



LATENT EXTINCTION—THE LIVING DEAD

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that 9000 years ago populated the New World. The elimination of this megafauna by hunting (of the herbivores) and starvation (of the herbivore-deprived carnivores) was probably the first, and certainly the most dramatically irreversible, of the anthropogenic macroalterations of New World ecosystems. Today, of the extinct Pleistocene megafauna, only the horse remains—evolutionarily invented in the New World but surviving in the Old World until brought back as a gift from the Pleistocene by Spanish soldiers.

GLOSSARY

agroscape The agricultural, ranching, and plantation countryside, with its roads, irrigation ditches, buildings, and so on. The agroscape stands in contrast to the wildland countryside that is not directly managed by humanity (though it is strongly impacted by it). The agroscape intergrades with wildlands in the form of woodlots, abandoned fields, poor soil sites, hedgerows, and edges of wildlands.

living dead An individual stripped of the ecological circumstances that allow it to be a reproductive member of its population, but which is living out its physiological life. Living dead are most easily observed as large trees remaining on the agroscape, but they are also present in natural ecosystems.

megafauna Large mammals that are wolf-sized, deer-sized, and larger. Commonly used in reference to the many species of extinct “Pleistocene megafauna”

TREES AND MANY OTHER organisms that dot the tropical agroscape are often living dead. These are those individuals that have been stripped of the ecological circumstances that allowed them to be a reproductive member of their populations but are living out a physiological life. The term may also be applied to a portion of a population or a patch of vegetation. There are degrees of “living deadness.” A living dead individual or even population may be resuscitated through ecosystem restoration. Ecosystem alteration by humans frequently produces living dead, but living dead are also part of natural ecosystem structure. The term and concept are conveniently applied to individuals that live long enough or are conspicuous enough to be included in the lay perception of the environment. The living dead are, in their sum, a latent extinction of a species in a place. This renders them a perceptual problem in the



FIGURE 1 Living dead trees isolated in pasture at the edge of the agroscape (background) as it creeps into old growth forest (foreground). Los Naranjos, Sector Cacao, Area de Conservación Guanacaste, July 29, 1987.

psychology of tropical conservation because their presence obfuscates pending extinction. But living dead are also primary elements of natural processes of local extinction, immigration, and population-community structural dynamics in response to short- and long-term environmental change, be it natural or anthropogenic. Extra-tropical habitats and extreme tropical ecosystems may have fewer living dead than do complex tropical ecosystems, but they are nevertheless present. As magnificent as the living dead may be on the tropical countryside, I suggest that we not be distracted by attempting to save them, but rather that we focus our conservation efforts on saving large blocks of wildland ecosystems that are relatively complete and (it is hoped) relatively poor in living dead.

I. INTRODUCTION

The idea of the living dead has gradually emerged in my ecological understanding as I have lived past and around the majestic forest giants left standing as the agroscape creeps into Costa Rica's forest ecosystems over the past 4 decades (Fig. 1 and Janzen, 1986a, 1986b). This creep gradually converts the forest to an agroscape of pastures, fields, and roadsides dotted with the occasional adult tree but few or no juveniles. This is an agroscape where a magnificent flower crop now

stands bee-less, an agroscape where fruit crops lie rotting below the pasture tree, an agroscape where tree seedlings wither in the dry-season sun or are turned to smoke in the dry-season anthropogenic fires.

I begin this article with a focus on adult large trees and use familiar examples from the Costa Rican countryside. To create breadth, I suggest that you join these verbs with the nouns from the ecosystems you know. This is a conservation biology question, but it applies to more than that, and it applies across the once-forested tropics as well as elsewhere.

Looking across the tropical landscape, the eye is greeted by stately single trees (Fig. 2), by patches of forest, by the blaze of a colorful flowering episode. Put an inventory to the plant species in a field, in a valley, in an ecosystem. All these species appear in the list. All is more or less well, we conclude, as 96.4% of the species that were here 50 years ago are still present. But are they? How many of them are living dead, part and parcel of latent extinctions?

We live a perceptual lie as we bustle about our agrosapes. That single stately green *Dipteryx* or *Hymenaea* or *Swietenia* or *Enterolobium*, standing in a field, pasture, or roadside, is often just as dead as if it were a log in the litter or the back of a logging truck. That tree was birthed in some favorable circumstance, a circumstance for pollination, seed dispersal, seed germination, and sapling survival.



