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Gradiental changes and temporal fluctuation of rove beetles (Coleoptera: Staphylinidae) in a northern German woodland

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Summary

In landscape gradients populations may interact or be separated by environmental barriers depending on the changing steepness of the gradient in a period of time. This problem was investigated by the rove beetle fauna of a woodland in northern Germany from 1989 to 1995. Rove beetles were recorded by handsorting and heat extraction to study the faunal interaction between different parts of the woodland caused by species fluctuations. The woodland was located on a gradient from dry site with beech wood via an intermediate mixed wood site to a wet site with alder wood. Additionally, climate and litter fall data of the beech wood were available. Population density decreased from the dry wood sites with 100 ind. m^{-2} on average to the alder wood with approximately 45 ind. m^{-2}. Overall, the long-term fluctuations of 9 species were examined in detail by cross correlation with climate and litter fall data. Most species of the dry sites correlated negatively with temperature, whereas the 2 species of the alder wood correlated negatively with groundwater level. Additionally, 4 species were also correlated with litter fall in the beech wood. The two species of the alder wood exhibited their optimal habitat in a short range of groundwater fluctuation and spatially shifted in a small area never using the whole alder wood area. None of the beech wood species significantly influenced the populations of the intermediate mixed or wet alder wood. Typical species of the intermediate mixed wood, only, significantly invaded into the beech and alder wood at high abundance periods. Thus, although species passed considerable fluctuations in the different parts of the woodland, interactions were small. Mainly species of the intermediate area showed highest influence on their adjacent conspecific populations.

Keywords: Staphylinidae, fluctuation, heterogeneity, habitat interaction, climate effects

Introduction

A global change is currently in progress, which can be referred to changes of climate and land use. However, long-term investigations regarding climate based fluctuations of soil fauna are up to date rare and hardly allow general conclusions. In forests, temporal changes in the fauna are referred to successions (NIEMELÄ at al. 1996), climate, litter fall and groundwater level changes (IRMLER 2004, 2006). Spatial heterogeneity can be either effected by forest management (ATLEGRIM & SJÖBERG 1996) or the heterogeneity of soil conditions, tree composition and cover or other small-scale habitat heterogeneity (NIEMELÄ at al. 1996, BORTMANN 1996). The present study focus on the question if a relationship exists between climate changes and heterogeneity in a woodland using rove beetles as indicators.

Rove beetles are one of the most frequent beetle groups in soils, but they are rarely investigated in ecological studies due to their difficult determination. Furthermore, with few exceptions, e.g. HARTMANN (1979), FRIEBE, (1983), PALMGREN & BISTRÖM (1979), most investigations based on pitfall traps that give no information on the population density and do not reflect a realistic species composition. Nevertheless rove beetles are regarded as valuable bioindicators for habitat interactions due to their high flight activity and for their sensitivity to management impacts in ecosystems (LEVESQUE & LEVESQUE 1995). In particular, they provide a variety of life forms concerning mobility, food demands, seasonal dynamics and development (BOHAC 1999).

The present study was performed in a woodland cross section from dry to wet conditions over a period of 7 years to investigate the long-term variance in densities caused by different environmental conditions with particular reference to climate changes and the interactions between the different sites. BOHAC et al. (1999) found that soil moisture was the most important factor regulating the beetle communities in abandoned fields and grassland during secondary succession. Furthermore, microclimate parameters were regarded to be responsible for occurrence and activity, too (HONEK 1988). Thus, rove beetles should be valuable soil organisms to indicate long-term environmental changes of sites and their interactions in a landscape gradient.

The following questions should be answered by the present investigation:

1) Which changes occur in the gradient from dry to wet conditions concerning species composition and population density? 2) Which environmental conditions are responsible for the long-term changes at the different sites? 3) Are their interactions between adjacent sites in the gradient reflected by shifting species abundance?

Study site and methods

The rove beetles were investigated between 1989 and 1995 in a woodland at Lake Belau about 30 km South of Kiel (federal state of Schleswig-Holstein: northern Germany) that is composed of a beech (*Fagus sylvatica*) wood situated on the hill top with acidic Dystric Cambisol soils, an afforested young mixed wood containing coniferous trees (*Pseudotsuga menziesii, Picea abies*) and hazel (*Corylus avellana*) at the hill slope and an alder wood on Histosol at the lake margin (Table 1). In the alder (*Alnus incana*) wood a central depression of the floor provided a small scale heterogeneity concerning the distance to the groundwater level (Fig. 1). In the alder wood sampling stations were in 2m, 4m, 9m and 12 m distance from the lake margin. Both mixed wood and beech wood were roughly 40 m and 300 m respectively away from the lake margin. Further characterisations of the three woodland areas, the vegetation and other groups of the soil fauna are described by IRMLER (1995). The soils were characterised in detail by SCHLEUß (1992).

Rove beetles were sampled from litter by a 0.1 m² frame. In the laboratory, they were collected from the litter by handsorting subsequently followed by heat extraction in a Macfadyen apparatus for 10 days (MACFADYEN 1962). Sampling was performed monthly. At each sampling date, in the beech wood 4 replicate samples were taken, in the mixed wood at the hill slope 2 replicate samples were taken and one sample was taken at each of the four subsites in the alder wood. In the beech and the mixed wood, distance between the subsites for the replicate samples were between 10 and 15 m. Distance of subsites in the alder wood are displayed in fig. 1.

