2. Species change in an urban setting – ground and rove beetles (Coleoptera: Carabidae and Staphylinidae) in Berlin

Abstract - The influence of environmental parameters on epigeic beetle communities of forest fragments in an urbanization gradient was studied in Berlin. Eight deciduous forests along a rural to urban gradient were sampled with pitfall traps. Species richness did not decline across the rural to urban gradient. As expected, impervious surface cover as an indicator of urbanization correlated not only with habitat fragmentation and heat island effect but also with altered soil properties. The proportion of forest specialist staphylinid species decreased with increasing urbanization. The differences between staphylinid communities of neighboring forest fragments were enhanced in the most urban parts, probably due to increased habitat fragmentation. Furthermore, the loss of flightless species with increasing habitat isolation emphasized the influence of habitat fragmentation. The carabid communities revealed the urbanization effects not as clearly as the staphylinid communities, but both taxa revealed that direct anthropogenic habitat alteration, indicated by removal of decaying wood, favors open-habitat specialists. The extent of the urbanization influence seems to vary seasonally. Environmental parameters associated with urbanization explain the ordination of species communities in the winter better than in the summer. Heat island effect is suggested as an explanation for this difference.

INTRODUCTION

With an estimated 2.4 billion people living as urban citizens in 1995 and this number expected to double by 2025 (Anthrop, 2000), cities serve primarily as human habitats. However, many other native and non-native organisms share this habitat. Dense street clusters, sealed parking lots and built-up areas, fallow lands, wastelands, and differently managed green spaces, including natural habitats

such as woods and bodies of water contribute to a rich variety of habitat types in urban areas. This mosaic habitat structure, but also the greater number of exotic species are reasons for the increased floristic richness in urban habitats (Tonteri and Haila, 1990; Kühn et al., 2004).

Nevertheless, it is the dense human population which defines urban spaces. Human activities affect natural habitats intensively in cities. Direct impacts include the reduction of habitat size, as well as disturbance, modification, and degradation of habitats. Additionally, indirect effects such as climatic change, introduction of non-native species, and environmental pollution contribute to changes in habitat quality. Gradient analysis along a rural-urban transect offers a good opportunity to obtain a better understanding of the mentioned anthropogenic influences on remnants of natural habitats in the urban context (McDonell et al., 1997; Niemelä et al., 2000).

This study was part of the interdisciplinary postgraduate research and study program "Perspectives on Urban Ecology - the Example of the European Metropolis of Berlin" which investigated the interrelations between non-biotic and biotic components of the urban ecosystem using a gradient analysis approach. Research was conducted in a transect from the center of Berlin to its south-eastern suburbs. It focused on the mechanisms of maintaining biodiversity in urban areas and unfolding its ecological significance in the urban environment. The objective of the study presented in this paper is to improve the understanding of urbanization effects on the biodiversity and community structure of epigeic beetle communities in deciduous forests.

Several authors reported a decline in epigeic species richness in forests along a rural to urban gradient (Schaefer and Kock, 1979; Davis, 1982; Ishitani et al., 2003; Magura et al., 2004; Weller and Ganzhorn, 2004). But these results do not reflect a general pattern (Niemelä et al., 2002; Alaruikka et al., 2003). However, the community structure changed in almost all of these case studies.

Urbanization influences several landscape properties, but not all of them to the same extent. This complicates the quantification of the urbanization (McDonell et al., 1997). So far, most studies on the influence of cities on epigeic invertebrates communities used the degree of urbanization, classified in three

classes (urban, suburban, rural), a dummy variable which was tested for correlations with different community properties. I think that splitting this complex variable into single components such as impervious surface cover, habitat structure, habitat fragmentation, and heat island effect will improve the understanding of the mechanisms of species change in the urbanization gradient.

Impervious surface cover is one of the primary characteristics of urbanization (Arnold and Gibbons, 1996). It influences secondary factors such as urban climate (Landsberg, 1981) and habitat patterns. Therefore, impervious surface cover was preferred to distance from the city center as the indicator of urbanization in this study.

Habitat structure in urban forests is altered due to not only the management of green spaces but also the increased usage for recreational purposes, which results for instance in a higher trampling intensity (Grandchamp et al., 2000). Other habitat structure properties such as the density of decaying wood and the change in soil characteristics probably influence the composition of epigeic beetle communities too.

Habitat fragmentation is one of the main influences on the community structure in patchy habitats (Niemelä, 2001; Tscharntke and Brandl, 2004). Edge effects, fragment size and habitat isolation contributed to this change (Mader, 1980; Halme and Niemelä, 1993). Several studies focused on the fragmentation effects on epigeic arthropods in urban areas but most of these studies neglected the partial effect of habitat structure alteration (Faeth and Kane, 1978; Miyashita, 1998; Bolger et al., 2000; Gibbs and Stanton, 2001; Weller and Ganzhorn, 2004). I incorporated both the effects of habitat fragmentation and the effects of habitat structure alteration as recommended by Gibb and Hochuli (2002). Habitat fragmentation influences habitat specialists and species that can survive in the neighboring habitats as well in different ways. Therefore, they must be treated independently in an analysis (Magura et al., 2001).

Altered climatic conditions obviously influence the urban flora (Hupfer and Chmielewski, 1990), but their effects on invertebrates have rarely been reported. Furthermore, the effects of climatic change on the species composition may differ between the summer and winter seasons. The heat island effect may be

more important in the winter. The freezing period, which is a critical factor for many arthropods (Vernon and Vannier, 2002), is approximately 30% shorter in the city than in the periphery and the minimal winter temperature can be up to 10°C higher (Landsberg, 1981).

Carabidae and Staphylinidae are the most abundant litter and soil surface dwelling beetle taxa in central Europe. Carabidae are valuable ecological indicators; they are taxonomically and ecologically well known and they are sensitive to environmental variation (Thiele, 1977). They have been widely studied in relation to habitat characteristics (Desender et al., 1994; Szyszko et al., 2002). Epigeic staphylinid beetles can be obtained by the same trapping procedure as carabid beetles. Staphylinid species can be found throughout the whole year and exhibit a greater species richness in wooded habitats than carabid beetles. Therefore staphylinid beetles were also incorporated in this study although the knowledge about their ecology is much more limited.

