Driving factors behind the eutrophication signal in understorey plant communities of deciduous temperate forests

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Summary

1. Atmospheric nitrogen (N) deposition is expected to change forest understorey plant community composition and diversity, but results of experimental addition studies and observational studies are not yet conclusive. A shortcoming of observational studies, which are generally based on resurveys or sampling along large deposition gradients, is the occurrence of temporal or spatial confounding factors.

2. We were able to assess the contribution of N deposition versus other ecological drivers on forest understorey plant communities by combining a temporal and spatial approach. Data from 1205 (semi-)permanent vegetation plots taken from 23 rigorously selected understorey resurvey studies along a large deposition gradient across deciduous temperate forest in Europe were compiled and related to various local and regional driving factors, including the rate of atmospheric N deposition, the change in large herbivore densities and the change in canopy cover and composition.

3. Although no directional change in species richness occurred, there was considerable floristic turnover in the understorey plant community and a shift in species composition towards more shade-tolerant and nutrient-demanding species. However, atmospheric N deposition was not important in explaining the observed eutrophication signal. This signal seemed mainly related to a

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shift towards a denser canopy cover and a changed canopy species composition with a higher share of species with more easily decomposed litter.

4. *Synthesis.* Our multi-site approach clearly demonstrates that one should be cautious when drawing conclusions about the impact of atmospheric N deposition based on the interpretation of plant community shifts in single sites or regions due to other, concurrent, ecological changes. Even though the effects of chronically increased N deposition on the forest plant communities are apparently obscured by the effects of canopy changes, the accumulated N might still have a significant impact. However, more research is needed to assess whether this N time bomb will indeed explode when canopies will open up again.

Introduction

Atmospheric nitrogen (N) deposition rates are markedly exceeding their historical background levels in industrialized regions of the world, and deposition rates will probably continue to rise in the 21st century (Dentener *et al.* 2006). Reductions in plant diversity and shifts in species composition through increased N deposition in ecosystems around the globe are common (Bobbink *et al.* 2010). For example, the effects of N enrichment on plant diversity in temperate grasslands have been well studied. Both experimental N addition studies (synthesized in, for example, Clark *et al.* 2007; De Schrijver *et al.* 2011) and observational studies along large deposition gradients (Stevens *et al.* 2004, 2010; Dupré *et al.* 2010; Maskell *et al.* 2010) indicate negative relationships between (cumulative) N addition and plant species richness. Therefore, N deposition would also be expected to impair forest plant diversity. Understorey plant communities support the majority of the plant diversity in temperate forests (Gilliam 2007). Moreover, levels of N deposition received by the understorey may be considerably higher compared with other vegetation types due to a higher aerodynamic roughness and intercepting surface of forest canopies (Erisman & Draaijers 2003). Yet, the effects of experimental N additions on forest understoreys seem less consistent compared with N additions in grassland (Gilliam 2006; Bobbink *et al.* 2010; De Schrijver *et al.* 2011). A recent meta-analysis of N addition experiments by De Schrijver *et al.* (2011) reported, for instance, a tendency towards decreasing biomass in the understorey and no significant effect of N addition on understorey plant species richness.

By contrast, many observational studies reported shifts in the understorey species diversity and composition and attributed those shifts to increased N deposition rates. In contrast to the N addition experiments on forest understoreys, which were mostly performed in North America, most of the observational studies were performed in Europe (cf. Gilliam 2006). For observational studies, two approaches have been used: (i) resurveys of permanent or semi-permanent plots (e.g. Thimonier, Dupouey & Timbal 1992; Thimonier *et al.* 1994; Lameire, Hermy & Honnay 2000; Kirby *et al.* 2005; Bernhardt-Römermann *et al.* 2007; Van Calster *et al.* 2007, 2008a) or (ii) changes in vegetation composition along large deposition gradients (e.g.

Tyler 1987; Brunet, Diekmann & Falkengren-Grerup 1998; van Dobben & de Vries 2010). A positive relationship between the increasing frequencies and abundances of nitrophilous species and (assumed) increased N availability was generally found. Yet, both approaches have shortcomings due to the possible occurrence of temporal or spatial confounding factors (Diekmann *et al.* 1999). Studies along large deposition gradients may include substantial differences in soil, climate and species pools between the study sites, making it difficult to isolate the effects of N deposition. Resurvey studies, on the other hand, are generally performed in single forests or landscapes, but the increased N deposition levels between the two survey dates often parallel other ecological changes that have taken place during the last decades (e.g. Hopkins & Kirby 2007). Many ancient, deciduous forests in lowland Europe have been managed as coppice or coppice with standards for many decades, if not centuries (e.g. Peterken 1993; Rackham 2003; Szabó 2010). This silvicultural system has now been abandoned or was replaced by a high forest management system in most regions resulting in important changes in the canopy structure and composition, which may have a significant impact on the understorey plant communities (e.g. Van Calster *et al.* 2008a). Densities of large herbivores (including roe deer – *Capreolus capreolus*, red deer – *Cervus elaphus* and fallow deer – *Dama dama*) and wild boar (*Sus scrofa*) have increased during recent decades in many regions across north-western Europe (Fuller & Gill 2001; Ward 2005; Milner *et al.* 2006; Bláha & Kotecký 2008). This increase is explained by land-use changes, milder winters and changes in game management. Rising herbivore populations have a large impact on the composition of the forest understorey (e.g. Welander 2000; Kirby 2001; Rooney & Waller 2003; Rooney 2009; Royo *et al.* 2010). These concurrent ecological changes make it inherently difficult to isolate N deposition from other drivers of forest vegetation change (e.g. Dzwonko & Gawronski 2002; Hofmeister *et al.* 2009).

