SHIELD BUGS AND WOODLAND COMPOSITION IN EPPING FOREST

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ABSTRACT

The distribution of five species of shield bug was studied with different host plant species, structure, condition and age in Epping Forest, Essex. Stands of beech, birch and oak-hornbeam, as well as scrubland gorse and hawthorn, were sampled, each tree being characterised by a variety of parameters including bole circumference, pollarding and defoliation class. Correlations between shield bug species and host plant character were expressed through chi-squared analyses of presence/absence data for the samples. Results suggest a high degree of host specificity amongst the phytophage species studied and probably a preference for early successional plant stages. Preferential utilisation of mature and non-defoliated hosts is also apparent. The results are discussed in terms of the requirements of the bugs and the nutritional value of the host. It is concluded that nitrogen availability within and between host plant species is likely to be highly influential in determining the diet and distribution of shield bugs, and indeed other selective-feeding heteroptera.

INTRODUCTION

Epping Forest comprises of 2430 hectares of woodland and grassland with small pockets of scrub and heathland, extending from the Wanstead Flats in the London Borough of Redbridge, north for approximately 19 km, just beyond Epping in Essex. The principal tree species are beech (Fagus sylvatica), birch (Betula pendula and B. pubescens), common oak (Quercus robur) and hornbeam (Carpinus betulus).

Pollen data indicate the late survival of the lime (Tilia) until about AD600 as the dominant tree species, then giving way to the familiar woodland associations seen today. The ecological trend over the last 100 years has been towards uniformity. Owing to the cessation of pollarding in 1878, previously pollarded beech growth has tended to out-top and kill off lower levels of oak and hornbeam. Birch has begun to colonise grassland areas formerly maintained by grazing (Baker et al., 1978).

The distribution and variation in quality of plants and their overall abundance must greatly affect the dynamics of any dependent insect species. At present the nature of these effects is largely a matter for speculation. Southwood (1961) found that the general number of phytophagous insects associated with a given tree species tended to reflect the abundance of that tree in recent times. Similarly Strong (Edwards and Wratten, 1980) showed that there was a positive relationship between phytophage number and host representation at a given time. Furthermore, on trees Southwood et al. (1982) found the distribution of sap-sucking insects to be non-uniform to a highly significant degree.

It is this aspect of the plant-insect relationship which is studied here, looking at the uniformity of distribution of five species of phytophagous shield bug (Pentatomoidea, Hemiptera-heteroptera) amongst woodland and scrubland in Epping Forest.

The subjects of the study are the hawthorn shield bug Acanthosoma haemorrhoidale (L., 1758), the birch shield bug Elasmostethus interstinctus (L., 1758), and the parent bug

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*Elastomucha grisea* (L., 1758) of the Acanthosomidae, and the gorse shield bug *Piezodorus lituratus* (Fabricius, 1794) and the forest bug *Pentatoma rufipes* (L. 1758) of the family Pentatomidae. Recent records show that all are widespread throughout the British Isles (Massee, 1955) and France (Villiers, 1945); hence Epping Forest would appear to be well within their northern European range. This suggests that nutritional preferences would have a greater effect on their distribution than climatic constraints.

The heteroptera are selective feeders on tissues of high protein content and, consequently, tend to occur in lower densities than groups utilizing a broader range of target tissues, such as defoliators. Even though a food plant may appear abundant, food may still be a limiting factor and absolute shortage may be very important in the regulation of phytophage populations (Van Emden, 1973). High protein tissues favoured by shield bugs include fruiting and flowering bodies, leaf buds and seed pods, and this reflects the nutritional selectivity of other heteroptera. It is unclear how host-specific these insects are, as are the relative roles of nutrients and secondary compounds in diet determination.

The preliminary step in elucidating these relationships is an examination of host plant variety and the way in which this affects shield bug representation within and between woodland plant species.

