The Extent, Distribution, and Fragmentation of Vanishing Montane Cloud Forest in the Highlands of Chiapas, Mexico

Luis Cayuela
Departamento de Ecología, Universidad de Alcalá, C.P. 28871, Alcalá de Henares, Madrid, Spain.

Duncan J. Golicher
Departamento de Ecología y Sistemática Terrestres, División de la Conservación de la Biodiversidad, El Colegio de la Frontera Sur, Carretera Panamericana y Periférico Sur s/n, C.P. 29290, San Cristóbal de las Casas, Chiapas, Mexico.

and

Jose María Rey-Benayas
Departamento de Ecología, Universidad de Alcalá, C.P. 28871, Alcalá de Henares, Madrid, Spain.

ABSTRACT
Montane cloud forest (MCF) has high levels of species diversity, contributes positively to the catchment water yield, and is a globally threatened habitat type. The shortage of reliable data regarding the area currently occupied by MCF remains an obstacle to operational conservation planning in Mexico. This paper assesses how much MCF remains in the central Highlands of Chiapas (Mexico) and how fragmented it is in relation to other forest cover. We estimated that the area covered by MCF was between 3700–5250 ha. This estimate contrasted with the approximately 40,000 ha reported for the same region by the Mexican National Forest Inventory in 2000. MCF was highly scattered and fragmented within a matrix of other tropical montane forest types. Other forest types may be partially buffering the remaining MCF habitats, however, mitigating their disturbance and enhancing their connectivity. We conclude that mechanisms should be sought to promote the protection of core areas containing MCF fragments in agreement with communal and private landowners and to conserve the ecological functions of surrounding buffer zones. Such a conservation strategy would match the natural configuration of these endangered habitats.

RESUMEN
El Bosque Mesófilo de Montaña o Bosque Nublado (BN) es un ecosistema único y de gran valor ecológico. Ello se debe, en parte, a la gran diversidad de especies que alberga y al papel que juega en la captación del agua. Aunque estos bosques se encuentran amenazados a nivel mundial, no existen datos fiables sobre la superficie que ocupan actualmente ni su distribución. Esto impide la elaboración de estrategias concretas de conservación. En el presente trabajo se investiga cuánto Bosque Nublado queda en Los Altos de Chiapas (México) y cuán fragmentado se encuentra en relación a otras formaciones forestales. Los resultados de este estudio sugieren que todavía existen entre 3700–5250 ha en el área de estudio. Estas cifras contrastan notablemente con las cerca de 40,000 ha obtenidas por el Inventario Forestal Nacional de México del año 2000. Los remanentes de BN se encuentran muy dispersos, fragmentados e inmersos en una matriz constituida mayormente por otros tipos de bosques tropicales de montaña. Sin embargo, la existencia de otras formaciones forestales que aparecen entremedias con el BN podría favorecer la conectividad de estos hábitats y mitigar, al menos en parte, la perturbación a la que están sometidos. Concluimos que es necesario buscar distintos mecanismos para promover la protección de áreas protegidas que contengan los remanentes actuales de BN en acuerdos establecidos con las comunidades y los propietarios de los predios, y la conservación de las funciones ecológicas de las áreas forestales colindantes.

Key words: Chiapas; Dempster-Shafer; Evergreen Cloud Forest; fragmentation; habitat mapping; Montane Cloud Forest; remote sensing.

Montane cloud forest (MCF) is a type of evergreen mountain forest distributed throughout the tropical belt at elevations between 1500 and 3000 m (but as low as 600 m in tropical island landscapes) and within a wide range of rainfall regimes (500–10,000 mm/yr; Hamilton et al. 1995). Because of the broad range of conditions in which it occurs, and the difficulty in finding consistent floristic differences between MCF and co-occurring forest types, there is no consensus definition of exactly what MCF is. Hamilton et al. (1995) and Hamilton (2001) outlined the following characteristics for MCFs: (1) capacity to capture or strip water from clouds which may result in increased catchment water yield when compared with other vegetation types; (2) soils that are wet, frequently waterlogged, and typically highly organic (histosols); (3) high proportion of its biomass in the form of epiphytes; (4) reduced load of woody climbers when compared with lower altitude tropical moist forest; and (5) high local biodiversity in terms of herbs, shrubs, and epiphytes, including a high proportion of endemic species.

