SPECIES RICHNESS OF PARASITES ON HOSTS: AGROMYZID FLIES ON THE BRITISH UMBELLIFERAE

By J. H. LAWTON AND P. W. PRICE

Department of Biology, University of York, Heslington, York, YO1 5DD and Department of Entomology, University of Illinois Urbana, Illinois, 61801 U.S.A.

SUMMARY

(1) The number of species of larval agromyzids (Diptera: Agromyzidae) mining plants in the family Umbelliferae within the British Isles is reviewed.

(2) A regression of the number of agromyzid species (S) on the geographical range of each plant (measured in 10 km squares, A) ($1_e S + 1$ vs $1_e A$) is highly significant, but explains only 32% of the variance. Several other 'species-area' curves are similar in this respect.

(3) Geometric mean size of the plants, leaf-form (both measures of plant 'architecture'), and whether or not they grow in aquatic habitats explains some of the residual variation, but approximately 50% remains unexplained.

(4) A wide variety of other characteristics of the plants, and their associated fauna (potential competitors and natural enemies) had no detectable influence on the number of Agromyzidae. Factors examined include taxonomic isolation, whether the plants were annual, biennial or perennial, the number of species of potentially competing microlepidoptera, and the number of species of parasitoids.

(5) We suggest that the number of agromyzid species on many common and widespread umbellifers is considerably below the number that could finally evolve to exploit these plants, and that guilds of specialized leaf-miners are not 'equilibrium assemblages'.

INTRODUCTION

Numerous authors have examined the factors that determine how many species of herbivorous insects are found on various species of plants. Thus, within a geographical region, more-widespread species of plants have more species of insects associated with them than do rare plants (Cornell & Washburn 1979; Lawton & Schröder 1977, 1978; Opler 1974; Southwood 1960; Strong 1974a). Lawton (1978), Southwood (1977) and Strong (1979) provide detailed reviews. Larger, architecturally more complex species of plants also support more species of insects than do smaller, architecturally simple ones (Price 1977; Strong & Levin 1979). Comparing plant-species with ranges of a similar size, trees have more species of insects associated with them than woody bushes, which in turn support more than perennial dicotyledenous herbs: weeds and other annuals are more impoverished, and monocotyledons (excluding grasses) the most impoverished of all (Lawton 1978; Lawton & Schröder 1977, 1978; Southwood 1977). Aquatic dicotyledons also have smaller insect faunas than terrestrial species with similar sized geographical ranges although the reasons for this are obscure (Cummins 1973; Lawton & Schröder 1977).

Somewhat surprisingly, introduced plants rapidly aquire an insect fauna that is commensurate with the size of their geographical range and architecture. Beyond a few hundred to a thousand years, time does not seem to have a significant effect on the total number of insect pest species associated with two species of plants (cacao and sugar cane) that have been widely introduced into different parts of the world (Strong 1974b; Strong, McCoy & Rey 1977). Nor does 'cumulative abundance' since the last ice-age appear to influence the number of insects found on British trees (Strong 1974a) although recently introduced species tend to fall below the general species-area regression (Southwood 1977).

In this paper we examine in more detail one family of plants, the Umbelliferae, and one family of their associated insects, the Agromyzidae, within the British Isles. The larvae of agromyzids are typical mining parasites; most species attack leaves, some the stems and a few, other parts of their hosts. Most are highly species-specific in the plants that they attack (Fig. 1) and all are highly specific to the plant part utilized. We refer to them as 'parasites' quite deliberately; in common with most other phytophagous insects the association which they have with their hosts is every bit as intimate and as specialized as more conventional parasites (Price 1977, in press).

The main difference between this study, and most of the earlier biogeographical work on phytophagous insect communities (*loc. cit.*) is its emphasis on a single insect taxon, rather than an entire faunal assemblage. Oplers' (1974) study on the microlepidoptera of Californian oaks and their allies is a notable exception. The paper has two main objectives. First, it asks whether data from a group of highly specialized plant parasites support or contradict the view that plants saturate with phytophagous insects in
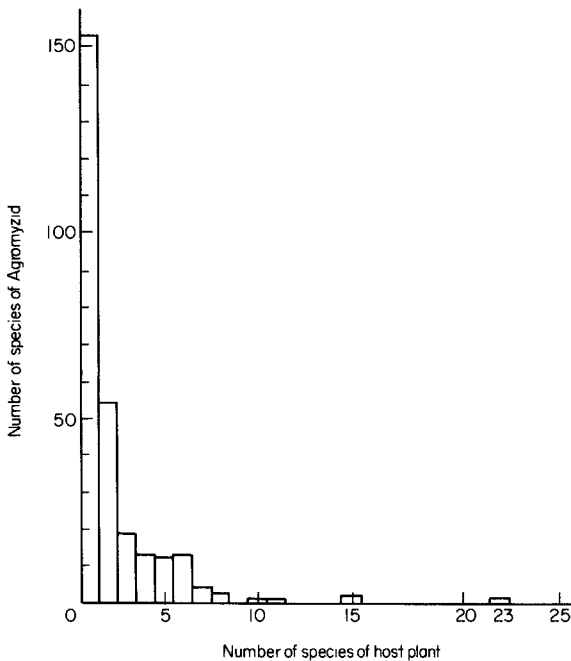

FIG. 1. The number of host-plants utilized by larvae of British Agromyzidae. The majority of species are monophagous or oligophagous (data from Spencer 1972).

ecological time (e.g. Strong, McCoy & Rey 1977) and evolutionary time (Janzen 1973). Although introduced plants quickly aquire a taxonomically diverse fauna commensurate with the size of their geographical range, many of these colonists appear to be unspecialized polyphages, feeding externally on the plant (Goeden 1971, 1974, 1976; Goeden & Ricker 1968; Strong 1979). Hence, analysis of the total fauna (Strong 1974b; Strong, McCoy & Rey 1977) may make it very difficult to detect slow colonization in a small subset of specialist parasites like the mining agromyzids. Second, we investigate whether other factors, for example plant architecture and habitat can explain differences in levels of colonization not accounted for by plant range.

Consider the data in Fig. 2, which shows the number of species of agromyzid flies associated with various families of plants (Price 1977). Although the number of herbivore species correlates with the number of hosts per taxon ($r = 0.71$), the slope of this relationship is less than one. Since most agromyzids are very specific in the plants which they attack (Fig. 1) the implication is that a large number of potential hosts remain uncolonized. Note also that there is a great deal of variation between families; some plant-groups are much richer in agromyzids than others. Similar relationships with similar low slopes hold for subfamilies of fleas (Price 1978), parasitic insects on mammals, birds and insects (Price 1978), mites on Lepidoptera (Treat 1975) and *Heliconius* butterflies on *Passiflora* (Benson, Brown & Gilbert 1975), again implying that a large number of apparently suitable hosts remain uncolonized, though to differing extents in different groups.

