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AN ABANDONED FIELD IS NOT A TREE FALL GAP

DANIEL H. JANZEN, Department of Biology, University of Pennsylvania, PA 19104, USA

The Neotropics are rich in mosaics of forest and ancient-to-modern pastures and fields. In most of these mosaics, the original and late second-growth forest is rapidly dwindling in area and the clearings are enlarging and coalescing. However, in some areas this process has been reversed; a field or pasture has been abandoned and is allowed to return to forest—usually due to changes in socio-politico-economic forces, forest-field rotations, or explicit conservation efforts.

At first glance, the forest invasion of an abandoned Neotropical clearing appears to have much in common with the forest invasion of a gap in a forest canopy—as though an abandoned field was just another kind of large gap in the canopy caused by a tree's death, landslide, tornado, riverbank erosion, etc. While there are some parallels between these two kinds of forest invasion of a deforested area, there are many ways that the reforestation process of abandoned fields and pastures differs from that of tree fall gaps and other natural holes in the canopy. Recent experiences with the restoration of lowland dry forest in northwestern Costa Rica (Janzen, 1988*a*,*b*) lead me to comment on these differences. Now that research in field and pasture restoration ecology is becoming important in the tropics (Uhl, 1983; Uhl and Jordan, 1984; Uhl and Buschbacher, 1985; Janzen, 1988*a-c*), it is appropriate to be cautious about whether our understanding of natural disturbance sites applies directly to the practice of restoring Neotropical old fields and pastures.

VERTEBRATE DISPERSERS OF SEEDS

It is virtually impossible for the fauna of seed dispersers that arrives in a tree fall or other natural gap to be similar in numbers and species to the dispersal fauna of an abandoned man-made clearing. For example, the humans responsible for the formation and use of clearings in Neotropical forests are usually hunters and/or facilitate access by other hunters. A major subset of the habitat's vertebrate disperser coterie is therefore almost always missing or severely reduced in the clearing, and in the forest adjacent to it, when the clearing is abandoned. Even if the abandoned clearing is then protected from hunters (by conservation measures or by site abandonment), the vertebrates that are large enough to have been hunted generally have a low reproductive rate. Many years will pass before their density returns to a level that matches that of forest that has been unoccupied by hunters for decades.

However, once a mosaic of large cleared areas and forest is several years into uninterrupted forest invasion, the large area of secondary vegetation offers far more food (fruits, leaves, insects) for certain species of vertebrates than would have the original forest on the site, with the result of an abnormally high density and omnipresence of certain members of the site's coterie of seed dispersers (monkeys, peccaries, deer, coatis, ctenosaurs, frugivorous birds, bats, etc.). This in turn results in a rain of animal-born seeds in intensities, compositions and patterns that are grossly different from those that would occur in a tree fall gap or other kind of natural opening in intact forest, or on the forest floor before an opening occurs (Janzen, 1983).

On the other hand, large clearings may also be low-grade habitat for many dispersers. Many kinds of newly abandoned old fields or pastures contain only herbs (including grasses), plants that offer little or no food to come of the species of vertebrates that eat and disperse the large seeds and fruits of many forest trees. Simply by being large, abandoned fields and pastures are a block of open space that many forest animals will not cross; the same seed dispersers regularly cross small natural disturbance sites. An agouti-dispersed species of tree may not get to the open part of an abandoned clearing simply because agoutis generally do not cross large open areas; however, there are numerous circumstances where an agouti will bury its seeds in a tree fall gap.

Seed dispersal is not one single ecological process. Fruit bats differ from agoutis, and agoutis differ from mice, and mice differ from tapirs, and tapirs differ from monkeys. It is my general impression that the inter-specific differences between the ways these animals disperse seeds are substantially greater in large clearings than in small natural disturbance sites. A bat or a monkey may swallow the same species of small seeds, but only one of them will fly across an abandoned clearing. Even if the seed dispersal is normal in some sense, the seeds fall into a competitive milieu generated by sets of plants that are either totally absent from the forest, or occur in very different proportions than they do in natural disturbance sites.

Understanding these anthropogenic and natural processes is further complicated because most abandoned clearings (and their surrounding forest) that are today being restored to forest have been under strong human use for decades to centuries. There is therefore no knowledge of the forest's carrying capacity for the vertebrates that disperse seeds. The biologist may easily be deceived into thinking that the current density of vertebrates is "natural" for the site, if for no other reason than local "knowledge" suggests that to be the case. This problem is exacerbated by the almost total absence of accessible unhunted areas at the present time, areas where the biologist can gain perspective of what sorts of vertebrate densities are possible in a variety of habitats.

