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Chapter 11

FOOD WEBS: WHO EATS WHAT, WHY, HOW, AND WITH WHAT EFFECTS IN A TROPICAL FOREST?

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INTRODUCTION

In this essay I paint a picture rich in extrapolation and conjecture, held in place by very few data points and much guided by my personal unpublished experiences. But this is the state of the art. My essay is about the animals that feed for the most part on living things, or things they have just killed. I shall discuss the animals that eat living things under six simple headings, but actually these headings are used only because field biologists have specialized in these areas in their studies of animal feeding relationships. Whether they represent fairly discrete islands of interaction in the ecosystem remains to be seen.

EATERS OF VEGETATIVE PARTS

The folivores, herbivores, plant parasites, and leaf eaters of tropical forests feed on a food that differs in one fundamental way from that eaten by carnivores. Their food contains large quantities of species-specific chemical defenses and therefore the food species are for the most part not readily interchangeable even when in hand, mouth, or gut. The entire structure of interactions of plant eaters with their food is centered on that trait. Thus, the impact of herbivores on plants and on plant arrays must be measured in the (often instantaneously trivial) amount eaten *plus* the much greater cost to the plant of producing the traits that keep it from being eaten by most animals most of the time. In short, the impact of the herbivore array cannot be measured observationally by the size of its bites nor experimentally by its removal. Rather, removal experiments must be coupled with the impossible task of allowing each individual plant to divert all of its huge herbivore defense budget to anti-edaphic, competitive and reproductive effort. Second, since prey items are at best poorly interchangeable, the spatial and temporal patterns of the edible ones become extremely important to the consumer. And why stress these two universal truths in an essay on tropical forests and their herbivores? Because the statements are most universally true in tropical forests.

Patterns of herbivory on individual plants

A misconception common among extra-tropical biologists is that tropical forest trees do not suffer total defoliation (and that "outbreaks" of tropical defoliators do not occur). In tropical forests made up largely of seasonally deciduous trees, total defoliation of adult individuals is commonplace during the first one to three months of the rainy season (Janzen, 1981a). Major defoliation is less commonplace, but nevertheless occurs on the evergreen species within the deciduous forest and on the members of evergreen lowland tropical forests (e.g. Anderson, 1961). Within evergreen forests, complete or nearly complete defoliation is more common among the tree species in the early stages of succession than later. The animals that defoliate tropical trees are most commonly moth larvae (Lepidoptera), adult beetles (Coleoptera), leaf-cutter ants (Attini, neotropical only), Orthoptera, and various groups of Homoptera. It is my subjective impression that on a world-wide basis, moth larvae are the most common offenders, both in numbers of cases and species. Defoliation in a tropical forest is less conspicuous than in extra-tropical forests because the defoliators are usually sufficiently stenophagous that they attack only one species of tree among the tens to hundreds at a site, because the lost leaves are usually replaced within two to four weeks, and because the inter-specific synchrony of defoliation is not great. A common impact of total defoliation is the shedding of set flowers or fruits, or failure to sexually reproduce in the following cycle (e.g. Rockwood, 1973) as well as reduced vegetative growth. There appears to be strong intra-year variation in the species and the individuals of trees which are defoliated, though some species seem to be especially likely to be defoliated (e.g., *Bombacopsis quinatum* and *Enterolobium cyclocarpum* in the lowland deciduous forests of Guanacaste Province, Costa Rica). Shrubs and understorey plants, while of less interest to foresters, are also often defoliated by insects (e.g. Janzen, 1981a).

As spectacular as total defoliation may be, a much larger bite of the leafy material is taken by the literally thousands of species of herbivores in a tropical forest that eat holes and notches in leaves, bite off shoot apices, suck phloem and xylem fluid from roots, stems and leaves, roll leaves, mine in leaves, scrape epidermis off leaf surfaces, web up young shoots, cut off the occasional leaf to carry off and eat in some more secluded place, etc. Each of these behaviors is often specific to certain species of immature insects or to a particular vertebrate at a particular time. Leigh (1975) calculates that for the Barro Colorado Island (Panama) forest the amount of leafy machinery eaten per year by insects is about 12.5% and by vertebrates 2.4%. However, this is a very severe underestimate of the insects' impact because it does not measure parts removed by sucking, leaves and apices eaten in entirety, leaves so severely damaged that they are aborted, the tree's loss in competitive or edaphic status caused by resource diversion to vegetative repair, and finally and worst, the costs of preventing greater amounts of damage.

The details of how the bites are taken do matter. Leaving seasonal considerations aside, a bite taken from a leaf is most damaging about the time it is a fully expanded photosynthetic machine but has not yet begun to repay its production costs (perhaps the 2nd to 4th weeks of visible life) and least damaging at the time it is being dehisced in senescence. The most damaging time of herbivory for a leaf on a deciduous tree should be near the half-way time of the leaf life span, as has been shown with extra-tropical crop plants (Chester, 1950). At this point in leaf age, there is no longer sufficient time to replace the lost leaf with a whole new leaf cycle, but the leaf has only just begun to repay the investment in its production.

A bite is not a bite is not a bite. A leaf roller may destroy much more of the leaf than it eats by greatly reducing its photosynthetic area. A leaf miner may do less damage than a chewer eating out the same amount because the miner does not produce such a large linear edge of opened leaf. A half gram of shoot tip eaten from the terminal axis may lower the competitive performance of a tree sapling more than the consumption of 10 kg of leaves (but see Harris, 1974). A 10% loss of seed material by drilling that mimics an insect attack caused a 30 to 50% reduction in seedling *Mucuna mutisiana* survival and shoot tip production in the face of severe herbivory (Janzen, 1976a). Even the distribution of bites should be of importance. For example, the role of inducible chemical defenses in deterring herbivores is recently getting much press (Ryan, 1978).

Apropos of this discussion, chemical defenses induced at the site of the bite may raise the fitness of the plant, not necessarily by reducing the percent of its foliage eaten but by causing the damage to be distributed in that pattern which least lowers the fitness of the plant (Janzen, 1979a). It seems likewise evident that the detailed distribution of a given amount of leaf removal (e.g., round holes, linear holes, marginal notches, a few big holes, many small holes, apical holes, distal holes, intervenation holes, etc.) will influence the impact of the herbivory on the host plant's fitness. We know nothing of this to date, but the combination of patterns offered by the fauna of insects in a tree species-rich tropical forest lends both realism and pertinence to the self-evident experiments.

