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# Effects of water regime and agricultural land use on diversity and species composition of vascular plants inhabiting temporary ponds in northeastern Germany

## Auswirkungen von Wasserstand und landwirtschaftlicher Nutzung auf Diversität und Artenzusammensetzung höherer Pflanzen an temporären Gewässern in Nordostdeutschland

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### Abstract

Fluctuations of the water level at the edges of temporary water bodies provide favourable living conditions for annual plant communities of the phytosociological class *Isoëto-Nanojuncetea*. Such communities of periodically flooded ponds within the agricultural landscape of NE Germany are particularly rich in rare plant species of that class. During the past decades drainage, fertilisation and herbicides in the surrounding arable fields have led to a severe decline in diversity of these species. To develop efficient conservation strategies it is essential to understand the factors driving the species composition. Therefore, we studied how varying water regimes, soil properties and agricultural practices affect the diversity and species composition of these temporary ponds.

The study was carried out in seven ponds on a conventionally managed farm in NE Brandenburg. At each of these wetlands mixed soil samples were taken to determine the pH, total nitrogen and phosphorus concentration. The plant species were recorded in 177 plots, each covering 1 x 1 m². For each plot, the water level was recorded in April, July and August 2013, respectively, resulting in five 'water level regimes'. Total species number and percentages of *Isoëto-Nanojuncetea* species were determined per plot, to evaluate water level effects on the vegetation. In addition, mean Ellenberg indicator values for light, moisture and nutrients were calculated to assess the environmental conditions.

Kruskal-Wallis tests with subsequent multiple comparisons showed significant differences between water regimes in both total species richness and percentage of *Isoëto-Nanojuncetea* species. *Isoëto-Nanojuncetea* species established best at sites with fluctuating water levels. Fitting environmental variables to NMDS ordination axes indicated that the water regime was the most significant factor for floristic variation. In plots with a more uniform water regime the species composition was explained mainly by the soil fertility. Farming practices showed less pronounced effects on species composition.

Our results suggest that maintaining water regimes with fluctuating water levels and keeping nutrient content low are crucial for the successful conservation of *Isoëto-Nanojuncetea* communities in arable landscapes.

**Keywords:** *Isoëto-Nanojuncetea*, kettle hole, NMDS, pond

**Erweiterte deutsche Zusammenfassung am Ende des Manuskripts**

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# 1. Introduction

Plants living at the shore of water bodies with dynamic water levels alternately have to cope with aquatic or terrestrial conditions. In Central Europe many species of these habitats belong to the class *Isoëto-Nanojuncetea* (ELLENBERG & LEUSCHNER 2010). One of the main factors differentiating the species composition of this vegetation are species-specific germination requirements. HEJNÝ (1957, 1962) divided the species of semi-terrestrial habitats into 'tenagophytes' (= plants of shallow waters) and 'pelochtophytes' (= plants of muddy littoral). Species of the first group are able to germinate in a completely flooded environment, whereas the latter preferably germinate in waterlogged soils. Additionally, the temperatures in water and soil affect the germination (PIETSCH 1999, CHYTRÝ & TICHÝ 2003, KIESSLICH et al. 2003). Small seed size, rapid germination, growth and reproduction under suitable conditions, and a long-term persistent seed bank are traits all species of semi-terrestrial habitats have in common (VON LAMPE 1996, THOMPSON et al. 1997, POSCHLOD et al. 1999).

Natural habitats of these communities are riverbanks and the edges of shallow lakes. In the cultural landscape the species can also colonize pig pastures, drained fish ponds and wet parts of arable fields (TÄUBER 2000). A common characteristic of these sites is the exclusion of competing plants by occasional flooding, tillage, trampling and uprooting animals.

During the past century this habitat type has experienced a severe decline due to the abandonment of traditional forms of land use and the reduction of flooding caused by more effective drainage (KALETTKA 1996, DEIL 2005). As a result, communities within the *Isoëto-Nanojuncetea* are threatened (RENNWALD et al. 2000), and many characteristic species are considered rare and endangered (LUDWIG & SCHNITTLER 1996).

To develop sustainable strategies to conserve this vegetation it is important to understand the individual habitat requirements of the respective species. To achieve a better understanding of the effects of water level dynamics on the species composition, we conducted a survey of seven ponds in an arable landscape of NE Germany. We address the following questions: (1) How does the flooding regime of the temporary ponds affect species composition and diversity? (2) Which flooding regime provides the most favourable conditions for species of the class *Isoëto-Nanojuncetea*? (3) How do farming and soil conditions influence the species composition? (4) Which management practices favour the establishment of rare and endangered *Isoëto-Nanojuncetea* species?

# 2. Materials and methods

### 2.1 Study area

The study was carried out in the year 2013 on two arable fields near Parstein, approx. 80 km northeast of Berlin, Germany (55 m a.s.l., 52°55'N, 14°02'E). This area is known for its rich flora of *Isoëto-Nanojuncetea* species (PIETSCH & MÜLLER-STOLL 1974).The area is part of the moraine landscape of the Pommern Stadium, which had been formed during the last glacial period (Weichsel). It is characterized by numerous kettle holes which are occasionally or permanently flooded. Most kettle holes in the study area presumably developed after the Mid Ages when extensive forest clearances induced soil erosion, which led to an accumulation of clayey impermeable layers in depressions and groundwater rise, because of reduced evapotranspiration after forest clearance (KLAFS et al. 1973). The water level of these so called 'pseudo-kettle holes' shows a particularly pronounced fluctuation. Here, glacial till formed fertile, alkaline Luvisols with almost neutral soil reaction.

The study area is characterized by a temperate, humid climate with a mean temperature of 8.3 °C and 532 mm precipitation (long-term mean from 1961–1990, weather station Angermünde; DEUTSCHER WETTERDIENST 2013a). The average temperature of the study year was 9 °C and had a precipitation of 483 mm (Angermünde; DEUTSCHER WETTERDIENST 2013b). Typical for the slightly continental climate are hot summers (longterm mean, 17 °C; 2013, 19 °C) with longer dry periods (longterm mean of summer precipitation, 177 mm; 2013, 165 mm) (DEUTSCHER WETTERDIENST 2013c).

We investigated seven temporary ponds with an area of 0.2–1.6 ha, scattered over an area of 60 ha (Fig. 1). To ensure comparability, all wetlands were situated within one farm that was conventionally managed.

### 2.2 Farming treatments

At the seven ponds, 177 sampling plots with 1 x 1 m$^2$ each were selected in summer 2012, based on to the occurrence of at least one of four characteristic species, i.e. *Elatine alsinastrum* L., *Limosella aquatica* L., *Myosurus minimus* L. and *Peplis portula* L. In autumn 2012, all plots were ploughed to ensure equal starting conditions, and excluded from agricultural management in the study year. To test the effects of different farming on species composition, combinations with and without crops, fertilization and herbicide applications, respectively, were randomly assigned to the plots and the corresponding treatment was applied manually. In addition, control plots without any management were established.

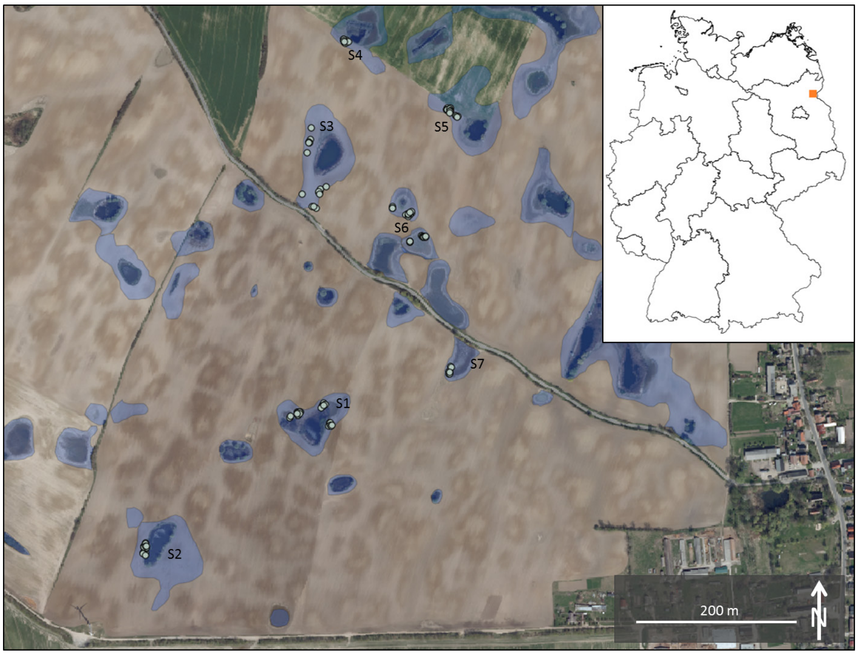


**Fig. 1.** Aerial picture of the study area with the seven wetlands (S1–S7) near Parstein in NE Brandenburg. The small map shows the location within Germany (orange dot). The blue shaded areas in the big map mark the highest flooding level of 2012 (digital orthophoto: LANDESVERMESSUNG UND GEOBASISINFORMATION BRANDENBURG).

