

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

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## 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 (3520–10,542), patch density (1.0–3.2 patches/100 ha), and total edge length (24,781–38,400 km) were associated with decreases in the mean patch size (65.0–8.7 ha), largest patch index (60.7–4.0%), total core area (99,422–9,611 ha), and mean proximity index (101,369–1405). The observed trends indicate increasing deforestation and fragmentation, particularly during the 1990–2000 period. Circa 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 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.

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## 1. Introduction

Forest loss and fragmentation are among the most important environmental issues now facing tropical developing countries (Laurance, 1999). These forests are home to indigenous peoples (Alcorn, 1993), supply natural timber and non-timber resources (Arnold and Ruiz Pérez, 2001), are pharmacopeias of natural products (Balick and 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 and 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 and 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 and 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 and Flamenco, 2003; González-Espinosa

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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 A.D., 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 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 and González-Espinosa, 2000).

Approximately 25–30% of Central America and northern South America belong to populated mountainous areas where slash-and-burn agriculture is practised. In such areas, low technology and subsistence agriculture predominate (Tinker et al., 1996; Rudel and 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 the 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 1974/1975, 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

### 2.1. Study area

The study area covers the Central Highlands of Chiapas, Mexico, and extends over ca. 3500 km<sup>2</sup> (Fig. 1). Elevation ranges from 600 to 2900 m (mostly above 1500 m). The topography is abrupt with fairly steep slopes. Mean annual temperature is 13–14 °C, and mean annual rainfall varies from 1200 to 1500 mm. The underlying geology of the area is carboniferous limestone with many rocky outcroppings. The soils are a mixture of thin lithic renzinas, deeper humic acrisols in forested areas, and rather infertile chromic luvisols.

### 2.2. 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 (see Cayuela et al., *in press-a,b*).

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. All forest types were native.

Classification of land cover was achieved using the Dempster–Shafer procedure as implemented in Idrisi 32

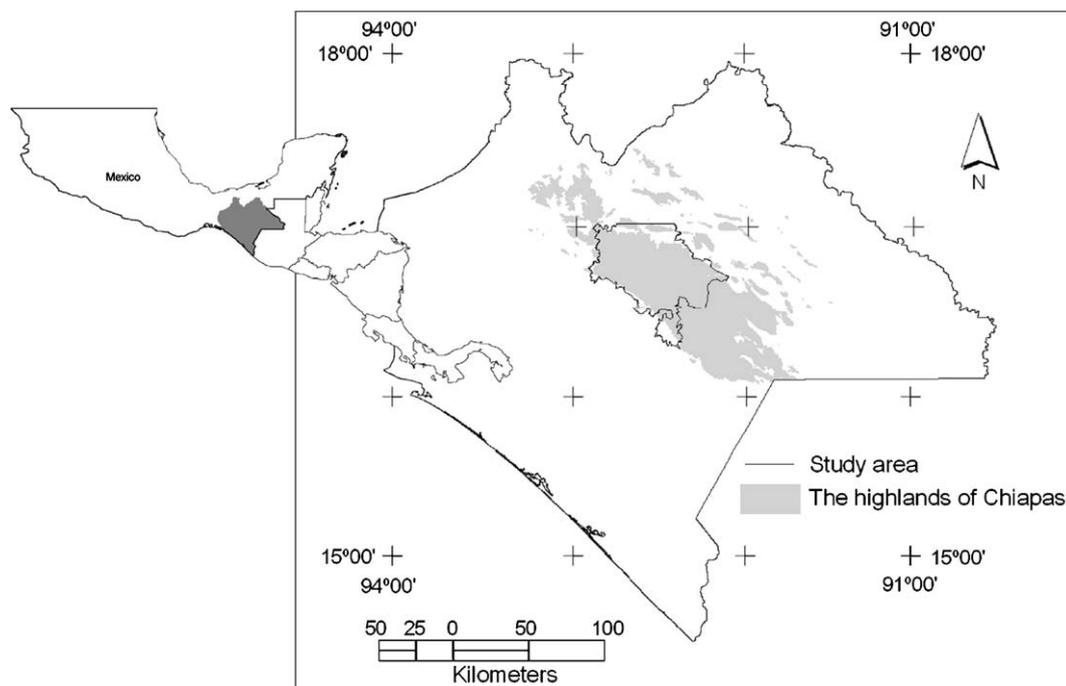


Fig. 1. Location map of the study area in the Highlands of Chiapas, Mexico.