One pattern of feeding seems to maximize the damage done to the plant, but it probably raises the fitness of the herbivore so much as to be selected for nevertheless. By far the bulk of tropical green tissue herbivory seems to occur between about sunset and midnight, that period in the 24 hour cycle when the nutrient content of green vegetation should be highest since it contains the day's photosynthate but has not yet translocated it or respired it, and that period when all the diurnal predators are blinded.

Ecosystem-level herbivory patterns

The overall quantity of leaf-eating, as measured by frass rain, caterpillar censuses, frequency of herbivore encounter, and appearance of leaf damage is highly seasonal in tropical forests. The longer and more well defined the dry season, the more concentrated the pulse of herbivory in the first one to three months of the following rainy season. One is left with the distinct impression that most of the leaf-eating insects in the habitat have a single generation of quite abundant larvae and adults at this time, and then either have a less abundant generation or very commonly remain dormant during the remainder of the rainy season. They then pass the dry season as active adults, migrants to a wetter area, or dormant eggs or pupae (and see Janzen 1973, 1976b). In evergreen tropical forests, if there is a sunnier and drier part of the year, as is usually the case, the peak of herbivory appears to occur during this time and immediately following it but is a gentler peak than in deciduous forests.

While it has never been measured, it is evident that there is severe supra-annual variation in the amount of herbivory in deciduous forests. For example, the first half of the 1977 and 1978 rainy seasons in Santa Rosa National Park (deciduous forest lowlands of Guanacaste Province, Costa Rica) were marked by extremely high general levels of herbivory and many species suffered total defoliation. In the rainy season of 1979, only one of the many previously severely defoliated species was again defoliated (*Enterolobium cyclocarpum*) and overall caterpillar densities were easily less than one tenth that of 1977 and 1978. A similar but less well documented situation appeared to occur in the lowland rain forests of Corcovado National Park (Costa Rica) in these three years.

There are conspicuous large differences in the amount of material eaten out of leaves in tree canopies in deciduous tropical forests as opposed to evergreen ones (and evergreen species in deciduous tropical forests; see Stanton, 1975). For example, in August 1979 there was a storm-produced tree fall of about 300 trees in Corcovado National Park. In clambering through the newly fallen crowns of at least 30 species of large trees I was struck by the presence of numerous crowns with no visible damage to their leaves and the fact that the others showed what would be deemed trivial damage as compared to the badly shot-holed, gouged and otherwise bitten-up leaves of a normal deciduous forest canopy. Within the Santa Rosa National Park deciduous forest there are a number of large evergreen species (e.g., *Andira inermis*, *Brosimum alicastrum*, *Ficus goldmani*, *Hymenaea courbaril*, *Manilkara zapota*, *Mastichodendron capiri*, *Sloanea terniflora*). There are numerous species of leaf-eaters that feed on the crowns of these plants, but the overall amount removed is much smaller than that removed from deciduous neighbors. Even when these trees have their new leaf crops the defoliation is trivial. (These "evergreens" are not truly evergreen, but drop their leaves synchronously at the beginning or the end of the dry season and immediately grow a new crop as is commonplace for "evergreen' trees in deciduous tropical forests in general.)

Shifting away from the food itself, one is struck by the extreme host-specificity of many of the insects that eat foliage in tropical forests. The details are only now beginning to be documented in a number of ongoing studies; it is a reasonable guess that when the votes are in, at least half of the foliage-eating insects will have only one species of host plant and none will eat more than 10% of the species present (except for leaf-cutter ants). If this statement is true, there are three obvious conclusions. Distances between host plants in time and space in a species-rich tropical forest can influence the intensity of impact of the herbivores on those plants. Second, species richness of herbivores in a forest should be at least in part dependent on the species richness of the plants (e.g. Janzen, 1977). Third, it should be impossible to predict the effect on the forest of the addition or deletion of a herbivore without knowing a very great deal about the ecology of the interaction of that herbivore with its food.

However, comparatively euryphagous insects do occur. For example, to date I have recorded that the larvae of *Hylesia lineata* (Saturniidae) feed and develop to adults on 44 species of Santa Rosa National Park foliage in 17 plant families (in a flora of approximately 575 species of plants). This caterpillar eats and grows well on *Zuelania guidonia* (Flacourtiaceae), a tree that has at least 40% dry weight phenols in its foliage, and eats many other species of leaves known to be rich in phenolics. It appears that *H. lineata* larvae thrive on phenol-rich foods but grow comparatively slowly. Sphinx moth larvae (Sphingidae) are much more stenophagous (1–4 host plants per species in this forest) and a 3 to 4 g larva matures in 3 to 4 weeks. *H. lineata* larvae weigh 2 to 4 g at the time of pupation but require 7 to 10 weeks to attain this size. In short, *H. lineata* is probably getting very little food per bite or stomach-full but can eat many kinds of plants, while the more stenophagous leaf-eaters such as sphinx moth larvae get more food per bite but can eat many fewer species of plants. The Santa Rosa National Park deciduous forest occupied by *H. lineata* also contains a highly euryphagous arctiid moth larva (a "woolly bear" in the genus *Hypercompe*). It has none of its 17 known hosts in common with *H. lineata*.

To this point I have restricted my discussion by and large to insects, but vertebrates are trivial neither in their selective impact nor in their daily removal of leafy plant parts (Leigh, 1975; McKey et al., 1978; Rockwood and Glander, 1979). Anyone seriously interested in this question cannot start without first reading the symposium volume *The Ecology of Arboreal Folivores* (Montgomery, 1978). Perhaps one of the more dramatic but poorly documented examples of the impact of vertebrates is the ability of a few free-ranging cattle to deflect succession following a year of slash and burn agriculture in a small patch cut out of a neotropical forest. This must be occurring in Africa with native mammals and natural tree falls, and must have occurred in the neotropics before and during the Pleistocene (Janzen and Martin, 1981).

