Age-dependent colonization of urban habitats: A diachronic approach using carabid beetles and spiders

Article *in* Animal Biology · January 2013

DOI: 10.1163/15707563-00002410

Françoise Burel
French National Centre for Scientific Research

Denis Lafage
LOGRAMI

Julien Pétillon
Université de Rennes 1

BRILL

Animal Biology 63 (2013) 257–269

Animal Biology
brill.com/ab

Age-dependent colonization of urban habitats: a diachronic approach using carabid beetles and spiders

Marion Varet[1,2], **Françoise Burel**[2], **Denis Lafage**[3,4] **and Julien Pétillon**[3,*]

[1] Université de Rennes 1, UMR CNRS 6553, 263 Avenue du Général Leclerc, CS 74205, 35042 Rennes Cedex, France
[2] Rennes Métropole, Communauté d'agglomération rennaise, 4 Avenue Henri Fréville, CS 20723, 35207 Rennes Cedex, France
[3] Université d'Angers, UNAM, GECCO, 2 Boulevard Lavoisier, 49045 Angers, France
[4] Université de Rennes 1, URU 420, UMR 7204 – Muséum National d'Histoire Naturelle, 263 Avenue du Général Leclerc, CS 74205, 35042 Rennes Cedex, France

Submitted: September 6, 2011. Final revision received: November 16, 2012. Accepted: November 19, 2012

Abstract

Urbanization creates human disturbance that plays an important role in ecosystem dynamics. Most of the time, there is a time lag between disturbance and colonization. Opportunistic species with high dispersal power colonize first, while habitat specialist species with a lower power of dispersal colonize later; the communities change with time after disturbance. We hypothesize that, following the establishment of a new neighbourhood, arthropod communities will change from habitat generalists to specialists, and will be more similar to those of the adjacent countryside. We selected two groups of invertebrates often used as bioindicators, spiders and carabid beetles. The following parameters were estimated: assemblage composition, species richness, activity-density total and per life history trait (broad habitat preference). The field data were collected in 2010 within 3 towns located in France. Neighbourhoods of 10 and 30 years old were pair-matched in these towns and sampled using pitfall traps set randomly in hedgerows (120 traps in total). 2101 adult spiders belonging to 89 species were collected, whereas the 643 captured carabid beetles belonged to 24 species. We found no evidence of any significant change in carabid beetle and spider communities according to neighbourhood age. The assemblages were mainly composed of habitat generalist species. These results suggest that urban areas can be seen to be in continual state of disruption, and colonization of these areas is assumed to be relatively rapid (i.e., less than 10 years in our case study), although incomplete.

Keywords

Araneae; Carabidae; Coleoptera; human disturbance; succession; urban ecology

*) Corresponding author; e-mail: julien.petillon@univ-rennes1.fr

DOI 10.1163/15707563-00002410

Introduction

The urbanization process is increasing in response to population growth and changes in lifestyle (Fenger, 1999; Weber, 2003). Urbanization can be defined as an implementation of anthropogenic structures (e.g., buildings, roads, etc.) to satisfy human population requirements at the expense of agricultural or natural areas (Germaine & Wakeling, 2001; McKinney, 2002). Thus, these modifications induce important changes in the long and short terms. In the long term, urbanization leads to landscape and physicochemical changes (Breuste et al., 1998; Baker et al., 2002): the creation of urban heat islands, concentrations of pollution (Fenger, 1999), fragmentation of natural areas (Antrop, 2004; Alberti, 2005) and the creation of new habitat types. In the short term, urbanization leads to habitat alteration by destruction and degradation (Davis & Glick, 1978; Niemelä, 1999; Tratalos et al., 2007). This important land-use change has a strong impact on biodiversity (e.g. Sanford et al., 2008; Fattorini, 2011). Most studies investigated the effects of urbanization by comparing urban and rural areas (Alaruikka et al., 2002; Sadler et al., 2006; Clark et al., 2007; Gaublomme et al., 2008; Niemelä, 2009), but in these studies, the age of the different neighbourhoods was usually not taken into account. However, the response of diversity is dynamic over time, often with a time lag between environmental change and biodiversity change (Forman, 1995; Foster et al., 1998; Łaska, 2001). Disturbance (whether associated with urbanization or not) plays an important role in ecosystem dynamics (White, 1979; Mooney & Godron, 1983; Łaska, 2001) and may lead to the dispersal or local extinction of plants and animals, thus drastically reducing diversity. Later, following the principles of ecological succession, the colonization of the area by new species is expected (Tilman, 1983; Pickett et al., 1989) if suitable habitats are available. Communities will then change during the colonization process. Recovery time varies according to target species and landscape connectivity (e.g. Connell & Slatyer, 1977).