(Eastman, 2001). This classifier allows for combination of different lines of evidence derived from both multi-spectral data and expert knowledge in order to develop statements of the degree to which each pixel belongs to each of the land cover classes being considered (Mertikas and Zervakis, 2001). The procedure is particularly useful when spectral data alone is insufficient to discriminate between some classification categories (Cayuela et al., in press-b). In these cases, expert knowledge can provide extra-evidence to improve land cover classification. Expert knowledge is a combination of a theoretical understanding of the problem and a collection of heuristic problem-solving rules that experience has shown to be effective in the domain. For example, there is theoretical and empirical support for some forest types to be associated to certain altitudinal ranges. The procedure can be summarised in three steps: (1) each line of evidence was formalised into one or various probability maps (with values between 0 and 1) supporting one or multiple land cover classes at the same time; (2) all evidences were combined by means of the Dempster–Shafer’s algorithm. This outputs different layers that defined the degree of belief or probability of each pixel belonging to each of the land cover classes being considered; and (3) a land cover classification map was obtained by assigning each pixel to the category that was the most probable after all evidences had been combined.

For classification of land cover in 2000, we used five lines of evidences: (i) multi-spectral data (channels 1–5 and 7) that was incorporated in the form of probabilities based on the variance/covariance matrix; (ii) elevation, assuming that montane cloud forest was more probable at higher elevations (above 2000 m) and coffee plantations at lower (below 2000); (iii) slope angle, assuming all forest types but pine forest to occur with higher probability at higher slopes, and pine forest, coffee plantations and non-forest areas at lower slopes; (iv) distance to human settlements and roadways, as evidence for presence of non-forest areas; (v) landscape perceptions regarding the main vegetation types, for which experts’ opinions were collected to

output a probability map resuming most widely accepted views of spatial patterns concerning vegetation types throughout the study area. In addition, a polygon layer displaying geo-referenced small coffee holdings was used as a hard evidence (i.e. no probabilistic) in support of coffee plantations. A detailed description of the classification procedure is provided in Cayuela et al. (in press-a).

Land cover classification in 1990 was based on the TM scenes (channels 1–5 and 7) in combination with evidences derived from the previously classified Landsat ETM+ scenes (Table 1). Although 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 1–4) and evidences derived from the previously classified Landsat TM scenes (Table 1).

### 2.3. Accuracy assessment

Accuracy assessment involves identifying a set of sample locations (ground verification points) that are visited in the field. The land cover found in the field is then compared to that which was mapped in the image for the same location by means of error or confusion matrices. 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). Based on the confusion matrices, different accuracy measures

Table 1  
Lines of evidence in support of different hypotheses used for Dempster–Shafer classification of land cover for the years 1975 and 1990

Supported hypotheses	Landsat TM (1990)		Landsat MSS (1975)	
	Line of evidence	Probability range	Line of evidence	Probability range
Remote sensing				
MCF	Supervised Bayes classification based on multi-spectral data	0.0–1.0	Supervised Bayes classification based on multi-spectral data	0.0–1.0
OF		0.0–1.0		0.0–1.0
POF		0.0–1.0		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

Maximum probability for evidence 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.

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

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

where  $\hat{N}_c$  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 was assessed by calculating the 95% confidence intervals of the estimator  $\hat{N}_c$ .

#### 2.4. 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 and Branthomme, 2001; Steininger et al., 2001; Staus et al., 2002; Armenteras et al., 2003; Millington et al., 2003; Echeverría et al., in press): (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

#### 3.1. 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 2a). However, classification accuracies increased to 89.8, 90.7 and 94.1%, respectively, when all forest types were combined into a single forest cover class (Table 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 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.

