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RESEARCH ARTICLE

Hydrology regime and hydrology recruitment niche predict changes in plant community composition across a pond habitat

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Abstract

Questions: Niche differentiation is widely accepted as a key mechanism important for species coexistence. Seed germination and seedling survival were recognized as important contributors to niche segregation and could be a crucial filter for determining species' distributions and community composition. Only a little is known about the direct relationship between hydrology recruitment niche, hydrology regimes, and community composition. Therefore, the main aim of this study is to identify the changes in the composition of a pond community with respect to the hydrological regime and predict them by the recruitment niche of species.

Location: The Gloggere pond in the Altdorfer forest (47.848 N, 9.698 E, Ravensburg vicinity, Upper Swabia, Baden-Wuerttemberg, Germany).

Methods: A transect with 46 permanent plots was established throughout the Gloggere pond, and species percentage cover was recorded in September 1992–1995, 2006, and 2017. Pond drawdown was implemented in 1993. Sediment samples were collected in March 1995 across the transect, and a pot germination experiment with six hydrological treatments was performed. The hydrology recruitment niche from the seed bank germination experiment was compared with the field hydrology niche to show the importance of the hydrology regime for community composition.

Results: The hydrological regime determined the community composition in both the germination experiment and the field. Species-specific hydrology niche from the field correlated with species-specific recruitment niche measured in the germination experiment.

Conclusions: Our results support the importance of recruitment niche as a driver of community composition for pond areas. For understanding and predicting changes in plant community composition, it is necessary to combine knowledge about the recruitment niche and the ability of seeds' survival in the sediment along a hydrological gradient with knowledge about abiotic filters, biotic interactions, and species-specific traits. Recognizing the recruitment niche is useful for better predicting the effect of future environmental changes, especially in the context of climate change and conservation management.

1 | INTRODUCTION

Niche differentiation is widely accepted as a key mechanism important for species coexistence, especially on relatively small scales (Grubb, 1977; Tilman, 1982). The concept of niche differentiation explains species distribution along environmental gradients due to interspecific differences in the ability to gather resources or use different areas of the environment in the adult stage. Moreover, early recruitment processes such as germination and seedling survival were also recognized as contributors to niche segregation (Evans & Etherington, 1990; Kotorová & Lepš, 1999; Marca et al., 2021). Recruitment niche, that is, environmental conditions suitable for seed germination and seedling establishment, therefore determines later adult species distribution and, consequently, community assembly and diversity (Poschlod et al., 2013; Fraaije et al., 2015; Valdez et al., 2019).

In wetland ecosystems, the most important drivers to create recruitment niches are water fluctuation regimes (Keddy & Reznicek, 1986) and flooding–drying patterns and timing (Riis & Hawes, 2002; Fischer et al., 2021) caused by, for example, rain or pond management. Year-to-year variability and/or huge variability within one year is a feature of hydrological niches not shared by other resources, such as light or nutrients, that tend to change gradually (Silvertown et al., 2014). Wetland species are adapted to their environment and occur under different hydrological conditions (Blom, 1999; Jensch & Poschlod, 2008; Colmer & Voesenek, 2009). Successful recruitment is dependent not only on suitable environmental conditions but also on seed availability in the soil seed bank (Keddy & Reznicek, 1986; Poschlod et al., 2013; Poschlod & Rosbakh, 2018; Valdez et al., 2019). Therefore, plant community composition results from a series of processes (that is, seed production and dispersal, soil seed survival, germination, and seedling establishment) influenced by abiotic filters (mostly water regime in wetland ecosystems), biotic interactions, and species-specific traits (Larson & Funk, 2016).

For artificial ponds, human management and the use of the surrounding land are important drivers of pond macrophyte and mudflat plant diversity and distribution patterns (Akasaka et al., 2010; Fares et al., 2020). Artificial fishponds have been an integral part of the European landscape since the Medieval Age (Poschlod, 2017). They provide a range of economic and ecosystem benefits, such as water retention, food production, and biodiversity (Lhotský, 2010; Popp et al., 2019). They serve as islands in the agricultural landscape and accumulate species more or less individualistically (Edvardsen & Økland, 2006). Species can stay hidden in the soil seed bank for more than 50 or even 100 years (Poschlod & Rosbakh, 2018) and germinate when suitable conditions, especially light and moisture, but without standing water, appear (Baskin et al., 2004).

