1 Introduction

Deciduous forests of the temperate zone harbour high densities of soil and litter-dwelling arthropods. Biomass estimates for many taxa revealed densities much higher than in most other biomes of the world (Peterson and Luxton, 1982). However, densities of arthropods vary considerably between forests. Differences in abundance can occur between forest types (Kautz and Topp, 1998, Scheu et al., 2003), between forests on slopes facing different directions (i.e. slope aspect) (Mudrick et al., 1994), forests situated at different altitudes (Ponge et al., 1997) or between forests characterized by differing soil chemical characteristics (Schaefer and Schauermann, 1990). Differences in abundance also occur within a certain forest. Apart from being affected by season (Beck, 1983, Friebe, 1983), density is affected by distance from the forest edge (Van Wilgenburg et al., 2001) and can change during successional stages (Paquin and Coderre, 1997).

Many forest floor species are patchily distributed. The variation in abundance of litter arthropods may be governed by the litter moisture content, which is higher on mounds than in pits (Levings and Windsor, 1984). In addition, litter chemical parameters differ spatially, e.g. are more acidic and leached in the vicinity of beech trunks. Such differences can affect the abundance of litter arthropods dramatically (Scheu and Poser, 1996). Furthermore, litter complexity and litter dry mass may serve as a measure of resource availability and habitat volume (Uetz, 1979). Structural components within stands may also alter density and diversity of arthropods. Structural diversity on the forest floor can be provided e.g. by downed coarse woody debris (CWD), which is a common and important structural element on the floor of primeval forests and can reach volumes of more than 450 $m^2 ha^{-1}$ (Saniga and Schütz, 2001). In managed forests, however, the amount of CWD rarely exceeds 3 $m^2 ha^{-1}$ (Ammer, 1991).

The direct effects of CWD have been well studied. CWD is known to serve as a “specific habitat” for a specialized fauna and microflora on the forest floor, providing shelter for a wide array of different species (Harmon et al., 1986, McMinn and Crossley, 1996). Numerous saproxylic arthropods depend on CWD (Jonsell et al., 1998, Sippola et al., 2002), and some of these species are involved in decomposition processes (Ausmus, 1977).

The indirect influence of CWD, however, on litter-dwelling arthropods of the forest floor has rarely been studied (Buddle, 2001, Marra and Edmonds, 1998). Preliminary investigations in a beech forest of the Westerwald (Germany), where management was “nature oriented”, indicated that most litter-dwelling arthropod taxa occurred in higher densities at sites close to CWD than at sites distant from CWD (Jabin et al., 2004). This effect was more pronounced at the forest edge than in its interior. The difference may be governed by climate, as macroclimatic conditions were more variable in the edge zone.

Two independent field investigations testing the general validity of the indirect effects of CWD were conducted. I concentrated on centipedes (Chilopoda), the only taxon that seemed to have several advantages for the study of indirect effects of CWD. Centipedes are widely distributed throughout the temperate regions of the world. They are abundant predators on the forest floor (e.g. Roberts, 1956, Fründ, 1983, Jabin et al., 2004) and are not directly dependent on CWD as a food source. Members of the chilopod taxa Lithobiomorpha, Geophilomorpha and Scolopendromorpha are feeding generalists (Poser, 1988) not associated to specific prey items which are only present at CWD.

Species richness, density and diversity of centipede assemblages were assessed in four primeval forests of Slovakia (Investigation I) and in twelve managed forests of western Germany (Investigation II).

The following hypotheses were addressed:

1. Sites close to CWD harbour higher species richness, higher density and also higher diversity of centipedes than sites distant from CWD.
2. The effect of CWD on the distribution pattern of centipedes is of general validity as it can be observed in managed and in primeval forests and is independent of altitude, parent material and slope aspect.

In the low mountain ranges of western Germany, numerous historical kiln areas which are characterized by high charcoal content in the upper soil horizon can still be found today. Charcoal has the ability to adsorb nutrients and can ameliorate the soil fertility (Oguntunde et al., 2004, Topoliantz et al., 2005). The effects of charcoal offer the opportunity to compare small-scale differences in soil chemistry. In a further study (Investigation III), the influence of soil chemistry on the small-scale distribution pattern of centipedes, other litter-dwelling arthropods and microbial parameters in temperate deciduous forests was assessed.

Two further hypotheses were addressed:

3. Charcoal in historical kiln areas alters soil chemistry in the A_h-horizon.
4. Centipedes, other litter-dwelling arthropods and soil microorganisms benefit from increased nutrient availability in historical kiln areas.

In Investigation IV, the effects of litter accumulation and CWD on microclimate and density of macroarthropods were studied. CWD is known to directly offer habitats with respect to suitable microclimate (Grove, 2002). Furthermore, litter habitats close to CWD, where litter strongly accumulates, were expected to buffer extreme microclimatic conditions (Kappes et al., 2006, Topp et al., 2006a,b). In a field experiment, I manipulated litter mass at different sites on the forest floor of two beech forests (Westerwald, Germany).