Table 2a

Confusion matrices for Dempster–Shafer classification of 1975, 1990, and 2000 Landsat satellite images using different categorisations of land cover: four forest types are identified (montane cloud forest, oak forest, pine–oak forest, and pine forest). 95% 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

Table 2b

Confusion matrices for Dempster–Shafer classification of 1975, 1990, and 2000 Landsat satellite images using different categorisations of land cover: a unique forest cover class is identified which includes all different forest types. 95% confidence intervals are shown for overall accuracies

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 (F)	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 3

Estimated area and corrected estimated area of land cover types in 1975, 1990, and 2000 in the Highlands of Chiapas

Cover type	1975				1990				2000			
	Map estimate		Corrected estimate		Map estimate		Corrected estimate		Map estimate		Corrected estimate	
	ha	%	ha	%	ha	%	ha	%	ha	%	ha	%
Native forest	231605	66.0	216363 ± 8066	61.7	183501	52.9	176953 ± 6260	51.0	98339	28.8	109087 ± 4272	32.0
Montane cloud forest	37312	10.6	69210 ± 9520	19.7	30939	8.9	50206 ± 6942	14.5	4654	1.4	8641 ± 2588	2.5
Oak forest	54131	15.4	34118 ± 6433	9.7	54499	15.7	34451 ± 6356	9.9	26133	7.7	25293 ± 3879	7.4
Pine–oak forest	48469	13.8	75035 ± 9953	21.4	39820	11.5	51085 ± 7504	14.7	31708	9.3	44479 ± 4609	13.0
Pine forest	91693	26.1	35899 ± 7990	10.2	58242	16.8	38367 ± 5615	11.1	35843	10.5	30556 ± 4708	9.0
Shade coffee plantations	27689	7.9	46388 ± 6272	13.2	19036	5.5	39208 ± 5780	11.3	15009	4.4	26457 ± 3714	7.7
Non-forest cover	91390	26.1	87933 ± 7068	25.1	144390	41.6	130765 ± 7054	37.7	227921	66.8	205725 ± 5411	60.3

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.

### 3.2. Changes in forest cover

Changes in land cover (Table 3) were derived from corrected area estimates using land cover maps (Fig. 2). 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  $2.7 \pm 0.3\% \text{ yr}^{-1}$  for the entire study period. Forest loss was moderately low in the first 15 years, at a deforestation rate of  $1.3 \pm 0.5\% \text{ yr}^{-1}$ , whereas it increased considerably to  $4.8 \pm 0.7\% \text{ yr}^{-1}$  in the 1990–2000 period.

### 3.3. Patterns of fragmentation

The total number of forest fragments increased from 3520 in 1975 to 6603 in 1990, and then to 10,542 in 2000 (Fig. 3). 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, respectively. By 1975, 91% of the forest area was concentrated in a large patch of approximately 211,000 ha,

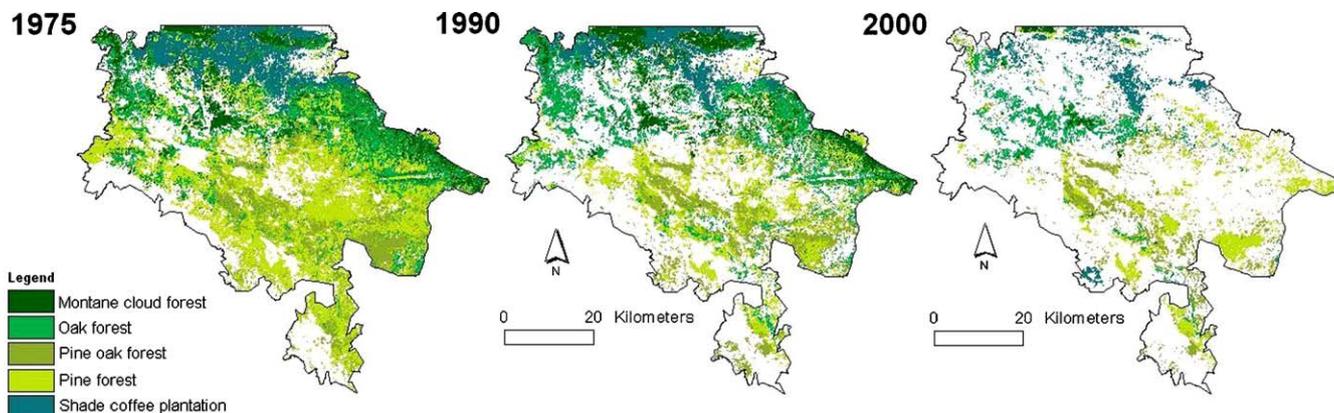


Fig. 2. Spatial variation of native forest and coffee plantations in the Highlands of Chiapas in the years (a) 1975, (b) 1990, and (c) 2000.