MCF is a rare type of forest, making up only 2.5 percent of the total area of the world’s tropical forests (Table 1). There are no accurate data as to how much MCF now remains worldwide. Accurate mapping is complicated by lack of resources and difficult ground access. This has led to a tendency to produce potential distributions for MCF within defined altitudinal ranges where it is likely to occur (Bubb et al. 2004). Despite this lack of information, there is a consensus that MCF is disappearing rapidly (Bruijnzeel & Hamilton 2000). For example, the Dominican Republic has lost 90 percent of its MCFs (Garcia & Roersch 1996). In Colombia, only

1 Received 14 January 2005; revision accepted 7 September 2005.
2 Corresponding author; e-mail: luis.cayuela@uah.es
10 percent of the Andean forests remain (Henderson et al. 1991). In Ecuador, MCF has disappeared completely from most of the central and western regions (Dodson & Gentry 1991). In Honduras, an annual rate of MCF loss of 4 percent has been estimated, and if these rates continue, MCF would almost completely disappear in less than 20 yr (Mejía 2001).

MCF provides important ecological services, the most notable being its potential for water-capture (Bruijnzeel 2001). The conversion of MCF to pasture and croplands often leads to loss of soil properties, resulting in reduced or erratic stream flows to adjacent lowlands (Hamilton 2001). The recognition of the hydrological value of MCF has been one of the main reasons for the establishment of protected areas within them. Examples include the Parque Nacional de la Tigra in Honduras, the Parque Nacional Henri Pittier in Venezuela, the Monteverde Reserve in Costa Rica, and the privately owned reserve of La Yerbabuena in Mexico.

In Mexico, the distribution of MCF is known to be highly fragmented and restricted to less than 1 percent of the country (Luna et al. 2001). It has been estimated that more than 90 percent of the original MCF has been lost, making this vegetation type one of the most threatened in the country. Chiapas has one of the largest areas of MCF in Mexico (Breedlove 1981, Ramírez-Marcial 2001). However, there are no accurate maps of where they can be found, no estimates of deforestation rates, and limited understanding of the socio-economic forces driving such change (Bubba et al. 2002).

In this context, we estimate MCF extent, distribution, and degree of fragmentation in the Highlands of Chiapas, Mexico. We performed a land cover classification of Landsat Enhanced Thematic Mapper (ETM+) satellite imagery based on Dempter-Shafer algorithm (Mertikas & Zervakis 2001). MCF extent was estimated from the resulting land cover classification. The probabilistic nature of this classification method allowed estimation of upper and lower credible bounds for the area covered by MCF by modifying the probabilities of each pixel to belong to this class. In addition, we examined the degree of fragmentation, exposure to disturbance, and isolation of the current MCF remnants. The analysis was performed at two different spatial scales: at the class level by considering MCF as a whole and at the patch level by considering only the largest habitat fragments. Two approaches were adopted based on the assumption that MCF habitat patches occur within a highly contrasting hostile surrounding habitat and the assumption that MCF patches intermingle with patches of other forest types that may be similar in structure and floristic composition to MCF.

The specific objectives of the study were: (1) to provide a reliable estimation of how much MCF remains in the central Highlands of Chiapas, Mexico, through the analysis of Landsat ETM+ satellite images; (2) to investigate the conservation value of the existing remnants in terms of size, shape, isolation, and distribution of MCF patches; and (3) to assess whether other forest formations play a role in maintaining the integrity of MCF remnants. Because MCF is vanishing rapidly from all of Central America, assessing potential sites for conservation must be mandatory in order to provide international organizations with the information they need to implement prompt action. These objectives have not been addressed before for this region and are crucial to help establishing guidelines that can be used in strategies for the conservation of this highly threatened habitat in Mexico.

