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Contemporary Neotropical Defaunation and Forest Structure, Function, and Diversity—A Sequel to John Terborgh*

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A series of long-term studies on the demography of tree seedlings and patterns of herbivory in the forest understory have been carried out at the Los Tuxtlas Tropical Research Station (southern Veracruz, Mexico) (see de la Cruz & Dirzo 1987; Dirzo 1984, 1987; Dirzo & Miranda 1990; Núñez-Farfán & Dirzo 1988). As a result of these studies, a number of features of this forest's understory became evident which, we believe, support Terborgh's contention (1988) that the "big [animal] things" of the tropical forest play an important though largely unappreciated role in the diversity and structure of these natural systems.

Such features of the forest understory at Los Tuxtlas include the following (1) A consistently low or total absence of damage by folivorous vertebrates. Practically none of the seedlings, which were individually marked and monitored for several years, show evidence of damage, other than by invertebrates (insects in several orders). Moreover, none of our permanent plots has shown damage by trampling, which is characteristic of other areas of tropical Mexico in which tapirs, white-tailed deer, mazama deer, and peccaries are present (personal observation). (2) A marked absence of several components of the forest floor–dwelling fauna that, presumably, should be trampling and feeding on the plants of this stratum. This absence is striking since 90 species of mammals are reported for the area, including several medium- to large-sized species of terrestrial herbivores (Navarro 1982). Evidence of a process of contemporary defaunation in Los Tuxtlas is presented elsewhere (Dirzo & Miranda 1990). (3) In the immediate vicinity of reproductive trees of several species with large seed crops (e.g., *Brosimum alicastrum, Dussia mexicana, Nectandra ambigens, Omphalea oleifera*), the forest floor is densely covered by carpets of these trees' seedlings. Due to the usually clumped distribution of the adult trees of these species, the carpets are often very extensive. These carpets are virtual monocultures in which insect herbivory (<10% leaf area eaten [de la Cruz & Dirzo 1987; Dirzo & Miranda, unpublished data]) and pathogenic infection (<5% leaf area damaged [García-Guzmán 1990]) are relatively low and the seedlings die mostly from shading by neighboring plants and from the physical damage caused by objects falling from the canopy. In areas not covered by tree seedlings, the carpets are replaced by dense mats of herbaceous plants, mostly in the Araceae (e.g., *Anthurium bombacifolium, Monstera acuminata, Syngonium podophyl-*

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lum — C. C. Horvitz & R. Dirzo, unpublished data). In these areas of herbaceous plant cover, herbivory is accounted for by insect and pathogen damage (García-Guzmán 1990) and no vertebrate herbivory has been detected. Furthermore, piles of seeds and fruits are occasionally left rotting on the ground, particularly in some areas of the forest (such as those on volcanic outcrops) where nesting sites and, presumably, densities of small rodents (mainly *Heteromys desmarestianus* and *Peromyscus mexicanus*) are rather low (R. Dirzo & S. Sinaca, unpublished data).

Are these features of the forest understory anomalous, and if so, to what extent are they a result of the presumed absence of mammalian vertebrates? The appropriate experiment to test this question at Los Tuxtlas would be to establish experimental plots with controlled and contrasting levels of grazing and trampling. However, our current level of knowledge on the ecology and management of this fauna, and the difficulty and potential dangers of a major "transplant" exercise, particularly for a site as small as Los Tuxtlas (700 ha the biological station itself, or ca. 4,000 ha if its still-forested western extension and surrounding fragments are considered — Dirzo 1990) prevent this experiment from being undertaken at the moment. In an attempt to carry our conjecture a bit farther, however, we conducted a comparative study between Los Tuxtlas and the Lacandon forest in Chiapas (southern Mexico), a major tract of forest some 500 km to the south of Los Tuxtlas and one in which the mammalian fauna was expected, in principle, to be much more intact than that of Los Tuxtlas (see Dirzo & Miranda 1990). This approach is the same as Terborgh (1988) used in comparing Cocha Cashu (Amazonian Peru) with the partly defaunated Barro Colorado Island (Panama) to assess the importance of top predators in the ecology of tropical forests.

In our study, we first documented that other alternative explanations, such as foliage unacceptability to vertebrates, do not seem to be the reason for the marked absence of vertebrate damage or trampling in the Los Tuxtlas understory. We then compared (1) the presence/absence and relative abundance of the mammalian faunas from both sites. This was accomplished by censusing, six times a year over two years, the presence of animal tracks on 100 quadrats (0.5 m × 0.5 m) of fine sand randomly positioned along a 0.5 km transect. Casts of the footprints were prepared and identified with Aranda's (1981) manual for mammalian tracks. Details of the technique are given in Miranda and Dirzo (1990). We also compared (2) the levels of herbivory by vertebrates, by censusing 300 individually tagged understory plants (seedlings and saplings) from each site. As a corollary, we compared (3) the structure and diversity of the two forests' understories based on the analysis of 20 1 m^2 quadrats on each site.

