
Species richness patterns in symbiotic gut fungi (Trichomycetes)

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The most common pattern in biology indicates that diversity (species number) increases with area and can be represented as species-area curves following a power model equation. Biogeographers and ecologists have observed this relationship both among larger areas of single biotas and among islands of one archipelago. Species-area relationships have not been well established for fungal communities. The few studies that exist show heterogeneous results. An attempt to test the species-area relationship in Trichomycetes was made for data collected between 1960-2000. During this period 46 species from different USA counties in Arkansas, Kansas, Missouri and Oklahoma were identified. Species numbers were plotted against county area as sample plots. The data strongly fit to a power regression curve ($r^2 = 0.92$). This suggests a strong biogeographic signal for the species-area relationship of these symbiotic fungi.

Key words: aquatic insects, biogeography, commensalism, Zygomycota.

Introduction

Spatial diversity patterns have long interested ecologists. The most common pattern indicates that diversity (species number) increases with area. The number of species inhabiting an ecosystem also increases along a gradient of increasing size. This pattern can be represented as species-area curves following the power model equation:

$$S = cA^z,$$

where S is the species number,

A the sampled area,

c a fitted constant and

z another constant that represents the slope when S and A are plotted in logarithmic scale.

A number of different hypotheses have been proposed to account for species-area relationships. One addresses habitat heterogeneity, which reflects the increase in niches available for new species as area increases (Lomolino, 2000). Another, the theory of island biogeography, posits that the number of

species inhabiting an island tends towards an equilibrium, which is the result of a balance between the immigration and extinction rates within the island (McArthur and Wilson, 1967). It has also been proposed that the correlation of species numbers with increased area might be an artefact due to the greater chance of discovering more rare species (Huston, 1994). In any case, the species-area pattern has its own value as a predictive tool in ecology.

The species-area pattern appears to be very common for different groups of organisms, but in fungal ecology it has been poorly studied. Species-area relationships have been investigated in a few fungal groups: aquatic hyphomycetes (Sanders and Anderson, 1979), fungal communities of the phylloplane (Andrews *et al.*, 1987; Kinkel *et al.*, 1987), soil fungi (Christensen, 1981; Wildman, 1987; 1992), wood rotting fungi (Chapela and Boddy, 1988) and ectomycorrhizal fungi (Bills *et al.*, 1986; Newton and Haigh, 1998), with heterogeneous results.

The relationship between species number and area for macro- or microfungi is unclear; in aquatic hyphomycetes and soil-borne fungi this pattern has been well established (Sanders and Anderson, 1979; Wildman, 1987, 1992). On the other hand, macrofungi associated with red spruce and hardwood forests in North America presented no indication of a species-area relationship (Bills *et al.*, 1986). In the UK, however, Newton and Height (1998) concluded the exact opposite for the same fungi. The data obtained with microfungi inhabiting the phylloplane did not support a species-area relationship for that community (Andrews *et al.*, 1987; Kinkel *et al.*, 1987; Wilson *et al.*, 1997).

Trichomycetes is a class of symbiotic fungi associated with arthropods. Their biology is unique among fungi because they have adapted to a constrained environment, attached to the lining of the arthropod gut. Trichomycetes are associated with various groups of Insecta, Crustacea and Diplopoda. Traditionally, the class has comprised four orders, *Amoebidiales*, *Asellariales*, *Eccrinales* and *Harpellales*. The *Amoebidiales* proved to be a group of protists that coexist with the gut fungi (Benny and O'Donnell, 2000). For the purpose of this study, *Amoebidiales* is included in the class since they share the same ecological niche with the fungi. Though the ecology of individual species might be well known in some cases, it is poorly understood for the class as a whole. The intent of this investigation is to test the species-area relationship in this unique group of microfungi.

Materials and Methods

The data were collected from different sources: literature, field notes and previous surveys carried out between 1960-2000 that were not conducted for

