13 Altered Patterns of Herbivory and Diversity in the Forest Understory: A Case Study of the Possible Consequences of Contemporary Defaunation

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A consistent pattern of the distribution of species on the planet is that biodiversity, in general, decreases from the tropics to the temperate zones (Krebs 1978; Raven and Johnson 1986). Prominent in this pattern is the overwhelming diversity in the tropics of insects—about 50% of which are herbivorous (Strong et al. 1984), of some groups of folivorous mammals (Eisenberg 1981) and flowering plants—the main food resource for herbivores (Strong et al. 1984). This suggests that tropical herbivory—a theme of this volume—should be particularly well represented and varied in the tropics and that its study is of fundamental importance to the understanding of the evolutionary biology of plants and animals. This situation also makes it mandatory to preserve representative portions of the tropics' biotic wealth. Currently, much of our knowledge on tropical biology is being derived from studies in preserved wildlands (see Clark et al. 1987, for an example). However, conservation problems in many tropical and semitropical countries are just formidable. This is so much so that even formally protected areas (e.g., biological stations and national parks) of countries such as Mexico are suffering from anthropogenic disturbances whose consequences are difficult to detect or predict. Also, research in such areas may generate findings which may not be representative of natural-system processes or which may be, at best, anomalous.

The existence of altered processes in tropical preserved wildlands has been suggested, for example, in the case of plant mating systems and their genetic and demographic consequences as a result of reduced population size (Lewin 1989), and in the patterns of tree-fall gaps and their turnover rates as a result of increased

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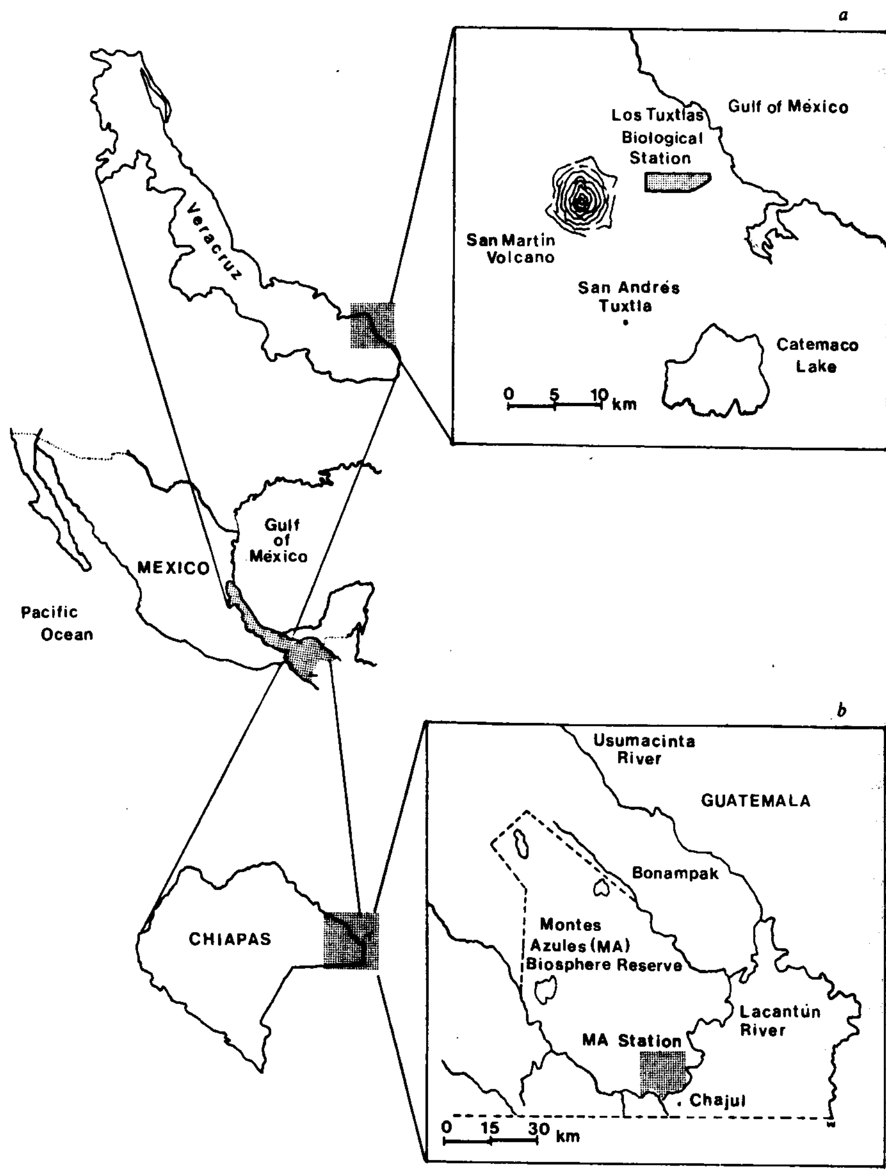

