

ARE ISOLATED REMNANT TREES IN PASTURES A FRAGMENTED CANOPY?

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ABSTRACT. It is generally thought that pastures are inhospitable habitats for rain forest organisms. This largely results from (i) using low resolution images when studying fragmented landscapes and (ii) ignoring the actual characteristics of pastures. In a highly fragmented landscape of Los Tuxtlas, Mexico, numerous remnants of the forest canopy are left when pastures are created. Most of these are undetected in deforestation studies and dismissed as irrelevant in fragmentation studies. Using aerial photographs and field verification, we analyzed the spatial distribution and physical and biotic characteristics of isolated trees in pastures, a common landscape element in this region. In 30 pastures there were 98 species of isolated trees, 76 of which were primary rain forest species. Isolated tree density averaged 3.3 tree/ha (range: 0.4–11.9) and decreased with slope. Variation in the species composition, density and canopy physiognomy of isolated trees greatly increases the biotic and physical heterogeneity of pastures. These remnant trees function as ‘stepping stones’ for native fauna and ‘safe sites’ for flora, favoring their maintenance in fragmented landscapes. We propose that, together with other forest remnants, isolated trees in pastures compose a physically discontinuous but functional canopy in the Los Tuxtlas landscape.

RESUMEN. Por lo general se considera a los potreros como habitats inhóspitos para organismos de selva, lo cual se debe en gran parte al uso de imágenes con baja resolución, así como al desconocimiento de las características de los potreros. En un paisaje muy fragmentado de la región de Los Tuxtlas, México, encontramos numerosos remanentes de selva al interior de los potreros. La mayoría no son detectados en estudios de deforestación y son ignorados en los de fragmentación. Mediante fotografías aéreas y verificación en terreno, se analizan las características físicas y bióticas de árboles aislados en potreros, mismos que constituyen un elemento del paisaje común en ésta región. En 30 potreros fueron registradas 98 especies de árboles aislados, 76 de ellas de la selva madura. La densidad de árboles aislados promedió 3.3 árboles/ha (intervalo: 0.4–11.9), decreciendo con la pendiente del terreno. La variación en densidad, fisonomía de copas y especies de árboles aislados aumenta considerablemente la heterogeneidad biótica y física de los potreros. Estos árboles operan como ‘sitios de relevo’ para la fauna y como ‘sitios seguros’ para la flora nativas. Proponemos que en conjunto con otros remanentes de selva, los árboles aislados en potreros componen un discontinuo pero funcional dosel en el paisaje de Los Tuxtlas.

INTRODUCTION

The deforestation of tropical rain forest (TRF) in the Americas is well documented (see review by Toledo 1992). The dramatic reduction of the original area covered by TRF, in addition to the spatial isolation of remnant fragments by the surrounding pastures and crop fields, presently represent the main threats to TRF biodiversity. However, the consequences of TRF fragmentation as well as the ecological dynamics of these fragmented landscapes in the humid tropics are still poorly understood.

Most studies on TRF fragmentation focused on the fragments per se, from the border to the interior, ignoring the characteristics of the habitat or types of habitats which surround these fragments (Saunders *et al.* 1991). Consequently, it is generally unknown how TRF organisms perceive, use or respond to habitat characteristics outside remnant fragments (Guevara 1995). In order to evaluate and understand the effects

of TRF fragmentation on biodiversity and ecological dynamics, an accurate description of landscape structure is a necessary first step. For this purpose information about species composition, abundance and spatial arrangement in pastures is particularly important. The types of elements present in a given landscape and their spatial arrangement define landscape structure (Forman & Godron 1986); i.e., “the distribution of energy, materials, and species in relation to the sizes, shapes, numbers, kinds and configurations of components” (Turner 1989). Landscape structure strongly influences important ecological processes within and among landscape components. The ecological dynamics of both the components and the mosaic which they usually form is known as landscape dynamics (Forman & Godron 1986, Turner 1989).

The exactness with which one can describe the structure of a landscape depends on the scale of the map used (Turner 1989). Studies of TRF deforestation commonly employ coarse or regional scales (e.g., 1:250,000), which are inappropriate for detecting the fine grained compo-

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nents of anthropogenic landscapes in the humid tropics. Contrary to conclusions drawn from deforestation data, TRF is not always completely replaced by a bare landscape. In many areas of the tropics numerous, scattered and relatively small TRF remnants are left behind as deforestation advances (Guevara 1986, Guevara *et al.* 1997).

