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Species richness of insects and mites on trees: expanding Southwood

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Summary

1. Data on the species richness of phytophagous insects and mites associated with 25 tree genera occurring as natives in Germany were compiled and compared to data for British trees published by Kennedy & Southwood (1984). For tree genera occurring in Germany and Britain patterns of species richness and composition of phytophage faunas were similar.
2. Present abundance of trees, their distributional history during the Holocene, morphological traits and taxonomic isolation were used to explain the variance of species richness and proportion of specialists across tree genera occurring as natives in Germany. Tree genera were either used as independent data points or to calculate phylogenetically independent contrasts. For the latter approach, a phylogeny for the tree genera was generated from published *rbc*L gene sequences. In general, the conclusions from the two types of analyses were similar.
3. The species richness of phytophages on German tree genera were positively related to present tree abundance, tree height and tree abundance derived from pollen samples. For phylogenetically independent contrasts the length of time a genus was present since the end of the last glaciation also became significant.
4. The proportions of specialists showed a negative relationship with present abundance of trees, a positive relationship with taxonomic isolation as well as the length of time of genus was present since the end of the last glaciation. For phylogenetically independent contrasts only the latter two variables remained significant.
6. Overall the results support the species–area and the coevolutionary hypotheses.

Key-words: coevolution, insects, mites, specialists, species–area relationship, species richness.

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Introduction

In 1984 the research efforts of Southwood culminated in a paper where Kennedy & Southwood (1984) presented an analysis of the species richness of phytophagous insects and mites associated with British trees. These authors reported that present abundance of trees in Britain, length of time a tree has been present in Britain since the end of the last glaciation, taxonomic isolation of trees, tree height and leaf length explained in decreasing order of importance a significant part of the variance in species richness of phytophages across trees. Altogether these five variables accounted for 82% of the variance. At least three classes of hypothesis were suggested to explain these patterns:

1. The *species–area* hypothesis: species–area curves are universal in ecology (Rosenzweig 1995). On a geographical scale several explanations of the species–area relationship have been specifically tallied for phytophages: the habitat–heterogeneity hypothesis (Williams 1943), the encounter–frequency hypothesis and the equilibrium theory hypothesis originally developed for islands (MacArthur & Wilson 1967; see Strong, Lawton & Southwood 1984 for a review). Together, all three hypotheses predict that species richness of phytophages should increase with abundance and distribution of a host species. In analogy to the explanations of the species–area hypothesis on a geographical scale, individual trees may be viewed as islands on a local

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scale and large trees should accumulate more phytophages than smaller ones. Since large trees provide many microhabitats, passive sampling increases with tree size and population size of phytophages increases with tree size which reduces extinction probabilities (Lawton & Schröder 1977; Strong & Levin 1979).

2. The *geological time* hypothesis: richness of phytophages on hosts may depend on how long a particular host has been able to accumulate phytophages either by collecting species from the available pool of phytophages or by evolutionary processes. Trees re-colonized Europe during the Holocene. Thus, the earlier a tree re-colonized an area in Europe, the more phytophages should occur on it (Birks 1980; Kennedy & Southwood 1984).

3. The *taxonomic isolation* hypothesis: related plants are likely to share chemical and physical traits. Phytophages are more likely to switch to closely related than to unrelated hosts as related potential hosts offer similar living conditions (e.g. chemical defence systems; Connor, Simberloff & Opler 1980; Strong, Lawton & Southwood 1984). Thus, tree species with co-occurring relatives (low taxonomic isolation) should have more phytophagous species than taxonomically isolated trees.

Subsequent to Southwood and coworkers, however, there were only few further attempts to analyse species richness of insects on trees (e.g. Leather 1986, 1991), but there are still several open questions and after 15 years some new perspectives.

1. Britain is an island. This geographical isolation certainly affected the re-colonization of organisms after the Pleistocene (e.g. Dennis 1977). For instance, there were no waves of different woodland types during the Holocene, as suggested for continental Europe (Ingrouille 1995). Nowadays, in Britain only 10–12% of the landscape is covered by woodland, one of the lowest values in Europe. In contrast, Germany has a woodland cover of 26% (WRI 1999). Thus the question arises as to whether the biogeographical patterns of species richness on trees obvious in Britain will also hold for continental Europe.

2. Kennedy & Southwood (1984) combined native and alien trees within their analyses. Rosenzweig (1995) showed that the correlation between g*eological time* and species richness is due to the inclusion of these alien trees. Thus, the *geological time* hypothesis is still a matter of debate (Southwood 1961; Strong 1974; Claridge & Wilson 1978; Birks 1980; Boucot 1983; Kennedy & Southwood 1984; Bush, Aho & Kennedy 1990; Price 1997).

The processes determining the proportions of specialists or generalists among plants are poorly understood (Lawton & Schröder 1978; Neuvonen & Niemelä 1981). The *plant predictability–apparency* hypothesis (Levins & MacArthur 1969; Feeny 1970; Strong & Levin 1979) predicts that apparent plants invest more into chemical defence and only specialists are able to exploit such hosts. Abundance is one component of apparency and thus one expects more specialists on abundant trees (Levins & MacArthur 1969; Rhoades & Cates 1976; Neuvonen & Niemelä 1981). The *coevolutionary* hypothesis (e.g. Berenbaum 1983) suggests that over time phytophages become increasingly specialized and in time evolve to specialists. Thus, the earlier a tree re-colonized an area the more specialized phytophages should occur on it.

The phylogenetic relatedness of taxa influences statistics (Harvey & Pagel 1991). Nowadays sophisticated methods exist which incorporate phylogeny into analyses (e.g. Felsenstein 1985). The development of laboratory techniques made DNA sequences available which can be used to infer the phylogenies of taxa to fuel phylogenetic controlled analyses (e.g. Chase *et al.* 1993). Kelly & Southwood (1999) already showed that the relationship between species richness of phytophages on British trees and tree abundance, at least, does not change by introducing phylogeny of trees into the analysis.

