

Leafhoppers (Hemiptera, Auchenorrhyncha) in fragmented habitats

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Abstract

The distribution of leafhoppers (including planthoppers, spittlebugs and treehoppers) largely depends on the distribution of their host plants. Plants occur more or less aggregated and frequently form discrete patches. In natural as well as in cultural landscapes these patches may be fragmented to some extent. A review of existing studies on leafhopper populations in fragmented landscapes summarises the current knowledge on the role of area and isolation on occurrence and density of leafhoppers. Whereas little information is available on the dynamics of occupancy

patterns in the habitat patches, in most leafhopper species effects of area and isolation on density and occupancy were reported. Increasing patch area often resulted in higher densities and higher incidences. On the other hand, increasing isolation was found to reduce the incidence in the patches. The relevance of these results are discussed in the light of recent metapopulation theory.

Key words: Auchenorrhyncha, host plant, habitat fragmentation, area, isolation

Introduction

The overall feature of leafhoppers (including planthoppers, spittlebugs and treehoppers) is their close relation to plants. The host plants provide nutrition (e.g. BACKUS 1985, COBBEN 1988), shelter for eggs (e.g. CLARIDGE et al. 1977) and transmission channels for bioacoustic signals (e.g. MICHELSEN et al. 1982). Accordingly, one major requisite of leafhopper habitats is the presence of the host plants. In particular in host plant specialists among leafhoppers the habitat is principally given by the distribution of the host plants.

Plants frequently occur aggregated to some extent and form discrete patches. The amount and physiology of the host plant may largely determine the quality of such host plant patches (e.g. PRESTIDGE 1982, MOON et al. 2000). However, some leafhopper species exhibit more complex habitat requirements. Additional factors like host plant architecture, vegetation structure or microclimate may be relevant (e.g. CLARIDGE 1986, DENNO & RODERICK 1991) and therefore the habitat may be not primarily defined by the occurrence of the host plants. In these species as well as in more generalist species with a broader range of host plants, the habitat patches may not be clearly delimited in the field. In contrast, in host plant specialists among the leafhoppers the survey of the distribution of the host plant was found to be a very feasible way to determine all potential habitats of a certain species in a landscape (DENNO et al. 1981, BIEDERMANN 2000).

In natural as well as in cultural landscapes the habitats of leafhoppers are frequently fragmented to some extent. In the recent two decades there is increasing concern about ongoing habitat fragmentation by human activities, especially in cultural landscapes (SETTELE et al. 1996). Fragmentation is suggested to be one major cause of the extinction of species and thereby declining biodiversity (MORRIS 1995). Looking at existing results on leafhoppers in fragmented habitats there are two levels of consideration, the population level and the community level. At the population level the occurrence, abundance and dynamics of particular species is of interest.

The analysis of leafhopper communities may yield additional information on, for instance, species richness or trophic interactions in relation to habitat configuration (e.g. DENNO & RODERICK 1991).

There are two major theoretical concepts dealing with the explanation of animal distributions on islands or habitat patches. The theory of island biogeography (MACARTHUR & WILSON 1967) predicts species numbers on islands or habitat patches in relation to isolation and area. In leafhoppers, the theory of island biogeography was studied, for instance, by NIEDRINGHAUS (1991) on dune islands in the North Sea. The application of island biogeography theory is confined to communities and seems not suitable for the analysis of populations of single species (see HANSKI 2001). Further, it assumes a mainland as a source of colonising individuals. In fragmented landscapes there is not necessarily a mainland, but a situation with a large number of patches of similar area may occur. The corresponding theory for populations on regional scales is the metapopulation theory (HANSKI 1998). Recent metapopulation theory is a spatially explicit attempt to describe the dynamics of a regional population with its members distributed over a set of habitat patches. The main feature of metapopulation dynamics is the occurrence of extinction and colonisation events in the habitat patches.

