

**Topoclimate and Microclimate  
in the Monarch Butterfly Biosphere Reserve**

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**Abstract.**

Overwintering monarch butterflies in Mexico select areas of the high elevation Oyamel fir -pine forest providing a canopy that protects them from extremes of cold, heat, sun, and wind. These exacting microclimatic conditions are found in relatively small areas of forest with appropriate topography and canopy cover. The major goal of this investigation is to map topoclimatic and microclimatic conditions within the Monarch Butterfly Biosphere Reserve by combining temperature monitoring (iButton Thermochnrons), hemispherical canopy photography, multiple regression, and GIS modeling. Temperature measurements included base weather stations and arrays of Thermochnrons (on the north-side of trees at 2m height) across local topographic and canopy cover gradients. Topoclimatic models of minimum temperatures included topographic position, slope, and elevation, and predicted that thermal belts on slopes and cold air drainage into canyons create local minimum temperature gradients of 2°C. Topoclimatic models of maximum temperatures models included elevation, topographic position, and relative solar exposure, with local gradients of 3°C. These models, which are independent of forest canopy structure, were then projected across the entire region.

Forest canopy structure, including direct and diffuse solar radiation, was assessed with hemispherical photography at each Thermochnron site. Canopy cover affected minimum temperatures primarily on the calmest, coldest nights. Maximum temperatures were predicted by direct radiation below the canopy. Fine-scale grids (25 m spacing) at three overwintering sites characterized effects of canopy gaps and edges on temperature and wind exposure.

The effects of temperature variation were considered for lipid loss rates, ability to take flight, and freezing mortality. Lipid loss rates were estimated by measured hourly temperatures. Many of the closed canopy sites allowed for substantial lipid reserves at the end of the season (March 15), but increases in average temperature could effectively deplete lipids by that time. The large influence of canopy cover on daytime maximum temperatures demonstrates that forest thinning directly reduces habitat suitability. Monarchs' flight behavior under warmer conditions suggests that daytime temperatures drive the dynamics of monarch distribution within colonies. Thinning also decreases nighttime minimum temperatures, and increases wind exposure. These results create a basis for quantitative understanding of the combinations of topography and forest structure that provide high quality overwintering habitat.

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**Introduction.**

Monarch butterflies in Mexico overwinter in high elevation forests in the Neo-Transvolcanic mountain range that provide appropriate temperature, solar radiation (insolation), moisture and wind (microclimatic) conditions (Brower 1985a, Brower 1985b, Brower 1995). Monarchs appear to be selecting a highly restricted microclimatic envelope, balancing between a set of climatic hazards (Brower 1999a, Brower 1999b). Sub-freezing temperatures directly kill monarchs and wet winter snow and rain storms followed by cold clear nights can lead to mass freezing mortality (Calvert et al. 1983, Alonso-Mejia et al. 1992, Anderson and Brower 1996, Brower et al. 2004). At the other extreme, warmer temperatures and direct insolation increase metabolism, fat loss, and water loss (Masters et al. 1998, Alonso-Mejia et al. 1997).

The microclimate at a specific location is the result of numerous physical and biological processes (Geiger et al. 2003, Barry 1992). The nested hierarchy of spatial variation in climate progresses downward through macroclimate, mesoclimate, topoclimate, and microclimate. Macroclimate characterizes the progression of air masses (synoptic meteorology) through a region (scale of 100+ km). Mesoclimates are subregional (scale of 1-10+ km) climates across broad topography. Topoclimates (scale of 10-1000 m) are a function of slope, aspect, and topographic position (ridge to valley/canyon) that affect solar radiation, wind, and cold air drainage. Microclimate (0.1-10m) is a function of vegetation canopy structure that modifies sunlight, wind, rainfall interception, evapotranspiration, and night-time thermal radiation balance. Geiger et al. (2003) provides an encyclopedic treatment of microclimatology.

This study uses temperature loggers, hemispherical photography, and GIS to measure and model maximum and minimum temperatures, to identify the range of topographic and canopy cover conditions across the Monarch Butterfly Biosphere Reserve that provide overwintering habitat. This study directly addresses the local impacts of canopy structure on microclimate, and can guide both management and restoration of overwintering monarch butterfly habitats.

**Methods**

The objective is to quantitatively map key temperature variables, particularly daytime maximum and nighttime minimum temperatures. The conceptual basis for fine-scale climate mapping is the establishment of temperature differentials for each topographic and canopy structure factor, and relating those differentials to a base station. For example, a typical lapse rate for average temperature is 3°C per 500 meters elevation. Drainage of cold air at night leads to distinct warm “thermal belts” at mid-slope and cold pockets below, as well as cold ridgetops and flats. During the overwintering season in the MBBR, south-facing slopes receive more solar radiation (insolation) than north-facing slopes, as a function of slope, aspect, and day of year. At the finest spatial scale, variation in minimum temperature within a forest stand is a function of local canopy cover and height above the ground. Insolation reaching the lower levels of the forest drives maximum temperatures, and the effects are modified by the penetration of wind

into stands. At the finest scale, there are differences within monarch clusters according to sky exposure.