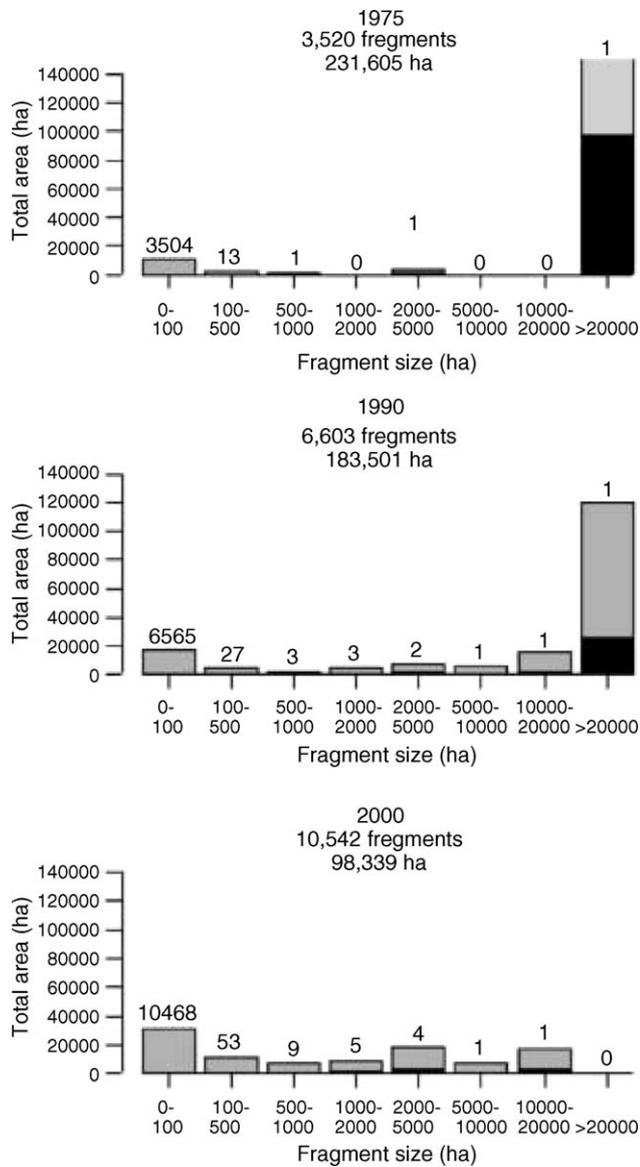


Fig. 3. Variation of forest fragment size (measured by bar height) and core area (in black) in the Highlands of Chiapas in the two study periods. Values on top of the bars represent the number of fragments belonging to each size interval.

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.

Table 4  
Change in spatial pattern of native forest in the Highlands of Chiapas in 1975, 1990, and 2000

Landscape indices	1975	1990	2000
Mean patch size (ha)	65.0 [0.45–211180]	26.9 [0.45–119516]	8.7 [0.45–13279]
Patch density ( $n/100$ ha)	1.0	1.9	3.2
Largest patch index (%)	60.7	35.1	4.0
Total edge length (km)	24781	50114	38400
Total core area (ha)	99422	29860	9611
Mean proximity	101369 [0.02–587150]	60017 [0–342240]	1,405 [0–34466]

For patch indices, median, minimum and maximum values are given.

Mean size of forest patch decreased from 65 ha in 1975 to 27 ha in 1990 (Table 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%) (Fig. 4a). By 1990, all cover types became less aggregated in the landscape 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 (Fig. 4a).

Forest fragments became increasingly adjacent to non-forest cover and, conversely, detached from shade coffee plantations (Fig. 4b). The greatest 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 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 (Fig. 4b).

