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

KEVIN LAMBEETS[1], MARTIJN L. VANDEGEHUCHTE[1], JEAN-PIERRE MAELFAIT[1,2] & DRIES BONTE[1,3]

[1]Ghent University, Dep. Biology, Terrestrial Ecology Unit (TEREC), KL Ledeganckstraat 35, B-9000 Ghent;
[2]Research Institute for Nature and Forest (INBO), Kliniekstraat 25, B-1070 Brussels;
[3]Wuerzburg University, Field Station Fabrikschleichach, Glashuettenstrasse 5, D-96181 Rauhenebrach, Germany
Correspondence: Kevin Lambeets, Terrestrial Ecology Unit (TEREC), Dep. Biology Ghent University, KL Ledeganckstraat 35, B-9000 Ghent, Belgium. Tel.: +3292645084; E-mail: Kevin.Lambeets@UGent.be

Summary

1. Species assemblages of naturally disturbed habitats are governed by the prevailing disturbance regime. So, stochastic flood events affect river banks and the inhabiting biota. Predatory arthropods predominantly occupy river banks in relation to 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.

Keywords: body size – dispersal ability – niche breadth – riparian ecology – trait-displacement

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, Nishizaki & Burns 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, Lens & Maelfait 2006a). Because this involves species assimilation, assemblage-wide changes in species diversity are predicted to result from species sorting. 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 2005). 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). Yet, responses depend on the type of disturbance and the relation with species functional traits (Bonte et al. 2006a; Moretti, Duelli & Obrist 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). Yet, spatially restricted disturbance can be important to facilitate the occurrence of specialized species that are able to react rapidly upon changing environment conditions (Bonn, Hagen & Wohlgemuth-von Reiche 2002; Rothenbücher & Schaefer 2006). Observed patterns may, however, vary considerably with the spatial scale of study (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, Tockner & Ward 2002; Naiman, Décamps & McClain 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 & Winterbourne 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 disturbance results from either equivalent or contrastive changes in assemblage-wide traits is virtually undocumented for 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. 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 community-wide character shifts and (iii) whether flooding disturbance (dis)favours species with distinct ecological traits.

Material and methods

STUDY SYSTEM & 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, Van Looy & Kurstjens 2000). Only when the river discharge drops below $200m^3/s$ (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. 2008).

All river banks along a continuous part of the river trajectory (Fig.1) 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 6.1m from the loamy river dyke for higher stations and 21.3m 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.

CHARACTERISATION 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 S1. 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 1). 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 emphasize 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.

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, Stöckli & Nentwig 1995; Harvey, Nellist & Telfer 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 female body size of 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 S2.

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 (GLMs; 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 information criteria (AIC), which are 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 were highly significant for average values (Araneae: $F_{2,80}>19.85$; all $p<0.0001$; Carabidae ($F_{2,80}>23.26$; all $p<0.0001$) and variances (Araneae: $F_{2,77}>15.36$; all $p<0.0001$; Carabidae ($F_{2,77}>21.17$; all $p<0.0001$), we performed trait analyses separately for the different distinguished taxonomic groups.

Results

SPECIES RICHNESS

Alpha diversity of carabid beetles (Fig. 2a) and numbers of resident species (Fig. 2b) 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. 2c). F-values, significance levels and AIC values are presented in Table 2.

ASSEMBLAGE-WIDE ECOLOGICAL TRAITS

Hereunder, 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 3.

Niche breadth, shading & moisture preference

Assemblage-wide niche breadth increased with increasing disturbance in Erigoninae, Lycosidae (Fig. 3a; Table 3a) and Bembidiini (Fig. 3b; Table 3b). Variance in niche breadth decreased monotonously with flooding for Pterostichini assemblages (Fig. 3c; Table 3d).

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. 4a; Table 3a). 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. Yet, this relation is highly influenced by the prevalence of agrobiont *Bembidion* carabids on the lowest river banks (skewed distribution at

Fig. 4b; Table 3b). Variance of shading preference peaked at intermediate degrees of flooding for Pterostichini (Fig. 4c; Table 3d).

Assemblage-wide xerophily of all spider (sub)families on average decreased with increasing flooding disturbance (Fig. 5a; Table 3a). Variance in xerophily decreased solely for Lycosidae (Fig. 5b; Table 3c). Bembidiini carabids showed a significant increase in xerophilic species with increasing disturbance (Fig. 5c; Table 3b).

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. 6a; Table3a). Significant linear decreases were found with respect to variance in assemblage-wide female size for Erigoninae and Lycosidae (Fig. 6b; Table 3c). Assemblage-wide average size of Pterostichini carabids increased significantly with increasing disturbance (Fig. 6c; Table 3b). Variance in carabid beetle body size was lower at more disturbed river banks for Bembidiini whereas it increased for Pterostichini (Fig. 6d; Table 3d).

