THE EFFECTS OF FLOODING DISTURBANCE ON THE DISTRIBUTION AND BEHAVIOUR OF RIPARIAN ARTHROPODS ALONG A LOWLAND GRAVEL RIVER

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The effects of flooding disturbance on the distribution and behaviour of riparian arthropods along a lowland gravel river

De effecten van overstromingsverstoring op de verspreiding en het gedrag van oevergebonden arthropoden langsheen een grindige laaglandrivier

by / door

Kevin Lambeets

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Frontcover: View at the riverine landscape at Maasmechelen (Photo: Kevin Lambeets)

Backcover: Male *Arctosa cinerea* (Fabricius, 1777), a rare, psammophilic wolf spider
of high conservation interest… (Photo: Rollin Verlinde, Vilda)

DANKWOORD

"Binnen een maand staat hij hier weer.", een uitspraak gericht naar mijn persoon tijdens m'n 16^{e} levensjaar. Ondertussen staat de wereld een luttele 10 jaar verder, zelf steeds verder struinend. De queeste die toen begon, bereikt een mijlpaal, een volgend baken. *Per aspera ad astra.* Edoch, zonder de hulp van een bont allegaartje mensen zou deze scriptie nooit het daglicht hebben gezien, noch worden neergelegd. Zij stonden me niet enkel bij met raad en daad... Velen onder hen hijsten, in beider betekenis van het woord, de krakende vracht, die ikzelf ter tijd en stond durfde te lossen, weer zorgvuldig op m'n schouders. Vandaar, een scriptie kan niet aanvangen zonder een oprechte dankbetuiging.

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Kevin Lambeets, 09 februari 2009

PUNK IS...

A BELIEF THAT THIS WORLD IS WHAT WE MAKE OF IT,
TRUTH COMES FROM OUR UNDERSTANDING
OF THE WAY THINGS ARE,
NOT FROM THE BLIND ADHERENCE TO PRESCRIPTIONS
ABOUT THE WAY THINGS SHOULD BE.

TAKEN FROM *"A PUNK MANIFESTO"* BY GREG GRAFFIN

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I. Introduction and Thesis outline

The river bank at Visserweert (Photo: Kevin Lambeets)

1.1 River banks within a human modified riverine landscape

The Common Meuse river reach

The Common Meuse is situated between Flanders (Belgium) in the West and the Netherlands in the East (Fig. I.1). It is the 45 km long non-impounded, non-navigable semi-natural reach of the River Meuse (925 km), and starts where the river descends from the rocky primary soils of the Ardennes and enters the loamy and sandy lowlands (adjacent to the “Kempisch Plateau”; Broothaers, 1996). The high slope, a fall of 30 to 60 cm per km, and the strong longitudinal gradient (0.45 m^1km^{-1}) are responsible for the fast flowing gravel-bed character of the Common Meuse. Since it is rain-fed, the River Meuse is characterised by strong water level fluctuations (Fig. I.2), yet only the Common Meuse comprises a wandering pattern of isolated river banks (Van Looy & De Blust, 1995; Table 1). Discharge regimes range from 10 m^3s^{-1} during dry periods up to 3,000 m^3s^{-1} in periods of heavy rainfall in the catchment area. Due to canalisation and normalisation of the River Meuse, starting around 1860, the historically shallow and wide river channel of the Common Meuse, still able to freely meander through the alluvial landscape, was replaced by a deep, small, uniform and fixed channel characterised by an increased water level and fast current velocity (van Winden et al., 2001). Consequently, a tendency for prolonged low flows and hydropeaking appears at present (Semmerkrot et al., 1997). Moreover, the transport of large gravel fractions halted, restricting the dynamic occurrence of newly formed gravel and sand bars. However, supplies of fine-grained sediment fractions such as sand-loam, loam and clay still proceeded. These sank and covered up the surrounding alluvial area after overbank flooding (Van Looy & De Blust, 1995; van Winden et al., 2001). Currently, concrete embankments or large stone boulders still demarcate parts of the Common Meuse which restrain natural dynamic processes such as recurrent, spacious but smooth flood events in spring. Over 50% of the alluvial plane is still intensively used for agricultural purposes while alluvial grasslands, sand-gravel bars or pioneer vegetations on overbank depositions only occupy 5% of the surface (Van Looy, 2006). The remaining landscape comprises riverine water bodies, gravel pits, marshland and woodland (Fig. I.1).

Fig. I.1 - Map of the Common Meuse river reach and its riparian margin. River banks along the trajectory are indicated by triangles, and were recorded during low flow discharge (day-average: 38 m^3s^{-1}). A complete survey of the river banks is provided in Table I.1.

Phyto-geographically, the Common Meuse is the only region in Belgium within the fluvial district (Lambinon et al., 1998), a sub-district of the Brabants district. It is situated along a prominent North-South axis (the River Meuse valley) and the transition zone between the Continental and Atlantic climate, resulting in a striking mixture of plants and animals. This region is characterised by rare river corridor plants ("stroomdalplanten"; cf. Burkart, 2001) confined to the typical microclimatic conditions along dikes and river banks (Peters et al., 2000) of which a multitude appears on the Red List of plants of Flanders and Brussels (Van Landuyt et al., 2006). Even at a European scale some habitats along the Common Meuse have the advantage of being officially protected. More particularly, remnants of the Arrhenatherion elatioris-association in the catchment area as well as the Bidention partitae and Polygono-Veronicetum anagallidis-aquaticae-associations along the riparian corridor ("Rivieren met slikoevers met vegetaties behordend tot het Chenopodion rubric p.p. en Bidention p.p."; code 3270, Sterckx et al., 2007) deserve special conservation attention. Therefore, substantial parts of the Common Meuse habitats have the advantage of being admitted to the NATURA2000-network (Van Looy, 2006).

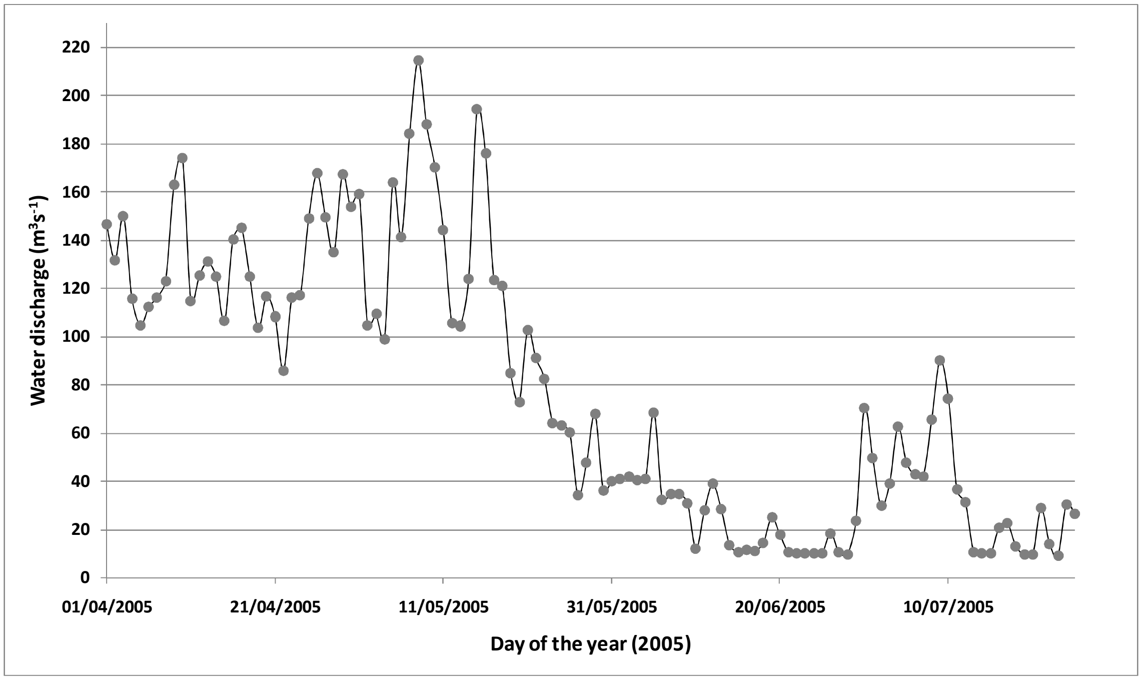

Fig. I.2 - Daily mean discharge regimes (m^3s^{-1}) for the Common Meuse river reach between April 1st and July 25th 2005, i.e. the period all river banks were sampled (see II.2. and II.3.). Data taken with permission from http://www.lin.vlaanderen.be/awz/waterstanden/hydra/maasbekken.htm

River banks and their ecological value

The environment of organisms living within the boundaries of riverine landscapes can be highly dynamic due to discharge fluctuations and sediment movements (Ward et al., 1998). Flood events reset riparian successional stages, thereby creating open pioneer conditions and increasing habitat heterogeneity on various spatiotemporal scales (Ward et al., 2002; Van Looy et al., 2006). The ecological quality of spatially structured river banks throughout Western-Europe and their related biota have suffered severely from human modifications in the past few centuries (Naiman et al., 2005; Tockner et al., 2006; Lake et al., 2007). Most river banks are highly disconnected and surrounded by agricultural land-use (Pedroli et al., 2002; Allan, 2004; Van Looy et al., 2006). Next to anthropogenic shifts in water discharge regimes of lowland rivers (Semmerkrot et al., 1997; Liefveld & Schulze, 2005), both habitat fragmentation by embanking and damming as well as the reclamation and deterioration of the surrounding alluvial landscape has negative consequences for many stenotopic riparian organisms (Ward et al., 1998; Van Looy et al., 2005; Laeser et al., 2005). The river banks along the Common Meuse which directly adjoin the channel are highly isolated and situated at the foot of steep dikes which consist of large stone boulders with a loamy or clayey in-between sediment fraction (Van Looy and De Blust, 1995; van Winden et al., 2001). The banks itself comprise an overburden of coarse gravel and a variable substrate in-between which ranges from sharp sand to a loamy substrate according to the banks' flooding susceptibility (cf. Paetzold et al., 2008); also related changes in vegetation manifest (Peters et al., 2000). Moreover, the lowest, most flood-disturbed banks are covered with an extensive silt layer (see Lambeets et al., 2007). Most of the river banks are regularly inundated during spring and summer, at least partly, but all banks annually experience long-lasting winter flooding (Van Looy & De Blust, 1995). The area adjacent to the banks consists of yearly-mown and fertilised agricultural meadows dominated by *Lolium perenne* and *Arrhenatherum elatius* (K. Van Looy, pers.comm.); rarely alluvial grasslands appear (e.g. at Meers, Roosteren, Kerkeweerd; Van Looy, 2005).

The Common Meuse still contains dynamic lowland river banks alongside its river channel which clearly differ in their vegetation composition. Typical riparian plants include *Rorippa sylvestris, Lythrum salicaria, Artemesia vulgaris, Polygonum aviculare, Xanthium orientale (*Peters et al., 2000); *Sisymbrium austriacum* is mainly found on higher banks or adjacent erosion channels (Van Looy, 2005; Lambeets et al., 2005). Additionally, these banks comprise variable arthropod assemblages (Desender et al., 1994; Vanacker, 2000; Lambeets et al., 2008a) which are characterised by many rare and stenotopic arthropods (Turin, 2000; Van Looy et al., 2005; Lambeets et al., 2007; Lambeets, 2008a). Conform with other river systems (Heidt et al., 1998; Sadler et al., 2004; Andersen & Hanssen, 2005), these riparian habitats also host a variety of rare hygrophilic and xerothermophilic species. Generally, for spatially and temporally highly variable habitats as river banks a conventional approach of static nature conservation would not meet the demands of these highly stenotopic species (Bonn et al., 2002; Palmer et al. 2005; Sabo et al., 2005; Van Looy et al. 2006).

River modification, restoration and biodiversity conservation

Ever since Roman times, the River Meuse was known as an important shipping way, providing essential goods and services (e.g. Quadflieg, 2005) and demarcated the Western border of the Holy Roman Empire from the 9th century onwards. Halfway the 19th century, mankind started to canalise and normalise the river trajectory of the Common Meuse to secure safe navigation, improve flood protection and support agriculture on the fertile floodplain soils (van Winden et al., 2001). The rugged pattern of sandy overbank depositions and flood channels disappeared (Fig. I.3) as the fertile riverine sediments of clay, loam and sand-loam were no longer displaced and rearranged, dependent on the distance from the river channel. The characteristic pattern of pools and riffles along the channel of the previously free-flowing gravel river was equalised as a consequence of substantial gravel mining practices between 1940 - 1970 (van Winden et al., 2001). Also, the vast deepening of the summer bed sharply separated the deeply scoured river channel from the remaining floodplains in the catchment area. Furthermore, the impounded character of the River Meuse in the Ardennes and the hydropower turbine at Lixhe contribute to extreme peaks in the discharge regime and sediment transport of the Common Meuse at present (Van Looy & De Blust, 1995; Semmerkrot et al., 1997). Next to the continuous network of river dikes, the agricultural intensification and extended urbanisation in the catchment area resulted in a faster drainage and precipitation discharge through the surface water; the ground water level declined and hence the water storage capacity of the alluvial floodplains decreased. Consequently, the frequency and magnitude of maximum (hydropeaking) and minimum (low flows) discharges increased (Fig. I.2), whereas sedimentation and erosion processes were disrupted, especially as the Common Meuse is a rain-fed river (Semmerkrot et al., 1997; Liefveld & Schulze, 2006). In general, perturbations of dynamic processes eventually lead to shifts in local conditions (e.g. vegetation structure, sediment composition) and channel connectivity (Naiman et al., 2005; Allan & Castillo, 2007). This can, in turn, affect habitat suitability for species which are adapted to short-term environmental changes and pioneer conditions induced by regular water level fluctuations (Robinson et al., 2002; Lytle and Poff, 2004; Lake et al., 2007). Reducing the sharp discharge fluctuations, hence, is a prerequisite for river restoration measures along the Common Meuse. Moreover, the water level should not drop over 30% per hour as an increased frequency and magnitude of discharge fluctuations causes downstream drift and stranding of rheophilic (in-stream) organisms (Semmerkot et al., 1997; Peeters et al., 2006) and negatively affects the riparian fauna (Bonn et al., 2002; Van Looy et al., 2005; Paetzold et al., 2008). Also, an ecological acceptable minimum discharge should always remain and never be too extensive (>10 m^3s^{-1}; Liefveld & Schulze, 2006).

As riparian and riverine habitats are amongst the most diverse but threatened ecosystems world-wide (ECE - River Convention, 1992), they in particular deserve conservation attention (Ward, 1998; Robinson et al., 2002; Naiman et al., 2005; Sterckx et al., 2007). As emphasised by several authors in the last decade (e.g. Buijse et al., 2002; Robinson et al., 2002; Tockner & Stanford, 2002; Lake et al., 2007), direct action is needed to preserve the rare and vulnerable organisms occurring throughout the riverine landscape. In Europe, over 90% of the riparian habitats have been reclaimed and currently lack natural river dynamics (Pedroli et al., 2002). Recently, ambitious European river restoration projects aim to re-establish natural riverine processes (e.g. by dike removal, restricting peak discharge regimes; Tockner et al., 1998; 2003; 2006; Palmer et al., 2005; Mant & Janes, 2006) and to restore the contact with the alluvial hinterland (Ward & Stanford, 1995; Buijse et al., 2002; Pedroli et al., 2002; Van Looy et al., 2006), thereby creating a more natural, continuous river valley in balance with socio-economic aspects (e.g. flood protection measures and recreation; Odou, 1998; Geilen et al. 2004). As enunciated by the **Living River Concept** (Nagels et al., 1999; Pedroli et al., 2002; Buijse et al., 2002), providing the necessary space for the river essentially relates to the rehabilitation of important ecological riverine processes on various spatial scales (e.g.

flooding, meandering). Consequently, dynamic processes will remodel both the riverine and riparian corridor, and reshape the surrounding landscape concordant with its physical characteristics (e.g. geomorphological stratification; Hupp & Osterkamp, 1996; van den Berg et al., 2000; Allan & Castillo, 2008) and its historical outline (Harding et al., 1998; Hérault & Honnay, 2005; see Fig. I.3). As the preservation and rehabilitation of (natural) floodplains and the widening of the river channel increase the ecological integrity of the riverine landscape as a whole (Ward & Stanford, 1995; Geilen et al., 2004), it also results in an increased water storage capacity, thus meeting the prerequisites and standards for ecological successful restoration (Palmer et al., 2005). For the riparian ecotone in specific, this will result in increased habitat heterogeneity at the local scale (habitat quality; Collinge et al., 2001; Lake et al., 2007) but also at the landscape scale (cf. species pool; Ward et al., 2002; Wiens, 2002; Riis and Sand-Jensen, 2006). Generally, scientifically-founded river restoration and rehabilitation of riparian habitats will enhance regional biodiversity (Ward et al., 1999; Sabo et al., 2005). With it, river dynamics are the key factor in determining the potential for persistent and viable populations of target plant and animal species along the river and the riparian ecotone (Pedroli et al., 2002; Nilsson & Svedmark, 2002; Robinson et al., 2002; Sadler et al., 2004; Riis et al., 2008; Paetzold et al., 2008). For the Common Meuse in particular, the Allier (France) serves as the ecological reference of a “pristine” lowland river (van den Berg et al., 2000); a self-regulating riverine ecosystem which is hardly touched by mankind and where biodiversity can be preserved in a sustainable way, yet restricted by the conditions of social stipulations (Buijse et al., 2002). The reference situation is mainly inspired by the historical state of the river system under consideration (Lake et al., 2007). Generally, the hydrogeomorphological processes that determine the ecology of the riparian ecotone should be sustained, and may be enhanced in cases such as the mid-section of the River Meuse (cf. Plachter & Reich, 1998; Mant & Janes, 2006; Tockner et al., 2006). Therefore, a more dynamic approach of river restoration and rehabilitation is needed, conform the Living River Concept (Pedroli et al., 2002; Palmer et al., 2005), which should be based on sound ecological principles and an understanding of dynamic processes (Giller, 2005; Jensen et al., 2006). Beside it, restoring and maintaining lateral and longitudinal connectivity along river corridors will enhance the rivers’ integrity and ecological sustainability (Palmer et al., 2005; Van Looy et al., 2006; Lake et al., 2007).

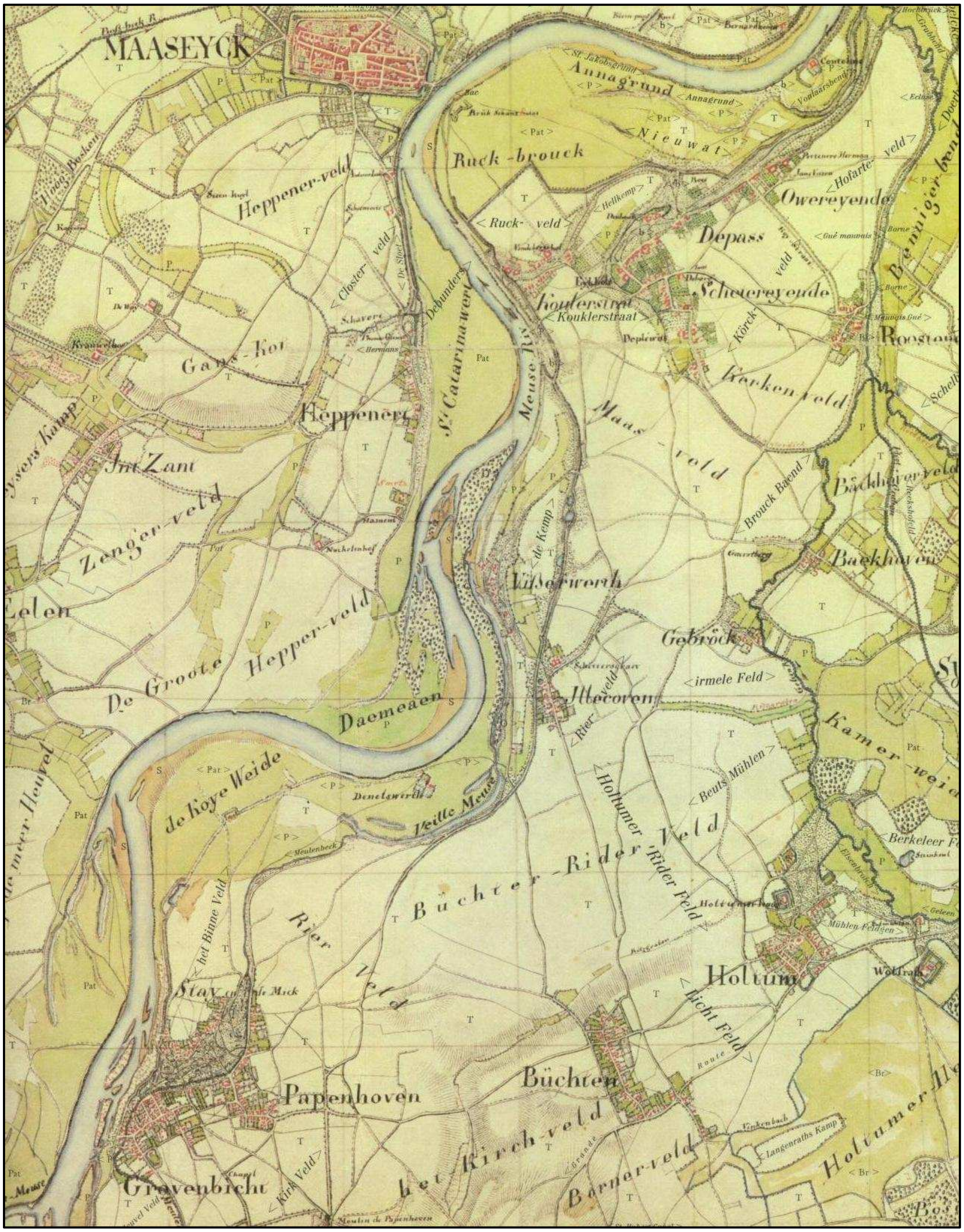

Fig. I.3 - The map of Tranchot with the Common Meuse (1800) nearby Maaseik. Notice the high degree of habitat diversity and landscape heterogeneity in general, with numerous gravel bars and isles along the fast flowing gravel bed (orange) bordered by rough growth, alluvial shrubs and woodlands (dotted) and alluvial grasslands (green). From 1860 onwards, the old river arms and side channels disappeared due to intensive river regulation practices.
With kind permission of Willem Overmars taken from http://www.wildernis.com/.

1.2 Environmental constraints for riparian arthropod assemblages

Predatory arthropods as ecological indicators for riparian habitats

Generally, the study of relationships between ecological parameters and the arthropod biota of ecosystems is considered to be useful for restoration assessment and conservation planning (Kremen et al., 1993; Maes, 2004; Fisher & Lindenmayer, 2007) and may guide future management (Greenwood et al., 1991; Kirby, 1992; Maes & Bonte, 2006). Arthropod spatial and temporal distributions span the ranges occupied by many vertebrate and plant species, but they also include more fine-grained patterns (e.g. patch size, habitat architecture etc.). Moreover, they cover a great variety of ecological niches and population properties, but also exhibit a great range of body sizes, dispersal traits and growth rates (see Kremen et al. (1993) for a vigorous review of the use of arthropods in conservation planning). Spiders (Araneae) and carabid beetles (Carabidae) are mobile predatory arthropods, abundantly occurring in any terrestrial ecosystem (Kirby, 1992; Turin, 2000; Harvey et al., 2002). Various studies acknowledge the value of spiders and carabid beetles for ecological research as they (1) are readily observed and easily collected (Maelfait & Baert, 1975; Andersen, 1995), (2) can be sampled *ad random* and in reproducible ways (Baars, 1979; Topping & Sunderland, 1992; Sunderland et al., 1995; Pekár, 2002) and (3) are well known taxonomically and ecologically (Maelfait et al., 1998; Harvey et al., 2002; Turin, 2000; Desender et al., 2008). As they are susceptible to various environmental changes (Kotze & O'Hara, 2003), and are able to persist in small habitat patches, just as plants (Le Viol et al., 2008), arthropods are becoming the focal species for the protection and management of small, remnant natural areas. Moreover, spiders and carabids clearly reflect shifts in local conditions (Ribera et al., 2001; Beals, 2006; Scott et al., 2006) and fragmentation on hierarchical spatiotemporal scales (Purtauf et al., 2004; Dauber et al., 2005; Schmidt et al., 2008). Hence, spiders and carabid beetles are considered as suitable ecological indicators for various ecosystems (New, 1999; Rainio & Niemelä, 2003; Maelfait et al., 2004).

Riparian habitats are known for their generally high biodiversity (Pollock et al., 1998; Ward et al., 1999; Mouw & Alaback, 2003). Despite the high heterogeneity of riverine ecosystems, which is met on different spatiotemporal scales (Ward et al., 2002), riparian habitats, however, do not necessarily harbour more species than other ecosystems, but rather comprise a specialised fauna as a result of environmental stressors as flood events and thermal fluctuations (Sabo et al., 2005; Baker et al., 2006). As a consequence of these stressful regimes, particularly predatory arthropod assemblages on river banks comprise many rare and stenotopic species (Desender et al., 1994; Bonn & Kleinwächter, 1999; Eyre et al., 2001; 2002; Andersen & Hanssen, 2005), which may vary greatly in their habitat requirements, dispersal ability, seasonal activity and body size (Desender, 1989a; Heidt et al., 1998; Bonn & Kleinwächter, 1999; Sadler et al., 2004; Andersen & Hanssen, 2005). Moreover, stenotopic riparian arthropods tend to disappear as a consequence of anthropogenic altered river discharges (Stelter et al., 1997; Bates et al., 2006; Paetzold et al., 2008 a.o.). Riparian spider and carabid beetle assemblages have proven to be valuable monitoring tools for habitat evaluation of riparian habitats (e.g. Bonn et al., 2002; Sadler et al., 2004; Van Looy et al. 2005; 2008) or other flood-disturbed habitats (Cattin et al., 2003; Pétillon et al., 2008). Environmental parameters affect the spatial distribution of predatory arthropods in flood-prone environments (Antvogel & Bonn, 2001; Van Looy et al., 2005; Bates et al., 2006; Lambeets et al., 2008a) and distribution patterns might differ according to species specific life-history traits such as habitat affinity and mobility (Desender, 1989a; Weigmann & Wohlgemuth-von Reiche, 1999; Rothenbücher & Schaefer, 2006). This was also proven for other invertebrate groups inhabiting flood-disturbed environments (Townsend & Hildrew, 1994; Plum, 2005; Foeckler et al., 2006; Paillex et al., 2007). Next to it, beneficial flood-avoiding strategies might increase spider and carabid beetle persistence in these habitats (Lang & Pütz, 1999; Rothenbücher & Schaefer, 2006; see below).

Therefore, considering a variety of riparian arthropods will provide valuable and complementary information for river restoration assessment and river management purposes. From a conservation perspective, especially threatened, representative species are considered to reflect the area’s naturalness more closely (Kremen et al., 1993; Fleishman et al., 2000). As riparian species are of great value to maintain biological diversity, they should be considered as the most important target group for the rehabilitation of riparian habitats (Sabo et al., 2005; Rothenbücher & Schaefer, 2006).

Species richness of riparian habitats

Riparian habitats are inherently species rich due to their highly heterogeneous and fluctuating character affected by flooding disturbance (Nilsson et al., 1989; Pollock et al., 1998; Bonn & Kleinwächter, 1999; Renofält et al., 2005). Several recent studies, however, proved they rather contain different and not necessarily more species (Sabo et al., 2005; Baker et al., 2006; 2007; Hylander, 2006). Generally, resident species are highly stenotopic and have adjusted to the extreme environmental circumstances induced by flooding (Plachter & Reich, 1998; Lytle & Poff, 2004). As a consequence they are rare both on national and international scales (Red Lists of Flanders: Maelfait et al., 1998; Desender et al., 1995; 2008; Hendrickx & De Bakker, forthcoming; Europe: Hänggi et al., 1995; Andersen, 1997; Harvey et al., 2002; Turin, 2000; Van Helsdingen, 2008a,b), but can occur abundantly on a local scale (Albert & Albert, 1976; Framenau et al., 1996; Heidt et al., 1998; Sadler et al., 2004). Moreover, assemblages of riparian arthropods comprise a high variety of opportunistic pioneer and eurytopic species (Bonn & Kleinwächter, 1999; Lang & Pütz, 1999; Bonn et al., 2002; Eyre et al., 2001; 2002; Henshall, 2003), which take advantage from the ephemeral and prey-rich conditions (Hering & Plachter, 1997; Briers et al., 2004; Paetzold et al., 2005; 2006). However, as the latter are still secure in the current (agricultural) landscape, attention should be paid especially to those species which are threatened in their future persistence by e.g. human mediated changes (Lambeck, 1997). Hence, focal arthropods for the conservation of riparian habitats should contain stenotopic species whose ecological requirements (1) accord with the specific conditions which characterise dynamic river banks (Aakra, 2000; Sadler et al., 2004; Andersen & Hanssen, 2005), but also (2) are believed to encapsulate the needs of other, more common species (Lambeck, 1997; Maes, 2004).

After the extreme floods in the ‘90s and the beginning of the 21st century, the Common Meuse showed itself to be a highly interesting system for nature restoration and rehabilitation (Van Looy & De Blust, 1995; Odou, 1998; Van Looy, 2005, 2006; Peters, 2006). Moreover, several studies indicated it still contained characteristic riverine and riparian species (Desender et al., 1994; Janssen, 1997; Peters et al., 2000; Vanacker, 2000; Lock & Vanacker, 2002; Usseglio-Polatera et al., 2000; Liefveld et al., 2001; Usseglio-Polatera & Beisel, 2002). Monitoring results showed that the restoration projects benefit both plants (Van Looy, 2005) and flight-active arthropods with an in-stream larval stage (Brugmans et al., 2005). In spite of these promising results, a scientifically-based research framework considering the rare riparian arthropods was still lacking. Therefore, pitfall samples from an extensive survey in 1998 (14 river banks; see Vanacker, 2000; Van Looy et al., 2005; 2008) were further identified and re-analysed (Lambeets et al., 2006; 2008a). Spider and carabid beetle assemblages were structured by similar environmental conditions, notwithstanding xerothermophilic and hygrophilic species were clearly confined to less dynamic and higher river banks, respectively. These results are presented in chapter II.1. Samples from an adjoining erosion channel which was naturally created during the extreme flood event of 1995 were identified as well (see Appendix A.1.). The channel serves to guide the flooding water during extreme flood events and was shown to contain a highly diverse and characteristic arthropod fauna. Lambeets et al. (2005) identified 2,109 adult spiders (Araneae) within 56 species (14 with a Red List-status in Flanders). Additionally, Lambeets & Struyve (2007) found 4,381 beetles (Coleoptera) spread over 152 species. Here, the arthropod fauna could be characterised as xerothermophilic and characteristic for disturbed areas in open, sandy areas with a scarce vegetation cover (cf. Van Looy, 2005). The presence of several rare, hygrophilic species could be attributed to the presence of riparian habitats in the vicinity. This small-scale study adds to the importance of the surrounding landscape which may act as a safe haven during high floods (Framenau et al., 1996; Rothenbücher & Schaefer, 2006) (see III.1.), just as argued for agricultural habitats during tillage (Pywell et al., 2005). A complete species list with the numbers trapped can be found in Appendix A1. for Araneae (Lambeets et al., 2005) and Coleoptera (Lambeets & Struyve, 2007), respectively.

The findings of previous studies founded the intensive survey carried out in 2005 (see II.2 and II.3) and 2006 (K. Lambeets, H. De Wandeler and colleagues, unpubl. data). Likewise, these studies were implemented using pitfall sampling (see Fig. I.4a,b).

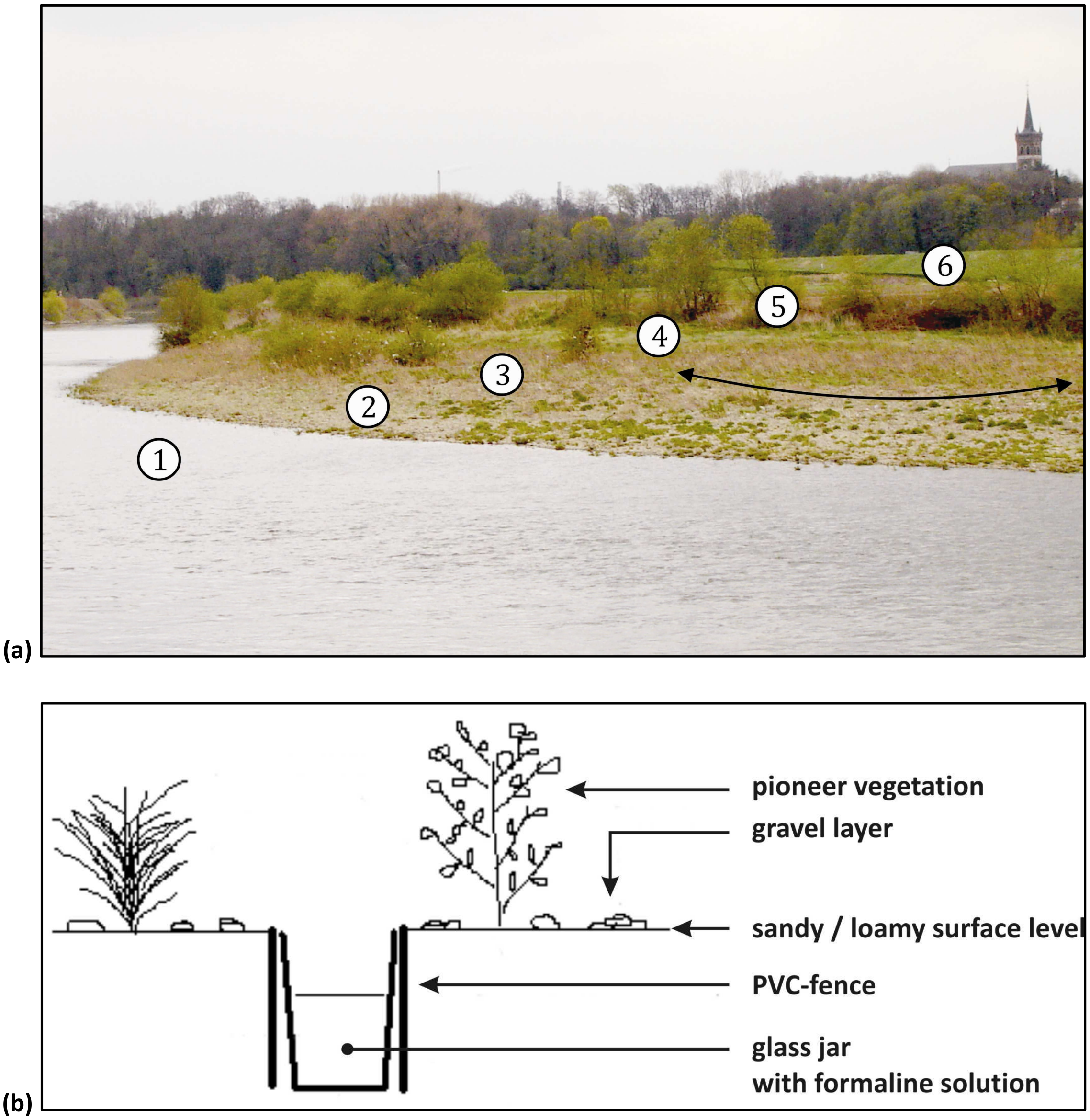

Fig. I.4 - Arrangement of the aquatic - terrestrial transition zone and positioning of the sampling set-up at the river bank at Ter Hagen (TH; Fig. I.1). Laterally from the river bank towards the alluvial hinterland, six zones were distinguished (a): (1) the fast-flowing gravel bed; (2) the bare gravel, proximate to the waterline; (3) & (4) the scarce pioneer vegetation, becoming more dense towards the river dike; (5) dense brushwood vegetation and scrubs along the dike (only if the embankments are not too vigorous); (6) the hinterland, which consists of (semi-natural) alluvial grasslands, meadows or intensively used agricultural fields. The arrow indicates where the pitfalls were positioned, i.e. along the transition between the open gravel and the scarce pioneer vegetation. (b) Pitfall sample set-up as it was used on the river banks along the Common Meuse.

Stochastic and sorting mechanisms in relation to flooding disturbance

Environments that are affected by natural or anthropogenic disturbances supposedly contain species assemblages that are structured by the prevailing disturbance regime as well as the ability of the inhabitants to deal with these stress factors (Lytle & Poff, 2004; Bonte et al., 2006a; Díaz et al., 2007). Environmental fluctuations keep a system away from a traditional equilibrium state (Vannote et al., 1980; Baker et al., 2006; Van Looy et al., 2006), provide renewed habitat opportunities and, by consequence, permit species with different functional life-history traits (e.g. habitat affinity and mobility) to occur on different spatiotemporal scales (Purtauf et al., 2004; Thompson & Townsend, 2006). Moreover, the general presumption that ecologically similar species in similar environments have similar traits, so there would be no phenotypic signature associated with contrasting distributions, seems not always to hold for dynamic systems (Bonte et al., 2006a; Ackerly & Cornwell, 2007). When *species sorting* occurs, sensu Leibold et al. (2004), all species can reach all patches, yet an environmental filtering effect causes the community that develops to be determined by the prevailing environmental conditions. Hence, species distributions are linked to local patch dynamics and the ability of species to react upon these conditions, and distributions are largely independent of purely spatial effects (Holyoak et al., 2005). When locations become unsuitable due to intense perturbations, however, only highly dispersive species will be able to persist due to substantial dispersal events and *mass effects* occur (Leibold et al., 2004; Holyoak et al., 2005). Consequently, seasonal activity patterns will confound distribution patterns as species presence can be expected to depend on the moment the river banks are exposed (Ribera et al., 2001; Rothenbücher & Schaefer, 2006; Bonte et al., 2006a). As a result, *colonisation windows* will be operative as well (Petersen, 1999; Bell et al., 2005). Therefore, a solid understanding of assemblage-wide functional responses provides insight in the vulnerability of certain ecological groups (Ribera et al., 2001; Foeckler et al., 2006; Violle et al., 2007) and should found nature management (Sutherland et al., 2004). By incorporating a trait-based approach, empirical and theoretical results can be more fully integrated into conservation measures (Driscoll & Weir, 2005; Bonte et al., 2006a; Le Viol et al., 2008).

River dynamics structure riverine and riparian landscapes (Ward et al., 2002) and consequently affect diversity patterns and assemblages of the inhabitants (Robinson et al., 2002; see 1.2.). For instance, Death & Winterbourn (1995) showed that an increase of the disturbance frequency primarily reduced stream invertebrate diversity by decreasing the time available for recolonisation following disturbance events. Bonn & Kleinwächter (1999) found that particularly mobile arthropods dominated highly flood-disturbed river banks, whereas flight-active beetles were the first to recover (Bonn et al., 2002). Studies considering patterns in plant traits showed seedling establishment to be clearly related to river dynamics (Shafroth et al., 2002) and consequently functional plant traits. Species adapted to flooding disturbance were clearly favoured, i.e. those plant species that displayed vegetative propagation (Rood et al., 2003), flood-synchronised seed dispersal (Karrenberg et al., 2002), flood-induced changes in root physiology (Blom & Voesenek, 1996), having large, hydrochorous, buoyant seeds (Lopez, 2001; Jäkäläniemi et al., 2004) or producing turions (Henry et al., 1996). Also, trait analysis proved to be a valid tool for analysing ecological patterns and functional changes of stream invertebrate assemblages (Usseglio-Polatera et al., 2000; Thompson & Townsend, 2006; Suren & Jowett, 2006; Díaz et al., 2007). More specifically, Lambeets et al. (2008a) showed that flooding structures riparian arthropod assemblages along the Common Meuse (see I.1.) but they did not find an answer for *"why"* xerothermophilic spiders and carabid beetles were favoured on more stable river banks and vice versa for hygrophilic species. The impact of flooding disturbance on the underlying mechanisms which structure arthropod assemblages on flood-disturbed river banks (cf. species sorting versus stochastic processes) is unravelled in chapter II.2. of this Ph.D.-thesis. Responses may be very species-specific, and therefore a beneficial management strategy for one species (umbrella species; Fleishman et al., 2000; Simberloff, 1998) may not be sufficient or will even disadvantage other species (Maes & Bonte, 2006; Maes & Van Dyck, 2005; Steck et al., 2007). Therefore, relying on a multi-species approach will generally benefit species diversity but also retain a higher degree of habitat heterogeneity on different spatiotemporal scales (Kremen et al., 1993; Lambeck, 1997). As riparian habitats contain many vulnerable and rare species, understanding the relationships between their distribution patterns and structuring environmental conditions as well as functional constraints (cf. Burkart, 2001; Sadler et al., 2004; Paetzold et al., 2008) will provide additional information for a sustainable river restoration and management. Chapter II.3. will provide more insight in these fundamental relationships.

river bank	country	locality	toponym	site description	UTMsq 5km	UTMsq 1km
TH1	NL	Ter Hagen	/		FS94A	FS9247
TH2	NL	Ter Hagen	/		FS94A	FS9347
KO1	BE	Kotem	/	arrival for recreational kayaking	FS94A	FS9348
KO2	BE	Kotem	/		FS94A	FS9348
KO3	BE	Kotem	/		FS94A	FS9349
KO4	BE	Kotem	/		FS94A	FS9249
ME2	NL	Meers	Weerterhof	trampling by Koniks, restored in 1998	FS94A	FS9149
ME1	NL	Meers	Weerterhof	trampling by Koniks, restored in 1998	FS94A	FS9149
MM	BE	Vucht	Langbroek	trampling by Koniks, restored in 2001	FS95C	FS9150
MB	NL	Maasband	/		FS95C	FS9251
MH	BE	Leut	Mazenhoven	trampling by Galloway	FS95C	FS9251
UM	NL	Urmond	/		FS95C	FS9352
MW	BE	Meeswijk	Palmenhof	restored in 2003	FS95C	FS9453
NH	NL	Berg aan de Maas - Nattenhoven	/	nearby ferry	FS95C	FS9454
KE	BE	Stokkem	Negenoord		FS95A	FS9456
OB1	NL	Obbicht - Grevenbicht	/	trampling by Koniks and Galloway	FS95A	FS9357
OB2	NL	Obbicht - Grevenbicht	/	trampling by Koniks and Galloway	FS95A	FS9357
OM	BE	Dilsen-Rotem	Oude Maas - Stokkemweerd	artificial dump of concrete blocks	FS95A	FS9357
VR	NL	Papenhoven	Kellerweerd, ferry		FS95A	FS9357
KW1	NL	Schipperskerk	Koeweide		FS96C	FS9460
KW2	NL	Schipperskerk	Koeweide		FS96D	FS9560
EL	BE	Elen	Elerweert		FS96D	FS9560
VW1	NL	Illikhoven	Visserweert	trampling by Galloway	FS96D	FS9561
VW2	NL	Illikhoven	Visserweert	trampling by Galloway	FS96D	FS9661
HE1	BE	Heppeneert	Heppeneert		FS96D	FS9662
HE2	BE	Heppeneert	Heppeneert		FS96D	FS9662
RO1	NL	Roosteren	Schansberg		FS96D	FS9563
RO2	NL	Roosteren	Schansberg	trampling by Koniks	FS96D	FS9663

Table I.1 - Survey of the sampled river banks and their specifications (see Fig. I.1).

1.3 Movement behaviour of riparian arthropods

Behavioural responses in unstable, flood-disturbed environments

Riparian habitats are liable to natural stochastic events, i.e. flooding disturbance, which determine the river's identity and integrity (Poff et al., 1997; Arthington et al., 2006, Tockner et al., 2006) and hence are important for the persistence of viable populations (Plachter & Reich, 1998; Geilen et al., 2004) (see above). Additionally, during the past two centuries most riverine ecosystems in Western Europe became highly fragmented as a consequence of exploitation practices such as gravel mining, and the intensification of the surrounding landscape for e.g. agricultural purposes (Ward & Stanford, 1995; Buijse et al., 2002; Mant & Janes, 2006; see above). Not only did many typical species disappear or became severely threatened (Burkart, 2001; Peters et al., 2000; Lambeets, 2008a), stenotopic riparian species are also expected to have adapted to the highly fluctuating environmental conditions (Lytle & Poff, 2004). For plants Blom & Voesenek (1996) and Karrenberg et al. (2002) discuss how certain life-history traits may involve increased persistence in flooded habitats. Adis & Junk (2002) and Lytle & Poff (2004) showed that behavioural, morpho-, pheno- and/or physiological adaptations benefit riparian and riverine organisms in relation to the (un)predictable character of riverine ecosystems, which is chiefly determined by the degree of flooding disturbance. DeVito et al. (2004) demonstrated how habitat affinity of riparian wolf spiders corresponds to thermal and desiccation stress regimes, which consequently determines their distribution patterns. Several studies considered ecomorphological adaptations of arthropods in other flood-prone habitats as salt-marshes (Foster, 2000; Pétillon et al., 2005a) or coastal shorelines (Morse, 2002; Kraus & Morse, 2005); others such as Desender (1989a), Plum (2005) and Bates et al. (2006) emphasised on riparian arthropods and benthic riverine species (Olden et al., 2004; Hoffman et al., 2006). Other studies recorded seasonal movements and concordant distribution patterns of riparian arthropods (Irmler, 1979; Lang & Pütz, 1999; Loeser et al., 2006; Rothenbücher & Schaefer, 2006) and attributed pattern divergence to important functional traits as habitat affinity and mobility. However, less attention was paid to the factors which directly guide movement decisions of the species under study.

Decision-making is essential to avoid costly situations by choosing more profitable outcomes, which enables an animal to anticipate environmental changes (Dall et al., 2005; Danchin et al., 2008) and to avoid ending up in unfamiliar (unsuitable) situations (Giraldeau, 1997; Bowler & Benton, 2005). As decision-making precedes movement behaviour, the factors guiding these decisions essentially relate to the beneficiality of this animal behaviour (Dall et al., 2005). Therefore, unravelling the relationships between the information which is used by organisms during movement decisions and their behavioural responses will lead to a better understanding of behavioural variation in general (Danchin et al., 2008). Within a drastically changing environment, as Planet Earth at present (e.g. Poff et al., 1997; Fahrig, 2003; 2007; Allan, 2004 a.o.), assessing the reliability of information resources will enable an organism to reduce the ecological uncertainty bound to that environment (Wehner, 1997; Dall et al., 2005) and consequently to make beneficial decisions and/or adjust its behaviour accordingly (Dingle, 1986; Both et al., 2006; Pulido, 2007; Wilcove & Wikelski, 2008). Moreover, environmental information might no longer be reliable due to anthropogenic interference as true habitat conditions can be concealed. These phenomena are referred to as *ecological traps* by Schlaepfer et al. (2002) and have been proven to occur in various ecosystems (e.g. Harding et al., 1998; Hérault & Honnay, 2005; Lunt & Spooner, 2005; Wolters et al., 2008). Dixit Schlaepfer et al. (2002), ecological traps occur when organisms make non-beneficial (poor) choices based on normal cues that no longer correlate with habitat quality, which especially occurs when an environment changes suddenly, for instance during anthropogenic perturbed floods. More particularly, it might be expected that species preferring dynamic or disturbed environments would show a higher degree of behavioural variability (phenotypic plasticity; Pigliucci, 2001), enabling them to respond efficiently to a quickly changing environment (Lytle & Poff, 2004; e.g. Scapini et al., 2002). Comparing behavioural responses between sets of sympatric species which differ in their degree of habitat specialisation will therefore provide valuable information about the adaptivity of certain behavioural traits (Zollner & Lima, 2005; Cézilly et al., 2008). Especially for organisms occurring in unpredictable, disturbed environments (Lytle & Poff, 2004), consistent (stereotyped) movement behaviour might be disadvantageous as decisions will probably not match the present conditions (Bowler & Benton, 2005; Fahrig, 2007). Therefore, behavioural flexibility benefits organisms inhabiting these stressful environments (e.g. Riechert & Hall, 2000; Scapini et al., 2002; Desender, 2000; Merckx & Van Dyck, 2006). Moreover, behaviour may be adjusted according to phenomenal (proximate) cues as pointed out for web-building spiders (Harwood et al., 2001; Bonte et al., 2008a), and can be refined and extended by learning (cf. experience; Persons & Uetz, 1996; Giraldeau, 1997).

The beneficiality of flood-adjusted movement behaviour

Riparian habitats are situated parallel with the river channel and hence are liable to fluctuations in water discharges (see above). As flood events both have a predictable (floods always occur in one direction, namely from the waterline towards the hinterland) and a stochastic component (especially in dynamic, rain-fed rivers the frequency and magnitude of flood events might be unpredictable; Van Looy, 2006), relying on one type of information (e.g. visual landmarks in the direct vicinity) can be costly as it might lead riparian organisms to unfamiliar or potentially unsuitable habitat (cf. Schlaepfer et al., 2002; Bonte et al., 2004a; Fahrig, 2007). As riparian habitats are extremely patchy, organisms inhabiting river banks should avoid to land offshore (on the water surface) as the uncertainty of ending up in suitable habitat during downstream drift is quite high, especially for less mobile species as wolf spiders, but less so for flight-active arthropods such as carabid beetles (Bonn, 2000; Bates et al., 2006). Avoiding flood events by moving upshore, i.e. away from the rising water en towards more stable, vegetated parts of the river bank, or anticipating flooding would benefit cursorial arthropods, especially before long-lasting winter floods set in (Lang & Pütz, 1999). Otherwise, species might choose to withstand flooding at the river bank level (Zulka, 1994; Plum, 2005; Rothenbücher & Schaefer, 2006). The latter option would enable less mobile arthropods to recolonise the bank quickly once the water retreats, thus directly benefiting from the ephemeral, prey-rich conditions (Briers et al., 2005; Paetzold et al., 2005; 2006). Movement patterns are hence expected to differ in agreement with their mobility (Bonte et al., 2006b). From that point of view, an accurate orientation will advantage river bank inhabitants; homeward orientation during sudden disturbance events will lead an individual back to its original habitat (Papi & Tongioirgi, 1963; Jander, 1975; Borgioli et al., 1999a). Innate (inherited) factors related to an individual's geographical origin and hence comprising habitat conditions at longer time frames, will provide essential information to sustain behavioural responses as they allow an individual to adequately relocate safe and suitable conditions (Papi & Tongiorgi, 1963; Ugolini et al., 1995).

Moreover, external (proximate) sensory stimuli (the spatial location of information and/or stress sources) will provide additional information and actualise movement decisions (Bowler & Benton, 2005), and hence reduce the ecological uncertainty of a variable environment (Schlaepfer et al., 2002). Tactile cues might be important to trigger a flight reflex away from the source of disturbance, e.g. the rising water level (Irmler, 1979; Morse, 1997; Bonn, 2000), whereas visual cues would rather guide directed movements (Colombini et al., 1995; Ortego-Escobar, 2002; Norgaard et al., 2007). Generally, a species that spends its entire life in spatially structured habitat patches is expected to be familiar with the arrangement of habitat structures; mainly relying on innate information might therefore restrict unnecessary movements. Its behaviour might be guided less by external visual input in comparison with a congeneric species with a wider niche range.

As river banks are prone to flooding disturbance which affects the occurrence of its inhabitants accordingly (see II.3.), and banks are highly isolated within an intensively used landscape (see above; Fig. I.1), movement behaviour is expected to accord with the prevalent disturbance regime (Plachter & Reich, 1998; Adis & Junk, 2002; Lytle & Poff, 2004). Besides flood-adjusted behaviour, movement patterns are expected to agree with a species' habitat affinity and mobility (see II.2.). Studies concerning lowland floodplains indicated this was the case for the resident arthropod fauna (Lang & Pütz, 1999; Weigmann & Wohlgemuth-von Reiche, 1999; Rothenbücher & Schaefer, 2006). As orientation precedes directed movements (Jander, 1975), accurately orienting and (re)locating suitable conditions will benefit the persistence of arthropods in flood-disturbed environments (Papi, 1955; Papi & Tongiorigi, 1963; Scapini et al., 1995; Borgioli et al., 1999a,b; Morse, 2002; Kraus & Morse, 2005). For instance, inadequate orientation may lead to low-quality habitats and cause locally perturbed population dynamics (Bonte et al., 2004a; Olden et al., 2004). How riparian arthropods (Araneae, Carabidae) with a varying habitat affinity and mobility differ in their migratory behaviour before the long-lasting winter flooding (see 1.2.) is dealt with in chapter III.1. More in-detail behavioural responses for two congeneric and sympatric wolf spiders (Lycosidae; *Pardosa agricola* (Thorell, 1856) and *P. amentata* (Clerck, 1757)) are analysed and discussed in chapter III.2. (orientation guided by visual stimuli), III.3. (zonal recovery during water surface locomotion) and III.4. (flood-avoidance and submersion tolerance), respectively.

1.4 Gene flow and genetic structure in linearly arranged ecosystems

Riverine and riparian environments are characterised by a unidirectional (downstream) flow gradient and a linear arrangement of habitat patches (Ward, 1998; Ward et al., 2002). Mostly the gradient in discharge regimes is correlated with shifts in environmental conditions (Naiman et al., 2005; Allan & Castillo, 2008) and functional grouping of its inhabitants (cf. the River Continuum Concept; Vannote et al., 1980; see II.2.). Moreover, the unidirectional gradient may guide drift processes along the stream channel. Dispersal mechanisms of in-stream invertebrates (Suren & Jowett, 2006; Hoffman et al., 2006), propagules of riparian plants (Riis & Sand-Jensen, 2006; Vogt et al., 2006; Bang et al., 2007) and freshwater fish (Lamouroux et al., 2002; Schick & Lindley, 2007) have already proven to depend on the prevailing discharge regime, at least to some extent. Generally, species capable of active dispersal may overcome downstream drift easily by active dispersal (MacNeale et al., 2005; Vignieri, 2005 a.o.). To fully understand dispersal processes and their effects on population dynamics, observational studies should be complemented by a genetic approach, otherwise important processes such as inbreeding depression or genetic drift might remain undiscovered (Lande, 1988; Frankham, 1995; Keller & Waller, 2002; Ronce, 2007). Recently, genetic studies considering hydrochorous riparian plants (Imbert & Lefèvre, 2002; Tero et al., 2003; Jacquemyn et al., 2006; Pollux et al., 2008) have shown that water-mediated (undirectional) dispersal is not necessarily the rank and file for these plants. Still, flood events might explain, at least partly, population dynamics and from that, patterns of genetic differentiation (Honnay et al., 2009; Van Looy et al., 2009).

Nevertheless the genetic structure of arthropods has been analysed sporadically the past decades (e.g. spiders: Boulton et al., 1998; Johannesen et al., 1998; Colgan et al., 2002; Bonte et al., 2003a; carabid beetles: Brouat et al., 2003; Dhuyvetter et al., 2004; Desender et al., 2005), studies concerning the population genetic structure of species inhabiting linearly arranged habitats are generally lacking in recent literature. In chapter IV.1., the spatial genetic structure of a stenotopic riparian wolf spider (Lycosidae) *Pardosa agricola* (Thorell, 1856) is unravelled. This cursorial wolf spider inhabits the dynamic river banks along the Common Meuse throughout the year (Lambeets et al., 2008a), but recently has been confined to the last 9 kms of the river reach (Lambeets et al., 2007; Lambeets, 2008a). Sensu Tero et al. (2003) and Pollux et al. (2008), different hypothetical models have been proposed concerning dispersal and (functional) connectivity between populations in ecosystems characterised by a unidirectional gradient (Fig. I.5), in this case, downstream flow:

(a) the *regional ensemble* represents highly isolated, persistent populations without any current migration between them (Fig. I.5a)
(b) unidirectional dispersal results in gene flow only between (temporally persistent) neighbouring populations (Fig. I.5b)
(c) the *stepping-stone model* also considers gene flow only to occur between adjacent population, yet with dispersal being bidirectional (Fig. I.5c)
(d) unidirectional dispersal and thus gene flow are not restricted to neighbouring populations but can occur between a series of ephemeral, local (sub)populations (Fig. I.5d), hence together forming a metapopulation
(e) the *classical metapopulation* model concurs with model (d), but dispersal can be bidirectional (Fig. I.5e)
(f) a *spatially extended population* is characterised by habitat patches with high rates of gene flow between them and hence form a single genetically uniform panmictic unit (Fig. I.5f)

As innate factors are expected to affect behavioural responses as well, and vice versa (Bossdorf et al., 2008), differences according to the geographical origin would also be reflected in the genetic structure of a highly stenotopic cursorial arthropod, which is not capable of (un)controlled flight. Individuals originating from the same river shore are expected to be genetically less differentiated than those from opposite shores as mobile arthropods, in contrast to riparian plants (Jacquemyn et al., 2006; Honnay et al., 2009; Van Looy et al., 2009), are able to effectively avoid and evade flooding. Nevertheless, genetic patterns might still differ in relation to river dynamics and hence habitat quality (Stelter et al., 1997; e.g. Scapini et al., 1995). *P. agricola* is capable of active water surface locomotion but clearly tends to avoid costs related with ending up offshore (see III.3. and III.4.) and, moreover, anticipates flooding by proactive (seasonal) migration (see III.1. and III.2.), genetic erosion of upstream populations might be expected (loss of alleles to drift) and consequently an accumulation of genetic diversity downstream (influx of alleles). Moreover, these results are best interpreted within a context of functional connectivity along the riparian corridor, as enunciated in chapter IV.1.

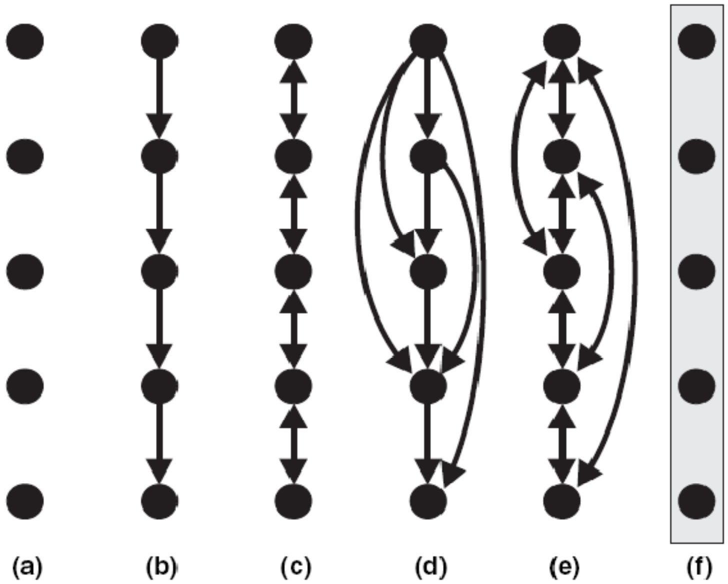

Fig. I.5 - Schematic representation of the different possible population models for linearly arranged habitats: (a) regional ensemble, (b) unidirectional gene flow, between adjacent populations only, (c) stepping-stone model, (d) unidirectional gene flow, yet possible between all (sub)populations, (e) classic metapopulation model and (f) spatially extended population with free gene flow. Figure after Pollux et al. (2009).

1.5 Objectives and outline of the thesis

The objectives outlined throughout this Ph.D.-dissertation find their origin in a preliminary survey of riparian arthropods in 1998 and 2000, after large-scale restoration efforts along the Common Meuse (Van Looy, 2005; Van Looy et al., 2005; 2008; Lambeets et al., 2008a). Building on the fundamental findings of these studies, this research project aims to address variation in distribution patterns and behavioural responses of riparian arthropods, particularly spiders (Araneae) and carabid beetles (Carabidae). As riverine ecosystems are basically non-equilibrium, dynamic ecosystems, flow regimes and flood pulse characteristics in particular are expected to shape both distribution and behaviour of mobile arthropod groups.

My research project, funded by a Ph.D. grant of the Institute for the Promotion of Innovation through Science and Technology in Flanders (IWT-Vlaanderen, N° 41328), attempts to unravel which environmental factors influence arthropod assemblage structure along spatially structured river banks of a lowland gravel river (Bonn & Kleinwächter, 1999; Sadler et al., 2004; Paetzold et al., 2008). As river banks are frequently disturbed by flood events and liable to extreme microclimatological conditions (Plachter & Reich, 1998; Robinson et al., 2002), functional life-history traits of the present species supposedly affect species composition as well (Wiens, 2002; McGill et al., 2006; Le Violle et al., 2007). More-over, the results are discussed in relation to the conservation of vulnerable riparian arthropods and a framework for river management and restoration (Pedroli et al., 2002; Van Looy, 2006; Lake et al., 2007; chapter II.1 – II.3). Due to riverine stress regimes, organisms which are repeatedly exposed to e.g. flooding are expected to have evolved or adjusted to these types of disturbance (Adis & Junk, 2002; Lytle & Poff, 2004). Therefore, different behavioural responses might be prevalent in accordance with their functional life-history traits (e.g. habitat affinity; Rothenbücher & Schaefer, 2006; chapter III.1 – III.4). Since the riparian corridor along the Common Meuse is embedded in a matrix of an intensively used hinterland and river banks are highly isolated, populations of stenotopic, less mobile species are expected to show variation in their spatial genetic structure (chapter VI.1). Chapter V. provides a general discussion and conclusions.