Altogether these arguments encouraged us to carry out an analysis of species richness of phytophagous insects and mites on their host trees in Germany. The aim of our study is threefold.

1. We will compare the species richness of the British insect fauna on trees with the fauna on trees also occurring in Germany. This will help to understand the effects of the special situation of Britain on biogeographic patterns.

2. We will analyse the variation in species richness across trees native to Germany in correlation of several independent variables using naive methods as well as modern comparative approaches.

3. We will analyse the variation in the percentage of specialized insect and mite species across tree genera.

Methods

HOST TREES

Species richness of phytophages was analysed on the level of tree genera. More precise data are not available (see also Neuvonen & Niemelä 1981; Kennedy & Southwood 1984). Among the 25 tree genera native to Germany (see Appendix 1) 20 are also native in Britain. We pooled the genus *Frangula* with the genus *Rhamnus* as suggested by some taxonomists (e.g. Fitschen 1987). For Britain Kennedy & Southwood (1984) handled *Picea abies* (L.) Karst as a native since it was present in Britain before the last glaciation. However, it was reintroduced by humans approximately 500 years ago (Birks 1980). Thus *Picea abies* was excluded when comparing the fauna of Britain and Germany.

HOST RECORDS

In order to compare the results with the results obtained by Kennedy & Southwood (1984), the same insect and mite taxa were considered (Appendix 1). Host records were compiled from published accounts. Only publications of renowned experts were selected. However, for some taxa information was scanty or outdated (Eriophyidae, Thysanoptera). From the lists we counted the overall species richness of insects and mites (subsequently simply called species richness) and the number of specialists (Appendix 2). Specialists were defined as phytophages restricted to one tree genus.

Undoubtedly, using published lists of phytophages introduces some bias (Kennedy & Southwood 1984; Gotelli & Graves 1996). Prominent critiques are the 'entomologist–area effect' (e.g. Connor & McCoy 1979) and that rare trees were sampled less frequently than common trees. However, as already suggested by Kennedy & Southwood (1984; see also Southwood 1961), the fauna of Britain as well as Central Europe has been studied for more than 100 years. Various studies also tested the reliability of published host records (Lawton *et al.* 1981; Southwood, Moran & Kennedy 1982; Niemelä & Neuvonen 1983; Leather 1990; but see Fielding & Coulson 1995). Most of them found no important differences in their analyses either using field samples or data retrieved from the literature.

TREE ABUNDANCE

Two surrogates of tree abundance were used in the analyses: grid occupancy across Germany and pollen samples across Europe. At present there are no grid maps of plant distribution available which cover Germany as a whole. Thus occupancy had to be combined from Häupler & Schönfelder (1989) covering the former BRD and Benkert, Fukarek & Korsch (1996) covering the former GDR (Appendix 2; 11 × 11-km grids, MTB-System). In tree genera with two or more species the total number of grids in which the genus was recorded was used. Claridge & Wilson (1978) and Kennedy & Southwood (1984) noted the all-or-nothing nature of grid occupancy as a surrogate of abundance (but see Kennedy & Southwood 1984). However, many macroecological studies demonstrate a correlation between abundance and occupancy (e.g. Hengeveld & Haeck 1982; Gaston & Blackburn 2000, and references therein) and thus in the present analyses the grid occupancy of tree species across Germany is used as a measure of present abundance of tree genera.

Huntley (1990) compiled a list of contemporary and fossil pollen samples of trees across Europe. These data rest on 500 localities studied for pollen-stratigraphy and more than 1000 localities with surface-samples (for details see Huntley 1990). This list, however, does not include data for the rosaceous trees. We use the number of samples in which a tree genus was recorded as a measure of abundance. Note that this measure of abundance is some kind of an average across time and space. At least in part the pollen data provide evidence for the abundance of tree genera during the Holocene. We call this measure of tree abundance derived from pollen samples 'pollen abundance'.

TREE HEIGHT

Tree height was measured by the maximum height (in m) of the tallest species within the genus (Rothmaler 1987). Leaf size, 'coniferousness' and 'evergreenness' (Kennedy & Southwood 1984) were not considered. Within Angiosperms and Conifers these variables show almost no variation and there are no degrees of freedom for meaningful phylogenetically controlled tests.

POSTGLACIAL OCCURRENCE OF TREES

To estimate the time span since the first fossil record of a tree in Central Europe after the last glaciation we compiled data from Firbas (1949), Sebald, Seybold & Philippi (1990a, 1990b, 1992, 1996), Lang (1994) and Burga & Perret (1998) (Appendix 2). Three problems arise. First, the time estimates are only approximate. Secondly, some trees produce very little pollen since they are pollinated by insects (e.g. *Rhamnus*, rosaceous trees). For these genera the probability of recording some fossil pollen is small. Thirdly, the genera of the rosaceous trees can not be distinguished by the morphology of their pollen (G. Lang, personal communication). Nevertheless, the length of time of occurrence since the last glaciation (further called postglacial occurrence) compiled for Germany showed good correlation with the data compiled for Britain (Birks 1980; $n = 20$, $r^2 = 0{\cdot}72$, $P < 0{\cdot}001$).

TAXONOMIC ISOLATION

Most researchers use the number of congeneric species as a measure of taxonomic isolation (e.g. Lawton & Price 1979). Kennedy & Southwood (1984) used the number of co-occurring species within the order (see also Neuvonen & Niemelä 1981). For statistical reasons we decided to use the number of congeneric species as the number of species within the order will have the same value for several tree genera which violates the assumption of independent data needed for statistical tests.

