Metacommunity responses of soil Collembola to inundation intensity in the Upper Rhine Valley

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Abstract

Over the last 10 years, soil Collembola were investigated in floodplain forest sites of the Upper Rhine Valley. The sites varied in elevation – and thus inundation intensity – and the hydrological regimes in different years ranged from intense flooding to strong drought. Spatial differences and temporal developments of the Collembolan communities were investigated and augmented by laboratory experiments. Experimental flooding produced severe effects mostly on species richness, but also facilitated individual species. The spatial studies showed that frequently flooded sites harbor species-poor, yet individual-rich communities, while less frequently flooded sites show species-rich, but individual-poorer communities. Specific community structures were found to be related either to frequent or rare inundation. Species composition and especially community structure were variable on one and the same site depending on the inundation intensity of the specific year. Temporal studies showed that within a given year – while being variable depending on site and flooding intensity – collembolan succession after floodwater withdrawal was regular and predictable. Changes in community structure during secondary succession were mostly due to dominance shifts of specific species. Specific adaptations and response patterns can be attributed to specific species. Although wide niche overlap between species was observed, strong differences in specific niche axes could be discerned. The spatio-temporal heterogeneity of the studied floodplains allow the differently reacting species to occur concomitantly. The regional mixture of differently reacting species allow local communities to react resiliently to inundation and thus maintain overall community stability despite variable flooding pressure.

Keywords: Collembola, floodplains, inundation, community ecology

1. Introduction

Natural river systems and their floodplains are characterised by recurring inundation events, which represent a natural disturbance for biotic communities (Junk et al. 1989, Fischer 1990). These biocoenoses are adapted to periodic flooding and show, over time, ecological stability despite regular inundation (Penka et al. 1985, 1991, Adis 1997, Magee et al. 1999). Larger, macrofaunal groups can periodically migrate out of and back into flooded soils in response to rising or falling water levels (Adis 1997). Collembola, with a smaller radius of action, have a much lower ability to migrate long distances in short time periods and can thus be highly affected by inundation (Palissa 1955, Beck 1972, Rusek 1984). Inundation can also heavily shape the landscape geomorphology, creating a high degree of habitat heterogeneity (Bayley 1995), which can presumably be reflected in collembolan metacommunity patterns. Although a number of studies have dealt with collembola in European riparian habitats (i.e. Franz et al. 1959, Tamm 1982, Rusek 1984, Griegel 1999, Sterzyńska & Ehrnsberger 1999), few of these have described their small-scale spatial heterogeneity or temporal dynamics (i.e.
Thus, the spatio-temporal distribution of Collembolan communities in relation to the spatial heterogeneity of and temporal disturbances in floodplains are still only fragmentarily known.

Beginning in the early 1990s, soil biological monitoring in floodplains of the Upper Rhine Valley in Germany showed that Collembola react quickly and differentially to differences in the inundation regime (LfU 1999, Russell et al. 2002). However, these early studies raised questions concerning natural collembolan responses to inundation and long-term community stability despite regular, yet variable inundation. Therefore, further investigations were undertaken in intact floodplains over the last decade to understand collembolan community responses to inundation and the role that small-scale habitat heterogeneity plays in community stability despite inundation disturbance. The present paper represents a summary of the major results from these studies, highlighting direct effects of inundation, spatial and temporal patterns relating to flooding intensity and responses within the communities. The specific aim of these studies was to determine the reactions of Collembolan communities due to spatio-temporally different inundation intensities and in relation to the spatial heterogeneity of floodplain forests. In general, these studies aimed at understanding how natural floodplain collembolan communities cope with the variable disturbance induced by recurring inundation.