Erigoninae and Lycosidae with known ballooning propensity are favoured by increased disturbance (Fig. 7a; Table3a). Variance in ballooning propensity of Erigoninae peaked at intermediate disturbance (Fig. 7b; Table3c). Assemblage-wide wing development on average increased for Bembidiini and Pterostichini (Fig. 7c; Table 3b).

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. Yet, 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. Yet, 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, colonise 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 2005; Öberg, Ekbom & Bommarco 2007). Generally, spider diversity is positively related to vegetation composition (Perner & Malt 2003; Beals 2006). As previous studies indicated flooding to homogenize vegetation structure (Peters et al. 2000; Shafroth, Stromberg & Patten 2002), increased flooding can result in a lowered diversity. Yet, studies concerning boreal or upland rivers showed positive relationships between flooding and vegetation heterogeneity *in 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 S1), it potentially affects species distribution patterns in a different way than flooding. The decrease in variance of xerophily indicates that assemblages are dominated by only few, ecological similar species, e.g. *Pardosa* species. 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, Stratton & Miller 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 (Manderbach & Hering 2001; Turin 2000), 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. 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-Polaterra & Beisel 2002; Suren & Jowett 2006). These patterns add to the prevalence of sorting mechanisms for Bembidiini assemblages, comparable to spiders. 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 changed 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. Especially floods 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. (1993), 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 nearby 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. Especially dispersive, common hygrophilous species are better represented as flooding increases. Yet, riparian species with well-developed dispersal abilities (e.g. Bembidiini) are well presented throughout the river system (Desender 1989a; Desender et al. 1993; Lambeets et al. 2008), thereby indicating their efficient movement throughout the system, probably resulting in one patchy population (Bates, Sadler & Fowles 2006). Patterns could at first sight be generated by the local landscape structure, but our analysis showed that the latter is independent of flooding regime. So, more intrinsic factors related to e.g. general activity or sediment preference should consequently 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 arthropod predators. 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. 2008). 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). Furthermore, 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).

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Supplementary Material

The following supplementary material is available for this article online**:**

Appendix S1: Pearson correlations with PCA-ordination axes of local topographical and regional chorological environmental parameters of river banks along the Common Meuse river reach.

Appendix S2: 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.

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

Fig. 2. 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.

Fig. 3. 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. 4. 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. 5. 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. 6. 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.

