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Author(s): Daniel H. Janzen
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No park is an island: increase in interference from outside as park size decreases

Daniel H. Janzen

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As areas of conserved pristine forest are reduced in size they are increasingly susceptible to significant immigration of animals and plants from nearby anthropogenic secondary successional habitats, and the animals of the pristine forest are also likely to forage outside of the pristine forest in the food-rich secondary succession. This phenomenon should be of particular importance to the interactions that occur in natural disturbance sites within pristine forest (e.g., succession in tree falls). However, since much large tree regeneration begins in tree fall gaps in the canopy, even the composition of the canopy may be influenced by large bodies of non-pristine vegetation surrounding the preserved area. From a conservation standpoint, this emphasizes that in some cases a patch of pristine forest may remain ecologically intact longer if surrounded by croplands and closely grazed pastures than if surrounded by extensive areas of secondary succession rich in plants and animals that will invade the pristine forest. Colonization of a tree fall by *Cecropia peltata* trees in pristine forest in Santa Rosa National Park, northwestern Costa Rica is used as an example. The phenomenon emphasizes some of the ways that small islands of vegetation may be only poorly analogous to more conventional islands surrounded by water.

D. H. Janzen, Dept of Biology, Univ. of Pennsylvania, Philadelphia, PA 19104, USA.

При сокращении территорий, занятых сохранившимися коренными лесами, в них повышается способность к восприимчивости растительных и животных иммигрантов из соседних антропогенных вторичных биотопов, а животные, обитающие в коренных лесах проводят фуражировку вне лесов, во вторичных биотопах, богатых пищей. Это явление имеет особое значение для взаимодействий, наблюдающихся в естественно нарушенных лесных участках (сукцессии при выпадении деревьев). Однако, т.к. восстановление многих крупных деревьев начинается на прогалинах в лесном покрове, даже состав покрова может находится под воздействием больших количеств вторичной растительности, окружающей сохранившуюся территорию. С точки зрения охраны подчеркивается, что в некоторых случаях участок коренного леса может дольше оставаться интактным, если он окружен пахотными землями и сильно выпасаемыми пастбищами, чем экстенсивными территориями вторичной сукцессии, обильными формами растений и животных, способными внедряться в коренные леса. Колонизация мест выпада деревьев *Cecropia peltata* в коренных лесах Национального Парка Санта Роза на сев.-западе Коста-Рики использована в качестве примера. Этот феномен выделяет некоторые из путей аналогизации маленьких островков растительности с обедненными вариантами обычных островов, окруженных водой.

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Introduction

There is evident conservation value to numerous small habitat preserves (parks) when large protected areas are impractical (Simberloff 1982). However, such a management policy brings to mind a caution that is often unappreciated for parks and other forms of conserved pristine vegetation, and becomes ever more appropriate as park size decreases. The smaller the patch (island) of habitat that is viewed as pristine, the greater the effect of the surrounding secondary successional vegetation and croplands as a source of 1) animals and seeds that enter the park and interact with the residents, and 2) food subsidy for residents capable of foraging outside of the pristine forest. Every field biologist working in or around apparently pristine vegetation is aware to some degree of this problem, but none of us wish to fully acknowledge its potential impact on biotic interactions and our ecological/evolutionary interpretations of them. It is a particularly inconvenient acknowledgment for studies of biotic interactions at levels of organization greater than pairs of individuals.

The problem arises because a park differs in one very substantial biological manner from a conventional island surrounded by water, a very different habitat. The conventional island is not surrounded by a habitat rich in organisms competent to forage extensively on the island (excluding beach inhabitants) and prone to bombard the island with juveniles quite capable of taking up residence. Likewise, the conventional island's residents are generally not inclined to forage heavily in the surrounding ocean. Oceanic birds nesting on small islands, and hermit crabs, are obvious exceptions. However, these sorts of animals are generally not included in discussions of how species-packing on islands relates to island size or to discussions of ecological interactions such as competition, mutualism, etc. In strong contrast, a park, and especially its naturally-occurring successional habitats in pristine vegetation (tree falls, landslides, large mammal trails, watercourse edges, etc.), is bombarded by an enormous multi-species seed shadow generated by the exploded populations of successional plants and associated animals of roadsides, abandoned croplands, brushy pastures, logged forest, etc. Furthermore, the animals of both natural disturbed sites and closed-canopy forest have many reasons to forage outside the park in these anthropogenic habitats.

Since the phenomenon I describe does not seem to threaten extinction, and may result in increased densities of desired species, it might seem so esoteric as to be not worrisome to park management (though its significance to more esoteric studies seems evident). However, parks differ quantitatively from zoos and botanical gardens in the interactions that are present in the park; parks function to conserve interactions, and the conservation of organisms is a happy by-product. A belt of food-rich secondary succession around a small park may be as destructive to these interactions as would be the elimination of the large carnivores within the park. The evolutionary ecology of large tree replacement in tree falls within the park may be rendered uninterpretable as much by heavy seed rain from outside the park as by deliberate planting in tree falls by park managers.

