Extinction risk modeling predicts range-wide differences of climate change impact on Karner blue butterfly

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Abstract

The Karner blue butterfly (*Lycaeides melissa samuelis*), an endangered species in decline due to multiple factors, including habitat loss, can be further threatened by climate change. Evaluating how climate shapes the population dynamics and distribution of the Karner blue (Kbb) is necessary for developing adaptive. Demographic models generally used for insect populations are often either density-dependent or applied to population presence-absence data in a density-independent manner. In contrast, we used scale-based, mixed density-dependent and density-independent (hereafter “endo-exogenous”) models for the Kbb, based on long-term count data of abundance during flight periods, to understand how different environmental variables, including climate, affected Kbb extinction risk through the middle of the 21st century. Our endo-exogenous models showed that density-dependent and environmental variables, including climate, topography, and tree canopy coverage, were essential drivers of Kbb population dynamics. We also found that Kbb’s response to climate differed between the species’ two annual generations and across its range: higher temperature and precipitation in summer generally benefited the second-generation populations, whereas there were uncertainties of the effects on the populations in different ecoregions during the first generation. These results imply that population-specific biotic/abiotic factors need to be incorporated into plans to manage the recovery of Kbb under climate change.

Introduction

Effects of climate change on biodiversity and ecosystems are well-documented [1-4], including changes in morphology, phenology, and species distributions [5-8]. Insects can be valuable indicators of how species respond to climate change [7-12] because they are ectotherms and are widespread across heterogeneous landscapes [13-14]. They also have complex life cycles with varying vulnerability throughout their life spans, challenging us to understand multiple ways in which climate change can affect a single species [15-16].

Widespread, increasing extinction risk has been documented across insect orders [60]. Therefore, improving the ability to predict extinction risk and relating that to drivers affecting that extinction risk is an important tool for conservation planning for at-risk species [61-63]. Elsewhere, we modeled extinction risk for an endangered butterfly, the Karner blue butterfly (Kbb, *Lycaeides melissa samuelis*), using an approach that incorporates both density-dependent and density-independent effects. We evaluated how density-dependent and density-independent factors might affect Kbb population size across generations.

The thermal regime controls the survival of many ectothermic organisms [17-19]. Climate change projections for the Midwest and the Northeastern United States (U.S.) predict higher temperatures, especially during the winter [20-21]. This could undermine the fitness of insect species [22] if it causes earlier maturation and smaller body sizes [23-24]. However, under warmer conditions and faster development, extra generations may appear, as has been reported for some species [25-27].

Precipitation patterns are varied due to climate change, and rainfall can be as significant as the temperature in affecting demography [28-29]. For insects, in particular, the effects of rain on demography can be complex and vary with temporal and spatial scales. For example, rainfall can interfere with pollen transport and dilute nectar, leading to lower pollinator visitation rates and poorer host plant reproduction [30-31]. In fact, for some butterfly species, total monthly precipitation is a better predictor of abundance than temperature and relative humidity [32-33].

Microclimates are mainly determined by terrain and canopy coverage [34]. Topographic conditions (i.e., slope, aspect, elevation) usually are decoupled from broad climatic gradients [35-37]. Wind speed/direction and solar radiation are affected by landscape texture [38] and, in turn, influence local thermal and rainfall patterns [39]. For instance, south-facing slopes are generally warmer than north-facing slopes in the northern hemisphere (Geiger et al., 2009). Higher elevations are colder and drier than lower altitudes [38]. This suggests that population survival models should incorporate fine-scaled, topo-climatic variables [41-43].

Multiple species in the butterfly family Lycaenidae share traits that make them prone to endangerment [44], including limited dispersal ability, monophagy or limited hostplant species, and specific habitat configuration requirements. The Kbb was listed as federally endangered in 1992 [48-49]. Today, native populations exist in isolated locations in New York, Michigan, and Wisconsin, U.S.; some have been reintroduced in Ohio, New Hampshire, Minnesota, U.S. [45-47]. The Kbb has an inherently limited dispersal range (less than 1 km), and habitat fragmentation further restricts their range expansion [49-50]. It resides in high-quality oak savanna and pine barren habitats, the landscape that supports its sole host plant, wild blue lupine (*Lupinus perennis*).

