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Hydrobiont animals in floodplain soil: Are they positively or negatively affected by flooding?

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A B S T R A C T

Small metazoans in soil are typically animals of hydrobiont origin: They live in small amounts of water in capillaries and water film around soil particles. We studied the effects of occasional flooding on communities of soil Rotifers in the Gemenc floodplain (Duna-Dráva National Park). Based on the abundances of 31 rotifer species, an ordination determined flood frequency as a significant driving factor in rotifer development. The effect of flooding is stronger than seasonality or forest type. Many species establish populations only in never flooded (*Encentrum* sp., *Adineta gracilis*) or rarely flooded areas, while some species are present in sites flooded from time to time. Species populations showed a continuum on the given gradient with no species having their optimum on frequently flooded sites. The impact of flooding on communities is much more important than the effect of forest type or season. Significant species responses to the effect of flood frequency have been determined, which demonstrate an occupation of different niches of each species. Based on this sample of soil rotifers, it appears that aquatic animals in floodplain soil are negatively affected by floods in general. This effect is comparable with the effect of seasonal changes in the community, but is much higher than the effect of forest type or differences among replicate series.

1. Introduction

Metazoan organisms, obligately living in soil, may be split into two main ecological groups according to their relation to water. Hydrobionts are strongly dependent on the presence of liquid water in which they live. Typical groups of soil hydrobionts are nematodes, rotifers, tardigrades, planarians and enchytraeids (Dunger, 1964). However, soil is typically a three-phase system in which solid particles, water and gases are in dynamic equilibrium affected by external conditions. Flooding of soil may strongly limit gas diffusion and change oxygen conditions in relation to present temperature (Higgins and Thiel, 1988; Greenway et al., 2006). In contrast to the benthic environment, the space among solid particles in soil is not ordinarily filled with water in pores and such a situation may produce anoxic conditions and strong gas limitation for organisms (Lavelle and Spain, 2001). Periodic sediment deposition during floods is accompanied by flushing of organic litter and partially decomposed organic matter from the riparian sites and clearing away litter from the soil surface (Bilby, 1988).

Floodplains commonly represent a transition zone between the aquatic and terrestrial phases, with high biodiversity and having one of the most diverse fauna in the temperate region (Shiel et al., 1998). The high biodiversity is regulated just by the frequency and importance of flooding events. On the other hand, soil hydrobionts leave the substrate if flooded and in this case they can be washed away during a flood (Devetter, 2010).

Rotifers, mainly bdelloids, are animals typical of soil (Pourriot, 1979; Donner, 1980), although they are common in most interstitial and open-water environments. On the other hand, many species have been reported as being able to live in any habitat, from proper water bodies to the water film surrounding soil particles, mosses and lichens (Donner, 1965; Fontaneto et al., 2011).

Rotifers are known to have a cosmopolitan and wide-spread distribution. They are able to spread by wind as well as water in an inundated area (Jenkins and Underwood, 1998; Fontaneto et al., 2008). Parthenogenetic reproduction and an ability for anhydrobiosis of bdelloids helps them to survive most unfavourable conditions (Ricci, 2001) and predetermines them to be good in colonizing and highly resistant to many factors which may drive the development of a community (Ricci, 1987). However, real communities are not similar and highly differ from place to place (Donner, 1972; Francez, 1980; Devetter, 2007, 2009; Fontaneto

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et al., 2011), being determined by a weak, but significant species-specific preference of species.

We studied the effect of overflow on a typical soil hydrobiont community, rotifers living in soil of an inundation area of large river. Specifically, we tested the hypothesis that frequency of flooding events affects the rotifer community. In the present study, the following questions were tested: 1) Are soil rotifers influenced by flooding? Does this affect their diversity or abundance? 2) Do species reflect a gradient of flooding frequency? 3) What is the relative importance of season, the effect of natural as well as artificial forest type and the effect of flooding?

2. Methods

2.1. Sampling area

The Gemenc floodplain is located in Hungary on the right bank of the Danube, between river kilometres 1503rd and 1469th (Fig. 1). It covers 18,000 ha, making it the only notable floodplain of the Middle-Danube in the Carpathian basin (Berczik and Buzetzky, 2006). It is also one of the largest floodplains in Europe, with unique natural value (Zinke, 1996). Characteristic hydrological processes of a river-floodplain system are still well preserved. The 30 km long and 5–10 km wide area lies completely within a dam system on the river. The stream gradient is about 5 cm km^{-1} in the main arm, with a flow velocity of 0.8–1.2 m s^{-1} at mean discharge. Daily water level data of the main arm are measured on an official gauge at Baja (1477.9 rkm, N 46° 10′ 41.73″ E 018° 55′ 29.43″; zero-point: 80.990 over the Baltic Sea) (Fig. 1).

