THE INFLUENCE OF FOREST FRAGMENTATION ON THE LOCATION OF OVERWINTERING MONARCH BUTTERFLIES IN CENTRAL MEXICO

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ABSTRACT. The endangered status of the overwintering phenomenon of monarch butterflies (*Danaus plexippus* L., Lepidoptera, Nymphalidae, Danainae) that migrate from eastern North America to Mexico has resulted from anthropogenic degradation of the forests where the butterflies spend the winter. During their five month overwintering period, the monarchs need to remain inactive and clustered in semi-closed or intact forests to reduce mortalities caused by freezing, lipid depletion and predation. We analyzed forest and landscape metrics to determine the forest characteristics preferred by monarchs when colonizing their overwintering sites.

Forest metrics at two different spatial scales were derived from a forest cover map generated from multi-spectral IKONOS satellite imagery. Landscape metrics of forest areas occupied by monarch colonies during the 2002–2003 overwintering season were significantly different than randomly selected non-colony areas. Colony sites had greater forest cover (> 60%), though even these forest patches were fragmented and thinned. Immediate colony areas (100 m radial from colony center) exhibited greater forest coverage in more closely spaced patches than did extended colony areas (1 km radial from colony center). Forest degradation was more evident in the extended colony landscapes than the immediate colony areas. Though forests in many of the immediate colony areas appeared to have been thinned and selectively logged, most have a semi-closed canopy.

Conservation efforts should focus on protecting the forest canopy. Continued forest degradation is likely to increase mortality for the eastern North American population of monarch butterflies, and may cause extinction both of its migration and the spectacular overwintering phenomenon in Mexico.

Additional key words: butterfly site selection, forest quality, habitat degradation, FRAGSTATS, IKONOS satellite imagery, landscape metrics

The destination of the fall migration of North American monarch butterflies that breed east of the Rocky Mountains was discovered in January 1975 by cooperators of Urquhart and Urquhart (1976, 1978). We now know that up to a billion butterflies migrate southward out of their nearly one million square mile breeding range (Brower, 1999a) and form overwintering colonies on approximately twelve separate densely forested mountain massifs in Central Mexico (Brower *et al*., 2002; Slayback *et al*., 2007). Recent data indicate that the colonies are astoundingly dense, with up to 50 million butterflies per hectare (Brower *et al*., 2004). The overwintering period lasts from November through March and is a unique biological phenomenon (Brower and Malcolm, 1991). Butterflies en route to the overwintering grounds can be up to four generations removed from their migrating ancestors, and frequently return to the same areas of trees as did their predecessors (Brower, 1986). The individual monarchs that survive the overwintering season return to the Gulf Coast states in early to mid-March when their larval food source, milkweed, is again available (Malcolm, 1993).

All known overwintering sites in Mexico occur in the states of Michoaçan and Mexico, within an area of approximately 10,000 km² (Brower *et al*., 2002; Bojórquez-Tapia *et al*., 2003). This area, part of which is shown in Fig. 1, is in the central part of the Neo-Transvolcanic belt that crosses Mexico just south of the Tropic of Cancer (Brower, 1995). Monarchs colonize in dense, protective, semi-closed oyamel fir forests (*Abies religiosa* H.B.K., Pinaceae) in order to conserve energy and avoid freezing and desiccation during the winter months (Masters *et al*., 1988; Weiss *et al*., 1991; Alonso-Mejia *et al*., 1997). Presumably, after the last glacial retreat, these oyamel forests retreated to the higher peaks in this area (Slayback *et al*., 2007) and are now restricted to elevations ranging from 2700 m to 3400 m and occur within the summer cloud belt (Brower, 1995). The oyamel forest micro-climate protects the butterflies from severe warm and freezing weather, and also from wind and desiccation. The cool temperature that is moderated by the high altitude forest canopy limits butterfly activity, thereby conserving their lipid reserves. The extreme concentration of the monarchs in so few small areas during the overwintering season makes the entire Eastern North American population vulnerable to minor perturbations to the forest system (Brower, 1977; Brower and Malcolm, 1991; Malcolm, 1993).

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Over the last few decades prior to 1986, forest degradation increased in and near critical monarch colony sites, primarily from logging for domestic or commercial use and clearance for cattle grazing or agriculture (Snook, 1993). Neither a 1986 presidential decree nor the 2000 Monarch Butterfly Biosphere Reserve (MBBR) (Fig. 1) has protected the colony sites from ascendant illegal logging. Destruction of the forest continued after the 1986 decree due to ignorance and deliberate exploitation (Malcolm and Zalucki, 1993b; Brower et al., 2002). The current extent and increasing rate of forest degradation and fragmentation within and around the core overwintering sites is of great concern (Brower et al., 2002; Ramírez et al., 2003; Honey-Roses and Galindo, 2004; Anon., 2006). These destructive practices not only remove sections of the habitat by clear-cutting, but they also degrade the forest through thinning and selective logging. Reductions in tree canopy cover alter the forest micro-climate, increase both exposure and access by predators, and ultimately lead to a severe increase in butterfly mortality, especially during strong winter storms (Calvert et al., 1983; Fink et al., 1983; Brower and Calvert, 1985; Anderson and Brower, 1996; Bebi et al., 2001; Brower et al., 2004). Monarchs are also sensitive to small perturbations that allow more sunlight to penetrate their overwintering environment. This can warm the butterflies and cause more rapid burning of their lipid reserves, which can become critically low during the overwintering season (Alonso-Mejia et al., 1997). The loss and fragmentation of the forest has impacted many of the traditional colony sites, some of which have moved, while several others have disappeared altogether (L. Brower et al., unpublished data). Continued reductions in forest cover may soon negatively affect the entire overwintering North American monarch populations, both east and west of the Rocky Mountains (Calvert et al., 1983; Brower and Malcolm, 1991; Snook, 1993; Brower et al., 2002; Brower and Pyle, 2004).

