Evidence of an extreme weather-induced phenological mismatch and a local extirpation of the endangered Karner blue butterfly

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Abstract
In 2011, an experiment was undertaken to examine spring synchrony between the endangered Karner blue butterfly (Lycaeides melissa samuelis) (Kbb) and its obligate host plant, wild blue lupine (Lupinus perennis) at Indiana Dunes National Lakeshore (INDU), where the southernmost population of Kbb occurred at the time of this study. From 2012 to 2014, field-placed Kbb eggs were observed for larvae hatching in conjunction with observations of lupine emergence in oak savanna habitat. In 2012, 61% of Kbb hatched when <5% of lupine had emerged due to an extreme early spring event as compared to subsequent years where temporal overlap was >15% between Kbb and lupine. Laboratory experiments testing the sensitivity of Kbb hatching to warm temperatures during the winter of 2011–2012 confirmed that Kbb eggs were susceptible to temperature-induced hatching. In the summer of 2012, second generation Kbb larvae feeding on sun-exposed lupine had higher mortality due to the heat and drought conditions that resulted in earlier plant senescence. Following 2012, Kbb were no longer observed at INDU. This observation illustrates the pressing need for adaptive management strategies that account for extreme weather events brought on by climate change.

KEYWORDS
climate change, drought, early spring, extirpation, extreme weather, Karner blue butterfly, phenologic mismatch, phenology

1 | INTRODUCTION

Studies of the effects of temperature and precipitation changes on timing and performance of the life events of species are important to understanding of the response of ecosystems to climate change and to inform adaptive management measures—iterative strategy development, monitoring, and decision making based on learning—that can help managers to respond to these variable climate change affects (Allstadt et al., 2015; Brown et al., 2016; Menzel et al., 2006). Temperature, precipitation, and photoperiod affect emergence, development, survival, abundance, and the behavior of many insect and plant species (Cohen, Lajeunesse, & Rohr, 2018;...
Piao et al., 2015; Van Asch & Visser, 2007). Because species rely on a variety of cues to time their life processes, and because weather, not photoperiod, is changing under climate change, interacting species may shift their phenological development at different rates or in different directions (Forrest & Thomson, 2011). Climate-related changes in phenology can cascade across trophic levels, affecting ecosystem food webs and driving biodiversity change and loss (Ellwood et al., 2011; Visser & Both, 2005).

Across North America, spring is arriving earlier (Allstadt et al., 2015; Piao et al., 2015). However, earlier leaf out or flowering is not consistent across plant classes, related sub-species, or within a single species. For example, trees have not advanced their phenology as much as other plant groups and some flowering forbs vary within genus (Gerst, Rossington, & Mazer, 2017; Root et al., 2003). Flowering among related species of plants may respond differently, with one subspecies blooming earlier and another remaining unchanged as demonstrated in Mertensia and Solidago (Hafdahl & Craig, 2014; Miller-Rushing & Inouye, 2009).

Likewise, as temperatures have increased, many insects have begun emerging earlier, with spring species advancing faster than summer species (Ellwood et al., 2011; O’Neill et al., 2012). In herbivorous insects, temperature is the dominant abiotic cue for diapause termination (Bale et al., 2002; Navarro-Canó et al., 2015; Wilson, Lewis, & Cunningham, 2009), but cues control the phenology of host plants differently (O’Neill et al., 2012). For example, forest tent caterpillars (Malacosoma disstria) overwinter as eggs and rely on temperature cues to synchronize their hatching with the bud bursts of their host trees, but warming experiments demonstrate asynchronous responses between hatching and hosts (Uelmen et al., 2016).

This phenomenon, temperature-induced emergence, applies to butterflies in general. Butterfly species with more developed overwintering life stages, narrower larval diet, or restricted ranges may be more at risk to the changing temperatures (Diamond, Frame, Martin, & Buckley, 2011). For instance, orange tip butterflies (Anthocharis cardamines) overwinter as pupae and require springtime warming conditions to induce eclosion while their Brassicaceae host plant species showed variable responses to warming conditions (Posledovich, Toftegaard, Wiklund, Ehrlén, & Gotthard, 2015).

Extreme weather events—occurrence of weather or climate variation above (or below) a threshold value, typically 5 or 1% of the upper (or lower) distribution of a the region’s historically observed climatic range—are compounding the consequences of mean temperature change (Seneviratne et al., 2012). Heatwaves, droughts, heavy precipitation, flooding, and periods of unseasonal temperatures have been increasing in recent years and will continue to grow in number and intensity as climate change proceeds (Byun & Hamlet, 2018; Planton, Déqué, Chauvin, & Terray, 2008; Ummenhofer & Meehl, 2017). In 2012, for example, many regions across northeast and Midwestern North America experienced an especially early spring warm up followed by severe summer drought (Ault et al., 2013; Mallya, Zhao, Song, Niyogi, & Govindaraju, 2013). These climate extremes can drive ecological change by differentially affecting interacting species, and these effects can cascade to broader ecosystem function (Butt et al., 2015; Ma, Rudolf, & Ma, 2015; Parmesan, Root, & Willig, 2000; Thibault & Brown, 2008).

