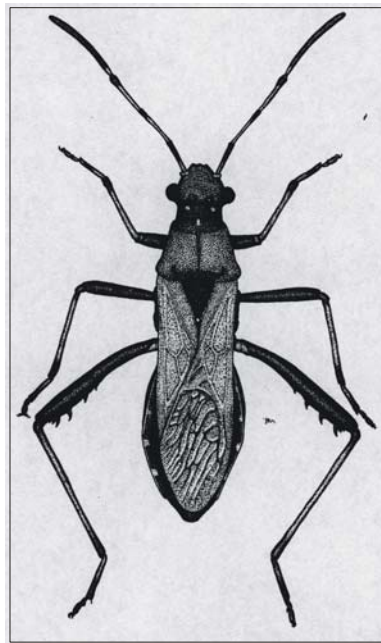


True bugs (Heteroptera) of steppes and extensive meadows in the Pfynwald (VS, Switzerland)

Diplomarbeit

der Philosophisch-naturwissenschaftlichen Fakultät
der Universität Bern



vorgelegt von
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Juni 2002

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Zusammenfassung

Die vorliegende Arbeit behandelt die Wanzenfauna von Steppen und extensiven Wiesen im Pfywald (VS, Schweiz). Das Hauptziel der Studie bestand darin, herauszufinden, welchen Einfluss die Bewirtschaftung auf die Wanzenfauna ausübt. Das Hauptaugenmerk lag dabei auf der Diversität der Wanzensynusien in Steppen und bewirtschafteten Wiesen, sowie dem Einfluss der Mahd.

Von Juli bis September 2001 wurden 10 verschiedene Flächen besammelt: 3 Steppen, 1 Halbtrockenwiese und 6 extensive Wiesen. Die Flächen befanden sich vorwiegend in der Milljeren, einem Teil des Pfywaldes.

Die Erfassung der Wanzen erfolgte mittels einer kombinierten Methode aus Kescher- und Sichtfang und dem Klopfrichter. Zusätzlich wurden auf jeder Fläche Umweltvariablen wie die Struktur und Zusammensetzung der Vegetation aufgenommen.

Im Untersuchungsgebiet wurden 144 Wanzenarten festgestellt, wovon 2 neu für die Schweiz und 41 neu für das Wallis sind. Verglichen mit anderen Arbeiten kann die Region als wertvoll für die schweizerische Wanzenfauna eingestuft werden.

Die Arten- und Individuenzahlen sind im Mittel in den Steppen höher als in den bewirtschafteten Wiesen.

Sowohl für die Steppen, die Halbtrockenwiese als auch für die Nutzwiesen wurden Spezies mit starker Affinität zu einem Biotoptyp (Bioindikatoren) gefunden.

Die Faunenverwandtschaft zwischen den Untersuchungsflächen wurde mit einer Clusteranalyse berechnet.

Die Beziehungen zwischen Wanzenzönosen und Umweltfaktoren wurde mit einer Canonical Correspondence Analysis (CCA) analysiert. Für die Wanzenzönosen der Steppen sind der Anteil der offenen Flächen, die Anzahl Pflanzenarten, die Vegetationsstruktur und die Strauchdeckung ausschlaggebend. Die Wanzenesellschaften der Halbtrockenwiese werden am besten durch die Strauchdeckung und die Vegetationsstruktur erklärt, diejenigen der Extensiven Wiesen durch die Feuchtigkeits- und Nährstoffzeiger.

Durch die Mahd werden sowohl die Arten- als auch die Individuenzahl signifikant reduziert, wobei räuberische und bodenlebende Wanzen weniger stark beeinflusst werden als phytophage Arten.

Summary

In this investigation the heteropteran fauna of unmanaged and managed xeric grassland was studied in the Pfynwald (VS, Switzerland). The main scope was to analyse the responses of true bugs to management with a focus on diversity of bug communities and the effects of mowing.

Samples were collected between July and September 2001 on 10 different plots: 3 steppes, 1 semi-natural grassland and 6 extensively managed meadows, situated in the Milljeren, part of the Pfynwald.

The true bugs were periodically sampled with the sweep-net, by visual search and the beating method. Additionally different environmental factors were measured such as the structure and the composition of the vegetation.

A total of 144 bug species were found. 2 species are new for Switzerland and 41 species are new for the canton of Valais. Therefore the region can be considered as rich in true bugs when compared with other Swiss areas.

On average the unmanaged steppes have a greater richness of species and higher abundances than the managed meadows.

Some species (indicators) were singled out with a great affinity either for steppes, semi-natural grassland or managed meadows.

A cluster analysis was carried out to detect the faunistical relationship between the Heteropteran fauna of the 10 sites.

The relationships between the bug communities and the environmental variables were analysed with canonical correspondence analysis (CCA). The percentage of open ground, number of plant species, total cover of shrubs and structure of vegetation are the decisive factors for the bug communities of the steppes. The bug community of the semi-natural grassland is best defined by the total cover of shrubs and the structure of the vegetation. For the extensive meadows the humidity and the value of nitrification of the soil – measured indirectly via the mean indicator values of the plant species – are determining.

By mowing the number of species and individuals were significantly reduced, predatory and ground-dwelling species less than phytophagous ones.

Introduction

Grasslands occur around the globe and are an important part of agriculture. They are characterized by a very high spatial and temporal heterogeneity determined by human activities. The present pattern of species diversity has been influenced by the history and the development of the landscape. How species are affected by this heterogeneity and how they can persist in agricultural systems is not entirely understood. There have been several studies on the influence of grassland management on insect diversity (e.g. MORRIS 1979, OTTO 1996, DUELLI & OBRIST 1998, DI GIULIO et al. 2001). As an example for management operations mowing has a direct effect on insects by damaging or killing individuals; mainly immobile species or developmental stages are affected. If management changes the habitat, e.g. alters the plant species composition or the structure of the vegetation, it also affects the microclimate that may alter community composition as many arthropods are very sensitive to microclimatic conditions (CURRY 1994).

The true bugs (Heteroptera) were chosen as an indicator group for insect diversity for various reasons: they are an ecologically very diverse group, including phytophagous, saprophagous and predatory species (DOLLING 1991). Some are generalists, with a ability to shift from one feeding type to another, while others are specialists (FAUVEL 1999). Furthermore both the larval stages and the adults live in the same habitat and react sensitively to environmental changes (MORRIS 1979, OTTO 1996). Finally DUELLI & OBRIST 1998 showed that the richness of the bug fauna strongly correlates with the total insect diversity.

In Switzerland some of the species richest habitats are natural xeric grasslands and traditional hay meadows. Some rare and endangered species are strongly associated with these habitats (BLAB et al. 1984 in OTTO 1996). Due to intensification in agriculture or abandonment many of these habitats have been lost throughout the last century. In Switzerland studies on true bugs in xeric grasslands have been carried out in the steppes of the Rhone valley by DELARZE & DETHIER (1988) and WITSCHI & ZETTEL (in press), by VOELLMY & SAUTER (1983) in the Swiss National Park and by GÖLLNER-SCHIEDING & REZBANYAI-RESER (1992) and OTTO (1996) in Ticino.

Due to climatic conditions (continental climate) an extraordinary flora and fauna was able to establish in the Rhone valley, including mediterranean elements.

Of special interest is the Pfywald (nature reserve since 1997) with its great diversity of habitats. The Rottensand, a dry floodplain, was already subject of several faunistic-ecological studies (GROSSENRIEDER & ZETTEL 1999, LOEFFEL et al. 1999, MÜLLER & ZETTEL 1999, ZEHNDER & ZETTEL 1999, WITSCHI & ZETTEL in press, WUNDER 2001). In this study the focus was put on agricultural land.

As an ecological compensation measure (since 1999) for a new motorway (A9), local agricultural policy encourages farmers to maintain traditional hay meadows as well as to reduce the intensity of grassland management by offering subsidies.

The aim of this study was firstly to contribute to the faunistic knowledge of the Heteroptera in the Rhone valley, especially the Pfywald area, secondly to study the responses of the true bugs to management, with a focus on diversity of bug communities in unmanaged and managed grasslands and the effects of mowing.

Hopefully the study will improve the understanding of applied grassland ecology and help to develop a suitable management policy to balance between sustainable production and the protection of grassland biodiversity.

Materials and methods

Research area and study sites

The research area is located in the Pfywald (VS, Switzerland). The soils are sandy sediments from an early glacial lake with a low capacity for water retention (BURRI & WINISTORFER in MATHIER et al. 1980). The mean yearly precipitation in Sion (elevation 482 m) is 649.9 mm, rainfall being lowest from March to July. The mean annual temperature is 10.3 °C with a maximum in August (20.1 °C) and a minimum in December (-1.7 °C). Mean annual sunshine duration is 2016.7 h (SMA, Anetz Station Sion 2001). The region is not only characterized by its low precipitation and high sunshine duration but also by its great daily and annual fluctuations in temperature and rather strong winds that intensify the effects of the dryness (WERNER 1985, BILLE & WERNER 1986). The study site (Milljeren) is an extensively managed area with a number of more or less isolated enclaves of agricultural land surrounded by a nature reserve. The Milljeren is characterized by a dense mosaic of different habitats: meadows, semi-natural grasslands, hedges, ponds, orchards and also more intensively managed cornfields.

For our study we focused on two types of grassland: extensively managed meadows and unmanaged steppes, including one semi-natural grassland. The steppes, occurring only in the driest and warmest places (WERNER 1985, DELARZE et al. 1999), are part of the protected area. We interviewed the farmers to assess the particular characteristics of their management: time and amount of irrigation, number and time of mowings, amount and type of fertilizer used, grazing, previous management (Tab. 1, Appendix 1). For the irrigation the farmers use a traditional system of water channels (Suonen); with the uneven terrain they do not allow a uniform irrigation of the meadows.

Sampling methods

Each site was sampled 5 times between 9. July and 28. September 2001. Sampling was carried out at intervals of 2 to 3 weeks (Tab. 2), and under good weather conditions only (minimal air temperature 14° C, no rainfall).

Combined sweep-net / visual search method

To compare the heteropteran communities in the different meadows we used a standardized sweep-net method after KONTKANEN (1950 in WITSACK 1975). On each site a transect of 1.5 x 100 m was established, which was sampled at each sampling series. Samples were collected by making 100 sweeps evenly distributed along the transect. After every 10th sweep the net was emptied, the Heteroptera and the Saltatoria being transferred to perspex tubes for later determination. The resulting 10 subsamples were considered as one series of samples. The round sweep-net had a diameter of 40 cm and was equipped with a handle of 1m length.

In addition to the sweep-net I searched the vegetation and the ground surface of the same transect for true bugs ca. 2 hours after the netting.

The animals were collected with an aspirator or a small net (15 x 20 cm). For each individual the host plant was recorded. This search was necessary as ground-dwelling or hidden species are usually missed

with the sweep-net. To guarantee comparability among sampling series the search was always carried out in the same way.

For the comparison of the sites the data of the two methods were pooled, as visual search is complementary to but not independent from the previous netting.

Both methods are semi-quantitative and in order to obtain comparable results it is important always to use the same procedure as well as work in good and comparable weather conditions (WITSACK 1975). This is especially true for the visual search, which strongly depends on the searchers skills; large, coloured and slow species are more easily sampled than small, cryptic and agile ones.

Beating method

As a completion of the species inventory several trees and shrubs were sampled along the edge of the meadows with the beating method. They were chosen at random and in terms of accessibility. To enhance the species richness several tree species were sampled, which are listed in Tab. 3.

With a padded bamboo stick all branches up to a height of 3 m were hit 10 times. The animals fell through a cloth funnel (fixed onto a square frame of 60 x 45 cm) held under the beaten area into a jar fixed underneath and were sorted out afterwards. In contrast to the sweep-net and the visual search, beating is only a qualitative method.

Identification

As a part of the research area is under natural protection only few individuals per species were killed and used as specimens. All the other sampled individuals were compared to these specimens in the field and provided with an identification code. They were kept until the end of the sampling and then released within the part of the transect they had been sampled.

Most species can only be identified under the microscope or by dissecting the genitalia. Therefore field identification may not be entirely accurate. For this reason some species were pooled as genera: *Nysius* sp. (*N. ericae*, *helveticus* and *senecionis*, possibly also *graminicola*, *thymi* and *cymoides*), *Alloeotomus* sp. (*A. germanicus* and *gothicus*), *Deraecoris* sp. (*D. punctulatus* and *serenus*), *Orthops* sp. (*O. campestris* and *kalmii*), *Phytocoris* sp. (*P. austriacus* and *varipes*), *Europiella* sp. (*E. albipennis* and *artemisiae*), *Nabis* sp. (*N. pseudoferus* and *punctatus*, possibly also *ferus*), *Carpocoris* sp. (*C. pudicus* and *purpureipennis*) and *Palomena* sp. (*P. prasina* and *viridissima*).

The adult insects were identified with the keys of WAGNER (1952, 1966, 1967, 1970/71) and PÉRICART (1983, 1984, 1987, 1998a, 1998b, 1998c). The nomenclature followed GÜNTHER & SCHUSTER (2000). All species identifications were confirmed by R. Heckmann (Germany). The reference collection is located at the Zoological Institute of the University of Berne.

Environmental factors

Vegetation

The plant species composition of each meadow was assessed before the 2nd cut, i.e. between the 25. July and the 20. August within a surface of 8 x 8 m. We identified all herbs and shrubs and estimated their relative abundances as well as the total cover of the herb layer, shrub layer, tree layer, moss layer and the percentage of open ground (after BRAUN-BLANQUET in

FREY & LÖSCH 1998). The Gramineae were not identified (except *Stipa capillata* L.) but their total abundance was determined. The plants were identified after LAUBER & WAGNER 1998 and ROTHMALER 1995.

Vegetation structure

For each series of samples the vegetation structure of each meadow was determined using the point-quadrat-method: at 20 points distributed evenly along the transect the number of contacts of the vegetation to a vertical metal rod ($\varnothing = 0.6$ cm) were counted in defined heights categories (0 - 10, 10 - 20, 20 - 40, 40 - 60 and 60 - 80 cm). For further analyses we used the total number of contacts per site.

The results for the managed sites must be dealt with care, as the mowing was not synchronized between the sites and therefore the number of sampling dates before and after mowing was not always the same.

Temperature

In the centre of each site a thermologger (LITE) was installed. At hourly intervals the temperature at 5, 20 and 80 cm above ground and the soil temperature at a depth of 20 cm were recorded. The thermocouples were shaded and free air circulation was guaranteed (Appendix 2). Only the temperature measurements of the sites TS2, HTW, EW2, EW3, EW5 and EW6 were available for analysis. Of these sites the mean daily temperature, the daily maximal and minimal temperature of 21 days before the mowing and 32 days after the mowing were analysed.

Statistical Analysis

For the data analysis, all series of samples were pooled over time, resulting in one sample per site. For species data only the adults were considered, as larvae cannot be identified to the species level. To compare the study sites only the data from the combined sweep-net / visual search method were used.

