



# Effects of habitat fragmentation on the buffering capacity of edge environments in a seasonally dry tropical oak forest ecosystem in Oaxaca, Mexico

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## Abstract

The composition, structure, and disturbance dynamics of the native oak forests in seasonally dry tropical highland regions throughout the world have been drastically altered due to human land use. Edge environments are a dominant feature in these highly fragmented landscapes, and may directly influence the capacity of the vegetation to ameliorate microclimate conditions and support the successful regeneration of disturbed habitat. In this study, microclimate variables (surface soil moisture, photosynthetically active radiation and ground, surface and air temperatures) were assessed across edge gradients occurring between forest remnants and openings of different sizes (<0.1 and >1 ha) in both a highly fragmented landscape and a relatively undisturbed adjacent landscape over a 2-year period. Surface soil moistures increased progressively from the open areas (10.8–40.1 g m<sup>-3</sup>) into the forest understory (16.8–54.7 g m<sup>-3</sup>). The steepness of the edge gradient was less pronounced in the highly fragmented landscape (23.02 g m<sup>-3</sup>) compared to the reference landscape (29.34 g m<sup>-3</sup>). These results suggest that microsite variability across edges was reduced in this landscape in response to fragmentation. Further, the occurrence of an extreme drought event during the second year diminished differences between the fragmented and reference landscapes, thereby leading to greater homogeneity of the microclimate across the edge environments. Structural differences in forest patches within the fragmented landscape were also found to interact synergistically with habitat fragmentation to influence patterns in microclimate across edge environments. The capacity of oak forests to ameliorate the availability and flux of surface soil moisture in seasonally dry tropical ecosystems through their effect on evaporative moisture loss, and the reduction of this buffering capacity in response to habitat fragmentation documented in this study, suggests that fragmentation has significantly altered the temporal and spatial heterogeneity of microclimate conditions in these landscapes.

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## 1. Introduction

In human-dominated agricultural landscapes in tropical highland regions throughout the world, much of the original forest cover has been converted to crops

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and pastures, often under shifting-cultivation or semi-permanent land-use systems that create mosaics of agricultural land, secondary forest and primary forest patches (Gonzalez-Espinosa et al., 1991; Thomlinson et al., 1996; Sarmiento, 1997; Rao and Pant, 2000). At the landscape scale, a common effect of forest conversion from land use is the formation of edges and the modification of pre-existing edges. These edge environments are often sites of rapid change, especially when abrupt transitions occur between vegetation communities having distinct structures and compositions. Consequently, edges within landscape mosaics play a pivotal role in determining the spatial and temporal heterogeneity of microclimatic conditions, and therefore the structure and functioning of ecosystems at the landscape level (Forman and Godron, 1986). Environmental heterogeneity is of fundamental importance to controlling ecological functions related to biodiversity, nutrient cycling, hydrologic regulation, and productivity (e.g., Pickett et al., 1997).

Growing recognition in recent years that the unique qualities and effects of edge environments need to be considered when managing landscapes has led to increased interest by managers and researchers in understanding edge dynamics. Studies have documented changes in abiotic conditions across edge gradients, particularly light, temperature, and moisture (Geiger, 1957; Ranney et al., 1981; Canham, 1988; Kapos, 1989; Williams-Linera, 1990; Ashton, 1992; Liechty et al., 1992; Chen et al., 1993; Matlack, 1993; Young and Mitchell, 1994; Camargo and Kapos, 1995; Ehrenfeld et al., 1997; Williams-Linera et al., 1997). These differences in microclimate across edges are related to the effects of different surfaces (e.g., forest cover, grass cover, bare soil) on light absorption and reflection, heat fluxes, temperature, and evapotranspiration (e.g., Geiger, 1957; Lowry and Lowry, 1989). Other studies have assessed how edges influence the dynamics of vegetation communities (Ehrenfeld, 1980; Whitney and Runkle, 1981; Fraver, 1994; Matlack, 1994; Jose et al., 1996; Ferreira and Laurance, 1997; Williams-Linera et al., 1997; Burke and Nol, 1998; Gelhausen et al., 2000; Euskirchen et al., 2001). Another important area of study has focused on determining the depth of edge influence into the adjacent forest (Chen et al., 1995; Camargo and Kapos, 1995; Saunders et al., 1999; Zheng and Chen, 2000).

Although these studies have elucidated many important patterns of edge behavior and effects on microclimate in landscapes following disturbance, studies that have examined relations between edge environments and soil moisture have often yielded contradictory results. Some studies report higher moisture in openings (Minckler et al., 1973; Becker et al., 1988; Liechty et al., 1992; Veenendaal et al., 1995; Breshears et al., 1997a), others report higher moisture in the understory (Mladenoff, 1987; Ashton, 1992; Joffre and Rambal, 1988, 1993; McDonald et al., 2002), while one found no difference between open and understory locations (Orwig and Abrams, 1995). Part of this discrepancy may be explained by variation due to edge orientation (Chen et al., 1993), time of year (which may affect the balance between evapotranspiration, rainfall, and interception; Belsky et al., 1989), and differences in sampling depths (which often are not adequately reported in the literature). However, interactions between local climatic conditions and the particular biophysical characteristics of the landscape matrix may also be important. For example, most studies on edge effects on soil moisture were conducted in moist climates where forest cover is relatively dense and productivity is not severely limited by water. In these environments, higher levels of canopy interception, water uptake and evapotranspiration by deeply rooted trees in forested areas compared to areas where the forest cover had been removed would likely lead to lower soil moisture in the former (Liechty et al., 1992; Bréda et al., 1995). In contrast, our understanding of how edges influence microclimate and vegetation dynamics in seasonally dry climates supporting more open forest and woodland ecosystems occurring is limited, and is primarily based on studies conducted on individual tree effects rather than edges between different vegetation communities created by disturbance (e.g., Belsky et al., 1993; Joffre and Rambal, 1988, 1993; but see Breshears et al., 1997a). Some evidence suggests that in drier climates, the moderating effects of increased shade by forest cover on reducing temperature, evaporation, and water pressure deficit may offset water losses due to canopy interception and transpiration by trees, thereby enhancing water availability under the forest canopy compared to in open areas (Fetcher et al., 1985; Belsky et al., 1993; Chen et al., 1999). Plants adapted to periodic drought also often shut down water conductance and tran-

spiration processes during dry periods (Bréda et al., 1993; Veenendaal et al., 1995), which would further reduce water loss. Enhancing our understanding of how edge dynamics influence microclimate conditions in dry climatic regions, especially in highly fragmented landscapes, is important because of the potential for these interactions to set thresholds beyond which the buffering capacity of the system is no longer strong enough to support restorative functions of forest regeneration and ecosystem sustainability.

