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Dynamics and trends of overwintering colonies of the monarch butterfly in Mexico

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ABSTRACT

There are two breeding migratory populations of the monarch butterfly (*Danaus plexippus*) in North America. A comparatively small, Western population migrates from states west of the Rocky Mountains to California, and a large Eastern population migrates from southern Canada and the United States to central Mexico. We monitored the dynamics and trends of monarch overwintering colonies in Mexico from the 2004–2005 to the 2013–2014 seasons. Of 19 colonies, 14 were inside the Monarch Butterfly Biosphere Reserve and five were outside the reserve. The number of colonies with butterflies varied among years, and in only three colonies were butterflies consistently present in all seasons. The total cumulative area of forest used by all monarch colonies in all seasons was 106.53 ha: 83.68% inside the reserve and 16.32% outside the reserve. By the 2013–2014 season, however, the surface occupied by monarchs (0.67 ha) had decreased 44% from the previous season, and is the smallest in two decades, far from the highest record of 18.19 ha in the 1996–1997 season. Extensive loss of breeding habitat by eradication of common milkweed (*Asclepias syriaca*, the primary food source for monarchs) from herbicide use and land-use changes in the United States, extreme climate conditions in Canada, the United States and Mexico, and deforestation and forest degradation in overwintering sites in Mexico all contributed to the steady decline in the abundance of monarch butterflies. Unregulated tourism also has become a threat to the dwindling colonies in Mexico. Protection of overwintering sites in Mexico is crucial to conserve this butterfly in North America. Given the rapid decline of monarch overwintering sites documented here, it is critical to initiate an immediate and concerted effort to protect and restore habitat along the migratory routes in the three countries.

"It was then that she realized that the yellow butterflies preceded the appearances of Mauricio Babilonia."
[One Hundred Years of Solitude, Gabriel García Márquez, 1927–2014]

1. Introduction

Animal migrations are natural phenomena that often transcend national political boundaries. Effectively conserving migratory species therefore requires long-term policies and actions at both national and international level in order to protect feeding, breeding and migrating habitat within different territories. In the Northern Hemisphere in particular, transboundary animal migrations often cross the territories of developed and developing nations. The type and effectiveness of conservation strategies and management measures therefore usually differ largely among countries, and heavily depend on the social, economic and political challenges each country has.

As many of the most spectacular migrations around the world have either disappeared due to human activities or are in steep decline, protecting the abundance of migrants is the key to protecting the ecological importance of migration (Wilcove and Wikelski, 2008). As the number of migrants declines, so too do many of the most important ecological services associated with them. Strategies aiming at protecting a particular migratory species often also offer opportunities for protection of additional habitat and species, for example, through the establishment of biological corridors. Furthermore, many migratory species are charismatic, which provide the opportunity to engage and educate the public in long-term conservation efforts.

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Reversing the trends of population decline in migratory species cannot be accomplished by policies in one country alone. This is certainly the case of efforts to conserve the monarch butterfly (*Danaus plexippus*) in North America, which offers a useful example of the challenges to protect migratory species and their habitat.

The monarch butterfly is the best known of all North American butterflies and one of the most studied insects. There are numerous nonmigratory populations and isolated records of this butterfly from around the world, including in the Cook Islands, the Solomon's, New Caledonia, Samoa, New Zealand, Australia, New Guinea, Ceylon, India, Saudi Arabia, Morocco, the Azores, the Canary Islands, the British Islands, Portugal, Central America, South America and the Caribbean (e.g. Ackery and Vane-Wright, 1984; Dockx et al., 2004; McCormack, 2005; Zhan et al., 2014).

After genetic analyses of specimens from around the world, Zhan et al. (2014) uncovered the history of the monarch's evolutionary origin and global dispersal. They speculated that monarchs originated in the southern United States or northern Mexico, where they originally undertook a shorter-distance annual migration, and that three subsequent, independent dispersal events led to the monarch's current distribution (Zhan et al., 2014): (i) towards the south, monarchs expanded from Belize to Costa Rica and into South America, as well as offshore, from south Florida to Bermuda and Puerto Rico; (ii) westwards, they expanded into Hawaii and then to Samoa and Fiji, and to New Caledonia, Australia and New Zealand; and (iii) across the Atlantic, monarchs established first in Portugal and then moved to Spain and Morocco.

The bulk of the species, however, is found in North America where two breeding migratory populations are recognized. One small population (hereafter referred as to the Western population) travels some 500 km from states west of the Rocky Mountains to overwinter in more than 390 sites, mainly in eucalyptus (*Eucalyptus globulus*), Monterey pine (*Pinus radiata*) and cypress (*Cupressus macrocarpa*) groves along the coast of California to as far south as Baja California in Mexico (Urquhart and Urquhart, 1977; Brower, 1995; Frey and Schaffner, 2004; Leong et al., 2004). The maximum number of overwintering monarchs for this population during a single season from 1990 to 2000 was estimated at 2,347,865 butterflies (Leong et al., 2004).

A much larger Eastern population travels over 4000 km from the Great Lakes region east of the Rocky Mountains in southern Canada and the United States to overwintering sites in central Mexico, performing the second longest migration of all known insects (Pence, 1998; Anderson, 2009). The overwintering sites of this population were discovered in Mexico in 1975 (Urquhart, 1976). Monarchs breed throughout the year in the Mexican states of Morelos, Guerrero, México, Oaxaca, Veracruz, San Luis Potosí, Chiapas, Michoacán, and Hidalgo, but the degree to which these local populations interbreed with the migratory butterflies is unknown (Commission for Environmental Cooperation, 2008). A nonmigratory population of monarch butterflies is also found throughout the year in southern Florida, which is genetically distinct from the other North American populations (Zhan et al., 2014), and they may have a significant influx of autumn migrants from the larger Eastern population (Altizer et al., 2000). Monarchs that overwintered in Mexico come from a wide breeding distribution spanning the northeastern coast of North America to western Texas (Flockhart et al., 2013), and about 50% were born in the central part (35°N–41°N) of eastern United States (Miller et al., 2012). Using distribution models generated from citizen scientist occurrence data and stable-carbon and -hydrogen isotope measurements, multi-generational colonization of monarch breeding grounds were tracked in eastern North America (Flockhart et al., 2013). Since the two populations form one genetic population, conservation of overwintering sites in Mexico is crucial to protect this butterfly in North America (Lyons et al., 2012).