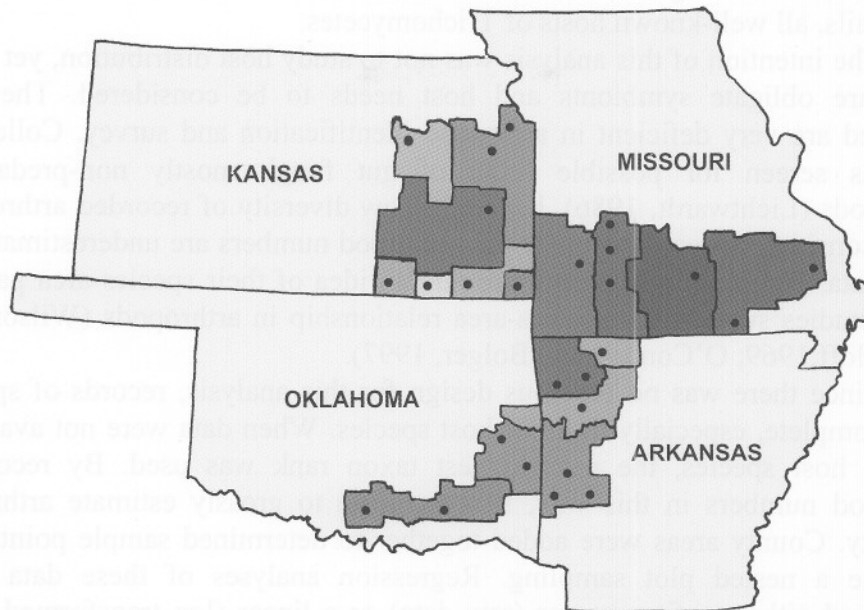


Fig. 1. Sampled area in four different states of the Midwest USA. Each grade of shade represents the sample point area (16 total). Black dots are the actual counties where collections were made.

the purpose of this analysis. During this period species of Trichomycetes and their hosts from different counties in the USA, Arkansas, Kansas, Missouri and Oklahoma were identified (Fig. 1). The published literature includes monographic work by Lichtwardt (1986) and its revised edition on-line by Lichtwardt *et al.* (2001) (www.nhm.ukans.edu/~fungi), and taxonomic papers with original descriptions of species and their hosts (Lichtwardt and Chen, 1964; Lichtwardt, 1972; Peterson *et al.*, 1981; Williams, 1982; Williams *et al.*, 1982; Peterson and Lichtwardt, 1983; Lichtwardt and Moss, 1984; Lichtwardt *et al.*, 1991a,b; 1999; Lichtwardt and Grigg, 1998) as well as biogeographic and ecological articles (Lichtwardt *et al.*, 1993, 1997; Slaymaker *et al.*, 1998). Field notes contain data for sites and localities, and species already described, but not recorded elsewhere in the literature.

Each data source presents limitations for consideration here. Sampling is incomplete and biased towards each project for which the data was collected. There is a strong bias towards aquatic insect associates in the last three decades since this was the main focus of the research carried out in Trichomycetes during that period. Reports on members of the *Amoebidiales*, *Asellariales* and *Eccrinales* are few. Occasionally surveys were limited to freshwater streams

and ponds, excluding terrestrial inhabitants such as isopods, millipedes and springtails, all well-known hosts of Trichomycetes.

The intention of this analysis was not to study host distribution, yet these fungi are obligate symbionts and host needs to be considered. The data collected are very deficient in arthropod identification and survey. Collecting methods screen for possible hosts of gut fungi, mostly non-predacious arthropods (Lichtwardt, 1986), hence the low diversity of recorded arthropods in the considered area. Obviously the arthropod numbers are underestimated in these data, but nevertheless they provide an idea of their species-area pattern. Many studies support the species-area relationship in arthropods (Wilson and Simberloff, 1969; O'Connell and Bolger, 1997).

Since there was no previous design for this analysis, records of species are incomplete, especially those of host species. When data were not available for the host species, the next highest taxon rank was used. By recording arthropod numbers in this way, it is possible to grossly estimate arthropod diversity. County areas were added together to determined sample points that simulate a nested plot sampling. Regression analyses of these data were performed either to fit a power (raw data) or a linear (log transformed data) function to test the species-area relationship for both arthropods and Trichomycetes.

Results

Forty-six species of Trichomycetes were identified from 26 counties (Table 1). Some records indicated new species yet to be described that were recorded as sp. # 1, 2. Only one sp. # was considered per genus, except for *Smittium* (the largest genus). This genus accounted for 35% of the variation among the fungi surveyed. There were 13 previously described species of *Smittium* recorded from midges (*Chironomidae*) and 3 unidentified ones in the same host family. The next most diverse genus was *Stachylina* with 4 species present in this survey also from chironomid hosts. The rest of the variation is distributed over several species from 19 genera of Trichomycetes.