Fig. 7. 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. 1

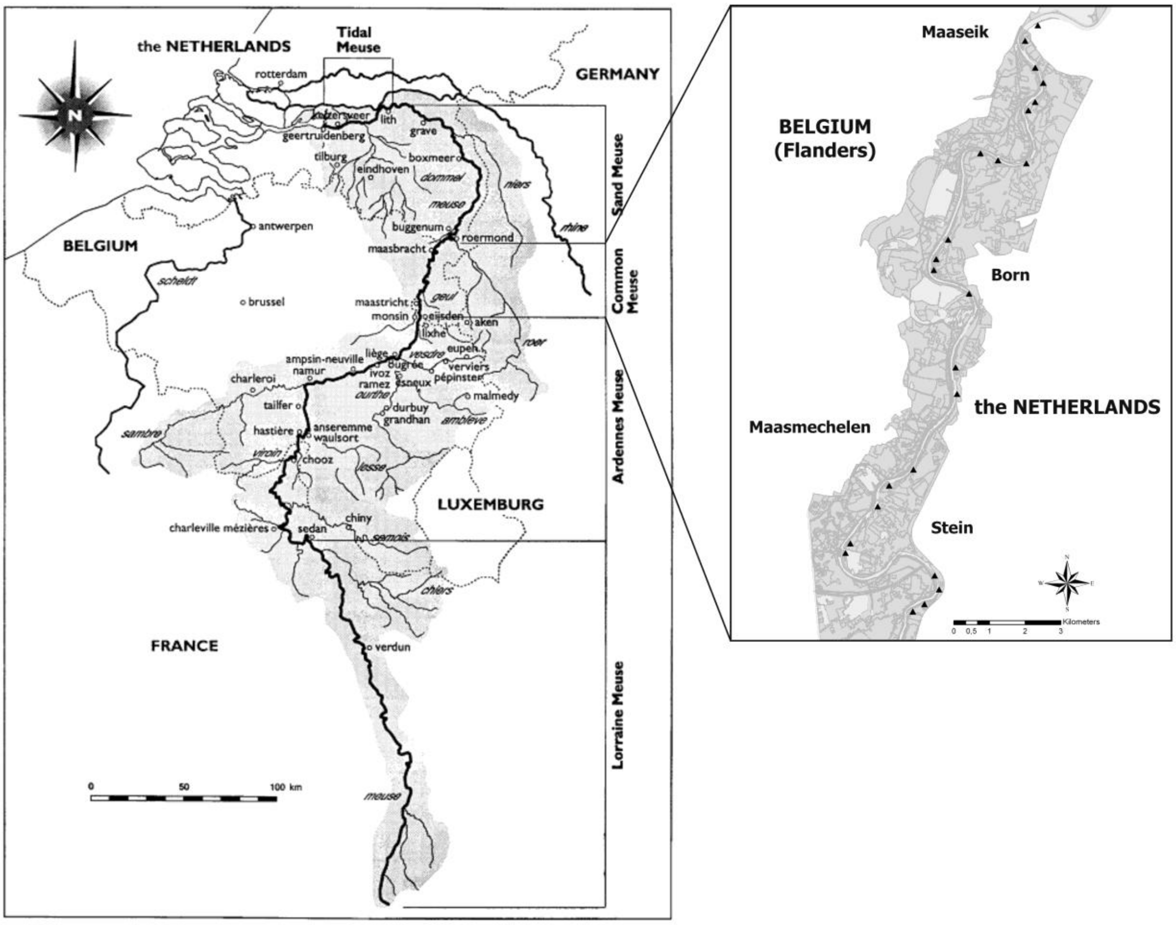

the NETHERLANDS
Tidal Meuse
GERMANY
N
rotterdam
keizersveer
lith
grave
geertruidenberg
tilburg
boxmeer
eindhoven
dommel
niers
meuse
Sand Meuse
rhine
antwerpen
buggenum
roermond
BELGIUM
maasbracht
Common Meuse
scheldt
brussel
maastricht
geul
monsin
eijsden
aken
lixhe
roer
liège
vesdre
eupen
ampsin-neuville
namur
ivoz
ramez
tilff
esneux
verviers
pépinster
charleroi
ourthe
malmedy
tailfer
durbuy
grandhan
amblève
hastière
anseremme
waulsort
sambre
viroin
chooz
lesse
Ardennes Meuse
LUXEMBURG
chiny
charleville mézières
sedan
semois
chiers
FRANCE
verdun
Lorraine Meuse
0
50
100 km
meuse
Maaseik
BELGIUM (Flanders)
Born
the NETHERLANDS
Maasmechelen
Stein
N
W
E
S
0
0,5
1
2
3
Kilometers