Table 1: Site characteristics (according to SCHLEUß 1992, SPRANGER 1992 and own measurements).

Environmental parameter	Beech wood	Mixed wood	Alder wood 4	Alder wood 3	Alder wood 2	Alder wood 1
Mean litter fall (kg ha^{-1} a^{-1})	3079	4489		6659		
Organic matter in top soil (%)	3.4	5.8		42.2		
Mean soil moisture (%)	26.0	31.6	33.6	56.6	63.8	59.5
Mean soil pH	3.7	3.8	4.2	5.5	6.0	5.3
Above mean groundwater level (m)	19	10	0.41	0.11	0.04	0.10

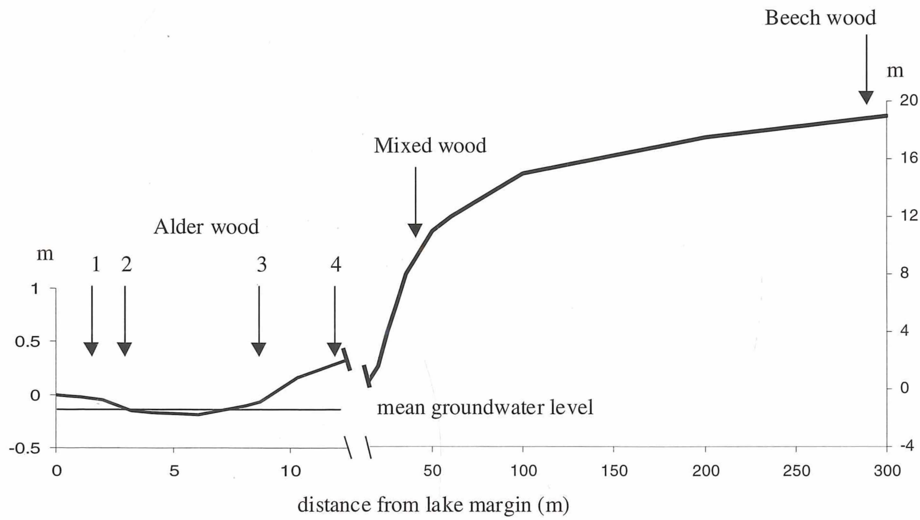

Fig. 1: Cross section of the investigated woodland (sampling sites are marked by arrows).

Climate data were obtained using the data of the climate station at Wankendorf, a village in 2.5 km distance from the investigated woodland. Monthly average temperatures and monthly sum of rainfall were used for the further analysis. In the beech wood only, litter was sampled by 1 m^2 funnel collectors directly adjacent to the rove beetle sample area and analysed in detail (SPRANGER 1992). For the further investigation in this study only the monthly sum of total litter has been used. In the alder wood additionally, groundwater level was determined monthly at each site using groundwater pipes 50 cm in length with openings at 5 cm intervals.

For the statistical analyses the program Statistica was used (STATSOFT 1996). Mean yearly abundance of species were correlated with mean annual temperature, mean January and July temperature, annual sum of rainfall, and annual sum of litterfall in the beech forest. For total means and standard deviations (s.d.) of species densities, the spatially replicate samples (4 in beech forest, 2 at mixed forest) were summarised for the seven years, for yearly means and s.d. the spatially replicate samples of each year were summarised separately. Thus, for densities at subsites in the alder wood no s.d. were calculated.

A Detrended Correspondence Analysis (DCA) and a Canonical Correspondence Analysis (CCA) were conducted by the program CANOCO (TER BRAAK & SMILAUER 1998) using the mean yearly abundance of the species and yearly climate values, e.g. mean annual temperature, January and July temperature, and annual sum of rainfall. A subsequent Monte-Carlo-Permutation test was performed to find significant parameters. The eigenvalues of DCA are equal to the sample or environmental parameter scores and are thus a measure of importance of ordination axes. According to JONGMAN et al. (1987) an eigenvalue more than 0.5 denotes a good separation along the axis.

Time series analysis was performed to determine long-term trends calculating seasonally adjusted curves to correlate climatic changes with the fluctuating abundance of the rove beetle species. The seasonal adjusted curves were chosen to focus on long-term trends and to avoid the correlation between the endogenous seasonality of species with the seasonality of climate factors. To produce the seasonally adjusted trend curve, the additive model was selected. Trend curves are calculated by the program Statistica using a 5 months smoothing mean. Cross correlation was performed to calculate the lag time. In cross correlation the environmental parameters analysed are successively correlated in monthly intervals with the abundance of the species. The shortest significant ($p < 0.05$) period between the change in an environmental parameter and the abundance of the species was taken as lag time, which can be presumed to be the reaction time between the abundance of the beetle species and the respective environmental factor. Lag time reflects the time between the occurrence of a triggering environmental situation, e.g. rainfall, and the reaction of the species expressed in abundance changes. The reaction time may be influenced either by different developmental times or by migration and the population dynamics effected by the ecological conditions. Lag times longer than 12 months were omitted. Counter plots of abundance were achieved by using distance weighted smoothing of smallest quadrates.

