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Diversity of ectomycorrhizal fungi in Britain: a test of the species–area relationship, and the role of host specificity

BY A. C. NEWTON* AND J. M. HAIGH†

Institute of Ecology and Resource Management, University of Edinburgh,
Darwin Building, Kings Buildings, Mayfield Rd., Edinburgh EH9 3JU, UK

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SUMMARY

The host range of ectomycorrhizal (ECM) fungi in Britain was examined by compilation of a data matrix from published literature sources, based primarily on accounts of sporocarp associations with particular host genera. Information was gathered for 577 species of ECM fungi belonging to 51 genera, and 25 genera of host trees, representing the majority of ECM fungal species and host genera recorded in Britain.

Pronounced variation was recorded in the number of ECM fungal species associated with different host genera, with over 200 species recorded with *Betula*, *Fagus*, *Pinus* and *Quercus*. There was a positive linear relationship ($r^2 = 0{\cdot}47$, $P = 0{\cdot}007$) between the number of species of ECM fungi associated with different host genera and the total area occupied by each tree genus in Britain (both values log-tranformed). There was also variation in the number of species of ECM fungi which were apparently specific to particular host genera, values ranging from zero (in 15 genera) to > 40 in the case of *Betula* and *Fagus*. In total, 233 fungal species appeared to be specific to a single host genus (i.e. 40% of those surveyed). Comparison of the ECM mycota associated with different host genera by PCA accounted for 17% of the total variation, with genera belonging to the Fagaceae (*Quercus*, *Fagus* and *Castanea*) tending to cluster together, indicating a degree of overlap in their ECM associates. Exotic conifer species, which displayed a lower ECM diversity than would be expected from their distributional areas, were characterized by a high degree of overlap with the ECM associates of *Pinus* and *Betula*.

These results indicate that the abundance of different genera of host trees and variation in host specificity could provide a basis for understanding patterns of diversity in ECM fungi within Britain.

Key words: Ectomycorrhiza, diversity, species–area relationship, host specificity.

INTRODUCTION

The relationship between species diversity and area has a long history in ecological science. A variety of relationships have been described for different organisms over a variety of scales (see Huston (1994)), such as flowering plants in Britain (Williams, 1964), birds on the Solomon islands (Diamond & Mayr, 1976), and mollusc species in lakes in New York state (Browne, 1981). Insects have received particular attention in this context, with species–area relationships described for phytophagous species on British perennial herbs (Lawton & Schröder, 1977), agromyzid flies on British Umbelliferae (Lawton & Price, 1979) and leaf-mining Lepidoptera on North American oaks (Opler, 1974), among many others (see Strong, Lawton & Southwood (1984)).

A number of different (but not mutually exclusive) hypotheses have been proposed to account for species–area relationships, including habitat heterogeneity, reflecting an increase in the number of habitat types with the area sampled (Williams, 1964); and the result of an equilibrium between the processes of extinction and immigration, as described by the equilibrium theory of island biogeography (MacArthur & Wilson, 1967). For the specific case of insects on plants, Southwood (1961) suggested that the probability of an insect encountering a suitable host depends on the frequency of the latter ('encounter frequency' hypothesis). It has also been suggested that species–area relationships might simply be the result of a sampling artefact, with increasing numbers of rare species being detected in larger samples by chance (Huston,

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* To whom correspondence should be addressed.
E-mail: `A.Newton@ed.ac.uk`
† Present address: Department of Biology, University of York, PO Box 373, York YO1 5YW, UK.

1994). Despite disagreement about the relative importance of these different mechanisms, and an increasing appreciation of the influence of scale (Gaston, 1996), species–area relationships remain an important predictive tool in ecological science (Peters, 1992).

No previous attempt appears to have been made to test whether species–area relationships apply to ectomycorrhizal (ECM) fungi. ECM fungi are an important component of biodiversity, particularly in temperate and boreal forest ecosystems, with over 148 genera and 5400 species described worldwide to date (Molina, Massicotte & Trappe, 1992). Many others clearly await description (Hawksworth, 1991): even in the UK, where the mycota is comparatively well documented, Orton (1986) notes that at least 15 *Cortinarius* species remain undescribed. Despite their ecological importance, the processes influencing the diversity of ECM fungi have rarely been examined (Allen *et al.*, 1995). Bruns (1995) hypothesized that high ECM diversity might result from resource partitioning, soil disturbance and competitive interactions between different ECM species; the relative importance of these different factors is unknown. One key factor influencing ECM diversity is host specificity (Molina *et al.*, 1992) or the 'preference' of ECM fungi for particular host trees (Newton, 1991). For example, the sporocarps of genera such as *Leccinum*, *Suillus*, *Rhizopogon* and *Hydnangium* are 80–100% restricted to individual plant genera or families (Molina *et al.*, 1992). Although host specificity is a well-known phemonenon to field mycologists, based on observations of sporocarp occurrence (e.g. see Watling (1984)), the extent of host specificity has never been critically examined for ECM fungi in Britain.

