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Autor: Schneller, Johann Jakob
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Spatial arrangement of phenotypes in populations of the common and widespread fern *Athyrium filix-femina*

Johann Jakob Schneller

Institut für Systematische Botanik, Universität Zürich, Zollikerstrasse 107,
CH-8008 Zürich, Switzerland; e-mail: schnell@systbot.unizh.ch

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Abstract

Schneller J.J. 2004. Spatial arrangement of phenotypes in populations of the common and widespread fern *Athyrium filix-femina*. Bot. Helv. 114/2: 101–107.

The distribution of eight different phenotypes in five populations of *Athyrium filix-femina* has been recorded. When calculating the Moran index it could be seen that no spatial autocorrelation occurs. *Athyrium filix-femina* is an outbreeding species and is characterised by highly effective gene flow and a considerable neighbourhood size. Its successful range of distribution seems to be mainly due to phenotypic plasticity.

Key words: Phenotype classes, population structure, spatial autocorrelation, gene flow, *Athyrium filix-femina*.

Introduction

Pteridophytes, as other cryptogamic plants, are characterised by the fact that the spore, which is the first gametophytic cell, is also the dispersal unit (diaspore). In contrast, both pollen and seed dispersal contribute to gene flow and influence spatial population genetic structure in flowering plants (Levin and Kerster 1974, Ennos 1994). In many seed plants, however, gene flow through pollen and seeds is spatially restricted and significant spatial genetic structure is expected. Most of the modern ferns develop only one type of spores (isospores) which are small and produced in great numbers. They are actively released from the leaves by the anulus mechanism of the sporangia. The influence of this first step is small, however, the main dispersal agent is thought to be the wind (Haider 1954, Straka 1962, Schneller 1995). Wind currents can transport spores over greater distances and may therefore increase effective gene flow. In spite of this, most of the fern spores are still dispersed to only a few meters of the source (Conant 1978). The spatial patterns of genotypes in populations further depend on breeding systems (Hamrick and Godt 1989, Murakami et al. 1997, Suter et al. 2000).

Tab. 1. Number of individuals and size and location of the investigated populations.

Population	Size of area m ²	Number of individuals	Altitude m	Swiss grid	International coordinates
Ricken, Bannwald	400	360	870	7215/2338	47° 14' 43"/9° 2' 41"
Rittmarren	400	292	1090	72285/23449	47° 15' 5"/9° 3' 46"
Feusisberg, Meinradsbrunnen	400	364	730	7013/22629	47° 10' 52"/8° 46' 34"
Schindellegi, Friesischwand	400	292	840	69695/22485	47° 10' 8"/8° 43' 7"
Sattelegg, Wilerzell	400	346	970	7049/22095	47° 7' 57"/8° 49' 21"

Athyrium filix-femina is a preferentially outbreeding species (Schneller 1979, Schneller 1998) and isozyme genotypes in populations are close to Hardy Weinberg equilibrium (Schneller, unpublished data). Most of the genetic variability has been found to occur within populations and considerable similarity among populations could be observed. The goal of this investigation was to learn more about the spatial distribution of different genetically determined phenotypes within and among different populations. Is there any spatial differentiation in the frequency of phenotypes in the form of clustering? Which factors are responsible for the spatial structure within and among populations?

Materials and Methods

Five well developed, individual-rich populations of *Athyrium filix-femina* growing under optimal conditions in colline to subalpine regions of northern Switzerland have been investigated (Tab. 1). In each location a square of 20 × 20 m out of a comparatively densely populated area was selected. Each individual within this square was characterised by its phenotype and its position (rectangular x, y co-ordinates) in relation to the zero point at the left lower corner.

Eight different leaf phenotypes were distinguished: Petiole and midrip green (green, G), petiole and midrip green with red line on the abaxial side (green and stripe, GS), petiole and midrip red (red, R), petiole and midrip red with darker red line on the abaxial side (red and stripe, RS), and the same four phenotypes mentioned above but covered with small unicellular hairs (pruinose, RH, GH, RHS, GHS). The phenotypes are stable and characterise the individual. They are determined by (Mendelian) genes; in preliminary experiments it was shown that "red" and "pruinose" are regulated by a dominant allele (unpubl.).

