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ORIGINAL PAPER

Ground beetle diversity in ancient woodland remnants in north-western Germany (Coleoptera, Carabidae)

Kerstin Sroka · Oliver-D. Finch

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Abstract We investigated ground beetle communities (Coleoptera, Carabidae) in ancient woodland remnants in north-western Lower Saxony, Germany. A total of 90 pitfall traps was exposed in a stratified design in 10 stands of mature oak–beech and oak–hornbeam forests in the year 2003. Overall, 47 species (10,676 individuals) were recorded. Among these were the two relict species *Carabus glabratus* and *Abax parallelus*, and 14 further eurytopic forest species. Eleven species exhibited a high frequency and were found in all of the ten stands. Multiple linear regressions showed several significant relationships at two scales for species richness of different groups of carabids and for several of the measured environmental factors. Forest area, litter depth, amount of dead wood, distance to forest edge, and soil moisture were found to be key factors determining species richness. Furthermore, recent disturbance by logging reduced the number of forest species. According to direct gradient analyses soil moisture and litter depth have greatest influence on species communities of both, forest species and widespread species. Habitat suitability models for the two recorded relict species, *A. paralellus* and *C. glabratus*, were developed using logistic regression. The presence of *A. parallelus* in the mature ancient woodland remnants depends mainly on higher values of soil moisture, whereas for *C. glabratus* none of the measured environmental variables appeared to be key factors. Implications for the conservation of carabid assemblages in mature ancient woodlands include the advice to spread out logging over long periods of time and over various woodlands in order to keep the stand disturbance at a long-term low level. Variation in logging practices may help to conserve diverse structures. Afforestation with non-native tree species should be avoided in the managed ancient woodlands. Finally, especially the preservation of a high soil moisture seems to be important to conserve typical carabid communities.

Keywords *Abax parallelus* · *Carabus glabratus* · Environmental factors · Relict species · Species richness

Introduction

In Central Europe, there is a clear difference between the species composition of ancient woodlands and that of recent woodlands. Ancient woodlands that have been wooded continuously at least since the end of the 18th century are known to serve as important relict habitats for various plant and animal species (e.g. Rackham 1980; Peterken 1993; Wulf 1997; Hermy et al. 1999). Having realized this importance, for conservation purposes the maintenance, investigation, and sustainable use of these woodlands were recommended by the Council of Europe since the 1980s (Speight 1989; Wulf and Kelm 1994).

A decline of specialized species has already been recorded, e.g. in Britain (Peterken 1993). Among epigeic arthropods, in particular among ground beetles, the relevance of ancient woodlands as habitat has been emphasized (e. g. Assmann 1999; Desender et al. 1999). Several carabid species show regionally a distinct

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K. Sroka · Oliver-D. Finch (✉)
Terrestrial Ecology Working Group, Faculty V, Biology, Geo- and Environmental-Sciences, University of Oldenburg, D-26111 Oldenburg, Germany
e-mail: oliver.d.finch@uni-oldenburg.de

preference for ancient woodlands (Assmann 1999), as previously shown for plant species (Wulf 1997).

Species richness and communities are influenced by a number of environmental factors, operating at different spatial scales (Begon et al. 1996). So far, at a large scale we have relatively detailed knowledge concerning the effects of habitat fragmentation, origin, and habitat size on forest carabids (e.g. Spence et al. 1996; Davies and Margules 1998; Magura et al. 2001a). The relationship between the age of a woodland and its carabid fauna was investigated in various countries (Terrell-Nield 1990; Niemelä et al. 1988; Spence et al. 1996; Desender et al. 1999; Assmann 1999). Between different types of woodland, coarse habitat associations of carabids were classified (e.g. Thiele 1977; Irmler 1999). Furthermore, also at the mesoscale of landscapes (i.e. large forests) habitat distribution patterns of carabids were investigated (Judas et al. 2002).

On the other hand, at a microscale, communities of forest carabids may be altered by biotic variables like e.g. the presence of red wood ants (*Formica rufa*-group), food conditions, or the presence or absence of competitors, as well as vegetation quality. Moreover, carabid species are associated with abiotic factors such as edaphic, temperature or (soil) moisture conditions (Thiele 1977; Niemelä et al. 1992; Baguette 1993; Bortmann 1996; Koivula et al. 1999; Antvogel and Bonn 2001; Rainio and Niemelä 2003). Nevertheless, previous work on the requirements of ancient woodland carabids often neglects environmental variables at a small spatial scale, as well as their effects on species distribution. Especially, investigation of environmental factors which are correlated with habitat factors of carabid beetles within a single forest type are lacking. Thus, overall knowledge about habitat factors determining the occurrence and describing the preferences of carabids in ancient woodlands, mainly on a microscale, is scarce—a good example for this is Northern Germany (Vossel and Assmann 1995; Assmann 1999; Finch 2005). This is also true for the defined stenotopic relict species. They require more, in-depth studies regarding their distribution patterns and their relationship with environmental factors in order to be able to use them as bioindicators and to preserve their specific microhabitats (Norden and Appelqvist 2001). For conservation purposes of an ecologically sustainable forestry, these relict species may represent target species of a high management priority (New 1995; Lindenmayer et al. 2000).

In north-western Germany, comparatively excellent information is available about the historical landscape development, as far as size and distribution of woodlands is concerned. First maps date back to the 18th century and additional references exist (Hesmer and Schroeder 1963; Pott and Hüppe 1991; see also Assmann 1999), thus allowing for a relatively precise differentiation of recent (grown on unwooded land after the end of the 18th century) and ancient woodlands.

We related our investigations to three perception scales ranging from whole woodlands of several hectares to microhabitats of just a few square metres. The research goals of the study were (1) to analyse the diversity and species communities of carabids in mature ancient forests, (2) to correlate their species richness, distribution and abundance with various environmental parameters in order to understand the relationships between these parameters and the most important habitat features, and (3) to develop habitat suitability models for single carabid species that show a regionally strong restriction to ancient woodlands in order to identify the most important factors controlling the occurrence of these species.

Methods

Study area and sampling

The study area is situated in the north-western part of Lower Saxony, Germany, between the two cities of Oldenburg (i.O.) and Bremen (8°30′ E and 53°4′ N) (Fig. 1). The climate is Atlantic, with a mean annual temperature of 8.7°C and an annual precipitation of about 750 mm (Behrends 1994).

The woodlands in the region are isolated and small in size when compared with the southern parts of Germany. We restricted our investigations to mature ancient woodland remnants with deciduous trees (mainly oak, beech and hornbeam). For studying carabid communities we selected seven mature ancient woodland remnants in the vicinity of a comparatively large, well studied woodland, the “Hasbruch” (NMELF 1999). A total of 10 plots (=stands) was chosen within these seven forests with the three larger forests being attributed two plots each. Each plot was subdivided into three sub-plots. Investigations were restricted to forests dominated by old, deciduous trees with an average age of 161 ± 40.5 years (mean ± SD; range 82–224). Ground vegetation types differed slightly between stands (Table 1), including seven oak–beech forests and three oak–hornbeam forests, with the latter commonly growing under moister conditions than the first.

