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Host plant pattern and variation in climate predict the location of natal grounds for migratory monarch butterflies in western North America

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Abstract The breeding grounds of migrant generation monarch butterflies in eastern North America are well known. In stark contrast the location of natal grounds of western migrants has not been delineated. We show that 55% of the area within seven western states was potential breeding range based on: (1) the occurrence of milkweed host plant species with phenology making them available during late-summer and (2) regional thermal conditions supportive of adult reproductive activity and development of immature stages. We next used a series of spatially explicit "bottom-up" regression models to test this first-approximation natal origins distribution. We tested for associations between variation in moisture availability at putative natal habitat and inter-annual variation in monarch abundance at western wintering sites for a 10 year period (1998–2007). Variation in moisture availability, as measured by Palmer's drought severity index (PDSI), across the western region predicted monarch abundance patterns. In contrast and as expected, PDSI across known eastern breeding grounds did not predict variation in western monarch migrant abundance. The pattern of moisture availability was not uniform between states or within states and permitted similar tests of association at a finer geographical level. PDSI for California, Idaho, Nevada, and Oregon (but not Arizona, Utah, or Washington) were each significantly associated with monarch wintering abundance patterns with California exhibiting the strongest relationship. At a more focused spatial scale we tested the local recruitment hypothesis. This is the notion that western coastal wintering monarch populations derive only from nearby coastal breeding habitat and that monarchs do not migrate from more distant natal grounds. Variation in moisture availability within a block of three contiguous central California climate divisions (Sacramento Drainage, San Joaquin Drainage, and Southeast Desert Basin) significantly predicted inter-annual abundance of migrant generation monarchs. In contrast PDSI patterns of three coastal California climate divisions, i.e., ones local to wintering sites, as well as that of climate divisions in western Nevada and Arizona did not predict variation in monarch abundance at this more focused spatial resolution. Our findings suggest that moisture regimes act as a strong bottom-up driver of monarch abundance pattern via resource availability in western USA.

Keywords *Danaus plexippus* (L.) · Degree-days · Local recruitment hypothesis · Milkweed · Monarch butterfly · Natal grounds · Palmer drought severity index

Introduction

The monarch butterfly (*Danaus plexippus* L.) exhibits a complex lifecycle based on environmental cues that results in two distinctly different generations; the summer (or breeding) generation and the migratory (or wintering) generation (Herman 1981; Goehring and Oberhauser 2002, 2004). Immature stage monarchs produced in late summer and early fall experience environmental cues such as shorter day lengths and declining temperatures and emerge as relatively longer-lived migratory generation butterflies. These cues initiate physiological processes leading to reproductive diapause and fall migration when the monarchs travel to milder overwintering habitats (Goehring and

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Oberhauser 2002, 2004). The migratory generation generally lives all winter, from about five to 9 months while spring and summer generation monarchs have much shorter lifespan, living from 2 to 5 weeks (Oberhauser 2004). Beginning in mid-January, wintering monarchs typically emerge from reproductive diapause and initiate mating activities (Leong et al. 1995; Frey 1999; Solensky 2003, 2004). Soon after, they disperse to their spring and summer breeding grounds where females lay their eggs on emerging milkweed host plant. These progeny of the winter generation are the first of several summer generations.

The North American monarch population is made up of three rather geographically distinct populations (Brower and Malcolm 1991; Brower et al. 1995; Altizer 2001; Oberhauser et al. 2008). One of the three populations consists of non-migratory monarchs, forming year-round populations inhabiting Florida and the Caribbean archipelago. Monarchs at these latitudes are not subject to the day-length and temperature cues that induce diapause and migration (Brower 1995; Farrey and Davis 2004). The largest population is the eastern migratory population and includes the majority of monarchs found east of the Rocky Mountains. While the eastern breeding range covers an extensive area, the migratory winter generation of monarchs coalesce spatially at a dozen focal overwintering sites in oyamel fir forests located in a relatively small area of the mountainous Transvolcanic Belt in the Mexican states Michoacan and Mexico (Brower et al. 2002; Slayback et al. 2007).

The western migratory population includes monarchs found west of the Rocky Mountains and is estimated to be two to three orders of magnitude smaller than the eastern population (Frey and Schaffner 2004; Taylor 2004). Monarch butterflies in western North America migrate to, and winter at, over 300 wooded sites along 1,000 km of coastline between Mendocino County California and Ensenada Baja California Mexico (Fig. 1; CNDDB 2002; Frey and Schaffner 2004; Stevens and Frey 2004).

Fall migration flyways of monarchs in eastern North America have been established (Howard and Davis 2008). Likewise the location and extent of the natal grounds of migrant generation monarchs in eastern North America are well known, having been identified from late summer field surveys (Oberhauser et al. 2001), tagging programs (Urquhart and Urquhart 1977, 1978; Rogg et al. 1999; Taylor 2005), and stable isotope research (Wassenaar and Hobson 1998; Dockx et al. 2004). Assessments of the influence of future climate change on the location and extent of both the wintering and breeding generations have also been made for eastern monarchs (Oberhauser and Peterson 2003; Batalden et al. 2007). In stark contrast there are few data on the location and range of summer breeding
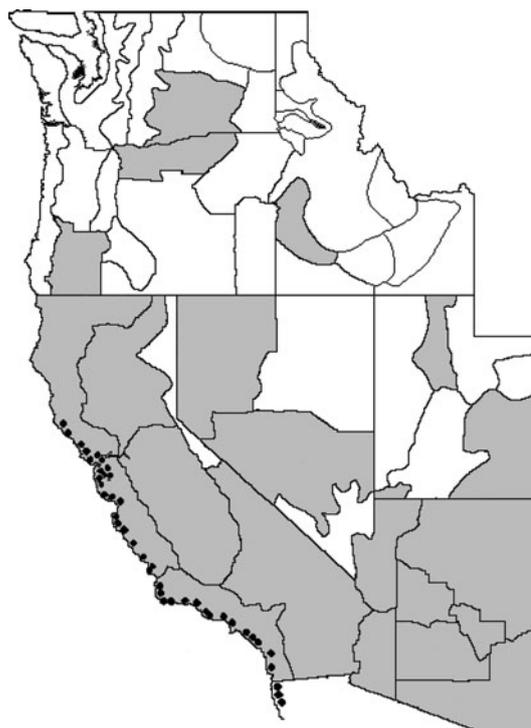

Fig. 1 Seven-state western regional map. *Dark points* along the Pacific Ocean coast represent the geographic extent of some of the over 300 western monarch wintering sites. *Boundary lines* delineate states and 54 NOAA/NCDC climate divisions within states. NCDC divisions were the finest-grain resolution of our milkweed and climate data sets. *Shaded regions* show the most probable location of breeding grounds that produce the migratory generation of monarchs based on the occurrence of late-summer milkweed and thermal constraints (degree days)

activity in the west and the natal grounds of the western migrant generation have not been delineated. This is of considerable conservation concern because climate change models predict that global change will likely result in 10–30% less precipitation and water availability across much of temperate western North America by 2050 (Milly et al. 2005; Christensen et al. 2007; Seager et al. 2007). These mid-latitude areas are significant because they likely encompass western monarch natal grounds and abundant quantities of milkweed, the monarch host plant.

Here we identify potential natal grounds of western migratory generation monarchs based on the spatial congruence of two requisite factors—occurrence of milkweed species (host plant) having late-summer phenology and regional thermal conditions during August and September that would support reproductive activity in adults and development of migrant generation immature stages. We next used a series of hierarchically nested spatially explicit "bottom-up" regression models to test this first-approximation natal origins map. We tested for associations between variation in moisture availability at putative natal

habitat and inter-annual variation in monarch abundance at western wintering sites for the 10 year period 1998–2007. A secondary goal during this phase of our study was to address two controversial and conservation relevant questions about western monarch migration and population dynamics. (1) There is disagreement as to whether western monarchs undergo long-distance migration. The *local recruitment hypothesis* suggests that they don't, that the monarchs in the coastal overwintering sites derive from nearby breeding sites (Wenner and Harris 1993). Alternatively, these monarchs may derive from more distant natal grounds throughout the western USA. These hypotheses can be tested by comparing the degree of association between conditions in different regions and the size of the wintering population. (2) There is also disagreement as to the degree to which the eastern and western populations are distinct. The *source sink hypothesis* suggests that the western population is rescued from extirpation by periodic immigration from the much larger eastern populations during the annual spring migration of the latter population from its Mexican wintering grounds (Brower and Pyle 2004; Vandenbosch 2007). This hypothesis would predict that the size of the western population would correlate with the size of eastern population during the previous year. Alternatively, the western population may be driven mainly by conditions within western breeding areas.

