

1 **Can urban consolidation limit local biodiversity erosion?**

2 **Responses from carabid beetle and spider assemblages in Western France**

3
4 **Marion Varet^{a,b}, Françoise Burel^a and Julien Pétilion^{c,*}**

5
6 ^a Université de Rennes 1, UMR CNRS 6553, 263 Avenue du Général Leclerc, CS 74205, 35042
7 Rennes Cedex, France

8
9 ^b Rennes Métropole, Communauté d'agglomération rennaise, 4 Avenue Henri Fréville, CS
10 20723, 35207 Rennes Cedex, France

11
12 ^c Université de Rennes 1, UMR 7204 – Muséum National d'Histoire Naturelle, 263 Avenue du
13 Général Leclerc, CS 74205, 35042 Rennes Cedex, France

14
15 * : Corresponding author. Tel: +33.22.323.68.51; Fax: +33.22.323.50.26. [julien.petillon@univ-](mailto:julien.petillon@univ-rennes1.fr)
16 [rennes1.fr](mailto:julien.petillon@univ-rennes1.fr)

1 **Abstract**

2

3 During the last decades, urban consolidation has been developed to minimize spatial expansion
4 of cities, yet very few studies investigated whether it would actually reduce some negative
5 effects of urbanization on biodiversity. In this study, we compared the invertebrate assemblages
6 associated with two distinct urban forms (compact vs. conventional), focusing on two arthropod
7 taxa often used as bioindicators, and dominant in urban habitats: spiders and carabid beetles. The
8 following parameters were estimated: assemblage composition, species richness, activity-density
9 total, per species (excluding seldom-recorded species) and per size class. The field collection was
10 performed in 2009 using pitfall traps randomly set in hedgerows within 6 sites (representing 251
11 traps). A total of 4413 spiders belonging to 117 species and 2077 adult carabid beetles belonging
12 to 39 species were collected. We found few significant differences in carabid beetle and spider
13 assemblages between the two urban forms. The species richness of both groups was independent
14 from the neighborhood design. Only four species of carabid beetles and ten of spiders
15 significantly reacted to the neighborhood design, and no difference was found among the two
16 designs for all other species. Large carabid beetles were more abundant and small spiders less
17 abundant in the new neighborhood design compared to the conventional one. For both carabid
18 beetles and spiders, no difference in assemblage composition was found between neighborhood
19 designs. We therefore conclude that urban consolidation, by permitting a higher human density
20 with similar arthropod assemblages, could contribute to reduce biodiversity loss in cities.

21

22 **Key words:** City compaction; Araneae; Carabidae; housing density; arthropods

23

1 **Introduction**

2 The world's urban population has increased considerably in the recent decades, reaching around
3 50% of the global population at present (United Nations Population Division 2012). This growth
4 is accompanied by an increase in the urbanization of land (Weber 2003; Grimm et al. 2008), and
5 frequently, negative effects on biodiversity (McKinney 2002). For plants, a lower α -diversity is
6 usually found in urban habitats compared to that in rural environments (e.g. McKinney 2002).
7 Arthropod species richness is also reported to decrease along rural to urban gradients (carabid
8 beetles: Niemelä and Kotze 2009, Magura et al. 2010; carabid beetles and spiders: Varet et al.
9 2011; arthropods in general: Gibb and Hochuli 2002, Kotze et al. 2011), with possible risks of
10 extinction predicted for several insect taxa (Fattorini 2011) and related changes in trophic
11 structure (Christie et al. 2010).

12 Given the spread of urban areas, it is thus important to understand the functioning of urban
13 ecosystems to plan the future development of cities and to minimize their negative
14 environmental impacts (Magura et al. 2004). Cities exhibit a specific environment in which the
15 conditions differ from those in natural habitats (Semenova, 2008), notably by the extent of
16 impervious surfaces (Weller and Ganzhorn 2004). However, the conservation of nature in the
17 city is increasingly important (Reduron 1996; Miller and Hobbs 2002; Jim and Chen 2008).
18 Currently, the desire and demand for nature in the city by urban residents and society in general
19 are clearly growing (Clergeau 2007). Thus, to meet these demands, new ways of thinking about
20 the city and new urban forms are developed, mostly to minimize their spatial expansion (Jenks et
21 al. 1996; Williams et al. 2000; Jenks and Dempsey 2005).

