

1 **Long-term effects of nutrient enrichment controlling plant species and**
2 **functional composition in a boreal rich fen**

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18

19 **Abstract**

20 Questions

21 How does long-term increase in nutrient availability affect species composition, species diversity and
22 functional composition in boreal rich fens, and how does this differ from short-term effects? What
23 are the possible mechanisms behind the observed changes and how does nutrient limitation
24 influence species diversity in these communities?

25

26 Location

27 Sølendet Nature Reserve, Central Norway (62° 40' N, 11° 50' E).

28

29 Methods

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30 A full-factorial field experiment. Plots in two localities received one of following treatments (n=3): no
31 nutrient addition (control), N, P, K, NP, NK, PK and NPK addition. Cover of plant species was recorded
32 before treatment, and after two and 15 years of treatment.

33

34 Results

35 Two years of nutrient addition caused small changes in species composition, but addition of NP led to
36 large increase in abundance of species with high ability to exploit the added nutrients - a direct result
37 of the elimination of nutrient limitation in the communities. 15 years of nutrient addition led to
38 significant changes following three different pathways, one for each of N, P and NP addition. The
39 addition of NP led to large community shifts, considerable species turnover, and reduced species and
40 functional richness, mainly caused by increase in cover of highly competitive and tussock-forming
41 grasses like *Deschampsia cespitosa*, *Festuca ovina* and *Molinia caerulea*, outcompeting other species,
42 especially bryophytes. Addition of N led to smaller changes in species turnover, and without clear
43 dominant species. Addition of P led to considerable species turnover, but no reduction in species or
44 functional richness, and the bryophyte diversity increased. This is explained by the bryophytes'
45 association with N-fixing cyanobacteria, suggesting less N limitation and a greater ability to utilise the
46 added P when vascular plants suffer from N-shortage. In addition, bryophytes are more sensitive to
47 low P availability, due to larger P requirements compared to vascular plants. There was no effect of K
48 addition.

49

50 Conclusions

51 Both N and P limitation is essential for the maintenance of high species diversity in boreal rich fens,
52 and P limitation controls bryophyte diversity. From a management perspective, N and P limitation is
53 vital in the conservation of boreal rich fens or when a functional fen system is re-established through
54 restoration measures.

55

56 **Keywords**

57 Bryophyte diversity, Functional richness, Functional traits, Mycorrhizal associations, N-fixation,
58 Norway, Nutrient limitation, Rich fen vegetation, Sloping fen, Species diversity

59

60 **Nomenclature**

61 Frisvoll et al. (1994) for bryophytes, Elven (2005) for vascular plants.

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62

63 Running head: Effects of nutrient enrichment in a boreal fen

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64 Introduction

65

66 Plant species diversity and composition of fen vegetation are largely controlled by hydrology and soil
67 chemistry. Both the poor-rich gradient, reflecting pH and mineral concentration (especially Ca), and
68 the fertility (or productivity) gradient, caused by variation in nutrient availability (nitrogen (N),
69 phosphorus (P), potassium (K)), are considered to be key factors (Sjörs 1948; Hájek et al. 2006;
70 Pawlikowski et al. 2013). The latter has rarely been studied in boreal fens where it is thought to be of
71 minor importance (Økland et al. 2001).

72 In large parts of Europe, nutrient enrichment has damaged the fens and strongly affected the
73 plant composition in various ways (Rydin & Jeglum 2013). For instance, through increased availability
74 of N as a result of hydrological alteration (drainage) which increases peat decomposition rates
75 (Holden et al. 2004), but also of input from airborne N deposition (Bobbink et al. 1998). Whereas P
76 levels may rise in fens which receive polluted groundwater or surface runoff (Beltman et al. 2000), or
77 as a result of restoration activities, e.g. from rewetting of highly decomposed peat on formerly
78 drained fens (Zak et al. 2010, Emsens et al. 2017). Increased levels of both abovementioned nutrients
79 are regarded as one of the major threats to biodiversity (Smith et al. 1999; Sala et al. 2000). Airborne
80 N loads correlate with the loss of rare plant species of grasslands (Stevens et al. 2004) while species
81 adapted to P-poor environments are outcompeted and face the risk of extinction as they typically are
82 small and invest little in sexual reproduction (Fujita et al. 2014). On the other hand, P pollution leads
83 to rapid changes in rich fen ecosystems through acidification (Kooijman 2012) and is also suggested
84 to be an important cause of species loss in grassland ecosystems, although the exact underlying
85 mechanisms are unclear (Ceulemans et al. 2013). On top of this, changes in climatic conditions affect
86 the nutrient dynamics and availability in fen ecosystems through changes in water level and
87 temperature (Jablonska et al. 2011; Cusell et al. 2013).

88 Despite these well-known relationships between nutrient enrichment and biodiversity in fen
89 systems, the nutrient dynamics and the effect of changes in the availability of N, P and K on the
90 species composition of rich fens, boreal fens in particular, are poorly understood. Most results so far
91 are based on analyses of edaphic conditions and biomass production along vegetation gradients
92 (Øien & Moen 2001; Rozbrojová & Hájek 2008; Peterka et al. 2014), or from analyses of short-term
93 response to fertilization (Güsewell et al. 2003; Øien 2004; van der Hoek et al. 2004). However, in
94 short-term fertilization experiments, the only response to increased nutrient availability is usually

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95 increased biomass production as a consequence of the temporary annulment of nutrient limitation.
96 There is normally little or no change in species composition in the short term (Pauli et al. 2002; Øien
97 2004; van der Hoek et al. 2004). Field experiments in areas with low availability of N or P or both,
98 indicate that the effects of increased P-availability appear more slowly and are more persistent than
99 those of increased N-availability (van der Hoek et al. 2004). In order to investigate how increased N-
100 and P-availability affects the species composition in the long run, more longer-lasting experiments
101 are needed. Interactions between N and P uptake, indirect effects caused by differences in retention
102 time, and effects on nutrient loss, need time to develop and to be detected (Güsewell et al. 2002,
103 2003).

104 The functional structure of a community, i.e. the distribution of functional traits in the
105 community and the surrounding species pool, is expected to reflect the mechanisms by which
106 communities respond to environmental factors (Lavorel & Garnier 2002). We expect that as a
107 consequence of changes in nutrient availability, processes such as competitive interactions or
108 environmental filtering will select for species with specific functional traits related to competitive
109 ability, resource acquisition and storage. Most plants characteristic of low-resource environments
110 share a common suite of traits, including low rates of growth, photosynthesis, and nutrient
111 absorption, high root: shoot ratios, low rates of tissue turnover, and high concentrations of
112 secondary metabolite. On the other hand, species adapted to high-nutrient environments have more
113 rapid acquisition of resources and low conservation of acquired resources (Chapin et al. 1993). A
114 trade-off is observed between attributes responsible for retention of resource capital in
115 unproductive habitats and those conditions conferring an ability for high rates of resource acquisition
116 in productive habitats (Berendse & Aerts 1987).

117 In boreal Fennoscandia, large fen areas are still unaffected by nutrient enrichment. Their
118 pristine conditions make them well suited to study the effects of changes in nutrient availability on
119 fen communities. In 1998, a fertilization experiment was set up in such an area, in the Sjølandet
120 Nature Reserve, Central Norway, which holds large areas of spring-water fed sloping rich fens
121 influenced by haymaking (Moen 1990). The original aims of the experiment were to determine which
122 nutrient (N, P, K) was limiting to 1) the plant production in the most common rich-fen communities,
123 and 2) the growth of some dominant and sub-dominant species. The fertilization caused increased
124 concentrations of N and P in several of the dominant and sub-dominant species and indicated a co-
125 limitation by N and P in the least productive communities and in most of the dominant and sub-
126 dominant species (Øien 2004). In order to increase the understanding of how anthropogenic nutrient

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127 enrichment affects rich-fen communities, and the potential implications for management of boreal
128 rich fens, the fertilization experiment in these communities was prolonged.