The following hypotheses were addressed:

5. Leaf litter and CWD alter the microclimate on the forest floor.
6. Centipedes and other litter-dwelling arthropods benefit from stable microclimatic conditions on the forest floor.

2 Material and methods

2.1 Investigation I (distribution pattern of centipedes in primeval forests)

Study area

The study areas are situated in the western Carpathians, central Slovakia, in two distinct mountain ranges: the Poľana and Kremnické vrchy Mountains. Both mountain ranges are of volcanic origin and are covered by broad-leaved, coniferous or mixed forests, of which only fragments can presently be considered to be natural. Four study areas were chosen in primeval forests: Either strictly protected forest reserves (Rohy in the Poľana mountains, and Boky and Badín in the Kremnické vrchy mountains) or forests classified as "protective forests on steep slopes" that have not been managed and are well preserved (Poľana – Poľana mountain range). The distances between the primeval forests range from 10-30 km. For more characteristics of the study areas see table 2.1.1.

Experimental design and field sampling

In each forest, 64 litter samples of 300 cm² were collected including all O-horizons. Sites close to coarse woody debris (c-CWD: mean distance <10 cm, $n = 32$) and sites distant from coarse woody debris (d-CWD: mean distance >200 cm, $n = 32$) were sampled. The minimum size of CWD chosen for sampling was represented by logs 20 cm in diameter and 200 cm in length. Minimum distances between sampling sites was 20 m. The total area coverage per forest and per c-CWD or d-CWD sites was 0.96 m². All forests were sampled in May and in July 2003, with specific logs chosen once only. All logs taken into consideration were at least moderately decayed (decomposition stage Z° 2 according to Albrecht, 1991).

Determination of centipedes

Soil arthropods were extracted from the litter using modified Tullgren funnels. Determination of Lithobiomorpha and Scolopendromorpha was carried out using the identification keys presented in Loksa (1954) and Eason (1964, 1982). Several morphological features of Lithobiomorpha which allow determination to the species level (e.g. female gonopods, modification of male legs) are only well-developed in the adult stage. The determination of Geophilomorpha was performed as according to Rosenberg (1989).

Data analysis

Both time periods were pooled to achieve yearly sums. Thus, the number of data sets per forest was $n = 32$, with 16 sampling sites at "c-CWD" and 16 sites at "d-CWD". Most of the data was not normally distributed. Consequently, median ± median absolute deviation values (MAD) are given and Mann-Whitney U-tests were performed to compare data sets between forests and between c-CWD and d-CWD sites within forests.

Species-area curves (species richness) and rarefaction diversity were calculated for each forest using the pooled data sets of scattered plots of 300 cm² ($n = 32$) separately for c-CWD and d-CWD sites. Rarefaction is a procedure for analysing the number of species among collections, when all collections are scaled down to the same number of individuals. The rarefaction analysis was fitted to regression lines ($y = a \ln(n) + b$). When the sample size is small, rarefaction diversity provides an alternative to conventional indices of species diversity such as Shannon diversity (H') (Smith and Grassle, 1977, Hsieh and Li, 1998).

Table 2.1.1: Main characteristics of the four primeval forests studied (Boky, Rohy, Pol'ana, Badín). Climatic data from Lapin et al. (2002).

	Boky	**Rohy**	**Pol'ana**	**Badín**
Mountain range	Kremnické vrchy	Pol'ana	Pol'ana	Kremnické vrchy
Size of reserve [ha]	176	25	40	31
Aspect of slope	S, SW	S, SW	E	N, NE
Gradient of slope [°]	10 – 40	10-40	20-60	10-40
Altitude [m above s.l.]	280 – 590	400-600	980-1100	700-780
Dominant tree species	*Quercus polycarpa, Quercus cerris*	*Quercus polycarpa*	*Fagus sylvatica, Abies alba*	*Fagus sylvatica, Abies alba*
Crown closure	0.8-2.0	0.8-2.0	0.7-2.0	>2.0
CWD [m^3 ha^{-1}]	20-40	150-280	150-280	250-350
Main soil type	eutric cambisol	eutric cambisol	dystric cambisol	dystric cambisol
Temperature in July (°C)	18.5-20.0	18.5-20.0	12.0-16.0	12.0-16.0
Annual rainfall (mm)	600-700	600-700	800-1100	800-1100
Nature reserve since	1986	1964	1981	1913