22 Urban consolidation, which aims at reducing the number of individual houses with gardens
23 (Grose 2009) in favor of grouped (semi-detached) or collective housing (Tratalos et al. 2007), is

1 developing fast (Searle 2011) due to several proved or supposed advantages like limited urban
2 sprawl, a more efficient use of land, a more efficient use of services, some shorter travel
3 distances, or a lower carbon footprint (Dodson 2010). Yet some disadvantages may occur (longer
4 travel distances to nature, less green space within the city, stormwater/air quality issues, health
5 issues, crowding), and among them, possible negative consequences on biodiversity (Gray et al.
6 2010). Very few studies have investigated the consequences of urban consolidation on
7 biodiversity, despite obvious potential impacts (Tratalos et al. 2007). Green spaces, developed in
8 order to promote outdoor recreational activities, social interactions (Grose 2009; Rogers and
9 Sukolratanamettee 2009) and environmental quality are used more and more by the public. Urban
10 green spaces can potentially contribute to enhancing biodiversity in the city (Kühn et al. 2004;
11 Jim and Chen 2008) including through the creation of microhabitat (Jim and Chen 2008). In
12 addition, the continuity of all the green areas is taken into account with the growing concept of
13 green urban corridors that are known to limit habitat fragmentation and to favor biodiversity
14 conservation (e.g. Vergnes et al. 2012). As a consequence, new neighborhood designs should
15 have higher housing density with a better continuity of public green space, thus promoting
16 increased connectivity for biodiversity. Conversely, conventional neighborhood designs are
17 likely characterized by a lower housing density, but with a strong fragmentation of public green
18 space.

19 The aim of the present study is to investigate whether and how the type of urban form will affect
20 two groups of arthropods (as a key component of biodiversity) in a single habitat type
21 (hedgerows, as an important habitat for urban biodiversity: Lövei et al. 2006) at a given time.
22 Spiders and carabid beetles were selected as model groups because they are known to react
23 strongly to changes in microhabitat conditions and therefore are often used as bioindicators

1 (Marc et al. 1999; Bell et al. 2001; Luff et al. 1992; Rainio and Niemelä 2003; Pearce and Venier
2 2006). They are also among the most diversified groups of ground-dwelling arthropods in urban
3 habitats (e.g. Dias et al. 2006; Sattler et al. 2011; Vergnes et al. 2012). In this research we tested
4 the following hypotheses more specifically. Hypothesis 1: The new neighborhood designs with
5 more public green spaces and hedgerows should accommodate more species and individuals
6 (total and by species). Hypothesis 2: The conventional neighborhood designs with less dense and
7 more fragmented public green spaces and hedgerows should accommodate more species with
8 high dispersal ability (the mean size of species was used here as a broad, negative proxy of long-
9 distance dispersal abilities: Southwood 1962; Magura et al. 2006; Desender et al. 2008; yet large
10 species tend to cover longer distances when they actively disperse: Jenkins et al. 2007). The
11 assumed differences in landscape parameters between the two designs were also tested for our
12 six study sites.

13

14 **Materials and methods**

15 *Study sites and sampling design*

16 To compare new and conventional urban designs, six neighborhoods, three of each type, were
17 selected within the conurbation of Rennes (Fig. 1). They are located in six cities: Brécé (N 48°
18 23', W 0° 48', coded A), Vezin-le-Coquet (N 48° 7', W 1° 45', coded B), Pacé (N 48° 8', W 1° 46',
19 coded C) (A to C: conventional design), Chantepie (N 48° 5', W 1°37', coded D), Saint Jacques
20 de la Lande (N 48° 3', W 1° 43', coded E) and Le Rheu (N 48° 6', W 1° 48', coded F) (D to F:
21 new design). All neighborhoods were built during the same period of time (between 1997 and
22 2000) and were adjacent to rural areas (field or meadow, so the colonization from surrounding
23 habitats is thus not seen as limited; Varet et al. 2011). Their area varied from 10 ha to 14.5 ha. All

1 sites were mapped using ArcView by interpretation of orthophotographs (2006), cadastral data
2 and ground-truthing. Mean house density was two times higher in the new neighborhood design
3 compared to that in the conventional one (31 vs. 16 houses/ha, respectively).

4 Sample points were randomly selected (Arcview, Geo Wizards) within public hedgerows, and
5 spaced at least by 10 meters so that the traps were considered independent (Topping and
6 Sunderland 1992). Hedgerows were planted and designed at the creation of the neighborhood.

7 Each sample point consisted of one pitfall trap (diameter at the surface: 85mm) covered with a
8 plastic roof. The pitfall traps were filled with a preservation solution composed of 50%
9 monopropylene glycol and 50% aqueous salt solution of 100g/l (best fluid for collecting ground-
10 dwelling spiders; Schmidt et al. 2006). At each site, between 40 and 44 traps were set up and
11 collected (some traps were stolen or damaged during the sampling period, which was taken into
12 account by dividing the total catches of each trap by the effective collection, see below). The
13 pitfall traps were emptied every two weeks for eight weeks between mid-April 2009 and mid-
14 June 2009. The temporal sampling effort was consequently limited to favor a larger spatial extent
15 (e.g. Lövei and Magura 2011); other studies in the same area also showed that most carabid
16 beetle and spider species were collected during the spring compared to an annual sampling
17 (sampling in one site over 3 years and use of rarefaction methods in three sites; Varet 2011).

18 Each site was characterized by the following landscape variables: length, number and mean
19 length of public hedgerows, proportion of public green space, number and mean size of public
20 green patches, shortest distance between two patches and index of contagion. One meter around
21 each pitfall trap, the following parameters were measured: litter depth (from 1=thin to 3=thick),
22 presence of grass, shrub and tree strata, origin of plant species (local and/or exotic).

