Synecology of spiders (Araneae) of gravel banks and environmental constraints along a lowland river system, the Common Meuse (Belgium, the Netherlands)

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Abstract: Gravel banks along the Common Meuse (Belgium) were sampled for epigeal invertebrates in order to investigate how assemblages are structured in relation to gravel bank characteristics (size, degree of isolation, vegetation cover, silt and periodic flooding). The spider species composition was dominated by Linyphiidae and Lycosidae. Species having short life cycles and well-developed aerial dispersal, litter-dependent hygrophiles and agrobionts were collected on all sites. The presence of xerothermic species and gravel-bank specialists was limited to scarcely covered, less dynamic gravel banks. By means of an ordination, we were able to reveal important characteristics that relate to invertebrate predator assemblage structure on the different gravel banks. Besides isolation and the level of flooding disturbance, the vegetation density and the presence of silt appeared to affect general diversity patterns, but also the diversity of species belonging to different ecological groups. The influence of the number and area of the banks in the vicinity can be interpreted as an ecological landscape effect. To preserve riparian specialists, river management along the Common Meuse should maintain disturbances caused by regular inundations of the riverine habitats. Overall we can state that there is not an univocal definition of "the" gravel bank. Therefore the aims of the current and future conservation policy should imply both dynamic and more elevated banks, in order to guarantee a high degree of local and regional heterogeneity throughout the river system.

Key words: spider assemblages, river banks, flood disturbance, landscape structure, river ecosystem

Introduction

Assemblages can be seen as local snapshots of a spatiotemporal continuous system, having no status as distinct biological entities and hence dependent of species' life history patterns, dispersal capacities and environmental constraints (HENGEVELD, HEMERIK 2002, BONTE *et al.* 2003). The understanding and structure of terrestrial predator assemblages from exposed riverine sediments along lowland river systems and their correlations with local habitat structure is poorly documented (ADIS, JUNK 2002, HENSHALL 2003). In these studies assemblages are characterized by fluvial dynamics and local habitat properties. Recent research of invertebrate assemblages focused upon upland and low mountainous stretches (BONN, KLEINWÄCHTER 1999, MANDERBACH, FRAMENAU 2001, ARMBRUSTER 2002, 2002, FRAMENAU *et al.* 2002, SADLER *et al.* 2004). The amount of litter and other micro-environmental factors were found to influence spider assemblages from riparian habitats like tidal marshes (HENDRICKX *et al.* 1998, PÉTILLON *et al.* 2004). With regard to the species-specific requirements of spiders, MAELFAIT *et al.* (2004) state that slight changes in habitat quality can cause important changes in the spider assemblage composition, making them useful indicators for nature conservation, comparable in that respect with carabid beetles (DESENDER, MAELFAIT 1999, JOCHEMS, VAN LOOY 2001, SADLER *et al.* 2004).

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The Common Meuse, forming both the natural and geographical border between Flanders (Belgium) and The Netherlands, is denominated as a lowland gravel river. In general riparian habitats (alluvial floodplains, gravel banks, etc.) are mostly characterized by a patchy spatial distribution along the river trajectory (PLACHTER, REICH 1998, SADLER *et al*. 2004). The main differentiating processes are related to the rain dependable water level fluctuations and the microclimatological circumstances of the gravel banks *in se* (RENÖFALT *et al*. 2005). Habitat fragmentation and in general landscape configuration, can have drastic consequences for all living organisms. At the moment it is one of the central themes regarding nature management and conservation (HEINO, HANSKI 2001, WIENS 2001). Gravel banks along the Common Meuse have always been present. Though from 1860 onwards dikes along the River Meuse were fortified to secure safe navigation, to improve flood protection and to allow agriculture on the fertile floodplain soils (VAN WINDEN *et al*. 2001). By consequence natural river dynamics became suppressed and natural riverine habitats were fragmented (VAN LOOY *et al*. 2002). Nowadays, following the "Living River"-concept (NAGELS *et al*. 1999), the natural river dynamics of the Common Meuse are being restored. The present habitat management attempts to re-establish the natural character of the Common Meuse and its surroundings (JOCHEMS, VAN LOOY 2001). Dikes are being removed, banks are lowered and the summer bed is widened (VAN LOOY, DE BLUST 1998) in order to restore the contact between the river and its winter bed and to re-create riverine habitats (NAGELS *et al*. 1999).

We investigated whether gravel banks under restoration support a typical spider fauna and if ecological species groups are evenly spread over all gravel banks or if they only occur in a selection of banks with distinct environmental properties.