To move from the vague to the specific, below I briefly comment on the primary and secondary succession in a tropical tree fall, a habitat where the phenomenon over which I worry is particularly evident. The question is simple. What determines the successional outsome in a particular tree fall in an essentially pristine forest? The answer is likewise simple. The outcome is determined by what plants were there when the tree fell, what plants arrive later, and how these plants interact. In a small park, all these processes are influenced by more than the organisms of the closed-canopy forest and its natural disturbance sites.

Replace a guapinol

In the eastern portion of Santa Rosa National Park in northwestern lowland Costa Rica (25 km south of La Cruz, 0–350 m a.s.l., see Boza and Mendoza 1981 for a general description), there is a 10 ha patch of apparently original forest (though the mahoganies, *Swietenia macrophylla,* were selectively removed in the 1940's). This forest is bounded on two sides by old pastures and in other directions grades into 10–80-yr old secondary successional forest. In the essentially pristine closed-canopy forest, the general canopy is 20–40 m in height; its undulation is accentuated by the very broken topography of ravines and small plateaus. At least 80% of the crowns of large trees are the following species: *Hymenaea courbaril* (Leguminosae), *Quercus oleoides* (Fagaceae), *Luehea speciosa* (Tiliaceae), *Brosimum alicastrum* and *Ficus obtusifolia* (Moraceae), *Zuelania guidonia* (Flacourtiaceae), *Manilkara zapota* and *Mastichodendron capiri* (Sapotaceae) (plant names used in this paper are in accordance with Janzen and Liesner 1980). There are another 30 species of rare large trees and sub-canopy level trees. *H. courbaril* or guapinol and *Q. oleoides* or roble encino are the most common large trees and one could easily describe the forest as being a guapinol-encino association, with the guapinol more common on the moist sites and the roble encino more common on the drier sites (the nearby pasture area was once a nearly pure roble encino forest, cf. Boucher 1981, and the guapinol forest may once have been little more than a fringe on the once much more extensive roble encino forest). The western edge of the guapinol-encino forest is cut through by the main blacktop road through the Park and the forest is generally referred to there as "bosque húmedo" or "bosque siempre verde". These names derive from the nearly evergreen pristine forest, which stands in strong contrast to the highly deciduous nature of the secondary successional forest that covers much of the remainder of the Park.

In late December 1978, one of the severe wind storms associated with the beginning of the rain-free dry season (December to mid-May) blew down a 31 m tall guapinol (three other large guapinoles were blown down within 1000 m of this one in the same storm). In falling, the guapinol left a gap in the canopy, produced a small patch of bare soil, exposed a large area of understory to direct insolation, and crushed a smaller area of understory vegetation. My question is, can the succession leading to the eventual replacement of this guapinol by another large tree or trees of the same or other species be studied as an example of succession in pristine forest of this type, and can the results be generalized to the evolutionary ecology questions currently fashionable about tropical forest dynamics? Has the succession in this tree fall been as altered by processes outside the pristine forest as if a forester had deliberately seeded the tree fall with a desirable tree species? For me, the best way to answer such questions, in the context of the subject of this essay, is to examine the guapinol tree fall at present, 3.5 growing seasons after the tree fell. My intent is to identify some of those interactions that may have been important so far and that may have been influenced by the area outside of the pristine forest.

Before examining this particular tree fall, more background is needed on the area. Santa Rosa National Park, 10800 ha in extent, was a cattle ranch for at least 200 yr. During that time, at least 30% of the forest was cleared and planted to grass. At least 70% of the remaining forest was lumbered and then allowed to return to secondary woody succession. The successional woody vegetation and pastures were variously grazed and browsed by cattle until 1978. The pastures are highly interdigitated with forest of all ages, and are presently gradually returning to woody vegetation (but the return is slowed by dry season grass fires). There has been essentially no hunting since 1971, when the Park was established.

Anatomy of a guapinol tree fall

The tree had 12.5 m of straight and unbranched 68.8 cm DBH bole, with a broadly conical crown 20.5 m in depth (distance from the first major fork to the uppermost layer of leaves). It was healthy and the crown symmetrical and intact. When the wind uprooted the guapinol at the beginning of the dry season, the soil was still moist. However, no rain fell for nearly 6 months on the newly bared soil, litter and understory vegetation. When uprooted, it produced a 2.3-m-tall hemispherical but thin mound of dirt and guapinol roots on the west side of an 80 cm deep hemispherical pit from which the root crown was torn. The soil was deep latosol with old volcanic ash intrusions. The guapinol fell such that the bole crushed a few understory saplings but the crown did not tear away portions of adjacent crowns of large trees. This was partly an accident of the way it fell and partly because, as is generally the case with this species of tree, the crown was free of large vines connecting it with other crowns. The gap in the canopy was 124 m^2 in extent. This tree fall and the succession in it is representative of numerous other tree falls that I have examined in pristine forest in the Park.