2.2 Investigation II (distribution pattern of centipedes in managed forests)

Study area

The study area was located in the low mountain ranges of western Germany. Twelve forests in which beech and oak trees dominated the natural woodland vegetation were selected for the study: (1) Königsberg, (2) Hübingen, (3) Alsbach, (4) Ehreshoven, (5) Urft, (6) Elbert, (7) Steinerberg-Plateau, (8) Achelshof, (9) Leyen, (10) Arzbach, (11) Steinerberg, (12) Immerkopf. Each study forest is situated in large forested areas which cover a minimum area of 10,000 ha. Forests in different geographic regions of the low mountain ranges (Eifel, Bergisches Land, Westerwald; Fig. 2.2.1) were selected on either southern slopes (forests 1 - 4), plateaus (forests 5 - 6) or northern slopes (forests 9 - 12) to investigate the effects of the exposure on slopes. To demonstrate the general validity of the effect of CWD, forests characterized by different environmental conditions were selected. In each aspect of slope, forests on different parent material were selected, resulting in soil pH-values of 3.0 - 7.0 (1M KCl). The elevation of the mesic forests ranged between 220 and 520 m.a.s.l. with an average precipitation of 800 - 1100 mm and an average annual temperature of 7.5 - 9.5°C (DWD, 1957, MURL, 1989). Leaf litter biomass ranged between 39.5 and 74.1 g 300 cm^{-2}. All forests were managed "close to natural", resulting in a considerable accumulation of coarse woody debris (CWD; 4 - 16 m^3 ha^{-1}) on the forest floor. For more details see table 2.2.1.

Field sampling and experimental design

The field investigations were carried out from spring 2002 to autumn 2004. All forests were sampled four times during different seasons (spring, summer, autumn, winter). In each forest, 32 litter samples of 300 cm^2 (including all O-horizons) were collected at sites close to CWD (c-CWD: mean distance <10 cm; $n = 32$) and at sites distant from CWD (d-CWD: mean distance >500 cm; $n = 32$). This resulted in 64 samples per forest and a total number of 768 samples during the investigation. An area of 0.96 m^2 was sampled per forest and site. The downed CWD (logs) chosen for sampling had a minimum diameter of 20 cm and a minimum length of 200 cm. The minimum distance between sampling sites was 20 m. All logs taken into consideration were at least moderately decayed (decomposition stage Z° 2 according to Albrecht, 1991) and only chosen once to avoid pseudoreplication (Hurlbert, 1984). The litter-dwelling arthropods were extracted using modified Tullgren funnels.

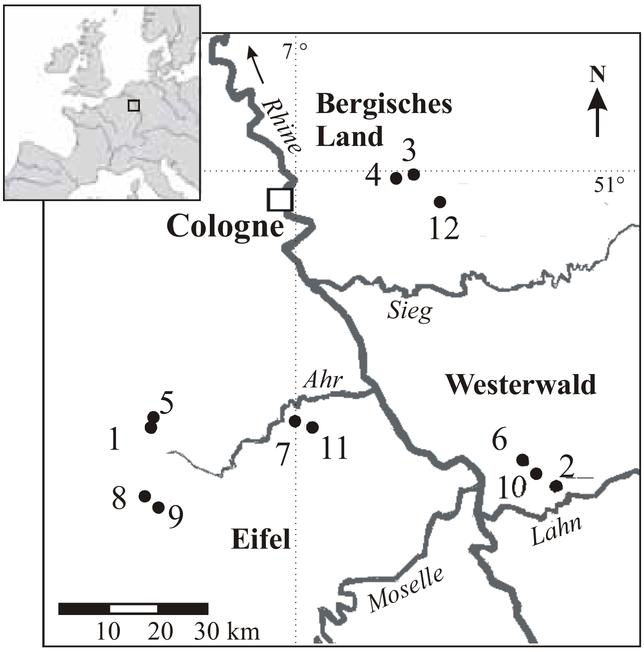

Fig. 2.2.1: Map of the study area showing the location of the twelve forests: (1) Königsberg, (2) Hübingen, (3) Alsbach, (4) Ehreshoven, (5) Urft, (6) Elbert, (7) Steinerberg-Plateau, (8) Achelshof, (9) Leyen, (10) Arzbach, (11) Steinerberg, (12) Immerkopf.

Table 2.2.1: Selected characteristics of the twelve forests studied. Average values are presented for altitude, CWD and litter mass (dry weight) and pH-value (mean, n = 8).

Forest	Aspect of slope	Altitude [m.a.s.l.]	CWD [m^3 ha^{-1}]	Litter mass [g 300 cm^{-2}]	pH [1 M KCl]
Königsberg	S	500	4	40.5	6.2
Hübingen	S	290	10	45.3	5.3
Alsbach	S	260	6	51.6	3.0
Ehreshoven	S	220	14	39.5	3.0
Urft	Plateau	500	4	59.0	5.5
Elbert	Plateau	400	12	50.1	5.5
Steinerberg-Plateau	Plateau	480	8	47.2	3.5
Achelshof	Plateau	520	8	38.9	3.5
Leyen	N	460	4	74.1	7.0
Arzbach	N	320	9	67.3	4.0
Steinerberg	N	490	16	51.2	3.4
Immerkopf	N	230	5	38.3	3.1