Plant Allelochemicals, Tritrophic Interactions and the Anomalous Diversity of Tropical Parasitoids: The "Nasty" Host Hypothesis

Ian D. Gauld; Kevin J. Gaston; Daniel H. Janzen

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Plant allelochemicals, tritrophic interactions and the anomalous diversity of tropical parasitoids: the "nasty" host hypothesis

Ian D. Gauld and Kevin J. Gaston, Dept of Entomology, Natural History Museum, Cromwell Rd, London, U.K. SW7 5BD – Daniel H. Janzen, Dept of Biology, Univ. of Pennsylvania, Philadelphia, PA 19104, USA

The number of species in many groups of parasitoid Hymenoptera does not increase rapidly with decreasing latitude. Discussion of the processes generating this pattern has focussed upon changes in host demographic traits and upon the effect of seasonality. Here we advance a further and compatible hypothesis, that tropical parasitoid hosts are less available to parasitoids than are extra-tropical hosts because their tissues are, on average, more chemically toxic than are the tissues of extra-tropical hosts. There is some evidence that suggests that tropical woody plants are, in general, richer in toxic secondary compounds than are extra-tropical species, and evidence exists to demonstrate that these allelochemicals may have adverse effects on parasitoids attacking phytophagous insects feeding on such plants.

The species richness of many groups of parasitoid Hymenoptera does not increase rapidly with decreasing latitude as does the species richness of most groups of arthropods that serve as parasitoid hosts (Owen and Owen 1974, Janzen and Pond 1975, Janzen 1981, 1983, Gauld 1986, Noyes 1989, Gauld, Hanson and Janzen, 10 years of Malaise trapping in Costa Rica; Janzen, 11 years of intensive rearing of parasitoids of macrocaterpillars in Costa Rica). Here we discuss the possibly major role of plant defensive chemistry in the processes that lead to a global pattern of parasitoids being less speciose in the tropics than would be expected from a consideration of the species richness of their hosts.

What are the processes that block an increase in the species richness of parasitoids as the species richness of potential hosts increases along a latitudinally decreasing gradient? To date, discussion driven by this question has focussed on three processes. First, changes in demographic traits of potential hosts along latitudinal gradients are expected to affect their parasitoids. For example, the population size of an "average" host species decreases from extra-tropical ecosystems to tropical low- and middle-elevation ecosystems. This means that the tropical parasitoid has to either be more adept at locating individual hosts, or be more generalist in its choice of hosts, if it is to harvest the same number of hosts per unit time or per generation as does its extra-tropical counterpart (Janzen and Pond 1975). Both of these demands on the parasitoid should lower the number of parasitoid species that will be able to survive per host species as the host species becomes scarcer. Put another way, the average species of tropical insect should be a suitable host for fewer species of parasitoids than will be the average species of extra-tropical host.

Second, the seasonality of a host species decreases from extra-tropical to tropical ecosystems. This decrease results in fewer and less intense seasonal peaks during which a parasitoid could encounter a high density of even a "rare" host.

Third, in the tropics parasitoids do not have a cool winter to aid them to pass the season(s) that are inimical to their hosts and invertebrate enemies. Whether the waiting tropical parasitoid is a dormant immature or potentially active adult, it is subject to many species of invertebrate predators and hyperparasitoids, as well as to heat and desiccation (Janzen 1973, 1976, 1983).

The "nasty" host hypothesis

Here we wish to advance a fourth and compatible hypothesis, that potential hosts in the tropics are also less available to parasitoids than are extra-tropical hosts because their tissues are, on average, more chemically toxic than are the tissues of extra-tropical hosts.

This primary hypothesis is based on a separate secondary hypothesis – that the overall greater chemical toxicity of tropical plants (Levin 1976) will result in the tissues of the insects that feed on them being more toxic in some way that is detrimental to the parasitoid. Although virtually no studies of such tritrophic interactions have been undertaken in natural tropical ecosystems, a considerable body of evidence now exists that shows that high levels of plant secondary chemicals in a herbivore's diet have detrimental effects on potential parasitoids (Flanders 1942, Smith 1978, Campbell and Duffey 1979, 1981, Duffey et al. 1986, Vinson and Barbosa 1987, McDougall et al. 1988, Barbosa et al. 1991).

