

Capítulo 5

Deforestación y fragmentación del bosque tropical montano en los Altos de Chiapas, México

Este capítulo reproduce el texto del siguiente manuscrito, a excepción de la sección de Métodos, que aparece resumida:

Cayuela, L., Rey Benayas, J.M. & Echeverría, C. 2006c. Clearance and fragmentation of tropical montane forests in the Highlands of Chiapas, Mexico (1975-2000). *Forest Ecology and Management*, under review.

Resumen

Los bosques tropicales montanos han sido reconocidos a escala global por su importancia para la conservación. A pesar de ello, estos bosques están desapareciendo rápidamente en muchas regiones del globo. Nuestro estudio analiza las tasas de deforestación y los patrones de fragmentación en los bosques tropicales montanos de los Altos de Chiapas, México, en un periodo de 25 años. A partir de la información procedente de imágenes satelitales de 1975 (MSS), 1990 (TM) y 2000 (ETM+) se calcularon tasas anuales de deforestación de 1.3% y 4.8% para los periodos comprendidos entre 1975-1990 y 1990-2000 respectivamente. Además de la deforestación, se ha producido una fuerte fragmentación de los remanentes de bosque. Los patrones espaciales de fragmentación fueron descritos utilizando diversos índices de paisaje. Se observó un aumento en el número de fragmentos forestales (de 3,520 a 10,542), la densidad de fragmentos (de 1.0 a 3.2 fragmentos/100 ha) y la longitud total del borde (de 24,781 a 38,400 km). De igual modo, se observó una disminución en el tamaño promedio del fragmento (de 65 a 8.7 ha), el porcentaje de área ocupado por el fragmento más grande (de 60.7 a 4%), el área núcleo total (de 99,422 a 9,611 ha) y el índice de proximidad entre fragmentos (de 101,369 a 1,405). Estas tendencias indican una creciente deforestación y fragmentación en el área de estudio, en particular entre los años 1990-2000. En 25 años se ha perdido alrededor de un 50% de la cobertura forestal en los Altos de Chiapas, y una parte importante de los bosques que quedan se han degradado como resultado del uso antrópico. El aumento de la población humana y el uso más intensivo de los suelos destacan como los principales causantes de la deforestación en el área de estudio. Dado que todavía queda cerca de un 20% de cobertura forestal, proponemos que los esfuerzos de conservación se centren en la protección de los bosques más maduros que aún existen y en la restauración de los bosques ya degradados, en vez de en mantener una determinada configuración espacial de los remanentes de bosque cuyo objetivo sea maximizar la conectividad entre fragmentos.

Clearance and fragmentation of tropical montane forests in the Highlands of Chiapas, Mexico (1975-2000)

Cayuela, L.¹, Rey Benayas, J.M.¹ & Echeverría, C.²

¹ Departamento de Ecología, Edificio de Ciencias, Universidad de Alcalá, E-28871 Alcalá de Henares. Madrid. Spain. Phone: +34 918856406; Fax: +34 918854929, E-mail: luis.cayuela@uah.es.

² Facultad de Ciencias Forestales, Universidad Austral de Chile, Casilla 567, Valdivia, Chile.

Abstract

Tropical montane forests have been recognised as having global conservation importance. However, they are being rapidly destroyed in many regions of the world. Our study focuses on the rate of loss and patterns of fragmentation in tropical montane forests in the Highlands of Chiapas, Mexico, during a 25-year period. Data from Landsat satellite imagery from 1975 (MSS), 1990 (TM) and 2000 (ETM+) were used to ascertain annual deforestation rates of 1.3% and 4.8% for the 1975-1990 and 1990-2000 periods respectively. Spatial patterns of forest fragmentation were identified using selected landscape indices. Increases in the number of forest fragments (3,520 to 10,542), patch density (1.0 to 3.2 patches/100 ha), and total edge length (24,781 to 38,400 km) were associated with decreases in the mean patch size (65.0 to 8.7 ha), largest patch index (60.7% to 4.0%), total core area (99,422 to 9,611 ha), and mean proximity index (101,369 to 1,405). The observed trends indicate increasing deforestation and fragmentation, particularly during the 1990-2000 period. Ca. 50% of the forest cover in the Highlands has been lost in 25 years, and a proportion of the remaining forests have been degraded as a result of human use. Increasing human population and a more demanding use of soils for agriculture and timber arise as the major causes of deforestation in the study area. We suggest that conservation efforts should be focused on habitat preservation and restoration rather than on maintaining a particular spatial configuration of the remaining forest habitats.

Keywords: Deforestation; GIS; Habitat fragmentation; Land-cover change; Mexico; Tropical montane forest; Remote sensing.

1. Introduction

Forest loss and fragmentation are amongst the most important environmental issues now being faced on tropical developing countries (Laurance 1999). These forests are home to indigenous peoples (Alcorn 1993), supply natural timber and non-timber resources (Arnold & Ruiz Pérez 2001), are pharmacopeias of natural products (Balick & Mendelsohn 1992), provide vital ecosystem services such as flood amelioration and soil conservation (Costanza *et al.* 1997), and have a major influence on carbon storage and climate at regional and global scales (Malhi & Phillips 2004).

One of the most alarming aspects of tropical deforestation is the unparalleled threat to biodiversity (Laurance 1999). Additionally, deforestation brings about the fragmentation of formerly continuous forest habitats (Saunders *et al.* 1991). At the landscape level, consequences of fragmentation include habitat loss for some plant and animal species, habitat creation for others, decreased connectivity of the remaining vegetation, decreased patch size, increased distance between patches, and an increase in edge at the expense of interior habitat (Skole & Tucker 1993, Mace *et al.* 1998). The ecological consequences of

fragmentation may differ depending on the patterns or spatial configuration imposed on a landscape and how it varies both temporally and spatially (Ite & Adams 1998, Armenteras *et al.* 2003). Therefore, an understanding of the relationship between landscape patterns and the ecological processes influencing distribution of species is required by resource managers to provide a basis for making land-use decisions (Ranta *et al.* 1998, Turner *et al.* 2001).

In this study we analyse the spatial patterns of deforestation and forest fragmentation in the Highlands of Chiapas, Mexico, over the period 1975-2000. The region is notable because of its high biodiversity and environmental heterogeneity (Ceballos *et al.* 1998, Wolf & Flamenco 2003, González-Espinosa *et al.* 2004). Fragmentation has been occurring in this mountainous area for centuries as a result of traditional slash-and-burn agricultural activities. By ca. 300 AD the Mayan people were already practising this type of agriculture based on the milpa system (corn, bean, and squash crops) and gathering firewood (Lee 1994). However, population has more than tripled over the last 30 years. Therefore, their traditional response to declining agricultural yields by moving human settlements to more fertile lands is no longer possible. This has resulted in an intensification of the agriculture through the expansion of areas for cultivation at the expense of forested lands, and an increase of extraction rates of forest products (Ochoa-Gaona & González-Espinosa 2000).