**Methods**

Sampling was carried out between 7 June and 20 September 1983 during which eighty sites were visited throughout Epping Forest. These were not chosen at random, but were selected with a view to sampling flora representative of the forest’s varied structural composition. Included were stands of birch, ancient beech woodland, mixed oak and hornbeam, and scrubland. In all, 1041 trees were sampled comprising 236 beech, 216 birch, 297 oak, 150 hornbeam, 100 hawthorn, 29 gorse and 13 holly.

Branches accessible from ground level were sampled by beating and fauna collected using a 1 m² beating tray. Experiments were conducted during the course of the study to look for variations in the distribution of *Elastomostethus* on birch at different sampling heights. The results had suggested that there is little difference between sampling heights and that low level samples should be representative of the whole tree. Within sites, usually ten to twenty trees were selected randomly for sampling. Owing to the paucity of Pentatomoid fauna in the Epping Forest area, and the sampling technique not permitting actual bug counts, the mere presence of a bug species in a sample was noted for a given tree. All the shield bugs under study are easily distinguishable and were identified in the field without the aid of keys. Nymphs and adults were assigned equal recording status; there is insufficient evidence to suggest any kind of nutritional transition between juveniles and adults.

Host plant type was recorded prior to sampling, each being defined according to nine parameters (after Moran and Southwood, 1982). In the event, however, only five were subsequently used in the analysis. These were species, circumference at 1.5 m, and pollarding to express host age and structure. Host condition was expressed by the percentage of leafless apices, and by defoliation. Categories of 0–20%, 20–40%, 40–60%, 60–80% and 80–100% enabled these measurements to be estimated satisfactorily in the field without necessitating the removal of plant material. The proportion of leafless apices is considered an expression of peripheral dead wood or reduction of leaf cover. Defoliation may be expected to cause nutrient loss, reduced photosynthesis and high expenditure in tissue replacement (Morris and Perring, 1974).
At the end of the sampling period, in order to simplify the large amount of data collected, tree circumference was used to define tree age, pollarding was the sole structural variable retained, and defoliation and leafless apices were examined to describe host condition. Specific relationships between shield bugs and their hosts were analysed statistically by chi-squared testing incorporating Yates’ correction factor (Siegel, 1956).

RESULTS

Host plant species

The results for each of the five Pentatomoid species recorded are shown in Fig. 1. Table 1 presents the significance levels of the associations.

Given that samples are likely to include a basal level of “tourists” (tourism here meaning the recovery of insects from plants with which they are unlikely to have any nutritional association), the results show highly significant relationships between shield bugs and host plants. Tourism, accounting for perhaps 5–10% of sampling successes, is largely attributable to adult flight activity. Particularly intimate are the associations between Acanthosoma and hawthorn, Elasmostethus and birch, and Piezodorus and gorse, though there were insufficient data to illustrate the latter statistically. Acanthosoma nymphs were occasionally taken from densely fruiting holly (Ilex), a stage at which it is not dissimilar in appearance to hawthorn.

Unfortunately, Elasmucha is not present in Epping Forest in sufficient numbers to determine its principal food plant, though birch would appear to be the most likely candidate. This may bring it into direct competition with Elasmostethus, which occurs in greater densities.

Pentatoma provides the main anomaly; the data show it to be strongly associated with beech, which is considered to be a rather poor host for invertebrates. Oak is the principal host elsewhere in Britain, though not so in Epping Forest. As well as oak, hornbeam is also shown to support few Pentatomoids. The “shift” towards beech occurs, perhaps significantly, in areas where beech growth has topped and is gradually eclipsing oak and hornbeam.

Host plant age

The relationship between age, measured by host circumference, and Pentatomoid distribution is expressed for Pentatoma and Elasmostethus on beech, birch, oak and hornbeam in Figs. 2 and 3.

Figure 2 (see also Tables 2 and 3) shows the effects of beech and birch age on the distribution of Elasmostethus. Since there is apparently no nutritional association between this bug species and beech the results produce a fairly uniform distribution irrespective of tree age, indicative of its presence as a tourist. The distribution of Elasmostethus on birch, however, is shown to be markedly irregular when samples are divided into those from <0.3 m circumference birches and those from ≥0.3 m ones; this bole circumference can be said to correspond to the maturation age of the birch, the approximate stage at which fruiting bodies may be expected to appear (Busgen et al., 1929; Forestry Commission, 1966; Wareing and Phillips, 1978).