The tree fall led to a strong and heterogeneous change in insolation at ground level. The freshly bared litter-free soil of the pit and mound was in direct sunlight or below open sky from about 0800 to 1600 hours (and most of it still was 3.5 yr later). The (previously) understory plants at the margins of the soil pit also received direct sunlight, as did much of the litter beneath them. The litter at this site received the most intense sunlight of any of that exposed by the tree fall because the understory vegetation tends to be most sparse around the bases of large trees such as this one. Immediately after the tree fell, the bole was partly covered by the crowns of 1–3 m tall understory shrubs and treelets whose crowns had merely been pushed to one side as the bole passed by. These small woody plant crowns shaded the litter somewhat and quickly responded to the increased insolation by producing more leafy crowns. By August 1982, these crowns generated as dense a shade, if not more so, as occurred before the tree fell. Where the crown of the guapinol landed, the understory plants were severely crushed and also covered with slowly decomposing medium-sized to large guapinol branches. Here, the overstory canopy was still intact, and therefore there was little or no change in insolation. By August 1982, the area where the crown fell was nearly bare of plants and littered with rotting vegetation.

By August 1982, 3.5 yr after the guapinol fell, the three new vegetation types are very different from each other in composition but strongly reflect the initial differences described above.

The soil pit and mound

This area of intense disturbance is highly heterogeneous in vegetation regeneration. On the bare soil, a few individuals of fast-growing "colonizing" species have taken root (Tab. 1) but they have not yet produced an approximation of a partly-closed canopy at any height. (I will later discuss *Cecropia peltata* as a detailed example). In addition to the plants that have grown on the bare soil from seedlings, 16 species of perennial vines that were present before the tree fell have grown into the open area over the bared soil or over the immediately adjacent vegetation (Tab. 1). Each of these species of vines is represented by only 1–2 individuals. Of similar biology to the vines, but more stationary, there were 14 species of saplings (juveniles) of self-supporting plants which had been rooted at the site when the tree fell but which would not have reached reproductive maturity in the shaded understory (as is

Tab. 1. Vegetation of the soil pit and its insolated immediate surroundings at ground level.

Plant species	Number of individuals	Height of tallest (cm)	Seed dispersal agents
Rooted from seed on the bared soil:			
Cecropia peltata (Moraceae)	4	800	birds, bats, coatis, monkeys, rodents
Adiantum conccinum (Adiantaceae)	5	25	?
Eupatorium quandrangulare (Compositae)	2	72	wind
Verbesina gigantea (Compositae)	2	145	wind
Cordia linnaei (Boraginaceae)	1	148	birds
Tetracera volubilis (Dilleniaceae)	1	6	birds
Cassia hayesiana (Leguminosae)	1	62	birds
Hamelia patents (Rubiaceae)	4	110	birds
Miconia argentea (Melastomataceae)	7	123	birds
Vismia baccifera (Guttiferae)	1	188	bats?
Solanum americanum (Solanaceae)	1	202	bats?
Piper marginatum (Piperaceae)	6	48	bats
Piper pseudo-fulligineum (Piperaceae)	3	87	bats
Pityrogramma calomelanos (Gymnogrammaceae)	2	36	?
Borreria ocimoides (Rubiaceae)	32	3	?
Philonotis sp. (Bartramaceae)	?	1	?
Prockia crucis (Flacourtiaceae)	1	110	birds
Vines growing across the bare soil and pit edge from old root stocks:			
Pithecoctinium crucigerum (Bignoniaceae)	2	20	wind
Gouania polygama (Rhamnaceae)	1	130	wind
Tetracera volubilis (Dilleniaceae)	1	30	birds
Serjania atrolineata (Sapindaceae)	1	20	wind
Paulinia cururu (Sapindaceae)	2	10	birds, coatis
Desmodium axillare (Leguminosae)	1	8	sticktight on mammal
Lygodium venustum (Schizaeaceae)	1	22	?
Petraea volubilis (Verbenaceae)	1	18	wind
Centrosema pubescens (Leguminosae)	1	40	explosive fruit
Discorea convolvulacea (Dioscoreaceae)	1	23	wind
Macfadyena unguis-cati (Bignoniaceae)	1	6	wind
Passiflora platyloba (Passifloraceae)	1	240	large mammals, rodents
Forsteronia spicata (Apocynaceae)	1	110	wind
Cissus rhombifolia (Vitaceae)	2	30	birds, mammals
Sicydium tamnifolium (Cucurbitaceae)	2	100	birds
Ipomoea squamosa (Convolvulaceae)	1	200	wind
Established prior to tree fall, self-supporting, not reproducing in forest understory:			
Annona purpurea (Annonaceae)	1	260	large mammals, rodents
Hymenaea courbaril (Leguminosae)	3	120	large mammals, rodents
Allophyllus occidentalis (Sapindaceae)	1	180	birds, large mammals
Sapium thelocarpum (Euphorbiaceae)	1	230	birds
Solanum accrescens (Solanaceae)	1	310	bats?
Malvaviscus arboreus (Malvaceae)	1	330	birds, mammals
Swartzia cubensis (Leguminosae)	1	110	birds, mammals
Spondias mombin (Anacardiaceae)	1	350	mammals
Astronium graveolens (Anacardiaceae)	1	130	wind
Lasiacis sorghidea (Gramineae)	2	110	?
Olyra latifolia (Gramineae)	2	60	rodents
Streptochaeta spicata (Gramineae)	2	80	sticktight on mammal
Panicum trichoides (Gramineae)	1	60	?
Scleria pterota (Cyperaceae)	1	90	?
Baccharis trinervis (Compositae)	1	210	wind
Manilkara zapota (Sapotaceae)	1	120	mammals
Established prior to tree fall, reproductive in forest understory:			
Rourea glabra (Connaraceae)	2	100	birds
Hirtella racemosa (Chrysobalanaceae)	3	240	birds, rodents
Eugenia aff. *oerstediana* (Myrtaceae)	2	300	birds
Ocotea veraguensis (Lauraceae)	1	140	birds, rodents
Piper pseudo-fulligineum (Piperaceae)	1	160	bats

