

The importance of Silver fir (*Abies alba* Mill.) in comparison to spruce (*Picea abies* (L.) Karst.) and oak (*Quercus petraea* (Matt.) Liebl.) for arboreal Heteroptera communities in Bavarian forests

Martin G o ß n e r

Abstract

Heteropteran communities in the canopies of Silver fir (*Abies alba*) and spruce (*Picea abies*) were studied at three lowland and three mountainous sites throughout Bavaria using flight-interception traps. At one lowland site sampling was extended to oak (*Quercus petraea*). A significantly higher number of species and specimens occurred on fir when compared to spruce. Including all sampled species, numbers on fir were even higher than on oak. Excluding tourists, oak was most species rich. Results demonstrate that fir, spruce, and oak harbour distinct communities. While specific communities including several rare species (e.g. *Actinonotus pulcher*, *Psallus punctulatus*) were found on fir, mainly generalists were found on spruce. *Pinalitus atomarius*, *Cremnocephalus alpestris*, *Phoenicocoris dissimilis* and *Orius minutus* significantly preferred fir. Therefore, with an increased cultivation of fir in lieu of spruce, an increase in Heteropteran diversity can be expected.

Introduction

Silver fir (*Abies alba*) was wide spread throughout Bavaria once and it is assumed that it covered around 8-15% of the potential natural forest area (WALENTOWSKI et al. 2004). In upland and mountain forests it was the most frequent coniferous tree species (SEITSCHKEK 1978, SCHMIDT 2004). Because of its broad ecological amplitude it colonised a diverse spectrum of sites after postglacial remigration from its refuges which included mountain as well as dry lowland sites in Franconia (KÖLLING et al. 2004, KÖLLING & BORCHERT 2004). However, the proportion of fir in Bavarian forests declined dramatically during the last two centuries (SEITSCHKEK 1978, SCHMIDT 2004). At present, only 2.1 % of forest area is stocked in fir (BAYER. LANDESANSTALT FÜR WALD UND FORSTWIRTSCHAFT 2004). There is a variety of reasons for this decline. Silvicultural support of spruce (*Picea abies*), grazing impact caused by high ungulate densities, and damage by pollution are the main factors (BROSINGER 2004, ELLING 2004). Recently an increasing cultivation of fir is dictated by forest management, not least because of increasing problems with spruce plantation as a consequence of climate warming (SCHMIDT 2004). Considering the variety of advantages compared to other tree species, fir seems to be an economically profitable tree species (KNOKE 2004).

From the faunistic point of view the importance of fir in Bavarian forests is scarcely known (e.g. MÜLLER & GOßNER 2004). Generally arthropod communities on fir are assessed as species poor in most taxa compared to other conifer species like spruce and pine (e.g. KLIMETZEK 1993, BÖHME 2001, BRÄNDLE & BRANDL 2001, SZENTKIRÁLYI 2001). However, GOßNER & BRÄU (2004) already pointed out that fir seems to be of faunistic interest for Heteroptera based on results of a study of three fir trees in Middle Swabia. Also, the studies in primary forest sanctuaries of Slovenia (FLOREN & GOGALA 2002) and in parks of Sweden (LINDSKOG & VIKLUND 2000) where fir is an ornamental plant give evidence for the importance of this tree species for several Heteroptera species. To enable a more reliable assessment of the importance of fir for arboreal Heteroptera communities, fir and spruce were sampled at three mountainous and three lowland forest stands across Bavaria. For a broader judgement the study was extended by a comparison to the communities on oak (i.e. *Quercus petraea*), the most species rich native tree genus relevant to forestry in Bavaria (e.g. BRÄNDLE & BRANDL 2001, WACHMANN et al. 2004, GOßNER 2005a).

Material und Methods

Heteroptera communities on fir (*A. alba*) and spruce (*P. abies*) were studied at six different sites across Bavaria, and those of oak (*Q. petraea*) at the site "Feuchtwangen" (Fig. 1). Fir is known to be autochthonous at all six sites. Three lowland (500-600 a.s.l.) and three mountainous (720-960 a.s.l.) sites, characterized by a high variety of substrate, were investigated (Table 1; see also GAUDERER et al. 2005). At site Feuchtwangen oak, spruce, and fir grow next to each other but lumped in a stand. At the other stands studied tree species occurred in a mixed stand, mainly together with beech (*Fagus sylvatica*) or pine (*Pinus sylvestris*).

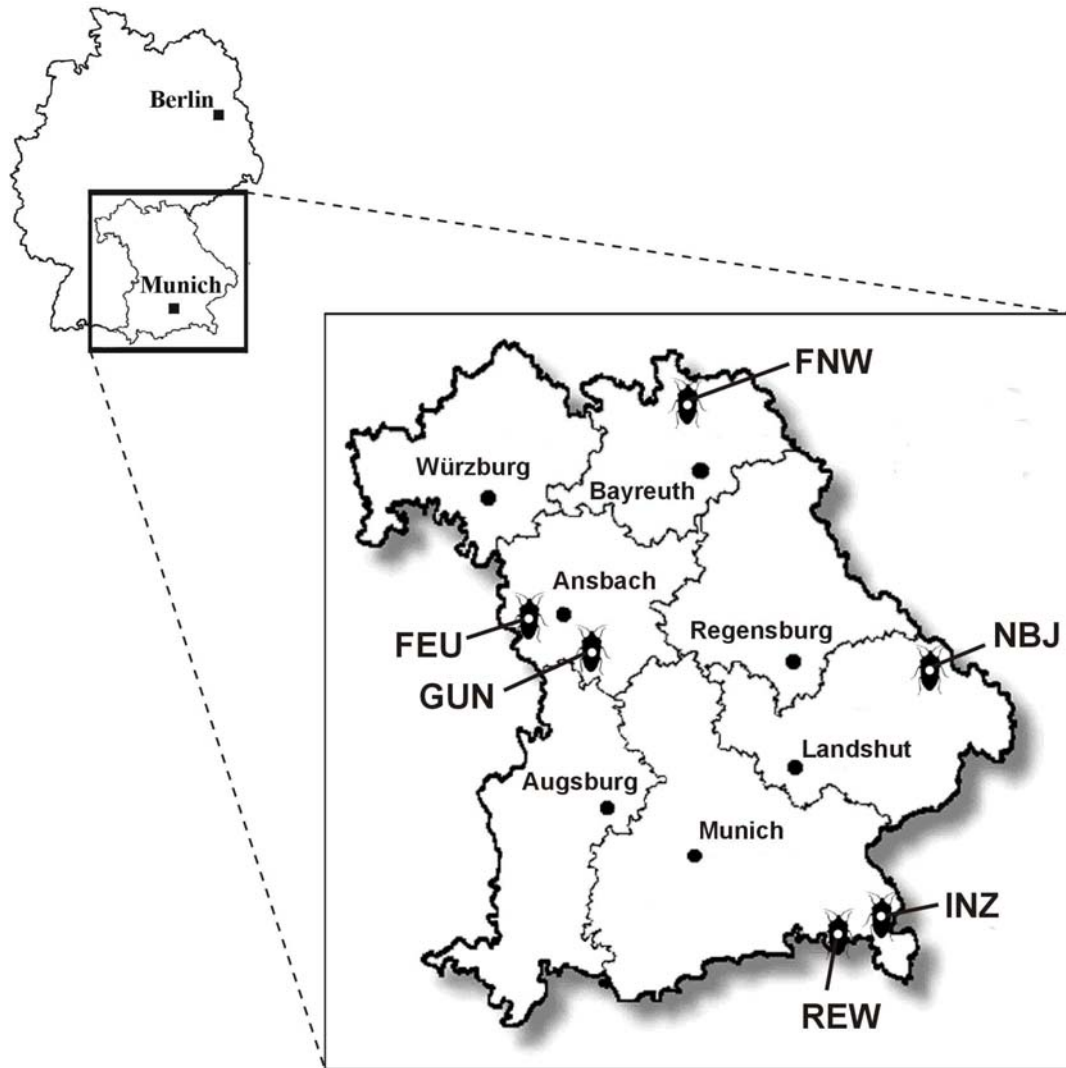


Fig. 1: Map of study sites. FEU = Feuchtwangen, GUN = Gunzenhausen, FNW = Frankenwald, NBJ = National Park "Bayerischer Wald", INZ = Inzell, REW = Reit im Winkl.