As a first measure of differences between the bug communities the dominance structure, heterogeneity and evenness were calculated. The dominance indices were calculated using the formula in MÜHLENBERG (1993). The Brillouin Index and Smith & Wilson's Index of Evenness were computed as measures for heterogeneity and evenness (Programs for Ecological Methodology, 2nd ed., KREBS 1999). Like the Shannon function the Brillouin index is most sensitive to the abundances of the rare species in the community, but can also be used when the community samples are not random samples, as it is the case by using the visual search. The Smith & Wilson's Index of Evenness is based on the variance in abundance of the species, is independent from species richness and is sensitive to both rare and common species in the community (KREBS 1999).

To compare the extensive meadows and the steppes Mann-Whitney U-Tests were performed on the species richness, the number of individuals, the structure of the vegetation before mowing and the temperature (SPSS, version 10.0).

The response of true bugs to mowing was tested with a Wilcoxon Signed Ranks Test (SPSS, version 10.0). As the mowing was not synchronized, only the sampling series directly before and after cutting were compared.

To assess the relationship between plant species richness and heteropteran bugs as well as between the number of woody plants sampled with the beating method and the bug diversity

correlations were calculated using Spearman's rho as the correlation coefficient for non-parametric data (SPSS, version 10.0).

Similarities between the species composition of the sites were analysed using the Spearman rank order correlation coefficient. As fusion strategies the average linkage technique (UPGMA) was chosen (Multivariate Statistical Package (MVSP), version 3.0). With this clustering method the patterns revealed in the dendrogram precisely represent the structure of the original data set.

Canonical correspondence analysis (MVSP, version 3.0; TER BRAAK 1986) was used to study the influence of environmental factors on the bug communities. The environmental factors included were: structure of vegetation, number of plant species, total cover of shrub layer, percentage of open ground, mean weighted indicator value for humidity and mean weighted indicator value for nitrogen after LANDOLT (1977 in LAUBER & WAGNER 1998). The species composition is strongly influenced by sample size and rare species being only recorded in large samples. To minimize sampling effects only species occurring at least in three sites, each with at least 5 individuals, were considered for analysis. The data was log-transformed to normalize the distribution.

Results

Species spectrum and comparison of methods

Between the 9. July and the 28. September, 144 bug species out of 17 families were sampled (Tab. 4). This corresponds to approximately 1/5 of the Swiss heteropteran fauna (758 species, A. OTTO, unpublished list). It is suggested that the presented list is not complete, as even in the last series 7 species were added to the list.

For Switzerland no Red List of the true bugs is available yet, but according to the Red List of Germany *Coranus griseus* is lacking in Germany, *Lygaeosoma sardeum*, *Pyrrhocoris marginatus* and *Dicranocephalus albipes* are threatened by extinction. 10 further species are endangered (*Atractotomus kolenatii*, *Carpocoris pudicus*, *Catoplatus fabricii*, *Elatophilus nigricornis*, *Europiella albipennis*, *Macroplox preyssleri*, *Odontotarsus purpurolineatus*, *Phymata crassipes*, *Phytocoris minor* and *Staria lunata*) (GÜNTHER et al. 1998).

For 41 species no records for the canton of Valais were found (CERRUTTI 1937, 1939a-c, DELARZE et al. 1988, DETHIER 1974, 1980, FREY-GESSNER 1863, WITSCHI & ZETTEL in press). *Stygnocoris similis* and *Phytocoris insignis* are new for the Swiss heteropteran fauna (RALF HECKMANN pers. comm., AUKEMA et al. 1996, 1999, DI GIULIO et al. 2000, FREY-GESSNER 1864-66, OTTO 1994, 1995, 1996). They are marked with VS and CH in Tab. 4.

As expected, the Miridae were the most common family represented by 54 species. The Lygaeidae was represented by 24, the Pentatomidae by 19 species. Their percentage is slightly above the Swiss average. All other families were represented by less than 10 species, the Ceratocombidae, Platapsidae, Pyrrhocoridae and Stenocephalidae being represented by a single species only (Tab. 5). It must be considered that these families are also only represented by one (Ceratocombidae, Platapsidae) or two species (Pyrrhocoridae, Stenocephalidae) in Switzerland (GÜNTHER & SCHUSTER 2000).

The species number as well as the number of individuals increased until the end of August. After a sudden decrease in early September, the number of species pooled over all sites as well as pooled only over the unmanaged or the managed sites remained constant, while the

number of individuals increased again towards the end of September (Fig. 1).

Figs. 2 and 3 show the seasonal phenology of the three species richest families, Miridae, Lygaeidae and Pentatomidae. In the unmanaged sites (TS1-3, HTW, Figs. 2 a, b) the species number of the Miridae attained its maximum at the end of August, while the species number of the Pentatomidae attained it already in early August and the Lygaeidae remained more or less constant throughout the season (Fig. 2 a). The abundance of the Pentatomidae was highest in July, while the Miridae were most abundant at the end of August. Due to high number of *Nysius sp.* the abundance of the Lygaeidae attained its maximum not until the end of September (Fig. 2 b).

The seasonal phenologies of the same families in the managed sites (EW1-6, Figs. 3 a, b) were similar to those in the unmanaged sites until the end of August when the meadows were cut. After the mowing the species number as well as the numbers of individuals remained at a low level.

The comparison of the sampling methods showed that more species were found with sweep-net and visual search than with beating, but the differences are not significant. There are also no significant differences between the methods when comparing the species recorded only with one method (Fig. 4).

Comparison of the study sites

Species richness and abundance

The number of species differed greatly between the different study sites. The unmanaged sites have a significantly higher richness than the managed sites ($Z = -2.138$, $p = 0.038$; Fig. 5 a). Within the unmanaged sites the steppe TS3 was with 49 species most diverse and TS3 (39 species) had the lowest diversity. Among the managed sites the species richness ranged between 16 (EW3) and 43 species (EW1 & EW2).

A similar difference was present between the unmanaged and the managed sites considering the total number of individuals ($Z = -2.558$, $p = 0.1$) (Fig. 5 b). In the steppe TS3 the bugs were most abundant (1190 individuals). The lowest abundance was recorded for the extensive meadows EW3 and EW4 (140 and 141 individuals, respectively).

For each of the 3 habitat types indicator species can be singled out. A species was considered to be characteristic when it was recorded with at least 20 individuals and 80 % of all individuals in one habitat type.

For the steppe 9 species (4 Miridae, 3 Lygaeidae, 1 Alydidae and 1 Rhopalidae) were characteristic, for the semi-natural grassland 3 (1 Miridae, 1 Pentatomidae and 1 Platapsidae) and for the meadows 6 species (3 Miridae, 1 Berytidae, 1 Pentatomidae and 1 Tingidae). 3 further species (*Macroplox preysleri*, *Alydus calcaratus* and *Aelia acuminata*) were characteristic for unmanaged sites, steppes and semi-natural grassland, together (Tab. 6). In

Tab. 6 all characteristic species are listed, including is also the percentage of all individuals recorded for the respective habitat type.

Dominance structure and Diversity

In general *Nysius sp.* was the eudominant species in the steppes, followed by *Chlamydatus pullus* and *Ortholmus punctipennis*. The semi-natural grassland HTW was characterized by one eudominant species, *Macrotylus paykulli*; all other species are either subdominant (*Coptosoma scutellatum*) or recedent. In the extensive meadows no species attained eudominance. The dominant species were *Adelphocoris lineolatus* followed by *Chlamydatus pullus* and *Nabis sp.* (Fig. 6).

Considering the dominance structure of each site by its own (Appendix 4) the steppes TS1 and TS2 and the extensive meadows EW1 and EW4-6 were characterized by one eudominant taxon each, the steppe TS3 and the extensive meadows EW2 and EW3 by dominant taxon.

In TS1 and TS2 *Nysius sp.* attained eudominance; all other species were either dominant (*Chlamydatus pullus*, *Europiella sp.* in TS2), subdominant (*Adelphocoris lineatus*, *Lygus gemmelatus*, *Ortholmus punctipennis* and *Alydus calcaratus* in TS1, *Adelphocoris lineatus* and *Lygus gemmelatus* in TS2) or recedent. In the steppe TS3 *Nysius sp.* attained only dominance followed by dominant the *Chlamydatus pullus* and *Ortholmus punctipennis* and the subdominant *Trapezonotus arenarius* and *Adelphocoris lineatus*.

In the extensive meadows *Adelphocoris lineatus* (EW1, EW5), *Trigonotylus caelestialium* (EW4) and *Chlamydatus pullus* (EW6) attained eudominance. They were followed either by the dominant *Adelphocoris sp.* (EW1, EW6) or *Nabis sp.* (EW4, EW5). In the extensive meadow EW2 *Chlamydatus pullus* and *Adelphocoris lineatus* attained dominance while all other species were either subdominant (*Rhyparochromus pini*, *Stictopleurus abutilon* and *Nabis sp.*) or recedent. The extensive meadow EW3 was slightly different in its dominance structure. *Nabis sp.*, *Lygus rugulipennis* and *Chlamydatus pullus* were dominant followed by *Notostira elongata* and *Lygus pratensis*.

Due to higher species richness the steppes and the semi-natural grassland showed a higher diversity than the extensive meadows. In contrast the extensive meadows showed a higher evenness due to the more even dominance structure (Fig. 7). The highest diversity as well as the highest evenness was calculated for the site EW2.

CCA and Cluster analyses

The ordination model in Fig. 8 explains 98.6 % of the total variance of species (sum of all canonical eigenvalues 0.429). Thereof the first two axes explain 75.0 % of the variation when the species-environment relationship is considered.

The first axis (eigenvalue 0.249) accounted for 41.1 % of the species variance, the second for 12.8 % (eigenvalue 0.077) and the third for 9.2 % (eigenvalue 0.056).

The ordination diagram shows that the extensive meadows and the steppes are clearly separated and that the semi-natural grassland HTW is separated from both the steppes and the extensive meadows (Fig. 9).

The arrows representing the environmental variables indicate the direction of maximum change of that variable across the diagram and its lengths is proportional to the rate of change: thus a long arrow indicates a big change and also indicates that the change in the environmental variable is strongly correlated with the ordination axes

and thus with the community variation shown. The position of a species point in relation to the arrows indicates the environmental preference of that species. Each site point lies in the centroid of the points for species that occur in those samples.

The most important environmental variable for the steppes TS1-3 are the percentage of open ground, number of plant species and the total cover of shrubs. For HTW the most explanatory variables are the structure of the vegetation and the total cover of shrubs, while for the extensively managed meadows the mean indicator values for humidity and nitrogen are the decisive factors.

There is a significant correlation between the species number of plants and true bugs (Spearman's $\rho = 0.72$, $p = 0.019$) (Fig. 9).

The similarity in the cluster analyses (Fig. 10) is based on species richness and species abundances.

The unmanaged and the managed sites were clearly separated (Spearman coefficient = 0.2).

Within the unmanaged sites the semi-natural grassland splits very early from the steppes (Spearman coefficient = 0.26) while the fauna of the steppes TS1 and TS2 were most similar (Spearman coefficient = 0.78).

Within the managed sites the groups EW1 and EW2 and EW3-6 split very early. Within the group EW3-6 EW3 and EW5 as well as EW4 and EW6 were among each other most similar (Spearman coefficient = 0.68, respectively 0.55).

Responses of true bugs to mowing

The number of species as well as the number of individuals were significantly reduced by mowing ($Z = -2.371$ and $Z = -2.366$, respectively, $p < 0.05$, $N = 7$) (Fig. 12). In the steppe TS3 the number of species as well as the number of individuals were less reduced by mowing (outliers in Figs. 11a and 11b). This is ascribed to the high number of Lygaeidae, especially *Nysius sp.* at this site.

After the mowing the variance in the number of species and individuals is much smaller, seen in the compression of the boxes in Fig. 12, as the rare species disappeared and only common, polyphagous species persisted.

Tab. 7 shows the reduction of bug diversity by mowing on the level of ecological groups. Phytophagous species were reduced most (29 out of 42 species disappeared). Zoophagous and especially ground-dwelling species are less influenced by mowing: only 4 out of 9 respectively 17 disappeared after the mowing.

Relationship between true bugs and plants

True bugs on selected woody plants

26 trees have been sampled with the beating method. On 2 species (*Lonicera xylosteum*, *Rosa canina*) no bugs were found. On 4 further species (*Alnus incana*, *Ligustrum vulgare*, *Salix eleagnos* and *Larix decidua*) only single individuals were captured.

A total of 31 bug species were sampled with at least 2 individuals (Tab. 8). Thereof 16 species were sampled on one host-plant only (*Deraeocoris ruber* on *Corylus avellana*, *Deraeocoris lutescens* on *Quercus pubescens*, *Charagochilus weberi* on *Juniperus communis*, *Malacocoris chlorizans* on *Viburnum lantana*, *Pilophorus clavatus* on *Salix caprea* and *Elatophilus nigricornis*, *Orius niger*, *Alloeotomus germanicus*, *A. gothicus*, *Phytocoris poni*, *Atractotomus kolenatii*, *Atractotomus parvulus*, *Chlamydatus pullus*, *Phoenicocoris obscurellus*, *Pilophorus connamopterus*, *Pentatoma rufipes* and *Rhaphigaster nebulosa* on *Pinus sylvestris*).

There is a strong correlation between the number of trees per species sampled with the beating method and the number of sampled bug species on a host-plant (Spearman's $\rho = 0.746$, $p < 0.001$, $N = 20$) (Fig. 12).

Kleidocerys resedae was the most abundant species on the selected trees and was sampled on 15 different tree species with a total of 1068 individuals (Tab. 8). It was most abundant on *Betula pendula*, followed by *Quercus pubescens*, *Berberis vulgaris* and *Pinus sylvestris*. Its abundance increased constantly until mid August and declined again in September (Appendix 5).

True bugs on herbage

By visual search 51 species were recorded with at least 2 individuals on each host-plant. Thereof 12 species were sampled on a single host-plant only (*Syromastes rhombeus* on *Trifolium pratense*, *Lygaeus equestris* on *Vincetoxicum hirundinaria*, *Macrotylus paykulli* on *Ononis natrix*, *Graphosoma lineatum* on *Peucedanum oreoselinum*, *Corizus hyoscyami* on *Achillea millefolium*, *Odontotarsus purpurolineatus* on *Globularia punctata*, *Dicranocephalus albipes* on *Euphorbia seguieriana*, *Orthops campestris* and *O. kalmii* on *Anthriscus sylvestris* and *Stenodema laevigatum*, *Aelia acuminata* and *Myrmus miriformis* on grasses) (Tab. 9). They are considered to be monophagous in our research area although some are mentioned to be polyphagous in literature.

Among the herbs *Achillea millefolium* hosted most species (12 bug species) followed by *Trifolium pratense* with 10 and *Artemisia vallesiaca* with 9 species (Tab. 9). On the family level the most frequently visited were the Fabaceae (8 species) with 21 recorded bug species including 3 (*Syromastes rhombeus*, *Macrotylus paykulli*, *Coptosoma scutellatum*) that were sampled exclusively on this family, followed by the Asteraceae (6 species) with 19 species.

19 species were recorded on Graminaceae (incl. *Stipa capillata*), thereof 3 species (*Stenodema laevigata*, *Aelia acuminata*, *Myrmus miriformis*) were monophagous.

According to literature 5 species are strictly graminisug (*Aelia acuminata*, *Myrmus miriformis*, *Notostira elongata*, *Stenodema laevigata*, *Trigonotylus caelestialium*) and the zoophagous species *Nabis sp.* and *Phymata crassipes* lay their eggs preferably on grass (PÉRICART 1983, 1984, 1987, 1998a, 1998b, 1998c, WAGNER 1952, 1966, 1967, 1970/71).

