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Plant functional diversity and nutrient availability can improve restoration of floating fens via facilitation, complementarity and selection effects

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Abstract

1. Peat-forming wetlands, particularly floating fens that form the initial stages of these ecosystems, are declining globally due to excavation, dehydration and eutrophication. Restoration typically involves reestablishment of early-successional open-water stages, with oligotrophic conditions that are characteristic for these systems. However, restoration success is notoriously limited. A potential improvement may be to initiate succession by reintroducing of target plant species. Knowledge is therefore needed on (a) which plant functional groups should be reintroduced to stimulate fen formation; and (b) how to manage nutrient levels during restoration, considering that plant growth may be slow in oligotrophic conditions.
2. We hypothesized that increasing functional diversity of introduced species would stimulate the formation of peat-forming target communities, their biomass accumulation and expansion onto open water. We also hypothesized that nutrient availability would mediate the relative contribution of specific functional groups to these effects. We investigated this in 36 artificial outdoor ponds by manipulating plant functional diversity (clonal dominants, clonal stress-tolerators and interstitials) on constructed rafts with fen-forming communities, and subjected these to a range of nutrient loadings over 2 years.
3. Increasing functional diversity as well as increasing nutrient loadings had stimulating effects on plant biomass accumulation, cover formation and rhizome growth onto open water. Both complementarity (due to niche partitioning or facilitation) and selection effects were mechanisms underlying the diversity effect, with a constant relative importance over the entire range of nutrient availabilities. Different functional groups were important for biomass production at different nutrient availabilities. Rhizome formation by clonal stress-tolerators contributed disproportionately to open water colonization, identifying this functional group as key across all nutrient levels.

*Both authors contributed equally.

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4. *Synthesis and applications.* Restoration of floating fen communities can be stimulated during the first 2 years by introducing a high functional diversity of plant species. These include fast-growing clonal species, clonal stress-tolerators and interstitials, which facilitate each other. Restoration is dependent on the presence of clonal stress-tolerators such as *Calla palustris*, *Comarum palustre* and *Menyanthes trifoliata* for expansion onto the open water. Furthermore, restoration can start under a wide range of water nutrient levels, including eutrophic conditions.

KEYWORDS

assisted colonization, floating fen, functional diversity, peat formation, restoration, rhizome formation, terrestrialization, wetlands

1 | INTRODUCTION

Peat-forming wetlands provide a multitude of services, including carbon storage, water purification, water retention and habitat provisioning for typical and endangered species; and are of great cultural value to humans (Chimner, Cooper, Wurster, & Rochefort, 2017; Lamers et al., 2015; Mitsch, Bernal, & Nahlik, 2013; Verhoeven, 1992). However, these ecosystems have severely declined on a global scale due to excavation, dehydration and eutrophication (Dahl, 2011; Zedler & Kercher, 2005). This applies particularly to the species-rich communities typical for the onset of peat formation by the colonization of open water, such as floating fens (Hajkova, Hajek, & Kintrova, 2009; Soomers, Karssenberg, Verhoeven, Verweij, & Wassen, 2013), which have become very rare and are difficult to restore (Chimner et al., 2017). Past restoration projects have shown that species-rich, peat-forming communities seldom return naturally after reestablishment of their typical abiotic conditions (Lamers et al., 2015). This may be due to dispersal limitation, slow colonization or low recruitment of arriving diaspores in the reestablished abiotic conditions (Brederveld, Jähnig, Lorenz, Brunzel, & Soons, 2011; Fraaije, ter Braak, Verduyn, Verhoeven, & Soons, 2015b; Fraaije et al., 2015a; Sarneel, Soons, Geurts, Beltman, & Verhoeven, 2011; Van Leeuwen, Sarneel, van Paassen, Rip, & Bakker, 2014). Consequently, restoration projects may greatly benefit from species reintroductions (Chimner et al., 2017; Rochefort et al., 2016).

Introducing a wide selection of plant species typically stimulates development of target communities during ecosystem restoration, especially if this includes keystone species with important ecosystem functions (Geist & Hawkins, 2016; Lunt et al., 2013). At a given nutrient availability, species-rich plant communities are generally more productive than species-poor communities, which is known as a positive diversity–productivity relationship or overyielding (Balvanera et al., 2006; Cardinale, 2011; Hooper et al., 2005; Spehn et al., 2005). Overyielding can be caused by two primary mechanisms. First, species complementarity can increase productivity if intraspecific competition in monocultures exceeds interspecific competition in mixed communities; either because species or functional groups partition available resources (niche partitioning) or

because of positive species interactions (i.e. facilitation) (Cardinale et al., 2012; Hooper et al., 2005; Loreau & Hector, 2001). Second, productivity can increase due to a selection effect: at higher diversity the chance increases that a highly productive species or functional group is present (Loreau & Hector, 2001; Wardle, 1999).

Overyielding is well-documented for terrestrial ecosystems (Hooper et al., 2005), in which its strength can depend on abiotic conditions including nutrient availability (del Río, Schütze, & Pretzsch, 2014; Schmid, 2002). In wetland ecosystems, plant functional diversity has been shown to increase plant biomass (Engelhardt & Ritchie, 2001), decrease methane effluxes (Bouchard, Frey, Gilbert, & Reed, 2007; Schultz, Andrews, O'Reilly, Bouchard, & Frey, 2011) and change nitrogen cycling (Schultz, Bouchard, & Frey, 2012). However, for wetland ecosystems, current knowledge on the diversity–productivity framework and potential mediating effects of nutrients on relations within this framework is still limited (Giller et al., 2004). Which keystone plant functional groups should be introduced, and at which nutrient levels, is largely unclear. Especially for nutrient levels, the question remains whether it is better to restore oligotrophic conditions typical for peat-forming wetland systems (Verhoeven, 1986) and the associated (red-listed) plant species (Rydin, Jeglum, & Jeglum, 2013); or to stimulate plant biomass production by providing more nutrients to initiate succession and peat formation (Lawlor, Schulze, Beck, & Müller-Hohenstein, 2010). Nutrients change many processes within plants and interactions among plants (Kraiser, Gras, Gutiérrez, González, & Gutiérrez, 2011), and may therefore also affect mechanisms such as complementarity and selection effects.

