

Ecological Niches in Sequential Generations of Eastern North American Monarch Butterflies (Lepidoptera: Danaidae): The Ecology of Migration and Likely Climate Change Implications

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ABSTRACT Eastern North American monarch butterflies (*Danaus plexippus* L.) show a series of range shifts during their breeding season. Using ecological niche modeling, we studied the environmental context of these shifts by identifying the ecological conditions that monarchs use in successive summer months. Monarchs use a consistent ecological regimen through the summer, but these conditions contrast strikingly with those used during the winter. Hence, monarchs exhibit niche-following among sequential breeding generations but niche-switching between the breeding and overwintering stages of their annual cycle. We projected their breeding ecological niche onto monthly future climate scenarios, which indicated northward shifts, particularly at the northern extreme of their summer movements, over the next 50 yrs; if both monarchs and their milkweed host plants cannot track these changing climates, monarchs could lose distributional area during critical breeding months.

KEY WORDS ecological niche modeling, monarch butterflies, climate change, geographic distributions, seasonal distributions

Monarch butterflies (*Danaus plexippus* L.) are perhaps the best known of migratory insects. Because they cannot overwinter in temperate climates, the eastern North American population migrates from broad summer breeding grounds in the United States and Canada to small areas of high-altitude fir forest in central Mexico. The same butterflies fly from Mexico to the southern United States in early spring, where they begin breeding. Their offspring continue northward, perhaps because of increasing heat and decreased host plant availability (Malcolm et al. 1987, 1993), and a subsequent generation returns to Mexico in the following fall. The close ties between this organism's annual cycle and climatic conditions suggest that monarchs could be impacted negatively by ongoing global climate change processes (Oberhauser and Peterson 2003).

Zalucki and Rochester (2004) predicted large-scale fluctuations in abundance of eastern North American monarchs resulting from effects of climate on phenology and fecundity. Prolonged rainy, cloudy, and cool conditions can reduce egg-laying and increase development time, whereas prolonged hot, dry spells can reduce adult lifespan and fecundity (Zalucki 1981). Extended exposure to temperatures of $\geq 36^{\circ}\text{C}$ can

cause significant larval mortality and developmental changes (Zalucki 1982, York and Oberhauser 2002). Climate can also influence the abundance and quality of monarchs' host plant; monarch larvae are specialist herbivores, feeding solely on plants in the genus *Asclepias* (milkweeds), and milkweed quality for developing larvae deteriorates at high temperatures (Zalucki and Kitching 1982).

Here, we assess seasonal variation in ecological niche characteristics of breeding monarch butterfly populations, taking advantage of recent advances in assessing seasonal niche variation (Joseph and Stockwell 2000, Martínez-Meyer et al. 2004, Nakazawa et al. 2004), to understand the constancy of monarchs' ecological requirements through the year. We studied likely effects of global climate change on these seasonal patterns, projecting the present day predictive models to future (2055) climate patterns to outline future potential distributional areas and migratory shifts. Results are interpreted in the context of migratory behavior in the eastern North American monarch population, emphasizing the unique nature of the annual migration and high-altitude tropical overwintering behavior of these populations.

Materials and Methods

Input Data Sets. Primary point-occurrence data for the eastern North American monarch population were obtained from the Monarch Larva Monitoring Project (MLMP). The MLMP has recruited a cadre of volunteers to obtain date-specific occurrence data for

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Table 1. MLMP data records in which one or more monarch eggs were observed and on which ecological niche models were based

Month	Occurrences with eggs present	Number of monitoring events	Number of U.S. states
Mar.	24	49	2
April	47	125	6
May	130	318	18
June	595	1,010	23
July	857	1,335	24
Aug.	677	1,223	25
Sept.	98	411	19

Number of U.S. states indicates the approximate geographic extent of the monitoring data for that particular month.

immature monarchs across 32 U.S. states and two Canadian provinces since 1997 (Monarch Larva Monitoring Project 2007). The MLMP data set describes spatial and temporal variation in juvenile abundance and survival, as well as in productivity across different habitat types (Prysbly and Oberhauser 2004). For this analysis, we only used egg occurrence data; similarly, for simplicity, we did not consider abundances, but rather, focused on presences at particular locations and times (Table 1).