Host identification was difficult since most are aquatic insect larvae, which have few species-specific characters. Only 111 different arthropod taxa were recorded; certainly the diversity of insects and other arthropods is far more complex than these records indicate. The surveyed arthropods correspond mostly to the *Chironomidae* (midges) (45%) and *Simuliidae* (blackflies) (19%) families in the order Diptera and in members of the order Plecoptera (stoneflies) (17%), all represented by aquatic larvae. Few members of Diplopoda (millipedes), Collembola (springtails), Coleoptera (beetles) (all less

Table 1. Trichomycetes and their hosts recorded in this study. Orders of the hosts in parenthesis.

Taxa	Hosts
<i>Arundinula orconectis</i>	<i>Orconectes nais</i> (Decapoda, Crustacea)
<i>Asellaria armadillidii</i>	<i>Armadillidium vulgare</i> (Isopoda, Crustacea)
<i>Asellaria unguiformis</i>	<i>Lirceus hoppinae</i> (Isopoda, Crustacea)
<i>Capniomyces stellatus</i>	<i>Allocapnia</i> spp. (Plecoptera)
<i>Ejectosporus magnus</i>	<i>Allocapnia</i> spp. <i>Zealeuctra</i> sp. (Plecoptera)
<i>Enterobryus elegans</i>	<i>Narceus americanus</i> (Diplopoda)
<i>Enterobryus euryhuri</i>	<i>Euryurus</i> sp. (Diplopoda)
<i>Genistelloides helicoides</i>	<i>Amphinemura</i> sp. (Plecoptera)
<i>Genistelloides hibernus</i>	<i>Allocapnia</i> spp. <i>Mesocapnia</i> sp. (Plecoptera)
<i>Genistellospora homothallica</i>	<i>Simulium</i> spp. (Diptera)
<i>Harpella melusinae</i>	<i>Simulium</i> spp. (Diptera)
<i>Lancisporomyces</i> sp.	<i>Amphinemura</i> sp. (Plecoptera)
<i>Legeriomyces ramosus</i>	<i>Baetis</i> spp. <i>Ephemerella</i> sp. (Ephemeroptera)
<i>Leidyomyces attenuatus</i>	<i>Passalidae</i> (Coleoptera)
<i>Orchesellaria pelta</i>	<i>Hydroisotoma schaefferi</i> (Collembola)
<i>Orphella hiemalis</i>	<i>Isoperla</i> sp. (Plecoptera)
<i>Paramoebidium corpulentum</i>	<i>Allocapnia</i> sp. (Plecoptera)
<i>Paramoebidium curvum</i>	<i>Simulium</i> spp. (Diptera)
<i>Paramoebidium</i> sp.	<i>Allocapnia</i> sp. (Plecoptera)
<i>Parataeniella armadillidii</i>	<i>Armadillidium vulgare</i> <i>A. nasatum</i> (Isopoda, Crustacea)
<i>Pennella angustispora</i>	<i>Simulium</i> spp. (Diptera)
<i>Pennella</i> sp.	<i>Simulium</i> spp. (Diptera)
<i>Simuliomyces microsporus</i>	<i>Simulium</i> spp. (Diptera)
<i>Simuliomyces spica</i>	<i>Allocapnia</i> sp. (Plecoptera)
<i>Smittium acutum</i>	<i>Chironomidae</i> (Diptera)
<i>Smittium alpinum</i>	<i>Diamesa</i> spp. (Diptera)
<i>Smittium caudatum</i>	<i>Orthocladus</i> sp. <i>Cricotopus</i> sp. <i>Hydrobaenus</i> sp. (Diptera)
<i>Smittium commune</i>	<i>Orthocladus</i> sp. <i>Cricotopus</i> sp. <i>Microtendipes</i> sp. <i>Phaenopsectra</i> sp. (Diptera)
<i>Smittium culicis</i>	<i>Culicidae</i> <i>Chironomidae</i> <i>Simuliidae</i> (Diptera)
<i>Smittium culisetae</i>	<i>Culicidae</i> <i>Chironomidae</i> <i>Simuliidae</i> <i>Ceratopogonidae</i> (Diptera)
<i>Smittium elongatum</i>	<i>Diamesa</i> spp. <i>Cricotopus</i> sp. (Diptera)
<i>Smittium gravimetallum</i>	<i>Dicrotendipes fumidus</i> (Diptera)
<i>Smittium kansense</i>	<i>Orthocladus</i> sp. <i>Hydrobaenus</i> sp. (Diptera)
<i>Smittium longisporum</i>	<i>Cricotopus</i> sp. (Diptera)
<i>Smittium orthocladii</i>	<i>Orthocladus</i> spp. <i>Diamesa</i> sp. (Diptera)
<i>Smittium simulii</i>	<i>Chironomidae</i> <i>Simuliidae</i> <i>Culicidae</i> (Diptera)
<i>Smittium</i> sp. 1	<i>Chironomidae</i> (Diptera)
<i>Smittium</i> sp. 2	<i>Chironomidae</i> (Diptera)

Table 1. (continued).