23

1 *Species identification and classification*

2 Carabid beetles and spiders were preserved in 70% ethanol and stored in the University
3 collection (Rennes, France). Adult carabid beetles were identified using Jeannel (1941; 1942)
4 and Trautner and Geigenmüller (1987), whereas adult spiders were identified using Roberts
5 (1987; 1995) and Heimer and Nentwig (1991). Catches in pitfall traps were related to trapping
6 duration and pitfall perimeter in order to calculate an ‘activity trappability density’ (number of
7 individuals per day and per meter; Sunderland et al. 1995), further abbreviated as ‘activity-
8 density’. Carabid beetles and spiders were classified into size classes (using mainly Roberts 1987
9 for spiders and Bouget 2004 for carabid beetles). The size classes (in mm, respectively size1,
10 size2, size3) were 0-3, 3-5, ≥ 5 for adult spiders and 0-5, 5-10, ≥ 10 for carabid beetles.

11

12 *Statistical analysis*

13 We performed multivariate analyses of activity-density of all species using the software
14 CANOCO (ter Braak and Šmilauer 2002) in order to analyze the patterns of species composition
15 in the 6 sites. The choice between linear (Principal Component Analysis: PCA) or unimodal
16 (Correspondence Analysis: CA) analyses depended on the length values of the first axis gradient
17 previously realized with DCA (Detrended Correspondence Analysis). To test for differences in
18 activity-density (total, per species represented by more than 1% of total catches and per size
19 class) and species richness between the neighborhood designs, we used nested general linear
20 model (GLM) with a quasi-Poisson distribution performed using data from the individual traps
21 (Vincent and Haworth 1983; O’Hara and Kotze 2010). City was nested within neighborhood
22 design. The resulting data were analyzed with R software (R Development Core Team 2009)
23 using the glmmPQL package (e.g. Venables and Ripley, 2002).

1

2 **Results**

3 *Description of the neighborhood designs*

4 The analysis of the landscape structure of the 6 neighborhoods from the 2 designs revealed that
5 the number of green patches and the length of public hedges were higher in the new
6 neighborhood design and that the index of contagion was almost significantly higher in the new
7 neighborhood design while the other parameters were not significantly different between the two
8 urban designs (Table 1). All sites were characterized by hedgerows with a medium-depth litter,
9 low percentages of herbaceous and tree strata, dense shrubs, and a dominance of local plant
10 species compared to exotic species (Table 1).

11

12 *Description of the fauna*

13 In total, 2077 carabid specimens belonging to 39 species were collected. Individuals of *Nebria*
14 *brevicollis* accounted for more than 50% of the total catch. The number of species varied
15 between the 6 neighborhoods (site A: 21, B: 21, C: 27, D: 17, E: 14, F: 20), as did the number of
16 individuals (site A: 249, B: 130, C: 423, D: 283, E: 158, F: 834). In total, 4413 spider specimens
17 belonging to 117 species were collected. Individuals of *Pardosa hortensis*, *Pardosa prativaga*,
18 *Ozyptila praticola*, *Zodarion italicum*, *Dysdera erythrina* and *Trochosa ruricola* accounted for
19 more than 40% of the total catch. The number of species and individuals were similar in all
20 neighborhoods (between 55 and 73 species; site A: 55, B: 73, C: 70, D: 71, E: 67, F: 58; and
21 between 616 and 891 individuals; site A: 714, B: 616, C: 891, D: 767, E: 742, F: 683).

22

23 *Species assemblages vs. urban forms*

1 Axis 1 of the CA on carabid beetle assemblages (Fig. 2) represented 10.3% of inertia and Axis 2,
2 8% of inertia. Axis 1 of the CA on spider assemblages (Fig. 3) represented 5.7% of inertia and
3 Axis 2, 5% of inertia. The neighborhood design variable on axis 1 and 2 of CAs was very close to
4 the origin for both groups, and neighborhood designs cannot be segregated by the global
5 composition of assemblages, (Figs. 2 and 3).

6

7 *Species activity-density and richness vs. urban forms*

8 The total activity-density of carabid beetles was significantly higher in the new neighborhood
9 design while the total activity-density of spiders and the species richness of both groups were
10 independent from the neighborhood design. Several species were significantly associated with
11 the neighborhood design. The carabid beetles *Harpalus rufipes* and *N. brevicollis* and the spider
12 *D. erythrina* were significantly more abundant in the new neighborhood design, while the
13 carabid beetles *Asaphidion stierlini* and *Pterostichus melanarius* and the spiders *Agoeca inopina*,
14 *Alopecosa pulverulenta*, *Hahnia nava*, *Pachygnatha degeeri*, *Pardosa amentata*, *Pardosa*
15 *saltans*, *Phrurolithus festivus*, *T. ruricola* and *Z. italicum* were significantly more abundant in the
16 conventional neighborhood design. Large carabid beetles (size class 3: Table 2) were more
17 abundant and small spiders (size class 1: Table 3) less abundant in the new neighborhood design
18 compared to the conventional one.

