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Eutrophication triggers contrasting multilevel feedbacks on litter accumulation and decomposition in fens

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Abstract. Eutrophication is a major threat for the persistence of nutrient-poor fens, as multilevel feedbacks on decomposition rates could trigger carbon loss and increase nutrient cycling. Here, we experimentally investigate the effects of macronutrient (NPK) enrichment on litter quality of six species of sedge (*Carex* sp.), which we relate to litter decomposition rates in a nutrient-poor and nutrient-rich environment. Our research focused on four levels: we examined how eutrophication alters (1) fresh litter production ("productivity shift"), (2) litter stoichiometry within the same species ("intraspecific shift"), (3) overall litter stoichiometry of the vegetation under the prediction that low-competitive species are outcompeted by fast-growing competitors ("interspecific shift"), and (4) litter decomposition rates due to an altered external environment (e.g., shifts in microbial activity; "exogenous shift"). Eutrophication triggered a strong increase in fresh litter production. Moreover, individuals of the same species produced litter with lower C:N and C:P ratios, higher K contents, and lower lignin, Ca and Mg contents (intraspecific shift), which increased litter decomposability. In addition, species typical for eutrophic conditions produced more easily degradable litter than did species typical for nutrient-poor conditions (interspecific shift). However, the effects of nutrient loading of the external environment (exogenous shift) were contradictory. Here, interactions between litter type and ambient nutrient level indicate that the (exogenous) effects of eutrophication on litter decomposition rates are strongly dependent of litter quality. Moreover, parameters of litter quality only correlated with decomposition rates for litter incubated in nutrient-poor environments, but not in eutrophic environments. This suggests that rates of litter decomposition can be uncoupled from litter stoichiometry under eutrophic conditions. In conclusion, our results show that eutrophication affects litter accumulation and -decomposition at multiple levels, in which stimulatory and inhibitory effects interact. The cumulative effect of these interactions ultimately determine whether peatlands remain sinks or become sources of carbon under eutrophic conditions.

Key words: carbon sequestration; decomposition; eutrophication; global change; litter; peatlands.

Introduction

More than an estimated one-quarter of the world's soil carbon is stored in peatlands (Joosten and Clarke 2002, Moore 2002). The prerequisite for net peat accumulation is a continuous input of fresh plant litter followed by partial decomposition (and long-term storage) of that litter (i.e., peat). As macronutrients are fixed in recalcitrant structures of the growing peat matrix, (inorganic) nutrient availability is generally low in peatlands (Joosten and Clarke 2002), which facilitates the presence of many rare, slow-growing plant species. However, widespread drainage coupled with peat mineralization, atmospheric nitrogen deposition, rising global temperatures, and the use of artificial fertilizer and manure is causing severe eutrophication of peatlands worldwide (van Diggelen et al. 2006, Lamers et al. 2015). To date, one of the major challenges is understanding how nutrient enrichment affects organic matter accumulation, decomposition, and net carbon fluxes in peatlands (Bragazza et al. 2006), as eutrophication-induced shifts in the carbon balance are likely. Eutrophication directly stimulates primary (and thus fresh litter) production (Kotowski et al. 2006, Hautier et al. 2009), and it may directly and indirectly alter decomposition rates of fresh litter and soil organic matter (Hessen et al. 2004). However, many studies of peatland eutrophication are biased by a (too) narrow scope, which has often resulted in oversimplified conclusions with respect to peat accumulation. In our paper, we argue that eutrophication-induced shifts occur at least at four different levels in the process of peat formation.

First, an increase in nutrient availability stimulates plant primary production (Hautier et al. 2009), and the

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concomitant increase in fresh litter production should directly increase rates of peat accumulation. In this paper, we refer to this as a "productivity shift." Second, nutrient enrichment may affect litter stoichiometry (e.g., litter quality indicators such as C:N ratios, C:P ratios, and lignin or cellulose contents) within individual plants of the same species (Aerts and de Caluwe 1997, Gusewell 2004). Such altered within-species stoichiometry can affect decomposition rates of freshly produced litter: a low litter C:N ratio or low lignin concentration can be indicative for a fast decay (Taylor et al. 1989, Gessner and Chauvet 1994). We refer to this eutrophication-induced within-species stoichiometric shift as an "intraspecific shift." Third, eutrophication may not only affect an individual plant's stoichiometry, it also affects the structure and composition of complete plant communities. If macronutrients are in ample supply, low-competitive, stress-tolerant plant species are generally outcompeted by taller, more competitive species (Kotowski et al. 2006, Hautier et al. 2009). Such changes in the composition of the vegetation can directly influence decomposition rates, as the quality of the litter (of the plant community as a whole) often changes as well (Hobbie 1992, Ward et al. 2015). This community level response to eutrophication is referred to as an "interspecific shift." Fourth, eutrophication affects the composition, biomass, and behavior of microbial communities in the soil (Wright et al. 2009, Kaštovská et al. 2012, Chen et al. 2014), which should again be mirrored in litter decomposition rates. To date, the exogenous effect of eutrophication on litter decomposition has remained unclear (Knorr et al. 2005). While some studies report high litter decomposition rates in eutrophic environments (Qualls and Richardson 2000, Bragazza et al. 2006, Kominoski et al. 2015), others report neutral or even opposite patterns (Craine et al. 2007, Hobbie 2008). The contrasting results led to the emergence of two seemingly competing theories with respect to effects of external nutrient supply on litter decomposition (Craine et al. 2007, Chen et al. 2014). The first theory of "stoichiometric decomposition" generally predicts higher decomposition rates with increasing exogenous nutrient input (the latter leading to, for example, lower soil and substrate C:N ratios; Hessen et al. 2004), whereas the second theory of "microbial nutrient mining" emphasizes the existence of a guild of micro-organisms that uses labile C as an energy source to decompose recalcitrant organic matter in order to gain access to organically bound nutrients (Moorhead and Sinsabaugh 2006). The latter theory predicts lower decomposition rates when the easily available exogenous nutrient pool increases, i.e., in response to eutrophication (Craine et al. 2007, Chen et al. 2014). We refer to this fourth eutrophication-induced shift as an "exogenous shift."

