36

1988. Tropical Rainforests: Diversity and Conservation.
California Academy of Sciences and AAAS, F. Almeda and
C. M. Pringle, eds., 306 pp. San Francisco, California.

COMPLEXITY IS IN THE EYE OF THE BEHOLDER

#283

DANIEL H. JANZEN

Department of Biology, University of Pennsylvania, Philadelphia, PA 19104

Complexity in biological systems cannot be measured by the number of species present, even though this parameter is traditionally used as an intuitive measure of complexity. What matters in complexity is how many kinds of organisms a given organism recognizes in its interactions with those organisms. Likewise, what matters is the number of species that a species is linked to in the habitat, since this number determines in part how much of a change in one species will be perceived as a change by other species. These generalities are illustrated with examples from the saturniid moth caterpillars and their predators and parasites in a Costa Rican dry forest in Santa Rosa National Park. It is possible to conclude that, for example, to a foraging bird, a tropical habitat rich in caterpillar species may be no more complex than is an extra-tropical habitat poor in species; ten species of green and edible caterpillars may be perceived as identical to 100 species of green and edible caterpillars.

Complexity is also related to the number of links and demographic patterns in food webs that are affected by the removal of a link. Owing to evolutionary conservatism, traits are often retained long after the events that selected for them have disappeared. This type of complexity in food webs and time is illustrated by considering the ecological impact of extinction of neotropical dispersal agents. The Pleistocene extinction of the horse probably caused substantial changes in the demography of the plants whose seeds it dispersed, and this in turn should have affected the demographies of the other animals that were dependent on those plants, which should in turn have affected the demographies of the other plants those animals serviced, etc. The example is then carried further by viewing the seemingly unoccupied Australian dry tropics as in fact a landscape that has suffered mass extinction of species and habitats through 30,000 years of dry season burning by indigenous peoples. Its complexity is the most difficult of all to see.

Copyright © 1988, California Academy of Sciences.

"Complexity" is often used to describe tropical forests. Its companion, great species richness, is used no less commonly. Just what is complexity? Is it in fact a long list of Latin binomials, the raw material for the trait of great species richness? As a tropical field biologist, my reply is that complexity is in the eye of the beholder. The length of a list of "species" in a habitat depends on who you ask. Furthermore, it is not so much how long is the list of species, but how the species interact that is the basis for biological complexity. A habitat whose vertebrates are six species of gazelles is likely to be less complex than one containing two species of gazelles, two species of large cats and two species of vultures. Again, how the parts interact may be very much a product of who is the beholder. There may be no interaction among three species of caterpillars eating three species of plants, but those three caterpillars may be very interactive parts of the diet of a bird that feeds on all three of them. Finally, the complexity of a tropical habitat is not something intrinsic to the site, but rather a delicate construction that changes as the ecological forces at a site change. These forces may no longer be visible to the beholder or even to the experimenter, but it is in the nature of nature that their impact on complexity is long-lasting.

THE SQUIRREL CUCKOO AS ETHNOZOOLOGIST

Santa Rosa National Park is 108 km^2 of dry tropical forest and abandoned pastures in northwestern lowland Costa Rica (Fig. 1). If we ask an insect taxonomist how many species of saturniid moth caterpillars (Fig. 2, and see figures in Janzen 1982a, 1985) occur in Santa Rosa, the reply will be "30 species" (Janzen 1982a), which is half as many as occur in all the U.S. and Canada (Hodges et al. 1983). Saturniids are the biggest moths in the world (Janzen 1984a), and are often called "giant silk moths" (e.g. Gardiner 1982); the cecropia, polyphemus, and luna moth are most familiar to North Americans (Ferguson 1972).

However, Santa Rosa is examined by more than insect taxonomists. The park is occupied by a healthy breeding population of squirrel cuckoos (*Piaya cayana*, Cuculidae; Fig. 3). These medium-size insectivorous birds are specialists at locating and preying on large caterpillars such as those in the Saturniidae.

If we ask an adult squirrel cuckoo how many species of saturniid caterpillars there are in Santa Rosa, it might reply "three kinds." First, there is the kind that when found is simply mauled and eaten or carried home to the nestlings. *Eacles imperialis, Rothschildia lebeau, Othorene purpurascens, Schausiella santarosensis* and *Caio championi* are examples from Santa Rosa. These large caterpillars (full-size *E. imperialis* caterpillars [Fig. 2a], weight 15-25 grams) are harmless to all vertebrate predators (though some are spiny

Fig. 1. Location of Santa Rosa National Park in northwestern Costa Rica. The volcanos that isolate the northwestern Pacific coastal lowland dry forest from the Atlantic rainforest lowlands are indicated by their specific names. The La Selva Biological Station, mentioned frequently elsewhere in this volume, is also indicated.

mimics of urticating caterpillars and therefore rejected by monkeys and perhaps by some other species of birds). They appear to escape mostly by being cryptic and by occurring as widely scattered individuals in the crowns of large trees.

The second kind consists of those caterpillars that are truly dangerous to vertebrates by virtue of extremely urticating spines (to a human, they hurt more than does stinging nettle) (Janzen 1984a,b). The squirrel cuckoo grabs one of these caterpillars (Fig. 2b) at the head with its bill and then bashes the caterpillar on a tree branch until it is quite dead. With death, the turgor