The process can be described by the following equation:

$$(1) T(\text{site}) = T(\text{base}) + \Delta T(\text{elev}) + \Delta T(\text{insolation}) + \Delta T(\text{hillslope}) + \Delta T(\text{canopy cover}) + \Delta T(\text{height})$$

The major goal of this research is to measure and model these temperature differentials.

#### *Temperature measurements*

Two Weatherhawk base stations were deployed, one in a clearing adjacent to the Chincua Guard Station (3160 m), and one at the western base (2415 m) of Cerro Pelon. These stations measured air temperature, relative humidity, solar radiation, wind speed and direction, and barometric pressure.

iButton Thermochrons (Thermochrons) measured air temperatures within the forests. These small (2 cm diameter, 0.75 cm depth) temperature loggers record up to 85 days of hourly average temperature to the nearest 0.5°C. They were deployed on the shaded N-sides of tree trunks at 2 m height on the underside of a 2 cm dowel extending ~ 6 cm from the tree trunk. Dowels were painted a dark color to be inconspicuous. Thermochrons were deployed in late November

Networks of Thermochrons were deployed, at Zapatero, Chincua Station, El Rosario, and Cerro Pelon (Figure 1). For this analysis, the primary network is the Zapatero network, deployed in late November (Figure 1). Following data quality controls (see Appendix A), 26 complete records for Dec. 1 – Apr 1 were obtained at Zapatero, along with 47 complete records for Feb 1 – Apr 1. The more spatially extensive Feb-Mar data were used to develop the primary temperature differential models. Data recovery, incorporation of partial time series, and the 2005-06 field season will provide more data for testing and refining the models.

#### *Hemispherical photography*

Hemispherical photographs were obtained in November 2004 and February 2005, using a Kodak DCS digital camera body and a Nikkor 8mm lens mounted on gimbals. Photos were taken in 3 megapixel JPEG format. Procedures followed those in Delta-T Hemiview Manual. Most photographs were taken at dawn, dusk or under cloudy conditions to maximize contrast between sky and obstructions. Because of the remote nature of some sites, some photographs were taken under less than ideal sky conditions and processed in Adobe Photoshop to better define the contrast.

Photographs were taken at each Thermochron site, approximately 1 meter N of the tree trunk at 1.75 m height. Grids of photographs were taken at 25 m or less intervals at three overwintering sites (Zapatero-Llanos de Torres, La Mesa, and Pelon) to characterize finer-scale variability in canopy cover

Photographs were analyzed using Hemiview 2.1 software (Delta-T Devices). The site factors extracted were:

- 1) ISFU – Indirect Site Factor Uncorrected: the overall proportion of sky visible.
- 2) ISFC – Indirect Site Factor Corrected: This measure includes a cosine correction to a horizontal surface, which emphasizes overhead openness and may be a better surrogate for night-time thermal IR balance.
- 3) DIRBEU by month – Total potential direct radiation (clear skies) below the forest canopy, calculated over the course of a month (21<sup>st</sup> to 21<sup>st</sup>); note that November and February have the same DIRBEU, as do December and January.
- 4) WSF<sub>dir</sub> – Wind Site Factor for eight directions: the proportion of open sky in each of eight 45° azimuth wedges, a measure of horizontal openness that is a first-order approximation of wind exposure. WSF is calculated by summing ISFU values for azimuth and dividing by 0.125 (1/8 of the sky is in each 45° azimuth wedge).

#### *GIS Analysis*

GIS analysis used ARCGIS 8 and 9. A 15 meter Digital Elevation Model (DEM) was created from the contours of 1:50,000 INEGI map. Slope and aspect were derived using ARCGIS functions, and combined into a “slope/aspect index” (SAI<sub>N</sub>) that quantified “northness” and is a reasonable surrogate for insolation:

$$2) \text{SAI}_N = \cos(\text{aspect}) * \sin(\text{slope})$$

A vertical north-facing slope has a value of 1.0, flats and due east/west facing slopes are 0, and a vertical south-facing slope has a value of -1.0.

Topographic position (TP150) was defined by the difference between the point elevation and the average elevation within 150 meters of the point. The window size can be varied according to application. It effectively differentiates canyon bottoms, slopes, and ridges/hilltops.

$$3) \text{TP150} = \text{DEM} - \text{mean DEM}(150\text{m radius})$$

Site factors in the fine-scale grids were interpolated to a 5 m grid with multiquadratic Radial Base Functions in the Geostatistical Analyst module in ARCGIS.

#### *Statistical analysis*

Empirical relationships between temperature and topographic and canopy factors were estimated with multiple regression in JMPIN 4.0 software. These regression parameters were then applied to the appropriate GIS coverages to predict temperatures across the MBBR region. Regression models between T<sub>max</sub> and DIRBEU were projected across the interpolated grids.

