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Comparative responses of spider and carabid beetle assemblages along an urban-rural boundary gradient

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Abstract. The urbanization process is the motor of deep environmental changes at both local and landscape levels. Although more and more studies are investigating the ecological consequences of urbanization, only a few have studied small-scale responses of biodiversity to urban-rural boundary gradients, and even fewer have compared different model groups synchronically. In this study, we compared the responses of two invertebrate groups often used as bioindicators, spiders and carabid beetles, along small-scale boundaries (around 1 km). The following parameters were estimated: assemblage composition, species richness, and activity-densities overall and per life history trait (habitat preference, dispersal abilities for carabid beetles and hunting guilds for spiders). The field data were collected in 2009 using pitfall traps set randomly in hedgerows within urban, boundary and rural zones (30 traps in total). 924 adult spiders belonging to 78 species were collected, whereas the 330 captured carabid beetles belonged to 25 species. We found no evidence of any significant change in carabid beetle activity-density (overall and for most life history traits) or in species richness along the urban-rural gradient. Conversely, there was a significant change in spider activity-density, both per habitat preference and per hunting guild. We also found a progressive change in community composition for spiders. Our results suggest that studying different model groups can provide complementary information about urbanization.

Keywords: Hedgerow, urbanization, habitat preference, trophic guild, dispersal abilities, Araneae, Carabidae

During the last decades the urban population has greatly increased, creating intensive urban areas and encroaching on adjacent rural areas (Douglas 1992; Fenger 1999; Weber 2003). Urbanization is defined as the installation process of anthropogenic structures (e.g., buildings, roads) in existing natural or farming areas, in order to satisfy human population requirements (Croci et al. 2008). According to this definition, the urbanization process is the motor of a deep modification in the environment. Urbanization affects energy flows, biochemical cycles, climate conditions, hydrology and soil properties (Breuste et al. 1998; Baker et al. 2002). This important land use change has a strong impact on biodiversity, and progressively more studies are examining the impact of urbanization. Currently, the main ecological questions are how species cope with the urban environment, pollution and the fragmentation of "natural habitats", and how this biodiversity is linked to the adjacent rural environment. Recent studies indicate that biodiversity is lower in urban environments than in agricultural landscapes (Niemelä 2009), with a decrease in both species richness and abundance in urban areas (Blair 1996, 1999; Clark et al. 2007; Clergeau et al. 1998; Denys & Schmidt 1998; Lehvävirta et al. 2006; McKinney 2002; Pacheco & Vasconcelos 2007; Sadler et al. 2006; Yamaguchi 2004). On this issue, the main bulk of recent research on invertebrates has concentrated on carabid beetles (Alaruikka et al. 2002; Niemelä et al. 2002; Ishitani et al. 2003; Gaublomme et al. 2008; Niemelä 2009). Until now, only a few studies have focused on spiders (Alaruikka et al. 2002; Magura et al. 2010).

Most of the information published to this day has considered long gradients (several km) from the center of the city to the rural areas, but it is not yet clear whether the changes are progressive along this gradient or if some sharp transitions occur between those two highly contrasted habitats. Transition zones between ecosystems (e.g., ecotones) may control the flow of energy, material and organisms between ecosystems. The functioning of the boundary is also one of the mechanisms that may explain biodiversity patterns (Di Castri & Hansen 1992). Most of the previous work hypothesized, for example, exchanges between rural and urban areas, rural areas being sources of individuals able to colonize the city. The aim of the present study is to investigate whether and how an urban-rural boundary will affect two groups of arthropods in a single habitat type (hedgerows) and over a short distance (around 1 km). Spiders and carabid beetles were selected as model groups because they are known to react strongly to changes in microhabitat conditions and therefore are often used as bioindicators (Marc et al. 1999; Bell et al. 2001; Luff et al. 1992; Rainio & Niemelä 2003; Pearce & Venier 2006).

In our research we tested the following hypotheses: 1) According to the conclusions of Alaruikka et al. (2002) spider and carabid beetle assemblages in urban areas differ in their responses to an urban-rural boundary. Spiders are expected to respond only slightly or not at all to the boundary, whereas carabid beetles are expected to respond strongly and suddenly to the boundary. 2) The urban environment selects for particular ecological traits (Blair 2001). In both groups, species from open habitats are expected to be more associated with urban areas due to a more open, mineralized environment. As the urban environment is composed of a hostile matrix, individuals with high capacity for (long-distance) dispersal are generally favored (Thiele 1977); more macropterous species of carabid beetles are therefore expected in urban habitats. The dispersal of spiders was not estimated since dispersal propensity is supposed to be a non-limiting factor in displacement and settlement for most species (e.g., Bell et al. 2005). As litter and vegetation structures in hedgerows are less complex in urban habitats (Frileux 2008), fewer web-building spiders and more cursorial spiders are expected there (Uetz 1979).