Similar tests were carried out on samples of Pentatoma from mature and immature beech, oak and hornbeam. Maturation ages were estimated to correspond to girths of 0.5 m for oak and hornbeam, and figures of 0.5 m and 1.0 m were studied for beech. The results are given in Tables 3, 4 and 5 and are illustrated in Fig. 3. Pentatoma is
non-uniformly distributed on beech, favouring mature hosts. For oak and hornbeam though there is no significant difference between samples from mature and juvenile hosts, perhaps emphasizing *Pentatoma*'s independence of these tree species in Epping Forest. There appears to be no evidence of reduced shield bug fauna from senile hosts. Samples of *Pentatoma* increase markedly during the maturation phase and do not decline in even the most aged beeches.
Table 1. Chi-squared tests of significance of associations between shield bug species and host plants (methods given in appendices)

<table>
<thead>
<tr>
<th>shield bug species</th>
<th>Pentatoma</th>
<th>Acanthosoma</th>
<th>Elasmostethus</th>
<th>Piezodorus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Beech</td>
<td>62.38</td>
<td>12.58</td>
<td>5.04</td>
<td>6.72</td>
</tr>
<tr>
<td>other flora</td>
<td>(+++)</td>
<td>(+++)</td>
<td>(+)</td>
<td>(+)</td>
</tr>
<tr>
<td>Birch</td>
<td>12.06</td>
<td>5.13</td>
<td>112.00</td>
<td>1.59</td>
</tr>
<tr>
<td>others</td>
<td>(+++)</td>
<td>(+)</td>
<td>(++)</td>
<td>(0)</td>
</tr>
<tr>
<td>Oak</td>
<td>0.01</td>
<td>12.05</td>
<td>12.99</td>
<td>1.25</td>
</tr>
<tr>
<td>others</td>
<td>(0)</td>
<td>(+++)</td>
<td>(+++)</td>
<td>(9)</td>
</tr>
<tr>
<td>Hornbeam</td>
<td>2.84</td>
<td>7.33</td>
<td>4.37</td>
<td>—</td>
</tr>
<tr>
<td>others</td>
<td>(0)</td>
<td>(+)</td>
<td>(+)</td>
<td>—</td>
</tr>
<tr>
<td>Hawthorn</td>
<td>7.05</td>
<td>277.20</td>
<td>6.35</td>
<td>—</td>
</tr>
<tr>
<td>others</td>
<td>(+++)</td>
<td>(+++)</td>
<td>(+)</td>
<td>—</td>
</tr>
</tbody>
</table>

for n = 1 degree of freedom:—

p ≤ 0.001, $\chi^2 = 10.827$ (++++, very highly significant).
p ≤ 0.01, $\chi^2 = 6.635$ (++, highly significant).
p ≤ 0.05, $\chi^2 = 3.841$ (+, significant).
p > 0.05, $\chi^2 < 3.841$ (0, not significant).

Fig. 2.
The effects of tree age on the distribution of Elasmostethus interstinctus. "R" represents the bug recovery rate, i.e. the successes per 100 trees sampled. The $\chi^2$ values are for comparisons between the distribution of Elasmostethus on juvenile and mature hosts of each tree species.
The effects of tree age on the distribution of *Pentatoma rufipes*. $\chi^2$ as in Fig. 2.