Table 1: Characterisation of studied sites. Pa=*Picea abies*, Aa=*Abies alba*, Qp=*Quercus petraea*, Ps=*Pinus sylvestris*, Fs=*Fagus sylvatica*. FNR=Forest Nature Reserve, NP=National Park.

site	Feuchtwangen	Gunzenhausen	Frankenwald	Bayer. Wald	Inzell	Reit im Winkl
abbreviation	FEU	GUN	FNW	NBJ	INZ	REW
geogr. coordinates	10°20'39"E 49°10'35"N	10°46'45"E 49°11'32"N	11°34'43"E 50°18'02"N	13°29'37"E 48°54'02"N	12°47'25"E 47°46'27"N	12°27'58"E 47°41'05"N
Size of stand (ha)	7.0	0.7	5.0	2.0	18.0	13.2
Tree age (mean) of studied tree species [years]	Pa 70 Aa / Qp 150	Pa / Aa 88	Pa / Aa 124	Pa / Aa 120	Pa / Aa 110	Pa / Aa / Ps 100
number of sampled trees (additional trees)	Pa 5, Aa 5, Qp 5	Pa 5, Aa 5	Pa 5, Aa 5	Pa 5, Aa 5	Pa 5, Aa 5	Pa 5, Aa 5(2), (Ps1)
a.s.l. [m]	500	510	550 - 600	870	720	960
geology	middle red marl	red marl sand	basement complex	crystalline basement complex	flysch	alpine lime(stone)
temperature in tree crown [°C]	15.1	14.6	13.5	12.8	12.6	12.4
precipitation [mm/a]	750	750	739	1360	1052	1052
Occuring tree species	Pa, Aa, Qp; Fs	Pa, Aa, Ps, Fs	Pa, Aa, Fs	Pa, Aa, Fs	Pa, Aa, Fs	Pa, Aa, Fs, (Ps)
forest type	managed	managed	unmanaged (FNR)	unmanaged (NP)	managed	managed

At each site five trees of each tree species were studied using flight interception traps (WINTER et al. 1999). At site Reit im Winkl two additional fir trees and one pine tree (*P. sylvestris*) were sampled. Traps consisted of a crossed pair of transparent plastic shields (40x60cm) with a funnel of smooth plastic cloth attached at the bottom and at the top; at the end of both funnels sampling jars were mounted filled with killing and preserving agent (1.5% copper-vitriol-solution). Flying arthropods are intercepted by the window, either they display a fright-reaction, fall down, and are sampled in the lower jar, or they try to avoid the window by flying upwards and are sampled in the upper jar. The traps were installed in the centre of each tree crown. Sampling took place during the vegetation period (April–October) of the year 2004 with a one-month sampling interval. Arthropods were transferred into alcohol (70%–ethanol) in the field. In the laboratory, samples were sorted into taxonomic orders. Species determination was done by the author using common identification keys (WAGNER 1952, 1966, 1967, 1971, 1973, 1975; WAGNER & WEBER 1978; PÉRICART 1972, 1987) and several other species-level publications. The determination of critical species was checked by G. SCHUSTER (Schwabmünchen). Based on expert knowledge the following species were classified as “tourists”: ground-living species, specialists of herbaceous plants, all broad-leaved tree specialists found on spruce/fir and vice versa.

For analysing differences in number of specimens or species Kruskal–Wallis–ANOVA (KW–ANOVA) and Mann–Whitney–U–test (MWU–test) were performed. For post–hoc–comparisons the Nemenyi post–hoc test was used (KÖHLER et al. 1996). For comparison of species richness on different tree species Shinozaki-rarefaction statistic (SHINOZAKI 1963) was applied. The curvature of the Shinozaki–curves depends on the heterogeneity of species composition and is a measure of beta–diversity. If the slope of a curve reaches zero the species are considered to be well represented in the samples. A deviation of the slope from zero indicates that further sampling will result in more species. For community–level analyses a Detrended Correspondence Analysis (DCA) was performed using abundance data (JONGMAN et al. 1995). Detrending was used to reduce the arch effect. DCA calculates eigenvalues (for all axes), which are equivalent to the correlation coefficient. Resulting axes are a measure of beta–diversity. By an Indicator Species Analysis (DUFRÈNE & LEGENDRE 1997) indicator values for each heteropteran species were computed based on information of the relative abundance and relative frequency of heteropteran species on a particular tree species. These were tested for statistical significance using a Monte Carlo technique.

Data analysis was done using common computer programs and PC–ORD 4.10 for Windows (McCUNE & MEFFORD 1999) for Correspondence and Indicator Species Analysis.

P–values between 0.05 and 0.10 were considered as a trend. This was done in order to present some conspicuous but not statistically provable differences between tree species.

Results

Diversity

A total of 2,690 specimens and 76 species of Heteroptera were caught on fir (30 trees), spruce (30 trees), and oak (5 trees). On two additionally sampled fir trees and one pine tree at site REW another 125 specimens (and one supplementary species) were sampled. This data is given in the Appendix (Table 5), but not included in statistical analysis.

Heteroptera on fir (species: 60%, specimens: 86%), spruce (species: 48%, specimens: 79%) as well as oak (species: 59%, specimens: 92%) were dominated by the family *Miridae*. Communities on fir exhibited a higher number of species (53) and specimens (1,800) than spruce (48 species, 663 specimens). This is illustrated by Shinozaki-curves in Fig. 2a. Oak was only sampled at site FEU. Intermediate numbers of species (29) and specimens (219) were found on oak when compared with fir (37 species, 639 specimens) and spruce (25 species, 178 specimens) (Fig. 2b). While communities on oak were influenced by “tourists” to a low extent, many “tourists” were found on fir and spruce (Fig. 2a). Excluding “tourists” from analysis, also a higher number of specimens (1,495 specimens) and species (32 species) were observed on fir when compared with spruce (27 species, 303 specimens) (Fig. 2a). However, oak was richer in species (28) than fir (19 species) and spruce (14 species) at site FEU (Fig. 2b). The abundance of Heteroptera was highest on fir (519 specimens) followed by oak (218 specimens) and spruce (44 specimens).

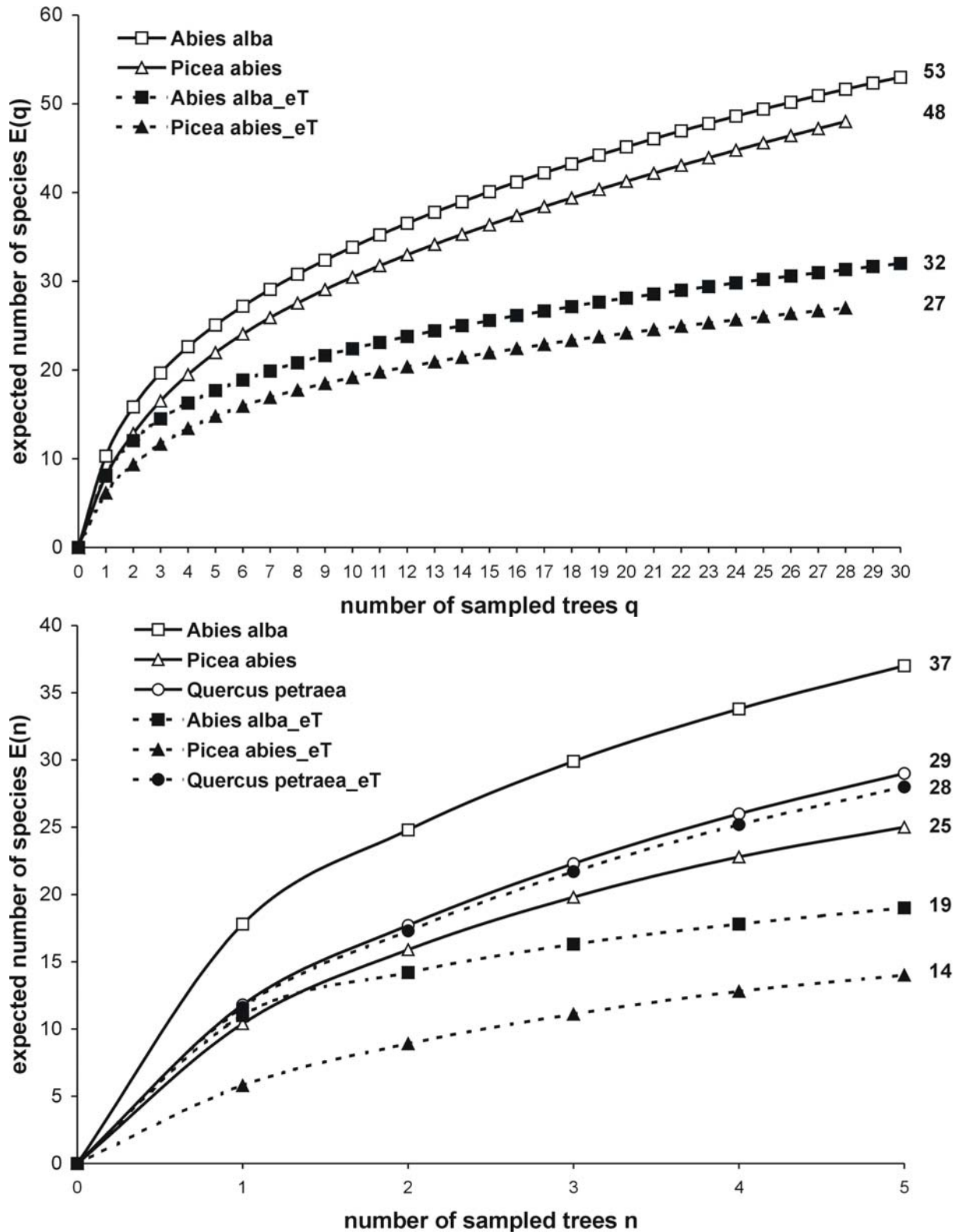


Fig. 2: SHINOZAKI-curves of Heteroptera communities on fir (*Abies alba*, squares), spruce (*Picea abies*, triangles) and oak (*Quercus petraea*, circles) over all stands (a) and at site Feuchtwangen (b). Because no heteropteran species was found on two spruce trees at site REW the length of the curves differ between *P. abies* and *A. alba* in Fig. 2a. eT=excluding "tourists".