Queen butterfly [*Danaus gilippus* Cramer (Lepidoptera: Nymphalidae)] eggs are indistinguishable from monarch eggs, but queen butterfly larvae possess a third set of filaments not present in monarchs. Because the ranges of these two species overlap in the southern United States, some MLMP volunteers may report monarch egg presence when they are actually seeing queen butterfly eggs. Hence, to verify data in the southern United States, we identified instances in which eggs were observed in 1 week but no monarch larvae were observed the following week. Without the confirmation of monarch larvae, these observations could be caused by the presence of queens. Volunteers at these five sites (all in Texas) were contacted and asked to confirm their data; none reported sightings of queen butterfly larvae near the time in question. Therefore, we assumed the observed eggs were monarchs and included these data in our models.

Ecological dimensions initially assessed included raster GIS data layers describing five climatic and four topographic parameters (maximum, minimum, and mean monthly temperatures; monthly solar radiation; monthly precipitation; elevation; slope; aspect; and tendency to pool water). Ecological niches were characterized using climatic variables for the period 1961–1990 (New et al. 1997), and topographic data were obtained from the Hydro-1K dataet (U.S. Geological Survey 2007). To permit efficient computing, all present day variables were resampled to 0.1° spatial resolution (≈ 10 km). Model development was limited to the area within 500 km of MLMP sampling points. We excluded occurrence data for the resident population in southern Florida and populations west of the Rocky Mountains, because their migratory habits (and perhaps their ecological requirements) differ from those of the eastern population (Brower and Malcolm 1991). We prepared month-specific data sets of mon-

arch occurrences and ecological variables for March through September, as well as for the overwintering period (December–February). We performed a jack-knife manipulation, in which single data layers were omitted sequentially and effects on omission error assessed, to identify data layers that did not contribute positively to overall predictive success, following Peterson and Cohoon (1999).

To predict future potential distributions, we used two scenarios of HadCM2, a general circulation model (Carson 1999) that has been used to create scenarios of future climate conditions. The HHGSDX50 scenario assumes 0.5%/yr CO₂ increase (IS92d) and incorporates mitigating effects of sulfate aerosol forcing, making it a relatively conservative estimate of climate change. The HHGGAX50 scenario assumes a 1%/yr CO₂ increase (IS92a) and does not allow for effects of sulfate aerosols and so is more extreme. As they are based on a 30-yr average around 2055, our models do not take into account potential effects of increased climate variability (El Niño events, in particular) on species' distributions. Because these future climate data are provided at a very coarse spatial resolution of $2.5 \times 3.75^\circ$, we calculated expected changes in temperature (°C) and precipitation (mm) under each scenario from the relatively coarse raw model results; these expected changes were applied to the original Intergovernmental Panel on Climate Change current climate data layers to provide a final pixel resolution of ≈ 30 by 30 km for future-climate data layers (Intergovernmental Panel on Climate Change 2007).

Niche Models. We modeled month-specific ecological niches using a desktop implementation of the Genetic Algorithm for Rule-set Prediction (GARP) (Stockwell 1992, 1999, Stockwell and Peters 1999). GARP is a machine-learning application that seeks nonrandom associations between point-occurrence data and ecological information in the form of raster GIS data layers in an iterative process of random rule generation, evaluation, perturbation, testing, and incorporation or rejection. The resulting models identify portions of ecological space that reflect the niche dimensions relevant to the geographic distributions of species. It should, of course, be borne in mind that these models are correlative and that niches almost certainly vary in ecological dimensions not included in this study. The approach has been described in detail elsewhere (Soberón and Peterson 2005).

We developed ecological niche models for March through September (the month on which a particular model is based is called the “focal month”) and projected each focal month model onto climatic conditions for each other breeding month, the winter months (December through February), and future climate scenarios for the focal month. We tested the robustness of the model using projections in which the focal month was projected onto itself and used to predict a random 50% of available occurrence points set aside for a relatively independent test of model quality. Projections of the focal month onto each other month indicated whether monarchs used the same ecological niches throughout the summer breeding

