

## Species richness on trees: a comparison of parasitic fungi and insects

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### ABSTRACT

We collected data on the species richness of parasitic fungi occurring on tree genera native to Germany. We explore variations of species richness of parasitic fungi in relation to present abundance of trees (a measure of host distribution), tree height (a measure of host size), the number of congeneric tree species (a measure of host isolation) and post-glacial occurrence of trees (a measure of host age). We compare the patterns to those retrieved for phytophagous insects from the very same data set.

In a univariate approach, we found only marginally significant relationships ( $P < 0.1$ ) between species richness of parasitic fungi and present abundance of trees, tree height and the number of congeneric tree species. After controlling for phylogenetic relatedness among hosts, these relationships became significant. However, the explained variance was always very low. Irrespective of the type of analysis, post-glacial occurrence of trees showed no significant relationship with species richness of parasitic fungi. Hierarchical partitioning showed that present abundance of trees, tree height and the number of congeneric tree species are of about equal importance to explain species richness of parasitic fungi. This result contrasts with that for phytophagous insects. For phytophagous insects, the present abundance of hosts explained by far the largest amount of variance in species richness.

The large and unexplained scatter around the species–area curve for parasitic fungi may be due to (1) idiosyncratic processes, (2) the composition of secondary metabolites among trees or (3) the co-occurrence of trees within habitats.

*Keywords:* insects, parasitic fungi, species–area relationship, species richness.

### INTRODUCTION

Most, if not all, organisms are hosts for parasites. The species richness of parasites, however, varies considerably between hosts (e.g. Southwood, 1961; Strong and Levin, 1975; Kennedy and Southwood, 1984; Gregory *et al.*, 1991; Brändle and Brandl, 2001). This variation is not random, but shows several striking patterns, especially for the species–area relationship (e.g. Connor and McCoy, 1979; Simberloff and Moore, 1997): widespread

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hosts tend to have more species of parasites than hosts with a restricted distribution. This pattern has been documented for phytophagous insects on plants (e.g. Strong, 1974; Kennedy and Southwood, 1984), parasitic fungi on trees and grasses (Strong and Levin, 1975; Clay, 1995), nematodes and trematodes on birds (e.g. Gregory *et al.*, 1991) and helminth parasites on freshwater fish (Price and Clancy, 1983). Despite this fairly general and robust positive relationship between parasite richness and host distribution, the processes behind this pattern remain elusive. At least three important processes are thought to be involved: passive sampling (Colemann, 1981), habitat heterogeneity (Williams, 1943) and an equilibrium between extinction and colonization (MacArthur and Wilson, 1967).

In addition to the difficulty of evaluating the relative importance of these three processes for generating the species–area curve in particular cases (Gotelli and Graves, 1996, pp. 207–238), the amount of variance explained by the species–area relationship varies considerably between taxa (e.g. Connor and McCoy, 1979). Hence some suggest that: (1) there is no single process which generates the variation in parasite richness among hosts (e.g. Kennedy and Southwood, 1984); (2) the importance of additional processes (see below) varies among assemblages of parasites and host taxa (e.g. Strong and Levin, 1975); and (3) patterns of parasite species richness are influenced by the idiosyncrasies of the host phylogeny (Gregory, 1997; Kelly and Southwood, 1999).

Apart from the species–area relationship, there are at least four additional processes that may influence species richness of parasites across hosts:

1. *Host size*. Analogous to explanations of the species–area hypothesis on a geographical scale, individual hosts may be viewed as islands on a local scale and large hosts should accumulate more parasite species than smaller ones. Larger hosts provide space for many individuals. This has two effects: first, passive sampling increases with host size; secondly, extinction probabilities of parasite populations within host individuals decrease with host size (e.g. Lawton and Schröder, 1977; Strong and Levin, 1979; Gregory *et al.*, 1991; Keymer *et al.*, 1991; Poulin, 1995).
2. *Taxonomic isolation*. Related hosts are likely to share physical, chemical and biological traits. Thus, parasites adapted to a particular host are more likely to switch to closely related than to unrelated hosts (Claridge and Wilson, 1981, 1982; Connor *et al.*, 1980; Strong *et al.*, 1985). Consequently, hosts embedded into a rich array of related species should be able to accumulate more parasite species than taxonomically isolated hosts.
3. *Host age*. Accumulation of parasites on a host species should increase with time, both on an evolutionary as well as an ecological time-scale (Birks, 1980; Kennedy and Southwood, 1984; Bush *et al.*, 1990).
4. *Dispersal*. The dispersal capacity of certain parasitic taxa may also influence the variation of species richness of parasites across hosts (e.g. Strong and Levin, 1975; Kennedy *et al.*, 1986; Gregory *et al.*, 1991; Keymer *et al.*, 1991). Parasites with good dispersal abilities may easily colonize suitable hosts. Strong and Levin (1975) show that the slope of the species–area curve of parasitic fungi associated with British trees is more shallow than the slope for phytophagous insects, a pattern which the authors attribute to differences in the dispersal of fungi and insects.