These landscapes have declined for decades due to fire suppression, agricultural expansion, and urbanization [54-56]. In recent years, oak savanna – pine barren areas have experienced new climate patterns, including prolonged summer drought and milder springs and winters. Specialist butterflies like the Kbb may be particularly susceptible to temperature changes if their hostplants are negatively affected by drought and other conditions, for example, host plant availability throughout the growing season [57-59]. Such influences may directly cause declines in Kbb survivorship and reproduction [60].

As a bivoltine species, first-generation Kbbs overwinter as an egg until mid-April, mature from larva to pupa through late May, and experience peak flight of emerging first-generation adults in June. In July, a second generation begins with peak flight and egg-laying in August [65]. The second generation is typically three to four times more abundant than the first generation [51, 66-67]. Thermal and drought tolerances are usually specific to each life stage [67-70], and climatic stress experienced by one stage can influence the next through ‘carry-over effects’ [71]. Conditions experienced by one generation also affect subsequent generations through ‘transgenerational effects’ [72-74]. Both carry-over and transgenerational effects are important considerations when modeling Kbb responses to temperature [75-76] to ensure that impacts throughout the life stages are modeled [77-79].

In a population viability analysis of the Kbb, [80] ranked the loss of habitat, fragmentation, and weather-related loss of eggs/larvae as critical bottlenecks for Kbb population viability. Several of these effects exhibited density dependency. Loss of overwintering eggs, effects of variable spring temperature and precipitation on larval survival, and effects of stress (often drought-induced) on hostplants affecting larval survival later in the year were climate change sensitive aspects of the Kbb life history that were most critical in determining population viability.

Here we modeled the effects of climate trends on both generations of the Kbb to identify significant predictors of population dynamics [81]. In addition, because both density dependence and independence influence insect population dynamics, we incorporated carry-over and transgenerational effects in a series of endo-exogenous models. The models captured both density dependence of the two generations of adult Kbb and corresponding density-independent environmental variables [82-83]. We used these models to test three central questions: first, if density independent factors were more critical than density-dependent effects in predicting population trends; second, how various density-independent environmental factors affected the two generations of Kbb; third, how best-fit models of Kbb abundance differed among locations and spatial scales.

Materials and Methods

Density-Dependent Data

We used time-series count data of adult Kbb from five populations across the species' range as the source of information on past population trends in Kbb abundance (S1 Table 1). Four populations were located on oak savannas in the Midwest U.S., and the fifth was found in eastern U.S. pine barrens habitats (Fig 1). Researchers sampled existing populations annually over time frames of 8 – 27 years at 48 sites in three states (Indiana, New York, Wisconsin), counting adult Kbb present along linear transects during the flight period – from late May to late June for the first generation, and from mid-July to mid-August for the second generation (S1 Table 2). Each of the five population groups was in a distinct ecoregion (S1 Fig 1) [84]. All populations within a given ecoregion were surveyed with consistent sampling strategies through time, usually by the same research teams at each location, allowing us to model across sites within the same ecoregions.

Fig 1. Locations of Karner blue butterfly's habitats in Central Wisconsin, Northwest Wisconsin, Fort McCoy (Wisconsin), Indiana Dunes National Park, and Albany Pine Bush (New York). White filled circles represent extant Karner populations, open circles represent historical Karner populations that are now extinct, and yellow filled circles represent sites with Karner reintroduction management ongoing.

Transect widths were not consistent among regions, so we calculated a population density index across all the surveys during each generation per site expressed as the number of individuals per kilometer of the transect. Although periodic habitat management at the sites, such

as mowing and burning, resulted in changes in vegetation conditions, variance caused by different management practices was not explicitly considered but may have affected our results. We assessed density-dependent effects for each generation by including flight-period population densities of the previous two generations. Including generations from more than the last year was unlikely to increase explanatory power [85].

