Short-term resilience of arthropod assemblages after spring flood, with focus on spiders (Arachnida: Araneae) and carabids (Coleoptera: Carabidae)

Denis Lafage,[1,2]* Charlotte Sibelle,[2] Jean Secondi,[2] Alain Canard[1] and Julien Pétillon[1]

[1] *EA 7316, Université de Rennes 1, Rennes, France*
[2] *Université d'Angers, UNAM, GECCO, Angers, France*

ABSTRACT

Despite the expected increase in extreme flood frequency, the manner in which terrestrial arthropods cope with regular submersion of their habitat remains poorly understood in meadows, especially in temperate floodplains. Here, we studied the recolonization dynamics of arthropods after a severe spring flood in the Loire Valley (France). We carried out analyses at the community (order or family identification level) and species scales, focusing on the assemblages of two dominant and diverse groups: carabids and spiders. Our objectives were the following: (i) to describe the temporal changes in community structure after flooding and (ii) to assess the influence of landscape configuration on recolonization patterns of species and their functional traits. Fieldwork was performed along three sampling transects, by using 75 pitfall traps, in 2012. A total of 14 767 arthropods belonging to 87 families were trapped, including 5538 spiders (55 species) and 3396 carabids (66 species). Multivariate analyses discriminated assemblages from flooded and non-flooded habitats and revealed changes over time in arthropod families and species after flood withdrawal. In particular, wolf spiders (Lycosidae) were the first to recolonize, whereas other groups clearly avoided flooded sites. Our results also revealed that short distances to hedgerows, and to a lesser extent, distance to woodlands, favoured the recolonization of large and ground-running spiders. In conclusion, our study shows the short-term resilience of certain groups or stenotopic species to flooding and also the relevance of multi-taxon-based studies. The presence of hedgerows has to be considered carefully in management plans because of their role of refuge during flooding. Copyright © 2015 John Wiley & Sons, Ltd.

KEY WORDS   disturbance; floodplain; recolonization; landscape; Coleoptera: Carabidae; Araneae; Loire/Maine

Received 16 May 2014; Revised 10 January 2015; Accepted 17 January 2015

INTRODUCTION

Natural floodplains are the most species-rich habitats in temperate regions (Gerken, 1988). Disturbance induced by flooding is an integral component of floodplain ecosystem function (Ward, New and Yen, 2001). As stated by the flood pulse concept (Tockner *et al.*, 2000; Adis and Junk, 2002; Junk and Wantzen, 2004), flow variations shape the riverbanks (Scott *et al.*, 1997), contribute to their dynamic equilibrium (Junk, 2005) and maintain biodiversity in the floodplains (Adis and Junk, 2002).

In Europe, large rivers have been highly modified by humans for protection against floods, mainly by building dykes and floodplain drainage. One of the expected effects of climate change is the increased frequency of extreme hydrological events on European rivers (Dankers and

Feyen, 2008). This situation is likely to increase the anthropogenic management of large rivers. Assessing the ability of organisms to recolonize supposedly virgin habitats after flooding, thereby maintaining local biodiversity, is essential to the establishment of management strategies that encompass biodiversity conservation.

Resistance and phenological strategies of ground-dwelling arthropods may have evolved before the colonization of floodplains ('predisposition'; Weigmann and Wohlgemuth-von Reiche, 1999). However, flood events frequently result in the displacement of interstitial (Marmonier *et al.*, 1992), benthic (Rempel *et al.*, 1999) and terrestrial (e.g., Lambeets *et al.*, 2008a) invertebrates, by either passive or active movements. In temperate regions, flooding is not as predictable because of less seasonal precipitation pattern and relatively unpredictable snowmelt (Adis and Junk, 2002). Flood timing, rather than magnitude, is also believed to determine the impact of floods on organisms (Junk, 2005). Arthropod communities of European rivers are likely to use a 'risk strategy' to

*Correspondence to: Denis Lafage, EA 7316, Université de Rennes 1, 263 Avenue du Général Leclerc, CS 74205, 35042 Rennes, France.
E-mail: lafage.denis@gmail.com

survive in this naturally disturbed habitat. The strategy consists of a suite of life history traits such as high productivity ('*r*-strategy'), high capacity for dispersion and active recolonization from areas that have been sheltered from flooding (Zulka, 1994). Vertical emigration to uplands or higher vegetation is also expected to increase recolonization success (Adis and Junk, 2002). A few terrestrial species also withstand short to prolonged (up to several weeks) periods of submersion (e.g., insects: Hoback and Stanley, 2001, and spiders: Pétillon *et al.*, 2009). Conversely, flood events can be seen as a way to colonize new habitats and exchange individuals between distant populations (Lambeets *et al.*, 2010). Strategies used by terrestrial arthropods to cope with the regular submersion of river banks have been widely studied (e.g., Hering, Gerhard, Manderbach and Reich, 2004; Lambeets, Vandegehuchte, Maelfait and Bonte, 2008b); salt marshes (e.g., Sudd, 1972; Pétillon, Montaigne and David, 2009) but were studied to a less extent in natural grasslands.

In this study, we assessed the recolonization process of grasslands by invertebrates, at both community and species scales, after a late spring flood in the Loire Valley (France). The Loire River is poorly affected by human modifications regarding hydrological functioning, especially when compared with other European large rivers (Descy *et al.*, 2014) and can be thus considered a reference, virgin system. We focused on carabids and spiders because these two groups are highly diverse and abundant in floodplains (Ballinger *et al.*, 2007; Lambeets *et al.*, 2008b; Lafage *et al.*, 2014) worldwide. Besides, because of their sensitivity to hydrological conditions, they are considered as good indicators of moisture (Greenwood *et al.*, 1991, 1995).

Although floods occurring in winter and early spring probably have less effect on most organisms than floods occurring in summer (Ilg *et al.*, 2008), we expected arthropod assemblages to change after flooding and to return more or less rapidly to an equilibrium, here estimated by a comparison with assemblages from non-flooded grasslands.

Macroinvertebrate traits seem to be particularly affected by hydrology (Tupinambás *et al.*, 2013). A comparison of time response to perturbations suggests that spiders have higher dispersal abilities than carabids (Hendrickx *et al.*, 2007; Lafage and Pétillon, 2014). We consequently expected spiders, particularly ground runners, to be faster recolonizers than carabids and, thus, to be more resilient. The two groups are also known to react to landscape characteristics and could use landscape elements to escape from floods. Carabids and large spiders are known to climb tree trunks, whereas ballooning spiders (Linyphiidae) are carried into the canopy by airflow (Adis and Junk, 2002). We hypothesized that increasing distances to refuges has an impact on recolonization and on functional traits, notably because of interactions between landscape configuration and body size and the dispersal abilities of the two groups. For instance, Andersen (2011) found large carabids to move away from water during winter, whereas small ones did not. Finally, we expected the large ground-dwelling spiders and carabids to be able to retreat into refuges and to recolonize from there, while small ballooning spiders and flying carabids could recolonize from adjacent habitats and, thus, experience little to no influence from the surrounding landscape on recolonization abilities.

MATERIAL AND METHODS

Sampling design

The study site was located in Western France (0°32′37·7″W, 47°30′05·6″N). The study area is an island (600 ha) encircled by three rivers. It is flooded yearly, mainly during late autumn and winter, for about 3 months. Spring floods occur approximately every 5 years. The river flow, after the confluence of the three rivers, was $135·8\,m^3\,s^{-1}$ in 2012. Three floods occurred during spring 2012: 26 April ($185·5\,m^3\,s^{-1}$), 2 May ($399·8\,m^3\,s^{-1}$) and 22 May ($184·8\,m^3\,s^{-1}$) (Figure 1). Land is mainly covered by hay meadows and a few poplar groves. The hedgerow network is poor, with a total length of only 22 km. Grasslands are cut in early or mid-summer and grazed by cattle in autumn.

Sampling design was based on vegetation maps produced using remote sensing techniques and topography. Fifteen sampling stations were chosen along three transects following the topographic gradient (five stations per transect, see Appendix A), with each station comprising five pitfall traps (100 mm diameter). The sampling design
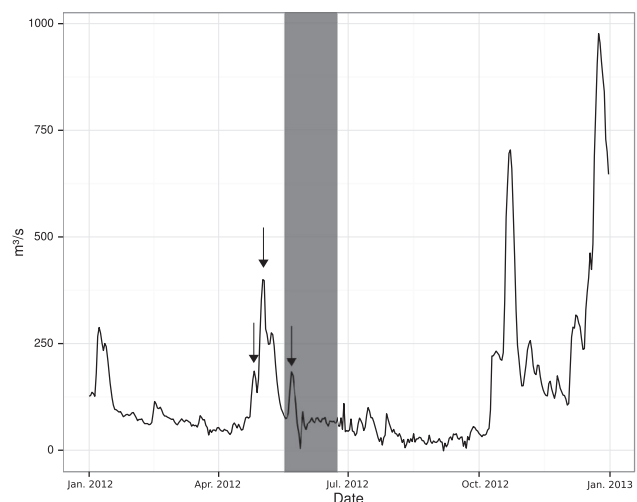

Figure 1. Average daily debit of the River Maine in 2012. Grey zone indicates sampling period, and arrows indicate major spring floods.

was stratified and encompassed six stations located in non-flooded grasslands (three xerophilous and three meso-hygrophilous stations) and nine stations located in flooded grasslands (five meso-hygrophilous and four hygrophilous stations). We hypothesized that xerophilous non-flooded stations provided refuge and sources for post-flood recolonization, which was tested by comparing their arthropod composition with the arthropod composition at non-flooded meso-hygrophilous stations.