In this study, we analyse species richness of parasitic fungi on tree genera native to Germany. As for Britain (e.g. Ellis and Ellis, 1997), host-associations of fungi and trees are fairly well understood (e.g. Braun, 1987, 1995). Furthermore, the variation in species

richness across tree genera has been intensively investigated and allows for a comparison between fungi and insects (e.g. Strong and Levin, 1975). Hence, the aims of our study were twofold: (1) to analyse the variation in species richness of parasitic fungi across trees using a cross-species as well as a phylogenetic controlled approach; (2) to compare patterns of relationships between species richness and host traits with those found for phytophagous insects within the very same data set (Brändle and Brandl, 2001).

## METHODS

### Parasitic fungi, phytophagous insects and hosts

Species richness of parasitic fungi was analysed at the level of tree genera (Strong and Levin, 1975; Kennedy and Southwood, 1984; Newton and Haigh, 1998; Kelly and Southwood, 1999). We have data for 25 tree genera that are native to Germany (see Table 1). We pooled the genus *Frangula* with the genus *Rhamnus* as suggested by some taxonomists (e.g. Fitschen, 1987). For these 25 host genera, we assembled lists of parasitic fungi that attack leaf tissue from the following sources: Erysiphales (powdery mildews): Braun (1987), Scholler (1996); Hyphomycetes: Braun (1995); Pucciniales and Ustilaginales (smuts): Brandenburger (1994), Scholler (1996). It is important to note that our species richness reflects the concept of *compound communities* (*sensu* Simberloff and Moore, 1997, p. 175). That is, our measure of species richness integrates across all individuals of all parasitic fungi species of all host populations in Germany.

Published lists introduce some bias into analyses of parasite–host associations (Kennedy and Southwood, 1984; Gotelli and Graves, 1996). To reduce the possible bias, we considered only taxa of fungi for which the taxonomy is well known. Nevertheless, when we compared species richness of fungi from our lists with species richness extracted from other sources that include additional taxa of fungi (Brandenburger, 1963, 1985), we found close correlations (with the data of Brandenburger, 1963:  $n = 25$ ,  $r = 0.70$ ,  $P < 0.001$ ; with the data of

**Table 1.** Number of parasitic fungi species on tree genera in Germany

Genus	<i>n</i>	Genus	<i>n</i>
<i>Abies</i>	14	<i>Picea</i>	5
<i>Acer</i>	4	<i>Pinus</i>	7
<i>Alnus</i>	3	<i>Populus</i>	16
<i>Betula</i>	5	<i>Prunus</i>	11
<i>Carpinus</i>	3	<i>Pyrus</i>	11
<i>Corylus</i>	2	<i>Quercus</i>	6
<i>Crataegus</i>	5	<i>Rhamnus</i>	2
<i>Fagus</i>	2	<i>Salix</i>	22
<i>Fraxinus</i>	6	<i>Sorbus</i>	11
<i>Ilex</i>	3	<i>Taxus</i>	0
<i>Juniperus</i>	1	<i>Tilia</i>	2
<i>Larix</i>	7	<i>Ulmus</i>	3
<i>Malus</i>	7		

Brandenburger, 1985:  $n = 25$ ,  $r = 0.77$ ,  $P < 0.001$ ). Moreover, the results of our analyses remained the same when we included other taxa of fungi. Hence, we are fairly sure that a bias in our data will have only minor effects on the results presented here.

