

THE ETERNAL EXTERNAL THREAT

Daniel H. Janzen

Once a preserve is established and once its neighbors accept its presence as a geographic entity, there is a strong inclination to turn to other conservation projects and leave the preserve to the managers and users. At this point the chainsaws and hunters can be stopped, but how do you keep out the moths that breed in a cotton field many kilometers distant? Who will stop agriculturally-induced rainfall reductions from drying out a tropical park? Who is going to remove the European ruderal herbs from the riparian succession in a New York state park? Who is going to stop the fast-growing legume trees that are being introduced for firewood from spreading into a tropical preserve? Are you going to tell the peccaries in your park they cannot maintain their density ten times higher than normal while feeding in the secondary succession around your park?

I do not have solutions to the class of problems that I discuss here. My only hope is that those in direct contact with this class of problems will encounter the solutions, case by case. Every case will have unique solutions that will be evident to the persons who are privy to the natural histories of the particular organisms and habitats in their care. I can say with certainty that this area of conservation has only one general principle: the only insular preserves are those that were insular to start with—and even these are subject to long-distance movements (or the lack of them) from human-generated habitats.

Preserve managers turn to ecologists (among others) for methodologies and principles that will give them a greater chance of management success. My opinion is that ecologists have only one rule to offer:

get to know the organisms and habitats in your care so well that you will recognize this class of problems at inception or earlier. In fact, knowledge of other systems and of general rules can even be counter-productive if they lead to watchfulness only for problems that have already been identified. Every nature preserve is guaranteed to have one or more major problems of this type that are unique to it and its communities.

There are two groups of external nonhuman and unintentional human threats to a preserve. First, there are biotic problems, based on wild or free-ranging domestic organisms to which the preserve boundaries mean little or nothing, or are just another habitat discontinuity. Second, there are human-induced changes in the physical world outside of the preserve, changes that wash over the preserve as well. In both cases, the threat is as much (if not more) to the interactions within the preserve as to the simple persistence of a species. The best guarantee of the latter is the maintenance of the former.

THE BIOLOGICAL WORLD

Animals and plants move. While a preserve's boundaries may serve well enough to stop direct human transgressions, the boundaries *per se* will mean nothing to most organisms. There are many biological facets to this problem, and I list a few below. A number of these facets are managerially contradictory, yet occur simultaneously in nature. As I emphasized in the introduction, each preserve will have its own variants and combinations. Preserve managers will have to come to their own decisions about which to ignore and which to attempt to modify.

Normal dispersal

Organisms normally leave a site by eruptive migration—fledging juveniles, seed and pollen dispersal, etc. If the site is an arbitrary patch in a continuous ocean of habitat or mosaics of habitat, this outflow is eventually matched by inflow. However, this statement becomes less true the more the site is on the margin of a major population discontinuity for the organism concerned. Preserve boundaries are very often major population discontinuities (and are becoming more so). Even if there is no habitat discontinuity at the preserve boundary, human harvest activities often generate a population discontinuity at the boundary. This means that for most populations on margins, the preserve boundary is a unidirectional filter. It lets members out, but few return. An animal that moves out of the preserve and disappears into

the outside world is just as dead as one that is shot by a poacher 2 km inside the preserve.

Such potentially severe losses occur without a human ever stepping foot in the preserve. How deeply these effects penetrate depends entirely on the behavior of the animal or the potential for pollen dispersal of a plant. For wide-ranging animals such as a herd of several hundred white-lipped peccary (*Tayassu peccari*), "the boundary" may be 10–30 km deep; for a howler monkey troop (*Alouatta palliata*), it is perhaps only a few meters from the forest–pasture habitat discontinuity. Imagine a large wind-pollinated beech tree (*Fagus*) that is growing on the margin between a 2-ha pristine forest preserve and an apple orchard. Half the tree's pollen is ecologically dead simply because it lands in the orchard. Furthermore, the beech tree's incoming pollen represents only half as many parents as does the pollen load that the tree would receive were it imbedded in a large pristine forest canopy.

There are two important components to this boundary effect. First, population density along boundaries may well be lower than in central areas simply because the rate of reproduction in this "habitat" is effectively reduced. This effect will be difficult to separate from other boundary effects to be discussed below. Second, this boundary effect depends on the habitat types surrounding the preserve. If the external habitats discourage animals from moving into them, they may have a less disruptive effect on the preserve than if they allow animals to go out but not to return. For plants, a preserve boundary is a sponge rather than a wall.