also the case with the above mentioned vines) (Tab. 1). These plants have responded to the insolation by enlarging their crowns into the insolated area. Finally, there were 5 species of shrubs and treelets that normally reproduce in the understory but responded to the increased light by increased foliation and by sexual reproduction (Tab. 1).

The newly insolated understory vegetation near the fallen bole

In strong contrast to the open and easily penetrable vegetation in the area of the soil pit, after 3.5 yr of growth the vegetation along the fallen guapinol bole is a nearly impenetrable stand of 1–10 cm diameter stems (measured 1 m above the ground) supporting a very dense canopy 2.5–4 m above the ground with emergents reaching 6 m. Large perennial vines course through the foliage at the level of the canopy. The following species constitute at least 90% of the volume of leafy vegetation: self-supporting – *Astronium graveolens* (Anacardiaceae), *Cecropia peltata, Brosimum alicastrum, Castilla elastica* and *Trophis racemosa* (Moraceae), *Trema micrantha* (Ulmaceae), *Cordia linnaei* (Boraginaceae), *Genipa americana* (Rubiaceae), *Casearia sylvestris* (Flacourtiaceae), *Annona reticulata* (Annonaceae), *Picramnia quaternaria* (Simaroubaceae), *Acacia collinsii* (Leguminosae); perennial vines – *Machaerium kegelii* and *Desmodium axillare* (Leguminosae), *Gouania polygama* (Rhamnaceae), *Paulinia cururu* (Sapindaceae), *Callichlamys latifolia, Pithecoctinium crucigerum* and *Cydista aequinoctialis* (Bignoniaceae), DHJ 12205 (Malpighiaceae), *Passiflora pulchella* (Passifloraceae). It is striking that only one of the above self-supporting species – the single 5-m tall *Brosium alicastrum* sapling – is a member of the 30–40 m canopy of this forest when mature. In contrast to the self-supporting plants leaning into the area around the soil pit at the base of the fallen guapinol, the trees near the bole have symmetrical crowns and straight vertical central axes.

The crushed understory where the guapinol crown fell

At this date, there appears to have been little or no replacement of the understory plants killed and branches stripped off by the guapinol crown when it fell. In view of the deep shade cast by the overstory canopy at this site, it will probably be scores of years before the vegetation again resembles normal understory.

Origin and survival of the plants in the tree fall

Where did they come from? Irrespective of whether the seeds arrived before or after the guapinol fell, every species of plant I have mentioned above as associated with the tree fall occurs commonly in the Park on roadsides, pasture edges, old fencerows, regenerating fields and other sites of primary and secondary anthropogenic succession. They also occur in what is in all likelihood pristine forest and its associated natural disturbance sites. Except for the two large trees, *Brosimum alicastrum* (ojoche) and *Hymenaea courbaril* (guapinol), and two large woody vines (*Callichlamys latifolia* and *Machaerium kegelii*) all of these species have large breeding populations in the anthropogenic portions of the Park vegetation. There are many more individuals, breeding individuals, and breeding individuals with extra-large flower and fruit crops in the anthropogenic vegetation than in the guapinol-encino forest and its tree falls. While the proportions of seeds in the seed rain from the two different origins need not reflect the absolute numbers of seeds produced in both habitats, it probably approximates it, at least in direction. It is therefore very likely that the seeds which produced the plants in the guapinol tree fall came from that portion of their population in anthropogenic vegetation. The nearest portion of this vegetation is approximately 60 m from the area of impact of the guapinol crown.