In the present study, we investigated how macronutrient (NPK) enrichment affects litter production, litter quality, and litter decomposition rates in groundwater-fed peatlands ("rich fens" hereafter). Undisturbed rich fens are oligo- to mesotrophic, waterlogged wetlands in which the peat-forming communities mainly consist of bryophytes and low-productive, stress-tolerant, small sedges of the *Carex* genus (Wheeler and Proctor 2000). In Europe and North America, however, eutrophication has affected a large proportion of the remaining fens (Lamers et al. 2015), leading to a loss of biodiversity and the replacement of small sedges by taller, more competitive sedges (Wheeler and Proctor 2000, van Diggelen et al. 2006). The majority of fen and peatland studies that addressed this eutrophication effect on ecosystem functioning have solely focused on effects of N enrichment (Aerts and de Caluwe 1997, Bragazza et al. 2012). Only relatively few studies experimented with P enrichment (Qualls and Richardson 2000, Sarneel et al. 2010) or the combined effects of NPK enrichment (Carfrae et al. 2007, Xing et al. 2011, Kaštovská et al. 2012). This has large implications for a good understanding of a potential shift in ecosystem functioning, since eutrophication of fens (in contrast to rainwater-fed bogs that are mainly affected by atmospheric N deposition) usually corresponds with a combined increase in pools of both inorganic nitrogen and phosphorus (Emsens et al. 2015, Lamers et al. 2015), as well as potassium if fertilizers are at the origin of the eutrophication (Wheeler 1983). Here, we aimed to disentangle the direction and magnitude of the different NPK eutrophication-induced shifts on litter decomposition, and related these results to actual peat accumulation. We selected six species of *Carex* that are naturally found along a fertility gradient in fens, and we varied NPK availability to quantify changes in litter production and litter quality. Litter quality was subsequently related to actual rates of litter decomposition in standardized nutrient-poor and nutrient-enriched decomposition beds. We hypothesized that (1) eutrophication increases plant biomass and litter production (productivity shift), (2) eutrophication increases litter quality and decomposability within the same species (intraspecific shift), (3) species typical for nutrient-enriched habitats produce litter that is more easily decomposable (interspecific shift), (4) eutrophic environments stimulate litter decomposition rates as predicted by stoichiometric theory, regardless of litter quality (exogenous shift).

We thus expected that eutrophication causes a multilevel shift in a fen's carbon balance by installing positive feedback loops on rates of litter production, litter quality, litter decomposition, and nutrient cycling. Theoretically, such feedbacks could hamper peat accumulation and further contribute to eutrophication, eventually turning a peatland from sink to source of carbon.

Materials and Methods

Species selection and classification

We selected six species of *Carex* that are typically found in fens and wet organic soils of the Northern hemisphere: *Carex paniculata*, *C. appropinquata*, *C. lepidocarpa*,

C. nigra, *C. diandra*, and *C. echinata.* The selected species occupy different parts of a fen along a fertility gradient. Therefore, we ranked the species according to their natural occurrence from eutrophic to oligotrophic conditions. We based this ranking on the species' revised Ellenberg values for nitrogen following Hill et al. (1999), in which *Carex paniculata* (6) > *C. appropinquata* (4) > *C. diandra* (3) > *C. lepidocarpa* (2) = *C. nigra* (2) = *C. echinata* (2). Note that Ellenberg-N values represent the general productivity of the system in which the species optimally occurs rather than solely N loading of the system (Klaus et al. 2012). Generally, low-competitive (low Ellenberg-N) species have their natural optimum in nutrient-depleted environments (Kotowski et al. 2006), which can be linked to their high nutrient use efficiency (Aerts 1999). In contrast, competitive (high Ellenberg-N) species only thrive in more eutrophic environments as they trade off nutrient use efficiency with rapid growth and foliar expansion (Aerts 1999). Although the latter strategy allows competitors to maximize light interception under eutrophic conditions (thereby outcompeting low-competitive species), it simultaneously hampers long-term survival in nutrient-depleted environments (Aerts 1999, Kotowski et al. 2006).

Germination and transplantation

In spring 2013, cold-moist stratified *Carex* seeds were germinated on moist filter paper in an incubator under a fluctuating day:night regime (24–15°C, 12:12 h photoperiod). After germination, seedlings were transported to a greenhouse nursery. Here, seedlings were temporarily grown on a moist mixture of standard potting soil and white sand to allow an optimal initial growth and establishment to an approximate height of 10 cm. After seven weeks, 180 healthy individuals (30 seedlings of each species) were carefully removed from their nursery pots and roots were rinsed to remove adherent soil particles. Seedlings were then transplanted into the experimental mesocosms.

Experimental design

Our study had a full-factorial design in which 30 seedlings of each of the six species were divided (in monocultures) over a total of 60 experimental mesocosms (volume 5 L), resulting in three (sub-replicate) seedlings of one species per replicate mesocosm. Next, one-half of the mesocosms received a nutrient-rich treatment while the other half was kept nutrient poor. In total, this setup resulted in five replicate mesocosms per species per nutrient treatment (2 nutrient levels × 6 species [3 individuals per mesocosm] × 5 replicate mesocosms). Mesocosms were placed in an unheated greenhouse (to prevent N deposition) in full daylight, and had a 2-cm layer of river gravel at the bottom. The remaining volume of the mesocosms was filled with clean white sand. Next, five multichannel peristaltic pumps (Masterflex 7521-57, Cole-Parmer, Chicago, Illinois, USA, each with 12 separate connections connected to light-sealed water reservoirs containing tap water) were connected to the 60 mesocosms. In each mesocosm, water from the reservoirs was pumped in at a constant rate of 0.18 L/d to compensate for evapotranspirational loss and to guarantee a constant basic supply of essential base cations, trace elements, and minimal amounts of nutrients (tap water characteristics in Appendix S1: Table S1). The inlets of the pumps were placed at the bottom of the mesocosms, in the river gravel, to ensure an equal distribution of water and nutrients as well as to simulate groundwater upwelling typical for fens. A water outlet was placed at the top of the mesocosms to allow runoff of excess water (Appendix S1: Fig. S1). When evapotranspiration exceeded water input (e.g., on warm and sunny days), demineralized water was added to keep the mesocosms continuously waterlogged cf. natural fens. Extra macronutrients (NPK) were injected biweekly directly into the mesocosm inlets, using a 2mL syringe, as dissolved KNO_3 (N and K) and KH_2PO_4 (P and K) from stock solutions so that total amounts of N, P, and K allocated to each mesocosm at the end of the growing season (n = 119 d) equaled 363.1, 21.1, and 959.8 mg, respectively, for the nutrient-rich treatment and 58.8, 3.8, and 88.6 mg, respectively, for the nutrient-poor treatment. These nutrient quantities were based on the range of values reported by Gusewell and Gessner (2009) who performed comparable mesocosm experiments with different species of *Carex* under different nutrient supplies. In our study, "nutrient-poor" implies conditions of severe macronutrient limitation whereas "nutrient-rich" implies a non-limiting macronutrient availability (for the selected species). In other words, the nutrient-poor treatment more closely resembles the natural range of the low Ellenberg-N species (e.g., *C. echinata* or *C. lepidocarpa*), whereas the nutrient-rich treatment more closely resembles the natural range of the higher Ellenberg-N species (e.g., *C. paniculata* or *C. appropinquata*). Every two weeks, the mesocosms were spatially randomized.