Our study conceptually originated from two features of wintering monarch population dynamics that emerged during the past decade. First, western wintering abundance (individuals per habitat) underwent a system-wide decline of approximately 80% (Stevens and Frey 2004; Stevens 2005); second, population abundance at individual (or different) California winter habitats was strongly correlated between successive years. Habitats that supported large populations were generally ranked relatively high year after year, regardless of whether the system-wide population was larger or smaller than the previous year. Conversely, the same was true for habitats with small populations; these habitats were almost always ranked low (Stevens and Frey 2004; Stevens 2005). This suggested that variation in abundance of the migratory generation was driven primarily by system-wide factors across the western natal grounds. Stevens and Frey (2004) hypothesized that increasing drought conditions in the west over this period of time were the most likely cause for declining monarch populations.

Variation in climate is generally regarded as a primary driver of large scale changes in biological processes (Parmesan et al. 2000; Hawkins et al. 2003; Parmesan and Yohe 2003; Root et al. 2003; Rosenzweig et al. 2008). This is supported by an extensive literature that shows variation in moisture availability, particularly in arid to semi-arid regions, accounts for the majority of variation in net primary productivity (Sala et al. 1988; Paruelo and Lauenroth 1995; Bell 1998; Oesterheld et al. 2001; Ciais et al. 2005). "Bottom up" models explain inter-annual variation in a variety of insect populations (Price and Clancy 1986; Hunter et al. 1997; Pollard et al. 1997; Hawkins and Holyoak 1998; McLaughlin et al. 2002; Price and Hunter 2005). Hawkins and Holyoak (1998) showed that 10 herbivorous insect species from five different orders had synchronous population declines across North America for which the timing and extent were congruent with a large-scale drought across the same region.

Methods

Spatial extent and study design

We carried out this work in two phases and focused on seven states that occur west of the USA. Continental Divide (Arizona, California, Idaho, Nevada, Oregon, Utah, and Washington; $\sim$1,857,000 km^2; Fig. 1). During the second phase of the study, for comparison and contrast, we also included information from six eastern states (Illinois, Iowa, Kansas, Maryland, Minnesota, and Pennsylvania; $\sim$885,618 km^2).

In Phase I of our study we used historical temperature data from the National Climatic Data Center (NCDC) to identify portions of the west that had long-term thermal conditions, i.e., degree-days, which could support late summer monarch recruitment. We also created a data set for presence/absence pattern for western milkweed species with life-history that made them available to monarchs during late-summer. A first-approximation natal grounds map for migrant generation monarchs was delineated as areas (NCDC climate divisions) where at least two species of late-phenology milkweed occurred and additionally generated a minimum of 400 Celsius degree-days during August and September.

In Phase II we identified a more probable sub-set of this hypothetical natal range by using hierarchically nested "bottom-up" regression models. For the 10-year period 1998–2007 we tested for associations between variation in moisture availability at putative natal habitat and inter-annual variation in monarch abundance at western wintering sites. We further used this approach to test predictions associated with the *local recruitment hypothesis* and the *source-sink hypothesis*.

Milkweed data sets

Diversity and presence/absence patterns of milkweed species available late in the summer was determined initially for the seven western states based on Woodson (1954). We

used Cronquist et al. (1984) to obtain more recent milkweed data for the inter-mountain states Idaho, Nevada, and Utah. We drew from Sundell (1994) for host plant patterns in Arizona. All three treatments provided information on milkweed distribution to county-wide spatial scale as well as information regarding species' life-history. These data were confirmed and supplemented by using searchable plant collection databases including the University and Jepson Herbaria/University of California Berkeley (Rosatti 2006); the Oregon Plant Atlas/the Oregon Flora Project (Hardison 2010); the Atlas of the Vascular Plants of Utah (Albee et al. 2002); and the Washington Herbarium Vascular Plant Database (Giblin 2010). We also communicated with experts on the systematics, biogeography, and ecology of milkweed for each western state (see *Acknowledgements for list of experts*). Together, this information was used to create a presence/absence milkweed data set for each state as well as diversity patterns within each state. We used NCDC maps of western state climate divisions with superimposed county-level boundaries to transform county-wide milkweed pattern to a somewhat less focused spatial scale involving the 54 climate divisions of our study (CPC 2005; Fig. 1). This was necessary since both phases of our study involved the use of other data that were available only to the climate-division level of spatial resolution (e.g., variation in moisture availability). There were a few cases in which a county where milkweed occurred overlapped two separate climate divisions. In these cases the milkweed species was documented as present in both divisions, possibly overestimating that species' geographic range.

Climate data sets

We obtained information about historical thermal conditions and moisture availability to create several climate related data sets used in this study. In Phase I we used NCDC temperature data to identify whether regional thermal conditions could support adult reproductive activity and development of immature stages during August and September, i.e., the months when the fall migratory generation is produced (Oberhauser 2007). Biologically relevant heat accumulated over time is expressed in units called degree-days (DD) (UCIPM Online 2003). Monarch eggs and immature stages need a minimum of 400 Celsius DD to successfully complete their development (Zalucki and Rochester 2004). For each of the 54 NCDC western climate divisions we computed the number of DD available for egg-to-egg monarch development based on temperature regimes averaged across the 30-year period 1970–2000. We used the method of Taylor and Lentz (2005) to calculate degree days with lower and upper monarch developmental thresholds set at 11.5 and 33°C, respectively. The

long-term monthly climate 'normals' (1971–2000) for maximum and minimum temperature were obtained from NCDC climate archives (NCDC 2002; http://www.ncdc.noaa.gov/oa/mpp/freedata.html). Maximum and minimum temperatures for August and September came from approximately 1400 weather stations across the seven-state region.

In Phase II we obtained data for the years 1998–2007 from the NCDC to estimate the amount of moisture available to regional flora each month. We used the Palmer Drought Severity Index (PDSI) as a relative measure of moisture availability and a proxy for regional net above-ground primary productivity of both host plants and nectar sources (Sala et al. 1988; Paruelo and Lauenroth 1995; Bell 1998; Oesterheld et al. 2001). This Index is expressed as departures from long-term temperature and precipitation data for a specific region. PDSI values generally range from −4.0, indicating extreme drought conditions, to +4.0, indicating a period of relative high moisture surplus (Palmer 1965; Hu and Willson 2000; Heim 2002). PDSI has been described as a hydrologic accounting system that incorporates precipitation, moisture supply, and moisture demand (Heim 2002). Daily precipitation and temperature (maximum and minimum) data from many weather stations within each climate division are used to produce the monthly PDSI estimates for each division. Climate divisions are encompassed by state boundaries, but are not constrained by county boundaries and in the western states, many of these divisions are organized around drainage basins (Smith 2004). Yearly PDSI values for our study were based on a 9 month time period, only including the months from January to September. October, November, and December were omitted because precipitation and temperature in these months occur after the recruitment period for that year's generation of fall migrant monarchs, and therefore would no longer be influential in the context of our model. To estimate inter-annual variation of western moisture conditions for each of the 54 divisions we obtained monthly PDSI values across the years 1998 to 2007 from NCDC climate archives (Smith 2004). We also obtained state-wide monthly PDSI values for six eastern states (Illinois, Iowa, Kansas, Maryland, Minnesota, and Pennsylvania) in order to test the general hypothesis that recruitment of western monarchs was a function of western climate-related drivers rather than eastern climate patterns.

Monarch abundance data sets

For Phase II of our study we obtained data for abundance patterns of migrant generation monarchs in western North America from the Western Monarch Thanksgiving Count (WMTC) data base. The WMTC program was initiated in 1997 by the Monarch Program, a non-profit organization.

Since 2001 it has been administered by a network of monarch researchers and naturalists in collaboration with the Xerces Society (Black 2007). The WMTC program monitored abundance at 83–140 sites annually across the wintering range in California and Baja California during the period of our study (1998–2007). Counts were conducted by monarch researchers and naturalists within a 2 week period centered on the Thanksgiving holiday using standardized protocols (Black 2007). We participated in counts for San Luis Obispo County, California and managed the system-wide WMTC data base during this period. The timing of the counts coincided with peak monarch abundance at western wintering sites since most migrants have arrived at their wintering destinations, but have not yet begun spring dispersal (Frey 1995; Frey and Schaffner 2004). Sites that were monitored but at which monarchs were not present were represented as zeros in the data set. We used these data to test whether variation in PDSI at system-wide spatial scale (seven western states or six eastern states), or for each western state or each eastern state separately, predicted inter-annual variation in monarch abundance (log mean WMTC abundance).