In particular, I analyzed the species change in a rural-urban gradient in Berlin to assess the following hypotheses: (1) Species richness decreases with urbanization. (2) Habitat degradation increases with urbanization and forest specialist beetles are most sensitive to this change. (3) Habitat fragmentation increases with urbanization. Beetle communities of smaller habitat patches tend toward an ecotone community structure with higher numbers of openland species due to increased edge effects. Habitat isolation has a negative impact on species with low dispersal ability. (4) The urban heat effect influences the species which are active in the winter in particular.

MATERIALS AND METHODS

Eight forests were selected along a rural to urban transect in southeastern Berlin, the largest city in Germany (fig. 1). The most central sites, Hasenheide (W8), Wildenbruchplatz (W7), and Treptower Park (W6) are managed parks,
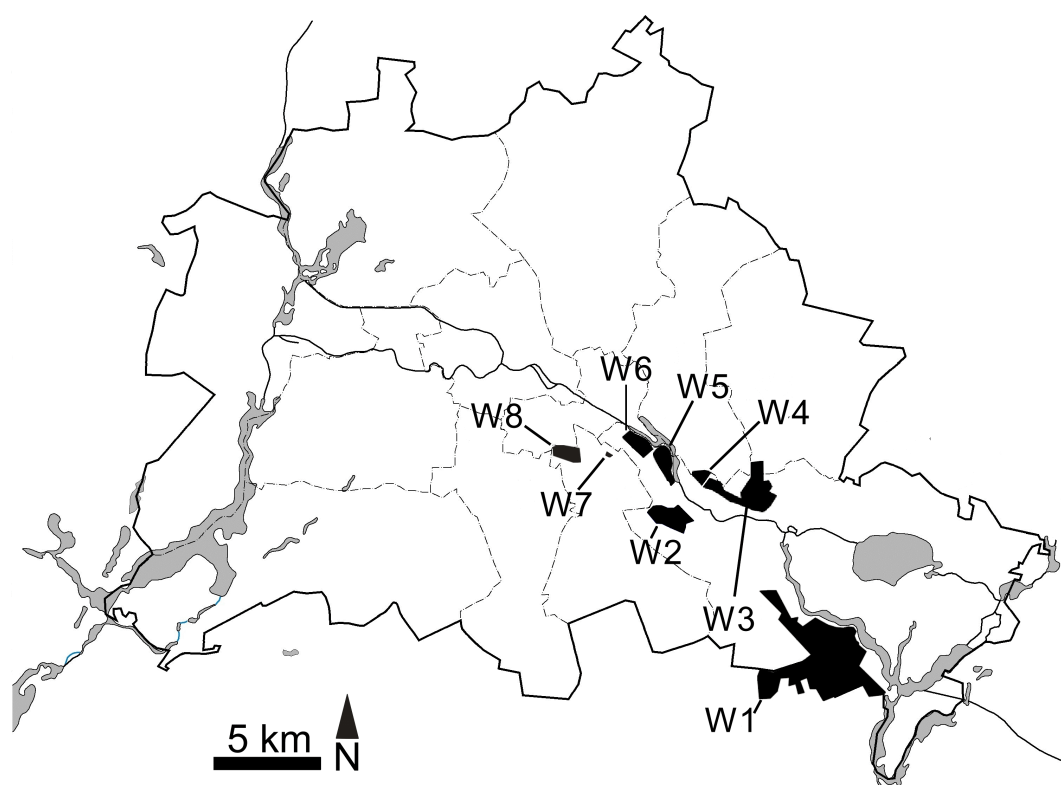
Figure 1. Location of the sampled woods in Berlin. Light gray: bodies of water; black: sampled woods. W1 – close to Karolinenhof; W2 – Königsheide; W3 – Eastern Wuhlheide; W4 – Western Wuhlheide; W5 – Plänterwald; W6 – Treptower Park; W7 – Wildenbruchplatz; W8 – Hasenheide.

including open habitats such as lawns. The Plänterwald (W5) borders on the Treptower Park but is not managed as a park. The Wuhlheide is a large forest which also includes managed park-like areas. Two sampling sites separated by a street with 4 lanes were selected here (W4, W3). The Königsheide (W2) is the largest unfragmented forest in the urban part of the transect. The most peripheral site is a forest situated close to Karolinenhof (W1) and bordering on the River Dahme. All woods except the small park W7 are mixed deciduous stands dominated by native oaks (*Quercus robur* and *Quercus petraea*). The tree composition of W7 is dominated by exotic tree species such as *Quercus rubra* or *Acer saccharinum*. The size of the study sites ranged from 2 ha (W7) to 1222 ha (W1).

At each site five pitfall traps (diameter: 6 cm), partly filled with saturated sodium chloride solution and a drop of detergent, were set up in a row approximately 10 m apart. The traps were covered with a 1-cm mesh grid to

prevent small vertebrates from entering the trap. A roof was not used – in the city it would attract the attention of passers-by, who might destroy the traps. Moreover, roofs were dispensable due to sampling frequency and low precipitation. In the parks the traps were positioned in least managed areas that appeared most natural. The traps were operated continuously from November 2002 to September 2003 and all were emptied on the same day at least every two weeks. The catch was preserved in 70% ethanol and sorted in the lab. Rove beetles (Staphylinidae: Coleoptera) and ground beetles (Carabidae: Coleoptera) were identified (to species level) using standard determination keys.

The species were classified into four categories: (1) forest species and eurytopic species more abundant in forests, (2) eurytopic species without habitat focus, (3) openland species and eurytopic species more abundant in openland habitats and (4) a few species that could not be classified. Sources with a regional background (Korge, 1991; Barndt et al., 1991) was used for this classification, because ecological range may vary between different regions.

The flight ability of each species caught was verified by using the available literature (Basedow et al., 1990; Barndt et al. 1991; Assing, 1992; Irmler, 1998; Markgraf and Basedow, 2002), by examining my own collection, by studying www-reports on catches with insect-nets mounted on cars, and through interviews with specialists (H. Korge, V. Assing).

Forest area and perimeter were determined from digital topographical maps (1:50000) published by the topographical agency of the federal state Brandenburg for each sampling site. Edge effects are more important in smaller areas but also in areas with an irregular shape because the proportion of unaffected core area decreases (Laurence and Yensen, 1991). Sampling sites were ranked according to the remaining core area. Although the core area cannot be calculated without knowledge about the width of the edge zone, the core area calculation according to Laurence and Yensen (1991) with different arbitrarily chosen edge width values showed that the rank order of the sampling sites did not change with the edge width.