Extreme events have had a demonstrated effect on butterflies previously. Climate extremes in 1989, 1990, and 1992 resulted in extirpation of Edith’s checkerspot (Euphydryas editha) butterfly from a montane population in Sequoia National Forest, California (Thomas, Singer, & Boughton, 1996). During the early spring of 1989, temperatures spiked and butterflies were documented in flight before nectar resources were available and starved within 2–3 days. In 1990, another early emergence followed by a snow storm buried the butterflies under snow for nearly a week. The population was extirpated in 1992 when unseasonably cold temperatures in July killed the butterfly’s larval host plant and the larvae starved (Singer & Thomas, 1996). Drought occurring in consecutive years also drove population losses in checkerspot butterfly (E. editha bayensis) in coastal areas (McLaughlin, Hellmann, Boggs, & Ehrlich, 2002).

Because early survivorship is a key aspect of insect fitness, understanding earlier life stage abiotic cues and the potential for phenological mismatches on food resource availability due to climate-induced weather variation is particularly important for predicting ecosystem change. Yet, many insect phenology studies and monitoring programs focus on adult emergence, or plant-pollinator interactions rather than herbivore-plant associations (Byers, 2017; Ellwood et al., 2011; Hodgson et al., 2011; O’Neill et al., 2012).

This study explored the impact of an extreme event on the phenology of spring larval emergence and the development of an endangered butterfly species, and its obligate larval food resource based upon a field experiment transformed by climate extremes. Laboratory experiments tested the effect of spring abiotic cues, temperature and photoperiod, on egg hatching. In the field, Kbb hatch timing was measured against the emergence of its host plant, wild blue lupine, to develop degree-day models. Larval development in the field, measured as successful adult eclosion, was examined across a range of topographic variations of naturally occurring lupine patches to assess topographic landscape variation effects on Kbb larval survival. Field experiments
incidentally documented the effect of unpredicted extreme weather events on this species.

2 | METHODS

2.1 | Study system

The Karner blue butterfly (Kbb) (Lycaeides melissa samuelis) is a native butterfly found in pine barrens and oak savanna habitats from the Northeastern United States to the upper Midwest of the United States and into southern Ontario, Canada (Andow, Baker, & Lane, 1994; Bernard et al., 2012). It has declined from a broader historical distribution to a relatively small set of isolated sites. Today, <1% of original temperate savannas of North America remains in the butterfly’s historic range and this system is considered one of the rarest and most critically endangered ecosystems in the world (Hoekstra, Boucher, Ricketts, & Roberts, 2005). The Kbb was listed in the United States as an endangered species in 1992 (Clough, 1992). Kbb larvae feed solely on wild blue lupine (Lupinus perennis), a disturbance-dependent perennial legume commonly found in savanna habitat. Where it still occurs, the Kbb is considered an indicator species for oak savanna ecosystems due to its association with quality savanna ecosystems (Ballard & Sterfa, 1991; Kerr, Sugar, & Packer, 2000). This study took place in the dune and swale oak savanna habitat of the Indiana Dunes National Lakeshore (INDU), located along the Indiana shore of Lake Michigan. This park was the southernmost refuge of the Kbb, although in steady decline since the 1990s and locally extinct after 2012.

Savanna ecosystems are heterogeneous in canopy cover and transition habitats between woodland-forest and prairie habitats (Albella, Jaeger, & Brewer, 2004). The savanna canopy at INDU is dominated by black oaks (Quercus velutina) and characterized by mixed canopy cover, early successional vegetation, sandy soils, and varying soil moisture as a result of the rolling dune and swale formations created by the last glacial episode (Thompson, 1992). The understory vegetation at INDU provides nectar for adult butterflies and includes native shrubs such as wild blueberry (Vaccinium spp.) and raspberry (Rubus spp.) mixed with a diversity of wildflowers including goldenrods (Solidago spp.), sunflowers (Helianthus spp.), milkweeds (Asclepias spp.), spiderwort (Tradescantia ohiensis), phlox (Phlox spp.), and wild blue lupine (L. perennis) (Grundel, Pavlovic, & Sulzman, 2000; Savanick, 2005). Disturbance by prescribed fire, mechanical alteration, chemical application, or natural processes such as bison grazing is needed to maintain the heterogeneous canopy structure indicative of quality Kbb habitat (Grundel, Pavlovic, & Sulzman, 1998b). The savanna canopy at INDU is dominated by black oaks (Quercus velutina) and characterized by mixed canopy cover, early successional vegetation, sandy soils, and varying soil moisture as a result of the rolling dune and swale formations created by the last glacial episode (Thompson, 1992). The understory vegetation at INDU provides nectar for adult butterflies and includes native shrubs such as wild blueberry (Vaccinium spp.) and raspberry (Rubus spp.) mixed with a diversity of wildflowers including goldenrods (Solidago spp.), sunflowers (Helianthus spp.), milkweeds (Asclepias spp.), spiderwort (Tradescantia ohiensis), phlox (Phlox spp.), and wild blue lupine (L. perennis) (Grundel, Pavlovic, & Sulzman, 2000; Savanick, 2005). Disturbance by prescribed fire, mechanical alteration, chemical application, or natural processes such as bison grazing is needed to maintain the heterogeneous canopy structure indicative of quality Kbb habitat (Grundel, Pavlovic, & Sulzman, 1998b;...