II. Environmental constraints for riparian arthropod assemblages

The river bank at Kerkeweerd was established after
the extreme flood event of 2003 (Photo: Kevin Lambeets)

II.1. Assemblage structure and conservation value of spiders and carabid beetles from restored lowland river banks

Lambeets K., Hendrickx F., Vanacker S., Van Looy K., Maelfait J.-P. & Bonte D. 2008. Biodiversity and Conservation 17, 3133-3148

Elaphrus riparius (Linaeus, 1758), a garish, riverine carabid beetle (Foto: Maarten Jacobs)

Abstract

We assessed the composition of spider and carabid beetle assemblages along river banks from the Common Meuse (Belgium) to determine their relationships with local topographical and landscape-related characteristics. Data were gathered with pitfall traps in 1998 and explored by ordination and grouping methods. Our analysis revealed that the presence of xerothermic spider species was limited to scarcely covered, less dynamic gravel banks. Riparian spider species were found on frequently flooded as well as on rather elevated and high gravel banks, while riparian carabid beetles were dominant on all sampled banks. The level of flooding disturbance, the vegetation density and the presence of silt appeared to be the most important environmental determinants of spider and carabid beetle assemblage structure. Consequently, local environmental factors influence species occurrence patterns in a similar way for the two investigated arthropod groups. Nevertheless, distinct ecological groups are differently ordered along the prime environmental gradients. Nature management should therefore consider the conservation, restoration and connectivity of both dynamic and more elevated banks in order to obtain a high degree of local and regional heterogeneity throughout the river system.

Key-words: Araneae, Carabidae, ecological groups, exposed riverine sediments, river dynamics, river restoration

Introduction

The structuring of arthropod assemblages from exposed riverine sediments (ERS) along lowland river systems and their relations with local habitat structures is to date poorly documented. Previous studies revealed the importance of fluvial dynamics and bar topography (Bonn and Kleinwächter, 1999; Manderbach & Framenau, 2001; Adis & Junk, 2002; Eyre et al., 2001; 2002; Sadler et al., 2004), substrate structure (Desender, 1989a; Manderbach & Framenau, 2001) and vegetation cover (Eyre et al., 2002). Because the majority of these studies focused on upland systems, it is not known whether the same factors are important in lowland gravel rivers. Stream canalization, subsequently leading to fragmentation of gravel banks (Naiman et al., 2005; Laeser et al., 2005) and alterations of the flooding regime (Bonn et al., 2002; Eyre et al., 2001; 2002) were found to impose drastic changes in riparian arthropod diversity. The Common Meuse (Fig. II.1), being a natural and geographical border between Flanders (northern Belgium) and the Netherlands, is a characteristic lowland gravel river. From 1860 onwards, dikes were fortified to secure safe navigation, improve flood protection and support agriculture on the fertile floodplain soils (van Winden et al., 2001). Consequently, natural river dynamics were modified resulting in a reduction in the size of gravel bars and their frequency of occurrence which increased their isolation (Van Looy et al., 2002). Elevated and less dynamic gravel banks are however still present along the Common Meuse (Van Looy & De Blust, 1998), mostly at the inside bends of large meanders in wider parts of the river channel. As for many riparian habitats (e.g. alluvial floodplains, river banks), a patchy spatial distribution along the river trajectory is characteristic (Plachter & Reich, 1998; Sadler et al., 2004), although the majority of the banks are not connected during low flows in the summer by exposed sediments. Currently, restoration efforts along the Common Meuse prioritise a re-establishment of its natural character (Nagels et al., 1999). Therefore, dikes have been removed, banks lowered and the summer bed widened in order to restore the aquatic-terrestrial linkages and, consequently, the contact between the river and its winter bed (Van Looy & De Blust, 1998).

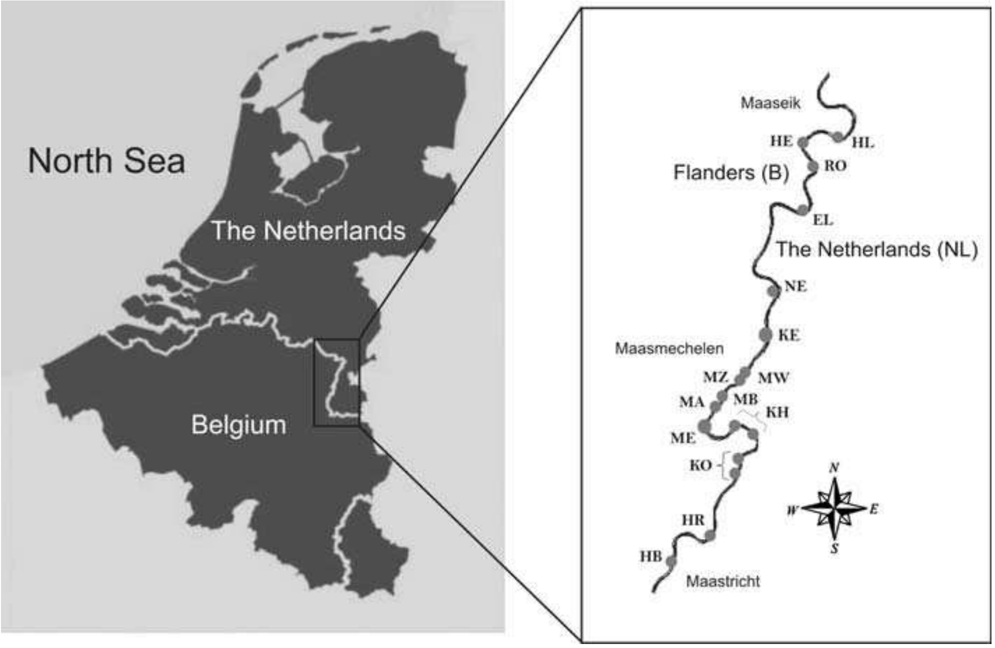

Fig. II.1 - Location of the gravel banks along the Common Meuse trajectory in 1998. All sampled gravel banks are indicated by dots and a subsequent code.

Because local environmental conditions largely depend on water level (Naiman et al., 2005) and microclimatological fluctuations (Renöfält et al., 2005), gravel banks comprise an extreme environment in which only well-adapted and highly dispersive species are expected to maintain viable populations (Stelter et al., 1997; Bonn, 2000). Therefore, we address whether (1) river banks along this lowland gravel river support a typical spider and carabid beetle fauna and (2) (dis)similarities are apparent in the occurrence of ecological groups within gravel banks. Based on these findings, we make suggestions for future river management and, more specifically, the conservation of riparian species.

Material and methods

Study area

The Common Meuse (45 km) is the shallow, less diked or dammed part of the River Meuse. It is the only gravel river in Flanders, and one of the few lowland gravel rivers in Europe (Van Looy & De Blust, 1998). The watercourse is characterized by strong river flow fluctuations and a wandering pattern of isolated gravel banks. The latter comprise a top layer of coarse shingle (10 – 100 mm) with in between a sharp sand-gravel or sand-loam fraction (Van Looy & De Blust, 1998), mostly covered with a thin layer of silt. Besides irregular spring and summer inundations, all gravel banks are permanently flooded during autumn and winter. Only when the river discharge drops below 200 m^3s^{-1}, gravel banks are exposed. Patch size and relative height consequently vary according to water level fluctuations (Plachter & Reich, 1998). Vegetation development depends on the river dynamics (Franklin et al., 2001) and silt deposition (Sluis & Tandarich, 2004) and is directly related to bank height and its location within the river system (Desender, 1989a). During peak transports, sediment is displaced and vegetation largely destroyed (Peters et al., 2000), (re)creating prime habitats for colonization of terrestrial plants and animal communities (Bonn & Kleinwächter, 1999).

Sampling protocol

In 1998 a total of 14 gravel banks were sampled along the 45 km length of the Common Meuse (Fig. II.1). At each bank, at least three pitfalls (Ø = 9.5 cm, 4% formalin solution) were placed from the end of May until the end of August, spaced 10 m apart and emptied fortnightly. This was considered sufficient to avoid interference between traps for arthropod catches (Topping & Sunderland, 1992). Vegetation composition was mapped in a range of 20 m around the pitfalls and characterized with respect to species composition and coverage in 1 m^2 plots around each pitfall. These data were used to define habitat heterogeneity and vegetation structure of the gravel banks. During field survey, gravel size fractions were estimated by eye and divided into size classes of 10 cm, ranging between 0 and 10 cm up and 40–50 cm. The presence or absence of sand and silt within 1 m^2 plots was recorded. In order to obtain appropriate estimates of local fluvial dynamics, the difference in water level (m) between 200 m^3s^{-1} and 10 m^3s^{-1} discharge was recorded as a measure for water level rise speed. Flooding susceptibility of each gravel bank was obtained by means of a regression analysis of the average distance between the pitfalls and the waterline during each sample period and discharges of the Common Meuse (Flemish River Administration, unpublished data) during the moment of the measuring. The discharge value at a distance equaling 0 m was used as an appropriate, relative measure of gravel bank height (i.e. the average discharge value at which pitfalls are flooded). Local geometrics of gravel banks (i.e. area (m^2), circumference (m) and length (m)) were calculated using ArcView GIS 3.2. Gravel bank location was defined with regard to its longitudinal position along the river trajectory. Gravel banks EL, HE, HR, KH, KO, MW are surrounded by arable land; KE, HB, HL, MA, MB, ME, MZ, RO by alluvial grasslands under nature management.

Data analysis

Pitfall sampling on river banks is often problematic. Water level fluctuations may affect yields as a consequence of inundations, and more epigeic than interstitial species are caught (Eyre et al., 2001). Therefore, pitfall captures per site were standardized to six pitfalls per gravel bank prior to further processing. Additionally capture rates in pitfall traps are influenced by population densities and intra- and interspecific differences in activity patterns and microhabitat structure (Topping & Sunderland, 1992; Antvogel & Bonn, 2001; Bonte et al., 2003b). For that reason we standardized species abundance on each bank towards relative abundance on the overall grand total (Maelfait & Baert, 1975; Baars, 1979; Desender & Maelfait, 1986). To minimise the influence of rare species in ordination analyses (McCune & Grace, 2002), species with less than 14 individuals were omitted (Maelfait & Baert, 1975), resulting in 31 spider and 51 carabid beetle species.

Intercorrelations of environmental properties (proc corr; SAS 9.1) were corrected for multiple comparisons by Bonferroni-adjustment. The assemblage structure and the reaction of the species to environmental gradients were explored by means of an unconstrained indirect gradient analysis (Detrended Correspondence Analysis (DCA); Hill, 1979a). Both species and samples were ordinated simultaneously (McCune & Grace, 2002) but environmental variables were restrained during analysis in order to present all conceivable variation related to species composition. Secondly, a non-hierarchical clustering method (relative Euclidean distance and Ward's method; Kaufman & Rousseeuw, 1990) was additionally applied to investigate similarity patterns in gravel banks, based on relative abundances of the two investigated arthropod groups. Similarity in ordinations between carabid beetles and spiders was tested by Mantel-test, based on 1000 Monte-Carlo permutations. Finally, Indicator Species Analysis (Dufrêne & Legendre, 1997) was applied to retrieve indicator species for gravel bank groups, as identified by cluster analysis. This analysis combines data on the relative abundance of a species with its fidelity in a particular group (= relative frequency of occurrence) to calculate its Indicator Value (IndVal). The statistical significance of the maximum indicator value was tested through Monte Carlo randomizations. All multivariate analyses were conducted with the PC-Ord package (McCune & Mefford, 1999).

Data on the general ecology of spiders and carabid beetles were derived from Hänggi et al. (1995), Roberts (1998), Harvey et al. (2002) and Entling et al. (2007), and Desender et al. (1995) and Turin (2000), respectively. Based on overall habitat preference of the species, we defined the following four ecological groups: (i) *xero- and thermophiles*: considered as species preferring arid circumstances and/or warm climatic conditions, mainly restricted to scarcely vegetated habitats; (ii) *hygrophiles*: occurring in a wide range of humid and moist circumstances, and habitats with a more dense vegetation cover (e.g. wetlands); (iii) *agrobionts*: considered as ubiquitous species occurring in a wide range of habitats and/or with a well developed dispersal capacity (especially species from arable land are considered as typical pioneers); (iv) *riparian species*: defined as species restricted to specific conditions in the proximity of the waterline, consequently only occurring along river banks. An overview of the different groups is given in Table II.1.

Results

General results

Environmental parameters showed significant interrelations. Gravel bank area and circumference ($r = 0.7326$; $P < 0.05$), rising speed of water and vegetation cover ($r = 0.5458$; $P < 0.05$) and rising speed and the presence of silt ($r = 0.7683$; $P < 0.05$) showed significant correlations after Bonferroni-correction. A total of 11,266 adult spiders were collected, belonging to 81 species and 11 families. The linyphiid spider *Oedothorax retusus* was the most common species, representing over 25% of the grand total of the catches. *Pardosa agricola* (Lycosidae) and *Erigone dentipalpis* (Linyphiidae) each made up about 12% of the catches. The two linyphiids occurred on all the sites, whereas *P. agricola* only appeared on nine of the 14 sampled gravel banks. The survey additionally revealed 23,331 carabid beetles belonging to 97 species. *Bembidion femoratum* represented 25% of the grand total, while *B. tetracolum* and *B. decorum*, respectively, comprised 16% and 6% of the catches. The cumulative number of all *Bembidion* species, comprise over 65% of carabid beetles collected. Except *B. decorum*, all previously mentioned species were present on all the sampled gravel banks. A complete species list and Red List status of the captured spiders and carabid beetles is given in Table II.1.

Spider assemblage structure

The ordination plot for spider species is shown in Fig. II.2. Axis 1 (eigenvalue 0.423) related to local vegetation cover (vegc: $r = 0.606$; $P < 0.05$), susceptibility to flooding disturbance of the gravel bank (height: $r = 0.711$; $P < 0.05$) and rising speed of the flooding water (ascent: $r = 0.534$; $P < 0.05$) and subsequently the presence of silt due to intercorrelation. Higher values on this axis indicate sites characterized by a more sparse vegetation cover, a lower relative elevation and a lower rising speed of the washing water. Axis 1 explained 40.6% of the total variance in the species data, while less than 1.1% was further explained by subsequent axes. Therefore, only the ranking of species along the first axis is discussed. Along this axis, hygrophilic species clustered together on the left side of the ordination, indicating their affinity towards densely vegetated gravel banks characterized by a rather high rising speed. These gravel banks were additionally characterized by a high number of eurytopic, frequently ballooning species (e.g. *Oedothorax* sp. and *Erigone* sp.). Riparian species were found on frequently flooded as well as on rather elevated and high gravel banks. Typical xerothermic species were captured in higher abundance on gravel banks with a slow water level ascent, and plotted at the right in the ordination. Eurytopic species, being good colonizers due to ballooning dispersal (Linyphiinae and Erigoninae) or cursorial movement (Lycosidae), were found in the middle of the output, signifying their overall presence on all gravel banks.

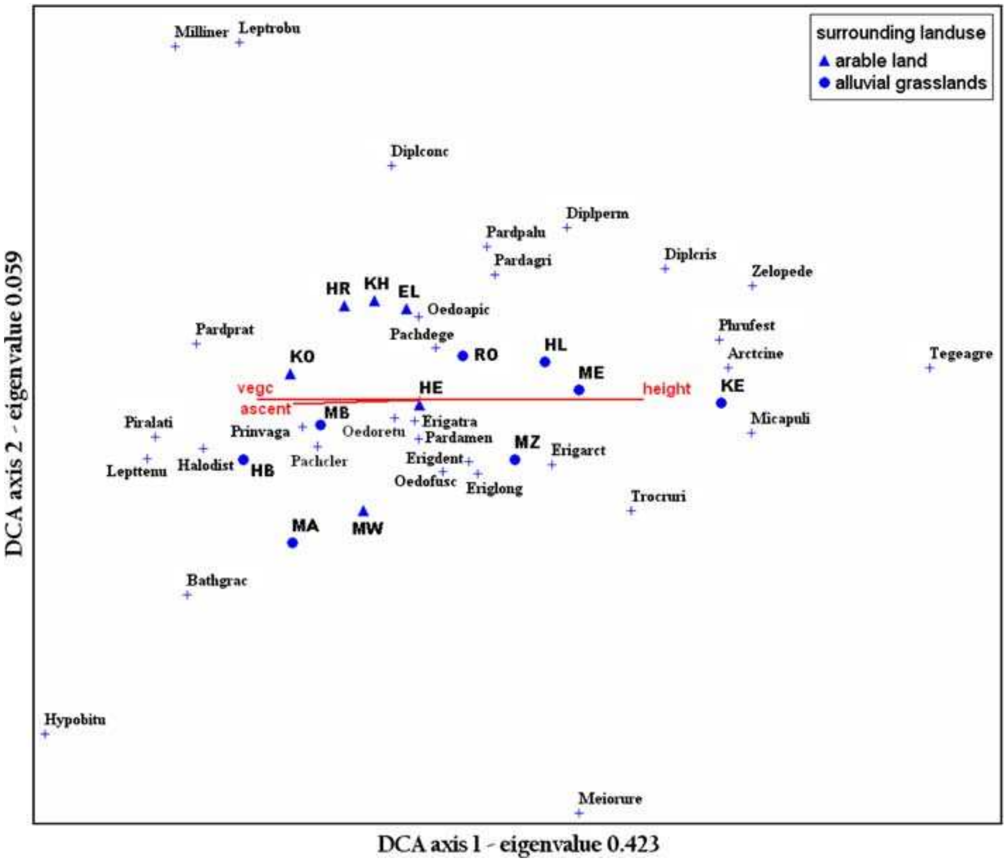

Fig. II.2 - DCA-ordination of spider pitfall data, after standardization for six pitfalls per site. Only most abundant species were taken in consideration (>14 ind.). Species are indicated by the first four letters of respectively genus and species name. Abbreviations of species names are listed in Table II.1. Symbols indicate land-use surrounding gravel banks. Environmental factors are indicated by vectors: ascent = local rising speed of water; height = relative flooding susceptibility of the gravel bank; vegc = mean vegetation cover around pitfalls on the gravel bank.

Carabid beetle assemblage structure

Ordination results of carabid beetle species are displayed in Fig. II.3. Axis 1 (eigenvalue 0.470), explaining 53.4% of the total variation in species composition is related to vegetation cover of the gravel banks (vegc: $r = 0.733$; $P < 0.05$), local gravel bank elevation (height: $r = 0.633$; $P < 0.05$) and water level rising speed (ascent: $r = 0.557$, $P <0.05$) and as a consequence of intercorrelation to the presence of silt. Higher values along the first axis indicated sites with a less dense vegetation, a lower degree of flooding susceptibility and a diminished water rising speed. Subsequent axes explained less than 2% of the total variation and are consequently omitted from the interpretation. Riparian species were scattered throughout the ordination, indicating their overall occurrence along the river system, although species-specific affinities towards environmental characteristics were recorded. Xerothermic species (mainly psammophiles), were restrained to the right side of the ordination. Carabid beetles from dynamic and humid environments (preferring loamy substrates), were found on the left. Moreover, agrobiont ubiquitous species were scattered throughout the ordination output, consequently occurring on all gravel banks.

Similarity of carabid beetle and spider assemblages

Mantel-test indicated that spider and carabid beetle assemblages are structured by similar environmental conditions, as indicated by correlated gravel bank ordination scores ($r = 0.477$; $P = 0.002$) between both groups.

Gravel bank clusters and indicator species

In agreement with the measured environmental properties, cluster analysis based upon spider and carabid beetle relative abundances, revealed two major groups of gravel banks, each characterized by several significant indicator species (Table II.2). The first group of gravel banks (HB, HR, KO, MA, MB, MW), enclosed hygrophilic carabid beetle species, preferring some degree of vegetation cover (e.g. *Paranchus albipes*, *Bembidion semipunctatum*, *Agonum micans*). Thermo- and xerophilic spiders and beetles (e.g. *Pardosa agricola, Phrurolithus festivus,* *Lionychus quadrillum, Amara aulica*) were found to be significant indicators for the second group of gravel banks (EL, HE, HL, KE, KH, ME, MZ, RO).

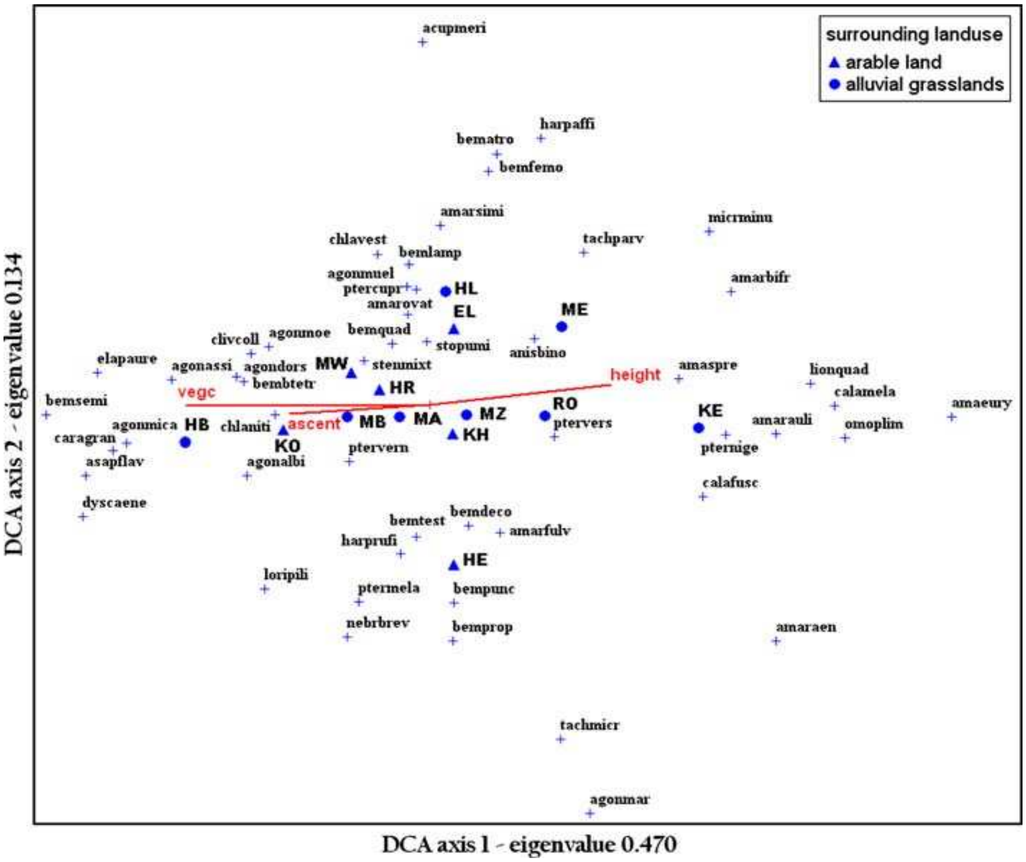

Fig. II.3 - DCA-ordination of carabid beetle data. Data is standardized for six pitfall traps per site. Only most abundant species were taken into account (>14 ind.), and represented by the first four letters of both genus and species name. Abbreviations of carabid beetle names are listed in Table II.1. Symbols indicate land-use surrounding gravel banks. Environmental factors are indicated by vectors: ascent = local rising speed of water; height = relative flooding susceptibility of the gravel bank; vegc = mean vegetation cover around pitfalls on the gravel bank.

Discussion

Spider synecology

In agreement with the dynamic character of gravel banks, spider species richness is rather low compared to other studies concerning recently fragmented dynamic habitats (Hendrickx et al., 1998; Bonte et al., 2002) and similar to the richness observed in agricultural landscapes (Perner & Malt, 2003).

gravel bank clusters	indicator species	IndVal
(1) HB, HR, KO, MA, MB, MW	*Paranchus albipes* (Fabricius, 1796)	88.9
	Agonum micans (Nicolai, 1822)	83.3
	Bembidion semipunctatum (Donovan, 1806)	81.7
	Elaphrus aureus Ph. Müller, 1821	66.7
(2) EL, HE, HL, KE, KH, ME, MZ, RO	*Lionychus quadrillum* (Duftschmid, 1812)	99.2
	Phrurolithus festivus (C.L. Koch, 1835)	93.3
	Amara aulica (Panzer, 1797)	92.8
	Pardosa agricola (Thorell, 1856)	87.0
	Diplocephalus cristatus (Blackwall, 1833)	81.3
	Calathus fuscipes (Goeze, 1777)	76.8
	Micaria pulicaria (Sundevall, 1831)	70.7

Table II.2 - Clusters of gravel banks, with indication of significant indicator species (Monte-Carlo permutations, $P < 0.05$) and indicator values (IndVal).

Generally, frequent aerial dispersers and cursorial meadow species can be considered as good colonizers of gravel banks, as recorded in other inundated ecosystems (Wohlgemuth-von Reiche & Grube, 1999). Our data, however, allow us to distinguish between species with distinct ecological affinities and dispersal capacities (Lambeets et al., 2006). The high abundance of cursorial lycosid spiders, especially the rare gravel bank specialists *Pardosa agricola* and *Arctosa cinerea*, on gravel banks surrounded by grasslands under nature management, suggests a dependence of other proximate natural habitat, possibly for seasonal migration towards hibernation sites during the subadult or juvenile life-phase (Albert & Albert, 1976; Alderweireldt & Maelfait, 1988). In contrast, short living pioneers, being good ballooners with short generation times (Bonte et al., 2002) colonize gravel banks directly after flooding (Wohlgemuth-von Reiche & Grube, 1999), without being dependent on nearby hibernation sites. The degree of local vegetation cover appears to influence the presence of riparian species (see e.g. Perner & Malt, 2003; Moring & Stewart, 1994; Laeser et al., 2005). As shown by Renöfalt et al. (2005) and Naiman et al. (2005) and confirmed in our study, vegetation cover is correlated with the water level rising speed and the presence of silt. Consequently, gravel banks that are characterized by an intermediate degree of flooding disturbance are more vegetated than those less susceptible to river dynamics, because the presence of silt has a self sustaining effect on the vegetation cover (Sluis & Tandarich, 2004). This is reflected in the species composition: hygrophiles prefer denser vegetated habitats consequently with a stable microclimate, while xero- and psammophiles are found on scarcely vegetated banks.

Carabid beetle synecology

On our studied gravel banks 97 carabid beetle species were found (representing more than 20% of the Belgian fauna; Desender et al., 1995). Because carabid beetles are able to react quickly to unpredictable gravel bank inundations by their well developed dispersal ability, they can reappear immediately after flood events (Bonn, 2000). The distribution pattern of the carabid beetles shows clear structuring: riparian species occur throughout the river system, as long as gravel banks are disturbed by some degree of flooding. Stenotopic hygrophiles prefer fairly loamy gravel banks, with a denser vegetation cover, while xerophiles mainly occur on sandy, elevated banks that are rarely inundated. Due to the possible presence of silt on more frequently inundated gravel banks, hygrophiles may also appear on the latter. Agrobionts, occur throughout the trajectory of the river system, indicating their opportunistic nature and preference for disturbed areas (Turin, 2000; Vanbergen et al., 2005). In general, our results are in concordance with those from upland rivers (Eyre & Luff, 2002; Sadler et al., 2004), in which sediment specialist species dominated exposed riverine sediments next to species from damp grassland habitat.

Similarity in Araneae and Carabidae assemblages

Both spider and carabid beetle assemblages are influenced in a similar way by local environmental parameters, but distinct ecological groups are differently ordered along the prime axis. The moistness of the local habitat, thus inundation susceptibility, is the main factor structuring both groups. This is in agreement with Bell et al. (1999) who studied the distribution of carabid beetle species in alluvial woodland adjacent to rivers in Western Europe. Although the relative height of the gravel banks appears to explain most variation in species occurrence, vegetation cover is a confounding important environmental property. Bonn et al. (2002) studied riparian habitats along several river systems in Germany and concluded that mainly vegetation heterogeneity, rather than different flood regimes, affected spider assemblages. In contrast, the latter found carabid beetle assemblages to be particularly influenced by fluvial dynamics. Other research on carabid beetles from exposed riverine sediments and their relation to microhabitat characteristics pointed out their affinity towards small-scale differences within the local habitat (e.g. soil moisture, substrate size; Antvogel & Bonn, 2001; Sadler et al., 2004; Phillips & Cobb, 2005). Due to this variation in local environmental properties, species richness of carabid beetles is rather high on gravel banks. In contrast, only some spider species appear to survive the extreme conditions met on gravel banks, because of higher desiccation tolerance or an adaptive morphology and behaviour (Bonte et al., 2006a). Subsequently, if vegetation succession on sandy gravel banks proceeds as a result of lower (anthropogenic induced) river dynamics, the few riparian species will disappear and be replaced by agrobionts (Wohlgemuth-von Reiche & Grube, 1999). In contrast to spiders, most of the specialist carabid beetles are able to react quickly to a changing environment (Desender, 1989a; Bonn, 2000; Driscoll & Weir, 2004) because of their well-developed flight ability. Since spiders mainly depend on passive dispersal, like ballooning or drifting, dispersal would imply high costs for reaching suitable habitat in highly fragmented systems (Bonte et al., 2006b). This subsequently accounts for the rarity of stenotopic spider species, even under suitable environmental conditions. Consequently, restoring cursorial connectivity by the restoration of suitable corridors appears urgent to prevent extinctions resulting from hampered upstream dispersal. Because landscape configuration potentially influences spider and carabid beetle assemblages, the level of bank connectivity and size (both contributing to the degree of fragmentation; Piessens et al., 2005) and the nature of the surrounding environment are a previously overlooked determinant of river bank arthropod assemblages. Neither did we found any evidence concerning longitudinal variation downstream with regard to differentiating species diversity, gradual shifts in sediment composition or fluvial dynamics (cf. Framenau et al., 2002), stressing the mutual variability across gravel banks. This is likely attributed to the relative short river trajectory of the Common Meuse (ca. 45 km), the selection of 14 gravel banks, the homogeneity of the river system studied (lowland gravel river; cf. Framenau et al. 2002; Eyre et al. 2001; 2002) and the influx of several tributaries (cf. link discontinuity concept; Rice et al., 2001).

Implications for conservation and restoration

Our study provides evidence that gravel banks enclose a characteristic spider and carabid beetle fauna. The respective assemblages differ according to one important environmental gradient related to flooding susceptibility. In general, our data suggest that heterogeneity within and among gravel banks are the prime factors to conserve the specific spider and carabid beetle diversity (cf. Naiman et al., 2005). Overall, many river habitat specialists show a restricted distribution in Europe (Hänggi et al., 1995; Harvey et al., 2002; Turin, 2000) and are consequently of high conservation value (Plachter & Reich, 1998). Since the conservation of regularly inundating river-ecosystems is a prerequisite for their occurrence, current river management should be revised and human impact needs to be minimized (Bonn et al., 2002). Especially gravel banks that host specialist spider species can be considered of great conservation value. More specifically, *A. cinerea* and *P. agricola* are listed as critical endangered on the Flanders Red List of spiders (Maelfait et al., 1998; Table II.1). In the Low Countries, both species are restricted to the Common Meuse river system. Given their specific habitat demands and their poorly developed aerial dispersal capacity, future restoration should emphasize simultaneously on habitat quality and gravel bank connectivity. Furthermore, because their survival directly depends on the presence of proximate suitable hibernation sites in alluvial grassland (Framenau et al., 1996; Lambeets & Bonte, subm.a), surrounding land-use needs to be considered. Concerning carabid beetles, especially *Bembidion* species are restricted to gravel banks (Turin, 2000; Manderbach & Hering, 2001). *B. atrocoeruleum*, a typical riparian carabid beetle with a preference for gravel and sharp sand (Turin, 2000), deserves special attention for conservation because of its rarity in the Low Countries. Moreover, because we found no evidence of directional downstream differences in gravel bank structure and species composition (e.g. Rice et al., 2001; Framenau et al., 2002), the restoration of connectivity through the establishment of gravel bar corridors within the river bed during low summer discharges is believed to be of primordial importance for the maintenance of viable populations of low dispersive (spider) species.

Acknowledgements

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Authors' contributions

The work presented here was carried out in collaboration between all authors and institutions. KVL and SV sampled the river banks, identified the carabid beetles and provided the environmental data. KL, FH and DB identified the spiders. KL wrote the paper. KL, JPM and DB conceptualised the research questions, analysed the data and interpreted the results. KVL, FH, JPM and DB discussed interpretation and presentation. KVL, JPM and DB conceived ideas for this project. All authors have read and approved the final manuscript version.

Table II.1 - Species list, abbreviations with indication of ecological group, total numbers of trapped individuals and red list status in Flanders of both spiders (Araneae) and carabid beetles (Carabidae) from gravel banks along the Common Meuse.

Abbreviation	**Species**	**Total**	**Red list**	**Abbreviation**	**Species**	**Total**	**Red list**
Oedoretu (pe)	*Oedothorax retusus* (Westring 1851)	2,793		Bemfemo (r-h)	*Bembidion femoratum* (Sturm 1825)	5,910	
Pardagri (r)	*Pardosa agricola* (Thorell 1856)	1,534	CR	Bembtetr (h)	*Bembidion tetracolum* (Say 1823)	3,740	
Oedofusc (pe)	*Oedothorax fuscus* (Blackwall 1834)	1,323		Bemdeco (r)	*Bembidion decorum* (Zenker 1810)	1,455	VU
Erigdent (pe)	*Erigone dentipalpis* (Wider 1834)	1,316		Bemprop (h)	*Bembidion properans* (Stephens 1829)	1,372	
Oedoapic (pe)	*Oedothorax apicatus* (Blackwall 1850)	1,060		Lionquad (r-xt)	*Lionychus quadrillum* (Duftschmid 1812)	1,216	SU
Erigatra (pe)	*Erigone atra* (Blackwall 1833)	859		Agonmuel (pe)	*Agonum muelleri* (Herbst 1785)	1,178	
Trocruri (pe)	*Trochosa ruricola* (De Geer 1778)	378		Bemquad (r)	*Bembidion quadrimaculatum* (Linnaeus 1761)	853	
Pardamen (pe)	*Pardosa amentata* (Clerck 1757)	378		Bempunc (r)	*Bembidion punctulatum* (Drapiez 1821)	760	SU
Diplconc (pe)	*Diplostyla concolor* (Wider 1834)	307		Harprufi (pe-xt)	*Pseudoophonus rufipalpis* (Degeer 1774)	551	SU
Pachcler (h)	*Pachygnatha clercki* (Sundevall 1823)	224		Tachparv (r-xt)	*Tachys parvulus* (Dejean 1831)	488	SU
Prinvaga (pe)	*Prinerigone vagans* (Audouin 1826)	97		Chlaniti (h)	*Chlaenius nitidulus* (Schrank 1781)	468	EN
Meiorure (pe)	*Meioneta rurestris* (C. L. Koch 1836)	88		Bemtest (r)	*Bembidion testaceum* (Duftschmid 1812)	445	IN
Eriglong (h)	*Erigone longipalpis* (Sundevall 1830)	84		Bematro (r)	*Bembidion atrocoeruleum* (Stephens 1821)	380	EW
Bathgrac (pe)	*Bathyphantes gracilis* (Blackwall	75		Ptercupr (h)	*Elaphrus cupreus* (Duftschmid 1812)	355	
Diplcris (pe)	*Diplocephalus cristatus* (Blackwall	74		Agonalbi (r-h)	*Paranchus albipes* (Fabricius 1796)	328	
Phrufest (xt)	*Phrurolithus festivus* (C. L. Koch 1835)	65		Tachmicr (r-xt)	*Tachys micros* (Fisher von Waldheim 1828)	297	SU
Pardprat (h)	*Pardosa prativaga* (L. Koch 1870)	57	VU	Harpaffi (xt)	*Harpalus affinis* (Schrank 1781)	280	
Lepttenu (pe)	*Tenuiphantes tenuis* (Blackwall 1852)	56		Clivcoll (h)	*Clivina collaris* (Herbst 1784)	275	
Halodist (r-h)	*Collinsia distincta* (Simon 1884)	45	EN	Agondors (pe)	*Anchomenus dorsalis* (Pontoppidan	271	
Arctcine (r-xt)	*Arctosa cinerea* (Fabricius 1777)	41	CR	Bemsemi (r-h)	*Bembidion semipunctatum* (Donovan 1806)	237	SU
Pachdege (pe)	*Pachygnatha degeeri* (Sundevall 1830)	39		Agonmar (r-h)	*Agonum marginatum* (Linnaeus 1758)	198	
Erigarct (xt)	*Erigone arctica* (White 1852)	27		Loripili (pe)	*Loricera pilicornis* (Fabricius 1775)	179	

Abbreviation	**Species**	**Total**	**Red list**	**Abbreviation**	**Species**	**Total**	**Red list**
Diplperm (pe)	*Diplocephalus permixtus* (O. P.-Cambridge 1871)	27		Ptermela (pe)	*Pterostichus melanarius* (Illiger 1798)	173	
Micapuli (xt)	*Micaria pulicaria* (Sundevall 1831)	23		Agonmica (h)	*Agonum micans* (Nicolai 1822)	169	SU
Tegeagre (xt)	*Tegenaria agrestis* (Walckenaer 1802)	22		Bemlamp (pe)	*Bembidion lampros* (Herbst 1784)	129	
Pardpalu (pe)	*Pardosa palustris* (Linnaeus 1758)	19		AsapXav (h)	*Asaphidion Xavipes* (Linnaeus 1761)	125	
Piralati (h)	*Pirata latitans* (Blackwall 1841)	17		Amaraen (xt)	*Amara aenea* (De Geer 1774)	117	
Leptrobu (h)	*Leptorhoptrum robustum* (Westring 1851)	16	VU	Amarbifr (xt)	*Amara bifrons* (Gyllenhal 1810)	110	
Milliner (h)	*Collinsia inerrans* (O. P.-Cambridge 1885)	16		Chlavest (h)	*Chlaenius vestitus* (Paykull 1790)	91	SU
Zelopede (xt)	*Trachyzelotes pedestris* (C. L. Koch 1837)	15	EN	Amarfulv (xt)	*Amara fulva* (Mueller 1776)	90	
Hypobitu (h)	*Hypomma bituberculatum* (Wider 1834)	14		Calamela (xt)	*Calathus melanocephalus* (Linnaeus 1758)	89	
Xeromini	*Xerolycosa miniata* (C. L. Koch 1834)	13	EN	Anisbino (h)	*Anisodactylus binotatus* (Fabricius 1787)	86	
Pardagre	*Pardosa agrestis* (Westring 1861)	13	EN	Agonassi (h)	*Limodromus assimilis* (Paykull 1798)	80	
Clubfris	*Clubiona frisia* (Wunderlich & Schuett 1995)	13	VU	Agonmoe (r-h)	*Agonum afrum* (Duftschmid 1812)	70	
Zelosubt	*Zelotes subterraneus* (C. L. Koch 1833)	11		Dyscaene (r-h)	*Dyschirius aeneus* (Dejean 1825)	70	
Steaphal	*Steatoda phalerata*(Panzer 1801)	10	VU	Ptervern (h)	*Pterostichus vernalis* (Panzer 1796)	62	
Zeloaene	*Zelotes aeneus* (Simon 1878)	10	RG	Calafusc (pe)	*Calathus fuscipes* (Goeze 1777)	60	
Pirapira	*Pirata piraticus* (Clerck 1757)	7		Elapaure (r-h)	*Elaphrus aureus* (Ph. Müller 1821)	55	SU
Trocterr	*Trochosa terricola* (Thorell 1856)	7		Amarauli (xt)	*Amara aulica* (Panzer 1797)	54	
Troxscab	*Troxochrus scabriculus* (Westring 1851)	7		Amarsimi (pe)	*Amara similata* (Gyllenhal 1810)	47	
Xystkoch	*Xysticus kochi* (Thorell 1872)	7		Amarovat (pe)	*Amara ovata* (Fabricius 1792)	39	
Porrconv	*Porrhomma convexum* (Westring 1851)	7		Nebrbrev (pe)	*Nebria brevicollis* (Fabricius 1792)	38	
Clubphra	*Clubiona phragmitis* (C. L. Koch 1843)	6		Amaeury (xt)	*Amara eurynota* (Panzer 1797)	24	VU

Abbreviation	**Species**	**Total**	**Red list**	**Abbreviation**	**Species**	**Total**	**Red list**
Arctleop	*Arctosa leopardus* (Sundevall 1833)	5	VU	Caragran (h)	*Carabus granulatus* (Linnaeus 1758)	20	
Pirahygr	*Pirata hygrophilus* (Thorell 1872)	5		Amaspre (xt)	*Amara spreta* (Dejean 1831)	18	
Baryprat	*Baryphyma pratense* (Blackwall 1861)	4	VU	Acupmeri (h)	*Acupalpus meridianus* (Linnaeus 1767)	18	
Heliaura	*Heliophanus auratus* (C. L. Koch 1835)	4	EN	Ptervers (pe)	*Poecilus versicolor* (Sturm 1824)	18	
Micrsuba	*Micrargus subaequalis* (Westring 1851)	4		Micrminu (xt)	*Microlestes minutulus* (Goeze 1777)	17	SU
Clubnegl	*Clubiona neglecta* (O. P.-Cambridge 1862)	4		Omoplim (xt)	*Omophron limbatum* (Fabricius 1776)	17	
Laricorn	*Larinioides cornutus* (Clerck 1757)	3		Pternige (pe)	*Pterostichus niger* (Schaller 1783)	17	
Ozypsimp	*Ozyptila simplex* (O. P.-Cambridge	3		Stenmixt (h)	*Stenolophus mixtus* (Herbst 1784)	15	
Nereclat	*Neriene clathrata* (Sundevall 1830)	3		Stopumi (h)	*Stomis pumicatus* (Panzer 1796)	14	
Pardpull	*Pardosa pullata* (Clerck 1757)	3		Clivfoss	*Clivina fossor* (Linnaeus 1758)	11	
Tetrexte	*Tetragnatha extensa* (Linnaeus 1758)	2		Amarapri	*Amara apricaria* (Paykull 1790)	11	
Bathparv	*Bathyphantes parvulus* (Westring 1851)	2		Ptermadi	*Pterostichus madidus* (Fabricius 1775)	11	
Euopaequ	*Talavera aequipes* (O. P.-Cambridge 1871)	2	VU	Trecquad	*Trechus quadristriatus* (Schrank 1781)	10	
Phlefasc	*Phlegra fasciata* (Hahn 1826)	2	VU	Synuniva	*Synuchus vivalis* (Illiger 1798)	9	
Synavena	*Synageles venator* (Lucas 1836)	2		Panabipu	*Panagaeus bipustulatus* (Fabricius 1775)	8	
Xystcris	*Xysticus cristatus* (Clerck 1757)	2		Elapripa	*Elaphrus riparius* (Linnaeus 1758)	7	
Diplconn	*Diplocephalus connatus* (Bertkau 1889)	2	IN	Amarfami	*Amara familiaris* (Duftschmid 1812)	6	
Leptpall	*Palliduphantes pallidus* (O. P.-Cambridge 1871)	1		Dyscglob	*Dyschirius globosus* (Herbst 1783)	6	
Dipllati	*Diplocephalus latifrons* (O. P.-Cambridge 1863)	1		Dysclued	*Dyschirius luedersi* (Wagner 1915)	6	
Cerabrev	*Ceratinella brevis* (Wider 1834)	1		Pterstre	*Pterostichus strenuus* (Panzer 1797)	6	
Clubpseu	*Clubiona pseudoneglecta* (Wunderlich 1994)	1	IN	Badisoda	*Badister sodalis* (Duftschmid 1812)	5	

Abbreviation	Species	Total	Red list	Abbreviation	Species	Total	Red list
Micrimpr	*Microlinyphia impigra* (O. P.-Cambridge 1871)	1	VU	Bemobtu	*Bembidion obtusum* (Serville 1821)	4	
Ozypprat	*Ozyptila praticola* (C. L. Koch 1837)	1		Bemquap	*Bembidion quadripustulatum* (Serville 1821)	4	SU
Pardprox	*Pardosa proxima* (C. L. Koch 1847)	1	RG	Notisubs	*Notiophilus substriatus* (Waterhouse 1833)	4	
Steaalbo	*Steatoda albomaculata* (De Geer 1778)	1	VU	Pternigr	*Pterostichus nigrita* (Paykull 1790)	4	
Stemline	*Stemonyphantes lineatus* (Linnaeus 1758)	1		Agonobsc	*Oxypselaphus obscurus* (Herbst 1784)	3	
Zelolatr	*Zelotes latreillei* (Simon 1878)	1		Amarpleb	*Amara plebeja* (Gyllenhal 1810)	3	
Agynsubt	*Agyneta subtilis* (O. P.-Cambridge 1863)	1		Badibull	*Badister bullatus* (Schrank 1798)	3	
Ostemela	*Ostearius melanopygius* (O. P.-Cambridge 1879)	1		Bemelon	*Bembidion elongatum* (Dejean 1831)	3	CR
Cerascab	*Ceratinella scabrosa* (O. P.-Cambridge 1871)	1		Pteranth	*Pterostichus anthracinus* (Illiger 1798)	3	
Pelepara	*Pelecopsis parallela* (Wider 1834)	1		Thallong	*Thalassophilus longicornis* (Sturm 1825)	3	
Zelolute	*Drassyllus lutetianus* (L. Koch 1866)	1	EN	Bemharp	*Bembidion harpaloides* (Serville 1821)	2	SU
Enopthor	*Enoplognatha thoracica* (Hahn 1833)	0.4		Cicihybr	*Cicindela hybrida* (Linnaeus1758)	2	NT
Euopfront	*Euophrys frontalis* (Walckenaer 1802)	0.4		Bembipu	*Bembidion bipunctatum* (Linnaeus 1761)	2	SU
LeptXav	*Tenuiphantes Xavipes* (Blackwall 1854)	0.4		Bemmini	*Bembidion minimum* (Fabricius 1792)	2	
Linyhort	*Linyphia hortensis* (Sundevall 1830)	0.4		Harpatte	*Harpalus attenuatus* (Stephens 1828)	2	
Robelivi	*Robertus lividus* (Blackwall 1836)	0.4		Harprubr	*Harpalus rubripes* (Duftschmid 1812)	2	
Trichack	*Trichoncus hackmani* (Millidge 1956)	0.4	CR	Pterlepi	*Poecilus lepidus* (Leske 1785)	2	
	Total	**11,266**	**23**	Trecdisc	*Trechus discus* (Fabricius 1792)	2	
				Trecobtu	*Trechus obtusus* (Erichson 1837)	2	
				Amacom	*Amara communis* (Panzer 1797)	1	

Abbreviation	Species	Total	Red list	Abbreviation	Species	Total	Red list
				Bembigu	*Bembidion biguttatum* (Fabricius 1779)	1	
				Bembgilv	*Bembidion gilvipes* (Sturm 1825)	1	
				Bradharp	*Bradycellus harpalinus* (Serville 1821)	1	
				Dromlin	*Paradromius linearis* (Olivier 1795)	1	
				Dyscinte	*Dyschirius intermedius* (Putzeys 1846)	1	VU
				Harpdist	*Harpalus distinguendus* (Duftschmid 1812)	1	
				Harplatu	*Harpalus latus* (Linnaeus 1758)	1	
				Patratro	*Patrobus atrorufus* (Stroem 1768)	1	
				Pteroblo	*Pterostichus oblongopunctatus* (Fabricius 1787)	1	
				Tachbist	*Tachys bistriatus* (Duftschmid 1812)	1	EN
				Tachquad	*Tachys quadristignatus* (Duftschmid 1812)	1	IN
				Demeatri	*Demetrias atricapillus* (Linnaeus 1758)	0.4	
				Dyscangu	*Dyschirius angustatus* (Ahrens 1830)	0.4	SU
					Total	**23,331**	**24**

Abbreviations for spiders were formulated as a combination of the first four letters of both genus and species epitheton. For carabid beetles abbreviations were taken from Boeken et al. (2002). Most abundant species (+14 individuals) were assigned to an ecological group according to their habitat preference based on available literature: (pe) = pioneer or eurytopic agrobionts - (h) = hygrophilic species - (xt) = xerothermic species - (r) = typical riparian species. Red list status is based on Desender et al. (1995) and in concordance with IUCN-categories; **EW**: extinct in the wild, **CR**: critical, **EN**: endangered, **VU**: vulnerable, **NT**: near threatened, **SU**: susceptible, **RG**: restricted geographically, **IN**: indeterminate.

II.2. Understanding the impact of flooding on trait-displacements and shifts in assemblage structure of predatory arthropods on river banks

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Depositions of silt at the river bank at Heppeneert (Foto: Kevin Lambeets)

Summary

1. Species assemblages of naturally disturbed habitats are governed by the prevailing disturbance regime. Consequently, stochastic flood events affect river banks and the inhabiting biota. Predatory arthropods occupy predominantly river banks in relation to specific habitat conditions. Therefore, species sorting and stochastic processes as induced by flooding are supposed to play important roles in structuring riparian arthropod assemblages in relation to their habitat preference and dispersal ability.

2. To ascertain whether assemblages of spiders and carabid beetles from disturbed river banks are structured by stochastic or sorting mechanisms, diversity patterns and assemblage-wide trait-displacements were assessed based on pitfall sampling data. We tested if flooding disturbance within a lowland river reach affects diversity patterns and trait distribution in both groups.

3. Whereas the number of riparian spider species decreased considerably with increased flooding, carabid beetle diversity benefited from intermediate degrees of flooding. Moreover, regression analyses revealed trait-displacements, reflecting sorting mechanisms especially for spiders. Increased flooding disturbance was associated with assemblage-wide increases of niche breadth, shading and hygrophilic preference and ballooning propensity for spider (sub)families. Trait patterns were comparable for Bembidiini carabids, but were less univocal for Pterostichini species. Body size decreased for lycosid spiders and Bembidiini carabids with increased flooding, but increased in linyphiid spiders and Pterostichini carabids.

4. Our results indicate that mainly riparian species are disfavoured by either too high or too low degrees of disturbance whereas eurytopic species benefit from increased flooding. Anthropogenic alterations of flooding disturbance constrain the distribution of common hygrophilous species and/or species with high dispersal ability, inducing shifts towards less specialized arthropod assemblages. River banks with divergent degrees of flooding impact should be maintained throughout dynamic lowland river reaches in order to preserve typical riparian arthropod assemblages.

Key-words: body size, dispersal ability, niche breadth, riparian ecology, species sorting

Introduction

The development of a trait-based ecology provides insight in assemblage-wide functional responses in environmentally variable environments (Van Looy et al., 2006; Violle et al., 2007). Changes in species distribution result from species sorting, mass effects or patch dynamics, eventually leading to community-wide character displacements or community-wide character shifts (Schluter 2000; Marchinko et al., 2004). For environments that are strongly affected by natural or anthropogenic disturbance, assemblages of species are expected to be structured by the ability of the species to react upon these disturbances (Plachter & Reich, 1998; Ribera et al., 2001; Bonte et al., 2006a). Because this involves species assimilation, assemblage-wide changes in species diversity are predicted to result from species sorting rather than substantial dispersal *per se* (Driscoll & Weir, 2005). In contrast, when the magnitude of disturbance is higher than tolerated by the potential inhabitants, only highly dispersive species will be able to persist due to repeated colonization events (McAuliffe, 1984; Ribera et al., 2001), with mass effects affecting species assemblages (e.g. Schmidt & Tscharntke, 2005a). Specialized species may be able to survive short-time disturbances, reappearing quickly after it subsides or benefiting from newly created structural elements (Weigmann & Wohlgemuth-von Reiche, 1999; Rothenbücher & Schaefer, 2006). However, responses depend on the type of disturbance and the relation with species' functional traits (Bonte et al., 2006a; Moretti et al., 2006; Papaik & Canham, 2006). When trait variation does not prevail in relation to disturbance regimes, species assemblages can be considered to be functionally equivalent (Ackerly & Cornwell, 2007). Consequently, assemblage-wide character displacements rather than trait shifts in response to species sorting take place (Schluter, 2000). This can be realized by shifts of taxonomically different species with similar functional traits within assemblages (Marchinko et al., 2004). Which patterns underlie assemblage structure are expected to depend on intrinsic dispersal abilities. Therefore, disturbance may act as an important trigger affecting assemblage structure in particular ways.

Localized rare disturbance events, irrespective of their magnitude or frequency, are expected to exert a minor effect on regional diversity (Chase, 2003; Bonte et al., 2006a). However, spatially restricted disturbance can be important to facilitate the occurrence of specialized species that are able to react rapidly upon changing environment conditions (Bonn et al., 2002; Rothenbücher & Schaefer, 2006). Observed patterns may, however, vary considerably according to the taxonomic group and with the spatial scale of study (Pollock et al., 1998; Prinzing et al., 2007; Sanders et al., 2007). Disturbance mechanisms appear to be especially relevant in riverine landscapes, in which flooding contributes to strong environmental heterogeneity (Naiman & Décamps, 1997; Ward et al., 2002) with subsequent highly structured assemblage patterns and related species diversity (Robinson et al., 2002; Naiman et al., 2005; Van Looy et al., 2005). Unravelling these patterns should be the foundation of riparian ecology (Jensen et al., 2006). As stated by Vannote et al. (1980) and Van Looy et al. (2006) assemblages from harsh riparian environments are assumed to shift constantly in relation to the prevalent disturbance regime, with synchronized species replacements throughout the river system. Therefore, if flooding disturbance affects environmental properties in a homogeneous way as induced by anthropogenic alterations of flooding (either extremely high or low flows), a high similarity in species diversity, assemblage structure and functionality would be expected. However, even if general environmental conditions are spatially similar under disturbance, temporal variation in disturbance will affect the distribution of mobile species, due to the creation of different colonization windows with subsequent species replacements under low frequencies of disturbance (McAuliffe, 1984; Death & Winterbourn, 1995). Therefore, different aspects of flooding disturbance should be studied simultaneously and in an integrated manner (Langhans & Tockner, 2005; Van Looy et al., 2005). In general, differences between local levels of species richness and patterns of species traits reflect the influence of local environmental fluctuations and suggest its possible interference in species interactions, eventually determining the composition of local and regional assemblages.

Whether assemblage composition affected by flooding results from either equivalent or contrastive changes in assemblage-wide traits is virtually undocumented for the riparian fauna (but see Desender, 1989a; Plachter & Reich, 1998). Given the general idea that sets of traits are related to species abilities to cope with stressful situations, we applied a functional trait approach for predatory arthropods to delineate relevant insights for the restoration and conservation of the vulnerable riparian biodiversity (Kremen et al., 1993). Therefore, we assessed diversity patterns, assemblage-wide shifts and variation in species traits of two well-studied and dominant groups of predatory arthropods, respectively spiders (Araneae) and carabid beetles (Carabidae), along riparian river banks. We particularly questioned: (i) whether patterns in diversity and species traits are affected by flooding disturbance among and within taxonomic groups; (ii) whether the underlying mechanisms are related to species sorting with congruent assemblage-wide character shifts; and (iii) whether flooding disturbance (dis)favours species with distinct ecological traits.

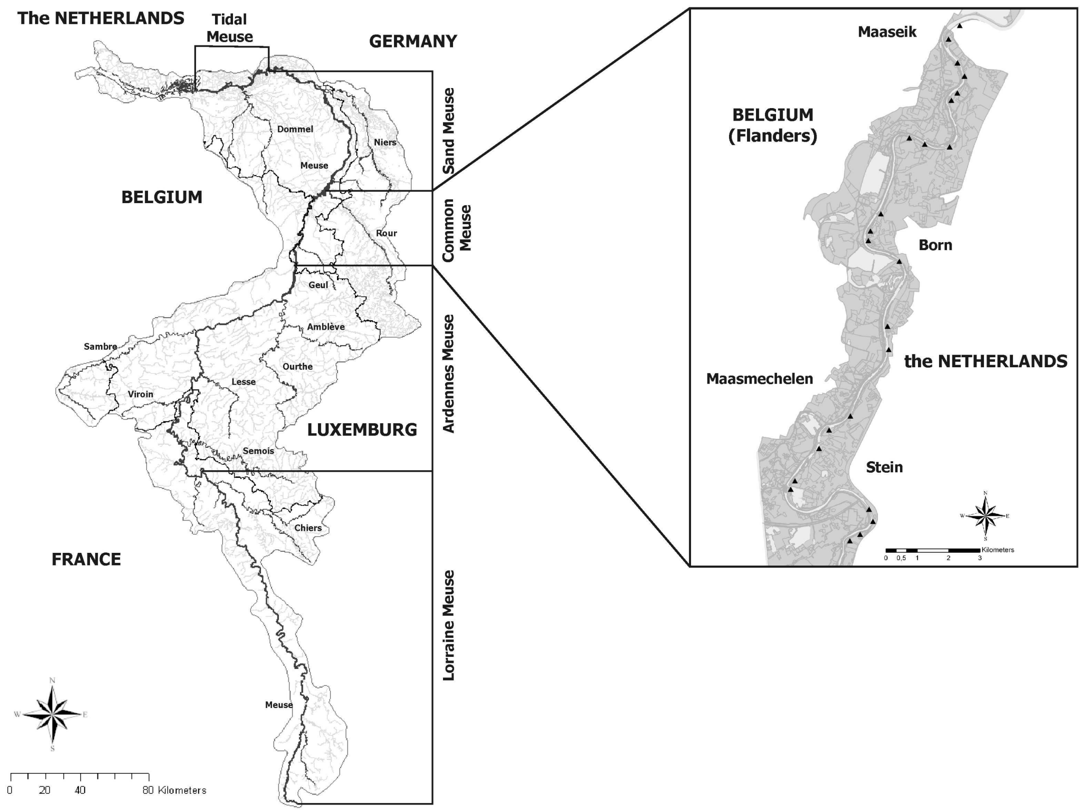

Fig. II.4 - Map of the River Meuse basin with inset for the Common Meuse river reach and its riparian margin; sampled river banks are indicated as triangles.

Material and methods

Study system and sampling protocol

The Common Meuse is the most natural part of the river Meuse and covers approximately 45 km of the total ca. 900 km river trajectory. Due to its rainfed character and the rocky soils of the upstream catchment, the watercourse is characterized by strong river flow fluctuations and a wandering pattern of isolated river banks (Pedroli et al., 2002; Van Looy et al., 2006). These banks comprise a top layer of coarse shingle with a sharp sand-gravel or sand-loam fraction in between and related changes in vegetation (Peters et al., 2000). Only when the river discharge drops below 200 m^3s^{-1} (from May until September), gravel banks are gradually exposed. At this rather restricted regional scale, no longitudinal downstream variation of gravel structure, vegetation composition or disturbance frequency occurs (all correlations $r < 0.24$), as reflected by species assemblage structure (Lambeets et al., 2008a).

All river banks along a continuous part of the river trajectory (Fig. II.4) were sampled from 06-04-2005 until 19-07-2005 with pitfall traps (Φ 9cm; 6% formaline solution; fortnightly emptied). Each gravel bank contained three to six pitfalls, divided over a maximum of two stations. Pitfalls were arranged parallel with the waterline, situated at an average distance of 6.1 m from the loamy river dyke for higher stations and 21.3 m for farthest stations on larger banks. As recommended by Topping & Sunderland (1992) pitfalls were spaced ten meters apart in order to avoid interference between the traps. Since unpredictable flood events caused data loss on several occasions, trapped species were interpolated distinctly for each sample date, pitfall trap and sample station. For each species, catches were pooled to total numbers per sample station. It is important to recognise that pitfall trapping has some inherent biases, and catches can be affected by factors including habitat structure, weather conditions and the used preservative (Topping & Sunderland, 1992). In this study, standardized pitfall trapping is an appropriate collection method, since we aimed to compare patterns of assemblage-wide (weighted) species traits as affected by flooding disturbance. Contrary to other studies (Andersen, 1995), cryptic and smaller sized individuals made up the majority of the catches (e.g. Bembidiini carabids and linyphiid spiders), by which our sample data is believed to reflect local arthropod composition well, hence liable for concrete interpretation.

Characterization of environmental parameters

Flooding is affected by local topography as well as by regional chorological factors (Pedroli et al., 2002; Naiman et al., 2005; Van Looy et al., 2006) and influences both local humidity and vegetation structure, being the most important drivers for habitat quality in the studied arthropod groups (Turin, 2000; Entling et al., 2007). Therefore, we recorded parameters related to flooding disturbance, river bank and channel geometry, substrate composition and vegetation structure. Measured landscape related parameters were sample site location, connectivity along the riparian corridor and surrounding landscape composition. For the ease of reading the measured variables, applied field methodology and interpretations of the main principal components are explained in Appendix A2. Principal component analysis (PCA; Goodall, 1954) revealed the prevalence of one “disturbance”-axis (PC_{dyn}; eigenvalue 7.102; explanatory value 18.69%) which correlated with flooding disturbance aspects and substrate composition after Bonferroni correction (Table II.3). Increasing values of PC_{dyn} indicate a higher frequency of flooding during the sample period, an increased rising speed of the washing water and a substrate composed of less coarse gravel, a fine-grained in between sediment fraction and increased siltation. Two other axes explained variation related to river bank and channel geometry (PC_{geo}; eigenvalue 5.166; explanatory value 13.59%) and patch size and vegetation structure (PC_{veg}; eigenvalue 4.284; explanatory value 11.27%). Because we emphasized on studying river bank arthropod diversity and assemblage-wide patterns of functional trait distribution in relation to flooding disturbance *sensu lato*, we retained gravel bank scores from the first principal component for further analyses.

Parameter	variable measured	Methodology	PC_{dyn}
Flooding disturbance	RSregr	Rising speed of washing water based on river discharge regimes and fortnightly measured distances pitfalls - water line	**-0.585**
Flooding disturbance	WFR	River bank water flow rate based on based on river discharge regimes and fortnightly measured distances pitfalls - water line	**-0.866**
Flooding disturbance	dayfl	Number of days flooded during sampling period based on river discharge regimes and WFR (log)	**0.811**
Flooding disturbance	dayfl5yr	Number of days flooded between 2000 and 2005 based on river discharge regimes and WFR (log)	**0.843**
River bank topography	orientcl	Orientation eighth of river bank	**-0.667**
Substrate composition	grav	Average gravel size (6 classes ranging from 0-10cm until >50cm)	**-0.782**
Substrate composition	sand	Sediment composition (sand - loam ratio)	**-0.852**
Substrate composition	silt	Siltation class index (none - covering 1/4 - half – up to dyke foot)	**0.771**

River discharge regimes taken from http://www.lin.vlaanderen.be/awz/waterstanden/hydra/ (hourly values). Substrate composition are estimated values based on digital pictures within a 1x1m quadrat surrounding each pitfall taken fortnightly during the field survey.

