Species Richness of the Parasitic Fungi of British Trees

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ABSTRACT The species richness of fungi associated with British trees is described by a significant species/area curve (r = 0.53, 0.01 > P > 0.001). Introduced tree species cannot be shown to have fewer fungal species than natives, per unit distributional range about Britain. Also, among natives and among introductions, older host taxa do not have more fungal species than do younger ones. This indicates the species richness of fungi to rapidly reach the limit set by host range, within ecological time. The slope of the species/area relationship for fungi is one-fourth that for insects; we propose that this is due to the inherently greater dispersability of fungi. Finally, the species/area regression residuals for fungi are correlated with those for insects (r = 0.65, 0.001 > P), suggesting plant defense mechanisms may be generally effective to plant parasites, be they insects or fungi.

The size of environments accounts for a great part of variation in species richness. This species/area phenomenon is generally true among close and ecologically similar situations when one compares actual islands (1), habitat “islands” in isolating “seas” of unsuitable environment (2), and serially self contained or contiguous regions (3). The relationship also exists between herbivores and the ranges of their hosts; the number of supported phytophagous insect species is a function of host plant range, when broadly sympatric host species are compared (4). As well, regionally isolated populations of a single host plant species support a number of insect phytophages that is set by the local area occupied by the host (ref. 5; E. McCoy, J. Rey, and D. R. Strong, manuscript in preparation). In this paper we show that parasitic fungal species richness is also set by host range, for British trees. This relationship appears to be attained within ecological time, and some of its properties are different from those of the species/area relationship of insects on British trees. We propose the differences to result from the greater dispersability of fungi, relative to insects.

Our data are given in Table 1. We have estimated host tree ranges from the Atlas of the British Flora (6), and from newer distributional information as yet unpublished†. Fungal/host species associations are estimated from various sources (7–17§). We use all appropriate data from all available sources.

Fig. 1 shows fungal species richness to be a function of host range for the trees of Britain. The evidence indicates that the fungal species/area relationship is generated rapidly, within ecological time, rather than over the longer periods usually required for evolutionary or geologic changes. This is suggested by the fact that introduced tree species tend not to be deficient in fungal species relative to natives. First, only four introduced species fall below the regression line of Fig. 1, whereas three fall above. Second, considering distances the points fall from the line the trend is likewise; introduced species do not tend to fall below the line and natives do not tend to fall above (Wilcoxon Two Sample Rank Test of regression residuals, natives contrasted with introduced species; P = 0.42, not significant including apple and lime among introduced species; P = 0.47, not significant including only lime; P = 0.38 including neither apple nor lime). Finally, the two groups do not describe different regression lines, as a function of host species area. By nonparametric analysis of covariance the slopes are not different [P > 0.11, not significant (18)], nor are the intercepts, of the introduced contrasted with the native species [P = 0.0474, not significant (19)].

Another method of assessing the influence of geologically long time periods upon accumulated parasite species richness is by search for correlation between number of associated fungal species and relative age in Britain of host species. From among the seven introduced hosts there are five for which the date of introduction is known (Table 1). There is no relationship between time since introduction and number of fungal parasite species associated with these host species (r = 0.18, not significant). We can also consider the relative age in Britain of native hosts. The “rational limit” of a host species is the time point where the frequency of pollen first rises to a sustained high value in the fossil record; hence it is an indication of how long host species have been abundant in Britain. Rational limits for a number of native host taxa have been verified with radiocarbon dating (20). These limits vary geographically, and we have calculated median values among British sites for the purposes of study (Table 1). With these data, older native host taxa do not have more associated fungal species than do younger ones; the correlation coefficient between median rational limit and number of associated fungi is negative and insignificant (r = −0.31, not significant n = 7). Given the concordant results from these several tests, there is no justification for assuming younger (native, introduced, or between native and introduced) host taxa to have fewer fungal pest species. Hence there is no justification for the idea that long periods of time will inexorably add pest species to these hosts (22, 23). A corollary is that a great proportion of the saturation number of parasite species is accumulated by these hosts within ecological time, i.e., within several hundred years.