TREE PHYLOGENY

Species or genera are not independent from each other but are linked by their evolutionary history (Felsenstein 1985; Harvey & Pagel 1991). Thus, two analyses were performed: first, a naive analysis using genera as independent data points (cross-genera analysis) and secondly, a phylogenetic controlled analysis (Harvey & Pagel 1991) with phylogenetic independent contrasts of traits calculated across a hypothesized phylogeny (called cladogram or sometimes tree; for definitions see Kitching *et al.* 1998).

To estimate a phylogeny for the tree genera, DNA sequences of the *rbc*L gene (ribulosebisphosphate-carboxylase, large subunit) were extracted from GenBank (GenBank accessions: X58391, L1318, X56618, L01889, X56621, X56619, U06799, L13340, AJ235804, L01928, L12573, X63663, AJ001766, X63660, X63665, AF133677, L01947, M58391, L13189, AB012793, U06827, AJ235811, AF022127, U00441). It was possible

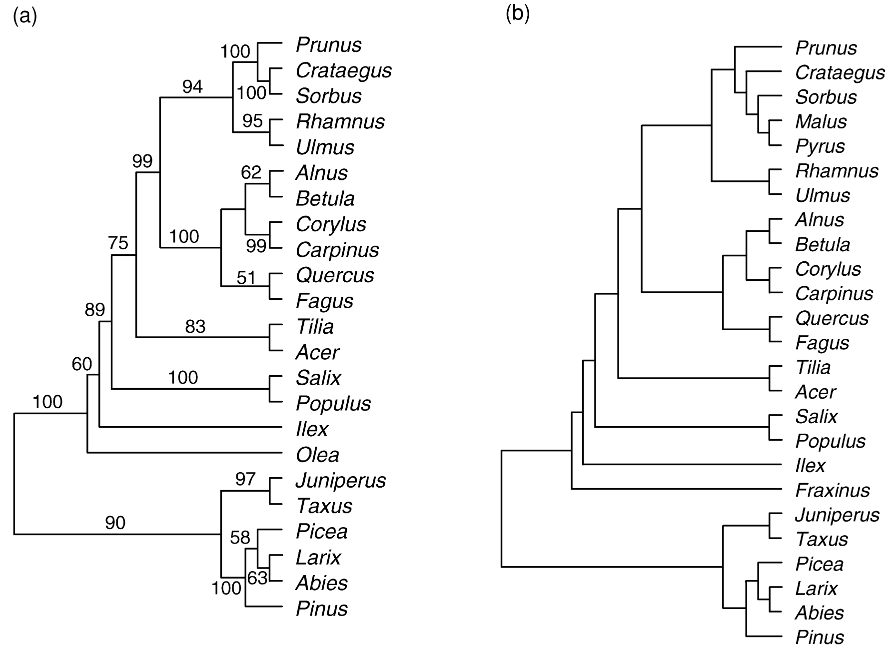

Fig. 1. Hypothesized phylogeny of tree genera native to Germany. (a) Majority rule consensus tree obtained by parsimony analysis of nucleotide sequences of the *rbc*L-gene rooted by *Ginkgo biloba*. Numbers indicate bootstrap support based on 100 replicates. (b) Final phylogeny used for calculating phylogenetically independent contrasts. This tree includes a phylogenetic hypothesis of the relationship among Maloidea proposed by Campbell *et al*. (1995).

to retrieve sequences for examples of species from most of the tree genera occurring in Germany. Exceptions were *Fraxinus*, *Malus* and *Pyrus*. Since *Fraxinus* was the only Oleaceae in the data set, the sequence from *Olea europaea* L. was used as a substitute. Note that the molecular data include species from all parts of the world. Thus, it is assumed that the genera are well defined. *Ginkgo biloba* L. was used to root the phylogeny. Sequences (1428 positions) were aligned by MultAlin 4·0 (Anonymous 1992) with the default option of gap penalty. Phylogenetic relationships were inferred using parsimony as implemented in PHYLIP 3·57c (Felsenstein 1993). DNAPARS resulted in four equally parsimonious trees of 907 steps. To find further support for relationships SEQUBOOT was used to produce 100 bootstrap replicates. Across these bootstrap replicates, DNAPARS found 281 most parsimonious trees. Subsequently, a majority rule consensus tree was computed with the program CONSENSE (Fig. 1a). To complete the phylogeny, information for the relationships among Maloideae given in Campbell *et al*. (1995, their Fig. 7) was used. The final hypothesized phylogeny (Fig. 1b) used for calculating phylogenetic independent contrasts is similar to the phylogeny used by Kelly & Southwood (1999).

The fully resolved phylogeny allowed calculation of phylogenetic independent contrasts according to the method developed by Felsenstein (1985). As branch lengths were not available, all branch lengths were set to be equal (Pagel 1992). Contrasts were calculated using CAIC (Purvis & Rambaut 1995). To analyse contrasts, least-squares regression with an intercept of zero was used (Garland, Harvey & Ives 1992; Pagel 1992).

GENERAL STATISTICAL ANALYSES

Prior to statistical analyses variables were either $\log_{10}$- or arcsine square root-transformed to reduce skewness and to attain equal variance (see Appendix 2). For all statistical tests significance was assumed when the error probability was below 5% (two-tailed). Error probabilities between 5 and 10% are marginally significant.