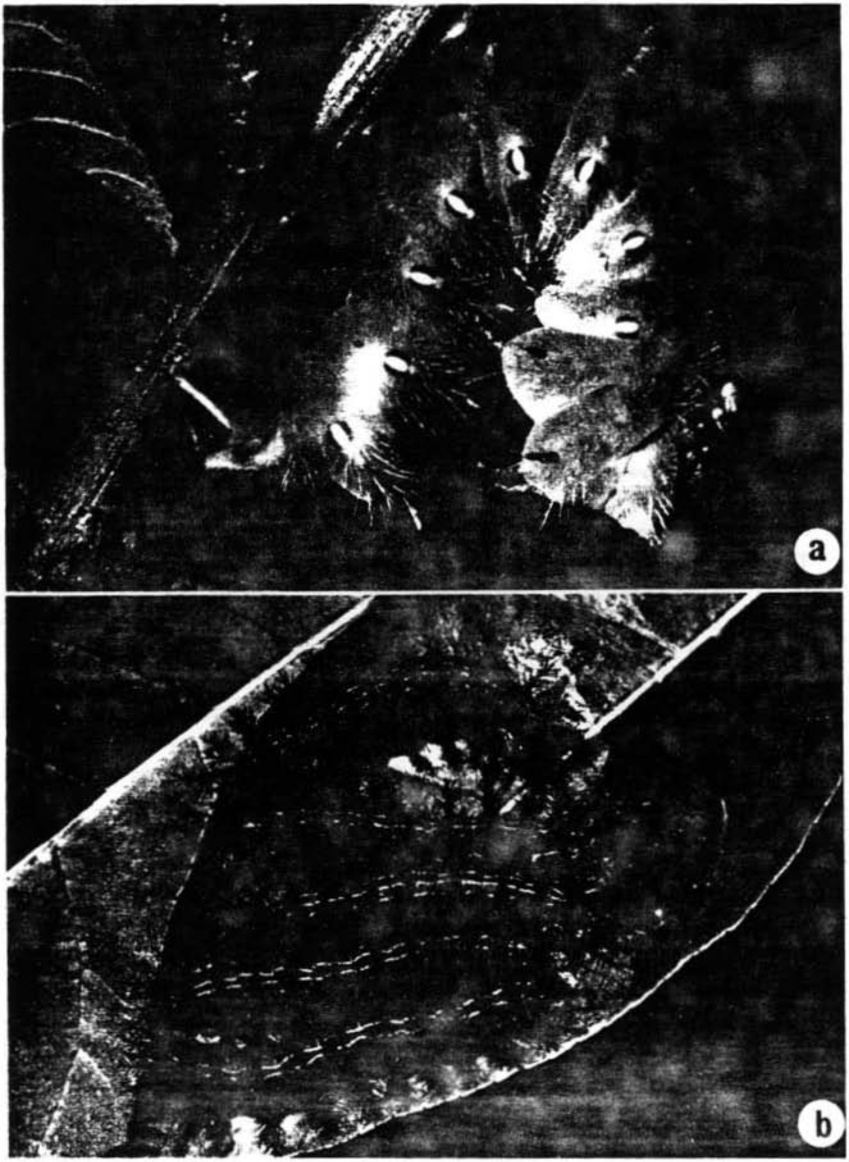

Fig. 2. a. Final instar caterpillar of *Eacles imperialis* (Saturniidae; 90 mm in length). b. Penultimate dark morph urticating caterpillars of *Hylesia lineata* (Saturniidae; 35 mm in length). Santa Rosa National Park, Costa Rica.

Fig. 3. Road-kill adult squirrel cuckoo (Cuculidae, *Piaya cayana*, 31 cm in length, Santa Rosa National Park, Costa Rica). Note the short, round wings and long tail–important features for agile and almost hovering flight in dense vegetation where it searches for caterpillars.

pressure of the body fluids declines and the urtication ability of the urticating spines (which are like liquid-filled syringes) is significantly reduced. The battered caterpillar is then swallowed entire. All hemileucine caterpillars at Santa Rosa (e.g. species of *Automeris, Molippa, Dirphia, Hylesia, Periphoba*) are of this kind. I do not know if the squirrel cuckoo is sufficiently deceived by the saturniid Batesian mimics of these urticating saturniid caterpillars (e.g. the harmless spiny caterpillars of *Ptiloscola dargei* and *Copaxa moinieri* [see figure in Batten 1984]) to process the mimics in this manner before eating them.

Finally, there is the kind of caterpillar that is found but rejected. There are only two saturniid Latin binomials in this category at Santa Rosa–*Arsenura armida* and *Rothschildia erycina*. I have watched adult squirrel cuckoos that were foraging for caterpillars hop within a few cm of large *R. erycina* caterpillars and simply ignore them. *Rothschildia erycina* caterpillars have the brilliant ringed color pattern of a coral snake (e.g. cover illustration of Janzen 1983a), as does *A. armida* (Janzen 1982a). There can be no doubt that the *R. erycina* caterpillars were seen and rejected, rather than simply overlooked. I have not yet witnessed a response to *A. armida* caterpillars, but I assume that these caterpillars are also seen and rejected. They occur in groups of hundreds of extremely ostentatious caterpillars within squirrel cuckoo foraging ranges but are not harvested by them. I assume that the squirrel cuckoo has the same avoidance response as do two other species of Santa Rosa birds that eat large caterpillars, a kiskadee and a motmot: these two birds have been shown to be genetically programmed to fear and avoid the coral snake color pattern (Smith 1975, 1977). I assume that the squirrel cuckoo has the same avoidance response. I hasten to caution, however, that other caterpillar-eating generalist vertebrates do not categorize the Santa Rosa caterpillar array as does the squirrel cuckoo. For example, I have watched the large *Ctenosaura similis* lizards in the same habitat repeatedly consume the brightly colored coral snake look-alikes (*R. erycina*) that are rejected by the squirrel cuckoo.

In sum, the squirrel cuckoo thinks that there are only three kinds of saturniid caterpillars in Santa Rosa. If there were some species of saturniid caterpillars so cryptic that they were never noticed by the squirrel cuckoo, there would also be a fourth kind of caterpillar—but the bird could not know this and therefore would not include it in its reply to your questionnaire.

Squirrel cuckoos also eat species of caterpillars that are in other families of Lepidoptera. The bird's three kinds of caterpillars—those eaten, those processed and then eaten, and those rejected—each include large caterpillars of other families as well (Sphingidae, Noctuidae, Notodontidae, Oxytenidae, Megalopygidae, Geometridae). This suggests that even with 3000-plus species of caterpillars at Santa Rosa (Janzen, in press), our squirrel cuckoo would still at best tell us that there are only three species of caterpillars at Santa Rosa. Furthermore, a medium-size caterpillar-eating bird of a large state park in the central U.S. would probably also reply "three" (though its kinds might be defined by different boundary traits than would be the kinds recognized by the squirrel cuckoo, as in the case of the *Ctenosaura* lizard mentioned above).

