

Insect diversity of a Costa Rican dry forest: why keep it, and how?

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The dry forest of the 108 km² Santa Rosa National Park in northwestern Costa Rica contains as many as 13 000 species of insects (including 3140 species of moths and butterflies) sustained by and sustaining about 700 species of plants and 400 species of vertebrates. These insects require explicit conservation attention. They are more than just decorations on the plants; rather, they are the building blocks and glue for much of the habitat. They are the food for much of the carnivore community, and the insect species are not merely interchangeable bits of nutrients. They are major killers of seeds, and thereby influence both the plant species composition of a habitat and prevent the better competitors from taking it over. They are the primary pollinators and are specific enough to be neither interchangeable nor replaceable with other animals; the seeds resulting from their pollination activities are major animal foods in the habitat. They are a diverse, puzzling, complex, intrinsically attractive, and major part of the intellectual display offered by tropical wildlands, the display that will be the eventual foundation for most of the reason why tropical wildlands will be retained as such in the future.

The retention and maintenance of insect species richness in a tropical wildland is strongly rooted in the preservation of plant species richness, in maintaining habitat mosaics (different members of which are used by a given insect in different seasons), in preserving a large diversity of habitats, and in recognizing the threat posed by insect crop associates in nearby agricultural lands.

KEY WORDS:—Tropical dry forest – insect conservation – Costa Rica – caterpillars – insect migration – seed predation – species diversity – tropical conservation – habitat diversity – pollination.

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INTRODUCTION

The conservation of tropical insect faunas (e.g. Elton, 1975) has received almost no explicit attention. However, the efforts to conserve vertebrate populations on the one hand, and major ecosystem fragments on the other hand, have conserved insect faunas (and other invertebrate faunas) as a byproduct. While this is all to the good, some characteristics of insects render insect conservation and importance in tropical wildlands worthy of explicit attention. Such

attention is also applicable to extra-tropical habitats, but they are beyond the scope of this essay.

A mainland Central American dry forest with a reasonable amount of topographic diversity and dry season moist refugia can contain as many as 13 000 species of insects (including 3140 species of moths and butterflies: Janzen, 1987a, b, c), sustained by and sustaining about 700 species of plants and 400 species of vertebrates. This is, for example, the approximate fauna and flora of Santa Rosa National Park, 108 km² in area and located in northwestern lowland Costa Rica (Janzen, 1986a). Here I address the question of why attempt to conserve and maintain such an insect fauna, and some of the ways to do so.

WHY ATTEMPT TO CONSERVE AND MAINTAIN A TROPICAL INSECT FAUNA?

The values of tropical wildlands range from repositories of genes, seeds and interactions to watershed protection to intellectual stimulation and recreation. These conservation reasons apply to insects as well as to magnificent trees, woolly animals, flashy birds and towering rainforest. Though the academic and conservation community has been lax in relating these reasons explicitly to insects, it generally assumes that insects are being adequately conserved as a by-product of the conservation of the more widely appreciated and better known large organisms and habitats. However, insects are much more than hitch-hikers on the plants and vertebrates.

Insects are an essential 'glue' and act as building blocks in the habitat structure and species lists that are the motivation for establishing wildland preserves. However, insects have been examined much less than have plants and vertebrates. There has been a strong tendency to study and survey tropical insects in relative isolation, rather than to investigate the impact of their addition to, or subtraction from, a habitat. Tropical conservation biology is in desperate need of observations and experiments with insects that are analogous to grazing exclosures, poacher decimation of large mammals, selective logging, weed introduction, man-made fires, etc. The progressive invasion of Central America by the Africanized honey bee (*Apis mellifera*) through its own movements (Taylor, 1985) is such an experiment, though the ecology of the bee's impact in its new-found habitats has not been studied in any serious manner (however, the subject has been superficially discussed at length). Changes in wildland plant arrays as mediated through decimation of wild herbivorous insects by pesticides and by habitat reduction in area would be another such experiment, though the subject is not being studied anywhere.

Below I outline just four of the many ways in which it is now becoming clear that insects are part of the 'glue and building blocks' in Santa Rosa's dry forest. That is to say, if that dry forest is to be maintained with its possible and original flora and vertebrate fauna, then insects are a critical part of that forest. Their elimination would result in a significantly altered habitat. I offer these four specific cases only as examples, and these examples are not intended to be universally applicable. However, I am confident that there are many analogous situations in other tropical habitats and geographic areas.