Not only is it likely that the seeds came from vegetation other than natural tree falls, but the number and patterns of arrival of these seeds are likely to be very different from those that would arrive as seed rain from natural tree falls. The species and numerical relations of the plants in the tree fall surely must be related to the numbers and timings of seeds that arrive. It follows from this that the proportions, ages, and fates of the plants in the guapinol tree fall cannot be viewed as "natural" in any sense of the word. That is to say, there is no reason to believe that for any given plant in the guapinol tree fall, the array of competitors and mutualists it now experiences approximates the array with which it on average interacted during its evolution.

Who brought them there? Just considering the 52 species of plants in the immediate vicinity of the soil pit and mound at the base of the guapinol, 62% of the plants are dispersed by birds and/or mammals (in addition, some of the wind-dispersed seeds are secondarily dispersed by seed predator rodents). Individuals of all of these vertebrates have foraging ranges large enough to encompass both the segment of pristine forest containing the guapinol tree fall and large areas of anthropogenic secondary woody succession. Of greater significance for this story, all of these animal species have populations sustained in great part by insects, fruits, flowers, foliage and seeds harvested from the anthropogenic vegetation. It is certain that their densities are much higher for the general region than would be the case were they being sustained only by the products of a large expanse of guapinol-encino forest. The anthropogenic forest can have highly diverse effects on the seed rain into the guapinol tree fall. On the one hand, it may be such a high-quality foraging area that animals that would normally frequent tree falls in pristine forest will find them comparatively poor as foraging sites and therefore the seed rain from these animals will be diminished. On the other hand, the anthropogenic vegetation may generate so many seeds or such intense portions of seed shadows that the tree fall receives far more seeds of this or that species than it ever would if far from such a source area. The actual situation for any given tree fall or class of tree falls cannot be determined any other way than through empirical observation.

How are plant-plant interactions affected by herbivores? Animals do more than bring seeds to the tree fall; by preying on dispersed seeds, trampling, and browsing, they further influence the outcome of this multi-specific vegetative melee. For example, one of the reasons why about 1 m^2 of the soil pit is bare of plants after 3.5 yr is that this portion of the site is crossed by a peccary trail. The peccaries both trample seedlings and browse certain species of foliage (cf. *Cecropia* below). *Liomys salvini* mice forage nightly in the tree fall. These heteromyid rodent seed predators both consume and disperse the seeds of almost every species of plant mentioned in this paper. For example, some individuals can live for months on a pure diet of guapinol seeds. The foliage of the plants in the guapinol tree fall is fed on by caterpillars, beetles, orthopteroids, true bugs and a miscellany of other insects. Just as with the plants, the individual insects are members of large populations distributed over the appropriate resource base. The densities of these insects, and those of the vertebrates mentioned above, are very different in the guapinol tree fall from what they would be were the tree fall part of a large expanse of intact forest. Furthermore, since the large "ocean" of anthropogenic vegetation generates carnivores that feed on the herbivores, as well as the herbivores themselves, it cannot be predicted at this stage of knowledge whether the herbivore density will be increased or decreased by the nearby anthropogenic vegetation.

Cecropia peltata as an example

To be more specific, I will examine *Cecropia peltata* (guarumo) in the context of the above generalizations. I chose this tree because it is familiar to many readers and to travellers in the tropics, and because it is a conspicuous member of the tree fall flora. However, a similar story can be told for each species that I have recorded growing in this particular tree fall.

Three of the four *Cecropia* saplings growing in the area of the soil pit are from seeds that germinated in the early wet season (May–June) of 1979 on the crest of the soil-root mound. One is 2.5 growing seasons of age, and unoccupied by ants. The three of equal age are 4, 7 and 8 m in height and the tallest will probably flower in 1983 for the first time. All three tall *Cecropia* are occupied by healthy colonies of *Azteca* ants, free of vines, and herbivorized to the degree normal for trees of this size.

The seeds of these *Cecropia* arrived at the site in the feces of a small to medium-sized bat (e.g., *Carollia, Artibeus*) or bird (e.g., *Chiroxiphia, Ramphastos*), or a non-volant mammal (e.g., *Tayassu, Capucinus, Nasua, Ototylomys*) that ate the fruit from the tree or ground below. The source tree was very likely one of the hundreds of adults growing along the roadside and in the several km^2 of late secondary succession within several km of the tree fall.

All of the animals that could defecate *Cecropia* seeds in the tree fall feed heavily not only on the abundant *Cecropia* fruits, but also on the abundant other fruits (and insects) of this vegetation. For example, the *Carollia* bats that could have defecated the seeds feed heavily on *Piper amalago* fruits (Fleming 1981) which occur at exceptionally high density in anthropogenic late secondary succession in the Park. In short, the *Cecropia* seed rain into the guapinol tree fall is generated by a density of *Carollia* and other frugivores far higher than could be supported by the pristine guapinol-encino forest with its sparse and highly pulsed seed, fruit and insect yield. For example, the guapinol trees produce fruit crops only at 3–5 yr intervals (Janzen 1978) and the understory fruiting shrubs (e.g., *Hirtella racemosa,* Chrysobalanaceae), *Ourata lucens* (Ochnaceae), *Psychotria nervosa* (Rubiaceae), *Mouriri myrtilloides* (Melastomataceae), *Picramnia quaternaria* (Simaroubaceae) have very small crops during only certain times of year. Except when one of the large moraceous trees or *Zuelania guidonia* (Flacourtiaceae) fruits in the guapinol-encino forest, the density of small juicy fruits is very low compared to late secondary succession.