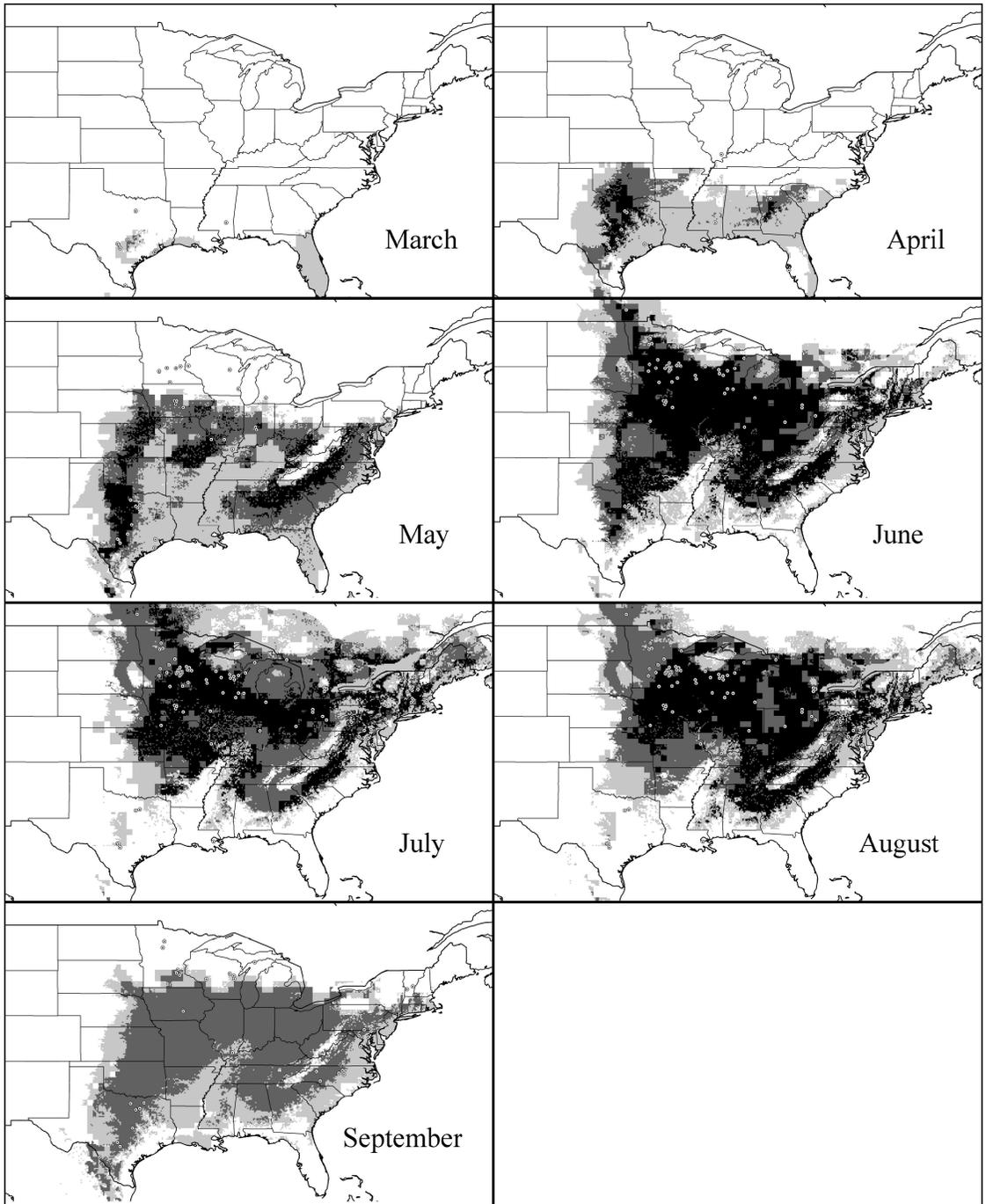


Fig. 1. Example of predictivity among monthly ecological and geographic distributions of monarch butterflies: the ecological niche model based on June points used to predict the geographic distribution of the species in March–September. Occurrence data from the month being predicted are overlaid as dotted circles. Predictions are summarized as light gray = any of 10 best subsets models predicts presence, dark gray = ≥ 6 of 10 best subsets models predict presence, and black = all 10 best subsets models predict presence.

period. The changed-climate projections allowed us to predict where acceptable breeding conditions might exist under future climates. Details for each of these steps follow.