Tropical folivorous vertebrates are quite euryphagous in nearly all cases but like euryphagous insects, they are by no means unselective hay balers. A captive tapir in Costa Rica rejected the foliage of at least 55% species of deciduous forest plants out of 381 species offered. It rejected all but one (*Pterocarpus rohrii*) of 55 species of tree legumes, and ate all but one (*Trema micrantha*) of the fast-growing secondary succession trees with large non-aromatic leaves (Janzen, 1981b). Free-ranging Malayan tapirs are very selective feeders on tree sapling species (Williams and Petrides, 1980), as are the tapirs on Barro Colorado Island (Terwiliger, 1978). Howler monkeys and colobus monkeys are very selective in the plant species, ages, parts and quantities that they eat (Struhsaker, 1975; McKey et al., 1978; Rockwood and Glander, 1979). While Kenyan elephants and giraffes consume some apparently very nasty foliage such as that of ant-acacias (*Acacia drepanolobium*), they are conspicuous in their avoidance of other plants such as introduced *Tecoma stans*, various Euphorbiaceae and Amaryllidaceae.

The choosiness exhibited by free-ranging folivorous vertebrates is undoubtedly based on achieving the most acceptable mixture of nutrients, and secondary compounds given the state of the animal (juvenile, pregnant, migrating, overweight), exposure to predators while foraging, and capability of the gut microbial flora as generated by the content of previous meals (Freeland and Janzen, 1974). In short, the foraging forest rhino or colobus monkey is eking a living on a battlefield generated by millennia of plant–herbivore evolutionary and coevolutionary skirmishes. However, I suspect that the bulk of the chemical defense traits it encounters were evolved in response to herbivory by insects rather than vertebrates.

While the biomass of forest folivorous vertebrates is generally low compared to forest insects (which also have a much higher turnover rate and therefore are extracting more from the system per gram of animal biomass), there is no doubt that they exert their own selective pressure on certain species of plants and influence the structure of the vegetation (e.g. Oppenheimer and Lang, 1969; Mueller-Dombois, 1972; Spatz and Mueller-Dombois, 1973). I predict that palms would be rare in species and individuals in the Neotropics if we had free-ranging elephants. Tangles of vines highly edible to cattle are largely absent in African and Asian forests and this is probably due at least in part to the presence of large herbivorous mammals. Two- and three-toed sloths seem to attain the highest biomass of any neotropical arboreal folivore (Montgomery and Sunquist, 1978), but this is probably related to the fact that they have the lowest foliage intake per gram of animal of any mammal that subsists largely or entirely on leaves and that they eat the mature leaves of many species of forest trees.

The work done to date on the impact of the herbivore array, insect and vertebrate, makes it clear that the emphasis needs to be shifted from how many of what sizes (e.g., Eisenberg, 1978), to either detailed physiological studies of how much materials the different life forms and species need and use, or to detailed studies of what they as individuals and populations are actually harvesting in the forest and how the cessation or intensification of this harvest would influence the vegetation. In short, we need natural history of the animals and their guts, with emphasis on the effects on vegetation. The content of the recent symposium on arboreal folivores (Montgomery, 1978) makes this very clear.

EATERS OF SEEDS

I have no doubt that, per gram eaten, the seed predators have the largest impact on tropical forest structure of any animal life form. In absolute overall effect they also probably have the largest impact as well. Just as the consumers of living vegetative parts have to deal with an incredible mixture of nutrient and chemical defense qualities, so do the seed predators (Janzen, 1978a). In addition, the seed predators have to deal with a food type that is usually absent for most of the year, is often absent or highly fluctuating in density from year to year (Janzen, 1978b), may be superabundant when present, and much scarcer in space than are the adult trees (since many individual adult trees do not bear fruits in a given year).

Most tropical seed predators can be grouped into three life forms: those that eat developing embryos in the developing fruit, those that eat full-sized nearly mature seeds, and those that act as post-dispersal seed predators.

Predators on young embryos

Aside from the large folivorous vertebrates that sometimes eat young green fruits along with the foliage or deliberately pick immature green fruits out of foliage, predators on young embryos are generally moth larvae (Lepidoptera) and sucking bugs (Coreidae, Lygaeidae, Pentatomidae, Pyrrhocoridae). In the former case, the caterpillars mine through the ovaries or web inflorescences together and eat many flowers and young fruits (e.g., Bawa and Opler, 1978). In the latter case, the attacked seeds (in a multiple-seeded ovary) appear to have been physiologically aborted and are often censused as such rather than as victims of sucking bugs. This type of seed predation is perhaps the mildest per seed killed because the parent plant has invested relatively little in fruit and seed at this stage, and because there is the possibility that it may be compensated for by the retention of other seeds or fruits that would have been aborted to tailor the fruit crop size to match food reserves or anticipated resource harvest. The moth larvae that eat very young seeds and fruits tend to be very stenophagous, but the bugs who play this game are often very euryphagous with respect to Latin binomials. They are avoiding most of a plant's unique chemical defenses by sucking from growing tissue, which is a tissue very likely to be similar among plant species (much as is the sapwood of tree trunks).

Predators on full-sized maturing seeds

Moth (Pyralidae) and beetle larvae (Bruchidae, Curculionidae, a few Cerambycidae) have specialized at eating full-sized maturing seeds while living inside them or their fruits (Janzen, 1980b), while squirrels, monkeys and parrots have specialized at eating them while living outside and moving from tree to tree (Emmons, 1975; McKey, 1978; Higgins, 1979). The insects tend to produce a single generation on a given seed crop, and then wait out the remainder of the year as active adults in the habitat. The amount of damage they do is generally related to the size of the seed crop (large seed crops may either swamp the ovipositional abilities of the arriving females or attract inordinate numbers of them), proximity of other seed crops in time and space (which may either dilute the number of arriving females or serve as a source for ovipositing females), and the suitability of the habitat in the vicinity of the seed crop for seed predator survival. The amount of damage done by the vertebrate seed predators involves these three parameters, but a fourth is also very important; the longer the immature but full-sized seeds are on the tree the more of them are eaten, thereby selecting strongly for rapid and synchronized seed and fruit maturation. That is to say, the functioning of predator satiation has a strong temporal component.

Predators on full-sized seeds have to deal with a wide array of seed secondary defensive compounds (Janzen, 1978a) and must have a wide variety of physiological and biochemical mechanisms for dealing with them (e.g., Rosenthal et al., 1976, 1977, 1978). In general they are highly stenophagous; for example, in a survey of seed-eating beetles in the deciduous forests in Guanacaste Province, Costa Rica, I found that of 110 species of beetle seed predators, 75% had only one host species, 13% had two, 8% had three and the maximum was eight in a flora of 975 plant species (Janzen, 1980b).