Most of what is known of the ecology and population biology of the monarch butterfly comes from studies during the last six decades at its breeding areas in the United States (for a review see Oberhauser and Solensky, 2004). In spring, adult butterflies that have overwintered in Mexico migrate north and reproduce in Texas and states to the north and east. Their offspring then move farther north into much of the eastern half of the United States and southern Canada, where they produce two or three more generations (Cockrell et al., 1993; Pleasants and Oberhauser, 2012). Most adults that emerge after mid-August migrate from the summer breeding range to their wintering grounds in Mexico, where they remain until spring. In February and March, adult monarchs in Mexico mate before migrating back north to recolonize their United States breeding range (Brower and Malcom, 1991). Monarchs are reproductive as they move north. Females lay eggs on milkweeds as they migrate north–northeast through Mexico and the southern United States from late February through April (Perez and Tailor, 2004).

There are three primary threats to the monarch butterfly in its range in North America (Brower et al., 2011): deforestation and degradation of forest by illegal logging of overwintering sites in Mexico; widespread reduction of breeding habitat, particularly in the Corn Belt region of the United States due to land use changes and the decrease of this butterfly's main larval food plant (common milkweed, *Asclepias syriaca*) associated with the use of glyphosate and other herbicides; and periodic extreme weather conditions throughout its range during the year. These threats are correlational, and combined are responsible for the dramatic decline in the number of monarchs in the hibernation colonies in Mexico (Vidal et al., 2014). Efforts by Mexican authorities to protect the monarch overwintering sites from illegal logging, together with the decade-long financial support from Mexican and international philanthropists and businesses to create local alternative income generation and employment, has resulted in the decrease of large-scale illegal logging from 731 ha affected in 2005–2007 to 5.18 ha affected in 2014 (the great majority in the indigenous community San Felipe de los Alzati in Michoacán state). Small-scale logging, which was a growing concern until 2013 (Vidal et al., 2014), was halted in 2014.

Monarchs are listed as a species of special concern by Canada's Species at Risk Act since 2003. There is no special protected legal status at the federal level for monarchs or their habitat in the United States. In Mexico monarchs are protected by the Species at Risk Norm, but the (small) colonies outside the Monarch Butterfly Biosphere Reserve need further protection. In 2008, the reserve became a World Heritage site (UNESCO, 2008). That year the Commission for Environmental Cooperation, established as part of the 1994 North American Free Trade Agreement (NAFTA), endorsed the North American Monarch Conservation Plan (Commission for Environmental Cooperation, 2008). Canada, the United States and Mexico agreed to protect breeding, overwintering and migrating habitat in their territories. Limited trilateral actions have been achieved to date, however, and monarchs were not even mentioned in the commission's 2010–2015 strategic plan (Commission for Environmental Cooperation, 2010).

Here we report upon the dynamics and sizes of overwintering colonies of the Eastern population of the monarch butterfly, which includes areas inside and outside the reserve. We assessed sizes of the colonies for 10 seasons, from the 2004–2005 to the 2013–2014 seasons. We also evaluated the impact of deforestation and forest degradation on the monarch overwintering sites during the last decade. Finally, we compare our data with available information from 1976 to 2003 to assess trends in the abundance of the Eastern population of the monarch butterfly in North America.

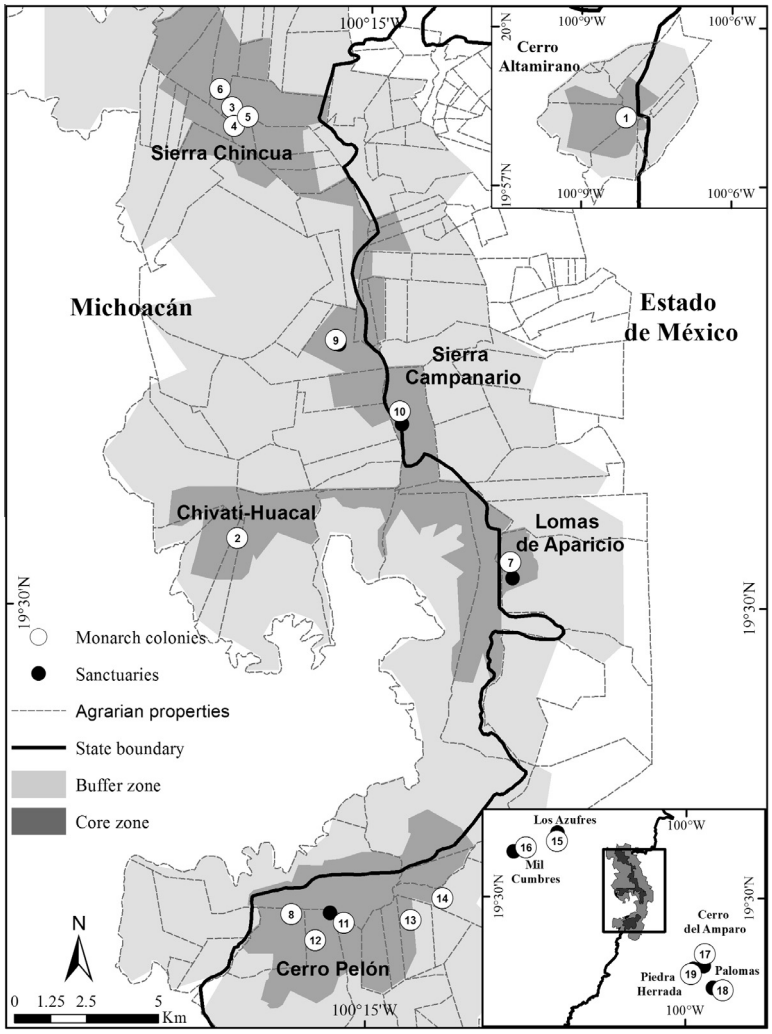

Fig. 1. Monarch sanctuaries and overwintering colonies inside and outside the monarch butterfly reserve. Numbers in circles refer to the names of colonies in Table 1.

2. Methods

2.1. Study area

In 2000, Mexico's federal government established the monarch reserve to protect 56,259 ha of forest along the mountains of the Trans-Mexican Volcanic Belt between the states of Michoacán and Estado de México. The reserve consists of 42,707 ha in two buffer zones and 13,552 ha in three core zones.