METHODS

Study sites and sampling design.—The study site was located at the boundary between urban and agricultural areas in Pacé (48°09′00″N, 01°46′00″W), a municipality of 8600 inhabitants located within the conurbation of Rennes (Brittany, France), which comprises 205,000 inhabitants. Sampling points were set in hedgerows, the main semi-natural structures in both areas, at five sites (with six sampling points per site), defined according to their distance to the boundary: two in the city (U1 and U2, respectively 0–150 m and 150–300 m from the boundary), one on the boundary (E) and two in the rural area (R1 and R2, respectively 250–450 m and 950–1150 m from the boundary) (Fig. 1). The percentage of asphalt cover was calculated by GIS (Geographic Information System) in a 100 m^2 perimeter around each site, and the percentage of plant cover was visually assigned to classes (0–1%,1–5%, 5–25%, 25–50, 50–75%, 75–100%). Soil water content and temperature were measured eight times at each site during the summer of 2009 using a W.E.T. sensor (5 cm deep) connected to a moisture meter HH2 (both by Delta-T Devices Ltd., Cambridge, UK). The percentage of asphalt cover decreased along the urban-rural gradient, whereas the percentage of plant cover increased along the same gradient (Table 1). Hedgerows were mostly oriented north/south, except those located at one urban site, which were oriented east/west. There was no effect of sites on other habitat characteristics (Table 1), indicating that conditions within hedgerows were similar in this respect.

Each sample point consisted of one pitfall trap (85mm diam.) covered with a plastic roof. The pitfall traps were filled with preservation solution composed of 50% monopropylen glycol 50% and 50% salt solution of 100 g/l (best fluid for collecting ground-dwelling spiders: Schmidt et al. 2006). The pitfall traps were emptied every two weeks for eight weeks between mid April 2009 and mid June 2009.

Species identification and classification.—Carabid beetles and spiders were preserved in 70% ethanol and stored in the University collection (Rennes, France). Adult carabid beetles were identified using Jeannel (1941, 1942) and Trautner & Geigenmüller (1987), whereas adult spiders were identified using Roberts (1987, 1995) and Heimer & Nentwig (1991). The nomenclature follows Lindroth (1992) for carabid beetles and Canard (2005) for spiders.

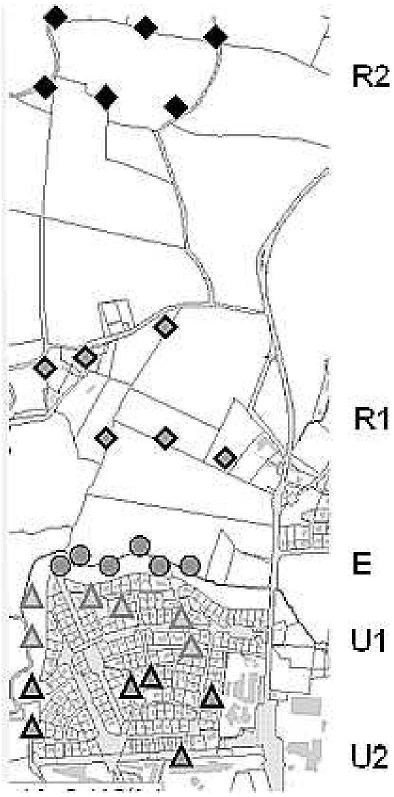

Figure 1.—Location of the sampling sites and traps in Pacé (Brittany, France). U2 (▲), U1 (▲), E (●), R1 (◆) and R2 (◆).

Catches in pitfall traps were linked to trapping duration and pitfall perimeter, in order to calculate an ‘activity trapability density’ (number of individuals per day and per meter: Sunderland et al. 1995), further abbreviated as ‘activity-density’. In order to analyze the community responses along the gradient, we studied species richness and total and per ecological trait activity-densities, as well as the assemblage composition (based on species activity-density).