Deforestation in Los Tuxtlas, Mexico, has dramatically reduced the original extent of TRF, leaving a highly fragmented landscape (Dirzo & García 1992) representative of other neotropical areas, particularly in Mexico and Central America (Guevara 1995). Cleared areas in Los Tuxtlas are much more complex than commonly thought. Crop fields and pastures are heavily dotted with isolated TRF trees and crossed by narrow bands of remnant TRF along rivers and streams (Guevara *et al.* 1992, 1997). A thorough description of all TRF remnants at Los Tuxtlas landscape would be time consuming and impractical. However, by focusing our efforts on one arboreal component of the landscape we can gain insight into its contribution to or importance in defining landscape structure, and establish its role in biological processes which influence landscape dynamics. In this study we have concentrated on isolated trees in pastures.

Isolated trees spared from forest cutting constitute the minimum remnant of the original TRF canopy. These Isolated Remnant Trees (IRTs) are common features of present agricultural landscapes throughout the tropics. They are commonly used as a source of shade for cattle, but also as complementary fodder, firewood, lumber and edible fruit (Guevara 1986, Guevara *et al.* 1997). Several studies have reported beneficial effects of the presence of IRTs in pastures on different TRF organisms, however little is known about the spatial distribution, species composition and physical characteristics of IRT.

First we address the importance of using appropriate scales for the study of fragmented TRF regions. Second, we describe important structural and floristic attributes of IRTs in Los Tuxtlas pastures. These include IRT density and its spatial variation, species composition, as well as tree and canopy dimensions. Finally we propose that, together with riparian corridors and larger fragments, IRTs function as a structurally discontinuous canopy. The spatial, physical and floristic characteristics of IRTs are key elements in biological processes involving TRF fauna (primarily volant) and flora. Consequently, these features are important for the management and conservation of TRF biodiversity in highly fragmented landscapes such as those used to raise cattle.

MATERIALS AND METHODS

The region of Los Tuxtlas, Veracruz (18°05'–18°43' N Lat. and 94°35'–95°25' W Long.), is a volcanic mountain range that rises from sea level up to 1,700 m a.s.l. The young volcanic soils are classified as vitric andosols, with poorly developed profiles and relatively high contents of organic material and nutrients. Mean annual precipitation is over 4,000 mm and mean annual temperature is 25° C. The original vegetation of the area is TRF, with a 20 to 30 m high canopy (Bongers *et al.* 1988). Between 80% to 90% of the original extent of TRF in Los Tuxtlas had been cleared by the year 1990. Deforestation is relatively recent, mostly occurring over the last three decades (Dirzo & García 1992). Currently, the Los Tuxtlas mountain range is covered by a vegetation mosaic dominated by cattle pastures and different types of crop fields which surround the remaining and diminishing TRF fragments.

For this study, an area 9.0 by 8.5 km (18°34'–18°39' N Lat. & 95°02'–95°07' W Long.), was selected (FIGURE 1). The study area is located between the San Martín Tuxtla volcano and the coast of the Gulf of Mexico, including the "Los Tuxtlas Biological Research Station" (with a 640 ha reserve) operated by the National Autonomous University of Mexico (UNAM). Total land surface included was 5,509 ha and the altitude ranged from 0 to 600 m a.s.l. From a 1991 aerial photograph (scale 1:75,000) the area covered by the following landscape elements was estimated: 1) rain forest fragments, 2) clear-cut open areas, 3) riparian corridors crossing open areas and 4) isolated trees in open areas. Using standard satellite image analysis on a 1990 Landsat TM scene, remnant forest was distinguished from cleared areas, and the results plotted on a map with a 1:250,000 scale, both for the selected study area and the whole region of Los Tuxtlas.

Aerial photo-interpretation was done with a dual stereoscopic magnifier to produce a 3D view of pastures, using 3× and 8× ocular lenses. Forty five pastures were randomly selected from those with visible limits (e.g., living fences) until 15 pastures for each of three slope categories had been identified (flat terrain, slight slope, steep slope). Land tenure status for the 45 pastures was: large private ranches (n = 14 pastures), small private ranches (n = 17) and communal or 'ejido' land (n = 14).

Using the aerial photo, the area of each pasture was estimated and isolated trees counted. Pasture area varied from 3.5 to 53.1 ha (mean = 19.0 ha ± 1.7 s.e.), and the total area of all pastures studied was 855 ha. Within the 45 pas-

