MANAGEMENT OF HABITAT FRAGMENTS IN A TROPICAL DRY FOREST: GROWTH[1]

Daniel H. Janzen[2]

ABSTRACT

Tropical conservation biology is inescapably the biology of habitat fragments and has been focused on habitat decay. Habitat restoration is primarily the initiation, growth, and coalescence of habitat fragments. Management of a tropical wildland will become the art and science of arresting the decomposition of habitat fragments and promoting their growth and coalescence. Forces that determine accumulation of structure and species are significantly within human control. Today's management actions will determine the nature of wildland habitats for centuries to come. Tropical dry forest is the most threatened of all the major lowland tropical forest habitats, simply because it has always occupied some of the lands most easily farmed in the tropics, and because it is so susceptible to fire. When dry forest and fields are abandoned and therefore allowed to return to dry forest, there are two principal kinds of forest initiation (assuming that there are nearby seed sources). a. When large pastures are downwind of a relatively intact forest, the initial invasion is primarily by individuals of large wind-dispersed trees that will persist and characterize the site for hundreds of years. However, these tree species are a minority of the total flora. Such forests of wind-dispersed trees are relatively inhospitable to animals, highly deciduous, and relatively species-poor. b. When there is any kind of attraction for animals in an abandoned open area, they may perch in it qr rest below it while crossing the open area. This results in accumulation of an entirely vertebrate-dispersed forest patch. Such patches may grow and coalesce to form a forest type as artificial as is a wind-generated forest. Vertebrate-generated forests contain more food items of interest to animals, are more species rich, and are more evergreen than are wind-generated forests. As large areas of abandoned low-grade farm and ranch land are returned to dry forest, the manager of national parks or other wildlands is confronted with the difficult decision of just which of the above, or other, forest types is to be promoted. The same will apply to rainforest when its restoration becomes a focus of concern.

Tropical conservation biology is inescapably the biology of habitat fragments. There are two kinds of fragments. First, much of what is worthy of conservation has already been broken into *decomposing habitat fragments* that are refugia and remnants. Even a large national park that is a solid block of pristine forest is a fragment. The biology of the decomposition process of these fragments is of intense contemporary interest to conservation planners and managers (e.g., Lovejoy et al., 1986; Diamond, 1986; Janzen, 1986a, c; Wilcove et al., 1986; Uhl & Buschbacher, 1985; Newmark, 1987). Second, habitat restoration is primarily the initiation and coalescence of *growing habitat fragments*. Management of a tropical wildland therefore becomes the art and science of arresting decomposition of habitat fragments and promoting their growth and coalescence. In such an arena, today's management actions will determine the nature of wildland habitats for centuries to come; forces that determine accumulation of structure and species are significantly within human control.

Here I examine the biology of habitat initiation and growth in a Costa Rican tropical dry forest. Dry forest is the most threatened of all the major lowland tropical forest habitats. It once covered more than half of the world's tropics (e.g., Brown & Lugo, 1982; Murphy & Lugo, 1986) but now supports a diverse array of breadbaskets, cotton fields, and pastures. In Pacific Mesoamerica, for example, less than 0.1% of the original tropical dry forest, which once covered an area the size of France (equal to five Guatemalas in area), has conservation status, and there

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TABLE 1. *Monthly precipitation (rounded to the nearest mm) in the administration area of Santa Rosa National Park, Guanacaste Province, Costa Rica (data collected by park rangers and extracted from the Meteorology Institute in San José).*

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
1980	1	0	5	0	184	175	139	159	331	417	240	9	1,660
1981	0	1	1	11	353	582	172	478	195	268	153	27	2,241
1982	16	2	0	41	919	129	117	34	328	197	37	1	1,820
1983	2	0	22	4	21	180	106	107	188	201	79	7	917
1984	6	8	0	0	118	218	278	162	613	261	52	7	1,723
1985	0	0	0	3	99	211	154	169	214	436	119	26	1,431

are no remaining large areas of even relatively pristine dry forest (Janzen, 1986a). This dry forest area exists almost entirely as habitat fragments and degraded patches, all of which are still shrinking if not in conserved areas. If there is ever to be a Pacific mesoamerican dry forest national park large enough to truly maintain the animals, plants, and habitats that greeted the Spaniards in the early 1500s, it will have to be grown rather than decreed (Janzen, 1986a).

The study site is the 108-km² Santa Rosa National Park and its immediate surroundings, the site of the proposed 800-km² Guanacaste National Park (GNP) (Janzen, 1986a). GNP is an approximate rectangle of variably damaged dry forest in northwestern Costa Rica, lying between Volcán Orosí and Volcán Cacao on the east and the Pacific Ocean to the west, with the Interamerican Highway cutting through the middle. From the ocean to the tops of the 1,500-m volcanoes is a moisture and elevational gradient that ranges from the driest part of Costa Rica (the sea level tip of the Santa Elena Peninsula, with less than 1 m of rainfall during its 5–6-month rainy season, Table 1) to seasonal rainforest on the volcano sides to ever-wet cloud forest on the volcano tops. The dry forest discussed here grows primarily within 10 km of the Administration Area of Santa Rosa National Park and is a mosaic of pristine forest, 0–400-year-old woody succession, and abandoned pastures of an introduced African pasture grass (jaragua, *Hyparrhenia rufa*). The Santa Rosa dry forest contains about 700 species of plants (Janzen & Liesner, 1980), 115 species of mammals (Wilson, 1983), 170

species of resident birds (Stiles, 1983), and 13,000 species of insects (including about 3,000 species of moths and butterflies, Janzen, 1988a, b).