Arthropod sampling was carried out from 18 May to 18 June 2012. Pitfall traps were located at least 20 m apart to avoid interactions between each other and yielded the calculation of 'activity density' for ground-dwelling arthropods (Topping and Sunderland, 1992). Traps were filled with preservative solution (50% monoethylene glycol, 50% water) and emptied every 3 or 4 days for a total of ten sampling periods.

Arthropod identification and classification

All terrestrial arthropods were identified to family level except springtails (Collembola), mites (Acari) and centipedes (Myriapoda), which were identified to the sub-order level; bees (Apoideae) to super-family level; and ants (Formididae) to sub-family level. Arthropods were preserved in 70% ethanol. Adult carabids and spiders were identified to species level. Spider nomenclature follows Platnick (2012). Carabid nomenclature follows Lindroth (1992).

Catches in pitfall traps were divided by trapping duration, in order to calculate activity density (Sunderland *et al*., 1995).

Statistical analyses

Prior to analyses, spatial autocorrelation was tested using Moran's I for arthropod, spider and carabid activity densities and species richness. Seasonal effect was tested on activity density and species richness of arthropods, spiders and carabids of non-flooded sites by using Box–Pierce tests.

The short-term recolonization of assemblages was first studied at the family level on all arthropods using correspondence discriminant analysis (CDA) (Perrière and Thioulouse, 2003). CDA categorizes observations in pre-defined groups. The dependent categorical variable was the class of time after flooding, and the response variable was the activity density of families. Permutation tests (999 iterations) were used to test class discrimination. Catches were classified according to five flood categories: three classes of time after flooding (1–9, 10–19 and >20 days) and two stations (non-flooded xerophilous and meso-hygrophilous).

We then focused on the short-term resilience of carabid and spider species using CDA with the same categorical variables but with activity density of species as explanatory variables. To identify spider and carabid species indicating a particular period in the recolonization process, we used the approach developed by Dufrêne and Legendre (1997), which statistically determines the association of a species to one or several groups by defining an indicator value (IndVal). IndVals were first calculated for flooded versus non-flooded sites and then for each of the five flood categories (see previous text). The enhanced method recommended by De Caceres and Legendre (2009) was applied using the R package 'Indicspecies' (De Caceres and Legendre, 2009). Significance of the indicator values was tested using 999-permutation test and Sidak's correction for multiple testing.

Analyses of similarity (ANOSIM) were then used to test differences in species composition between flood categories for both spiders and carabids, using the R package 'vegan' (Oksanen *et al*., 2013). The recolonization process was assessed by testing for some differences in activity density and species richness between the five flood categories using nonparametric Kruskal–Wallis tests followed by two-sample Wilcoxon tests.

In order to test the effect of landscape on the functional composition of spider and carabid assemblages, multivariate analyses of variance with Tukey honest significant difference (HSD) post-hoc tests were used with classes of distance to the nearest potential refuges (minimal distance to hedgerows, woodlands and non-flooded meso-hydrophilous grasslands) as independent explanatory variables and activity densities per functional trait as response variables. Three classes of distance, chosen to obtain comparable numbers between classes, were used for each landscape variable. For distance to the nearest hedgerow, non-flooded habitat and refuge, distance classes were 0–100, 101–200 and >200 m. For distance to the nearest woodland, distance classes were 0–300, 301–600 and >600 m. Only flooded sites were included in the analysis. Functional traits included dispersal ability and size of carabids and spiders, as displacements of these two traits have already been observed on riverbanks in relation to increasing flooding disturbance (Lambeets *et al*., 2008a). Dispersal ability of carabids was estimated by the development of wings in adults (e.g., Hendrickx *et al*., 2007). Species were classified as macropterous, apterous or dimorphic following Desender *et al*. (2008). For dimorphic species, wing development was checked on all individuals. Spiders were classified according to their dispersal habits as adults (Uetz *et al*., 1999): runners versus balloons. Carabids were divided into three size classes: small, 0–5 mm; medium, 5–10 mm; and large, >10 mm. Spiders were also divided into three size classes: small, 0–3 mm; medium, 3–5 mm; and large, >5 mm (Varet *et al*., 2013, 2014).

RESULTS

We found no seasonal effect on activity density or on species richness (Appendix B). Autocorrelation was significant but low enough to be neglected (Gerisch *et al.*, 2012).

Description of assemblages

A total of 14 767 arthropods belonging to 87 families (Appendix C) were trapped. Arthropod assemblages were dominated by one spider family (Lycosidae: 30·8% of total catches) and one carabid beetle tribe (Harpalini: 11·4% of total catches).

A total of 5538 spiders (4674 adults) of 55 species (Appendix D) representing 11 families were trapped. Lycosidae were highly dominant (83·4% of individuals). One species accounted for almost 50% of adult individuals: *Pardosa prativaga*.

A total of 3396 adult carabids belonging to 66 species (Appendix E) and 17 tribes were collected. Three species (*Poecilus cupreus*, *Harpalus affinis* and *Harpalus dimidiatus*) accounted for more than 40% of individuals.

Change in communities after flooding

The first two axes of the CDA on arthropods explained 71·89% of the total variance. Permutation tests showed that the group discrimination was significant ($P < 0·001$). Assemblages from the flooded xerophilic habitat presented a clearly different species composition (ANOSIM, Table I) and was characterized by Histeridae, Acrididae, Gnaphosidae and Harpalini (Figure 2). Assemblages from habitats 1–9, 10–19 and >20 days after flood withdrawal, characterized by Lycosidae (Figure 3),
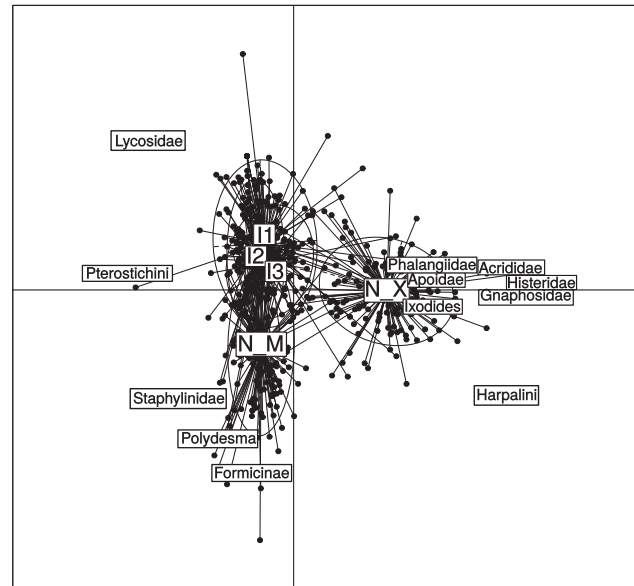

Figure 2. Correspondence discriminant analysis of the arthropod groups classified by time class since water withdrawal. Groups presented are the ones that contributed most to the axes. Ellipses represent the summarized weighted scatter plot for each class. Classes of time since water withdrawal: 1–9 (I1), 10–19 (I2) and more than 20 days (I3). N_X, non-flooded xerophilous stations; N_M, meso-hygrophilous stations.

presented no significantly different species compositions from each other (ANOSIM, Table I). Non-flooded meso-hygrophilous sites, characterized by the presence of Formicinae, Polydesmidae and Staphylinidae, presented a significantly different species composition from all other classes (ANOSIM, Table I).

The two first axes of the CDA on spiders explained 74·7% of the total variance. Permutation tests showed that

Table I. Analyses of similarity testing for differences in assemblage composition between classes of time since water withdrawal (I1: 1–9 days; I2: 10–19 days; I3: more than 20 days; N_X: non-flooded xerophilous grasslands; and N_M: meso-hygrophilous grasslands).

Group	I1	I2	I3	N_M
Arthropods				
I2	R = −0·06, P = 0·994			
I3	R = −0·07, P = 0·966	R = 0·019, P = 0·16		
N_M	R = 0·14, P = 0·001	R = 0·016, P = 0·001	R = 0·14, P = 0·001	
N_X	R = 0·36, P = 0·001	R = 0·48, P = 0·001	R = 0·40, P = 0·001	R = 0·36, P = 0·001
Spiders				
I2	R = 0·01, P = 0·454			
I3	R = 0·02, P = 0·202	R = 0·02, P = 0·158		
N_M	R = 0·03, P = 0·002	R = 0·14, P = 0·001	R = 0·01, P = 0362	
N_X	R = 0·17, P = 0·001	R = 0·05, P = 0·008	R = 0·02, P = 0·048	R = 0·18, P = 0·001
Carabids				
I2	R = 0·01, P = 0·206			
I3	R = 0·01, P = 0·531	R = 0·01, P = 0·746		
N_M	R = 0·19, P = 0·001	R = 0·17, P = 0·001	R = 0·17, P = 0·001	
N_X	R = 0·49, P = 0·001	R = 0·57, P = 0·001	R = 0·48, P = 0·001	R = 0·64, P = 0·001