The objective of this review is to make a survey on existing studies on leafhopper populations in fragmented habitats and to discuss the results in regard to metapopulation theory. According to recent theory, the occurrence and density of leafhoppers in a particular habitat patch may depend on area, isolation, quality and surrounding landscape structure of the patch. The quality of a patch is the fundamental factor for the survival and reproduction of leafhoppers and is not a particular issue of fragmented habitats. The role of surrounding landscape structure on leafhopper distribution in habitat patches is largely unknown (but see JONSEN & FAHRIG 1997). Thus, in the following the current knowledge on the role of area and isolation on occurrence and density of leafhoppers will be summarised.

Habitat fragmentation and metapopulation theory

Habitat fragmentation describes the decrease in number and size of suitable habitats for species (e.g. HARRISON & BRUNA 1999, HUXEL & HASTINGS 1999). The processes which lead to habitat fragmentation are decreasing area of patches up to their complete elimination and consequently increasing isolation of patches. The term fragmentation describes both the processes and the outcome. It often implies a loss of habitat due to human activities. As in natural landscapes suitable habitat may be patchy without anthropogenic influence, here the term patchiness may be more appropriate. However, in the following the term fragmentation will be used for both fragmented and patchy habitats.

Living in such a set of patches animals build up structured populations (HARRISON 1991), with its members distributed over a number of habitats. In recent years the analysis of spatial population structure has made a rapid development, both in theoretical (e.g. HANSKI 2001) and empirical studies (e.g. GUTÉRREZ et al. 2001). The results suggest that animals build up a wide continuous range of spatial population structures from isolated patches with virtually no immigration, over metapopulations with a limitation in the dispersal between patches, up to patchy populations with high colonisation and thus low extinction rates (HARRISON 1991, THOMAS & KUNIN 1999). According to metapopulation theory (HANSKI 1998) the dynamics of the occurrence of a species in its habitat patches is determined by local extinction and colonisation. The extinction rate is assumed to decrease with increasing patch area and the colonisation rate depends on the degree of isolation of a patch. For the long-term persistence of a metapopulation an equilibrium between extinction and colonisation is required.

Leafhopper populations in fragmented habitats

The distribution of species in a number of habitat patches of various area and isolation was analysed in several studies on leafhoppers (HALKKA et al. 1971, LAWTON 1978, RAUPP & DENNO 1979, DENNO et al. 1981, MACGARVIN 1982, BIEDERMANN & APPELT 1996, BIEDER-

MANN 1997, BIEDERMANN 1998, ZABEL & TSCHARNTKE 1998, BIEDERMANN 2000, BIEDERMANN unpubl. data). The main focus of these studies was on the dependency of the incidence (= probability of occurrence) and density of a particular species on area and isolation of patches. In nearly all studies the first step was a complete survey of the host plant patches in the study area providing the area and isolation of the patches. This step was followed by a survey of the leafhopper occurrence or density in these patches. In order to quantify extinction or colonisation events in some studies the survey for the occurrence of species has been repeated for several years or generations.