**Abb. 1.** Luftbild des Untersuchungsgebietes mit sieben Gewässern (S1–S7) in der Nähe von Parstein in NO-Brandenburg. Die kleine Karte zeigt die Lage innerhalb Deutschlands (orange markierte Fläche). Die blau schattierten Flächen in der großen Karte markieren den höchsten Wasserstand von 2012 (digitales Orthophoto: LANDESVERMESSUNG UND GEOBASISINFORMATION BRANDENBURG).

Winter wheat was sown in autumn 2012 (200 kg $ha^{-1}$), herbicides were applied in spring 2013 (Diflufenican, Flurtamone, Diflufenican), and fertilizer (in total 160 kg N $ha^{-1}$) in three consecutive applications.

### 2.3 Vegetation sampling and nomenclature

Plant species composition within the 177 plots was recorded at the beginning of August 2013. On each plot all vascular plant species were recorded. In addition, percentage cover of the herbal layer was estimated and the mean height of the vegetation measured. The nomenclature of plant species follows WISSKIRCHEN & HAEUPLER (1998), for the phytosociological units OBERDORFER (2001); the assignment of individual species to phytosociological classes follows ELLENBERG et al. (2001). All vegetation samples and the environmental data are available in the electronic appendices S1–S7.

### 2.4 Environmental variables

To characterise soil conditions, one representative mixed sample of the plough layer (0–20 cm) was taken from each of the seven wetlands in summer 2012. The samples were air dried and sieved with a 2 mm sieve. Measurements were conducted at the Adam Mickiewicz University Poznań, Poland. There, the pH (determined in 100 ml deionized water) and the concentrations of organic and ammonia nitrogen (digestion in sulphuric acid and colourimetrical determination of ammonia after absorption in boric acid), phosphorus (extraction in hot acidic aqueous solution and determination by molybdate method), and potassium (digestion in hydrochloric acid and determination using atomic emission spectrometry) in soil were analysed. The summary statistics of the soil properties are given in Table 1.

For each of the plots the mean Ellenberg indicator values for light (L), moisture (F) and nutrients (N) were calculated (ELLENBERG et al. 2001). Additionally, the number of species typical for the phytosociological class *Isoëto-Nanojuncetea* was determined per plot. Plant species were classified as belonging to the *Isoëto-Nanojuncetea* based on ELLENBERG et al. (2001), when they are character species of any phytosociological group within the class (see Appendix S1).

The water level of each plot was assessed three times in 2013, i.e. in mid April, early July and early August, respectively. The observations were assigned to one of the categories 'moist', 'waterlogged' or 'flooded'. Plots were defined as moist, when the soil moisture was similar to the neighbouring arable fields. Waterlogged conditions were defined, when the soil was saturated but not covered by water. Plots with water level above the soil surface were defined as flooded. The observed combinations of water levels in April, July and August resulted in five 'water level regimes'.

### 2.5 Data analyses

The effects of water regime and farming practices on species richness were tested by carrying out Kruskal-Wallis tests with subsequent multiple comparisons of group means with Bonferroni correction to identify differences between the water level regimes. The tests were run using the package agricolae (DE MENDIBURU 2013) within the software environment R (R CORE TEAM 2013).

**Table 1.** Summary statistics of the measured chemical soil parameters of all seven wetlands.

**Tabelle 1.** Zusammenfassende Statistik der gemessenen chemischen Bodenparameter aller sieben Gewässer.

| | median | 95 % conf. interval mean | minimum | maximum |
|---|---|---|---|---|
| pH | 6.8 | ±0.01 | 6.8 | 7.0 |
| total nitrogen (mg $kg^{-1}$) | 1316 | ±176.89 | 1204 | 3920 |
| total phosphorus (mg $kg^{-1}$) | 33.3 | ±0.49 | 31.8 | 39.3 |
| potassium (mg $kg^{-1}$) | 78.5 | ±2.83 | 50.1 | 94.6 |

In order to reveal patterns of floristic composition and their relationship to the different water regimes Nonmetric Multidimensional Scaling (NMDS) was used, where Bray-Curtis dissimilarities described distances between the samples (MINCHIN 1987, FAITH et al. 1987). The ordination used three dimensions and was run with several random starts. Two plots (Ela38, Ela71) with only four and five species, respectively, were excluded from the ordination and model fitting.

To assess the environment-vegetation relationships linear trends and smooth surfaces of the environmental variables and the indicator values were fitted on the NMDS ordination. Generalized additive models were chosen to fit smooth surfaces with thin plate splines. The linearity of the relationship between environmental variables and the site scores was tested by comparing the coefficient of determination ($R^2$) of a linear model fitting and a generalized additive model fitting (GAM). If the $R^2$ of the GAM was higher than that of the linear model, a non-linear relationship with the ordination result was assumed (VIRTANEN et al. 2006). NMDS ordination and fitting of linear models was carried out using the R package vegan (OKSANEN et al. 2013).

## 3. Results

### Overall vegetation patterns

In total, 70 plant species were recorded at the study ponds, including 54 broad-leaved herbs and 16 graminoids (see Appendix S1); 39 species were annuals and 31 perennials. According to phytosociological categories, six species belong to the class *Isoëto-Nanojuncetea,* among them the 'critically endangered' *Elatine alsinastrum* and *Juncus tenageia,* and the 'endangered' *Ranunculus sardous* (LUDWIG & SCHNITTLER 1996). The most abundant species were *Tripleurospermum perforatum* (135 plots), *Polygonum aviculare* agg. (133), *Myosurus minimus* (116) and *Alopecurus aequalis* (100). Table 2 gives the mean frequencies of all species according to the five different water regimes.

### Effects of water regime on species richness

The highest number of species was observed in plots with fluctuating water level ('moist-waterlogged-moist'; see Table 3); plots with a more constant water level had significantly fewer species ('flooded-flooded-moist', 'moist-moist-moist'; Kruskal-Wallis test, $p < 0.001$). The highest percentage of annuals was found in plots that were not flooded in spring ('waterlogged-flooded-moist', 'moist-moist-moist', 'moist-waterlogged-moist'), while the highest percentage of perennials was observed in spring-flooded plots ('flooded-flooded-moist', 'flooded-waterlogged-moist'). Furthermore, *Isoëto-Nanojuncetea* species dominated also in plots with fluctuating water levels and which were waterlogged at least during parts of the growing season ('flooded-flooded-moist', 'flooded-waterlogged-moist', 'waterlogged-flooded-moist', 'moist-waterlogged-moist'; Kruskal-Wallis test, $p < 0.001$, see Fig. 2).

### Effects of farming practices on species richness

The effects of farming were less clear than of the water regime. The highest species numbers were recorded in plots with crops and no other treatment, whereas lowest species numbers were observed under combined treatments of crop, fertilizer and herbicide application, and crop and herbicide application, respectively (Kruskal-Wallis test, $p < 0.001$, Fig. 3A).

**Table 2.** Mean constancy (%) of all species according to their appearance on plots with different water regimes. Each column represents all vegetation relevés of one water regime. Species are ordered according to their phytosociological status. Abbreviations of water regimes: For abbreviation of water levels see Figure 2. Last column gives the abbreviations of species names used in the NMDS plot.

