## 1 Integrating environmental conditions and functional life-history traits

2 for riparian arthropod conservation planning.

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#### 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' occurrence 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 species composition of predatory riparian arthropod assemblages. Mainly flooding disturbance appeared to affect spider and carabid beetle species composition. 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. Whereas hygrophilic species benefited from increased vegetation cover, xerothermophilic specialists were favoured by increased flooding disturbance. 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. We show the importance of a dynamic and evidence-based approach of river management on a local scale to preserve vulnerable riparian arthropods. 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 riverine landscapes. More-over, we argue that the understanding of functional responses towards environmental factors results in general and widely applicable guiding concepts for species conservation.

- **Key-words:** carabid beetles flooding disturbance multi-species approach lowland
- 48 river banks river restoration spiders

#### Introduction

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Riverine ecosystems are characterized 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 specialized and vulnerable fauna as a result of environmental stressors such as flood events and thermal fluctuations (Andersen and 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; Renöfalt 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 and 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 generally 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), thereby creating 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 (cf. species pool; Riis and Sand-Jensen, 2006).

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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 and 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. 2006; Violle et al., 2007). Spiders (Araneae) and carabid beetles (Carabidae) are mobile 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 and Malt, 2003; Vanbergen et al., 2005). Particularly riparian habitats host many rare and stenotopic arthropods (Turin, 2000; Sadler et al., 2004; Andersen and Hanssen, 2005). A preliminary study considering the predatory arthropod fauna along the Common Meuse (Lambeets et al., in press a) indicated that the environmental conditions affecting assemblage structure of riparian spiders and carabid beetles were similar. Yet, information about responses of riparian species towards environmental conditions is

greatly lacking, especially at restricted spatial scales (but see Rothenbücher and Schaefer, 2006; Bates et al., 2006; Lambeets et al., 2008).

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 hypothesized 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). More-over, community analyses are complemented with a multi-species approach (Kremen et al., 1993; Maes and 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.

#### **Material 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. 1). Due to its rain-fed character and the rocky soils of the upstream catchments, 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, with 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 200m<sup>3</sup>/s (from May 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 vegetation 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., 2008).

#### Sampling protocol

All river banks along a continuous part of the Common Meuse river reach (n=24; Fig. 1) were sampled from 06-04-2005 until 19-07-2005 with pitfall traps (diameter 9cm; 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 6.1m from the loamy river dyke and 21.3m for more distant (lower) stations on larger banks. As recommended by Topping and Sunderland (1992) pitfalls were spaced ten meters 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 pitfalls not flooded. 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 and Sunderland, 1992; Pékar, 2002). In this study, standardized 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.

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#### Characterization 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., in press a). 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 1. Since distribution patterns of spiders and carabid beetles clearly relate to functional species characteristics (Ribera et al., 2001; Lambeets et al., 2008; 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 and O'Hara, 2003; Bonte et al., 2006; 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 and Schaefer, 2006). For a brief explanation of the functional traits and literature overview see Table 2.

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### Assemblage structure and constraints

Multivariate and univariate techniques were used to identify patterns of change in arthropod assemblages and species abundance 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 and 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 and 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 stressfactor 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 standardized 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 and Sunderland, 1992), species counts were adjusted by the maximum number of individuals of each species occurring within a sample station (Maelfait and 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 BrayCurtis distance measure and a flexible beta group linkage method ( $\beta = -0.25$ ; McCune and Grace, 2002). To relate multivariate assemblage structure with environmental parameters or species traits, the BIO-ENV procedure (PRIMER 5; Clarke and 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 (p) 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 analyzed by generalized linear models. Responses of riparian species were analyzed by regression of their total catch number (from hereon referred to as "density", although a relative measure because pitfalls register density-activity) on the earlier retrieved important community-structuring environmental parameters. Poisson regression models (SAS 9.1.3, proc glimmix) were applied with Satterthwait's procedure to compute corrected degrees of freedom (Verbeke and Molenberghs, 2000). In all cases, models were corrected for overdispersion and normality of residuals was checked.