Santa Rosa is covered with a mosaic of deciduous to semi-deciduous dry forest (0–350 m elevation). This forest ranges from small patches of virtually pristine vegetation through zero to 400-year old secondary succession in a complex

mosaic that is distributed over a diverse topography of mesas, slopes, ravines and valley bottoms. There is a 6-month rain-free season and a 6-month rainy season during which 1.0–2.5 m of rain falls, distributed around two peaks (Table 1). Santa Rosa's dry forest is representative of much of the vegetation that once clothed the dry Pacific side of Mesoamerica, but today has been largely replaced by fields and pastures.

Bird food

If you lose the insects you lose the insectivorous birds and many other small carnivores. The potential repercussions of the loss of a large and species-rich body of small carnivores needs no discussion. However, vertebrates do not eat just any insect, and therefore conservation needs to be directed at more than just insects in general. Insects are not simply interchangeable parts in the natural machine.

The diet of a species of bird, for example, is often reported as simply 'insects', or 'caterpillars', when the bird is in fact dependent on a very specific set of species of insects (but see Janzen, 1986d). This dependency is nicely displayed by the elegant trogon (*Trogon elegans*), a prominent and beautiful member of the bird fauna in Santa Rosa's dry forest. The elegant trogon nests in holes in trees. The parents bring caterpillars to the nestlings. A nestling fitted with a soft collar of pipe cleaner wire cannot swallow a caterpillar, which can then be collected later for identification (e.g. Orians & Horn, 1969). Using this method, it is easy to show that the caterpillars eaten by nestling elegant trogons are not a random sample of the caterpillars in the forest (Janzen, Joyce & Isenhardt, 1987). For example, during July 1986 we captured 82 insects that had been brought to three *T. elegans* nests. All were identified: 74% of them were large sphingid caterpillars, and 96% of these were green species or green morphs of polymorphic species (e.g. *Manduca* spp., *Erimyia* spp., *Pachylioides resumens*, *Perigonia lusca*, *Eupyrrhoglossum sagra*, *Amplypterus gannascus*, *Protambulyx strigilis*). At that time of year it was clear that both parents were unambiguously specializing at finding large (1–10 g) green sphingid moth caterpillars. This specialization occurred in a habitat and time of year rich in other species of large and small caterpillars of many colors (as well as rich in other insects). The deletion of the sphingid moths (less than 3% of the moth fauna) from this habitat could remove at least 74% of the items brought to the nestlings and well over 90% of the weight of the items brought during the time of year in which most *T. elegans* nest.

The removal of the sphingids from Santa Rosa might well result in the trogons' compensating by finding other kinds of caterpillars and other insects (as observation of nestling food later in the rainy season shows they do). However, this would probably result in significant losses in efficiency for the parents. For example, Santa Rosa trogons breed almost entirely at the time of year (June–July) when there is a conspicuous peak in the biomass of large sphingid larvae. I suspect that only at this time of year can they usually find larvae in sufficient numbers per hour or day to properly feed the nestlings and simultaneously maintain their other activities at a normal level.

However, a reduction in sphingid caterpillar abundance might lead to a much more complex and trogon-specific perturbation. Sphingid caterpillars feed

Table 1. Monthly precipitation (rounded to the nearest millimetre in the administration area of Santa Rosa National Park, Guanacaste Province, Costa Rica (data collected by Park Rangers and extracted from the Meteorology Institute in San Jose)

Year	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
1980	1	0	5	0	184	175	139	159	331	417	240	9	1660
1981	0	1	1	11	353	582	172	478	195	268	153	27	2241
1982	16	2	0	41	919	129	117	34	328	197	37	1	1820
1983	2	0	22	4	21	180	106	107	188	201	79	7	917
1984	6	8	0	0	118	218	278	162	613	261	52	7	1723
1985	0	0	0	3	99	211	154	169	214	436	119	26	1431

on plants whose foliage is rich in potentially toxic small molecules (Janzen & Waterman, 1984). Each time a nestling trogon digests a sphingid caterpillar, it is getting a heavy dose of these potentially toxic small molecules from the leaf fragments in the gut of the caterpillar (an adult trogon kills the caterpillar brought to the nestling, but does not strip out the caterpillar's gut contents). The chemicals in the caterpillar gut may well be inducing the physiological ability to withstand or otherwise detoxify toxic plant compounds by the nestling, or modifying the nestling's gut flora through selection for resistant bacterial strains. Alternatively, the nestling may even be obtaining an inoculum of detoxifying bacteria from the caterpillar.