Figure 13-1. Location of the region and Biological Station of Los Tuxtlas in the State of Veracruz (*a*), and of the Montes Azules Biosphere Reserve (Lacandon forest) in the State of Chiapas (*b*).

edge effects (Martinez-Ramos, unpublished data). In this chapter we attempt to integrate our findings on the patterns of herbivory in tropical rain forests of Mexico with our preoccupations for rain forest conservation, with the aim of illustrating (1) how the study of plant–herbivore interactions in some neotropical wildlands may be affected by subtle conservation problems and (2) the ecological (and potentially evolutionary) consequences this may have on the plant–herbivore interface. The conservation problem we address in particular is contemporary defaunation affecting herbivorous vertebrates of a Mexican rain forest.

This study is centered at the Los Tuxtlas tropical research station (Figure 13-1). Los Tuxtlas, is in the State of Veracruz, Southeast Mexico (95° 04′ West long. and 18° 30′ North lat.). It is one of the best-studied areas in the country (see Gòmez-Pompa et al. 1976; Còmez-Pompa and del Amo 1985) and probably in Latin America. Moreover, the area is important for it constitutes the northern-most limit in the distribution of the tropical rain forest in the New World (Dirzo 1987). However, despite its latitudinal position the area is still highly diverse and it combines species of Neotropical origin with Nearctic and endemic species (Andrle 1964; Dirzo 1987; Ibarra-Manriquez and Sinaca 1987; Pérez-Higareda et al. 1987). Yet recent evidence suggests that a number of natural processes under study at the site may be influenced by human activities taking place in the vicinity of the preserved areas. In particular, we submit that the patterns of herbivory on the understory plants may be determined by a process of vertebrate defaunation that has been taking place over the last 20 years or so (see below).

THE ALTERED PATTERNS OF HERBIVORY

The patterns of herbivory in the understory of Los Tuxtlas have been studied in some detail and the main results are summarized here.

Studies with Seedlings in Permanent Quadrats

Continuous observations on individual leaves of seedlings of five species (*Nectandra ambigens, Omphalea oleifera, Pterocarpus rohrii, Faramea occidentalis, Psychotria faxlucens*) in the understory of mature forest showed that the predominant scores of leaf damage were 0 (no damage) and 1–25% of leaf area damaged and that insects (of various orders) were the only herbivores responsible for the damage (Dirzo 1984 and unpublished data). Similar results were obtained with seedlings of *Cecropia obtusifolia* and *Heliocarpus appendiculatus* studied in tree-fall gaps (Nùñez-Farfàn and Dirzo 1988). For these two species yearly averages of the standing levels of damage were close to 15% of leaf area eaten. In all cases there was evidence of insect damage (scars) and no evidence of damage by vertebrates (browsing, pull-out).

In a study directed to assess the rates of pathogen infection on the foliage of 10 understory species in the mature forest (Garcia-Guzmàn 1989), long-term observations on individually marked leaves showed that most of the damage was due to insects and pathogens and none to vertebrates.

Community-Level Surveys of Leaves

For each of 52 species of seedlings, a random sample of 50 leaves was collected and the standing levels of damage were measured to the nearest square millimeter (de la Cruz and Dirzo 1987). The results of this survey (Fig. 13-2) show that 76% ($N = 3394$) of them had levels of damage lower than 10% and 41% were intact or damaged by pathogens. A minimum fraction of the sample (0.5%) bore damage greater than 25% and the overall mean was 10.5%. This information was complemented by an analysis of the types of damage observed (Dirzo unpublished data): 75% of the leaves were damaged by insects and pathogens, 9% were damaged by pathogens alone, 16% were intact, and none of the leaves bore recognizable evidence of damage by vertebrates.