Data on phytophagous insects associated with the tree genera, together with data for the independent variables which characterize hosts, were taken from Brändle and Brandl (2001; see their Appendix 2). We used the following independent variables:

1. *Present abundance of trees.* We used grid occupancy from the former Federal Republic of Germany (Häupler and Schönfelder, 1989) and the former Democratic Republic of Germany (Benkert *et al.*, 1996) to estimate tree abundance. In the former, grid occupancy is reported across  $11 \times 11$  km grids (MTB-system); in the latter, grids are subdivided into tetrads. We combined both sources by counting the number of  $11 \times 11$  km grids occupied by a tree genus. For genera with two or more species, we used the total number of squares in which the genus was recorded. Overall present tree abundance characterizes the distribution of a host genus.
2. *Tree height.* Tree height was measured using the maximum height (in metres) of the tallest species within the genus (Rothmaler, 1987). We did not consider leaf size (for reasons, see Brändle and Brandl, 2001).
3. *Re-colonization of trees during Holocene.* We used the time span since the first fossil record of a tree in Central Europe during the Holocene (Brändle and Brandl, 2001). Three problems arise: (i) The data are only approximate. (ii) Some trees produce very little pollen, since they are pollinated by insects (e.g. *Rhamnus* and the rosaceous trees); the probability of finding fossil pollen of these genera is thus low (Birks, 1980). (iii) The genera of the rosaceous trees cannot be distinguished by the morphology of their pollen (G. Lang, personal communication).
4. *Taxonomic isolation.* Most researchers use the number of congeneric species as an indirect measure of taxonomic isolation (Lawton and Price, 1979; Claridge and Wilson, 1981, 1982). Kennedy and Southwood (1984) used the number of co-occurring tree species within the order (see also Neuvonen and Niemelä, 1981). For statistical reasons, we used the number of congeneric species, as the number of species within orders will have the same value for a number of tree genera, which violates the assumption of independent data required for statistical tests.

### Statistical analyses

Before the statistical analyses, richness of parasitic fungi was  $\log_{10}(x + 1)$  and all other variables  $\log_{10}$ -transformed to make the variables more suitable for parametric statistical tests. For all statistical tests, significance was assumed when two-tailed error probabilities were below 5%. When probabilities were between 5 and 10%, we considered the relationships 'marginally significant'.

When using tree genera in a comparative analysis, one has to be aware that genera are not independent from each other but are linked by their evolutionary history (Felsenstein, 1985; Harvey and Pagel, 1991). Thus, we followed two lines of analyses: (1) a naive analysis using genera as independent data points in all statistical analyses (cross-genera analyses) and (ii) a phylogenetically controlled analysis (Harvey and Pagel, 1991). For the latter analysis, we calculated phylogenetically independent contrasts across a hypothesized phylogeny. For all analyses, we used the phylogeny published in Brändle and Brandl (2001). The fully resolved

phylogeny allowed us to calculate phylogenetically independent contrasts (PICs) according to the method developed by Felsenstein (1985). However, we were unable to generate meaningful branch lengths for the phylogeny and we had to assume an equal length for all branches (Pagel, 1992). This assumes a punctual view of evolution. Calculations were done using CAIC (Purvis and Rambaut, 1995). For regression analyses of contrasts, it is necessary to set the intercept to zero (Garland *et al.*, 1992; Pagel, 1992).

Macroecological studies are confounded by complex interrelationships between variables. To estimate the importance of the independent variables for the explanation of species richness in parasitic fungi and insects, we applied hierarchical partitioning, a technique which recently percolated into ecology (Chevan and Sutherland, 1991; MacNally, 2000). The aim of hierarchical partitioning is not to identify a single optimal model or to generate a predictive equation. Rather, all possible regression models are used to estimate the average independent contribution of a given independent variable to the dependent variable (MacNally, 2000). To assess the statistical significance of independent contributions, we used randomizations (999 randomizations). We considered independent contributions as significant if  $\leq 5\%$  of the randomizations generated contributions equal to or larger than the contribution calculated from the original data.

To compare the importance of independent variables on species richness between parasitic fungi and phytophagous insects, we compared the patterns of independent contributions for parasitic fungi and phytophagous insects for the raw data as well as the contrasts. For statistical assessment, we used bootstrapping. For each bootstrap sample, we calculated the difference between the independent contributions on species richness of fungi and insects and assessed whether the difference was larger than or equal to the difference calculated from the original data.

