Eur. J. Entomol. **106**: 241–252, 2009
http://www.eje.cz/scripts/viewabstract.php?abstract=1448
ISSN 1210-5759 (print), 1802-8829 (online)

Light intensity affects spatial distribution of Heteroptera in deciduous forests

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Key words. Light regime, diversity, Heteroptera, community structure, vertical and horizontal stratification, nemoral fauna

Abstract. Studies on the effect of varying light intensity on the spatial distribution of flying insect communities are rare, particularly in complex ecosystems like forests. The horizontal and vertical distribution of Heteroptera was studied at different scales in a large deciduous forest area, the "Steigerwald", in southern Germany. Diversity was affected by (1) vertical position: it was significantly higher near the ground than in the canopy of beech-dominated forests but similar in oak-dominated forests; within the canopy of beech-dominated forests, diversity was significantly higher in the upper than in the lower canopy of intermixed oak trees but similar in beech trees; (2) canopy cover, but in oak forests the response depended on the vertical position: increasing significantly close to the forest floor with decreasing canopy cover, but showing an opposite trend in the canopy; so that in sparse stands (little canopy cover) diversity was significantly higher near the ground, whereas where the forest canopy was medium or dense diversity was higher in the canopy. Moreover, community composition of Heteroptera near the ground differed from that in the canopy in both forest types and near the ground between stands in oak-dominated forest that had canopies of different densities. Results clearly indicate that light intensity is an important direct or indirect factor structuring Heteroptera communities. While in the canopy differences in leaf quality and microhabitats might be important, near the forest floor it is more likely to be the diversity of herbaceous plants.

INTRODUCTION

Light is known to be an important abiotic factor influencing the distribution, biomass and diversity of terrestrial plants and animals (Begon et al., 1998; Reynolds, 1999; Aavik et al., 2008). Within productive sites like tropical rainforests it might be expected that high light intensities, combined with a greater range of light intensities and spectra, provide more opportunities for specialization and increases in plant species richness (Begon et al., 1998). The same mechanism may also apply in temperate regions.

The light intensities in central European biotopes differ greatly. Generally, open habitats like meadows or grassland are exposed to high levels of solar radiation, especially intensively managed grasslands where periodical mowing results in low growing vegetation. Forests, however, have a much more complex structure. Natural forests contain a mosaic of different sized openings, caused by natural die back, windblow and insect outbreaks, as well as areas of closed forest of different ages and structures (Franklin et al., 2002; Rademacher et al., 2004). According to the gap dynamic theory, gap formation increases abiotic and biotic heterogeneity and enables species to coexist (Shugart, 1984; Laska, 2001). For example different gap sizes will favour either shade-intolerant or shade-tolerant plant species (Runkle, 1985; Kneeshaw & Bergeron, 1996; Huth & Wagner, 2006). In the interior of most mature managed forests little light reaches the forest floor (Szwagrzyk et al., 2001). But the rarer forest management practice of coppicing with standards results in more open forests, with a changing light regime during the rotation period (Buckley, 1992; Bärnthol, 2003). This form of management creates an artificial disturbance similar to canopy gap formation (Peterken, 1996).

Furthermore, there is a vertical stratification in light intensity. For example, there is great change in light intensity from the canopy to the ground in an old growth Douglas-fir-Helmlock forests in North America (Parker, 1997). Moreover, the degree of change from canopy to forest floor depends on the tree species present (Häberle et al., 2003). Depending on the level of illumination trees produce either sun or shade leaves (Urban et al., 2007).

Plant performance, composition and diversity change in response to changes in illumination (Pavlovic et al., 2006), which indirectly affect insect distribution and diversity (De Cauwer et al., 2006; Richards & Windsor, 2007). In addition, the intensity of sunlight affects the concentration of secondary plant compounds in leaves and therefore insect performance (Dudt & Shure, 1994; Le Corff & Marquis, 1999). In addition to the indirect responses via plants insects might also be directly affected by light intensity. Temperature, which is linked to the intensity of sun light, strongly affects the rate of reproduction in insects (Liu et al., 1995) and therefore might affect the distribution and diversity of insects, as reported for agricultural crops (Cauwer et al., 2006). Similarly, in forests lace-wings (Gruppe & Schubert, 2001; Duelli et al., 2002a) and saproxylic beetles (Jonsell et al., 1998; Sverdrup-Thygeson & Ims, 2002) prefer sunny areas. Moreover the importance of openings in the forest and forest edges is revealed by several studies (Bouget & Duelli, 2004; Ulyshena et al., 2004; Wermelinger et al., 2007; Müller et al., 2008). These studies, however, focused either solely on outer forest edges, adjacent to agricultural land (Duelli et al., 2002a; Duelli & Obrist, 2003) or on gaps caused by windblow or insect outbreaks (Duelli et al., 2002b; Müller et al., 2008). Natural openings in the forest canopy are characterized not only by higher levels of illumination at ground level, but also by an increase in structural diversity (e.g. dead wood) compared to areas of the forest where the canopy is closed (Bouget & Duelli, 2004). Therefore it is difficult to separate the effect of light intensity on insects from that of other effects. In managed forests, however, most of the cut wood is removed, which makes it easier to study the effects of illumination. Few studies, however, have looked at the effect of the different levels of illumination resulting from different types of management on forest insects (Koivula, 2002; Huber & Baumgarten, 2005; Gossner et al., 2006).