Material and Methods

The Common Meuse (45 km) is the shallow, less diked or dammed part of the River Meuse (LIEFVELD *et al*. 2001). It marks the border between The Netherlands and Flanders (Belgium) (Fig. 1). The strong river flow fluctuations, coarse gravel and sharp sand characterize the watercourse (LIEFVELD *et al*. 2001). The gravel banks situated along the trajectory of the Common Meuse can be defined as a top layer of coarse shingle with between a sharp sand-gravel fraction, mostly covered with a thin layer of silt (VAN LOOY, DE BLUST 1998), shifting into steep loamy banks towards the dike. It is the only gravel river in Flanders, and one of the few lowland gravel rivers in Europe (VAN LOOY, DE BLUST 1998). The extreme microclimatic conditions of the gravel banks are caused by the bare gravel (LOMMELEN 2000). Besides irregular spring and summer inundations, all sites are permanently flooded during autumn and winter. Only when the river discharge drops below 200 m^3/s, the gravel banks are exposed (VANACKER 2000). Patch size and relative height of the gravel banks varies from day to day and depends of the water level fluctuations (PLACHTER, REICH 1998). The degree of vegetation succession depends both on the silt deposition (SLUIS, TANDARICH 2004, NEUMEIER 2005), the river dynamics (FRANKLIN *et al*. 2001) and the morphological structure of the substrate (BONN, KLEINWÄCHTER 1999, EYRE *et al*. 2002). A species-poor and scarce pioneer vegetation appears some meters from the waterline (SCHAMINÉE *et al*. 1998), changing into brushwood towards the dike (VANACKER 2000). Flooding offers new habitats for succession of terrestrial plants and animal communities (BONN, KLEINWÄCHTER 1999). Yet many riparian species, e.g. *Pardosa wagleri, Pirata knorri* (MANDERBACH, FRAMENAU 2001), *Bryodema tubercultata* (STELTER *et al*., 1997), depend on inundations so that specific habitat characteristics are provided. The temporary nature of gravel banks makes them unique habitats for several highly specialized invertebrates of great conservational value (HENSHALL 2003, SADLER *et al*. 2004). Gravel banks along the Common Meuse are surrounded by a variety of biotopes, enclosing both arable land and alluvial grasslands.
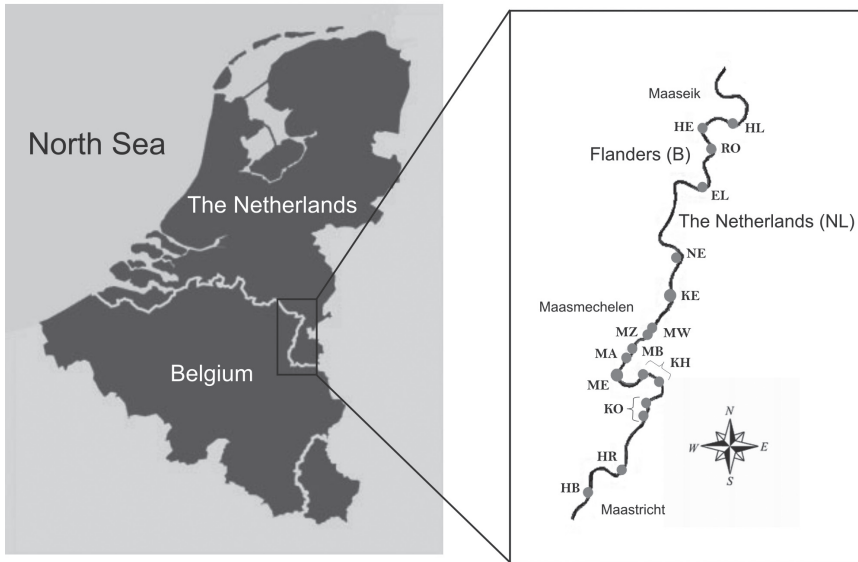
Fig. 1. Location of the gravel banks along the Common Meuse trajectory in 1998. Sampled gravel banks are indicated by dots.

In total 17 gravel banks, situated both on Belgian and Dutch side of the river, were sampled along the 45 km long trajectory of the Common Meuse (Fig. 1). At each sample site, three or more pitfalls (Ø = 9.5 cm, 4% formalin solution) were placed from the end of May until the end of August, spaced ca. 10 meter apart, which should suffice to avoid interference between traps for spider catches (Topping, Sunderland 1992, Pétillon *et al.* 2004). During the field survey several parameters were measured: 1) vegetation cover, 2) substrate structure (mean gravel size, presence of sand and/or silt), 3) relative height of the gravel banks (inverse measure; calculate as the slope of the regression line that symbolizes the relation between the discharge of the river at the moment of each pitfall collecting (X) and the distance of the pitfalls to the waterline (Y), troughout the sample period), 4) gravel bank dimensions (area, circumference, length) and 5) distance to and total area of nearest banks. Pitfall traps register arthropod activity patterns, and are affected by both population density and species-specific movement rates (Maelfait, Baert 1975). Furthermore microhabitat structure and movement behaviour could also affect trappability in spiders (Topping, Sunderland 1992).