The spatial autocorrelation index I, proposed by Moran, was calculated using the program SAAP (Wartenberg 1989). Nineteen distance classes were chosen. Six of the eight phenotypes were used for the calculation of I. Additionally, the frequency of the eight different phenotypes for each population have been calculated and the similarities of the different populations were estimated using BIOSYS (Swofford and Selander 1989). The phenotypes were genotypically interpreted using two different estimates. Either the frequency of three 'loci' (green/red, stripe/without stripe and

pruinose/not pruinose) or the frequency of the eight phenotypes was assumed. Both were used for analysis.

Results

The distribution of the phenotypes within the sampling plots is shown in Figure 1. The comparison of the frequencies among populations is seen in Figure 2. Although the general pattern of the distribution of *A. filix-femina* is, due to environmental conditions, not purely random, Moran I statistics of the spatial correlations showed no significant substructuring (i.e. clustering; Fig. 3). The results of the similarity calculations are given in Figures 4 and 5.

Discussion

The spatial autocorrelation of fern populations has been demonstrated in only a few cases. When comparing the spatial structure of *A. filix-femina* with that of *Asplenium trichomanes* subsp. *quadrivalens* (Suter et al. 2000) and *Pteris multifida* (Murakami et al. 1997) clear differences can be observed. Whereas the latter two species show substructuring due to clonality and/or breeding system and range of gene-flow, *A. filix-femina* lacks any clear structuring (Fig. 3). *Asplenium trichomanes* and *Pteris multifida* both are rock inhabiting species and show naturally fragmented populations. Populations of *A. filix-femina* on the other hand are much less fragmented and form rather a continuum. In *A. filix-femina* individuals may sometimes develop more than one shoot apex. In such cases, the shoots are clumped and remain connected to each other. However, the vegetative reproduction (clonal growth) is very limited. These results show that in *Athyrium* the neighbourhood size is large (efficient gene flow) and the composition of populations is very similar over larger distances (Figs. 2, 4, 5). Although most of the spores will be deposited only within a few meters from the point of release, their dispersion leads to a random distribution of genotypes. An additional factor responsible for the big population size is considered to be the age structure of its plants, with some individuals reaching ages of much greater than 50 years. So, many differently aged individuals live together.

Due to the well developed antheridiogen system and the high inbreeding depression (Schneller 1979) the species is preferentially outbreeding. Structuring of populations may be found only under very special conditions (well isolated populations with only few individuals). Significant differences in phenotype and allele frequencies will be found when considering much larger distances, e.g., south or north of the Alps, or between central and southern Europe (Schneller, unpubl.).

The degree of fragmentation of populations, the breeding system, and stochastic processes all together influence the spatial structure. When considering the potential evolutionary implications, it seems likely that ferns with a wide distribution and more or less continuous populations (such as *A. filix-femina*) evolve slower because of their highly effective gene flow and considerable neighbourhood size. This suggests that phenotypic plasticity (robustness) is likely to be an important factor contributing to their wide and successful distribution.

I thank all the students of the fern course (summer 1998) for their help collecting raw data.