2.2 | Laboratory experiments

A captive breeding colony of Kbb was established in June 2010 from butterflies obtained from INDU (U.S. Fish and Wildlife Service permit #TE10887 A) and reared in environmental chambers (Conviron MTR30) with temperature programs that mimicked historic average temperatures at Indiana Dunes. Temperature profiles were changed every 10 days to replicate the 1952–1999 mean temperature (designated +0 treatment) and varied cyclically between daily minimum and maximum during a 24-hr day. Additional treatments reared Kbb under temperature regimes deviated by a set number of degrees (+2, +4, +6°C) from the historical mean on the same 10-day, diurnally varying cycle. Light to dark cycles were set to the mean sunrise and sunset times for each 10-day period. Date of larval hatching was recorded for these laboratory reared Kbb.

Wild blue lupine is a moderately shade-intolerant, perennial legume native to the sandy glacial outwash regions from Minnesota and southern Ontario, Canada, to Maine (Pavlovic & Grundel, 2009). Lupine can be found in prairies, open barrens, savanna, and woodlands and its phenology varies across the gradient of canopy covers in these habitats. Sun-exposed plants (<30% canopy cover) emerge earlier, grow denser, and are more abundant, while shaded plants (>70% canopy cover), in comparison, emerge and senesce later in the season (Maxwell, 1998; Pavlovic & Grundel, 2009). Under certain weather conditions, the shaded lupine plants are larger and can be of higher nutritional quality facilitating faster larval development and increased Kbb larval survival compared to sun-grown plants (Grundel, Pavlovic, & Sulzman, 1998a; Lane & Andow, 2003). The Kbb is typically bivoltine, with the first generation of adults emerging in late May to June and a second generation of adults occurring in mid to late July into August ending with the diapause of the second generation eggs for the winter (Savignano, 1990; Swengel & Swengel, 1999). Shortly after breeding, first-flight females lay single eggs primarily on the leaves, petioles, and stems of wild lupine plants and occasionally on nearby plants (Pickens & Root, 2008; Lane, 1999). These first-flight females preferentially oviposit on shaded lupine that can provide quality forage further into the growing season in hot, dry years and can increase larval survivorship (Benjamins, 2003). Second-flight females lay their eggs in small clumps or close together on lupine stems, blades of grass, or other leaf litter for overwintering (Grundel et al., 1998b).
To test whether warmer temperatures might induce early hatching of Kbb, wintering laboratory Kbb eggs were exposed to late April temperatures in February and March in an “early spring” experiment. Eighty eggs were obtained from four females from each experimental treatment (+0, +2, +4, +6) and then evenly distributed into treatment cohorts of 10 each to decrease potential maternal effects from the trials (Van Asch, Julkunen-Tiito, & Visser, 2010). The “early spring” treatment was simulated in an environmental chamber (Conviron MTR30) running a temperature profile varying diurnally between 11.2 and 16.7°C, mimicking the historical temperatures between April 20th and 29th, a period when Kbb eggs might typically hatch. Light regimes were unchanged from the programmed schedules. Experiments began on February 19, 2012, more than 2 months before the first laboratory egg hatch date of the warmest treatment recorded in the previous year (April 25, 2011). The experiment was repeated every 10 days for a total of four trials. Half of each cohort was returned to its source treatment following 10 days of exposure to the “early spring” temperatures (10-day treatment), and the remaining half resided in the “early spring” temperatures indefinitely (prolonged treatment). Subsequent trials began on February 28, 2012, March 10, 2012, and March 20, 2012. Eggs were checked daily for hatching.

To determine the lower threshold temperature for the accumulated degree-days that cause hatching, Kbb eggs were incubated in small, individual incubators (ReptiPro 6000 manufactured by ReptiPro), at a constant 2.8°C (n = 40), 6.1°C (n = 40), 7.8°C (n = 41), 10°C (n = 41), 12.2°C (n = 41), and 15.6°C (n = 40) (corresponding to incubator settings of 37, 43, 46, 50, 54, and 60°F). In each incubator, five to six eggs from each of eight random +0 colony females were placed in vented 0.2 ml micro-centrifuge tubes (USA Scientific). Eggs were monitored for hatching for 10 days of exposure to the temperature treatment for each cohort. Each cohort was returned to its source treatment following 10 days of exposure to the “early spring” temperatures (10-day treatment), and the remaining half resided in the “early spring” temperatures indefinitely (prolonged treatment). Subsequent trials began on February 28, 2012, March 10, 2012, and March 20, 2012. Eggs were checked daily for hatching.