#### 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.

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#### Riparian arthropod assemblage structure

Cluster analysis for spider records separated the 28 sample stations into five groups (Fig. 2a), 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. 2a). The nMDS plots less disturbed river banks on top, i.e. higher and 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. 2b), 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 was conform 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 analyzed in more detail below.

#### Species richness and functional diversity

We found clear differences in total species richness between river bank clusters (Fig. 3) 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 groups. Differences in species richness within functional groups per taxon were significant for eurytopic / pioneer 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 spiders species richness was highest on higher river banks ( $F_{3,24}$ =3.03, p=0.038), yet 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. 4a and Fig. 4b for spiders and carabid beetles respectively.

#### **Environmental constraints**

Variation in spider assemblage structure along the Common Meuse was best explained by water flow rate solely ( $\rho$ =0.387, p<0.05). Second best was the combination of sand-loam ratio, the water flow rate and the rising speed of the washing water ( $\rho$ =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 ( $\rho$ =0.492, p<0.01). Including the rising speed of the washing water (cf. spiders) was nearly as good ( $\rho$ =0.491, p<0.01). These parameters logically

differ between the river bank clusters (see Appendix A.1), hence, are useful to relate to species specific occurrences (see below).

#### **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 ( $\rho$ =0.288, 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), none the less 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 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 3.

## Flooding disturbance

An increase of the discharge regime at which the river banks are inundated, 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.

#### **Sediment composition**

An increase of the sand-loam ratio and accordingly a decrease of the river bank siltation 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.

#### 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.

#### 331 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, 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 conditions and functional life-history traits result in a different assemblage structure.

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#### 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, typical 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 and 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 concordant effects for the riparian arthropod fauna (Sadler et al., 2004; Van Looy et al., 2005), even on a microhabitat level (Bonn and Kleinwächter, 1999)and differences between species responses can be expected since variation in functional traits affects their distribution patterns (Bonte et al., 2006; Lambeets et al., 2008).

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#### 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 and Kleinwächter, 1999; Van Looy et al., 2005; Rothenbücher and 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 structure 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 and Kleinwächter, 1999; Baker et al., 2006). Laeser et al. (2005) and Paetzold et al. (2008) found arthropod abundance and diversity to decrease steeply along channelized river sections that are affected by anthropogenic flow regulation (hydropeaking; Semmerkrot et al., 1997). Since disturbance sets back succession, resulting in a complex and highly diverse microhabitat mosaic (Sadler et al., 2004; Wintle and Kirkpatrick, 2007), and intervenes in competitive relations (McCauliffe, 1984), species preferring ephemeral conditions as well as specialized species are favoured (Baker et al., 2006). Therefore, a complete lack of flooding

disturbance would prove to be pernicious for typical riparian organisms (Renöfalt et al., 2005; Stromberg et al., 2007; Paetzold et al., 2008). Even on this small scale, river banks differ in abiotic parameters (see Appendix A.1), 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., 2006; Lambeets et al., 2008). 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: *Arctosa cinerea, Pardosa agricola, P. agrestis*) are restrained by a lack of ballooning dispersal (Bonte and Lambeets, unpubl. data), contrary to small flight-active carabid beetles as *Bembidion* species (Bates et al., 2006). Desender (1989) 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 (Jäkäläniemi et al., 2005). Bonn and 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 and 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 and Plachter, 1997; Briers et al., 2005). Carabid beetles differing in their activity period might colonize 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. (2008), 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, the degree of 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 species (Bonn and Kleinwächter, 1999). Also, sediment composition affects carabid assemblage structure (Eyre et al., 2001; Sadler et al., 2004; Lambeets et al., in press a). This holds true especially for riparian species (Desender, 1993; Bates et al., 2007). Interestingly, metallic colouration of carabid beetle elytra is an additional factor affecting their occurrence. Desender (1989) 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

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al., 2002; Bonte et al., 2004) stressing the importance of habitat specialization 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., 2006).