The main goal of this study was to determine how the water regime affects the plant community composition and whether the hydrological recruitment niche of species can predict changes in community composition under the different hydrology regimes. The species-specific hydrological recruitment niche was determined by a seed bank germination experiment and compared with the observed plant communities across a transect from the study area. The second goal was the long-term development of the pond macrophyte community. We asked three specific questions: (i) is the germination of seeds from the seed bank affected by the hydrology regime? (ii) Does a hydrological gradient across the pond correlate with the species-specific hydrological recruitment niche determined by the seed bank experiment? (iii) Is there any species turnover of the macrophyte community over a period of 25 years?

2 | METHODS

2.1 | Study area

The study area is located in the Altdorfer forest in the vicinity of Ravensburg (47.848 N, 9.698 E, Upper Swabia, Baden-Württemberg, Germany). The Gloggere pond is situated at 561 m a.s.l. on the Würm ice moraine wall of the Waldburg ridge of clay tufa without lime, measures 0.8 ha with a maximal depth of 2.8 m, was created by humans more than 200 years ago, and is used extensively for fish breeding. The first known summer drawdown was in 1993. The drawdown lasted seven months, from mid-March to mid-October. The pond area was not completely dry; the substrate remained more or less muddy. Before that, there was only drainage in winter, but not every year. The pond is fed by rainwater only (Poschlod et al., 1996). The pond area can be divided into an edge part which is terrestrialized (further referred to as the edge part), and an open-water area (further referred to as the pond part). The edge part was covered by reed plants, with *Carex elata* being the most dominant plant species. Depending on the elevation, *Phragmites australis* and herbs accompanied the reeds. The open-water area contained a species-rich, macrophytic aquatic flora with *Nymphaea alba* as the most dominant plant species (Figure 1).

2.2 | Field observations

A transect of 92 m in length was established throughout the pond, along which 46 permanent plots of 2 m × 2 m. The transect started and ended in the edge part of the pond, so 14 plots were in the edge terrestrialized zone, and 32 plots were in the open-water area (Figure 1; Appendix S3). Plots were arranged along a line and
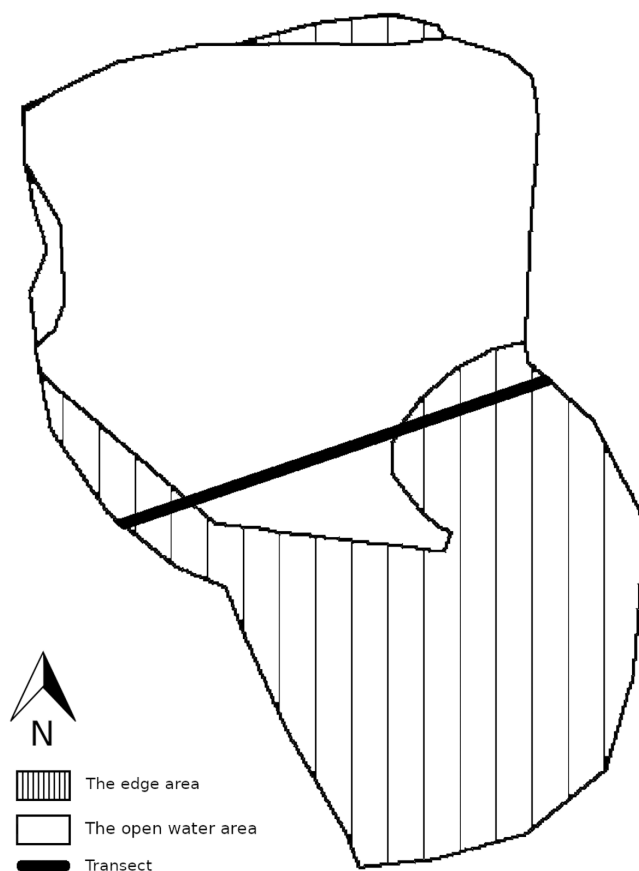
FIGURE 1 Gloggereweiher pond with the transect of permanent plots.

touched each other at the corner. If a plot was on the right side of the line, the next was on the left side, then again on the right side, etc. In September 1992–1995, 2006, and 2017 species percentage cover using the Braun–Blanquet scale was recorded (Appendix S1).