As deforestation throughout the world continues to increase at alarming rates (Wilson, 2002), research into the ecological impacts caused by forest fragmentation on specific species has also increased. There are two primary components to fragmentation, total reduction of specific habitat types, and the reduction of habitat into small isolated patches (Meffe et al., 1997). Even slight perturbations to the quality of the habitat caused by initial fragmentation can affect the availability of resources for sensitive species using or living within the habitat area (Hargis et al., 1999; Ramírez et al., 2003; Ramirez et al., 2005).

Early habitat fragmentation studies concentrated on remnant habitat patches (Diamond, 1975; Verboom and Van Apeldoorn, 1990), while more recent studies have focused on the configuration of habitat patches (Hargis et al., 1999). Many fragmentation studies are consistent in stating that no single metric can be used to describe the response of a species to alterations in forest configuration (Haines-Young and Chopping, 1996; Gustafson, 1998; Hargis et al., 1999). The specific metrics, or combination of metrics, used to answer a particular research question need to be determined separately for each independent study. For example, Luoto et al. (2002) used a number of landscape metrics derived from satellite imagery, including habitat composition and largest patch size. They discovered that spatial variation of habitat (which was not originally considered a critical factor) is the dominant factor in determining the distribution of Clouded Apollo butterflies (Parnassius mnemosyne (Linnaeus), Papilionidae) in southwestern Finland.

Forest fragmentation can have a critical impact on the survival of the monarch butterflies (Calvert and Brower, 1981; Calvert et al., 1982; Weiss et al., 1991; Brower, 1999b; Ramírez et al., 2003). However, limited research has been conducted on the detailed forest requirements of colonizing monarchs at the landscape scale and, therefore, the full extent to which forest degradation affects the overwintering monarchs remains unknown.

We addressed two general research questions in this paper: (1) What are the forest fragmentation characteristics of monarch colony overwintering sites and how do they differ relative to non-colony sites? (2) How do characteristics of forests utilized by monarch colonies vary at two different spatial scales, one that is an immediate (100 m) and one that is an extended (1 km) radial area, as measured from the center of the colony?

The answers to these questions can help explain the relationship between forest degradation caused by human practices, i.e. clearcutting and thinning, and monarch colony locations. Answering these questions will also lead to a better understanding of the monarch's overwintering biology, which in turn should lead to more effective conservation efforts to prevent the loss of the monarch's migration and overwintering behavior that clearly has become a severely endangered biological phenomenon (Brower and Malcolm, 1991; Honey-Roses and Galindo, 2004).

METHODS

The study area. The general study area is the Monarch Butterfly Biosphere Reserve (MBBR) as decreed by Mexican President Ernest Zedillo (2002) and is located in central Mexico in the states of

Michoaçan and Mexico. Our primary study area was delineated by the extent of coverage of specific IKONOS satellite imagery (Fig. 1).

Colony and non-colony location data. A number of trained field personnel from the MBBR and Universidad Nacional Autónoma de México (UNAM) recorded the locations of monarch colonies (L. Brower, unpublished data) between 31 December 2002 and 8 January 2003. The team first conversed with local people to locate possible colonies and then traversed on foot through the forest to determine whether colonies were actually present. Colony locations were recorded
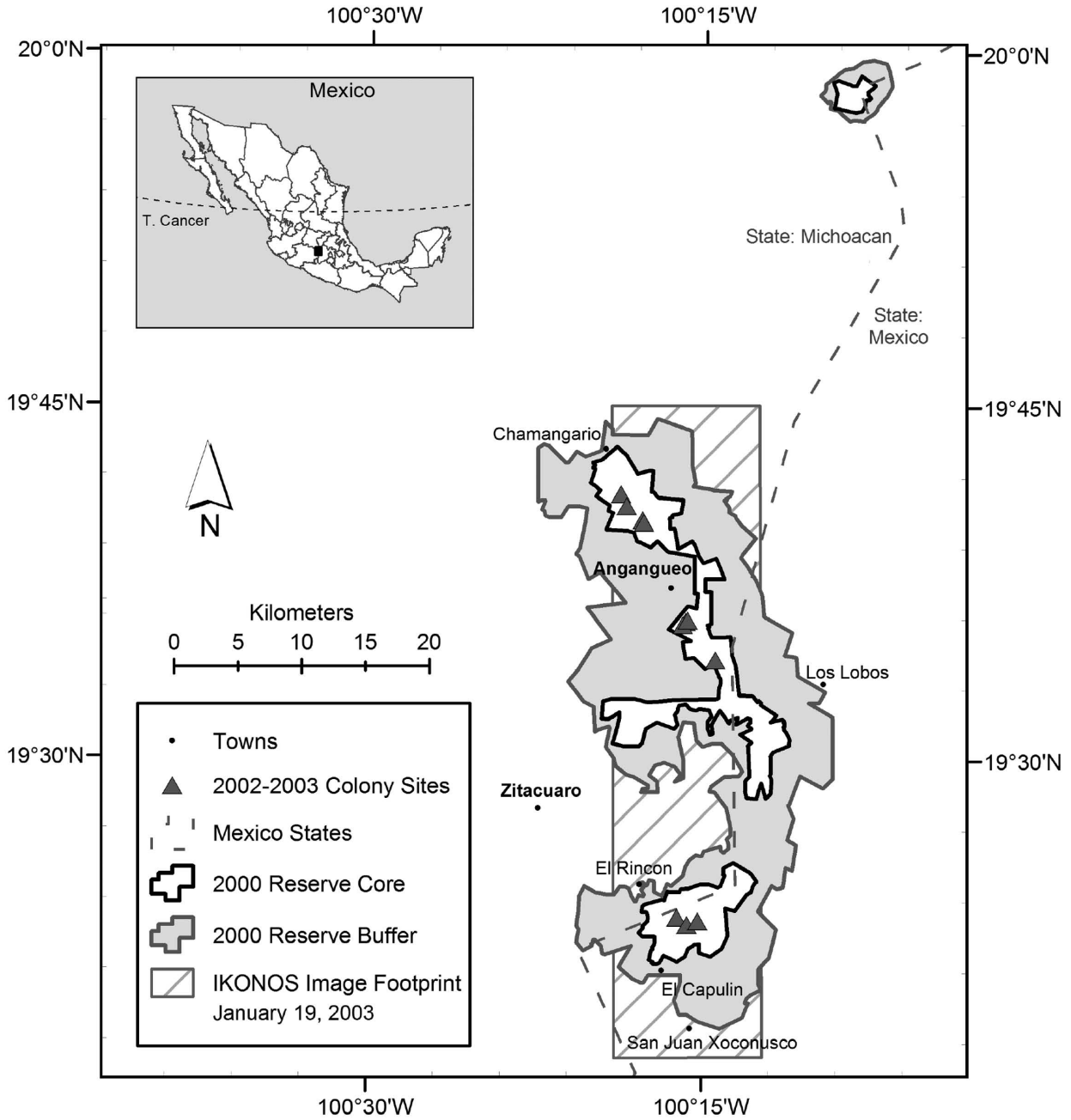