Approximately 25%-30% of Central America and northern South America belong to populated mountainous areas where slash-and-burn agriculture is practiced. In such areas low technology and subsistence agriculture predominate (Tinker *et al.* 1996, Rudel & Roper 1997, Ochoa-Gaona 2001). In this context, the objective of this study is to contribute to the understanding of the patterns of deforestation and fragmentation in tropical mountain forests of Central America, where indigenous communities play a central role in the dynamics of land cover change. In particular we aim at: (1) providing an estimate of deforestation rates over the period 1975-2000 using satellite scenes acquired in 1974/75, 1990 and 2000; and (2) assessing changes in the spatial configuration of

native forests over time by using selected landscape indices. The information generated may be directly applied to management strategies as the present research identifies the spatial and temporal trends of processes that might affect future conservation programmes. In particular, further restoration programmes of native forests, estimates of potential diversity loss and setting nature reserves need the outcomes of this study.

2. Methods

Study area

The study area covers the Central Highlands of Chiapas, Mexico (**Figure 4.1**). A detailed description can be found in **chapter 4**.

Land cover classification

To analyse temporal changes in area and spatial pattern of native forests a set of three Landsat scenes were acquired for the years 1975 (MSS), 1990 (TM), and 2000 (ETM+). In order to carry out a quantitative comparison of the images, the original 79 m MSS raster grids were resampled to the resolution of the TM and ETM+ 30 m raster grids (Steininger *et al.* 2001, Staus *et al.* 2002). Each image was geometrically, atmospherically and topographically corrected as described in **chapter 3**.

We defined six classes of land cover: (1) montane cloud forest; (2) oak forest; (3) pine-oak forest; (4) pine forest; (5) shade coffee plantations; and (6) non forest cover. Non forest cover corresponded to agriculture fields, pasturelands, recent fallows, cleared areas, bare ground, and urban areas.

Classification of land cover was achieved using the Dempster-Shafer procedure (see **chapters 3 and 4**). For classification of land cover in 2000 we used the ETM+ scenes (channels 1 to 5 and 7) and evidences derived from expert knowledge as described in Cayuela *et al.* (2006b) (**chapter 4**).

Land cover classification in 1990 was based on the TM scenes (channels 1 to 5 and 7) in combination with evidences derived from the previously classified

Landsat ETM+ scenes (**Table 5.1**). Despite the successional dynamics in the region are quite difficult to generalise, the following vegetation gradient can be assumed to occur: non forest → pine forest → pine-oak forest → oak forest → montane cloud forest (González-Espinosa *et al.* 1997, Ramírez-Marcial *et al.* 2001, Galindo-Jaimes *et al.* 2002). Given this gradient, we assumed that the probabilities for a pixel to belong to a certain forest class in 1990 were somehow determined by its assignment to the same or close-related forest class in 2000. For instance, if in 2000 we had a pixel classified as oak forest, this was likely to have been either oak forest or montane cloud forest in 1990. Similarly, for classification of land cover in 1975 we used the MSS scenes (channels 1 to 4) and evidences derived from the previously classified Landsat TM scenes (**Table 5.1**).

Accuracy assessment

Confusion matrices were developed to assess the accuracy between verification sites and the classification maps. Validation of the ETM+ land cover map was achieved using 303 independent ground control

points. The TM and MSS land cover maps were verified based on an interpretation of ground control points that had not changed over time (193 and 157 respectively). Different accuracy measures were calculated: producer's accuracy, user's accuracy, and overall accuracy. In order to summarise the classification results, overall accuracies with 95% confidence intervals were also reported.

Based on the confusion matrices we used the direct approach formulated by Card (1982) to correct the estimates of land cover area. For the case of r classes we calculated the corrected area of class j as:

$$\tilde{N}_c = \sum_{j=1}^r (n_{cj} / n_j) N_j$$

where \tilde{N}_c is the corrected area estimate, n_{cj} is the number of ground control points for class j that have been classified as class c , n_j is the total number of control points for class j , and N_j is the map area estimate for class j . The accuracy of these area estimates were assessed by calculating the 95% confidence intervals of the estimator \tilde{N}_c .

Table 5.1. Lines of evidence in support of different hypotheses used for Dempster-Shafer classification of land cover for the years 1975 and 1990. Maximum probability for evidences derived from expert knowledge was set at 0.8 thus allowing uncertainty to be incorporated in the classification procedure. MCF = Montane cloud forest; OF = Oak forest; POF = Pine-oak forest; PF = Pine forest; CP = Coffee plantation; NF = Non forest.

Type	Supported hypotheses	Landsat TM (1990)		Landsat MSS (1975)	
		Line of evidence	Prob. range	Line of evidence	Prob. range
REMOTE SENSING	MCF		0.0-1.0		0.0-1.0
	OF		0.0-1.0		0.0-1.0
	POF	Supervised Bayes classification based on multi-spectral data	0.0-1.0	Supervised Bayes classification based on multi-spectral data	0.0-1.0
	PF		0.0-1.0		0.0-1.0
	CP		0.0-1.0		0.0-1.0
	NF		0.0-1.0		0.0-1.0
EXPERT KNOWLEDGE	MCF	MCF in 2000 classification	0.0/0.8	MCF in 1990 classification	0.0/0.8
	MCF, OF	OF in 2000 classification	0.0/0.8	OF in 1990 classification	0.0/0.8
	OF, POF, PF	POF in 2000 classification	0.0/0.8	POF in 1990 classification	0.0/0.8
	POF, PF	PF in 2000 classification	0.0/0.8	PF in 1990 classification	0.0/0.8
	CP	CP in 2000 classification	0.0/0.8	CP in 1990 classification	0.0/0.8

Deforestation and fragmentation analysis

Maps were analysed using ARC VIEW version 3.2 (ESRI 1999) and its extension Arc View Spatial Analyst 2.0 for Windows to quantify land cover change and forest loss and to configure grid covers for the application of landscape spatial indices. Because the presence of small patches can be only assessed using high spatial resolution imagery (Millington *et al.* 2003), the smallest forest patches (less than 5 pixels) were removed from all the images.

Annual deforestation rates were calculated using the compound-interest-rate formula due to its explicit biological meaning (Puyravaud 2003). This is:

$$P = \frac{100}{t_2 - t_1} \ln \frac{A_2}{A_1}$$

where P is percentage of forest loss per year, and A_1 and A_2 are the corrected forest cover estimates at time t_1 and t_2 respectively. Bounds to deforestation rate estimates were calculated by using the upper 95% confidence interval for A_1 and the lower 95% confidence interval for A_2 and *vice versa*.

Quantification and comparison of the spatial configuration of native forest fragments were conducted based on the following set of key landscape metrics selected after reviewing recent forest fragmentation studies (Imbernon & Branthomme 2001, Steininger *et al.* 2001, Staus *et al.* 2002, Armenteras *et al.* 2003, Millington *et al.* 2003, Echeverría *et al.* 2006): a) patch area (ha); b) patch density (number of patches per 100 ha); c) largest patch index (% of the landscape comprised by the largest patch); d) total edge length (km); e) total core area (total patch size remaining after removing a specific buffer edge; 100 m in this study) (ha); f) mean proximity index (ratio between the size and proximity of all patches whose edges are within 1 km of the focal patch); g) aggregation index (% of like adjacencies between cells of the same patch type); and h) adjacency index (length in km of edge between native forest and other cover types). These indices or spatial metrics were computed by FRAGSTATS version 3.3 (McGarigal *et al.* 2002).