The three core zones contain the majority of the monarch's sanctuaries (Fig. 1, Vidal et al., 2014): a northern zone (558 ha) includes Cerro Altamirano; a central zone (9671 ha) includes Sierra de Chincua, Sierra El Campanario, and Cerro Chivatí-Huacal; and a southern zone (3339 ha) includes Cerro Pelón. The three core zones include parts of the land of 38 communities and are surrounded by two buffer zones that provide connectivity. In the core zone, logging permits on 17 properties were rescinded when the reserve was established.

Monarchs mostly formed their colonies on oyamel fir (*Abis religiosa*) and pine (*Pinus* spp., mostly *P. pseudostrobus*, associated with *P. montezumae*, *P. michoacana*, *P. tenuifolia*, and *P. leiophylla*), and occasionally on white cedar (*Cuppressus lindleyi*) and oak (*Quercus rugosa* and *Q. laurina*).

2.2. Identification and measure of butterfly colonies

In this paper a *colony* refers to one or more aggregations of clustering butterflies that were relatively close to each other and that over time exhibited a clear preference for a particular area of forest. A cluster is a well-defined aggregation of butterflies. All colonies were well established by the second half of December. We named each colony after the agrarian, state, federal or private property where the colony was located. Clustering butterflies from different years within the same property were considered the same colony.

There have been failing attempts to find additional monarch colonies from aerial surveys (Slayback and Brower, 2007; Slayback et al., 2007). A combination of our on-ground surveys with those aerial surveys provides a more comprehensive search for colonies. Every November from 2004 to 2013 we visited all sites where colonies of butterflies were historically recorded, a region located between 99°52′5.7″W, 19°05′24.82′N and 100°48′23.87″W, 19°05′49.35″N (Fig. 1). We began measuring the colonies in early December, and continued doing so every two weeks until the end of March. Data for the 2002–2003 and 2003–2004 seasons were collected in the second half of December by personnel of the monarch reserve and by one of us (E.R.-S.), respectively. A team of at least

four experienced individuals from the World Wildlife Fund (WWF) and the National Commission on Protected Areas (CONANP) of the Secretariat of the Environment and Natural Resources (SEMARNAT), accompanied by at least one local forest owner, collected the data for each colony.

We recorded the exact location (at center of the colony) and measured each colony by tracing a polygon containing the trees with the butterfly clusters in which the original vertex was the tree at the highest point of the slope, located with a Garmin eTrex H global positioning system in projection Universal Transverse Mercator System and datum World Geodesic System 84. That tree was referenced with a color plastic band. We recorded the geographical directions and distances among the peripheral trees (containing butterfly clusters) near to the original vertex with a Suunto KB-20 sighting compass and metric open reel fiberglass tape. Those trees were also referenced with color plastic bands.

With ArcGis 10.2 derive aspect function we also determined the slopes preferred by the butterfly colonies and defined eight categories of slope orientation: N (0–22.5°, 337.6–360°), NE (22.6–67.5°), E (67.6–112.5°), SE (112.6–157.5°), S (157.6–202.5°), SW (202.6–247.5°), W (247.6–292.5°), and NW (292.6–337.5°).

2.3. Data analysis

Estimating the numbers of monarch butterflies in the overwintering sites in Mexico is virtually impossible due to the compacted nature of their clusters and the complex architecture of the tree branches where they congregate. We used, therefore, the area of forest occupied by butterflies as an indirect indicator of their abundance. There have been attempts to quantify the density of monarch colonies (Calvert, 2004).

All data were recorded in Excel sheets. Using these data and the ArcView 3.3 geographic information system we estimated the surface occupied by each colony for each of eight bi-weekly measurements (1–14 December, 15–31 December, 1–14 January, 15–31 January, 1–14 February, 15–28 February, 1–14 March, and 15–31 March). We overlapped the data for each measurement for each colony with ArcGis (version 10.2) global information system (GIS) to map the dynamics of the colonies and their distribution in the forest each year, and throughout the 10 years of our study. The use of GIS allows the presentation of a temporal cartography to illustrate the changes on colony location along the study period.

In most years we selected the surface occupied by the colonies during the second part of December – when the colonies were essentially fully established – as an indicator of abundance of butterflies for the season. Exceptions were 2004 (we measured the colonies in 1–14 December) in colonies Cerro Prieto, San Mateo Almomoloa, and San Antonio Albarranes; 2005 and 2007 (1–14 January) in colony Río de Parras; 2008 (1–14 January) in colony Carpinteros; and 2012 (1–14 January) in colony San Antonio Albarranes.

We overlapped the locations of the monarch colonies we recorded in the last decade, with the forest affected by illegal logging in the same period, to show the impact on the habitat of the butterfly colonies (online Appendixes 1 and 2).

3. Results

3.1. Habitat use and spatial dynamics of colonies

Every year, from the 2004–2005 to the 2013–2014 season, monarchs usually arrived at the overwintering sites in late October-

Table 1
Size of 19 monarch butterfly overwintering colonies from 2004–2005 to 2013–2014.