However, not only vertebrates have opinions as to the number of kinds of caterpillars in Santa Rosa. There are, for instance, at least 40 species of parasitic wasps in the genus *Enicospilus* (Ichneumonidae) in Santa Rosa; there are at best 25 species of *Enicospilus* in all of the continental U.S. (I. Gauld, pers. comm.). *Enicospilus* wasps (Fig. 4) lay their eggs in caterpillars. The wasp larva develops within a caterpillar and consumes its body tissues. There are four widespread species of *Enicospilus* in the U.S., and each specializes in a different group of species of caterpillars (I. Gauld, pers. comm.). One, *E. americanus*, attacks only the larvae of saturniid caterpillars, but it attacks many species of them (e.g. Peigler 1985; Krombein et al. 1979). It sees many Latin binomials as a single kind of host.

In Santa Rosa, there are three species of *Enicospilus* that attack Saturniidae, and they attack three species of them. Each wasp species is specific to its own host species. Hundreds of rearing records in an ongoing six-year study of caterpillar parasitoids suggest that each wasp species attacks only one species of Santa Rosa saturniid. For example, one species of *Enicospilus* has been reared over 300 times from the caterpillars of *Rothschildia lebeau*

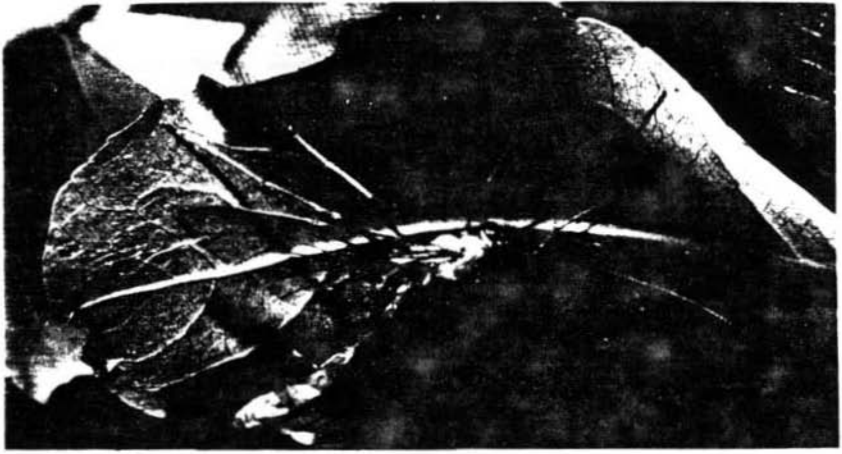

Fig. 4. Adult *Enicospilus* wasp (Ichneumonidae, 38 mm body length, Santa Rosa National Park, Costa Rica).

but never from the caterpillars of *Rothschildia erycina* (53 rearings of wild caterpillars to date), even when the two saturniid caterpillars developed simultaneously on the same individual host plant. In sum, each of these three species of *Enicospilus* that parasitizes saturniid caterpillars counts only one species and kind of caterpillar at Santa Rosa. I must be careful to note, however, that the wasp does not eat even a single Latin binomial. The moth, pupa, and eggs of the saturniids no more exist to the *Enicospilus* wasps than do all the other caterpillar species, leaves, hummingbirds, rocks, and snakes at Santa Rosa.

At this point you may conclude that each of the three species of *Enicospilus* that attacks saturniids in Santa Rosa views the tropics as having fewer kinds of caterpillars than does the single *Enicospilus* that attacks many species of saturniids in the U.S. However, recall the example of the squirrel cuckoo. One can argue that all attackable caterpillars belong to one kind and the remainder are non-existent. In this view, both the Santa Rosa *Enicospilus* and the U.S. *Enicospilus* think that there is only one kind of caterpillar in their habitats–the caterpillar in which they can oviposit.

This ecosystem tangle applies to all of the thousands of species in Santa Rosa and in the U.S. It is apparent why biologists are fond of using Latin binomials rather than biological perceptions as a standard unit of description. But this fondness has also led to a focus on species lists as descriptors of tropical habitats, rather than to a focus on the actual biological processes as descriptors. I might also note that *Homo sapiens* is particularly prone to act like a squirrel cuckoo or an *Enicospilus* wasp when it has to deal with biology that is beyond its direct personal perception. Botanists are forever speaking of the biology of this or that species of plant, when in fact they ignore the seeds and seedlings and really are concerned with adult plants. Lepidopterists commonly think only of adult butterflies and moths when they speak of Lepidoptera. Ornithologists virtually never count the eggs in nests as part of a bird population, and if a species is territorial, they often ignore the adults that do not hold a territory.

But then does it really make no difference to the squirrel cuckoo that there are 3000-plus species of caterpillars in Santa Rosa? Does it not matter if an edible kind is made up of one or many Latin binomials? Does it matter to an *Enicospilus* if its host is made up of one or twenty species? It does matter, but putting numbers on how much it matters requires a knowledge of natural history much greater than we have at present.

For example, as the density of an *Enicospilus* single species of host declines, so also may decline the number of caterpillars that a wasp can find. However, if the wasp treats several species of caterpillars as a single kind, then when there is a decline in the density of one, others may serve as food in its stead. In short, the more species of caterpillars a wasp can use, the less likely is the wasp population to decrease following a reduction in density of one of them. Viewed the other way around, it matters to a caterpillar just how many other species of caterpillars one of its parasites feeds on. The more species of caterpillars fed on by one of its parasites, the less likely is a depression of caterpillar density to be reflected in a later depression in the percent of parasitization of that caterpillar. Finally, it is evident that the more different are the biologies of the hosts used by one wasp species, the greater will be the probability that a change in density of one host will not be synchronized with a change in the density of another host species.

And the squirrel cuckoo is in exactly the same situation as is the parasitic wasp. However, at a minimum, a female wasp only has to find two individual host caterpillars to replace herself. Owing to mortality of her offspring, she generally has to find more—perhaps even several hundred more since she can lay that many eggs. The female cuckoo, weighing several thousand times as much as does the 3-4 cm long wasp and living many years instead of a few weeks, has to find tens of thousands of large caterpillars to replace and maintain herself (the female wasp eats only flower nectar). Small wonder that the squirrel cuckoo does not specialize in foraging on the caterpillars of one or even a few Latin binomials.