Figure 1. Location of the Monarch Butterfly Biosphere Reserve zones showing 11 overwintering sites located during the 2002–2003 season (the third black triangle from the top represents two sites and the fourth three).

using a Garmin Global Positioning System (GPS) with an estimated 5–15 m horizontal positional error. The error is a function of the instruments positional accuracy (Garmin, 2003) and a reduced signal caused by dense canopy cover.

To account for a broader range of forest conditions (Pereira and Itami, 1991), in addition to data from the 11 observed colony locations, we generated 33 random sample points, referred to as 'available' or likely non-colony points for the MBBR area. These non-colony locations may have been utilized by monarchs during the study period, but extensive aerial and field surveys during four subsequent overwintering seasons (Slayback *et al*., 2007; and Slayback and Brower, in press) indicated that no colonies were located at these sites.

Fine spatial resolution satellite data. IKONOS imagery has been used in many studies to map and classify land cover categories (Franklin *et al*., 2001; Song and Woodcock, 2002; Asner and Warner, 2003; Roberts *et al*., 2003; Thenkabail *et al*., 2004). The high spatial resolution (1 m) of the IKONOS panchromatic data enables individual plant canopies to be detected (Asner and Warner, 2003). IKONOS multi-spectral image data, with a nominal ground sampling distance of 4 m also has a very high spatial resolution by satellite image standards (Cablk and Minor, 2003), and provides information that can be utilized to separate subtle differences within cover types, such as tree cover, urban areas, or riparian zones (Goetz *et al*., 2003).

We acquired IKONOS panchromatic and multi-spectral imagery (11-bit radiometric quantization) of the Central Mexico study area for 13 January 2003, coinciding with the winter dry season for which the colony data were recorded. We ortho-rectified the IKONOS imagery to the UTM WGS84 coordinate system, using a digital elevation model based on a 12 m grid. The ortho-rectification procedure accounted for the extreme relief displacement in the study area and transformed the image so that it was planimetrically correct and therefore aligned to the monarch colony site locations. A scene-specific IKONOS rational polynomial coefficients (RPC) model was used in the ortho-rectification procedure to define the interior and exterior geometry of the sensor (Dial *et al*., 2003). The root mean square error of the ortho-rectification was approximately 2 pixels (or 8 m), based on 124 independent checkpoints.

We visually interpreted digital color imagery (2 m spatial resolution) produced by scanning color aerial photographs captured by Armando Peralta of UNAM in 2003, and IKONOS panchromatic imagery (1 m spatial resolution) captured by Space Imaging, Inc. in 2003, to identify canopy reference data points (randomly generated) as either open or closed forest. Sample data (1200 points) were randomly generated to achieve approximately one point per 50 hectares. Congalton (1991) suggested that at least 250 reference pixels are required to determine the mean accuracy to within + 5% (assuming an overall accuracy of 85%). Thus, we used three-quarters of the canopy reference data (900 points) to train the image classification processes, and the remaining one-quarter (300 points) to validate the output classification image.

We produced a map of forest and non-forest pixels using an expert classifier approach with inputs from supervised and unsupervised classification procedures, as well as by selecting class-boundary thresholds for spectral and spatial transform images (Stow *et al*., 2003). The fine 4 m spatial resolution of the IKONOS multi-spectral imagery enabled tree canopy cover and occasionally individual trees to be identified. To effectively distinguish tree canopy from shadow or agricultural vegetation, the expert classifier incorporated both IKONOS spectral band and image transform data, such as the normalized differential vegetation index (Read and Lam, 2002; Staus *et al*., 2002; Goetz *et al*., 2003; Chen *et al*., 2004), tasseled cap indices (Horne, 2003), and texture enhancement (Franklin *et al*., 2000; Franklin and Wulder, 2002). We integrated these image-based products into the ERDAS Knowledge Engineer software tool to produce a digital map consisting of forest and non-forest cover classes. We generalized this two-category map through the elimination of single pixels of a given class, so that forest fragmentation parameters could be extracted more effectively and efficiently. The accuracy of the classification was determined from 300 randomly generated points visually interpreted as forest or non-forest from the IKONOS panchromatic image and the aerial photographs. While image classification procedures were used to extract forest canopy patches, the canopy/non-canopy classification process and resultant map are referred to as forest and non-forest areas in this study, the more common terminology used in forest fragmentation studies.

Fragmentation analysis. To quantify the pattern of forest cover, we used FRAGSTATS version 3.3 (McGarigal *et al*., 2002) to create 250 landscape metrics, such as patch size, edge length, and patch density, from the forest and non-forest map. For those unfamiliar with the FRAGSTATS procedure and landscape metrics terminology, see Anon. (2007). The landscape metrics were calculated at the IKONOS pixel resolution (4 m) and extracted at two different scales, immediate colony (circle with 100 m radius) and extended colony (circle

with 1000 m radius) centered on the 11 monarch colony and 33 random non-colony sites (Fig. 2). The radial distance used to generate the immediate colony landscapes was determined from the average radial size of colonies (100 m) and the estimated penetration range of edge effects, such as changes to microclimate and predation rate (Chen and Franklin, 1990; Staus et al., 2002). The radial distance for the extended colony landscapes was based on the estimated active range of monarchs within the overwintering area. Research shows that most colonies are located within 1 km of a water source to and from which monarchs regularly fly (Calvert et al., 1983; Masters et al., 1988; Calvert and Lawton, 1993; Alonso-Mejia et al., 1998; Brower et al., unpublished data).