Here, we aim to provide recommendations for the restoration of peat-forming, floating fen wetland communities by evaluating the effectiveness of manipulated functional diversity of introduced plants during the initial phase of restoration across a gradient of nutrient availability. We hypothesized that (a) increasing functional diversity of introduced species would stimulate the formation of peat-forming target communities, their biomass accumulation and expansion onto open water; and that (b) nutrient availability would affect the underlying mechanisms and mediate the relative contribution of specific functional groups

to these effects. We expected most biomass accumulation in the vegetation at very high nutrient levels (mediated by rapid biomass production of fast-growing, competitive helophytes such as *Phragmites australis*), but most expansion of the communities onto open water at low-to-intermediate nutrient levels (mediated by rapid clonal expansion of rhizomatous helophytes such as *Comarum palustre*). Furthermore, we anticipated that a third functional group, nonclonal helophytes, would be facilitated by the floating fen formation by either of the two other groups. We investigated this by manipulating functional diversity of experimental wetland plant communities for 2 years, after which we measured the accumulation of biomass as a proxy for vegetation carbon storage, and the formation of plant cover and rhizomes as proxies for colonization of open water.

2 | MATERIALS AND METHODS

2.1 | Experimental design

We experimentally studied the influence of functional plant diversity on biomass accumulation, cover and rhizome formation by wetland plant species over a nutrient gradient in 36 artificial outdoor ponds in Loenderveen, the Netherlands (52°12'41"N, 5°2'18"E). The ponds were square, 1.5 m deep, 5.0 × 5.0 m wide at the top and 3.0 × 3.0 m wide at the bottom and lined with waterproof foil. Each pond was filled with a 0.3 m layer of sand-clay mixture (10:1), and a 0.7 m water column from a nearby lake ("Waterleidingplas"). This lake water was used to initially fill the ponds, and subsequently used to control the water level via an overflow mechanism. This water was oligotrophic due to phosphate removal for drinking water (measured monthly during the 2-year experimental period ($n = 24$): mean total N = $2.71 \pm 0.42SD$ mg/L, mean total P = $0.008 \pm 0.005SD$ mg/L; Waternet, unpubl. data). No fish were present in the ponds. To prevent variation among ponds in possible nutrient uptake, submerged vegetation was removed each July from ponds with a submerged plant cover >60%. The artificially created ponds enabled us to experimentally manipulate nutrient availability and the functional diversity of introduced plants without interference of existing vegetation and/or environmental conditions.

We studied growth of nine typical wetland plant species in these ponds from September 2012 to September 2014. Seedlings of all species were grown from seeds in potting soil. When their above-ground parts measured ~0.05 m in height, the seedlings were divided over 126 artificial mats or rafts ("Röhrichtmatten," Bestmann Green Systems, Tangstedt, Germany) that were randomly distributed across all the ponds. Each pond received either three or five mats to ensure complete randomization of the experimental treatments. The mats (1.0 × 1.0 m) were made of a base layer of floating polyethylene strings with a coconut fibre mat fixed on top (Figure S1). The polyethylene strings were tied together, creating a floating mat with an open structure through which roots could grow into the water. The mats did not contain any nutrients, and were kept apart by a fixation

to the bottom of the ponds to prevent plant interactions between mats.

At the start of the experiment, 24 young plants were inserted into small holes cut into the coconut fibre top of each mat. Each mat received 24 individual plants belonging to one, two or three functional groups based on the classification method as initially proposed by Boutin and Keddy (1993) (Figure 1). These three functional groups differ in their functional morphology: clonal dominants (represented by *Typha latifolia*, *P. australis* and *Phalaris arundinacea*), clonal stress-tolerators (*Calla palustris*, *C. palustre* and *Menyanthes trifoliata*) and interstitials (*Alisma plantago-aquatica*, *Iris pseudacorus* and *Acorus calamus*). All species (except *A. plantago-aquatica*) are rhizomatous to some extent, but the tall clonal dominants typically have much longer creeping rhizomes than the shorter interstitials, while the much shorter clonal stress-tolerators proliferate via rhizomes and creeping stems extensively. The optimal habitat of the clonal stress-tolerators is more oligotrophic than that of the other two groups (species traits presented in Table S1). We manipulated functional diversity by regulating functional richness (i.e. the number of functional groups) instead of species diversity to make our results more widely applicable, and avoid the implicit assumption that all species are equally different from each other (Hooper et al., 2005). Our selection of three different species within each functional group makes the results per group more representative for species with that same functional role.

To investigate interactions among the three functional groups, mats received plants from either only one, two or all three of the functional groups—resulting in seven combinations of functional groups (Figure 1). Each functional group was always represented by all three species from that group. If multiple functional groups were present, the number of individual plants was the same for each functional group (Figure 1, Table S2). Planting densities on the mats resembled realistic and cost-effective planting schemes as applied locally in restoration projects in the Netherlands.

To investigate possible effects of nutrient availability on the developing plant communities, we manipulated nutrient loadings in the ponds throughout the experiment. Nine different loadings of both nitrogen and phosphorus were applied by weekly additions of NO_3NH_4 and KH_2PO_4 to the water column in the ponds (range 0–5.0 mg N and 0–0.5 mg P/L, details in Table S3) from April until October in both study years. Loadings mimicked a full range from oligotrophic to hypertrophic waters. To avoid stoichiometric effects, KH_2PO_4 and NO_3NH_4 were added in a ratio of 1:12.6 to obtain a N:P ratio of 10:1 g/g throughout all treatments. All combinations of functional groups were exposed to the whole nutrient gradient, with two replicates per combination in every nutrient treatment (Figure S2). Few species other than those selected for the functional groups spontaneously colonized on the mats. In total these were <5 species, dominated by *Mimulus guttatus* and *Bidens frondosa*, with a combined fresh weight always <10% of the total vegetation fresh weight. These species were removed in May, June, August and October 2013 and April, May, June and July 2014.

