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Monarch butterflies overwinter in restricted areas in montane oyamel fir forests in central Mexico with specific microclimates that allow the butterflies to survive for up to 5 months. We use ecological niche modeling (ENM) to identify areas adequate for overwintering monarch colonies under both current and future climate scenarios. The ENM approach permits testing and validation of model predictivity, and yields quantitative, testable predictions regarding likely future climate change effects. Our models predicted monarch presence with a high degree of accuracy, and indicated that precipitation and diurnal temperature range were key environmental factors in making locations suitable for monarchs. When we projected monarch distribution onto future climate scenarios (Hadley Centre climate models), we found that conditions were likely to be inadequate across the entire current winter range, particularly owing to increased cool-weather precipitation that could cause increased mortality. This study applies ENM to understanding the seasonal dynamics of a migratory species under climate change, and uses ENM to identify key limiting environmental parameters in species' responses to climate change.

The eastern migratory population of monarch butterflies (*Danaus plexippus*) presents an enormously complex life cycle. They winter in extremely limited areas in central Mexico, undergo multiple annual breeding generations east of the Rocky Mountains, and migrate between these breeding and overwintering grounds each spring and fall. Conservation concerns for this species have focused on the restricted wintering area (1, 2), and recent winter mortality events (3) reinforce this worry. The relationship between winter mortality and weather conditions suggests that climate change may have important impacts on monarch butterflies.

Monarchs that winter in central Mexico are restricted to oyamel fir (*Abies religiosa*) forests. These forests are part of a high-altitude ecosystem limited to montane "islands" on high peaks in Mexico (<0.5% of Mexico's land area, 40,000–50,000 hectares). They are apparently relictual, reflecting the southward advance of boreal forests during glaciations, but most were subsequently displaced by other floras. Only at 2,400- to 3,600-m elevations in central Mexico do cold climates permit firs to dominate (4, 5), coinciding with a fog-and-rain belt during the summer wet season. Overwintering monarch colonies have been reported on 12 such montane islands in the Transvolcanic Belt in central Mexico (2, 6, 7), all within a small area (≈30 × 60 km) and almost always on southwest slopes (8).

The ≈135-day monarch overwintering period (early November to late March) falls in the dry season, in which relative humidity is greatly reduced. Although some freezing and snow do occur during the winter, temperatures characteristic of boreal climates farther north are moderated this far south. Limited long-term temperature records in the Chincua and Rosario colonies indicated no temperatures below freezing in the winters of 1994 and 2001, respectively (E. Rendón Salinas, personal communication).

Monarchs are sensitive to microclimatic conditions, particularly temperature, during the overwintering period (9–12). Monarchs exposed to low temperatures can freeze, and a combination of cold and wet conditions makes them considerably more vulnerable to freezing (13); low temperatures also reduce flying ability and increase vulnerability to predation (13, 14). Although less attention has focused on effects of high temperatures, they are likely to deplete lipid reserves, cause premature reproductive development, and promote early departure from the overwintering areas (6, 15–17). These observations suggest that monarchs survive the winter within a narrow microclimatic window.

Several major weather-related winter mortality events have been caused by precipitation followed by low temperatures. For example, in January 1981, when storms over a 10-day period dropped 43 cm of snow in the Sierra Chincua at temperatures to −5°C, ≈42% of one wintering population died (11). A February 1992 storm killed 82% of one small colony (18). In 1995, 6% of another aggregation on Sierra Chincua died after a late December snowstorm (E. Rendón Salinas, personal communication). Finally, 70–80% of the two largest overwintering populations died as a result of a January 2002 storm in which cold and wet conditions dominated (3). During the following summer, a large-scale monitoring project documented the second-lowest summer populations recorded during the 7 yr of data (www.mlmp.org), suggesting that winter mortality affects abundance in succeeding generations.