Our primary hypothesis is also based on the observation that the number (and in some groups, at least, the proportion) of warningly-coloured (aposematic) insects is higher in the tropics. Such warningly-coloured insects (excluding their Batesian mimics) are also likely to have tissues that are potentially toxic to parasitoids, irrespective of the origin of the toxic compounds (Brower 1984, Guilford 1990). Our intent is not to discuss whether insect tissues are actually more toxic in the tropics, but rather to take this as a basic assumption so as to be able to further discuss our primary hypothesis.

The "nasty" host hypothesis states that, quite aside from whether the tropical resource for a parasitoid community is more finely subdivided than is the extra-tropical resource, each resource bit is better defended – by accident of chemical processing or by the evolution of defensive traits – than is an equal-sized resource bit in an extra-tropical ecosystem. This means that the tropical parasitoid must be yet either more specialized, if it feeds on one host species, or more versatile if it feeds on multiple species, than need be its extra-tropical counterpart. Either challenge should result in a net lowering of the number of species of parasitoids that can persist in a habitat.

Mechanics of being a "nasty" host

For the purposes of this discussion, we treat lowland to intermediate elevation (below about 2500 m) tropical rain forest and dry forest mainland ecosystems as representative of "the tropics". These tropical ecosystems are substantially richer in kind and quantity of directly toxic secondary compounds (alkaloids, uncommon amino acids, flavonoids, cyanogenic glycosides, steroids etc.) in their plants than are extra-tropical ecosystems (e.g. Levin 1976). Plant families well-known to be rich in toxic compounds, such as the Anacardiaceae and Solanaceae, are primarily tropical centred (Heywood 1985). Furthermore, it has been demonstrated repeatedly that closely related, sympatric rain forest tree species that produce toxic allelochemicals differ from each other in their allelochemical composition (Waterman 1983, and references therein). While the toxic secondary compounds are highly variable in their physiological impact on different taxa, we treat them here as overall "toxic", "inimical" and/or "repellent" to carnivorous parasitoids. Parenthetically, we note that these plants may also be richer in certain digestion inhibitors (polyphenols, etc.) and other large molecules that protect plants (e.g. proteinase inhibitors, lectins) than are extra-tropical plants, but we assume here that these molecules are largely irrelevant to the hypothesis since they do not find their way into potential host tissue as intact molecules.

The group of insects that feed on tropical plants are substantially richer in toxic secondary compounds than are extra-tropical insects. Whilst this fact has not been documented through an all-encompassing review, it forms a major part of the field observations of anyone who works for extended periods of time with tropical insects in the field. This increased toxicity comes about through a) direct synthesis of toxins, b) modification of toxins extracted from host plants, c) sequestration of toxins extracted from host plants, and d) presence of these compounds in digestive tracts. An array of tropical potential hosts, therefore, is likely to represent a more diverse and more potentially dangerous array of dietary items to a parasitoid, than does an array of extra-tropical potential hosts.

Microecological distribution of the "nasty" host effect

Actual or potential tissue toxicity is not distributed uniformly amongst potential hosts for parasitoids, within or between tropical ecosystems. It is also clear that the ability to deal with actual or potentially toxic secondary compounds will not be distributed evenly within or between parasitoid taxa. The heterogeneity of these distributions reveals several interesting aspects of the "nasty" host effect.

Insect eggs, insect pupae, carnivorous larvae, sap-sucking immature hemimetabolous insects, and insects that bore in dead sapwood are examples of groups of parasitoid hosts that generally lack self-generated secondary compounds or secondary compounds derived from plants (e.g. Orians and Janzen 1974, Brower 1984). This is the case irrespective of whether the potential host is from a tropical or an extra-tropical ecosystem. It is within these groups of hosts that the "nasty" host effects are unlikely to be involved in whatever gradients of species richness are displayed by their parasitoids, and one may predict – other factors being equal – that parasitoid species richness will increase with potential host species richness. In many groups this is indeed so. For example, Kamath and Gupta (1972) noted that the Rhyssinae, a cosmopolitan group of ichneumonids attacking borers in wood, are more species rich in lowland tropical forests than they are in extra-tropical forests.