FIGURE 2 A living dead *Terminalia* tree stands in silhouette, left behind as the rain forest was cleared around it, the natural tree falls in which its seedlings might have survived long since removed. Rincon Rainforest, Area de Conservación Guanacaste, January 6, 2000.

But one or more of these circumstances is now gone. It was carried away with the forest, put on the hunter's table, pesticided out of existence, or global warmed into oblivion. The long-lived tough adult lives out its physiological life, in the absence of the carpenter with a chain saw, but it is evolutionarily dead. Its pollen no longer flows to other members of the population, its seeds are no longer carried away from seed predators, or its seeds are no longer carried to a favorable site for seedling growth and sapling survival to adulthood.

But because the adult lives on, we are lulled into thinking that the environmental damage really is not all that bad, that extinction has not already occurred. If we can still show the tree to our children, it seems not to be extinct. It is so big and green and strong. Every year we see its flowers, and maybe we even see its fruits on the ground below. And after all, it has clearly weathered all that we have thrown at it. What ever can the matter be?

Humanity's interaction with the world's ecosystems has an enormous perceptual element. We act on what we perceive, be it threat or opportunity. Much of our

conservation pragmatics and understanding is based on our knowledge that we really are losing species, losing ecosystems, losing the capacity of the environment to absorb our footprints. But that knowledge comes from what we see and measure. If all members of a tree species were to have the trait that each abruptly falls over dead the moment that it ceases to be a reproductive member of its population in its ecosystem, there would be far stronger alarm cries across the tropics about extinction rates and realities. If trees, the largest organisms on most of our landscapes, were very short lived as compared with humans, there would be less of perceptual problem—though just as large a conservation problem.

When the terrestrial world was covered with forest ecosystems, the single tree left standing in an aboriginal cornfield may well have been living dead, but the population from which it was derived was not usually at risk of anthropogenic extinction, unless perhaps dependent on a seed disperser targeted by that aboriginal population (Janzen and Martin, 1982). But when the agroscape is dotted with living dead in the wake of contemporary omnipresent ecosystem alteration, latent extinction is very real. A tree species may be ranked as "common"—meaning visible from a car window along many roads—yet be effectively extinct in a county, state, or region. And since the agroscape now stretches from horizon to horizon, the plant may well be absolutely extinct, since all of its former range may be populated by living dead.

II. DEFORESTATION AND THE LIVING DEAD

The forest need not be removed to convert trees to living dead. It is just that when the forest is partly removed, there is a very high chance that this alone will ecologically deprive many individuals of the remaining tree species sufficiently to convert them to living dead status. And, it certainly leaves the living dead very visible.

But even when the forest is left in place, that is no guarantee of a healthy tree population. When the Pleistocene hunters and their carnivorous helpers hunted out the neotropical mastodons and gomphotheres, the glyptodonts and camels, the ground sloths (Janzen, 1983b; Janzen and Martin, 1982), they did not do it by forest clearing. For decades to millennia after this 9000-year-old event, many of the remnant individuals of the tree populations that these big mammals



FIGURE 3 A living dead *Crescentia alata* fruit crop presented to earthbound extinct megafauna (Fig. 4). Sector Poco Sol, Area de Conservación Guanacaste, May 28, 1988.

dispersed (Fig. 3), and for which they created safe sites for seedlings by their browsing and trampling, would have been living dead scattered in the forest.

If some particular species—a pollinator or dispersal agent, for example—in the forest is extinguished, by whatever cause, there will often be surrogates and alternates that will assume, in some form, some portion of the “role” of the extinguished mutualist. The tree species will live on, albeit in some other ecological morph, and therefore in some technical sense will not be extinct. The tree that was “dependent” on the extinguished species will not, then, be living dead. But the devil is in the details. We need to go case by case. The suite of interactants with a tree species generates a given seed shadow, pollen rain, sapling demography, and microgeographic distribution. Remove one species of interactant. The entire n -dimensional hyperspace shifts in this or that direction. In some places this is toward eventual extinction, in other places it is just a change in demography and microgeographic distribution.

The history of any surviving species is that it must have survived thousands of such handoffs from one mutualist to another, from one moment to the next (e.g., Hallwachs, 1986). What bumps individuals into the category of living dead is the serendipitous event of losing irreplaceable partners. Humanity has a way of removing not only partners, but whole suites of them, as well as altering the physical environment. Our thoroughness and omnipresence creates ecological irre-

placeability. Yes, when we lose one ground sloth, a glyptodont picks up some of the slack, though the tree is now a different beast. And at some time, likely as not, some new slothoid arrives by evolution or immigration over the millennia. But lose all these big mammals at once, and the result is guaranteed to be large arrays of living dead.