The paper is organized as follows. First, we examine the relationship between the number of agromyzid species and the geographical range of each potential host umbellifer
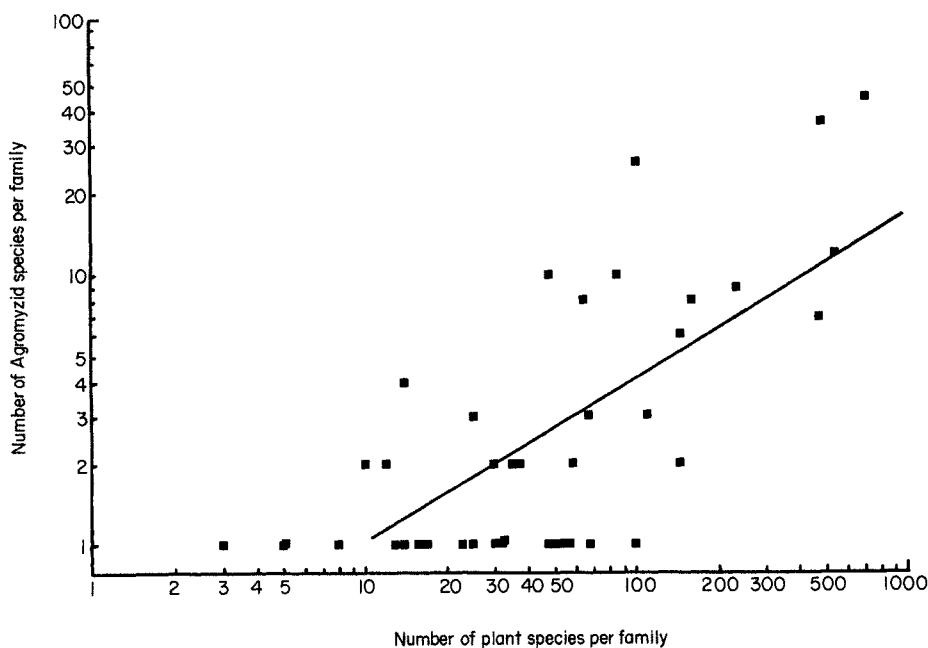

FIG. 2. Relationship between the number of species in each plant family and the number of agromyzid flies attacking each family in Canada and Alaska (Price 1977). The regression is $\log_e Y = 0.613 \log_e X - 1.416$ ($F_{1,39} = 39.94$; $P < 0.001$)

in Britain. We then try to account for the large amount of unexplained variation in this relationship by other characteristics of the host-plants, their size, leaf-form, habitat and so on. We also look for effects imposed on the agromyzids by interactions with potential competitors (other groups of miners), and natural enemies (insect parasitoids). Sufficient variation in the number of agromyzid species remains unexplained for us to tentatively conclude that communities of parasitic insects may not be at equilibrium; that not enough evolutionary time has elapsed to allow speciation by specialized leaf-miners to utilize all the potential hosts at their disposal.

METHODS

The data on agromyzids are from the detailed study of Spencer (1972), yielding host-parasite records for the agromyzids of the British Isles. Information on the sizes of the geographical ranges of plants in the family Umbelliferae were obtained from Perring & Walters (1962), expressed as the number of 10 km squares occupied by each species in Britain (including Ireland). Information on the host plants other than range (e.g. size, habitat and life-history) were taken from Clapham, Tutin & Warburg (1962), supplemented, where necessary, by reference to Fitter, Fitter & Blamey (1974), Martin (1974), McClintock & Fitter (1961), or from Dr A. H. Fitter (personal communication).

Taxonomic categories in the Umbelliferae, such as genus, may not reflect plant characters that are biologically significant for the parasites. Therefore, inter-generic affinities in biochemistry and taxonomy (described in Heywood 1971) were examined. We also used the number of native British species in each genus as a simple index of 'taxonomic isolation' (Lawton & Schröder 1977, 1978).

The leaves of the umbellifers were classified into five categories from 1 (all leaves extremely finely divided) to 5 (most leaves broad, flat and undivided), as an index of increasing suitability for leaf-miners. This process was carried out independently three times, by referring to the illustrations in three floras (Fitter, Fitter & Blamey 1974; Martin 1974; and McClintock & Fitter 1961) each illustrated by different artists. Sixty-three per cent of the plants were assigned to the same category using all three texts; there were very few major disagreements. Where plants had been placed in different categories using different books, the scores were first checked, and the plants then assigned to the largest category.

Information on associated fauna was taken from a variety of sources. Leaf mining Lepidoptera (whose host associations are given by Ford (1949)) are the group most similar in their ecology to the agromyzids. Hering (1957) also provides host-parasite lists for leaf-miners in Europe although the hosts are listed as genera only and not as species. The major natural enemies of agromyzids are parasitoids, recorded by Bouček & Askew (1968), Fischer (1962), Graham (1969) and Griffiths (1964–68). Most records provided the host agromyzid and the plant species with which the parasitoid was associated.

The complete data are given in Appendix 1. Inevitably there are some missing values, and in consequence sample-sizes differ in different analyses.

RESULTS

Agromyzid Species and Plant Range Relationship

The relationship between the number of species of agromyzids associated with, and the geographical range of, each species of umbellifer in the British Isles is shown in Fig. 3.
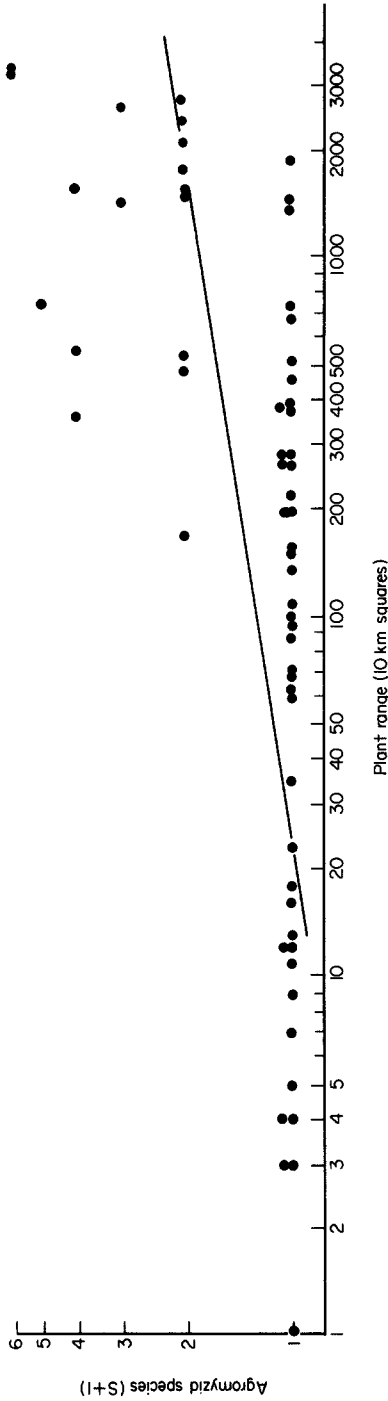
Fig. 3. The number of species of agromyzid flies on umbellifers in Britain: plant range is measured by the number of 10 km squares in which the plant is found. The fitted regression line is given by eqn (1).

The equation is

$$\log_e(S + 1) = 0{\cdot}139 \log_e(A) - 0{\cdot}410, \tag{1}$$

where S is the number of agromyzid species, and A is the size of the plant's geographical range in 10 km squares ($F_{1,59} = 27{\cdot}70$: $P < 0{\cdot}001$).

Although this relationship is highly significant, only 32% of the variation in agromyzid species is accounted for by the regression ($r = 0{\cdot}57$). The notable features in Fig. 3 are as follows.

(1) Many plant species have no agromyzid parasites, although they occupy an area as large as others that have parasites. All seventeen of these species are thought to be native to the British Isles (Clapham, Tutin & Warburg 1962).

(2) Several common plant species support only one parasite species whereas species of similar range support four and five times as many.

(3) The two species of plant with the widest range, *Heracleum sphondylium* and *Angelica sylvestris*, each with five agromyzid species, have fewer parasites than plants outside the Umbelliferae with similar ranges, for example *Senecio jacobaea*, *Taraxacum officinale* (Compositae) and *Ranunculus acris* (Ranunculacea), each with eight agromyzid species.