2. Materials and methods

**Sampling and laboratory methods** – Collembolan communities were studied between 1995 and 2005 in a number of sites (mainly floodplain forests) from six locations in the Upper Rhine Valley in Germany between Strasbourg and Mannheim. During this period, observations of the immediate effects of inundation were complicated, i.e. by site inaccessibility, and samples taken from under floodwater in other sites failed to show animal-free soil. Therefore, laboratory inundation experiments were undertaken. Hereby, 50 soil cores (10 groups of 5 samples each, Ø 6.4 cm; 5 cm depth, 3 – 5 cm between each sample of a group) were taken from two softwood forests each (Leopoldshafen [May 2003] and Rastatt [July 2003], see below) and brought to the laboratory. From each location, the microarthropods from 10 cores (one from each group) were extracted immediately, while the remaining 40 were placed in aquariums under aerated (= O2-saturated) water (20 °C) of similar chemical properties as the Rhine River (i.e., pH 8 – 8.5; 400 – 550 µS/cm; 0 mg NO2- and NH4+/l, 25 mg NO3-/l). Ten samples (again one from each group) were subsequently removed after 3 days, 2, 4 and 6 weeks, allowed to drip dry for 3 days and the animals subsequently extracted (see below) for 10 days. Further faunal analysis was as below.

**Spatial studies** – Field investigations began with studies of floodplain spatial heterogeneity in sites of varying inundation intensity. In 1995 and 1996, 7 sites within a 520-ha area near Altenheim (separated by 200 – 400 m from each other), differing in elevation and ranging from reeds (site 1), softwood (sites 2A, 2B, 2C), lower-hardwood (site 3) to upper-hardwood forests (sites 4A and 4B), were sampled. For details of the sites, soils and flooding regime, see Russell et al. (2002). Collembolan data from 1993 and 1994 for these sites were obtained from GEFU (1994, 1995). In 1999 – 2001, a subset of these sites representing the main softwood and hardwood forest types and experiencing regular but different inundation intensities (2A, 2C, 4A, 4B) were studied further. In each year, five soil cores (6.4 cm Ø, 5 cm depth) were taken three times per year (May – July depending on inundation, August, late September) from the same 25 m² sampling area of each site, beginning after the spring/early-summer floods.
Between 2002 and 2005 the studied spatial scale was reduced. Hereby, three sites located in transects perpendicular to the water line, separated by 20 – 30 m each and of increasing elevation (and thus lower average inundation intensity) were sampled (lower softwood forest [l-SW], upper softwood forest [u-SW] and lower hardwood forest [l-HW]). As the original location of Altenheim represented anthropogenically influenced floodwater-control sites, two replicated transects (blocks) were studied in natural floodplains in 2002 and 2003 (near Rastatt in the nature reserve »Rastatter Rheinauen« and near Karlsruhe in the floodplain forests of Leopoldshafen), and were increased to four transects in 2004 and 2005 (additionally: floodplain forests in Altenheim [including the site 2A from above as o-SW] and in the nature reserve »Bremsengrund«). Replicated sites of the different transects were flooded at similar Rhine River water levels. For details of the sites and flooding regime, see Russell (2005), Russell & Griegel (2006). In these sites, sampling was increased to 15 cores per site and sampling date (dimensions and depths as above) in 2002 and 2003 (to evaluate in-site variability) and reduced again to 10 cores in 2004 and 2005 (due to the increased number of sites and based on the variability results of 2002 and 2003).

**Temporal studies** – Field studies were also designed so that temporal within-site reactions to inundation could be discerned. Average community changes due to year-to-year differences in inundation intensity were observed by studying the same sites (i.e., in Altenheim and the small-scale transects) over 2 – 5 years. Furthermore, within-year community responses following flooding incidences were investigated by reducing the temporal scale of sampling. In 2001, three upper-softwood forests (in Ketsch near Heidelberg, Leopoldshafen and Rastatt [see above]), separated by approximately 30 – 40 km but of similar elevation (and thus inundation duration) were sampled every 14 days between August and September after being flooded for approx. 155 days. For details of the sites, see Russell & Hauth (2002). In each site, 15 soil cores (as above) were taken along a 10 – 15 m transect parallel to the water line. The small-scale transects in Rastatt and Leopoldshafen were sampled (see above) in 2002 biweekly approximately 2 weeks after floodwater withdrawal and in 2003 in early spring before regular flooding as well as in 3- to 4-week intervals beginning approximately 4 weeks after floodwater withdrawal in June.

**Sample treatment** – In each study, microarthropods were extracted from the soil cores in Macfadyen-type, high-gradient extractors for 10 – 14 days. Collembola were sorted out under a stereomicroscope at maximally 50× magnification and determined to species level under an interference-contrast microscope at up to 1000× magnification.