For all arthropods, family differences in composition were tested; for spiders and carabids, differences in species composition were tested.
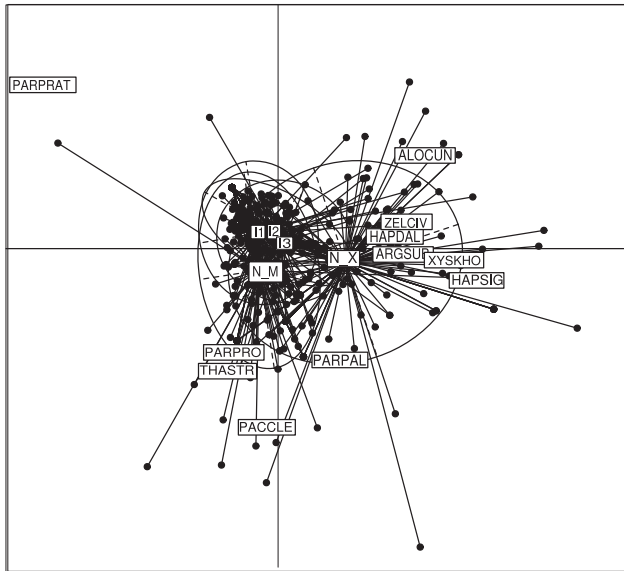
Figure 3. Correspondence discriminant analysis of the spider species classified by time class since water withdrawal. Species presented are the ones that contributed most to the axes. Ellipses represent the summarized weighted scatter plot for each class. Classes of time since water withdrawal: 1–9 (I1), 10–19 (I2) and more than 20 days (I3). N_X, non-flooded xerophilous stations; N_M, meso-hygrophilous stations; PARPRAT, *Pardosa prativaga*; PARPRO, *Pardosa proxima*; THASTR, *Thanatus striatus*; PACCLE, *Pachygnatha clercki*; PARPAL, *Pardosa palustris*; HAPSIG, *Haplodrassus signifer*; XYSKHO, *Xysticus kochi*; ARGSUB, *Argenna subnigra*; HAPDAL, *Haplodrassus dalmatensis*; ZELCIV, *Zelotes civicus*; ALOCUN, *Alopecosa cuneata*.
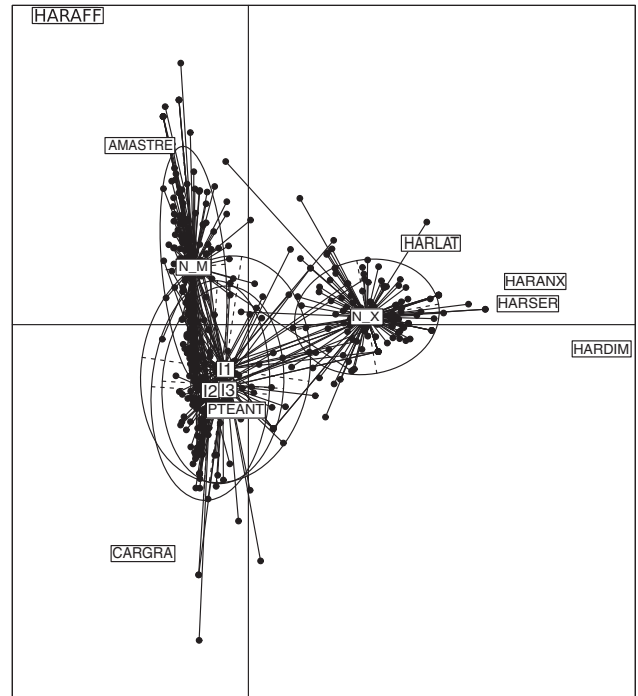

Figure 4. Correspondence discriminant analysis of the carabid species classified by time class since water withdrawal. Species presented are the ones that contributed most to the axes. Ellipses represent the summarized weighted scatter plot for each class. Classes of time since water withdrawal: 1–9 (I1), 10–19 (I2) and more than 20 days (I3). N_X, non-flooded xerophilous stations; N_M, meso-hygrophilous stations; CARGRA, *Carabus granulatus*; HARAFF, *Harpalus affinis*; AMASTRE, *Amara strenua*; PTEANT, *Pterostichus anthracinus*; HARLAT, *Harpalus latus*; HARANX, *Harpalus anxius*; HARSER, *Harpalus serripes*; HARDIM, *Harpalus dimidiatus*; CARGRA, *Carabus granulatus*.

the group discrimination was significant ($P < 0.001$). The assemblage from the non-flooded xerophilic stations presented a clearly different species composition (Figure 4; ANOSIM: Table I) and was characterized by *Haplodrassus signifer* (confirmed by IndVal = 0.52, $P = 0.005$), *Haplodrassus dalmatensis* (confirmed by IndVal = 0.45, $P = 0.005$), *Zelotes civicus* (confirmed by IndVal = 0.39, $P = 0.005$), *Xysticus kochi* (confirmed by IndVal = 0.36, $P = 0.005$) and *Argenna subnigra* (confirmed by IndVal = 0.17, $P = 0.005$). Assemblages from habitats 1–9, 10–19 and >20 days after flooding had subsided presented no significantly different species compositions from each other (ANOSIM, Table I). Assemblages from habitats 1–9 and 10–19 days after flooding had subsided were characterized by *P. prativaga* (Figure 4; confirmed by IndVal = 0.77, $P = 0.004$, and IndVal = 0.55, $P = 0.01$, respectively). *Ozyptila simplex* was an indicator of stations that had been free from floodwater for more than 20 days (IndVal = 0.48, $P = 0.005$). Non-flooded meso-hygrophilous stations were characterized by the presence of *Pardosa proxima* (confirmed by IndVal = 0.31, $P = 0.005$), *Pachygnatha clercki* (confirmed by IndVal = 0.22, $P = 0.005$) and *Thanatus striatus* (confirmed by IndVal = 0.16, $P = 0.05$) and presented a significantly different species composition from flooded stations

(ANOSIM, Table I). Regarding flooding specifically, *Pardosa prativa* was an indicator of flooded sites (IndVal = 0.77, $P = 0.004$), whereas *H. signifer* (IndVal = 0.73, $P = 0.002$), *H. dalmatensis* (IndVal = 0.64, $P = 0.002$), *X. kochi* (IndVal = 0.64, $P = 0.002$), *Z. civicus* (IndVal = 0.58, $P = 0.004$), *Pelecopsis mengei* (IndVal = 0.54, $P = 0.04$), *A. subnigra* (IndVal = 0.45, $P = 0.018$) and *P. clercki* (IndVal = 0.45, $P = 0.036$) were indicators of non-flooded stations.

The two first axes of the CDA on carabids explained 87.4% of the total variance and permutation tests showed that the group discrimination was significant ($P < 0.001$). The assemblage from non-flooded xerophilic stations presented a clearly different species composition (ANOSIM, Table I) and was characterized by *H. dimidiatus*, *Harpalus serripes*, *Harpalus anxius* and *Harpalus latus* (Figure 4). Assemblages from stations free from floodwater for 1 to more than 20 days were characterized by *Carabus granulatus* and *Pterostichus anthracinus* and presented no significantly different species compositions (ANOSIM, Table I). Non-flooded meso-hygrophilous stations, characterized by the presence
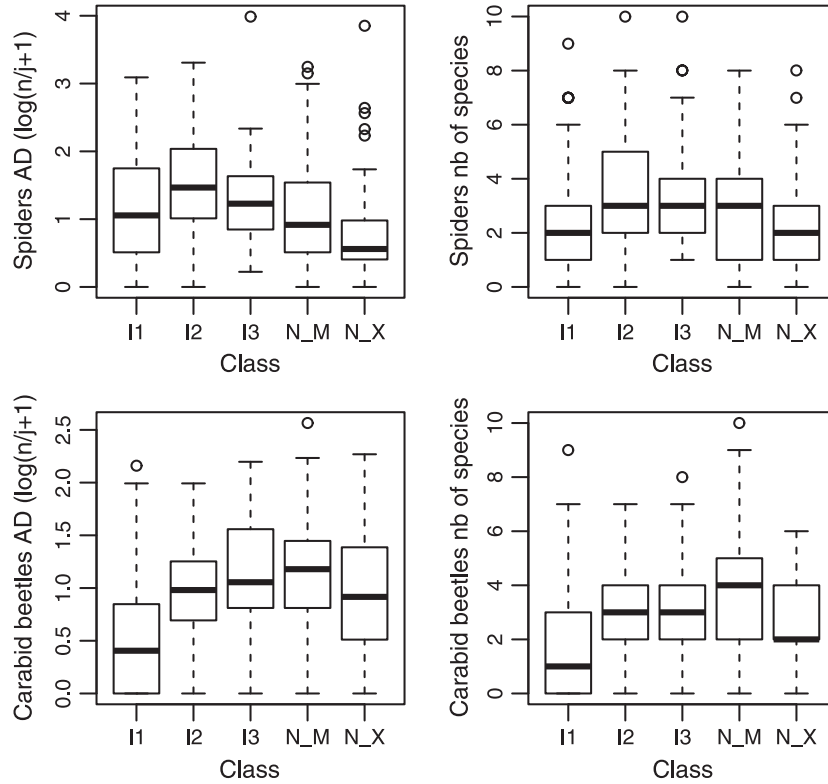
Figure 5. Activity density (AD) and species richness of spiders and carabids for each time class since water withdrawal [1–9 days (I1), 10–19 days (I2), more than 20 days (I3), non-flooded xerophilous (N_X), number (NB) and non-flooded meso-hygrophilous (N_M)]. Box plots represent median, 25% and 75% quartiles and max/min values.

of *H. affinis* (confirmed by IndVal = 0·40, $P = 0·015$) and *Amara strenua*, presented a significantly different species composition from all other stations (ANOSIM, Table I). Regarding flooding specifically, *C. granulatus* was an indicator of flooded stations (IndVal = 0·59, $P = 0·024$), whereas *H. affinis* (IndVal = 0·85, $P = 0·002$), *H. latus* (IndVal = 0·84, $P = 0·002$), *Harpalus luteicornis* (IndVal = 0·72, $P = 0·002$), *H. serripes* (IndVal = 0·68, $P = 0·002$), *A. strenua* (IndVal = 0·67, $P = 0·006$), *H. dimidiatus* (IndVal = 0·66, $P = 0·002$), *H. anxius* (IndVal = 0·64, $P = 0·002$), *Harpalus rufipes* (IndVal = 0·48, $P = 0·024$) and *Amara rufipes* (IndVal = 0·48, $P = 0·024$) were indicators of non-flooded stations.