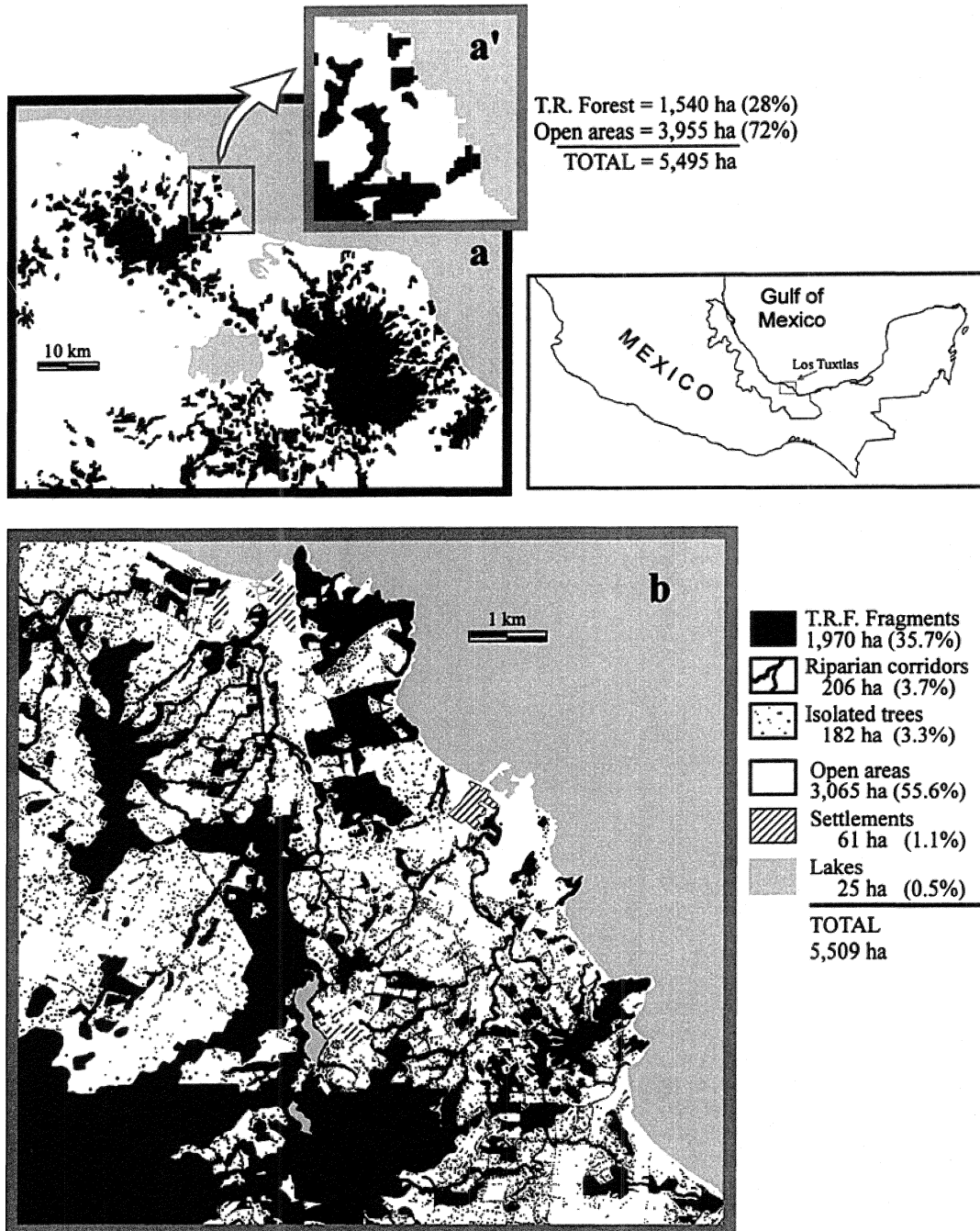


FIGURE 1. Rain forest fragmentation in the Los Tuxtlas region, Mexico viewed with two different scales; a: from a map with an original scale of 1:250,000 of the whole mountain range and obtained from a 1990 satellite image (study site amplified in a'); b: study site from a 1991 aerial photograph with an original scale 1:75,000.

tures 2,428 isolated trees were counted. To test whether density of isolated trees varied with slope or with land tenure the data were analyzed with one way ANOVAs (Sokal & Rohlf 1981) and Tukey's multiple range test (Steel & Torrie 1980).

In the field isolated trees were identified to species in 30 of the 45 pastures. Owners denied access to remaining pastures, or they were inaccessible. A total of 735 isolated trees were registered in these pastures over a total sampling area of 173 ha. To ensure common land use history, tree identification was only done within a single management unit for a given pasture. Management subdivisions and wide variations in pasture size and topography resulted in different sampling sizes for each pasture. Sampling area varied from 1.1 to 10.0 ha for 29 pastures and 35.0 ha for one pasture.

Canopy dimensions were measured for 20 isolated individuals of five species (100 trees). *Brosimum alicastrum*, *Nectandra ambigens*, *Poulsenia armata*, *Ficus yoponensis* and *F. tecolutensis* were selected since all are canopy TRF species and are among the most common in the pastures of the study area. Measured trees were located within the 30 pastures sampled, except four trees of *F. tecolutensis*, which had to be measured in nearby additional pastures. Total height, height of lowest foliage, and two perpendicular diameters of the canopy were measured for each tree. Vertical canopy depth (difference between total height and the height of lowest foliage) and canopy cover were calculated for each tree. These measurements were compared among species with one-way ANOVAs (Sokal & Rohlf 1981) and Tukey's multiple comparison test (Steel & Torrie 1980).