Average number of species and specimens was higher at the lowland stands (FEU, GUN, FNW) compared to the mountainous stands (Fig. 3). This was significant regarding fir (species: $Z=3.22$ $p<0.01$, specimens: $Z=2.68$ $p<0.01$) as well as spruce (species: $Z=3.59$ $p<0.001$, specimens: $Z=4.05$ $p<0.0001$) (MWU-test), although Heteroptera communities on fir in National Park "Bayerischer Wald"

was relatively rich in species and specimens (Fig. 3). Abundance and species number of Heteroptera were higher on fir compared to spruce at all stands, but this was not statistically significant in all cases (Fig. 3). Communities on fir exhibited a higher number of species and specimens compared to oak regarding all species (statistical trend $p < 0.10$) but not when “tourists” were excluded from analysis. The difference between spruce and oak was more evident when “tourists” were excluded.

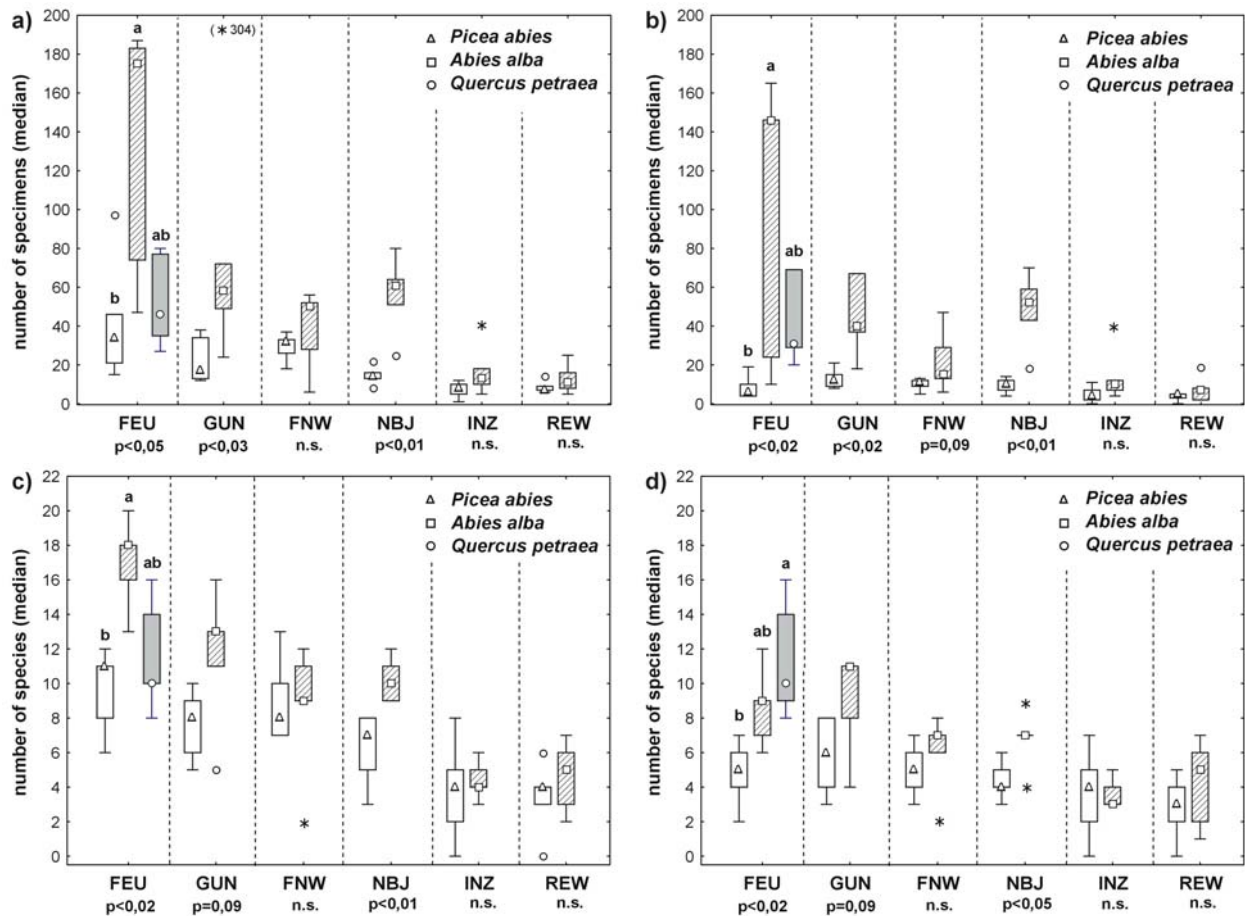


Fig. 3: Average number (median) of sampled specimens (Figs. 3a, b) and species (Figs. 3c, d), separated by stands. Figs. 3a, c: all species, Figs. 3b, d: excluding “tourists”. Results of a MWU-test or a Kruskal-Wallis-ANOVA (FEU) with Nemenyi post-hoc-test (letters are symbolising significant differences) between tree species. Box=25%/75%-percentiles, Whisker=Min-Max-values. A circle indicates extreme values between one and three times the box length, an asterisk even larger value.

The effect of “tourists” on the communities of the studied conifers was caused mainly by Heteroptera species inhabiting broad-leaved tree species. The proportion was highest at site FEU where it reached an average value of around 50% (Table 2). No significant difference could be found between spruce and fir at most stands. An exception was site FNW where a higher proportion was observed on spruce compared to fir.

Table 2: Average proportion (median) of broad-leaved tree species on Heteroptera communities on spruce (*Picea abies*) and fir (*Abies alba*).

	FEU	GUN	FNW	NBJ	INZ	REW
<i>P. abies</i>	0.45	0.20	0.30	0.16	0.00	0.13
<i>A. alba</i>	0.50	0.18	0.22	0.30	0.17	0.00
MWU-test	n.s.	n.s.	Z=1.98 $p < 0.05$	n.s.	n.s.	n.s.

Canopy community

Communities (excluding “tourists”) on spruce and fir differed conspicuously, illustrated by the separation along dimension 1 by a correspondence analysis (except REW-fir/NBJ-spruce). This indicates that communities on spruce and fir were differently structured. Species decisive for the separation of the communities on spruce and fir are shown in Fig. 4. In total no captured species

exhibited higher abundance on spruce, even though the proportion of some species (species in the right part of Fig. 4) on total community was higher on spruce. Only at site FEU *Parapsallus vitellinus* was slightly more abundant on spruce (Table 3). Several species were obviously more abundant on fir and four of these exhibited a significant preference of fir; *Cremnocephalus alpestris* (Indicator-values: fir: 71, spruce: 1), *Orius minutus* (fir: 51, spruce: 3), *Phoenicocoris dissimilis* (fir: 47, spruce: 0), and *Pinalitus atomarius* (fir: 66, spruce: 3) (Monte-Carlo-test, $p < 0.001$).

Regarding both conifers, Heteroptera communities of lowland and mountain stands were separated by a correspondence analysis along dimension 2 (Fig. 4). While *Pinalitus atomarius* and *Phytocoris intricatus* clearly preferred mountain sites, *Phoenicocoris dissimilis*, *Orius minutus*, *Phoenicocoris modestus*, and *Parapsallus vitellinus* did so in lowland sites (Fig. 4).