This scenario suggests that the nestling trogon that develops on a diet of non-sphingid caterpillars or other insects that feed on foods containing less noxious chemicals may well be less competent at dealing with adult food. For example, adult trogons at Santa Rosa consume a wide variety of extremely bad-tasting (to humans) small fruits (e.g. *Ocotea veraguensis* (Lauraceae), *Picramnia quaternaria* (Simarubaceae), *Desmopsis bibracteata* (Annonaceae)) as well as numerous fruits that taste 'good' (e.g., *Hirtella racemosa* (Chrysobalanaceae), *Allophylus occidentalis* (Sapindaceae), *Ixora floribunda* (Rubiaceae)). The chemicals that make the fruits taste bad to humans probably function in keeping the wrong potential frugivores from eating these fruits, and thereby raise the chance that a trogon will have time to get to them. A nestling diet of sphingid caterpillars may be the mechanism that generates an adult trogon capable of having such a relationship with certain fruiting plants.

On the other hand, trogons may be genetically programmed for the capacity to detoxify or avoid plant toxins. This suggests that *T. elegans* may specialize at feeding large sphingid caterpillars to its offspring (and not forage for the other large caterpillars in the habitat) because the abundant sphingid larvae are biochemically available to this bird. Again, this emphasizes the potentially strong dependence of *T. elegans* on the array of sphingid larvae that occur in abundance in the early rainy season, but it is a dependence that may be quite different than if the bird needs sphingids in the diet to induce (or shape) detoxification ability.

While this example concerns only a single species of bird, many preliminary field observations suggest that numerous other species of insectivorous medium-sized birds are similarly dependent on large sphingid larvae for nestling food (e.g. squirrel cuckoo, *Piaya cayana*; black-headed trogon, *Trogon melanocephalus*; violaceous trogon, *Trogon violaceus*; turquoise-browed mot-mot, *Eumomota superciliosa*; blue-crowned mot-mot, *Momotus momota*; collared aracari, *Pteroglossus torquatus*). The hypotheses developed for the elegant trogon potentially apply to all of these species.

Seed killers

The Santa Rosa dry forest has a rich fauna of bruchid (Bruchidae) and weevil (Curculionidae) seed predators (Janzen, 1980). This is not the place to discuss the potential and actual great impact of insect seed predators on plant species composition and food availability to vertebrates in tropical habitats. Here I briefly sketch a single example. *Ateleia herbert-smithii* is a fast-growing legume tree that occurs with moderate abundance in the secondary succession in a small area of the eastern part of Santa Rosa (Janzen, 1987d). In the vicinity of adult

seed trees, its light-demanding seedlings are prominent in the early stages of succession and it accumulates height and dominance as rapidly as does any tree in the habitat. Where there has been a high input of seeds, it is often one of very few tree species present—a true dominant. However, *A. herbert-smithii* foliage and its wind-dispersed seeds are not food for any of the park's vertebrates. An increase in abundance of *A. herbert-smithii* will also lower the carrying capacity of the habitat for numbers of individuals and species of plants and insects. The foliage of *A. herbert-smithii* is fed on by only one species of insect, a noctuid moth caterpillar (*Parachabora abydas* H.S.). In fact, the few small pure stands of *A. herbert-smithii* saplings in Santa Rosa are occupied by conspicuously reduced arrays of insect species and individuals as compared with those in the species-rich mix of vegetation only a few meters away.

How could *A. herbert-smithii* become abundant? A large adult *A. herbert-smithii* may produce 50 000–1 000 000 seeds in a single year's crop, and do so every other year (and the population is synchronized in its fruiting periodicity). However, the trees lose 80% or more of their seed crops to seed predation by a single species of a tiny weevil, *Apion johnschmiti* Whitehead. In the 1982, 1984 and 1985 seed crops in Santa Rosa, the average seed predation was greater than 90% (Janzen, 1987d). The apparently unimportant event of the loss of this weevil from the habitat would undoubtedly cause a great increase in the abundance of *A. herbert-smithii*. Such a loss is biologically possible if the dry forest occupied by *A. herbert-smithii* is severely agriculturalized, thereby eliminating the refugia in which the adult weevils pass the two years that usually occur between the synchronized seed crops. This appears to have already occurred with the small Nicaraguan population of *A. herbert-smithii* (Janzen, 1987d).

Pollinators

The potential impact of the removal of insects that are pollinators from a tropical habitat is self-evident. However, there is always the temptation to assume that if a major group of pollinators is removed, some other group will take its place.