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2.3 | Field study of spring Kbb and lupine phenology

To test the potential for springtime phenological mismatch, Kbb egg hatching and lupine emergence were observed simultaneously in the field at INDU. In January 2012, 640 Kbb eggs were deployed at 40 sites (n = 16 egg/site) in vented 0.2 ml micro-centrifuge tubes (USA Scientific). Eggs were sourced from laboratory +0 and +4 laboratory treatment Kbb stocks and evenly distributed between naturally occurring canopy and fully-shaded environments at each site. Sites were located in known Kbb areas and distributed across naturally shaded to open canopy conditions. In subsequent years, 2013–2014, fewer eggs were available, requiring the number of sites and number of eggs placed per site to be reduced (n = 8–10 eggs per site at 20 sites in 2013 and n = 6–8 eggs per site at 16 sites in 2014). Several Kbb eggs were deployed at an easily accessible site and monitored daily to increase the likelihood of observing initial hatching events at field sites. Eggs at field sites were monitored regularly for signs of larval emergence and the date of observed hatching recorded. The proportion of hatched eggs was calculated for each observation date.

During the summers of 2010–2012, the distribution of lupine was mapped across the study area. Mapping entailed walking the study area using GPS units (Garmin 64S and Trimble Juno 3B) to demarcate observed lupine plants across the different dune aspects. Lupine patches were required to be at least three meters apart to be recorded as a distinct plant or patch. Because lupine is a long-lived perennial plant, the resulting map represents where lupine likely existed on the landscape during the years of spring emergence monitoring (Grigore & Tramer, 1996; Michaels, Shi, & Mitchell, 2008).

To document spring timing of lupine emergence in 2012–2014 relative to Kbb hatching, emerging lupine plants were documented in the field with the same methodology as above. The spring sampling paths started from points scattered across the study site and crossed topographic gradients within areas of known lupine presence between deployed Kbb field sites to reduce topographic bias. The newly emerged lupines were recorded as GPS points for each survey date. Known lupine points that had not yet emerged were identified in a GIS overlay analysis and labeled as “absent” if a plant was known from previous surveys and was greater than 3 meters from any emerged lupine point (ESRI, 2016). Absent lupine was assumed to have been absent on prior survey dates. Likewise, when lupine emergence was recorded, the plant was marked as emerged for subsequent survey dates. For each survey date, the percent of lupine was calculated as the number of emerged lupine points divided by the total number of potential lupine points along the survey routes by date (Equation 1).

\[
\% \text{daily lupine} = 100 \times \left( \frac{\text{Number of confirmed emerged lupine points}}{\text{Number of total potential lupine points}} \right)
\] (1)

Degree day values were also estimated for Kbb hatching to compare with lupine phenology across the study
years (Cesaraccio, Spano, Duce, & Snyder, 2001; Zalom & Goodell, 1983). Degree-days is a time-based integral calculation of heat accumulation with a minimum and an optional maximum threshold temperature (Bonhomme, 2000; Cesaraccio et al., 2001). The lower cutoff temperature was determined from laboratory experiments. Lupine degree-days were calculated from hourly ambient temperatures \( T_t \) using the integration method of growing degree-day calculation with a lower cutoff temperature \( T_{base} \) (Equation 2).

\[
\text{Degree day} = \sum_{t=1}^{24} (T_t - T_{base})dt
\]

where \( T = \) temperature, \( t = \) time, and \( T_{base} \) is the minimum threshold temperature.

Hourly temperature data were retrieved from the weather station located at the INDU headquarters complex ~10 km from the furthest study area (MesoWest http://mesowest.utah.edu/ Station Name: BAILLY Station ID: TS480). Each day’s accumulated degree-day value was summed from January 1 to 9:00 a.m. on the day of the survey.

2.4 | Field study of larval development and adult eclosion

Field experiments examined how Kbb larval developed and eclosed into adults relative to lupine phenology. On May 18, 2012, 990 first generation Kbb larvae were released at 33 lupine sites of varying aspect and canopy cover at INDU. At each site, three areas (~2 m\(^2\)) containing ample lupine plants were enclosed with fine mesh nets and 0, 10, or 20 larvae, respectively, were placed under each set of three nets. GPS coordinates and canopy cover measurements were collected at each site and slope and aspect were extracted from a digital elevation model (DEM) in GIS (ESRI, 2016). Nets were checked regularly from May 30 to June 20, 2012 for the presence of adult Kbb. The zero-larvae nets served as a control in Kbb inhabited sites where naturally occurring eggs or larvae may have been present prior to the experiment.

For the second generation larvae, a single larva was placed under a net at each of the same 33 locations. Nets were placed around small wire frames and located over a mass of lupine stems that included at least 15 green leaves. Nets were securely closed on the bottom and top to eliminate possible movement of larvae away from the location. Larvae were introduced into the nets between June 30 and July 6, 2012. Nets were monitored for the presence of an adult Kbb from July 20 to August 8, 2012. In total, 35 larvae were deployed. Lupine senescence was recorded as complete loss of leaves.