Soil moistures of all soil cores were determined graviometrically (before/after extraction). After animal extraction, pH (electrometrically in CaCl₂) as well as C- and N-content (in a C-N-S analyser) was determined for each soil core.

**Metacommunity dynamics** – Further investigations of between-site dispersal were carried out in 2002. Directional migration was determined through barriered mini-pitfall traps (Mebes & Filser 1997). Four series of 5×5 traps (before/behind a covered barrier, 1.5 cm Ø each, separated laterally by 30 cm) each were set in two locations (the transects of Leopoldshafen and Rastatt described above) between the lower hardwood and lower softwood sites directly after inundation in July and collected biweekly until September. Drifting litter material was collected by hand in 2002 from floodwaters of the same two locations and checked for Collembola.
Data analysis – Densities were calculated for total Collembola as yearly averages (spatial-distribution studies) or sampling-date averages (temporal-dynamic studies) from the geometric means of individuals/sample and were standardized to individuals m\(^{-2}\). Species richness was determined as sampling-date averages per year (spatial distribution) or sampling-date sums (temporal dynamics). Due to the non-normal distribution of soil microarthropods, differences in density (community total or of individual species) and species richness (as species per sample) between floodplain levels or between sampling dates or years were tested for significance using a non-parametric one-way ANOVA for multiple observations (= samples) per cell (= site and sampling date) (modified Friedman test; Zar 1999). This ANOVA is based on ranked per sample data and on the \(\chi^2\) rather than the F distribution. A post-hoc Tukey-like multiple comparison procedure for this non-parametric ANOVA (Zar 1999) subsequently tested for significant differences between specific sites and sampling dates, respectively.

For the collembolan assemblages of each site and sampling date, respectively, the relative abundances of the individual species were calculated to determine community structure. Since stochastic differences in individual species’ densities created much noise in the data, the species were divided into ecological groups for comparison of community structure. For this, a cluster analysis of the Spearman correlation matrices of the species abundance data (from Altenheim and the transects from 2002) as well as a correspondence analyses of the abundances were carried out (see Russell et al. 2002, Russell & Griegel 2006). Furthermore, non-parametric ANOVAs (as above) of the individual species’ abundances were carried out to test for site (spatial) or sampling-date (temporal) preferences. From these results, groups of ecologically isovalent species (cf. Weigmann 1997) were constructed\(^1\). The species of these groups are listed in the appendix. Community structures are presented here based on these groups, with each group representing the cumulative relative abundances of the constituent species per year (spatial distribution) or sampling-date (temporal dynamics).

Small-scale temporal changes in community structure were analysed by constructing semi-logarithmic rank-abundance curves (RADs) for the communities per site and sampling date. The RADs of each sampling per site were tested for significant differences by ANCOVA or – after converting the curves to linear cumulative-dominance curves – by a Kolmogorov-Smirnov K-test. The RADs were then fitted to various community niche-apportionment models using the Software RAD 4.1 (Ulrich 2003).

Finally, species’ affinities for various environmental parameters were analysed using the complete data from all studies. For this, various abiotic parameters (i.e., soil moisture, pH, organic content etc.) were grouped into linearly arranged value-classes, the data from soil samples grouped in these classes according to their respective abiotic values, and the cumulative abundances of the individual species from these sample groups averaged as above to individuals m\(^{-2}\). Since most species showed at most unimodal rather than linear relationships to the abiotic parameters, correlation analyses were not carried out.

3. Results

Laboratory experiments – After experimental flooding, species richness was strongly reduced (\(\chi^2 = 14.2, P = 0.007\)), especially in samples from Rastatt (Fig. 1). After 4 – 6 weeks of inundation, almost only hygrophilous or hygrotolerant species remained (i.e. Sminthurides Peckiana_5_Final_1.qxp 26.11.2008 14:10 Seite 130

\(^1\) The classification of the species into the various groups was based on the data and, thus, determined according to ecological behaviour on site (= a posteriori), not primarily according to the known autecology (= a priori, cf. Weigmann 1997). Nonetheless, the results of our classification are in accordance with literature information for many species occurring in riparian habitats (i.e. Rusek 1984, Bretfeld 1999, Griegel 1999, Palissa 2000).
spp., *Podura aquatica, Isotomiella minor, Sminthurinus aureus, Sphaeridia pumilis*). Their populations often increased with inundation time ($P = 0.03 – 0.001$), leading to increasing total densities in Leopoldhafen samples ($\chi^2_r = 22.8, P < 0.001$; Fig. 1). Strong population growth of these species resulted mainly from large proportions of early-instar juveniles.