The aim of this investigation was to test whether diversity of ECM fungi in Britain is related to the area of the host genera with which they are associated. Data on ECM associations were obtained from a variety of published sources. In addition, these data were used to examine the extent of host specificity in different genera of ECM fungi in Britain. The data sources used in these analyses were subject to a number of different limitations, principally as a result of their contrasting breadth and depth of coverage. In addition, virtually all of the data sources referred to associations of sporocarps with particular tree species, rather than to direct assessment of ECM colonization on root systems. It was therefore assumed that such sporocarp associations give an indication of the actual association of ECM fungal species with particular hosts, and that the inclusion of data from a wide range of sources would compensate for the limitations intrinsic to each source.

METHODS

Compilation of data on host associations of ECM fungi in Britain

Data on the association between different ECM fungi and the host tree species with which they are associated were collated from a variety of published sources. As host-associations of ECM fungi might differ between geographical areas, only sources specific to Britain were used. Four main sources of information were employed:

(i) Taxonomic monographs of specific groups of ECM genera: Gasteromycetes, Pegler, Læssøe & Spooner (1995); *Russula*, Rayner (1985); truffles, Pegler, Spooner & Young (1993); Boletaceae, Gomphidiaceae, Paxillaceae, Watling (1970).
(ii) Regional floras: Hebrides, Dennis (1986); Mull, Henderson & Watling (1978), Watling (1985); Shetland, Watling (1992*b*); Warwickshire, Clark (1980); Yorkshire, Bramley (1985).
(iii) Field guides (Phillips, 1981).
(iv) Surveys of ECM fungi associated with particular tree genera: *Betula*, Watling (1984); *Quercus*, Watling (1974); *Picea sitchensis*, Alexander & Watling (1987); *Salix* spp., Watling (1981, 1987, 1992*a*).

Other publications used but not included in the above list largely consisted of articles with references to individual ECM associations (Elkington, 1971; Read, Kianmehr & Malibari, 1977; Nannfeldt, 1979; Watling, 1981, 1987, 1988; Orton, 1986; Ingleby *et al.*, 1990). In exception to the other sources used, which were based on sporocarp associations, Ingleby *et al.* (1990) described associations of ECM fungi with host tree species based on microscopic examination of the mantle structure of the mycorrhizas themselves.

Limitations of the data

Each data source suffers from a number of intrinsic limitations, the most important of which is the problem of uneven coverage. For example, taxonomic monographs are only available for a limited number of genera of ECM fungi, and relatively few regional floras have been published in Britain. Taxonomic monographs have the advantage of being based on accurate determinations by specialists, supported by reference collections in national herbaria, but suffer from limited breadth, reflected in the limited number of collections included. Field surveys and regional floras tend to be based on a much larger number of observations, but are nevertheless subject to bias with respect to the areas surveyed. As a result of uneven coverage, the data compiled are clearly limited, both in terms of the tree

Table 1. *The total number of ectomycorrhizal fungi associated with each tree/shrub genus, the number of these which are specific to the host genus, and the area occupied by each host genus in Britain*

Host genus	Number of associated species of fungi	Number of specific ectomycorrhizal associates	Area occupied by host genus in Britain (ha)	Number of 10-km plots in Britain occupied by host genus
Abies	1	0	7944	—
Acer*	5	0	75767	—
Alnus	47	7	32423	2184
Betula	245	43	149968	1808
Carpinus	8	2	3823	670
Castanea	11	0	30338	936
Cedrus*	3	0	—	—
Corylus	21	2	11656	2204
Crataegus*	2	0	—	—
Eucalyptus	2	1	—	—
Fagus	223	40	85457	2059
Fraxinus*	2	0	115167	—
Ilex*	7	0	—	—
Larix	46	2	154720	478
Nothofagus	2	0	—	—
Picea	151	3	646847	—
Pinus	201	14	421021	—
Populus	9	0	18153	725
Pseudotsuga	2	0	—	—
Quercus	233	30	229334	1907
Salix	146	8	13215	1946
Sequoiadendron*	1	0	—	—
Taxus*	5	0	—	—
Tilia	33	2	3264	1237
Ulmus*	1	0	16734	—
Arctostaphylos	5	0	—	—
Dryas	5	1	—	57
Helianthemum	2	0	—	699