It should now be clear that the complexity of a habitat is not measured in the simple length of the list of its Latin binomials. What matters to an insect or bird is how many species of caterpillars it pools as one kind, rather than how many Latin binomials there are overall. What matters is whether the wasp can use or persist on one or two or three species of saturniid caterpillars, not whether there are 3000 species of caterpillars in the habitat. What matters to a saturniid caterpillar is not how many caterpillar species are in the habitat, but rather how many of those Latin binomials are supporting carnivores (predators and parasites) during the time when the caterpillar is scarce and how many Latin binomials are a food base on which the carnivores build up populations that later wreak havoc on the caterpillar population. In other words, 29 species of sympatric saturniid caterpillars may be as dangerous to a *Rothschildia lebeau* caterpillar as would be only one other species of saturniid caterpillar that is much loved by squirrel cuckoos, very common, and not prone to fluctuate in numbers.

THE FRUITS THE MEGAFAUNA LEFT BEHIND

As alluded to in the previous section, complexity may also be measured by the number of connections between an organism and the other organisms along the food chain. This may be dramatically illustrated by asking how far along in the food chain are the effects felt if a member of the food chain is removed. This experiment has been performed for us more times than we might like in humanity's frantic rush to destroy the tropics, but one case has an instructive special twist to it.

Ten thousand years ago, and for at least 3 million years before that, horses and numerous other large herbivorous mammals (the herbivorous megafauna) browsed, grazed, and harvested fruit over Central America just as they did in North America and others did in South America (Janzen and Martin 1982). The first wave of human hunters eliminated nearly all of these animals (Martin 1984). The Spaniards brought one back to us, the horse (horses originated in the New World and moved across the Bering Straits into the Old World before the Pleistocene hunters got to the New World by the same route).

This Spanish gift from the past found the fruits of the jicaro tree (Figs. 5-7, *Crescentia alata*, Bignoniaceae, the catalpa family). It found them in those few habitats where a megafauna-dispersed tree can grow without its dispersal agents and/or around Indian villages where the 5-20 cm diameter hard (Janzen 1982b,c) and spherical jicaro fruits were used for food and bowl-like utensils. The Spanish riding horse cracked the hard shells of the jicaro fruit with its incisors (Fig. 6), swallowed the seed-rich and molasses-rich pulp with little chewing, and defecated viable seeds far and wide in many habitats (Janzen 1982b,c).

Jicaro spread and became a widespread tree once again—the Spaniards had returned one of its original dispersal agents. Jicaro enjoyed 400 years again as a widespread tree, so much so that it became widely regarded as a

Fig. 5. Jicaro tree (*Crescentia alata*, Bignoniaceae), more than 150 years old, growing in a very old pasture (Santa Rosa National Park, Costa Rica).

native (wild) part of the flora. But very modern man controls his horses. For example, in the mid-1970s he removed them from Santa Rosa National Park, for 400 years a cattle ranch, so as to create a more "natural habitat." The jicaro fruits lay rotting beneath the parent trees (Fig. 7), and seed dispersal stopped. Dry-season fires went uncontrolled, fueled by the ungrazed grass in abandoned pastures. Jicaro saplings and seedlings were killed by the fires and competition from 1-2 m tall grass, and repeated burning incinerated the adult trees. Santa Rosa still has some adult jicaro, but the population is dwindling fast. In 1985, fire control was initiated and horses were again allowed to range free. This may reverse the decline of the jicaro population, but for the moment we can examine what it means for a forest/grassland mosaic to lose its jicaro trees.

When Santa Rosa had a free-ranging horse population and enough livestock to eat the grass back to a density where it was not a severe competitor with jicaro seedlings, jicaro was common and occurred on many drainage and soil types. Each adult jicaro tree makes huge flower crops during 1-2 week periods several times a year. Since many jicaro trees flower somewhat out of synchrony with each other, there are abundant jicaro flowers available for four or more months of each year. These flowers are heavily visited by long-tongued, narrow-faced, tiny *Glossophaga* bats (Howell 1983). These bats are the primary (if not exclusive) pollinators of jicaro flowers and obtain a major part of their food from jicaro flowers at certain times of the year. This implies that when the jicaro trees are eliminated, the *Glossophaga* bat density or seasonal presence will be substantially reduced.

Fig. 6. Adult range horse in the process of cracking a jicaro fruit prior to eating the pulp inside (Santa Rosa National Park, Costa Rica).

However, these flower-visiting bats are also major pollinators of other woody plants in Santa Rosa, such as *Bauhinia ungulata, Hymenaea courbaril* and *Ceiba pentandra* (cf. Heithaus et al. 1975). The removal of jicaro will lower the density of *Glossophaga* bats in the park, which will in turn reduce and alter gene flow, reduce fruit crop sizes, and eventually change the abundance of other species of trees. The latter two consequences may well reduce the density of some other animals, such as the agouti (*Dasyprocta punctata*). This large diurnal rodent, a major consumer of *H. courbaril* seeds and fruits in some habitats, is also a major disperser of the seeds of many species of trees at Santa Rosa (W. Hallwachs, pers. comm.). The interaction goes on and on.

There are many ways that a deleted interaction may be replaced by another interaction in nature. On the other hand, the loss of a single species of animal such as the horse may lead to a major ripple of quantitative and qualitative interactions through and beyond the habitat. Species such as the horse have been termed "keystone" species (Gilbert 1977), as if there were something special about them. However, it is becoming my experience that what is special about a keystone species is that an investigator happens to know enough about its natural history to see the changes that occur following its removal. All species that I have worked with in detail in the tropics have the property that the demise of one of them will cause an ecological ripple in the habitat. Some species make bigger ripples than do others when removed, but even this trait will vary in the eyes of the beholder. Yes, the addition or deletion of species only sometimes creates a ripple so great that *Homo sapiens* is directly affected through its physical needs, but it is not necessarily useful to put ourselves at the head of the importance list when trying to understand ecology.

THE GREAT AUSTRALIAN BARBECUE

The Australian dry tropics seem hardly to have been touched by the hand of man, as compared to the obvious and intense agricultural and wild harvest pressure that characterizes the remainder of the dry tropics. The Australian haven of about 2 million square kilometers of essentially unoccupied dry tropical forest seems at first glance to be a place where one can study the dry tropics as they once were.