The vulnerability of monarchs during winter has received intense public and scientific attention, with most interest focusing on habitat reduction resulting from logging and clearing (1–3, 19). The Mexican government responded to threats to overwintering populations by creating the Monarch Butterfly Special Biosphere Reserve in 1986, in which 16,110 hectares of key habitat were protected, and the Monarch Butterfly Biosphere Reserve in 2001, with 56,259 hectares including both a core zone and a buffer zone (20, 21).

Here, we explore likely effects of global climate change on monarch distributions by using ecological niche modeling (ENM), and point out that predicted changes pose potential threats to monarch survival. This contribution represents a first application of ENM to understanding climate change effects on the seasonal dynamics of a migratory species, and is particularly attractive in that model parameters can be compared directly with key limiting ecological parameters known to affect populations of the species in question.

Methods

Our general approach to using ENM to predict climate change effects on biodiversity is summarized below, with greater detail

available elsewhere (22, 23); similarly, the algorithm used for modeling species' ecological niches is described here, but more detail is provided in separate publications (24–26).

Input Data. Distributional data in the form of unique occurrence points for overwintering monarchs were obtained from published literature (27). Although additional unpublished finer-scale locations for overwintering monarchs are available, their close proximity to published locations would result in pseudoreplication of points. For oyamel, we drew occurrence information from natural history museum specimen records in the Red Mundial para la Información de la Biodiversidad (www.conabio.gob.mx).

Ecological niche models require that occurrence points be placed in a continuous, raster-based (gridded) ecological/environmental context. We obtained the following environmental data sets for all of Mexico from the Intergovernmental Panel on Climate Change (www.ipcc.ch): annual and January means for cloud cover; diurnal temperature range; precipitation; maximum, minimum, and mean temperature; and vapor pressure. We obtained topographic data (elevation, slope, and aspect) from the U.S. Geological Survey's Hydro-1K data set (http://edcdaac.usgs.gov/gtopo30/hydro). To provide a finer-scale view of current distributions, we also developed analyses using topographic data plus coverages representing seasonal (3 month) composites of advanced very high-resolution radiometer (AVHRR) normalized difference vegetation index data (28). All environmental data were gridded at 1-km spatial resolution for analysis. These data were used to generate models of the current ecological niche of overwintering monarchs.

ENM. The ecological niche of a species can be defined as the conjunction of ecological conditions within which it is able to maintain populations without immigration (29–31); as such, it is defined in multidimensional ecological–environmental space. The ecological niche of a migratory species includes a succession of conditions that are periodically and regularly occupied; our focus here is one part in this succession, monarch overwintering sites in central Mexico.

Several approaches have been used to approximate ecological niches (32–34). Of these, among the most robust is the genetic algorithm for rule-set prediction (GARP), which includes several inferential approaches in an iterative, artificial-intelligence-based framework (24–26). GARP provides greater flexibility than the traditional bioclimatic envelope approaches, and does not require enormous sample sizes (35). Moreover, GARP has been subjected to extensive testing in diverse taxa and regions (35–43).

GARP resamples known occurrence points (points in space at which a species is known to occur) and "pseudoabsence" points (sites at which the species is not known to occur) randomly with replacement to create training and test data sets (up to 1,250 points each) (24–26). It works in an iterative process to develop rules that identify key niche parameters, evaluate their importance and predictivity, and either incorporate them into a model or reject them. After an initial phase of rule generation based on the training data, GARP evaluates the "fitness" (predictivity based on test data) of a particular rule set using the test data, and then "evolves" that rule set via a series of perturbations mimicking DNA evolution: rule sets can be truncated, particulars of criteria in rules can be changed, rules can "cross over" (e.g., trade segments), etc. Rule sets showing improved fitness are retained, whereas rule sets for which fitness is reduced are eliminated from consideration. Change in predictive accuracy from one iteration to the next is used to evaluate whether a particular rule should be incorporated into the model, and the algorithm runs either 1,000 iterations or until convergence. GARP models thus provide a heterogeneous rule-set that iden-

tifies an ecological niche space hypothesized to be habitable for a species. Ecological niche spaces identified with GARP can then be projected onto landscapes to identify potential distributional areas.