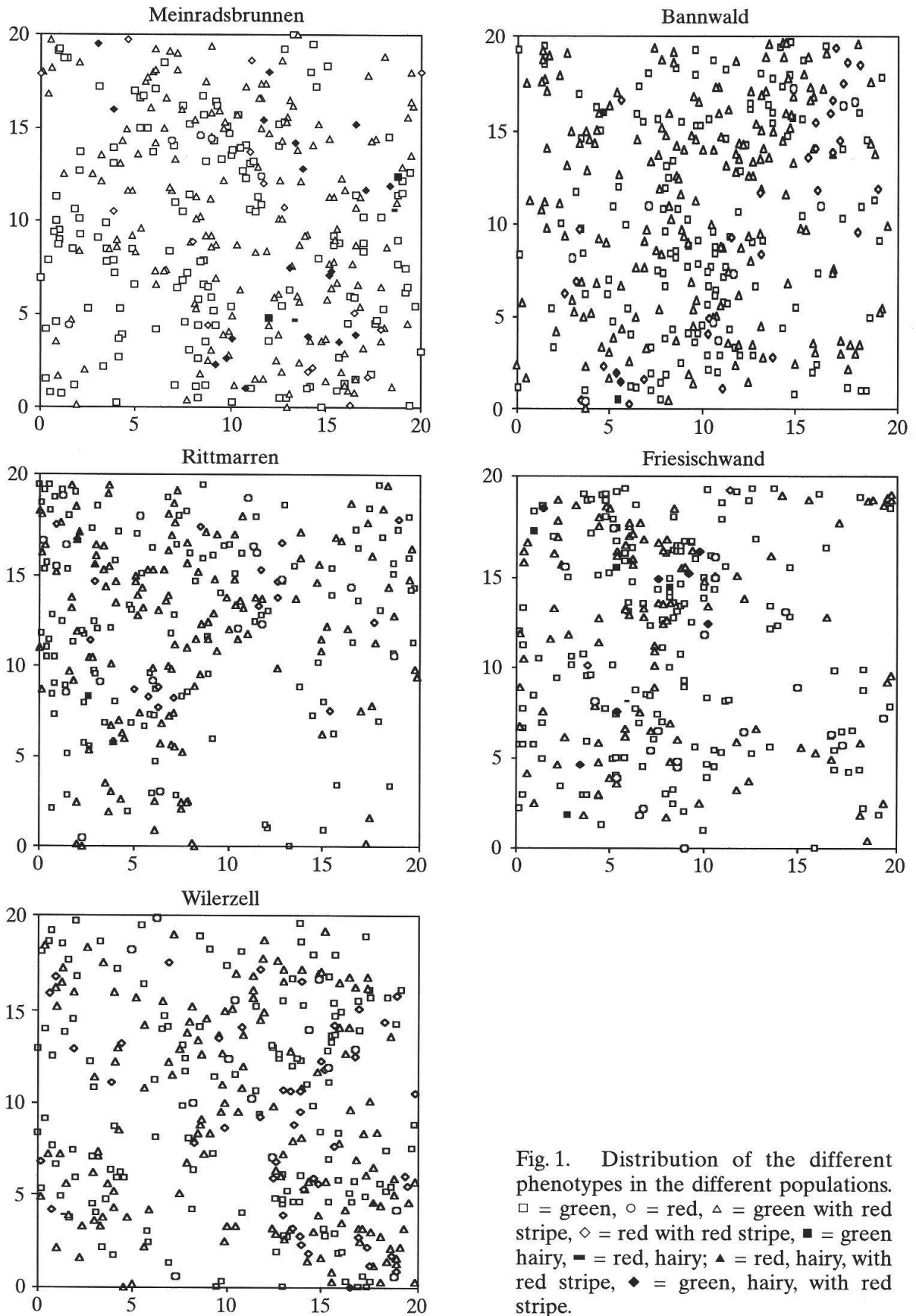


Fig. 1. Distribution of the different phenotypes in the different populations. □ = green, ○ = red, △ = green with red stripe, ◇ = red with red stripe, ◻ = green hairy, ◻ = red, hairy, △ = red, hairy, with red stripe, ◇ = green, hairy, with red stripe.