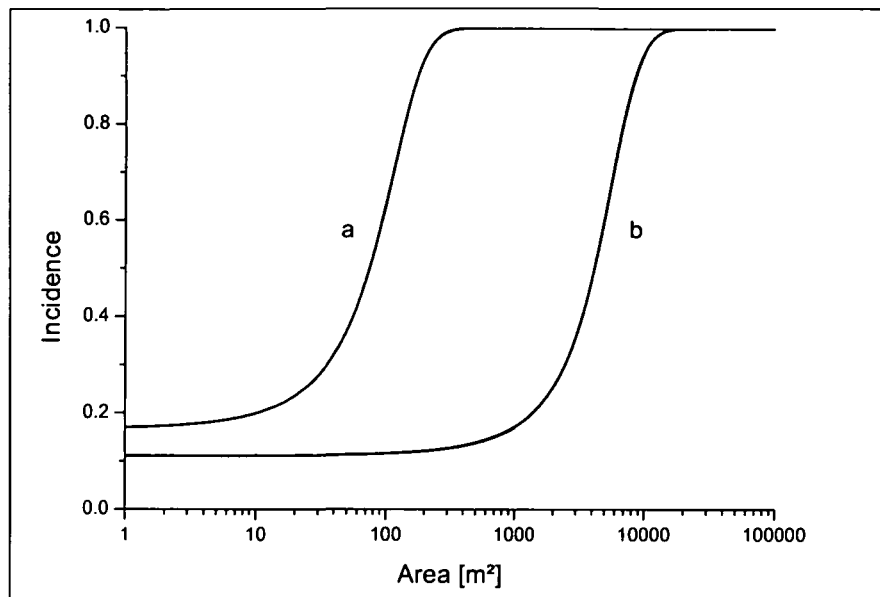
Incidence and area

The first study on the relationship between the occurrence of leafhoppers and the area of their habitats was performed by HALKKA et al. (1971) on the spittlebug *Philaenus spumarius* (Aphrophoridae). They were analysing the distribution of *Philaenus spumarius* in island habitats in an archipelago of 135 islands in the Baltic Sea.

A method to analyse the role of patch area on the occurrence of leafhoppers in host plant patches is the use of incidence functions (ADLER & WILSON 1985, TAYLOR 1991). Incidence functions quantify the relationship between species presence and area in a set of patches of various area. In order to calculate incidence functions, in each patch the presence or absence of the species is recorded. The resulting occupancy patterns are related to patch area using logistic regression (HOSMER & LEMESHOW 2000). Logistic regression is a statistical method which detects relationships between a dependent binary variable and one or more independent variables. Here, the dependent variable is the presence-absence pattern in the patches and the independent variable is the area of the patches. The resulting incidence functions show the relationship between the probability of occurrence (= incidence) and area (Fig. 1).

In order to obtain the incidence function of *Philaenus spumarius* a re-analysis of the data (HALKKA et al. 1971) was performed. The results showed a positive relationship between the occurrence of *Philaenus spumarius* and the suitable habitat area on the islands.

Fig. 1: Examples of incidence functions of (a) *Gargara genistae* and (b) *Ribautodelphax pungens* demonstrating the positive relationship between the incidence (= probability of occurrence) and area (= patch size), based on logistic regression using data from BIEDERMANN (unpubl.) and BIEDERMANN & APPELT (1996).



Directly using the technique of logistic regression, BIEDERMANN & APPELT (1996) calculated incidence functions of five monophagous leafhoppers occurring in host plant patches of various area in fragmented dry grassland: the leafhopper *Adarrus multinotatus* (Cicadellidae), the spittlebug *Neophilaenus albipennis* (Aphrophoridae) in 506 patches, the planthopper *Ribautodelphax pungens* (Del-

was increasing with increasing area of the host plant patches. In a second study of the treehopper *Gargara genistae* in another landscape with 237 patches of *Sarothamnus scoparius* a similar result was found (BIEDERMANN unpubl. data), the incidence is increasing with increasing patch area (Fig. 1). These results indicate a high variability in the incidence-area relationship among species, even within one guild.

In a study of several phytophagous and predatory insects on *Urtica dioica* ZABEL & TSCHARNTKE (1998) recorded a positive relationship between the area of the host plant patches and the incidence of the monophagous leafhopper *Macropsis scutellata* (Cicadellidae).

In general, the effects of patch area are of relevance for the explanation of the distribution of leafhoppers as in all species a significant relationship exists between incidence and area. In order to analyse the differences in the incidence-area relationship between species, from the existing results area thresholds were calculated. Based on the incidence functions area thresholds were taken as a measure of the characteristic of the incidence function. As thresholds the area at an incidence of 0.5 and 0.95 were chosen. The comparison shows a high variability among species (Table 1). Some species like the leafhopper *Adarrus multinotatus* or the planthopper *Kelisia haupti* occupy even very small patches of only a few square meters, whereas in other species like the spittlebug *Neophilaenus albipennis* or the planthopper *Ribautodelphax pungens* only large patches have a considerable incidence.