3. Results

Accuracy assessment

Overall agreement for classification was 62.4% for the 1975 MSS image, 70.5% for the 1990 TM image, and 75.3% for the 2000 ETM+ image (**Table 5.2a**). However, classification accuracies increased to 89.8%, 90.7% and 94.1% respectively when all forest types were bound into a single forest cover class (**Table 5.2b**). Overall, for the classification by forest types, the lowest values of the producer's accuracy corresponded to pine-oak forest and montane cloud forest (i.e. these classes were underestimated in the classification), and the lowest values of user's accuracy corresponded to pine forest and oak forest (i.e. these classes were overestimated in the classification). Montane cloud forest and oak forest are very similar in their spectral signatures, and so they are pine-oak forest and pine forest. This is because they correspond to stages in a continuous succession process, which may easily produce misclassifications between the categories assigned in the training site and those classified by the algorithm. These misclassifications are more evident for the lower resolution TM and MSS satellite imagery.

Changes in forest cover

Changes in land cover (**Table 5.3**) were derived from corrected area estimates using land cover maps (**Figure 5.1**). The estimated area of native forests decreased from 216,363 ha (61.7% of the study area) in 1975 to 109,087 ha (32.0%) in 2000. In other words, almost 50% of the native forest existing in 1975 was deforested by 2000. Shade coffee plantations also decreased from 46,388 ha (13.2%) in 1975 to 26,457 ha (7.7%) by 2000. On the contrary, non forest cover increased from 25.1% to 60.3% of the study area. When identifying different forest types, montane cloud forest was the forest type that suffered the largest decrease, from 19.7% of the study area in 1975 to 2.5% in 2000. Annual deforestation rate was $2.7 \pm 0.3\%$ yr^{-1} for the entire study period. Forest loss was moderately low in the first fifteen years, at a deforestation rate of $1.3 \pm 0.5\%$ yr^{-1} , whereas it increased considerably to $4.8 \pm 0.7\%$ yr^{-1} in the 1990-2000 period.

Table 5.2. Confusion matrices for Dempster-Shafer classification of 1975, 1990, and 2000 Landsat satellite images using different categorisations of land cover: (a) four forest types are identified (montane cloud forest, oak forest, pine-oak forest, and pine forest); (b) a unique forest cover class is identified which includes all different forest types. 95 percent confidence intervals are shown for overall accuracies.

Land cover map	Ground verification points																				
	1975 MSS Imagery						1990 TM Imagery						2000 ETM+ Imagery								
	CF	OF	POF	PF	CP	NF	User's accuracy	CF	OF	POF	PF	CP	NF	User's accuracy	CF	OF	POF	PF	CP	NF	User's accuracy
Cloud Forest (CF)	18	4	2	0	0	1	72.0	23	3	4	0	1	0	74.2	25	9	2	2	0	0	65.8
Oak forest (OF)	6	13	3	0	3	0	52.0	10	15	3	0	3	2	45.4	9	39	6	1	1	3	66.1
Pine-oak forest (POF)	5	0	13	3	0	1	59.1	5	3	20	3	0	0	66.5	0	3	33	5	0	1	78.6
Pine forest (PF)	7	0	13	9	3	3	25.7	2	0	5	16	0	4	59.3	2	0	18	24	0	1	53.3
Coffee plantation (CP)	0	0	0	0	18	0	100.0	0	0	0	0	20	0	100.0	0	0	0	0	20	1	95.2
Non forest cover (NF)	0	0	1	2	2	27	84.4	0	1	2	0	5	43	87.5	0	2	1	3	5	87	88.8
Total	36	17	32	14	26	32		40	22	34	19	29	49		36	53	60	35	26	93	
Producer's accuracy	50.0	76.5	40.6	64.3	69.3	84.4	62.4 ±7.6	57.5	68.2	58.8	84.2	69.0	85.7	70.5 ±6.4	69.4	73.6	55.0	68.6	76.9	93.5	75.3 ±4.8

Land cover map	Ground verification points											
	1975 MSS Imagery				1990 TM Imagery				2000 ETM+ Imagery			
	F	CP	NF	User's accuracy	F	CP	NF	User's accuracy	F	CP	NF	User's accuracy
Forest cover (FC)	96	6	5	89.7	112	4	6	91.8	178	1	5	96.7
Coffee plantation (CP)	0	18	0	100.0	0	20	0	100.0	0	20	1	95.2
Non forest cover (NF)	3	2	27	84.4	3	5	43	84.3	6	5	87	88.8
Total	99	26	32		115	29	49		184	26	93	
Producer's accuracy	97.0	69.2	84.4	89.8 ±4.7	97.4	69.0	87.8	90.7 ±4.2	96.7	76.9	93.5	94.1 ±3.9

Table 5.3. Estimated area and corrected estimated area of land cover types in 1975, 1990, and 2000 in the Highlands of Chiapas. The sum of the corrected estimated areas for the different forest types can differ slightly from the total native forest area due to rounding effects.

COVER TYPE	1975			1990			2000					
	Map estimate	Corrected estimate	Map estimate	Corrected estimate	Map estimate	Corrected estimate	Map estimate	Corrected estimate				
	(ha)	(%)	(ha)	(%)	(ha)	(%)	(ha)	(%)				
Native forest	231,605	66.0	216,363 ± 8,066	61.7	183,501	52.9	176,953 ± 6,260	51.0	98,339	28.8	109,087 ± 4,272	32.0
Montane cloud forest	37,312	10.6	69,210 ± 9,520	19.7	30,939	8.9	50,206 ± 6,942	14.5	4,654	1.4	8,641 ± 2,588	2.5
Oak forest	54,131	15.4	34,118 ± 6,433	9.7	54,499	15.7	34,451 ± 6,356	9.9	26,133	7.7	25,293 ± 3,879	7.4
Pine-oak forest	48,469	13.8	75,035 ± 9,953	21.4	39,820	11.5	51,085 ± 7,504	14.7	31,708	9.3	44,479 ± 4,609	13.0
Pine forest	91,693	26.1	35,899 ± 7,990	10.2	58,242	16.8	38,367 ± 5,615	11.1	35,843	10.5	30,556 ± 4,708	9.0
Shade coffee plantations	27,689	7.9	46,388 ± 6,272	13.2	19,036	5.5	39,208 ± 5,780	11.3	15,009	4.4	26,457 ± 3,714	7.7
Non forest cover	91,390	26.1	87,933 ± 7,068	25.1	144,390	41.6	130,765 ± 7,054	37.7	227,921	66.8	205,725 ± 5,411	60.3