A combination of a temporal and spatial approach allows the assessment of the relative contribution of N deposition compared with other ecological changes on forest understorey plant communities. Dupré *et al.* (2010) recently demonstrated the usefulness of a similar spatiotemporal approach to assess deposition effects in acidic grasslands. Diekmann *et al.* (1999) and Köchy & Bråkenhielm (2008) had previously used this

approach in forest ecosystems, but included only a small number of regions (2) or plots (9), respectively, in their analyses. In the present study, data from 1205 (semi-) permanent vegetation plots taken from 23 rigorously selected understorey resurvey studies along a large deposition gradient across the temperate zone of Europe were used to assess (i) whether species richness and vegetation composition have changed during the period between the surveys, (ii) whether changes in richness and composition were larger in regions with higher N deposition rates and (iii) the relative importance of other ecological factors, notably canopy structure, canopy composition and grazing pressure, compared to N deposition.

Material and methods

STUDY SITES

The sample sites are all described as ancient, semi-natural temperate forest in Europe (cf. Peterken 1993; Hermy *et al.* 1999). Temperate zones on other continents were not considered because Ellenberg indicator values (Ellenberg *et al.* 1992), which are important for the indirect assessment of changes in environmental conditions, are not available. All records were from sites in which no stand-replacing management actions (e.g. clear-cuttings followed by replanting with conifers) have taken place since the date of the first survey. We looked for studies with data for at least *c.* 20 permanent or semi-permanent plots. These plots had to be independent (e.g. no subplots of a single larger plot), and the interval between the first and the last survey had to be at least *c.* 20 years. This large time interval is needed to account for the long life span of many (understorey) forest species (e.g. Ehrlén & Lethilä 2002). Plot-level presence/absence data of all species in the understorey layer (here defined as all vascular plant species < 1 m) for both survey dates were available in all cases. Where possible, plot-level cover data for the shrub and tree layers were included as well.

Potentially suitable studies were found using Web of Science (http://www.isiknowledge.com) and by contacting researchers through the FLEUR-network (a European network of forest understorey researchers; http://www.fleur.ugent.be) in the different regions of the temperate forest zone. Data from 23 studies and eight countries were obtained, ranging from the United Kingdom to the Czech Republic and from Switzerland to mid Sweden (Fig. 1; Table 1). The soil types covered by the studies ranged from relatively poor, sandy soils (Zoerselbos, Be; Speulderbos, Nl) to rich, clay soils (Dalby, Se; Göttingen, Ge) and deep calcareous rendzinas or luvisols (Děvín and Milovice Wood, CZ). However, most study sites were located on moderately rich, loamy soils. We cannot independently assess the representativeness of our samples, but we consider that a large part of the potential variation has been covered because of the geographic and edaphic distribution spread of the samples.

The first surveys were carried out between 1935 and 1986/89 and the recent surveys between 1987/88 and 2009. The time interval between the two surveys ranged between 17 and 67 years. The forests were either not managed (seven studies), only extensively managed (11 studies), or a mixture of both (five studies) at the time of the most recent survey (Table 1). Management frequency and intensity decreased since the time of the first survey in 10 study regions. The number of plot pairs per study ranged between 17 and 139, with an average of 52 per study. In total, understorey plant community data from 1205 plot pairs were included in the data base.
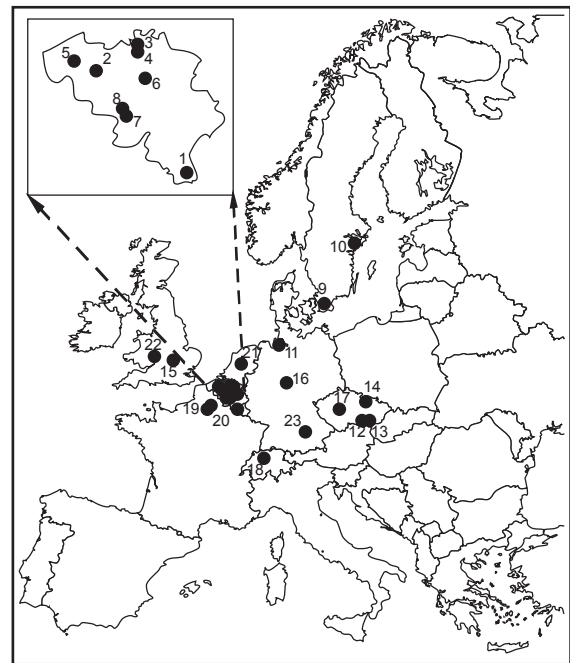

