THE NUMBER OF SPECIES OF INSECT ASSOCIATED WITH VARIOUS TREES

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It is common knowledge amongst ecologists and collectors that some trees have many species of insect denizen and others, usually recently introduced, comparatively few. But the number of species of insect associated with a certain tree would seem to reflect not only the actual time it has been present in Britain but also, and of rather more importance, its general abundance or scarcity throughout this period. If this hypothesis is correct, then in other parts of the world where the pattern of tree dominance is different from that in Britain, we should expect the comparative numbers of insect species to vary accordingly.

The coniferous forest belt is far more extensive in Russia than in Britain and thus pine, spruce, larch and fir (the last three introduced species in Britain) will be comparatively

Table 1. *Comparative series of the numbers of insect species on various deciduous (unmarked) and coniferous* forest trees in Britain and European Russia*

Tree	Britain	Russia
Oak (*Quercus*)	284	150
Willow (*Salix*)	266	147
Birch (*Betula*)	229	101
Hawthorn (*Crataegus*)	149	59
Poplars (*Populus*)	97	122
Apple (*Malus*)	93	77
*Pine (*Pinus*)	91	190
Alder (*Alnus*)	90	63
Elm (*Ulmus*)	82	81
Hazel (*Corylus*)	73	26
Beech (*Fagus*)	64	79
Ash (*Fraxinus*)	41	41
*Spruce (*Picea*)	37	117
Lime (*Tilia*)	31	37
Hornbeam (*Carpinus*)	28	53
*Larch (*Larix*)	17	44
*Fir (*Abies*)	16	42
Holly (*Ilex*)	7	8

more abundant. The numbers of insect species on certain deciduous and coniferous trees in Britain and in Russia are given in Table 1. The figures for Britain are taken from Table 4 and are for certain major groups, those for Russia from Gusev & Rimsky-Korsakov's (1940) list of pests and so, although it is of no importance in the present discussion, the actual values are only directly comparable within series. It will be seen that there is a considerable measure of agreement between the two sets of figures, but that the coniferous trees all have comparatively more associated insect species in Russia than in England. This is supported by the correlation coefficients; for all the trees the coefficient is $+0{\cdot}62$, but when the conifers are excluded it rises to $+0{\cdot}84$. In other words the numbers of insect species on the conifers in the two countries are much less closely associated than

the numbers on the trees of the deciduous forest belt. Thus this comparison between Britain and Russia supports the hypothesis; the trees that are more abundant in Russia have comparatively more insect species.

The second area with which comparison will be made is Cyprus. Some idea of the relative abundance of various trees in that island can be obtained from Holmboe (1914). The more important trees are *Juniperus foetidissima* (forests, especially on the higher mountains and in mountain meadows), *J. phoenicea* (maquis scrub-woods of lowlands), *Pinus nigra*, sub-species *pallasiana* (upland forest), *P. halepensis* (lowland forests), *Quercus alnifolia* (evergreen oak of forests), *Q. infectoria* (deciduous oak of lowland regions), *Alnus orientalis* and *Platanus orientalis* (dominant trees of marshes and river valleys) and *Crataegus azarolus* ('all over the island'). The endemic *Cedrus libani* sub-species *brevifolia* is mentioned as an important forest tree in Cyprus by Pliny and Theophrastus, but it had become rare by 1900, probably owing to extensive felling since the

Table 2. *Comparison of the number of Heteroptera and Homoptera Auchenorrhyncha on various trees in Britain and Cyprus*

Tree type	Britain		Cyprus	
	Species	Number	Species	Number
Deciduous oaks (*Quercus*)	*robur* L. *petraea* (Matt.) Liebl.	47	*infectoria* Oliv.	6
Evergreen oaks (*Quercus*)	**ilex* L.	0	*alnifolia* Poech.	2
Alder (*Alnus*)	*glutinosa* (L.) Gaertn.	18	*orientalis* Decaisne	3
Hawthorn (*Crataegus*)	*oxyacanthoides* Thuill. *monogyna* Jacq.	18	*azarolus* L.	4
Mountain ash (*Sorbus*)	*aucuparia* L.	1	*cretica* Fritsch	1
Maple (*Acer*)	*campestre* L.	4	*obtusifolium* Sibth. et Smith	1
Plane (*Platanus*)	**orientalis* L.	0	*orientalis* L.	4
Apple (*Malus*)	spp.	19	*spp.	1
(*Prunus*)	*spinosa* L.	5	*spp.	1
Juniper (*Juniperus*)	*communis* L.	6	*foetidissima* Willd.	10
			phoenicea L.	5
Pine (*Pinus*)	*sylvestris* L.	17	*nigra pallasiana* Loub.	6
			halepensis Mill.	3
Cedar (*Cedrus*)	**libani* L.	0	*libani brevifolia* J. D. Hooker	1