Results

Changes in the environmental conditions

The investigated years between 1989 and 1995 provided different climatic situations (Fig. 2). The year 1990 was the warmest year of the studied period, which is referred to the warm winter with mean January temperature of 4.4 °C, while the summer was cool with a maximum mean monthly temperature in August of 17.8 °C. Mean annual temperature in 1994 was intermediate, but the year provided the warmest summer with 20.0 °C in July. Both years were characterised by the highest annual rainfall of the studied period with more than 970 mm. The years 1991 and 1994 represented the coldest winter of the period, while 1994 and 1995 reached highest summer temperatures. The driest year of the studied period was in 1995 with 686 mm.

Litter fall as well showed high fluctuations between the years. In 1992 litter fall was nearly twice as high as in the preceding year 1991. The year 1993 was characterised by a very high litter fall also. The mean yearly litter inputs of the studied period into the different parts of the wood are listed in table 1. Highest inputs in this period were measured for the alder wood, lowest for the mixed wood, but variance between the years determined in the beech wood were larger than differences between the sites.

The groundwater level fluctuated corresponding to the seasons, with high levels in the early spring and low levels in autumn (Fig. 4). In 1994 and 1995 groundwater levels were above average of the studied years, which caused long-term waterlogged periods at the stations 2 and 1 in the alder wood. In contrast, the years 1992 and 1993 were dry and the groundwater level was below soil surface throughout the year.

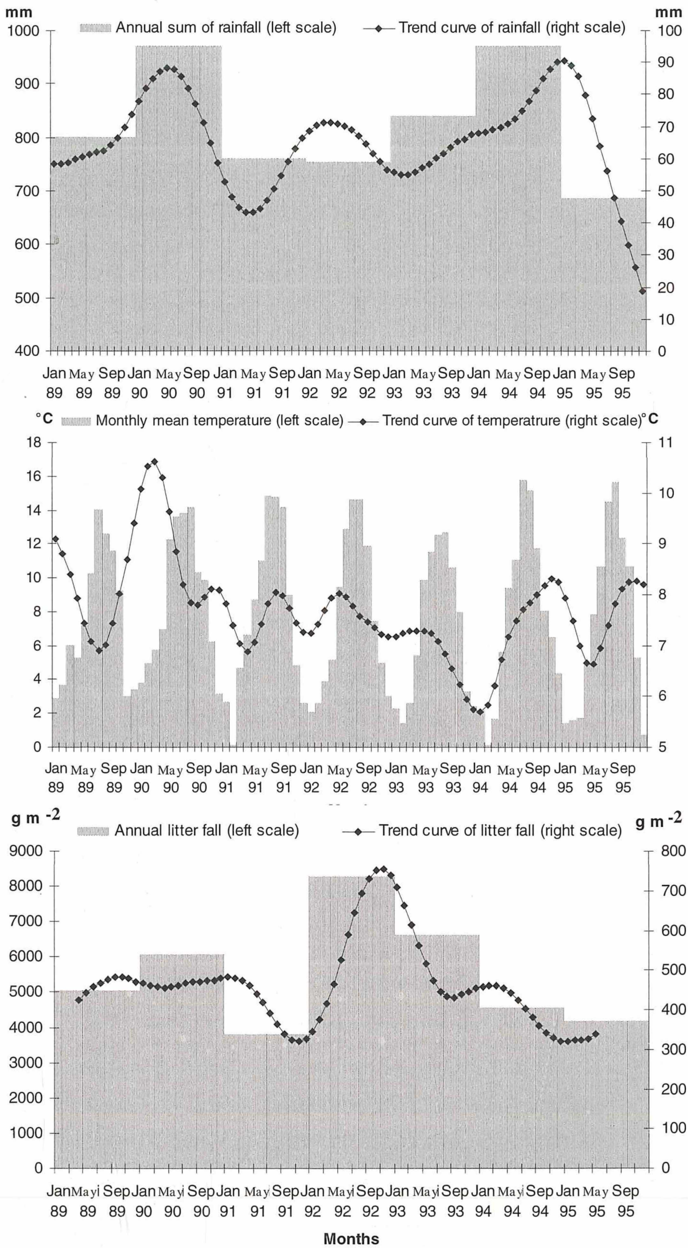

Fig. 2: Fluctuation of rainfall, temperature and litter fall in the beech wood during the 7 investigated years. The trend curves based on the results of the times series analysis.

Table 2: Density (ind. m^{-2}) of rove beetle species and species richness 0.1 m^{-2} at the investigated sites of the woodland (species with less than 0.1 ind. m^{-2} are omitted).