Morphological measurements and plant harvest

During the growing season, we determined the specific leaf area (SLA) of all plants. Next to a species' Ellenberg-N value, SLA indices are also used as a proxy for plant-growth strategy: fast-growing, competitive species (typical for eutrophic systems) tend to have higher SLA indices than slow-growing, stress-tolerant species (typical for nutrient-limited systems; Westoby 1998). For SLA determination, we randomly collected one fresh, fully expanded, and illuminated leaf per individual plant in the middle of the day at the end of August 2013. Next, we cut out a 5–6 cm fragment from the middle of the leaf, and immediately calculated the surface area of one side of the fragment by combining digital photography with image-processing software ImageJ (Schneider et al. 2012). Next, all fragments were oven dried (70°C) for 24 h and weighed. SLA was calculated as leaf area divided by dry mass (cm^2/g). We used mesocosm averages of SLA (three

sub-replicates) for further data analysis. From October onward, senesced leaves (litter) were collected every week, rinsed, air dried, and stored in dry paper bags. At the end of the growing season (November 2013, $n = 119$ d), we counted the total number of living leaves per individual plant (leaf count), and we averaged the lengths of the two longest leaves per plant (leaf length). Next, the mesocosms were placed in a dark cooling room to simulate winter conditions and to initiate rapid leaf senescing. Mid-January 2014, all sedges were removed from the cooling room and aboveground (senesced) biomass was harvested and carefully rinsed with deionized water to remove any adherent soil particles. Per mesocosm, litter from the final harvest was mixed with the senesced leaves that had been collected in the weeks before. Next, all biomass was dried at 45°C and then weighed (g). We used this 45°C-dried rather than 70°C-dried material in subsequent decomposition experiments as this more closely resembles natural material for decomposition. To estimate total (70°C-dried) biomass per mesocosm, subsamples (1.4–1.9 g) of each 45°C-dried homogenized sample were oven-dried at 70°C to calculate a conversion factor per sample. Total biomass was then calculated by multiplying this conversion factor with the mass of the total collected 45°C-dried material. We only report the latter biomasses per plant (total biomass per mesocosm/3 plants) in this paper. The 70°C-dried litter was then ground using a rotary mill (Retsch zm 200, Retsch, Haan, Germany) and used for chemical analysis.

Chemical analyses

We made a selection of chemical (plant litter) variables that are most commonly used as indicators of litter quality: N, P, K, C, lignin, and cellulose content (and mass ratios between these variables). Additionally, we determined litter Ca and Mg contents as these parameters may also correlate with decomposition rates. Total N, P, K, Ca, and Mg contents were determined following Walinga et al. (1989), in which ground samples were digested with H_2SO_4, salicylic acid and H_2O_2. N and P were analyzed on a segmented flow analyzer (Skalar, Breda, the Netherlands); K, Ca, and Mg were analyzed on ICP (Thermo Fisher, Franklin, Massachusetts, USA). Total C contents were analyzed though combustion of oven-dried and mill-ground plant material, using a CN-analyzer (Flash 2000, Thermo Fisher Scientific, Waltham, Massachusetts, USA). We used the van Soest method to analyze plant material for alpha-cellulose ("cellulose" hereinafter) and ADF-lignin content ("lignin" hereinafter; Van Soest 1963). In this method, cetyltrimethylammonium-bromide (CTAB) is added to 0.5–1 g of ground plant material and heated, which dissolves proteins. Samples were then rinsed, dried at 105°C, and weighed. Next, 72% sulfuric acid (H_2SO_4) was added to dissolve cellulose, after which samples were again rinsed, dried, and weighed. Mass loss, corrected for initial mass of the sample, was used to calculate cellulose content. Finally, lignin was removed from the samples by ashing the remaining material at 550°C for 4 h. Again, mass loss was used to calculate lignin content. Due to unforeseen procedural errors during the heating phase and sulfuric-acid phase, respectively, we lost two cellulose and three lignin samples (out of the 60 samples). Contents are reported in mg/g dry mass.

Decomposition experiments

Decomposition experiments were run in 10 closed artificial decomposition beds (57 cm long × 39 cm wide × 28 cm high). Each bed was filled with 25 kg of limed (25 g $CaCO_3$) clean white sand, and inoculated with 1 L fresh peat soil from a *Scorpidium scorpioides*-dominated rich fen (collected in the Weerribben, the Netherlands; 52°47′02.4″ N 5°58′58.8″ E) to attain a decomposer community typical for rich fens. Beds were placed in a basement with relatively stable temperatures (minimum–maximum range between 15.2°C and 19.9°C) in full darkness. To allow establishment of the decomposer community, mesocosms had been established six months prior to initiation of the decomposition experiment. Water levels were manually kept at surface level with a mixture of 90% demineralized water and 10% tap water, the latter to provide a minimal supply of essential trace and base elements (Appendix S1: Table S1) to mimic rich fen conditions. Soil pH in the decomposition beds equaled 7.2 ± 0.04 (measured with a HI 99121 portable pH meter [Hanna Instruments, Woonsocket, Rhode Island, USA]). After five months (one month prior to actual litter incubation), one-half of the beds (five) were heavily eutrofied by mixing 200 g slow-release NPK fertilizer (17-9-11 Substral Osmocote Scotts Benelux, Sint-Niklaas, Belgium) with the soil. The other one-half of the decomposition beds was kept nutrient poor; soil was also "mixed" to guarantee an equal treatment but no fertilizer was added.