Location	State	Sanctuary	Colony (property)	Surface (ha)per season in second half of December									
				2004	2005	2006	2007	2008	2009	2010	2011	2012	2013
Inside monarch reserve	Michoacán	Cerro Altamirano	E. Contepec	–[a]	–[a]	0.09	–[a]	0.01	–[a]	–[a]	–[a]	–[a]	–[a]
		Chivatí-Huacal	I. C. Carpinteros	–[a]	0.10	0.39	0.06	0.17	0.29	0.35	0.20	–[a]	0.01
		Sierra Chincua	Federal property	0.20	–[a]	–[a]	–[a]	0.47	–[a]	–[a]	–[a]	–[a]	–[a]
			State property	–[a]	0.57	1.34	–[a]	0.53	–[a]	–[a]	–[a]	0.18	–[a]
			E. Cerro Prieto	–[a]	–[a]	–[a]	0.29	–[a]	0.47	–[a]	0.27	–[a]	0.02
			E. El Calabozo Fracción I	–[a]	–[a]	–[a]	–[a]	0.59	–[a]	0.44	–[a]	–[a]	–[a]
		Lomas de Aparicio	I. C. Crescencio Morales	0.10	0.46	0.16	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]
	Estado de México	Cerro Pelón	E. Nicolás Romero	–[a]	–[a]	–[a]	–[a]	0.38	–[a]	0.56	0.17	0.03	–[a]
		Sierra	E. El Rosario	1.06	1.23	2.49	1.48	2.37	0.50	1.74	1.37	0.63	0.52
		Campanario	E. La Mesa	–[a]	0.22	0.61	0.33	–[a]	–[a]	–[a]	–[a]	0.03	–[a]
		Cerro Pelón	I. C. San Juan Xoconusco	–[a]	1.92	0.98	0.43	–[a]	–[a]	–[a]	0.36	–[a]	–[a]
			E. El Capulín	0.24	0.08	–[a]	0.25	–[a]	0.53	–[a]	–[a]	–[a]	0.03
			E. Mesas Altas de Xoconusco	–[b]	–[b]	–[b]	0.38	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]
			I. C. San Pablo Malacatepec	–[b]	–[b]	–[b]	–[b]	–[b]	–[b]	–[b]	–[b]	0.06	0.04
Occupation inside monarch reserve				1.60	4.58	6.06	3.22	4.52	1.79	3.09	2.37	0.93	0.62
Outside monarch reserve	Michoacán	Los Azufres	P. P. San Andrés	–[a]	0.22		0.31	0.03	0.04	0.10	0.10	0.01	–[a]
		Mil Cumbres	E. Río de Parras	–[a]	0.28	0.07	0.27	0.13	–[a]	0.28	0.04	–[a]	–[a]
	Estado de México	Cerro del Amparo	E. San Francisco Oxtotilpan	0.10	0.11	0.10	–[a]	0.01	–[a]	0.10	0.05	0.02	–[a]
		Palomas	E. San Antonio Albarranes	0.35	0.56	0.17	0.40	0.19	0.03	0.20	0.19	0.11	0.02
		Piedra Herrada	E. San Mateo Almomoloa	0.14	0.17	0.27	0.41	0.18	0.06	0.25	0.14	0.12	0.03
Occupation outside monarch reserve				0.59	1.34	0.61	1.39	0.54	0.13	0.93	0.52	0.26	0.05
Total occupation per season				2.19	5.92	6.67	4.61	5.06	1.92	4.02	2.89	1.19	0.67
Number of colonies				7	12	11	11	12	7	9	10	9	7

E = ejido, I. C. = indigenous community, P. P. = private property.
[a] No monarch butterfly colony present in second half of December.
[b] No monarch butterfly colony recorded before.

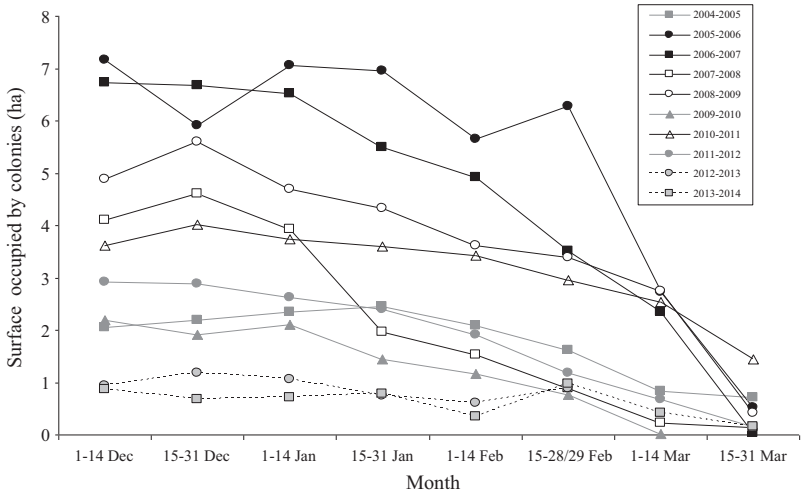

Fig. 2. Size and dynamics of the monarch butterfly overwintering colonies from the 2004–2005 to the 2013–2014 seasons.

early November, and departed in late March-early April (with the notable exceptions of the 2012–2013 and 2013–2014 seasons when they arrived in early December) (Table 1 and Fig. 2). After arriving the butterflies rested on tree branches. In December they began forming colonies with well-defined aggregations (clusters). Colonies were well established by the second half of December (see Table 2 for exact location of all colonies), when monarchs perched on tree trunks, indicating that the colonies will stay in that area. The area of forest occupied by butterflies decreased from the second half of December, when the colonies were fully established, until the first half of February when the clusters and colonies were more dispersed.

The larger the colonies, the more compacted the butterflies became. During our 10 overwintering seasons the colonies remained in the higher areas in the mountains, where they had been established, and from there the butterflies began their migration north.

The number of colonies with butterflies varied among years. For example, in the 2005–2006 season we visited 17 colonies and found butterflies in 12, while in the 2012–2013 season we visited 19 colonies and found butterflies in nine. We consistently found butterflies in all seasons in only three colonies, El Rosario, San Antonio Albarranes, and San Mateo Almomoloa (Table 1 and Fig. 3). In colony Carpinteros we found butterflies in all but two seasons, while in colony Mesas Altas de Xoconusco we found butterflies in only one season.

Of the 19 colonies we registered, 11 were located in Michoacán state (nine inside the reserve, two outside the reserve) and eight were located in Estado de México (five inside the reserve, three outside the reserve) (Tables 1 and 2, Fig. 1 and online Appendixes 1 and 2).

3.2. Space occupied by colonies

Although the area occupied by each and all colonies varied significantly over the last two decades, our data show a clear declining trend in the abundance of monarchs overwintering in Mexico, in particular during the last seven seasons (Fig. 4). By the 2013–2014 season the surface occupied by monarchs (0.67 ha) had decreased 44% from the previous season, and is the smallest in two decades, far from the highest record of 18.19 ha in the 1996–1997 season (Table 1 and Fig. 4). The largest colony we recorded was El Rosario, with 2.49 ha, and the smallest colonies were Contepec, San Francisco Oxtotilpan, San Andrés, and Carpinteros, with 0.01 ha each. Observations in the breeding grounds in the United States indicate that the surface occupied by monarchs in the hibernation sites in the 2014–2015 season is expected to increase at least twice compared to the 0.67 ha in the 2013–2014 season (Chip Taylor, Monarch Watch, personal communication, 30 September 2014).

The total cumulative area of forest used by monarchs in the 19 overwintering colonies during the last decade was 106.53 ha (Table 3): 89.15 ha (83.68%) were inside the monarch reserve and 17.38 ha (16.32%) were outside the reserve. Five colonies occupied 64% of the area within the reserve, El Rosario, the Michoacán state property, El Capulín, San Juan Xoconusco, and Cerro Prieto.