	Beech		Mixed		Alder (subsites)			
Total number of adult specimens	2008		1449		280	231	161	280
Species	Mean	S.d.	Mean	S.d.	4	3	2	1
Geostiba circellaris	51.7	17.9	23.6	5.9	16.3	1.2		0.6
Othius myrmecophilus	19.6	4.4	19.2	5.2	5.2	1.6	0.1	0.7
Atheta fungi	6.7	1.1	7.2	0.5	2.4	0.6	0.1	0.1
Tachyporus hypnorum	0.7	0.6	0.8	0.3	0.3	0.3	0.1	0.3
Philonthus cognatus	1.8	0.9	0.2	0.3			0.1	0.1
Mycetoporus mulsanti	0.5	0.6	1.3	0.5	0.1			
Mycetoporus lepidus	0.5	0.5	0.1	0.1	0.1	0.1		
Aleochara bipustulata	0.1	0.2						
Tachyporus solutus	0.3	0.1	0.2	0.0				
Mycetoporus rufescens	0.3	0.2	0.5	0.4				
Othius punctulatus	4.0	0.9	8.3	10.7	0.7	0.6		0.1
Oxypoda annularis	2.6	0.5	1.2	2.3	0.4	0.1		
Lathrimaeum atrocephalum	1.8	0.5	12.0	11.6	2.5	2.7	1.0	2.8
Lathrimaeum unicolor	0.0	0.1	10.7	10.3	1.0	1.5	1.6	0.4
Rugilus rufipes	0.9	0.4	2.5	0.1	0.9	0.3	0.1	0.3
Amischa decipiens	0.5	0.2	1.0	0.1	0.1	0.3		0.1
Stenus impressus	0.4	0.4	1.5	0.5	0.4	0.3	0.1	0.6
Amischa analis	0.3	0.2	0.9	0.5	0.0	0.3		0.1
Lathrobium brunnipes	0.1	0.2	2.0	0.7	0.3	0.6		0.1
Tachyporus obtusus	0.1	0.1	0.8	0.4	0.1			
Proteinus micropterus	0.0	0.1			0.0	0.6	0.1	0.1
Tachinus signatus	0.3	0.1			0.1	0.3	0.1	0.0
Liogluta alpestris	0.1	0.2	0.3	0.4	0.1	0.3	1.3	0.3
Anotylus rugosus	0.4	0.2	1.4	0.7		0.9	0.3	0.9
Carpelimus corticinus	0.0	0.1	0.1	0.1				0.1
Gabrius breviventer	0.2	0.4	0.4	0.5	0.3	0.6	0.4	0.1
Carpelimus elongatulus			0.1	0.1		0.1	0.4	1.2
Ocalea picata					4.0	8.7	3.3	3.3
Myllaena intermedia					0.1	7.8	2.4	5.1
Olophrum piceum					0.1	0.1	0.6	0.6
Oxypoda brevicornis						0.1	0.1	
Atheta elongatula					1.0	0.3	1.0	
Lesteva longoelytrata					0.1		0.7	
Atheta aquatica						0.6	3.3	
Myllaena infuscata							0.1	0.3
Stenus bipunctatus							1.8	0.3
Deubelia picina							0.3	
Average density of adults (Ind. m^{-2})	71.9	19.1	120.8	26.7	53.2	40.0	27.0	29.7
Average density of larvae (Ind. m^{-2})	53.2	64.8	71.9	47.9	133.	240.	113.3	180.0
Species richness / subsite	37.3	1.5	44.5	6.3	42	49	41	46

Composition of the rove beetle fauna

A total of 118 rove beetle species out of 4409 specimens was recorded in the woodland with 57, 60 and 80 species in the beech, mixed and alder wood respectively. Although the alder wood represented the highest species richness, it provided the lowest density (Table 2). Furthermore, within the alder wood density decreased with decreasing distance from the lake margin. However, the high densities of rove beetles in the beech and the mixed wood was mainly referred to the high abundance of *Geostiba circellaris* that accounted for half of the staphylinid abundance in the beech wood. The species was the most dominant species regarding beech and mixed wood and even in the upper part of the alder wood. A similar distribution was found for *Othius myrmecophilus,* the other frequent species in the dry parts of the woodland. *Lathrimaeum atrocephalum* and *L. unicolor* showed their highest abundance in the mixed wood. Most of the species recorded in the beech and the mixed wood also occurred in the alder wood, whereas only few species that were frequent in the alder wood, e.g. *Lathrobium brunnipes* and *Anotylus rugosus,* were found in the drier parts of the woodland. Some species only occurred in the wettest part near the lake margin, e.g. *Stenus bipunctatus, Deubelia picina,* and *Myllaena infuscata.*

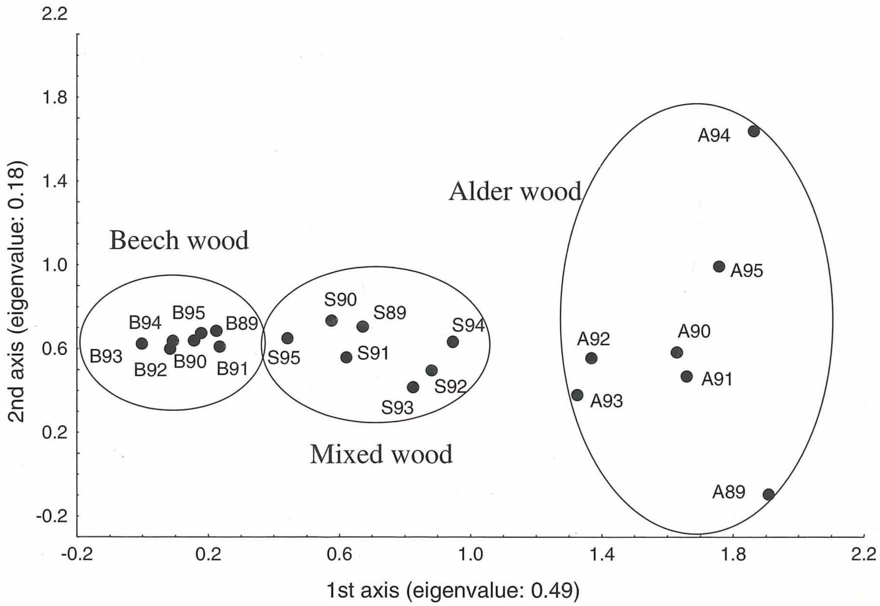

Fig. 3: Result of the Detrended Correspondence Analysis of sites and years in the studied woodland (B: beech wood, S: mixed wood at slope, A: alder wood; the numeric characters indicate the respective year).