(4) Plant hosts recorded from less than 160 10 km squares support no agromyzid species.

We enquire next whether any of this variation in the number of agromyzid species can be accounted for by differences in plant structure (architecture), life-history, biochemistry or taxonomic affinity.

Effects of Plant Characteristics other than Range

The residuals (R_{es}) generated by the agromyzid species-plant range regression (eqn (1)) were tested under the null hypothesis that they were not significantly correlated with any of the four following plant characteristics.

(a) Geometric mean size (cm): the geometric mean of the normal maximum and minimum sizes of mature plants given in Clapham, Tutin & Warburg (1962).

(b) Leaf-form, scored 1–5 as an index of increasing suitability for life-miners (see methods).

(c) Life-history, by classifying the plants as annuals (score 1), biennials (score 2·5) or perennials (score 5) (or intermediate values where plants could be in one of two different categories).

(d) Taxonomic isolation: the number of native British species in the genus.

Size and leaf-form are components of plant architecture (Lawton 1978): we hypothesized that larger plants, and plants with broad, undivided leaves should support more species of agromyzid than small plants, and plants with very fine, highly divided leaves.

In the analysis carried out by Lawton & Schröder (1977, 1978), weeds and other annuals (plants of low 'apparency' *sensu* Feeny 1976) appeared to support fewer species of insects than perennial plants. We therefore expected to see proportionately more agromyzids on the perennial umbellifers, and fewest on the annuals.

We were uncertain what the effects of taxonomic isolation might be. Lawton & Schröder (1977) tested the hypothesis that taxonomically isolated species might support fewer parasites than plants with a large number of relatives in the same geographical region, but they were unable to show significant effects in any of the plant-groups which they examined, except the monocotyledons. At best we expected a weak, positive relationship between taxonomic isolation and the residuals round the regression predicted by eqn (1).
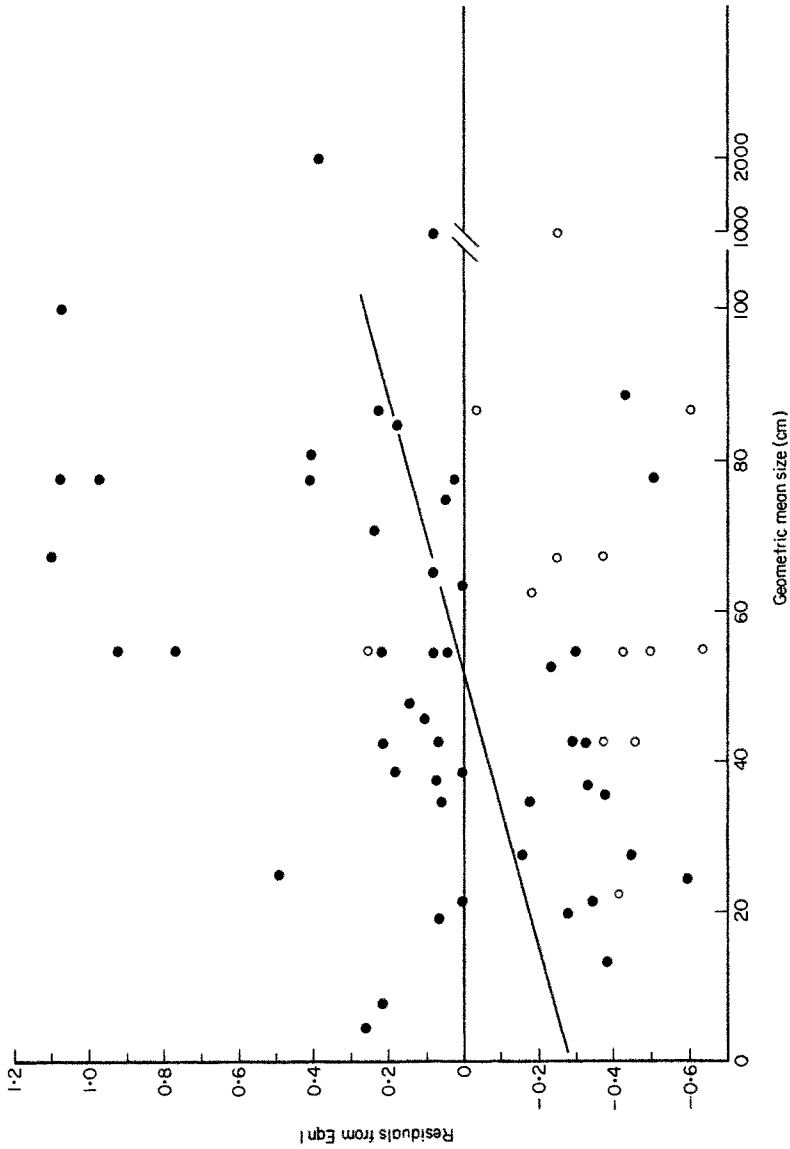
Fig. 4. The residuals from the species plant-range regression (eqn (1) and Fig. 3) as a function of the geometric mean size of the hostplant. The fitted regression (omitting the three extremely large plants) is given by eqn (2b) (○ plants from aquatic habitats: ● all other species).

Finally we separated out the aquatic umbellifers (species growing in littoral communities, ponds, fens, etc.), to see if they too were impoverished, as is apparently the case with other aquatic dicotyledons (Lawton & Shröder 1977).

Plant size contributes significantly to the scatter round the regression shown in Fig. 3. The correlation between residuals (R_{es}) and geometric mean size (Z) is significant, but only if three plants that are at least an order of magnitude larger than any of the others are excluded from the analysis (Fig. 4) (*Conium maculatum*, *Sium latifolium* and *Heracleum mantegezzianum*). The equations are:

All data

$$R_{es} = 0.0001Z - 0.016 \qquad (2a)$$

$$(F_{1,59} = 0.60; P = 0.44 \text{ NS}).$$

(Fitting the logarithm of the geometric mean size for all the data does not improve this relationship.)

Excluding three extreme plants

$$R_{es} = 0.0055Z - 0.286 \qquad (2b)$$

$$(F_{1,56} = 5.08; P = 0.028; r^2 = 0.08).$$

Leaf-form also has a significant effect, although the relationship is complicated by the aquatic umbellifers (Fig. 5). The Spearman rank correlation (r_s) (Siegel 1956) between leaf-form and the residuals from the species-plant range regression is significant ($r_s = 0.342$; $t_{41} = 2.33$; $0.025 > P > 0.01$) only if the aquatic umbellifers are excluded. All but one of the thirteen aquatic umbellifers have negative residuals (see Figs 4 and 5), and hence support fewer agromyzids than predicted by eqn (1). (The mean residual for the aquatics (-0.321) differs significantly from zero: $t_{12} = 4.75$; $P < 0.001$.) Note that these same aquatic species also weaken the correlation between plant size and the residuals from the species-plant range regression shown in Fig. 4.

The remaining plant characteristics have no detectable effects. The scores for annual biennial or perennial plants (life-history effects) are not significantly correlated with the residuals ($r_s = -0.069$; NS); combining leaf-form and life-history characteristics merely weakens the influence of the former; and the effects of taxonomic isolation also appear to be negligible, although again they are complicated by the aquatic umbellifers. Thus, the residuals from the species-plant range regression and taxonomic isolation are significantly *negatively* correlated (not positively correlated as hypothesized) if all the data are included ($r = -0.278$; $F_{1,59} = 4.96$; $P = 0.030$), but this effect is almost entirely attributable to the aquatic members of the largest genus, *Oenanthe*. If we exclude all aquatics, or the genus *Oenanthe*, taxonomic isolation no longer has any significant effect.