We have all been nourished by the marvels of evolutionary understanding, leading to the temptation to wonder if rapid evolution will not resuscitate a living dead population, if not many of its individuals. Novel pollinators, dispersal agents, fruit morphology, flowering phenology—all could save the day. In theory yes, but in reality not on the timescales ordained by humanity’s charge across the landscape. How long will it take to evolutionarily reinvent a neotropical herbivorous/frugivorous megafauna? Fracture the remaining forest, with its living dead, into small ecological islands (also known as national parks and reserves). Thereby create ideal circumstances for rapid and novel evolution. We still cannot expect natural selection to create a mastodon from a white-tailed deer in anything like the speed required to be an antidote for neotropical rain forest anthropogenic alteration, beginning with the megafauna extinctions.

Certain kinds of habitat destruction are compatible with some tree natural histories. Two common trees, the guanacaste (*Enterolobium cyclocarpum*, Fabaceae) and jicaro (*Crescentia alata*, Bignoniaceae), owe their



FIGURE 4 An earthbound extinct megafauna returned from the Costa Rican Pleistocene by Spanish immigrants, breaking a *Crescentia alata* fruit (Fig. 3) to eat the molasses and seeds inside. Sector Santa Rosa, Area de Conservación Guanacaste, 1980.

contemporary prominence on the Mesoamerican Pacific coastal landscape to a particular kind of habitat destruction. For both, large mammals—such as free-ranging horses—swallow the seeds while eating the content of indehiscent fruits fallen below the parent tree (Figs. 3 and 4), and later defecate them in open sunny habitats (Janzen, 1981, 1982a, 1982b). Forest clearing unto brushy pastures and scraggly roadsides, populated by widely circulating working horses, maintains a healthy population of reproducing guanacaste and jicaro trees in a precarious balance with humanity.

What did these trees do before the Spaniards brought the horse back from its Old World refuge after its neotropical extinction by Pleistocene hunters (Janzen and Martin, 1983)? They probably survived in a peculiar habitat characterized by ample insolated ground yet sufficient rain for there to be large trees and sloppy seed predator rodents (or human fruit and seed harvesters), which offered sufficient seed dispersal. River edges, marsh edges, and the interface between tropical dry forest and desert are such habitats, and the aboriginal

village/field edge adds a serendipitous fourth. The Spanish working horse (Fig. 4) found the fruits abandoned by their extinguished ancestors and spread these two trees so thoroughly that today they are viewed by Mesoamerican societies as native and natural. And, in the case of *Enterolobium cyclocarpum*, cattle are surrogate horses (Janzen, 1982a).

However, as the motorbike and car replace the horse today, and as the cattle industry fades, these two trees are left as very visible living dead scattered across the former ranch lands, their abundant fruits rotting below the parent tree, the newly germinated seedlings killed by fungal pathogens nourished by the annually replenished seed crop, and the rare escaped seedling killed by herbicides, grass fires, and cosmetic cleansing.

III. WHEN IS A TREE NOT LIVING DEAD?

Earlier I noted that if each member of a tree species were to abruptly fall over dead the moment that it ceases to be a reproductive member of its population in its ecosystem, there would be far stronger alarm cries across the tropics about extinction rates and realities.

However, the isolated tree, left an adult in the open as the forest is mined away from around it (Fig. 2), is not necessarily or automatically a member of the living dead, or at least not necessarily at that moment. At least two circumstances may help to avoid this label. First, the pollinator community and the seed dispersal community for that tree may still be of a structure such that they confer sufficient amounts and patterns of their services and do so with the new reproductive phenology that will be expressed by the tree in its “new” habitat. And males do have fitness. A plant may never set a fruit or never have a surviving seedling from its seed crop, yet it still may be very much a member of the reproducing population (e.g., Aldrich and Hamrick, 1998). Plants contribute pollen “outward” as well as receive it from unseen members of the population. There may be some circumstances where this or that member of the pollinator guild will in fact carry pollen from that isolated tree back into the forest. At least potentially this may remove the living dead label.

Second, the new pattern of seed/seedling/sapling safe sites for that species may be sufficient for population survival, even if different. A novel demography, reproductive phenology, and microgeographic structure will ecologically emerge, reflecting the serendipitous matching of the tree’s traits to these new conditions.