The DCA shows that the three study sites in the woodland are well separated by the ordination (Fig. 3). On the one hand, differences between the years are distinctly lower than the spatial differences based on the change of environmental parameters within the gradient. Ordination along 1st axis is sufficient concerning the eigenvalue of 0.49 and corresponds with the moisture gradient with the wet alder site on the right hand and dry beech site on the left hand. On the other hand, similarities in the ordination of years within the three sites can be detected. The year 1993 is ordered on the left side of the sites' plot. This fits well with the overall ordination of the 1st axis along the soil moisture gradient, because 1993 was the driest year during the study period. This is underlined by the ordination of the year 1994 at the right side of the plots for the mixed and the alder wood as it represented the wettest year. However, the CCA revealed no significant results using annual rainfall as well as mean annual January and July temperatures. The higher variance at the alder wood might be referred to the variance in groundwater level, but the low eigenvalue of the 2nd axis with 0.18 indicates only small differences between the years.

Long-term changes

For the time series analysis 9 species were selected that were most abundant at least in one of the sites (Table 2). With the exception of the two species from the alder wood, i.e. *Ocalea picata* and *Myllaena intermedia,* and *Othius punctulatus* all other species studied correlated negatively with temperature reflecting a decrease in abundance in response to high temperature (Table 3). Time lags of temperature varied between 1 and 12 months. Thus, temperature was the factor showing the highest number of significant correlations in the rove beetle species. The four most abundant species of the beech wood also significantly correlated with litter fall that was only measured in the beech wood. Time lags of 12 months were determined for these relations reflecting that the species' abundance maxima of the total period occurred one year after the high litter fall events in 1992 and 1993 (Fig. 4).

Table 3: Results of cross correlation between environmental parameters and abundance of species (only significant results displayed; R: correlation coefficient; Lag: time lag in months between triggering parameter and abundance response).

	Temperature		Rainfall		Litter fall		Groundwater		Site
Species	R	Lag	R	Lag	R	Lag	R	Lag	
Oxypoda annularis	-0.68	5			0.59	12			Beech
Geostiba circellaris	-0.71	3			0.50	12			Beech
Atheta fungi	-0.56	1			0.66	12			Beech
Atheta fungi	-0.59	1							Mixed
Othius myrmecophilus	-0.39	6							Beech
Othius punctulatus					0.63	12			Beech
Lathrimaeum atrocephalum	-0.39	12	0.36	2					Beech
Lathrimaeum atrocephalum			0.38	0					Mixed
Lathrimaeum unicolor	-0.45	6							Mixed
Ocalea picata							-0.45	3	Alder
Myllaena intermedia							-0.39	4	Alder

The two species studied occurring in the alder wood, i.e. *Ocalea picata* and *Myllaena intermedia,* were negatively correlated with groundwater level. Regarding the situation at site 3 of the alder forest, both species were highly abundant during the beginning of the study period with medium groundwater levels of 10 to 12 cm under floor (Fig. 4). Abundance decreased if the groundwater level at site 3 was beneath 14 cm under floor and their density also decreased if groundwater level was higher than 10 cm under floor.

