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Seven years of spider community succession in a Sphagnum farm

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Abstract. Sphagnum farming is paludiculture aiming to produce *Sphagnum* biomass as a sustainable alternative to peat in horticultural growing media. Here we focus on the habitat value of artificial Sphagnum farming sites for peatland species. We report results from seven years of biodiversity monitoring (2011–2018) in a 14 ha Sphagnum farm in north western Germany, using spiders and harvestmen as indicator groups for succession of invertebrate communities. Species richness and abundance more than doubled in the first two years of *Sphagnum* growth, but remained rather constant since then. Peatland generalists rapidly colonized the site and constitute some 30%–40% of activity dominance since the second year. Stenotopic peatland spiders arrived later, but their abundance proportion increased significantly from 2014 to 2017. Nevertheless, the spider communities remain distinct from (semi-)natural reference sites. Highly characteristic species of pristine bogs are still lacking. We conclude that a novel community has assembled that bears only moderate resemblance to natural peatlands. Persisting high annual turnover rates in terms of species composition and dominance structure (both > 30%) corroborate high levels of ongoing dynamics and the significance of stochastic processes. The long-term trajectory of community succession in the Sphagnum farm remains vague.

Keywords: Arachnida, biodiversity monitoring, paludiculture, peatlands, surrogate habitat

Worldwide each year approximately 5000 km^2 of actively growing (peat accumulating) peatland (=mire, ~ 0.1% of the global land surface) is destroyed by human activities (Joosten 2016). Europe is the continent with the highest proportion of degraded peatland (44%), and in some central-European countries — such as Germany — less than 2% of peatlands remain intact (Barthelmes 2016). Currently two particularly problematic tendencies are recognizable with respect to peatland conservation. First, the rapidly growing demand for biomass drives agriculture (back) into peatlands, despite the fact that drainage-based agriculture on organic soils is unsustainable and a major source of greenhouse gas emissions (Joosten et al. 2016b). Second, *Sphagnum* peat has emerged as the most important constituent of growing media in horticultural industry (Schmilewski 2008). Worldwide 40 million m^3 of *Sphagnum* peat are used annually (Block et al. 2019). While the few remaining bogs (mires only fed by precipitation, often dominated by *Sphagnum* vegetation) in central Europe are strictly protected as priority habitat by the EU Habitats Directive (92/43/EEG) and by national laws, peat is increasingly imported from North- and East-European countries and Canada. Peat extraction destroys bogs and their ecosystem services, including carbon storage capacity, water regulation, biodiversity protection and their function as palaeo-environmental archives (Gaudig 2019). With a global perspective, there is one promising way out: paludiculture, or wet agriculture on peatlands (Joosten et al. 2016a).

Paludiculture is a peat-conserving sustainable agricultural production system under wet site conditions that stops subsidence and minimizes emissions (Joosten et al. 2016a; Wichtmann et al. 2016). A novel form of paludiculture is Sphagnum farming, aiming at the cultivation of *Sphagnum* biomass on rewetted, formerly drained peatland (Gaudig et al. 2018). *Sphagnum* biomass has similar properties to slightly humified *Sphagnum* peat ('white peat') and is therefore suitable for the production of high-quality horticultural growing media (e.g., Emmel 2008; Oberpaur et al. 2010; Reinikainen et al. 2012; Blievernicht et al. 2013). Despite its multiple environmental benefits, Sphagnum farming is still in its infancy (Gaudig et al. 2018). Only since 2004 has peatmoss been cultivated in field experiments in Canada and Germany (Gaudig et al. 2014, 2018; Pouliot et al. 2015). The largest Sphagnum farm in Europe to date is situated near Rastede in northwestern Germany. Its total size is 14 ha, with a net *Sphagnum* production area of 5.6 ha (Gaudig et al. 2018). Calculations show that upscaling Sphagnum farming and large-scale commercial implementation will become economically feasible in the near future (Wichmann et al. 2017, 2020).

Besides producing *Sphagnum* biomass and halting greenhouse gas emissions from drained peat, Sphagnum farming may have a positive impact on biodiversity conservation. Peatlands host highly specialized biota (Minayeva et al. 2016) with a high proportion of rare and threatened species. It is, however, largely unknown and unpredictable to which extent the artificial Sphagnum farms may act as substitute habitats for the threatened fauna of natural bogs. To answer this question, we have monitored biodiversity at the Rastede Sphagnum farm since its establishment in 2011. We studied the succession of spider communities, because spiders are highly diverse top-predators with dominant abundance in the macrofauna of peatland habitats (Muster et al. 2015; Gaudig & Krebs 2016). In the first years of study, we focused on comparing the spider communities of the Sphagnum farm with (semi-)natural reference plots in the surroundings. After three years, peatland generalist species made up more than 40% of the spider abundance in the Sphagnum farm, but stenotopic, poor-dispersing bog specialists were largely lacking (Muster et al. 2015). The communities remained distinct from those of the reference sites, indicating that a novel type of habitat with no equivalence in natural environments has been created. But how would succession proceed in the long term?