FRAGSTATS metrics were generated from the classified image representing forest cover (Fig. 3) at both the class-level (forest only) and landscape-level. Class-level metrics refer to the relationship between forest and non-forest pixels, while landscape-level metrics refer to the composition or configuration of forest and non-forest land within a specified area. Similar to the methods of Imbernon and Branthomme (2001), several steps were followed to select appropriate metrics. We generated a correlation matrix for all the landscape pattern metrics and removed redundant metrics where correlation values were greater than 0.8. Descriptive and inferential statistics were used to compare landscape pattern metrics for colony and non-colony ('available') sites. Based on interpretation of statistical boxplots, metrics with similar distributions for colony and non-colony forest areas were removed from further analysis, i.e., were deemed to have no explanatory power for colonization requirements. We
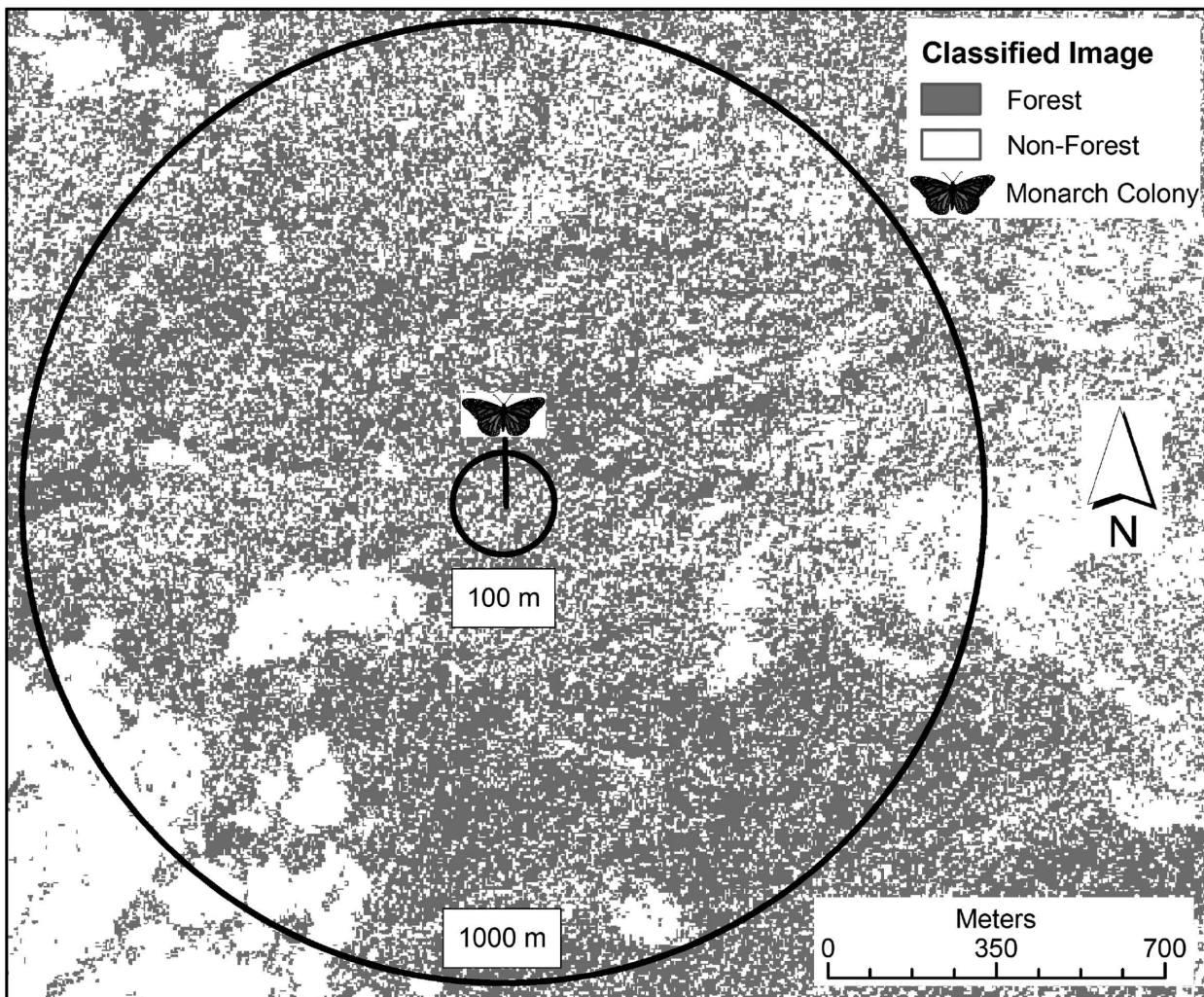

Figure 2. Concentric radial landscapes extend from the monarch colony centroid.
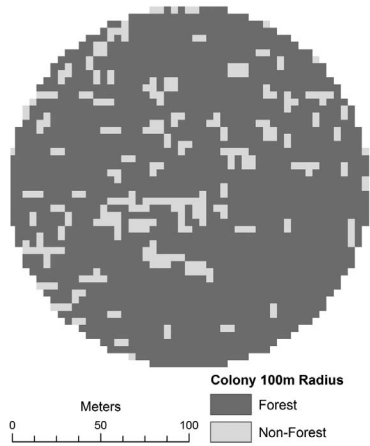
Figure 3. An example of colony areas at the immediate colony scale (100 m radius).