2.2. Rotifer sampling and processing

Sampling was done twice, on 2–3 June and 19–20 October 2010 using a hierarchical design. At each sampling time, we sampled four series of sites in two types of lowland forests: Two replicate series with four plots each, were sampled in near natural lowland forests and two series in hybrid poplar plantations. In each series, samples were taken in four plots situated at 580, 615, and 800 cm elevations related to the official gauge at Baja and differently threatened by flood. Site I is situated behind the dike and never flooded by river water (Fig. 1, Table 1). We also determined the time in days spent from the last flooding of a given site in which the former community may regenerate. In each plot, three random replicate samples were taken within a distance of 3 m from each other to determine population variability. In total 48 samples were taken per sampling date. Rotifer samples were taken with a 10 cm^2 cylindrical soil corer down to a depth of 10 cm. Each sample was placed in a separate plastic bag and stored in a refrigerator. Samples were processed as soon as possible in random order, but not later than one month after collection to prevent changes in the community. The content of each bag was gently homogenized in the lab and a proportion of the material (10–20 g) was subjected to extraction. Rotifers were extracted from soil to distilled water using the L-C extraction method (Devetter, 2010). Living specimens were determined and counted using a counting chamber. The keys of Bartoš (1959) and Donner (1965) were used for species identification. Nomenclature followed Segers (2007). Water content of fresh soil samples were measured by the gravimetric method, while conductivity and pH in distilled water were measured in the lab. The character of each soil type was similar in all sampling sites as long as fluvial sediments with very similar granularity was present. Soil pH ranged from 6.9 to 7.8 and conductivity ranged from 84 to 381 μS cm^{-1}. In total, 96 samples were analysed.

Table 1
Characterization of sampling sites according to flood frequency. In each series, samples are taken in four plots situated in different elevation related to official gauge at Baja and differently threatened by flood.

Sites	Flooded if water is over	2–3. June	19–20. October	Flooded days in 2010 (%)	Flooded days in 2003–2010 (mean)
I.	Never	Dry	Dry	0 (0%)	0 (0%)
II.	800 cm	Dry for 329 days	Dry for 125 days	9 (3%)	3.9 (1.1%)
III.	615 cm	Dry for 5 days	Dry for 39 days	41 (14%)	22.6 (6.2%)
IV.	580 cm	Flooded	Dry for 38 days	53 (18%)	30.0 (8.2%)

2.3. Statistical analyses

A couple of statistical methods were used to process the data. Multivariate analysis was conducted by the direct, partial redundancy analysis method, using CANOCO (4.5) (ter Braak and Šmilauer, 1998), in three steps: 1) Forward selection of environmental variables and Monte-Carlo permutation test (999 permutations) were used to determine the proportion of variability explained by each variable and its significance. 2) The effects of the gradient of flooding events and season on the rotifer community was analysed if the effect of replicates, parallel gradients and forest type were partialled out as covariables. 3) Species – response curves were fitted using general linear models using a unimodal response. Data were log-transformed in all cases. In the ordination diagrams, the species were labelled by the first three letters of the generic and first three letters of the specific names.

Nested ANOVA was used to analyse the effect of season, forest type, parallel gradients and gradient of flooding risk on general

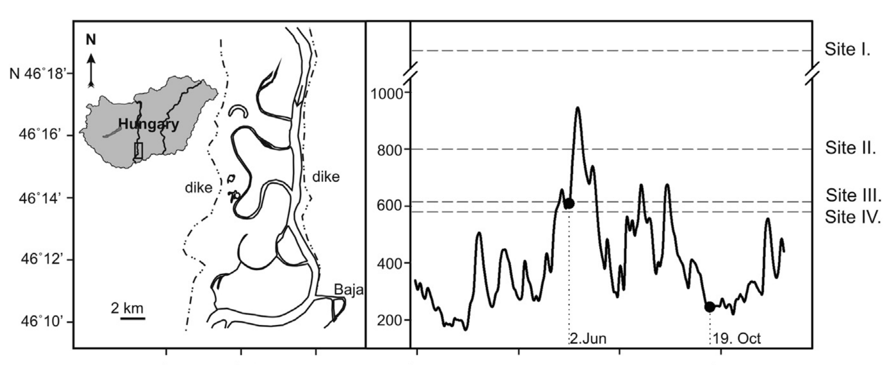

Fig. 1. Map of the Gemenc floodplain with variation of water level in 2010 and elevation of sampling sites.