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ORGANIZATION OF APHID GUILDS IN DISCRETE HABITAT PATCHES

Ph.D. Theses

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Szeged, Hungary

2003

Introduction

The ecological study of aphids (*Aphidina*) is in most cases motivated by pest control issues. Population dynamics, the quality the host-plant and the role of natural enemies in fluctuations in abundance of this insect group are the primary targets of study. Less attention is directed towards their role in natural and semi-natural communities and the joint behaviour of co-exsistent aphid populations. This successful insect group is able to achieve large individual numbers in short time due to their parthenogenetic reproduction and rapid developmental period. They are very responsive to changes in their environment, thus their population size fluctuates intensively within a wide range. They co-exist with other organisms (phytophagy, predation, symbiosis, mutualism, competition), thus it is worthwhile to study their roles in various interactions.

The life cycle of aphids and the development of vegetation are synchronized within a year. It is characteristic of most aphid species' seasonal dynamics that the abundance has two peaks – one in spring and one in autumn – and the individual number significantly decreases during summer. The abundance changes are caused by a number of reasons and population dynamics are influenced by both abiotic and biotic factors. Density-dependent factors may also have a role in the regulating the abundance of populations, however these become relevant at extreme abundance values only. The spatial distribution of host-plants and changes in the quality of phloem sap has an effect on population dynamics of both monoecious and heteroecious species as well. Furthermore, intra- and interspecific interactions also influence the spatial distribution and temporal fluctuations of aphids. Among these, the mutualistic interaction with ants (*Formicidae*) is of particular significance.

It is well-known that during their feeding aphids produce honeydew. This substance provides a food source rich in sugar and amino acid for ants which – in exchange for the food – protect aphids from their natural enemies, make them to feed more intensively, decrease their dispersal thus have a positive effect on their survival and growth rate. In most cases the interaction is facultative and a number of its characteristics (e.g. its strength and symmetry) changes with time and space. The mutualistic interaction depends on the quality of the host-plant, the species involved in the interaction and the everchanging environmental conditions. The nature of the mutualism may change by the increase of aphid density and it sometimes switches to predation. The intra-, or interspecific competition between aphids for the service of the ants has been proven several times. Thus it is reasonable to say that the mutualism between aphids and ants is rather complex due its facultative nature. The most recent studies investigate the various characteristics of conditional mutualism. Our knowledge about the seasonal changes of the interaction, the significance of species specificity and the effect of ant-attendance on aphid communities, and diversity is still incomplete.

Aims of the study

We studied spatial pattern of aphid populations in discrete habitat patches (on scattered willows). The following questions were addressed:

- How can the habitat selection of aphids be realized?
- What is the structure of the aphid guild like?
- How does the aphid-ant mutualism effect on spatial distribution?
- Do the attending ants influence the diversity of aphids?
- Do the two similar habitat differ in the spatial pattern of aphids?

The other main goal of our study was to characterize the seasonal dynamics of aphid populations. Questions are:

- In what respect does the abundance changes of populations differ from each other?
- What effects do climatic factors have on different species?
- Do interactions between populations have an effect on life cycles?
- What are the characteristics of the seasonal dynamics of aphid-ant mutualism, and does the intensity of attendance change seasonally?
- How are species-specific effects realized in the case of aphids and ants?

Materials and Methods

We studied the factors influencing habitat selection and spatial distribution of aphid populations living on White Willow (*Salix alba*) in two areas where the host-plant are dispersed: in Inérhát kaszálórét (Kesznyéten Nature Reserve) and Szücsi-rét (outside Kiskőrös). We also studied population dynamics in one of the areas. The aphid populations on this host-plant and the ants visiting them provide an ideal opportunity for the investigation of the temporal aspects of mutualist interactions, since most of the small number of species (9) are monoecious (*Tuberolachnus salignus*, *Pterocommna* and *Chaitophorus* species) and all of them are attended by ants from different species (mainly *Lasius* species).