*Introduced species

Middle Ages. Neither the apple (*Malus* sp.) nor the cherry, plum or sloe (*Prunus* spp.) figure in either Holmboe's list of 'spontaneous vascular plants in Cyprus' or that of the 'more important wild plants of gardens and plantations', although he quotes an author writing in 1563 who said that 'apples are rare at Famagusta and of bad quality' and says that cherries (*P. cerasus*) thrive in some village gardens.

Lindberg (1948) gives an account of the Heteroptera and Homoptera Auchenorrhyncha collected in Cyprus. The number of species on the various trees are given in Table 2, together with those on the same or closely allied trees in Britain (data from Table 4). Whereas in Britain the dedicuous oaks (*Quercus*) are the dominant tree species, in Cyprus, *Juniperus* and *Pinus* share this position and all these trees have comparatively large numbers of associated Hemiptera. Another noteworthy feature of Table 2 is a comparison of the introduced species in both countries: *Platanus*, *Cedrus* and *Quercus alnifolia* all have associated Hemiptera in Cyprus where they are native, in Britain there are none on the same species of the two former or on *Q. ilex*, closely allied to *Q. alnifolia*.

The reverse appears to hold for *Malus* and *Prunus*, species of which are native in Britain, whilst in Cyprus they seem to be comparatively rare introductions.

The British fauna may also be compared with that of Sweden. The number of species of Lepidoptera and the main groups of phytophagous Coleoptera (Phytophaga and Rhynchophora) associated with the various Swedish trees has been obtained from Aurivillus (1917, 1920, 1924) Benander (1929, 1950, 1953), Nordström & Wahlgren (1935-41) Spessivtsaff (1925) and Wahlgren (1915).

The data for Britain are based on Stokoe & Stovin (1944, 1948), Ford (1949) and Walsh (1954) and are given in detail in Table 4. An exact comparison based on the number of species is precluded because these different authorities, standards of 'major host plants' may not be the same. However, it is legitimate to compare the ranks of the trees in the two countries (Table 3).

Table 3. *Comparative series of the number of species of Lepidoptera and Coleoptera associated with various trees in Sweden and Britain*

	Sweden		Britain	
	No. spp.	Rank	No. spp.	Rank
Willows (*Salix* spp.)	198	1	224	2
Birch (*Betula* spp.)	177	2	213	3
Oak (*Quercus* spp.)	146	3	237	1
Poplars (*Populus* spp.)	114	4	78	6
Spruce (*Picea abies*)	93	5	27	14
Pine (*Pinus sylvestris*)	90	6	73	7
Sloe (*Prunus spinosa*)	90	6	103	5
Alder (*Alnus glutinosa*)	63	8	68	10
Apple (*Malus* spp.)	63	9	72	8
Hawthorn (*Crataegus* spp.)	54	10	131	4
Elm (*Ulmus* spp.)	46	11	69	9
Beech (*Fagus sylvatica*)	46	12	57	11
Hazel (*Corylus avellana*)	34	13	55	12
Mountain Ash (*Sorbus aucuparia*)	32	14	27	14
Lime (*Tilia* spp.)	31	15	22	17
Ash (*Fraxinus excelsior*)	17	16	29	13
Hornbeam (*Carpinus betulus*)	11	17	27	14

If the present hypothesis is correct, then the following trees which have higher ranks in Sweden than Britain, should be relatively more abundant in Sweden than Britain: willow, birches, poplars, spruce, pine, alder and lime. Likewise oak, sloe, hawthorn, elm, hazel, ash and hornbeam should be rarer in Sweden, and apple, beach and mountain ash of similar relative abundance in the two countries. Dr A. Melderis, of the Botany Department, British Museum (N.H.), who is conversant with the floras of both countries, has been kind enough to comment on these comparisons and considers that, in general, they are correct. There are certain discrepancies, lime and sloe are probably equally common in both countries and mountain ash more abundant in Sweden than in Britain. It is felt that the measure of agreement (fourteen out of seventeen comparisons) is so large as to support the present hypothesis.