19

20 **Discussion**

21 From a strictly urbanistic point of view, the two urban forms are obviously distinct (type and
22 density of housing, coverage ratio, floor area ratio; Chapuis et al. 2005), but from a landscape
23 perspective, the distinction was less obvious in this study. In terms of composition, urban forms

1 could be distinguished according to two parameters. The higher density and length of hedgerows
2 and the higher number of public green space patches in the new urban design are in accordance
3 with the goals aimed at the conception of these neighborhoods, and supported our hypotheses.
4 Regarding landscape connectivity, both urban forms were not really different. Indeed, whatever
5 the urban form, the neighborhood was split by dense public roads. This analysis at a landscape
6 scale of the two urban forms was yet based on six sites only, and nevertheless there was a trend
7 for the new, compact, urban form to offer a better connectivity between green habitats. The goals
8 set by new urban form designers are thus not all reached here.

9 Several, although not numerous, species had some population activity-densities dependent on
10 urban form. Most of these species were more abundant in neighborhoods of conventional design.
11 This can be explained by the fact that most of these species are generalist or open field species,
12 like the carabids *Asaphidion stierlini* and *Pterostichus melanarius* (Luff 1998; Bouget 2004) and
13 the spiders *Agoeca inopina*, *Alopecosa pulverulenta*, *Pachygnatha degeeri*, *Pardosa amentata*,
14 *Phrurolithus festivus*, *T. ruricola* and *Z. italicum* (Hänggi et al. 1995; Harvey et al. 2002).
15 Indeed, the conventional neighborhood has a lower density of public hedgerows and is
16 consequently likely to host more species preferring open environments. Yet, two forest species,
17 the spiders *Hahnina nava* and *Pardosa saltans*, were significantly more abundant in the
18 conventional design than in compact neighborhoods, but they occurred at low numbers in both
19 urban forms (although sufficient to be included in the individual species analysis). More
20 generally, forest species were little represented in both urban forms and species richness of
21 carabid beetles and spiders did not differ among the neighborhoods, contrary to our first
22 hypothesis with the activity-density of forest species not higher in new urban forms. This can be
23 partly due to the similarity of the urban forms when considering certain landscape indexes.

1 Indeed, the diversity of assemblages is partly shaped by the landscape structure (e.g. Le Coeur et
2 al. 2002; Schmidt et al. 2005; Schweiger et al. 2005; Hendrickx et al. 2007). But habitat quality
3 (including frequency and intensity of disturbances) also determines the local presence of
4 specialist or generalist species. The lack of an effect of urban forms on species richness, as well
5 as the low occurrence of forest species, can then be also attributed to the similarity in quality and
6 management of the hedgerows between the two urban forms. It should be emphasized that
7 hedgerows in both new and conventional urban forms are managed by the same people, who
8 apply their skills independently from the urban form itself (in the conurbation of Rennes; Le
9 Rudulier 1994). Yet the management of green spaces made up of non-native species may re-
10 create and maintain some diversified assemblages (e.g. for carabid beetles; Magura et al. 2000),
11 intensive management is well-known to homogenize invertebrate faunas, and maintain species of
12 young successional stages even in older neighborhood (comparisons between 14 and 30 year-old
13 sites in the same study area; Varet et al. in press.).

14 Confirming our second hypothesis, the total activity-density of large individuals (carabid beetles)
15 was higher and small individuals (spiders) were lower in the new urban design than in the
16 conventional urban designs with individual houses and gardens. Large individuals (carabid
17 beetles), considered to have a lower dispersal capacity (den Boer 1977; Dajoz 2002), are more
18 numerous in new urban designs. These designs include more hedgerows and seem to offer a
19 better connectivity than conventional designs. New urban designs include more continuous
20 suitable elements, favoring the dispersal of large carabid individuals (Burel 1989), as opposed to
21 neighborhoods with more fragmented public green spaces and hedgerows due to individual
22 houses. Small individuals (spiders), considered as having a higher dispersal capacity (size and
23 mass limitation of long-distance dispersal in spiders; e.g. Coyle et al. 1985), were also more

1 numerous in conventional neighborhoods. The lower number of hedgerows in these
2 neighborhoods allows for a better dispersal of small spiders using ballooning as a main dispersal
3 method (Dean and Sterling 1985), mostly by decreasing the number of barriers to (aerial)
4 dispersers (Larrivé and Buddle 2009).

5 Although obvious differences in some landscape parameters were highlighted, only slight,
6 mostly non-significant differences were found in arthropod assemblages, despite the use of
7 complementary biological models (e.g. Desender and Maelfait 1999; Pétilion et al. 2008). This
8 can be explained by the fact that urban environments, whatever their design, are considered
9 highly disturbed (Blair 1996; Ormerod 2003) and consequently host mostly species of young
10 successional stages. This study also underlines the need to conduct trait-based analyses on top of
11 classical species richness approach (see also Magura et al. 2008; Tóthmérész et al. 2011; Horváth
12 et al. 2012). As an applied conclusion, urban consolidation, by permitting a higher housing
13 density with similar arthropod assemblages, is likely to reduce biodiversity loss in cities.