Table 1: Comparison of the area requirements (in m²) of eight leafhopper species for two given incidence thresholds (I = 0.5 and I = 0.95), calculated by incidence functions using logistic regression; references: 1: BIEDERMANN & APPELT (1996), 2: ZABEL & TSCHARNTKE (1998), 3: recalculated from HALKKA et al. (1971), 4: BIEDERMANN (unpubl. data).

Species	Number of patches	Incidence	
		0.5	0.95
<i>Adarrus multinotatus</i> ¹	506	-	8
<i>Kelisia haupti</i> ¹	21	10	18
<i>Gargara genistae</i> ¹	24	24	79
<i>Philaenus spumarius</i> ³	135	56	301
<i>Gargara genistae</i> ⁴	237	75	212
<i>Macropsis scutellata</i> ²	32	493	1229
<i>Neophilaenus albipennis</i> ¹	506	747	1976
<i>Ribautodelphax pungens</i> ¹	73	4162	10052

phacidae) in 73 patches of *Brachypodium pinnatum*, the planthopper *Kelisia haupti* (Delphacidae) in 21 patches of *Carex humilis* and the treehopper *Gargara genistae* (Membracidae) in 24 patches of *Sarothamnus scoparius*. In all species a significant relationship exists between incidence and area. The incidence

Density and area

The relationship between the density and the area of host plant patches was analysed in several studies on leafhoppers (Table 2). In the planthopper *Ditropis pteridis* (Delphacidae) a positive relationship was detected between density and patch area of the host

plant *Pteridium aquilinum* (LAWTON 1978). In a guild of leafhoppers on *Spartina patens* RAUPP & DENNO (1979) and DENNO et al. (1981) reported high variability in the response of species density on patch area. A positive relationship between area and density was found in the planthoppers *Tumidagena minuta* (Delphacidae), *Delphacodes detecta* (Delphacidae) and *Aphelonema simplex* (Issidae), whereas the densities of the planthopper *Megamelus lobatus* (Delphacidae) and the leafhoppers *Amplicephalus simplex* (Cicadellidae) and *Destria bisignata* (Cicadellidae) were not affected by area.

In a study of the density of the spittlebug *Philaenus spumarius* in 24 patches of *Chamerion angustifolium* no significant relation could be detected between area and density (MACGARVIN 1982). In the leafhopper *Adarrus multinotatus* no correlation was found between density and patch area in 14 patches of *Brachypodium pinnatum* (BIEDERMANN 1997). A similar result was obtained in the treehopper *Gargara genistae*. There was no relationship between density and patch area in 17 patches of *Sarothamnus scoparius* (BIEDERMANN unpubl. data).

Incidence and isolation

Among the existing investigations on the spatial distribution of leafhoppers in habitat patches no study was available on the relationship between density and isolation. However, there are a few studies testing the effect of isolation on the occupancy of patches (Table 3). The analysis of *Philaenus spumarius* on small islands in the Baltic Sea (HALKKA et al. 1971) showed a significant effect of isolation on the distribution of the spittlebug. In a study of the spittlebug *Neophilaenus albipennis* BIEDERMANN (1997) was using logistic regression (as the independent variable the distance to the next occupied patch was used as a measure of isolation) to detect effects of isolation on the incidence of the spittlebug in the 506 patches of its host plant *Brachypodium pinnatum*. The results clearly state that the incidence of *Neophilaenus albipennis* was reduced in the more isolated patches. Another study using logistic regression was performed in the treehopper *Gargara genistae* in a set of 237 patches of the host plant *Sarothamnus scoparius* (BIEDERMANN unpubl. data). Again, the inci-

dence was significantly affected by isolation, increasing distance to the next occupied patch was reducing the probability of occurrence in the patches.

In contrast, in other leafhopper species no effect of isolation could be detected. The spatial analysis of the distribution of the leafhopper *Adarrus multinotatus* showed no effect of isolation on the occupancy in the patches of the host plant *Brachypodium pinnatum* (BIEDERMANN 1997). In a set of 506 patches even patches with large distances to other patches had a high incidence. In the leafhopper *Macropsis scutellata* isolation had no effect on the incidence in 32 patches of *Urtica dioica* (ZABEL & TSCHARNTKE 1998).