Table 2. BIRCH. Chi-squared tests of significance of associations between shield bugs and host plant morphology

<table>
<thead>
<tr>
<th></th>
<th>Pentatoma</th>
<th>Elasmostethus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Circumference:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>under 0.3 m</td>
<td>0.083</td>
<td>13.52</td>
</tr>
<tr>
<td>over 0.3 m</td>
<td>(0)</td>
<td>(+ + +)</td>
</tr>
<tr>
<td>Leafless species:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>under 20%</td>
<td>—</td>
<td>13.71</td>
</tr>
<tr>
<td>over 20%</td>
<td>—</td>
<td>(+ + +)</td>
</tr>
<tr>
<td>Defoliation:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>under 20%</td>
<td>—</td>
<td>8.07</td>
</tr>
<tr>
<td>over 20%</td>
<td>—</td>
<td>(+ + +)</td>
</tr>
</tbody>
</table>

The uniform distributions, reflecting the tourist associations of *Elasmostethus* and *Pentatoma* on beech and birch respectively, provide standards which allow comparisons with more intimate relationships. Their uniformity suggests the absence of any major sampling bias.

**Pollarding**

This structural variation is shown to have no significant effect on samples of *Pentatoma* from hornbeam or oak. Though pollarding induces fresh young growth, the cessation of
this practice during the last century means that all pollarded growth in Epping Forest is now mature*. This would explain the significant relationship between \textit{Pentatoma} and pollarded beech, the link between faunal distribution and host maturity having already

*A small amount of experimental re-pollarding has been undertaken in recent years as part of a plan to revive traditional management. The newly-pollarded area was not included in the sampling (Ed).

### Table 3. Beech. Chi-squared tests of significance of associations between shield bugs and host plant morphology

<table>
<thead>
<tr>
<th></th>
<th>\textit{Pentatoma}</th>
<th>\textit{Elasmostethus}</th>
</tr>
</thead>
<tbody>
<tr>
<td>Circumference:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>under 0.5 m</td>
<td>6.94</td>
<td>—</td>
</tr>
<tr>
<td>over 0.5 m</td>
<td>(+ +)</td>
<td></td>
</tr>
<tr>
<td>under 1.0 m</td>
<td>5.57</td>
<td>0.076</td>
</tr>
<tr>
<td>over 1.0 m</td>
<td>(+)</td>
<td>(0)</td>
</tr>
<tr>
<td>Pollarding:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>pollarded</td>
<td>4.61</td>
<td>0.067</td>
</tr>
<tr>
<td>unpollarded</td>
<td>(+)</td>
<td>(0)</td>
</tr>
<tr>
<td>Leafless apices:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>under 20%</td>
<td>1.79</td>
<td>0.072</td>
</tr>
<tr>
<td>over 20%</td>
<td>(0)</td>
<td>(0)</td>
</tr>
</tbody>
</table>

### Table 4. Oak. Chi-squared tests of significance of associations between shield bugs and host plant morphology

<table>
<thead>
<tr>
<th></th>
<th>\textit{Pentatoma}</th>
<th>\textit{Elasmostethus}</th>
</tr>
</thead>
<tbody>
<tr>
<td>Circumference:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>under 0.5 m</td>
<td>2.90</td>
<td>—</td>
</tr>
<tr>
<td>over 0.5 m</td>
<td>(0)</td>
<td></td>
</tr>
<tr>
<td>Pollarding:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>pollarded</td>
<td>1.04</td>
<td>—</td>
</tr>
<tr>
<td>unpollarded</td>
<td>(0)</td>
<td></td>
</tr>
<tr>
<td>Leafless apices:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>under 20%</td>
<td>2.31</td>
<td>0.59</td>
</tr>
<tr>
<td>over 20%</td>
<td>(0)</td>
<td>(0)</td>
</tr>
<tr>
<td>Defoliation:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>under 20%</td>
<td>0.41</td>
<td>—</td>
</tr>
<tr>
<td>over 20%</td>
<td>(0)</td>
<td></td>
</tr>
</tbody>
</table>
Table 5. hornbeam. *Chi-squared tests of significance of associations between shield bugs and host plant morphology*