Such replacement is certainly possible, but unlikely for many species of plants. Furthermore, even when replacement occurs, the resultant pattern of pollen reception and donation will certainly change. There are 125 species of Leguminosae in Santa Rosa's flora of about 600 broad-leaved angiosperms (21% of the flora) (Janzen & Liesener, 1980). One of these legumes is wind-pollinated (*A. herbert-smithii*), one is bird-pollinated (*Caesalpinia exostemma*), two are bat-pollinated (*Hymenaea courbaril* and *Bauhinia unguolata*) and the remainder are insect-pollinated. The loss of the insect fauna of Santa Rosa—and primarily that of solitary bees and moths—would have a catastrophic effect on the representation of legumes in this dry forest. Yes, a few species would probably limp along with a small amount of self-pollination, but all the circumstantial evidence and two explicit studies (Bawa, 1974; Bullock, 1985) suggest that these dry forest plants set very few seeds by self-pollination. Furthermore, it is highly unlikely that the quality of the seeds set would be equal to what is produced by outcrossing. The removal of the legumes from Santa Rosa would have catastrophic effects on the kind and abundance of food for virtually the entire trophic web. Legume seeds are a major part of the diet of parrots, rodents, peccaries and Bruchidae. Legume leaves support a substantial fraction of the

species of caterpillars in Santa Rosa (especially in the families Noctuidae, Notodontidae, Geometridae, and Saturniidae). Shade from deciduous and evergreen legumes plays an important role in determining the mosaic of temperature and moisture conditions in different microsites during the progression of the six month dry season. Finally, the loss of legumes would strongly alter nitrogen cycling.

Equally tempting is the thought that since plants make very many flowers in excess of the (very large) number of seeds that they set, most of the pollination activity could be excised out of a habitat with little effect on an ecological time scale. However, the act of recruitment of a new plant into the population is very much a game of repeated tries for particular combination of microhabitat conditions. Within certain boundaries, the more tries, the more recruitment (though it is often forgotten that optimal microhabitat conditions may consist in part of the absence of conspecifics). Even a small reduction in a numerically large seed crop can have very severe effects on the amount and location of recruitment of the next generation of adults. It is likewise often forgotten that a plant's fitness, and its ecological impact, is measured by the amount and direction of outgoing pollen as well as the number of seeds set (Janzen, 1977, 1983a). Large outcrossed flower crops that are generating no outgoing pollen because of the demise of their pollinators imply that there are elsewhere large flower crops receiving little or no incoming pollen.

Some pollinating insects require more than an intact dry forest habitat. In Santa Rosa, there are at least 40 species of sphingid moths that have one generation in the park during the first 2–3 months of the rainy season, and then leave as adults for some other part of Costa Rica, where they remain (and probably breed) until the following rainy season in Santa Rosa (Janzen, 1987a, c). As implied above, when they are caterpillars, they are important sources of food for the park's carnivores (some species of parasitoid wasps and tachinid flies, as well as more generalist vertebrates). But when the adults arrive and while they are laying their eggs, and after they have enclosed but before they migrate away, they are very active visitors and presumed pollinators of at least 50 species of Santa Rosa plants (e.g. Haber, 1983; Haber & Frankie, 1982). It is not known what fraction of these plants are pollinated in great part or totally by sphingids, but the proportion is certainly greater than half.

The removal of these sphingids by the act of destroying the other habitats to which they migrate (and from which they return at the beginning of Santa Rosa's rainy season), would have a severe impact on the pollination regimes of a large number of plants and plant species. This removal could also be generated by the loss of particular species of plants within Santa Rosa, plants that maintain the adult sphingids at key times of the year. Such a removal will, just as with the examples mentioned earlier, cause a subsequent ripple in the relationships between other organisms in the park (just as occurred when the megafaunal mammal extinctions occurred 10 000 years ago, Janzen & Martin, 1982). Since all sphingids appear to have about the same general morphological aspect (e.g. Janzen, 1984), it is tempting to suggest that the removal of some species will be compensated for by increased flower visitation by others. However, direct observation of many of the species of plants visited by sphingids in the park makes it quite clear that any given species of flower is visited by only a very small subset of the total set of species of adult sphingids in the habitat.

Biocultural value of insects

The tropical world is entering what might well be considered Stage II in conservation biology (Stage I is the identification of important areas to conserve and give them legal conservation status). In a small but significant number of tropical countries, what is potentially non-marine wildland is more-or-less fixed in area, and the question becomes how to involve the wildland's neighbours in its preservation. Educational development is a major answer. But if wildlands are to be sufficiently mysterious, complex, beautiful and instructive for them to be desired for their intrinsic traits, then their participant parts need to be on display and within reach of the personal experience of visitors. Wildlands have three major groups of organisms: plants, vertebrates and insects. The plants and insects are by far the easiest to find, examine closely, puzzle over and be intrigued by. However, plants have the nasty habit of seeming to be basically green blobs (because we cannot see their enormous chemical diversity and are poorly equipped to appreciate their behaviour). This leaves insects as the potential major showpieces of the future, the future when people are bored with one or more placid lion, gaudy quetzal and fleeing hummingbird. Insects display far more kinds of form and function than do other major groups of organisms, they often do their thing at arm's length without fleeing from the observer, and they are so species-rich that it is commonplace to find a different one at each stop in the visitor's itinerary.