In the seasonally dry highlands of southeastern Mexico, processes of habitat fragmentation have created landscape mosaics characterized by patches of native oak forests, open areas cleared of their original forest vegetation for agriculture or grazing, and successional vegetation communities establishing following abandonment from land use. This research examined changes in microclimate (temperature, light, and soil moisture) across edges created by forest openings of different sizes as a result of habitat fragmentation in a seasonally dry tropical oak forest ecosystem in the highlands of southern Mexico. The main hypothesis addressed by this research was that fragmentation processes in seasonally dry climates reduces soil moisture availability and microclimate heterogeneity across edges, and that this trend will be more pronounced in more highly fragmented landscapes and in larger forest openings due to reduced buffering capacity of the forest to moderate environmental conditions. We also specifically examined the impact of an extreme drought event on microsite conditions and heterogeneity, and hypothesized that this impact would be more pronounced with increasing degree of fragmentation and in larger forest openings. The implications of the research results are discussed in relationship to the capacity of the forest to moderate environmental fluctuations and maintain resilience in response to future disturbance.

## 2. Site description

The study site is located in the Mixteca Alta region in the Nochixtlán District, in the State of Oaxaca in southeastern Mexico, at approximately 17°N latitude. The Mixteca Alta region is orographically complex, comprised of many distinct mountain ranges not belonging to a single structural entity, but which to-

gether are considered to form the “Sierra Madre del Sur” (García-Mendoza and Cruz, 1993). Geologically, the region is comprised of a combination of sedimentary, igneous and metamorphic rock, while the study area is part of the Yanhuítlán Formation, which was formed by quaternary alluvium comprised of silt and red clays that cover the floor of the Yanhuítlán valley (Ferrusquia-Villafranca, 1976). Some authors have considered that primary soils of this region include lithosols, regosols, and small areas with andisols (García-Mendoza and Cruz, 1993). According to our field observations, the study area corresponds to an association of Rendzic Lithosols (the former Rendzinas), defined as soils having a dark surface horizon, rich in organic matter, with a high base status directly overlying a highly (>40%) calcareous rock or sediment (FAO–UNESCO–ISRIC, 1990; ISSS, ISRIC and FAO, 1994). Most of the soils have AC, A–C, and AB–C horizon that have clayey textures (e.g., clay, clay loam and silty clay loam) and colors ranging from dark brown to red. In a few profiles an incipient B horizon was observed, probably indicating that the soil development tendency is from Rendzic Lithosols to Vertic Cambisols.

The study was conducted in two adjacent villages (Santiago Huaucuililla and San Pedro Cántaros Coxcaltepec), which supported communal forest lands that had experienced different degrees of habitat fragmentation: (1) ‘low fragmentation’ (Santiago Huaucuililla) consisting of a forested landscape with relatively small clearings embedded within the forest matrix, and (2) ‘high fragmentation’ (San Pedro Cántaros Coxcaltepec) consisting of an open landscape matrix that included both small and large forest clearings interspersed with small forest remnants. Combined, the study sites comprised a total area of approximately 100 ha that supported relatively similar edaphic, topographic, and climatic conditions.

Although both sites were affected by human land-use activities, there was a clear gradient of disturbance intensity between the ‘high fragmentation’ (Cántaros) and ‘low fragmentation’ (Huaucuililla) sites. In Cántaros, small openings had been created as a result of clearing of trees for charcoal production, and the forest matrix in which these openings were embedded contained multiple openings separated by relatively short distances (30–50 m). Closer to the village of Cántaros, larger areas of forest had been cleared for cultivation,

most of which had been abandoned within the last 8–10 years. In Huauclilla, the small openings were likely created for agricultural production, but had been abandoned decades earlier and not utilized within the time period of local people's recorded memories. In contrast to Cántaros, land-use activities were largely absent during recent history at the Huauclilla site due to a predominance of productive activities within the village that were not based on agricultural or forest products.

Under the Köppen system, the study sites in San Pedro Cántaros and San Miguel Huauclilla are classified as seasonally dry temperate (BSkw(w)) (Salas et al., 1994). Climate is seasonal with a 6–8-month dry season (November–April). Mean annual precipitation ranges between 450 and 800 mm of rain annually (Silva Riquer, 1990). The wet season (May–October) is characterized by frequent torrential rains, with an interseasonal dry period (*canícula*) sometimes occurring in July–August.

The dominant vegetation type at the two study sites was drought deciduous oak forest, which typically occurs in the region between 1500 and 2500 m elevation and has an average canopy tree height of 10–15 m (Salas et al., 1994). Dominant mature forest species included: *Q. acutifolia* Neé, *Q. segouiensis* Liebm., *Q. castanea* Neé, *Juniperus deppeana* Adams, and *Arbutus glandulosa* DC. Early- and late-successional species that established in the forest clearings and edges following abandonment of agricultural lands included: *Pinus oaxacana* (Mart.) Mirov, *P. lawsonii* Roetzl ex Gord., *Rhus virens* Gray, *Baccharis conferta* H.B.K., *Arctostaphylos pungens* Kunth., *Dodonaea viscosa* (L.) Jacq., and *J. deppeana* Adams. All openings supported predominantly grass vegetation with occasional shrubs and trees, with more dense early-successional shrub and tree vegetation near the forest edge. Although species composition of the forest vegetation was similar at the two sites, forest structure varied according to their different land-use histories, with Huauclilla predominantly supporting mature old growth, and Cántaros supporting young successional forest, much of which had regenerated from sprouting after cutting.

The assumption that both research sites had supported the same original vegetation prior to changes caused by land-use activities was supported by the similar biophysical and climatic conditions. The lack

of true interior forest habitat in the landscape precluded the use of true controls in the study; therefore, the relatively less disturbed mature forests in the low fragmentation site served as 'reference' conditions to which the high fragmentation site could be compared.