Density-Independent Data

We downloaded monthly climatic data (S1 Table 3) from the Parameter-elevation Relationships on Independent Slopes Model (PRISM Climate Group) as raster maps at a resolution of 30 arc-seconds (1/40th of a decimal degree). Each pixel was 800 m x 800 m [86]. PRISM's temperature and precipitation are gridded interpolations of climate data and digital elevation models (DEM) [87-88]. As environmental factors vary throughout the growing season, it was necessary to examine the two generations separately to understand their interactions with Kbb life cycles [89-90].

For each Kbb population, we used monthly climatic data corresponding to the location and time over which surveys were conducted. We examined four climate variables – monthly minimum, maximum, and mean temperature, and total precipitation – over periods approximating three life stages: egg (Dec-Mar as overwintering), larvae and pupae (Apr-May as spring), and peak adulthood (Jun) for the first generation; egg (Jun), larvae and pupae (Jul), and peak adulthood (Aug) for the second generation.

We included two additional topographic variables: slope and aspect. They were derived from 30 m DEMs obtained from USGS (U.S. Geological Survey) in ArcGIS [91]. The circular aspect layer was converted to a topographic solar radiation index (i.e., *trasp*), using the following linear transformation:

$$trasp = \frac{1 - \cos \left[\frac{\pi}{180} * (aspect - 30) \right]}{2}$$

The transformation output was a continuous variable between 0 and 1 where north-oriented slopes were assigned 0, and south-oriented slopes were given 1 [92].

We also extracted canopy coverage from the 2011 National Land Cover Database (NLCD) and USFS Tree Canopy Cover for CONUS from the Multi-Resolution Land Characteristics (MRLC) Consortium at 30 m resolution [93]. We assumed that both topography and tree canopy cover had been constant over the past two decades at the level of individual sites [51].

Modeling Process

We combined our density data with environmental explanatory variables to create endo-exogenous models using 18 predictor variables per generation. Our statistical models were built at two spatial scales: i) population grouped by each ecoregion, and ii) all populations combined across ecoregions. We modeled population group as the unit rather than specific populations for

three reasons: first, density estimates for each population were too small to create robust models; second, variation among transect measurements at an individual site could be very high, particularly when local population density was low; third, there was no variance of topography or canopy cover within individual sites. Sample sizes and the number of years surveyed in our data set varied among regions (S1 Table 1). Therefore, when integrating all populations, we reduced estimation bias using bootstrapping to balance oversampled and underrepresented population groups, following [94-95].

We applied six modeling algorithms of R package “caret” [96] to check model performance with mean absolute error, root-mean-square error, and adjusted R-squared: two were regression-based (i.e., generalized linear model and multivariate additive regression spline, and four were machine-learning (i.e., random forest, gradient boost machines, support vector machines, neural network analysis). We preprocessed low-variance and colinear predictors to reduce the high-dimensionality of data space and standardized variables in regression-based algorithms with centering and scaling. After reviewing initial models (S1 Table 4), we limited further modeling efforts to the use of random forests, a non-parametric approach that did exceptionally well for multivoltine species, guaranteeing robust model outputs in other studies [97-98].

We then used the genetic algorithm (GA) for selection among random forest models [99]. Genetic algorithm, as a computationally efficient approach, generated an entire population of feasible solutions that were repeatedly subjected to “cross-over” and “random mutation” until the combinatorial optimum with the lowest Akaike Information Criterion (AIC) was identified [100]. A concern with GA applications is the potential to overfit the models. Therefore, we also applied jack-knife partial least squares (PLS) using the R package “mdatools” [101]. This linear latent approach is suitable when the matrix of predictors has more variables than observations [102], identifying the estimated coefficient, standard error, and p-value of each predictor. The sample R codes were included in S2 Appendix.