**Tabelle 2.** Mittlere Stetigkeit (%) aller Arten hinsichtlich ihres Auftretens in Plots mit verschiedenen Wasserstandsregimes. Jede Spalte gibt die mittleren Frequenzen der Arten in allen Flächen eines Wasserregimes wider. Die Arten sind nach Ihrer Zuordnung zu pflanzensoziologischen Klassen sortiert. Abkürzungen der Wasserregimes siehe Abbildung 2. Die letzte Spalte enthält die Abkürzungen der Artnamen, die im NMDS-Ordinationsdiagramm verwendet wurden.

| | **mmm** | **mwm** | **wfm** | **fwm** | **ffm** | Abbreviations |
|---|---|---|---|---|---|---|
| number of relevés | 120 | 6 | 31 | 5 | 13 | of species names |
| ***Chenopodietea* species** | | | | | | |
| *Tripleurospermum perforatum* | 87 | 83 | 81 | . | . | Tripperf |
| *Chenopodium album* | 33 | 33 | . | . | . | Chenalbu |
| *Conyza canadensis* | 16 | . | . | . | . | Conycana |
| *Geranium dissectum* | 16 | . | . | . | . | Geradiss |
| *Persicaria maculosa* | 9 | 83 | 10 | . | . | Persmacu |
| *Stellaria media* agg. | 7 | . | . | . | . | Stelmedi |
| *Capsella bursa-pastoris* | 6 | . | . | . | . | Capsburs |
| *Chenopodium polyspermum* | 1 | . | 3 | . | . | Chenpoly |
| *Sonchus arvensis* | 1 | 17 | . | . | . | Soncarve |
| ***Secalietea* species** | | | | | | |
| *Apera spica-venti* | 56 | . | . | . | . | Aperspic |
| *Fallopia convolvulus* | 46 | . | . | . | . | Fallconv |
| *Viola arvensis* | 37 | . | . | . | . | Violarve |
| *Anagallis arvensis* | 9 | 33 | 19 | . | . | Anagarve |
| *Vicia hirsuta* | 7 | . | . | . | . | Vicihirs |
| *Matricaria recutita* | 3 | . | . | . | . | Matrrecu |
| *Papaver rhoeas* | 3 | . | . | . | . | Paparhoe |
| ***Artemisietea* species** | | | | | | |
| *Urtica dioica* | 8 | 33 | . | . | . | Urtidioi |
| *Stellaria aquatica* | 3 | . | . | 20 | . | Stelaqua |
| *Artemisia vulgaris* | 3 | . | . | . | . | Artevulg |
| ***Molinio-Arrhenatheretea* species** | | | | | | |
| *Poa trivialis* | 10 | 17 | . | . | . | Poatriv |
| *Leontodon autumnalis* | 1 | . | . | . | . | Leonautu |
| *Myosotis scorpioides* | . | . | . | 80 | 62 | Myosscor |
| ***Agrostietea* species** | | | | | | |
| *Myosurus minimus* | 72 | . | 87 | 60 | . | Myosmini |
| *Agrostis stolonifera* | 56 | 50 | 32 | . | 15 | Agrostol |
| *Plantago major* ssp. *intermedia* | 48 | 100 | 68 | 100 | 8 | Planmajo |
| *Trifolium hybridum* | 13 | . | . | . | . | Trifhybr |
| *Rumex crispus* | 12 | . | 48 | 80 | 46 | Rumecris |
| *Ranunculus sardous* | 7 | . | . | . | . | Ranusard |
| ***Bidentetea* species** | | | | | | |
| *Alopecurus aequalis* | 52 | 83 | 48 | 100 | 100 | Alopaequ |
| *Rorippa palustris* | 30 | 83 | 55 | 60 | 38 | Roripalu |
| *Bidens frondosa* | 27 | . | 81 | . | 15 | Bidefron |

| number of relevés | **mmm** 120 | **mwm** 6 | **wfm** 31 | **fwm** 5 | **ffm** 13 | Abbreviations of species names |
|---|---|---|---|---|---|---|
| *Rumex maritimus* | 23 | 17 | 26 | . | 23 | Rumemari |
| *Rumex palustris* | 4 | . | . | 40 | 69 | Rumepalu |
| *Persicaria lapathifolia* | 3 | . | 13 | . | . | Perslapa |
| *Persicaria minor* | 2 | 33 | . | . | . | Persmino |
| *Bidens cernua* | . | 83 | 10 | . | 15 | Bidecern |
| *Potentilla supina* | . | . | 19 | . | . | Potesupi |
| *Ranunculus sceleratus* | . | 17 | . | 20 | . | Ranuscel |
| ***Isoëto-Nanojuncetea* species** | | | | | | |
| *Peplis portula* | 25 | 100 | 94 | 100 | 85 | Peplport |
| *Limosella aquatica* | 17 | . | 68 | 100 | 8 | Limoaqua |
| *Gnaphalium uliginosum* | 14 | 50 | 39 | . | . | Gnapulig |
| *Elatine alsinastrum* | 3 | 100 | 10 | 60 | 23 | Elatalsi |
| *Juncus bufonius* | 3 | 50 | 52 | . | . | Juncbufo |
| *Juncus tenageia* | . | . | 3 | 60 | . | Junctena |
| ***Phragmitetea* species** | | | | | | |
| *Phalaris arundinacea* | 8 | . | . | . | 8 | Phalarun |
| *Lycopus europaeus* | 4 | 83 | . | . | 8 | Lycoeuro |
| *Scutellaria galericulata* | 3 | . | . | . | 8 | Scutgale |
| *Oenanthe aquatica* | 3 | 50 | . | 80 | 92 | Oenaaqua |
| *Phragmites australis* | 1 | . | . | . | . | Phraaust |
| *Alisma lanceolatum* | . | 67 | 29 | 100 | 92 | Alislanc |
| *Epilobium parviflorum* | 3 | 33 | 39 | 20 | 8 | Epilparv |
| *Alisma plantago-aquatica* | . | . | 32 | 100 | 100 | Alisplan |
| *Bolboschoenus maritimus* | . | . | . | 20 | . | Bolbmari |
| *Eleocharis palustris* | . | . | . | 20 | 15 | Eleopalu |
| *Sparganium erectum* | . | . | . | 60 | 77 | Sparerec |
| *Typha latifolia* | . | . | . | 40 | 8 | Typhlati |
| **Other classes:** | | | | | | |
| *Polygonum aviculare* | 87 | 83 | 61 | 40 | 15 | Polyavic |
| *Echinochloa crus-galli* | 55 | 100 | 87 | . | . | Echicrus |
| *Poa annua* | 49 | 17 | 94 | . | . | Poaannu |
| *Elymus repens* | 40 | . | 3 | . | . | Elymrepe |
| *Cirsium arvense* | 8 | . | 3 | 20 | . | Cirsarve |
| *Taraxacum officinale* agg. | 8 | 17 | . | . | . | Taraoffi |
| *Veronica arvensis* | 7 | . | . | . | . | Veroarve |
| *Lysimachia vulgaris* | 4 | . | . | . | . | Lysivulg |
| *Persicaria amphibia* | 4 | . | . | . | 46 | Persamph |
| *Medicago lupulina* | 2 | . | . | . | . | Medilupu |
| *Juncus articulatus* | 2 | 17 | . | . | . | Juncarti |
| *Tussilago farfara* | 1 | . | . | . | . | Tussfarf |
| *Vicia sepium* | 1 | . | . | . | . | Vicisepi |
| *Trifolium campestre* | . | . | 10 | . | . | Trifcamp |

**Table 3.** Annual, perennial and total species numbers (mean ± SD) and numbers and percentage of *Isoëto-Nanojuncetea* species (I-N) under different water regimes. For abbreviation of water levels see Figure 2.