2.5 | Adult Kbb field census

To help inform Kbb management at INDU, Kbb butterfly adults were counted during the first and second adult generations between 1999 and 2014. From 1999 to 2012, six routes were walked and adult Kbbbs observed were mapped along the route. This was repeated two to three times per adult flight. The highest adult count for each route for each generation was used as a measure of Kbb abundance. After 2012, larger areas were searched along routes for Kbb. The survey count data was examined with a time series trend analysis.

3 | RESULTS

Statistical analyses (one-way \( t \) test, ANOVA and Tukey HSD post-hoc tests) were performed with SPSS v20 (IBM Corp., 2011).

3.1 | Laboratory experiments

The “early spring” laboratory trials exposing wintering Kbb eggs to late April temperatures determined that Kbb eggs could be induced to emerge early compared to those maintained at the historical temperature regimes. Eggs from the +0 and +2 colonies exposed to April temperatures in both the 10-day and the prolonged treatments hatched sooner than colony eggs (+0 10-day: \( SD = 2.4, n = 7, t = 117.9, df = 6, p < .0001 \); +0 prolonged: \( SD = 10.6, n = 25, t = 39.1; df = 24; p < .0001 \); +2 10-day: \( SD = 2.3, n = 6, t = 113.3; df = 5; p < .0001 \); +2 prolonged: \( SD = 10.4, n = 24, t = 39.9; df = 23; p < .0001 \)). Eggs from the +4 treatment colony in the 10-day treatment hatched 3.2 days later (\( SD = 2.5; n = 5 \)) than colony eggs (\( t = 93.9; df = 4; p < .0001 \)); however, +4 eggs in the prolonged treatment hatched 11.1 days sooner (\( SD = 9.6; n = 11 \)) than those from the +4 colony (\( t = 31.9; df = 10; p < .0001 \)). Eggs from the +6 treatments failed to hatch (Figure 1).

Degree day accumulation for Kbb hatching begins when temperature exceed a minimum lower threshold temperature value. Peterson et al. (2006) employed 12°C as a minimum cutoff for calculating Kbb degree-days; however, the laboratory experiments indicated that 10°C is the appropriate minimum threshold value for Kbb degree-day calculations. The constant-incubated eggs at
2.8, 6.1, 7.8, 10°C failed to hatch after 15 days of incubation, while egg incubated at 12.2°C (n = 4) and 15.6°C (n = 13) hatched within 10 days. After 21 days, the unhatched eggs were moved to room temperature (>16°C) and viable eggs from the 2.8°C (n = 5), 6.1°C (n = 4), 7.8°C (n = 1), and 10°C (n = 11) hatched within 2 days. The value of 10°C is a standard threshold in pest management and is consistent with other butterfly studies (Cayton, Haddad, Gross, Diamond, & Ries, 2015; Herms, 2004; Pruess, 1983; Roltsch, Zalom, Strawn, Strand, & Pitcairn, 1999).

3.2 Field study of spring Kbb and lupine phenology

The timing of Kbb hatching in the field differed by year. The mean hatch day was 76.6 in 2012, 117.2 in 2013, and 111.1 in 2014 and was significantly different across all years (ANOVA $F_{2,491} = 10,423$, $p < .0001$; Tukey HSD $p < .0001$) (Table 1). However, the mean degree-days for Kbb egg hatching were not significantly different across all 3 years: 51.4 degree-days in 2012, 47.9 degree-days in 2013, and 47.7 degree-days in 2014 (ANOVA $F_{2,490} = 1.720$, $p = .180$; Tukey HSD $p > .19$) (Table 2). Hatching initiated at 36 degree-days and was nearly complete by 80 degree-days.

The spring emergence of lupine also differed by year. In 2012, half of known lupine had emerged by March 19 (Day of year 79), while this same amount of lupine did not emerge until April 29 (day of the year 119) in 2013 and April 24 (day of the year 114) in 2014. The mean day for emerged lupine was 79 in 2012, 113 in 2013, and 116 in 2014 (ANOVA $F_{2,2,261} = 5,898$, $p < .0001$; Tukey HSD $p < .0001$) (Table 1). However, in 2012, lupine emergence required additional degree-day accumulation for emergence than in subsequent years. Lupine emergence in 2012 was delayed with a mean degree-day accumulation of 76.5 compared with mean degree-days of 42.1 in 2013, and 59.1 in 2014 (ANOVA $F_{2,2,261} = 629.8$, $p < .0001$; Tukey HSD $p < .0001$) (Table 2).

INDU, like other areas of the Midwest United States in 2012, experienced the earliest false spring to date (Ault et al., 2013). An early false spring occurs when unseasonably warm temperatures in late winter trigger an untimely break in dormancy of plants and animals and can result in phenological mismatches between species.

