Some Observations on the Structure of Phytophagous Insect Communities: The Implications for Biological Control

by

J. H. Lawton and D. Schröder[1]

INTRODUCTION

Considerable attention has been paid to the number of species of insects associated with various species of trees (Opler 1974; Southwood 1961, 1973; Strong 1974a, b; van Valen 1975). The purpose of the present investigation is to analyse the structure of the insect communities associated with higher plants other than trees. The work is a co-operative venture between a practical biological control worker (D.S.) and theoretical community ecologist (J.H.L.). A great deal of the information which we have used was collected for biological control purposes. In analyzing just a small fraction of this high quality, empirical data we hope to stimulate other biological control workers to undertake similar 'follow up' and 'synthesis' studies wherever possible, if only to prove that our generalisations are wrong! The more we know about plant-insect associations, the more we are likely to be able to manipulate them successfully, and to anticipate problems before they occur (Wapshere 1974).

We direct ourselves to five basic problems. First we ask how various types of higher plants (specifically woody shrubs, perennial herbs, weeds and other annuals, and monocots excluding grasses) differ in the number of species of insects which they support. This analysis is carried out by comparing standard species-area curves (Dritschilo *et al.* 1975; May 1975; Opler 1974; Strong 1974a) for the various species of plants in each of these four groups. (A brief consideration is also given to the small quantity of data available for aquatic perennial dicots.)

In the second section, we consider how the 'taxonomic isolation' of a plant, measured simply as the number of related species in the same genus and geographical region, might also influence the total number of insect species to be found on it.

Questions one and two deal with the total species of insects accumulated by a particular plant species over evolutionary time. We are not concerned, in this paper, with the problem of newly introduced plant species (Strong 1974b).

As well as the total number of species, we also look at the 'fine structure' of these insect guilds. Section three examines the taxonomic composition of the total insect faunas of particular types of plants, and section four considers the problem of specialist (monophagous) and generalist (polyphagous) insects. In particular, we enquire whether there are any systematic patterns in the types of insects added by plants as their associated faunas grow in size; for example do plants with particularly well developed associated faunas number proportionally more 'generalists' amongst them, and so on?

Finally, section five looks briefly at feeding types, (i.e. chewers, gall-formers, miners, suckers and fruit and flower feeders), again in relation to the type of plant, its geographical abundance, and taxonomic isolation.

DATA SOURCES

We have drawn on data from two primary sources, namely the accounts of individual plant-species given in the *Biological Flora of the British Isle*, published in the *Journal of Ecology* between Volume 36 (1948) and 61 (1973) (Lawton 1976) and the published and unpublished survery data of the Commonwealth Institute of Biological Control's European Station at Delémont, Switzerland. It is particularly important to realise at this stage that our analyses are based entirely on European data. As such, they may be less, or in some cases entirely, inappropriate when considering plant-herbivore associations from other geographical regions.

The C.I.B.C. data is of two main sorts; Zwölfers' extensive analyses of the phytophagous insects attacking wild Cynareae (thistles, burdocks, knap-

[1] Department of Biology, University of York, Hestlington, York, YO1 5DD U.K. and C.I.B.C. European Station, 1 Chemin de Grillons, Delémont, Switzerland.

weeds etc.) in Europe (Zwölfer 1965a), and the combined survey work of several of the staff on various species of woody shrubs (Herting 1964; Malicky, Sobhian & Zwölfer 1970; Scheibelreiter 1973; Zwölfer 1964, 1965b). In addition to these two main bodies of survey data, we also touch on survey data from a range of other species of plants.

We do not propose to list the data in full; a copy of the original information is available on request.

INSECT SPECIES ASSOCIATED WITH VARIOUS TYPES OF HIGHER PLANTS: SPECIES-AREA CURVES

This part of the work draws almost entirely on the *Biological Flora,* which deals in detail with the biology and ecology of over 100 species of plants. We excluded several from this analysis, for a variety of reasons.

a) We did not include any trees because similar, and more extensive data have already been very adequately analysed elsewhere (Southwood *loc cit*; Strong *loc cit*).

b) The grasses (Graminae) were also omitted because the insect data appeared to be particularly unreliable. (The entomological literature on which the accounts are based frequently records 'grass' as a food plant, rather than the species of grass involved.)

c) A fairly arbitrary series of decisions, which inevitably introduced a certain amount of error, had to be made about the accounts which listed no insect species associated with particular plants. Where an author used a term like 'none observed' we included the record as a zero; where he used a term like 'no information' we excluded it.

It is important to realize some of the other limitations of this *Biological Flora* data. First, insects may be 'associated' with a plant for a variety of reasons, and it is not always apparent from the accounts whether the species listed are all herbivores, or whether some of them are nectar feeders, casual visitors or predators, for example; the great majority appear to be 'herbivores' of one sort or another (i.e. leaf, root, stem seed or flower eaters). Second, we are in no way suggesting that the *Biological Flora* accounts are complete lists of the insects normally associated with each particular plant. We are well aware that they are of variable quality and that some are certainly very incomplete. Since they are compiled by a large number of different authors over a long period of time, this seems merely to have increased the variance in the data, rather than introduced any systematic errors. It does mean, however, that our statements about the insects associated with different types of plants are based on relative and not absolute comparisons.

The present geographical ranges of each of the plants in the British Isles, excluding Ireland (where there are grounds for believing that both the plant distribution and insect data may be less reliable) and the sites of known introductions, were obtained from the *Atlas of the British Flora* (Perring and Walters 1962). The *Atlas* gives the distribution of each species on a presence or absence basis using grid squares of 10 km × 10 km ('10 km squares'). The main ecological characteristics of each plant were obtained from Clapham, Tutin and Warburg (1962). Within the *Biological Flora* data, four distinct groups of plants could be recognised:

i. A group made up predominantly of perennial dicotyledonous herbs. Twenty-eight of the species fell into this category, which for convenience also included two dicots that can be either bienniel or perennial, and one perennial fern with a similar herbaceous growth form, giving a total sample size of thirty one.

ii. A group of ten species made up of perennial, dicotyledenous woody bushes and undershrubs.

iii. A group of sixteen predominantly annual dicots. Eight of these species are common agricultural weeds, of which seven are annuals and one a perennial weed. The other eight species are all annuals (or in one case annual/biennial) from a variety of natural open and disturbed habitats.

iv. A group of fourteen monocotyledonous herbs, which do not include any Graminae, but which otherwise embraces a wide range of plants within the monocots.

For convenience, these four categories will be referred to as 'Perennial Herbs', 'Woody Shrubs', 'Weeds and other Annuals' and 'Monocots'. Fig. 1 shows their species-area relationships, with S as the number of species of insect associated with each plant species, and A its present geographical range within the British Isles, in terms of the number of '10 km squares' occupied by the plant. Since the axes are logarithmic, $S + 1$ was used in the regressions in order to be able to include those species of plants from which no insects have been recorded. The equations are:

(1) *Perennial Herbs* (Fig. 1a)

$\ln [S+1]=0.54 \ln A-0.95$

$r^2=0.71$; $F_{1,29}=69.57$; $P<0.001$

(2) *Woody Shrubs* (Fig. 1b)

$\ln [S+1]=0.45 \ln A+0.005$

$r^2=0.85$, $F_{1,8}=45.51$; $P<0.001$

(3) *Weeds and other annuals* (Fig. 1c)

$\ln[S+1]=0.47 \ln A-1.33$

$r^2=0.59$; $F_{1,14}=20.32$; $0.005>P>0.001$

(4) *Monocots* (Fig. 1d)

$\ln[S+1]=0.39 \ln A-1.60$

$r^2=0.51$; $F_{1,12}=12.64$; $.005>P>0.001$

Table 1 summarizes a statistical comparison of the four fitted lines. Note that none of the regressions differs from any of the others in either residual variance or slope; they differ only in intercept. It appears from these regressions that each of the four groups of plants has a quite characteristic number of insect species associated with it, for a particular size of geographical range, in the sequence

Woody shrubs = Perennial Herbs > Weeds and other Annuals > Monocots.

Notice that the regression line for the woody shrubs lies above that for the Perennial Herbs, but that this difference is not statistically significant.