It may be suggested that it is unreasonable to compare islands, such as Britain or Cyprus, with continental areas, as the fauna of islands may be impoverished during successive climatic changes and be unable to replenish completely from the main land mass. However, the great majority of insects, even wingless Collembola, are carried on air currents to some extent, as evidenced by Elton's (1925) observations on Spitzbergen and

the work of others on the insects in the upper air (Hardy & Milne 1938, Freeman 1945, 1952, Glick 1939), that small sea barriers such as the English Channel are unlikely to be of any significance. If the abundance of a tree alters greatly in an area, one might expect corresponding changes in the fauna, and these might show the effect of insular isolation, if such exist. As juniper has become rarer in southern England one Heteropteran attached to it appears to have become extinct, whilst in contrast four new species have recently become established on pine since the extensive conifer afforestation (Southwood 1957). Two of these may have spread from Scotland, but the other two were formerly unknown in Britain and their introduction from the Continent, together with three new species of Micro-Lepidoptera with the same host plant, may be modern evidence of the relative unimportance of the English Channel as a barrier. (Plant quarantine regulations have prevented the importation of nursery stocks during this period.)

Another approach to this problem would be to compare two continental areas such as Russia and Sweden. Unfortunately, the necessary data on the exact relative abundance of different trees in Russia are not available, nor is such a comparison easily made for an area so large and diverse. However, some brief comparison may be made between the Russian (Table 1) and the Swedish data (Table 3) already given. One of the largest changes in rank is the case of hornbeam, which has more insect species in Russia where indeed it is more abundant. Pine, spruce (both also in the southern Russian forests) and beech are somewhat more strongly represented in the Russian flora than in the Swedish, and this is what would be expected from a study of their associated insect species. In contrast, there is relatively less arctic tundra scrub with dwarf birch, willow and alder in Russia than in Sweden, and these trees have higher ranks in Sweden than in Russia.

Only general comparisons are possible with Russia, Sweden and Cyprus; a more detailed study has been made in the case of Hawaii and this shows the same relation of abundance and number of insect species (Southwood 1960a). However, lack of a quantitative measure of the relative abundance of the different trees throughout recent geological history precludes a detailed numerical test of the hypothesis for these countries. But for Britain Godwin (1956) has compiled all the Quaternary records of plant remains. The number of records for each tree is a combined measure of the length of time it has been in Britain and its abundance throughout this time. Godwin stresses that, as some plants are more likely to be preserved or identified than others, and as sampling has been more extensive in some areas and strata than others, the data should not be regarded as strictly quantitative. None the less, it is felt that the number of different records for a tree in Godwin (1956) does give a numerical assessment, albeit approximate, of its history that is of value for the present comparison.

Godwin's (1956) records for each tree together with the number of species of the major groups of plant feeding insects associated with it are given in Table 4. The figures for the Heteroptera are based on Appendix 3 of Southwood & Leston (1959), those for the Homoptera Auchenorrhyncha and Psylloidea mainly on Edwards (1896), for the Macro-Lepidoptera on the 'main host plants' given for each species by Stokoe & Stovin (1944, 1948) the Micro-Lepidoptera on Ford (1949) and the Coleoptera on Walsh (1954). The latter unfortunately is not completely satisfactory for the present purpose, often referring to genera rather than species.

The correlation coefficient of the relationship between the history of the tree (Godwin's records) and the total number of insect species (given in Table 1) is highly significant ($0{\cdot}85$, $P < 0{\cdot}001$). It is noteworthy too that even when the introduced species belong to the same genus as a native tree, *e.g.* sycamore (*Acer pseudoplatanus*) and common maple

(*A. campestre*), not all the insects of the indigenous tree are able to transfer to the alien, even though they may have another unrelated tree as an alternate host; Hering (1951) made similar observations on leaf-miners in the Berlin botanic gardens. Of the introduced trees, spruce (*Picea abies*) has the largest number of associated insect species, whilst the firs (*Abies* spp.) also have a comparatively high number; it is interesting that Godwin