Considering the clear difference in the composition of non-flooded xerophilic stations and other stations (see Figures 2, 3 and 5 and preceding texts), non-flooded xerophilic grasslands were removed from further analyses, because they could not be considered as refuges or sources for recolonization.

Recolonization process

Activity density and species richness of spiders varied significantly between flood categories ($\chi^2 = 19·08$, $P < 0·001$ and $\chi^2 = 35·45$, $P < 0·001$, respectively). There was no significant difference between activity density in

Table II. Values of mean activity density (AD ± SD) and species richness (S ± SD) of carabids and spiders.

df = 3	I1	I2	I3	N_M	Test	Post-hoc
Spider AD	1·13 ± 0·85	1·49 ± 0·76	1·29 ± 0·65	1·06 ± 0·73	$\chi^2 = 19·08$, df = 3, $P < 0·001$	N_M < I3 < I2; I1 < I2
Spider S	2·16 ± 1·78	3·52 ± 2·13	3·55 ± 1·91	3·02 ± 2·11	$\chi^2 = 35·45$, df = 3, $P < 0·001$	I1 < I2 = I3 = N_M
Carabid AD	0·54 ± 0·53	0.95 ± 0·48	1·10 ± 0·52	1·11 ± 0·52	$\chi^2 = 77·88$, df = 3, $P < 0·001$	I1 < I2 = I3 = N_M
Carabid S	1·76 ± 1·78	3·15 ± 1·61	3·32 ± 1·69	3·95 ± 2·06	$\chi^2 = 82·27$, df = 3, $P < 0·001$	I1 = I2 = I3 < N_M

AD, activity density; S, species richness; SD, standard deviation.
Nonparametric Kruskal–Wallis tests and two-sample Wilcoxon post-hoc tests for comparisons of activity density and species richness between classes of time since water withdrawal (I1: 1–9 days; I2: 10–19 days; I3: more than 20 days; N_X, non-flooded xerophilous grasslands; N_M, meso-hygrophilous grasslands).

Table III. Multivariate analyses of variance and Tukey honest significant difference post-hoc tests for comparison of spider and carabid activity density of each class of functional traits between classes of distance to the nearest hedgerow, woodland, non-flooded site or to the nearest refuge.

	Hedgerow	Woodland	Non-flooded site	Nearest refuge
Spiders				
Length	$F_{2494} = 6.41$, $P < 0.001$	$F_{2494} = 3.90$, $P < 0.001$	$F_{2494} = 2\,0.40$, $P = 0.027$	$F_{2494} = 1.85$, $P = 0.087$
C1	DH1 < DH3	DW1 = DW2 < DW3	n.s.	
C2	DH3 < DH2 = DH1	n.s.	n.s.	
C3	DH3 < DH2 < DH1	DW3 < DW2	n.s.	
Dispersion	$F_{2494} = 12.05$, $P < 0.001$	$F_{2494} = 2.55$, $P = 0.080$	$F_{2494} = 8.16$, $P < 0.001$	$F_{2494} = 1.11$, $P = 0.33$
Running	DH3 < DH2 < DH1		DNF3 < DNF2 < DNF1	
Ballooning	DH1 < DH3		n.s.	
Carabids				
Length	$F_{2494} = 9.87$, $P < 0.001$	$F_{2494} = 3.88$, $P < 0.001$	$F_{2494} = 1.63$, $P = 0.138$	$F_{2494} = 0.64$, $P = 0.696$
C1	DH1 = DH2 < DH3	n.s.		
C2	DH2 = DH3 < DH1	DW1 = DW2 < DW3		
C3	DH2 = DH3 < DH1	n.s.		
Wing development	$F_{2494} = 2.97$, $P = 0.019$	$F_{2494} = 4.87$, $P < 0.001$	$F_{2494} = 2.51$, $P = 0.041$	$F_{2494} = 1.64$, $P = 0.162$
Brachypterous	n.s.	n.s.	n.s.	
Macropterous	n.s.	DW1 = DW2 < DW3	n.s.	

n.s., non-significant, Bold values correspond to significant p values.
For spiders, size classes are C1: 0–3 mm; C2: 3–5 mm; and C3: >5 mm. For carabids, size classes are C1: 0–5 mm; C2: 5–10 mm; and C3: >10 mm. Distance classes to the nearest hedgerow are DH1: 0–100 m; DH2: 101–200 m; and DH3: >200 m. Classes to the nearest woodland are DW1: 0–300 m; DW2: 301–600 m; and DW3: >600 m. Distance classes to the nearest non-flooded habitats are DNF1: 0–100 m; DNF2: 101–200 m; and DNF3: >200 m.

the stations 1–9 days after flood withdrawal or in non-flooded meso-hygrophilous stations (Table II and Figure 4). Activity density was highest for stations free from floodwater for 10 to more than 20 days after water withdrawal. Spider species richness observed for stations free from floodwater for 1–9 days was significantly lower than species richness observed for stations non-flooded for 10 to more than 20 days or for non-flooded meso-hygrophilous stations (Table II and Figure 4).

Activity density and species richness of carabids were significantly different between flood categories (respectively, $\chi^2 = 77.88$, $P < 0.001$ and $\chi^2 = 82.27$, $P < 0.001$). Activity density and species richness in stations 1–9 days after water withdrawal were significantly lower than they were in other stations (Table II and Figure 4). Species richness of stations 10 to more than 20 days after floodwater withdrawal was significantly lower than species richness in non-flooded meso-hygrophilous stations (Table II and Figure 4).

Effect of landscape configuration

Multivariate analyses of variance on spider activity density for the three size classes showed significant differences between classes of distance to the nearest hedgerow ($F = 6.41$, $P < 0.001$), woodland ($F = 3.90$, $P < 0.001$) and non-flooded meso-hygrophilous grassland ($F = 2.40$, $P = 0.027$). Post-hoc Tukey HSD tests showed different effects of distance to hedgerow on the size classes. Activity density of medium and large spiders was greater near hedgerows, whereas activity density of small spiders was highest far from hedgerows (Table III). Distance to the nearest woodland also had contrasting effects: Activity density of small spiders was highest far from woodlands, whereas activity density of large spiders was highest near woodlands (Table III). Post-hoc Tukey HSD tests were not significant for distance to the nearest non-flooded meso-hygrophilous grassland.

Multivariate analyses of variance on spider activity density observed for the dispersal habits showed significant differences between classes of distance to the nearest hedgerow ($F = 12.05$, $P < 0.001$) and to the nearest non-flooded meso-hygrophilous grassland ($F = 2.14$, $P = 0.047$; Table III). Post-hoc Tukey HSD tests showed contrasting effects of distance to hedgerow, with greater activity density of ground-running spiders near hedgerows, whereas activity density of ballooning spiders was highest far from hedgerows (Table III). Activity density of ground-running spiders was also greater when distance to the nearest non-flooded meso-hygrophilous grassland decreased (Table III).

Multivariate analyses of variance on carabid activity density for the three size classes showed significant differences between classes of distance to the nearest hedgerow ($F = 9.87$, $P < 0.001$) and to the nearest woodland ($F = 2.95$, $P = 0.007$; Table III). Post-hoc Tukey HSD tests showed contrasting effects of distance to hedgerow, with the activity density of medium and large carabids being greater near hedgerows, whereas activity density of small carabids was highest far from hedgerows (Table III).

Activity density of medium carabids was highest far from woodlands (Table III).

Multivariate analyses of variance on carabid activity density observed for the two classes of wing development showed significant differences between classes of distance to the nearest hedgerow ($F = 2.97$, $P < 0.019$) and to the nearest woodland ($F = 4.87$, $P < 0.001$) (Table III). Post-hoc Tukey HSD tests showed significant effects of distance to woodlands for macropterous carabids, with the activity density of these species being higher far from woodlands (Table III).