The essay presented here is based on processes observed within the area of the proposed Guanacaste National Park. Space does not permit review of the pertinent literature from other habitats, but this will be done in a later publication.

WHAT ARE THE TRAITS OF THE TWO PRINCIPAL KINDS OF HABITAT FRAGMENTS?

DECOMPOSING HABITAT FRAGMENTS

As logging, burning, and clearing for pastures and agriculture have whittled away at Guanacaste Province's dry forest in northwestern Costa Rica (e.g., Uhl & Buschbacher, 1985; Janzen, 1986a), the large and multi-habitat dry forest expanses have been reduced to fragments ranging in size from a few hundred hectares to areas containing only a single remaining tree. Species richness in these fragments is decaying to substantially lower equilibrium densities than once existed, but many decades will pass before a stable equilibrium level is reached (if ever). The rate and depth of decay depends on at least three major variables:

1. How directly prejudicial is the forest fragmentation process to the organisms in the remaining fragments? This aspect of fragmentation cannot be separated from the simple effects of reducing the size of the habitat (and thus the sizes of the constituent populations). Except in experiments (e.g., Lovejoy

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et al., 1986) and massive logging or resettle-
ment schemes, habitat is almost never re-
duced in area as if a giant cookie-cutter had
cut out a small relict piece in one fell swoop.
For example, the fragmentation and decom-
position of dry forest by repeated fires has a
quite different effect on its species composi-
tion than if some of the forest is left standing
and some is bulldozed for cotton fields that
are then allowed to change to brushy pastures.

2. Are there other areas that continually
generate incoming individuals? In other words,
is the population of any given species in a
habitat fragment maintained by internal re-
cruitment, colonists, or both? Incoming in-
dividuals may originate in the same or dif-
ferent kinds of habitat as the recipient habitat
(e.g., Janzen, 1986e).

3. What proportion of the species have
what population decay rates and individual
life spans? A tree species whose individuals
have a 400-year life span may persist in a
habitat fragment long after that fragment can
support a breeding population of the species,
while an insect population might well disap-
pear within weeks of the time when its pop-
ulation no longer achieves recruitment.
Whether the observer is left with a feeling of
pending doom as a dry forest is increasingly
fragmented depends in great part on which
kinds of organisms are censused as indicators.
Agroecosystems based on what once was trop-
ical dry forest are especially rich in the living
dead—individuals living out a physiological
life span but no longer occupying a habitat
in which recruitment occurs (Janzen, 1986b).

GROWING HABITAT FRAGMENTS

The second kind of habitat fragment is very
different from the shrinking relict mentioned
above. In the long view of tropical conser-
vation, growing habitat fragments are ex-
tremely important and complex; while shrink-
ing habitats may even be accepted as they
stand, growing habitats require management
technology and choices. As more tropical res-
toration projects take root, there will be more
efforts at initiating habitats, reconstructing
habitats from fragments, and even reinstalling

species from distant habitats and geographies.
Restoration will often initiate growing habitat
fragments that accumulate species richness
to equilibrium levels as yet unknown. As they
grow and coalesce, the three variables men-
tioned above will generally apply, but with
different relative importance.

1. The selection of ecological processes
(e.g., fire, hunting, grazing) to be stopped will
determine the species richness, life forms, and
habitat structure. Stopping hunting but allow-
ing fire to continue yields a very different
kind of habitat fragment than does allowing
hunting but stopping fires. Stopping anthro-
pogenic fires has a very different effect than
does stopping natural fires. While the site may
initially have had an equilibrium array of
species, for all practical purposes and for many
centuries it can sustain many different kinds
of habitats during the restoration phase. Which
habitat occurs will depend on the initiation
and management processes.

2. Proximity of source areas for incoming
species, as measured by the ability of indi-
viduals of species to arrive, establish, and
recruit once present, will be very important
in determining whether a growing fragment
quickly or slowly rises to an equilibrium value.
Since different groups of organisms have ex-
tremely different abilities to colonize, and since
the chance of establishment in a habitat de-
pends at least on what species have colonized
earlier and the environmental traits of the
habitat, I expect the rate of species buildup
to be very irregular, with long periods of
relative stasis.

3. Species will appear in a fragment long
before they have attained a density at which
their population can survive through recruit-
ment and/or persistence within the habitat.
That is to say, the species richness of a grow-
ing habitat fragment can easily be greater
than the equilibrium density for a fragment
of that size and set of conditions.

Study of the decay of species richness with-
in a fragment requires either actual or infer-
ential knowledge of reference or benchmark
habitat. This is becoming extremely difficult
in dry forest because this forest type has
already been thoroughly fragmented for de-

cades or even centuries. On the other hand, there are numerous opportunities to study species accumulation in growing habitat fragments, even if there are not enough species in the region to completely restore the habitat.