Table II.3 - Pearson correlations with the first principal component (PC_{dyn}) of measured parameters of river banks along the Common Meuse river reach. Parameters were transformed accordingly if they did not meet the normality assumption (McCune & Grace, 2002). Only significant parameters are shown. Correlation coefficients $r > 0.570$ are significant after Bonferroni correction. For an overview of the environmental characterization based on the measured parameters and a concise explanation of the applied field methodology see Appendix A2.

Species richness and species traits

Species richness (alpha diversity, being the total species richness within one sample station equal to three pitfall traps) was calculated as the total number of species caught in each sample station. Since this measure is affected by rare accidental vagrants we used the richness of resident species, i.e. species appearing with at least ten individuals within one sample station (Bonte et al., 2006a), as a more stringent measure. Riparian diversity was calculated as the species richness of riparian specialists. Thereby, species were defined as “riparian” based on relevant literature handling ecological requirements of spiders (Hänggi et al., 1995; Harvey et al., 2002) and carabid beetles (Desender et al., 1995; Turin, 2000).

Five traits were chosen to represent important life history features of spiders and carabid beetles. Niche breadth was considered as the number of habitat types (related to the species' geographical rareness) in which spider and carabid beetle species were caught, as derived from Hänggi et al. (1995) and Boeken et al. (2002), respectively. Shading and moisture preference were obtained from habitat type preferences as calculated by Entling et al. (2007) for spiders (xerophily) and ecological group classification as summarized by Turin (2000) and Boeken et al. (2002) for carabid beetles (hygrophily). Average body size of female spiders was derived from Roberts (1987; 1998), while Boeken et al. (2002) was consulted for the average body size of carabid beetles. Ballooning propensity of spiders, i.e. whether or not aerial dispersal can be performed by a species, was taken from the review of Bell et al. (2005) and extended with new experiments for riparian spiders (Bonte & Lambeets unpub. data). Flight ability of carabid beetles was assessed by relative wing development in relation to body size as defined by Desender (1989b). A complete list of trapped numbers and species trait values can be found in Appendix A3.

Data analysis

Our trait-based approach was based on the weighted averages and the variances of trait values of species co-occurring in local assemblages. Average values serve as comparable measures in order to array assemblages along a one-dimensional gradient. The analysis of trait variance is complementary and essential because weighted averages can be the same despite variation in trait variance and therefore ease the distinction between prevalent structuring processes (Ackerly & Cornwell 2007) and thus assembly rules (Holdaway & Sparrow 2006). Consequently, we were able to distinguish between assemblage-wide ecological mean values and their amplitudes.

General linear models (GLM; proc mixed, SAS 9.1) were used to assess the influence of disturbance on species richness and species traits. Number of species, weighted averages and variances of trait values were the dependent variables, whereas the first principal component (PC_{dyn}) was considered as the continuous factor reflecting flooding disturbance *sensu lato*. Both linear and quadratic functions were modelled. The most reliable model was inferred by Akaike's information criteria (AIC), based on model fit and model complexity criteria (Johnson & Omland, 2004). In all cases, normality of residuals was checked (proc univariate, SAS 9.1). Because patterns in life history traits are highly interdependent according to common phylogenetic origin (Bonte et al., 2006a), analyses were performed at the lowest workable phylogenetic level, being the subfamily-level for spiders (Erigoninae, Linyphiinae, Lycosidae) and the tribe level for carabid beetles (Bembidiini, Pterostichini). Because the interaction between taxonomic group and traits was highly significant for average values (Araneae: $F_{2,80} > 19.8$; all $p < 0.0001$; Carabidae ($F_{1,54} > 10.2$; all $p < 0.0023$) and most variances (Araneae: $F_{2,77} > 15.3$; all $p < 0.0001$; Carabidae ($F_{1,54} > 21.1$; all $p < 0.0001$ except hygrophily: $F_{1,54} = 1.00$; $p = 0.3212$ and wing development: $F_{1,54} = 0.02$; $p = 0.8774$), we performed trait analyses separately for the differently distinguished taxonomic groups.

Results

Species richness

Alpha diversity of carabid beetles (Fig. II.5a) and numbers of resident species (Fig. II.5b) peaked at an intermediate degree of flooding disturbance, whereas no significant patterns were found for spider species richness. The relation between the richness of stenotopic riparian species and PC_{dyn}, revealed a linear decrease for spiders and an intermediate optimum for carabid beetles with increased flooding (Fig. II.5c). F-values, significance levels and AIC values are presented in Table II.4.

Assemblage-wide ecological traits

In the following, we only present significant relationships between flooding disturbance (PC_{dyn}) and assemblage-wide species traits. F-values, significance levels and AIC values are presented in Table II.5.

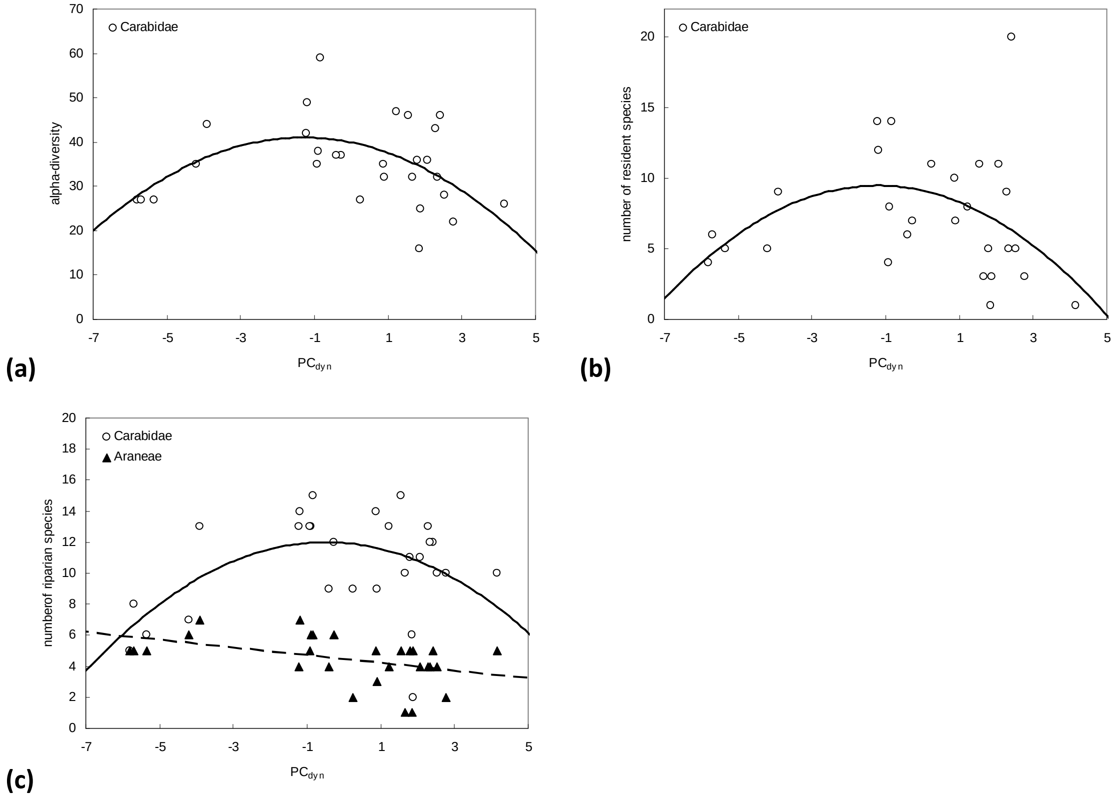

Fig. II.5 - Relationship between spider and carabid diversity and the degree of flooding disturbance along a lowland gravel river. (a) Alpha diversity; (b) richness of resident species; (c) richness of riparian species. The principal component scores arising from a PCA-analysis of site specific habitat characteristics (PC_{dyn}) are used to indicate the degree of flooding disturbance along the X-axis.

		second order relation		**first order relation**	
diversity measure	**regression statistics**	**Araneae (1, 25)**	**Carabidae (1, 25)**	**Araneae (1, 26)**	**Carabidae (1, 26)**
alpha diversity	F	0.57	8.68	2.89	0.05
	p	0.4562	**0.0069**	0.1012	0.8228
	AIC	180.9	195.6	179.7	202.2
resident diversity	F	1.45	4.94	0.84	0
	p	0.2399	**0.0356**	0.3677	0.9643
	AIC	146.2	160	144.5	162.1
riparian diversity	F	0.33	6.82	6.12	1.53
	p	0.5697	**0.015**	**0.0202**	0.227
	AIC	107.2	141.7	102.7	144.6

Table II.4 - Influence of flooding disturbance on species richness of spider and carabid beetle assemblages of river banks. General linear model (GLM) regression statistics and Akaike's information criteria (AIC) values are shown for spiders and carabid beetles. Degrees of freedom are indicated below each taxonomic group as (numerator degrees of freedom; denominator degrees of freedom).

Niche breadth, shading & moisture preference

Assemblage-wide niche breadth increased with increasing disturbance in Erigoninae, Lycosidae (Fig. II.6a; Table II.5a) and Bembidiini (Fig. II.6b; Table II.5b). Variance in niche breadth decreased monotonously with flooding for Pterostichini assemblages (Fig. II.6c; Table II.5d).

All spider (sub)families showed an increased preference for shaded conditions with increasing flooding disturbance. Assemblages with on average a higher degree of shading preference occurred at more disturbed river banks (Fig. II.7a; Table II.5a). In contrast, shading preference for Bembidiini was lower at low degrees of flooding and a monotonous increase of shading preference is noticed as flooding increases. However, this relation is highly influenced by the prevalence of agrobiont *Bembidion* carabids on the lowest river banks (skewed distribution at Fig. II.7b; Table II.5b). Variance of shading preference peaked at intermediate degrees of flooding for Pterostichini (Fig. II.7c; Table II.5d).

Assemblage-wide xerophily of all spider (sub)families on average decreased with increasing flooding disturbance (Fig. II.8a; Table II.5a). Variance in xerophily decreased solely for Lycosidae (Fig. II.8b; Table II.5c). Bembidiini carabids showed a significant decrease in hygrophilic species with increasing disturbance (Fig. II.8c; Table II.5b).

Body size and dispersal ability

Female size of Lycosidae decreased to a minimum at intermediately disturbed sites, whereas an increase with disturbance was prevalent in Erigoninae and Linyphiinae (Fig. II.9a; Table II.5a). Significant linear decreases were found with respect to variance in assemblage-wide female size for Erigoninae and Lycosidae (Fig. II.9b; Table II.5c). Assemblage-wide average size of Pterostichini carabids increased significantly with increasing disturbance (Fig. II.9c; Table II.5b). Variance in carabid beetle body size was lower at more disturbed river banks for Bembidiini, whereas it increased for Pterostichini (Fig. II.9d; Table II.5d).

Erigoninae and Lycosidae with known ballooning propensity are favoured by increased disturbance (Fig. II.10a; Table II.5a). Variance in ballooning propensity of Erigoninae peaked at intermediate disturbance (Fig. II.10b; Table II.5c). On average, assemblage-wide wing development increased for Bembidiini and Pterostichini (Fig. II.10c; Table II.5b).

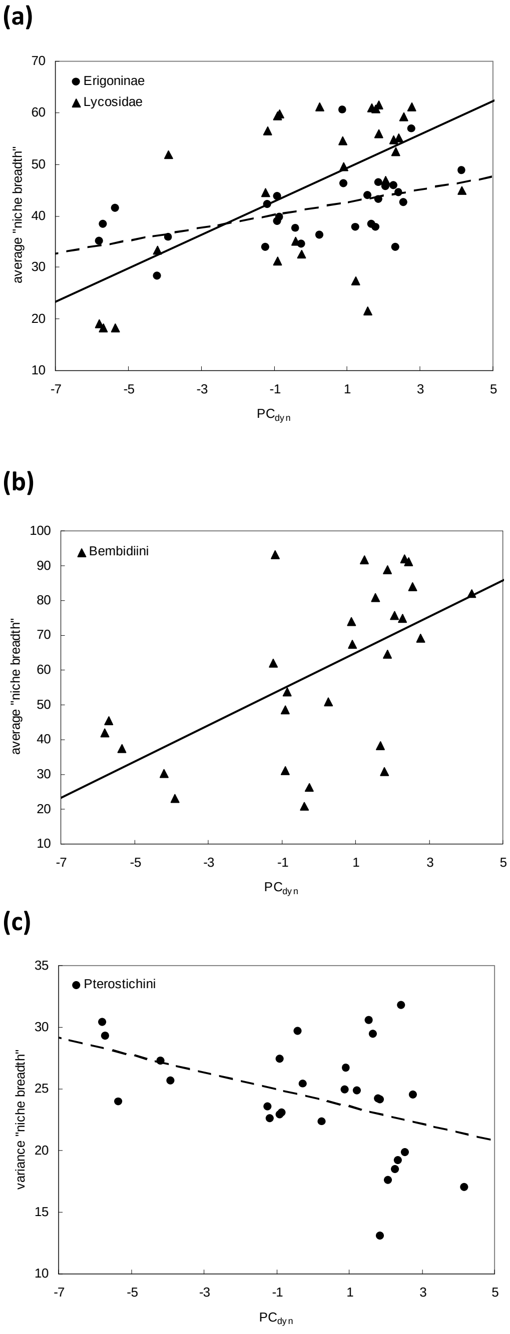

Fig. II.6 - Relationship between spider and carabid beetle niche breadth and the degree of flooding disturbance (PC$_{dyn}$) along a lowland gravel river. (a) Weighted average Erigoninae, Lycosidae; (b) weighted average Bembidiini; (c) variance Pterostichini.

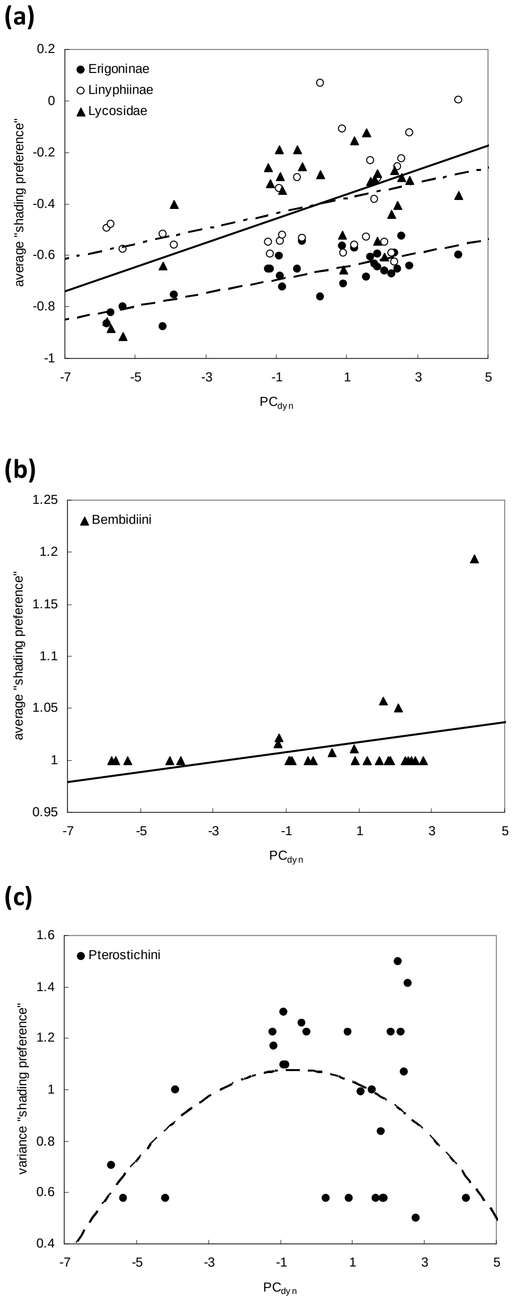

Fig. II.7 - Relationship between spider and carabid beetle shading preference and the degree of flooding disturbance (PC$_{dyn}$) along a lowland gravel river. (a) Weighted average Erigoninae, Linyphiinae, Lycosidae; (b) weighted average Bembidiini; (c) variance Pterostichini.

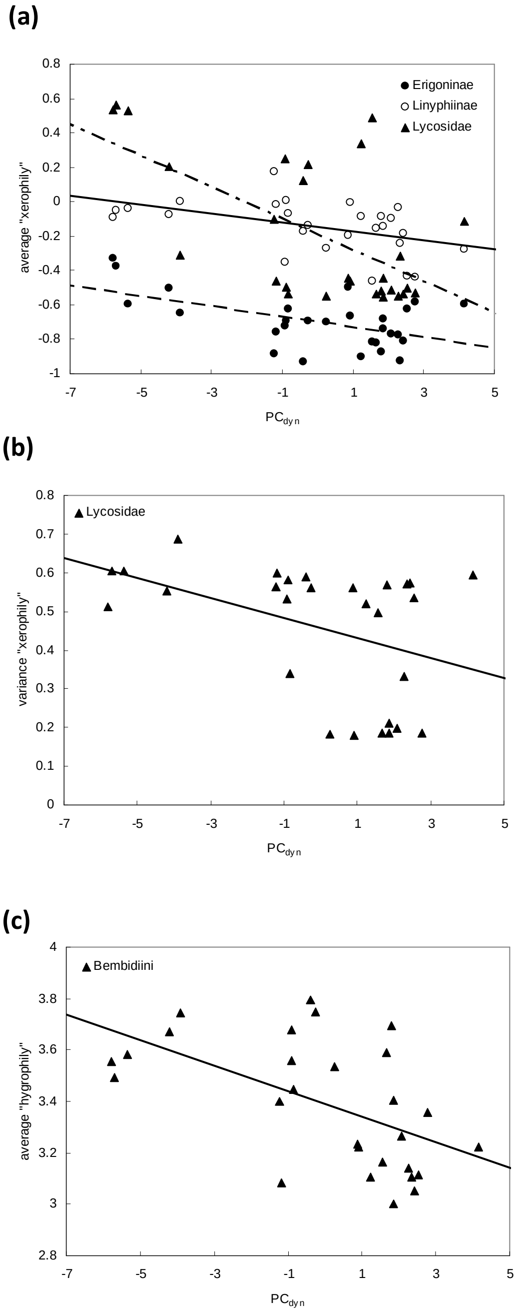

Fig. II.8 - Relationship between spider xerophiliy and carabid beetle hygrophily and the degree of flooding disturbance (PC_{dyn}) along a lowland gravel river. (a) Weighted average Erigoninae, Linyphiinae, Lycosidae; (b) variance Lycosidae; (c) weighted average Bembidiini.

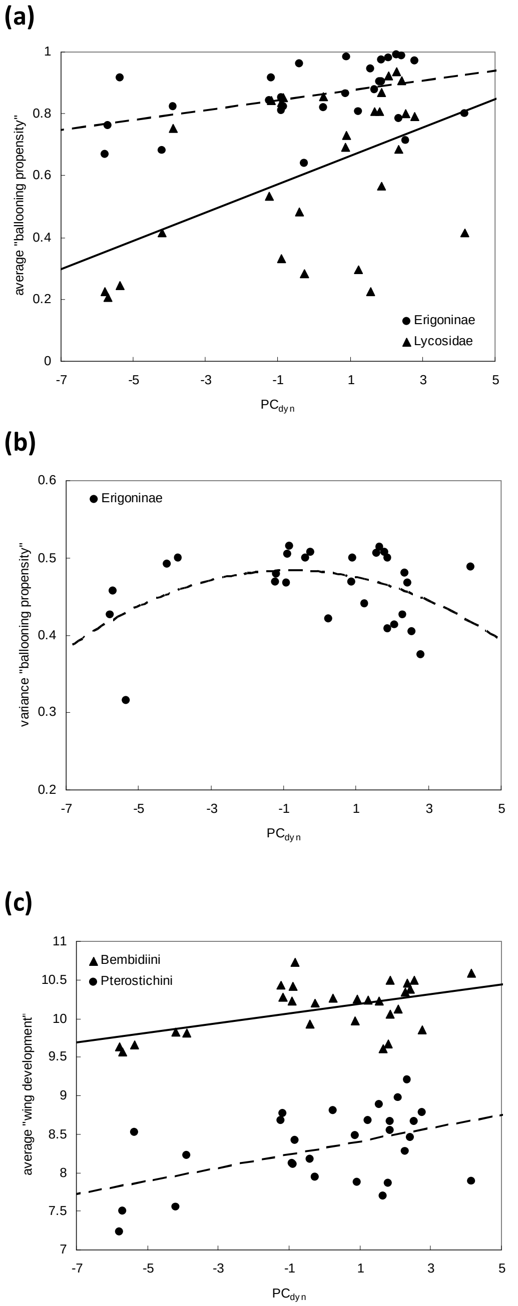

Fig. II.10 - Relationship between spider ballooning propensity and carabid beetle wing development and the degree of flooding disturbance (PC_{dyn}) along a lowland gravel river. (a) Weighthed average Erigoninae, Lycosidae; (b) variance Erigoninae; (c) weighted average Bembidiini, Pterostichini.

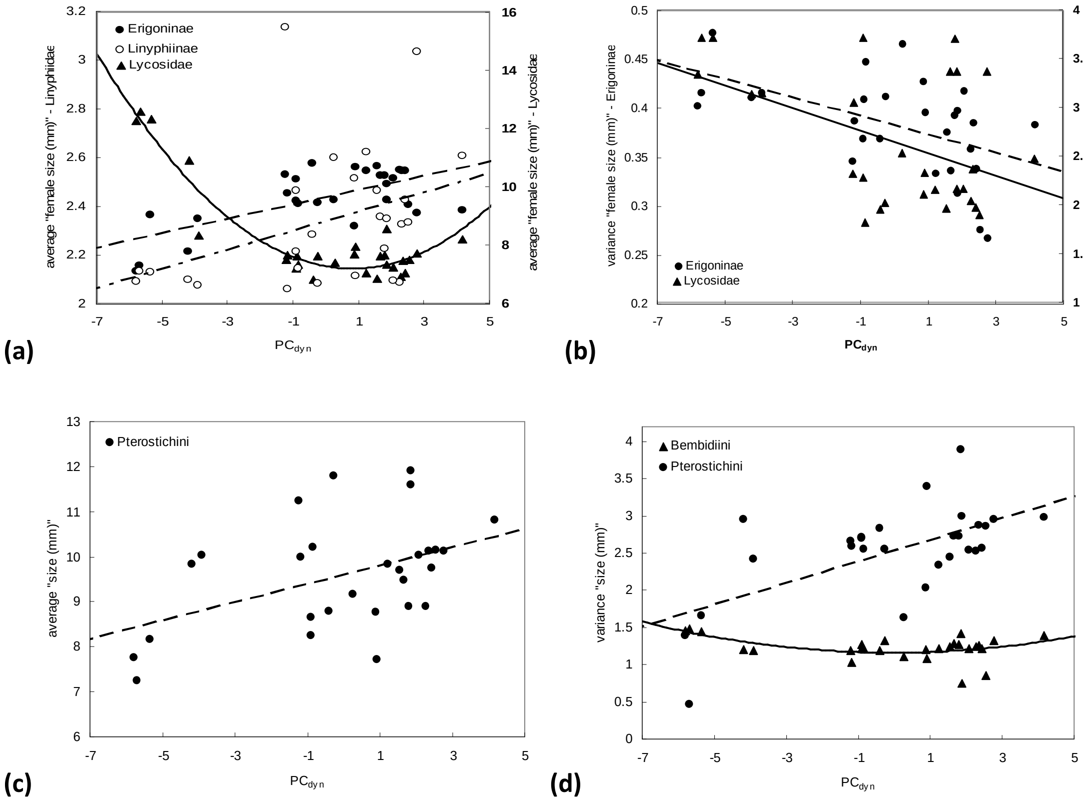

Fig. II.9 - Relationship between spider female body size and carabid beetle body size and the degree of flooding disturbance (PC$_{dyn}$) along a lowland gravel river. (a) Weighted average Erigoninae, Linyphiinae, Lycosidae; (b) variance Erigoninae, Lycosidae; (c) weighted average Pterostichini.

Discussion

Our study contributes to a solid understanding of functional species traits of component predatory arthropods of river banks and their responses to flooding disturbance, thereby affecting species assemblage structure. Species richness of carabid beetles benefits from intermediate flooding disturbance whereas the richness of stenotopic riparian spiders increases with subsiding flooding. Congruent assemblage-wide shifts in species traits show that species sorting in response to flooding is the underlying mechanism within spider (sub)families and Bembidiini carabids. However, sorting mechanisms appear contrastive in Pterostichini carabid assemblages.

Only the number of riparian spider species decreases with increasing flooding disturbance. This suggests that increased flooding facilitates the settlement of eurytopic species, while specialists tend to disappear. The increase in eurytopic species is reflected in assemblage-wide shifts towards higher dispersal ability, higher shading and moisture preference (lower xerophily) and a smaller body size in Lycosidae. Moreover, lycosid and erigonid spiders with aerial dispersal capacity dominate lower river banks, although both highly mobile and sedentary erigonids are present on banks with an intermediate degree of disturbance, whereas variance in ballooning propensity remained constant for lycosid spiders. This indicates a clear shift towards generally mobile species, but with sorting mechanisms prevalent at high and low flooding for erigonids and species replacements for lycosids. The overall presence of highly dispersive, rather generalist agrobionts indicates that species from neighbouring arable habitats, colonize river banks and dominate assemblages under intensive flooding disturbance. Mass effects, by which a continuous input of species from source habitat is expected (Leibold et al., 2004), is consequently prevalent, comparable with results for spiders from agricultural ecosystems (Schmidt & Tscharntke, 2005a; Öberg et al., 2007). Dispersal of specialist species might be important on a more restricted spatial scale, adding to subsequent recolonisation or successfully escaping flooding (Morse, 1997; Kraus & Morse, 2005). Generally, spider diversity is positively related to vegetation composition (Perner & Malt, 2003; Beals, 2006). As previous studies have indicated flooding to homogenize vegetation structure (Peters et al., 2000; Shafroth et al., 2002), increased flooding can result in a lowered diversity. Nevertheless, studies concerning boreal or upland rivers showed positive relationships between flooding and vegetation heterogeneity *per se* (Nilsson et al., 1989; Renöfält et al., 2005), with concordant effects on riparian arthropod diversity (Bonn et al., 2002). Since vegetation composition is not related to flooding disturbance at our considered spatial scale (see Appendix A2.), it potentially affects species distribution patterns differently to flooding. The decrease in variance of xerophily indicates that assemblages are dominated by only few, ecological similar species, e.g. *Pardosa* sp. This pattern is similarly reflected by assemblage-wide decreases of both average body size and its variance with increased flooding disturbance. For Erigoninae an opposite pattern was found, with mainly larger species on more disturbed river banks, whereas small linyphiids are replaced by larger species since the variance in body size remained constant. Because larger Erigoninae are the dominant dispersers during early summer, this pattern can be expected to be caused by a replacement of specialist species (often xerophilic species) by highly dispersive agrobionts and hygrophilous species. Agrobionts, however, may not be able to survive flooding events due to the lack of behavioural or physiological adaptations (Suter et al., 2004; Rothenbücher & Schaefer, 2006), thereby experiencing river banks as sink habitat.

In contrast to spiders, carabid beetle species richness peaks at intermediate levels of disturbance. Shifts in traits suggest that species sorting is mainly prevalent for Bembidiini species. Interestingly, assemblage-wide changes in dispersal ability are comparable. While Bembidiini species are often considered as inherent elements of the riparian carabid fauna (Turin, 2000; Manderbach & Hering, 2001), preferring dynamic and moist circumstances, our results demonstrate that specialist species tend to disappear at highly disturbed river banks. On average, shading preference was lowest at higher river banks whereas hygrophily decreased with increased flooding. Variance patterns of body size, however, show that only a restricted subset of Bembidiini species is able to persist on river banks at both ends of the disturbance gradient. These patterns indicate that species tend to be lost as flood pulses rise or at lower degrees of flooding, adding to the prevalence of sorting mechanisms for Bembidiini assemblages, comparable to spiders. Both floods and low flows are often related to anthropogenic alterations of the flooding regime and shown to be detrimental for the invertebrate fauna (Usseglio-Polatera & Beisel, 2002; Suren & Jowett, 2006). Sorting mechanisms appear less obvious for Pterostichini assemblages. Niche breadth variance is low especially at the most disturbed river banks whereas larger species with well developed wings (cf. Bembidiini) become dominant. Therefore, increased flooding is clearly responsible for the elimination of smaller, more specialized Pterostichiini species from local assemblages, yet they are known to colonize flooded sites quickly by means of epigeal locomotion (Lang & Pütz, 1999). Next to it, Pterostichini species tend to profit from intermediate degrees of disturbance as shown by the variance in shading preference. Assemblages of Pterostichini species are mainly structured by changes in dispersal capacity rather than by replacements of species with idiosyncratic ecological needs. Therefore, sorting mechanisms seem to affect Pterostichini assemblages in other ways than Bembidiini, but effects of anthropogenically altered flood regimes are equally prevalent. Floods, in particular, cause shifts towards eurytopic Pterostichini assemblages, hence specialized species are lost. In general, carabid beetle trait patterns in relation to flooding are more variable and specific according to the considered phylogenetic level compared to spiders. This may be caused by conservative traits like elytra coloration and diurnal activity patterns (related to desiccation tolerance; Desender, 1989a). Sorting mechanisms related to local habitat conditions at both ends of the disturbance gradient are in concordance with Bonn & Schröder (2001), who demonstrated incidence patterns to vary in opposite directions for a specialized *Agonum* and a eurytopic *Pterostichus* species. Bonn & Kleinwächter (1999) indicated apparent sorting mechanisms for riparian carabid beetle assemblages with specialized species closer to the waterline, shifting to a less specialized carabid fauna further away. In concordance with our results and earlier studies of Desender et al. (1994), they clearly showed wing development to be related to the distribution of *Agonum* and *Bembidion* species (increased overall macroptery at sites near the water edge) and *Pterostichus* species (reduction of hind wings near dykes). Although different flood regimes benefit different species, an optimum in species richness at intermediately disturbed banks is assumed to be maintained by increased microhabitat heterogeneity (Pollock et al., 1998). This allows for a narrow niche separation (Bonn & Kleinwächter, 1999), hence benefiting the persistence of species with divergent habitat preferences and interrelated sets of species traits (e.g. dispersal ability) (Ward et al., 2002; Vanbergen et al., 2005). Either low flows or increased flooding would disfavour riparian carabid beetles, leading to constraints on the local assemblages (cf. Vanbergen et al., 2005; Stromberg et al., 2007).

Notwithstanding the prevalence of mobile species on all river banks, sorting mechanisms underlie species assemblage structure. In particular, common hygrophilous species are better represented as flooding increases. However, riparian species with well-developed dispersal abilities (e.g. Bembidiini) are well presented throughout the river system (Desender, 1989a; Desender et al., 1994; Lambeets et al., 2008a), thereby indicating their efficient movement throughout the system, probably resulting in one patchy population (Bates et al., 2006). Patterns could, at first sight, be generated by the local landscape structure, but our analysis showed that the latter is independent of the flooding regime. Therefore, more intrinsic factors related to, for example, general activity or sediment preference should influence trait patterns. As shown by Bonte et al. (2006b), dispersal mode (passive controlled in carabid beetles *versus* predominantly uncontrolled passive in spiders) could additionally underlie differences of the observed species distribution patterns, with stronger resemblance in carabid assemblages due to their better-developed colonisation abilities.

In conclusion, flooding disturbance is responsible for variable species sorting in two groups of opportunistic predatory arthropods. Assemblage-wide shifts in species traits were directional for spider (sub)families, with concordant effects regardless of their dispersal abilities. Shifts for carabid beetle tribes were similar for Bembidiini, yet less univocal for Pterostichiini. Since eurytopic as well as specialist species are locally present, our results indicate that variation in riparian arthropod assemblages is enhanced by different flood regimes. If we take into account that especially cursorial spider species with larger body sizes and a higher degree of habitat specialization, and hygrophilous carabid beetles with smaller body sizes are more vulnerable to extinction (Bonte et al., 2006a; Niemelä et al., 2002), human-driven alterations in flooding disturbance, i.e. either too high or too low, can be expected to have a major impact on arthropod assemblages and the distribution of rare riparian species (Bonn et al., 2002; Lambeets et al., 2008a). Moreover, a homogenization of habitat structure as a consequence of repetitive flood events or its absence will result in a more uniform and less specialized species composition (Bonn & Kleinwächter, 1999; Vanbergen et al., 2005; Van Looy et al., 2006). Species are added to local communities as disturbance seizes for spiders or at intermediate degrees of disturbance for carabid beetles, thereby increasing alpha diversity (Robinson et al., 2002; Bonte et al., 2006a; Jonsen & Fahrig, 1997). Due to generally better developed dispersal abilities, riparian carabid beetles appear more resilient and able to persist under increased dynamics (Van Looy et al., 2005).

Acknowledgements

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Authors' contributions

KL sampled the river banks, gathered environmental measures, performed the analyses and drafted the manuscript. KL and DB conceptualized the research questions and interpreted the results. MLV identified the carabid beetles. JPM discussed presentation and was involved in the final preparation of the manuscript. All authors read and approved the final draft.

Supplementary Material

Appendix A2.: Pearson correlations with principal component analysis-ordination axes of local topographical and regional chorological environmental parameters of river banks along the Common Meuse.

Appendix A3.: Species list, trapped numbers and trait values of spiders (Araneae: Erigoninae, Linyphiinae, Lycosidae) and carabid beetles (Carabidae: Bembidiini, Pterostichini) from river banks along the Common Meuse.

Table II.5 - Influence of flooding disturbance on niche breadth, shading preference, drought/moisture preference, body size, flight ability (spider ballooning propensity and carabid beetle wing development) of spider and carabid beetle assemblages from river banks. General linear model (GLM) regression statistics and Akaike's information criteria (AIC) values are shown for weighted averages (Table II.5a and 5b) and variances (Table II.5c and 5d), respectively, for each of the spider (sub)families (Lycosidae, Erigoninae, Linyphiinae) and carabid beetle tribes (Bembidiini, Pterostichini). Degrees of freedom are indicated below each taxonomic group as (numerator degrees of freedom; denominator degrees of freedom).

(a)

		second order relation			**first order relation**		
life history trait	**regression statistics**	**Lycosidae (1, 25)**	**Erigoninae (1, 25)**	**Linyphiinae (1, 24)**	**Lycosidae (1, 26)**	**Erigoninae (1, 26)**	**Linyphiinae (1, 25)**
Niche breadth	F	2.45	1.24	0.14	14.2	8.27	2.84
	p	0.1304	0.2752	0.7157	**0.0009**	**0.0079**	0.1044
	AIC	213.1	179.1	190.1	215	178.5	189.1
Shading preference	F	17.02	3.37	1.37	14.2	38.13	5.07
	p	**0.0004**	0.0784	0.2528	**0.0009**	**<.0001**	**0.0334**
	AIC	-9.3	-54.3	4.8	-5.2	-62.2	-2.7
Xerophily	F	2.05	10.58	1.81	15.47	10.71	7.3
	p	0.1645	**0.0033**	0.1912	**0.0006**	**0.003**	**0.0122**
	AIC	32.7	-20.4	-10.6	27	-21.1	-18.3
Female size	F	74.46	13.12	0.01	42.62	20.85	4.43
	p	**<.0001**	**0.0013**	0.9433	**<.0001**	**0.0001**	**0.0456**
	AIC	58	-40.1	23.1	87.2	-39.8	15.1
Ballooning	F	1.92	0.32	0.33	8.43	5.83	0.61
	p	0.1786	0.5792	0.5737	**0.0074**	**0.0231**	0.4437
	AIC	13.5	-28.6	-21.3	6.9	-38.5	-30.9

(b)

		second order relation		first order relation	
life history trait	**regression statistics**	**Bembidiini (1, 25)**	**Pterostichini (1, 25)**	**Bembidiini (1, 26)**	**Pterostichini (1, 26)**
Niche breadth	F	1.64	0.44	14.16	0.05
	p	0.2126	0.5120	**0.0009**	0.8302
	AIC	237.3	183.5	239.5	182.2
Shading preference	F	7.71	0.01	3.45	2.24
	p	**0.0103**	0.9281	0.0745	0.1462
	AIC	-82.1	24.1	-87.5	16.1
Hygrophily	F	1.81	2.55	11.28	0.28
	p	0.1901	0.1231	**0.0024**	0.6000
	AIC	10.2	5.3	3.4	-1.0
Body size	F	0.36	0.45	1.41	1.64
	p	0.5554	0.5084	0.2450	0.2115
	AIC	10.7	94.5	2.4	73.2
Wing development	F	2.36	1.99	9.75	7.68
	p	0.1373	0.1710	**0.0044**	**0.0102**
	AIC	25.1	46.9	19.4	41.7

(d)

		second order relation		first order relation	
life history trait	**regression statistics**	**Bembidiini (1, 25)**	**Pterostichini (1, 25)**	**Bembidiini (1, 26)**	**Pterostichini (1, 26)**
Niche breadth	F	0.31	0.44	0.28	5.62
	p	0.5813	0.5133	0.6026	**0.0254**
	AIC	189.5	161.1	188.4	159.0
Shading preference	F	0.17	4.84	1.23	0.28
	p	0.6863	**0.0376**	0.2782	0.5983
	AIC	34.0	27.8	26.5	24.6
Hygrophily	F	0.02	0.08	0.94	0.05
	p	0.8859	0.7771	0.3417	0.8174
	AIC	-25.2	2.4	-35.2	-6.4
Body size	F	5.25	2.76	3.21	15.84
	p	**0.0306**	0.1090	0.0850	**0.0005**
	AIC	-8.0	54.6	-12.4	50.5
Wing development	F	1.38	2.03	0.94	0.75
	p	0.2524	0.1675	0.3424	0.3935
	AIC	5.9	30.6	-1.5	25.0

(c)

life history trait	**regression statistics**	**second order relation**			**first order relation**		
		Lycosidae (1, 25)	**Erigoninae (1, 25)**	**Linyphiinae (1, 24)**	**Lycosidae (1, 26)**	**Erigoninae (1, 26)**	**Linyphiinae (1, 23)**
Niche breadth	F	1.31	0.42	0	3.65	0.05	0
	p	0.2624	0.524	0.9561	0.0672	0.8186	0.9504
	AIC	168.1	133.6	191.4	167.2	130.3	190.6
Shading preference	F	0.05	0.41	0	0.05	0.07	0.26
	p	0.8314	0.5256	0.978	0.8186	0.8005	0.6165
	AIC	-71.5	24.3	-9.6	-83.3	-33.9	-19.1
Xerophily	F	0.11	0.22	1.52	5.31	3.34	3.25
	p	0.7471	0.6465	0.2295	**0.0295**	0.0791	0.0841
	AIC	-1.8	-51.8	-34.9	-10.8	-62.7	-43.9
Female size	F	2.95	0.58	3.23	7.55	9.58	0.02
	p	0.0982	0.4528	0.0853	**0.0108**	**0.0047**	0.8867
	AIC	61.6	-67.5	52.9	57.9	-78.6	49.3
Ballooning	F	1.54	5.18	0.28	0.23	0.33	0
	p	0.2266	**0.0317**	0.6044	0.6329	0.5694	0.9753
	AIC	-44.2	-65.6	7.7	-53.5	-72.3	-0.8

II.3. Integrating environmental conditions and functional life-history traits for riparian arthropod conservation planning

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A female *Arctosa cinerea* (Fabricius, 1777), leering from its refuge (Photo: Rollin Verlinde, Vilda)

Agonum marginatum (Linnaeus, 1758), a scarce hygrophilic carabid (Photo: Maarten Jacobs)

Abstract

River banks are naturally disturbed habitats, in which local flood events and the landscape structure are expected to govern riparian species assemblages. Not solely effects of flooding *per se*, but also related changes in vegetation structure will affect species distribution. By elucidating the relationships between species occurrences and multivariate habitat conditions on a restricted spatial scale, insight into conservation strategies to preserve riparian species is gained. Ordination and grouping methods revealed important environmental and functional trait constraints on the composition of predatory riparian arthropods. Mainly flooding disturbance appeared to affect spider and carabid beetle assemblages. Habitat affinity and dispersal ability were retained as important traits explaining similarity between arthropod assemblages. River banks similar in species composition differed in absolute and functional group species richness. Furthermore, Poisson regressions demonstrated the importance of variation in discharge regime, sediment composition and vegetation structure for the preservation of rare riparian arthropods. Xerothermophilic specialists were disfavoured by increased flooding disturbance, whereas hygrophilic species benefited from increased vegetation cover. In contrast to flight-active riparian carabids, occurring throughout the river system, especially cursorial spiders are expected to go extinct under increased anthropogenic alterations of discharge regimes. In general, river restoration should generate the required heterogeneity in environmental conditions (e.g. dynamic processes) at the river bank level, thereby increasing the sustainability of dynamic riverine landscapes and the conservation of vulnerable riparian arthropods. Moreover, we argue that the understanding of functional responses towards environmental factors on a local scale results in general and widely applicable guiding concepts for species conservation and ecosystem management.

Key-words: carabid beetles, flooding disturbance, multi-species approach, lowland river banks, river management, spiders

Introduction

Riverine ecosystems are characterised by spatial and temporal variation in local and regional environmental parameters (Ward et al., 2002), thereby showing a considerable variation in riverine and riparian biodiversity (Pollock et al., 1998; Robinson et al., 2002). Despite this high heterogeneity, they do not necessarily harbour more species than other ecosystems, but rather comprise a specialised and vulnerable fauna as a result of environmental stressors such as flood events and thermal fluctuations (Andersen & Hanssen, 2005; Sabo et al., 2005; Baker et al., 2006). Since river banks are situated at the interface between aquatic and terrestrial environments, they are subject to repeated inundations and affected by intensive agricultural practices in the catchment area (Ward et al., 2002; Renöfält et al., 2005). Currently, anthropogenic alterations cause unnatural fluctuations of river discharge regimes, i.e. prolonged low flows and hydropeaking (Semmerkrot et al., 1997), thereby altering erosion and sedimentation processes. This eventually leads to shifts in local conditions (e.g. vegetation structure) and channel connectivity (Naiman et al., 2005). In turn this can affect habitat suitability for species which are adapted to short-term environmental changes and pioneer conditions induced by regular flood events (Robinson et al., 2002; Lytle & Poff, 2004; Lake et al., 2007).

As riparian and riverine habitats are amongst the most diverse yet threatened ecosystems world-wide (ECE - River Convention, 1992), they in particular deserve conservation attention (Ward, 1998; Naiman et al., 2005). As suggested by several authors in the last decade (e.g. Buijse et al., 2002; Tockner & Stanford, 2002; Lake et al., 2007), direct action is needed to preserve the rare and vulnerable organisms occurring within the riverine landscape, thereby increasing regional biodiversity (Sabo et al., 2005). Recently, ambitious European river restoration projects have been aiming to re-establish natural discharge regimes (dike removal, preventing hydropeaking or low flows) and to restore the contact with the alluvial hinterland (Buijse et al., 2002; Pedroli et al., 2002). Their main objective is to create or to restore a more natural, continuous river valley in balance with socio-economic aspects. For the riparian ecotone in specific, this will result in increased habitat heterogeneity at the local scale (habitat quality; Collinge et al., 2001) but also at the landscape scale (species pool; Riis & Sand-Jensen, 2006).

The study of relationships between ecological parameters and the arthropod biota provides valuable and complementary information for restoration assessment and conservation planning (Kremen et al., 1993; Fisher & Lindenmayer, 2007) and may guide future management (Palmer et al., 2005). We especially argue that a more functional understanding of this relationship is of wider applicable conservation interest (Bonte et al. 2006a; Violle et al., 2007). Spiders (Araneae) and carabid beetles (Carabidae) are mobile predatory arthropods, found in any terrestrial ecosystem. Changes in their species composition clearly reflect shifts in local environmental conditions (Ribera et al., 2001; Pétillon et al., 2005; Scott et al., 2006), habitat fragmentation (Dauber et al., 2005; Major et al., 2006; Schmidt et al., 2008) and the surrounding land-use (Perner & Malt, 2003; Vanbergen et al., 2005). Particularly riparian habitats host many rare and stenotopic arthropods (Turin, 2000; Sadler et al., 2004; Andersen & Hanssen, 2005). A preliminary study considering the predatory arthropod fauna along the Common Meuse (Lambeets et al., 2008a) indicated that the environmental conditions affecting assemblage structure of riparian spiders and carabid beetles were similar. However, information about responses of riparian species towards environmental conditions is greatly lacking, especially at restricted spatial scales (but see Rothenbücher & Schaefer, 2006; Bates et al., 2006; Lambeets et al., 2008b).

Based on an intensive sampling campaign, we here unravel patterns of change in the assemblage structure and corresponding functional groups of riparian arthropods. Spiders and carabid beetles are supposed to be constrained by important environmental parameters such as flooding disturbance. Otherwise, we expect functional life-history traits (e.g. dispersal ability, ecological habitat affinity) to affect assemblage structure as well (Violle et al., 2007). Moreover, community analyses are complemented with a multi-species approach (Kremen et al., 1993; Maes & Bonte, 2006) to investigate relationships between distribution patterns of vulnerable riparian species and structuring habitat conditions. Consequently, these results provide complementary information for riparian arthropod conservation and river management purposes.

Materials and Methods

Study area

The Common Meuse is the most natural reach of the River Meuse and covers approximately 45 km of the total ca. 900 km river trajectory (Fig. II.4). Due to its rain-fed character and the rocky soils of the upstream catchments, the watercourse is characterised by strong river flow fluctuations and a wandering pattern of isolated river banks (Pedroli et al., 2002; Van Looy et al., 2006). These banks comprise a top layer of coarse shingle completed with a sharp sand-gravel or sand-loam fraction, and related changes in vegetation (Peters et al., 2000); the lowest gravel bars are covered with an extensive layer of silt. Only when the river discharge drops below 200 m^3s^{-1} (roughly from April until September), river banks are gradually exposed. Currently, large parts along the Common Meuse trajectory are still heavily diked with concrete embankments or large stone boulders, restraining natural dynamic processes (van Winden et al., 2001). Over 50% of the alluvial plain is still in intensive agricultural use while alluvial grasslands, sand-gravel bars or pioneer vegetations on overbank sediment depositions only occupy 5% of the surface (K. Van Looy, pers. comm.). At this rather restricted regional scale, no longitudinal downstream variation of disturbance frequency, substrate structure or vegetation composition occurs. This is demonstrated by the lack of any correlation between environmental factors and river bank downstream position (all $r < 0.24$; Lambeets et al., 2008b).

variable class	**parameter measured**	**methodology**
flooding disturbance	**WFR**	(log) River bank water flow rate (cf. river bank flood frequency)
flooding disturbance	**RSregr**	(log) Rising speed of the washing water
river bank topography	**orientcl**	Orientation quarter of the river bank (1 = ZO, 6 = W)
river bank topography	**area**	Patch size (based on redrawn detailed maps, ArcGIS 9.1)
river bank topography	**wd**	River channel width-depth ratio (cf. water storage capacity)
river bank topography	**alpha**	River bank steepness
river bank topography	**wdst**	Width-depth ratio restricted to river bank level
substrate composition	**gravel**	Gravel size class (1 = small-sized gravel, 5 = coarse shingle)
substrate composition	**sand**	Composition of the in-between sediment fraction ((sharp) sand - loam ratio)
substrate composition	**silt**	Silt cover (none - covering 1/4 - half or up to dike foot)
vegetation structure	**avVegc**	(sqrt) Average vegetation cover (digital photos)
trampling	**catt**	Grazing intensity class (0 = no cattle, 4 = up to 25 grazers)
channel connectivity	**downstr**	Number of river banks in downstream direction
channel connectivity	**RTnneigh**	(sqrt) Nearest neighbour distance to most approximate river bank
channel connectivity	**PBwsum**	Patch-based weighted sum of river bank
landscape composition	**landu**	Surrounding land use (alluvial grasslands, brushwood shoulders, meadows, crop fields)
landscape composition	**arabl100**	(sqrt) Area of arable land within 100 m radius
landscape composition	**brush100**	(sqrt) Area of brushwood vegetation within 100 m

Table II.6 – Environmental parameters of river banks along the Common Meuse used in the BIO-ENV procedure. Parameters were transformed a priori if they did not meet the normality assumption (Shapiro-Wilkinson >0.90), indicated by (log) if logarithmic and (sqrt) if square root.

Sampling protocol

All river banks along a continuous part of the Common Meuse river reach (n = 24; Fig. II.4) were sampled from 06-04-2005 until 19-07-2005 with pitfall traps (diameter 9 cm; 6% formaline solution; fortnightly emptied). Each river bank contained three up to six pitfalls, divided over a maximum of two stations. Sample stations (n = 28) were arranged parallel with the waterline, situated at an average distance of 6.1 m from the loamy river dike and 21.3 m for more distant (lower) stations on larger banks. As recommended by Topping & Sunderland (1992) pitfalls were spaced 10 m apart to avoid interference between the traps. Since unpredictable flood events caused data loss on several occasions, numbers of individuals caught were interpolated distinctly for each species, sample date, pitfall trap and sample station. Average numbers of trapped individuals were calculated based on trap data from remaining unflooded pitfalls. For each species, catches were pooled to total numbers per sample station. It is important to recognise that pitfall trapping has some inherent biases, and catches can be affected by factors including habitat structure, weather conditions and the preservative used (Topping & Sunderland, 1992; Pekár, 2002). In this study, standardised pitfall trapping is an appropriate collection method, since we aim to compare distribution patterns as affected by environmental conditions. Contrary to other studies (e.g. Bonn et al., 2002), cryptic and smaller sized individuals, such as *Bembidion* carabids and linyphiid spiders, made up the majority of the catches so our sample data are believed to reflect local arthropod composition well. Moreover, pitfalls were constantly operative from the moment the river banks were exposed until mid-summer. Therefore, sampling took place during the general activity period of both focal groups and within one habitat type (river banks), adding to the usefulness of pitfall catches in this case and its liability to concrete interpretation (Baars, 1979). All species were assigned to following functional groups: riparian, hygrophilic, xerothermophilic and eurytopic / pioneer species based on relevant literature resources (Araneae: Roberts, 1987; 1998; Harvey et al., 2002; Entling et al., 2007; Carabidae: Turin, 2000; Boeken et al., 2002). Additionally, species restricted to the alluvial plain were considered for carabids.

Characterisation of environmental parameters and functional traits

Discharge regimes are affected by local topography as well as regional chorological factors (Pedroli et al., 2002; Van Looy et al., 2006) and influence both local humidity and vegetation structure, being the most important drivers of habitat suitability for the studied arthropod groups (Turin, 2000; Entling et al., 2007). Therefore, we selected a suite of 18 environmental variables which have proven to relate to arthropod occurrence on river banks (Van Looy et al., 2005; Lambeets et al., 2008a). We recorded parameters related to flooding disturbance (2), river bank and channel geometry (5), substrate composition (3) and vegetation structure (1). Additionally, local trampling intensity, if any, was quantified (1). Measured landscape-related parameters were connectivity along the riparian corridor (3) and surrounding land-use (3). Environmental variables were checked for normality using the Kolmogorov-Smirnov test and transformed if necessary. For the ease of reading the measured variables and applied field methodology are concisely explained in Table II.6.

Since distribution patterns of spiders and carabid beetles clearly relate to functional species characteristics (Ribera et al., 2001; Lambeets et al., 2008b; Le Viol et al., 2008), functional life-history traits were determined based on literature resources. We consider functional life-history traits as those traits that potentially affect species occurrence and persistence in a fundamental ecological context (cf. Violle et al., 2007). As these species traits concern an amalgam of eco-, morpho-, pheno- , and physiological characteristics, we selected those which have been proven to effectively affect spider and carabid beetle occurrence patterns (Ribera et al., 2001; Kotze & O'Hara, 2003; Bonte et al., 2006a; Le Viol et al., 2008). Ecological preference was split up into niche breadth, shading and moisture preference and additionally sediment preference for carabids. Morphological features enclosed body size, flight ability and also metallic lustre of the elytra for carabid beetles. Main activity periods were taken into account since species presence can be expected to depend on the moment when habitat patches become available (Ribera et al., 2001; Rothenbücher & Schaefer, 2006). For a brief explanation of the functional traits and literature overview see Table II.7.

Assemblage structure and constraints

Multivariate and univariate techniques were used to identify patterns of change in arthropod assemblages and species densities in relation to environmental constraints, respectively. Since river banks are known to be inhabited by a heterogeneous mixture of rare, riparian species and eurytopic (agrobiont) species, non-metric multidimensional scaling analysis (nMDS, PRIMER 5; Kruskal & Wish, 1978) was used to assess why sample stations were separating. We used nMDS since it is an iterative ordination method that places sample units in a k-dimensional space using ranked distances between them (McCune & Grace, 2002). Because nMDS does not assume linearity or monotonicity of the underlying data structure, it is particularly appropriate for the kinds of ecological data in this study (Beals, 2006; Major et al., 2006), and provides a stress-factor which indicates the stability of the ordination. Similarity matrices were based on Bray-Curtis distance measures. Prior to nMDS, species catches were pooled to total numbers per sample station and standardised towards three trapping devices. To minimise the influence of vagrants, species with less than 30 individuals were omitted. Because of prevalent pitfall bias caused by e.g. different activity patterns, population densities or (micro) habitat structure (Topping & Sunderland, 1992), species counts were adjusted by the maximum number of individuals of each species occurring within a sample station (Maelfait & Baert, 1975). Similarity in Bray-Curtis distance matrices of spiders and carabid beetles was tested by a Mantel-test, based on 1000 Monte-Carlo permutations. Furthermore, the sample stations were grouped based upon their similarity of arthropod occurrence, using a hierarchical cluster analysis with a Bray-Curtis distance measure and a flexible beta group linkage method ($\beta = -0.25$; McCune & Grace, 2002).

To relate multivariate assemblage structure with environmental parameters or species traits, the BIO-ENV procedure (PRIMER 5; Clarke & Ainsworth, 1993) was used. Based on the agreement between the biotic and abiotic similarity matrices BIO-ENV calculates which combination of environmental parameters explains assemblage structure best. Biotic similarities were based on the Bray-Curtis distance measures, whereas abiotic distance matrices were based on Euclidean distances; Spearman rank correlation (ρ) was used to indicate the matching.

Species richness and densities of riparian arthropods

Absolute species richness per arthropod group (Araneae; Carabidae) and species richness per functional group were analysed by generalised linear mixed models (GLMM). Responses of riparian species were analysed by regression of their total catch number (from hereon referred to as "density", although a relative measure because pitfalls register activity- density) on the earlier retrieved community-structuring environmental parameters. Poisson regression models (SAS 9.1, proc glimmix) were applied, with Satterthwait's procedure to compute corrected degrees of freedom (Verbeke & Molenberghs, 2000). In all cases, models were corrected for overdispersion and normality of residuals was checked.

functional trait	**explanation**	**literature Araneae**	**literature Carabidae**
Shading preference	Preference for habitat openess (cf. vegetation cover)	Entling et al. (2007)	Turin (2000); Boeken et al. (2002)
Moisture preference	Preference for habitat moistness or dryness	Entling et al. (2007)	Turin (2000); Boeken et al. (2002)
Niche breadth	The number of habitat types (related to species' geographical rareness) in which the species was caught	Hänggi et al. (1995)	Boeken et al. (2002)
Flight ability	Ballooning propensity for spiders (0/1) and relative wing development in relation to body size for carabids	Bell et al. (2005); Bonte & Lambeets (unpub. data)	Desender (1989a)
Body size	Average female size for spiders and average size for carabids	Roberts (1987; 1998)	Boeken et al. (2002)
Activity period	Activity period, based on the reproductive peak	Roberts (1987; 1998)	Turin (2000)
Sediment preference	Preference for substrate composition	/	Turin (2000); Boeken et al. (2002)
Metallic lustre	Elytra colouration (cf. reflection)	/	Boeken et al. (2002)

Table II.7 – Functional species traits chosen to represent important life-history features of spiders and carabid beetles (see Lambeets et al., 2008b). Functional traits were based on valuable literature resources describing ecological habitat affinity and morphological species characteristics.

Results

General results

We recorded a total of 107 spider (25,964 individuals) and 105 carabid beetle species (21,803) across the sampled river banks. After omitting species represented by less than 30 individuals, 25,413 adult spiders (97.9% of total numbers trapped) and 21,367 adult carabid beetles (98.0%) remained for further analysis, spread over, respectively, 28 and 39 species.

Riparian arthropod assemblage structure

Cluster analysis for spider records separated the 28 sample stations into five groups (Fig. II.11a), corresponding to their positions in relation to flooding susceptibility and vegetation openness. Ordination by nMDS supported the results of the cluster analysis and the 2D-configurational state of species composition was considered stable (stress: 0.18; Fig. II.11a). The nMDS plots less and highly disturbed river banks on top, i.e. higher as well as lower yet wide banks, whereas banks with an intermediate, more natural, degree of flooding are found below. River banks with a dense vegetation cover are found on the right side of the nMDS; vegetation openness increases to the left. Concordant patterns were found for carabid beetles (stress: 0.18; Fig. II.11b), with a clear separation of the highest from more disturbed river banks on the right and the left side of the nMDS respectively. Banks with a dense vegetation cover are found on top, more open banks below. This pattern confirms the cluster analysis. The Mantel-test indicated that spider and carabid beetle assemblages are structured by similar environmental conditions (r = 0.352, p = 0.001). Since the nMDS configurations differ slightly, other aspects of, mainly, flooding disturbance affect species composition according to the arthropod group under consideration. Therefore, factors that separate river banks are analysed in more detail below.

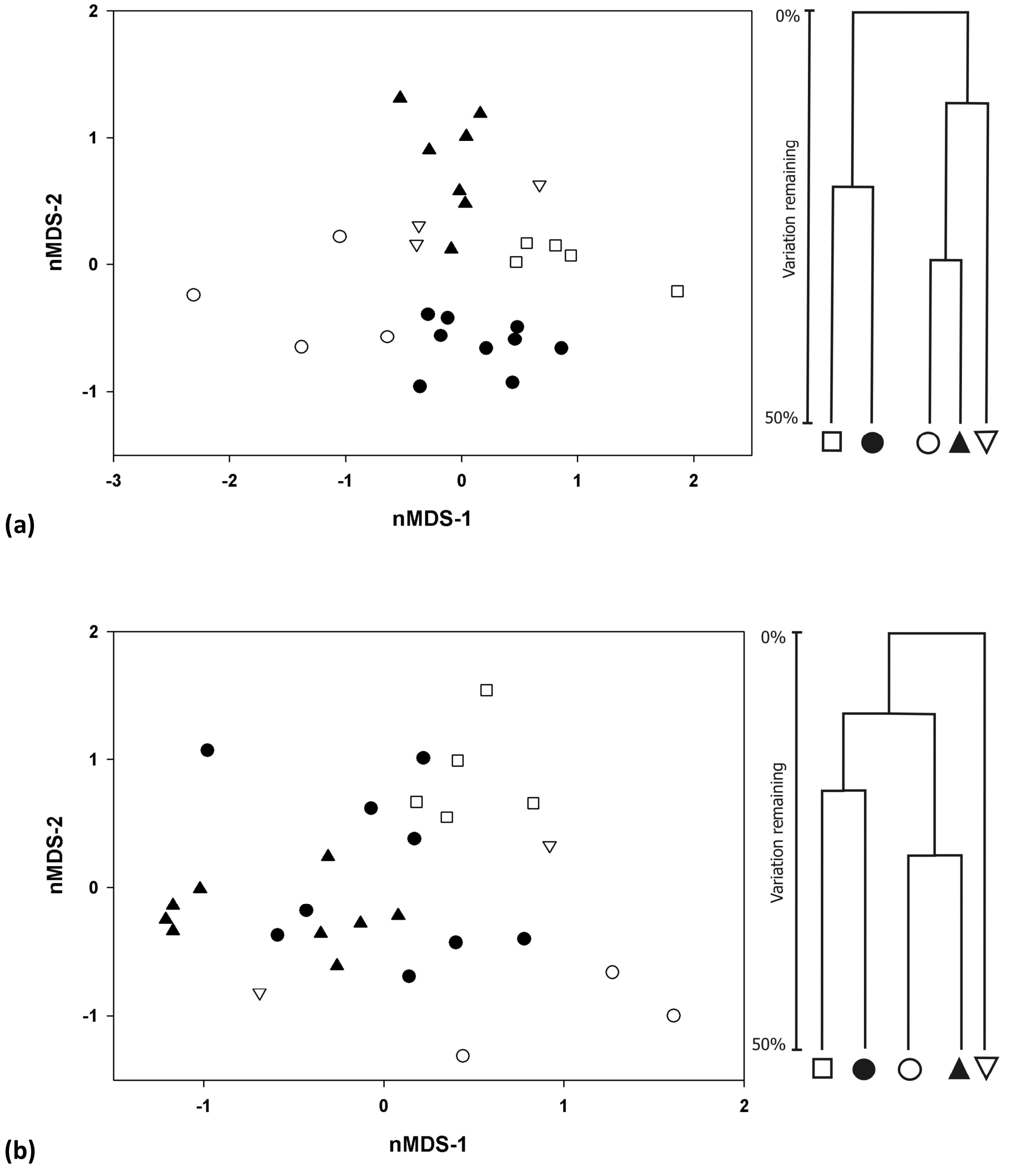

Fig. II.11 – Results of the nMDS ordination (left) and Bray-Curtis similarity tree (right, branches of the sample stations belonging to the same group are merged) of the sample stations, based on the relative abundances of (a) spider and (b) carabid beetle species. Clustered sample station groups are indicated with different symbols; (X,Y) indicate the number of river banks enclosed within each cluster for respectively spiders and carabid beetles: □: Cluster1 (5;5); ●: Cluster2 (9;9); ▲: Cluster3 (7;9); △: Cluster4 (3;2); ○: Cluster5 (4;3).