### 3. Methods

#### 3.1. Experimental design

Three replicate plots for each of the following types of forest openings were selected in the summer of 1994: (1) 'small' openings (<0.1 ha), (2) 'large' openings (>1.0 ha), both located in the highly fragmented landscape of Cántaros, and (3) 'reference' openings located within the less fragmented landscape of Huauclilla (<0.1 ha). The forest edge was defined as the base of the bole of the trees growing at the open-forest boundary. Each plot was stratified by the following microsites (subplots) located along a transect from the center of the forest opening into the forest interior perpendicular to the south facing edge (Fig. 1):

- (1) 'open' microsite = approximate center of the clearing;
- (2) 'shrub' microsite = 5 m into the shrub vegetation from the forest edge;
- (3) 'edge' microsite = 5 m into the forest vegetation from the forest edge;
- (4) 'forest' microsite = 30 m into the forest vegetation from the forest edge.

The depth-of-edge-influence on microclimate reported in the literature generally ranges between 15 and 50 m, depending on the parameter being measured and the particular ecosystem being studied (Williams-Linera, 1990; Matlack, 1993; Chen et al., 1995; Jose et al., 1996). A distance of 30 m was considered appropriate for detecting significant patterns in microsite conditions and plant response along edge gradients for this forest ecosystem. Several studies have shown that environmental gradients in the northern hemisphere are the steepest and longest on edges facing south (Matlack, 1993; Chen et al., 1995; Fraver, 1994). Locating the experiment transects on south facing edges was therefore expected to capture the maximum edge gradient in the landscape.

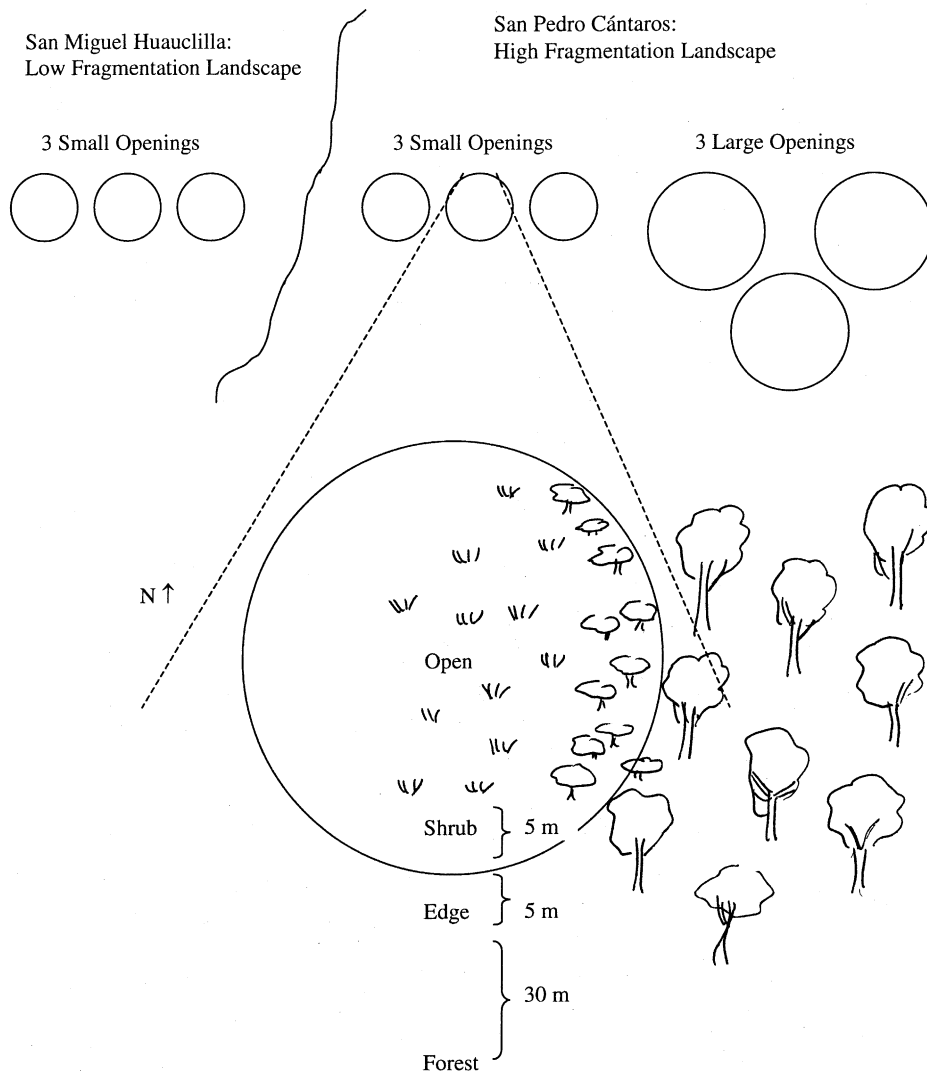


Fig. 1. Schematic diagram of experimental design.

### 3.2. Light and temperature

Photosynthetically active radiation (PAR) and surface soil temperature were measured using Li-cor quantum sensors (LI-190SA and 190SZ), recorded on a LI-1000 data logger (Li-cor Inc., Lincoln, NE). PAR and temperature measurements were recorded on sunny, cloudless days during the dry season between February–April of 1997 and January–March of 1998, for a total of 20 days, in order to provide maximum uniformity of environmental conditions and allow for

reliable comparisons of data across microsites and sampling periods. For each plot, light and temperature measurements were taken simultaneously during the sampling period on a given day for the four different microsites (only one plot was monitored per day). Data recording was conducted between the hours of 07:00–15:00 h (24 h sampling was not possible due to equipment and field logistics limitations; therefore minimum temperatures and frost events were not recorded). Measurements were registered every 10 s and the mean value recorded by the data logger every

10 min. Sensors were placed on wooden platforms positioned 30 cm above the ground. A level was used to ensure that the light sensors were horizontal to the ground. The temperature probes were placed in the approximate center of each microsite subplot to a depth of 5 cm in the mineral soil. The Li-cor light and temperature sensors and data loggers were rotated between plots such that the same equipment was consistently used for each measurement period. On the same day as the Li-cor measurements were taken, additional temperature readings were recorded every 30 min at each microsite using a portable meter with detachable temperature probes suitable for different substrate types (Cole Palmer Inc., Chicago, IL). Three different substrates were measured at each microsite: air (1 m above the soil surface), soil surface (surface litter layer gently removed), and upper mineral soil horizon (10 cm depth). Both the data loggers and portable temperature meter were battery operated.