DISCUSSION

Changes in arthropod composition over time

The CDA and ANOSIM on the whole arthropod assemblage demonstrated that flooded sites presented similar compositions over time, suggesting slow resilience of ground arthropod communities to spring floods. A spider family (Lycosidae), with high dispersal abilities, was characteristic of all flooded habitats. The habitats only flooded in winter were characterized by Staphylinidae, Polydesmidae and Formicinae. Staphylinids have been reported to survive 30 days of immersion at low (i.e., winter) temperatures (Adis and Junk, 2002) and are usually associated with wet habitats (Greenwood *et al.*, 1991). Polydesmidae can be encountered from very dry to very wet habitats (Voigtländer, 2011); but to our knowledge, no study has investigated their resilience after flooding. Ants, and especially the Formicinae sub-family, are known to adapt very well to extreme perturbation including unpredictable flooding (Lenoir, 2006; Nielsen, 2011). In our study, even if ants appear to be characteristic of non-flooded meso-hygrophilous sites, they represent 6% of arthropods collected in the 10 first days after the water receded and 11% of arthropods caught between 10 and 20 days after the water subsided. This suggests that some colonies resisted inundation of their nests.

Comparison of spider and carabid recolonization after flooding

In this study, spiders and carabids were the two most highly dominant groups of arthropods, reinforcing the need to focus on their species composition. Species composition of the spider assemblage 20 days after the water had subsided was not different from that observed in non-flooded meso-hygrophilous grasslands, whereas the composition of carabid assemblage differed until the end of our study. Additionally, species richness of spiders reached the same level as non-flooded meso-hygrophilous grasslands between 10 and 20 days after the floodwater had receded, whereas species richness of carabids did not, even after more than 20 days. This is in accordance with the findings of Gerisch *et al.* (2012) for carabids after a summer flood but contrary to numerous studies stating that riparian ground beetles are highly resilient to regular and periodic floods (Uetz, 1979; Zulka, 1994; Adis and Junk, 2002; Lessel *et al.*, 2011).

The spider assemblage in flooded habitats was clearly dominated by a ground-dwelling species: *P. prativaga*. This species is associated with open habitats and is considered ubiquitous (Harvey *et al.*, 2002). Like most lycosids, this species has high dispersal abilities; Richter *et al.* (1971) estimated a mobility of $34.5\,\mathrm{cm\,min^{-1}}$, in a straight line, in the field (i.e., around 500 m a day). *P. prativaga* activity density decreased from 75.8% of total activity density of spiders in the 10 first days after water withdrawal to 53.7% after 20 days from water withdrawal. This suggests that *P. prativaga* is the first species to recolonize grasslands after floodwater has receded. The species can thus be considered an indicator of flooded habitats, and its presence would indicate ongoing recovery (Gerlach *et al.*, 2013). Non-flooded-hygrophilous grasslands are characterized by two hygrophilous species, *P. proxima* and *P. clercki* (Harvey *et al.*, 2002), but are numerically dominated by *P. prativaga* (51% of all spiders). Flooded habitats are thus dominated by an opportunistic spider species with a typical risk strategy, whereas non-flooded meso-hygrophilous grasslands are characterized by stenotopic (hygrophilous) species. This segregation between sites that are flooded only in winter and those flooded in both winter and spring is in accordance with Sudd (1972) and Uetz (1979); both the studies showed that flooding frequency was an easy way to discriminate spider assemblages. However, this is in opposition with the findings of Bell *et al.* (1999), who showed that spider assemblages are shaped according to whether or not a site is flooded.

Flooded habitats were characterized by two hygrophilous (Desender *et al.*, 2008) carabid species, *C. granulatus* and *P. anthracinus*, and numerically dominated by *P. cupreus*. *P. cupreus* is considered eurytopic, with an affinity for wet habitats and with high dispersal abilities (up to $30\,\mathrm{m\,days^{-1}}$ in the field: Thiele, 1977). Its ability to swim across small water bodies has also been reported (Sienkiewicz and Zmihorski, 2012). Non-flooded meso-hygrophilous grasslands are characterized by two carabid species with unclear habitat requirements: *H. affinis* and *A. strenua*. *H. affinis* is considered a eurytopic species with affinities for dry grasslands by Desender *et al.* (2008), but Van Looy *et al.* (2007) found that this species is a quick colonizer of riparian habitats, although it is also sensitive to rapid flow increases. The rising water observed in 2012 could have been slow enough to allow *H. affinis* to retreat into non-flooded habitats, explaining its dominance in the non-flooded meso-hygrophilous stations (27% of total catches). *A. strenua* is considered by Luff (1998) to be a

coastal species that can be found on riverbanks. Follner and Henle (2006) consider *A. strenua* a resident of transition zones between dry and wet habitats, which is in accordance with our findings.

The low richness of hydrophilic species in flooded sites is in opposition with Lessel *et al.* (2011) who found an increased number of hygrophilic species with increasing soil moisture. The long period without spring flood in the Loire Valley (8 years) could have allowed eurytopic species to colonize grasslands and exclude hygrophilic species.

The non-flooded xerophilous sites were characterized by species of dry habitats: *H. latus*, *H. anxius*, *H. serripes* and *H. dimidiatus* (Luff, 1998; Desender *et al.*, 2008) for carabids and *X. kochi* and *H. dalmatensis* for spiders. Therefore, these grasslands cannot be considered refuges. Results of the IndVal approach confirmed the CDA for carabids when looking at flooded site versus non-flooded site indicators but did not function very well when looking at indicators of time classes since the water had receded, suggesting that carabids are less resilient than spiders.

The variations in activity density between the flood categories presented different patterns between spiders and carabids. The activity density of spiders reached the same level as non-flooded meso-hygrophilous grassland immediately after water receded and was the highest 10–19 days after flooding. The lack of spatial competition after flooding could explain this observation (Hering *et al.*, 2004). Besides, on river banks, prey sources of spiders and carabids are known to switch from terrestrial to aquatic after flooding (Paetzold *et al.*, 2005; O'Callaghan *et al.*, 2013). The same prey shift in flooded grasslands could explain the high activity of Lycosidae. Indeed, this behaviour is mainly observed in species with traits that favoured rapid dispersal (O'Callaghan *et al.*, 2013). The fast resilience of spiders compared with carabids has recently been reported after severe disturbance (e.g., Varet *et al.*, 2013, 2014). The dominance of adult lycosids at the beginning of water withdrawal (92·6%) suggests that spiders of this family avoid flooding by actively retreating to refuges or by resisting it. The activity density is greatest between 10 and 20 days after the water receded, suggesting active colonization of empty habitats.

For carabids, the important difference in activity density (−49%) between non-flooded habitats and habitats 1–10 days after water withdrawal suggests high mortality caused by the flood. Activity density did not reach the level observed in the non-flooded habitats, even after 30 days after the water receded, suggesting a medium-term to long-term resilience of the assemblage. Those findings are in accordance with the results of Hering, Gerhard, Manderbach and Reich (2004), which

found carabid density to be the lowest 1 month after a 100-year flood, and highest 2 months after the flood. These results are also in accordance with the findings of Rothenbücher and Schaefer (2006) on strategies used by spiders during winter flooding but not by carabids. These authors found that leafhoppers and planthoppers could tolerate winter flooding, whereas spiders and carabids emigrate to safe places. Spring flooding could have occurred faster than winter flooding, allowing spiders, but not most carabids, to emigrate. Gerisch *et al.* (2012) found that the total species richness of carabids reached a level similar to that of pre-flood condition within 2 years of an extreme summer flood.

Influence of landscape configuration in the recolonization process

As expected, landscape configuration had an impact on some functional traits of spiders and carabids. Activity density of medium and large individuals of the two groups was higher near hedgerows, and the activity of small species was greater farther from them. Hedgerows could constitute a refuge for medium-sized carabids and large species of spiders with high active dispersal abilities. Such vertical migrations have been reported in ants and millipedes in the Pantanal (Adis *et al.*, 2001). For large carabids, usually considered to have a lower dispersal capacity (Dajoz, 2002), natural hedgerows are frequently used as overwintering sites. Higher activity density of large carabids species could thus reflect the emergence of adults in early spring. Higher activity density of small species far from hedgerows could result from a barrier effect of hedgerows on aerial dispersers (Larrivée and Buddle, 2009). A significant effect of distance to hedgerows was found for the dispersal habits of spiders. As ground runners are usually medium or large species and ballooners are small species, our results are obviously in accordance with those found for the size class analysis. We found no impact of distance to hedgerows on the wing development of carabids. Indeed, only one species (*C. granulatus*) was brachypterous, and half of its population was located in a site next to a hedgerow (30 m). This suggests that this hygrophilous species, usually associated with grasslands, is also dependent on the presence of hedgerows in flooded sites. However, the species is able to survive for over 10 days under water (Decleer, 2003), which probably explains its presence on the study site.

The influence of distance to woodlands is less clear, as it influenced the activity density of small and large spiders only. This is probably due to the spatial distribution of the two small woodlands that were relatively far from the flooded habitats. Distances to non-flooded meso-hygrophilous grasslands and to the nearest refuge did not

affect the functional traits of spiders and carabids, suggesting that these taxa are likely to actively retreat into hedgerows and woodlands, even if there is another, nearer, refuge available. Thus, it seems that never-flooded sites that serve as refuges during winter floods (Andersen, 2011) do not serve as refuge during spring floods.

In conclusion, we showed that spring-flooded, winter-flooded and never-flooded habitats presented clear, discrete compositions. As expected, spiders and carabids were the most resilient arthropod groups after a severe spring flood, especially Lycosidae and Pterostichini. Surprisingly, spiders almost recovered only 20 days after flooding, suggesting that spring floods are, as expected, less severe than summer floods for this group. Carabids, despite being known to be well adapted to floodplain ecosystems, appeared less resilient than spiders, confirming the relevance of multi-taxon-based studies. Finally, we found that the role of landscape in the recolonization by spiders depends on their body size and dispersal habits. Recolonization of carabids was mainly dependent on their size and on the presence of hedgerows. For both spiders and carabids, hedgerows, and to a lesser extent woodland, seem to constitute preferential refuges, which should be considered carefully, as hedgerows are continuously decreasing in agricultural landscapes.