To test the *source-sink hypothesis* we evaluated associations between inter-annual variation in abundance of western winter generation monarchs (WMTC) and three independent indices of historical eastern monarch abundance. We used a series of linear regression models over the 10 year period 1998–2007. In each model the response variable was western monarch abundance (log transformed annual WMTC means). The three eastern USA monarch population data sets used as predictor variables were: (1) late summer eastern egg densities, (2) transect counts of fall migrating monarchs, and (3) the forest area occupied by eastern monarchs at Mexican wintering colonies. Late summer egg densities were the peak number of eggs per milkweed stem reported by the Monarch Larval Monitoring Project (MLMP) across the four-state monitoring region Minnesota, Michigan, Wisconsin, and Iowa during late July and August. Mean eggs per stem were based on counts at 13–70 milkweed sites per year within the four-state region over the 9 year period (1998–2006). Our data set for this index consisted of values published in the MLMP annual report (Oberhauser 2007). Our second index of eastern monarch abundance was derived from weekly counts of migrating monarchs along an eastern seaboard flyway near Cape May, New Jersey conducted by biologists at the Cape May Bird Observatory. Counts were made between 1 September and 31 October each year (Walton et al. 2005). We created a data set of the average annual count (log count) across the 9-week migratory period for the years 1998–2007 (Walton 2008). The third index of inter-annual eastern abundance was based on measurements of the total forest area (Ha.) occupied by wintering

monarchs at 12 mountainous wintering colonies in Mexico in December or January (Rendon-Salinas and Galindo-Real 2005; Oberhauser et al. 2008). Details of the specific procedures and/or databases for each index can be found in their original sources (Walton et al. 2005; Oberhauser 2007; Rendon-Salinas and Galindo-Real 2005). We ran each specific regression model twice, resulting in two separate tests for each of the three predictor variables. In the first analysis, predictor and response variables were conducted for the same year. The second comparison involved a 1 year time lag between predictor and response variables to test whether eastern monarch abundance for 1 year predicted western abundance for the following year.

Statistical analyses and test of the local recruitment hypothesis

All analyses were conducted with Minitab® Statistical Software, version 15.1 (Minitab Inc., State College, PA, USA). Alpha level for statistical tests of significance was 0.05 unless otherwise indicated. Linear regression analyses were carried out in Phase II to assess the relationship between wintering monarch abundance and system-wide or state-by-state PDSI patterns from 1998 to 2007. For tests at both spatial scales the response variable was the annual region-wide log mean wintering monarch abundance. The predictor variable was the system-wide (western or eastern) average January to September PDSI or each state's average PDSI index for each year.

Our test of the *local recruitment hypothesis* involved a multiple regression analysis to evaluate the association between inter-annual variation of WMTC abundance at individual wintering sites and moisture availability (PDSI) from three blocks of NCDC climate divisions considered as putative natal grounds for the migratory generation (Fig. 2). The groupings of climate divisions were increasingly more distant inland from the coastal wintering sites to test the *local recruitment hypothesis* prediction that only local events (drivers) should influence recruitment. Specifically, each WMTC habitat's abundance ($\log_{10} + 1$) was tested against the yearly divisional PDSI average for the division in which the habitat was located (i.e., within the *coastal block* of division groupings), the next closest division (within the *central block* of division groupings), and the most distant division (within the *interior block* of division groupings). We also included in the model a linear and quadratic term to account for variation due to the geographic location of each wintering site across the 1000 km. western wintering range. This site-location term was necessary because wintering abundance pattern was known to vary spatially (Stevens and Frey 2004; Frey and Schaffner 2004; Stevens 2005). The coastal climate division block contained all the wintering habitats and
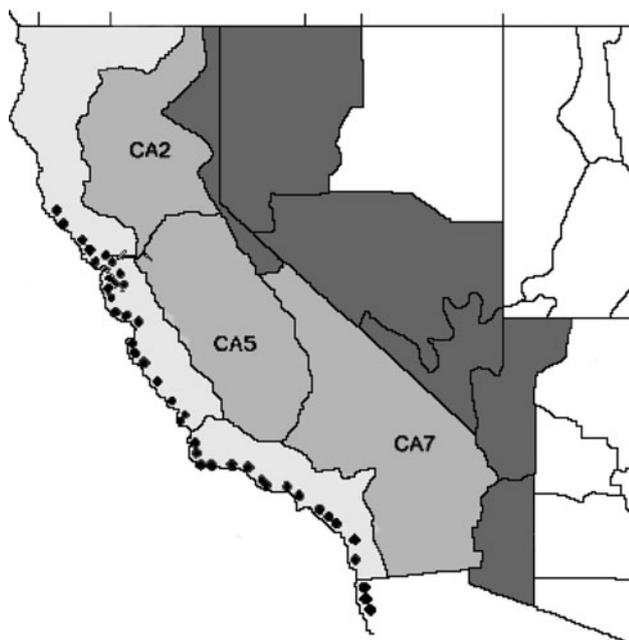
Fig. 2 *Map* showing the location of coastal (*lightest grey*), central, and interior (*darkest grey*) climate division blocks from which historical moisture availability (PDSI) was used in a multiple regression model to test the *Local Recruitment Hypothesis* for the years 1998–2007. *Dark points* along the Pacific Ocean coast illustrate the geographic extent of some of the 195 monarch wintering populations in the Western Monarch Thanksgiving Count (WMTC). Only variation in PDSI of the central climate block predicted WMTC inter-annual abundance. The central climate block of divisions includes CA2—Sacramento Drainage, CA5—San Joaquin Drainage, CA7—Southeast Desert Basin

consisted of the following California climate divisions: North Coast Drainage (CA1), Central Coast Drainage (CA4), South Coast Drainage (CA6). The central climate division block contained the following climate divisions: Sacramento Drainage (CA2), San Joaquin Drainage (CA5), Southeast Desert Basins (CA7). The most distal interior climate division block was made up of the following divisions in Arizona, California, and Nevada: Northeast Interior Basins (CA3), Northwestern (NV1), South Central (NV3), Extreme Southern (NV4), Northwest (AZ1), Southwest (AZ5). Individual WMTC wintering sites were linked to the PDSI of a particular climate division within a block of divisions based on proximity and an assumed monarch southwesterly fall migration flight direction. Southwesterly flight paths of fall migrants have been well documented from studies that employed a wide variety of techniques including tag and recapture research (Rogg et al. 1999), vanishing bearing measurements (Perez et al. 1999; Calvert 2001), and the orientation of individual monarchs tethered in flight mills (Mouritsen and Frost 2002). The mean migration orientation, relative to North, from these studies has ranged from 196° to 239°. The overall multiple regression model took the form:

$$\text{Log}_{10}(A + 1) = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_4 x_4 + \beta_5 x_4^2 + \varepsilon$$

where A is the annual WMTC monarch abundance at a specific wintering habitat, x_1 is the 9-month PDSI for a climate division within the coastal region, x_2 is the PDSI for a climate division within the central region, x_3 is the annual PDSI for a climate division(s) within the interior region, x_4 is the location of the wintering site relative to the most northern site (linear term), and x_4^2 is the quadratic term relative to location along the coast.

Results

Phase I: Host plant pattern and thermal regimes

Western region host plant pattern

We identified 29 species of monarch host plant (*Asclepias* sp.) listed as present in the seven-state western region. The two most ubiquitous species were *Asclepias fascicularis* and *A. speciosa*, occurring in the majority of the 54 NCDC climate divisions across the region. Milkweed was present in all climate divisions across the seven states with the exception of two coastal climate divisions in Washington (WA1—West Olympic Coast; WA2—NE Olympic San Juan). Species richness varied greatly across the western states. At state-wide spatial scale three to six milkweed species occurred in Idaho, Nevada, Oregon, and Washington while Arizona, California, and Utah had 22, 13, and 14 species, respectively. Only seven species had growing seasons that extended into August and September (*Asclepias california, A. eriocarpa, A. erosa, A. fascicularis, A. linaria, A. speciosa, A. tuberosa*). Thirty-five of the 54 NCDC divisions, comprising 78% of the region's area, had at least two of these late maturing species present. After controlling for variation in area among the 54 climate divisions California had significantly greater richness of these late phenology species (California median number of late-season species per division was five; the remaining western states median species per division was two. Mann–Whitney $w = 1133$, $n = 7$ and 47; $P = 0.0001$).

Late summer regional thermal patterns

Twenty-nine of the 54 climate divisions of the western states (64% of the area) generated conditions that were thermally favorable for monarch reproductive activity and immature stage development, i.e., locations with greater than 400 C degree days, during the combined 2 month period August/September when monarchs would be recruited to the migrant generation. Twenty-one of the 25

climate divisions that failed our thermally conducive screening criteria were located in the three northern states—Idaho, Oregon, and Washington.

Congruence of host plant pattern and thermal regimes

Twenty-two climate divisions comprising 55% of the area within the seven western states met both screening criteria, i.e., the occurrence of two or more species of late-summer milkweed and conditions thermally supportive for adult reproduction and larval development. The location of these divisions provided a first-approximation of natal grounds for western migrant monarchs (Fig. 1). A strong latitudinal gradient was evident as none of the divisions within the four southern states failed both screening criteria, while 12 northern divisions within Idaho, Oregon, and Washington (38% of the three-state northern area) failed both screens.