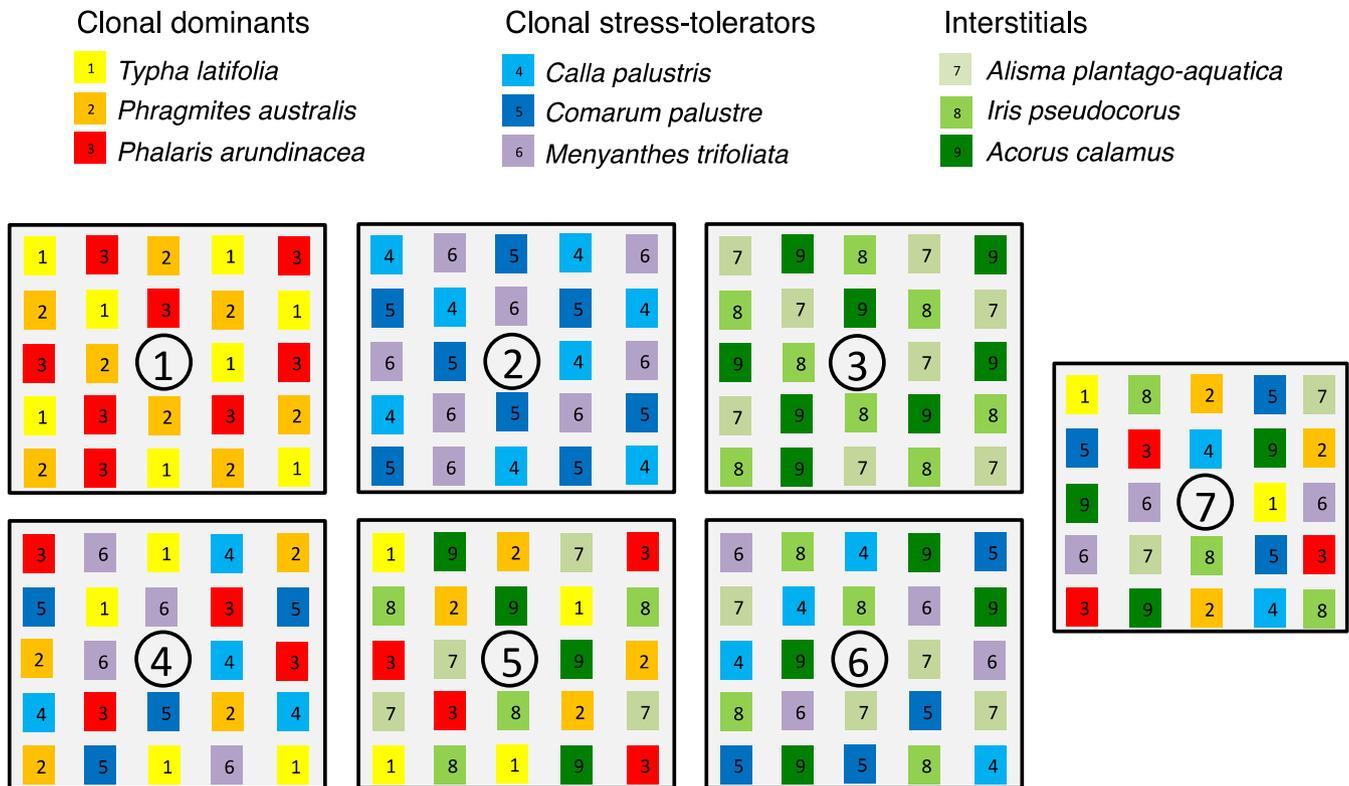


FIGURE 1 Schematic overview of the seven different possible planting combinations (indicated by encircled numbers) for the 126 experimental mats. Each mat (large squares) was planted with 24 individual plants (filled coloured squares) from nine different species belonging to three different functional groups

2.2 | Data collection

Data were collected per plant species per mat at the end of the experiment. First, we estimated the percentage of cover on each mat. Second, we recorded the presence (yes/no) and length (total in m) of rhizomes growing onto the open water surface (measured starting from the edges of the mats). Third, as an indicator of fen formation and ultimately vegetation carbon storage, all above-ground biomass per plant species that formed on the mats (so excluding rhizome biomass) was destructively harvested by collecting all plant material growing above the mats. All plant material was dried for at least 48 hr at 70°C, and weighed on a scale ($d = 0.1$ g). Most roots had grown into the polyethylene of the mat, which made it impossible to harvest root biomass representatively.

2.3 | Data analysis

We analysed how the development of vegetation on the mats was affected by the functional groups, combinations of functional groups, functional diversity and nutrient availability in multiple general(ized) linear mixed-effects models in R for statistics (R-Development-Core-Team, 2017).

Four dependent variables were used in all statistical analyses, calculated per mat (Model I) or per individual plant per functional group (Model II, III and IV): (a) above-ground living plant biomass, hereafter "biomass," which after two growing seasons ranged from

0.0 to 532.0 g dry weight per individual plant with a mean of 41.5 g; (b) percentage cover on the mats, hereafter "cover," after two seasons ranging from 0% to 25.3% formed by individual plants with a mean of 4.3%; (c) presence of rhizomes growing onto the open water from the sides of the floating mats, hereafter "rhizome presence," modelled as binomial variable (present on 79 of the 126 mats after two seasons); (d) length of rhizomes formed by individual plants, hereafter "rhizome length" (ranging from 0 to 9.63 m, with a mean of 0.45 m).