Since pitfall trapping is considered to be the only available method for large scale studies (Spence and Niemelä 1994), in each sub-plot three pitfall traps were

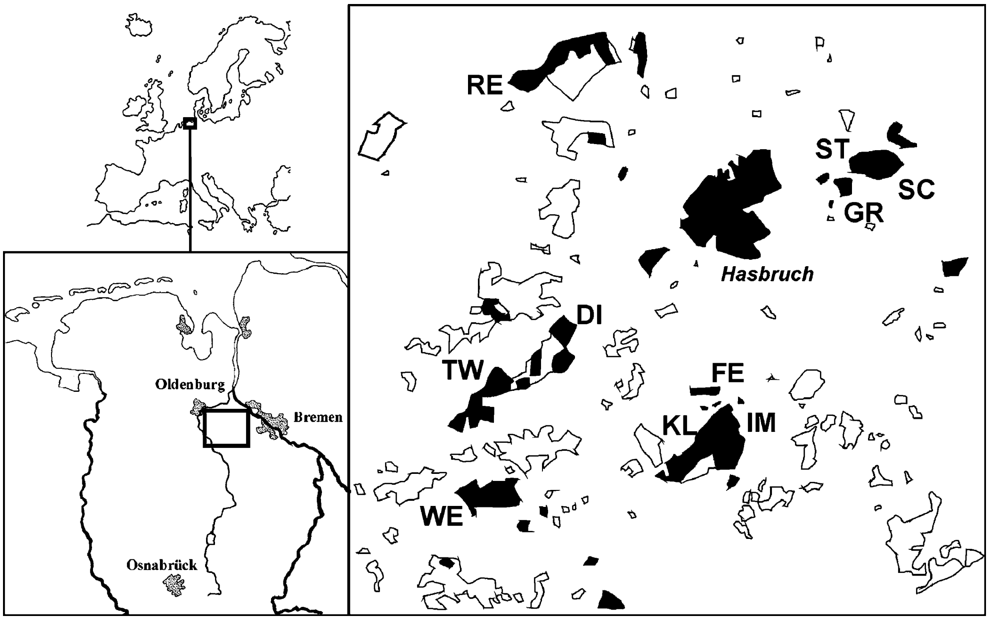


Fig. 1 Location of the study area and the ten sampled forest stands (north-western part of Germany, Lower Saxony; recent woodlands shown with bold border, ancient woodlands black)

placed (glasses with an upper diameter of 5.4 cm and a volume of 0.5 l) for standardized trapping, resulting in a total of 90 traps. The distance between the sub-plots amounted to at least 50 m. At each sub-plot, traps were set out in a triangular pattern. Single traps were placed at a distance of 14 m from the centre. Thus, influence of depletion should have been sufficiently avoided between sub-plots and individual traps (Digweed et al. 1995).

Pitfall traps were partially filled with a 2% formaldehyde killing and preserving solution and a detergent to reduce surface tension. A wire net of 8 × 8 cm with a mesh size of 1 cm was placed 1.5–2 cm above each trap to keep small vertebrates out. The continuous sampling period lasted from 9th May, 2003 until 25th October, 2003 (11 610 trap-days) and thus covered most of the growing season. The nomenclature of carabids is in accordance with Assmann et al. (2003).

Table 1 Characteristics of the 10 investigated forest stands

Frest stand (code)	Woodland (name)	Vegetation type	Dominant plant species in the field layer	Total size of woodland (ha)
DI	Hatter Wald	Milio-Fagetum	*Rubus idaeus*, *R. fruticosus*, *Hedera helix*, *Milium effusum*, *Oxalis acetosella*	323
FE	Feldhorst	Milio-Fagetum	*Ilex aquifolium*, *Rubus fruticosus*, *Dryoperis filix-mas*	20
GR	Großer Mittelhoop	Fago-Quercetum	*Milium effusum*, *Avenella flexuosa*, *Maianthenum bifolium*, *Rubus idaeus*, *R. fruticosus*	18
IM	Stühe	Milio-Fagetum	*Rubus fruticosus*, *Oxalis acetosella*	326
KL	Stühe	Vilio-Quercetum	*Rubus fruticosus*, *Dryoperis filix-mas*, *Oxalis acetosella*	326
RE	Reiherholz	Stellario-Carpinetum	*Hedera helix*, *Milium effusum*, *Polygonatum multiflorum*	343
SC	Stenumer Holz	Stellario-Carpinetum/ Fago-Quercetum	*Hedera helix*, *Ilex aquifolium*, *Rubus fruticosus*, *Deschampsia cespitosa*, *Oxalis acetosella*	95
ST	Stenumer Holz	Milio-Fagetum	*Ilex aquifolium*, *Hedera helix*, *Rubus idaeus*, *Milium effusum*	95
TW	Hatter Wald	Milio-Fagetum	*Hedera helix*, *Dryopteris filix-mas*, *Oxalis acetosella*, *Milium effusum*	323
WE	Wehe	Stellario-Carpinetum	*Hedra helix*, *Oxalis acetosella*	124

Data analysis

A regional species pool for Lower Saxony was taken from this federal state's current Red List of carabids (Assmann et al. 2003). From a biogeographic point of view, this is a comparatively well fitted regional pool. Habitat specificity was taken from Dülge (1992), Turin and Heijerman (1988), and additionally from Turin et al. (1991), since The Netherlands are next to our study area and have a similar Atlantic climate. We distinguished stenotopic and eurytopic forest carabid species, as well as carabids of open habitats and eurytopic carabids.

Multiple linear regression analyses using the backward selection procedure were calculated using an exclusion *P*-value of 0.1, as recommended by Hosmer and Lemeshow (2000). At two different spatial scales the effect of variables on species richness was investigated: the plot scale and the sub-plot scale. For individual traps, no multiple linear regressions were conducted, since it was assumed that species richness had not been recorded in a representative way in individual traps. Three different categories of species numbers were used: the total number of species, the number of woodland carabid species, and the number of widespread species, the latter representing open habitat and eurytopic species (Magura et al. 2001a).

Recording of environmental variables depended on spatial scale. At plot level we measured the (1) total area of deciduous forest within a radius of 2 km around each plot (%), (2) forest area (log ha), and (3) shape of woodland. For the latter, a shape index was calculated according to Magura et al. (2001a). It was defined as $P/(200\times(\pi \times A)^{-1/2})$, where P is the perimeter expressed in m, and A is the area in hectares. This index has a value of 1 for a circular forest, and values >1 for forests with deviation from the circular shape.

At the sub-plot level (Table 2), we measured the distance to the forest edge (m), soil moisture (mean plant indicator values as provided by Ellenberg et al.