Ethics Statement

The study did not involve human subjects, vertebrates, or cephalopods, nor any kind of animal sacrifice. It did involve observational and field studies of a federally listed endangered species – Karner blue butterfly. Approval from the U.S. Fish and Wildlife Service and relevant state agencies to conduct Kbb counts were obtained when required by those agencies. Data were collected on federal, state, and non-governmental organization lands managed by the U.S. National Park Service (Indiana Dunes National Park populations), U.S. Department of Defense (Fort McCoy populations), and the Albany Pine Bush Commission (Albany Pine Bush populations), with the permission of those entities. For the Central and Northwest Wisconsin populations, all the surveys were legally carried out on public-access land (state- and county-owned, or public access rights-of-way immediately along public roads) without intentionally handling, harassing, or taking specimens.

Results

For the first generation, the population density of both first and second generations in the previous year were positively related to current-generation density, except the populations of Northwest Wisconsin (Table 1). Among 12 climate variables, population density increased with warmer overwintering minimum temperature at the whole-species scale in Central Wisconsin and decreased in Fort McCoy and Albany Pine Bush; it also reduced with higher overwinter and spring total precipitation except in Northwest Wisconsin. In contrast, none of the June predictors and spring minimum temperature were significant in any ecoregion. Specifically, in populations of Northwest Wisconsin and Indiana Dunes National Park, canopy cover, elevation, slope, and trasp were negatively associated with current-generation density.

Table 1. Best-fit endo-exogenous partial least squares regression model regression coefficients at whole-species scale and (five) ecoregion for the first-generation Kbb populations, separately. The adjusted-R² values were attached to the last row of the table.

	Whole Species			Central Wisconsin			Northwest Wisconsin			Fort McCoy			Indiana Dunes National Park			Albany Pine Bush		
	EC	SE	p	EC	SE	p	EC	SE	p	EC	SE	p	EC	SE	p	EC	SE	p
PS	0.38	0.08	0.007	0.25	0.10	0.050	0.08	0.06	0.230	0.77	0.10	0.001	0.58	0.08	0.002	0.48	0.10	0.007
PF	0.23	0.06	0.014	0.17	0.05	0.029							0.32	0.04	0.001			
MT_OW																-0.10	0.03	0.036
MT_SP	0.05	0.02	0.040							0.04	0.05	0.125						
MT_JN																		
AT_OW																-0.02	0.03	0.026
AT_SP	0.05	0.01	0.010	0.09	0.03	0.056												
AT_JN																		
IT_OW	0.03	0.01	0.072	0.14	0.03	0.024				-0.11	0.06	0.022				-0.14	0.01	0.001
IT_SP																		
IT_JN																		
PT_OW										-0.22	0.04	0.004	-0.14	0.06	0.088	-0.19	0.04	0.008
PT_SP	-0.21	0.03	0.003	-0.35	0.03	0.000				-0.18	0.08	0.085						
PT_JN																		
Canopy							-0.03	0.01	0.060				-0.02	0.01	0.074			
Elevation							-0.08	0.02	0.014				-0.04	0.06	0.380			
Slope							-0.04	0.01	0.011				-0.03	0.03	0.254			
Trasp							-0.04	0.01	0.018				-0.01	0.07	0.263			
adj-R ²	0.409			0.418			0.606			0.424			0.753			0.615		

EC, Estimated Coefficient; SE, Standard Error; p, p-value; PS, Previous-Year Second-Generation Density; PF, Previous-Year First-Generation Density; MT, Mean Temperature; AT, Maximum Temperature; IT, Minimum Temperature; PT, Total Precipitation; OW, Overwinter; SP, Spring; JN, June. Blank cells indicate non-significant ($p > 0.1$) predictors.

For the second generation, four variables were significant across spatial scales and among ecoregions: population density of previous-year second-generation (positive), current-year first generation (positive), August maximum temperature (positive in Northwest Wisconsin and Fort McCoy, and negative in Central WI and at whole-species scale), and July total precipitation (positive, except in Fort McCoy and Albany Pine Bush) (Table 2). Total precipitation for June and August were the only variables not significant in any ecoregion. Canopy cover was positively associated with current-generation density in Northwest Wisconsin but negative in Indiana Dunes National Park. The three topographic predictors were consistently negative in Indiana Dunes National Park but insignificant.

