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Slow Recovery of Mire Vegetation from Environmental Perturbations Caused by a Heat Wave and Experimental Fertilization

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Abstract We monitored vegetation changes in an alpine mire after stopping an experiment of nutrient addition, during which the mire experienced a heat wave. We aimed at assessing the capacity of mire vegetation to recover towards the original state. Nitrogen and phosphorus were added during the growing seasons of 2002–2009. We recorded periodically the cover of all vascular plant species and moss species from 2002 to 2012, i.e., 9 years after the heat wave and 3 years after discontinuing fertilization. The principal effect of the 2003 heat wave consisted in a rapid increase in cover of vascular plants and a parallel decrease in cover of mosses. These trends slowed down after 6 years and almost totally halted 9 years after the heat wave. The heat wave was the main driver of vegetation changes but the vegetation also responded to fertilization. Species within plant functional types (PFTs) showed differing responses to the heat wave and/or fertilization. The mire vegetation showed poor capacity to recover towards the initial conditions. Changes in vegetation composition were determined by individualistic responses of species to varying ecological factors. Grouping plant species into PFTs may conceal important differences in the responses of mire vegetation to environmental changes.

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Introduction

Peatlands have the by far greatest capacity to store carbon (C) among all terrestrial ecosystems. Frequent waterlogging, nutrient scarcity and strong acidity are the main ecological factors responsible for low rates of organic matter decomposition in peatlands, which allow partly decayed plant material to accumulate as peat. All of these features are in turn controlled by a key environmental factor, i.e., water table (WT) level (Limpens et al. 2008). Climate change scenarios predict warmer and drier summers for northern cold regions (Meehl et al. 2007; Briffa et al. 2009) including more frequent, stronger and longer-lasting drought events (Meehl and Tebaldi 2004). This is expected to lower the summer WT in peatlands, especially if higher evapotranspiration rates are not offset by increased summer precipitation (Gong et al. 2012). Such hydrological changes, besides decreasing the water content in the surface peat layer, can improve the soil nutrient status through accelerated peat mineralization (Bridgham et al. 1998; Olde Venterink et al. 2009). Inorganic nutrient, especially nitrogen (N) availability, can be further raised because of increasing atmospheric N deposition rates which in turn stimulates litter decomposition in peaty soils (Bragazza et al. 2012). The effects of WT lowering and/or higher nutrient availability are hence expected to impair the C budget of peatland ecosystems which can so shift from C sinks to C sources. Peatlands also occur on mid-latitude mountains. Mountain peatlands are threatened by environmental changes triggered by climate warming to a similar, or even greater extent than boreal and subarctic ones. Summer drought is also

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expected to become more frequent in mountain regions but soil water content in mountain peatlands may decrease even more as an effect of shorter snow-cover duration (Brown and Mote 2009), especially at mid altitudes where peatlands are most abundant. Mountain peatlands are of high importance owing to aesthetic and recreational values and, especially, for biodiversity conservation. In particular, mountain peatlands shelter protected habitats and plant species, some of which have in these peatlands the southernmost outposts of their distribution range in the Northern Hemisphere (Krisai and Schmidt 1983; Grünig et al. 1986; Gerdol and Tomaselli 1997).

The peculiar mechanisms controlling the functioning of these unique ecosystems have fostered recent research in peatland ecology. Several studies have addressed the direct effects of ecological factors on peatland ecosystems. Manipulative approaches have been used with this respect, such as warming (Breeuwer et al. 2008), fertilizing (Xing et al. 2011), or manipulating WT level (Breeuwer et al. 2009), snow-cover (Bombonato and Gerdol 2012), or more factors in combination (see, for example, Weltzin et al. 2000; Keuper et al. 2011). An increasing body of evidence suggests that the direct effects of varying ecological factors on the functioning of peatland ecosystems are often overruled by changes in vegetation composition (Heijmans et al. 2008; Strakova et al. 2012). Responses of peatland vegetation to environmental perturbations have been often synthesized by grouping plant species into plant functional types (PFTs). Indeed, PFTs show major differences in terms of nutrient concentrations (Ward et al. 2009; Bombonato et al. 2010), which can in turn affect C storage in plant tissues and its subsequent cycling in the soil (De Deyn et al. 2008). However, when assessing vegetation changes based on PFT grouping the overall responses at the ecosystem level can be biased by differing responses of individual species within a given PFT. For example, in a fertilization experiment in Alaskan tussock tundra declining dominance of a deciduous shrub species was compensated for by accelerated growth of sub-dominant graminoids, rather than by subordinate shrubs, showing that individual species within different PFTs can have similar capacity to take up nutrients in excess (Bret-Harte et al. 2008). Jägerbrand et al. (2009) also observed varying responses of species, particularly within the moss and lichen PFTs, to combined treatments of warming and fertilization at a subarctic heath. Vegetation composition can, hence, be a proxy for estimating greenhouse gas fluxes from peat soils (Couwenberg et al. 2011). As a consequence, it is important to detect vegetation changes considering the individual responses of all plant species.

In 2002 we initiated an experiment of fertilization in a peatland in the Italian Alps. The following year (2003) this peatland experienced a strong heat wave, which affected a vast area in Central-Southern Europe (García-Herrera et al. 2010). The heat wave brought about severe desiccation of the peatland surface (Gerdol et al. 2007). We, thus, had the unforeseen opportunity to test the combined effects of our manipulative experiment of nutrient addition with those deriving from a natural extreme event. Two years after the heat wave (2005), vegetation composition and net CO_2 exchange were both affected by the heat wave to a greater extent than by nutrient addition (Gerdol et al. 2008). Afterwards, the experimental fertilization continued until 2009 when we detected notable interactions between the ongoing effects of nutrient addition and the after-effects of the heat wave on the peatland vegetation. In addition, the interactive responses of vegetation to nutrient addition and to the heat wave differed in relation to habitat (Brancaleoni and Gerdol 2014). In 2009, the experimental fertilization was stopped as we decided to monitor the recovery of peatland vegetation at regular intervals. Recent research has shown that mire vegetation has the potential to recover after disturbance, deriving either from natural events such as fire (Sillasoo et al. 2011), anthropogenic interventions such as peat cutting (Kollmann and Kjørup Rasmussen 2012) or changes in atmospheric input (Paal et al. 2010; Vellak et al. 2014). On the other hand, there is still poor understanding of whether and how peatland vegetation can adapt to climatically-driven environmental changes and/or recover after mitigations of human impact. Our objective was to assess the capacity of mire vegetation to recover 9 year after the heat wave and 3 years after fertilization was stopped.