Species richness and functional diversity

We found clear differences in total species richness between river bank clusters (Fig. II.12) both for spiders ($F_{4,23} = 5.74$, p = 0.0023) and carabid beetles ($F_{4,23} = 7.22$, p = 0.0006). Disturbed river banks generally contained the lowest number of species for both arthropod groups. Differences in species richness within functional groups per taxon were significant for pioneer/eurytopic spider species ($F_{3,24} = 2.85$, p = 0.0471) and carabid beetles ($F_{3,24} = 5.7$, p = 0.0024) with the lowest species richness on the most disturbed river banks. This also applies for species richness of hygrophilic spiders ($F_{3,24} = 7.31$, p = 0.0006) and carabids ($F_{3,24} = 5.36$, p = 0.0034). Riparian spider species richness was highest on higher river banks ($F_{3,24} = 3.03$, p = 0.038), yet was not different for carabids ($F_{3,24} = 1.12$, p = 0.3724). No significant differences were found for xerophilic species (Araneae: $F_{3,24} = 2.48$, p = 0.0723; Carabidae: $F_{3,24} = 1.6$, p = 0.2069), or for alluvial carabid species ($F_{3,24} = 1.37$, p = 0.2749). Pairwise differences are indicated in Fig. II.13a and II.13b for spiders and carabid beetles, respectively.

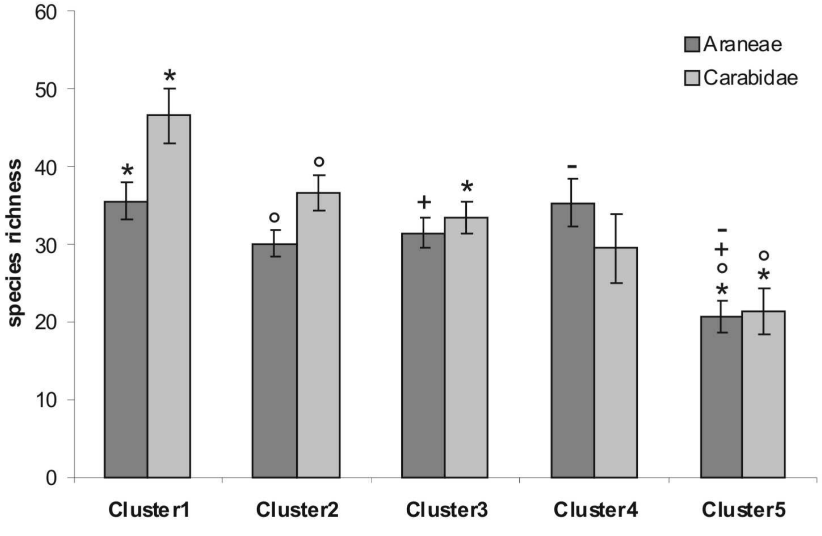

Fig. II.12 – Differences in total species richness per sample station between river bank clusters which are based on spider and carabid beetle catch numbers respectively (Sorensen distance, flexible β = -0.25). Error bars indicate standard errors of the mean. Significance pairwise comparisons within arthropod groups are indicated by the same symbols (post hoc Tukey-Kramer test; *, °, +, -).

Environmental constraints

Variation in spider assemblage structure along the Common Meuse was best explained by water flow rate solely (ρ = 0.387, $p < 0.05$). Second best was the combination of sand-loam ratio, water flow rate and rising speed of the washing water (ρ = 0.381, $p < 0.05$). Concordantly, a combination of sediment composition (sand-loam ratio and silt cover), vegetation cover and water flow rate, were found to match carabid beetle assemblage structure best (ρ = 0.492, $p < 0.01$). Including the rising speed of the washing water (cf. spiders) was nearly as good (ρ = 0.491, $p < 0.01$). These parameters logically differ between the river bank clusters (see Appendix A4.) and hence are useful to relate to species specific occurrences (see below).

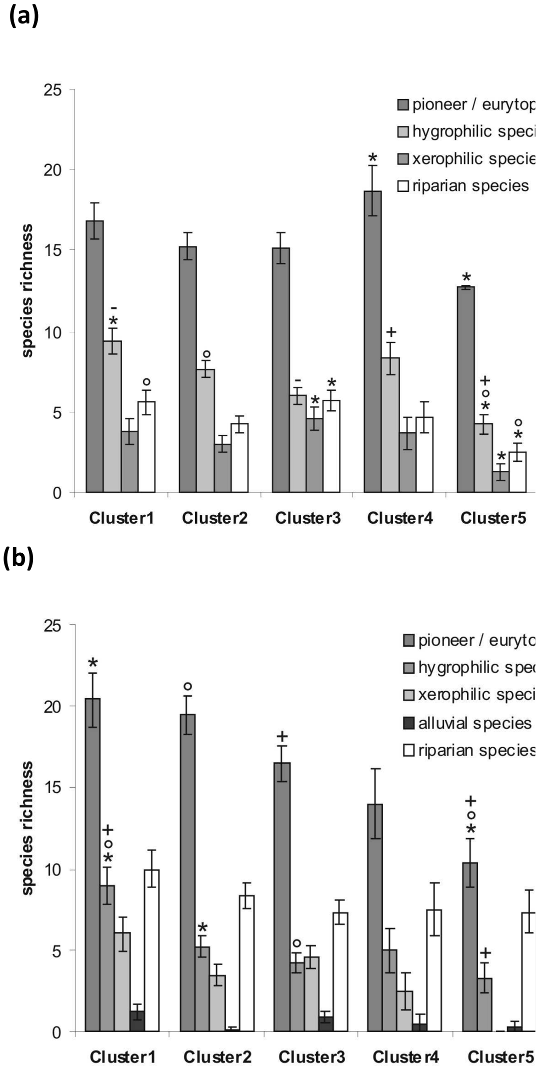

Fig. II.13 – Differences in functional group species richness per sample station between river bank clusters for spiders (a) and carabid beetles (b), i.e. riparian, hygrophilic, xerothermophilic and pioneer/eurytopic species and additionally alluvial species for carabids. Clusters are based on spider and carabid beetle catch numbers respectively (Sorensen distance, flexible β = -0.25). Significant pairwise comparisons within functional groups are indicated by the same symbols (post hoc Tukey-Kramer-test; *, °, +).

Functional constraints

A combination of shading and moisture preference and ballooning propensity was found to explain variation in spider assemblages from river banks best ($\rho = 0.290$, $p < 0.1$). Yet, leaving out shading preference proved to perform equally well ($\rho = .288$, $p < 0.1$). Variation in carabid beetle assemblages was best explained by a combination of niche breadth, activity period, average body size, relative wing development, sediment preference and with ($\rho = 0.212$, $p<0.1$) or without ($\rho = 0.211$, $p < 0.1$) metallic lustre of the elytra. We acknowledge these results are nearly significant ($p < 0.1$), nonetheless they indicate the importance of life-history traits affecting species occurrence and by consequence species composition.

Riparian species' responses

Below, the effects of important (manageable) environmental conditions (cf. habitat quality determining assemblage structure of predatory arthropods on river banks as mentioned above) on the densities of stenotopic riparian spiders ($n = 9$) and riparian carabid beetles ($n = 11$) are presented. In order to improve readability, an overview of Poisson model fit statistics is provided in Table II.8.

(a) Flooding disturbance

An increase of the discharge regime at which the river banks are inundated (WFR), i.e. a decrease of the local flood frequency, had a positive effect on the local density of the jumping spider *Heliophanus auratus*, the wolf spider *Arctosa cinerea*, the linyphiids *Caviphantes saxetorum* and *Troxochrus scabriculus* and the carabid *Lionychus quadrillum*. In contrast, densities of *Agonum afrum* were negatively affected. Additionally, *A. cinerea* and *T. scabriculus* are positively affected by a decrease in water rising speed (RSregr).

(b) Sediment composition

An increase of the sand-loam ratio (Sand) and accordingly a decrease of the river bank siltation (Silt), increased local densities for the spiders *A. cinerea*, *H. auratus* and *T. scabriculus* and the carabids *Bembidion atrocaeruleum* and *L. quadrillum*. *Tachys parvulus* was positively affected by an increased sand fraction, whereas densities of *Tachys micros* and *A. afrum* increased when the loam fraction increased. *C. saxetorum* was disadvantaged by an increased siltation of the river bank.

(c) Vegetation cover

Densities of two riparian spiders, *Pardosa agrestis* and *Collinsia distincta*, and three carabids, *Paranchus albipes*, *Bembidion testaceum* and *T. micros*, increased with increasing vegetation cover (AvVegc).

Discussion

The species composition of spiders and carabid beetles from lowland river banks differs strongly on a restricted spatial scale, the Common Meuse river reach. Similarity of respective species compositions was constrained by similar habitat quality factors (e.g. flooding disturbance) and functional species traits (e.g. dispersal ability). Clearly, the most disturbed sites are the least species rich and differ notably in functional species richness, especially for spiders. Furthermore, stenotopic riparian species with different habitat affinities vary strongly in their response to environmental conditions, indicating the importance of heterogeneity of river bank properties. These patterns indicate that species sorting affects arthropod species composition since variance in local environmental conditions and functional life-history traits results in a different assemblage structure.

Table II.8 – Density patterns of riparian spiders and carabid beetles were analysed using Poisson regression models. Significance levels of the environmental parameters are indicated as *** (p < 0.001), ** (p < 0.01) or * (p < 0.05). Whether or not the parameter had a positive effect on species density is indicated as **“+”** or **“-“**. Nomenclature for spiders and carabids is based on Bosmans & Vanuytven (2001) and Boeken et al. (2002) respectively. Red list-status is taken from Maelfait et al. (1998) for spiders and Desender et al. (1995) for carabids, and are in concordance with IUCN-categories: **EW**: extinct in the wild, **CR**: critical, **EN**: endangered, **VU**: vulnerable, **SU**: susceptible, **IN**: indeterminate.

		sand		**silt**		**avVegc**		**WFR**		**RSregr**	
species	**Red List**	***F***	***effect***	***F***	***effect***	***F***	***effect***	***F***	***effect***	***F***	***effect***
Heliophanus auratus C.L. Koch, 1835	*EN*	**6.94***	**+**	**4.48***	**-**	0.25	.	**7.92****	**+**	0.94	.
Arctosa cinerea (Fabricius, 1777)	*CR*	**19.96*****	**+**	**6.37***	**-**	2.17	.	**64.13*****	**+**	**20.12*****	**+**
Pardosa agrestis (Westring, 1861)	*EN*	2.77	.	1.12	.	**18.21*****	**+**	0.31	.	0.12	.
Pardosa agricola (Thorell, 1856)	*CR*	0.17	.	0.72	.	1.75	.	0.21	.	0.03	.
Baryphyma pratense (Blackwall, 1861)	*VU*	0.02	.	0.23	.	0.55	.	0.71	.	0.16	.
Caviphantes saxetorum (Hull, 1916)	*IN*	3.75	.	**5.53***	**-**	0.96	.	**4.36***	**+**	2.31	.
Collinsia distincta (Simon, 1884)	*EN*	3.07	.	0.93	.	**8.6****	**+**	0.17	.	2.61	.
Hypomma bituberculatum (Wider, 1834)	.	0.14	.	1.4	.	0	.	0.67	.	0.02	.
Troxochrus scabriculus (Westring, 1851)	.	**5.73***	**+**	**6.09***	**-**	1.27	.	**5.16***	**+**	**10.24****	**+**
Paranchus albipes (Fabricius, 1796)	.	0.4	.	0.02	.	**7.49***	**+**	0.44	.	0.05	.
Agonum marginatum (Linnaeus, 1758)	.	0.2	.	0.07	.	2.5	.	0.12	.	0.09	.
Agonum afrum (Duftschmid, 1812)	.	**4.25***	**-**	2.97	.	1.61	.	**11.24***	**-**	0.04	.
Bembidion atrocoeruleum (Stephens, 1829)	*EW*	**5.06***	**+**	**6.3***	**-**	0.73	.	0.95	.	2.83	.
Bembidion decorum (Zenker, 1801)	*VU*	0.66	.	0.33	.	1.94	.	0.03	.	3.98	.
Bembidion punctulatum (Drapiez, 1820)	*SU*	0.01	.	0.88	.	3.1	.	0.27	.	0.01	.
Bembidion testaceum (Duftschmid, 1812)	*IN*	0.2	.	0.2	.	**5.74***	**+**	0.14	.	0.18	.
Chlaenius tibialis Dejean, 1826	*IN*	0.04	.	0.56	.	3.52	.	0.13	.	0	.
Lionychus quadrillum (Duftschmid, 1812)	*SU*	**15.61*****	**+**	**12.57****	**-**	2.83	.	**15.50*****	**+**	3.03	.
Tachys micros (Fischer Von Waldheim, 1828)	*SU*	**9.18****	**-**	2.91	.	**5.37***	**+**	1.24	.	0.95	.
Tachys parvulus (Duftschmid, 1812)	*SU*	**4.39***	**+**	3.46	.	0.14	.	1.45	.	1.25	.

Similarity in spider and carabid beetle species composition

Similar environmental conditions constrain the species composition of riparian spiders and carabid beetles s.l., with distinct differences for functional groups. The nMDS separates the river banks according to different aspects of flooding disturbance and to the arthropod group, which is elucidated by a different order of the river banks. This is reflected in the species composition since xerothermophilic species separate from species preferring more moist conditions. Remarkably, stenotopic riparian carabid beetles appear on all river banks, whereas riparian spiders clearly separate according to their habitat affinity. Agile pioneers and eurytopic species seem to occur throughout the river system. Studies on a larger spatial scale, i.e. river systems as a whole (Bonn & Kleinwächter, 1999) or comparing different rivers (Bonn et al., 2002; Framenau et al., 2002), confirm the importance of fluvial dynamics affecting spiders and carabid beetles in slightly diverse ways, yet with comparable distribution patterns. On the other hand, Paetzold et al. (2008) proved species richness and abundance of riparian arthropod groups to be divergently affected by anthropogenic flow modification. Overall, flooding relates to heterogeneity in river bank conditions with corresponding effects for the riparian arthropod fauna (Sadler et al., 2004; Van Looy et al., 2005), even on a microhabitat level (Bonn & Kleinwächter, 1999), and differences between species responses can be expected since variation in functional traits affects their distribution patterns (Bonte et al., 2006a; Lambeets et al., 2008b).

Environmental constraints for riparian arthropod species composition s.l.

Local river bank conditions constrain species composition of the inhabiting arthropods in similar ways, but neither topographical features nor the surrounding landscape composition are explanatory. In concordance with other studies (Bonn & Kleinwächter, 1999; Van Looy et al., 2005; Rothenbücher & Schaefer, 2006), flooding disturbance and sediment composition structure spider and carabid beetle assemblages as well as vegetation cover for carabids. Absolute and functional species richness is lower on more disturbed river banks for both groups. Additionally, riparian spider richness is significantly lower on disturbed banks, whereas it is not the case for flight-active carabids. Bonn et al. (2002) argued that spiders along three major German rivers are affected by structural parameters as vegetation architecture rather than habitat quality in se (cf. hydrogeomorphical dynamics). The latter was found to be more important for carabids (Van Looy et al., 2005), but similar patterns in functional group distribution can still prevail (Bonn & Kleinwächter, 1999; Baker et al., 2006). Laeser et al. (2005) and Paetzold et al. (2008) found arthropod abundance and diversity to decrease steeply along channelised river sections that are affected by anthropogenic flow regulation (hydropeaking; Semmerkrot et al., 1997). Since disturbance sets back succession, which results in a complex and highly diverse microhabitat mosaic (Sadler et al., 2004; Wintle & Kirkpatrick, 2007), and intervenes in competitive relations (McCauliffe, 1984), species preferring ephemeral conditions (cf. pioneers) as well as specialised species are favoured (Baker et al., 2006). Therefore, a complete lack of flooding disturbance would prove to be pernicious for typical riparian organisms (Lytle & Poff, 2004; Renöfalt et al., 2005; Paetzold et al., 2008). Even on this small scale, river banks differ in abiotic parameters (see Appendix A4.), with resemblant constraints for arthropod occurrence, hence, indicating the importance of local habitat quality. Therefore, conserving habitat heterogeneity along river systems and restoring natural hydrogeomorphical processes (Ward, 1998; Tockner et al., 2006) is necessary to increase overall riparian biodiversity. Next to it, quantifying response patterns on a more specific (species) level provides purposive information for the rehabilitation of the riparian corridor and future river management (Pedroli et al., 2002). More specifically, our results impart to the use of arthropods as ecological indicators for river health assessment and for evaluating riparian habitat integrity (Van Looy et al., 2005; Paetzold et al., 2008).

Functional constraints for riparian arthropod species composition s.l.

We found tendencies for functional life-history traits to affect species composition of spiders and carabid beetles. Although not significant, we consider them as relevant given the correlation at the community level (Bonte et al., 2006a; Lambeets et al., 2008b). We showed a prominent role for species' dispersal ability (Steinitz et al., 2006) to structure predatory arthropod assemblages. Especially large cursorial spiders (e.g. Lycosidae: *A. cinerea, Pardosa agricola, P. agrestis*) are restrained by a lack of ballooning dispersal (Bonte & Lambeets, unpubl. data), contrary to small flight-active carabid beetles as *Bembidion* species (Bates et al., 2006). Desender (1989a) demonstrated that carabids on more disturbed river banks possess better developed wings than those on stable banks. In that way, species on stable banks might suffer from abrupt flooding caused by hydropeaking, possibly resulting in local extinction events (cf. Jäkäläniemi et al., 2005). Bonn & Kleinwächter (1999) found the relative frequency of macropterous carabids to increase with the proximity to the waterline. Small riparian carabids respond fairly to disturbance by dispersing, thereby increasing their overall fitness (Bates et al., 2006), in contrast to larger species from stable systems (Kotze & O'Hara, 2003). Therefore, large carabids are also considered more sensitive to disturbance. Remarkably, the proportion of cursorial lycosid spiders increased as well, probably benefiting from increased prey-subsidy nearby the waterline (Hering & Plachter, 1997; Briers et al., 2005). Carabid beetles differing in their activity period might colonise banks varying in exposure date and hence depend on a suitable surrounding landscape (Vanbergen et al., 2005; Lake et al., 2007). In concordance with Lambeets et al. (2008b), ecological habitat preferences relate to riparian assemblages in taxon specific ways. Spiders seem to sort according to their moisture preference, whereas geographical rareness was retained to affect carabid species composition. Therefore, moistness and the vegetation cover, which relate to the local disturbance regime, are essential in providing suitable habitat conditions on river banks for a variety of arthropod species (Bonn & Kleinwächter, 1999). Also, sediment composition affects carabid assemblage structure (Eyre et al., 2001; Sadler et al., 2004; Lambeets et al., 2008a). This holds true especially for stenotopic riparian species (Desender et al., 1994; Bates et al., 2007). Interestingly, metallic colouration of carabid beetle elytra is an additional factor affecting their occurrence. Desender (1989a) states that elytra colouration, shiny metallic vs. dull, relates to desiccation tolerance. None the less, unambiguous evidence for this concern is still lacking. Our results demonstrate a tendency of the importance of functional traits at the community level. They confirm earlier studies (Alaruikka et al., 2002; Framenau et al., 2002; Bonte et al., 2004b) stressing the importance of habitat specialisation and dispersal ability in structuring arthropod assemblages. In general, we here highlight the importance of understanding both environmental and functional constraints in conservation research, especially when these functional traits are directly related to species' vulnerability (Bonte et al., 2006a).

Idiosyncratic ecological needs of stenotopic riparian arthropods s.s.

Both hygrophilic and riparian species are relatively well presented along the Common Meuse, often locally, and have been shown to reflect changes in hydrogeomorphical dynamics closely (Desender, 1989a; Geilen et al., 2004). Yet, habitat specialists tend to disappear or are replaced during detrimental circumstances (Lambeets et al., 2008b). Small stenotopic carabids, e.g. *B. atrocaeruleum,* are able to (re)colonise river banks quickly after flooding as their dispersal is triggered by the timing of flood events, local habitat quality and the interspersion of river banks (Bates et al., 2006). As this species is indicative for less disturbed gravel bars (Van Looy et al., 2005), it tends to disappear on highly unstable loamy banks with an extensive silt layer. Therefore, anthropogenic flood modification, especially low flows or hydropeaking during spring and summer, predominantly restrict riparian carabid occurrence. Paetzold et al. (2008) stressed that the interstitial holes that result from erosion and sediment deposition during flooding, which are used by arthropods as refuges during inundations, are silted up during low flows by fine-grained deposits. Among others, the rare psammophilic lycosid *A. cinerea* is known to use interstitial burrows as a refuge (Framenau et al., 1996). Also the salticid *H. auratus* and the linyphiid *C. saxetorum* prefer dry sandy substrates interspersed with refuges (Harvey et al., 2002). Consequently, these spiders tend to decline with increasing flooding disturbance. The same arguments account for *L. quadrillum* and *T. parvulus*, both xerothermophilic carabids occurring mainly on sandy soils. These circumstances are met on higher river banks, less susceptible to spring-flooding. Although hygrophilic species richness was lowest on disturbed river banks, the macropterous *A. afrum* was favoured by flooding; it prefers frequently disturbed habitats and a water-saturated, muddy underground (Turin, 2000). Remarkably, the lycosid *P. agricola*, the linyphiid *Baryphyma pratense* and the carabids *B. decorum* and *Chlaenius tibialis* were not confounded by any of the environmental conditions. Albert & Albert (1976) already suggested that other conditions, such as suitable hibernation sites nearby, affect the distribution of *P. agricola*. Petersen (1999) indicated seasonal migration of a common *Bembidion* species to depend on the nearby habitat, whereas Rothenbücher & Schaefer (2006) stressed the general importance of adequate overwintering sites for floodplain arthropods. Furthermore, the presence of carabids typically restricted to the surrounding alluvial area on river banks, e.g. *Philorhizus sigma* (Rossi, 1790), *Carabus auratus* Linnaeus, 1761, indicates the input from accidental or vagrant species (Sadler et al., 2004). Allowing for overbank flooding to take place, thereby creating sandy patches with an open vegetation cover, will decrease matrix hostility for rare cursorial species by creating small-scale open, ephemeral conditions. In that opinion, the re-establishment of, for instance, erosion channels (Lambeets & Struyve, 2007), will prove valuable for conservation purposes and the conservation of riparian biodiversity. These patches might prove valuable colonisation gaps for typical riparian plants as well (Hölzel, 2005; Wintle & Kirkpatrick, 2007). In general, changes in lateral and longitudinal connectivity may affect species differently according to their habitat preferences and the spatial scale of study (Dauber et al., 2005; Schmidt et al., 2005; 2008) or the degree of habitat specialisation (Jonsen & Fahrig, 1997, Henle et al., 2004). To account for viable and persistent populations of low dispersive target species, restoring cursorial connectivity by establishing sustainable river bank corridors appears urgent to prevent extinctions resulting from hampered upstream dispersal (Collinge et al., 2001; Lambeets et al., 2007). Yet, this may not hold for riparian plants (Imbert & Lefèvre, 2003; Jacquemyn et al., 2006) or other flight-active arthropods (MacNeale et al., 2005).

Implications for riparian arthropod conservation and river management

Lowland river banks are threatened habitats world-wide (ECE - River Convention, 1992) and their associated arthropod fauna is of high conservation value (Sadler et al., 2004). Obviously, less dynamic as well as disturbed lowland river banks along the Common Meuse contain typical species that elsewhere would be lost (see Appendix A5. for total species densities). Yet, river banks with a high flood impact were the least species rich and harboured less riparian species. Our study indicates that rare river bank-inhabiting arthropods can be preserved if river restoration and rehabilitation of the riparian corridor increase habitat heterogeneity, especially of the river banks itself (e.g. sediment composition, vegetation structure). Habitat heterogeneity has already proven to be highest at intermediate disturbance rates (Wintle & Kirkpatrick, 2007) and stenotopic riparian species tend to disappear at either high or low flooding disturbance rates (Rothenbücher & Schaefer, 2006). Therefore, the restoration of natural hydrogeomorphical processes is essential to maximise the biodiversity of riparian habitats in general (Ward et al., 1999). The human impact on riverine water discharge regimes, such as hydropeaking and prolonged low flows or large-scale embankments, disadvantages riparian arthropods (Paetzold et al., 2008) as well as the riverine biota (Semmerkrot et al., 1997; Suren & Jowett, 2006). Anthropogenic fluctuations in discharge regimes should be minimised as they counteract natural hydrogeomorphical dynamics (Geilen et al., 2004; Arthington et al., 2006; Stromberg et al., 2007) and negatively affect connectivity (Ward et al., 2002), factors to which riparian specialists are adapted (Lytle & Poff, 2004; Bates et al., 2006). Additionally, an increased heterogeneity will enhance functional and response diversity and consequently benefit the resilience of riparian species and the riverine ecosystem as a whole (Groffman et al., 2006). Therefore, river management and policy making should take species specific ecological requirements into consideration when (re)defining river restoration objectives (Arthington et al., 2006; Lake et al., 2007). In that way, the persistence of vulnerable riparian species and biodiversity in general will be sustained, and rehabilitation of the ecological river integrity in the long term is possible (Poff et al., 1997; Pedroli et al., 2002).

We stress the importance of considering faunal patterns on hierarchical scales (Lake et al., 2007) and across taxa. Spiders and carabid beetles provide different but additional information on the ecological integrity of riverine ecosystems as demonstrated also by Bonn et al. (2002) for floodplains along three major German rivers or Paetzold et al. (2008) for braided Alpine rivers. Patterns, however, may differ according to the specific characteristics of the system (e.g. altitude) and according to its geographical location (Framenau et al., 2002). The success of river restoration for riparian arthropods might also depend on the lateral and longitudinal connectivity of the river system (Bates et al., 2006). A less hostile transversal connection, with the hinterland acting as a species source, contributes to overall species richness and functionality (Renöfält et al., 2005; Lake et al., 2007), whereas restoring corridor connectivity enables species exchange and (re)colonisation of suitable patches upstream (Jäkäläniemi et al., 2005). However, to sustain the persistence of riparian arthropods, ecological rehabilitation should focus on the enlargement of riparian habitat patches, thus increasing habitat heterogeneity (Báldi, 2008), prior to optimising habitat connectivity (Geilen et al., 2004).

As enunciated by the Living River Concept (Pedroli et al., 2002; Palmer et al., 2005), our results suggest a more dynamic point-of-view for the restoration of lowland rivers and their riparian ecotone to benefit stenotopic riparian species. River management should be based on sound ecological principles and an understanding of the impact of hydrogeomorphic processes on multiple species (Tockner et al., 2006; Jensen et al., 2006). In general, river integrity will increase by creating a cohesive network of riverine and riparian habitats functionally connected to the alluvial hinterland, and allowing for dynamic processes to take place (Buijse et al., 2002; Pedroli et al., 2002; Geilen et al., 2004). Future river management should not only consider river channel qualities as for in-stream biota (e.g. Suren & Jowett, 2006), but also account for environmental constraints affecting the vulnerable arthropod fauna from the riparian transition zone. River restoration should, therefore, focus on restoring natural discharge regimes as they are crucial for preserving habitat heterogeneity and consequently supporting rare riparian arthropods.

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Authors' contributions

KL sampled the river banks, gathered environmental data, performed the analyses and drafted the manuscript. KL and DB conceptualised the research questions, interpreted and discussed the results. MLV identified the carabid beetles and skimmed the manuscript for writing errors. JPM discussed the interpretation and presentation, and was involved in the final preparation of the manuscript. All authors read and approved the final draft.

Supplementary Material

Appendix A4. - Pairwise differences of environmental conditions between river bank clusters: water flow rate, water rising speed, composition of the in-between sediment fraction, extent of the silt cover and average vegetation cover.

Appendix A5. - Total numbers of individuals caught (species densities) of riparian species on the river banks along the Common Meuse.

III. Movement behaviour of riparian arthropods

Males of *Pardosa agricola* (Thorell, 1856) and *P. amentata* (Clerck, 1757), the most abundant wolf spiders along the Common Meuse (Photo: Dries Bonte & August Verbruggen)

III.1. Do riparian arthropods proactively evade annual flooding by seasonal migration?

Lambeets K. & Bonte D. Subm. Freshwater Biology

The river bank at Elerweert during late summer (Photo: Hans de Wandeler)

Summary

1. Organisms that inhabit (ir)regularly disturbed environments benefit from evading seasonal changes in habitat quality by migration. The riparian transition zone along lowland rivers shows unpredictable floods in spring and summer but also regularly occurring (annual) long-lasting inundations from autumn till winter. Organisms that inhabit these river banks are expected to show adaptive responses to both, yet migratory responses may only be synchronised with respect to floods in autumn.
2. We tested the prediction that riparian arthropods show proactive flood avoidance strategies by means of an intensive pitfall survey on a river bank along a rain-fed gravel river, the Common Meuse (Belgium).
3. Stenotopic riparian, cursorial spiders clearly evaded the annual flood in autumn before the river bank completely inundated, a strategy which might be attributed to flood avoidance. In contrast, the river bank acted as sink for eurytopic (pioneer) spiders as they end-up in the riparian zone during slightly windy days in autumn which provide ideal weather conditions for ballooning or rappelling (passive, uncontrolled flight). Flight-active riparian carabids did not show any pattern of proactive avoidance in pitfall traps and are therefore hypothesised to evacuate the river bank habitat by flight once flooding sets in.
4. Proactive seasonal migration towards higher and non-flooded winter habitats (i.e. brushwood vegetation and litter hovels alongside the river banks), is only observed for larger, cursorial riparian spiders. Therefore, they might be more sensitive to anthropogenic changes in water discharge than more mobile, flight-active arthropods. The conservation and rehabilitation of riparian habitats should therefore not be decoupled from an optimal management of the alluvial hinterland.

Key-words: Araneae, Carabidae, hibernation, lowland river, migratory behaviour, movement mode

Introduction

Migration has evolved as a specialised strategy to maximise fitness, that is, to secure optimal environmental conditions at all times. Consequently, it allows organisms to exploit different habitats in different ontogenetic stages or habitats that change seasonally, successionally, or as a result of resource depletion. Its onset, frequency and extent depend, however, on multiple factors (Dingle, 1986). As for dispersal (Bowler & Benton, 2005), migratory strategies differ between species because they differ in geographical distribution, but also because each species is characterised by its specific evolutionary background that shapes ecological, morphological and physiological traits which are essential for repetitive long-distance movements between e.g. foraging and breeding grounds. Nonetheless migration often involves distant “round-trips”, for short-lived species short-distance or one-way movements actually concern migratory movements (Dingle, 1986). Generally, individuals use information from the environment, which may also trigger physiological (internal) mechanisms, as an embarkation for migration. These cues often relate to photoperiod, temperature or even chemical cues in case of seasonal movements between different habitat types (Adis & Junk, 2002; Ward et al., 1998; Alerstam et al., 2003; Pulido 2007).

Movement patterns of flight-active arthropods have been studied quite extensively during the past decade (Thomas, 2000; Schtickzelle & Baguette, 2003; Chapman et al., 2005; Matter et al., 2005; Brattström et al., 2008). For these insects, long-distance movements (migration) merely serve to meet their habitat requirements or avoid (seasonally) unsuitable conditions. Habitat shifts of species with a passive, uncontrolled flight (Topping & Sunderland, 1998; Bonte et al., 2004b; 2006b; Schmidt & Tscharntke, 2005b) or cursorial species (Petersen, 1999; Bonte et al., 2000; 2003a; 2004a) have also received substantial attention. For the latter, however, migration involves much larger risks of ending up in unsuitable habitat (Bonte et al., 2003c; 2008b) and limited time windows for dispersal are hypothesised to synchronise mass dispersal events (Bell et al., 2005). Especially species that inhabit regularly disturbed environments such as arable fields (Petersen, 1999; Samu & Szinetár, 2002; Schmidt & Tscharntke, 2005b; Öberg et al., 2008), tidal zones (Pétillon et al., 2004; Kraus & Morse, 2005) or river banks (Irmler, 1979; Framenau et al., 1996; Lang & Pütz, 1999; Bates et al., 2006) will benefit from evading their habitat before it becomes unsuitable due to e.g. crop harvesting or inundations.

Adis & Junk (2002) and Lytle & Poff (2004) discuss how behavioural, morphological and physiological adaptations may benefit riparian organisms in relation to the (un)predictable character (cf. flooding disturbance) of riverine landscapes. Short-term flooding events during peak waters cannot be predicted and many arthropods withstand this disturbance by distinct behavioural and physiological adaptations like retreating into caveats combined with inundation tolerance (Ward et al., 1998; Plum, 2005; Rothenbücher & Schaefer, 2006; Lambeets et al., 2008c). In contrast, it is unlikely that terrestrial arthropods can withstand long-term winter-flooding (Zulka, 1994; Decleer, 2003). However, these annually returning events can be predicted and more synchronised, hence proactive flood avoidance strategies are expected. Seasonal evacuations of the river bank towards higher and non-flooded winter habitats, such as the dense brushwood vegetation and litter hovels alongside the river banks (Lang & Pütz, 1999; Loeser et al., 2006; Baker et al., 2006) are already shown to benefit riparian species persistence. Seasonal migration of riparian arthropods towards hibernation habitat mostly occurs shortly before flooding (Adis & Junk, 2002) and hence offers the opportunity for direct reimmigration after the flooding water seizes (Weigmann &Wohlgemuth-von Reiche, 1999; Hering et al., 2004; Rothenbücher & Schaefer, 2006). Both changes in multi-habitat availability (Van Looy et al., 2005; Laeser et al., 2005; Lambeets et al., 2008a; 2009) and extremely modified inundation regimes (Semmerkrot et al., 1997) may hypothecate the persistence of riparian arthropods. However, to our knowledge, the extent to which riparian species of various mobility and river bank specialisation differ in their temporal distribution and along a flooded river bank has not been tested before (but see Bonn (2000) for differentiation in flight activity of riparian carabids from spring until autumn).

According to Adis & Junk (2002), long-lasting seasonal floods, and not general winter conditions, are considered as the proximate factors inducing (seasonal) habitat shifts (see also Lang & Pütz, 1999). Consequently, we would expect stenotopic riparian species to show this proactive migratory behaviour, in contrast to more eurytopic species. Moreover, arthropods with well-developed active flight as carabid beetles are capable of exploiting the mosaic of temporary habitat patches, typical for riparian habitats (e.g. Chapman et al., 2005). Therefore, riparian carabids can easily escape flooding (Zulka, 1994; Bonn, 2000; Bates et al., 2006) and are expected to profit maximally from thermal conditions and the prey abundance on river banks (Paetzold et al., 2005; Kleinwächter & Bürkel, 2008). Consequently, no proactive migration is expected in arthropods that possess the ability for the onset of long-distance movements when conditions deteriorate due to e.g. rising water levels. Therefore, we tested the hypothesis that proactive retreating movements (further referred to as seasonal migration) of dominant riparian, terrestrial arthropods will differ between species, and especially between different functional groups. We surveyed terrestrial migration movement during late summer and autumn on an annually winter-flooded river bank by means of an intensive sampling campaign. This study took place at a river bank along the Common Meuse (Belgium). River banks from this lowland gravel river are inundated both by irregular floods in spring and early summer and a long-lasting flood that lasts from autumn until next years' early spring (Van Looy & De Blust, 1995; van den Berg et al., 2000). More specifically, we predict proactive migration in those arthropods that depend entirely on river banks for their occurrence but are not able to move large distances instantly when flooding takes place (here stenotopic, larger spiders), while not so in eurytopic (spiders and carabid beetles) and flight-active arthropods (stenotopic riparian carabids).

Material and Methods

Experimental set-up

From 23-08-2005 until 13-12-2005 a river bank along the Common Meuse, a semi-natural lowland river reach forming the geographical border between Flanders (Belgium) and the Netherlands, was sampled by means of a 12 x 4 pitfall screen. Generally, river banks along the Common Meuse are highly isolated and situated at the foot of steep embankments which consist of large stone boulders or concrete slabs with a loamy or clayey in-between sediment fraction (Van Looy & De Blust, 1995). The river bank under study (Area: 15.9 m^2) is regularly disturbed during spring and early summer. It is typified by a well-developed vegetation cover upon a gravel fraction of intermediate size with an in-between sand-loam fraction covered with an extensive silt-layer (see Lambeets et al., 2007). The direct surrounding consists of yearly-mown and fertilised alluvial meadows (Lambeets et al., 2008a). All pitfall traps (Ø 9 cm; 6% formaline solution; emptied weekly) were arranged in twelve parallel rows and four perpendicular columns covering a shoreline - river dike gradient (see Fig. I.4: from (2) until (5)), and stages in vegetation succession from bare gravel towards dense brushwood vegetation, respectively (Peters et al., 2000). The first ten pitfalls rows covered the river bank itself, whereas the last two rows were situated at the dike just next to a yearly-mown meadow dominated by *Lolium perenne* and *Arrhenatherum elatius*. As the sampling took place after the main growing period of most plants typical for lowland river banks along the Common Meuse (e.g. *Rorippa sylvestris, Lythrum salicaria, Artemesia vulgaris, Polygonum aviculare, Xanthium orientale*; Peters et al., 2000), the vegetation cover gradient barely altered throughout the sampling period. However, the mean vegetation cover along the gradient (based on digital photographs covering 1 m^2 around each pitfall taken in November) significantly increased towards the dike, i.e. from 17.5% nearby the waterline to 99% at the dike ($r = 0.97$; $F_{11,33} = 10.59$, $p < 0.0001$). Moreover, vegetation cover at the river bank level in se was significantly lower than the brushwood cover at the loamy dike (bank: 50.4% +/- 4.6SE, dike: 96.9% +/- 10.4SE; $F_{1,43} = 17.04$, $p = 0.0002$). Therefore, the gradient which is covered by the pitfalls also corresponds to a gradient in vegetation cover. Pitfalls were spaced widely apart in order to avoid interference between the traps and hence pseudo-replication (Topping & Sunderland, 1992). During the last week (week 17), the water level reached up to the dike foot, inundating all pitfall traps on the river bank. We only analysed the most common species found along the river bank: *Pardosa agricola* (Thorell, 1856), *P. amentata* (Clerck, 1757), *Trochosa ruricola* (De Geer, 1778) and *Centromerita bicolor* (Blackwall, 1833) which are cursorial spiders, not capable of performing ballooning dispersal during autumn (group 1), *Oedothorax apicatus* (Blackwall, 1850), *O. fuscus* (Blackwall, 1834), *O. retusus* (Westring, 1851) and *Troxochrus scabriculus* (Westring, 1851) which are small-sized (agrobiont) spider species with a well-developed ballooning dispersal capacity (group 2), and *Amara bifrons* (Gyllenhal, 1810), *A. eurynota* (Panzer, 1797), *Bembidion femoratum* (Sturm, 1825), *B. tetracolum* (Say, 1823), *Nebria brevicollis* (Fabricius, 1792) and *Ophonus puncticeps* (Stephens, 1828), macropterous (i.e. with well developed flight muscles and wings) carabid beetles (group 3). Only *P. agricola*, *T. scabriculus* and *O. puncticeps* can be regarded as riparian specialists (Turin, 2000; Harvey et al., 2002).

In order to analyse shifts in species abundance, we standardised to total numbers for each species during each week (n = 16) per pitfall column (n = 4). We further refer to these numbers as "relative abundance". It is important to recognise that pitfall sampling has some inherent biases, and catches can be affected by factors including habitat structure, weather conditions and the preservative used (Topping & Sunderland, 2002). In this study, standardised pitfall trapping, however, is considered appropriate as we aimed to unravel species-specific temporal habitat shifts along a unilateral gradient.

Statistical analysis

We tested if relative abundances of spiders and carabid beetles in- or decreased with date of sampling and according to the distance on the river bank from the dike (pitfall row). Standardised sampling data were analysed by generalised linear mixed models for binomial data (GLMM with logit link, SAS 9.1). Corrected degrees of freedom were approximated by the Satterthwaite procedure (Verbeke & Molenberghs, 2000). Pitfall column (the replica) and its interactions with row and date were modelled through random effects because they consist of interdependent data (trapping data are standardised per column - see higher). Because plausible autocorrelation between our samples is exogenous, i.e. rather resulting from spatially structured environmental factors, traditional, non-spatial statistics are believed to describe the relationship between species density along the gradient in time (pitfall row x sample date) perfectly well (Currie, 2007).

We first tested interactions between species (nested within functional groups) and functional groups with date and row (distance from dike). Because species from different functional groups behaved differently (see results), we decided to present statistics (i.e. relative abundance tested against date, row and the interaction row x date) for all species.

(a)

	species	*P. agricola*	*P. amentata*	*T. ruricola*	*C. bicolor*	*O. apicatus*	*O. fuscus*	*O. retusus*	*T. scabriculus*
	functional group	[1] ripa	[1]	[1]	[1]	[2]	[2]	[2]	[2] ripa
parameter	**numbers caught**	***7,386***	***698***	***745***	***687***	***764***	***1,436***	***3,832***	***870***
*pfrow*date*	F-value	10.10	6.29	0.31	5.29	7.96	0.03	14.20	0.97
	p-value	0.0015	0.0123	0.5783	0.0219	0.0049	0.8620	0.0002	0.3250
pfrow	F-value	129.72	28.59	0.37	0.23	39.37	51.27	41.82	102.69
	p-value	<.0001	<.0001	0.5432	0.6300	<.0001	<.0001	<.0001	<.0001
date	F-value	7.14	5.53	0.00	5.13	7.14	0.00	11.79	0.00
	p-value	0.0077	0.0190	1.0000	0.0240	0.0077	1.0000	0.0060	1.0000

(b)

	species	*A. bifrons*	*A. eurynota*	*B. femoratum*	*B. tetracolum*	*N. brevicollis*	*O. puncticeps*
	functional group	[3]	[3]	[3]	[3]	[3]	[3] ripa
parameter	**numbers caught**	***2,479***	***646***	***1,181***	***598***	***889***	***601***
*pfrow*date*	F-value	4.46	40.95	2.02	0.75	1.88	0.00
	p-value	0.0351	<.0001	0.1554	0.3870	0.1714	0.9582
pfrow	F-value	18.83	0.30	121.19	0.00	68.05	0.00
	p-value	<.0001	0.5846	<.0001	1.0000	<.0001	1.0000
date	F-value	3.24	25.71	0.02	95.26	0.00	3.40
	p-value	0.0724	<.0001	0.8829	<.0001	1.0000	0.0661

Table III.1 - Fit statistics of generalised linear mixed models (GLMM) for seasonal shifts in relative abundances during late summer and autumn of (a) spiders (Araneae) and (b) carabid beetles (Carabidae) on a lowland river bank. Legend: pfrow = pitfall row with the lowest value for traps nearby the waterline, increasing towards the dike; date = sample date, covering 16 weeks between the end of August and mid-December. Functional grouping: [1] cursorial spiders not capable of ballooning in autumn – [2] small-sized spiders with well-developed ballooning capacity – [3] macropterous (flight-active) carabid beetles; "ripa" indicates it concerns a stenotopic riparian species.

Results

In total 19,327 spiders and 11,046 carabid beetles were caught, representing 72 and 71 species, respectively. From these captures, the studied spider species (see above) made up 84.9% (16,418 individuals), contrary to 57.9% (6,394) for the carabids. Total numbers caught per species and per sample period are presented in Fig. III.1. Moreover, not all species were caught from the first week of sampling onwards (see Fig. III.2).

Migration behaviour differs significantly between the three delineated functional groups (group*row*date: $F_{2,8907} = 55.38$, $p < 0.0001$). This effect is caused by shifts in relative abundance in riparian species from group 1 (cursorial spiders). Within functional groups, changes in relative abundances in relation to distance from the river bank shoreline (pitfall row) and sample date are similar for the different species (species[group]*date*row: $F_{13,8830} = 0.05$, $p = 1.000$). Below, we only present those spider and carabid species that showed a significant relation with either date of sampling and/or the distance from the waterline. All further test-statistics are presented in Table III.1a (Araneae) and Table III.1b (Carabidae) for the ease of reading.

Within the group of riparian spiders, relative abundances of the cursorial wolf spider *Pardosa agricola* (Fig. III.2a) are higher nearby the waterline in the beginning of the sampling and decreases towards the dike, but this pattern switches as time progresses with higher relative abundances towards the dike. Relative abundance of *P. amentata* and *Centromerita bicolor* shift in the same way, but both are more common near the dike during the entire period (*P. amentata*; Fig. III.2b) or from the sixth week onwards (*C. bicolor*; Fig. III.2c). *Trochosa ruricola* showed the same pattern as the latter species, but changes in relative abundance are not significant.

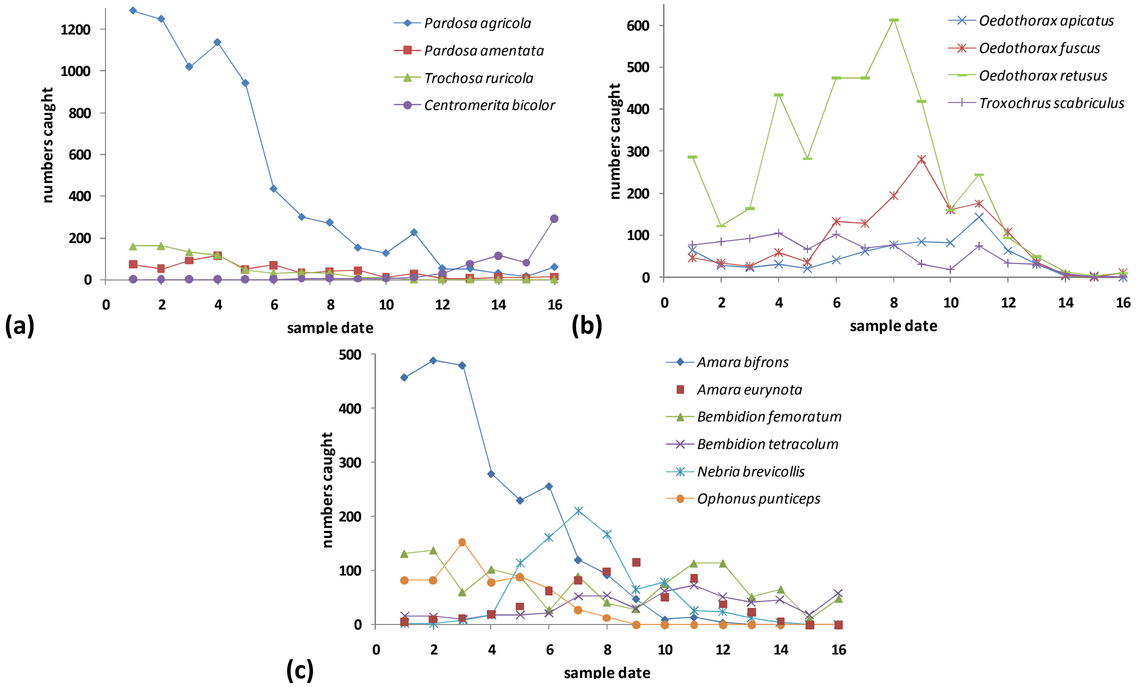

Fig. III.1 – Total numbers of predatory arthropods caught on a lowland river bank along the Common Meuse in function of the sampled period (sample date). Figures are presented per functional group (see Table III.1): (a) cursorial spiders not capable of ballooning in autumn [1], (b) small-sized spiders with well-developed ballooning capacity [2], (c) macropterous carabid beetles [3]; *Pardosa agricola, Troxochrus scabriculus* and *Oedothorax punticeps* concern stenotopic riparian species.

Eurytopic, agrobiont species do not show clear shifts in relative abundance in relation to the oncoming flood. For both *Oedothorax apicatus* (Fig. III.2e) and *O. retusus* (Fig. III.2f) relative abundances were higher towards the dike foot throughout the sampling period. For both linyphiids, however, a slight increase at the waterline is noticeable at the end of the sampling. This pattern is more pronounced for *O. retusus*. Additionally, *O. fuscus* and *Troxochrus scabriculus* did not show any shifts along the gradient between the waterline and the dike. Their relative abundances were always higher nearby the dike (Fig. III.2d).

As for eurytopic spiders, we did not find any evidence for proactive seasonal migration in carabid beetles. *Amara bifrons* (Fig. III.3a) and *A. eurynota* (Fig. III.3b) showed generally higher relative abundances closer to the waterline, even increasingly later in the season. Comparably, the relative abundance of *Bembidion femoratum* was highest at all times closer to the waterline. Relative abundances remained higher towards the dike at all times for *B. tetracolum*, *Nebria brevicollis* and *Ophonus puncticeps* (Fig. III.3c).

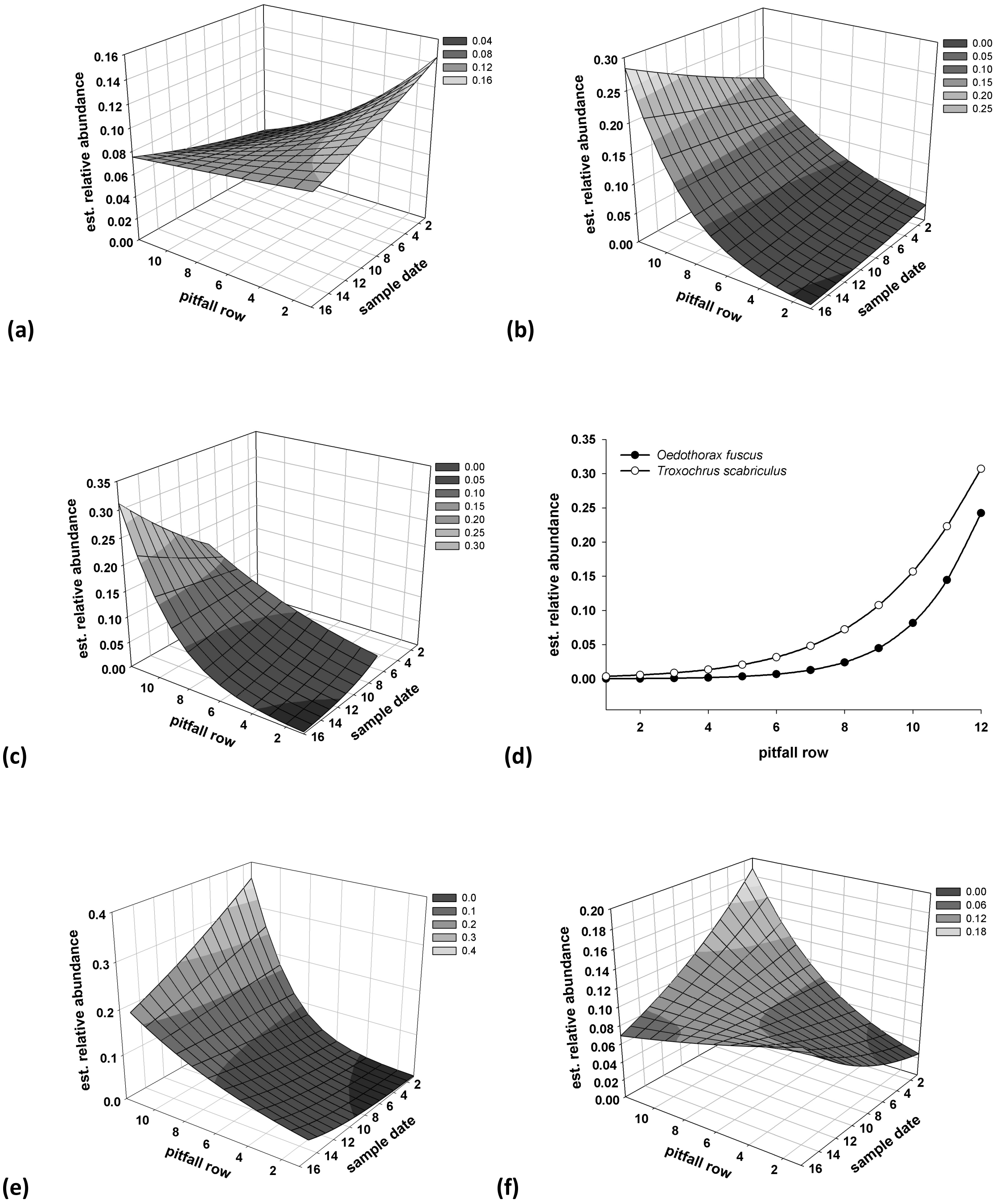

Fig. III.2 - Estimated relative abundances, based on pitfall captures, for spiders (Araneae) during autumn (August-December) on a lowland river bank. Pitfall row values increase from the dynamic area nearby the waterline to the densely vegetated river dike. Each sample date corresponds to one week. Wolf spiders (Lycosidae): (a) *Pardosa agricola* [1] ripa, (b) *P. amentata* [1] and dwarf spiders (Linyphiidae): (c) *Centromerita bicolor* [1], (d) *Troxochrus scabriculus* [2] ripa and *Oedothorax fuscus* [2], (e) *O. apicatus* [2], (f) *O. retusus* [2]. Fit statistics and functional grouping are presented in Table III.1a.

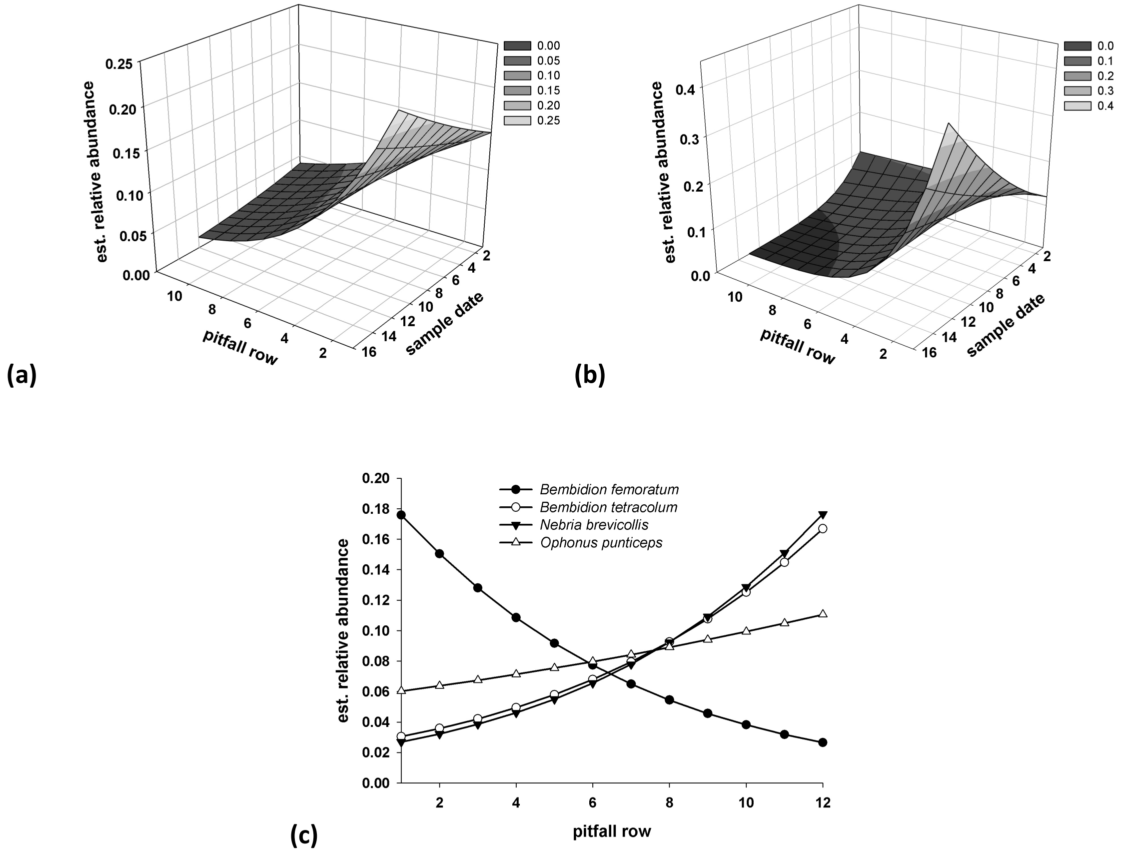

Fig. III.3 - Estimated relative abundances, based on pitfall captures, for carabid beetles (Carabidae) during autumn (August-December) on a lowland river bank. Pitfall row values increase from the dynamic area nearby the waterline to the densely vegetated river dike. Each sample date corresponds to one week. (a) *Amara bifrons* [3], (b) *A. eurynota* [3], (c) *Bembidion femoratum* [3], *B. tetracolum* [3], *Nebria brevicollis* [3] and *Ophonus puncticeps* [3] ripa. Fit statistics and functional grouping are presented in Table III.1b.

Discussion

Based on an intensive field survey, we show that larger, cursorial riparian spiders migrate towards dike vegetation before the onset of long-lasting flooding in winter. This contrasts with patterns for small-sized eurytopic spiders and carabid beetles. For eurytopic agrobiont spiders, flooding is expected to be detrimental because movement entirely depends on aerial dispersal (either ballooning or rappelling). Carabid beetles are hypothesised to profit maximally from environmental conditions on gravel banks because they are able to respond quickly (active flight) when the bank is flooded (Bonn, 2000; Bates et al., 2006; Rothenbücher & Schaefer, 2006).

In lowland river banks flooding and temperature fluctuations result in a distinct zoning of vegetation patterns (Nilsson et al., 1989; Pollock et al., 1998; Burkart, 2001; van Eck et al., 2004) and animal distributions (Antvogel & Bonn, 2001; Bonn & Kleinwächter, 2002; Van Looy et al., 2005). In contrast to unpredictable spring and summer-floods, annual winter floods last for several months (Van Looy & De Blust, 1995). The majority of terrestrial arthropods are not able to withstand long-lasting flooding (i.e. more than three months for most of the river banks) and need to avoid this severely stressful situation (Zulka, 1994; Lang & Pütz, 1999; Decleer, 2003). Because the ability to cope with these flooding stress inevitably depends on the organisms' functional traits (DeVito et al., 2004; Rothenbücher & Schaefer, 2006; Lambeets et al., 2008b; 2009), different seasonal migration strategies were expected according to (i) the species' affinity to river bank habitats and (ii) their movement mode (Lang & Pütz, 1999; Bates et al., 2006; Lambeets et al., 2008c).

Because river banks along the Common Meuse are situated within an agricultural matrix, riparian species are expected to spend their entire life on the river banks. However, only *Pardosa agricola*, *Troxochrus scabriculus* and *Ophonus puncticeps* can be considered truly stenotopic species of riverine habitats. Although proactive seasonal migration patterns are clear for all cursorial riparian spider species, only *P. agricola* showed a clear shift in abundance from the waterline in early autumn towards the dike in winter. The other species (*P. amentata* and *Centromerita bicolor*) always occurred prominently near the dike vegetation (because of covariation with vegetation structure and litter deposition), but decreased in relative abundance from the bank in a similar way as *P. agricola*. While the obvious pattern in the latter can almost certainly be attributed to a strategy of flood avoidance (Albert & Albert, 1976; Framenau et al., 1996), it may be less clear for the more eurytopic riparian spiders. As shown for other *Pardosa*-species (Edgar, 1971; Bonte et al., 2001; Kraus & Morse, 2005), a retreat towards the dike may equally be a strategy of hibernation and therefore independent of flood-avoiding behaviour. Because seasonal migration towards hibernation habitats occurs before flooding, changes in temperature, precipitation or day-length are expected to be the cue for the onset of this migration event (Petersen, 1999; Bonn, 2000). Alternatively, motivation for seasonal habitat shifts might be cued by changes in prey availability as well. However, this would rather be expected in food-limited habitats (Harwood et al., 2001) rather than in prey-rich riparian ecotones (Wenninger & Fagan, 2000; Paetzold et al., 2005) or woodland habitats (Edgar, 1971).

Agrobiont spider species that possess well-developed ballooning capacities (*Oedothorax*, *Erigone*-species) show different temporal distribution patterns. Studies concerning crop-field and adjacent perennial habitats (Schmidt & Tscharntke, 2005b; Öberg et al., 2008) also demonstrated the importance of seasonal migration strategies for crop colonisation out of suitable overwintering sites (i.e. non-crop habitat). In our study, these species slightly increase alongside the waterline in late summer and even decrease nearby the river dike. This indicates the absence of any proactive retreating but instead an increased colonisation during the late summer and autumn. Indeed, warm, slightly windy days during autumn provide ideal weather conditions for ballooning, and induce mass ballooning events in crop inhabiting spiders (Bell et al., 2005). This aerial dispersal (whether by ballooning or rappelling; Bonte et al., 2008b) enables agrobiont spiders to leave crops before harvesting, but probabilities of landing in unsuitable habitat are equally high because trajectories cannot be controlled (passive, uncontrolled flight; Bonte et al., 2006b). River banks are therefore considered as potential sinks for pioneer species when they are colonised in that season (i.e. due to mortality during flooding; Lang & Pütz, 1999).

Because carabid beetles posses well-developed flight abilities (Chapman et al., 2005), especially under harsh environmental conditions (Desender, 1989a; Zulka, 1994; Bonn & Kleinwächter, 1999), they may gain from residing on the river bank until it is effectively flooded (cf. exploiting its resources; Paetzold et al., 2005; 2006). Xerophilic carabid beetles with a preference for sandy substrates like *Amara bifrons* and *A. eurynota* (Turin, 2000) suspend retreat from river banks, just as the eurytopic, hygrophilic carabid *Bembidion femoratum*. Thereby, unnecessary movement costs are avoided and species may profit maximally from enhanced thermal conditions on the river bank (Zulka, 1994). Lang & Pütz (1999) indicated that carabid beetles also emigrate from flood-prone habitats towards non-inundated sites by cursorial movement. *O. puncticeps*, a xerophilic, alluvial species, however, does not show a distinct seasonal migration and occurs predominantly on vegetated parts of the river bank. This pattern also applies for eurytopic carabid beetles such as *B. tetracolum* and *Nebria brevicollis*. They colonise open-gravel habitat less frequently and do, as a consequence, not show distinct migration patterns along the entire river bank.