For the survivor, such ecological fitting (Janzen, 1985) of an individual (or a population) into the environment newly thrust upon it is the same process as occurs when a tree species is anthropogenically introduced to a new place. Whether introduced by humans or by natural processes, its survival there demonstrates that it has ecologically fit in. Such introduction may occur into a natural ecosystem or one variously anthropogenically perturbed. Sloppy deforestation may create many living dead, only mildly impact some other species, and favor yet new introductions into the region by having removed competitors or consumers.

A population of plants in a newly altered landscape is not necessarily at a given moment either “dead” or “alive.” Just as the relationships of an individual to its ecological circumstances may decay slowly, it is also easy to visualize a population being sufficiently anthropogenically impacted that it gradually decays over several decades-to-centuries-long generations. This state of decay is an intermediate between living dead and “normal surviving.” The portion of a population of trees at some geographic point may be in a constant state of swinging between being “okay” and living dead, as its associated climate and community of interactors goes through their own changes.

A species’ population in its totality may also be waxing or waning in geographic coverage, density, “living deadness,” or all three. Living dead are found at the geographic or demographic margins of all populations. It is just that human activity in ecosystem modification (elimination, simplification) simultaneously impacts so many species, and is so omnipresent, that it creates large numbers of living dead in the same place at the same time. These then carry the tragic perceptual load of tricking us into thinking that all is much more well than it actually is.

But ecological neutering, expressed as here in the terms “living dead” or “latent extinctions,” is not restricted to the circumstance of the single tree in the field or a single portion of a population. The living dead are an integral part of natural age-structured mortality. Any field biologist can identify a large number of young individuals—seeds, seedlings, saplings—that have a vanishingly small chance of survival as individuals. The forest understory is densely populated with them, as is each squirrel’s winter seed cache, as is the patch of seedlings below the healthy parent tree, as is the ground covered with epiphyte seeds that fell past the branches of the trees above, as is the floor of the cave littered with bat-dispersed seeds. A very large part of the world’s herbivore machine is run with this fuel and actually should be labeled “detritivore” rather than herbivore.

The implications for evolutionary biology are huge, given that no matter how much herbivory occurs on these living dead, there can be no natural selection inflicted on the food populations.

Living dead adult individuals are also a prominent part of many undisturbed habitats and ecosystems. These are the waifs, the strays. Each of these is a plant whose seed arrived, grew to an adult, but found itself in a place lacking whatever is needed to maintain a viable population (Janzen, 1986c). In complex interwoven tropical habitats and ecosystems, the species list in a given place may contain as many as 10 to 20% of these kinds of living dead. For example, if a valley-bottom forest is eliminated, over time a significant number of tree species may disappear from the adjacent ridge, not because of any direct impact on the ridge forest but because the portions of the populations that were there are no longer maintained by seed flow into them from the valley bottom. This phenomenon is particularly visible where a particular soil or slope is thoroughly cleared for a crop, and the natural vegetation is left relatively intact in a neighboring habitat, ostensibly to protect it. Some species disappear because the conserved habitat did not really have its mutualist animals and physical climate conserved, or because it is too small, but others disappear simply because they were naturally occurring living dead.

Not to belabor the obvious, a tree standing dormant in the tropical dry season is not reproducing in the narrow sense, but it is also not necessarily living dead. But this is tricky for the observing human. We are very accustomed to being around trees that are not, at that moment, undergoing anything that appears to be reproduction, yet are members in good standing of quite surviving populations. The living dead tree does not display anything much different at first glance. Recognition of living dead status requires in-depth knowledge of its activities over decades, requires knowing if and where its pollen is going, and requires knowing where its seeds are moving to and what happens to them when they get there. This understanding is not acquired with the casual glance (e.g., Aldrich and Hamrick, 1998; Curran *et al.*, 1999; Hallwachs, 1986).