We developed 100 replicate niche models, and used a new procedure (36) for choosing best rule-sets. The procedure is based on the observations that (*i*) models vary in quality owing to the random-walk nature of the genetic algorithm approach, (*ii*) variation among models involves an inverse relationship between error of omission (leaving out appropriate conditions) and commission (including sets of conditions not actually appropriate), and (*iii*) the best models cluster in a region of minimum omission of independent test points (i.e., models are able to predict independent points with few failures) and moderate area predicted (an axis related directly to commission error; such models neither under- nor over-predict distributional areas) (36). Hence, to identify a best subset among the 100 replicate models, we (*i*) eliminated all but 20 models that had low omission error (<5%) based on the independent test points, (*ii*) calculated the average proportion of the area predicted to be adequate habitat for monarchs among these low-omission models, and (*iii*) identified 10 models closest to the overall average distributional area. The sums of these 10 models were used as our best predictions of potential monarch distributions.

We tested model quality via a simple χ^2 approach. The proportion of the area of analysis, which varied between models (see below), predicted to be appropriate for monarchs multiplied by the test data sample size provides an estimate of occurrence points that would be correctly predicted were the prediction to be random with respect to the distribution of the test points. A χ^2 test based on observed correct and incorrect predictions of test points and expected numbers from the random model is used to assess the probability that a random model could account for observed predictive success of models (note that both omission and commission error are taken into account in this test: omission directly, and commission via the proportional area calculations). As a method of identifying environmental dimensions important for defining monarchs' geographic potential, we conducted a series of sequential jackknife manipulations in which all possible combinations of a reduced set (e.g., $N - 2$) of N environmental coverages were used to generate models; model quality was assessed in these manipulations via inspection of patterns of correlation between variable inclusion and levels of omission error (type I error) (37).

Climate Change Scenarios and Projection Techniques. Once current ecological niche models were developed, explored, and validated, we applied them to the challenge of understanding future potential distributions. The ordered series of if–then statements that make up GARP models and predict either presence or absence can be applied to transformed landscapes to identify areas in which a species can survive in the future.