2.3 | Seed bank experiment

Sediment samples were collected in March 1995 from the flooded bottom of the pond across the transect. In total, 40 sediment samples of 1.5 L were taken along the transect. For taking soil samples a hemispherical metal instrument was used with a of volume 0.25 L. Each sample was located beside a transect plot, but only the plots of the open-water area were sampled. Samples were mixed well to achieve the evenest distribution of diaspores and distributed in equal proportions in plastic pots (diameter 27.5 cm, height 24 cm). The pots were filled with 9 L of a sterile composts + sand mixture first, over which 0.75 L of the sediment of the field site was applied to a thickness of about 1.3 cm because it is known that species of pond bottoms usually germinate in light conditions of the upper soil layer (Phartyal et al., 2020; Rosbakh et al., 2020). We used six treatments that differed in water level, with ten replicates for each treatment. Hydrological treatments were permanently dry to moist (water level approx. 20 cm below the surface), permanently wet (water level

near the surface), permanently flooded 10 cm above the surface, permanently flooded 40 cm above the surface, and two temporarily flooded treatments (pots were flooded 40 cm above the surface and then dried in June or August respectively). Permanent hydrological treatments were chosen to reflect different water conditions across the transect. Temporarily flooded treatments were chosen to test different possibilities in summer drawdown. A seed bank experiment was performed in water basins in the Philipps-University of Marburg Botanical Garden from March 1995 until October 1995. Germinated seeds were recorded and removed from the pots until no more seedlings appeared (Appendix S2).

2.4 | Data analysis

To display the differences in species composition across transects through the pond and their changes over time, we used non-parametric multidimensional scaling (NMDS) ordination as the most robust unconstrained ordination method (Minchin, 1987). NMDS uses plant occurrence data alone to identify the axes that best explain variation in plant species composition. NMDS does not assume linear relationships and also allows the use of any distance measure of the samples. We used the "metaMDS" function with Bray–Curtis distances from the *vegan* R package (version 2.5–7; Oksanen et al., 2020). The Braun–Blanquet cover–abundance scale was converted to the midpoint of the cover range. As environmental variables, we used year and water level as ordered factors (water level was set to 1 for plots from the pond part and 0 for plots from the edge part of the transect). For a detailed examination of community structure and its relationship to environmental variables, we performed two NMDS separately for edge and pond plots. As environmental variables, we used year and water level (water level was approximated as the distance from the pond's shore in the case of edge plots and distance from the center of the pond in the case of pond plots).

To investigate the impact of water level on species germination during the seed bank experiment, we performed NMDS with germination data in different hydrology treatments. We removed species with low total germination counts (three or fewer) from the analyses. We included the six treatments as unordered factors in the NMDS and additionally ordered them according to their water level (dry to moist — drainage June — drainage August — wet — Flooded10 — Flooded40) as an environmental variable. We used the "envfit" function from the *vegan* package to perform a permutation test for testing the significance of water levels to an established community.

To compare the field observations and seed bank experiment, we calculated Spearman correlations between the hydrological axes of the NMDS. We used the first NMDS axis for the field observations because the water level was projected nearly exclusively on this axis. For the seed bank experiment, we rotated the NMDS ordination based on the species position projected on the water level vector. We performed all statistical analyses in R software (version 4.1.2; R Core Team, 2021).