One group, so far not dealt with at all, are the submerged or semi-submerged aquatics, all perennial dicots. These are shown for convenience in Fig. 1a as open circles. (They were not, for obvious reasons, included in the data used to calculate equation 1.) The much smaller numbers of species of insects associated with these submerged aquatics, compared with terrestrial Perennial Herbs which have a geographical range of a similar size is obvious. On the limited data available, they appear to occupy a position somewhere between the Weeds and Other Annuals, and the Monocots.

Zwölfer's Cynareae data, and the C.I.B.C. survey data on Woody Shrubs (Fig. 2) complement these conclusions, although a certain amount of caution is necessary before they can be used in this context. In neither case are the true geographical areas occupied by each of the plants on the Continent of Europe accurately known. However, widespread plants were sampled more frequently than those with a restricted distribution, so that the total number of locations sampled for each species scales roughly with their geographical range. This inter-

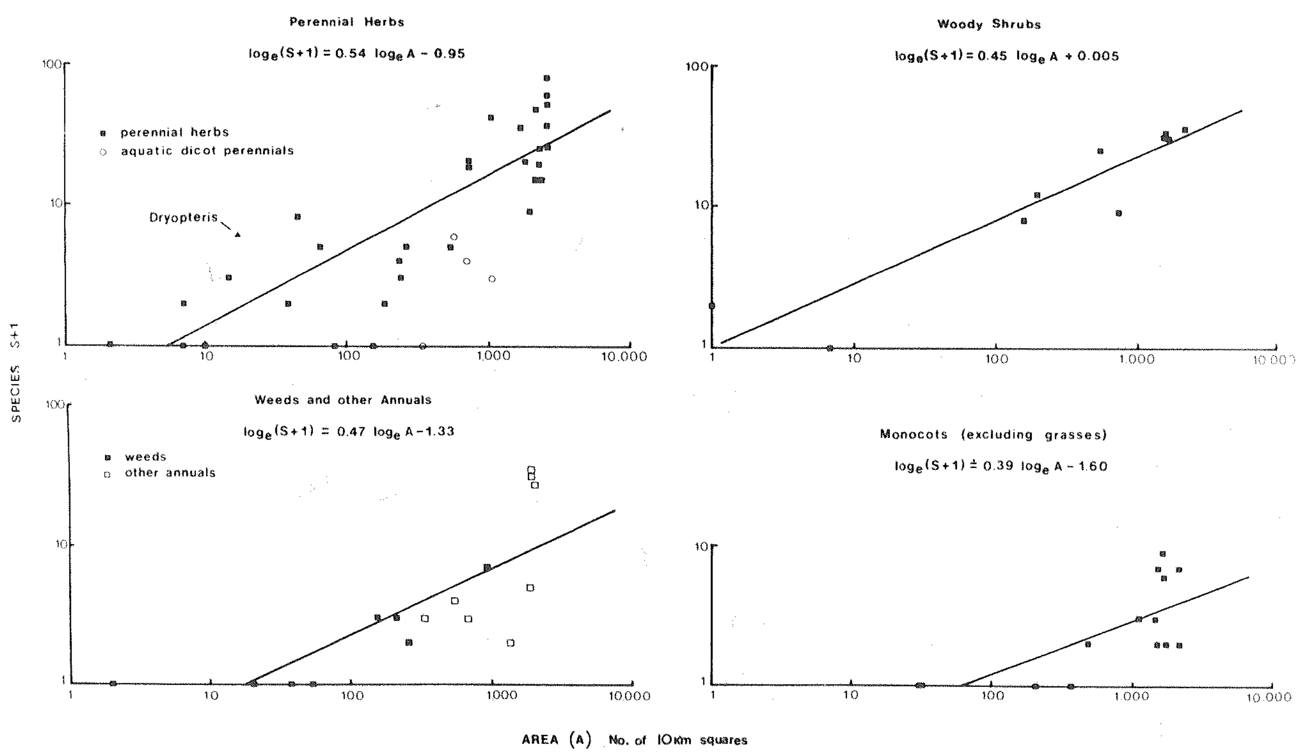


Fig. 1. The total number of insect species associated with four different groups of plants. Plant distributional range is measured in terms of the total number of 10km squares in the Atlas of the British Flora. (Biological Flora data; see text for details).

TABLE 1
Statistical compariosn of regressions 1-4.

	Woody Srhubs (2)	Weeds and other Annuals (3)	Monocots (4)
Perennial Herbs (1)	V:F =2.37 NS b:F =0.65 NS c:F =2.79 $0.25>P>0.1$ } NS	V:F =1.01 NS b:F =0.34 NS c:F =10.41 $.005>PP>0.001$ }	V:F =1.89 NS b:F =0.96 NS c:F =44.30 $P<0.001$ }
Woody Shrubs (2)		V:F =2.39 NS b:F =0.02 NS c:F =19.20 $P<0.001$ }	V:F =1.25 NS b:F =0.21 NS c:F =72.6 $P<0.001$ }
Weeds and other Annuals (3)			V:F =1.91 NS b:F =0.23 NS c:F =8.51 $0.01>P>0.005$ }

V=comparison of residual variances
b= " " " slopes
c= " " " intercepts

pretation is supported by the fact that in general, increasing sampling effort alone would yield a relationship of the form $S \sim l_n A$ and a true 'island effect' (like that seen in the *Biological Flora* data) one of the form $l_n S \sim l_n A$ (May 1975).

For the Cynareae and Woody Shrubs the relationships are:

Cynareae

$S=0.0088 \ln N+2.33$
$r^2=0.40$; $F_{1,42}=27.85$; $P<0.001$ (5)

or

$\ln S=0.65 \ln N+0.85$
$r^2=0.74$; $F_{1,42}=130.38$; $P<0.001$ (6)

C.I.B.C. Woody Shrubs

$S=0.012 \ln N+2.45$
$r^2=0.79$; $F_{1,5}=18.30$; $.01>P>0.005$ (7)

or

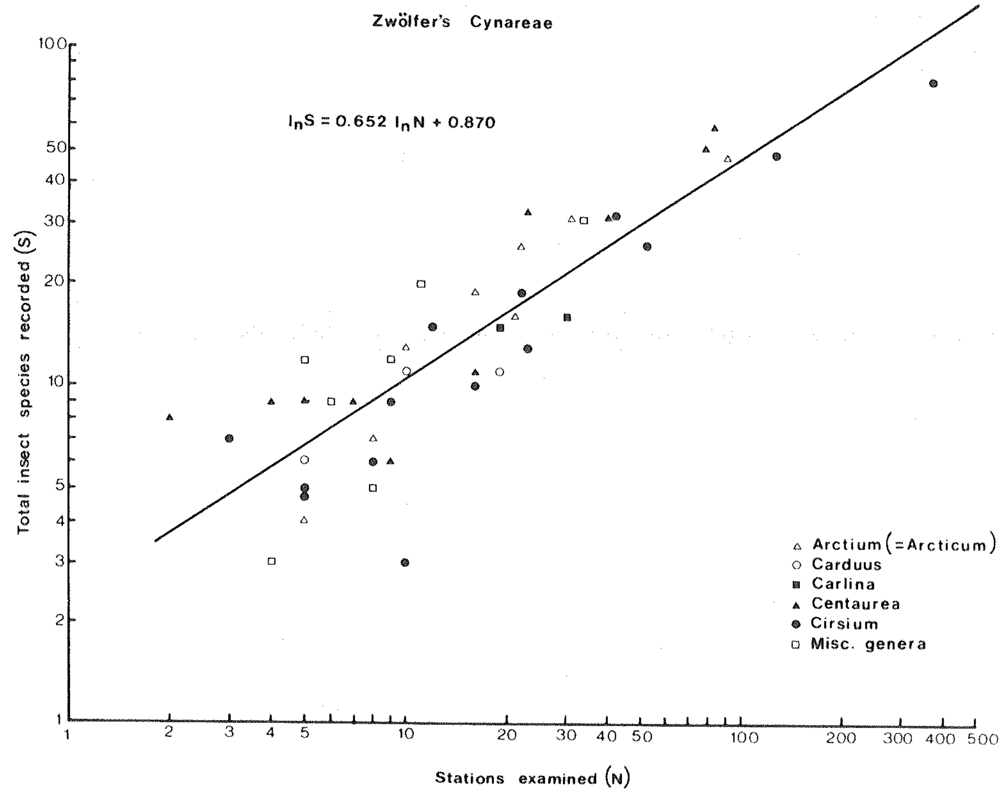
$\ln S=0.64 \ln N+1.12$
$r^2=0.91$; $F_{1,5}=49.01$; $P<0.001$ (8)

where S is the number of species, and N is the number of sites sampled.