In this study, we compared the response of two groups of invertebrate species, carabid beetles and spiders, which are known to react strongly to changes in microhabitat conditions and are often used as bioindicators (for spiders see Marc et al., 1999; Bell et al., 2001; for carabid beetles see Luff et al., 1992; Rainio & Niemelä, 2003; for both groups see Pearce & Venier, 2006). Following the principle of colonization (e.g. White, 1979), we hypothesized that habitat generalist species (often having high dispersal power) are the first to colonize urban areas, while habitat specialist species (generally having low dispersal power) colonize later (see, e.g., Southwood, 1962). To test for such a colonization process, we compared assemblages from sites differing in building age, i.e., 10 vs. 30 years. These ages were chosen because, in a previous study (Varet et al., 2011), we found that 10-year neighbourhoods were ‘still’ dominated by pioneer species, with a lot of forest and/or low-disperser species missing (i.e., present in the surroundings but not in the town), although the habitat quality was apparently sufficient.

Material and methods

Study sites and sampling design

The study sites were located within the conurbation of Rennes, Brittany, France, in three towns: Acigné (N48°08′05″, W01°32′07″) (coded A), Vezin-le-Coquet (N48°7′7″, W1°45′0″) (coded B) and Pacé (N48°8′52, W1°46′0″) (coded C). In each town, two zones (neighbourhoods) were selected depending on the date when they were built: one neighbourhood was 10 years old and the other one was 30 years old. All sites (A10, A30, B10, B30, C10 and C30) had at least one side adjacent to the rural (agricultural) area, so that colonization from source habitats could not be seen as limited (Varet et al., 2011). All selected neighbourhoods were built with a "traditional design" (i.e., single houses with private gardens), and had similar population density (around 16 inhabitants/ha), percentage of impervious area (ranging from 27 to 33%) and total surface (between 10 and 14.5 hectares for the six neighbourhoods).

At each site, 20 randomly located sample points were set up (Arcview, Geo Wizards) in public shrubby areas previously mapped by GIS. Two criteria, however, were applied to the location of sampling points; first, for security reasons, no traps were placed in sparsely vegetated hedgerows near playgrounds for children and second, the points had to be at least 10 metres apart so that the data were independent from one trap to another (Topping & Sunderland, 1992). We limited the sampling to hedgerows because they were dominant in the green spaces of new neighbourhoods. Hedgerows were planted at the creation of the neighborhood. Each sample point consisted of one pitfall trap (cylinder height: 100 mm, diameter: 85 mm) covered with a plastic roof. The pitfall traps were filled with about 75 ml of a preservation solution composed of 50% monopropylen glycol and 50% salt solution of 100 g/l (the best collecting fluid for spiders: Schmidt et al., 2006). The traps were monitored every two weeks for eight weeks between mid April 2010 and mid June 2010. This sampling period corresponds to the period when 75% of the total number species present in urban hedgerows during one year are found (Varet, 2011).

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

Catches in pitfall traps actually estimate the 'activity-trappability-density' of species (number of individuals dependant of trap duration and perimeter Sunderland et al., 1995), further abbreviated as 'activity-density'. The life history trait considered in this study is habitat preference. Carabid beetles and spiders were classified into two classes of habitat preference (see Hänggi et al., 1995 for spiders; Luff, 1998 and Bouget, 2004 for carabid beetles): generalist species and specialist species, e.g., species of wet habitats, forest species and open habitat species.

Statistical analysis

To detect differences in activity-density (per species, per life history trait and total) and species richness between ages (fixed factor) and towns (random factors), we used a generalised linear mixed model (GLMM). Poisson distribution was applied to data from individual traps because counts of activity-density are assumed to conform to such a distribution (Vincent & Haworth, 1983; O'Hara & Kotze, 2010). A first complete model was created (catches $\sim$ age + town + age $\times$ town) and, when the interaction between the two discrete factors was not significant, a second model with only fixed factors (i.e., without interactions) was made (catches $\sim$ age + town).

Data were analysed with R software (R Development Core Team, 2009), using the lmer() function of the lme4 package (e.g., Bates et al., 2012). The analyses on activity-densities were done species by species, only for the species with an activity-density higher than 1% of the total activity-density (i.e., non-rare species). Moreover, to analyse similarity in species composition, Bray-Curtis distances between individual traps were calculated using activity-density data transformed by double square-root to downweight the effects of dominant species as recommended by Legendre & Legendre (1983). Bray-Curtis distances were then subjected to hierarchical cluster analyses using Ward's method, and statistically analysed by some Analyses of Similarity (ANOSIM; dissimilarity ranks between classes by age and town factors; 999 permutations), on both carabid and spider catches.

Results

General description

In total, 643 individual carabid beetles belonging to 24 species were collected (see complete list in supplementary table S1). Individuals of *Nebria brevicollis* accounted for more than 80% and *Notiophilus quadripunctatus*, *Notiophilus biguttatus* and *Pterostichus madidus* accounted for more than 10% of the total catch. In total, 2101 individual spiders belonging to 89 species were collected (see complete list in supplementary table S2). Individuals of *Pardosa hortensis* accounted for more than 35% and *Pardosa prativaga*, *Alopecosa pulverulenta* and *Ozyptila praticola* accounted for more than 15% of the total catch. Beetle and spider assemblages were mainly composed of large individuals, generally considered having a low dispersal power. Moreover, these individuals were also predominantly generalist (more than 75% of individuals belonged to generalist species for both spiders and carabids).