Methods

Study Area, Experimental Design and Climate

The study was carried out in a transitional mire in the Italian Dolomites (Torbiera di Passo San Pellegrino, ca. 4 ha area; 46°21′N, 11°44′E; 1800 m). The mire surface presented a small-scale mosaic of drier hummocks and wetter lawns. In hummocks, *Sphagnum fuscum* (henceforth *S. fuscum*) was the dominant moss species and *Calluna vulgaris* (henceforth *C. vulgaris*) and *Eriophorum vaginatum* (henceforth *E. vaginatum*) were the co-dominant vascular plant species. In lawns, *Sphagnum russowii* (henceforth *S. russowii*) and *Sphagnum magellanicum* (henceforth *S. magellanicum*) were the most abundant species in the moss layer while the vascular plant layer was dominated by graminoids, principally *E. vaginatum*, *Carex nigra* (henceforth *C. nigra*) and *Molinia caerulea* (henceforth *M. caerulea*). A more detailed description of the vegetation can be found in Brancaleoni and Gerdol (2014).

Our experiment of nutrient addition lasted 8 years. During each of the growing seasons 2002–2009, we added N (as NH_4NO_3) at three levels and phosphorus (P) (as NaH_2PO_4) at two levels. The experimental design was full factorial, with six combinations of treatment levels: −N–P (no N or P

addition); −N + P (no N, 1 g P m^{-2} yr^{-1}); LN–P (1 g N m^{-2} yr^{-1}, no P); LN + P (1 g N m^{-2} yr^{-1}, 1 g P m^{-2} yr^{-1}); HN–P (3 g N m^{-2} yr^{-1}, no P); HN + P (3 g N m^{-2} yr^{-1}, 1 g P m^{-2} yr^{-1}). The experiment was carried out in 60 permanent plots of 1 × 1 m, that were arranged in ten blocks, six in hummocks and four in lawns. Each block contained all six combinations of treatment levels. The nutrients were sprayed in solutions (1 L m^{-2}), five times during the growing season. The same amount of distilled water was sprayed onto the control plots. No manipulation was carried out from 2010 onwards.

The climate in the study area is cool-humid montane (mean annual temperature: ca. 3 °C; mean total annual precipitation: ca. 1000 mm). The growing season lasts ca. 90 days (from the beginning of June to the end of August). During the 2003 season air temperatures were very high (Fig. 1), especially in August (Brancaleoni and Gerdol 2014). Although precipitation was fairly high throughout the 2003 season (Fig. 1), the peatland experienced desiccation in that season because of exceptionally high evapotranspiration rates (Brancaleoni and Gerdol 2014). In the subsequent seasons weather fluctuated considerably but air temperatures never approached the peak values recorded in 2003 (Fig. 1).

Vegetation Analysis and Statistics

Vegetation was surveyed at the peak of the growing season (end July) in the following years: 2002 (prior to the heat wave,
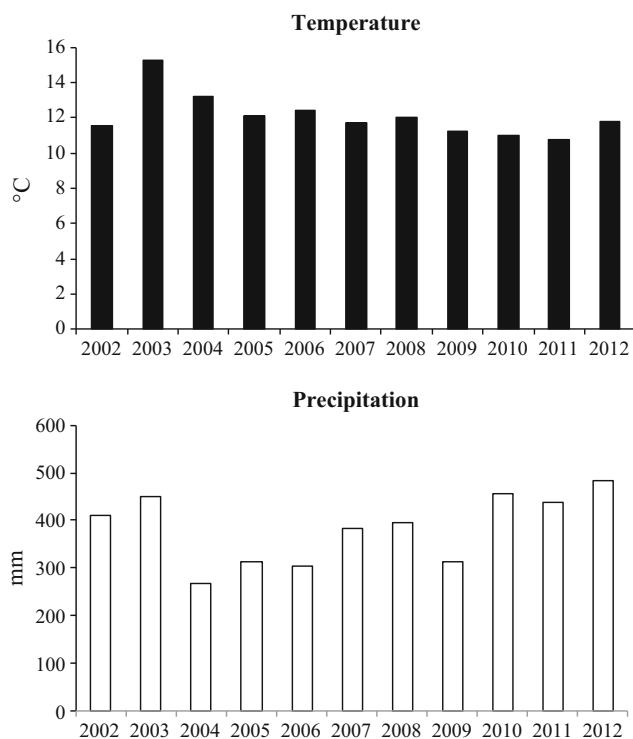

Fig. 1 Mean air temperature and mean total precipitation during the growing seasons 2002–2012

start of the fertilization experiment), 2005 (2 years after the heat wave, fertilization ongoing), 2009 (6 years after the heat wave, end of the fertilization experiment) and 2012 (9 years after the heat wave, 3 years after stopping experimental fertilization). Individual species abundance was recorded as described in Brancaleoni and Gerdol (2014). Briefly, the percentage cover of moss species was estimated visually in all of the 60 plots. At each plot, the cover of vascular plant species was assessed non-destructively by the point-intercept method (Jonasson 1988) in a 50 × 50 cm sub-plot. On the same occasions, the total cover of vascular plants was determined at each plot by measuring the Leaf Area Index (LAI) using a PAR/LAI ceptometer (Decagon, LP-80). In order to account for micro-scale variability in the distribution of vascular plants, at each plot the LAI was measured ten times at regular distance within the plot. The highest and lowest values were discarded and the mean of the remaining eight values was used as the LAI value for that plot. Species nomenclature follows Conti et al. (2005) for vascular plants; Laine et al. (2009) for *Sphagnum* mosses; Cortini Pedrotti (2001) for non-*Sphagnum* mosses.

In a previous study, we observed habitat-dependent variations in the responses of mire vegetation to the heat wave and the experimental fertilization (Brancaleoni and Gerdol 2014). Therefore, all statistics were run separately for hummocks and lawns. Key to discussions of recovery is how it is defined (Jones and Schmitz 2009). In this study, we focussed our attention on the trajectory of vegetation changes after the experimental treatments were discontinued. We defined recovery as the capacity of the vegetation to revert to a state comparable to that observed before the heat wave and prior to the start of the experimental fertilization (Mountford et al. 1996). To determine changes in community composition we used a multivariate approach, based on constrained redundancy analyses (RDA) in which the blocks (six blocks for hummocks and four blocks for lawns, respectively) were included as covariables in the RDAs. The 'species' matrix contained the percentage covers of moss species (assessed visually) and the percentage covers of vascular plant species (calculated as a percentage of the total number of intercepts) determined in 2002, 2005, 2009 and 2012 in all plots. Only species achieving at least 5 % percentage cover in one of the 4 years were included in the analyses. The sizes of the matrices were 13 × 144 for hummocks and 17 × 96 for lawns, respectively. The 'environment' matrix contained N addition, P addition and Year (Yr) as the three variables (Lepš and Šmilauer 2003). The RDAs were run using CANOCO 5.0 (ter Braak and Šmilauer 2012). Changes in LAI, total moss cover (henceforth, moss cover) and individual species cover were detected, separately for hummocks and lawns, by mixed-model ANOVAs with block as random factor and Yr, N addition and P addition as fixed factors. Significance of