Data for area occupied by host genera from Locke (1987); number of 10-km plots occupied by host genera derived from Perring & Walters (1962). All of the genera included have been recorded as at least sometimes forming ECM associations; those marked with an asterisk are thought usually to form arbuscular mycorrhizas (see Harley & Harley (1987)).

and fungal species included. It should also be recognized that these different data sources differ in their degree of precision with respect to the association of a sporocarp with a particular host species. For example, taxonomic monographs and detailed field surveys may include specific records of associations, contrasting with the unsupported generalizations to which field guides are prone.

The main additional problem with the majority of these data sources is that they are based on observations of sporocarps with particular tree genera, rather than on direct observations of mycorrhizas. The analyses presented here are based on the assumption that sporocarp association gives an indication of mycorrhizal association, which is clearly subject to an unknown degree of error, and might tend to exaggerate the ECM species richness associated with particular tree genera. Ideally this survey would have been based solely on studies of a similar nature to those undertaken by Ingleby *et al.* (1990). However, since the literature consists overwhelmingly of field observations of sporocarps, it has been necessary to base the study largely on this information. It should be emphasized that the data compiled consisted of putative mycorrhizal relationships based on sporocarp associations, rather than confirmed associations, in most cases.

Data analysis

The information gathered was incorporated into a presence/absence matrix of ECM fungi and their host genera. Only when a specific tree genus was mentioned was this added to the matrix. For example, sporocarps recorded 'under birch and pine' were incorporated into the matrix as associated with both genera, whereas sporocarps observed 'in birch/pine woodland' were ignored, since it is not clear in such cases which tree genus is the putative host. Fungal species were only included in the matrix if information was found on associated host genus, and many species have been omitted from the matrix because no published information was available. The check list of British agarics and boleti by Dennis, Orton & Hora (1960) was used to determine the proportion of known species which have been included in the matrix, in order to assess the extent of the omissions. Some genera that have previously been suggested to form ECM associations were excluded from the analysis, namely *Clavulina*, *Collybia*, *Entoloma*, *Lepiota*, *Pholiota* and *Psathyrella*, because of the uncertainty surrounding their mycorrhizal capability.

In order to test the species area relationship, data for the area occupied by 18 different tree genera in Britain was obtained from Locke (1987). These figures are the results of a woodland and trees census by the Forestry Commission between 1979 and 1982. In addition, the *Atlas of the British Flora* (Perring & Walters, 1962) was used to provide an alternative estimate of area, based on the number of 10 × 10 km squares from which each species was recorded. Records marked as pre-1930 were ignored and recorded introductions were included; data for the most abundant species of each genus has been used to represent the distribution of the genus as a whole. The relationship between ECM species diversity and distributional area of the host genus, was examined by regression of $\log_e$-transformed values, using data from Locke (1987) and Perring & Walters (1962) in separate analyses.

To examine the degree of similarity between the ECM fungi associated with different host genera, the data matrix was analysed by principal component analysis (PCA) using xlSTAT (T. Fahmy, Paris, France), denoting 'presence' and 'absence' as one and zero respectively.

RESULTS

The data matrix contained 577 species of ECM fungi in 51 genera. An additional 79 species for which no host was mentioned explicitly were encountered in the literature survey; these were excluded from the analysis. As the majority of the literature sources referred only to the host genus rather than to the species, the analysis is based on comparisons between host genera. To assess the degree of coverage of different fungal genera, the number of species from each genus considered was compared with those included in the most recent checklist available (Dennis *et al.*, 1960). In 75% of the ECM genera listed by Dennis *et al.* (1960), information was gathered on 100% or more of the species listed in the checklist. The degree of coverage of the current survey varied between genera, the proportion of species of a particular genus included ranging from 11·5% (*Hygrophorus*) to 300% (*Leccinum*; the value of > 100% resulting from taxonomic revision subsequent to publication of the checklist). With respect to host trees, 25 genera were included in the survey, which represents all genera of ectomycorrhizal trees which are either native or planted on a significant scale in Britain. The shrubs *Arctostaphylos uva-ursi*, *Dryas octopetala* and *Helianthemum chamaecistus* were also included because of their association with ECM genera, although the mycorrhizal status of these species is in some cases enigmatic (Harley & Harley, 1987).