In a more extensive survey using 1103 randomly chosen plants from four 1000-m^2 plots (Garcia-Guzmàn and Dirzo unpublished data), we found (Table 13-1) that damage by insects and pathogens was the most frequent type of damage, while nearly 40% of the leaves were intact and, again, none of the plants or leaves from such a large sample were damaged by vertebrates.

In summary, the understory vegetation of this forest shows that (1) insects are

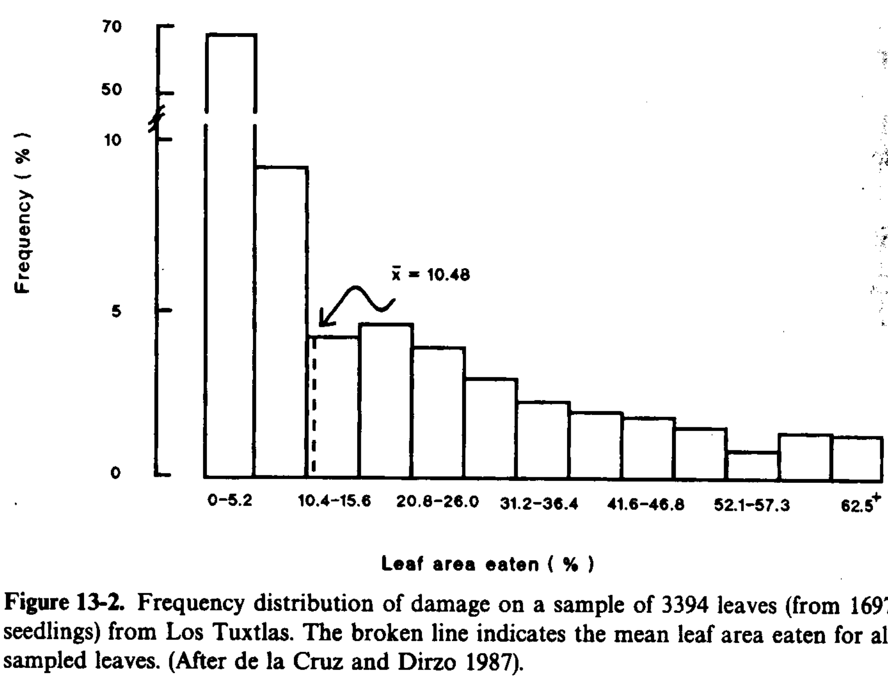

Figure 13-2. Frequency distribution of damage on a sample of 3394 leaves (from 1697 seedlings) from Los Tuxtlas. The broken line indicates the mean leaf area eaten for all sampled leaves. (After de la Cruz and Dirzo 1987).

TABLE 3-1. Types of Damage on the Foliage of Understory Plants from Los Tuxtlas[a]

Type of Damage	Frequency (%)	
	Plants[b]	Leaves[c]
Insects alone	36.7	15.9
Insects plus pathogens	58.2	43.1
Pathogens alone	1.7	1.4
Intact	3.5	39.6
Vertebrate	0	0

[a]The plants for this survey were randomly chosen from four 1000-m^2 plots. After Garcia-Guzmàn and Dirzo (unpublished).
[b]$N = 1103$.
[c]$N = 8365$.

the main herbivores and, more importantly, (2) there is a consistent absence of damage by vertebrate folivores. The predominant role of insects as foliage consumers has been well established for several tropical sites (e.g., Leigh and Smythe 1978; Janzen 1981b; Dirzo 1987), but this finding has been largely based on the study of the foliage of trees and plants of upper strata and not seedlings or herbs of the forest understory. These insects (together with pathogens and perhaps other invertebrates) should be the exclusive consumers at this level is somewhat surprising, for several folivores, in particular gregarious (e.g., peccaries, coatis) and large (e.g., tapirs, white-tailed deer) ground-dwelling vertebrates should be expected to be important consumers. Absence of evidence of damage by vertebrates, low levels of herbivory, and extremely high-density carpets of seedlings and herbs (see below) are striking and, apparently, recently acquired (G. Pérez-Higareda personal communication) features of the understory of this and other neotropical forests. Are these features anomalous? If so, what are the possible reasons for such a scenario?

POSSIBLE REASONS FOR THE OBSERVED PATTERNS

Three possible reasons could account for the observed patterns: (1) a biogeographical limitation in the distribution of vertebrates, (2) unpalatability of the foliage, and (3) contemporary defaunation. We shall discuss each in turn.