Carabid beetles and spiders were classified into three classes of habitat preference using Hänggi et al. (1995), Harvey et al. (2002), Luff (1998) and Bouget (2004): forest species (species predominantly found in forest areas), open habitat species (species which occur predominantly in open habitats), other (species occurring in wet habitats and generalist species). The dispersal abilities of carabid beetles were estimated by the

Table 1.—Habitat characteristics of five sampling sites (percentage min and max of classes of herbaceous cover, mean (± SE) for litter depth, temperature and moisture).

	U2	U1	B	R1	R2
Asphalt cover (%)	48	50	12.5	4	0.5
Hedgerow exposition	N-NE/S-SW	E/W	N/S	N-NE/S-SW	N/S
Herbaceous cover (%)	1–5	5–25	25–50	25–50	25–50
Litter depth (cm)	0.83 ± 0.31	1.83 ± 0.56	1.08 ± 0.30	2.33 ± 0.56	1.25 ± 0.34
Temperature (° C)	14.57 ± 0.45	13.61 ± 1.07	12.97 ± 0.18	14.28 ± 0.65	15.01 ± 0.67
Moisture (%)	15.90 ± 1.19	14.21 ± 0.48	11.93 ± 1.1	13.19 ± 1.55	12.45 ± 2.04

development of wings (e.g., Hendrickx et al. 2007), and species were classified as macropterous, apterous or dimorphic, in accordance with research by Lindroth (1992) and Desender et al. (2008). Spiders were classified according to their hunting habits (Uetz et al. 1999): web builders, ambushers and ground runners.

Statistical analysis.—In order to analyze patterns of species composition along the urban-rural boundary gradient, multivariate analyses on activity-density of all species were performed using the software CANOCO (Ter Braak & Šmilauer 2002). The choice between linear (Principal Component Analysis: PCA) or unimodal (Correspondence Analysis: CA) analyses depended on the length values of the first axis gradient previously realized with DCA (Detrended Correspondence Analysis).

In order to test differences in species richness and density-activity (total and per ecological trait) between the five sites, GLM with quasi-Poisson distribution was performed using data from the individual traps (Vincent & Haworth 1983; O'Hara & Kotz 2010). When GLM revealed a significant effect of site factor, Tukey's post-hoc tests with Bonferroni correction for multiple comparisons were performed between mean parameters. The resulting data were analysed with R software (R Development Core Team 2009).

RESULTS

Description of the fauna.—In total, 924 spiders of 78 species representing15 families were collected, among which Lycosidae were dominant (51% of all individuals), followed by Linyphiidae (14.5%); Thomisidae (5.9%); Dysderidae (4.9%) and Gnaphosidae (3.9%). Individuals from five species, *Pardosa prativaga* (Koch 1870), *Pardosa amentata* (Clerck 1757), *Alopecosa pulverulenta* (Clerck 1757), *Pardosa lugubris* (Walckenaer 1802), and *Ozyptila praticola* (Koch 1837), accounted for more than 40% of all catches.

In total, 330 individuals of carabid beetles belonging to 24 species and 15 genera were collected. Three species, *Nebria brevicollis, Pterosticus cupreus* and *Notiophilus quadripuncatus*, accounted for more than 50% of all catches.

Changes in species assemblage along the gradient.—Axis 1 of the PCA on spider assemblages (Fig. 2) represented 24.6% of inertia, and Axis 2 represented 11.0% of inertia. Axis 2 segregated urban sites from rural ones; the boundary traps were located between those from urban and rural sites. Rural traps were characterized by *P. lugubris*, *Tegenaria picta* Simon 1870, *Dysdera erythrina* (Walckenaer 1802) and *Pardosa saltans* Töpfer-Hofmann 2000.

Axis 1 of CA on carabid beetle assemblages (Fig. 3) represented 15.9% of inertia, and Axis 2 13.0% of inertia. Boundary sites were included in envelope rural group. Axis 1 segregated urban traps from rural-boundary ones. Urban traps were mainly characterized by *N. brevicollis*, *Badister bipustulatus* and *Asaphidion stierlini*, whereas boundary and rural traps were characterized by *Carabus intricatus*, *Harpalus tardus* and *Agonum moestum*.