Groups of egg parasitoids, such as Trichogrammatidae, Scelionidae and Mymaridae, appear to be more species rich in the tropics than in extra-tropical habitats (Noyes 1989, Askew 1990). This could easily be due to two processes. First, the general palatability of insect eggs removes the nasty host hypothesis from consideration. Second, owing to the chemical, morphological and behavioural similarity of eggs (Orians and Janzen 1974), an increase in egg species richness does not automatically result in an inimical subdivision of the egg resource for egg parasitoids. For example, 1000 eggs of one species of notodontid moth in England are probably not much different from 1000 eggs of 20 species of notodontid moths in Costa Rica. However, an array of 1000 notodontid caterpillars of 20 species is a much more diverse host substrate than is a monospecific array of 1000 notodontid caterpillars, in part because of the "nasty" host effect, and in part because of morphological, physiological, phenological and behavioural considerations of the caterpillars.

The distribution of species among ichneumonid subfamilies along extra-tropical to tropical species gradients offers a third example. Campoplegine and banchine ichneumonids, whose larvae feed directly in the larvae of exposed or weakly concealed leaf-eating Lepidoptera larvae, are generally less species rich in the tropics than outside. Pimpline and mesostenine ichneumonids, whose larvae develop in Lepidoptera pupae, show the opposite trend (Janzen 1981, Gauld 1986, 1987, 1991). However, we recognize that this process is compatible with other processes that may generate the same phenomenon.

As a general rule, insect larvae that live outside the leaf and consume whole or nearly whole bites of leaf tissue are consuming maximum amounts of toxic compounds. On the other hand, those that mine in galls, leaves and stems often select only the most nutrient-rich and/or most toxin-poor part of the tissue to consume (e.g. Lin and Trumble 1986, Cornell 1989). It is quite striking that the hymenopterous parasitoid assemblages of larvae inside plant tissues in the tropics are of similar species richness to those in extra-tropical zones, while the assemblages of parasitoids attacking exophytic larvae decrease with decreasing latitude (Hawkins 1990).

Homoptera probe specific host-plant tissue and ingest xylem or phloem-sap (Dolling 1991). They are thus probably able to avoid a substantial number of the plant allelochemicals compartmentalized in other cells or intracellular vacuoles. The chalcidoid parasitoids of sternorrhynchine Homoptera and the dryinid parasitoids of Auchenorrhyncha are known to be very species rich in tropical habitats (Olmi 1984, Noyes 1989). Soil inhabiting phytophagous insects, which probably also ingest less toxic compounds than do consumers of green leaves, also have parasitoid assemblages of approximately the same size in tropical and extra-tropical habitats (Hawkins 1990).

Within those parasitoids that have leaf-eating hosts there should be another ecological dichotomy. As mentioned earlier, many tropical plants have leaves that are rich in tannins and other digestion inhibitors, whilst a much greater array of tropical plants of all life forms are rich in those relatively small molecules that are directly toxic to physiological systems. Parasitoids should find those hosts that feed on plants rich in digestion inhibitors to be substantially less toxic than are those hosts that feed on plants rich in small toxic molecules. This leads to the straightforward prediction that increased species richness in the former group of potential hosts is less likely to make life difficult for parasitoids than will increased species richness in the latter group of potential hosts. Survey data that could be used to examine this hypothesis do not exist at present.

However, there are some tantalizing examples. *Enicospilus americanus* is a large ophionine ichneumonid parasitoid that attacks many species of saturniid caterpillars in extra-tropical North America and southern South America (Townes and Townes 1966, Gauld 1988a, b); similarly *Enicospilus texanus* attacks a wide range of *Hemileuca* species (Saturniidae) in the southern United States and northern Mexico (Gauld 1988a). However, neither of these "generalist" parasitoid species extends into the neotropics, and all rearings to date among the more than 100 species of *Enicospilus* in Costa Rica suggest that they have but one host, or several extremely similar hosts (Gauld 1988b, D. H. Janzen, unpubl.). It is consistent with the "nasty" host hypothesis that when *Enicospilus* parasitizes caterpillars that feed on the relatively atoxic trees and shrubs of extra-tropical forests it can have a long host list, but when it is parasitizing caterpillars that feed on relatively toxic trees and shrubs of tropical forests, it is restricted to one of these host species (and presumably has the micro-behaviour and/or metabolic ability to avoid the toxins in that host).

