

10 | Comments on Host-Specificity of Tropical Herbivores and its Relevance to Species Richness

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Abstract: We have the working hypothesis that the high species richness of lowland tropical forests is maintained in major part by the herbivore community. The ecological process is that these consumers prevent the best competitors within a given life form from becoming common enough to eliminate competitively the other species of that life form from the community. In short, the herbivores are making space for the poorer competitors. The effectiveness of such a process depends in great part on the degree of host-specificity displayed by the members of the herbivore community. In general, the highly host-specific fraction of the herbivore community should be responsible for the density-dependent responses that result in heavier damage per plant as the plant or plant part becomes more abundant.

Even at this embryonic stage, we can identify three major aspects of the way host-specificity relates to plant species diversity. (1) How does host-specificity differ from the viewpoint of the animal as contrasted with that of the plant? The animal is concerned with what proportion it can eat of the plant species and plant parts in the habitat. It is further concerned with its relative fitness on each. The plant is concerned with what proportion of the herbivore community will respond in a density-dependent manner to the plant's frequency in time and space. (2) Why are tropical herbivores more host-specific than temperate ones (if they are)? The selective pressures in the coevolution of feeding efficiency and plant defenses are such that the larger the plant resource base, and the more constantly it is present (in both cases, from the perspective of the animal), the more host-specific will be the animals and the more species of animals can coexist in a given plant community. (3) Who should win the coevolutionary race between a particular plant population and the herbivores in its habitat? The more effectively the herbivore community counters the plant's chemical and behavioral defenses, the shorter should be the half-life of a plant population in a given habitat. We may conclude from this that extinction rates should be higher in the tropics than in temperate zones. Further, the number of plant species in a habitat should be only indirectly related to rates of speciation.

INTRODUCTION

We have the working hypothesis that the high species-richness of lowland tropical forests is maintained in great part by the herbivore community. The

ecological process is as follows. The herbivores present the best competitors within a given life form by becoming common enough to eliminate competitively the other species with that same form from the habitat; the herbivores are making space for the poorer competitors. The effectiveness of such a process depends in great part on the degree and kind of host-specificity displayed by the members of the herbivore guild. In general, it is the highly host-specific fraction of the herbivore guild that should be responsible for the density-dependent responses which result in heavier damage per plant as the plant becomes more abundant (Janzen, 1970, 1971a, b, c, d, 1972a, b, c; May *et al.*, 1970; Connell, 1971).

I shall discuss three aspects of the relationship of herbivore host-specificity to tropical tree species richness. The first is methodological: How does host-specificity differ from the viewpoints of the animal and the plant? The second deals with the species richness of the herbivore guild: Why are tropical herbivores more host-specific than temperate ones (if they are)? The third links herbivory and extinction rates: What is the structure of the coevolutionary race between a particular plant population and the herbivores in its habitat?

HOST-SPECIFICITY FROM THE ANIMAL AND PLANT VIEWPOINT

We must first clarify an important aspect of terminology. There are two pairs of words which are often confused in the literature: generalist versus specialist, and host-specific versus not host-specific (and various Latin and Greek transliterations). The first pair usually refers to the length of the list of plant parts or species on which the individuals of the herbivore species may be found feeding. The second pair often refers to this as well, but may also incorporate some measure of the relative abundance on each host species. Statements on host-specificity may even incorporate some measure of how reliably the population displays this relative abundance in different habitats, at different times, etc. Furthermore, the issue is almost never discussed in respect of the obvious problem that there is variance in host-specificity by the individual and by the population as a whole; it is almost impossible to discriminate between these two types of variance with a sample taken at just one time. If one quarter of the herbivore population is found on one species of plant and three-quarters on another, this may be due to all the herbivores feeding indiscriminately on both and the plants being in a 1 : 3 ratio, or due to the herbivore population being heterozygous at a 1 : 3 ratio with respect to its genetic programming in host-specificity. Finally, we must accept the possibility that the host population is heterozygous with respect to susceptibility (Jones, this volume).

