early senescence could cause larvae to starve. Thus, the lack of a significant relationship between ants and second brood Karner blue butterflies in native lupine plots at our site may be due to either a more scattered distribution of Karner blue butterflies while they search for nectar plants after lupine senescence, or to reduced Karner blue butterfly larval survival resulting from lupine senescence. Either scenario coupled with the likelihood of higher overall ant activity during the second brood would reduce the strength of their relationship.

The trend we observed in the varying significance of the Karner blue butterfly–ant relationship between broods in native lupine plots also occurred in burned plots. Their relationship was significantly positively correlated in burned plots during the first brood, which suggests that burning to facilitate lupine at the Concord Pine Barrens does not compromise the ant–Karner blue butterfly mutualism. Fire can alter ant species diversity (Underwood and Christian 2009) or have little to no impact on ant species diversity (Jackson and Fox 1996; Houdeshell et al. 2011), depending upon the habitat (Farji-Brener et al. 2002; Parr et al. 2004) and ant nesting behavior (Arnan et al. 2006; Frizzo et al. 2012). Fire can directly affect ants by increasing mortality or forcing colony dispersal (Andersen 1991; Underwood and Christian 2009), but fire more often affects ants indirectly by modifying habitat structure, microclimate, food supply, and interspecific competition (Andersen 1991; Farji-Brener et al. 2002, Houdeshell et al. 2011). Regardless, studies show that the direct and indirect effects of fire on ants are relatively short-lived and that ant communities recover in 8–18 mo (Jackson and Fox 1996; York 2000; Farji-Brener et al. 2002; Parr et al. 2004; Vasconcelos et al. 2008; Underwood and Christian 2009). Thus, it is likely that ant populations at our study site had ample time to recover since the last prescribed burns in 2010.

Shared habitat plays an important and complex role in the relationship between ants and Karner blue butterflies. Managers at our study site can address the role of habitat and encourage the interaction between ants and butterflies by managing for particular habitat characteristics attractive to both. Ants have habitat preferences that differ by species and include specific preferences for a variety of food sources, nesting sites, temperature, humidity, and population interactions that regulate access to available resources (Agosti et al. 2000). Thus, determining which ant species positively interact with Karner blue butterflies should be a priority, so managers can identify and effectively manage for the habitat requirements those species share with Karner blue butterflies. For example, prescribed fire is a useful habitat management tool for wild blue lupine and thus Karner blue butterflies, but fire can also be detrimental to Karner blue butterflies by killing eggs, larvae, and adults caught in burn plots (Swengel 1994; Maxwell 1998; U.S. Fish and Wildlife Service 2003). To support the long-term viability of Karner blue butterfly populations, managers must address the balance between the short-term detrimental effects and long-term habitat improvements of fire (Swengel 1994; U.S. Fish and Wildlife Service 2003). They must also consider differences in how ant species react to burning. Prioritizing and balancing these habitat needs and management activities will both ensure the recovery of ant communities after a burn, and encourage positive interactions between Karner blue butterflies and ants that enhance Karner blue butterfly survival and population viability.

Further research into the ant community at this site and its relationship with local Karner blue butterflies is essential to understanding the significance of its role in Karner blue butterfly survival in the Concord Pine Barrens, and possibly in the survival of the species as a whole. Future studies at this site should include more pitfall traps to shed more light on ant species richness and the strength of the relationship between ants and Karner blue butterflies, both of which we may have underestimated due to our relatively small number of pitfall traps. Greater understanding of ant community composition would also provide insight, because not all ant species provide the same degree of benefit to Karner blue butterflies (New 1993; Fraser et al. 2001; Pierce et al. 2002). Thus, future studies that evaluate which ant species provide the most benefit to Karner blue butterflies, and the distribution of these species, may be vitally important for the effective management and conservation of Karner blue butterflies.

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