Figure 4. An example of non-colony areas at the immediate colony scale (100 m radius)

used the small sample Student's t-tests and one-sided unequal variance Welch's tests to compare the mean values of the colony and non-colony landscapes for the remaining metrics. Metrics showing no significant difference ($p > 0.05$) between the landscapes were removed. The final set of selected metrics indicated specific monarch colony habitat characteristics, and differentiated between colony and non-colony sites. The complete set of metrics used to quantify landscape pattern, structure and composition at both the single-class (forest) and multiple-class (forest and non-forest,
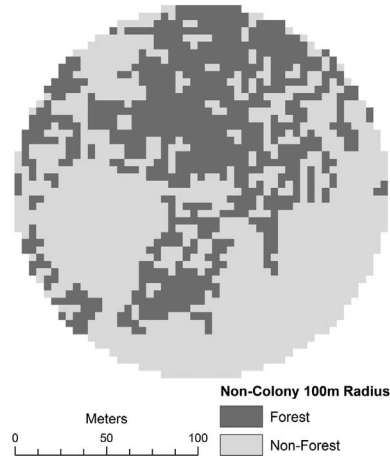
indicating landscape heterogeneity) are listed in Table 1 (for a detailed explanation of FRAGSTATS metrics, see Williams, 2005, Appendix D). Abbreviations for landscape metrics listed in Table 1 are provided within parentheses throughout the Results section.

We also used Student's t-tests to assess differences in landscape metrics for the immediate and extended colony areas. This was done to explore whether or not differences were evident in the spatial characteristics of forests required by the monarchs to colonize (immediate colony) and to fly to water sources

Table 1. Selected FRAGSTATS fragmentation metrics, (modified from McGarigal and Marks, 1994, p. 24).

Patch density and size metrics		**Core area metrics**	
PD	Patch Density (#/100 ha)	TCA	Total Core Area (ha)
PLAND	Percentage of Landscape (%)	CORE	Core Area
AREA	Patch Area Distribution	CAI	Core Area Index Distribution
		NDCA	Number of Disjunct Core Areas (#)
Edge metrics		DCAD	Disjunct Core Area Density (#/100 ha)
ED	Edge Density (m/ha)		
Shape metrics		**Isolation and proximity metrics**	
LSI	Landscape Shape Index	ENN	Euclidean Nearest Neighbor Distance
GYRATE	Radius of Gyration Distribution		Distribution
SHAPE	Shape Index Distribution		
		Contagion metrics	
FRAC	Fractal Dimension Index Distribution	AI	Aggregation Index (%)
CIRCLE	Related Circumscribing Circle Distribution	PLADJ	Percentage of Like Adjacencies (%)
CONTIG	Contiguity Index Distribution	**Diversity metrics**	
		PRD	Patch Richness Density (#/100 ha)
Connectivity metrics			
COHESION	Patch Cohesion Index		

(extended colony) during the 2002–2003 overwintering season.

The comparison of colony to non-colony areas was conducted in order to determine (1) whether specific forest characteristics affect where monarch colonies are located, or (2) whether colony locations are determined independently of forest characteristics, i.e. forest characteristics in colony and non-colony areas are not significantly different. The comparison of immediate and extended colony areas characterized the whole environment in which the monarchs reside and interact whilst overwintering, rather than just their colony site. This may indicate that for an area to be suitable for monarchs to colonize, the forest composition and configuration at both the immediate and extended scales must match the monarchs' forest requirements.

RESULTS

Classification accuracy. Overall classification accuracy values for the forest/non-forest map derived from IKONOS multi-spectral data were 92.3% and 88.6%, with kappa values of 0.847 and 0.766, when compared against reference data generated from visual interpretation of IKONOS panchromatic imagery and aerial photography, respectively. The kappa statistic incorporates omission and commission errors and corrects for chance agreement between reference and classified data (Jensen 1996, Lillesand and Kiefer 2000).

The average overall classification accuracy estimated with the two reference sets was 90.4% and the average kappa value was 0.806. For the forest category, user's (commission) accuracy values were 92.3% and 87.3%, and producer's (omission) accuracy values were 92.9% and 92.9%, based on IKONOS panchromatic imagery and aerial photography, respectively. For the non-forest category, user's (commission) accuracy values were 92.4% and 90.3%, and producer's (omission) accuracy values were 91.8% and 83.2%, based on IKONOS panchromatic imagery and aerial photography, respectively. All of these measures suggest that the forest cover map is a highly accurate representation of forest cover in 2003 and a reliable source for quantitatively assessing forest fragmentation.

Influence of forest fragmentation on colony locations. Examples of the more discriminatory landscape metrics, their distributions, and significance levels in relation to variations in colony and non-colony sites at the 100 m radial scale are shown in Table 2. Significance levels for all other metrics are listed in the text. At this scale, colony sites contained more forest (PLAND) in fewer patches (PD) than the non-colony sites. In addition the forest patches of the colony sites were more complex (FRAC 0.0332, TCA), elongated

(GYRATE 0.0374), and irregular in shape (SHAPE 0.0417). However, they were also less contiguous (CONTIG 0.0396) and aggregated (LSI, AI) than the non-colony sites. The aggregation index (AI) (approximately 73%) indicated that colony sites contained closely spaced patches, but in general, colony sites were less aggregated than non-colony sites. This may be due, in part, to aggregated non-forest patches at the non-colony sites. Despite high edge densities (ED) within colony sites, the high percentage of forest in combination with the close proximity of forest patches (AI) appears to provide habitat conditions suitable for monarch colonies (e.g., good canopy cover and protection). In some cases the negative effects of edge (or high edge density, ED), such as high predation, may be reduced or counter-acted by positive edge effects, such as slight increases in insolation, when patches are located in close proximity (Weiss *et al.*, 1991).

Examples of the more discriminatory landscape metrics at the 1 km radial scale are shown in Table 3. Colony landscapes contained smaller forest patches (AREA, ED 0.0042), which were more complex (FRAC), elongated (GYRATE), irregular in shape (SHAPE 0.0009), contained less core area (CORE 0.0005), and were higher in density (PD 0.0499), than the non-colony sites. The forest canopy in the extended colony landscape was more highly fragmented than the non-colony sites, there were fewer core areas (CORE 0.0005) and as a result, much of the forest area contained a high proportion of 'edge'. The forest patches in the colony landscapes were less contiguous (CONTIG), connected (COHESION 0.0418), and circular (CIRCLE 0.0111) than the non-colony landscapes, but were also less isolated (ENN). Low patch connectivity (COHESION) may indicate that when monarchs fly through the landscape they use both the forest and non-forest patches (Masters *et al.*, 1988). Shape complexity (SHAPE, GYRATE, FRAC 0.006) and associated edge density (PD) were higher for colony landscapes, but the patches were less isolated (ENN). However, there is no significant difference in the percentage of forest cover (PLAND 0.1717) between the colony and non-colony landscapes.