## RESULTS

The species richness of parasitic fungi on German tree genera varied considerably. The largest number of species (22) occurs on *Salix*, whereas none was found on *Taxus* (see Table 1). A comparison of the variation of species richness across hosts shows that the variation coefficient of log-transformed data is 41% for fungi and 20% for insects. Furthermore, the richness of parasitic fungi was closely related to the richness of phytophagous insects (cross-genera:  $n = 25$ ,  $r^2 = 0.36$ ,  $P = 0.002$ ; PICs:  $n = 25$ ,  $r^2 = 0.45$ ,  $P < 0.001$ ).

Across tree genera, we found weak and only marginally significant correlations between species richness of parasitic fungi and the present abundance of trees, tree height and the number of congeneric tree species (Table 2). Controlling for the phylogenetic relatedness among tree genera, these three relationships became significant (Table 2, Fig. 1). Independent of the type of analysis (cross-genera or PICs), post-glacial occurrence was not correlated with the richness of parasitic fungi (Table 2, Fig. 2).

For phytophagous insects, relatedness among tree genera, present abundance of trees, tree height and the number of congeneric species, all are significantly correlated with insect species richness (Table 2) either using genera as independent data points or using PICs. Again, post-glacial occurrence showed no significant correlation with the species richness of phytophagous insects.

Hierarchical partitioning suggested that the number of congeneric species and tree height were the most important variables for species richness of parasitic fungi across tree genera. However, only the contribution of the number of congeneric tree species is marginally

**Table 2.** Coefficients of determination ( $r^2$ ) of species richness ( $\log_{10}$ -transformed) of parasitic fungi and phytophagous insects occurring on tree genera native to Germany versus various independent variables

Independent variables	$\log_{10}$ species richness			
	Fungi	Insects	Fungi	Insects
	$r^2_{\text{cross}}$	$r^2_{\text{cross}}$	$r^2_{\text{con}}$	$r^2_{\text{con}}$
Present abundance	0.14 <sup>(*)</sup>	<b>0.65***</b>	<b>0.25*</b>	<b>0.59**</b>
Tree height	0.14 <sup>(*)</sup>	<b>0.21*</b>	<b>0.20*</b>	<b>0.29**</b>
Post-glacial occurrence	0.00	0.02	0.05	0.09
Congeneric species	0.14 <sup>(*)</sup>	<b>0.22*</b>	<b>0.33**</b>	<b>0.30**</b>

*Note:* The analysis of contrasts ( $r^2_{\text{con}}$ ) uses a regression with an intercept of zero. Thus there is no direct way to compare  $r^2$  between an analysis which uses tree genera as independent data points and an analysis using PICs.

The left-hand columns show the results of the cross-genera analyses ( $r^2_{\text{cross}}$ ,  $n = 25$ ), the right-hand columns the analysis of phylogenetic independent contrasts ( $r^2_{\text{con}}$ ,  $n = 24$ ). Significant coefficients of determination ( $P < 0.05$ ) are indicated in **bold** (error probabilities: <sup>(\*)</sup> $P < 0.1$ ,  $*P < 0.05$ ,  $**P < 0.01$ ,  $***P < 0.001$ ). Regressions on contrasts were calculated with an intercept of zero. Note that all independent variables were  $\log_{10}$ -transformed. The results of the phytophagous insects were taken from Brändle and Brandl (2001, Table 2).