INITIATION AND GROWTH OF HABITAT FRAGMENTS

The manner of initiation and growth of habitat fragments in Santa Rosa's dry forest is a novel process in the evolutionary and ecological history for these habitats and for this fauna and flora (just as it would be for other tropical restoration projects). Even though much of Santa Rosa has been cleared to bare ground by volcanic activity in the past, habitat restoration (primary succession) on such a site is different in many ways from the secondary succession that occurs when habitats are initiated and grow in old fields, abandoned pastures, or repeatedly burned forest. However, be they novelties or otherwise, understanding the biology of growing fragments is critical to survival and maintenance of Santa Rosa's tropical dry forest.

Growing habitat fragments in Santa Rosa are most commonly initiated in abandoned pastures. Even if land is lumbered or cleared for fields, it is usual for such areas to be converted to pastures before the restoration process is allowed. Most Santa Rosa pastures are almost pure jaragua (*Hyparrhenia rufa*) with a sprinkling of native herbs, though a few pastures of native grasses remain on the poorest, driest, and/or rockiest soils (e.g., Santa Elena Peninsula and Cerro El Hacha), and pastures of other introduced grasses occur on the moister volcanic slopes. The abandoned or lightly used pastures in Santa Rosa range from grass patches of less than a hectare to several km² in area.

Abandoned pastures initially range from virtually lacking trees and treelets to quite rich in sucker shoots from old and large root systems. Santa Rosa pastures are also dotted with the occasional seedling or sucker shoot from a sapling tree or treelet. The numbers, sizes, and kinds of large woody plants in a newly abandoned pasture depend on its age, frequency and timing of burning, timing of pasture "cleaning," proximity to forest (e.g., Purata, 1986), kind of livestock, stocking density, and numerous other variables (just as is the case in extratropical invasion of abandoned fields and pastures by forest, e.g., Olsson, 1984, and included references). All of the initially present woody plants are potential starting points for dry forest habitat initiation (see "nuclear trees" discussed below) and add to the composition of a growing habitat fragment without having to arrive by dispersal.

Expanding and filling habitat fragments range from being totally isolated to being expansions of an existing forest into an adjacent pasture. Placement of these fragments is not haphazard and often has clear relationships to fire patterns, wind direction, animal availability, soil moisture and contour, kinds of nearby forest, and other factors.

TWO PRINCIPAL KINDS OF HABITAT INITIATION

Almost all fires were stopped in abandoned pastures in Santa Rosa's dry forest through an active fire control program initiated in the 1984 dry season. All modern fires in the Santa Rosa area are set by humans or arrive as free-running wildfires that were set by humans. In some of the park pastures, fires even stopped at the time of park establishment in 1972 (or later, 1972–1983) because they were sufficiently isolated that only deliberately set fires got to them. There are even some old pastures or pasture remnants in the park that have not been burned for many decades because woody succession isolated them from the pastures that traditionally burned. As a general rule in Santa Rosa, when woody succession has proceeded to the point where the overstory canopy shades out the grasses and herbs, the forest does not carry a fire (though there are special circumstances, to be described elsewhere, in which enough dry forest can burn to initiate a return to grassland).

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When livestock were finally removed from Santa Rosa in 1978–1979, an important ecological process was altered. Livestock had maintained the jaragua at a low level through heavy grazing. Grass fires had relatively little fuel, and a conspicuous equilibrium was maintained between forest/pasture edges; in dry years or when the fire was late in the dry season, it nibbled away the margins of the forest. In wet years or when there was an early burn, the forest margins moved slightly into the pasture. When the cattle were removed, the jaragua formed dense stands 1–2 m in height within a single rainy season. These stands shade woody plant seedlings and provide enough fuel to support very hot and thorough fires at any time in the dry season (such stands even support fires during droughts in the rainy season). This initiated a rapid decline in the area and quality of dry forest fragments surviving in the abandoned pastures and on their margins. This decline stimulated the fire control program initiated in the 1984 dry season.

The two processes of forest initiation described below are occurring in fire-free and cattle-free contemporary Santa Rosa. Were the park to be returned to either cattle-rich, fire-rich, or cattle- and fire-rich status, the details of these processes would undoubtedly be different.

Habitat establishment through seed dispersal by wind.

In many of Santa Rosa's abandoned pastures free of cattle and fire, a distinctive set of woody species has appeared as the forest moves into the pasture. At least 90% of the trees and treelets have wind-dispersed seeds. The vertebrate-dispersed initial colonizers, such as *Cecropia obtusifolia*, *Piper* spp., *Trema micrantha*, *Muntingia calabura*, *Spondias mombin*, and *Bursera simaruba*, are almost entirely absent. For example, the oldest explicit regeneration plot (CT Regeneration Plot, on soils derived from a flat, volcanic welded ashflow) in the park was last swept by fire in the 1979 dry season (it was a jaragua pasture that had been frequently burned pas-

ture of some kind for several hundred years). Today (end of the 1986 rainy season), the following 12 species constitute at least 90% of the 5,000-plus individuals and biomass of trees and treelets in the 3-ha plot (all trees of all sizes in the plot are registered and mapped): *Ateleia herbert-smithii*, *Acosmium panamensis*, *Lysiloma auritum*, *Dalbergia retusa* (Leguminosae); *Rehdera trinervis* (Verbenaceae); *Cordia alliodora* (Boraginaceae); *Luehea speciosa* (Tiliaceae); *Swietenia macrophylla* (Meliaceae); *Tabebuia rosea* and *T. ochracea* (Bignoniaceae); *Cochlospermum vitifolium* (Cochlospermaceae); and *Hemiangium excelsum* (Hippocrateaceae). All plants in this plot arrived by their own means, and the vegetation was not manipulated.