Finally, inter-generic affinities in the Umbelliferae that were biologically meaningful to agromyzids could not be adequately assessed from information in Heywood (1971), particularly in the absence of a pharmacopedia relevant to agromyzids (or any other insect herbivores) on this family. We found no compelling evidence for uniting any genera into a single assemblage for regression purposes. However, four species of umbellifer may harbour agromyzids that are sustained in the biogeographic sense by more common species: one species on *Heracleum mantegazzianum* may owe its presence to the much more common *H. sphondylium*; similarly one species on *Pimpinella major* and *Silaum silaus* may be largely supported by *P. saxifraga*, and two species on *Pastinaca*
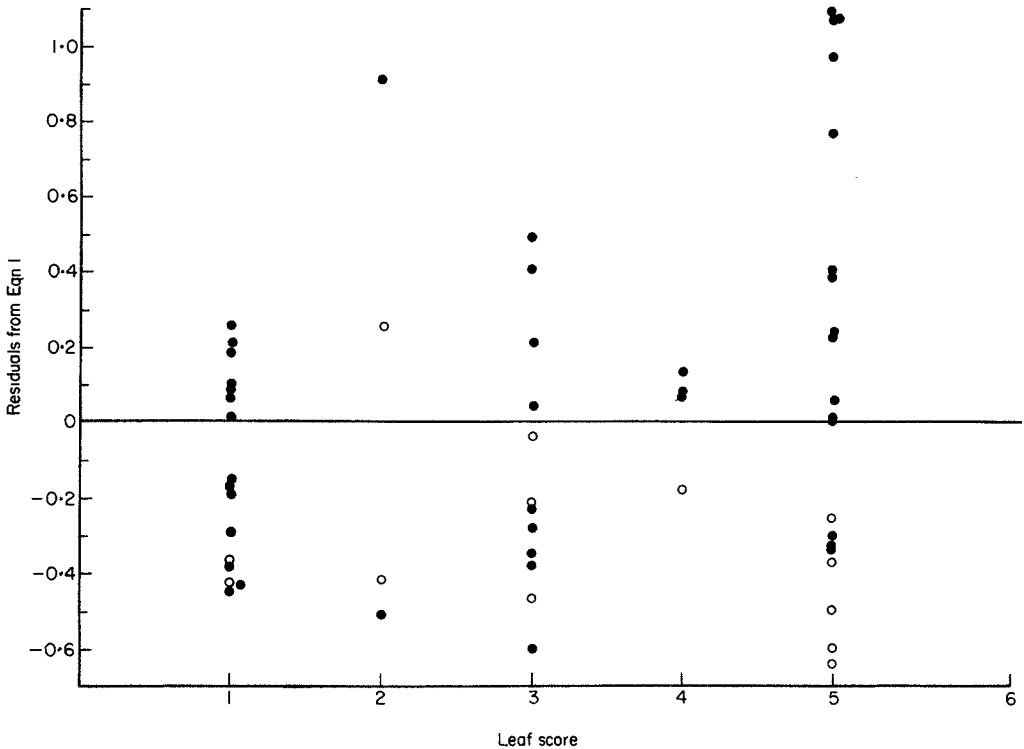
FIG. 5. The residuals from the species plant-range regression (eqn (1) and Fig. 3) plotted against leaf-score. Very finely divided leaves score 1; very broad, undivided leaves score 5. (O plants from aquatic habitats: ● all other species.)

sativa may be supported by the more common *Heracleum sphondylium*. When the numbers of agromyzid species per plant species were reduced because of this possibility, the agromyzid species-plant range relationship was only marginally better than portrayed by eqn (1):

$$\log_e(S + 1) = 0.127 \log_e(A) - 0.371 \quad (F_{1,59} = 30.36; P < 0.001; r^2 = 0.34),$$

(3)

accounting for only 2% more of the variance. These effects are clearly negligible.

In summary, part of the variance round the regression line shown in Fig. 1 can apparently be attributed to three plant characteristics, namely size, leaf-form and whether or not the plants are aquatic. All three operate in the direction that we predicted. None of the other plant characteristics that we can measure have any significant effects.

Unfortunately, this simple picture is complicated by two things. First, plant size and leaf-form are themselves correlated ($r_s = 0.369$; $t_{54} = 2.91$; $0.005 > P > 0.001$), implying that the large umbellifers also tend to have large, broad and undivided leaves. Second, and more surprising, there are significant (though weak) positive relationships between leaf-form and range ($r_s = 0.292$; $t_{54} = 2.25$; $0.025 > P > 0.01$), and plant size and range ($F_{1,56} = 4.66$; $P = 0.035$; $r^2 = 0.08$) again omitting the three extremely large plants. In other words, the most widespread umbellifers tend to be bigger and have larger, less divided leaves than umbellifers with restricted ranges. Such correlations between the independant variables make it extremely difficult to disentangle their

relative contributions, the more so because leaf-form is a rank-score. However, we can obtain a rough indication of how much of the variation in agromyzid species-richness we can explain by treating leaf-score as an interval-scale, and fitting standard multiple regressions. The two best, yielding significant fits to all the independent variables, were as follows:

Agromyzid species v. range and leaf-forms

$$\log_e(S + 1) = 0{\cdot}146 \log_e (A) + 0{\cdot}102L - 0{\cdot}657 \tag{4}$$
$$\text{Range } (A) \ F_{1,40} = 23{\cdot}21; P < 0{\cdot}0001$$
$$\text{Leaf-form } (L) \ F_{1,40} = 6{\cdot}50; P = 0{\cdot}015.$$

(Excluding from the analysis five plants with no data on leaf-form, and aquatics.) A slightly better alternative model was:

Agromyzid species v. range and geometric mean size

$$\log_e(S + 1) = 0{\cdot}140 \log_e(A) + 0{\cdot}008Z - 0{\cdot}715 \tag{5}$$
$$\text{Range } (A) \ F_{1,38} = 20{\cdot}28; P = 0{\cdot}0001$$
$$\text{Size } (Z) \ F_{1,38} = 8{\cdot}17; P = 0{\cdot}0069.$$

(Excluding the same data as in eqn (3) to facilitate comparison, and the two remaining plants of extreme size.)

The multiple correlation coefficients for these regressions were 0·699 (eqn (4)) and 0·715 (eqn (5)), implying that at best, approximately 50% of the variation in the number of agromyzid species still remains unexplained.

Effects of other insects

Conceivably, part of the unexplained variation in agromyzid species could be accounted for by interactions with other organisms on the host plant. We tested two hypotheses: (1) the guild of leaf-miners is in dynamic equilibrium and therefore taxonomic units within this guild will display complementary abundances on a range of plants; (2) extinction rates of agromyzids or resistance to colonization are higher for some species of host plant because natural enemies of agromyzids are very effective on these hosts.

The major taxonomic group of miners other than agromyzids is the microlepidoptera. Theoretically, these may compete with agromyzids for resources and preempt potential niche space; in practice this does not appear to be the case. The species-area relationship for microlepidoptera on Umbelliferae in Britain is very similar to that for agromyzids ($r^2 = 0{\cdot}24$) (Fig. 6a) and the regression of agromyzids plus microlepidoptera on plant area accounts for only 34% of the variance ($F_{1,57} = 29{\cdot}57, P < 0{\cdot}001; r = 58$). A positive relationship exists between the number of species of agromyzids and the number of microlepidoptera species per host in Britain ($F_{1,57} = 50{\cdot}91; P < 0{\cdot}001; r^2 = 0{\cdot}47$) and a similar relationship is seen between agromyzids and all the other leaf miners in Europe ($F_{1,33} = 15{\cdot}71; P < 0{\cdot}001; r^2 = 0{\cdot}32$). It therefore appears that each group of parasites is colonizing host plants in a similar way.