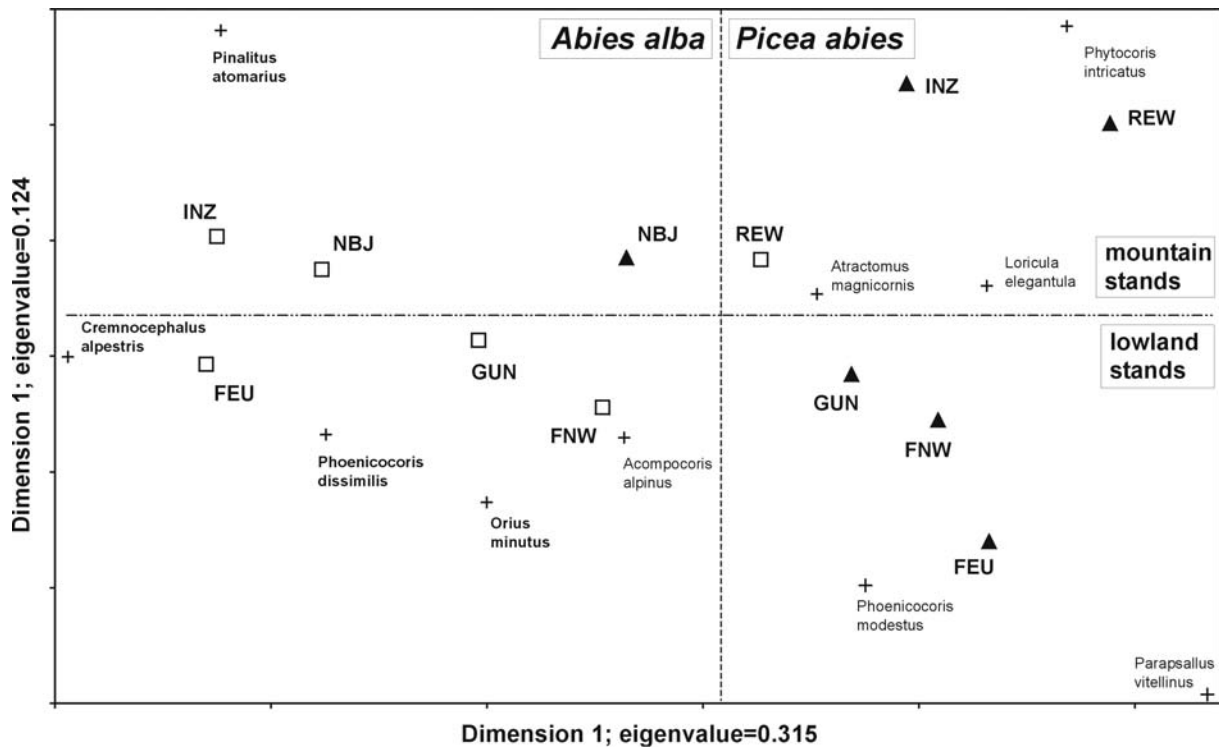


Fig. 4: Ordination diagram (DCA) of Heteroptera communities (excluding “tourists”), separated by site and tree species (□ fir *Abies alba*, ▲ spruce *Picea abies*). Only species with more than 30 specimens are shown. Species that exhibited significant difference in abundances between spruce and fir are bolded (Monte-Carlo-test $p < 0.05$).

At site FEU communities of oak were conspicuously different from that on conifers even when all species were taken into account (Fig. 5). In this single tree comparison moreover, distinct communities on spruce and fir were found (except one fir tree). Heteroptera communities on spruce and oak were more similar than that of fir and oak. *Cremnocephalus alpestris*, *Orius minutus*, *Phoenicocoris dissimilis*, and *Pinalitus atomarius* preferred fir (Table 3). Additionally, *Atractotomus magnicornis* and *Actinonotus pulcher* were conspicuously more abundant on fir when compared to spruce and oak. Several species were more abundant on oak than on the conifers. Of these *Psallus mollis*, *Rhabdomiris striatellus* and *Deraeocoris lutescens* significantly preferred oak. Only for *Parapsallus vitellinus*, even though not significant, an affinity to spruce can be supposed. Surprisingly, *Harpocera thoracica*, an oak specialist, was more abundant on spruce (108 specimens) and fir (43 specimens) than on oak (11 specimens). However, the difference was not statistically significant. The position of the data point representing *Psallus varians* close to spruce in the ordination diagram (Fig. 5) is not because of a high abundance on this tree species (1 specimen), but high abundance on fir (23 specimens) and oak (21 specimens). As well, at site FNW *P. varians* occurred in high numbers on spruce (52 specimens) and fir (57 specimens).

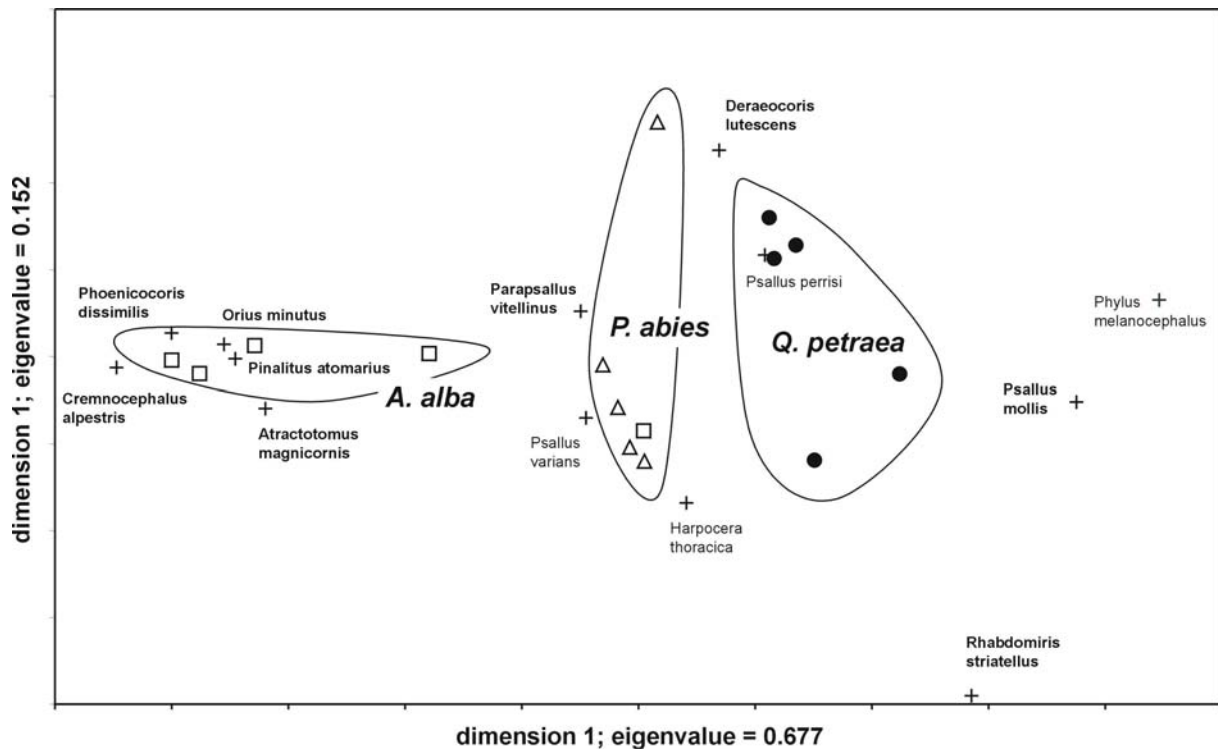


Fig. 5: Ordination diagram (DCA) of Heteroptera communities (single trees, including “tourists”) on spruce (*Picea abies*, Δ), fir (*Abies alba*, \square) and oak (*Quercus petraea*, \bullet) at site FEU. Only species with more than 15 specimens are shown. Species that exhibited significant difference in abundances between spruce, fir and oak are bolded (Monte-Carlo-test $p < 0.10$).

Table 3: Results of a Monte-Carlo-Test (indicator-values, p-values) for difference activity of heteropteran species ($p < 0.10$) between oak (*Quercus petraea*), spruce (*Picea abies*), and fir (*Abies alba*) at site FEU.

	<i>Q. petraea</i>		<i>P. abies</i>		<i>A. alba</i>		p
	Abundance	Indicator value	Abundance	Indicator value	Abundance	Indicator value	
<i>Cremnocephalus alpestris</i>	0	0	3	0	351	99	0.001
<i>Orius minutus</i>	2	1	3	3	39	89	0.001
<i>Pinalitus atomarius</i>	0	0	0	0	15	100	0.001
<i>Psallus mollis</i>	35	90	1	1	3	3	0.005
<i>Atractotomus magnicornis</i>	0	0	10	18	34	77	0.014
<i>Phoenicocoris dissimilis</i>	0	0	0	0	22	80	0.016
<i>Rhodomiris striatellus</i>	13	65	0	0	3	8	0.029
<i>Deraeocoris lutescens</i>	80	62	16	12	34	26	0.032
<i>Actinonotus pulcher</i>	0	0	0	0	4	60	0.068
<i>Parapsallus vitellinus</i>	0	0	13	58	5	11	0.084

The single pine tree at site REW revealed a Heteroptera community different from that of fir and spruce (Appendix, Table 5). *Alloeotomus germanicus* and *Phoenicocoris obscurellus* exhibited conspicuous higher abundances on the pine tree compared to the other conifer species.