Fig. 2

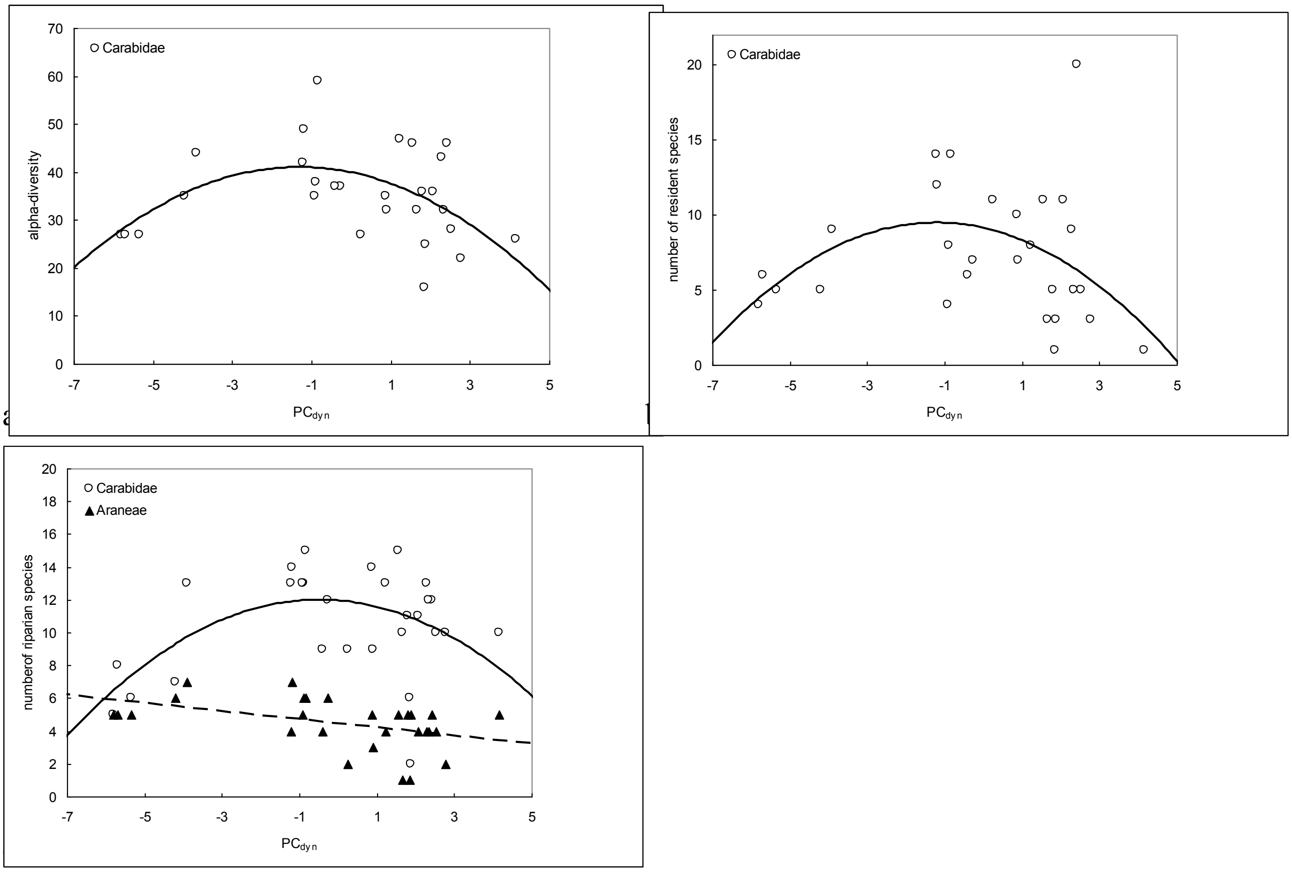
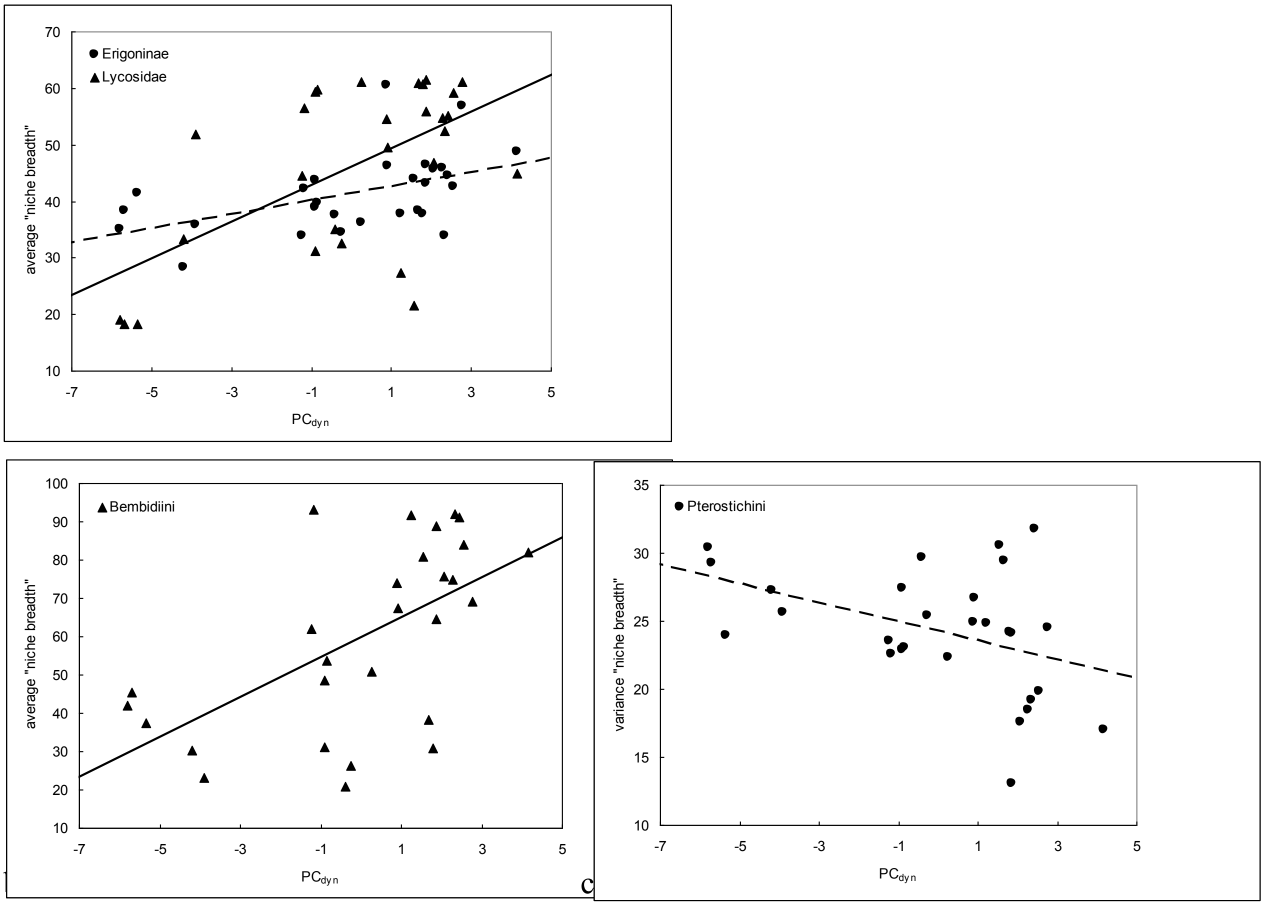

Carabidae
alpha-diversity
70
60
50
40
30
20
10
0
-7
-5
-3
-1
1
3
5
PC_{dyn}
Carabidae
number of resident species
20
15
10
5
0
-7
-5
-3
-1
1
3
5
PC_{dyn}
Carabidae
Araneae
numberof riparian species
20
18
16
14
12
10
8
6
4
2
0
-7
-5
-3
-1
1
3
5
PC_{dyn}