† Range data for walnut and Norway spruce have kindly been supplied us by Monks Wood Experimental Station, Abbots Ripton, Huntingdon, PE 17 2LS, England.

§ Numerous authors (1960–1974); Review of Plant Pathology and Review of Applied Mycology, all first reports of single plant/fungi associations.
Fig. 1. Species/area relationship for the fungi of British trees. $r = 0.53$, $0.001 < P < 0.01$. Log $S = (0.26) \log$ host species range + (0.26). Introduced species are indicated as solid points, natives as hollow points.

The inherently different dispersal patterns of fungi and insects may explain the difference between the species/area curves for these two groups. In Fig. 2 we show these comparatively. Fungi regularly undergo long-distance dispersal by wind transport of spore clouds (24–26). For example, there is an annual arrival into Britain of spores of Puccinia graminis from across the Baltic, from Northern Europe (27). And spore rains originating from fungal populations hundreds of kilometers away are known in other plant-attacking fungi (28–33). Spore viability after long-distance transport is high in the cases studied (34–36). The majority of fungi associated with plants infect as well as disperse passively; although there are

**Table 1.** Range in Britain of host tree taxa; number of species of associated fungi; median rational limits, and age of introduction into Britain of non-native hosts (21)

<table>
<thead>
<tr>
<th>Host taxon</th>
<th>Present range in Britain (100 km)</th>
<th>No. of associated fungal species</th>
<th>Median rational limit of natives, if known, years before present</th>
<th>Year of introduction into Britain A.D. (21)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oak (Quercus petraea &amp; Q. robur)</td>
<td>3,593</td>
<td>41</td>
<td>8787.5</td>
<td></td>
</tr>
<tr>
<td>Birch (Betula spp.)</td>
<td>4,217</td>
<td>12</td>
<td>9625</td>
<td></td>
</tr>
<tr>
<td>Hazel (Corylus avellana)</td>
<td>2,885</td>
<td>10</td>
<td>9000</td>
<td></td>
</tr>
<tr>
<td>Willow (Salix spp.)</td>
<td>14,358</td>
<td>32</td>
<td>6250</td>
<td></td>
</tr>
<tr>
<td>Alder (Alnus glutinosa)</td>
<td>2,931</td>
<td>23</td>
<td>6250</td>
<td></td>
</tr>
<tr>
<td>Hawthorn (Crataegus spp.)</td>
<td>4,648</td>
<td>11</td>
<td>6250</td>
<td></td>
</tr>
<tr>
<td>Ash (Fraxinus excelsior)</td>
<td>3,187</td>
<td>22</td>
<td>4037.5</td>
<td></td>
</tr>
<tr>
<td>Holly (Ilex aquifolium)</td>
<td>2,388</td>
<td>6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sloe (Prunus spinosa)</td>
<td>2,564</td>
<td>17</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Poplar (Populus spp.)</td>
<td>2,834</td>
<td>19</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Elm (Ulmus spp.)</td>
<td>2,984</td>
<td>14</td>
<td>8750</td>
<td></td>
</tr>
<tr>
<td>Beech (Fagus silvatica)</td>
<td>2,639</td>
<td>19</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Common maple (Acer campestre)</td>
<td>1,277</td>
<td>9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hornbeam (Carpinus betulus)</td>
<td>683</td>
<td>11</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Juniper (Juniperus communis)</td>
<td>624</td>
<td>9</td>
<td>9875</td>
<td></td>
</tr>
<tr>
<td>Mountain ash (Sorbus aucuparia)</td>
<td>2,446</td>
<td>16</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lime (Tilia spp.)</td>
<td>1,634</td>
<td>15</td>
<td></td>
<td>Native &amp; introduced</td>
</tr>
<tr>
<td>Sweet chestnut (Castanea sativa)</td>
<td>986</td>
<td>7</td>
<td>100</td>
<td>Native &amp; introduced</td>
</tr>
<tr>
<td>Apple (Malus spp.)</td>
<td>1,651</td>
<td>12</td>
<td>1,629</td>
<td></td>
</tr>
<tr>
<td>Larch (Larix decidua)</td>
<td>608</td>
<td>9</td>
<td>1,600</td>
<td></td>
</tr>
<tr>
<td>Horse chestnut (Aesculus hippocastanum)</td>
<td>1,692</td>
<td>4</td>
<td>1,400</td>
<td></td>
</tr>
<tr>
<td>Walnut (Juglans regia)</td>
<td>118</td>
<td>8</td>
<td>1,500</td>
<td></td>
</tr>
<tr>
<td>Norway spruce (Picea abies)</td>
<td>1,094</td>
<td>16</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