Not only the common animals of secondary succession, such as *Carollia,* are affected by the large amounts of this vegetation. In the vicinity of the tree fall, birds that are generally thought of as deep forest birds, such as the long-tailed manakin *(Chiroxiphia linearis)*, feed heavily on the small fruits of the forest understory shrubs listed above (Janzen unpubl., Foster 1976). However, these birds also make long foraging forays into secondary succession (and more rarely nest there) to feed on fruits at abundant *Cecropia, Hamelia patens* (Rubiaceae), *Casearia corymbosa* and *Casearia sylvestris* (Flacourtiaceae), *Trema micrantha* (Ulmaceae), *Clidemia octona* (Melastomataceae), *Alophyllus occidentalis* (Sapindaceae), etc. If the density of these birds is raised by increased fruit availability, they will be at a higher density in pristine forest near late secondary succession than in pristine forest alone. Not only does the secondary succession contain more fruiting species (and fruit through more of the year) than does the pristine forest, but when understory shrubs of the pristine forest are exposed to insolation along roadsides and other kinds of edges, they often bear exceptionally heavy fruit crops.

It is probably not an accident that the four *Cecropia* seedlings that survived to sapling status in the guapinol tree fall soil pit area were all on the very steep-sided mound. Peccaries are fond of *Cecropia* seedlings (5–30 cm tall, months before they have acquired an obnoxious ant colony) and I suspect that they ate every seedling that appeared on the bare soil of the pit or its edges. While the peccary troup in this area forages throughout the pristine forest (and seeks shade and water there), there is far more browse and fallen fruit forage for them in the secondary succession than in the pristine forest. Their visitation rate and their density are undoubtedly higher in the guapinol tree fall because of the nearby secondary succession.

To mature in the guapinol tree fall, these *Cecropia* saplings had to do more than just arrive and survive herbivory. They had to be found by one or more *Azteca* ant queens. The founding queens originated in the same large adult *Cecropia* as produced the seeds, and the density of founding queens in the vicinity of old secondary succession is much higher than in large expanses of pristine forest, even if it does contain an occasional mature *Cecropia* in an old tree fall.

A major value of the *Azteca* ant colony is in keeping the tree free from climbing vines (Janzen 1969, 1973). The ocean of late secondary succession generates enormous numbers of seeds of the species of vines that are a threat to *Cecropia* saplings (all those listed in Tab. 1 except *Callichlamys latifolia* and *Machaerium kegelii*). The ants are also functional in removing pyraustine pyralid larvae that do severe damage by rolling and consuming leaves. However, they do not remove the insects that specialize at avoiding the patrolling ants (just as is the case with acacia-ants and acacias, Janzen 1967). For example, there are large populations of three butterflies *(Historis odius, Historis acheronta, Colabura dirce)*, one skipper (Hesperiidae) and one chrysomelid beetle (probably *Coelomera atrocaerulea*) that feed solely on the leaves of the population of *Cecropia* in late secondary succession. The ants cannot thoroughly remove these five species of herbivores. It would not be surprising to find that the density of *Cecropia* in natural tree falls in pristine guapinol-encino forest is too low to sustain one or more of these species.

The *Azteca* ants are usually effective at deterring the *Atta cephalotes* leaf-cutter ants from harvesting *Cecropia* leaves at Santa Rosa. However, for other less well-protected plants in the tree fall, it is an important fact that the anthropogenic secondary succession maintains a very high density of large *Atta* colonies. Whether leaf-cutters forage in any given tree fall depends on the proximity of a leaf cutter nest, and this in turn is related to nest density. The density of leaf-cutter nests is related to both the quality of the habitat and the amount of colonization by new queens. This is in turn related to the number of large mature colonies in the general vicinity. The particular guapinol tree fall under scrutiny here is within foraging range of a large leaf cutter colony. Of the three guapinol saplings growing at the margin of the original soil pit and therefore potential candidates to replace the one that fell, two had over 90% of their 1982 leaf crop removed by leaf cutters in May, and by the end of August 1982 these leaves had not been replaced. Such defoliations have a strong potential for influencing the competitive interactions between *Cecropia,* guapinol, and other woody plants in the tree fall.