As a final test, we regressed the residuals from the species-geographical range relationship for the microlepidoptera against the equivalent residuals for agromyzids. Competitive interactions between these two groups (so that plants with more microlepidoptera than expected have fewer agromyzids and vice-versa) should generate a significant negative relationship. The actual relationship is significant, but positive (with the agromyzid residuals from eqn (1) as the independent variable: $F_{1,57} = 23{\cdot}99; P < 0{\cdot}001$;
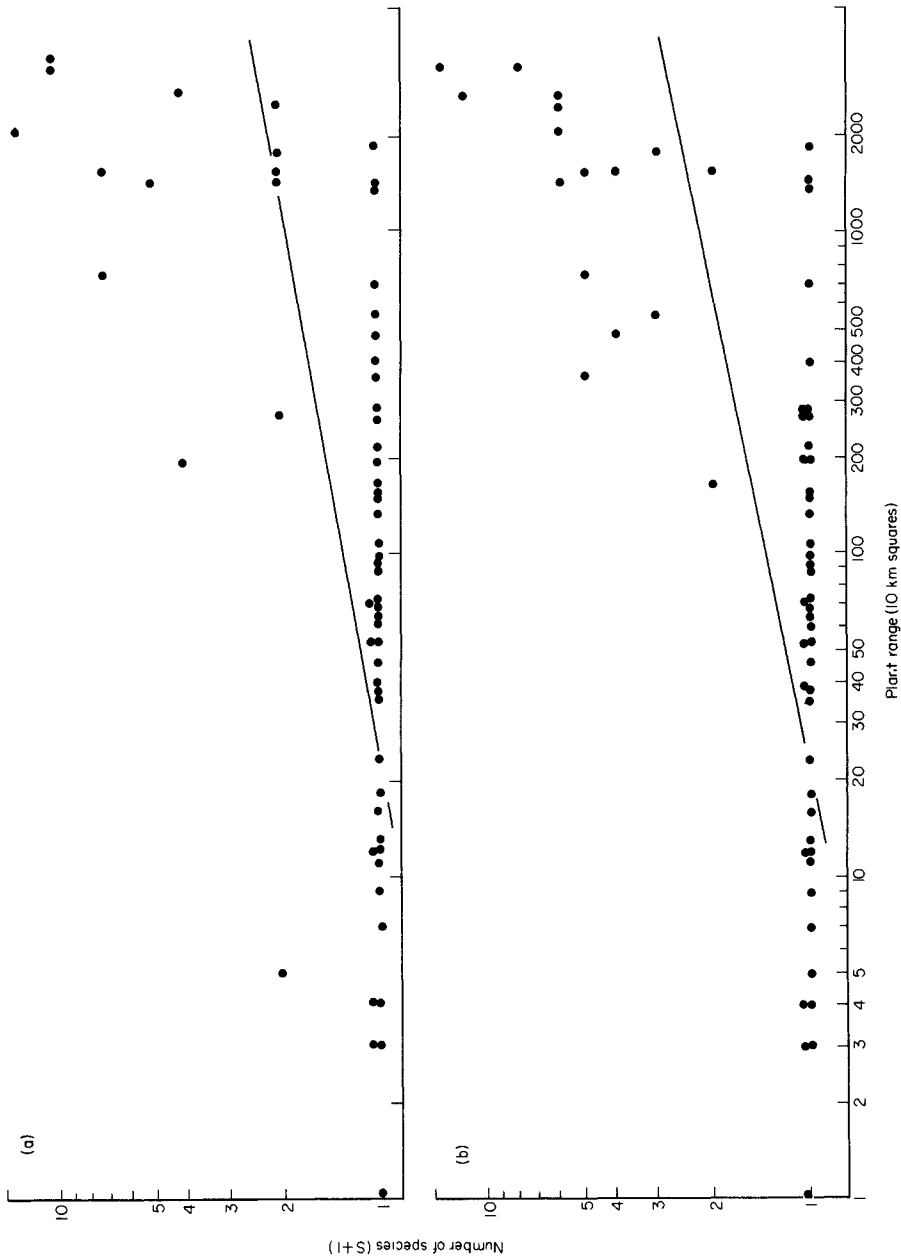
FIG. 6(a). The number of species of microlepidoptera (S_m) on umbellifers in Britain; plant range (A) is measured by the number of 10 km squares. Microlepidoptera are potential competitors of leaf-miners. The equation is: $\log_e(S_m + 1) = 0.16 \log_e A - 0.49$ ($F_{1,57} = 18.80$; $P < 0.001$). (b) The number of species of parasitoids (S_p) on umbellifers in Britain. The equation is: $\log_e(S_p + 1) = 0.201 \log_e A - 0.60$ ($F_{1,59} = 31.82$; $P < 0.001$).

$r^2 = 0.29$) implying, if anything, that the plants tend to vary together, i.e. Umbelliferae with more agromyzids than expected also have more microlepidoptera.

Natural enemies could also conceivably play an important role in modifying or preventing the colonization of potential host plants by agromyzids (Holt 1977; Lawton 1978). Some plant species may be more favourable to parasites than others, or exist in more favourable plant assemblages (Atsatt & O'Dowd 1976). But again the parasitoids show a species-area relationship with plants similar to that of the agromyzids (Fig. 6(b)) and provide no evidence that plants with few agromyzids support more species of parasitoids than average. A positive correlation exists between number of agromyzids per host plant in Britain and number of parasitoids associated with that host plant species ($F_{1,57} = 31.82$; $P < 0.001$; $r^2 = 0.35$) and the number of agromyzids per host plant genus in Europe and the number of parasitoids associated with that genus ($F_{1,34} = 18.09$; $P < 0.001$; $r^2 = 0.34$). Finally, as with the microlepidoptera, the residuals from the agromyzid species-geographical range regression are positively, not negatively, correlated with the equivalent relationship for the parasitoids ($F_{1,59} = 119.5$; $P < 0.001$; $r^2 = 0.67$). There is no evidence that umbellifers with fewer agromyzids than expected support a larger than usual guild of parasitoids: quite the reverse.

DISCUSSION

Although the more widespread Umbelliferae support more species of agromyzid parasites than do the rarer ones, plant range accounts for only 32% of the variation in agromyzid species. Some of the residual variation can apparently be attributed to three plant characteristics; namely size, leaf-form and whether or not the plants grow in aquatic habitats.

Since size and leaf-form are themselves correlated, it is not clear whether both contribute to the variation. But three umbellifers that are each at least an order of magnitude larger than any other species are not noticeably richer in agromyzids; indeed because of their undue influence on the regression, the effects of plant size are only apparent if these three unusually large plants are excluded from the analysis. Hence, leaf-form rather than size *per se* may well be the important variable. The general problem of how much 'size *per se*', compared with more complex architecture, contributes to the enhanced number of species of insects associated with larger plants requires further work (Strong 1979; Strong & Levin 1979). The present study suggests that quite subtle effects of plant architecture can be detected within a closely related group of species, and that they are not just apparent in gross comparisons between major life-forms and taxa (Lawton 1978; Lawton & Schröder 1977, 1978; Strong & Levin 1979).