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#### Idiosyncratic ecological needs of 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, 1989; Geilen et al., 2004). Yet, habitat specialists tend to disappear or are replaced during detrimental circumstances (Collinge et al., 2001; Lambeets et al., 2008). Small stenotopic carabids, e.g. Bembidion atrocaeruleum, are able to (re)colonize 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 their 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 Arctosa cinerea is known to use interstitial burrows as a refuge (Framenau et al., 1996). Also the salticid *Heliophanus auratus* and the linyphiid Caviphantes 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 Lionychus quadrillum and Tachys parvulus, both xerothermophilic carabids occurring mainly on sandy soils. These circumstances are met on higher river banks, less susceptible to flooding. Although hygrophilic species richness was lowest on disturbed river banks, the macropterous A. afrum was favoured by flooding, preferring frequently disturbed habitats and a watersaturated, muddy underground (Turin, 2000). Remarkably, the lycosid *Pardosa* agricola, the linyphiid Baryphyma pratense and the carabids Bembidion decorum and Chlaenius tibialis were not confounded by any of the environmental conditions. Albert and 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 and Schaefer (2006) stressed the general importance of convenient 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 and Struyve, 2007), will prove valuable for conservation purposes and sustainability of riparian biodiversity. These patches might prove valuable colonization gaps for typical riparian plants as well (Hölzel, 2005; Wintle and Kirkpatrick, 2007). In general, changes in lateral and longitudinal connectivity may affect species differently

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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 specialization (Jonsen and Fahrig, 1997, Henle et al., 2004). To account for viable and persistent populations of low dispersive target species, restoring cursorial connectivity by restoring 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 and 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 A.2 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 and Kirkpatrick, 2007) and stenotopic riparian species tend to disappear at either high or low flooding disturbance rates (Rothenbücher and Schaefer, 2006). Therefore, the restoration of natural hydrogeomorphical processes is essential to maximize the biodiversity along riparian systems in general (Ward et al., 1999). The

human impact on riverine water discharge regimes of 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; Arthington et al., 2006). Anthropogenic fluctuations in discharge regimes should be minimized 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 specialist are adapted (Lytle and 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. Yet, patterns may differ according to the specific characteristics of the system (e.g. altitude) and according to its geographical location (Framenau et al., 2002). 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 species.

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River management should be based on sound ecological principles and an understanding of the impact of hydrogeomorphical processes on multiple species (Tockner et al., 2006; Jensen et al., 2006). 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)colonization 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 optimizing habitat connectivity (Geilen et al., 2004). 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 and Jowett, 2006) but as well 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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800	The following supplementary material is available for this article online:
800	The following supplementary material is available for this article online:  Appendix A.1: Pairwise differences of environmental conditions between river bank
801	<b>Appendix A.1:</b> Pairwise differences of environmental conditions between river bank
801 802	<b>Appendix A.1:</b> Pairwise differences of environmental conditions between river bank clusters: water flow rate, water rising speed, composition of the in-between sediment
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801 802 803 804	Appendix A.1: 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.