4. Discussion

4.1. Dynamics of monarch colonies

As noted above, not all colonies had butterflies in all 10 overwintering seasons. A similar pattern was documented for the Western monarch population in California. Of 331 monarch sites monitored there during 10 overwintering seasons (1990–2000), 136 had no winter aggregations of butterflies (Leong et al., 2004). The loss of these monarch habitats in California was attributed to loss of trees due to urban or agricultural development, diseases, selective cutting, storms, fires, and flooding. Furthermore, 11 of 88 monarch overwintering sites disappeared in Santa Barbara County in California in 1990–2000 due to agricultural, commercial, and municipal development (Frey and Schaffner, 2004).

Given that most (67%) of their colonies formed on the slopes in the SW quadrant, Calvert and Brower (1986) concluded that this location (which receives more insulation) satisfies the butterflies' requirements for flying and deter bird predators. Direct and indirect solar radiation, augmented by a SW exposure and favorable slope inclination, allows the butterflies to warm enough to fly when temperatures are below flight threshold. A similar correlation was found for the overwintering sites of the Western monarch population along the coast of California. Of 195 sites with roosting monarchs, 136 (79%) occurred on slopes with SW orientation, which provide optimal exposure to sunlight and possibly protection from wind (Leong et al., 2004). Our data from the Mexican overwintering sites support the butterflies' preference for the SW quadrant, but monarchs also concentrated in the W and NW quadrants.

Table 2
Geographical location of 19 overwintering colonies of the monarch butterfly (on 15–31 December) from the 2004–2005 to the 2013–2014 seasons.

Location	State	Sanctuary	Colony (property)	Geographical coordinates per season in second half of December																			
				2004		2005		2006		2007		2008		2009		2010		2011		2012		2013	
				N	W	N	W	N	W	N	W	N	W	N	W	N	W	N	W	N	W	N	W
Inside monarch reserve	Michoacán	Cerro Altamirano	E. Contepec	–[a]	–[a]	–[a]	–[a]	19°58′16.34″	100°08′07.20″	–[a]	–[a]	19°58′25.64″	100°07′52.59″	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]
		Chivatí-Huacal	I. C. Carpinteros	–[a]	–[a]	19°31′39.35″	100°18′02.13″	19°31′33.77″	100°18′02.83″	19°31′30.20″	100°17′56.65″	19°31′27.01″	100°18′02.02″	19°31′32.27″	100°17′56.58″	19°31′24.70″	100°17′58.80″	19°31′25.27″	100°18′02.54″	–[a]	–[a]	19°31′29.01″	100°17′58.28″
		Sierra Chincua	Federal property	19°40′41.09″	100°18′12.31″	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]	19°40′34.71″	100°18′08.79″	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]
			State property	–[a]	–[a]	19°40′18.35″	100°17′52.23″	19°40′32.67″	100°17′58.98″	–[a]	–[a]	19°40′30.34″	100°17′53.44″	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]	19°40′30.20″	100°17′49.43″	–[a]	–[a]
			E. Cerro Prieto	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]	19°40′02.74″	100°17′14.86″	–[a]	–[a]	19°40′20.24″	100°17′43.57″	–[a]	–[a]	19°40′27.85″	100°17′44.17″	–[a]	–[a]	19°40′22.11″	100°17′32.95″
			E. El Calabozo Fracción I	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]	19°41′07.64″	100°18′27.25″	–[a]	–[a]	19°41′08.92″	100°18′20.48″	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]
		Lomas de Aparicio	I. C. Crescencio Morales	19°30′28.45″	100°12′04.36″	19°30′30.31″	100°12′02.43″	19°30′36.15″	100°12′09.41″	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]
		Cerro Pelón	E. Nicolás Romero	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]	19°23′19.91″	100°16′40.96″	–[a]	–[a]	19°23′14.49″	100°16′39.64″	19°23′40.60″	100°16′32.03″	19°23′23.85″	100°16′22.17″	–[a]	–[a]
		Sierra	E. El Rosario	19°35′43.15″	100°15′44.36″	19°35′30.23″	100°15′46.21″	19°35′41.22″	100°15′45.65″	19°35′59.65″	100°15′48.98″	19°35′58.91″	100°15′48.09″	19°35′31.88″	100°15′48.52″	19°35′54.24″	100°15′47.09″	19°35′30.89″	100°15′45.29″	19°35′58.47″	100°15′48.59″	19°36′06.52″	100°15′43.71″
	Estado de México	Campanario	E. La Mesa	–[a]	–[a]	19°33′45.52″	100°14′14.39″	19°33′55.47″	100°14′31.31″	19°33′49.98″	100°14′05.47″	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]	19°34′10.37″	100°14′17.89″	–[a]	–[a]
		Cerro Pelón	I. C. San Juan Xoconusco	–[a]	–[a]	19°23′06.60″	100°15′32.90″	19°23′09.00″	100°15′32.46″	19°23′16.34″	100°15′36.29″	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]	19°23′21.67″	100°15′34.73″	–[a]	–[a]	–[a]	–[a]
			E. El Capulín	19°23′19.66″	100°16′15.40″	19°23′13.42″	100°16′05.92″	–[a]	–[a]	19°23′12.84″	100°16′16.84″	–[a]	–[a]	19°23′04.57″	100°16′11.67″	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]	19°23′17.55″	100°16′07.16″
			E. Mesas Altas de Xoconusco	–[b]	–[a]	–[b]	–[b]	–[b]	–[b]	19°23′17.45″	100°13′59.48″	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]	–[a]
			I. C. San Pablo Malacatepec	–[b]	–[a]	–[b]	–[b]	–[b]	–[b]	–[b]	–[b]	–[b]	–[b]	–[b]	–[b]	–[b]	–[b]	–[b]	–[b]	19°24′07.02″	100°13′47.38″	19°23′54.04″	100°13′51.47″
Outside monarch reserve	Michoacán	Los Azufres	P. P. San Andrés	–[a]	–[a]	19°47′17.92″	100°36′20.41″	–[a]	–[a]	19°46′57.99″	100°35′56.46″	19°47′08.71″	100°36′10.87″	19°47′01.25″	100°35′53.75″	19°47′10.95″	100°36′17.72″	19°47′04.99″	100°35′53.19″	19°47′09.66″	100°36′20.04″	–[a]	–[a]
		Mil Cumbres	E. Río de Parras	–[a]	–[a]	19°42′06.89″	100°48′45.06″	19°41′22.71″	100°48′39.93″	19°41′29.57″	100°48′27.51″	19°41′36.53″	100°48′24.86″	–[a]	–[a]	19°41′26.72″	100°48′34.21″	19°41′30.45″	100°48′28.88″	–[a]	–[a]	–[a]	–[a]
	Estado de México	Cerro del Amparo	E. San Francisco Oxtotilpan	19°11′50.77″	99°54′48.01″	19°11′50.98″	99°54′40.81″	19°11′50.49″	99°54′49.09″	–[a]	–[a]	19°11′50.07″	99°54′48.34″	–[a]	–[a]	19°11′42.06″	99°54′44.79″	19°11′47.37″	99°54′49.22″	19°11′52.16″	99°54′49.20″	–[a]	–[a]
		Palomas	E. San Antonio Albarranes	19°05′59.51″	99°52′09.74″	19°06′01.20″	99°52′11.41″	19°06′00.77″	99°52′16.53″	19°05′50.68″	99°52′09.63″	19°05′58.76″	99°52′10.99″	19°05′54.22″	99°52′07.50″	19°05′52.76″	99°52′09.33″	19°06′02.77″	99°52′15.76″	19°05′58.59″	99°52′12.37″	19°06′00.79″	99°52′09.35″
		Piedra Herrada	E. San Mateo Almomoloa	19°11′06.28″	99°57′41.45″	19°11′06.82″	99°57′43.82″	19°11′09.49″	99°57′45.44″	19°10′59.35″	99°57′43.17″	19°11′13.10″	99°57′25.57″	19°11′00.24″	99°57′42.03″	19°11′05.55″	99°57′45.03″	19°11′02.07″	99°57′44.49″	19°11′06.42″	99°57′41.57″	19°11′10.54″	99°57′37.17″