Table 2 Characterization of the studied sub-plots by selected environmental variables

Sub-plot (code)	Distance to forest edge (m)	Age of forest stand (years)	Litter depth (cm)	Coverage of field layer (%)	Soil moisture	Soil acidity (pH)	Recent disturbance by logging
DIa	141	178	0.04	31	5.5	3.2	No
DIb	160	178	0.05	43	5.5	3.3	No
DIc	252	178	0.04	9	5.5	3.7	No
FEa	55	172	0.06	7	5.5	3.3	No
FEb	61	172	0.07	5	5.5	3.3	No
FEc	51	172	0.09	23	5.5	3.2	No
GRa	19	163	0.02	3	5	3.6	No
GRb	31	163	0.04	28	5	3.5	No
GRc	75	163	0.08	12	5.5	3.5	No
IMa	67	182	0.06	33	5	3	No
IMb	145	172	0.05	17	5	3.1	Yes
IMc	123	172	0.04	57	5	3.3	Yes
KLa	284	168	0.04	33	5.5	3.2	No
KLb	230	206	0.06	30	5.5	3.7	No
KLc	133	206	0.07	11	5.5	3.4	No
REa	59	100	0.02	32	6	4.1	No
REb	85	100	0.04	58	6	4.4	No
REc	63	100	0.03	58	6	3.9	No
SCa	214	164	0.03	20	6	4.9	No
SCb	192	164	0.03	37	6	4.5	No
SCc	142	113	0.05	10	5	3.1	No
STa	93	224	0.06	7	5.5	3.3	Yes
STb	126	224	0.07	14	5	3.1	Yes
STc	129	56	0.06	2	5	3.1	No
TWa	146	173	0.05	57	5.5	3.8	No
TWb	94	173	0.04	25	5.5	3.6	No
TWc	67	173	0.05	3	5.5	3.2	No
WEa	99	92	0.03	18	6	3.4	No
WEb	182	92	0.04	1	5.5	3.1	No
WEc	219	82	0.04	4	6	3.3	No

All data at plot level and the variables light intensity, downed dead wood, height of tree-, shrub-, and field-layer as well as coverage of tree-, shrub-, and litter-layer at sub-plot level are not presented in detail; data for soil moisture are mean indicator values as provided by Ellenberg et al. (1992)

(1992) of all plant species recorded at a sub-plot), and age of forest stand (years). Furthermore, we considered the two categorical variables 'recent (in the last two years) disturbance by logging' and 'presence of ditches'. For regressions of species numbers at the sub-plot scale, the average of the values measured at the trap scale was calculated (e.g. the light intensity of a sub-plot is the average of the light intensities measured for each of the 3 traps of this sub-plot). The environment of each trap was characterized by

(1) light intensity (measured with a light meter),
(2) soil acidity (pH values measured in $CaCl_2$ from soil samples of the top layer),
(3) downed dead wood (three size classes for wood: <2 cm, 2–7 cm and >7 cm in diameter),
(4) total of dead wood,
(5) height (cm) and vegetation cover (%) in the tree-, shrub-, and field-layer,
(6) and litter depth (cm) and cover (%).

A Shapiro–Wilks-test was used to check the dependent variable (species number) for a normal distribution. Environmental variables were tested for correlations between one another. From pairs of correlated variables ($P < 0.01$, Spearman-Rho > 0.5), one of the variables was not considered further during analyses.

Influence of the categorical variables was tested using Mann–Whitney-*U*-tests. As we focus on abiotic explanations of species richness and structure of species communities, biotic factors like competition (e.g. Günther and Assmann 2000) and prey availability (Guillemain et al. 1997) were neglected or treated as unknown sources of variation. All areas and distances were measured by the ArcView GIS program. For regression analyses and tests we used SPSS 12.0 (SPSS Inc. 2003).

Multivariate analysis

For the multivariate statistical analysis, in order to overcome some of the inconsistencies of the trapping method (e.g. Adis 1979; Lövei and Sunderland 1996), species that occurred with ≤ 5 individuals in the total catch of all 10 plots were excluded. Species caught in such low numbers can usually be seen as accidental migrants that do not support reproducing populations within the investigated site (Desender 1996) or for which the pitfall trapping method is inadequate (e.g. carabids that spend considerable time on trees like *Calosoma* spec.). Hence, as in numerous other studies based on pitfall trapping (e.g. Antvogel and Bonn 2001; Koivula et al. 2004), these purely accidental species were excluded from multivariate statistical analyses.

Furthermore, abundance data were square-root transformed (Jongman et al. 1995). In order to study the effects of several environmental parameters and of forest management on the species communities, we carried out canonical correspondence analysis (CCA) as a method of direct gradient analysis. Environmental variables were standardized to zero mean and unit variance (Jongman et al. 1995). In order to focus the analyses on key factors, we included only environmental variables that proved to be uncorrelated during linear regressions, as well as the categorical variable 'recent disturbance by logging' (see above). All other environmental variables were omitted in the CCA. Row and column scores were standardized by Hill's method. Scaling was optimized for species. A Monte Carlo Test was included (50 runs) in order to test the null hypothesis stating that there is no relationship between the two matrices (species versus environmental matrix). CCA was carried out at the sub-plot level using the PC-Ord 4.0 software package (McCune and Mefford 1999).

Habitat suitability modelling

At a species level, our study intended to develop habitat models for the stenotopic forest carabid relict species that were present in the investigation area. These models lead to formalized relationships between site characteristics and the presence of the species (Guisan and Zimmermann 2000; Berg et al. 2004; Binzenhöfer et al. 2005). Incidence values (0/1) were established using the 90 individual traps. Sites were characterized at sub-plot and trap-scale as mentioned above. In cases when strong correlation between variables was found (see above), one was not included in the further analyses so as to avoid multicollinearity (Binzenhöfer et al. 2005). In order to construct multivariate habitat suitability models, we used multiple logistic regression in the stepwise backward mode (Kleyer et al. 2000; Hosmer and Lemeshow 2000). The level of significance to include variables was $p_{\text{in}} = 0.05$ and to exclude variables was $p_{\text{out}} = 0.10$ (e.g. Binzenhöfer et al. 2005). Incidence probability was predicted and presence–absence-response curves were constructed using the site parameters. Nagelkerke's R^2 was used to quantify model calibration. Furthermore, for the assessment of the discriminative power of models, receiver operating characteristic (ROC) curves with their corresponding AUC values were used (e.g. Peeters and Gardeniers 1998; Bonn and Schröder 2001; Binzenhöfer et al. 2005). For habitat modelling, the program SPSS 12.0 (SPSS Inc. 2003) was used.

Results

General aspects

A total of 10,676 individuals representing 47 species (23 genera) were recorded during the year 2003 (Table 3). Both, the genus *Carabus* (seven species; 33% of the regional species pool of 21 species) and the genus *Pterostichus* (seven species; 32% of the regional species pool of 22 species), were rich in species. Furthermore, two out of four *Abax* species occurring in Lower Saxony were recorded. Eleven of the 47 species

Table 3 Distribution and abundance of the carabid species recorded in the ten forest stands.