The top priority for monarchs seems to be the colonization of immediate sites that contain the greatest total forest cover even though many of these forest areas are fragmented and appear to be thinned.

Comparison of fragmentation at site and landscape scales. The monarchs seem to have different forest composition and configuration requirements for areas in which they colonize, than the more extensive areas in which they interact and move.

Table 2. Selected fragmentation metrics used to compare colony and non-colony sites at the 100 m radial scale.
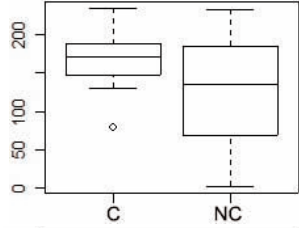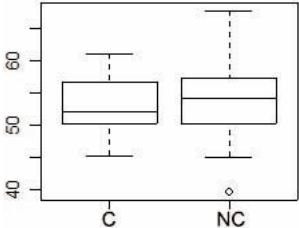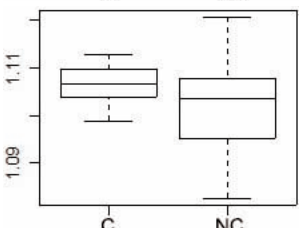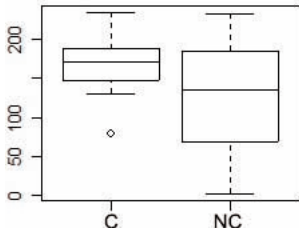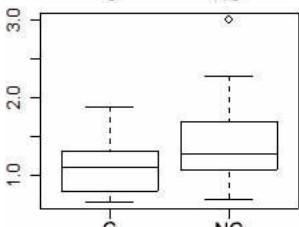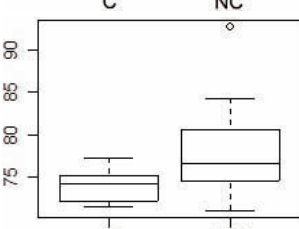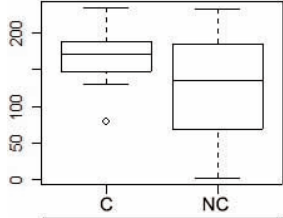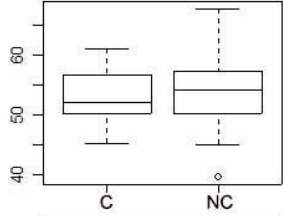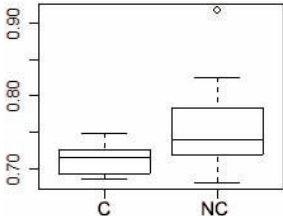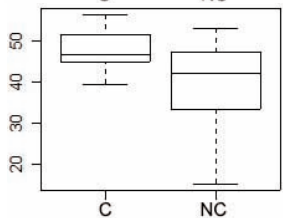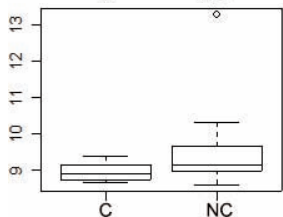
Landscape Metrics	T-test (2-tail)	Boxplot	Ecological interpretation of colony landscapes
Class Level (Forest Patches)			
Edge Density (ED)	0.0385		greater edge density
Patch Density (PD)	0.0413		fewer patches
Percentage of Landscape (Forest) (PLAND)	0.0455		greater forest cover
Landscape Level (Forest and Non-Forest patches, indicating landscape heterogeneity)			
Landscape Shape Index (LSI)	0.0242		less aggregated
Total Core Area (TCA)	0.0376		less core area
Aggregation Index (AI)	0.0374		less patch aggregation

C = Colony site, NC = Non-colony site
T-test significance difference < 0.05

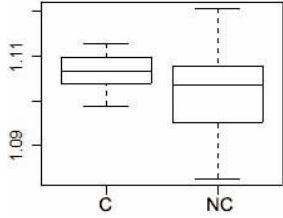Table 3. Selected fragmentation metrics used to compare colony and non-colony sites at the 1 km radial scale.

Landscape Metrics	T-test (2-tail)	Boxplot	Ecological interpretation of colony landscapes
Class Level (Forest Patches)			
Patch Area Distribution (AM)	0.0311		Landscape: Smaller patches
Radius of Gyration Distribution (AM)	0.0083		Patch: Less elongated and compact
Fractal Dimension Index Distribution (MN)	0.0007		Landscape: More complex and convoluted
Landscape Level (Forest and Non-Forest patches, indicating landscape heterogeneity)			
Contiguity Index Distribution (AM)	0.0006		Landscape: Less contiguous
Shape Index Distribution (AM)	0.0007		Patch: More irregular and complex
Euclidean Nearest Neighbor Distance Distribution (MN)	0.0068		Patch: Less isolation

Distribution metrics measure the aggregate properties of the patches: FRAGSTATS computes the following: (1) mean (MN), (2) area-weighted mean (AM), (3) median (MD), (4) range (RA), (5) standard deviation (SD), and (6) coefficient of variation (CV).
T-test significance difference < 0.05.

The metrics used for this analysis are summarized in Table 4.

In general, the immediate colony sites contained a greater percentage of forest cover (PLAND), had greater edge densities (ED), had more elongated (GYRATE), complex (FRAC), irregular (SHAPE), and less compact (CIRCLE) forest patches than the 1 km colony landscapes. However, they also had larger core areas (CORE) and were less isolated (ENN) than the extended colony landscapes. The immediate colony sites

Table 4. Comparison of landscape metrics between immediate and extended colony landscape scales.