Dried plant litter (0.82 ± 0.08 g [mean ± SD]) was manually cut into 5-cm fragments and then put in litter bags. As plants from the nutrient-poor treatment had not produced sufficient biomass for incubation, we were restricted to incubating litter from plants that had grown under the nutrient-rich treatment. Ten replicate litterbags of each of the six species (two litter samples were collected from each of the 30 nutrient-rich mesocosms) were divided pairwise over the nutrient-poor and nutrient-rich decomposition beds. Additionally, we incubated one piece of standard (alpha-)cellulose filter paper (0.78 ± 0.006 g) in each mesocosm.

The litter bags (8 × 5.5 cm) were made from polyester netting with mesh size 325 μm (TopZeven, Haarlem, the Netherlands). We chose this fine mesh size, as the use of a too large mesh size in narrow-leaved grasses causes unacceptable litter loss through the maze (Aerts et al. 2003). Litter bags were placed horizontally on the soil surface and were then pushed 2–3 mm into the top soil to guarantee contact of the plant litter with surrounding soil and pore water; this is also the zone where leaf litter would be deposited under natural conditions.

TABLE 1. Plant leaf length, leaf count, total aboveground biomass, and specific leaf area (SLA) of the study species (averages ± SD) under low and high nutrient treatments at the end of the experiment ($n = 5$).

Species and nutrient treatment	Leaf length (cm)		Leaf count, *n*		Total aboveground biomass (g)		SLA (cm^2/g)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Carex paniculata								
Low	25.6	3.4	30.1	8.2	0.65	0.14	297	32
High	36.0	4.3	51.7	9.5	1.73	0.38	315	34
C. appropinquata								
Low	16.1	1.5	24.9	5.6	0.48	0.13	298	27
High	39.5	5.9	60.8	11.3	2.45	0.74	292	24
C. diandra								
Low	23.2	1.3	35.7	10.6	0.57	0.08	201	31
High	31.6	4.5	64.1	18.3	1.43	0.53	206	18
C. lepidocarpa								
Low	14.1	0.9	36.1	7.0	0.92	0.14	300	27
High	17.9	1.3	78.3	11.2	2.03	0.14	289	25
C. nigra								
Low	16.4	1.7	22.9	3.5	0.45	0.04	252	51
High	21.4	2.4	50.1	20.4	1.07	0.11	260	34
C. echinata								
Low	15.5	1.9	60.8	4.3	0.80	0.18	215	21
High	17.9	2.5	120.8	5.8	2.16	0.50	226	20

All litterbags were retrieved after 116 d (0.32 yr). Litter samples were carefully rinsed with demineralized water, dried (45°C), and remaining mass (g) was determined. To correlate litter decomposition rates with measures of litter quality, we calculated decomposition constants k for each litter replicate from a single-exponential decay model (Wider and Lang 1982), which has been proven to be a solid indicator for decomposition rates (Hobbie 2008)

$$\ln\left(M_t/M_0\right) = -\mathrm{k} \times t,$$

where M_t is the mass at time t, M_0 is the initial mass, k is the decay constant, and t is time (yr).

Data analysis

We analyzed our data using linear mixed effect (LME) modelling with REML in SPSS 22 (IBM Corp. 2013), in which we treated Species (1–6) as well as Nutrient level (rich or poor) as fixed-effect predictors. Data were log-transformed wherever this resulted in a better approximation of the normal distribution of the model residuals. Next, we ran separate models to test for the effects of species and nutrient level on each of the following response variables: total (litter) biomass, leaf count, leaf length, SLA, litter C:N and C:P ratios, litter contents of cellulose, lignin, Ca, Mg, and K, and litter decomposition constants (k). In each model, we always tested for possible interactions between the two fixed factors. If interactions were nonsignificant, we additionally ran a model that only included the main effects of the two predictors. In this paper, we only report the outcome of these main-effect models if the significance of any of the parameters had changed. Finally, we ran Spearman correlation tests to correlate (untransformed) widely used litter quality indicators (N, P, C:N, C:P, lignin, cellulose, lignin:N, lignin:P, K, Ca, Mg), as well as Ellenberg-N values and SLA indices, with actual litter decomposition constants (k). Correlation tests were run for the nutrient-poor and nutrient-enriched decomposition beds separately. For all tests, significance was accepted at $P < 0.05$.

RESULTS

Plant morphology

Plants grown in the nutrient-rich treatment produced more (factor 1.7–2.5×) and longer (factor 1.1–2.5×) leaves compared to the nutrient-poor treatment. Total aboveground litter production per plant (biomass) more than doubled (by a factor of 2.2–5.2×; Table 1) in the nutrient-rich treatment. The fixed-effect model indicated significant interaction effects between species and nutrient treatment for biomass production, leaf count, and leaf length (Appendix S1: Table S2), indicating that the magnitude of the positive effect of nutrient enrichment on litter production was species dependent. Specific leaf area (SLA), however, was not affected by nutrient treatment, but differed significantly between species (Appendix S1: Table S2).