Fig. 1. Map showing the location of the 23 regions included in this study (the numbers refer to Table 1).

CALCULATION OF THE RESPONSE VARIABLES

Nomenclature was standardized based on Ellenberg *et al.* (1992), and understorey data were transformed to presence/absence records to standardize the recording scale among studies. Next, three plant community descriptors were derived for both the plots in the old (o) and recent (r) surveys: the species richness (S_o, S_r) and the mean Ellenberg indicator values for light availability (mL_o, mL_r) and soil nitrogen availability (mN_o, mN_r) based on presence/absence data. In the absence of actual measurements of environmental variables, the use of Ellenberg indicator values to document environmental preferences and changes in environmental conditions is an acceptable, widely used, alternative (Diekmann 2003), especially when used within a single vegetation type (Wamelink *et al.* 2002) such as (ancient) forest (Dzwonko 2001). Considering the ordinal nature of the indicator values, calculation of mean indicator values is strictly speaking not fully appropriate, but the vast majority of plant ecologists use calculated means as they work very well (Diekmann 2003). Potential time-lags in the response of the vegetation due to changes in environmental conditions were accounted for by selecting only studies with a sufficiently long time interval (> 17 years) between the two surveys. Ellenberg indicator values for light availability range from 1 (species can grow in very deep shade and rarely occurs in more open conditions) to 9 (species only occurs in open conditions). Soil nitrogen availability values range from 1 (species occurs on sites with very low N availability) to 9 (species only occurs on sites with very high N availability). It should be noted that the Ellenberg N values indicate more than N availability alone and reflect general nutrient availability (Schaffers & Sýkora 2000; Diekmann 2003; Ellenberg & Leuschner 2010). Hence, in the remainder of the text, we will denote Ellenberg N as soil nutrient availability and increasing mN values will be referred to as eutrophication. Indicator values for soil reaction (mR) were not used due to the strong, positive correlation with the mN values (r_{so} = 0.71, P < 0.001; r_{sr} = 0.78, P < 0.001; n = 1201 and with

Table 1. Ecological details of the 23 studies included in this meta-analysis. The ID of each study refers to Fig. 1

ID	Author(s)	Study region, Country	Lat °N	Long °E	MAT* °C	MAP* mm	Plot size (range) m²	Number of plots	Survey year(s) Old	Survey year(s) Recent	Grazing* Density (no. 100 ha⁻¹)	Change	Atmospheric deposition* N_mean (kg ha⁻¹ year⁻¹)	Management† Old	Management† Recent
1	T. Vandenbroeck, unpublished data	Gaume, Be	49.6	5.5	8.2	852	100	43	1950s	2008	16	Stable	17.0	3	2
2	Baeten et al. (2010)	Binnen-Vlaanderen, Be	51.0	4.5	9.7	798	150	47	1977–1980	2009	0	Stable	22.1	3	2
3	S. De Smet, unpublished data	Zoerselbos, Be	51.2	4.7	9.7	798	100	17	1982	2008	8	Stable	24.2	1	1
4‡	Cornelis, Rombouts & Hermy (2007)	Herenbossen, Be	51.1	4.8	9.7	798	196	111	1980	2004	8	Stable	21.9	3	2
5‡	Lameire, Hermy & Honnay (2000)	Vorte Bossen, Be	51.1	3.4	9.7	798	150	26	1977–1980	1998	0	Stable	22.3	2	1 and 2
6	Baeten et al. (2009)	Meerdaalwoud, Be	50.8	4.7	9.7	798	125–225	21	1954	2000	18	Stable	18.3	3	2
7‡	Van Calster et al. (2008a)	Florenne, Be	50.3	4.6	9.7	798	100	58	1957	2005	8	Stable	19.7	2	2
8	Van Calster et al. (2008a)	Tournibus, Be	50.3	4.6	9.7	798	100	139	1967	2005	8	Stable	20.9	2	2
9	von Oheimb & Brunet (2007)	Dalby, Se	55.7	13.3	7.9	652	1 (16 for canopy)	74	1935	2002	15	Increase	8.5	1	1
10‡	O. Eriksson, unpublished data	Tullgarn, Se	58.1	17.1	6.8	509	100	127	1971	2003	14	Increase	8.3	2	2
11	Naaf & Wulf 2010	Elbe-Weser, Ge	53.6	9.0	8.3	761	100–400	50	1986–1989	2008	7	Increase	24.9	2	2
12	R. Hédl, unpublished data	Děvín, CZ	48.9	16.6	8.6	490	100–1000	50	1953–1963	2002–2003	12	Decrease	14.3	2 and 3	1 and 2
13	Hédl, Kopecký & Komárek (2010)	Milovice Wood, CZ	48.8	16.7	8.6	490	500	46	1953–1954	2006	2	Increase	13.3	2 and 3	1 and 2
14	Hédl (2004)	Rychlebské hory Mts., CZ	50.3	17.1	7.2	976	315	21	1941–1943	1998–1999	1	Increase	13.0	2	1 and 2
15	Kirby & Morecroft (2010)	Wytham Woods, UK	51.8	−1.3	9.9	631	100	49	1974	1999	100	Increase	14.5	1	1
16	Dierschke (2009)	Göttingen, Ge	51.5	10.1	8.5	643	250 (100–400)	42	1980	2001	0	Stable	18.8	1	1
17	Petřík (2009)	Milíčovský les, CZ	50.0	14.5	8.6	516	240 (50–625)	19	1986	2008–2009	10	Stable	13.5	2	1 and 2