The vertical structure of forests may also affect insect distribution (Le Corff & Marquis, 1999; Basset et al., 2003; Vance et al., 2007; Müller et al., 2008). As Su & Woods (2001) demonstrate it is essential also to sample vertically in order to reliably describe the effects of forest management on a horizontal scale. Studies of vertical stratification within forests do not consider fine scale differentiation: in Central Europe most studies have focused on sampling at two heights, with a few exceptions (Irmler, 1998; Gruppe et al., 2008).

Previous studies of horizontal and vertical stratification have mainly focused on Lepidoptera or Coleoptera (Gering et al., 2003; Summerville et al., 2003, 2006; Murakami et al., 2005; Crist et al., 2006; Hirao et al., 2007). Although important taxa in forest ecosystems (Achtziger et al., 2007; Gossner et al., 2008) the spatial distribution of Heteroptera in forests is not well studied. Current knowledge comes mainly from studies of forest edges (e.g. Müller et al., 2008).

To determine the effects of light intensity on Heteroptera communities I focused on gradients of light intensity occurring within regular managed forest systems, i.e. coppice with standards in an oak-dominated forest and a high forest system in a beech-dominated forest in the "Steigerwald" in Northern Bavaria. I hypothesised that gradients in light intensity would affect the diversity and structure of Heteroptera communities vertically (1) as well as horizontally (2). (1) Light intensity decreases from the canopy to the ground and therefore Heteroptera communities might be influenced by their vertical position on a "rough" scale (canopy vs. near the ground) as well as on a "finer" scale (within the canopy). (2) In coppiced oak forests with standards, the different stages during a rotation are characterized by different levels of canopy cover and thus different light regimes at ground level. In beech dominated forests gaps and gap edges resulting from forest management and closed forest areas differ in canopy cover. The different canopy cover leads to horizontal differences in light intensity at ground level in both forest types, which might affect the diversity and structure of Heteroptera communities.

MATERIAL AND METHODS

The study was conducted in the 20,000 ha Steigerwald in northern Bavaria (10°29′E, 49°50′N). It is dominated by broadleaved trees: beech (*Fagus sylvatica* L.) in the north and oak [*Quercus petraea* (Matt.) Liebl.] in the south. Average daily temperatures range from 7.5 to 8.5°C and average annual precipitation from 650 to 800 mm. The northern part of this area is dominated by high forest. The southern part is made up of smaller areas of coppice with standards and stands undergoing conversion. The oak forests were sampled in 2002 (Müller et al., 2004) and the beech forests in 2004 (Müller, 2005).

Arthropods were sampled using flight-interception traps (Basset et al., 1997), which were placed just above ground level (1.5 m) and at different heights in beech and oak trees (Table 1 and 2). Sampling jars were filled with killing and preserving fluid (1.5%-$CuSO_4$-solution) and emptied monthly from March to October. The samples were sorted and Heteroptera subsequently identified to species level using Wagner (1952, 1966, 1967), Péricart (1972, 1983, 1987) and recent taxonomic publications. Only adult bugs were included in the analyses.

TABLE 1. Vertical positions of the traps used to sample flying arthropods in beech and oak dominated forests. Note that identical traps were used for the canopy vs. ground and the within canopy (upper and lower canopy) analyses. n = number of traps .

Canopy vs. ground	Oak-dominated		Beech-dominated		
	canopy	near ground	canopy	near ground	
height [m]	10–30	1.5	10–30	1.5	
oak (n)	40	25	–	–	
beech (n)	–	–	53	69	
Within the canopy			upper canopy	lower canopy	trunk layer
height [m]			20–30	10–20	2–10
oak (n)			13	14	–
beech (n)			15	38	35

TABLE 2. Position and number of traps used to sample flying arthropods in order to determine the effects of canopy cover. Note that the analysis uses the same data as the analysis for vertical position of the traps (Table 1). n = number of traps .

Canopy cover	Oak-dominated			Beech-dominated		
	dense	medium dense	sparse	forest interior	edge of gap	centre of gap
near ground (n)	5	10	10	31	30	8
canopy (n)	15	15	10	–	–	–

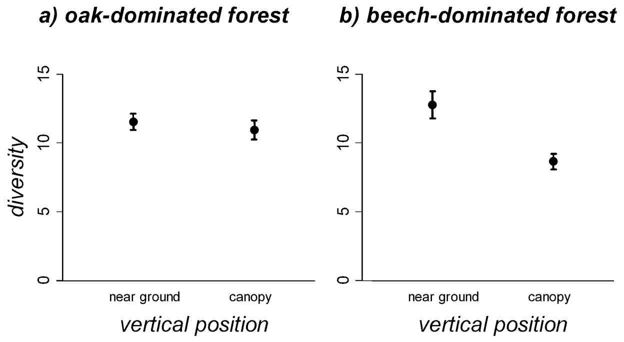

Fig. 1. Diversity (Fisher's alpha) of Heteroptera corrected for sample size. a) oak-dominated forest n = 25 traps, t-test: df = 48, t = 1.00, p > 0.10; b) beech-dominated forest n = 53 traps. t-test: df = 104, t = 5.04, p < 0.0001.