A GIS model used the 10<sup>th</sup> and 90<sup>th</sup> percentiles of T<sub>max</sub>, T<sub>min</sub>, and aspect at historical monarch sites to spatially define topoclimatic habitat suitability.

*Lipid depletion analysis*

Complete ThermoChron records at Zapatero, Chincua Station, and El Rosario from Dec 1 – Mar 15 were converted into lipid losses by the equation (Masters et al. 1988, Alonso-Mejia et al. 1997):

$$4) \text{ lipids/hour} = \log_{10}E = 0.048T_{(h)} - 0.368,$$

E is energy expenditure in Joules/hour,  $T_{(h)}$  is hourly temperature. Energy was converted into lipid mass at 37.66 J/mg. Lipid mass was started at 113 mg on December 1 (Alonso-Mejia et al. 1997). The sensitivity of lipid loss to higher temperatures was explored by increasing all hourly temperatures by 1° and 2°C.

## Results

### *Macroclimate*

December 2004- March 2005 was rather mild, with no major storms recorded. From December 1 through April 1, average daily  $T_{\max}$  at Chincua Station was  $14.3^{\circ}\text{C}$ , average daily  $T_{\min}$  was  $0.3^{\circ}\text{C}$  (Table 1). Absolute  $T_{\min}$  was  $-5.0^{\circ}\text{C}$ .  $T_{\max}$  at Pelon West was  $4.3^{\circ}\text{C}$  warmer,  $T_{\min}$  was  $6.6^{\circ}\text{C}$  warmer, and absolute  $T_{\min}$  was  $3.3^{\circ}\text{C}$ . Calculated seasonal average lapse rate for  $T_{\max}$  is  $-0.9^{\circ}\text{C}/500\text{m}$ , and for  $T_{\min}$  is  $-4.4^{\circ}\text{C}/500\text{m}$ . These lapse rates are not necessarily used in the topoclimatic models, where the Thermochron networks extended over a much smaller elevational range.

### *Topoclimatic analysis*

This analysis considers topographic factors only; the effects of canopy cover are treated below. All comparisons were for clear days/nights in from Feb 1 through Mar 31 unless otherwise noted. Average  $T_{\min}$  in forested sites was  $3.4^{\circ}\text{C}$  (range  $2.5$  to  $4.5^{\circ}\text{C}$ ) warmer than  $T_{\text{base}}$  on average (i.e.  $\Delta T_{\min} = +2.5$  to  $+4.5^{\circ}\text{C}$ ). The best model for  $\Delta T_{\min}$  included elevation, TP, the absolute value of TP (ABS TP), and slope (Table 1):

Table 1. Topoclimatic model for  $\Delta T_{\min}$  in February and March

<b>Term</b>	<b>Estimate</b>	<b>Std Error</b>	<b>t Ratio</b>	<b>Prob&gt; t </b>
<b>Intercept</b>	16.708721	4.789477	3.49	0.0012
<b>ELEVATION</b>	-0.004226	0.001492	-2.83	0.0071
<b>TP150</b>	0.0233024	0.005566	4.19	0.0001
<b>ABS TP</b>	-0.021172	0.00886	-2.39	0.0216
<b>Slope</b>	0.0261518	0.007178	3.64	0.0007

$$R^2_{\text{adj}} = 0.58, \text{RMSE} = 0.27^{\circ}\text{C}$$

This model predicts a lapse rate of  $2.1^{\circ}\text{C}/500$  meters, less than that calculated from Chincua Station to Pelon West, and likely reflects a relatively limited elevational gradient within the Zapatero array. TP drives a gradient from cold canyon bottoms through warmer slopes and ridgetops. ABS TP cools down ridgetops and canyon bottoms. Steeper slopes allow for more cold air drainage away from the site. The net effect of these factors is that the range of  $\Delta T_{\min}$  across a local canyon profile at Zapatero is  $1.2^{\circ}\text{C}$  from the warmer mid-slope thermal belt to the cooler canyon bottom. Ridgetops are about  $0.6^{\circ}\text{C}$  cooler than the thermal belts. Steeper canyons have slightly greater  $T_{\min}$  gradients.

Maps of predicted  $\Delta T_{\min}$  with  $T_{\text{base}} = -10^{\circ}\text{C}$  (a cold extreme) at Chincua Station were produced at 1:24,000 scale at three overwintering regions (Figs. 2-4). The Sierra Chincua map (Fig. 2) shows, at any given elevation, repeating patterns of colder canyon bottoms, warmer thermal belts, and colder ridgetops, nested within the elevational lapse rate. The very coldest areas, scattered above 3300 meters are  $-8.5^{\circ}\text{C}$ .  $T_{\min}$  within the Zapatero colony area at 3050-3250 meters is  $-6$  to  $-7^{\circ}\text{C}$ . Pelon West (Fig. 3) and El Rosario (Fig. 4) show the similar local structures superimposed across sharper topography at Pelon, and across a broader mountain massif at Rosario. The major colonies in 2004-2005 were all the same  $T_{\min}$  zones. The relationship of  $T_{\min}$  (and  $T_{\max}$ ) with monarch use will be discussed in detail below.