While tens of species of vertebrate seed dispersal agents disperse seeds into a given tropical site, hundreds of species of animals are busily trimming the seed and seedling shadows. All of the above differences between abandoned clearings and tree fall gaps apply to the seed predators, but more so. It is my experience that while at least half of the species of vertebrate seed dispersers at a site may at least cross an abandoned clearing on occasion, not more than a few percent of the total suite of seed predator species will search for or find seeds there. On the other hand, just as with certain species of seed dispersers, some of the seed predators that are there may be excessively abundant in comparison with a tree fall or other natural gap in the forest.

The issue is confused even more since almost all species of vertebrate-dispersed seeds cannot arrive at the interior of an abandoned clearing without being carried there by a vertebrate. In contrast, virtually every tree fall gap will receive some vertebrate-dispersed species of seeds that arrive simply by falling off the parent tree before or after the gap occurred. Thus, for many species of vertebrate-dispersed seeds, some tree recruitment may occur within the forest even if the relevant vertebrates have been extinguished and the species is dependent on tree fall gaps. Whether this recruitment is sufficient to maintain a breeding population of the tree is a different question.

DISPERSAL BY WIND

It is tempting to view the final product of woody invasion of an abandoned clearing as some kind of a copy of the adjacent forest, just as is normally the case with a tree fall or other natural gap. Dispersal of seeds by wind, however, offers a clear example of why this view is untenable. There is usually a consistent direction to the wind during the time of year when wind-dispersed woody plants mature their fruits. The invasion of an abandoned field by the wind-dispersed subset of the flora is therefore extremely directional (e.g., upwind invasion does not occur, which automatically introduces major heterogeneity into the forest invasion of any clearing). In addition, the wind enters many vertebrates refuse to go. The outcome is that seed flow from a forest that is a mix of wind-dispersed species and animal-dispersed species can easily generate a forest that is made up almost entirely of wind-dispersed species (e.g., Janzen, 1988*a*). Such a forest may require many centuries for the wind-dispersed species to die out and the animal-dispersed species to invade to a "natural" density.

Tropical dry forests have a much greater absolute number of wind-dispersed species than do tropical wet forests (e.g., Gentry, 1982). Abandoned clearings in dry forest may therefore be invaded by dry forest much more rapidly than those in wet forest. In addition, the large or obvious wind-dispersed seeds are usually toxic to vertebrates (e.g., Janzen, 1986*a*) and the small ones are hard to find once dispersed. The wind-dispersed forest that can appear in an abandoned clearing may have a very reduced food supply for a vertebrate that both preys on and disperses seeds. This may strongly retard the flow of animal-dispersed seeds into the site (Janzen, 1988*a*).

THE FIELD'S NEIGHBORS

The inter-field and inter-pasture variation in the age, history and species composition of neighboring vegetation—hence variation in source of seeds and their dispersers—is enormous. It ranges from bare ground to large expanses of herb-tree mixes to uncut forest. It is common for two equal-sized and equal-aged abandoned clearings on the same soil in the same climate to have very different rates and patterns of invasion by forest because the vegetation type adjacent to each is different. Adjacent clearings may also have different disturbance histories, resulting in very different seed banks, herb plant layers, animal arrays, mycorrhizal populations, populations of root stocks, soil chemistry, water retention, etc. This situation is compounded by the agriculturalists' and pastoralists' habit of using abrupt changes in vegetation, soil, slope, etc., as boundaries for their clearings. The consequence is that the seed rain from the neighboring uncut vegetation may consist largely of species that did not originally occur on the site of the abandoned clearing (and see Janzen, 1986*b*, 1987).

PHYSICAL ENVIRONMENT

The physical environment in an abandoned clearing is dramatically different from that in a tree fall gap, but the direction of the differences is not always as one would intuit. It has been my experience that the dense herb layer of an abandoned field, for example, can act as a sponge and moist air mat, keeping the soil much more moist during short rainy season droughts than can the forest understory; on the other hand, during a long rainy season drought, the clearing dries out much more than does a tree fall gap in the adjacent forest. The unobstructed sunlight of a clearing and a gap may be the same for a given leaf, but lateral air movement within the forest may cause the growing plant in the gap to be bathed in cooler and more humid air than is the case in a nearby clearing. All parts of a natural gap are near the forest, but only a small fraction of an abandoned clearing can be near a forest since abandoned clearings are usually much larger than natural gaps in the canopy. All of these differences will differentially affect competitive, growth and herbivory regimes in an abandoned clearing as contrasted with a tree fall.