14

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1 **Table 1:** Landscape indexes for each neighborhood and comparison of means between the two
 2 urban designs (significance by Mann-Whitney tests indicated with bold font). Bold font indicates
 3 significant difference among urban designs. For information, the following local parameters are
 4 also provided: mean litter depth (see the scores in Material and Methods), occurrence of grass,
 5 shrub and tree strata and local and exotic species.

	New design			Conventional design			U-value	p-value
	Site D	Site E	Site F	Site A	Site B	Site C		
length of public edges (m)	281.6	335.5	252.9	138	221.1	95.5	U1=0 (U2=9)	0.0495
number of public edges	6.4	9	9.1	3.6	9.1	1.5	U1=2.5 (U2=6.5)	0.3827
mean length of public edges (m)	44.1	37.4	27.9	38.6	21.4	66	U1=4 (U2=5)	0.8273
the proportion of public green space	34.4	34.3	13.3	12.3	22.6	11.6	U1=1 (U2=8)	0.1266
number of public green patches	4.3	3.9	5.1	2.4	3.6	2.7	U1=0 (U2=9)	0.0495
mean size of public green patch (ha)	756	884	261	502	621	421	U1=3 (U2=6)	0.5127
the shortest distance between two patches (m)	5.3	4.2	6.3	8.1	4.4	9.9	U1=2 (U2=7)	0.2752
index of contagion	35	36	38	35	32	34	U1=0.5 (U2=8.5)	0.0765
Mean litter depth	2.23	1.80	1.43	1.86	1.71	1.84		
Occurrence (%) of								
Herbaceous stratum	43.18	40.91	11.36	42.11	32.56	55.26		
Shrub stratum	100	100	100	100	100	100		
Tree stratum	25.00	15.90	0	0	25.58	23.68		
Native species	68.18	51.16	81.81	97.37	74.42	50.00		
Exotic species	40.91	60.47	34.09	44.74	39.53	63.16		

1 **Table 2.** Result of the GLM analysis of the effect of neighborhood design (CD=Conventional design; ND=new design) on species richness and
2 activity-density (total, mean per species and per size class) for the most abundant carabid beetle species (i.e. represented by at least 1% of total
3 catches). Bold font indicates significant difference among urban designs.

4

Genus species	Authority, year	code	Effect of city		Effect of neighborhood design				5		
			F-ratio	p-value	Means in ND	Means in CD	F-ratio	p-value	result		
<i>Amara sp.</i>		AMAR	2.23	0.066	0.013	±0.003	0.015	±0.003	0.12	0.733	6
<i>Asaphidion flavipes</i>	(Linnaeus, 1761);	ASFL	3.44	0.009	0.047	±0.014	0.038	±0.017	0.23	0.633	
<i>Asaphidion stierlini</i>	(Heyden, 1880)	ASST	3.24	0.013	0.003	±0.001	0.016	±0.013	5.17	0.024	ND<CD ⁷
<i>Bembidion lampros</i>	(Herbst, 1784)	BELA	4.21	0.003	0.005	±0.002	0.014	±0.006	3.75	0.054	
<i>Harpalus affinis</i>	(Fabricius, 1792)	HAAE	1.07	0.37	0.005	±0.002	0.006	±0.002	0.05	0.820	8
<i>Harpalus rufipes</i>	(De Geer 1774)	HARF	8.39	<0.001	0.023	±0.012	0.003	±0.002	12.22	<0.001	ND>CD
<i>Nebria brevicollis</i>	(Fabricius, 1792)	NEBR	8.89	<0.001	0.364	±0.086	0.174	±0.030	8.38	0.004	ND>CD
<i>Notiophilus biguttatus</i>	(Fabricius, 1779)	NOBI	7.88	<0.001	0.047	±0.010	0.029	±0.007	2.98	0.086	
<i>Notiophilus quadripunctatus</i>	(Dejean, 1826)	NOQU	7.42	<0.001	0.055	±0.011	0.044	±0.009	0.80	0.378	
<i>Pterostichus cupeus</i>	(Linnaeus, 1758)	PTCU	3.93	0.004	0.004	±0.002	0.007	±0.002	1.24	0.266	
<i>Pterostichus madidus</i>	(Fabricius, 1775)	PTMA	9.40	<0.001	0.009	±0.005	0.016	±0.006	2.27	0.133	
<i>Pterostichus melanarius</i>	(Illiger, 1798)	PTME	3.22	0.013	0.000	±0.000	0.013	±0.013	9.45	0.002	ND<CD
Size class	Size 1		6.12	<0.001	0.162	±0.027	0.147	±0.038	0.14	0.710	
	Size 2		1.03	0.391	0.037	±0.006	0.047	±0.008	0.92	0.338	
	Size 3		9.95	<0.001	0.401	±0.087	0.219	±0.036	6.70	0.010	ND>CD
Species richness			12.65	<0.001	2.333	±0.145	2.403	±0.204	0.09	0.761	
Total activity-density			12.43	<0.001	0.603	±0.093	0.421	±0.060	4.14	0.043	ND>CD