Data analysis and statistics

The effects of vertical position and canopy cover on the diversity and species composition of Heteroptera were analysed. It was assumed that the light intensities would be higher in the canopy than near the ground and in more open than in dense forests. Vertical distribution was analysed in two ways (Table 1).

(1) The communities in the canopy and near the ground were compared, in both oak and beech forests, using only the samples collected from canopies of the dominant tree species.

(2) At a finer within canopy scale, communities in the upper and lower canopy of oak and upper/lower canopy and trunk layers of beech, at the beech-dominated forest site, were compared.

The effect of the assumed higher light intensities in areas with little canopy cover and complete canopy cover was analysed in two ways (Table 2). Differences between:

(1) stands with a dense, medium dense or sparse forest canopy in the oak-dominated forest and

(2) plots deep in the forest, at the edge of a gap or in the centre of a gap in beech-dominated forest, were analysed.

Both the diversity and community structure of Heteroptera were analysed. α-diversity was measured as the α-value of the log-series, described as Fisher's alpha (Fisher et al., 1943), because of its favourable statistical properties (May, 1975; Taylor, 1978; Wolda, 1983; Magurran, 2004). The computer program EstimateS generates a standard deviation for Fisher's alpha (Colwell, 1997), which is presented in the figures and validated statistically (t-test, single-factor ANOVA).

Differences in community structure were analysed using a one-way Analysis of Similarity (ANOSIM). This was used to determine differences between a priori defined groups of community samples using permutation/randomisation methods on a similarity matrix (for details see Clarke & Warwick, 1994). In this study the Bray-Curtis dissimilarity matrix was used because it captures differences in assemblage structure due to both the abundance of shared species and species composition. It is one of the most robust measures of ecological distance (Faith et al., 1987) and therefore frequently used in ecological studies (e.g. Rodgers & Kitching, 1998). All analyses were done using the Primer 5 computer program (Primer-E 2002).

An Indicator Species Analysis (Dufrêne & Legendre, 1997) gave indicator values for each heteropteran species, based on the relative abundance and relative frequency of each species in samples collected from a particular stratum. These were tested for statistical significance using a Monte Carlo technique. Analyses were performed with PC-ORD for Windows (Version 3.05).

TABLE 3. Rough indication of the species mainly flying close to the ground or in the canopy in oak-dominated (a) and beech-dominated forests (b). Results of an indicator species analysis (p < 0.10). n = total number of specimens caught.

(a) oak-dominated forest	n	Indicator value		p
		ground	canopy	
Drymus ryei	60	**36**	0	0.001
Nabis pseudoferus	39	**30**	0	0.002
Stenodema laevigata	43	**27**	0	0.005
Aradus depressus	24	**20**	0	0.005
Dolycoris baccarum	32	**22**	1	0.027
Orius majusculus	24	**18**	1	0.044
Himacerus apterus	13	**11**	0	0.049
Palomena prasina	77	**32**	3	0.051
Scolopostethus thomsoni	16	**12**	0	0.051
Deraeocoris ruber	16	**12**	0	0.056
Dryophilocoris flavoquadrimaculatus	232	**33**	5	0.078
Deraeocoris lutescens	1253	19	**66**	0.001
Harpocera thoracica	791	12	**73**	0.001
Pentatoma rufipes	50	2	**36**	0.020
Psallus variabilis	13	0	**20**	0.031
Temnostethus gracilis	11	0	**20**	0.033
Loricula elegantula	36	3	**26**	0.069
Piesma maculatum	8	0	**15**	0.081
Σ species mainly caught in a particular stratum		**11**	7	
(b) beech-dominated forest				
Dolycoris baccarum	51	**34**	0	0.001
Stenodema laevigata	12	**13**	0	0.005
Nabis pseudoferus	9	**13**	0	0.016
Megalonotus chiragra	8	**10**	0	0.023
Carpocoris fuscispinus	9	**9**	0	0.034
Troilus luridus	14	**12**	0	0.045
Palomena prasina	53	**25**	5	0.049
Drymus ryei	6	**7**	0	0.062
Deraeocoris lutescens	326	3	**80**	0.001
Psallus varians	1179	28	**68**	0.001
Pentatoma rufipes	72	1	**37**	0.001
Anthocoris confusus	102	12	**44**	0.003
Orius minutus/vicinus	43	5	**26**	0.008
Loricula elegantula	22	0	**17**	0.009
Harpocera thoracica	212	1	**28**	0.022
Temnostethus pusillus	4	0	**8**	0.028
Phytocoris tiliae	10	0	**11**	0.039
Psallus perrisi	13	0	**10**	0.048
Σ species mainly caught in a particular stratum		8	**10**	

RESULTS

The results presented are for 10,372 specimens of 125 species of Heteroptera. 6,193 specimens of 93 species were collected in the oak-dominated forest and 4,179 specimens of 87 species in the beech-dominated forest. A complete list of all the species collected is given in the Appendix.