**Tabelle 3.** Anzahl annueller und ausdauernder Arten, sowie Gesamtartenzahl (Mittelwert ± SD) und Anzahl und Anteil der *Isoëto-Nanojuncetea*-Arten (I-N) bei verschiedenen Wasserregimes. Abkürzungen der Wasserregimes siehe Abbildung 2.

| Water regime | | annual | perennial | total | I-N species | I-N species (%) |
|---|---|---|---|---|---|---|
| mmm | (*n* = 122) | 7.5 ± 2.3 | 2.9 ± 1.3 | 10.4 ± 2.9 | 1.1 ± 1.3 | 9.8 ± 10.8 |
| mwm | (*n* = 6) | 10.2 ± 1.3 | 5.2 ± 1.8 | 15.3 ± 1.9 | 4.0 ± 1.1 | 25.8 ± 5.0 |
| wfm | (*n* = 31) | 9.2 ± 2.0 | 3.0 ± 1.5 | 12.2 ± 2.5 | 3.5 ± 1.1 | 29.1 ± 8.3 |
| fwm | (*n* = 5) | 6.2 ± 1.5 | 7.6 ± 1.3 | 13.8 ± 2.6 | 4.2 ± 0.8 | 30.5 ± 3.3 |
| ffm | (*n* = 13) | 3.9 ± 1.5 | 6.0 ± 1.2 | 9.9 ± 2.0 | 1.2 ± 0.8 | 12.3 ± 7.5 |

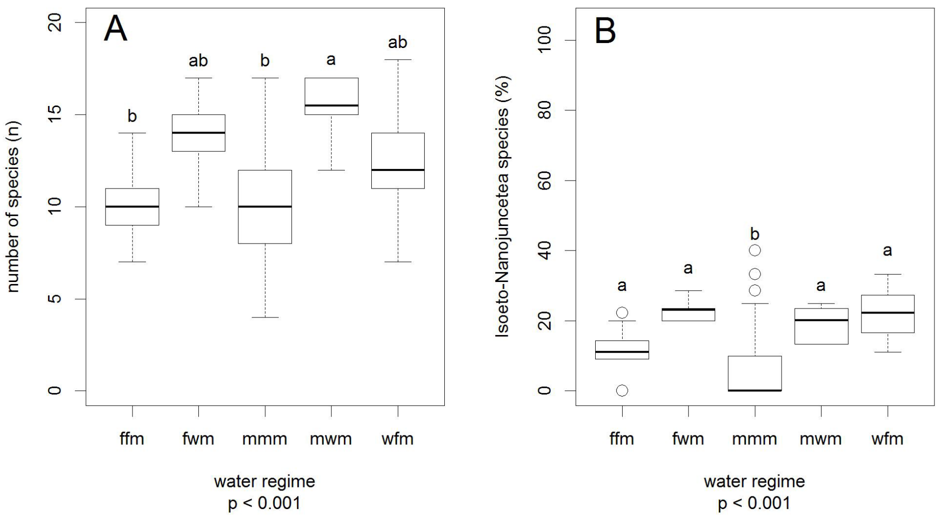


**Fig. 2.** Boxplots of number of species (A) and percentage of *Isoëto-Nanojuncetea* species (B) under different water regimes (multiple comparisons, α = 0.05). Lowercase letters indicate differences between groups. Abbreviations of water levels in April-July-August: mmm, moist-moist-moist; mwm, moist-waterlogged-moist; wfm, waterlogged-flooded-moist; fwm, flooded-waterlogged-moist; and ffm, flooded-flooded-moist.

**Abb. 2.** Boxplots der Gesamtartenzahl (A) und des prozentualen Anteils der *Isoëto-Nanojuncetea*-Arten (B) bei verschiedenen Wasserregimes (Multiple Mittelwertvergleiche, α = 0,05). Kleinbuchstaben zeigen Unterschiede zwischen den Gruppen an. Abkürzungen der Wasserstände (April-Juli-August): mmm – feucht-feucht-feucht; mwm – feucht-wassergesättigt-feucht; wfm – wassergesättigt-überflutet-feucht; fwm – überflutet-wassergesättigt-feucht; und ffm – überflutet-überflutet-feucht.

The proportion of *Isoëto-Nanojuncetea* species was highest in plots with only herbicide application. The lowest proportions were found in plots with fertilization as well as with combinations of crop and fertilization, crop and herbicide application, fertilization and herbicide treatment, respectively (Fig. 3B).

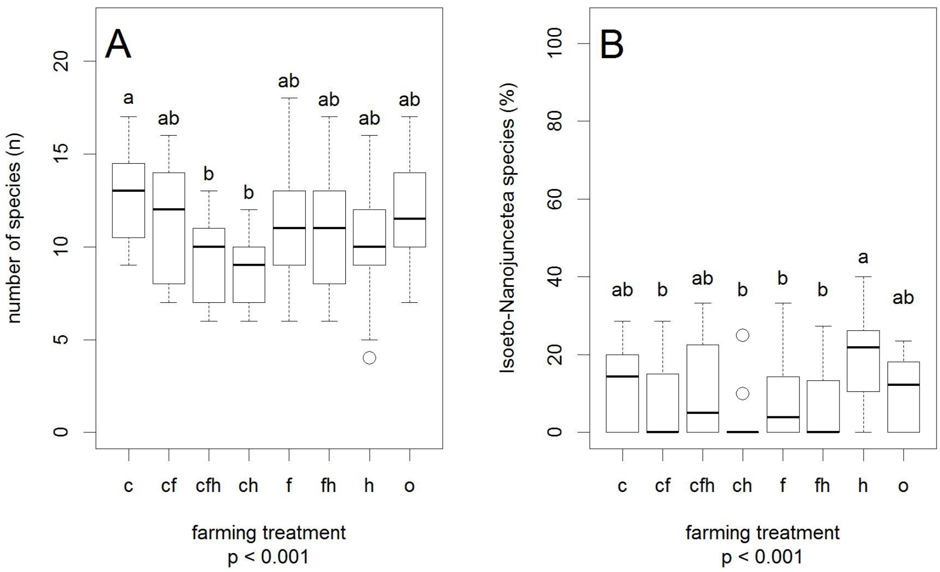


**Fig. 3.** Effects of farming practices on the total number of species (A) and on the percentage of *Isoëto-Nanojuncetea* species (B). Lowercase letters indicate differences between groups. Abbreviations of treatments: c, crop; cf, crop and fertilizer; cfh, crop, fertilizer and herbicide; ch, crop and herbicide; f, fertilizer; fh, fertilizer and herbicide; h, herbicide; and o, control without treatment.

**Abb. 3.** Auswirkungen der Bewirtschaftungsmaßnahmen auf die Gesamtartenzahl (A) und den prozentualen Anteil von *Isoëto-Nanojuncetea*-Arten (B). Kleinbuchstaben kennzeichnen Unterschiede zwischen den Gruppen. Abkürzungen der Behandlungen: c – Kultur; cf – Kultur und Düngung; cfh – Kultur, Düngung und Herbizid; ch – Kultur und Herbizid; f – Düngung; fh – Düngung und Herbizid; h – Herbizid; und o – Kontrolle ohne Bewirtschaftung.

### Effects on species composition

Nonmetric Multidimensional Scaling (NMDS) mainly ordered the sampling plots along a moisture gradient (Fig. 4). Species belonging to arable plant communities (*Secalietea cerealis*, *Chenopodietea*; Fig. 5) represented the largest group and were mostly located on the left hand side of the ordination, representing drier sites, which were never flooded, and therefore allowed the development of typical arable plant communities. Most of them were common weeds which indicate regularly managed arable fields (*Apera spica-venti*, *Chenopodium album* agg., *Echinochloa crus-galli, Tripleurospermum perforatum*). The species plotted in the upper right and in the centre of the ordination represented a mixture of plants belonging to frequently disturbed (*Isoëto-Nanojuncetea*, *Bidentetea tripartitae*) and unfrequently disturbed communities of temporary ponds (*Agrostietea stoloniferae*). Species adapted to permanent flooding (*Phragmiti-Magnocaricetea*), like *Alisma plantago-aquatica* and *Sparganium erectum*, were displayed at the lower right.