Braithwaite et al. (in press) open their discussion of mammal assemblages with: "Tropics in Australia are extensive, relatively unpopulated and undisturbed." However, this is very much an illusion: the Australian dry tropics are one of the most severely human-influenced areas in the world's tropics. Yes, some faunal and floral species lists for dry tropical Australia are respectably long (e.g., Taylor and Dunlop, in press; Braithwaite et al., in press), but it is clear that these species are only remnants of what existed prior to invasion of Australia by hunting and firing humans.

Fig. 7. Accumulated rotting and (few) ripe jicaro fruits below a several hundred-year-old jicaro tree to which horses do not have general access: a small number of fruits have been opened by a single horse that passed through just prior to the photograph (Santa Rosa National Park, Costa Rica).

Human hunters and harvesters have been collecting food in dry tropical Australia for at least 30,000 years and probably for 10-50 thousand years before that (e.g. Merrilees 1968; Gill 1975; Kershaw 1984; White and O'Connell 1983; Singh et al. 1981; Ingram 1985). Everything known of their hunting methods, and those of hunters in dry habitats elsewhere, suggests that grass fires (Fig. 8) were major tools of the harvest (e.g. Stocker 1966; Singh et al. 1981; Ridpath 1977). At the time of European contact, the fires were widespread but patchy in thoroughness owing to their occurrence in the early rainy season, when the world is only heterogeneously dry (cf. Stocker 1966; Ridpath 1977; Stocker and Mott 1981; Mott and Andrew, in press; Braithwaite and Estbergs, in press).

Apparently the function of fire was that of concentrating game animals in unburned sites, producing patches of post-fire new sprouts that attracted game, aiding in game ambush, clearing out the understory for visibility and projectile passage (ever try to throw a boomerang in a forest?), and removing spear grass (*Heteropogon contortus*, a very annoying Australian grass whose seeds are dispersed by penetrating mammal fur and even skin). These fires burned relatively unchecked (small patches of forest were explicitly protected by aborigines) and a single fire could easily burn through thousands of square kilometers just as it does today. It is likely that much of dry tropical Australia was burned in most years. Catling and Newsome (1981) have productively deduced that such fires should have selectively eliminated some species of vertebrates and altered the geographical demography of others. Likewise, experimental burning in Australia (e.g. Unwin et al., in press) is making it quite clear that tropical rainforest or dry forest will be replaced by eucalypt-forested grasslands under ordinary burning regimes. For the purposes of this discussion, however, it is instructive to return to Guanacaste Province on the dry Pacific coastal plain of northwestern Costa Rica with the above fire story in mind.

When the Spaniards arrived in northwestern Costa Rica about 1523, all indications are that they encountered a forested landscape that was sparsely populated by shifting agriculturalists and patches of variously-aged secondary forest succession and uncut forest. The largely deciduous forest experienced a six-month rain-free dry season, just as it does today and as does dry tropical Australia (Taylor and Tulloch, in press). During the following 450 years, European agriculture (and livestock-culture) cleared ever more extensive patches of forest. By 1940 most and by 1977 all of the area was officially viewed as free of forest (Sader and Joyce 1984). Where the cleared land was not used for fixed-field agriculture, it was burned more or less annually to convert it ever more thoroughly to grassland. African grasses such as *Hyparrhenia rufa* (Pohl 1983) were introduced to complete the conversion into pasture (Parsons 1972). The more fire, the more complete the conversion. The more complete the conversion, the more easily and thoroughly the habitat is burned. This lamentably self-reinforcing process has occurred throughout Central America.

Start with a dry and largely deciduous forest, make some clearings, and burn them annually. The clearings spread as the fire eats into the margins.

Fig. 8. a. *Eucalyptus*-clothed grassland prior to dry season fires. b. *Eucalyptus*-clothed grassland immediately after a dry season fire. Both photographs taken 30 m apart in mid-August, 1985, near Katharine, Northern Territory, Australia.

Within a few hundred years on ranches of several hundred km^2 (large enough that there are large expanses of vegetation unbroken by barriers of roads and croplands), the final result is a grassy plain. This plain is, however, dotted with forest fragments associated with habitats that are difficult to burn (marshes, cliff faces, spits of land between river forks, river banks, hills surrounded by rock faces deep ravines, rock outcrops, etc.). In Guanacaste Province, the only tropical habitat that I have watched carefully for a long time (24 years), these tiny habitat fragments (Fig. 9) are still in the process of losing species because of their small size. They are also still losing species because of the long-term persistence of root stocks remaining from the original forest; these plants take tens to hundreds of years to die out of habitats that cannot support them as breeding populations. These habitat fragments take time to lose many of their species because the loss does not occur until an exceptionally dry year, in which the usually unburnable site becomes burnable. At present, the tiny forest fragments (a few hectares to much less in size) contain approximately 20% of the original dry forest flora and fauna that once occupied Guanacaste. This is an overall figure. The species of plants, insects, and other animals have been extinguished differentially, since they have different needs, inter-fragment mobility, ability to colonize and recolonize fragments, etc. All of the large vertebrates and many of the large trees are gone from these fragments. Some herbs, vines, and fast-growing small trees are more common than they were in the original forest; these are among the species commonly viewed as roadside and fencerow weeds.

Dry tropical Australia has been treated like Guanacaste, but for 30,000 years. The tiny pieces of closed canopy or "monsoonal" dry forest scattered through Australia's dry tropics are the true remnants of what was once virtually the entire forest cover of an area as large as a quarter of the United States. The habitat ocean surrounding these forest bits is in fact an enormous undulating plain of largely native grasses. However, this habitat is not generally perceived as grassland by Australian biologists because viewed laterally, it looks like a "forest." That is, when you look at it, you see a lot of trees (Fig. 8). Viewed from above or below, Australia's (eucalypt) forests are just grassy plains dotted with amazingly fire-tolerant *Eucalyptus* trees (and their relatives). The trees are spaced far enough apart that direct sunlight penetrates to ground level in sufficient quantity to support a dense stand of grassy fuel.