### 3.3. Surface soil moisture

Percent surface soil moisture was determined gravimetrically every 2 weeks for each of the four microsites in all nine sites from August 1996 to August 1998. Soil was collected from the surface mineral horizon to a depth of 10 cm. Three replicates were collected for each microsite within a 1 m radius of permanently marked sampling points (total  $n = 3$  replicates  $\times$  4 microsites  $\times$  9 sites = 108). Care was taken to avoid selecting points near areas where soil had previously been collected. Samples were sealed in air-tight tin cans, and total wet weight determined within 2 days of collection at the National Institute of Forestry and Agricultural Research (INIFAP) Experimental Station in Yanhuítlán, Oaxaca. The samples were then dried to a constant weight at 105 °C in a drying oven, weighed again to determine dry weight, and sieved using a 2 mm mesh screen. All remaining materials  $>2$  mm were weighed to determine the weight of the non-soil component, which was subtracted from the total wet and dry soil weights. Percent soil moisture by soil weight was determined separately for each sample and converted to volumetric measures using soil bulk density measurements. (Bulk density was determined by carefully removing each soil sample from the top 10 cm of the soil horizon, lining the hole

with thin plastic (saran wrap), and filling the hole with water of a known volume. The soil samples were later dried and bulk density calculated as dry weight per volume and expressed as the average of three replicate samples for each microsite.) The percent soil moisture data were further stratified into dry and wet seasons for the 2 years of the study for further statistical analysis.

### 3.4. Statistical analysis

Analysis of variance for a split plot design (whole-plot = size; subplot = micro; subsubplot = season) was used to test for significant main effects and interactions among treatments on soil moisture (SAS Institute, 1995). Temperature and light were only tested for whole-plot (size) and subplot (micro) effects since measurements were not collected over time. Contrasts were performed to understand interaction terms and differences between individual treatment effects. When necessary, the data were log-transformed in order to normalize the data or account for the use of percentage data. Differences in the variability of surface soil moisture (i.e., maximum – minimum) were determined by performing an analysis of variance on mean maximum range in surface soil moisture across the edge gradient.

## 4. Results

### 4.1. Precipitation, light and temperature

Daily mean PAR and temperature varied substantially among the four different positions along the edge gradient from the open into the forest ( $***P < 0.001$ ), with an abrupt decrease occurring when moving from the shrub to the edge microsites for both variables (Fig. 2). Maximum fluctuation in daily PAR and temperature values (maximum – minimum) also varied among microsites ( $***P < 0.001$ ), with the greatest fluctuation occurring in the open and decreasing progressively into the forest. The maximum temperature occurred around 14:00 h in the open and shrub microsites, and 13:30 h in the edge and forest microsites. Maximum PAR occurred around noon, but was more variable among microsites than temperature.

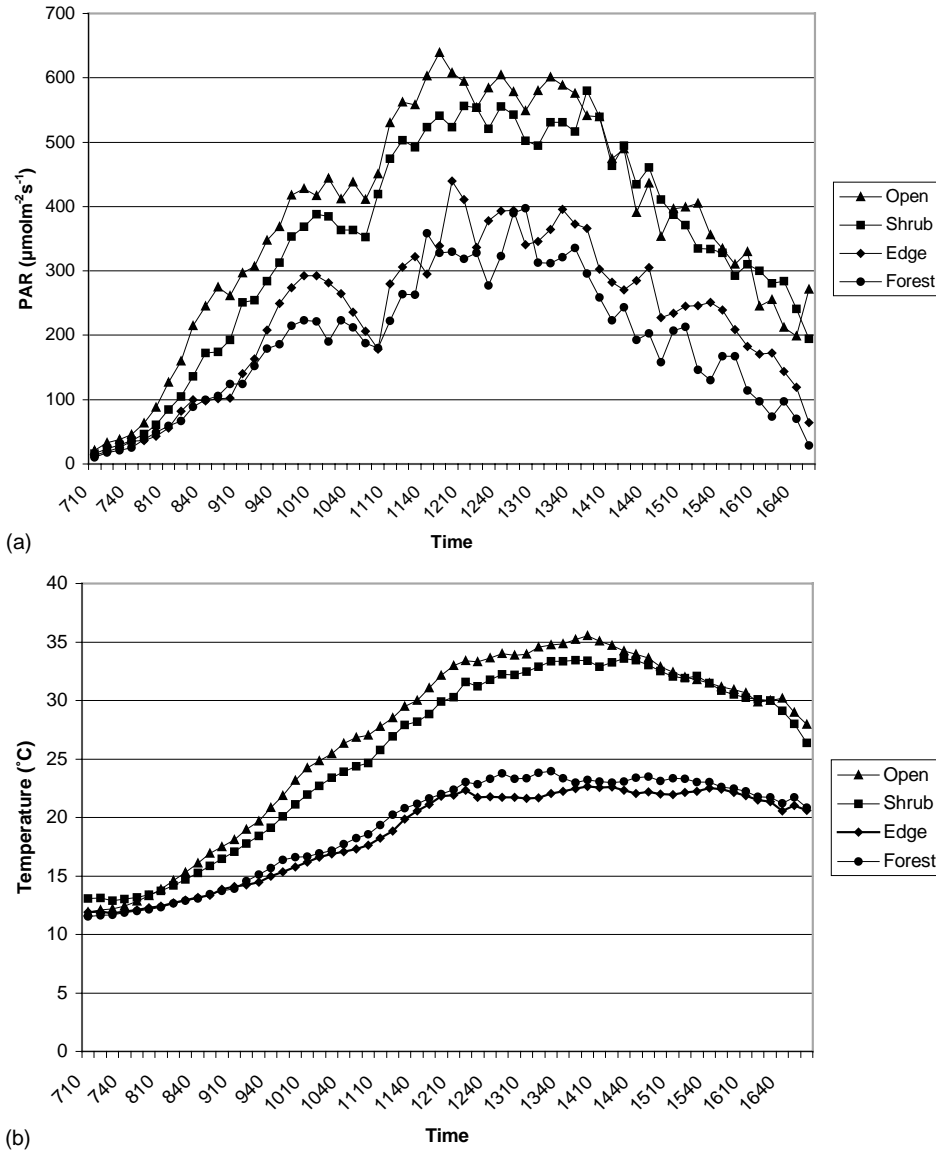


Fig. 2. (a) Mean daily photosynthetically active radiation (PAR); and (b) air temperature (30 cm above the ground), collected for 20 sunny, cloudless days during the dry season (February–April 1997), comparing between different microsites (Nochixtlán District, Oaxaca, Mexico) (data from the high and low fragmentation sites were pooled by microsite due to lack of significant differences between sites).