Figure 6 shows an overlay of the NMDS ordination with the fitted vectors and smoothed surfaces for the mean Ellenberg indicator values and plant height. The strongest linear correlation to the ordination space ($R^2$ = 0.90) was found for soil moisture values. The values in Figure 6A represented a gradient from moderate soil moisture at the left (mean 5.5) to values of 9 indicating wet sites at the right side of the plot. As the mean Ellenberg indicator value for light was highly correlated with the mean indicator value for moisture ($R^2$ = 0.68,

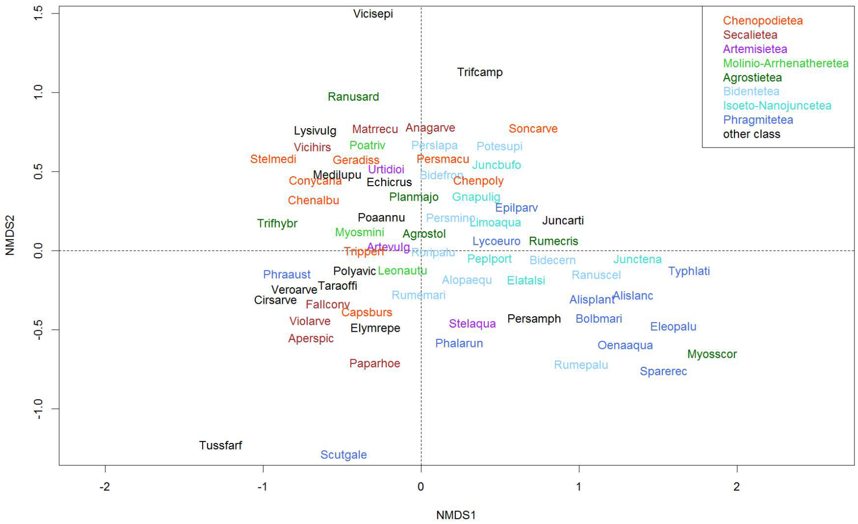


**Fig. 4.** NMDS plot of all species (stress 15.3%). Species belonging to one phytosociological class are marked by the same colour. Species were assigned to phytosociological units according to ELLENBERG et al (2001). Species which couldn't be assigned to phytosociological classes which contained only one or two species were marked black. To improve readability species names are abbreviated and sites are not shown. In Table 2 all species names are listed with their corresponding abbreviations.

**Abb. 4.** NMDS-Plot aller Arten (Stress 15,3 %). Arten, die zu einer pflanzensoziologischen Klasse gehören, werden in der gleichen Farbe dargestellt. Die Zuordnung der Arten erfolgte nach ELLENBERG et al. (2001). Alle Arten, für die eine eindeutige Zuordnung nicht möglich ist und pflanzensoziologische Einheiten, denen nur eine oder zwei Arten zugeordnet wurden, sind schwarz dargestellt. Für eine bessere Lesbarkeit wurden Artnamen abgekürzt und Punkte der Aufnahmeflächen nicht dargestellt. In Tabelle 2 sind alle Artnamen mit den dazugehörigen Abkürzungen aufgeführt.

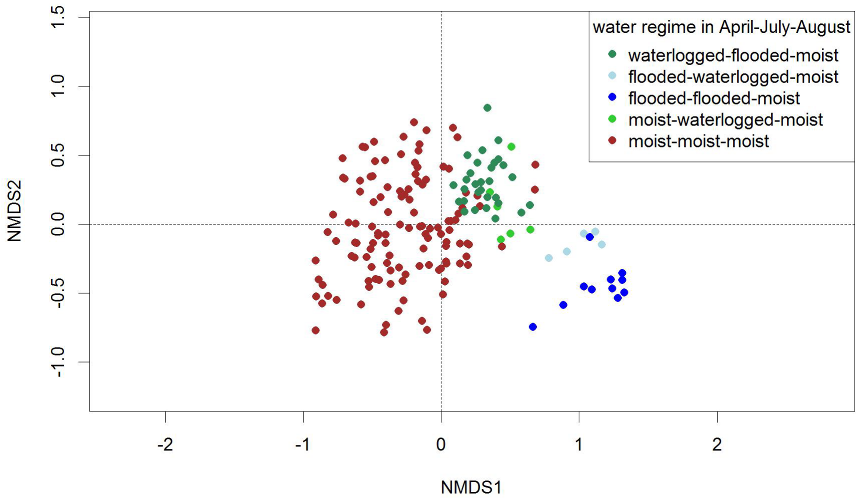


**Fig. 5.** NMDS ordination plot of all sampling plots (stress 15.3%). Different water regimes are marked by different colours. To improve readability species names are not shown.

**Abb. 5.** NMDS-Plot aller Aufnahmeflächen (Stress 15,3 %). Die unterschiedlichen Wasserregimes sind durch verschiedene Farben dargestellt. Zur besseren Lesbarkeit wurden die Artnamen nicht geplottet.

$p$ < 0.001), it was also closely related to the first NMDS dimension (Fig. 6B). The mean vegetation height described an orthogonal gradient with low growing communities in the upper part of the plot and taller plants at the opposite side (Fig. 6C). Collinearity between the fitted surface for the mean vegetation height and the nitrogen indicator values (Fig. 6D) suggested a soil fertility gradient along the second NMDS dimension. Measured soil factors revealed little variation among the seven ponds, except for nitrogen, which showed one outlier (Table 1); due to this low variation and few samples we did not plot these values on the NMDS ordination. The different farming practices had only a low correlation to the site scores ($R^2$ = 0.11, $p$ < 0.01), indicating that farming only had a minor impact on sites with water level fluctuations (Table 4).

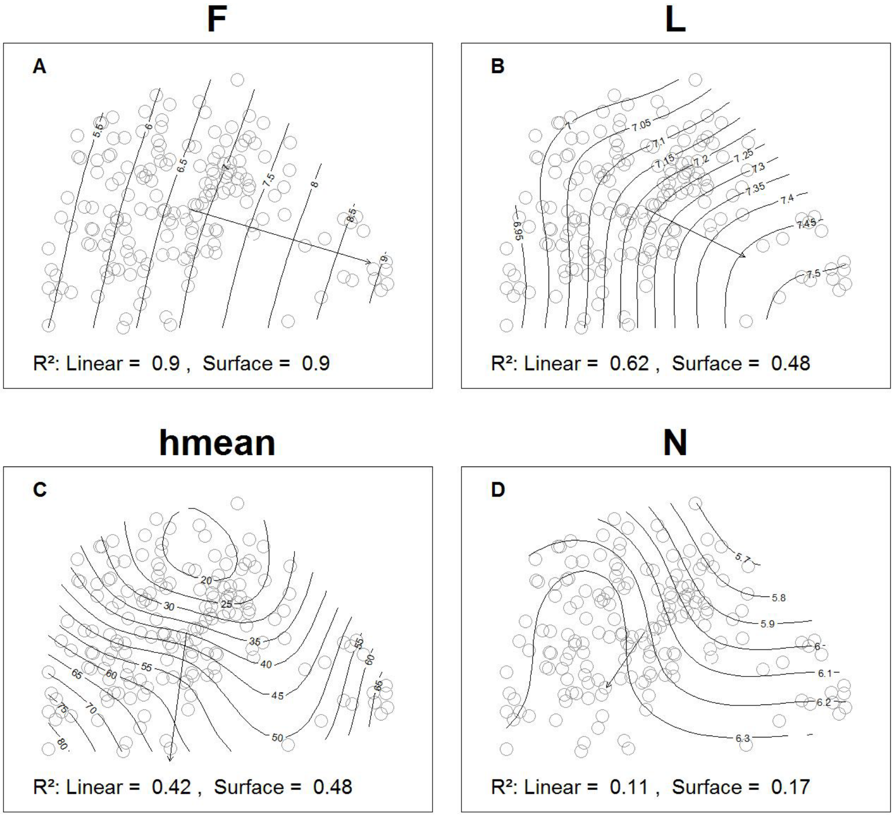


**Fig. 6.** NMDS ordination with fitted vectors and smoothed surfaces for the mean Ellenberg indicator values for A: soil moisture (F), B: light (L), C: the mean vegetation height (hmean) and D: nutrients (N). The coefficient of determination ($R^2$) is given for the linear and the surface fit. Arrows indicate the direction of the most rapid change along the gradient. Sampling plots are marked by grey circles, species names are not shown.

**Abb. 6.** NMDS-Plot mit den angepassten Vektoren und geglätteten Oberflächen für die mittleren Zeigerwerte für A: Bodenfeuchte (F), B: Licht (L), C: die mittlere Vegetationshöhe (hmean) und D: Nährstoffe (N) . Für jede Variable ist das Bestimmtheitsmaß ($R^2$) sowohl für die Anpassung des linaren Modells als auch der angepassten Oberfläche angegeben. Die Pfeile zeigen die Richtung der stärksten Änderung der Umweltvariablen entlang des Gradienten an. Die Untersuchungsplots sind als graue Kreise eingezeichnet, Artnamen sind nicht dargestellt.

**Table 4.** Results of the vector and smoothed surfaces fitting of the environmental variables. Values given in the columns NMDS1 and NMDS2 represent the direction cosines of continuous variables along the two axes. p values are based on 999 random permutations. Code for significance levels: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$; n.s.,p$P > 0.05$.