Environmental factors

Vegetation

There is no significant difference in the plant diversity between the unmanaged and the managed sites ($Z = -1.283$, $p = 0.257$, $N_1 = 4$, $N_2 = 6$). Within the unmanaged sites the number of species ranged from 21 to 41 species, whereas they ranged from 11 to 30 in the managed sites. Of each site the plant species composition is given in Appendix 6, including abundances.

The analysis of the indicator values showed that the managed sites are significantly more humid and rich in nitrogen than the unmanaged sites ($Z = -2.467$, $p = 0.014$ and $Z = -2.245$, $p = 0.025$, respectively, $N_1 = 4$, $N_2 = 6$) (Fig. 13).

Overall no significant differences between the vegetation structure of the unmanaged and the managed grasslands could be found ($Z = -0.107$, $p > 0.9$, $N_1 = 4$, $N_2 = 6$) (Tab. 10). Also the comparison of the structure before the cutting (sampling series 1 and 2) does not reveal any differences ($Z = -0.64$, $p > 0.9$, $N_1 = 4$, $N_2 = 6$). The highest value was determined for the semi-natural grassland HTW.

Temperature

Significant temperature differences between sites occurred only at 5 and 20 cm above ground, and for mean and maximal temperatures only (Appendix 7).

Before mowing the mean daily temperature as well as the daily maximal temperature were significantly higher in the unmanaged steppes compared to the managed meadows ($T_{\text{mean}5}$: $Z = -4.488$, $p < 0.001$, $T_{\text{max}5}$: $Z = -5.574$, $p < 0.001$; $T_{\text{mean}20}$: $Z = -2.373$, $p = 0.018$, $T_{\text{max}20}$: $Z = -2.945$, $p = 0.003$; $N_1 = 42$, $N_2 = 84$) (Appendix 7).

After the mowing the only significant differences were between the daily maximal temperature ($T_{\text{max}5}$: $Z = -2.891$, $p = 0.004$; $T_{\text{max}20}$: $Z = -2.345$, $p = 0.019$; $N_1 = 64$, $N_2 = 128$).

Discussion

Species richness and comparison of methods

With the methods used it was impossible to cover the whole heteropteran fauna. Some families, especially ground-dwelling species like the Lygaeidae or the Cydnidae, which were not found at all, may be underestimated. There are three explanatory reasons:

1. We did not use pitfall traps because the number of bug species sampled by the pitfall traps is very low compared to the captured non-target organisms, e.g. ground beetles (STANDEN 2000) and because part of the research area is under natural protection. Nevertheless it must be taken into consideration that pitfall traps capture a different selection of Heteroptera compared with the sweep net (CHERRILL et al. 1994 in STANDEN 2000, DANA HAR 1998 in STANDEN 2000).
2. As already mentioned the visual search depends strongly on the searchers skills. Small, cryptic and agile species are easily missed, especially in dense vegetation.

3. Only few individuals per species were killed and identified. All the other individuals caught were compared to these specimens and identified in the field. Therefore it is likely that similar species could have been missed.

Xeric grasslands are species rich habitats, not only in regard to the Heteropterans but also to plants and other arthropods. With 144 species our research area can be considered as species rich, especially when is considered that only a relative small area was sampled in just one season, in comparison to the studies of OTTO 1996, where in 1994 and 1995 a total of 212 species were found on 23 different plots (semi-natural grasslands, meadows and pastures) in the Ticino and DELARZE & DETHIER (1988) where through two seasons 109 species were found on 10 steppes in the Rhone valley.

The found species composition is characteristic for xeric grassland. 73 species (50.7%) were also found in xeric grasslands in the Ticino (OTTO 1996). According to DI GIULIO et al. (2001) & OTTO (1996) the zoogeographical region is a main factor responsible for species composition, either due to historical factors (e.g. differences in former land use) or today's differences in landscape structure. It seems that the geographical distribution of terrestrial invertebrates tends to be patchier, with more species having restricted ranges than terrestrial vertebrates and plants (OTTO 1996).

As expected, the Miridae were the most common family. They prefer herbage as habitat (DOLLING 1991) and the sweep net is an adequate method for sampling them. Their percentage (37.5%) in the research area corresponds to the Swiss average (38%). The percentage of the Lygaeidae and the Pentatomidae, next to the Miridae the most common families, were also slightly above the Swiss average. The Lygaeidae occurred preferably in the steppes, due to their high percentage of open ground, while the Pentatomidae were most frequent in the semi-natural grassland.

With the beating fewer species were found than with the combined sweep-net / visual search method. This is due to the fact that with the beating a lower plant diversity was sampled and that many bugs live in the crown of woody plants which were out of reach.

Comparison of the study sites

General

The distribution of Heteroptera is strongly influenced by climate and vegetation (DOLLING 1991, CURRY 1994). The composition of a local heteropteran community seems to depend upon five main characteristics of the site:

(1) the climatic area and the micro-climatic characteristics of the site, (2) the vegetation type together with the existence of several strata, (3) the season, (4) the presence of prey for predatory species and (5) the influence of human practices (FAUVEL 1999, CURRY 1995).

When combining the results of species richness, diversity, cluster analysis and canonical correspondence analysis three habitat types can be discerned in the study area: the steppes TS1, TS2 and TS3, the semi-natural grassland HTW and the extensively managed meadows EW1 - EW6.

Steppe:

The steppes are characterized by high temperatures, low humidity, open ground and high plant diversity, including several specialized plant species (Caryophyllaceae, *Centaurea vallesiaca*, *Helianthemum nummularium*, *Astragalus onobrychis*, *Potentilla sp.* and *Stipa*

capillata). The heterogeneity of the vegetation structure and ground cover as well as the plant species richness provide a great number of niches for true bugs with different ecological needs.

The steppes were richest in bug species, including some generalists (e.g. *Adelphocoris lineolatus*, *Chlamydatus pullus*) but also rare and specialized species (e.g. *Lygaeosoma sardeum*, *Phymata crassipes*, *Coranus griseus*). A great number are xero-thermophilic (Tab. 4) and also some mediterranean species were found (e.g. *Staria lunata*, *Odontotarsus purpurolineatus*, *Gonocerus acuteangulatus*).

Semi-natural grassland:

Like the steppes the semi-natural grassland is characterized by rather high temperatures, low humidity and characteristic plants (*Ononis natrix*, *Onobrychis sp.*) but additionally by a dense vegetation cover and the stratification of the vegetation, including several shrubs within the sampling site.

The bug community in the semi-natural grassland is rather different from the other habitat types. Beside a few generalists the semi-natural grassland provides many niches for more or less specialized species, mostly xero-thermophilic or mediterranean species (*Cyrtopeltis geniculata*, *Pyrrhocoris marginatus*, *Dicranocephalus albipes*,). Hardly any ground-dwelling species were found as they normally need some open ground. The semi-natural grassland does not only provide niches for typical grassland species but, due to the shrubs, also for woodland species (e.g. *Macrolophus pygmaeus*).

Extensive meadows:

Generally the extensive meadows are characterized by a more temperate microclimate, a lower temperature and a higher humidity due to regular irrigation. The vegetation cover is more dense than in the steppes and nearly no open ground exists. The plant species composition is dominated by Gramineae, Fabaceae and Asteraceae.

Within the meadows three groups of bug communities can be recognized:

- (1) EW3 and EW5, the most intensively managed meadows (EW3 mowed 3 times, EW5 intensively irrigated) with a low plant diversity. They are very poor in species and the abundances are very low. Only more or less eurytope bug species were recorded, including mesophilic species (*Berytinus minor*, *Nabis sp.*).
- (2) EW4 and EW6, now extensively managed meadows, but formerly intensive cultures (corn) with the use of fertilizer and biocides. Like EW3 and EW5 they are very species poor and the abundances are very low. But unlike in EW3 and EW5 also xero-thermophilic species, mostly Lygaeidae were recorded (*Peritrechus geniculatus*, *P. gracilicornis*, *Trapezonotus arenarius*).
- (3) EW1 and EW2, since approximately 15 years extensively managed meadows with adjacent natural, xeric habitats. The bug communities were nearly as rich in species as the steppes. The vegetation structure and the plant diversity provide niches for generalists as well as for rare and specialized species (*Ceratocombus coleoptratus*, *Berytinus montivagus*, *Dicyphus annulatus*).

The variance within the managed meadows is rather high. Widespread, polyphagous species were found in all the extensive meadows in high abundances but rare and specialized species were only found in EW1 and EW2. In general, common, polyphagous species seem to persist

better in managed meadows than specialists. Some species may even profit from more intensive management (DI GIULIO et al. 2001). According to OTTO (1996) extensively managed xeric grasslands (cut once a year, no fertilizer and no irrigation) are the species richest biotops, combining a great number of generalists and specialists.

From our data we are not able to conclude that grazing has an effect on bugs. The meadows were only extensively grazed in autumn (October), and not every meadow is grazed every year. Several studies (BORNHOLDT 1991, OTTO 1996) showed that intense grazing reduces the diversity as well as the abundance of true bugs by defoliation, trampling and fertilizing by dung.

The study suggests that for maintaining species richness on a regional scale it is crucial to preserve a range of sites with a focus on natural xeric grasslands (steppes) and extensively managed meadows.

To some extent the results are comparable with the study of GRICHTING (2002) who investigated grasshoppers on the same transects and could also identify three distinct grasshopper communities for the habitat types steppe, semi-natural grassland and extensive meadow.

Indicator species

The occurrence of an indicator species is strongly correlated with environmental factors, either biotic (e.g. food, predators) or abiotic (e.g. humidity, temperature) (MARCHAND 1953). By definition indicator species have to be stenotopic. But it is important to realize that in different regions a species can behave differently according to different environmental factors (e.g. competition). Therefore one species can be used as an indicator in a restricted area only (OTTO 1996), and our selected indicator species may only be characteristic for grasslands in the Pfynwald area.

Steppe:

The indicator species of the steppes are generally adapted to dry and warm places. The majority of the species are xerophilic (*Nysius sp.*, *Ortholmus punctipennis*, *Trapezonotus arenarius*, *Europiella sp.* and *Charagochilus weberi*), some also thermophilic (*Nysius sp.*, *Ortholmus punctipennis*) two belonging to the mediterranean fauna (*Lygus gemmelatus*, *Camptopus lateralis*).

Lygaeidae were only characteristic for the steppes; most of them need open ground and a great number are xero-thermophilic and restricted to xeric grasslands.

Overall the most abundant species was *Nysius sp.* It is suggested that from this genus *N. ericae* was most abundant, since nearly 85% of all identified individuals belonged to this species. *N. helveticus* (4 identified individuals) and *N. senecionis* (2 identified individuals) were present in a much lower abundance. It is still possible that *N. thymi* and *graminicola* were present in the research area as these species often occur in the same places. Apart from occurring in the steppes *N. sp.* was represented by single individuals in 3 extensive meadows (EW2, EW4, EW5). According to PUTSHKOV (in PÉRICART 1998a) and MARCHAND (1953) *N. ericae* is xero-thermophilic and prefers sandy sites with little vegetation. In Europe at least two generations developed each year (PÉRICART 1998a), but it is possible that up to five generations may develop, as observed in the semi-arid plains in the USA (MILLIKEN 1918). *N. ericae* is polyphagous and feeding on seeds of Asteraceae and Fabaceae as well as on Chenopodiaceae and Rosaceae. It may occur in aggregations of hundreds of individuals per m² (PÉRICART 1998a) and become a severe cereal pest as observed in the USA (MILLIKEN 1918). *Nysius sp.* is widespread, adapted as well to mediterranean as to more temperate climates.

Semi-natural grassland:

The three species characteristic for the semi-natural grassland are all xero-thermophilic. Thereof *Graphosoma lineatum* is a mediterranean species and specialized on Apiaceae (*Peucedanum oreoselinum*) (WAGNER 1966).

In the semi-natural grassland *Macrotylus paykulli* was the eudominant species. It is of east-mediterranean origin (AUKEMA & RIEGER 1999). *M. paykulli* is a specialist feeding preferably on *Ononis natrix* (WAGNER 1952) and is therefore confined to arid meadows and semi-natural grasslands, where *Ononis sp.* as well as Apiaceae are typical plants.

Extensive meadows:

The majority of the indicator species of extensive meadows belong to the Miridae. They are either polyphagous (*Adelphocoris seticornis*, *Polymerus unifasciatus*) or grass-feeding species (*Trigonotylus caelestialium*). All indicator species of the extensive meadows are more or less eurytope or mesophilic, like *Berytinus minor* (PÉRICART 1984), which was restricted to the most irrigated and presumably most humid meadow EW5.

Among characteristic species *Trigonotylus caelestialium* was most abundant in the managed meadows. It is a eurytop grass-feeder with a holarctic distribution. At least 2 generations develop each year: the first one turns up mid May to mid June, the second one mid August. In Germany it was found in extremely dry sites as well as in humid meadows (RIEGER 1978). At Pfyf *T. caelestialium* prefers the more temperate managed meadows.

Responses of true bugs to mowing

It is known that a intensification of management (3 to 6 cuts per year, more fertilizer) causes a loss of species diversity in flora and fauna, and this is also true for Heteroptera. By mowing, the habitat of true bugs is changed suddenly. Not only the structure of the habitat and therefore the micro-climate is changed (BORNHOLDT 1991) but also nearly all food resources (blossoms, seeds, leaves) of phytophagous species disappear. Mowing also has a direct effect on adults and especially larvae by damaging or killing them. Furthermore by removing the swath eggs laid in plants may be removed from the habitat. DI GIULIO et al. (2001) found out that not only the number of mowings but also the timing in relation to the life cycle is important since mainly the immobile larval and egg stages are influenced by mowing. In general more widespread species with several generations per year have a better chance of persisting in highly disturbed habitats than specialized or rare ones which are monovoltine (MORRIS 1979, OTTO 1996, DI GIULIO et al. 2001).

It seems that abundances of phytophagous species are more reduced by mowing than those of predatory or ground-dwelling species. This findings are supported by the studies of MORRIS (1979, 2000) and OTTO (1996).

Mowing can be beneficial for ground-dwelling and predatory species as it firstly prevents the succession of the meadows, secondly reduces the spatial resistance and thirdly causes a rise in temperature at the micro-climatic level which is especially beneficial for ground-dwelling xero-thermophilic species.

Within the mowed sites the steppe TS3 is a special case as also after the mowing a high number of species and individuals were recorded, mainly due to the high number of Lygaeidae which may benefit from mowing. Compared to the other sites not all swath is cleared away after mowing and so the bugs may still feed on seeds. Further some

plants remained in the steppe and not the whole site was mowed (refuge habitats).

In agricultural landscape suitable food is often available only temporarily (seasonally or according to management). Invertebrates may have the problem of colonise suitable habitats in a different place after mowing or after hibernation. Therefore a mosaic of different habitats as it is present at Milljeren (including meadows cut at different times) are important as refuges for the persistence of populations.

