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ORIGINAL PAPER

Species richness of saproxylic beetles in woodlands is affected by dispersion ability of species, age and stand size

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Abstract This study examines the occurrence of saproxylic beetles in woodlands of different size and age and their potential to leave woodland areas and cross open grassland in northern Germany. The beetles were recorded by emergence traps and flight-intercept-traps. The investigated sites were dominated by beech, oak and alder, but other tree species also occurred in low abundance. Species richness showed a positive relation to stand size and age of woods. Both total and rarefaction species richness were the lowest in small and young woods and highest in old and large woods. Species richness decreased asymptotically from the inner-wood habitat to a distance greater than 80 m from the wood margin. 80 species were classified into 46 low mobile species found at a distance <30 m from wood margins and 34 high mobile species found >30 m from wood margins. The most mobile species were found the most frequently in all woods; but they contributed less to species richness in wood stands than did the species with low mobility. The contribution of the least mobile species to species richness in wood stands increased with the age and size of the stands, with the effect of stand size being the greater. We conclude that in our study region woods larger than 100 ha are necessary to maintain the highest richness of the least mobile saproxylic beetles.

Keywords Mobility · Wood size · Wood age · Biodiversity · Species richness · Wood fragmentation

Introduction

In the last two decades, discussions of biodiversity frequently mention the status of saproxylic beetles, and conservation strategies have been demanded for single highly endangered species in a European context (Rauh and Schmitt 1991; Speight 1989; Ranius et al. 2005; Gibb et al. 2006b). In Germany, for example, saproxylic beetles account for 59% of the endangered species of beetles and similar percentages are found in other European countries (Geiser 1998; McLean and Speight 1993; Siitonen 2001).

Management of forests which controls the amount of dead wood and the age of forest sites is the main influence on species richness (Similä et al. 2003; Dobelin 2006). During the twentieth century, old-growth forests, with old, dying and dead trees declined dramatically. In Scandinavian boreal forests, only one-third of old Scots pines and Norway spruces found in the 1920s can be found today (Andersson and Östlund 2004). Major isolation and fragmentation of forests began in Central Europe in the Middle Ages and has thus effected the saproxylic beetles for over 500 years. A low dispersion potential of saproxylic species is supposed to be one reason for their endangered status (Ammer 1991; Schiegg 1999).

Flight ability differs between saproxylic beetle species and different movement strategies exist, with short-distance movements being more frequent than long-distance movements (Jonsell et al. 2003). Although, long distance movement seems to be more frequent in some species than in others, high dispersion ability need not confer frequency of occurrence (Jonsell et al. 1999).

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Regions with highly fragmented woodland areas in an agricultural matrix (e.g. northern Germany) are ideal for investigating dispersal of saproxylic beetles in modern mosaic landscapes. Hitherto, dispersion of saproxylic beetles has been mainly investigated for single species (Ranius and Hedin 2001; Jonsson 2002; Rink 2006) or specific fungus dwelling species (Komonen and Kouki 2005; Jonsell et al. 1999). Investigations of the relative dispersive ability of saproxylic beetles in landscape mosaics are lacking.

Here, we focus on the following questions: (1) How do small, isolated woodland areas influence the biodiversity of saproxylic species in a semi-open grassland? (2) How far can saproxylic species travel over open grassland areas? (3) Do these processes affect the biodiversity of wood area differing in size and age?

Sites and methods

Studies were conducted in 2000 and 2001 in the valley of the upper river Eider approximately 10 km south of the city of Kiel (northern Germany). The total area is approximately 350 ha, comprising semi-open moist grassland in the river valley and mainly deciduous forests on the slopes. In the valley itself small wood sites are distributed over the whole area. Most of these are moist alder woods, but also sometimes drier hedgerows or single large oak trees. The mean annual temperature of the region is 8.1°C and mean annual rainfall is 697 mm. In the study period, temperature from March to May was higher, and from June to August, slightly lower than the 30 year average. Annual rainfall from March to August in 2000 was lower than the 30 year average.

The occurrence of saproxylic beetles in relationship to age and size of woody stands was investigated at 57 sites distributed throughout the 350 ha study area. The age of the single wood stands was estimated from a map published in 1877 by the Prussian government and they were classified as young (younger than 130 years) or as old (older than 130 years). The area of the woods was determined with the program ArcView GIS 3.2 (Environmental Research Institute 1999) and classified into 3 groups: 1: <10 ha, 2: between 10 ha and 100 ha, and 3: >100 ha.