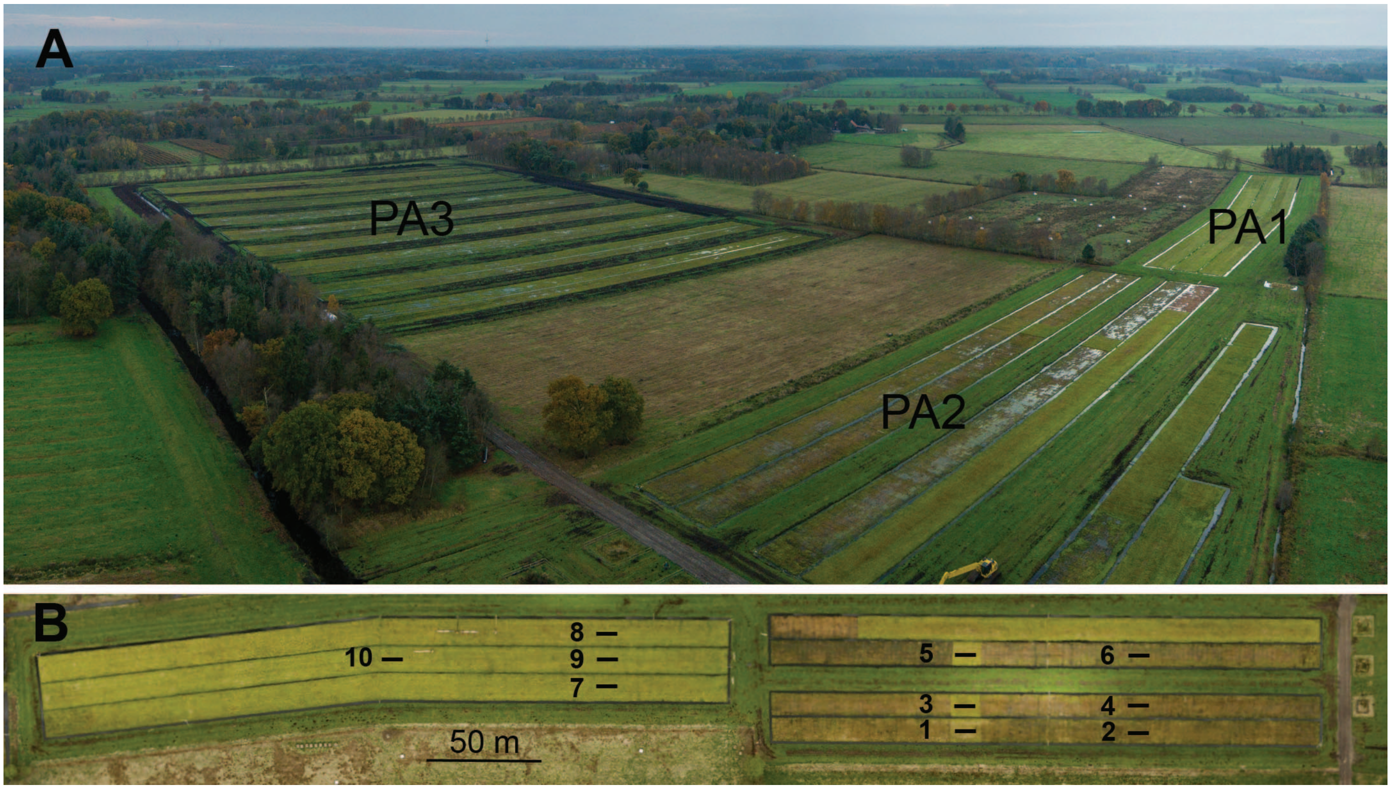

Figure 1.—A. Aerial view of the Rastede Sphagnum farm with three production areas (PA1–PA3). B. Position of the pitfall transects in PA1 (plots 7–10) and PA2 (plots 1–6). Fotos: Tobias Dahms, Stephan Busse.

Here we present data from seven years of spider community succession in the Rastede Sphagnum farm (2011–2018). According to our working hypothesis, communities of the Sphagnum farm would slowly converge with those of more natural peatlands. We furthermore predicted an increase in species richness and abundance of stenotopic peatland spiders, and a decrease in annual turnover rates with age of the Sphagnum farm.

METHODS

Study site.—The Rastede Sphagnum farm (Fig. 1) is situated in northwestern Germany at 53°16′N, 8°16′E (see Muster et al. 2015 for a map). The farm was established in 2011 on 4 ha of formerly drained bog grassland with a net moss area of 2.025 ha. *Sphagnum* production fields were arranged in stretches of 10 m width separated by irrigation ditches (0.5 m width, 0.5 m depth). The area was divided in two production units. Production area 1 (PA1) consisted of 3 *Sphagnum* production fields surrounded by causeways, whereas production area 2 (PA2) included 2x2 *Sphagnum* production fields that were separated by elevated causeways for management and harvesting. In 2016, the size of the Rastede Sphagnum farm was tripled to a total of 14 ha (net moss area 5.6 ha) by the installation of production area 3 (PA3). For technical details concerning establishment and management of the farm, see Wichmann et al. (2017) and Gaudig et al. (2018).

Sampling.—We used pitfall trapping to study the succession of spider communities at the Rastede Sphagnum farm. From 2011 to 2018, 6–10 plots distributed in production areas PA1 and PA2, all from continuously growing peatmoss lawn (i.e., not meanwhile harvested) were studied. At each plot, five pitfalls were installed in linear transects parallel to the ditches in the center of the *Sphagnum* production field (c. 5 m distance to the ditch) with trap interdistances of 1 m. This is one of the most commonly used inter-trap spacings, and Ward et al. (2001) found no significant difference in abundance and composition among 1, 5 and 10 m treatments for any invertebrate taxa. We used plastic cups with opening diameter of 7.5 cm, filled with 4% formaldehyde solution plus neutral detergent, and protected by 15x15 cm metal roofs. Traps were fixed to the moss with tent pegs to prevent uplifts. Floating events were rare due to maintenance of almost constant water tables by a sophisticated water management system (Brust et al. 2018). Traps were active during two 4-week periods in spring of each year (May and June, supplementary Table S1, online at http://dx.doi.org/10.1636/JoA-S-19-074.s1).

Determination, nomenclature and habitat association.—Adult spiders were determined to species level using Roberts (1998) and Nentwig et al. (2019). Nomenclature and family allocation follow the World Spider Catalogue (WSC 2019). Harvestmen were identified using Martens (1978), nomenclature follows Muster et al. (2016). Voucher specimens are deposited in the collection Christoph Muster, Putbus, Germany. Species were classified in three categories according to the strength of association with peatland habitats. Peatland specialists (PS) are stenotopic, tyrphobiont species that exclusively inhabit peatland habitats. Peatland generalists (PG) show strong habitat priority for peatlands, but they may occur in other habitats as well. Peatland tolerants (PT)

Table 1.—Correlation of environmental variables with the NMDS ordination of the spider communities. Significance levels: *** $P \leq 0.001$, ** $P < 0.01$, *$P < 0.05$.

variable	description	R^2	P	
hum	mean humidity during trapping period (%)	0.3870	0.001	***
rad	mean radiation during trapping period (W/m^2)	0.1347	0.023	*
temp	mean temperature during trapping period (°C)	0.4086	0.001	***
wind	mean wind speed during trapping period (m/s)	0.3886	0.001	***
prec	mean monthly precipitation during trapping period (mm)	0.2408	0.001	***
y_hum	mean humidity of previous 12 months (%)	0.5898	0.001	***
y_rad	mean radiation of previous 12 months (W/m^2)	0.0580	0.204	
y_temp	mean temperature of previous 12 months (°C)	0.5875	0.001	***
y_wind	mean wind speed of previous 12 months (m/s)	0.1337	0.027	*
y_prec	mean precipitation of previous 12 months (mm)	0.0371	0.353	
veg_cov	cover of vascular plants (%)	0.2604	0.001	***
peat_cov	cover of *Sphagnum* moss (%)	0.8017	0.001	***
moss_cov	cover of non-*Sphagnum* mosses (%)	0.3880	0.001	***
peat_h	*Sphagnum* lawn thickness (cm)	0.6585	0.001	***
water	mean water table (relative to surface of *Sphagnum* lawn) (cm)	0.2655	0.001	***

inhabit a wide variety of habitats, including peatlands. Classification was based on Platen et al. (1999) following details described in Muster et al. (2015). The species quality index (SQI), a single numerical descriptor for the quality of a species assemblage (Foster et al. 1990), was calculated as described in Muster et al. (2015) based on rarity categories taken from Blick et al. (2016).

Environmental data.—We collected data on 15 environmental variables with potential impact on the spider communities (Table 1). Climate data (temperature, relative humidity, wind speed, radiation) were downloaded from https://uol.de/wetter for the weather station at the University of Oldenburg (ca. 15 km south of the Sphagnum farm). Precipitation data for Rastede (ca. 4 km southwest of the farm) were extracted from DWD Climate Data Center (2019). For the climate data, we included mean values for the trapping period of each year as well as mean values for the 12-months prior to the trapping period.

Cover of *Sphagnum* mosses, other moss species and vascular plants (estimated visually 'by eye' in percentages), as well as *Sphagnum* lawn thickness (five measurements *per* plot), were recorded in >350 permanent observation plots of 25 × 25 cm that were randomly distributed over the study site. Data were recorded once annually during May to June. We used annual mean values for the *Sphagnum* production fields in which the pitfall plots were located.

Water tables were monitored using automatic data loggers in ditches, one logger in each production system (Brust et al. 2018). As the *Sphagnum* lawn is highly permeable, water tables in the lawn are similar to the ditch water tables (Brust et al. 2018). The water tables were expressed relative to the (upgrowing) peatmoss surface in the pitfall plots. We calculated mean values for the active trapping periods (May and June) of each year, except for water level 2011 for which – in absence of data for May and June – the July 2011 value was taken.