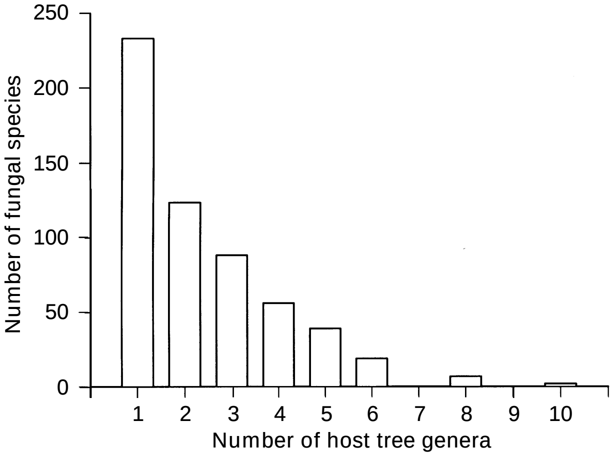

Figure 1. The number of ectomycorrhizal fungal species associated with different numbers of host tree genera.

Pronounced variation was recorded in the number of ECM fungal species associated with different host genera, values ranging from one (e.g. *Abies*) to > 200 in the case of *Betula*, *Fagus*, *Pinus* and *Quercus* (Table 1). Variation was also recorded between host genera in the number of species of ECM fungi which appeared to be specifically associated with them, values ranging from zero (in 15 host genera) to > 40 in the case of *Betula* and *Fagus* (Table 1). In total, 233 fungal species appeared to be specific to a single host genus (i.e. 40% of those surveyed), with only nine fungal species recorded in association with eight or more host genera (Fig. 1). In general, those host genera with a large number of apparently host-specific ECM associates tended to have a large total number of ECM fungi associated with them (Table 1).

Variation in the host range of different fungal genera was also apparent (Table 2). In general, the larger fungal genera tended to be associated with a relatively broad host range. For example, the two largest genera considered, *Cortinarius* and *Russula* (with 136 and 89 species respectively), were found to associate with a total of 14 and 12 host genera respectively. Over 40% of the species within these genera were found to associate with a single host genus. By contrast, many smaller genera such as *Suillus* and *Naucoria* (with a total of 11 and 14 species respectively) were found to associate with fewer host genera (9 and 5 respectively), with over 50% of species in these genera associated with a

Table 2. *The number of species, occurrence of host specificity and host range within Britain for the genera of ectomycorrhizal fungi included in this survey*

Fungal genera	Number of species included in matrix	Number of host-genus-specific species	Number of associated host genera
Amanita	16	4	7
Amphinema	1	0	3
Aureoboletus	1	1	1
Bankera	1	1	1
Boletinus	1	1	1
Boletus	34	8	16
Cantharellus	6	2	7
Cenococcum	1	0	4
Chroogomphus	3	2	3
Cortinarius	136	63	14
Craterellus	2	0	5
Elaphomyces	5	3	8
Gautieria	1	1	1
Gomphidius	4	2	3
Gymnomyces	1	0	2
Gyroporus	2	1	5
Hebeloma	17	4	10
Humaria	1	1	1
Hydnangium	1	1	1
Hydnellum	2	2	2
Hydnotria	1	1	1
Hydnum	2	0	6
Hygrophorus	10	5	5
Inocybe	59	17	13
Laccaria	9	3	8
Lactarius	59	23	13
Leccinum	15	10	11
Leucocortinarius	1	0	2
Leucogaster	1	0	2
Melanogaster	2	0	6
Naucoria	14	9	5
Paxillus	3	0	8
Phellodon	1	0	3
Phylloporus	1	0	3
Pisolithus	1	0	2
Porphyrellus	1	0	2
Rhizopogon	4	3	3
Rozites	1	1	1
Russula	89	38	12
Sarcodon	1	0	2
Scleroderma	5	3	7
Strobilomyces	1	0	2
Suillus	11	6	9
Thelephora	1	0	4
Tomentella	1	0	2
Tricharina	1	0	3
Tricholoma	33	13	10
Tuber	10	2	18
Tylopilus	1	0	7
Uloporus	1	1	1
Zelleromyces	1	0	2

single host genus. In this context, it is striking that the genus *Tuber*, represented by only 10 species, was found to associate with the largest number of different tree genera (18).

