Herbivory at the Limits

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THE TROPICAL FOREST CANOPY has been described as the last biotic frontier[1]. It has a number of features which make this characterization particularly apt: until recently it has been largely inaccessible, our knowledge of its inhabitants is poor, and discussions of its features are prone to become polarized – opinions are rife and facts few; any generalizations are likely to become targets for debate.

Against this background, Basset's[2] recent discussion of the host specificity of herbivorous insects in rain forests is likely to attract close attention. In particular, his suggestion that polyphagy may be more widespread than previously thought will almost certainly receive some intense scrutiny, even if it is not likely to be viewed, in some quarters at least, as a contentious statement. More specifically, information on the numbers and patterns of interspecific interactions in rain forests is central to an understanding of the basic structure of these systems and to questions of their temporal stability and resilience to perturbation.

Basset restricts his considerations to arboreal and free-living insect herbivores. Whether, as he suggests, these represent the majority of the species of herbivorous insects in rain forests could perhaps be contested, but they undoubtedly constitute a significant proportion of herbivore–plant interactions in these habitats. Support for arguments as to the host specificity of these organisms is derived from two sources, first, from Basset's own interpretation of the available literature, and second, from a detailed investigation of the arboreal arthropod fauna of the Australian rainforest tree black booyong [*Argyrodendron actinophyllum* (Sterculiaceae)]. From the former, he can glean little more than that evidence is growing for the existence of polyphagous herbivorous arthropods in rain forests. Indeed, one might expect this to be an inevitable consequence of increases in both host records and the numbers of investigations with time. Perhaps more important is the recognition that many of the oft-cited examples of the high specificity of rainforest herbivores relate to insects that are concealed feeders or are mainly restricted to herbaceous plants and vines. Arboreal free-living insect herbivores have received rather little attention, even by rainforest standards. It might also be observed that levels of host use in any sample of herbivorous insects are almost invariably right skewed. Most species have comparatively few hosts, while a few have many hosts (Table 1). The length of the right-hand tail is probably less important to an understanding of patterns of host specificity than is the degree of skew.

Most of the hard data in Basset's paper are from his own field studies, and his case for levels of polyphagy having been underestimated previously largely stands or falls upon his results and their interpretation. His studies, which were carried out in warm subtropical rain forest north of Brisbane, have spawned many papers (see Ref. 2 for references), are impressive in scope, and have not, as far as I am aware, been paralleled for any other large rainforest tree. Over three years, more than 50 000 arthropods were obtained from the crowns of mature specimens of *A. actinophyllum*, by the use, in all seasons, of quantitative collecting techniques. With the assistance of specialist taxonomists, a large proportion of these specimens were sorted to species, providing a detailed picture of the fauna associated with this tree. Insights into the host specificities of the herbivores were sought through feeding trials with the foliage of *A. actinophyllum* and other trees, through direct observation in the field, through rearing and from information on the spatial occurrence of species in the forest.

From this work, eleven percent (17 species out of the 156 recognized) is considered to be a conservative estimate of the proportion of herbivorous insect species foraging within *A. actinophyllum* crowns which are monophagous (restricted to host species belonging to the same family) or oligophagous (restricted to a few hosts from related families or to very few hosts from unrelated families). Inevitably, this figure is open to a number of questions. Exclusion of species based on inference, or even on the basis of feeding trials might be challenged; species may feed successfully on hosts upon which they never naturally occur. Equally, one might also ask how representative of the entire herbivorous insect fauna of the tree are samples obtained from one site in its geographic range (the range of *A. actinophyllum*, although not continuous, spans some 13° of latitude[4]). Nonetheless, even if only approximately correct, this result would not appear to substantiate the idea that herbivorous rain forest insects tend to be specialists.

Taking the results for the insect herbivore assemblage of *A. actinophyllum* at face value, one is led to ask what features this tree might possess that promote polyphagy amongst the herbivores which feed upon it. Basset identifies several possibilities. These include the apparent scarcity of qualitative defences, the low nutrient levels and high fibre content of the foliage, the relatively unpredictable availability of young foliage, and possible low levels of predation pressure. The impact of the results pertaining to this tree species upon our understanding of the specificity of insect herbivores in rain forests essentially rests upon how typical such characteristics are of other rainforest tree species (it has been estimated that there are some 50 000 species of tropical trees[5], most of which will occur in rain forests).