**Spatial studies** – In the field studies of spatial distribution in Altenheim between 1993 and 1996, average species richness increased ($\chi^2_r = 36.5, P < 0.001$) and average total densities decreased ($\chi^2_r = 17.1, P = 0.009$) from the lowest softwood to the highest hardwood sites. In the sites studied later at a reduced spatial scale, species richness was lower in the lower softwood forests compared to the two higher-level sites ($\chi^2_r = 125.7, P < 0.001$; Fig. 2), while average densities were often highest in the mid-level upper-softwood sites ($\chi^2_r = 34.4, P < 0.001$; Fig. 2).

Community composition and structure differed in relation to average flooding intensity of the site. In Altenheim, the most frequently flooded lower-softwood sites were strongly dominated by hygrophilous (i.e. *Sminthurides* spp.) and hygrotolerant species (i.e. *I. palustris* s.l. and *S. aureus*; Fig. 3). In the mid- and upper-softwood sites, these species occurred in reduced populations while the populations of generalist and wetness-avoiding species (i.e. *I. minor*, *Protaphorura aurantiaca* and *Folsomia quadrioculata*) increased, resulting in more evenly distributed dominances. The less-intensely flooded hardwood forests, on the other hand, were dominated by flooding-avoiding (i.e. *Megalothorax minimus*, *Stenaphorurella denisi*) and intolerant species (i.e., *Parisotoma notabilis*, *Tomocerus baudoti*).

[Fig. 1] Direct effects of inundation. Impact of experimental flooding on species richness and total densities in samples from two different sites. Vertical dotted lines denote begin of inundation.

At the reduced spatial scale, the differences in inundation intensity were less dramatic between closely neighbouring sites. Nonetheless, with decreasing flooding intensity, similar shifts from hygrophilous communities, through balanced communities, to flooding-avoiding and –intolerant communities were observed (Fig. 4). Which species occurred dominant in the individual floodplain levels was, however, site specific.
Temporal studies – The communities within a site differed from year to year depending on inundation intensity. Species richness and total densities were strongly reduced in Leopoldshafen and Rastatt from the intensely flooded year 2002 to the dry year 2003 ($\chi^2_r = 23.6$ and $\chi^2_r = 102.5$, respectively, both $P < 0.001$; Fig. 2). In general, community composition and structure (as yearly averages) showed the strongest year to year changes (Fig. 4). Hygrophilous, hygrotolerant or generalist species dominated the communities in frequently flooded years. In years with minimal inundation, these species’ populations were reduced and – within the same site – wetness – avoiding and flooding-intolerant species dominated. In years with intermediate inundation, the communities consisted of mixtures of these species.

In-site community changes also occurred within a year, especially after strong inundation. For instance, in 2001 and 2002, species richness and density declined directly following inundation and increased within weeks after floodwater withdrawal ($\chi^2_r = 29.3$, $P < 0.001$ and $\chi^2_r = 32.3$, $P < 0.001$, respectively). Species dominances showed particularly rapid changes.