When the number of species of ECM fungi associated with different host genera was regressed against the total area occupied by each tree genus in Britain (both values $\log_e$-transformed), a positive linear relationship was recorded ($r^2 = 0{\cdot}47$, $P = 0{\cdot}007$; Fig. 2). For this analysis, the area data used were derived from Locke (1987) (see values in Table 1). When the proportion of ECM species which are host-specific to a particular genus was included as an additional variable in the regression analysis, the

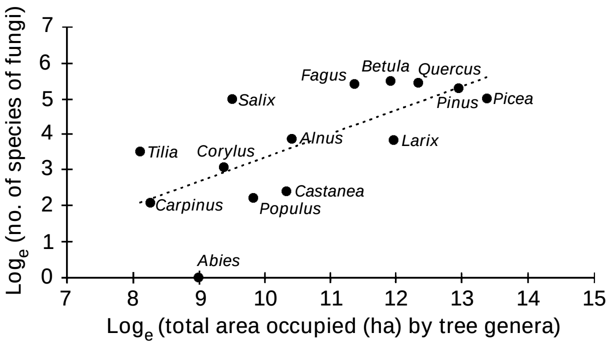

Figure 2. The relationship between the number of species of ectomycorrhizal fungi associated with different host genera, and the distributional area of the host genus (from Locke (1987)). The regression line of log$_e$-transformed values is presented ($y = 0{\cdot}665 \times -3{\cdot}306$; $r^2 = 0{\cdot}47$; $P = 0{\cdot}007$).

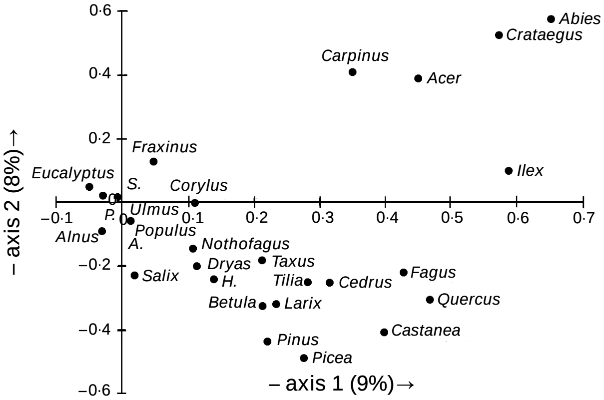

Figure 3. Principal-components analysis of different genera of host trees, using the species of ectomycorrhizal fungi with which they are associated as a basis for comparison. The total variation accounted for by the analysis was 17 % (axes 1 and 2 accounted for 9 and 8 % of the variation respectively; only these axes are illustrated). (For clarity, some genera have been abbreviated, as follows: *A.*, *Arctostaphylos*; *H.*, *Helianthemum*; *P.*, *Pseudotsuga*; *S.*, *Sequoiadendron*).

proportion of variation accounted for increased from 47 to 60 %. *Acer*, *Fraxinus* and *Ulmus* were excluded from these regression analyses, as these genera predominantly form arbuscular mycorrhizas in nature (Harley & Harley, 1987). However, even when these three genera were included in the analysis, a significant proportion of the variation was accounted for by area ($r^2 = 0{\cdot}25$; $P = 0{\cdot}038$). When numbers of associated ECM fungal species were regressed against areas of host genera calculated from Perring & Walters (1962), no significant relationship was recorded ($r^2 = 0{\cdot}01$, $P = 0{\cdot}673$; data not illustrated).

When the data matrix was analysed by PCA, axes 1 and 2 accounted for 9 % and 8 % of the variation respectively, giving a total of 17 % (Fig. 3). This low value is unsurprising, given the fact that such a high proportion of ECM species were restricted to a single host genus. Most genera grouped in the same cluster, the outliers being *Abies*, *Acer*, *Carpinus*, *Crataegus* and *Ilex* (Fig. 3). With respect to these genera, these results should be viewed with great caution as the total number of ECM associates was relatively low (< 10) in each case, which will have biased the analysis. Despite such limitations, some notable patterns are apparent. Genera belonging to the Fagaceae (*Quercus*, *Fagus* and *Castanea*) tended to cluster together, indicating a degree of overlap in their ECM associates. *Pinus* and *Picea* also grouped closely together, despite only the former of the two genera being native to Britain. *Alnus*, *Populus* and *Salix* were also relatively close to each other.