### METHODS

**STUDY AREA.**—The study area covers the central Highlands of Chiapas, Mexico, and extends over ca 3500 km² (Fig. 1). Several forest types are found in the Highlands, including oak, pine-oak, pine, and MCFs (Rzedowski 1978). Elevation ranges from 600–2900 m (mostly above 1500 m). The topography is abrupt with fairly steep slopes (mean = 14.8°, SD = 9.6°). Mean annual temperature is 13–14°C, and mean annual rainfall is 1200–1500 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. Most inhabitants belong to Mayan ethnic groups. The main economic activities are traditional agriculture and non-commercial forestry. The traditional shifting cultivation of *milpa* is a rain-fed, labor-intensive system using different cultivars of maize in association with beans, squash, chili, and other edible vegetables.

### DEFINITION OF LAND COVER CLASSES

We defined six classes of land cover: (1) MCF; (2) oak forest, (3) pine-oak forest, (4) pine forest, (5) shade coffee plantations, and (6) non forest cover. Non forest cover constituted agriculture fields, pasturelands, recent falls, cleared areas, bare soil, and urban areas. The forests themselves have been continuously disturbed over a long time period, creating a complex mosaic of successional stages of development (Ramírez-Marcial et al. 2001, Galindo-Jaimés et al. 2002). The successional dynamics in the region are quite difficult to generalize. There is a tendency for early successions to be dominated by pine species.
Floristic, structural, and physiognomic attributes were used as ground-based criteria for identification of MCF habitats. Some indicators of MCF were presence of wet soils during the dry season, abundance of mosses, vascular epiphytes, and lianas, and preponderance of broad-leaved species. Preferential genera of Mexican MCF conditions are Clethra L., Magnolia L., Meliosma Blume, Styrax L., Symplocos Jacq., and Ternstroemia Mutis ex L.f. (Alcántara et al. 2002). Only a few species from these genera occur in oak forest or coniferous forest. Indicator species for MCF include Persea americana Miller, Cinnamomum spp., Nectandra spp., Ocotea spp., Magnolia sharpii Miranda, Drimys granadensis L.f., Meliosma dives Standl. et Steyerm., Microtropis contracta Lundell, Podocarpus matudae (Buchholz & Gray), Weinmannia pinnata L., or the arborescent fern Cyathea fulva Fée. Oak species also tend to differ in these formations from those found in oak and pine-oak forests. Examples include Quercus acatenangensis Trel., Q. benthamii A.D.C., Q. lancifolia Cham. and Schltld., and Q. sapatofolia Liebm. Pine-oak-liquidambar forests were also included as a successional stage of MCF following Breedlove (1981) and Rzedowski (1978).

PRELIMINARY DATA PROCESSING.—A subset from three Landsat ETM+ scenes with a resolution of 30 m were used (path 21 row 48 taken on 3 April 2000; path 21 row 49 taken on 19 April 2000; path 22 row 48 taken on 25 March 2000). Geometric rectification was performed using a 1:50,000 road map (LAIGE 2000) and a second-order polynomial nearest neighbor algorithm (root mean square error <0.5 pixels). To reduce the external effects on vegetation reflectance, an atmospheric correction was applied, assuming a flat surface, null diffuse irradiance, and Lambertian reflectance. The technique used was the default transmittance method proposed by Chavez (1996). Effects on shaded slopes were accounted for by performing topographic corrections using a C model (Teillet et al. 1982), which is recommended for high solar angles as it was the case of our satellite images (solar angles >45°). All the processing work was performed using the PCI 7.0 software package (PCI 2001).

CLASSIFICATION PROCEDURE.—Land cover classification was performed with the Dempster–Shafer classifier (Eastman 2001). The Dempster–Shafer theory of evidence is a generalization of the Bayesian theory of subjective probability which allows for combination of different independent lines of evidence derived from various sources in order to obtain degrees of belief for different hypotheses (Kontoes et al. 1993, Mertikas & Zervakis 2001). The procedure is particularly useful when spectral data alone is insufficient to discriminate between some classification categories (Cayuela et al. in press). Detailed applications of this methodology to remote sensing can be found in Kontoes et al. (1993) and Mertikas & Zervakis (2001).