Table 2: Summary of the results on the relationship between leafhopper density and patch area, +: positive, 0: no relationship; references: 1: LAWTON (1978), 2: RAUPP & DENNO (1979), 3: DENNO et al. (1981), 4: MACGARVIN (1982), 5: BIEDERMANN (1997), 6: BIEDERMANN (unpubl. data).

Species	Number of patches	Density-area relationship
<i>Ditropis pteridis</i> ¹	9	+
<i>Delphacodes detecta</i> ²	25	+
<i>Tumidagena minuta</i> ³	25	+
<i>Aphelonema simplex</i> ³	25	+
<i>Amplicephalus simplex</i> ³	25	0
<i>Destria bisignata</i> ³	25	0
<i>Megamelus lobatus</i> ³	25	0
<i>Philaenus spumarius</i> ⁴	24	0
<i>Adarrus multinotatus</i> ⁵	14	0
<i>Gargara genistae</i> ⁶	17	0

Species	Number of patches	Incidence-isolation relationship
<i>Philaenus spumarius</i> ¹	135	-
<i>Neophilaenus albipennis</i> ⁴	506	-
<i>Gargara genistae</i> ⁵	237	-
<i>Adarrus multinotatus</i> ²	506	0
<i>Macropsis scutellata</i> ³	32	0

Incidence, area and isolation

The simultaneous analysis of both area and isolation of the patches was performed in three species. In the spittlebug *Neophilaenus albipennis* both factors have a significant effect on the occurrence in the host plant patches. These two factors yet account for 27.2 % of the variance in the occurrence when analysed in a multiple logistic regression analysis (BIEDERMANN 1997). That is, even without considering habitat quality of the patches a rather high amount of variance was explained by these two factors of spatial configuration. In the treehopper *Gargara genistae* the relationship between occurrence and these two factors was similar. The amount of variance explained was 25.4 % (BIEDERMANN unpubl. data).

Table 3: Summary of the results on the relationship between leafhopper incidence and patch isolation, -: negative, 0: no relationship; references: 1: HALKKA et al. (1971), 2: BIEDERMANN (1997), 3: ZABEL & TSCHARNTKE (1998), 4: BIEDERMANN (2000), 5: BIEDERMANN (unpubl. data).

Using the same statistical procedure in another spittlebug, *Philaenus spumarius*, in the joint analysis of area and isolation of patches (data from HALKKA et al. 1971) these two factors even account for 57.5 % of the variance in the distribution.

Dynamics of incidence

Surveys of the distribution of species in several subsequent years or generations yield the dynamics of patch occupancy. The species may get extinct in some patches and other previously empty or new patches may be (re-) colonised. Metapopulation theory suggests that the extinction rate of species depends on patch area. In fact, in the spittlebug *Neophilaenus albipennis* the extinction rate is positively correlated with patch area (BIEDERMANN 2000). The extinction rate is high in small patches and decreases with increasing patch area. The mean yearly rate of extinction was estimated 3.9 %. The colonisation rate was comparable, the yearly rate was 4.9 %. The treehopper *Gargara genistae* showed a comparable turnover in patch occupancy (BIEDERMANN unpubl. data) with a shifted balance between the yearly extinction rate (11.1 %) and the yearly colonisation rate (1.9 %). In the spittlebug *Cercopis sanguinolenta* in a three-years period no extinction was recorded in ten local populations (BIEDERMANN 1998). Obviously, the yearly rate of extinction varies among leafhopper species. However, the database is too weak to deduce general conclusions from these results.