RESULTS

At the regional scale (1:250,000) small remnants of TRF, such as forest fragments smaller than 20 ha, riparian corridors and isolated trees are undetectable (FIGURE 1a). However, at the local scale with higher resolution (1:75,000), it is evident that these elements are common and widespread throughout the study area (FIGURE 1b). Of the 5,484 ha of TRF which originally covered the selected study area, less than 2,000 ha remained in 1991 (36% of total area). This was distributed in fragments varying in size from <5 to >500 ha. Areas disturbed by human activities totalled more than 3,500 ha (64%) including pastures, crop fields, urban areas, riparian corridors and isolated trees. The isolated trees detected with the aerial photo had an esti-

TABLE 1. Variation in isolated tree density in pastures of Los Tuxtlas with slope and land tenure. Data obtained from a 1991 aerial photograph (scale 1:75,000).

	Total no. of trees	Density (IRT/ha)			
		Avg.	SE*	Min.	Max.
Slope					
Flat	756	1.7	(0.3) ^a	0.4	4.6
Slight	653	3.8	(0.7) ^b	0.9	11.9
Steep	1,019	4.4	(0.5) ^b	2.2	9.1
Land tenure					
'Ejido'	614	3.4	(0.5) ^{ns}	1.0	7.8
Small landholder	1,111	4.1	(0.7) ^{ns}	0.9	11.9
Large ranch	703	2.2	(0.3) ^{ns}	0.4	4.6
Total	2,428	3.3	(0.3)	0.4	11.9

* Different letters indicate significant differences ($P \leq 0.001$).

mated total cover of 3.3% of total area (FIGURE 1b), and 5.2% of disturbed areas.

IRT DENSITY. In the 45 pastures selected from the aerial photo, density of isolated trees ranged from 0.4 to 11.9 trees/ha, with a mean density of 3.3 trees/ha (± 0.3 s.e.). Density of trees varied significantly with respect to slope ($F_{(2,42)} = 13.3$, $P < 0.001$). On flat terrain mean density was lower than on slight and steep slopes (TABLE 1). Although density was slightly lower on large private ranches, it was not significantly different from that of small land holdings, or 'ejido' lands ($F_{(2,42)} = 2.7$, $P = 0.07$).

For 28 of the 30 pastures surveyed *in situ*, density of isolated trees ranged from 0.3 to 12.4 trees/ha. The remaining two pastures had atypically high densities (28.2 and 29.1 trees/ha; TABLE 2). Excluding the two atypical pastures, mean density of the isolated trees registered on site, was 5.2 trees/ha (± 0.7 se). When two or more trees were very close together, they looked like a single crown from the aerial photo, in addition isolated trees with a small canopy cover (<50 m²) were not detected in the photos. This explains the higher IRT densities registered in the field.

IRT SPECIES. A total of 98 species belonging to 33 families were registered as isolated trees (list available on request) in 30 pastures (total sampled area = 173 ha). Families with the greatest number of species were: Leguminosae (18 spp.), Moraceae (12 spp.), Lauraceae and Sapotaceae (6 spp. each), and Apocynaceae, Bombacaceae, Euphorbiaceae, Meliaceae and Myrtaceae (4 spp. each). Of the 98 species, 76 were primary TRF trees, 11 were late secondary succession

TABLE 2. Richness, density and most abundant species of isolated trees in 30 pastures of the Los Tuxtlas region.