From the herbivore's viewpoint, we want to know what proportion of the

total nuts, fruits, leaves, etc. in the habitat are acceptable food. Furthermore, we want to know its relative fitness when feeding on each species. In such a calculation we cannot afford to forget that herbivores do not eat Latin binomials. They feed on specific parts of the plant, or if they feed on several parts of one species (e.g. old and new foliage) they have quite different relative fitnesses on each. They may even have different fitnesses on the same plant part when that part is in different microhabitats or when taken from plants growing under different nutrient-competition-herbivory regimes.

Let us consider a *Curculio* weevil that matures in the nuts of an oak and two hickories in a temperate zone forest composed of maple, tulip, poplar, beech, oak and two species of hickory. The weevil may be regarded as a generalist in that 50% of the tree species serve as hosts. On the other hand, if we add in a measure of nut abundance, the weevil may be labeled a specialist if the oaks and hickories are rare. Furthermore, if only a few of the trees produce large nut crops at intervals of several years, then the trees may be much rarer for the weevil than for the forester. To complicate the picture further, we must remember that the acorns may have a high tannin concentration and thus female weevils reared from them might have much lower fecundity than those from the hickory nuts.

There is, however, another set of confounding factors in host-specificity from the animal's viewpoint. If we look at all the weevils in the genus *Curculio* (which feed on the large nuts of Fagaceae and Juglandaceae in North America (Gibson, 1969)), we find that most have 3-5 host species and it appears that if these hosts are growing in the same site, a single species of weevil may be breeding in all of them. In this context the weevil mentioned in the previous paragraph is neither an extreme specialist nor extreme generalist. On the other hand, out of well over 100 species of seed-eating weevils and bruchids reared to date in a host-specificity study in Costa Rica (Janzen, 1972c), only 8 occur on more than one host species. Here, a weevil that matures in seeds of three tree species could be labeled an extreme generalist even though it feeds on less than 1% of the plant species in the habitat. This actually makes sense biochemically. The marked specialization cited above is probably based on differences in secondary compounds in the seeds, and thus an insect that feeds on more than one or two may have to have an extremely generalized gut biochemistry.

From the plant's viewpoint, the critical variable is what proportion of the plant is consumed by the herbivore each time the plant produces a new set of whatever parts the herbivore eats. This is related in a very complex manner to the fate of the herbivore population when the food item is absent (e.g. during a year between seed crops). For convenience, at this point we may recognize a

dichotomy between the physical environment and the biotic environment as represented by alternate hosts. Forgetting alternate hosts for the moment, the herbivore population will be variably decimated when crossing the same metric distances in space and time between hosts. For example, to a herbivore moving between two host trees, 300 m along a dry ridge crest may be ten times as far as 300 m across a humid swamp. A two-month wait between seed crops may be twice as lethal to a bruchid population during the rainy season as during the dry season.

With respect to alternate hosts, the situation is equally complex. When the primary host is absent, we may profitably distinguish between alternate hosts that simply slow the rate of population decline, and those that lead to population increase. Slowing of the rate of population decline may be accomplished in two ways: (1) Commonly an alternate host only provides water, sugar or other compounds which help keep the animal alive but do not sustain reproduction (e.g. "non-hosts as well as leaves and stems of host plants serve for water supply" —Eggerman and Bongers, 1971). This phenomenon is manifested in tropical deciduous forest by the fact that many species of insects pass the dry season as active adults in reproductive diapause; during the dry season their host-specificity decreases greatly as they feed on a number of plants and plant parts they ignore in the rainy season (Janzen, 1973a, b). (2) Small amounts of reproduction on a sub-optimal host may also suppress the rate of population decline when the primary host is absent. A striking example is provided by temperate zone conifers. When the host population has a three-year reproductive (mast) cycle, some species of cone-infesting insects have a three-year diapause. However, a small percentage of their populations does not go into diapause, and reproduces on the cone crops of the few trees that are out of phase with the remainder of the tree population. They do poorly on these "alternate" hosts, yet it is this sub-population that keeps the herbivore in the game when the tree occasionally waits four years between mast crops (Janzen, 1971b).