3 | RESULTS

3.1 | Field observations

We found 57 species in the above-ground vegetation across the transect — 39 species in the pond part, 47 species in the edge part, and 29 species (51%) shared among both parts. When we analyzed all plots together, the NMDS projected water regime (pond vs edge) mainly on the first NMDS axis and time mainly on the second NMDS axis (stress = 0.13; Figure 2). When we analyzed pond and edge plots separately, for pond plots, the NMDS projected time mainly on the first NMDS axis, whereas the distance from the pond center did not play a significant role in the vegetation composition (stress = 0.17; Figure 3a). For the edge plots, the NMDS projected distance from the shore of the pond mainly on the first NMDS axis and the time mainly on the second NMDS axis (stress = 0.13; Figure 3b). Species typical for forest and forest edges like *Alnus glutinosa*, *Brachypodium sylvaticum*, *Betula verrucosa*, *Dryopteris carthusiana*, *Eupatorium cannabinum*, *Fagus sylvatica*, *Hypericum maculatum*, *Picea abies*, *Rubus fruticosus*, and *Rubus idaeus* appeared in vegetation in 2006 and 2017 and slowly overgrew the part of the transect farthest from the pond. See Appendix S3 for details on species-specific changes in vegetation cover across time.

3.2 | Seed bank experiment

More than three seedlings were established during the experiment for 24 species (from 33 recorded species). Species composition significantly differs under the different water levels ($p < 0.001$, $R^2 = 0.66$). NMDS showed clear differences in germination under the flooded and non-flooded conditions (stress = 0.09; Figure 4). Dry and wet treatments were separated from each other, and the treatment drained in June was between these. A large number of species appeared in the three above-mentioned treatments; the largest was in the treatment drained in June (Table 1). Species unable to germinate under the flooded treatment, such as *Bidens* sp., *Carex* sp., *Cyperus fuscus*, and *Rorippa palustris*, germinated only in treatments without flooding or after early drainage. Both flooded treatments, as well as the treatment drained in August, clustered together. The flood level and drainage later in the season was only of little importance for seed germination in terms of the number of established seedlings as well as species composition. The number of species increased only a little after drainage in August compared to both flooded treatments (Table 1). The vector arrow from the ordered treatment indicates that the treatment as factor closely followed the assumed water gradient, except for the treatment drained in August.
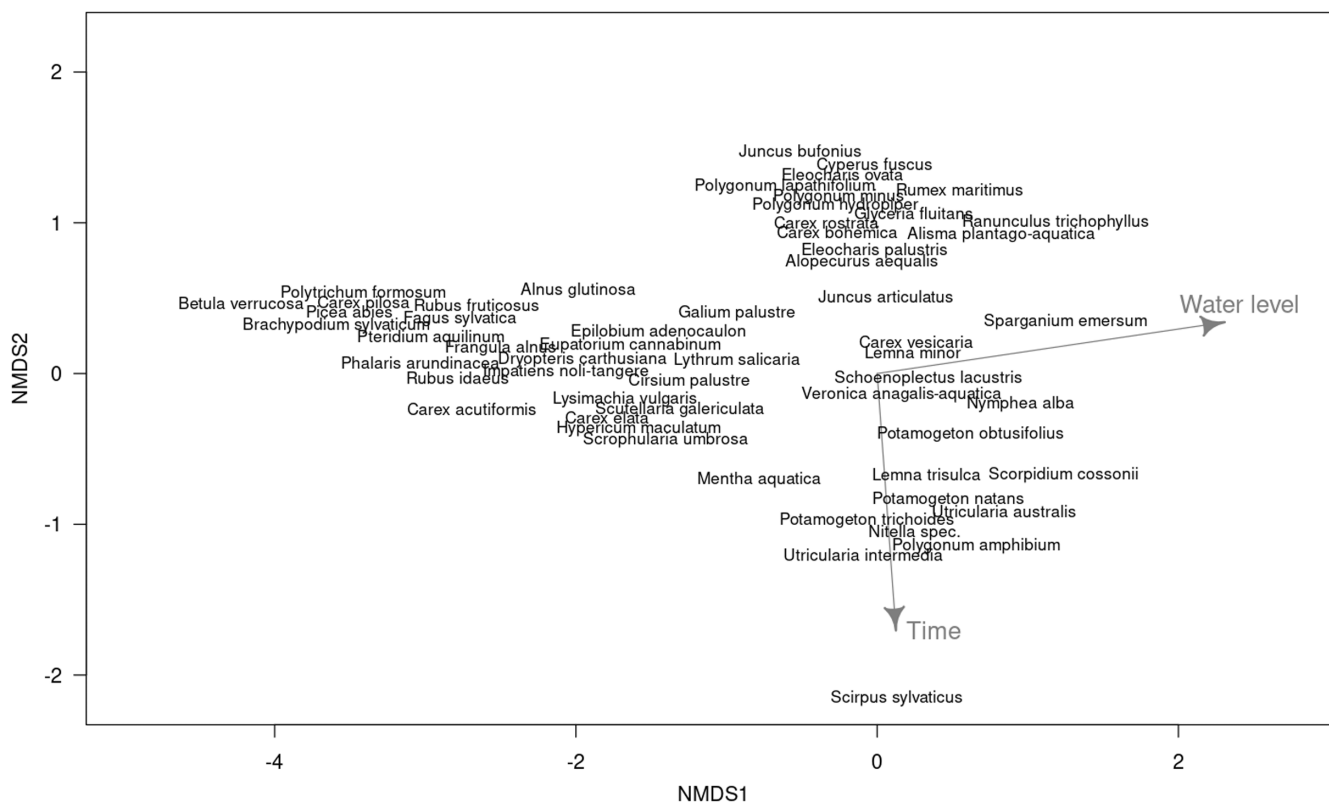