Data analysis.—To assess community changes over time, we applied generalized estimating equations (GEEs) to account for temporal pseudoreplication (i.e., non-independence of samples). Data were averaged per plot, except for abundance, for which individual traps were analysed. GEEs were run using the *geeglm* function in the R package 'geepack' (Højsgaard et al. 2006) with Poisson error structure for the count data (richness, abundance), Gaussian error distribution (proportion of peatland spiders, Shannon diversity index) and Gamma error structure with log-link (proportion of peatland specialists). The correlation structure was defined as 'exchangeable' with plot as the grouping variable (and trap for abundance). To test for significant differences between years, Tukeys post hoc tests were performed, using the *lsmeans* function in the R package 'emmeans' (Lenth 2020) to adjust for multiple comparisons.

We applied non-metric multidimensional scaling (NMDS) to visualize changes in the spider community composition over time. NMDS was performed on the Hellinger-transformed matrix of annual plot means of standardized abundance (specimens/trap/day) with the *metaMDS* function in the R package 'vegan' (Oksanen et al. 2019), using the Bray-Curtis dissimilarity index. In a first analysis, we put the observed temporal community pattern in the Sphagnum farm into context with neighboring peatland habitats that show various degrees of anthropogenic impact. The reference plots were studied from 2011 to 2013 and are described in detail in Muster et al. (2015). We used indicator species analysis (De Cáceres & Legendre 2009) to identify species that are significantly associated either with the Sphagnum farm or with the seminatural reference plots. Indicator species analysis was performed on the matrix of standardized abundance (specimens/trap/day) for annual means (Sphagnum farm) and plot means (reference sites) using the function *multipatt* in the R package 'indicspecies' (De Cáceres et al. 2020).

A second ordination analysis aimed to identify relationships between community succession and environmental variables in the Sphagnum farm. Environmental vectors from the parameters in Table 1 were fitted onto the NMDS ordination and tested for significance by 999 permutations (*envfit* function in 'vegan'). Environmental vectors with $P < 0.05$ were considered significant, but only vectors with $P \leq 0.001$ were plotted onto the ordination (Fig. 4).

A quantitative assessment of compositional change through time was approached by estimation of biodiversity turnover rates. We calculated the richness-based species-exchange ratio

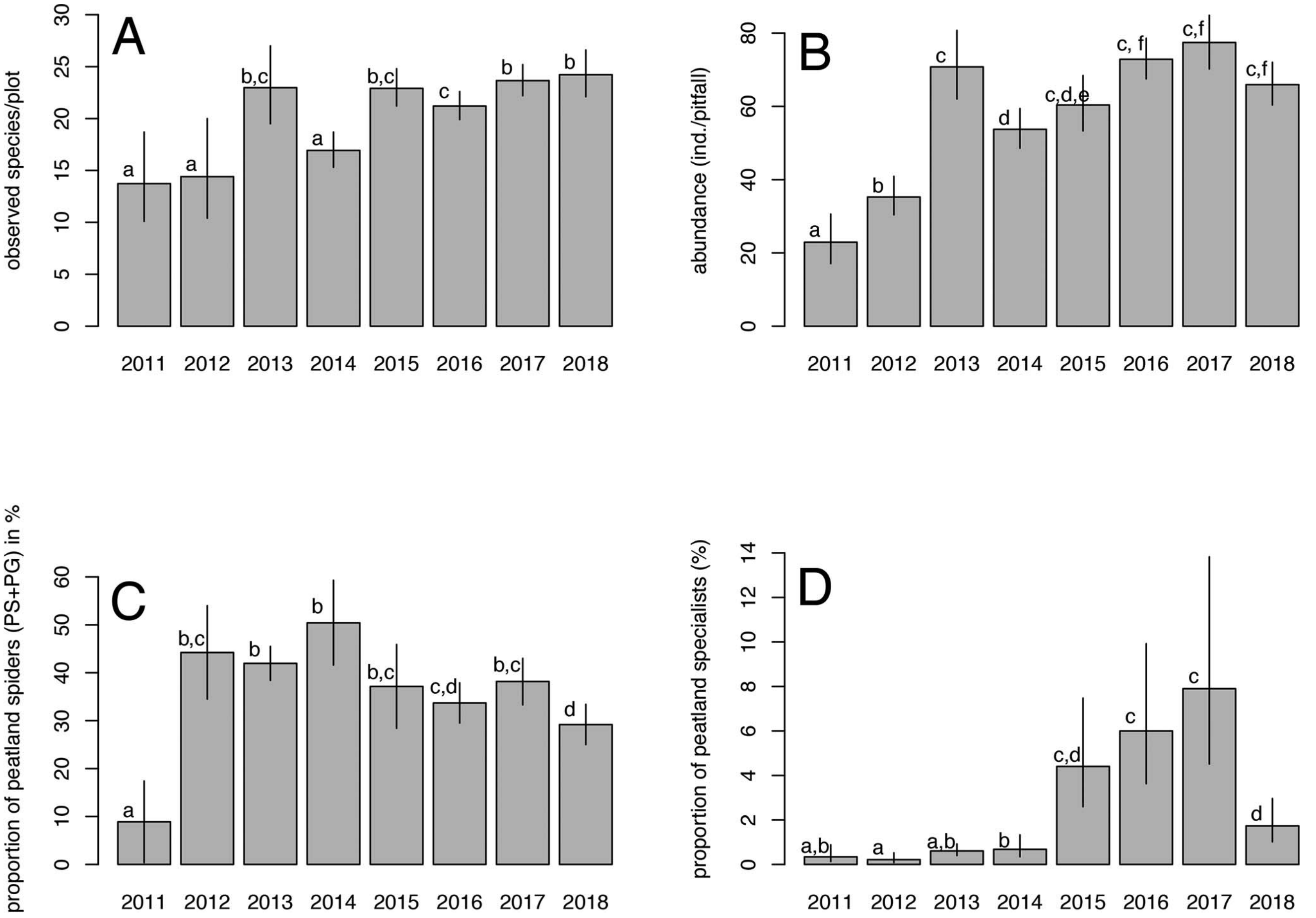

Figure 2.—Change in biodiversity parameters of spider assemblages in the Rastede Sphagnum farming site from 2011 to 2018. A. Differences in species richness (GEE-p, $\chi2 = 3268$, $df = 7$, $P < 0.001$). B. Differences in abundance (GEE-p, $\chi2 = 164$, $df = 7$, $P < 0.001$). C. Differences in the abundance proportion of peatland spiders (PS+PG) (GEE-n, $\chi2 = 395$, $df = 7$, $P < 0.001$). D. Differences in the abundance proportion of peatland specialist species (GEE-g, $\chi2 = 1216$, $df = 7$, $P < 0.001$). Bars indicate 95% confidence intervals. Pairwise comparisons (Tukeys post hoc test, $P < 0.05$) are presented with lower case letters, values with identical letters are not significantly different.

(SERr), which is the complement of Jaccard's similarity index, and the abundance-based species-exchange ratio (SERa), which is closely related to Simpson's diversity index, as described in Hillebrand et al. (2018). Both metrics reflect the proportional exchange between earlier and later samples in a time series and can take values between 0 (no exchange) and 1 (complete exchange of species and their relative abundances). We calculated the exchange ratios among subsequent years by treating each plot of five pitfalls as an individual site. All statistical analyses were carried out in R (R Development Core Team 2019).

RESULTS

Within the first seven years since establishment of the Rastede Sphagnum farm (2011–2018), a total of 16,247 specimens of 68 species of spiders and one harvestman species were collected from non-harvested *Sphagnum* plots. 14,212 adult specimens (87%) were determined to species level (Appendix 1). Original data are available in supplementary Table S2, online at http://dx.doi.org/10.1636/JoA-S-19-074.s2.