DISCUSSION

The results of this investigation must clearly be treated with caution, given the fact that the data sources employed suffered from a number of limitations. One of the most important of these, as noted earlier, is that most of the published data on ECM associations in Britain refer to associations of sporocarps with particular hosts. Such surveys are prone to inaccuracy, simply because of the capricious and seasonally dependent fruiting behaviour of many ECM fungi. Many species, particularly those that produce hypogeous or inconspicuous sporocarps, tend to be under-recorded in field surveys. As sporocarp associations are no proof of a mycorrhizal association, it is conceivable that some of the species included in this survey are saprotophic or pathogenic, at least in some situations. It should also be emphasized that absence of proof of an association is not proof of absence of that association. It is very probable that the host ranges of many of the fungi included here might be broader than that indicated by the available literature, simply because of the limitations of the data available.

Although the current survey included the majority of ECM species recorded in Britain, a number of species were omitted because information on their host associations is lacking. For example, the exclusion of 79 species for which no host genus was explicitly mentioned in the surveyed literature might have biased the analyses. The associations of these species were described simply in terms of habitat type (e.g. deciduous and/or coniferous woodland), and might therefore have included a number of taxa with very broad host ranges. However, on inspection, the vast majority (> 90 %) of these species are very infrequent taxa for which detailed information is entirely lacking.

Bias in the data set might also have arisen from variation in recorder effort. Field surveys of ECM fungi tend to focus on particular habitats which are relatively rich in species, such as semi-natural woodland, rather than plantation forests. Field surveys also tend to be biased towards those fungi that are relatively easy to identify; many of the more critical species (such as many *Cortinarius* spp.) are likely to be under-recorded. It might also be significant that many of the host genera with the highest number of ECM associates, such as *Betula*, *Quercus* and *Pinus* (but not *Fagus*), were those for which specific accounts have been written. However, the current analysis more than doubled the number of associates for each of these genera listed in previous accounts (Watling, 1974, 1984; Alexander & Watling, 1987). The consideration of host genera, rather than species, will also have influenced the results, as genera with a relatively large number of species would tend to have a larger number of ECM fungi associated with them. As most of the tree genera native to Britain contain a small number (1–3) of species, this is unlikely markedly to have influenced the results. A possible exception is *Salix*, which includes a relatively large number of species colonizing a range of different habitats (Watling, 1992*a*). It might be significant that a far higher ECM diversity was associated with this genus than would be expected from its distributional area alone.

Despite these biases and limitations, the results indicate that ECM fungi in Britain can be described by a species–area relationship, in that variation in ECM diversity is associated with the distributional area of different genera of host trees. This relationship might be of value in understanding patterns of ECM diversity. For example, the high number of ECM species associated with genera such as *Betula*, *Fagus*, *Quercus*, *Pinus* and *Picea* can be attributed, at least in part, to the relatively high abundance of these genera. A number of hypotheses may be proposed to account for this relationship. Regional variation in ECM mycotas might result in host genera with broader distributional ranges coming into contact with a larger number of potential ECM symbionts. Alternatively, higher abundance of the host might in some way facilitate diversification of fungal symbionts, perhaps as a result of the greater edaphic tolerance ranges characteristic of widespread tree species. A third possibility is that a high diversity of ECM associates has actually enabled particular host tree genera to colonize larger areas.

The current results may be usefully compared with previous analyses of species–area relationships in insects. Strong (1974*a*, *b*) analysed the species–area relationship for phytophagous insects in Britain, and found that the relationship accounted for *c.* 61% of the variation, when fitted as a linear regression on log-transformed values. From this, Strong (1974*a*, *b*) suggested that the diversity of the insect fauna associated with a tree species in any region was determined largely by the present area of distribution of the tree species concerned. Further analysis by Kennedy & Southwood (1984), using improved sources of data, accounted for 58% of the variance, rising to 74% when other variables ('time' and 'evergreenness') were included in the regression model. Claridge & Evans (1990) re-analysed the species–area relationship for insects associated with tree species in Britain, using forest inventory data provided by Locke (1987). Although such data are considerably more accurate than the distribution maps used in previous analyses, these re-analyses led to a reduction in the variance attributable to area, with a figure of 17% derived from analysis of both broadleaved and coniferous tree species combined (Claridge & Evans, 1990). The proportion of variation in ECM diversity attributable to area (47%) recorded in this study is therefore considerably higher than that recorded for phytophagous insects using the same inventory data for host distribution (Claridge & Evans, 1990).