FIGURE 2 Non-metric multidimensional scaling ordination (NMDS) of species composition across the transect. Water level (water level was set to 1 for plots from the pond part and 0 for plots from the edge part of the transect) and time were fitted as environmental vectors (arrows).
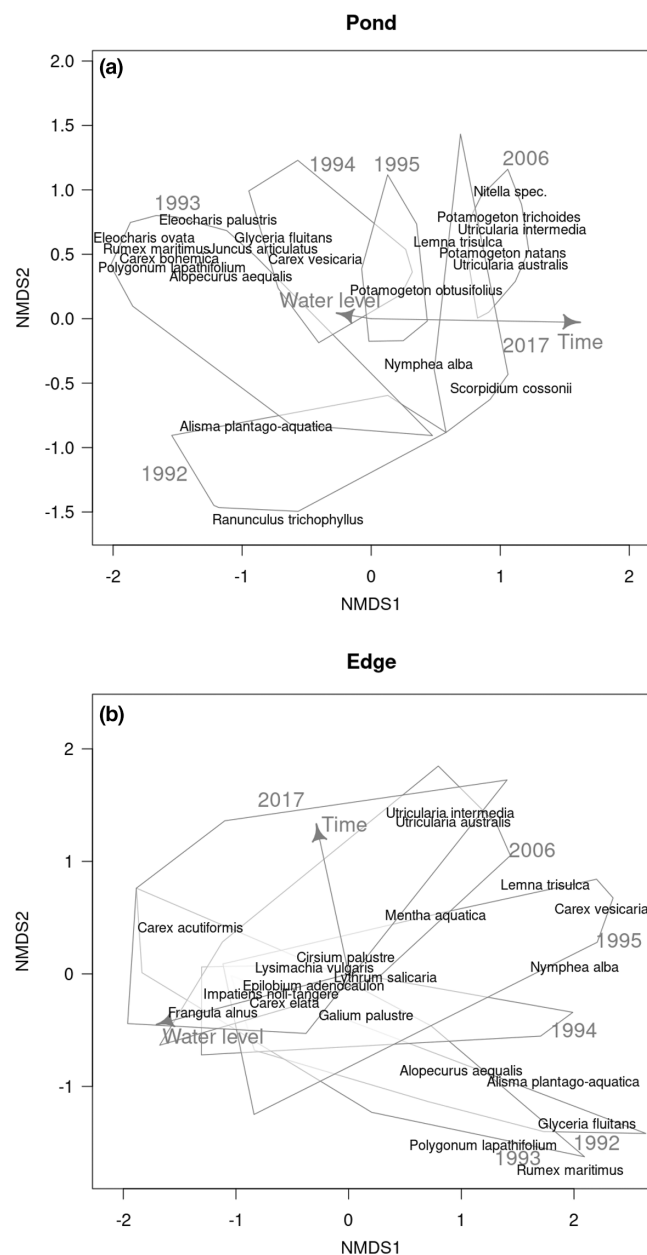
FIGURE 3 Non-metric multidimensional scaling ordination (NMDS) of species composition of pond plots (a) and edge plots (b) of the transect. Water level (water level was approximated as the distance from the shore of the pond in case of edge plots and distance from the center of the pond in case of pond plots) and time were fitted as environmental vectors (arrows). The twenty most abundant species shown.