![FIGURE 1](image.png) Change in hatch timing of Kbb eggs in days resulting from the laboratory “early spring” experiment where eggs from three laboratory temperature Kbb colonies—historic (1951–1999) mean temperature (+0), +2°C above historic temperature (+2), and +4°C above historic temperature (+4)—were exposed to 10 days (10-day) or continuous duration (Prolonged) historic late April temperatures; * indicates significance based on t test. Kbb, Karner blue butterfly.

| Field results | Treatment | Mean | Median | SD  | n   |
|---------------|-----------|------|--------|-----|-----|
| 2012 Kbb Hatch | Field     | 76.6 | 76.0   | 2.1 | 382 |
| 2013 Kbb Hatch | Field     | 117.2| 119.0  | 3.1 | 18  |
| 2014 Kbb Hatch | Field     | 111.1| 111.5  | 3.2 | 96  |
| 2012 lupine emergence | Field | 79.2 | 78.0  | 2.0 | 531 |
| 2013 lupine emergence | Field | 113.4| 114.0 | 7.4 | 1325|
| 2014 lupine emergence | Field | 116.0| 113.0 | 7.1 | 406 |

| Lab results | Treatment | Mean | Median | SD  | n   |
|-------------|-----------|------|--------|-----|-----|
| 2012 Kbb Hatch | +0        | 117.4| 117.0  | 4.9 | 741 |
| 2012 Kbb Hatch | +2        | 110.0| 110.0  | 4.3 | 292 |
| 2012 Kbb Hatch | +4        | 103.8| 105.0  | 6.5 | 228 |
| 2012 Kbb Hatch | +6        | 96.0 | 97.0   | 5.2 | 113 |

Abbreviation: Kbb, Karner blue butterfly.

TABLE 1 Day of the year summary statistics of Kbb hatching in the field from 2012 to 2014, lupine emergence in the field from 2012 to 2014, and Kbb hatching in the laboratory in 2012 under increasing temperature treatments—historic temperature (+0), +2°C above historic temperature (+2), +4°C above historic temperature (+4), and +6°C above historic temperature (+6).
and food resources (Allstadt et al., 2015; Bale et al., 2002; Ellwood et al., 2011). The early spring was followed by record-breaking high July heat and extensive drought in the region (Karl et al., 2012; Mallya et al., 2013). Due to this extreme early spring event, temperatures were above 25°C at INDU in mid-March of 2012 and Kbb began hatching on March 15. However, by degree-days, Kbb hatching was not significantly different across the study

**Table 2** Degree-day summary statistics of Kbb hatching in the field from 2012 to 2014, lupine emergence in the field from 2012 to 2014, and Kbb hatching in the laboratory in 2012 under increasing temperature treatments—historic temperature (+0), +2°C above historic temperature (+2), +4°C above historic temperature (+4), and +6°C above historic temperature (+6)

| Field results            | Treatment | Mean | Median | SD   | n  |
|--------------------------|-----------|------|--------|------|----|
| 2012 Kbb Hatch Field     | 51.4      | 44.3 | 19.8   | 382  |
| 2013 Kbb Hatch Field     | 48.0      | 50.5 | 10.4   | 18   |
| 2014 Kbb Hatch Field     | 47.8      | 50.1 | 10.0   | 96   |
| 2012 lupine emergence    | 76.5      | 75.3 | 20.5   | 531  |
| 2013 lupine emergence    | 42.1      | 37.3 | 19.5   | 1325 |
| 2014 lupine emergence    | 59.1      | 56.5 | 16.1   | 406  |

| Lab results              | Treatment | Mean | Median | SD   | n  |
|--------------------------|-----------|------|--------|------|----|
| 2012 Kbb Hatch +0        | 38.6      | 35.6 | 13.9   | 741  |
| 2012 Kbb Hatch +2        | 42.1      | 40.7 | 14.1   | 292  |
| 2012 Kbb Hatch +4        | 52.6      | 54.2 | 22.7   | 228  |
| 2012 Kbb Hatch +6        | 54.9      | 56.1 | 19.1   | 113  |

Abbreviation: Kbb, Karner blue butterfly.

**Figure 2** (a) Percent of wild blue lupine present compared to percent of hatched Karner blue butterfly larvae present by day of the year at INDU in 2012, 2013, and 2014. (b) Percent of wild blue lupine present compared to percent of hatched Karner blue butterfly larvae present by degree-day at INDU in 2012, 2013, and 2014. INDU, Indiana Dunes National Lakeshore; Kbb, Karner blue butterfly.
years, while lupine emergence was delayed in 2012 as compared to 2013 and 2014 (Figure 2,b). Kbb hatched prior to lupine emergence in 2012, based on both day of the year ($t = -18.4$; $df = 911$; $p < .0001$) and degree-day ($t = -18.5$; $df = 911$; $p < .0001$) (Tables 1 and 2). In 2013, Kbb and lupine emergence were not significantly different, based on both day of the year ($t = 2.2$; $df = 1,341$; $p = .30$) and degree-day ($t = 1.3$; $df = 1,341$; $p = .21$). In 2014, mean Kbb hatch was sooner than lupine emergence, on average, in both day of the year ($t = -6.2$, $df = 495$; $p < .0001$) and degree-days ($t = -6.5$; $df = 495$; $p < .0001$). In 2012, 43% of Kbb emerged with <2% of anticipated coverage of lupine on the landscape and another 18% of Kbb emerged with <5% lupine coverage (Figure 2). In years without an early spring extreme event (2013 and 2014), lupine emergence and larval hatching had temporal overlap such that >15% of lupine had emerged across the studied landscape when Kbb larvae began emerging.