Fig. 2 Spatial patterns: species richness (top) and average densities (bottom), both as sampling date averages, in two to four small-scale gradients in three different years. Sites in each gradient range from lower softwood forests (l-SW) through upper softwood forest (u-SW) to lower hardwood forests (l-HW). Numbers below site designations indicate average inundation (in days).
following flooding events. Populations of hygrophilous, hygrotolerant species or the generalist I. minor increased strongly directly following inundation, decreasing again a few weeks after floodwater withdrawal ($\chi^2_r = 95.2, 82.8, 53.4$, respectively, all $P < 0.001$; Fig. 5). As these species’ proportions decreased, the populations of mesophilous, wetness-avoiding and flooding-intolerant species increased significantly ($\chi^2_r = 64.6, 12.5, 15.6$, respectively, all $P < 0.001$). In years with less inundation, i.e. 2003, these later species, but also floodplain untypical (»remaining«) species developed large populations and thus high dominances throughout the year ($\chi^2_r = 49.5, 40.4, 35.8, 49.2$, respectively, all $P < 0.001$; Fig. 5). Furthermore, in these dryer years, community differences between closely neighbouring sites diminished as the inundation differences decreased (Fig. 4). Moderate inundation in 2004 did not return the communities of the upper-level sites to hygrophilous communities (Figs. 4 and 5). Only in the lower softwood sites did hygrophilous, hygrotolerant and generalist species increase again.
These changes in species dominances also caused rapid changes in community structure, especially following strong flooding. Directly after inundation, especially high dominances of hygrophilous species caused very steep initial slopes of rank-abundance curves, which became smoother with time after floodwater withdrawal (Fig. 6). Recurring inundation caused renewed strong dominances of single species and thus steep initial slopes, which again became shallower with time as species richness increased and dominances became more even. These rank-abundance curves differed significantly (ANCOVA: F(6, 131) = 4.98, P > 0.001; Kolmogorov-Smirnov K = 1.59 – 1.73, P = 0.031 – 0.005). However, differences in niche-partitioning processes associated with these community changes were not evident, as the rank abundance curves of the different dates all fit best to Zipf-Mandelbrot community models (data not shown).
Nonetheless, niche differences between species were apparent. Using complete data from all studies, species showed different affinities especially for soil moisture, with population maxima at high, moderate or low moistures (Fig. 7), even though they usually occurred throughout the entire range of soil moisture. Closely related species often exhibited density maxima in different moisture ranges (Fig. 7).

Fig. 5  Temporal patterns: changes in community structure within different years in two upper softwood forests: Leopoldshafen (top), Rastatt (bottom). Vertical dotted lines indicate inundation events (numbers below lines indicate duration of inundation in days). For legend of species groups, see Fig. 4.
Fig. 6  Temporal patterns: community structure (as rank-cumulative dominance) after 2 flooding incidences (June and August 2002). Data from upper softwood forest in Leopoldshafen.

Fig. 7  Niche differentiation: abundances of different species against soil moistures. Data from all studies used for analyses; only a few species shown as examples.
**Metacommunity dynamics** – Dispersal and colonization mechanisms between sites varied between species. In the inundation experiments, strong population development especially of early-instar juveniles (i.e. of *Sminthurides* spp., *S. pumilis*, *S. aureus*, *I. minor*) even after weeks of inundation indicate hatching from flood-resistant eggs. Other species were regularly found on plant debris floating on the floodwater surface (i.e., *Sminthurides* spp., *P. aquatica*, *Friesea* spp., *Tomocerus* spp., *F. quadrioculata*). Using barriered pit-fall traps, no migration could be detected for some species (i.e. *S. pumilis*; Fig. 8). Others showed directional migration from dryer, upper-level sites to lower-level sites directly after floodwater withdrawal. Based on comparison with data from soil sampling above and below the trap complexes, some mesophilous and wetness-avoiding species were dispersing from high population densities into soils newly freed from floodwaters (i.e. *S. aureus*, *I. anglicana*, *I. palustris*), while other, hygrophilous species were migrating back into moister soils after being deposited into higher-level sites by inundation (i.e., *P. aquatica*, *S. aquaticus*, *S. malmgreni*; Fig. 8).

![Metacommunity responses of soil Collembola](image)

**Fig. 8** Dispersal: average activities in mini-pitfall traps (in individuals per trap per 2 weeks) on either side of a barrier (left: towards upper-level sites, right: towards sites recently freed from floodwater).
4. Discussion

Flooding is at first a disturbance for collembolan communities, causing significant reductions in densities and species richness. Collembola are generally capable of tolerating only short periods of inundation, with longer periods reducing densities by up to 90-100% (Beck 1972, Weigmann 1973, Zinkler & Rüssbeck 1986). However, populations can regenerate within a year, often only after six weeks, depending on flooding intensity (i.e. Palissa 1955, Wink 1971, Beck 1972, Russek 1984, present studies). Collembolan assemblages as a whole can therefore respond very resiliently to flooding, quickly regenerating the communities after the disturbance of inundation.