Obviously, relationships of the form $l_n S \sim l N$ provide a better fit to the data than $S \sim \ln N$, supporting the interpretation that the most widespread plants appear to have more species of insects on them not just because they were sampled more intensively, but because they are more widespread.

If this interpretation is correct, it suggests that the non-significant difference found in the *Biological Flora* analysis between the number of species of insect on Woody Shrubs and on Perennial Herbs with a geographical range of a similar size may, in fact, be real. Note that as in the *Biological Flora* data, eqns. 6 and 8 are identical in slope and differ only in intercept, with the C.I.B.C. Woody Shrubs yielding approximately 1.3 times more species of insects per station sampled than the Cynareae.

The Cynareae, in fact, consist of perennial, biennial and annual herbs, (Polunin 1969; A. H. Fitter, *pers. comm.*) so that we can extend this analysis further, to examine species-area relationships within these three groups. There is no significant difference between the regression line for Perrenial



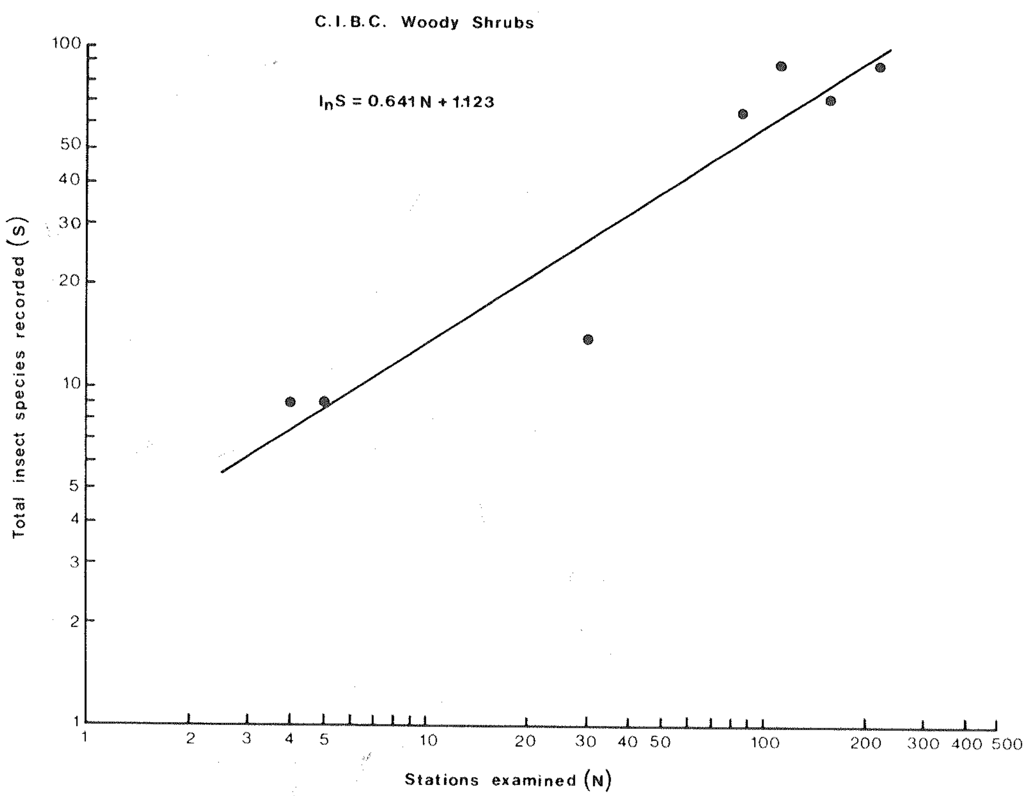


Fig. 2. Relationship between stations examined and insect species recorded on various species of (a) Cynareae, and (b) Woody Shrubs. (C.I.B.C. survey data see text for details).

Cynareae and that for Annual and Biennial Cynareae in combination (residual variance F =1.68; slope F =0.47; intercept F =0.004). The data were not extensive enough for the Annuals and Biennials to be analysed separately. (Sample sizes differ slightly from those for the overall Cynareae regression, because a small number of species could not be allocated to one of the three groups). These data, therefore, fail to support the *Biological Flora* analysis, in that the Perennial Cynareae do not apparently have a larger insect community associated with them than the annuals and biennials.

THE EFFECTS OF 'TAXONOMIC ISOLATION'

The idea that the 'taxonomic isolation' of a plant may have an effect on the number of species of herbivores which feed on it has been touched on by several authors (e.g. Janzen 1968; Feeny 1977; Simberloff 1974), but it has never been quantified or rigorously tested. In this section we test the hypothesis that the more taxonomically isolated a plant is, the fewer the species of insects it will have associated with it, on the grounds that the 'exchange' of herbivores between closely related plant species will in general be easier than 'exchange' between unrelated species. This, of course, assumes that in general closely related plants are likely to biochemically and structurally more similar than are less closely related plants, which does not seem unreasonable (see, for example Futuyama 1976; Feeney 1977; Southwood, 1961). 'Exchange' is used here to denote the aquisition of a herbivore guild on an evolutionary time-scale.

For each of the plant-genera in the *Biological Flora* accounts, we recorded the number of native species within the British Isles, and also the approximate number of species in the genus on a world-wide basis (both from Clapham *et al.* 1962). The world-wide species per genus failed to yield any sensible patterns and will not be considered further.

Fig. 3 shows the residuals (*R*) derived from the appropriate species-area curves shown in Fig. 1 (eqns 1-4), plotted against the number of plant plant species in the genus (*G*) within the British Isles. Log. transformations of the number of species in the genus provide the best fits to these data, yielding for:

Perennial Herbs (Fig. 3a)

$$R = 0.19 \ln G - 0.32 \quad (9)$$

$r^2 = 0.07$; $F_{1,29} = 2.07$; $0.25 > P > 0.1$ (N.S.)

Monocots (Fig. 3b)

$$R = 0.30 \ln G - 0.43 \quad (10)$$

$r^2 = 0.46$; $F_{1,12} = 10.28$; $.01 > P > 0.005$

There is obviously no relationship between the residuals and the total plant species in the genus for either the Woody Shrubs (Fig. 3d) or the Weeds and Other Annuals (Fig. 3c). The Perennial Herbs (eqn. 9) show signs of the positive relationship predicted by the hypothesis, but this is not statistically significant. Only the Monocots (eqn. 10) provide unequivocal evidence to support the notion that taxonomically isolated plants have fewer species of insects associated with them than do plants with several relatives in the same geograhphical area.

The effects of area and taxonomic isolation may be combined as follows:

Monocots

$$\ln S = 0.39 \ln A + 0.29 \ln G - 2.11 \quad (11)$$

$F_{2,11} = 13.65$; $P < 0.001$

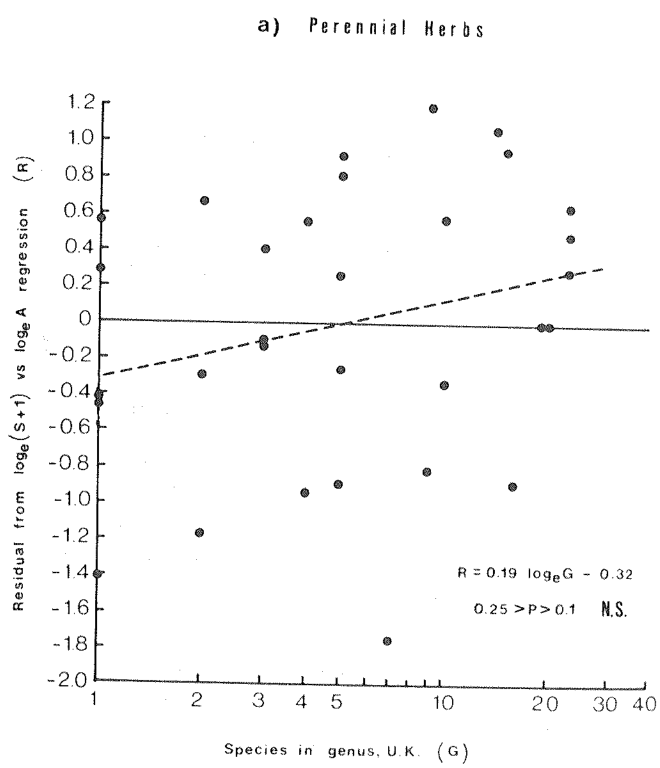
and with somewhat less justification

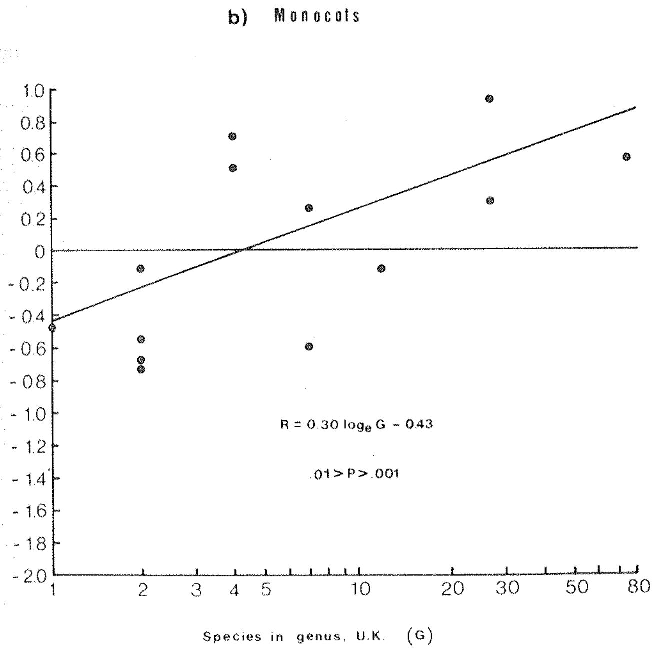
Perennial Herbs

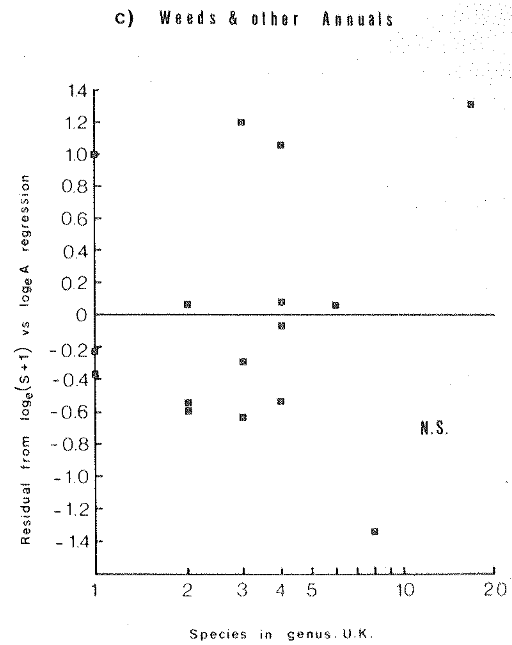
$$\ln S = 0.51 \ln A + 0.21 \ln G - 1.14 \quad (12)$$

$F_{2,28} = 37.27$; $P < 0.001$

Zwölfer's Cynareae data were analysed in a similar way, but using the residuals from eqn. 6 and the total number of species in the genus on the Continent of Europe (Polunin 1969). None of the relationships tested was significant.







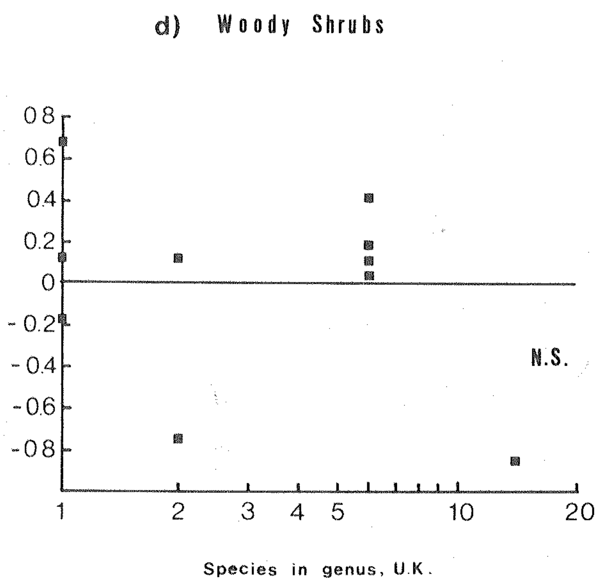


Fig. 3. The residuals from the fitted regression lines in Fig. 1, plotted against the number of species of plants in the genus (taxonomic isolation). Only the data for Monocots shows a signficant relationship.

THE TAXONOMIC COMPOSITION OF THE ASSOCIATED INSECT FAUNA

Up to this point, we have been concerned with the total numbers of species of insects, without enquiring what the types of insects are.In this section, we ask whether there are any obvious differences in the faunal assemblages associated with plants of a particular type. A preliminary analysis of this kind was carried out by Lawton (1976) using the *Biological Flora* data in its entirety, to provide a base line against which the herbivore community found on bracken (*Pteridium*) could be compared. Here, we treat each of the four plant-groups separately, and look for gross differences between them in terms of the orders of insects which occur on them. This analysis is then extended by reference to Zwölfer's Cynareae data, and the C.I.B.C. survey data on Woody Shrubs.

The analyses are carried out by simply summing the available records from each plant, and no attempt has been made to allow for the fact that commoner plants contribute proportionally more records (because they have more species in total) than rarer plants. There are a number of interesting but small changes in the composition of the faunas of plants in each group depending on how widespread they are, but we have not yet finished analysing these trends, and still less understand their significance; overall, these do not appear to influence the main results of this section.

Table 2 summarizes the total number of insects in each of five major orders associated with the four groups of plants recognised in the *Biological Flora* data. A simple pair-wise comparison using χ^2 shows that the proportions of insects in each taxonomic group do not differ significantly from one another, except that the Woody Shrubs depart markedly from all the others (from Perennial Herbs, $P<0.001$; from Weeds and other Annuals, $P<0.001$, and from Monocots, $0.05>P>0.025$). Woody Shrubs appear to have considerably more Lepidoptera and fewer Diptera (and possibly Co-

TABLE 2

Taxonomic composition of the insect faunas of various plant groups (total records from all species in the group). The figures in brackets are proportions.

Plant-group	Total Records in Each Group				
	Hemiptera	Lepidoptera	Coleoptera	Diptera	Hymenoptera
Biological Flora					
Perennial Herbs	97 (0.21)	166 (0.36)	91 (0.20)	74 (0.16)	28 (0.06)
Woody Shrubs	39 (0.24)	108 (0.65)	8 (0.05)	6 (0.04)	3 (0.02)
Weeds and other Annuals	14 (0.15)	32 (0.33)	23 (0.24)	20 (0.20)	8 (0.08)
Monocots	8 (0.24)	14 (0.42)	7 (0.21)	4 (0.12)	0 (0)
C.I.B.C. Surveys					
Cynarea	92 (0.11)	226 (0.27)	315 (0.38)	184 (0.22)	9 (0.01)
Woody Shrubs	51 (0.15)	163 (0.47)	98 (0.28)	2 (0.01)	30 (0.09)

leoptera, but see below) than the three other plant groups.

Table 2 also summarizes the taxonomic composition of the insects recorded by the C.I.B.C. One point that is immedately obvious is the proportionately greater representation of Coleoptera in these surveys, compared with the *Biological Flora* accounts.We feel that this probably reflects more thorough collecting and greater taxonomic skill rather than any subtle biological differences between the plants. With this important caveat in mind, the general conclusion that woody shrubs have a greater proportion of Lepidoptera (between 1.5 and 2.0 times more) and perhaps fewer Diptera than non-woody herbs would appear to be substantiated.