Saproxylic beetles were recorded using 57 metal emergence-traps, each of which was 1 m^2 and 0.2 m high. The bottom of the emergence-traps were covered by a PVC-sheet to avoid invading soil species and filled with the dead wood from a radius of 20 m around the trap site. To achieve a representative composition of the saproxylic beetles at the trap sites, dead wood in different decay status was sampled from the floor and from standing trees. A catching box was installed at the side of each trap and filled with 4% formaldehyde and a detergent liquid. Samples were taken in monthly intervals from 17 March to 8 August 2000 and from 1 April 2001 to 18 August 2001. The tree species that were used to fill the emergence traps was recorded.

For the measurement of dispersal of saproxylic beetles over grassland a smaller area in the centre of the study site was selected. In this area several small woody sites in the valley connected slightly larger woods at both slopes. A total of 67 flight-intercept-traps were installed in this area including the slopes of the valley, amongst linear alder woods, hedgerows and in the intermediate grassland. The flight-intercept-traps were set on 1.5 m high stakes. On the top of each stake a PVC-tub with 30 cm side length was installed into which a cross of two transparent PVC-plates with side lengths of 50 cm were placed. The PVC-tub was filled with 4% formaldehyde. Flight-intercept-traps were emptied at monthly intervals from March to August 2000.

A Canonical Correspondence Analysis (CCA) was used to study the composition of saproxylic beetles in the 57 woody sites using the program CANOCO (Ter Braak and Smilauer 1998) with age, size and species richness of trees included as environmental factors. A subsequent Monte-Carlo-Permutation test was performed to find significant parameters. Only those ordination axes with eigenvalues >0.5 were retained, as these are likely to have the most discriminatory power (Jongman et al. 1987).

Further statistical analyses were performed using the program STATISTICA (Statsoft 1998). As species richness and rarefaction species richness were normal distributed, a multifactorial ANOVA was used to test the relationship between total species richness and rarefaction species richness to age and stand size. Fisher LSD tests were used to differentiate homogenous groups. Rarefaction species richness, calculated using the program 'Ecological Methodology' (Krebs 1994), was limited to 20 specimens, which was the minimum number of specimens per emergence trap.

To address how far saproxylic beetles flew over open grassland, species that were not found in the emergence traps were omitted; 80 species were included in the dispersion analysis. The distance moved by each species was recorded as the distance between the wood where the species was recorded in an emergence trap, and the most distant flight-intercept-trap record, estimated using ArcView GIS. This distance is the minimum dispersal distance species fly over open grassland and is assumed to indicate the relative dispersive ability compared to other species. The species were classified according to these distances as follows (DC): 1 only in woods, 2 between >0 and 30 m distance, 3 between >30 m and 80 m distance and 4 >80 m distance from wood margin. For the comparison between wood stands, the classes 1 and 2 were combined into low mobile class and classes 3 and 4 into a high mobile class.

The placing of a species into a dispersal class will be affected by the abundance of the species in the emergence traps, with highly abundant species being more likely to be found more frequently in the flight-intercept-traps than rare species. Therefore, the following two statistical approaches were taken: (1) The abundances in emergence traps (EA) and flight-intercept-traps (IA) were normalised with a natural log transformed, then the species of the emergence traps were ordered in decreasing abundance and correlated with abundances in the flight-intercept-traps in the same species order using Pearson correlation coefficient. (2) To integrate distance classes (DC), abundances at emergence traps (EC) were also classified into four classes: (1) <6, (2) 6–20, (3) 21–60, and (4) >60 specimens. Subsequently, the effect of the distance classes (DC) and the abundance classes (EC) on the abundance in the flight-intercept-traps (IA) was analysed using a multifactorial ANOVA.

Nomenclature follows the recent catalogue of Central European beetles (Böhme 2005) and Conservation listing [Red list (RL) categories 1, 2 and 3] is derived from the regional Red List of Schleswig–Holstein (Ziegler and Suikat 1994)

Results

Effects of age and area on species richness

In total, out of 38 beetle families 4,360 specimens in 137 species were recorded by flight-intercept-traps and 3,890 specimens in 123 species were recorded by emergence traps. 80 species were found in both trap types. Four highly endangered species (RL 1) and 44 endangered species (RL 2 and 3) were found in the 188 species, which amounts to 25% of all species recorded in the investigation. The most species rich families were the log-feeding Scolytidae, Cerambycidae, and Anobiidae with 30, 23, and 13 species, while fungi-feeding families, e.g. Cisidae, contributed only 14 species (Fig. 1). The majority of the families were represented by only 3 to 1 species.

Alder, oak and beech were the most frequent tree species of logs in the emergence traps. The species richness of saproxylic beetles in emergence traps was not significantly different between tree species. Mean species richness in alder dominated traps ($n = 22$) was 13.0 ± 5.5, in oak dominated traps ($n = 13$), 13.5 ± 5.3, and in beech dominated traps ($n = 11$), 14.7 ± 6.3.

