

Managing plant species diversity under fluctuating wetland conditions: the case of temporarily flooded depressions

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Abstract Temporarily flooded depressions in arable fields support populations of specialised plant species that are affected by flooding and agricultural management. Depending on the degree of flooding, different proportions of wetland and arable species contribute to the seed bank. This is reflected by high inter-annual variations in plant communities with a high conservation value. Due to ongoing agricultural intensification, the biodiversity of temporarily flooded depressions has declined, and several plant species have become regionally extinct. Because seed banks harbour persistent seeds over long periods, they play a crucial role in the conservation and restoration of temporary wetland vegetation. This study focuses on the effects of different flooding regimes on plant species emerging from seed banks of temporarily flooded depressions in arable fields

in northeast Germany. We cultivated soil samples from upper and lower wetland zones under short, intermediate and long-term flooding (5, 15 and 40 cm above soil surface) in a common garden experiment over 2 years. We observed significant changes in species composition depending on the flooding duration. Species richness declined and evenness increased with increasing flooding duration. Upper and lower zones showed similar species richness and evenness, but species compositions differed. Red List species emerged from all treatments although the species differed, indicating that all communities emerging under different flooding regimes have a high conservation value. Seed banks under fluctuating site conditions can constitute a series of alternating plant communities. This could be used to develop management strategies that benefit different communities with high conservation values.

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Keywords Temporarily flooded depressions · Conservation management · Flooding regime · Rare plant species · Soil seed bank · Therophytes

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Introduction

Seed banks have great potential for the conservation and restoration of degraded habitats because they may contain seeds of regionally extinct species (Bernhardt et al. 2004; Poschlod 1993). Particularly, in ecosystems with environmental fluctuations, many species only emerge periodically and they can survive these

unfavourable periods in the seed bank (Poschlod et al. 1999). The dynamics of fluctuating systems favour contrasting plant communities depending on the site conditions, and the seed bank will reflect these different communities. Adaptive management may facilitate the establishment of a series of alternating communities, thus, maximising plant diversity over time. Many conservation studies have assessed the soil seed bank and its importance for the conservation and restoration of wetlands in agricultural landscapes (Bissels et al. 2005; Casanova 2012). In the prairie pothole region and in coastal plain depressions in the United States, for example, several studies have focused on different approaches to restore the natural vegetation after long-term agricultural use of these wetlands (De Steven et al. 2006; Galatowitsch and van der Valk 1996). Other studies focused on restoring wet meadows after long periods of intensive (arable) land use, using the soil seed bank (Bekker et al. 2000; Hölzel and Otte 2004; van Dijk et al. 2007). However, studies assessing the soil seed bank of temporarily flooded depressions in arable fields in temperate climates have so far been rare (Bissels et al. 2005).

Because of the intensification of agricultural management, many regions that formerly harboured a great variety of species specifically adapted to traditional farming practices have experienced a considerable decline in arable plant species diversity in the past decades (Burrichter et al. 1993; Meyer et al. 2013; van Zanten et al. 2014). One example is wet field depressions that have been ameliorated by more efficient drainage. Many arable and amphibious plant species are adapted to disturbance and variable site conditions through the development of a long-term persistent seed bank (Brock 2011; Thompson et al. 1998). In temporarily flooded fields, both regular arable weeds and wetland plants are found in the seed bank (Albrecht 1999; Bissels et al. 2005). Thus, the soil seed bank of such sites can harbour complementary plant communities that markedly exceed the species diversity in the apparent vegetation.

In large parts of Europe, deforestation during the medieval age promoted the development of wet field depressions due to rising ground water. This led to the flooding of local depressions, where colluvial clay deposits inhibited water infiltration of Klafs et al. (1973). Such man-made wetlands also developed in abandoned marl or clay pits (Day et al. 1982). As habitat quality has deteriorated due to widespread

drainage, the biodiversity of these habitats has markedly declined and many plant species are threatened by the loss of flooding and water level fluctuations (Zacharias and Zamparas 2010). Moreover, climate change is expected to have a negative impact on temporarily flooded depressions as the weather is predicted to become more extreme with mild wet winters and hot dry summers (IPCC 2007). This may shorten the flooding duration, which is a disadvantage for plant species that require flooding for germination (e.g. Kwon et al. 2013). Conversely, precipitation is predicted to become more uneven and more intense (Madsen et al. 2009), which could benefit species assemblages dependent on temporarily flooded depressions (Kappelle et al. 1999). Thus, new concepts are needed to preserve the vegetation of these habitats.