This resilience is based on the capability of, i.e., hygrophilous and –tolerant species to quickly develop populations following inundation, at times to densities beyond those before inundation. Only in very frequently flooded sites are total densities and species richness continuously suppressed. Regeneration is further facilitated by rapid dispersal of species into recently flooded sites, for which different mechanisms exist. Passive dispersal by floodwaters is especially important for hygrophilous species (Griegel 1999, present studies). A further, widely distributed mechanism is hatching from flood-resistant eggs present in soils or sediments (analogous to a seed bank) after inundation, i.e. in Sminthurides spp., Sminthurinus aureus, S. pumilis or I. minor (Beck 1972, Tamm 1984, 1986, Gauer 1997, present studies). Fluctuating water levels can thus disperse these species or their eggs throughout the floodplains. Some of these species have very short generation times (3 – 21 days: Palissa 1959, Blancquaert et al. 1981a, b), allowing very rapid population growth after recolonization. After frequent inundation, Collembolan communities thus apparently regenerate, at least at first, through the rapid colonization by and population development of a hygrophilous or –tolerant subset of the communities. These few species then develop strong dominances within the regenerating communities, leading to the strongly skewed community structures directly after inundation.

Conversely, wetness-avoiding and flooding-intolerant species were persistently affected negatively by inundation and were widespread only in infrequently flooded sites. Inundation pressure obviously imposes constraints upon the occurrence and development of these species. In less intensely flooded sites, on the other hand, the greater occurrence of these species-richer groups leads to significantly higher species richness. Although common in upper-level floodplain sites (Tamm 1982, Pichard et al. 1989, Farkas 1995, Griegel 1999), the population sizes of these species are nonetheless small compared to the strong populations of species-poor hygrophilous groups in frequently flooded sites. This results in the inverse relationship between densities and species richness in upper- and lower-level floodplains. Palissa (1959) and Lek-Ang & Deharveng (2002) similarly found species-poor, yet individual-rich hydrophilous community components in frequently flooded sites and non-hydrophilous components showing an inverse species-individuals relationship under low inundation pressure.

Between these two response extremes, generalist and mesophilous species are intermediary in their reactions to flooding, occurring in higher abundances in sites experiencing moderate inundation. These and many hygrotolerant species are euryoecous. Weigmann & Wohlgemuth-von Reiche (1999) call the ability of such species to develop individual-rich populations after medium intensities of inundation »opportunistics« and a »risk strategy«, since they quickly recolonize floodplains after inundation, but are strongly effected by renewed flooding.
Due to the inherent habitat heterogeneity of floodplains, inundation is spatially variable, with the same flooding incident affecting various sites differently and thus creating spatially different local conditions. The different and at times opposite population responses to different inundation intensities (Russell & Griegel 2006) leads to species sorting (Leibold et al. 2004). Depending on average inundation intensity, the species groups dominating in specific local sites then differ, which in turn causes differences in community composition and structure. A marked gradient can thus be regularly observed through different floodplain levels, even at very small spatial scales: from hygrophilous and -tolerant species dominating in very intensely flooded sites, generalist and mesophilous species being dominate in areas of medium inundation intensity, to wetness-avoiding and flooding-intolerant species dominating communities in the least flooded sites (Rusek 1984, Pichard et al. 1989, Čarnogurský et al. 1994, Griegel 1999, Sterzyńska and Ehrnsberger 1999, Russell et al. 2002).

Inundation also varies from year to year, so that local habitat conditions are temporally variable as well. The local communities follow these conditions, so that in-site community composition and structure also vary from year to year, depending on the hydrological regime. Further, after floodwater withdrawal, the hydrology of the soils alters, creating in-site environmental changes also at very small temporal scales. Again, the various response abilities of the different species groups result in short-term local community assembly following these habitat changes. The different community structures observed spatially thus also delineate the temporal phases of community regeneration after flooding, with initially abundant hygrophilous components reducing with time and, depending on inundation intensity, mesophilous or flooding-avoiding species increasing (Russell et al. 2004, Russell & Griegel 2006). These temporal changes are also attributable to the dispersal and colonization mechanisms during community assembly after inundation. For instance, slower or delayed population growth of non-hygrophilous species deposited with plant debris by floodwaters are likely. Recolonization of flooded habitats through active immigration from peripheral areas are probably ongoing processes (Frenzel 1936, Weigmann 1973). These temporal community changes are apparently due more to the differences in dispersal and population responses to hydrological conditions (= metacommunity dynamics) rather than changes in niche-appointment processes, since all the observed community structures fit similar models in the present studies. Finally, with much time after floodwater withdrawal or in dryer years, environmental conditions then become spatio-temporally more similar and dominance becomes determined more by comparable colonization-competition trade-offs (patch dynamics, Leibold et al. 2004). In the present studies, lack of inundation allowed species that had been negligible in heavily flooded years to develop strong populations and become dominant throughout many sites. Local community composition then became spatio-temporally more similar and β-diversity decreased.