The Hadley Centre Climate Models of climate change and dispersal (HadCM2) (44) include several scenarios: we assessed both a conservative and a less conservative view of climate change over the next 50 yr by using the HHGSDX50 and HHGGAX50 scenarios. The HHGSDX50 scenario assumes 0.5% per yr CO_2 increase and incorporates the buffering effects of sulfate aerosol forcing, making it a relatively conservative estimate of climate change. The HHGGAX50 scenario assumes a 1% per yr CO_2 increase and does not allow for sulfate aerosol effects, and so is less conservative. Results are based on a 30-yr average around 2,055 (2,040–2,059), and are provided at a spatial resolution of $2.5° \times 3.75°$. To improve resolution, following recommended approaches for first-level downscaling (www.ipcc.ch), we extracted coverages summarizing expected percent change in each climate parameter and used them to increment present-day temperature and precipitation maps (0.5°
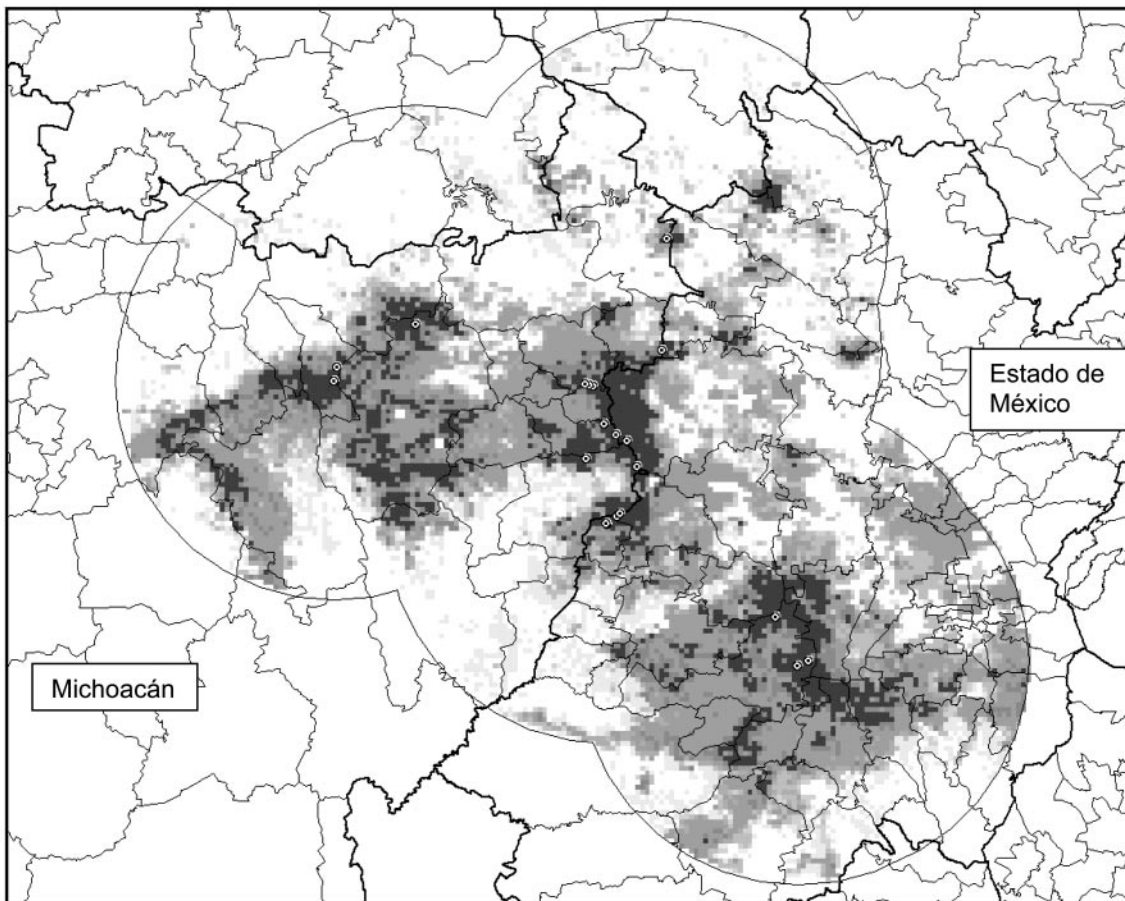
Fig. 1. Ecological niche model based on 22 known monarch butterfly overwintering sites (dotted circles) in relation to AVHRR imagery and topographic data. Increasingly dark shades of gray indicate greater model agreement. The area included in the model (areas <50 km from known overwintering sites) is indicated by the overlapping circles.

× 0.5° resolution), thus improving future-climate resolution somewhat. The result is a series of maps summarizing present and future climate conditions, all at similar levels of resolution.

Analyses. We modeled current and future potential monarch distributions by using GARP in the following ways. (*i*) Current monarch distributions were modeled at fine scale (1 × 1 km resolution) based on AVHRR plus topographic data to produce a detailed view of the species' potential geographic distribution within 50 km of known overwintering sites. (*ii*) Oyamel distributions were modeled over all of Mexico to summarize potential fir distributions in the country based on coarser-resolution climate and topographic data. (*iii*) Climate plus topography plus actual oyamel distribution were used to obtain a Mexico-wide view of monarch potential distributions. (*iv*) Climate plus topography (but not including elevation or oyamel distributions) were used to model monarch overwintering distribution over all of Mexico, projecting over the next 50 yr by using the future climate scenarios (elevation per se was excluded from this analysis owing to its changing implications for species' distribution in the face of changing climates). Steps *i* and *ii* produce a best hypothesis of monarch and oyamel distributions (AVHRR data are not available for oyamel distributions owing to the historical nature of the available data), step *iii* uses the oyamel distributional information to educate predictions for monarch distributions, and step *iv* projects the monarch model to future modeled climates.