All these species have wind-dispersed seeds. However, Santa Rosa has a native tree and treelet flora of 215 species (Janzen & Liesner, 1980) of which 25% are wind dispersed; 64% are vertebrate dispersed. More than 100 species of vertebrate-dispersed trees and treelets maintain breeding populations within 200 m of the CT Regeneration Plot. It is clear that habitat initiation in this plot is based on an ecologically distinctive subset of the species pool (cf. Beyer, 1975, for a curiously similar extratropical example).

There is one major reason why vertebrate-dispersed species are scarce in this restoration site. Among the many seed-dispersing vertebrates in the park, only white-tailed deer (*Odocoileus virginianus*) and coyotes (*Canis latrans*) encounter resources in a pure stand of jaragua. A deer sometimes uses it for cover when resting and spits out *Spondias mombin* (Anacardiaceae) and *Byrsonima crassifolia* (Malpighiaceae) nuts when chewing its cud (Janzen, 1985). Coyotes hunt there for cotton rats, *Sigmodon hispidus*, and defecate tree seeds such as *Manilkara chicle* (Sapotaceae) and *B. crassifolia*. Other vertebrates that disperse trees and treelets (e.g., collared peccaries (*Tayassu tajacu*), coatimundis (*Nasua narica*), magpie jays (*Calocitta formosa*), and tapirs (*Tapirus bairdii*)) only defecate in the pasture when they happen to cross it on their

way from one forest to another; in addition to the two plants listed above, these animals have dispersed a few individuals of *Enterolobium cyclocarpum* and *Acacia collinsii* (Leguminosae), *Genipa americana* and *Alibertia edulis* (Rubiaceae), and *Annona reticulata* (Annonaceae) into the CT Regeneration Plot. This particular abandoned pasture did not have a tree that served as a nuclear tree (see below) though the single old *Acrocomia vinifera* palm could have served that role. Also, animal-rich forest only occurs along one side of the plot and so there is little reason for animals to cross it.

There are many places in Santa Rosa where patches of wind-generated forest have recently been initiated as major protrusions into abandoned pastures. Examination of these forest fragments (or peninsulas) over the past few years allows a number of generalizations:

1. Not only is an abandoned jaragua pasture initially unattractive to seed-dispersing animals because the grass usually does not represent food or other resources, but the growing forest made up predominantly of wind-dispersed trees offers no food for frugivory (by monkeys, bats, coatis, tayras, tapirs, peccaries, deer, numerous birds) compared with a forest fragment containing a more balanced mix of seed dispersal types. Since the wind-dispersed trees are first to colonize the site, they physically and numerically dominate it for many decades as they live out their life spans. While the site does offer shade and some foliage and seeds, it still lacks a major class of food.

2. The wind-dispersed initial colonizers are large trees (attaining heights of 15–25 m) and live for 50 to several hundred years. There is no wave of early successional, short-lived, and comparatively small species. It is even tempting to suggest that a wind-dispersed colonizing tree has to be tall in dry forest, or it won't be tall enough to have its seeds blow over the canopy and into tree falls and other gaps in the canopy. Put another way, in a climatic regime that grows a tall forest, only canopy-level or emergent trees (and high-climbing vines) will successfully colonize that forest via wind-dispersal or evolve wind-dispersal.

3. Not only does a wind-dispersed dry forest lack fruit, but all its seeds are well protected against vertebrate postdispersal seed predators. The species with big seeds in conspicuous fruits or other dispersal units (e.g., *Lonchocarpus* spp., *Acosmium*, *Swietenia*, *Hemiangium*, *Ateleia*) have very toxic seeds (e.g., Janzen, 1986d). Those with edible seeds (e.g., *Cochlospermum*, *Rehdera*, *Luehea*) have very small seeds that easily escape by self-burial in the litter.

4. As the first wave of wind-dispersed trees reaches maturity and begins bearing seeds, the dispersal process in the fragment does not change. By contrast, in a site that is invaded by vertebrate-dispersed tree species, the pattern of the dispersal process will change as the trees come into reproductive maturity and begin to attract animals. Some of these animals (e.g., agoutis (*Dasyprocta punctata*)) play no part in initiating the forest fragment. This attraction will increase the rate of accumulation of plant species in the habitat fragment.

5. The majority of the large trees in Santa Rosa (many with fruits eaten by vertebrate dispersal agents) require at least as much sunlight as is made available when a tree falls to grow into saplings (the evergreen *Manilkara chicle* is the only obvious exception). Once the habitat fragment is occupied by large wind-dispersed trees, the species composition of the canopy will not significantly change its composition until these wind-dispersed trees begin to die of senescence (and create tree falls) many decades later, even if there is a very heavy flow of vertebrate-dispersed seeds into the site during intervening years.

6. A wind-dispersed forest does not expand into a pasture from all compass directions. A pasture on the downwind side of a forest of mixed dispersal types receives a heavy inoculum of wind-dispersed seeds, but a pasture upwind of forest receives none. This process is especially critical to restoration efforts if the upwind margin of the pasture borders

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on a park boundary with agricultural land, ocean, or other nonforest habitat. Vertebrate-dispersed seeds in a pasture may have come from any direction. In Santa Rosa, the dry season winds blow almost invariably from northeast to southwest; rainy season winds blow in many different directions, but there are no wind-dispersed trees or treelets that mature their seeds at this time (see 10 below).