Migration

Anyone concerned with songbirds understands the omnipresence and importance of seasonal migrations in the biology of a preserve (e.g. Howe, 1984). It is likewise fully appreciated that if such migrants are to arrive, they have to come from somewhere. We all know the story: no matter how magnificent the waterfowl refuges along migratory flyways, if you eliminate the prairie pothole nesting grounds you eliminate the ducks. Conservation thus becomes a game of simultaneous and unerring maintenance of distant habitats connected by biological threads tens to thousands of kilometers in length. The interruption of either end of the cycle leads not only to the loss of the migrant population, but may also result in the loss of "cultural" knowledge of migratory endpoints for the species as a whole. A California monarch butterfly (*Danaus plexippus*) will have no idea of how to get to the traditional overwintering grounds of the eastern monarch in the Mexican highlands (e.g. Brower et al., 1985; Urquhart and Ur-

quhart, 1976). This means that it is unlikely that the former, if introduced into the eastern United States, would become easily established.

We are only now beginning to dimly focus on the fact that migrations within the tropics are an integral part of the biology of many tropical organisms. This has been appreciated by biologists in Africa for some time; seasonal movements (and forced cessation of seasonal movements) of big game and birds have been a constant source of anguish for conservationists on that continent. Biologists are just beginning to discover the intratropical migration patterns of the Neotropics (e.g. Stiles, 1983; Leck, 1985; Janzen, 1984a, 1986), but I suspect that for many species the discovery is coming too late. A very great external threat from agriculture is that it will eliminate one of the end points in a migratory cycle. Here I offer a single example from Santa Rosa National Park in northwestern Costa Rica.

Large moths of the family Sphingidae are prominent visitors (and presumed pollinators) of flowers in the Park (Haber, 1984; Haber and Frankie, 1982). Their large caterpillars are conspicuous consumers of foliage and they are major dietary items for certain species of insectivorous birds and parasitic insects. There are at least 64 species of sphingids that breed in Santa Rosa during the first two months of the rainy season (Janzen, 1984a and in press), and it is clear that they interface with many points in the Park's ecosystem. There are at least 40 species that appear to have the following life history. At the beginning of the rainy season (mid-May) the adult moths arrive in the Park in large numbers. They visit flowers and oviposit on more than 100 species of plants (Janzen, 1984a and in press). Within three months, they have passed the first generation in the Park and emerged from their pupae. During this first generation, the carnivores that feed on them have built up from their annual low at the end of the dry season to their annual high at the end of this first generation. At this time many individuals of most species of sphingids leave the park. A few appear to stay there and have a second generation, but it appears that the majority fly to the rainforest side of Costa Rica, 15–50 km to the east.

By the end of the rainy season, all the adults of at least 40 sphingid species seem to have left the park, and they leave no residual dormant pupae or eggs. Also at this time, these adults of the migrant species are common on the rainforest side of Costa Rica. Because seemingly freshly emerged adults appear at lights for the following six months in the rainforest, I assume that one or more generations occur there. At the end of the Santa Rosa dry season, these adults fly back across the central mountain ranges to the dry forest on the Pacific side of Costa Rica for their (next) generation in their food-rich and relatively predator-poor habitats.

that are using the pristine habitat for shelter from the sun and weather require no elaboration.

Many animals eat fruits and defecate (or regurgitate) the seeds (Janzen, 1984b). This seed rain falls wherever the animals go. If a pristine preserve is embedded in secondary succession, the pristine habitat fragment is bombarded by a far higher density of these propagules than it would be if that site were simply part of a large piece of pristine vegetation (Janzen, 1983; Ranney et al., 1981; Estrada et al., 1984). Since microsuccession in treefalls and other kinds of natural disturbance sites is dependent as much on the numbers of seeds as on the kinds of seeds that arrive, this bombardment has a high potential for altering the course of succession and eventually the overall structure of the pristine vegetation.

The alteration is exacerbated not only by the seed dispersal activities of the animals, but also by the occurrence of the secondary successional plants around the pristine area at much higher densities than they were prior to human intervention. Rare plants and very patchily distributed plants in natural disturbance sites become the common ones in old field, pasture, and roadside regeneration (Marks, 1983; Janzen, 1984b). This means, for example, that a Santa Rosa treefall is not only getting traversed by more collared peccaries (*Tayassu tajacu*) per week, but those peccaries leave more seeds from secondary successional plant species per defecation than would peccaries living in a very large expanse of pristine vegetation.

Denizens of the crop habitat

Crop and pasture lands (abandoned or in production) generally contain large populations of many species of animals and plants. Many of these are exotics, and they are strongly dependent on the crop and its microhabitat. However, there are also many species that eruptively migrate (or colonize) into neighboring preserves from agricultural land (e.g. Marks, 1983). There are also indigenous species on agricultural land that still have noncrop populations in more pristine neighboring preserves.