The mixed-effects models were fitted with one of four possible dependent variables: (a) biomass, (b) cover, (c) rhizome presence and (d) rhizome length. Residuals were normalized by natural log-transformations of biomass, cover and rhizome length, and analysed using package "nlme" (Pinheiro, Bates, DebRoy, & Sarkar, 2015). The presence of rhizomes was analysed as a binomial dependent variable using package "lme4" (Bates, Mächler, Bolker, & Walker, 2015). Nutrient loading into the ponds (ranging from 0 to 5.0 mg N/L and 0 to 0.5 mg P/L) was included as continuous predictor variable numerically ranging from 0 to 5, hence, estimated effect sizes in the models are presented on the scale of nitrogen loadings. Nutrient loading was centred by subtracting the mean from all values to improve interpretability (Raudenbush & Bryk, 2002). Intercepts in all models were allowed to vary by pond by including individual pond (36 levels) as random factor.

In Model I we tested whether cumulative values per mat calculated for either one of the four vegetation variables responded

to diversity (modelled as continuous predictor variable, ranging from one to three functional groups per mat), nutrient availability and their interaction. In Models II, III and IV we evaluated effects of treatments on vegetation variables calculated per individual plant. Model II analysed possible effects on vegetation variables of clonal dominants, Model III for clonal stress-tolerators and Model IV for the interstitials. Models II, III and IV tested whether particular functional groups responded to the presence of particular other functional groups, and hence examined possible complementarity effects in more detail. The presence of the other two functional groups was modelled as binomial fixed factors: either present (1) or not (0). For example, in Model II the biomass of clonal dominants was the dependent variable, therefore the presence of clonal stress-tolerators (1/0) and presence of interstitials (1/0) were included as fixed factors. Details on model selection are provided in Supporting Information Methods.

In addition to the mixed models, we applied randomization tests to quantify the effects of functional groups expressed in standard deviation units on three variables: total plant biomass, total plant cover and total rhizome length per mat (Gotelli, Ulrich, & Maestre, 2011). Our working hypothesis was that the presence or absence of a particular functional group significantly affected all three of these variables. The null hypothesis was that mats with and without a particular functional group would not differ more than expected by chance. This method has been developed for species, but we here applied it analogously to functional groups. More details can be found in Supporting Information Methods.

To disentangle possible complementarity and selection effects as underlying mechanisms explaining observed net diversity-productivity effects, we used the additive partitioning technique as described by Loreau and Hector (2001). For every mixture and for every nutrient level we calculated the net effect, the complementarity effect and the selection effect. More details can be found in Supporting Information Methods.

3 | RESULTS

3.1 | Effects of functional diversity and nutrient loading

Mean biomass (dry weight in g), cover (in %) and the probability of rhizome formation on the mats increased with functional richness and nutrient loading (Table 1, Figure 2, Table S4). The positive effects of increasing functional diversity were consistent across different levels of nutrient loading. The vegetation transgressively overyielded, that is, the maximum biomass and cover produced by the best mixed community (1,894 g dry weight and 100% cover per mat for mats with all three functional groups) exceeded the maximum biomass and cover produced by the best monoculture (1,288 g for the monoculture with interstitials and 90.5% cover per mat for the monoculture with clonal stress-tolerators). Biomass production, cover formation and the probability of rhizome formation on the mats increased with the number of functional groups

that were present (Figure 2a–c, Model Ia, b and c in Table 1, respectively). Rhizome length did not increase due to functional diversity (Figure 2d, Model Id in Table 1).

Nutrient addition had a much stronger effect than functional diversity on final plant biomass (Figure 2a–c, see also Figure S1). Mean biomass of all mats was 40 g when no nutrients were added, which increased 26-fold to 1,048 g at the highest nutrient loading. Nutrients affected coverage less than biomass, but again had a stronger effect on coverage than functional diversity. Mean cover ranged from 15% at the lowest nutrient level to 72% cover at the highest nutrient level (a fourfold increase). At the lowest nutrient level, rhizomes formed on 7 of 14 mats (50%), and at the highest nutrient level on 11 of 14 mats (79%); a relative increase by 58%. Furthermore, nutrient loading increased rhizome length >19-fold, from $0.90 \text{ m} \pm 0.45\text{SD}$ at the lowest, to $17.9 \text{ m} \pm 17.0\text{SD}$ at the highest nutrient level (Figure 2d).

3.2 | Relative contributions of the three functional groups

The three functional groups differed in their relative contributions to the vegetation that had formed on the mats after 2 years, and this relative importance depended on nutrient loading (Figure 3). Summed over all nutrient levels, biomass formed by clonal dominants was 11.7% of all formed biomass, which was less than the biomass formed by the clonal stress-tolerators (35.2%) or the interstitials (53.1%). At low nutrient loadings clonal stress-tolerators contributed most to biomass, while at high nutrient loadings the interstitials contributed more (significantly so if a functional groups standardize effect size exceeds 2.0, Figure 3a). Cover on the mats, summed over all nutrient levels, was mostly formed by the clonal stress-tolerators and interstitials (Figure 3b). Clonal dominants contributed 19.2% of the cover, clonal stress-tolerators 42.7% and interstitials 38.1%. Clonal stress-tolerators formed rhizomes on 64 of the 72 mats (89%) on which they were present, the clonal dominants on 29 of the 72 (40%) of the mats on which they were present, and the interstitials did not form rhizomes. The clonal stress-tolerators contributed most to the presence of rhizomes on the mats at all nutrient levels, while the relative contribution of clonal dominants to rhizome presence increased with increasing nutrient availability (Figure 3c). Clonal stress-tolerators also formed the longest rhizomes at all nutrient levels (Figure 3d): the rhizomes of clonal stress-tolerators grew farther onto the open water (mean distance from mats: $1.48 \text{ m} \pm 2.18\text{SD}$, maximum: 9.63) than rhizomes of clonal dominants (mean distance from mats: $0.09 \text{ m} \pm 0.13\text{SD}$, maximum: 0.52).