To optimize ecological niche model quality, we developed 100 replicate models for each month-to-month comparison based on random 50–50 splits of available occurrence points. One half of the occur-

rence points were used to build models; the others were used to test them. Of these 100 models, we selected the 10 “best” based on error component distributions (Anderson et al. 2003). This procedure is based on the observations that (1) models vary in quality, (2) variation among models involves an inverse relationship between error of omission (leaving out true distributional area) and commission (including areas not actually inhabited), and (3) best models (as judged by experts blind to error statistics) are clustered in a region of minimum omission of independent test points (obtained from the 50–50 splits) and moderate area predicted present (an axis related directly to commission error). The position of a particular model in relation to the two error axes provides an assessment of the relative accuracy of each model. To choose best subsets of models, we (1) eliminated all models that had >5% omission error based on independent test points, (2) calculated the median area predicted present among these low-omission models, and (3) retained models within the central 50% of the overall frequency distribution of area predicted present.

Ecological similarity among monthly ecological niche models was assessed through interpredictivity calculations (Peterson et al. 1999, Peterson and Vieglais 2001, Martínez-Meyer 2002), which are based on the premise that, if two populations share similar ecological niches, the models for one will predict the distribution of the other accurately and vice versa. This approach involved projection of models for the focal month onto the environmental data sets for each other month and overlay of occurrence data for the other months. Niche similarity was measured as the percentage of occurrence data points falling within the prediction area of the model (Peterson and Vieglais 2001), reported in a matrix, in which cell values summarize the percentage of occurrences predicted correctly by a 1-mo model in each other month studied. To assess statistical significance, we compared observed predictive success with the expected based on random association between predictions and test points: the proportion of the study area predicted present or absent by the model multiplied by number of test points yielded random expectations (Peterson 2001, Peterson and Vieglais 2001). Observed and expected numbers were compared using a one-tailed Pearson χ^2 test, with 1 df (calculated in Microsoft Excel). (It should be noted that, lacking data on absences of the species across the landscape, the more customary κ and receiver operating characteristic–area under curve (ROC AUC) statistics are not applicable.)

Future potential monthly distributional areas were estimated through methods described in detail elsewhere (Araújo et al. 2005, Peterson et al. 2001, 2002, Peterson 2003, Thomas et al. 2004). In brief, we projected the present day, month-specific ecological niche models onto future month-specific climate data and averaged the projections from the two future-climate scenarios for simplicity. We summarized climate change effects as (1) raw area predicted present

Table 2. Summary of interpredictivity tests among month-specific ecological characteristics and geographic distributions of monarch butterflies

Month being predicted	Month predicting						
	Mar.	April	May	June	July	Aug.	Sept.
Mar.	100 ^a	100 ^a	70 ^a	40 ^a	0	0	60 ^a
April	100 ^a	94 ^a	94 ^a	88 ^a	19	81 ^a	0
May	49	91 ^a	100 ^a	72 ^a	54 ^a	70 ^a	47 ^a
June	54	100 ^a	96 ^a	100 ^a	89 ^a	86 ^a	0
July	65	100 ^a	94 ^a	96 ^a	100 ^a	79 ^a	17 ^a
Aug.	89	100 ^a	93 ^a	96 ^a	80 ^a	100 ^a	76 ^a
Sept.	97 ^a	89 ^a	91 ^a	83 ^a	0	46	100 ^a

Columns are months used to generate predictions (focal months); rows are months predicted. Cell contents are percent correct prediction of independent test data by any of the 10 best-subsets models.

^a Predictions significantly ($P < 0.05$) better than random models (Pearson χ^2 tests, $df = 1$).

before climate change, (2) raw area predicted present after climate change, and (3) area of overlap between (1) and (2). (2) is equivalent to a “universal dispersal” assumption, whereas (3) is equivalent to a “no dispersal” assumption (Thomas et al. 2004).

Results

Initial jackknife manipulations of the climatic and topographic parameters found that aspect, solar radiation, and tendency to pool water did not contribute significantly to model quality, so our models of present day distributions were based on maximum, minimum, and mean monthly temperatures; precipitation; elevation; and slope. This suite of variables allowed highly accurate month-specific models, as assessed in predicting independent test data sets (Pearson χ^2 values ranged from 12.7 to 50.6 for all seven monthly χ^2 tests, $df = 1$, all $P < 0.05$).