Changes in species density and species richness along the gradient.—There was a significant effect of sites on the total activity-density of spiders and the activity-density of "other habitat" species ($F_{1,4} = 4.90$, $P = 0.005$ and $F_{1,4} = 4.45$, $P = 0.007$, respectively), but post-hoc tests did not reveal significant differences between sites. The species richness and activity-density of forest species and web builders were not significantly different between sites ($F_{1,4} = 0.66$, $P = 0.625$; $F_{1,4} = 0.73$, $P = 0.578$ and $F_{1,4} = 0.18$, $P = 0.946$, respectively), but there was a significant effect of sites on the activity-densities of open-habitat species ($F_{1,4} = 4.88$, $P = 0.005$; Fig. 4a), ambushers ($F_{1,4} = 4.19$, $P = 0.009$; Fig. 4b) and ground runners ($F_{1,4} = 6.06$, $P < 0.001$; Fig. 4c).

For carabid beetles, sites had no significant effect on most explanatory variables tested (species richness: $F_{1,4} = 1.24$, $P = 0.321$; total activity-density: $F_{1,4} = 1.93$, $P = 0.14$; activity-densities of dimorphic and macropterous species: $F_{1,4} = 0.50$, $P = 0.738$ and $F_{1,4} = 2.29$, $P = 0.087$, respectively; activity-densities of forest, open and other habitat species: $F_{1,4} = 2.24$, $P = 0.094$; $F_{1,4} = 1.48$, $P = 0.237$ and $F_{1,4} = 2.16$, $P = 0.103$, respectively). There was a significant effect of sites only on the activity-density of apterous species ($F_{1,4} = 2.78$, $P = 0.048$), but post-hoc tests did not reveal significant differences between sites.

DISCUSSION

Contrary to carabid beetles, the composition of spider assemblages in the boundary was intermediate between those from urban and rural habitats. Characteristic species for urban habitats were *Enoplognatha thoracica* (Hahn 1833), *Tiso vagans* (Blackwall 1834) and *Troxochrus scabriculus* (Westring 1851) and, for rural habitats, *P. lugubris*, *T. picta*, *D. erythrina* and *P. saltans*. In addition, changes in activity-density were either null, or progressive, indicating a general non-sharp response of spider assemblages to the boundary. That result was mainly due to species with low to medium activity-densities, whereas dominant species (i.e., *A. pulverulentata*, *P. amentata* and *P. prativaga*) were distributed along the whole urban-rural transect. The latter species are all widely distributed in Europe and occur in a wide variety of habitats (Harvey et al. 2002; Le Péru 2007).

This progressive change between urban and rural habitats was also observed in relation to habitat preferences. The activity-densities of species from open habitats increased smoothly from urban to rural habitats. That result is quite different from previous studies (and from our expectation), which showed that species from open habitats were associated with urban areas, whereas forest species were more frequently found in rural habitats (e.g., Magura et al. 2004). Yet, it is important to note that most previous studies were carried out in woodlands, not in hedgerows, as was the case here. No response was found from the web-builder guild, but that can be easily explained by the lack of efficiency of pitfall trapping for that guild (e.g. Churchill 1993). The patterns of hunter guilds (ambushers and ground runners) along the gradient do not especially support the view of a progressive response, but instead present, as expected, a lower activity-density in urban habitats. That general negative impact of urbanization is in accordance with most studies carried out along (long) urban-rural transects (Denys & Schmidt 1998; Blair 1999; Yamaguchi 2004; Lehvävirta et al. 2006; Sadler et al. 2006; Clark et al. 2007; Pacheco & Vasconcelos 2007), but appears more in contradiction to the few studies specifically focused on spiders along large-scale urban-rural gradients (Alaruikka et al. 2002; Magura et al. 2010).