In our study, the Dempster–Shafer classification procedure was implemented by combining evidence derived from both multispectral data and expert knowledge. Each line of evidence was formalized into one or various probability maps (with values between 0 and 1) supporting one or multiple hypotheses at the same time. After combining all evidences by means of the Dempster–Shafer’s algorithm, results were obtained in the form of layers that defined the degree of belief or probability of each pixel belonging to each of the hypotheses or classification categories. A land cover classification map was then obtained by assigning each pixel to the category that was the most probable after the spectral and ancillary information had been combined (hardening process). We used five lines of evidence (Table 2):
TABLE 2. Lines of evidence in support of different hypotheses (MCF = Montane cloud forest; OF = Oak forest; POF = Pine-oak forest; PF = Pine forest; CP = Coffee plantation; NF = Non forest) used in Dempster–Shafer classification procedure. Function type refers to the manner in which the knowledge regarding a certain hypothesis was shaped. Note that maximum probability for evidences derived from expert knowledge was set at 0.8 and 0.6 leaving room for uncertainty concerning our knowledge about the system.

<table>
<thead>
<tr>
<th>Type</th>
<th>Line of evidence</th>
<th>Supported hypothesis</th>
<th>Function type</th>
<th>Probability range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Remote sensing</td>
<td>Multi-spectral data worked out through Bayes classification</td>
<td>MCF</td>
<td>Variance/Covariance matrix</td>
<td>0.0–1.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>OF</td>
<td>0.0–1.0</td>
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<td></td>
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<td>POF</td>
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<td>PF</td>
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<td>CP</td>
<td>0.0–1.0</td>
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<td></td>
<td></td>
<td>NF</td>
<td>0.0–1.0</td>
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</tr>
<tr>
<td>Expert knowledge</td>
<td>Elevation</td>
<td>MCF, OF, POF, PF, NF</td>
<td>Linear</td>
<td>0.0–0.8</td>
</tr>
<tr>
<td></td>
<td></td>
<td>CP, OF, POF, PF, NF</td>
<td>Linear</td>
<td>0.0–0.8</td>
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<td></td>
<td>Slope</td>
<td>MCF, OF, POF</td>
<td>Linear</td>
<td>0.0–0.8</td>
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<td></td>
<td></td>
<td>PF, CP, NF</td>
<td>Linear</td>
<td>0.0–0.8</td>
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<tr>
<td></td>
<td>Distance to human settlements</td>
<td>NF</td>
<td>Distance-based</td>
<td>0.0–0.8</td>
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<tr>
<td>Landscape perception</td>
<td>regarding main vegetation types</td>
<td>POF, PF, NF</td>
<td>Fixed probability</td>
<td>0.0/0.6</td>
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<td></td>
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<td>OF, POE, PF, NF</td>
<td>Fixed probability</td>
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<td>OF, POE, NF</td>
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<td>MCF, OF, NF</td>
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<td>MCF, OF, POF, NF</td>
<td>Fixed probability</td>
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<td>CP, NF</td>
<td>Fixed probability</td>
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</table>

(1) Remote sensing data (bands one, two, three, four, five, and seven) that was incorporated into the analysis in the form of Bayes probabilities based on the variance/covariance matrix derived from training sites;
(2) Elevation, assuming that MCF was more probable at higher elevations (above 2000 m) and coffee plantations at lower ones (below 2000 m);
(3) 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;
(4) Distance to human settlements and roadways, using updated roadway and human settlement maps as an evidence for presence of non forest areas. This information was derived from a road map and a map of localities containing data from population censuses. As the map did not specify the size of the settlements, only the geographical position of the settlement center, a map representing the effect of settlement size was derived based on a function inferred from population data (see Cayuela et al. in press);
(5) Landscape perception regarding main vegetation types, for which experts’ opinions were collected through participatory mapping. This output a probability map that represented the consensual view of the spatial patterns of vegetation types throughout the study area based on over 10 yr field experience.

In addition, a polygon layer displaying georeferenced small coffee holdings (COMCAFE 2001) was used as hard evidence in support of coffee plantations. Further information about this procedure is described by Cayuela et al. (in press).