Endangered species

Not only more specimens and species in total but also more endangered species were found on fir as compared to spruce during the presented study (Table 4). Interestingly, with *Pinalitus atomarius* and *Phoenicocoris dissimilis* two of these species were found in quite high numbers and at almost all studied stands. Noteworthy is the occurrence of two mistletoe-specialists, *Pinalitus visicola* and *Hypseloecus visci* on fir at site FEU and GUN. At both sites mistletoes grew on the studied fir trees. The finding of *Actinonotus pulcher*, *Deraeocoris trifasciatus* and *Psallus punctulatus*, known from broad-leaved trees, on fir is worth mentioning. While the two latter could only be observed at site FEU,

A. pulcher occurred also at the alpine sites INZ and REW. The record of *A. pulcher* at site REW was made on the two additionally sampled old fir trees. *Alloeotomus germanicus* has an affinity to pine.

Table 4: Species that are listed in the Red List of endangered species of Bavaria (RLB, ACHTZIGER et al. 2003) and Germany (RLG, GÜNTHER et al. 1998) found on spruce (Pa, *P. abies*), fir (Aa, *A. alba*), oak (Qp, *Q. petraea*), and pine (Ps, *P. sylvestris*) (in brackets: total number of sampled trees). FG=feeding guild (z=zoophagous, p=phytophagous, o=omnivorous, ?=unknown), H=habitat (t=tree, h=herbaceous plant, m=mistletoe), TH=tree habitat (c=coniferous trees, b=broad-leaved trees).

	FG	H	TH	RLB	RLG	Pa (30)	Aa (30)	Qp (5)	Ps (1)	site
Microphysidae										
<i>Loricula ruficeps</i>	z	t	b+c	R	A 1	2	1	1	0	FEU, GUN
<i>Myrmedobia distinguenda</i>	z	t	c	R	A 2/3	0	1	0	0	INZ
Miridae										
<i>Alloeotomus germanicus</i>	z	t	c	3		1	0	0	5	GUN, REW
<i>Actinonotus pulcher</i>	?	t	b	R	A 0	0	6*	0	0	FEU, INZ, REW*
<i>Orthotylus obscurus</i>	p	t	c	R	A 1	0	1	0	0	FEU
<i>Psallus piceae</i>	o	t	b	R		1	0	0	0	FEU
<i>Psallus pinicola</i>	o	t	c	R		1	0	0	0	INZ
<i>Deraeocoris trifasciatus</i>	z	t	b	V		0	2	0	0	FEU
<i>Psallus punctulatus</i>	o	t	b	new	A 2/3	0	3	3	0	FEU
<i>Pinalitus viscidola</i>	p	m	c	R		0	4	0	0	FEU
<i>Pinalitus atomarius</i>	p	t		R	A 1	12	111	0	0	FEU, GUN, FNW, NBJ, INZ, REW
<i>Hypseloecus visci</i>	p	m		G		0	3	0	0	FEU, GUN
<i>Phoenicocoris dissimilis</i>	?	t	c	R	A 1	0	51	0	0	FEU, GUN, FNW, NBJ, REW
Anthocoridae										
<i>Elatophilus nigricornis</i>	z	t	c	R	A 2/3	0	0	0	1	REW
Aradidae										
<i>Aradus obtectus</i>	m	t	b+c	R	A 1	0	1	0	0	REW
Lygaeidae										
<i>Metopoplax origani</i>	p	h		1		0	1	0	0	NBJ
Rhopalidae										
<i>Brachycarenum tigrinus</i>	p	h		2		1	2	1	0	FEU, GUN
Reduviidae										
<i>Empicoris baerensprungi</i>	z	t	b+c	R	A 2/3	0	0	1	0	FEU
Total number of RL-specimens						18	186	6	6	
Total number of RL-species						6	13	4	2	

* one specimen was found on an additional fir tree not included in the analyses.

Discussion

Diversity on different tree species

Heteroptera communities on fir (*Abies*) are supposed to be less diverse than those of other conifer species like spruce (*Picea*) or pine (*Pinus*) in Germany. BRÄNDLE & BRANDL (2001) reported about six phytophagous Heteroptera on *Abies*, 21 on *Picea* and 26 on *Pinus*. In a recently published book on the biology and ecology of plant bugs (*Miridae*) of Germany, WACHMANN et al. (2004) described 11 *Miridae* that were regularly found on *Abies*, 24 on *Picea* and 26 on *Pinus* (excl. *Pinus mugo*), excluding species that use conifers only as overwintering habitat. For none of these species is *Abies* specified as main host tree. In contrast, I found a significantly higher diversity on fir than on spruce (Fig. 2, 3). The low species number of *Abies* in previous publications is most probably a consequence of the low number of studies on Heteroptera communities on this tree species in the past. It is assumed that the experimental designs of these studies were not adequate to collect the canopy community of fir representatively. On the one hand investigations were only snapshots, like the fogging of fir trees in Slovenia at one date (end of June) by FLOREN & GOGALA (2002). On the other hand most information on fir communities is gained via ground based hand collecting. Also, regarding

other insect taxa like Coleoptera, Neuropterida, Aphidoidea, Symphyta, and Lepidoptera fir is expected to be species poor compared to spruce and pine (BÖHME 2001, BRÄNDLE & BRANDL 2001, SZENTKIRÁLYI 2001) and this might be also a consequence of less intense research activities on this tree species (MÜLLER & GOßNER 2004, MÜLLER et al. 2005).

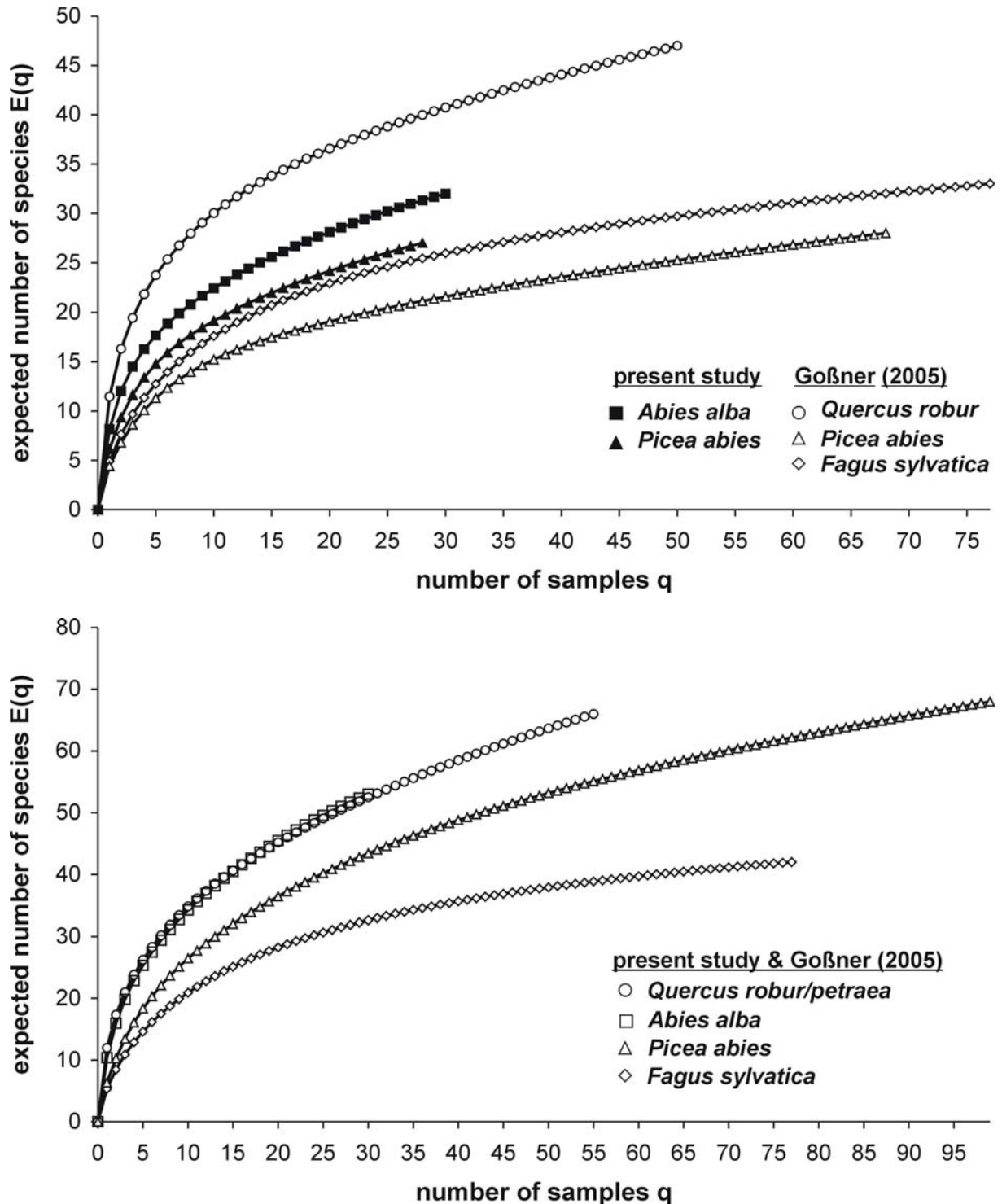


Fig. 6: Shinozaki curves of Heteroptera communities found on oak (*Quercus robur/petraea*), spruce (*Picea abies*), and beech (*Fagus sylvatica*) in the study of GOßNER (2005a) and on spruce (*P. abies*) and fir (*Abies alba*) in the present study. a) Excluding and b) including "tourists".