7. The only parents of wind-generated fragments in pastures are trees near the forest–pasture interface. Even a few tens of meters of forest thoroughly filter out wind-borne tree seeds (e.g., Augspurger, 1986). On the other hand, the vertebrate-dispersed seeds falling into a growing habitat fragment in an abandoned pasture may have passed through forest expanses hundreds to thousands of meters wide.

8. Wind-dispersed seeds at Santa Rosa move up to about 200 m into pastures, but a more common distance is 0–100 m. The seeds move greater distances if the parents are maximally tall individuals that have grown up in competition with other forest trees (i.e., near forest margins) rather than shorter isolated trees in open pastures. This means that wind-generated growing habitat fragments will always be near another forest with adult trees in it.

9. Wind-generated seed shadows are often dense and very uniform compared with vertebrate-generated seed shadows (which have conspicuous heterogeneity associated with perches, waterholes, trails, shade, steep contour, tourist presence, and other factors). If there is one member of a wind-dispersed species of tree maturing in a growing habitat fragment, there are likely to be numerous others (unique individuals of vertebrate-dispersed trees are commonplace in growing habitat fragments, see below).

10. Forests of wind-dispersed species bear no ripe fruits or seeds throughout the rainy season (no Santa Rosa species of wind-dispersed tree or treelet ripens its fruits in the rainy season). Associated with this, the wind does not blow with equal intensity and pattern throughout the year. The highest average wind

velocity occurs during the first half of the dry season (December through early March). The days with the strongest wind occur in late December and January. During the dry season the most intense winds occur during the central part of the day (when it is driest and fruits are most likely to be shed or broken off, and fruits are most likely to dehisce). During the rainy season, there are many nearly calm days, and winds often occur during rainstorms (when a wind-dispersed fruit or seed would have little or no chance of dispersal). Another barrier to wind-dispersal during the rainy season is that wind-dispersed units of dispersal lose weight at maturity by drying out, which does not occur readily in the rainy season.

Along the same lines, almost all wind-dispersed seeds at Santa Rosa appear to germinate within a few weeks of being wetted by the first rains. There is a major pulse of seedling appearance with the first rains (from seeds accumulated during the dry season) followed by no further seedling input or site colonization during the six-month rainy season. Vertebrate-dispersed seeds in Santa Rosa display many kinds of dormancy and new seedlings of many species appear at different times during the rainy season. Since many of these seeds are dispersed during the rainy season, a habitat fragment can be initiated at this time of year from dispersing seeds or from seeds in the soil.

Habitat establishment through seed dispersal by vertebrates.

Vertebrates play a much more complex role than does wind in initiation and growth of habitat fragments. This is because:

a) There are nearly three times as many species of vertebrate-dispersed than wind-dispersed trees and treelets in Santa Rosa, and they bring with them more life forms and kinds of ways to occupy a site than are found among the wind-dispersed species.

b) There are many more kinds of vertebrate-generated seed shadows than wind-dispersed seed shadows in Santa Rosa.

c) The pattern of forest initiation depends

on the biology of the animals as well as on the biology of the plants. The wind has not evolved and coevolved with plants, and the plants can only evolve, not coevolve with the wind.

Here, I focus on one particular kind of vertebrate-generated forest initiation in Santa Rosa pastures, that which is associated with nuclear trees.

A nuclear tree is a single tree that appears in a pasture and is then attractive to animals that defecate or otherwise drop seeds in its vicinity (see McDonnell & Stiles, 1983; Beckwith, 1954; Debussche et al., 1982, for ornithological extratropical examples). The animals go to the tree as a perch, for shade, to eat its fruits, to mark ranges, and other reasons. Whether a nuclear tree and its associated seed rain actually becomes a growing fragment of forest habitat depends on numerous environmental variables ranging from the rate and kind of seed rain to the depth of the grass, soil conditions, species of nuclear tree, fire regime, and other factors. For example, many of the best contemporary examples of vertebrate-generated growing habitat islands in Santa Rosa are centered on guanacaste trees (*Enterolobium cyclocarpum*) on small rocky outcrops that protected the sapling from low grass fires (in the heavily grazed pastures). Within a few years after cattle were removed from Santa Rosa, the high grass fires swept across these small fragments and obliterated many of them and their nuclear guanacaste trees.

Representative nuclear trees in Santa Rosa are guanacaste, cenizaro (*Pithecellobium saman*, Leguminosae), guacimo (*Guazuma ulmifolia*, Sterculiaceae), jobo (*Spondias mombin*, Anacardiaceae) and figs (*Ficus* spp., Moraceae), but many other species can serve this function (some are remnant wind-dispersed trees standing as the sole survivors of a dwindled forest fragment).

A growing dry forest fragment that has been generated by vertebrates around a nuclear tree in the center of an abandoned pasture has a number of distinctive traits:

1. Wind-dispersed species of trees and treelets are absent (unless they were present as persistent suckers at the time of fragment initiation). That is to say, the species pool from which the fragment is potentially drawn is some subset of the 138 species of vertebrate-dispersed trees and treelets in Santa Rosa.