Table 2. Best-fit endo-exogenous partial least squares regression model regression coefficients at whole-species scale and (five) ecoregion for the second-generation Kbb populations, separately. The adjusted-R² values were attached to the last row of the table.

	Whole Species			Central Wisconsin			Northwest Wisconsin			Fort McCoy			Indiana Dunes National Park			Albany Pine Bush		
	EC	SE	p	EC	SE	p	EC	SE	p	EC	SE	p	EC	SE	p	EC	SE	p
CF	0.36	0.08	0.013	0.38	0.10	0.052				0.16	0.04	0.010	0.48	0.11	0.012	0.68	0.15	0.011
PS	0.24	0.08	0.045	0.18	0.07	0.062	0.06	0.02	0.019	0.18	0.05	0.016	0.35	0.07	0.009	0.17	0.10	0.039
MT_JN																0.07	0.04	0.198
MT_JL										0.08	0.01	0.003						
MT_AG				0.03	0.01	0.053	0.03	0.02	0.074							0.05	0.02	0.035
AT_JN													0.05	0.03	0.089			
AT_JL	-0.04	0.02	0.063							0.07	0.02	0.037						
AT_AG	-0.06	0.03	0.098	-0.06	0.02	0.032	0.03	0.01	0.025	0.10	0.02	0.007						
IT_JN	0.06	0.02	0.019	0.03	0.02	0.249	0.02	0.01	0.016									
IT_JL							0.05	0.02	0.094	0.09	0.01	0.001						
IT_AG																0.06	0.03	0.068
PT_JN																		
PT_JL	0.06	0.02	0.019	0.08	0.06	0.025	0.04	0.03	0.024				0.08	0.05	0.062			
PT_AG																		
Canopy							0.06	0.02	0.049				0.02	0.03	0.304			
Elevation													-0.02	0.05	0.306			
Slope	-0.07	0.02	0.011										-0.07	0.06	0.293			
Trasp													-0.06	0.03	0.154			
adj-R ²	0.468			0.447			0.523			0.478			0.785			0.733		

EC, Estimated Coefficient; SE, Standard Error; p, p-value; PS, Previous-Year Second-Generation Density; PF, Previous-Year First-Generation Density; MT, Mean Temperature; AT, Maximum Temperature; IT, Minimum Temperature; PT, Total Precipitation; OW, Overwinter; SP, Spring; JN, June. Blank cells indicate non-significant (p > 0.1) predictors.

Adjusted R^2 of model equations ranged from 0.22 to 0.85, with values smaller at whole-species than ecoregion scale, and more significant in Northwest Wisconsin, Indiana Dunes National Park, and Albany Pine Bush (Tables 1 and 2). Not all variables kept in the equations were statistically significant, especially for the populations of Indiana Dunes National Park, because GA provided combinatorial optimization. Estimated coefficients of density-dependent variables (0.06 – 0.68) were almost twice as large as those of density-independent variables (0.01 – 0.22). In addition, the standard errors of climatic variables were generally small (0.01 – 3.00). They were much smaller than their estimated coefficients, indicating relatively high certainty about our understanding of Kbb responses to climate change.

Discussion

Best-fit PLS models differed among generations and ecoregions. Still, at least one density-dependent variable, previous-year second-generation population density, and several density-independent variables were retained in each model equation, suggesting that both influence population dynamics of the Kbb across its range [103]. However, consistent with [104-105], we found density-dependence is always more influential than any density-independent environmental factors, implicating that climatic effects could be overshadowed by density-dependent effects in the absence of persistent ecological changes and extreme climate events [106-107] and that the positive density dependence in the models, in the form of steadily decreasing population trends, might have been related to population bottlenecks and Allee effects [108-109].