According to the Canonical Correspondence Analysis (CCA) with the species found in emergence traps, two factors; wood area ($F = 2.94$, $P = 0.005$, $P = 199$) and age ($F = 2.47$, $P = 0.005$, $P = 199$) significantly affected the distribution of the saproxylic beetles, whereas tree species richness had no significant effect (Fig. 2). Ordination along 1st axis corresponded with wood site area and along the second axis with age. According to the ordination of species along the two axes several species were found only in large woods, but the majority were also recorded in small woods.

Species richness and rarefaction species richness of emergence traps were related to stand size and age of woods (Table 1; multifactorial ANOVA for species richness: size: $F = 1.42$, $P = 0.25$, $\mathrm{DF} = 2$, age: F: 8.48, $P = 0.005$, $\mathrm{DF} = 1$, both effects: $F = 5.10$, $P = 0.009$, $\mathrm{DF} = 2$). Thus, age of woods is the most important factor for species richness at emergence traps. According to the homogeneous groups the steepest step was at young and intermediate sized woods. Young and large woods showed similar species richness to old and small woods. Thus, low species richness can be expected in young and small woods, whereas large and old woods have approximately twofold higher species richness.

For rarefaction species richness only size had an effect (mulitfactorial ANOVA: $F = 3.32$, $P = 0.047$, $\mathrm{DF} = 2$, age: $F = 0.53$ $P = 0.98$, $\mathrm{DF} = 1$, both effects: $F = 1.23$,

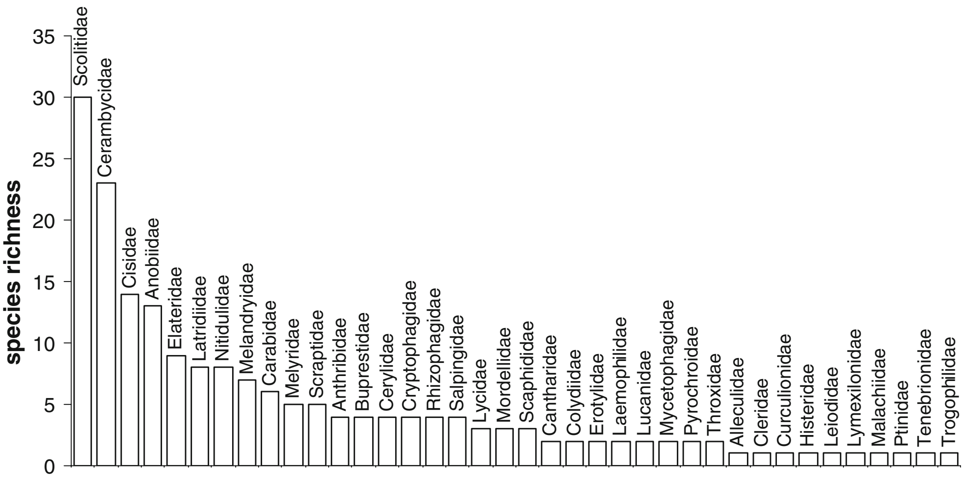

Fig. 1 Species richness of saproxylic beetle families recorded in woodland emergence traps