2. Certain vertebrate-dispersed species are missing because they are usually dispersed by vertebrates that either never cross pastures or are very unlikely to carry one of these seeds when they do. For example, agoutis and monkeys are very unlikely to carry the large seeds of guapinol (*Hymenaea courbaril*, Leguminosae), panamá (*Sterculia apetala*, Sterculiaceae), and tempisque (*Mastichodendron capiri*, Sapotaceae) across a pasture.

3. The species and age of the nuclear tree will influence the species composition of arriving seeds. If it bears edible fruits (which is very likely since wind-dispersed nuclear trees are almost nonexistent in large pastures), the species composition of the seed rain during fruiting will be strongly influenced by the assortment of animals attracted to its fruit. Additionally, different species of trees offer different kinds of perches and shade, which likewise will influence animal visitors and their seed cargoes.

4. The species and age of the nuclear tree will influence the survival of the seedlings below it through differential shade effects on grasses and woody seedlings, protection of seedlings from fire through shading out grasses and keeping the soil moist, and the duration of its deciduousness during the dry season.

5. The trees accumulating around a nuclear tree are usually smaller and shorter than the nuclear tree because they are younger than it and because they compete with it. The canopy is therefore dome-shaped with the nuclear tree near the center rather than flat-topped (as is the case in wind-generated habitat fragments).

6. The understory of a vertebrate-generated habitat fragment often contains reproducing treelets and shrubs, e.g., *Chomelia spinosa*, *Alibertia edulis*, *Psychotria* spp.

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(Rubiaceae); *Piper* spp. (Piperaceae); *Erythroxylon havanense* (Erythroxylaceae); *Malvaviscus arboreus* (Malvaceae), *Hirtella racemosa* (Chrysobalanaceae); *Ximenia americana* (Olacaceae); *Casearia* spp. (Flacourtiaceae); *Ocotea veraguensis* (Lauraceae); and *Annona reticulata* (Annonaceae). Reproducing small plants are generally missing from the understory of a wind-generated forest fragment.

7. Owing to the larger species pool and area from which the species are drawn, species richness of trees and treelets is substantially greater in growing vertebrate-generated habitat fragments than in wind-generated ones. However, if there is frequent animal movement through a wind-generated habitat fragment, the sum of the wind-dispersed species and the animal-dispersed species gives the most species-rich habitats of all.

8. Except for the very large seeds that are not carried out into a pasture (see 2 above), all sizes of seeds arrive at a vertebrate-generated habitat fragment. However, there should be some sorting with distance as fragments get so far out into a pasture that small frugivorous birds are less likely to go to them. In contrast, a wind-generated growing forest fragment should also display sorting whereby the species with lighter seeds move further downwind in the initial invasion.

9. A vertebrate-generated habitat fragment can grow in any direction, rather than downwind as does a wind-generated habitat fragment; and a vertebrate-generated fragment can range from a distant island to a peninsula, while a wind-generated fragment is usually a peninsula from an established forest.

10. The seeds in a vertebrate-generated habitat fragment may come from as far as many thousands of meters from the fragment, and from any compass direction. The tree species in the fragment are thus likely to represent a much greater portion of their respective populations than is the case with a wind-generated patch (which is derived from the immediately adjacent forest). Associated with this process is the fact that vertebrate-generated habitat fragments often contain isolated representatives of a species; whether these individuals can reproduce (through long-distance pollination or by being self-compatible) varies with the species. However, it is quite likely that such species occasionally exceed the species carrying capacity of the fragment, since if it does not maintain itself in the fragment, it is not present in some senses.

11. Since there are some vertebrate-dispersed tree species in fruit throughout the year in Santa Rosa, there are likewise trees and treelets in fruit throughout the year in the vertebrate-generated growing habitat fragments.

12. As a habitat fragment grows by vertebrate input of seeds (and by internal recruitment), its margins become less likely sites of seed deposition. The rate of expansion of a habitat fragment noticeably declines as it becomes more than about 0.5–1 ha in area.

Discussion

I have briefly described two prominent kinds of forest habitat initiation and growth in abandoned pastures in Santa Rosa's dry forests. There are also many other kinds of habitat initiation occurring in this park at present. It is evident that the initial processes in habitat initiation will determine the species composition and structure of the forest for many centuries on these sites. It is equally evident that the actions of park managers will determine the kinds of habitat initiation that occur. If the park is left completely to itself, one kind of mosaic will occur. If livestock are used to depress the grass in certain areas, a different kind of mosaic will occur. If nuclear trees are planted far out into pastures or seeded there in the dung of cattle (as occurs with guanacaste and cenizaro trees if the cattle have access to fruit crops), a third kind of mosaic will occur. If native timber trees are seeded in by air or hand, and then natural succession is allowed to continue (as an example for those who want to know how to return worthless dry forest pastures to timber production), the resultant forest will depend

in great part on the particular species of tim-
ber trees used (fleshy fruit-bearing versus
wind-dispersed, evergreen versus deciduous,
fast- versus slow-growing). Pastures near for-
ests rich in seed-dispersing mammals and birds
will initiate quite different kinds of forest than
will those in areas relatively free of verte-
brates due to poaching, heavy tourist use, or
experimental removal.

It is clear that the managed fate of the
entire area of tens of km² of pasture in Santa
Rosa or several hundred km² of pasture in
Guanacaste National Park should not be the
same from area to area. But whatever kinds
of management of habitat fragment initiation
and growth are to be applied, it will require
basic research into the multiple pathways that
secondary succession can follow in this species-
rich situation. Whether these pathways will
finally converge on a single kind of vegetation
for any given site is almost irrelevant, since
this will take thousands of years to occur and
we have to deal with the situation at hand.