The original conclusions drawn here from less-studied habitats, flooded meadows, should be tested in other large European streams with few disturbed hydrological functioning.

APPENDIX A. Localization of the sampling sites along each transect. stars correspond to flooded stations (white: meso-hygrophilous, black: hygrophilous) and dots to non-flooded stations (white: xerophilous, black: meso-hygrophilous).
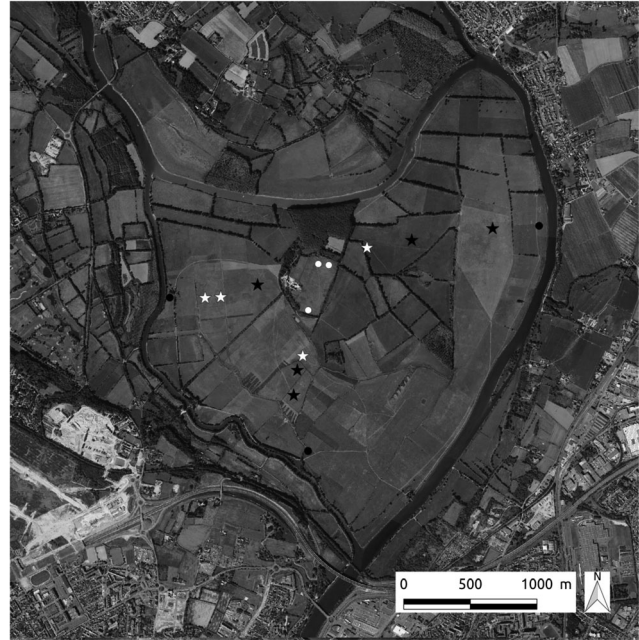
APPENDIX B. Spatial autocorrelation tests (moran's i values; significance of tests $* = 0.05$) and seasonality tests (box–pierce tests) for activity density and species richness of arthropods, spiders and carabids.

	Activity density	Species richness
Autocorrelation		
Arthropods	$I = 0.44*$	$I = 0.48*$
Spiders	$I = 0.41*$	$I = 0.46*$
Carabids	$I = 0.40*$	$I = 0.45*$
Seasonality		
Arthropods	$\chi2 = 0.46$	$\chi2 = 1.33$
Spiders	$\chi2 = 0.22$	$\chi2 = 0.32$

APPENDIX C. Number of individuals per class of time since water receded (i1: 1–9 days; i2: 10–19 days; and i3: more than 20 days) for all taxa.

	I1	I2	I3	N_M	N_X	Total
Acaridida	42	121	11	12	3	189
Acrididae	18	7	17	11	153	206
Aphididae	10	11	54	9	55	139
Apidae		1			2	3
Apoidae	3	1	1	1	21	27
Araneidae					3	3
Arionidae	48	26	15	147	128	364
Asellidae	86		1	1		88
Bembidiini	14	8	7	17	2	48
Brachinini			1	12		13
Byrrhidae	3	9	5	13	13	43
Calliphoridae			1			1
Cantharidae	1			2	4	7
Carabini	51	58	23	36	2	170
Cassidae	1	2			2	5
Chlaeniini	3	2		5		10
Chloropidae	7	2		20	10	39
Cicadellidae	3	1	3	13	7	27
Clivinini	66	31	14	64	4	179
Coccinellidae	16	4		7	23	50
Curculionidae	56	53	30	140	102	381
Cydnidae		1	2	2	20	25
Cynipidae		2	1	1	1	5
Diapriidae					1	1
Dictynidae	1			1	7	9
Dyschiriini	1			1		2
Elaphridae	1			2		3
Elateridae	31	21	11	28	18	109
Entomobryomorpha	139	407	94	46	11	697
Evanoidea	1	1	1	1	6	10
Formicinae	137	130	69	801	222	1359
Gamasides	4	2	11	24	2	43
Gnaphosidae	2	23	12	20	156	213
Harpalini	128	140	118	500	843	1729
Helicidae				6	3	9
Helophoridae	5	18	6	2	23	54
Histeridae	17	6	2	11	201	237
Ichneumonoidea	2	7	4	8	13	34
Ixodides	1		1	6	51	59
Lauxaniidae	1			1		2
Lebiini	21	64	73	55	28	241
Linyphiidae	80	123	63	154	64	484
Lithobiomorpha	1			20	2	23
Lulomorpha			1	8	1	10
Lycosidae	1269	978	538	1135	634	4554
Lygaeidae	1				1	2
Miridae		3	1	1	11	16
Muscidae	14	2		12	17	45
Myrmicinae	160	185	224	59	134	762
Nebriini	1	1		1		3
Nitidulidae		3		3	9	15
Omophronidae	3	1				4
Oniscidae		1	6	25	5	37
Oodini	4					4
Panagaeini		1				1
Pentatomidae	2	1	1	1	6	11
Phalangiidae	3	1	7		49	60

(Continues)

APPENDIX C. (Continued)

	I1	I2	I3	N_M	N_X	Total
Philodromidae		4	2	11	35	52
Piophilidae				1		1
Pisauridae					1	1
Platynini			1	6		7
Polydesma	3	9	3	69		84
Pselaphidae	11	18	10	15	8	62
Pterostichini	144	135	136	240	21	676
Salticidae					2	2
Scarabaeidae	2	1	1	4	2	10
Scatopsidae	14	4	1	10	3	32
Sciaridae	11	12	6	12	11	52
Sironidae		2				2
Sphaeroceridae	3		1	4		8
Sphodrini					2	2
Staphylinidae	29	52	23	148	9	261
Symphypleona	27	4	1	6	1	39
Tephritidae	2	2	1	2		7
Tetragnathidae			2	13	2	17
Tetrigidae	4	2		4		10
Tettigoniidae				1	5	6
Theridiidae	1			3	5	9
Thomisidae	23	39	41	46	8	157
Tingidae	1			2	13	16
Tipulidae		1		1	1	3
Trechini				1		1
Trombidiformes	24	30	71	33	19	177
Vespidae			3	3	1	7
Zabrini	13	21	14	128	25	201
Zuphiin		1				1

APPENDIX D. Number of individuals per class of time since water receded (i1: 1–9 days; i2: 10–19 days; and i3: more than 20 days) for all spider species.

Species	Dispersal	Size	I1	I2	I3	N_M	N_X	Total
Alopecosa barbipes	GR	C3	0	0	0	0	2	2
Alopecosa cuneata	GR	C3	8	29	4	0	38	79
Arctosa leopardus	GR	C3	4	1	1	1	2	9
Argenna subnigra	B	C1	1	0	0	1	7	9
Diplostyla concolor	B	C1	0	0	0	0	1	1
Drassodes lapidosus	GR	C3	0	0	0	0	4	4
Drassyllus pusillus	GR	C2	0	0	1	2	0	3
Enoplognatha mordax	GR	C2	0	0	0	3	2	5
Enoplognatha sp.	GR		1	0	0	0	0	1
Erigone atra	B	C1	1	0	1	1	0	3
Erigone dentipalpis	B	C1	42	24	12	39	2	119
Erigone sp.	B		0	1	0	0	0	1
Euophrys frontalis	GR	C1	0	0	0	0	1	1
Gnaphosa sp.	GR		0	0	0	0	1	1
Haplodrassus dalmatensis	GR	C2	0	1	0	0	40	41
Haplodrassus signifer	GR	C3	0	3	0	2	57	62
Haplodrassus sp.	GR		0	0	0	0	1	1
Hypsosinga albovittata	B	C1	0	0	0	0	3	3
Linyphiidae	B		3	3	0	4	1	11
Lycosidae	GR		0	134	173	154	283	744

(Continues)

APPENDIX D. (Continued)