129 In this paper, we use data from 15 years of nutrient addition to investigate 1) how a long-
130 term increase in nutrient availability affects species composition, species diversity and functional
131 composition of boreal rich fen plant communities, and 2) how these effects differ from short-term
132 effects. Possible mechanisms causing the observed changes are discussed. We expect a clear
133 difference between the short-term (after two years) and long-term (after 15 years) effect. As the
134 studied fens have been shown to be co-limited by N and P, we expect the addition of N and P
135 together to have the largest effects through competitive exclusion, and addition of K to have no or
136 little effect. A number of studies indicate that N-limited environments favour fast-growing strong
137 competitive species, in contrast to P-limited environments where nutrient-conservative, stress-
138 tolerant strategies are more decisive (e.g. Ceulemans et al. 2011, Fujita et al. 2014). Since fertilization
139 modifies or even reverses limitation patterns, we expect N addition to favour species more adapted
140 to reducing the nutrient loss (i.e. retaining P) as it becomes limiting, e.g. species with evergreen or
141 thick leaves (high leaf dry matter content), and species that acquire P from association with
142 arbuscular mycorrhizal fungi. Regarding P addition, we expect an increase of canopy height and
143 specific leaf area, as well as a raise of species able to acquire N through associations with ericoid- or
144 ectomycorrhizal fungi.

145

146 **Methods**

147 **Study area**

148 The fertilization experiment was carried out in the Sølendet Nature Reserve, Central Norway
149 (62° 40' N, 11° 50' E), situated at 700-800 m a.s.l. The area has an annual precipitation of 637 mm,
150 and a long-lasting snow cover (210-220 days per year). The mean annual temperature is +0.6 °C, with
151 a January mean of -9.5 °C and a July mean of 10.5 °C. The vegetation is dominated by birch woodland
152 and sloping fens. Three localities with rich-fen vegetation were chosen for the fertilization
153 experiment in 1998. The initial phase of the experiment ended in 2000, after which the fertilization
154 treatment continued in two of the localities (named site 2 and 3 in Øien (2004), here we name them
155 A and B respectively). The experiment was located in a part of the reserve with large fens sloping (3-
156 5°) towards south-southeast. In this area, waterlogging, through an upward discharge of
157 groundwater, sustains a thin peat layer (15-45 cm). Eustatic springs rising in the upper parts of the

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158 reserve provide the fens with calcareous, mineral-rich water throughout the year. For centuries,
159 these fens were harvested for hay, a land-use that ceased about 1950, and the area was abandoned
160 until restoration and management started in 1974. Today the area in this part of the reserve is mown
161 approximately once every 10 years to maintain an open cultural landscape without shrubs (Moen
162 1990). The experimental localities have similar biogeochemical properties, with pH in the peat
163 around 6.5 and low availability of N, P and K (Øien 2004). Both localities were mown twice after the
164 management started and before the experiment was carried out; locality A in 1979 and 1994, and
165 locality B in 1983 and 1993. During the course of the experiment, the localities were mown after the
166 data sampling in 2000.

167 The vegetation in both localities consists of rich-fen communities belonging to the Caricion
168 atrofuscae alliance (Moen 1990; Moen et al. 2012), and the field layer is dominated by sedges and
169 grasses (*Carex dioica*, *C. panicea*, *Eriophorum angustifolium*, *Molinia caerulea*, *Trichophorum*
170 *cespitosum*). Brown mosses, especially *Campylium stellatum* and *Scorpidium cossonii*, dominate in
171 the bottom layer, and liverworts (e.g. *Aneura pinguis* and *Gymnocolea borealis*) are also common.
172 The production in the field layer (standing crop) is around 140 g/m² (Moen et al. 2015). Further
173 details about the study area can be found in Moen (1990) and Moen et al. (2012).

174

175 **Experimental design and sampling**

176 The effect of nutrient application was assessed using a full-factorial fertilization experiment (BACI
177 design). At each of the two localities, an area of 100-150 m² with vegetation as homogeneous as
178 possible was marked in August 1998. Twenty-four plots of 1 x 1 m separated by at least 1 m in the
179 direction of the slope (SE) were randomly arranged within each locality, avoiding hummocks and
180 small trickles of surface water. The plots were fertilized with the following nutrient combinations: no
181 nutrients (control), N, P, K, NP, NK, PK and NPK; each treatment replicated in three plots per locality.
182 Nutrient solutions (Supplementary material 1) were mixed by dissolving salts in deionized water.
183 Small amounts of concentrated HCl or 1 M NaOH (a few ml in a 10 l solution) were added to adjust
184 the pH to between 5.0 and 6.0 to resemble the pH of the precipitation. The amount of supplied
185 nutrients, given separately or in combination, was 12 g/m² N, 3 g/m² P and 12 g/m² K per year on
186 each plot during the initial phase of the experiment (1999-2000). Half of the amount was applied in
187 the first fertilization at the beginning of June, the rest in two applications, one later in June and one
188 in the beginning of July. During the latter phase of the experiment (2001-2013) the amount of

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189 supplied nutrients was halved (6 g/m² N, 1.5 g/m² P and 6 g/m² K per year), by leaving out the two
190 latter of the annual applications. One litre of solution was applied with a spraying can to each plot on
191 each occasion. The control plots received one litre of deionized water at each application.

192 Within a 0.5 x 0.5 m area in the centre of each plot the species composition was recorded
193 estimating the cover of all vascular plants and bryophytes using an adjusted Hult-Sernander-Du Rietz
194 scale (Moen 1990) with 9 classes: 1: recorded at the border outside the plot, 2: < 1 %, 3: 1-3.125 %, 4:
195 3-6.25 %, 5: 6.25-12.5 %, 6: 12.5-25 %, 7: 25-50 %, 8: 50-75 %, 9: 75-100 %. Cover values that were
196 used in statistical testing were transformed to the middle value of each class: 0=0 %, 1= 0%, 2=0.5 %,
197 3=2.0625 %, 4=4.6875 %, 5=9.375 %, 6=18.75%, 7=37.5 %, 8=62.5 %, 9=87.5%. Cover values were
198 recorded before fertilization (1998), after two years of fertilization (2000), and after 15 years of
199 fertilization (2013); each year in the first half of August.

200

201 **Data analysis**

202 Multivariate plant species responses (plant community matrices with cover values) over time were
203 examined by distance-based, nonparametric MANOVA (Legendre & Anderson 1999; McArdle &
204 Anderson 2001) using the computer program DISTLM ver. 5 (Anderson 2004). The experiment had a
205 full factorial, repeated measures design with locality as a random, blocking factor and treatments
206 replicated within localities. The experimental treatments were represented in the ANOVA-model as
207 three orthogonal, fixed, binary factors (nutrient not supplied, nutrient supplied), here referred to as
208 Nf, Pf and Kf. All terms for possible interactions among the three factors were included in the
209 models. Locality (two levels) and plots were modelled as random factors. The plot factor was nested
210 within combinations of locality and treatments. Time (three levels: 1998, 2000, 2013) was included in
211 the linear model as a fixed factor together with terms representing all interactions among
212 treatments, locality and time. Construction of test statistics followed the same principles as for
213 univariate analyses. Permutation test with 4 999 permutations of residuals under the full model
214 provided the p-values (Anderson 2001; Anderson & ter Braak 2003). See Supplementary material 2
215 for further details about the MANOVA analyses.

216 An unconstrained ordination (PCA) of species cover values with fertilization treatments as
217 supplementary variables was performed to explore the community changes from 1998 to 2013. PCA
218 was chosen for his purpose as responses to treatments were mostly quantitative, there was no
219 outliers and an initial analysis revealed short gradient lengths within the sampled material (2.21 SD

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220 units for the first axis when the whole data set was analysed). To track (the direction of) community
221 shifts over time, 95 % confidence ellipses of centroids of plots receiving the same nutrient treatment
222 were calculated for each year and locality. The ordination analyses were carried out using the
223 computer program Canoco 5 for Windows (Ter Braak & Šmilauer 2012).