1 **Table 3.** Result of the GLM analysis of the effect of neighborhood design (CD=Conventional design; ND=new design) on species richness and
2 activity-density (total, mean per species and per size class) for the most abundant spider species (i.e. represented by at least 1% of total catches).
3

Genus species	Authority, year	code	Effect of city		Effect of neighborhood design						
			F-ratio	p-value	Means in ND		Means in CD		F-ratio	p-value	result
<i>Agroeca inopina</i>	Cambridge, 1886	Agrin	2.44	0.047	0.009	±0.003	0.018	±0.004	4.47	0.036	ND<CD
<i>Alopecosa pulverulenta</i>	(Clerck, 1757)	Alopu	6.07	<0.001	0.017	±0.003	0.041	±0.013	6.98	0.009	ND<CD
<i>Clubiona comta</i>	Koch, 1839	Cluco	5.34	<0.001	0.018	±0.004	0.018	±0.004	0.01	0.906	
<i>Clubiona terrestris</i>	Westring, 1851	Clute	2.22	0.07	0.016	±0.003	0.012	±0.003	0.72	0.397	
<i>Diplostyla concolor</i>	(Wider, 1834)	Dipco	0.89	0.47	0.009	±0.002	0.014	±0.003	2.25	0.14	
<i>Drassodes lapidosus</i>	(Walckenaer, 1802)	Drala	7.96	<0.001	0.015	±0.003	0.013	±0.004	0.35	0.555	
<i>Dysdera erythrina</i>	(Walckenaer, 1802)	Dyser	3.10	0.016	0.046	±0.008	0.026	±0.005	4.87	0.028	ND>CD
<i>Enoplognatha thoracica</i>	(Hahn, 1833)	Enoth	5.03	<0.001	0.012	±0.003	0.022	±0.007	2.98	0.085	
<i>Erigone dentipalpis</i>	(Wider, 1834)	Eride	1.88	0.120	0.017	±0.005	0.011	±0.005	0.1.00	0.319	
<i>Hahnia nava</i>	(Blackwall, 1841)	Hahna	1.71	0.148	0.008	±0.002	0.027	±0.006	10.37	0.001	ND<CD
<i>Microneta viaria</i>	(Blackwall, 1841)	Micvi	4.07	0.003	0.028	±0.004	0.022	±0.005	1.27	0.261	
<i>Neriere clathrata</i>	(Sundevall, 1830)	Nercl	1.83	0.124	0.020	±0.004	0.017	±0.004	0.36	0.549	
<i>Ozyptila praticola</i>	(Koch, 1837)	Ozypr	3.82	0.005	0.079	±0.010	0.068	±0.009	0.69	0.406	
<i>Pachygnatha degeeri</i>	Sundevall, 1829	Pacde	6.62	<0.001	0.009	±0.003	0.023	±0.008	5.42	0.021	ND<CD
<i>Pardosa amentata</i>	(Clerck, 1757)	Param	4.93	<0.001	0.002	±0.002	0.027	±0.015	12.76	<0.001	ND<CD

<i>Pardosa hortensis</i>	(Thorell, 1872)	Parho	3.04	0.018	0.226	±0.038	0.244	±0.036	0.13	0.722	
<i>Pardosa prativaga</i>	(Koch, 1870)	Parpr	12.16	<0.001	0.100	±0.032	0.052	±0.011	4.87	0.028	
<i>Pardosa pullata</i>	(Clerck, 1757)	Parpu	9.00	<0.001	0.028	±0.011	0.017	±0.007	1.75	0.187	
<i>Pardosa saltans</i>	Töpfer-Hofmann, 2000	Parsa	3.95	0.004	0.009	±0.005	0.025	±0.012	3.67	0.057	ND<CD
<i>Phrurolithus festivus</i>	(Koch, 1835).	Phrfe	2.92	0.022	0.009	±0.002	0.021	±0.004	7.38	0.007	ND<CD
<i>Pisaura mirabilis</i>	Clerck, 1757	Pismi	5.43	<0.001	0.027	±0.004	0.023	±0.006	0.39	0.532	
<i>Scotina celans</i>	(Blackwall, 1841)	Scoce	0.67	0.620	0.014	±0.003	0.015	±0.004	0.09	0.767	
<i>Tenuiphantes tenuis</i>	(Blackwall, 1852)	Lepte	3.17	0.015	0.016	±0.003	0.020	±0.004	0.75	0.386	
<i>Trochosa ruricola</i>	(de Geer, 1778);	Troru	8.06	<0.001	0.016	±0.004	0.057	±0.011	20.92	<0.001	ND<CD
<i>Zelotes pedestris</i>	(Koch, 1837)	Zelpe	4.06	0.003	0.016	±0.011	0.012	±0.004	0.28	0.597	
<i>Zodarion italicum</i>	(Canestrini, 1868)	Zodit	11.17	<0.001	0.029	±0.007	0.049	±0.009	4.53	0.034	ND<CD
Size class	Size 1		4.59	0.001	0.258	±0.018	0.336	±0.027	6.98	0.008	ND<CD
	Size 2		1.98	0.098	0.381	±0.043	0.385	±0.040	0.00	0.947	
	Size 3		0.46	0.766	0.321	±0.033	0.352	±0.034	0.44	0.509	
Species richness			3.34	0.011	7.515	±0.353	7.958	±0.363	0.80	0.372	
Total activity-density			1.86	0.118	1.031	±0.080	1.142	±0.081	0.96	0.327	

1 **Fig. 1.** Location of the 6 neighborhoods (conurbation of Rennes, Brittany, France); sites A to
2 C have conventional designs and sites D to F have new designs.