Comparisons of this nature are obviously crude, and within major plant groups we must expect particular species or genera to depart from the norm. These discrepancies, however, are in themselves potentially interesting, because it is not until we know what is normal that we can begin to speculate about, and understand, what is special. Here we draw attention to just one striking feature in the Cynareae data. Table 3 shows their faunal composition, broken down by genera. Whereas the data *in toto* suggest that phytophagous Hymenoptera are unimportant (constituting only 1% of the fauna), all but one of the records are from the genus *Centaurea*. Why? In fact, if we take the *Biological Flora* accounts for Perennial Herbs together with that for weeds and other Annuals as 'normal' then it is *Centaurea* amongst the Cynareae which has its proper compliment of Hymenoptera, and most of the other genera that are deficient. It is tempting to speculate that we have here an example of the barriers to colonisation that arise due to taxonomic isolation of the host-plant, dealt within the previous section. What these barriers are, of course, is a different question.

Sow thistles (*Sonchus*), reinforce these points, because they too depart significantly from the general picture (Table 3, after Schröder 1974), particularly in the numbers of Diptera which they support. In this, as in other cases, a further uncertainty is whether this is a genuine difference, or due to the particular interests and skills of the investigator. In this particular case, the differences are probably genuine (because they are apparent in both literature and independent field survesy), but they serve to remind us that whilst the patterns look interesting we must be particularly careful about making generalizations using data that are simply not up to it.

THE PROPORTIONS OF 'SPECIALISTS' AND 'GENERALISTS'

A fourth question of interest concerns the proportions of 'specialist' and 'generalist' species amongst the insects found on a particular plant. For example widespread plants have more species associated with them than rare plants; are there

TABLE 3
Taxonomic composition of the insect faunas of particular genera of herbaceous dicots (see text for details)

Plant genus	Total records in each genus				
	Hemiptera	Lepidoptera	Coleoptera	Diptera	Hymenoptera
Zwölfer's Cynareae					
Arctium (=*Arcticum*)	6 (0.21)	10 (0.36)	7 (0.25)	5 (0.18)	0 (0)
Carduus	21 (0.13)	31 (0.19)	79 (0.48)	35 (0.21)	0 (0)
Cirsium	34 (0.12)	60 (0.21)	110 (0.39)	76 (0.27)	0 (0)
Centaurea	21 (0.09)	79 (0.33)	65 (0.27)	65 (0.27)	12 (0.05)
Carlina	4 (0.12)	12 (0.38)	12 (0.39)	3 (0.10)	0 (0)
Onopordum	1 (0.02)	12 (0.28)	23 (0.53)	7 (0.16)	0 (0)
Five monospecific genera	6 (0.12)	13 (0.26)	19 (0.38)	10 (0.20)	1 (0.02)
Schröder (1974)					
Sonchus (Field Survey	7 (0.23)	2 (0.06)	0 (0)	20 (0.66)	1 (0.03)
Sonchus (Literature)	13 (0.24)	17 (0.31)	1 (0.19)	22 (0.41)	1 (0.02)

proportionally more specialists in these larger associations, or more generalists, or are there no discernable patterns? As in so much of this work, the *a priori* formulation of a specific hypothesis is extremely difficult. Rhoades and Cates (1977), for example, have gone as far as suggesting that nothing can be said about the relative proportions of specialist and generalist species on a plant, because it is the total grazing pressure, and not simply the presence of a species (which may be too rare to be of any significance) which is of key importance in the coevolution of a plant and its guild of herbivores. However, they do make the specific prediction that the total *grazing pressure* exerted by generalists herbivores should be greater on 'ephemeral' plant resources than on 'predictable' plant resources. This is an interesting, and important prediction. Furthermore we can deduce from it that in a large sample of plants, unless the grazing pressures exerted are very curiously distributed amongst the various associated species of insects (which is not impossible!), and despite what Rhoades and Cates themselves suggest, we would still expect to see a higher proportion of generalist *species* feeding on ephemeral plant-tissue than on predictable plant tissue. (Before we could tell whether this was a reasonable deduction we would have to know not only the number of specialist and and generalist species on each kind of plant, but also their 'normal' population sizes, characteristic feeding rates and so on. Needless to say, we do not have this sort of information at our disposal). Elsewhere in the same paper, Rhoades and Cates conclude that ephemeral plant tissue include both anuals and rare species. Hence, we have the (admittedly weak) hypothesis that the proportion of generalist herbivores should be greater on rare than on common species and greater on annuals than perennials. Neither prediction appears to be substantiated by the data. Quite the reverse.

Zwölfer's Cynareae data provides extensive information on the food-plant specificity of the insects. For simplicity we have reduced his five feeding categories to three, namely:

Polyphagous (generalist) species which regularly feed on plants in more than one Tribe or Family.

Oligophagous species feeding on more than one species of plant, but all the food plants are in one Tribe.

Monophagous (specialist) insects feeding on only one species of host plant, at least within the geographical region under investigation.

Fig. 4 shows the proportions of polyphagous and monophagous insects associated with each of the

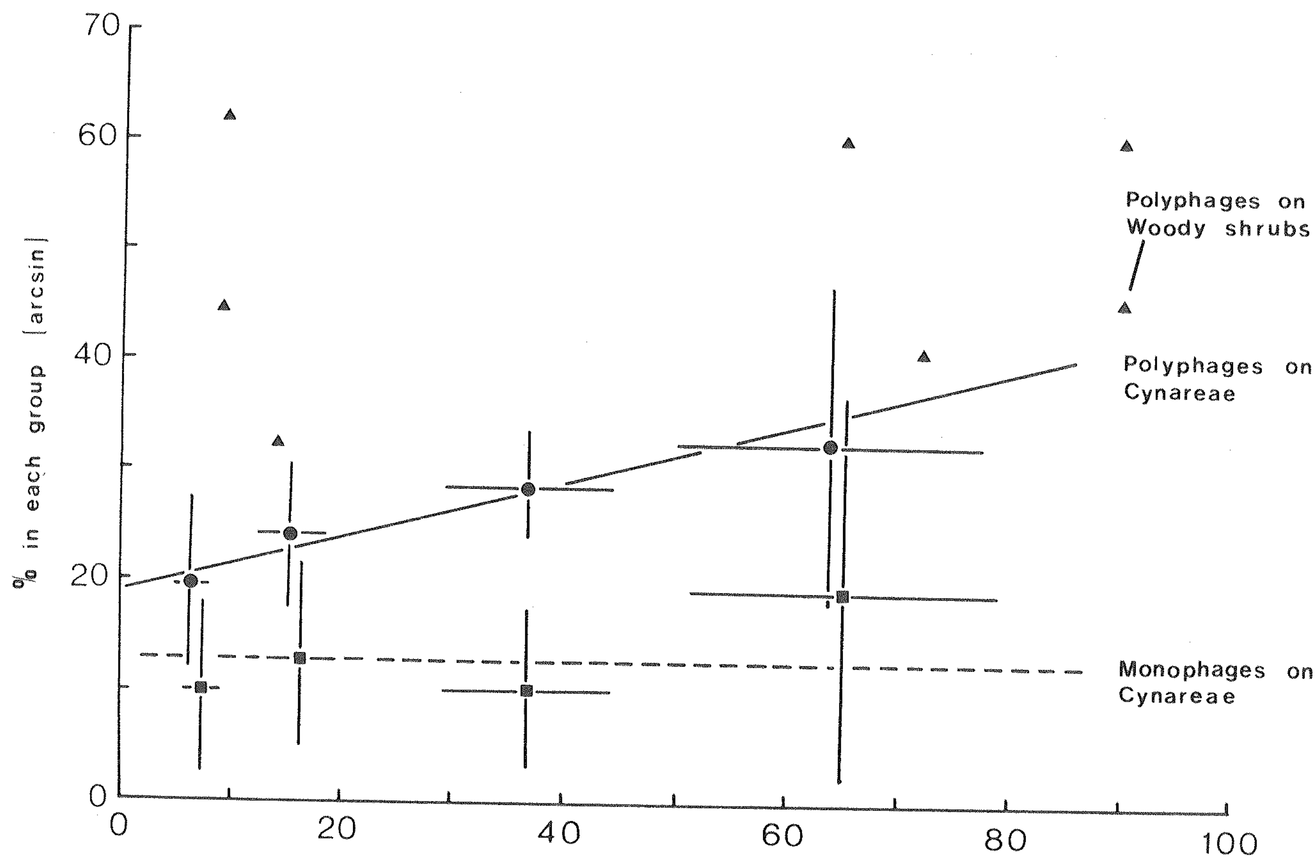


Fig. 4. Proportionsof polyphagous and monophagous species of insects associated with Woody Shrubs and Cynareae, as a function of the total number of insect species recorded on the plant. (C.I.B.C. survey data). Means and 95% confidence intervals of grouped data are shown for the Cynareae.