We verified our classification using 303 independent ground field points. The areas where points were taken had an extension of at least 90 × 90 m (i.e., 3 × 3 pixels) and were located at least 30 m from the border to avoid positional errors in geo-referencing control points. Completely randomized selection of verification sites was impossible as ground access in the region was limited. A confusion matrix was generated and three kinds of errors were calculated: (1) error of omission, (2) error of commission, and (3) overall error with 95 percent confidence intervals. The Tau coefficient, which is a variation of the commonly used Kappa coefficient, was calculated to evaluate the improvement of the classification over a random assignment of pixels to groups (Ma & Redmond 1995). The transformed divergence technique was used to find the separability between the land cover spectral signatures. A value of 2000 may be considered as excellent “between-class” separability, values above 1900 can be considered good separability, and values below 1700 suggest very poor separability. All classification procedures and analyses were implemented with Idrisi 32 (Eastman 2001).

ESTIMATING MONTANE CLOUD FOREST EXTENT.—For each of the six thematic classes, we obtained a layer showing the degree of belief
given the relevant lines of evidence. Subsequently, each pixel was assigned to the class for which it had the highest degree of belief. From the resulting thematic map, we estimated the area covered by MCF as well as for the remaining classes. Sensitivity analysis was carried out by modifying the degree of belief in MCF at regular intervals up and down to 50 percent of its initial value. Following each of these transformations, a hardening process was implemented and MCF area was estimated in relation to changes in area for other forest classes. This procedure did not produce conventional confidence intervals based on the likelihood of data given a hypothesis. Instead, the subjective interpretation of probability led to upper and lower credible limits for the amount of MCF remaining that were consistent with the available expert knowledge.

**Spatial pattern analysis.**—We analyzed the spatial configuration of MCF fragments using the following progressive relaxations of the definition of MCF: (1) MCF treated as a completely contrasting habitat with regard to all other classes; (2) MCF and oak forest treated as similar habitats as opposed to any other class; and (3) MCF, oak forest and pine-oak forest as similar habitats as opposed to any other class. All these analyses were conducted on simple binary maps by combining the target habitats in one group and merging all the other classes in another group. In addition, we calculated a co-occurrence matrix based on the original six classes of land use, from which we estimated the percentage of adjacencies (i.e., pairs of patch types appearing side by side on the map) between MCF and other classes.

Analyses of spatial patterns were carried out at two different scales: at the class level, considering MCF as a whole and at the patch level, with particular focus on the 20 largest MCF patches. Quantification of the spatial configuration of forest fragments was conducted based on the following set of key metrics selected after reviewing recent forest fragmentation studies: (1) area (ha); (2) core area (total patch size remaining after removing the outer part of the patch; we selected a 30 m edge following Williams-Linera et al. 1998) (ha); (3) edge density (m/ha); (4) perimeter–area ratio (equals the ratio of the patch perimeter (m) to area (m²)); and (5) patch contiguity index (a measure of patch shape, where values close to 0 indicate low contiguity among pixels within a grid-cell patch and increase to a limit of 1 as connectedness among pixels increases). These analyses were computed using the software FRAGSTATS 3.3 (McGarigal et al. 2002).

**RESULTS**

**Extent of montane cloud forest.**—Using the categorical land-cover map obtained through the Dempster–Shafer classification procedure, we estimated MCF extent in the study area as 4650 ha, equivalent to 1.4 percent of the total area. Overall, forest cover occupied 28.1 percent of the total area (MCF = 1.4%, oak forest = 7.7%, pine-oak forest = 8.4%, pine forest = 10.6%), whereas non forest and coffee plantations occupied ca 67.4 and 4.4 percents of the study area, respectively.

By modifying our degree of belief in MCF by ±50 percent, we estimated the amount of MCF as between 3700 and 5250 ha. These changes in estimated area associated with shifts in the degree of belief in MCF were linked mainly to changes in estimated area of oak forest and, to a lesser extent, of pine-oak forest and pine forest.

**Spatial pattern of montane cloud forest.**—MCF exhibited an intermediate frequency of adjacency between pixels of the same type (51.0%), an intermediate frequency of adjacency with other forest types (43.2%), and low frequency of adjacency with non forest fragments and coffee plantations (2.9%).