A total of 67 and 60 willow trees were sampled in Kesznyéten Nature Reserve in spring 1998 and 1999, respectively. We gathered samples from 33 trees on 15 occasions in Szücsi-rét in 1999 between april and november for the studies on population dynamics. The aphid colonies were gathered from the same, marked trees within the areas. On every occasion 10 randomly chosen shoots were examined on each tree. In both areas the ant fauna was surveyed and the characteristics of the host-plants (trunk diameter, trunk height, canopy area) were recorded and the trees were mapped in both areas.

The following methods were employed in the data analysis: Spearman rank correlations were computed between the parameters of willow trees and the number of individuals of aphids for the investigation of habitat selection. The associations of aphid species were analysed with test of independence (χ^2-test). We calculated percentage difference between the trees based on composition of aphid and ant assemblages, and correlations between the similarity matrices were calculated, as well. We carried out hierarchical classification and principal coordinate analysis (PCoA) of willows based on both aphids and ants. We compared aphid groups with Mann-Whitney tests in the investigations based on presence/absence of attending ants.

We used climate data to analyse the potential environmental correlates of the aphids' population dynamics. The amount of rainfall (in mm) and the average of the daily maximum temperatures two weeks before the sampling date were taken into account. We computed Spearman rank correlation coefficients between the changes of the abundance of aphids and the climate data. To determine the changes of diversity the Shannon formula was used.

The dynamic features of aphid-ant mutualism were also investigated. We calculated Spearman rank correlations between the size of aphid colonies and the number of individuals of the three attending ant species, summerized seasonally. We counted Kruskal-Wallis test to assess the seasonal changes of the individual number of ants attending a certain aphid colony. In order to establish the preferences of aphid and ant species a test of independence (χ^2-test) was carried out.

Results

1. Spatial patterns

1.1 A total of 85212 individuals of nine aphid species were collected from the two areas of investigation. One group of individuals were a subspecies of *Plocamaphis flocculosa bracysiphon* – a so far unrecorded species in the Hungarian fauna – and *Salix alba* was not included as a host-plant in the species records. We recorded 15 ant species on the willows in the two areas.

1.2 Aphid immigration to habitat islands can be considered random, however, colonization depends on a number of factors. Among the various habitat selective factors the role of ants is particularly significant in Inérhát rét. The size of trees is a dominant feature in the Kiskőrös area, though only in the case of *Pterocomma rufipes* species. The distances of the nearest trees are a decisive feature in the spatial distribution of aphids, however this effect is indirect and mediated by the ants.

1.3 It is true of both areas that abundant aphid species associate independently of each other on willow trees thus their spatial distribution is not a sign of interaction (e.g. competition for mutualists).

1.4 Comparison of the similarity matrices of the trees based on the ants and aphids indicated significant differences. Positive correlation in Inérhát rét is probably due to the closer association of ant and aphid species. Most important mutualist ant species in the Kiskőrös area participate in the interactions with more or less the same intensity and the aphid preference is not so pronounced. On the basis of multivariate analyses of willows the role of spatiality in the similarities can be ruled out in both areas. The ant species distinguish trees much better than the aphid species, since the ants show a mosaic-like distribution pattern due to interspecific competition. There is no conflict between the aphid species neither on food, nor on mutualists, hence their populations can freely combine on willow trees. At the most, the association of a few species to ants is indicated by the results of multivariate analyses.

1.5 The presence of mutualist ants on willow trees increases the diversity of aphids. This indicates that the ants do not choose between the aphid species, thus the survival of more colonies is possible as a result of their attendance.

1.6 The myrmecophily of all willow-dwelling aphid species is facultative, however their association is species-dependent. *Chaitophorus vitellinae* is involved in the strongest mutualism with ants and *Pterocomma* species are less frequently visited by mutualists.