The actual vegetation that develops in temporarily flooded depressions in arable fields depends on agricultural management, soil and climatic conditions (Pinke et al. 2014). Most importantly, the species diversity of these depressions is affected by the flooding regime (Casanova and Brock 2000), controlling germination via soil temperature and light and oxygen concentrations (e.g. Matsuo et al. 1984). At the initial stage of secondary succession, competition is low, and most species best establish under terrestrial conditions, as long as the soil moisture is sufficient. Only submersed macrophytes and those with floating leaves are unable to survive at terrestrial sites, and most of them cannot establish without inundation (Baskin and Baskin 2014). During flooding, the depth of a waterbody can affect water plant germination through daily changes in light availability and temperature (Pons and Schröder 1986). High water levels and a long flooding duration promote the establishment of water plant species, whereas a short flooding duration is more advantageous for terrestrial species. During the draw-down, amphibious and terrestrial plant species can emerge under damp but not flooded conditions. An intermediate flooding duration with a slow drawdown or slowly rising water levels throughout a vegetation period can stimulate a sequence of water plant, amphibious plants or terrestrial species. Thus, the highest species diversity is expected under intermediate flooding. Moreover, as temporary wetlands harbour many rare and endangered plant species (Casanova and Brock 1990; Lentz and Dunson 1999; Lukacs et al. 2013; Mann and Raju 2002; Pukacz et al. 2009), the number of Red List species will increase concurrently

with flooding. Species evenness is often negatively correlated to species richness (Weiher and Keddy 1999). In aquatic ecosystems, the limited availability of light and chemical growth factors can significantly limit competition by reducing the productivity of dominant species (Li et al. 2015; Slivitzky 2002). In contrast, this may also reduce species richness by excluding species without appropriate adaptations. However, as dominance is reduced and most of the remaining species find conditions suitable in which to establish, we expect that species are more likely to be equally abundant and that evenness will increase based on the intensity of flooding. In the lower wetland zone, where flooding occurs more frequently over a longer duration than in the upper wetland zone, seeds can accumulate in the soil because the germination of most species is inhibited under anaerobic conditions (Saatkamp et al. 2014). Moreover, as flooding gradients lead to differences in species composition in the apparent vegetation (Keddy and Reznicek 1986), a similar pattern can be expected in the composition of the soil seed bank. Thus, we expect the soil seed bank to reflect the flooding history of the different wetland zones.

In this study, we investigate how soil seed banks in upper and lower wetland zones of temporarily flooded depressions reflect the past flooding regime, and how flood management could be used to create a series of different plant communities. We analysed the species diversity of plant communities emerging from soil samples in experiments with different flooding durations and water levels. Specifically, we hypothesise that (i) plant communities emerging from the seed bank are different along a flooding gradient, both in the upper and lower zones of temporarily flooded depressions, (ii) seedling densities emerging from the seed bank are highest under intermediate flooding, particularly in samples from the lower zone, (iii) species richness of the seed bank will decrease with flooding in samples from the upper zone, (iv) species evenness is highest at high flooding in both zones and (v) the number of rare species increases with flooding.

Methods

Study sites and seed bank sampling

Soil samples were collected at Parstein, northeast Germany (northeast of Berlin, 53°0′52N, 13°59′E,

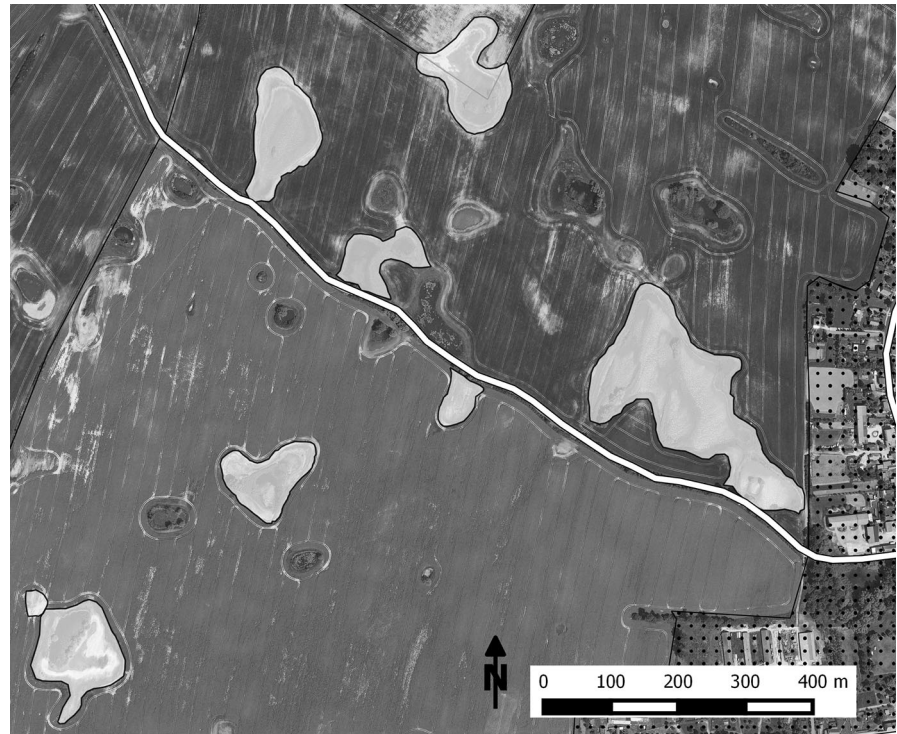
55 m above sea level). This region is characterised by a temperate, humid climate with an average annual temperature of 9 °C and 500 mm precipitation (1981–2010; DWD 2014); one-third of the precipitation occurs in the summer. The glacial moraine landscape has fertile luvisols with an almost neutral soil reaction. Glacial processes and former land use has resulted in numerous wet field depressions with great differences in both the frequency and duration of flooding (Klafs et al. 1973). As natural and man-made depressions have many common ecological characteristics, we refer to both of them as ‘temporarily flooded depressions’.