Figure 2 illustrates the extent and spatial distribution of MCF cover in simple binary maps when considered: on its own, in combination with oak forest, and in combination with oak and pine-oak forest. Metrics for MCF patches are shown in Figure 3. Because edge density and the contiguity index were highly correlated with patch area and the perimeter–area ratio, respectively ($r > 0.9$), we did not report these metrics in the results. Core area was also highly correlated with patch area ($r > 0.9$). However, we considered it interesting to report these two metrics separately as they both provide important information about the spatial configuration of MCF. Total area was estimated in 4600 ha. Adding the oak forest buffer around the MCF patches increased total area to 19,000 ha. When considering pine-oak forest in addition to oak forest buffers, total area rose to 30,000 ha. When using an oak forest buffer number of patches decreased to 5400 and mean patch area increased to 3.6 ha. When both oak forest and pine-oak forest were considered as buffers for MCF, number of patches decreased to 3000 and mean patch area increased to 10.1 ha.

Total core area represented a small fraction of total area, ranging from 550 to 1000 ha when lower and upper bounds under the sensitivity analysis were considered. However, it increased to 7300 ha when including contiguous oak forest habitat patches. This quantity increased to 13,000 ha when pine-oak forest habitat patches were included. Mean core area behaved in a similar way to mean patch area but with much lower values. Estimated mean core area was 0.1 ha and increased up to 4.4 ha when considering all woody buffers.

Distribution of fragments based on the perimeter–area ratio was highly skewed toward large values. The perimeter–area ratio for most fragments decreased considerably when other forest formations surrounding MCF patches were considered. Such a response revealed a tendency toward agglomeration of different forest subtypes in larger and less exposed forest fragments.

**Quantifying spatial pattern on the largest montane cloud forest fragments.**—Metrics were computed for the 20 largest patches. These occupied some 31 percent of the total area covered by MCF. Figure 4 shows the patch area, the core area, and the perimeter–area ratio for the 20 largest MCF habitat patches when considering MCF habitat patches on their own and bound to contiguous similar forest habitats (oak forest and oak plus pine-oak forest). The largest patch (L) had an area of 550 ha, excluding forest formations other than MCF. The following three largest patches A,
D, and E had estimated areas of 210, 135, and 95 ha, respectively. All the remaining 16 largest patches did not exceed 50 ha. Core area was much lower than patch area, the largest patch (L) having some 250 ha, less than half the total area of its corresponding patch area. The perimeter–area ratio was generally lower for the largest patches.

We restate that the decision to analyze the effect of adding the oak forest and pine-oak forest around MCF was taken in order to draw out the effect of these formations in preventing complete fragmentation and isolation of the remaining MCF patches. In the middle column of Figure 4, it is possible to observe that nine patches...
FIGURE 4. Metrics for the 20 largest patches showing the area (top), core area (middle row), and perimeter–area ratio (bottom row), when considering MCF only (left), in conjunction with oak forest (middle) and in conjunction with pine-oak and oak forests buffers (right).

(A–I) in the Tzontehuitz mountain range were embedded within a common matrix of oak forest (see Fig. 5a). In this case, all the MCF patches and the surrounding oak forest matrix comprised an area of ca 2300 ha. Adding to this area the cover of pine-oak forest in close contact with MCF (left column), the resulting forested patch area increased up to ca 2800 ha and led to the incorporation of one new MCF patch that was otherwise unconnected (J). Similarly, oak forest cover brought together two of the largest MCF habitat patches at Huitepec Nature Reserve (M–N), leading to a comparatively large mixed forest patch of about 800 ha when pine-oak forest was also considered. In all other cases, inclusion of other forest formations did not result in the linkage of otherwise separated MCF habitat patches, only in an increase in area and core area. This increase was in some cases quite large, such as in El Extranjero (S) where some scattered small patches of MCF (the largest consisting of 23 ha) were surrounded by ca 1600 ha of uninterrupted pine-oak forest.

ACCURACY ASSESSMENT.—A confusion matrix between thematic classes (Table 3) revealed the classes that were commonly mixed in the classification process. The Tau coefficient showed a 70.6 percent of agreement between the predicted land covers and field data. This demonstrated an acceptable level of agreement between the predicted land covers and field data (following Monserud & Leemans 1992). The transformed divergence index established a poor spectral separability between pine-oak and pine forests, and between MCF and oak forest in one of the scenes (path 22 row 48). A regular degree of separability was achieved between MCF and pine-oak forest, MCF and pine forest, and oak forest and coffee plantation in some of the satellite scenes. For all other classes, the spectral separability was good.