Results

All GARP models of present distributions of monarchs predicted independent test data sets with high statistical significance. Models based on AVHRR and topography were most precise, given that analysis was restricted to an area within 50 km of known overwintering sites (χ^2 tests, df = 1, all best-subsets models $10^{-95} < P < 0.03$). Models based on climate and topography were similarly significant (χ^2 tests, df = 1: models without oyamel distributions included, all best-subsets models $10^{-4} < P < 0.03$; models that included oyamel distributions, all best-subsets models $10^{-4} < P < 0.004$), although not so impressively so, given the broader areas analyzed. Finally, predictions for oyamel distributions were also highly predictive (χ^2 tests, df = 1, all best-subsets models $10^{-29} < P < 10^{-18}$). This ability to predict patterns of distribution of independent sets of occurrence points indicates that our models hold significant predictive power for distributional phenomena for monarchs and firs.

Inspection of models based on AVHRR and topographic data provided a detailed prediction of overwintering site distribution (Fig. 1), including several areas within 50 km of current overwintering sites not currently known to be used by monarchs. Correspondence of the areas identified in these analyses with the modeled distribution of oyamel was excellent (Fig. 2), even when analyses were based on nonoverlapping data sets, suggesting that monarchs and the firs obey similar ecological "rules" in their ecological and geographic distributions, at least in broad terms.

Geographic distributions reconstructed from climate and topographic data only (not shown) were necessarily less detailed
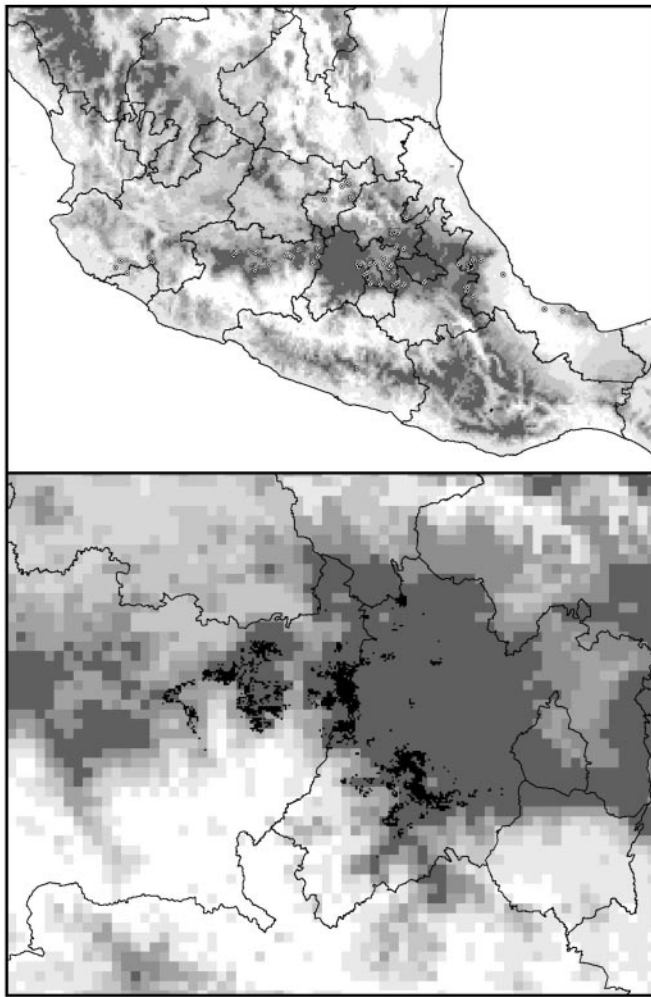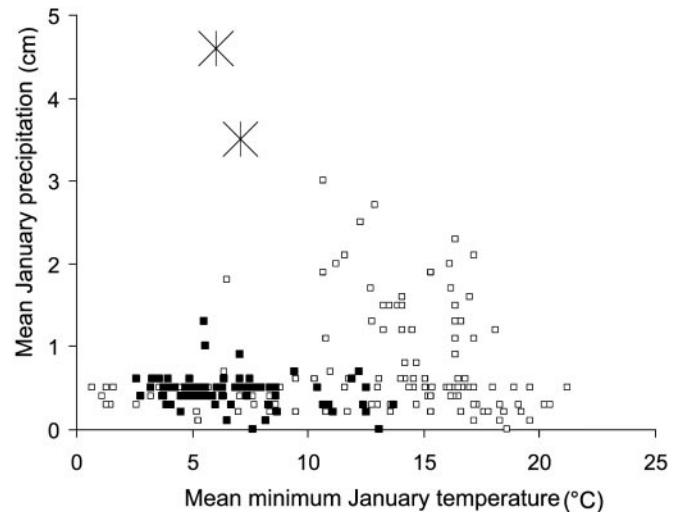
Fig. 2. Ecological niche model based on 121 known occurrence points (dotted circles; herbarium specimen records) for oyamel fir in relation to climate and topographic data. Increasingly dark shades of gray indicate greater model agreement. (*Upper*) View of model projected across central Mexico to indicate broad-scale oyamel potential distribution. (*Lower*) Close-up of monarch overwintering area, with the best locations identified by the independently derived monarch model overlaid in black to illustrate the close agreement between the two modeling efforts.