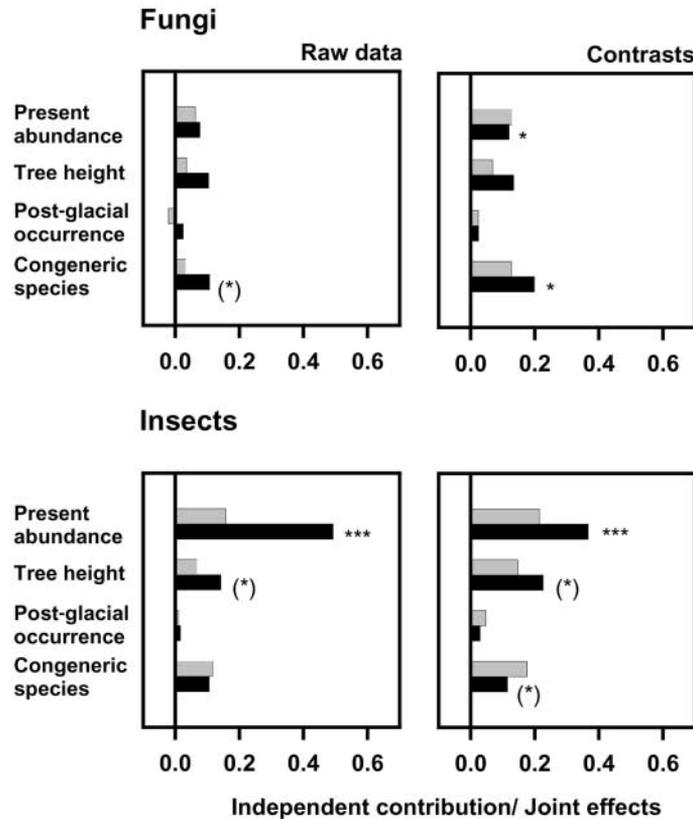
significant. The present abundance of trees and post-glacial occurrence explained only limited variance in species richness. When we analysed PICs, the number of congeneric species became the most important variable, followed by the present abundance of trees.

For phytophagous insects, the present abundance of trees was the most important significant variable. The number of congeneric species and tree height had marginally significant independent contributions. The contribution of post-glacial occurrence was low. In general, the patterns generated using tree genera as independent data points and PICs were similar.

When we compared the independent contributions of the independent variables between parasitic fungi and phytophagous insects, we found only one significant difference: the contribution of the present abundance of trees was significantly greater in the analyses of insects than in the analyses of parasitic fungi for the cross-species data as well as the independent contrasts.

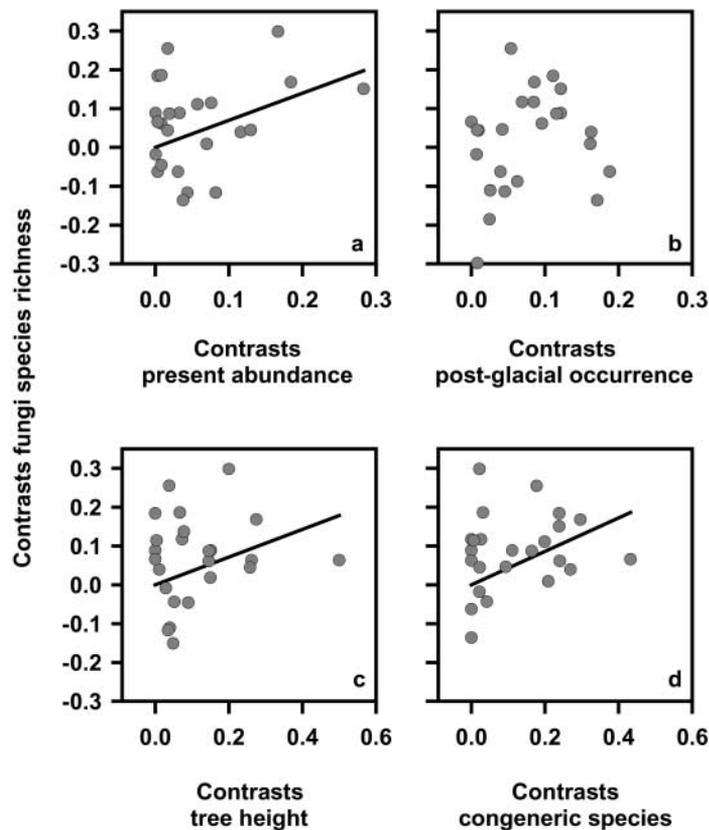
## DISCUSSION

Strong and Levin (1975) and Clay (1995) noted that about 30% of the variance in species richness of parasitic fungi was explained by the species–area relationship. In the present study, the species–area relationship accounted for only 14% of the variation in species richness. For phytophagous insects, the species–area relationship explains more than 50% of the variance in species richness across hosts (Kennedy and Southwood, 1984; Brändle and Brandl, 2001). Thus there is a robust difference in the scatter around the species–area relationship between fungi and insects. Nevertheless, we want to add three cautionary notes (see also Connor and McCoy, 1979). First, in the case of fungi or insects on trees, some authors included introduced hosts into their analyses. The compound communities of