224 To further characterize the results and to aid the interpretation of the mechanisms behind
225 the observed changes, we tested the treatment effects after two and 15 years on six functional
226 groups (sedges, dwarf shrubs, forbs, grasses, mosses and liverworts), 14 functional traits (reflecting
227 species strategies according to nutrient acquisition and competition abilities), including mycorrhizal
228 associations (see list of traits in Supplementary material 3), and on 14 plant species (11 vascular
229 plants and 3 bryophytes) of the rich fen communities. The species were chosen among common and
230 characteristic rich-fen species representing the various functional groups and among more sparsely
231 occurring species that showed a clear response to nutrient addition during the initial phase of the
232 experiment. The vascular plant species were: one dwarf-shrub *Andromeda polifolia*, four sedges
233 *Carex dioica*, *C. lasiocarpa*, *C. panicea*, and *Trichoporum cespitosum* ssp. *cespitosum*, three grasses
234 *Deschampsia cespitosa*, *Festuca ovina* and *Molinia caerulea*, and three forbs *Saussurea alpina*,
235 *Succisa pratensis*, and *Thalictrum alpinum*. The bryophytes were (only mosses): *Campylium stellatum*,
236 *Scorpidium cossonii* and *Tomentypnum nitens*. Trait values were obtained from the TRY database
237 (Kattge et al. 2011; see also Supplementart material 4), the LEDA database (Kleyer et al. 2008), the
238 CLO-PLA database (Klimešová & De Bello 2009), and the local flora (Elven 2005). A few values missing
239 in the databases were extracted either from Elven (2005) or obtained from measurements in the
240 field based on the authors own observations. Information about mycorrhizal associations (in vascular
241 plants only) was obtained from MycoFlor database (Hempel et al. 2013), cross-checked with data
242 from Akhmetzhanova et al. (2012), and supplemented with data from Veselkin et al. (2014) for *Carex*
243 spp. Main types of mycorrhizal associations (obligatory OM, ectomycorrhizal EcM, ericoid ErM,
244 arbuscular AM) were defined according to Hempel et al. (2013) and Moora (2014). When we refer to
245 functional group- and traits-names further in the text, we refer to their community weighted means
246 for plots (CWM, Lavorel et al. 2008).

247 We used univariate ANOVA to test for treatment-related changes in community weighted
248 means of functional groups and traits, and changes in abundance of species. For each of these
249 response variables we based the ANOVA on a univariate version of the linear model used in the
250 MANOVA analyses described above, however, with the following modification. Multivariate analyses
251 indicated that turnover in species composition during the experiment followed 3 distinct pathways

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252 associated with the N, P and NP treatments respectively (see Results). Thus, in order to answer our
253 research questions, it became relevant and necessary to compare the effect of each treatment with
254 the effects of each of the other treatments and the controls instead of testing for main effects of the
255 Nf and Pf factors. We therefore modelled the experimental treatments as one factor with four levels,
256 N, P, NP, and control, and performed all pairwise contrasts between these levels when ANOVA
257 revealed significant treatment effects. Treatments involving K was pooled with the corresponding
258 treatment without K in these analyses as MANOVA revealed that addition of K had no effect on
259 species composition. As in the multivariate analyses, p-values were obtained by permutation of
260 residuals. In the pairwise contrasts significance was evaluated according to the Holm-Bonferroni
261 sequential procedure (Holm 1979) with a familywise error rate ≤ 0.05 . Analyses of species responses
262 were based on log-transformed cover values.

263 Using the same approach, we also tested the effect of nutrient addition on species diversity
264 (species number and Shannon evenness E) and functional richness (Villegger et al. 2008). The
265 calculation of functional richness include six different functional traits for vascular plants (see
266 Supplementary material 3 for details). Statistical modelling of diversity, functional traits and species
267 responses were performed in the R statistical environment (R Core Team 2013).

268

269 **Results**

270

271 We found no effect of fertilizing plots with K on species composition, whether K was added alone or
272 together with N, P, or both (Fig. 1, Supplementary material 2). In the following, we do not present
273 results for K, except in the abovementioned figure and supplementary material. Treatments that
274 included the addition of K are pooled with parallel treatments that did not include K. So, henceforth
275 (including in tables and figures) "N" treatment actually refers to the pooled "N and NK" treatment,
276 "NP" treatment refers to pooled "NP and NPK" and so on.

277

278 **Community changes**

279 At the start of the experiment in 1998, there was no systematic variation in species composition
280 related to the assigned treatments. However, the two localities differed in species composition,
281 particularly among graminoids. *Carex lasiocarpa*, a common species in locality A, was not present in
282 locality B. *Deschampsia cespitosa* and *Festuca ovina*, two species that responded strongly to nutrient

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283 addition, occurred only in locality B. The moss *Tomentypnum nitens*, another species with strong,
284 positive response to nutrient addition, was present in the bottom layer of most plots in locality B, but
285 hardly found in locality A. For further details, see Supplementary material 5 and Øien (2004). As the
286 initial composition of species that later responded to the experimental treatments, was different
287 between the two localities, the overall MANOVA revealed significant treatments by locality by time
288 interactions for both addition of N and P (Supplementary material 2). We therefore also analysed
289 each locality separately in order to confirm that the species composition responded to the same
290 treatments at both localities, which was generally the case (Supplementary material 2).

291 Two years into the experiment, there were significant effects of P addition on the floristic
292 composition in the experimental plots of locality B (Fig. 1, Supplementary material 2), and there was
293 a marginally significant interaction between Nf and Pf in the same locality. The largest turnover in
294 species composition had thus occurred in the NP-plots (Tab. 1). After 15 years of nutrient
295 enrichment, the turnover in species composition was larger (Fig. 1, Tab. 1). Both enrichment with N
296 and enrichment with P had led to significant differences in floristic composition compared to the
297 controls in both localities (Supplementary material 2). In addition, there was an interaction between
298 the Nf- and Pf factors. Plots receiving both N and P were different both from plots receiving only N
299 (non-parametric MANOVA of plots fertilized with N: df = 1, 10, locality A: pseudo-F = 3.572, p <
300 0.001, locality B: pseudo-F = 6.605, p < 0.001) and plots receiving only P (non-parametric MANOVA of
301 plots fertilized with P: df = 1, 10, locality A: pseudo-F = 3.682, p < 0.001, locality B: pseudo-F = 6.542,
302 p < 0.001). So, the turnover in species composition followed 3 distinct pathways in both localities
303 depending on experimental treatment, one associated with the addition of N, one with the addition
304 of P, and a third pathway associated with the addition of both nutrients (Fig. 1).

305

306 **Fertilization with both nitrogen and phosphorus**

307 The proportion of tussock-forming grasses increased strongly in plots fertilized with both N and P
308 (Fig. 2), and the increase was most evident in locality B (Supplementary 6). *Deschampsia cespitosa*
309 and *Festuca ovina* were barely present prior to the experiment but dominated these plots in locality
310 B after 15 years. In locality A, where these species were not present initially, *Molinia caerulea*
311 dominated after 15 years (Fig. 6). During the initial phase, the treatment had a positive effect on the
312 majority of the most common species in the field layer. Both, forbs (e.g. *Saussurea alpina*,
313 *Thalictrum alpinum*), and dwarf shrubs (*Andromeda polifolia*), increased in cover (Figs. 2 and 5).

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314 However, the expansion of grasses during the second phase occurred at the expense of all other
315 functional groups in the field layer (Fig. 2). Although some larger forbs (e.g. *S. alpina*) maintained
316 their increased cover from the first phase in some plots, several species disappeared, both some
317 relatively common (e.g. *Saxifraga aizoides* and *Tofieldia pusilla*) and some characteristic rich-fen
318 species that were present in most plots at low abundances (e.g. *Eriophorum latifolium*, *Kobresia*
319 *simpliciuscula* and *Pedicularis oederi*). Two of the most common species of the field layer, *Carex*
320 *dioica* and *Trichophorum cespitosum*, were reduced to a fraction of their original cover (Fig. 5).