The grass understory occurs even when large adult trees are as abundant as they are in a Central American dry forest. This begs the question of why eucalypt crowns do not close up the canopy, grow out to fill in the space between them. A similar question is why it is that within a eucalypt crown the leafing is not thorough enough to form a solid barrier to sunlight, as is the common case with dry forest deciduous trees when they are in leaf in the rainy season. It may be that the eucalyptus tree crown is evolutionarily

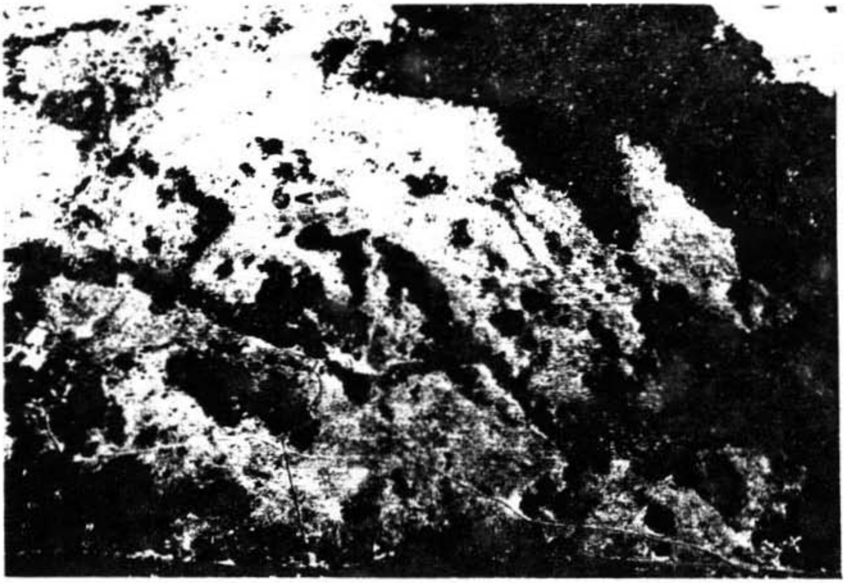

Fig. 9. Aerial view of several hundred-year-old pastures in Santa Rosa National Park. All of the light-colored area is jaragua (*Hyparrhenia rufa*) grass monoculture that was burned almost annually up through the 1984 dry season. Forest and forestlets are variously aged secondary succession that were being eradicated before the fire was halted. Arrow indicates a forest island under a single large guanacaste tree (*Enterolobium cyclocarpum*) whose crown is 40 m in diameter. Park entrance highway (two-lane) passes along base of photograph and center is Presa Pinuela. January 1985, Santa Rosa National Park, Costa Rica.

designed to let the heat from a grass fire pass quickly through, rather than form a tent to trap rising hot air that would kill branches and leaves. Equally, concentrations of individuals may be thinned by the lethal effect of their combined crowns accumulating hot air rising from the burning grass below. Many of the other species of trees that co-occur with *Eucalyptus* in frequently burned areas have deciduous crowns at the time of fires, stand far apart, and/or have very diffuse crowns.

There are many species of *Eucalyptus* trees in the dry Australian tropics (accompanied by the equally species-rich sister genus *Melaleuca* in the Myrtaceae, and the unrelated species-rich legume genus *Acacia*). If a fire-rich habitat is only 30,000 years old, are we to guess that the trees that occupy most of the habitat have speciated in this short time? Perhaps, but it is not necessarily so. The fire-resistant Myrtaceae could be serendipitously fire-resistant and have been much older occupants of dry forest unburned habitats with a high frequency of disturbance (landslides, cliff faces, erosion ravines, marsh-stream-river-flood plain banks, heavily browsed/grazed areas, hurricane impact areas, etc.). Some species could even have been selected for fire tolerance in areas with exceptionally frequent lightning fires at the beginning of the rainy season (end of the dry season). But whatever habitats the fire-resistant *Eucalyptus* occupied originally, owing to their high fire tolerance they undoubtedly underwent an explosion in population size and geographic coverage when the original human occupants of dry tropical Australia began their burning regime.

The original occupants were, above all else, hunters and gatherers. In the Neotropics, the first waves of Neotropical hunters eliminated the bigger and slower of the Neotropical herbivores (Martin 1973, 1984) (and caused their predators and scavengers to starve; Janzen 1983b). The original human invaders of Australia did the same (Martin 1984). They certainly had a diverse fauna of large animals to hunt (Murray 1984) and those animals are no longer with us. It is not hard to imagine that the removal of these large animals reduced the frequency and extent of small-scale vegetation disturbance (leading to a more homogeneous fire regime) and reduced the dispersal of dry-forest tree seeds (leading to slower reinvasion of sites that were occasionally cleaned of their plants by exceptional fires). Australia also went through periods of climatic changes during this time. Habitats move, fragment, and coalesce as the climate changes. The movement of seeds by animals is an integral and important component to this habitat movement, and thus an important part of whether a climate change leads to species or habitat movement or to species or habitat extinction.

But then, enter the Europeans as a major agricultural force between 1800 and 1900 (depending on where you are in Australia, they and their influence on the fire regime arrived at different times). Aside from largely eliminating the original inhabitants and therefore indirectly eliminating their practice of burning early in the dry season, the Europeans were interested in raising cattle. And to do this, late dry season fires seemed best because they yielded a dry season harvest of green sprouts. Additionally, once the traditional early dry season fires were gone, the tinder-box nature of the habitat by the end of the dry season led to rapid and thoroughly widespread fires from accidents, ranches, or lightning. A small patch of deciduous dry forest that would be protected by a moist area or rocky outcrops from a weak fire early in the dry season will often be overrun by a raging fire late in the dry season.

The consequence of the shift in fire regime has been dramatic. The original eucalypts still stand over their grassy plain, but their recruitment is severely limited. Annual fires in the late dry season repeatedly eliminate all but the most robust adult trees, and even these eventually succumb. Where grazing is severe enough to reduce grass fuel to non-inflammable levels, the eucalypt seedlings and sucker shoots are also eaten, and introduced grazing-resistant woody plants invade the forest understory. One day, within 100 years or so, Australians are going to wake up to find that almost overnight their dry tropical eucalyptus forests have been converted to treeless grassland habitats and deciduous forest scrub that is largely inedible to cattle.