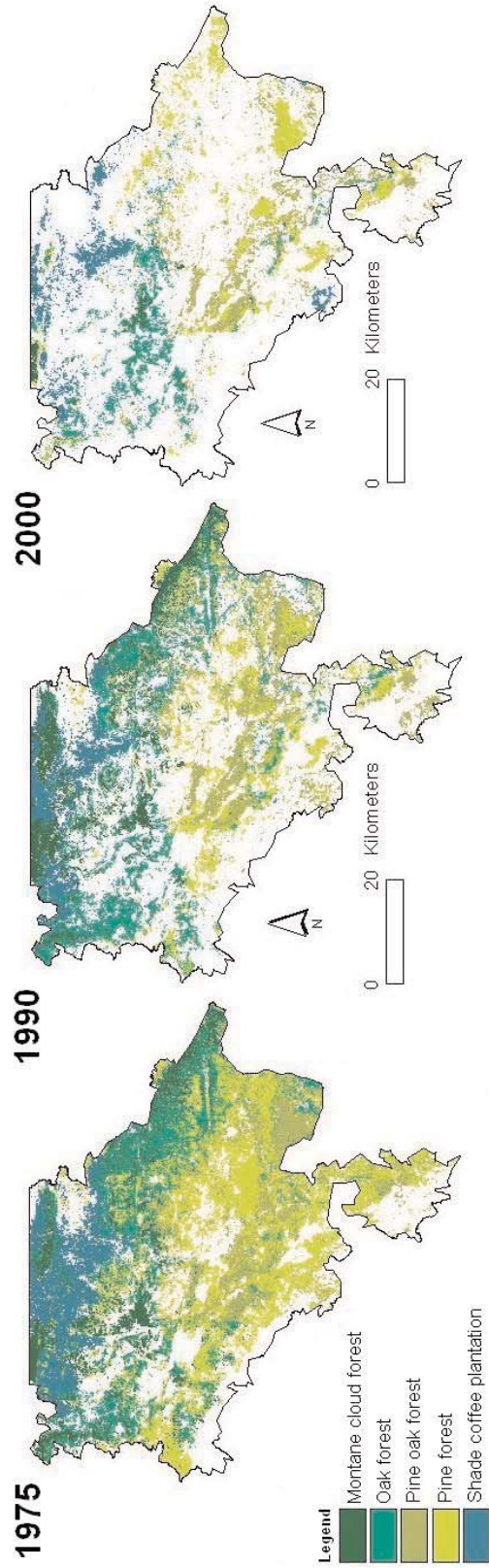


Figure 5.1. Spatial variation of native forest and coffee plantations in the Highlands of Chiapas in the years (a) 1975, (b) 1990, and (c) 2000.

Patterns of fragmentation

The total number of forest fragments increased from 3,520 in 1975 to 6,603 in 1990, and then to 10,542 in 2000 (Figure 5.2). This corresponds to an annual increase in the number of fragments of 12.5% and 16.0% in the 1975-1990 and 1990-2000 periods res-

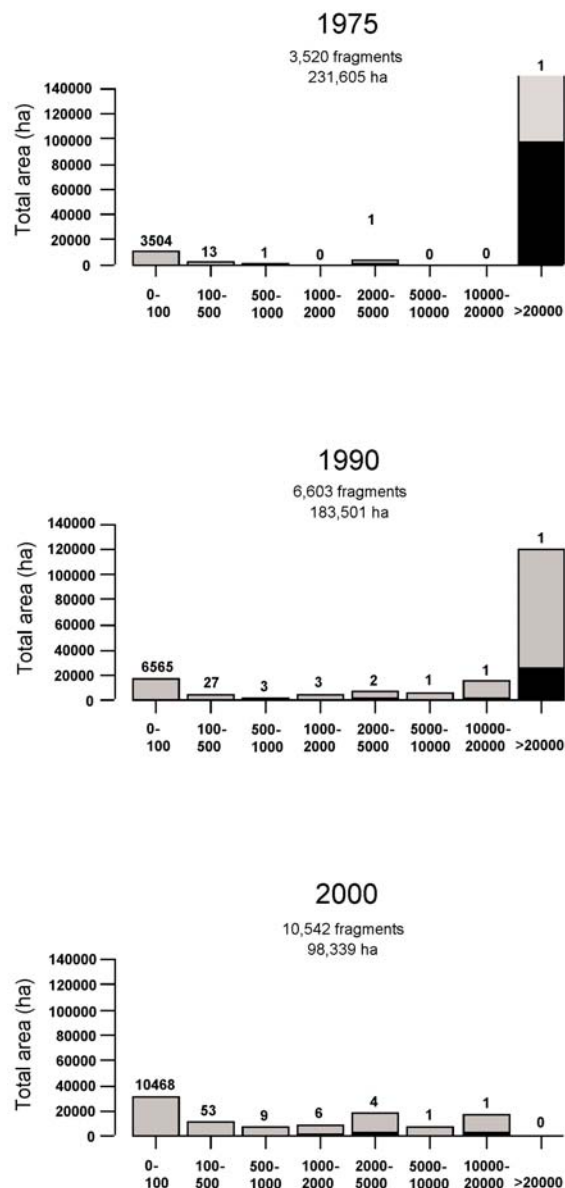


Figure 5.2. Variation of forest fragment size (measured by bar height) and core area (in black) in the Highlands of Chiapas in the two study periods. Values on top of the bars represent the number of fragments belonging to each size interval.

pectively. By 1975, 91% of the forest area was concentrated in a large patch of approximately 211,000 ha, and most of the remaining forest occurred in isolated patches of less than 500 ha. In 1990, 65% of the remaining forest was still concentrated in the same large patch, and 13% in small forest fragments of less than 100 ha. By 2000, this percentage increased to 39%, and the largest patch was reduced to 14% of the total forest area.

Mean size of forest patch decreased from 65 ha in 1975 to 27 ha in 1990 (Table 5.4). This rapid decline in patch size was associated with a rapid increase in the patch density for the same period, and a substantial reduction in the size of the largest forest patch, from 61% of the total study area in 1975 to 35% in 1990. Total edge length doubled in this period, whereas total core area decreased to less than one third of its value in 1975. Between 1990 and 2000 there was also an important decrease in the mean forest patch. The patch density increased and the largest patch index decreased to one tenth of its value in 1990. Contrary to the trend observed in the former period, there was a reduction in total edge length from approximately 50,000 ha in 1990 to less than 40,000 ha in 2000. Total core area decreased in almost one third of its value in 1990, and the mean proximity between forest fragments sharply declined from 1990 to 2000 indicating an increase in the distance between forest patches.

In 1975 the forest and non-forest covers exhibited a high frequency of aggregation (92% and 84% respectively), whereas shade coffee plantations were less aggregated (67%) (Figure 5.3a). By 1990 all cover types became less aggregated in the landscape as compared to 1975. In 2000, the rapid deforestation occurred in the previous decade led to a further segregation of forest patches, decreasing the index of aggregation to 76%. Conversely, the index of aggregation for non-forest cover and shade coffee plantations increased to 87% and 71% respectively (Figure 5.3a).