Alternate hosts, on which the herbivore does not reproduce, may also strongly influence the herbivore's fitness when it finally locates the primary host. For example, the seed-eating bruchids mentioned earlier lay their eggs on the host fruits or seeds, and the larvae mature within. The percentage of the seed crop eaten is directly related to the number of eggs that the female beetle can lay. Her fecundity may be nearly doubled by having had the opportunity to feed on flower nectar (and pollen?) during the time between emerging from last year's seed crop and finding this year's seed crop (Janzen, 1971b). Here we may expect female bruchids, whose larvae are so specialized, to be generalists owing to the chemical similarity of flower nectar and pollen.

The abundance of the primary host should be especially sensitive to the presence of alternate hosts which provide a food supply on which the herbivore can multiply. On a contemporary time scale, the plant should be indifferent to whether the non-host plants are of many or few species; these plants may almost be regarded as inert "stuffing" between the primary host plants and the alternate hosts. We are then concerned with how many species of alternate hosts are present, their timing, their relative abundance, and their spacing with respect to the primary host. Cotton stainer bugs (*Dysdercus* spp.) and Malvales provide a good tropical example (Janzen, 1972a). These bugs feed and reproduce on the seeds of tropical Malvaceae and Sterculiaceae, and have received special attention because of their importance as cotton pests. They build up large densities on the seed crops of wild Malvales; then, as that food supply is exhausted, they move *en masse* to nearby cotton fields. The reverse also occurs. It is easy to see how there would be selection favoring either strong interspecific synchrony (to satiate the bugs) or maximal asynchrony among the wild species of Malvales in a tropical forest. Every time a new malvaceous species immigrated to a given habitat, there was a strong possibility of its either raising the amount of damage done to the seed crops of other Malvales, or incurring unusually heavy destruction of its own seed crop.

We should also turn the question upside down and ask what fraction of the total herbivore guild can feed on any given species of plant. Since ecologists are not yet in the habit of characterizing entire herbivore guilds, I have to let the reader's imagination wander on the subject. For a start, however, we can be assured that in a tropical habitat it will be only a tiny fraction, while in a temperate habitat it may be a very large fraction. Ironically, this suggests that a new chemical defense in a temperate tree may be subject to a much more severe herbivore test than it would in a tropical tree. We may also note that the answer depends to a large extent on what portion of the herbivore guild is vertebrate and what part arthropod, as vertebrates appear to have much greater generalist abilities as based on the detoxification ability of their complex gut microflora.

WHY SHOULD TROPICAL HERBIVORES BE MORE SPECIALIZED?

There are two causally related short answers to this question. First, the food items of tropical herbivores display more spatial, chemical and behavioral heterogeneity than do those of temperate herbivores. Second, there is a theoretical answer that has been around a long time: the more predictably available a specific food item (e.g. new leaves on the lower branches of heavily shaded crowns of tree species x), the more a herbivore can afford to specialize in the face of interspecific competition for that general class of food items (e.g. all

new leaves). We can then see that the number of herbivore species in the habitat should be a function of the size of each kind of food relative to the size of the herbivore, the distinctness and predictability of the food items in the eyes of the herbivore, and the total amount of food that can be harvested without generating effective defense mechanisms through natural selection (see also Southwood, 1961; Janzen, 1968). Let us examine several applications of these ideas.

I have recently found that there are substantially more species and individuals of herbivorous insects (and associated parasites) at intermediate elevations (900–1300 m) on tropical mountains than at sea level. The provisional explanation is that the increased insect community is living off the photosynthate that is not metabolized by the plants during the cool nights at higher elevations (Janzen, 1973a, b). However, there is no dramatic increase in plant species at this elevation. In accordance with the ideas expressed in the previous paragraph, I interpret these data in the following manner. In their biochemical-behavioral “eye”, the herbivores divide each plant in the community into a number of parts (shoot tips, upper crown-leaves, shade-leaves, flowers, anthers, etc.). In the lowlands, a number of these plant fractions will not be an adequate food supply to support a completely specialized herbivore. The herbivore that might have been supported by it will be more of a generalist (and competitively displace some other herbivore) or be itself absent. As the size of the plant’s total energy budget increases with elevation, the replacement rate for specific fractions eaten off the plant should increase, allowing any given species of plant to support more species or herbivores. This assumes that the plant has some absolute percentage of its total budget that must be expended on maintenance; if the percentage needed for maintenance declines with an increasing overall budget, there should be even more which the herbivore can remove without generating selective pressures sufficient to produce a chemical defense to exclude or debilitate the herbivore.