Phase II: Associations between monarch abundance and moisture availability

Inter-annual migrant generation monarch abundance based on Western Monarch Thanksgiving Counts (WMTC) varied substantially across the range of western wintering sites during the period 1998–2007. Monarch abundance was greatest in 1998 and smallest in 2002 and 2007 (Fig. 3a). Larger populations tended to occur at sites along central coastal California while smaller populations were more prevalent in the northern and southern extremes of their western wintering range and resembled a pattern reported earlier (Stevens and Frey 2004; Frey and Schaffner 2004; Stevens 2005).

System-wide western moisture availability over the 10 years, as measured by Palmer's drought severity index (PDSI), was also highly variable, ranging from the wettest conditions in 1998 to extremely dry conditions in 2002 and 2007. Mean annual PDSI values for the seven state area ranged from +2.4 (NCDC category—moderately moist) to −3.2 (NCDC category—severe drought) for 1998 and 2002, respectively (Fig. 3b solid points). In contrast moisture regimes averaged across six eastern states experienced less year-to-year variation and during no year did drought conditions exist (Fig. 3b open circles).

Regional and state-wide "bottom-up" regression models

Inter-annual variation in moisture availability, as measured by Palmer's drought severity index (PDSI), across the seven-state western region predicted monarch migrant generation abundance patterns, i.e., log mean WMTC abundance (Table 1; Regression: $F = 8.27$, $P = 0.021$, $R^2 = 51\%$). No significant relationship was found between variation in eastern breeding habitat moisture availability
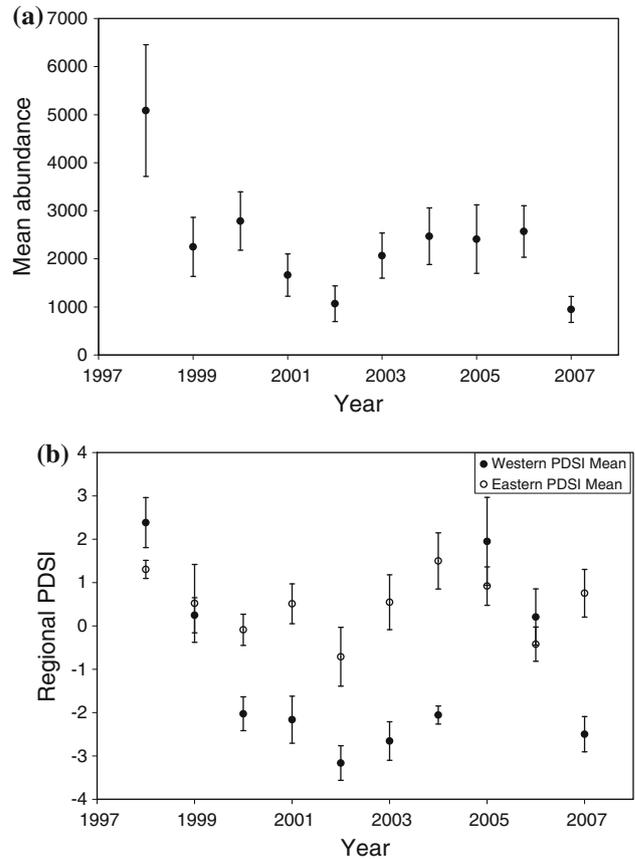

Fig. 3 Pattern of abundance of western wintering generation monarchs and variation in regional moisture availability for the years 1998–2007. **a** Mean abundance per wintering site based on Western Monarch Thanksgiving Counts. **b** Regional moisture availability (PDSI) averaged across seven western states (*solid points*) or six eastern states (*open circles*). Negative PDSI values represent increasing severe drought conditions. *Bars* represent standard errors

regimes, averaged over the six-state region (Illinois, Iowa, Kansas, Maryland, Minnesota, and Pennsylvania), and the pattern of western wintering monarch abundance (Table 1; Regression: $F = 1.41$, $P = 0.269$, $R^2 = 15\%$).

At state-by-state level of resolution, PDSI patterns within California, Idaho, Nevada, and Oregon each significantly predicted inter-annual wintering generation monarch abundance (Table 1; Regression—California: $F = 14.22$, $P = 0.005$, $R^2 = 64\%$; Idaho: $F = 6.65$, $P = 0.033$, $R^2 = 45\%$; Nevada: $F = 6.34$, $P = 0.036$, $R^2 = 44\%$; Oregon: $F = 8.79$, $P = 0.018$, $R^2 = 52\%$). There was not a significant relationship however between the PDSI patterns for Arizona, Utah, or Washington and variation in western monarch abundance (Table 1). Among the seven separate state-wide linear regression models, variation in California's PDSI history accounted for the greatest amount of variation in western monarch wintering population abundance (Table 1; $R^2 = 64\%$).

Table 1 Results from linear regression models for regional moisture availability (Western or Eastern states PDSI) as a predictor of western monarch migratory wintering generation abundance (Log_{10} mean abundance per site) for the years 1998–2007

Predictor variable	Model statistics		
Region or state PDSI	P^a	R^2 (%)	$F_{1,9}$
Western region	**0.021**	50.8	8.27
Arizona	0.204	19.3	1.92
California	**0.005**	64.0	14.22
Idaho	**0.033**	45.4	6.65
Nevada	**0.036**	44.2	6.34
Oregon	**0.018**	52.4	8.79
Utah	0.103	29.8	3.40
Washington	0.520	5.3	0.45
Eastern region	0.269	15.0	1.41
Illinois	0.734	1.5	0.12
Iowa	0.852	0.5	0. 04
Kansas	0.635	3.0	0.24
Maryland	0.137	25.5	2.74
Minnesota	0.558	4.5	0.37
Pennsylvania	0.578	4.0	0.34

[a] Bold print P-values indicate that the variation in moisture availability (PDSI) for a particular region or state was a significant predictor of western North America wintering monarch abundance

All of the six eastern states (Illinois, Iowa, Kansas, Maryland, Minnesota, and Pennsylvania) whose moisture regimes (PDSI history) we tested individually failed to predict inter-annual variation in western monarch abundance (Table 1).

Test of the local recruitment hypothesis

This test represented the smallest scale of our hierarchically nested spatial approach. Overall, the multiple regression model demonstrated significant relationships (Table 2; $F_{5, 1059} = 56.30$, $P < 0.001$, $R^2 = 21\%$). Three of the five predictive terms in the model accounted for significant portions of variation in wintering migrant abundance. The significant linear and quadratic *"Up coast vs. down coast"* terms confirmed that the coastal distribution of wintering populations across this time span followed a 2nd order inverted U-shaped spatial pattern with greater abundance per site toward the center of the wintering range (Table 2; linear term: $t = 10.93$, $P < 0.001$; quadratic term: $t = -12.17$, $P < 0.001$).

Variation in moisture availability (PDSI) during the years 1998–2007 for some climate divisions, but not those expected by the *local recruitment hypothesis*, significantly predicted variation in monarch wintering abundance at this spatial scale. There was a significant positive relationship between PDSI values for the centrally located block of divisions and wintering abundance at monarch habitats (Fig. 2, intermediate grey area; Table 2, $t = 4.16$, $p < 0.001$). The central block included California NCDC climate divisions CA2 (Sacramento Drainage), CA5 (San Joaquin Drainage), and CA7 (Southeast Desert Basin). Increasing drought severity was associated with smaller same-year wintering populations of monarchs. In contrast, variation in PDSI in the "local" or coastal block of climate divisions (Fig. 2, lightest gray areas; CA1—North Coast Drainage, CA4—Central Coast Drainage, CA6—South Coast Drainage) and PDSI of the interior block of climate divisions (Fig. 2, darkest grey area) were not significant predictors of winter generation abundance (Table 2; $P = 0.856$, $P = 0.161$, respectively).