Fig. 3



Erigoninae
Lycosidae
average "niche breadth"
PC$_{dyn}$
70
60
50
40
30
20
10
-7
-5
-3
-1
1
3
5
Bembidiini
average "niche breadth"
100
90
80
70
60
50
40
30
20
10
PC$_{dyn}$
Pterostichini
variance "niche breadth"
35
30
25
20
15
10
PC$_{dyn}$

Fig. 4

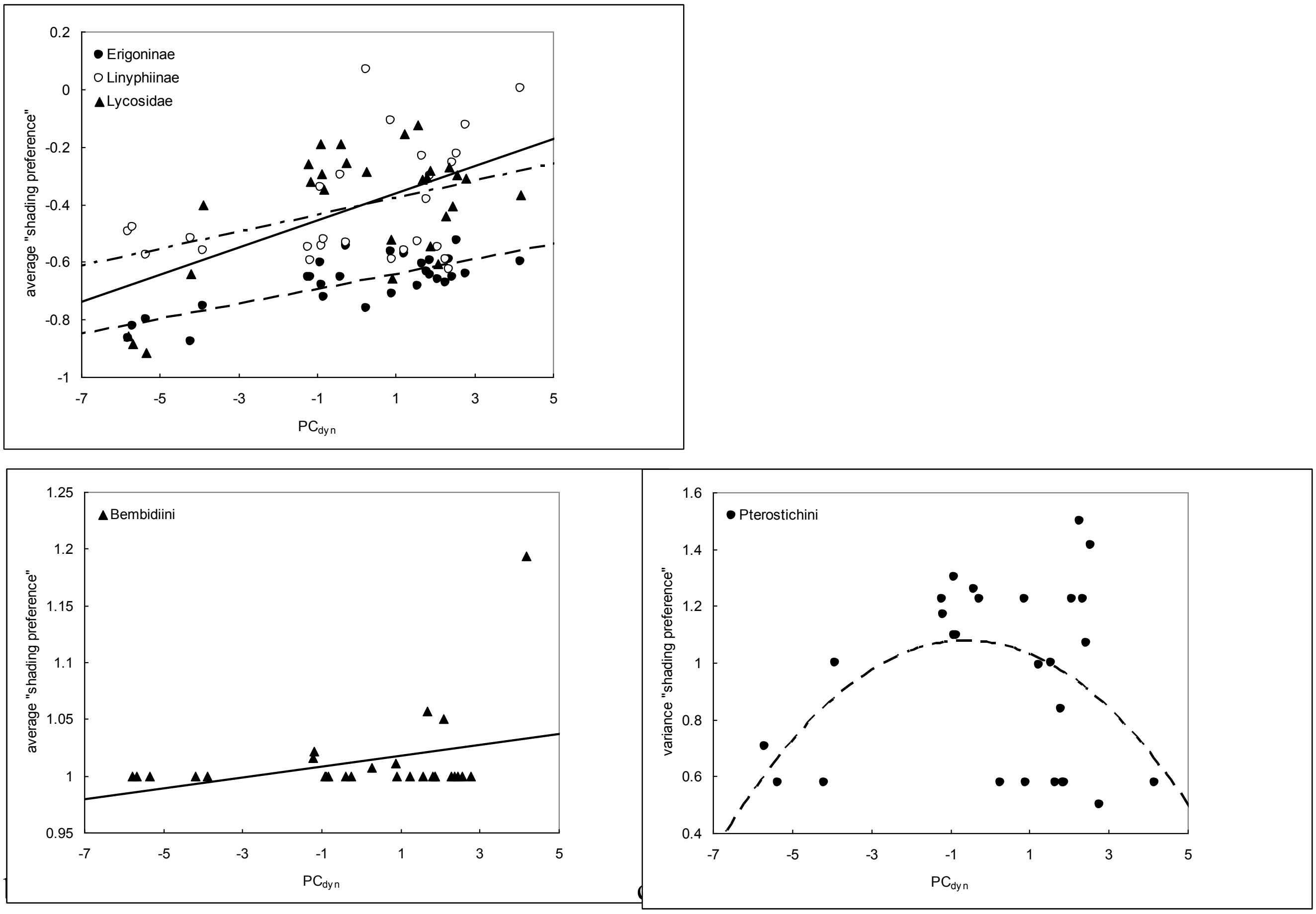

Erigoninae
Linyphiinae
Lycosidae
average "shading preference"
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
-7
-5
-3
-1
1
3
5
PC_{dyn}
Bembidiini
average "shading preference"
1.25
1.2
1.15
1.1
1.05
1
0.95
-7
-5
-3
-1
1
3
5
PC_{dyn}
Pterostichini
variance "shading preference"
1.6
1.4
1.2
1
0.8
0.6
0.4
-7
-5
-3
-1
1
3
5
PC_{dyn}