3

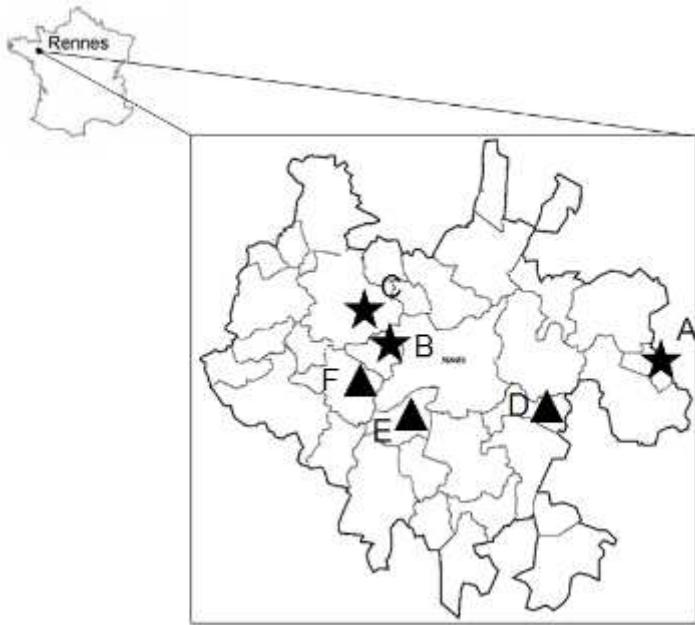
4 **Fig. 2.** Ordination diagram of the first two axes of Corresponding Analysis for 26 carabid
5 beetle species and 251 samples. For projection, the species fit range is from 3% to 100%; 14
6 species are represented. The inverted triangle represents the new neighborhood design and the
7 star represents the conventional neighborhood design. Species codes are given in Table 2 and:
8 Haru=*Harpalus rubripes* (De Geer, 1774); Lefu=*Leistus fulvibarbis* (Dejean, 1826); Lopi=*Loricera pilicornis*
9 (Fabricius, 1775); Trec=*Trechus* sp.

10

11 **Fig. 3.** Ordination diagram of the first two axes of Corresponding Analysis for 69 spider
12 species and 251 samples. For projection, the species fit range is from 3% to 100%; 39 species
13 are represented. The inverted triangle represents the new neighborhood design and the star
14 represents the conventional neighborhood design. Species codes are given in Table 3 and:
15 Alocu=*Alopecosa cuneata* (Clerck, 1757); Atyaf=*Atypus affinis* Eichwald, 1830; Censy=*Centromerus sylvaticus*
16 (Blackwall, 1841); Clure=*Clubiona reclusae* Pickard-Cambridge, 1863; Draso=*Drapetisca socialis* (Sundevall,
17 1833); Hapsl=*Haplodrassus silvestris* (Blackwall, 1833); Harho=*Harpactea hombergi* (Scopoli, 1763);
18 Micpu=*Micaria pulicaria* (Sundevall, 1831); Micsu=*Micrargus subaequalis* (Westring, 1851); Ozysi=*Ozyptila*
19 *simplex* (Cambridge, 1862); Pansu=*Panamomops sulcifrons* (Wider, 1834); Phrmi=*Phrurolithus minimus* Koch,
20 1839; Pirpi=*Pirata piraticus* (Clerck, 1757); Robar=*Robertus arundineti* (O. Pickard-Cambridge, 1871);
21 Steli=*Stemonyphantes lineatus* (Linnaeus, 1758); Trosc=*Troxochrus scabriculus* (Westring, 1851);
22 Trote=*Trochosa terricola* Thorell, 1856; Walac=*Walckenaeria acuminata* (Blackwall, 1833); Zelap=*Zelotes*
23 *apricorum* (Koch, 1876); Zelsu=*Zelotes subterraneus* (Koch, 1833); Zorsp=*Zora spinimana* (Sundevall, 1833).