Table 1. (Continued)

ID	Author(s)	Study region, Country	Lat °N	Long °E	MAT* °C	MAP* mm	Plot size (range) m²	Number of plots	Survey year(s) Old	Survey year(s) Recent	Grazing* Density (no. 100 ha⁻¹)	Grazing* Change§	Atmospheric deposition* N_{mean} (kg ha⁻¹ year⁻¹)	Management† Old	Management† Recent
18	Walther & Grundmann (2001)	Switzerland, CH	47.3	7.8	9.4	782	100–400	37	1940–1965	1998	18	Stable	17.8	2	2
19	G. Decocq, unpublished data	Hirson/Saint-Michel, Fr	49.9	4.1	10.2	869	500–800	22	1956–1965	1996–1998	18	Increase	18.9	2	2
20	G. Decocq, unpublished data	Andigny, Fr	50.0	3.6	9.9	685	500–800	19	1957–1963	1995–1996	20	Increase	21.2	2	2
21	P. Hommel, unpublished data	Speulderbos, Nl	52.3	5.7	9.3	820	100–250	27	1957–1959	1987–1988	9	Increase	35.7	2	1
22‡	K. Vanhuyse, unpublished data	Lady Park, UK	51.7	−2.7	9.3	719	32	35	1979	2009	10	Decrease	14.4	1	1
23	Bernhardt-Römermann et al. (2007)	Münich, Ge	48.3	11.7	7.5	793	100	125	1986	2003	10	Decrease	21.5	1	1

MAP, mean annual precipitation; MAT, mean annual temperature.
*See text for a detailed description.
†Management classes were defined as follows: 1: no management, 2: low intensity cuttings (i.e. removal of a small fraction of canopy trees) at a low frequency (i.e. <1× per 10 year) and 3: high intensity cuttings (i.e. removal of a significant fraction of canopy trees) at a higher frequency (i.e. more than 1× per 10 year).
‡Studies for which no canopy data were available.

r_s = Spearman rank correlation for the old and new survey, respectively). Hence, we cannot fully disentangle the effects of eutrophication and acidification. To determine the change in species richness and Ellenberg indicator values, response ratios were calculated according to Hedges, Gurevitch & Curtis (1999) as $\ln(X_r/X_o)$, with X being one of the three response variables. These response ratios are further denoted as RR_S, RR_L and RR_N. Response ratio means per study and across all studies were calculated according to the weighting proposed in Hedges, Gurevitch & Curtis (1999). A fourth response variable was the plot-level floristic turnover. We calculated the Lennon dissimilarity (Lennon et al. 2001) in floristic composition between a plot in the first survey and the same plot in the second survey as $\min(b, c)/[\min(b, c) + a]$, with a representing the number of species shared by both plots; b the number of species that occur in the plot only during the first survey and c the number of species that occur in the plot only during the second survey. The dissimilarity was modified to a similarity measure: similarity = 1 − Lennon index. This simple presence/absence-based index is less sensitive to differences in species richness between the plots than the commonly used Jaccard index (Koleff, Gaston & Lennon 2003) and is therefore more appropriate to determine real floristic turnover, which was appropriate for the purposes of the current study.