Species richness changed significantly over time (GEE-p, $\chi2 = 3268$, $df = 7$, $P < 0.001$), but remained almost constant from 2013–2018 (Fig. 2A). Similarly, spider abundance changed significantly over time (GEE-p, $\chi2 = 164$, $df = 7$, $P < 0.001$) with a plateauing trend since 2013 (Fig. 2B). The Shannon diversity index (H) showed an increasing trend through time (GEE-n, $\chi2 = 1549$, $df = 7$, $P < 0.001$), with lowest mean in 2012 (1.89) and highest mean in 2017 (2.62) (Table 2).

The species pool of 69 observed species comprised seven peatland specialists (10%) and eleven peatland generalists (16%), all others were classified as peatland tolerants (Appendix 1). The abundance proportion of spiders with strong association to peatlands (PS+PG) showed significant temporal variation (GEE-n, $\chi2 = 395$, $df = 7$, $P < 0.001$). Peatland spiders were rare in the year of establishment of the farm, but achieved the ultimate level at an early stage of the succession (Fig. 2C). Considering peatland specialists separately, again we observed significant changes in abundance proportion through time (GEE-g, $\chi2 = 1216$, $df = 7$, $P < 0.001$). Up to 2014, the stenotopic peatland species were recorded only in few specimens, but from 2014 to 2017, there was a significant increase up to 8% of the activity dominance (Fig. 2D). On the other hand, the species quality index (SQI), which takes into account the frequency distribution of all

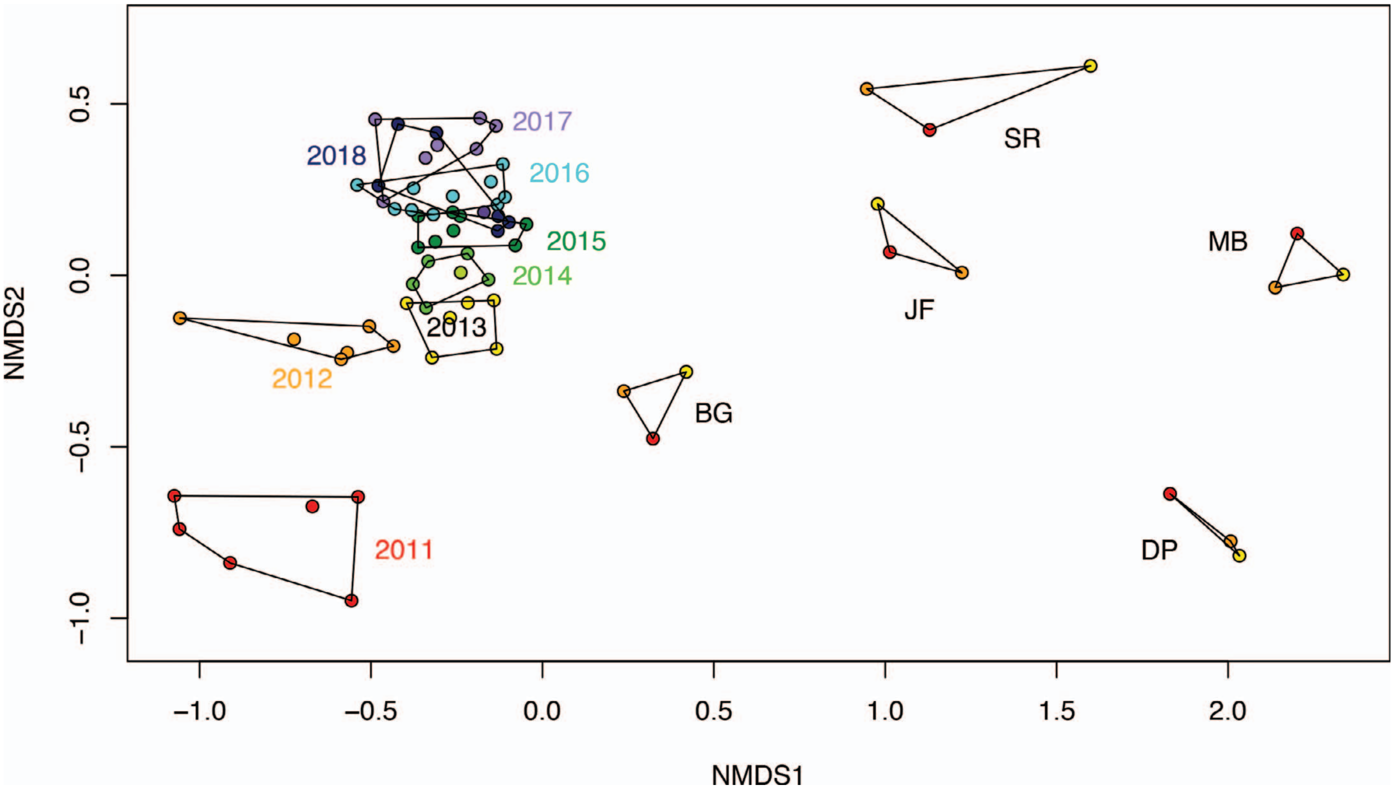

Figure 3.—Non-metric multidimensional scaling (NMDS) ordination of spider community composition for a time series in the Rastede Sphagnum farm (annual plot means for 2011 to 2018) compared to seminatural reference sites (annual plot means for 2011 to 2013). Each year is shown in a different colour. Convex hulls designate year for the plots of the Sphagnum farm and site for the reference plots. Reference site abbreviations: BG–bog grassland, DP–degraded bog, JF–*Juncus* fallow, MB–myrtle bushes, SR–sedge reed. Ordination of samples is based on Hellinger-transformed species abundances (individuals/pitfall/day) and Bray Curtis dissimilarities. Stress = 0.11.

species in the assemblage, showed a decreasing tendency as succession proceeded. The regression became more pronounced with higher weighting of rare species categories (Table 2).

Ordination analysis of the spider communities of the Sphagnum farm as compared to those of seminatural reference sites revealed distinctiveness of the Sphagnum farming sites through time (Fig. 3). There was a drastic shift of the Sphagnum farming site along the second NMDS axis within the first two years of Sphagnum farming, but since then overall compositional change in the communities has been marginal. Irrespective of the time since establishment, the communities of the farm remain completely separated from those of seminatural peatlands along ordination axis 1. At the species level, indicator species analysis revealed 11 species that were significantly associated with the Sphagnum farm, and 21 species with significant association to the reference plots (Table 3). Note that the indicator species of the Sphagnum farm include the Red-listed *Pirata piscatorius* (Clerck, 1757), which is threatened in Germany according to Blick et al. (2016).

Most of the examined environmental variables were significantly correlated with the temporal community pattern in the Sphagnum farm (Table 1, Fig. 4). *Sphagnum* cover was identified as the most influential parameter, as it showed the highest correlation coefficient with community-level variation. Merely radiation and precipitation in the 12 months prior to the trapping period had no explanatory value ($P > 0.05$). The directions of the temperature and humidity vectors demonstrate that the weather conditions became progressively warmer and less humid during our 7-year investigation period.

Analysis of biodiversity change over time revealed high annual turnover rates throughout the entire investigation period. Annual turnover in species identity (SERr) shows a slightly descending tendency over time (Fig. 5A). Nevertheless, the exchange in the species inventory did not fall below 30% between subsequent years. We observed a strong initial decline in the abundance-based exchange ratios (SERa) (Fig. 5B). In the first year of the succession in the Sphagnum farm, the dominance structure of the spider community changed almost completely. Since then, annual abundance-based turnover rates settled down on average values between 30%–40%, with a slightly increasing trend in recent years.

