Anthropogenic disturbances infiltrate forest fragments

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In the years after Edward O. Wilson and Robert MacArthur's seminal book, *The Theory of Island Biogeography* (1), which laid the foundations for understanding species diversity and extinction rates in isolated habitats, was published in 1967, a flurry of papers erupted on the effect of fragmentation in tropical rainforests. The big question at that time was whether it would be more advisable to protect massive tracts of continuous rainforest or smaller patches forming an archipelago of forest fragments within an anthropogenic matrix of pasturelands and tropical farms. Tom Lovejoy, who, like MacArthur, had earned his doctoral degree at Yale University under the mentorship of G. Evelyn Hutchinson, decided to put the question to a test by taking advantage of the ongoing land clearings around Manaus, Brazil, to create a large-scale experiment. In collaboration with Amazonian ranchers, the team cleared the trees around a series of fragments of rainforest of varying sizes to create islands of intact forest, and have been monitoring the plots since 1978, carefully documenting how deforestation harms neighboring pristine fragments as plants and animals of the mature forest give way to more opportunistic species that thrive in disturbed habitats (2–4). The Manaus experiment has been replicated in many different tropical regions with similar results, showing the vulnerability of small reserves to large-scale human disturbance. The detailed underlying mechanisms of biodiversity loss, however, remained to be unraveled. In PNAS, a group of Mexican ecologists tackle the problem of ecosystem fragmentation from a different perspective, the demography of understory plants, adding important information to our knowledge on the dynamics of forest fragments (5).

Demography of the Rainforest's Understory

In 1973, after finishing his doctoral degree in Bangor, North Wales, under the mentorship of John Harper, José Sarukhán returned to his native Mexico. Sarukhán had completed a series of studies, which he published in collaboration with Harper (6) and Madhav Gadgil (7), in which they showed that despite the challenge that the simultaneous occurrence of vegetative propagation and sexual reproduction may pose, plant populations can be studied and modeled with the tools and techniques of quantitative demography, including the estimation of Markovian transition probabilities between life-history stages. Sarukhán's work with buttercups in North Wales spread among the scientific community and was hailed by Hutchinson (8), the mentor of MacArthur and Lovejoy, as a groundbreaking initiative. He wrote "the fact that the smallest individual plant can be entered on a large-scale map [. . .], directly copying the distribution in the field, makes the study of plant demography far more accurate than is possible in most studies of animals, provided that the investigator has almost limitless patience."

Upon returning to Mexico, Sarukhán decided to extend his studies in plant demography to Mexico's tropical rainforests. He realized that the ecological dynamics in the shaded understory were immensely important to understanding and predicting the fate of the rainforest because, decades into the future, the forest canopy will be dominated by those species that manage to germinate and survive in the understory at present. Thus, he chose as his study species the understory palm *Astrocaryum mexicanum* at the Los Tuxtlas Tropical Field Station, the northernmost tropical rainforest reserve in Mexico. Armed with Hutchinson's proverbial limitless patience, the team started the demographic monitoring of *Astrocaryum* in 1975, and has continued to this day. The group, all researchers from Mexico's National University (UNAM), tagged thousands of palms in permanent plots and developed some ingenious tools to study the demographic dynamics of the palms (9): They correlated stem growth and leaf scars with plant age. Because trees or large tree parts that fall, opening gaps in the canopy, bend in their collapse the palm shoots, which regain vertical growth leaving behind a kink in the stem, they used the twisted palm shoots to estimate frequency and date of gap formation (10). They recorded seed production, estimated seed predation, and followed in detail the survivorship of tagged cohorts, while quantifying at the same time detailed parameters describing the community structure of the rainforest, including species richness, floristic composition, and spatial pattern.

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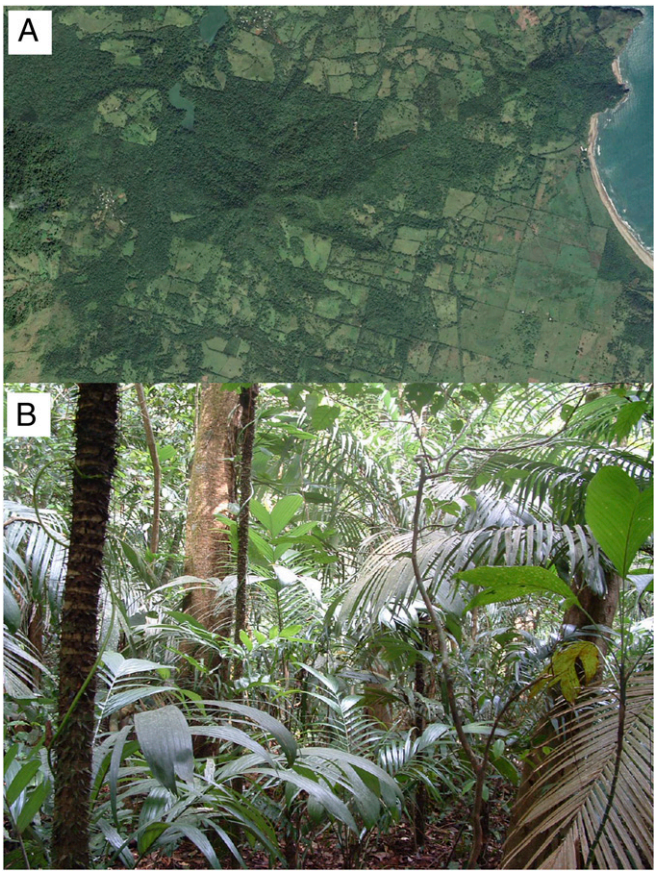