What message does Australia's dry tropical forest story have for the understanding of tropical complexity? Australia is a marvelous example of how what you see in the tropics, species-rich as it may be, can still be but a tattered ecological remnant rather than an evolutionarily fine-tuned ecosystem millions of years old. Yes, there are hundreds of species of plants in dry tropical Australia. But this list is undoubtedly much shorter than it was 30,000 years ago, and it is going to get abruptly shorter as the European-style fire regime eliminates the last relict dry forest pockets.

Dry tropical Australia displays the striking ecosystem pattern of enormous areas covered with a few species-rich genera of grasses, trees, and shrubs, with a sprinkling of tiny refugee habitats containing many other species. However, it is likely that these plants did not come to have their current habitat status through evolution under a severe fire regime, but rather have been put in their places by a process of ecological fitting of fire-tolerant parts evolved in other disturbed habitats. Yes, dry tropical Australia has its spectacular vertebrates–goannas, wallabies, emus, bower birds, megapodes, cockatoos, magpie geese, etc. But this fauna is only a pale shadow of the marsupials that were as large as tapirs and rhinos, the huge ratites, giant kangaroos, etc., that early humans confronted. The impact of the extinct megafauna is still everywhere to be seen or tasted–thorns, burs, large fleshy fruits with woody or fibrous coverings around seeds, leaf defensive chemistry. Such an impact will require a special kind of reconstruction ecology to understand (e.g. Janzen and Martin 1982). This is an area of field biology very much in its infancy.

In sum, dry tropical Australia is complex and spectacular just as is (was) much of the remainder of the dry tropics. However, this complexity is only that which can survive the great homogenizers, fire and humanity. The regime of nearly annual burning and continuous hunting has been forced onto a complex tropical habitat. The effects have been indelibly recorded through extinctions and novel geographic distributions well before any evolution can occur to compensate for them. This type of complexity is also in the eye of the beholder, but the beholder is blind.

CONCLUSION

The tropics are a complicated environment. The direction and intensity of ecosystem processes are as much based on the idiosyncracies of the natural history of particular species as on major climatic and geological variables. One of those particular species is *Homo sapiens*. *Homo sapiens* has clearly beaten nature, and in doing so continues to convert habitats to the vegetation type that grows the resources to support a very large herd of human draft animals. May I only add that humanity has never displayed the trait of developing the brains of its draft animals. The bits of complex tropical nature that are still within the grasp of tropical peoples are perhaps this portion of humanity's last chance for mental stimulation extraneous to the pitiful stimuli offered by humanity itself. Life in a sugar cane plantation is not substantially improved by even two TV channels playing ten-year-old re-run movies from the U.S.

In the not-too-distant future, the most valuable pieces of real estate in the tropics will be the less than 10% that will be in national parks or other biological reserves. Can you imagine the intellectual response by Europe if 100 km^2 of Pleistocene forest and its animals could be made to reappear in central France? I do not intend to depreciate the complexity of human society. Rather I note that this complexity is only a very incomplete representation of what the human mind is capable of absorbing, using, and enjoying. The natural world, tropical or otherwise, at least allows the chance for a substantial increase in the completeness of that representation. Complexity is in the eye of the beholder, but there has to be something left to behold.

ACKNOWLEDGMENTS

This study was supported by Santa Rosa National Park and the Servicio de Parques Nacionales of Costa Rica, by travel funds from the Australian government (CSIRO), and by NSF DEB 83-08388 and 84-03531. Neotropical organism identification was provided by C. Lemaire, I. Gauld, N. Woodley, M. Wood, F. Joyce, and W. Hallwachs. Australian field work was greatly assisted by CSIRO and M. Andrew, W. Freeland, K. Harley, M. Ridpath, F. Crome, G. Stocker, E. Henzell, P. Murray, M. Westoby, B. Rice, J. Kikkawa, W. Winter, R. Braithwaite, J. Mott, M. Hegarty, E. Hegarty, J. McIvor, C. Gardener, J. Taylor, A. Newsome, J. Calaby, B. Walker, R. Jones, L. Corbett, M. Lonsdale, T. Press, B. Gald, S. Morton, A. Chapman, D. Tulloch, P. Johnson, R. Jones, and many others in Australia (August 1985). The manuscript was constructively commented on by I. Gauld and W. Hallwachs.

I dedicate this paper to the right-minded persons in the Australian government who are willing to plan the long-term use and perpetuation of the Australian tropics, rather than simply to harvest them.

LITERATURE CITED

Batten, M. 1984. The ant and the acacia. Science 84 5(3):58-67.

Braithwaite, R. W., and J. A. Estbergs. In press. Fire patterns and woody vegetation trends in the Alligator Rivers region of northern Australia. *In* J. C. Tothill and J. J. Mott, eds. The Ecology and Management of the World's Savannas. Australian Academy of Science, Canberra.

Braithwaite, R. W., J. W. Winter, J. A. Taylor, and B. S. Parker. In press. Patterns of diversity and structure of mammalian assemblages in the Australian tropics. Austr. J. Mam.

Catling, P. C., and A. E. Newsome. 1981. Responses of the Australian vertebrate fauna to fire: An evolutionary approach. Pages 273-310 *in* A. M. Gill, R. A. Groves, and I. R. Noble, eds. Fire and the Australian Biota. Australian Academy of Science, Canberra.

Ferguson, D. C. 1972. Saturniidae (Part). Bombycoides. Pages 155-275 *in* The Moths of America North of Mexico. Fascicle 20.2B. E. W. Classey, London.

Gardiner, B. O. C. 1982. A silkmoth rearer's handbook. The Amateur Ent. 12:1-255.

Gilbert, L. E. 1977. Development of theory in the analysis of insect-plant interactions. Pages 117-154 *in* D. J. Horn, G. R. Stairs, and R. D. Mitchell, eds. Analysis of Ecological Systems. Ohio State University Press, Columbus, Ohio.

Gill, A. M. 1975. Fire and the Australian flora: A review. Austr. For. 38:4-25.

Heithaus, E. R., T. H. Fleming, and P. A. Opler. 1975. Foraging patterns and resource utilization in seven species of bats in a seasonal tropical forest. Ecology 56:841-854.