Synthesis

The fragmentation of habitats may have severe consequences on animal distribution (HARRISON & BRUNA 1999). Fragmentation leads to reduced patch area and as a result the extinction probability of local populations is high in small patches. Below a certain threshold a patch may be too small to maintain viable populations. The comparison of studies on leafhoppers demonstrated that the area requirements vary in a broad range. This variability may be attributed to parameters of population dynamics or life-history traits. Species which are able to build up high densities in their patches could reach sufficient population sizes to

reduce the extinction risk due to environmental stochasticity (LANDE 1993). Additionally, the resource concentration hypothesis (ROOT 1973, CONNOR et al. 2000) predicts higher densities in larger patches as a result of e.g. greater reproduction, reduced edge effect or reduced predator density.

On the other hand, dispersal could obscure the correlation between density and area. In species with a high dispersal ability like *Amplipcephalus simplex* or *Adarrus multinotatus*, all patches could be reached with high probability. Thus, initial differences in densities due to reduced performance in small patches may be levelled off by dispersing individuals. As a result, small patches may be sink-habitats (PULLIAM 1996). The outcome of such a process would be an equal density in all patches irrespective of its area. In fact, for the guild of leafhoppers on *Spartina patens* DENNO et al. (1981) suggest an association between positive area-density relationship and low dispersal ability of species (e.g. measured by the fraction of macropterous individuals).

The dispersal ability differs between species and may be correlated with the effect of isolation on the distribution in fragmented landscapes. Dispersing individuals may (re-) colonise patches which were empty or newly emerged. For instance, in the spatial analysis of the distribution of the leafhopper *Adarrus multinotatus* no effect of isolation on patch occupancy could be detected. In the same landscape a parallel investigation of the population genetics of *Adarrus multinotatus* was conducted. The results showed a concordant result, a high gene flow is suggested to exist between local populations at the regional scale (VEITH et al. 1996). In the spittlebug *Neophilaenus albipennis* which was studied in the same set of habitat patches, the distribution was significantly affected by isolation. As expected, in a mark-recapture experiment in *Neophilaenus albipennis* low dispersal rates were recorded (BIEDERMANN 1997).

The existing case studies on leafhoppers clearly demonstrate the effects of area and isolation on distribution and density in fragmented habitats. A set of hypotheses is available to explain these static patterns. However, these studies give only an idea of the importance of dynamic spatial processes. In particular, stu-

dies on the dynamics of the distribution (extinction and colonisation) in the habitat patches would be required in order to enhance our knowledge of spatial processes (e.g. turnover rates) at the regional scale. Effects of spatial configuration of patches on incidence and density as well as spatial dynamics of incidence are expected to be scale-dependent (WEBB & THOMAS 1994, KOENIG 1999, HE & GASTON 2000). Thus, future studies on several, hierarchically nested scales would assess the importance of scale on the identification of effects of area and isolation. The consideration of dynamic habitat patches (e.g. mosaic cycles) would incorporate an additional time scale into the analysis of regional leafhopper populations.

Zusammenfassung

Die Verbreitung von Zikaden ist in starkem Masse abhängig von der Verbreitung ihrer Wirtspflanzen. Pflanzen treten meist aggregiert auf und bilden oft gut abgrenzbare Bestände. Diese Bestände können sowohl in Natur- als auch in Kulturlandschaften zu einem gewissen Grad fragmentiert sein. Ein Überblick über die vorhandenen Untersuchungen an Zikaden in fragmentierten Landschaften stellt die Ergebnisse zum Einfluss von Flächengröße und Isolation der Wirtspflanzenbestände auf das Vorkommen und die Abundanz von Zikaden zusammen. Während nur wenige Informationen zur zeitlichen Dynamik der Verbreitungsmuster verfügbar sind, konnte in den meisten untersuchten Zikadenpopulationen ein Effekt von Flächengröße und Isolation auf die Dichte und das Verbreitungsmuster in den Wirtspflanzenbeständen nachgewiesen werden. Zunehmende Flächengröße resultiert häufig in höheren Dichten und höheren Inzidenzen, mit zunehmender Isolation hingegen sinkt die Inzidenz. Die Bedeutung dieser Ergebnisse wird im Hinblick auf die aktuelle Metapopulationstheorie diskutiert.

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