The vertebrate seed predators, on the other hand, are as euryphagous as their more folivorous relatives and seem to overcome seed defenses by having guts highly skilled at the necessary biochemistry and by being able to consume relatively small amounts of each species owing to the high nutrient content of the food (see especially McKey, 1978 on this point).

Pre-dispersal seed predators are relatively common and as a rough estimate attack a third to half of the species of seed crops in a lowland tropical forest on normal soil. In the deciduous forest study mentioned above, about 20% of all species of plants in the forest have pre-dispersal seed predation by insects and another 20 to 40% are attacked by some vertebrate. Percent seed predation within a crop is very difficult to determine unless very close watch is kept of the fruit and seed crop during its development. Immature fruits opened by vertebrates are often shed early and rotted away by the time the intact fruits fall or dehisce. Apparently intact seeds often have developing or dead insects inside of them (X-ray works well to detect these animals). Fruits with insects inside are often shed slightly earlier than are mature fruits and seeds, and if the sample is derived from this or early fallen fruits, a very misleading percent mortality may be obtained. Simultaneously, dispersal agents are often adept at removing the healthy fruits with intact seeds, which biases the sample percent mortality upwards in a crop of ripe nuts on or below the parent tree.

In short, pre-dispersal seed predation on nearly mature seeds reduces the size of the final seed crop and kills offspring on which maximum parental investment has been bestowed. Furthermore, the parent cannot replace the dead offspring with new ones even if it can physiologically perceive the death of its offspring, since fruits generally mature long after flowering occurs. I suspect that it is escape from both insect and vertebrate pre-dispersal (as well as post-dispersal) seed predators which is the driving selective pressure behind much of tropical tree species' mast-seeding at supra-annual intervals (Janzen, 1974, 1976c, 1978b). It is therefore these animals which are in great part responsible for the highly pulsed input of seeds into many tropical forest habitats, a pulsation that should influence regeneration patterns and abundance of frugivores and other users of fruits and seeds. This pulsation also renders impossible the measurement of total harvestable productivity in a forest with any kind of study extending over only a year or two.

Post-dispersal seed predators

During and after seed dispersal the vertebrates become prominent as seed killers. Part of this seed predation is pure seed predation and part of it is the price paid for dispersal. Which interpretation is to be given to a given act of seed predation depends on the animal's species and state and on the species and location of seed under consideration. Baird's tapir (*Tapirus bairdii*) is a pure predator of *Mastichodendron capriri* seeds (by mastication), a 78% predator (by digestion) of *Enterolobium cyclocarpum* seeds, and apparently a pure disperser of fig seeds (Janzen, 1981c). Oil-birds are killers of the seeds in the fruits they feed to their nestlings, since these seeds are regurgitated to the floors of caves, but dispersers of the seeds (an unknown percent) that they consume and regurgitate while in flight in the forest (Snow, 1976). The agouti (*Dasyprocta*) is a predator on *Scheelca* palm nuts (seeds) but buries many for later consumption; some of these dispersed seeds are missed and become the recruitment into the palm population (Bradford and Smith, 1977). However, even this interaction may be only a remnant of a more complex Pleistocene one (Janzen and Martin, 1981).

Post-dispersal seed predators are of course confronted with the same seed chemicals as are the late pre-dispersal ones (though there may be some chemical changes as a seed matures) and may have to deal with a much harder seed coat or nut wall. However, the physical location of dispersed seeds is much more diffuse than that of the seed crop on the parent. The forest floor is constantly being searched by insect seed predators (sucking bugs, ovipositing beetles). These insects treat the seeds they find much as do the pre-dispersal seed predators but they will search until they exhaust the seed supply or the seeds escape by germination since a dispersed seed does not leave them behind. The bugs appear to be euryphagous within a set of closely related seeds, e.g., seeds of *Bombacopsis*, *Sterculia*, *Ceiba* and other Malvaceae and Sterculiaceae are preyed upon by Pyrrhocoridae (Janzen, 1972a), while legume seeds are preyed on by highly stenophagous beetles.

Peccaries (*Tayassu*) and forest-floor rodents are major predators on dispersed Neotropical forest tree seeds. The peccaries use odor and landmarks (such as the stumps around which agoutis have buried seeds) to locate seeds and nuts in the litter (Kiltie, 1981). Even extremely hard palm nuts are cracked by white-lipped peccaries (Kiltie, 1979). It is my impression that the large soft seeds enclosed in a very hard nut are usually poorly defended chemically (e.g., Malaysian *Lithocarpus*, African *Coula edulis*, Neotropical *Astryocaryum* and *Acrocomia* palm nuts).

While agoutis have received a great deal of attention as dispersers and killers of large seeds on the forest floor (e.g. Smythe, 1970) small heteromyid rodents, such as *Liomys salvini* in Guanacaste, Costa Rica, deciduous forests, are also impressively deadly. Captive *L. salvini*, weighing only 45 to 60 g, may consume as many as 15 to 20 newly germinated seeds of *Enterolobium cyclocarpum* per night to maintain their body weight. A *Liomys* will even keep itself alive by consuming 4 to 8 hard ungerminated 0.5 to 1.0 g *E. cyclocarpum* seeds per night and notching the remainder so that they will germinate for future meals (W. Hallwachs, pers. comm.).

The interaction between *L. salvini* and *E. cyclocarpum* illustrates well the behavioral complexity of prey location in this portion of the forest food web. *L. salvini* harvests *E. cyclocarpum* seeds directly from the fruits fallen below the parent tree. But these are the fruits that were not eaten by large mammals. Horses and cows are contemporary dispersal agents and digestive seed predators (and the horse is a Pleistocene one, see below) and defecate *E. cyclocarpum* seeds in a variety of habitats along with a huge odor cue, the pile of dung. *L. salvini* quickly seek out these piles and burrow through them after seeds. As many as six *Liomys* may arrive at one pile of horse dung the first night, and they may remove as many as 500 *E. cyclocarpum* seeds from a dung pile in one night. An *E. cyclocarpum* seed has three hopes: to be dumped in a habitat lacking *L. salvini* (e.g. in a river by a tapir that ate the fruit; Janzen, 1981c), to be buried shallowly by the dung beetles (Scarabaeidae) as they go about their work, or to be cached by a *Liomys* that is shortly subsequently eaten by a predator (Janzen, unpubl.).