<table>
<thead>
<tr>
<th></th>
<th>Pollarded</th>
<th>Unpollarded</th>
</tr>
</thead>
<tbody>
<tr>
<td>Circumference:</td>
<td>0.09</td>
<td>(0)</td>
</tr>
<tr>
<td>under 0.5 m</td>
<td></td>
<td></td>
</tr>
<tr>
<td>over 0.5 m</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pollarding:</td>
<td>0.81</td>
<td>(0)</td>
</tr>
<tr>
<td>pollarded</td>
<td></td>
<td></td>
</tr>
<tr>
<td>unpollarded</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Defoliation:</td>
<td>2.25</td>
<td>(0)</td>
</tr>
<tr>
<td>under 20%</td>
<td></td>
<td></td>
</tr>
<tr>
<td>over 20%</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

---

been stressed. The results are shown in Fig. 4. *Acanthosoma*’s association with hawthorn appears to be unaffected by pollarding.

**Host condition**

Figure 5 shows the detrimental effects of poor tree condition on the distribution of Pentatomoidea. Since the results were very similar for each bug–host relationship (see Appendices), data have been “lumped” for representative purposes. Samples from trees
Table 6. HAWTHORN. Chi-squared tests of significance of associations between shield bugs and host plant morphology

<table>
<thead>
<tr>
<th>Acanthosoma</th>
<th>Circumference:</th>
<th>2.17</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>under 0.5 m</td>
<td></td>
</tr>
<tr>
<td></td>
<td>over 0.5 m</td>
<td>(0)</td>
</tr>
<tr>
<td>Pollarding:</td>
<td>pollarded</td>
<td>0.045</td>
</tr>
<tr>
<td></td>
<td>unpollarded</td>
<td>(0)</td>
</tr>
<tr>
<td>Leafless apices:</td>
<td>under 20%</td>
<td>0.046</td>
</tr>
<tr>
<td></td>
<td>over 20%</td>
<td>(0)</td>
</tr>
</tbody>
</table>

![Graph showing host condition and defoliation percentages]

The effects of tree condition on the distribution of shield bugs.

with <20% defoliation were compared with those from ≥20%. Chi-squared analysis (Table 7) showed these samples to be very highly significantly different, the bugs favouring lightly-defoliated hosts. The corresponding test for the proportion of leafless apices indicated a slight preference for hosts with well-foliated apices.

Figure 6 shows the relationship between Elasmostethus and birch condition, supplementing the “group” data. Results of tests (as described above) were very highly and
highly significant for leafless apices and defoliation respectively; in both cases the bug was more common on healthy birches.

This suggests that the physiological drain of defoliation and the side-effect of cover reduction causes significant loss of Pentatomoid fauna.

There is no link between beech condition and the distribution of either Pentatoma or Elasmucha. This may well be attributable to the high nutritive value of the buds present at the leafless apices of beech (Van Emden, 1973); the inconspicuous brown colour of Pentatoma may also offset any loss of cover.

There were insufficient data to fully examine the relationships between Piezodorus and Elasmucha and their host species. The former, however, was shown to have no significant association with birch or oak, and an aversion to beech. Table 6, showing the

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Table 7. *Chi-squared tests of significance of the distribution of shield bugs between hosts of varied condition*

<table>
<thead>
<tr>
<th></th>
<th>Pentatomoidae (all five species)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Leafless apices:</strong></td>
<td></td>
</tr>
<tr>
<td>under 20%</td>
<td>4.38</td>
</tr>
<tr>
<td>over 20%</td>
<td>(+)</td>
</tr>
<tr>
<td><strong>Defoliation:</strong></td>
<td></td>
</tr>
<tr>
<td>under 20%</td>
<td>22.60</td>
</tr>
<tr>
<td>over 20%</td>
<td>(+ + +)</td>
</tr>
</tbody>
</table>

---

**Fig. 6.**

The effects of host condition on the distribution of *Elasmucha* on birch.
Acanthosoma–hawthorn relationship, suggests the insignificance of the parameters studied.

Percentage sampling success for Pentatomoid species on varieties of oak, beech, birch and hornbeam are given in the Appendices.