Changes in species assemblages

The ascending hierarchical clustering of carabid beetle and spider communities (figs. 1 and 2) did not segregate assemblages according to neighbourhood age, or by site. Young and old sites were represented by similar percentages (around

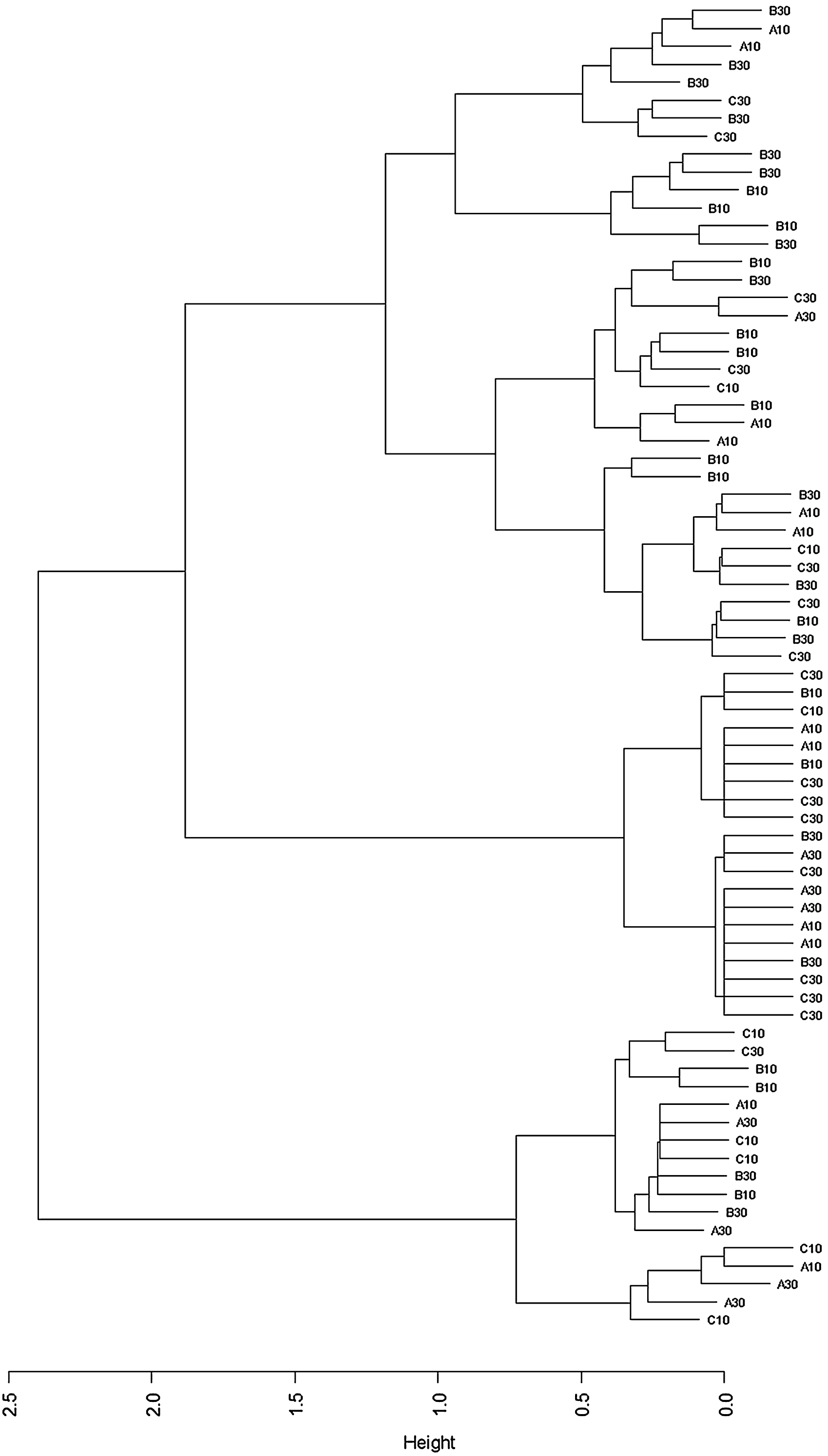

Figure 1. Ascending hierarchical clustering of carabid beetle assemblages based on 78 individual traps (traps with no carabid beetles were removed from the analysis). The cluster dendrogram was constructed using the Ward method based on distances calculated by the Bray-Curtis on square root double data activity-density. Sites are given by letters (A, B, C; see text for details) and age by numbers (10 vs. 30 years old).