Stand	DI	FE	GR	KL	IM	RE	SC	ST	TW	WE	total	Presence
Number of individuals	1010	540	1021	680	599	965	1073	520	1674	2594	10676	
Number of species	23	26	28	20	17	23	23	26	21	24	47	
Abax parallelepipedus (Piller & Mitterpacher, 1783)	246	69	268	128	92	275	193	48	304	738	2361	10
Abax parallelus (Duftschmid, 1812)	–	–	–	–	–	172	9	–	–	8	189	3
Agonum fuliginosum (Panzer, 1809)	–	–	–	1	–	–	–	–	–	–	1	1
Agonum marginatum (Linné, 1758)	–	–	–	–	–	–	–	1	–	–	1	1
Agonum muelleri (Herbst, 1784)	–	–	1	–	–	–	–	–	–	–	1	1
Agonum viduum (Panzer, 1797)	–	–	–	–	–	–	–	2	–	–	2	1
Amara plebeja (Gyllenhal,1810)	–	3	2	–	1	–	–	3	–	–	9	5
Amara similata (Gyllenhal,1810)	1	1	1	1	3	–	–	–	–	–	7	8
Anisodactylus binotatus (Fabricius, 1787)	–	–	1	–	1	–	–	2	–	–	4	3
Asaphidion curtum Heyden, 1870	–	–	11	–	–	–	–	–	2	2	15	3
Badister lacertosus Sturm, 1815	–	–	2	2	–	1	2	2	–	–	9	5
Badister sodalis (Duftschmid, 1812)	1	–	–	–	–	2	–	–	–	–	3	2
Bembidion guttula (Fabricius, 1792)	–	3	–	–	–	–	2	3	–	2	10	4
Bembidion lampros (Herbst, 1784)	–	–	–	–	–	–	–	–	2	1	3	2
Calathus melanocephalus (Linné, 1758)	–	–	1	–	–	–	–	–	–	–	1	1
Calathus rotundicollis Dejean, 1828	–	–	9	–	–	–	–	–	–	6	15	2
Calosoma inquisitor (Linné, 1758)	–	1	–	–	–	–	–	–	–	–	1	1
Carabus cancellatus Illiger, 1798	–	–	–	1	–	–	–	–	1	–	2	2
Carabus coriaceus Linné, 1758	57	56	–	34	76	91	–	–	108	55	477	7
Carabus glabratus Paykull, 1790	47	–	–	–	–	86	–	–	112	–	245	3
Carabus granulatus Linné, 1758	19	12	17	16	7	25	3	20	144	33	296	10
Carabus nemoralis O.F. Müller, 1764	3	3	19	1	2	25	8	2	3	16	82	10
Carabus problematicus Herbst, 1786	12	46	58	104	82	20	21	18	86	158	605	10
Carabus violaceus Linné, 1758	120	53	79	84	46	28	94	39	63	89	695	10
Clivina fossor (Linné, 1758)	1	–	1	1	–	1	6	1	–	–	11	6
Cychrus caraboides (Linné, 1758)	1	8	9	3	5	4	2	3	6	2	43	10
Elaphrus cupreus Duftschmid, 1812	–	1	–	–	–	–	–	–	–	–	1	1
Harpalus laevipes Zetterstedt, 1828	–	–	17	–	–	3	–	–	8	–	28	3
Harpalus latus (Linné, 1758)	–	–	1	–	1	4	–	–	2	–	8	4
Leistus rufomarginatus (Duftschmid, 1812)	–	6	1	–	–	–	–	–	1	2	10	4
Limodromus assimilis (Paykull, 1790)	1	2	178	–	–	15	22	3	5	92	318	4
Loricera pilicornis (Fabricius, 1775)	2	1	–	–	–	2	2	2	1	4	14	7
Nebria brevicollis (Fabricius, 1792)	59	31	92	7	4	63	86	12	100	757	1211	10
Notiophilus biguttatus (Fabricius, 1779)	9	9	38	11	1	1	5	4	13	20	111	10
Notiophilus rufipes Curtis, 1829	–	2	13	1	–	–	4	1	–	–	21	5
Patrobus atrorufus (Stroem, 1768)	–	–	–	–	–	–	49	–	–	–	49	1
Poecilus cupreus (Linné, 1758)	–	–	–	–	–	–	1	1	–	–	2	2
Poecilus versicolor (Sturm, 1824)	–	1	–	–	–	–	–	–	–	–	1	1
Pterostichus melanarius (Illiger, 1798)	14	1	9	1	2	10	215	1	1	227	481	10
Pterostichus niger (Schaller, 1783)	273	148	79	189	198	73	319	271	358	142	2050	10
Pterostichus nigrita (Paykull, 1790)	2	–	1	–	–	3	3	21	–	1	31	6
Pterostichus oblongopunctatus (Fabricius, 1787)	113	44	106	93	64	53	4	29	354	230	1090	10
Pterostichus rhaeticus Heer, 1837	3	1	–	1	–	–	21	4	–	4	34	6
Pterostichus strenuus (Panzer, 1797)	24	33	–	1	14	8	2	26	–	2	110	8
Pterostichus vernalis (Panzer, 1796)	–	–	–	–	–	–	–	1	–	–	1	1
Stomis pumicatus (Panzer, 1796)	1	1	2	–	–	–	–	–	–	3	7	4
Trechus obtusus Erichson, 1837	1	4	5	–	–	–	–	–	–	–	10	3

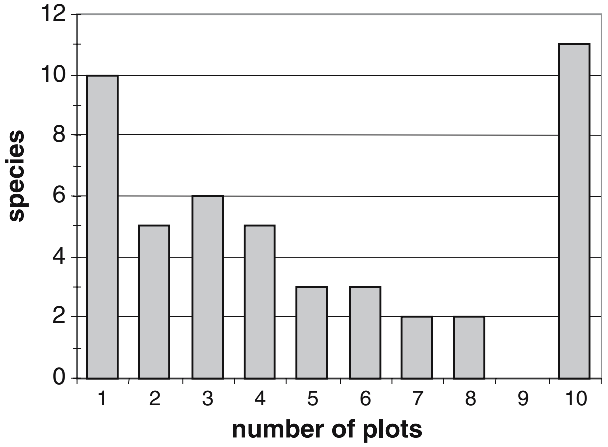
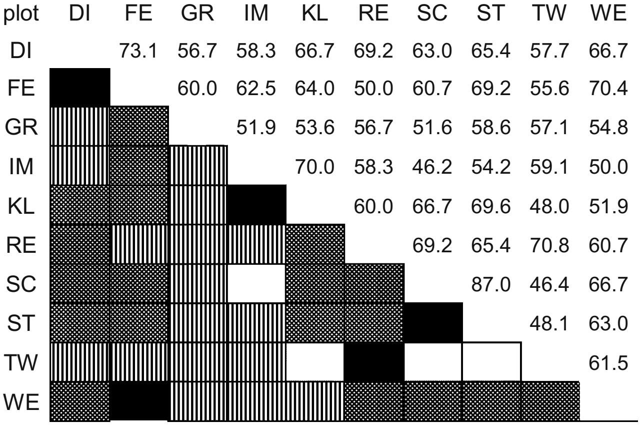


Fig. 2 Number of records per carabid species in different plots



plot	DI	FE	GR	IM	KL	RE	SC	ST	TW	WE
DI		73.1	56.7	58.3	66.7	69.2	63.0	65.4	57.7	66.7
FE	■		60.0	62.5	64.0	50.0	60.7	69.2	55.6	70.4
GR	▥	▒		51.9	53.6	56.7	51.6	58.6	57.1	54.8
IM	▥	▒	▥		70.0	58.3	46.2	54.2	59.1	50.0
KL	▒	▒	▥	■		60.0	66.7	69.6	48.0	51.9
RE	▒	▥	▥	▥	▒		69.2	65.4	70.8	60.7
SC	▒	▒	▥	□	▒	▒		87.0	46.4	66.7
ST	▒	▒	▥	▥	▒	▒	■		48.1	63.0
TW	▥	▥	▥	▥	□	■	□	□		61.5
WE	▒	■	▥	▥	▥	▒	▒	▒	▒	