Vertical position

Heteroptera diversity was influenced by vertical position in beech but not oak forests. In beech forests there was a greater diversity of Heteroptera near the ground

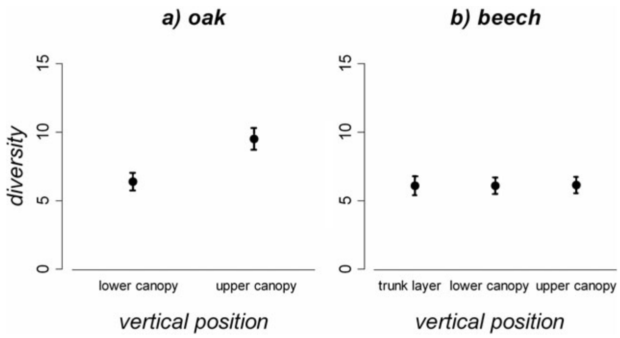

Fig. 2. Fine scale differences in the diversity (Fisher's alpha) of Heteroptera at different heights in beech-dominated forest corrected for sample size: a) oak n = 13, t-test: df = 24, t = 4.35, p < 0.001; b) beech n = 15, ANOVA: df = 44, F < 0.01, p > 0.10.

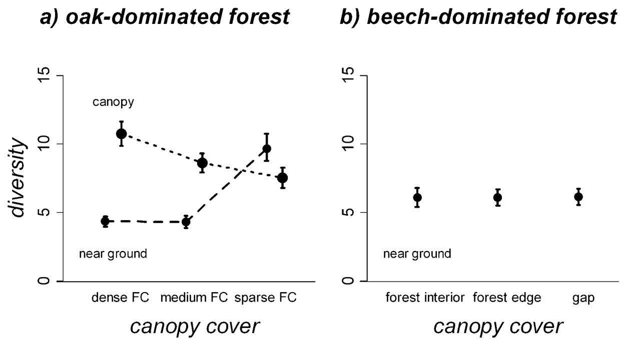

Fig. 3. Diversity (Fisher's alpha) of Heteroptera along a horizontal gradient of light intensity in oak- (a) and beech- (b) dominated forest, corrected for sample size: a) near the ground n = 5; df = 14, F = 25.31, p < 0.0001; in the canopy n = 10; df = 29, F = 4.49, p < 0.05, b) near the ground n = 8, ANOVA: df = 23, F = 2.80, p > 0.10. FC = forest canopy cover.

than in the canopy (Fig. 1). The community composition was affected by vertical position in both types of forest (oak: ANOSIM; Global R = 0.607, p < 0.001; beech: ANOSIM; Global R = 0.221, p < 0.001). In both forests several species also significantly preferred one of the two strata (Table 3). While in oak forests there were more indicator species near the ground the opposite occurred in beech forests.

At a finer scale within the canopy of beech dominated forests, the diversity of species in the upper canopy layer of oak trees was higher than in the lower canopy layer. Within the canopy of beech trees, there were no differences in the diversity measured at three vertical positions (Fig. 2).

Community structure was not affected by the vertical position within the canopy of either beech or oak trees (ANOSIM; oak: Global R = –0.009, p = 0.506; beech: Global R = 0.04, p = 0.083). Some species, however, showed a significant preference for the upper canopy layers of oak and beech (Table 4), but none showed a preference for the lower canopy or the trunk layer.

Canopy cover

Canopy cover affected the diversity of heteropterans in oak (Fig. 3a) but not beech forests (Fig. 3b). In oak forests the effect of canopy cover on diversity was different for insects collected in the canopy compared to near the ground: while diversity significantly increased with increasing light intensity near the ground, in the canopy it decreased with decrease in canopy cover (Fig. 3a). That is, diversity was significantly higher in the canopy of dense (t-test: df = 13, t = 8.93, t < 0.001) and medium dense (t-test: df = 13, t = 7.29, p < 0.001) stands. In sparse forests diversity was higher near the ground (t-test: df = 13, t = 7.95, t < 0.001).

Differences in canopy cover did not affect community structure in the canopy of oak-dominated forest (ANOSIM; oak: Global R = 0.02, p = 0.321) or near the ground in beech-dominated forest (Global R = 0.05, p = 0.094). Near the forest floor in oak-dominated forests, however, community structure was significantly associated with differences in canopy cover (Global R = 0.25, p < 0.001). A post hoc test revealed significant differences between sparse and medium (p = 0.011) as well as between sparse and dense canopy cover (p = 0.003).

In oak forests, several species were mainly caught near the ground at sites with a dense or sparse forest canopy, and in the canopy at sites with medium forest canopy cover (Table 5). In beech forests species were mainly caught near the ground at sites where there were gaps in the forest canopy, except for *Psallus varians*, which was caught mainly at forest edge sites.

DISCUSSION

This study revealed that the diversity and community composition of Heteroptera are associated with differences in light intensity in a Central European forest. It

TABLE 4. Heteroptera caught at different heights by traps placed in oak and beech trees in beech dominated forests. Results of an indicator species analysis (p < 0.10). n = total number of specimens caught.

Beech-dominated forest	n	Indicator value			p
		Trunk layer	Lower canopy	Upper canopy	
Oak					
Phytocoris dimidiatus	28	–	1	**42**	0.028
Beech					
Psallus perrisi	13	1	1	**20**	0.013
Pentatoma rufipes	75	2	11	**34**	0.019
Phytocoris dimidiatus	5	0	0	**16**	0.023
Psallus varians	1121	23	29	**45**	0.032
Σ species preferring strata		0	0	**5**	

TABLE 5. Heteroptera caught at sites with different canopy cover (FC = forest canopy cover) in oak (a) and beech dominated forests (b). Results of an indicator species analysis ($p < 0.10$). n = total number of specimens caught.