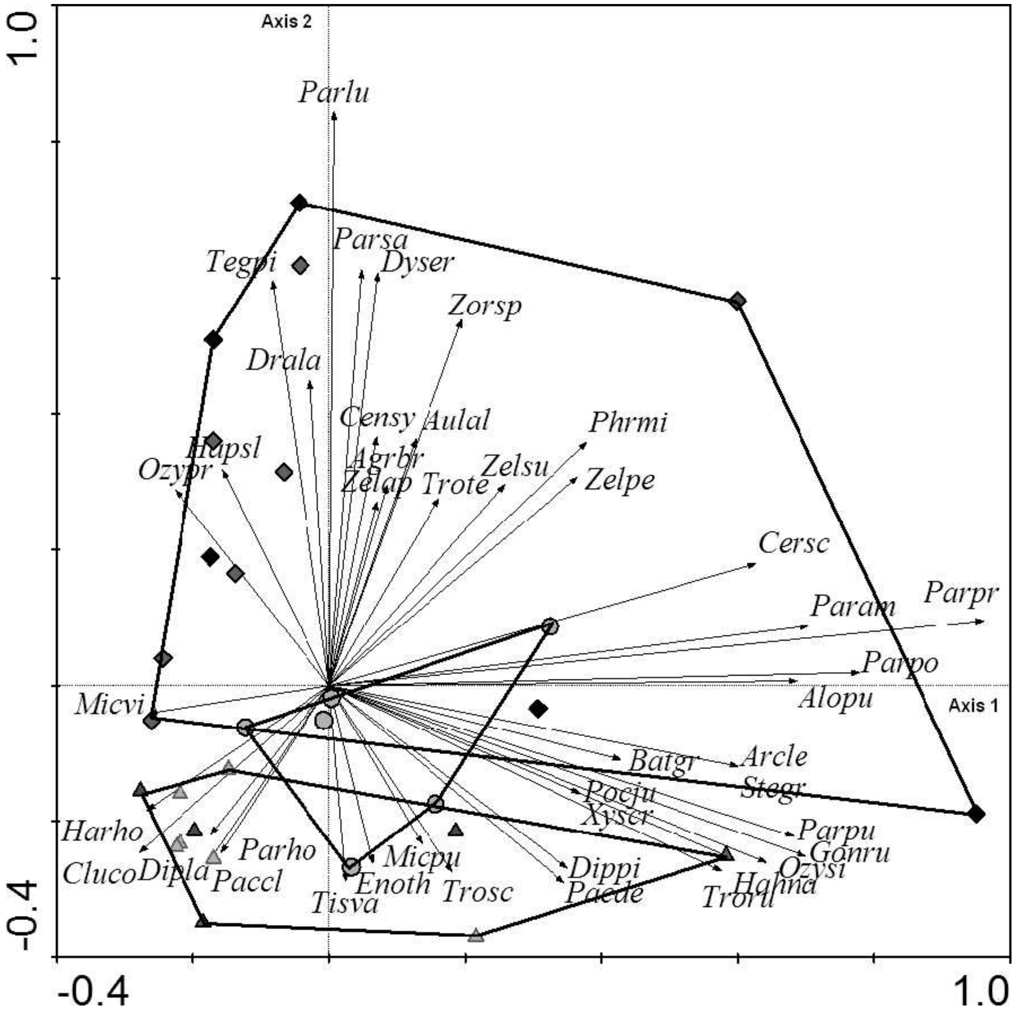

Figure 2.—Ordination diagram of the first two axes of Principal Component Analysis for 75 spider species (asterisk). For projection, the species fit range is from 7% to 100%; 43 species are represented and 30 samples. Abbreviations: U2 (▲), U1 (▲), E (●), R1 (◆) and R2 (◆). The envelopes (solid lines) group urban (U1-U2), rural (R1-R2) and boundary (E) sites. Species: Agrbr = *Agroeca brunnea* (Blackwall 1833); Alopu = *Alopecosa pulverulenta* (Clerck 1757); Arcle = *Arctosa leopardus* (Sundevall 1833); Aulal = *Aulonia albimana* (Walckenaer 1805); Batgr = *Bathyphantes gracilis* (Blackwall 1841); Censy = *Centromerus sylvaticus* (Blackwall 1841); Cerbr = *Ceratinella brevipes* (Westring 1851); Cersc = *C. scabrosa* (Cambridge 1871); Cluco = *Clubiona comta* Koch 1839; Dipla = *Diplocephalus latifrons* (Cambridge 1863); Dippi = *D. picinus* (Blackwall 1841); Drala = *Drassodes lapidosus* (Walckenaer 1802); Dyser = *Dysdera erythrina* (Walckenaer 1802); Enoth = *Enoplognatha thoracica* (Hahn 1833); Gonru = *Gongylidium rufipes* (Linnaeus 1758); Hahna = *Hahnia nava* (Blackwall 1841); Hapsl = *Haplodrassus