FLOWER VISITORS

The tropics are famous for the complexity and spectacular nature of their flower–visitor relationships, most of which are based on the animal providing outcrossing and the plant providing food. The bees (Hymenoptera) form a fairly distinct subset of the trophic web. These flying penises prey exclusively on pollen and drink nectar (sugar, protein- and/or oil-rich; and see Baker, 1978) and only connect directly with the trophic web by being prey for some predators and parasitoids and by being models in many mimicry systems. Also, as with other flower visitors, bees form a tight but diffuse connection with the general food web in that resources spent on them (production and strategic costs of flowers, nectar, pollen) are resources not available for defenses, repair of damage by herbivores, seed production, etc. They thereby constrict the size of the base of the food web that is used by consumers of other plant parts.

Most other flower visitors have at least one stage or time in their life when they feed on something quite different from flower nectar and/or pollen. *Heliconius* butterflies have larvae that are major parasites on *Passiflora* vines, the flowers of which are not visited by *Heliconius* (Gilbert, 1975). The *Glossophaga* bats that pollinate *Crescentia* flowers eat many insects (Howell and Burch, 1974; Heithaus et al., 1975) and are fig seed dispersers as well. Hummingbirds (Trochilidae) and sunbirds (Nectariniidae) are expert insect hawkers (Skead, 1967; Stiles, 1973; Gill and Wolf, 1975). Fig wasps (Agaontidae) that pollinate fig florets are also intense fig seed predators (Janzen, 1979b). *Polybia* wasps are intense predators on caterpillars and male ants yet visit flowers frequently for nectar. Being a system very poor in wind-pollinated species (i.e. cheap pollen flow between conspecifics standing shoulder to shoulder) tropical forests abound with complex systems for moving pollen via animals among widely dispersed individuals. However, the aspect of interest is not the actual food or its small cost to the total tree resource budget but rather the large influences that can be gained with such small expenditures of resources. For example, it is probable that fig trees are reliably outcrossed over distances of many kilometers and at extremely low densities of flowering individuals by releasing a pheromone that serves as a locator cue to the minute wasps that have just left a far distant conspecific (Janzen, 1979b). The amount of resource allocated to pheromones in a fig tree's budget is probably minute, yet this one trait may be in great part responsible for *Ficus* being one of the largest tropical tree genera (over 900 species), for *Ficus* occurring in almost every kind of tropical forest, and for *Ficus* being a common tree genus in most forest types around the tropics of the world (Janzen, 1979b). Certainly bats, birds, large moths and large bees move pollen over distances of 0.1 to 1 km or more (e.g., Janzen, 1971; Feinsinger, 1976, 1978; Frankie et al., 1976; Gould, 1978; Stiles, 1978) in return for a small fraction of the total plant budget. Furthermore, since the plant approximately controls the amount taken per unit photosynthate eaten, a much larger portion of the food web should be contributed by these animals than by consumers which generate large strategic losses, large insurance costs, and much literal waste. All three of these latter categories are losses to the plant yet support no part of the trophic pyramid.

There is another reason besides the dual trophic role of many species of flower visitors that interactions with flower visitors are one of the most interactive parts of tropical forest food webs. To the plants, flower visitors are a resource to be competed for. They therefore are one of the major causes of both synchronized flowering within species (e.g. Augsperger, 1978) and asynchronous flowering between species. Both these patterns should in turn strongly influence the availability of reproductive and vegetative resources to other consumers. Furthermore, since flower visitors are not under the complete evolutionary control of the trees, they may well prevent or constrain many of the imaginable patterns of tree behavior (as well as spatial distribution) in a tropical forest. Yet, dipterocarps seem to have solved the problem of synchronized outcrossing at many-year intervals even in a forest very rich in dipterocarps. They are pollinated by thrips (P.S. Ashton, pers. comm.), which presumably feed on some vegetative plant part during the years of flower absence. Thrips are hardly more than animate wind. However, the chances of such a system arising to meet the needs of tree spacing and timing patterns in more normal tropical forests are much lower than are the chances of the evolution of more conventional plant–pollinator interactions.

SEED MOVERS

Seed movers, or dispersal agents are analogous in many ways to flower visitors. Many seeds are effectively contaminants of the disperser, stuck on the outside or imbedded in the digesta on the inside. Many of these are killed by being shed, regurgitated, or defecated in the wrong place, or by being digested as a minor part of the potential disperser's diet. Others are more deliberately carried off to be eaten at a later date but survive through errors of recovery by the owners (agoutis and *Liomys* mice are the bees of the forest seed world). Just as many tropical flowers are conspicuously engineered to keep out the bulk of the animals that would eat their nectar and pollen if they could gain entry, a given species of ripe fruit is undoubtedly designed by natural selection to be uninteresting or even distasteful to the majority of the frugivores in the habitat (Janzen, 1975). It should be designed to be attractive only to that set of seed and fruit consumers that, working in consort, generate the highest quality seed shadow for that parent tree. However, just as there are many flower visitors that get to a flower's rewards through the channels opened for the pollinators, fruit eaten by undesired animals is probably a major part of the fuel that runs the animal array of a tropical forest. For example, Howe and Vandekerckhove (1979) have found only one bird to be a likely high quality seed disperser for the deciduous forest shrub *Casearia corymbosa*, yet fourteen species of birds eat the fruit. Even the carnivores eat fruit — bats and birds that feed insects to their offspring and eat some themselves are often heavy fruit eaters as well. Even proper Carnivora such as jaguars, tayras, coatimundis, jackals, and tigers are heavy fruit eaters (just as are northern bears and foxes).

The numbers and species of vertebrates that subsist entirely or in large part on ripe fruits (with some green ones thrown in) vary enormously among tropical forest habitats. The rain forests of

Panama, perhaps most closely studied for primates, bats and birds (Hladik and Hladik, 1969; Karr 1976; Morrison, 1978) literally teem with frugivores while they are scarce in the Malaysian forests rich in Dipterocarpaceae on very poor soils (Janzen, 1980a). Yet the Indian–Southeast Asian–Australian tropics are (were) extremely rich in large fruit-pigeon numbers and species while the neotropics hardly have any; neotropical forest parrots (all Psittacidae) are very abundant in species and numbers primarily as predators on full-sized maturing seeds, while they are scarce in numbers and species in the Southeast Asian tropics. All of the large terrestrial vegetarian mammals in Africa eat many species of fruits, and disperse as well as prey on many species of seeds in the process; an analogous fauna is by and large missing from the neotropics after the Pleistocene megafaunal extinctions (Janzen and Martin, 1981).