	Landscape Metrics	T-test (2-tail)	Ecological Interpretation of Landscapes (immediate colony > or < extended colony)
Class-Level Metrics (Forest Patches)			
PLAND	Percentage Land Cover (Forest)	0.002	> percentage forest cover
ED	Edge Density	0.004	> edge density
GYRATE	Radius of Gyration Distribution (MN)	0.011	> elongation and compaction
SHAPE	Shape Index Distribution (MN)	0.000	> irregularity and complexity
FRAC	Fractal Dimension Index Distribution (MN)	0.011	> complexity and convolution
FRAC	Fractal Dimension Index Distribution (SD)	0.000	> heterogeneity in patch fractal dimensions
CIRCLE	Related Circumscribing Circle Distribution (MN)	0.017	< circularity and compaction
CORE	Core Area Index Distribution (MN)	0.036	> patch core area
ENN	Euclidean Nearest Neighbor Distance Distribution (MN)	0.019	< patch isolation
COHESION	Patch Cohesion Index	0.020	< connectivity and greater division
Landscape-Level (Forest and Non-Forest patches, indicating landscape heterogeneity)			
PD	Patch Density	0.006	> patch density
AREA	Patch Area Distribution (MN)	0.042	< patch size
GYRATE	Radius of Gyration Distribution (MN)	0.004	> elongation and compaction
GYRATE	Radius of Gyration Distribution (SD)	0.002	> uniformity in gyration
SHAPE	Shape Index Distribution (MN)	0.014	> irregularity and complexity
CORE	Core Area Index Distribution (MN)	0.009	> patch core area
CORE	Core Area Index Distribution (SD)	0.000	> heterogeneity in patch core area
COHESION	Patch Cohesion Index	0.000	< connectivity and greater division

Distribution metrics measure the aggregate properties of the patches: FRAGSTATS computes the following: (1) mean (MN), (2) area-weighted mean (AM), (3) median (MD), (4) range (RA), (5) standard deviation (SD), and (6) coefficient of variation (CV).

T-test significance difference < 0.05

also had less space between patches, which suggests that the extended colony landscapes were more open, possibly due to greater forest degradation. In general, the immediate colony sites contained forest patches that were greater in density and more complex, irregular and small in shape than the extended landscapes, suggesting that the immediate landscapes may have been more fragmented than the extended landscapes. Some landscape metrics (ED, PD and COHESION) suggest that the immediate colony landscapes were patchier than the extended sites. However, when combined with their greater total forest cover (PLAND), many of the immediate colony landscapes may actually be considered less fragmented. This suggests that forest patch composition should be assessed along with forest patch configuration to properly characterize forest fragmentation.

In addition to the significantly greater percentage of forest cover in immediate colony areas, the range of forest cover was different for the two spatial scales selected for fragmentation analysis (Table 5). The majority of the immediate colony sites had between 60% and 75% forest cover, while the majority of the extended colony landscapes had between 54% and 66% forest coverage. The 2002–2003 colony extended landscapes were more frequently associated with moderate forest cover than the immediate colony landscapes, suggesting that the monarchs utilized areas of forest in the extended landscapes that were somewhat fragmented or semi-open.

DISCUSSION

Reliability of the fragmentation analysis. The reliability of the fragmentation analysis was dependent on the accuracy of image georeferencing and classification procedures for the forest and non-forest pixels. This was challenging in a few areas, particularly for northwest facing slopes. However, the high average overall accuracy of 90.44% and a kappa value of 0.8064 for the image classification suggest that the satellite image-driven map of forest cover was suitable for fragmentation analysis.

Colony and non-colony forest characteristics. Certain forest configuration and composition characteristics of the colony sites and surrounding landscapes were significantly different than those of the randomly generated non-colony ('available') sites and landscapes. In general, the analysis suggests that the monarchs colonize areas containing at least 60% forest cover, with trees frequently arranged in closely packed, small irregular patches. However, as most of the MBBR has been subjected to some level of forest degradation and ongoing forest incursions (Snook, 1993; Brower *et al*., 2002; Ramírez *et al*., 2003; Honey-Roses and Galindo, 2004; Ramirez *et al*., 2005), many of the current overwintering sites may contain sub-optimum colonizing conditions and may have only represented the best forests available.

Forest characteristics of immediate and extended colony areas. The immediate and extended colony areas had significantly different forest configuration characteristics. Monarchs appear to have colonized the immediate sites that had the maximum amount of forest cover, provided that the location also had suitable environmental conditions such as close proximity to water (< 1 km), cool moist micro-climate, south-west facing slopes and an approximate elevation of 3000m (Bojórquez-Tapia *et al*., 2003). This is possibly because greater forest cover in the immediate colony sites enables larger numbers of monarchs to be supported on branches or trunks, and the higher the density of monarchs in the clusters, the greater protection afforded against weather and predators.

Differences in forest pattern or fragmentation between the two spatial scales of analysis may be related to actual differences in forest disturbances, deforestation practices, and/or total forest cover. The selective logging of larger trees may have occurred within the densely forested colony sites (Brower *et al*., 2002; Honey-Roses and Galindo, 2004), resulting in fragmented and closely spaced forest patches, as quantified by the landscape metrics (ED, COHESION

Table 5. Frequency distribution of forest cover (PLAND) for colony sites.

Colony Cover (%)	Cover Type	Minimum	1st Quartile	Mean	Median	3rd Quartile	Maximum
100 m radius	Forest	42.05	59.88	67.53	67.66	74.36	90.28
	Non-Forest	9.72	25.64	32.47	32.34	40.12	57.95
1 km radius	Forest	48.27	53.69	59.72	58.83	65.94	74.74
	Non-Forest	20.21	34.06	39.36	41.17	46.31	51.73

and PLAND) (Calvert *et al.*, 1983; Brower and Calvert, 1985; Anderson and Brower, 1996; Bebi *et al.*, 2001).