To compare the patterns of species richness and faunal composition, species richness in Britain was plotted against species richness in Germany. This was performed across tree genera using the species richness of all phytophages as well as the richness of single groups (Fig. 2; Appendix 1). In such a plot each symbol indicates the species richness of the total fauna or certain groups on a certain tree genus. Furthermore, for the total fauna or single tree genera we plotted the richness of each group of phytophages in Germany against the richness of this group in Britain. Thereby each symbol represents one of the phytophagous groups listed in Appendix 1. If the composition of the fauna of phytophages is similar in Britain and Germany, one expects high correlations in the latter type of plot. If richness values are $\log_{10}$-transformed, a slope of one indicates similarity in the composition of the faunas (Frenzel & Brandl 2000). Slopes were estimated by the reduced major axis approach (Rayner 1985) as the estimates of species richness in Britain and Germany have a substantial error (McArdle 1988).

A correlation matrix was computed to show relationships among independent variables (Table 1). Further, multiple regression analyses were carried out using ordinary least squares with a backward elimination of

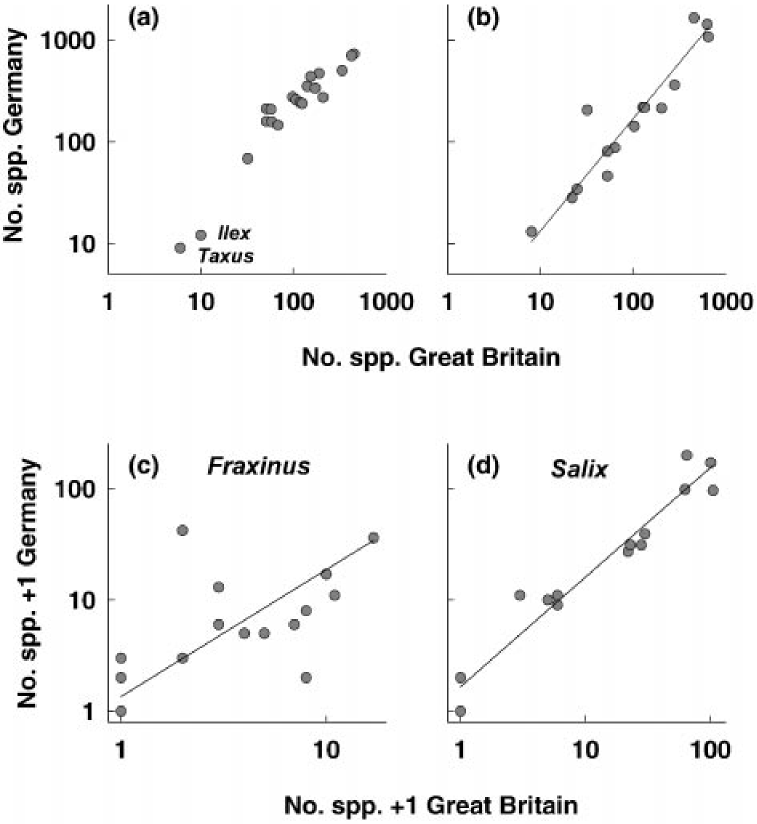

Fig. 2. (a) Cross-genera relationship between the species richness of phytophagous insects and mites on tree genera which are native to Britain and Germany ($n = 20$, tree genera $r^2 = 0{\cdot}92$, $P < 0{\cdot}001$). (b) Cross-taxa relationship between number of phytophage records within taxonomic groups on tree genera which are native to Britain and Germany ($n = 15$ taxonomic groups, $b_{RMA} = 1{\cdot}10$, 95% confidence limits 0·88–1·37, $r^2 = 0{\cdot}88$, $P < 0{\cdot}001$). (c, d) Cross-taxa relationship between number of phytophage records within taxonomic groups on *Fraxinus* and *Salix* (for statistics see text). Note that all axes are $\log_{10}$-transformed and regression lines are reduced major axis regressions.

Table 1. Correlations among independent variables: (a) cross-genera, (b) phylogenetic independent contrasts. For illustrative reasons individual significant correlation coefficients ($P < 0{\cdot}05$) are indicated in bold. Both matrices are strongly correlated ($r = 0{\cdot}95$)

	Pollen abundance	Tree height	Postglacial occurrence	Congeneric species
(a)				
Present abundance	**0·61**	0·18	0·25	**0·51**
Pollen abundance		**0·48**	0·10	0·31
Tree height			−0·03	0·13
Postglacial occurrence				**0·66**
(b)				
Present abundance	**0·55**	0·26	0·37	**0·53**
Pollen abundance		**0·59**	0·19	**0·47**
Tree height			0·13	0·20
Postglacial occurrence				**0·58**

variables (Crawley 1993). A significance level of 0·1 for the elimination of independent variables was chosen.

Results

COMPARISONS OF FAUNAS ON TREES: GERMANY VS. BRITAIN

In total the compiled list accumulated 6632 host records for 3016 insect and mite species (see Appendix 1). Species richness among native trees in Germany showed considerable variation. Most insects and mites were recorded on *Salix* (728 species of phytophages) and *Quercus* (699), whereas only few species were recorded on *Ilex* (12) and *Taxus* (nine). Most of the phytophages belong to the Lepidoptera (35% of all species) and Coleoptera (23%). For all 20 tree genera native to Britain and Germany the fauna was more species-rich in Germany than in Britain (sign-test: $P < 0{\cdot}001$).