Fig. 3 Similarity matrix at plot-scale (Jaccard Index; black: >70%; dotted: 60–69%; striped: 50–59%; grey: 40–49%)

showed a high presence and occurred in all 10 plots (*Abax parallelepipedus*, *Carabus violaceus*, *C. problematicus*, *C. granulatus*, *C. nemoralis*, *Cychrus caraboides*, *Nebria brevicollis*, *Notiophilus biguttatus*, *Pterostichus melanarius*, *P. niger* and *P. oblongopunctatus*). On the other hand, more than 50% of the species were recorded in less than five plots, including 10 species recorded in only one plot (Fig. 2). The most numerous species (>1000 individuals) were *A. parallelepipedus*, *P. niger*, *N. brevicollis*, and *P. oblongopunctatus*. These four species represented 62.9% of the total catch. Among the recorded species were also the two stenotopic forest species *Carabus glabratus* and *Abax parallelus*, as well as 14 additional eurytopic forest species. Twenty-two species were considered as characteristic of open habitats, two of wet habitats and seven were generalist species with a wide distribution, typical both of forest and open habitats. Between most plots, species similarity (Jaccard index) amounts to more than 50%, in several cases reaching values above 70% (Fig. 3). Only four comparisons have less than 50% of the recorded species in common.

Species richness

Per plot (9 traps) the mean species richness averaged 23.10 ± 3.21 carabid species (mean ± SD; range: 17–28) and 1067.60 ± 637.85 individuals (range: 520–2594) (Table 3). The largest number of individuals per sub-plot (3 traps) was captured at the WEA sub-plot (1141 individuals; 10.7% of the total catch), followed by the WEC (979 individuals; 9.2%) and the TWA (567 individuals; 5.3%) sub-plots (the mean for all sub-plots was 355.87 ± 240.40; range: 125–1141). At this scale, an average of 15.77 ± 3.81 species were recorded (range: 10–22).

The species richness of each of the three species categories (total species richness, number of forest species, and the number of widespread species) followed a normal distribution (Shapiro–Wilks-test, $P > 0.05$).

Multiple linear regressions between the number of carabid species of the three categories (see above) and the environmental variables measured at different scales were conducted. At plot scale, these resulted in significant negative relationships between total number of species and forest area (Table 4). This variable also had significant negative correlation with the richness of widespread species.

At the sub-plot scale there was a small significant negative correlation between the distance to the forest edge and the number of forest species ($B = 0.012$). Soil moisture showed a significant positive correlation with forest species richness. Other variables correlated negatively, although not significantly at the $P < 0.05$-level (litter depth, amount of dead wood). Moreover, for the woodland carabids a significant negative correlation between recent disturbance by logging and their species richness was also found.

Total species richness exhibits a negative correlation with distance to forest edge at the $P = 0.1$-level. On the other hand, a highly significant positive correlation existed between the total species richness and soil moisture. The occurrence of widespread species showed significant positive correlation with soil moisture. All other environmental variables under consideration did not correlate significantly with total species richness, the number of forest species, or the number of widespread species at both scales—or they were correlated significantly with other variables and thus not considered separately during multiple linear regressions.

Table 4 Relationships between environmental variables measured at two different scales and total number of species, number of forest species, and number of widespread species

	Total number of species	Number of forest species	Number of widespread species	Variable correlated with (Spearman-Rho ≥ 0.5)
Plot scale (multiple linear regressions)				
Total area of deciduous woodland (%)	n.s.	n.s.	n.s.	
Forest area (log ha)	−5.135**	n.s.	−3.737*	(−) Shape-index**
r^2	0.592	.	0.495	
F	14.083	.	9.833	
df	9	.	9	
$P =$	0.006	.	0.014	
Sub-plot scale (multiple linear regressions)				
Distance to forest edge (m)	−0.018 ($P = 0.059$)	−0.012**	n.s.	
Soil moisture	5.823**	1.792*	3.047*	(+) Soil acidity** (−) tree height**
Light intensity	n.s.	n.s.	n.s.	(+) Height** and (+) coverage** of field- and (−) coverage** of tree-layer
Total of dead wood	n.s.	−0.407 ($P = 0.068$)	n.s.	(+) All three classes of downed dead wood**
Age of forest stand (years)	n.s.	n.s.	n.s.	(+) Height of tree-layer**
Coverage (%) of shrub-layer	n.s.	n.s.	n.s.	(+) Height of shrub-layer**
Litter depth (cm)	n.s.	−26.955 ($P = 0.087$)	n.s.	(+) Litter cover**
r^2	0.285	0.437	0.120	
F	6.774	6.625	4.960	
df	29	29	29	
$P =$	0.004	< 0.001	0.034	
Categorical variables on plot scale (Mann–Whitney-U-tests)				
Recent disturbance by logging	n.s.	Negative effect*	n.s.	
Presence of ditches	n.s.	n.s.	n.s.	

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, n.s. = not significant ($P \geq 0.1$); the B value of multiple linear regressions is given when significant, i.e. when $P < 0.05$

Ordination of species communities

Direct gradient analyses were calculated separately for the woodland carabid species and the number of widespread species. Fourteen species and only 24 individuals were excluded from multivariate analyses as they were represented by less than six individuals in the total catch. Thus, a dataset consisting of 10,652 individuals and 33 species remained. Of these species 15 (6217 individuals) were regarded as forest species.

The ordination of forest species and investigated deciduous mature ancient woodland stands resulted in an axis 1 (eigenvalue 0.136) differentiated by a combination of soil moisture (inter-set correlation IC: −0.61) and litter depth (IC: 0.68; Fig. 4a). Secondary variation (eigenvalue 0.083) was related to a small extent to litter depth (IC: −0.26), and to a greater extent than to litter depth only to the total amount of dead wood (IC: 0.41). Relationships between variables and species data along the third axis were weak (IC < 0.40), as were relationships between the other five environmental variables and the first two axes. Most forest species were clustered in the center of the ordination, except for a few species that showed mostly only a low (≤50%) presence in the total data set (e.g. *A. parallelus*, *C. glabratus*, *L. assimilis*). The eigenvalue of the first three axes is much higher than the range expected by change (Monte Carlo Test, $P < 0.05$). Thus, relationships between the species data and the measured environmental factors were significant. The total inertia in the species data was 0.709 and the amount of variance explained along the first three axes was 38.1% for the forest species dataset.