This is to say, an integral part of the 'matrix and glue' of a wildland habitat is public support, both political and financial. The public needs more than economic arguments to remain strongly in favour of conservation as the business climate waxes and wanes. There is a reason why libraries are not converted to newsprint when there is a paper shortage. Insects possess an enormous wealth of intriguing information. This information is, at present, essentially untouched in the educational development of tropical national parks and other kinds of wildlands. My experience in Santa Rosa's dry forest has been that insect biology is a quickly and readily accepted advertisement and attention-holder for a tropical dry forest. Large caterpillars are particularly useful in this context. Furthermore, insects tend to be especially available and spectacular during the first three months of the rainy season. This is precisely the time of year when mammals are the most difficult to observe, and most plants are involved in their most boring activity (photosynthesizing in abstinence).

HOW TO KEEP THE DIVERSITY

As suggested earlier, maintenance of the high insect species richness found in tropical wildlands today is partly achieved simply through overall maintenance of the habitat. However, insects do have some peculiarities that add to the complexity of maintaining tropical wildlands. In the four points above, I have already implied a number of things that are necessary to maintain an intact array of insects in a tropical dry forest. For example, a dry forest national park, such as Santa Rosa, must have sister rainforest national parks that its migrant species can go to and return from. But there are more things to do than insure a network of wildlands.

Plant species richness

A very substantial part of the great species richness of insects in a tropical dry forest is based on plant species richness and on the number of kinds of habitats.

A consequence is that an entire block of phytophagous species may be removed by the deletion of a particular species of plant. That is to say, a small reduction in the number of species of plants in a wildland may seriously depress insect species-richness if some of the plants removed are those that are fed on by many species of insects. This is because of the very high species-specificity displayed by many tropical herbivorous insects (e.g. bruchids—Janzen, 1980; sphingid caterpillars—Janzen, 1984). For example, the evergreen treelet *Ocotea veraquensis* is the sole native member of the Lauraceae in Santa Rosa's dry forest. Its elimination would delete at least one of the most seasonally omnipresent sphingids (*Amphypterus gannascus*), a rare congener (*Amphypterus ypsilon*), a medium-sized saturniid moth (*Copaxa moinieri*), a seasonally omnipresent epipaschiine pyralid moth (*Stericta albifasciata*), a euteliine noctuid moth (*Paectes* sp.), two limacodid moths, three nymphalid butterflies (*Prepona* sp., *Anaea* spp.) and a seed predator weevil (*Heilipus draco*). On the other hand, it is impossible at this time to know if the addition of more species of Lauraceae to the Santa Rosa flora would result in an increase in species of herbivores that specialize at feeding on Lauraceae, because there is no way to know if there are additional (potentially invasive) herbivores restricted to Lauraceae in adjacent rainforest that could survive the other conditions in Santa Rosa.

In other words, when a park planner notes that a reduction in park area will result in, for example, a 2% loss of tree species because there is not enough area to maintain them, there will be an associated but less visible loss of insects. This loss may be large or small, depending on the particular tree species lost. Herbivorous insects, like other organisms, require a certain area of habitat to maintain a population, but they first require that the species of food they eat is present in that habitat. A very small amount of habitat may be adequate to maintain an insect population, if that habitat is rich in the right species of plants and not too rich in threatening carnivores. On the other hand, a very large amount of habitat may not support an insect population if, for example, the adult trees that it feeds on have been removed by very selective logging that otherwise seems to have little effect on forest structure.

The habitat

Phytophagous insects need substantially more than just their host plants (e.g. Janzen, 1985). The heavily agriculturalized areas around Santa Rosa still have many large adult trees standing individually in pastures, fence rows and small woodlots. These trees conspicuously lack many of the specialist insects that feed on them in intact or relatively intact forest, even though at times they are only a few hundred metres from blocks of intact forest. For example, the large weevil *Rhinochenus stigma* (Curculionidae) is a common seed predator of *Hymenaea courbaril* (Leguminosae) in intact forest but totally absent from the *H. courbaril* fruit crops on trees isolated in pastures; *Rhinochenus transversalis* is abundant in the fruit crops both in the forest and in isolated trees (Janzen, 1983b). The cause is that *R. stigma* adults can get out of the indehiscent fruits on their own, but *R. transversalis* adults require that the hard fruit be gnawed open by an agouti (*Dasyprocta punctata*, Rodentia) in order to escape. Agoutis do not live in pastures. The fruits of *Cedrela odorata* (Meliaceae) are mined by pyralid moth larvae (*Hypsipyla grandella*) and weevil larvae (Curculionidae) in the forest in Santa Rosa, but the fruits of trees isolated in pastures and roadsides only a few

hundred meters outside the forest are attacked only by the moth larvae. The caterpillars of the saturniid moth *Copiopteryx semiramis* are absent from its sapotaceous host plant, *Manilkara chicle* (Sapotaceae), where it has been left standing in open pasture, but are present on the same species of tree in nearby forest.