Table 2. Coefficients of determination (r^2) of species richness ($\log_{10}$-transformed) and proportions of specialists (arcsine square root transformed) occurring on tree genera native to Germany vs. various independent variables (error probabilities: ns = $P > 0{\cdot}05$, *$P < 0{\cdot}05$, **$P < 0{\cdot}01$, ***$P < 0{\cdot}001$). The left columns show the results of the cross-genera analyses (r^2_{cross}, $n = 25$, pollen abundance $n = 20$), the right columns the analysis of phylogenetic independent contrasts (r^2_{con}, $n = 24$, pollen abundance $n = 19$). Significant coefficients of determination ($P < 0{\cdot}05$) are indicated in bold. Regressions using contrasts were calculated with an intercept of zero. Note that all independent variables were $\log_{10}$-transformed

	Dependent variables Log_{10} species richness		Arcsine (% specialists)	
Independent variables	r^2_{cross}	r^2_{con}	r^2_{cross}	r^2_{con}
Present abundance	**0·65*****	**0·59*****	0·02NS	0·13NS
Pollen abundance	**0·59*****	**0·63*****	0·04NS	0·02NS
Tree height	**0·21***	**0·29****	0·01NS	0·01NS
Postglacial occurrence	0·02NS	0·09NS	**0·38****	**0·37****
Congeneric species	**0·22***	**0·30****	**0·22***	**0·53*****
Species richness	–	–	0·03NS	0·09NS

The proportions of specialists showed also considerable variation. Proportions of specialists were high on *Juniperus* (66%) and *Pinus* (47%), whereas the phytophage faunas of *Carpinus* (8%) and *Malus* (11%) were less specialized.

Species richness was closely correlated across tree genera native to Britain and Germany (Fig. 2a). The genera *Taxus* and *Ilex* have impoverished phytophage faunas and thus dominate the correlation. Nevertheless, the relationship remained highly significant ($n = 18$, $r^2 = 0{\cdot}86$, $P < 0{\cdot}001$), even without the data from *Taxus* and *Ilex*. When correlating the richness for individual phytophage groups, significant positive relationships again appeared, except for the Coccoidea. The significant coefficient of determinations (r^2; $P < 0{\cdot}05$) ranged between 0·33 (Thysanoptera) and 0·91 (Microlepidoptera).

In the analyses of species richness across the phytophage groups, a high correlation also appeared (Fig. 2b). Furthermore, the confidence limits of the reduced major axis slope of the regression line includes one. When the species richness of groups in Germany and Britain were plotted against each other for each tree genus, significant positive relationships were again found in all cases ($P < 0{\cdot}05$). The coefficients of determination ranged between 0·29 (*Fraxinus*, Fig. 2c) and 0·93 (*Salix*, Fig. 2d), the reduced major axis slopes between 0·98 (*Salix*) and 1·52 (*Acer*). In most cases the slopes were not significantly different from one (except *Ulmus*).

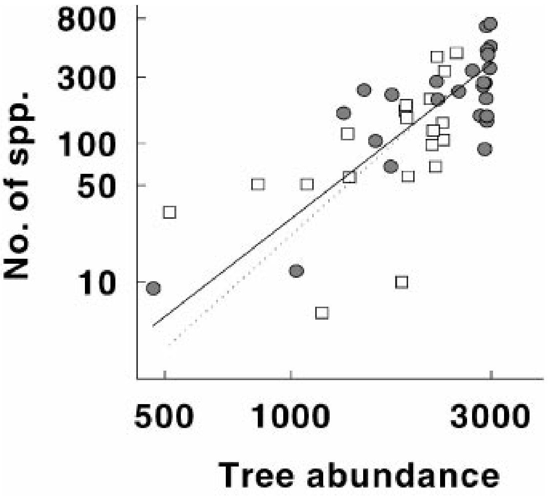

Fig. 3. Species–area relationship for the number of phytophagous insect and mite species on native British trees ($n = 20$, quadrates, dotted regression line) and on native German trees ($n = 25$, circles, solid regression line). Present tree abundance was measured as the number of 10 × 10 grids occupied in Britain and the number of 11 × 11-km grids occupied in Germany. Britain: $n = 20$, $r^2 = 0{\cdot}30$, $P = 0{\cdot}011$, $b_{RMA} = 2{\cdot}72$, 95% confidence limits 1·02–7·26; Germany: $n = 25$, $r^2 = 0{\cdot}65$, $P < 0{\cdot}001$, $b_{RMA} = 2{\cdot}34$, 95% confidence limits 1·70–3·25. Axes are $\log_{10}$-transformed. Note that regression lines are reduced major axis regressions.

SPECIES RICHNESS OF PHYTOPHAGES ON TREE GENERA IN GERMANY

The strongest relationship was found between species richness and present tree abundance (Table 2, left columns). The species–area relationship did not differ significantly from the model obtained in Britain (Fig. 3; slopes are not significantly different: t-test: $t = 1{\cdot}55$, $P > 0{\cdot}05$). However, as shown in Table 3, there were also other variables with significant correlations to species richness: the pollen abundance, the number of congeneric tree species and tree height. Controlling for phylogenetic relatedness the results did not change. Moreover, values of r^2 from cross-genera comparisons and from independent contrasts were highly correlated ($n = 5$, $r = 0{\cdot}99$, $P = 0{\cdot}002$).

Using multiple regression analysis, present abundance was the most important variable influencing species richness, as judged by the standardized regression coefficient (Table 3). Other significant variables or marginally significant variables were tree height and pollen abundance. In total all variables explain 88% of the total variance, which is a little higher compared to Kennedy & Southwood (1984). Additionally, in the analysis of phylogenetic contrasts the postglacial occurrence of trees entered into the regression equation with marginal significance. Judged by the standardized

Table 3. Summary table of four stepwise multiple regression models (backward elimination) to predict species richness and the proportions of specialists on tree genera native to Germany. r^2 of the models, standardized regression coefficients (beta) and error probabilities are given. Significant betas ($P < 0·05$) are indicated in bold. Prior to the analyses species richness was $\log_{10}$-transformed and the proportions of specialists were arcsine square root transformed. Regressions on contrasts were calculated with an intercept of zero. Note that all independent variables were $\log_{10}$-transformed

	Independent variables		beta	*P*
Species richness				
Cross-genera ($n = 20$)	Present abundance		**0·65**	**< 0·001**
	Pollen abundance		0·22	0·063
	Tree height		**0·28**	**0·011**
r^2		**0·88**		**< 0·001**
Phylogenetic contrasts ($n = 19$)	Present abundance		**0·51**	**0·010**
	Tree height		**0·27**	**0·007**
	Postglacial occurrence		0·18	0·083
	Pollen abundance		**0·33**	**0·015**
r^2		**0·90**		**< 0·001**
Proportion of specialists				
Cross-genera ($n = 20$)	Present abundance		**−0·51**	**0·013**
	Congeneric species		0·45	0·061
	Postglacial occurrence		**0·44**	**0·046**
r^2		**0·59**		**0·001**
Phylogenetic contrasts ($n = 19$)	Congeneric species		**0·59**	**0·004**
	Postglacial occurrence		0·33	0·075
r^2		**0·63**		**< 0·001**

regression coefficients, the importance of the other independent variables did not change.