Forest fragments became increasingly adjacent to non-forest cover and, conversely, detached from shade coffee plantations (Figure 5.3b). The greatest

LANDSCAPE INDICES	1975	1990	2000
Mean patch size (ha)	65.0 [0.45-211,180]	26.9 [0.45-119,516]	8.7 [0.45-13,279]
Patch density (n/100 ha)	1.0	1.9	3.2
Largest patch index (%)	60.7	35.1	4.0
Total edge length (km)	24,781	50,114	38,400
Total core area (ha)	99,422	29,860	9,611
Mean proximity	101,369 [0.02-587,150]	60,017 [0-342,240]	1,405 [0-34,466]

Table 5.4. Change in spatial pattern of native forest in the Highlands of Chiapas in 1975, 1990, and 2000. For patch indices, mean, minimum and maximum values are given.

increase in adjacency with the non-forest cover occurred between 1975 and 1990. Then, this index faintly declined between 1990 and 2000, due to the substantial reduction in forest cover reported for this period (**Table 5.3**). There was a slight decline in the index of adjacency between 1975 and 1990 for shade coffee plantations, which was followed by a greater reduction in the last period (**Figure 5.3b**).

4. Discussion

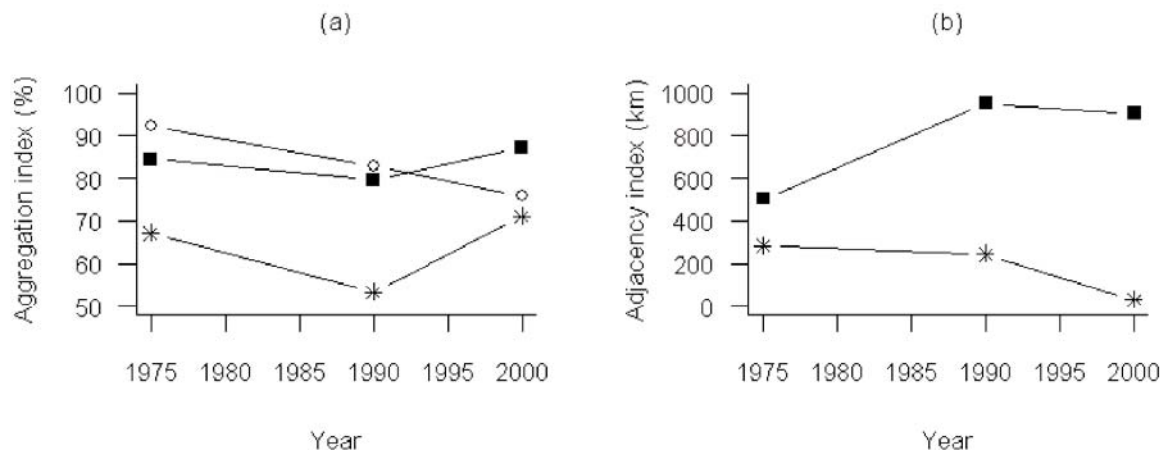
Evaluation of methods and results

Monitoring of land cover change based on remote sensing data is certainly a hazardous task (Foody 2002). Due to our estimates of forest loss are based on classification maps, and maps are simply a model

or generalization of reality, it is important to acknowledge that these will contain error. Despite different studies have stressed the importance of correcting land cover area estimates from the confusion matrix (e.g. Card 1982, Dymon 1992, Gallego 2004), these corrections have been rarely applied in studies on land cover change (but see Reams & van Deusen 1999). Our study is robust from a methodological standpoint as it incorporates this error into the estimation of land cover area in a consistent manner.

An additional complication appears because land cover classification can be difficult to apply in practice due to the existence of transitional vegetation gradients (Foody & Hill 1996, Cayuela *et al.* 2006a). Forest loss estimates are particular sensitive to what is being defined as 'forested area' (Ochoa-Gaona & González-Espinosa 2000). Despite we attempted to

Figure 5.3. Changes in (a) aggregation index; and (b) adjacency index applied to the major land cover types in the Highlands of Chiapas. Land cover types: ○ = native forest; ■ = non forest cover; and * = shaded coffee plantation.



discriminate between different successional forest types, the low classification accuracy obtained from ground truthing, particularly for the lower resolution MSS images, prevented us from using these results to estimate deforestation rates. Consequently, all successional forest categories were grouped together into one 'forest class' resulting in higher percentages of classification accuracy.

How much forest has been lost?

Deforestation rates in Mexico during the second half of the 20th century have been considered among the highest in the world (Repetto 1988, Sayer & Whitmore 1991, Masera *et al.* 1992, Cairns *et al.* 1995). For the whole country, Masera *et al.* (1992) estimated an overall annual deforestation rate of 1.56% during the mid-1980s. For tropical forests in Mexico, Repetto (1988) estimated annual deforestation rates of 1.0%. Ochoa-Gaona & González-Espinosa (2000) found that deforestation rates for the 1974-1990 period in the central Highlands were much higher than these national estimates. Our estimates of forest loss for the 1990-2000 period considerably exceed the already high rates that had previously been reported and are one of the highest rates found in tropical and temperate forests of the world (Dirzo & García 1992, Ite & Adams 1998, Sierra 2000, Cohen *et al.* 2002, Staus *et al.* 2002, but see Sader & Joyce 1988, Steininger *et al.* 2001). The rates of forest loss reported in this study do not exclude the secondary vegetation developed several years after crop abandonment. These abandoned fields were mostly classified either as non-forest areas or as pine and pine-oak forests. Therefore, actual rates of forest loss may be even higher than those reported here.

A study conducted in two municipalities of the Highlands revealed an increasing trend in the deforestation rates of 1.58%, 2.13%, and 4.75% for the 1974-1984, 1984-1990, and 1990-1996 periods respectively (Ochoa-Gaona & González-Espinosa 2000). Our results indicate that these trends can be extrapolated to the entire Highlands of Chiapas and that deforestation in the late 1990s continued increasing until 2000. However, comparison of deforesta-

tion rates can be sometimes deceptive due to the use of different criteria for vegetation classification (Foody & Hill 1996) and formulae (Puyravaud 2003).

In addition to forest loss, there are more subtle changes that affect the structure and composition of the forests and result in their degradation (Ochoa-Gaona 2001). Oak species in the Highlands, for instance, are frequently subjected to selective logging for firewood. Under intensive human use, pine-oak forests would be expected to shift to pine forests (Ochoa-Gaona & González-Espinosa 2000, Galindo-Jaimes *et al.* 2002). Our analyses have not directly accounted for shifts between forest cover states, but the relative temporal changes in the corrected estimates of the different forest types indirectly show these trends. The most remarkable point is the severe decrease in montane cloud forest cover (one eighth of its original cover). This decline does not imply that all this forest has been cleared, but it might rather be indicating that some proportion of it may have been degraded to other forest types, mostly oak forest, but also pine-oak and pine forests depending on the intensity and nature of indigenous management. Similarly, disturbances in oak forests might result in a shift to pine-oak forest, and so on (González-Espinosa *et al.* 1997, Ramírez-Marcial *et al.* 2001, Galindo-Jaimes *et al.* 2002). This might explain why both oak and pine forests showed a slight increase in area in the 1975-1990 period and only a modest decrease in the 1990-2000 period.