The absence of an herbivorous insect from its host plant in a pasture or other disturbed site may be due to novel microclimate, lack of sites in which to pass the inimical non-breeding season, lack of mutualists, increased exposure to predators or rigid behavioural programming that results in the adult insect not searching for its host plants in very exposed sites. However, whatever the cause, it is clear that one cannot predict from a simple list of plant species which insects or how many will occupy a site. It is quite conceivable that a host-specific moth, for example, may be extinguished by agriculturalization of a large area, even though its host plant is still widespread in that area and even viewed as being in no danger of extinction.

The size of the habitat

There may be one trait that compensates for the susceptibility to local extinction brought about by the narrow host specificity of many species of herbivorous insects. Insects are small, and for many species, a large number of individuals (that appear to be an adequate breeding population) can be maintained in a relatively small area of relatively intact habitat, compared with the average size area required to maintain a healthy breeding population of most species of vertebrates. However, there is a complication. Many tropical dry forest insects use different habitats for different life stages. A seed predator beetle may have its one annual generation during the dry season in the drying fruits of a legume vine that lives only on dry ridges. Upon emerging from the legume seeds, the adults may then migrate to a sheltered and moist creek bed and remain there during the rest of the dry season. Then, with the oncoming rainy season, the adults may move into the most disturbed part of the habitat where they may find herbaceous plant flowers where they can feed on nectar and pollen. The consequence is that small insects, having little ability to manipulate their physical and biotic environment, may require a relatively small area at any one time but require different small areas in different seasons. That is to say, a conservation area for such a beetle may have to be large enough or carefully located to include all three of the habitats needed by the beetle and to include them in sufficient proximity.

Unfortunately, the multiple habitat needs of different groups of insects are not congruent. The combination of habitats that will be needed to maintain 50 species of bruchid beetles in a dry tropical forest will not be the same as the combination needed to maintain 30 species of anthophorid bees. The outcome is that the 150 species of seed predator bruchids and weevils in a dry forest, for example, may need as much area of habitat as do the 175 species of birds, even though one might be able to argue that any 'average' species of bruchid could maintain a breeding population in an area considerably smaller than is needed to maintain a breeding population of some 'average' species of bird.

There is a second way that great species richness of insects in a given site is dependent on a much larger area than would seem to be necessary considering just the absolute number of hectares needed to support a large breeding

population of an insect species. Any large sample of insects in a tropical habitat contains a significant (but presently unknown) proportion of species that are wanderers or transients that do not maintain breeding populations in the site but nevertheless participate in its ecological interactions (Janzen, 1986c). The larger the number of different habitats that lie near the habitat from which the sample has been taken, the greater the proportion of the sample that will be wanderers and transients. That is to say, the elimination of habitats from a habitat mosaic will lead not only to loss of the species breeding in the habitats eliminated, but reduce the species richness of the remaining habitats.

Habitat diversity

A large area of pristine forest probably has a lower species richness of insects than will the same forest after it has been slightly agriculturalized. In the present day, a national park or other kind of wildland is often selected for conservation status just at the moment that extensive agricultural practices begin to threaten the site. The site is therefore often a mosaic of relatively pristine forest with patches of various ages of secondary succession (started before and after the conservation decree). There is no doubt that mild opening up of a large pristine forest block by agriculture, especially if this agriculture is then followed by abandonment of fields and pastures, raises the species richness of insects in the site overall (it does the same for plants and vertebrates). Human farming activities act like any other predator in this context. By breaking up a large forest block with, for example, scattered fields and brushy pastures, humans open the way for many species characteristic of secondary succession to enter the site and raise the overall number of species and life forms in the site. A 10% reduction in the area of a large block of pristine forest, for example, is unlikely to extinguish more than a few pristine forest species but will generate sufficient habitat for many species of secondary succession that were absent from the original site. As the secondary successional forest patches gradually return to pristine forest stature and closure, species richness of insects will then decline.