PROPORTIONS OF SPECIALIZED PHYTOPHAGES ON TREE GENERA IN GERMANY

Postglacial occurrence and the number of congeneric species were positively related to the proportion of specialists (Table 2, right columns). These results did not change after controlling for the phylogenetic relatedness among tree genera. As in the analyses of species richness, values of r^2 from cross-genera comparisons and from independent contrasts were highly correlated ($n = 6$, $r = 0·81$, $P = 0·05$).

In the regression model with tree genera as independent data points three independent variables remained in the regression (Table 3): present abundance of trees, postglacial occurrence and the number of congeneric species. Note that the relationship between proportion of specialists and present abundance is negative. That is, tree genera which are abundant have a lower proportion of specialized phytophagous species in their fauna than rare trees. However, only the number of congeneric species and postglacial occurrence remained significant or marginally significant in a phylogenetically controlled analysis.

Discussion

The comparisons between Britain and Germany revealed that the patterns of species richness as well as the composition of faunas among and within tree genera are approximately similar in Britain and Germany (Southwood 1961). The only non-significant relationship within the Coccoidea may be explained by the fact that in both countries this group harbours a large number of introduced species (Kostarab & Kozár 1988). The major implication of these comparisons is that the fauna of phytophages in Britain is not affected by the special island situation. Consequently, the biogeographical patterns derived from the British fauna are also valid for continental situations.

SPECIES–AREA RELATIONSHIP

As in many other studies, the species–area relationship accounted for a substantial amount of variance in species richness across tree genera in Germany. All studies which measured abundance of trees considered only parts of the distributional ranges of tree species or genera, and the present paper is no exception. Abundances were estimated for areas selected mainly on the basis of political boundaries, but political boundaries are not the limits an insect would recognize (Kuris *et al.* 1980). Nevertheless the species–area curve derived for Britain predicts species richness of tree genera in Germany and *vice versa*, a clear indication how robust the species–area relationship is. However, pollen abundance also explained an additional part of the variance in species richness. Note that pollen abundance was derived from samples across Europe and thus covers a larger spatial scale compared to present abundance.

The pollen abundance covers not only a broader spatial scale than present abundance, but also includes an historical perspective. Fossil abundance based on the number of Quartenary remains was first used as a substitute of present tree abundance by Southwood (1961).

He found a strong positive relationship, but he did not use multivariate approaches. Thus we re-analysed the data of Kennedy & Southwood (1984; only native species) using the data of Huntley (1990). A strong relationship appeared (cross-genera: $n = 16$, $r^2 = 0{\cdot}63$, $P < 0{\cdot}001$; phylogenetic independent contrasts: $n = 15$, $r^2 = 0{\cdot}70$, $P < 0{\cdot}001$). Moreover, in a multiple regression analysis both present abundance in England and pollen abundance entered significantly into the model. Pollen abundance was much more important than present abundance, as judged by the standardized regression coefficients (cross-genera: $n = 16$, pollen abundance: beta = 0·68, $P < 0{\cdot}001$; present abundance: beta = 0·31, $P = 0{\cdot}077$; phylogenetic independent contrasts: $n = 15$, pollen abundance: beta = 0·58, $P < 0{\cdot}001$; present abundance: beta = 0·22, $P = 0{\cdot}325$).

The major drawback of the pollen abundance is that this measure mixes spatial and temporal components. Thus at present it is not possible to decide whether the additional explanatory power of the pollen abundance is due to the temporal or spatial component. The use of pollen records as a measurement of tree abundance through time was criticized by Birks (1980), on the grounds that each tree genus produces very different amounts of pollen and fossil pollen preservation depends on morphology and the sediments in which pollen were located. However, the pollen data used by Southwood (1961), as well as those from Huntley (1990) which were used in the present study, are based on presence/absence data.

Explicit tests for these mechanisms which generate the species–area curve are beyond the possibilities of the present study. One may only suggest that the passive sampling is probably of minor importance. The passive sampling hypothesis predicts that there is no substantial species turnover among trees (Gotelli & Graves 1996, p. 210). The large number of phytophages restricted to only one tree genus suggests that impoverished faunas are not nested subsets of rich faunas.

After controlling for the species–area relationship, Neuvonen & Niemelä (1981) as well as Kennedy & Southwood (1984) found a significant contribution of tree height on species richness, although it does not contribute greatly to the explained variance. Also in the present study tree height explained a significant part of the variance in species richness, even after controlling for phylogenetic relatedness. Thus, this relationship seems to be robust across areas and methods. Two main explanations have been suggested: first, the correlation results from a common species–area relationship. Secondly, architectural complexity increases with tree size and large trees provide more niches (Lawton & Schröder 1977; Lawton 1978; Strong & Levin 1979; Kennedy & Southwood 1984; Strong *et al.* 1984). Neuvonen & Niemelä (1981) doubt the architectural hypothesis since they included only trees and shrubs into their analysis, which in their opinion show little variations in size and therefore architectural complexity. However, there are great differences in size between shrubs and trees. For example, *Picea abies*, the tallest species in the study by Neuvonen & Niemelä (1981), reaches 25 m whereas the smallest, *Rubus ceasius* L., reaches only 0·25 m (see also Appendix 2). Nevertheless, one may argue that height *per se* is not a suitable measure of architectural complexity. Various other morphological features, such as branching structure, are more convincing surrogates for architectural complexity, although it may be difficult to design a measure of complexity which allows comparison of the architecture across tree genera. Nevertheless, such attempts are needed in future studies.