Community structure and reaction of the species to environmental gradients were indirectly explored by means of an unconstrained indirect gradient analysis (DCA = Detrended Correspondence Analysis (Hill 1979)). Only the more abundant species were taken into account for the ordination analysis (Bonte *et al.* 2002). Thereby a multidimensional ordering of the traps is revealed based on their species composition similarity. Sample sites, in this case gravel banks, with a similar assemblage are closely ordered, while those with a completely different species composition are ordered distantly (Bonte *et al.* 2002). Ecological characteristics of spiders were mainly derived from Hänggi *et al.* (1995), Maelfait *et al.* (1998), Roberts (1998), Nentwig *et al.* (2002) and Harvey *et al.* (2002).

Results

After Bonferroni-correction, only the presence of silt and both the vegetation cover (r = 0.61; p<0.05), and the total area of banks in the vicinity (r = -0.63; p<0.05) showed a significant cor-

relation. In total 11.438 spiders (not standarized numbers) were collected from 14 gravel banks along the Common Meuse, divided over 82 species and 11 families (Table 1). About half of the catches belonged to the Linyphiinae and Erigoninae. The linyphiid *Oedothorax retusus* was the most common species, representing over 25% of the grand total of the catches. *Pardosa agricola* as well as *Erigone dentipalpis* took up about 12% of the catches. Both linyphiids occurred on all the sites, whereas *P. agricola* only appeared on 9 of the gravel banks.

Ordination of spider data revealed an axis 1 (eigenvalue 0.423), showing a clear relationship with the environmental factors and the spreading of the gravel banks and explaining 22.67% of the total variance in the species data (Fig. 2). Less isolated gravel banks ($r_{(2)12} = 0.746$, $p<0.05$), thus with higher extent of connectivity, were situated more towards the left side of the ordination plot. Furthermore a landscape effect is signified by the number of gravel banks in the vicinity of the bank under consideration ($r_{(2)12} = -0.587$, $p<0.05$). On the left of the plot banks situated relatively lower in respect to the water level ($r_{(2)12} = -0.560$, $p<0.05$) could be found, as well as banks with a denser vegetation ($r_{(2)12} = -0.606$, $p<0.05$) and mostly covered with a layer of silt ($r_{(2)12} = -0.529$, $p<0.05$). Eurytopic, frequently ballooning species were centered in the ordination, and thus present on all gravel banks, just as several ubiquitous ground dwelling grassland species. Hygrophiles cluster together on the left of the output (gravel banks HB, KO, MB). Specialized xerophiles and psammophiles cluster together on the right side of the ordination (HL, KE, ME). Additionally typical xerothermic species are found in high abundance on KE in comparison with the other banks. Typical riverine species can be found on both frequent flooded as rather elevated gravel banks (resp. EL, HE, HL, RO and KE, ME). Moreover axis 2 (eigenvalue 0.126) explained 6.79% of the scattering of species. Along axis 2 perennial species with a short life-cycle are found on the right and on the left side long-lived species with an annual life-cycle. These eurytopic species probably colonize the gravel banks from the adjacent habitats, comparable with source-sink dynamics (JOHNSON 2004). Overall axis 2 probably accounts for a landscape-effect, though no clear explanation could be restrained.

Discussion

Spider synecology

The total number of spider species is rather low in comparison with other studies concerning recently fragmented and dynamic biotopes (BONTE *et al*. 2003, HENDRICKX *et al*. 1998). Possible reasons could be the long-lasting winter inundations, making the gravel banks unsuitable for colonization (BONN *et al*. 2002), and the large-scale fluctuations in temperature. Frequent ballooners and cursorial meadow species can be considered as typical pioneers of gravel banks as well as other terrestrial habitats which are regularly flooded (cf. WOHLGEMUTH - VON REICHE, GRUBE 1999). Though when looking at the ordination a clear distinction can be made between annual and perennial pioneer species. Former, for instance cursorial lycosids, seem to be present once gravel bank stability increases, thus probably colonizing the banks from the adjacent habitats, which seem to be mostly grasslands under nature management (source-sink dynamics (cf. JOHNSON 2004)). While frequent ballooning, short-living species colonize the banks from the first moment on (SCHMIDT, TSCHARNTKE 2005). Overall many of the habitat specialists show a limited distribution, at least in Flanders (MAELFAIT *et al*. 1998) or even in Europe (HÄNGGI *et al*. 1995, HARVEY *et al*. 2002), thus representing high values for regional conservation or even on European scale (PLACHTER, REICH 1998).

Hygrophiles clearly prefer denser vegetated habitats, consequently characterized by a more stable microclimate with regard to temperature and humidity (PHILLIPS, COBB 2005). Xerophiles and psammophiles can be found on scanty vegetated banks with a lower extent of connectivity.

Table 1. Relative number of spider species from gravel banks along the Common Meuse (standardized for 6 pitfall traps per sample site), and classification as listed in the Red List of Flanders (Maelfait *et al.* 1998) (in concordance with IUCN-categories; **CR**: critical, **EN**: endangered, **IN**: indeterminate, **RG**: rare geographically, **VU**: vulnerable).