Throughout this and the following discussion, I have been treating the habitat as ecologically “full”. I assume that the number of herbivore species in the habitat is set by energy and competitive relationships, and has little to do with rates of speciation; these rates are assumed to be high enough such that far more species arrive at any given habitat than that habitat can absorb. This assumption is explicitly contradictory to the hypothesis that the tropics have so many species because they are a benevolent repository for species from harsher environments.

What happens when the resource base becomes more finely divided? In a temperate zone deciduous forest-field mixture, there is a large guild of seed-

eating insects. Many anecdotal reports suggest that the majority of these species of seed-eaters are parasitized by one or more species of parasitic Hymenoptera. Further, the proportion of the individuals that are parasitized appears to be high enough to have at least the potential for influencing the dynamics of the density of their prey. In a tropical forest-field mixture, the story is quite different. Of more than 100 species of weevils and bruchids reared from seeds in Costa Rica, not more than 35% had any parasites at all. Furthermore, most of those with parasites experienced parasitization well below 10%. There is no reason to postulate that the overall biomass of seed-eating insects is any less in the tropical forest than in the temperate zone forest. If anything, it might be higher in the tropics owing to the steadier input of seeds.

However, at the tropical site, the parasites' food resource is much more finely divided than in the temperate zones; there are more species of bruchids at the tropical site (about 50 × 100 miles) than in all the United States (which has about 100 species (Johnson, 1970)). One of the major problems facing a hymenopterous parasite is to have the morphology and behavior to penetrate the fruit and seed wall with its ovipositor so as to reach the bruchid or weevil larva within. It may also have to deal with toxic secondary compounds that the larva has derived from the seed. We may expect a parasite that can deal with any one bruchid, but the tropical parasite will have to have an attack repertoire that allows effective parasitization of several species of bruchids or weevils, if it is to have a host population large enough for survival. It is significant in this connection that most of the Costa Rican bruchid parasites recorded to date parasitize several species of bruchids, and the hosts of these bruchids usually have very similar fruit morphology.

A third elaboration of tropical herbivore specificity is brought to mind by the mixed dipterocarp forest growing on white sand hillside soils in Bako National Park (sea level to 100 m elevation), Sarawak. At first glance, this rain forest appears unexceptional. It has a high tree species richness, a generally closed canopy at 30–40 m, and a shrub- and sapling-filled understory. However, two important things strike the observer on closer examination. First, the rate of regeneration of cleared forest is extraordinarily slow. A 40 acre field on a broad and flat ridge top had scattered shrubs and small trees 2–4 m tall among a sedge and herb ground layer; it had never been grazed by cattle and was reputed to have been last cleared in the early 1940s. For a site with about 4 m of relatively evenly distributed rainfall per year (similar to Kuching, cf. Fogden, 1971), this suggests exceptionally low primary productivity, which is probably due to the white sand soil. Second, the vertebrate community was almost non-existent, despite this being a national park that was rarely visited. During two weeks of

field work in the rainy season, I saw only two insectivorous lizards; I rarely saw more than three small to medium sized birds during a clear morning. There were almost no mammal tracks on the clean sand and mud paths, and rodent runways were only very rarely observed.

In this strange community, foliage-inhabiting herbivorous insects (and their arthropod predators) were almost completely absent. Unfortunately, standardized samples were not taken, but my experience with taking tropical sweep samples (Janzen, 1973a, b) leads me to feel certain that the quantity of insects taken would have been similar to that on the top of a 3300 m Costa Rican mountain. This would be about one tenth what one would get in a Costa Rican sample from an environmental regime like the Sarawak site, but on better soil. Yet the Sarawak site has a very high diversity of plants in the forest (the old field, however, was very impoverished). If tropical herbivorous insects are not forced to be highly specialized, as the overall productivity declines in the habitat they should increase the list of acceptable host plants. The number of species of insects is expected to decline, but some should remain common. The only other option would be for each species to become very rare; however, the small number of species of insects observed on the foliage does not support this idea.