We also found that the population size of the first generation was consistently smaller than the second generation in the same year, and that might have been influenced by the timing of wild lupine growth: first-generation larvae survive several months overwinter and feed on smaller, newly sprouted wild lupine leaves as the insects emerge from dormancy; second-generation larvae hatch a week after eggs are laid on mature lupine leaves which can have better nutrient quality [109-110]. However, [111] found that leaf nutrients were even poorer in the second generation, because of worsening climate conditions, such as drought, in the summer. Thus, an alternative explanation could be that high overwinter mortality of eggs drove down overall population abundance.

The detrimental effects of higher overwinter temperatures and total precipitation on the first-generation flight-period density in most ecoregions and the whole-species model were consistent with previous research on the butterflies in the UK [112-115]. [108] showed three major mechanisms to be essential to overwinter survival of Kbb. First, higher temperature causes snow cover to thaw more quickly, increasing the chance of overwintering stage exposure due to loss of insulation [116]. Second, warm, moist conditions might cue earlier hatching during late winter, resulting in mortality of hatched individuals because of limited food sources [117-119]. Third, overwintering diseases, such as fungal infections, increase with elevated temperature and precipitation [120].

Elevated spring temperatures were positively associated with first-generation flight-period density, suggesting that spring temperature might be critical to the final larval instar stage, accelerating metamorphosis [121]. In addition, higher temperatures during the pupal stage have been demonstrated to cause earlier maturation in other butterfly species, including the Eastern monarch butterfly [122-125]. However, for the Kbb, like other multivoltine species, earlier maturation often results in smaller adult sizes and reduced fitness [126-127]. The solid adverse effects of higher spring total precipitation on some populations were indicative that rainfall shortage might not necessarily hamper larval and pupal developments, and wild lupine was relatively drought-tolerant, supporting the negative association between seasonal butterfly abundance and spring monthly precipitation observed in previous research on butterflies in neotropics [128].

There was a strong, positive association between flight-period density and temperature for the second generation. [129] reported that warm summers were generally beneficial to multivoltine species for several reasons. First, higher June mean and minimum temperature might promote better host plant quality (i.e., wild lupine), thus enhancing larval feeding and providing a longer growing season with increased sunny days. Second, higher July temperatures could lead to earlier adult emergence, with a higher probability that a third generation would be produced [123]. Third, lower August temperatures (maximum temperature, in particular) may result in localized extinction [130-131]. In contrast, a warmer August may facilitate the growth of plants as food sources for the Kbb during extended flight periods [132]. There is also evidence that higher August temperature correlates with enhanced egg-laying rate, so the benefit of warming could be passed to the next overwinter generation [133].

The uniformly positive influence of increased total summer precipitation, especially in July, suggests that rainfall may partially alleviate water stress [134-135]. In recent decades, the extinction of populations at Indiana Dunes National Park has been attributed to summer drought [119]. Such drought led to the desiccation of host and nectar plants, impairing Kbb reproduction [33]. Therefore, according to our model outputs, a combination of temperature, precipitation, and density dependence best predicted Kbb population dynamics. Consistent with the finding of [136-139], monthly climate predictors, like mean temperature and total precipitation, had twice the explanatory power for Kbb abundance as did extreme climate predictors, perhaps because the monthly climate had more direct and proximal influences on their physiological responses. Temperature can positively affect cold-adapted insect species except during winter [140]. It's possible that elevated temperature enabled individuals to reach their physiological optimum [141], overriding the harmful effects of a warmer winter [142]. The mean temperature was often considered the primary climatic driver for some pollinator species [143-145]. However, our study showed that minimum and maximum temperatures, and total precipitation (especially in spring and July), appeared to be as crucial as mean temperature.