Western versus eastern monarchs: tests of the source-sink hypothesis

No association existed between PDSI patterns in eastern North America compared to those in the west from 1998 to 2007 (Pearson's correlation coefficient $= 0.355$; $P = 0.313$; $n = 10$). The annual pattern for each region clearly demonstrates the highly variable moisture availability of the west

Table 2 Results from multiple regression test of the *Local Recruitment Hypothesis*

Variable related to location of	Predictor variable	Model statistics	
		P	t
Wintering site	"Up coast vs. down coast" (linear term)	**<0.001**	10.93
Wintering site	"Up coast vs. down coast" (quadratic term)	**<0.001**	−12.17
Breeding habitat	PDSI—Coastal block of climate divisions	0.856	0.18
Breeding habitat	PDSI—Central block of climate divisions	**<0.001**	4.16
Breeding habitat	PDSI—Interior block of climate divisions	0.161	−1.40

Relationships are between five predictor variables and inter-annual variation in monarch wintering abundance. See text for full description of the model. Figure 2 shows the location of the coastal, central, and interior blocks of climate divisions from which historical moisture availability (PDSI) was used to test for putative natal grounds of the migratory generation

Overall regression model: F-statistic $= 56.30$; $df = 5, 1059$; $P < 0.001$; $R^2 = 21\%$

P values less than 0.05 are shown in bold

Table 3 Results of linear regression tests for the relationship between variation in eastern monarch abundance and western wintering generation abundance (log mean WMTC) using three different indices of eastern population size

Model category: predictors[a]	Same year model			1 year lag model		
	P	R^2 (%)	$F_{1,9}$	P	R^2 (%)	$F_{1,8}$
Midwestern egg densities	0.561	5.1	0.37	0.149	27.3	2.63
Cape May transect counts (log mean)	0.842	0.5	0.04	0.433	9.0	0.69
Mexico colony size	0.588	3.8	0.32	0.824	0.8	0.05

This relationship was tested for same year comparisons, as well as modeled with a 1 year lag in order to assess whether eastern abundance in a given year predicted western abundance the following season

[a] See Methods for descriptions of the three indices of eastern monarch abundance

in contrast to much less variation and the absence of drought conditions in the eastern region (Fig. 3b).

Support for the *source-sink hypothesis* was not found as none of the three indices of inter-annual variation of eastern monarch abundance (Midwestern USA breeding generation egg densities, Cape May migration transect counts, and Mexico wintering colony size—hectares) predicted population dynamics of western monarchs. Significant relationships between eastern and western monarch abundance were absent for models involving both same year comparisons as well as those with a 1 year time lag or offset year comparisons (Table 3).

Discussion

Protection and conservation planning for monarch butterflies in western North America is problematic for several reasons. While the location and habitat quality of the majority of wintering sites are known, the location of the breeding grounds for the western migratory generation has not been established (Stevens and Frey 2004; Frey and Schaffner 2004). Another major limitation to conservation planning for this species is a lack of understanding of the primary drivers or causes of inter-annual variation in monarch abundance (Stevens and Frey 2004). In addition a sense of urgency overshadows conservation planning because of a consensus that arid and semi-arid mid-latitude areas of temperate western North America will become even drier in the near future scenario of global climate change (Milly et al. 2005; Christensen et al. 2007; Seager et al. 2007).

In the initial phase of our study we mapped the occurrence of western milkweed species that did not senesce until late summer and would thus provide host plant for migratory generation monarchs. Late-season milkweed species were more prevalent in southern portions of the west than in Idaho, Oregon, and Washington based on screening at both state-wide and climate-division spatial scales. Climate divisions in California had significantly

greater diversity of these late season milkweed species than other western states. In a review of the relationship between climate and broad-scale geographic patterns of species richness, Hawkins et al. (2003) identified 20 of 21 (95%) studies where water-related variables explained the majority of variation in plant taxa species richness. Richerson and Lum (1980) concluded that variation in regional precipitation accounted for the majority of diversity of California perennial herbaceous plants ($R^2 = 59\%$). This suggested that at a landscape spatial scale multi-year droughts, such as recently occurred in western North America, would result in reduced milkweed diversity, as well as lower diversity of monarch nectar sources.

Milkweed distribution in the west establishes range boundaries for monarch butterfly occurrence but it cannot be used solely to predict breeding grounds for the migratory generation of this species. In addition to the necessary presence of the larval host plant, suitable temperature regimes are also required for the development of monarch immature stages and for adult reproductive activity (Taylor and Lentz 2005). Monarch butterfly recruitment in a given area is thus constrained by both milkweed distribution and regional temperatures (Zalucki and Rochester 2004).

Regional temperature patterns, like host plant availability, have direct effects on breeding ground recruitment in the Lepidoptera (MacNally et al. 2003). This is because both the rate of larval development and the rate at which females produce and deposit eggs are constrained by low temperature. Adult monarch's minimum flight threshold and the developmental minimum temperature of immature stages are 11–12°C (Zalucki 1981; Cockrell et al. 1993; Masters 1993; Zalucki and Rochester 1999, 2004). Large areas of the western USA become increasingly cool in late summer and early fall, especially at higher elevations and more northern latitudes. We demonstrated that in the northern-latitude states Idaho, Oregon, and Washington, even though milkweed was documented to occur in some areas, the majority of climate divisions were likely too cold (i.e., insufficient number of degree-days) in August and September for most larvae to complete growth cycles.

Similarly the cumulative thermal regime would severely restrict female search time for host plant and depositing eggs; thus few western migrant-generation monarchs were likely recruited from most climate divisions within these states during most years (Fig. 1).

Temperature generally decreases with increases in altitude, while cloud cover and wind speed increase, a combination of conditions that reduce butterfly flight time and fecundity (MacNally et al. 2003). Utah, Nevada, and Idaho are dominated by mountainous topography with average mean elevations of 1800, 1700, and 1500 m, respectively (Infoplease 2005; WRCC n.d.). In contrast California's average elevation is 880 m and only its Northeast Interior Basins climate division (Fig. 2) generated less than 400 C degree-days during August/September. This climate division is dominated by the Warner and Sierra Nevada Mts. The majority of Utah and all of Nevada occurs within the Great Basin desert which comprises 23% of the seven-state western region. This cold desert receives little precipitation making water a primary limiting resource for both plants and animals in this region (Seto et al. 2004).

Western North America experienced dramatic extremes in moisture availability during the time frame of our study (1998–2007; Cook et al. 2004, 2008). In the context of the previous 100 year period (1908–2007), El Niño Southern Oscillation (ENSO) conditions produced California's wettest year in 1998, its second driest year in 2002, and its seventh driest year in 2007 (Smith 2004). The multi-year post-ENSO drought was spatially extensive, reaching into western Canada and northwestern Mexico (Cook et al. 2004, 2008). Obvious indicators of this drought's severity were dramatically shrinking reservoirs throughout the arid and semi-arid west. Two of the region's largest reservoirs, Lake Mead and Lake Powell, reached record low-water levels (Piechota et al. 2004). The extreme nature of biota effects of this drought was demonstrated in episodic mortality (55–100% die-off) among six species of long-lived desert perennials monitored since 1984 at a study site in California's Southeast Desert Basin (Miriti et al. 2007). Extremely high mortality of *Pinus edulus* trees in pinon-juniper woodlands across Arizona, Colorado, New Mexico, and Utah was also attributed to this multi-year post-ENSO drought (Breshears et al. 2005). While extreme weather events such as hurricanes, floods, or catastrophic winter storms may impact animal abundance directly, in most cases, weather anomalies such as drought affect food web dynamics, therefore indirectly impacting abundance (Hawkins and Holyoak 1998; Parmesan et al. 2000; Brower et al. 2004).

Bottom-up effects resulting from drought can greatly reduce Lepidoptera resource availability (Seto et al. 2004; Fleishman et al. 2005), and the relationship between plants and available moisture has been identified as a primary driver of population dynamics for a number of herbivorous insects (Ehrlich et al. 1980; Pollard et al. 1997; Bell 1998; Hawkins and Holyoak 1998; Koricheva and Larsson 1998; McLaughlin et al. 2002; Price and Hunter 2005). In terms of monarch breeding habitat, drought reduces milkweed germination, survivorship, growth, and seed production (Miller and Dingle 1982; Bell 1998; Bowles et al. 1998). Bell (1998) showed that supplemental water provided to milkweed (*A. eriocarpa*) in a seasonally dry western habitat resulted in longer growing seasons for the plants, which enhanced the survival and development rates of monarch larvae that fed on them. This suggests that increased moisture availability translates into higher host plant availability, which in turn yields larger wintering monarch populations.

Water availability can also cause changes in plant properties, such as latex concentration, that can affect larval performance (Bell 1998). Milkweed plants with low water availability often have more viscous latex which can make leaf eating more difficult for larvae, which may lead to declines in larval survival (Buttery and Boatman 1976; Gershenzon 1984; Bell 1998).

In the second phase of our study we used spatially explicit bottom-up regression models to test our first-approximation natal origins map that had been based on milkweed distribution and thermal regimes. This study shows, for the first time, that a pattern of moisture availability, i.e. inter-annual PDSI, across a 10-year period was a strong predictor of inter-annual variation of system-wide western monarch abundance. Moisture variation across the western region and more specifically patterns in California, and to a lesser extend Idaho, Nevada, and Oregon, significantly predicted wintering monarch, i.e., migrant generation, abundance (Table 1).