HUMMOCKS
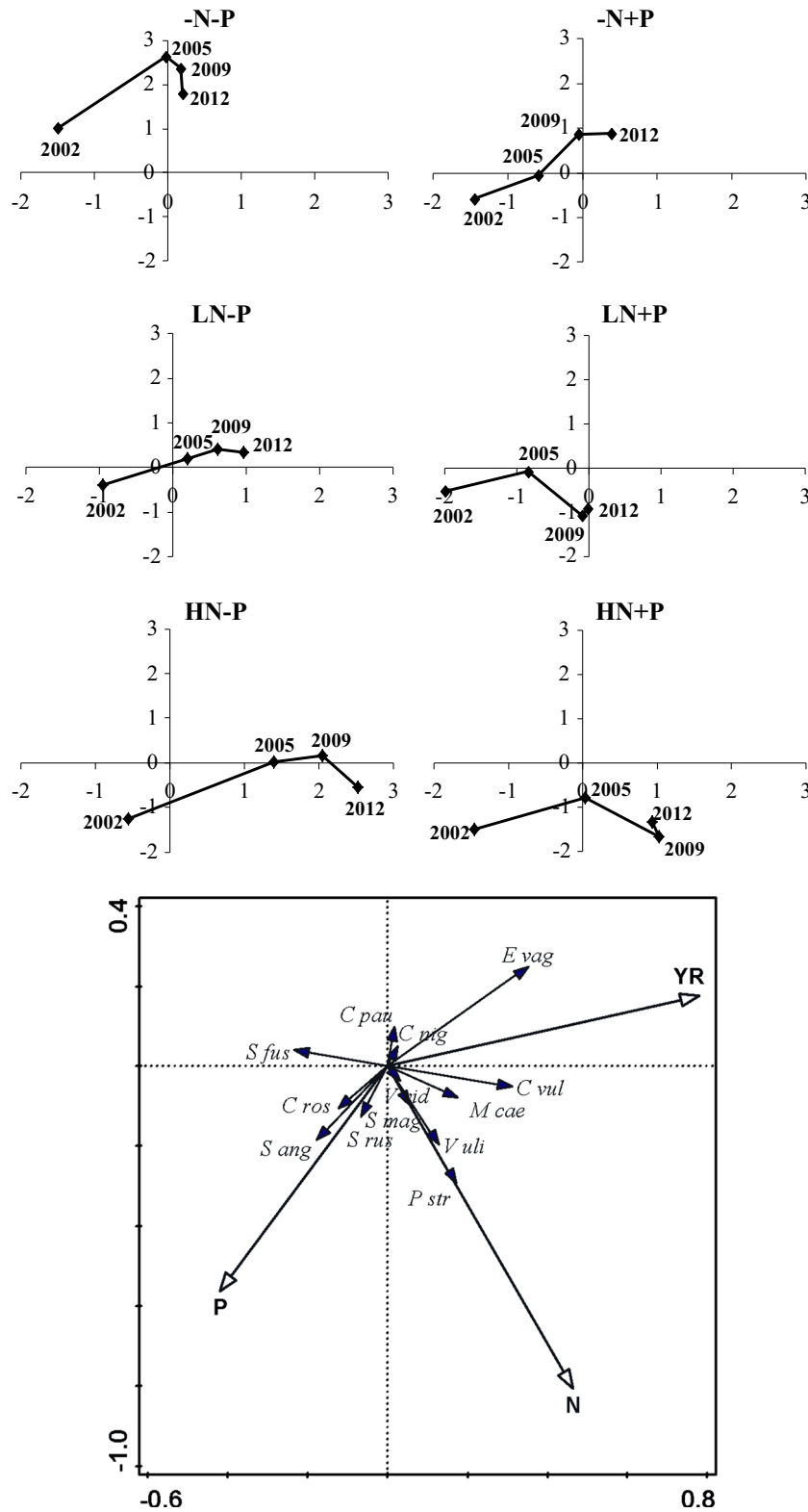
differences between mean values was assessed by post-hoc Fisher's LSD tests. Heteroscedastic data were log-transformed prior to statistical analysis, after checking for homogeneity of variances by Kolmogorov-Smirnov tests. All univariate statistics were run by the package STATISTICA (Release 6; StatSoft Inc. ©, Tulsa, OK, USA).

◄ **Fig. 2** Constrained RDA ordination on the first two axes for hummocks, showing the centroids of the plots subjected to experimental fertilization and their shifts from 2002 to 2012 and the species-treatment biplot. Treatment abbreviations: −N–P (control, no N or P addition); −N + P (no N, 1 g P m^{-2} yr^{-1}); LN–P (1 g N m^{-2} yr^{-1}, no P); LN + P (1 g N m^{-2} yr^{-1}, 1 g P m^{-2} yr^{-1}); HN–P (3 g N m^{-2} yr^{-1}, no P); HN + P (3 g N m^{-2} yr^{-1}, 1 g P m^{-2} yr^{-1}). Species abbreviations: *C vul Calluna vulgaris, C nig Carex nigra, C pau Carex pauciflora, C ros Carex rostrata, E vag Eriophorum vaginatum, M cae Molinia caerulea, P str Polytrichum strictum, S ang Sphagnum angustifolium, S fus Sphagnum fuscum, S mag Sphagnum magellanicum, S rus Sphagnum russowii, V uli Vaccinium uliginosum, V vid Vaccinium vitis-idaea*

Results

Community Composition

The first two RDA axes explained 52 and 34 % of the total variance for hummocks, and 45 % and 29 of the total variance for lawns, respectively. The displacement of the plot centroids in the RDA ordination diagram documented changes in community composition over time (Figs. 2 and 3). The first RDA axis presented a positive correlation with LAI in both habitats (higher for hummocks: $r=0.40$, $n=144$, $p<0.01$ than for lawns: $r=0.27$, $n=96$, $p<0.05$) and a negative correlation with moss cover (lower for hummocks: $r=-0.16$, $n=144$, $p<0.05$ than for lawns: $r=-0.51$, $n=96$, $p<0.05$). Shifts of the plot centroids towards higher values of the first RDA axis were, hence, generally associated with increasing vascular plant cover and/or decreasing moss cover. The length of centroid displacements along the first RDA axis can be regarded as an estimate of the magnitude of variation in community composition. Further information about the trajectory and magnitude of vegetation changes, and their relationships with the fertilization treatments, was provided by mixed-model ANOVAs of LAI and moss cover (Table 1; Figs. 4 and 5). In both hummocks and lawns, LAI and moss cover changed significantly over time while fertilization exerted overall lower, habitat-dependent, effects. Indeed, P addition had a significant effect on LAI in hummocks (Table 1) where the LAI increased more over time under P addition (Fig. 4). Nitrogen addition influenced moss cover in hummocks (Table 1) where moss cover decreased less, and even increased under LN addition (Fig. 5). Conversely, fertilization did not affect either LAI or moss cover in lawns (Table 1). However, significant interactions of nutrient additions with Yr and Block indicated that the temporal trend of community composition in lawns fluctuated presumably owing to block-related differences in floristic composition among plots (Table 1).