## 4. Discussion

### 4.1. Evaluation of methods and results

Monitoring of land cover change based on remote sensing data is certainly an imprecise task (Foody, 2002). Although 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 might contain errors.

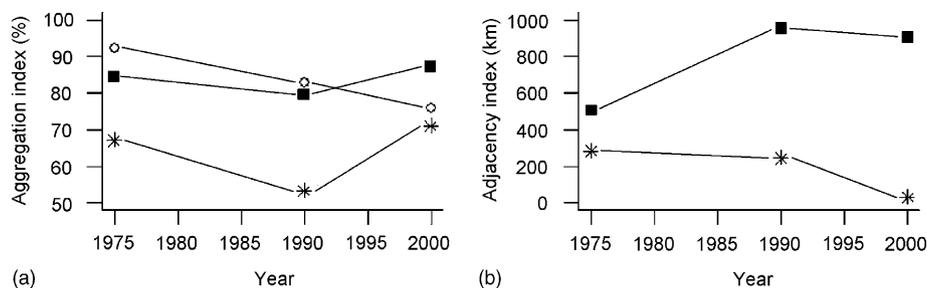


Fig. 4. Changes in (a) aggregation index and (b) adjacency index applied to the major land cover types in the Highlands of Chiapas. Land cover types: (○) native forest; (■) non-forest cover; and (\*) shaded coffee plantation.

Different studies have stressed the importance of correcting land cover area estimates from the confusion matrix (e.g. Card, 1982; Dymond, 1992; Gallego, 2004) but these corrections have been rarely applied in studies of land cover change (but see Reams and 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 and sound 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 and Hill, 1996; Cayuela et al., in press-b). Forest loss estimates are particularly sensitive to what is being defined as ‘forested area’ (Ochoa-Gaona and González-Espinosa, 2000). Despite our attempt to 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.

#### 4.2. 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 and 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 and 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 and García, 1992; Ite and Adams, 1998; Sierra, 2000; Cohen et al., 2002; Staus et al., 2002; but see Sader and 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 and 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 deforestation rates can be sometimes deceptive due to the use of different criteria for vegetation classification (Foody and 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 and 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 indicate 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.

Among the main causes of deforestation are human population pressure and an increasing demand of land for agriculture and timber products from tropical forests (Rudel and Roper, 1997; Lawrence et al., 1998; Laurance, 1999; Ochoa-Gaona and 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% (Gobierno de Chiapas, 1971; INEGI, 2000). 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 practised 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), and 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).

#### 4.3. 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 (Fig. 2). The general trend was towards an increase in the number of fragments (Fig. 3) and isolation of patches, and a decline in the mean patch size (Table 4). However, total edge length increased in the earliest stage of forest loss and fragmentation but decreased during the later stages. Echeverría et al. (in press) 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., in press).

The connectivity between forest fragments, or its opposite, the degree of isolation, has frequently been considered as one of the most important factors on population dynamics (Tischendorf and 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 almost 100-fold during the period studied. This effect of deforestation was also observed by Imbernon and Branthomme (2001) and Echeverría et al. (in press) 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 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 (Fig. 4a) and with an abrupt separation of shade coffee plantations surrounding forest fragments during the 1990–2000 period (Fig. 4b). Shade coffee plantations have been shown to act as refuges for the biodiversity of the surrounding forest habitats (Perfecto et al., 1996; Moguel and Toledo, 1999; Mas and 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., in press-a). Due to this, the positive effect that these low impact agro-ecosystems may be exerting on the surrounding forest may diminish.

#### 4.4. 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). The reason for this is that confounding factors can mask many fragmentation effects (Ewers and Didham, 2006). For instance, there are multiple ways in which species traits like trophic level, dispersal ability and degree of habitat specialisation influence species-level responses. The temporal scale of investigation may have a strong influence on the results of a study, with short-term crowding effects eventually giving way to long-term extinction debts (Hanski and Ovaskainen, 2002). Moreover, many fragmentation effects like changes in genetic, morphological or behavioural traits of species require time to appear. In addition, 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). According to Ewers and Didham (2006), actual empirical measurements of the landscape threshold suggest that a figure like 20% is far too simplistic. In fact, the threshold for some species is as high as 95%, and varies widely from species to species.