We next demonstrated that variation in moisture regimes across eastern North America breeding grounds did not drive variation in western inter-annual monarch winter generation abundance (Table 1). We also showed that variation in monarch abundance in western North America was unrelated to variation in indices of inter-annual abundance of eastern monarchs. This latter pattern of independence existed with models which incorporated a 1 year lag for western monarch abundance (Table 3). Taken together these findings demonstrated the independence of population dynamics of monarchs in eastern and western North America and discounted the *source-sink hypothesis* (Brower and Pyle 2004; Vandenbosch 2007) as an explanation for our findings.

Moisture availability varied significantly among western states and within each state during our study (Stevens 2005). Based on these discordant patterns of moisture we used multiple regression analysis to predict the location of western North America monarch natal grounds at a finer-

grained spatial scale, i.e., at the level of climate divisions within states for PDSI and monarch abundance at individual wintering sites rather than system-wide average annual abundance. Variation in moisture availability within a block of three contiguous central California climate divisions (Sacramento Drainage, San Joaquin Drainage, and Southeast Desert Basin) significantly predicted interannual abundance of migrant generation monarchs at wintering sites (Table 2; Fig. 2). In contrast PDSI patterns of three coastal California climate divisions, i.e., ones local to the wintering sites, as well as those of climate divisions in northeastern California, western Nevada and western Arizona did not predict variation in monarch abundance at this spatial resolution. These findings do not support the *local recruitment hypothesis* which posits that western monarchs do not migrate but coalesce over relatively short distances from coastal milkweed habitat to nearby wintering sites (Wenner and Harris 1993). The distance from the spatial centers of eleven coastal California counties along the range of western monarch wintering sites to the nearest local wintering site is only 30.1 ± 4.4 km (mean $\pm$ SE). The distance between winter habitats and putative natal grounds identified in Phase II of our study however was nearly an order of magnitude greater (213.0 ± 2.7 km; Fig. 2).

The three California climate divisions that we identified as the primary natal grounds for western migrant monarchs comprised an area of 274,176 km^2 or 15% of the western region (Fig. 2). This is considerably smaller than the first-approximation natal area we delineated in phase I of our study based on host plant distribution and thermal regimes (1,023,021 km^2 or 55% of the west; Fig. 1). The existence of a smaller western late-summer core recruitment area resembles the spatial pattern for recruitment of migrant generation monarchs in eastern North America. Using stable isotopes Wassenaar and Hobson (1998) identified a nine-state core natal area of 1,523,037 km^2 which included Illinois, Indiana, Iowa, Kansas, Michigan, Missouri, Nebraska, Ohio, and Wisconsin. This area was approximately 25% of the potential breeding habitat for this population yet accounted for 50% of migrant monarchs sampled at Mexico wintering sites. At landscape-scale, agricultural lands in eastern North America natal grounds (e.g., corn and soy fields in Iowa, Minnesota, and Wisconsin) recruited 45–70 times more monarchs to summer and migratory populations than non-agricultural habitats (Oberhauser et al. 2001). This has relevance to our identification of western North America natal grounds since approximately 25% of California's landscape is classified as agricultural land and located primarily in the Sacramento Drainage and San Joaquin Drainage climate divisions and to a lesser extent in the Southeast Desert Basin division (USDA 2002; Fig. 2).

It was not surprising that two of these climate divisions, the Sacramento Drainage (CA2) and San Joaquin Drainage (CA5), had such high diversity of late-season milkweed species as they are part of the California Floristic Province. This province is one of 34 global conservation hotspots or regions identified by their unusually high diversity of vascular plants (Meyers et al. 2000). The region's rich variety of late-summer host plant species predicts that nectar sources would also be abundant to support recruitment of migratory generation adult monarchs. These two climate divisions, as well as the Southeast Desert Basin division, are characterized by hot, dry summers with most precipitation limited to cool winters. Less than 7% of the annual precipitation budget of climate divisions CA2 and CA5 (Fig. 2) occurs from May through August, resulting in conditions in which late summer moisture availability is extremely limiting and is likely a strong bottom-up driver of western monarch population dynamics. The seasonal pattern of annual moisture availability in western North America is opposite from the pattern across the natal grounds in eastern North America where approximately 40% of annual precipitation typically occurs from May through August (NCDC 2002). The Intergovernmental Panel on Climate Change projects that western USA will very likely experience more frequent, more intense and longer duration heat waves in the 21st century (Christensen et al. 2007). Snyder et al. (2007) used a high resolution regional climate model (40 km grids) under a scenario of increasing carbon emissions and predicted that the Sacramento Drainage and San Joaquin Drainage climate divisions will likely receive significantly less December through March precipitation in the future.

The unique migratory nature of North American monarchs is a phenomenon without parallel, but it makes conservation of this insect inherently difficult. Conservation efforts in western North America have focused almost exclusively on wintering habitat issues at a local level (Wells et al. 1983; Brower and Malcolm 1991; Frey and Schaffner 2004; Oberhauser et al. 2008). An increasing understanding of the likely effects from global climate change during the twenty-first century mandates that all portions of a species life-cycle must be taken into account. This is especially true for species like the monarch butterfly that spend most of the year occupying a much wider geographical range associated with their multi-generational breeding grounds (Batalden et al. 2007; Oberhauser et al. 2008).

References

Albee B, Shultz L, Goodrich S (2006) The atlas of the vascular plants of Utah. Utah State University. http://www.gis.usu.edu/Geography-Department/utgeog/utvatlas/

Altizer SM (2001) Migratory behaviour and host-parasite co-evolution in natural populations of monarch butterflies infected with a protozoan parasite. Evol Ecol Res 3:611–632

Batalden R, Oberhauser KS, Peterson AT (2007) Ecological niches in breeding generations of Eastern North American monarch butterflies. Ecol Entomol 36:1365–1373

Bell E (1998) Multitrophic level influences on the population ecology of the monarch butterfly (*Danaus plexippus* L.). Doctoral Thesis, University of California at Santa Cruz, Santa Cruz

Black S (2007) California Monarch Butterfly Conservation Campaign. The Xerces Society. http://www.xerces.org/california-monarchs/

Bowles M, McBride J, Betz R (1998) Management and restoration ecology of the federal threatened Mead's milkweed, *Asclepias meadii* (Asclepiadaceae). Ann Missouri Botan Garden 85:110–125

Breshears D, Cobb N, Rich P, Price K, Allen C, Balice R, Romme W, Kastens J, Floyd M, Belnap J, Anderson J, Myers O, Meyer C (2005) Regional vegetation die-off in response to global-change-type drought. Proc Natl Acad Sci 102:15144–15148

Brower LP (1995) Understanding and misunderstanding the migration of the monarch butterfly (Nymphalidae) in North America: 1857–1995. J Lepid Soc 49:304–385

Brower LP, Malcolm S (1991) Animal migrations: endangered phenomena. Am Zool 31:265–276

Brower LP, Pyle R (2004) The interchange of migratory monarchs between Mexico and the Western United States, and the importance of floral corridors to the fall and spring migrations. In: Nabhan G (ed) Conservation of migratory pollinators and their nectar corridors in North America. Arizona-Sonora Desert Museum, Natural History of the Sonoran Desert Region, No. 2. University of Arizona Press, Tucson, Arizona, pp 144–166

Brower LP, Fink LS, Brower AVZ, Leong K, Oberhauser K, Altizer SM, Taylor O, Vickerman D, Calvert WH, Hook TV, Alonso-Mejia A, Malcolm SB, Owen DF, Zalucki MP (1995) On the dangers of interpopulational transfers of monarch butterflies. Bioscience 45:540–544

Brower LP, Castilleja G, Peralta A, Lopez-Garcia J, Bojorquez-Tapia L, Diaz S, Melgarejo D, Missrie M (2002) Quantitative changes in forest quality in a principal overwintering area of the monarch butterfly in Mexico, 1971–1999. Conserv Biol 16:346–359

Brower LP, Kust DR, Rendon-Salinas E, García Serrano E, Kust KR, Miller J, Fernandez del Rey C, Pape K (2004) Catastrophic winter storm mortality of monarch butterflies in Mexico during January 2002. In: Oberhauser KS, Solensky MJ (eds) Monarch butterfly ecology and behavior. Cornell University Press, Ithaca, pp 151–166

Buttery BR, Boatman SG (1976) Water deficits and flow of latex. In: Kozlowski TT (ed) Water deficits and plant growth. Academic Press, New York, pp 233–289

Calvert WH (2001) Monarch butterfly (*Danaus plexippus* L., Nymphalidae) Fall migration: flight behavior and direction in relation to celestial and physiographic cues. J Lepid Soc 55:162–168

Christensen JH, Hewitson B, Busuioc A, Chen A, Gao X, Held I, Jones R, Kolli RK, Kwon WT, Laprise R, Magaña Rueda V, Mearns L, Menéndez CG, Räisänen J, Rinke A, Sarr A, Whetton P (2007) Regional climate projections. In: Climate change 2007: the physical science basis. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change. Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller H (eds) Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA

Ciais P, Reichstein M, Viovy N, Granier A, Ogee J, Allard V, Aubinet M, Buchmann N, Bernhofer C, Carrara A, Chevallier F, De Noblet N, Friend A, Friedlingstein P, Grunwald T, Heinesch B, Keronen P, Knohl A, Krinner G, Loustau D, Manca G, Matteucci G, Miglietta F, Ourcival J, Papale D, Pilegaard K, Rambal S, Seufert G, Soussana J, Sanz M, Schulze E, Vesala T, Valentini R (2005) Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature 437:529–533

CNDDB (2002) Monarch Habitats. California Natural Diversity Database (CNDDB), Wildlife and Habitat Data Analysis Branch, Department of Fish and Game. http://www.dfg.ca.gov/biogeodata/cnddb/cnddb_info.asp

Cockrell B, Malcolm S, Brower LP (1993) Time, temperature, and latitudinal constraints on the annual recolonization of eastern North America by the monarch butterfly. In: Malcolm SB, Zalucki MP (eds) Biology and conservation of the monarch butterfly. Science Series No. 83. Natural History Museum of Los Angeles County, Los Angeles, pp 233–252

Cook E, Woodhouse C, Eakin C, Meko D, Stahle D (2004) Long-term aridity changes in the western United States. Science 5698:1015–1018

Cook ER, Bartlein PJ, Diffenbaugh N, Seager R, Shuman BN, Webb RS, Williams JW, Woodhouse C (2008) Hydrological variability and change. In: Abrupt climate change. A report by the US climate change science program and the subcommittee on global change research. US Geological Survey, Reston, VA, pp 143–257

CPC (2005) Monitoring and Data: United States Climate Data and Maps. Climate Prediction Center (CPC), NOAA/National Weather Service. http://www.cpc.ncep.noaa.gov/products/monitoring_and_data/us.shtml

Cronquist A, Holmgren A, Holmgren N, Reveal J, Holmgren P (1984) Intermountain Flora: Vascular Plants of the Intermountain West, USA Volume Four. The New York Botanical Garden, Bronx

Dockx C, Brower LP, Wassenaar L, Hobson K (2004) Do North American monarch butterflies travel to Cuba? Stable isotope and chemical tracer techniques. Ecol Appl 14:1106–1114

Ehrlich PR, Murphy D, Singer MC, Sherwood CB, White RR, Brown IL (1980) Extinction, reduction, stability, and increase: the responses of checkerspot butterfly (*Euphydryas*) populations to the California drought. Oecologia 46:101–105

Farrey B, Davis A (2004) Monarch butterfly larvae (Lepidoptera: Nymphalidae) with 3 tubercle pairs in South Florida. Florida Entomol 87:408–411

Fleishman E, Murphy D, Austin GT (2005) Biodiversity patterns of spring-associated butterflies in a Mojave Desert mountain range. J Lepid Soc 59:89–96

Frey D (1995) Monarch population trend—California overwintering sites. Monarch Newsletter 5:6–7

Frey D (1999) Resistance to mating by female monarch butterflies. In: Hoth J, Merino L, Oberhauser K, Pisanty I, Price S, Wilkinson T (eds) 1997 North American conference on the monarch butterfly-paper presentations: biology, conservation, sustainability and development, and environmental education. Printed by the Commission for Environmental Cooperation, pp 79–87

Frey D, Schaffner A (2004) Spatial and temporal pattern of monarch overwintering abundance in western North America. In:

Oberhauser KS, Solensky MJ (eds) Monarch butterfly ecology and behavior. Cornell University Press, Ithaca, pp 167–176

Gershenzon J (1984) Changes in the levels of plant secondary metabolites under water and nutrient stress. In: Timmerman B, Steelink C, Loewus F (eds) Phytochemical adaptations to stress. Plenum Press, New York, pp 273–321

Giblin D (2010) County-level distribution maps for Washington state. University of Washington. http://biology.burke.washington.edu/herbarium/resources/wtucountyquery.php

Goehring L, Oberhauser K (2002) Effects of photoperiod, temperature and host plant age on induction of reproductive diapause and development time in *Danaus plexippus*. Ecol Entomol 27:674–685

Goehring L, Oberhauser K (2004) Environmental factors influencing postdiapause reproductive development in monarch butterflies. In: Oberhauser KS, Solensky MJ (eds) Monarch butterfly ecology and behavior. Cornell University Press, Ithaca, pp 187–198

Hardison LK (2010) The Oregon plant atlas. Oregon State University. http://colleges.ecoplexity.org/oregon_plant_atlas

Hawkins BA, Holyoak M (1998) Transcontinental crashes of insect populations? Am Nat 152:480–484

Hawkins BA, Field R, Cornell HV, Currie DJ, Guegan JF, Kaufman DM, Kerr JT, Mittelbach GG, Oberdorff T, O'Brian EM, Porter EE, Turner JRG (2003) Energy, water, and broad- scale geographic patterns of species richness. Ecology 84:3105–3117

Heim R (2002) A review of twentieth-century drought indices used in the United States. Bull Am Meteor Soc 83:1149–1165

Herman WS (1981) Studies on the adult reproductive diapause of the monarch butterfly, *Danaus plexippus*. Biol Bullet 160:89–106

Howard E, Davis A (2008) The fall migration flyways of monarch butterflies in eastern North America revealed by citizen scientists. J Insect Conserv 13:279–286

Hu Q, Willson GD (2000) Effects of temperature anomalies on the Palmer drought severity index in the central United States. Internat J Climatol 20:1899–1911

Hunter MD, Varley GC, Gradwell GR (1997) Estimating the relative roles of top-down and bottom-up forces on insect herbivore populations: a classic study revisited. Proc Natl Acad Sci 94:9176–9181

Infoplease (2005) Highest, lowest, and mean elevations in the United States, Information Please Database, Pearson Education, Inc. http://www.infoplease.com/ipa/A0873836.html

Koricheva J, Larsson S (1998) Insect performance on experimentally stressed woody plants: a meta-analysis. Ann Rev Entomol 43:195–216

Leong K, O'Brian E, Lowerisen K, Colleran M (1995) Mating activity and status of overwintering monarch butterflies (Lepidoptera: Danaidae) in central California. Ann Entomol Soc Am 88:45–50

MacNally RE, Fleishman E, Fay JP, Murphy DD (2003) Modeling butterfly species richness using mesoscale environment variables: model construction and validation. Biol Conserv 110:21–31

Masters AR (1993) Temperature and thermoregulation in the monarch butterfly. In: Malcolm SB, Zalucki MP (eds) Biology and conservation of the monarch butterfly. Science Series No. 83. Natural History Museum of Los Angeles County, Los Angeles, pp 147–156

McLaughlin JF, Hellman JJ, Boggs CL, Ehrlich PR (2002) The route to extinction: population dynamics of a threatened butterfly. Oecologia 132:538–548

Meyers N, Mittermeier R, Mittermeier C, da Fonseca G, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858

Miller E, Dingle H (1982) The effect of host plant phenology on reproduction of the milkweed bug, *Oncopeltus fasciatus*, in tropical Florida. Oecologia 52:97–103

Milly P, Dunne K, Vecchia A (2005) Global pattern of trends in streamflow and water availability in a changing climate. Nature 438:347–350

Miriti M, Rodríguez-Buriticá S, Wright S, Howe H (2007) Episodic death across species of desert shrubs. Ecology 88:32–36

Mouritsen H, Frost B (2002) Virtual migration in tethered flying monarch butterflies reveals their orientation mechanisms. Proc Natl Acad Sci 99:10162–10166

NCDC Normals (2002) Climatography of the United States No. 81— Monthly Normals of Temperature, Precipitation, and Heating and Cooling Degree Days for 1971–2000. National Oceanic and Atmospheric Administration (NOAA), National Climatic Data Center (NCDC), Asheville, NC. http://www.ncdc.noaa.gov/oa/mpp/freedata.html

Oberhauser K (2004) Overview of monarch breeding biology. In: Oberhauser KS, Solensky MJ (eds) Monarch butterfly ecology and behavior. Cornell University Press, Ithaca, pp 3–7

Oberhauser K (2007) Monarch numbers update. Monarch Larva Monitoring Project- a North American Citizen Science Program 8:2. http://www.mlmp.org/Newsletters/mlmp_newsletter_2007.pdf

Oberhauser KS, Peterson T (2003) Modeling current and future potential wintering distributions of eastern North American monarch butterflies. Proc Natl Acad Sci 100:14063–14068

Oberhauser K, Prysby M, Mattila H, Stanley-Horn D, Sears D, Dively G, Olson E, Pleasants J, Lam W, Hellmich R (2001) Temporal and spatial overlap between monarch larvae and corn pollen. Proc Natl Acad Sci 98:11913–11918