3.3 | Comparison of field observations and seed bank experiments

We had 18 species in both experiments; six of these species were found only in pond plots, and 12 in both pond and edge plots. The species' NMDS hydrological position from the field observations was strongly correlated with the species' NMDS hydrological position from the seed bank experiment ($\rho = 0.705$, $p = 0.001$).

4 | DISCUSSION

We investigated the community composition of the Gloggereweiher pond area for 25 years. We showed the importance of the hydrological gradient for changes in community composition. The hydrology niche of species, measured from the field observations, and their hydrological recruitment niche, measured from the germination experiment in a controlled environment under the different hydrology regimes, were strongly correlated. Our findings confirm that the recruitment niche drives species composition in hydrological gradients, or that the recruitment niche of wetland species is very similar to their adult niche (Valdez et al., 2019). In both cases, species cannot be part of the community if environmental conditions are not suitable for their germination, even if they are part of a regional species pool (Jiménez-Alfaro et al., 2016).

Summer drawdown in 1993 had a strong effect on community composition in open-water plots. A certain group of species (*Carex bohemica*, *Carex rostrata*, *Cyperus fuscus*, *Eleocharis ovata*, *Juncus bufonius*, *Polygonum hydropiper*, *Polygonum lapathifolium*, *Rumex maritimus*, and *Sparganium emersum*) appeared only for one season during the drawdown in 1993. Except for *Carex rostrata* and *Sparganium emersum*, these species are annuals, dependent entirely on suitable germination conditions, which are light, alternating temperatures, and oxygen (Phartyal et al., 2020; Rosbakh et al., 2020). *Alopecurus aequalis*, *Carex vesicaria*, *Eleocharis palustris*, and *Juncus articulatus* also appeared in the open-water plots after the summer drawdown in 1993 but, in contrast to the species mentioned above, persisted in the vegetation for two or more seasons. They are perennial and can remain in the community for more than one season without regeneration via seeds. Nevertheless, none of them have appeared in vegetation in the last two samplings (years 2006 and 2017), indicating that more than one drawdown is necessary for their persistence in the community. *Schoenoplectus lacustris* appeared in the open-water community in the next two years, that is, in 1994 and 1995, but disappeared later. The changes in hydrology itself cannot explain this because *Schoenoplectus lacustris* is known as a perennial species of continuously flooded ecosystems. More likely, summer drawdown leads to changes in community composition, creating favorable conditions for this species during the next few years. Unlike the species that appeared after the summer drawdown, the macrophyte *Potamogeton obtusifolius* showed the opposite pattern and was not present in the open-water vegetation during the drawdown in 1993. Therefore, not annual but occasional summer drawdown leads to the highest diversity of pond community (Higgisson et al., 2018; Fischer et al., 2021).