Species	Dispersal	Size	I1	I2	I3	N_M	N_X	Total
Meioneta rurestris	B	C1	9	2	5	13	1	30
Micaria albovittata	GR	C2	0	0	0	0	1	1
Micrargus subaequalis	B	C1	0	0	0	2	0	2
Oedothorax fuscus	B	C1	5	1	1	9	5	21
Oedothorax retusus	B	C1	0	1	0	0	0	1
Ozyptila simplex	GR	C2	18	34	43	46	5	146
Ozyptila sp.	GR		3	5	0	1	2	11
Ozyptila trux	GR	C2	2	1	0	0	0	3
Pachygnatha clercki	B	C3	0	0	2	12	2	16
Pachygnatha sp.	GR		0	0	0	1	0	1
Panamomops sulcifrons	B	C1	0	0	1	0	0	1
Pardosa agrestis	GR	C3	19	10	3	16	8	56
Pardosa amentata	GR	C3	2	0	0	1	0	3
Pardosa palustris	GR	C2	88	77	38	180	93	476
Pardosa prativaga	GR	C2	1117	668	312	616	34	2747
Pardosa proxima	GR	C2	52	29	5	93	25	204
Pardosa pullata	GR	C2	1	1	0	2	5	9
Pardosa sp.	GR		1	1	0	1	6	9
Pelecopsis mengei	B	C1	1	1	6	6	13	27
Pelecopsis parallela	B	C1	3	3	4	1	16	27
Phrurolithus festivus	GR	C1	0	0	0	0	1	1
Pirata piraticus	GR	C3	0	1	0	0	0	1
Pisaura mirabilis	GR	C3	0	0	0	0	1	1
Prinerigone vagans	B	C1	1	0	0	3	0	4
Steatoda phalerata	GR	C2	0	0	0	0	3	3
Talavera aperta	GR	C1	0	0	0	0	1	1
Tenuiphantes tenuis	B	C1	19	50	37	65	24	195
Thanatus sp.	GR		0	0	0	1	0	1
Thanatus striatus	GR	C2	0	3	1	9	0	13
Tiso vagans	B	C1	1	0	1	1	0	3
Trachyzelotes pedestris	GR	C2	0	0	0	1	0	1
Trochosa ruricola	GR	C3	38	69	62	52	12	233
Trochosa sp.	GR		1	0	0	0	4	5
Trochosa spinipalpis	GR	C3	7	1	0	2	1	11
Trochosa terricola	GR	C3	4	5	1	8	1	19
Troxochrus scabriculus	B	C1	0	0	0	1	0	1
Xysticus acerbus	GR	C2	0	0	0	0	1	1
Xysticus kochi	GR	C2	0	1	1	1	34	37
Zelotes civicus	GR	C2	0	2	0	0	34	36
Zelotes latreillei	GR	C3	0	1	0	0	1	2

APPENDIX E. Number of individuals per class of time since water receded (i1: 1–9 days; i2: 10–19 days; i3: more than 20 days; n_x: non-flooded xerophilous grasslands; and n_m: meso-hygrophilous grasslands) for all carabid species.

Species	Wing development	Size	I1	I2	I3	N_M	N_X	Total
Acupalpus exiguus	Macropterous	C1	19	14	9	23	2	67
Agonum gracile	Macropterous	C2			1	1		2
Amara aenea	Macropterous	C2	6	2	3	21	3	35
Amara anthobia	Macropterous	C2		1				1
Amara communis	Macropterous	C2				1		1
Amara concinna	Macropterous	C2		1	4	1		6
Amara equestris	Macropterous	C3				1	1	2
Amara familiaris	Macropterous	C2		1		1	1	3
Amara floralis	Macropterous	C2				2		2
Amara fulvipes	Macropterous	C2				2	2	4

(Continues)

APPENDIX E. (Continued)

Species	Wing development	Size	I1	I2	I3	N_M	N_X	Total
Amara kulti	Macropterous	C2	1					1
Amara lunicollis	Macropterous	C2			1	4	1	6
Amara montivaga	Macropterous	C2					1	1
Amara plebeja	Macropterous	C2				2		2
Amara rufipes	Macropterous	C2	2	4		11	8	25
Amara similata	Macropterous	C2			1	1		2
Amara strenua	Macropterous	C2	2	10	6	86	7	111
Amara tricuspidata	Macropterous	C2					1	1
Anchomenus dorsalis	Macropterous	C2				4		4
Anisodactylus binotatus	Macropterous	C3	30	19	10	6	34	99
Anisodactylus poeciloïdes	Macropterous	C3	1					1
Anthracus consputus	Macropterous	C1	3			1		4
Brachinus elegans	n.a.	C2			1	12		13
Calathus fuscipes	Apterous	C3					2	2
Carabus granulatus	Polymorphic	C3	36	48	25	18	2	129
Carabus monilis	Brachypterous	C3	4	6	4	17		31
Chlaeniellus nigricornis	Macropterous	C3	3	2		5		10
Clivina fossor	Polymorphic	C2	59	30	19	68	4	180
Cryptophonus tenebrosus	Macropterous	C2	2				1	3
Diachromus germanus	n.a.	C2	4	26	20	91		141
Dyschiriodes globosus	Polymorphic	C1	1					1
Dyschirius angustatus	Macropterous	C1				1		1
Elaphrus riparius	Macropterous	C2	1			2		3
Harpalus affinis	Macropterous	C3	21	23	26	288	30	388
Harpalus anxius	Macropterous	C2	4		1		111	116
Harpalus cupreus	Macropterous	C3	8	22	8	26	6	70
Harpalus dimidiatus	Macropterous	C3	13	24	37	1	345	420
Harpalus dispar	Macropterous	C3				1		1
Harpalus latus	Macropterous	C2	3	3	4	31	116	157
Harpalus luteicornis	Macropterous	C2	5	3	5	31	39	83
Harpalus melancholicus	Macropterous	n.a.					1	1
Harpalus modestus	Macropterous	C2					10	10
Harpalus serripes	Macropterous	C3	9	2		1	146	158
Loricera pilicornis	Macropterous	C2	3	1				4
Metallina lampros	Polymorphic	C3				3	1	4
Metallina properans	Polymorphic	C1	1	1	1			3
Microlestes minutulus	Macropterous	C1	1	2	12	1	19	35
Nebria brevicollis	Polymorphic	C3		1		1		2
Notaphus dentellus	Macropterous	C3				1		1
Notiophilus biguttatus	Macropterous	C1	14	8	6	11	1	40
Oodes helopioides	Brachypterous	C2	3					3
Ophonus ardosiacus	Macropterous	C3				9		9
Panagaeus cruxmajor	Macropterous	C2		1				1
Parophonus mendax	n.a.	C2				1		1
Platynus livens	n.a.	n.a.				1		1
Poecilus cupreus	Macropterous	C3	122	125	143	239	15	644
Poecilus kugelanni	Macropterous	C3	1		1		2	4
Polystichus connexus	Macropterous	C2		1				1
Pseudoophonus rufipes	Macropterous	C3	2	2	2	19	2	27
Pterostichus anthracinus	Polymorphic	C3	3	2			1	6
Pterostichus melanarius	Polymorphic	C3	3			8		11
Pterostichus vernalis	Polymorphic	C3		1				1
Stenolophus mixtus	Macropterous	C2		1	1			2
Stomis pumicatus	Polymorphic	C3	1					1
Syntomus obscuroguttatus	Brachypterous	C1	21	62	61	54	8	206
Trechoblemus micros	Macropterous	C1				1		1

REFERENCES

Adis J, Junk WJ. 2002. Terrestrial invertebrates inhabiting lowland river floodplains of Central Amazonia and Central Europe: a review. *Freshwater Biology* **47**: 711–731.

Adis, J, Marques MI, Wantzen M. 2001. First observations on the survival strategies of terricolous arthropods in the northern Pantanal wetland of Brazil. *Andrias* **15**: 127–128.

Andersen J. 2011. Winter quarters of wetland ground beetles (Coleoptera, Carabidae) in South Scandinavia. *Journal of Insect Conservation* **15**: 799–810.

Ballinger A, Lake PS, Nally RM. 2007. Do terrestrial invertebrates experience floodplains as landscape mosaics? Immediate and longer-term effects of flooding on ant assemblages in a floodplain forest. *Oecologia* **152**: 227–38.

Bell D, Petts GE, Sadler JP. 1999. The distribution of spiders in the wooded riparian zone of three rivers in Western Europe. *Regulated Rivers: Research & Management* **158**: 141–158.

Dajoz R. 2002. *Les Coléoptères Carabidés et Ténébrionidés: écologie et biologie.* Tec & Doc: Paris, France.

Dankers R, Feyen L. 2008. Climate change impact on flood hazard in Europe: an assessment based on high-resolution climate simulations. *Journal of Geophysical Research* **113**: 2156–2202.

De Caceres M, Jansen F. 2010. Package 'indicspecies'. *Function to assess the strength and significance of relationships of species site group associations.*

De Caceres M, Legendre P. 2009. Associations between species and groups of sites: indices and statistical inference. *Ecology* **90**: 3566–3574.

Decleer K. 2003. Population dynamics of marshland spiders and carabids beetles due to flooding : about drowning, air bubbling, floating, climbing and recolonisation. In *Towards natural flooding reduction strategies*. Warsaw **1**: 1–6.

Descy J-P, Leitao M, Everbecq E, Smitz JS, Deliège J-F. 2014. Phytoplankton of the River Loire, France: a biodiversity and modeling study. *Journal of Plankton Research* **34**:120–135,

Desender K, Dekoninck W, Maes D, Crevecoeur L, Dufrêne M, Jacobs M, Lambrechts J, Pollet M, Stassen E, Thys N. 2008. *Een nieuwe verspreidingsatlas van de loopkevers en zandloopkevers (Carabidae) in Belgie. Rapporten van het Instituut voor Natuur- en Bosonderzoek.* Brussel (Belgium). 208 pp.

Dufrêne M, Legendre P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* **67**: 345–366.

Follner K, Henle K. 2006. The performance of plants, molluscs, and carabid beetles as indicators of hydrological conditions in floodplain grasslands. *International Review of Hydrobiology* **91**: 364–379.

Gerisch M, Dziock F, Schanowski A, Ilg C, Henle K. 2012. Community resilience following extreme disturbances: the response of ground beetles to a severe summer flood in a central European lowland stream. *River Research and Applications* **28**: 81–92.

Gerken B. 1988. *Auen Verborgene Lebensadern der Natur.* Rombach Verlag, Freiburg.

Gerlach J, Samways M, Pryke J. 2013. Terrestrial invertebrates as bioindicators: an overview of available taxonomic groups. *Journal of Insect Conservation* **17**: 831–850.