Basset recognizes that other tree species may be very different. It is difficult, however, to reach general conclusions as to what form any differences may take, and hence predict their consequences. The case of plant defences provides a good example of the problems. Although variation in the defences exhibited by plant species at the same latitude and by temperate and tropical trees has frequently been remarked upon, we remain some way from a sound understanding of the relative roles of different forms of defence in different forest systems. Nonetheless, the broad conclusion that alkaloids are both more common and more toxic in tropical plant species than in their temperate counterparts[6–8], implies that unlike *A. actinophyllum* many rainforest trees employ qualitative defenses.

An obvious problem in attempting to evaluate the relative preponderance of conditions favouring narrow or broad host specificities lies in judging the relative importance of the various factors promoting monophagy or polyphagy. It is salutary that various authors (see Refs 9,10 for some references) have found grounds for arguing that herbivorous tropical insects are more specialized, less specialized or no different in their host use when compared with their temperate counterparts. In major part, this apparent confusion results from the recognition of

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Table 1. Patterns in the number of host species per consumer species for various groups of herbivorous tropical insects[a]

Insect	Site	n[b]	Number of plant species per herbivore species: Mean (SD)	Median	Range
Seed weevils	Guanacaste, Costa Rica	110	1.4 (1.0)	1	1–8
Butterflies[c]	La Selva, Costa Rica	75	1.7 (1.8)	1	1–7
Butterflies	Corcovado, Costa Rica	49	1.6 (1.4)	1	1–6
Butterflies	Santa Rosa, Costa Rica	50	1.2 (0.5)	1	1–3
Ithomiinae	Limoncocha, Ecuador	27	1.4 (2.7)	1	1–5
Heliconius	La Selva, Costa Rica	7	2.3 (2.6)	1	1–8
Heliconius	Arima valley, Trinidad	14	1.8 (1.0)	1	1–5
Heliconius	Rincon, Costa Rica	15	1.5 (0.7)	1	1–3
Geometridae on *Piper*	La Selva, Costa Rica	20	2.6 (1.4)	2	1–6
Ithomiinae	Campinas, Brazil	18	4.3 (3.0)	3	1–12
Hispine beetles	Caribbean, Costa Rica	8	4.6 (3.4)	4	1–11
Flea beetles	La Selva, Costa Rica	7	3.4 (2.1)	2	2–7
Heliconius	Rio de Janeiro, Brazil	11	3.2 (2.1)	3	1–6
Seed weevils on *Parkia*	South America	10	3.6 (2.3)	3	1–7
Leaf weevils on *Piper*	La Selva, Costa Rica	25	4.4 (4.5)	3	1–18

[a]Modified from Ref. 3, where the sources are given.
[b]n is the number of insect species in each case.
[c]'Butterflies' consists of Nymphalidae, Pieridae and Papilionidae.

different factors as being of primary importance in moulding host ranges, and occasionally from a failure to acknowledge that individual factors may influence different groups of herbivorous insects in very different ways. As Basset recognizes, although various factors can be identified as likely contributors to the host ranges of free-living arboreal insect herbivores in rain forests, these may be interrelated and interact in potentially complex ways.

Any fresh comments on levels of host specialism in habitats rich in insect species seem likely to be incorporated into a further evaluation of the probable global number of extant species in this taxonomic class. Although they retain interest, personally I doubt whether calculations necessitating the direct input of host-specificity parameters will provide a robust basis for estimates. Calculations tend to be sensitive to this variable; assumed levels of herbivore specificity has been identified as one of the more important contributors to estimated numbers of insect species[11–13]. Our understanding of the patterns of host use of herbivorous rainforest insects will have to be vastly improved before adequate levels of certainty can be achieved. There are no obvious short cuts to this end. Sound information on host use has to be built up over long periods of time and, if the errors contained within many host lists are to be avoided, with great patience. Basset's work demonstrates that this can be achieved even for rainforest trees of up to 50 m high. It will take many more such studies to substantiate his general contention that polyphagy is more prevalent in such systems than previously thought.

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