IV. WHAT OF SMALL PLANTS?

The isolated tree in the pasture has been a convenient illustrative example, but the world to which these ideas apply is far greater than that of large tropical trees. A small herbaceous plant may be a perennial with longevity like that of a tree. When the euglossine bees are

extinguished through forest partial clearing, a *Catsetum* orchid they pollinated is left high on the main trunk of a shade tree left behind, a living dead in its own right. The orchid may flower for a century, waiting in vain for its long-distance pollinators (Janzen, 1974). They are long gone, their year-round nectar and pollen sources turned to charcoal. A living dead clump of perennial grass on a landslide scar may for many decades produce its small hard seeds, designed millions of years ago for a trip through a seed-dispersing, now-extinguished, large herbivore to a new disturbed site (Janzen, 1984). It finally succumbs to its individual sterile fate as the landslide scar revegetates to forest. A living dead herbaceous morning glory (Convolvulaceae), sprouting and flowering year after year into the insulated roadside ditch from its underground tuber, may never again see the bees that once moved among its flowers and the flowers of the many other forest-edge species that once sustained them (e.g., Frankie *et al.*, 1998).

But as mentioned earlier for a population of trees, even a population of annuals may also be a living dead population. Yes, each year it may flower and seed and disperse and then again germinate with the next rains. But did it make “enough” seeds? Were they set at the “right” time? Did they have the right genetic composition? Did they move to the right safe sites? Were those sites there to be moved to? Does the population do all this and much more to hold its place in the naturally shifting nature of its surroundings? Each year the population may decline a bit. Maybe even in some years it recovers. But overall, gradually it slides into local extinction.

Looking backward at the history of a plant population “going extinct,” it may be possible to describe the decay of such a living dead population. Looking forward, however, it is much harder to label than is the living dead tree in a cornfield. After all, all populations have their ups and downs. How to know, other than retroactively, when a down is a downswing versus a slide into extinction? When the habitat destruction is major and obvious, the prediction is much easier, but perhaps more scientifically trivial, than when the habitat destruction is piecemeal, fuzzy, or widespread yet light.

V. WHAT OF ANIMALS, THOSE THINGS THAT MOVE?

Reproduction—that is, membership in the population—has two components. On the one hand, it is self-

evident that the individual needs to be physiologically able to reproduce. On the other hand, if it is ecologically neutered, it is as dead as if sliced off with a chain saw. Selection has not generally favored the ability of a tree to “know” that it has been ecologically neutered by the removal of its pollinators, its dispersal agents, or the safe sites for its juveniles, and then take remedial action. What would the mutant tree have to be able to do? Walk back to the forest? Animals, with their chance to move to a new ecological circumstance, get horny. They search for nesting sites and mates, they may fight harder for their surviving fewer children, or they may migrate or emigrate to other places. But, in the face of the sweeping and omnipresent hand of humanity, busily extending its extended genome to cover the globe with both people and their domesticates (Janzen, 1998), where is the potentially living dead animal to go, and how long does it have to get there? One can search only so long before dying of old age, becoming a road kill, or running out of stored food reserves.

The tropical agroscape, and most wildlands as well, are awash with living dead animals, animal populations, and animal arrays (also known as “communities,” whatever those are). Latent extinction is everywhere, but it operates more rapidly on animals with their high turnover rate and their lower capacity for extended lives as dormant seeds, resprouting root stocks, clonal patches, and so on.

Humans contribute in a curious perceptual manner to us being less aware of the animal living dead. At the level of the large animals, “everybody knows” that jaguars and tapirs are still “here” because everyone knows someone who knows someone who saw one once. One sighting of one 10-year-old jaguar crossing the road at noon 12 years ago will sustain the living dead jaguar in that area for decades, long past its consignment to the litter. It has taken more than three decades for the myth of Costa Rican giant anteaters, which once ranged these forests, to die a natural death.

Collectors and collections do their part as well. There is a snapshot of history present in our museum drawers, each specimen with its neat locality label. These collections continue the illusion of survival long past the reality. Retroactive data capture from museums gives a distribution map not of what is today on the Costa Rican countryside, but rather what once roamed where today sweeps unbroken waves of sugarcane, pasture, plantations, and horticulture. Intellectually every taxonomist knows this, but the orderly march of specimens across the museum drawers that read Panama, Costa Rica, Nicaragua, Guatemala, Veracruz, and San Luis Potosí lull one into thinking “surely over that huge

geographic range there are still viable populations.” Plants are not immune to these processes. It is just that with the more illusive, the shorter lived, the more mobile, the animal living dead may be more easily manifest in historical collections than on looking out the car window at 70 kmph.

And, when one descends from a field vehicle somewhere, a rare butterfly flutters from the museum drawer and down the roadside ditch, the cruel illusion is reinforced. Highly mobile animals are particularly effective at hiding the living dead from perception. The last living dead Costa Rican green macaws will fly across the countryside for decades. One small viable population of butterflies can create hundreds of living dead individuals searching across the food-plant-free agroscape until dying on windshields, of pesticides, or in the collector’s net.

