Ann. Zool. Fennici 24:239–247. 1987

Biogeographical and evolutionary aspects of insect herbivory

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Tahvanainen, J. & Niemelä, P. 1987: Biogeographical and evolutionary aspects of insect herbivory. — Ann. Zool. Fennici 24:239–247.

The composition and diversity of phytophagous insect communities associated with various plants are reviewed. Emphasis was placed on variation and anomalies in species-area relationships of insect-plant associations. The extent of variation in the number of phytophagous insect species, as explained by the range and abundance of the plants, was consistently higher for trees and shrubs, polyphagous insect groups and generally and weakly defended plants than for herbs, specialized insect groups and strongly and distinctively defended plants. Good species-area relationships are mainly due to simple mechanical processes, while anomalous or poor species-area relationships evidently reflect intricate ecological and evolutionary interaction between the insects and plants studied. The rate of insect recruitment by introduced plants is highly variable. Chemically isolated and strongly defended plants accrue insects very slowly and mainly through evolutionary processes, while poorly defended plants are quickly colonized by local polyphagous insect species. Old, declining plant taxa, such as ferns and gymnosperms, have impoverished phytophagous faunae as compared with angiosperms, angiosperms presumably being inherently more responsive to coevolutive processes. This leads to the high taxonomic and chemical diversity today apparent among both angiosperms and their herbivores. The coevolutionary history of insects and plants is demonstrated by the fact that even today phylogenetically old phytophagous insect groups tend to be concentrated on old plant taxa while young insect phytophages are associated mainly with angiosperms.

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1. Introduction

In recent years, numerous investigations on the interaction between plants and herbivorous animals have shown interesting patterns in the life strategies and diversity of phytophagous insects associated with various plants. These studies have shown that there is a positive correlation between the species richness of herbivorous insects and the range and/or abundance of the plant (for references see Table 1). Plant characteristics such as size, structural complexity, time of occurrence in a particular area, number of habitats occupied and degree of taxonomic isolation also explain the variation in insect species diversity (for reviews see Kennedy & Southwood 1984, Srong et al. 1984, Leather 1986).

There are consistent differences in the species richness and composition of the insect faunae associated with plants of different growth form and different evolutionary age (Table 1, Zwölfer 1978, Hendrix 1980). Thus there are more herbivorous insect species on trees and shrubs than on herbs, and the herbivorous insect associations on old, primitive plant taxa appear to be impoverished as compared with the angiosperms.

While significant correlations have been found between the properties of plants and the diversity of their associated insect communities, very little is known of the actual ecological and evolutionary mechanisms responsible for these patterns. Since Southwood's (1961) paper on species-area relationships between herbivorous insects and British trees, surprisingly little has been learnt about the biological and evolutionary processes responsible for the relationships observed (see also Neuvonen & Niemelä 1983).

This paper discusses the present state of research concerning phytophagous insect species richness and the structure of insect communities on plants of differing abundance, geographical distribution, growth form and evolutionary status.

Table 1. Summary of published species-area relationships for insects and different types of plants. S = number of insect species. A = geographical range of the plant. AF = geographical range and frequency (abundance) of the plant. – = slope not given. * = analysis based on tree genera. Statistical differences between the groups A, B and C were tested using the Mann-Whitney U-test.