The impervious surface cover around the sampled habitat patches was estimated within 500 m of the boundary of the habitat. The impervious surface

cover map from the data base: Berlin Urban and Environmental Information System (UEIS, 2005) was analyzed using the software Multispec (Landgrebe and Biehl, 2005). Due to the data quality mean impervious surface cover could be calculated as a range only. The upper bound was used in the analysis (the lower bound yielded similar results).

The density of decaying wood structures (branches thicker than 5 cm or tree stumps), which are important habitat structures for instance as overwintering sites, was estimated using the point-centered-quarter-method (PCQ: Mueller-Dombois and Ellenberg, 1974). PCQ was also used to measure the distance between the borders of the sampling sites and the borders of the nearest habitat patches of wood as an indicator of habitat isolation. The adjacent sites W3 and W4 as well as W5 and W6 were united for this calculation. The thickness of the humus layer was measured once close to each trap. At the same time two litter samples were taken randomly with a 15 cm core sampler close to each of five traps, dried (24 h at 80°C) and the leaf litter was weighed after removal of twigs. The mean of humus thickness and leaf litter amount for each sampling site was used in the analysis. Both values influence epigeic beetles because most of them are part of the decomposition food web which depend on the resources of their prey indirectly. Furthermore, humus and litter layers are the microhabitats of larvae and imagines (Coleman et al., 2004). Soil properties were measured in January 2005, assuming that the change in soil properties was negligible since the beetle sampling. Mean annual air temperature, as an indicator of the heat island effect, was taken from the data base Berlin Urban and Environmental Information System (UEIS, 2005).

Changes in the composition of the staphylinid and carabid communities across the transect were examined using hierarchical cluster analysis based on a non-weighted pair-group average algorithm with the Jaccard index.

In addition to species richness, rarefaction was used to estimate the species diversity at the different sites because differences in trapping efficiency could bias the number of species detected (Gotelli and Colwell, 2001). Rarefaction yields comparable species accumulation curves which were used to rank the different assemblages (Magurran, 1988). Rarefaction curves were calculated with

the program EstimateS (Colwell, 2004). Subsequently, Spearman rank correlation was used to assess the relationship between species diversity and the impervious surface cover around the sites as a indicator for urbanization but also the other environmental parameter measured.

To examine the hypothesis that forest species are most sensitive to urbanization, Spearman rank correlation between the percentage of forest species of both taxa and impervious surface cover was calculated. Density of decaying wood was assumed to be an indicator for habitat quality which is affected by urban landscape management. It was tested whether or not forest and open-habitat species percentage were correlated with this indicator. Percentage species was used in this analysis and the next analysis because it may reflect sensitivity to urbanization respectively habitat fragmentation of an ecological group relative to other groups.

Spearman rank correlation was also applied to investigate the relationship between habitat fragmentation parameters and fauna. First it was tested whether a statistically significant correlation existed between habitat patch size respectively core area adjusted for edge effects and proportion of openland species. Accordingly, the correlation between habitat isolation and number of flightless species was tested for statistical significance.

Finally, indirect gradient analysis was used to discriminate seasonally different responses of the community structure to environmental variation. Therefore, detrended correspondence analysis was applied using the community ecology package (Oksanen et al., 2005) of the statistical software R (R Development Core Team, 2005). Subsequently, environmental vectors (impervious surface cover, core area, habitat isolation, decaying wood density, humus thickness, leaf litter density, mean annual air temperature) were fitted to this ordination using the function "envfit" of the same software package. This function finds directions in the ordination space towards which the environmental parameters change most rapidly. The significance of the fitted vectors was assessed using 1000 permutations of the environmental parameters (Oksanen et al., 2005). In contrast to a direct gradient analysis like canonical correspondence analysis this

procedure is not influenced by a priori assumptions about the influence of environmental gradients.

The dataset was divided into a winter (November-March) and a summer part (April-September), integrating spring and autumn. The limits of the two parts were set when the activity of autumn and winter species decreased and the activity of spring and summer species increased and vice versa. The datasets included the square-root-transformed numbers of caught individuals of the different species in each of the nine sites. Species were omitted if they were caught with only one individual per site in the entire dataset.

All statistics except otherwise stated were calculated with STATISTICA (StatSoft, 2001).

RESULTS

Altogether 47 carabid beetle species (919 individuals) and 92 staphylinid beetle species (2111 individuals) were collected across the Berlin rural-urban
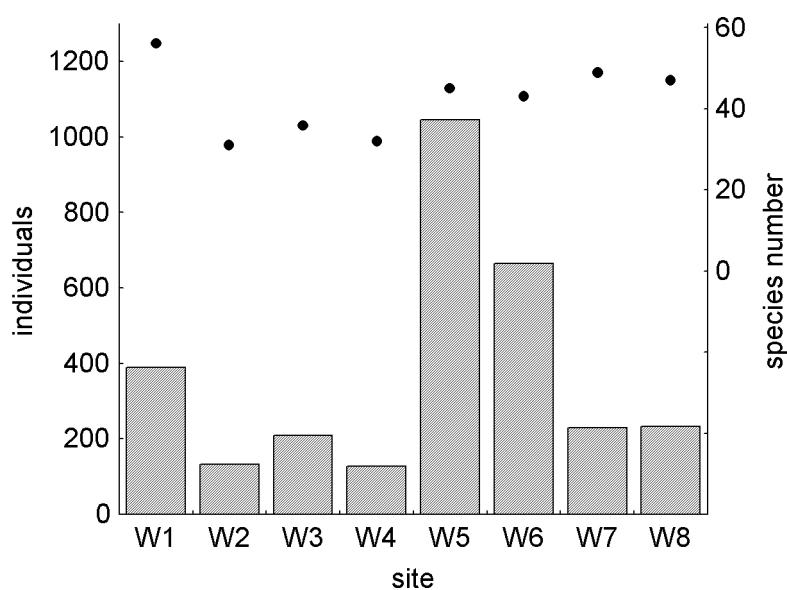

Figure 2. Differences in beetle catch (bars represent beetles per sampling site) and species richness (circles) between eight forest sampling sites across a rural-urban gradient in Berlin.

gradient (appendices 1 and 2). Species richness was highest in the most rural sampling site W1 (fig. 2). The highest number of individuals was captured at W5. The most abundant species were the staphylinid species *Philonthus decorus* (20.5% of total catch) and *Tachinus signatus* (14.4%). The most abundant carabid species was *Nebria brevicollis* (5.0%).