**Discussion**

Evident from the results is the relationship between shield bugs and the early successional stages of woodland vegetation. This would appear to be true for most British Pentatomoidea (Douglas and Scott, 1865; Butler, 1923; Southwood and Leston, 1959). Those associations highlighted were Acanthosoma and hawthorn, Elasmostethus and birch and Piezodorus and gorse. This situation may be attributable to variations in the availability of nitrogen between plant species and successional stages (Heilman, 1966; Woodwell et al., 1975; Mattson, 1980). The need to satisfy nitrogen requirements is reflected by the affinity of many phytophagous insects for high-protein tissues (Van Emden, 1973). In Epping Forest, mineral-deficient soils would further reduce nitrogen levels in plant tissues, accentuating this problem. Birch is known to contain relatively high levels of nitrogen, in common with alder (Alnus) and both are early successional species in Epping Forest. Nitrogen-fixing legumes are also largely colonising plants. Hence if high levels of nitrogen are a feature of the faster growing early successional flora, then the Forest’s shield bug fauna may be expected to be associated with early stages of succession. The “dual discrimination” theory (Edwards and Wraatten, 1980) of balancing nutritional requirements with secondary compound tolerance (sometimes equated to flavour) may account for deviations of host specificity from this theme.

Low densities of Elasmucha suggest that competition for birch resources with Elasmostethus may be a limiting factor. An alternative explanation is one of host specificity. Both Betula pubescens (red or black birch) and B. pendula (silver birch) are present in Epping Forest, the latter in greater numbers. Unfortunately, the relative numbers in the samples were not noted. It is possible, though, that Elasmostethus is more specific to B. pendula and Elasmucha to B. pubescens. This would explain the prevalence of Elasmucha elsewhere in Britain in areas where the black birch may predominate.

Pentatoma, the only species found to be associated with climax vegetation, was noteworthy for its preference for beech hosts. Beech provides a major, relatively untapped food resource in Epping Forest, and, therefore, it is hardly surprising that at least one species of bug is utilising it. Ford (Southwood, 1957) suggests the possibility of localised populations becoming increasingly specialised to the point of race emergence; this may indeed be occurring in Epping Forest’s beech-feeding Pentatoma, particularly given the apparently low affinity for the more common native host, the oak.

Recordings of Acanthosoma on holly may be attributable to visual confusion or to multiple host tolerance.

The relation of tree age to circumference, and in turn to maturity, is an approximation based on a highly variable situation. Reference literature suggests that the estimates of flowering/maturation ages used in the statistical tests are appropriate (see results). Not noting the presence and density of flowering and fruiting bodies was an important omission. However, without the reproductive tissues of mature trees juvenile hosts are still utilised to a minor degree owing to the presence of young buds and leaf tissue, rich in mobilised nitrogen. The relationship between Pentatoma and mature beech, weaker than that of Elasmostethus and birch, reflects a greater dependence on leaf buds for food rather than reproductive material.
The paucity of Pentatomoid fauna on hornbeam may be due to its status as a climax species in Epping Forest today or its comparatively late (Medieval) arrival in the flora. Young pollarded growth may be expected to be less successful in attracting shield bugs than mature fruiting growth (either pollarded or unpollarded). However, the general effect of pollarding, maintaining woodland diversity, would vastly outweigh any detrimental effects.

Available evidence shows that tree condition has a marked effect on the presence of nitrogen in tissues (Morris and Perring, 1974). This may account for the observation by Southwood et al. (1982) that a higher proportion of leaf-chewing insects were associated with fewer sap-suckers. Hence the very highly significant relationship between shield bugs and lightly-defoliated hosts. Heavy Tortix caterpillar defoliation of oak in areas of Epping Forest early in the season contributes to the avoidance of this species as a host. Foliage as a source of cover may be particularly important to the green-pigmented phytophagae.

The results suggest that future studies which include a closer examination of the distribution of nitrogen within and between host plant species of varying successional status are likely to be highly rewarding. Indeed this might allow shield bug data to be used to construct a model applicable to other selective-feeding heteroptera.