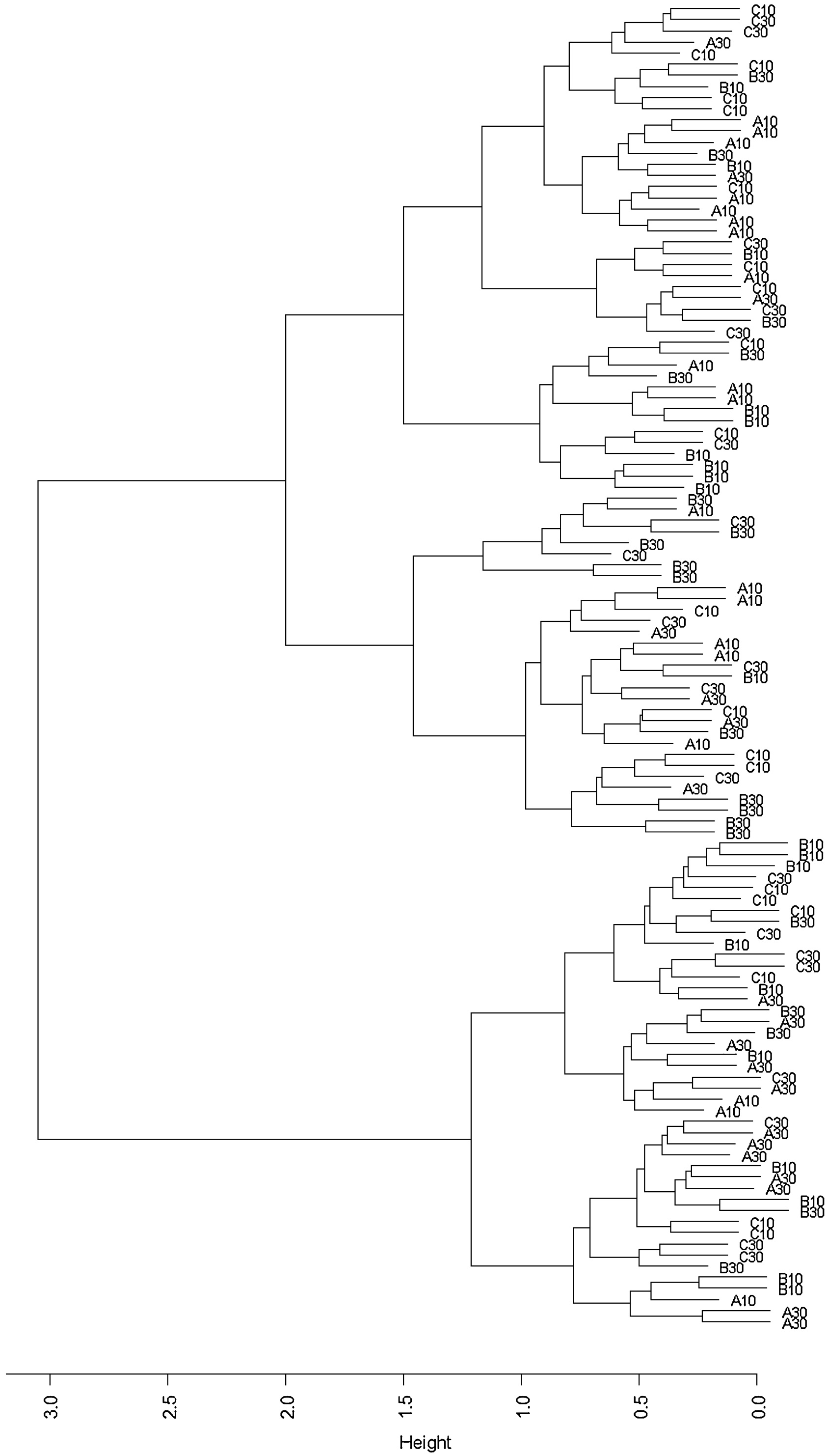

Figure 2. Ascending hierarchical clustering of spider assemblages based on 120 individual traps. The cluster dendrogram was constructed using the Ward method based on distances calculated by the Bray-Curtis on square root double data activity-density. Sites are given by letters (A, B, C; see text for details) and age by numbers (10 vs. 30 years old).

50%) of individual traps, both within and between the three main clusters. However, one cluster contained more individual traps from site B for carabid beetles (more than 56% of traps from site B in the left cluster: fig. 1) and another regrouped slightly more young sites for spiders (68% of old sites in the left cluster: fig. 2). ANOSIMs confirmed these results, with traps significantly grouped by the town (carabids: $R = 0.13$, $P = 0.002$; spiders: $R = 0.03$, $P = 0.014$), but not by the age of construction (carabids: $R = 0.03$, $P = 0.053$; spiders: $R < 0.01$, $P = 0.214$).