Santa Rosa, with its complex mosaic of many ages of regenerating forest may well be at its peak species richness at present. However, Santa Rosa is dry forest with extreme seasonality of rainfall (Table 1). Its dry forest once graded into Costa Rica's rainforest at distances of 1–13 km. When the entire area was a relatively unbroken expanse of pristine forest, the characteristic rainforest species undoubtedly penetrated the dry forest along the riparian bottomlands that extend from the rainforest to Santa Rosa (Janzen, 1987e). A few hectares of relict fragments of these penetrations still exist today in Santa Rosa. Clearing for agriculture and pasture between Santa Rosa and the rainforest has converted this complex vegetation to a much more homogeneous and deciduous secondary successional forest. This forest undoubtedly lacks many species of plants and insects that will return from the rainforest (provided there is rainforest then) as the dry forest returns to a more pristine (and therefore more humid) state. I cannot know if this gain in species will compensate for the loss in species of disturbed and drier sites that will occur.

If the primary goal is maximum species richness in a conservation area, then a certain amount of anthropogenic disturbance will further that goal. At present, the species that are added by disturbance are also often well represented in nearby areas not under conservation. However, as agriculture

becomes more intensive, these species are obliterated from roadsides, unkempt pastures, small scale fields, etc. In the near future, conserved but not truly pristine wildlands may be the sole remaining habitat for many of those seemingly anthrophilic species.

Threat from human associates

There is a peculiar and small set of insects that maintain large breeding populations in croplands, pastures and other cultivated portions of the agroecosystem (Janzen, 1986b). There are two ways that such insects threaten the insects of nearby wildlands. First, if these insects have conspecifics living in the wildlands, the agroecosystem genotypes will flood the wildland gene pools. This is brought to mind by logic, by seeing Santa Rosa periodically invaded by masses of insects from nearby agricultural lands, and by the fact that throughout the world there are pesticide-resistant strains of insects in many habitats that have never been subjected to pesticides.

Second, the cropland insects sometimes support enormous numbers of individuals of parasites, predators and diseases. These carnivores will certainly wash over neighbouring wildlands with as much effect, if not more in some cases, as a major pesticide application. It is striking to note how many people speak of the introduction of biological control agents as being environmentally safe, even when the agent is as generalist a carnivore as is a disease.

CONCLUSION

The designers of today's and tomorrow's conserved wildlands cannot just be mammalogists, ornithologists, botanists, etc. They must think and act like biologists with the goal of conserving interactions and interacting systems. As such, the effect of the loss or alteration of a particular species' population cannot be considered as proportional to its interest to humans or to its conspicuousness. However, conservation directed at inconspicuous small organisms—insects—will always be an uphill battle. There is only one solution. Make insects highly conspicuous through the medium of educational development of their homelands. The day will come when people travel to Santa Rosa in the first week of June because they want to see adults of *Schausiella santarosensis*, one of the very few saturniid moths in Costa Rica that has a very restricted range distribution. They will puzzle over why this moth has only one generation per year; they will wonder why it lies dormant as a pupa for 3 months in moist soil as well as for the 6 months of the dry season, in a habitat in which its legume host plant (*Hymenaea courbaril*) is evergreen. Marine turtles and wildebeest are not the only organisms with puzzling and spectacular seasonal breeding.

It is clear that conserving areas large enough to maintain healthy populations of vertebrates and large plants will also serendipitously conserve major sets of insect populations. However, one cannot succumb to the temptation to view insects as necessarily needing much less area than is needed by large organisms. Many insects, especially those in very seasonal tropical habitats, are highly migratory for distances of hundreds of metres to hundreds of kilometres. While it is as yet unknown to what degree the vegetation between two points in the migratory cycle need to be conserved, it is certain that the two end points of the migration have to be conserved if the population is to persist. One cannot speak of a dry forest national park as an object unto itself.

Insects are major connectors between different species in their habitat, including species that have long been in the eye of the conservation community. By consuming large quantities of plants and plant parts on the one hand, and by being consumed in enormous amounts by vertebrates on the other hand, insects in great part determine the structural relationships between larger organisms. Those of you who wish to see vertebrates in tomorrow's national parks need to give serious consideration to the place of insects in the food and competition webs leading to those vertebrates. Tropical islands, relatively free of insects (Janzen, 1973, 1981) illustrate this very well. The reason that most mainland tropical species of birds could not survive on Caribbean Islands is not the weather. Likewise, it is not the weather that leads to the species of plants that occur on Caribbean islands to most commonly occur in large monospecific stands. The person who wishes to maintain a high species richness of plants in a tropical habitat definitely has the herbivorous insects, vertebrates and diseases on his or her side.

Insects are not lots of little interchangeable creepy-crawlies. The agriculturalist may view them as the scourge of the earth, but that position was long ago pre-empted by *Homo sapiens*. To the conservationist constructing and managing wildlands, and constructed and managed they must be, insects are a diverse educational fodder, food for the vertebrates, and dampeners of competitive ability among plants. All of these things raise the carrying capacity of the site for species and populations of organisms.