The hierarchical cluster analysis showed that communities from adjacent sites grouped together in most cases. The staphylinid communities of the adjacent sites W3 and W4 did not group together like the carabid communities. Staphylinidae communities showed a high dissimilarity in the city center which declined towards the periphery, whereas Carabidae communities followed a different pattern. The sites closest to the rivers Spree and Dahme (W1, W5, W6) were more similar to each other than to the other sites which form another cluster excluding W2. The latter had the smallest number of captured carabid individuals and was very different from the communities at the other sites (fig. 3).

Significant positive correlations were found between urbanization indicated by the mean impervious surface cover around the sampling sites and isolation ($R=0.80$, $p=0.02$), mean annual air temperature ($R=0.94$, $p<0.001$) as well as litter amount ($R=0.73$, $p=0.04$). Humus thickness decreased with increasing urbanization ($R=-0.83$, $p=0.01$). The density of decaying wood was lowest in the most urbanized park and highest in the most rural forest (fig. 4), but the
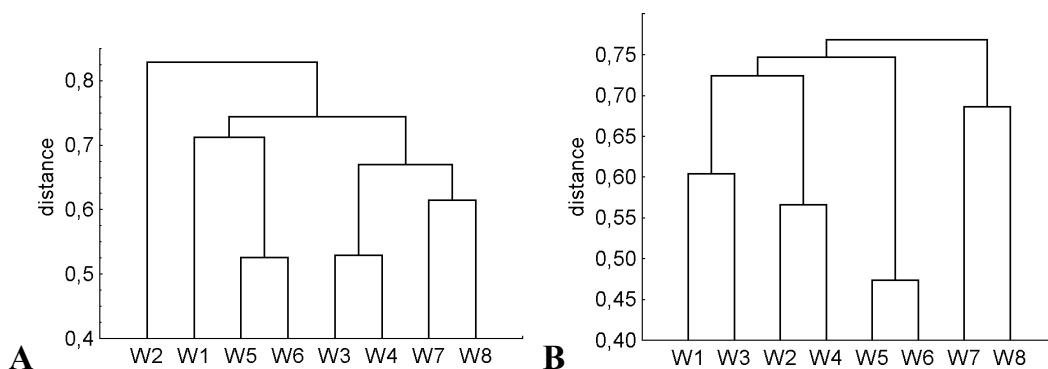

Figure 3. Cluster trees based on fauna similarity (Jaccard index) for (A) Carabidae and (B) Staphylinidae from epigeic beetle communities in eight forests across a rural-urban gradient (W1-rural to W8-urban) in Berlin.
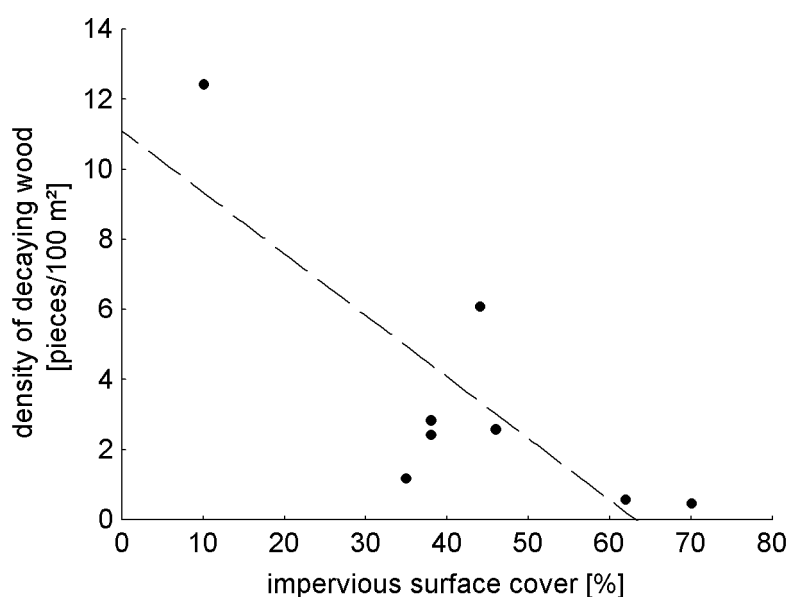
Figure 4. Relationship between urbanization indicated by impervious surface cover and density of decaying wood in eight forests across a rural-urban transect in Berlin.

Spearman rank correlation narrowly missed statistical significance (R=-0.62, p=0.10). Neither species number nor species richness rank after rarefaction were correlated with one of the measured environmental parameters.

The proportion of forest staphylinid species in the communities decreased with the impervious surface cover (R=-0.93, p<0.001), whereas the forest carabid species proportion did not show this pattern. The proportion of forest carabid species was highest at the site W5 and W6 with an intermediate impervious surface cover (fig. 5A). The number of open-habitat carabid beetles (R=-0.93, p=<0.001) as well as staphylinid beetles (R=-0.71, p=0.047) increased with decreasing density of decaying wood (fig. 5B), but the number of forest specialists did not decrease with decreasing density of decaying wood (fig. 5C).