$\Delta T_{\max}$  in forested sites averaged  $-1.15^{\circ}\text{C}$ , with a low extreme of  $-2.5^{\circ}\text{C}$ . 7/46 stations were warmer than the base station, with a high outlier at  $+3.7^{\circ}\text{C}$ . The best topographic model includes elevation, TP, and SAI-NS (Table 2).

Table 2. Topoclimatic model for  $\Delta T_{\max}$  in February and March

<b>Term</b>	<b>Estimate</b>	<b>Std Error</b>	<b>t Ratio</b>	<b>Prob&gt; t </b>
<b>Intercept</b>	39.456608	14.95676	2.64	0.0116
<b>ELEVATION</b>	-0.008064	0.004731	-1.70	0.0957
<b>TP150</b>	0.0837026	0.01617	5.18	<.0001
<b>SAI-NS</b>	-2.127113	0.868478	-2.45	0.0186

$R^2_{\text{adj}} = 0.42$ , RMSE =  $0.96^{\circ}\text{C}$

This model predicts a lapse rate for  $T_{\max}$  of  $-4.0^{\circ}\text{C}/500$  meters, greater than that calculated from the overall Chincua-Pelon gradient, and reflects a relatively limited elevational gradient within the Zapatero array. TP creates a  $3^{\circ}\text{C}$  ridgetop-canyon bottom gradient, and SAI creates a  $2^{\circ}\text{C}$  gradient from N to S slopes.

Maps of  $\Delta T_{\max}$  with  $T_{\text{base}} = 15^{\circ}\text{C}$  were produced at 1:24,000 scale at three overwintering regions (Figs. 5-7). The Sierra Chincua map (Fig. 5) shows the pattern of colder canyon bottoms, warmer ridgetops, cooler N-facing versus warmer S facing slopes, within the elevation gradient. Temperatures within the general Zapatero colony area are predicted to be  $12.5 - 14.5^{\circ}\text{C}$ , and local ridgetops exceed  $15^{\circ}$ . The maps for Pelon (Fig. 3) and El Rosario (Fig. 4) show the same patterns across differing topography.

#### *Microclimatic effects of Canopy Cover*

Hemispherical photographs show the range of canopy cover and other characteristics at representative sites (Fig. 8). Each photo has a table with the site factors described above, and will be briefly discussed to illustrate components of the analysis.

Reading a hemispherical photograph is straightforward. The photographs are  $180^{\circ}$  field of view – the horizon is at the outer edge of the photograph and the zenith (directly overhead) is in the center of the image. East and west are reversed because the photograph is looking up. Sunpaths are superimposed in the arched grid - the most southerly sun path is Dec. 21 (the winter solstice); the next line north is Nov/Jan. 21, then Feb/Oct 21, and the center line is Mar/Sep 21, and on to the summer solstice at the northernmost line. There is also a circular grid of eight  $45^{\circ}$  azimuth wedges, divided into eighteen  $5^{\circ}$  zenith angle slices (not shown, but easily visualized). Hemiview calculates the open proportion in each division, and applies the appropriate corrections for direct and diffuse radiation intensity.

Figure 8A shows a site occupied by monarchs (the dark shapes in the trees to the S and SE) in the Zapatero colony in November 2005. ISFU is 0.12 (12% of the sky is visible). ISF (cosine corrected to a horizontal surface) is slightly higher (0.15). The site receives a potential  $170-190 \text{ MJ}/\text{m}^2$  per month (a small range) – note that most of this insolation is dappled light filtering through the trees to the west. The greatest wind exposure (0.23) is from the NW, the lowest is S

Figure 8B shows an unoccupied site about 100 meters NE of Photo 8A. The site is approximately twice as open as 8A. 8B receives similar insolation in Jan and Feb, with a large increase to  $>300 \text{ MJ/m}^2$  in March – note how the March sun path traverses the large overhead gap in the early afternoon. The greatest wind exposure (0.38-0.41) is from the W and SW, with 0.31 from the NE.

Figure 8C shows the clearing at the south end of the Zapatero colony. ISF and ISFU are high. Potential direct insolation is  $>625 \text{ MJ/m}^2$  in each month. Wind exposure is highest ( $>0.5$ ) from the S and SW, and E, SE, and W are relatively high.

Figure 8D shows the least open site (ISFU= 0.04), with low values of all site factors, in a dense stand of pole-sized trees 7-10 m ta.

Figure 8E is at Mil Cumbres, below a former roost tree, with moderate ISFU (0.18), with high NE wind exposure (0.45). This site will be discussed later in some detail.

Figure 8F is a very sheltered Thermochron site on a steep ( $26^\circ$ ) NE-facing slope. The Thermochron is on the tree directly south, about 1m away. The sky is more visible through trees looking downslope than looking upslope. Site factors are generally low, with highest wind exposure to the E.