Some animals, like some plants, thrive in the agroscape. Are they living dead as well? The agroscape changes its biotic and its physical traits at the whim of some combination of the market and our technical ability to (re)engineer our domesticates (and produce new ones). Overnight the agroscape can flip from heaven to hell for a particular species. When cotton was the crop of choice on the Costa Rican countryside, the world was an ocean of food for native *Dysdercus* cotton-stainer bugs (as well as for a number of other native cotton herbivores). The local extinction of the bugs’ original wild food plants (Malvaceae, Sterculiaceae, Bombacaceae) that accompanied the forest clearing for cotton fields was invisible. But when the downstream shrimp industry decided that it could no longer tolerate the pesticide runoff from the cotton fields, and cotton went the way of history, then so did the populations of cotton stainers. Some remain on as tiny (living dead?) populations on the seeds of local roadside malvaceous and sterculiaceae herbs, but even these may be living dead with their food plants easing their slide into extinction.

Does the ecologically neutered tree try harder, as an animal might? Could there be selection for such behavior? What does the isolated tree in the field perceive? What is perceived by an elephant-dispersed tree in a forest where the elephants have been extinguished? The tree in the field can know that much less pollen of this or that genetic composition now arrives, and may adjust accordingly—it may flower longer, it may set more seeds that are fertilized with its own pollen. It may make more flowers more regularly or it may set more wood or grow a larger crown. All of these things are simple responses to a circumstance that must occur in a natural forest to this or that individual that is

not living dead. But the extinction of animal dispersal agents and safe sites for juvenile plants goes unheralded, with not even a potential feedback loop.

VI. AND WHAT OF THE THINGS THAT EAT THE LIVING DEAD?

All have their predators, their parasites, their mutualists, their scavengers. Many of these are quite dependent on the traits of their hosts. Food is not food is not food. Narrowly host-specific specialists abound.

For every living dead individual, population, or species, there is a large suite of consumers—individuals, and even species—living at the margin of their existence. A seed predator weevil—*Rhinochenus stigma*—passes its larval stages in the pods of guapinol (*Hymenaea courbaril*) on the Costa Rican countryside (Janzen, 1974). It maintains what appears to be a healthy population in the annual to supra-annual fruit crops that are destined to fall and rot below the parent in the absence of both the Pleistocene megafauna and the agouti (*Dasyprocta punctata*), contemporary inheritor of the guapinol (Hallwachs, 1986). But as each of those old guapinol trees dies at the end of its 200 to 500 year life span, the weevil population takes another hit. One day the last living dead guapinol trees will die, and along with them will go what appears today to be a perfectly healthy community of weevils.

The guapinol is also fed on by leaf-eating caterpillars. One, a large saturniid, *Schausiella santarosensis*, eats only guapinol leaves and will go the way of the *Rhinochenus* weevil. Another, *Dirphia avia*, also a large saturniid, feeds also on the foliage of Spanish cedar (*Cedrela odorata*), mahogany (*Swietenia macrophylla*), oak (*Quercus oleoides*), and guarea (*Guarea excelsa*) (Janzen and Hallwachs, 2000). As the adult guapinol trees dwindle in number, how the *Dirphia avia* population will twist and change will depend in part on how many individuals of the other living dead remain. (You guess: How many Spanish cedar, mahogany and oak trees will be left standing by the Costa Rican roadside?) Perhaps *Guarea excelsa*, its wood of no commercial value, will be the only host plant left. Enough to sustain *Dirphia avia*? Who knows, but it certainly won’t be the same moth population that it was before.

The flowers of the living dead *Andira* trees were once a primary food source for tens of thousands of individuals of hundreds of species of bees; today they are visited by only a pale shadow of this bee community (Frankie *et al.*, 1998). But those old adult *Andira* con-