All centroids moved towards higher values of the first RDA axis from 2002 to 2005 both in hummocks and in lawns (Figs. 2 and 3). This is in line with consistent increases in LAI and consistent decreases in moss cover even in the untreated control plots of both habitats (Figs. 4 and 5). Afterwards, the trajectory and the magnitude of shifts of the plot centroids varied somewhat in relation to habitat and treatment. In hummocks, the centroids of all treatments moved again towards higher values of the first RDA axis both in 2009 and, generally, in 2012 as well. Indeed, the vascular plant cover still increased although the moss cover generally stopped decreasing. In particular, the moss cover in the HN + P treatment increased significantly after the initial decline, which was mirrored by a slight reversion of trajectory of change for the HN + P centroid in 2012 (Fig. 2). In lawns, the centroids of the –N plots moved little along the first RDA axis from 2005 to 2009 (Fig. 3) whereas the magnitude of the centroid shifts was greater for the LN and HN plots, where the vascular plant cover still increased and the moss cover still declined during that period (Fig. 3). Conversely, all centroids in lawns underwent poor shifts along the first RDA axis from 2009 to 2012 because the vascular plant cover stopped increasing and the moss cover stopped decreasing during that period. The trajectory of change of the LN–P and HN + P centroids even reverted, in line with increasing moss cover in those plots (Fig. 3). Overall, only in few cases did the centroids revert their trajectory towards lower values of the first RDA axis after the fertilization treatment was discontinued, either in hummocks or in lawns. In addition, the magnitude of such backward shifts was very modest which indicates poor capacity of vegetation to revert to the original state.

Individual Species

Temporal changes in the cover of individual species, and their responses to the treatments, were documented by the direction of the species arrows in the RDA space (Figs. 2 and 3) and by the results of the mixed-model ANOVAs (Figs. 6 and 7; Appendix). In hummocks, four vascular plant species increased in cover over time. The two dominant species *E. vaginatum* and *C. vulgaris* increased in cover most strongly (Fig. 6) and, therefore, presented long arrows oriented towards the right sector of the RDA diagram (Fig. 2). However, these two species responded differently to the fertilization treatments. The temporal increase in *E. vaginatum* cover was independent of nutrient addition, while *C. vulgaris* was definitely enhanced by N addition at high level (HN) independent of concomitant P amendment (Fig. 6; Appendix). Significant N × Yr interaction indicated differential effects of treatment over time for *C. vulgaris*. Indeed, *C. vulgaris* increased in cover under N addition until 2009, but not after stopping fertilization (Fig. 6). Two subordinate vascular plant species also presented significant changes in cover over time, again with different responses to treatments. *Vaccinium vitis-idaea* (henceforth *V. vitis-idaea*) increased strongly after 2009 in the plots where P had been added (Fig. 6). In contrast, the cover of *C. nigra* increased until 2009 and decreased somewhat thereafter with no effects of treatments (Fig. 6). The two most abundant moss species in hummocks presented different temporal trends and

LAWNS
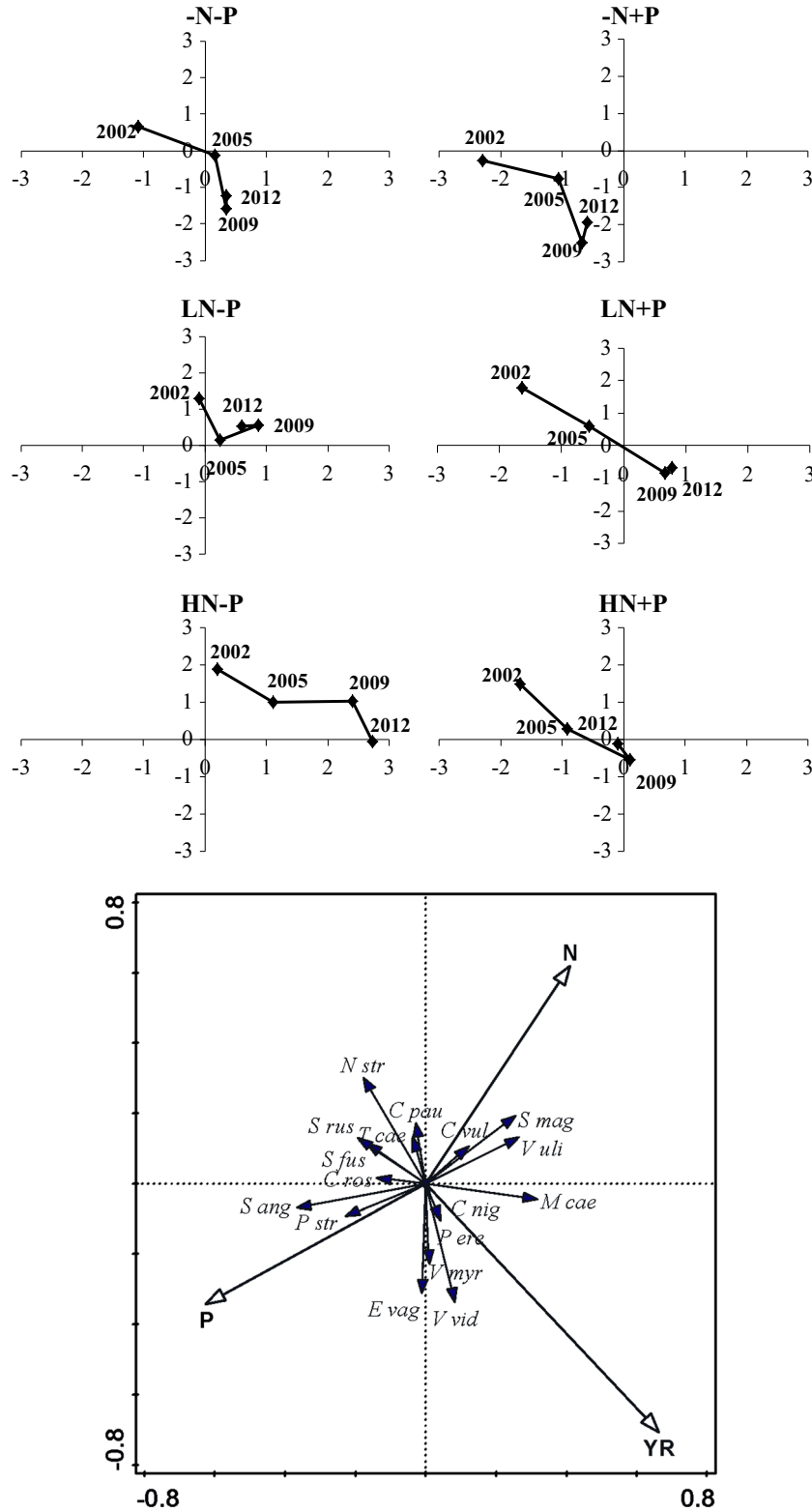
responded differently to the treatments. Indeed, N addition had a negative effect on *S. fuscum* that decreased in cover even after 2009 where N had been added at high level without concomitant P addition (HN–P), as documented by the significant effect of N and N×P (Fig. 6). Adding N increased the cover of *Polytrichum strictum* (thereafter *P. strictum*).