Biogeographical Limitation

Given that Los Tuxtlas is the northernmost limit of the distribution of the tropical rain forest on this continent, it could be expected that this location is out of the range of distribution of some of the typical ground-dwelling neotropical vertebrates, including some folivorous species which, presumably, feed on the plants of the forest understory. However, there is solid evidence in the literature suggesting that Los Tuxtlas is not out of the range of distribution of numerous species relevant to this discussion. Literature accounts include information both at a global level (i.e., the country and the North American region) (Hall 1981; Leopold 1959; Ramirez-Pulido et al. 1983, 1986) and at a more local level (i.e., the State of Veracruz and the specific region of Los Tuxtlas) (Hall and Dalquest 1963; Navarro 1980, 1982). This information and that provided by naturalists and researchers with a long working experience in the area allows us to confidently state that up to some 20 years ago the area maintained sizable populations of ground-dwelling folivorous (or partly folivorous) species such as *Tapirus bairdii, Tayassu pecari, Tayassu tajacu, Mazama americana, Odocoileus virginianus, Dasyprocta mexicana, Agouti paca, Nasua nasua*, as well as arboreal herbivores such as *Ateles geoffroyi, Coendu mexicanus*, and *Potos flavus*. Consequently, we are led to conclude that biogeographic limitation is not responsible for the currently observed patterns of herbivory.

Foliage Unpalatability

An alternative explanation is that chemical characteristics of understory plants, for example high concentrations and diversity of secondary metabolites, low-water contents or other nutritional limitations, render the foliage of these plants highly unacceptable to vertebrate herbivores. We assessed this possibility by means of acceptability experiments in which we offered the foliage of five representative species of seedlings and five representative species of saplings from Los Tuxtlas to four species of folivorous vertebrates (*Tapirus bairdii*, the baird tapir; *Tayassu tajacu*, the collared peccari; *Tayassu pecari*, the white-lipped peccari; and *Odocoileus virginianus*, the white-tailed deer) kept in captivity at the Instituto de Historia Natural in the city of Tuxtla Gutiérrez, Chiapas. We chose the plant species based on their frequency and abundance in randomly established plots. The five species with the highest scores of an index of frequency (number of plots in which a species appeared/total number of plots) × abundance (numbers of individuals) were included in the experiments. Live plants of these species were collected in pots and offered simultaneously to each of the vertebrates. The plants were left in the animals' cages and we observed the herbivore's reactions until feeding was completed. The results of these experiments are given in Table 13-2. It was quite evident that, with one exception (*Omphalea oleifera*), all plant species were readily acceptable to and avidly eaten by the four species of vertebrates. *O. oleifera* was rejected by the tapir and was found moderately acceptable by the two peccaries and the deer. In addition to these short-term responses, we found no evidence that any of the animals used for the experiments experienced any longer-term negative effects associated with their feeding on the experimental plants. Although acceptability trials have a number of limitations (see Dirzo 1980), the results were so clearcut that we conclude that unpalatability is not responsible for the absence of vertebrate damage on these plants in the field.

TABLE 13-2. Acceptability of Foliage of Plants from Los Tuxtlas to Four Species of Vertebrates Maintained in Conditions of Captivity[a]

Plant Species	Baird's Tapir			White-Lipped Peccari			Collared Peccari			White-Tailed Deer		
	RA	PA	R	RA	PA	R	RA	PA	R	RA	PA	R
Seedlings												
Nectandra ambigens	×	—	—	×	—	—	×	—	—	×	—	—
Psychotria faxlucens	×	—	—	×	—	—	×	—	—	×	—	—
Poulsenia armata	×	—	—	×	—	—	×	—	—	×	—	—
Faramea occidentalis	×	—	—	×	—	—	×	—	—	×	—	—
Rinorea guatemalensis	×	—	—	×	—	—	×	—	—	×	—	—
Saplings												
Omphalea oleifera	—	—	×	—	×	—	—	×	—	—	×	—
Chamaedorea tepejilote	×	—	—	×	—	—	×	—	—	×	—	—
Psychotria faxlucens	×	—	—	×	—	—	×	—	—	×	—	—
Faramea occidentalis	×	—	—	×	—	—	×	—	—	×	—	—
Schaueria calycobractea	×	—	—	×	—	—	×	—	—	×	—	—
Overall (*n*/10)	9	0	1	9	1	0	9	1	0	9	1	0

[a]RA = readily eaten, PA = partly eaten, R = rejected.