Taxa	Hosts
<i>Smittium</i> sp. 3	Chironomidae (Diptera)
<i>Smittium stenosporum</i>	<i>Cricotopus</i> sp. (Diptera)
<i>Stachylina grandispora</i>	<i>Chironomus</i> sp. (Diptera)
<i>Stachylina pedifer?</i>	Chironomidae (Diptera)
<i>Stachylina penetralis?</i>	Chironomidae (Diptera)
<i>Stachylina</i> sp.	Chironomidae (Diptera)
<i>Trichozygospora</i> <i>chironomidarum</i>	<i>Orthocladius</i> spp. <i>Cricotopus</i> sp. <i>Diamesa valkanovi</i> (Diptera)
<i>Zygopolaris ephemeridarum</i>	<i>Baetis</i> spp. (Ephemeroptera)

than 1%) and Crustacea (isopods) (4%) were surveyed from terrestrial habitats as stated above.

When the numbers of species of Trichomycetes and of their hosts were regressed against the area sampled (all values log transformed), a positive linear relationship was registered (Fig. 2). The data were also analysed against a power regression curve of the type $S = cA^z$ (Fig. 3), with a strong fit ($r^2 = 0.91$ for both arthropod and trichomycete diversity). The estimated value of z for the Trichomycetes was 0.55 and for arthropods 0.67. The latter seemed high for arthropods, but for the fungi it is similar to previous reports in the literature (0.36-0.66). It should be acknowledged that there is still no clear biological interpretation of how these z values vary (Lomolino, 2000). Crawley and Harral (2001) found that z values are dependent not only on taxa and sampling techniques, but also on spatial scales in plants. The slope of the log-log plot is not constant and might increase at intermediate scales such as the one used in this investigation.

Discussion

The results of this study strongly indicate that the Trichomycetes follow a species-area relationship. This is also true for their hosts that represent a small subset of the arthropods that bear these fungi. The increase in the number of fungi can be explained as a direct function of arthropod species increase with area. It is clear that diversity of Trichomycetes is tightly linked to host diversity. Fungal numbers follow arthropod numbers, which in turn follow a well-established species-area pattern of diversity. This relationship might help us understand the general distribution pattern of these fungi and their diversity. The curve for Trichomycetes has a lower slope than for the arthropod hosts that reflects the difference in abundance that exists between the fungi and their hosts, the latter being more common. The number of arthropod species to be

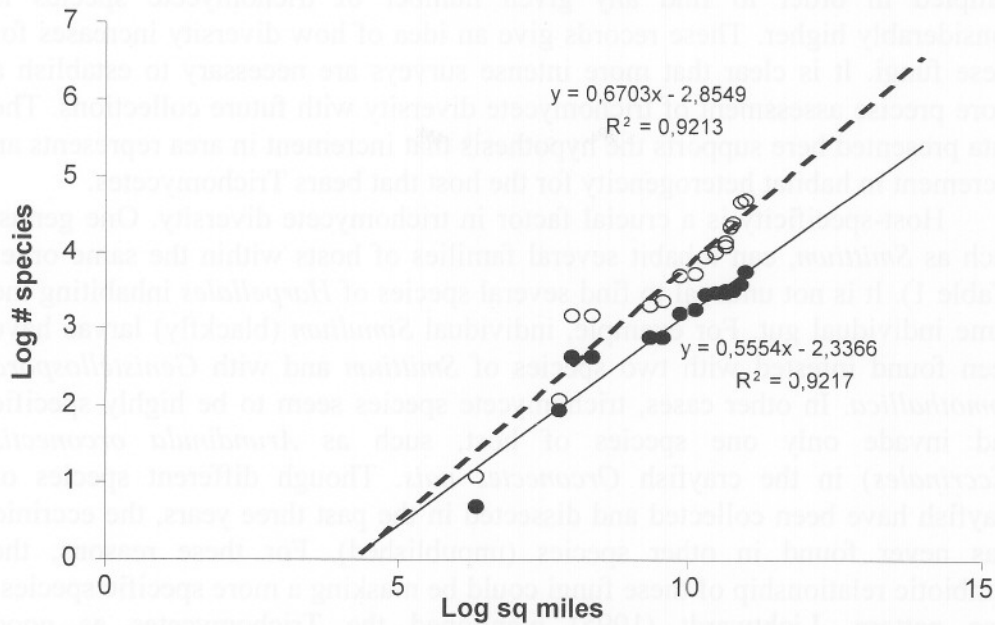


Fig. 2. Linear regression showing the species-area pattern for the Trichomyces (●) and for the arthropod hosts (○).