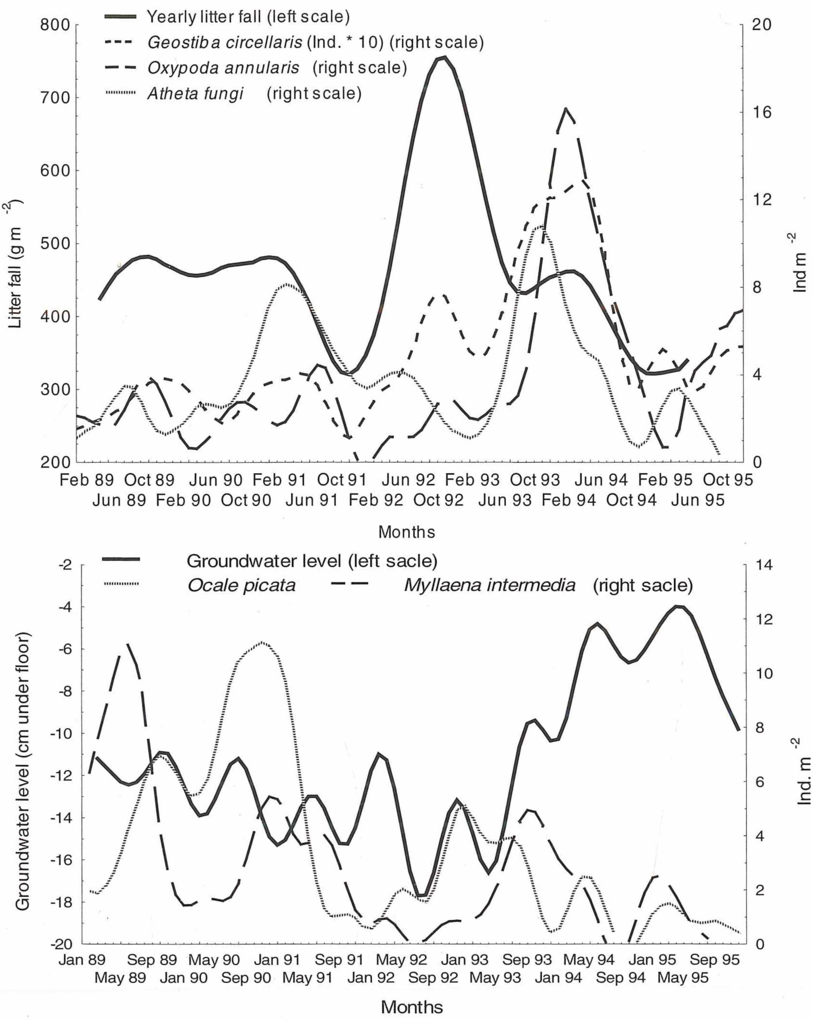

Fig. 4: Time series analysis of 5 rove beetle species with litter fall in the beech wood and groundwater level at subsite 3 in the alder wood.

Interactions between sites

The above selected species were tested by cross correlation if their population fluctuations corresponded particularly between adjacent sites. No correlation was found for *Othius myrmecophilus* and *Geostiba circellaris* between beech, mixed and alder wood. This can be also seen by the counter plots that resulted in more or less parallel counter lines (Fig. 5). However, abundance relationships were found for species occurring mainly at the hill slope in the mixed forest. Abundance of *Othius punctulatus* and *Lathrimaeum atrocephalum* in the beech and in the alder forest significantly corresponded with density fluctuations in the mixed forest. This is also obvious by a higher number of vertical counter lines in the counter plots (Fig. 5). Time lags between the intermediate mixed wood and both the upper and lower adjacent beech wood and alder wood respectively varied between 1 and 3 months meaning that an increase in density in the mixed wood resulted in an increase of density in the beech or alder wood 1 to 3 months later. Correlation in *Atheta fungi* was significant between mixed and beech wood only (Table 4).

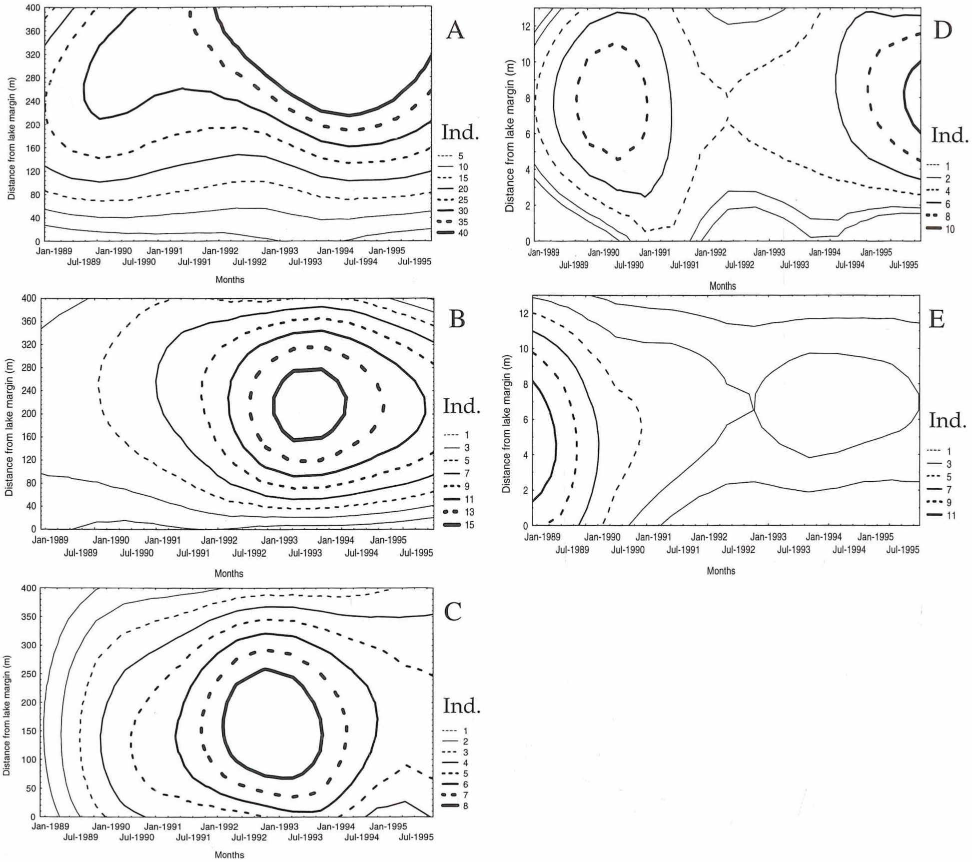

Fig. 5: Counter plots of the density (Ind. m^{-2}) of 5 rove beetle species in the cross section from alder wood at the lake margin to the 350 m distant beech wood during the study period of 7 years (A: *Geostiba circellaris*, B: *Atheta fungi*, C: *Lathrimaeum atrocephalum*, D: *Ocalea picata*, E: *Myllaena intermedia*).