Contemporary Defaunation

The previous results, together with an evident, ongoing process of contemporary defaunation, suggest that the latter may be responsible, at least in part, for the altered patterns of herbivory we described above. Defaunation in Los Tuxtlas, as in many other forests, has been occurring because of anthropogenic activities such as hunting, illegal trading of animals and their products (e.g., pelts), collection of specimens for pets, and quite importantly, habitat destruction in the immediate vicinity of the preserve. Adequate documentation of this phenomenon is very difficult, partly owing to its illegal nature, the difficulty of studying these animals, and because their absence is not readily evident. In the following section we describe studies attempting to assess the level of defaunation in Los Tuxtlas and to test the hypothesis that contemporary defaunation plays a role in the altered patterns of herbivory and diversity of the forest understory.

THE DEFAUNATION HYPOTHESIS

Clearly, the test of this hypothesis is difficult. As a first approximation we decided to carry out a comparative study, whereby Los Tuxtlas could be compared with a similar site in which the mammalian fauna was adequately represented. Unfortunately, such a site was not to be found within the region of Los Tuxtlas and the comparable area had to be found elsewhere. After an intensive search throughout the remaining distribution of the tropical rain forest in Mexico, we chose the Montes Azules Biosphere Reserve, located in the Lacandon Forest (Selva Lacandona) in the State of Chiapas (Fig. 13-1). This site was chosen for it appeared to be the most promising in terms of its mammalian fauna.

The Selva Lacandona used to be an extensive tract of rain forest covering about 1.3 million ha extending throughout the northeast of the State of Chiapas and into the Petén Zone in Guatemala (Diechtl 1988). Currently, it constitutes the largest tract of tropical rain forest in Mexico, covering an area of approximately 600,000 ha (Diechtl 1988), 300,000 of which have been assigned (as from 1978) to the Montes Azules Biosphere Reserve. This impressive forest is extremely diverse (see Medallin 1986), but its biota is still largely unexplored. Although deforestation has been intensive, the extant large tracts of forest would suggest that most of the faunal elements of tropical rain forests are still well represented.

In this study we included the following aspects: an assessment of the mammalian fauna, analysis of the patterns of herbivory and, as a corollary, an assessment of the structure and diversity of the forest understory. In all cases, the same methodologies were used at both sites.

Comparison of the Mammalian Faunas

To compare both faunas we used a technique of foot-print detection with 100 50 × 50 cm plots of fine sand randomly positioned along a 500-m transect. The tracks were identified by preparing casts of the foot prints and keying them out with manuals for the identification of animal tracks (Aranda 1981; Murie 1974). Censuses of the 100 plots were done three times during each field session. (There were two field sessions per year, during two years.) This method provided qualitative information regarding the presence–absence of animals. The details and the reliability of this technique are given in Miranda and Dirzo (1990). This survey was complemented with diurnal and nocturnal sightings along the same 500-m transect.

The results of this comparison showed many more species present at Montes Azules than at Los Tuxtlas (15 vs. 9 by the method of tracks and 12 vs. 5 by sightings; Table 13-3). The species list given in Table 13-3 only includes taxa that, by the literature, are expected to occur in Los Tuxtlas. The species detected only

TABLE 13-3. Comparison of the Mammalian Fauna Between Montes Azules and Los Tuxtlas Using Two Methods: Detection of Animal Tracks and Direct Sighting[a]

	Montes Azules		Los Tuxtlas	
Species	Track	Sighting	Track	Sighting
Didelphis sp.	*	*	*	*
Philander opossum	*	*	*	—
Alouatta sp.[b]	—	*	—	*
Ateles geoffroyi[b]	—	*	—	—
Dasypus novemcinctus	*	*	*	—
Sciurus sp.[b]	*	*	*	*
Agouti paca[b]	*	*	*	*
Dasyprocta sp.[b]	*	—	*	*
Nasua nasua[b]	*	*	*	—
Potos flavus[b]	—	*	—	—
Procyon lotor	*	—	*	—
Lutra longicaudis	*	—	—	—
Felis onca	*	—	—	—
Felis pardalis	*	—	*	—
Tapirus bairdii[b]	*	—	—	—
Tayassu tajacu[b]	*	*	—	—
Tayassu pecari[b]	*	*	—	—
Mazama americana[b]	*	*	—	—
Total	15	12	9	5

[a] *, present;—, absent.
[b] Mainly herbivores.