A host is not a simple bag of fat, muscle, water and secondary compounds. Equally, a parasitoid may not eat, or be subjected to, all parts of the host in space or time. For example, many koinobiont (sensu Askew and Shaw 1986) endoparasitoids that have protracted first larval instars often wait in a very specific part of the host such as in the salivary glands or cerebral ganglion, or reside within a trophamnionic membrane (Gauld and Bolton 1988), and therefore may not be exposed to potentially toxic compounds that are present in some parts of the host. Many parasitoids, especially ichneumonids, do not eat their host until it has voided its gut contents (Gauld 1988c), whilst many endoparasitic braconid larvae initially feed on teratocytes – cells derived from the braconid embryonid trophamnion which absorb nutrients from the host (Polaszek 1986). Whilst not enough is known of the detailed distribution of secondary compounds in potential hosts or of where parasitoids spend their time and feed in the host, it is certainly predictable that there will be found to be groups of parasitoids that are strongly influenced by the secondary compound chemistry of potential hosts, and others that are quite unaffected, according to the parts of host that are eaten and the places in the host where the parasitoid larvae reside.

The "nasty" host hypothesis predicts, just as do other associated hypotheses, that there should be more tropical species that are completely free of parasitoids than there are extra-tropical species that are completely free of parasitoids. Direct tests of this prediction must await long-term thorough faunal surveys. However, there certainly are numerous tropical species of potential parasitoid hosts that lack Hymenoptera, Diptera or both parasitoids; many of these partially or totally parasitoid-free tropical hosts are aposematically coloured (D. H. Janzen, unpubl.).

We expect parasitoid Hymenoptera and Tachinidae to respond differently to increases in host secondary compound toxicity, reflecting their very different evolutionary ancestry (Eggleton and Belshaw, in press). Parasitoid Hymenoptera have a long evolutionary history as carnivores, feeding on the muscle, fat, haemolymph etc. of their hosts. Their closest link to herbivory as a phylogenetic lineage is with distant sawflies that fed on wood or in the relatively innocuous inner stem tissues of plants (Königsmann 1978, Rasnitsyn 1980). Tachinidae have as their phylogenetic ancestors a group of taxa whose larvae generally feed in decomposing materials, and therefore have long dealt with bacterial and fungal toxins in their diet and immediate habitat. We predict, therefore, that parasitoid Hymenoptera will be more affected by an increase in host toxicity than will be Tachinidae, and that Tachinidae will be more "generalist" than will be Hymenoptera with respect to the species richness of the array of hosts used by a single species. However, we recognize that this potential effect can easily be confounded by a greater impact of host behavioural and morphological specialization on tachinids than on parasitoid Hymenoptera. For example, parasitoid Hymenoptera can evolutionarily track their hosts from day to night (tachinids are diurnal), and from eggs or larvae to pupae (tachinids generally do not oviposit in eggs or on pupal stages). Tachinids may be quite robust in the face of increased host toxicity but exceptionally susceptible to other forms of host specialization.

In conclusion

Available data show that tropical woody plants are, in general, richer in toxic secondary compounds than are extra-tropical species. Ample evidence exists to demonstrate that these allelochemicals may have adverse effects on parasitoids attacking phytophagous insects feeding on such plants. Combining these observations, the "nasty" host hypothesis identifies yet another ecological process that probably influences tropical-extratropical gradients in parasitoid species richness. Any given set of parasitoid taxa will be potentially influenced by this process to the degree that the life styles and natural histories of the parasitoids and their potential hosts interact with secondary plant chemistry. To determine the latter we need both basic survey data as to which parasitoids use which hosts, and as to which hosts they do not use. Equally, we need detailed anatomical/biochemical studies to know the degree to which parasitoids actually interact with, or are constrained in their potential evolution by, the secondary compound chemistry of their hosts.

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