The results from the temperature probe readings for the three different substrates (air, surface, and belowground) indicate that for all substrates, temperatures did not vary significantly among opening types (Table 1). Comparing across microsites, mean air temperatures were similar ( $P = 1.0$ ); however, both soil surface ( $***P < 0.001$ ) and belowground

( $***P < 0.001$ ) mean soil temperatures showed consistent differences, with values being greatest for open microsites, intermediate for shrub and edge microsites, and lowest for forest microsites (Table 1). Contrasts comparing across microsites indicated a clear difference between mean surface and belowground temperatures, with open and shrub microsites

Table 1

Means ( $\pm$ S.E.) of daily average and maximum fluctuation (maximum – minimum,  $\Delta$ ) of air temperatures (height = 30 cm), ground surface temperatures, and belowground soil temperatures (depth = 10 cm), comparing between: (a) different microsites, (b) opening types and (c) showing maximum range (i.e., difference, maximum – minimum value) of soil temperatures across the edge gradient for different opening types<sup>a</sup>

	Air		Surface		Belowground	
	$x$ ( $^{\circ}$ C)	$\Delta$	$x$ ( $^{\circ}$ C)	$\Delta$	$x$ ( $^{\circ}$ C)	$\Delta$
(a) Microsite ( $n = 12$ )						
Open	21.8 (0.7)	21.3 (1.6)	28.7 (1.5)	37.4 (2.6)	25.0 (0.9)	27.8 (2.4)
Shrub	22.1 (0.8)	21.0 (1.8)	27.6 (1.5)	35.4 (2.8)	23.8 (1.0)	26.1 (2.9)
Edge	21.9 (0.8)	21.9 (2.2)	23.0 (1.1)	30.7 (2.8)	19.9 (0.6)	22.0 (2.4)
Forest	21.8 (0.7)	19.5 (1.1)	21.4 (0.9)	24.6 (2.2)	18.6 (0.7)	18.4 (2.2)
(b) Opening type ( $n = 9$ )						
Reference	22.0 (0.9)	19.4 (1.8)	26.1 (1.5)	32.0 (2.9)	21.6 (0.9)	21.2 (2.0)
Small	21.6 (0.4)	21.5 (0.9)	24.3 (1.0)	32.9 (1.9)	21.8 (0.9)	26.0 (2.2)
Large	22.4 (0.3)	22.4 (1.3)	25.4 (1.1)	30.3 (2.6)	22.3 (1.1)	23.0 (2.3)
(c) Range across edge gradient ( $n = 9$ )						
Reference	3.2 (0.4)		18.3 (1.1)		3.6 (0.7)	
Small	4.9 (1.2)		13.8 (1.0)		10.4 (0.7)	
Large	3.0 (0.5)		15.0 (1.1)		10.3 (0.7)	

<sup>a</sup> Analysis of variance for the full split plot design: \*\*\* $P < 0.001$  (Nochixtlán District, Oaxaca, Mexico).

having greater values than forest and edge microsites (\* $P < 0.05$ ).

Maximum fluctuation in temperatures (maximum – minimum) within microsite was greater in open and shrub microsites compared to edge and forest microsites for both surface (\*\* $P < 0.001$ ) and belowground temperature (\*\* $P < 0.01$ ), but not for air temperature ( $P = 0.35$ ) (Table 1). Maximum temperature fluctuation did not vary significantly between opening types (data not shown). The steepness of the temperature gradient of the ground surface across the edge gradient (maximum range) was greatest for the reference openings, intermediate for large openings, and least for small openings; although differences were not significant ( $P = 0.30$ ; contrast comparing reference with large and small:  $P = 0.14$ ) (Table 1). Differences in the temperature gradient across the edge were not significant for air ( $P = 0.62$ ) or belowground ( $P = 0.71$ ) substrates.

#### 4.2. Surface soil moisture

Analyses of mean surface soil moisture patterns in the landscape indicate a significant difference for all three main effects (size, microsite, and season; \*\*\* $P < 0.001$ ) (Table 2). Interactions were observed between

Table 2

Means ( $\pm$ S.E.) of soil moisture content ( $\text{g m}^{-3}$ ) in the surface soil horizon (depth = 10 cm) by microsite and opening type for four different seasons: (a) first wet season (wet1 = August–November 1996), (b) first dry season (dry1 = December 1996–April 1997), (c) second wet season (wet2 = May–November 1997), and (d) second dry season (dry2 = December 1997–April 1998) (Nochixtlán District, Oaxaca, Mexico)

	Microsite			
	Open	Shrub	Edge	Forest
(a) wet1				
Reference	40.1 (2.7)	43.6 (2.6)	52.1 (3.7)	54.7 (2.8)
Small	31.9 (2.8)	35.1 (3.6)	50.4 (4.3)	39.4 (3.2)
Large	36.6 (3.7)	37.1 (3.6)	51.7 (4.5)	51.8 (4.0)
(b) dry1				
Reference	22.4 (1.3)	25.5 (1.1)	30.6 (1.5)	33.9 (1.1)
Small	19.0 (1.4)	18.9 (1.7)	28.1 (1.6)	25.2 (1.4)
Large	20.2 (1.6)	20.4 (2.0)	28.1 (2.0)	31.7 (1.8)
(c) wet2				
Reference	28.3 (1.9)	36.5 (2.0)	40.3 (2.1)	42.8 (2.0)
Small	23.3 (1.7)	25.4 (1.7)	34.9 (1.6)	29.9 (1.6)
Large	27.2 (1.9)	28.8 (1.9)	31.9 (2.0)	38.3 (2.3)
(d) dry2				
Reference	10.3 (1.4)	15.2 (2.0)	20.5 (2.9)	21.0 (2.7)
Small	11.1 (1.4)	11.2 (1.4)	21.1 (2.0)	16.8 (2.1)
Large	10.8 (1.4)	10.6 (1.6)	17.3 (2.7)	19.8 (2.8)