All samples were taken from seven temporarily flooded field depressions within a 60-ha area. They were selected on the presence of *Elatine alsinastrum*, a rare and strongly endangered amphibious species (Landesumweltamt 2006; Lansdown 2014; Ludwig and Schnittler 1996). Due to the restricted distribution of this species and to facilitate field access and soil collection, samples were taken on one conventionally managed farm. According to information from the farmer, the arable fields are cultivated in a four-course crop rotation (winter barley, winter rape, winter wheat and maize) using a field cultivator and disc harrow (plough level 0.2 m) for soil tillage. Mineral NPK fertilisers and herbicides are applied depending on the nutrient needs of the individual crops and weed abundance. All temporarily flooded parts are cultivated if the water level and soil moisture content allow the use of machinery. In May 2012, the sizes of the waterbodies ranged from 0.3 to 4.2 ha with geographical distances between them of 0.2–1.0 km (mean 0.5 km; see Fig. 1).

As the vegetation at the edges of wetlands follows a clear zonation according to soil moisture and flooding (Keddy and Ellis 1985), we assumed that such a zonation also might exist in the seed bank composition. Therefore, we differentiated between the upper zone that was flooded until late May, and the lower zone that was flooded until late July.

In August 2012, we took soil samples from both of these zones. At depressions with permanently flooded core areas (marked by a shoreline with perennial plants like *Salix* spp. or *Phragmites australis*), the permanently flooded parts experienced a different disturbance regime than the arable fields. Therefore, we also presumed that there would be differences in the species composition of the soil seed bank and

Fig. 1 Position of the seven temporarily flooded depressions (*shaded areas*) within two arable fields. Aerial picture from Bing (2012)



excluded these parts from sampling. At each depression, 30 soil cores were randomly collected from both the upper and lower zones. Soil corers had a diameter of 3.3 cm, and samples were taken down to 20 cm, corresponding with the depth of ploughing practised on the farm. According to Gruber et al. (2010), regular tillage leads to an even seed distribution within this plough layer. The samples from each zone were combined and mixed thoroughly to remove any site-specific seed bank variation. This resulted in two composite samples, one from the upper and one from the lower zone, representing a contrasting flooding history.

Flooding experiment

To test the effects of different water levels and flooding duration combinations on the emergence of plant communities, the composite samples were transferred to a set of artificial outdoor water basins and split into different treatments. As the depressions in the study area were usually flooded in the winter, we also maintained the samples in flooded basins at that time. We defined the start of the vegetation period as

the first week with mean daily temperatures above 5 °C, which was early April in 2013 and early March in 2014. Usually, the upper zone of flooded field depressions dries up within approximately 2 weeks after the start of the vegetation period; in the lower zone, this takes approximately 8 weeks (Altenfelder, pers. obs.). Therefore, we selected flooding durations of 2 and 8 weeks. To examine the full gradient of possible flooding durations, we included a permanently flooded treatment (>16 weeks flooded) and an unflooded control (water level 15 cm below the soil surface). To test for the effects of different water levels, we established water levels of 5, 15 and 40 cm above the soil surface. Moreover, each water level was combined with the three flooding treatments of 2, 8 and >16 weeks. All combinations of flooding duration and water level resulted in 10 treatments that can be interpreted as gradients of flooding intensity.

For each treatment combination we used six replicates, resulting in a total of 118 plastic pots ($18 \times 18 \times 18 \text{ cm}^3$). Approximately, three quarters of each pot were filled with sterilised soil and covered with 2 cm of soil from the upper or lower zone. To evaluate seed contamination, we additionally set up

controls with autoclaved soil (four replicates per flooding treatment and six replicates for the unflooded control). Because *Epilobium* spp., *Juncus effusus*, *Lythrum salicaria*, *Sonchus arvensis* and *Taraxacum* spp. emerged from these pots we considered them as seed contaminants and excluded them from further analyses. Nomenclature follows Wisskirchen and Haeupler (1998) for vascular plants and Blümel and Raabe (2004) for charophytes.

