

SYMBIOTIC DRIFT AS A CONSEQUENCE OF DECLINING HOST PLANT POPULATIONS

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In this paper we present a hypothesis about the loss of organisms associated with hosts in small populations. Data for fungi specific to arcto-alpine plants are presented. We found that the number of fungal species on plants is directly proportional to the size of the host population. This conforms to MacArthur and Wilson's theory of island biogeography. Once the host population is below a critical size, some fungal species are lost. We term this process 'symbiotic drift.'

Key words: *Dryas*, *Juncus*, habitat island biogeography, fungi.

INTRODUCTION

Populations are susceptible to extinction as a result of habitat loss (Fahrig, 1997). Small populations are likely to suffer from random processes like genetic drift (Amos and Balmford, 2001) or the allee effect (Dennis, 2002). Populations of parasites may also be affected by habitat loss when the host population declines or disappears. According to MacArthur and Wilson (1963), the number of species on an oceanic island is correlated with the area of that island. In our investigation, the host populations were considered as habitat islands.

The effect of host abundance on parasites has attracted considerable attention from researchers; however, the effect on other associated organisms such as semiparasitic symbionts has not been adequately investigated. In this paper we suggest that a small host population is likely to lose its symbionts in a process we term 'symbiotic drift.'

From the perspective of symbiotic species, a declining host population should be regarded as one affected by reduction and fragmentation of its habitat, which is likely to have a negative effect on the species (Fahrig, 1997, 2003). If individuals of a host population are treated as sites available for colonization, then their reduction below a certain extinction level might cause the symbiotic population to

become extinct as predicted by Lande (1987). Similarly, Nee (1996) in his analysis of the predator-prey relationship predicted the existence of an eradication threshold – the minimum prey-carrying capacity below which the predator population will not be sustained. This suggests that the population of a symbiotic species may decline at a faster rate, even to the point of disappearance, than would be predicted based solely from the presence or absence of the host population. We propose the term 'symbiotic drift' to describe the decline and disappearance of host-specific symbiotic species due to the processes associated with declining host populations. Symbiotic drift should lead to a positive correlation between host population size and the number of symbionts, unless the declining number of the symbiotic species is counterbalanced by immigration of different symbiotic species.

MATERIALS AND METHODS

To test our hypothesis we analyzed the number of fungal symbionts in relation to the size of host plant populations in the Czech Republic, Poland, Ukraine, Romania, Russia and Greenland. Some host plants were deemed inappropriate for the investigation because a majority of their fungal symbionts were

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not host-specific (Chlebicki, 2002). Nonspecific fungi can migrate between different host species, and therefore the size of a particular host population does not affect the population level of the symbionts. We studied two host plant species: *Dryas octopetala* with more than 20 host-specific fungal species, and *Juncus trifidus* with 11 fungal species restricted to *Juncaceae* and *Cyperaceae*. The genus *Dryas* consists of four diploid species (Hultén, 1959) and several intermediate forms of various taxonomic ranks. In Europe, three-leaved rush (*Juncus trifidus* L.) consists of a widely distributed type variety and an Alpine population named *J. trifidus* var. *monanthos* (Jacq.) Bluff & Fingerhuth.

The material gathered by the authors came from the Sudetes, Šumava Mts. and Carpathians. The biggest populations of *Dryas octopetala* inhabit the Západné and Belianske Tatry Mts. Smaller populations were noted in the Malá Fatra Mts., Chočské vrchy Mts., Nízke Tatry Mts., Svidovets Mts. and Raráu Mts. Thirty specimens of the plant were collected from each big population. Very small relict populations have survived on a single rock wall in the 'Biała Woda' Nature Reserve in the Pieniny Mts. (Kornaś, 1958). Other very small populations were noted on Mt. Bába in the Nízke Tatry Mts. and the slope of Mt. Pop Ivan and Mt. Berbenieskul, both in the Chornohora Mts. Only parts of some specimens were collected for investigation of these small *Dryas* populations. In addition, the 248 collections of *Dryas octopetala* in Czech and Polish herbaria such as PRC (70), PR (82) and KRAM (95) were researched using Rostrup's method. The fungi were extracted from phanerogam herbaria and placed in paper bags.