Table 4. *The commoner British trees, their history and associated insects*

	History in Britain since Pleistocene Period	Number of records in Godwin (1956)	Associated insect species: Heteroptera	Homoptera (part)	Macro-Lepidoptera	Micro-Lepidoptera	Coleoptera	Total
Oak (*Quercus robur* L. and *Q. petraea* (Matt.) Liebl.	Native	197	37	10	106	81	50	284
Birch (*Betula* spp.)	,,	182	12	4	94	84	35	229
Hazel (*Corylus avellana* L.)	,,	136	16	2	18	28	9	73
Willow (*Salix* spp.)	,,	134	22	20	100	73	51	266
Alder (*Alnus glutinosa* (L.) Gaertn.)	,,	87	14	8	28	27	13	90
Hawthorn (*Crataegus* spp.)	,,	67	17	1	64	53	14	149
Ash (*Fraxinus excelsior* L.)	,,	59	10	2	16	9	4	41
Pine (*Pinus sylvestris* L.)	,,	54	15	3	10	28	35	91
Holly (*Ilex aquifolium* L.)	,,	44	0	0	2	2	3	7
Yew (*Taxus baccata* L.)	,,	42	0	0	1	0	0	1
Sloe (*Prunus spinosa* L.)	,,	30	4	2	48	43	12	109
Poplars (*Populus* spp.)	,,	30	8	11	33	26	19	97
Elm (*Ulmus*) spp.)	,,	30	11	4	33	26	10	82
Beech (*Fagus sylvatica* L.)	,,	27	4	3	24	16	17	64
Common maple (*Acer campestre* L.)	,,	18	2	2	8	12	2	26
Hornbeam (*Carpinus betulus* L.)	,,	17	1	0	7	16	4	28
Juniper (*Juniperus communis* L.)	,,	17	6	0	4	8	2	20
Spruce (*Picea abies* (L.) Karst.)	Native in interglacial reintroduced *c.* 1500	15	9	1	6	13	8	37
Lime (*Tilia* spp.)	Native and introduced	14	7	2	15	5	2	31
Mountain ash (*Sorbus aucuparia* L.)	Native	13	0	1	2	17	8	28
Fir (*Abies* spp.)	Native in interglacial reintroduced *c.* 1600	10	5	0	2	1	8	16
Sweet chestnut (*Castanea sativa* Mill.)	Introduced A.D.100	10	0	0	0	5	0	5
Apple (*Malus* spp.)	Native and introduced	7	18	3	21	42	9	93
Walnut (*Juglans regia* L.)	Introduced *c.* 1400	3	0	0	0	1	2	3
Holm oak (*Quercus ilex* L.)	Introduced 1580	2	0	0	0	2	0	2
Larch (*Larix decidua* Mill.)	Introduced 1629	1	3	0	6	6	2	17
Sycamore (*Acer pseudoplatanus* L.)	Introduced *c.* 1250	1	1	0	5	8	0	15
Horse-chestnut (*Aesculus hippocastanum* L.)	Introduced *c.* 1600	0(?11)	0	2	1	1	0	4
Acacia (*Robinia pseudacacia* L.)	Introduced 1601	0	0	0	0	1	0	1
Plane (*Platanus orientalis* L.)	Introduced *c.* 1520	0	0	0	0	0	0	0

(1956) considers that these trees were native in Britain before the last glacial phase, apparently becoming extinct by the post-glacial.

The regression equation of the number of insect species on the history and abundance of the tree (Godwin's records) has been calculated and is drawn in Fig. 1. Because of the inherent weaknesses in the data too much stress should not be laid on the precise position of the line, but it is apparent that certain trees have either far more or far fewer insects than can be accounted for in terms of their history. In other words when the effect of

their history is removed some trees stand out as being 'good' host plants for insects and others especially 'bad'.