**Fig 1.** Summary of the results of four separate hierarchical partitions. The left-hand panels present the results for the raw data, the right-hand panels those for the phylogenetically independent contrasts. Solid bars indicate independent effects, stippled bars joint effects. The abscissa indicates the explained variance which may be interpreted as  $r^2$ -values. Asterisks correspond to the significance of the independent contribution obtained by bootstrapping (see Methods).

parasites on alien hosts may be structured by processes quite different from the processes on native hosts. Therefore, results may change with the inclusion of introduced hosts (e.g. Rosenzweig, 1995; Kelly and Southwood, 1999; but see Strong and Levin, 1975). Moreover, the parasites of introduced hosts are often less well known than those of the natives and alien hosts may also bring parasites with them (Strong *et al.*, 1985). Secondly, researchers have calculated species–area relationships across different taxonomic subsets of parasites. For instance, we found little agreement in the species richness of fungi when we compared the database used during our study and the data published in Strong and Levin (1975). A correlation analysis between the number of parasitic fungi in England versus the data of the present study (only host species which are native to both countries) accounted for only 27% of the variation ( $n = 17$ ,  $P = 0.03$ ). This is in contrast to a comparison of the richness of phytophagous insects on native trees in Britain and Germany, where 92% of the variation was accounted for (Brändle and Brandl, 2001). Note that in the latter study, the very same set of phytophagous insect taxa was used to estimate species richness of phytophages. Thirdly, our measure of the present abundance of trees covers only a small part of the total



**Fig. 2.** The relationship between parasitic fungi richness on native German tree genera and various independent parameters. The plots show the patterns using phylogenetically independent contrasts. Richness versus: (a) present abundance of trees in Germany; (b) years after the first post-glacial record in Central Europe until present; (c) maximal tree height within genus; (d) the number of congeneric species. Regression lines represent significant relationships ( $P < 0.05$ ; see Table 2). Note that regressions are calculated with an intercept of zero.

distributional ranges of the hosts. Most distributional ranges span across large parts of the Palaearctic realm (Meusel and Jäger, 1992). Thus, the importance of the species–area relationship may change if we consider the total distributional range size of hosts.

In the present study, all the other processes suggested to account for some of the variance in parasite species richness across hosts appear to have little explanatory power. Tree height was suggested to influence parasite richness either via a species–area relationship or via architectural complexity (Lawton and Schröder, 1977; Lawton, 1978; Strong and Levin, 1979; Kennedy and Southwood, 1984; Strong *et al.*, 1985). However, the evidence for a correlation of architecture and tree size is, at least for our data set, rather tenuous. Furthermore, we only considered parasitic fungi that attack leaf tissue. Thus, tree height may be an inadequate surrogate of the architectural complexity for fungi which attack leaves (e.g. Strong and Levin, 1975). Future studies should develop more elaborate measures of architectural complexity that consider the niches of the parasites in a more direct way.

In the case of leaves, however, such measures may only differ between gymnosperms with rather simple leaves and the more complex leaves of angiosperms. This hampers a meaningful phylogenetic analysis (Harvey and Pagel, 1991).

Taxonomic isolation was introduced by Kennedy and Southwood (1984) to explain some of the variance in species richness of phytophagous insects across trees. Although the flow of arguments to describe the possible influence of taxonomic isolation on species richness of parasites is straightforward, we found no strong and convincing influence of taxonomic isolation on the species richness of fungi. Again, this agrees with the analysis of phytophagous insects on trees. For insects also, taxonomic isolation explained only a minor part of the variance in species richness (Kennedy and Southwood, 1984; Brändle and Brandl, 2001).