Figure 8G is a ridgetop in thinned forest, with high ISFU, insolation, and wind exposure.

Figure 8H is intact forest in a canyon bottom at Zapatero. The stream runs SE to NW, and the two canyon walls are visible to the SW and NE. Like 8F, the site has generally low site factors.

#### *Effects on $T_{\min}$*

The effects of forest cover on  $T_{\min}$  can be complex and conditional, because wind, cold air drainage, and radiational cooling interact at very local scales. ISF and ISFU were non-significant regressions parameters for overall Feb-Mar  $\Delta T_{\min}$ .  $\Delta T_{\min}$  for only those hours when  $T < 0^\circ\text{C}$  and Wind = 0 at Chincua Station did show a significant relationship with ISFU (Table 3), in addition to the same parameters that were in the pure topoclimatic model. The leverage of ISFU over the range from 0.08 to 0.43 is  $\sim 0.5^\circ\text{C}$ . Calm conditions allow for relatively warmer forest understory relative to the open;  $\Delta T_{\min}$  is greater on calm nights by  $\sim 2^\circ\text{C}$  as a result of lack of mixing from wind.

Table 3. Topoclimatic and canopy cover model for  $T_{\min}$  when  $T < 0$ , Wind = 0 at Chincua

Term	Estimate	Std Error	t Ratio	Prob> t
Intercept	20.687505	4.950055	4.18	0.0002
Slope	0.0384841	0.006916	5.56	<.0001
TP150	0.0529177	0.006695	7.90	<.0001
ABS TP150	-0.021676	0.008559	-2.53	0.0154
ELEVATION	-0.004815	0.001529	-3.15	0.0031
ISFU	-1.674206	0.778003	-2.15	0.0375

$$R^2_{\text{adj}} = 0.81, \text{RMSE} = 0.26^\circ\text{C}$$

The effect of canopy cover on  $\Delta T_{\max}$  is a linear relationship with DIRBEU (direct radiation below the canopy uncorrected) and a marginally significant relationship with elevation (lapse rate =  $2.9^{\circ}\text{C}/500\text{m}$ ) (Table 4). Direct radiation uncorrected for slope and aspect produced slightly higher  $R^2_{\text{adj}}$  values than corrected values, likely because most radiation is being absorbed by foliage and trunks that face in all directions. The effect of slope and aspect is expressed in the density of canopy facing upslope versus downslope (see Fig. 8 F). Variability of DIRBEU creates a  $4.5^{\circ}\text{C}$  gradient.

Table 4. Canopy cover model for  $\Delta T_{\max}$

Term	Estimate	Std Error	t Ratio	Prob> t
Intercept	-21.37409	10.95645	-1.95	0.0576
ELEVATION	0.0058147	0.003476	1.67	0.1017
DIRBEU Mar-Feb	0.0076155	0.001	7.61	<.0001

$R^2_{\text{adj}} = 0.57$ , RMSE =  $0.90^{\circ}\text{C}$

Average  $T_{\max}$  over the entire Dec1-Apr 1 growing season (for 26 Thermochrons) was also predicted by DIRBEU, with the best relationship using only March DIRBEU (Table 5).

Table 5. Canopy cover model for Dec-Mar average  $T_{\max}$  with DIRBEU-Mar

Term	Estimate	Std Error	t Ratio	Prob> t
Intercept	-20.22013	16.92938	-1.19	0.2445
DIRBEU-Mar	0.0071741	0.001182	6.07	<.0001
ELEVATION	0.0098289	0.005368	1.83	0.0801

$R^2_{\text{adj}} = 0.62$ , RMSE =  $0.89^{\circ}\text{C}$

ISFU, which is a much more general measure of canopy cover, can be substituted for DIRBEU-Mar in a model with slightly less predictive power (Table 6).

Table 6. Canopy cover model for Dec-Mar average  $T_{\max}$  with ISFU

Term	Estimate	Std Error	t Ratio	Prob> t
Intercept	-21.33567	18.10105	-1.18	0.2511
ELEVATION	0.0100302	0.005738	1.75	0.0944
ISFU	14.119239	2.46132	5.74	<.0001

$R^2_{\text{adj}} = 0.60$ , RMSE =  $0.93^{\circ}\text{C}$

This model indicates that for every 10% increase in ISFU,  $T_{\max}$  over the season will increase by  $0.7^{\circ}\text{C}$ .

#### *Fine-scale photo grids (Figs. 9-14)*

The interpolated photo grids document variable canopy structure at each site, as interpolated. The DIRBEU map of the Chincua grid (Fig. 9) shows canopy gaps and edges on the southern edge, and a thinning towards the NE. The sites occupied by monarchs are shown as the white circles. The densest forest sites have potential direct insolation  $50\text{-}100\text{ MJ m}^{-2}\text{ month}^{-1}$  the majority is in the range of  $200\text{-}500\text{ MJ m}^{-2}\text{ month}^{-1}$  and the gaps and edges receive up to  $700\text{-}800\text{ MJ m}^{-2}\text{ month}^{-1}$ . These values range from

<5% to >50% potential insolation. The monthly shifts in intensity are relatively subtle, and high insolation areas remain largely in the same place. The conversion of DIRBEU-Mar to average  $T_{\max}$  from Dec-Mar shows the denser forests at 11-13°C and the open gaps and edges at 15-17°C. Monarchs were present (in November) in the area of 12.5-15°C Dec-Mar  $T_{\max}$ .