Fig. 5

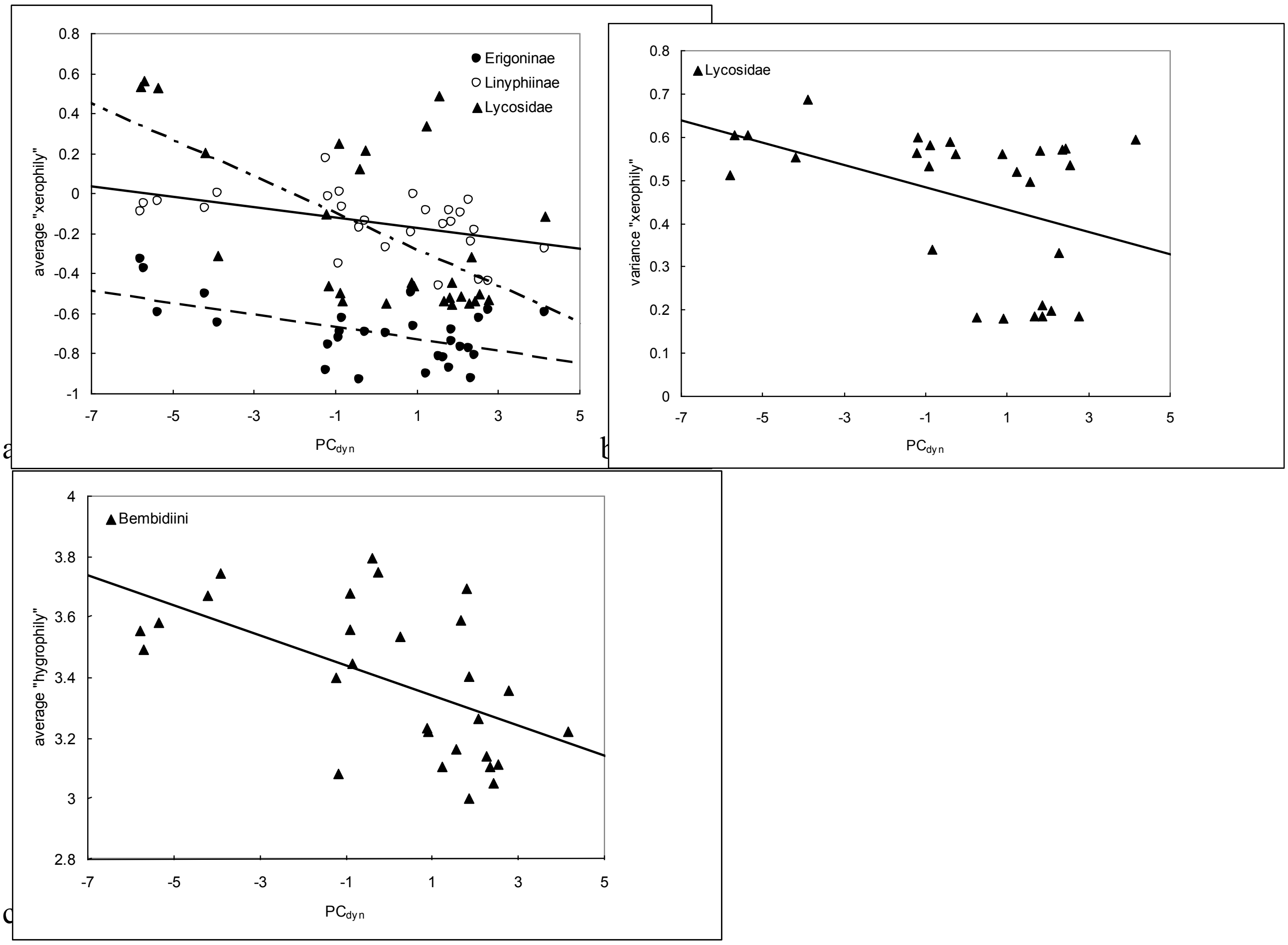

a
average "xerophily"
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
-7
-5
-3
-1
1
3
5
PC$_{dyn}$
● Erigoninae
○ Linyphiinae
▲ Lycosidae
b
variance "xerophily"
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
-7
-5
-3
-1
1
3
5
PC$_{dyn}$
▲ Lycosidae
c
average "hygrophily"
4
3.8
3.6
3.4
3.2
3
2.8
-7
-5
-3
-1
1
3
5
PC$_{dyn}$
▲ Bembidiini