Size (ha)	No. spp.	No. trees	Density (trees/ha)	Most abundant species (no. trees)
1.1	19	31	28.2	<i>Ficus yoponensis</i> (4); <i>Inga quaternata</i> (3).
1.1	15	32	29.1	<i>Zanthoxylum kellermannii</i> (8); <i>Ceiba pentandra</i> (3).
1.6	11	12	7.5	<i>Pouteria sapota</i> (2).
2.3	15	19	8.3	<i>F. yoponensis</i> (4); <i>Nectandra ambigens</i> (2).
2.5	7	11	4.4	<i>Ampelocera hottlei</i> (2); <i>F. yop.</i> (2); <i>N. ambigens</i> (2).
3.0	9	18	6.0	<i>Z. kell.</i> (5); <i>Cordia megalantha</i> (3); <i>Inga pavoniana</i> (3).
3.0	14	22	7.3	<i>Bursera simaruba</i> (3); <i>Lonchocarpus guatemalensis</i> (2).
3.0	14	31	10.3	<i>B. sim.</i> (7); <i>Cordia alliodora</i> (4); <i>Pseudolmedia oxyphyllaria</i> (4).
3.5	12	21	6.0	<i>Trichospermum galeottii</i> (4); <i>Robinsonella mirandae</i> (3).
4.0	8	14	3.5	<i>F. yoponensis</i> (3); <i>Z. kellermannii</i> (3).
4.0	20	35	8.8	<i>Sapium nitidum</i> (6); <i>Z. kell.</i> (5); <i>Poulsenia armata</i> (3).
4.0	12	38	9.5	<i>B. sim.</i> (10); <i>Z. kell.</i> (10); <i>Tabebuia guayacan</i> (6).
4.5	6	7	1.6	<i>N. ambigens</i> (2).
4.5	15	56	12.4	<i>Cupania glabra</i> (14); <i>Z. kellermannii</i> (8); <i>S. nitidum</i> (7).
5.0	7	9	1.8	<i>P. armata</i> (2); <i>P. sapota</i> (2).
5.0	10	14	2.8	<i>R. mirandae</i> (4); <i>T. galeottii</i> (2).
5.0	9	17	3.4	<i>Vatairea lundellii</i> (7); <i>C. alliodora</i> (3).
5.0	11	19	3.8	<i>S. nitidum</i> (6); <i>Cupania macrophylla</i> (3).
5.0	23	40	8.0	<i>Spondias radlkoferi</i> (6); <i>F. yoponensis</i> (3); <i>P. sapota</i> (3).
5.2	11	18	3.5	<i>F. yop.</i> (5); <i>S. radlkoferi</i> (2); <i>Dendropanax arboreus</i> (2).
6.0	8	11	1.8	<i>S. radlkoferi</i> (3); <i>Ficus tecolutensis</i> (2).
6.0	24	45	7.5	<i>F. tecolutensis</i> (4); <i>F. yoponensis</i> (4); <i>S. radlkoferi</i> (4).
6.5	4	4	0.6	—
6.5	31	74	11.4	<i>N. ambigens</i> (9); <i>P. oxyphyllaria</i> (9); <i>P. sapota</i> (5).
6.6	15	37	5.6	<i>N. ambigens</i> (14); <i>P. armata</i> (9).
7.0	8	13	1.9	<i>Gliricidia sepium</i> (4); <i>C. alliodora</i> (3).
8.5	14	35	4.1	<i>B. sim.</i> (8); <i>Omphalea oleifera</i> (5); <i>L. gua.</i> (4); <i>S. rad.</i> (4).
9.0	17	21	2.3	<i>N. ambigens</i> (4); <i>Brosimum alicastrum</i> (2).
10.0	17	20	2.0	<i>Cornutia grandifolia</i> (3); <i>Cordia stellifera</i> (2).
35.0	11	11	0.3	—
173.4	98	735	*5.2	—

* Average: the first two pastures were excluded from calculations (see text).

species and the other 11 were pioneer species or gap colonizers.

The most abundant species were *Bursera simaruba* (53 trees), *Zanthoxylum kellermannii* (46), *Nectandra ambigens* (45), *Ficus yoponensis* (36), *Poulsenia armata* (30), *Spondias radlkoferi* (30), *Sapium nitidum* (30), *Pouteria sapota* (25) and *Brosimum alicastrum* (21). These nine species were also the most frequent, occurring in 10 or more of the 30 sampled pastures. Species composition varied widely among pastures, making it impossible to consider a single species or group of species as dominant IRT in Los Tuxtlas pastures (TABLE 2). Of the 98 species registered, there were 16 species with just two trees and 22 with a single tree.

These 98 species represent 33% of total tree flora (298 species) registered in the TRF protected area (640 ha) of the UNAM research station. Of the total tree flora in this area, 131 species of canopy or subcanopy trees commonly grow taller than 15 m as adults (Ibarra & Sinaca 1995, 1996) and of this subset 67 species (51%)

were registered as isolated trees in the 30 pastures studied.

IRT DIMENSIONS. The five species selected for canopy measurements were among the most abundant and frequent in the studied pastures. For these species, mean tree height was greater than 20 m (TABLE 3) and similar among species ($F_{(4,99)} = 1.43$, $P = 0.23$). All other canopy measurements varied among species. Mean height of lowest foliage was different among species ($F_{(4,99)} = 4.7$, $P < 0.001$). *P. armata* trees had the shortest distance to lowest foliage, whereas *N. ambigens* and *F. yoponensis* trees had the highest values (Tukey MSD_{0.05} = 4.62). Mean vertical canopy depth was also different among species ($F_{(4,99)} = 3.81$, $P < 0.001$). *B. alicastrum* and *P. armata* had the deepest canopies (Tukey MSD_{0.05} = 6.36), and *N. ambigens* the smallest. Mean canopy cover also differed among species ($F_{(4,99)} = 9.7$, $P < 0.001$), ranging from 158 to 462 m². Trees of the two fig species had the largest values of canopy cover (Tukey MSD_{0.05}

TABLE 3. Average measurements for 5 rain forest species (20 trees per species) common as isolated remnant trees in pastures of Los Tuxtlas (standard error in parenthesis). Different letters indicate significant differences ($P < 0.001$).