A field is also fuel. When a pasture or a field is abandoned, it rapidly accumulates a very large amount of herbaceous fuel that rots only slowly because of its extreme exposure to drying sun and wind (even in the rainy season); the absence of livestock exacerbates the phenomenon (Janzen,

1988*b*). It is often much more inflammable than is the litter and understory of the forest that will eventually replace it. While a lightning strike to an isolated tree in such a field may ignite a fire, even in the wet season, a fire is much less likely to start or continue in a tree fall gap in a closed forest. Because of the large amount of fuel, this fire will also be much more severe for any woody plants in the field—isolated trees or regenerating patches—than it would have been while burning through the sparse fuel in the understory of the forest or through a tree fall gap (Uhl and Buschbacher, 1985; Janzen, 1988*b*).

AT THE END

The processes referred to above result in an abandoned clearing being a species-rich jumble of dying, abnormally reproducing, normally reproducing, and growing individuals. They have ecologically fit into the site, but they cannot be said to have evolved into the site (Janzen, 1985*a*). Virtually none of the plants and animals are present in patterns, relationships, densities, etc., that are the same as those under which their traits evolved. The abandoned clearing is about as "natural" as an unplanned zoo and botanical garden.

But then again, any given tree fall gap has an enormous stochastic element in determining its processes and species composition. The difference is that the tree fall gap is filled by processes that we believe relate directly to the supposed function of the traits of the organisms. The abandoned clearing, however, is filled by processes that do not relate well to the organisms' evolutionary histories. For example, tapir density in an abandoned field may depend on the proximity of a military base and weekend hunting by soldiers, and fruit bat density in an abandoned field may depend on the proximity of old roadsides covered with fruit-bearing trees. A big-seeded forest tree that can live 400 years may grow well if it is planted in the field by a horse defecation, but die if washed there by surface erosion. Which species of trees grow up and shade out the grass in an abandoned pasture may depend little on the competitive abilities of either the trees or the grasses, and much on whether a rancher left an upwind patch of trees when clearing for the pasture 200 years ago.

The apparent predictability or "naturalness" of the forest invasion of a natural gap and the disorderliness of the invasion of an abandoned clearing are deceptive. The individuals of the species filling a natural gap are also there because they ecologically fit there; a given natural gap does not usually contain a significant portion of the breeding population. The processes in the forest put them there and they survived once they arrived (at least for a while). Exactly the same may be said for the species filling the abandoned clearing. The problem is that we are inclined to view the pattern of forest invasion in the forest as "natural" (and therefore logical—produced by evolution) and that of forest invasion of an abandoned pasture as "unnatural" (and therefore illogical—produced by random processes). But in both cases, the invasion is simply the product of current ecological processes that operate on the traits of the plants to put them there and kill them.

The difference is that in the case of the forest gap, we know something of these ecological processes (e.g., Hubbell and Foster, 1986; Martínez-Ramos and Alvariz-Buylla, 1986). The demographic composition of a tree fall gap, and the progression of its species, therefore seems to become predictable. (However, I cannot resist adding that if we were to add back in the herbivorous megafauna with which these plants undoubtedly evolved long ago (e.g., Janzen, 1985*b*), the Neotropical "tree fall gap" would be a totally different—and much more variable—habitat, just as is the case with African tree fall gaps where the megafauna is still in place.) In the case of the abandoned clearing, we know little of the processes (but see McDonnell and Stiles, 1983; Robinson and Edgemon, 1988; Uhl et al. 1988; Buschbacher et al., 1988; McCune and Allen, 1985; Archer et al., 1988; Gomez-Pompa and del Amo, 1985; Whitmore, 1983; Stocker, 1981). Further, the processes of invasion of a tropical clearing relate very poorly to the apparent function of the evolved traits of the invaders. The resultant composition and progression of the forest invasion of an abandoned human clearing is less predictable to us at present than is that of a tree fall gap, but certainly not less interesting. A major research effort on forest invasion of tropical abandoned fields and pastures, both for esoteric and conservation purposes, is overdue. It is an effort that can be undertaken much more readily than can the study of the nearly extinct "natural" gap in "undisturbed" forest.

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