Likewise, what they eat varies greatly among groups of frugivores. Small to medium-sized birds that eat many insects as well as fruits tend to be heavy consumers of small-seeded juicy fruits rich in sugars and vitamins; various fruit specialists of all sizes consume many species of fruits whose pulp is rich in oil and protein (McKey, 1975; McDiarmid et al., 1977). These seeds are often very large and are often regurgitated rather than passed all the way through the digestive tract. The large indehiscent relatively dry legumes and other fruits that are picked up off the forest floor by large mammals are very different in flavor and consistency from the large juicy fruits eaten by large forest primates. While one species of fig may be fed on by tens of species of birds, bats and mammals, another species only a few meters away may have its fruits eaten solely by squirrels.

Animate dispersers of seeds generate very different seed shadows than does wind, the wind that is such a prominent disperser of extra-tropical seeds (though there are many tropical wind-dispersed seeds as well). Animal-generated seed shadows tend to have large lacunae with no seeds and strong local peaks at resting places, sleeping places or other high concentrations of animals (e.g. Janzen et al., 1976). Such seed shadows can be attenuated in time far past the time when the mature fruits appeared on the tree, owing to the delay in passage through the animal gut. This delay may be as much as two weeks or more in a large vertebrate (Janzen, 1981c). Seeds dispersed by animals may be especially conspicuous as when in piles of odoriferous dung, or especially cryptic as when buried individually by rodents. Animal-generated seed shadows often contain much heavier seeds than those dispersed by wind, and animals will orient the directions of their movement in response to many different variables rather than a single major direction as is often the case with a tropical wind-generated seed shadow.

The composite seed shadow generated by the entire forest is the base of the food chain for a large number of animals. In short, the forest supports these animals rather than a seedling lawn. When the animals are missing, as when a seed and seedling species is very well protected chemically (e.g. Rankin, 1978), the vertebrates have been hunted out (e.g., many African forests), the forest is on an island (e.g. Janzen, 1972b), or the vertebrates are largely missing because of low or too pulsed seed production (e.g. Janzen, 1974), the seedling lawns are truly impressive. In these cases the bulk of the plants die through intra-specific competition and a much greater and different form of nutrient flow enters the detritivores in the form of dead seedlings rather than as feces and carcasses of seed predators.

Fruit is a peculiar kind of food. Not only should it be engineered to be ignored by most of the animals except those that will put the seeds in the right place, it will have odd nutrient traits for the animals that should eat it. It must be rich in those chemical traits that make life difficult for microbes (Janzen, 1977). It should be rich in some nutrients and very poor in others; the optimal fruit will be an important yet small part of the diet of an animal who will deposit the seeds elsewhere while in search of its other resource needs. The worst fruit would be one that would allow the dispersal agent to sit in or near the parent tree and satisfy all of its dietary needs. Ironically, some fruit bats and figs may represent such a combination (Janzen, 1979b). If it were not for their need to roost in cavities, and (inexplicably) to carry the fruit away from the fig tree before eating it, bats would be terrible dispersal agents for the figs that they seem to be able to subsist on for long periods. Since humans are very fond of sugar, water and vitamin-rich fruits (even tending to call the others vegetables: avocados, eggplants, peppers), we have a fairly biased image of a tropical fruit as something that is rich in calories and water. A very large number of species of wild tropical fruits, however, is protein- and oil-rich and supports a set of birds that get the bulk of their food from these "foul-tasting" fruits [e.g., trogons, toucans, puff-birds, cotingas, oil-birds, bell-birds, manakins in the neotropics (McKey, 1975; Snow, 1976; McDiarmid et al., 1977)].

ANIMAL PARASITOIDS

In discussing whole tropical forest ecosystems, insect parasitoids (tachinid flies, parasitic Hymenoptera, etc.) would appear to be hardly more than a fine fuzz sprinkled across the upper reaches of the food web. The amount of nutrient and caloric resource they process is minute compared to the resource budget of a large tree. However, as with many seed-eaters, bud-biters and pollen carriers, the parasitoids have an enormous potential influence on which of the many potential players is on stage in a given tropical forest act. And since the players vary greatly in their contribution to the form of the overall ecosystem, this is not a trivial influence.

Tropical parasitoids have life cycles like those of extra-tropical ones. They lay their eggs on, in or near a host insect, the larvae develops on or in the host and eventually kills it, and the adult emerges shortly thereafter from a pupa or cocoon inside or near the debris from the dead host. As an adult, the insect is usually a flower visitor for nectar (and pollen?) while it searches for new hosts.

However, there is mounting evidence (Owen and Owen, 1974; Janzen, 1981d) that parasitoid species richness does not march ever upward as the species richness of the total pool of available prey rises in moving from extra-tropical to tropical regions of the earth. A theoretical explanation seems to be in order here. Parasitoids are numerically much less abundant than their hosts. As we move into the tropics, the increase in potential prey species richness is associated with a severe decline in the average density of a prey species. This means that the parasitoids must either exist at an even much lower density, become more euryphagous, or become more adept at prey location. All three undoubtedly occur, but one cannot expect all parasitoids to meet the challenge over evolutionary time. All three challenges mean that parasitoids should become progressively proportionately rarer as the species richness of potential prey rises. Associated with this, for example, I have found that the greatest species richness of Ichneumonidae (a major hymenopterous parasitoid family) per unit area lies between about 37.5 and 42.5°N latitude in North America (Janzen, 1981d). I am finding that many species of potential prey (seed predator beetles in the Bruchidae and Curculionidae) seem to have no parasites in the lowland deciduous forests around Santa Rosa National Park (Janzen, 1980b).

We do not yet know enough of the interactions of tropical parasitoids with wild host populations to even guess the consequences of increased euryphagy and comparatively reduced parasitoid species richness with decrease in latitude. However, it should make one very wary of extrapolating from extra-tropical systems of parasitoid and host populations. It may well be that fluctuations of tropical host populations are much less influenced by parasitoids than is generally believed of their northern relatives. Likewise, it may well be that the future of biological control of crop insects in tropical systems lies more in manipulating the spatial and temporal juxtaposition of plants inedible and edible to the pest than in augmenting populations of parasitoids and arthropod predators.