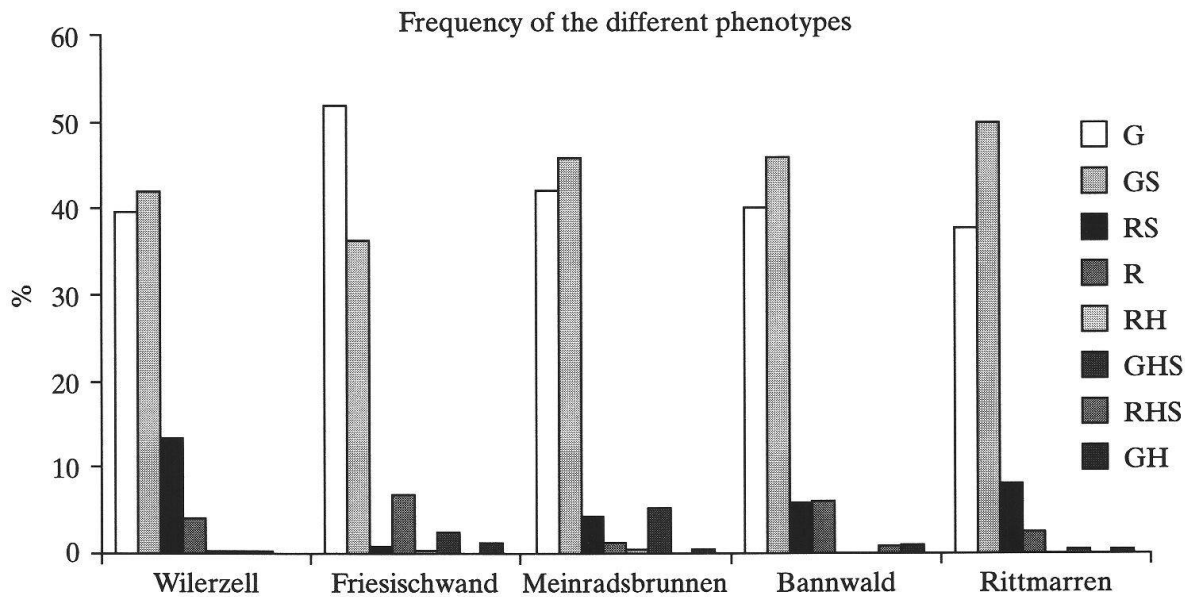


Fig. 2. Frequencies of the different phenotypes among the five populations (abbreviations see text).

Zusammenfassung

Die räumliche Verteilung von acht verschiedenen Phänotypen in fünf Populationen von *Athyrium filix-femina* wurde aufgenommen. Der Moran Index zeigte keine räumliche Autocorrelation. *Athyrium filix-femina* ist fremdbefruchtet und zeichnet sich durch einen sehr wirksamen Genfluss und eine beachtliche effektive Populationsgrösse aus. Die Art ist durch ein grosses Verbreitungsareal gekennzeichnet und ist sehr häufig. Dies verdankt sie wohl massgeblich ihrer grossen, phänotypischen Plastizität.

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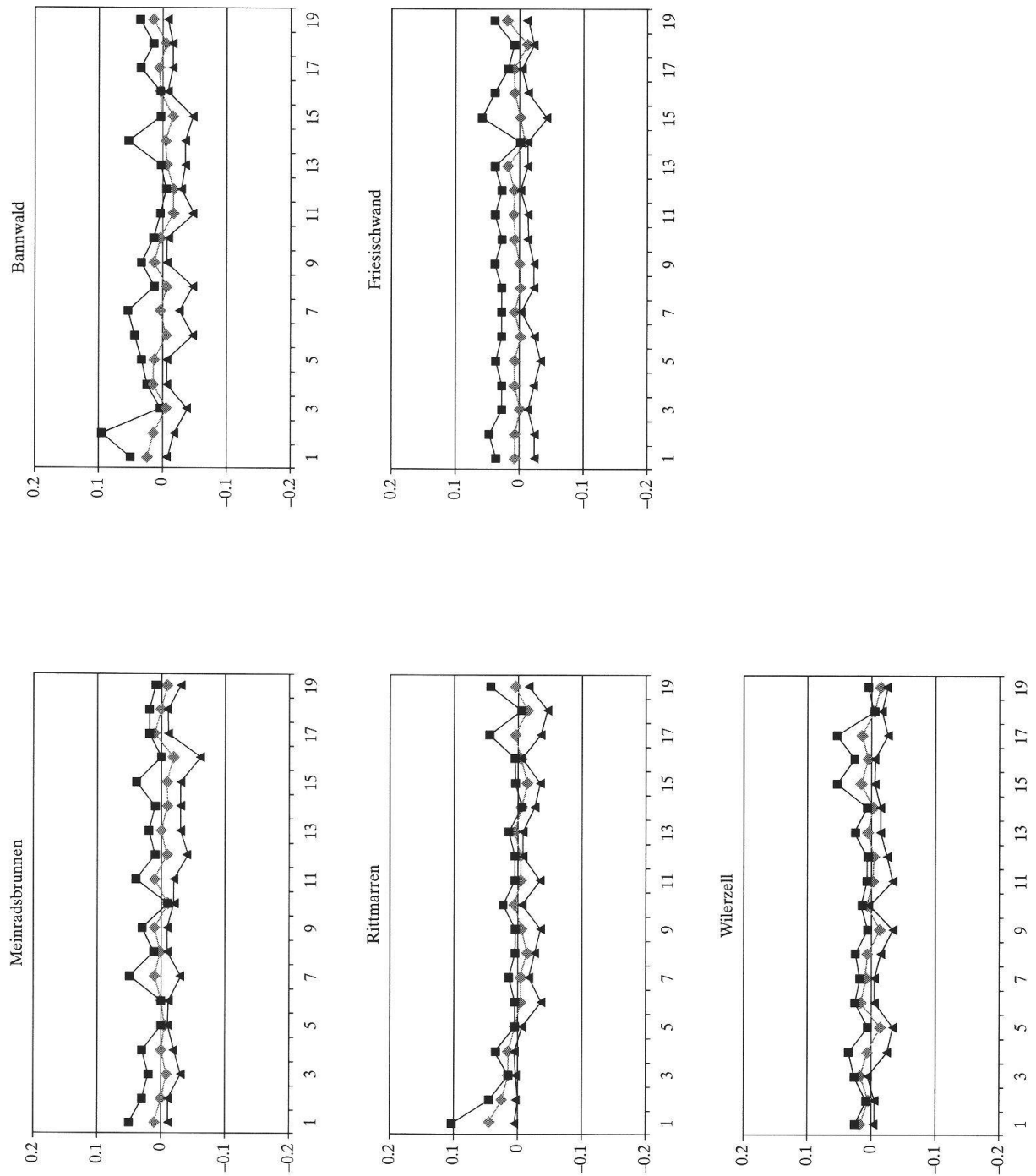