Predictivity among monthly ecological and geographic distributions was excellent (Fig. 1): coincidence between predictions and relatively indepen-

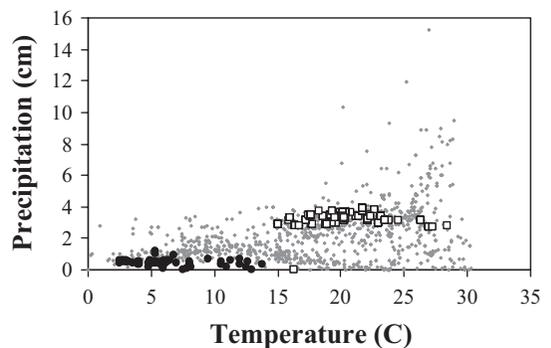


Fig. 2. Temperature and precipitation combinations across North America (small gray points, based on June conditions), showing sets of conditions predicted to be suitable for monarchs based on ecological niche models from June occurrence data (white squares) and from winter occurrence data of the Mexican overwintering populations (black circles) (Oberhauser and Peterson 2003).

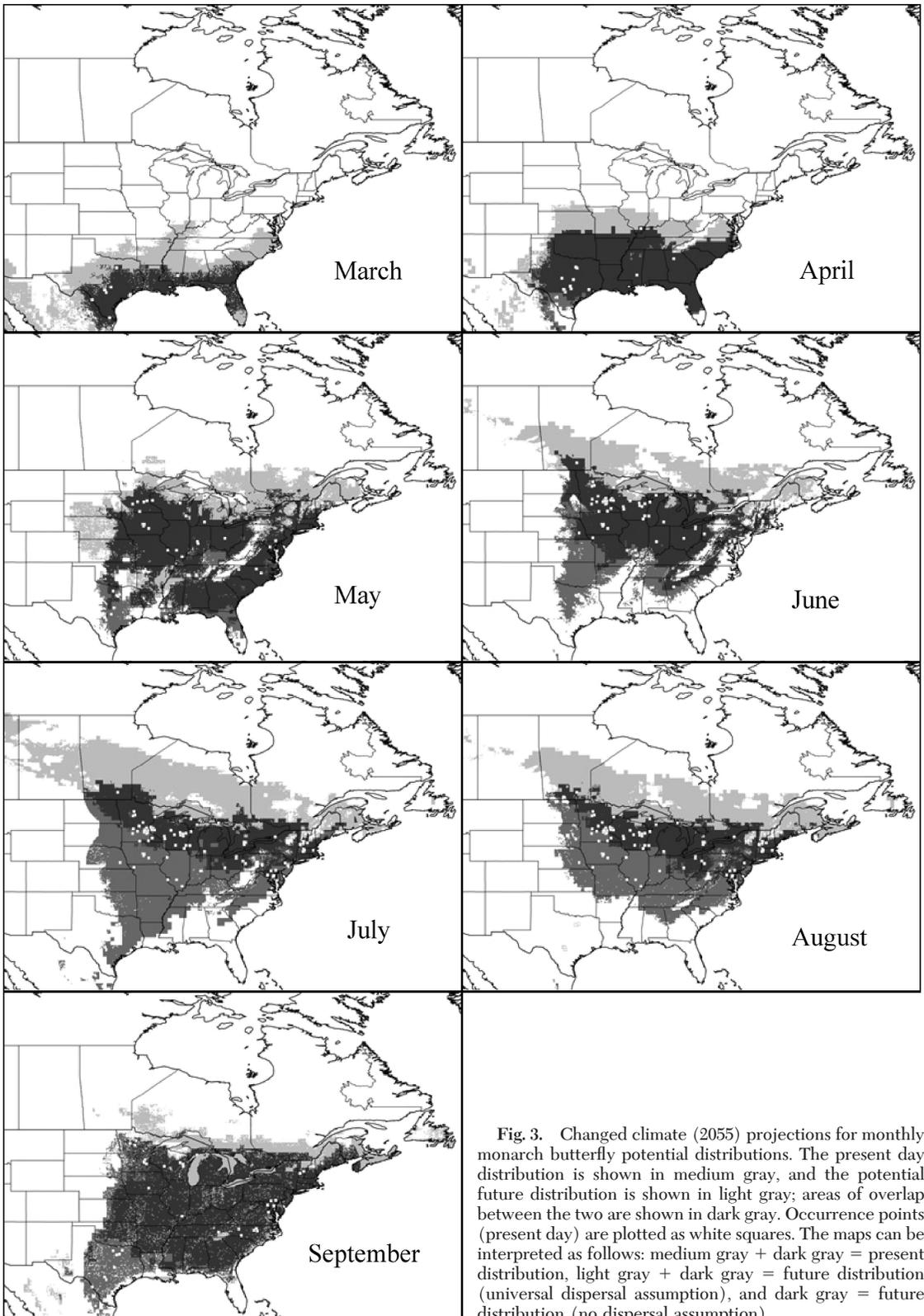


Fig. 3. Changed climate (2055) projections for monthly monarch butterfly potential distributions. The present day distribution is shown in medium gray, and the potential future distribution is shown in light gray; areas of overlap between the two are shown in dark gray. Occurrence points (present day) are plotted as white squares. The maps can be interpreted as follows: medium gray + dark gray = present distribution, light gray + dark gray = future distribution (universal dispersal assumption), and dark gray = future distribution (no dispersal assumption).

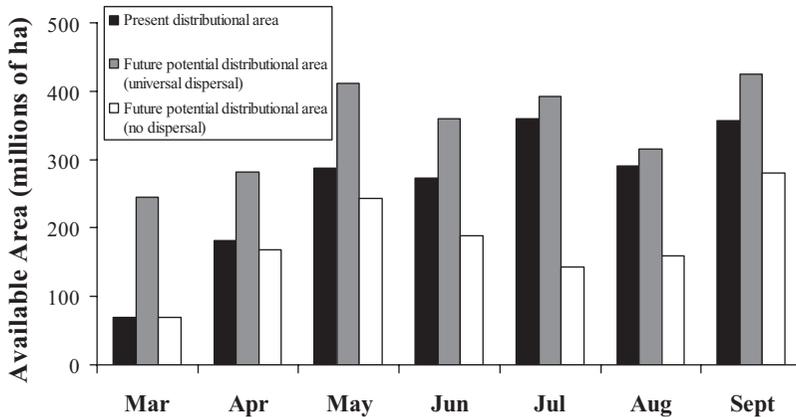


Fig. 4. Summary of area estimates for present and future monthly distributional areas for monarch butterflies. Present day distributional area is shown in black. Projected future potential distributional areas are shown in gray (universal dispersal assumption) and white (no dispersal assumption).