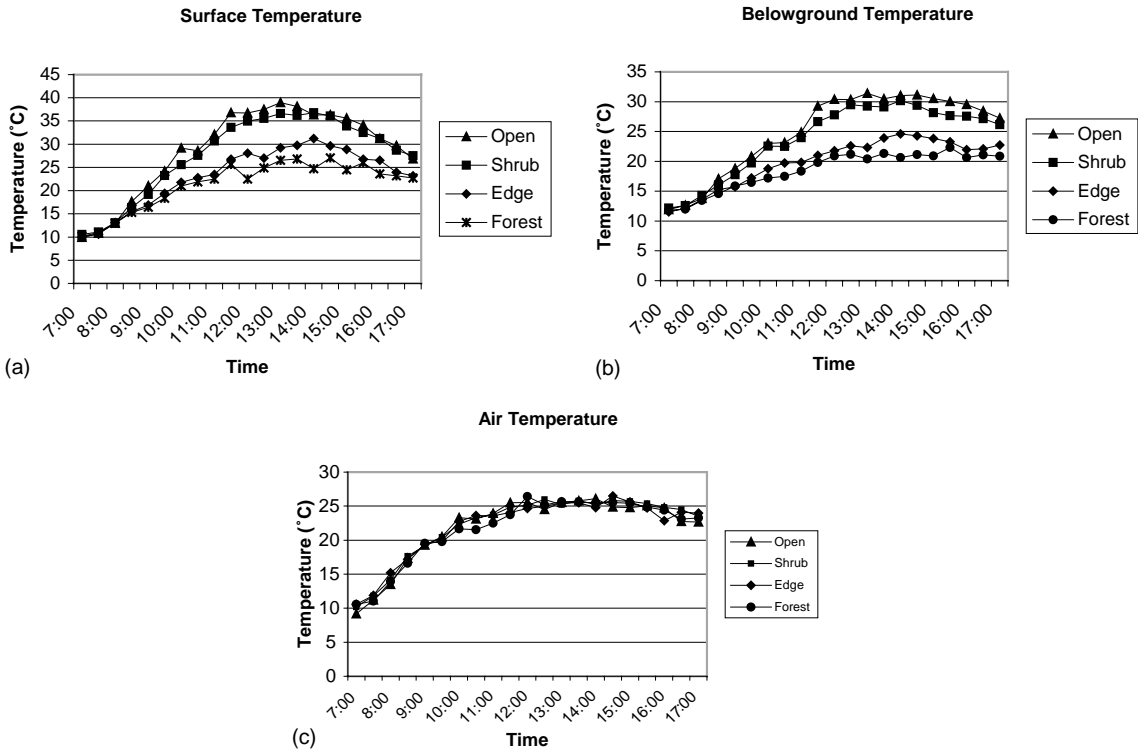


Fig. 3. Mean daily temperatures for: (a) soil surface, (b) belowground soil 5 cm, and (c) aboveground air (30 cm above the ground), comparing between different microsites (Nochixtlán District, Oaxaca, Mexico).

season and opening size ( $***P < 0.001$ ), season and microsite ( $**P < 0.01$ ), and size and microsite ( $***P < 0.001$ ), but not between all three variables combined ( $P = 0.85$ ). As expected, mean soil moistures were lower during the second year compared to the first year for all four microsite locations when comparing between respective seasons and opening types, reflecting the effects of the extreme drought of 1997–1998 (Fig. 3). Overall, surface soil moistures were greatest in the reference openings, intermediate in the large openings, and lowest in the small openings. However, these differences among microsites were most pronounced during the two wet seasons, and were essentially eliminated during the extreme drought in the second dry season (Fig. 3). Contrasts comparing mean surface soil moisture between different opening sizes for each of the four seasons supported these conclusions (wet1,  $P = 0.01$ ; dry1,  $P = 0.17$ ; wet2,  $P = 0.01$ ; dry2,  $P = 0.78$ ). Thus, during wetter periods microsite conditions were more

variable across the landscape, while the drought had a homogenizing effect on microsite conditions. Overall, openings within the less fragmented landscape, which were surrounded by a matrix of more dense and contiguous forest cover than the highly fragmented landscape, maintained higher levels and more moderate fluctuations in soil moisture conditions than in the adjacent open environment throughout the study period.

Comparing mean surface soil moistures between different microsites, the forest and edge microsites consistently had greater soil moisture than the open and shrub microsites ( $***P < 0.001$ ) for all collection times (Fig. 4). Within season, forest and edge microsites maintained similar surface soil moistures during all seasons (Fig. 5a). In contrast, there was a trend suggesting that the shrub microsites maintained greater soil moistures than the open microsites during the two wet seasons, while these differences disappeared during the two dry seasons (Fig. 5a). Further

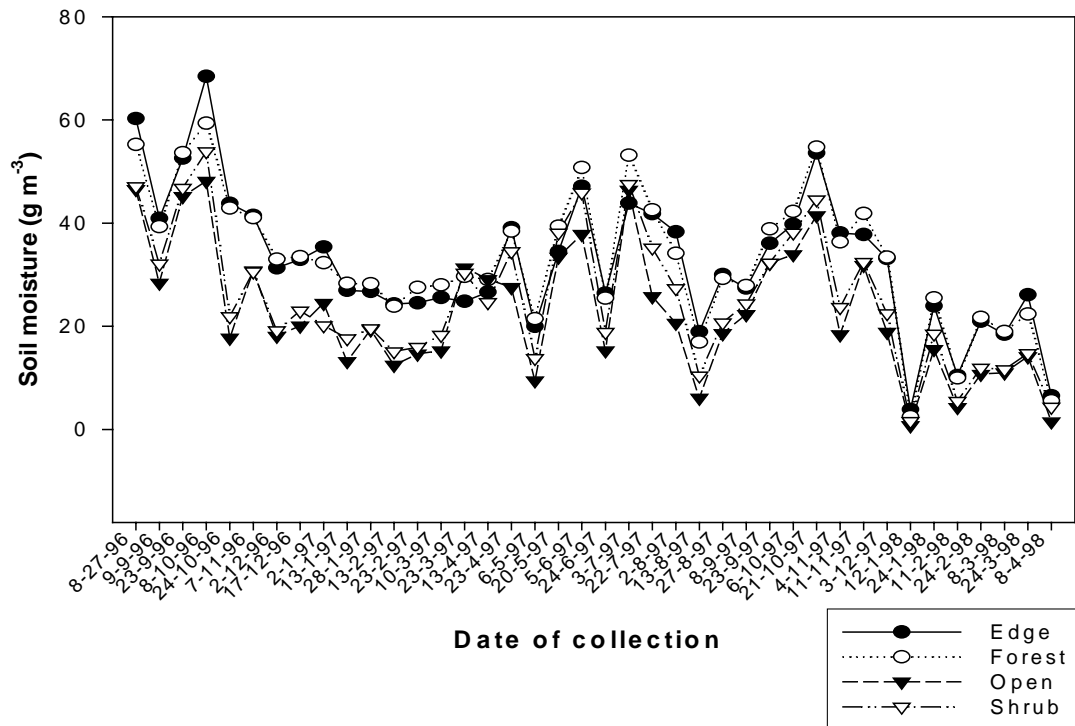


Fig. 4. Mean surface soil moisture (depth = 10 cm) for four microsite locations (open, shrub, forest, and edge) collected bi-monthly during a 2-year period (Nochixtlán District, Oaxaca, Mexico).