Our study showed the unique long-term development of pond macrophytic vegetation over 25 years. To our best knowledge, the development of pond macrophytic vegetation has never been studied for such a long time. In 1992, before the summer drawdown, the macrophytic vegetation of the open-water area was dominated by only a few species (mainly *Alisma plantago-aquatica*, *Nymphaea alba*, and *Ranunculus trichophyllus*). After the summer drawdown in 1993, many species appeared, and species composition changed
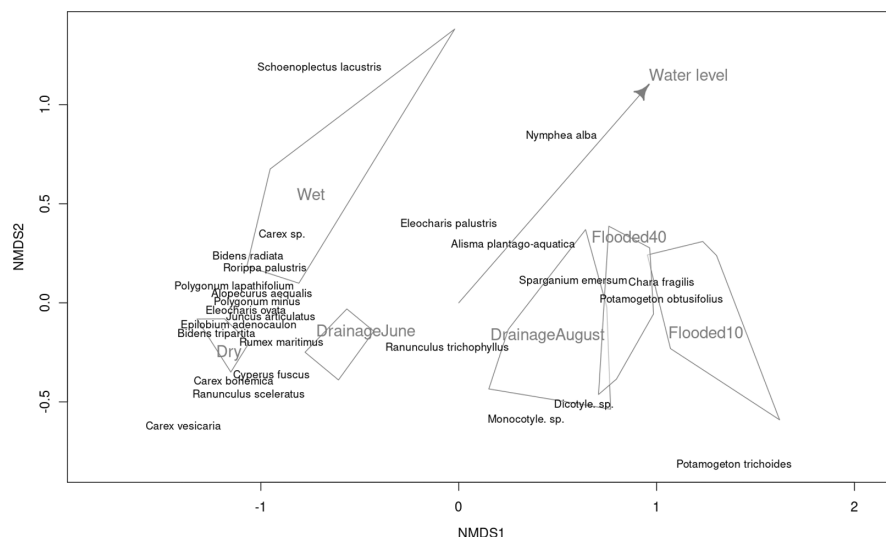
FIGURE 4 Non-metric multidimensional scaling ordination (NMDS) of the germination experiment. Different flooding treatments were represented as categorical variables (polygons) and fitted as an environmental vector (arrow).

TABLE 1 The number of species germinating in different treatments and the total number of seedlings established in all samples per treatment

Treatement	Number of species	Total number of seedlings
Dry (drainage March)	17	1570
Drainage June (flooded March to June)	22	1724
Drainage August (flooded March to August)	14	466
Wet	19	385
Flooded 10 cm	5	117
Flooded 40 cm	10	306

substantially (see above for details). Nevertheless, the number of species decreased over time. In 2006 and 2017, the vegetation was again dominated by a few species, mainly *Lemna trisulca*, *Potamogeton natans*, *Utricularia australis*, and *Utricularia intermedia*, that is, species with floating leaves, which can inhibit the presence of other species. Only *Nymphaea alba* remained in the vegetation throughout the observation period.

In contrast with the open-water community, the community composition of edge plots was only slightly affected by the summer drawdown. The hydrological gradient, that is, the distance from the pond shore, was indicated as the main driver of community composition — the farther the shore, the smaller the effect of summer drawdown. Changes over time were driven not only by the vegetation development after the summer drawdown but also by the surrounding vegetation. Species typical for forest and forest edges, including *Betula verrucosa*, *Dryopteris carthusiana*, *Eupatorium cannabinum*, *Fagus sylvatica*, *Picea abies*, *Rubus fruticosus*, and *Rubus idaeus*, appeared and slowly overgrew edge plots.

Huge differences between non-flooded and flooded treatments in the controlled-germination experiment demonstrate that hydrological conditions are the major environmental driver of germination for the investigated plant community. At scales of 10 or 40 cm, the water levels of flooded treatments played only a minor role, and mainly seedlings of species that grow as adults under submerged conditions, such as *Chara fragilis*, *Potamogeton obtusifolium*, *Potamogeton trichoides*, and *Sparganium emersum* established

there. In contrast, *Alisma plantago-aquatica*, *Eleocharis palustris*, and *Ranunculus trichophyllus*, that is, species that grow as adults in the water conditions, germinated in all treatments, which proves differences between adult and regeneration niches (Grubb, 1977). These findings are in accordance with previous studies (Facelli et al., 2005; Valdez et al., 2019) and emphasize the importance of a drawdown of water level for the germination of certain species. On the other hand, the timing of drainage played a substantial role in germination. Drainage in June allows germinating for the highest number of species, and the highest number of individual seedlings was found under this treatment. Drainage later in the season, that is, in August, had only a small effect on the number of germinated species and seedlings. NMDS projected this treatment closely to and partly overlapping with the other two flooded treatments. Day length could be responsible for this as a known mechanism to effectively restrict seed germination to favorable seasons (Densmore, 1997).