silvestris* (Blackwall 1833); Harho = *Harpactea hombergi* (Scopoli 1763); Micpu = *Micaria pulicaria* (Sundevall 1831); Micvi = *Microneta viaria* (Blackwall 1841); Ozypr = *Ozyptila praticola* (Koch 1837); Ozysi = *O. simplex* (Cambridge 1862); Paccl = *Pachygnatha clercki* Sundevall 1823; Pacde = *P. degeeri* Sundevall 1829; Param = *Pardosa amentata* (Clerck 1757); Parho = *P. hortensis* (Thorell 1872); Parlu = *P. lugubris* (Walckenaer 1802); Parpo = *P. proxima* (Koch 1848); Parpr = *P. prativaga* (Koch 1870); Parpu = *P. pullata* (Clerck 1757); Parsa = *P. saltans* Töpfer-Hofmann 2000; Phrmi = *Phrurolithus minimus* Koch 1839; Pocju = *Pocadicnemis juncea* Locket & Millidge 1953; Stegr = *Steatoda grossa* Koch 1838; Tegpi = *Tegenaria picta* Simon 1870; Tisva = *Tiso vagans* (Blackwall 1834); Troru = *Trochosa ruricola* (de Geer 1778); Trosc = *Troxochrus scabriculus* (Westring 1851); Trote = *Trochosa terricola* Thorell 1856; Xyscr = *Xysticus cristatus* (Clerck 1757); Zelap = *Zelotes apricorum* (Koch 1876); Zelpe = *Z. pedestris* (Koch 1837); Zelsu = *Z. subterraneus* (Koch 1833); Zorsp = *Zora spinimana* (Sundevall 1833).