Tree species	Tree height (m)	Lowest foliage (m)	Canopy depth (m)	Canopy cover (m ²)
<i>F. yoponensis</i>	27.7 (1.2) ^a	10.2 (1.2) ^b	17.5 (1.5) ^{ab}	461.9 (49.5) ^c
<i>F. tecolutensis</i>	24.4 (1.8) ^a	9.8 (1.3) ^{ab}	14.6 (1.1) ^{ab}	371.0 (53.0) ^{bc}
<i>B. alicastrum</i>	26.7 (2.1) ^a	7.8 (0.9) ^{ab}	18.9 (2.4) ^a	267.1 (40.1) ^{ab}
<i>P. armata</i>	23.9 (1.6) ^a	5.2 (0.8) ^a	18.7 (1.5) ^a	212.0 (27.2) ^a
<i>N. ambigens</i>	23.3 (1.3) ^a	11.9 (1.5) ^b	11.4 (1.5) ^b	158.3 (12.5) ^a
Total ($N = 100$)	25.2 (0.7)	9.0 (0.6)	16.2 (0.8)	296.0 (20.7)

= 155.6), and those of *N. ambigens* had the smallest (TABLE 3).

DISCUSSION

Our results demonstrate that the accuracy of the description of landscape structure depends heavily on the scale of the photos or images employed for analysis. Regional scales (e.g., 1:250,000) provide important and reliable data for temporal and spatial analyses of deforestation and resulting fragmentation over a vast region (1×10^5 ha). From this type of analysis Dirzo and García (1992) showed that total area and rate of TRF canopy elimination in Los Tuxtlas are very high. However, these scales are inadequate for perceiving the fine grain structure of local landscapes (1×10^3 ha). This requires a higher limit of resolution, such as that obtained with a scale of 1:75,000. With this more detailed description it is clear that the fragmented landscape in Los Tuxtlas cannot simply be viewed as a forest vs. non forest scenario; rather, it is composed of many distinct elements that create a complex and heterogeneous land mosaic. What appears to be an area deprived of trees on a low resolution map, in fact has numerous scattered remnants of the original TRF with canopies as high as 20 m, and these add a visible and functional dimension which interrupts an otherwise flat and barren landscape element.

IRTs AND LANDSCAPE STRUCTURE IN LOS TUXTLAS. The density and spatial distribution of IRT species in pastures are the combined results of the original TRF floristic composition and structure, coupled with the management history. The presence of IRTs in pastures, and the variation in IRT density observed for different degrees of slope, are linked with traditional agricultural practices and present needs (e.g., shade for cattle). Particularly important are the choices made by each landholder during forest cutting and burning (Guevara 1986, Guevara *et al.* 1997). Easy to work on and more productive, flat terrain is always cleared first and thus has

had a more prolonged use, frequently being converted from pasture to crop field and vice-versa, depending on the farmer's needs. Trees that interfere with plowing and crop yield are felled.

Since the derived benefits of valuable tree species are very important to local inhabitants (Guevara 1986), it was expected that land tenure would be related to IRT density. The pastures of small landholders and those on communal lands (ejidos) are in the hands of local inhabitants living in small settlements, while those of large private ranches are run by owners who live in distant cities. Although there was no significant difference in IRT density with respect to land tenure (possibly because of small sample size), IRT density was higher on properties owned by small landholders (4.1 trees/ha) and 'ejidos' (3.4) than those of city ranchers (2.2), suggesting that the former group conserves more of the extended discontinuous TRF canopy.

The density of large trees (DBH > 10 cm) in undisturbed TRF at Los Tuxtlas is higher than 300 trees/ha (Bongers *et al.* 1988). By 1991, in those areas converted to pastures, tree density was reduced by two orders of magnitude (3 trees/ha). In the context of this dramatic reduction in tree density and the resulting minimal IRT canopy cover ($\approx 5\%$ of disturbed area), it is remarkable that one third of the local TRF tree flora was represented by isolated trees in the 30 active pastures. Furthermore, when we only consider those tree species which grow taller than 15 m as adults, IRTs represent half of the TRF tree flora. The notable richness and prevalence of TRF canopy and subcanopy species as IRTs, are a direct result of the selective habits of farmers during forest cutting and the fact that clearing of the area is relatively recent (<50 years).

Given the remarkable richness of TRF species that IRTs represent in a sample of only 30 pastures, it is conceivable that an inventory of all the arboreal elements in modified areas, that is, of IRTs, riparian corridors and living fences, would reveal that 100% of the TRF tree species are represented. Even though species richness per unit area of pasture is insignificant in com-

parison to that of the original TRF, the fact that this richness exists is extraordinary in itself and is contrary to what we would expect on analyzing low resolution images in which pastures appear to be completely devoid of trees (FIGURE 1a'). This becomes even more significant when we consider that in Mexico more than three quarters of the original expanse of TRF has already been converted into pastures (Toledo 1992). While every effort should be made to reduce this dire loss of canopy cover, we cannot afford to overlook the importance of the arboreal elements conserved in pastures.