Abbreviation	Species	EL	HB	HE	HL	HR	KE	KH	KO	MA	MB	ME	MW	MZ	RO	Total	Red list
Agynsubt	*Agyneta subtilis* (O. P.-Cambridge, 1863)	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	
Arctcine	*Arctosa cinerea* (Fabricius, 1777)	0	0	0	0	0	0	0	0	0	0	37	0	4	0	41	CR
Arctleop	*Arctosa leopardus* (Sundevall, 1833)	0	2	0	0	0	0	0	0	0	3	0	0	0	0	5	VU
Baryprat	*Baryphyma pratense* (Blackwall, 1861)	2	0	0	0	0	0	0	0	0	2	0	0	0	0	4	VU
Bathgrac	*Bathyphantes gracilis* (Blackwall, 1841)	2	2	10	4	3	0	4	30	6	8	0	5	1	1	75	
Bathparv	*Bathyphantes parvulus* (Westring, 1851)	0	2	0	0	0	0	0	0	0	0	0	0	0	0	2	
Cerabrev	*Ceratinella brevis* (Wider, 1834)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	
Cerascab	*Ceratinella scabrosa* (O. P.-Cambridge, 1871)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	
Clubfris	*Clubiona frisia* Wunderlich, Schuett, 1995	0	0	2	0	0	0	1	2	0	2	1	0	1	3	13	VU
Clubnegl	*Clubiona neglecta* O. P.-Cambridge, 1862	0	0	1	0	0	0	0	1	0	0	0	1	1	0	4	
Clubphra	*Clubiona phragmitis* C.L. Koch, 1843	0	2	0	0	0	0	1	0	0	3	0	0	0	0	6	
Clubpseu	*Clubiona pseudoneglecta* Wunderlich, 1994	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	IN
Diplconc	*Diplostyla concolor* (Wider, 1834)	6	36	10	82	3	2	88	14	0	21	2	13	14	16	307	
Diplconn	*Diplocephalus connatus* Bertkau, 1889	0	0	0	0	0	0	1	0	0	0	0	0	0	1	2	IN
Diplcris	*Diplocephalus cristatus* (Blackwall, 1833)	0	0	4	48	3	4	5	0	0	1	4	0	3	2	74	
Dipllati	*Diplocephalus latifrons* (O. P.-Cambridge, 1863)	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	
Diplperm	*Diplocephalus permixtus* (O. P.-Cambridge, 1871)	1	0	4	12	1	0	4	0	0	0	0	0	5	0	27	
Enopthor	*Enoplognatha thoracica* (Hahn, 1833)	0	0	0	0	0	0	0.4	0	0	0	0	0	0	0	0.4	
Erigarct	*Erigone arctica* (White, 1852)	0	0	3	16	0	0	2	2	0	1	0	2	0	2	27	
Erigatra	*Erigone atra* Blackwall, 1833	53	50	100	150	14	36	66	91	6	139	34	58	36	26	859	
Erigdent	*Erigone dentipalpis* (Wider, 1834)	61	72	156	254	23	88	105	116	2	142	55	133	57	52	1316	
Eriglong	*Erigone longipalpis* (Sundevall, 1830)	4	8	13	18	0	6	2	13	0	4	4	5	4	3	84	
Euopaequ	*Talavera aequipes* (O. P.-Cambridge, 1871)	0	0	0	0	0	2	0	0	0	0	0	0	0	0	2	VU
Euopfront	*Euophrys frontalis* (Walckenaer, 1802)	0	0	0	0	0	0	0.4	0	0	0	0	0	0	0	0.4	
Halodist	*Collinsia distincta* (Simon, 1884)	2	2	0	0	2	0	3	11	0	12	1	7	1	4	45	EN
Heliaura	*Heliophanus auratus* C.L. Koch, 1835	2	0	0	0	1	0	0	0	0	1	0	0	0	0	4	EN
Hypobitu	*Hypomma bituberculatum* (Wider, 1834)	0	8	1	0	0	0	0	0	0	3	0	2	0	0	14	
Laricorn	*Larinioides cornutus* (Clerck, 1757)	0	0	0	0	0	2	0	0	0	1	1	0	0	0	3	
Leptflav	*Tenuiphantes flavipes* (Blackwall, 1854)	0	0	0	0	0	0	0.4	0	0	0	0	0	0	0	0.4	

Table 1. Continued.