GEOLOGICAL TIME HYPOTHESIS

When Rosenzweig (1995) reanalysed the data of Kennedy & Southwood (1984) he failed to find support for the *geological time* hypothesis. In his analysis he excluded trees introduced by man (see also Birks 1980). Similarly, in the analysis of species richness of phytophages on tree genera in Germany the time a species was present since the last glaciation (postglacial occurrence) did not remain in the multiple regression model. However, note that for phylogenetic contrasts postglacial occurrence had some marginal significance. In general, the available analyses do not provide convincing support for the *geological time* hypothesis. The results so far are not robust across areas and methods.

As well as technical problems with the measure used to estimate postglacial history, two arguments may cause doubts about a simple correlation between species richness and postglacial occurrence. First, all tree genera have evolved before the Pleistocene. Thus, the time for the evolution of a phytophage–host association may be independent of re-colonization patterns of trees after the Pleistocene and consequently the time measure used in the analyses operates on the wrong scale. Secondly, the *geological time* hypothesis assumes that trees bring few phytophages from their Pleistocene refuges. Phytophages certainly followed their hosts (see Eber & Brandl 1994).

TAXONOMIC ISOLATION HYPOTHESIS

Despite the different methods applied to measure taxonomic isolation, most studies found a significant contribution of taxonomic isolation on host phytophagous species richness (Lawton & Schröder 1977; Connor, Simberloff & Oppler 1980; Neuvonen & Niemelä 1981; Kennedy & Southwood 1984; Leather 1990). In the present study, taxonomic isolation showed only in the univariate analysis a significant positive relationship with species richness of phytophages. Thus, the importance of taxonomic isolation affecting species richness of phytophages remains dubious.

PLANT PREDICTABILITY–APPARENCY AND THE COEVOLUTIONARY HYPOTHESIS

The processes shaping the specialist/generalist ratio on hosts are far from clear, as results varied greatly between studies (e.g. Lawton & Schröder 1978). Neuvonen & Niemelä (1981) favoured the *plant predictability–apparency* hypothesis (Levins & MacArthur 1969) when they analysed the proportions of specialized Macrolepidoptera on Finnish deciduous trees and shrubs. They found a significant positive relationship between proportions of specialists (or negative relationship of proportions of polyphagous, respectively) and the total number of species as well as the abundance of trees as predicted by the *plant predictability–apparency* hypothesis. The data from this study failed to find such a correlation (see also Andow & Imura 1994). On the contrary, the findings of the present study provide some support for of the *coevolutionary* hypothesis: postglacial occurrence and the number of congeneric species were positively related to the proportions of specialists even when we controlled for phylogenetic relatedness. To find further support for a correlation between the proportion of specialists and postglacial occurrence, the data of Neuvonen & Niemelä (1981) on tree-feeding Macrolepidoptera were analysed. Although the authors defined specialists as species restricted to one host plant family, and we used the postglacial occurrence data from Germany, a marginally positive relationship appeared (cross-genera: $n = 14$, $r^2 = 0{\cdot}25$, $P = 0{\cdot}07$; phylogenetic independent contrasts: $n = 13$, $r^2 = 0{\cdot}17$, $P = 0{\cdot}14$; proportions of specialists were arcsine square root-transformed). Andow & Imura (1994) provided further more direct support for the *coevolutionary* hypothesis. They found that arthropod communities on invasive crops in Japan become increasingly specialized over time.

Conclusions

In sum, the results of the present study expand Kennedy & Southwood (1984) and demonstrate that the patterns reported by them also hold for Germany. Thus, the fact that Britain is an island has not biased the analyses of Southwood and coworkers. Furthermore, most of the patterns reported by Kennedy & Southwood are not affected by the phylogenetic relationships of tree genera. However, it should be noted that some patterns are not testable within a phylogenetic framework. In Europe, most of the gymnosperm trees are evergreen whereas most angiopserm trees are deciduous. Thus with European trees it is not possible to test whether 'evergreenness' has an effect on species richness of phytophages. Beyond Southwood, the present study emphasizes the role of coevolutionary processes for the composition of phytophage faunas, especially the relative number of specialized phytophages.

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Appendix 1

The number of phytophages associated with trees in Germany: Buhr (1965)[1], Vitzthum (1929)[2], Freude, Harde & Lohse (1965–85)[3], Lohse & Lucht (1989, 1992, 1994)[4], Lucht (1998)[5], Pfeffer (1994)[6], Bense (1996)[7], Dieckmann (1972, 1974, 1980, 1988)[8], Hering (1957)[9], Spencer (1990)[10], Skuhravá & Skuhravý (1997)[11], Wagner (1952, 1966, 1967, 1970/71, 1973, 1975, 1978)[12], Péricart (1983, 1984)[13], Moulet (1995)[14], Ossiannilsson (1978, 1981, 1983)[15], Nast (1972)[16], Klimaszewski (1973)[17], Börner (1952)[18], Blackmann & Eastop (1994)[19], Zahradnik (1963)[20], Mound & Halsey (1978)[21], Schmutterer (1959)[22], Kostarab & Kozár (1988)[23], Muche (1968, 1969a, 1969b, 1970, 1974, 1975, 1977)[24], Schwenke (1972, 1982)[25], Koch (1988)[26], Ebert & Rennwald (1991a, 1991b)[27], Ebert (1994a, 1994b, 1997a, 1997b, 1998)[28], Eckstein (1933)[29], Hannemann (1961, 1964, 1977, 1995, 1997)[30], Schliephake & Klimt (1979)[31]. ERI = Eriophyidae (Acarina), COL = Coleoptera, AGR = Agromyzidae (Diptera), CEC = Cecidomyiidae (Diptera), HET = Heteroptera, AUC = Auchenorrhyncha (Homoptera), PSY = Psylloidea (Homoptera), APH = Aphidoidea (Homoptera), ALE = Aleyrodoidea (Homoptera), COC = Coccoidea (Homoptrea), SYM = Symphyta (Hymenoptera), CYN = Cynipoidea (Hymenoptera), MAC = Macro-Lepidoptera, MIC = Micro-Lepidoptera, THY = Thysanoptera.