## **Captions** 808 809 810 Fig. 1 – Map of the River Meuse basin with an inset for the Common Meuse river reach 811 and its riparian margin; sampled river banks are indicated as **\( \Lapla \)**. 812 813 Fig. 2 – Results of the nMDS ordination (left) and Bray-Curtis similarity tree (right, 814 branches of the sample stations belonging to the same group are merged) of the sample 815 stations, based on the relative abundances of (a) spider and (b) carabid beetle species. 816 Clustered sample station groups are indicated with different symbols; (X,Y) indicate the 817 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); 818 O: Cluster5 (4;3). 819 820 Fig. 3 – Differences in total species richness per sample station between river bank 821 822 clusters which are based on spider and carabid beetle catch numbers respectively 823 (Sorensen distance, flexible $\beta = -0.25$ ). Error bars indicate standard errors of the mean. 824 Significance pairwise comparisons within arthropod groups are indicated by the same symbols (post hoc Tukey-Kramer test; \*, °, +, -). 825 826 827 Fig. 4 – Differences in functional group species richness per sample station between 828 river bank clusters for spiders (a) and carabid beetles (b), i.e. riparian, hygrophilic, 829 xerothermophilic and pioneer/eurytopic species and additionally alluvial species for 830 carabids. Clusters are based on spider and carabid beetle catch numbers respectively

(Sorensen distance, flexible  $\beta = -0.25$ ). Significant pairwise comparisons within

832 functional groups are indicated by the same symbols (post hoc Tukey-Kramer-test; \*, °, 833 +). 834 835 **Table 1** – Environmental parameters of river banks along the Common Meuse used in 836 the BIO-ENV procedure. Parameters were transformed a priori if they did not meet the 837 normality assumption (Shapiro-Wilkinson >0.90), indicated by (log) if logarithmic and 838 (sqrt) if square root. 839 840 **Table 2** – Functional species traits chosen to represent important life history features of spiders and carabid beetles (see Lambeets et al., 2008). Traits were based on valuable 841 842 literature resources describing ecological habitat affinity and functional species 843 characteristics. 844 845 **Table 3** – Density patterns of riparian spiders and carabid beetles were analysed using 846 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 847 848 had a positive effect on species density is indicated as "+" or "-". Nomenclature for 849 spiders and carabids is based on Bosmans and Vanuytven (2001) and Boeken et al. 850 (2002) respectively. Red list-status is taken from Maelfait et al. (1998) for spiders and 851 Desender et al. (1995) for carabids, and are in concordance with IUCN-categories: EW: 852 extinct in the wild, CR: critical, EN: endangered, VU: vulnerable, SU: susceptible, IN: 853 indeterminate.

# **Fig. 1** – Map of the River Meuse basin with an inset for the Common Meuse river reach and its riparian margin; sampled river banks are indicated as ▲.

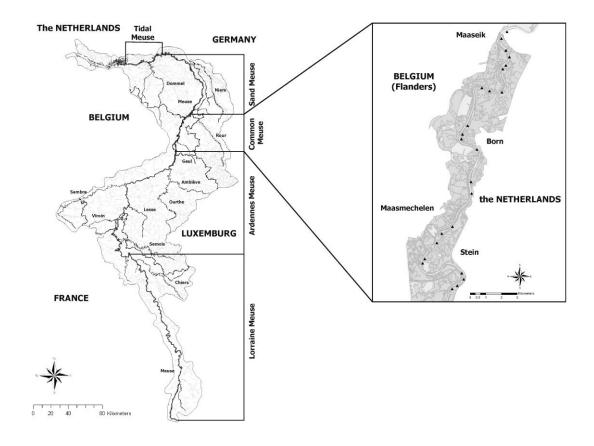
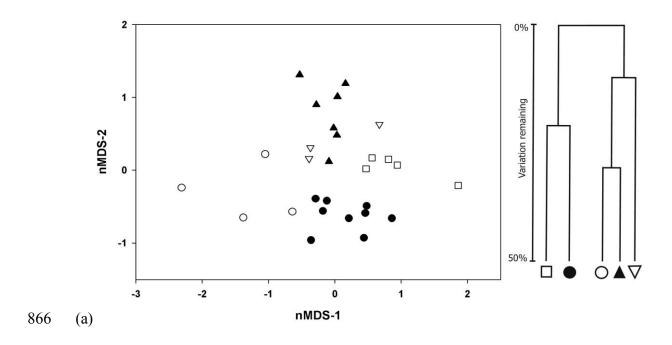
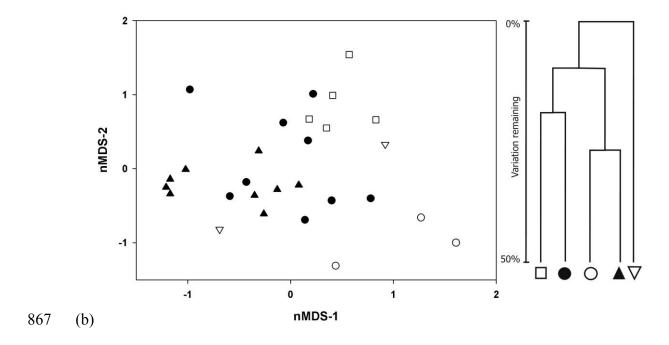
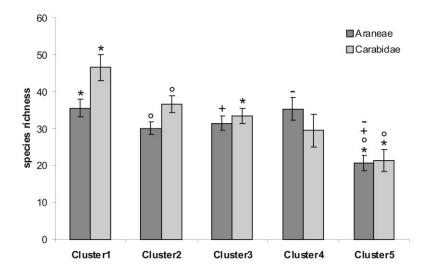