Our germination experiment confirmed that differences in water management lead to different community compositions, potentially impacting the restoration and conservation of artificial water ecosystems. Community assembly of non-natural habitats is often dependent on anthropogenic disturbances. Some species, considered threatened due to changes in anthropogenic impact during the last decades, can be present in the soil seed bank, survive there for a long time, and germinate under the appropriate management (Poschlod & Rosbakh, 2018). Fifteen out of 33 species germinating in the controlled experiment were never present

in the vegetation sampling, emphasizing the importance of persistence in the soil seed bank for these species. Understanding the species-specific requirements and their hydrological recruitment niche allows for designing appropriate management for target species or influencing community composition using different hydrology regimes. Therefore, the hydrological recruitment niche should be just as crucial for decision-making in restoration ecology as knowledge of population biology, genetics, and the impact of other environmental factors.

Only 46% of the species found in the vegetation of the pond germinated in the controlled experiment. There are several reasons for this relatively small overlap, which was also obvious in another experiment (Valdez et al., 2019). Sediment samples were not collected at the terrestrial edge of the pond since the focus of this study was on the vegetation of the terrestrialization and open-water zones in the pond. The main reason, however, may be that certain species have only a transient seed bank, such as, for example, *Lemna trisulca* and *Phragmites australis* among many others (Kleyer et al., 2008) which means they were not part of the seed bank of the sediment samples. This fact is often combined with clonality. Many wetland and aquatic species reproduce mainly clonally. Clonally reproducing species also produce only a very limited number of seeds, and processes such as seed germination and seedling establishment are irrelevant to their population dynamics (Eckert, 2002). Low amounts of seed may also be a reason. Some species in the sediment seed bank were probably not detected since we only collected 1.5 liters of sediment per plot throughout a single transect (Saatkamp et al., 2009). Finally, species could migrate to the transect later from the regional species pool. Seed reproduction can be of the same importance for them as for species germinating in our controlled experiment. Moreover, the dispersal strategy of these species cannot be neglected (Soons et al., 2017).

5 | CONCLUSION

Our study shows the unique long-term vegetation mapping of pond habitat and supports the importance of hydrological recruitment niche as a driver of community composition for pond areas. The highest plant diversity was only found during the first two years after the pond was drained in summer. This also corresponds with the highest plant diversity in the germination experiment in the treatment drained in June. Therefore, creating variable conditions for seedling recruitment is the driving force of plant diversity in this area. Understanding changes in plant community composition is necessary if the knowledge about the hydrological recruitment niche and the ability of seeds to survive in the sediment along the hydrology gradient is to be combined with knowledge about abiotic filters, biotic interactions, and species-specific traits. Recognizing the hydrological recruitment niche is helpful for better predicting the effect of future environmental changes, especially in the context of climate change and conservation ecology.

DATA AVAILABILITY STATEMENT

The data supporting the findings of this study are available in Appendix S1 and S2.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Percentage species cover recorded across the transect with 46 permanent plots using the Braun–Blanquet scale in September 1992–1995, 2006, and 2017.

Appendix S2. Numbers of seeds that germinated during the water basin experiment. Used hydrological treatments were permanently dry (water level approx. 20 cm below the surface), permanently wet (water level near the surface), permanently flooded 10 cm above

the surface, permanently flooded 40 cm above the surface, and two temporarily flooded treatments (pots were flooded 40 cm above the surface and then dried in June or August respectively).

Appendix S3. Percentage species cover across the transect and over time — the darker the green color, the higher the percentage cover of species in the given plot.