Generally, suitable refuges nearby the river bank seem of prime importance alongside semi-natural river stretches to support the persistence of mobile arthropods in winter (Lang & Pütz, 1999; Loeser et al., 2006; Baker et al., 2006). Based on a wide array of riparian arthropods that differ in movement mode and habitat preference, we here provide evidence that different species show distinct shifts in distribution patterns before an annual, long-lasting flood event. These findings highlight that the lateral connectivity between the river bank habitat and inland dike vegetation, and the adjacent hinterland, is essential for the survival of riparian arthropods, especially for those with rather poor-developed movement capacities such as cursorial riparian wolf spiders (Lambeets et al., 2008b; 2009). In order to conserve migration processes, preservation of riparian habitats should not be decoupled from an optimal management of the alluvial hinterland (Buijse et al., 2002; Pedroli et al., 2002; Lake et al., 2007). Evidently, because seasonal migration in riparian spiders occurs before flooding sets in, anthropogenic changes in water discharge (especially higher discharge regimes earlier in the season; Semmerkrot et al., 1997; Paetzold et al., 2008) may disadvantage the persistence of many riparian arthropods.

Acknowledgements

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Authors' contributions

KL obtained the samples, analysed the data and wrote the paper. KL and DB conceptualised the research questions, interpreted the results and discussed the presentation of the results. Both authors have contributed to, seen and approved the manuscript.

III.2. Movement behaviour of riparian wolf spiders as a response to visual stimuli

Lambeets K., Van Ranst J. & Bonte D. In prep.

Female *Pardosa agricola* (Thorell, 1856) on a gravel and sand-loam substrate
(Photo: Rollin Verlinde, Vilda).

Abstract

Orientation necessarily precedes movement behaviour and is controlled by both innate factors and cues obtained from external sensory stimuli (the spatial location of information and/or stress sources), yet can be refined and extended by experience. Particularly in habitats that can suddenly be disturbed (such as river banks), an accurate orientation is of prime importance to ensure persistence. In a field experiment, we studied between-population variation in movement responses towards dike vegetation (winter habitat) of two congeneric and sympatric riparian wolf spiders. Behavioural responses of a stenotopic riparian species *Pardosa agricola* (Thorell 1856) and a generalist *P. amentata* (Clerck 1757), were tested in relation to their location on the river bank (distance from dike vegetation) and under different weather conditions. Two populations of each species from both river sides were tested within a common arena. The stenotopic riparian wolf spider showed movements towards its overwintering habitat in accordance to the location and its natal river bank shore. The responses were additionally dependent on the ambient weather conditions. For *P. amentata*, we also recorded between-population variation, although not in correspondence with its original location along the river. Our results indicate that between-population variation in movement behaviour of wolf spiders is prevalent in relation to habitat affinity. Moreover, factors related to population of origin (either genetics or experience) influence orientation outcomes for the stenotopic species. The generalist shows less between-population variation and results indicate it might be guided mainly by proximate cues. Therefore, the observed movement behaviour is expected to benefit the stenotopic wolf spider in particular by restricting unnecessary movements and efficiently avoiding potentially threatening situations, such as winter flooding, by guiding them towards upland hibernation sites.

Key-words: between-population variation, Lycosidae, orientation behaviour, visual cues

Introduction

Movement behaviour is a key characteristic affecting population dynamics, especially in fragmented landscapes (Zollner & Lima, 1999; 2005; Fahrig, 2007). Foregoing movement decisions and factors affecting movement direction essentially sustain risk-avoidance (Dall et al., 2005). Therefore, a lack of accurate orientation preceding movement can lead an organism into unsuitable conditions (Jander, 1975) or even cause locally perturbed population dynamics (Bonte et al., 2004a).

Innate knowledge related to an individual's geographical origin guides an adequate orientation (Papi & Tongiorgi, 1963; Jander, 1975), yet it might not be adaptive in unfamiliar conditions (cf. Schlaepfer et al., 2002). Therefore, its importance is relative to proximate factors which influence behavioural decisions as well (Bowler & Benton, 2005). Orientation is a movement behaviour based on the spatial location of information and/or stress sources, yet can berefined and extended by learning (Jander, 1975). Learning results from the spatial relationships among objects in the organism's perceptible range and from previous experienced proximate cues (Persons & Uetz, 1996; Giraldeau, 1997). Among these, homeward orientation mechanisms, comparable with unidirectional zonal recovery in intertidal zones (e.g. for sandhoppers: Borgioli et al., 1999b, Ugolini, 2001; wolf spiders: Morse, 2002), are considered as beneficial risk-avoiding strategies. Homeward orientation essentially leads to profitable outcomes in familiar environments, guiding cursorial organisms as wolf spiders directly towards suitable conditions (Morse 1997; 2002). Furthermore, visual cues, either local landmarks (e.g. vegetation structure; Bonte et al., 2004a) or celestial cues, sustain accurate orientation (Jander, 1975). By gathering information from its surroundings, organisms reduce the ecological uncertainty bound to that environment (Wehner, 1997; Dall et al., 2005), eventually leading to movement decisions (Lima & Zollner, 1996; Pulido, 2007). For cursorial spiders in particular, there can be no doubt that perceptible factors are effectively integrated into orientation and movement decisions (Persons, 1999; Norgaard et al., 2007; Rypstra et al., 2007). This perception, however, mainly depends upon their sensory abilities (Land, 1971; Ortega-Escobar & Muñoz-Cuevaz, 1999).

Since consistent (stereotyped) movement behaviour might be disadvantageous (Bowler & Benton, 2005), especially for organisms occurring in unpredictably disturbed environments (Lytle & Poff, 2004), orientation behaviour has to be flexible to some extent (Jander, 1975). Whenever different modalities that guide orientation decisions are opposed (e.g. accustomed cues of the location vs. celestial information), an inaccurate orientation and movement direction might predominate (Papi & Tongiorgi, 1963; Jander, 1975). Therefore, plasticity in orientation or movement will benefit organisms occurring in disturbed environments (Scapini et al., 1988; 2002; Bonte et al., 2007a). Moreover, as lowland river banks are subject to sudden changes due to flooding disturbance, stereotyped responses (low behavioural variability) may not allow individuals to cope with this kind of environmental variation.

As flooding disturbance implies potential fitness costs for shore-inhabiting species by being washed away or drowned, mobile species are expected to show a directed response perpendicular to the rising water level (moving ashore) and even withstand flooding during transient inundation events (Rothenbücher & Schaefer, 2006; Lambeets et al., 2008c). Moreover, preliminary movements towards adjacent upland overwintering sites before the onset of long-lasting winter flooding have been recorded for mobile, predatory arthropods from river bank habitats (Lang & Pütz, 1999; Lambeets & Bonte, subm.a). Earlier results indicated that tactile cues cause a fleeing response in riparian wolf spiders (Lambeets et al., 2008c), whereas accurate (homeward) orientation when ending up on the water mainly depended on their natal origin (Lambeets & Bonte, subm.b), leading individuals directly back to the accustomed river bank. Here, we want to determine whether between-population variation in behavioural responses of riparian wolf spiders also remains under pure visual stimuli when they are tested just before the onset of the long-lasting winter flood. Therefore, orientation behaviour and subsequent movement of two congeneric and sympatric wolf spiders (Araneae; Lycosidae) with a different habitat affinity were studied in the field. *Pardosa agricola* (Thorell, 1856) is considered as a stenotopic riparian species (Harvey et al., 2002) that inhabits unpredictably disturbed (dynamic) river banks throughout the year (Lambeets et al., 2008a). In contrast, *P. amentata* (Clerck, 1757) occurs commonly in a wide range of humid habitats (Alderweireldt & Maelfait, 1988). Thus, the latter is considered to encounter the typical river bank conditions only sporadically once they are exposed because its main habitat are the surrounding humid grasslands. By employing a comparative approach, we discern between the effects of factors related to natal origin (river shore) and visual stimuli (local landmarks related to the experiment location on the river bank, weather conditions). Since *P. agricola* spends its life entirely in spatially structured river banks, it is expected to be familiar with the spatial arrangement of river bank structures; mainly relying on innate information might restrict unnecessary movements. Therefore, visual cues are expected to guide orientation of a stenotopic riparian wolf spider less than of *P. amentata* for which vegetation rather acts as an orientation landmark, leading to suitable habitat accordingly. The latter is, therefore, not expected to move according to the location of winter habitat nor its natal habitat.

Methods

Experimental field set-up

During August 2005 and 2006, before the onset of the long-lasting winter flood (Van Looy & De Blust, 1995), (sub)adult individuals of *Pardosa agricola* and *P. amentata* were collected from four highly isolated river banks in the downstream section of the Common Meuse. This dynamic semi-natural section of the river Meuse is non-impounded and non-navigable, forming the geographical border between Flanders (Belgium) in the West and the Netherlands in the East. Two isolated populations of each species (mean inter-population geographical distance: 2504 m +/- 532SE; mean F_{st} = 0.0291 +/- 0.0076SE (Lambeets et al., in prep.)) were sampled on both river shores and only individuals occurring on the bare gravel were collected. The sampled river banks were always oriented in the same direction, i.e. predominantly eastward for the left shore and westward for the right shore. These river banks were similar with respect to flooding susceptibility (flooded at 179 m^3s^{-1} +/- 13SE), size (area: 10202 m^2 +/- 1940SE) and vegetation structure (see Lambeets et al., 2007). Behavioural differences arising from dissimilar stand conditions may consequently be ruled out (cf. Papi & Syrjämäki, 1963), and therefore between-population differences result from the wolf spiders' geographical (natal) origin and/or experience. All individuals collected were kept in separate plastic vials with a humid plaster bottom and fed *ad libitum* with *Drosophila* *melanogaster* prior to testing (climatic chamber under ambient light conditions and constant temperature, 15°C). Earlier experiments already showed that a short time under controlled conditions did not change behaviour under tactile stimuli (Lambeets & Bonte, subm.b). Within a week, orientation behaviour was tested in a large arena constructed of transparent plexi-glass sides (160*60*25 cm) of which the bottom was covered with a sand-gravel fraction. The arena was placed on an unfamiliar river bank upstream which was structurally the same as the natal river bank habitat (soft slope, bare gravel for >20 m from the waterline onwards), alternately directly along the waterline and the dike (location) which were approximately 40 m apart during the experiments. With it, weather conditions (sunny, overcasted) were recorded. All spiders were tested in groups of ten individuals per population and per species. Per group they were released in the middle of the arena. We scored whether or not individuals were inclined to move ashore, i.e. perpendicular to the waterline or towards the vegetation. Ashore movement was considered as a proxy for unidirectional orientation. For all groups each test was repeated three times for both locations (water, vegetation), yet in a random order to skirt experience (cf. Papi & Tongiorgi, 1963; Persons & Uetz, 1996). If ambient conditions exceeded 30°C the field experiment was stopped because of severe dehydration. In total 28 groups of *P. agricola* and 21 groups of *P. amentata* were tested.

Statistical analysis

We analysed whether orientation behaviour differed according to natal origin (two populations from each river shore), weather conditions, local landmarks (water, vegetation) and their interactions. Repeated tests were treated as a random factor. The binomially scored responses were analysed by generalised linear mixed models with logit-link (GLMM, SAS 9.1). Non-explanatory factors were sequentially removed. Groups were modelled through random effects. Corrected degrees of freedom were calculated by Satterthwait's procedure (Verbeke & Molenberghs, 2000). Post-hoc Tukey tests were applied to reveal significant proportional differences in ashore movement.

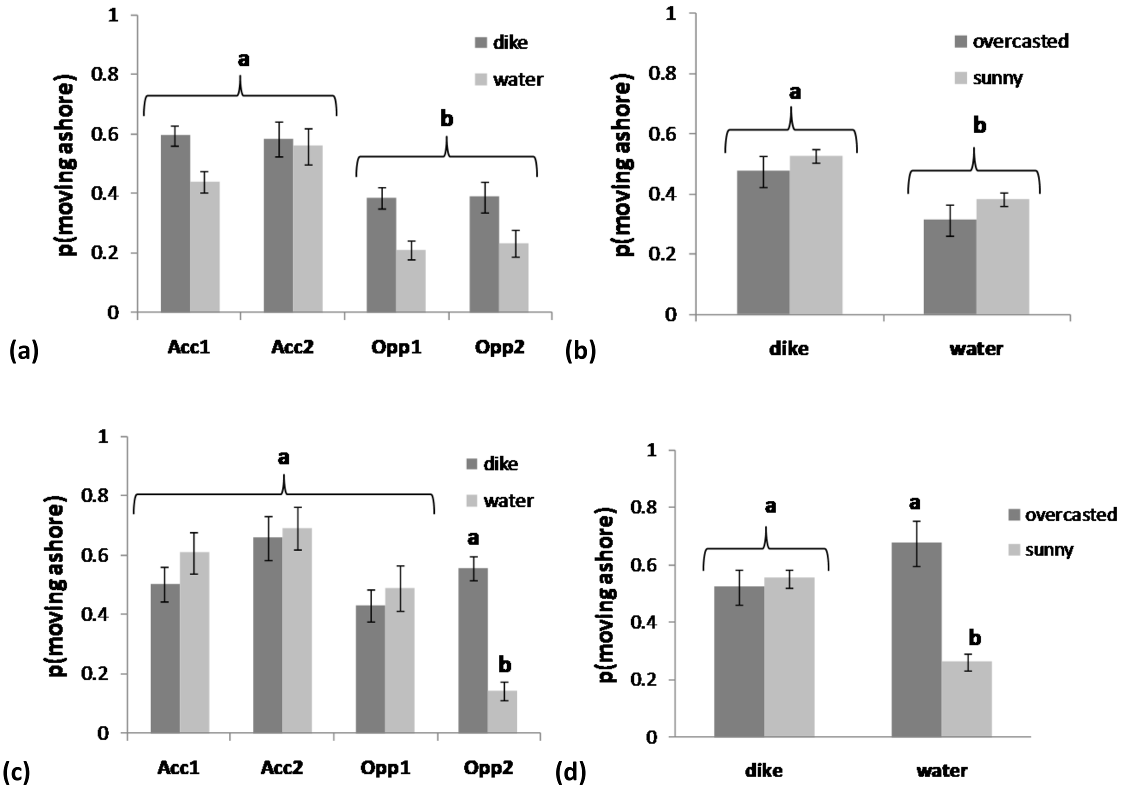

Fig. III.4 - Estimated mean proportions for orientation behaviour of (a,b) the stenotopic riparian wolf spider *Pardosa agricola* and (c,d) the generalist *P. amentata*. Four populations, two from each river shore, were tested during a field experiment, alternately at two locations (waterline, dike-vegetation) and under ambient conditions (sunny, overcasted). Acc1, Acc2 indicate individuals were collected at the same river shore (accustomed) as where they were tested; Opp1, Opp2 point to individuals ascending the opposite shore. Error bars indicate the standard error of the mean. Different letters indicate significant proportional differences in ashore movement after post-hoc Tukey-tests (all $p < 0.001$).

Results

Wolf spiders clearly differed in their orientation behaviour according to their geographical origin, the weather conditions and with respect to the location of testing (location*origin*weather*species: $F_{2,263} = 0.01$, $p = 0.9860$; location*origin*species: $F_{3,263} = 4.94$, $p = 0.0023$; location*weather*species: $F_{1,263} = 7.29$, $p = 0.0074$). Therefore, further analyses were applied for each species separately (Fig. III.4a-d; Table III.2a-b).

Between-population variation in orientation behaviour was clear for *Pardosa agricola*. Individuals appeared to move more ashore when originating from the same river shore population as where tested (i.e. accustomed populations) compared to when originating from the opposite shore (Fig. III.4a; Table III.2a). Moreover, ashore movement increased proportionally when vegetation was perceptible (tests close to the dike) (Fig. III.4b). Behavioural responses of *P. amentata* were more variable. There were no significant differences in ashore movement between the accustomed populations (Fig. III.4c; Table III.2b) or even between populations from different river shores (Opp1 vs. Acc1,2). Moreover, between-population differences only appeared for those *P. amentata* groups originating from the opposite shore (Opp2; Fig. III.4c). Weather conditions did not affect ashore movement differently when tested adjacent to the dike, but did so when tested at the waterline; sunny conditions led to a decreased tendency to move ashore (Fig. III.4d).

(a)

parameter	**NumDF**	**DenDF**	**F-value**	**p-value**
loc*orig*cond	1	149	0.03	0.868
loc*cond	1	150	0	0.9583
orig*cond	1	151	0.01	0.914
loc*orig	3	152	1.52	0.212
cond	1	155	3.29	0.0718
loc	1	156	28.44	<.0001
orig	3	156	22.52	<.0001

(b)

parameter	**NumDF**	**DenDF**	**F-value**	**p-value**
loc*orig*cond	1	114	0	0.9783
orig*cond	1	115	3.87	0.0517
loc*cond	1	116	12.81	0.0005
loc*orig	3	116	7.22	0.0002
loc	1	116	2.08	0.2522
cond	1	116	9.69	0.0023
orig	3	116	9.68	<.0001

Table III.2 - Generalised linear mixed models (GLMM) for wolf spider orientation behaviour during a field experiment: (a) the stenotopic riparian species *Pardosa agricola* and (b) the generalist *P. amentata*. Legend: loc – location of the arena at the river bank (cf. distance from the dike); orig – population of origin (4); cond – weather conditions at the time of testing (sunny, overcasted).

Discussion

Two river bank wolf spiders with a different habitat affinity orientated towards the dike vegetation according to the distance at which they were released and factors related to their natal origin. However, differences between populations from opposite river shores were less distinct for the generalist species. The stenotopic riparian wolf spider showed clear between-population differences in orientation in response to the vegetation landmark, whereas both vegetation and weather conditions affected orientation of the generalist. These data suggest that factors related to natal origin and visual cues (vegetation, waterline) guide orientation and movement behaviour of wolf spiders on river banks.

Factors underlying variability in orientation responses of arthropods in unstable environments have been studied mainly in predictably disturbed intertidal zones (e.g. Scapini et al., 1988; Borgioli et al., 1999a,b; Morse, 2002). Behavioural responses at infrequently disturbed habitats as river banks were subject to earlier studies (Papi & Tongiorgi, 1963; Papi & Syrjämäki, 1963). These studies did merely consider typical riparian species and did not compare behavioural traits between sympatric congeners. A comparative approach, however, elucidates the adaptive value of alleged beneficial responses (Krebs & Davies, 1997; Cézilly et al., 2008). As a risk-avoiding strategy, i.e. evading the rising water level, has an obvious survival value along flood-disturbed shorelines, adjusting movement behaviour in response to predictable (accustomed) or sudden perceptible environmental variation is essentially advantageous (Jander, 1975; Scapini et al., 1999). From this, it is evident that a riparian species, assumed to be adapted to flood events (Lytle & Poff, 2004), would benefit from weighing costs and benefits of movement by integrating various information sources. This is demonstrated here by the orientation behaviour related both to local cues, population of origin and weather conditions. Moreover, movement behaviour can be expected to change over the season or with the life-stage (Papi & Tongiorgi, 1963; Scapini et al., 1999), with orientation being mainly directed towards suitable overwintering sites before the onset of annually reoccurring floods (Lang & Pütz, 1999). Correspondingly, Morse (1997) argued movement of intertidal wolf spiders to increase when occurring nearby the edge of the water, and even more when being splashed by surf. On the other hand, Kraus & Morse (2005) clearly associated seasonal habitat shifts of an intertidal wolf spider to environmental variation.

Between-population variation was noticed for both species, indicating that orientation tendencies coincide with a direction towards river bank vegetation on their natal river shore in the field. This surprisingly led to directional movements away from their preferred habitat when originating from the opposite shore, especially for a stenotopic riparian wolf spider. Papi & Syrjämäki (1963) proved *Pardosa agricola* to rely on an internal solar compass as well, even adjusting its orientation according to the time of day (time-compensatory mechanisms; Jander, 1975). Despite this apparent necessity of sunny conditions for orientation, *P. agricola* behaved more consistently compared to *P. amentata* under different weather conditions (Fig. III.4a,b). This may be due to early-life experiences with visual and tactile cues, as also suggested for other wolf spiders in disturbed environments (Papi & Tongiorgi, 1963; Persons & Uetz, 1996; Morse, 2002). Moreover, differences in orientation might be less pronounced after captivity (Papi & Syrjämäki, 1963; K. Lambeets, unpubl. data). Comparably, Ortega-Escobar (2002) and Norgaard et al. (2007) showed the necessity of visual input during homing behaviour of two wandering spiders. As *P. amentata* prefers moist grassland habitats (Alderweireldt & Maelfait, 1988), it is expected to lack sufficient information for accurate orientation on the river banks itself and, consequently, to show increased variation in its responses to pure visual landmarks in the direct vicinity (Fig. III.4c). Therefore, it is expected to orient entirely on visual stimuli and not on innate information related to the population of origin. This might be the most beneficial strategy for *P. amentata*, because it leads individuals directly to suitable habitat in a variety of situations (Jander, 1975). The water landmark did not led to an increased ashore movement for *P. amentata*, which might indicate it is unfamiliar with the visual perception of flooding (Fig. III.4d).

Our results indicate that factors related to population of origin might affect orientation behaviour less under more benign circumstances compared with stressful situations as being washed offshore (Morse, 1997). However, Papi & Tongiorgi (1963) and Riechert & Hall (2000) showed the ability of spiders to change behaviour quickly in their own benefit. Experience, for instance with geotactic landmarks as bank inclination or a humidity gradient (Papi & Tongiorgi, 1963), might be necessary to develop a precise orientation strategy (Scapini et al., 1999; Morse, 2002). Moreover, other factors such as temperature, dietary conditions or population density might underlie specific behavioural responses as well (Nylin

& Gotthard, 1998; for wolf spiders: Wagner & Wise, 1997; Walker et al., 1999). As factors related to both the population of origin and mainly vegetation landmarks guide movement behaviour of a stenotopic riparian species, it may result in a more efficient movement strategy to carry these wolf spiders adequately to their upland hibernation sites in autumn. A generalist wolf spider, on the other hand, might be negatively affected by flooding as its orientation behaviour seems to be chiefly guided by proximate cues. Generally, decision-making that precedes movement is guided both by factors related to natal origin and proximate cues as discernible visual landmarks (Ugolini et al., 1995), yet individuals from different populations may transfer inherited or experienced information differently into behaviour (Scapini et al., 2002; Bonte et al., 2006b).

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Authors' contributions

JVR and KL were responsible for the experimental work. KL analysed the data and drafted the manuscript. KL and DB composed the experimental design, formulated research questions and interpreted and discussed the results. All Authors have read and approved the final manuscript version.

III.3. Interdemic variation in homeward orientation behaviour in two riparian wolf spiders

Lambeets K. & Bonte D. Subm. Behavioural Processes

River bank at Mazenhoven, the bank of testing (Photo: Kevin Lambeets).

Abstract

Animals make decisions based on various sources of information that differ in their spatial and temporal scale of validity and/or acquisition. This decision-making is expected to be shaped by evolutionary processes and is especially relevant in stressful situations. The importance of ultimate sources of information or experience involved in orientation behaviour remains to date unclear. By means of a field experiment, we evaluated variation in zonal recovery of two sympatric, riparian *Pardosa* wolf spiders after releasing individuals offshore from a non-familiar river bank. After acclimatisation under controlled laboratory conditions, both species showed strong directional movements towards the natal river bank shore. Additionally, the most stenotopic riparian wolf spider showed considerable between-individual variation in orientation behaviour across populations, but reacted less variable across individuals within populations. This indicates the importance of individual variation in movement behaviour. In conclusion, information with respect to an individual's geographical origin acts as an important cue for wolf spider orientation during movement. Our findings provide insights into decision-making processes in stressful situations and point to between-population variation in orientation behaviour, which relates to ultimate (inherited) factors and/or early-life (learned) experience.

Key-words: decision-making, geographical origin, Lycosidae, variation partitioning, water surface locomotion, zonal recovery

Introduction

The information collected over substantial, temporal and spatial scales provides the basis for adaptive decision-making (Dall et al., 2005; Danchin et al., 2008). Especially for movement, the acquisition of reliable information on the state of the physical environment will reduce the uncertainty and thus costs involved with ending up in unsuitable conditions (Giraldeau, 1997; Bowler & Benton, 2005). An accurate integration of information will therefore lead to beneficial decision-making and the minimisation of risks concerned with habitat unpredictability or unsuitability. In first instance, an individual may use prior information about its personal condition, i.e. innate information comprising both genetic information and information expressed in body condition (Dall et al., 2005). For example, movement behaviour may change with the internal condition of an animal (Persons, 1999; Walker et al., 1999; Bonte et al., 2008b), its gender (Freake, 1998; Bonte et al., 2004a) or its genetic composition (Bonte & Lens, 2007; Berwaerts et al., 2008).

Because many behaviours show a strong additive genetic component (Colombini et al., 1994; Bonte et al., 2006b; 2007a) or are transgenerational by epigenetic effects (Bossdorf et al., 2008), between-population variation can be expected in spatially structured populations. Even with considerable gene flow, behavioural differences between populations may remain for some generations if local selection pressures are strong (Riechert & Hall, 2000). When behavioural decisions are primary based on these ultimate sources of information (so an individual’s evolutionary history), predictable responses may be expected for individuals from the same population under certain circumstances. For example, a preferred movement direction is often evoked in individuals that descend from equally and predictably disturbed sites such as tidal zones (Morse, 2002; Scapini et al., 1995; 2002).

Because these innate sources of information directly relate to habitat conditions at longer time frames, they may be deceivable if the environment changes suddenly (Schlaepfer et al., 2002). Therefore, decisions can be actualised by integrating information about the individual’s recently experienced social environment (e.g. species density; Wagner & Wise, 1997) or its (direct) abiotic environment (Hill, 1979b; Norgaard et al., 2007). Genotype x Environment interactions are, consequently, expected. This was illustrated for aerial dispersing spiders, in which dispersal behaviour was affected by an individual’s genetic background and its specific reaction towards wind velocity (Bonte et al., 2007a).

Additionally, individuals may gain experience with local conditions (Lima & Zollner, 1996). This experience can then be used in decision-making, as shown for movement behaviour (Scapini et al., 1999; Pulido, 2007) and orientation (Jander, 1975; Hill, 1979b). Relying on a simple strategy, e.g. by employing a non-informational (random) movement process, may also lead to profitable outcomes in movement dilemmas (Zollner & Lima, 1999). However, this is very unlikely for animals with well-developed sensory capacities and a quite complex behaviour (Lima & Zollner, 1996; Bowler & Benton, 2005). Because the integration of these different sources of information over an individual's lifetime (and even longer in case of genetically build information) is expected to result in beneficial decision-making, we expect that an individual, familiar with certain stressful situations (experienced) will respond more accurately compared to one only sporadically meeting these conditions. This has, for instance, been documented for stress related to flooding (Papi & Tongiorgi, 1963; Morse, 2002; Scapini et al., 2002).

Flooding disturbance is generally considered as a potentially lethal form of stress which disadvantages riparian organisms in several ways (Adis & Junk, 2002; van Eck et al., 2004; Plum, 2005). Notwithstanding typical shoreline and floodplain inhabiting arthropods may withstand flooding temporarily (Foster, 2000; Rothenbucher & Schaefer, 2006; Lambeets et al., 2008c), especially blatant disturbances of water discharge regimes could disadvantage species adapted or experienced with local circumstances along spatially structured river banks (Semmerkrot et al., 1997; Lytle & Poff, 2004). Efficiently locating the shore after being washed away, and subsequent perpendicular movement to the shore, will benefit terrestrial species living in inundation-prone environments (Shultz, 1987; Morse, 2002; Stratton et al., 2004; Bates et al., 2006). This necessitates the ability to perform effective water surface locomotion in the first place (Suter, 1999; Suter et al., 2004). By contrast, simply drifting along-stream would involve more risks as it is a directionally, passive uncontrolled movement (Suter, 1999). It does not require additional muscular input and hence is a remarkably cheap form of transport. However, the elevated uncertainty of a suitable destination downstream can be expected to stimulate homeward movement behaviour. In contrast to drifting, active walking on the water surface can be controlled to some extent. Decision-making by either choosing to move shoreward (this is defined as zonal recovery;

Scapini et al., 1995; 2002; Morse, 2002) or to drift away is therefore of prime importance for riparian arthropods that experience sudden flooding (Papi, 1955; Morse, 2002).

Between-population variation in orientation behaviour of cursorial terrestrial arthropods has been documented before (Bonte et al., 2004a; Papi & Tongiorgi, 1963). Previous studies, however, did not emphasise on the decision-making process during sudden stressful situations under which decisions need to be taken swiftly. We performed a common-garden field experiment to test whether two congeneric, sympatric species of wolf spiders (Araneae; Lycosidae) differ in orientation behaviour (zonal recovery) and to unravel the factors explaining this behaviour, accordingly. *Pardosa agricola* (Thorell 1856) is considered as a stenotopic riparian species (Harvey et al., 2002) that inhabits dynamic river banks throughout the year (Lambeets et al., 2008a). In contrast, *P. amentata* (Clerck 1757) occurs commonly in a wide range of humid habitats (Alderweireldt & Maelfait, 1998). Thus, the latter is considered to encounter the typical conditions met on river banks only sporadically once they are exposed because its main habitat are the surrounding humid grasslands. Because risks of mortality during or after drifting are expected to be high for both species, we expect strong shoreward orientation (zonal recovery) in both species. However, because *P. agricola* spends its life entirely in spatially structured river banks, we expect the species to rely on innate sources of information to return consistently to the natal shore, even if released on shores at the opposite side of the river. By contrast, *P. amentata* is expected to show more random orientation because inherited decision rules might not be fine-tuned to deal with sudden unpredictable changes.

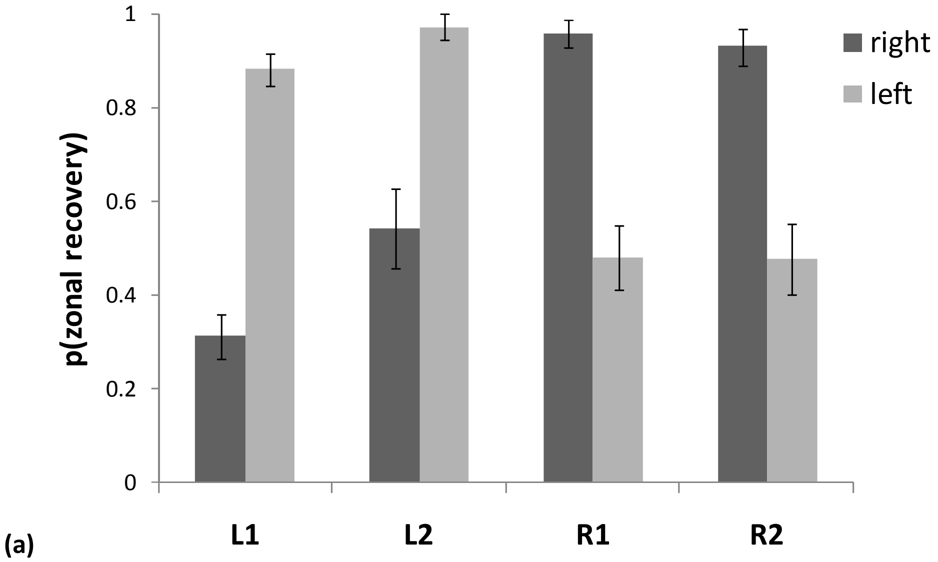
Material and methods

Experimental set-up

During June 2005 and 2006 adult *Pardosa agricola* and *P. amentata* individuals were collected from four river banks along the Common Meuse, a semi-natural river reach forming the geographical border between Flanders (Belgium) and the Netherlands. Two populations of each species on both sides of the river were sampled: Flemish populations (left river shore) L1, L2 and Dutch populations (right river shore) R1 and R2. These river banks are similar with respect to flooding susceptibility, size and vegetation structure (see Lambeets et al., 2007); behavioural differences related to dissimilar stand conditions (Papi & Syrjämäki, 1963) can, consequently, be ruled out. All individuals were collected in separate opaque vials and transported to the lab. After an acclimatisation period of one week under controlled conditions (individual vials with a humid plaster bottom, 15°C, fed *ad libitum* with *Drosophila melanogaster*), homeward orientation behaviour (zonal recovery) was tested in the field by means of a common-garden experiment. The wolf spiders were individually released from a large opaque plastic cup on the water surface 1.25 m offshore. All tests were performed in the morning when the sun was at the south-east quarter (9 - 12 am). The opposite river shore was approximately 50 m away, and therefore indiscernible for the wolf spiders. We recorded whether or not zonal recovery occurred (returning shoreward), a simple binary measure of homeward orientation. Once a wolf spider reached the shore or spent more than 90 sec passively drifting along-stream without showing a propensity for shoreward movement, it was recollected to avoid genetic erosion downstream. To test whether zonal recovery was transferable, all spiders were tested once at both sides of the river (reciprocal transplant; Riechert & Hall, 2000; Bélisle, 2005) along unfamiliar shorelines which were structurally the same as their natal habitat (soft slope, bare gravel for >20 m from the waterline onwards). In total 241 individuals of *P. agricola* and 201 of *P. amentata* were tested randomly.

Statistical analysis

Variation in behavioural responses is expected to be statistically divided over variation within the different sources of information that affect these responses (Zollner & Lima, 2005; Cézilly et al., 2008). We tested if zonal recovery differed according to species, gender, the river bank of origin (four populations), the bank where the tests were performed (two sides) and their interactions. The binary scored responses were analyzed by generalised linear mixed models with logit-link (GLMM, SAS 9.1). Individuals and the dates of testing were modelled through random effects. By including the date of testing, we corrected for confounding climatological variables such as humidity, temperature and light conditions. Consequently, we specifically tested for the effect sizes of innate information (i.e. population of origin) upon homeward orientation behaviour. Non-explanatory factors were sequentially removed departing from full models. Corrected degrees of freedom were approximated by the Satterthwaite procedure (Verbeke & Molenberghs, 2000). To assess the relative importance of relevant sources of innate information during zonal recovery, variation partitioning techniques were applied for each species separately in which all factors (individual, date, gender, bank of testing, origin) were modelled as random effects.



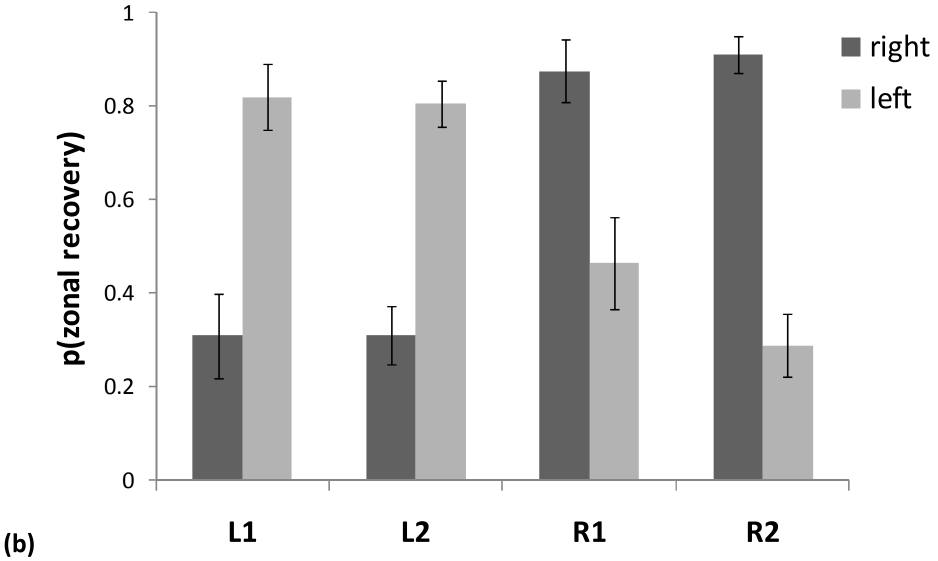


Fig. III.5 - Mean estimated proportions per population tested for two riparian wolf spiders performing zonal recovery (river banks on the left river side: L1, L2; on the right side: R1, R2) on both river bank shores (left, right). Error bars indicate the standard error of the mean. (a) *Pardosa agricola*, a stenotopic riparian species and (b) *P. amentata*, a wide-spread generalist colonising the river banks once exposed.

Results

Zonal recovery during water surface locomotion

Zonal recovery behaviour (i.e. the probability of returning shoreward) differed between wolf spider species (Table III.3), but both species reacted similar according to the other tested parameters (interactions were not significant). Overall, *Pardosa agricola* showed 11.1% higher zonal recovery rates that *P. amentata* (respectively, 80.3% +/- 4.1SE; 69.2% +/- 5.7SE). For both *P. agricola* (Fig. III.5a) and *P. amentata* (Fig. III.5b), zonal recovery differed according to the interaction between their population of origin and the bank of testing (Table III.3). No differences were found between populations originating from the same side of the river. Thus, both wolf spider species rather returned shoreward when tested at the corresponding river shore (Fig. III.5). When tested at the opposite shore than their natal origin, they decided to drift along-stream more often, sometimes after moving away from the shore (i.e. in the direction of the accustomed shore) for a couple of seconds, rather than to return shoreward. The interaction between gender and population of origin was retained as significant, but neither males nor females responded consistently according to their origin (Table III.3).

parameter	NumDF	DenDF	F-value	p-value
species (spec)	1	381.5	8.45	0.0039
population of origin (orig)	3	435	3.93	0.0087
sex	1	335.8	3.52	0.0616
test bank (test)	1	2.165	0.82	0.4547
test*orig	3	442.6	87.94	<.0001
orig*sex	3	395.8	4.97	0.0021
test*spec	1	581.5	1.60	0.2062
orig*spec	3	418.3	1.27	0.2831
test*sex	1	436.3	0.06	0.8092
spec*sex	1	360.6	0.01	0.9408
test*orig*spec	3	440.9	1.20	0.3078
test*orig*sex	3	430.7	1.27	0.2852
orig*spec*sex	3	374.6	0.87	0.4571
test*spec*sex	1	423.2	0.40	0.5259
spec*orig*test*sex	3	594.2	0.68	0.5643

Table III.3 - Statistical results of generalised linear mixed models (GLMM) for homeward orientation behaviour (zonal recovery) in two sympatric riparian wolf spiders (*Pardosa agricola* and *P. amentata*). A stepwise backward selection procedure was used to omit non-explanatory parameters departing from full models. (NumDF = numerator degrees of freedom; DenDF = denumerator degrees of freedom).

Variation partitioning of orientation behaviour

Conform the results above, the interaction between natal origin and river shore explained substantial variation in zonal recovery in both species (Fig. III.6). Yet, less variation due to geographical origin was explained in *P. agricola* compared to *P. amentata* (variation explained respectively, 43.81% - 58.48%). Individual variation was high in *P. agricola* (41.19% vs. none for *P. amentata*): 39.9% of *P. agricola* individuals consistently returned shoreward irrespective of the test-bank or consistently choose to drift along-stream (5.3%). 54.8% of the tested individuals showed inconsistent behaviour compared to 62.8% in *P. amentata*. Gender explained only a minor part of behavioural variation of *P. agricola* (0.65%) as a factor, as did the interaction with origin and river shore (2.77%). In contrast, gender in interaction with river shore explained 8.18% for *P. amentata*. Unexplained, residual variability was quite low for *P. agricola* (2.98%), but substantial for *P. amentata* (33.34%). Interestingly, the date of testing explained 8.59% of behavioural variation for *P. agricola*, alluding to the importance of external (environmental) cues.

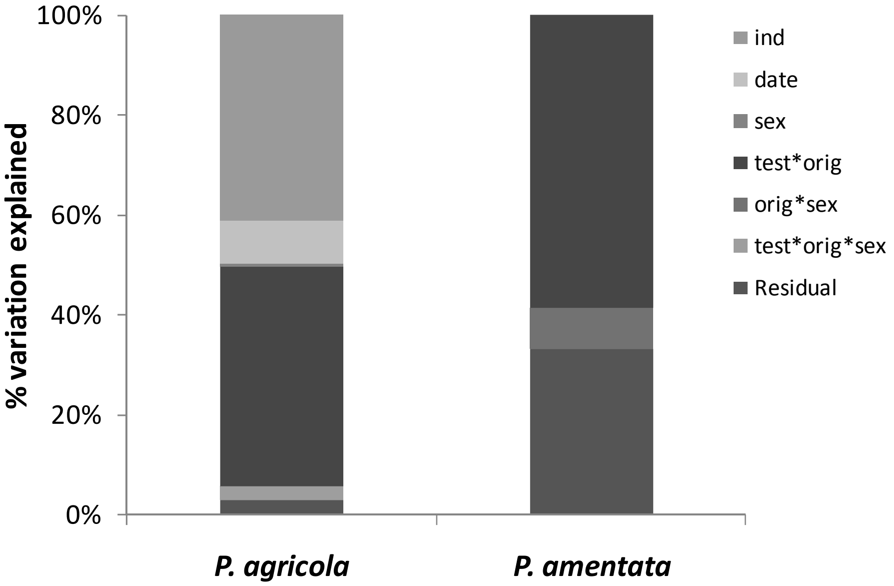


Fig. III.6 - Assessment of available sources of information explaining variation in homeward orientation decisions (zonal recovery) of two sympatric riparian wolf spiders, *Pardosa agricola* (stenotopic) and *P. amentata* (wide-spread generalist), using variation partitioning. The parameters tested for were date = date of testing, ind = individual, orig = natal population (origin), sex (male, female) and test = river bank shore where the wolf spiders were tested (left, right) and their mutual interactions. Residual variation due to other, not identified factors is indicated as well.

Discussion

Zonal recovery of *Pardosa agricola* and *P. amentata* was similar in relation to the river side of origin. Despite prior acclimatisation under laboratory conditions, individuals oriented and moved more shoreward when tested on a river bank on their accustomed shoreline compared to the opposite side. Population of origin explained the major part of variation in orientation decisions which adds to the profitability of direct zonal recovery. But, in line with our key-predictions, *P. agricola* showed more overall similarity in orientation behaviour, independent of the river side where tested. This alludes to the existence of distinct movement phenotypes, i.e. walkers and drifters in *P. agricola*. Next to inconsistent decisions, a substantial proportion of the individuals decided to return shoreward (active locomotion; walkers) or to drift along-stream (passive locomotion; drifters) consistently. This distinction corresponds to the locomotion gaits as defined by Suter (1999) and Suter et al. (2003), who distinguished water surface locomotion by spiders into sailing (passive), rowing (active) and galloping (active). *P. amentata* resided more on other, unidentified information sources and, hence, showed more inconsistent movement.

Our release-experiment showed clear between-population variation in orientation behaviour for two sympatric wolf spider species. Concordantly with early results from Papi (1955) and Papi & Syrjämäki (1963), most individuals selected their accustomed river shore when displaced, even after acclimatisation. Efficient (homeward) orientation enables organisms to retrieve their original habitat, especially under stressful situations (cf. for butterflies: Merckx & Van Dyck, 2007; sandhoppers: Scapini et al., 1995; 2002; Borgioli et al., 1999b; spiders: Ortega-Escobar & Muńoz-Cuevas, 1999; Morse, 2002). In the case of river banks, which are inherently prey-rich (Paetzold et al., 2005) and spatially structured (Ward et al., 2002; Wiens, 2002), swiftly returning shoreward is expected to be more beneficial relative to downstream drift, unless local conditions deteriorate (Bates et al., 2006). The effect of bank location on the wolf spider's mobility appeared to be similar in both species, despite a much broader habitat range for *P. amentata.* This suggests that costs related to drift are not due to risks of reaching unsuitable habitat (with wide habitat availability for *P. amentata*), but rather relate to direct costs by increased risks of direct mortality during transfer (e.g. predation, drowning; Suter, 1999). Due to the inherent fragmented character of riverine ecosystems, zonal recovery is a beneficial strategy to avoid costs related with sudden flooding.

The two species make similar adaptive decisions, preventing costly downstream drift by zonal recovery. Although general outcomes, i.e. effectively returning shoreward, were similar for both wolf spider species*,* variation partitioning points to a lower degree of individual variation in *P. amentata* compared to *P. agricola*. Relying on orientation towards its geographical origin keeps down costs when decisions need to be taken quickly and/or when costs related to superfluous movements are high (Fahrig, 2007). Generally, orientation reflexes based on ultimate cues, like a preferred geographical direction (Scapini et al., 1995; Morse, 2002), appear to be common zonal recovery mechanisms for shoreline inhabiting terrestrial organisms which are frequently exposed to flooding disturbance. However, proximate cues have been shown to affect the behaviour of spiders as well. For instance, especially cursorial spiders make use of celestial cues (solar compass; Ortega-Escobar & Muńoz-Cuevas, 1999; Dacke et al., 2001) or orient based on local visual landmarks (Hill, 1979b; Norgaard et al., 2007). For instance, Papi & Syrjämäki (1963) showed a decreased orientation precision in *P. agricola* when descending from overgrown habitats. Similarly, Papi (1955) showed the ability of *Arctosa perita* (Latreille 1799) to select the accustomed site of a stream, but only when the sky was clear. Furthermore, patterns in vegetation transition have been proven to aid homeward orientation of *Pardosa monticola* (Clerck 1757) during terrestrial movement (Bonte et al., 2004a).

Since our results show the importance of a wolf spider's origin as the prime source of information to explain variation in homeward orientation behaviour, geographical origin is supposed to reliably lead a wolf spider shoreward (Papi & Syrjämäki, 1963). Therefore, directed orientation when landing offshore is in line with an adaptive response in a risky, flood-prone environment. It reduces the time spent on the water surface and limits potential costs related to downstream drift. This does, however, not imply that local adaptation in orientation behaviour is prevalent (Papi & Syrjämäki, 1963; Merckx & Van Dyck, 2007). A learned orientation component, concordant with local environmental conditions, is manifested during the early lifetime but can disappear quickly once "adapted" individuals are transferred (Papi & Tongiorgi, 1963; Riechert & Hall, 2000). Morse (2002) showed that individuals of *Pardosa lapidicina* Emerton 1885 descending from locations less prone to tidal floods, moved unidirectionally rather than individuals occurring nearby the shoreline, and concluded that experience affected their orientation and movement decisions directly.

From an adaptive point of view, our results suggest that individuals familiar with flooding disturbance (*P. agricola*) are better able to deal with sudden stressful situations by relying more on population-specific (homeward) information and individually-gained information, consequently reacting less variable across individuals within populations, but not among populations (high between-individual variation). However, our study does not allow to distinguish whether direct sensory input and/or early-life time experience are the rank and file of divergent behaviour between two sympatric wolf spiders. Still, after a long period of acclimatisation in the lab both species possessed orientations in agreement with their origin, irrespective of their habitat specialisation, and individual decisions do affect variation in wolf spiders' responses. This indicates that at least some aspects of orientation behaviour are inherited (Jander, 1975) and that individuals do gain early-life experience with local conditions (e.g. former floods or celestial cues; Papi & Syrjämäki, 1963; Persons & Uetz, 1996; Scapini et al., 1999; Morse, 2002). In conclusion, we here showed how two riparian wolf spiders with a dissimilar habitat affinity integrated prior sources of information differently into beneficial orientation decisions during flooding, despite overall similar behaviour in the end.

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Authors' contributions

KL composed the experimental design, performed the experiments, analysed the data and drafted the manuscript. KL and DB formulated the research questions, interpreted and construed the results and discussed the presentation. Both authors have contributed to, seen and approved the manuscript.

III.4. Plasticity in flood-avoiding behaviour in two congeneric riparian wolf spiders

Lambeets K., Maelfait J.-P. & Bonte D. 2008. Animal Biology 58, 389-400

Experimental set-up to test flood-avoiding behaviour of wolf spiders and a female *Pardosa agricola* (Thorell, 1856) being completely submerged… (Photo: Kevin Lambeets)

Abstract

The ecological effects of disrupted flooding are known to be pernicious for the occurring riparian fauna. As flooding disturbance is argued to structure species assemblages, behavioural aspects may be affected just as well. Generally, eurytopic inhabitants possess a well-developed dispersal ability allowing frequent recolonisation, whereas specialised stenotopic species are expected to be adapted to these stress regimes. This study aims at determining whether flooding induces different behavioural responses in two congeneric wolf spider species. Variation in flood-avoiding behaviour was evaluated by means of individual tests performed under different ambient conditions. We considered sheltering behaviour preceding flooding, a direct flight reflex induced by the flood event, an escape reaction away from the rising water and submersion tolerance. Our findings indicated clear flood-avoiding behaviour for both species, yet a higher degree of plasticity in individual behaviour for a riparian wolf spider, *Pardosa agricola* (Thorell, 1856), in contrast to a generalist species, *P. amentata* (Clerck, 1757). Nonetheless the former species systematically reacted under different ambient conditions, a generalist shifts responses, displaying a higher degree of between-individual variation. Submersion tolerance was equivalent, emphasising similar morphological characteristics. We argue habitat specialisation and/or experience with local conditions to influence behavioural responses in order to optimise long-term persistence under flood stress. Future studies of behavioural variation should consider temporal variation in species condition, thus employing distinct populations thriving under different local stress regimes.

Key-words: behavioural plasticity, habitat specialisation, Lycosidae, *Pardosa agricola*, *Pardosa amentata*, submersion tolerance.

Introduction

Flooding and low flows are hydrological events affecting river ecosystems and consequently their biotic components. Generally, the ecological effects of flooding disturbance are assumed to be more pernicious than periods of low flow (Suren & Jowett, 2006). In temperate regions, flooding events are charged by seasonal and weather dependable processes (Adis & Junk, 2002), although they are currently artificially controlled by humans due to e.g. upstream weirs and embankments (Semmerkrot et al., 1997; Pedroli et al., 2002).

Wolf spiders (Araneae; Lycosidae) belong to the most abundant arthropods on river banks along the Common Meuse river reach (Lambeets et al., 2006; 2008a). They are perfectly suited to study behavioural mechanisms or mobility patterns (e.g. foraging strategies) since wolf spiders readily react upon small-scale environmental perturbations according to their idiosyncratic ecological needs, and are easily collected or surveyed (Samu et al., 2003; Bonte et al., 2004a; Pétillon et al., 2005b). As previously documented, this river is prone to substantial winter inundation and unpredictable inundation during spring and autumn (Geilen et al, 2004; Liefveld & Schulze, 2005). Species living at the riparian interface, situated at the terrestrial – aquatic transition, are consequently exposed to stress induced by flooding disturbance and periods of drought. In contrast to eurytopic inhabitants, generally acknowledged to possess a well-developed dispersal capacity that allows frequent recolonisation after dispersal (Zulka, 1994), specialised stenotopic species are expected to be adapted to these extreme environmental fluctuations (Foster, 2000; Adis & Junk, 2002). These adaptations comprise a.o. adjusted dispersal power (Desender, 1989a; Bonn, 2000; Bonte et al., 2003c), beneficial behavioural responses (Joy & Pullin, 1997; Decleer, 2003; Pétillon et al., 2004) or specifically developed physiological tolerances (Hebets & Chapman, 2000; Messner & Adis, 2000; Suter et al., 2004). Previous studies indicated clear behavioural (Witteveen & Joosse, 1988; Borgioli et al., 1999) or eco-physiological responses (Hoback & Stanley, 2001) as induced by hypoxia or flooding. Both Weigmann & Wohlgemuth-von Reiche (1999) and Rothenbücher & Schaefer (2006) discussed survival strategies of soil dwelling arthropods from lowland floodplains according to their degree of eurytopicity. Field studies concerning sympatric wolf spiders of the genus *Pardosa* report of divergent physiological adaptations determining distribution patterns (DeVito et al., 2004). Morse (2002) showed clear differences in movement patterns and orientation ability within an intertidal *Pardosa* species along the tide line. Additionally, Kraus & Morse (2005) found seasonal shifts for the same species, being associated with various proximal cues. In contrast, our study indicates behavioural responses induced by simulated disturbance to differ between mobile, congeneric *Pardosa* species characterised by a different habitat preference.

Here, we empirically studied whether two closely related species of wolf spiders, differing in their degree of habitat specialisation, show a divergent tolerance withstanding inundation and if behavioural responses during flood events differ. More specifically, we expected well-developed adaptive (*sensu* beneficial) responses in the riparian specialist *Pardosa agricola* (Thorell, 1856), but less so in the congeneric eurytopic species *P. amentata* (Clerck, 1757).

Material and Methods

Study species and collecting method

The two most dominant wolf spider species, and in general the most dominant spider species along the Common Meuse, were chosen as a model for this study. *Pardosa agricola* is a riparian specialist species, in the Low Lands mainly found on river banks along the Common Meuse characterised by flooding after heavy rainfall (Lambeets et al., 2007). Contrary, *P. amentata* is a generalist species found in a large variety of humid habitats (Alderweireldt & Maelfait, 1988). The two species were hand collected from the river bank at Elerweert along the Belgian side of the Common Meuse, where they occur sympatrically. All specimens were collected along a strip no further than 10 m out of the rough, river dike vegetation and approximately 15 m from the waterline. Since we wanted to test behavioural responses of wolf spiders towards flood events, hand collecting took place in November, just before the long-lasting, seasonal winter flood. In total 293 subadult individuals were tested, 68 specimens in 2005 (*P. agricola*: #35; *P. amentata*: #33) and 225 individuals in 2006 (*P. agricola*: #157; *P. amentata*: #68). All individuals were tested three times according to the experimental design, hereunder described in detail.

Experimental design

Since we wanted to test behavioural responses of wolf spiders prior to upcoming inundations and assess their individual submersion tolerance, we created surrogate gravel banks (Fig. III.7) and simulated flooding disturbance. The experimental set-up consisted of plastic, conical test tanks (Φ 12 cm, height 7 cm) filled with a layer of minimum 3 cm of industrially cleaned sharp sand on which larger shingle (width range: 3 - 7 cm) was randomly deposited. In order to simulate natural temperature fluctuations, the test tanks were placed outside throughout the testing period. Experiments were performed in two subsequent years (2005 - 2006), with significantly different means of daily outdoor temperatures during the testing periods ($F = 12.78$, $df = 1$, $p = 0.0005$). Average temperature in 2005 (5.65°C +/- 0.49SE) was higher than in 2006 (3.47°C +/- 0.37SE). Inundation was simulated by means of manually raising the water level of each test tank from the bottom on applying a small rubber funnel (Fig. III.7). If individuals decided to stay hidden and withstand inundation, the test tanks were covered with a large plexi-glass to keep the wolf spiders from climbing out once they decided to leave their refuge. Before and between repeated tests, depending whether or not an individual was submerged, the spiders were kept in a climatic chamber in individual plastic vials filled with a thin layer of humid plaster. The temperature of the climatic chamber was constant (10°C), with dark/light conditions consistent with diurnal regime, thus adjusted accordingly on weekly intervals. Before and after each test, all spiders were fed *ad libitum* with fruit flies (*Drosophila melanogaster*). All individuals were acclimatised to ambient conditions in the test tank for 2 hours.

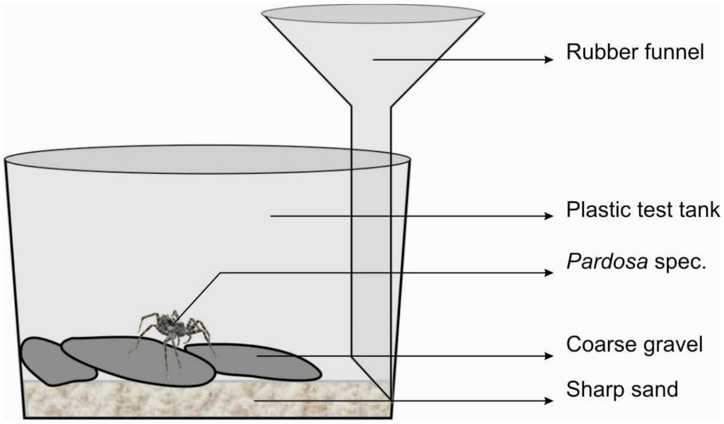

Fig. III.7 - Experimental design of a test tank used to study the effects of simulated flooding on individual wolf spider behaviour and submersion tolerance.

Monitoring of wolf spiders during simulated inundation

The following behavioural responses of individual wolf spiders were observed during the induction of the inundation: (i) whether the wolf spider was hidden or not before the water level was raised, (ii) in case the individual was hidden in a refuge whether it remained there and (iii) whether individuals showed a clear flight reflex, i.e. seeking higher ground during the escape reaction, away from the rising water. Submersion tolerance was consequently only assessed for individuals that decided to stay submerged after the induced inundation. For the latter, we recorded the time they withstand submergence until they appeared at the water surface or their survival (in case they died before coming to the surface). Submerged individuals were checked after 1, 2, 4, 8 hours and subsequent mid-daily intervals, respectively.

Statistical analyses

The three behavioural responses are binomially distributed and subsequently analysed by generalised linear mixed models with logit-link (GLMM; SAS 9.1, proc glimmix). We applied general linear mixed models (GLM; SAS 9.1, proc mixed) to test whether the time withstanding submergence significantly differed between species, test years and their interaction. Species and test year were taken up as fixed variables in all the models. Individuals were included as repeated measures and modelled through random effects. The interaction between species and test year was omitted from further analyses if not significant. Post-hoc comparisons between factors and/or interactive effects were made with Tukey tests. Backwards procedures were applied departing from full models. Corrected degrees of freedom were calculated by Satterthwait's procedure (Verbeke & Molenberghs, 2000). Estimations of individual repeatability were based on covariance parameter estimates, calculated as the ratio of estimated individual variation and the sum of former added to the estimated residual variation.

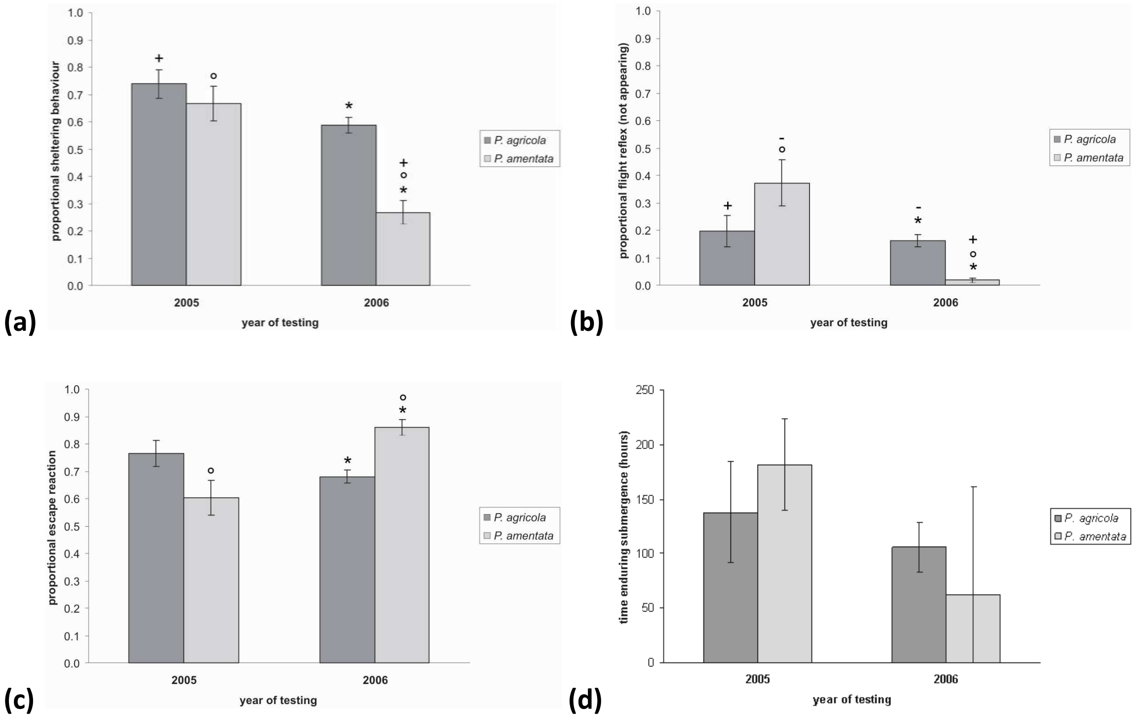

Fig. III.8 - (a) Proportional differences between species and test years concerning sheltering behaviour of individual wolf spiders after acclimatisation; (b) proportional differences between species and test years considering a flight reflex of individual wolf spiders once inundation was set in; (c) proportional differences regarding an escape reaction of individual wolf spiders, i.e. clear-cut running from the rising water, between species and between test years applying an individual test set-up; (d) differences between species and test years for individual wolf spiders for the time withstanding submergence after induced inundation. Significant pairwise comparisons are indicated by symbols (*, °, +, -).

Results

Induced behavioural responses

Sheltering behaviour prior to inundation differed, between years (F = 25.79, df = 290.9, p < 0.0001), between species (F = 13.13, df = 290.9, p = 0.0003) and was affected by their interaction (F = 4.72, df = 290.9, p = 0.0306; Fig. III.8a). No differences between the species were retrieved in 2005 (t = 0.86, df = 297.7, p = 0.8268), yet responses varied in 2006 with *Pardosa agricola* hiding more after acclimatising (t = 5.44, df = 274.5, p < 0.0001). *P. agricola* showed consistent behaviour over the years (t = 2.29, df = 285.4, p = 0.1037), while *P. amentata* was more prone to hide in 2005 than in 2006 (t = 4.70, df = 294.6, p < 0.0001). Individual repeatability was lower for *P. agricola* (σ_{ind} = 0.5827 +/- 0.2234SE, R = 0.3976) than for *P. amentata* (σ_{ind} = 2.2762 +/- 0.7657SE, R = 0.6666).