For the widespread species, the variation along the first axis (eigenvalue 0.188) again appeared to be a product of soil moisture (IC: −0.65; Fig. 4b) and of litter depth (IC: 0.71). Along the second axis (eigenvalue 0.12), differences resulted from all the remaining

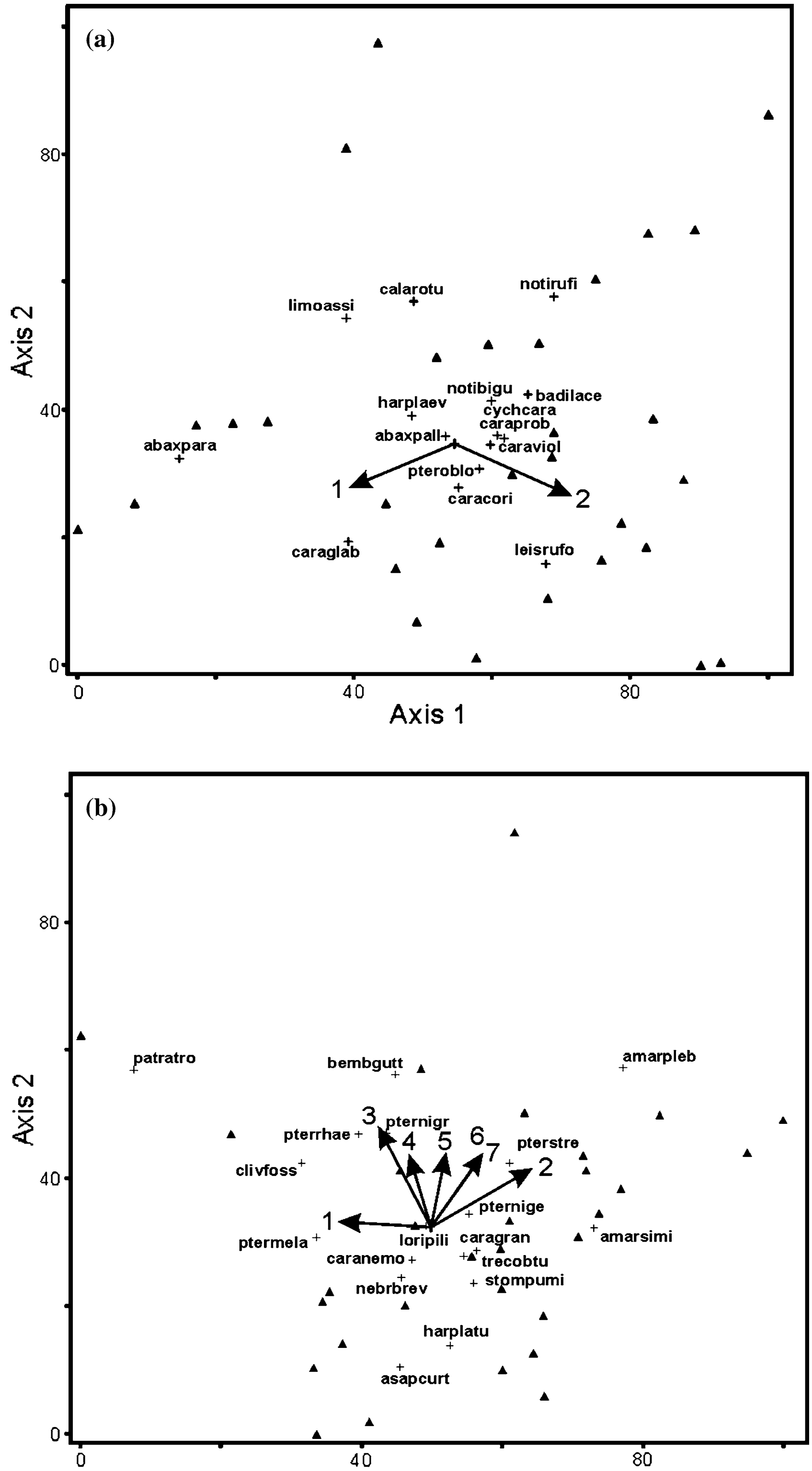


Fig. 4 CCA-biplot for forest species (**a**) and widespread species (**b**). Carabid species are named (with the first four letters from their generic and the first four letters from their species names, e.g. *Carabus glabratus* = caraglab) and marked with crosses, environmental variables are represented by arrows ((1) soil moisture, (2) litter depth, (3) shrub layer coverage (%), (4) total amount of dead wood, (5) light intensity, (6) age of forest stand, (7) recent disturbance) and individual sub-plots by triangles (proximity in sub-plots means similarity of communities)

environmental variables that were included in the analyses and which were often associated with conditions of rather open habitats (light, and recent disturbance). Along this axis, correlations (IC > 0.4) existed with the shrub cover (IC: 0.69), light intensity (IC: 0.51), age of woodland (IC: 0.51), total amount of dead wood (IC: 0.5), recent disturbance (IC: 0.45), and litter depth (IC: 0.40). The remaining variable (distance to forest edge) exhibited a weaker (IC < 0.40) relationship with the data. The eigenvalue of the two first axes is much higher than the range expected by change (Monte Carlo Test, $P < 0.05$). The third axis failed the Monte Carlo Test ($P > 0.05$). For the widespread species, the first three axes explained 35.1% of the total variance (inertia: 1.042).

Habitat models for relict species

The two relict species, *C. glabratus* (stands DI, RE, TW) and *A. parallelus* (stands RE, SC, WE) were each recorded at three out of ten plots. *A. parallelus* was present in 17, *C. glabratus* in 27 out of 90 pitfall traps. Although the models for each of these species make correct predictions (AUC values >0.9), they differ clearly. For the occurrence of *A. parallelus* within the habitat type "mature ancient woodland remnants", a highly significant model with high explanatory power (AUC: 0.973, $R^2_{\mathrm{Nagelkerke}}: 0.844$) was created. It included soil moisture as sole parameter. On the other hand, in the model for *C. glabratus* (AUC: 0.905, $R^2_{\mathrm{Nagelkerke}}: 0.569$), none of the site parameters could be excluded during the stepwise backward logistic regression procedure (distance to forest edge, light intensity, total amount of dead wood, age of forest stand, litter depth, height of vegetation in the shrub-layer, recent disturbance by logging, and soil moisture). Explanatory power of the model is considerably lower, as indicated by its $R^2_{\mathrm{Nagelkerke}}$. Here, the model gives no further information on the occurrence of the species.

Discussion

Species richness and environmental variables

At two scales, several ecological factors were found to influence the species richness pattern of carabids in mature ancient woodland stands. Magura et al. (2001a) and Assmann (1999) analysed effects of large scale environmental variables on species richness of carabid beetles in forests of a fragmented landscape. As in the present study, they found significant negative correlations between total species richness and forest area. Although this seems to contradict many papers that report positive correlations between habitat size and number of species, for carabids such negative correlations with patch size had already been shown in several studies on several habitat types (e.g. Usher et al. 1993; Magura et al. 2001a). This reduction in species numbers may be due to a loss of habitat heterogeneity in closed, large woodlands and the subsequent exclusion of eurytopic or open habitat species.

On the other hand, Magura et al. (2001a) were able to detect a positive correlation between the number of forest specialist carabids and the size of the forest patch. This is in accordance with previous studies that proved that a decrease of forest area leads to a decrease of the number of forest specialists and, simultaneously, to an increase of the number of generalists (Halme and Niemelä 1993; Spence et al. 1996). Such a correlation was not found in our data set. In our case, forest size seems not to fall below the critical threshold of most forest carabid species. Even the smallest (18 ha) of the investigated ancient woodland remnants of our study supported a typical forest carabid assemblage with a large number of forest species. As Halme and Niemelä (1993) showed, critical values of forest size are species specific. They reported for boreal forests an absence of *C. caraboides* in forest fragments <20 ha, while *C. hortensis* only became scarce in fragments <3 ha. Populations of strict forest specialists were not supported in fragments below 21.5 ha. Such critical thresholds have been published also for birds. Above a threshold of 10 ha, avian diversity is high and similar to that of larger contiguous woodland (Nikolakaki and Dunnett 2005).