Material of *Juncus trifidus* was collected in the Sudetes and Šumava Mts. The same method was used in collection of rushes. Only small parts of tufts were collected from the small populations of the Hrubý Jeseník Mts. and Mt. Králický Snižník (see Tab. 2). We did not research phanerogam collections of *Juncus trifidus*.

Analyses of spatial patterns in the distribution of fungi employed the Mantel randomization test using the algorithm described by Manly (1977). The relationship between population size and number of fungal species was analyzed using Spearman rank correlations. Prior to the analysis, host population size was estimated and categorized in five size classes. Our criterion for host population size estimation was the area it occupied.

RESULTS AND DISCUSSION

Among the host plants investigated, we distinguished host-specific fungi (mostly semiparasitic folliculus symbionts) that occurred only on the host

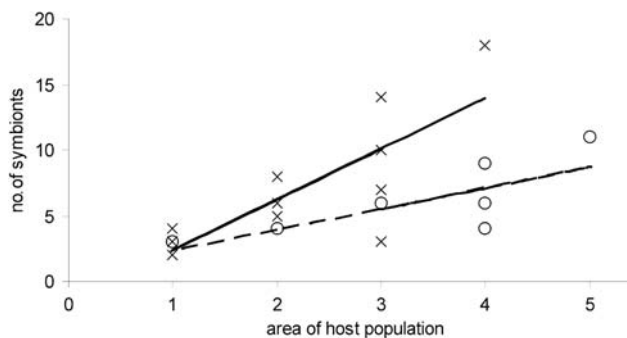


Fig. 1. Correlation between area occupied by host populations and number of host-specific fungal species. × – *Dryas octopetala*; o – *Juncus trifidus*; 1 – up to 5 m²; 2 – 25 m²; 3 – 1 ha; 4 – 1 km²; 5 – more than 1 km² for *Dryas octopetala*; 1 – up to 10 dm² (two tufts); 2 – up to 25 dm² (several tufts); 3 – up to 150 m²; 4 – up to 10 ha; 5 – more than 10 ha for *Juncus trifidus*.

plant, as well as nonspecific species known on other plants. Host-specific fungi can be used to explore phylogeographical questions such as the origin and direction of migrational host plants (Chlebicki, 2002; Chlebicki and Olejniczak, 2003; Chlebicki and Suková, 2004; Chlebicki et al., 2005). The same host plant populations were widely distributed in the Carpathians and their foothills during the last glacial period (Tralau, 1961), but now are divided into discrete populations that occur in disjunct 'islands' of various sizes (Tabs. 1, 2).

The number of fungal species on *Juncus trifidus* and *Dryas octopetala* are presented versus host population size divided into five size classes (Fig. 1). We found a significant correlation between population size estimates and the number of fungal species inhabiting populations of *Dryas octopetala* (Spearman rank correlation, $N = 12$; $r = 0.731$; $p < 0.01$; Fig. 1).

Fungi on *Juncus trifidus* have been studied in Central Europe, especially in the Hercynian and Sudetan mountains. Large populations of *Juncus trifidus* in the Alps and Carpathians host more species of ascomycetes than the small to fragmentary populations in the Hercynian mountains and Sudetes (Scheuer, 1988, 1999; Chlebicki, 2002; Suková, 2004; Suková and Chlebicki, 2004). Most fungi associated with *J. trifidus* are not highly specialized species. Five fungal species analyzed here can infect many species of *Cyperaceae* and *Juncaceae*, and six are strictly juncicolous, among them one specific to *Juncus trifidus*. The significant correlation between host plant population size and number of fungal species (Spearman rank correlation, $N = 8$; $r = 0.791$; $p < 0.05$) confirmed the inadvertent extinction of some fungi in the smallest 'islands' (Fig. 1, Tab. 1, 2). In declining ecosystems,