The wind exposure grids for Chincua (Fig.10) show the effects of edges and gaps as well. The brown background of ISFU (range 0.05-0.40) provides an overall measure of wind exposure from all directions. Each point has a unique wind profile. There are protected areas available in the grid under all wind directions, and the November monarch distribution tends to be in well sheltered areas, except for relatively high exposure to SW winds in the western portion. Note that the higher exposure of a gap can extend 25 meters in the downwind direction.

The partial grid at Pelon (Figs. 11 and 12) was much more open than either Chincua or La Mesa. A U-shaped zone of relatively dense forest (easiest to see in March) supported the actual clusters of butterflies during field visits in November and late February (but butterflies were more widely distributed than these areas). This zone has estimated Dec-Mar  $T_{\max}$  in the 11.5-13°C range, the same as the cluster sites at Chincua. The more open areas have estimated Dec-Mar  $T_{\max}$  >15°C. Wind exposure varies with wind direction, but note that the sites within the denser U-shaped zone are relatively well protected from most directions.

The grid at La Mesa (Figs. 13 and 14) had similar characteristics to that at Chincua, with two prominent gaps. The cluster sites noted from 2003-2004 were in the range 11.5-13°C, as at Zapatero.

The interpretation of wind exposure must account for prevailing wind directions. Hourly wind speed and directions for the season show the highest wind speeds (4 m/s) from WSW through SSE, with another peak around E (3 m/s). Pelon has the same maximum wind speeds, sharper peaks at E and W, and fewer higher S and SW winds. Further investigation of wind exposure should concentrate on those directions.

#### *Topoclimatic suitability map*

The topoclimatic suitability map was created from the following data from the monarch colony data set overlaid with the  $T_{\max}$ ,  $T_{\min}$ , and aspect (Table 7). Note that because the temperature predictions are based on differentials from  $T_{\text{base}}$ , the absolute value of those predictions does not affect the classification.

Table 7 Percentiles of environmental factors at monarch colonies (N=123)

Term	Mean	10%	90%
$T_{\max}$ (15°)	14.27°C	12.2°C	16.7°C
$T_{\min}$ (-10°)	-6.33°C	-5.45°C	-7.20°C
Aspect	216	102	317

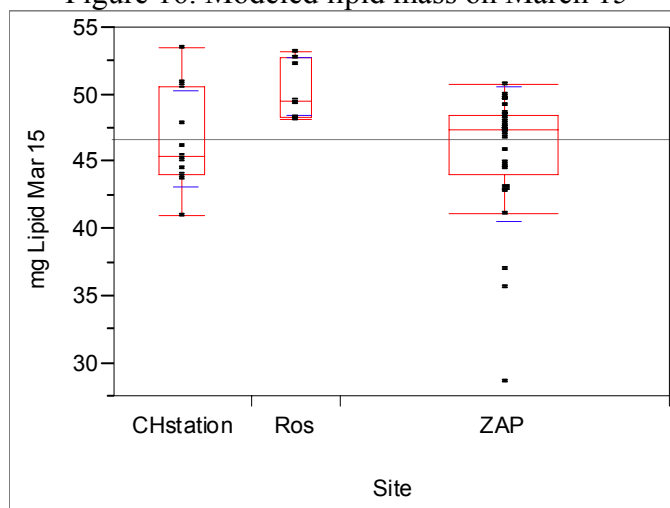
12,016 ha of predicted suitable habitat are distributed between 2517 and 3524 meters elevation. The highest elevations are too cold, and the lower elevations are too warm. The preference for southern and western aspects creates a more continuous belt on the western slopes of the Sierra Chincua and Sierra Campanario. Suitable habitat on the eastern slopes is more fragmented, and largely restricted to the south-facing slopes, because the preference for south-western aspects eliminates much of the intervening E and N-facing slopes. Note that predicted suitable habitat extends down many deep canyons below the main elevational belt.

The topoclimatic suitability maps assume that forest cover is not limiting. Incorporation of a forest cover map with appropriate cover classes (not currently available) will provide a final map of current potential habitat.

#### *Lipid loss rates*

Lipid remaining on March 15 at the ThermoChron sites varied from 53 mg to 29 mg with a mean of 47 mg (Fig. 16). Lipid mass of monarchs at the end of the overwintering season were estimated at 58 mg (Alonso-Mejia et al. 1997). Lipid masses were measured by the Brower team in 2004. The breakdown by sites shows that the lowest lipids were at Zapatero, at three sites that were on warm ridgetops in thin forest.