How broadly applicable is the philosophy
espoused in this essay? Rainforest restoration
has not been explicitly tried, but it is an in-
tegral part of traditional shifting agriculture
in some areas and has occurred throughout
the wet tropics where farms and homesteads
have been abandoned when farmers have been
relocated out of an area slated to become a
rainforest national park. The details of rain-
forest restoration will obviously be different
from those in dry forest, but there will be
many similarities.

One difference is apparent even at this
early stage of understanding. When a clean
pasture is abandoned next to a pristine rain-
forest, the rate of rainforest tree and treelet
movement into it appears to be much slower
than in seemingly equivalent cases in dry
forest. This is the case even in the wetter
eastern end of Guanacaste National Park as
compared with the central drier part. There
are at least three possible causes. First, rain-
forest vertebrates may be even more reluctant
to enter rainforest pastures and use nuclear
trees, for example, than are dry forest ver-
tebrates. Second, the general lack of strong

directional winds in rainforest may impede
movement of wind-dispersed species into pas-
tures. Third, and I suspect the most likely
case, a seedling from a dry-forest seed dis-
persed into a dry-forest pasture finds itself in
a much more foreign environment than does
a seedling from a rainforest seed dispersed
into a rainforest pasture. The heat, sun, wind,
dryness, and fluctuations of an open pasture
are much more similar to the rigors of dry
forest than they are to the understory of a
rainforest (even in a tree fall). Additionally,
dry-forest pasture soils are rich in spores of
endomycorrhizal fungi while rainforest pas-
ture soils are generally very poor in them (D.
Janos, pers. comm.). Certainly at Santa Rosa
there is no indication that the physical con-
ditions of open pasture habitat are lethal to
tree seedlings, even when they are species
commonly associated with relatively moist
habitats (e.g., *Hymenaea courbaril, Manil-
kara chicle*).

Blydenstein (1967) described the mosaic
of Venezuelan grazed pasture and forest
patches as the result of a dynamic interaction
between dryness and fire, just as occurred in
Santa Rosa before the fire and cattle were
eliminated. In some ways, this dynamic is a
fine-scale version of the global balance be-
tween the dwindling tropical wildlands and
restoration systems such as that occurring in
Santa Rosa National Park and the proposed
Guanacaste National Park area. At present
we are in a continuous drought and fire phase,
with the forest patches shrinking very, very
rapidly. If the dynamic is to have any sig-
nificant balance, forest restoration is going to
have to start up throughout the tropics. It
must start not only in places like Guanacaste
National Park, where remnants of the plants,
animals, and habitats are still present, but
also in the large expanses of the tropics where
there is virtually nothing left. For example,
in countries like Costa Rica, virtually all rain-
forest parks are on hilly to mountainous soils,
with the true flatlands either cleared or almost
cleared. The real challenge is whether with
fencerow populations, woodlot populations,
and living dead (Janzen, 1986f) one can put

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back together even a first approximation of the flatland rainforests that once stood on the enormous acreages of low-yield rainforest fields and pastures.

The question has been raised as to why Guanacaste National Park needs to be as large as 800 km², especially since about 90% of the habitat has been partly homogenized through partial destruction. The traditional answer is that a large area is needed to maintain even minimal populations of the wide-ranging large animals and the big trees. A less traditional, but nonetheless compelling, answer is that the area must be large to maintain intact wildlands *and* be extremely accessible to tourists, researchers, managers, and school groups; these are the people whose votes and long-term use will keep GNP alive. But there is also a less conventional biological reason that is especially pertinent to dry forest. Intact dry forest is a very complex mosaic of many small fragments of habitat types nestled in amongst each other, generated by soil type, drainage, wind exposure, slope, and rainfall. This mosaic of conditions and species is largely responsible for the many pathways that may be taken by secondary succession in an abandoned pasture; two pastures with identical conditions may easily be positioned next to two quite different source areas for the species that will colonize it. A given animal or plant species exists as a population supported by one or more of these habitat types, but the support base is highly fragmented. A dry forest wildland must be big so that the total area contains enough pieces of a given habitat type (e.g., dry ridges) to support healthy populations of the species that are supported by that habitat type. Yes, there are 800 km² of dry forest in GNP, but, for example, less than 100 km² supports the endemic population of the tree *Ateleia herbertsmithii*, the only legume in the world that is known to be wind-pollinated (Janzen, 1988c).

This worry applies to rainforest as well. Yes, it all appears to be just a sheet of green, but as soon as it is necessary to find any tree species, or any constellation of species, the biologist learns to search for the subtle dif-

ferences in drainage, soil, and other factors that lead to the highly localized target. When the professional conservationists tell us that X% of the rainforest still remains, and that Y% of X is disappearing daily, it is imperative to remember that 0% of many of the habitat types of tropical rainforest remain. Furthermore, that Y% is not spread proportionately over the remaining types, giving us an equal amount of time to crusade for what remains. It is critical to identify those rainforest habitat types that are as threatened as is the tropical dry forest and focus restoration projects on them. The battle for mesoamerican tropical dry forest conservation should have been fought in the year 1800; don't wait until the year 2000 to begin to fumble with the rainforest pieces worth restoration.