The hypothesis that the habitat fragmentation influences the species composition of the epigeic beetle assemblages was supported only in some points. That openland species should be more present in species assemblages of small habitat patches was not supported by the data. Neither sampling site area nor core area size were correlated with the percentage of openland species (figure 5D), but Carabidae and Staphylindae followed the same pattern with very low percentages of openland species at W 4, W5, and W6. The number of flightless

species decreased as patches became more isolated (R=-0.90, p=0.01). Nine of the caught species were classified as always flightless: the carabid species *Calathus micropterus*, *Carabus nemoralis*, and *Stomis pumicatus* and the staphylinid species *Astenus gracilis*, *Drusilla canaliculatus*, *Ocypus brunnipes*, *Ocypus melanarius*, *Oxypoda praecox*, and *Xantholinus tricolor*. Three of these were widespread across the transect: *Carabus nemoralis* occuring at all
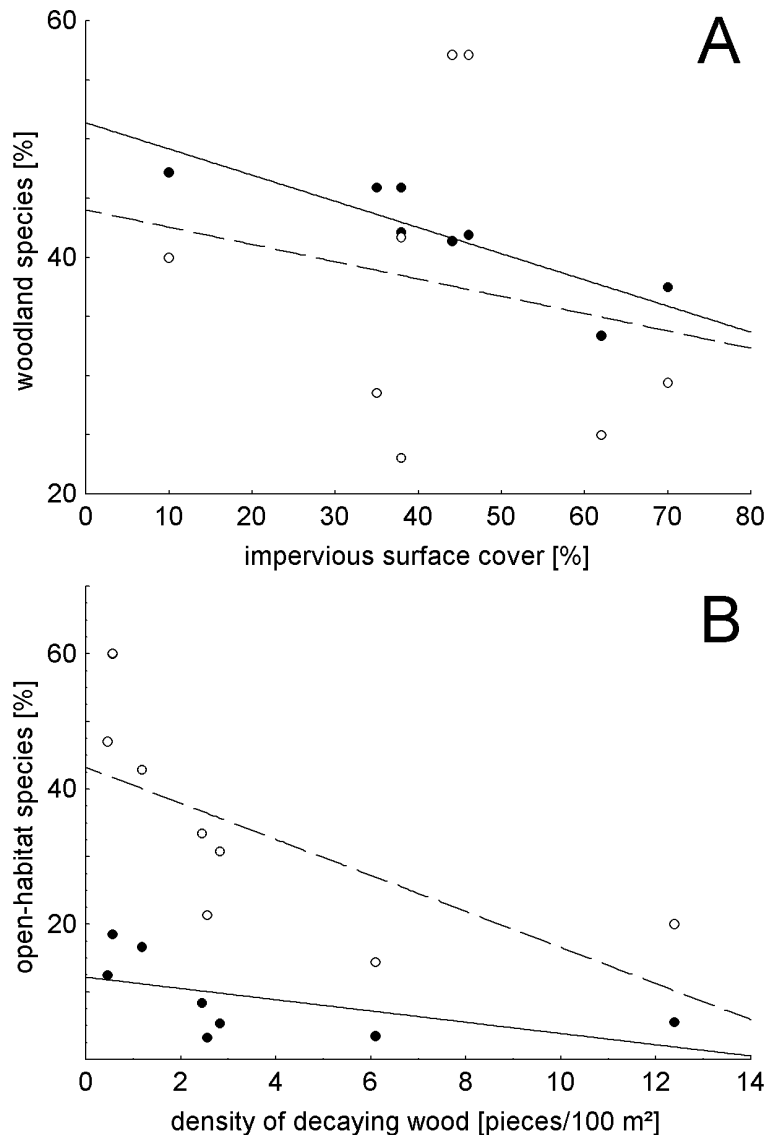

Figure 5. Relationships between impervious surface cover and percentage of forest species (A), between density of decaying wood and percentage of openland species (B) respectively forest species (C) and between habitat area and percentage of openland species (D). All graphs for Staphylinidae (closed circles) and Carabidae (open circles).
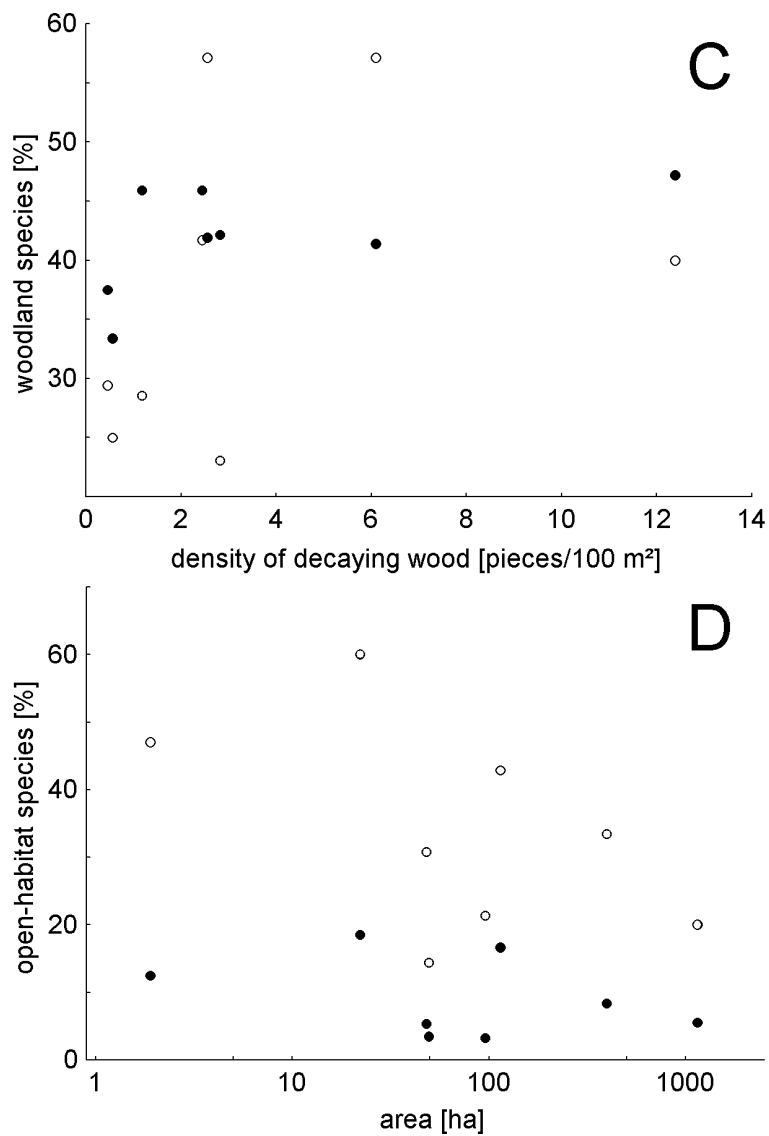
Figure 5 (continued). Relationships between impervious surface cover and percentage of forest species (A), between density of decaying wood and percentage of openland species (B) respectively forest species (C) and between habitat area and percentage of openland species (D). All graphs for Staphylinidae (closed circles) and Carabidae (open circles).