analysis revealed that the higher values in the shrub microsites during the wet seasons were primarily due to more moist conditions in the reference openings compared to the small and large openings (Table 2). Variability, as indicated by the standard errors, was generally greatest for the forest and edge microsites, and least for the open and shrub microsites (Table 2). For the forest microsites, both reference and large openings had higher soil moisture compared to small openings, while for the edge, shrub and open microsites differences among opening size were less pronounced (Table 2). Differences in mean soil moistures between opening sizes were also more pronounced during the wet seasons compared to the dry seasons, with reference openings having greater values than small or large openings (Fig. 5b).

The moisture gradient across the edge environment (maximum range) for the surface soil horizon was steeper for both the reference and large openings compared to small openings ( $P = 0.16$ ). This gradient was least pronounced during the second dry (Table 3),

again indicating decreasing variability across the gradient under conditions of increasing drought severity and moisture limitation.

## 5. Discussion

Our results indicate that for this seasonally dry forest ecosystem surface soil moistures was least in the open environment dominated by herbaceous vegetation and increased progressively across the shrub-forest edge and into the forest understory. This pattern was consistent for openings in both highly fragmented and relatively intact landscapes, as well as for openings of different sizes, and for both wet and dry seasons. Although other studies have reported seasonal changes in moisture relations, with soil moistures under tree canopies (Belsky et al., 1989) or in edge environments (Chen et al., 1993) being lower than in openings during certain times of the year, this reversal in soil moisture patterns did not occur in our study.

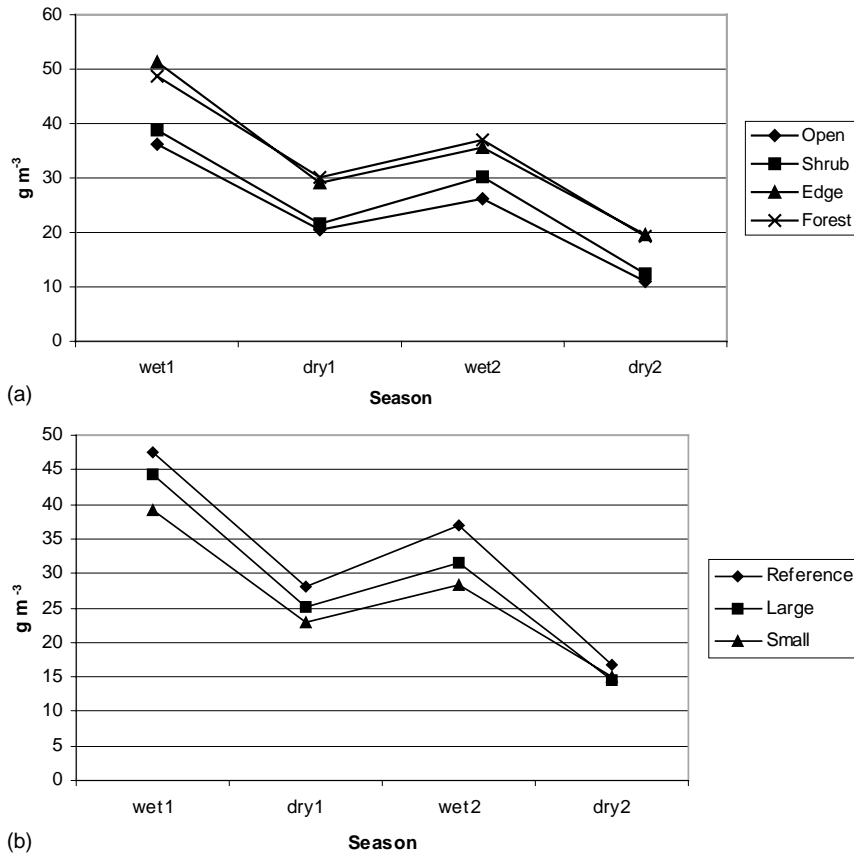


Fig. 5. Mean surface soil moisture (depth = 10 cm): (a) comparing between different microsites by season; and (b) comparing between different opening types and four different seasons: first wet season (wet1 = August–November 1996), first dry season (dry1 = December 1996–April 1997), second wet season (wet2 = May–November 1997), and second dry season (dry2 = December 1997–April 1998) (Nochixtlán District, Oaxaca, Mexico) (S.E. comparing between means of the same size = 1.12; S.E. comparing between means of different sizes = 2.87).

Position along the edge gradient also affected the degree of microclimate variation. Within the four microsites studied (open, shrub, edge, and forest), variability in surface soil moisture, temperature and light were consistently least for open and shrub microsites

and greatest for edge and forest microsites for all seasons and opening sizes. Similarly, [Chen et al. \(1993\)](#) found that variability in soil moisture was highest at the edge, intermediate in the forest, and lowest in an open clearcut. Higher variability in the edge and forest

Table 3

Maximum range (i.e., difference, maximum – minimum value) of mean surface soil ( $\text{g m}^{-3}$ ) moisture across the edge gradient for different opening types (Nochixtlán District, Oaxaca, Mexico)

Opening type	Season			
	wet1	dry1	wet2	dry2
Reference	29.34 (3.87)	15.74 (1.63)	16.7 (1.98)	10.07 (1.03)
Small	14.63 (6.15)	11.07 (3.04)	11.71 (2.0)	7.39 (2.5)
Large	23.02 (4.22)	18.57 (3.77)	13.85 (3.34)	10.91 (4.89)

understory in our study may be due to more diverse and heterogeneous above- and belowground communities caused by the presence of trees (Wilson and Kleb, 1996). Others have also observed that cultivation has a homogenization effect on soil properties, resulting in lower variability in agricultural landscapes compared to non-agricultural landscapes (Jenny, 1941; Sandor, 1983; Zhang et al., 1988; Sandor and Eash, 1991), and potentially an overall reduction in habitat complexity (Pogue and Schnell, 2001).