For carabid beetles, neither classical parameters (density-activity and species richness) nor parameters derived from life history traits varied along the urban-rural boundary gradient, invalidating pro parte our expectations. That result is also contradictory to most studies that reveal a strong negative impact of urbanization (e.g., Alaruikka et al. 2002; Ishitani et al. 2003). It must be stressed that our study originally investigated a very small-scale response (around 1 km), whereas most studies indicated some changes in carabid beetle species richness only after more than 3 km (e.g., Weller & Ganzhorn 2004). The length of the gradient studied here would thus be too short to reveal some responses of carabid beetles, known to react to changes in landscape structure (Burel et al. 1998). Changes in assemblage composition along the urban-rural boundary gradient as revealed by multivariate analysis included the discrimination of two groups, associated with the urban and rural-boundary habitats. Urban habitats were dominated by *N. brevicollis*, whose activity-densities strongly decreased in rural habitats. That species was already known to occur mainly in urban areas (Weigmann 1982).

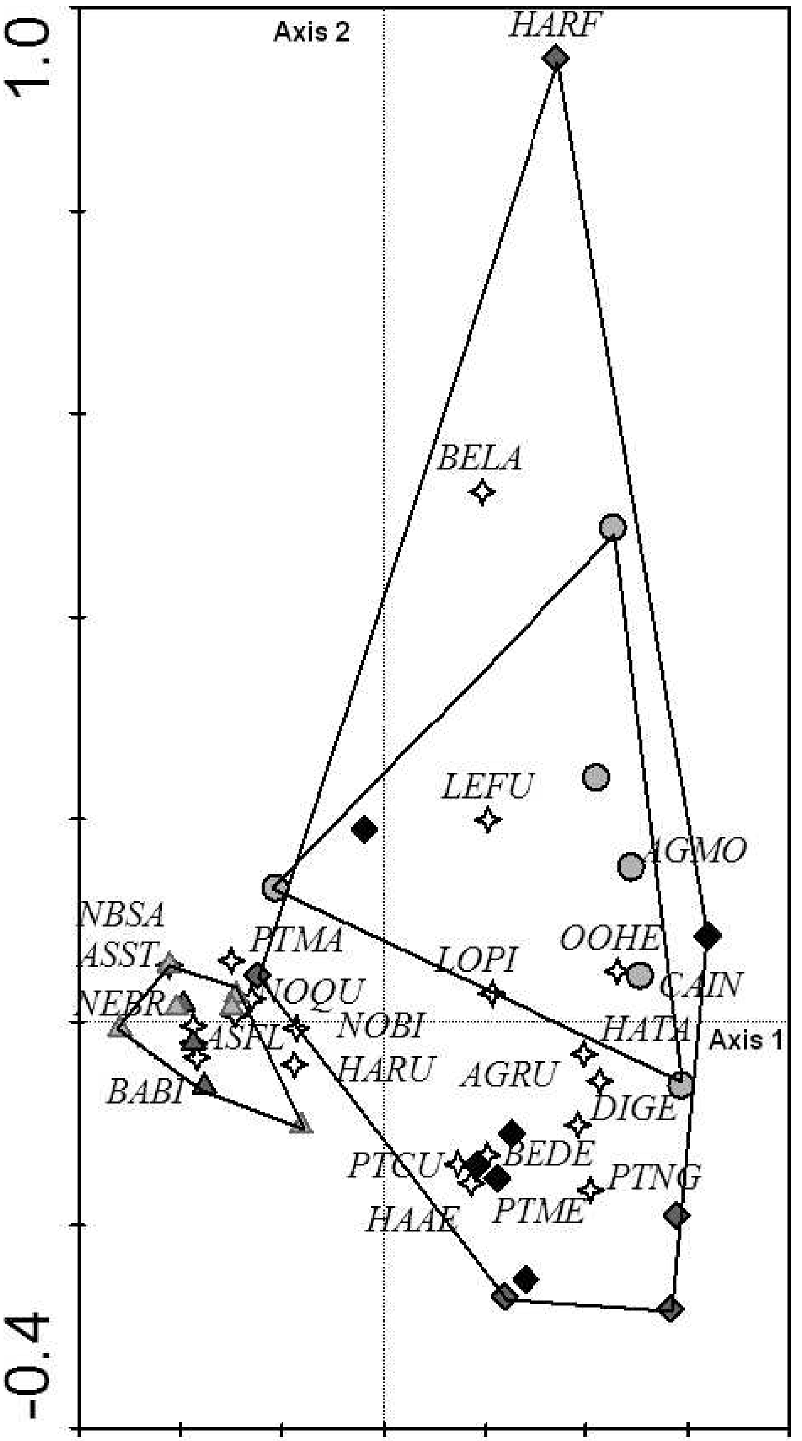

Figure 3.—Ordination diagram of the first two axes of Correspondence Analysis for 25 carabid species (asterisk) and 30 samples. Abbreviations: U2 (▲), U1 (▲), E (●), R1 (◆) and R2 (◆).The envelopes (solid lines) group urban (U1-U2), rural (R1-R2) and boundary (E) sites. Species: AGRU = *Agonum dorsalis* (Pontoppidan); AGMO = *A. moestum* (Dufts 1812); ASFL = *Asaphidion flavipes* (Linnaeus 1761); ASST = *Asaphidion stierlini* (Heyden 1880); BABI = *Badister bipustulatus* (Fabricius 1792); BEDE = *Bembidion dentellum* (Thunberg 1787); BELA = *B. lampros* (Herbst 1784); CAIN = *Carabus intricatus* Linnaeus 1761; DIGE =*Diachromus germanus* (Linnaeus 1758); HAAE = *Harpalus affinis* (Fabricius 1792); HARU = *H. rubripes* (De Geer 1774); HARF = *H. rufipes* (De Geer 1774); HATA = *H. tardus* (Panzer 1796); LEFU = *Leistus fulvibarbis* (Dejean 1826); LOPI = *Loricera pilicornis* (Fabricius 1775); NEBR = *Nebria brevicollis* (Fabricius 1792); NBSA = *N. salina* Fairmaire & Laboulbene 1854; NOBI = *Notiophilus biguttatus* (Fabricius 1779); NOQU = *N. quadripunctatus* (Dejean 1826); OOHE = *Oodes helopioides* (Fabricius 1792); PTCU = *Pterostichus cupreus* (Linnaeus 1758); PTMA = *P. madidus* (Fabricius 1775); PTME = *P. melanarius* (Illiger 1798); PTNG = *P. nigrita* (Paykull 1790).