◀ **Fig. 3** Constrained RDA ordination on the first two axes for lawns, showing the centroids of the plots subjected to experimental fertilization and their shifts from 2002 to 2012 and the species-treatment biplot. Treatment abbreviations as in Fig. 2. Species abbreviations: *C vul Calluna vulgaris; C nig Carex nigra, C pau Carex pauciflora, C ros Carex rostrata, E vag Eriophorum vaginatum, M cae Molinia caerulea, N str Nardus stricta, P str Polytrichum strictum, P ere Potentilla erecta, S ang Sphagnum angustifolium, S fus Sphagnum fuscum, S mag Sphagnum magellanicum, S rus Sphagnum russowii, T cae Trichophorum caespitosum, V myr Vaccinium myrtillus, V uli Vaccinium uliginosum, V vid Vaccinium vitis-idaea*

However, the temporal trend differed in relation to level of N addition with strongest increase after 2009 in HN (Fig. 6).

In lawns, the cover of the most abundant evergreen shrub (*V. vitis-idaea*) increased steadily over time, even after stopping fertilization, with no effects of treatment (Fig. 7; Appendix). The cover of all three dominant graminoids (*E. vaginatum, C. nigra* and *M. caerulea*) varied significantly over time but with differing temporal trends and responses to the treatments. *E. vaginatum* increased in cover until 2009, independent of treatment (Fig. 7). The cover of *M. caerulea* increased more rapidly until 2009, then it increased only in plots that had received N addition at high level with no P addition (Fig. 7). Conversely, the cover of *C. nigra* increased until 2009 but decreased afterwards, with no significant after-effects of the treatments (Fig. 7). The cover of the most abundant moss species in lawns, *S. magellanicum*, was significantly affected by Yr and N addition, with a significant N×Yr interaction. Indeed, *S. magellanicum* cover slightly declined until 2009 independent of treatment, but increased strongly in the plots that had experienced N addition at high level after the experimental fertilization was discontinued (Fig. 7).

Table 1 *p*-values of the mixed-model ANOVAs of Leaf Area Index (LAI) and moss cover for hummocks and lawns

	LAI		Moss cover	
	Hummocks	Lawns	Hummocks	Lawns
N	0.62	0.12	**0.03**	0.52
P	**0.05**	0.25	0.06	0.19
Yr	**<0.001**	**0.01**	**<0.001**	**0.02**
Block	0.08	0.17	0.63	0.85
N×P	0.80	0.91	0.26	0.24
N×Yr	0.36	0.43	0.13	**0.03**
N×Block	0.62	0.70	0.43	0.93
P×Yr	0.41	0.41	0.50	0.58
P×Block	0.75	0.99	0.15	0.41
Yr×Block	0.65	0.70	0.35	0.10
N×P×Yr	0.56	0.33	0.81	0.45
N×P×Block	0.17	**<0.001**	0.10	**<0.001**
N×Yr×Block	0.79	0.10	0.97	0.92
P×Y×Block	0.98	**<0.01**	0.62	0.23

Significant (*p*<0.05) values in bold character

Discussion

Vegetation Layers

The vegetation changed rapidly, as a consequence of the 2003 heat wave, with secondary effects of the experimental fertilization. The main change consisted in a strong increase in cover of vascular plants, especially in hummocks, and a parallel decrease in moss cover, especially in lawns. Increasing vascular plant cover has been recorded in several European mires during the last decades (Gunnarsson and Rydin 1998; Frankl and Schmeidl 2000; Gunnarsson et al. 2002; Freléchoux et al. 2004). Such vegetation changes were principally caused by direct and indirect effects of climate warming that overruled between-year fluctuations of plant species populations (Gunnarsson and Flodin 2007) or dynamic processes associated with autogenic succession (Zobel 1988). Although the nature of the vegetation changes was very similar to that found in other sites, the magnitude of the change was much greater. For example, in a Swedish bog no species varied in frequency by more than 25 % over a 54-years period (1954–2008) during which mean annual temperature increased gradually by ca. 0.7 °C (Kapfer et al. 2011). Conversely, the cover of the vascular plant layer in the untreated control plots increased by 78 % in hummocks and 64 % in lawns, respectively, over 7 years (2002–2009). Indeed, the 2003 heat wave caused warming and consequent desiccation of the upper peat layers (Gerdol et al. 2008), which probably stimulated vascular plant growth by reducing temperature limitations to root growth (Schenker et al. 2014) or by increasing biomass allocation to aboveground organs (Sullivan et al. 2008). Higher soil temperatures could also enhance vascular plant growth through higher nutrient mineralization (Carbutt et al. 2013). However, relationships between soil temperature and nutrient mineralization rates are not always straightforward in soils of cold regions (Sistla and Schimel 2013; Yano et al. 2013). It is also uncertain whether surface desiccation affected nutrient mineralization because recent studies have not observed any significant changes in peatland soil nutrient availability after dehydration (Macrae et al. 2013; Briones et al. 2014).