Change in species activity-density and richness

Activity-densities of both spiders and carabid beetles, either total, per habitat preference and for most species, were independent of the age of the sites (tables 1 and 2), except for the spiders *Diplocephalus picinus*, *Pardosa pullata* and *P. saltans* which were more densely active in recently created neighbourhoods. Other species also reacted to the age of the sites, but with an interaction with the town studied (*Nebria brevicollis*: table 1; *Harpactea hombergi*: table 2). The species richness was also independent of site age (tables 1 and 2), for both carabid beetles and spiders.

Discussion

Contrary to our initial hypothesis, spider and carabid beetle assemblages did not change with time between 10 and 30 years. Species richness and most of the activity-densities did not significantly differ according to the age of the neighbourhoods, and the assemblage composition remained similar for the six studied sites. Two hypotheses could help explain these results.

The first is that 30 years might not be a long enough period to allow the colonization of urban green spaces from the adjacent countryside by habitat specialist species with a low dispersal power. The second hypothesis is that 10 years are sufficient to reach an optimal colonization of urban green spaces. We reject the first hypothesis because this period is ecologically long for the model groups used here, carabid beetles (see also Verschoor & Krebs, 1995) and spiders (Thomas et al., 1992; Buddle et al., 2003). As an example, Cristofoli & Mah (2010) have shown that spiders only need 15 years to recolonize a peat bog. Besides, the urban areas are adjacent to rural areas, so that the limiting effect of "habitat islands" is highly reduced (Clergeau et al., 2006); a relatively fast colonization of new environments – much inferior to 30 years – is consequently expected. Finally, the assemblages observed are mostly made up of opportunistic generalist species, mainly large individuals with rather low long-distance dispersal capacities. Thus, the first hypothesis can be dismissed in favour of the second one.

Despite the age difference between neighbourhoods, arthropod assemblages were all made up of mainly generalist species. This could be due to the general environment of the urban area. Urban green spaces (potential habitats) are often maintained by man (cutting, litter input, weeding, etc.) and are considered a regular

Table 1.
Influence of town and age factors on species richness and activity-density (total, per non-rare species and per life history trait) on carabid beetles (GLMM with quasi-Poisson error distribution). In case of significant interaction, effects of town and age factors are those from the full model.

	Town × age		Town		Age	
	Wald χ^2	P-value	Wald χ^2	P-value	Wald χ^2	P-value
Mean species richness	7.00	0.030	8.92	0.012	0.37	0.542
Mean activity density	84.19	<0.001	150.37	<0.001	1.71	0.190
Mean activity-density per habitat preference						
generalists	86.25	<0.001	124.91	<0.001	1.81	0.179
specialists	0.34	0.846	23.12	<0.001	1.78	0.183
Mean activity-density per species						
Nebria brevicollis	87.41	<0.001	96.98	<0.001	6.97	0.008
Notiophilus biguttatus	0.20	0.903	5.31	0.070	1.11	0.292
Notiophilus quadripunctatus	5.82	0.055	1.69	0.430	2.7	0.100
Notiophilus rufipes	0.00	1.000	2.19	0.334	<0.01	0.996
Pterostichus madidus	0.00	1.000	2.12	0.347	0.01	0.920

Table 2.
Influence of town and age factors on species richness and activity-density (total, per non-rare species and per life history trait) in spiders (GLMM with quasi-Poisson error distribution). In case of significant interaction, effects of town and age factors are those from the full model.

	Town × age		Town		Age	
	Wald χ^2	P-value	Wald χ^2	P-value	Wald χ^2	P-value
Mean species richness	20.08	<0.001	1.26	0.532	0.91	0.339
Mean activity-density	79.71	<0.001	109.43	<0.001	9.38	<0.001
Mean activity-density per habitat preference						
generalists	30.21	<0.001	63.96	<0.001	0.01	0.91
specialists	56.03	<0.001	49.93	<0.001	21.42	<0.001
Mean activity-density per species						
Agroeca inopina	2.72	0.257	5.00	0.082	0.59	0.441
Alopecosa pulverulenta	21.49	<0.001	1.9	0.386	2.78	0.096
Clubiona terrestris	7.64	0.022	4.00	0.135	1.83	0.177
Diplocephalus picinus	<0.01	1.000	19.91	<0.001	10.47	0.001
Drassodes lapidosus	1.33	0.515	9.49	0.009	0.47	0.494
Dysdera erythrina	0.46	0.796	7.98	0.018	0.64	0.425
Harpactea hombergi	<0.01	0.009	4.45	0.108	6.78	0.009
Lepthyphantes tenuis	2.56	0.279	5.85	0.054	1.27	0.261
Microneta viaria	3.32	0.190	3.73	0.155	0.99	0.321
Neriene clathrata	2.53	0.282	0.41	0.815	0.12	0.732
Ozyptila praticola	26.54	<0.001	3.97	0.137	0.43	0.511
Pardosa hortensis	2.89	0.236	87.26	<0.001	3.66	0.056
Pardosa prativaga	<0.01	1.000	<0.01	1.000	0.32	0.571
Pardosa pullata	<0.01	0.999	6.22	0.045	6.66	0.009
Pardosa saltans	1.24	0.539	27.76	<0.001	24.29	<0.001
Pisaura mirabilis	1.01	0.603	9.13	0.01	1.37	0.241
Scotina celans	<0.01	1.000	<0.01	1.000	<0.01	0.999
Trochosa ruricola	0.61	0.737	8.11	0.017	2.04	0.153
Trochosa terricola	8.83	0.012	0.44	0.803	0.32	0.571
Zodarion italicum	2.75	0.253	0.35	0.839	2.33	0.127