Abbreviation	Species	EL	HB	HE	HL	HR	KE	KH	KO	MA	MB	ME	MW	MZ	RO	Total	Red list
Leptpall	*Palliduphantes pallidus* (O. P.-Cambridge, 1871)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	
Leptrobu	*Leptorhoptrum robustum* (Westring, 1851)	5	2	0	0	1	0	2	3	0	2	0	0	1	1	16	VU
Lepttenu	*Tenuiphantes tenuis* (Blackwall, 1852)	2	4	4	0	0	0	2	18	2	20	1	1	0	2	56	
Linyhort	*Linyphia hortensis* Sundevall, 1830	0	0	0	0	0	0	0.4	0	0	0	0	0	0	0	0.4	
Meiorure	*Meioneta rurestris* (C.L. Koch, 1836)	0	0	3	8	0	10	5	5	2	3	1	18	32	1	88	
Micapuli	*Micaria pulicaria* (Sundevall, 1831)	0	0	2	6	0	8	0	0	0	1	1	0	1	4	23	
Micrimpr	*Microlinyphia impigra* (O. P.-Cambridge, 1871)	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	VU
Micrsuba	*Micrargus subaequalis* (Westring, 1851)	0	0	0	0	0	2	0	1	0	0	0	0	1	0	4	
Milliner	*Collinsia inerrans* (O. P.-Cambridge, 1885)	1	0	2	0	1	0	4	7	0	1	0	0	0	0	16	
Nereclat	*Neriene clathrata* (Sundevall, 1830)	0	0	0	0	0	0	1	0	0	2	0	0	0	0	3	
Oedoapic	*Oedothorax apicatus* (Blackwall, 1850)	195	36	131	100	15	22	69	76	8	119	65	51	51	123	1060	
Oedofusc	*Oedothorax fuscus* (Blackwall, 1834)	101	80	210	260	15	28	68	90	18	124	66	81	95	87	1323	
Oedoretu	*Oedothorax retusus* (Westring, 1851)	306	122	398	226	82	82	194	151	24	540	196	206	82	185	2793	
Ostemela	*Ostearius melanopygius* (O. P.-Cambridge, 1879)	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	
Ozypprat	*Ozyptila praticola* (C.L. Koch, 1837)	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	
Ozypsimp	*Ozyptila simplex* (O. P.-Cambridge, 1862)	0	0	0	2	0	0	0	0	0	1	0	0	0	0	3	
Pachcler	*Pachygnatha clercki* Sundevall, 1823	11	12	46	8	5	2	9	19	0	75	16	7	5	10	224	
Pachdege	*Pachygnatha degeeri* Sundevall, 1830	1	8	5	8	1	2	2	2	0	0	0	1	1	8	39	
Pardagre	*Pardosa agrestis* (Westring, 1861)	0	0	0	6	0	2	2	0	0	2	0	0	0	1	13	EN
Pardagri	*Pardosa agricola* (Thorell, 1856)	327	0	110	106	1	2	4	1	0	6	40	0	0	939	1534	CR
Pardamen	*Pardosa amentata* (Clerck, 1757)	28	48	27	50	1	12	13	5	0	71	22	21	16	64	378	
Pardpalu	*Pardosa palustris* (Linnaeus, 1758)	3	0	1	6	0	0	1	2	0	2	1	0	1	2	19	
Pardprat	*Pardosa prativaga* (L. Koch, 1870)	4	18	0	4	0	0	6	0	0	15	0	4	1	5	57	VU
Pardprox	*Pardosa proxima* (C.L. Koch, 1847)	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	RG
Pardpull	*Pardosa pullata* (Clerck, 1757)	0	0	0	2	0	0	1	0	0	0	0	0	0	0	3	
Pelepara	*Pelecopsis parallela* (Wider, 1834)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	
Phlefasc	*Phlegra fasciata* (Hahn, 1826)	0	0	0	0	0	2	0	0	0	0	0	0	0	0	2	VU
Phrufest	*Phrurolithus festivus* (C.L. Koch, 1835)	1	0	1	30	0	14	4	1	0	0	2	2	5	5	65	
Pirahygr	*Pirata hygrophilus* Thorell, 1872	0	0	0	0	1	0	1	1	0	2	0	0	0	0	5	
Piralati	*Pirata latitans* (Blackwall, 1841)	2	8	0	2	0	0	1	1	0	2	0	2	0	0	17	

Table 1. Continued.