CARNIVOROUS PREDATORS

The tropics are famous as a place of intensive and extensive predation by carnivores, leading to such things as large and exact mimicry complexes, amazing camouflage, elaborate escape behaviors, etc. (Robinson, 1969; Rettenmeyer, 1970; Andrews, 1979). From the viewpoint of food webs, however, this may mean little more than that there is less prey escape generated by unequal seasonal depression of predators and their various prey species than in extra-tropical areas. It may also mean that a given biomass of potential prey supports a smaller biomass of predators than does the same amount of prey in more northern areas. It is striking that tropical forests are particularly poor in those masses of highly edible prey that are so abundant in the spring in northern climates, and form the basis of the food web for so many northern predators. Aphids, large numbers of conspicuous and edible caterpillars and grasshoppers, masses of nesting birds, periodical cicadas, mayfly emergences, hordes of small rodents in peak years, passenger pigeons, salmon runs, etc., are prey types that are by and large missing from tropical forests. Termite swarms, at best an evening or two in duration, are about the only easily available and poorly protected analogue. Of course there is the odd year or place where caterpillars or grasshoppers, for example, are very abundant but these are very often highly distasteful insects and their location in time and space is highly unpredictable.

While it is difficult to ascertain the impact on the ecosystem of carnivore density heterogeneity among tropical habitats, it is certainly true that it exists. Small Caribbean islands are disproportionately rich in carnivorous insect groups (Janzen, 1973; Becker, 1975) and very poor in vertebrate predators. Presumably this is because the former are good at starving and the latter are poor at swimming. Africa contains conspicuously more species and biomass of predators on small animals such as snakes, lizards, mice, nesting birds, etc., than are found in comparable neotropical habitats. I have hypothesized that this is due to the living and dead large herbivores aiding in keeping the density of carnivores high in Africa (Janzen, 1976d), and have postulated that the greater predator density is responsible for the apparent lower density of lizards, snakes, bird nests, wasp nests, etc., as compared to similar neotropical habitats. Habitats with apparent low primary productivity, such as those growing on white sand soils in Asia, Africa and the neotropics, tend to have conspicuously reduced number and species richness of both carnivorous vertebrates and insects (as well as scavengers) (Janzen, 1980a).

It is certainly true that the tropics contain some extremely long food chains, but I suspect that this is brought out by the predictable presence of certain components of the system rather than the size of the base of the food pyramid. Furthermore, the long food chains in the tropics certainly cannot be thought of as standing on their own as populations subsisting free of the remainder of the food web.

In the following Central American food chain, it is obvious that there are as many lateral moves as vertical ones: sun to *Enterolobium cyclocarpum* fruits to *Liomys* mice to *Bothrops* viper to colubrid snake (Colubridae) to ocelot (*Felis pardalis*) to large boa. All four of the carnivores are taking prey from all potential levels of the food web except the plant (and even ocelots eat fruit).

INTEGRATION

Observers of ecosystems are fond of documenting how much energy or resource flows through the various linkages described in earlier pages, and how much accumulates at various points in the ecosystem. The driving emotion for such a query or documentation is easy to locate. It lies in the insatiable human, and very human, trait of really only caring about nature to the extent it yields resources that raise our fitness or that of our extended families. That is to say, ecosystem research is basically a harvest exercise. As such I find it totally uninteresting and therefore shall not waste space on harvest questions such as what is the productivity of the animals in a tropical forest, or what is the productivity of a tropical forest with and without its animals, or what is the standing crop of carnivores as compared to herbivores, etc.

However, ecosystem biologists do on occasion ask a question that is of more general interest as well. They ask things like what role do the parasitoids, the seed predators, the leaf eaters, etc. play in the ecosystem? Of course they play no role, but we can avoid that philosophical confrontation by asking what would happen in a forest were the fruit eaters, the flower visitors, the tapir killers, etc., to be magically removed or augmented. The answers will be of interest to both those who wish to harvest nature and to those who wish to understand her. In a real sense, I would like to ask what is the effect of a mutation that results in change in the relationships described or alluded to in the previous sections.

There are at least three ways to ask this question: logic, experiments, and observation of natural experiments. This is not the place for an essay on the relative merits of these three, rather it is my opinion that we know so little about the real world in tropical forests that logic is by far the poorest pathway and should be used only as a last resource. All the inference we can bring to bear may dictate that catastrophic disturbance and random colonization processes are adequate to "explain" the structure of tree species relationships in a tropical forest (Connell, 1978; Hubbell, 1979) but we will only know why *Enterolobium cyclocarpum* is a rare tree and found only in very select habitats adjacent to 300 other species of trees when we know the frequency distributions of what, how and when, destroys the thirty million large seeds, seedlings and saplings produced by the adult tree in its lifetime.

In short, then, what would be the effect of the removal of various subsets or all of the food web described in earlier sections on a tropical forest? Perhaps the most extreme case would be the removal of the herbivores that are parasitic and predaceous on plants. On a contemporary time scale, the absence of herbivores would lead to an immediate choking of the understorey with seedlings from the many surviving seeds and from the enlarged seed crops that come about due to no repairs and losses to leaf- and stem-eaters. This should result in more litter, more litter degraders, and intense competition among seedlings and between seedlings and the species of plants that normally pass their entire developmental cycle in the understorey (such is presently visible in Malaysian dipterocarp forest). Even a dying seedling takes up resources. The increased volume of roots and mycorrhizae, fed not so much by self-harvested resources as by seed reserves, should result in more thorough capture of minerals released by detritivores. The species composition of the understorey should change, since some of the usual residents will not be able to cope with the diffuse competition from the sudden influx of invaders. The species composition of the overstorey, whether from trees coming up in tree falls or from interstitial species insinuating their crowns into the canopy, should change rapidly as the numerical aspects of inter-specific competition change; species whose seeds and seedlings suffered no mortality from animals will suddenly have to endure many competitive bouts with species that previously they only rarely encountered. The increased density of seed shadows should result in the low probabilities of survival in this or that microhabitat being multiplied by numbers of tries quite high enough to result in whole successes. All of this assumes the fairly unlikely case that the dispersal agents and the pollinators will be up to harvesting and moving this suddenly increased seed and pollen resource. Their failure, guaranteed to be heterogeneous in quality and quantity, will increase the difficulty of predicting the outcome in species composition and relative abundances of the winners, though it will not necessarily make the system more stochastic.