Figure 16. Modeled lipid mass on March 15



These estimates represent a monarch roosting in the understory all season long, and do not account for flight activity, exposure to direct sun, or variations of temperature with height. The sensitivity to overall increased temperature at three sites indicates that lipid mass decreases by 7 to 10 mg/°C. The largest effects were at the warmest ThermoChron (IB47, on an open south-facing ridgetop), because the rate of lipid loss is an exponential function of temperature. IB2 was on a mid-slope position within the November colony area, and IB59 was the coolest canyon bottom with intact forest, in an area occupied by the colony in March.

## Discussion

Overwintering monarch butterflies live on a climatic knife-edge between risks of freezing and exhausting lipid reserves before the end of the season in mid-March. Topoclimatic and microclimatic variability afford the butterflies a choice of temperature regimes across the landscape, according to elevation, local topography, and forest canopy cover. This study has quantified many of those temperature gradients, and has generated topoclimatic suitability maps into which local variability in canopy cover can be nested.

The effective temperature differentials across the topoclimatic and microclimatic factors in this study are summarized in Table 8. Topoclimatic factors are readily mapped from a DEM, but local canopy cover requires hemispherical photography, or a remotely sensed forest cover map at appropriate resolution. The combination of topoclimate and canopy microclimate will predicts air temperatures at shaded sites at ~ 2m height. The challenge is then to project to body temperature ( $T_{\text{body}}$ ) of monarchs clustering at various heights in the canopy, and at different positions within clusters.

The ground to crown gradient for dense and open stands differ during the day and night (Geiger 1965). Nighttime gradients are larger in thin forest because an inversion layer can develop as the ground is more exposed to the night sky, whereas in the dense forest, only the tree crowns are exposed and the ground cools less. Daytime gradients are larger in dense forest, because most insolation heats the tree crowns, little reaches the ground, and mixing is poor; whereas in the thin forest, air more freely mixes and reduces temperature differences.

$T_{\text{body}}$  is the same as  $T_{\text{air}}$  under complete cover in a dense forest, or the underside of clusters. ISFU necessarily gets greater on average as one ascends in the forest canopy, and will have a direct effect on  $T_{\text{body}}$  of exposed butterflies.  $T_{\text{body}}$  can be 4°C below  $T_{\text{air}}$  with complete sky exposure, such as on the upper side of a cluster high in the canopy (Anderson and Brower 1996).

$T_{\text{body}}$  of butterflies in direct sun can be as great as 10°C above ambient when in optimal basking posture, and less than 3°C when in heat avoidance posture (Masters et al. 1988). Exposure to direct sun, in addition to higher  $T_{\text{max}}$  in open forests, can drive lipid depletion to unacceptable levels.

Table 8. Temperature differentials

Term	$T_{\text{max}}$	$T_{\text{min}}$	Butterfly
Elevation (500m)	4	2	--
Topographic position	3	2	--
Aspect	2	--	--
Slope	--	0.75	--
ISFU	4.5	0.5	4
DSFU	4.5	--	10
Ground-Crown Dense	+6	-1	
Ground-Crown Open	+1	+5	

All of these temperature differentials are additive, and can be assembled to assess freezing and lipid depletion risks in intact and thinned forests.

*Effects of  $T_{min}$ : Freezing risks*

Dry monarchs have 15% freezing mortality when  $T_{body} = -5^{\circ}\text{C}$ , 50% mortality at  $-8^{\circ}\text{C}$ , and 90% mortality at  $-11^{\circ}\text{C}$  (Anderson and Brower 1996). In 2004-2005, the extreme low at Chincua Station was  $-5^{\circ}\text{C}$ , with 315 hours  $< 0^{\circ}\text{C}$ . Extreme  $T_{min}$  within forests was  $-0.5^{\circ}\text{C}$  (one site), and  $0^{\circ}\text{C}$  at two others. The remainder of the sites had  $T_{min}$  extremes of  $0.5$ - $1.5^{\circ}\text{C}$ . However,  $T_{air}$  higher in the canopy in a dense forest may be  $1^{\circ}\text{C}$  cooler, and  $T_{body}$  an individual completely exposed to the night sky is  $4^{\circ}\text{C}$  cooler. Adding the cool extremes together and assuming  $-5^{\circ}\text{C}$  at Chincua Station on a calm night, estimated  $T_{body}$  of a completely exposed monarch in the tree crown is  $-4.5^{\circ}\text{C}$ . On calm clear nights, the forest is a more effective blanket, so  $\Delta T_{min}$  at 2 m height is around  $2^{\circ}\text{C}$  warmer relative to  $T_{base}$ , but there may be greater differences with height. Quantification of height gradients in open and closed forests is a future research priority. Extreme  $T_{min}$  in the MBBR is approximately  $-10^{\circ}\text{C}$ , so even in the most sheltered forest canopies, dry monarchs may be at freezing risk during these extremes. If monarchs are wet,  $T_{body}$  of  $-4.5^{\circ}\text{C}$  presents a 70% mortality risk;  $-6^{\circ}\text{C}$  presents a 99% mortality risk.