Species input from agricultural habitats has two possibly severe impacts. First, as implied above, migrating or colonizing species may simply consume preserve organisms (and serve as food for them), thereby altering the preserve (see the discussion of nest predation in habitat edges by Wilcove et al., Chapter 11). This applies to parasites and diseases as well as to the traditional carnivores. Second, and much more insidious, these large widespread agricultural populations may homogenize the gene pools of the preserve's "wild" conspecifics. There may be a quick loss of whatever genetic adaptations there have been

to local biotic and physical conditions (see Templeton, Chapter 6). Pesticide resistance, high reproductive rates, peculiar dormancy physiologies, and other traits that are strongly selected for in agricultural species should appear in the wild population where they may depress fitness. We know very little about the swamping of the gene pool of a small and locally adapted population by a large and widespread population that is subject to somewhat different selective pressures (but see Ledig, Chapter 5).

The crops themselves

There is a widespread lack of fear of the spread of crop organisms and horticultural varieties, both because they are "good" and because they are widely thought of as being so heavily dependent on humans for protection that they will not be a threat to relatively pristine areas. There are two conspicuous kinds of exceptions. First, when crop organisms have been introduced to islands (or to other naturally impoverished areas) there is little ecological resistance to their spread; this has been documented extensively (see Pimm, Chapter 14).

Second, there is the widely unappreciated problem that today's agriculturalists (in the broad sense) are busy looking for new organisms to cultivate as crops, organisms with properties that are not represented among traditional cultivars. Such neocultivars are but little different from truly wild phenotypes. The introduction of the Africanized honeybee into the Neotropics is perhaps the most widely popularized example. Introduction of *Eucalyptus* into the Neotropics is a threat in progress (somewhat less so, however, because its wind- and gravity-dispersed seeds are slow invaders, and because particular human-induced burning regimes are probably necessary to maintain a resident *Eucalyptus* breeding population).

A storm cloud on the horizon is the well-meaning but potentially catastrophic widespread introduction of fast-growing tropical firewood trees (Hughes and Styles, 1984). These are mostly ruderal legumes, and are the sorts of trees that will become prominent members of natural disturbance sites in relatively pristine vegetation. The introduced plants have a strong chance of influencing the outcome and speed of succession and competitively eliminating some of the habitat's members.

As humanity becomes ever more imaginative in building agroecosystem habitats that are constituted of a diverse array of organisms, the intercontinental and interhabitat movement of species will be ever more widespread. The steps are largely irreversible. Except for very large (and slowly reproducing) organisms, or those with peculiarly susceptible individuals (e.g., the dodo, *Raphus cucullatus*), our chances

of eliminating introduced and established organisms is nil except at very high cost. As a general statement, a large pristine habitat is probably the only effective barrier to such external threats, and even that will be penetrated by a variety of introduced organisms (Africanized honeybees, for example, maintain established breeding populations in Costa Rican pristine forests).

The threat from the preserve

As any African farmer next to a national park well knows, there are animals in a preserve that can be incompatible with contemporary agriculture. Indeed, if the Pleistocene hunters had not eliminated the New World herbivorous megafauna, the post-Pleistocene farmers certainly would have; glyptodonts, ground sloths, and gomphotheres (Janzen and Martin, 1982) would not have been miscible with corn fields. Complaints that protected animals damage crops range from Swedish wolves killing the occasional sheep (for which the owners are compensated by the government), to ducks feeding in North American grain fields, to vampire bats in Santa Rosa National Park feeding on cattle on neighboring ranches. As agricultural intensity and refinement increase around a preserve, the chance for such interaction creating ill will toward the preserve increases. Simultaneously, increasing educational sophistication of the neighboring landowners should result in greater tolerance to damage and the suggestion of intricate solutions. The balance between these two processes can only be determined on a case-by-case basis, but this balance does need to be considered if one is to understand the interaction of a preserve with its surroundings.

THE PHYSICAL WORLD

The threatening physical environment around a preserve ranges from that which is under the direct control of humans (e.g., pesticides and fire) to uncontrollable weather modification by humans.

Pesticides

The avoidance of pesticide and other agrochemical contamination of a preserve appears to be little more than a direct struggle between the humans that apply them and those concerned with the preserve. Spray plane overflights and nearby pesticide applications on windy days are generally a legal matter between the preserve and surrounding areas, as if the preserve were simply another farm. Pesticide contamination

of wide-ranging vertebrates that sometimes feed outside of the preserve is a battle that hardly needs mention. However, there are three aspects of pesticide dynamics that deserve emphasis.

