6. SUMMARY

Title: Structure of insect communities on scrubs: The Hemipteran fauna as an example of biodiversity in hedge and forest edge ecosystems

In this investigation aspects of organization and biodiversity of insect communities in hedgerow and forest edge ecosystems were analysed by studying the Hemipteran fauna [Insecta: Hemiptera: Heteroptera (bugs), Auchenorrhyncha (planthoppers, leafhoppers etc.), Aphidina (aphids) and Psyllina (fleahoppers)] on the scrub species rose (*Rosa* spp.), sloe (*Prunus spinosa* L.) and hawthorn (*Crataegus* spp.). For this purpose from 1989 until 1993 data on distribution and abundance of 80 Hemipteran species (54 on rose, 61 on sloe, 54 on hawthorn) were collected in different regions of Bavaria by beating at hedges and forest edges varying in habitat conditions and age. Community structure at young forest edges that were constructed experimentally within the study project „construction of rich structured forest edges" was compared with old ones. Based on these data, general structural patterns, aspects of biodiversity in local Hemipteran communities (species-abundance patterns, species composition, guild structure, diversity) and dynamics in space and time were presented, followed by the study of major influences for the generation of these patterns.

(A) Local dynamics of populations and communities

(1) Species abundance patterns of established Hemipteran communities at old forest edges mainly followed logarithmic models. They consistently yielded three species groups on all scrubs and sites of the study region: (a) Species with extremely high population densities in all or only certain years (i.e. aphids, psyllids); (b) species showing high to intermediate densities and nearly similar dominance ranks in all three study years (basic species pool) and (c) rare species with very small abundances. Temporal stability of community structure mainly depended on population dynamics of the dominant species (a,b).

(2) Fluctuations between years of dominant representatives of a guild could be explained by the actual dynamics and predictability of the resource used (e.g. phloem-sap, xylem-sap, mesophyll-sap, fruits or prey) and species-specific resource use strategy. In the resulting two-dimensional matrix (resource/strategy) all dominant species could be ranked within a continuum from „pulsing and low predictable ressources/opportunistic strategy and high fluctuations" (aphids, entomophagous Heteroptera, hibernating as adults) to „resources with relatively constant availability/less density fluctuations" (mesophyll feeders and entomophytophagous Heteropteran species, hibernating in the egg stage).

(3) There were no signs of density regulation as a result of strong intra- or interspecific competition, e.g. negative correlations between population densities of potential competitors or density compensation / competitive exclusion within one guild. Among the other mortality factors potentially influencing or controlling individual population densities (like abiotic environmental variability, predator and parasitoid pressure), none could be identified to play a dominant role for community structure. This „diffusive density control" usually kept individual population densities below a threshold beyond that competition may become important. Hence local Hemipteran communities are not saturated with species. Population dynamics of most Hemipteran species were independent of those found for other species on the same trophic level (individual density control). The actual community structure is influenced mainly by vertical, trophic interactions and less by horizontal, interspecific interactions (non-interactive communities).

(4) Dominant aphid species on rose and sloe presented a highly fluctuating and therefore unpredictable system component: In 1991 aphid reached extremely high densities at all sites, affecting Hemipteran community structure (guild structure, species-abundance patterns) in that

year, probably due to specific weather conditions that altered synchronisation with resource quality and predator activity.

(5) With the exception of such gradations, essential community features as species ranks, identity of dominant species (basic species pool, see above), guild structures and local species richness remained relatively stable and were reasonablely predictable both in temporal (within a season, between years) and spatial terms (within a region).

(B) Aspects of biodiversity in local communities

(6) Parameters measuring quantity and diversity of trophic and structural resources („habitat heterogeneity") on scrub level (fractal dimension of branch sections, scrub height) and on hedge level (e.g. hedge width, hedge structure) were the main determinants of biodiversity in local Hemipteran communities (species composition, species richness, diversity indices). As could be shown on scrub and site level, both development of habitat heterogeneity and colonization are dependend on time, especially in the first decades. Therefore, age plays a key role in determining actual community structure in hedges or forest edges: Old and/or rich-structured scrubs and biotopes generally had higher Hemipteran diversities than young and/or poor-structured ones.

(7) Hemipteran colonization of young woody species at experimentally constructed forest edges showed similar patterns at all sites of the study region: While assemblages in the first and second year of colonization were constituted mainly by chance, typical first colonization communities followed with high portions of species dwelling both on herbs and scrubs. From the fourth year onwards species composition approaches the situation in established communities as a result of increase in species numbers, especially in scrub-dwelling species. After 15-20 years of colonization, Hemipteran species numbers in planted hedges or forest margins reached similar levels compared with 50year old sites, but there still were differences concerning species-abundance patterns and community composition.

(8) Other variables like area, fragmentation and isolation of the biotopes showed less influence; they could explain local species numbers only according to their degree of correlation with resource and habitat diversity parameters. On average there were slightly higher species numbers at forest edges compared with hedgerows. The number of woody species per site did not affect local Hemipteran species richness on a specific scrub species. Total Hemipteran species richness of a hedge or forest edge, however, was positively related to the number of the scrub species (this was also true for Auchenorrhyncha species richness in herbaceous field edges).

(9) Analysis of data sets of different spatial scales and under varying regional conditions reveiled positive relations between local abundance and regional distribution in all cases (abundance-frequency relations). As could be shown for most Hemipterans, species with low ecological specificity reached high local average densities and a wide regional distribution, thus building a common species pool of "core species" [see (1)]. The remaining species, partly showing higher ecological specificity could be found only locally and/or in low abundances (complementary or "satellite species"); they were the reason for spatial or temporal species turnover. Depending on regional habitat diversity, sample effort and spatial scale, the patterns of regional distribution showed unimodal or bimodal species frequency curves.

(10) On sloe Hemipteran species numbers and community composition (especially of core species) showed only insignificant variability among 10 hedgerow areas on a North-to-South transect through Bavaria. The change of regional species pools resulting from observable recent range extensions in certain species indicate that local species richness of Hemipteran communities may also be affected or even determined by biogeographical processes.

(C) Basic patterns of the Hemipteran fauna of hedges and forest edges

(11) Body size of the 80 Hemipteran species studied covered three orders of magnitude, with small species being more numerous than large-sized ones. On average, oligophagous species were significantly smaller than polyphagous ones, likewise phytophagous species were smaller than entomophagous ones. Patterns of species-body size distributions were consistent among the three scrub species and frequently explained by or related to resource use (ecological constraints, e.g. resource or habitat size) and/or phylogenetic constraints. Studying abundance-body size relationships allways reveiled negative correlations, in which bigger species showing low abundances whereas small species were found in both high and low densities. Most Hemipteran species therefore did not follow the „rule of energy-equivalence".

(12) The Hemipteran fauna on rose, sloe and hawthorn in hedges and at forest edges shows a consistent and specific mixture of species with different life history strategies and ecological niches. This biodiversity is the result of constraints by the specific ecological conditions (resource distribution, habitat structure etc.) in hedges and forest margins.

The structure of present Hemipteran communities in hedges and at forest edges might be regarded as the actual result of „self-organizing processes", acting on different temporal (and spatial) scales, i.e. ecological time (population dynamics, succession and colonization), historical time (formation of hedges and forest edges in the course of human land use), prehistorical time (postglacial range extension) and evolutionary time (processes of speciation and adaptation). Compared with other plant-insect systems the species system studied takes an intermediate position within a continuum from "highly organized systems/predictable structure" and "chance-constructed systems/without predictable structure".