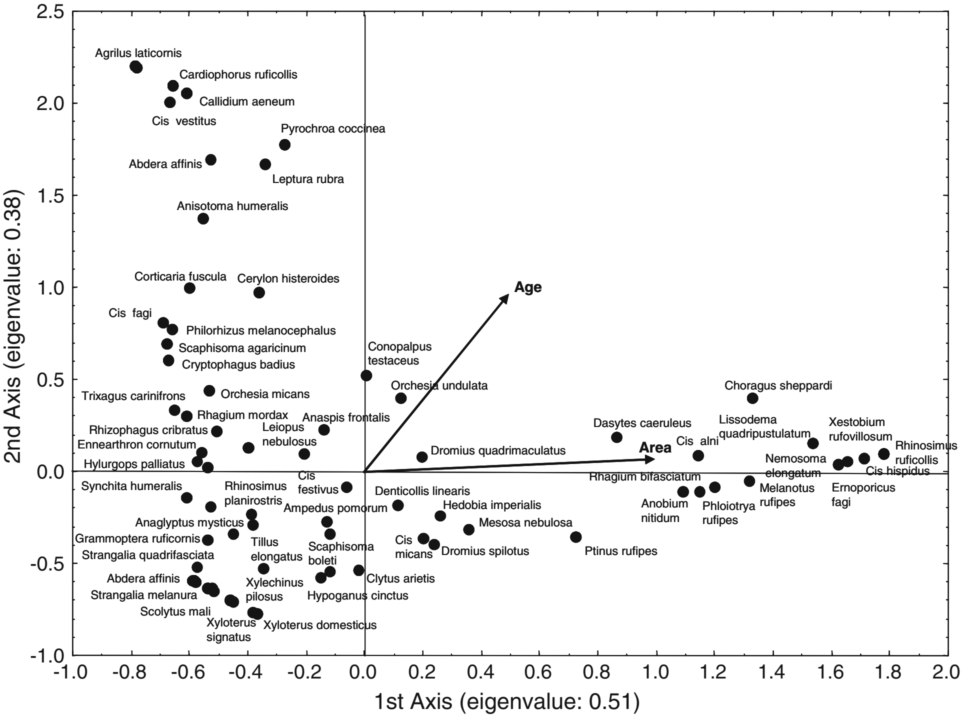

Fig. 2 Canonical Correspondence Analysis with wood area and age as significant environmental parameters

Table 1 Total species richness and rarefaction species richness (species/20 specimens) in samples from different wood age and stand sizes

Area	Age									
	n	Species richness				*n*	Rarefaction species richness			
		<130 years		>130 years			<130 years		>130 years	
		m	SD	*m*	SD		*m*	SD	*m*	SD
<10 ha	18	10.89[1]	4.51	15.67[2,3]	6.43	3	5.37[1]	1.73	5.42[1,2]	1.55
>10–100 ha	12	10.58[1]	3.12	21.25[3]	2.60	8	6.34[1,2]	1.02	7.13[2]	0.92
>100 ha	2	17.00[2,3]	9.90	19.54[2,3]	5.66	13	6.32[1,2]	0.52	6.44[1,2]	1.74

n number of samples, *m* mean, *SD* standard deviation

$P = 0.38$, $DF = 2$). In this analysis, old and large woods have on average between one and two species more than young and small woods.

Mobility of saproxylic beetles

The spatial pattern of species richness in the flight-intercept-traps showed that the majority of saproxylic beetles were found in or nearby the woods (Fig. 3). In the flight-intercept-traps of open grasslands located no more than 30 m distant from the nearest wood, species richness was on average not higher than 10 species, while it was more than 20 species in woods. Species richness decreased asymptotically from inner-wood-traps to traps >80 m distance from woods (Fig. 4). There was a significant difference in the species richness of the inner-wood-traps compared to the outer-wood-traps. (Kurskall Wallis ANOVA, $\chi^2 = 20.23$; $P = 0.0002$), whereas the outer-wood-traps were not significantly different from the grassland traps. The ability of species with different dispersive abilities to cross open grassland is illustrated by *Anobium nitidum* and *Rhizophagus bipustulatus* (Fig. 5). *Anobium nitidum* mainly emerged from logs in a large western beech forest and in the north-western mixed forest with only a few specimens being found in the flight-intercept-traps which were mainly located in the row of small alder woods in the centre of the study area. A distance of 20 m was measured from the nearest wood to the most distant flight-intercept-trap with a positive record in open grassland. *Rhizophagus bipustulatus* was as abundant as *Anobium nitidum* in emergence traps but was more frequently caught at flight-intercept traps. The furthest flight-intercept-trap that recorded *Rhizophagus bipustulatus* was 120 m from the nearest wood.

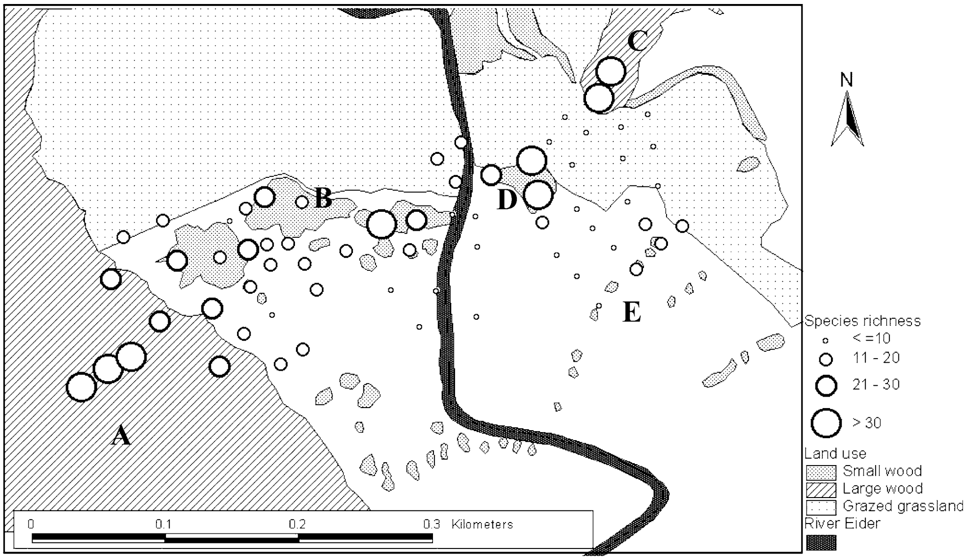

Fig. 3 Spatial distribution of species richness of saproxylic beetles in the flight-intercept-traps