Amongst the main causes of deforestation are human population pressure and an increasing demand of land for agriculture and timber products from tropical forests (Rudel & Roper 1997, Lawrence *et al.* 1998, Laurance 1999, Ochoa-Gaona & González-Espinosa 2000, Ochoa-Gaona 2001). In the Highlands of Chiapas, human population increased from 165,500 to 458,500 inhabitants in the period 1970-2000, and the relative proportion of indigenous population increased from 56.9% to 71.2% (source: <http://www.conapo.gob.mx>). As a consequence, between 1990 and 2000 the total consumption of timber for firewood, charcoal, and construction increased by 19.4%, 24.1% and 20.1%, respectively (SEMARNAP 2000). The lack of alternative economic opportunities

in Chiapas and the increase in the number of households have forced people to open up marginal lands for cultivation and intensified the crop cycles. Consequently, deforestation is practiced in the region only as a low-income extractive activity that lacks long-term objectives aimed at sustainable management. Other factors have promoted deforestation, such as the steady fall in coffee prices in international markets since the 1980s (Collier *et al.* 1994), or the lack of governance following the Zapatista rebellion of 1994, which allowed rampant illegal clearing for agriculture, livestock ranching, and human settlement (González-Espinosa 2005).

Patterns of forest fragmentation

We observed drastic changes in the spatial pattern of the native forests since 1975. Whereas in 1975 the landscape was mostly dominated by a continuous forest cover (largest patch index 60.7%), in 2000 there were only a few large forest fragments (largest patch index 4.0%) and a myriad of very small ones (>10,000 fragments smaller than 100 ha) scattered across the landscape (**Figure 5.1**).

The general trend was towards an increase in the number of fragments (**Figure 5.2**) and isolation of patches, and a decline in the mean patch size (**Table 5.4**). However, total edge length increased in the earliest stage of forest loss and fragmentation but decreased during the later stages. Echeverría *et al.* (2006) also observed this trend in Rio Maule-Cobquecura, Chile, together with a reduction in patch density between 1990 and 2000. In the Highlands of Chiapas, the increase in patch density possibly involved the reduction in size and the modification of geometrically complex-shaped fragments created during the first study period rather than the elimination of forest patches as in Rio Maule-Cobquecura. The total core area also decreased as a result of forest loss and increasing fragmentation. This decline in core area was proportionally much greater than the loss of habitat itself.

The remarkable heterogeneity of the study landscape, however, suggests that careful consideration is needed when assessing some of the consequences

of fragmentation. Fragment edges may be inhospitable to some forest species, but they are not universally adverse to all forest organisms (Turner 1996). In addition, the gradients produced by forest edges may depend on the scale of the organisms or processes involved. This has possibly led to a broad array of interpretations of edge distance thresholds in the scientific community that ranges from 30 m (e.g. Williams-Linera *et al.* 1998, López-Barrera *et al.* 2005) to 300 m (Millington *et al.* 2003, Echeverría *et al.* 2006).

The connectivity between forest fragments, or its opposite, the degree of isolation, has frequently been considered as one of the most impacting factors on population dynamics (Tischendorf & Fahrig 2000). The ability of species to colonize a forest fragment depends to some extent on the distance of the fragment from other areas of native vegetation. The time since isolation, and the dispersal abilities of organisms are also important determinants of the biotic response to fragmentation (Saunders *et al.* 1991).

In the Highlands of Chiapas, the degree of isolation between forest fragments increased in almost one hundredth during the studied period. This effect of deforestation was also observed by Imbernon & Branthomme (2001) and Echeverría *et al.* (2006) in tropical and temperate forests respectively. Such a large increase in the patch isolation may suggest a vast loss of forest connectivity (e.g. Ochoa-Gaona *et al.* 2004). It is important, however, to consider the absolute values of the mean proximity index in addition to the observed trends. For example, a patch of 100 ha separated from the closest forest patch by a distance of 100 m would result in a proximity index value of 100; our mean value by 2000 was about 14 times this, indicating still a relatively large degree of connectivity among fragments.

The increase in aggregation of the non forest cover during the last time interval was strongly associated with an increase in forest loss rate (**Figure 5.3a**) and with an abrupt separation of shade coffee plantations surrounding forest fragments during the 1990-2000 period (**Figure 5.3b**). Shade coffee plantations have been shown to act as refuges for the biodiversity of

the surrounding forest habitats (Perfecto *et al.* 1996, Moguel & Toledo 1999, Mas & Dietsch 2004). In the Highlands, shade coffee plantations have become altitudinally isolated from the nearby montane cloud forests due to intense deforestation at lower altitudes (Cayuela *et al.* 2006b). Due to this, the positive feedback that these low impact agro-ecosystems may be exerting on the surrounding forest may diminish.

Management and policy implications

Empirical evidence to date suggests that, whereas the loss of habitat has large negative effects on biodiversity, the breaking apart of habitat, independent of habitat loss, has rather weak effects on biodiversity, which are as likely to be positive as negative (Fahrig 2003). It has been suggested that there is a threshold value of habitat amount, at about 20% of habitat, below which the effects of habitat fragmentation on population persistence may become more evident (Fahrig 1997, 2001). Given that there is still some 30% of the area covered by forest in the Highlands of Chiapas, conservation efforts should be focused on habitat preservation and restoration.

In the Highlands of Chiapas, forest degradation towards open/disturbed forest and secondary vegetation has been an ongoing severe process during the last decades (Ochoa-Gaona 2001) in addition to forest fragmentation and overall deforestation. This may have important implications for the conservation of biodiversity. For instance, many large animal species have already become extinct or are extremely rare in the Highlands (M. González-Espinosa and N. Ramírez-Marcial, pers. comm.) despite there are still large forest fragments where these animal species might thrive. This suggests that maintenance of large forest blocks is not a straightforward solution and certainly not a feasible one for the conservation of some species. As Redford (1992) pointed out, large forest tracts do not necessarily contribute to preserve the ecological integrity of the forest and/or support high species diversity. For this reason, we should rather focus our attention on: (1) management of the natural system; and (2) management of the external influences on the natural system (Saunders *et al.* 1991). Management of the natural system implies

prioritising areas for conservation according to different criteria, e.g. presence of rare species or species under some category of endangerment (Rey Benayas & de la Montaña 2004). This issue is tackled in **chapter 6**.

On the other hand, management of the external influences on the natural system might involve maintenance of a diverse landscape structure, which increases the survival of dispersers by providing a moderated microclimate, food resources for some species, and shelter from predators (Fahrig 2001). Two conditions provide a high quality matrix in the Highlands of Chiapas: (1) the rotary and extensive character of the agricultural system; and (2) the high resilience of vegetation under traditional slash-and-burn agriculture (milpa system) and extensive use (selective timber, extraction, firewood collection, grazing, or human induced fire) (García-Romero *et al.* 2005). A shift from extensive agriculture towards more intensive crops or the increase of cattle-raising activities is thus likely to decrease the buffering properties of the existing matrix.

Overall there is a need to depart from the traditional notions of reserve management, and look instead towards integrated landscape management (Saunders *et al.* 1991). Policies designed to reduce the pressure to clear forested land are useful (Rudel & Roper 1997). The reinforcement of communal forest ownership appears to be one way of achieving this (Bray *et al.* 2005). Land tenure laws have only given farmers the right to use the land and to some extent the wood resource (Ochoa-Gaona 2001). They have no jurisdiction over other resources, such as water, wildlife, fish, etc., which are the exclusive property of the federal government (Thoms & Betters 1998). The farmers are therefore not encouraged to use an integrated multiple-resource approach. This leads to a lack of environmental concern and a decline in people's identification with the landscape. In this context, community management would be able to set broader strategic goals and adopt a long-term perspective on management decisions (Bray *et al.* 2005).