	ERI[1,2]	COL[3,4,5,6,7,8]	AGR[1,9,10]	CEC[1,11]	HET[12,13,14]	AUC[15,16]	PSY[17]	APH[18,19]	ALE[20,21]	COC[22,23]	SYM[24,25]	CYN[1,25]	MAC[26,27,28]	MIC[29,30]	THY[31]
Abies	–	73	–	3	6	3	–	9	–	11	15	–	14	31	–
Acer	8	51	–	8	6	11	1	16	4	13	10	1	44	37	–
Alnus	9	96	2	3	17	27	4	9	–	9	28	–	86	52	7
Betula	8	106	2	7	8	20	3	18	1	13	51	–	140	115	7
Carpinus	–	53	1	6	3	8	–	1	2	10	6	–	39	27	2
Corylus	4	90	1	9	13	11	1	2	1	11	11	–	63	38	4
Crataegus	4	73	1	6	2	11	2	10	1	11	16	–	67	68	1
Fagus	3	99	–	8	12	7	–	2	1	12	5	–	72	47	7
Fraxinus	4	41	1	5	10	2	4	2	1	12	7	–	35	16	5
Ilex	–	6	1	–	–	–	–	2	–	2	–	–	1	–	–
Juniperus	1	11	–	6	13	2	–	1	–	4	2	–	10	15	3
Larix	1	48	–	1	5	–	–	8	–	–	14	–	11	15	1
Malus	4	55	2	1	5	4	2	15	–	14	4	–	60	75	1
Picea	–	127	–	6	21	6	–	20	–	8	24	–	30	34	3
Pinus	1	160	–	4	26	5	–	24	–	11	31	–	24	43	6
Populus	7	139	7	12	10	19	1	26	–	10	32	–	130	71	6
Prunus	6	90	1	5	4	9	4	16	–	12	18	–	147	121	3
Pyrus	4	56	–	3	9	2	3	17	1	15	7	–	49	58	1
Quercus	4	208	–	8	39	24	1	14	1	19	22	45	168	137	9
Rhamnus	1	13	–	2	4	4	5	7	–	5	–	–	30	20	–
Salix	10	197	8	38	26	30	8	30	1	10	95	–	169	97	9
Sorbus	3	36	1	2	1	6	2	9	–	10	12	–	28	47	–
Taxus	2	1	–	1	–	–	–	–	–	3	–	–	1	1	–
Tilia	5	52	–	8	9	8	–	2	–	11	3	–	77	26	6
Ulmus	4	81	–	4	9	13	1	17	–	7	7	–	54	36	4

Appendix 2

List of untransformed dependent and independent variables: Benkert *et al.* (1996)[1], Häupler & Schönfelder (1989)[2], Huntley (1990)[3], Fitschen (1987)[4], Lang (1994)[5], Firbas (1949)[6], Burga & Perret (1998)[7], Sebald *et al.* (1990a, 1990b, 1992, 1996)[8], Rothmaler (1987)[9]. Transformation of variables as used for statistical analyses in brackets.

	Total number of phytophages ($\log_{10}$)	Number of specialists (arcsine – square root)	Present abundance[1,2] ($\log_{10}$)	Pollen abundance Europe[3] ($\log_{10}$)	Congeneric species in Germany[4] ($\log_{10}$)	Postglacial occurrence[5,6,7,8] ($\log_{10}$)	Tree height (m)[9] ($\log_{10}$)
Abies	165	31	1335	795	1	5 000	50
Acer	210	77	2917	292	5	8 000	25
Alnus	349	82	2976	3419	3	8 000	25
Betula	499	133	2987	4103	5	14 000	25
Carpinus	158	13	2825	788	1	4 000	20
Corylus	259	33	2871	2904	1	9 500	6
Crataegus	273	43	2901	–	2	5 500	10
Fagus	275	44	2878	1026	1	6 000	40
Fraxinus	145	43	2928	900	2	8 000	40
Ilex	12	3	1030	49	1	6 500	6
Juniperus	68	45	1729	784	3	14 000	12
Larix	104	27	1590	106	1	11 000	35
Malus	242	29	1493	–	1	6 000	10
Picea	279	75	2222	2048	1	5 200	50
Pinus	335	157	2708	4122	3	14 000	40
Populus	470	151	2936	208	3	12 000	30
Prunus	436	94	2945	–	5	12 000	25
Pyrus	225	29	1738	–	1	4 500	20
Quercus	699	252	2921	2702	3	10 000	40
Rhamnus	91	29	2896	67	3	12 000	4
Salix	728	312	2983	2087	22	12 000	30
Sorbus	157	31	2928	–	4	12 000	15
Taxus	9	4	470	51	1	8 000	15
Tilia	207	28	2238	1535	2	9 000	30
Ulmus	237	61	2514	2236	3	10 000	40