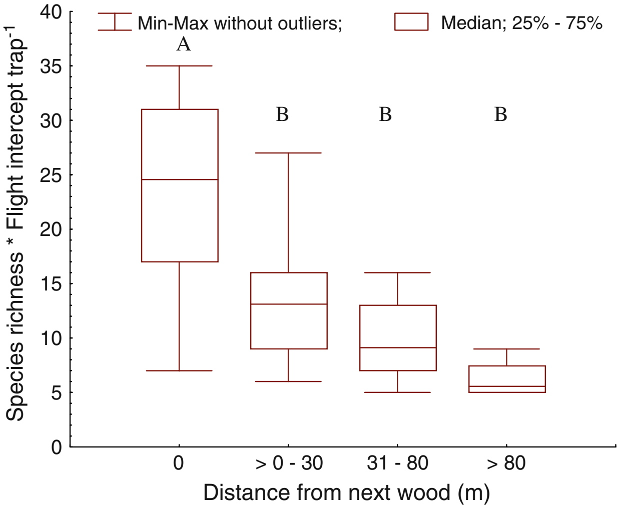

Fig. 4 Species richness of saproxylic beetles in flight-intercept-traps at different distances from the nearest wood. *Different characters* indicate significant difference according to ANOVA and LSD post-hoc test

Using the 80 species which occurring in both trap types, species abundance in the flight-intercept-traps (IA) was positively correlated with their abundance in the emergence (EA) traps ($r = 0.33$; $P = 0.003$) indicating that species abundance in emergence traps affected abundance in the flight-intercept-traps. Hence, only 11% ($r^2 = 0.11$) of the species abundance in the flight-intercept-traps was explained by abundance in the emergence traps.

The classification of the 80 species into the 4 distance classes had the following results (Table 2): 24 species were classified to the dispersion class 1, distance classes 2 and 3 had 22 and 21 species respectively, whereas only 13 species were classified to class 4. In a multifactorial ANOVA using the distance classes (DC) and the emergence classes (EC) the effect of both parameters on the abundance of the flight-intercept-traps (IA) was separated. The results show that EC has a lower insignificant affect ($F = 2.4, P = 0.07, \mathrm{DF} = 3$) on IA than DC ($F = 20.8$, $P < 0.001$, $\mathrm{DF} = 3$; Table 3).

Effect of dispersion ability on species richness

Overall, both low (DC 1 and 2) and high (DC 3 and 4) mobile classes contributed to the total species richness with 57.5 and 42.5%, respectively. Although the species richness of DC 1 was highest, its contribution to the average species richness of emergence traps was low. On average, both 16 and 24% of the mean species richness in the emergence traps was provided by the classes with the lowest (DC 1) and the highest (DC 4) dispersion potential, respectively. Therefore, the contribution of the two distance classes to the species composition in the emergence traps is contradictory to the relation found in total species richness. The fractions of both low and high mobile species amounted to 27.4 and 52.8% of the species richness in the emergence traps. In respect of the three classes of stand size and the two age classes, the species with low mobility were rarest in small and young wood stands, while they were more frequent in old and large stands (Table 4). In contrast, highly mobile species accounted for the highest percentage in small and young wood stands. According to the ANOVA, the difference is significant for age as a co-variable ($F = 3.9$ and $P = 0.01$, $\mathrm{DF} = 2$) for low mobility species, but not for highly mobile species.

Discussion

Effort has been made to investigate the different factors that may influence the diversity of saproxylic beetles in