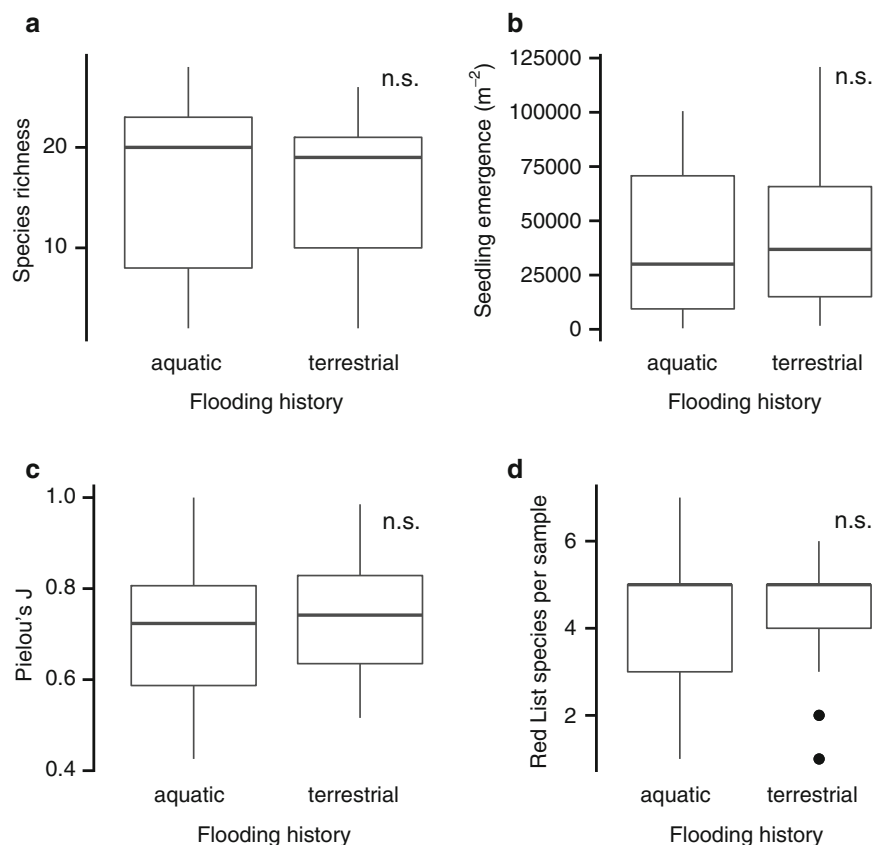
The experiment started in August 2012 and ran for 2 years, finishing in August 2014. All emerging seedlings were identified, counted and removed bi-weekly over the whole study period. Soil was mixed when seedling emergence declined. Plants that were difficult to identify were grown until they could be identified to species. Within the *Alisma plantago-aquatica* group, three different taxa occurred; however, as most individuals did not flower, it was impossible to determine their abundance. The Red List of the Federal State of Brandenburg (Kabus and Mauersberger 2011; Landesumweltamt 2006) was used to assess the conservation values of plants emerging from the soil samples.

Data analyses

Seed numbers were calculated by extrapolating the numbers of seeds detected in the surface area of the soil cores to 1 m². Two pots of the upper zone (2 weeks at 40 cm; permanently flooded 40 cm) were lost during the experiment and had to be removed from the analyses.

Response variables were species richness, evenness of seedling communities and number of Red List species as a measure of the conservation value. These variables could not be transformed to achieve a normal distribution. Therefore, we performed Kruskal–Wallis tests using the package agricolae (de Mendiburu 2014) in R (R Core Team 2013) to determine the effects of water level and flooding duration on soil samples. As there was no significant difference in seedling density, species richness, evenness and conservation value between the two wetland zones (Fig. 2), these zones were no longer distinguished in further analyses of diversity. To test for differences between the treatment combinations, group means were compared at the

Fig. 2 Species richness (a), seedling density (b), evenness (c) and number of Red List species (d) in the soil seed bank of the *upper* (aquatic) and *lower* (terrestrial) zones of temporarily flooded depressions in arable fields (Kruskal–Wallis test, $p < 0.05$)



95 % confidence interval level with Bonferroni corrections. Interaction effects were tested using dummy variables. As a measure for evenness we calculated Pielou's J ($J = H'/\ln s$), with $H' = -\sum p_i \times \ln p_i$, where p_i is the proportional abundance of species i and s is the number of species. To calculate the number of Red List species, we included those species with a Red List status of 'near-threatened', 'vulnerable', 'endangered' and 'critically endangered'.