The most noteworthy statistical difference between the immediate and extended colony areas was the forest composition metric PLAND (percentage of forest cover). Forest cover was both greater within the immediate colony sites and more uniform (ENN) than in the extended colony landscapes. This suggests that the monarchs tended to colonize areas where forest canopy protection immediately surrounding their colony was the greatest and where evenly spaced forest patches in the extended landscape (used occasionally by the overwintering monarchs to fly out to find water or food) provided some forest protection to the immediate colony area (Calvert *et al.*, 1979; Masters *et al.*, 1988; Weiss *et al.*, 1991). Many of these immediate colony areas were fragmented and had been thinned (Honey-Roses and Galindo, 2004).

Colony forest fragmentation caused by forest degradation. The fragmentation of the forest caused by anthropogenic forest degradation or natural forest disturbances (e.g., fire or tree fall) could not be distinguished. However, the monarch colony fragmentation analysis was used to indicate or infer the impact that various disturbance and forest degradation practices may have had on the location of monarch colonies at two different scales.

The immediate colony sites contained a high percentage of forest (PLAND) in many closely spaced forest patches (AI, PD). If forest degradation had occurred in these sites, it was most likely to have been the result of forest thinning and selective logging practices (Honey-Roses and Galindo, 2004). In general, the extended colony landscapes were subject to more forest disturbance, degradation and deforestation than the immediate colony areas. Tree clearance practices seem to have been more common in the extended colony landscapes (Brower *et al.*, 2002; Honey-Roses and Galindo, 2004), as indicated by the simple forest patch shapes (GYRATE, FRAC, SHAPE, CIRCLE) and lower total percentage of forest cover (PLAND) than the 100 m landscapes. In addition, the high patch density (PD) and low isolation (ENN) of forest patches in the 1 km landscapes indicate that forest degradation caused by forest thinning or selective logging had also taken place in the remaining or remnant forest patches.

In general, deforestation seems to be more detrimental than forest thinning for the overwintering monarchs, if it occurs close to persistent colony sites, because it increases the impact of edge effects on the monarch colonies (Calvert and Brower 1981; Calvert *et al.*, 1981, 1982). However, forest thinning can also have a negative effect on the monarch colonies, as it decreases the protection afforded by the forest canopy. Though the monarchs may continue to colonize a site that has been subject to some forest thinning, this thinning may have adverse effects on the monarch colony population, such as reduced survival (Anderson and Brower, 1996). These effects have not been adequately studied and documented.

Despite widespread forest degradation, the MBBR is still able to provide some suitable habitat for monarchs to colonize. However, further forest degradation activity within the MBBR could negatively impact the colonizing monarchs (Alonso-Mejía *et al.*, 1993). Though logging is legally restricted in the MBBR buffer and supposedly prohibited in the MBBR core zones, extensive illegal logging and clear cutting activities continue. The effects that these activities have on the overwintering monarch colonies and population may not be fully understood, but clearly, the loss of forest or increased fragmentation of existing forest within the MBBR will produce a steady decrease in areas suitable for monarchs to colonize (Calvert and Brower, 1981; Brower, 1996, 1999b; Brower, 1999a; Ramírez *et al.*, 2003). The findings of this study provide a better understanding of the relationship of forest fragmentation and the locations used by monarchs to colonize throughout the overwintering season.

CONCLUSIONS.

The use of high resolution IKONOS imagery with 4 m spatial resolution allowed a unique, spatially-detailed assessment of forest fragmentation in this study and has enabled the habitat for overwintering monarch butterflies to be characterized in terms of forest patches and gaps within the forest canopy. As a result, the forest composition and configuration metrics were produced at a fine spatial scale, comparable to the scale at which the monarchs use and interact with the forest canopy. Forest characteristics govern forest micro-climate, the maintenance of which is critical to the winter survival of the monarchs. The more predictive landscape metrics may well be surrogates for micro-climate conditions, though this could not be verified in our study.

The research literature indicates that high levels of forest degradation in or near habitat traditionally used for colonization will result in fewer monarchs surviving the overwintering season (Calvert *et al.*, 1983; Fink *et al.*, 1983; Brower and Calvert, 1985; Anderson and Brower, 1996; Brower *et al.* 2004). This study increases the understanding of forest conditions required by monarchs to colonize and, as a result, may allow further insight into the parameters of forest degradation (such as opening of the canopy) that may have the greatest negative impact on overwintering monarch colonies.

Results from this study show that the monarchs colonize areas having specific composition and configuration of forest patches, as well as specific environmental conditions (Bojórquez-Tapia *et al.*, 2003). Both the immediate site and extended colony landscape scales should be considered when determining the effects of forest configuration and composition on the location of monarch colonies. The butterflies seem to require a combination of semi-closed protective forests to colonize and semi-open extended colony landscape to enable them to fly to water sources. Forest degradation is seen to have a mainly negative effect with respect to a forest area's suitability as a colony site, with low forest cover rather than forest patchiness appearing most detrimental to colonizing monarchs. This is because large openings in the forest canopy lead to increased exposure, freezing and monarch mortality, especially during storms (Anderson and Brower, 1996; Brower, 1996; Brower *et al.*, 2004). Information from this study also suggests that continued forest degradation in the MBBR will have a negative affect on overwintering monarchs as their colony locations change as the dry season progresses and also from year to year.

Several important research tasks need to be undertaken on overwintering monarchs. A coordinated method of ground searching and aerial reconnaissance (Slayback *et al.*, 2007) can provide a more complete colony location dataset, as well as a definite record of areas without colonies. These data will provide a better non-colony dataset than the randomly generated points used in this study. A multi-temporal image-based analysis of forest fragmentation for both colony and non-colony areas should also be undertaken. This could determine the total amount and spatial distribution of changes in forest cover that are occurring throughout the MBBR relative to the forests chosen by monarchs to colonize. The forest conditions required by the monarchs may or may not remain the same as winter progresses and the colonies move downhill closer to water sources. Colony location data that are based on tracking each colony throughout the overwintering season would provide a more in depth understanding of the monarchs forest requirements for their immediate colony landscape throughout the winter.

Acknowledgments

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