As inundation was set in, most of the individuals tried to escape from the rising water (see above), therefore the species effect was not withhold as explaining significantly variation of flight reflex (F = 0.42, df = 306, p = 0.5195; Fig. III.8b). Nevertheless, both year (F = 4.46, df = 306, p = 0.0356) and the interaction between both singular effects turned out to be significant (F = 15.95, df = 306, $p < 0.0001$). In concordance with pairwise comparisons concerning hiding behaviour, *P. agricola* left its refuge proportionally less than *P. amentata* in 2006 (t = -3.99, df = 383.5, p = 0.0005), whereas latter species was less apt to appear in 2006 (t = -3.93, df = 314.8, p = 0.0006). Interestingly, the flight reflex did not differ between years for *P. agricola* (t = 1.50, df = 293, p = 0.4408), nor between species in 2005 (t = 2.06, df = 273.5, p = 0.1693). Repeatability for the flight reflex was lowest of all recorded behaviours for *P. agricola* (σ_{ind} = 0.4299 +/- 0.2266SE, R = 0.3264) and intermediate, yet comparably higher for *P. amentata* (σ_{ind} = 1.9894 +/- 0.6035SE, R = 0.7703).

Escape reaction, running away from the rising water, differed again between species and year (F = 20.50, df = 352.4, $p < 0.0001$; Fig. III.8c), between species (F = 4.28, df = 352.4, p = 0.0394) and between years (F = 26.94, df = 352.4, $p < 0.0001$). Here, *P. agricola* was not found to react significantly different between subsequent years (t = 0.61, df = 216.8, p = 0.9301) and neither species showed a different response in 2005 (t = -1.74, df = 207.2, p = 0.3027). During the tests of 2006 *P. agricola* was inclined to escape the flood proportionally more than *P. amentata* (t = 4.65, df = 605.8, $p < 0.0001$) and the latter was more apt to run from the rising water in 2006 than in 2005 (t = 5.80, df = 438.7, $p < 0.0001$). Individual repeatability was lower for *P. agricola* (σ_{ind} = 2.0855 +/- 0.4170SE, R = 0.7777) contrary to *P. amentata* (σ_{ind} = 5.2378 +/- 1.2730SE, R = 0.9513).

Submersion tolerance

On average, *P. agricola* spent 103.53h +/- 16.91SE (max. 840h) being submerged whereas the average for *P. amentata* was slightly higher (129.94h +/- 37.06SE, max. 744h). The reported differences are, however, not significant (F = 0.14, df = 102, p = 0.7125; Fig. III.8d). Effects of testing year (F = 1.08, df = 104, p = 0.3007), or its interaction with species (F = 0.54, df = 104, p = 0.4649) were neither significant. Individual repeatability was lower for *P. agricola* (σ_{ind} = 12237 +/- 11846SE, R = 0.3521) than for *P. amentata* (σ_{ind} = 56299 +/- 18008SE, R = 0.9018), indicating that eurytopic individuals responded more similar than individuals of a specialist species.

Discussion

Notably, *Pardosa agricola* and *P. amentata* are capable of surviving short term submergence as induced by flood events notwithstanding most of the individuals rather try to elude flooding. Although our results indicate no significant differences regarding tolerance levels, probably due to similar morphological characteristics (Stratton et al., 2004; Suter et al., 2004) resulting from a common origin (cf. periodically disturbed ephemeral habitats; Marshall & Rypstra, 1999), behavioural responses of sympatrically occurring species are clearly divergent with pronounced effects of test year. A riparian specialist species was seemingly less liable to differences between years than a generalist wolf spider. Our study does, however, not allow to distinguish which factors (e.g. experience with flooding, ambient conditions or others) are the rank and file of divergent behaviour between years. Moreover, these results only concern behavioural responses during autumn.

In general, *P. agricola* seeks refuge underneath coarse gravel, whereas on average activity levels of *P. amentata* differ between years, possibly as a consequence of different ambient conditions. Spiders may be restricted in movement during unfavourable temperatures (Cushing & Opell, 1990) whereas threshold temperature for activity may be related to habitat preference (Kirchner, 1973). As shown by Walker et al. (1999) and Samu et al. (2003) foraging strategies may differ between congeneric species, favouring prey encounters. Similarly, Kraus & Morse (2005) demonstrated an increased preference for refuge sites for an intertidal wolf spider when ambient temperatures fell. They emphasised seasonal variation in behaviour to be prominent, probably because seasonal changes are associated with different internal states (Bonte et al., 2007c). Overall, the responses of both species can be considered as a beneficial risk-avoidance strategy with regard to habitat specialisation, adding to their persistence in the long term (Joy & Pullin, 1997).

As disrupted flooding disturbance is regarded as a pernicious event decreasing riparian spider persistence (Bonn & Kleinwächter, 1999; Decleer, 2003), both species appear to escape once inundation sets in. Joy & Pullin (1997) and Konvicka et al. (2002) have proven flood events to decrease survival rates of hibernating butterfly larvae. Similarly, a large-scale study of Weigmann & Wohlgemuth-von Reiche (1999) clearly indicated negative effects of prolonged inundation for several arthropod groups. Since *P. agricola* is a stenotopic river bank species in our country (Lambeets et al., 2007), flood events may select for individuals displaying beneficial behaviour and efficiently escaping sudden floods (Morse, 2002; Lambeets & Bonte, subm.b). On average, *P. agricola* displayed similar behaviour systematically regardless of the test year, thereby escaping inundation more efficiently. Similar to the responses discussed above, *P. agricola* was more likely to leave its shelter once flooding was simulated over the years. Apparently, rising water induces a clear flight reflex, equivalent with results of Bates et al. (2006) concerning a riparian carabid beetle. Since wolf spiders are only able to detect proximate objects (Foelix, 1996), tactile cues especially are expected to act as an important trigger for flight responses (Kraus & Morse, 2005). Cushing & Opell (1990) proved simulated tactile stimuli to act as an important trigger inducing flight of an *Uloborus* spider. *P. amentata* rarely endured inundation and exhibited lower hiding propensity. As pointed out by Wenninger & Fagan (2000), temperature regimes can affect wolf spider condition directly. Despite a general decrease of activity, thereby probably restricting energy dissipation, *P. amentata* clearly attempts to escape harmful flooding even under colder conditions.

Moreover, our results show a higher individual repeatability in the eurytopic species, despite larger between-individual variation in behaviour. This individual variation potentially underlies its wide distribution range. In contrast, individuals of *P. agricola* are behaviourally less consistent and show consequently less individual variation. This agrees with findings of Cushing & Opell (1990) that behavioural consistency under specific conditions, combined with different responses under altered conditions, eventually benefit species persistence by means of risk spreading.

Although wolf spiders are able to cope with flood events to some extent (Rovner, 1986; Decleer, 2003; Pétillon et al., 2005b), vigorously disrupted discharge regimes will certainly have a negative effect irrespective of habitat specialisation or interrelated beneficial behavioural responses (Adis & Junk, 2002; Lytle & Poff, 2004).

Consequently, our results indicate efficient flood-avoiding behaviour in two related wolf spiders, presumably in accordance with their contemporary distribution and physiological constraints (DeVito et al., 2004). For a eurytopic species, the high degree of between-individual behavioural plasticity is assumed to be responsible for its persistence under a wider range of environmental circumstances. In contrast, higher individual plasticity in the stenotopic species is suggested to be beneficial for the species' persistence on the long term.

Acknowledgements

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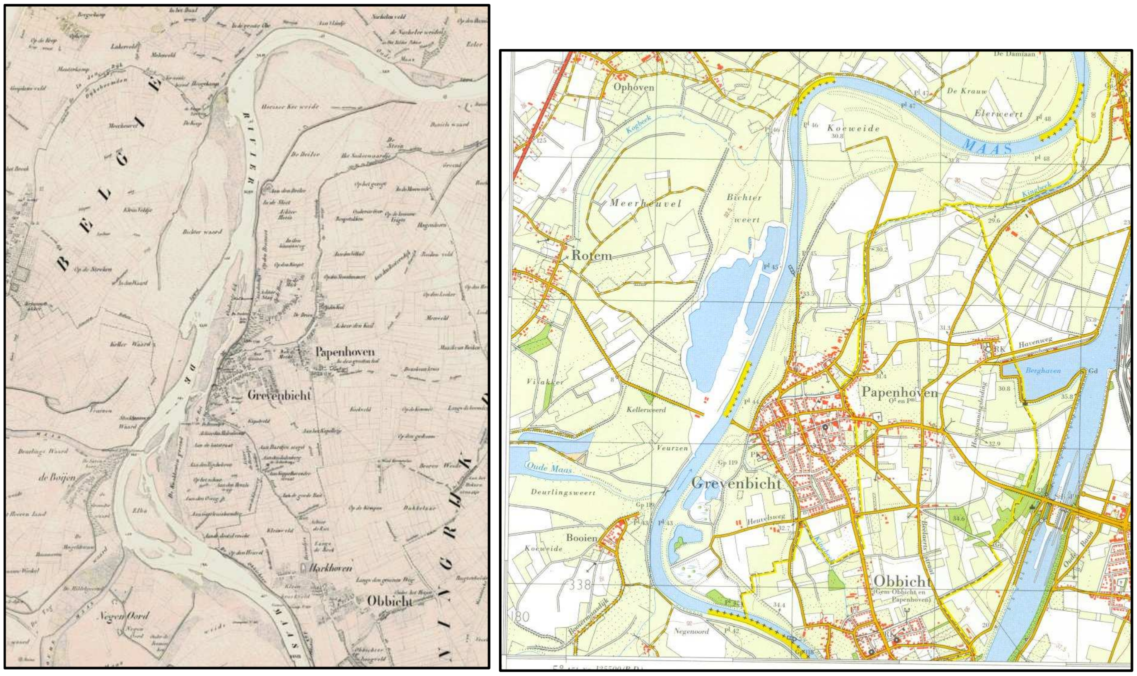
Authors' contributions

KL composed the experimental design, performed the experiments, analysed the data and drafted the manuscript. KL and DB formulated the research questions, interpreted and construed the results. JPM discussed the experimental set-up and was involved in the interpretation and presentation of the manuscript. All Authors have read and approved the final manuscript version.

IV. Population genetic structure of riparian arthropods



The Common Meuse trajectory between Dilsen-Stokkem and Elen (Belgium) // Obbicht and Illikhoven (the Netherlands) in 1849 (Gelderland Bibliotheek, Arnhem), and after river regulation from 1860 onwards (Topografische Dienst Nederland, 1979). The historical, broad gravel bed with rough river banks, old river arms and side-channels still showed numerous isles and gravel bars…

IV.1. Spatial genetic variation of a riparian wolf spider *Pardosa agricola* (Thorell, 1856) on lowland river banks

Lambeets K., Maelfait J.-P., Breyne P. & Bonte D. In prep.

River bank at Koeweide, one of the last strongholds of
Pardosa agricola (Thorell, 1856) (Photo: Kevin Lambeets)

Abstract

Habitat patches along lowland river systems are often highly structured and show a high degree of habitat heterogeneity on both spatial and temporal scales. The connectivity between river banks directly adjoining the river channel is often highly disturbed due to river regulation, and depends on a species' habitat affinity and dispersal capacity (functional connectivity). Moreover, natural stochastic events as flooding directly affect habitat and species distribution. As downstream drift of organisms might be expected in linear river ecosystems subject to unidirectional flow, asymmetric gene flow will manifest consequently. While flight-active arthropods easily disperse upstream, less mobile (cursorial) species are expected to show typical patterns hypothesised for linear populations and hence isolation-by-distance might occur. Here we analyzed patterns of genetic variation within and among nine spatially structured populations of the highly stenotopic wolf spider (Lycosidae) *Pardosa agricola* (Thorell, 1856) using Amplified Fragment Length Polymorphism (AFLP) markers. Genetic diversity is still very high in all populations and no downstream accumulation was found nor was genetic diversity higher in larger populations. Furthermore, nearby populations on the same river shore were clearly less genetically differentiated compared with populations far away and/or on the opposite shore; no isolation-by-distance patterns were present. This indicates short-distance dispersal still occurs, but the river channel forms a physical barrier for species exchange. Probably historical gene flow was higher and extended over the whole river reach. The disappearance of river banks upstream and their isolation downstream indicate river regulation measures corrupt gene flow, hence causing genetic differentiation to occur over a short period of time and on a small spatial scale. The rehabilitation of the riparian corridor is therefore needed to restore (upstream) functional connectivity for cursorial arthropods, whereas periods of sustainable low flow-discharges will benefit the exchange of individuals between opposite shores, additionally.

Key-words*:* AFLP, functional connectivity, genetic differentiation, Lycosidae, river regulation

Introduction

The interaction between demographic and genetic processes ultimately affects the persistence of species in spatially structured systems and should therefore underlie conservation efforts (Lande, 1988; Keller & Waller, 2002). While intensive ecological studies that aim to relate environmental parameters with species distribution patterns are a crucial first step, it is clear that insights into the genetic structure of complex populations, and thus the direction of species exchange (gene flow), provide additional information for species conservation (Frankham, 1995; Vernesi et al., 2008; Van Looy et al., 2009).

Because natural stochastic events are important for the persistence and the development of ecosystems, they concordantly affect population dynamics (Bonn et al., 2002; Robinson et al., 2002; Lake et al., 2007). The effects of these events will also depend on the traits of the inhabitants and the resulting distribution of their habitats (Johst et al., 2002; Bélisle, 2005). Consequently, disturbance events impact the genetic structure of their residents as well, especially in linear ecosystems where unidirectional drift of organisms (and genes) is expected (Stelter et al., 1997; Arens et al., 1998; Jacquemyn et al., 2006; Honnay et al., 2009). Moreover, asymmetric dispersal rates and reduced functional connectivity may decrease metapopulation viability (Vuillemier & Possingham, 2006) and limit behaviourial adaptations to the local conditions (Riechert, 1993a,b).

Rivers divide the landscape and create highly diverse ecosystems with increased habitat heterogeneity on different spatiotemporal scales (Ward et al., 2002; Wiens, 2002). The spatial distribution of habitat patches along a river's trajectory is often highly structured and functional connectivity generally depends on species' habitat affinity and their mobility (Dìaz et al., 2007; Paillex et al., 2007). This does not necessarily mean that more mobile species show a lower degree of genetic differentiation or vice versa since propagules can be obtained by water-mediated dispersal from upstream populations and/or zoochorous transfer (hydrochorous riparian plants; Tero et al., 2003; Pollux et al., 2009), resulting in a bidirectional pattern of gene flow (see Fig. I.5 for an overview of plausible configurations of the genetic structure of linear populations). However, for organisms with a more active dispersal mode evidence in this matter is still scarce (but see Stelter et al., 1997; Vignieri, 2005). Human practices often interrupt the connectivity between these patches (Ward & Stanford, 1995). River regulation (e.g. embankments, weirs) not only disrupts water discharge regimes but also modifies the patchiness of habitats which are directly affected by flooding (e.g. in-channel substrates, river banks), and additionally affects habitat suitability by sedimentation processes (Allan & Castillo, 2008). Moreover, disturbed water level fluctuations may distort dispersal movements of stenotopic riparian species (Plachter & Reich, 1998; Ward et al., 1998; Bates et al., 2006) and thus (re)colinisation events (Collinge et al., 2001). Next to it, the agricultural intensification and degradation of the surrounding catchment area (e.g. floodplains, riparian forest) intervenes in the lateral exchanges of organisms and obstructs migration movements from and towards overwintering sites (Rothenbücher & Schaefer, 2006).

While flight-active arthropods easily spread upstream (Stelter et al., 1997; MacNeale et al., 2005; Bates et al., 2006), cursorial arthropods are restricted by both environmental factors and their dispersal/movement ability (Bonte et al., 2003a). Lambeets et al. (2008b) showed that especially larger, cursorial, stenotopic riparian arthropods are subject to increased flooding disturbance. Although unidirectional (downstream) dispersal may still be possible (e.g. by water surface locomotion; Stratton et al., 2004; Lambeets & Bonte, subm.b), upstream transport of propagules is often hampered by the high degree of isolation and the low quality of remaining habitat patches along the riparian corridor (cost-distance effects; Fahrig, 2007). Population responses to stochastic events as flooding do not necessarily need to be attributed to purely environmental factors. Instead, they may be affected by interactions between "non-genetic" factors and genetic variation, i.e. by the interaction between demographic and genetic stochasticity (Frankham, 1995; Keller & Waller, 2002; Bossdorf et al., 2008).

We investigated patterns of genetic variation within and among spatially structured (sub)populations of the riparian wolf spider (Lycosidae) *Pardosa agricola* (Thorell, 1856) along the Common Meuse using dominant Amplified Fragment Length Polymorphism (AFLP) markers. The Common Meuse is the most undisturbed, dynamic mid-section of the River Meuse and still contains several isolated gravel bars and islands along its trajectory. AFLP-analysis has been proven useful to study genetic diversity in wolf spiders (Fu et al., 2008) and generally to study genetic differentiation with supposed asymmetric dispersal (Arens et al., 1998; Jacquemyn et al., 2006; Honnay et al., 2009). *P. agricola* is considered as a rare stenotopic riparian species (Albert & Albert, 1976; Harvey et al., 2002) that inhabits dynamic river banks throughout the year (Lambeets et al*.,* 2008a). As upstream populations were still present in 1998 along the Common Meuse, we noticed populations of *P. agricola* became isolated in the downstream section (Lambeets et al., 2007; Lambeets, 2008a). The presence of open, pioneer conditions created by regular flooding disturbance, benefits *P. agricola* (Lambeets et al., 2009). Therefore, the extinction of upstream populations might be caused by large scale flood events (discharges >2,500 m^3s^{-1}), from which the last-one dates back to January 2003 (see Honnay et al., 2009; Van Looy et al., 2009), and additionally due to unsuitable or unreachable flood-refuges nearby. Otherwise, the disruption of the flow regime, either by hydropeaking or extensive low flows (Semmerkrot et al., 1997; Liefveld & Schulze, 2005), might effectively degrade habitat suitability of the river banks for highly stenotopic species, e.g. by an overburden of loamy deposits on the bare gravel or siltation of the interstitial crevices (Paetzold et al., 2008). Currently, river restoration projects aim at restoring the connectivity between the river and the hinterland as well as the longitudinal connectivity of the riparian corridor by locally removing embankments and restoring a more natural discharge regime respectively (Van Looy & De Blust, 1995; Peters, 2006).

The general aims of this study were to assess whether the population structure of *P. agricola* matches the supposed asymmetric (unidirectional) pattern (i.e. a linear population structure caused by the water current; see Fig. I.5) of downstream habitat colonisation (Kawecki & Holt, 2002). As historical data suggests populations are disappearing in a downstream direction, unidirectional gene flow and genetic erosion of upstream populations, and thus isolation-by-distance, is expected to result from genetic differentiation. Hence, an increased genetic diversity might be expected in downstream populations due to the unidirectional influx of individuals and hence alleles. Additionally, between-population gene flow should be higher between adjacent (highly connected) populations on the same river shore compared with populations which are further away and/or on opposite shores. Based on the AFLP-derived genetic structure, implications for the rehabilitation of the riparian corridor are provided in the context of further river restoration efforts.

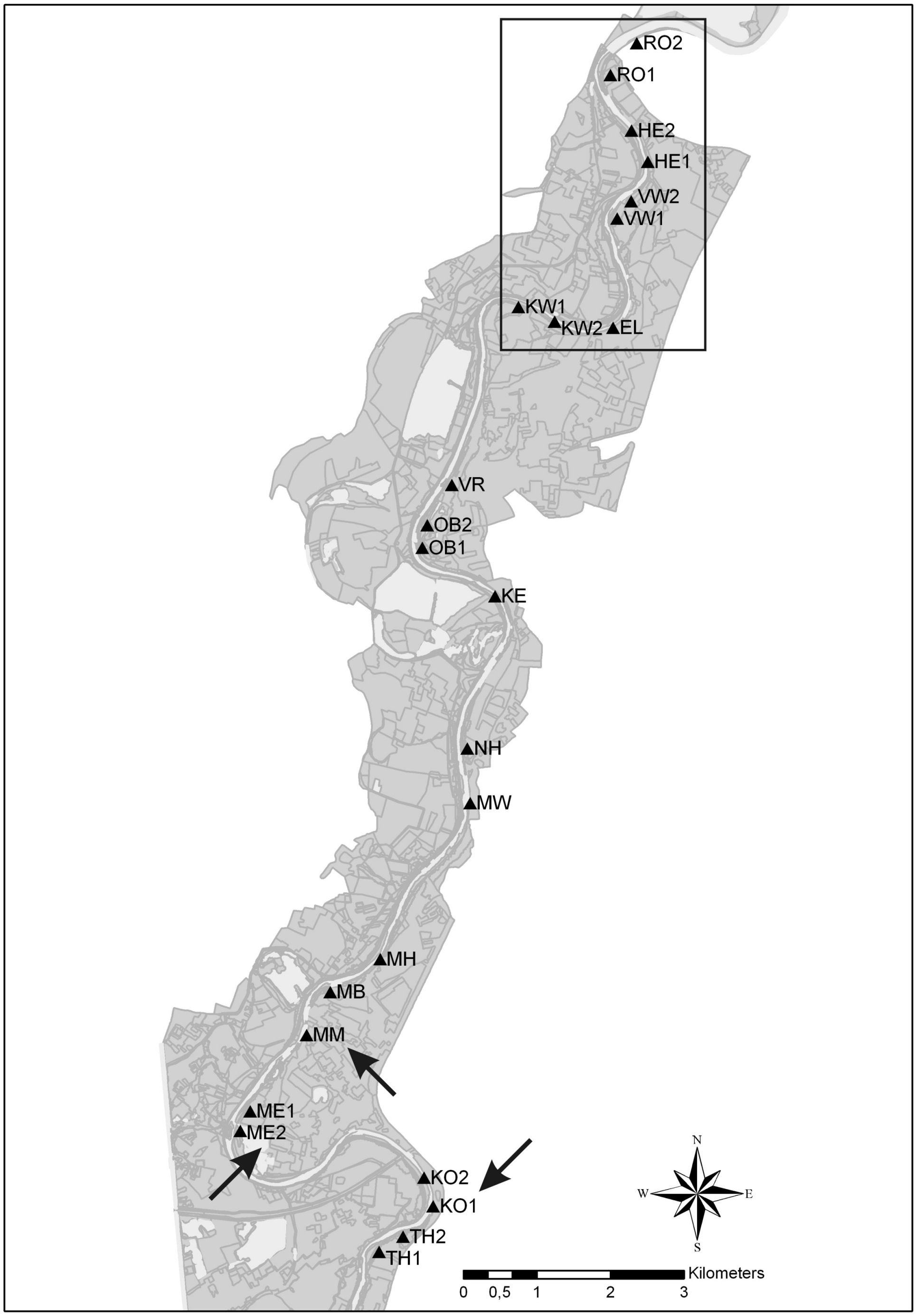


Fig. IV.1 - Locations of the nine sampled populations of *Pardosa agricola* along the Common Meuse. All sampled river banks (rectangular in-set) were situated in the most downstream part of this section of the River Meuse, just before the embanked section of the Sand Meuse which lacks gravel bars along its trajectory. Sample data from 1998 yet confirmed the presence of *P. agricola* upstream (arrows); some historical populations are not shown as these river banks have disappeared after the extreme flood event of 2003 (K. Van Looy, pers. comm.).

Material and methods

Study area, species and sampling

The Common Meuse is situated between Flanders (Belgium) in the West and the Netherlands in the East (Fig. IV.1). It is the 45 km long non-impounded, non-navigable semi-natural section of the River Meuse, and starts where the river descends from the rocky primary soils of the Ardennes and enters the lowlands. The high slope is responsible for its fast flowing gravel-bed character. Since it is rain-fed, the Common Meuse is characterised by strong water level fluctuations and a wandering pattern of isolated river banks (Van Looy & De Blust, 1995). Discharge regimes range from 10 m^3s^{-1} during dry periods up to 3,000 m^3s^{-1} in periods of (extremely) heavy rainfall in the catchment area. Due to canalisation and normalisation of the River Meuse, a tendency for prolonged low flows and hydropeaking along the Common Meuse occurs (Semmerkrot et al., 1997). Currently, parts of the Common Meuse are still heavily diked with concrete embankments or large stone boulders which restrain natural dynamic processes (van Winden et al., 2001). Over 50% of the alluvial plane is still intensively used for agricultural purposes while alluvial grasslands, sand-gravel bars or pioneer vegetation on overbank depositions only occupy 5% of the surface (K. Van Looy, pers. comm.).

Along the Common Meuse the stenotopic riparian wolf spider *Pardosa agricola* is one of the most abundant spider species (Lambeets et al., 2007; 2009). Controlled lab experiments with *P. agricola* juveniles (n = 340; 20 specimens per taken from each 17 females) showed no ballooning propensity at all for this wolf spiders species (Bonte & Lambeets, unpubl. data). The river banks where *P. agricola* still occurs in high numbers (rectangular in-set Fig. IV.1) are flooded after heavy rainfall in spring and early summer but remain inundated throughout late autumn and winter. This implies that all spiders have to move to higher ground during winter in order to hibernate (Lambeets & Bonte, subm.a) as they are merely able to survive submergence up to one month (Lambeets et al., 2008c). These river banks differ in their flooding susceptibility (discharge when flooded ranges from (dynamic) 76 m^3s^{-1} up to (more stable) 247 m^3s^{-1}, mean 172 m^3s^{-1} +/- 16SE), but still provide enough suitable habitat for *P. agricola* to establish viable populations (see Lambeets et al. 2007). On average the inter-patch distance amounts to 2521 m +/- 261SE (range: 390 m – 3354 m; Table IV.2). Furthermore, these banks are characterised by a clear succession of typical riparian plants such as *Rorippa sylvestris, Lythrum salicaria, Artemesia vulgaris, Polygonum aviculare* and *Xanthium orientale* (Peters et al., 2000). Despite extensive survey efforts in the surrounding grassland habitats, no specimens of *P. agricola* were found, even along the river dikes or at distances only a few meters away (K. Lambeets, pers. obs.), except for a small relict population at an erosion channel nearby river bank KE (Fig. I.1.; Lambeets et al., 2005). During an intensive sampling in 2005, however, six individuals were caught on KE and one at MB and MW (arrows Fig. IV.1), each in July; KE concerns a newly formed river bank after the extreme flood of 2003 whereas the river bank at MW was restored in 2001 (Van Looy, 2004). This might indicate that, certainly at KE, a relict population might still be present.

In May and August 2007, *P. agricola* individuals of the downstream river banks were collected by hand sampling. We were not able to find any individuals at KE. We collected between 9-23 individuals per population (Table IV.1). All wolf spiders were stored in large plastic vials with a humid tissue and transported to the laboratory where they were individually separated into smaller plastic vials with a humid plaster bottom before DNA extraction.

river bank	**river shore**	**x**	**y**	**n**	**H_j**	**PPL**
KW1	right (NL)	248896	195570	**23**	**0.3952**	**96.6**
KW2	right (NL)	249387	195369	**13**	**0.3962**	**96.6**
EL	left (VL)	250184	195286	**25**	**0.4073**	**100**
VW1	right (NL)	250239	196771	**15**	**0.3899**	**93.2**
VW2	right (NL)	250428	197006	**14**	**0.3768**	**93.2**
HE1	left (VL)	250655	197545	**11**	**0.3873**	**96.6**
HE2	left (VL)	250432	197967	**9**	**0.4101**	**96.6**
RO1	right (NL)	250145	198723	**18**	**0.3919**	**98.3**
RO2	right (NL)	250505	199156	**23**	**0.3693**	**91.5**
			Mean (SE)	**16.8 (1.9)**	**0.3915 (0.0043)**	**95.8 (0.9)**

Table IV.1 - Characteristics of the nine *Pardosa agricola* populations on river banks along the Common Meuse. *n*: number of individuals; H_j: expected heterozygosity; *PPL*: percentage polymorphic loci; *x* and *y* coordinates according to Belgian Lambert grid; NL: shore at the Dutch river side (the Netherlands) and VL: shore at the Flemish side (Belgium).

AFLP analysis

The day after sampling, all wolf spiders were frozen in liquid nitrogen, freeze-dried for 48h and homogenised with a mill (Retsch MM 200) to fine powder. DNA was extracted from the thorax and legs using the DNeasy Blood & Tissue kit (Qiagen). DNA quality and concentration were estimated on 1.5% agarose gels. Hundred ng of DNA was used for AFLP analysis according to Vos et al. (1995). Restriction and ligation was performed in a single step. Amplification of fragments was performed in 2 steps using the primer combinations P*st*I+A/M*se*I+A for preamplification and P*st*I+AGT/M*se*I+ACC, P*st*I+ACT/M*se*I+ACC, P*st*I+ACT/M*se*I+AGA, P*st*I+ACT/M*se*I+AGG for selective amplification. Fragment separation and detection took place on a Nen IR^2 DNA analyzer (Licor) using 36 cm denaturing gels with 6.5% polyacrylamide. IRDye size standards (50 to 700 bp) were included for sizing of the fragments. Control samples were included in each gel to check for reproducibility between gels. Only clear, intense bands were scored. Scoring was done using the SAGAmx software (LI-COR Biosciences). We scored the presence or absence of every marker in each individual as 1 or 0 (present or absent) to form a binary data matrix.

Data analysis

Based on allele frequencies, within-genetic diversity was estimated by the proportion of polymorphic loci (PLP) and Nei's genetic diversity (expected heterzygosity, H_j and average heterozygosity, H_w) as well as the proportion of total genetic variability within a population compared to the total genetic variability (population differentiation; F_{ST}; 500 permutations) and total metapopulation diversity (H_t) (Lynch & Milligan, 1994). These measures were calculated by AFLP-SURV (Vekemans et al., 2002). To identify whether or not larger populations are genetically more diverse, a linear regression was performed between a surrogate measure for local population size and H_j as well as PPL (SAS 9.1, proc reg). Population size was approximated by using the numbers of individuals caught during an intensive pitfall sampling campaign (see Lambeets et al., 2008b; 2009) multiplied by the river bank width at that moment (a proxy for the amount of suitable habitat). As samples were collected during the main activity period of *P. agricola* (May - June) and in the same habitat type, this product represents a relative proxy for population size (Baars, 1979), notwithstanding pitfall traps rather reflect activity-densities (Maelfait & Baert, 1975).

To assess the degree of molecular variation within and among populations, total genetic diversity was partitioned by applying a hierarchical analysis of molecular variance (AMOVA; Table IV.2) on Euclidean pairwise genetic distances using GENALEX 6.1 (Peakall & Smouse, 2005). Significances were determined based on 999 permutations. The $Ø_{ST}$ is an analogue for F_{ST}-values used for dominant markers such as AFLP, and was derived from the Euclidean genetic distances. Its significance was calculated using the Monte Carlo procedure in GENALEX 6.1 (999 permutations).

Pairwise genetic distances among the nine investigated populations and their level of significance were obtained from AMOVA. Again 999 permutations were applied. A principal coordinates analysis (PCoA) was performed on this matrix using GENALEX 6.1 and the first two axes were plotted graphically. The relationship between pairwise genetic distances (F_{ST}), derived from AFLP-SURV, and geographic distances (Table IV.3), respectively along the river channel and Euclidean distances (calculated by ArcGIS 9.1), was assessed with Mantel-tests implemented within the ade4 package of R statistical software v. 2.6.0 (R Development Core team; 999 replicates). In order to test for the existence of functional connectivity, we similarly performed a Mantel-test between pairwise genetic distances and pairwise river bank ranking according to their degree of functional connectivity as estimated by previous experimental work (Lambeets & Bonte, subm.b). River banks that are connected during summer and reachable by cursorial movement were ranked 1, those that are situated at the same river side, but only reachable by cursorial movement during extremely low water flows as 2, those close together but separated by the river as 3 and those distantly located and on the opposite river side as 4 (Table IV.3).

Source of variation	**df**	**SS**	**MS**	**Est. Var.**	**%**
Among populations	8	157.864	19.733	0.585	6%
Within populations	144	1430.403	9.933	9.933	94%
Total	**152**	**1588.267**		**10.518**	**100%**

Table IV.2 - Hierarchical analysis of molecular variance (AMOVA) based on 59 AFLP loci in nine populations of *Pardosa agricola*.

To test the hypothesis of upstream genetic erosion due to downstream drift after being washed away, a linear regression was performed between the distances from the banks along the river channel in a downstream direction and H_j as well as PPL (SAS 9.1; proc reg). Similarly we tested the hypothesis that genetic variation would be negatively related to the magnitude of local flooding disturbance because of frequent colonisation/extinction events. A previously derived compound measure of flooding disturbance (PC_{dyn}; see Lambeets et al., 2008b) was used to test the relation with expected heterzygosity (H_j).

Population	**KW1**	**KW2**	**EL**	**VW1**	**VW2**	**HE1**	**HE2**	**RO1**	**RO2**
KW1	0	542 [1]	1333 [3]	2963 [2]	3354 [2]	3898 [4]	4361 [4]	5296 [2]	6030 [2]
KW2	0^{ns}	0	791 [3]	2421 [2]	2812 [2]	3356 [4]	3819 [4]	4753 [2]	5488 [2]
EL	0.0211*	0.0228*	0	1630 [4]	2021 [4]	2565 [2]	3028 [2]	3962 [4]	4697 [4]
VW1	0.0195**	0.0159*	0.0099**	0	390 [1]	934 [3]	1397 [3]	2332 [2]	3067 [2]
VW2	0.0371**	0.0226**	0.0321**	0.001^{ns}	0	544 [3]	1007 [3]	1941 [2]	2676 [2]
HE1	0.0591**	0.0703**	0.046**	0.0332**	0.0587**	0	463 [1]	1397 [3]	2132 [3]
HE2	0.0375**	0.0402**	0.0298**	0.0303**	0.0583**	0.0015^{ns}	0	934 [3]	1669 [3]
RO1	0.0415**	0.0373**	0.0309**	0.0285**	0.0574**	0.0359**	0.0143^{ns}	0	734 [1]
RO2	0.0247**	0.0283**	0.0199**	0.011**	0.0406**	0.0546**	0.0372**	0.0231**	0

Table IV.3 - Pairwise genetic (F_{ST}; below the diagonal) and geographic distances (m; above the diagonal, [functional connectivity ranking]) for nine populations of *Pardosa agricola* along the Common Meuse (* $p < 0.05$; ** $p < 0.01$; *ns* not significant).

Results

The four AFLP primer combinations resulted in 59 highly reliable polymorphic markers. Our data-set contained information for 153 wolf spider individuals spread over nine populations with different population sizes (Lambeets et al., 2007; Lambeets, 2008a).

Genetic diversity within populations was high (Table IV.1), with the percentage of polymorphic loci (PPL) ranging from 91.5 to 100 (mean: 95.84). Concordantly, the average expected heterozygosity (H_w) was 0.392 (range per population, H_j: 0.370 – 0.413). PLP nor H_j were significantly related to population size (resp. $t = 0.65$, $p = 0.5379$; $t = 0.91$, $p = 0.3921$). Genetic diversity (H_j) is not accumulating downstream ($t = -1.35$, $p = 0.3611$) nor is it affected by flooding disturbance ($t = 0.98$, $p = 0.3611$), ruling out upstream erosion and local colonisation-extinction dynamics.

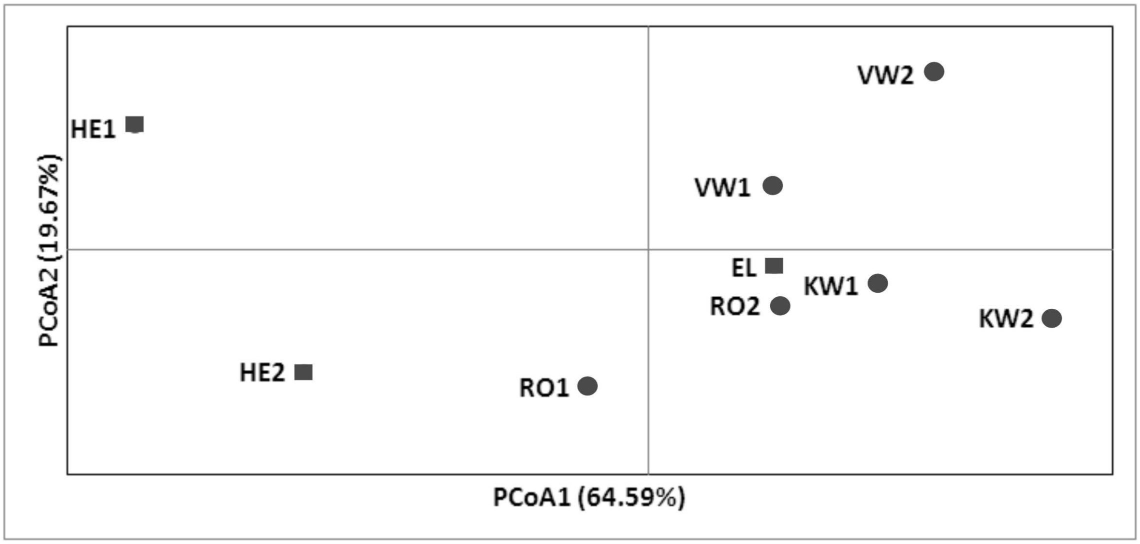


Fig. IV.2 - Principal coordinates (PCoA) plot of first two axes calculated based on 59 polymorphic markers and using Nei's genetic distances between populations. River banks at the left river shore (Flanders, Belgium) are indicated by a square, banks at the right river shore (the Netherlands) by a circle. The codes referring to the populations are described in Table IV.1.

Total genetic diversity (H_t) was 0.4043. F_{ST} of the actual (sampled) population was 0.0316 and differed significantly from a random assemblage of individuals (500 permutations; $p < 0.0001$). This indicates actual populations are genetically more differentiated than random assemblages of individuals. The AMOVA-derived $Ø_{ST}$ value was 0.056 (99 permutations; $p = 0.01$) was very similar to F_{ST}. Nonetheless, only 6% of the genetic variation could be attributed to variation between populations ($p = 0.001$; Table IV.2), whereas 94% was explained by intra-population differentiation ($p = 0.001$).

The first two principal components (PCoA; Fig. IV.2) explained 64.6% and 19.7% of the total variance in genetic variation. Remarkably, this pattern deviates from our expectancy of unidirectional gene flow. The Mantel-tests showed no significant relationship between pairwise F_{ST}-values and pairwise geographic distances (i.e. distance along the river channel; $r = 2x10^{-6}$, $p = 0.1931$) or Euclidean distances ($r = 4x10^{-6}$, $p = 0.1708$), respectively (Fig. IV.3a,b; Table IV.3), which indicates the lack of isolation-by-distance. However, a significant positive correlation was found according to the functional connectivity ranking between river banks ($r = 0.0067$, $p = 0.0096$; Fig. IV.3c). This demonstrates the isolation of river banks along the same shore versus on opposite shores (Table IV.3), just as was revealed by the PCoA.

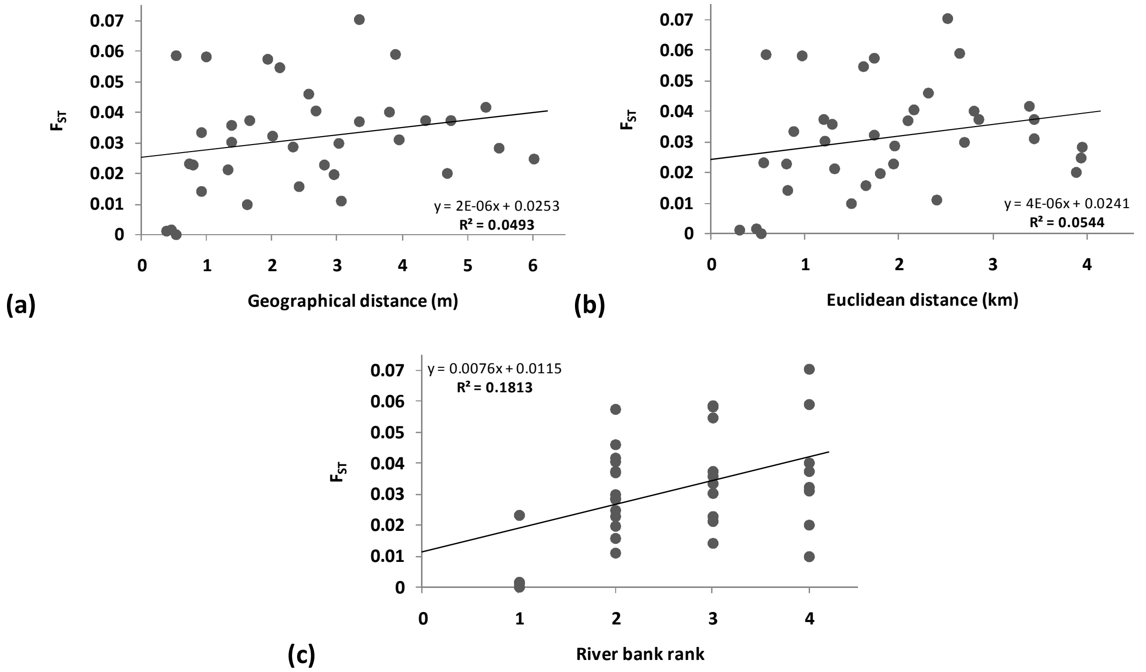


Fig. IV.3 - Relationship between pairwise genetic distances (F_{ST}) and (a) pairwise geographic distances (along the river channel), (b) Euclidean distances and (c) functional connectivity (ranking over river banks), representing isolation-by-distance relations for a metapopulation of 173 *Pardosa agricola* individuals.

Discussion

Genetic differentiation and genetic diversity in a wolf spider population

The studied populations of a stenotopic riparian wolf spider of nine river banks along the semi-natural Common Meuse suggest that river regulation and the isolation of the river banks did not strongly affect the genetic diversity of *Pardosa agricola*. Yet, our results provide evidence of decreasing functional connectivity since populations originating from opposite river shores are more genetically differentiated.

The within-population genetic diversity found for *P. agricola* (H_W: 0.392; PPL: 95.8) was considerably higher than for a recent AFLP-based study of Fu et al. (2008) considering widely dispersed populations of the wolf spider *P. pseudoannulata* (H_W: 0.2554; PPL: 72.99). The high levels of genetic diversity also indicate that the populations of *P. agricola* are likely to be of a common ancestry since it takes time for diversity to decrease (Keller & Waller, 2002).

Moreover, our results suggest that river regulation and the resulting fragmentation of populations or the disappearance of upstream populations did not strongly affect genetic diversity in *P. agricola*. Given the intensification of the surrounding land-use during the past century, the time since fragmentation of the river banks (by the erection of a substantial network of dikes the past century) might have been too short to reduce population genetic diversity within populations, notwithstanding the low dispersal power of *P. agricola* (cf. Boulton et al., 1998; Bonte et al., 2003a). Genetic diversity did not increase downstream, by which the hypothesis of unidirectional, asymmetric dispersal, presumably underlying genetic structure in linear ecosystems, can be rejected (Tero et al., 2003; Vuillemier & Possingham, 2006).

As our study was implemented along a 9 km-long river section, a low degree of genetic differentiation between *P. agricola* populations could be expected (F_{ST}: 0.0316; $Ø_{ST}$: 0.056). To compare, riparian plants occurring along the Common Meuse generally show higher differentiation, such as the perennial pioneer *Sisymbrium austriacum* (F_{ST}: 0.097; $Ø_{ST}$: 0.091; Jacquemyn et al., 2006) and the dry grassland species *Origanum vulgare* ($Ø_{ST}$: 0.24; Van Looy et al., 2009). Honnay et al. (2009) found genetic differentiation of the pioneer plant *Erysimum cheiranthoides* to increase over three years of sampling (F_{ST}: 0.06, 0.11, 0.17; $Ø_{ST}$: 0.06, 0.08, 0.18). Yet, studies considering wolf spider populations in other dynamic, not linear organised systems also showed low genetic differentiation, even at much larger scales (coastal dunes - *P. monticola*, allozyme-based F_{ST}: 0.011 (Bonte et al., 2003a) and *Geolycosa pikei*, allozyme-based F_{ST}: 0.020 (Boulton et al., 1998); pine woodlands within an agricultural matrix – morphospecies “Wirra”, mitochondrial DNA-based F_{ST}: 0.086 (Colgan et al., 2002)).

The effects of fragmentation on metapopulations depend on the mobility and thus dispersal rates of species (Casagrandi & Gatto, 2002). Therefore, arthropods capable of active flight (cf. ballooning in spiders) may encounter little difficulty maintaining gene flow among populations surrounded by an unfavourable matrix (Ramirez & Haakonsen, 1999; MacNeale et al., 2005). Cursorial species with restricted mobility might experience more hindrance of impassable boundaries (Bowler & Benton, 2005), with a decreased genetic exchange as result (e.g. Vignieri, 2005). However, such expectations may not always be fulfilled, as shown by Desender et al. (2005) for stenotopic, brachypterous carabid beetles from woodland patches within an urbanised landscape matrix. Desender and colleagues suggested that genetic diversity might even increase as an adaptation to increased habitat heterogeneity. Additionally, the degree of habitat specialisation may confound genetic structure as it is often correlated to dispersal capacity. Gene flow of specialist species, often being less mobile (Bonte et al., 2003b; 2004), might be more hampered by (physical) barriers than of generalists (Bonte et al., 2003a; Brouat et al., 2003). Still, genetic differentiation of *P. agricola* is mainly explained by within-population variation (94%), as is often the case for sedentary predatory arthropods as spiders (Ramirez & Haakonsen, 1999; Pedersen & Loeschke, 2001; but see Fu et al., 2008), confirming genetic diversity is still high.

Functional connectivity affects *P. agricola*'s genetic structure more than geographic isolation, obviously because the species will not spontaneously cross the current river channel (Lambeets & Bonte, subm.b). Studies showing isolation-by-distance or downstream (unidirectional) accumulation of genetic diversity often consider much longer river trajectories (Imbert & Lefèvre, 2003; Van Looy et al., 2009). But even for plants this does not necessarily imply the presence of isolation-by-distance effects (Tero et al., 2003; Jacquemyn et al., 2006; Honnay et al., 2009; Pollux et al., 2009). Unfortunately, evidence of isolation-by-distance for arthropods inhabiting linear ecosystems with a unidirectional gradient could not be found in recent literature (but see Peterson et al., 2001; Bonte et al., 2003a; Desender et al., 2005 for other habitat types). Lab experiments indicated the absence of ballooning in the species in accordance with the theory that costs of landing offshore or reaching unsuitable habitat can be expected to be too high (Bonte et al., 2003b; 2006; 2007). Because currently occupied patches are also hypothesised to be functionally isolated in order to allow gene flow between distant populations, we attribute the low genetic differentiation more to historical than to recent gene flow, i.e. due to recent colonisation of a highly dynamic ecosystem (cf. Honnay et al., 2009; Van Looy et al., 2009).

Geologically, the recent location of the River Meuse became relatively stable only 10.000 BP (Broothaers, 1996). Consequently, riparian patches along its trajectory could only been colonised recently (post-glacial range expansion), which may result in low genetic variation and between-population differentiation (cf. Pederschen & Loeschke, 2001). Particularly isolated patches along the river shoreline might have been liable to founder effects by repeated events of genetic drift after (re)colonisation (Boulton et al., 1998), contrary to more contiguous alluvial grasslands (Van Looy et al., 2009). Moreover, F_{ST}-values may rather reflect historical patterns of between-population genetic exchange than current levels of migration (Bonte et al., 2003a; Imbert & Lefèvre, 2003) and may differ according to the technique used (Dhuyvetter et al., 2004). Besides the relatively young geological history of the River Meuse, river banks along the Common Meuse only became highly isolated after the intensification of gravel mining practices and the exploitation of the hinterland (ca. 150 ago; Van Looy & De Blust, 1995). Hence, the currently observed low levels of genetic differentiation might stem from higher levels of gene flow in the past. The surrounding landscape may, nevertheless, play an important role for between-population exchanges of cursorial arthropods (Desender et al., 2005; Jopp & Reuter, 2005; Fahrig, 2007). Therefore, genetic differentiation of *P. agricola* populations might still increase if the exchange of individuals between river banks, and hence functional connectivity, will not be re-established (cf. Honnay et al., 2009).

Nearby populations were less genetically differentiated, which suggests short-distance exchange of individuals during periods of benign low flow still occurs. Although unlikely in our model system, nearby river banks may also have been colonised by the same founding group (Van Looy et al., 2009). The higher pairwise F_{ST}-values, e.g. between HE and the other river banks (Table IV.3), indicate that founder effects might have caused the genetic variation in the study system (Frankham, 1995; Boulton et al., 1998), yet no relationship between flooding disturbance and genetic diversity was found. Moreover, higher genetic differentiation of populations from opposite river shores confirms the validity of our functional connectivity approach which is based on the flood-avoiding behaviour of *P. agricola* (cf. Riechert, 1993a,b). Nevertheless *P. agricola* is capable of active water dispersal, landing offshore is costly and the probability of effectively relocating suitable patches downstream might be extremely low due to the fragmented character of the river banks and will depend on the local conditions permitting retention of drifting propagules (Riis & Sand-Jensen, 2006) and hence stream size (Bang et al., 2007).

Riparian corridor connectivity and species conservation

Along with the extreme flood event of 2003 an impressive influx of plant species was recorded and several newly formed gravel bars occurred along the river corridor (K. Van Looy, pers. obs.). Still, cursorial arthropods such as wolf spiders are disadvantaged by extreme and sudden floods (Lambeets et al., 2008b) as they might not be able to escape the flooding in time or when suitable flood refuges become unreachable (Rothenbücher & Schaefer, 2006; Lambeets & Bonte, subm.a). Smaller, flight-active arthropods such as carabid beetles, however, may re-establish viable populations quickly (Bonn et al., 2002; Hering et al., 2004; Brugmans et al., 2005) since they are able to escape sudden floods efficiently or they may even extend their distribution when more suitable patches become available (MacNeale et al., 2005; Bates et al. 2006). Generally, short-lasting low flows in summer will prove beneficial particularly for cursorial riparian arthropods as it allows them to migrate upstream when gravel bars are exposed and hence (re)colonise available habitat patches. But even low flow conditions during summer are highly disturbed as a consequence of upstream weirs and the draining of large amounts of cooling water by the upstream hydropower plant at Lixhe (Semmerkrot et al., 1997). As proven by Van Looy et al. (2008), the resulting sudden changes in water discharge were more adverse for carabid beetle assemblages directly downstream of the power plant, i.e. at the origin of the Common Meuse river section. In addition, this may explain why *P. agricola* and other large riparian wolf spiders such as *Arctosa cinerea* (Fabricius, 1777), disappeared from river banks upstream (KO and further upstream). By weighing the costs and benefits of an ecologically sustainable discharge regime, however, a minimal water level and discharge should always remain to preserve rheophilic species as well (Liefveld & Schulze, 2005). As dispersal is assumed to be asymmetric in river ecosystems (mainly downstream; e.g. Pollux et al., 2009; Van Looy et al., 2009; but see MacNeale et al., 2005; Honnay et al., 2009), reconnecting patches by the reestablishment of an extensive riparian corridor is unlikely to lead to an increased metapopulation persistence (Veullemier & Possingham, 2006), unless *P. agricola* individuals show a tendency to predominantly disperse along the river shoreline in an upstream direction (cf. Riechert, 1993b).

Genetic diversity is still very high in all populations, yet we found prove that isolation, even on this small spatial scale and by the physical presence of the river, affects the genetic structure of a cursorial stenotopic wolf spider. Therefore, rehabilitation of the riparian corridor is needed, functionally reconnecting existing populations on a landscape scale and giving cursorial species the chance to disperse upstream or to cross the river at low costs. Current river restoration projects implemented by dike removal and a widening of the current channel will prove beneficial in that opinion (Van Looy, 2004; Peters, 2006), certainly when they would, effectively, integrate the requirements of stenotopic riparian arthropods (Lambeets et al., 2008a,b; 2009). Additionally, conservation and restoration efforts should integrate spatial and temporal patterns of water discharges regime (Geilen et al., 2004; Liefveld & Schulze, 2005; Van Looy et al., 2006). Hence, allowing for a more natural flooding frequency and magnitude within a less intensively used landscape will preserve and increase heterogeneity along different spatiotemporal scales and consequently re-establish and connect suitable habitat patches along-stream (Ward & Stanford, 1995; Lake et al., 2007).

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Authors' contributions

The work presented here was carried out in collaboration between all authors and institutions. KL and JPM collected the specimens. KL extracted DNA, performed AFLP scoring, analysed the data and wrote the paper. PB provided the necessary facilities and verified AFLP scoring. KL, JPM and DB conceptualised the research questions, interpreted and discussed the results. JPM and DB conceived ideas for this project and discussed the presentation. All authors have contributed to, seen and approved the final version of the paper.

V. Synthesis and Conclusions

The Common Meuse at Meers during early summer; one of the first (successful) river restoration projects within the framework of the *Living River Concept* (Photo: Kevin Lambeets)

5.1 General conclusions

Arthropod assemblages from lowland river banks

The assemblages of spiders (Araneae) and carabid beetles (Carabidae) on river banks of the Common Meuse were proven to be highly heterogeneous in their species composition (see II.1., II.3.). Typical riparian species appeared on specific river banks according to their habitat affinity, complemented by xerothermophilic species on higher, more stable gravel bars and hygrophilic species on less stable, rather loamy banks. Beside that, pioneer species and agrobionts with optima in the surrounding, intensively used agricultural landscape, were present on all river banks. These habitats are in a way comparable with river banks due to their disturbed character (cf. Samu & Szinetár, 2002), e.g. tillage during winter. Our data also showed that carabid beetles are more resilient to changes in water flow conditions than spiders (see II.2.). Concordantly, stenotopic riparian carabids are less restricted to certain river banks conditions (see Appendix A6. for a complete list and functional group classification). However, small-sized, hygrophilic carabids appear more vulnerable to disrupted flooding, in contrary to what has been suggested in other studies (Bates et al., 2006). Particularly, larger, cursorial riparian spiders are disadvantaged by increased flooding disturbance (see II.2.). Generally, species sorting under influence of increased or too low flooding caused more specialised assemblages of riparian arthropods to be replaced by assemblages of eurytopic species on, respectively, less or more stable river banks along the Common Meuse. Highly dispersive, eurytopic species from the neighbouring arable habitats dominate highly disturbed river banks, indicating mass effects structure riparian arthropod assemblage under intensive flooding. Assemblage shifts of spiders and carabid beetles, however, could not always be explained by similar trait-displacements; often differences appeared according to the lower phylogenetic level studied (subfamily for spiders; tribe for carabids). In agreement with the results of Lambeets et al. (2008a), species composition of spiders and carabid beetles was influenced by the same environmental factors (see II.3.). Primarily flooding disturbance of the river banks constrained species composition of both groups, but sediment composition and vegetation cover also explained variation therein. Not surprisingly, these factors restricted the distribution of rare stenotopic riparian species. By employing a functional group and a multi-species approach, increased flooding disturbance was shown to disfavour xerothermophilic specialists and larger, cursorial spiders (e.g.

Caviphantes saxetorum, *Arctosa cinerea*) but not macropterous carabid beetles (e.g. *Agonum marginatum*, *Bembidion atrocaeruleum*). Hygrophilic species benefited from a denser vegetation cover, in agreement with results of Kleinwächter & Rickfelder (2007) for a rare riparian carabid beetle, *Bembidion velox* (only found in small numbers along the Common Meuse; see Appendix A6.). Since each river bank is characterised by a certain flow regime by which it is inundated, species composition also depended on the moment when the banks are exposed. Hence, the main activity period of each species will also influence its occurrence (see II.3.). These so-called *colonisation windows* were also shown to operate and determine assemblage structure in other ecosystems such as arable fields (Ribera et al., 2001; Petersen, 1999) and coastal grey dunes (Bonte et al., 2006a). Moreover, the flooding susceptibility of river banks affects also the life-history cycle of riparian wolf spiders (K. Lambeets and colleagues, unpubl. data). First of all, *P. agricola* cohorts shifted towards generally larger individuals on less disturbed river banks, whereas its reproductive output remained similar irrespective of the local conditions. Contrasting patterns were found for *P. amentata*. These results confirm the assumption that the moment of exposure does affect life history patterns, yet more in-detail studies are still advisable.

From these results it is obvious that variation in assemblages of riparian arthropods is enhanced by different flood regimes and thus a high environmental heterogeneity. Anthropogenic alterations of the water discharges, resulting in either too high or too low degrees of flooding disturbance *sensu lato*, can be expected to alter these assemblages drastically. Emphasizing on functional responses besides environmental constraints will increase our understanding of the functioning of riverine ecosystems on a local scale and, more specifically, how to preserve the rare riparian arthropods inhabiting these highly threatened and dynamic transition zones. The restoration of more natural hydrogeomorphic processes is essential for the rehabilitation of the river's integrity (Poff et al., 1997; Pedroli et al., 2002) and hence to maximise biodiversity in general (on a larger spatial scale; Ward et al., 1999; Sabo et al., 2005), by preserving its vulnerable inhabitants (Sadler et al., 2004; Paetzold et al., 2008). Considering response patterns on hierarchical scales and across taxa provides policy makers with complementary information for sustainable river management (Tockner et al., 2006; Lake et al., 2007).

Variation in movement behaviour and genetic structure

Although flooding disturbance and functional life-history traits simultaneously affect the assemblage structure and species composition of riparian arthropods along the Common Meuse, other aspects such as movement behaviour, might do so as well (Ward et al., 1998). In chapter III we discussed that mobility, amongst other traits, intervened in the occurrence of arthropods throughout the river reach. By analysing (flood-avoiding) movement behaviour (see III.1., III.4.) and the stimuli guiding movement decisions (III.2., III.3.), we proved that behavioural responses of a stenotopic riparian wolf spider clearly diverged from a less specialised congener. As arthropods capable of active flight can easily escape flood events by simply flying away when necessary, it might benefit them to avoid excess energy expenditure by leaving the river banks before it is inundated (see III.2.). The results from chapter II.2. indicated that particularly wolf spiders (Lycosidae) are vulnerable to increased flooding, whereas ballooning, agrobiont linyphiid spiders (Erigoninae, Linyphiinae) increase. But, their higher mobility, being passive-uncontrolled and influenced by thermal conditions (Bonte et al., 2008b), also increases their vulnerability to winter flooding as they end up on the river bank in autumn and may not able to escape flooding in time. Hence, river banks rather act as sink habitats for agrobiont spiders (cf. cereal fields after ploughing; Topping & Sunderland, 1998; Öberg et al., 2008). Another option is to leave the river bank before it is flooded. Nevertheless relative numbers of other spiders also decreased throughout autumn (see III.2.), only the highly stenotopic wolf spider *P. agricola* showed a proactive migration movement towards the denser dike vegetation (cf. Lang & Pütz, 1999). These results emphasize the importance of suitable hibernation habitats in the direct vicinity of the river banks (Loeser et al., 2006; Rothenbücher & Schaefer, 2006), which coincides with results from similar studies concerning arable land habitats (Pywell et al., 2005; Schmidt & Tscharntke, 2005b). This confirms the results of chapter II.2., that larger, cursorial riparian spiders are the most vulnerable to human-induced changes in water discharge regimes. Although carabids may easily escape sudden flood events (Bonn, 2000; Bates et al., 2006), their (re)colonisation rates will also depend on the surrounding landscape composition (Petersen, 1999; Purtauf et al., 2004). Also, for agricultural environments, it has been generally acknowledged that the surrounding landscape matrix influences arthropod occurrence patterns and species richness, next to local habitat quality and the applied disturbance regime (Niemelä et al., 2002; Öberg et al., 2007; Drapela et al., 2008). Hence, a fluent transition from the riparian corridor towards the hinterland and an increased quality of nearby habitats for overwintering, will add to the conservation of, especially, less mobile riparian arthropods.

Directed movement, such as gradually migrating from the proximity of the river channel towards the dike vegetation, and possibly further on, also implies there are certain factors that guide the way. Indeed, an accurate orientation which precedes movement reduces costs involved with ending up at unsuitable conditions (Jander, 1975). As wolf spiders in general appeared most sensitive to flooding (see II.2., III.1.), we selected two closely related wolf spider species that differed in their degree of habitat specificity and tested their orientation and movement behaviour under field conditions. Apparently, mainly internal factors, related to their geographical origin (river bank side), guide their movement towards the winter habitat in late summer (see III.2.). Their decisions under sudden stressful situations (zonal recovery after landing offshore) are mainly based on population-specific information (see III.3.). The stenotopic riparian wolf spider, *P. agricola*, was found to make use of proximate cues rather under stressful circumstances, compared to when plausible threatening conditions were absent (no direct contact with water). Consequently, by restricting unnecessary movements and avoiding costly situations involved with flooding both in autumn (winter flooding; see III.1, III.4.) and spring (unpredictable floods; see III.3.), beneficial decisions arise. Moreover, our results suggest that other, not-identified factors confound the movement behaviour of the generalist wolf spider *P. amentata*, resulting in less consistent behavioural responses. This might be explained as it only sporadically inhabits river banks, and probably shows other movement behaviour in its preferred habitat (moist grassland habitats; Alderweireldt & Maelfait, 1988; cf. *P. lugubris*: Edgar (1971); *P. agrestis*: Samu et al. (2003)). Zollner & Lima (2005) discuss how behavioural strategies can differ according to the prevailing conditions. By simulating a river bank environment and yet keeping the wolf spiders under ambient conditions, we found clear differences in active flood-avoiding behaviour (see III.4). In agreement with the higher behavioural consistency during zonal recovery (see III.3.), *P. agricola* also showed more systematic responses under simulated flooding than *P. amentata*. Still, both species were equally able to withstand inundation, but not more than five days on average (maximum period of submersion tolerance: 35 days). This indicates wolf spiders are able to survive short-lasting flood events easily (flood pulses in spring often only last one day; Van Looy & De Blust, 1995) by hiding in flood refuges (Zulka, 1994; Framenau et al., 1996; Decleer, 2003). Earlier experiments concerning the submersion tolerance of wolf spiders from alluvial grasslands confirm our results (maximum period of submersion tolerance: *P. amentata*, 9 days; *P. proxima*, three days; *P. purbeckensis*, 11 days, and other wolf spiders of the genus *Pirata*: *P. hygrophilus*, 24 days; *P. latitans*, 16 days; *P. piraticus*, 27 days; Lambeets, Dedeyne, Maelfait & Alderweireldt, unpubl. data).