source of disturbance, thereby limiting the colonization by habitat specialists. According to the source-sink model resulting from island theories (here habitat islands: Clergeau et al., 2006), there should still be an input of biodiversity from the rural environment to the urban environment (following the colonization movements that could be expected intuitively). In this study, assemblages (especially for carabids) are composed of relatively few individuals compared to those found in rural areas of the region (Brittany), and their species richness is rather low (24 species here, as compared with 53 species in Burel et al., 1998, despite the same regional species pool and the use of the same sampling technique, pitfall traps, and a comparable effort, 6720 traps/day here vs. 5376 in Burel et al., 1998). Moreover, urban carabid assemblages are dominated by *Nebria brevicollis*, a relatively scarce species in European rural areas (Niemelä et al., 2002; Saska, 2007).

Nevertheless, the urban environment is clearly colonized and many studies have even highlighted a certain degree of diversity in urban habitats (Croci et al., 2008; Niemelä, 2009). The landscape structure does not seem to be the only determining element for the colonization of urban environments. Habitat quality seems to be crucial too. Urban hedgerows are indeed very different from those in rural areas in terms of the nature, quality and habitat management. Urban hedgerows are often made up of exotic species (which is the case here, although with percentage cover inferior to 20%: Varet, 2011), and the tree and herbaceous strata are frequently low, and may not be suitable for the rural species, thus limiting their role as corridors. Conversely, urban habitats offer rather good quality habitats (Croci et al., 2008), and can thus be a refuge for grassland species (e.g. Carpaneto et al., 2005).

Finally, other results from the same study sites suggest that the "source-sink" model between rural and urban areas does not always seem to be effective (Varet et al., 2011). Moreover, the urban area can be seen as being continually disrupted and the colonization of urban areas is assumed to be relatively rapid (i.e., less than 10 years), although incomplete.

Acknowledgements

We would like to thank Marie Trang and Aurore Bréan for their help in collecting individuals and identifying carabid beetles, and the following people for their help in identifying problematic spiders: Alain Canard, Robert Bosmans (genera *Lepthyphantes* and *Zodarion*) and Christophe Hervé (genus *Drassodes*). Our thanks to Boris Leroy for help with multivariate analyses. Sandrine Baudry, Simone Fattorini, Aldyth Nyss and three anonymous referees are acknowledged for useful comments on earlier drafts. This study was funded by Rennes Métropole.

References

Alaruikka, D., Kotze, D.J., Matveinen, K. & Niemelä, J. (2002) Carabid beetle and spider assemblages along a forested urban-rural gradient in southern Finland. *J. Insect Conserv.*, 6, 195-206.

Alberti, M. (2005) The effects of urban patterns on ecosystem function. *Int. Regional Sci. Rev.*, 28, 168-192.

Antrop, M. (2004) Landscape change and the urbanisation process in Europe. *Landscape Urban Plan.*, 67, 9-26.

Baker, L.A., Brazel, A.J., Selover, N., Martin, C., McIntyre, N., Steiner, F.R., Nelson, A. & Musacchio, L. (2002) Urbanisation and warming of Phoenix (Arizona, USA): impacts, feedbacks and mitigation. *Urban Ecosyst.*, 6, 183-203.

Bates, D., Maechler, M. & Bolker, B. (2012) lme4: Linear mixed-effects models using S4 classes. R package version 0.999999-0. http://CRAN.R-project.org/package=lme4

Bell, J.R., Wheater, C.P. & Cullen, W.R. (2001) The implications of grassland and heathland management for the conservation of spider communities: a review. *J. Zool.*, 255, 377-387.

Bouget, C. (2004) *Chablis et diversité des coléoptères en forêts de feuillus de plaine: Impact à court terme de la trouée, de sa surface et de son contexte paysager*. Ph.D. thesis, Museum National d'Histoire Naturelle, Paris.

Breuste, J., Feldamenn, H. & Ohlmann, O. (1998) *Urban ecology*. Springer Verlag, Berlin.

Buddle, C.M., Walker, S.E. & Rypstra, A.L. (2003) Cannibalism and density-dependent mortality in the wolf spider *Pardosa milvina* (Araneae: Lycosidae). *Can. J. Zool.*, 81, 1293-1297.