Fig. 3. Visualization of ecological niches of wintering monarch butterflies in relation to availability of ecological conditions. Open squares indicate environmental conditions that are not predicted to be suitable; filled squares indicate environmental conditions that are predicted to be suitable for the species; and crossed X's indicate the raw results of the global climate change models, which are the conditions predicted across the current monarch wintering areas under HHGSDX50 (upper) and HHGGAX50 (lower) scenarios of the Hadley global climate change simulation.

than the more finely resolved AVHRR-based predictions, but reflected the overall distributional pattern (i.e., a disjunct potential distributional area in the Transvolcanic Belt of central Mexico) quite well. Inclusion of oyamel distributions in the ecological niche model for monarchs refined the prediction of present distributional area considerably.

Projected onto future climates predicted by the two climate change scenarios, in neither case did more than half of the models predict continued suitability of the present overwintering distribution for monarchs. Because the two climate change scenarios were chosen on purpose to represent relatively conservative and relatively liberal views of likely climate change effects, this result suggests that our projections are likely to be robust to deviations of actual trajectories from model predictions. In the majority of replicate models developed, no coincidence was found between future potential monarch overwintering areas and any present oyamel distributional areas.

Jackknife manipulations of the different climate coverages (37) pointed to the critical roles of precipitation and temperature in constituting the ecological niche of overwintering monarchs;

only precipitation and diurnal temperature range correlated positively with improvement in avoiding omission error. To explore the role of these environmental parameters in influencing monarch overwinter survival in more detail, we plotted mean January precipitation against mean January minimum temperature for potential distributional areas versus areas identified as not suitable for overwintering monarchs (Fig. 3). The concentration of suitable areas in cool (not cold, not warm) temperatures and low precipitation is clear, and illustrates the importance of these factors in determining whether a location is suitable for overwintering monarchs. However, inspection of the two future climate scenarios indicates that climates in the single future-climate pixel that covers the entire winter range of monarchs are likely to be considerably worse for the species, combining cool temperatures with much-increased precipitation.

Discussion

Ecological niche models predict the current distribution of overwintering monarchs with high accuracy, demonstrating that the approach has utility for understanding the ecological niche and distributional ecology of this species during the winter phase of its annual cycle. In addition, environmental parameters identified as key to predicting monarch presence (temperature and precipitation) have been implicated as important factors in past mortality events (3, 13); exploration of the expected future values of these parameters underscores the concern for monarch overwintering areas in changing climate regimes.