During the period 2002–2009, mosses declined to a lesser extent compared to the increase in cover of vascular plants (moss cover decreased by 4 % in hummocks and 21 % in lawns, respectively). The decrease in cover of mosses was similar to that observed in some European mires experiencing gradual climatic warming (Frankl and Schmeidl 2000; Nordbakken 2001). Possible causes explaining the decrease in moss cover were: reduced moss growth as an effect of dehydration of moss tissues (Gerdol et al. 2007), reduced performance of mosses out-shaded by higher vascular plant cover (Ohlson et al. 2001; van der Wal et al. 2005) or a combination of these two causes. Whatever the mechanisms involved, the

Fig. 4 Mean (+1SE) values of Leaf Area Index (LAI) in hummocks and lawns from 2002 to 2012. Treatment abbreviations as in Fig. 2
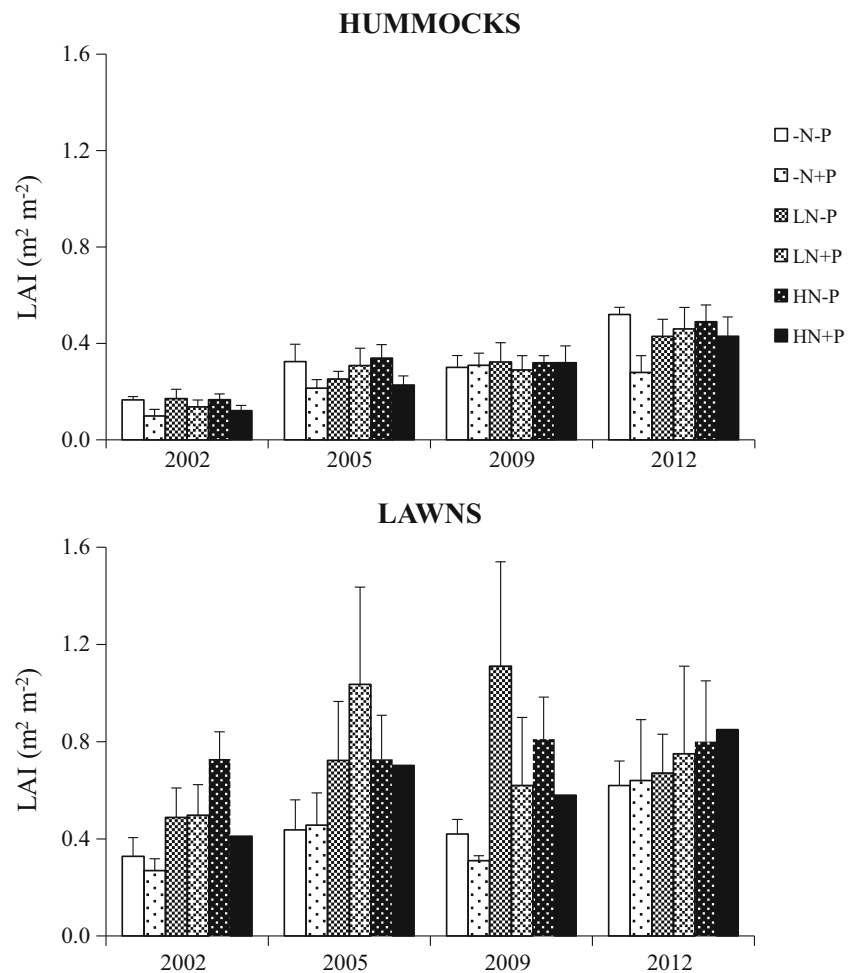
decrease in moss cover can be ascribed to desiccation of the mire surface because of very high evapotranspiration rates (Brancaleoni and Gerdol 2014). In fact, no decline in moss cover has been observed under a warming climate in mires of wet oceanic regions where higher temperatures did not raise evapotranspiration rates (Gunnarsson and Flodin 2007; Kapfer et al. 2011).

Three years later (2012), no sign of vascular plant cover reduction was yet visible even if the increasing trend strongly declined (+3 % in hummocks and +1 % in lawns, respectively). In 2012 the moss cover was stable in hummocks (+1 %) and even reversed the decreasing trend (−7 %) in lawns. In conclusion, the short-term changes in vegetation composition triggered by the heat wave suggest that mire ecosystems, although possessing a quite good capacity to recover from gradual environmental changes (Rydin and Barber 2001; Belyea and Baird 2006; Gunnarsson and Flodin 2007; Heijmans et al. 2008), are very sensitive to abrupt events (Dise 2009). On the other hand, the vegetation exhibited low ability to recover at least in the short term. Slow recovery of mire vegetation has been observed following abrupt events, either natural such as fire (Sillasoo et al. 2011) or anthropogenic such as mining for

peat extraction (González et al. 2014; Konvalinková and Prach 2014) or mechanical damage by vehicle tracks (Charman and Pollard 1995). In some sites, the vegetation of disturbed mires was still dissimilar to that of natural sites several decades after the triggering event(s) (Sillasoo et al. 2011; Pouliot et al. 2012).

Responses of Individual Species

Six out of 13 species in hummocks and five out of 17 species in lawns presented significant changes in cover with time and/or treatment. Interesting, all of them had high cover in at least one of the two habitats prior to the start of our study. These species belong to three PFTs: dwarf shrubs, graminoids and mosses. Contrary to several mires in Northern or Central Europe (Gunnarsson and Rydin 1998; Freléchoux et al. 2004; Heijmans et al. 2013), there was no encroachment either of tall shrubs or of trees that were never recorded in this mire since 1981 (Gerdol, personal observation). This suggests that vegetation dynamics in mire ecosystems depends more on vegetation composition and, presumably, abundance of individual species than on invasion of new species from outside.