In Los Tuxtlas, most if not all of the canopy and subcanopy tree species that we see today as IRTs, grew and attained their adult size as part of a dense and continuous TRF canopy. The isolation of these trees in pastures resulted in the modification of their canopy physiognomy. The exposed trunks of these trees receive direct sunlight, stimulating the sprouting of new twigs and explaining the low heights of lowest foliage recorded for IRTs (TABLE 2). In contrast, in undisturbed TRF the five species studied do not have such low foliage (pers. obs.). After neighboring trees are felled, IRT canopy expands, resulting in a larger canopy cover than that characteristic of forest counterparts (unpubl. data). Similar canopy modifications are reported for trees bordering canopy light gaps (Young 1995), or at the edges of wide rivers (Hallé *et al.* 1978).

Tree species respond differently to isolation. For example, the canopies of isolated *N. ambigua* trees were narrower, smaller in cover area and began higher off the ground, showing a more conservative response than the other four species. Variation in size and shape of individual canopies and in foliage density, results in environmental differences both within and under the canopy of isolated trees (Parker 1995). Thicker and wider canopies produce more shade, offer more sites for colonization by epiphytes, and more perching sites for birds and bats. Those that produce fleshy fruit offer more food for frugivores.

BENEFITS OF IRTs ON TRF BIOTA. The presence of IRTs in pastures has beneficial effects for canopy dwelling biota and other TRF organisms in landscapes modified by human activities in of the Neotropics. Favored native forest organisms include birds (Bronstein & Hoffman 1987, Nadkarni 1988, Saab & Petit 1992, Guevara & Laborde 1993), woody plants which grow under the canopy of IRTs (Guevara *et al.* 1986, 1992, Janzen 1988, Gerhardt 1993, Otero 1995) and epiphytic plants (Nadkarni 1988, Williams-Linera *et al.* 1995, Hietz-Seifert *et al.* 1996). Few of these studies have examined these beneficial

effects in the larger context of a fragmented landscape. The following benefits for TRF biota and related ecological processes are directly linked with IRT density, species composition and the whole landscape structure of our study area.

Of the frugivorous avifauna reported for the UNAM research station (145 spp.), almost one third (47 spp.) was registered visiting only four IRTs of two fig species. Visitation rates to IRTs are strongly influenced by fruit type and availability offered by the tree (Guevara & Laborde 1993). Even when the IRTs are not fruiting they are frequently visited by frugivorous birds, indicating that IRT are highly valuable perching sites in pastures. Remarkable temporal variation in fruit phenologies has been reported for TRF tree species in Los Tuxtlas (Carabias & Guevara 1985) and, as we have seen, a high number of TRF species were registered as IRTs. Consequently, in addition to being spatially discontinuous, IRTs represent a temporally discontinuous source of food for frugivorous birds. When flying through pastures frugivorous birds closely follow riparian corridors and the scattered IRT, showing a marked preference for the remnants of the TRF canopy (Laborde 1996). Traditionally, the definition of a corridor is based on human perceptions which, from a bird's eye-view, may be meaningless. Our observations of flight patterns in Los Tuxtlas pastures indicate that birds perceive and routinely take advantage of a network of connected TRF remnants in which IRTs are the nodes. The lower values for lowest foliage and greater canopy cover of the IRTs may make them even more attractive to avifauna.

Beneath the canopies of IRTs there is a dense and species rich deposition of seeds of zoochorous woody species. Seed deposition is numerically dominated by pioneer and secondary woody species with tiny seeds (seed width < 3 mm), whereas seeds of TRF primary species with larger seed sizes are deposited in very low quantities (Guevara & Laborde 1993). In addition to defecating previously ingested seeds while at the IRT canopy, frugivorous birds also ingest fruit and seeds, carrying them to other trees in pastures or even into TRF fragments. At Los Tuxtlas, TRF fragments are the most important seed source of TRF species. Outside these fragments, IRTs are also seed sources of TRF species, but in addition they are seed concentration points of zoochorous TRF plants in pastures. In this respect, IRTs function as an extension of TRF canopy.