### 3.3 | Field study of larval development and adult eclosion

Larval success, measured as presence of an adult Kbb from larvae placed under nets in the field, was assessed for both generations across a range of topographic variation in 2012. Larval to adult eclosion success in the first generation was 2.22% based on a total of 22 adult Kbbbs recovered from the enclosure nets ($n = 990$) and lacked a discernable pattern in the topography. In the second generation, two individuals were found as adults, for a 5.7% success rate ($n = 35$). These second brood successful sites were northern facing slopes with mean canopy cover of 71.4% ($SD = 4.3%$; $n = 2$) as compared to unsuccessful sites on non-northern aspects with mean canopy cover of 56.5% ($SD = 21.1%$; $n = 30$). Due to the summer drought of 2012, 27% of lupine sites ($n = 9$) fully senesced as indicated by the complete loss of leaves, before the end of July (Figure 3).

### 3.4 | Adult field census

From 1999 to 2012, the Kbb population at INDU was in decline ($y_t = 471.4–16.1 x_t$, adjusted $R = .74$; $df = 23$; $p < .0001$). The Kbb population at INDU peaked at the start of population surveys in 1999. Between 2012 and 2013, the population count fell significantly and after 2012, Kbb butterflies were no longer found in or around INDU (Figure 4).

### 4 | DISCUSSION

The observed mismatch in Kbb and wild blue lupine phenologies in 2012 compared to subsequent years suggest that interacting insect-plant associations can be affected by extreme weather events and that these altered phenologies can be detrimental for insect-plant interactions. Here, the early spring event of 2012 induced Kbb larvae...
to begin hatching on March 15, ~2 days prior to sufficiently available food resources on the landscape at INDU. The timing of Kbb hatching was rapid, initiating at ~36 degree-days; by 60 degree-days, 80% of Kbb eggs had hatched; and within the week, nearly all eggs had hatched. The phenology of its host plant, wild blue lupine, was delayed in 2012 despite the early spring event as compared to other years and suggests that environmental factors beyond air temperature contribute to signaling growth in this perennial plant. Because of its precipitous hatching, its limited dispersal ability, and specialization on a single plant species, Kbb may be more at risk than other butterfly species to phenological mismatching (Eskildsen et al., 2015; Miller-Rushing, Høye, Inouye, & Post, 2010).

Drought conditions by early July of 2012 resulted in water-stressed lupine plants, especially on warmer aspects, and by late July, lupine plants had senesced (Kar et al., 2012; Mallya et al., 2013). Lupine of poor nutritional quality can slow Kbb growth rate, reduce larvae size at pupation, and undermine fitness (Grundel et al., 1998a). Senesced lupine plants led to observed failure of second generation larvae to reach adulthood, while lupine on northern slopes with greater canopy cover maintained sufficient quality to foster larval growth and successful adult eclosion, thus providing a refugia for Kbb. Shade-grown lupine tends to be sparse, but can be of higher nutritional value, and more drought-tolerant than full-sun grown lupine (Grundel et al., 1998a; Hellmann, 2002). The observed survival on northern aspects highlights the importance of climate refuges, particularly those on northerly facing slopes, especially during dry weather years. Drought stress can also negatively affect nectar food sources for adult pollinators (Carroll, Pallardy, & Galen, 2001; Huberty & Denno, 2004; Walsh, 2017). Reduced adult nutritional status can reduce adult weight, decrease adult longevity, reduce egg production, and decrease egg overwintering survival (Carroll et al., 2001; Hellmann, 2002; Murphy, Launer, & Ehrlich, 1983; Wyatt, Broyles, & Derda, 1992).

While the reasons for the decline of Kbb at INDU from 1999 to 2011 remain uncertain, the less extreme effects of climate change such as advancing onset of spring and longer growing seasons may have stressed Kbb, its host plant, or both at INDU during that time (Posledovich et al., 2015). Like other Lepidoptera, Kbb may exhibit multi-voltinism if exposed to signaling temperature and light conditions (Altermatt, 2010). Warmer springtime temperatures can trigger earlier Kbb larval emergence and result in the failure of a fraction of second generation Kbb eggs to undergo diapause. These individuals may subsequently fail to complete a third life cycle as lupine senescence would have likely occurred before the Kbb larva could fully mature (Altermatt, 2010).

Intermittent summer droughts may have decreased food resources during Kbb adult flights thereby reducing fitness (Cope et al., 2017; Huberty & Denno, 2004). Retrospectively investigating historic temperature and precipitation patterns in comparison to Kbb surveys, lupine phenology, degree-day models, and management practices may help to unravel the circumstances around the decline of Kbb at INDU. Further investigations of lupine phenology and the abiotic factors that affect its life history like temperature and precipitation could prove valuable to predicting Kbb-lupine interactions into the warming future. The low larval survivorship in the first generation field experiment despite protection and abundant green lupine indicates that additional factors like predation, parasitism, or competition may be negatively affecting larval survivorship.