Fig. 5 Mean (+1SE) values of total percentage moss cover in hummocks and lawns from 2002 to 2012. Treatment abbreviations as in Fig. 2
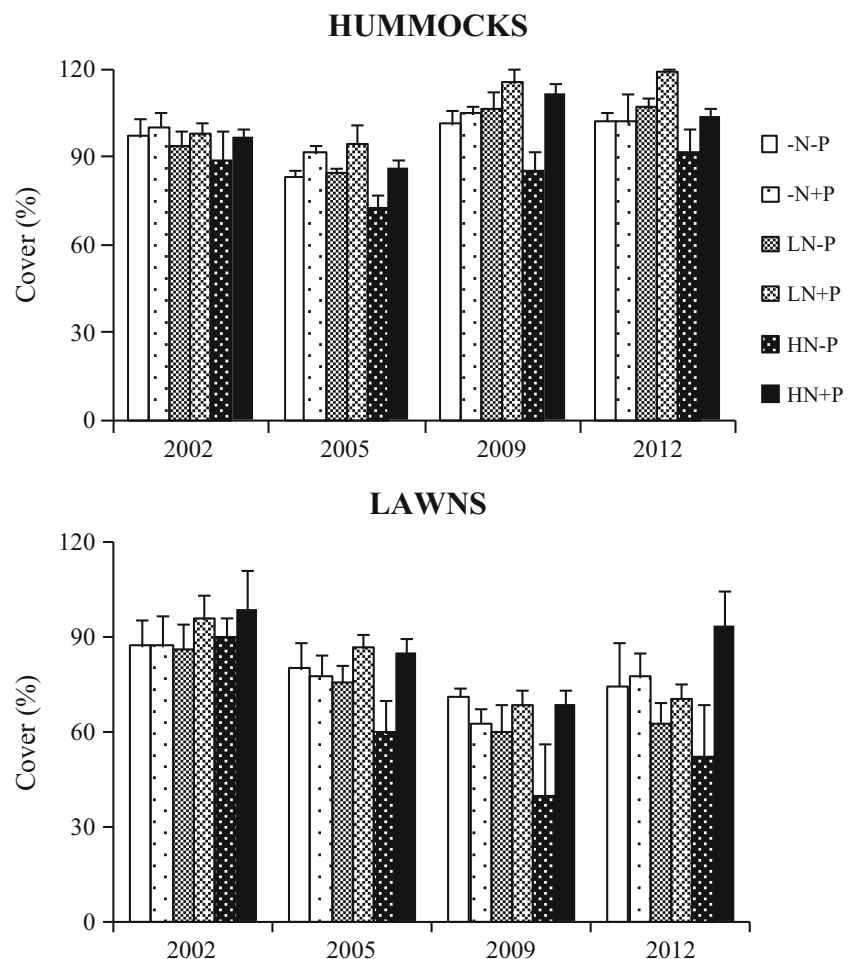
In half of these cases (Figs. 6 and 7; Appendix), changes over time in the cover of individual species were unaffected by the treatments. This, again, demonstrates that the heat wave was the main driver of vegetation changes in this mire. However, individual species did respond to the experimental fertilization especially in the nutrient-poorer habitat of hummocks (Gerdol et al. 2008). Our study also revealed differing responses to nutrient addition for individual species within PFTs and, to a lesser extent, for individual species across habitats.

Within dwarf shrubs, growth enhancement of *C. vulgaris* by N addition in hummocks was caused by alleviation of N limitation (von Oheimb et al. 2010). Adding P did not affect *C. vulgaris* in spite of low P availability in hummocks (Gerdol et al. 2008). This presumably depends on a side-effect of N addition which increases P acquisition in this species (Rowe et al. 2008; Jones and Power 2012). It is difficult to explain why growth enhancement by N addition was not sustained after stopping experimental fertilization. We speculate that this shallow-rooting species (Wallén 1987) had no longer access to the applied N that migrated downwards because of its high mobility in peaty soils (Blodau et al. 2006). Enhancement of *V. vitis-idaea* growth by P addition in hummocks was

probably caused by release of P limitation. In nutrient-poor habitats, *V. vitis-idaea* is able to cope with P deficiency by accessing biologically unavailable P pools with help of mycorrhizal associates (Gerdol et al. 2004; Cairney 2011). However, adding easily accessible inorganic P in hummocks was of benefit to *V. vitis-idaea*. The longer lasting enhancement of *V. vitis-idaea*, that persisted after discontinuing fertilization may be due to the low mobility of P in soils (Jalali and Matin 2013; Messiga et al. 2013).

Within graminoids, *E. vaginatum* has been found to respond to warming in cold ecosystems, independent of nutrient availability (Chapin and Shaver 1996). This explains why *E. vaginatum* increased in cover, independent of treatment both in hummocks and in lawns, in spite of the different soil nutrient status in the two habitats. Conversely, *M. caerulea* increased in cover in lawns when adding N without concomitant P addition because of its adaptation to P-limiting conditions (Tomassen et al. 2004) and its superior competitive performance under N fertilization (Friedrich et al. 2011). The increase in growth of *C. nigra* may represent a transient response to warming. Contrary to the other graminoids, *C. nigra* did not respond to nutrient addition. Similarly, short-term

Fig. 6 Mean (+1SE) number of intercepts of vascular plant species and mean (+1SE) percentage cover of moss species in hummocks over the period 2002–2012. Only significant (*p*<0.05) effects of the three main factors (Yr, N addition, P addition or N×P interaction) are shown.
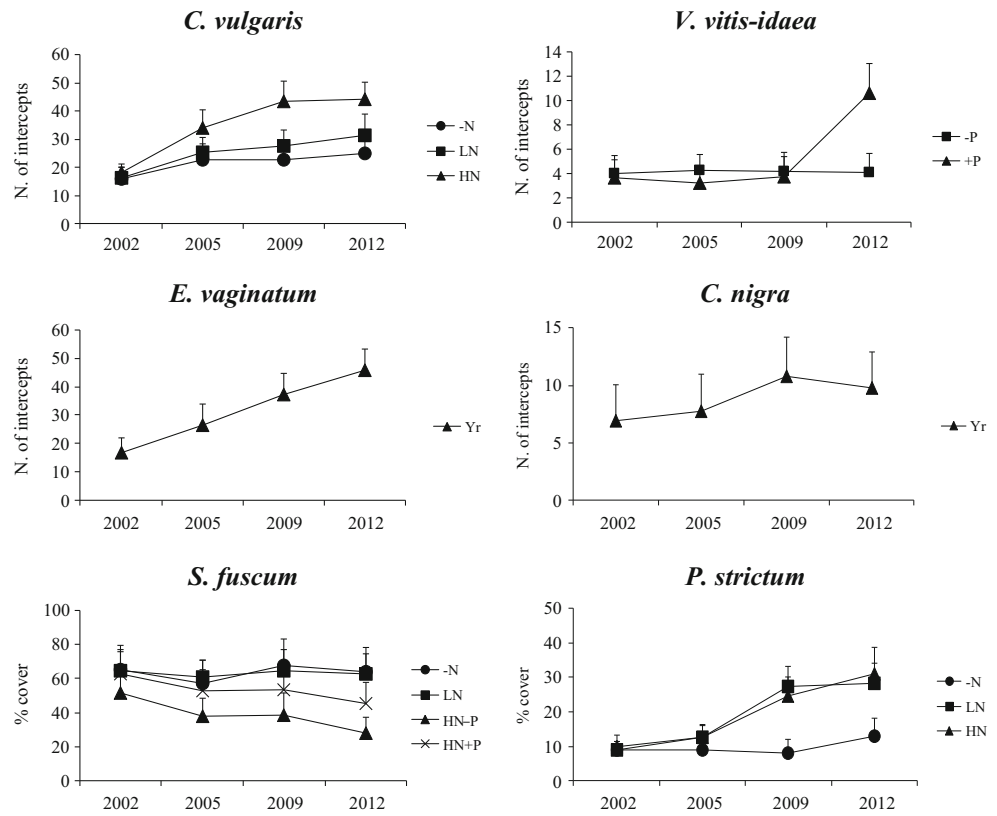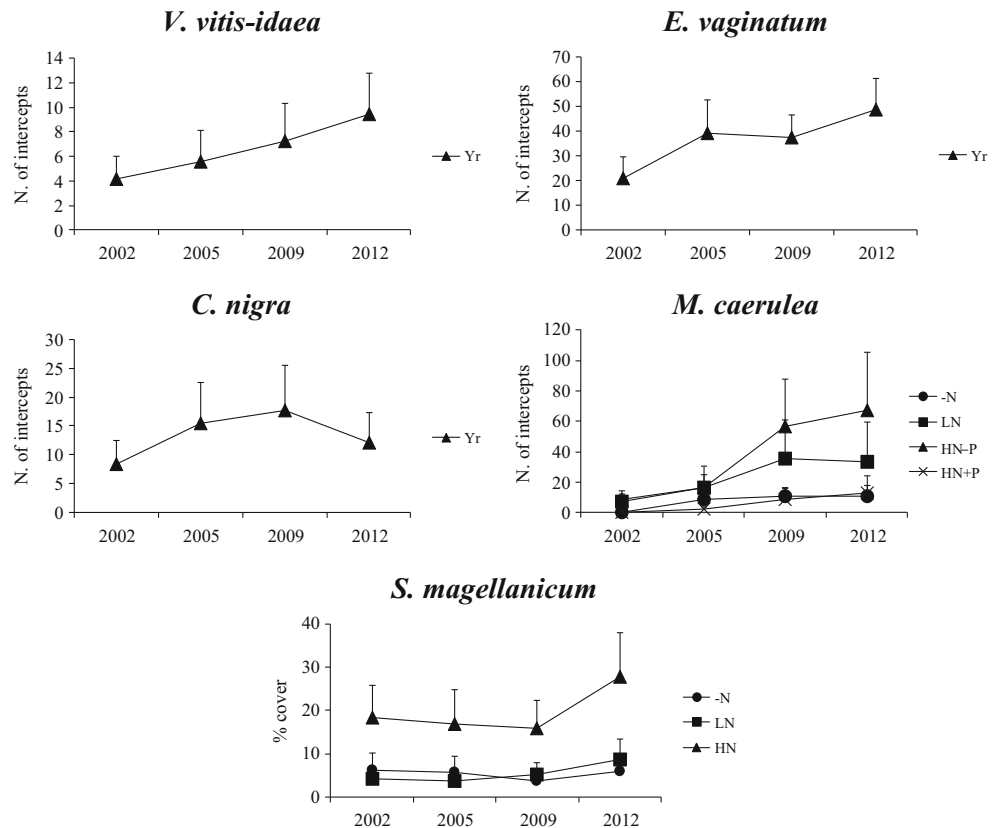