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 degradation 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 (González-Espinosa and Ramírez-Marcial, personal communication). 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. We believe that large forest tracts do not necessarily contribute to the preservation of the ecological integrity of the forest and/or support high species diversity (see Redford, 1992). 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 and de la Montaña, 2004). Cayuela et al. (in press-c) found that hotspots of tree diversity were mostly associated to ridge-top montane cloud forests, a habitat that is rapidly disappearing in the region (Cayuela et al., in press-a). A first priority thus could be preserving forest fragments containing some of these highly diverse habitats. Management of the external influences on the natural system should be also an important component of any conservation strategy (Saunders et al., 1991). Maintenance of a diverse landscape structure increases the survival of seed 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 and 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 and 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 provides further evidence of the usefulness of remote sensing approaches to monitor deforestation rates and

patterns of fragmentation in inaccessible 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 minimise 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.

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## References

- Alcorn, J.B., 1993. Indigenous peoples and conservation. *Conserv. Biol.* 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. *Biol. Conserv.* 113, 245–256.
- Arnold, J.E., Ruiz Pérez, M., 2001. Can non-timber forest products match tropical forest conservation and development objectives? *Ecol. Econ.* 39 (3), 437–447.
- Balick, M.J., Mendelsohn, R., 1992. Assessing the economic value of traditional medicines from tropical rain forests. *Conserv. Biol.* 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? *J. Forest.* 93, 21–24.
- Card, D.H., 1982. Using known map category marginal frequencies to improve estimates of thematic map accuracy. *Photogramm. Eng. Remote Sens.* 44, 1033–1043.
- Cayuela, L., Golicher, J.D., Rey Benayas, J.M., in press-a. The extent, distribution, and fragmentation of vanishing montane cloud forest in the Highlands of Chiapas, Mexico. *Biotropica*.
- Cayuela, L., Golicher, J.D., Salas Rey, J., Rey Benayas, J.M., in press-b. Classification of a complex landscape using Dempster–Shafer theory of evidence. *Int. J. Remote Sens.*
- Cayuela, L., Rey Benayas, J.M., Justel, A., Salas Rey, J., in press-c. Modelling tree diversity in a highly fragmented tropical montane landscape. *Glob. Ecol. Biogeogr.*
- Ceballos, G., Rodríguez, P., Medellín, R.A., 1998. Assessing conservation priorities in megadiverse Mexico: mammalian diversity, endemism, and endangerment. *Ecol. Appl.* 8, 8–17.
- Cohen, W., Spies, T., Alig, R., Oetter, D., Maiersperger, T., Fiorella, M., 2002. Characterizing 23 years (1972–1995) 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. *Conserv. Biol.* 6 (1), 84–90.
- Dymond, J.R., 1992. How accurately do image classifiers estimate area? *Int. J. Remote Sens.* 13 (9), 1735–1742.
- Eastman, J.R., 2001. Idrisi 32, release 2 Guide to GIS and Image Processing. Clark Labs, Clark University, Massachusetts.
- Echeverría, C., Coomes, D., Salas, J., Rey Benayas, J.M., Lara, A., Newton, A., in press. Rapid deforestation and fragmentation of Chilean temperate forests. *Biol. Conserv.*
- ESRI, 1999. ArcView 3.2. Environmental Systems Research Institute, Inc., Redlands, California, USA.
- Ewers, R.M., Didham, R.K., 2006. Confounding factors in the detection of species responses to habitat fragmentation. *Biol. Rev.* 81 (1), 117–142.
- Fahrig, L., 1997. Relative effects of habitat loss and fragmentation on population extinction. *J. Wildl. Manage.* 61 (3), 603–610.
- Fahrig, L., 2001. How much habitat is enough? *Biol. Conserv.* 100, 65–74.
- Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol., Evol. Systemat.* 34, 487–515.
- Foody, G.M., 2002. Status of land cover classification accuracy assessment. *Remote Sens. Environ.* 80, 185–201.