Litter chemistry

Under the nutrient-rich treatment, *Carex* species produced litter with lower C:N ratios, C:P ratios, and lignin

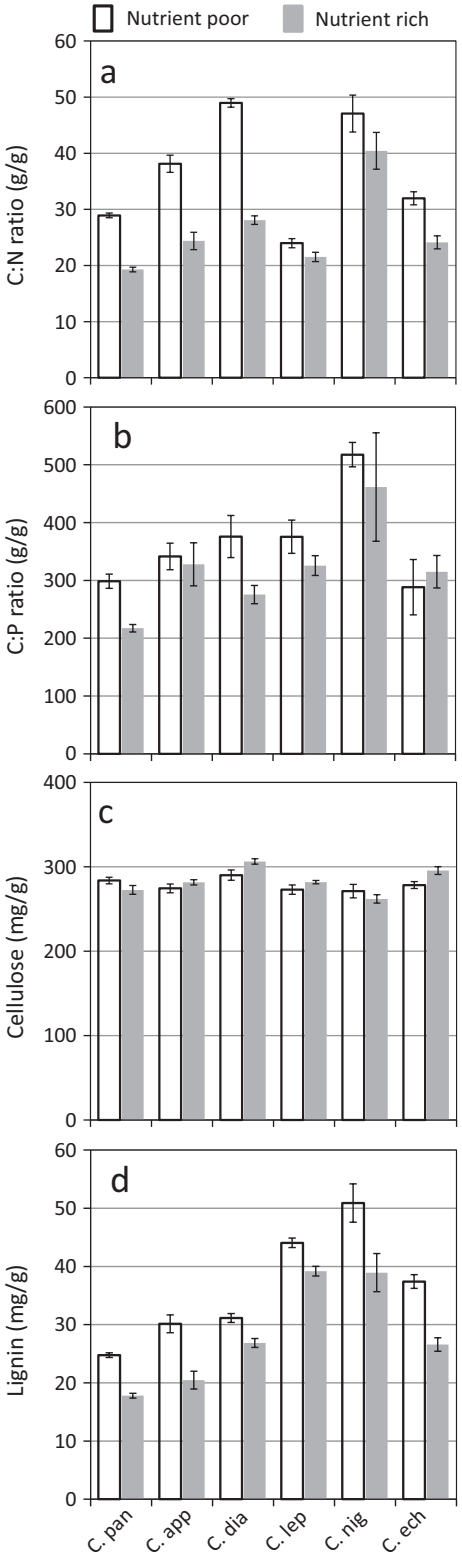

FIG. 1. Effects of nutrient availability on leaf litter (a) C:N ratios, (b) C:P ratios, (c) cellulose, and (d) lignin content of six species of *Carex*: *C. paniculata, C. appropinquata, C. lepidocarpa, C. nigra, C. diandra,* and *C. echinata*. Bars represent mean ± SE (n = 5).

contents, while cellulose contents remained unaltered and only differed between species (Fig. 1; Appendix S1: Table S3). Additionally, litter Ca and Mg contents were significantly lower in the high-nutrient treatment, while K contents increased (Fig. 2; Appendix S1: Table S3). Significant interaction effects between "species" and "nutrient level" were present for litter C:N ratios, cellulose contents, and K and Mg contents (Appendix S1: Table S3). When we re-ran all models without interaction terms to test for the main effects of species and nutrient levels, all main effects retained their significance.

Decomposition rates

At the end of the decomposition experiment (n = 116 d), soil pH in the nutrient-enriched decomposition beds had dropped slightly (6.3 ± 0.1), while pH in decomposition beds without nutrient addition had risen (8.0 ± 0.1). Nutrients that had been released from the slow-release fertilizer into the pore water of the nutrient-rich decomposition beds had accumulated to final hypertrophic concentrations of (in mg/L): PO_4^3-P, 348 ± 80; NH_4-N, 2,430 ± 135; NO_3-N, 2,243 ± 48. *Carex* litter in the nutrient-enriched decomposition beds had decomposed approximately twice as slowly as litter in the nutrient-poor beds (Fig. 3; Appendix S1: Table S4). In contrast, the cellulose paper had a seemingly higher decomposition constant in the nutrient-enriched beds, but this difference was nonsignificant (Mann-Whitney U test, P = 0.15). The fixed-effect model indicated a

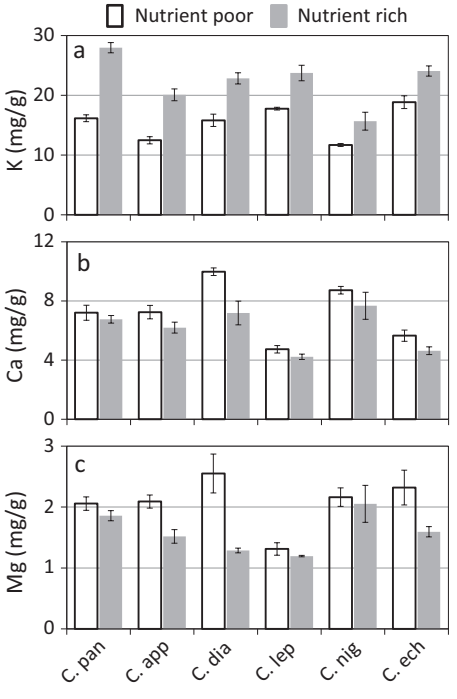

FIG. 2. Effects of nutrient availability on leaf litter (a) K, (b) Ca, and (c) Mg content of six species of *Carex*. Bars represent mean ± SE (n = 5).

significant interaction effect between species (including the cellulose paper) and nutrient level on the decomposition constant k (Appendix S1: Table S4). The main effects remained significant when omitting the interaction term, indicating that both species and nutrient treatment determine the rate of litter decomposition.

Finally, we correlated litter decomposition constants k with indicators of litter quality in the nutrient-poor and the nutrient-rich decomposition beds separately. For the nutrient-poor decomposition beds, correlations were significantly negative for litter C:N, C:P, lignin:N, lignin:P ratios as well as lignin contents, while litter K, N, and P content correlated positively with the decomposition constants (Table 2). Moreover, both the species' Ellenberg-N values and SLA indices correlated positively with the decomposition constants in the nutrient-poor decomposition beds, indicating a higher decomposability of litter from competitive (high Ellenberg-N, high SLA) species. Correspondingly, the species' Ellenberg-N values correlated with SLA indices (Spearman's rho = 0.304, n = 60, P = 0.018). However, in the nutrient-enriched decomposition beds, none of the litter quality indicators correlated with the decomposition constants, and neither did Ellenberg-N values or SLA indices (Table 2). Finally, litter cellulose, Ca, and Mg content did not correlate with the decomposition constants, and this pattern was consistent in both nutrient treatments (Table 2).