First, in developing countries the concern over pesticides is generally directed at human health hazards. As concern becomes more sophisticated, it is generally directed at vertebrates, and especially those found dead after severe sloppiness in pesticide applications. Insects and other arthropods often escape this concern. They are small (their carcasses are inconspicuous), generally feared and disliked by most people, and not a focus for preserve establishment. It has been my experience that very substantial pesticide damage to insect populations in a preserve can occur in areas marginal to agricultural land, with no notice taken by preserve managers who are quite eager to eliminate fires, poachers, and timber thieves. At least part of this oversight is due to a misconception about pesticides. Bulk containers identify not only the chemicals, but give warnings such as "mildly toxic," "extremely toxic," etc. Suspicious preserve managers who investigate pesticide operations near the boundaries are likely to have their fears diminished by reading that a pesticide being applied is only "mildly toxic." However, pesticides are designed to kill invertebrates; the warning labels refer to toxicity to humans and other warm-blooded vertebrates, not to the target organisms.

Second, many preserves are established simply by taking in as much preserve-worthy habitat as is available. When more choice is possible, a time-honored criterion is the inclusion of entire drainage systems within the preserve. This is more than an ecological nicety and must be done even if the drainage basin contains croplands which have to be abandoned. Recent incidents with pesticide threats to Santa Rosa National Park in northwestern Costa Rica have underscored the need for a more thorough look at a drainage system.

Santa Rosa contains the upper drainage basin for several large dry river systems. However, those who established the Park boundaries did not notice that a tiny number of feeder streams and small slopes above those streams were left outside of the park. In no case does the area outside the Park make up more than 1-3 percent of the total catchment of the drainage systems. However, in recent years the cattle pastures that previously occupied the southern boundaries of the park have been converted to cotton and other croplands. The outcome is that each river system gets a major pulse of pesticides (all correctly applied on calm mornings by spray planes) and silt via rainwash surface runoff from the fields. One of the dry river systems (Quebrada Guapote) has been sterilized, and a second is very likely to be destroyed unless some kind of alternate land use can be assigned. A tiny

error in boundary demarcation can have a very large effect on a preserve if extremely toxic chemicals are being pushed into the habitat.

Third, as any farmer knows, pesticide applications in fields do not eliminate pest populations but rather (it is hoped) depress them enough to allow a crop to develop. Associated with this, the populations of insects in fields are often resistant to pesticides. This often leads to the impression that pesticides are a nuisance to insects but not likely to exterminate them. What such observers generally do not know is that when the same pesticides are applied to wild vegetation, they are effective at eliminating wild insect populations. Perhaps the most dramatic examples of this come from small woodlots and low forest strips between cotton, sorghum, and other crops in Costa Rica and Nicaragua. Airplanes commonly spray this remnant vegetation at the same time that the crop is sprayed, and the small bits of wild vegetation become impressively free of insects. The foliage of the plants growing within the bits is so free of herbivory that it appears made in a florist's shop. However, the field itself is often quite rich in insects (which are presumably resistant to the pesticides). I suspect the cause of this pattern is that the wild insects are initially at a low density, as is their food. They are also not likely to be parts of large crop-adapted resistant populations. When hit with a pesticide, their numbers are severely depressed and the survivors have the added problem of locating food. When a population of a crop insect is hit with a pesticide, even if there are only a few survivors, those few are sitting on mountains of food.

Fire

This is not the place to enter into a discussion of whether inflammable preserves should be maintained so as to simulate precolonial fire regimes (or the lack of them). However, if the decision has been made to exclude fire, firing practices in neighboring grasslands (pasture or otherwise) are a severe threat. Fire moves with the wind and the wind knows no boundaries. Decades of a successful fire control program can be lost with a single error; even more threatening, the probability of catastrophe rises with each year since the last fire (at least until the vegetation has developed enough of a woody closed canopy to have a nonflammable understory). Perhaps worse, though inconspicuous, is that agrofiring regimes are generally different in intensity and seasonality than are natural ones (if there are such), and can as surely lead to gross alterations of habitats as can the elimination of fire from a naturally burned preserve.

In areas where pasture and woody secondary vegetation are frequently burned, the local attitude is often that fires are inevitable. Associated with this, unless special relationships exist with neighbors of the preserve, fires will usually be allowed to burn directly up to the preserve boundaries, thereby placing the onus of stopping them on the preserve. Fires, unlike cattle, are not viewed as belonging to anybody, and nobody retrieves them when they wander into your park.