Effects of tree canopy on Kbb population density were mixed between the two generations since we found that more extensive canopy cover led to the decline of the first-generation

population and the reverse for the second generation. In early spring, canopy gaps could promote lupine photosynthetic activity [146], compensating for relatively low atmospheric and soil temperatures [147]. In summer, extensive canopy shading might not only offer thermal refugia for the Kbb [111, 149], but suitable moisture conditions for lupine and other nectar species, preventing them from senescing too early [149-151]. However, canopy shading caused a tradeoff limiting host and nectar plant growth due to insufficient solar radiation [152]. Thus, an intermediate canopy cover with moderate shading might best be able to support a high abundance of Kbb [111, 153-156]. In addition, adverse effects of both slope and trap were consistent with the findings of [157-158]: north- and east-facing gentle slopes were much cooler than south- and west-facing steep slopes in the northern hemisphere, leading to higher survivorship of wild lupine and reproductive success of the butterflies.

Microclimate variables were not as instructive as coarse-scale climatic factors except in Indiana Dunes National Park and Northwest Wisconsin. Habitat specialist species, like the Kbb, can have a more significant margin of thermal tolerance at the northern edge than at the southern edge of their range in the northern hemisphere [9, 18, 81, 159]. This asymmetrical response to thermal gradients [19] could explain why we found that none of the climatic variables were significant for Northwest Wisconsin populations during the first generation. Northwest Wisconsin is located at the northern edge of the current Kbb range, where annual temperatures were lowest and growing seasons were shortest among the five ecoregions. Under these conditions, lupine quality and phenology could be a more substantial limiting factor than climate [160-161]. In contrast, Indiana Dunes National Park is located close to the southern edge of the range and often experiences mild winters, cool summers, and high humidity because it is adjacent to Lake Michigan [162]. These ideal climate conditions may have buffered Kbb populations against the geographical gradient effects until the long-lasting drought of 2012.

Conclusions

Examining both generations separately helped identify the timing of long-term effects of temperature and precipitation on lifecycles: the first-generation adult stage typically showed lower sensitivity to climate variables compared to the second generation. As did [129], we found that unusually low temperatures under climate change might be tolerated by overwintering eggs, and high temperatures were beneficial to all the other life stages of the Kbb, while water stress is a significantly limiting factor during the summer. The effects of weather conditions on earlier life stages or the previous generation could be carried over to later life stages or the subsequent generation, altering survivorship and population abundance. In addition, population-specific differences of significant variables may suggest local adaptation because each ecoregion had a unique combination of climate, topography, soil, hydrology, and plant communities. Conversely, the integration of all populations across regions obscured the patterns of local spatial heterogeneity. Therefore, confirming the finding of [163], models at ecoregion or finer scales appear to be

preferable to whole-species levels for conservation purposes and for directing management plans. Because most previous studies either used density-dependent models or were based on presence-absence data rather than population count data, our study adds new insight into how the Kbb might respond to various climate change effects.

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Supporting Information

S1 Table 1. The states, counties, latitudes, and longitudes of 48 Kbb populations in five ecoregions.

S1 Table 2. Summaries of long-term Karner blue population count data during flight periods, including sampling methods, sampled populations, dates & durations, and data contributors.

S1 Table 3. Descriptions of each category of density independent data used to model populations of the Kbb.

S1 Table 4. Performance comparisons for six modeling algorithms used to select significant predictors describing adult abundance of first and second generation Kbb population.

Abbreviations used: MAE—Mean Absolute Error, RMSE—Root-Mean-Square Error, R^2 -adj—adjusted R-squared, GLM—Generalized Linear Model, MARS—Multivariate additive regression spline, GBM—Gradient Boost Machines, RF—Random Forest, ANN—Neural Network Analysis, SVM—Support Vector Machines. The top three models for each of the accuracy metrics were bolded.

812 **S1 Fig 1. EPA ecoregions level III illustrating the ecoregions associated with the study sites.**
 813 The five groups of the Karner blue populations (Central Wisconsin, Northwest Wisconsin, Fort
 814 McCoy, Indiana Dunes National Park, and Albany Pine Bush) belong to five distinct ecoregions
 815 (North Central Hardwood Forests, Northern Lakes and Forests, Driftless Area, Southern
 816 Michigan/Northern Indiana Drift Plain, and Northeastern Coastal Zone, respectively).

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 818 **S2 Sample R codes of statistical analysis and modeling**

Figure