Fig. 6

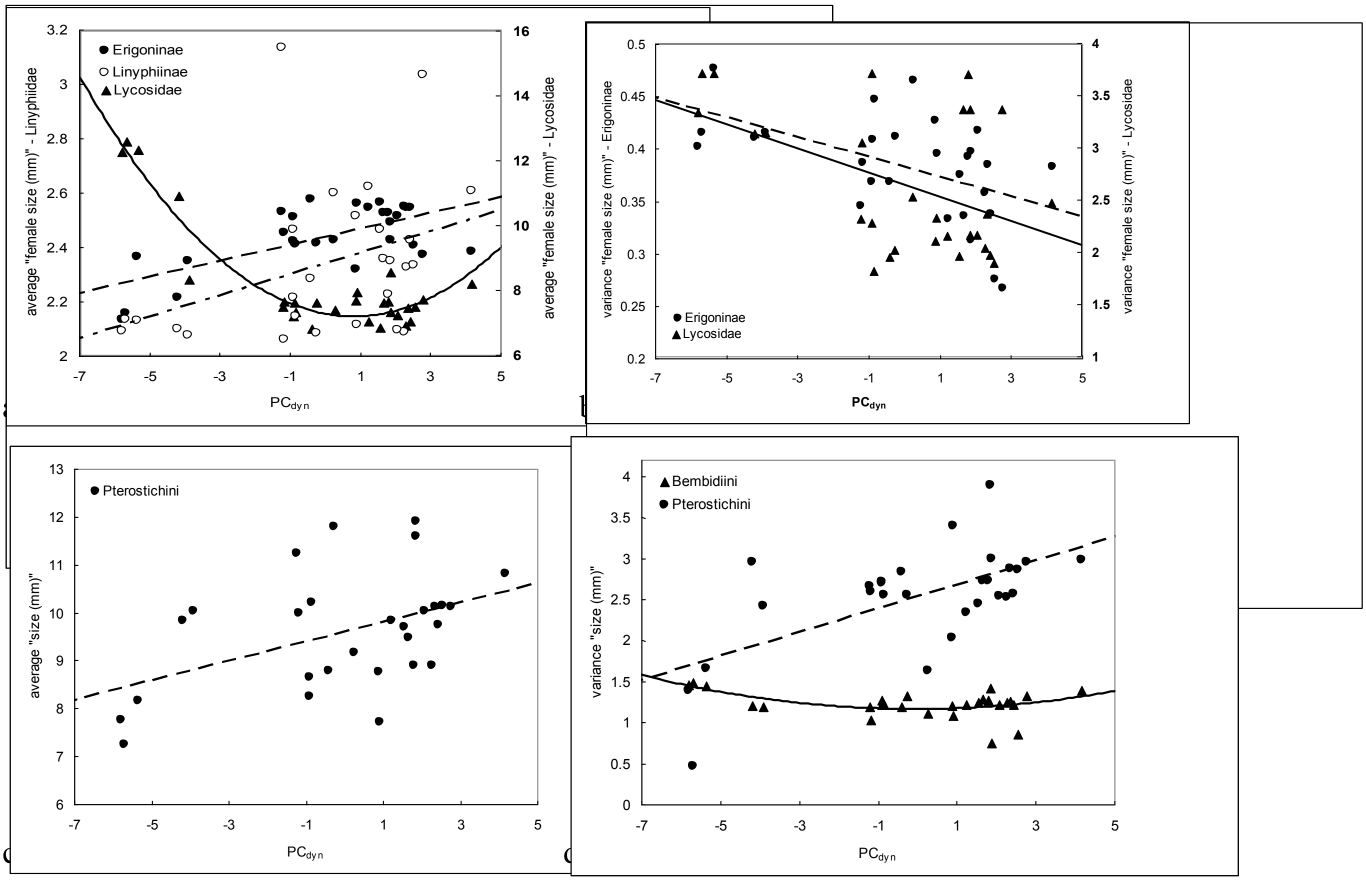
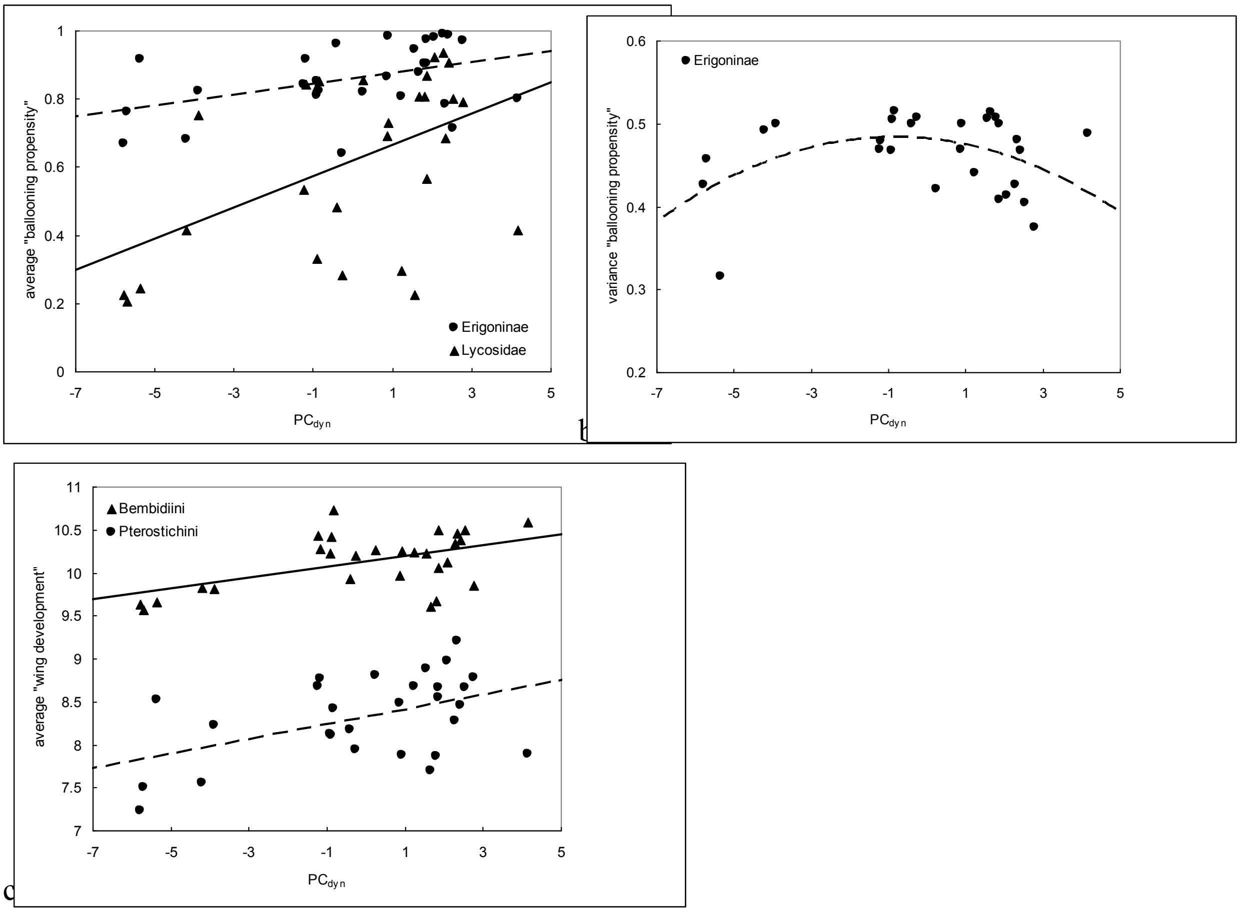