As I demonstrated, Heteroptera communities on oak exhibited higher number of species compared to spruce and fir, when "tourists" were excluded from analyses (Fig. 2b, 3d). This confirms the studies of BRÄNDLE & BRANDL (2001) (39 species) and WACHMANN et al. (2004) (47 species) mentioned above. A comparison to the study of GOßNER (2005a), who studied Heteroptera communities in tree crowns of oak, spruce, and beech at three different sites in Southern Bavaria by using "same trapping

method, reveals other interesting aspects. Within tree species relevant to forestry in Bavaria, Heteroptera communities on oak are most diverse, followed by fir (Fig. 6a). Diversity on spruce was higher in the present study compared to that of GOßNER (2005a) where spruce was examined on sites outside its natural growth range. In the present study three sites within the natural growth range of spruce were investigated; National Park "Bayerischer Wald", Inzell, and Reit im Winkl. However, communities on spruce were not more diverse and not richer in specialists at sites where spruce is native than on sites where it is not native. Climatic constraints at the mountainous sites led to lower abundance and species number of Heteroptera (Fig. 3) when compared to lowland sites. Therefore, climatic conditions were the key factors for differences in Heteroptera diversity between sites in present study.

"Tourists" had a conspicuous effect on the total species number on fir, although the proportion of broad-leaved tree species was not higher on fir as compared to spruce (Table 2). This was true for the dry lowland site of Feuchtwangen, where species numbers on fir was even higher than on oak (Fig. 3c). This might be explained by the fact that fir is an autochthonous element of colline forests (WALENTOWSKI et al. 2001, KÖLLING et al. 2004), while spruce has been cultivated in this region for not longer than a few centuries. In some species direct adaptation to deciduous trees (oak) and fir might have occurred (1), in other species structural elements (e.g. mistletoes) have to be seen as ecological links between deciduous trees and fir (2).

1.) Examples for the first group are the rarely found species *Actinonotus pulcher* and *Psallus punctulatus*. WACHMANN et al. (2004) described *Quercus* and *Acer* as main host genera of the montane-mediterranean *A. pulcher*. Southeast Europe is its central distribution area and only a few, mostly old records from mountainous regions are known from Germany (GOßNER & BRÄU 2004, WACHMANN et al. 2004). However, GOßNER & BRÄU (2004) found six specimens of *A. pulcher* on fir at a lowland forest site (630m a.s.l.) in Southern Bavaria; no specimen could be observed on other coniferous and broad-leaved trees. In the present study *A. pulcher* also occurred exclusively on fir, mainly at the dry, lowland forest site of Feuchtwangen. Therefore the preference neither for broad-leaved trees nor for mountainous sites was confirmed by the present study. FLOREN & GOGALA (2002) captured *A. pulcher* in their study of the canopy fauna of beech and fir in primary forest sanctuaries of Slovenia exclusively on fir using canopy fogging. Based on these recent records from fir, an affinity of *A. pulcher* to fir is assumed. Therefore an adaptation to fir and oak can be suggested. *P. punctulatus* is described as species occurring exclusively on *Quercus*, possibly only on *Q. petraea* (WACHMANN et al. 2004). GOßNER (2005b) demonstrated that *P. punctulatus* occurs on *Quercus* species at several sites in northern Bavaria. In the present study *P. punctulatus* was found on *Q. petraea* and *Abies alba* at site Feuchtwangen and this indicates that an adaptation to both species might have occurred.

2.) Two species that are known to live phytophagously on mistletoes (mainly *Viscum album* spp. *album*) were captured on fir, *Hypseloecus visci* and *Pinalitus viscicola*. Both species have been rarely found, because of difficulty of accessing mistletoes in tree crown. However, they also occur on *Viscum album* growing on other broad-leaved tree species and *P. viscicola* is also known from *Loranthus europaeus* on oak (WACHMANN et al. 2004). The records of *H. visci* and *P. viscicola* on fir at site Feuchtwangen and Gunzenhausen, where mistletoes grow on sampled trees indicate that *H. visci* and *P. viscicola* also colonise fir-mistletoes (*Viscum album* spp. *abietis*). FLOREN & GOGALA (2002) also found *Hypseloecus visci* on fir in Slovenia. Therefore, mistletoes might be seen as a structural link between broad-leaved trees and fir. Another link seems to exist between broad-leaved trees and pine. *H. visci* was already recorded from pine-mistletoes (*Viscum laxum* on *Pinus sylvestris*) (WACHMANN et al. 2004).

With *Psallus varians* and *Harpocera thoracica* two other Heteroptera species of broad-leaved trees were observed in high numbers on spruce and fir. For *P. varians* this confirms results from GOßNER (2005a), who studied tree crown communities of spruce at three different sites in Bavaria. WACHMANN et al. (2004) described that *P. varians* sometimes occurs on conifers, but they suggested conifers not to be host trees. The high abundance of this species on conifers remains unclear. This also applies to the numerous catches of *Harpocera thoracica* on spruce and in lower numbers on fir. WACHMANN et al. (2004) described this species as an oak specialist, sucking on pollen bags of young floescence, but also on aphids. In the study of GOßNER (2005a) *H. thoracica* significantly preferred oak to beech and spruce. Only a very few specimens of this species were captured on spruce. Considering all data on Heteroptera species (including "tourists") found on oak, spruce, fir, and beech in the present study as well as in the study of GOßNER (2005a), a similar number of species is expected for oak and fir (Fig. 6b). Which of the "tourist"-species (known from broad-leaved trees only) found on fir, use this conifer species as food resource and for larval development remains unknown.

Canopy community

Distinct communities were found more often on mountainous as compared to lowland stands on fir or on spruce (Fig. 4). This indicates that communities in mountain areas are not only poorer in species and specimens but also differently structured. Some species like *Pinalitus atomarius* and *Phytocoris intricatus* exhibited a higher proportion of the total community in mountain sites, others like *Phoenicocoris dissimilis*, *Orius minutus*, *Phoenicocoris modestus*, and *Parapsallus vitellinus* did so in lowland sites. This difference in community structure can be interpreted as more severe climatic conditions at mountain compared to lowland sites. The high proportion of *P. atomarius* and *P. intricatus* at the mountain sites confirms data on their distribution given by WACHMANN et al. (2004) (see also WAGNER 1952, 1970, STICHEL 1958, JOSIFOV 1986).