None of the umbellifers growing in aquatic habitats support any agromyzids, and all but one have negative residuals in Fig. 3. This impoverished fauna resembles that of other dicotyledons from similar habitats (Lawton & Schröder 1977, 1978). The agromyzids that mine the leaves of umbellifers all pupate outside their host plant (see Spencer 1972) so that plants growing in water, or in habitats liable to flooding, may be unfavourable to the pupal stage. Stem borers and miners pupate in the plant but may be carried into water as the vegetation dies down. Thus emergent aquatic plants may present a serious barrier to colonization by agromyzids.

We were unable to detect any differences between annual, biennial or perennial umbellifers. In this respect the umbellifers resemble European Cynareae (Lawton & Schröder 1978), and it now seems possible that the reduced number of species noted by Lawton &

Schröder (1977) on weeds and other annuals, compared with perennial herbs is a direct effect of differences in size and/or architecture rather than 'apparency' (Feeny 1976). Further work is required on this point.

Contrary to expectation, none of the other plant characteristics or associated fauna had any detectable effects on agromyzid species richness. Obviously, it was not possible to measure everything, although we considered a number of other possibilities. Thus, we looked at stem-form (because a small minority of the agromyzids are stem miners), and classified the stems into whether or not they were hollow. None of the variations in the number of stem miners could be accounted for by this refinement.

The most serious omissions are probably as follows. (i) The number of different habitats occupied by each umbellifer. (ii) The geographical spread of the records; umbellifers which occupy the same number of 10 km squares may differ markedly in the position and extent of their actual ranges (contrast *Myrrhis odorata* and *Pastinaca sativa* for example, each occupying just over seven hundred squares, with the former having a more diffuse and northerly distribution than the latter). (iii) Plant abundance and density within each 10 km square. (iv) Plant history. (v) Plant chemistry. Attempts to quantify (i) and (ii) in a simple and satsifactory manner proved to be impossible. We have no data on (iii), and under (iv) are cautioned by Godwin (1975) that his compilation of plant remains in Britain from the Quaternary should not be used to measure the relative abundance of species through time. Thus the absence of records (which applies to 44% of the umbellifers in our study) does not imply absence of a species, and we were therefore unable to examine the important historical aspects of the agromyzid-umbellifer relationship. (v) Without knowing the pharmacological effects of umbellifer chemicals on agromyzids we submit that there is no evidence that presence of any chemical, or combination of chemicals, acts as a complete barrier to colonization. The plant most toxic to vertebrates, *Conium maculatum*, has been colonized by one agromyzid and four microlepidopterans. Other plants that might be assumed to be chemically resistant to colonization because agromyzids are absent have been successfully colonized by microlepidopterans (three species on *Eryngium maritimum*, and one each on *Oenanthe crocata*, *O. aquatica* and *Peucedanum officinale*) showing that chemical barriers are unimportant. Other cases could be cited where herbivores are known to utilize umbellifers with no agromyzids (e.g. *Foeniculum vulgare* is used by *Papilio machaon* larvae). Plant-chemistry in general appears to have little influence on the number of insect species which eventually evolve to exploit a plant (Lawton 1978).

Obviously, the possibility also remains that despite our impression to the contrary, the agromyzid and plant range data are sufficiently unreliable to introduce considerable bias (and therefore inexplicable variation) into our study. The fact that the number of agromyzid species on a plant can only be a small integer, whereas the range data are effectively continuous over an interval of four orders of magnitude will also introduce a small amount of scatter round the most deterministic of species-area regressions.

Put simply, we have not, and cannot measure everything that might contribute to variation round the regression line predicted by eqn (1); nor do we really know how much of the variation we need to account for before we have nothing very interesting left to explain!

These caveats are very important; but they are not a counsel of despair. Given that we have a large amount of unexplained variation in our data (approximately 50%), the hypothesis that a significant part of this is due to non-equilibrium conditions—the failure of agromyzids to colonize all the suitable resources—is plausible, economic and

worth pursuing, albeit difficult to test. Since we have tested as best we can the effects of competition and enemies which would lead to increased extinction with higher species richness and the maintenance of an equilibrium number of species (as explained by MacArthur & Wilson 1967), and we have found an absence of these effects, we are left with no alternative more parsimonious than to conclude that non-equilibrium, non-asymptotic conditions prevail.

Although almost all species-area relationships for plants and their associated parasites are highly significant statistically, the amount of variation which they explain varies markedly. Some studies find that most of the variation is accounted for by the regression (Opler (1974), $r^2 = 0.90$; Lawton & Schröder (1977), woody shrubs $r^2 = 0.85$, perennial herbs $r^2 = 0.71$; Cornell & Washburn (1979), Californian oaks $r^2 = 0.72$). Others find less satisfactory fits; Strong (1974a), $r^2 = 0.61$; Strong, McCoy & Rey (1977), $r^2 = 0.61$; Lawton & Schröder (1977), weeds and other annuals $r^2 = 0.59$, monocotyledons $r^2 = 0.51$: and some that less than 50% of the variance has been accounted for (Strong (1974b), $r^2 = 0.47$; Cornell & Washburn (1979), Atlantic oaks $r^2 = 0.41$; Strong & Levin (1975) $r^2 = 0.28$). There is even one study that finds no significant relationship of any kind (Claridge & Wilson 1976, 1978). Although it is not known for any of these plant-insect associations how much of the residual variation could be accounted for by other characteristics of the host-plant, they show that the agromyzid data shown in Fig. 3 are not particularly unusual. It also seems likely that an understandable reluctance on the part of ecologists to report, and editors to publish, results with low (or zero) levels of statistical significance will distort our impression of the real world in favour of high correlation coefficients (Strong 1979).

Strong's studies omitted records of plants with no herbivore species, which raises the question of whether different methodologies may yield very different results. When zero records were omitted from our data, all correlations on host plant area (for agromyzids, microlepidoptera and parasitoids) were less significant, and in the first two cases accounted for only 3% ($P < 0.50$) and 15% ($P < 0.10$) of the variance respectively. The correlation for parasitoids accounted for 6% more of the variance than when zero records were included (41% ($P < 0.005$) versus 35%). We believe many of the zeros to be genuine, and that they should be included. In so doing, our analyses are actually conservative, because for the agromyzids, correlations that omit the zero records account for very little variance, and hence place an even greater onus on factors other than the geographical range of the host plant to explain differences in agromyzid species richness.

Within the Umbelliferae, many of the potential hosts that remain uncolonized have small geographical ranges and provide no challenge to the equilibrium theory. But also many common plant species have resources unutilized by agromyzid species. Given enough evolutionary time there is no apparent reason why common host plants should not continue to accumulate species for as long as competition and enemies remain unimportant. We are aware that colonization and speciation can occur rapidly in some phytophagous Diptera (Bush 1975), and apparently in other groups (Zimmerman 1960). We do not know whether these examples are typical of phytophages in general, or agromyzids in particular. If they are, they may be fatal for our hypothesis. Nor do we know, with the possible exception of the aquatic umbellifers, what it is about certain very widespread plants that has, so far, prevented colonization by agromyzids. Chance, presumably, plays an important part.