It has been my experience that a fire moving across a large inflammable area will slightly penetrate or at least kill the margins of unburnable forest at the line of contact. The fire-damaged edge will then grow substantial amounts of herbaceous material in the following growing season, thereby extending the margin of the inflammable area. If the process continues annually, at least in the tropical dry forest areas of Costa Rica, Africa and Australia, grassland will gradually replace the forest (except for portions on exceptionally moist sites). Even these moist areas may be burned in dry years or in dry seasons that follow exceptionally heavy fuel accumulation in the grassland. In short, a forested preserve surrounded by pasture or young to middle-aged secondary succession in a tropical area dry enough to burn (and this includes almost all of the lowland tropics) is at exceptional fire risk because the large external inflammable area will carry a large fire to the preserve boundaries.

Even if the preserve boundaries are controlled by firebreaks that are wide and burned annually, more distant fires are also a threat. Wind carries glowing embers. When they land on forest litter or living trees, they are usually harmless. However, if they land on a dry rotting log or standing dead tree (or even on a dead branch of a living tree) within the forest, they can and do start that material on fire. It is this kind of fuel that accumulates in large amounts in seasonally dry forests, and such fuel is exceptionally abundant following a dry rainy season (due to slow decomposition rates). In normal years such burning material produces nothing more than a pile or line of ash, standing out strongly from the surrounding unburnable leaf litter. However, on occasion a small patch of forest understory burns. This creates a light-rich site that grows more herbaceous material. This site in turn has a higher chance of catching fire or sustaining a fire than does an intact forest. Likewise, if one of these small fires encounters a patch of secondary succession within the forest (e.g., an old roadside or home-site), the patch may contain ample fuel to accelerate the process of producing a sheet of highly inflammable vegetation within the forest.

Finally, there is an insidious trait of the small and seemingly trivial fires that enter a forest preserve. A light fire creeping along through the leaf litter appears to kill only seedlings and small woody plants, leaving the larger trees unscathed. However, in Costa Rican

dry forests, such fires are often hot enough to kill small areas of the cambium near ground level, resulting in almost unnoticeable sloughing of bark and dead tissue at these points in subsequent years. If there is another light fire in the litter within the 5–20 year period that it may take a tree to grow over these small fire scars, the fire then has access to the internal dead wood of the tree trunk. A light litter fire, then, cuts down large living trees as surely as if done with a chainsaw. What would appear to be a trivial fire can convert a closed-canopy forest into a tangle of secondary succession that is ideal fuel for a serious fire in a subsequent dry season.

Climate

The most conspicuous external threat to a preserve is climate modification by humans, who are clearing forests and other pristine habitats. Speaking of the Amazon basin, Camara (1983) noted that “large scale destruction of it could change dramatically the amount of water in the drainage system of the basin and profoundly affect the ecosystems of all protected areas, indirectly. If such a situation arises, the aims of the creation of these areas may be frustrated by human action beyond their border.” While it may as yet be undecided as to when regional climate changes (as expressed in standard weather records) occur following deforestation, there are clearly many local effects of deforestation that impinge directly on the climate of a preserve. Before discussing the details, there is a philosophical point that needs elaboration.

It may be argued that climate modification by clearing of forest is not necessarily bad for the people living on that land; whatever the climate and soils, humans will eventually grow (or select for) the crops that grow best there. In only a few cases will the habitat be so close to the margin of usability that climate modification will eliminate all agricultural possibilities. But reserves are not as flexible as agriculturalists. Let us say that the climate change induced by forest clearing is a 20 percent reduction in annual rainfall and a two-week shortening of a six-month rainy season. This kind of a change will have a dramatic effect on the habitat. There will be local extinctions, modifications of population densities, changes in microhabitat distributions, and changes in proportional representation of species.

Why should we worry about human-induced changes in climate? Hasn't every point in space and every species been subject to such changes in the past? Natural changes generally fall on continuous gradients of habitats. As species change geographically and demographically in response to climate changes, other species move into the site from previously wetter or drier areas. In short, arrays of

organisms and their component parts get pushed around over the countryside as climates change. However, when the climate changes on a small habitat island in an agricultural ocean, the species simply get shoved into the ocean, and the island is so far from “land” (if there is any left) that there are no incoming species to constitute new arrays.

Species that inhabit seasonal climates (virtually all of the world's terrestrial organisms in virtually all habitats) are periodically subject to multiple-year runs of exceptional deleterious weather. While a local population may be decimated by this event, a number of years of deleterious weather are generally required to cause extinction of a species. This is due to on-site population residuals, including seed banks (e.g. Baskin and Baskin, 1978), robust adults, ratooning root stocks, refugia with exceptional peaks in resource abundance, and dormant pupae. However, when climate modification induced by humans mimics such a naturally-occurring weather event, the climate does not return to the original state after a few years. Population residuals can persist only so long.