dent test points was considerably better than random expectations when models for focal months were used to predict occurrence data from most other months (Table 2). Models for April, May, and June predicted monarch distributions for every month significantly better than random models. The July ecological niche model predicted independent test data sets well for May through August and August predicted April through August. March and September were more erratic in their ability to predict other months, likely reflecting lower sample sizes available for model-building and the fact that temperatures are more variable in those 2 mo. Hence, monarchs seem to be faithful niche followers (Nakazawa et al. 2004) throughout their breeding period.

Comparing ecological niches as modeled for the breeding (herein) and overwintering stages (Oberhauser and Peterson 2003), however, revealed a niche shift between the two seasons. The breeding season niche is characterized by warmer and wetter conditions than monarchs occupy during the winter (Fig. 2); this difference is reflected in poor (no) coincidence between predictions from models based on breeding sites and overwintering points. During the winter months, breeding niche conditions are manifested in Atlantic coastal portions of Central America, as opposed to the central Mexican highlands where monarchs overwinter (Oberhauser and Peterson 2003).

Projecting month-specific ecological niche models onto future climate scenarios suggests complex effects of climate change on the seasonal potential geography of monarchs (Fig. 3). Early in the breeding season, monarchs could see an increase in the area of ecologically suitable habitat, assuming that they can migrate more quickly and somewhat longer distances. In June–August, however, ideal conditions shift northward and separate more from the current range. The amount of suitable area available in the present and future, based on different assumptions of dispersal ability (universal dispersal or no dispersal assumption), is shown in Fig.