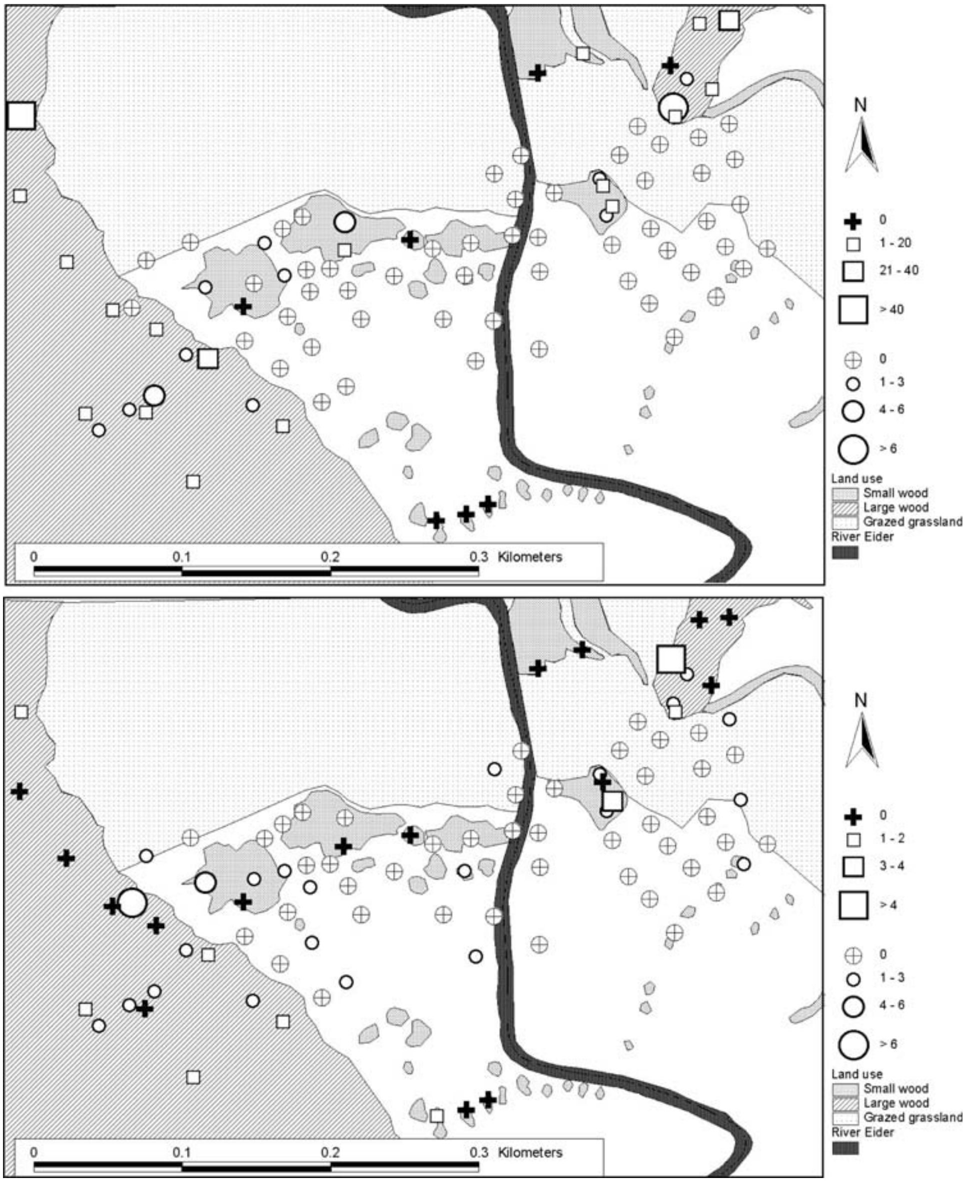

Fig. 5 Distribution pattern of abundance in emergence traps and flight-intercept-traps of a species with low mobility (*Anobium nitidum, upper graph*) and high mobility (*Rhizophagus bipustulatus, lower graph*) in open habitats (white area abandoned grassland; *squares*: emergence traps, *circles*: flight-intercept-traps)

forests. Besides the amount of dead wood, the original tree species and its condition as log, snag or limb is of importance (e.g. Irmler et al. 1996; Grohmann et al. 2004; Dobelin 2006). An intensive study on substrate requirement in Sweden discovered tree species as highly important, but with ongoing wood decay, the host range of saproxylic beetle species broadens and decay fungi become the most important factor (Jonsell et al. 1998). In this study, oak and beech were the trees with the most species rich assemblages of saproxylic beetles. Oak was also the tree species with the highest number of beetle species specialised on only one tree species. In our investigation, beech was the tree with the highest number of saproxylic beetle species. This might be due to the low number of oak trees growing in the woods investigated and the young age of the trees. Oak exhibits its greatest species richness in large free-standing trees under high insolation, and high canopy cover is detrimental for many beetle species (Ranius and Jansson 2000; Vodka et al. 2009). In contrast to oak, beech is the dominating tree in the study area and it also provided the greatest number of old trees which support fungi and provide hollows which are important resources for many saproxylic beetles. High numbers of both are found in natural old forests and might explain the higher species richness in old forests (Junninen et al. 2006; Ranius 2002).