There is no perfect timing of mowing as species respond differently. Generally one late mowing (mid August) is recommended for invertebrates, so that many species can develop undisturbed (OTTO 1996). Early mowing (May) reduces the abundance of many species, as many true bugs hibernate as eggs laid on the leaves of herbs or grasses or their larval development is not yet finished and are therefore damaged or killed by mowing. For many species a strip-management could permit a withdrawal to either a uncut part of the meadow or a part where the plants are already regrown.

Relationship between true bugs and plants

The majority of Heteroptera feed on vascular plants. The plant species richness and also the vegetation structure provide a great number of trophic niches. In most of the natural habitats dicotyledons are the dominant form of vegetation. They greatly outnumber the other vascular plants in terms of species. Herbs normally die down in winter and are also structurally simpler than trees and shrubs, providing fewer ecological niches. For these reasons, herbs generally host fewer insects species than woody plants, but there are much more species of herbs so that roughly equal numbers of insects are associated with the two structural types (DOLLING 1991). Next to herbs grasses are a major feature of meadows. They owe their present-day predominance to human activities in managing the countryside for pastures and extensive meadows and to the fact that our major food crops are cereals. Before Man cleared the forest, grasses must have covered a small fraction of the area now dominated by them.

Many species could be found only once on a host plant. Some of these single captures were surely made by chance; because monophagous species are often rare and polyphagous ones are found on many host plants but not necessarily in high abundances (MARCHAND 1953).

True bugs on woody plants

The most abundant species on woody plants was *Kleidocerys resedae*, a phytophagous bug usually feeding on Betulaceae and other broad-leaved trees (PÉRICART 1998a, WAGNER 1966). In northern regions (Finland, Sweden) the species was also found on different species of Ericaceae. The major host plant for *K. resedae* in the research area was *Betula pendula*, but it seems that with high abundances also *Pinus* can be used as a host plant.

A great number of zoo- or zoo-phytophagous species live preferably on trees, feeding on other bugs, psyllids, aphids or caterpillars. Being often more agile than phytophages (GÖLLNER-SCHEIDING 1989) they have a natural advantage in the trees.

True bugs on herbage

The important host plants in the research area belong to the families Fabaceae and Asteraceae, the most abundant families in the research area, including some species that are essential for specialists (e.g. *Ononis natrix*, *Onobrychis viciifolia*). Some plants occurring only in xeric

grasslands, like *Peucedanum oreoselinum*, *Euphorbia seguieriana* and *Vincetoxicum hirundinaria* are important hosts for specialists (*Graphosoma lineatum*, *Dicranocephalus albipennis* and *Lygaeus equestris*).

Most phytophagous true bugs feed on seeds and leaves, few on blossoms. WITSCHI & ZETTEL in press (2001) reported, that the number of bug species and individuals on *Centaurea vallesiaca* correlated with the flowering stage. Interestingly the highest abundances on e.g. *Achillea millefolium* and *Globularia punctata* were recorded after bloom. It seems that many species profit from ripening ovules and seeds which are known to be very nutritious. It is also possible that these plants are not only a food resource but are also important shelters.

Next to herbs grasses are an important food resource for true bugs (leaves and grains). Unlike herbs they are nearly available all year as they grow very fast either in spring or after a disturbance like mowing. Most grass-feeding Heteroptera belong to the family Miridae. These include all european members of the specialized tribe Stenodemini (*Stenodema*, *Notostira*, *Trigonotylus*). In the research area the Stenodemini are predominantly found in the extensive meadows (> 90%). Other grass-feeding Heteroptera are found in the extensive meadows as well as in the steppes and semi-natural grassland. Among the Heteroptera some Pentatomoidea are major pests of cereals in Europe. Predominant among these are the genera *Eurygaster* and *Aelia* which normally feed on the vegetative parts and grains of wild and pasture grasses (DOLLING 1991).

Acknowledgements

I would like to thank all the people who helped me carrying out this investigation:

First of all Jürg Zettel, the leader of our group, for the support and constructive critics. Ralf Heckmann for helping me with the determination and for many useful hints. Stefan Grichting who carried out his study on grasshoppers on the same sites for the good team work. Dita Vizoso for her critical reading of the manuscript and her friendship. Jean-Pierre Airoidi for statistical help. All the farmers for permission to work on their fields.

I would also like to express my gratitude to Fam. Bieri and Fam. Salamin for their hospitality throughout the field season. To Corinne Mosimann, Daniela Mühlheim, Irene Künzle and Cyrill Rémy for the good working climate. And to my family for their support and love.

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Tables

Figures

Appendix

Tables

- Tab. 1:** Study sites
- Tab. 2:** Sampling dates
- Tab. 3:** Tree and shrub species sampled with the beating method. Given are the number of trees and shrubs sampled.
- Tab. 4:** Complete list of the recorded bug species in alphabetical order, the nomenclature following GÜNTHER (2000). Single captures are listed under First catch. Species difficult to identify in the field were pooled (}).
- For **study sites** abbreviations see Tab. 1.
- Sampling method:** SN = sweep-net; VS = visual search; B = beating method
- Diet:** z = zoophagous or partly zoophagous according to literature (WAGNER 1952, 1966, 1967, 1970/71; PÉRICART 1983, 1984, 1987, 1998, FAUVEL 1999); ph = phytophagous; m = monophagous, recorded more than once on one host plant only; p = polyphagous, sampled on more than one host plant, each with at least two individuals
- CH** = record new for Switzerland; **VS** = record new for the canton Wallis
- Tab. 5:** Number of species per family and the relative abundance of the families. As a comparison the relative abundance in the Swiss heteropteran fauna is given.
- Tab. 6:** Bug species characteristic for the three types of habitat, steppe, semi-natural grassland and extensive meadow. % = percentage of all recorded individuals which was found in this habitat type.
* = species that were recorded with less than 20 individuals.
- Tab. 7:** Number of species present before and after the mowing. After the mowing only species were considered that were present also before mowing.
- Tab. 8:** True bugs on selected woody plants. Only species are listed that were recorded with at least two individuals on one host plant. Species recorded outside the sampling site are marked (*). Nr. = species number according Tab 4.
- Tab. 9:** True bugs on herbage. Only species are listed that were recorded with at least two individuals on one host plant. Zoophagous or partly zoophagous species are marked (z). Species recorded outside the sampling sites are marked (*).
- Tab. 10:** Vegetation structure of each meadow determined with the point-quadrat-method. Given are the total number of contacts of the vegetation to a vertical metal rod pooled over all sampling series.

Tab. 1:

Study sites		Vegetation type	Swiss coordinates
TS1	unaffected/uninfluenced steppe	Stipo-Poion carniolicae	610375 / 127625
TS2	unaffected/uninfluenced steppe		610177 / 127423
TS3	steppe, cut once or twice a year, used as a training field for dogs		610150 / 127386
HTW	Semi-natural grassland, former vineyard (30 years ago), strong exposure to sunlight	Mesobromion	611066 / 128071
EW1	Extensive meadow, cut twice, mid June and late august, grazed with sheeps, no fertilizer, irrigated	Arrhenatherion	610792 / 127842
EW2	Extensive meadow, cut twice late June and late august, no fertilizer, irrigated, until 20 years ago intensive corn culture		610809 / 127540
EW3	Extensive meadow, cut three times, late May, early July and late August, grazed with sheeps, fertilized every 2 to 3 years with dry sheep dung, watered, until 6 years ago intensive rye culture		610536 / 127607
EW4	Extensive meadow, cut twice, late June and late August, fertilized, irrigated, until 20 years ago intensive corn culture		610532 / 127475
EW5	Extensive meadow, cut twice, late June and late August, grazed with horned cattle or sheeps, irrigated		711643 / 127424
EW6	Extensive meadow, cut twice, mid June and mid august, in some years grazed with sheeps, fertilized every two or three years with dry sheep dung, until 7 years ago intensive corn culture		610598 / 127062

Tab. 2:

Serie of samples	1	2	3	4	5
TS1	11. 7.	6. 8.	23. 8.	11. 9.	25.9
TS2	23. 7.	13. 8.	27. 8.	15.9	28. 9.
TS3	22. 7.	7. 8.	24. 8.	9. 9.	21.9
HTW	24. 7.	12. 8.	28. 8.	13. 9.	27.9
EW1	9. 7.	31. 7.	15. 8.	29. 8.	18.9
EW2	12. 7.	1. 8.	16. 8.	5.9	19.9
EW3	21. 7.	5. 8.	26. 8.	8.9	22.9
EW4	13.7	3.8	25.8	12.9	26. 9.
EW5	14. 7.	30. 7.	21. 8.	3. 9.	17. 9.
EW6	17.7	2. 8.	22. 8.	6. 9.	20. 9.

Tab. 3:

Nr.	Species	TS1	TS2	TS3	HTW	EW1	EW2	EW3	EW4	EW5	EW6	Tot
	Broad-leaved trees											
1	<i>Alnus incana</i>								1			1
2	<i>Berberis vulgaris</i>	1		2								3
3	<i>Betula pendula</i>		2	5	1	2		2			3	15
4	<i>Cornus sanguinea</i>					2		3				5
5	<i>Corylus avellana</i>						1		1			2
6	<i>Fraxinus excelsior</i>			1								1
7	<i>Hippophaë rhamnoides</i>					2						2
8	<i>Ligustrum vulgare</i>				1					1		2
9	<i>Lonicera xylosteum</i>						1					1
10	<i>Populus alba</i>				2			1	2		1	6
11	<i>Populus nigra</i>	2			1	1	3	2	2	2	3	16
12	<i>Populus tremula</i>		1		1		1			1		4
13	<i>Prunus avium</i>					1						1
14	<i>Prunus mahaleb</i>		1	3		2	1			1		8
15	<i>Quercus pubescens</i>	2	1		2	2	4	1	3		2	17
16	<i>Robinia pseudoacacia</i>									1		1
17	<i>Rosa canina</i>	1										1
18	<i>Salix caprea</i>									2		2
19	<i>Salix eleagnos</i>	2	2	1								5
20	<i>Salix purpurea</i>		1			1						2
21	<i>Sorbus aria</i>	1	1		1		1					4
22	<i>Viburnum lantana</i>					1	1	1	1		1	5
	Conifers											
23	<i>Juniperus communis</i>	1	2					1				4
24	<i>Larix decidua</i>										1	1
25	<i>Picea abies</i>										1	1
26	<i>Pinus sylvestris</i>	5	4	3	6	1	2	4	5	2	3	35
	Total:	9	9	12	9	14	13	10	10	8	10	

Tab. 4:

Tab. 4 cont.:

Tab. 4 cont.:

Tab. 5:

Family	N species	% at Pfyf	% in CH
Miridae	54	37.50	37.9
Lygaeidae	24	16.67	15.3
Pentatomidae	19	13.19	7.2
Anthocoridae	7	4.86	3.6
Coreidae	6	4.17	3.3
Rhopalidae	6	4.17	1.9
Nabidae	5	3.47	2.0
Scutelleridae	5	3.47	1.0
Tingidae	4	2.78	5.9
Berytidae	3	2.08	1.3
Reduviidae	3	2.08	2.0
Acanthosomatidae	2	1.39	1.0
Alydidae	2	1.39	0.6
Ceratocombidae	1	0.69	0.1
Platapsidae	1	0.69	0.0
Pyrrhocoridae	1	0.69	0.3
Stenocephalidae	1	0.69	0.0
17 families	144 species		

Tab. 6:

	Species	%
Steppes	<i>Ortholmus punctipennis</i>	100.0
	<i>Europiella sp.</i>	100.0
	<i>Nysius sp.</i>	99.4
	<i>Lygus gemmelatus</i>	98.8
	<i>Rhopalus parumpunctatus</i>	85.9
	<i>Trapezonotus arenarius</i>	85.7
	<i>Phytocoris insignis</i>	84.0
	<i>Camptopus lateralis</i>	80.6
	<i>Charagochilus weberi</i>	80.0
Semi-natural grassland	<i>Macrotylus paykulli</i>	100.0
	<i>Coptosoma scutellatum</i>	85.3
	<i>Graphosoma lineatum</i>	84.2
steppes and semi-natural grassland	<i>Macroplox preysleri</i>	100.0
	<i>Alydus calcaratus</i>	80.3
	<i>Aelia acuminata</i>	80.0
Extensive meadows	* <i>Berytinus minor</i>	100.0
	* <i>Kalama tricornis</i>	100.0
	<i>Adelphocoris seticornis</i>	98.7
	<i>Eysarcoris aenaeus</i>	96.2
	<i>Polymerus unifasciatus</i>	85.7
	<i>Trigonotylus caelestialium</i>	98.9

Tab. 7:

	before mowing	after mowing
Phytophagous species (others than Miridae)	25	6
Phytophagous Miridae	17	7
Zoophagous species	9	5
Ground-dwelling species	17	13

Tab. 8:

Nr.		<i>Berberis vulgaris</i>	<i>Betula pendula</i>	<i>Cornus sanguinea</i>	<i>Corylus avellana</i>	<i>Fraxinus excelsior</i>	<i>Hippophaë rhamnoides</i>	<i>Populus alba</i>	<i>Populus nigra</i>	<i>Populus tremula</i>	<i>Prunus avium</i>	<i>Prunus mahaleb</i>	<i>Quercus pubescens</i>	<i>Robinia pseudoacacia</i>	<i>Rubus sp.</i>	<i>Salix caprea</i>	<i>Salix purpurea</i>	<i>Sorbus aria</i>	<i>Viburnum lantana</i>	<i>Juniperus communis</i>	<i>Picea abies</i>	<i>Pinus sylvestris</i>	Total number of individuals
2	<i>Elasmucha grisea</i>		4								4												8
7	<i>Elatophilus nigricornis</i>																					3	3
8	<i>Orius horvathi</i>				2																	2	4
10	<i>Orius niger</i>																					2	2
16	<i>Coreus marginatus</i>		3						6*						6*				2*				17
18	<i>Gonocerus acuteangularis</i>	2		3																			5
24	<i>Kleidocerys resedae</i>	70	673	13		7	20	17	17	6	14	4	143	3		3			10			68	1068
49/50	<i>Alloeotomus germanicus/gothicus</i>																					42	42
53	<i>Deraeocoris ruber</i>				2																		2
54	<i>Deraeocoris lutescens</i>												3										3
60	<i>Charagochilus weberi</i>																			3			3
69/70	<i>Phytocoris austriacus/varipes</i>	2																				2	4
74	<i>Phytocoris pini</i>																					4	4
75	<i>Phytocoris reuteri</i>			2																		14	16
81	<i>Blepharidopterus angulatus</i>		7						8														15
85	<i>Malacocoris chlorizans</i>																						5
87	<i>Atractotomus kolenatii</i>																					2	2
88	<i>Atractotomus parvulus</i>																					12	12
89	<i>Chlamydatus pullus</i>																					2	2
95	<i>Phoenicocoris obscurellus</i>																					6	6
96	<i>Pilophorus cinnamopterus</i>																					52	52
97	<i>Pilophorus clavatus</i>															2							2
101	<i>Himacerus apterus</i>		4	4			2	4	2			2								2	2	30	52
109	<i>Dolycoris baccarum</i>		2									3						2				5	12
110	<i>Eurydema oleracea</i>																			2			2
111	<i>Eurydema ornatum</i>											2											2
114/115	<i>Palomena prasina/viridissima</i>		2	3																		5	10
116	<i>Pentatoma rufipes</i>																					2	2
118	<i>Piezodorus lituratus</i>							3					7									3	13
119	<i>Rhaphigaster nebulosa</i>																					3	3
132	<i>Rhopalus parumpunctatus</i>																				2		2
	Total number of species	3	7	5	2	1	2	2	5	1	2	3	4	1	1	1	1	1	3	4	1	19	
	Total number of individuals	74	695	25	4	7	22	21	30	6	18	9	155	3	6	3	2	2	15	9	2	259	