At sub-plot scale, species richness also showed a negative correlation with the distance to the forest edge. Since many of the investigated forest fragments are jagged by agricultural areas, this suggests that this also may be an important factor influencing carabid species richness in woodlands. On one hand, core zones of the forest interior are reduced. On the other hand, however, species richness is increased at edge zones due to several effects (Saunders et al. 1991; Magura et al. 2001b; Molnar et al. 2001; Magura 2002; Koivula et al. 2004). Open land generalist species are capable of invading the forest edge because microclimatic conditions at the edge are not the same as in the forest interior. Thus, our results (1st) confirm that with increasing forest habitat size the total number of carabids may decrease, the reason for this being that (2nd) the influence of the edge effect and thus of the areas usually richer in species is reduced.

Besides the effect of the distance to the forest edge, a positive correlation between species richness and soil moisture was found at sub-plot scale. Soil moisture was positively correlated with soil acidity. A positive correlation between species richness and soil acidity was also found by Magura et al. (2003), who identified soil acidity beneath compaction of the soil and leaf litter cover as one of the most important factors determining carabid diversity. Soil acidity was identified as being responsible for spatial distribution and habitat preferences of several carabid species (e.g. Thiele 1977; Paje and Mossakowski 1984).

Also, at a sub-plot scale, current disturbance by logging had a negative effect on forest carabids. Similar effects were described for clear-cuts of boreal forests (e.g. Niemelä et al. 1993; Niemelä 1997; Koivula 2002) as well as for small clearings in managed spruce forests (Huber and Baumgarten 2005). Clear-cuts are known to have a severe impact on carabid communities (Niemelä 1997; Koivula 2002).

The negative influence of the two factors litter depth and amount of dead wood on the number of forest species was unexpected. This effect may be a result of the used trapping method: since both a deep litter and a large quantity of dead wood may reduce the carabids' mobility, an increase of these factors leads to a decrease of the number of species captured. Greenslade (1964) already had pointed out that at a trap site local microhabitat factors like dense vegetation—or, as in our case, a thick layer of litter or a large amount of dead wood—may reduce the sampling efficiency of pitfall traps. The high movement obstruction reduces individual walking distance which may in turn result in a lower number of species caught (Christ and Wiens 1995). Contrasting with our results, for downed dead wood we expected neutral or positive effects for carabid populations. For example, dead wood may serve as an important hiding place during day-time or for overwintering (Thiele 1977). Nevertheless, studies investigating causality are still lacking (Bortmann 1996) and, unfortunately, we were not able to obtain consistent results concerning this habitat feature either. A negative effect of leaf litter cover on diversity of ground beetles was also shown in other studies (Guillemain et al. 1997; Molnar et al. 2001). Nevertheless, generally, and especially when there is a shortage, litter is an important habitat factor, having undoubtedly positive effects on forest carabids (Thiele 1977; Loreau 1987; Niemelä et al. 1992; Magura et al. 2003).

Most present studies of forest carabids focus only on one perception scale (e.g. regional scale or microhabitat), while the other scales are often neglected (e.g. Assmann 1999; Magura et al. 2001a). Thus, having found significant correlations at two spatial scales, our study clearly underlines the importance of investigating relationships between species richness and habitat at different spatial scales. When different scales are taken into account, a more comprehensive understanding of the patterns and processes that determine species richness of carabids in woodlands becomes possible.

Species communities and environmental variables

The differences between the species composition of carabid communities in the various ancient oak–beech forests investigated in this study were not large. Pairwise comparison showed that only in four out of 45 cases less than 50% of species were shared. Thus, species composition was comparatively homogeneous, especially when compared with other types of woodland (e.g. Irmler 1999; Finch 2005). Several species were frequent, thus they can be regarded as regular inhabitants of mature ancient deciduous woodlands. A few species (*A. parallelepipedus*, *P. niger*, *N. brevicollis*, and *P. oblongopunctatus*) predominated (62.9% of the total catch). Similar dominance structures with a few very abundant species and a lack of medium common species were reported from other forests, e.g. boreal woodlands (Niemelä 1993; Niemelä et al. 1993) and a spruce forest (Huber and Baumgarten 2005).

A separate gradient analysis (CCA) of the two ecological groups (woodland carabids and widespread carabids) is justified by former studies. For example, Huber and Baumgarten (2005) also found clear clusters of forest and eurytopic or open habitat species, respectively. Thus, in order to clarify habitat associations of both groups, in our opinion a separate CCA-analysis seems more promising. At the microscale, species communities of forest carabids are determined by soil moisture (and the positively correlated soil acidity) and litter depth. Humidity gradients often have been identified as most important in shaping carabid communities (e.g. Turin et al. 1991; Baguette 1993; Bonn and Schröder 2001), whereas the effect of litter depth is less obvious. It may be attributed to a better food availability (e.g. Loreau 1987; Niemelä et al. 1992) or to a higher movement obstruction, as discussed above. Overall, at this finest scale many of the typical forest species seem to have only one requirement: living in an ancient, mature deciduous woodland. All of the other factors studied seem to have no influence whatsoever. These species are eurytopic forest generalist species which were ordinated in the center of the CCA-plot and showed an undifferentiated pattern (e.g. *A. parallelepipedus*, *C. coriacaeus*, *C. violacaeus*, *C. problematicus*, *C. caraboides*, *P. oblongopunctatus*). In other studies, for example of *A. parallelepipedus*, a significant correlation with abiotic factors could not be found either (Guillemain et al. 1997).

Although altogether 19 variables were measured, the variance in data sets of both ecological groups was explained by the CCA only to a relatively small extent (38.1% and 35.1%, respectively). As expected, among the various ecological groups present the widespread species showed additional correlations with further environmental factors besides soil moisture and litter depth, factors which are often associated with more open habitat conditions (light, and recent disturbance).

Further environmental factors may shape carabid communities but were not considered in our study. For example, Judas et al. (2002) found that the topoclimatic differentiation of a landscape may also influence the distribution patterns of carabids. This seems to be particularly important in mountainous landscapes with variation in exposure, as studied by Judas et al. (2002). By contrast, our study took place in the woodlands of the north-western German Lowland, where variation of local temperature due to different exposure was expected to play a minor role.

Moreover, Koivula et al. (1999) as well as Hawes et al. (2002) detected interspecific relationships between carabids and ants of the *Formica rufa*-group. These ants were nearly absent in the deciduous woodlands investigated in our study, therefore the potential to interact with the carabid assemblage was ignored.