Fig. 2 – Results of the nMDS ordination (left) and Bray-Curtis similarity tree (right, branches of the sample stations belonging to the same group are merged) of the sample stations, based on the relative abundances of (a) spider and (b) carabid beetle species. Clustered sample station groups are indicated 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).

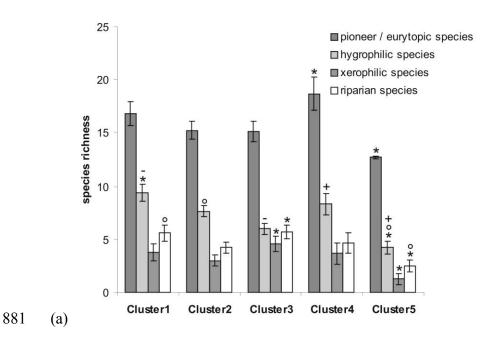


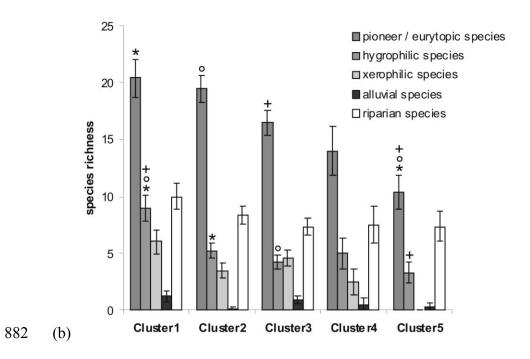


**Fig. 3** – Differences in total species richness per sample station between river bank clusters which are based on spider and carabid beetle catch numbers respectively (Sorensen distance, flexible  $\beta$  = -0.25). Error bars indicate standard errors of the mean. Significance pairwise comparisons within arthropod groups are indicated by the same symbols (post hoc Tukey-Kramer test; \*, °, +, -).



**Fig. 4** – 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  $\beta$  = -0.25). Significant pairwise comparisons within functional groups are indicated by the same symbols (post hoc Tukey-Kramer-test; \*, °, +).





**Table 1** – 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.

variable class	parameter measured	methodology
flooding disturbance	WFR	(log) river bank water flow rate
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	wd 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 (gravel – (sharp) sand - loam ratio)
substrate composition	silt	silt cover (none - covering 1/4 - half or up to dyke 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 bank 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 connectivity
landscape composition	landu	surrounding land use (alluvial grasslands, brushwood shoulders, meadows, crop fields)
landscape composition	arabl100	(sqrt) amount of arable land within 100m radius
landscape composition	brush100	(sqrt) amount of brushwood vegetation within 100m radius

**Table 2** – Functional species traits chosen to represent important life history features of spiders and carabid beetles (see Lambeets et al., 2008). Traits were based on valuable literature resources describing ecological habitat affinity and morphological species characteristics.