E = ejido, I. C. = indigenous community, P. P. = private property.
[a] No monarch butterfly colony present in second half of December.
[b] No monarch butterfly colony recorded before.

Table 3
Cumulative forest occupied by 19 overwintering colonies of monarch butterflies from the 2004–2005 to the 2013–2014 seasons.

	State	Sanctuary	Colony (agrarian property)	Surface (ha) 2004–2013
Inside monarch reserve	Michoacán	Cerro Altamirano	E. Contepec	0.38
		Chivati-Huacal	I. C. Carpinteros	3.77
		Sierra Chincua	Federal property	10.85
			State property	2.11
			E. Cerro Prieto	4.30
			E. El Calabozo Fracción 1	3.10
		Lomas de Aparicio	E. Crescencio Morales	1.89
		Cerro Pelón	E. Nicolás Romero	3.65
		Sierra Campanario	E. El Rosario	35.14
			E. La Mesa	3.91
			I. C. San Juan Xoconusco	7.28
	Estado de México	Cerro Pelón	E. El Capulín	10.15
			E. Mesas Altas de Xoconusco	2.18
			I. C. San Pablo Malacatepec	0.44
	Total occupation inside the monarch reserve			89.15
Outside monarch reserve	Michoacán	Los Azufres	P. P. San Andrés	2.21
		Cerro Garnica	E. Río de Parras	2.10
		Cerro del Amparo	E. San Francisco Oxtotilpan	1.21
	Estado de México	Palomas	E. San Antonio Albarranes	5.12
		Piedra Herrada	E. San Mateo Almomoloa	6.74
	Total occupation outside the monarch reserve			17.38
	Total occupation in the monarch region			106.53

E = ejido, I. C. = indigenous community, P. P. = private property.

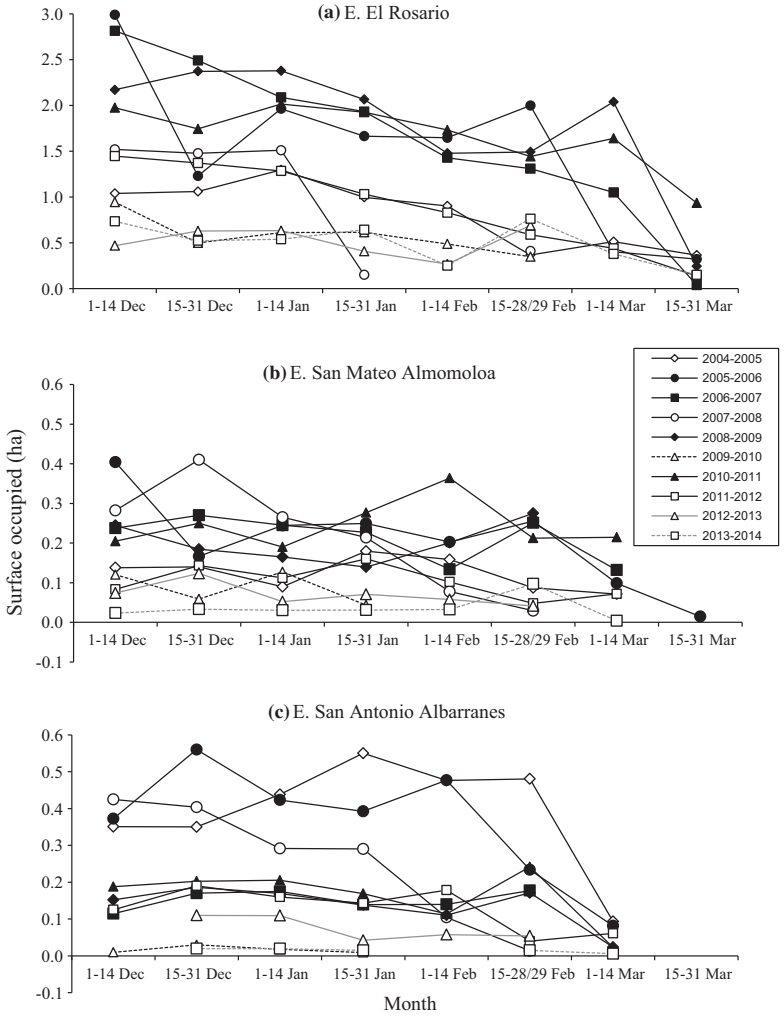

Fig. 3. Size of three monarch colonies (El Rosario, San Mateo Almomoloa, and San Antonio Albarranes) with butterflies present from the 2004–2005 to the 2013–2014 seasons.