Nonetheless upstream river banks disappeared over the years due to extreme flood events during the past two decades (K. Van Looy, pers. obs.), viable and large populations of *P. agricola* are still present in the Northern (downstream) part of the Common Meuse. These populations, however, are highly isolated within the current landscape. An unbroken shore defence of concrete slabs (ca. 3 km, between Koeweide (KW) and Obbicht (OB); Fig. I.1, Fig. II.4) and an intensively used agricultural landscape separate these river banks from the rest of the system. As *P. agricola* is capable of passive (uncontrolled) water surface locomotion (see III.3), it might be expected there exists a unidirectional gradient in gene flow, along with the water current. Based on AFLP-analysis, we did not find evidence for isolation-by-distance nor did genetic diversity increase in the downstream populations. Lower pairwise genetic F_{ST}-values indicated that the exchange of individuals is still possible between highly connected populations along the same river shore, whereas genetic differentiation between populations from opposite river shores was higher. The increased genetic differentiation of populations from opposite river shores, confirms the flood-avoiding behaviour of *P. agricola*. In chapter III.5., the onset of flooding was shown to induce a flight reflex away from the rising water level. However, as wolf spiders are capable of effective water surface locomotion (Stratton et al., 2004) individuals might relocate their original river bank shore adequately when being washed away during a sudden and unpredictable flood event in spring (see III.3.). Migratory movements in autumn, which are guided by visual landmarks on the river bank (see III.2.), are directed towards suitable hibernation sites nearby, thereby anticipating the long-lasting winter flood and reaching higher grounds safely (see III.1.). Combined, these results suggest that different behavioural mechanisms might originate the genetic differentiation of spatially structured populations of a stenotopic wolf spider inhabiting lowland river banks (see IV.1.). A decreased functional connectivity along the riparian corridor and the physical obstacle of the water counteract the exchange of individuals bidirectional along and across the river channel, respectively. The currently high genetic diversity might be a consequence of the only recent fragmented character of the Common Meuse and stem from higher gene flow in the past. As upstream populations have disappeared only recently (see 1.2), historical gene flow and thus genetic drift, could operate over a wider geographical scale (>30 km before 1998 vs. approximately 6 km at present). The sampled populations may concern just those at the end of a linear population with unidirectional dispersal between them (Fig. I.5b,d). Based on our behavioural observations, it is more likely, however, that populations of *P. agricola* are spatially structured, with high connectivity between adjacent populations from the same river shore. Moreover, the river channel and the surrounding landscape represent barriers for species dispersal and hence the exchange of alleles, functionally isolating the populations even further. Generally, the results indicate that habitat quality, apparently determined by flooding disturbance *sensu lato* (see II.2., II.3.), affects the genetic structure of *P. agricola* populations next to connectivity *per se*. Nonetheless we did not find unique alleles and generally low F_{ST}-values, applying an assignment analysis (Duchesne & Bernatchez, 2002) might still prove valuable to unravel contemporary gene flow between populations (cf. Pollux et al., 2009).

5.2 Conservation of riparian arthropods

The predatory arthropod assemblages from 24 river banks along the Common Meuse were proven to be quite heterogeneous and to be structured by flooding disturbance. Generally, communities of terrestrial riparian arthropods are more prone to local environmental conditions (Bonn et al., 2002; Sadler et al., 2004; Baker et al., 2007), than to regional factors (but see Townsend et al., 2003; Renöfält & Nilsson, 2008). Mixtures of xerothermophilic species alternate with hygrophilic and eurytopic species, whereas rare stenotopic riparian species were either found on differently structured river banks (Fig. V.1; mostly carabid beetles: *Agonum marginatum*, *Bembidion atrocaeruleum*, *Lionychus quadrillum*) or confined to very specific conditions, which accounts for less mobile wolf spiders in particular (*Arctosa cinerea*, *P. agrestis*, *P. agricola*), but also aerial dispersive linyphiids such as *Caviphantes* *saxetorum* and *Collinsia distincta*. One spider species was found for the first time in Belgium: *Pelecopsis mengei* (Simon, 1884), and was given the name "Grindoeverballonkopje" (Lambeets, 2008b), whereas the carabid beetle *Dicheirotrichus rufithorax* (Sahlberg, 1827), although found before in Belgium at Voeren (T. Struyve, pers. comm.), still does not occur on the species list of Flanders (Desender et al., 2008). As suggested by Sabo et al. (2005) and Rothenbücher & Schaefer (2006), particularly stenotopic riparian species are of conservation interest as the others are still secure in the current landscape. Generally, river banks act as sink habitats for non-riparian species, occurring abundantly on the river banks as well (Van Looy, 2006; Vogt et al., 2006). This was also indicated for the Common Meuse (see Appendix A6.), although eurytopic and pioneer spiders did not show proactive migration before winter flooding.

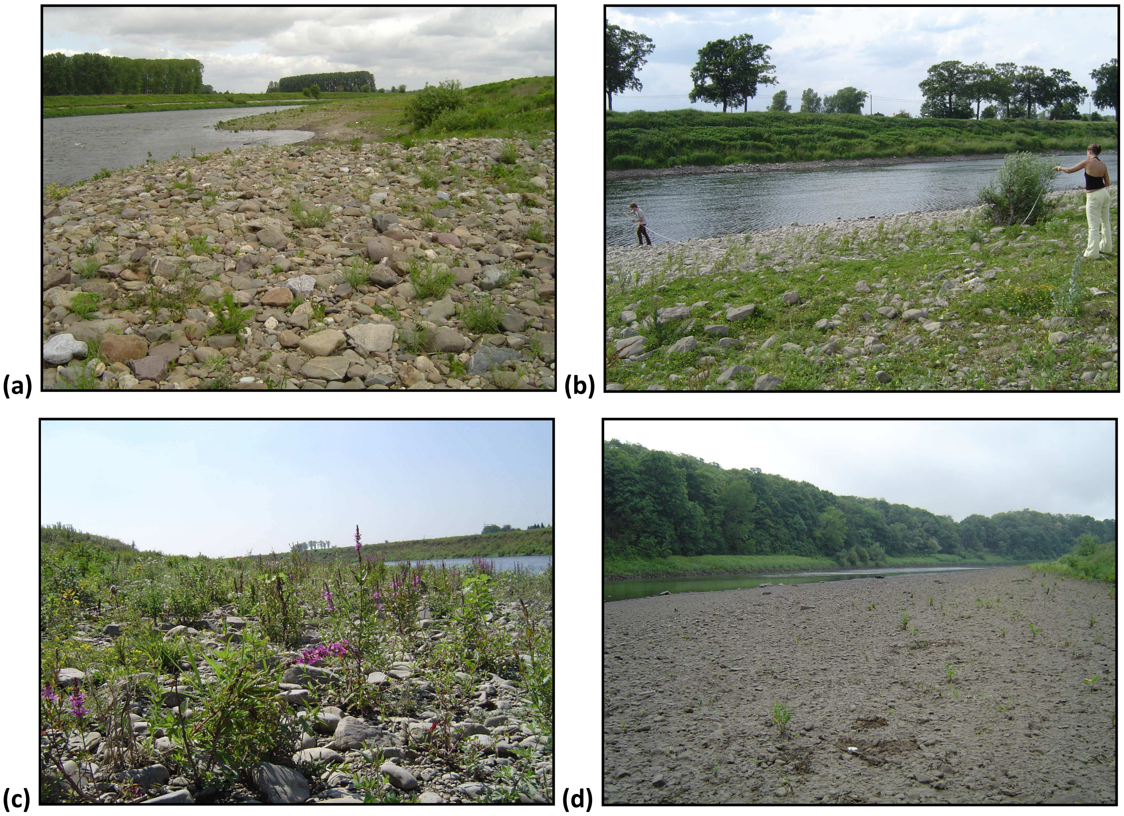


Fig. V.1 – The susceptibility of river banks to flooding disturbance is often indicated by its architectural prospects: **(a)** higher river bank with coarse gravel and an in-between sediment fraction of sharp sand, situated at the pilot-project Meers (ME; see Fig. I.1); **(b)** densely covered river bank with coarse gravel at Neerhagen (NE); **(c)** sand-loamy river bank with typical riparian vegetation succession, along the nature restoration project at Visserweert (VW); **(d)** river bank covered with a thick layer of silt, located near a road verge overgrown with dense brushwood and shrubs (KO2).

Low flows during summer are a natural phenomenon along lowland rivers (Van Looy & De Blust, 1995; 1998) and may benefit the exchange of cursorial, terrestrial species along and across the riparian corridor. Because of the construction of upstream weirs for water retention (Borgharen, Linne) and the hydroelectric power plant at Lixhe, water discharges in summer are highly disrupted along the Common Meuse (Semmerkrot et al., 1997); prolonged water retention and the drainage of cooling water from the power station, respectively, result in unnatural discharge regimes. Sudden peak flows up to 80 m^3s^{-1}, defined as hydropeaking and with the water level rising more than 1 m per hour, are an almost daily recurring event. In a lateral direction along the river banks (from water line to dike), the water may even expand up to 10 m per hour (K. Lambeets, pers. obs.). As proven by Van Looy et al. (2008) the increase in discharge is much higher closer to the hydropower plant (upstream from our sampled plots, at Lanaken-Smeermaas), and reduces gradually along the trajectory of the Common Meuse (ca. 20 m^3s^{-1} at Roosteren (RO); Fig. I.1). Van Looy and colleagues showed that these hydropeaking events are particularly pernicious for the carabid beetle fauna during periods of low flows. Additionally, this might explain why species such as *A. cinerea* and *P. agricola* have disappeared from river banks upstream at Kotem, Maasmechelen and Mazenhoven (respectively KO, MM and MH; Fig. I.1; K. Lambeets, pers. obs.). Some river banks which contained vital populations of *P. agricola* (see Lambeets et al., 2007; 2008a) even completely vanished after the extreme flood of 2003 (K. Van Looy, pers. comm.). Especially lower river banks with a soft slope at embanked sections of the Common Meuse are liable to these disrupted water level fluctuations, and consequently their inhabiting fauna as well (Paetzold et al., 2008; Fig. V.1).

River banks where *A. cinerea* occurs, appear to be the most differentiated, and so their respective xerothermophilic assemblages (Lambeets et al., 2007; 2008a; 2009). As these higher river banks (Fig. V.1) are highly isolated along the Common Meuse (Meers (ME) and Obbicht (OB); Fig. I.1), their inhabiting arthropod fauna is also the most vulnerable to disrupted flood pulses, particularly for spiders. By weighing the costs and benefits of an ecologically sustainable discharge regime, however, a minimal water level and discharge should always remain to preserve rheophilic species as well (Liefveld & Schulze, 2005). In contrast, communities of benthic invertebrates may recover more quickly and even to a comparable level of less-perturbed reaches (Usseglio-Polaterra & Beisel, 2002). This illustrates that river management should not only account for the needs of the in-stream biota (e.g. water quality, substrate structure; Petts et al., 1993), but just as well consider habitat requirements of riparian arthropods. Moreover, biodiversity conservation also requires the consideration of the upland ecosystems, as they represent important sources of propagules (Bang et al., 2007). This might be more important for vascular plants (Mouw & Alaback, 2003) and benthic invertebrates (Usseglio-Polatera & Beisel, 2002; Reese & Batzer, 2007) in agreement with the *River Continuum Concept* as specified by Vannote et al. (1980).

Generally, flood events are necessary to reset habitat succession and thus create open (ephemeral) conditions for riparian species (Sadler et al., 2004), and otherwise to generate habitat by overbank depositions (Wintle & Kirkpatrick, 2007). This may be complemented by allowing large grazers to the river banks such as hardy Konik horses and Galloway cattle (Van Braeckel, 2002; Table I.1). Trampling prevents fixation of the sediment and restrains vegetation succession. By keeping the sediment loose, extensive grazing creates substrate cavities which provide important shelter for arthropods during high temperatures in summer and refuges during flooding. The drawback of too intensive grazing is the increased soil erosion and hence decreased stability of the gravel bars (McInnis & McIver, 2006), whereas dung locally fixates the substrate. Consequently, intensive grazing reduces the conservation value of high quality river banks as shown by Bates et al. (2007). Beside the effects of eolic dynamics on stenotopic arthropods from calcareous dune grasslands, Bonte & Maes (2008) indicated that trampling affects the distribution of arthropods, yet in accordance with their habitat affinity and mobility (Maes & Bonte, 2006).

Unravelling behavioural strategies and population dynamic processes of terrestrial riparian arthropods allows the identification of important corridor functions and the effects of functional connectivity (Bélisle, 2005). By applying a metapopulation approach, Stelter et al. (1997) illustrated that even for a mobile riparian grasshopper *Bryoderma tuberculata*, large numbers of river banks are needed to support viable populations. Moreover, older more stable banks, which are less prone to inundation, provide sources for recolonisation after severe flood events. In its current state, the Common Meuse still provides suitable habitat for *P. agricola* (e.g. no environmental constraints were found), yet this easily recognisable remains a valuable ecological indicator for (intact) river banks surrounded by alluvial grasslands (Lambeets et al., 2008a; Fig. V.1c), just as *A. cinerea* for higher river banks

(Lambeets et al., 2007; Fig. V.1a). Moreover, by analysing movement behaviour of *P. agricola*, i.e. responses which are supposedly important to survive in flood-disturbed habitats (cf. Framenau et al., 1996; Morse, 2002), in comparison with a sympatric, generalist congener, between-population variation in movement behaviour was prevalent irrespective of the degree of habitat specialisation. Evidence was given that movement decisions of a stenotopic riparian wolf spider that spends its entire life in spatially structured, dynamic river banks, are more beneficial in relation to the risks involved with flooding. Hence, *P. agricola* avoids potential costs related to flooding more efficiently than *P. amentata*. Notwithstanding these behavioural decisions were indicated to increase the survival in a flood-disturbed environment, they also counteract species exchange and hence may increase genetic differentiation in time. Nevertheless the genetic structure of *P. agricola* showed that the network of populations in the downstream section of the Common Meuse is still strong, it appears to be highly isolated. The rehabilitation of the riparian corridor will certainly decrease the isolation between river bank patches and benefit the upstream exchange of individuals. For instance, the removal of the dike improvement along the river bank at Elerweert (EL; Fig. I.1) re-established open, pioneer conditions and increased the contact with the hinterland, hence providing the necessary conditions for *P. agricola*, amongst others, and facilitating the transition between the river bank and the adjacent alluvial meadows (see Peters (2006) for a survey of the planned restoration projects). In contrast, the erection of the river dike at Roosteren (RO) clearly had a negative effect as no specimens of *P. agricola* were encountered afterwards (K. Lambeets, pers. obs.). However, the construction of an adjoining erosion channel in contact with the river channel might prove beneficial on the long term to sustain persistent populations of various riparian arthropods (Lambeets et al., 2005; Lambeets & Struyve, 2007; see Appendix A1.) and biodiversity in general (Van Looy, 2005). As suggested by Van Looy et al. (2008), widening and enlarging the river bed successfully dampens discharge fluctuations and moderates hydropeaking events. The NATURA2000 pan-European network of protected areas and species (see Decleer, 2007) demands clear definitions to achieve a *good ecological status* for a sustainable conservation status. Many stenotopic riparian arthropods are scarce, even on an international scale (Van Helsdingen, 2008a; Kotze & O'Hara, 2003), and restricted to very specific environmental conditions, yet none of them are included in the Appendices of the Habitat Directive (Sterckx et al., 2007; cf. ECE – River Convention, 1992). Nonetheless, the inclusion of the River Clubtail (*Gomphus flavipes*), a highly stenotopic dragonfly which is restricted to lowland and mid-reaches of large rivers with coarse-grained sand and gravel bars, as a focal species opens perspectives for the future. Moreover, this species was recently discovered along the Common Meuse (H. Matheve, pers. comm.), indicating water quality and habitat suitability have improved the last decade (recent values of the Belgian Biotic Index (BBI), a proxy for the water quality based on the presence of macro-invertebrate taxa, were shown to be "good" up to "very good": BBI >= 7; data from the Flemish Environment Agency (VMM)). However, river management should ensure less abrupt fluctuations of the water discharge regime and allow the river to create its own river banks (De Knijf et al., 2006), the same story line as for many of the predatory riparian arthropods quoted in this PhD-dissertation…

5.3 Future perspectives for river restoration

Within ecosystems, disturbance may have non-uniform effects due to the fact that ecosystems are themselves heterogeneous with respect to their abiotic characteristics and history (Fraterrigo & Rusak, 2008). Rivers, nor their associated habitats, are continuous and equilibrium-state systems. Stochastic processes primarily induced by flow regimes and flood pulse characteristics, shape patterns in habitat heterogeneity and biodiversity (Ward et al., 2002; Robinson et al., 2002), but are also influenced by river management and the surrounding land-use (Allan, 2004; Pedroli et al., 2002). As proposed by Van Looy (2006), conservation and restoration objectives for river ecosystems should be defined by a multi-dimensional and multi-scale approach (cf. Buijse et al., 2002; Pedroli et al., 2002), rather than by stand-still principles. The supporting management framework should be based on sound-ecological principles (Jensen et al., 2006; Lake et al., 2007) and derived from the observed patterns and structures in the riverine and riparian landscape. As hydro- and geomorphological dynamics are tightly and reciprocally linked to ecological and physiochemical processes within and along rivers, changes in either of them will induce shifts in the other (see Naiman et al. (2005) and Allan & Castillo (2008) for a comprehensive overview). Understanding the functioning of a river ecosystem, therefore, demands an integrated and integral picture of the processes that found a river's integrity (Van Looy, 2006). As stated by Poff et al. (1997) in the **Natural Flow Regime Concept**, biodiversity patterns can best be interpreted with regard to river specific variation in discharge and disturbance regimes. Generally, due to the scale-sensitivity, complexity and specificity of a river system's functioning and processes, restoration and conservation approaches cannot be generalised towards other river systems (e.g. Bonn et al., 2002; Paetzold et al., 2008). Therefore, the multi-scale **River Disorder Approach** as discussed by Van Looy (2006) provides a valuable and comprehensive framework for restoration and biodiversity conservation in riverine and riparian habitats. Sensu Van Looy (2006, p.305): *"The disorder concept depicts the riverine ecosystem as a complex, discontinuous system with characteristics that reflect the influence of the river's catchment area (geo-ecoregions), hydroregions and bioregions and the processes determining fluxes of matter and species."*, which coincides with the target fields for conservation (see below). From here, it is obvious that a generalised strategy for species conservation in riparian habitats is not feasible. Moreover, a river's identity in succession, local topographical structure and regional chorological appearance delineates the possibilities for biodiversity, and hence conservation and restoration strategies. Consequently, self-sustainability of river systems depends not merely on the water discharge regime and related geomorphologic processes, but also incorporates functional and structural connectivity and patterns of biodiversity on different spatiotemporal scales (Wiens, 2002; Townsend et al., 2003; Allan, 2004). This Ph.D.-thesis provides a further understanding of the disorder in the middle reach of the River Meuse by associating the effects of flooding disturbance *sensu lato* on a (local) river bank level, an integration of the pillars of the Natural Flow Regime paradigm (Poff et al., 1997), with biodiversity and other biotic patterns. However, (dis)similarities with and between the surrounding floodplain meadows, dry river grasslands (cf. lateral connectivity; Van Looy et al., 2006; cf. Paillex et al., 2007) or other reaches (cf. longitudinal connectivity; Usseglio-Polaterra & Beisel, 2002; Bij de Vaate et al., 2007) along the River Meuse's trajectory still remain notional for riparian arthropods (but see Van Looy et al., 2005). In line with the Disorder Approach, different groups and/or species might be indicative at different spatial and temporal scales. This has cogently been reasoned for arthropods in arable land habitats: Purtauf et al. (2004), Schmidt & Tscharntke (2005a), Öberg et al. (2007; 2008), Drapela et al. (2008) and Schmidt et al. (2008) a.o. Data from the sampling at Elerweert suggest that, indeed, other assemblages are present at the alluvial meadows (K. Lambeets, unpubl. data).

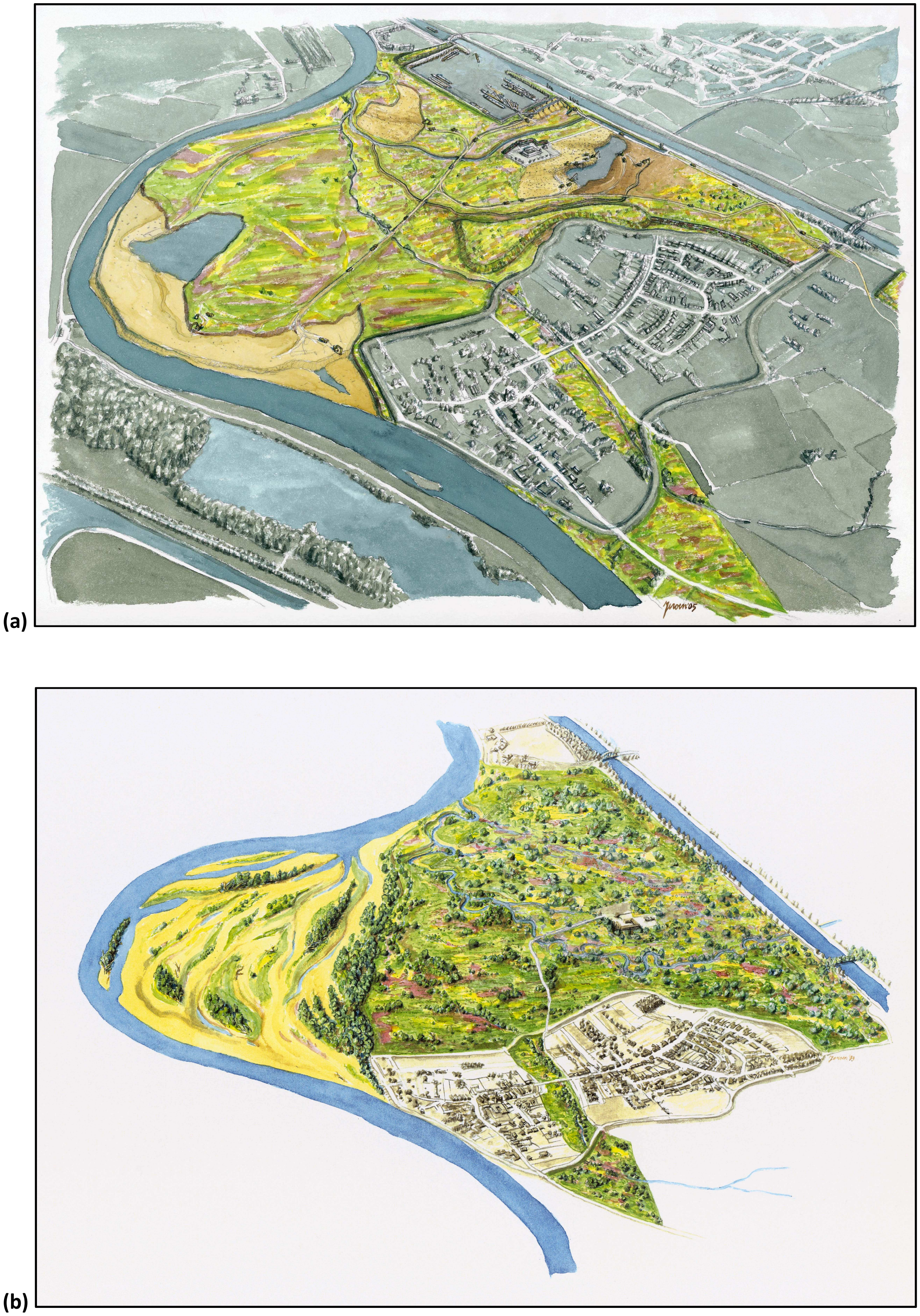
However, more evidence is clearly needed to define specific targets and guidelines for rehabilitation strategies of the hinterland as a suitable haven for riparian and alluvial arthropods, and not merely for river corridor or floodplain plants (Mouw & Alaback, 2003; Hérault & Honnay, 2005; Stromberg et al., 2007).

As summarised by Van Looy (2006), target fields for conservation in riverine ecosystems should be fourfold:

(1) the biodiversity of the river system as a whole, including healthy populations and gene pools, this is termed the **river corridor reservoir** (Naiman & Décamps, 1997)
(2) **connectivity**, both structural and functional (Ward & Stanford, 1995; Wiens et al., 2002)
(3) a **natural flow regime** (Poff et al., 1997; Arthington et al., 2006), based on five cornerstone aspects: magnitude, frequency, duration, timing and rate of change
(4) **geomorphodynamical processes** such as sedimentation and erosion, induced by the hydrological cycle, are essential for structuring the riverine landscape (Steiger et al., 2005) and biodiversity concordantly (Ward et al., 1998; Allan, 2004)

The idiosyncratic ecological needs of the inhabiting organisms, whether plants (Pollock et al., 1998; Burkart, 2001; Renöfält et al., 2005; Stromberg et al., 2007), rheophilic fish species (Lamouroux et al., 2002; Schick & Lindley, 2007), benthic macro-invertebrates (Petts et al., 1993; Usseglio-Polaterra & Beisel, 2002; Suren & Jowett, 2006; Bij de Vaate et al., 2007) or arthropods (Bonn & Kleinwächter, 1999; Eyre et al., 2001; 2002; Paetzold et al., 2008), should be fully integrated into restoration and rehabilitation perspectives. As argued by Arthington et al. (2006), evidence-based restoration and purposive management should also be the rank and file in riparian and riverine ecology. This study proves spiders and carabid beetles, as separate but complementary taxonomic groups, to be valuable indicators to assess the effects of (disrupted) flow regimes and flood pulses (cf. Kremen, 1992; Van Looy et al., 2008; see Kremen et al. (1993) for a review of the use and value of terrestrial arthropods in conservation planning). Moreover, stenotopic riparian species tend to have very specific ecological requirements, and will hence prove valuable as ecological indicators and/or sentinel species. As argued by Simberloff (1998), umbrella species are not necessarily outmoded, but considering multiple species, each covering a certain ecological or functional group (see Appendix A6. for functional grouping), will certainly add to the concept of selecting indicator and umbrella species for conservation and monitoring purposes (Lambeck, 1997; Maes & Van Dyck, 2005). Kleinwächter & Rickfelder (2007) argued that the protection of a highly specialised riparian carabid endorses support for other riparian species as well, whereas Van Looy et al. (2008) showed carabid beetle functional groups to be good indicators for river bank habitat quality and disrupted discharge regimes, respectively. Therefore, analysing the environmental and functional constraints for the distribution of multiple arthropod species from various taxonomic groups (target (1) - (3)), and on different spatiotemporal scales, as well as trying to understand the behavioural mechanisms underlying these patterns (in relation to functional connectivity; target (2)), will add to our understanding of the functioning of highly dynamic and non-equilibrium riverine ecosystems. Moreover, as the climate of Planet Earth is quickly and drastically changing under influence of anthropogenic activities, alterations in the flow and flood regimes will be accentuated (Tockner & Stanford, 2002). Also, the intensification of the hydrological cycle as a consequence of greater pressures on the freshwater resources due to economic expansion (Poff et al., 2003), the increased discharge of pollutants due to further land conversion and land-use intensification (Buijse et al., 2002) and the proliferation of invasive species (Olden et al., 2004) are major obstacles to restore riverine and riparian habitats world-wide (Naiman et al., 2005; Bernhardt & Palmer, 2007; Allan & Castillo, 2008). River restoration objectives, however, need to stay realistic (a pristine state can never be restored; Buijse et al., 2002; Lake et al., 2007) and meet the social standards of e.g. flood protection strategies (Geilen et al., 2004). Therefore, 1900 might an appropriate reference situation for river restoration strategies, i.e. the period before industrialisation and land-use intensification (Van Looy, 2005). Integrating a network for soft recreation throughout the riverine landscape will certainly benefit the common goods, and with it, the social appreciation for large-scale landscape-ecological reformation and nature development will increase. An ongoing restoration project is presented at Fig. V.2, by which natural, dynamic processes are being restored by means of removing the shore defences locally, the widening of the summer bed and the shallow extraction of the top-gravel layer of the nearby (alluvial / arable) parcels, but also the reestablishment of the dike fortification nearby the village.

Fig. V.2 – Rough draft of the river restoration management at Itteren by Jeroen Schelmer (Consortium Grensmaas, 2005): (a) transitional stage and (b) final stage.



Albeit, the seemingly insurmountable problems related to the river's identity, its restoration management and the rehabilitation of a suitable and sustainable riparian corridor certainly create new challenges for enthusiastic, dynamic (young) scientists! Whatever the arthropods decide, *"Should I stay or should I go?"* remains a fundamental question being inherently part of an exceptional life in an extreme and dynamic environment…

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SUMMARY

Building on the fundamental findings of a preliminary survey of riparian arthropods in 1998 and 2000, this research project aims to address variation in distribution patterns and behavioural responses of riparian arthropods, particularly spiders (Araneae) and carabid beetles (Carabidae). As riverine ecosystems are basically non-equilibrium, dynamic ecosystems, mainly flow regimes and flood pulse characteristics are expected to shape both distribution and behaviour of these mobile arthropods.

My research project attempts to unravel which environmental factors influence arthropod assemblage structure along spatially structured river banks of a lowland gravel river, the Common Meuse. As these river banks are (in)frequently disturbed by flood events and liable to extreme microclimatological conditions, functional life-history traits of the present species supposedly affect species composition as well. Moreover, organisms occurring within a highly structured system and which are repeatedly exposed to flooding disturbance, are expected to have evolved or adjusted their behavioural responses in accordance with their functional life-history characteristics such as habitat affinity and mobility. Correspondingly, less mobile species are expected to show variation in their spatial genetic structure as well.

The Common Meuse is situated between Flanders (Belgium) in the West and the Netherlands in the East. It is the 45 km long non-impounded, non-navigable semi-natural reach of the River Meuse (925 km). Due to a high slope and rain-fed character, the common Meuse is characterised by a fast flowing gravel-bed and hence strong water level fluctuations. Discharge regimes range from 10 m^3s^{-1} during dry periods up to 3,000 m^3s^{-1} in periods of heavy rainfall in the catchment area. Due to canalisation and normalisation of the River Meuse, starting around 1860, the historically shallow and wide river channel of the Common Meuse, was replaced by a deep, small, uniform and fixed channel characterised by an increased water level and fast current velocity. Consequently, a tendency for (human-mediated) prolonged low flows and hydropeaking appears at present. Over 50% of the alluvial plane is still intensively used for agricultural purposes while alluvial grasslands, sand-gravel bars or pioneer vegetations on overbank depositions only occupy 5% of the surface.

The remaining landscape comprises riverine water bodies, gravel pits, marsh- and woodlands.

The environment of organisms living within the boundaries of riverine landscapes is highly dynamic due to discharge fluctuations and sediment movements. River banks in particular are susceptible to flood events, which reset riparian successional stages and affect the assemblage structure of its inhabitants. By analyzing the effects of flooding disturbance *sensu lato* on diversity patterns and assemblage-wide trait distribution of spiders and carabid beetles, the underlying mechanisms structuring arthropod assemblages were unravelled. The results, based on an intensive pitfall sampling during spring and early summer in 2005, indicated that shifts towards less specialised arthropod assemblages are prevalent as flooding disturbance increases. Mainly stenotopic riparian species are disfavoured by either too high or too low flooding, whereas eurytopic species and agrobionts benefit from increased disturbance. Species sorting appeared particularly for spiders. Next to it, the relationships between species occurrences and the multivariate environmental and functional constraints were unravelled to gain insight into conservation strategies to preserve rare riparian arthropods. Absolute species richness was clearly lower on more disturbed river banks and functional diversity differed according to the arthropod group. Moreover, analysing occurrence patterns on a species level revealed the importance of variation in flooding disturbance, sediment composition and vegetation architecture for the preservation of rare riparian spiders and carabid beetles. In general, increased anthropogenic alterations of low flows and flood pulse characteristics will cause the loss of stenotopic, xerothermophilic and less mobile riparian arthropods. River restoration and riparian rehabilitation should generate the required heterogeneity at the river bank level, hence increasing the sustainability of dynamic lowland river ecosystems and the conservation of vulnerable riparian arthropods.

Notwithstanding exploitation practices and the intensification of the hydrological cycle as well as the surrounding landscape negatively affect riverine ecosystems and hence their inhabitants, stenotopic riparian species are also expected to have adapted to these highly fluctuating environmental conditions within a fragmented landscape. Hence, behavioural, morpho-, pheno- and/or physiological adaptations will benefit riparian and/or riverine organisms in relation to the (un)predictable character (cf. flooding disturbance) of riverine ecosystems. By means of an intensive pitfall survey during autumn 2005, field- and controlled lab-experiments, insights were gained into movement behaviour of riparian arthropods. Only larger, cursorial riparian spiders showed proactive seasonal migration towards higher and non-flooded winter habitats alongside the river bank. In contrast, the riparian zone acted as a sink for agrobiont spiders, whereas flight-active riparian carabid beetles probably evacuate the river bank once winter-flooding sets in. These results indicate that river management should incorporate an optimal management of the alluvial hinterland besides the rehabilitation of the riparian corridor *in se*.

As decision-making processes precede movement behaviour, the factors guiding these decisions essentially relate to the beneficiality of this animal behaviour. Therefore, unravelling the relationships between the information which is used by organisms during movement will lead to a better understanding of behavioural variation in general. The results of two field experiments indicated that movement decisions of two sympatric wolf spiders are guided, particularly, by factors related to their population of origin (side of the river; either genetics or experience). However, a stenotopic riparian wolf spider, *Pardosa agricola* (Thorell, 1856), was inclined to rely on individual information (i.e. proximate cues) only during sudden stressful situations (tactile contact with the water surface). A generalist species, which only occurs on the river banks sporadically, *P. amentata* (Clerck, 1757), also showed strong directional movements towards the shore once on the water surface, but relied less on individual information. Still, as between-population variation remained for a stenotopic species, it was less clear for a generalist under pure visual stimuli (no contact with the water). Flood-avoiding behaviour was also prevalent for both wolf spiders during a controlled experiment, with the stenotopic *P. agricola* reacting systematically under different conditions and hence showing a lower degree of repeatability in individual behaviour (higher plasticity). Furthermore, no differences in submersion tolerance were found.

Additionally, the fragmented character of riparian habitat patches, and thus the low degree of functional connectivity, and the unidirectional flow of the river may confound the exchange of species and individuals. However, particularly less mobile (cursorial) species are expected to show typical gene flow patterns hypothesised for linear populations, and hence isolation-by-distance might occur. By using Amplified Fragment Length Polymorphism (AFLP) markers, the genetic population structure of the highly stenotopic wolf spider *P. agricola* was studied. Genetic diversity appeared still very high in all populations and no downstream accumulation was found, nor was genetic diversity higher in larger populations. Furthermore, nearby populations on the same river shore were clearly less genetically differentiated compared with populations far away and/or on the opposite shore; no isolation-by-distance patterns were present. This indicates short-distance dispersal still occurs, but the river channel forms a physical barrier for species exchange. The rehabilitation of the riparian corridor is needed to restore (upstream) functional connectivity for cursorial arthropods on river banks, whereas periods of sustainable low flow-discharges will benefit the exchange of individuals between opposite shores.

Generally, a multi-scale approach as outlined by the *River Disorder Approach* provides a valuable and comprehensive framework for river restoration and biodiversity conservation in riverine and riparian habitats. River management emphasising the restoration and rehabilitation of a sustainable river integrity should certainly involve the functioning of dynamic processes, driven by flow regimes and flood pulses, and incorporate the idiosyncratic, ecological needs of riparian arthropods. Thereby, obtaining insight into functional and behavioural responses towards environmental conditions on a local scale, and aspects of flooding disturbance in particular, will increase our understanding of highly dynamic ecosystems and result in widely applicable guiding concepts for species conservation and ecosystem management.

SAMENVATTING

Verdergaand op de bevindingen van staalnames met betrekking tot oevergebonden arthropodengemeenschappen in 1998 en 2000, tracht deze doctoraatsscriptie de variatie in verspreidingspatronen en het gedrag van spinnen (Araneae) en loopkevers (Carabidae) voorkomend langsheen laaglandoevers van een grindrivier te ontrafelen. Rivieren vertonen een erg variabel karakter, gedefinieerd als een *dynamisch evenwicht*, en worden derhalve gekenmerkt door hun afvoerregime en (over)stromingskarakteristieken. Bijgevolg valt te verwachten dat de overstromingsgevoeligheid van de habitaten langsheen een rivier de verspreiding alsook het gedrag van mobiele arthropoden beïnvloedt.

Dit onderzoek ontrafelt welke omgevingscondities de gemeenschapsstructuur van arthopoden vormgeeft binnen ruimtelijk verspreide oevers langsheen een laaglandriver, de Grensmaas. Aangezien deze oevers onderhevig zijn aan (on)regelmatige overstromingsverstoring en een erg extreem microklimaat vertonen, wordt tevens een structurend effect verwacht van de functionele levensgeschiedeniskenmerken van de aanwezige soorten. In overeenstemming met soortspecifieke karakteristieken zoals habitatpreferentie en mobiliteit, wordt verwacht dat de soorten binnen dit dynamische en ruimtelijk gefragmenteerd systeem welbepaalde gedragsmatige aanpassingen hebben ontwikkeld in de loop der tijd. Minder mobiele soorten zouden eveneens overeenkomstige genetische variatie vertonen.

De Grensmaas situeert zich op de grens tussen Vlaanderen (België) in het oosten en Nederland in het westen. De 45 km-lange Grensmaas omvat het quasi-natuurlijke ongestuwde, onbevaarbare gedeelte van de Maas (totaal traject 925 km). Ten gevolg van het regengevoede karakter en de sterke helling van het verloop, wordt dit deel gekenmerkt door een snelstromende grindbedding en groffe waterpeilfluctuaties. De waterafvoer varieert van 10 m^3s^{-1} tijdens droge periods tot 3000 m^3s^{-1} bij hevige regens in het afwateringsgebied. De rechttrekking van de rivierbedding en de normalisatie van het waterpeil van de gehele Maas vanaf 1860, vormde het historische, zachtglooiende rivierkanaal van de Grensmaas om tot een diepe, smalle, uniforme en gefixeerde bedding gekarakteriseerd door een hoger waterpeil en toegenomen afvoersnelheid. Heden zijn anthropogeen-gestuurde langdurige lage waterstanden en afvoerpieken legio voor de Grensmaas. Ook het omliggend alluviale landschap veranderde drastisch in de loop der tijd en omvat tegenwoordig meer dan 50% intensief gebruikte landbouwgronden (akkers, hooilanden,...). Amper 5% van de oppervlakte in het afwateringsgebied zijn (ongerepte) alluviale graslanden, rivieroevers of pioniervegetaties op overdijkse sedimentafzettingen. Het resterende deel van de vallei bestaat uit waterlichamen, grind- en zandwinningsgebieden, broeklanden en bosgebied.

De leefomgeving binnen de grenzen van een riviergebonden landschap is hoog-dynamisch als een gevolg van waterpeilschommelingen and sedimentverplaatsingen. Oevers in het bijzonder zijn onderhevig aan overstromingsverstoring die zowel de successie terugdringt als de gemeenschapsstructuur van de aanwezige organismen stuurt. Door na te gaan welke effecten deze intense verstoring heeft op de diversiteit van zowel spinnen als loopkevers en het optreden van gemeenschapsbrede kenmerkverschuivingen te bestuderen, worden de onderliggende mechanismen aangaande de gemeenschapsstructuur blootgelegd. Resultaten gebaseerd op een intensieve bodemvalbemonstering tijdens de lente en zomer van 2005, tonen aan dat bij toenemende overstromingsverstoring verschuivingen optreden naar minder gespecialiseerde gemeenschappen. Vooral stenotope oeversoorten moeten het ontgelden bij zowel een te hoge als een te lage mate van overstroming. Onder invloed van deze verstoring worden soorten met welbepaalde ecologische kenmerken duidelijk bevoordeeld (*species sorting*). Dit was vooral duidelijk voor spinnen, minder voor loopkevers. Daarnaast werden de onderlinge relaties bestudeerd tussen het voorkomen van soorten op zich en de verschillende omgevingscondities alsook functionele beperkingen. Op die manier werden maatregels aangaande het behoud van kwetsbare oevergebonden arthropoden gedefinieerd. De totale soortenrijkdom was beduidend lager op meer verstoorde oevers, terwijl de functionele diversiteit verschilde afhankelijk van de bestudeerde groep van arthropoden. Analyses op soortsniveau onthulde het belang van een afwisselende overstromingsverstoring, de sedimentsamenstelling en de vegetatiestructuur voor het voorkomen van oevergebonden spinnen en loopkevers. Anthropogene veranderingen van zowel het afvoerregime als de overstromingskarakteristieken leiden tot een verlies van oevergebonden, warmte- en droogteminnende, minder mobiele soorten. Bijgevolg dient rivierherstel en de heropwaardering van de oeverzone de benodigde heterogeniteit ook op kleinere schaal, namelijk die van de oevers *sensu stricto*, te genereren. Zowel de duurzaamheid van dynamische laaglandrivieren als het behoud van zeldzame oevergebonden soorten wordt hierbij bewerkstelligd.

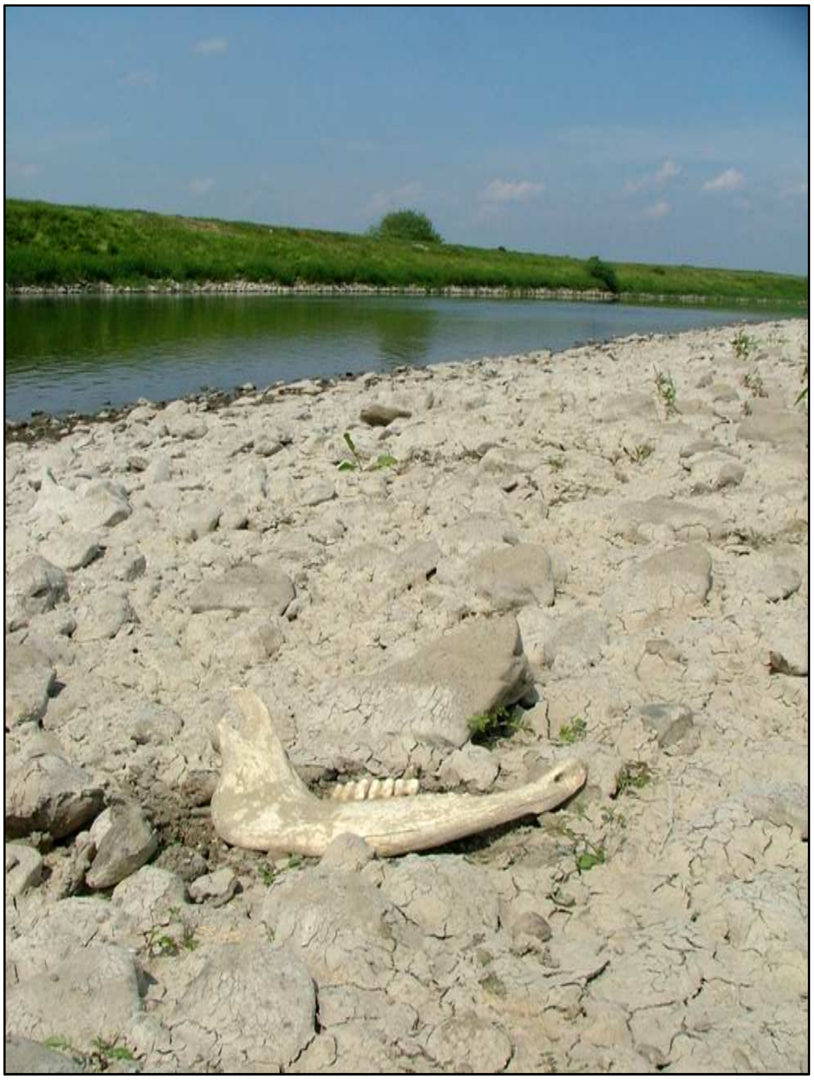
Niettegenstaande de negative gevolgen van de doorgedreven ontginningen, het intensief watergebruik en de omvorming tot een agrarisch landschap voor het rivierecosysteem en de aanwezige organismen, worden voor stenotope oeversoorten aanpassingen verwacht die inspelen op enerzijds de sterk afwisselende omgevingscondities en anderzijds de hoge mate van isolatie van geschikte habitatfragmenten. Specifieke gedragsmatige, morfo-, feno- en/of fysiologische aanpassingen met betrekking tot het (on)voorspelbaar overstromingskarakter van rivieren bevoordelen zowel rivier- als oeversoorten. Door middel van een intensieve bodemvalbemonstering tijdens het najaar van 2005 naast veld- en gecontroleerde laboexperimenten, werd het bewegingsgedrag van soorten voorkomend langsheen de oevers bestudeerd. Enkel grotere, cursorische oevergebonden spinnen vertoonden proactieve migratie (dus vòòr de overstroming) in de richting van hogergelegen overwinteringshabitaten. Daarentegen fungeert de oeverzone als een immigratie-afhankelijk habitat (*sink habitat*) voor agrobionten, en loopkevers verlaten de oever pas zodra deze overstroomt. Dit impliceert dat rivierbeheerders zich niet enkel moeten richten op de heropwaardering van de oevercorridor op zich, maar eveneens de herinrichting van het alluviale hinterland moeten in rekening brengen.

Besluitsvorming (*decision-making*) vormt een inherent onderdeel van bewegingsgedrag. De factoren deze besluiten sturen, beïnvloeden tevens de voordeligheid van de getroffen beslissingen. Nagaan welke informatiebronnen de verplaatsingen van organismen onderbouwen, draagt bij tot een beter begrip van gedragsmatige variatie van mobiele soorten. De resultaten van twee veldexperimenten toonden aan dat de besluitvorming van twee samen-voorkomende wolfspinsoorten onderhevig is aan de populatie van herkomst (zijde van de rivier; of ervaring of genetisch bepaald). Een stenotope oeversoort, *Pardosa agricola* (Thorell, 1856) - Ruigtewolfspin, vertrouwde echter meer op individuele informatie (proximate signalen) tijdens stressvolle situaties (contact met water). Een generalist daarentegen, *P. amentata* (Clerck, 1757) - Tuinwolfspin, die enkel sporadisch op de grindoevers voorkomt, vertoonde tevens een gerichte verplaatsing conform haar herkomst, maar vertrouwde minder op individueel vergaarde informatie. Onder puur visuele prikkelingen bleef de variatie tussen populaties van de stenotope oeversoort bestaan, maar verdween meer voor de generalist. Overstromingsontwijkend gedrag werd eveneens opgemerkt tijdens een gecontroleerd laboexperiment, ongeacht de habitatspecificiteit. De stenotope *P. agricola* reageerde systematisch onder verschillende omstandigheden en vertoonde derhalve een lagere gedragsmatige herhaalbaarheid in individueel gedrag (hogere plasticiteit). Er werden geen verschillen in overstromingstolerantie aangetoond.

Daar het fragmentarische karakter van oeverhabitaten, en bijgevolg de lage functionele connectiviteit, alsook de unidirectionele stroming van de rivier de uitwisseling van soorten en individuen beïnvloedt, wordt verondersteld dat minder mobiele (cursorische) soorten een typische patroon vertonen qua genenuitwisseling zoals vooropgesteld door modellen voor lineaire populaties; daarom wordt isolatie-door-afstand (*isolation-by-distance*) verwacht. Op basis van Amplified Fragment Length Polymorphism (AFLP) merkers, werd de populatiegenetische structuur van de stenotope, oevergebonden wolfspin *P. agricola* bestudeerd. De genetische diversiteit was nog steeds erg hoog in alle populaties en srtoomafwaartse accumulatie werd niet aangetroffen. Genetische diversiteit was niet hoger in grotere populaties. Voorts waren naastliggende populaties aan dezelfde zijde van de rivier minder genetisch gedifferentieerd in vergelijking met verder uiteen gelegen populaties en/of populaties aan weerszijden van de rivier; isolatie-door-afstand werd niet weerhouden. Deze resultaten duiden erop dat uitwisseling over kortere afstanden nog steeds mogelijk is, maar dat de diepe rivierbedding een onoverkomelijke barrière vormt voor genetische uitwisseling, en bijgevolg voor de uitwisseling van soorten / individuen. De heropwaardering en herinrichting van de oevercorridor is noodzakelijk om (stroomopwaartse) functionele connectiviteit te herstellen voor cursorische, oevergebonden arthropoden. Bijkomend zullen periodes van duurzame lage waterstanden de uitwisseling van soorten en individuen tussen tegenoverliggende oevers ten goede komen.

Een aanpak overheen verschillende ruimtelijke en temporele schalen, zoals voorgesteld binnen de *River Disorder Approach*, verschaft een waardevolle en geïntegreerde omkadering voor rivierherstel en het behoud van biodiversiteit in rivier- en oeverhabitaten. Beheersmaatregelen met de nadruk op het herstel en de heropwaardering van een duurzame integriteit voor de rivier, dienen het functioneren van dynamische processes te omvatten, maar eveneens rekening te houden met de idiosyncratische, ecologische noden van oevergebonden arthropoden. Bovendien leidt een beter inzicht in de functionele en gedragsmatige reacties in relatie tot omgevingscondities, en meer specifiek overstromingsverstoring op zich, tot een beter begrip van deze hoog-dynamische ecosystemen. Deze inzichten zullen resulteren in breder toepasbare, begeleidende concepten voor soortsbehoud en ecosysteembeheer.

Appendices



The river bank, a dynamically extreme environment…
or was it the other way around?! (Photo: Dries Bonte)

Appendix A1. - Species list and number of (a) spiders (Araneae) and (b) beetles (Coleoptera) caught in the erosion channel at the nature reserve "De Groeskens", Dilsen-Stokkem (2004). See (a) Lambeets K., Bonte D. & Maelfait J.-P. 2005. De spinnenfauna (Araneae) van een erosiegeul in het natuurreservaat "De Groeskens" langsheen de Grensmaas (Dilsen-Stokkem). Nieuwsbrief van de Belgische Arachnologische Vereniging 20(1), 10-21 and (b) Lambeets K. & Struyve T. 2007. De keverfauna van een erosiegeul langs de Grensmaas (De Groeskens, Dilsen-Stokkem, België). Natuurhistorisch Maandblad 96(4), 105-111.

(a)

Family	Species	#mm	#ff
Gnaphosidae	Drassodes lapidosus (WALCKENAER, 1802)	1	0
Gnaphosidae	Drassyllus pusillus (C.L. KOCH, 1833)	0	1
Gnaphosidae	Micaria pulicaria (SUNDEVALL, 1831)	4	0
Gnaphosidae	Trachyzelotes pedestris (C.L. KOCH,1839)	5	2
Clubionidae	Clubiona lutescens WESTRING, 1851	1	0
Clubionidae	Clubiona phragmitis C.L. KOCH, 1843	1	1
Clubionidae	Clubiona reclusa O.P.-CAMBRIDGE, 1863	0	1
Liocranidae	Phrurolithus festivus (C.L. KOCH, 1835)	1	1
Thomisidae	Ozyptila simplex (O.P.-CAMBRIDGE, 1862)	1	0
Thomisidae	Xysticus acerbus THORELL, 1872	10	1
Thomisidae	Xysticus cristatus (CLERCK, 1757)	0	1
Thomisidae	Xysticus erraticus (BLACKWALL, 1834)	2	0
Thomisidae	Xysticus kochi THORELL, 1872	18	2
Thomisidae	Xysticus ulmi (HAHN, 1832)	0	1
Salticidae	Heliophanus flavipes (HAHN, 1832)	3	0
Lycosidae	Alopecosa pulverulenta (CLERCK, 1757)	9	0
Lycosidae	Pardosa agrestis (WESTRING, 1861)	146	87
Lycosidae	Pardosa agricola (THORELL, 1856)	3	9
Lycosidae	Pardosa amentata (CLERCK, 1757)	487	280
Lycosidae	Pardosa hortensis (THORELL, 1872)	3	2
Lycosidae	Pardosa palustris (LINNAEUS, 1758)	11	1
Lycosidae	Pardosa prativaga (L. KOCH, 1870)	78	3
Lycosidae	Pirata latitans (BLACKWALL, 1841)	3	0
Lycosidae	Pirata piraticus (CLERCK, 1757)	0	1
Lycosidae	Trochosa ruricola (DEGEER, 1778)	258	64
Lycosidae	Xerolycosa miniata (C.L. KOCH, 1834)	20	2
Pisauridae	Pisaura mirabilis (CLERCK, 1757)	3	0
Agelenidae	Tegenaria silvestris L. KOCH, 1872	0	2
Hahniidae	Hahnia nava (BLACKWALL, 1841)	13	1
Theridiidae	Robertus lividus (BLACKWALL, 1836)	0	1
Theridiidae	Steatoda phalerata (PANZER, 1801)	0	1
Tetragnathidae	Pachygnatha clercki SUNDEVALL, 1823	30	28
Tetragnathidae	Pachygnatha degeeri SUNDEVALL, 1830	13	2
Tetragnathidae	Tetragnatha extensa (LINNAEUS, 1758)	0	1
Linyphiidae	Bathyphantes gracilis (BLACKWALL, 1841)	1	0
Linyphiidae	Bathyphantes parvulus (WESTRING, 1851)	1	0
Linyphiidae	Caviphantes saxetorum (HULL, 1916)	1	0
Linyphiidae	Centromerita concinna (THORELL, 1875)	0	6
Linyphiidae	Centromerus sylvaticus (BLACKWALL, 1841)	0	1
Linyphiidae	Diplostyla concolor (WIDER, 1834)	2	10
Linyphiidae	Erigone atra (BLACKWALL, 1841)	7	5
Linyphiidae	Erigone dentipalpis (WIDER, 1834)	63	11
Linyphiidae	Collinsia distincta (SIMON, 1884)	3	3

Family	Species	#mm	#ff
Linyphiidae	Linyphia triangularis (CLERCK, 1757)	1	0
Linyphiidae	Meioneta rurestris (C.L. KOCH, 1836)	118	38
Linyphiidae	Mioxena blanda (SIMON, 1884)	0	3
Linyphiidae	Oedothorax apicatus (BLACKWALL, 1850)	9	26
Linyphiidae	Oedothorax fuscus (BLACKWALL, 1834)	30	40
Linyphiidae	Oedothorax retusus (WESTRING, 1851)	53	36
Linyphiidae	Pelecopsis parallela (WIDER, 1834)	2	3
Linyphiidae	Pocadicnemis juncea LOCKET & MILLIDGE, 1953	1	0
Linyphiidae	Porrhomma microphthalmum (O.P.-CAMBRIDGE, 1871)	1	0
Linyphiidae	Prinerigone vagans AUDOUIN, 1826	0	3
Linyphiidae	Stemonyphantes lineatus (LINNAEUS, 1758)	6	2
Linyphiidae	Troxochrus scabriculus (WESTRING, 1851)	2	0
Linyphiidae	Walckenaeria vigilax (BLACKWALL, 1833)	1	0
Total	**2109 individuals, 56 species**	***1426***	***683***

(b)

Family	Beetle species	25Mrch-5Apr	5-30Apr	30Apr-3Jun	3Jun-19Jul
Anthicidae	Anthicus flavipes (Panz.)	0	0	2	0
Byrrhidae	Curimopsis paleata (Er.)	0	0	0	1
Byrrhidae	Cytilus sericeus (F.)	0	3	1	2
Byrrhidae	Lamprobyrrhulus nitidus (Schall)	17	48	42	25
Byrrhidae	Simplocaria semistriata (F.)	5	0	4	0
Cantharidae	Cantharis livida (L.)	4	0	0	0
Cantharidae	Rhagonycha fulva (Scop.)	2	0	0	0
Carabidae	Acupalpus meridianus (L.)	0	7	9	5
Carabidae	Agonum marginatum (L.)	0	0	1	0
Carabidae	Agonum muelleri (Herbst)	6	16	9	15
Carabidae	Agonum sexpunctata (L.)	0	1	0	0
Carabidae	Amara aenea (De Geer)	22	16	31	114
Carabidae	Amara aulica (Panzer)	1	3	5	4
Carabidae	Amara bifrons (Gyll.)	0	0	1	1
Carabidae	Amara consularis (Duft.)	0	0	0	1
Carabidae	Amara fameliaris (Duft.)	0	0	4	1
Carabidae	Amara montivaga (Sturm)	0	0	0	1
Carabidae	Amara ovata (F.)	18	10	2	14
Carabidae	Amara similata (Gyll.)	2	1	1	3
Carabidae	Asaphidion curtum (Heyden)	1	0	1	0
Carabidae	Asaphidion flavipes (L.)	4	1	0	2
Carabidae	Badister bullatus (Schrank.)	0	5	2	1
Carabidae	Badister unipustulatus (Bonelli)	0	0	1	0
Carabidae	Bembidion femoratum (Sturm)	38	73	12	53
Carabidae	Bembidion lampros (Herbst)	3	9	13	18
Carabidae	Bembidion obtusum (Serville)	0	5	0	0
Carabidae	Bembidion properans (Stephens)	8	13	33	83
Carabidae	Bembidion quadrimaculatum (L.)	1	4	11	18
Carabidae	Bembidion tetracolum (Say)	74	231	22	18
Carabidae	Carabus granulatus (L.)	1	5	0	0
Carabidae	Carabus violaceus (L.)	0	1	0	0
Carabidae	Chlaenius nitidulus (Schrank)	0	3	2	4
Carabidae	Chlaenius tibialis (Dej,)	7	41	32	71
Carabidae	Cicindela campestris (L.)	385	1049	3	0
Carabidae	Cicindela hybrida (L.)	0	1	0	0

Family	Beetle species	25Mrch-5Apr	5-30Apr	30Apr-3Jun	3Jun-19Jul
Carabidae	Clivina collaris (Herbst)	0	1	2	1
Carabidae	Clivina fossor (L.)	1	4	0	3
Carabidae	Dyschirius angustatus (Ahrens)	0	0	0	1
Carabidae	Dyschirius globosus (Herbst)	0	0	0	1
Carabidae	Harpalus affinis (Schrank)	18	27	26	37
Carabidae	Harpalus attenuatus (Steph.)	0	0	0	1
Carabidae	Harpalus distinguendus (Duft.)	17	21	24	10
Carabidae	Harpalus latus (L.)	0	0	1	5
Carabidae	Harpalus rubripes (Duft.)	0	2	0	7
Carabidae	Lionychus quadrillum (Duft.)	1	0	0	0
Carabidae	Microlestes maurus (Sturm)	0	0	1	5
Carabidae	Nebria brevicollis (F.)	0	0	2	0
Carabidae	Notiophilus substriatus (Waterhouse)	2	1	1	1
Carabidae	Panangeus cruxmajor (L.)	0	0	0	2
Carabidae	Parophonus maculicornis (Duft.)	0	0	1	3
Carabidae	Platynus albipes (F.)	5	4	0	0
Carabidae	Platynus assimilis (Paykull)	8	8	1	5
Carabidae	Platynus dorsalis (Pontoppidan)	0	2	23	8
Carabidae	Poecilus cupreus (L.)	0	154	24	55
Carabidae	Pseudophonus rufipes (De Geer)	2	0	19	242
Carabidae	Pterostichus anthracinus (Ill.)	1	15	0	0
Carabidae	Pterostichus madidus (F.)	1	0	4	8
Carabidae	Pterostichus niger (Schaller)	0	0	0	4
Carabidae	Pterostichus nigrita (Paykull)	1	2	3	0
Carabidae	Pterostichus strenuus (Panzer)	5	12	5	0
Carabidae	Pterostichus vernalis (Panzer)	0	4	0	6
Carabidae	Pterostichus melanarius (Ill.)	1	2	2	10
Carabidae	Stenolophus teutonus (Schrank)	0	0	0	2
Carabidae	Stomis pumicatus (Panzer)	0	0	5	3
Carabidae	Syntomus truncatellus (L.)	0	0	0	1
Carabidae	Tachys bistriatus (Duft.)	10	2	3	8
Carabidae	Tachys micros (Ficher von Waldheim)	0	2	1	0
Carabidae	Trechus obtusus (Er.)	0	0	1	0
Catopidae	Ptomophagus subvillosus (Goeze)	0	0	1	0
Chrysomelidae	Chaetocnema hortensis (Geoffr.)	0	2	8	3
Chrysomelidae	Chrysomela staphylea (L.)	1	0	0	0
Chrysomelidae	Crepidoptera ferrugineum (Scop.)	0	0	1	0
Chrysomelidae	Haltica oleracea (L.)	0	0	1	0
Chrysomelidae	Hippuriphila modeeri (L.)	0	1	0	0
Chrysomelidae	Longitarsus dorsalis (F.)	8	14	7	2
Chrysomelidae	Longitarsus ganglbauri (Hktr.)	8	0	0	1
Chrysomelidae	Longitarsus luridus (Scop.)	4	12	2	0
Chrysomelidae	Longitarsus melanocephala (Deg.)	0	1	0	1
Chrysomelidae	Phyllotreta atra (F.)	0	0	3	1
Chrysomelidae	Phyllotreta diademata (F.)	0	0	0	2
Chrysomelidae	Phyllotreta nemorum (L.)	0	1	0	0
Clambidae	Clambus armadillo (De Geer)	0	1	0	0
Coccidulidae	Coccidula septempunctata (L.)	1	0	0	2
Coccidulidae	Hippodamia tredecimpunctata (L.)	0	0	0	3
Coccidulidae	Platynaspis luteorubra (Goeze)	0	0	1	4
Coccidulidae	Scymnus frontalis (F.)	0	0	0	2
Cryptophagidae	Atomaria linearis (Steph.)	0	0	1	5
Curculionidae	Apion flavipes (Payk.)	0	0	1	0
Curculionidae	Apion virens (Herbst)	0	1	0	1