321 The bottom layer in plots fertilized with both N and P decreased during the whole
322 experimental period (Figs. 2 and 5). The mean cover of the dominant bryophyte species, *Campyllum*
323 *stellatum*, decreased from > 40 % prior to the fertilization, to < 10 % after 15 years of nutrient
324 addition (Fig. 5). The other most common bryophyte species *Scorpidium cossonii* had disappeared,
325 along with the most common liverwort prior to the experiment, *Gymnocola borealis*
326 (Supplementary material 5).

327 The plant communities' functional composition changed accordingly. Canopy height and
328 relative abundance of competitors and hummock-/tussock-forming species increased, while stress
329 tolerators and species with clonal spread decreased (Fig. 3a and Supplementary material 6). There
330 were also changes in the relative abundance of species with specific mycorrhizal associations. ErM
331 plants increased after 2 years and AM plants after 15 years (Fig. 4). For the other traits, including leaf
332 dry matter content or specific leaf area, we could not distinguish any significant change as a result of
333 addition of both N and P.

334

335 **Fertilization with nitrogen**

336 In plots fertilized with N, there was in general a much lower turnover during 15 years of nutrient
337 addition than in plots receiving both N and P. None of the common species had disappeared and
338 there were no clear dominants after 15 years. The most common species in the field layer were the
339 same as prior to fertilization: *Carex panicea*, *Molinia caerulea* and *Trichophorum cespitosum*. In
340 contrast to the NP treatment, there was no increase in the relative abundance of grasses under the N
341 treatment (Fig. 2), only *M. caerulea* showed a significant increase (in locality A) during the
342 experimental period (Fig. 5, Supplementary material 6). The sedges, as a group, increased their
343 relative abundance in N-fertilised plots during the experimental period (Fig. 2). This in contrast to all
344 other treatments, including controls, where the share of sedges decreased. The increase was due to

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345 an increase in cover of *Carex panicea* during the first phase of the experiment, and *Trichophorum*
346 *cespitosum* regaining its former cover during the second phase after an initial decline (Fig 5).

347 The relative abundance of mosses was negatively affected by N-addition (Fig. 2). The bottom
348 layer was much reduced after 15 years. *Campylium stellatum* was still the dominating species, but
349 the cover of both *C. stellatum* and *Scorpidium cossonii* had decreased (Fig. 5).

350 The effects on functional composition were small. After two years there was no significant
351 changes, and after 15 there was an increase in the share of hummock-/tussock-forming species in
352 locality A (Supplementary material 6), and in the relative abundance of species with arbuscular
353 mycorrhizal associations (Fig. 4).

354

355 **Fertilization with phosphorus**

356 Addition of P led to a strong increase in the relative abundance of dwarf shrubs (Fig. 2). After 15
357 years *Andromeda polifolia* was the most common species in the field layer in these plots together
358 with the forb *Thalictrum alpinum* (Fig. 5). Other forbs, i.e. *Saussurea alpina*, also increased in cover,
359 while the small sedge *Carex dioica* was negatively affected.

360 In the bottom layer, addition of P had a positive effect on liverworts (Fig. 2), and a negative
361 effect on mosses (significant only in locality B). There was also a large turnover among the
362 dominating moss species. *Campylium stellatum* and *Scorpidium cossonii* were significantly reduced,
363 while *Tomentypnum nitens* became a new dominant together with *C. stellatum* (Fig. 5). Several
364 bryophytes that were not found in the communities prior to the fertilization (e.g. *Rhizomnium*
365 *pseudopunctatum*, *Dicranum bonjeani*, *Barbilophozia quadriloba*, *Scapania* sp.) appeared in these
366 plots after 15 years, increasing the overall bryophyte diversity (see below). The most common of
367 these were the pleurocarpous moss *R. pseudopunctatum* (see Supplementary 4).

368 In terms of the plant communities' functional composition, there were few effects of P
369 addition in the first phase of the experiment. The relative abundance of ErM species had increased
370 (Fig. 4), and stress tolerators had decreased (Fig. 3a). On the other hand, addition of P over 15 years
371 also led to increase in the relative abundance of woody species, OM forming species (only significant
372 in locality A), continued increase in ErM forming species, while AM forming species decreased (Figs.
373 3, 4 and Supplementary material 6). There was also an increase in hummock/tussock forming species
374 in locality B (Supplementary material 6).

375

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376 **Changes in species and functional diversity**

377 The total number of species changed very little after two years of nutrient application but had
378 increased slightly from a mean \pm SD of 25 ± 5.0 species to 27 ± 5.0 species in plots where P was
379 added alone. After 15 years of nutrient application, addition of N and NP had a negative effect on the
380 species number compared with control (ANOVA: $F = 24.01$, $df = 3, 43$, $p < 0.001$). The species richness
381 had decreased under these treatments from 25 ± 3.8 and 25 ± 4.4 to respectively 18 ± 4.0 and $15 \pm$
382 2.4 species. A similar decline did not occur in plots fertilized with P. In these plots the number of
383 species in the bottom layer had increased, compared with the controls (ANOVA: $F = 18.04$, $df = 3, 43$,
384 $p < 0.001$), from a mean number of 5 ± 1.5 species to 7 ± 2.7 species. Shannon evenness showed no
385 treatment related changes during the experiment, neither after two years nor after 15 years of
386 nutrient addition. Functional richness showed no change after two years of fertilization. However,
387 after 15 years functional richness was lower in plots fertilized with NP than in other plots (ANOVA: $F =$
388 3.81 , $df = 3, 43$, $p < 0.01$). Functional richness in NP plots had decreased from 0.019 ± 0.017 in 1998
389 to 0.002 ± 0.002 in 2013.

390

391 **Discussion**

392

393 Our results show that the mechanisms behind the observed changes differ between the
394 experiments' two phases. After two years of increased nutrient availability, the changes in species
395 composition in the investigated rich fen communities were small for all treatments, but treatments
396 where both N and P were added had led to increased abundance for many species, especially those
397 with a high ability to exploit the added nutrients (e.g. *Festuca ovina*). These changes were most
398 probably a direct result of the elimination of nutrient limitation, where variation in the ability to
399 exploit increased nutrient supply determined the outcome.

400 In the second phase of the experiment, elevated availability of N or P had changed the
401 competitive conditions, resulting in significant changes in species composition. The changes followed
402 three different pathways of compositional turnover, one for each of N, P and NP. The vegetation in
403 the plots fertilized with both N and P had changed from a community dominated by stress tolerant
404 and highly clonal species (many sedges) in the field layer and a high diversity of bryophytes in the
405 bottom layer, to a community characterized by a few dominant, and highly competitive, tussock
406 forming grasses in the field layer, and a strongly reduced bottom layer with the resulting loss both in

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407 species diversity and functional richness. The P-plots, despite a high species turnover, had no clear
408 dominant species in the field layer, with both herbs, dwarf-shrubs and sedges among the common
409 species. The bottom layer was still well developed and species rich. The functional composition had
410 changed little, apart from the increase in dwarf-shrubs and a few other wooded species, i.e. species
411 adapted to resources retention. There was no loss of species diversity; on the contrary, the number
412 of bryophyte species (especially liverworts) had increased. Fertilization of N alone led to a third
413 outcome, clearly different from both those fertilized with P alone and those fertilized with both N
414 and P. Similarly to the NP treatments, the N-plots had a clearly reduced bottom layer and reduced
415 species diversity, but without clear dominants in the field layer. Although the hummock species and
416 sedges had increased, the most common species were the same as prior to the fertilization.