TABLE 2. Spearman's correlations between initial litter quality parameters and decomposition constants k of *Carex* leaf litter incubated in nutrient-poor (left) and nutrient-rich (right) decomposition beds.

Parameter	Nutrient-poor beds k		Nutrient-rich beds k	
	Spearman's rho	P	Spearman's rho	P
N (mg/g)	**0.57**	**0.001**	−0.16	0.412
P (mg/g)	**0.50**	**0.005**	−0.05	0.787
C:N ratio (g/g)	**−0.55**	**0.002**	0.17	0.376
C:P ratio (g/g)	**−0.49**	**0.006**	0.07	0.718
Lignin (mg/g)	**−0.41**	**0.034**	0.27	0.171
Lignin:N ratio (g/g)	**−0.53**	**0.005**	0.33	0.094
Lignin:P ratio (g/g)	**−0.43**	**0.027**	0.18	0.380
K (mg/g)	**0.47**	**0.009**	−0.23	0.215
Ca (mg/g)	0.07	0.709	0.18	0.338
Mg (mg/g)	0.03	0.880	0.12	0.516
Cellulose (mg/g)	−0.08	0.678	−0.08	0.688
Ellenberg-N ranking	**0.74**	**<0.001**	0.03	0.865
SLA (cm^2/g)	**0.43**	**0.018**	0.11	0.580

Notes: Measurements are based on litter from six species of *Carex*, each with five replicates per nutrient treatment. Sample size n = 30 for both nutrient-poor and nutrient-rich beds. Values shown in boldface indicate significance ($P < 0.05$).

Discussion

We investigated how eutrophication of fens by primary nutrients (NPK) affects litter production, litter stoichiometry, and litter decomposition rates of six species of *Carex*. The effects of eutrophication were contrasting: although *Carex* plants grown on eutrophic soils produced more than double the amount of fresh litter (productivity shift), a concomitant increase in litter quality both within (intraspecific shift) and between (interspecific shift) species clearly stimulated litter decomposition rates. However, the stimulant effect of such eutrophication-induced higher litter quality on decomposition rates only held if litter was deposited in nutrient-poor (exogenous) environments. In eutrophic environments, decomposition rates were uncoupled from litter stoichiometry, and *Carex* decomposition rates were twice as low (exogenous shift). This suggests a dominant role of the external environment on litter decomposition rates.

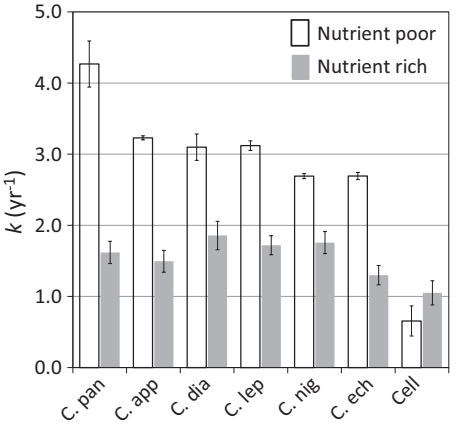

FIG. 3. Decomposition constants k (yr^{-1}) of litter of six *Carex* species grown under nutrient-rich conditions and cellulose paper ("Cell"). Litter was incubated pairwise in nutrient-poor (white bars) and nutrient-rich (gray bars) decomposition beds. Bars represent mean ± SE (n = 5).

Productivity shifts

It is well known that eutrophication causes an increase in primary biomass production and concomitant competition for light (Kotowski et al. 2006, Hautier et al. 2009). In response, rates of fresh litter input toward the peat soil increase correspondingly. In our data set, plants grown in the nutrient-rich treatments had produced 2.2–5.2 times more litter (in g dry mass) by the end of the experiment than plants grown in the nutrient-poor treatment. Such significant nutrient-induced increase in primary production should favor peat accumulation and thus carbon sequestration (Oechel et al. 2000).

Plant litter quality shifts and litter decomposition rates

Apart from the direct positive effects of eutrophication on fresh litter production, indirect effects of eutrophication on rates of litter decomposition co-determine whether fens will be long-term net sinks or sources of carbon. Nutrient

additions can affect litter stoichiometry within plants of the same species (Aerts and de Caluwe 1997, Gusewell 2004). Our study showed that indicators of high litter quality (i.e., low C:N and C:P ratios, high K contents, and low lignin contents) were indeed significantly altered in response to nutrient enrichment. Individuals of the same species that had grown in the nutrient-rich mesocosms consistently produced higher-quality litter than individuals grown in the nutrient-poor mesocosms. Stoichiometric intraspecific shifts occurred in all of the six *Carex* species, and appeared to be independent of the species' natural (optimal) occurrence along a fertility gradient (Ellenberg-N values). Moreover, species with the highest Ellenberg-N values (e.g., *C. paniculata*, *C. appropinquata*) generally produced more easily degradable litter than did species with lower Ellenberg-N values (e.g., *C. echinata*, *C. nigra*). According to plant-strategical theory (Westoby 1998), fast-growing, competitive species should primarily invest in rapid expansion of (photosynthetic) leaf area rather than investing in structural strength and defensive degradation-inhibiting compounds. Indeed, we found that the species' Ellenberg-N values correlated positively with SLA indices, which indicates rapid expansion of assimilation-related tissue in competitive plants. Accordingly, specific leaf area (SLA) of the plants correlated positively with litter decomposition constants, in line with other research (Cornelissen and Thompson 1997, Gusewell and Verhoeven 2006). Since fen eutrophication triggers a plant-strategical shift from slow-growing, small-sedge communities toward communities dominated by tall, competitive sedges and helophytes (Wheeler and Proctor 2000), the concomitant interspecific shift in vegetation composition coupled with shifts in dominant plant strategies and overall tissue quality will expectedly accelerate rates of litter decomposition and nutrient cycling (Cornwell et al. 2008).