investigated sites; *Drusilla canaliculatus* at W1, W2, W4, and W8; and *Ocypus brunnipes* at W4, W5, and W8. Most flightless species occurred only at the peripheral sites W1 and W2 (fig. 6).
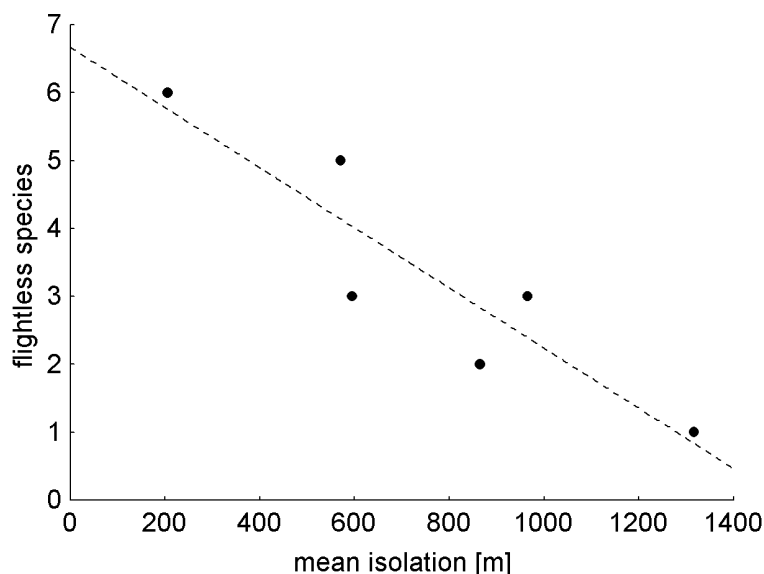
Figure 6. Relationship between habitat isolation and number of flightless species in epigeic beetle communities of forests across a rural-urban transect in Berlin. The sampling sites W3 and W4 respectively W5 and W6 were united as adjacent sites for this analysis.

The first axis of the ordination plot for the summer data accounted for 45.3% of the species variance, the second axis for 21.1%. The first axis of the ordination plot for the winter data accounted for 37.3% of the species variance, the second axis for 15.4%. The most common species, e.g. *Carabus nemoralis*, *Notiophilus biguttatus*, or *Nebria brevicollis*, grouped around the origin (fig. 7). The sampling sites W5 and W6, which formed a cluster with high similarity in the cluster analysis (fig. 3) were also close to each other in both ordination plots, but were more separated from the other sites in the summer than in the winter (fig. 7). The characteristic distinctness of the most peripheral site W1 was revealed by both ordination plots. A thick humus layer characterized the soil at the sampling sites W2 and W4. The ordination of the winter beetle communities separated these sites from the others (fig. 7B).

In contrast to the results from the direct correlation between the different environmental properties of the sites, the species ordination plots showed that the environmental parameters habitat isolation, habitat area, mean annual air temperature, impervious surface cover, and density of decaying wood seem to form a single gradient. Another gradient was represented by the soil properties humus thickness and litter amount. The different orientation of these two

gradients was more pronounced in the winter plot. The correlation of the environmental vectors with the summer ordination plot had weak statistical
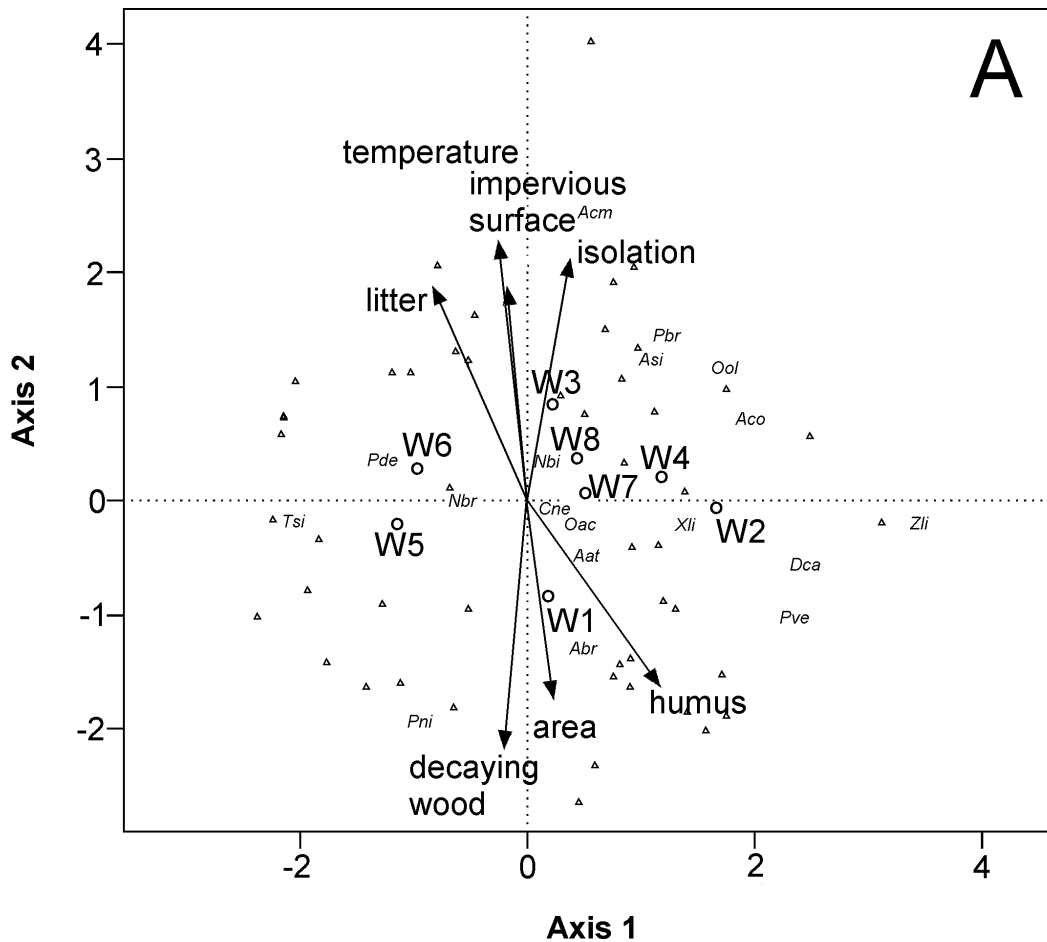