Significant abundance relationships were also found for *Ocalea picata* and *Myllaena intermedia* between the subsites in the alder wood. *Ocalea picata* abundances at subsites 3 and 2 corresponded with the abundance of subsite 4 with a time lag of 0 to 3 months. The shorter time lag of 0 months was at the directly adjacent subsite 3, whereas the more distant population at subsite 2 reacted with a longer delay. No correlation was found to subsite 1. In contrast, abundance of *Myllaena intermedia* at subsite 3 showed no correlation to subsite 4, but only to subsites 2 and 1 with time lags between 2 and 3 months. Increments based on the linear regressions were between 0.2 and 0.7 reflecting that an increase of 1 specimen at subsite 3 resulted in an increase in either 0.2 or 0.7 specimens at subsites 2 and 1.

Table 4: Results of cross correlation between abundance in the mixed wood and in the beech or alder wood and between different subsites in the alder forest (R: regression coefficient, I: increment of linear regression, L: time lag in months; number in brackets of the alder wood indicate the subsite).

Species	Beech			Alder		
Mixed wood	R	I	L	R	I	L
Lathrimaeum atrocephalum	0.33	0.4	2	0.36	0.7	1
Othius punctulatus	0.37	0.3	2	0.46	0.5	3
Atheta fungi	0.30	0.3	1	.	.	.
	Alder (3)			Alder (2)		
Ocalea picata (Alder 4)	0.45	0.6	0	0.50	0.5	3
	Alder (2)			Alder (1)		
Myllaena intermedia (Alder 3)	0.38	0.2	2	0.51	0.7	3

Discussion

Concerning to the Detrended Correspondance Analysis the three sites located on the cross section are strictly separated throughout the years. An overlap of adjacent sites for species assemblages could not be found. Referring to the ordination results the species composition in the beech wood showed the lowest variance during the period studied, whereas in the alder wood the highest variance between the years were recorded and the mixed wood reflected an intermediate situation. Although the distance between the mixed wood and the alder wood is much lower than between mixed wood and beech wood, the similarity of species composition between mixed and beech wood was higher. The strong separation of the three assemblages is mainly based on the restriction of alder wood species to their habitat. Whereas most species that mainly occurred in the beech wood were also found in the alder wood, at least at higher elevations up to 0.5 m above ground water level, none of the typical alder wood species invaded into the mixed or beech wood. Within the cross section different environmental parameters are changing from alder to beech wood, i.e. humus form, soil moisture and vegetation. According to results of ANDERSEN et al. (1990) vegetation cover has no remarkable influence on the species composition of rove beetles, whereas litter layer and soil moisture were found to be highly responsible for species composition changes (BOHAC et al. 1999).

In a comparison of 37 forest sites in Schleswig-Holstein (northern Germany), soil moisture was also found to be the most effective parameter for ground beetles (IRMLER 1999). Organic matter and sand content of soil were mostly correlated with soil moisture meaning that their effect on the species distribution cannot be separated. Soils with high moisture were also characterised by high organic matter and low sand content. Thus, species living on soils with high moisture seem to prefer also soil with high organic matter and low sand content. To separate the different parameters a higher number of sites varying independently in parameter values than in the present study must be investigated.

The rough step from alder wood to mixed wood is also reflected in the population density with distinctly low densities in the alder wood and high densities in the mixed and beech wood. Only few data are available on densities of rove beetles in forests. PALMGREN & BISTRÖM (1979) published 120 ind m^{-2} in Scandinavian coniferous forests and HARTMANN (1979) and FRIEBE (1983) recorded densities of approximately 100 ind. m^{-2} from German beech woods on a density level that is similar as the densities in the dry parts of the woodland. According to data listed by BOHAC (1999) densities of rove beetles varied between 5 and 470 ind. m^{-2} in forests of Czech-Republic and Slovakia with highest values in wet forest types. This is in contrast to the present investigation, where lowest densities were found in the wet parts of the studied forest. The density decrease from dry to wet conditions in the woodland is also supported by the density gradient in the alder wood, as with increasing distance from the groundwater table the density increased. At 0.5 m above groundwater, the density was nearly twice as high than at 0.2 m. The discrepancy between the present findings and those of BOHAC (1999) may be explained by the relatively long waterlogged period in the ground depression of the alder wood that cause an oxygen deficit in lower soil layers.

Species richness, however, was on a similar level throughout the whole studied forest with a minor not significant decrease from alder to beech wood. This supports the overall situation in the beech wood with high dominance of few species, whereas in the alder wood a more even dominance structure was found. This is in correspondence with the findings of BOHAC (1999), who compared different forest types in Europe and also found the highest species richness in wet forests.

In the alder wood, groundwater fluctuation seems to be the major environmental factor influencing the density fluctuation of rove beetles. Neither temperature nor rain fall gave significant results due to the time series analysis in the two species examined, *Ocalea picata* and *Myllaena intermedia*. It is interesting that both species were negatively correlated to groundwater level concerning the cross correlation which indicates that they prefer wet conditions, but not too high groundwater tables. Densities decreased during periods of low groundwater levels as well as during high groundwater levels. The rough decrease when groundwater level was higher than 6 to 8 cm under floor might be referred to the oxygen deficit in this soil layer and means that at least larvae use the soil up to 6 to 8 cm depth. The optimal range of groundwater level seems to differ between the two species examined. While *Myllaena intermedia* had its highest density at a groundwater level between 10 and 12 cm under floor, *Ocalea picata* was most frequent if groundwater level was between 12 and 15 cm under floor. Experiments on flood sensitivity of staphylinids display a high submergence mortality. Even species of floodplains do not exceed a period of 18 days of submergence (ANDERSON 1968, HEYDEMANN 1967).