3.3 | Complementarity and selection effects among the functional groups

The positive effect of functional richness on biomass accumulation and cover formation could almost entirely be attributed to a species complementarity effect (Figure 4a,b). The positive

TABLE 1 Final model-averaged parameter estimates (β), their standard errors (SE), 95% confidence intervals and p -values for significant terms remaining in the models after model selection (for details on model selection see Table S4)

Model	Dependent variable	Predictor variable ^a	β^b	SE	95% CI	p -value	Back-transformed effect sizes ^c		
Ia	Biomass per mat	Intercept	4.45	0.23	4.00–4.90	<0.001			
		Nutrient	0.56	0.14	0.28–0.84	<0.001	Min: 40 g	Max: 1,048 g	26-fold increase
		Richness	0.26	0.11	0.037–0.49	0.02	Min: 251 g	Max: 367 g	1.46-fold increase
Ib	Cover per mat	Intercept	2.70	0.12	2.47–2.93	<0.001			
		Nutrient	0.29	0.05	0.18–0.40	<0.001	Min: 15%	Max: 72%	4-fold increase
		Richness	0.30	0.06	0.18–0.42	<0.001	Min: 25%	Max: 36%	1.48-fold increase
Ic	Rhizome presence per mat	Intercept	0.22	0.12	0.089–0.52	0.06			
		Nutrient	0.061	0.027	0.006–0.12	0.03	Min: 7/14 50% of mats	Max: 11/14 79% of mats	1.29-fold increase
		Richness	0.19	0.06	0.071–0.30	0.002	Min: 27/54 50% of mats	Max: 16/18 89% of mats	1.39-fold increase
Id	Rhizome length per mat	Intercept	0.27	0.33	–0.40 to 0.93	0.43			
		Nutrient	0.53	0.11	0.31–0.75	<0.001	Min: 0.90 m	Max: 17.9 m	19-fold increase
<i>Clonal dominants</i>									
IIb	Cover per plant	Intercept	0.82	0.08	0.67–0.98	<0.001			
		Presence clonal stress-tolerators	0.40	0.07	0.26–0.55	<0.001	Absent: 1.60%	Present: 3.34%	2-fold increase
		Presence interstitials	0.23	0.08	0.08–0.38	<0.01	Absent: 1.96%	Present: 2.98%	1.5-fold increase
IIc	Rhizome presence per plant	Intercept	0.52	0.08	0.37–0.69	<0.001			
		Presence interstitials	–0.25	0.11	–0.46 to –0.03	0.02	Absent: 19/36 mats rhizomes	Present: 10/36 mats rhizomes	2-fold lower chance with interstitials present
<i>Clonal stress-tolerators</i>									
IIIa	Biomass per plant	Intercept	3.27	0.09	3.08–3.51	<0.001			
		Nutrient	0.52	0.07	0.38–0.66	<0.001	Min: 9.3 g	Max: 144.1 g	16-fold increase
IIIb	Cover per plant	Intercept	1.62	0.08	1.46–1.78	<0.001			
		Nutrient	0.30	0.05	0.20–0.40	<0.001	Min: 1.98%	Max: 15.12%	7-fold increase
IIIc	Rhizome presence per plant	Intercept	0.90	0.04	0.81–0.98	<0.001			
		Nutrient	0.047	0.023	2.8×10^{-5} to 0.094	0.05	Min: 6/8 mats	Max: 8/8 mats	Minor effect
IIId	Rhizome length per plant	Intercept	–0.54	0.12	–0.84 to –0.23	<0.001			
		Nutrient	0.69	0.08	0.54–0.85	<0.001	Min: 0.13 m	Max: 5.0 m	38-fold longer
<i>Interstitials</i>									
IVa	Biomass per plant	Intercept	2.99	0.13	2.67–3.25	<0.001			
		Nutrient	0.88	0.08	0.71–1.00	<0.001	Min: 2.72	Max: 271.00	100-fold more
IVb	Cover per plant	Intercept	1.35	0.07	1.21–1.49	<0.001			
		Nutrient	0.30	0.026	0.25–0.36	<0.001	Min: 2.03 g	Max: 12.78 g	6-fold increase
		Presence clonal dominants	0.21	0.09	0.03–0.39	0.02	Absent: 4.49%	Present: 5.30%	1.18-fold increase
		Presence clonal stress-tolerators	0.29	0.09	0.10–0.47	<0.01	Absent: 4.21%	Present: 5.58%	1.33-fold increase

Notes. ^aFor binomial factors of functional group presence, the absence of functional groups was always the intercept. ^bFor nutrients, effect sizes are presented on the scale for nitrogen concentrations (ranging from 0 to 5.0 mg N/L). ^cEffect sizes on back-transformed scales are indicated with minimal and maximal values.