DISCUSSION

Sphagnum farming is a new type of paludiculture, hence the suitability of artificial *Sphagnum* lawns as potential habitat for the specialised fauna of bogs has not been explored over longer periods. For the initial two years of peatmoss growth, Muster et al. (2015) demonstrated a rapid change in the spider communities of the Rastede Sphagnum farm, with dominance shifting from disturbance specialists (pioneer species) towards generalised peatland species. Spider communities of the

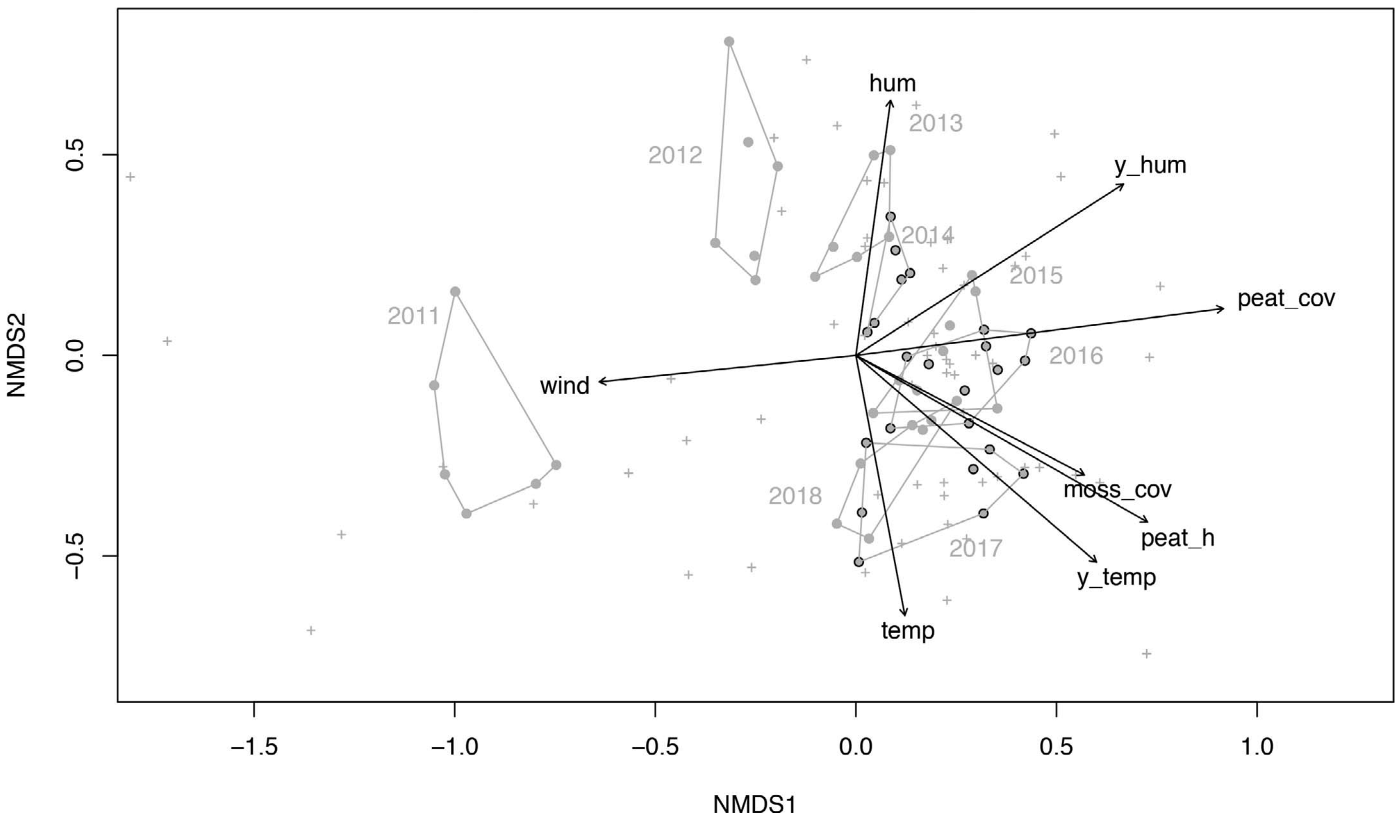

Figure 4.—Fitting of significant environmental vectors ($P \leq 0.001$) to the NMDS ordination of spider communities in the Rastede Sphagnum farm. Ordination of plots (means of 5 pitfalls) is based on Hellinger-transformed species abundances and Bray Curtis dissimilarities. Stress = 0.13. Plots of identical years are enclosed by convex hulls. Grey crosses denote species positions. See Table 1 for variable codes.

Sphagnum farm did not converge with assemblages of simultaneously studied (very small) remnants of natural peatlands in the vicinity, but we still expected that communities would become more similar to those of the reference plots within longer time periods. This was based on ecological succession theory, whereby a gradual, continuous change along a monotonic path would be anticipated (Zedler & Callaway 1999). Spider community data from five more years of monitoring in the Rastede Sphagnum farm (2014–2018), however, do not support this hypothesis. The spider assemblages of the Sphagnum farm remained equally distant from the seminatural reference sites through the entire time series (Fig. 3). From 2013 onwards, the Sphagnum farm clustered tightly in the ordination space and did not show signals of an inherent trajectory. Is convergence towards more natural peatland communities only a very slow process, or will novel communities with a new balance persist through time?

To answer this question, we can learn from experience in wetland restoration, a widely used and intensely studied practise to compensate for historic and ongoing wetland losses. In both systems, i.e., newly created wetlands (e.g., Sphagnum farms) and restored wetlands, the abiotic condi-

Table 2.—Biodiversity estimators for the spider community in the Rastede Sphagnum farm from 2011 (year of establishment) to 2018. SQI-L – Species quality index with linear weighting of rare species; SQI-E – Species quality index with exponential weighting of rare species.

	2011	2012	2013	2014	2015	2016	2017	2018
no. pitfalls	30	30	30	30	40	50	35	35
total abundance	629	947	2021	1523	2395	3642	2748	2342
individuals (pitfall mean)	20.97	31.57	67.37	50.77	59.88	72.84	78.51	66.91
adult spiders (total)	600	880	1812	1313	2075	3149	2340	2043
adults (pitfall mean)	20.00	29.33	60.40	43.77	51.88	62.98	66.86	58.37
no. observed species	29	26	39	30	43	40	44	40
species (plot mean)	13.50	14.17	22.67	16.67	23.00	21.20	23.43	24.00
Shannon-H (pitfall mean)	2.02	1.89	2.25	2.13	2.59	2.49	2.62	2.59
SQI-L (plot mean)	1.69	1.58	1.67	1.57	1.60	1.63	1.61	1.55
SQI-E (plot mean)	2.97	2.85	2.79	2.63	2.56	2.65	2.50	2.48

Table 3.—Significant indicator species ($P < 0.05$) for the Sphagnum farm and seminatural peatland habitats in the surroundings.