Habitat modelling

The association of various species with ancient woodlands was reported by several authors for different European countries. For most species, regional variations of this association were observed. Besides plant species (Wulf 1997 and references therein), these observations focussed on carabids (Desender et al. 1999; Assmann 1999). In contrast to the well known importance of habitat continuity for species showing a low dispersal power, the contribution of further habitat factors to the regional stenotopy is insufficiently studied. Until today, only the stenotopy of several plant species is known in sufficient detail (Norden and Appelqvist 2001; Wulf 2003). Habitat suitability models can supply further data for successful conservation strategies of the relict carabid species in focus in our study. The new insights regarding the importance of key environmental parameters can be used to improve habitat quality in a more effective and controlled way (e.g. Bonn and Schröder 2001; Berg et al. 2004). Our habitat modelling for the two recorded stenotopic forest carabid species for which a strong restriction to ancient woodlands is known (Dülge 1992; Assmann 1999), lead to a very concise habitat model for *A. parallelus* and to a rather vague model for *C. glabratus*. The status of the species is ‘‘not threatened’’ (*A. parallelus*) and ‘‘near threatened’’ (*C. glabratus*), respectively, according to the current Red Data Book of Lower Saxony (Assmann et al. 2003).

In our dataset, the habitat of *A. parallelus* is characterized by soils with a relatively high moisture, indicated by a vegetation with a mean plant indicator value of ‘‘6’’, according to Ellenberg et al. (1992). Thus, *A. parallelus* seems to select the site on at the intermediate scale (sub-plot scale), at which soil moisture was measured. Although also included, the finer scale (trap scale) contributed variables to the model that turned out to be not significant. Higher soil moisture coincided with the oak–hornbeam forests. The restriction of *A. parallelus* to this forest type was also mentioned for The Netherlands (Turin et al. 1991). Soil acidity had a smaller influence, as the species was recorded on soils with pH-values ranging from 3.0 to 5.1. The pronounced moisture requirement of this species was already noticed in former studies (e.g. Assmann 1994) and is in accordance with the requirement of a constant soil moisture during the stage of maternal care of eggs (Löser 1970; Dülge 1992). Thus, moisture is a valuable key factor determining the occurrence of this species in ancient woodlands.

For *C. glabratus* it was not possible to find a key factor comparable to the one found for *A. parallelus*. Even the model including as sole variable the type of habitat is insufficient, as the species was recorded only in three out of 10 plots in the preselected habitat type ‘‘mature deciduous ancient woodland’’. We recorded this species only in the two largest forests (>300 ha; see also Dülge 1992), but Assmann (1999) found populations also in much smaller forests (60–90 ha). Thus, above this threshold, forest area seems not to influence occurrence. A decline of *C. glabratus* in all of north-western Central Europe has been reported (Desender and Turin 1989; Assmann et al. 2003). The species is already extinct in The Netherlands (Turin 2000). In northern Europe this species occurs in open habitats like bogs and alpine heaths (e.g. Eyre et al. 2003; Naujok and Finch 2004). Previous studies in Central Europe were not able to identify specific habitat parameters either, i.e. parameters which might act as key factors for the occurrence of this species in ancient woodlands (Assmann 1994; Assmann and Günther 2000). Therefore, so far it was impossible to develop species specific management strategies of this possibly declining species which could be used as target species for nature conservation measures.

Conclusions for the management of ancient woodland sites, and consequences for the conservation of their carabid beetle communities

Generally, a further reduction in size and a further fragmentation of ancient woodlands has to be prevented in order to keep core habitats of the specialised flora and fauna large enough (e.g. Assmann 1999; Magura et al. 2001a). Presently, this appears not to be a major problem, as none of the ancient woodlands seem to be endangered by clear-felling (e.g. in order to expand agricultural areas).

Overall, it is widely accepted to manage forests in an ecologically sustainable way (United Nations 1992; Lindenmayer et al. 2000). Current changes within the investigated ancient woodlands are subtle and usually caused by forestry measures. None of the sites investigated during this study is protected by nature conservation measures and all are being tended by the public forestry authority of Lower Saxony. Logging, especially in old stands, has a negative influence on the species richness of forest carabids, at least for a few years immediately after harvesting. Although selective cutting—as practised in the investigated stands—conserves species communities of forest carabids best (Koivula 2002; Huber and Baumgarten 2005), this may result in a threat to the population when too many stands or too large areas of mature forest are subject to cutting within only a few years. In this case, the undisturbed area left for a possible retreat of forest specialists may be insufficient, leading to the common trend observed that small generalist species with good dispersal abilities increase while large specialists decrease (Raino and Niemelä 2003). Thus, cutting should be spread out over a longer time span and should never affect individual woodlands intensively, in order always to leave connected and undisturbed mature forest stands. The conservation of different structures at each site can be achieved by using a variety of logging practices (varying levels of stand retention including mature forests, selective cutting and single, small open clear-cuts). This management strategy was recently suggested by Huber and Baumgarten (2005) for the conversion of spruce forests to mixed forests in Bavaria. It may also improve diversity of carabids and of other animal groups (like spiders, wasps, and bees, etc.) in ancient woodlands when carried out at various spatial scales (see also Niemelä 1997; Lindenmayer et al. 2000). Additionally, this strategy may reproduce historical forms of woodland use (with an overall more open canopy due to e.g. grazing) better than current management which is restricted to selective felling and leads to a more or less closed canopy (Pott 1999; Falke et al. 2000). During this study, soil moisture has been shown to correlate positively with species richness, to be a factor shaping carabid communities, and to be a key factor for the occurrence of *A. parallelus*. Thus, from a nature conservation point of view a higher soil moisture should be preserved. On the contrary, at many sites intensive drainage measures were erected and are regularly managed. Soil structure and ground vegetation is often heavily affected by vehicles used to harvest and transport the tree trunks.

Furthermore, at least in the past, many sites in ancient woodlands were afforested with conifers, e.g. spruce (*Picea* spp.). At present, afforestation with the neophytic Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) is of special interest because of its high productivity and economic importance. Supported by the decree of the ‘‘long-term ecological forestry’’ (Otto 1991), during the next decades the Douglas fir should reach an average proportion of 10% within the forested area of the public forests in Lower Saxony. In practice, this means that values of up to 40% should be expected in certain forest areas (Scherzinger 1996). Even if planted as mixed forests, as proposed, this would change the character of the deciduous forests and thus of the main habitat of the characteristic communities of carabid beetles investigated in this study.

Outside of the existing forests, an arrondation of the woodland edge may be desirable in order to enlarge core habitats within the woodlands. In many cases woodland edges border on arable land that was formerly extensively used—thus, one has to be cautious in order not to destroy relicts of extremely valuable open habitats (Butterfield et al. 1995; Finck and Schröder 1997; Klein 1997; Finch 2005). Forest corridors and windbreaks might be used to link isolated forest patches of ancient woodland (e.g. Gruttke 1994; Sustek 1994; Nikolakaki and Dunnett 2005). On the other hand, an additional planting of deciduous forest stands may be more useful for the connection of populations of forest carabids, at least, when distances between forests are large, as in our investigation area (Magura et al. 2001a; Wulf 2003). Nevertheless, there again, valuable open habitats should not be affected adversely. Overall, in order to preserve a high value for nature conservation, forestry in ancient woodland stands should act with consideration and in a strict, ecologically sustainable way. Therefore, the main rules which can be derived from our results (see also Wulf 2003) are avoiding disturbance of soil characteristics (including moisture level; Wilson et al. 1997) and of ground vegetation, preventing the conversion from deciduous to coniferous stands, and variation of logging in space and time thus maintaining a considerable amount of mature stands at a long-term, low level disturbance.

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