417 The results after 15 years clearly demonstrate the general understanding that when the
418 limiting resources are made available in excess, which in this case is both N and P (Øien 2004), a few
419 highly competitive species with some of the traits mentioned above, would outcompete other
420 species due to the effect of nutrient enrichment on productivity (Grime 2001; Cusell et al. 2014).
421 Both *Deschampsia cespitosa*, *Festuca ovina* and *Molinia caerulea* have the ability to form dense mats
422 or tussocks crowding out other species. *F. ovina* and *M. caerulea* have also a relatively good ability to
423 exploit increased nutrient availability under nutrient-poor conditions (Kachi & Rorison 1990; Hansson
424 & Göransson 1993; Taylor et al. 2001). Especially *M. caerulea* is well known to be responsive to high
425 N influx (Friedrich et al. 2011). The literature is inconclusive when it comes to *D. cespitosa*. Grime et
426 al. (2007) classified it as intermediate between C-S-R and stress tolerant competitor. However, based
427 on our results this species is capable of a more effective exploitation of nutrients than most species
428 in the investigated fen communities, which in addition to its ability to form dense mats, gives it a
429 competitive advantage.

430 The experiment also shows that the initial species composition strongly affects the outcome
431 of the nutrient addition even after 15 years of experimental treatment, possibly through founder
432 control (Rees & Bergelson 1997) or pre-emption of the resources (Olde Venterink & Güsewell 2010).
433 For example, a characteristic fen species like *M. caerulea* was common and evenly distributed in the
434 two localities at the start of the experiment, while *D. cespitosa*, a species with a wider ecological
435 amplitude and that normally is found scattered at low abundance throughout the rich-fen lawns of
436 the study area, was only found in locality B (Fig. 5, Supplementary material 5). After 15 years *D.*
437 *cespitosa* dominated in plots fertilized with both N and P in locality B, and *M. caerulea* dominated in

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438 plots under the same treatment, but only in locality A where *D. cespitosa* was lacking at the start of
439 the experiment.

440 We did not observe any clear trend in the functional composition related to specific leaf area
441 (SLA) and leaf dry matter content which are related to each other by a physiological trade-off,
442 despite that they are believed to play a key role in plants nutrient acquisition strategies (Reich 2014).
443 A probable mechanism, which explains higher SLA values in plants adapted to nutrient-richer
444 habitats, is that of adaptation to reduced light availability as a consequence of increased productivity
445 (Freschet et al. 2015). Given the functional structure of the boreal fen system investigated, this
446 suggests that the productivity changes are not high enough to favour this trait, even after 15 years of
447 fertilization.

448 Fertilization with both N and P revealed small effects on relative abundance of traits related
449 to mycorrhizal associations. An initial increase in abundance of ErM forming plants (*Andromeda*
450 *polifolia* and *Vaccinium uliginosum*) was probably simply related to plant growth stimulation by the
451 surplus of nutrients. The long-term effect (increase in AM and OM forming plants) which is clearly
452 associated with the dominance of obligatorily AM *Molinia caerulea*, could potentially be caused by
453 the differences in relative availability of added N and P. For example, Johnson (2009) presented
454 important conceptual trade balance model, which predicts four types of ecological interactions
455 between plant and AM fungal symbiont depending on the relative availability of N and P. According
456 to this model the best situation for the evolvement of strong mutualism is P limitation with the
457 excess of N. C-limited mutualism will occur at N and P limitation, N limitation and excess of P will lead
458 to commensalism, while excess of N and P to parasitism (Johnson 2009). It has to be pointed out that
459 EcM and ErM fungi may supply plants also with P, while AM fungi have the ability to provide N,
460 although the overall importance of these processes for plant nutrition and competitive interactions
461 within a community is still not well understood (Read et al. 2004; Plassard et al. 2011; Whiteside et
462 al. 2012).

463 Based on earlier investigations in these fen systems (Øien & Moen 2001; Øien 2004), one can
464 safely assume that plots receiving N in the current experiment experienced P limitation after 15 years
465 of nutrient addition, and that plots receiving P experienced N limitation. The vegetation is not
466 influenced by long transported atmospheric N deposition, as the area where the experiment was
467 conducted receive close to background deposition of N (Holland et al. 2005). Given these
468 assumptions the results from our experiment do not support the suggested mechanisms that predict
469 higher species diversity under P limitation compared to N limitation. On the other hand, our results

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470 support the suggestion that most plant species in the boreal (northern temperate) regions are
471 adapted to N limitation, not to P limitation (Vitousek & Howarth 1991; Reich & Oleksyn 2004),
472 including species found in mires and fens.

473 In the plots receiving N (i.e. P-limited) the few species that benefit from the excess N are
474 those that already are common in the community. The observed changes are mainly the result of the
475 common species outcompeting some of the less common ones, especially some bryophytes. Among
476 the common species are several grasses, of which many are able to form facultative associations with
477 AM fungi (Akhmetzhanova et al. 2012, Hempel et al. 2013) to alleviate P limitation, explaining the
478 significant increase in AM forming species. This has also been proposed as a plausible mechanism in
479 other studies (Aerts 2002; Olsson & Tyler 2004) and agrees with the abovementioned model by
480 Johnson (2009). Interestingly, a meta-analysis by Treseder (2004) did not show significant differences
481 in the responses of EcM and AM fungi to N fertilization, and the study by Gerz et al. (2016) showed
482 even a negative correlation between soil N content and AM mycorrhization in forest and grassland
483 ecosystems in Estonia.

484 The maintenance of high diversity in plots receiving P (i.e. N-limited) suggest that there is a
485 large pool of plant species that are able to tolerate severe N limitation. This could explain the
486 increase in some vascular plants, like the herbs *Saussurea alpina*, *Succisa pratensis* and *Thalictrum*
487 *alpinum*, and especially the ErM forming dwarf-shrub *Andromeda polifolia*. The induced N limitation
488 clearly allow ErM forming plants to have competitive advantage over other species, including AM
489 forming ones, since ErM fungi are especially efficient in N acquisition from organic sources (Read et
490 al. 2004; Averill et al. 2014).

491 The species turnover among bryophytes and the increase in certain species like
492 *Tomentypnum nitens* in plots receiving P may have several explanations. It has been shown that
493 species of hornworts and liverworts receive much of their N through symbiotic associations with N-
494 fixing cyanobacteria (Adams & Duggan 2008). This is also true for moss species common in nutrient
495 poor boreal forests (Zackrisson et al. 2009, Rousk et al. 2013). Whether this also is the case for
496 mosses in fens is not known. However, such associations have been found to be relatively common in
497 *Sphagnum* and other mire bryophytes in boreal and arctic environment (Basilier 1979; Solheim &
498 Zielke 2002). Some bryophytes are also known to form associations with various fungi, including
499 endophytes, AM, and even EcM and ErM fungi (Davey & Currah 2006; Ligrone et al. 2007; Zhang &
500 Guo 2007; Pressel et al. 2010), although the function of these is still poorly understood. In addition,
501 Niinemets & Kull (2005) concluded from fertilization experiments on calcareous grassland that

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502 bryophyte productivity is mainly limited by P due to larger P requirements compared to vascular
503 plants. They explain this from the circumstance that bryophytes photosynthesize under CO₂-
504 saturated conditions underneath the vascular plant layer with a high fraction of cytosolic P bound in
505 sugar esters, making them more sensitive to low P availability. These relationships and properties
506 implicate that some bryophytes do not (or to a lesser degree) experience N limitation or are P
507 limited. In the absence of highly competitive vascular plant species the competitive conditions are
508 changed, more bryophytes are able to utilise the added P to growth. The dominating pleurocarpous
509 mosses (e.g. *Campylium stellatum* and *Scorpidium cossonii*), on the other hand, are outcompeted due
510 to a relatively low ability for vertical growth.

511 The results of this study clearly demonstrate the importance of nutrient availability in
512 controlling the plant species composition and diversity in boreal fens. They also suggest that both N
513 and P limitation is essential for maintaining high species diversity. Large pools of vascular plants are
514 adapted to N limitation, while low availability of P apparently control bryophyte diversity. From a
515 management perspective, maintenance of N and P limitation is therefore of vital importance in order
516 to succeed in the conservation of boreal rich fens or when a functional fen system are re-established
517 through restoration measures.