species of Cynareae examined by Zwölfer. The proportion of polyphagous species (p) increases significantly as the total number of species of insects on the plant (S) increases, (which is equivalent to the plant itself becoming more widespread) :

$$p=0.265\ S+19.00 \qquad (13)$$

$r^2=0.12$; $F_{1,40}=5.71$; $0.025>P>0.01$

where p is expressed as the usual arcsin transformation. For clarity, Fig. 4 shows the means of grouped data, together with similar information on the proportion of strictly monophagous species on the same plants. The latter show no discernable trends; rather it is the proportion of oligophages which decrease in line with the increasing proportion of polyphages.

Within the Cynareae themselves, we may further examine the relative proportions of monophages, oligophages and polyphages on annual plus biennial species compared with the perennials. Separate regression lines for these two groups equivalent to eqn. 13 (above) are virtually identical (residual variance $F_{18,15}=1.18$; slope $F_{1,32}=1.52$; intercept $F_{1,34}=0.03$) and provide no evidence that the proportion of polyphages is different on perennial Cynareae than on annual and biennial species.

Finally, we can compare the proportions of specialist and generalist species on the Cynareae with those given in the C.I.B.C. data on Woody Shrubs. Our simple deduction derived from Cates and Rhoades' hypothesis leads us to predict a greater proportion of specialists on the woody shrubs (which are more persistent and hence more predictable in time and space than most, or all, of the Cynareae). Again, exactly the opposite is found to be true. Fig. 4 shows that the proportion of polyphages on each of the woody shrubs lies well above the data for the Cynareae.

Within the Woody Shrubs themselves, the proportion of specialists and generalists shows no relationship with the total number of species found on the plant. This may merely reflect the much smaller amount of data available for this group although interestingly enough, a consideration of the Lepidoptera alone (which are proportionally

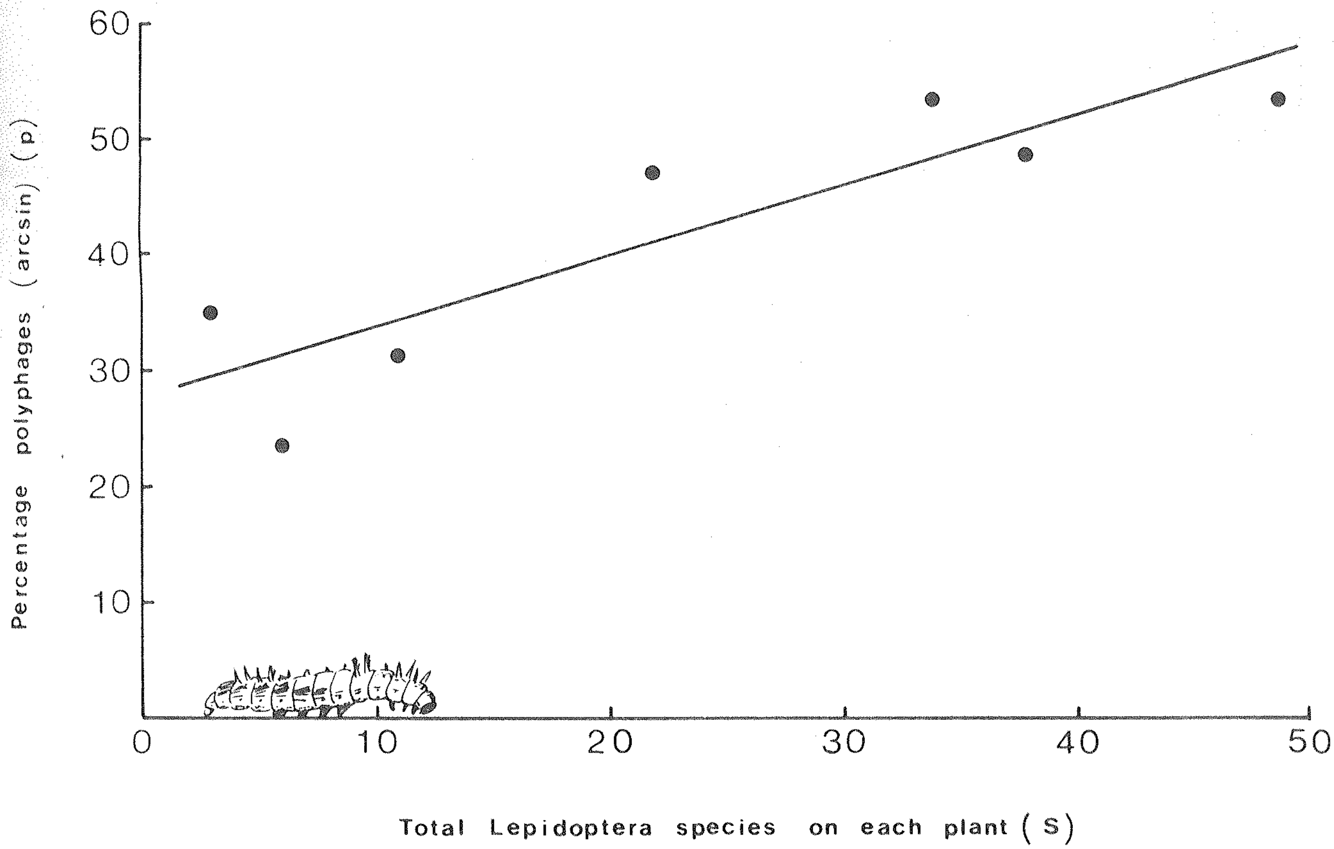


Fig. 5. Proportion of polyphagous Lepidoptera (p) recorded on Woody Shrubs, as a function of the total number of species of Lepidoptera (S) recorded on the plant (C.I.B.C. survey data). The equation is $p=0.595+27.99$ ($F_{1,42}=18.03$; $.01>P>0.005$), with p expressed as the usual arcsin tranformation.

much commoner on the woody shrubs than on the Cynareae—see above) again shows a strong positive relationship between the total number of species and the proportion of generalists (Fig. 5).

Preliminary analyses suggest that consideration of the proportions of oligophages and polyphages within other taxonomic groups, rather than entire insect assemblages, may prove to be particularly interesting. This work is at a very preliminary stage and will not be developed further here.

THE STRUCTURE OF INSECT ASSEMBLAGES BY FEEDING TYPE

Insects exploit plants in a variety of ways. In the last part of this analysis we ask whether there are any systematic changes in the relative proportions of five basic feeding types, drawing once more on Zwölfer's data for Cynareae. The five categories are:

a) Chewers; species feeding externally on the leaves. The insects involved are either Lepidoptera larvae, or larval and adult Coleoptera.
b) Miners; including root, stem and leaf miners, from the Lepidoptera, Diptera and Coleoptera.
c) Gall formers; both leaf and stem galls, formed by larval Diptera and Hymenoptera.
d) Suckers; all Hemiptera.
e) Seed and flower feeders; a somewhat miscellaneous assemblage of larval Lepidoptera, Diptera and larval and adult Coleoptera.