**Tabelle 4.** Ergebnisse der Modellanpassung. Werte in den Spalten NMDS1 und NMDS2 stellen jeweils den Richtungskosinus der kontinuierlichen Variablen entlang der beiden Achsen dar. P-Werte basieren auf 999 Permutationen. Code für Signifikanzniveaus: *, $p < 0,05$; **, $p < 0,01$; ***, $p < 0,001$; n.s., $p > 0,05$.

| | Linear Model Fit | | | | | Surface | | |
|---|---|---|---|---|---|---|---|---|
| | NMDS1 | NMDS2 | R² | p | | R² | p | |
| Mean height | -0.13 | -0.99 | 0.41 | 0.001 | *** | 0.48 | 0.001 | *** |
| pH | -0.87 | 0.20 | 0.37 | 0.001 | *** | 0.52 | 0.001 | *** |
| Phosphorus | -0.18 | 0.84 | 0.49 | 0.001 | *** | 0.49 | 0.001 | *** |
| Potassium | 0.07 | -0.99 | 0.04 | 0.066 | | 0.26 | 0.001 | *** |
| Nitrogen | 0.05 | 0.44 | 0.38 | 0.001 | *** | 0.08 | 0.001 | *** |
| L | 0.63 | -0.31 | 0.62 | 0.001 | *** | 0.48 | 0.001 | *** |
| F | 0.96 | -0.28 | 0.90 | 0.001 | *** | 0.90 | 0.001 | *** |
| N | -0.56 | -0.83 | 0.11 | 0.001 | *** | 0.18 | 0.001 | *** |
| Factors: | | | | | | | | |
| Treatment | | | 0.11 | 0.002 | ** | | | |
| Water regime | | | 0.47 | 0.001 | *** | | | |

## 4. Discussion

### Richness of *Isoëto-Nanojuncetea* species

DREGER (2002) found within the biosphere reserve Schorfheide-Chorin similar species numbers for small kettle holes (< 1 ha). FISCHER (1983) and HOFFMANN et al. (2000) reported similar numbers of endangered species in ponds in other parts of Brandenburg. The number of *Isoëto-Nanojuncetea* species within our study was reasonably low. This can be related to the unfavourable weather conditions during the study year, as PIETSCH & MÜLLER-STOLL (1974) noted, that several factors like the weather conditions and the management of the fields influence the opportunity to find species of the dwarf rush communities.

### Effects of water regime and farming on species richness

Our investigations showed that strong fluctuations of the water level with flooding in spring or summer positively affect both the total richness of vascular plants and the number of *Isoëto-Nanojuncetea* species. We suppose that these site conditions favour high species numbers by increasing the range of favourable habitat conditions. These results are consistent with GREET et al. (2013) that duration and frequency of flooding positively affect the plant species richness in amphibious habitats including the *Isoëto-Nanojuncetea* and related communities. A study on Australian temporary wetlands contrastingly resulted in highest total species richness without any inundation (CASANOVA & BROCK 2000). These contradicting results may be due to differences in the study sites. The Australian study was conducted at wetlands surrounded by relatively undisturbed grass- und shrublands, whereas in our study regular farming may have reduced the diversity of the arable plant community, which would dominate these sites under terrestrial conditions.

An unexpected result concerning the arable farming treatments was that richness of *Isoëto-Nanojuncetea* species was highest in plots solely treated with herbicides. As most *Isoëto-Nanojuncetea* species germinate well after application of pre-emergence herbicides, they may be scarcely affected by this treatment and possibly benefit from the reduced competition of other species (POSCHLOD et al. 1999). This also matches with BROSE & TIELBÖRGER (2005) who found that removal of competitive species can increase the richness of wetland species. However, as our study covers the time span of only one year (with unfavourable germination conditions) and we tested only one herbicide, more detailed investigations are necessary before general conclusions on the effects of herbicides on *Isoëto-Nanojuncetea* species are possible. Fertilization and competition by crops resulted in particularly low numbers of such species.

### Effects of water regime on community composition

Ordination of plant communities of the 177 plots with differing water regimes, soil properties and farming practices revealed fluctuations of the water level to be most decisive for community composition. CASANOVA & BROCK (2000) and BROCK et al. (2005) came to the same conclusions by testing effects of different water regimes on the establishment of wetland plant communities in seed bank investigations. A long-term study on the effects of the timing of flooding on the species composition showed that seasonality (flooding in spring or summer) altered the community more than the frequency of flooding (ROBERTSON et al. 2001). Also other studies showed that flooding in general, and duration of flooding in particular, control the composition of wetland communities (BROCK et al. 2005, CHERRY & GOUGH 2006, ROBERTSON & JAMES 2007, DELLA BELLA et al. 2008). PÄTZIG et al. (2012) found annual 'hydroperiod' (defined as the number of months a site was flooded) to be significantly related to the occurrence of amphibious plants.

Mean Ellenberg indicator values for moisture and light showed a strong relationship with the first ordination axis, representing the influence of the water level fluctuations on the plant species composition. This result agrees with TÄUBER & PETERSEN (2000) who found that the water regime and availability of light both are essential factor for the successful establishment of *Isoëto-Nanojuncetea* species. Germination experiments by SALISBURY (1970) and POSCHLOD et al. (1999) demonstrated that an insufficient light supply can limit germination of these species in deep water bodies.

Mean vegetation height and the mean Ellenberg indicator value for nutrients showed a good relationship to the floristic variation, indicating that the communities emerging under different water regimes are related to the nutrient content in the soil. Similar conclusions were drawn by PÄTZIG et al. (2012) who found a positive relationship of nitrate-nitrogen in the water to amphibious plants. Depending on the soil nutrient content, *Isoëto-Nanojuncetea* communities establish under low or medium nutrient levels and they are replaced by more nitrophilous *Bidentetea* communities (KIESSLICH et al. 2003).

### Implications for conservation and management

As temporary ponds are well known for their richness of annual species and often harbour numerous rare and endangered species, they significantly contribute to the biodiversity of the study area in NE Brandenburg (DREGER 2002) and similar agricultural landscapes (DAVIES et al. 2008). The main factors creating suitable habitat conditions for the *Isoëto-Nanojuncetea* as well as other plant communities, like those within the class *Bidentetea*, in arable fields are regular human disturbances by ploughing and the change between flooding and drought. Drainage or local excavation of temporary ponds, as it took place during the past century (KALETTKA 1996) and is still done by some farmers, severely threaten these plant communities by discontinuing the water level fluctuations. Even macrophyte communities, which also harbour several rare and endangered plant species (RAABE 2008, PUKACZ et al. 2009) and offer breeding habitat for amphibian species, benefit from regular soil disturbance and water level fluctuations. Observations during the past 8 years confirm that the species richness and the number of rare plant species are remarkably higher in temporary ponds than in perennial ponds in the study area (U. Raabe, unpubl. results).

Furthermore, setting aside these areas as suggested by BERGER et al. (2003) would cause a decline of the *Isoëto-Nanojuncetea* communities in favour of mid- and late-successional plant communities of less conservation concern. As all these communities contribute to the species richness of these field ponds, a more differentiated management is recommended that should create and maintain a high diversity of habitat types at the temporary ponds.

## Erweiterte deutsche Zusammenfassung

**Einleitung** – Die Wasserstandsschwankungen an den Ufern flacher Gewässer bieten ideale Voraussetzungen für die Entwicklung annueller Pflanzengesellschaften der Klasse *Isoëto-Nanojuncetea*. In der Agrarlandschaft Nordostdeutschlands haben sich an ackerbaulich genutzten und temporär überfluteten Senken Bestände entwickelt, die sich durch einen großen Reichtum an Arten der Zwergbinsen-Gesellschaften auszeichnen.

Dort und in anderen Teilen Deutschlands haben Nutzungsaufgabe und die Regulierung der Wasserstandsdynamik in den vergangenen Jahrzehnten zu einem starken Rückgang dieser Pflanzengesellschaften geführt. Viele Arten der *Isoëto-Nanojuncetea* gelten daher heute als gefährdet. Um diesen Vegetationstyp langfristig zu schützen, ist es wichtig, die Habitatansprüche der entsprechenden Arten zu kennen. In der vorliegenden Studie haben wir die Auswirkungen verschiedener Wasserstandsregimes, Bodeneigenschaften und Landbewirtschaftung auf den Artenreichtum und die Artenzusammensetzung dieser temporären Gewässer untersucht.