Erigoninae
Linyphiinae
Lycosidae
average "female size (mm)" - Linyphiidae
average "female size (mm)" - Lycosidae
3.2
3
2.8
2.6
2.4
2.2
2
16
14
12
10
8
6
-7
-5
-3
-1
1
3
5
PC$_{dyn}$
variance "female size (mm)" - Erigoninae
variance "female size (mm)" - Lycosidae
0.5
0.45
0.4
0.35
0.3
0.25
0.2
4
3.5
3
2.5
2
1.5
1
Erigoninae
Lycosidae
PC$_{dyn}$
Pterostichini
average "size (mm)"
13
12
11
10
9
8
7
6
PC$_{dyn}$
Bembidiini
Pterostichini
variance "size (mm)"
4
3.5
3
2.5
2
1.5
1
0.5
0
PC$_{dyn}$

Fig. 7



average "ballooning propensity"
1
0.8
0.6
0.4
0.2
0
-7
-5
-3
-1
1
3
5
PC$_{dyn}$
● Erigoninae
▲ Lycosidae
variance "ballooning propensity"
0.6
0.5
0.4
0.3
0.2
● Erigoninae
average "wing development"
11
10.5
10
9.5
9
8.5
8
7.5
7
▲ Bembidiini
● Pterostichini

Table 1: 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 S1.

Parameter	**variable measured**	**Methodology**	**PC_{dyn}**
flooding disturbance	RSregr	rising speed of washing water based on river discharge regimes and fourthnightly measured distances pitfalls - water line	**-0.585**
flooding disturbance	WFR	river bank water flow rate based on based on river discharge regimes and fourthnightly 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 - upto dyke foot)	**0.771**

Remarks:

- **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 1*1m quadrat surrounding each pitfall taken fourthnightly during the field survey

Table 2. Influence of flooding disturbance on species richness of spider and carabid beetle assemblages of river banks. GLM regression statistics and 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).

		second order relation		**first order relation**	
diversity measure	**regression statistics**	**Araneae**	**Carabidae**	**Araneae**	**Carabidae**
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 3. 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. GLM regression statistics and AIC values are shown for weighted averages (Table 3a and 3b) and variance (Table 3c and 3d) 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).

Table 3a

		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 propensity	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

Table 3b

		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

Table 3c

		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, 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 propensity	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

Table 3d

		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

Supplementary Material - LAMBEETS ET AL. – ARTHROPOD ASSEMBLAGE STRUCTURE FROM RIVER BANKS

Appendix S1: 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**
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	scrub100	amount of scrubland 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	scrub250	amount of scrubland 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 approximate 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 (McCune & Grace 2002); 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 scrub 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: $38m^3/s$)
- **Vegetation and substrate features** are estimated values based on digital pictures within a 1*1m 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 (100m and 200m radius)

Appendix S2: Species list, trapped numbers and trait values of three spider (sub)families (Araneae: Erigoninae, Linyphiinae, Lycosidae) and 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.

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
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
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

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
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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