Insect–plant associations	Dependent/ independent variable	Slope of species-area graph (z)	Variation in insect numbers explained by range (and frequency) of plant (R^2)
A. *Wide insect taxa on trees or shrubs*			
All insects on woody shrubs (Lawton & Schröder 1978)	ln S / ln A	0.64	0.91
All insects on British trees (Strong & Levin 1979)	log S / log A	0.89	0.58
Insects and mites on British trees (Kennedy & Southwood 1984)	log (S+1) / log AF	0.46	0.59
Lepidoptera, Hymenoptera, Homoptera and Diptera on Rosaceous trees (Leather 1986)	log (S+1) / log AF	0.82	0.65
All insects on British shrubs (Strong & Levin 1979)	log S / log A	0.66	0.49
All insects on British shrubs (Lawton & Schröder 1977)	log (S+1) / log A	0.45	0.85
Lepidoptera, Hymenoptera, Homoptera and Diptera on Rosaceous shrubs (Leather 1986)	log (S+1) / log AF	0.43	0.62
B. *Restricted insect taxa on trees or shrubs*			
Macrolepidoptera on Finnish trees (Neuvonen & Niemelä 1981)	S / ln AF	–	0.35
Macrolepidoptera on Finnish deciduous trees (Neuvonen & Niemelä 1981)	S / ln AF	–	0.57
Sawflies on Finnish trees (Neuvonen & Niemelä 1983)*	log (S+1) / log AF	–	0.30
Macrolepidoptera on British trees (Neuvonen & Niemelä 1983)	log S / log A	–	0.35
Microlepidoptera on British trees (Neuvonen & Niemelä 1983)	log S / log A	–	0.36
Leaf-mining Lepidoptera on American oaks (Opler 1974)	log S / log A	0.47	0.90
Cynipid gall wasps on American oaks (Cornell & Washburn 1979)			
– Atlantic region	log S / log A	0.25	0.41
– California region	log S / log A	0.65	0.33
Leaf hoppers on British trees (Claridge & Wilson 1981)	log (S+1) / log A	0.34	0.16
Leaf miners on British trees (Claridge & Wilson 1982)	log (S+1) / log A	0.34	0.19
Leaf miners on British trees (Godfray 1984)	log (S+1) / log A	0.50	0.13
C. *Insects on herbs*			
All insects on British herbs (Strong & Levin 1979)	log S / log A	0.49	0.28
All insects on perennial herbs (Lawton & Schröder 1977)	ln (S+1) / ln A	0.54	0.71
All insects on weeds and other annuals(Lawton & Schröder 1977)	ln (S+1) / ln A	0.58	0.47
All insects on monocots (Lawton & Schröder 1977)	ln (S+1) / ln A	0.39	0.51
All insects on Cynareae (Lawton & Schröder 1978)	ln S / ln A	0.65	0.74
All insects on ferns (Auerbach & Hendrix 1980)	S / log A	0.29	0.18
Agromyzids on British Umbelliferae (Lawton & Price 1979)	log (S+1) / log A	0.14	0.32
Microlepidoptera on British Umbelliferae (Lawton & Price 1979)	log (S+1) / log A	0.16	0.24
Lepidoptera, Hymenoptera,Homoptera and Diptera on Rosaceous herbs (Leather 1986)	log (S+1) / log AF	0.37	0.32

Differences between the groups A, B and C:	ln z :	A/B	NS	ln R^2:	A/B	$p<0.01$
		A/C	$p<0.01$		A/C	$p<0.05$
		B/C	NS		B/C	NS

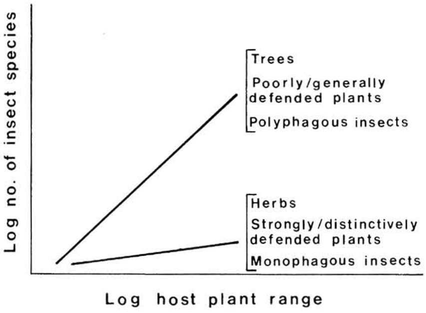

Fig. 1. Some key properties of plants and insects characteristic to a high and low slope of the species-area graph.

2. Species-area relationships of herbivores

Widespread plant species tend to have many associated phytophagous insect species. Positive species-area relationships have been established for all insects on plants of variable taxonomic groups and for only distinct taxonomic or ecological groups of either insects or plants (Table 1).

A study of the published species-area relationships reveals interesting variation and anomalies. Firstly, there are clearly more insect species on trees and shrubs than on herbs. Secondly, there are profound differences in individual case studies as to the extent of variation in numbers of herbivorous insect species explained by the range and/or abundance of the plant. The explained variation tends to be higher for trees and shrubs than for herbs, higher for taxonomically diverse or polyphagous insect groups, and higher for taxonomically homogeneous plant groups (Table 1). Thirdly, the slope of the species-area graph, that is, the rate of accrual of insect species as a function of plant's range appears to be steeper for trees and shrubs than for herbs (Table 1, Fig. 1).