1 Fig. 1.

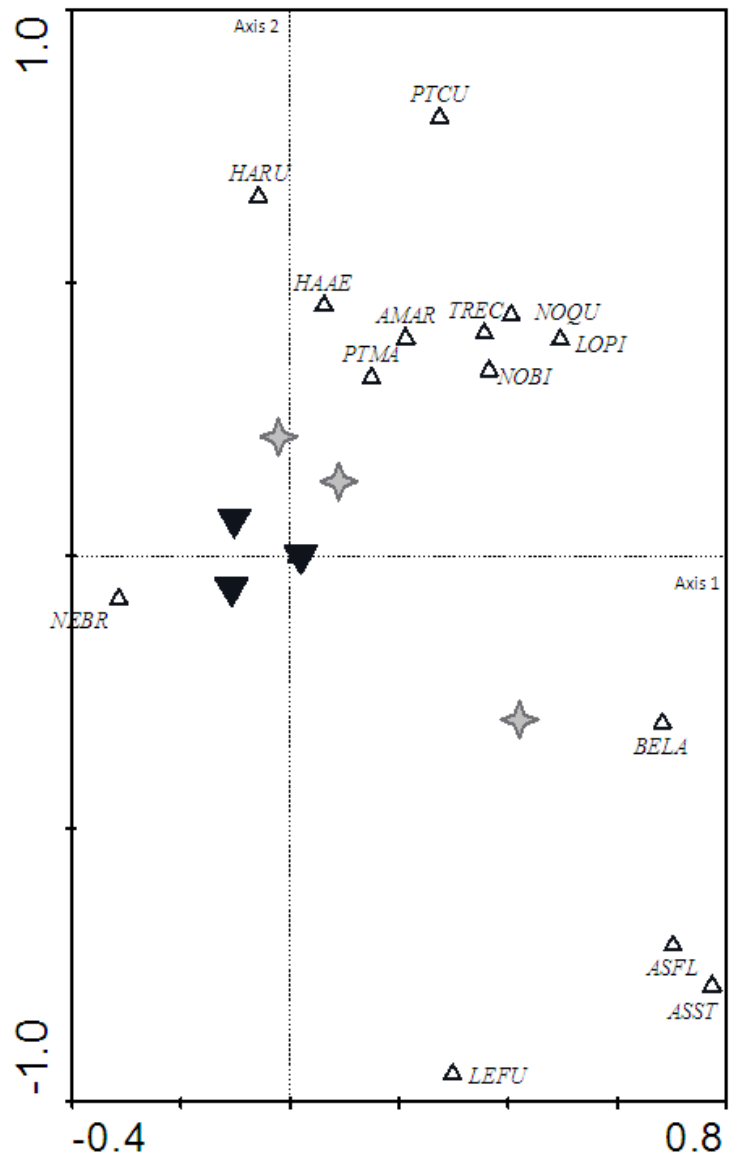
2



3

1 Fig. 2.

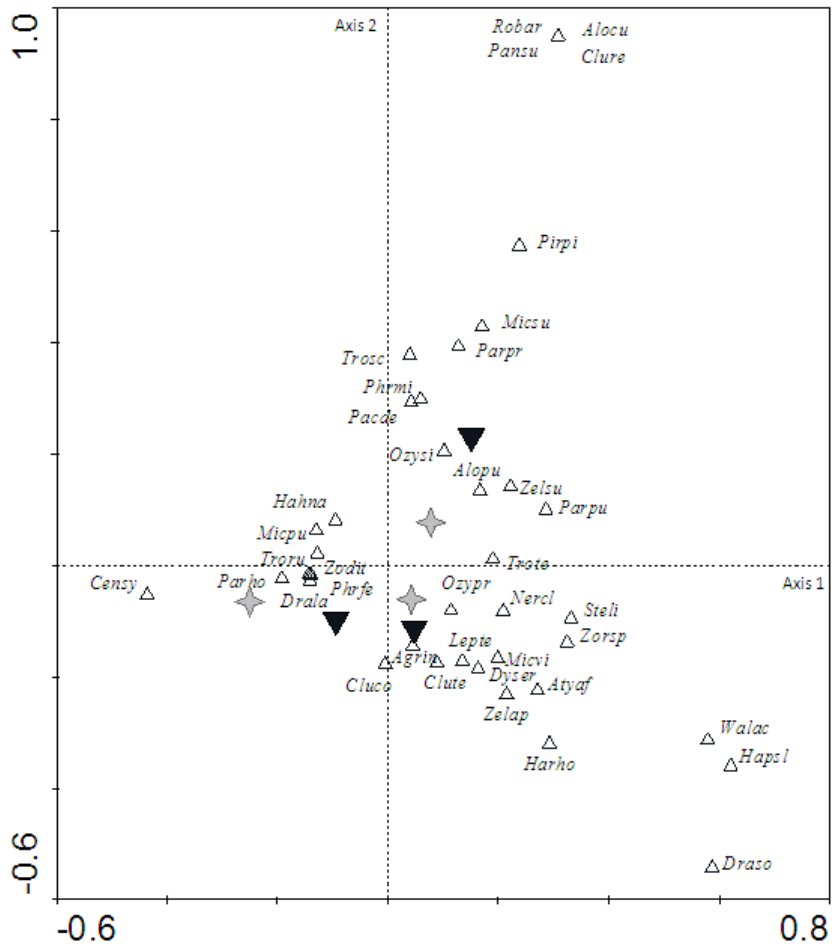
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3

1 Fig. 3.

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4