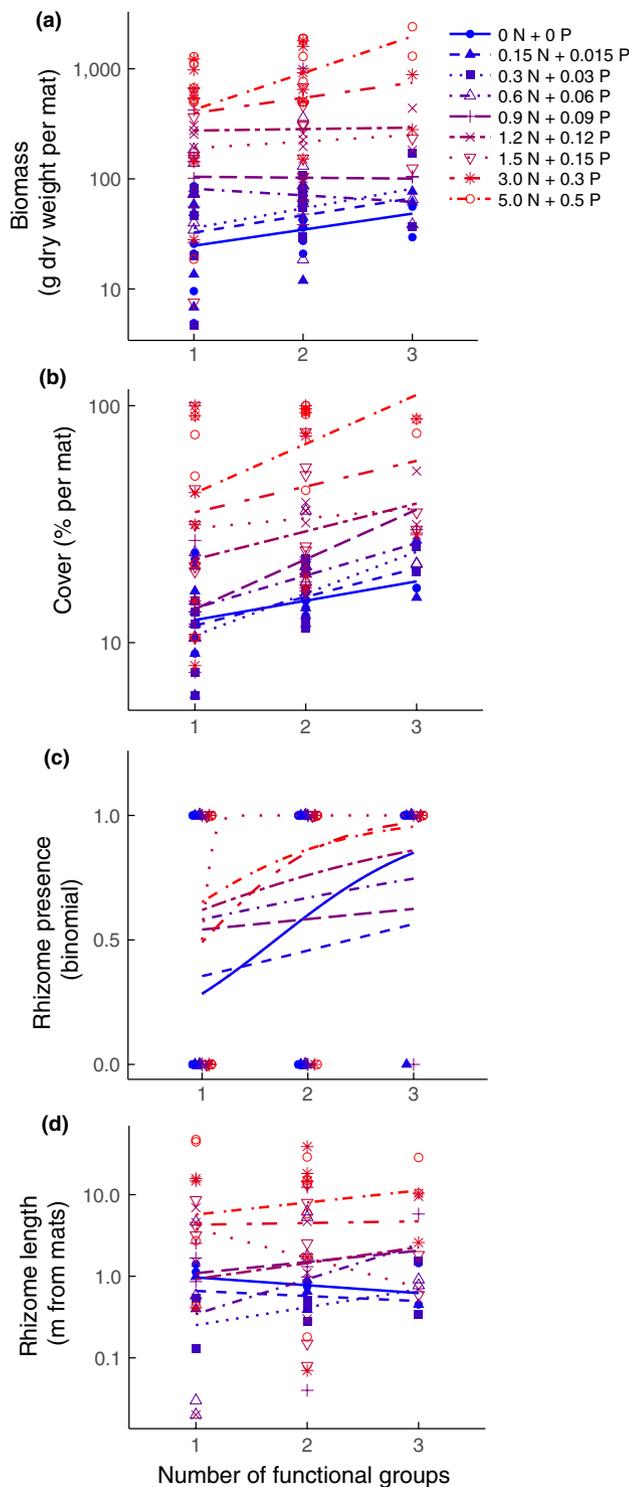


FIGURE 2 Biomass as gram dry weight per mat (a), coverage in percentage per mat (b), rhizome presence (1/0) (c) and rhizome length (d) in response to functional diversity (one, two or three functional groups) and nutrient loadings of nitrogen (N) and phosphorus (P). The vertical axes are log-scaled in panels a, b and d. (c) Overlapping points are staggered on the horizontal axis

relation between richness and the probability of rhizome formation was mostly due to a selection effect (Figure 4c), related to the increased probability to have clonal stress-tolerators present

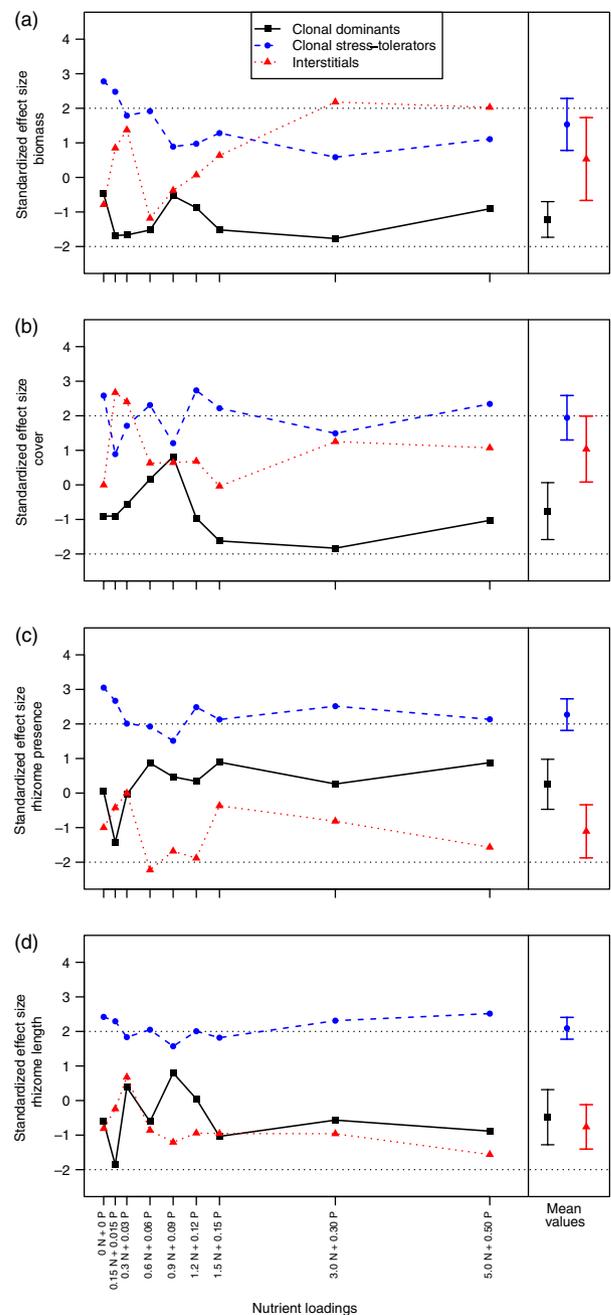


FIGURE 3 The relative contributions of the three different functional groups to (a) biomass, (b) cover, (c) rhizome presence and (d) rhizome length per mat at the different levels of nutrient loadings in mg/L. The vertical axis depicts the number of standard deviations that a functional group deviates from a random expected mean of equal contribution by every functional group, which is expressed in units of standardized effect size (SES). SES-values deviating more than the thresholds of 2.0 (dashed lines) from zero indicate that a functional group contributes significantly more (>2.0) or less (<-2.0) to a vegetation parameter than expected. SES-values are indicated for different nutrient loadings, and as mean values per functional group (\pm SE)

on mats with higher diversity. The same mechanisms remained important across the gradient of nutrient loadings, although the effect sizes increased proportionally to the increases of biomass and