Oberhauser KS, Cotter D, Davis D, Décarie R, Behnumea AE, Galino-Leal C, Gallina Tessaro MP, Howard E, Lauriault J, Maczieski W, Malcolm S, Martínez F, González JM, McRae M, Nernberg D, Pisanty Baruch I, Ramírez I, Reyes JJ, Wilson A (2008) North American Monarch Conservation Plan. Commission on Environmental Cooperation, Montreal

Oesterheld M, Loreti J, Semmartin M, Sala O (2001) Inter-annual variation in primary production of a semi-arid grassland related to previous-year production. J Vegetation Sci 12:137–142

Palmer WC (1965) Meteorological drought. Research Paper No. 45. US Department of Commerce Weather Bureau, Washington, DC

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42

Parmesan C, Root TL, Willig MR (2000) Impacts of extreme weather and climate on terrestrial biota. Bullet Am Meterol Soc 81:443–450

Paruelo J, Lauenroth W (1995) Regional patterns of normalized difference vegetation index in North American shrublands and grasslands. Ecology 76:1888–1898

Perez S, Taylor O, Jander R (1999) Testing monarch butterfly orientation in the field during the autumn migration. In: Hoth J, Merino L, Oberhauser K, Pisanty I, Price S, Wilkinson T (eds) 1997 North American conference on the monarch butterfly-paper presentations: biology, conservation, sustainability and development, and environmental education. Printed by the Commission for Environmental Cooperation, pp 127–132

Piechota T, Timilsena J, Tootle G, Hidalgo H (2004) The western US drought: how bad is it? Eos 85:301–308

Pollard E, Greatorex-Davies J, Thomas J (1997) Drought reduces breeding success of the butterfly *Aglais urticae*. Ecol Entomol 22:315–318

Price P, Clancy K (1986) Multiple effects of precipitation on *Salix lasiolepis* and populations of the stem-galling sawfly, *Euura lasiolepis*. Ecol Res 1:1–14

Price P, Hunter M (2005) Long-term population dynamics of a sawfly show strong bottom-up effects. J Anim Ecol 74:917–925

Rendon-Salinas E, Galindo-Real C (2005) Monitoreo de las colonias de hibernacion de la mariposa monarcha, Diciembre 2004:

reporte preliminar. In: World Wildlife Fund Programa Mexico, Mexico City, pp 1–9

Richerson P, Lum K (1980) Patterns of plant species diversity in California: relation to weather and topography. Am Nat 116: 504–536

Rogg K, Taylor O, Gibo D (1999) Mark and recapture during the monarch migration: a preliminary analysis. In: Hoth J, Merino L, Oberhauser K, Pisanty I, Price S, Wilkinson T (eds) 1997 North American conference on the monarch butterfly- paper presentations: biology, conservation, sustainability and development, and environmental education. Printed by the Commission for Environmental Cooperation, pp 133–137

Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA (2003) Fingerprints of global warming on wild animals and plants. Nature 421:57–60

Rosatti TJ (2006) The Jepson online interchange–California floristics. University of California, Berkeley. http://ucjeps.berkeley.edu/interchange/index.html

Rosenzweig C, Karoly D, Vicarelli M, Neofotis P, Wu Q, Casassa G, Menzel A, Root T, Estrella N, Seguin B, Tryjanowski P, Liu C, Rawlins S, Imeson A (2008) Attributing physical and biological impacts to anthropogenic climate change. Nature 483:353–357

Sala O, Parton W, Joyce L, Lauenroth W (1988) Primary production of the central grassland region of the United States. Ecology 69:40–45

Seager R, Ting M, Held I, Kushnir Y, Lu J, Vecchi G, Huang H-P, Harnik N, Leetmaa A, Lau N-C, Li C, Velez J, Naik N (2007) Model projections of an imminent transition to a more arid climate in southwestern North America. Science 316:1181–1184

Seto KC, Fleishman E, Fay JP, Betrus CJ (2004) Linking spatial patterns of butterfly and bird species richness with Landsat TM derived NDVI. Int J Remote Sens 25:4309–4324

Slayback DA, Brower LP, Ramírez MI, Fink LS (2007) Establishing the presence and absence of overwintering colonies of the Monarch butterfly in Mexico by the use of small aircraft. Am Entomol 53:28–40

Smith C (2004) Monthly mean timeseries. NOAA-CIRES Climate Diagnostics Center. http://www.cdc.noaa.gov/Timeseries/index.html

Snyder M, Sloan L, Bell J (2007) Modeled regional climate change in the hydrologic regions of California: a CO2 sensitivity study. J Am Water Resour Assoc 40:591–601

Solensky MJ (2003) Reproductive Fitness in Monarch Butterflies, *Danaus plexippus*. PhD Thesis, University of Minnesota, St. Paul

Solensky MJ (2004) The effect of behavior and ecology on male mating success in overwintering monarch butterflies (*Danaus plexippus*). J Insect Behav 17:723–743

Stevens S (2005) Migration and Dynamics of the Monarch Butterfly in Western North America. MS Thesis, California Polytechnic State University, San Luis Obispo, CA

Stevens S, Frey D (2004) How the other half lives: monarch population trends west of the great divide. Monarch Watch Update—July 23, 2004. http://www.monarchwatch.org/update/2004/0723.html#4

Sundell E (1994) A new flora for Arizona in preparation: Asclepiadaceae. J Arizona-Nevada Acad Sci 27(2):169–187

Taylor O (2004) Fourth of July/Mid-summer counts. Monarch Watch Update. July 23, 2004. http://www.monarchwatch.org/update/2004/0723.html#7

Taylor O (2005) Monarch Watch. The University of Kansas Entomology Program. http://www.monarchwatch.org

Taylor O, Lentz J (2005) Monarchs, cold summers, jet streams, volcanoes, and more. Monarch Watch Update. January 14, 2005. http://www.monarchwatch.org/update/2005/0114_teaching.html

UCIPM Online (2003) Degree-days: about degree-days. In: University of California Integrated Pest Management (UC IPM), Regents of the University of California

Urquhart F, Urquhart N (1977) Overwintering areas and migratory routes of the eastern populations of the monarch butterfly (*Danaus p. plexippus*, Lepidoptera: Danaidae) in North America with reference to the western populations. Canadian Entomol 109:1583–1589

Urquhart F, Urquhart N (1978) Autumnal migration routes of the eastern population of the monarch butterfly (*Danaus p. plexippus* L.; Danaidae: Lepidoptera) in North America to the overwintering site in the neovolcanic plateau of Mexico. Can J Zool 56:1754–1764

USDA (2002) Census of Agriculture. Table 1: State summary highlights. http://www.agcensus.usda.gov/Publications/2002/Volume_1,_Chapter_2_County_Level/California/index.asp

Vandenbosch R (2007) What do monarch population time series tell us about eastern and western population mixing? J Lepid Soc 61:28–31

Walton RK (2008) Natural History Services Monarch Monitoring Project. Cape May Point, NJ. http://rkwalton.com/mon.html

Walton R, Brower LP, Davis AK (2005) Long-term monitoring and fall migration patterns of the monarch butterfly in Cape May, NJ. Ann Entomol Soc Am 98:682–689

Wassenaar L, Hobson K (1998) Natal origins of migratory monarch butterflies at wintering colonies in Mexico: new isotopic evidence. Proc Natl Acad Sci 95:15436–15439

Wells S, Pyle R, Collins N (1983) The IUCN invertebrate red data book. Gland, Switzerland: IUCN, 632 pp

Wenner A, Harris A (1993) Do California monarchs undergo long-distance directed migrations? In: Malcolm SB, Zalucki MP (eds) Biology and conservation of the monarch butterfly. Science Series No. 83. Natural History Museum of Los Angeles County, Los Angeles, pp 209–218

Woodson RE (1954) The North American species of Asclepias L. Ann Missouri Bot Garden 41:1–211

WRCC (n.d.) Historical Climate Information, Western Regional Climate Center (WRCC). http://www.wrcc.dri.edu/

Zalucki MP (1981) The effects of age and weather on egg laying in *Danaus plexippus* L. (Lepidoptera: Danaidae). Res Popul Ecol (Kyoto) 23:318–327

Zalucki MP, Rochester W (1999) Estimating the effect of climate on the distribution and abundance of *Danaus plexippus*: a tale of two continents. In: Hoth J, Merino L, Oberhauser K, Pisanty I, Price S, Wilkinson T (eds) 1997 North American conference on the monarch butterfly- paper presentations: biology, conservation, sustainability and development, and environmental education. Printed by the Commission for Environmental Cooperation, pp 151–164

Zalucki MP, Rochester W (2004) Spatial and temporal population dynamics of monarchs down under: lessons for North America. In: Oberhauser KS, Solensky MJ (eds) Monarch butterfly ecology and behavior. Cornell University Press, Ithaca, pp 219–228