Abbreviation	Species	EL	HB	HE	HL	HR	KE	KH	KO	MA	MB	ME	MW	MZ	RO	Total	Red list
Pirapira	*Pirata piraticus* (CLERCK, 1757)	0	2	0	0	0	4	0	1	0	0	0	0	0	0	7	
Porrconv	*Porrhomma convexum* (WESTRING, 1851)	2	0	0	0	0	2	1	0	0	1	1	0	0	0	7	
Prinvaga	*Prinerigone vagans* (AUDOUIN, 1826)	5	2	19	10	4	0	4	31	2	4	2	5	3	6	97	
Robelivi	*Robertus lividus* (BLACKWALL, 1836)	0	0	0	0	0	0	0.4	0	0	0	0	0	0	0	0.4	
Steaalbo	*Steatoda albomaculata* (DE GEER, 1778)	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	VU
Steaphal	*Steatoda phalerata* (PANZER, 1801)	0	0	0	0	0	8	0	1	0	0	1	0	0	0	10	VU
Stemline	*Stemonyphantes lineatus* (LINNAEUS, 1758)	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
Synavena	*Synageles venator* (LUCAS, 1836)	0	0	0	2	0	0	0	0	0	0	0	0	0	0	2	
Tegeagre	*Tegenaria agrestis* (WALCKENAER, 1802)	0	0	0	2	0	20	0	0	0	0	0	0	0	0	22	
Tetrexte	*Tetragnatha extensa* (LINNAEUS, 1758)	0	0	1	0	0	0	0	0	0	1	0	0	0	0	2	
Trichack	*Trichoncus hackmani* MILLIDGE, 1956	0	0	0	0	0	0	0.4	0	0	0	0	0	0	0	0.4	CR
Trocruri	*Trochosa ruricola* (DE GEER, 1778)	29	24	30	44	1	86	2	11	2	64	19	29	3	33	378	
Trocterr	*Trochosa terricola* THORELL, 1856	0	4	1	0	0	2	0	0	0	0	0	0	0	0	7	
Troxscab	*Troxochrus scabriculus* (WESTRING, 1851)	0	4	0	2	0	0	0	0	0	1	0	0	0	0	7	
Xeromini	*Xerolycosa miniata* (C.L. KOCH, 1834)	0	0	0	0	0	8	0	3	0	2	0	0	0	0	13	EN
Xystcris	*Xysticus cristatus* (CLERCK, 1757)	0	0	0	0	0	2	0	0	0	0	0	0	0	0	2	
Xystkoch	*Xysticus kochi* THORELL, 1872	0	0	0	0	0	6	0	0	0	0	0	0	0	1	7	
Zeloaene	*Zelotes aeneus* (SIMON, 1878)	0	0	0	10	0	0	0	0	0	0	0	0	0	0	10	RG
Zelolatr	*Zelotes latreillei* (SIMON, 1878)	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	
Zelolute	*Zelotes lutetianus* (L. KOCH, 1866)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	EN
Zelopede	*Trachyzelotes pedestris* (C.L. KOCH, 1837)	3	0	1	4	0	6	0	0	0	1	0	0	0	0	15	EN
Zelosubt	*Zelotes subterraneus* (C.L. KOCH, 1833)	1	0	0	0	0	10	0	0	0	0	0	0	0	0	11	EN
	Total	1164	558	1297	1482	177	482	678	710	72	1407	572	653	426	1588	11266	23
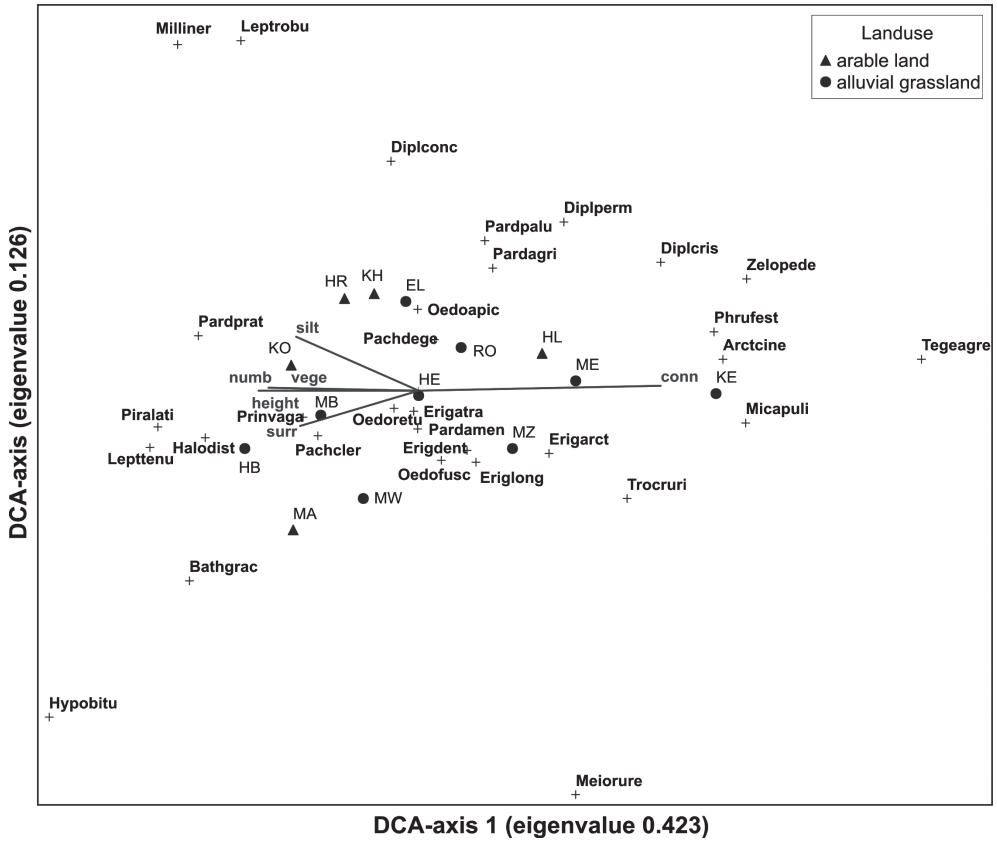
Fig. 2. DCA-ordination of spider pifall data, after standardization for 6 pitfalls per site. Only most abundant species are taken in consideration. Species are listed by respectively first 4 letters of genus and species epitheton. Gravel banks are grouped by means of surrounding land-use (gravel bank characteristics: height - flooding disturbance measure, i.e. relative height ot the gravel bank; silt - absence or presence of a silt layer; connectivity measure, i.e. nearest neighbour distance; numb and surr - respectively number and area of gavel banks in the vicinity; vege - amount of vegetation cover.