Dynamic equilibrium levels of the type envisaged in 'classical' island biogeography (MacArthur & Wilson 1967; Janzen 1973), if they exist at all may be much higher than

the number of agromyzid species found on any umbellifer in Britain today. Among the leaf-blade miners, by far the largest group of agromyzids, three species are known to coexist on the same host (e.g. on *Heracleum sphondylium*, *Pimpinella saxifraga*), and six and seven species on one host is commonly observed in other plant families. Four leaf midrib miners occur on *Taraxacum officinale* (Compositae) and three stem borers on *Senecio jacobaea* (Compositae). Two stem miners are found on *Melandrium rubrum* (Caryophyllaceae) and three on *Galium mollugo* (Rubiaceae). Ignoring the other plant parts that are not commonly utilized by agromyzids we could conservatively expect twelve to fifteen species of agromyzid to coexist on hosts with the largest geographical ranges. Competition for plant resources, as envisaged by Janzen (1973) is probably unimportant. Patchiness of plants, low colonization rates in ecological time, and the usually low level of resource utilization on any one plant, will dilute the intensity of interactions even when several agromyzid species occur in the same vicinity. Rathcke (1976a, b) supports our contention since she found that competition was not an organizing influence in the stem-boring guild of a tall grass prairie, and competition in general does not seem to be important in structuring phytophagous insect communities (Lawton 1978; Rathke 1976b; Strong 1979).

Our main conclusions may be less at variance with those of Strong (1974a, b) and Strong, McCoy & Rey (1977) than they appear to be at first sight. Thus, analysis of a complete fauna may mask a much slower colonization by specialized leaf-miners, which naturally make up a rather small proportion of the total species of insects on plants (e.g. 21% in European Cynareae, and 15% in several woody shrubs: Lawton & Schröder 1978: unfortunately, we do not have comparable data for the Umbelliferae). Interestingly miners make up a significantly larger proportion of the total insect species on widespread Cynareae than they do on the rarer ones (Lawton & Schröder 1978). This is again consistent with the hypothesis than many plant species have not yet come into equilibrium with their mining parasites, and that common and widespread plants are the ones that are more likely to have been 'found' in evolutionary time (Southwood 1977, and references therein).

We do not wish to take issue with the general view that the gross number of arthropod species on introduced plants reaches some sort of asymptote fairly quickly, particularly if, as appears to be the case, most of these species are relatively unspecialized external feeders (Goeden 1971, 1974, 1976; Goeden & Ricker 1968). Rather, we wish to draw attention to the fact that the subtle accumulation of specialists (e.g. miners and gall formers) may continue over very long periods of evolutionary time. Strong (1979) concurs in this view. The native Umbelliferae of Britain appear to offer numerous possibilities for further colonization by agromyzids.

ACKNOWLEDGMENTS

REFERENCES

Atsatt, P. R. & O'Dowd, D. J. (1976). Plant defecne guilds. *Science*, 193, 24–29.
Benson, W. W., Brown, K. S. Jr & Gilbert, L. E. (1975). Coevolution of plants and herbivores: passion flower butterflies. *Evolution*, 29, 659–660.

Bouček, Z. & Askew, R. R. (1968). *Index of Palearctic Eulophidae, Index of Entomophagous Insects* 3 (Ed. by V. Delucchi and G. Remandiere). Le Francois, Paris.

Bush, G. L. (1975). Sympatric speciation in phytophagous parasitic insects. *Evolutionary Strategies of Parasitic Insects* (Ed. by P. W. Price), pp. 187–206. Plenum, New York & London.

Clapham, A. R., Tutin, T. G. & Warburg, E. F. (1962). *Flora of the British Isles*. Cambridge University Press.

Claridge, M. F. & Wilson, M. R. (1976). Diversity and distribution patterns of some mesophyll-feeding leafhoppers of temperate woodland canopy. *Ecological Entomology* 1, 231–250.

Claridge, M. F. & Wilson, M. R. (1978). British insects and trees: a study in island biogeography or insect/plant coevolution? *American Naturalist*, 112, 451–456.

Cornell, H. V. & Washburn, J. O. (1979). The richness-area correlation for Cynipine galls on oak trees: a comparison of two geographical areas. *Evolution* (in press).

Cummins, K. W. (1973). Trophic relations of aquatic insects. *Annual Review of Entomology*, 18, 183–206.

Feeny, P. (1976). Plant apparency and chemical defense. *Recent Advances in Phytochemistry*, 10, 1–40.

Fischer, M. (1962). Beitrag zur Kenntnis der Wirte von *Opius. Arten. Entomophaga*, 7, 79–90.

Fitter, R., Fitter, A. & Blamey, M. (1974). *The Wild Flowers of Britain and Northern Europe*. Collins, London.

Ford, L. T. (1949). *A Guide to the Smaller British Lepidoptera*. South London Entomology and Natural History Society, London.

Godwin, H. (1975). *The History of the British Flora*. Cambridge University Press, Cambridge.

Goeden, R. D. (1971). The phytophagous insect fauna of milk thistle in Southern California. *Economic Entomology*, 64, 1101–1014.

Goeden, R. D. (1974). Comparative survey of the phytophagous insect faunas of Italian thistle, *Carduus pycnocephalus*, in Southern California and Southern Europe relative to biological weed control. *Environmental Entomology*, 3, 464–474.

Goeden, R. D. (1976). The Palearctic insect fauna of milk thistle, *Silybum marianum*, as a source of biological control agents for California. *Environmental Entomology*, 5, 345–353.

Goeden, R. D. (1968). The phytophagous insect fauna of Russian thistle (*Salsola kali* var. *tenuifolia*) in Southern California. *Annals of the Entomological Society of America*, 61, 67–72.

Graham, M. W. R. de V. (1969). The Pteromalidae of North-western Europe (Hymenoptera: Chalcidoidea). *Bulletin of the British Museum (Natural History) Entomology Supplement* 16, 1–908.

Griffiths, G. C. D. (1964–68). The Alysiinae (Hym. Brackonidae) parasites of the Agromyzidae (Diptera). *Beitraege zur Entomologie*, 14, 823–914; 16, 551–605; 16, 775–951; 17, 653–696; 18, 5–62; 18, 63–152.

Hering, E. M. (1957). *Bestimmungstabellen der Blattminen von Europa*. Vols. 1–3. Junk, The Hague.

Heywood, V. H. (1971) (Ed.). *The Biology and Chemistry of the Umbelliferae*. Academic Press, London.

Holt, R. D. (1977). Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology*, 12, 197–229.

Janzen, D. H. (1973). Host plants as islands. II. Competition in evolutionary and contemporary time. *American Naturalist*, 107, 786–791.

Lawton, J. H. (1978). Host-plant influences on insect diversity: the effects of space and time. *Symposia of the Royal Entomological Society of London* 9, *Diversity of Insect Faunas* (Ed. by L. A. Mound and N. Waloff), pp. 105–125. Blackwell Scientific Publications, Oxford.

Lawton, J. H. & Schröder, D. (1977). Effects of plant type, size of geographical range and taxonomic isolation on number of insect species associated with British plants. *Nature*, 265, 137–140.

Lawton, J. H. & Schröder, D. (1978). Some observations on the structure of phytophagous insect communities: the implications for biological control. *Proceedings of the IV International Symposium on Biological Control of Weeds* (Ed. by T. H. Freeman), pp. 57–73. Centre for Environmental Programs, University of Florida, Gainesville.

MacArthur, R. H. & Wilson, E. O. (1967). *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey.

Martin, W. K. (1974). *The Concise British Flora in Colour*. Ebury Press & Michael Joseph, London.

McClintock, D. & Fitter, R. S. R. (1961). *The Pocket Guide to Wild Flowers*. Collins, London.

Opler, P. A. (1974). Oaks as evolutionary islands for leaf-mining insects. *American Scientist*, 62, 67–73.

Perring, F. H. & Walters, S. M. (Eds.) (1962). *Atlas of the British Flora*. B.S.B.I., Nelson, London.