TABLE 13-4. Index of Occurrence of Tracks of a Selected Number of Vertebrate Species from Los Tuxtlas and Montes Azules[a]

	Index of Occurrence	
Species	Los Tuxtlas	Montes Azules
Agouti paca	1.52	3.04
Dasyprocta mexicana	0.30	0.23
Felis onca	0	2.46
Felis pardalis	0.46	1.59
Mazama americana	0	2.07
Tapirus bairdii	0	0.30
Tayassu pecari	0	0.15
Tayassu tajacu	0	0.30
Mean $\pm$ SD	0.29 ± 0.53	1.27 ± 1.17

[a] See text and Miranda and Dirzo (1990) for details on the index used.

in Montes Azules included the tapir, the white-lipped peccary, the collared peccary, and the mazama deer. By their number and biomass (or both) these four species are expected to be important ground-dwelling herbivores. Table 13-3 includes a number of nonherbivorous species whose presence, only in Montes Azules, is indicative of the "health" of the trophic chain in this site and of the converse situation in Los Tuxtlas.

We also calculated a weighted index of occurrence for a number of important species of mammals (Table 13-4). (This index is the product of the frequency with which a species occurs in the plots and the number of recording sessions in which the tracks appeared (for details see Miranda and Dirzo, 1990.) It is clear that the frequency of occurrence of the important herbivores and top predators is substantially larger in Montes Azules (Mann-Whitney's $U = 53$; $P < 0.05$). Moreover, species such as the tapir, the jaguar, the peccaries, and the mazama deer never did appear in the surveyed plots of Los Tuxtlas.

Comparison of the Patterns of Herbivory

The levels of herbivory were determined in permanently marked seedlings (up to 50 cm in height) and saplings (50–150 cm in height). The seedlings were studied in 20-m^2 permanent quadrats and the saplings in ten 10-m^2 quadrats. In both cases, 10 plants were randomly chosen from each individual quadrat, thus totalling 200 seedlings and 100 saplings in each site. The topmost leaves, up to five per seedling and ten per sapling, were individually marked with plastic color rings. At each recording date, all leaves were individually relocated and recorded as intact or eaten with the level of damage and the agent responsible for it noted.

The results of this comparison are summarized in Table 13-5. Although the levels of vertebrate herbivory in Montes Azules would seem to be rather low (overall ca. 29% of the plants and 27% of the leaves were damaged), the comparison with Los Tuxtlas is overwhelming: none of the surveyed plants or leaves were damaged. The implication of this result is that the consistent absence

TABLE 13-5. Damage by Folivorous Vertebrates on Seedlings and Saplings from Both Sites[a]

	Seedlings		Saplings		Overall	
	Plants	Leaves	Plants	Leaves	Plants	Leaves
Montes Azules	58 (29)	289(30.5)	30 (30)	240(24)	88 (29.3)	529(27.2)
Los Tuxtlas	0	0	0	0	0	0

[a]Data are the numbers (percentages) of damaged plants and leaves; pooled values from all quadrats. Original sample sizes for seedling: plants = 200, leaves = 948; saplings: plants = 100, leaves = 1000.

of damage by vertebrates in Los Tuxtlas is, very likely, associated with the marked rarity of this fauna in this site.

Structure and Diversity of the Forest Understory

As a corollary to the comparative study, we included an analysis of the structure and diversity of the understory of the forest from both sites. We surveyed the floristic composition and number of individuals in the same quadrats used for the study of herbivory on seedlings. Seedling density was considerably higher in Los Tuxtlas (Table 13-6, ratio Los Tuxtlas/Montes Azules = 2.3; $P < 0.05$). Nearly 67% of the quadrats from Los Tuxtlas and only 10% from Montes Azules had one dominant species. Likewise, the mean number of different species per quadrat in Los Tuxtlas was about one third that of Montes Azules and, consequently, the mean diversity index is significantly higher in the latter site ($P < 0.001$). These results suggest that the absence of vertebrates may bring about dramatic changes in the structure and diversity of the forest understory.