5. Conclusions

Our research is a further evidence of the usefulness of remote sensing approaches to monitor deforestation rates and patterns of fragmentation in little accessible tropical areas. The high rates of deforestation and forest fragmentation reported here show that this area of the Neotropics is being rapidly altered. In particular, the highly diverse montane cloud forest has almost disappeared completely. It is urgent to define political and conservation actions that minimize the impact of human activities on the remaining native forests. The spatial patterns of forest fragmentation were characterized by an increase in the number of forest fragments, patch density, and total edge length coupled with a decrease in mean patch size, largest patch index, total core area, and mean proximity index. Conservation efforts in the Highlands of Chiapas should be based upon the management of the natural system and the management of the external influences on it, particularly the detection of hotspots, passive and active restoration and sustainable forest exploitation by the local indigenous communities.

Acknowledgements

Satellite imagery and ancillary data were provided by LAIGE-ECOSUR. This work was financed by the European Commission, BIOCORES Project, INCO Contract ICA4-CT-2001-10095.

References

- Alcorn, J.B. 1993. Indigenous peoples and conservation. *Conservation Biology* 7: 424-426.
- Armenteras, D., Gast, F. & Villareal, H. 2003. Andean forest fragmentation and the representativeness of protected natural areas in the eastern Andes, Colombia. *Biological Conservation* 113: 245-256.
- Arnold, J.E. & Ruiz Pérez, M. 2001. Can non-timber forest products match tropical forest conservation and development objectives? *Ecological Economics* 39(3): 437-447.
- Balick, M.J. & Mendelsohn, R. 1992. Assessing the economic value of traditional medicines from tropical rain forests. *Conservation Biology* 6: 128-130.
- Bray, D.B., Merino-Pérez, L. & Barry, D. 2005. The community forests of Mexico. *Managing for Sustainable Landscapes*. University of Texas Press, Texas, USA.
- Cairns, M.A., Dirzo, R. & Zadroga, F. 1995. Forests of Mexico: a diminishing resource? *Journal of Forestry* 93: 21-24.
- Card, D.H. 1982. Using known map category marginal frequencies to improve estimates of thematic map accuracy. *Photogrammetric Engineering and Remote Sensing* 44: 1033-1043.
- Cayuela, L., Golicher, J.D., Salas Rey, J. & Rey Benayas, J.M. 2006a. Classification of a complex landscape using Dempster-Shafer theory of evidence. *International Journal of Remote Sensing*, in press.
- Cayuela, L., Golicher, J.D., Rey Benayas, J.M. & 2006b. The extent, distribution, and fragmentation of vanishing Montane Cloud Forest in the Highlands of Chiapas, Mexico. *Biotropica*, in press.
- Ceballos, G., Rodríguez, P. & Medellín, R.A. 1998. Assessing conservation priorities in megadiverse Mexico: mammalian diversity, endemism, and endangerment. *Ecological Applications* 8: 8-17.
- Cohen, W., Spies, T., Alig, R., Oetter, D., Maierberger, T. & Fiorella, M. 2002. Characterizing 23 years (1972-95) of stand replacement disturbance in western Oregon forest with Landsat imagery. *Ecosystems* 5: 122-137.
- Collier, G.A., Mountjoy, D.C. & Nigh, R.B. 1994. Peasant agriculture and global change. *BioScience* 44: 398-407.
- Costanza, R., Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P. & van den Belt, M. 1997. The value of the world's ecosystem services and natural capital. *Nature* 387: 253-260.
- Dirzo, R. & García, M.C. 1992. Rates of deforestation in Los Tuxtlas, a Neotropical area in Southeast Mexico. *Conservation Biology* 6(1): 84-90.
- Dymond, J.R. 1992. How accurately do image classifiers estimate area? *International Journal of Remote Sensing* 13(9): 1735-1742.
- Echeverría, C., Coomes, D., Salas, J., Rey Benayas, J.M., Lara, A. & Newton, A. 2006. Rapid deforestation and fragmentation of Chilean temperate

- forests. Biological Conservation, in press.
- ESRI. 1999. Environmental Systems Research Institute. Inc., Redlands, California, USA.
- Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. *Journal of Wildlife Management* 61(3): 603-610.
- Fahrig, L. 2001. How much habitat is enough? *Biological Conservation* 100: 65-74.
- Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution and Systematics* 34: 487-515.
- Foody, G.M. 2002. Status of land cover classification accuracy assessment. *Remote Sensing of the Environment* 80: 185-201.
- Foody, G.M. & Hill, R.A. 1996. Classification of tropical forest classes from Landsat TM data. *International Journal of Remote Sensing* 17: 2353-2367.
- Galindo-Jaimes, L., González-Espinosa, M., Quintana-Ascencio, P. & García-Barrios, L. 2002. Tree composition and structure in disturbed stands with varying dominance by *Pinus* spp. in the highlands of Chiapas, Mexico. *Plant Ecology* 162: 259-272.
- Gallego, F.J. 2004. Remote sensing and land cover area estimation. *International Journal of Remote Sensing* 25(15): 3019-3047.
- García-Romero, A., Oropeza-Orozco, O. & Galicia-Sarmiento, L. 2005. Land-use systems and resilience of tropical rain forests in the Tehuantepec Isthmus, Mexico. *Environmental Management* 34(6): 768-785.
- González-Espinosa, M. 2005. Forest use and conservation implications of the Zapatista rebellion in Chiapas, Mexico. In: Kaimowitz, D. (ed.) *Forests and Conflicts*. ETFRN News No. 43-44 (European Tropical Forest Research Network), Wageningen, The Netherlands. pp 74-76.
- González-Espinosa, M., Ochoa-Gaona, S., Ramírez-Marcial, N. & Quintana-Ascencio, P.F. 1997. Contexto vegetacional y florístico de la agricultura. In: Parra-Vázquez, M.R. & Díaz-Hernández, B.M. (eds.) *Los Altos de Chiapas: Agricultura y crisis rural*. Tomo I. Los Recursos Naturales. El Colegio de la Frontera Sur, San Cristóbal de las Casas, Chiapas, México. pp. 85-117.
- González-Espinosa, M., Rey-Benayas, J.M., Ramírez-Marcial, N., Huston, M.A. & Golicher, D., 2004. Tree diversity in the northern Neotropics: regional patterns in highly diverse Chiapas, Mexico. *Ecography* 27: 741-756.
- Imbernon, J. & Branthomme, A. 2001. Characterization of landscape patterns of deforestation in tropical rain forests. *International Journal of Remote Sensing* 22: 1753-1765.
- Ite, U.E. & Adams, W.M. 1998. Forest conversion, conservation and forestry in Cross River State, Nigeria. *Applied Geography* 18: 301-314.
- Laurance, W.F. 1999. Reflections on the tropical deforestation crisis. *Biological Conservation* 91: 109-117.
- Lawrence, D.C., Peart, D.R. & Leighton, M. 1998. The impact of shifting cultivation on a rainforest landscape in West Kalimantan: Spatial and temporal dynamics. *Landscape Ecology* 13: 135-148.
- Lee, T.A. 1994. La antigua historia de las etnias de Chiapas. In: Armendáriz, M.L. (ed.) *Chiapas: una Radiografía*. Fondo de Cultura Económica, Distrito Federal, México. pp. 55-69.
- López-Barrera, F., Newton A. & Manson R. 2005. Edge effects in a tropical montane forest mosaic: experimental tests of post-dispersal acorn removal. *Ecological Research* 20: 31-40.
- Mace, G., Balmford, A. & Ginsberg, J.R. 1998. *Conservation in a changing world*. Cambridge University Press, United Kingdom.
- Malhi, Y. & Phillips, O.L. 2004. Tropical forests and global atmospheric change: a synthesis. *Philosophical Transaction of the Royal Society of London B* 359: 549-555.
- Mas, A.H. & Dietsch, T.V. 2004. Linking shade coffee certification to biodiversity conservation: butterflies and birds in Chiapas, Mexico. *Ecological Applications* 14(3): 642-654.
- Masera, O., Ordoñez, M.J. & Dirzo, R. 1992. Carbon emissions from deforestation in Mexico: current situation and long term scenarios. In: Makundi, W. & Sathaye, J. (eds.) *Carbon emissions and sequestration in forests: case studies from seven developing countries*. University of California, Berkeley, CA. pp. 1-49.
- McGarigal, K., Cushman, S.A., Neel, M.C. & Ene, E. 2002. FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps. Computer software