Figure 7. Ordination diagrams of the first two axes of detrended correspondence analyzes for epigeic beetle communities from eight forests (W1-W8) across a rural-urban gradient in Berlin during the summer (A) and the winter season (B). The arrows represent environmental gradients fitted to the ordination space. Species that made up 50% of all collected individuals are abbreviated, the other species are drawn as triangles. Aat - *Anthobium atrocephalum*, Abr - *Amara brunnea*, Acm - *Amara communis*, Aco - *Amara convexior*, Acr - *Acidota cruentata*, Asi - *Amara similata*, Cne - *Carabus nemoralis*, Dca - *Drusilla canaliculata*, Nbi - *Notiophilus biguttatus*, Nbr - *Nebria brevicollis*, Oac - *Oxypoda acuminata*, Oba - *Ocalea badia*, Omy - *Othius myrmecophilus*, Ool - *Ocypus olens*, Opu - *Othius punctulatus*, Pbr - *Plataraea brunnea*, Pde - *Philonthus decorus*, Pni - *Pterostichus niger*, Pve - *Poecilus versicolor*, Qsc - *Quedius scintillans*, Tob - *Trechus obtusus*, Tsi - *Tachinus signatus*, Tsu - *Tachinus subterraneus*, Xli - *Xantholinus linearis*, Zli - *Zyras limbatus*.
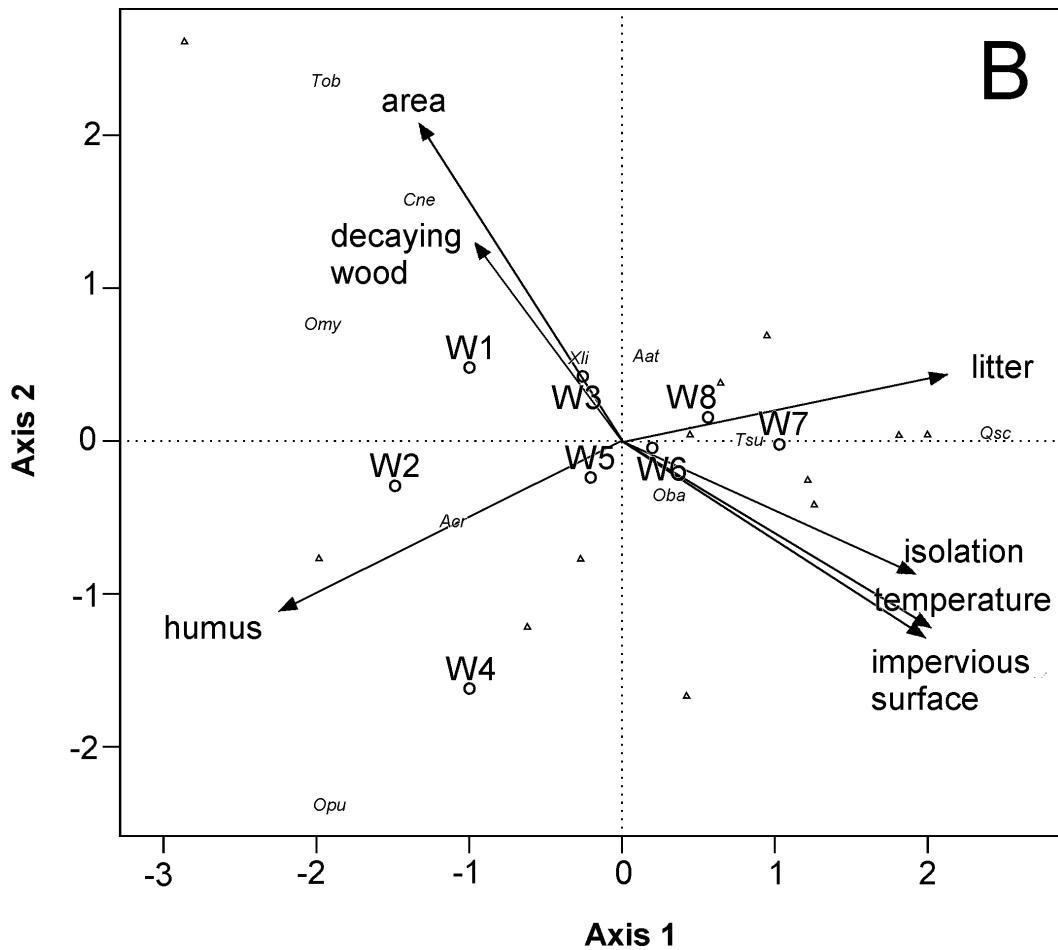
Figure 7 (continued). Ordination diagrams of the first two axes of detrended correspondence analyzes for epigeic beetle communities from eight forests (W1-W8) across a rural-urban gradient in Berlin during the summer (A) and the winter season (B). The arrows represent environmental gradients fitted to the ordination space. Species that made up 50% of all collected individuals are abbreviated, the other species are drawn as triangles. Aat - *Anthobium atrocephalum*, Abr - *Amara brunnea*, Acm - *Amara communis*, Aco - *Amara convexior*, Acr - *Acidota cruentata*, Asi - *Amara similata*, Cne - *Carabus nemoralis*, Dca - *Drusilla canaliculata*, Nbi - *Notiophilus biguttatus*, Nbr - *Nebria brevicollis*, Oac - *Oxypoda acuminata*, Oba - *Ocalea badia*, Omy - *Othius myrmecophilus*, Ool - *Ocypus olens*, Opu - *Othius punctulatus*, Pbr - *Plataraea brunnea*, Pde - *Philonthus decorus*, Pni - *Pterostichus niger*, Pve - *Poecilus versicolor*, Qsc - *Quedius scintillans*, Tob - *Trechus obtusus*, Tsi - *Tachinus signatus*, Tsu - *Tachinus subterraneus*, Xli - *Xantholinus linearis*, Zli - *Zyras limbatus*.

support, whereas all environmental vectors except density of decaying wood were correlated significantly with the ordination space of the winter data (Table 1).