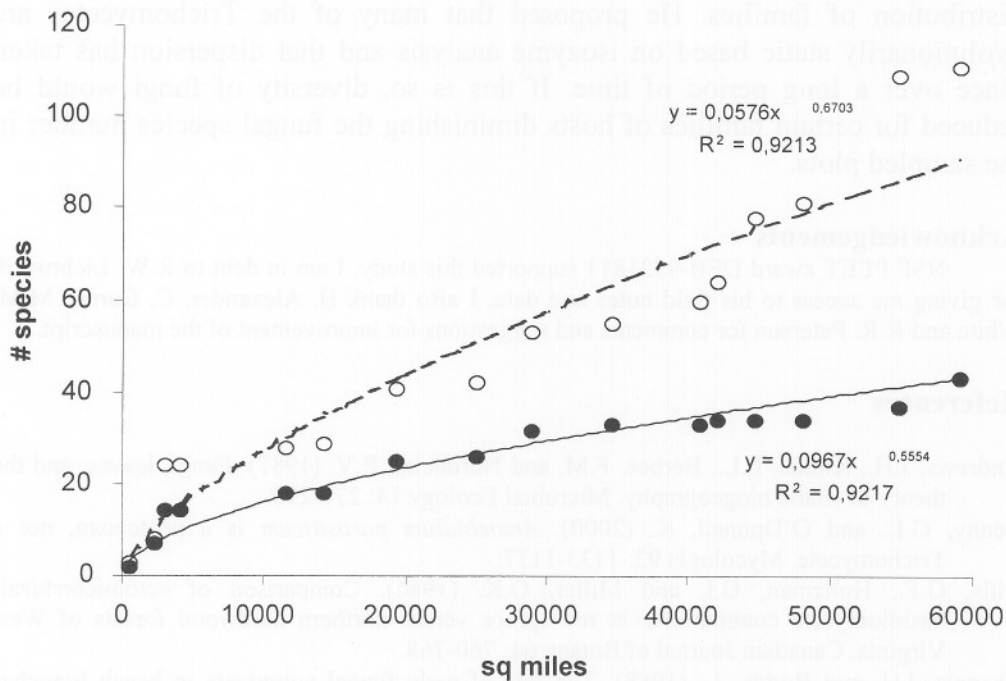


Fig. 3. Power regression showing the species-area pattern for the Trichomyces (●) and for the arthropod hosts (○).

sampled in order to find any given number of trichomycete species is considerably higher. These records give an idea of how diversity increases for these fungi. It is clear that more intense surveys are necessary to establish a more precise assessment of trichomycete diversity with future collections. The data presented here supports the hypothesis that increment in area represents an increment in habitat heterogeneity for the host that bears Trichomycetes.

Host-specificity is a crucial factor in trichomycete diversity. One genus, such as *Smittium*, can inhabit several families of hosts within the same order (Table 1). It is not unusual to find several species of *Harpellales* inhabiting the same individual gut. For example, individual *Simulium* (blackfly) larvae have been found infested with two species of *Smittium* and with *Genistellospora homothallica*. In other cases, trichomycete species seem to be highly specific and invade only one species of host, such as *Arundinula orconectis* (*Eccrinales*) in the crayfish *Orconectes nais*. Though different species of crayfish have been collected and dissected in the past three years, the eccrinid was never found in other species (unpublished). For these reasons, the symbiotic relationship of these fungi could be masking a more specific species-area pattern. Lichtwardt (1995) mentioned the Trichomycetes as good biogeographic subjects because of their symbiotic relationship, host-specificity, ancient origin, low vagility of many arthropod hosts, and the widespread distribution of families. He proposed that many of the Trichomycetes are evolutionarily static based on isozyme analysis and that dispersion has taken place over a long period of time. If this is so, diversity of fungi would be reduced for certain families of hosts diminishing the fungal species number in the sampled plots.

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