Hodges, R. W., et al. eds. 1983. Check list of the Lepidoptera of America north of Mexico. E. W. Classey, London.

Howell, D. J. 1983. *Glossophaga soricina*. Pages 472-474 *in* D. H. Janzen, ed. Costa Rican Natural History. University of Chicago Press, Chicago, Ill.

Ingram, M. 1985. Aboriginal vision. Earthwatch 5(1):13-17.

Janzen, D. H. 1982a. Guia para la identificacion de mariposas nocturnas de la familia Saturniidae del Parque Nacional Santa Rosa, Guanacaste, Costa Rica. Brenesia 19/20:255-299.

Janzen, D. H. 1982b. Fruit traits, and seed consumption by rodents, of *Crescentia alata* (Bignoniaceae) in Santa Rosa National Park, Costa Rica. Amer. J. Bot. 69:1258-1268.

Janzen, D. H. 1982c. How and why horses open *Crescentia* fruits. Biotropica 14:149-152.

Janzen, D. H., ed. 1983a. Costa Rican natural history. University of Chicago Press, Chicago, Ill.

Janzen, D. H. 1983b. The Pleistocene hunters had help. Amer. Nat. 121:

598-599.

Janzen, D. H. 1984a. Two ways to be a tropical big moth: Santa Rosa saturniids and sphingids. Oxford Sur. Evol. Biol. 1:85-140.

Janzen, D. H. 1984b. Natural history of *Hylesia lineata* (Saturniidae: Hemileucinae) in Santa Rosa National Park, Costa Rica. J. Kans. Ent. Soc. 57:490-514.

Janzen, D. H. 1985. A host plant is more than its chemistry. Ill. Nat. Hist. Sur. Bull. 33:141-174.

Janzen, D. H. In press. Ecological characterization of a Costa Rican dry forest caterpillar fauna. Biotropica.

Janzen, D. H., and P. S. Martin. 1982. Neotropical anachronisms: The fruits the gomphotheres ate. Science 215:19-27.

Kershaw, A. P. 1984. Late Cenozoic plant extinctions in Australia. Pages 691-707 *in* P. S. Martin and R. G. Klein, eds. Quaternary Extinctions, A Prehistoric Revolution. University of Arizona Press, Tucson, Ariz.

Krombein, K. V., P. D. Hurd, D. R. Smith, and B. D. Burks, eds. 1979. Catalog of Hymenoptera in America north of Mexico. Smithsonian Institution Press, Washington, D.C.

Martin, P. S. 1973. The discovery of America. Science 179:969-974.

Martin, P. S. 1984. Prehistoric overkill: The global model. Pages 354-403 *in* P. S. Martin and R. G. Klein, eds. Quaternary Extinctions, A Prehistoric Revolution. University of Arizona Press, Tucson, Ariz.

Merrilees, D. 1968. Man the destroyer: Late Quaternary changes in the Australian marsupial fauna. J. Royal Soc. West. Aust. 51:1-24.

Mott, J. J., and M. H. Andrew. In press. The effect of fire on the population dynamics of native grasses in tropical savannas of north-west Australia. Proc. Ecol. Soc. Aust. 13.

Murray, Peter. 1984. Extinctions down under: A bestiary of extinct Australian Late Pleistocene Monotremes and Marsupials. Pages 600-628 *in* P. S. Martin and R. G. Klein, eds. Quaternary Extinctions, A Prehistoric Evolution. University of Arizona Press, Tucson, Ariz.

Parsons, J. J. 1972. The spread of African pasture grasses into the New World tropics. J. Range Manage. 20:13-17.

Peigler, R. S. 1985. Recent records for parasitism in Saturniidae (Lepidoptera). Nach. ent. Ver Apolla, Frankfurt, N. F. 5:95-105.

Pohl, R. W. 1983. *Hyparrhenia rufa* (jaragua). Pages 256-257 *in* D. H. Janzen, ed. Costa Rican Natural History. University of Chicago Press, Chicago, Ill.

Ridpath, M. G. 1977. Ecological consequences of fire for animal communities. Pages 48-55 *in* R. E. Fox, ed. Report on the use of fire in National Parks and Reserves. Government Printer, Darwin, Australia.

Sader, S. A., and A. T. Joyce. 1984. Relationship between forest clearing and biophysical factors in tropical environments: Implications for the design of a forest change monitoring approach. National Aeronautics and Space Administration Report No. 230.

Singh, G., A. P. Kershaw, and R. Clark. 1981. Quaternary vegetation and fire history in Australia. Pages 23-54 *in* A. M. Gill, R. A. Groves, and I. R. Noble, eds. Fire and the Australian Biota. Australian Academy of Science, Canberra.

Smith, S. M. 1975. Innate recognition of coral snake pattern by a possible avian predator. Science 187:759-760.

Smith, S. M. 1977. Coral-snake pattern recognition and stimulus generalization by native great kiskadees (Aves: Tyrannidae). Nature 265:535-536.

Stocker, G. C. 1966. Effects of fires on vegetation in the Northern Territory. Aust. For. 30:223-230.

Stocker, G. C., and J. J. Mott. 1981. Fire in the tropical forests and woodlands of northern Australia. Pages 427-439 *in* A. M. Gill, R. H. Groves, and I. R. Noble, eds. Fire and the Australian Biota. Australian Academy of Science, Canberra.

Taylor, J. A., and C. R. Dunlop. In press. Plant communities of the wet-dry tropics of Australia: The Alligator Rivers region. *In* M. G. Ridpath and L. K. Corbett, eds. Ecology of the wet-dry tropics. Proc. Ecol. Soc. Aust. 13.

Taylor, J. A., and D. Tulloch. In press. Rainfall in the wet-dry tropics: Extreme events at Darwin and similarities between years during the period 1870-1983 inclusive. Aust. J. Ecol. 10.

Unwin, G. L., G. C. Stocker, and K. S. Sanderson. In press. Fire and the forest ecotone in the Herberton highland, north Queensland. Proc. Ecol. Soc. Aust. 13.

White, P. J., and J. F. O'Connell. 1983. A prehistory of Australia, New Guinea, and Sahul. Academic Press, New York, N.Y.