**Methoden** – Die Untersuchungen wurden an sieben Gewässern eines konventionell bewirtschafteten Agrarbetriebs im Nordosten Brandenburgs durchgeführt. Auf 177 Untersuchungsplots von 1 x 1 $m^2$ wurden alle Gefäßpflanzenarten erhoben. Für alle Flächen wurden mittlere Zeigerwerte für Licht, Feuchte und Nährstoffe berechnet. Um Auswirkungen verschiedener Wasserregimes, Bodeneigenschaften und Bewirtschaftung auf Arten der *Isoëto-Nanojuncetea* zu ermitteln, wurde die Anzahl der Kennarten aller pflanzensoziologischen Einheiten innerhalb dieser Klasse ermittelt. Die Wasserstände in jedem Plot wurden im April, Juli und August 2013 erfasst und den Kategorien ‚feucht', ‚wassergesättigt' oder ‚überflutet' zugeordnet. Die Kombination der Wasserstände im Laufe der Vegetationsperiode führte zu fünf verschiedenen Wasserstandsregimes. Bodenreaktion, Gesamtstickstoff und Gesamtphosphor wurden aus Mischproben für jedes der sieben Gewässer ermittelt. Um die Auswirkungen der landwirtschaftlichen Nutzung zu testen, wurden nach randomisierter Zuweisung in den verschiedenen Plots eine Kombination der Behandlungen mit/ohne Kultur, mit/ohne Düngung bzw. Herbizidanwendung durchgeführt.

**Ergebnisse** – Multiple Mittelwertvergleiche zeigten, dass sich die Gesamtartenzahl und der Anteil an *Isoëto-Nanojuncetea*-Arten signifikant zwischen den verschiedenen Wasserregimes unterscheiden. Bezüglich der Landnutzung führte der Anbau von Winterweizen ohne weitere Bewirtschaftungsmaßnahmen zur höchsten Gesamtartenzahl; die niedrigsten Artenzahlen wurden auf Flächen mit Kombinationen von Deckfrucht, Düngemittel- und Herbizideinsatz, sowie Deckfrucht und Herbizidbehandlung festgestellt. Der Anteil von *Isoëto-Nanojuncetea*-Arten war auf herbizidbehandelten Flächen am höchsten.

Eine Ordination mittels einer nichtlinearen multidimensionalen Skalierung (NMDS) zeigte, dass das Wasserregime die floristische Variation auf den Erhebungsflächen am besten erklärt. Auf Flächen mit gleichem Wasserregime wird die Artenzusammensetzung vor allem durch die Nährstoffgehalte des Bodens bestimmt. Die Bewirtschaftungsmaßnahmen zeigten keine deutlichen Auswirkungen auf die Artenzusammensetzung.

**Diskussion** – Kleingewässer, wie die brandenburgischen Pseudo-Sölle, können eine große Artenvielfalt und zahlreiche seltene und gefährdete Arten aufweisen, und tragen damit wesentlich zur Agrobiodiversität bei. Die wichtigsten Faktoren, die eine Etablierung der *Isoëto-Nanojuncetea*-Gesellschaften auf Ackerflächen ermöglichen, sind regelmäßige Störung durch Bodenbearbeitung und der Wechsel von Überflutung und Austrocknen. Drainieren oder punktuelles Eintiefen von temporären Gewässern führen zu einem Verlust dieser Dynamik und stellen damit eine erhebliche Gefährdung der Pflanzengesellschaften dar. Auch andere Gesellschaften wie die der Makrophyten, die ebenfalls einige seltene Arten aufweisen, profitieren von der regelmäßigen Störung durch Bodenbearbeitung und Wasserstandsschwankungen. Eine Nutzungsaufgabe würde einen Rückgang dieser Vegetation zugunsten anderer mehrjähriger Gesellschaften bedeuten. Da diese Pflanzengesellschaften zur Gesamtbiodiversität der Kleingewässer beitragen, wird ein diversifiziertes Management empfohlen, das zur Schaffung oder zum Erhalt vielfältiger Habitatstrukturen beiträgt.

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## Supplements and Appendices

**Additional supporting information may be found in the online version of this article.**

**Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.**

**Appendix S1.** Species traits, classification as *Isoëto-Nanojuncetea* species and assignment to phytosociological classes.

**Anhang S1.** Artmerkmale, Klassifikation als *Isoëto-Nanojuncetea*-Arten und Zuordnung der Arten zu pflanzensoziologischen Klassen.

**Appendix S2.** Site parameters of all plots of temporary wetlands in Brandenburg.

**Anhang S2.** Standortparameter aller Aufnahmeflächen von temporären Gewässern in Brandenburg.

**Appendix S3.** Vegetation Relevés of all plots with water levels dry-dry-dry in April-July-August.

**Anhang S3.** Vegetationsaufnahmen aller Plots mit Wasserständen trocken-trocken-trocken in April-Juli-August.

**Appendix S4.** Vegetation Relevés of all plots with water levels dry-waterlogged-dry in April-July-August.

**Anhang S4.** Vegetationsaufnahmen aller Plots mit Wasserständen trocken-feucht-trocken in April-Juli-August.

**Appendix S5.** Vegetation Relevés of all plots with water levels flooded-waterlogged-dry in April-July-August.

**Anhang S5.** Vegetationsaufnahmen aller Plots mit Wasserständen überflutet-feucht-trocken in April-Juli-August.

**Appendix S6.** Vegetation Relevés of all plots with water levels waterlogged-flooded-dry in April-July-August.

**Anhang S6.** Vegetationsaufnahmen aller Plots mit Wasserständen feucht-überflutet-trocken in April-Juli-August.

**Appendix S7.** Vegetation Relevés of all plots with water levels flooded-flooded-dry in April-July-August.

**Anhang S7.** Vegetationsaufnahmen aller Plots mit Wasserständen überflutet-überflutet-trocken in April-Juli-August.

## References


BERGER, G., PFEFFER, H., KÄCHELE, H., ANDREAS, S. & HOFFMANN, J. (2003): Nature protection in agricultural landscapes by setting aside unproductive areas and ecotones within arable fields ("In-field Nature Protection Spots"). – J. Nat. Conserv. 11: 221–233.

BROCK, M.A., NIELSEN, D.L. & CROSSLE, K. (2005): Changes in biotic communities developing from freshwater wetland sediments under experimental salinity and water regimes. – Freshwater Biol. 50: 1376–1390.

BROSE, U. & TIELBÖRGER, K. (2005): Subtle differences in environmental stress along a flooding gradient affect the importance of inter-specific competition in an annual plant community. – Plant Ecol. 178: 51–59.

CASANOVA, M.T. & BROCK, M.A. (2000): How do depth, duration and frequency of flooding influence the establishment of wetland plant communities? – Plant Ecol. 147: 237–250.

CHERRY, J.A. & GOUGH, L. (2006): Temporary floating island formation maintains wetland plant species richness: the role of the seed bank. – Aquat. Bot. 85: 29–36.

CHYTRÝ, M. & TICHÝ, L. (2003): Diagnostic, constant, and dominant species of vegetation classes and alliances of the Czech Republic: a statistical revision. – Folia Fac. Sci. Nat. Univ. Masarykianae Brunensis 108: 1–231.

DAVIES, B., BIGGS, J., WILLIAMS, P., WHITFIELD, M., NICOLET, P., SEAR, D., BRAY, S. & MAUND, S. (2008): Comparative biodiversity of aquatic habitats in the European agricultural landscape. – Agr. Ecosyst. Environ. 125: 1–8.

DE MENDIBURU, F. (2013): agricolae: Statistical Procedures for Agricultural Research. R package version 1.1–4.

DEIL, U. (2005): A review on habitats, plant traits and vegetation of ephemeral wetlands – a global perspective. – Phytocoenologia 35: 533–705.

DELLA BELLA, V., BAZZANTI, M., DOWGIALLO, M.G. & IBERITE, M. (2008): Macrophyte diversity and physico-chemical characteristics of Tyrrhenian coast ponds in central Italy: implications for conservation. – Hydrobiologia 597: 85–95.