Fig. 7 Mean (+1SE) number of intercepts of vascular plant species and mean (+1SE) percentage cover of moss species in lawns over the period 2002–2012. Only significant (*p*<0.05) effects of the three main factors (Yr, N addition, P addition or N×P interaction) are shown.

increase in growth rates of two dominant *Carex* species has been observed at a passively warmed grassland in Germany although experimental warming had not improved the soil nutrient status (Kudernatsch et al. 2008). In an Irish fen *Carex* species did not respond to N addition while grasses did, thus indicating that increasing the vascular vegetation can shift in dominance from *Carex* to grasses (Verhoeven et al. 2011).

The extent of the moss cover decline was definitely smaller in hummocks than in lawns owing to two reasons. First, the hummock-forming species *S. fuscum* has a superior capacity to avoid desiccation than the lawn species *S. russowii* and *S. magellanicum* (Gerdol et al. 1996; Robroek et al. 2009). Second, the slight decline in cover of *S. fuscum* in hummocks was almost totally offset by increased cover of *P. strictum*, a desiccation-tolerant moss species settled in the driest habitats (Tuittila et al. 2000). Nutrient addition exerted a stronger influence on mosses than on vascular plants both during the experiment and afterwards. Adding N at high level had a negative effect on all *Sphagnum* species. Indeed, high N influx hampers *Sphagnum* production (Granath et al. 2012) because of direct toxic effects on the cells (Limpens and Berendse 2003) and/or indirect effects associated with P limitation (Phuyal et al. 2008). In particular, increased N deposition with no concomitant P supply strongly limits *Sphagnum* growth because of impaired N:P ratio in the tissues (Bragazza et al. 2004). For this reason, adding P somewhat attenuated the negative effect of N addition especially on *S. fuscum*. In hummocks, N addition had an opposite effect on the non-*Sphagnum* moss *P. strictum* that increased strongly in cover under high N influx. This is in line with the results of several studies reporting enhanced growth of *P. strictum* after experimental N amendment (Berendse et al. 2001; Hoosbeek et al. 2002; Bubier et al. 2007). The strong increase in cover of *P. strictum*, and concomitant decline of *S. fuscum* even after stopping fertilization in HN–P, suggests that *P. strictum* can even out-compete the associated *Sphagnum* species at a certain cover threshold (González et al. 2013). Mitchell et al. (2002) also observed contrasting effect of high N deposition on *P. strictum* and the co-existing *Sphagnum* species *S. fallax*. In lawns, the initial negative effects of high N influx on *S. magellanicum* were even reversed after stopping N addition. Indeed, *S. magellanicum* is quite resistant to high N influx thanks to its ability to mitigate N-toxicity by lower uptake (Fritz et al. 2014). Furthermore, *S. magellanicum* capitula quickly respond to reductions in excess nutrient supply (Limpens and Heijmans 2008) which makes it highly competitive against co-existing species (Mulligan and Gignac 2002).

Conclusion

The principal effect of the 2003 heat wave consisted in a rapid increase in cover of vascular plants and a parallel decrease in cover of mosses. These trends became evident immediately after the heat wave (Gerdol et al. 2008). Subsequently, they slowed down after 6 years and almost totally halted 9 years after the heat wave. There were poor indications of recovery towards the initial vegetation conditions. The heat wave was the main driver of vegetation changes but vegetation also responded to nutrient additions whose after-effects were still detectable 3 years after stopping fertilization. While the vegetation changes triggered by the heat wave and the experimental fertilization were habitat-dependent (Brancaleoni and Gerdol 2014), hummocks and lawns did not differ remarkably from each other in their capacity to recover from the environmental perturbations. Species within PFTs showed differing responses to the heat wave and/or the experimental fertilization, with additional habitat-dependent variations. This supports results of previous studies that observed individualistic responses of mire species to varying ecological factors (Chapman and Rose 1991; Hájková et al. 2011; Kapfer et al. 2011). Therefore, grouping plant species into PFTs may conceal important differences in the responses of mire vegetation to environmental changes.

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