A. cinerea and *P. agricola* are considered as stenotopic riparian species having a clear preference for sandy and shingly soils (ALBERT, ALBERT 1976, FRAMENAU *et al.* 1996), just as *Diplocephalus connatus.* In Belgium *Halorates distinctus* only occurs in freshwater marshes along large rivers (HENDRICKX *et al.* 1998), consequently can be considered as a riparian species. Still *A. cinerea* is markedly isolated within the DCA-output from *P. agricola.* This niche-differentiation appears to be in concordance with a field survey along the Common Meuse of 2005 (K. Lambeets, unpubl. data). *A. cinerea* occurs on more elevated, sandy gravel banks with rather scarce vegetation cover and a relative high amount of coarse gravel. This in contrary to *P. agricola* which inhabits more loamy, denser vegetated gravel banks with a silt layer present. *P. agricola* is almost absent from high gravel banks (KE), thus not in direct contact with the river (VAN LOOY, DE BLUST (1998), while *Zelotes subterraneus* and *Xysticus kochi,* both occurring in rather dry and non-shaded habitats (ROBERTS 1998), are only found on KE. Furthermore, we can state that the adjacent habitat plays a role in the survival of both *A. cinerea* and *P. agricol*a because former seems to hibernate in natural alluvial grasslands (FRAMENAU *et al.* 1996) and *P. agricola* is found in pitfalls situated in yearly mown meadows from September onwards (K. Lambeets, unpubl. data).

Overall gravel banks where habitat specialist species occur in rather high numbers, can be considered of being of great conservational value for future nature management. Taken into consideration the different habitat requirements of these species, several types of gravel banks and ecological managed alluvial grasslands have to be preserved during future nature management and restoration of the Common Meuse.

Spider assemblage responses

Overall we can state that the spider assemblages are influenced by local environmental factors and in some degree by the landscape configuration. This is consistent with similar studies from exposed riverine sediments (EYRE *et al.* 2002) and other dynamic habitats, like agricultural landscapes (JEANNERET *et al.* 2003). The high supply of allochtonous organic matter by the river is posed by ADIS, JUNK (2002) and FRAMENAU *et al.* (2002) as another explanation for the high abundance of more mobile groups (e.g. ground beetles and spiders) on river banks. BONN *et al.* (2002) studied riparian habitats along several river systems in Germany and concluded that mainly vegetation heterogeneity, rather than different flood regimes, influenced spider assemblages. PERNER, MALT (2003) showed that vegetation structure indirectly explained most of the variance in the spider data-set along a decreasing management gradient of grasslands. In our study, the separation of araneid groups is less apparent. Nevertheless from the spider data onwards an obvious difference between the characterisation of gravel banks is noticeable, pointing out their singularity. Once the water level drops, gravel banks become exposed and quickly are colonized by a pioneer vegetation, with a characteristic vertical zonation pattern (SCHAMINÉE *et al.* 1998, NEUMEIER 2005). Gravel banks situated lower above the water level are more susceptible to flooding disturbance, thus getting covered with a silt layer more often. This in turn enhances vegetation succession. Stronger vegetated banks are able to accumulate a higher amount of silt, which has a self-reinforcing effect upon the vegetation *in se* (SLUIS, TANDARICH 2004). Due to the denser vegetation cover, relative lower banks can maintain a more stable micro-climate concerning humidity, temperature etc. (SOUZA, MARTINS 2004).