(a) oak-dominated forest	n	Indicator value			p-value
Near the ground		dense FC	medium FC	sparse FC	
Harpocera thoracica	136	**78**	11	11	0.02
Orthotylus tenellus	72	**72**	28	0	0.038
Dolycoris baccarum	28	**86**	14	0	0.066
Rhabdomiris striatellus	152	**74**	26	0	0.067
Kleidocerys resedae	1996	0	30	**70**	0.015
Anthocoris confusus	28	17	0	**83**	0.017
Elasmucha fieberi	8	0	0	**100**	0.03
Loricula elegantula	8	0	0	**100**	0.031
Anthocoris nemorum	8	0	0	**100**	0.033
Σ species preferring each stratum		**4**	**0**	**5**	
In the canopy		dense FC	medium FC	sparse FC	
Rhabdomiris striatellus	149	**44**	26	30	0.036
Loricula elegantula	28	0	**71**	29	0.015
Pentatoma rufipes	42	17	**70**	13	0.07
Eurydema oleracea	3	0	**100**	0	0.092
Palomena prasina	13	11	15	**74**	0.015
Dryophilocoris flavoquadrimaculatus	56	10	5	**84**	0.051
Σ species preferring each stratum		**1**	**3**	**2**	
(b) beech-dominated forest	n	Indicator value			p-value
Near the ground		forest interior	forest edge	gap	
Psallus varians	406	25	**45**	30	0.053
Carpocoris fuscispinus	9	11	0	**89**	0.001
Carpocoris purpureipennis	4	8	0	**92**	0.002
Anthocoris confusus	38	23	22	**54**	0.006
Palomena prasina	42	8	18	**74**	0.007
Aelia acuminata	10	3	3	**94**	0.011
Rhabdomiris striatellus	3	11	0	**89**	0.015
Piezodorus lituratus	3	11	0	**89**	0.06
Stenodema laevigata	12	0	44	**56**	0.078
Harpocera thoracica	15	19	23	**58**	0.081
Deraeocoris lutescens	40	19	25	**56**	0.09
Σ species preferring each stratum		0	1	**10**	

was clearly demonstrated that Heteroptera are not evenly distributed within forests, which agrees with previous studies (Štepanovičová & Lapková, 1988; Müller & Gossner, 2007; Gruppe et al., 2008), but that their distribution is associated with different light intensities within forests is a new finding. It is reported that in temperate forests the effects of light on flying insect communities is associated with changes in canopy cover (Štepanovičová, 1981; Gossner et al., 2006; Yi, 2007) or distance from the ground (Irmler, 1998). This study shows that both processes are important and can interact with each other, so that the effect of changes in canopy cover differs at different heights within a forest.

Diversity was higher near the ground in beech forests but did not differ between the canopy and near the ground in oak forests. This is surprising because the canopy contains most of the photosynthetically active tissue in forests and is exposed to more sunlight. However, this might caused, first, by the fact that independently of light intensity, Heteropteran diversity associated with beech is less diverse than that associated with oak (Gossner, 2008): almost 20 monophagous species occur on oaks in Central Europe, while there are no true bugs monophagous on beech (Wachmann et al., 2004). Alternatively, oak specialists were mainly found in the canopy, while species associated with beech tend to occur also frequently near the ground (Gruppe et al., 2008). This was exemplified by the high indicator values of *Psallus varians* and *Anthocoris confusus*, the only two Heteroptera species in Central Europe that are more abundant in beech dominated forests (Gossner, 2006). These effects resulted in the community structure differing between strata with some species mainly found in the canopy and others near ground.

Differences in diversity and community composition were found within the canopy of beech forests. The upper crown of oaks growing in beech dominated forest contained a higher diversity of Heteroptera than the lower crown. Light availability determines the distribution of leaves within the canopy and vice-versa (Norman & Campbell, 1989; Kucharik et al., 1999) leading to a spatial variation in leaf energy balance, water content and photosynthesis, and therefore in herbivore distribution (Murakami & Wada, 1997; Basset, 2001). According to Ellsworth & Reich (1993), differences in the physical environment determine differences in the leaf quality between forest strata. As Southwood (1973) demonstrated, structure of herbivorous communities is often affected by the nutritional condition of plants, specifically their low protein and other nutrient content might be crucial. Moreover, digestibility-reducing factors affect insect feeding, growth rates and survival and therefore population size and community structure of herbivorous insects (Feeny, 1970; Basset, 1996). Consequently, variation in leaf quality might affect the diversity of herbivorous communities. As Murakami et al. (2005) demonstrated for Lepidoptera larvae, leaf quality of oak decreases from the upper canopy to the understory in spring, but this pattern reverses during summer. The pattern reflects temporal differences in bud burst. Like lepidopterous larvae most oak Heteroptera are early spring feeders (Wachmann et al., 2004) and therefore their distribution might reflect leaf quality at that time, with the higher diversities in the upper canopy associated with the higher leaf quality there.