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REFERENCES

- BAWA, K. S., 1974. Breeding systems of tree species in a tropical lowland community. *Evolution*, 28: 85-92.
- BULLOCK, S. H., 1985. Breeding systems in the flora of a tropical deciduous forest in Mexico. *Biotropica*, 17: 287-301.
- ELTON, C. S., 1975. Conservation and the low population density of invertebrates inside neotropical rain forest. *Biological Conservation*, 7: 3-15.
- HABER, W. A., 1983. *Hylocereus costaricensis*. In D. H. Janzen (Ed.), *Costa Rican Natural History*: 252-253. Chicago: University of Chicago Press.
- HABER, W. A. & FRANKIE, G. W., 1982. Pollination of *Luehea* (Tiliaceae) in the Costa Rican deciduous forest. *Ecology*, 63: 1740-1750.
- JANZEN, D. H., 1973. Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. *Ecology*, 54: 687-708.
- JANZEN, D. H., 1977. A note on optimal mate selection by plants. *American Naturalist*, 111: 365-371.
- JANZEN, D. H., 1980. Specificity of seed-attacking beetles in a Costa Rican deciduous forest. *Journal of Ecology*, 68: 929-952.
- JANZEN, D. H., 1981. Reduction in euglossine bee species richness on Isla del Caño, a Costa Rican offshore island. *Biotropica*, 13: 238-240.
- JANZEN, D. H., 1983a. Seed and pollen dispersal by animals: convergence in the ecology of contamination and sloppy harvest. *Biological Journal of the Linnean Society*, 20: 103-113.
- JANZEN, D. H., 1983b. *Hymenaea courbaril*. In D. H. Janzen (Ed.), *Costa Rican Natural History*: 253-256. Chicago: University of Chicago Press.
- JANZEN, D. H., 1984. Two ways to be a tropical big moth: Santa Rosa saturniids and sphingids. *Oxford Surveys in Evolutionary Biology*, 1: 85-140.

- JANZEN, D. H., 1985. A host plant is more than its chemistry. *Illinois Natural History Bulletin*, 33: 141-174.
- JANZEN, D. H., 1986a. Guanacaste National Park: tropical ecological and cultural restoration. Editorial Universidad Estatal a Distancia, San Jose, Costa Rica.
- JANZEN, D. H., 1986b. The future of tropical ecology. *Annual Review of Ecology and Systematics*, 17: 305-324.
- JANZEN, D. H., 1986c. Lost-plants. *Oikos*, 46: 129-131.
- JANZEN, D. H., 1986d. Complexity is in the eye of the beholder. Proceedings of a symposium on diversity at the California Academy of Natural Sciences, San Francisco, California (in press).
- JANZEN, D. H., 1987a. How moths pass the dry season in a Costa Rican dry forest. *Insect Science and its Application* (in press).
- JANZEN, D. H., 1987b. Ecological characterization of a Costa Rican dry forest caterpillar fauna. *Biotropica*: in press.
- JANZEN, D. H., 1987c. Biogeography of an unexceptional place: what determines the saturniid and sphingid moth fauna of Santa Rosa National Park, Costa Rica, and what does it mean to conservation biology. Proceedings of a biogeography symposium in Merida, Mexico: in press.
- JANZEN, D. H., 1987d. Natural history of a wind-pollinated Central American dry forest legume tree (*Ateleia herbert-smithii* Pittier). In press, *Legume Conference*, St. Louis, June 1986.
- JANZEN, D. H., 1987e. Habitat sharpening. *Oikos*, 48: 1.
- JANZEN, D. H. & LIESNER, R., 1980. Annotated check-list of plants of lowland Guanacaste Province, Costa Rica, exclusive of grasses and non-vascular cryptogams. *Brenesia*, 18: 15-90.
- JANZEN, D. H. & MARTIN, P. S., 1982. Neotropical anachronisms: the fruits the gomphotheres ate. *Science*, 215: 19-27.
- JANZEN, D. H. & WATERMAN, P. G., 1984. A seasonal census of phenolics, fibre and alkaloids in foliage of forest trees in Costa Rica: some factors influencing their distribution and relation to host selection by Sphingidae and Saturniidae. *Biological Journal of the Linnean Society*, 21: 439-454.
- JANZEN, D. H., JOYCE, F. J. & ISENHART, F., 1987. *Trogon elegans* and sphingid caterpillars in a tropical dry forest. *Biotropica* (submitted).
- ORIAN, G. H. & HORN, H. S., 1969. Overlap in foods and foraging of four species of blackbird in the potholes of central Washington. *Ecology*, 50: 930-936.
- TAYLOR, O. R., 1985. African bees: potential impact in the United States. *Bulletin of the Entomological Society of America*, 31(4): 14-24.