Our results indicated, first, that at Los Tuxtlas, forest floor–dwelling vertebrates are very poorly represented. In terms of their presence in the sand quadrats, we detected nine species, whereas fifteen were found in the Lacandon forest. The species detected only in the Lacandon forest include the tapir, the mazama deer, the white-lipped peccary, and the collared peccary — species which by their number and/or biomass are expected to be important understory herbivores. Likewise, other nonherbivorous species (including top predators such as the jaguar) were present only in the Lacandon forest. A weighted index of animal occurrence (details of the index in Miranda & Dirzo 1990), calculated for a select list of herbivorous species (tapir, mazama deer, white-lipped and collared peccaries, paca, agouti) and predators (jaguar, ocelot), indicated that the frequency of occurrence of some of the important understory mammals is very low at Los Tuxtlas (overall mean [s.d.] index difference: Los Tuxtlas 0.29 [0.53]; Lacandon forest 1.27 [1.17]; U-test, $P < 0.05$). Although our emphasis was on the terrestrial mammals and we do not have comparable quantitative information on the arboreal ones, diurnal (06–08 hrs) and nocturnal (20–22 hrs) censuses by direct sightings on both sites indicated the total absence at Los Tuxtlas of at least one species, the spider monkey (which, indeed, we have not seen in the forest for the last nine years), and the low abundance of other species, such as the kinkajou. Thus, by "defaunation" at Los Tuxtlas we imply the absence or low occurrence of many of the components of the forest floor–dwelling mammals, ranging from the size of agouties (~2.5 k) to jaguars (~80 k), and the absence or low abundance of some arboreal ones too. Second, while at the Lacandon forest 29% of the sampled seedlings and 30% of the saplings were damaged by vertebrates, none of the plants from Los Tuxtlas were damaged by these organisms. Third, the density of seedlings was 2.33 times higher (58.2 vs. 22.6 m^{-2}; U-test difference, $P < 0.05$) and the understory diversity 3.46 times lower (Shannon's Index, H', 2.3 vs. 6.65; modified t-test for H' comparison, $P < 0.001$) in Los Tuxtlas than in the Lacandon forest.

Additionally, the absence or low abundance of some understory mammals at Los Tuxtlas might imply reduced levels of seed predation for some relatively large-seeded species (which typically produce dense seedling carpets) such as *Brosimum alicastrum, Dussia mexicana, Nectandra ambigens,* and *Omphalea oleifera.* These species are readily eaten when offered to some captive mammals such as peccaries and white-tailed deer (R. Dirzo, unpublished data).

These results are highly suggestive, but association of facts does not guarantee causality and experiments are still needed. However, we are now much more confident about the potential value of the experimental ma-

nipulation, and moreover, as a result of this prospective study, we now have a more practical alternative experiment: instead of "retransplanting" the mammalian fauna to Los Tuxtlas (with all the problems this would imply), we will establish exclosures at the Lacandon forest to see if we can generate patches of forest understory with the "defaunation syndrome" of Los Tuxtlas. As a control, comparable exclosures will be set up at Los Tuxtlas. The value of such experiments cannot be overemphasized, not only for their potential to help us understand nature, but because of their far-reaching implications "for the future management of isolated forest fragments" (Terborgh 1988, p. 403), which are an increasingly common feature of tropical areas.

What we have described as "anomalous" features of the understory of Los Tuxtlas do not constitute a "defaunation syndrome" of general applicability, for the absence or low abundance of vertebrate animals may be a natural aspect of some forests (see Janzen 1974). However, the image of the defaunation syndrome of the understory (seedling carpets, vertebrate damage-free understory herbs and seedlings, piles of uneaten rotting fruits and seeds) comes to mind when we think of areas of intense perturbation by gold miners (and their hunting), as compared to nondisturbed areas in Corcovado National Park, Costa Rica (Janzen et al. 1985; R. Dirzo, personal observation). Are other protected forests already experiencing the same phenomenon? It might be worth considering and studying the ecological implications of defaunation in such important sites.

We believe that our preliminary findings constitute a sequel to Professor Terborgh's contention that tropical "big things" are important, although our case differs from his in some respects. Terborgh discusses a situation of "selective defaunation" whereby the top predators are missing and the herbivores, lacking a controlling agent, have a negative impact on some components of the vegetation, presumably via intensive seed predation on the large-seeded species. Our case is a situation of more "general defaunation," in which the top predators, as well as the herbivores, are missing and it is the vegetation (or some of its components) that lacks some of its controlling agents, apparently via reduced herbivory (and perhaps seed predation and trampling). It would seem premature to conclude, for our studied system, that its big things "hold the key to its stability and to the maintenance of its extraordinary diversity of plants and animals" (Terborgh 1988, p. 402). However, our studies suggest that medium to large mammalian herbivores may play an important role in the structure and diversity of the understory (and perhaps in the long-term dynamics of the forest). Quite clearly, this is an area of tropical conservation biology that warrants further study.

Finally, two other important lessons emerge from this kind of study. First, tropical biologists frequently tend to gain an idea of the degree of conservation of a given site on the basis of physiognomy-related macro attributes of the forest (e.g., the relative abundance and distribution of secondary species, or the frequency distributions of tree diameters). Obviously these are useful, but they can also yield a very misleading image: a forest such as Los Tuxtlas has a splendid botanical (macrophysiognomic) appearance, but it is a very dramatically altered forest. Second, these studies point out to the tremendous value of the few large and relatively well-conserved (botanically *and* zoologically) sites that still exist in the tropics. Many important lessons for understanding, managing, and conserving tropical ecosystems (and their agroecosystems too) remain to be learned from the relatively undisturbed areas of the world.

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