The most bizarre "herbivore" threat to *Cecropia* saplings in the Park is the large lineated woodpecker *(Dryocopus lineatus)* that tears open the stems to prey on the ant colony. It weakens the stems so badly that they are permanently deformed and often break off at the damage point in a windstorm. The large number of *Cecropia* in late secondary succession may be instrumental in leading to the bird learning to exploit this food source. Further, the late secondary succession contains very large numbers of dying trunks and stems in which this bird forages heavily for wood-mining insects; its density is likely to be much higher in the presence of such a food source than in pristine forest.

Once the *Cecropia* in the guapinol gap attain flowering size, they will still be influenced by the other *Cecropia* in the secondary succession. *C. peltata* (like other species of *Cecropia*) is dioecious and therefore must outcross. It is also believed to be wind-pollinated. The large number of trees in secondary succession must create an enormous group pollen shadow that must greatly facilitate pollination of the female trees in tree falls. However, the importance of this process will depend on the way wind moves between the pristine forest and the secondary successional forest, and how far *Cecropia* pollen moves on it. It is possible that for a female *Cecropia* to be successfully pollinated in a tree fall it may have to have a male of equal reproductive state so close as to be within the same tree fall, and therefore the *Cecropia* trees in nearby secondary succession are irrelevant to the tree fall *Cecropia* except as sources of animal-dispersed seed and herbivores.

If a *Cecropia* tree attains fruiting status in the guapinol tree fall, the same processes that put its seed into the tree fall also apply in dispersing its seeds to new tree falls. Its seeds are likely to be more broadly dispersed within and between habitats than were there no secondary succession in the vicinity. Whether its fruits will be more thoroughly eaten (removed) will depend on the relative fruit abundance of *Cecropia* and other plants in the secondary succession and to what degree this attracts the animals that would otherwise be getting their fruit in the guapinol tree fall.

If one examines third- or greater order interactions of the *Cecropia* with the other members of the habitat, the connections are clear but their numerical values even more difficult to divine than would be those of the above discussion. For example, as mentioned above, a major challenge to *Cecropia* saplings is being used as a vine trellis. *Passiflora platyloba* is one such vine; at Santa Rosa it is fed on by the caterpillars of three species of heliconiine butterflies all of which have large populations in the secondary succession around the pristine forest but also oviposit on the *P. platyloba* in the forest tree falls. One of these, *Heliconius hecale,* is a prominent visitor (and probable pollinator) to the flowers of *Hamelia patens.* This shrubby treelet occurs in the tree fall and is common in the anthropogenic secondary succession, where partly insolated plants bear huge fruit crops. These fruit crops are heavily fed on by the long-tailed manakins mentioned earlier as an example of one of the birds that lives in the understory of the pristine forest but forages for fruits in both tree falls and the anthropogenic secondary succession. A manakin could well have been the bird that defecated *Cecropia* seeds in the guapinol tree fall.

The above considerations of *Cecropia* biology bring to mind the possibility that *Cecropia* is not even a natural member of guapinol (or other large tree) tree falls in pristine guapinol-encino forest at Santa Rosa National Park. It may well have been a tree of much larger disturbance sites such as new river terraces created by exceptional rainy seasons, cliff edges, and landslide scars. In these sites, just as in anthropogenic secondary succession in logged areas, abandoned fields and roadsides, the local density could have been high enough for high-quality cross-pollination, coupled with sufficient site duration for a long life as a seed-producing adult (*C. peltata* can live to at least 12–20 yr of age at Santa Rosa, as determined by counting the cycles of long and short internodes associated with the long rainy and dry seasons). If the above supposition was in fact the case, the natural sub-populations of *Cecropia* would have hit forest tree falls in their vicinity with seeds, just as they would hit other larger and more long-lived disturbance sites. The degree to which the resulting *Cecropia* adults in tree falls were part of the breeding population, as opposed to being as dead as is a rainforest tree seedling that comes from a seed carried to the sea in a river and washed up on an island beach, depends on the numerical values of all the various interactions mentioned earlier for the *Cecropia* in the guapinol tree fall.

At Santa Rosa there are no areas of pristine forest far enough from anthropogenic secondary succession to test the above hypothesis on *Cecropia* population structure. However, such forest exists in the rainforest inland from Llorona in northern Corcovado National Park on the Osa Peninsula of southwestern Costa Rica. Here, *Cecropia peltata* is a common member of the succession in anthropogenic disturbance sites as well as along rivers, in landslide scars, etc. However, it is generally absent from natural tree falls several kilometers into the forest from abandoned fields and roadsides. When a large portion of the soil of this forest is bared by clearing or by a major storm, it remains free of *Cecropia* seedlings for 1–3 yr. On the other hand, when old fields are recleared or "primary" forest near old fields is cleared, the bare ground is immediately colonized by seedlings of *Cecropia, Piper, Trema* and other fast-growing trees. Presumably these appear from a soil seed bank rather than immediate seed-rich fecal input. Such an observation is hardly new in human experience, and probably was a major driving force in the cultural evolution of true slash and burn agriculture. Where it seems to need reappreciation is in understanding tree-fall vegetation composition in pristine forest within foraging and dispersal range of the animals and plants of anthropogenic secondary succession. For example, Holthuijzen and Boerboom (1982) studied the seed bank in the soil of "pristine Surinam lowland rainforest" and found an average of 73 *Cecropia* seeds per square meter of litter and topsoil. However, their description of the study site says "the nearest *Cecropia* stand, bordering a forest road, was about two km from the sample area"; this puts their "pristine" rainforest sample well within daily movement range of the host of animals that would feed on the anthropogenic roadside *Cecropia* fruits.