Host-specificity is clearly another factor influencing ECM diversity, as indicated by the additional 13% of variation explained by this variable when included in the regression model. The analysis described here indicates that a high proportion (40%) of ECM species in Britain is apparently specific to a single host genus. The fact that genera such as *Fagus*, *Quercus* and *Betula* displayed a higher ECM diversity than could be accounted for by distributional area alone, might be attributable to the relatively high degree of host-specificity recorded by ECM associates of these genera compared with the others surveyed (17·9%, 12·9% and 17·6% respectively). Patterns of host-specificity in ECM fungi have received relatively little attention. Although many ECM species are able to form mycorrhizas with a wide range of hosts in axenic conditions, sporocarp associations between ECM species and particular hosts indicate that host-specificity (or 'ecological specificity' *sensu* Harley & Smith (1983)) is widespread in nature. For example, in a survey of 29 genera of ECM fungi, Molina *et al.* (1992) found that the proportion of species restricted to a single host genus varied between 20–100%.

Another factor which accounts for some of the variation in ECM diversity recorded here is whether the host tree is native to Britain, or has recently been introduced. Coniferous genera such as *Larix*, *Abies* and *Picea*, which have been introduced relatively recently, were each found to be associated with fewer fungal taxa than would be expected from their distributional areas. The results of the PCA analysis supports the suggestion that since their introduction into Britain, *Picea* spp. have tended to form ECM associations preferentially with fungi associated with *Pinus* and *Betula* (Alexander & Watling, 1987), particularly the former. This might account for the fact that of 151 associated species of fungi recorded with *Picea*, only three are apparently host-specific. In the case of *Larix*, although the PCA analysis again indicated a high degree of similarity with *Pinus*, a higher degree of overlap of ECM associates was recorded with *Betula*. This might be attributable to the presence of relict *Betula* on plantation sites acting as a source of inoculum (c.f. Alexander & Watling (1987)). The very low number of associates recorded with *Abies* spp. and *Pseudotsuga* spp. is perhaps more an indication of how coniferous plantations in general have been neglected in fungal surveys, rather than an accurate assessment of their current ECM status.

Ultimately, the factors influencing ECM diversity need to be appreciated in terms of speciation processes in ECM fungi, which remain very poorly understood (Molina *et al.*, 1992). It is conceivable that a tendency towards host-specificity might promote speciation within ECM fungi, by acting as a form of reproductive isolation. The high diversity within highly speciose genera such as *Cortinarius* and *Russula*, for example, can be seen as partly the consequence of the development of large numbers of host-specific species with a wide range of different host genera. Some smaller genera of ECM fungi, such as *Leccinum*, *Suillus* and *Naucoria*, appear to be specialist associates with a restricted range of hosts. In this context, the exceptionally wide host-range recorded here for *Tuber* is enigmatic, and appears to contrast with data from other hypogeous genera (Molina *et al.*, 1992). The overlap in ECM fungal species associated with different host genera from the same family, as recorded here in the Fagaceae, also illustrates the need to consider the influence of evolutionary history on diversity in ECM fungi.

The biases and inadequacies in the data sources used here clearly limit the weight which can be accorded to the main trends detected. It was assumed at the outset that the intrinsic limitations in the data would be compensated by the inclusion of a wide variety of data sources. Although the validity of this assumption remains open to question, the significant species–area relationship recorded here at least provides a basis for future testing. A more detailed analysis awaits more thorough field surveys, perhaps targetting little-studied tree genera such as *Abies* or *Pseudotsuga*, and the detailed assessment of different host species as well as genera. Surveys of sporocarp association should be supported by analysis of mycorrhizal colonization of root systems. Taxonomic revisions are also required in a number of ECM genera; the lack of an up-to-date checklist of British fungal species is a hindrance to estimations of total diversity. Nevertheless, the British mycota is probably one of the best documented currently available, having been supported by the field activity of both professional and amateur mycologists for over a century (Watling, 1986, 1988). It is therefore salutory to consider that the ECM fungal associates of so few tree genera in Britain are known in any detail. Considerable research is still required if the diversity relationships of ECM fungi are to be fully elucidated, particularly in areas where taxonomic efforts are still at an early stage.

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