Family	Beetle species	25Mrch-5Apr	5-30Apr	30Apr-3Jun	3Jun-19Jul
Curculionidae	Baris lepidii (Germ.)	1	2	0	1
Curculionidae	Ceutorhynchus litura (F.)	1	0	0	0
Curculionidae	Cidnorhinus quadrimaculatus (L.)	0	0	1	0
Curculionidae	Grypus equiseti (Steph.)	1	0	0	0
Curculionidae	Gymnaethron tetrum (F.)	0	0	0	1
Curculionidae	Hypera pedestris (Payk.)	0	1	0	0
Curculionidae	Hypera postica (Gyll.)	1	2	3	3
Curculionidae	Hypera zoilus (Scop.)	9	12	1	0
Curculionidae	Phyllobius urticae (Deg,)	0	0	1	0
Curculionidae	Rhinoncus gramineus (F.)	0	1	1	0
Curculionidae	Sitona flavescens (Mrsh.)	7	20	17	9
Curculionidae	Sitona hispidulus (F,)	30	42	16	9
Curculionidae	Sitona humeralis (Steph)	2	6	9	5
Curculionidae	Tanymecus palliatus (F.)	5	4	6	1
Curculionidae	Tychius junceus (Reich.)	0	0	1	4
Curculionidae	Tychius picirostris (F.)	0	0	0	5
Elateridae	Adelocera murina (L.)	0	0	0	1
Elateridae	Agriotes lineatus (L.)	0	0	1	0
Elateridae	Agriotes obscurus (L.)	0	1	2	1
Elateridae	Pseudathous niger (L.)	0	0	0	1
Elateridae	Zorochrus dermestoides (Herbst)	1	3	23	55
Hydrophilidae	Sphaeridium scaraboides (L.)	0	0	1	0
Liodidae	Liodes pallens (Strm.)	0	0	0	3
Nitidulidae	Meligethes ovatus (Sturm)	0	1	0	0
Phalacridae	Olibrus corticalis (Panz.)	0	0	1	0
Scarabaeidae	Aphodius granarius (L.)	0	2	1	0
Scarabaeidae	Aphodius prodromus (Brahm)	4	6	0	0
Scarabaeidae	Onthophagus joannae (Goljan)	1	0	0	0
Scarabaeidae	Onthophagus similis (Scriba)	0	1	0	0
Scarabaeidae	Rhyssemus germanus (L.)	1	0	0	0
Scarabaeidae	Valgus hemipterus (L.)	0	0	0	1
Silphidae	Necrophorus vespillo (L.)	1	0	0	0
Silphidae	Phosphuga atrata (L.)	1	1	1	0
Staphylinidae	Aloconota gregaria (Er.)	2	1	0	0
Staphylinidae	Aleochara curtula (Goeze)	0	0	4	0
Staphylinidae	Amarochara forticornis (Boisd)	0	0	1	0
Staphylinidae	Amischa analis (Grav.)	0	0	2	0
Staphylinidae	Bledius opacus (Block.)	4	6	10	1
Staphylinidae	Bryocharis analis (Payk.)	1	1	0	0
Staphylinidae	Callicerus rigidicornis (Er.)	2	0	0	0
Staphylinidae	Dinaraea angustula (Gyll.)	0	0	1	0
Staphylinidae	Drusilla canaliculata (F.)	0	1	0	0
Staphylinidae	Gabrius subnigritulus (Rtt.)	0	0	1	0
Staphylinidae	Ilyobates subopacus (Palm)	1	0	3	0
Staphylinidae	Lathrobium fulvipenne (Grav.)	3	8	1	7
Staphylinidae	Mycetophorus ruficornis (Kr.)	0	1	0	0
Staphylinidae	Ocypus melanarius (Heer)	5	2	0	3
Staphylinidae	Ocypus olens (Müll.)	0	0	0	1
Staphylinidae	Ontholestes murinus (L.)	0	1	0	0
Staphylinidae	Oxytelus sculpturatus (Grav.)	0	2	0	0
Staphylinidae	Oxytelus tetracarinatus (Block)	0	0	1	0
Staphylinidae	Paederus litoralis (Grav.)	0	0	2	0
Staphylinidae	Philonthus varius (Gyllh.)	0	0	1	0
Staphylinidae	Quedius molorchinus (Grav.)	0	0	0	1

Family	Beetle species	25Mrch-5Apr	5-30Apr	30Apr-3Jun	3Jun-19Jul
Staphylinidae	Scopaeus cognatus (Rey)	0	0	2	0
Staphylinidae	Stenus biguttatus (L.)	1	0	0	0
Staphylinidae	Tachinus corticinus (Grav.)	3	2	0	0
Staphylinidae	Tachyporus chrysomelinus (L.)	1	0	0	0
Staphylinidae	Tachyporus nitidulus (F.)	1	2	7	4
Staphylinidae	Trogophloeus pusillus (Grav.)	0	1	0	0
Staphylinidae	Xantholinus linearis (Ol.)	1	2	1	0
Staphylinidae	Xantholinus longiventris (Heer)	17	17	10	6
Staphylinidae	Zyras limbatus (Payk.)	1	0	0	0
Totaal	**4381 individuals, 152 species**	***803***	***1994***	***550***	***1034***

Appendix A2. - Pearson correlations with PCA-ordination axes of local topographical and regional chorological environmental parameters of river banks along the Common Meuse river reach. Prior to PCA-analysis parameters were transformed if they did not meet the normality assumption (McCune & Grace, 2002), indicated by (log) for logarithmic and (sqrt) for square-root transformation. Correlation coefficients r > 0.570 are significant after Bonferroni correction.

parameter	**variable measured**	**methodology**	**PC_{dyn}**	**PC_{geo}**	**PC_{veg}**
flooding disturbance	RSregr	rising speed of washing water based on river discharge regimes and fourthnightly measured distances pitfalls - water line	**-0.585**	0.081	-0.094
flooding disturbance	WFR	river bank water flow rate based on based on river discharge regimes and fourthnightly measured distances pitfalls - water line	**-0.866**	-0.203	0.061
flooding disturbance	dayfl	number of days flooded during sampling period based on river discharge regimes and WFR (log)	**0.811**	0.264	-0.133
flooding disturbance	dayfl5yr	number of days flooded between 2000 and 2005 based on river discharge regimes and WFR (log)	**0.843**	0.193	-0.189
river bank topography	ddike	average distance pitfalls - dike	*-0.516*	-0.386	-0.314
river bank topography	hw	ratio elevation - width river bank (cf. ascent)	-0.113	**0.625**	**0.497**
river bank topography	alpha	river bank steepness	-0.372	0.348	**0.577**
river bank topography	hwst	hw restricted to river bank level	-0.102	-0.238	-0.011
river bank topography	orientcl	orientation eighth of river bank	**-0.667**	*0.408*	0.086
river bank topography	area	patch size	0.048	**-0.799**	0.152
river bank topography	watl	length of interface river bank - river channel (cf. waterline)	0.307	**-0.576**	0.242
river channel topography	wd	ratio width-depth river channel (cf. water storage capacity)	0.167	-0.26	-0.043
river channel topography	hd	elevation river bank - depth river channel ratio (river corridor geometry)	-0.295	0.379	**0.592**
river channel topography	wdst	wd restricted to river bank level	0.085	*0.502*	-0.144
river channel topography	hdst	hd restricted to river bank level	0.131	**0.676**	-0.062
substrate composition	grav	average gravel size (6 classes ranging from 0-10cm until >50cm)	**-0.782**	-0.13	0.19
substrate composition	sand	sediment composition (sand - loam ratio)	**-0.852**	-0.08	-0.074
substrate composition	silt	siltation class index (none - covering 1/4 - half - upto dyke foot)	**0.771**	0.232	-0.052
vegetation structure	shad	percentage of vegetation shading	0.221	-0.268	**0.586**
vegetation structure	vegh	average vegetation height	0.022	0.361	*0.514*
vegetation structure	avVegc	average vegetation cover	0.214	0.069	**0.617**

parameter	variable measured	methodology	PC_{dyn}	PC_{geo}	PC_{veg}
vegetation structure	sdVegc	variation in vegetation cover	0.221	-0.04	*0.509*
vegetation structure	vegsucc	vegetation succession (sqrt)	0.047	0.034	0.214
landscape composition	alluv100	amount of alluvial grasslands within 100m radius (log)	-0.237	0.371	**-0.574**
landscape composition	arabl100	amount of arable land within 100m radius (log)	0.35	-0.33	0.238
landscape composition	brush100	amount of brushwood vegetation within 100m radius (log)	-0.335	0.206	-0.173
landscape composition	shrub100	amount of shrubland within 100m radius (log)	-0.104	*-0.516*	-0.355
landscape composition	water100	amount of waterbodies within 100m radius (log)	*0.508*	-0.287	-0.368
landscape composition	alluv250	amount of alluvial grasslands within 200m radius (log)	-0.38	**0.672**	-0.332
landscape composition	arabl250	amount of arable land within 200m radius (log)	*0.4*	0.144	-0.074
landscape composition	brush250	amount of brushwood vegetation within 200m radius (log)	*-0.505*	0.019	-0.117
landscape composition	shrub250	amount of shrubland within 200m radius (log)	-0.176	**-0.601**	-0.17
landscape composition	water250	amount of waterbodies within 200m radius (log)	-0.31	-0.382	0.298
channel connectivity	RTnneigh	nearest neighbour distance to most proximate river bank	*0.441*	-0.317	0.334
channel connectivity	PBwsum	patch-based weighted sum of river bank connectivity	*0.441*	0.373	-0.198

Environmental characterization:

Streamflow regimes are affected by local topography as well as by regional chorological factors (Pedroli et al., 2002; Van Looy et al., 2006) and influence both local humidity and vegetation structure, being the most important drivers for habitat suitability in the studied arthropod groups (Turin, 2000; Entling et al., 2007). Therefore, we recorded parameters related to flooding disturbance, river bank and channel geometry, substrate composition and vegetation structure. Measured landscape related parameters were sample site location, connectivity along the riparian corridor and surrounding land-use. For the ease of reading the measured variables and applied field methodology are concisely explained in Appendix S1. The large set of parameters was condensed into compound variables by means of Principal Component Analysis (PCA; Goodall, 1954). In this way, covariation between variables is represented and conclusions can be made regarding mutual correlations between habitat properties; Pearson correlation coefficients were calculated for these axes. PCA revealed the prevalence of one "disturbance"-axis (PC_{dyn}; eigenvalue 7.102; explanatory value 18.69%) which correlated with flooding disturbance aspects and substrate composition after Bonferroni-correction (Table 1). Increasing values of PC_{dyn} indicate a higher number of days the river banks were flooded during the sample period, an increased rising speed of the washing water and a substrate composed of less coarse gravel, a fine-grained in between sediment fraction and increased siltation. Two other axes explained variation related to river bank and channel topography (PC_{geo}; eigenvalue 5.166; explanatory value 13.59%) and vegetation structure (PC_{veg}; eigenvalue 4.284; explanatory value 11.27%). Thereby, increasing values of PC_{geo} represent a smaller patch size, a higher ascent of the gravel banks, a lower water storage capacity of the river channel and a lower degree of shrub vegetation nearby yet more alluvial grasslands. PC_{veg} can be described as vegetation complexity; increasing values lead to a higher degree of vegetation cover and height, hence, more shaded conditions.

Remarks:

- **River discharge regimes** taken from http://www.lin.vlaanderen.be/awz/waterstanden/hydra/ (hourly values)
- **River bank and channel topography** based on GPS-data and manual measurements taken during field survey of 2005 (low flow rate: 38 m^3s^{-1})
- **Vegetation and substrate features** are estimated values based on digital pictures within a 1x1 m quadrat surrounding each pitfall taken during the field survey at a fourthnightly basis
- Measures of channel connectivity based on definitions within Winfree et al. (2005)
- **Landscape composition** based on redrawn detailed maps of both sides of the Common Meuse river reach (Flemish: ECODYN model (Van Looy et al., 2005); Dutch: RES (Thijs, 2004)); values calculated applying ArcGIS 9.1 landscape sectors at two different spatial scales (100 m and 200 m radius)

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Appendix A3. - Species list, trapped numbers and trait values of (a) three spider (sub)families (Araneae: Erigoninae, Linyphiinae, Lycosidae) and (b) two carabid beetle tribes (Carabidae: Bembidiini, Pterostichini) from river banks along the Common Meuse. Nomenclature is according to Bosmans & Vanuytven (2001) for spiders and Boeken et al. (2002) for carabid beetles. Information about the life history trait values and their calculation is provided in chapter II.2. (see Lambeets et al., 2008).

(a)

spider (sub)family	*species*	*trapped numbers*	*Niche Breadth*	*Shading preference*	*Hygrophily*	*female size (mm)*	*Ballooning propensity*
Erigoninae	Baryphyma pratense (Blackwall, 1861)	307	5	-0.32	-1.48	2.75	0
Erigoninae	Caviphantes saxetorum (Hull, 1916)	225	1	-1.59	0.46	1.50	0
Erigoninae	Ceratinella brevipes (Westring, 1851)	2	40	-0.60	-0.85	1.70	0
Erigoninae	Dicymbium nigrum (Blackwall, 1834)	13	52	-0.41	-0.34	2.20	1
Erigoninae	Dicymbium tibiale (Blackwall, 1836)	90	31	-0.41	-0.34	2.35	0
Erigoninae	Diplocephalus cristatus (Blackwall, 1833)	53	45	-0.65	-0.23	2.15	1
Erigoninae	Diplocephalus permixtus (O. P.-Cambridge, 1871)	2	19	0.16	-0.88	1.70	0
Erigoninae	Diplocephalus picinus (Blackwall, 1841)	1	57	0.51	-0.36	1.70	0
Erigoninae	Dismodicus bifrons (Blackwall, 1841)	2	33	-0.48	-0.14	2.25	1
Erigoninae	Erigone atra Blackwall, 1833	713	77	-0.47	-0.42	2.30	1
Erigoninae	Erigone dentipalpis (Wider, 1834)	689	73	-0.69	-0.32	2.20	1
Erigoninae	Erigone longipalpis (Sundevall, 1830)	4	9	-1.53	-1.58	2.95	1
Erigoninae	Gongylidium rufipes (Linnaeus, 1758)	4	29	0.17	-0.83	3.15	0
Erigoninae	Collinsia distincta (Simon, 1884)	116	4	0.89	-0.29	2.10	0
Erigoninae	Hypomma bituberculatum (Wider, 1834)	161	23	-0.92	-1.29	2.70	1
Erigoninae	Lessertia dentichelis (Simon, 1884)	1	15	-0.92	-0.48	3.10	0
Erigoninae	Maso sundevalli (Westring, 1851)	2	53	0.39	-0.05	1.55	1
Erigoninae	Micrargus herbigradus (Blackwall, 1854)	3	76	0.36	-0.14	1.70	1
Erigoninae	Micrargus subaequalis (Westring, 1851)	1	46	-0.82	0.03	1.80	1
Erigoninae	Collinsia inerrans (O. P.-Cambridge, 1885)	21	5	-0.74	-0.39	2.25	1
Erigoninae	Monocephalus fuscipes (Blackwall, 1836)	1	33	0.38	-0.41	1.95	1
Erigoninae	Oedothorax apicatus (Blackwall, 1850)	944	47	-0.88	-0.48	2.80	1
Erigoninae	Oedothorax fuscus (Blackwall, 1834)	808	55	-0.81	-0.79	2.65	1
Erigoninae	Oedothorax retusus (Westring, 1851)	4568	36	-0.63	-0.98	2.55	1

spider (sub)family	***species***	***trapped numbers***	***Niche Breadth***	***Shading preference***	***Hygrophily***	***female size (mm)***	***Ballooning propensity***
Erigoninae	Pelecopsis mengei (Simon, 1884)	7	12	0.27	0.15	2.20	0
Erigoninae	Pelecopsis parallela (Wider, 1834)	69	42	-1.03	-0.35	1.75	1
Erigoninae	Peponocranium ludicrum (O. P.-Cambridge, 1861)	4	12	-0.25	0.56	1.92	0
Erigoninae	Pocadicnemis juncea Locket & Millidge, 1953	14	31	-0.59	-0.46	1.95	0
Erigoninae	Prinerigone vagans (Audouin, 1826)	21	9	-0.86	-0.85	2.60	1
Erigoninae	Troxochrus scabriculus (Westring, 1851)	52	28	-0.76	-0.40	1.85	1
Erigoninae	Walckenaeria atrotibialis (O. P.-Cambridge, 1878)	2	58	0.25	-0.27	2.50	1
Erigoninae	Walckenaeria dysderoides (Wider, 1834)	15	46	0.77	0.12	2.00	0
Erigoninae	Walckenaeria nudipalpis (Westring, 1851)	1	45	-0.26	-0.75	2.80	1
Erigoninae	Walckenaeria unicornis O. P.-Cambridge, 1861	3	33	-0.39	-0.41	2.55	0
Erigoninae	Walckenaeria vigilax (Blackwall, 1853)	1	34	-0.90	-0.50	2.30	1
Linyphiinae	Araeoncus humilis (Blackwall, 1841)	1	49	-1.11	-0.34	1.60	1
Linyphiinae	Bathyphantes gracilis (Blackwall, 1841)	23	78	-0.37	-0.51	2.20	1
Linyphiinae	Bathyphantes nigrinus (Westring, 1851)	2	50	0.59	-0.51	2.60	1
Linyphiinae	Bathyphantes parvulus (Westring, 1851)	1	44	-0.06	-0.12	2.25	1
Linyphiinae	Diplostyla concolor (Wider, 1834)	181	69	0.07	-0.27	2.60	1
Linyphiinae	Palliduphantes insignis (O. P.-Cambridge, 1913)	3	15	-0.96	-0.35	2.05	0
Linyphiinae	Leptorhoptrum robustum (Westring, 1851)	3	15	-0.51	-0.77	3.90	1
Linyphiinae	Tenuiphantes tenuis (Blackwall, 1852)	29	69	-0.39	-0.32	2.65	1
Linyphiinae	Meioneta rurestris (C.L. Koch, 1836)	403	76	-0.64	0.04	2.00	1
Linyphiinae	Microlinyphia pusilla (Sundevall, 1830)	2	44	-0.54	0.08	4.00	0
Linyphiinae	Neriene clathrata (Sundevall, 1830)	7	57	0.42	-0.35	4.35	1
Linyphiinae	Ostearius melanopygius (O. P.-Cambridge, 1879)	4	12	-0.97	-0.32	2.30	0
Linyphiinae	Porrhomma microphthalmum (O. P.-Cambridge, 1871)	14	36	-0.68	-0.44	1.95	1
Linyphiinae	Porrhomma pygmaeum (Blackwall, 1834)	4	39	-0.31	-0.93	2.25	1
Linyphiinae	Stemonyphantes lineatus (Linnaeus, 1758)	3	54	-0.37	0.45	5.40	1
Lycosidae	Alopecosa cuneata (Clerck, 1757)	6	45	-0.63	1.10	7.00	1
Lycosidae	Alopecosa pulverulenta (Clerck, 1757)	23	65	-0.45	0.22	8.25	1
Lycosidae	Arctosa cinerea (Fabricius, 1777)	683	3	-0.97	1.01	14.50	0
Lycosidae	Arctosa leopardus (Sundevall, 1833)	9	26	-1.09	-0.49	9.00	1
Lycosidae	Pardosa agrestis (Westring, 1861)	443	34	-1.16	-0.41	7.50	1

spider (sub)family	***species***	***trapped numbers***	***Niche Breadth***	***Shading preference***	***Hygrophily***	***female size (mm)***	***Ballooning propensity***
Lycosidae	Pardosa agricola (Thorell, 1856)	4047	9	-0.06	0.83	6.75	0
Lycosidae	Pardosa amentata (Clerck, 1757)	7584	63	-0.18	-0.60	6.75	1
Lycosidae	Pardosa nigriceps (Thorell, 1856)	1	31	-0.25	-0.11	6.00	1
Lycosidae	Pardosa palustris (Linnaeus, 1758)	225	51	-0.85	-0.27	5.75	1
Lycosidae	Pardosa prativaga (L. Koch, 1870)	546	49	-0.85	-0.58	5.00	1
Lycosidae	Pardosa proxima (C.L. Koch, 1847)	199	2	-0.38	-0.69	6.00	1
Lycosidae	Pardosa pullata (Clerck, 1757)	9	66	-0.57	-0.07	5.00	1
Lycosidae	Pirata hygrophilus Thorell, 1872	5	45	-0.04	-0.48	5.75	0
Lycosidae	Pirata latitans (Blackwall, 1841)	45	45	-0.66	-0.38	4.50	1
Lycosidae	Pirata piraticus (Clerck, 1757)	16	35	-0.74	-0.86	6.75	1
Lycosidae	Trochosa ruricola (De Geer, 1778)	1661	55	-0.75	-0.27	11.50	0
Lycosidae	Xerolycosa miniata (C.L. Koch, 1834)	19	20	-1.01	0.29	6.00	1

(b)

carabid beetle tribus	***species***	***Trapped numbers***	***Niche breadth***	***Shading preference***	***Hygrophily***	***Body size***	***Wing development***
Bembidiini	Asaphidion flavipes (Linnaeus, 1761)	61	51	0	3	4.35	8.5
Bembidiini	Bembidion atrocoeruleum (Stephens, 1829)	989	0	1	4	4.75	9.5
Bembidiini	Bembidion decorum (Zenker, 1801)	779	6	1	4	5.6	10.5
Bembidiini	Bembidion dentellum (Thunberg, 1787)	1	72	3	4	5.5	10
Bembidiini	Bembidion elongatum (Dejean, 1831)	1	1	1	4	4	.
Bembidiini	Bembidion femoratum (Sturm, 1825)	2556	80	1	3	4.85	10.5
Bembidiini	Bembidion harpaloides (Serville, 1821)	3	25	3	4	5.1	.
Bembidiini	Bembidion lampros (Herbst, 1784)	242	137	0	0	3.5	.
Bembidiini	Bembidion obtusum (Serville, 1821)	6	60	3	0	3.2	.
Bembidiini	Bembidion properans (Stephens, 1829)	1115	108	0	3	4	.
Bembidiini	Bembidion punctulatum (Drapiez, 1820)	508	4	1	4	5.05	11.5
Bembidiini	Bembidion quadrimaculatum (Linnaeus, 1761)	119	102	1	3	3.15	9
Bembidiini	Bembidion semipunctatum (Donovan, 1806)	3	23	3	4	3.7	10

carabid beetle tribus	*species*	*Trapped numbers*	*Niche breadth*	*Shading preference*	*Hygrophily*	*Body size*	*Wing development*
Bembidiini	Bembidion stomoides (Dejean, 1831)	1	2	3	4	5.5	5.5
Bembidiini	Bembidion testaceum (Duftschmid, 1812)	47	4	1	4	5	10.5
Bembidiini	Bembidion tetracolum (Say, 1823)	1836	104	0	3	5.5	.
Bembidiini	Bembidion velox (Linnaeus, 1761)	1	2	1	4	5.75	.
Bembidiini	Tachys bistriatus (Duftschmid, 1812)	2	2	0	4	2.95	10
Bembidiini	Tachys micros (Fischer Von Waldheim, 1828)	88	8	1	4	2.15	.
Bembidiini	Tachys parvulus (Duftschmid, 1812)	206	8	1	4	2.05	7.5
Bembidiini	Tachys quadrisignatus (Stephens, 1829)	1	1	1	4	2.55	6.5
Pterostichini	Paranchus albipes (Fabricius, 1796)	125	101	4	4	7.9	.
Pterostichini	Limodromus assimilis (Paykull, 1790)	54	86	0	4	10.5	5.5
Pterostichini	Anchomenus dorsalis (Pontoppidan, 1763)	436	111	0	0	7	7.5
Pterostichini	Agonum marginatum (Linnaeus, 1758)	91	86	1	4	9.5	10
Pterostichini	Agonum micans (Nicolai, 1822)	2	21	3	4	6.85	9.5
Pterostichini	Agonum afrum (Duftschmid, 1812)	36	76	3	4	8.7	8.5
Pterostichini	Agonum muelleri (Herbst, 1785)	593	101	0	3	8.2	9
Pterostichini	Oxypselaphus obscurum (Herbst, 1784)	13	107	0	4	5.7	.
Pterostichini	Agonum sexpunctatum (Linnaeus, 1758)	17	55	2	3	8.5	7
Pterostichini	Calathus fuscipes (Goeze, 1777)	17	81	0	0	11.7	.
Pterostichini	Calathus melanocephalus (Linnaeus, 1758)	3	97	2	0	7.5	.
Pterostichini	Pterostichus anthracinus (Illiger, 1798)	8	48	3	4	10.75	.
Pterostichini	Poecilus cupreus (Linnaeus, 1758)	1090	68	4	3	11.25	9
Pterostichini	Pterostichus gracilis (Dejean, 1828)	2	20	3	4	9.2	11.5
Pterostichini	Pterostichus melanarius (Illiger, 1798)	278	98	0	0	15.5	.
Pterostichini	Pterostichus niger (Schaller, 1783)	3	95	0	4	18	8
Pterostichini	Pterostichus nigrita (Paykull, 1790)	1	69	0	4	10.65	.
Pterostichini	Pterostichus strenuus (Panzer, 1797)	28	135	0	3	6.1	.
Pterostichini	Pterostichus vernalis (Panzer, 1796)	95	127	3	3	6.75	.
Pterostichini	Poecilus versicolor (Sturm, 1824)	224	71	0	0	10.1	7
Pterostichini	Stomis pumicatus (Panzer, 1796)	50	56	3	3	7.65	.
Pterostichini	Synuchus vivalis (Panzer, 1797)	6	40	0	3	7.5	6

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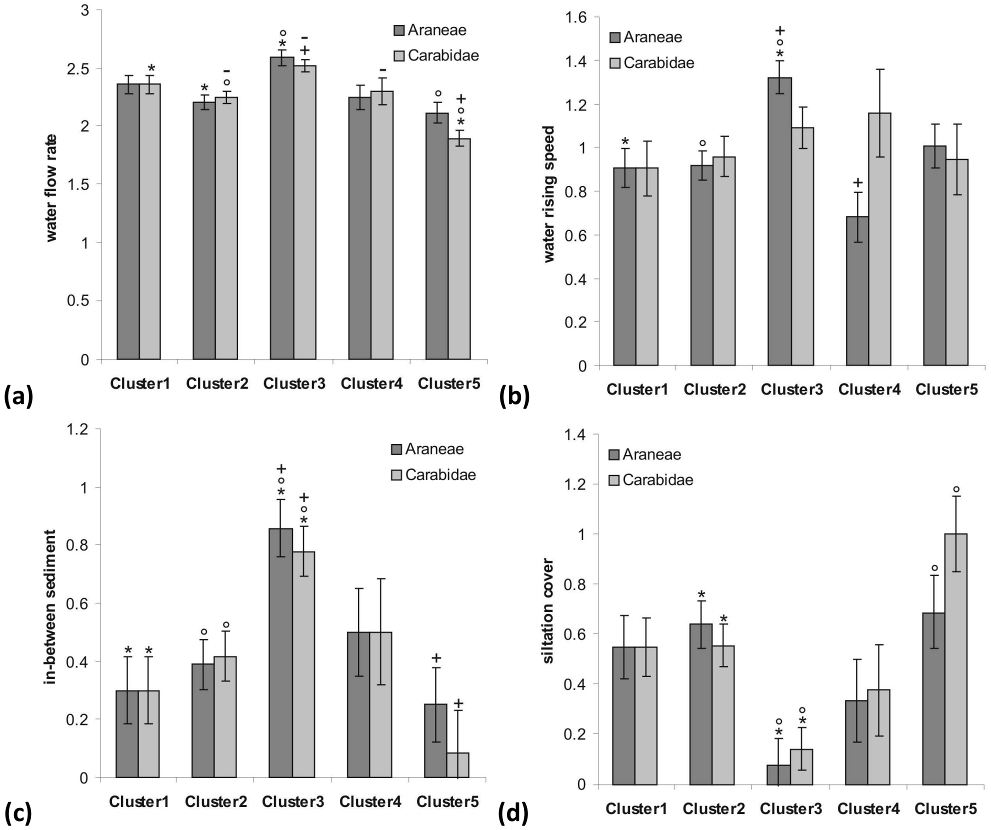
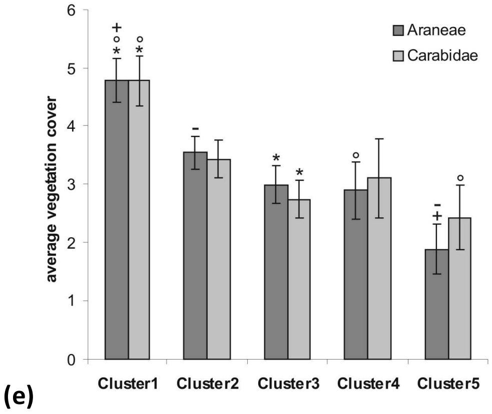
Appendix A4. - Pairwise differences of environmental conditions between river bank clusters (SAS 9.1; proc mixed): (a) water flow rate, (b) water rising speed, (c) composition of the in-between sediment fraction, (d) extent of the silt cover, (e) average vegetation cover. Clusters are based on spider and carabid beetle catch numbers (Sorensen distance, flexible β = -0.25). Error bars indicate standard errors of the mean. Significant pairwise comparisons within arthropod groups are indicated by symbols (post hoc Tukey-Kramer test; *, °, +, -). Table (f) represents differences in environmental conditions between river bank clusters were analysed by one-way ANOVA's.





(f)

environmental parameter	taxon	F-value	p-value
water flow rate	Araneae	5.99	0.0019
water flow rate	Carabidae	8.48	0.0002
water rising speed	Araneae	7.16	0.0007
water rising speed	Carabidae	0.6	0.6633
in-between sediment composition	Araneae	5.37	0.0033
in-between sediment composition	Carabidae	5.55	0.0028
silt cover	Araneae	5.05	0.0045
silt cover	Carabidae	7.11	0.0007
average vegetation cover	Araneae	7.06	0.0007
average vegetation cover	Carabidae	4.41	0.0086

Appendix A5. - Total numbers of individuals caught (species densities) of riparian species on the river banks along the Common Meuse. High species abundances are highlighted. The riparian linyphiid spider *Pelecopsis mengei* (Simon, 1884) was caught with seven individuals at river bank cluster three (1) and four (6) respectively, whereas the riparian carabid beetle *Bembidion velox* (Linnaeus, 1761) was encountered with only one individual at cluster one.

Scientific Name	**Cluster 1**	**Cluster 2**	**Cluster 3**	**Cluster 4**	**Cluster 5**	**species total**
Pardosa agricola (Thorell, 1856)	2	**3887**	0	6	*152*	**4047**
Heliophanus auratus C.L. Koch, 1835	2	2	**26**	13	0	**42**
Baryphyma pratense (Blackwall, 1861)	40	**175**	46	29	17	**307**
Collinsia distincta (Simon, 1884)	**58**	45	4	1	9	**116**
Arctosa cinerea (Fabricius, 1777)	60	0	**620**	3	0	**683**
Pardosa agrestis (Westring, 1861)	**370**	9	52	2	11	**443**
Caviphantes saxetorum (Hull, 1916)	*83*	23	**113**	0	6	**225**
Troxochrus scabriculus (Westring, 1851)	12	5	**31**	5	0	**52**
Bembidion atrocoeruleum (Stephens, 1829)	172	*233*	**387**	172	10	**973**
Bembidion decorum (Zenker, 1801)	61	**269**	129	*233*	12	**703**
Agonum afrum (Duftschmid, 1812)	9	7	1	5	**15**	**36**
Bembidion punctulatum (Drapiez, 1820)	**179**	89	*117*	98	17	**500**
Chlaenius tibialis Dejean, 1826	*97*	**313**	37	11	16	**473**
Paranchus albipes (Fabricius, 1796)	**43**	29	*34*	5	15	**125**
Agonum marginatum (Linnaeus, 1758)	**48**	29	13	0	0	**90**
Tachys micros (Fischer Von Waldheim, 1828)	**37**	20	14	0	17	**88**
Bembidion testaceum (Duftschmid, 1812)	14	**21**	7	3	3	**47**
Lionychus quadrillum (Duftschmid, 1812)	96	718	**4546**	*1116*	26	**6500**
Tachys parvulus (Duftschmid, 1812)	38	34	**96**	27	5	**199**
river bank total	**1417**	**5907**	**6269**	**1726**	**330**	***15649***

Appendix A6. - Species list and (standardized, total) numbers of arthropods caught on the river banks of the Common Meuse river reach in 2005: (a) spiders (Araneae) and (b) carabid beetles (Carabidae). All observations are entered in the data-bank of Belgian spiders (Hendrickx & De Bakker, forthcoming) and have been implemented in the new distribution atlas of the ground and tiger beetles of Belgium (Desender et al., 2008). Functional grouping is based on relevant literature resources (spiders: Hänggi et al., 1995; Maelfait et al., 1998; Harvey et al., 2002; carabid beetles: Turin, 2000; Desender et al., 1995; Boeken et al., 2002; see also Lambeets et al., 2008): h - hygrophilic, pe - pioneer/eurytopix, r - stenotopic riparian, xt - xerothermophilic. Seasonal activity patterns (activity period; ActPer) are based on Schaefer (1976): arthropods were assigned to one of four classes: eurychrone species, in which adults are active throughout the year (type I); stenochrone species, with their main activity during March-June (type IIa); stenochrone species, with an activity peak during June-September (type IIb); and stenochrone or diplochrone species, with their main activity during October – March (type IV-V).

(a)

Family	**species code**	**Scientific name**	**Funct. group**	**Total**	**ActPer**
Lycosidae	**Pardamen**	Pardosa amentata (Clerck, 1757)	pe	7584	IIa
Erigoninae	**Oedoretu**	Oedothorax retusus (Westring, 1851)	pe	4568	I
Lycosidae	**Pardagri**	Pardosa agricola (Thorell, 1856)	r	4047	IIa
Lycosidae	**Trocruri**	Trochosa ruricola (De Geer, 1778)	pe	1661	IIb
Erigoninae	**Oedoapic**	Oedothorax apicatus (Blackwall, 1850)	pe	944	I
Erigoninae	**Oedofusc**	Oedothorax fuscus (Blackwall, 1834)	pe	808	I
Erigoninae	**Erigatra**	Erigone atra Blackwall, 1833	pe	713	I
Erigoninae	**Erigdent**	Erigone dentipalpis (Wider, 1834)	pe	689	I
Lycosidae	**Arctcine**	Arctosa cinerea (Fabricius, 1777)	r-xt	683	IIa
Lycosidae	**Pardprat**	Pardosa prativaga (L. Koch, 1870)	h	546	IIb
Tetragnathidae	**Pachcler**	Pachygnatha clercki Sundevall, 1823	h	456	I
Lycosidae	**Pardagre**	Pardosa agrestis (Westring, 1861)	r-xt	443	IIa
Linyphiinae	**Meiorure**	Meioneta rurestris (C.L. Koch, 1836)	pe	403	I
Erigoninae	**Baryprat**	Baryphyma pratense (Blackwall, 1861)	r-h	307	IIa
Erigoninae	**Cavisaxe**	Caviphantes saxetorum (Hull, 1916)	r-xt	225	I
Lycosidae	**Pardpalu**	Pardosa palustris (Linnaeus, 1758)	pe	225	IIb
Lycosidae	**Pardprox**	Pardosa proxima (C.L. Koch, 1847)	h	199	IIa
Linyphiinae	**Diplconc**	Diplostyla concolor (Wider, 1834)	pe	181	I
Erigoninae	**Hypobitu**	Hypomma bituberculatum (Wider, 1834)	h	161	IIa
Erigoninae	**Halodist**	Collinsia distincta (Simon, 1884)	r-h	116	IIa
Erigoninae	**Dicytibi**	Dicymbium tibiale (Blackwall, 1836)	pe-h	90	IIb
Gnaphosidae	**Micapuli**	Micaria pulicaria (Sundevall, 1831)	xt	74	IIa
Erigoninae	**Pelepara**	Pelecopsis parallela (Wider, 1834)	pe-xt	69	I
Erigoninae	**Diplcris**	Diplocephalus cristatus (Blackwall, 1833)	pe	53	I
Erigoninae	**Troxscab**	Troxochrus scabriculus (Westring, 1851)	r-xt	52	IIa
Lycosidae	**Piralati**	Pirata latitans (Blackwall, 1841)	h	45	IIb
Salticidae	**Heliaura**	Heliophanus auratus C.L. Koch, 1835	r	42	IIb
Thomisidae	**Ozypsimp**	Ozyptila simplex (O. P.-Cambridge, 1862)	h	33	IIa
Liocranidae	**Phrufest**	Phrurolithus festivus (C.L. Koch, 1835)	xt	29	IIb

Linyphiinae	**Lepttenu**	Tenuiphantes tenuis (Blackwall, 1852)	pe	29	I
Clubionidae	**Clubfris**	Clubiona frisia Wunderlich & Schuett, 1995	xt	27	I
Clubionidae	**Clubrecl**	Clubiona reclusa O. P.-Cambridge, 1863	h	27	IIb
Tetragnathidae	**Pachdege**	Pachygnatha degeeri Sundevall, 1830	pe	25	I
Lycosidae	**Aloppulv**	Alopecosa pulverulenta (Clerck, 1757)	pe-h	23	IIa
Linyphiinae	**Bathgrac**	Bathyphantes gracilis (Blackwall, 1841)	pe	23	I
Erigoninae	**Milliner**	Collinsia inerrans (O. P.-Cambridge, 1885)	h	21	I
Erigoninae	**Prinvaga**	Prinerigone vagans (Audouin, 1826)	pe	21	I
Lycosidae	**Xeromini**	Xerolycosa miniata (C.L. Koch, 1834)	xt	19	IIb
Gnaphosidae	**Zelolute**	Drassyllus lutetianus (L. Koch, 1866)	xt	16	IIb
Lycosidae	**Pirapira**	Pirata piraticus (Clerck, 1757)	h	16	IIb
Erigoninae	**Walcdysd**	Walckenaeria dysderoides (Wider, 1834)	pe-xt	15	I
Linyphiinae	**Porrmicr**	Porrhomma microphthalmum (O. P.-Cambridge, 1871)	pe-xt	14	I
Erigoninae	**Pocajunc**	Pocadicnemis juncea Locket & Millidge, 1953	pe-xt	14	IIa
Erigoninae	**Dicynigr**	Dicymbium nigrum (Blackwall, 1834)	pe	13	IIa
Clubionidae	**Clubphra**	Clubiona phragmitis C.L. Koch, 1843	h	13	IIb
Thomisidae	**Xystkoch**	Xysticus kochi Thorell, 1872	pe	12	IIa
Thomisidae	**Xystacer**	Xysticus acerbus Thorell, 1872	xt	11	IIa
Lycosidae	**Arctleop**	Arctosa leopardus (Sundevall, 1833)	h	9	IIb
Lycosidae	**Pardpull**	Pardosa pullata (Clerck, 1757)	pe-xt	9	IIb
Thomisidae	**Xystulmi**	Xysticus ulmi (Hahn, 1831)	h	9	IIa
Theridiidae	**Robenegl**	Robertus neglectus (O. P.-Cambridge, 1871)	h	8	I
Agelenidae	**Agellaby**	Agelena labyrinthica (Clerck, 1757)	pe	7	IIa
Linyphiinae	**Nericlat**	Neriene clathrata (Sundevall, 1830)	pe	7	I
Pisauridae	**Pisamira**	Pisaura mirabilis (Clerck, 1757)	pe	7	IIa
Erigoninae	**Pelemeng**	Pelecopsis mengei (Simon, 1884)	r-h	7	I
Lycosidae	**Alopcune**	Alopecosa cuneata (Clerck, 1757)	xt	6	IIa
Salticidae	**Synavena**	Synageles venator (Lucas, 1836)	xt	6	IIb
Clubionidae	**Clubnegl**	Clubiona neglecta O. P.-Cambridge, 1862	xt	6	I
Theridiidae	**Enopmord**	Enoplognatha mordax (Thorell, 1875)	h	5	IIa
Lycosidae	**Pirahygr**	Pirata hygrophilus Thorell, 1872	h	5	IIb
Hahniidae	**Hahnnava**	Hahnia nava (Blackwall, 1841)	xt	5	IIa
Theridiidae	**Steaphal**	Steatoda phalerata (Panzer, 1801)	xt	5	IIb
Thomisidae	**Xystcris**	Xysticus cristatus (Clerck, 1757)	pe	5	IIa
Erigoninae	**Eriglong**	Erigone longipalpis (Sundevall, 1830)	h	4	I
Erigoninae	**Gongrufi**	Gongylidium rufipes (Linnaeus, 1758)	h	4	IIa
Linyphiinae	**Ostemela**	Ostearius melanopygius (O. P.-Cambridge, 1879)	pe	4	I
Erigoninae	**Pepoludi**	Peponocranium ludicrum (O. P.-Cambridge, 1861)	xt	4	IIa
Gnaphosidae	**Zelopede**	Trachyzelotes pedestris (C.L. Koch, 1837)	xt	4	IIb
Linyphiinae	**Porrpygm**	Porrhomma pygmaeum (Blackwall, 1834)	pe-h	4	I
Clubionidae	**Clublute**	Clubiona lutescens Westring, 1851	h	3	IIb
Linyphiinae	**Leptinsi**	Palliduphantes insignis (O. P.-Cambridge, 1913)	pe-xt	3	I

Linyphiinae	**Leptrobu**	Leptorhoptrum robustum (Westring, 1851)	h	3	I
Erigoninae	**Micrherb**	Micrargus herbigradus (Blackwall, 1854)	pe-h	3	I
Salticidae	**Phlefasc**	Phlegra fasciata (Hahn, 1826)	xt	3	IIb
Linyphiinae	**Stemline**	Stemonyphantes lineatus (Linnaeus, 1758)	pe	3	IV-V
Erigoninae	**Walcunic**	Walckenaeria unicornis O. P.-Cambridge, 1861	h	3	I
Linyphiinae	**Bathnigr**	Bathyphantes nigrinus (Westring, 1851)	h	2	I
Erigoninae	**Diplperm**	Diplocephalus permixtus (O. P.-Cambridge, 1871)	pe	2	I
Pisauridae	**Dolofimb**	Dolomedes fimbriatus (Clerck, 1757)	h	2	IIa
Erigoninae	**Masosund**	Maso sundevalli (Westring, 1851)	h	2	I
Theridiidae	**Robelivi**	Robertus lividus (Blackwall, 1836)	pe-xt	2	I
Erigoninae	**Walcatro**	Walckenaeria atrotibialis (O. P.-Cambridge, 1878)	pe-h	2	IIa
Erigoninae	**Cerabrep**	Ceratinella brevipes (Westring, 1851)	pe-h	2	I
Erigoninae	**Dismbifr**	Dismodicus bifrons (Blackwall, 1841)	pe-h	2	IIa
Theridiidae	**Enopthor**	Enoplognatha thoracica (Hahn, 1833)	xt	2	IIa
Linyphiinae	**Micrpusi**	Microlinyphia pusilla (Sundevall, 1830)	pe-h	2	IIb
Linyphiinae	**Araehumi**	Araeoncus humilis (Blackwall, 1841)	pe-h	1	I
Linyphiinae	**Bathparv**	Bathyphantes parvulus (Westring, 1851)	pe	1	IIb
Theridiidae	**Crusgutt**	Crustulina guttata (Wider, 1834)	xt	1	I
Dictynidae	**Dictlate**	Dictyna latens (Fabricius, 1775)	xt	1	IIa
Dictynidae	**Dictunci**	Dictyna uncinata Thorell, 1856	pe	1	IIa
Erigoninae	**Diplpici**	Diplocephalus picinus (Blackwall, 1841)	pe-h	1	IIb
Salticidae	**Euopaequ**	Talavera aequipes (O. P.-Cambridge, 1871)	xt	1	IIb
Salticidae	**Evarfalc**	Evarcha falcata (Clerck, 1757)	xt	1	IIb
Gnaphosidae	**Haplsign**	Haplodrassus signifer (C.L. Koch, 1839)	xt	1	IIa
Araneidae	**Laricorn**	Larinioides cornutus (Clerck, 1757)	pe-h	1	I
Erigoninae	**Lessdent**	Lessertia dentichelis (Simon, 1884)	h	1	IIa
Erigoninae	**Micrsuba**	Micrargus subaequalis (Westring, 1851)	pe-h	1	IIb
Erigoninae	**Monofusc**	Monocephalus fuscipes (Blackwall, 1836)	h	1	I
Salticidae	**Myrmform**	Micaria formicaria (Sundevall, 1831)	xt	1	IIa
Lycosidae	**Pardnigr**	Pardosa nigriceps (Thorell, 1856)	xt	1	IIa
Liocranidae	**Phrumini**	Phrurolithus minimus C.L. Koch, 1839	xt	1	IIb
Tetragnathidae	**Tetrexte**	Tetragnatha extensa (Linnaeus, 1758)	pe	1	IIb
Erigoninae	**Walcnudi**	Walckenaeria nudipalpis (Westring, 1851)	h	1	I
Erigoninae	**Walcvigi**	Walckenaeria vigilax (Blackwall, 1853)	h	1	IIb
Thomisidae	**Xysterra**	Xysticus erraticus (Blackwall, 1834)	xt	1	IIa
Gnaphosidae	**Micasubo**	Arboricaria subopaca (Westring, 1861)	xt	1	IIa
		107 species	**Total**	**25964**	

(b)

Tribus	species code	Scientific name	Funct. group	Total	ActPer
Lebiini	LIONQUAD	Lionychus quadrillum (Duftschmid, 1812)	r-xt	6751	IIa
Bembidiini	BEMBFEMO	Bembidion femoratum (Sturm, 1825)	h	2556	IIa
Bembidiini	BEMBTETR	Bembidion tetracolum (Say, 1823)	pe	1836	IIa
Bembidiini	BEMBPROP	Bembidion properans (Stephens, 1829)	h	1115	IIb
Pterostichini	PTERCUPR	Poecilus cupreus (Linnaeus, 1758)	pe-h	1090	IIa
Bembidiini	BEMBATRO	Bembidion atrocoeruleum (Stephens, 1829)	r	989	IIa
Harpalini	HARPRUFP	Harpalus rufipalpis (Fabricius, 1792)	pe	937	IV-V
Bembidiini	BEMBDECO	Bembidion decorum (Zenker, 1801)	r	779	IIa
Pterostichini	AGONMUEL	Agonum muelleri (Herbst, 1785)	pe	593	IIa
Bembidiini	BEMBPUNC	Bembidion punctulatum (Drapiez, 1820)	r-h	508	IIa
Chlaeniini	CHLATIBI	Chlaenius tibialis Dejean, 1826	r-h	477	IIb
Pterostichini	AGONDORS	Anchomenus dorsalis (Pontoppidan, 1763)	pe	436	IIa
Harpalini	HARPAFFI	Harpalus affinis (Schrank, 1781)	pe-xt	345	I
Zabrini	AMARAENE	Amara aenea (De Geer, 1774)	xt	296	IIa
Pterostichini	PTERMELA	Pterostichus melanarius (Illiger, 1798)	pe	278	IV-V
Bembidiini	BEMBLAMP	Bembidion lampros (Herbst, 1784)	pe	242	IIa
Pterostichini	PTERVERS	Poecilus versicolor (Sturm, 1824)	pe	224	IIa
Bembidiini	TCHSPARV	Tachys parvulus (Duftschmid, 1812)	r-xt	206	IIa
Zabrini	AMAROVAT	Amara ovata (Fabricius, 1792)	pe	185	IIa
Nebriini	NEBRBREV	Nebria brevicollis (Fabricius, 1792)	pe	175	IV-V
Scaritini	CLIVCOLL	Clivina collaris (Herbst, 1784)	pe-h	163	IIb
Pterostichini	AGONALBI	Paranchus albipes (Fabricius, 1796)	r-h	125	I
Bembidiini	BEMBQMAC	Bembidion quadrimaculatum (Linnaeus, 1761)	pe-h	119	IIa
Pterostichini	PTERVERN	Pterostichus vernalis (Panzer, 1796)	pe-h	95	IIa
Pterostichini	AGONMARG	Agonum marginatum (Linnaeus, 1758)	r-h	91	IIa
Bembidiini	TCHSMICR	Tachys micros (Fischer Von Waldheim, 1828)	r-h	88	IIa
Zabrini	AMARAULI	Amara aulica (Panzer, 1797)	xt	84	IV-V
Zabrini	AMARSPRE	Amara spreta (Dejean, 1831)	pe-xt	62	IIa
Loricerini	LORIPILI	Loricera pilicornis (Fabricius, 1775)	pe	62	IIa
Bembidiini	ASPHFLAV	Asaphidion flavipes (Linnaeus, 1761)	h	61	IIa
Zabrini	AMARBIFR	Amara bifrons (Gyllenhal, 1810)	xt	57	IV-V
Pterostichini	AGONASSI	Limodromus assimilis (Paykull, 1790)	h	54	IIa
Harpalini	ANISBINO	Anisodactylus binotatus (Fabricius, 1787)	h	53	IIa
Pterostichini	STOMPUMI	Stomis pumicatus (Panzer, 1796)	pe-h	50	IIb
Zabrini	AMARSIMI	Amara similata (Gyllenhal, 1810)	pe	50	IIa
Bembidiini	BEMBTEST	Bembidion testaceum (Duftschmid, 1812)	r-h	47	IIa
Zabrini	AMARPLEB	Amara plebeja (Gyllenhal, 1810)	pe	39	IIa
Pterostichini	AGONMOES	Agonum afrum (Duftschmid, 1812)	r	36	IIa
Zabrini	AMAREYRI	Amara eurynota (Panzer, 1797)	xt	31	I
Pterostichini	PTERSTRE	Pterostichus strenuus (Panzer, 1797)	pe	28	IIa
Zabrini	AMARFAMI	Amara familiaris (Duftschmid, 1812)	pe	21	IIa
Carabini	CARAGRAN	Carabus granulatus Linnaeus, 1758	pe-h	20	IIa
Chlaeniini	CHLANITI	Chlaenius nitidulus (Schrank, 1781)	h	20	IIa
Carabini	CARAAURA	Carabus auratus Linnaeus, 1761	(r)xt	19	IIa
Pterostichini	AGONSEXP	Agonum sexpunctatum (Linnaeus, 1758)	h	17	IIa

Pterostichini	**CALAFUSC**	Calathus fuscipes (Goeze, 1777)	pe	17	IIb
Zabrini	**AMARCOMM**	Amara communis (Panzer, 1797)	pe	16	IIa
Harpalini	**HARPDIST**	Harpalus distinguendus (Duftschmid, 1812)	xt	16	IIa
Elaphriini	**ELAPAURE**	Elaphrus aureus P.H. Müller, 1821)	h	14	IIa
Pterostichini	**AGONOBSC**	Oxypselaphus obscurum (Herbst, 1784)	pe-h	13	IIa
Nebriini	**NEBRSALI**	Nebria salina Fairmaire & Laoulbene, 1854	xt	13	IV-V
Lebiini	**DROMSIGM**	Philorhizus sigma (Rossi, 1790)	(r)h	12	IIa
.	**CICICAMP**	Cicindela campestris Linnaeus, 1758	xt	11	IIa
Scaritini	**CLIVFOSS**	Clivina fossor (Linnaeus, 1758)	pe	11	IIa
Harpalini	**HARPLATU**	Harpalus latus (Linnaeus, 1758)	pe	11	I
Zabrini	**ZABRTENE**	Zabrus tenebrioides (Goeze, 1777)	.	11	IV-V
Licinini	**BADIBULL**	Badister bullatus (Schrank, 1798)	pe	9	IIb
Notiophilini	**NOTISUBS**	Notiophilus substriatus Waterhouse, 1833	h	9	IIa
Pterostichini	**PTERANTH**	Pterostichus anthracinus (Illiger, 1798)	h	8	IIa
Harpalini	**STENMIXT**	Stenolophus mixtus (Herbst, 1784)	h	8	IIa
Lebiini	**MICRMINU**	Microlestes minutulus (Goeze, 1777)	xt	7	IIb
Bembidiini	**BEMBOBTU**	Bembidion obtusum (Serville, 1821)	pe	6	IIa
Harpalini	**OPHORUFB**	Ophonus rufibarbis (Fabricius, 1792)	xt	6	IIa
Licinini	**BADISODA**	Badister sodalis (Duftschmid, 1812)	h	6	IIa
Elaphriini	**ELAPRIPA**	Elaphrus riparius (Linnaeus, 1758)	h	6	IIa
Pterostichini	**SYNUVIVA**	Synuchus vivalis (Panzer, 1797)	pe-h	6	IV-V
Harpalini	**ACUPMERI**	Acupalpus meridianus (Linnaeus, 1767)	xt	5	IIa
Licinini	**BADILACE**	Badister lacertosus (Sturm, 1815)	pe	5	IIa
Harpalini	**STENTEUT**	Stenolophus teutonus (Schrank, 1781)	h	5	IIa
Trechini	**THALLONG**	Thalassophilus longicornis (Sturm, 1825)	h	5	IIa
.	**CICIHYBR**	Cicindela hybrida Linnaeus, 1758	xt	5	IIa
Harpalini	**HARPRUBR**	Harpalus rubripes (Duftschmid, 1812)	xt	5	I
Trechini	**TRECQSTR**	Trechus quadristriatus (Schrank, 1781)	pe	5	IV-V
Zabrini	**AMARCURS**	Amara cursitans (Zimmerman, 1831)	xt	4	IV-V
Harpalini	**HARPTARD**	Harpalus tardus (Panzer, 1797)	pe	4	I
Harpalini	**ACUPPARV**	Acupalpus parvulus (Sturm, 1825)	h	3	IIa
Zabrini	**AMARFULV**	Amara fulvipes (Serville, 1821)	xt	3	IV-V
Bembidiini	**BEMBHARP**	Bembidion harpaloides (Serville, 1821)	(r)h	3	IIa
Pterostichini	**CALAMELA**	Calathus melanocephalus (Linnaeus, 1758)	xt	3	IIb
Chlaeniini	**CHLAVEST**	Chlaenius vestitus (Paykull, 1790)	h	3	IIa
Pterostichini	**PTERNIGE**	Pterostichus niger (Schaller, 1783)	pe	3	IV-V
Bembidiini	**BEMBSEMI**	Bembidion semipunctatum (Donovan, 1806)	(r)h	3	IIa
Pterostichini	**AGONMICA**	Agonum micans (Nicolai, 1822)	h	2	IIa
Zabrini	**AMARMONT**	Amara montivaga (Sturm, 1825 R)	xt	2	IIa
Chlaeniini	**CHLANIGR**	Chlaenius nigricornis (Fabricius, 1787)	h	2	IIa
Panagaeini	**PANABIPU**	Panagaeus bipustulatus (Fabricius, 1775)	xt	2	IIa
Panagaeini	**PANACRUX**	Panagaeus cruxmajor (Linnaeus, 1758)	h	2	IIa
Scaritini	**DYSCPOLI**	Dyschirius politus (Dejean, 1825)	h	2	IIb
Pterostichini	**PTERGRAC**	Pterostichus gracilis (Dejean, 1828)	(r)h	2	IIa
Bembidiini	**TCHSBISU**	Tachys bistriatus (Duftschmid, 1812)	(r)h	2	IIa
Harpalini	**ACUPDUBI**	Acupalpus dubius Schilsky, 1888	h	1	IIa
Zabrini	**AMARCULA**	Amara convexiuscula (Marsham, 1802)	h	1	IIb
Bembidiini	**BEMBDENT**	Bembidion dentellum (Thunberg, 1787)	(r)h	1	IIa

Bembidiini	**BEMBELON**	Bembidion elongatum (Dejean, 1831)	h	1	IIa
Bembidiini	**BEMBLUNU**	Bembidion lunulatum (Fourcroy, 1785)	h	1	IIa
Bembidiini	**BEMBSTOM**	Bembidion stomoides (Dejean, 1831)	h	1	IIa
Bembidiini	**BEMBVELO**	Bembidion velox (Linnaeus, 1761)	r-h	1	IIa
Harpalini	**BRADHARP**	Bradycellus harpalinus (Serville, 1821)	pe	1	IV-V
Lebiini	**DROMLINE**	Paradromius linearis (Olivier, 1795)	pe-xt	1	I
Scaritini	**DYSCAENE**	Dyschirius aeneus (Dejean, 1825)	h	1	IIa
Harpalini	**HARPANXI**	Harpalus anxius (Duftschmid, 1812)	xt	1	I
Harpalini	**OPHOPCEP**	Ophonus punticeps Stephens, 1828	xt	1	IV-V
Harpalini	**PAROMACU**	Parophonus maculicornis (Duftschmid, 1812)	xt	1	IIa
Pterostichini	**PTERNIGR**	Pterostichus nigrita (Paykull, 1790)	pe-h	1	IIa
Bembidiini	**TCHSQSIG**	Tachys quadrisignatus (Stephens, 1829)	pe-xt	1	IIa
		105 species	**Total**	**21804**	

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The Common Meuse under barrage.
…opposing the fast-flowing gravel bed.
(Photo: Marcel Lambeets)

CURRICULUM VITAE

Kevin G. Lambeets werd op 25 juni 1982 geboren te Tienen. Hij groeide op te Linter, een pittoreske gemeente die zich uitstrekt langsheen de vallei van de Grote Gete. Van 1994 tot 2000 werd de tijd gesleten op de banken van de VIA-scholengroep te Tienen. Deze turbulente periode is karakteriseerd door een omzwerving van ASO naar Elektro-Mechanica, om later met brio te slagen binnen Wetenschappen-Wiksunde. Aangezien een gemis aan wetenschappen zich huisvestte in zijn nog prille grijze massa, werden de studies aan de Faculteit Wetenschappen van de Universiteit Gent (UGent) verder gezet. De licentiaatsscriptie rondde hij onder het toeziend oog van Dominque Adriaens af, en droeg de titel: “Vergelijkend myo-osteologische studie van het kopbouwplan binnen de Ordo Anguilliformes (*Anguilla anguilla* & *Conger conger*)”. Na vier jaar zwoegen behaalde hij grote onderscheiding als Licentiaat Biologie, optie Dierkunde. Edoch, het verhaal rolt verder... Door toedoen van een enthousiaste begeleider gedurende de licentiaatsjaren, Dries Bonte met name, werd de zindering voor natuurstudie en ecologie gewekt. Ondertussen ontdekte Kevin “de eigen streek”, in den beginne op zijn eentje, later bijgestaan door de vrijwilligers van Natuurpunt Gete-Velpe-Mene. Dit resulteerde niet enkel in een engagement voor natuur in eigen regio, waarbij hij zich engageerde als conservator van het natuurreservaat Doysbroek-Viskot en lid werd van de Jeugdbond voor Natuur(studie) en Milieu(bescherming) (JNM), maar bewerkstelligde tevens de verdere prikkeling van zijn interesse voor de natuur. Daarnaast vervoegde hij de gelederen van Arachnologia Belgica, de Belgische Arachnologische Vereniging (ARABEL), waarbinnen sinds 2009 de functie van web-master werd opgenomen.

Tijdens de hete zomer van 2004 stelde Kevin samen met Dries Bonte en Jean-Pierre Maelfait een IWT-onderzoeksaanvraag op m.b.t. een specialisatiebeurs als doctoraal onderzoeker. In januari 2005 werd de toekenning van deze beurs bevestigd en kreeg hij zijn plaatsje binnen de onderzoeksgroep Terrestrische Ecologie (TEREC) van de Universiteit Gent. Al snel maakte hij deel uit van een jonge, enthousiaste en dynamische groep onderzoekers onder leiding van Luc Lens. Betreffende het eigen onderzoek, werden de banden met Kris Van Looy (INBO) aangehaald, de verantwoordelijke aangaande de beheersmonitoring en de ecologische gebiedsvisie van de Grensmaas. Enkele maanden later struinde Kevin langs de oevers van diezelfde laaglandrivier... naarstig op zoek naar grindbanken, spinnen en loopkevers. Niettemin de Grensmaas ter tijd en stond zijn dynamiek gelden liet, werd na vier jaar en half onderzoek een doctoraatsscriptie afgewerkt. Het voorliggend resultaat omvat acht internationaal (ge)publiceer(de)bare hoofdstukken. Gemeenschap- en gedragsecologische aspecten wisselen elkaar af, maar ook genetisch onderzoek werd niet geschuwd. Dit zorgt voor de nodige variatie en complementariteit van het onderzoek. De sterke inslag naar natuurbehoud toe kenmerken de scriptie, maar tevens het interessevlak van de schrijver.

Een referentiekader, op maat asjeblieft.. of zowel van dichtbij als veraf kijken,
zo doe je kennis op, ja!

The intensive field-survey along the Common Meuse…

Bij dromen begint de verandering van de wereld!

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Decision-making in a dynamic environment particularly involves one critical question: ***"Should I stay or should I go?"***, a matter of vital importance which has been considered before by Joe Strummer and The Clash, as early as 1982.

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Faculteit Wetenschappen

Terrestrial Ecology

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