The slope of the species-area correlation and the percentage of insect species diversity, as explained by the host plant's range, is disappointingly lower for herbs than for shrubs and trees (Lawton & Price 1979, Leather 1986), and there are certain instances in which these figures are conspicuously low even for trees (Claridge & Wilson 1981, 1982). These differences and anomalies can be explained by the variation in host plant specificity of the insects and the taxonomic/chemical isolation of the plants studied (Table 2). Thus, in cases where the insect group is composed of very specialized feeders and the plant group in question contains strongly and distinctively defended species, the evolutionary ties between the plant and the insects are so strict and dominating that, beyond a certain limit, expansion of the range cannot add new insect species to the association. Thus the pool of specialist herbivores on a particular plant soon become exhausted and the generalist feeders encountered through range expansion are unable to overcome the plant's strong and distinctive defence. Agromyzids on British Umbellifers studied by Lawton & Price (1979) may represent this kind of insect-plant association. Also British trees, when considering the rather specialized feeding habits by leaf hoppers and leaf miners (Claridge & Wilson 1981, 1982), may form such a heterogeneous group of plants that only weak species-area relationships can be created. The better species-area relationship between American leaf-mining Lepidoptera and oaks, which appear to be rather generally defended, than between cynipid gall wasps and oaks (Opler 1974, Cornell & Washburn 1979) may simply reflect a higher host specificity among the species of the latter insect group. On Finnish trees the number of plant species in the host plant taxon explained 84 % of the species richness of sawflies, which are extremely specialized feeders (Neuvonen & Niemelä 1983).

In general, herbaceous plants are more qualitatively defended, having alkaloids and other low molecular toxins, than shrubs and trees which are characterized by non-specific quantitative defences

Table 2. Combinations of insect and plant characteristics producing species-area relationships with a low or high percentage of variation in insect species richness explained by host plant range/abundance.

Insect characteristics	Plant characteristics
Low	
Taxonomically restricted insect groups	Herbaceous plants
Mono- and oligophagous insect groups	Strongly/distinctively defended plants
Miners and gallers	Chemically heterogenous groups of plants
High	
Taxonomically wide insect groups	Trees and shrubs
Polyphagous insect groups	Poorly/generally defended plants
Chewing (and sucking) insects	Chemically homogenous plant groups

(Feeny 1976, Rhoades 1979, Harborne 1982). Quite logically herb feeding insects seem to be more specific in their food selection than tree and shrub feeders (Futuyma 1976, Niemelä et al. 1982). Both the accrual rates (slope) and the percentage of variation in insect species richness explained by the range/ abundance of the plant should therefore be higher for trees and shrubs than for herbs (Table 1, Table 2, Fig. 1).

Deviations and anomalies in species-area relationships may actually reflect fundamental ecological and evolutionary differences between different insect-plant associations. In fact, so-called good species-area cases, usually obtained from studies on wide taxonomic entities of plants and insects and from generalized herbivores on generally (or poorly) defended plants, may not be particularly interesting ecologically. Instead, they may be products of simple mechanical processes which automatically add new, more or less generalized feeders when a plant's range expands. More attention should be paid to different types of species-area relationships and to the insect and plant taxa deviating from the general pattern. In this approach, however, more detailed information is needed both on the ecology of insects and on the qualities of plants important for food utilization by herbivorous insects. Probably the most crucial factor in need of further study is plant's secondary chemistry (see also Neuvonen & Niemelä 1983, Kennedy & Southwood 1984, Leather 1986). Taxonomic relation is too robust a character to indicate the critical qualitative (secondary chemical) differences between plant species. This is clearly demonstrated by North European willows (*Salix* spp.), among which morphologically and taxonomically very similar species may differ dramatically in their phenolic glycosides, a group of secondary phenolics, basically toxic to all kinds of animals (Julkunen-Tiitto 1985, 1986, Tahvanainen et al. 1985a, 1985b). Recently, Taper & Case (1987) showed that the variation in leaf tannin levels was the most significant predictor (with $r^2 = 47$ %) of the number of leaf-galling cynipid wasp species on American oaks. The addition of host plant range to the regression improved the amount of variance explained by only 11 per cent.

An additional factor, so far very little studied, which may explain the differences in insect species diversity and the species-area relationship between trees and herbs is the length of the active growing period of the plant foliage. Woody plants (trees and shrubs) bear green foliage most of the growing season while the foliage of most herbaceous species are present for a much shorter period of time. Most importantly, most deciduous trees produce new leaves during rather a long period of time. This means that trees and shrubs are for herbivores renewing source of food during the progress of the growing season. This allows herbivore species with differing food preferences to colonize the plant (Niemelä & Haukioja 1982). In addition to the low resource diversity, shortage of time for larval development may limit the number of insect species capable of utilizing herbaceous plants (Niemelä et al. 1982).