CALCULATION OF THE EXPLANATORY VARIABLES

The variables used to explain the changes in the understorey plant community were the average rate of atmospheric N deposition, the climate in the study region, the actual density of large herbivores and the change therein and the change in canopy cover and composition which may reflect changes in management.

The rate of N deposition was quantified using the EMEP data base (http://www.emep.int), which allows deposition data for the whole of Europe to be derived with a resolution of 50 km × 50 km. We extracted wet and dry deposition data of reduced and oxidized N and for the year 2000 (N_{2000}, expressed in kg ha^{-1} year^{-1}). This year was chosen as it represents the average of the interval in which the recent surveys were performed. De Schrijver et al. (2011) recently showed that the modelled EMEP data and locally observed N deposition data are very well correlated. Significant underestimations only occur at sites where nearby point sources (e.g. large animal husbandry farms) are present. However, the throughfall deposition on the forest floor will likely be between 1.5× and 2× higher than the open field N deposition due to the high aerodynamic roughness of forest canopies (ICP 2005).

To obtain a mean N deposition rate over the period between the two surveys (N_{mean}), we accounted for the variation in deposition rates over time by calculating the cumulative deposition between the two survey years (N_{cum}) using correction factors for the different decades, based on the year 2000 deposition rates (see Dupré et al. (2010) for more information on the correction factors and the calculation methods). Then, the N_{cum} was divided by the time interval between the two surveys. N_{mean} ranges between 8.3 and 35.7 kg ha^{-1} year^{-1} (Table 1). Sulphur (S) deposition also contributes to the potential acidifying deposition rate, but this rate (expressed in keq ha^{-1} year^{-1} and calculated as: $N_{2000}/14 + (S_{2000}/32.06)*2$) was very strongly correlated (r_s = 0.93, P < 0.001, n = 23) to the N_{2000} deposition values. Hence, the sulphur deposition variable was not included in the analysis.

Climate may influence the rate and nature of vegetation changes both directly (e.g. through its influence on germination and growth rates) and indirectly (e.g. through its influence on biogeochemical cycling). Therefore, we derived the mean annual temperature (MAT)

and precipitation (MAP) for the period 1961–1990 for each of the study sites using the program NewLocLim v1.10 (FAO 2005; Table 1).

Local expert knowledge was used to estimate the present density of the three most common large herbivores in Europe (i.e. numbers of roe deer, fallow deer and red deer per 100 ha) in each study area and to indicate whether these numbers have increased (nine studies), decreased (three studies) or remained stable (11 studies) in the period between the two surveys (see also Table 1). To account for differences in the density estimates, densities were $\ln(x + 1)$ transformed. The trend variable was recoded into two dummy variables (HERBI−, HERBI +).

The change in the cover and composition of the canopy (including both the shrub and tree layers) was quantified using three variables: the change in the total cover of the canopy, the change in the shade casting ability of the canopy species and the change in the litter quality. Canopy data were available for all but five studies (numbers 4, 5, 7, 10 and 22 in Table 1). The total cover of the shrub and tree layers was calculated as the sum of the cover percentages of all species occurring in these layers. The change in cover was calculated using the response ratio: $\ln(Cover_r/Cover_o)$, further denoted as RR_{cover}. The shade casting ability and the litter quality were calculated as a cover weighted average of, respectively, the shade casting ability and litter quality index scores listed in Appendix A (see also Van Calster et al. 2008a; Baeten et al. 2009). The scores range between 1 (very low shade casting ability and very low decomposition rate) and 5 (very high shade casting ability and very high decomposition rate). Index scores were not available for all species, and so plot values were only used when > 70% of the total cover was comprised by species with a known score, resulting in 787 plots that could be used for further analysis. Finally, response ratios for shade casting ability (RR_{shade}) and litter quality (RR_{litter}) were calculated to determine the change in these variables. The three canopy response ratios were not correlated (r_s RR_{litter} − RR_{cover} = 0.08, r_s RR_{litter} − RR_{shade} = 0.03, r_s RR_{shade} − RR_{cover} = −0.02; n = 787). Response ratio means per study and across all studies were calculated according to Hedges, Gurevitch & Curtis (1999).

STATISTICAL ANALYSIS

Linear mixed models were used to relate each of the four understorey response variables to the explanatory variables at the study level (number of years between surveys, N_{mean}, MAT, MAP, actual grazing pressure and trend in grazing pressure) and at the individual plot level (RR_{cover}, RR_{shade}, RR_{litter} and the initial Ellenberg values mL_o and mN_o). The initial Ellenberg values mL_o and mN_o were not included as explanatory variables for the responses RR_L and RR_N as they form the denominator of the respective RRs. The modelling was carried out using the *lme* function in the *nlme* library in R 2.10.1 (Pinheiro et al. 2009; R Development Core Team 2009).