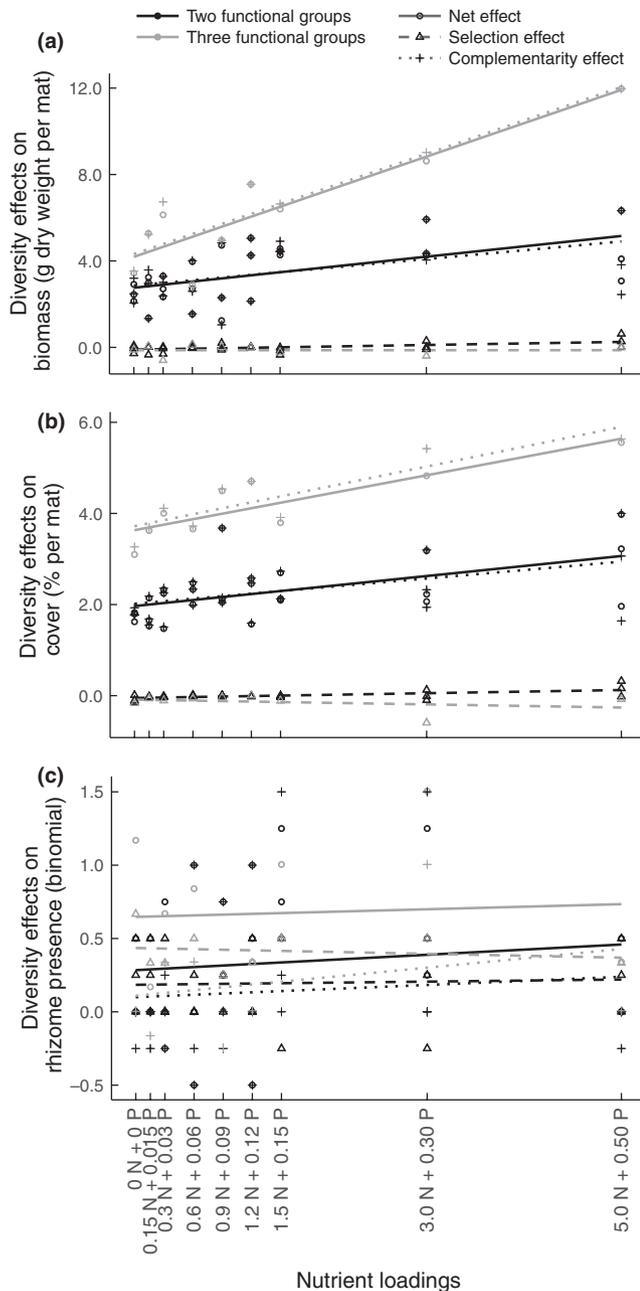


FIGURE 4 This figure visualizes the net, complementarity and selection effects of functional diversity on (a) biomass production in grams per mat, (b) percentages of mats covered by vegetation and (c) the presence of rhizomes per mat (1 = rhizomes, 0 = no rhizomes), and how they change over the gradient of experimental nutrient loadings (in mg/L). In general, an increase of diversity to three functional groups (grey lines) affected the vegetation parameters stronger than an increase to two functional groups (black lines); and the strength of the effects increased with nutrient loadings. For biomass and cover formation, the net effect could almost completely be explained by the complementarity effect—over the entire gradient of nutrient loadings. For rhizome presence, the selection effect was the most important mechanism. The vertical axis is natural log-scaled for biomass and cover (a and b), and a binomial scale for rhizome presence (c). Statistical details are available in Table S5

cover formation caused by higher nutrient availability (Figure 4, Table S5). Effects were in most cases stronger on mats with three functional groups than on mats with two functional groups (Table S5). For biomass production, the mean proportion of the net effect that was explained by the complementarity effect was $1.00 \pm 0.07SD$, the selection effect was close to zero, and this pattern was largely consistent over the different nutrient loadings (Table S5). For cover formation, the proportion explained by the complementarity effect was $0.99 \pm 0.04SD$ and the selection effect was again close to zero. For the presence of rhizomes, the selection effect did explain a large proportion of the net effect: the net effect consisted of $0.25 \pm 0.24SD$ selection, and $0.15 \pm 0.50SD$ complementarity effect across all nutrient loadings and diversity levels (details in Table S5).

A more detailed investigation of possible positive interactions among functional groups underlying the complementarity effect indicated both facilitation and competition (Models II, III and IV in Table 1 and Table S4). Cover formation by interstitials increased by 18% if clonal dominants were present. Clonal stress-tolerators facilitated cover formation by clonal dominants (+109%) and interstitials (+29%). The presence of interstitials increased cover formation by clonal dominants (+52%), but decreased the chance that this functional group formed rhizomes (−50%).

4 | DISCUSSION

Our results show that restoration of peat-forming ecosystems may benefit from increasing plant functional richness and nutrient availability for the developing communities, because this stimulates plant growth and the colonization of open water by floating vegetation in the initial years after species reintroduction. In our experimental setup, the most functionally diverse communities formed more biomass and cover due to complementarity and facilitation among introduced functional groups. Additionally, the presence of the functional group of clonal stress-tolerators strongly enhanced rhizome growth and thereby colonization of open water, indicating a strong positive selection effect. Together, these results support our hypothesis that increasing functional diversity can stimulate initial growth and expansion of plant species typical for peat-forming communities. This knowledge can help to increase the success of wetland restoration projects.

Our observation of overyielding in mixed wetland communities is in line with the general diversity–productivity framework in terrestrial ecosystems (Balvanera et al., 2006; Cardinale, 2011; Hooper et al., 2005; Spohn et al., 2005) and confirms previous studies in wetland ecosystems (Engelhardt & Ritchie, 2001; Schultz et al., 2011, 2012). Our study expands the available knowledge for wetland systems by using different species and a different approach, and—most importantly—specifically tests the mediating role of nutrient availability in the diversity–productivity

framework. In contrast to our expectation that clonal dominant species such as *P. australis* would thrive at high nutrient conditions and form the most rhizomes on the open water, rhizome formation could be attributed almost entirely to clonal stress-tolerators at all nutrient conditions. Rapid growth and rhizome formation by the clonal stress-tolerators probably explains why this functional group facilitated cover formation of the interstitials and clonal dominants. However, this effect was smaller than anticipated. No interstitials were found outside the mats, and clonal dominants only formed few rhizomes in comparison to the clonal stress-tolerators. Hence, the strong selection effect for the presence of the clonal stress-tolerators makes them crucial for the expansion of vegetation onto the open water.