In the same context, when a local population is extinguished in “nature,” it is commonly reestablished by haphazard immigration or even by traditional migration movements. As preserves become ever more insular and islands are pushed ever further from other islands or from the “mainland” (if any exists), the opportunity for such reestablishment declines.

There is a second major way in which agricultural activities influence preserves via the physical climate. Most preserves have vegetation that is grossly different in overall structure from that of the agricultural land that is immediately adjacent. The difference is usually in the direction of more extreme fluctuations and absolute values in the agricultural land. They are hotter in the day, colder at night. It is drier and sunnier in the day. It is windier. This means that, quite irrespective of the overall climate modification by agricultural lands, lands adjacent to a preserve will create maximal edge effects within the preserve and thereby render small preserves even smaller than they seem to be. Ten preserves of 10 ha each may be all edge (see Lovejoy, Chapter 12 for a tropical rainforest example), while one preserve of 100 ha may contain a small core area that is relatively free of physical edge effects. The core would probably not persist in the face of biological interactions from the area that is rich in edge effects, however.

The oak and Santa Rosa

The demise of the population of the lowland tropical oak, *Quercus oleoides*, in Santa Rosa National Park is instructive on some of the

above points. The park covers an area of 10,000 ha from the Pacific Ocean to about 350 m elevation along the gradual rise up to the steep sides of the recent 1650 m Volcan Cacao in the northwestern corner of Costa Rica (11° N latitude). Prior to Spanish occupation of the site in the late 1500s, a semi-evergreen forest composed primarily of *Quercus oleoides* occupied the northeastern and most upland portions of the park and continued up the slopes of the volcano to at least 500 m elevation. This region is the southernmost portion of the *Q. oleoides* population, a population ("superspecies") that extends through dry-forest Central America north to the Texas coastal border and through the eastern coastal United States (under the name of *Quercus virginiana*).

In Santa Rosa, *Q. oleoides* occupies original and only slightly degraded volcanic tuff substrates. These soils are so poor that agriculture has traditionally failed on them. Part of their low quality derives from the fact that when the rainy season stops or falters, they dry out very rapidly owing to their high porosity. When the northeastern part of Santa Rosa had a continuous moderately-to-highly evergreen oak forest canopy, the incessant winds that accompany the end of the rainy season and the first half of the six-month dry season blew across the top of this canopy and the shaded soil remained relatively moist for at least the first several months of the dry season. The oaks drop their acorns during the last two months of the rainy season. If the litter-soil surface is moist, the acorns germinate within weeks. An acorn's shoot tip grows straight down, however, and comes to rest several centimeters below the soil surface. The contents of the acorn are then rapidly transferred to a tuberous swelling on the underground stem. If the soil remains moist, an above-ground shoot is produced and the seedling grows. If the soil is very dry, however, the seedling remains dormant and produces an above-ground shoot only when the soil is again moistened. If the litter-soil surface is dry, the acorn does not germinate; after several months it is dead, its seed contents dry and rock-hard. In short, the acorn is self-burying during the moist end of the rainy season, the function of burial being escape from the upcoming dry season (and escape from the very active acorn harvest by a variety of mammalian seed predators). This portion of the story is inferred and observed from minute remnants of intact oak forest that still remain in the park.

At present, the northeastern portion of the Park is occupied by a mosaic of fragments (usually a fraction of a hectare in area) of the original oak forest, interspersed with grass pastureland and patches of woody succession ranging from one to hundreds of years of age. The pastures were cleared between the late 1500s and 1940s, and converted from native grasses to jaragua (*Hyparrhenia rufa*, an introduced East

African grass; Pohl, 1983) in the 1940s. The pastures are maintained by fire, though the park is currently engaged in a fire control program that will lead to their eventual demise through woody succession. The oaks are well known in the region, and there is a strong desire to see the Santa Rosa oak forest return to its original state. The prospects for this, however, are grim.