Price, P. W. (1977). General concepts on the evolutionary biology of parasites. *Evolution*, 31, 405–420.

Price, P. W. (1978). The extent of adaptive radiation in fleas (Siphonaptera). *Fleas—Proceedings of an International Conference* (Ed. by R. Traub). Balkerna, Rotterdam (in press).

Price P. W. (1980). *Evolutionary Biology of Parasites*. Princeton University Press, Princeton, New Jersey (in press).

Rathcke, B. J. (1976a). Insect-plant patterns and relationships in the stem-boring guild. *American Midland Naturalist*, 96, 98–117.

Rathcke, B. J. (1976b). Competition and coexistence within a guild of herbivorous insects. *Ecology*, 57, 76–87.

Siegel, S. (1956). *Nonparametric Statistics for the Behavioural Sciences*. McGraw-Hill, New York.

Southwood, T.R.E. (1960). The abundance of the Hawaiian trees and the number of their associated insect species. *Proceedings of the Hawaiian Entomological Society*, 17, 299–303.

Southwood, T.R.E. (1977). The stability of the trophic milieu, its influence on the evolution of behaviour and of responsiveness to trophic signals. *Colloques Internationaux du C.N.R.S. 265, Comportement des Insectes et Milieu Trophique*, pp. 471–493.

Spencer, K. A. (1972). *Handbooks for the Identification of British Insects*. Diptera Agromyzidae. Royal Entomological Society, London.

Strong, D. R. Jr (1974a). Non-asymptotic species richness models and the insects of British trees. *Proceedings of the National Academy of Science, U.S.A.*, 71, 2766–2769.

Strong, D. R. Jr (1974b). Rapid asymptotic species accumulation in phytophagous insect communities: the pests of cacao. *Science*, 185, 1064–1066.

Strong, D. R. Jr (1979). Biogeographic dynamics of insect-host plant communities. *Annual Review of Entomology*, 24, 89–119.

Strong, D. R. Jr & Levin, D. A. (1975). Species richness of the parasitic fungi of British trees. *Proceedings of the National Academy of Science, U.S.A.*, 72, 2116–2119.

Strong, D. R. Jr & Levin, D. A. (1979). Species richness of plant parasites and growth form of their hosts. *American Naturalist* (in press).

Strong, D. R. Jr McCoy, E. D. & Rey, J. R. (1977). Time and the number of herbivore species: the pests of sugarcane. *Ecology*, 58, 167–175.

Treat, A. (1975). *Mites of Moths and Butterflies*. Cornell University Press.

Zimmerman, E. C. (1960). Possible evidence of rapid evolution in Hawaiian moths. *Evolution*, 14, 137–138.

APPENDIX I

Data on British Umbelliferae and Agromyzidae on which the analyses were performed (see text for details)

Plant Species	No. 10 km squares	No. agromyzid species	Geometric mean size (cm)	Leaf form score	Life history score	Taxonomic isolation native species in genus, U.K.	No. microlep. species	No. parasitoid species
Sanicula europaea	1752	1	34·6	5	5	1	1	2
Eryngium maritimum	196	0	42·4	5	5	2	3	0
Eryngium campestre	12	0	42·4	4	5	2	0	4
Chaerophyllum temulentum	1545	1	54·7	4	2·5	1	1	0
Anthriscus caucalis	281	0	35·3	3	1	2	–	5
Anthriscus sylvestris	2637	2	77·5	3	3	2	–	0
Scandix pecten-veneris	453	0	27·4	1	1	1	0	5
Myrrhis odorata	720	0	77·5	2	5	1	0	0
Torilus japonica	1425	2	25·0	3	1	3	0	5
Torilus arvensis	137	0	20·0	3	1	3	0	0
Torilus nodosa	285	0	13·2	1	1	3	0	0
Caucalis platycarpos	12	0	19·0	1	1	0	0	0
Caucalis latifolia	11	0	37·5	–	1	0	0	0
Smyrnium olusatrum	538	1	86·6	5	2·5	1	0	0
Physospermum cornubiense	7	0	47·4	4	5	1	0	1
Conium maculatum	1510	1	1000·0	1	2·5	1	4	0
Bupleurum rotundifolium	18	0	21·2	5	1	4	0	0
Bupleurum baldense	3	0	4·5	1	1	4	0	0
Bupleurum falcatum	1	0	80·6	5	5	4	0	0
Buplcurum tenuissimum	59	0	27·4	1	1	4	0	0
Trinia glauca	4	0	7·8	1	5	1	0	0
*Apium graveolens**	267	0	42·4	5	2·5	3	0	0
*Apium nodiflorum**	1856	0	54·8	5	5	3	0	0
*Apium inundatum**	371	0	22·4	1	5	3	0	0
Petroselinum crispum	98	0	52·5	–	2·5	1	0	0
Petroselinum segetum	157	0	54·8	5	2·5	1	0	0
Sison amomum	484	1	70·7	5	2·5	1	0	3
*Cicuta virosa**	68	0	62·5	4	5	1	0	0
Carum verticillatum	150	0	42·4	1	5	2	0	0
Carum carvi	70	0	38·7	1	2·5	2	0	0

Species								
Bunium bulbocastanum	9	0	45·8	1	5	1	0	0
Conopodium majus	2468	1	38·7	1	5	1	1	5
Pimpinella saxifraga	1576	3	54·8	5	5	2	6	3
Pimpinella major	354	3	77·5	5	5	2	0	4
Aegopodium podagraria	2742	1	63·2	5	5	1	3	11
Sium latifolium*	109	0	1000·0	5	5	1	0	0
Berula erecta*	683	0	54·8	5	5	1	0	0
Crithmum maritimum	219	0	21·2	3	5	1	0	0
Seseli libanotis	4	0	42·4	3	5	1	0	0
Oenanthe fistulosa*	515	0	42·4	3	5	7	0	0
Oenanthe pimpinelloides	94	0	54·8	3	5	7	0	0
Oenanthe silaifolia	13	0	75·0	—	5	7	0	0
Oenanthe lachenalii*	386	0	54·8	2	5	7	1	0
Oenanthe crocata*	1448	0	86·6	5	5	7	1	0
Oenanthe aquatica*	270	0	67·1	1	5	7	0	0
Oenanthe fluviatilis*	88	0	67·1	3	5	7	0	0
Aethusa cynapium	1358	0	24·5	3	1	1	0	0
Foeniculum vulgare	393	3	88·3	1	5	1	0	0
Silaum silaus	547	0	54·8	2	5	1	0	2
Meum athamanticum	63	0	34·6	1	5	1	0	0
Selinum carvifolia*	3	0	54·8	2	5	1	0	0
Ligusticum scoticum	196	0	36·7	5	5	1	0	0
Angelica sylvestris	3259	5	77·5	5	5	1	9	13
Angelica archangelica	16	0	77·5	—	5	1	0	0
Peucedanum officinale	5	0	84·9	1	2·5	2	1	0
Peucedanum palustre*	23	0	86·6	3	5	2	0	0
Peucedanum ostruthium	35	0	65·0	—	2·5	2	0	0
Pastinaca sativa	740	4	67·1	5	2·5	1	6	4
Heracleum sphondylium	3292	5	100·0	5	2·5	1	9	7
Heracleum mantegazzianum	166	1	2000·0	—	2·5	1	0	1
Daucus carota	2035	1	54·8	3	2·5	1	12	5

* Plants from aquatic habitats (fens, marshes, damp places, ditches, ponds, lakes, etc.)