**CONCLUSIONS**

Epping Forest Pentatomoidea show a high degree of host specificity, though facultative polyphagism cannot be ruled out. They appear to prefer early successional stages to slower-growing “climax” vegetation which is likely to contain lower levels of accessible nitrogen. An affinity for mature hosts could relate to relatively protein-rich reproductive tissues. This is supported by the observed aversion of shield bugs to physiologically drained defoliated hosts.

The colonisation of beech by Pentatoma appears to be linked to the increasing dominance of this tree species in the nucleus of the Forest, and also by competition on oak, its common host, with high density invertebrate populations.

Further work on the limiting role of nitrogen in the distribution of these phytophagae species is envisaged and is likely to be rewarding.

**ACKNOWLEDGEMENTS**

I would like to thank Paul Moxey and the staff of Epping Forest Conservation Centre, High Beach, Essex, for their help and use of facilities during the study period, to Dr. J. C. Hartley of the University of Nottingham for academic advice, and to the University of Nottingham Science and Agricultural libraries for reference facilities. This work was financed by a British Ecological Society Small Projects Grant.
### Shield bugs and woodland composition in Epping Forest


### APPENDICES

#### A. Birch sampling data (N = 216)

<table>
<thead>
<tr>
<th>Circumference</th>
<th>Pentatoma</th>
<th>Elasmostethus</th>
<th>Piezodorus</th>
<th>Elasmucha</th>
<th>Overall</th>
<th>(n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0–0.5 m</td>
<td>07.14</td>
<td>31.13</td>
<td>04.64</td>
<td>03.31</td>
<td>41.06</td>
<td>(151)</td>
</tr>
<tr>
<td>0.5–1.0 m</td>
<td>03.70</td>
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### B. Beech sampling data (N = 236)

#### Sampling success (%o)

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<td>03.85</td>
<td>34.62</td>
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<td>(34)</td>
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<tr>
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<td>08.33</td>
<td>45.83</td>
<td>(24)</td>
</tr>
<tr>
<td>3.0–3.5 m</td>
<td>38.89</td>
<td>16.67</td>
<td>55.56</td>
<td>(18)</td>
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<td>3.5–4.0 m</td>
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#### Leafless apices:

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#### Defoliation:

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### C. Oak sampling data (N = 297)

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<th>Overall</th>
<th>(n)</th>
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<th>Overall</th>
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E. Statistical tests—methods

Chi-squared contingency tables (2 × 2), incorporating Yates’ correction factor.

Example 1:

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<tr>
<th></th>
<th>Pentatoma present</th>
<th>Pentatoma absent</th>
<th>(r)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Beech</td>
<td>69 (32)</td>
<td>167 (204)</td>
<td>236</td>
</tr>
<tr>
<td>Other species</td>
<td>71 (108)</td>
<td>734 (697)</td>
<td>805</td>
</tr>
<tr>
<td>(c)</td>
<td>140</td>
<td>901</td>
<td>1041 (N)</td>
</tr>
</tbody>
</table>

where E is the number of scores expected (bracketed) and O is the number of scores observed.

\[ E = \frac{r \cdot c}{N} \]

\[ \chi^2 = \frac{\sum (O - E - \frac{1}{2})^2}{E} = 62.38, \ p \leq 0.001 \text{ (one degree of freedom)} \]

Example 2:

<table>
<thead>
<tr>
<th></th>
<th>Elasmostethus present</th>
<th>Elasmostethus absent</th>
<th>(r)</th>
</tr>
</thead>
<tbody>
<tr>
<td>birch defoliation 20°o</td>
<td>66 (59)</td>
<td>123 (130)</td>
<td>189</td>
</tr>
<tr>
<td>birch defoliation 20°o</td>
<td>2 (9)</td>
<td>25 (18)</td>
<td>27</td>
</tr>
<tr>
<td>(N)</td>
<td>68</td>
<td>148</td>
<td>216</td>
</tr>
</tbody>
</table>

\[ \chi^2 = \frac{\sum (O - E - \frac{1}{2})^2}{E} = 8.09, \ p \leq 0.01 \text{ (one degree of freedom)} \]