Vegetation established under the IRT canopy is more similar to that of undisturbed TRF, than to that of nearby sites in the open pasture, as

measured by floristic composition, species richness and tree density (Guevara *et al.* 1986, 1992, Guevara 1995). Management practices such as frequent weeding, herbicide spraying, cattle grazing and trampling prevent the development of TRF woody species that have successfully dispersed and established under IRT canopies. However, when these disturbances were experimentally stopped, a continuous, 5 m tall canopy developed under the crowns of IRT in only three years. The fast growing canopy was dominated by a few secondary and pioneer tree species. Under this secondary canopy, ruderal herbaceous species typical of pastures were overshadowed and almost completely eliminated, whereas numerous mature TRF tree species established successfully (Guevara, *et al.* in press). Even though the deposition of large seeds (width > 7 mm) corresponding to TRF tree species is relatively low, their establishment success is clearly higher than that of pioneer and secondary woody species with tiny seeds (Guevara 1995). Favorable conditions for seed dispersal, germination and seedling establishment of TRF tree species, previously believed to occur exclusively in undisturbed TRF or large TRF fragments, also occur in pastures under IRT canopies.

Epiphytic plants are characteristic and important components of TRF biodiversity, and are particularly sensitive to the conversion of TRF into pastures (Nadkarni 1988). There are, of course, no epiphytes in a treeless land. However, in our study site of 38 IRTs, a total of 58 species of vascular epiphytes and hemi-epiphytes were registered (Hietz-Seifert *et al.* 1996). This richness represents a notable proportion (37%) of the epiphytic flora (157 spp.) reported for the UNAM research station (Ibarra & Sinaca 1995). The number of epiphytes per unit area in pastures with IRTs is much lower than that in undisturbed TRF. However contrary to expectation, the epiphytic species richness per tree for IRTs in this pasture was not significantly different from trees of similar sizes (same DBH classes) in undisturbed TRF (Hietz-Seifert *et al.* 1996). Although located in an environment that might be considered too harsh for epiphytes, IRTs appear to offer habitats that are just as favorable as those found in undisturbed TRF.

IRTs AND LANDSCAPE DYNAMICS. Studies of TRF fragmentation have concentrated on describing the characteristics of fragments, including size, shape, species composition and distance to other fragments. Results on species richness per fragment, community and population parameters, and habitat use by TRF biota are commonly explained in relation to fragment

characteristics (Saunders *et al.* 1991). The structure and floristics of the anthropogenic habitats which surround TRF fragments are often disregarded, or briefly and incompletely described. It is because of these types of studies that the idea of 'forest islands' immersed in an inhospitable sea of grasses has prevailed. This, however, is an oversimplified scenario which ignores the fact that pastures do not have the same isolation effects as the ocean (Forman & Godron 1986, Turner 1989, Saunders *et al.* 1991). Habitats modified by human activity have traditionally been recognized as a source of invasive species which interfere with the internal dynamics of TRF fragments (Janzen 1983). Curiously, both the presence and beneficial effects of arboreal elements, such as IRTs, within pastures and crop fields have been repeatedly ignored. The role of these elements in mitigating the effects of isolation on TRF organisms, and consequently improving their chances of persisting in an anthropogenic landscape is rarely considered (Guevara 1995). Accurate quantitative and qualitative descriptions of landscape structure in today's fragmented landscapes of the humid tropics are badly needed. Valid comparisons of results among different sites or landscapes depend on it.

In fragmented landscapes where seed sources of TRF plants are abundant and profusely distributed, such as the landscape of our study area, IRTs could function as regeneration nuclei of the TRF if pastures were abandoned (Guevara *et al.* 1986). The prolific regeneration of TRF trees beneath IRT canopies could be used as the replacement or renewal mechanism of IRTs. Temporary exclusion of weeding and cattle disturbances under the canopy of an IRT will suffice for this purpose, and selective weeding or thinning will ensure that the original IRT will be replaced by another TRF tree species. The presence of IRTs in Los Tuxtlas pastures greatly contributes to the resilience of the system.

In undisturbed TRF, the renewal and maintenance of the forest depend largely on biotic interactions that take place within the forest canopy twenty or more meters above the ground (Nadkarni 1988). Most TRF tree species depend on canopy dwelling fauna for reproduction, i.e. insects for pollination and vertebrate frugivores for seed dispersal. The beneficial effects of IRTs on some of the TRF canopy-dwelling biota, as well as the significant role of IRTs in the maintenance of biotic interactions between TRF flora and fauna in the middle of pastures, demonstrates that they are of vital importance where the original TRF has been fragmented.

IRTs are conspicuous features of landscape structure in our study area. The high variation in the density and species composition of the IRTs

studied greatly increase the biotic and physical heterogeneity of the landscape matrix in which the remaining fragments of TRF are embedded. However, the mere presence of IRTs in pastures does not guarantee these favorable effects. Landscape dynamics, including the benefits of IRTs, is strongly influenced by landscape structure (Turner 1989). In particular, the occurrence or degree of modification of those ecological processes that are crucial for TRF fauna and flora, are largely dependent on the extent, spatial distribution, shape, size and species composition of every remnant of the TRF canopy. Together these physically separated arboreal elements create a fragmented canopy which, although discontinuous, is ecologically functional.

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