To identify major gradients in species composition, a detrended correspondence analysis (DCA) was used (Hill and Gauch 1980). We preferred this method to non-metric multidimensional scaling (NMDS), even though both operations led to almost identical results (results of NMDS are not shown), because DCA fits species response curves to standard deviations and provides more detailed information on beta diversity along the first ordination axis. The effect of high seedling densities was reduced by square root transformation and subsequent Wisconsin double standardisation. To assess relationships between seedling composition and different water regimes, linear trends of water level, flooding duration and median Ellenberg indicator values for moisture (Ellenberg et al. 2001) were fitted on the ordination results. Both ordination and fitting of linear models were carried out using the R package *vegan* (Oksanen et al. 2013).

Results

Effects on diversity

During the 2-year sampling period, a total of 19,966 seedlings emerged from all samples. Seedling density was highest under no flooding ($74,282 \pm 15,015$ seedlings m^{-2} , mean \pm SD) or short-term flooding ($71,427 \pm 15,015$ seedlings m^{-2}). Density decreased with increasing duration of inundation (Kruskal–Wallis test: $H = 105.0$, $p < 0.0001$; Fig. 3). Under intermediate- and long-term flooding, there was an effect of water level with higher seedling densities at water tables of 5 cm compared with higher water levels within the same flooding duration treatment.

A total of 65 species emerged from the soil samples, nine of them are considered to be endangered according to the Red List of the Federal State of Brandenburg (see Online Resource 1). In total, 54 species emerged from soil samples from the upper zone and 60 from the

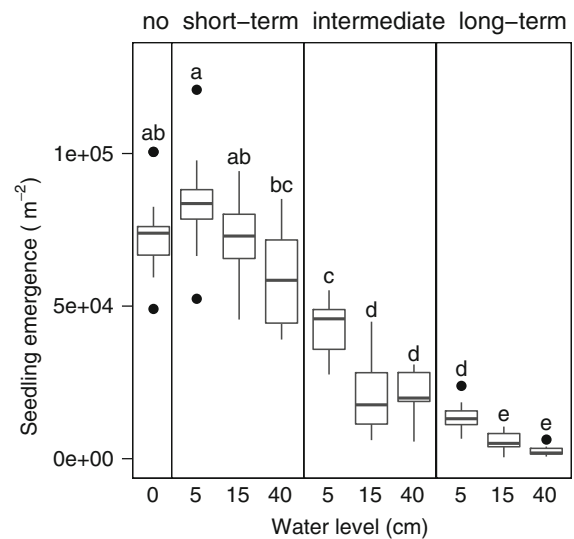


Fig. 3 Differences in seedling emergence from soil samples of temporarily flooded depressions in arable fields in response to experimental flooding. Lowercase letters indicate significant differences among groups according to multiple comparisons following a Kruskal–Wallis test ($p < 0.05$)

lower zone, with 49 species in common. The most abundant species were *Alisma plantago-aquatica* agg. and *Peplis portula*, both of which emerged from 93 % of all pots.

Species richness was highest under no and short-term flooding (22 ± 2 species per pot with no flooding and 22 ± 3 with short-term flooding). Flooding duration significantly reduced species richness (Kruskal–Wallis test: $H = 88.1$, $p < 0.0001$); water level had no effect on species richness (Fig. 4). Evenness significantly increased with increasing flooding duration (Kruskal–Wallis test: $H = 86.7$, $p < 0.0001$; Fig. 5), while water level had no effect on evenness.

The highest number of Red List species was observed under no or short-term flooding, as well as intermediate flooding with shallow water levels (no flooding: 5.1 ± 0.5 ; short-term flooding: 5.1 ± 0.6 ; intermediate with a water level of 5 cm: 5.2 ± 0.6 Red List species per sample). Increasing flooding duration significantly decreased the number of Red List species (Kruskal–Wallis test: $H = 67.9$, $p < 0.0001$; Fig. 6). Water level changed the number of Red List species under intermediate- and long-term flooding between 5 and 40 cm water levels. In the unflooded and temporarily flooded treatments almost all emerging Red List species were amphibious plants,