When drawing conclusions the following points must be remembered. The insect faunae associated with trees and shrubs are probably more thoroughly recorded than those associated with herbs and grasses (Leather 1986). It is also possible that the commonly used estimates of plant range and abundance may not give an ecologically reliable measure of plant quantity, and the estimates may not be comparable for plants of different growth form or for different subsets of the entire herbivore faunae (Kennedy & Southwood 1984, Janzen 1986). The parameters of different species-area correlations must be compared with caution, since both the method of data transformation and the type of regression model used can considerably affect both the slope and the explanatory power of the regression (Connor & McCoy 1979). Fortunately, however, the methods of data processing are quite similar in the three groups of cases (Table 1, groups A, B and C) compared in this paper.

3. Insect recruitment by introduced plants

3.1. Variable accrual rates on introduced plants

Plants transferred either accidentally or intentionally to other continents or remote areas provide interesting large-scale experiments for the study of insect community dynamics. The better documented cases come from cultivated crops or ornamental trees (Strong et al. 1984). Some tropical and subtropical crops such as sugar cane, cocoa, coffee, coconuts, citrus, cotton and rice have been introduced for cultivation in all continents. All these crops have accumulated herbivorous insect pests extremely rapidly; a few hundred years after introduction the area where they were planted becomes the main factor explaining the variation in insect numbers (McCoy & Rey 1983). The amount of time after introduction does not seem to have any influence on the insect species richness. It is also known that some other cosmopolitan crops and weeds mainly growing in middle latitudes, such as maize, soya bean and thistles, accumulate a "normal" number of insect herbivores within a few hundred of years. The colonizers of introduced plants are almost exclusively local polyphagous, externally feeding insects (Strong et al. 1984).

Sometimes the recruitment of insect herbivores by some introduced plants takes place very slowly. For example *Opuntia* from the New World introduced to South Africa and Australia and *Eucalyptus* from Australia introduced to Africa and to North and South America have been colonized by hardly any local phytophagous insects since their introduction a hundred or more years ago (Strong et al. 1984). Quite slow insect recruitment is also exhibited by deciduous trees transferred from Great Britain to South Africa and vice versa. The insect fauna on introduced species is conspicuously impoverished as compared with native trees in both areas (Southwood et al. 1982, see also Southwood & Kennedy 1983).

Very rapid recruitment of insect herbivores by introduced plants has evidently been overemphasized due to disproportionate information on cultivated crops. Crops represent plants with a rather poor chemical defence especially after being transferred to cultivated and often heavily fertilized monocultures. Thus they are very easily colonized by mobile polyphagous insects (see Janzen 1986).

We conclude that the rate of herbivore recruitment varies greatly among introduced plants and obviously depends on the general level and distinctiveness of their chemical defence as compared with local plants. The role of taxonomic (chemical) isolation in the rate of insect accrual on introduced plants was clearly demonstrated by Connor et al. (1980). The results showed that those introduced Fagaceous trees having consubgeneric species in the locality of introduction accrued a nearly normal number of leaf miner within a hundred years of introduction. By contrast, few species of leaf miners were recruited by taxonomically more distant tree species.

3.2. Two superimposed phases of insect accrual

We believe that there is a wide continuum of cases among introduced plants as to the speed of herbivorous insect recruitment. At one extreme we have poorly defended cultivated crops with very rapid asymptotic recruitment and at the other strongly defended and/or taxonomically (chemically) isolated plants, such as *Opuntia* and *Eucalyptus,* with very slow accrual. The former are mainly colonized by polyphagous species (Strong et al. 1984) without need of evolutionary adaptation. The latter, on the other hand, appear to be inaccessible to any kind of local insect and are slowly colonized either after evolutionary adaptation by local insect species or by insects introduced from the plant's original range.