518

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529

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- 728
- 729 **List of appendices**
- 730 Supplementary material 1: Nutrient solutions added
- 731 Supplementary material 2: Results from distance-based, nonparametric MANOVA of multivariate
732 plant species responses
- 733 Supplementary material 3: List of functional traits and mycorrhizal associations
- 734 Supplementary material 4: List of databases and datasets for calculation of trait values accessed
735 through the TRY trait-database
- 736 Supplementary material 5: List of species found in the experimental plots
- 737 Supplementary material 6: Changes in community weighted means in each locality for functional
738 groups and traits with significantly different responses to treatments at the two localities.

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739 **TABLES**

740

741 **Table 1.** Mean (\pm SD) turnover in species composition per plot measured as Euclidean distance (ED) after two
 742 and 15 years of nutrient addition. Turnover significantly different from control in pairwise tests are in bold. An
 743 initial two-way ANOVA revealed main effects of locality on compositional turnover in both periods, but no
 744 interaction between treatments and localities. Pairwise comparisons between treatments and control were
 745 therefore done under linear models that included main effects of locality.

746

	1998-2000		1998-2013	
	Loc A	Loc B	Loc A	Loc B
Contr	4.96 \pm 1.18	6.08 \pm 1.11	6.07 \pm 1.11	8.83 \pm 1.66
N	5.00 \pm 0.99	6.62 \pm 1.22	9.46 \pm 0.89	10.54 \pm 1.68
P	5.49 \pm 0.44	7.39 \pm 1.29	10.34 \pm 1.61	15.95 \pm 1.51
NP	6.66 \pm 0.49	9.50 \pm 0.81	12.95 \pm 1.69	16.01 \pm 1.81

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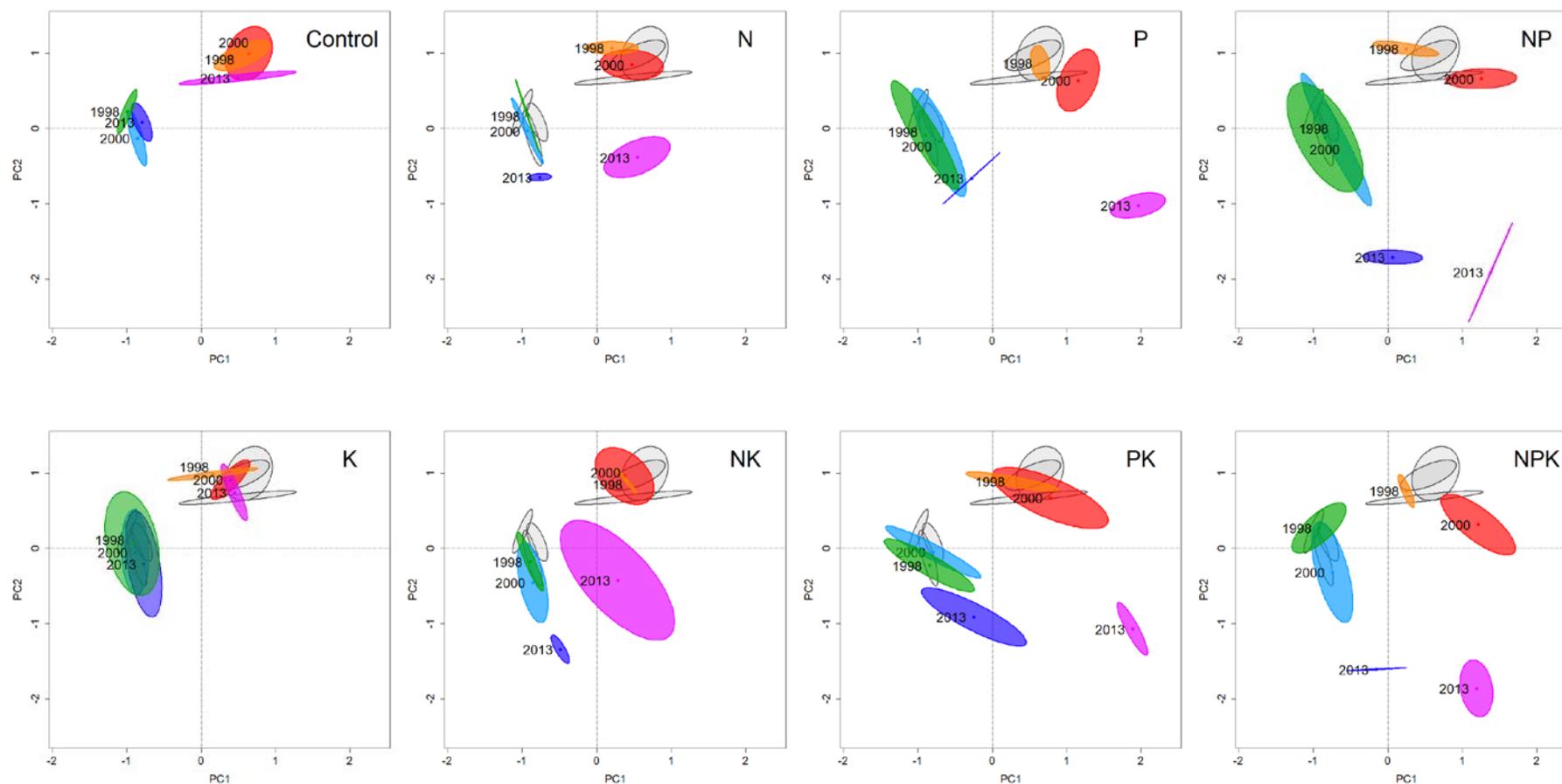
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FIGURES



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Figure 1. Centroids of plots with similar treatment together with their 95% confidence ellipses in unconstrained ordination (PCA), and their shifts from 1998-2013 along the first and second axis. Ellipses in green or blue colours are from locality A, while ellipses in orange, red or purple colours are from locality B. Ellipses in grey colour indicate the control treatment ellipses inserted into the diagrams of the other treatments for comparison.

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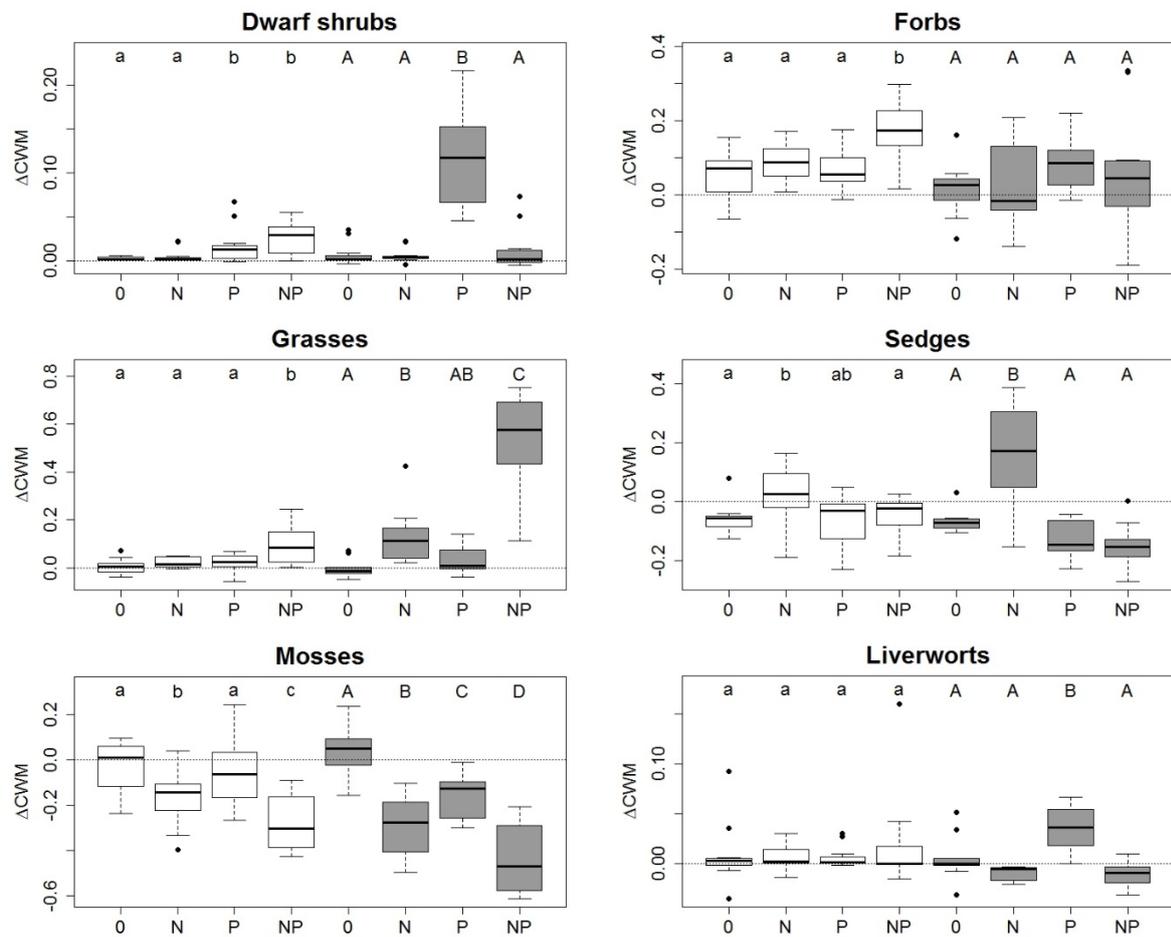