The distinct communities on spruce and fir were traced back mainly to the preference of *P. atomarius*, *Cremnocephalus alpestris*, *Phoenicocoris dissimilis* and *Orius minutus* for fir. Interestingly, WACHMANN et al. (2004) described *Picea* as a main host tree genus of phytophagous *P. atomarius* and the omnivorous *C. alpestris*. Almost no specimens of *P. atomarius* were found on *Picea* in the present study. This confirms the study of LINDSKOG & VIKLUND (2000) on Heteroptera on different conifer species (*A. alba*, *A. nordmanniana*, *P. abies*) in parks of Stockholm. They found *P. atomarius* exclusively and numerous on *A. alba*, which is planted in Sweden only for ornamental purposes. Based on this data and on the close correspondence observed between the zonal-geographic ranges of *P. atomarius* and *A. alba* in Central and South Europe they suggested *A. alba* as the primary or original host plant of *P. atomarius*. This is clearly supported by the results of the present study. FLOREN & GOGALA (2002) demonstrated that *P. atomarius* also occurs in high numbers in the canopy of fir trees in Slovenia. The reason for the few records of *P. atomarius* in Bavaria may result from the low study intensity of Heteroptera on *A. alba*. *C. alpestris* is phytophagous during larval and mainly aphidophagous during adult stages (WACHMANN et al. 2004). Therefore, the high abundance of this species on fir might be a consequence of higher prey availability. The same can be suggested for *O. minutus*, which is an important aphid-antagonist, and is therefore used as biological control agent (e.g. SHOJAI et al. 1996). For site NBJ also ZÖBL et al. (2005) reported about a higher number of aphidophagous species and specimens on fir compared to spruce. However, aphid quantity was not significantly higher on fir, but of different quality: Mainly *Lachnidae* were found on fir, while *Adelgidae* dominated on spruce (MÜLLER et al. 2005). This might explain the higher abundance of this species on fir. GOBNER et al. (2005) studied aphidophagous communities on introduced Douglas-fir and spruce in Southern Bavaria. They found a significantly higher abundance of *C. alpestris* and *O. minutus* on introduced Douglas-fir and traced it back to the high densities of Douglas-fir woolly aphid (*Adelges cooleyi*) which is also introduced from North America. Regarding *C. alpestris* it cannot be excluded that a preference for fir exists due to the phytophagous habit of their larvae. Either due to larval or adult habits, *C. alpestris* seems to have an affinity to fir. This is also confirmed by high numbers of this species sampled by FLOREN & GOGALA (2002) on fir trees in Slovenia. Only very few previous records are known from *P. dissimilis*, all sampled from conifers. Nothing is known about its feeding habit. In the present study it was observed quite numerously on fir at the dry lowland sites of Feuchtwangen and Gunzenhausen. No specimen were captured on spruce or oak. A preference for fir is therefore suggested and the low number of previous records might be explained by the less intensive studies on Heteroptera in fir crowns.

Communities on oak at site Feuchtwangen were distinct from those on spruce and fir, characterised by several oak specialists (Fig. 5). This, and the fact that with the exception of *Parapsallus vitellinus*, no Heteroptera species with an affinity to spruce was observed, communities between spruce and oak were more similar than communities between fir and oak. However, this is not conflicting with the assumption that some heteropteran species of broad-leaved trees adapted to fir. It is only a consequence of a specific community, typical of coniferous-Heteroptera on fir. This result supports the hypothesis that spruce plantations outside the natural growth range are dominated by generalists and species from neighbouring tree species (in this case oak and fir). Therefore, a distinct crown community is lacking.

Conclusions

The results of the present study demonstrated that fir is of high significance regarding the political directive (e.g. convention of biological diversity, CBD) of maintaining a high Heteroptera diversity in managed forests of Bavaria. It harbours a community distinct from spruce which can be characterised by several species - including endangered ones - exhibiting a clear preference for fir. Consequently, an increase in fir cultivation in lieu of spruce will most likely lead to an increase of biodiversity while the reverse may be expected with the continued preference in cultivation of spruce, and no additional

biodiversity profits can be gained. Foresters are therefore advised to optimise game management to promote the natural regeneration of fir. With a higher percentage of fir, managed forests will be augmented economically as well as ecologically.

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Appendix

Table 5: List of sampled Heteroptera species in tree crowns of spruce (Pa, *Picea abies*), fir (Aa, *Abies alba*), oak (Qp, *Quercus petraea*) and pine (Ps, *Pinus sylvestris*). EntGerm-Nr=Species number in Entomofauna Germanica (HOFFMANN & MELBER 2003). The data of additionally sampled fir trees at REW is given in brackets. Most of the specimens that were not determinable to species level were juveniles.

Ent Germ Nr		FEU			FNW			GUN			INZ			REW		
		Pa	Aa	Qp	Pa	Aa	Pa	Aa	Pa	Aa	Pa	Aa	Pa	Aa	Ps	
106	<i>Acalypta parvula</i> (Fallén, 1807)	1	0	1	0	0	0	0	0	0	0	0	0	0	0	
162	<i>Loricula elegantula</i> (Baerensprung, 1858)	2	2	2	2	3	5	16	1	1	5	3	2	1 (4)	0	
163	<i>Loricula pselaphiformis</i> Curtis, 1833	0	0	0	0	0	1	0	0	0	0	0	0	0 (0)	0	
164	<i>Loricula ruficeps</i> (Reuter, 1884)	1	0	1	0	0	1	1	0	0	0	0	0	0 (0)	0	
167	<i>Myrmedobia distinguenda</i> Reuter, 1884	0	0	0	0	0	0	0	0	1	0	0	0	0 (0)	0	
168	<i>Myrmedobia exilis</i> (Fallén, 1807)	0	0	0	0	1	0	0	1	1	0	0	0	0 (0)	0	
187	<i>Alloeotomus germanicus</i> Wagner, 1939	0	0	0	0	0	1	0	0	0	0	0	0	0 (0)	5	
188	<i>Alloeotomus gothicus</i> (Fallén, 1807)	0	0	0	0	0	0	2	0	0	0	0	0	0 (0)	1	
196	<i>Deraeocoris ruber</i> (Linnaeus, 1758)	0	0	1	0	0	0	0	0	0	0	0	0	0 (0)	0	
198	<i>Deraeocoris trifasciatus</i> (Linnaeus, 1767)	0	2	0	0	0	0	0	0	0	0	0	0	0 (0)	0	
200	<i>Deraeocoris lutescens</i> (Schilling, 1837)	16	34	80	9	9	19	20	1	1	0	7	0	0 (0)	0	
201	<i>Actinonotus pulcher</i> (Herrich-Schaeffer, 1835)	0	4	0	0	0	0	0	0	1	0	0	0	0 (1)	0	
221	<i>Dichroscytus intermedius</i> Reuter, 1885	1	0	0	0	0	0	1	0	0	0	0	0	0 (2)	0	
242	<i>Phytocoris dimidiatus</i> Kirschbaum, 1856	0	0	3	0	0	0	0	0	0	0	0	0	0 (0)	0	
244	<i>Phytocoris intricatus</i> Flor, 1860	1	4	0	4	7	3	9	3	0	4	4	3	3 (0)	0	
245	<i>Phytocoris longipennis</i> Flor, 1860	0	0	1	0	0	0	0	0	0	0	0	0	0 (0)	0	
246	<i>Phytocoris pini</i> Kirschbaum, 1856	0	0	0	0	0	1	0	0	0	0	0	0	0 (5)	0	
249	<i>Phytocoris tiliae</i> (Fabricius, 1776)	0	0	1	1	0	0	0	0	0	1	1	0	0 (0)	0	
251	<i>Rhabdomiris striatellus</i> (Fabricius, 1794)	0	3	13	0	0	0	0	0	0	0	0	0	0 (0)	0	
268	<i>Lygocoris pabulinus</i> (Linnaeus, 1761)	0	0	0	0	0	0	0	1	0	0	0	0	0 (0)	0	
274	<i>Lygus gemellatus</i> (Herrich-Schaeffer, 1835)	0	1	0	0	0	0	0	0	0	0	0	0	0 (0)	0	
285	<i>Pinalitus atomarius</i> (Meyer-Dür, 1843)	0	15	0	1	0	3	12	2	20	6	60	0	4 (6)	0	
287	<i>Pinalitus rubricatus</i> (Fallén, 1807)	0	0	0	0	0	0	0	0	1	0	0	1	1 (0)	0	
288	<i>Pinalitus viscidola</i> (Puton, 1888)	0	4	0	0	0	0	0	0	0	0	0	0	0 (0)	0	
305	<i>Leptopterna dolabrata</i> (Linnaeus, 1758)	0	0	0	0	0	0	0	0	0	0	0	1	0 (0)	0	
344	<i>Blepharidopterus angulatus</i> (Fallén, 1807)	0	0	0	1	0	0	0	0	0	0	0	0	0 (0)	0	
347	<i>Cylloceria histronius</i> (Linnaeus, 1767)	0	1	5	0	0	0	0	0	0	0	0	0	0 (0)	0	
349	<i>Dryophilocoris flavoquadrimaculatus</i> (De Geer, 1773)	1	2	3	0	0	0	0	0	0	0	0	0	0 (0)	0	
374	<i>Orthotylus obscurus</i> Reuter, 1875	0	1	0	0	0	0	0	0	0	0	0	0	0 (0)	0	
377	<i>Orthotylus tenellus</i> (Fallén, 1807)	0	0	3	0	0	0	0	0	0	0	0	0	0 (0)	0	
383	<i>Orthotylus fuscescens</i> (Kirschbaum, 1856)	0	1	0	0	0	0	0	0	0	0	0	0	0 (0)	0	
387	<i>Hypseloecus visci</i> (Puton, 1888)	0	1	0	0	0	0	2	0	0	0	0	0	0 (0)	0	
391	<i>Pilophorus perplexus</i> Douglas & Scott, 1875	0	1	0	0	0	0	0	0	0	0	0	0	0 (0)	0	
393	<i>Cremnocephalus albolineatus</i> Reuter, 1875	0	0	0	0	0	0	1	0	0	0	0	0	0 (0)	0	
394	<i>Cremnocephalus alpestris</i> Wagner, 1941	3	351	0	3	33	2	181	2	40	10	99	1	2 (20)	0	