Opening the forest canopy has three impacts on  $T_{body}$ , therefore – the direct effect on air temperature ( $-0.5^{\circ}\text{C}$  from ISFU 0.08 to 0.43, only on calm nights), the degree of temperature stratification, and the impact of sky exposure of individual monarchs ( $4.0^{\circ}\text{C}$ ). The mid-winter distribution of monarchs in thermal belts also reduces risks of freezing.

*Impacts of  $T_{max}$ : Lipid depletion, flight ability, and dehydration*

The effects of  $T_{max}$  on monarchs are twofold. First, high temperatures in shaded roosting sites increase resting metabolic rates, and deplete lipid reserves faster. If roosting sites are in direct sun, monarch body temperatures can be  $3$ - $10^{\circ}\text{C}$  above air, depending on basking posture. Sunlit clusters may rapidly reach unacceptably high temperatures, and monarchs react by taking flight, which cools them down but also is energetically expensive, and moving to new roost sites that are acceptably cool. On the opposite end, monarchs require  $> 12.8^{\circ}\text{C}$  ambient air temperatures in the shade to allow for flight, but only after shivering which is energetically expensive (Masters et al. 1988), so if monarchs settle in too cool a spot, they are essentially trapped for long time periods. This problem likely restricts large aggregations of butterflies on N-facing slopes. Higher temperatures also reduce relative humidity and increase vapor saturation deficits, which dehydrates monarchs who then must fly to re-hydrate at water sources. Monarchs tend to move downslope into more protected canyons near water sources in March, when air temperatures and insolation are on the increase in most years.

A thinned forest creates warmer air temperatures throughout the lower canopy; a forest with ISFU of 0.25 will be  $1^{\circ}\text{C}$  warmer during the day on average than one with ISFU of 0.10. Thinning also increases the likelihood that monarch clusters will be in direct sun. Butterflies will tend to leave such sites, and accumulate in cooler, denser forests. This movement will also indirectly provide more shelter from nighttime lows.

### *Wind*

With maximum mean hourly wind speeds of 3-4 m/s, wind did not appear to be a significant stress in 2004-2005. Monarchs leave California sites when wind at ground level in the forest reaches 2 m/s (Leong 1990a, Leong and Frey 1991). Winter storm winds in California regularly exceed 10 m/s in the open, and monarchs were sensitive to WSF >0.4 at Andrew Molera State Park (Weiss and Luth 2002). Wind direction in Mexico is likely to be most important when combined with rain, which wets butterflies and makes them more vulnerable to freezing. Anderson and Brower (1996) report rain and wind approaching from the NE, but SW can also be an important rain direction. The lack of storms in 2004-2005 did not allow for detailed investigation of wind dynamics during rainfall/snowfall events.

One example of potential wind impacts comes from Mil Cumbres (Fig. 8E). This photo, taken in February, was directly beneath a tree with thousands of dead butterflies at its base – monarchs had occupied the site in November, but had left in December (I. Ramirez pers. comm.). The area to the north was logged recently, which opened the canopy and greatly increased wind exposure from that direction, especially higher in the canopy. There were several periods in December when relatively high (>2 m/s) ENE winds brought low relative humidity (<30%), which may explain why the butterflies left the site, but more investigation of these phenomena is required.

### *Aspect*

The preference for more westerly aspects over easterly aspects may reflect the availability of late afternoon sun when monarchs choose roost sites at the end of the day, but this is speculation. On a broader scale, the high proportion of large colonies on the western slope of the Sierra Chincua, Sierra Campanario, and Cerro Pelon may reflect upward movements of warm air from the lowlands, but this mesoclimatic phenomenon has not been rigorously investigated.

### *Longer-term risks*

This study was necessarily restricted to one overwintering season, which was relatively mild. While the temperature differentials will likely not dramatically change, since they are based on principles of environmental biophysics, estimation of the annual risks of warm temperatures, freezing, and storm mortality will require examination of historical weather data, as well as continued monitoring at the base stations and selected Thermochron sites within the forest.

### *Conservation implications*

These results lead to the following conservation implications:

- 1) Topoclimatically suitable habitat in the absence of forest disturbance extends across ~12,000 ha. This will shrink if climate change leads to warmer temperatures as the suitable zone moves upslope.
- 2) Forest thinning increases daytime temperatures by increasing direct insolation, which will drive faster lipid depletion and reduce relative humidity. Because of air circulation

within the understory, it may require only a fraction of the forest to be opened to affect adjacent closed canopy areas.

3) Forest thinning can reduce nighttime minima, especially on calm, clear nights, and increases the sky exposure of monarchs in addition to effects on air temperature.

4) Except in the densest forests, there will be some periods of direct light in the understory that can provide a window for flight even if air temperatures remain too cool for flight.

5) Protection of closed canopy stands, and restoration of thinned forest will be necessary for long-term habitat requirements.

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