Consider a representative large adult Santa Rosa oak within one of these small patches of forest at the end of the rainy season. Its neighboring adult conspecifics are 5 to 50 m away; the intervening area is filled with vegetation that ranges from a 1–2 m stand of jaragua to closed-canopy forest understory. It obtains enough pollen to set a crop of tens of thousands of acorns at several year intervals. Such a crop is usually synchronized with a year of massive acorn production by many of its conspecifics. The acorns begin to fall in late October, and the bulk fall in November. In late October and early November, the rainy season wanes, with more and more breezy sunny days of blue skies. The sun has direct access to the soil in open areas and the winds are everywhere at ground level. Where there is forest, the edge is within 100 m of any oak, and the wind blows directly through the forest; even dense coniferous forests are viewed as needing at least 100 m of width before winds blowing into the interior from an edge are stopped (Harris, 1984). The forest leaf litter dries rapidly and the acorns lie on the dry soil without germinating, either in the forest or under the grass. The grass grows in small tight clumps, with bare soil and a few oak leaves between. Acorns are slippery and smooth; they end up on the soil and not beneath a moisture-retaining grass turf or mat. The herbaceous vegetation dries very rapidly, and when not excluded, the human-generated fires begin spreading by December. Because of the very high fuel load (since 1978 there has been essentially no livestock in the Park), even an early dry season fire is hot enough to kill any acorn, as well as any above-ground seedling or sucker shoot. The dry season continues for another five months, with wind, insolation and fire prominent throughout.

At present there are *no* oak seedlings in the disturbed parts of Santa Rosa. Prior to fire control but after the removal of cattle, the Santa Rosa oak population was steadily diminishing as root systems were gradually killed through the production of sucker shoots that were killed annually by fire, and large adults were gradually eliminated by fires burning through their bases at access points in old fire scars. The fires have been stopped, but there is no sign of seedlings; they are killed by the dry season starting 1–2 months early, from the viewpoint of the acorn exposed on the soil surface. As the vegetation gradually succeeds back to forest within the Park, will soil conditions at the end of the rainy season remain moist long enough to allow

acorn germination? Perhaps in some sites, but the situation is complicated by the fact that the first several hundred years of succession in this dry forest is performed almost entirely by dry season-deciduous species of trees, and they do little to prolong the moistness of the rainy season.

Assuming that the Santa Rosa forest gradually returns to its semi-evergreen original status (there are slow-growing evergreen trees in the area that may aid the evergreen oaks in this context), will the overall climate of the region allow oak regeneration? All of the area around the park has been or is being cleared for agricultural purposes. The late rainy season winds and the early dry season winds sweep for 10-20 km across fully insolated dry pastures and fields before hitting the 1000-ha area that may someday again become an oak forest. It is highly doubtful that such a patch of forest, even if it has a closed canopy, can sustain an internal blanket of moist soil and air for the length of time necessary for oak seedling recruitment. Furthermore, the terrain is highly dissected, a situation resulting in numerous edges that are exposed to the drying wind. Santa Rosa's upcoming oak forest has as much chance to influence the overall climate of the Park as does an ice cube.

IN CLOSING

If nuclear winter threatens all of us and all those things we work to save, then the nucleotide summer is surely on the other side of the coin. Yes, genetic engineering can undoubtedly produce all kinds of fantastically useful organisms. But if you are worried about what the rabbit did in Australia, how the sea lamprey clobbered Lake Michigan, and how European diseases exterminated the original human occupants of the New World, "you ain't seen nothin' yet." The metazoans and microbes that humanity is gearing up to produce are without doubt the largest threat of all to nature as we know it. In Australia humans have managed to destroy easily 90 percent of the habitats and organisms in the past 40,000 years, first by hunting and burning, then following up with a small number of introductions of relatively ordinary animals and plants from other continents. When humans start releasing organisms that have been explicitly engineered to eat the world to the ground, turning it into hamburger, cotton, and honey, then you can kiss our "natural" preserves goodbye. You can legislate nuclear power plants out of existence. But there is no way to recall a genetically engineered product that is found to have seriously destructive effects on preserves (and it is highly doubtful that the commercial world would have the incentive to even attempt a recall).

And what do I have to offer of a concrete nature to a preserve manager? Within a tropical forested habitat, expect edge effects anywhere within 5 km of the preserve boundary. However, for wide-ranging vertebrates and the seeds they carry, the edge effects will be much greater. Know the details of the natural history of your organisms well enough that you can both anticipate their interactions and know at what distance their populations can be perturbed by a preserve edge. Be as concerned about the composition of the surrounding habitat as about the area you wish to conserve. Above all, be a field biologist who works with your preserve's neighbors to keep out what should be kept out.