Table 1. Correlation between environmental vectors and ordination plots from detrended correspondence analysis for two seasonal aspects of epigeic beetle communities from forests across a rural-urban transect in Berlin.

environmental parameter	summer		winter	
	r^2	p	r^2	p
impervious surface cover	0.37	0.36	0.84	<0.01
area	0.32	0.42	0.90	<0.01
isolation	0.50	0.21	0.65	0.04
mean air temperature	0.55	0.17	0.83	<0.01
density of decaying wood	0.49	0.20	0.39	0.22
leaf litter amount	0.44	0.31	0.71	0.01
humus thickness	0.42	0.31	0.94	<0.01

DISCUSSION

The results of this study showed that urbanization had no effects on the species richness of epigeic beetle assemblages in forest fragments across a rural-urban gradient. However, the variation of the species composition of the epigeic beetle assemblages was partly related to the urbanization.

Some earlier studies described a decline in species richness with increasing urbanization (Niemelä et al., 2002; Ishitani et al., 2003; Weller and Ganzhorn, 2004) while other studies did not reveal such an effect (Klausnitzer and Richter, 1983; Alaruikka et al., 2003; Magura et al., 2004). Such differing conclusions might result from small differences. Niemelä et al. (2002) and Alaruikka et al. (2003) sampled the same rural-urban gradient with the same sampling effort in different years. Their conclusions differed due to five species each found only once that were not captured by Alaruikka et al. (2003) in the rural part. Thus, the

species number may be influenced also by other sources of variation, for instance the climatic variation.

A decreasing dominance of forest specialists in urban sites compared to rural sites was observed in almost all studies on rural-urban gradients. Staphylinid beetles followed this pattern in this study, but carabid beetles did not. The variation of forest carabid species number was very high at the intermediate level of impervious surface cover. Especially the sites W5 and W6 had many forest carabid species. A possible explanation for this peak might be a difference in the vegetation cover. W2 and W4 with few forest carabid species were more dominated by oaks than the forests W5 and W6 which were rich in forest carabid species. Nonetheless, this does not explain the great deviation from the other sampling sites.

The loss of decaying wood was the only indicator for habitat degradation by human management which was applied in this study. Open-habitat specialists might profit from management practices including the removal of decaying wood from urban parks as implied by the increase of such species with decreasing density of decaying wood. The opposite assumption, that forest specialists suffer from this kind of habitat alteration, was not confirmed. The loss of forest specialists across the rural-urban gradient as shown for the staphylinid beetles might be a result of other forms of habitat degradation such as trampling (Grandchamp et al., 2000), which are more directly associated with urbanization.

Habitat fragmentation, especially the size reduction of the patches, can favor open-habitat species in woodland habitats (Mader, 1980). Invasion of open-habitat species from the surrounding grasslands increases with the decreasing size of forest patches in rural environments (Halme and Niemelä, 1993; Usher et al., 1993). However, my study did not reveal clear evidence for such size-dependent effects. Neither the total area of the forest fragments nor the area after subtracting the edges probably affected by the surrounding area were correlated with the number of open-habitat species. Other studies found open-habitat carabid beetle species more frequently in urban forests compared to rural forests but gave no evidence that habitat size was the crucial factor (Irmler, 2001; Alaruikka et al., 2003).

Isolation influences carrion beetle species richness (Gibbs and Stanton, 2001), spider species richness (Miyashita et al., 1998), and carabid beetle species richness (Weller and Ganzhorn, 2004) negatively in urban areas. To understand isolation, one must consider both the hostility of the environment in which the habitat fragments are embedded (matrix habitat) and the organism's gap-crossing ability (Tscharntke and Brandl, 2004). High traffic density, built-up areas, and sealing of the soil seem to contribute to a high degree of isolation due to hostile matrix habitat. The increasing differences between the species composition of neighboring forests with increasing urbanization is an indicator of this effect. Staphylinid beetle communities revealed this pattern clearly in this study. The effect of the urban habitat hostility is particularly important for forest species. Czechowski (1982) studied the urban carabid beetle communities of Warsaw and found the highest dissimilarities between forest communities compared to other habitat types like allotment gardens or lawn greenery.

Focusing on species with restricted dispersal abilities, the effect of urban habitat isolation is much more enhanced. The number of flightless species depended on the isolation of the forests. Only three flightless species occured at the two most isolated sites in the city center. Two of these are comparably large species (*Carabus nemoralis* and *Ocypus brunnipes*). Larger species mostly have a higher walking speed (Klazenga and de Vries, 1994), which may partly compensate for the inability to fly.

Little is known about the seasonal variation of the response of epigeic beetle communities to urbanization. The small number of active species during the cold season is certainly one reason for this lack of knowledge. However, the results of my study suggest that the difference between the communities of urban and rural woods are more conspicuous in the winter season. All environmental parameters of the sampling sites that were correlated with urbanization e.g. habitat fragmentation, impervious surface cover, mean air temperature, and soil properties, could be fitted clearly to environmental gradients occurring in the winter ordination plot but not in the summer plot. As an observational and correlational study my gradient analysis cannot reveal a reason for this phenomenon, but I suggest that the heat-island effect is responsible for this

seasonal difference because it is more relevant in the winter. The differences in frost intensity and lowest winter temperature between rural and urban areas (Landsberg, 1981) might form a relevant gradient that influence the species composition strongly. In addition, the winter plot revealed that the effects of the urbanization gradient represented by the differences in impervious surface cover, habitat fragmentation, and mean air temperature differ from the effects of the soil gradient. In the correlation analysis both gradients were correlated, but this relationship seems to be artificial, especially in the case of leaf litter amount.

My study gave indications of the factors that may influence the species composition of epigeic beetles in urban forests. Instead of a uniform urbanization gradient, a complex interaction including the effects of habitat fragmentation, habitat alteration, and climatic change seem to influence the beetle communities. I suppose that additional properties such as the climatic differences between different sampling years, the variance in local habitat productivity (Shochat et al., 2004) as well as historical differences influence the species change too. Further research is needed to examine the influence of the history of the habitat fragments. The history of each forest fragment varies broadly not only within a particular city but also between cities. Differences in the age of a city as well as the type of urban development can be expected to affect the fauna of each local wooded habitat differently. Although area and isolation of a habitat patch might be similar in a spatial sense the effective isolation due to the history can differ. The integration of such effects might help us to understand contradicting results from different urban settings better.