- re program produced by the authors at the University of Massachusetts, Amherst. URL: www.umass.edu/landeco/research/fragstats/fragstats.html.
- Millington, A.C., Velez-Liendo, X.M. & Bradley, A.V. 2003. Scale dependence in multitemporal mapping of forest fragmentation in Bolivia: implications for explaining temporal trends in landscape ecology and applications to biodiversity conservation. *Photogrammetry & Remote Sensing* 57: 289-299.
- Moguel, P. & Toledo, V.M. 1999. Biodiversity conservation in traditional coffee systems of Mexico. *Conservation Biology* 13: 11-21.
- Ochoa-Gaona, S. 2001. Traditional land-use systems and patterns of forest fragmentation in the Highlands of Chiapas, México. *Environmental Management* 27(4): 571-586.
- Ochoa-Gaona, S. & González-Espinosa, M. 2000. Land use and deforestation in the highlands of Chiapas, Mexico. *Applied Geography* 20: 17-42.
- Ochoa-Gaona, S., González-Espinosa, M., Meave, J.A. & Sorani, V. 2004. Effect of forest fragmentation on the woody flora of the highlands of Chiapas, Mexico. *Biodiversity and Conservation* 13(5): 864-884.
- Perfecto, I., Rice, R.A., Greenberg, R. & van der Voort, M.E. 1996. Shade coffee: a disappearing refuge for biodiversity. *BioScience* 46: 598-608.
- Puyravaud, J.P. 2003. Standardizing the calculation of the annual rate of deforestation. *Forest Ecology and Management* 177: 593-596.
- Ramírez-Marcial, N., González-Espinosa, M. & Williams-Linera, G. 2001. Anthropogenic disturbance and tree diversity in Montane Rain Forests in Chiapas, Mexico. *Forest Ecology and Management* 154: 311-326.
- Ranta, P., Blom, T., Niemela, J., Joensuu, E. & Siitonen, M. 1998. The fragmented Atlantic rain forest of Brazil: size, shape and distribution of forest fragments. *Biodiversity and Conservation* 7: 385-403.
- Reams, G.A. & van Deusen, P.C. 1999. The Southern Annual Inventory System. *Journal of Agricultural, Biological, and Environmental Statistics* 4(3): 108-122.
- Redford, K.H. 1992. The empty forest. *BioScience* 42(6): 412-422.
- Repetto, R. 1988. *The forest for the trees? Government policies and the misuse of forest resources*. World Resources Institute, New York.
- Rey Benayas, J. M. & de la Montaña, E. 2004. Identifying areas of high-value vertebrate diversity for strengthening conservation. *Biological Conservation* 114: 357-370.
- Rudel, T. & Roper, J. 1997. The paths to rain forest destruction: crossnational patterns of tropical deforestation, 1975-1990. *World Development* 25: 53-65.
- Sader, S.A. & Joyce, A.T. 1988. Deforestation rates and trends in Costa Rica, 1940 to 1983. *Biotropica* 20: 11-19.
- Saunders, D.A., Hobbs, R.J. & Margules, C.R. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5: 18-32.
- Sayer, J.A. & Whitmore, T.C. 1991. Tropical moist forests destruction and species extinction. *Biological Conservation* 55: 199-213.
- SEMARNAP. 2000. *Estadísticas básicas del sector forestal*. Secretaría de Medio Ambiente, Recursos Naturales y Pesca. URL: <http://www.energia.gob.mx/publicaciones>.
- Sierra, R. 2000. Dynamics and patterns of deforestation in the western Amazon: the Napo deforestation front, 1986-1996. *Applied Geography* 20: 1-16.
- Skole, D. & Tucker, C. 1993. Tropical deforestation and habitat fragmentation in the Amazon: satellite data from 1978 to 1988. *Science* 260: 1905-1909.
- Staus, N., Strittholt, J., Dellasala, D. & Robinson, R. 2002. Rate and patterns of forest disturbance in the Klamath-Siskiyou ecoregion, USA, between 1972 and 1992. *Landscape Ecology* 17: 455-470.
- Steininger, M., Tucker, C., Ersts, P., Killeen, T., Villegas, Z. & Hecht, S. 2001. Clearance and fragmentation of tropical deciduous forest in the Tierras Bajas, Santa Cruz, Bolivia. *Conservation Biology* 15: 856-866.
- Thoms, C.A. & Betters, D.R. 1998. The potential for ecosystem management in Mexico's forest ejidos. *Forest Ecology and Management* 103: 149-157.
- Tinker, B.P., Ingram, J.S.I. & Struwe, S. 1996. Effects

- of slash-and-burn agriculture and deforestation on climate change. *Agriculture, Ecosystems and Environment* 58: 13-22.
- Tischendorf, L. & Fahrig, L. 2000. On the usage and measurement of landscape connectivity. *Oikos* 90: 7-9.
- Turner, M.G. 1996. Species loss in fragments of tropical rain forest: a review of the evidence. *Journal of Applied Ecology* 33: 200-209.
- Turner, M.G., Gardner, R.H. & O'Neill, R.V. 2001. *Landscape Ecology in Theory and Practice: Pattern and Process*. Springer, New York.
- Williams-Linera, G., Domínguez-Castelú, V. & García-Zurita, M.E. 1998. Microenvironment and floristics of different edges in a fragmented tropical rainforest. *Conservation Biology* 12(5): 1091-1102.
- Wolf, J.H.D. & Flamenco, A. 2003. Patterns in species richness and distribution of vascular epiphytes in Chiapas, Mexico. *Journal of Biogeography* 30: 1689-1707.