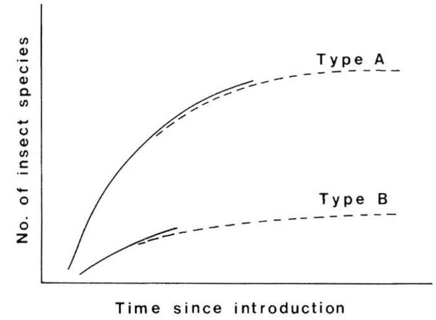

Fig. 2. Two extreme types of insect recruitment curves exhibited by introduced plants. Poorly or generally defended plants approach type A recruitment dominated by a rapid ecological phase of accrual (solid line). Strongly defended or chemically isolated plants become mainly colonized through evolutionary processes (broken line) leading to a very slow recruitment (type B curve).

Thus in insect recruitment by introduced plants it can be seen that rapid initial colonization by polyphagous species is governed mainly by ecological factors and that slow evolutionary recruitment occurs by either local or introduced insects (see also Janzen 1986). The colonization of poorly protected plants should be primarily governed by ecological factors, while strongly defended plants require special adaptations before local insects are able to utilize them (Fig. 2). Slow evolutionary accrual continues also on poorly defended plants after the rapid phase of ecological colonization. It is important to note, however, that both types of recruitment processes are superimposed; their relative contribution varies according to the level of the plant's resistance and the colonization ability of the local insect species.

In herbivorous insect recruitment on different types of introduced plants we can see a trend parallel to the species-area relationships of differentially defended local plants, discussed in the previous chapter. In both processes polyphagous insects on weakly defended plants produce good species-area relationships while on distinctly or strongly defended plants the evolutionary adjustment between trophic levels dictate the insect species richness to the extent that only poor species-area relationships can be obtained.

4. Herbivorous insect communities on major plant taxa

4.1. Coevolution of major plant and phytophagous insect taxa

The majority of existing higher plants belong to three main subsections of the plant kingdom: pteridophytes (mainly ferns), gymnosperms and angiosperms. Phylogenetically they represent the old and primitive (ferns) to the young and advanced (angiosperms) types of vascular plants. Ferns originate from the Devonian some 400 million years ago. Gymnosperms are a somewhat younger group, but angiosperms did not appear until the late Jurassic, less than 200 million years ago (Niklas et al. 1983).

First phytophagous insects, probably sap-sucking Collembolans or Homopterans, appeared either in the Devonian or during the Carboniferous (Strong et al. 1984). Leaf-chewing tenthredinid sawflies (Symphyta) have been present since the Permian. Ecologically most sophisticated phytophagous insects such as leaf miners and gallers and certain taxonomic groups such as Lepidopterans and phytophagous Dipterans have developed within the past 100 million years in close association with angiosperms (Zwölfer 1978, Strong et al. 1984). Both taxonomic and ecological diversification of phytophagous insects is closely tied with the evolution of higher vascular plants.

Since ferns, gymnosperms and angiosperms represent different evolutionary phases of the plant kingdom, in a clear sequential order, it is interesting to see if the composition of present insect faunae on these plant taxa reflect to any extent the coevolutionary development of plant and insect taxa. This is particularly relevant if we assume that plants and insect herbivores have evolved through coevolutionary processes as proposed by Ehrlich & Raven (1964).

Definite questions can be presented in this respect: 1) Are there significant differences in insect species richness on three major plant taxa? 2) Is there any relationship between the phylogenetic age of these plant taxa and their associated phytophagous insects? and 3) Are there any apparent patterns in feeding mode and the degree of specificity of insects associated with ferns, gymnosperms and angiosperms?

4.2. Insect species diversity on major plant taxa

Few attempts have been made to compare herbivorous insect species diversity on major plant taxa. It is well known but only superficially documented that mosses and lichens are very resistant to herbivorous insects and are, consequently, utilized by a very low number of insect species (Gerson 1969, Seppänen 1970, Emmet 1979). According to Balick et al. (1978) ferns are utilized by phytophagous insects to an extent quite comparable with higher plants. Later Hendrix (1980) came to the conclusion that significantly fewer insect species than expected utilize ferns as a food source; the ratio of fern feeding insect species to fern species being 1:19 while the ratio of phytophagous insects to angiosperms is less than 1:1 (Hendrix 1980). In a separate analysis Auerbach & Hendrix (1980) found a lower number of Macrolepidopteran species per plant species on ferns than on angiosperms but the difference was not statistically significant. However fern feeders are more polyphagous than angiosperm feeders (Hendrix 1980) so that the total number of Macrolepidopteran species in relation to the plant species diversity must be much lower for ferns than for angiosperms.