Pioneer spider species like *Oedothorax* spp. and *Erigone* spp. clearly dominate gravel banks, just as outlined by a study considering several river-floodplains in Germany (BONN, KLEINWÄCHTER 1999, WOHLGEMUTH - VON REICHE, GRUBE 1999). Next to vegetation density, gravel size increases from the sharp sand fraction along the water line, onwards to the coarse gravel of the dike, where a ruderal and dense vegetation is found. Thus gravel banks enclose a wide range of small-scale microclimatological differences, causing a more heterogeneous habitat with varying substrate structure and vegetation cover, both in time and space (BONN, KLEINWÄCHTER 1999). Former authors noticed that the narrow niche separation in Araneae and Carabidae assemblages was due to the high heterogeneity, enhancing general biodiversity. PHILLIPS, COBB (2005) found proof that micro-scale differences of vegetation type and substrate structure around pitfalls can obscure trapping of certain species. In contrary to carabid beetles (grand total of 98 species, K. Lambeets unpubl. data), only some spider species are able to survive the extreme conditions met on gravel banks, which can serve as one of the main reasons of the poor species richness. Next to the long-lasting winter and regular springtime flood events, possibly most of the spider species are more sensitive to desiccation due to a non-adapted morphology and behaviour (FOELIX 1996). Certain types of gravel and other substratum (e.g. sand, loam and silt), with regard to physical composition, size and ability to restrain heat, can play a decisive role in the thermal balance of river bank habitats. But if vegetation succession on sandy gravel banks would proceed, due to a decrease in river dynamics, typical riverine species would disappear and on the other hand an increase in habitat generalists could be noticed (WOHLGEMUTH - VON REICHE, GRUBE 1999). Furthermore connectivity, considered as the interpatch distance between consecutive banks, can be looked at as an isolation effect, while secondly the patch area contributes to the degree of fragmentation

(Piessens *et al.* 2005). Within our study, only the degree of isolation had a significant effect upon species distribution, especially habitat specialists seem susceptible to an increase of fragmentation (landscape effect).

Conservation and restoration issues

For conservational purposes, one can state, in order to preserve specialist species within a river-ecosystem, regular disturbance by inundation within the ecosystem should be maintained. In order to enhance natural water dynamics, present river management should be revised. In other words the human impact, e.g. river bed modifications, damming, stone embankments, etc., should be minimized (Bonn *et al.* 2002). Yet it is important to account for flood protection measures, like is the case along the Common Meuse (Nagels *et al.* 1999). But rather small-scale habitat restoration would be beneficial for conservational purposes (Lin, Xie 2005), otherwise the initial amplitude of species adjustment could be too large, and species would ultimately face extinction. This can be a reason for the slow reaction of spider assemblages after habitat restoration, like Bonte *et al.* (2003) pointed out for dune landscapes. Further research will reveal if this is also the case along the Common Meuse (K. Lambeets, unpubl. data). Although not measured in this study, other properties of exposed riverine sediments such as grazing intensity, surrounding land-use or exposure to environmental factors as wind, shadowing, water chemistry or pollution may also influence communities of cursorial predators (Framenau *et al.* 2002).

In conclusion we can state that there isn't a unequivocal definition of "the" gravel bank. In order to preserve typical riverine species by means of river ecosystem restoration, both dynamic and more elevated gravel banks should be taken in consideration. Overall promoting heterogeneity in local gravel bank characteristics and landscape composition, e.g. surrounding land-use, could be one of the keys promoting spider diversity along a river system, just as Clough *et al.* (2005) have shown for spider diversity in cereal fields. Thereby a variety in local habitat characteristics should be retained, especially by means of a differentiating substrate structure and a vertical zonation pattern in vegetation succession, caused by natural flooding of the gravel banks. River management should be adjusted in order to maintain a natural river corridor and surrounding riverine landscape, as well as the conservation of natural river flow regimes.

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Синекология на паяците (Araneae), обитаващи чакълестите брегове на равнинната речна система Мюз (Белгия, Холандия) и факторите, които ги ограничават

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(Резюме)

Чакълестите брегове на речната система Мюз са изследвани за епигейни безгръбначни животни, с цел да се установи как са структурирани съобществата по отношение на характеристиките на речния бряг (размер, степен на изолираност, растителност, наличие на наноси и периодичност на заливанията). Семействата Linyphiidae и Lycosidae доминират сред установените при изследването паяци. Видове с кратки жизнени цикли и по-добри възможности за разпространение по въздуха, както и подстилъчно живеещи хигрофили и агробионти са установени във всички изследвани стации. Присъствието на ксеротермни видове и такива, специализирани за живот в чакълести крайречни брегове, са регистрирани само на места с рядка растителност и по-малко динамични брегове. Чрез ординационен анализ са установени факторите, които определят структурата на хищните безгръбначни животни в различните чакълести брегове. Изолацията, степента на заливност, гъстотата на растителната покривка и наличието на наноси са сред факторите, които определят основните типове на разпространение. Според авторите, за да се опазят видовете, живеещи само в чакълестите брегове на реките, е необходимо да бъдат поддържани естествените процеси на периодичното им заливане. Тъй като няма еднозначна дефиниция на това, какво е речен чакълест бряг, предлага се при природозащитни действия терминът да се прилага в по-широк смисъл, като по този начин бъдат включени по-динамичните и по-издигнатите речни брегове, за да се гарантира опазването на хетерогенността по дължината на речната система.