Patterns of surface soil moisture on the landscape scale in our study appeared to be related to differences in the size of forest openings and the characteristics of the matrix forest as influenced by human land-use activities and fragmentation processes. As expected, openings in the reference landscape where fragmentation processes were less pronounced maintained overall higher surface soil moisture compared to openings in the more highly fragmented landscape. These results again suggest that forest cover exerts a buffering influence over soil moisture conditions, both in the adjacent opening and in the forest understory, and that loss of forest cover due to habitat fragmentation leads to drier soil conditions.

A somewhat more surprising result was that small openings in the fragmented landscape had lower surface soil moistures than large openings, and the steepness of both the soil moisture gradient and ground surface temperature across the edge was also less pronounced in small openings (less edge heterogeneity). These patterns may be related to the more patchy distribution (less contiguous cover) of the forest surrounding the small openings, due to historically greater harvesting pressures for charcoal production in that area. Tree basal area of the surrounding forest was lower for small openings ( $165 \text{ m}^2 \text{ ha}^{-1}$ ) compared to both large ( $330 \text{ m}^2 \text{ ha}^{-1}$ ) and reference ( $390 \text{ m}^2 \text{ ha}^{-1}$ ) openings (Asbjornsen, unpublished data). Thus, large openings adjacent to forests with relatively undisturbed canopy cover may more effectively maintain surface soil moisture than small openings surrounded by patchy forest cover. These observations indicate that relatively small forest patches embedded within a matrix landscape dominated by open vegetation communities can still exert a significant controlling influence on microclimate conditions in adjacent environments. Further, not only are differences in the sizes of openings and forest patches within fragmented

landscapes important to understanding patterns in microclimate conditions across edge environments, but the particular characteristics of the forest patches located within or adjacent to the matrix may also play a critical role in determining these patterns. In our study, structural differences in the forest patches caused by differing historical land-use intensities appeared to have caused unexpected patterns in surface soil moisture across the edge gradient. Thus, not only did loss of forest cover due to habitat fragmentation reduce microsite heterogeneity across edge gradients, but increased human disturbance intensity in remaining forest patches further reduced variability across edges (overriding the effects of opening size), suggesting a synergistic interaction between habitat fragmentation and patch structure.

In addition to possible effects of forest structure on soil moisture, water uptake by trees from the adjacent forest may also have contributed to the drier surface soils in the small openings, since the proximity of the forest to the center of the opening was greater in the small openings compared to in the large openings. In a semiarid pine–juniper woodland, trees were found to use shallow intercanopy soil moisture up to 8 m away from the canopy patches (Breshears et al., 1997b). Although oaks are well-known for their deep rooting habit (Bréda et al., 1993; Abrams, 1996), blue oak (*Q. douglassi*) common to dry oak savanna ecosystems in California was found to have relatively high fine root biomass in the upper soil horizon for up to 5 m from the tree (Millikin and Bledsoe, 1999). Further, the lower stand basal area of the forest surrounding the small openings would have reduced canopy cover, potentially leading to reduced shading and greater evaporative loss of soil moisture in small openings.

Another phenomenon in forest openings that may directly influence surface soil moisture patterns is the redistribution of surface runoff from open areas to forest edges, due to the greater abundance of bare soil areas and the more sparse vegetation and litter layer characteristic of the open areas. Although we did not specifically investigate the possible influence of this phenomenon in our study, others (Breshears et al., 1997a; Joffre and Rambal, 1988, 1993) have shown that redistribution of runoff from intercanopy sites to canopy patches can contribute to lower soil moistures in more open areas.

The occurrence of an extreme drought in the second year of this study appeared to interact with landscape features to significantly change how microsite conditions and heterogeneity were expressed across edges in the landscape. Overall, soil moisture was less for all microsites and opening types during both the second wet and dry seasons (the drought year) compared to the corresponding previous wet and dry seasons. Further, not only was the steepness of the moisture gradient across the edge reduced in both the highly fragmented landscape and the reference landscape, the differences in the gradient intensity between the two landscapes was also diminished. These patterns support the notion of declining environmental heterogeneity in areas maintaining less forest cover and the occurrence of synergistic interactions between habitat fragmentation and microclimate under extreme drought conditions that lead to reduced buffering capacity of the forest to mitigate environmental fluctuations.

Although few studies have specifically considered the effects of extreme climatic events on microsite heterogeneity across edge gradients, other studies have reported similar interactions between microsite heterogeneity (e.g., soil moisture, light, temperature) and climatic conditions associated with different seasons. A study investigating temporal changes in edge effects on microclimate and vegetation dynamics for a fragmented tropical broadleaf forest in New Zealand reported strong microclimate gradients for PAR, vapor pressure deficit and air temperature across forest margins during the summer period, while in the winter these gradients broke down (Young and Mitchell, 1994). Liechty et al. (1992) found that differences in surface soil moisture contents between intact hardwood stands and stands converted to red pine plantations in the Great Lakes Region only occurred during the summer months when evapotranspiration was greatest, and that these differences were not apparent during early spring when transpiration was minimal. However, in this same study differences in soil moisture contents between the two stands were more pronounced during a drought year than during normal years, which is contradictory to the results reported in our study. These differences between the two studies may again reflect site-specific interactions between local climate, vegetation, and the landscape mosaic, especially when comparing regions with distinctly different precipitation regimes. These patterns

need to be further analyzed using comparative studies designed to incorporate such regional differences.

## 6. Conclusions

Our results indicate that habitat fragmentation in seasonally dry forests leads to reduced soil moisture and microsite heterogeneity across edge environments occurring between forest patches and open clearings. These patterns were attributed to the loss of ameliorating effects of shading by the forest canopy on reducing evaporative moisture loss. These effects appear to be the reverse as those typically observed in more moist climates, and emphasize the importance of climate–vegetation interactions in determining water balance. Further, our study showed that interactions between an extreme drought event and landscape features created by habitat fragmentation (edges, openings, forest patches) led to a reduction in both moisture availability and heterogeneity in the landscape. This trend was especially pronounced in the more fragmented landscape. Changes in the capacity of the ecosystem to buffer against extreme microclimate fluctuations and to maintain heterogeneity across edges in fragmented landscapes, may set environmental constraints that determine ecosystem functioning and resilience following disturbance. These constraints have important implications for the design of management and conservation strategies aimed at ensuring the long-term renewal and maintenance of high-elevation tropical oak forests that have been heavily disturbed by human land-use and subsequent habitat fragmentation.

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