See text for explanation and data sources.
a few known cases of fungal dispersal and infection by animals, anemophily is the common mode (37). Thus, distant host infection and host switching in parasitic fungi are not usually limited by the behavior, or lesser dispersability, of spore-carrying animals. Only a subsample of insect species is dispersed over great distances by wind, only the lighter, smaller species (38-43). The propensity to be wafted great distances is primarily a function of mass and surface/volume ratio, in fungi as well as in insects; smaller spores have a lower rate of settling from the aeroplankton and can be expected to be carried in spore clouds for greater distances (26). Given that fungal spores are an order of magnitude smaller, and lighter, than the smallest arthropods, it is reasonable that fungal species as a group disperse more widely than insect species (42, 43). Greater dispersability should lower the slope of the species/area plot (lower the value of z in $S = kA^z$) by making the compared regions less species-distinct, that is, by increasing the number of host species regularly colonized by each fungus species. The difference in slope between the two species/area curves is consistent with this. The slope of the insect relationship is 1.12, compared with 0.26 for fungi. The difference is significant by nonparametric analysis of covariance [0.005 < P < 0.007 (44)]. See the legend of Fig. 2 for details.

The patterns of insect and fungal species richness over these trees are not independent; hosts deficient in insect species relative to their ranges also tend to be deficient in fungal species. This is shown by the correlation between insect and fungal regression residuals (Fig. 3), and suggests that plant defenses effective against species of one parasite type (e.g., insects) may also be generally effective against another (fungi). There is evidence that some secondary plant compounds can serve in this fashion, simultaneously as insect repellent/insecticides and as fungicides (45). Alpha-tomatine, produced by species in the plant family Solanaceae, depresses growth of the parasitic fungus Fusarium, as well as reduces leaf damage by the Colorado beetle. It also prevents inhibition by, and at high concentrations kills, nymps of the potato leaf hopper, and interferes with the development of the two-striped grasshopper and of Aedes aegypti (46). Gossypol, a phytoalexin-like alkaloid produced by cotton, may perform

in a similarly general antiparasite fashion; it inhibits fungal spore germination in boils and simultaneously is found in very high concentrations in pigment glands; pigment glands are responsible for toxicity of cotton to insects (47).

Other factors contributing to variation in pest species richness include morphological heterogeneity within individuals of the host plant species. This heterogeneity factor is demonstrated by the fact that British herbs support fewer insect species than do shrubs, than do trees, per area of distribution (Strong, manuscript in preparation). Similarly, United States herbs support fewer fungal species than do shrubs, than do trees, per area of distribution (Levin, manuscript in preparation). We assume here that trees provide a greater diversity of niches for parasites, than do shrubs, than do herbs. But our data cannot explore the influence of size alone; that is, we hypothesize that more insect species will be supported per unit standing crop by a tree species than by an herb species by virtue of the greater morphological diversification within individuals not by the greater size, per se, of the tree.

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