For the species mainly living in the mixed or beech wood temperature and litter fall were the most important factors to explain the long-term fluctuation. Regarding to the correlation coefficients, both high temperatures and litter have a negative and positive effect respectively on the density. According to laboratory experiments of TOPP (1978) the species that were also found in the present study, i.e. *Atheta fungi, Othius myrmecophilus, Geostiba circellaris* and *Lathrimaeum atrocephalum,* are not counted to freeze tolerant species. They are freeze sensitive, but still survive supercooling points between –5.0°C to –10.0°C, a temperature that was rarely found in the years investigated. As these species reached their maximum abundance in 1994, after the coldest winter in 1993/94 winter temperature seem to be more important than summer temperature. However, there is also high evidence, that litter fall is the triggering factor of the density for *Geostiba circellaris* and *Othius myrmecophilus* in 1994 as the 1994-maximum occurred in the beech wood only. Moreover, *Geostiba circellaris* maximum started in autumn 1992 with a premaximum and passed a long period of high density during 1993 and 1994. In contrast, *Atheta fungi* correlated with temperature in both beech and mixed wood that implies that likely temperature is the triggering factor for this species. Additionally, *Atheta fungi* exhibited another abundance maximum after the winter 1990/91 that was the next coldest one in the study period. The positive effect of the high litter fall on the rove beetle species can be referred either to a higher food supply or to a better temperature buffer in winter time.

Response time on triggering environmental factors highly depends on the developmental time of the species. For *Othius punctulatus* the reproduction dynamics are well known already. It passed a stringent seasonal development with one reproduction period per year that was also found for the small *Geostiba circellaris* (KASULE 1970, HARTMANN 1979). In contrast, *Othius myrmecophilus, Oxypoda annularis* and *Atheta fungi* have no seasonally defined reproduction periods (KASULE 1970, TOPP 1974, HARTMANN 1979). The short response lag on triggering temperature of *Atheta fungi* is referred to the partly parthenogenic reproduction in this species (TOPP 1974). The longer time lags of the other staphylinid species can be the result of the longer delay by mating that occurred mainly in spring. This is also due to *Othius myrmecophilus,* although females lay eggs throughout the year (KASULE 1970).

The last question concerns the interactions between adjacent parts of the woodland meaning that density fluctuations in one part of the forest influences the density in other parts. As can be seen from the cross correlations high densities of species living mainly in the beech wood, i.e. *Geostiba circellaris* and *Othius myrmecophilus,* seem to have no enhancing effect on the populations of the lower parts of the woodland. Although *Geostiba circellaris* and *Othius myrmecophilus* inhabited nearly the whole woodland, the high increase in the abundance from autumn 1992 to autumn 1994 in the beech wood produced no higher densities in the mixed or the upper alder wood. This low dispersal power is referred to the lack of hind wings in both species that inhibits a fast dispersal. The species occurring mainly in the mixed forest showed a more flexible behaviour. The populations of the three species examined from that part of the woodland positively influences the populations in the adjacent parts. All three species have well developed hind wings. The high dispersal power of these species is also documented by the short time lag, but also reflects the environmental barriers in the woodland. Although the distance from the mixed wood to the beech wood was much higher than to the alder wood, time lags between mixed and beech wood were generally lower than between mixed wood and alder wood. In particular, species of often inundated habitats are assigned by a high dispersal power (KUNZE & KACHE 1998). Thus, it was expected that species of the alder wood often shift between sites. However, these species lived in spatially more restricted habitats than do species of the higher elevations. *Ocalea picata* that mainly occurred in higher elevated parts of the alder wood scarcely invaded to the site directly adjacent to the lake margin even in dry periods, e.g. in the year 1993. Vice versa, *Myllaena intermedia* living on slightly lower elevated parts did not invade to the high elevated site 4 even during the long water logged period in 1993/94.

It could be shown that rove beetle populations exhibited considerable abundance fluctuations mainly as response on temperature changes. In the beech wood, litter fall seems to be also a triggering parameter likely in correspondence with temperature and at wet groundwater near sites, the groundwater table was the main factor affecting the population densities of species. Species of the near groundwater located sites are restricted to a small-scale habitat with a short range of groundwater fluctuation that likely depend on the specific moisture conditions and the sensitivity to an oxygen deficit in the soil layer. Dispersal of both species mainly living in the beech wood and in the alder wood is low due to the reduction of hind wings and the specific preference of moisture condition respectively. Species living in intermediate habitats showed the highest dispersal power invading into the beech wood as well as into the alder wood. Regarding global climate change, changing rainfall and temperature may drastically change the staphylinid community. If winter temperatures will increase as predicted by CUBASCH (1998), in particular rove beetle species of the beech wood will suffer due to their sensitivity to high winter temperatures.

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