- Foody, G.M., Hill, R.A., 1996. Classification of tropical forest classes from Landsat TM data. *Int. J. Remote Sens.* 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 Ecol.* 162, 259–272.
- Gallego, F.J., 2004. Remote sensing and land cover area estimation. *Int. J. Remote Sens.* 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. *Environ. Manage.* 34 (6), 768–785.
- Gobierno de Chiapas, 1971. Censo General de Población 1970/1971. Estado de Chiapas, México, D.F.
- 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.
- Hanski, I., Ovaskainen, O., 2002. Extinction debt at extinction threshold. *Conserv. Biol.* 16, 666–673.
- Imbernon, J., Branthomme, A., 2001. Characterization of landscape patterns of deforestation in tropical rain forests. *Int. J. Remote Sens.* 22, 1753–1765.
- INEGI, 2000. Censo de Población y Vivienda. Instituto Nacional de Estadística, Geografía e Informática, México.
- Ite, U.E., Adams, W.M., 1998. Forest conversion, conservation and forestry in Cross River State, Nigeria. *Appl. Geogr.* 18, 301–314.
- Laurance, W.F., 1999. Reflections on the tropical deforestation crisis. *Biol. Conserv.* 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 Ecol.* 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. *Ecol. Res.* 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. *Phil. Trans. Roy. Soc. London, Ser. B* 359, 549–555.
- Mas, A.H., Dietsch, T.V., 2004. Linking shade coffee certification to biodiversity conservation: butterflies and birds in Chiapas, Mexico. *Ecol. Appl.* 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 program produced by the authors at the University of Massachusetts, Amherst, Available at: [www.umass.edu/landeco/research/fragstats/fragstats.html](http://www.umass.edu/landeco/research/fragstats/fragstats.html).
- Mertikas, P., Zervakis, M.E., 2001. Exemplifying the theory of evidence in remote sensing image classification. *Int. J. Remote Sens.* 22 (6), 1081–1095.
- 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. *Photogramm. Remote Sens.* 57, 289–299.
- Moguel, P., Toledo, V.M., 1999. Biodiversity conservation in traditional coffee systems of Mexico. *Conserv. Biol.* 13, 11–21.
- Ochoa-Gaona, S., 2001. Traditional land-use systems and patterns of forest fragmentation in the Highlands of Chiapas, Mexico. *Environ. Manage.* 27 (4), 571–586.
- Ochoa-Gaona, S., González-Espinosa, M., 2000. Land use and deforestation in the highlands of Chiapas, Mexico. *Appl. Geogr.* 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. *Biodivers. Conserv.* 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. *For. Ecol. Manage.* 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. *For. Ecol. Manage.* 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. *Biodivers. Conserv.* 7, 385–403.
- Reams, G.A., van Deusen, P.C., 1999. The southern annual inventory system. *J. Agric. Biol. Environ. Stat.* 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, J.M., 2004. Identifying areas of high-value vertebrate diversity for strengthening conservation. *Biol. Conserv.* 114, 357–370.
- Rudel, T., Roper, J., 1997. The paths to rain forest destruction: crossnational patterns of tropical deforestation, 1975–1990. *World Dev.* 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. *Conserv. Biol.* 5, 18–32.
- Sayer, J.A., Whitmore, T.C., 1991. Tropical moist forests destruction and species extinction. *Biol. Conserv.* 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. *Appl. Geogr.* 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 Ecol.* 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. *Conserv. Biol.* 15, 856–866.
- Thoms, C.A., Betters, D.R., 1998. The potential for ecosystem management in Mexico's forest ejidos. *For. Ecol. Manage.* 103, 149–157.
- Tinker, B.P., Ingram, J.S.I., Struwe, S., 1996. Effects of slash-and-burn agriculture and deforestation on climate change. *Agric. Ecosyst. Environ.* 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. *J. Appl. Ecol.* 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. *Conserv. Biol.* 12 (5), 1091–1102.
- Wolf, J.H.D., Flamenco, A., 2003. Patterns in species richness and distribution of vascular epiphytes in Chiapas, Mexico. *J. Biogeogr.* 30, 1689–1707.