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 carabid beetles	Bell et al., 2005; Bonte and Lambeets, unpub. data	Desender, 1989
Body size	average female size for spiders and average size for carabid beetles	Roberts, 1987; 1998	Boeken et al., 2002
Activity period	activity period, based on the reproductive peak	Roberts, 1985; 1998	Turin, 2000
Sediment preference	preference for substrate composition	1	Turin, 2000; Boeken et al., 2002
Metallic lustre	elythra colouration (cf. reflection)	1	Boeken et al., 2002

**Table 3** – 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 and 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.

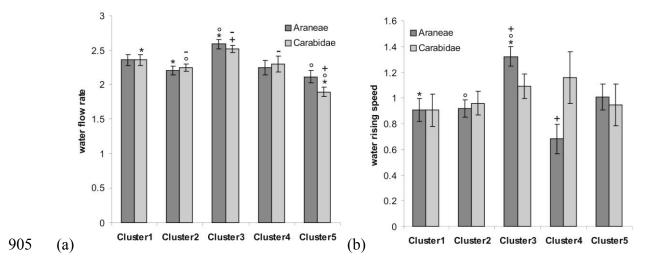
		sand		silt		avVegc		WFR		RSregr	
species	Red List	F	effect	F	effect	F	effect	F	effect	F	effect
Heliophanus auratus C.L. Koch, 1835	EN	6.94*	+	4.48*	-	0.25		7.92**	+	0.94	
Arctosa cinerea (Fabricius, 1777)	CR	19.96***	+	6.37*	-	2.17		64.13***	+	20.12***	+
Pardosa agrestis (Westring, 1861)	EN	2.77		1.12		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	

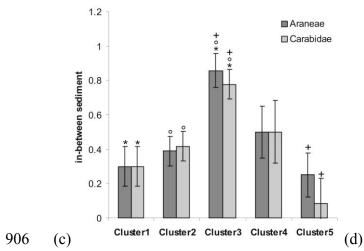
Tachys micros (Fischer Von Waldheim, 1828)	SU	9.18**	-	2.91	5.37*	+	1.24	0.95	
Tachys parvulus (Duftschmid, 1812)	SU	4.39*	+	3.46	0.14		1.45	1.25	

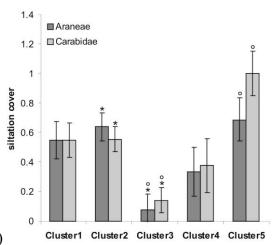
**Supplementary Material** – Lambeets et al. - Integrating environmental conditions and functional life-history traits for riparian arthropod conservation planning.

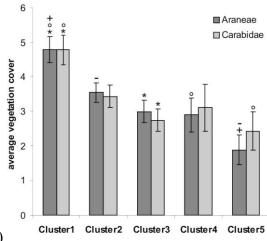
**Appendix A.1:** Pairwise differences of environmental conditions between river bank clusters (SAS 9.1.3; proc mixed): (a) water flow rate, (b) water rising speed, (c) composition of the in-between sediment fraction, (d) extent of the silt cover, (e) average vegetation cover. Clusters are based on spider and carabid beetle catch numbers (Sorensen distance, flexible  $\beta$  = -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.











(e)

## 909 (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	Araneae	5.37	0.0033
composition			
in-between sediment	Carabidae	5.55	0.0028
composition			
silt cover	Araneae	5.05	0.0045
silt cover	Carabidae	7.11	0.0007
average vegetation	Araneae	7.06	0.0007
cover			
average vegetation	Carabidae	4.41	0.0086
cover			

**Appendix A.2:** 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 linyphild 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.

ScientName	Cluster1	Cluster2	Cluster3	Cluster4	Cluster5	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