We adopted an information-theoretic approach of data modelling in which sets of models are compared in a symmetric way, which avoids problems associated with multiple pairwise testing (cf. Bolker 2008; Bolker et al. 2009). Here, we used the Akaike Information Criterion (AIC) to compare the competing models. First, we related a response variable to each of the explanatory variables separately using mixed models with the intercepts varying randomly by study, that is, 'Study ID' as random effects term. A null model with the intercepts varying by study, but with no explanatory variables, was also calculated. The ΔAIC of a model was then calculated as the difference in AIC value for that model and the model with the lowest AIC value (best fit to the data). Models with ΔAIC > 4 may be considered
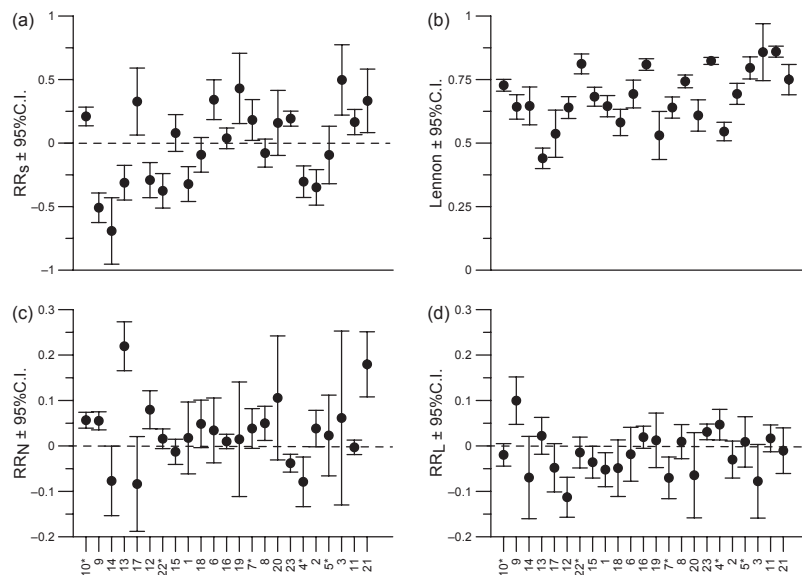
Fig. 2. Species richness, soil nutrient and light availability, and community shifts for the 23 studies included in this study. Mean (±95% confidence interval) response ratios are given based on the plot values in the old and recent surveys for understorey species richness (RR_S) (a), and the mean Ellenberg values for nutrient availability (RR_N) (c) and light (RR_L) (d). Panel b depicts the mean Lennon similarity coefficients between the understorey composition in the old and recent survey. Due to the bounded nature (between 0 and 1) of the Lennon similarity coefficients, the 95% confidence intervals were based on 2000 bootstrap resamples within each study. The studies are ranked according to increasing mean atmospheric N deposition, and a * indicates studies for which no canopy data were available.

clearly distinguishable, while all models with $\Delta AIC < 4$ may be kept under consideration (Bolker 2008). Then, we constructed a second set of models with all possible combinations of the explanatory variables that proved to be equivalent in the previous modelling step (here $\Delta AIC < 4$). For instance, if explanatory variables *a*, *b* and *c* were retained, all combinations were $a + b + c, a + b, a + c, b + c, a, b, c$. The $\Delta AICs$ for this set of models will be reported. Finally, the parameter values of the model that showed the best fit (in terms of AIC value) were re-estimated with restricted maximum likelihood estimation and reported.

Results

Across all studies, the species richness did not change over time, but significantly increased in eight studies and decreased in eight others (Fig. 2a). The mean (exp-transformed) response ratio for species richness was 0.97 (95% confidence interval: 0.87–1.09). The mean species number across all plots in both the old and recent surveys was c. 17. The mean Lennon similarity was 0.69 (Fig. 2b), which implies that on average one-third of the species in each plot pair has been replaced. An overview of the fifty most frequent species and their average change in frequency is given in Table 2. The species decreasing in frequency were mostly herb species, whereas ferns and seedlings of tree and shrub species increased. The Ellenberg indicator value for nutrient availability significantly increased in six studies and decreased in two studies (Fig. 2c), and across all studies, a significant increase was found (RR_N: 1.03; 95% CI: 1.01–1.05). The Ellenberg indicator value for light availability significantly decreased in four and increased in three studies (Fig. 2d) and exhibited a (marginally significant) decrease across all studies (RR_L: 0.99; 95% CI: 0.97–1.01). RR_L and RR_N were negatively correlated ($r_s = -0.15$, $P < 0.001$,

$n = 1201$), suggesting that a decreasing proportion of more light-demanding species in the understorey plant community goes along with an increasing proportion of more nutrient-demanding species.