Nutrient loading affected the relative importance of the different functional groups for biomass accumulation, and hence the potential of the vegetation to form peat during later developmental stages. In line with our second hypothesis, the clonal stress-tolerators were the most important for biomass accumulation under low and intermediate nutrient conditions. However, with increasing nutrient availability the interstitials became more important. We expected a hump-shaped relation between nutrient loadings and biomass accumulation, with low plant growth at low nutrient availability and high nutrient levels hampering the expansion of fringe (edge) vegetation, such as observed in the field (e.g. Lamers et al., 2015). However, both biomass and cover formation increased consistently with increasing nutrient loading, suggesting that nutrient additions can have positive effects on biomass accumulation and plant expansion during the first years of wetland restoration. This experiment therefore shows that increasing functional diversity can enhance initial restoration success of peat-forming communities, and that this phase does not necessarily require oligotrophic conditions.

4.1 | Complementarity and selection effects among the functional groups

Productivity in our experimental wetlands increased with functional diversity due to both complementarity and selection effects. Complementarity was the dominant mechanism causing overyielding for biomass accumulation and cover formation in the mixed communities, and the selection effect for the presence of clonal stress-tolerators was the most important for rhizome formation. Observing a complementarity effect suggests that there was interspecific resource partitioning among the three functional groups, or that the groups facilitated each other (Hooper et al., 2005). Because positive interactions (facilitation) were much more common than negative interactions (competition), facilitation provides a likely explanation for the observed complementarity effect.

Observing facilitation is in line with some previous studies (Le Bagousse-Pinguet, Liancourt, Gross, & Straile, 2012), but deviates from most studies describing competition among wetland plants (Doherty & Zedler, 2014; Engelhardt & Ritchie, 2001; Valiente-Banuet & Verdú, 2008; Weis, Cardinale, Forshay, & Ives, 2007). This may be explained by (a) the short duration of our experiment,

representing the initial phase of species establishment in which competition may not yet have played a dominant role; (b) the use of artificial floating mats, on which facilitation may have occurred because plant and rhizome growth seemed to stabilize the mats—suggesting our results are particularly applicable to situations in which floating vegetation reaches far onto the open water and is subjected to wind and water flow; and (c) spatial effects: in contrast to terrestrial ecosystems (Tilman, 1994) competition for space may be lower in range expanding ecosystems such as vegetation expanding onto open water. The complementarity effect remained the dominant mechanism across all levels of nutrient availability. Overall, our results therefore suggest that under range-expanding conditions such as the colonization of open water, facilitation among wetland functional groups may increase resource use efficiency and biomass accumulation over a broad gradient of nutrient availabilities.

4.2 | Floating fen restoration

Difficulties with restoration of floating fens are a problem because of the rapid losses of this important ecosystem type world-wide (Chimner et al., 2017; Lamers et al., 2015). Even after abiotic conditions have been restored in degraded systems, propagules of target plants need to arrive (Soomers, Karssenberg, Soons, et al., 2013) and establish (Sarneel & Soons, 2012) at suitable shallow shorelines for rhizomatous growth to expand onto open water (Sarneel, Huig, Veen, Rip, & Bakker, 2014; Sarneel et al., 2011). Our study shows the added value of introducing multiple, carefully selected target species during restoration, and the relevance of nutrient availability for these plants during the initial years of restoration projects. This knowledge can be applied when selecting plant species for introduction and when determining whether or not to manipulate nutrient levels during wetland restoration practises. For example, the process of nutrient reduction need not necessarily be finished before species are reintroduced at a site, as the availability of nutrients appears not to be a limiting factor for restoration success during the establishment phase. After this phase, nutrient levels should be more tightly managed to ensure development and persistence of target species known to respond negatively to nutrient-rich conditions (e.g. Lamers et al., 2015).

Our experiment did not fully resemble the natural field situations. Two important differences between our experiments and field situations are (a) the absence of herbivores such as waterbirds, which can severely reduce expanding vegetation in fen systems (Dingemans, Bakker, & Bodelier, 2011; Sarneel et al., 2014), so that the effect of any species reintroductions is likely to be strongly reduced; and (b) a lack of water flow around the mats. In most field situations, debris, sediments and plant seeds will become trapped in expanding rhizomes analogous to the way described in tussocks (Ervin, 2009). This could provide a suitable substrate for new seedlings or other species to establish and expand, thereby contributing to the developing community. Addressing these additional aspects in long-term field evaluations could further improve wetland restoration practises.

4.3 | Conclusions and implications for wetland restoration

This study implies that for restoration of the initial succession stages of peat-forming ecosystems, increasing plant functional diversity in peat-forming ecosystems can accelerate community development during restoration of the initial stages, both as establishment of new ecosystems or expansion of existing systems. Community biomass accumulation, cover and rhizome formation all increased with functional group richness. Peat-forming communities can benefit from facilitation among different functional groups, and initially develop under a surprisingly wide range of nutrient availabilities. The observed facilitation effects suggest that increasing functional diversity can stimulate terrestrialization and peat formation. However, apart from facilitation we also observed a positive selection effect. In our experiment, the impact of adding clonal stress-tolerators to mats was very large. Clonal stress-tolerators acted as a keystone functional group for the colonization of open water, and importantly contributed to the early phase of fen restoration.

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AUTHORS' CONTRIBUTIONS

J.V.Z., J.V. and M.B.S. conceived the ideas and designed the experiment; J.V.Z. and S.I.J. collected the data; C.V.L., M.B.S. and E.S.B. analysed the data; E.P. and B.V.Z. contributed to the data analysis; C.V.L. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.4t5q437> (van Zuidam et al., 2018).

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SUPPORTING INFORMATION

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