Tab. 10:

Sampling sites	Vegetation structure
TS1	356
TS2	292
TS3	371
HTW	913
EW1	468
EW2	351
EW3	371
EW4	368
EW5	609
EW6	349

Figures

- Fig. 1:** Seasonal phenology of the total number of species and individuals, pooled over all sites.
- Fig. 2:** Seasonal phenology of the total number of (a) species and (b) individuals of Miridae, Lygaeidae and Pentatomidae pooled over the unmanaged sites, steppes TS1-3 and fallow HTW.
- Fig. 3:** Seasonal phenology of the total number of (a) species and (b) individuals of Miridae, Lygaeidae and Pentatomidae pooled over the managed sites, extensive meadow EW1-6.
- Fig. 4:** Efficiency of the sampling methods. Grey: number of species sampled exclusively with this method. SN = sweep-net; VS = visual search; B = beating method
- Fig. 5:** Comparison of number (a) of species and (b) individuals in unmanaged (steppes) and managed (extensive meadows) sites. For significance see text.
- Fig. 6:** Dominance structure for steppes (TS1-3), semi-natural grassland (HTW) and extensive meadows (EW1-6). Dominance index D after MÜHLENBERG (1993).
- Fig. 7:** Diversity and Evenness of each study site. Bars = the Brillouin's Index, points = Smith & Wilson's Index of Evenness.
- Fig. 8:** Ordination diagram based on canonical correspondence analysis. Environmental variables are represented as vectors, site scores and species scores as centroids. Site score abbreviations see Tab. 1, species scores are labeled with species number according to Tab. 4. For further information see text.
- Fig. 9:** Correlation between the species number of plants and heteropteran bugs (Spearman's $\rho = 0.72$, $p = 0.019$, $N = 10$, confidence interval set at 95 %).
- Fig. 10:** Cluster analysis of the study sites using the Spearman rank order correlation coefficient as a measurement of similarity, based on species richness and abundance.
- Fig. 11:** Responses of the bug community to mowing. A pairwise comparison was conducted with a Wilcoxon Signed Ranks Test. (a) numbers of species, (b) numbers of individuals. For significance see text. °TS3, *TS3 = outliers
- Fig. 12:** Correlation between the number of trees per species sampled and the heteropteran bugs (Spearman's $\rho = 0.746$, $p < 0.001$, $N = 20$, confidence interval set at 95 %).
- Fig. 13:** Mean indicator values for (a) humidity and (b) nitrogen in unmanaged and managed sites. For significance see text.

Fig. 1:

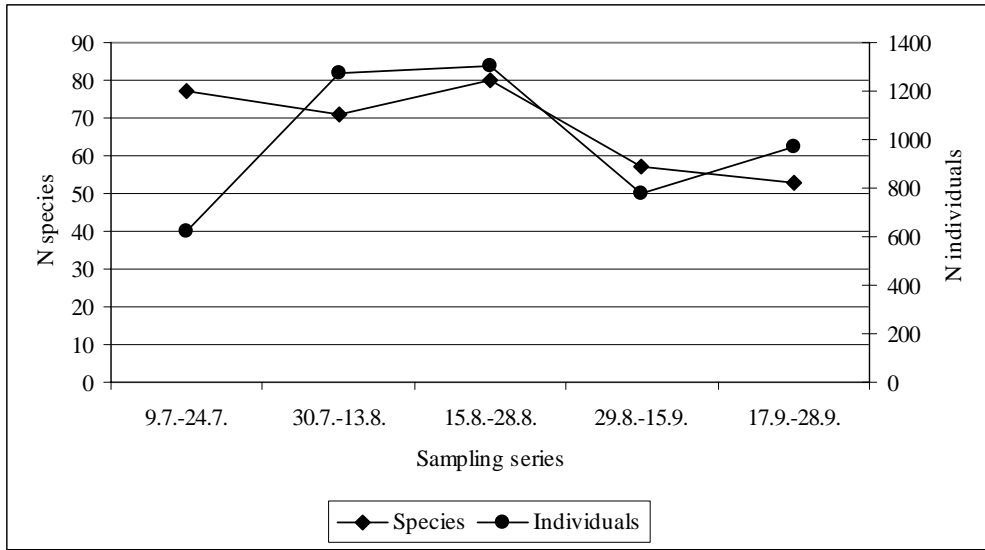


Fig. 2a:

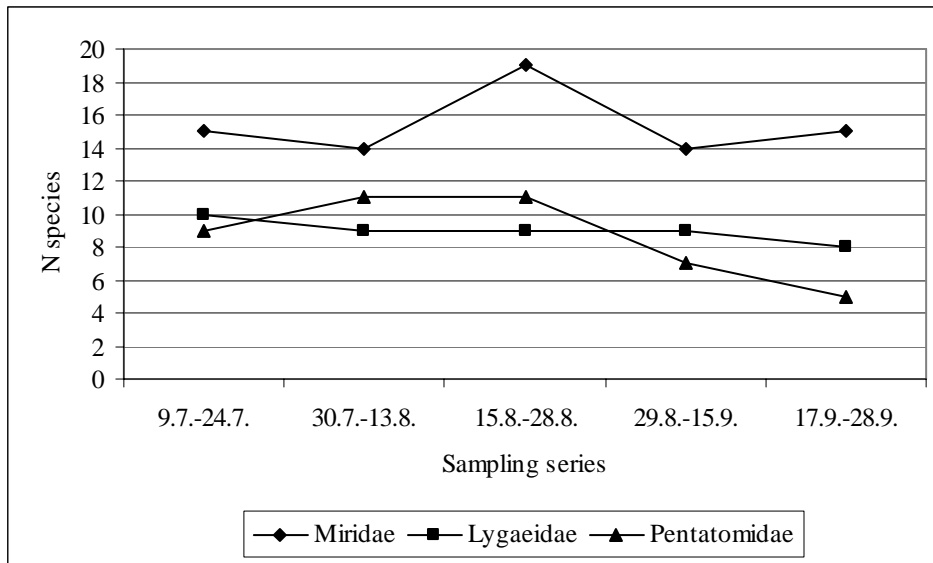


Fig. 2a:

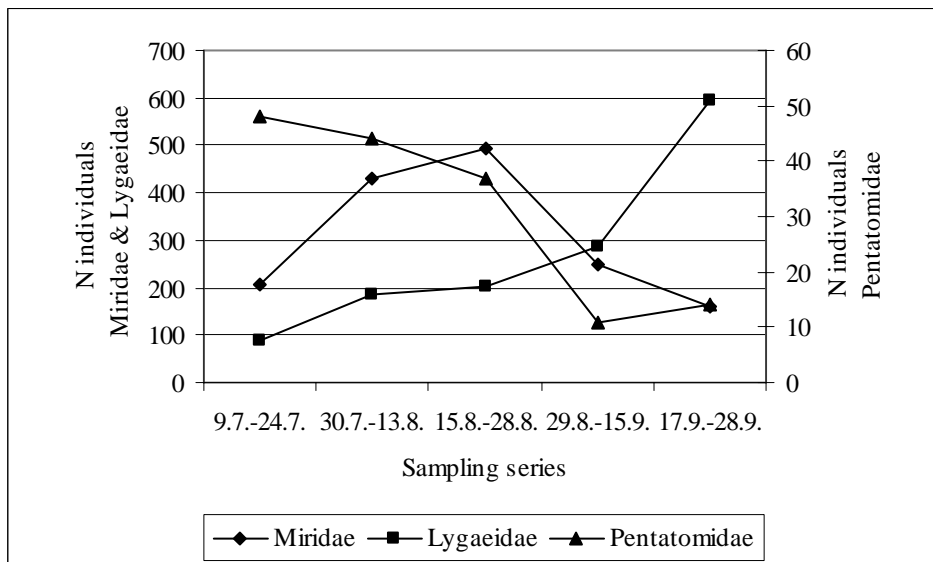


Fig. 3a:

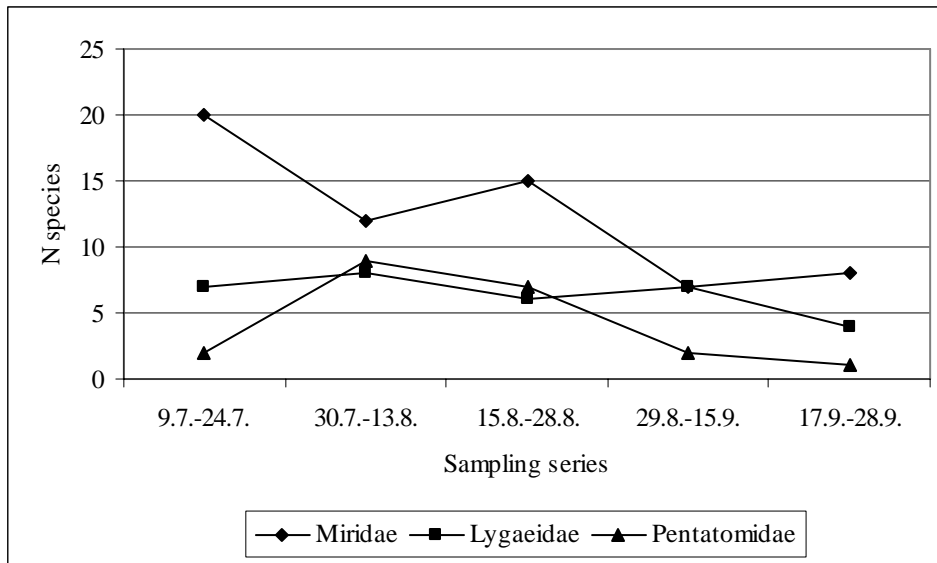


Fig. 3b:

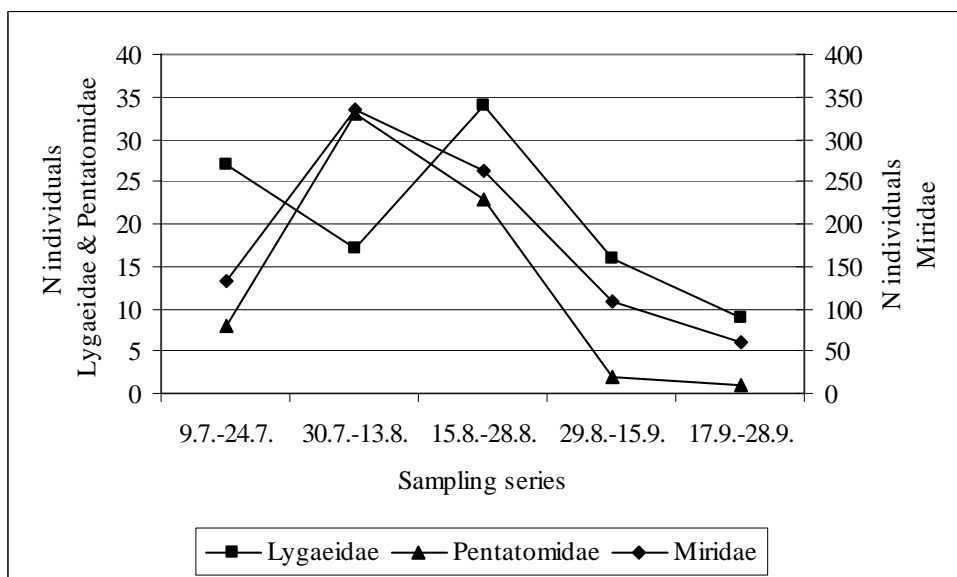


Fig. 4:

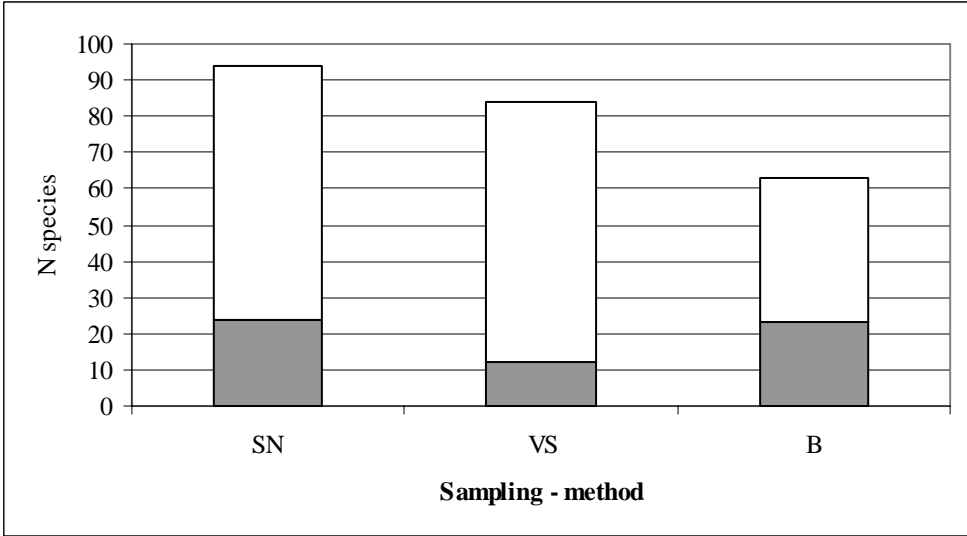


Fig. 5a:

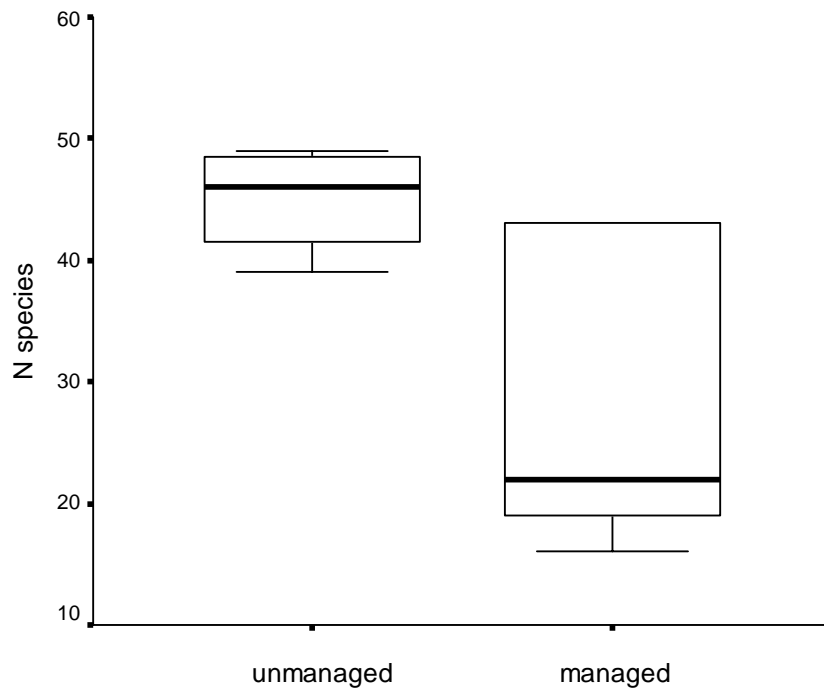


Fig. 5b:

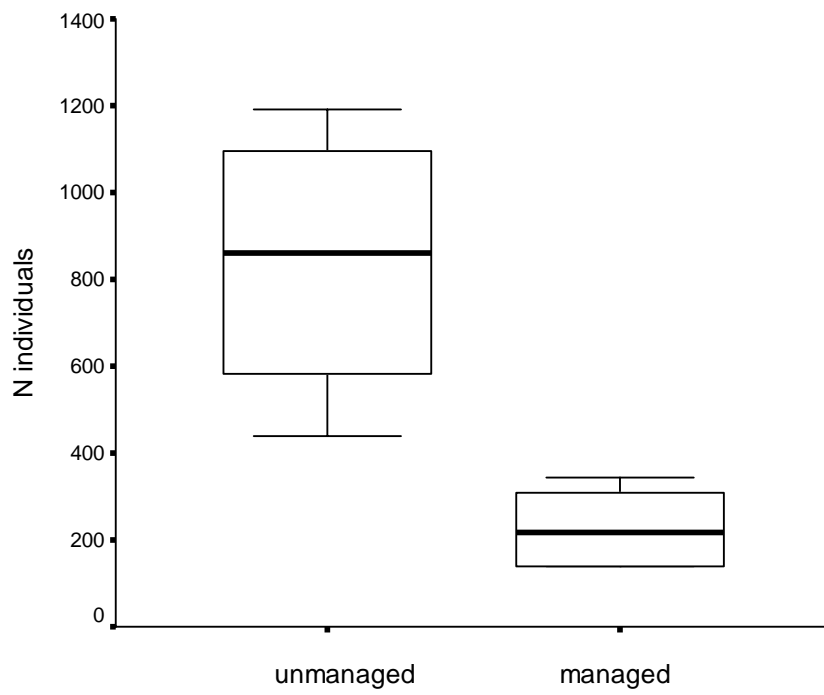


Fig. 6:

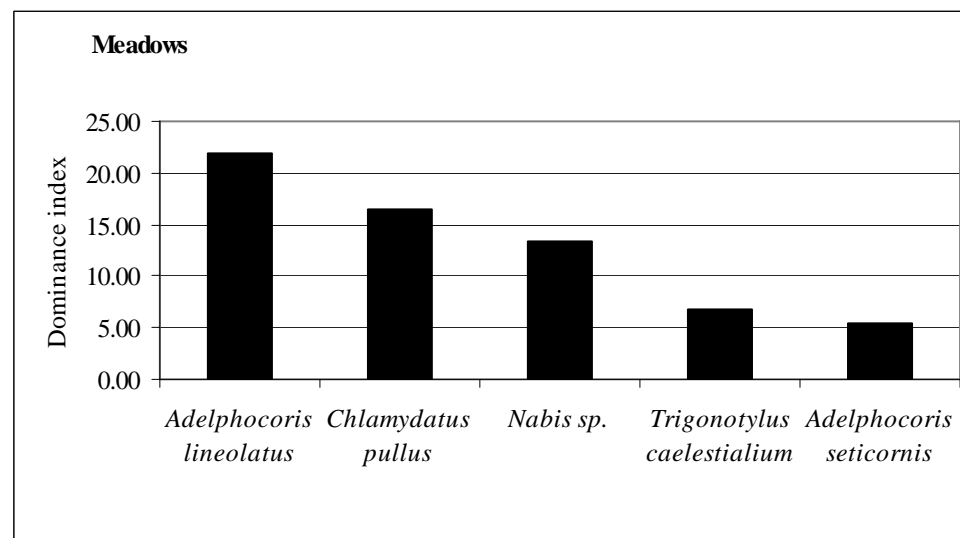
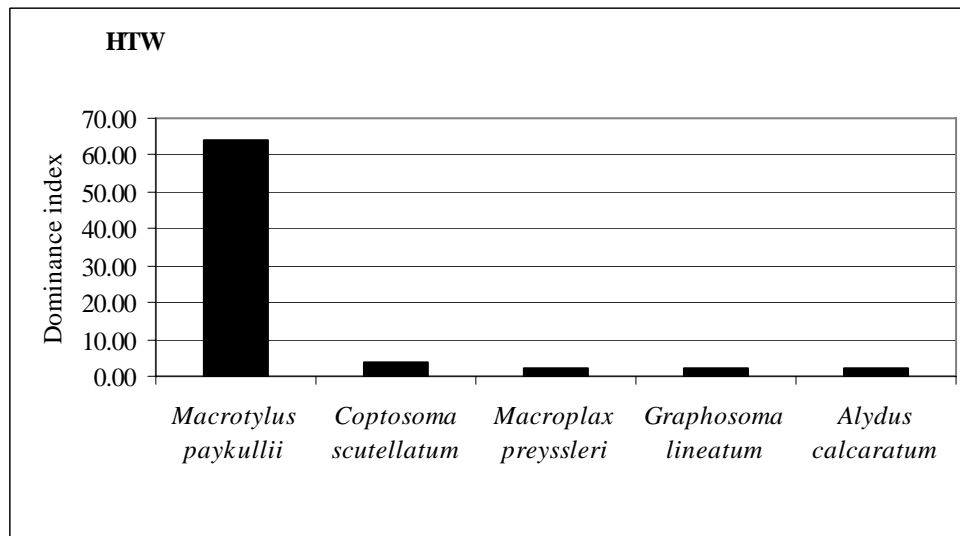
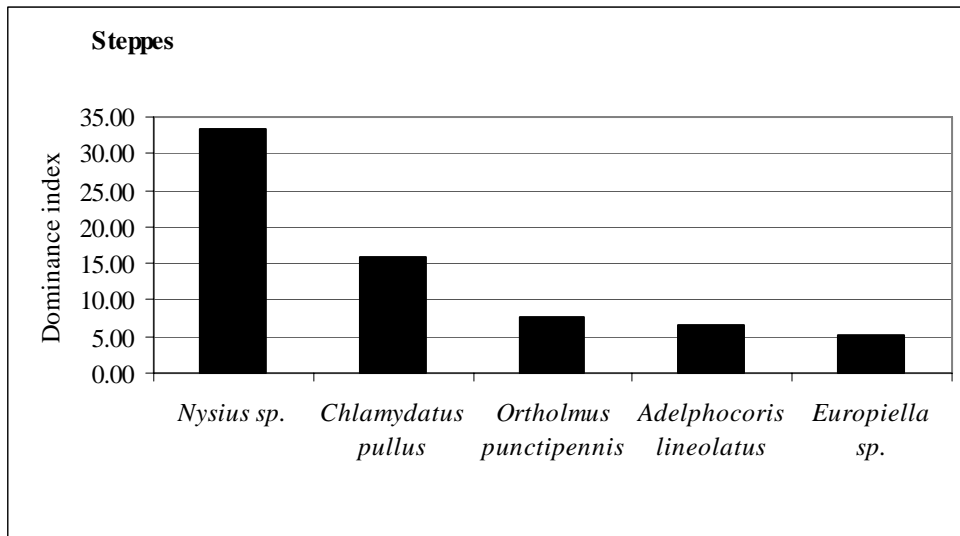


Fig. 7:

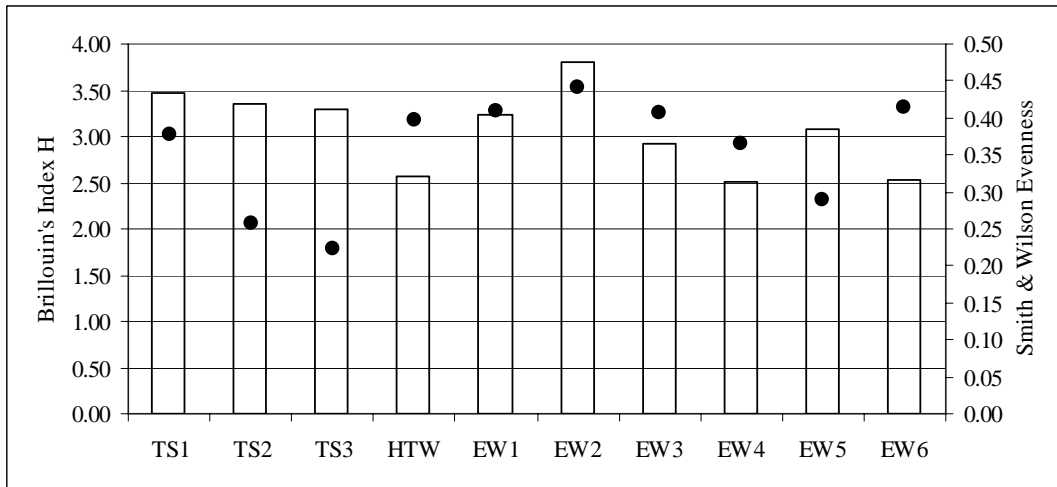
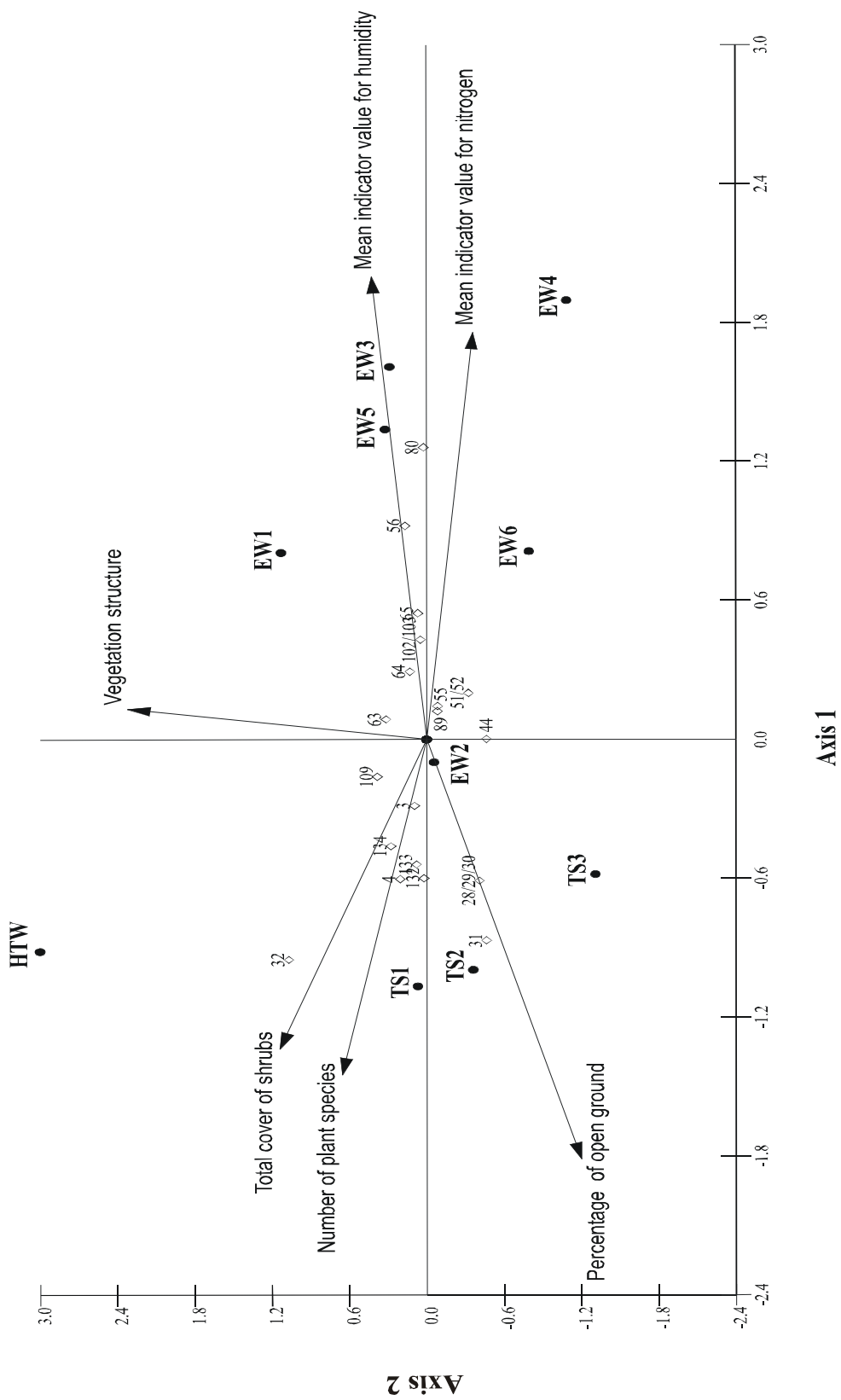


Fig. 8:
Fig. 9:



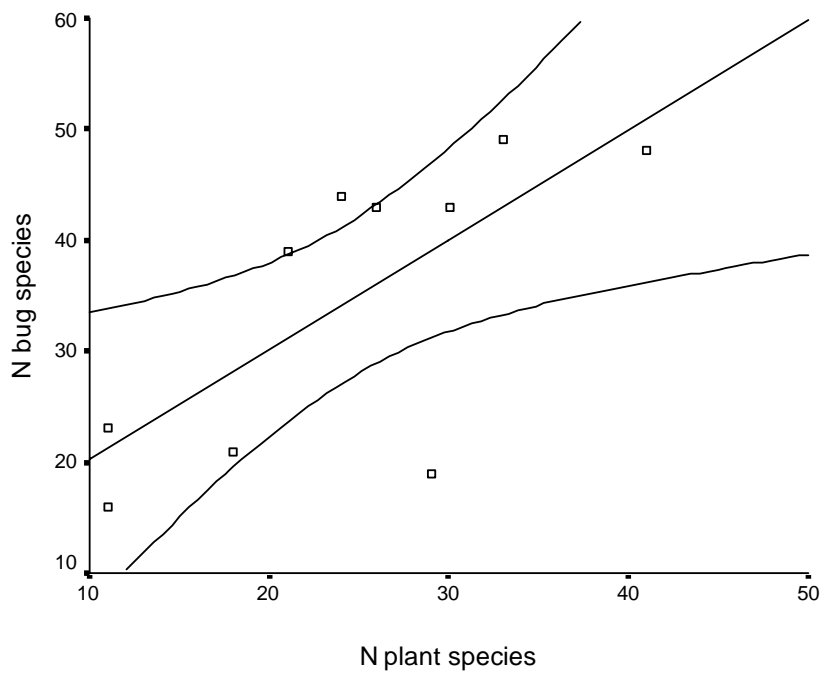


Fig. 10:

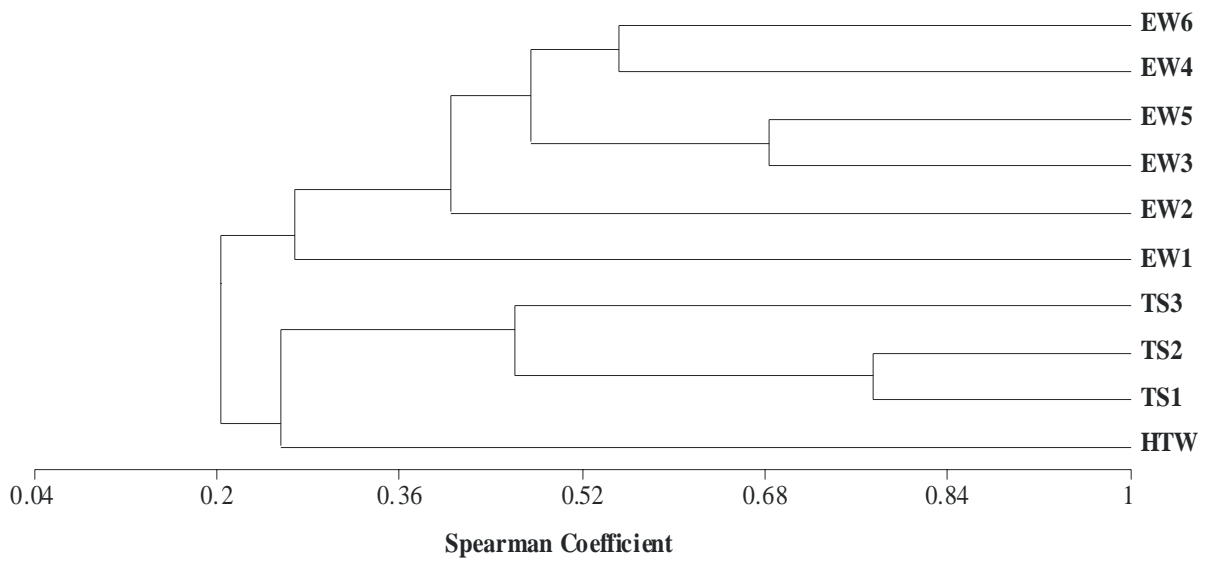


Fig. 11a:

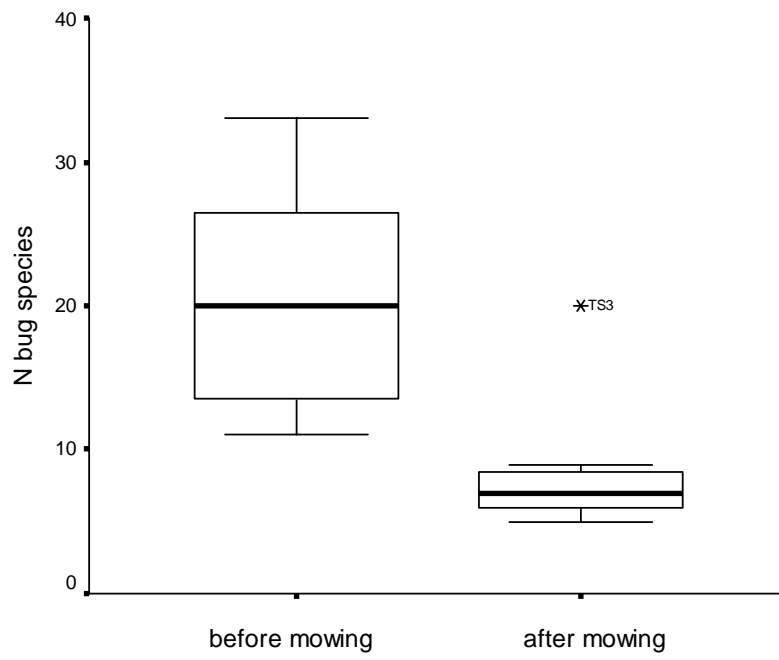


Fig. 11b:

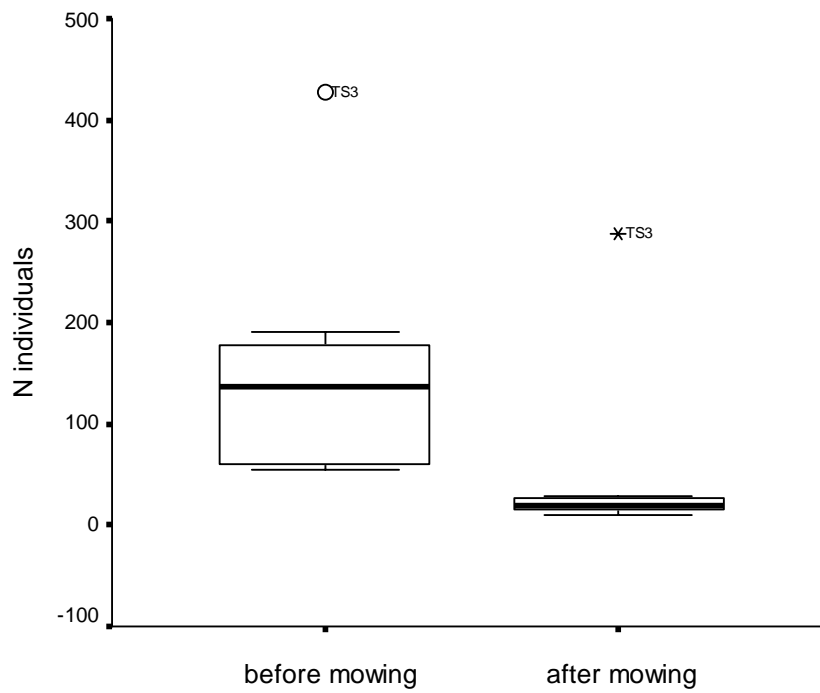


Fig. 12:

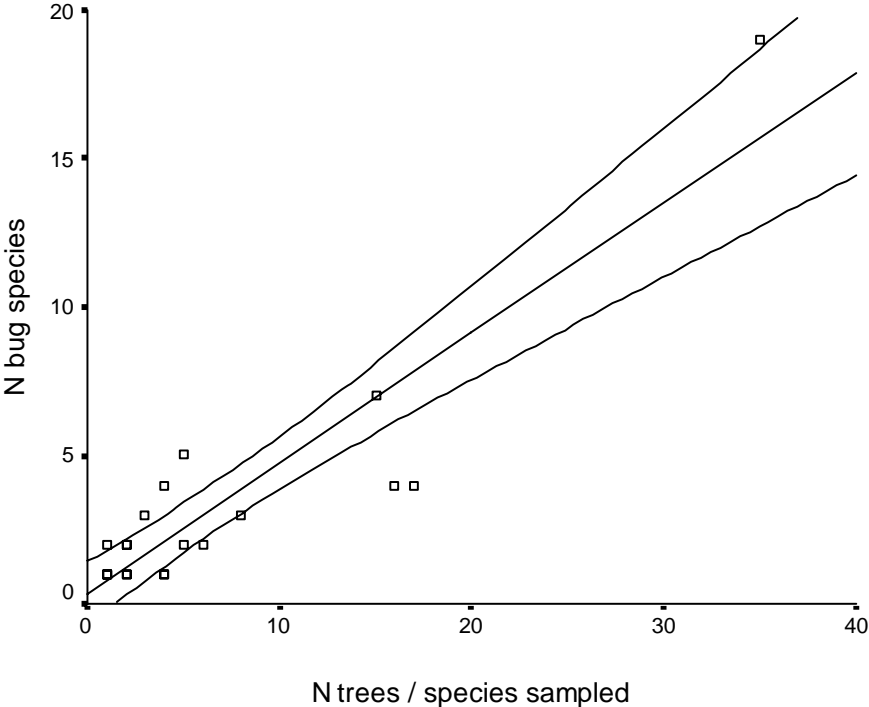


Fig. 13a:

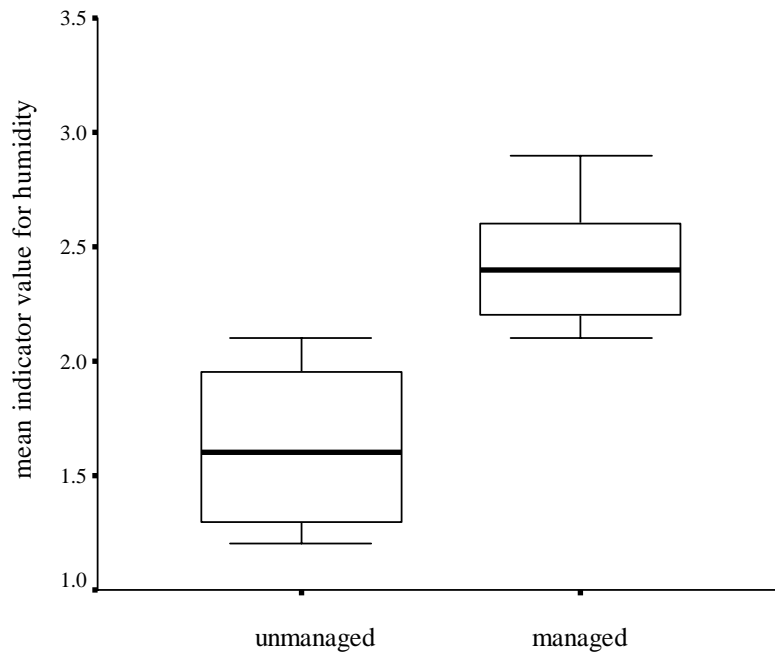
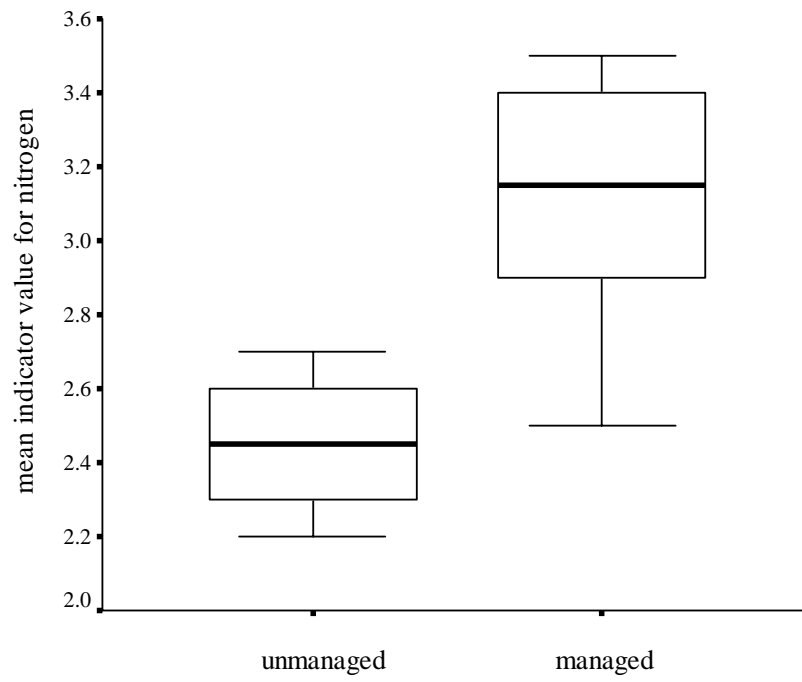


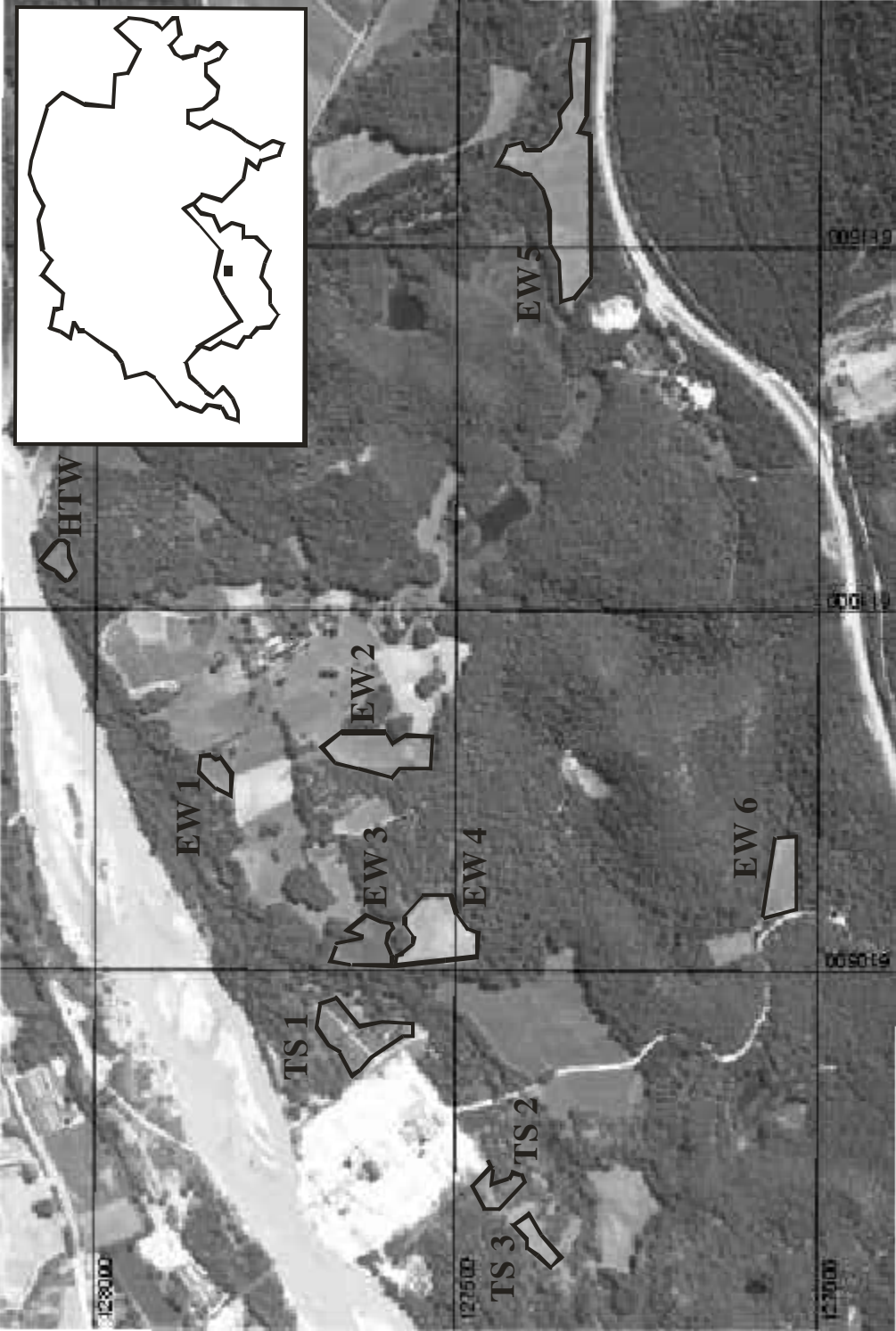
Fig. 13b:



Appendix

- Appendix 1:** Site plan of the sampling area
- Appendix 2:** Thermologger (LITE) with shaded thermocouples.
- Appendix 3:** *Stygnocoris similis*. A new record for Switzerland. From PÉRICART (1998b)
- Appendix 4 :** Dominance structure of each site. On the left sites with a eudominant species, on the right sites with a dominant species. Dominance index D after MÜHLENBERG (1993). For species number see Tab. 4.
- Appendix 5:** Seasonal phenology of *Kleidocerys resedae*.
- Appendix 6:** Plant species composition of each site. Given is the abundance after BRAUN-BLANQUET 1964 (in FREY ET AL. 1998). R = Number of sites for which the species was recorded.
- Appendix 7:** Temperatures. (a) Mean daily temperature and maximal temperature at 20 and 5 cm above ground before mowing and (b) maximal temperature at 20 and 5 cm above ground after mowing. For significance of differences see text.