Fig. 1. (*A*) Los Tuxtlas Tropical Field Station, in the coastal plains of Veracruz, is now besieged by encroaching tropical pastures and a deforested landscape. Image copyright Google Earth Pro, DigitalGlobe; imagery date 10/26/2014. (*B*) As a result of anthropogenic disturbances, gaps open more frequently in the canopy of the 640-ha reserve, whereas foraging by large herbivores has dwindled, allowing the understory palm *A. mexicanum* to become dominant and control the regeneration dynamics of the forest. Image courtesy of Miguel Martínez-Ramos.

During the four decades that have passed since the project started, deforestation and other anthropogenic disturbances have ravaged the rainforests of Veracruz (11). Ironically, while the team of ecologists from UNAM grew and consolidated into one of the best research groups in Latin America, almost all of the forests along the coastal plains of the Gulf of Mexico were felled and turned into farm fields or, more often, pastures. Despite efforts by the UNAM researchers to protect the regional forests in the form of a large biosphere reserve, during the 40-y study period, the Los Tuxtlas field station gradually became isolated into a 640-ha fragment of zealously protected forests surrounded by a matrix of induced pasturelands, a true ecological island. This growing besiegement gave the research team the opportunity to follow the changing dynamics of the forest within the protected reserve as anthropogenic destruction progressed outside its boundaries, providing an answer to the fundamental question about the viability of isolated reserves when destruction reigns all around (Fig. 1).

Fragmentation and Loss of Large Animals

As the team suspected when they started the project in 1975, looking in detail at the demography of understory species can provide critically important elements to understand the dynamics, and ultimately the fate, of the rainforest in a rapidly changing environment. As the forest fragments become smaller and more isolated, the dominant trees, especially those trees near the edge of the fragment, become more vulnerable to extreme weather and desiccation, and fall more easily. Because of the large perimeter-to-area ratio, edge effects seriously affect small fragments: Forest gaps open more frequently, leading to increased light availability and higher photosynthesis rates for understory plants (12). Increased photosynthesis in the beleaguered field station allowed *A. mexicanum* to devote more of its energy budget for reproduction, and, as a result, seed production tripled during the study period. Rising frequencies of gap formation also allowed young palms to elongate faster and reach reproductive age sooner, whereas the older, tall palms, which could not withstand the physiological damage of direct sunlight exposure, started to die. As the Los Tuxtlas fragment shrunk, gaps increased and the palms switched to a different demographic mode with shorter life spans and earlier reproduction but with a dramatically increased fecundity.

Contemporary defaunation, the loss of large animals through hunting and habitat destruction, also played a critical role (13). A small forest fragment cannot support the home ranges needed by many large herbivores, and hunting around the embattled reserve decimates the populations of those large herbivores that migrate in and out of the fragment. As a result, deer, peccaries, and tapirs have all but disappeared from Los Tuxtlas, whereas mice and squirrels have increased fivefold. These small rodents move the hard nuts of *Astrocaryum* into caches, but rarely damage them to lethal levels (14). As a result, more seeds are able to germinate successfully and transition into seedlings. In addition, *Astrocaryum* seedlings, which are unarmed and have grass-like leaf blades, were browsed and consumed in the past by the now-gone large mammals. Their absence from the reserve allows seedling survivorship to be much higher at present than ever before.

Cascading Effects

The dramatic increase in palm density and cover had cascading effects on other ecosystem components. The population explosion of *Astrocaryum* reduced space and resource availability for trees in the understory. As the palm expanded, the diversity and density of understory trees declined in a similar proportion. The species that did manage to survive in the palm-dominated understory were fewer and more similar in composition between plots, leading to the homogenization of the forest understory and a loss of spatial diversity.

Looking at the complex network of connected effects from a demographic perspective through the dynamics of the *Astrocaryum* palm, Martínez-Ramos et al. (5) were able to identify the mechanisms and drivers of anthropic disturbances to a fine degree, and how they cascade onto the structure and function of the rainforest ecosystem. Instead of focusing on canopy species to understand the effects of forest fragmentation, this new study focused on the less visible understory plants, and, using the tools of plant population biology, it shows how these plants play important roles in the maintenance of forest structure and functioning, and how, when affected, they can become major drivers of rapid ecosystem change.

The study's message is that even in apparently well-preserved natural areas, the influence of surrounding anthropogenically modified ecosystems can drive forest degradation and a decline in biodiversity if the size of the protected forest fragment is not large enough. Additionally, the painstakingly gathered 40-y dataset describes the complex cascading mechanisms that link

human disturbances to plant demography and to a decline in ecosystem function and services. Through a combined impact on the population ecology of understory palms, the joint effects of fragmentation and defaunation may render conservation efforts ineffective. The cascading disruptions derived from human disturbances in the Anthropocene can affect even the best-protected natural areas if they are not large enough. Unfortunately, this rapid disruption of tropical forests driven by the anthropogenic degradation of the surrounding habitats is not unique to Los Tuxtlas. Recent studies have shown that the phenomenon is widespread and progressing rapidly on all continents, putting global biodiversity under serious risk (15).

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