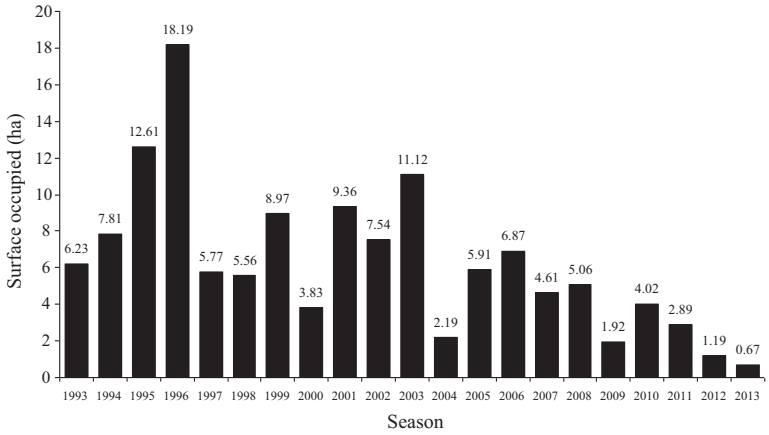

Fig. 4. Size of monarch butterfly colonies from the 1993–1994 to the 2013–2014 seasons. Data from 1993–1994 to 2001–2002 are from García-Serrano et al. (2004), and data for 2003–2004 and 2004–2005 to 2013–214 are from the authors.

In February, when the temperature increases, monarchs break the reproductive diapause, became more active, clusters break, colonies disperses, and mating begin (Calvert and Brower, 1986), which corresponds to our measurement on the second half of February. Those authors note that from mid-February colonies progressively move towards the lower areas in the mountains and from there they began the spring migration to the north in mid-March. However, during our 10 overwintering seasons the colonies did not move to the lower areas. Instead, monarchs departed directly from the high altitudes where they had established. We have no explanation for this, but note that as colonies became smaller they seem to prefer to establish and stay in higher areas. It is important to note that the area occupied by all colonies decreased over the last decade (Table 1 and Fig. 4).

4.2. Decline of monarch colonies

Brower et al. (2011) documented a statistically significant decline in the monarch butterfly colonies. Our data allowed us to document in detail the steady decline of the monarch colonies in the overwintering sites over the last decade, as well as to examine and describe for the first time the spatial and temporal dynamics of the colonies.

Calvert and Brower (1986) estimated the surface area occupied by "30" butterfly colonies between the 1976–1977 and 1981–1982 seasons, but their high number of colonies are an artifact of double counting (or more) several of the same colonies in different days and months in the same season. It is difficult to compare their study with ours with respect to the size of the colonies reported because they mapped very few colonies each year (only one colony in the 1976–1977 season), and measured them within a wide range of dates throughout their six wintering seasons. Nevertheless, the sizes of colonies reported by Calvert and Brower (1986) give an indication of the minimum abundance of butterflies during their study period.

García-Serrano et al. (2004) monitored monarch colonies from the 1993–1994 to the 2001–2002 seasons using a methodology similar to ours, and recorded 22 colonies (15 inside the reserve, seven outside the reserve). They compared their data with those from 1976–1977 to 1981–1982 (Calvert and Brower, 1986), but incorrectly chose the surface reported by Calvert and Brower (1986) for only a few colonies (just one colony – 1.5 ha – for the 1976–1977 season) and reported them as the "total" surface occupied during those seasons (E. García-Serrano, personal communication). There is an additional set of original field data, an unpublished undergraduate thesis by Mejía in 1996 (cited in García-Serrano et al., 2004), from the 1984–1985 to the 1990–1991 season.

4.3. Continuing threats

Threats to the monarch populations in North America are both abiotic and biotic. Based on a spatially structured, stochastic and density-dependent periodic projection matrix model that integrates patters of migratory connectivity and demographic vital rates across the annual cycle, Flockhart et al. (2014) concluded that the dramatic decline of monarchs has been caused by the reduction in milkweed in the United States due to the increase use of genetically modified crops and land-use change. Those authors concluded that reducing the negative effects of these host plants on the breeding grounds is therefore the top conservation priority to slow or halt population decline of monarchs in North America. After overlapping the locations of the monarch colonies with the forest affected by illegal logging in the last decade (Vidal et al., 2014), we demonstrated that the habitat of several butterfly colonies has been severely impacted (online Appendixes 1 and 2). The forests most affected were those in colonies Crescencio Morales (3.2 ha of forest affected), El Rosario (1.6 ha), Nicolás Romero (1 ha), La Mesa (0.9 ha), Cerro Prieto (0.8 ha), and San Juan Xoconusco (0.5 ha). In Crescencio Morales we had recorded monarchs in three consecutive seasons, but none have been recorded there since the 2007–2008 season because the forests they used to hibernate are gone (Vidal et al., 2014). We do not know whether the butterflies that abandoned Crescencio Morales or any other colonies relocated to other sites. In the 2007–2008 season, however, we found a new colony in Mesas Altas de Xoconusco (15 km from Crescencio Morales), and in 2012–2013 and 2013–2014 we found another new one in San Pablo Malacatepec (12.5 km from Crescencio Morales).

Extreme weather conditions are also a major threat to this butterfly throughout its range (Harvell et al., 2002; Oberhauser and Peterson, 2003; Batalden et al., 2007). One hundred fifteen ha of forest in the monarch reserve were affected by floods, strong winds, droughts, and fires from 2009 to 2011, and 29 ha more were affected by drought and parasitic plants in 2012 and 2013 (Vidal et al., 2014). In 2014, 2.81 ha more were degraded by drought. Severe rain, snow and freezing temperatures caused mass mortalities of monarchs in the overwintering sites, including a severe storm that killed an estimated 2.5 million butterflies in January 1981 (Calvert et al., 1983). Eighty-three percent of butterflies in colony San Mateo Almomoloa (reported as "Herrada") perished in 1992 due to extreme cold weather (Culotta, 1992). Storms and

extreme cold temperature in January 2002 (Brower et al., 2004), and in January 2004 were probably the cause of the reduced areas occupied by monarchs in the 2002–2003 and 2004–2005 seasons. We witnessed the devastation of colony El Rosario by the storm of January 2004, when only 1.06 ha were occupied by butterflies that season, compared with 2.49 ha in the 2006–2007 season. In December 1995, E.R.-S. observed the impact of a less intense storm in colony San Andrés which was particularly affected due to its smaller size and because it was located in an open area.