Greenwood MT, Bickerton MA, Castella E, Large ARG, Petts GE. 1991. The use of Coleoptera (Arthropoda: Insecta) for floodplain characterization of the river Trent, U.K. *Regulated Rivers: Research & Management* **6**: 321–332.

Greenwood MT, Bickerton ME and Petts GE. 1995. Spatial distribution of spiders on the floodplain of the River Trent UK: the role of hydrological setting. *Regulated Rivers: Research and Management* **10**: 303–313.

Harvey PR, Nellist DR, Telfer, MG. 2002. *Provisional Atlas of British Spiders (Arachnida, Araneae)*, vols. 1 and 2. Biological Records Center: Huntingdon, Cambridgeshire, UK.

Hendrickx F, Maelfait J-P, Van Wingerden W, Schweiger O, Speelmans M, Aviron S, Bugter R. 2007. How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. *Journal of Applied Ecology* **44**: 340–351.

Hering D, Gerhard M, Manderbach R, Reich M. 2004. Impact of a 100-year flood on vegetation, benthic invertebrates, riparian fauna and large woody debris standing stock in an alpine floodplain. *River Research and Applications* **20**: 445–457.

Hoback WW, Stanley DW. 2001. Insects in hypoxia. *Journal of Insect Physiology* **47**: 533–542.

Ilg C, Dziock F, Foeckler F. 2008. Long-term reactions of plants and macroinvertebrates to extreme flood in floodplain grassland. *Ecology* **89**: 2392–2398.

Junk WJ, Wantzen KM. 2004. The flood pulse concept: new aspects, approaches, and applications. An update.

Junk WJ. 2005. Flood pulsing and linkages between terrestrial, aquatic, and wetland systems. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie* **29**: 11–38.

Lafage D, Pétillon J. 2014. Impact of cutting date on carabids and spiders in a wet meadow. *Agriculture, Ecosystems & Environment* **185**: 1–8.

Lafage D, Secondi J, Georges A, Bouzillé J-B, Pétillon J. 2014. Satellite-derived vegetation indices as surrogate of species richness and abundance of ground beetles in temperate floodplains. *Insect Conservation and Diversity* **7**: 327–333.

Lambeets K, Breyne P, Bonte D. 2010. Spatial genetic variation of a riparian wolf spider *Pardosa agricola* (Thorell, 1856) on lowland river banks: the importance of functional connectivity in linear spatial systems. *Biological Conservation* **143**: 660–668.

Lambeets K, Hendrickx F, Vanacker S, Van Looy K, Maelfait JP, Bonte D. 2008a. Assemblage structure and conservation value of spiders and carabid beetles from restored lowland river banks. *Biodiversity and Conservation* **17**: 3133–3148.

Lambeets K, Vandegehuchte ML, Maelfait JP, Bonte D. 2008b. Understanding the impact of flooding on trait-displacements and shifts in assemblage structure of predatory arthropods on river banks. *The Journal of Animal Ecology* **77**: 1162–74.

Larrivée M, Buddle CM. 2009. Diversity of canopy and understorey spiders in north-temperate hardwood forests. *Agricultural and Forest Entomology* **11**: 225–237.

Lenoir J-C. 2006. Structure sociale et stratégie de reproduction chez Cardiocondyla elegans. Université de Tours. 132 p.

Lessel T, Marx MT, Eisenbeis G. 2011. Effects of ecological flooding on the temporal and spatial dynamics of carabid beetles (Coleoptera, Carabidae) and springtails (Collembola) in a polder habitat. *Zookeys* **100**: 421–446.

Lindroth CH. 1992. *Ground Beetles (Carabidae) of Fennoscandia, a Zoogeographic Study, Part I.* (Intercept.). Andover, UK.

Luff ML. 1998. *Provisional atlas of the ground beetles (Coleoptera, Carabidae) of Britain.* Biological Records Centre Institute of Terrestrial Ecology: Huntingdon, UK.

Marmonier P, Dole-Olivier M-J, Creuze des Chatellier M. 1992. Spatial distribution of interstitial assemblages in the floodplain of the Rhone River. *Regulated Rivers* **7**: 75–82.

Nielsen MG. 2011. Ants (Hymenoptera: Formicidae) of mangrove and other regularly inundated habitats: life in physiological extreme. *Myrmecological News* **14**: 113–121.

O'Callaghan MJ, Hannah DM, Boomer I, Williams M, Sadler JP. 2013. Responses to river inundation pressures control prey selection of riparian beetles. *PloS One* **8**: e61866.

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Wagner S. 2013. Vegan: community ecology package. http://cran.r-project.org/package=vegan

Paetzold A, Schubert CJ, Tockner K. 2005. Aquatic terrestrial linkages along a braided-river: riparian arthropods feeding on aquatic insects. *Ecosystems* **8**: 748–759.

Perrière G, Thioulouse J. 2003. Use of correspondence discriminant analysis to predict the subcellular location of bacterial proteins. *Computer Methods and Programs in Biomedicine* **70**: 99–105.

Pétillon J. Montaigne W, David R. 2009. Hypoxic coma as a strategy to survive inundation in a salt-marsh inhabiting spider. *Biology Letters* **5**: 442–445.

Platnick NI. 2012. The World Spider Catalog, version 13·0. The American Museum of Natural History. http://research.amnh.org/iz/spiders/catalog/.

Rempel LL, Richardson JS, Healey MC. 1999. Flow refugia for benthic macroinvertebrates during flooding of a large river. *Journal of the North American Benthological Society* **18**: 34–48.

Richter CJJ, Den Hollander J, Vlijm L. 1971. Differences in breeding and motility between *Pardosa pullata* (Clerk) and *Pardosa prativaga* (L. Koch), (Lycosidae, Araneae) in relation to habitat. *Oecologia* 327: 318–327.

Rothenbücher J, Schaefer M. 2006. Submersion tolerance in floodplain arthropod communities. *Basic and Applied Ecology* 7: 398–408.

Scott ML, Auble GT, Friedman JM. 1997. Flood dependency of cottonwood establishment along the Missouri river, Montana, USA. *Ecological Applications* 7: 677–690.

Sienkiewicz P, Zmihorski M. 2012. The effect of disturbance caused by rivers flooding on ground beetles (Coleoptera: Carabidae). *European Journal of Entomology* 109: 535–541.

Sudd J. 1972. The distribution of spiders at Spurn Head (E. Yorkshire) in relation to flooding. *The Journal of Animal Ecology* 41: 63–70.

Sunderland KD, De Snoo GR, Dinter A, Hance T, Helenius J, Jepson P, Kromp B, Samu F, Sotherton NW, Toft S, Ulber B. 1995. Density estimation for invertebrate predators in agroecosystems. In S. Toft & W. Riedel (Eds.), *Acta Jutlandica* 133–162. Aarhus University Press: Aarhus, Denmark.

Thiele HU. 1977. Carabid beetles in their environments. *Zoophysiology and Ecology* 10: 372.

Tockner K, Malard F, Ward JV. 2000. An extension of the flood pulse concept. *Hydrological Processes* 14: 2861–2883.

Topping C, Sunderland KD. 1992. Limitations to the pitfall traps in ecological-studies exemplified by a study of spiders in a field of winter-wheat. *Journal of Applied Ecology* 29: 485–491.

Tupinambás TH, Cortes RMV, Varandas SG, Hughes SJ, França JS, Callisto M. 2013. Taxonomy, metrics or traits? Assessing macroinvertebrate community responses to daily flow peaking in a highly regulated Brazilian river system. *Ecohydrology* 7: 828–842.

Uetz GW. 1979. The effect of flooding on floodplain arthropod distribution, abundance and community structure. *American Midland Naturalist* 101: 286–299.

Uetz GW, Halaj J, Cady AB. 1999. Guild structure of spiders in major crops. *The Journal of Arachnology* 27: 270–280.

Van Looy K, Jochems H, Vanacker S, Lommelen E. 2007. Hydropeaking impact on a riparian ground beetle community. IV.3. *River Research and Applications* 23: 223–233.

Varet M, Burel F, Lafage D, Pétillon J. 2013. Age-dependent colonisation of urban habitats : a diachronic approach using carabid beetles and spiders. *Animal Biology* 63: 257–269.

Varet M, Burel F, Pétillon J. 2014. Can urban consolidation limit local biodiversity erosion? Responses from carabid beetle and spider assemblages in Western France. *Urban Ecosystems* 17: 123–137.

Voigtländer K. 2011. Preferences of common Central European millipedes for different biotope types (Myriapoda, Diplopoda) in Saxony-Anhalt (Germany). *International Journal of Myriapodology* 6: 61.

Ward DF, New TR, Yen AL. 2001. Effects of pitfall trap spacing on the abundance, richness and composition of invertebrate catches. *Journal of Insect Conservation* 5: 47–53.

Weigmann G, Wohlgemuth-von Reiche D. 1999. Vergleichende Betrachtungen zu den Überlebensstrategien von Bodentieren im Überflutungsbereich von Tieflandauen. *Das Untere Odertal: Auswirkungen der periodischen Uberschwemmungen auf Biozonosen und Arten. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart,* 229–240.

Zulka KP. 1994. Carabids in a Central European floodplain: species distribution and survival during inundations. In *Carabid Beetles: ecology and evolution.* Springer Netherlands; 399–405.