WHAT IS THE STRUCTURE OF THE COEVOLUTIONARY RACE?

Let us construct a hypothetical evolutionary history for a tree species in a particular tropical habitat in a particular region (e.g. the site represented by well drained north-facing lateritic slopes of valleys with permanent rivers). Shortly after the species arrived in the habitat the ensuing population probably increased after a period of physiological evolutionary adjustment to as high a density as would ever be experienced in that habitat. This is because in the initial immigration it left all its herbivores behind and was at first faced only by those herbivores that could shift over from the resident plants. It should thus have been at its competitive best. This phenomenon is currently manifested in the practice of establishing tropical tree plantations on foreign continents. As the tree progresses through evolutionary time, it should gradually acquire an array of host-specific herbivores, as ways evolve to breach the tree's chemical and behavioral defenses. Since the herbivores have many more generations per year than the tree, it seems likely that were they to be super-proficient at locating their food, the tree would have a short history indeed. However, as the herbivore load builds up, the density of the tree should decline, causing some of its herbivores to switch to other plant species or even become locally extinct. The rate of decline of the tree's density may also be slowed by the local extinction of other species of trees that were major competitors with our exemplar tree. We

may expect the tree eventually to become so rare that it becomes locally extinct through a perturbation of the habitat or through failure to outcross. It is noteworthy that in the latter case the failure to outcross may not only be directly lethal for an obligatory outcrosser, but also may result in new resistant genes or recombinants being lost from a facultatively outcrossing population before they can spread through the susceptible tree population.

We now have a plot of tree density (survivorship) against evolutionary time, that looks roughly like a jagged negative exponential that eventually drops abruptly to the x-axis. At any one time, we would expect most of the tree species in the habitat to be fairly low on the long right-hand tail of their evolutionary survivorship curve (i.e. most of the trees should be moderately rare). There should be very few common species. The abundance of the common species should be directly proportional to how recently they immigrated and how different a habitat each immigrated from. There should be no excessively rare species (e.g. one or two adults per habitat).

How would the evolutionary survivorship curves differ for the tree species in a temperate zone habitat? They should start off in the same manner, but once into their downward decline, they should level off well above the x-axis. This sustained high density and low rate of local extinction is postulated because long before a temperate zone tree species gets very rare, it can escape from potential herbivores through greater than annual synchronized timing of its nut, flower, leaf, etc. production on a population- or habitat-wide basis (Janzen, 1971b). A newly invading temperate zone tree should also have a more difficult time in becoming established than its tropical counterpart, because the temperate zone tree's competitors will be a few very common species, each highly adapted to the peculiar weather and edaphic circumstances of that habitat. In a tropical forest, almost every time an invasion is attempted, the new seedling or sapling will be competing with a new array of species, each of which has similar abiotic needs to the others and to the immigrant. On the average, we may expect that at least 50% of the time the immigrant should be at a competitive advantage when compared with the tree with which it is most directly competing.

I expect to find that once established in a temperate zone habitat, a tree species persists almost indefinitely. On the other hand, there should be a comparatively high local extinction rate from any given tropical habitat. That is, extinction rates should be higher in the tropics, rather than lower, as is often assumed to be the case.

I should emphasize that owing to the highly heterogeneous physical environment of the tropics as a whole, there should be intra-tropical gradients in extinction rates as well. We should expect the highest extinction rates in those

sites where conditions favor the rapid development of an effective and highly host-specific herbivore load on each tree species, and where the tree species lack environmental cues adequate to allow population-wide behavioral synchrony on a greater than annual basis.

In closing, I might add that the more skewed to the right the average evolutionary survivorship curve and the closer to the x-axis it is, the more species there should be in the habitat at any one time. In short, the more the conditions favor survivorship of the average tree population at a low density, the greater should be the species richness of the habitat.

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