Figure 2. Changes in community weighted means (ΔCWM) of functional groups after two years (white boxes) and 15 years (grey boxes) of fertilization. Thick, horizontal lines represent median changes, boxes cover interquartile ranges, while whiskers extend to the most extreme data point which is no more than 1.5 times the interquartile range from the box. Different letters above boxes indicate significantly different treatment effects according to multiple comparisons among treatments within periods. Lower case letters are used for comparisons among changes in CWM over the period 1998-2000, while upper case letters are used for 1998-2013. Multiple comparisons were made in light of results from repeated measurement ANOVAs which included tests for differences between localities and interactions between treatments and locality on CWM. For functional groups responses to treatments were similar in both localities, even though there were weak treatment by locality interactions for grasses and mosses (cf. supplementary material 6). However, we found time-independent differences between localities for most groups. Differences between the two localities were therefore accounted for when comparing treatments. Note different scaling of vertical axes.

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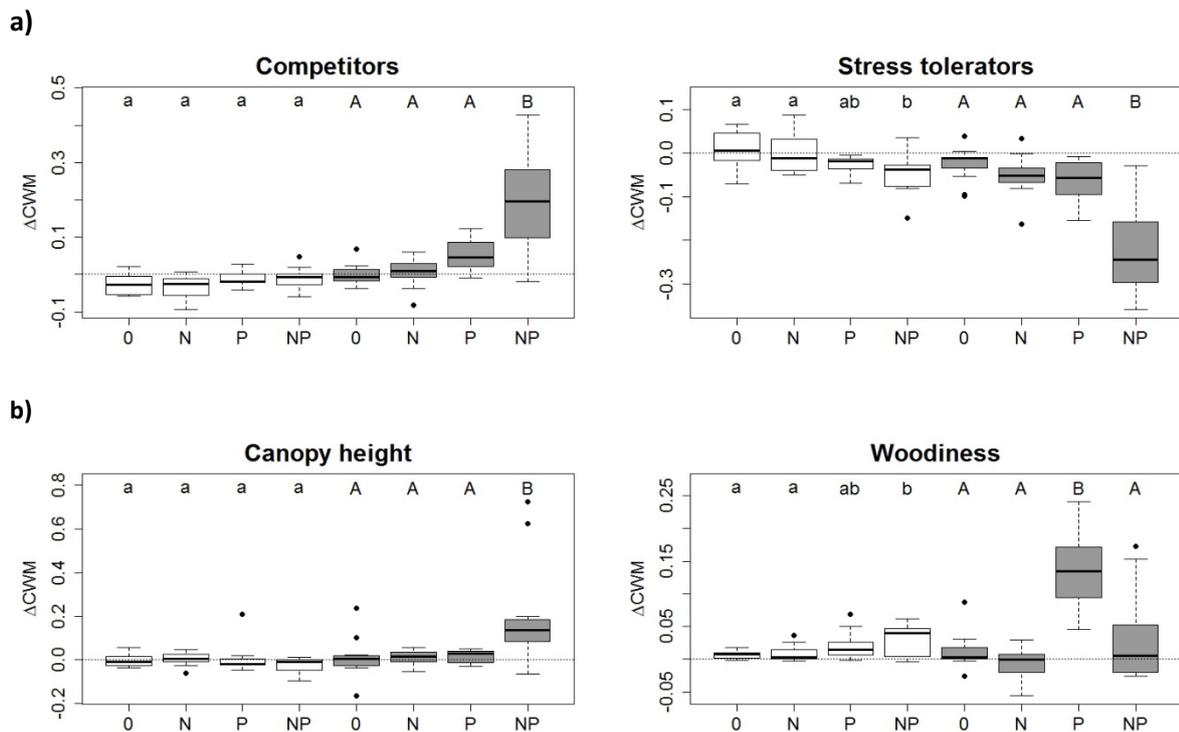


Figure 3. Changes in community weighted means (ΔCWM) of various plant functional traits after two years (white boxes) and 15 years (grey boxes) of fertilization of rich fen vegetation. For further explanations, see Fig. 2, and for explanation of traits, see Supplementary material 3. Repeated measurement ANOVAs revealed time-independent differences in CWM between localities for all traits shown here. Differences between the two localities were therefore accounted for when comparing treatments. Only traits with similar responses at both localities are shown here. Results for traits where ANOVA revealed significantly different responses at the two localities to some treatments, are presented in supplementary material. a) Traits based on plant strategies according to Grime (2001). b) Traits based on quantitative measures. Note different scaling of vertical axes.

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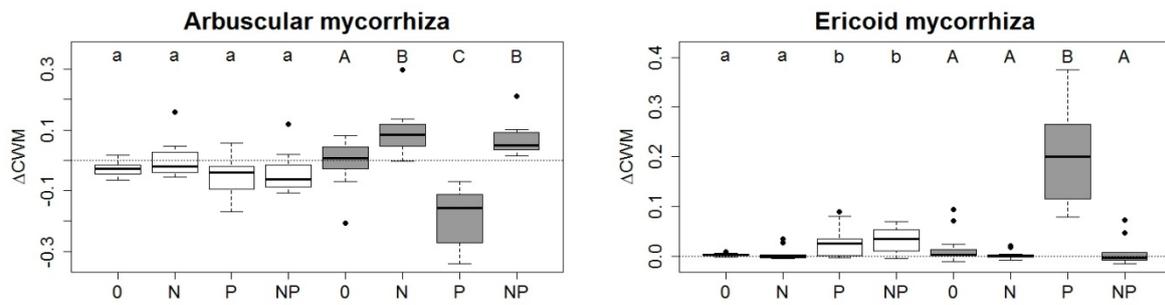


Figure 4. Changes in community weighted means (ΔCWM) of species groups with various mycorrhizal associations after two years (white) and 15 years (grey) of fertilization of rich fen vegetation. For further explanations, see Fig. 2. Repeated measurement ANOVAs revealed time-independent differences in CWM between localities for both traits shown here. Differences between the two localities were therefore accounted for when comparing treatments. Note different scaling of vertical axes.