A priori, we might expect that mining and in particular gall forming, would involve a greater degree of specialization on the part of the exploiting insect than simple external feeding (i.e. chewing and sucking). The host specificity of gall-formers, for example, is emphasised by Went (1970) ; the same is true of the (mining) Agromyzid Diptera (Hussey and Gurney 1962; Spencer 1972) and leaf-mining Lepidoptera (Opler 1974). A simple hypothesis would then be that more widespread plants, and plant species that are not taxonomically isolated, present gall formers and miners with a proportionally greater opportunity for colonization in evolutionary time than less widespread and taxonomically isolated species. Further, since the overall proportion of miners and gall formers

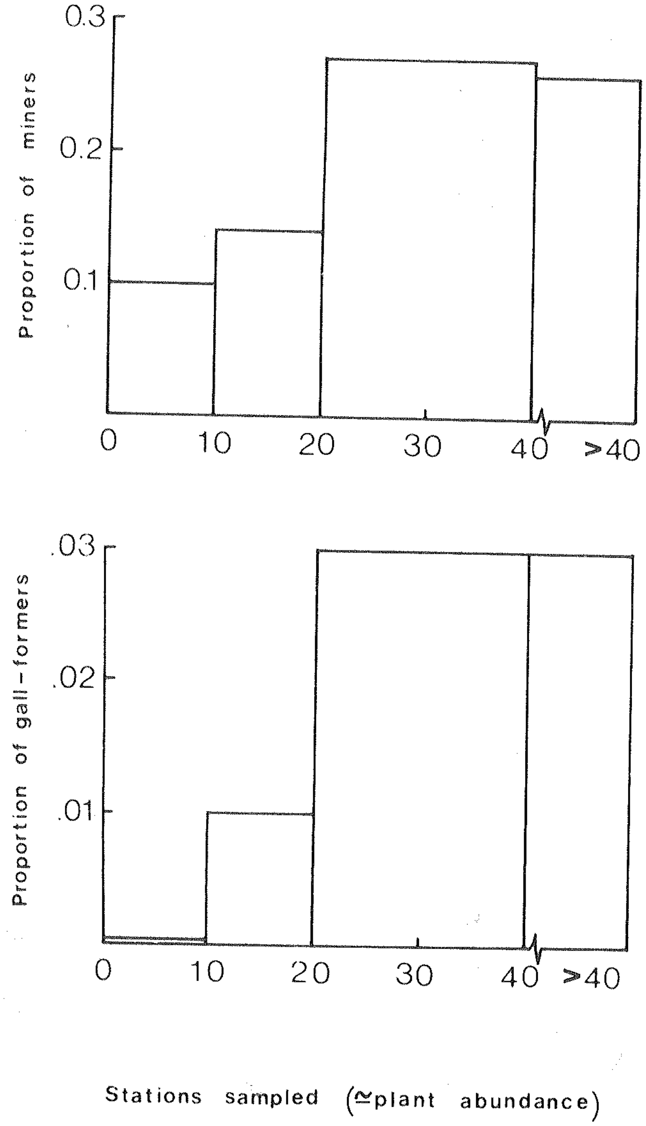


Fig. 6. Proportion of miners and gall formers in European Cynareae as a function of the number of stations examined.

is rather small, this prediction need not be contradictory to the more general observation made in the previous section that the total proportion of polyphagous (generalist) species increases on more widespread plants.

Fig. 6 shows that the proportion of miners and gall-formers does indeed increase as the plants become more widespread, and that these differences are highly significant (Table 4). The effects of taxonomic isolation are more difficult to establish, but it may be significant that a much greater proportion of the gall-formers occurs on *Centaurea* than the other genera (Table 5), and that *Centaurea* itself contains more species than any other member of the group in Europe (Polunin 1969). Since most of the galls are made by Hymenoptera, this is merely another way of looking at the very uneven distribution of the members of this order amongst the various genera of Cynareae, touched on in the previous section. (Note that within *Centaurea,* restricted species with less than 11 stations sampled appear to have no gall-formers, so that the effects of plant distribution and taxonomic isolation are acting independently, although the data are by this time becoming so divided that more precise analyses are impossible).

The remaining feeding categories show no clearly discernible patterns, either with plant abundance or amongst the various genera of Cynareae.

As a parting gesture, we can compare the distribution of feeding types on the Cynareae with that on Woody Shrubs, again using the C.I.B.C. survey data (Table 6). Most of the differences reflect common-sence observations. Thus the larger proportion of Lepidoptera on Woody Shrubs is partly responsible for the larger proportion of chewers, although some of the Lepidoptera mine, and some of the chewers are Coleoptera, so that the relationship is not a simple one. Miners are rather rarer on Woody Shrubs, probably reflecting the fact that their stems are not so readily mined as the stems of Cynareae (it may also reflect human fraility—woody shrubs are less easy to dig up than thistles, and hence root miners may be under recorded!). Cynareae flowers are obviously particularly attractive. At this stage, such comparisons are merely anecdotal. We know too little about the processes controlling the gross structure of herbivore guilds for them to be any more.

DISCUSSION

Our results can be discussed in two quite separate ways; in relation to the growing body of ecological theory concerned with the structure of plant-herbivore communities (Feeney 1977; Futuyma 1976; Murdoch Evans and Peterson 1972; Rhoades and Cates 1977; Otte 1975) and in relation to the search for, and use of, insects in the biological control of plants (Harris 1974; Wapshere 1974). At the moment, these two bodies of knowledge share a relationship that is very similar to that between predator-prey and host-parasite theory in insect population dynamics, and the use of natural enemies in the biological control of insect pests (Huffaker 1971). The former ought to be of use to the latter, but in fact very rarely is.

Obviously, ecological theory has a very long way to go before it is sufficiently robust to be of major

TABLE 4

Numbers of gall-formers and leaf-miners on Cynareae in four different abundance categories; numbers in brackets are the expected distributions of feeding-types on the null hypothesis of no significant difference between plant-abundance categories.

Abundance Category (Stations sampled)	Gall-formers	Miners	Others	£
1-10	0 (2.58)	13 (26.46)	111 (94.93)	124
11-20	2 (4.16)	28 (42.69)	170 (153.12)	200
21-40	6 (4.69)	61 (48.02)	158 (172.26)	225
> 41	10 (6.51)	82 (66.79)	221 (239.63)	313
£	18	184	660	862

$\chi^2=32.08$; d.f.$=8$; $p<0.001$

TABLE 5

Proportions in each feeding type in relation to the various genera of Cynareae.

Genus	No. of species examined	Chewers	Miners	Gall-formers	Seed and Flower feeders	Suckers
Carduus	8	70	34	0	58	21
Cirsium	14	94	68	2	110	35
Centaurea	10	49	54	15	93	21
Arctium	3	5	4	0	13	5
Others	8	43	26	1	36	9

Note 1 The distribution of Gall formers amongst the groups *Carduus, Cirsium, Centaurea* and *Arctium* and Others departs markedly from random ($\chi^2=29.76$; d.f.$=2$; $P<0.001$).
Note 2 None of the other feeding groups show any clearly discernable patterns.

TABLE 6

Comparison of feeding types on Cynareae and Woody Shrubs (Proportions in brackets)

	Chewers	Miners	Gall-formers	Seed, fruit and flower feeders	Suckers
Cynareae	261 (0.30)	184 (0.21)	18 (0.02)	310 (0.36)	91 (0.11)
Woody Shrubs	209 (0.60)	54 (0.15)	13 (0.04)	24 (0.07)	50 (0.14)

help in many practical biological control programmes. But both sides of the subject must at least try to draw closer together, otherwise biological control programmes will continue to be developed piecemeal, perhaps incurring needless expense, and a higher proportion of failures than is really necessary, and theoretical ecologists will continue to make generalisations that every practical worker knows are untrue, and solve fascinating but irrelevant problems.

The overriding impression to emerge from this work is that phytophagous insect communities have some remarkable regularities in their structure. This is true both in terms of the total number of species associated with a particular plant, as well as in taxonomic composition, the proportions of polyphages and monophages and the various means of exploiting the plant. Of course, these patterns are an average picture. Certain groups of plants appear to depart quite markedly from the norm, and not all the predictions made from the *Biologicl Flora* are borne out by an analysis of the C.I.B.C. survey data (or vice versa). These anomalies can only be resolved by further work.