4. This shows the complexities of likely climate change effects on monarch seasonal geography.

Discussion

Recent years have seen many applications of ecological niche modeling approaches to questions of distributional biology of species. Applications have included describing distributions, discovering new populations and species, describing historical distributional shifts, predicting the geographic potential of species' invasions, and anticipating future distributional shifts in the face of changing conditions (Zalucki and Rochester 1999, Guisan and Hofer 2003, Pearson and Dawson 2003, Thuiller et al. 2005, 2006, Wiens and Graham 2005, Araújo and Guisan 2006, Araújo et al. 2006, Pearson et al. 2006). Although methodologies and thought frameworks are in the process of rapid development, applications to seasonal biology are still few (Martínez-Meyer et al. 2004, Nakazawa et al. 2004, Peterson et al. 2005). As such, this review of seasonal ecology of monarchs represents an important addition to a growing literature.

The ability of ecological niche models to predict month-to-month distributional dynamics shows that sequential generations of breeding monarchs are effectively niche followers across the changing ecological landscape of spring, summer, and fall. Some focal months were better able to predict seasonal shifts than others, with March and September being the least predictive. Causes may include the smaller occurrence data sets available in March and September (Table 1), the fact that monarchs are switching from migratory to breeding behavior, and the accelerated rate at which seasonal climates change during these months. Because MLMP volunteers do not always record absence data, input data from the beginning and end of the breeding season may be less reliable. More generally, our monthly resolution may provide a temporal scale too coarse for precise predictions,

particularly in spring and fall when climates are changing more rapidly.

The lack of correspondence between the breeding season niche and the winter niche used by monarch butterflies is evidence that monarchs switch niches as they migrate to and from their wintering sites in central Mexico, even though their breeding niche is available in other (albeit more distant) parts of Mexico and Central America during the winter months. This result effectively combines the niche follower and niche switcher dichotomy of Nakazawa et al. (2004) within a single species—monarchs follow a breeding-season niche from March–October but spend the remainder of the year under very different conditions.

Future climate projections of month-specific ecological niche models predict marked changes in the species' seasonal potential distribution. Currently, monarchs migrate from Mexican wintering grounds to breed in the southern United States, and their offspring migrate into more northern areas. The current spatial manifestation of the niche shifts northward during March–May but remains relatively stationary in June–August (Fig. 1). With climate change, habitable areas are predicted to continue shifting northward through July (Fig. 3). The seasonal potential distribution contracts in August, perhaps necessitating relocation of all local populations of monarchs before breeding. It is unclear whether monarchs will be able to adjust their seasonal movement patterns to accommodate these changing conditions or what the consequence of lost breeding locations will be.

Mobile species such as monarchs may be able to track the geographic distribution of their breeding ecological niches seasonally as climates change; evidence indicates that some European butterflies have achieved such tracking (Parmesan et al. 1999, Hill et al. 2003). Additionally, monarch diapause behavior and movement patterns have changed as the species has expanded into new habitats (Zalucki and Rochester 1999). If monarchs can indeed track the shifts in ecological niche conditions (universal dispersal assumption), they stand to gain a significant amount of habitat (Fig. 4). Currently, the range of milkweed extends only 160 km into Canada, so it is absent from the regions of Canada to which monarchs' potential distributions are projected to shift (Woodson 1954). Milkweed may not be able to colonize northward as rapidly as monarchs might require, which may make these habitats nonetheless uninhabitable. Without such universal dispersal potential (no dispersal assumption), monarchs could lose considerable potential distributional area in June–August (Fig. 4), the most critical breeding portion of the annual cycle.

The research reported here used monarch habitat use to define their ecological niche. This approach differs from that of Zalucki and Rochester (1999, 2004), who used temperature constraints determined from laboratory studies to construct models of monarch distributions in Australia and North America. We suggest that future research combine these two approaches, addressing the physiological constraints that limit monarchs to their current range. Although

MLMP data do not place monarchs above a mean monthly temperature of 30°C, tolerance of hotter temperatures would alter the range shifts predicted here. For example, York and Oberhauser (2002) showed that limited exposure to temperatures as high as 36°C is not detrimental; high temperature tolerance should be explored further using realistic exposure durations. We also suggest that future studies determine behavioral responses of monarchs to unfavorable conditions. Directional movement could indicate an ability to track changes to shifting niche locations. Finally, we suggest that the ecological niche defined in these models be used to predict distributions of other monarch populations, including those in southern Florida and west of the Rocky Mountains.

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