LITERATURE CITED

- Baskin, J. M. and C. C. Baskin 1978. The seed bank in a population of an endemic plant species and its ecological significance. Biological Conservation 14:125-130.
- Brower, L. P., B. E. Horner, M. A. Marty, C. M. Moffitt, and B. Villa-R. 1985. Mice (Peromyscus maniculatus, P. spicilegus, and Microtus mexicanus) as predators of overwintering monarch butterflies (Danaus plexippus) in Mexico. Biotropica 17:89-99.
- Camara, I. de G. 1983. Tropical moist forest conservation in Brazil. In Tropical Rain Forest: Ecology and Management, S. L. Sutton, T. C. Whitmore and A. C. Chadwick (eds.). Special Publication, British Ecological Society, No. 2, pp. 413-421.
- Estrada, A., R. Coates-Estrada and C. Vazquez-Yanes 1984. Observations on fruiting and dispersers of Cecropia obtusifolia at Los Tuxtlas, Mexico. Biotropica 16:315-318.
- Haber, W. A. 1984. Pollination by deceit in a mass-flowering tropical tree Plumeria rubra L.(Apocynaceae). Biotropica 16:269-275.
- Haber, W. A. and G. W. Frankie 1982. Pollination of Luehea (Tiliaceae) in the Costa Rican deciduous forest. Ecology 63:1740-1750.
- Harris, L. D. 1984. The fragmented forest. University of Chicago Press, Chicago. 211 pp.
- Howe, R. W. 1984. Local dynamics of bird assemblages in small forest habitat islands in Australia and North America. Ecology 65:1585-1601.
- Hughes, C. E. and B. T. Styles 1984. Exploration and seed collection of multiple-purpose dry zone trees in Central America. International Tree Crops Journal 3: 1-31.

- Janzen, D. H. 1971. Seed predation by animals. Ann. Rev. Ecol. Syst. 2:465-492.
- Janzen, D. H. 1974. Tropical blackwater rivers, animals, and mast fruiting by the Dipterocarpaceae. Biotropica 6:69-103.
- Janzen, D. H. 1978. Seeding patterns of tropical trees. In Tropical trees as living systems. P. B. Tomlinson and M. H. Zimmerman (eds.), Cambridge University Press, New York, pp. 83-128.
- Janzen, D. H. 1983. No park is an island: increase in interference from outside as park size increases. Oikos 41:402-410.
- Janzen, D. H. 1984a. Two ways to be a tropical big moth: Santa Rosa saturniids and sphingids. Oxford Surveys in Evolutionary Biology 1:85-140.
- Janzen, D. H. 1984b. Dispersal of small seeds by big herbivores: foliage is the fruit. Amer. Nat. 123:338-353.
- Janzen, D. H. 1986. Biogeography of an unexceptional place: what determines the saturniid and sphingid moth fauna of Santa Rosa National Park, Costa Rica, and what does it mean to conservation biology? Proc. 1984 Merida symposium in Mesoamerican Biogeography (in press).
- Janzen, D. H. and P. S. Martin 1982. Neotropical anachronisms: the fruits the gomphotheres ate. Science 215:19-27.
- Lovejoy, T. E., R. O. Bierregaard, J. M. Rankin and H. O. R. Schubart 1983. Ecological dynamics of tropical forest fragments. In Tropical Rain Forest: Ecology and Management, S. L. Sutton, T. C. Whitmore and A. C. Chadwick (eds.). Special Publication, British Ecological Society, No. 2, pp. 377-384.
- Lovejoy, T. E., J. M. Rankin, R. O. Bierregaard, Jr., K. S. Brown,

- Jr., L. H. Emmons, and M. E. Van der Voort 1984. Ecosystem decay of Amazon forest remnants. In Extinctions, M. H. Nitecki (ed.) University of Chicago Press, pp. 295-325.
- Marks, P. L. 1983. On the origin of the field plants of the northeastern United States. American Naturalist 122:210-228.
- Myers, N. 1985. The end of the lines. Natural History 94 (February):2-12.
- Pohl, R. W. 1983. Hyparrhenia rufa (jaragua). In Costa Rican Natural History, D. H. Janzen (ed.). University of Chicago Press, Chicago, p. 256.
- Ranney, J. W., M. C. Bruner and J. B. Levenson 1981. The importance of edge in the structure and dynamics of forest islands. In Forest Island Dynamics in Man-Dominated Landscapes, R. L. Burgess and D. M. Sharpe (eds.). Springer-Verlag, New York.
- Silvertown, J. W. 1980. The evolutionary ecology of mast seeding in trees. Biol. J. Linn. Soc. 14:235-250.
- Stiles, F. G. 1983. Birds. In Costa Rican Natural History, D. H. Janzen (ed.), University of Chicago Press, Chicago, pp. 502-530.
- Urquhart, F. A. and N. R. Urquhart 1976. The overwintering site of the eastern population of the monarch butterfly (Danaus p. plexippus, Danaidae) in southern Mexico. J. Lepid. Soc. 30:153-158.