Fig. 3. Morans Index (I) in the five different populations. Six common phenotypes were analysed and maximum-, average- and minimum-values are indicated.

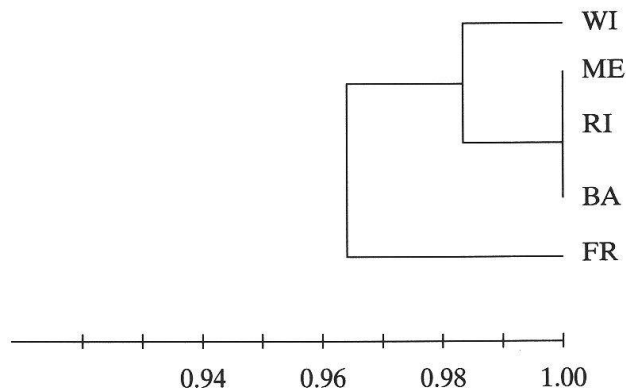


Fig. 4. Nei's genetic similarity among populations when considering three loci behind the phenotypes. BA = Bannwald, FR = Friesischwand, ME = Meinradsbrunnen, RI = Rittmarren, WI = Wilerzell.

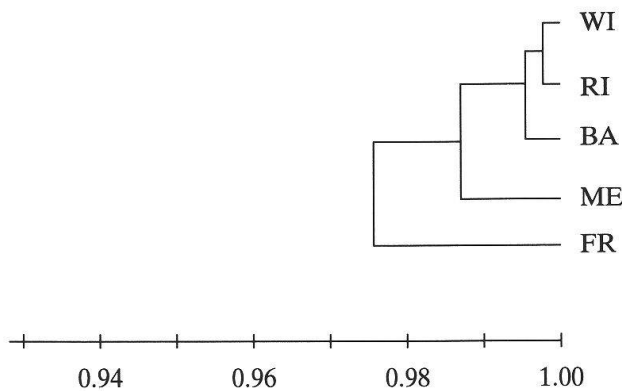


Fig. 5. Nei's similarity among populations considering the frequency of the eight phenotypic classes. BA = Bannwald, FR = Friesischwand, ME = Meinradsbrunnen, RI = Rittmarren, WI = Wilerzell.

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