While predicting extreme weather events is difficult, if not impossible, managers may endeavor to understand the effects of such extreme climatic variation on their managed habitats and species and adapt their management practices accordingly. Adaptive management, a framework of iterative goal setting, monitoring, strategy development, action implementation, and informed decision making based on learning and knowledge building from feedback, is a proven method for successful natural resource conservation and may be an increasing valuable tool for adapting to climate change (Lawler, 2009; Patterson & Grundel, 2014). For example, here, modifying canopy cover and managing for a mosaic of shading on hill aspects has proved a valuable climate adaption strategy. Great effort is expended in habitat restoration and species management, but unfortunately, few track ecosystem responses (Schultz, Russell, & Wynn, 2008). Structured annual monitoring and tracking of proximate indicators based on habitat goals can provide quantitative information for adaptive decision making (Bried et al., 2014; Landres, Morgan, & Swanson, 1999; Murphy & Weiland, 2011). For example, in this case, tracking degree-days, rain-free days, and summer heat indices in conjunction with tree bud burst, wildflower blooming observations, or monitoring plant phenology plots such as lupine may serve as viable tracking metrics for availability of food resources for pollinators like the Kbb. A degree-day metric, calculated from daily weather observations, would have informed management of the 2012 early spring event that unfolded. Similarly, if a summer metric like rain-free days was tracked with flowering observations, the lack of summer food sources may have also become apparent to management. Employed tracking metrics in 2012 may have triggered a resource supplementation strategy like providing additional nectar sources for pollinators and a precautionary approach to the following year's management actions like withholding spring...
prescribed burning. This type of regular habitat assessment is particularly important for species-specific monitoring (Scott et al., 2005). As demonstrated here with the endangered Kbb, endangered species recovery may be better served if recovery plans expanded beyond simple population metrics to integrated habitat and weather metrics and precautionary decision making in the face of uncertain climate patterns as the consequences can be lethal for a species already under stress (Bernazzani, Bradley, & Opperman, 2012; Campbell et al., 2002; Gerber & Hatch, 2002; Neel, Leidner, Haines, Goble, & Scott, 2012). A shared, cohesive adaptive strategy of goals, metrics, monitoring, and assessment across management units could allow for transparent decision making and provide a collective knowledge base for resource managers. Climate change and extreme weather events will continue to strain interactions between species and habitats with potentially deadly consequences as was the case here of the local Kbb extirpation at INDU where employing a cohesive adaptive strategy may serve to offset negative climate impacts.

Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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CONFLICT OF INTEREST
The authors declare no potential conflict of interest.

AUTHOR CONTRIBUTIONS
R.G., J.H. conceived and secured funding for the larger study: effects of climate change on endangered Karner blue butterfly (Kbb). T.P. and R.G. completed field and constant incubation experiments. J.D. oversaw laboratory Kbb propagation, provided stock for field experiments, and completed laboratory early spring hatch experiment. R.K. collected adult Kbb count field data. T.P. preformed GIS and data analysis and contributed the bulk of manuscript preparation with input from R.G., J.D., and J.H.

DATA AVAILABILITY STATEMENT
The data that supports the findings of this study are openly available in ScienceBase under Karner blue butterfly field datasets (https://www.sciencebase.gov/catalog/item/5b80299ee4b05f6e32194d3e): Karner blue butterfly adult count surveys at Indiana Dunes National Lakeshore, 1994–2014 (https://doi.org/10.5066/P9S9D95J0), Karner blue butterfly egg hatching observation at Indiana Dunes National Lakeshore, 2012–2014 (https://doi.org/10.5066/P9T8HFQ9), Karner blue butterfly larval success observations at Indiana Dunes National Lakeshore, 2012 (https://doi.org/10.5066/P95GFNGQ); Karner blue butterfly laboratory datasets (https://www.sciencebase.gov/catalog/item/5b8029b6e4b05f6e32194d40): Karner blue butterfly early spring laboratory experimental hatching observations (https://doi.org/10.5066/P9S7086U), Karner blue butterfly eggs constant temperature incubation in 2013 (https://doi.org/10.5066/P9L3Q0KR); and Habitat, microclimate, and phenological patterns of Wild Lupine project (https://www.sciencebase.gov/catalog/item/5b7b54ce4b0f368e932cac): Wild blue lupine spring survey points at Indiana Dunes National Lakeshore, 2012–2014 (https://doi.org/10.5066/P9T8HFQ9), Wild blue lupine summer survey points at Indiana Dunes National Lakeshore, 2010–2012 (https://doi.org/10.5066/P96F3DQH), and Wild blue lupine survey tracks at Indiana Dunes National Lakeshore, 2010–2014 (https://doi.org/10.5066/P9B93C17).

ETHICS STATEMENT
Handling, rearing, and disposition of Karner blue butterfly eggs, larvae, and adult butterflies was approved by U.S. Fish and Wildlife Service under Endangered Species Act Section 10 permit #TE10887A.

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