The small-scale conditions in floodplain habitats thus periodically change dependant upon the hydrological regime and are highly variable. Due to the various physiological adaptations, population responses and dispersal mechanisms of the constituent species of the metacommunity, different species can become locally dominant, »drivers« (Walker 1992, 1995), at different times under different conditions. The differences found in local collembolan community structure and composition – deriving from the same (small-scale) regional species pool – are therefore a function of the high spatio-temporal habitat heterogeneity in combination with the metacommunity dynamics occurring in large
floodplain ecosystems. The variability in reactions among the species of the metacommunity enables the resiliency of the (spatially and temporally variable) local coenoses and, thus, functional stability of the collembolan communities as a whole in light of the recurring, yet variable disturbance of inundation.

5. References


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Appendix: Species included in the various ecologically isovalent species groups

**Hygrophilous species**
- *Podura aquatica* Linnaeus, 1758
- *Sminthurides aquaticus* (Bourlet, 1842)
- *Sminthurides malmgreni* (Tullberg, 1876)
- *Sminthurides signatus* (Krausbauer, 1898)
- *Sminthurides spec. juv.*

**Hygrotolerant species**
- *Isotomurus plumosus* Bagnall, 1940
- *Oligaphorura groenlandica* (Tullberg, 1876)
- *Sminthurides parvulus* (Krausbauer, 1898)
- *Sminthumurus aureus* (Lubbock, 1862)
- *Sphaeridia pumilis* (Krausbauer, 1898)

**Generalist species**
- *Anurida uniformis* Gisin, 1953
- *Isotomiella minor* (Schäffer, 1896)
- *Mesaphorura hygrophila* (Rusek, 1971)
- *Protaphorura aurantiaca* (Ridley, 1880)

**(Hygro-) Mesophilous species**
- *Arrhopalites acanthophthalma* Gisin, 1958
- *Arrhopalites caecus* (Tullberg, 1871)
- *Arrhopalites aleholvae* Rusek, 1970
- *Isotomurus palustris* (Müller, 1776)
- *Mesaphorura krausbaueri* Börner, 1901
- *Xenyllodes armatus* Axelson, 1900

**Wetness-avoiding species**
- *Dicrorytoma minuta* (Fabricus, 1783)
- *Folsomia candida* (Willem, 1902)
- *Folsomia quadriculata* (Tullberg, 1871)
- *Folsomia manolachei* Bagnall, 1939
- *Friesea mirabilis* (Tullberg, 1871)
- *Isotoma anglicana* Lubbock, 1862
- *Megalothorax minimus* Willem, 1900
- *Mesaphorura macrochaeta* Rusek, 1976
- *Stenaphorrella denisi* (Bagnall, 1935)
- *Stenaphorrella quadrispina* (Börner, 1901)
- *Xenyllodes armatus* Axelson, 1903

**Flooding-intolerant species**
- *Dicrorytoma fusca* (Lubbock, 1873)
- *Lepidocyrtus cyaneus* Tullberg, 1871
- *Neanura muscorum* (Templeton, 1835)
- *Onychiurus spinularius* Gisin, 1952
- *Parisotoma notabilis* (Schäffer, 1896)
- *Protaphorura armata* (Tullberg, 1896)
- *Pseudosinella alba* (Packard, 1873)
- *Tomocerus baudoti* Denis, 1932
- *Tomocerus minor* (Lubbock, 1862)
- *Tomocerus vulgaris* (Tullberg, 1871)