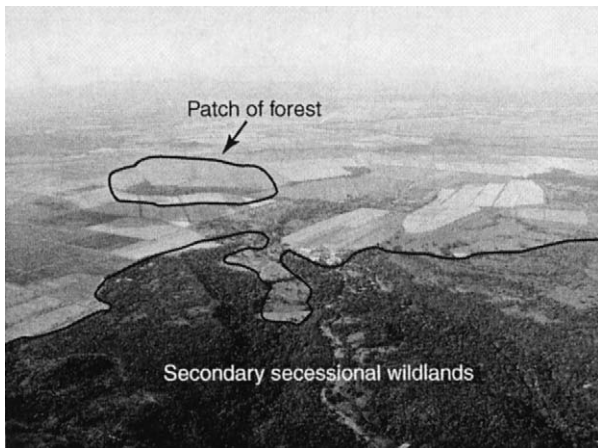


FIGURE 5 A living dead patch (left center) of natural vegetation, composed primarily of living dead individuals, among rice fields. There is essentially no gene flow between the patch and the secondary successional wildland in the foreground despite the thin connecting strip of riparian vegetation. Southwest of Liberia, Guanacaste Province, Costa Rica, December 14, 1999.

tinue to produce their massive flower crops and will do so for many decades to come. Its copious fruits, now largely from pollination by domestic honey bees, lie rotting below their parents in the absence of the masses of frugivorous bats that once dispersed them (Janzen *et al.*, 1976).

As noted earlier, the living dead are a “natural” part of any plant population. They are those individuals that have fallen where they have no chance of survival to reproduction. There are even living dead that have lived past their reproductive age. However, these living dead differ from the tree in the field in a very critical way for those who consume them. These living dead are being continually replenished by the natural dispersal process. They do not herald an invisible walk to extinction for the consumer.

VII. ARE THERE LIVING DEAD HABITATS AND ECOSYSTEMS?

Even when heavily agroindustrialized, the tropical agroscape often has patches of wildlands (Fig. 5)—forests along rivers and ravines, broken topography, swamps and marshes, vegetation on bad soil, no-man’s land between rival owners, woodlots, hunting preserves, industrial accidents, parks, and parklets. This remaining natural vegetation is a patchwork and a dot map, and it appears to be 1 to 20% of the original vegetation. And it gives one hope.

One says, “aha, there are remnants. There is wild biodiversity on the countryside, in the agroscape. There is hope outside of the reserves” (which are so hard to maintain and seem so expensive in national park status). This is a cruel illusion. Descend to one of these patchlets of forest, so green, so tree-filled. It is a biodiversity desert, lacking 50 to 99% of its original biodiversity that it had when it was once part of a forested landscape. As a package it is a vegetational living dead. Its species list is a mix of actual living dead and a few species that can maintain viable populations under these circumstances. Our major problem is that we visit these patches as tourists. We were not there in 1965 to see their earlier biodiversity, to compare it with its pale shadow in 1999 (but see Frankie *et al.*, 1998).

Why are the survivors living dead, and what happened to those that have gone locally extinct? Part of them went when the area got so small that there were no longer circumstances for a viable population size. Part of them were explicitly mined or hunted. Part of them went when their mutualists, prey, and hosts went. Part of them went when the neighboring habitat, a habitat that spit seeds into the remaining forest and thereby maintained a population there, went to croplands. Part of them went when the seasons got drier, or wetter, or windier, or more fire-rich, or longer, or shorter, or, or, or.

Even those national parks that seem so secure are at major risk from this phenomenon. When the Southeast Asian dipterocarp trees fruit, the wild pigs come from everywhere and the collective seed crop of the preserved forest patch has no chance of satiating these seed predators (e.g., Curran *et al.*, 1999). It may be better to surround a conserved wildland with wild animal-free rice fields than oceans of secondary succession subsidizing waves of animals that then turn the small old-growth forest into yet more secondary succession by defecating seeds all over it (e.g., Janzen, 1983a).

The bottom line is that the complex fabric woven from thousands of interacting species has been ripped to bits. Many of those that seem to have survived are living dead, or the serendipitous few that find this new impoverished habitat to their competitive liking. In short, these patches are only pseudo-remnants, not really smaller pieces of what once was. Even those ecosystems and habitats that have always existed as small units—a marsh, a landslide scar, a volcano top, a patch of serpentine soil—did not live in isolation. Rather, each was maintained by a complex ebb and flow of immigrants, waifs, and influences from the neighbors. When the neighboring natural system is turned to cropland, the integrity of the small natural patch (e.g., Fig.

5) is usual trashed almost as badly as if an army of chain saws had run through it. It just takes a bit longer for the living dead to live out their physiological lives.

These impoverished patches are especially deceptive for the bioilliterate. For those to whom a forest is just a batch of large woody plants, for those who cannot or will not read the differences between an advertising ditty and a complex poem, the agroscape with its living dead and pseudo-remnant natural vegetation appears to be not much different from a glade and forest mix in a national park. All seems to be well. But when humanity expects something from that wildland patch, it discovers that almost all of its tropical biodiversity is gone.