The mean (exp-transformed) RR_{cover} across studies was 1.05 (95% CI: 0.95–1.16) and the canopy cover increased in nine and decreased in five studies (Fig. 3a). The RR_{shade} and RR_{litter} exhibited a significant (1.04; 95% CI: 1.01–1.07) and marginally significant (1.03; 95% CI: 0.99–1.07) increase, respectively. Both the shade casting ability of the canopy and the litter quality index significantly increased in three studies and decreased in one (Fig. 3b,c). Scatterplots (not shown) of the values of the three canopy variables in the old surveys with their respective response ratios indicated that the largest increases took place in plots with low values in the old surveys. An overview of the ten most frequent tree and shrub species in the recent surveys and their changes in frequency and cover is given in Table 3. It appears that the increasing importance of shade casting species and/or species with a better litter quality is mainly due to the increases of *Acer pseudoplatanus*, *Carpinus betulus* and *Fraxinus excelsior*.

The results of the null models indicate that variation of the change in species richness (RR_S) is more or less equally distributed at the study (41%) and plot level (59%). The variation partitioning in the Lennon similarity coefficients is comparable: 36% variation at the study level and 64% at the plot level. The linear mixed models with RR_S and the Lennon similarity coefficients retained the same set of explanatory variables (Table 4), and also the best-fitting model was similar. The $\Delta AICs$ between the best-fitting models and the null models were 15.4 and 16.1 for RR_S and the Lennon coefficient, respectively, which indicates that the explanatory variables do

Table 2. Overview of the fifty most frequent understorey species with their average study-level frequency in the recent surveys and the change in frequency compared to the old surveys. The species are ranked according to increasing change in frequency; tree and shrub species that occurred as seedlings in the understorey are marked with (TS), ferns are marked with (F)

Species	Average frequency (%) in recent survey	Change in frequency (%) compared to old survey	Species	Average frequency (%) in recent survey	Change in frequency (%) compared to old survey
Ajuga reptans	10	−5.8	*Stachys sylvatica*	15	+ 2.0
Poa nemoralis	17	−5.4	*Urtica dioica*	26	+ 2.0
Mercurialis perennis	24	−4.6	*Melica uniflora*	15	+ 2.0
Convallaria majalis	17	−3.2	*Carpinus betulus (TS)*	13	+ 2.1
Paris quadrifolia	14	−3.2	*Glechoma hederacea*	17	+ 2.3
Primula elatior	12	−2.7	*Dryopteris filix mas (F)*	24	+ 2.4
Ranunculus ficaria	17	−2.4	*Arum maculatum*	17	+ 2.7
Lonicera periclymenum	22	−2.2	*Circaea lutetiana*	17	+ 2.8
Asarum europaeum	11	−2.0	*Stellaria holostea*	13	+ 2.9
Anemone nemorosa	39	−1.8	*Geum urbanum*	30	+ 3.1
Ranunculus auricomus	10	−1.0	*Athyrium filix-femina (F)*	25	+ 3.8
Polygonatum multiflorum	31	−0.8	*Sorbus aucuparia (TS)*	17	+ 3.9
Viola reichenbachiana	14	−0.5	*Coryllus avellana (TS)*	16	+ 4.2
Geranium robertianum	10	−0.3	*Brachypodium sylvaticum*	18	+ 4.8
Pteridium aquilinum (F)	19	+ 0.2	*Quercus robur (TS)*	15	+ 5.1
Adoxa moschatellina	11	+ 0.3	*Poa trivialis*	16	+ 5.3
Maianthemum bifolium	13	+ 0.3	*Oxalis acetosella*	30	+ 5.5
Scilla non-scripta	13	+ 0.6	*Rubus fruticosus* coll.	54	+ 6.4
Carex sylvatica	23	+ 0.8	*Galeopsis tetrahit*	12	+ 7.1
Moehringia trinervia	13	+ 0.9	*Acer pseudoplatanus (TS)*	21	+ 7.3
Galium odoratum	20	+ 1.0	*Hedera helix*	31	+ 7.4
Milium effusum	23	+ 1.1	*Fagus sylvatica (TS)*	30	+ 8.4
Lamiastrum galeobdolon	30	+ 1.2	*Fraxinus excelsior (TS)*	27	+ 9.8
Galium aparine	12	+ 1.4	*Dryopteris carthusiana (F)*	24	+ 10.7
Deschampsia cespitosa	29	+ 1.9	*Dryopteris dilatata (F)*	17	+ 12.6

explain a significant part of the variation. The RR_S and the Lennon similarity coefficient decreased with an increasing number of years between the two surveys, that is, plots in studies with longer time intervals between surveys lost more species and exhibited higher turnover. Species richness decreased most, and turnover was highest in plots where the light availability at the time of the first survey was relatively high. The mean N deposition rate exhibited a (weak) positive relationship with RR_S and the Lennon similarity coefficient.