Species diversity did not differ with position within the canopy of beech trees. This reflects the different ecologies of oak and beech. While oak is a shade-intolerant species with an open crown structure, beech is a shade-tolerant tree species with a denser crown structure (Erlbeck et al., 1998). This results in proportionally more light reaching the lower parts of the canopy of oak than beech trees. This might result in a higher microclimatic diversity and thus in a higher number of niches within oak crowns, which promotes Heteroptera diversity. Moreover, as already discussed above, as a consequence of more light reaching the lower canopy in oak crowns, leaf quality varies within trees to a greater extent than within beech trees resulting in greater differences in herbivore diversity within the crowns of oak trees (Murakami et al., 2005). This might however only occur within oak crowns in managed forests (e.g. high forestry systems) in which the lower canopy is shaded by surrounding trees, especially when the dominant tree species is shade tolerant like beech. Similar patterns might occur in other shade-intolerant species like ash and alder.

Changes in the densities of tree crowns had large but different effects on Heteropteran diversity and species composition in the canopy and near the ground: while diversity in the canopy decreased with increasing light intensity the opposite occurred near the ground. That is, the diversity was higher in oak crowns in dense and medium dense forest stands and near the ground in stands with a sparse canopy. Four major effects could explain this pattern: (1) the higher light intensity near the ground at sites where the canopy was sparse, resulted in higher plant diversity and therefore higher Heteroptera diversity (Siemann et al., 1998; Brandle et al., 2001); in beech forest with only small gaps in the canopy no horizontal gradient in plant species diversity was recorded, (2) oak trees produce branches lower down the trunk if there is sufficient light and therefore canopy species are also able to occur near the ground (Su & Woods, 2001; Gruppe et al., 2008), (3) light intensity within the lower canopy of trees might not be as low as expected because of lateral illumination, and (4) with a decrease in canopy cover the diversity of Heteroptera might decrease due to a decrease in the amount of habitat (species-area relationship, Rosenzweig, 1995).

Changes in canopy cover did not alter community structure in the canopy but did affect species composition near the ground (this supports explanation 1). This might be due to the host plant canopy remaining the same, whereas at ground level there was a high species turnover of herbaceous plants (Müller et al., 2004). Insects are known to respond to plant diversity, structure, density and spatial variation in community composition (Andow, 1991; Siemann et al., 1998; Tscharntke & Brandl, 2004; Crist et al., 2006). The current results indicate that changes in the community structure of Heteroptera are associated with spatial variation in herbaceous plant communities.

Direct and indirect effects of light intensity, however, might be not the only factors affecting the distribution of Heteroptera. Although the bottom-up effects of plants are important in trophic interactions in terrestrial systems (Stiling & Rossi, 1997; Karimzadeh et al., 2004), top-down effects are also known to be important in some terrestrial systems (Roininen et al., 1996; Stadler, 2004). Thus changes in the occurrence of predators and parasites might also affect the distribution of Heteroptera. Moreover, intra- and inter-specific competition is known to be important in structuring insect communities. Further studies on the importance of these effects on the distribution of Heteroptera in forests are needed.

CONCLUSION

The results of this study clearly indicate that the distribution of Heteroptera in continuous deciduous forests is highly stratified spatially and light intensity is an important factor in structuring communities, either directly or indirectly. This emphasizes the importance of tree species with a more open crown, or sparse forests with lower canopy cover for maintaining a high insect diversity in managed Central European forests, as Dolek et al. (in press) demonstrated for ants on oaks and Freese et al. (2006) for the endangered butterfly *Euphydryas maturna*. This can be achieved not only by supporting traditional coppice with standard forestry management, but also by forest management that results in a mosaic of different canopy cover including gaps, and by increasing the proportion of shade intolerant species like oak.

ACKNOWLEDGEMENTS. This study is based on material sampled by J. Müller (Grafenau) and U. Simon (Freising), who generously offered me to process the Heteroptera samples. I thank the forestry departments of Ebrach, Eltmann, Uffenheim, Iphofen and the "Rechtlergemeinschaft" Welbhausen, for their generous support, and to W. Rabitsch (Wien) and three anonymous referees for critical remarks on the manuscript. Thanks to E. Allan (Jena) for language improvements. Finally, many thanks to all those who helped install the traps and the students who sorted the samples. The study was financed by grants from the "Kuratorium Wald" of the Bavarian State Forestry Administration (project no. V56, V62).

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Received November 24, 2008; revised and accepted January 5, 2009

Appendix. List of species caught in the traps.

	Oak-dominated		Beech-dominated			Total
	C	NG	C_beech*	C_oak	NG	
Acanthosomatidae						
Acanthosoma haemorrhoidale (Linnaeus, 1758)	8	8	2	0	1	19
Elasmostethus interstinctus (Linnaeus, 1758)	7	12	2	3	1	25
Elasmostethus minor Horváth, 1899	0	4	0	0	0	4
Elasmucha fieberi (Jakovlev, 1864)	1	8	0	1	1	11
Elasmucha grisea (Linnaeus, 1758)	6	20	7	0	5	38
Anthocoridae						
Anthocoris confusus Reuter, 1884	9	28	83	34	38	192
Anthocoris nemoralis (Fabricius, 1794)	0	0	0	1	0	1
Anthocoris nemorum (Linnaeus, 1761)	0	8	0	0	0	8
Orius majusculus (Reuter, 1879)	4	20	3	2	0	29
Orius minutus/vicinus	11	32	38	12	14	107
Temnostethus gracilis Horváth, 1907	11	0	7	0	0	18
Temnostethus pusillus (Herrich-Schaeffer, 1835)	4	0	4	2	0	10
Xylocoris galactinus (Fieber, 1836)	0	0	0	1	0	1
Aradidae						
Aneurus avenius (Dufour, 1833)	0	0	1	0	0	1
Aradus conspicuus (Herrich-Schaeffer, 1835)	0	0	0	0	2	2