species	A[a]	B[b]	IndVal[c]	*P* value[d]
Sphagnum farm				
Pirata piscatorius (Clerck, 1757)	0.9865	1	0.993	0.005**
Bathyphantes gracilis (Blackwall, 1841)	0.953	1	0.976	0.004**
Oedothorax fuscus (Blackwall, 1834)	0.95	1	0.975	0.004**
Arctosa leopardus (Sundevall, 1833)	0.9269	1	0.963	0.007**
Xysticus kochi Thorell, 1872	1	0.875	0.935	0.012*
Pirata piraticus (Clerck, 1757)	0.8617	1	0.928	0.011*
Pardosa amentata (Clerck, 1757)	0.855	1	0.925	0.014*
Gongylidiellum vivum (O. Pickard-Cambridge, 1875)	0.9432	0.875	0.908	0.034*
Xysticus cristatus (Clerck, 1757)	0.8872	0.875	0.881	0.03*
Araeoncus humilis (Blackwall, 1841)	1	0.75	0.866	0.039*
Diplocephalus permixtus (O. Pickard-Cambridge, 1871)	0.9985	0.75	0.865	0.028*
Seminatural reference plots				
Diplostyla concolor (Wider, 1834)	1	1	1	0.004**
Trochosa spinipalpis (F. O. Pickard-Cambridge, 1895)	0.9967	1	0.998	0.006**
Pelecopsis radicicola (L. Koch, 1872)	0.9925	1	0.996	0.006**
Ozyptila trux (Blackwall, 1846)	0.989	1	0.994	0.006**
Piratula hygrophila (Thorell, 1872)	0.989	1	0.994	0.015*
Pocadicnemis juncea Locket & Millidge, 1953	0.9694	1	0.985	0.004**
Rilaena triangularis (Herbst, 1799)	0.9601	1	0.98	0.005**
Bathyphantes parvulus (Westring, 1851)	1	0.8	0.894	0.01**
Euryopis flavomaculata (C.L. Koch, 1836)	1	0.8	0.894	0.01**
Paranemastoma quadripunctatum (Perty, 1833)	1	0.8	0.894	0.01**
Saaristoa abnormis (Blackwall, 1841)	1	0.8	0.894	0.01**
Tallusia experta (O.P.-Cambridge, 1871)	1	0.8	0.894	0.005**
Drassyllus pusillus (C.L. Koch, 1833)	1	0.6	0.775	0.043*
Micaria pulicaria (Sundevall, 1831)	1	0.6	0.775	0.035*
Nemastoma lugubre (O.F. Müller, 1776)	1	0.6	0.775	0.035*
Robertus lividus (Blackwall, 1836)	1	0.6	0.775	0.026*
Trochosa terricola Thorell, 1856	1	0.6	0.775	0.04*
Walckenaeria vigilax (Blackwall, 1853)	1	0.6	0.775	0.032*
Zora spinimana (Sundevall, 1833)	1	0.6	0.775	0.035*
Oedothorax gibbosus (Blackwall, 1841)	0.9398	0.6	0.751	0.035*
Micrargus herbigradus (Blackwall, 1854)	0.9392	0.6	0.751	0.035*

[a] Positive predictive value of the species as indicator of the site group

[b] Sensitivity of the species as indicator of the site group

[c] Indicator value: a measure of the association between a species and a site group

[d] *P* value from 1000 permutations, * < 0.05, ** < 0.01

tions may correspond to the target sites (natural peatland habitats), but biotic colonization often lags behind, as it depends largely on landscape context (source populations in the vicinity) and dispersal abilities of particular taxa. There is growing evidence suggesting that wetland restoration fails to recover function and structure of natural wetlands (Moreno-Mateos et al. 2012; Anderson & Rooney 2019). Experience from restoration studies has also demonstrated that commonly used metrics to detect biodiversity trends (species richness, abundance/density, Shannon-diversity, evenness) are inadequate to describe faunal change and rehabilitation success. For example, macroinvertebrate richness and abundance of restored and created wetlands converged within 5 to 10 years with reference assemblages (Moreno-Mateos et al. 2012). Similarly in restored mines, almost half of the taxa attained equal or better density and species richness values in rehabilitated areas as compared to undisturbed areas, but community similarity was hardly ever achieved (Cristescu et al. 2012). The contrast between remarkably fast recovery in species richness and abundance as opposed to persistent compositional differences from the pre-disturbed stage can now be considered as a general pattern in biodiversity restoration. In particular, the small, native, poor-dispersing taxa remain absent or considerably less abundant in rehabilitated areas (Watts & Mason 2015; Alignan et al. 2018).

We observed an intriguingly similar pattern for spider community succession in the Sphagnum farm. Species richness as well as spider abundance reached plateau values within the first three years of *Sphagnum* growth. Wetland-dependent spiders rapidly colonized the Sphagnum farm, and several years after establishment the spider assemblages were dominated by wolf spiders classified as peatland generalists, such as *Pirata piraticus*, *P. piscatorius* and *Piratula latitans* (Blackwall, 1841), or wetland opportunists, such as *Arctosa leopardus*, *Pardosa amentata* and *P. prativaga* (L. Koch, 1870). Nevertheless, only a subset of characteristic spiders of natural peatlands were recorded in the Sphagnum farm. Even though we observed a significant increase in the proportion of specialized peatland species from 2014 to 2017, stenotopic target species of ombrotrophic peatlands (bogs fed exclusively

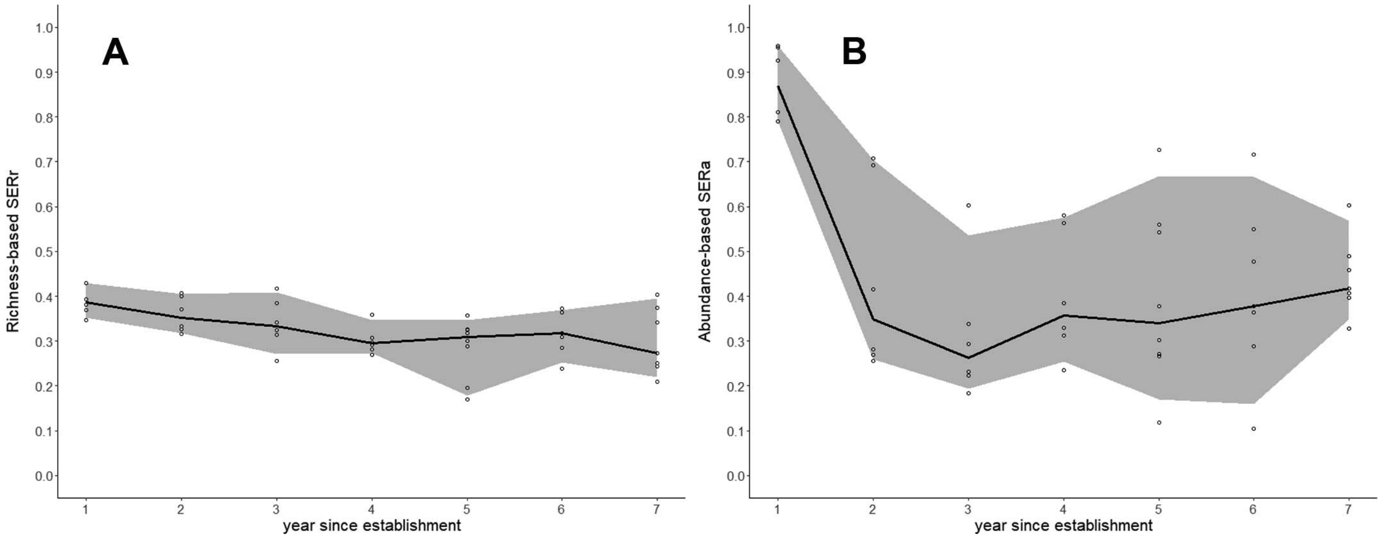

Figure 5.—Annual turnover rates in spider communities in the Rastede Sphagnum farm based on plot means. A. Richness-based species exchange rate (SERr). B Abundance-based species exchange rate (SERa). Grey shading represents 5%–95% quantiles, the black lines represent the median.

by direct precipitation), for example *Agyneta mossica* (Schikora, 1993), are still absent from the study site. Such rare, specialized, and apparently little dispersing species are systematically disadvantaged on isolated habitat fragments (Tscharntke et al. 2002). But dispersal limitation may not be the only constraint. This is demonstrated by the stenotopic wolf spider *Pardosa sphagnicola* (Dahl, 1908), which has been recorded in the Rastede Sphagnum farm in 2013 by a single female. Since then, no more specimens of this species have been collected in the study site. Thus, habitat deficiency may also impede successful establishment of populations of peatland specialists. Muster et al. (2015) already stressed the structural homogeneity of Sphagnum farming sites as opposed to pristine bogs, as caused, among other factors, by weed management necessary due to high nutrient inflow via the irrigation system (Temmink et al. 2017).