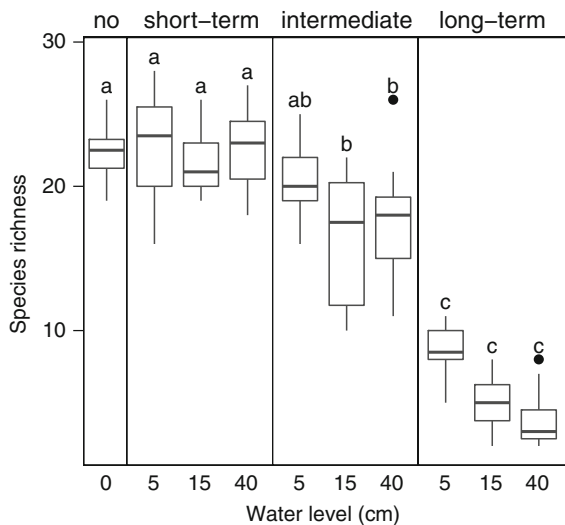


Fig. 4 Species richness in soil samples from temporarily flooded depressions in arable fields under experimental flooding. Lowercase letters indicate significant differences among groups according to multiple comparisons following a Kruskal–Wallis test ($p < 0.05$)

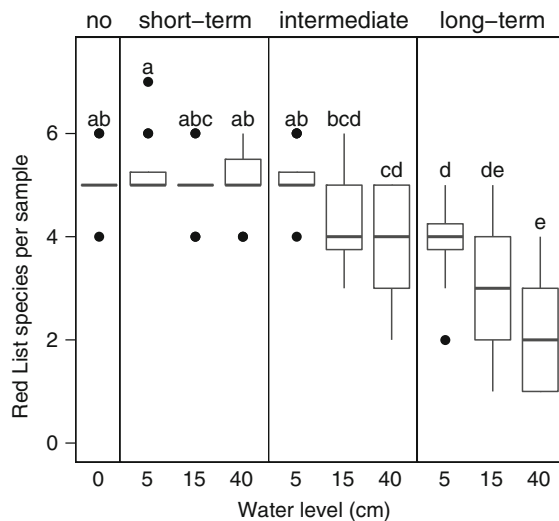


Fig. 6 Red List species emerging from soil samples of temporarily flooded depressions in arable fields under experimental flooding. Lowercase letters indicate significant differences according to multiple comparisons following a Kruskal–Wallis test ($p < 0.05$)

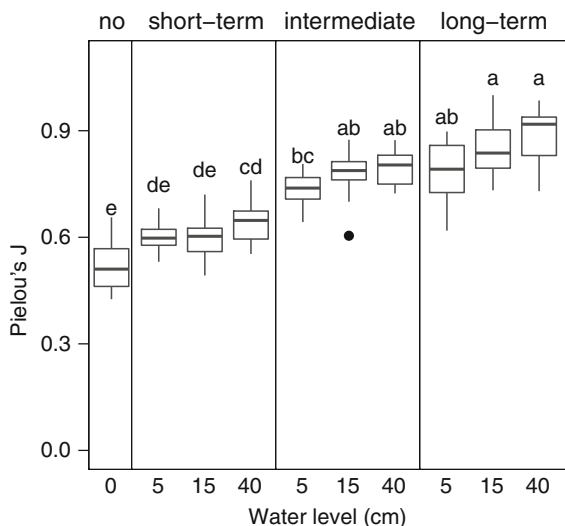


Fig. 5 Evenness of the species emerging from soil samples of temporarily flooded depressions in arable fields under experimental flooding. Lowercase letters indicate significant differences according to multiple comparisons following a Kruskal–Wallis test ($p < 0.05$)

including *Elatine alsinastrum*, *Limosella aquatica* and *Myosurus minimus*. Under permanent flooding these species also emerged but more rarely; instead, the threatened charophyte *Tolypella prolifera* exclusively emerged under intermediate or permanent flooding.

Variation in species composition along a flooding gradient

The gradient length of 3.7 along the first DCA ordination axis indicated an almost complete turnover in plant species composition emerged from the soil samples (Fig. 7). This change in species composition was mainly determined by differences between temporary and permanent flooding; few differences were observed among the unflooded and short- to intermediate-term flooded treatments. The gradient was closely correlated with flooding duration and indicator values for moisture ($p < 0.001$; Table 1). Along the second ordination axis the species composition changed according to the wetland zone ($p < 0.001$; Table 1). This gradient indicates that species composition among both wetland zones increasingly differed with flooding duration. The experimental water levels were not significantly correlated with the species composition.

Discussion

Effects on seedling abundances, diversity and conservation value

Contrary to our hypotheses, the seedling abundance and species richness were highest with no or short-