Aradus depressus (Fabricius, 1794)	0	24	0	0	1	25
CIMICIDAE						
Cimex dissimilis sensu Péricart 1972	0	0	1	0	0	1
COREIDAE						
Coreus marginatus (Linnaeus, 1758)	0	0	0	0	3	3
Enoplops scapha (Fabricius, 1794)	0	4	0	0	0	4
CYDNIDAE						
Tritomegas bicolor (Linnaeus, 1758)	1	0	0	0	0	1
GERRIDAE						
Gerris lacustris (Linnaeus, 1758)	0	4	0	0	0	4
LYGAEIDAE						
Drymus ryeii Douglas & Scott, 1865	0	60	2	0	6	68
Eremocoris podagricus (Fabricius, 1775)	0	4	0	0	0	4
Gastrodes abietum Bergroth, 1914	1	4	1	0	0	6
Gastrodes grossipes (De Geer, 1773)	0	0	0	2	0	2
Kleidocerys resedae (Panzer, 1797)	104	1996	33	11	33	2177
Megalonotus chiragra (Fabricius, 1794)	0	8	0	1	8	17
Metopoplax ditomoides (A. Costa, 1847)	0	0	2	1	0	3
Peritrechus lundii (Gmelin, 1790)	0	4	0	0	0	4
Platyplax salviae (Schilling, 1829)	1	0	0	1	0	2
Scolopostethus affinis (Schilling, 1829)	0	4	0	0	0	4
Scolopostethus decoratus (Hahn, 1833)	1	0	0	0	0	1
Scolopostethus grandis Horváth, 1880	0	4	0	0	2	6
Scolopostethus thomsoni Reuter, 1874	0	16	0	0	0	16
Sphragisticus nebulosus (Fallén, 1807)	0	0	1	0	1	2
Stygnocoris sabulosus (Schilling, 1829)	0	4	0	0	0	4
Trapezonotus arenarius (Linnaeus, 1758)	0	0	0	0	1	1
Trapezonotus dispar Stal, 1872	0	8	0	0	0	8
MICROPHYSIDAE						
Loricula elegantula (Baerenspung, 1858)	28	8	24	4	3	67
Loricula pselaphiformis Curtis, 1833	0	0	6	0	1	7
Loricula ruficeps (Reuter, 1884)	5	0	3	0	0	8
MIRIDAE						
Atractotomus magnicornis (Fallén, 1807)	0	0	1	0	0	1
Blepharidopterus angulatus (Fallén, 1807)	1	0	1	0	1	3
Campylomma annulicorne (Signoret, 1865)	0	0	1	0	0	1
Campyloneura virgula (Herrich-Schaeffer, 1835)	1	4	1	0	3	9
Closterotomus biclavatus (Herrich-Schaeffer, 1835)	2	4	0	0	0	6
Closterotomus fulvomaculatus (De Geer, 1773)	1	0	0	0	0	1
Cyllecoris histrionius (Linnaeus, 1767)	59	84	3	14	2	162
Deraeocoris annulipes (Herrich-Schaeffer, 1842)	0	0	0	1	0	1
Deraeocoris lutescens (Schilling, 1837)	945	308	547	290	40	2130
Deraeocoris ruber (Linnaeus, 1758)	0	16	0	0	0	16
Deraeocoris trifasciatus (Linnaeus, 1767)	4	4	0	3	1	12
Dichrooscytus intermedius Reuter, 1885	0	4	0	0	0	4
Dryophilocoris flavoquadrimaculatus (De Geer, 1773)	56	176	1	7	1	241
Harpocera thoracica (Fallén, 1807)	655	136	205	183	15	1194
Horistus orientalis (Gmelin, 1790)	0	0	1	0	0	1
Isometopus intrusus (Herrich-Schaeffer, 1835)	1	0	0	0	0	1
Liocoris tripustulatus (Fabricius, 1781)	0	4	0	0	1	5
Neolygus contaminatus (Fallén, 1807)	1	0	0	0	0	1
Neolygus viridis (Fallén, 1807)	2	0	0	0	0	2
Lygus punctatus (Zetterstedt, 1839)	1	0	0	0	1	2
Lygus pratensis (Linnaeus, 1758)	6	4	2	0	0	12
Lygus rugulipennis Poppius, 1911	0	4	0	0	0	4
Malacocoris chlorizans (Panzer, 1794)	2	0	0	0	0	2
Mermitelocerus schmidtii (Fieber, 1836)	0	4	0	0	0	4
Miris striatus (Linnaeus, 1758)	2	0	3	0	0	5
Orthocephalus saltator (Hahn, 1835)	0	4	0	0	0	4