In our study the age of the stands in combination with stand size influences the species richness of saproxylic beetles, a finding which corroborates many other studies (e.g. Dobelin 2006). Lowest species richness was found in small and young stands, highest species richness in old and large stands. Species richness of large young stands was

Table 2 Classification of saproxylic beetles into 4 distance classes (DC); 1: inner-wood class, 2: >0–30 m, 3: >30–80 m, 4: >80 m; total number of specimens in 57 emergence traps (EA) and in 67 flight-intercept-traps (IA); homogeneous groups at $P < 0.05$ indicated by different exponents

Species	EA	IA	DC	Species	EA	IA	DC
Abdera affinis	1	4	1	*Scolytus intricatus*	25	3	2
Anaglyptus mysticus	43	2	1	*Scolytus rugulosus*	57	1	2
Anaspis thoracica	70	4	1	*Dissoleucas niveirostris*	12	1	2
Cis alni	15	1	1	*Sulcacis fronticornis*	1	1	2
Cis festivus	14	5	1	*Synchita humeralis*	46	30	2
Choragus sheppardi	78	1	1	*Xyloterus signatus*	6	42	2
Cis nitidus	1	1	1	*Abdera flexuosa*	9	3	3
Conopalpus testaceus	115	6	1	*Anaspis humeralis*	70	12	3
Dryocoetes villosus	4	2	1	*Anaspis maculata*	243	113	3
Enicmus testaceus	1	7	1	*Anaspis rufilabris*	162	76	3
Ennearthron cornutum	29	1	1	*Anisotoma humeralis*	70	4	3
Mesosa nebulosa	5	1	1	*Cis micans*	3	5	3
Grammoptera ruficornis	30	7	1	*Crypturgus cinereus*	35	8	3
Grynobius planus	10	2	1	*Dromius quadrimaculatus*	34	10	3
Hypoganus inunctus	7	1	1	*Dryocoetes alni*	143	73	3
Lissodema quadripustulatum	19	2	1	*Dryocoetes autographus*	5	46	3
Malachius bipustulatus	4	2	1	*Hedobia imperialis*	88	14	3
Mycetochara linearis	2	4	1	*Litargus connexus*	7	17	3
Phymatodes testaceus	2	1	1	*Melanotus rufipes*	5	23	3
Pityophthorus pubescens	101	4	1	*Pyrochroa coccinea*	1	3	3
Ptilinus pectinicornis	429	8	1	*Pyrochroa serraticornis*	7	4	3
Rhagium bifasciatum	4	2	1	*Rhagium mordax*	6	19	3
Saperda scalaris	4	2	1	*Rhinosimus ruficollis*	1	16	3
Xestobium rufovillosum	2	1	1	*Strangalia melanura*	1	29	3
Anobium nitidum	240	44	2	*Strangalia quadrifasciata*	30	13	3
Anthribus albinus	7	2	2	*Xestobium plumbeum*	66	4	3
Cerylon fagi	1	1	2	*Xyloterus domesticus*	10	38	3
Cerylon histeroides	3	5	2	*Ampedus pomorum*	29	75	4
Clytus arietis	10	2	2	*Anaspis frontalis*	51	485	4
Dromius spilotus	3	3	2	*Cerylon ferrugineum*	18	33	4
Leiopus nebulosus	42	6	2	*Cis pygmaeus*	1	10	4
Leptura rubra	16	8	2	*Dasytes aerosus*	23	11	4
Mordellochroa abdominalis	3	3	2	*Dasytes plumbeus*	145	1,628	4
Nemosoma elongatum	14	15	2	*Denticollis linearis*	48	83	4
Orchesia micans	24	11	2	*Ernoporicus fagi*	273	36	4
Orchesia undulata	15	2	2	*Hylurgops palliatus*	4	142	4
Phloiotrya rufipes	11	3	2	*Lygistopterus sanguineus*	9	51	4
Ptinus rufipes	2	7	2	*Mordella holomelaena*	7	29	4
Rhizophagus dispar	3	4	2	*Rhinosimus planirostris*	67	241	4
Scaphisoma boleti	6	8	2	*Rhizophagus bipustulatus*	24	49	4

approximately the same as in small old stands. Similä et al. (2003) stressed the importance of the continuity of dead wood in semi-natural stands for the persistence of saproxylic beetles and found this more important than the total amount of dead wood. Other studies obtained no relationship between continuity indicator species for unbroken input of dead wood and species richness, while single species were positively correlated with the abundance of indicator species (Sverdrup-Thygeson 2001).