These patches have also played a mean trick on the conservation community. A huge portion of the world's conservation policy is based on the understandings of nature held largely intuitively by those who have grown up extra-tropical and learned their lessons from extra-tropical ecosystems. They easily adopt the mantra of trying to save the biodiversity remnants scattered across the agroscape. They are especially prone to do so in the face of the frustration of trying to save very large (and commercially juicy) blocks of intact vegetation. The forest-patchlet-dotted agroscape of Minnesota or Sweden still collectively contains easily more than 80% of the species that were there when the European colonists arrived. However, the same snapshot of a Costa Rican agroscape contains at best 5 to 20% of what once was. And the percent is still falling rapidly because a huge fraction of what remains today is living dead.

The more biodiverse and the more complex an ecosystem, the more likely that human perturbation will create anthropogenic living dead among the species with longer-lived individuals. This is because perturbations strip away mutualists and other biointeractors, leaving behind the physiologically functional individuals to live out their neutered life spans. The more biodiverse and the more complex, the more likely any given individual is to be dependent on one or more of these interactants to remain a member of the population.

This tropical-to-extra-tropical comparison, derived by spending my life peering closely at both tropical and extra-tropical habitats is a major driver behind the conclusion that in the tropics a triage decision is needed. The living dead are writhing in lethal pain on the battlefield of the tropical agroscape. If we expend our scarce financial, political, and social resources on them instead of saving a few large coherent blocks of multi-ecosystem biophysical units, in the end we will live an even yet more impoverished biodiversity existence.

The future of real conservation in the tropics lies in by-and-large focusing our efforts on the survival of a relatively small number of very large and diverse biophysical units, each complicatedly integrated with local, national, and international societies (Janzen, 1998, 1999). Painful as it may be, resources spent on trying to save individual species and small habitat fragments scattered across the agroscape, often living dead, is bad conservation economics and creates an angry antagonistic *Homo sapiens*.

We have no option in the tropics but to recognize that conserved wildlands are and always will be islands in an ocean of agroscape. Our task is to get on with rendering them into the highest quality islands possible, and not be distracted by, nor lulled by, the living dead individuals and islandlets. Yes, if there remains but just one Rembrandt painting, we of course save it even if it is bullet-holed and faded. However, we must recognize it for what it is and not convince ourselves that by doing so we have preserved our knowledge of European history.

VIII. RESTORATION BIOLOGY

The living dead are largely a negative force in the algebra of conservation biology and conservation reality. However, in those few cases where ecosystem restoration is desired or serendipitous, their life span delimits a window of opportunity for the reintegration of their species into the restoring ecosystem. Reintegration is not an unqualified given, however. A single large tree in a pasture being restored to forest may be dropping its seeds and fruits into an early successional old-field community that for decades is still way too unattractive to contain the seed dispersal coterie that will begin to restore the demography of that tree species. Equally, the pollinators of its flowers may already be extinct, or abhor the young secondary succession coming up below the large old parent. And finally, the physical climate of the highly deciduous and dry-season blasted secondary succession may well be a dismal place for a seedling or sapling of that old-growth giant. As every plantation initiator knows, the act of stuffing seeds into the ground does not a plantation make.

Until a very short time ago, the California condor was made up of living dead individuals. They were brought into captivity (e.g., transplanted to a safe field), reproduced (e.g., seeds collected and grown in pots), and have been put back out, hopefully in an agroecosystem with a friendly sociology. This habitat is, however, very seriously impoverished through reduction of ma-

rine mammal populations that so kindly generated the cadavers for lunch, and the California condor may always be dependent on human subsidy.

Many species of living dead may be rescued in this manner, if we care enough to spend the resources on them and gather information about them. But before racing out to apply the same technique to the living dead guapinol trees in the centers of Costa Rican pastures, a question very much needs to be addressed. Would not the same money spent on saving large blocks of guapinol-occupied wildlands, complete with their pollinators and dispersal agents, not generate vastly more conservation of guapinol and its hundreds of thousands of compatriot species? Yes, even these large blocks of wildland will contain some living dead. The wildland's biodiversity will attain an equilibrium density at whatever number of species survive the reduction from a continent of wildland to a large island of wildland. Those who are extinguished during this process will suggest the list of who were the living dead.

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