Predictable patterns and structure, of course, imply that there are ecological and evolutionary 'rules' governing them. If we view the number of species on a particular plant as a balance between colonization and extinction, then geographically more widespread plants have a larger number of species associated with them because they are more likely to be found and colonized in evolutionary time (Janzen 1968; Opler 1974; Southwood 1961; Strong 1974a,b). In Feeney's (1977) terminology, they are more 'apparent'. Unpredictability in time and space (Weeds and other Annuals) reduces this 'apparency' and hence the equilibrium number of species is less. Why Perennial Monocots should have even lower equilibria is less obvious. We are inclined to the view that this is a function of their 'architecture', with the Woody Shrubs, Perennial Herbs and Monocots forming a series of decreasing structural complexity. Structurally more complex plants permit greater niche-diversification (both for competitor avoidance and the avoidance of your neighbours' predators or parasites (see Zwölfer 1975)), and hence have a bigger equilibrium species pool. Trees are even more structurally complex and (with the possible exception of very rare species) Strong's (1974a) data for British trees suggest higher numbers of associated species, area for area, than Woody Shrubs or Perennial Herbs. (A direct comparison is impossible, because Strong's equation appears to be in error in that it does not fit his own results, and predicts ridiculously high numbers of species on common trees! Allowance has also to be made for the fact that he included, and we excluded Ireland from the plant-area measurements). Visual inspection of his results however suggests that in terms of associated insects, trees have more species of insects associated with them than have Woody Shrubs with a geographical range of the same size. The complete series therefore appears to be Trees>Woody Shrubs>Perennial Herbs>Weeds and other Annuals>Monocots.

The paucity of insects on aquatic Macrophytes (which appear to fall in this series somewhere between Weeds and other Annuals and Monocots) is well known (e.g. Cummins 1973), and presumably reflects low colonization (or higher extinction) rates; why this should be, however, is very uncertain.

What are the implications of these results for biological control? In the simplest possible terms, they mean that a control worker faced with a new problem to solve and a control programme to instigate may now be able to get some help with estimating part of his costs before he starts. If the plant to be controlled is a perennial herb, and geographically widespread in its native environment, there will be a large pool of species from which to select possible control agents. If on the other hand his plant is a monocot, and naturally rather rare, the number of species in the available pool is going to be very small indeed, perhaps none of them will be suitable.

Monocots excepted, the taxonomic isolation of the plant seems to be unimportant. Why Monocots should show such a clear effect of taxonomic isolation whilst plants in the other groups do not is far from clear.

These are not the only considerations, of course. Not all the species of insects will occur in all parts of the host plant's range, although more widespread oak-tree species with bigger total pools of insects do support more species at any one locality (Opler 1974). This important point is obviously something that requires further work, in combination with the notion that more of the insect species are likely to be found toward the centre of the plant's geographical range (e.g. Goeden 1971). In other words, although we now know that the total species pool of a plant is determined by the size of its geographical range, the processes that determine how many species, from the total, will be found at any one place within that range requires further work. This also raises the important problem of matching the climatic tolerance of a particular insect in its native environment with that in the proposed site of introduction. In that widespread plants have more insects in total, and on present limted evidence, more species at any one locality, the chances of finding the 'right' insect on a widespread plant would appear to be enhanced.

Polyphagy is an additional complication. What limited data we have suggests that the proportion of polyphages increases on more widespread plants (all groups on the Cynareae, and polyphagous Lepidoptera on the Woody Shrubs). Furthermore, the proportion of polyphages on Woody Shrubs is much greater than on a typical group of herbaceous dicots, the Cynareae. This latter observation is in line with Futuyma's (1976) recent independent analysis, which also presents sound ecological reasons why it should be so. Hence, the biological control worker faced with a woody shrub to control is in all probability going to have to do a lot more work screening polyphages than a colleague working with an herbaceous dicot.

The effects of plant abundance on the proportion of polyphages are more difficult to interpret. The most likely explanation we can offer is that this reflects changes in the preferred host-plant(s) of a particular species of insect in different parts of its geographical range. The phenomenon is well documented for a variety of groups e.g. aphids (Eastop 1973; Pathak 1975); a mirid (McNeill in prep.); heliconid butterflies (Benson, Brown and Gilbert 1975); weevils (Zwölfer, Frick and Andres 1971) a dipteran (Hussey & Gurney 1962) and several groups with different food plants on the North and South Islands of New Zealand (Dugdale 1975). As the geographical area sampled increases, one is increasingly likely to detect changes in the preferred food plant(s) of a particular insect, which is therefore more likely to be classified as 'polyphagous'. It is interesting, however, that if this is the explanation, it manifests itself in an increase in polyphagy (and a decrease in oligophagy) with no apparent change in monophagy (Figs. 4 and 5). It seems odd that a similar decrease in insects classified as monophages does not occur with increasing host area. We do not understand this last point, but given that the effect is real, and generally applicable to groups other than the Cynareae, it implies that the chance of hitting on a really good, monophagous control agent is greater for a widespread plant than a rare plant (because the total number of species increases on a common plant, and the proportion of monophages stays constant). In terms of anticipating costs, this would again seem to be a sufficiently important result to jutisfy further investigation.

Our interpretation that the apparent increase in polyphagy on more widespread plants is due to species swapping hosts touches on the central problems of the selection of the correct geographical race for biological control, already dealt with by a number of other people (e.g. Wapshere 1974). An apparently polyphagous species may, in fact, be a very good and quite specific control agent if individuals from a particular local population are selected. This, of course, raises the question of why insects change host plants. In the case of the mirid *Leptoterna dolobrata* (Linn.) it is because in different parts of the insect's range, the timing of flowering of certain species of grass get 'out of phase' with the insect's life-history; *Leptoterna* than 'moves over' onto more appropriately timed species (McNeill, in prep.). In other cases, the shift appears to be due to competition (Zwölfer 1970, 1975; Zwölfer, Frick and Andres 1971), which would be in keeping with our view that phytophagous insect communities are highly structured and that one of the processes determining this structure is competition.

Understanding the reason for these shifts, however, is important. If they can be selected for easily (say over a few generations) than an apparently safe control agent may actually prove to be a dangerous thing to introduce. It would pay to do more fundamental work on the problem of polyphagy, oligophagy and monophagy, particularly in relation to host-plant distribution.

Our remaining remarks are four-fold and can be brief. First, the patterns which we observe in taxonomic composition and the proportions of feeding types reinforce the view that there is still a great deal to be discovered about the 'rules' governing the structure of phytophagous insect communities, but that as yet, this does not much help the practical worker. One possibility comes to mind; may it sometimes be better to introduce a set of herbivore species onto a plant for control purposes, rather than just one? This is analogous to the problem of whether one should release one, or more than one species of predator or parasite for biological control purposes in insect pest control (Hassell and Varley 1969; Huffaker 1971). If we understood the 'assembly rules' better, then multiple introductions might be easier.

Second, if competition and the pressures induced by predators and parasites are major forces in moulding the structure of the insect communities on plants, we should not necessarily confine our search for suitable control agents to species of insects that are common and widespread. Relieved from the pressures of its competitors or natural enemies, an insect may be capable of inflicting considerable damage—perhaps the more so because the plant may not be adapted to withstanding a high level of attack from the species in question.

Third, the implications of this work and the growing body of ecological theory that goes with it (loc. cit) are that taxonomically related and/or biochemically and structurally similar plants are more likely to be invaded by an insect than taxonomically unrelated and/or biochemically and structurally very different plants. Prescreening programmes for potential introductions obviously need to concentrate on as small a range of plants as possible to cut down costs, but as many as possible to be safe. Relatives of the target plant and local crops are obviously tested; the rapid growth in our knowledge of plant chemistry (e.g. Farnsworth 1966) may, however, make the discovery of unrelated but biochemically similar plant-species in the target area much easier and hence improve prescreening programmes. Much, however, would depend on the costs of obtaining the biochemical fingerprints.

Finally, it goes without saying that we have relied extremely heavily on published lists, many of which are notoriously unreliable. Zwölfer's data on the Cynareae are outstanding both for their detail and their accuracy. Above anything else, our analyses have made us acutely aware of the shortage of work of this quality. Our understanding of phytophagous insect communities is unlikely to advance without detailed and extensive surveys. We need good insect species lists from as many plant species as possible. We need to know the geographical range of each plant, and of its insects; we need to know more about the food plant specificity of the insects, and how they make their living on the plant. Only then will a better understanding of phytophagous insect communities emerge. People working in the field of biological control of weeds are privileged in so far as they can study insect plant relationships in much more detail and over much larger areas than most other biologists. We hope that in future, they will make good use of these unique opportunities.

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