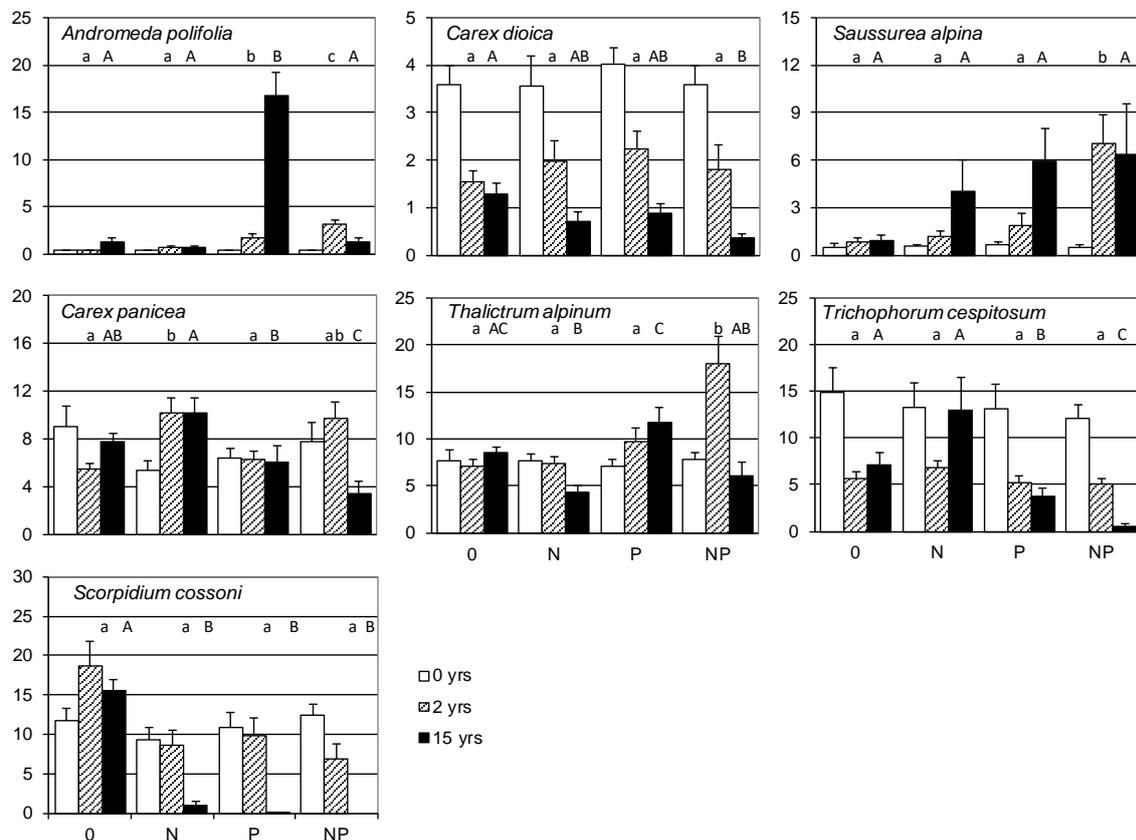


Figure 5. Abundance (% cover) of common and characteristic species of the rich fen communities with a clear pattern in relation to year and nutrient addition. White bars show the abundance before fertilization, hatched bars after two years, and filled bars after 15 years. Thin bars denote s.e. Different letters above bars indicate significantly different treatment effects (lower case after two years, upper case after 15 years) according to multiple comparisons of log-transformed cover values. Multiple comparisons were made in light of results from repeated measurement ANOVAs which included tests both for differences between localities and interactions

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between treatments and locality on species cover. For species shown here we did not find such interactions. However, we found time-independent differences between the localities. Differences in cover between the two localities were therefore accounted for when comparing treatments. Note different scaling of vertical axes.

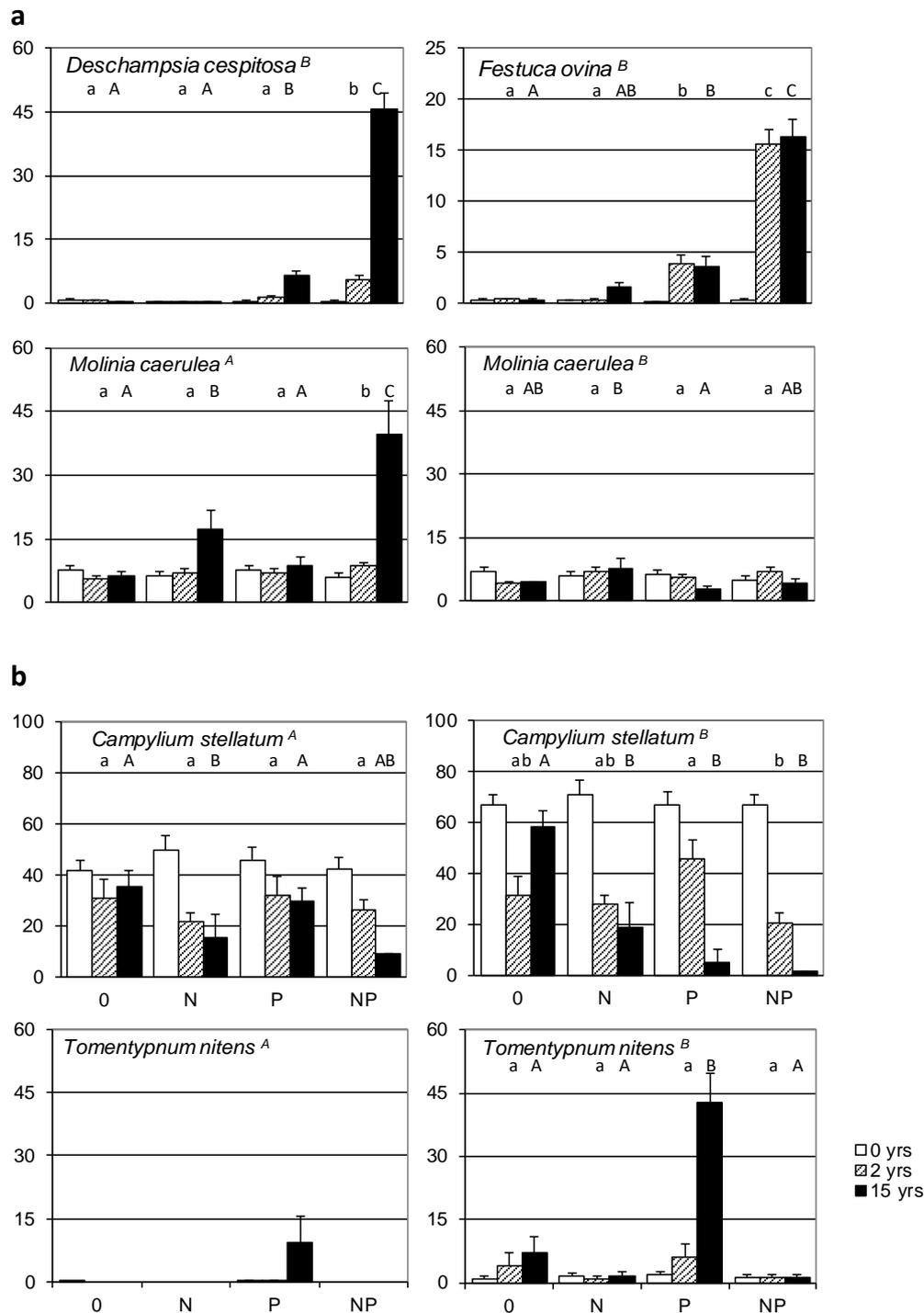


Figure 6. Abundance (% cover) of two groups of species where competitive interactions among the species may have affected their responses to a) addition of both N and P, and b) addition of P. The groups include both common rich-fen species and more sparsely occurring species that became dominant under some treatments

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during the experiment. White bars show the abundance before fertilization, hatched bars after two years, and filled bars after 15 years. Thin bars denote s.e. Different letters above bars indicate significantly different treatment effects (lower case after two years, upper case after 15 years) according to multiple comparisons of log-transformed values. As explained for figure 5, multiple comparisons were made in light of results from repeated measurement ANOVAs. For *Molinia caerulea* and *Campylium stellatum* these analyses revealed significantly different responses to treatments at the two localities. For *Deschampsia cespitosa*, *Festuca ovina* and *Tomentypnum nitens* it was not meaningful to perform overall analyses for both localities together as they had low frequency in locality A and were not present under all treatments. Results are shown for each locality separately ("A" or "B" after species names). Note different scaling of vertical axes.

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