Birks (1980) and Kennedy and Southwood (1984) introduced host age to explain some of the variation in parasite richness across hosts. Both studies, however, incorporated introduced trees into their analyses (see above). Rosenzweig (1995) failed to find support for the host age hypothesis when he excluded introduced hosts. Therefore, he concluded that the host age hypothesis only works over short time periods on artificially introduced hosts (see also Frenzel *et al.*, 2000). However, there are at least two other obvious limitations of our measure of host age. First, our estimate considers only a small part of the total evolutionary history of trees, the post-glacial period. The time for the evolution of a parasite–host association may be independent of the re-colonization patterns of trees after the Pleistocene. Consequently, the measure used in our analyses operates on the wrong time scale (Brändle and Brandl, 2001). Secondly, our analyses assumed implicitly that trees were free of parasites when they colonized the more northern parts of Europe from the Pleistocene refuges. At least some parasites will have followed their hosts (see also Eber and Brandl, 1994). Overall, although historical and palaeogeographic factors are essential to understand species diversity and community structure (Ricklefs and Schluter, 1993), there is at present little support for the host age hypothesis for fungi and phytophagous insects on trees.

Strong and Levin (1975) report that the slope of the species–area curve for phytophagous insects is steeper than that for parasitic fungi. They argue that fungal species disperse more widely than insects, which should increase the probability of host switches. This should lead to a smaller  $z$  in  $S = kA^z$ . Our analysis does not support this hypothesis. Note that the coefficient of variation in species richness across hosts is higher in fungi than in insects. If dispersal increases the colonization probability of hosts, this should also lead to a decrease in the variation of species richness across host species, as dispersal will tend to homogenize differences between species.

From the above discussion, it would appear that our efforts to explain the variation in richness in fungi across host trees was not very successful. We wish to suggest three lines of argument for further discussion. First, the variation may be due to idiosyncratic processes. Such idiosyncratic processes may be evolutionary processes. Fungi disperse by an enormous amount of spores and all trees sample these spores passively from the environment. This initiates complex interactions, whereby most of the spores fail to infect a host. Nevertheless, in the case a species is able to infect a host, interactions between fungi and host may ultimately lead to speciation of a new parasitic fungi species. The details of the interactions which may lead to failure or success and the details of the speciation process will depend on the traits of parasite and host. In part, these interactions should be predictable from phylogenetic relatedness and from the similarity of secondary metabolites between species

(see below). The complex interactions between the ecology and evolution of parasite and host may generate considerable and idiosyncratic variation across species. In passing, we wish to make two notes: (1) The management of tree populations by humans may have also influenced the patterns of species richness across hosts in an idiosyncratic way. (2) The statement that processes are idiosyncratic is not strictly correct, since it precludes any valid research project. Thus, scientists have to pinpoint the idiosyncratic processes to reach a more detailed understanding.

Secondly, variation between species may be due to differences in diversity or uniqueness of secondary metabolites (Jones and Lawton, 1991). On the one hand, it has been hypothesized that a diverse and unique suite of secondary metabolites reduces the probability that parasites are able to colonize a host. This should result in a negative correlation between species richness of parasites and the diversity of secondary metabolites (the 'divers defence' or 'biochemical barrier' hypothesis *sensu* Jones and Lawton, 1991). On the other hand, the 'common chemistry' hypothesis predicts a positive correlation between richness of parasites and the diversity of secondary metabolites. Plants with diverse chemistry have a higher probability of sharing chemicals with other plants. This may facilitate host shifts (Jones and Lawton, 1991). However, Jones and Lawton (1991) found only little support for these two hypotheses when they examined the insect species richness of British Umbellifers. Nevertheless, we believe that secondary metabolites are of some importance, especially for parasitic fungi. Compared with phytophagous insects, parasitic fungi have a very close relationship with their hosts (germination, growing within leaf tissue). Thus, these parasites may be confronted with plant secondary metabolites in a very direct way.

Thirdly, species richness of fungi is influenced by the habitat niche of the host. Host expansions, host switches and the evolution of a new species may be more likely among tree species that share the same habitats. Species with broad niches are more likely to co-occur relative to pairs of specialized species. Thus generalists may accumulate more species than specialists.

Overall, our results indicate that there is no single and simple process to account for the outstanding variance in the species richness of parasitic fungi across tree genera. The predictive power of the species–area relationship is poor for parasitic fungi compared with that for phytophagous insects. Although the dispersal ability of fungi via spores may influence host distribution, other explanations – such as the diversity and composition of plant secondary metabolites and the habitat distribution of trees – may provide further keys to understand the fascinating diversity of parasitic fungi on trees.

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