Certain habitat-wide traits can be expected to change as well. The species richness of trees at a site should decrease because the increased number of reproductive tries and the increased intensity of trying should speed competitive bouts (and therefore speed the rate of arrival at equilibria) and should allow the best competitors for microhabitats to attain their maximum density as they will not be suffering from density-dependent disease and pest problems. The standing crop of adult plants on the site should probably not change except to the degree that reserves not needed for repair are channelled into vegetative growth rather than sexual reproduction. The poorer the habitat, the less of this type of change there should be, since the poorer the site the more of the budget must be going into vegetative parts of the plant. I would also expect a reduction in the finer kinds of variation in plant life form, since there are a smaller number of "best" kinds of life form if there is a smaller number of kinds of challenges facing the plants.

Over evolutionary time, the latter reduction should be even more intense. Non-biotic challenges and resources tend to be relatively monomorphic within a habitat and change little over evolutionary time compared to biotic challenges. Selection for the diversion of resources from repair, defense and sexual reproduction should result in a few super-competitors for the homogeneous resources characterizing a habitat. It is not hard to envision thousands of square miles of *Phyllostachys* bamboo in a tropical Indian deciduous forest habitat or the same of *Brosimum utile* in a Costa Rican lowland rain forest, with each doing most of the replacement in the occasional tree falls as senescence occurs (much as is the case in some monospecific tropical forest stands today). At present we can only examine island floras for evidence to support this scenario, and none have been examined with this in mind.

On a less dramatic, and therefore more focused scale, the late Pleistocene extinction of much of the neotropical herbivorous megafauna (and its associated carnivores) was a true experiment over nearly evolutionary time in trophic ecology (Janzen and Martin, 1981). The seeds these animals used to disperse probably lay rotting in fruit, were eaten by small seed predators, or died as seedlings in competition with the parent tree. The parental tree species populations probably shrank in area and density to extinction or to those habitats where dispersal was minimally necessary. In a few cases, what had been trivial dispersal agents (e.g., perhaps agoutis with *Scheelea* palm seeds) became major ones. As the plants dependent on the large mammals dwindled in density and area of coverage, I expect that others took their place through expanding populations and occupation of new microhabitats. The understorey palms, so abundant in species and individuals in neotropical rain forests, are probably one such group of plants. Wind-dispersed species are probably others. The reduction in frequency of small tree falls trampled and browsed open repeatedly by proboscidians and other large forest herbivores would surely have had a depressant effect on vines and herbaceous upright plant species richness and density in mature forest. Moving up the food chain, it is easy to postulate that the same fauna of small carnivores, as is found today in Africa, with its postulated depressant effect on other small animals, would have occurred in the neotropics in the Pleistocene and its removal has led to the lizard-rich habitats we see today.

In yet another scenario, I can ask what would happen were I to hit the food pyramid at its very base, by reducing the substrate nutrient quality to that represented by silicon sand as is indeed found in the so-called "white sand and blackwater river" regions of the tropics today (Janzen, 1974). Throughout such forest we find the lavish displays of fruits and flowers, so common in many microhabitats on better tropical soils, to be largely absent; with them go the insects and small vertebrates that depend on them. But then, perhaps it is the other way round; dependency on other forms of pollination and dispersal take prominence as the overall level of food offered declines, leading to an ever-greater downward spiral. When such a forest is cleared by landslide, flood or other agent, the replacement rate is excruciatingly slow — peoples living in such areas regard a meter regrowth of early successional vegetation per year as phenomenally high. This means that the leaf-eaters from cows to caterpillars have slim pickings and what they pick is slow to be replaced.

Moving up the food chain in such a forest I expect the top levels to be worst hurt. Not surprisingly, scavengers should be few and especially proficient at surviving long fasts between meals. The aerial insect pickers should be scarce along with the foliage gleaners. Seed escape from the few seed-eaters present should be especially easy through satiation generated by high inter- and intraspecific synchrony of seed production at long intervals, long intervals being required to store enough reserves to make a large seed crop. Again, as with flowers and fruits, this should make life particularly difficult for the seed predators because even if there is a high average amount of food coming in, it comes at pulses too long for the animal machine to easily average it through fat storage, dormancy and migration (pigs seem to be about the best at all three).

But whence the pollinators for the large-scale flowerings that must accompany the large-scale seedings? Wind or wind-like organisms (animals that can subsist on other foods in between) will have to do it. But then again, cross-pollination may be of lesser importance in this land of reduced biotic challenge where the survival game is played by dormancy, excessive chemical defenses, slow growth rates, and edaphic specialization. Why edaphic specialization? If there is little or no escape from seed predators by distance movement, local timing and pattern, then it is by satiation, which by its very nature means that most seeds end up in the immediate vicinity of the parent. Here, then, there should be strong selection for a dispersal system that moves the seed just past the crown of the parent and into the area occupied on average by the soil type that supported the parent. Here the seedling will have to compete largely with sibs and conspecifics, and thinning will be achieved by crowding rather than intensive seed predation and herbivory. But if there is strong selection for competitive ability in the exact micro-habitat of one's parent, then the best genes to carry are likely to be those of individuals surviving close to your parent or even those of your parents. In losing the animal interaction we have lost a substantial fraction of the reason for continually trying out new combinations and for being open to receive those found successful by conspecifics.

This is not the place to discuss the various experiments that agricultural humans inflict on tropical forests. I have tried to outline some of the ways that the trophic web interacts with tropical forests and with itself. If there is any message to the agricultural experimenter it is that tropical vegetation and the animal interactions it contains tends to be highly tailored to the habitat. Predictions of outcomes have to be cast in percent yes and percent maybe and percent no. Pull the elephants out of a highland rain forest, a lowland rain forest and a lowland deciduous tropical forest and the species richness of trees may go down, stay the same and go up respectively. Put an irrigation ditch through a deciduous forest and the density of malvaceous seed predators will rise and the density of leguminous seed predators will fall. Put a 1-ha bean field in rain forest and the two may have virtually no insects in common after six months; do the same in deciduous forest and most insects in the bean field may also be found in the forest (in the rainy season, if there are any bean plants left). Superimposed on this stochastic heterogeneity, the best way to fulfil human highly idiosyncratic demands becomes virtually impossible to predict. For one society, the best replacement of its forest will be cattle ranches, for another a twenty species mixed plantation of cabinet-grade timber, and for a third simply a large sign introducing the world's finest museum of the organisms and interactions that produced *Homo sapiens* and all his friends and relations.

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