The spatial pattern of forests in a landscape also influences the species richness of saproxylic species. Gibb et al. (2006a) supposed that a distance shorter than 100 m between coarse woody debris within a forest has no effect on the dispersion of early succession saproxylic beetles, but the availability of suitable habitats at a scale of 1–10 km was important for the survival of many saproxylic species. According to their investigation, red-listed species had a more localised distribution than other species. This might

Table 3 Results of the multifunctional ANOVA using abundance classes of emergence traps (EC) and dispersion classes (DC) to explain mean abundance in flight-intercept-traps

Emergence classes	Dispersion classes	*n*	Flight intercept abundance (ln)
1	1	5	0.58^{1}
2	1	1	0.68^{1}
3	1	9	0.83^{1}
1	2	2	1.19^{1}
4	1	13	$1.33^{1,2}$
2	2	6	$1.53^{1,2,3}$
2	3	7	$1.89^{1,2,3,4}$
4	2	14	$2.07^{1,2,3,4}$
3	2	10	$2.10^{1,2,3,4}$
3	3	11	$2.64^{2,3,4}$
1	3	3	$2.65^{3,4}$
4	3	15	$3.04^{4,5}$
2	4	8	$3.63^{4,5,6}$
1	4	4	$3.65^{4,5,6}$
3	4	12	$4.12^{5,6}$
4	4	16	5.49^{6}

Homogenous groups are indicated by the same exponents

n number of species by class

be the reason for the low fraction of poorly mobile species in the different woods investigated here, although they mainly contributed to total species richness.

Colonisation probability by beetles depends on a variety of factors: flight ability, density of populations, age of woods, character of habitats between woods, and size of woods (Jonsell et al. 1999). Dispersal ability also depends on different preconditions and can vary within a population, e.g. fewer individuals of *Oplocephala haemorrhoidalis* had flight muscles than of *Bolithophagus reticulates* which induced higher site constancy in the first species (Jonsson 2002). Furthermore, 75 and 60% of *Osmoderma eremite* and *Lucanus cervus*, respectively, were found not disperse from the tree hole or stump where they developed (Ranius and Hedin 2001; Rink 2006). However, once flying saproxylic beetles can travel large (Rink 2006; Hedin and Ranius 2002). Our approach to determine the dispersion ability using distances between woods and records by flight-intercept-traps certainly does not reflect the absolute dispersal ability of the species, but it shows the minimum distance that species can cross open grassland. It was not the aim of the investigation to study the dispersion ability of saproxylic beetles, but to compare species in their relative dispersion ability. This can be seen by the abundance pattern of species in the two trap types. Whereas a majority of species was found in higher abundance in emergence traps than in flight-intercept-traps, a number of species showed the opposite abundance relationship between the two trap types. The latter were rarely found in emergence traps, but frequently found in flight-intercept-traps, indicating high mobility. According to our results the abundance of species in the flight-intercept-traps can be mainly explained by the dispersal ability of the species because only 11% of abundance in the flight-intercept-traps is explained by the abundance of species in the different wood stands. Furthermore, if distance classes and emergence classes that represent the abundance of the species in the wood stands are analysed according to their effect on the abundance in the flight-intercept-traps, the effect of the distance classes was higher than the effect of emergence classes.

In our investigation, large and young wood stands had nearly the same fraction of low mobile species as large and old wood stands. Small and old wood stands revealed an intermediate level between small young woods and large old woods for low mobile species. The most mobile species were the more common species in all wood stands, but as small young stands exhibited only a low number of low mobile species, the percentage of the most mobile species increased in this size class.

Saproxylic beetles are of conservation concern in Central European forests because they account for a high percentage of the endangered species in forested areas. In this respect old forests or old trees are mostly the focus of conservation effort as they provide the most species rich locations for endangered saproxylic species. Our investigations document that age and size of forests are important

Table 4 Percent of low and high mobile saproxlic beetle species detected in emergence traps of wood stands differing in size and age

Area	EA	Age									
		n	Low mobile		High mobile		*n*	Low mobile		High mobile	
			<130 years		<130 years			>130 years		>130 years	
			m	SD	*m*	SD		*m*	SD	*m*	SD
<10 ha	1.15	18	20.9	11.4	59.5	11.6	3	25.8	11.3	44.2	11.5
>10–100 ha	1.37	12	28.5	13.9	49.5	12.9	8	26.3	10.5	55.8	13.2
>100 ha	1.87	2	30.8	12.3	39.6	0.6	13	32.5	10.0	50.8	17.6

EA effect of age as co-variable, *n* number of samples, *m* mean, *SD* standard deviation factors for colonisation by low mobile species for which crossing non-forest areas appears to be an obstacle to colonisation. Colonisation of reforested woods by specific low mobile insect groups like ants is also slow (Dekoninck et al. 2008). According to our investigation low mobile species reach their highest richness in forests larger than 100 ha and older than 130 years. Our results indicate that the long process of colonisation for the low mobile species can be accelerated by forest size. Reforestation policies should therefore take this into account.

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