Exogenous environment shifts and litter decomposition

Decomposition rates in the nutrient-enriched decomposition beds were, for the litter of the *Carex* species, approximately twice as low as in the nutrient-poor decomposition beds. Since litter was of equal quality in both treatments (pairwise incubations), such pronounced difference can only be due to differences in the external environment. This implies that the effect of the external environment on decomposition processes can easily outweigh the previously described intra- and interspecific litter quality shifts. However, we found a strong interaction effect between litter type (*Carex* species and cellulose filter paper) and nutrient treatment on decomposition rate, indicating that the effect of external eutrophication on litter decomposition is highly dependent of litter type and quality. In contrast to the *Carex* litter, the cellulose filter paper decomposed slightly faster (although nonsignificant, $P = 0.15$) in the nutrient-enriched mesocosms. Such litter-dependent response to fertilization has been suggested by other researchers as well (Sinsabaugh et al. 2002, Moorhead and Sinsabaugh 2006).

Although we did not quantify microbial activity nor qualify the composition of microbial communities, we can discuss our results in the light of existing knowledge. Primarily, our results are in accordance with the concept of "microbial nutrient mining" (Moorhead and Sinsabaugh 2006, Craine et al. 2007). This theory predicts that, under nutrient-limited conditions, slow-growing microbial "miner" guilds will thrive, as they specialize in retrieving nutrients that are stored in recalcitrant organic matter (in our case in the *Carex* litter; Moorhead and Sinsabaugh 2006). Microorganisms that do relatively well under nutrient-poor conditions are presumably slow-growing *K* strategists, including many fungi (Fontaine et al. 2003, Chen et al. 2014). Consequently, the rate of decomposition under such conditions should primarily depend on how easily the organic matter can be decomposed (i.e., the relative amount of defensive and recalcitrant structures in the material), which is in line with our observed correlations between litter quality indicators (e.g., C:N and C:P ratios, lignin contents, K contents) and litter decay constants in the nutrient-poor decomposition beds.

Interestingly, we found that litter decomposition rates were uncoupled from litter stoichiometry in the nutrient-enriched decomposition beds. Here, none of the well-known litter quality indicators correlated with the decomposition constants. Whenever inorganic nutrients are excessively available in the abiotic environment, difficult-to-retrieve organically bound nutrients no longer need to be mined from recalcitrant organic matter. Here, we expect a microbial shift toward dominance of guilds of fast-growing opportunistic competitors (mainly bacteria) that thrive on the readily available inorganic nutrients and on soluble polymers from fresh litter (Fontaine et al. 2003, Moorhead and Sinsabaugh 2006). Presumably, such "eutrophic" communities consist of rapidly reproducing *r* strategists (Chen et al. 2014), which could (under these conditions) outcompete *K* strategists (Fontaine et al. 2003). Indeed, changes in microbial community due to nutrient (mainly nitrogen) amendment have been linked to a suppressed activity of lignin-degrading enzymes and a stimulated activity of cellulose-degrading enzymes (Fog 1988). An increase in external nutrient availability should thus lead to a decreased breakdown of lignified organic matter and an increased breakdown of cellulosic organic matter (Sinsabaugh et al. 2002), which is in line with our observation of relatively faster decomposition of the cellulose filter paper but slower decomposition of lignified *Carex* litter in the nutrient-rich decomposition beds. Finally, we emphasize that we investigated the effects of ambient nutrient levels on litter decomposition based on two extremities (no nutrient addition and hypertrophic nutrient levels), and we did not investigate the effects of all possible nutrient levels between these two extremities. The final nutrient concentrations released by the Osmocote fertilizer can be considered hypertrophic and resemble conditions of heavy anthropogenic NPK fertilization without subsequent runoff, uptake, or dilution of nutrients (as is the