There are some indications that macrolepidopteran species diversity on gymnosperms is also lower than on angiosperms (Holloway & Hebert 1979, Neuvonen & Niemelä 1981). If this trend holds for other groups of insects as well, we can conclude that also on gymnosperms the herbivorous insect species diversity is lower than on angiosperms. There are several explanations for these trends. Firstly ferns and gymnosperms represent old plant taxa which have clearly passed the peak of their species diversity (Niklas et al. 1983). The species richness of ferns reached its maximum already during the Carboniferous and has declined since then (Fig. 3). The species diversity of gymnosperms has also decreased significantly within the last 100 million years (Niklas et al. 1983). It seems probable that the decline in species diversity has been associated with a decline in chemical and ecological diversity as well thus leading to the narrowing in the variety of resources available to herbivorous insects. Furthermore the reproductive strategy of ferns and gymnosperms characterized by a large effective population size and by a generalist pollen and propagule dispersal may not be particularly favourable to speciation and local differentiation (Niklas et al. 1983). Consequently the coevolutionary mechanisms between herbivorous insects and ferns and gymnosperms have probably never reached

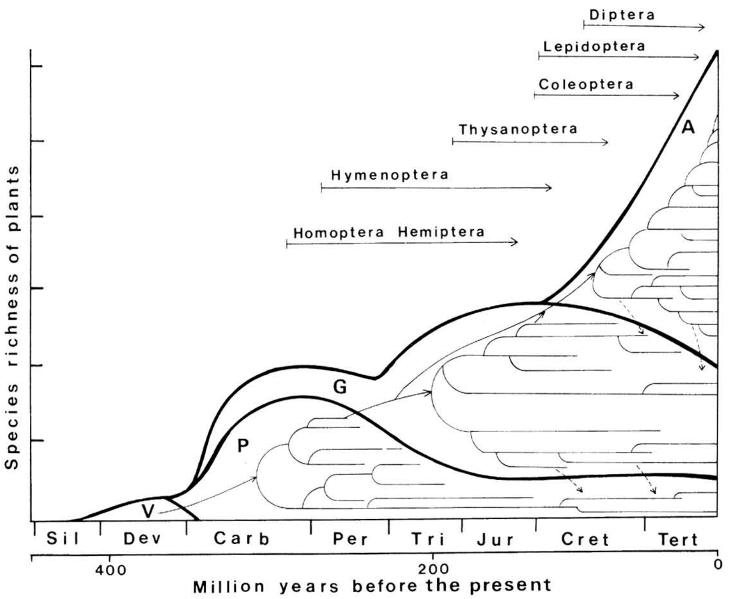

Fig. 3. Geological patterns in species diversity of major taxa of vascular plants (thick lines) and hypothetical diversification of phytophagous insects (thin lines) associated with them. Switching of phytophagous insects between plant taxa has taken place mainly from more advanced towards more primitive groups (broken arrows). First appearance of phytophagous forms in major insect orders is indicated. V = primitive vascular plants, P = Pteridophytes, G = Gymnosperms, A = Angiosperms. Modified from Zwölfer (1978), Niklas et al. (1983) and Strong et al. (1984).

a very high level of intensity. On the other hand, angiosperms with small effective population sizes and specialized mechanisms of pollen and propagule dispersal may have been more responsive to interactive processes between plants and their herbivores. This leads to an extraordinary high species diversity apparent both in angiosperm plants and their associated insect herbivores.

4.3. Phylogenetic relationships of plant-insect associations

The phylogenetic diversification of phytophagous insects coincides very closely with the evolution of major taxa of higher vascular plants (Zwölfer 1978, Strong et al. 1984). It is tempting to believe that insect groups originating during the peak diversity of a certain plant taxon should be well represented on that particular taxon also later. Thus the oldest phytophagous insect groups should dominate on ferns and gymnosperms while young insect taxa should be relatively more common on angiosperms. According to the analysis of Hendrix (1980), the relative numbers of insect species from different insect orders utilizing ferns are not representative of the taxonomical distribution of phytophagous insects in general. Somewhat surprisingly Hendrix (1980), however, concludes that juxtaposition of the evolutionary histories of ferns and phytophagous insects fails to adequately explain the anomalies since evolutionarily old groups are no better represented on ferns than on younger groups. Reanalysis of Hendrix's (1980) data reveils, however, that the insect orders containing the oldest phytophagous insect groups are better represented on ferns than expected (Fig. 4).