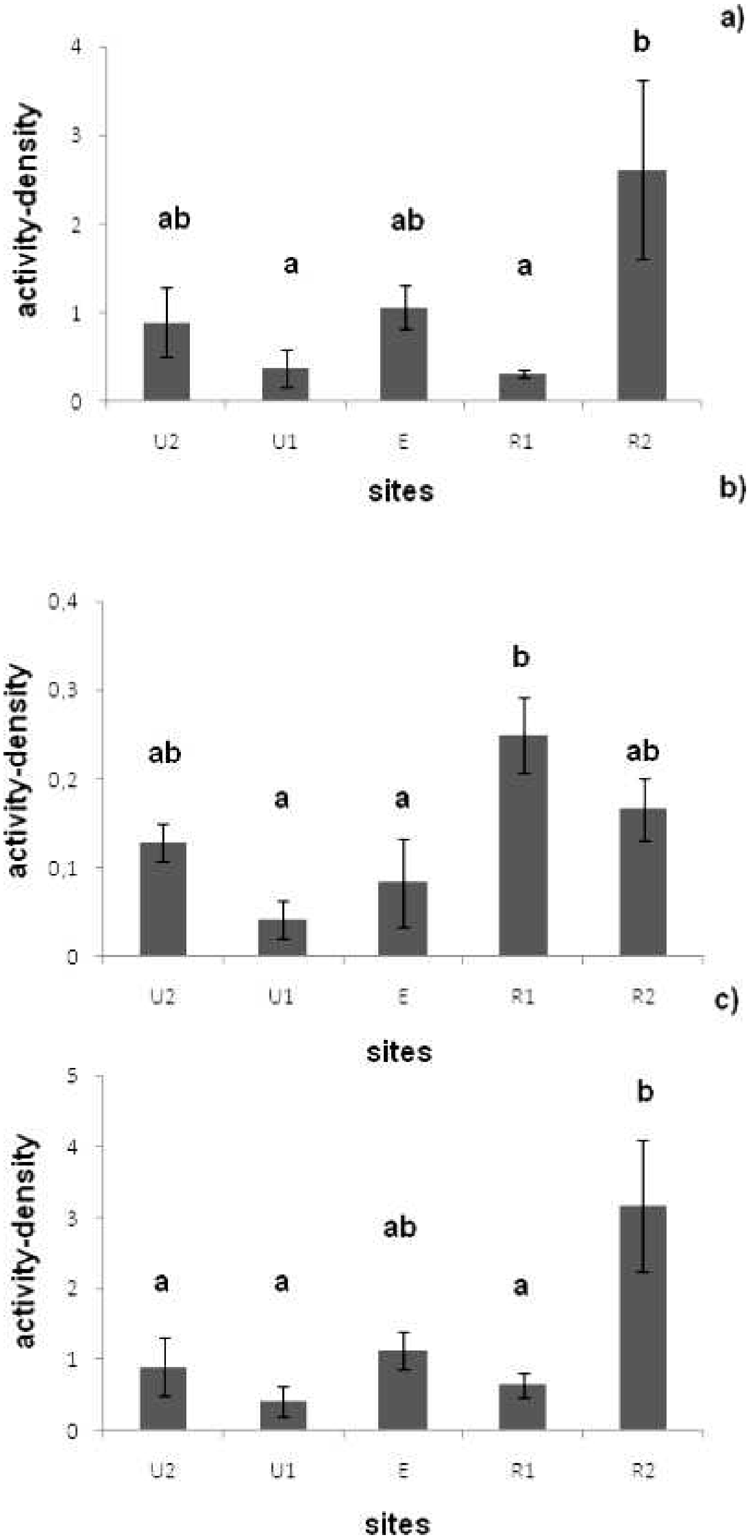

Figure 4.—Mean activity-density (± SE) of spiders per site along the urban-rural boundary gradient. a) open habitat species, b) ambushers, c) ground runners. Significant differences are assigned by different letters above bars.

Boundary and rural habitats were conversely characterized by *C. intricatus,* a forest species (e.g., Desender et al. 2008). Further studies should thus investigate the importance of hedgerow connectivity in forest species colonization.

As revealed by multivariate analyses, spider and carabid beetle assemblages exhibited different types of responses along an urban-rural boundary gradient. Spiders exhibited a rather progressive response, whereas it was almost null for carabid beetles. This difference may be attributed to differences in dispersal abilities and in sensitivity to environmental factors, or to an interaction between these two variables. Spiders are, for example, known to be sensitive to variation in litter depth (Uetz 1979), possibly at a higher magnitude than carabid beetles (Pétillon et al. 2008). It has been shown that species with high dispersal abilities are more sensitive to local habitat factors, whereas species with poor dispersal capacity are more dependent on large-scale, landscape factors (Croci et al. 2008). Carabid beetles would thus respond strongly to changes in landscape structure and spiders to continuous changes in local factors, which could explain, together with their high dispersal tendency (for both short and long distances: Bell et al. 2005), their progressive response along an urban-rural boundary gradient. It must finally be stressed that the different responses of the two groups studied may also be attributed to the low number of carabids caught and to some co-varying factors likely to create heterogeneity among traps or sites from one single area. Differences in hedgerow orientation are, for example, known to influence spider assemblage composition, at least for vegetation-dwelling species (Ysnel & Canard 2000).

In conclusion, this study highlights the importance of comparing several model groups synchronically, since their scale of sensitivity to environmental factors, and thus their response to a given process, may differ.

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