Orthonotus rufifrons (Fallén, 1807)	0	12	0	0	0	12
Orthops kalmii (Linnaeus, 1758)	0	4	0	0	0	4
Orthotylus bilineatus (Fallén, 1807)	0	8	0	0	0	8
Orthotylus prasinus (Fallén, 1829)	11	4	0	0	0	15
Orthotylus tenellus (Fallén, 1807)	34	72	1	2	0	109
Plagiognathus vitellinus (Scholtz, 1846)	0	0	2	0	0	2
Phoenicocoris modestus (Meyer-Dür, 1843)	1	0	1	0	0	2
Phoenicocoris obscurellus (Fallén, 1829)	0	0	0	0	1	1
Phylus melanocephalus (Linnaeus, 1767)	45	20	5	12	1	83
Phytocoris dimidiatus Kirschbaum, 1856	6	4	5	11	1	27
Phytocoris intricatus Flor, 1860	0	0	1	0	0	1
Phytocoris longipennis Flor, 1860	4	0	4	2	1	11
Phytocoris meridionalis (Herrich-Schaeffer, 1835)	0	0	2	1	0	3
Phytocoris populi (Linnaeus, 1758)	1	0	0	0	0	1
Phytocoris reuteri Saunders, 1875	0	0	0	1	1	2
Phytocoris tiliae (Fabricius, 1776)	2	4	9	6	2	23
Pilophorus perplexus Douglas & Scott, 1875	1	0	0	0	0	1
Pinalitus atomarius (Meyer-Dür, 1843)	1	0	0	0	0	1
Pinalitus cervinus (Herrich-Schaeffer, 1842)	2	0	0	0	0	2
Plagiognathus arbustorum (Fabricius, 1794)	0	12	0	0	0	12
Psallus albicinctus (Kirschbaum, 1856)	17	8	0	1	0	26
Psallus ambiguus (Fallén, 1807)	1	12	0	0	0	13
Psallus lepidus (Fieber, 1858)	0	4	0	0	0	4
Psallus mollis (Mulsant, 1852)	51	36	7	57	5	156
Psallus perrisi (Mulsant & Rey, 1852)	61	84	13	16	2	176
Psallus punctulatus Puton, 1874	6	0	0	15	0	21
Psallus variabilis (Fallén, 1807)	13	0	1	2	0	16
Psallus varians (Herrich-Schaeffer, 1841)	17	32	1121	337	406	1913
Psallus wagneri Ossiannilsson, 1953	0	0	4	0	0	4
Rhabdomiris striatellus (Fabricius, 1794)	149	152	4	17	3	325
Stenodema calcarata (Fallén, 1807)	0	4	0	0	0	4
Stenodema laevigata (Linnaeus, 1758)	3	40	0	0	12	55
NABIDAE						
Himacerus mirmicoides (O. Costa, 1834)	0	0	0	1	0	1
Himacerus apterus (Fabricius, 1798)	1	12	4	2	0	19
Nabis pseudoferus Remane, 1949	3	36	2	4	9	54
PENTATOMIDAE						
Aelia acuminata (Linnaeus, 1758)	0	8	1	1	10	20
Arma custos (Fabricius, 1794)	0	0	0	0	1	1
Carpocoris fuscispinus (Boheman, 1849)	0	0	2	0	9	11
Carpocoris purpureipennis (De Geer, 1773)	0	4	0	0	4	8
Chlorochroa pinicola (Mulsant & Rey, 1852)	0	0	1	0	0	1
Dolycoris baccarum (Linnaeus, 1758)	4	28	5	5	49	91
Eurydema dominula (Scopoli, 1763)	0	8	0	0	0	8
Eurydema oleracea (Linnaeus, 1758)	3	0	0	0	3	6
Holcostethus strictus (Wolff, 1804)	0	4	0	0	1	5
Palomena prasina (Linnaeus, 1761)	13	64	19	9	42	147
Palomena viridissima (Poda, 1761)	0	0	0	0	2	2
Pentatoma rufipes (Linnaeus, 1758)	42	8	75	23	9	157
Piezodorus lituratus (Fabricius, 1794)	0	0	0	2	3	5
Pinthaeus sanguinipes (Fabricius, 1787)	0	0	3	0	6	9
Troilus luridus (Fabricius, 1775)	0	0	5	0	13	18
PIESMATIDAE						
Piesma maculatum (Laporte, 1833)	8	0	0	0	1	9
REDUVIIDAE						
Empicoris vagabundus (Linnaeus, 1758)	1	0	0	0	0	1
RHOPALIDAE						
Brachycarenus tigrinus (Schilling, 1829)	2	0	4	3	1	10
Corizus hyoscyami (Linnaeus, 1758)	0	0	0	0	1	1

Saldidae						
Saldula saltatoria (Linnaeus, 1758)	0	4	0	0	0	4
Scutelleridae						
Eurygaster testudinaria (Geoffroy, 1785)	1	12	0	0	1	14
Tingidae						
Acalypta musci (Schrank, 1781)	0	0	1	0	0	1
Acalypta parvula (Fallén, 1807)	0	0	0	0	1	1
Σ specimens (n)	2445	3748	2288	1104	787	10372
Σ species (n)	62	67	56	43	56	125

C = canopy, NG = near the ground, * including trunk layer, lower and upper canopy.