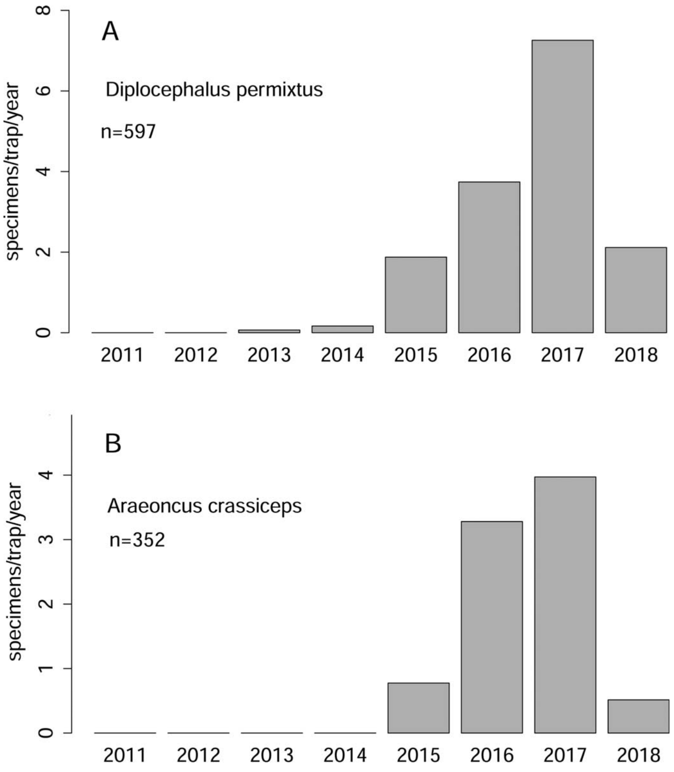

Figure 6.—Temporal pattern of population growth in two species of dwarf spiders (Linyphiidae) in the Rastede Sphagnum farm. A. *Diplocephalus permixtus*. B. *Araeoncus crassiceps*.

The observed levelling-off in species richness and abundance trends should not be mistaken as indication for reaching equilibrium state in the spider communities. Biodiversity change comprises more than variation in species richness, it includes the identity of species and the associated functional traits (Hillebrand et al. 2018). Our analysis revealed steady and high composition turnover rates in the Sphagnum farm since establishment of the *Sphagnum* lawn. High turnover rates are characteristic for communities of small habitat islands (Tscharntke et al. 2002). The dimension of unpredictable compositional change is best demonstrated by the temporal dynamics in two species of dwarf spiders (Linyphiidae). *Diplocephalus permixtus* inhabits a variety of wetland habitats, but is a poor-dispersing species (Buchar & Růžička 2002). The first specimen in the Rastede Sphagnum farm was recorded in 2013. Since 2015 the species has shown a rapid proliferation and in 2017 it reached 10.8% of the total spider abundance at the site (Fig. 6A). *Araeoncus crassiceps* (Westring, 1851) has been rated as a peatland specialist by Buchar & Růžička (2002). This species arrived at the study site no earlier than 2015, but only one year later it reached a dominance of 5.8% (Fig. 6B). As the first records of these spiders (and some other rare peatland species) coincide with the beginning of our sampling in PA1, one might assume prevalence of spatial over temporal effects. However, we did not find consistent tendencies across species. The relative abundance of *Diplocephalus permixtus* was not different in both sections of the farm (Mann-Whitney test, W = 121.5, $P = 0.88$), while it differed between PA1 and PA2 in *Araeoncus crassiceps* (Mann-Whitney test, W = 121.5, $P = 0.0028$). On the other hand, both species experienced strong declines in 2018, the year of the "summer of the century" in Germany with exceptionally warm and dry conditions. Averaged over Germany, the mean temperature in spring 2018 (March–May) was 10.2°C and in summer (June–August) it was 19.3 °C, an anomaly of plus 2.5 K and 3 K, respectively, compared to the international climatological reference period 1961–1990. Mean precipitation was 140.6 mm in spring and 129.4 mm in summer, corresponding to anomalies of minus 24.4% and minus 45.9 % compared to the average for 1961–1990 (DWD 2020). We suspect that the observed reduction in activity densities (this is what pitfalls measure) of these species may be attributable to the particular weather circumstances in that year. Our analyses have shown significant effects of weather variables on the activity pattern of the spider communities. Peatland species are adapted to cold microclimatic conditions. Thus, they may show less activity in warm periods, even if the water level remains constantly high, as assured through water management in the Sphagnum farm (Brust et al. 2018). Would we ever be able to predict such colonization dynamics that depend on highly stochastic components? We argue that even sophisticated modelling will not be able to substitute for continuous biodiversity monitoring of faunal succession in novel created habitats.

The final trajectory of the communities remains unclear. The main environmental driver for structuring the spider assemblages in the Rastede Sphagnum farm – *Sphagnum* cover – approached 100% in the recent years and therefore will become less influential in future. Our study period is still too short to deduce the final state of the succession course, and also effects of harvesting were not yet included in the analysis. Recovery times in case of spontaneous wetland regeneration were estimated to be very long, with 52% of wetlands having a recovery time > 1,000 years (Pezzati et al. 2018). Therefore, management activities have been proposed to assist the ecosystem to rebuild its diversity, including assisted dispersal or introduction of poor-dispersing target species. Active intervention has been shown to speed up the recovery process by two orders of magnitude (Pezzati et al. 2018). For example, soil transfer did promote the establishment of characteristic beetle assemblages in rehabilitation of a Mediterranean steppe territory (Alignan et al. 2018). Given the large potential of Sphagnum farms as a surrogate habitat for at least a selection of endangered bog species, translocation of faunal species or peatmoss material could be considered to raise peatland specific biodiversity. Alternatively, we should accept the distinctiveness of the invertebrate communities in Sphagnum farming sites from communities in natural peatlands and consider Sphagnum farming as a large-scale experiment for the colonization and community formation of *de novo* created wetlands. Our results indicate that new community members and transient species may further enhance the conservation value of the site, as seen in the high species quality index values in the initial phase. However, the first objective of Sphagnum farming is commercially profitable biomass production. Thus, timing, frequency and techniques of harvesting will have a crucial impact on the development of the sites and their communities. Harvesting cycles of 3–5 years are envisioned (Wichmann et al. 2020), but field experience is restricted and innovative harvesting machinery still needs to be developed (Gaudig et al. 2018). In this paper, we focussed on the invertebrate succession in the relatively undisturbed phase of initial peatmoss growth. The effects of harvesting are currently being studied in the Rastede Sphagnum farm in a follow-up project. Preliminary results one year after harvest indicate a decrease of population density but not in species composition and diversity, illustrating that Sphagnum farming – in contrast to drainage-based land use – has a large potential as a surrogate habitat for at least a selection of endangered bog species.