DEUTSCHER WETTERDIENST (2013a): Download of the long-term mean of temperature and precipitation (1961–1990). – URL: http://www.dwd.de [accessed 2014-01-27].

DEUTSCHER WETTERDIENST (2013b): Download of the monthly climate data for 2013 of the weather station Angermünde. – URL: http://www.dwd.de [accessed 2014-01-27].

DEUTSCHER WETTERDIENST (2013c): Download of the monthly climate data for Brandenburg. – URL: http://www.dwd.de [accessed 2014-01-27].

DREGER, F. (2002): Sölle – Bedeutung für die Biodiversität in Agrarlandschaften unterschiedlicher Landschaftsräume. – Beitr. Forstwirtsch. Landschaftsökol. 36: 88–92.

ELLENBERG, H. & LEUSCHNER, C. (2010): Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht. 6 Aufl. – Ulmer, Stuttgart: 1333 pp.

ELLENBERG, H., WEBER H.E., DÜLL, R., WIRTH, V. & WERNER W. (2001): Zeigerwerte von Pflanzen in Mitteleuropa. 3 Aufl. – Scr. Geobot. 18: 1–262.

FISCHER, W. (1983): Vegetationsmosaike in vernässten Ackerhohlformen mit einem Beitrag zu segetalen Zwergbinsen- und Zweizahn-Gesellschaften. – Wiss. Z. Päd. Hochsch. Potsdam, Math.-naturwiss. R. 27: 495–516.

FAITH, D.P., MINCHIN P.R. & BELBIN, L. (1987): Compositional dissimilarity as a robust measure of ecological distance. – Vegetatio 69: 57–68.

GREET, J., COUSENS, R.D. & WEBB, J.A. (2013): Seasonal timing of inundation affects riparian plant growth and flowering: implications for riparian vegetation composition. – Plant Ecol. 214: 87–101.

HEJNÝ , S. (1962): Über die Bedeutung der Schwankungen des Wasserspiegels für die Charakteristik der Makrophytengesellschaften in den mitteleuropäischen Gewässern. – Preslia 34: 359–367.

HEJNÝ, S. (1957): Ein Beitrag zur ökologischen Gliederung der Makrophyten der tschechoslowakischen Niederungs-Gewässer. – Preslia 29: 349–368.

HOFFMANN, J., MIRSCHEL, W., CEBULSKY, I. & KRETSCHMER, H. (2000): Zur Soziologie und witterungsabhängigen Ausbildung von Zwergbinsen-Gesellschaften auf Ackerböden in Ostbrandenburg. – Verh. Bot. Ver. Berlin Brandenburg 133: 119–144.

KALETTKA, T. (1996): Die Problematik der Sölle (Kleinhohlformen) im Jungmoränengebiet Nordostdeutschlands. – Natursch. Landschaftspfl. Bbg. Sonderheft Sölle: 4–12.

KIESSLICH, M., DENGLER, J. & BERG, C. (2003): Die Gesellschaften der *Bidentetea tripartitae* Tx. et al. ex von Rochow 1951 in Mecklenburg-Vorpommern mit Anmerkungen zur Synsystematik und Nomenklatur der Klasse. – Feddes Rep. 114: 91–139.

KLAFS, G., JESCHKE, L. & SCHMIDT, H. (1973): Genese und Systematik wasserführender Ackerhohlformen in den Nordbezirken der DDR. – Arch. Naturschutz Landschaftsforsch. 13 (4): 287–302.

LANDESVERMESSUNG UND GEOBASISINFORMATION BRANDENBURG (2013): Digital aerial photographs. – URL: http://isk.geobasis-bb.de/ows/dop20c.php [accessed 2014-01-27].

LUDWIG, G. & SCHNITTLER, M. (1996): Rote Liste gefährdeter Pflanzen Deutschlands. – Schriftenr. Vegetationskd. 28: 1–744.

MINCHIN, P.R. (1987): An evaluation of relative robustness of techniques for ecological ordination. – Vegetatio 69: 89–107

OBERDORFER, E. (2001): Pflanzensoziologische Exkursionsflora für Deutschland und angrenzende Gebiete. 8. Aufl. – Ulmer, Stuttgart: 1051 pp.

OKSANEN, J., BLANCHET, F.G., KINDT, R., LEGENDRE, P., MINCHIN, P.R., O'HARA, R.B., SIMPSON, G.L., SOLYMOS, P., STEVENS, M.H.H. & WAGNER, H. (2013). vegan: Community Ecology Package. R package version 2.0–9.

PÄTZIG, M., KALETTKA, T., GLEMNITZ, M. & BERGER, G. (2012): What governs macrophyte species richness in kettle hole types? A case study from Northeast Germany. – Limnologica 42: 340–354.

PIETSCH, W. & MÜLLER-STOLL, W.R. (1974): Übersicht über die im brandenburgischen Gebiet vorkommenden Zwergbinsen-Gesellschaften (*Isoëto-Nanojuncetea*). – Verh. bot. Ver. Prov. Brandenburg 109: 56–95.

PIETSCH, W. (1999): Zum Keimverhalten ausgewählter Arten mitteleuropäischer Zwergbinsengesellschaften. – Mitt. Bad. Landesver. Naturkunde u. Naturschutz N.F. 17: 261–274.

POSCHLOD, P., BÖHRINGER, J., FENNEL, S., PRUME, C. & TIEKÖTTER, A. (1999): Aspekte der Biologie und Ökologie von Arten der Zwergbinsenfluren. – Mitt. Bad. Landesver. Naturkunde u. Naturschutz N.F. 17: 219–260.

PUKACZ, A.. PEŁECHATY, M. & RAABE, U. (2009): Pierwsze stanowisko *Chara baueri* (*Characeae*) w Polsce (First locality of *Chara baueri* (*Characeae*) in Poland) [in Polish]. – Fragm. Floristic. Geobot. Polonica 16: 425–429.

R CORE TEAM (2013). R: A language and environment for statistical computing. – R Foundation for Statistical Computing, Vienna, Austria.

RAABE, U. (2008): Die Sprossende Armleuchteralge, *Tolypella prolifera* (Ziz ex A. Braun) Leonh., in Brandenburg wieder aufgefunden. – Verh. Bot. Ver. Berlin Brandenburg 141: 145–152.

RENNWALD, E. (2000): Verzeichnis und Rote Liste der Pflanzengesellschaften Deutschlands. – Schriftenr. Vegetationskd. 35: 1–800.

ROBERTSON, A.I., BACON, P. & HEAGNEY, G. (2001): The responses of floodplain primary production to flood frequency and timing. – J. Appl. Ecol. 38: 126–136.

ROBERTSON, H.A. & JAMES, K.R. (2007): Plant establishment from the seed bank of a degraded floodplain wetland: a comparison of two alternative management scenarios. – Plant Ecol. 188: 145–164.

SALISBURY, E. (1970): The pioneer vegetation of exposed muds and its biological features. – Philos. T. Roy. Soc. B 259: 207–255.

TÄUBER, T. (2000): Zwergbinsen-Gesellschaften (*Isoëto-Nanojuncetea*) in Niedersachsen – Verbreitung, Gliederung, Dynamik, Keimungsbedingungen der Arten und Schutzkonzepte. – Cuvillier, Göttingen: 238 pp.

TÄUBER, T. & PETERSEN, J. (2000): *Isoëto-Nanojuncetea* (D1) Zwergbinsen-Gesellschaften. – Synopsis Pflanzenges. Dtschl. 7: 1–88.

THOMPSON, K., BAKKER, J.P. & BEKKER, R.M. (1997): The soil seed banks of North West Europe: methodology, density & longevity. – Cambridge Univ. Press, Cambridge: 276 pp.

VIRTANEN, R., OKSANEN, J., OKSANEN, L. & RAZZHIVIN, V.Y. (2006): Broad-scale vegetation-environment relationships in Eurasian high-latitude areas. – J. Veg. Sci. 17: 519–528.

VON LAMPE, M. (1996): Wuchsform, Wuchsrhythmus und Verbreitung der Arten der Zwergbinsengesellschaften. – Diss. Bot. 266: 1–353.

WISSKIRCHEN, R. & HAEUPLER, H. (1998): Standardliste der Farn- und Blütenpflanzen Deutschlands. – Ulmer, Stuttgart: 765 pp.