The numbers and behavior of visitors pose an additional threat to the monarch colonies. We often observed groups of tourists approaching the colonies too close. As a result, the butterfly clusters broke, the colonies dispersed and relocated to areas nearby. We repeatedly documented this in colonies that are open to tourists (Cerro Prieto, Sengio, El Rosario, El Capulín, La Mesa, and San Mateo Almomoloa) and in colonies not open to tourists (the federal property, and the Michoacán state property). Since monarchs apparently do not feed when they overwinter in Mexico, they depend on their lipid reserves (Rendón-Salinas, 1997; Alonzo-Mejía et al., 2007). When butterflies are disturbed regularly by tourists throughout the season, they are forced to fly more often and spend their energy reserves, which would affect their ability to migrate north.

4.4. Recommendations

Reversing the trend of population decline in the monarchs cannot be accomplished by policies and actions in one country alone. We believe that the three countries must re-energize efforts to conserve the Eastern and Western monarch populations.

As priorities for the United States and Canada we recommend (K. Oberhauser, personal communication): (i) support of state and federal agricultural conservation programs that protect and restore habitat for monarch foraging, breeding, and migration; (ii) decrease harmful effects of insecticides by improving integrated pest management practices, limiting the use of neonicotinoids, and by reducing off-target exposure (see Pleasants and Oberhauser, 2012); (iii) the provision of tools and guidelines to inform monarch conservation efforts (e.g. promoting mowing, burning, thinning, and harvesting regimes to restore ecosystem structure and species composition); and (iv) propagation of milkweed for increasing seed stock availability, and inclusion of species of milkweed native to the location being planted to restore habitat.

Priorities in Mexico should focus on (see also Vidal et al., 2014): (i) stopping permanently large-scale and small-scale illegal logging in the core zones and restore the habitat that has been degraded in the overwintering sites; (ii) compliance of tourist guides and visitors to stricter rules when visiting the reserve; (iii) increasing focused and coordinated action with regards to the payments for environmental services to local communities; and (iv) protecting the monarch reserve's buffer zones from unsustainable forest exploitation, fires, grazing, and agricultural expansion. Critical areas along monarch migratory corridors across Mexican states (e.g. Nuevo León, Coahuila, Tamaulipas, San Luis Potosí, and Querétaro) also need to be identified and protected.

The United States and Mexico share a wide array of habitats and species, including 450 species listed under the Convention on the International Trade in Endangered Species (CITES) and over 100 species on the U.S. Endangered Species list (Canada/Mexico/US Trilateral Committee for Wildlife and Ecosystem Conservation and Management, 2014; U.S. Fish & Wildlife Service, 2014). These include species of migratory mammals and birds, as well as native fish, amphibians, reptiles, and insects. Given that wildlife migrations to and from U.S. national parks have not been central to management policies, despite recognition that migrations are disappearing, a long-term migratory species initiative was recently recommended to the U.S. National Park System, which includes habitat conservation and restoration (Berger et al., 2014)

Successful examples of international action to protect migratory species in North America are, however, not common. A well-known, successful case is the recovery of the eastern North Pacific population of the gray whale (*Eschrichtius robustus*), which travels from feeding grounds in the Chukchi, Beaufort and the northwestern Bering Seas and along the coast of the United States and Canada, to the breeding and calving lagoons in the Baja California peninsula and the Gulf of California in Mexico (Findley and Vidal, 2002; Swartz et al., 2006). This population was almost exterminated by whalers in the 19th and 20th centuries, but is now believed to have reached its carrying capacity thanks to international cooperation.

Efforts to conserve the monarch butterfly and its habitat in North America offer a useful example of the challenges to protect migratory species and their habitat. Even though most flagship species have historically been large mammals, monarchs can be a powerful vehicle and a charismatic species to help educate and engage the public in conservation efforts (Guiney and Oberhauser, 2008).

5. Conclusions

Our data, collected systematically during 10 consecutive seasons, document the rapid decline of the overwintering colonies of the Eastern population of the monarch butterfly. The total cumulative area of forest (106.53 ha) used by all monarch colonies during the last decade is of the highest priority for conservation and restoration. Of utmost importance are the largest colonies El Rosario, the Michoacán state property, El Capulín, San Juan Xoconusco, and Cerro Prieto, where the bulk of the overwintering butterflies congregate. The colonies outside the reserve also warrant protection. The smaller the colonies become, the highest the risks of disappearing due to additional threats such as extreme climatic conditions, predation, diseases, and human disturbance.

Given the relatively high numbers of tourists visiting the butterfly colonies every year (Vidal et al., 2014), we believe it is urgent to improve the management of this industry to protect the butterflies and also to ensure that tourism-related activities continue providing important economic benefits to the communities. Monarch conservation and sustainable activities, such as well-planned tourism, should help improve local social and economic conditions, which in turn would contribute to the long-term protection of the monarch overwintering sites.

Ninety percent of monarchs overwintering in Mexico had fed as larvae on the common milkweed (Malcom et al., 1993). After 1999, increased production of genetically modified glyphosate-resistant soy and maize resulted in a significant reduction of milkweed and the loss of monarch breeding habitat in its eastern North American breeding range. Pleasants and Oberhauser (2012) estimate a 58% decline in milkweeds and an 81% decline in monarch production in the U.S. Midwest from 1999 to 2010, and conclude that a loss of agricultural milkweed is a major contributor to the Eastern monarch population decline. A similar decreasing pattern was documented in the overwintering sites of the Western population from 1997 to 2009, and the numbers of monarchs in California in the winter of 2009–2010 were the lowest on record (Jepsen et al., 2010). Climate change and deforestation have less influence on projected population declines of monarchs compared to the effects of milkweed declines on the breeding grounds (Flockhart et al., 2014), which contradicts the longtime advocated view that these butterflies were most vulnerable to deforestation and degradation of their hibernation sites (Brower et al., 2002, 2004). Conserving monarchs by addressing the negative impacts of land-use change and the use of genetically modified, herbicide-resistant

crops on milkweed abundance are therefore the highest conservation priority (Flockhart et al., 2014).

Twenty years ago, NAFTA was created with the aim of encouraging the free movement of goods and capital between Mexico, the United States, and Canada. Those countries choose the monarch butterfly as an emblem for their cooperation. Today, the monarch migration is an endangered biological phenomenon (Brower and Malcom, 1991). Only through an immediate, coordinated and well-funded effort that involve politicians, managers, scientists and the public to protect and restore habitat along its migratory route in the three countries, this dazzling natural wonder can be saved for this and for future generations.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2014.09.041.

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