An obvious alternative explanation for the difference is that Montes Azules, as a forest, has a higher diversity than Los Tuxtlas which, in turn, would determine the differences in the understory. This possibility was explored with a comparative analysis of the diversity of the upper strata of both forests, following the method depicted by Gentry (1982). The survey was carried out in a 0.1-ha plot and included all plants ⩾ 1.0 cm dbh.

Both the number of species and the diversity index were higher in Montes Azules than in Los Tuxtlas (Table 13-7; $P < 0.001$ for the index comparison). However, even if Montes Azules is more diverse, the difference between the two forests could still be used to explore the question, by comparing differences in the upperstory communities with the differences between the two understories. For example, while the ratio of the number of species in Montes Azules to Los Tuxtlas is 1.12, the corresponding value for the understory is 2.6 times higher. Likewise, the ratio of Montes Azules to Los Tuxtlas for the diversity index is 1.14 for the upper strata, while that of the understory is 3.46, that is, over three times higher. These relationships suggest that the differences in the upperstory may not be the sole explanation for the differences in the understories.

TABLE 13-6. Structure and Diversity of the Understory from Both Sites[a]

	Los Tuxtlas	Montes Azules
Mean density (range)	52.8 (11–204)	22.6 (10–62)
Number of quadrats with one dominant species[b]	14	2
Mean number of different species[c]	2.3	6.65
Mean diversity index (H′)	1.07	3.71

[a]Data from 20 1-m^2 quadrats.
[b]Dominant species = 5 or more conspecific individuals.
[c]Based on 10 randomly chosen plants per quadrat.

in Montes Azules included the tapir, the white-lipped peccary, the collared peccary, and the mazama deer. By their number and biomass (or both) these four species are expected to be important ground-dwelling herbivores. Table 13-3 includes a number of nonherbivorous species whose presence, only in Montes Azules, is indicative of the "health" of the trophic chain in this site and of the converse situation in Los Tuxtlas.

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TABLE 13-7. Number of Species and Diversity Index for the Trees and Understory of Both Sites

	Number of Species		Diversity Index	
	Trees	Understory	Trees	Understory
Montes Azules (MA)	90	6.65	1.690	3.710
Los Tuxtlas (LT)	81	2.30	1.482	1.071
Ratio MA/LT	1.12	2.89	1.140	3.460

It is instructive to compare the diversity of the upper strata and the understory for each of the two sites. Owing to reasons such as higher species packing and higher turnover rates of individuals and species in the understory, we would expect understories to be more diverse than their corresponding upper strata. Such is clearly the case in Montes Azules, where the diversity index of the understory is 2.2 times higher, whereas in Los Tuxtlas the diversity index of the understory is, surprisingly, even lower than that of the upper strata (Table 13-7). This relationship suggests an anomalous situation in the structure and diversity of the understory of a defaunated forest.

EPILOGUE

Evidence of the role of herbivores as agents that increase vegetational diversity has been documented for agronomic systems (Harper 1969), marine communities (Lubchenco 1978), and grasslands (Harper 1969; Tansley and Adamson 1925), and has been suggested for tropical rain forests (Janzen 1970; Connell 1971). Our results seem to point in this direction. The impact of herbivorous vertebrates on the diversity of this kind of community may be largely augmented because they do not only feed on the foliage, but they also consume and kill large quantities of seeds (Janzen 1981a; Hallwachs 1986).

Our conclusions regarding the role of vertebrate herbivores on the patterns of herbivory and vegetational structure and composition of the understory of Los Tuxtlas is based on correlative findings. Unequivocal conclusions demand experimental, noncircumstantial evidence. In particular, two kinds of experimental manipulation are amenable: (1) reintroduction of vertebrate herbivores to Los Tuxtlas to see if the patterns of herbivory, structure, and diversity of the understory will then resemble those of Montes Azules and (2) the establishment of selective exclosures in Montes Azules to assess the relative importance of different kinds of herbivores (e.g., insects, vertebrates) and to see if, in the absence of grounddwelling herbivores, the understory resembles that of Los Tuxtlas.

If the kind of experimental manipulations we propose here do confirm our findings, they will unequivocally support the hypothesis that herbivorous vertebrates play an important role in the patterns of herbivory in the forest understory and, in the long term, on the structure and dynamics of some tropical rain forests.

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