Burel, F., Baudry, J., Butet, A., Clergeau, P., Delettre, Y., Le Cœur, D., Dubs, F., Morvan, N., Paillat, G., Petit, S., Thenail, C., Brunel, E. & Lefeuvre, J.C. (1998) Comparative biodiversity along a gradient of agricultural landscapes. *Acta Oecol.*, 19, 47-60.

Canard, A. (2005) Catalogue of spider species from Europe and the Mediterranean basin. *Rev. Arachnol.*, 15, 1-408.

Carpaneto, G.M., Mazziotta, A. & Piattella, E. (2005) Changes in food resources and conservation of scarab beetles: from sheep to dog dung in a green urban area of Rome (Coleoptera, Scarabaeoidea). *Biol. Conserv.*, 123, 547-556.

Clark, P.J., Reed, J.M. & Chew, F.S. (2007) Effects of urbanisation on butterfly species richness, guild structure, and rarity. *Urban Ecosyst.*, 10, 321-337.

Clergeau, P., Jokimäki, J. & Snep, R. (2006) Using hierarchical levels for urban ecology. *Trends Ecol. Evol.*, 21, 660-661.

Connell, J.H. & Slatyer, R.O. (1977) Mechanisms of succession in natural communities and their role in community stability and organization. *Am. Nat.*, 111, 1119-1144.

Cristofoli, S. & Mahy, G. (2010) Comment les espèces réagissent-elles face à la fragmentation et face à la restauration des milieux tourbeux en Haute Ardenne ? *Forêt Wallonne*, 109, 25-33.

Croci, S., Butet, A., Georges, A., Aguejdad, R. & Clergeau, P. (2008) Small urban woodlands as biodiversity conservation hot-spot: a multi-taxon approach. *Landscape Ecol.*, 23, 1171-1186.

Davis, A.M. & Glick, T.F. (1978) Urban ecosystems and island biogeography. *Environ. Conserv.*, 5, 299-304.

Fattorini, S. (2011) Insect extinction by urbanization: A long term study in Rome. *Biol. Conserv.*, 144, 370-375.

Fenger, O. (1999) Urban air quality. *Atmos. Environ.*, 33, 4877-4900.

Forman, R.T.T. (1995) *Land mosaics: the ecology of landscapes and regions*. Cambridge University Press, Cambridge.

Foster, D.R., Motzkin, G. & Slater, B. (1998) Land-use history as long-term broad-scale disturbance: regional forest dynamics in Central New England. *Ecosystems*, 1, 96-119.

Gaublomme, E., Hendrickx, F., Dhuyvetter, H. & Desender, K. (2008) The effects of forest patch size and matrix type on changes in carabid beetle assemblages in an urbanized landscape. *Biol. Conserv.*, 141, 2585-2596.

Germaine, S.S. & Wakeling, B. (2001) Lizard species distributions and habitat occupation along an urban gradient in Tucson, Arizona, USA. *Biol. Conserv.*, 97, 229-237.

Hänggi, A., Stocklie, E. & Nentwig, W. (1995) *Habitats of Central European spiders*. Centre Suisse de cartographie de la faune, Neuchâtel.

Heimer, S. & Nentwig, W. (1991) *Spinnen Mitteleuropas*. Verlag Paul Parey, Berlin.

Jeannel, R. (1941-1942) *Faune de France 39, Coléoptères carabiques première et deuxième parties*. Paul Lechevalier et fils Eds, Paris.

Łaska, G. (2001) The disturbance and vegetation dynamics: a review and an alternative framework. *Plant Ecol.*, 157, 77-99.

Legendre, L. & Legendre, P. (1983) *Numerical ecology*. Elsevier, Amsterdam.

Lindroth, C.H. (1992) *Ground beetles (Carabidae) of Fennoscandia, a zoogeographic study, Part I*. Intercept, Andover.

Luff, M.L. (1998) *Provisional atlas of the ground beetles (Coleoptera, Carabidae) of Britain*. Biological Records Centre, Huntington.

Luff, M.L., Eyre, M.D. & Rushton, S.P. (1992) Classification and prediction of grassland habitats using ground beetles (Coleoptera, Carabidae). *J. Environ. Manage.*, 35, 301-315.

Marc, P., Canard, A. & Ysnel, F. (1999) Spiders (Araneae) useful for pest limitation and bioindication. *Agri. Ecosyst. Environ.*, 74, 229-273.

McKinney, M.L. (2002) Urbanisation, biodiversity, and conservation. *Bioscience*, 52, 883-890.

Mooney, H.A. & Godron, M. (1983) *Disturbance and ecosystems: components of response*. Springer-Verlag, Berlin.

Niemelä, J. (1999) Ecology and urban planning. *Biodivers. Conserv.*, 8, 119-131.

Niemelä, J. (2009) Carabid beetle assemblages along urban to rural gradients: A review. *Landscape Urban Plan.*, 92, 65-71.