407	<i>Atractotomus magnicornis</i> (Fallén, 1807)	10	34	0	16	15	28	160	8	7	12	26	3	13 (22)	0
431	<i>Harpocera thoracica</i> (Fallén, 1807)	108	43	11	0	0	2	0	0	0	0	0	0	0 (0)	0
452	<i>Parapsallus vitellinus</i> (Scholtz, 1846)	13	5	0	3	5	7	12	0	0	1	0	0	2 (2)	0
453	<i>Phoenicocoris dissimilis</i> (Reuter, 1878)	0	22	0	0	3	0	22	0	0	0	1	0	3 (14)	0
454	<i>Phoenicocoris modestus</i> (Meyer-Dür, 1843)	3	7	0	0	12	3	5	0	0	0	0	0	0 (0)	0
455	<i>Phoenicocoris obscurellus</i> (Fallén, 1829)	0	0	0	0	0	0	8	0	0	0	0	0	0 (0)	11
457	<i>Phylus melanocephalus</i> (Linnaeus, 1767)	0	1	14	1	0	0	0	0	0	0	0	0	0 (0)	0
468	<i>Psallus perrisi</i> (Mulsant & Rey, 1852)	7	8	6	0	0	0	2	0	0	0	0	0	0 (0)	0
470	<i>Psallus variabilis</i> (Fallén, 1807)	0	1	1	0	0	0	0	0	0	0	0	0	0 (0)	0
471	<i>Psallus wagneri</i> Ossiannilsson, 1953	0	0	0	0	0	0	0	0	0	0	0	0	0 (0)	1
472	<i>Psallus ambiguus</i> (Fallén, 1807)	0	0	1	0	0	0	0	0	0	0	0	0	0 (0)	0
476	<i>Psallus piceae</i> Reuter, 1878	1	0	0	0	0	0	0	0	0	0	0	0	0 (0)	0
477	<i>Psallus pinicola</i> Reuter, 1875	0	0	0	0	0	0	0	1	0	0	0	0	0 (0)	0
487	<i>Psallus mollis</i> (Mulsant & Rey, 1852)	1	3	35	0	0	0	0	0	0	0	0	0	0 (0)	0
488	<i>Psallus punctulatus</i> Puton, 1874	0	3	3	0	0	0	0	0	0	0	0	0	0 (0)	0
490	<i>Psallus varians</i> (Herrich-Schaeffer, 1841)	1	23	21	52	57	3	1	0	0	4	7	0	1 (5)	8
501	<i>Himacerus mirmicoides</i> (O. Costa, 1834)	0	0	2	0	0	0	0	0	0	0	0	0	0 (0)	0
510	<i>Nabis pseudoferus</i> Remane, 1949	0	1	0	0	0	0	0	0	0	0	0	0	0 (0)	0
513	<i>Acomporis alpinus</i> Reuter, 1875	0	0	0	4	0	0	0	0	0	4	21	0	2 (1)	0
515	<i>Acomporis pygmaeus</i> (Fallén, 1807)	0	0	0	0	0	0	0	0	0	2	2	1	1 (3)	0
518	<i>Anthocoris confusus</i> Reuter, 1884	0	1	0	5	5	0	2	0	0	1	1	0	0 (0)	0
528	<i>Elatophilus nigricornis</i> (Zetterstedt, 1838)	0	0	0	0	0	0	0	0	0	0	0	0	0 (0)	1
533	<i>Temnostethus gracilis</i> Horváth, 1907	0	1	0	0	0	0	0	0	0	0	0	1	0 (0)	0
543	<i>Orius minutus</i> (Linnaeus, 1758)	3	39	2	0	18	6	21	0	0	1	13	0	1 (2)	1
555	<i>Xylocoris galactinus</i> (Fieber, 1836)	1	0	0	0	0	0	0	0	0	0	0	0	0 (0)	0
564	<i>Empicoris baerensprungi</i> (Dohrn, 1863)	0	0	1	0	0	0	0	0	0	0	0	0	0 (0)	0
566	<i>Empicoris vagabundus</i> (Linnaeus, 1758)	2	0	0	0	0	0	0	0	0	0	0	0	0 (0)	0
591	<i>Aradus obtectus</i> Vasarhelyi, 1988	0	0	0	0	0	0	0	0	0	0	0	0	1 (0)	0
619	<i>Kleidocerys resedae</i> (Panzer, 1797)	3	5	1	1	3	0	0	0	2	2	2	1	1 (1)	0
639	<i>Metopoplax ditomoides</i> (A. Costa, 1847)	1	0	0	0	0	0	0	0	0	0	0	0	0 (0)	0
640	<i>Metopoplax origani</i> (Kolenati, 1845)	0	0	0	0	0	0	0	0	0	1	0	0	0 (0)	0
650	<i>Drymus ryeii</i> Douglas & Scott, 1865	1	0	0	0	0	0	0	0	0	0	0	0	0 (0)	0
656	<i>Gastrodes abietum</i> Bergroth, 1914	0	0	0	2	2	1	0	2	0	1	2	5	2 (1)	0
657	<i>Gastrodes grossipes</i> (De Geer, 1773)	2	3	1	11	7	1	0	0	0	0	1	0	0 (0)	0
688	<i>Megalonotus chiragra</i> (Fabricius, 1794)	0	1	0	0	0	0	0	0	0	0	0	1	0 (0)	0
729	<i>Piesma maculatum</i> (Laporte, 1833)	2	2	2	0	0	0	1	0	0	0	0	0	0 (0)	0
769	<i>Brachycarenum tigrinus</i> (Schilling, 1829)	0	1	1	0	0	1	1	0	0	0	0	0	0 (0)	0
813	<i>Troilus luridus</i> (Fabricius, 1775)	0	0	0	0	1	0	0	0	1	0	1	0	0 (0)	0
828	<i>Chlorochroa pinicola</i> (Mulsant & Rey, 1852)	0	0	0	0	0	0	0	2	0	0	0	0	0 (0)	0
831	<i>Palomena prasina</i> (Linnaeus, 1761)	2	8	1	3	0	0	0	0	0	0	0	0	0 (0)	1
840	<i>Pentatoma rufipes</i> (Linnaeus, 1758)	0	0	2	3	1	1	1	0	1	6	4	0	0 (0)	1
853	<i>Eurydema oleracea</i> (Linnaeus, 1758)	0	0	0	1	0	0	0	0	0	0	0	0	0 (0)	0
865	<i>Elasmucha grisea</i> (Linnaeus, 1758)	0	0	0	0	0	1	0	0	0	0	0	0	0 (0)	0

Acomporis sp.	0	0	0	0	0	0	0	0	0	1	0	0	1 (0)	0
Anthocoridae sp.	0	0	0	3	3	0	2	1	0	2	10	0	5 (2)	0
Anthocoridae/Microphysidae	0	0	1	0	0	0	0	0	0	0	0	0	0 (0)	0
Cremnocephalus sp.	0	0	0	1	0	0	0	0	0	0	2	0	0 (0)	0
Gastrodes sp.	0	0	0	2	0	2	0	0	0	0	1	0	1 (0)	0
Loricula sp.	0	1	0	1	2	0	7	1	0	0	6	1	0 (0)	0
Miridae sp.	13	19	31	10	1	18	13	9	8	5	1	8	7 (1)	1
Mirinae sp.	0	0	0	0	0	0	1	0	0	0	0	0	0 (0)	0
Orthotylinae sp.	0	0	0	0	0	0	0	0	0	1	0	0	0 (0)	0
Pentatomidae sp.	1	2	4	0	0	0	1	0	0	1	0	3	3 (0)	0
Phoenicocoris sp.	0	0	0	0	1	0	0	0	0	0	0	0	0 (0)	0
Phytocoris sp.	1	2	0	5	3	3	2	1	4	3	4	11	10 (0)	1
Psallus sp.	9	3	10	0	0	0	0	0	0	0	1	0	0 (0)	0
Psallus/Parapsallus sp.	2	0	0	1	0	1	0	0	0	0	0	0	0 (0)	0
Phylinae sp.	0	0	0	0	0	0	0	0	0	0	0	0	0 (1)	0
number of specimens	213	666	265	146	192	114	507	36	89	73	281	43	65 (93)	32
number of species	25	37	29	19	17	20	22	11	12	15	19	11	15 (15)	9

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Dr. Martin Goßner

Loricula – Agentur für Kronenforschung, ökologische Studien und Determination, Schussenstr. 12, 88273 Fronreute, Germany, FAX: 08161-714671,

e-mail: martin.gossner@loricula.de

internet: www.loricula.de