DISCUSSION

IMPLICATIONS OF THE STUDY.—From the general trends observed in all Central America, and particularly in Mexico (Cairns et al. 1995, Bubb et al. 2004), we can assume that MCF loss has been large in the last decades. Current evidences also show that deforestation rates have considerably increased in the last decades in the region (Ochoa-Gaona & González-Espinosa 2000, Cayuela et al. 2006), although it is difficult to ascertain how much of this forest loss could be attributable to MCF due to the low resolution of temporal satellite data (particularly MSS Landsat satellite imagery). Thus, it is very difficult to find a suitable historical reference point.

Today, the amount of MCF that remains in the Highlands of Chiapas is extremely small compared to the 350,000 ha that make up the study area. We found two previous estimates of MCF extent in the study area: the Mexican National Forestry Inventory (SEMARNAP 2000) and a report on the situation of the cloud forest in northern Chiapas (Bubb 1991). Our results differed in important respects from those presented in these studies. The SEMARNAP study reports 22,400 ha of mature MCF and 16,200 ha of disturbed MCF with secondary vegetation for the same area. It is not clear how the SEMARNAP study made this distinction due to the difficulties to separate primary MCF from secondary MCF consistently using Landsat satellite imagery (see Sader et al. 1989, Steininger 1996). Comparisons with our maps (see Fig. 5b)
revealed that most of the disturbed MCFs in the SEMARNAP map were in fact coffee plantations that had been misclassified. The buffering property of other mountain forests which can shelter MCF remnants may extend to agro-ecological shade coffee plantations (Moguel & Toledo 1999). However, in the Highlands of Chiapas, coffee plantations have become altitudinally isolated from the forest type we define as MCF and should not have been classified as MCF.

Bubb’s (1991) study reported only 3500 ha of MCF and provided much more reliable insight in current patterns of MCF distribution. The principal sources for his maps of MCF distribution were 1982 aerial photographs and 1:250,000 scale maps of land use and vegetation from the National Institute of Statistics, Geography and Information (INEGI) in addition to limited field surveys. Given the large rates of deforestation observed in this area in the last decade (Cayuela et al. 2006), we believe that at the time of the study (1990) MCF occupied a much larger area than that reported by Bubb. Apart from changes that may have occurred since this period, the reasons for the differences between our study and this report are clearly due to methodological issues. Bubb’s report was limited to sites with 500 ha or more of continuous forest cover as portrayed by the INEGI 1:250,000 map. Therefore, small MCF patches, many of them interspersed with other vegetation types, were disregarded. Here, we reiterate a key virtue of our method—unlike other approaches to imprecise estimation, we did not overlook small forest patches. This is important in this particular conservation context, as these habitats are known to harbor isolated individuals of endangered species, maintain habitat heterogeneity and diversity at the landscape level, and act as natural seed sources for restoration of nearby degraded natural areas (Turner & Corlett 1996).

**HOW THREATENED IS THE REMAINING MONTANE CLOUD FOREST?**—
A key finding of this study was that MCF habitat patches by themselves do not contain large undisturbed core areas. Exposure to disturbance is partly diminished through the existence of the woody buffers. However, these larger assorted forest patches often have very intricate shapes due to human disturbance operating inside the forest in addition to disruption from the patch border inward, probably due to clearance for agriculture at a very local scale (Ochoa-Gaona & González-Espinosa 2000). Thus, MCF core areas embedded within assorted forest patches are also exposed to some degree of human disturbance despite being buffered by other intervening forest types (Ramírez-Marcial et al. 2001).

The remarkable heterogeneity of this landscape suggests that careful consideration is needed when assessing the consequences of fragmentation. In contrast with classical island biogeography, landscape-mosaic-based approaches attempt to model the way organisms perceive and interact with landscape patterns. Their underlying logic assumes a detailed understanding of organisms’ ecology (McGarigal et al. 2002). Dispersal of some organisms and permeability to ecological processes between the MCF patches occurring within a cluster may be favored by the intervening forest habitats (Gascon et al. 1999). There is thus a need for much more work in this region on how specific organisms are being affected by changes in landscape structure.