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Appendix 1. —Species occurrence data from the Rastede Sphagnum farming site from 2011 to 2018 with ecological classification. RC – rarity category (from Blick et al. 2016): vc very common, c common, mc moderately common, r rare, er extremely rare. PA – peatland association (based on Platen et al. 1999): PS peatland specialist, PG peatland generalist, PT peatland tolerant. DT – disturbance tolerance (based on *Originaliy of habitat* as given by Buchar & Růžička 2002): DI disturbance intolerants, DG disturbance generalists, DS disturbance specialists.

family/species	2011	2012	2013	2014	2015	2016	2017	2018	∑	RC	PA	DT
Theridiidae												
Enoplognatha mordax (Thorell, 1875)				1	4	2			**7**	mc	PT	DI
Robertus heydemanni Wiehle, 1965	11	3	1	2	9	2	10	1	**39**	er	PT	DS
Theonoe minutissima (O. Pickard-Cambridge, 1879)					1				**1**	r	PS	DI
Linyphiidae												
Agyneta decora (O. Pickard-Cambridge, 1871)		1	2				1		**4**	mc	PS	DI
Agyneta rurestris (C. L. Koch, 1836)					1				**1**	vc	PT	DS
Araeoncus crassiceps (Westring, 1861)					31	164	139	18	**352**	mc	PS	DG
Araeoncus humilis (Blackwall, 1841)	12		2	1	1		3	1	**20**	vc	PT	DS
Bathyphantes approximatus (O. Pickard-Cambridge, 1871)			5		4	2	2	1	**14**	vc	PT	DG
Bathyphantes gracilis (Blackwall, 1841)	16	24	111	72	84	68	139	78	**592**	vc	PT	DS
Centromerita bicolor (Blackwall, 1833)			1					1	**2**	vc	PT	DS
Ceratinella brevipes (Westring, 1851)	1			1	20	23	120	30	**195**	c	PT	DG
Ceratinella brevis (Wider, 1834)			1						**1**	vc	PT	DG
Cnephalocotes obscurus (Blackwall, 1834)	1		1				1	2	**5**	vc	PG	DG
Dicymbium nigrum brevisetosum Locket, 1962			4	1	2	3	1	3	**14**	vc	PT	DS
Diplocephalus permixtus (O. Pickard-Cambridge, 1871)			2	5	75	187	254	74	**597**	c	PT	DI
Dismodicus bifrons (Blackwall, 1841)					1				**1**	vc	PT	DG
Erigone arctica (White, 1852)	1								**1**	r	PT	na
Erigone atra Blackwall, 1833	183	21	7	4	8	1	11	4	**239**	vc	PT	DS
Erigone dentipalpis (Wider, 1834)	158	2			5	1	2	4	**172**	vc	PT	DS
Erigone longipalpis (Sundevall, 1830)	5	1							**6**	mc	PT	na
Erigonella hiemalis (Blackwall, 1841)					1				**1**	vc	PT	DG
Erigonella ignobilis (O. Pickard-Cambridge, 1871)			1			4	6	3	**14**	r	PS	DI
Glyphesis servulus (Simon, 1881)						1			**1**	r	PT	DI
Gnathonarium dentatum (Wider, 1834)			3	1	1	2		1	**8**	c	PT	DG
Gongylidiellum vivum (O. Pickard-Cambridge, 1875)	2		2	6	48	21	46	15	**140**	c	PS	DG
Lophomma punctatum (Blackwall, 1841)			1				1		**2**	c	PS	DG
Mermessus trilobatus (Emerton, 1882)					2		1		**3**	vc	PT	DS
Micrargus herbigradus (Blackwall, 1854)					1				**1**	vc	PT	DG
Micrargus subaequalis (Westring, 1851)							1		**1**	vc	PT	DG
Oedothorax apicatus (Blackwall, 1850)	1						1		**2**	vc	PT	DS
Oedothorax fuscus (Blackwall, 1834)	118	128	40	15	93	129	195	320	**1038**	vc	PT	DS
Oedothorax gibbosus (Blackwall, 1841)							1		**1**	vc	PG	DG
Oedothorax retusus (Westring, 1851)	6	5				1	7	11	**30**	vc	PT	DS
Palliduphantes pallidus (O. Pickard-Cambridge, 1871)							1		**1**	vc	PT	DG
Pelecopsis parallela (Wider, 1834)	2	2	1		1	4			**10**	vc	PT	DS
Pelecopsis radicicola (L. Koch, 1872)					1				**1**	c	PT	DG
Pocadicnemis juncea Locket & Millidge, 1953					1			2	**3**	vc	PT	DG
Porrhomma campbelli F. O. Pickard-Cambridge, 1894							1		**1**	mc	PT	DI
Porrhomma microps (Roewer, 1931)							1		**1**	mc	PT	DI
Prinerigone vagans (Audouin, 1826)	1								**1**	mc	PT	na
Styloctetor compar (Westring, 1861)								1	**1**	mc	PT	DG
Tapinocyba insecta (L. Koch, 1869)						1			**1**	vc	PT	DG
Tenuiphantes tenuis (Blackwall, 1852)	1		4	8	2	9	1	3	**28**	vc	PT	DS
Tiso vagans (Blackwall, 1834)	7	1	4		1	6	2	5	**26**	vc	PT	DG
Walckenaeria nudipalpis (Westring, 1851)			1	2	4	5	7	5	**24**	vc	PG	DG
Tetragnathidae												
Pachygnatha clercki Sundevall, 1823		36	42	2	23	10	11	6	**130**	vc	PT	DS
Pachygnatha degeeri Sundevall, 1830	6	1	7	1	16	13	96	18	**158**	vc	PT	DS

Appendix 1.—Continued.

family/species	2011	2012	2013	2014	2015	2016	2017	2018	∑	RC	PA	DT
Lycosidae												
Alopecosa cuneata (Clerck, 1757)	1	3	20			3	1	19	**47**	vc	PT	DS
Alopecosa pulverulenta (Clerck, 1757)	1	2	6	1	18	49	3	19	**99**	vc	PT	DS
Arctosa leopardus (Sundevall, 1833)	2	12	30	151	330	737	309	318	**1889**	c	PT	DG
Hygrolycosa rubrofasciata (Ohlert, 1865)			1						**1**	r	PG	DG
Pardosa amentata (Clerck, 1757)	14	163	412	133	99	355	52	76	**1304**	vc	PT	DS
Pardosa palustris (Linnaeus, 1758)	1	5	27	30	37	52	23	18	**193**	vc	PT	DS
Pardosa prativaga (L. Koch, 1870)	8	7	146	138	377	303	153	298	**1430**	vc	PT	DS
Pardosa pullata (Clerck, 1757)						1		1	**2**	vc	PG	DS
Pardosa purbeckensis F. O. Pickard-Cambridge, 1895	15	70	89	45	42	26	6	21	**314**	r	PT	na
Pardosa sphagnicola (Dahl, 1908)			1						**1**	r	PS	DI
Pirata piraticus (Clerck, 1757)	21	369	592	491	391	550	257	198	**2869**	vc	PG	DG
Pirata piscatorius (Clerck, 1757)	1	7	115	95	194	113	14	57	**596**	mc	PG	DG
Piratula hygrophila (Thorell, 1872)		2	16	8	11	10	6	4	**57**	vc	PT	DG
Piratula latitans (Blackwall, 1841)	3	2	47	80	68	182	414	293	**1089**	vc	PG	DG
Trochosa ruricola (De Geer, 1778)	1	7	22	11	34	72	28	55	**230**	vc	PT	DS
Trochosa spinipalpis (F. O. Pickard-Cambridge, 1895)					2	1			**3**	vc	PG	DG
Thomisidae												
Ozyptila trux (Blackwall, 1846)				1				1	**2**	vc	PT	DG
Xysticus cristatus (Clerck, 1757)		4	31	4	24	28	7	43	**141**	vc	PT	DS
Xysticus kochi Thorell, 1872		2	12	1	6	7	4	15	**47**	vc	PT	DG
Salticidae												
Attulus caricis (Westring, 1861)					1				**1**	r	PG	DG
Attulus floricola (C. L. Koch, 1837)							1		**1**	c	PG	DG
OPILIONES: Phalangiidae												
Rilaena triangularis (Herbst, 1799)			2	2		1			**5**	vc	PT	na