TABLE 1. Distribution of specific and plurivorous fungi on *Dryas octopetala* in the Carpathians

Region	<i>Dryas</i> -specific fungi	Plurivorous	Size of the host population*
Malá Fatra Mts.	14	1	++++
Chočské vrchy	6	1	+++
Západné Tatry Mts.	18	7	+++++
Wysokie Tatry Mts.	8		++3
Belianske Tatry Mts.	7		+++++
Pieniny Mts.	2	4	++
Nízke Tatry Mts.: Krakova hoľa	6	2	++
Nízke Tatry Mts.: Bába	4	2	+
Svidovets Mts.	5		++
Chornohora Mts.	3		+
Maramureş	3		+++
Rarâu Mts.	10	2	+++

* + - up to 5 m²; ++ - 25 m²; +++ - 1 ha; ++++ - 1 km²; +++++ - more than 1 km².

TABLE 2. Distribution of specialized and plurivorous fungi on *Juncus trifidus* in the Sudetes and Šumava Mts.

Region	Specialized fungi	Plurivorous fungi	Size of host population*
Šumava Mts.: Velký Ostrý	5	7	++++
Šumava Mts.: Jezerní stěna	7	5	++++
Krkonoše Mts.: Sněžka Mt.	8	7	+++++
Králický Sněžník	4	6	+++
Hrubý Jeseník Mts.: Keprník	3	3	++++
Hrubý Jeseník Mts.: Vozka	6	4	++++
Hrubý Jeseník Mts.: Červená hora	3	6	++
Hrubý Jeseník Mts.: Petrovy kameny	3	0	+

* + - up to 10 dm² (two tufts); ++ - up to 25 dm² (several tufts); +++ - up to 150 m²; +++++ - up to 10 ha; ++++++ - more than 10 ha.

increased colonization by autochthonic as well as allochthonic parasites has been reported (Combes, 1995). The loss of symbionts as a result of symbiotic drift should involve only host-specific (mostly autochthonic) fungi. Nonspecialized fungi (mostly allochthonic) are predicted to occur in both big and small 'islands.' We suggest that symbiotic drift in small host populations may result from extinction of symbiotic organisms due to habitat shrinkage. This conforms to MacArthur and Wilson's (1967) model of island biogeography. Simpson (1974) also noted very rapid readjustment of species numbers following changes in island area.

In small populations with a decreasing opportunity for sexual processes to occur, Muller's ratchet effects (MR) as well as genetic drift may result in extinction (Chao et al., 1992). It may also result from mutational meltdown, especially in asexual populations (Gabriel et al., 1993; Lynch and Gabriel, 1990). Loss of mutualistic endophytes in grasses is a conse-

quence of deleterious mutation according to the MR hypothesis (Howard and Lively, 1994). However, these theories are based particularly on animals and do not seem to hold true for fungi. There is increasing evidence to suggest that MR does not occur in fungi, especially mitotic ascomycetes, possibly due to parasexuality (Bidochka and Koning, 2001).

Symbiotic drift is strictly connected with shrinking of the host plant population. Gotelli's (1991) metapopulation model shows the effect of propagule immigration while the existing population size is decreasing. Levis and Culver (1971) and Frank (1991) noted that migration among patches has a strong effect on global dynamics, but in the Carpathians, migration between small alpine populations should be limited. Our results support this hypothesis. No correlation was found between geographic distance and similarities based on the fungal composition of ten Carpathian populations (Mantel test, $r = 0.290$, NS). In fact, these patches are independent and do not have a metapop-

ulation structure. The extinction of such small populations need not have any effect on the rest of the sites (Saloniemi, 1997).

Thus, as a host plant population declines, we expect the host plant to lose many of its parasites and to increase its population, as the enemy release hypothesis (Mitchell and Power, 2003) or taxon cycle theory would predict (Ricklefs and Bermingham, 2002), but at the same time, fragmentation, habitat loss and genetic drift of the host plant population may pull the symbiotic fungi (parasite) populations into the 'extinction vortex', which from the perspective of the host can be seen as symbiotic drift.

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