Those trees which have a large number of insects attached to them (when the effect of history is eliminated) fall into two families. Three are Rosaceae — hawthorns (*Crataegus*), sloe (*Prunus spinosa*) and apple (*Malus*) — although the point for the fourth common tree member of the family, the mountain ash (*Sorbus aucuparia*), lies on the regression line. The others are the two Salicaceae — the willows (*Salix*) and poplars (*Populus*); the records for each genus have to be lumped as many of the plant records cannot be determined to species (Godwin 1956). It is probable that as each of these genera contain a large

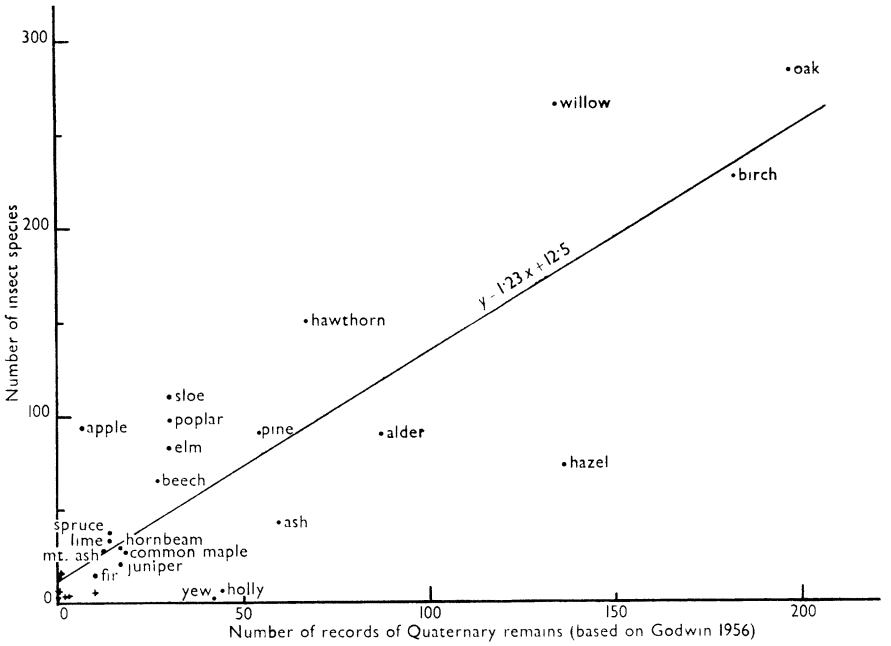

FIG. 1. Graph showing the relationship between a tree's history (x) and the number of associated insect species (y). (+, introduced trees).

number of species compared with the other tree genera, (*e.g.* birch 3, oak 2, beech 1) they provide a larger number of niches than the other trees. Alternatively, the Salicaceae may be especially favourable host plants for insects; this appears to be the case with Rosaceae and it is interesting, as Hering (1951) has remarked, that a number of insects feed only on these two comparatively unrelated plant families. In some cases the assumption of the second host seems to have been comparatively recent; *e.g.* the *Salix* feeding bug *Orthotylus marginalis* Reuter, seldom found an apple at the beginning of this century, is now common in many orchards. Apple has, of course, become increasingly abundant in Britain in the last centuries.

There are four trees which have remarkably few associated insects: hazel (*Corylus avellana*), ash (*Fraxinus excelsior*), holly (*Ilex aquifolium*) and yew (*Taxus baccata*). The presence of hazel in this group is surprising since it is in the Fagales group of tree families and not an isolated taxonomic position as is the ash (family Oleaceae), the only British tree in the second main series of the Dicotyledones, the Metachlamydeae. The paucity of

insects on the holly and yew, which is true throughout their range, is especially marked and must be associated with their structural or biochemical features.

The probable mechanism underlying this relationship between tree abundance and the number of insect species is outlined by Southwood (1960b).

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SUMMARY

1. The hypothesis is suggested that the number of insect species associated with a tree is a reflection of the cumulative abundance of that tree in the particular country throughout recent geological history (*e.g.* in the Quaternary period). This means that the dominant native trees will have most insect species, and recently introduced ones fewest.

2. General comparisons between the insect fauna of certain trees in Britain, Sweden, Russia and Cyprus support the hypothesis.

3. A more detailed test is made for Britain, where it is shown that the number of species of the major plant feeding orders of insects (Lepidoptera, Coleoptera and most groups of Hemiptera) associated with British trees is closely correlated with the number of records of their Quaternary remains recorded by Godwin (1956).

4. Using such data it is possible to eliminate the effect the history (cumulative abundance) of the tree on the number of insect species, when it is seen that some trees are evidently especially resistant or unsusceptible to insect colonization, and others probably the reverse.

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