A positive note is that no evidence has yet been produced of recent extinction of plant species (M. González-Espinosa & N. Ramírez-Marcial, pers. obs. 2004). Isolated and small patches may maintain large numbers of species (e.g., >50 tree species/ha, L. Cayuela, pers. obs.). Yet this trend may be changing, as birds and mammals are especially vulnerable to high rates of MCF fragmentation (Pattanavibool & Dearden 2002).

**HOW CAN ECOLOGICAL FUNCTIONS BE CONSERVED?**—Recent deforestation and agricultural exploitation have increased the natural fragmentation of Mexican cloud forests (Luna et al. 2001). As we have stated, however, MCF habitats in the central Highlands of Chiapas are typically buffered by relatively large amounts of montane forest habitats. This buffering effect is particularly important in the context of maintaining ecological processes related to water capture.
Because MCF currently occupies only 1.4 percent of the study area, maintenance of other surrounding forest formations is necessary to retain the water captured by MCF in the subsoil. Furthermore, MCF that has degraded to oak forest or pine-oak forest due to low-intensive, long-duration disturbance regimes (e.g., selective logging) can still play some role in capturing atmospheric water. In contrast, plantations of fast growing exotic species are generally considered to be water consumers rather than water producers (e.g., Sahin & Hall 1996). We therefore stress the need to place more emphasis on MCF conservation rather than reforestation if maintaining or augmenting hydrological function is the goal.

MECHANISMS FOR CONSERVATION.—A critical challenge for conservation planning in this region is the complex social context. Insecure land tenure is a major barrier to establishing a coherent conservation strategy (Thoms & Betters 1998). Progress toward operational prioritization of areas for conservation has been slow. An exception is the private Huitepec nature reserve. However, most of the MCF area remains outside the reserve and is exposed to logging or permanent deforestation. The threat to this forest is immediate. For example, at least 10 ha of the most valuable species-rich forest are known to have been converted to other uses since the images used in this study were taken.

Communal forest ownership causes both challenges and opportunities in the context of management for conservation goals. One of the challenges is that the criteria used for evaluating the success of communal management are inevitably biased toward social and political concerns (Bray et al. 2003). Ecological and economic sustainability may be evaluated much less rigorously than would be the case when forests are under state or private ownership. One of the opportunities is that community management is able to set broader strategic goals. The region is moving toward a more secure system of land tenure. Thus, communities can be encouraged to adopt a long-term perspective on management decisions. It is important to draw on positive experiences at a national level. However, there is a danger of overgeneralization. Most of the models of large-scale community forest management that have been implemented in other regions of Mexico (Bray et al. 2003) have limited transferability to the conservation of small areas of fragmented forest containing species of little commercial value.

An additional hurdle to overcome before small fragments of MCF can receive adequate protection is the historical trend in Mexico toward focusing conservation initiatives around extensive protected areas. In the context of the fragmented forests and densely populated landscapes of Chiapas, there is scope for learning from the European experiences of plant microreserves in Valencia, Spain (Laguna et al. 2003), or even sites of Special Scientific Interest (SSI) in the United Kingdom (Barton & Buckley 1983). Such schemes rely not only on legislation, but also on negotiations based on the good will of the landowners. Recently, a national initiative has been proposed that could enable landowners to obtain benefits from the ecological services that forests provide (SEMARNAT 2003). Because the special importance of MCF is recognized by the inhabitants of the region, implementation of any of the initiatives mentioned above would bring a hope for the future of this threatened vanishing forest.

CONCLUSIONS

We estimated the area covered by MCF to be between 3700 and 5250 ha. This contrasts with the approximately 40,000 ha reported by the Mexican national forestry inventory in 2000. MCF was found to be highly scattered and fragmented within a matrix of other tropical montane forest types. These other forests may be buffering the remaining MCF habitats, mitigating their disturbance and enhancing their connectivity. We conclude that mechanisms should be sought that promote: (1) The protection of core areas containing MCF fragments in agreement with communal and private landowners; and (2) Conservation of the ecological functions of surrounding buffer zones.
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