We do not begin to know enough of the biology of tropical animals and plants to know what that foraging range might be (and it surely varies with the species). However, distances of 1–5 km are certainly within that range. The *Carollia* in the vicinity of the guapinol tree fall regularly forage 1–3 km (Fleming and Heithaus 1981). The peccaries in a preserve of similar vegetation 50 km to the south move over an area 1–10 km in diameter during the day and year (C. Vaughan, pers. comm.). *Heliconius hecale* moves 0.1 to 2 km in vegetation like that at Santa Rosa on a daily and life-span basis in search of flowers, mates, and oviposition sites (L. Gilbert, pers. comm.). I have found the large mammal-dispersed seeds of *Mastichodendron capiri,* which had to originate in the guapino-lencino forest or further away, in the secondary succession 2.5 km from the guapinol tree fall.

On a larger scale

The problem I discuss here exists on a scale much larger than one tropical park and its secondary succession. The patterns and densities of migratory birds in, within, and out of the tropics have undoubtedly been strongly altered by anthropogenic alteration of extra-tropical and tropical regions far from any specific tropical "pristine" segment of vegetation (Keast and Morton 1980). The "pristine" forests we study in the best-preserved portions of Neotropical parks are about as natural as will be the forest parks of Uganda 10000 yr from now after all the big game animals have been shot out (cf. Janzen and Martin 1982). I think we have no choice but to abandon any hope of studying the ecology of large ecosystems as systems in evolutionary equilibrium and to deal with ecosystems as only quite rough approximations of evolutionary steady states. Such a view brings to mind a generally unstudied trait of ecosystems, the degree of which the ecologically interacting organisms have been moved out of evolutionary equilibrium, and how much the "inefficiency" of the phenotypes results from the new levels and directions of resource flow.

To bring up the *Cecropia* example again, to what degree are some animals of the guapinol tree fall subsisting on *Cecropia* seed rain from the secondary succession? Might we expect the next million years of *Cecropia* life in anthropogenic secondary succession to generate a *Cecropia* fruit type that generates a much more directed seed shadow into some type of regularly recurring anthropogenic vegetation type (e.g., roadsides) and away from tree falls in pristine forest where survivorship of first or second generation offspring is essentially nil? Is the "natural" *Cecropia* genotype already severely contaminated with genes that have been highly successful in anthropogenic secondary succession but have low fitness in tree fall succession in pristine forest?

In closing

Natural secondary and primary disturbance sites in pristine forest are likely to pick up or contain a fauna and flora that will be the same as or strongly influenced by anthropogenic successional habitats within 5 km (or perhaps more) of the sites. While I have not discussed this, the animal visitors to a pristine forest canopy fruit crop are subject to the same process. For me this means that small parks (small islands of relatively pristine vegetation in a sea of secondary succession) may well maintain nearly all the *species* that they always had, but the densities and ecological relationships (hence selective pressures) may be altered strongly. It is hard to avoid the conclusion that in some circumstances, it may be much better to surround a small patch of primary forest with species-poor vegetation of non-invasive species of low food value (e.g., grain fields, closely cropped pastures, cotton fields, sugar cane) than to surround it with an extensive area of secondary succession rich in plants and animals that will invade the pristine forest.

From the conservation standpoint, one is tempted to say that invasion of secondary successional species doesn't matter as long as the habitat and its species are conserved. However, there are two reasons why it matters. The first is speculative, but probably real. If, for example, a tree like *Cecropia* becomes a prominent part of guapinol tree falls at Santa Rosa, it could well alter the competitive successes of the various canopy-level tree species that normally develop in the tree fall. This could well change the species composition of the canopy, and even something as prominent as the guapinol might disappear. The second reason is a recognition of the nature of a park or other habitat preserve. As mentioned in the introduction, all the *species* at Santa Rosa could be maintained (at enormous expense) in zoos, botanical gardens and game preserves. But a park is not so much a living museum of the species as of their interactions. We have to ask if the function of a park or other primary forest preserve is to conserve species we all like or if its function is the much more complex act of conserving that set of interactions we view as characteristic of pristine forest. The interactions are often what we put up park boundaries for. If you alter a species' interactions, you have altered it as much as if you changed its color, diet or teeth. What we always seem to bemoan is the extinction of species from natural areas, when we should be just as worried about the addition of species. That *Cecropia* tree may not belong in the Santa Rosa guapinol tree fall any more than an *Eucalyptus* sapling belongs there.

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