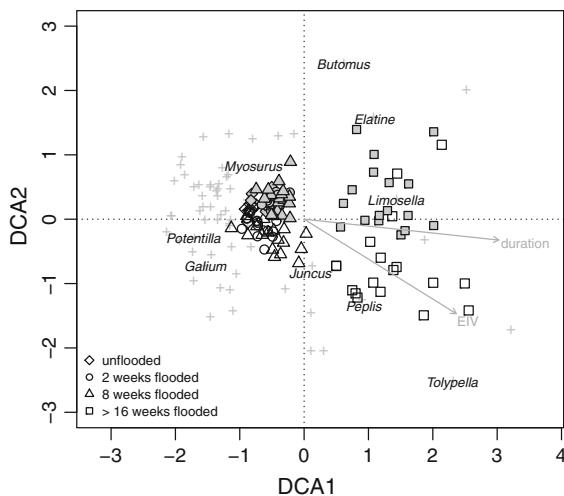


Fig. 7 Detrended correspondence analysis (DCA) of the species composition in soil samples responding to experimental flooding from the upper (filled symbols) and lower zones (transparent symbols) of temporarily flooded depressions in arable fields. Arrows indicate the correlation of flooding duration and the median Ellenberg indicator values for moisture (EIV moisture) to the ordination results from the linear models. The length of the arrows indicates the strength of the correlation. Different flooding durations are represented by different symbols; species without Red List status are represented by 'plus'. Full names of Red List species *Butomus umbellatus*, *Elatine alsinastrum*, *Galium palustre* agg., *Juncus tenageia*, *Limosella aquatica*, *Myosurus minimus*, *Peplis portula*, *Potentilla supina* and *Tolypella prolifera*

term experimental flooding. It made no difference whether samples came from the upper or lower wetland zone. This is in agreement with other studies, where the highest species richness was observed in unflooded samples (AponTE et al. 2010; Casanova and Brock 2000). The cause for these high numbers of seedlings and species establishing from the soil seed

bank is because both terrestrial and amphibious plant species find suitable germination conditions when flooding is short or absent, as long as competition is low. Furthermore, many amphibious plant species emerge in high numbers as soon as environmental conditions favour germination (Bliss and Zedler 1998; von Lampe 1996). Under flooded conditions, where temperatures are constant during day and night, most amphibious plants fail to germinate as they need diurnally fluctuating temperatures (Baskin and Baskin 2014; Poschlod et al. 1999). Furthermore, only few species are known to optimally germinate when they are submerged (Poschlod et al. 1999), and seedling densities are usually higher under unflooded conditions (Collins et al. 2013). Obligate water plants, which depend on continuous flooding, had a minor emergence in all treatments and, therefore, they did not significantly contribute to the species richness in the temporary flooded treatments.

In our study, evenness increased with flooding duration. This observation is consistent with the findings of Weiher and Keddy (1999) in riverine wetlands, where species evenness also increased with decreasing species richness and abundance. These results may be caused by increasing stress associated with the flooding duration. Thus, species unable to tolerate flooding are inhibited, and species richness decreases. The remaining stress-tolerant species are more likely to emerge with similar abundances leading to an increased evenness. As stress is usually associated with decreasing plant biomass and size (Grime 1979), competitive interactions could favour small-sized species contributing to plant communities with low species richness but high evenness, where all species present were equally uncommon (Bock et al.

Table 1 Relationship between flooding duration, median Ellenberg indicator value for soil moisture (EIV moisture), water level and wetland zone to the first two DCA axes

	DCA axis 1	DCA axis 2	R ²	p value
Flooding duration	0.994	−0.107	0.8	0.001
EIV moisture	0.850	−0.527	0.7	0.001
Water level	0.683	0.730	0.0	0.080
Upper wetland zone	0.034	0.301		
Lower wetland zone	−0.032	−0.291		
Wetland zone			0.1	0.001

p values are based on 999 random permutations. Bold p values indicate significant correlations

2007). In contrast, there are also studies that found inconsistent patterns for species richness and evenness (Soininen et al. 2012; Stirling and Wilsey 2001). They concluded that both measures of biodiversity depend on different and independent ecological processes. Thus, Ma (2005) related these patterns to a deviating response to soil conditions, i.e. C:N ratio and phosphorus concentration. However, in our study, such effects can be excluded because we thoroughly mixed the soil samples.

We used the number of Red List species as an indicator of the conservation value of the plant communities emerging from the soil samples. Other studies have shown that the conservation value of temporarily flooded depressions can be very high (Bell et al. 2012; Casanova and Brock 1990; Lukacs et al. 2013). Indeed, we also found endangered species in most of the soil samples. This indicates that the soil seed banks of temporary wetlands are an important reservoir for rare species, which can be activated for conservation purposes or used during the restoration of degraded sites. Faist et al. (2013) reported that rare species in the aboveground vegetation were more abundant in the seed bank in vernal pools in California, showing the potential for the future establishment of rare species from the seed bank.

As in other studies on the soil seed bank of wetlands (e.g. Aponte et al. 2010), a few species account for the main share of the seed bank, which is a common characteristic for this habitat type (Harper 1987). Some rare plants that are reported for the study area, i.e. *Schoenoplectus supinus* and *Chara baueri*, could not be found (Hoffmann 1996; Raabe 2009) although this might be due to their rarity and the limited amount of soil analysed. The differences in the number of Red List species between the different experimental flooding regimes were marginal, but all species groups from terrestrial, amphibious and water plants were included. This result indicates the favourable conditions to promote endangered species from different plant communities along a flooding gradient.