Representation of appropriate, intact habitat is, of course, key to conservation efforts; indeed, butterfly species with ranges expected to expand under changing climates have declined owing to habitat loss (45). Degradation of forests in which monarchs overwinter is a real and serious threat to their survival (20, 46). Conversion of forested land to agriculture, legal and illegal logging, harvesting of wood for domestic use, charcoal production, livestock grazing, and intentional forest fires have all been implicated in loss of key habitat for monarch overwintering (2, 47). Our analyses suggest that climate change effects may

pose an additional long-term risk to monarchs. Two general circulation model scenarios that differed in assumptions about CO_2 levels and sulfate aerosols suggest that current overwintering sites will become considerably less suitable for monarchs over the next 50 yr; although temperatures are predicted to be similar to those found currently, increased precipitation combined with these cool temperatures is likely to result in more frequent large-scale mortality events. In fact, when current oyamel distribution was included in models to be projected to future climates, none of the present wintering sites was predicted to be suitable in 50 yr.

Our use of current ecological niches to predict monarchs' potential distributions under climate change scenarios is subject to a number of assumptions: that species' niches are conserved (38, 48), that monarch dispersal is limited by presence of oyamel forests, and that global-scale climate models have sufficient detail to permit inferences. The approach has also been criticized under the reasoning that shifting interspecific interactions are likely to influence potential distributions much more than species' autecology (49). However, across numerous spatial scales, niche models do predict current geographic distributions (31, 37, 38, 40, 41, 50, 51); ecological niches have been shown to be conserved over significant periods of evolutionary time (38, 48, 52); and models show excellent predictivity even when transplanted to other regions and completely different community contexts (39, 53–57). In addition, both empirical evidence (8–10, 12, 13) and our modeling point to the importance of two key environmental features, temperature and precipitation. Given the absolute nature of the mass mortality events, we doubt that shifting interactions could improve the forecast of increased frequency of such events and their catastrophic effects on monarchs.

Butterflies have been the subjects of other studies of the effects of past and future climate change on species distribution (45, 58, 59). Some mobile species appear to have tracked changing climates by shifting ranges northward (58), but sedentary species have failed to do so (59), which will likely result in loss of distributional area for many species. This study represents an assessment of implications of global climate change for a migratory butterfly; future steps, including using regional climate models with much-improved spatial resolution, would be quite rewarding, as would incorporating the migrating and breeding stages of the monarchs' annual cycle.

Monarchs present an interesting case, as they recolonize overwintering areas every year, and might thus be better able to encounter areas of suitable habitat than species with restricted dispersal capabilities. The importance of dispersal was highlighted by a recent survey of climate change effects on birds, mammals, and butterflies in Mexico, in which methods identical to those used here were applied to 1,870 species (22): dispersal was key in determining what outcome awaits each species; under assumptions of universal dispersal ability, species on average neither increased nor decreased in potential distributional area; under assumptions of no dispersal, however, all species declined, with a nontrivial portion seeing catastrophic declines in habitable area.

It is important to bear in mind that ecological niche models attempt to portray the geographic distribution of areas appropriate for the species in ecological terms. For a variety of historical and ecological reasons, species rarely inhabit the entire spatial manifestation of their ecological niches (38). Monarchs do not appear to be using all habitable areas even within 50 km of known overwintering colonies. It is possible that the benefits of very dense aggregations means that only a subset of potential habitat will be used, although the frequent discovery of new colonies (61) suggests that more monarch overwintering areas remain to be discovered. Certainly, areas of suitable conditions (Fig. 1) would be excellent candidates for inspection. Effective long-term conservation, although appearing more complex even than previously appreciated, will depend on effective detection and monitoring of monarch overwintering areas.

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