1.7 The spatial distribution and habitat selection of aphid populations is influenced mostly by attendant ants in a species-dependent manner. In Inérhát rét the dominant *Lasius fuliginosus* participates the most intensively in the interactions and in Kiskőrös three attending species (*L. niger*, *L. brunneus*, *Dolichoderus quadripunctatus*) visits the colonies with about the same intensity (though less actively than *L. fuliginosus*). This explains the differences in the spatial colonization of aphids in the two areas.

2. Seasonal dynamics

2.1 The investigations of the temporal characteristics of spatial patterns were conducted in Szücsi-rét near Kiskőrös. The habitat selection factors and the features determining spatial patterns do not change significantly throughout the year. The significance of mutualists changes seasonally only in the case of *Chaitophorus vitellinae* species. In summer their spatial pattern is shaped in accordance with their stronger interaction with ants. The cumulative species richness and the seasonal increase of cumulative frequency of species indicate that the common aphid species of the area are mobile.

2.2 On the basis of the investigations conducted throughout the year point to the fact that the seasonal dynamics of most aphid species is characterized by a spring and an autumn abundance peak. Comparison of the individual numbers and climatic data revealed that the quantity of precipitation and temperature has an indirect effect on the abundancy of aphids through influencing the quality of the host-plant.

2.3 Similarly to the abundance changes the diversity of aphids on a species level has two peaks: in summer the species number decreases and the individual numbers of most species drops below detectable levels. The dominance of *Chaitophorus vitellinae* is characteristic of this season as it tolerates high temperature and maintains the strongest interaction with ants. Assessing the changes in willow-occupancy – as habitat islands – species by species we conclude that the structure of the aphid guild in the canopy is rearranged at least in terms of common species.

2.4 The seasonal dynamics of some aphid species is different from each other, even though they live on the same host-plant. On the basis of population dynamics the nine observed species fall into four types.

2.5 We examined the differences in life cycle in the case of two *Pterocomma* species with similar behaviour and feeding characteristics. In spring there is a marked temporal shift in the appearance of the different morphs of the two species. There is no shift in the autumn peak, however the density of *P. pilosum konoi* is lower, though it is present for a longer time on the willow trees than the *P. rufipes*. Parasitoids prefer the colonies of *P. pilosum konoi* in spring and in autumn as well.

2.6 While aphids show seasonal dynamics, in the ants' case it is the activity and the intensity of visiting that change throughout the year. According to our results in spring, but mainly in autumn ants do not utilize the high levels of diversity and abundance of aphids characteristic of these seasons. They are the most active in the summer, when individual numbers are at minimum values, however in this season, they fully utilize the available resources: mutualists can be observed in practically all aphid colonies. Our studies point to the fact that the seasonal dynamics of aphids and the activity of ants throughout the year are not adjusted to each other. Thus it follows that the interactions between populations are facultative and their strength changes with time.

.7 Ant populations differ from each other and can be classified on the basis of the seasonal intensity of attendance. The role of *Lasius* species (*L. niger*, *L. fuliginosus*, *L. brunneus*) in mutualistic interactions is prominent, although *Dolichoderus quadripunctatus* is also a significant aphid visitor in summer. The seasonal changes in the aphid preference of ants are also a species-specific effect.

2.8 In the case of three ant species there is a positive trend between the colony size of aphids and the individual number of mutualistic ants in all seasons, but a significant positive correlation is only detectable in the case of

Lasius brunneus and *Dolichoderus quadripunctatus* species in summer and in the case of *L. niger* in spring. There is no detectable correlation between the colony size and the species number of ants. This suggests that ants already appear in groups with a few members, and they cannot manage colonies with large numbers. The positive correlation is explained by the fact that aphid colonies are generally smaller in size at this time of the year and they are better suited to the ants' requirements thus it is more rewarding to visit a larger colony with greater number of workers.

2.9 Aphid species differ in their association with ants. The most common *Chaitophorus vitellinae* is involved in the strongest mutualism with ants, their colonies can occur with any ant species and they are frequently attended in all seasons. The less preferred aphid species (*Ch. salijaponicus niger*, *Pterocomma rufipes*) are attended intensively only in summer.

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