There were no differences in seedling abundance, diversity or conservation value between the upper and lower wetland zones. This shows that even in the areas that are less frequently flooded and farmed when dry enough, the diversity and conservation value are comparable with the more frequently and longer flooded lower wetland zone. The year in which our

soil samples were collected was at the end of several years of high precipitation, which resulted in regular flooding of the upper wetland zone and a lack of farming, except for soil tillage. Thus, the seed bank might have recovered from a prior phase of more regular farming. In semi-arid gypsum vegetation, Olano et al. (2012) observed that the soil seed bank can rapidly recover after disturbance, if the seed bank in the surrounding area is still intact. For the conservation management of such habitats, this suggests that populations of rare plant species can recover, as long as flooding recurs within a certain period. Consequently, supporting a fluctuating hydrological regime is crucial for preserving these rare species. In contrast, a changing climate and altering the flooding regime might lead to a further decline of temporarily flooded depressions and the related plant communities. In the Mediterranean region, the predicted decrease of precipitation (IPCC 2007) may lead to shortened hydro-periods that are likely to reduce the spatial extent of amphibious plant communities (Ghosn et al. 2010).

Species composition changes along flooding gradients

The emerging seedling communities were strongly differentiated by flooding duration, indicating that the seed bank of temporarily flooded depressions has the potential to promote different plant communities depending on the actual water regime. The increasing duration of inundation impaired the living conditions for terrestrial species and improved the establishment of water plants, and the gradient from temporary to permanent flooding caused a nearly complete species turnover. Similar to field studies, which observed a clear moisture gradient in the communities of temporarily flooded depressions (Altenfelder et al. 2014; Hoffmann 1996), the species composition of seed bank samples from the upper and lower wetland zones differed. This is consistent with findings of Aponte et al. (2010), who found a gradient in seed bank composition along a moisture gradient. Additionally, regular water level changes, transporting hydrochore seeds at the water surface or zoochorous dispersal by birds may contribute to this difference between the two wetland zones.

The experimental water level had no effect on the species composition, probably because flooding at any

depth provides constant temperatures under which only a certain set of species are able to germinate (Pons and Schröder 1986). It might also be that plant species react more strongly to light availability, which is not necessarily dependent on the depth of the water column (Wetzel 2001). Light availability can be affected by the turbidity of the water as well as by shading from vegetation cover. During our experiment, all ponds were mostly clear, and light availability was high even at the flooding level of 40 cm. This is consistent with seed bank analyses by Casanova and Brock (2000) who found minor effects of inundation depth on species composition in Australian temporary wetlands. There, depth had an effect in separating groups under waterlogged conditions or no flooding. Among treatments with fluctuating water levels there were no effects of inundation depth as in our experiment. As the influence of flooding depth on seedling establishment might have been of greater importance in turbid water, and as arable field depressions are often muddy, further investigations with water samples of standardised light transmissivities would be reasonable.

Management implications

Our results suggest that the most promising approach to establish and maintain a series of plant communities with high conservation values is to manage water level fluctuations. The most effective way to create diverse communities would be to realise the whole spectrum of flooding situations in a rotational order. According to our results, a short flooding duration leads to the highest species richness but evenness is highest under long-term flooding. Therefore, creating shallow zones around temporarily flooded depressions that can slowly dry up after flooding would benefit many plant species and prevent the dominance of a single competitive species. In contrast, it is important to create adequate conditions for water plants by ensuring that flooding takes place regularly. This can be done by preventing or removing drainage of temporarily flooded depressions. Of course, the flooding regime should particularly focus on the habitat requirements of the species in individual field depressions. To achieve wide species diversity, different field depressions should be included in corresponding programs.

Besides these management treatments that directly affect the depressions, more variable agricultural land use may improve the diversity of the ephemeral plant communities. Devictor et al. (2007) showed that soil tillage is an important management aspect that can enhance the species richness of these plant communities. Also, rare species that occur at temporarily flooded depressions are annuals, and they rely on regular disturbance by soil tillage (Online Resource 1). Setting aside these areas would lead to a rapid change in the species composition towards perennial communities suppressing rare plants (Hoffmann 1996). Furthermore, more restrictive applications of herbicides and fertiliser will improve the diversity of temporarily flooded depressions (Altenfelder et al. 2016). These conservation measures would provide suitable habitat conditions for different plant communities along a flooding gradient. They could enable the whole set of endangered species and rare communities to establish over a sequence of wet and dry years at the same location.

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Compliance with ethical standard

Conflicts of interest The authors declare that they have no conflicts of interest.

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