Niemelä, J., Kotze, D.J., Venn, S., Penev, L., Stoyanov, I., Spence, J., Hartley, D. & Montes de Oca, E. (2002) Carabid beetle assemblages (Coleoptera, Carabidae) across urban-rural gradients: an international comparison. *Landscape Ecol.*, 17, 387-401.

O'Hara, R.B. & Kotze, D.J. (2010) Do not log-transform count data. *Methods Ecol. Evol.*, 1, 118-122.

Pearce, J.L. & Venier, L.A. (2006) The use of ground beetles (Coleoptera: Carabidae) and spiders (Araneae) as bioindicators of sustainable forest management: A review. *Ecol. Indic.*, 6, 780-793.

Pickett, S.T.A., Kolasa, J., Armesto, J.J. & Collins, S.L. (1989) The ecological concept of disturbance and its expression at various hierarchical levels. *Oikos*, 54, 129-136.

R Development Core Team (2009) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna.

Rainio, J. & Niemelä, J. (2003) Ground beetles (Coleoptera: Carabidae) as bioindicators. *Biodivers. Conserv.*, 12, 487-506.

Roberts, M.J. (1987) *The spiders of Great Britain and Ireland*. Harley Books, Colchester, Essex.

Roberts, M.J. (1995) *Spiders of Britain and Northern Europe*. HarperCollins Publishers, London.

Sadler, J.P., Small, E.C., Fiszpan, H., Telfer, M.G. & Niemelä, J. (2006) Investigating environmental variation and landscape characteristics of an urban-rural gradient using woodland carabid assemblages. *J. Biogeogr.*, 33, 1126-1138.

Sanford, M.P., Manley, P.N. & Murphy, D.D. (2008) Effects of urban development on ant communities: implications for ecosystem services and management. *Conserv. Biol.*, 23, 131-141.

Saska, P. (2007) Diversity of carabids (Coleoptera: Carabidae) within two Dutch cereal fields and their boundaries. *Balt. J. Coleopt.*, 7, 37-50.

Schmidt, M.H., Clough, Y., Schulz, W., Westphalen, A. & Tscharntke, T. (2006) Capture efficiency and preservation attributes of different fluids in pitfall traps. *J. Arachnol.*, 34, 159-162.

Southwood, T.R.E. (1962) Migration of terrestrial arthropods in relation to habitat. *Biol. Rev.*, 37, 171-214.

Sunderland, K.D., De Snoo, G.R., Dinter, A., Hance, T., Helenius, J., Jepson, P., Kromp, B., Samu, F., Sotherton, N.W., Toft, S. & Ulber, B. (1995) Density estimation for invertebrate predators in agroecosystems. In: S. Toft & W. Riedel (Eds.) *Arthropod natural enemies in arable land. I. Density, spatial heterogeneity and dispersal*, pp. 133-162. Aarhus University Press, Århus.

Thomas, M.B., Wratten, S.D. & Sotherton, N.W. (1992) Creation of 'island' habitats in farmland to manipulate populations of beneficial arthropods: predator densities and species composition. *J. Appl. Ecol.*, 29, 524-553.

Tilman, D. (1983) Plant succession and gopher disturbance along an experimental gradient. *Oecologia*, 60, 285-292.

Topping, C.J. & Sunderland, K.D. (1992) Limitations in the use of pitfall traps in ecological studies exemplified by a study of spiders in a field of winter wheat. *J. Appl. Ecol.*, 29, 485-491.

Tratalos, J., Fuller, R.A., Warren, P.H., Davies, R.G. & Gaston, K.J. (2007) Urban form, biodiversity potential and ecosystem services. *Landscape Urban Plan.*, 83, 308-317.

Trautner, J. & Geigenmüller, K. (1987) *Tiger beetles, ground beetles: Illustrated key to the Cicindelidae and Carabidae of Europe*. Josef Margraf Eds, Aichtal.

Varet, M. (2011) *Biodiversité et aménagements urbains : réponse des assemblages de carabiques et d'araignées dans les haies publiques de Rennes Métropole*. Ph.D. thesis, Université de Rennes 1, Rennes.

Varet, M., Pétillon, J. & Burel, F. (2011) Comparative responses of spider and carabid beetle assemblages along an urban-rural ecotone. *J. Arachnol.*, 39, 236-243.

Verschoor, B.C. & Krebs, B.P.M. (1995) Successional changes in a saltmarsh carabid beetle (Coleoptera, Carabidae) community after embankment of the Markiezaat area. *Pedobiologia*, 39, 385-404.

Vincent, P.J. & Haworth, J.M. (1983) Poisson regression models of species abundance. *J. Biogeogr.*, 10, 153-160.

Weber, C. (2003) Interaction model application for urban planning. *Landscape Urban Plan.*, 63, 49-60.

White, P.S. (1979) Pattern, process, and natural disturbance in vegetation. *Bot. Rev.*, 45, 229-299.