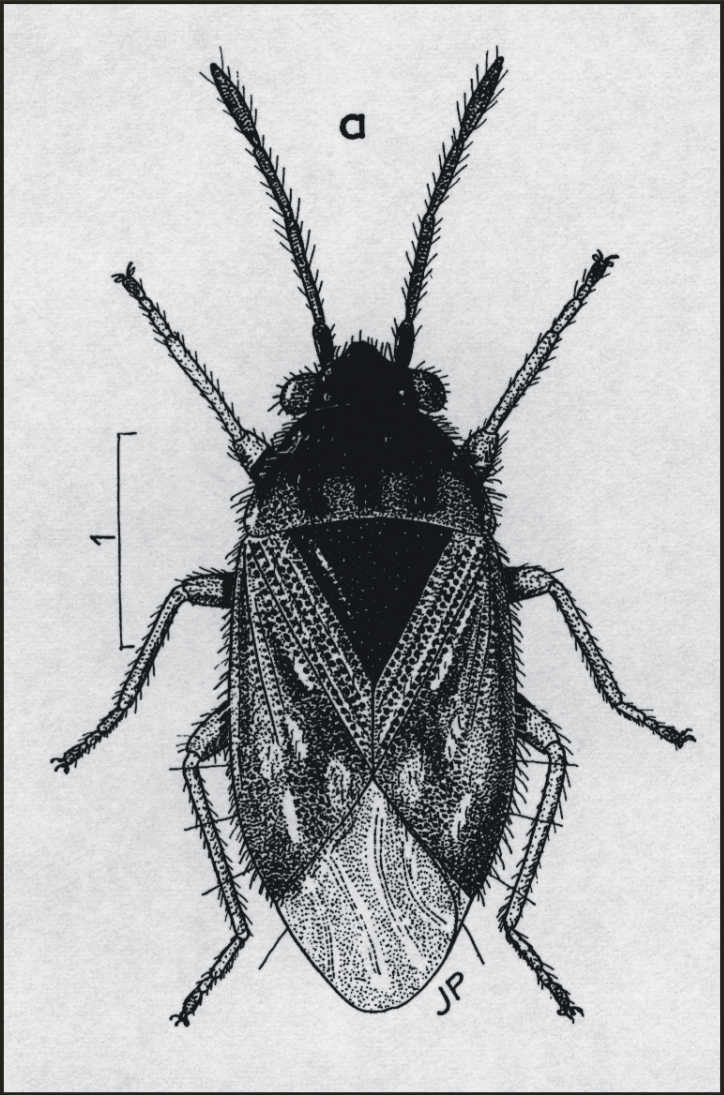
Appendix. 1:



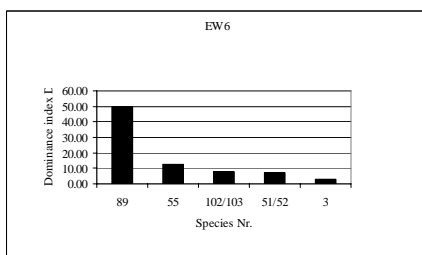
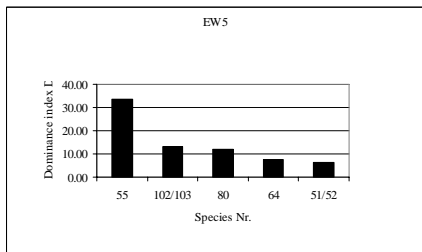
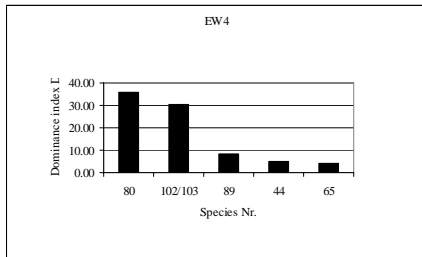
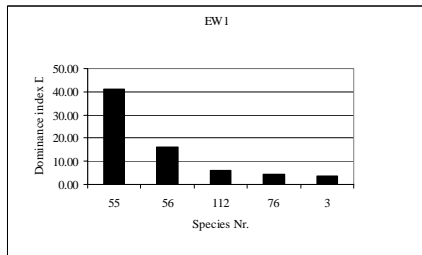
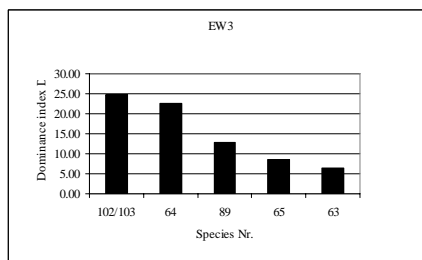
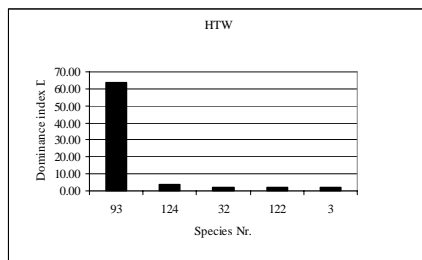
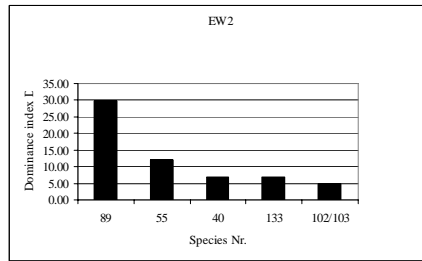
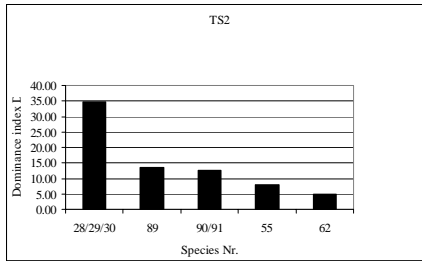
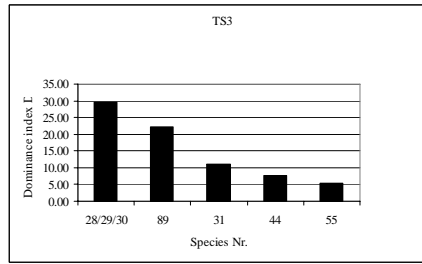
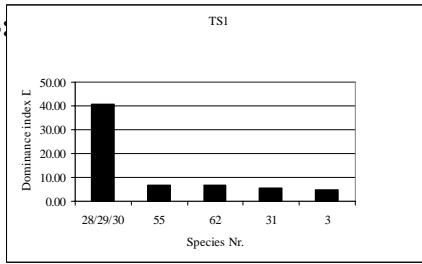
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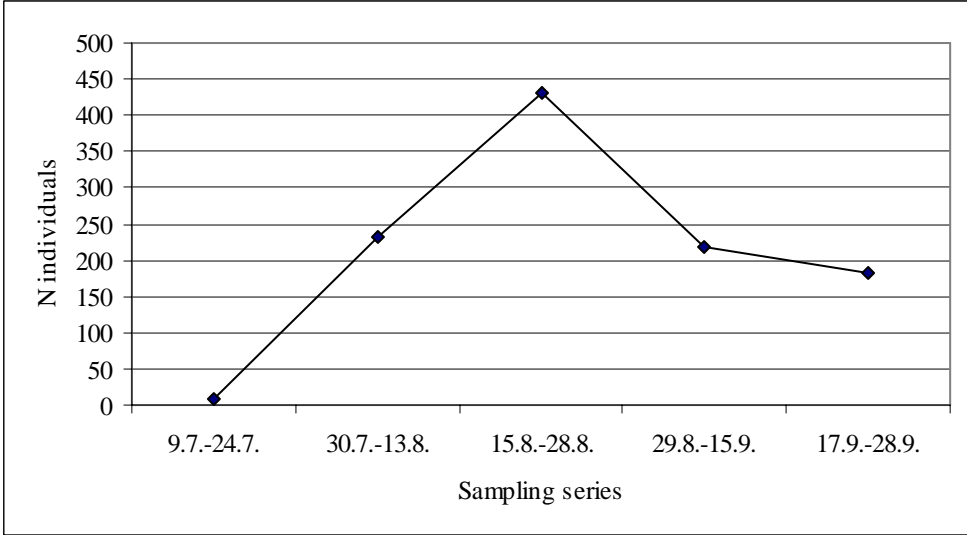
Appendix. 3:



Appendix 4



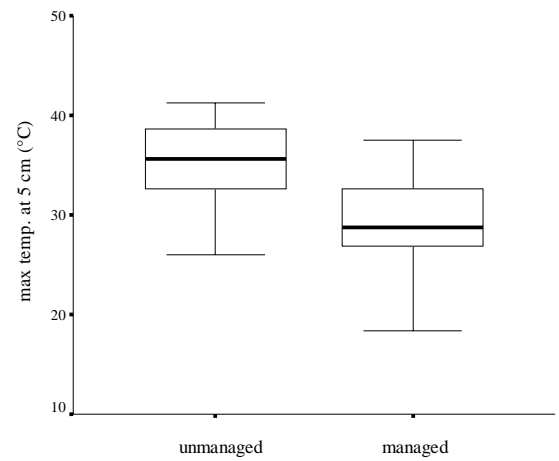
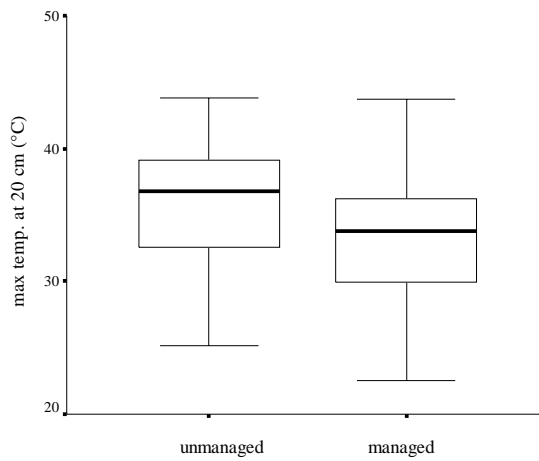
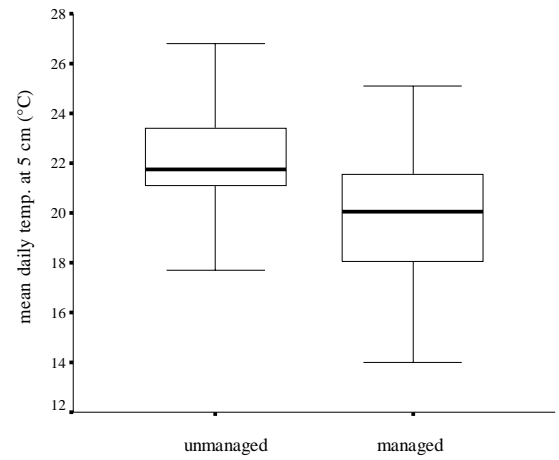
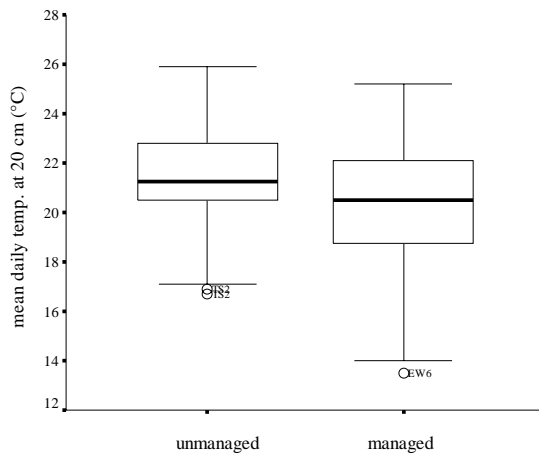
Appendix 5:



Nr.	Art	TS1	TS2	TS3	HTW	EW1	EW2	EW3	EW4	EW5	EW6	R
	Fabaceae cont.											
52	<i>Oxytropis campestris campestris</i> L.	x										1
53	<i>Securigera varia</i> LASSEN				x							1
54	<i>Trifolium pratense (pratense)</i> L.			x	1	1	1m	1m	r	2b	2a	8
55	<i>Trifolium repens</i> L.			x		x	x	1m	x	1	1m	7
56	<i>Vicia cracca (cracca)</i> L.			x	1	x	x	x	1		1	7
57	<i>Quercus pubescens</i> WILLD.				x							1
	Globulariaceae											
58	<i>Globularia punctata</i> LAPEYR.	1										1
	Lamiaceae											
59	<i>Acinos arvensis</i> DANDY	+		x								2
60	<i>Prunella vulgaris</i> L.						1	x				2
61	<i>Salvia pratensis</i> L.	x	x	r		2b	+					5
62	<i>Thymus praecox</i> OPIZ	r	1		x							3
	Liliaceae											
63	<i>Asparagus officinalis</i> L.	x			1							2
	Plantaginaceae											
64	<i>Plantago lanceolata</i> L.			x		1m	+		x	1m	1	6
65	<i>Plantago major (intermedia)</i> LANGE			1							+	2
66	<i>Plantago media</i> L.					x	+					2
	Polygalaceae											
67	<i>Polygala vulgaris (vulgaris)</i> L.				1							1
	Ranunculaceae											
68	<i>Clematis vitalba</i> L.				+							1
69	<i>Ranunculus acris (friesianus)</i> SYME					1m	1			2a		3
	Resedaceae											
70	<i>Reseda lutea</i> L.			x							1	2
	Rosaceae											
71	<i>Potentilla argentea</i> L.		+	1m								2
72	<i>Potentilla recta</i> L.										r	1
73	<i>Potentilla reptans</i> L.	1m	2a	1m	x							4
74	<i>Prunus mahaleb</i> L.		r									1
75	<i>Sanguisorba minor (minor)</i> SCOP.						x					1
76	<i>Sorbus aria</i> CRANTZ				r							1
	Rubiaceae											
77	<i>Asperula aristata</i> L.	1										1
78	<i>Galium mollugo (album)</i> MILLER				x	+	r		x	+	+	6
79	<i>Galium verum (verum)</i> L.		x	+	1	1						4
	Scrophulariaceae											
80	<i>Euphrasia rostkoviana</i> HAYNE										r	1
81	<i>Odontites luteus</i> CLAIRV.	2a	2a	r	x							4
82	<i>Verbascum thapsus (crassifolium)</i> MURB.			x								1
83	<i>Veronica spicata</i> L.				1							1
	Vitaceae											
84	<i>Vitis vinifera</i> L.				1							1
	Graminaceae incl. <i>Stipa capillata</i> L.	2b	2b	2b	5	3	1m	3	5	3	3	10
85	<i>Stipa capillata</i> L.	2b	2a	2a								
	Shrubs											
86	<i>Berberis vulgaris</i> L.	x	+									2
87	<i>Crataegus monogyna</i> JACQ.				r							1
88	<i>Cornus sanguinea</i> L.				+							1
89	<i>Ligustrum vulgare</i> L.				x							1
90	<i>Lonicera xylosteum</i> L.				r							1
91	<i>Populus alba</i> L.				x	x						2
92	<i>Rosa</i> sp.				x							1
93	<i>Rubus</i> sp.			x	2a						+	3
	Total number of species	24	21	33	41	30	26	11	18	11	29	

Appendix 7:

a)



b)