These contrasting conclusions from the same data are evidently due to different way of defining the phylogenetic age of insect groups used in the analysis: Hendrix (1980) presumably used the absolute age of insect orders in his analysis while we base our conclusion on the actual age of phytophagy in each insect order. For example, the order Orthoptera is very old but herbivorous orthopterans did not appear earlier than the middle Cretaceous (Strong et al. 1984).

Detailed analysis of the species distribution of central European insect families on the phylogenetic sequence of vascular plants supports the conclusion that the old phytophagous insect groups tend to be concentrated on old plant taxa while the younger insect groups mainly use young angiosperm taxa. It is interesting that different families within the same insect order follow this rule rather consistently (Zwölfer 1978). Also the insect faunae associated with even more primitive plant taxa, such as mosses, are predominantly composed of phylogenetically old insect types (Gerson 1969).

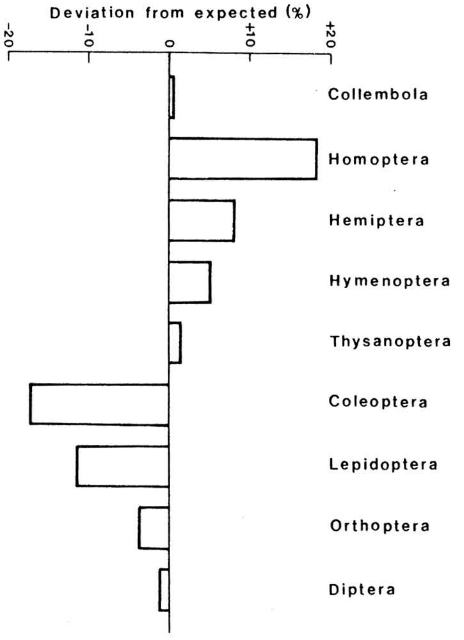

Fig. 4. The difference between observed and expected (zero line) numbers of insect species of major phytophagous insect orders on ferns. The null hypothesis is that the insect species distribution between orders is the same on ferns as among phytophagous insects in general. Insect orders are placed in order on the basis of the first appearance of phytophagy. Data after Hendrix (1980).

As Hendrix (1980) pointed out there are few insect taxa that are solely restricted to ferns. The contemporary fern fauna seems to be a mixture of original fern feeders and representatives of insect taxa which recently switched from phylogenetically younger plants (Fig. 3, see also Strong et al. 1984). Thus the insects feeding presently on ferns and gymnosperms do not form a pure line of adaptive radiation coevolved with their original host taxa but a significant portion of their present phytophages are newcomers from rather recently diversified insect associations of young angiosperms.

The present, undoubtedly insufficient, information indicates that fern feeding insects are more polyphagous as compared with insects associated with angiosperms (Hendrix 1980). According to Holloway & Hebert (1979) conifer feeding Macrolepidopterans in Canada are more generalized in host selection than macrolepidopterans associated with deciduous trees. This trend in feeding specialization of phytophagous insects can logically be explained by lower diversity in secondary chemistry of ferns and gymnosperms as compared with angiosperms (Balick et al. 1978, Hendrix 1980, Harborne 1982). Thus, regardless of the time available for coevolutionary diversification and specialization among fern and gymnosperm feeding insects the major taxonomical and ecological explosion of phytophagous insects has taken place recently and in a very short period of time on angiosperms. This supports the argument proposed by Niklas et al. (1983) that there is an inherent difference between angiosperms and lower vascular plant taxa in their predisposition to diversify taxonomically or chemically and consequently to create, either through coevolutionary or one-directional adaptive processes, highly diverse phytophagous insect associations.

Acknowledgements. We wish to thank Ilkka Hanski, Olli Järvinen and an anonymous reviewer for valuable criticism on the manuscript.

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Received 26.I.1987, revised 8.VII.1987
Printed 30.IX.1987