LITERATURE CITED

AUGSPURGER, C. 1986. Morphology and dispersal potential of wind-dispersed diaspores of neotropical trees. Amer. J. Bot. 73: 353–363.

BECKWITH, S. L. 1954. Ecological succession on abandoned farm lands and its relationship to wildlife management. Ecol. Monogr. 24: 349–376.

BEYER, W. N. 1975. Types of seed dispersal: their effects on species diversity of trees. Amer. Nat. 109: 103–104.

BLYDENSTEIN, J. 1967. Tropical savanna vegetation of the llanos of Colombia. Ecology 48: 1–15.

BROWN, S. & A. E. LUGO. 1982. The storage and production of organic matter in tropical forests and their role in the global carbon cycle. Biotropica 14: 161–187.

DEBUSSCHE, M., J. ESCARRE & J. LEPART. 1982. Ornithochory and plant succession in Mediterranean abandoned orchards. Vegetatio 48: 255–266.

DIAMOND, J. 1986. The design of a nature reserve system for Indonesian New Guinea. Pp. 485–503 in M. J. Soulé (editor), Conservation Biology. Sinauer, Sunderland, Massachusetts.

JANZEN, D. H. 1983. No park is an island: increase in interference from outside as park size decreases. Oikos 41: 402–410.

———. 1985. *Spondias mombin* is culturally deprived in megafauna-free forest. J. Trop. Ecol. 1: 131–155.

———. 1986a. Guanacaste National Park: Tropical Ecological and Cultural Restoration. Editorial Universidad Estatal a Distancia, San José, Costa Rica.

———. 1986b. The future of tropical ecology. Annual Rev. Ecol. Syst. 17: 305–324.

———. 1986c. The eternal external threat. Pp. 286–303 in M. E. Soulé (editor), Conservation Biology. Sinauer, Sunderland, Massachusetts.

———. 1986d. Mice, big mammals, and seeds: it matters who defecates what where. Pp. 251–271 in

A. Estrada & T. H. Fleming (editors), Frugivores and Seed Dispersal. W. Junk Publishers, Dordrecht.

———. 1986e. Lost plants. Oikos 46: 129–131.

———. 1986f. The future of tropical ecology. Annual Rev. Ecol. Syst. 17: 305–324.

———. 1988a. Ecological characterization of a Costa Rican dry forest caterpillar fauna. Biotropica (in press).

———. 1988b. 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. Brenesia (in press).

———. 1988c. Natural history of a wind-pollinated Central American dry forest legume tree (*Ateleia herbert-smithii* Pittier). Legume Conference, St. Louis, Missouri, June 1986 (in press).

——— & R. LIESNER. 1980. Annotated check-list of plants of lowland Guanacaste Province, Costa Rica, exclusive of grasses and non-vascular cryptogams. Brenesia 18: 15–90.

——— & P. S. MARTIN. 1982. Neotropical anachronisms: the fruits the gomphotheres ate. Science 215: 19–27.

——— & P. G. WATERMAN. 1984. A seasonal census of phenolics, fibre and alkaloids in foliage of forest trees in Costa Rica: some factors influencing their distribution and relation to host selection by Sphingidae and Saturniidae. Biol. J. Linn. Soc. 21: 439–454.

LOVEJOY, T. E., R. O. BIERREGAARD, JR., A. B. RYLANDS, J. R. MALCOLM, C. E. QUINTELA, L. H. HARPER, K. S. BROWN, JR., A. H. POWELL, G. V. N. POWELL, H. O. R. SCHUBART & M. B. HAYS. 1986. Edge and other effects of isolation on Amazon forest frag-

ments. Pp. 257–285 *in* M. J. Soulé (editor), Conservation Biology. Sinauer, Sunderland, Massachusetts.

McDONNELL, M. J. & E. W. STILES. 1983. The structural complexity of oldfield vegetation and the recruitment of bird-dispersed plant species. Oecologia 56: 109–116.

MURPHY, P. G. & A. E. LUGO. 1986. Ecology of tropical dry forest. Annual Rev. Ecol. Syst. 17: 67–88.

NEWMARK, W. D. 1987. A land-bridge island perspective on mammalian extinctions in western North American parks. Nature 325: 430–432.

OLSSON, G. 1984. Old Field Forest Succession in the Swedish West Coast Archipelago. Ph.D. Dissertation. University of Lund, Sweden.

PURATA, S. E. 1986. Floristic and structural changes during old-field succession in the Mexican tropics in relation to site history and species availability. J. Trop. Ecol. 2: 257–276.

STILES, F. G. 1983. Checklist of birds. Pp. 530–544 *in* D. H. Janzen (editor), Costa Rican Natural History. Univ. Chicago Press, Chicago.

UHL, C. & R. BUSCHBACHER. 1985. A disturbing synergism between cattle ranch burning practices and selective tree harvesting in the eastern Amazon. Biotropica 17: 265–268.

WILCOVE, D. S., C. H. McLELLAN & A. P. DODSON. 1986. Habitat fragmentation in the temperate zone. Pp. 237–256 *in* M. J. Soulé (editor), Conservation Biology. Sinauer, Sunderland, Massachusetts.

WILSON, D. E. 1983. Checklist of mammals. Pp. 443–447 *in* D. H. Janzen (editor), Costa Rican Natural History. Univ. Chicago Press, Chicago.