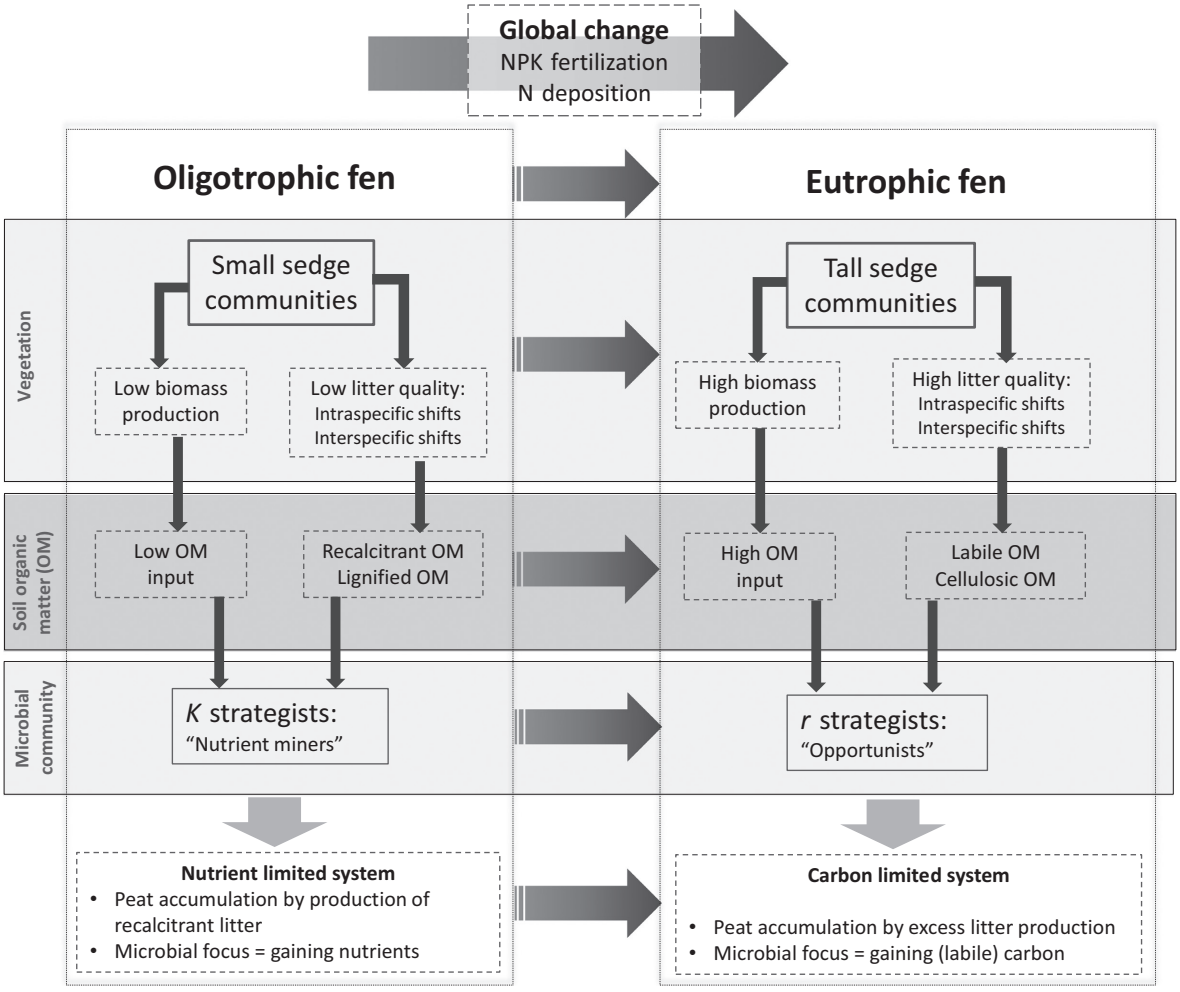

FIG. 4. Simplified hypothetical flowchart showing contrasting pathways for peat accumulation in oligotrophic (left) and eutrophic (right) fens. Eutrophication causes a decline in the area covered by oligo- and mesotrophic small-sedge fens in favor of eutrophic tall-sedge fens.

case in a closed mesocosm). It is thus possible that different or less pronounced patterns emerge under field conditions, or if a different range of ambient nutrient levels is applied. The latter supposition requires future investigation. Taken together, our results suggest that, in oligotrophic ecosystems, microorganism vigor can be nutrient limited (or, at least, nutrient–carbon co-limited). Despite widespread belief that soil microorganisms are usually C limited, the concept of microbial macronutrient limitation is not new (Egli 1991, Schimel and Weintraub 2003). Under eutrophic conditions, potential nutrient limitation is evidently lifted (Fig. 4), so that microbial vigor is determined mainly by the availability of high-quality labile carbon (e.g., sugars and cellulose).

Critical remarks on extrapolation: below- vs. aboveground decomposition

It should be noted that we only investigated eutrophication-induced shifts in aboveground litter production and chemistry, whereas belowground root decay contributes to peat formation as well (Saarinen 1996). The litter bags in our decomposition experiment were buried in the top layer of the waterlogged soil at the oxic/anoxic interface, where aboveground litter would be deposited under natural conditions. In this zone however, oxygen depletion is less severe than in deeper fully anoxic peat layers, which implies that in our experiment fungal growth may not have been hampered by oxygen depletion. Indeed, typical fungal degraders of recalcitrant polymers ("nutrient miners") are rarely extracted from deep anoxic peat layers as they generally cannot survive anoxia (Thormann 2006). This has important implications with respect to the generalization of our results: although it is likely that (fungal) recalcitrant polymer degraders could have thrived on the litter in our experiment, they would probably have been excluded if litter had been buried deeper within the anoxic soil. Therefore, we suggest that future research on peat accumulation should also focus on the quantification and qualification of root production, root decay, and decomposer communities in deeper, fully anoxic,

peat layers. Finally, although our research focused on groundwater-fed peatlands in the Northern hemisphere, environmentally induced shifts in the quantity and quality of plant litter should also play a key role in peat formation in a broader range of peatland types, e.g., tropical peatlands (Sjogersten et al. 2014).

Cumulative effects of eutrophication on peat accumulation and carbon sequestration

We have shown that fen eutrophication triggers contrasting multilevel effects on litter accumulation and decomposition. When nutrient-poor fens are enriched with nutrients, e.g., in response to anthropogenic disturbances, a strong increase in rates of fresh litter production combined with generally lower rates of litter decomposition (the latter due to likely shifts in microbial activity) should favor peat accumulation and thereby carbon sequestration. This implies that if both conditions of high rates of fresh litter input and high exogenous nutrient availability are satisfied, decomposer communities do not decompose "older" more recalcitrant litter to gain nutrients, resulting in its net accumulation. However, we also found that eutrophication increases plant litter quality and thereby the overall degradability of litter. Indeed, individuals of the same species produced higher-quality tissue, and a shift from small, stress-tolerant, plant species toward fast-growing competitors increases overall tissue quality of the vegetation. The latter (intra- and interspecific) litter-quality shifts should, on the other hand, lead to higher decomposition rates in eutrophic systems, contrary to the aforementioned findings. In the end, these contrasting results suggest that oligotrophic, as well as eutrophic, fens can accumulate peat and sequester carbon, but we hypothesize that the underlying mechanisms are different: peat accumulation in nutrient-poor fens is primarily due to a high recalcitrance (e.g., higher lignin content) of fresh litter and organic matter, whereas peat accumulation in nutrient-rich fens is due to high rates of fresh litter input combined with decreased nutrient-mining by microbial communities (Fig. 4). These predictions are supported by field observations that peat layers of groundwater-fed fens can either consist of small sedge and bryophyte fragments (indicating peat accumulation under nutrient limitation), or, on the other extreme, of tall sedge and reed fragments (indicating peat accumulation under higher nutrient availability; Succow and Joosten 2001). Finally, we should note that our results only apply to non-drained fens, as we did not manipulate water levels. Drainage triggers rapid peat and litter mineralization and concomitant eutrophication, and permanent aerobic conditions will hamper peat formation regardless of nutrient levels (Lamers et al. 2015). Conclusively, it is clear that eutrophication can affect litter (and eventually peat) accumulation and decomposition at multiple levels, in which stimulatory and inhibitory effects may simultaneously interact. We urge future studies to take these multiple levels into account.

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Supporting Information

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