The variation of RR_L and, to a lesser extent, of RR_N largely occurred at the plot level (91% and 68%, respectively). For both response variables, only the canopy change variables were retained (Table 5). The ΔAICs between the best-fitting models and the null models were 12.6 and 11.5 for RR_L and RR_N, respectively. RR_N increased with increasing canopy cover and increasing quality of the litter. RR_L also increased with increasing quality of the litter and decreased with increasing canopy cover and increasing shade casting abilities of the canopy species.

Discussion

During the last decades, large changes in the understorey vegetation of the studied ancient, semi-natural deciduous woodlands have taken place. Although no directional change in species richness occurred, there was considerable floristic turn-

over and species composition shifted towards more shade-tolerant and nutrient-demanding species. In contrast to the expectations, atmospheric N deposition was not important in explaining the observed eutrophication signal. This signal seems mainly caused by a shift towards a denser canopy cover and a changed canopy species composition with a higher share of species with more easily decomposed litter.

Below, we first discuss the ecological changes that have taken place in the studied forests during recent decades and elaborate the way in which these ecological changes relate to the observed shifts in the understorey plant communities. We end by interpreting our results in terms of a model recently developed by Smith, Knapp & Collins (2009), which presents ecological change as a response to chronic resource alterations.

ECOLOGICAL CHANGES IN ANCIENT, SEMI-NATURAL DECIDUOUS FORESTS IN EUROPE

The range of open field N deposition rates (between 8.3 and 35.7 kg ha⁻¹ year⁻¹) included in this study is very similar to the range in N deposition rate across temperate forest in Europe (Holland *et al.* 2005). Bobbink *et al.* (2010) state that there is evidence for N deposition effects on understorey biodiversity in temperate forests at deposition rates < 20 kg ha⁻¹ year⁻¹ and perhaps even as low as 10–15 kg ha⁻¹ year⁻¹. As the N deposition on the forest floor will probably be one-and-a-half
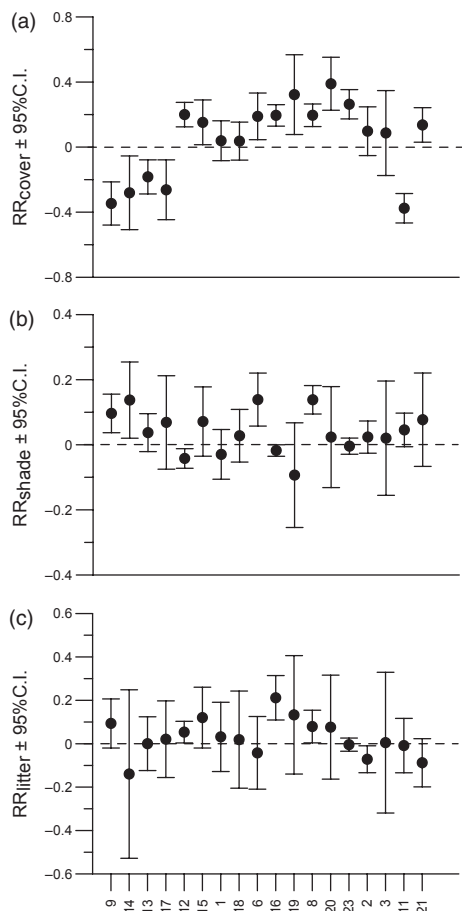
Fig. 3. Canopy cover, shade casting ability and litter quality changes for the 18 studies for which canopy data were available. Mean (±95% confidence interval) response ratios (RRs) are given based on the plot values in the old and recent surveys for canopy cover (RR_{cover}) (a), the shade casting ability of the tree and shrub species in the canopy (RR_{shade}) (b) and the quality of the litter shed by the species in the canopy (RR_{litter}) (c). The studies are ranked according to increasing mean atmospheric N deposition.

to two times higher than the cited open field values (ICP 2005), the critical load value has been exceeded in many of the study regions. Therefore, large N-driven changes in the understorey plant community were expected.

The decrease in management intensity in our study sites since the time of the first surveys is mainly the result of two factors: (i) many of the ancient, semi-natural deciduous forests have been given a more protected status (e.g. under the EU Habitat Directive) during the last decades because of their conservation value; (ii) more importantly, the coppice or coppice with standards management system, which was very common in much of Europe, has largely been abandoned or replaced by high forest systems characterized by much longer rotations due to a changing socio-economic context (Kirby & Watkins 1998; Szabó 2010). The decreased management intensity, especially in semi-natural, deciduous forests, is probably a general trend across north-western and central Europe (e.g. Hopkins & Kirby 2007; Ellenberg & Leuschner 2010; Hédl, Kopecký &

Komárek 2010). This trend is also exemplified by increasing stocks of wood in European forests; for example in Western European forests, standing volumes per ha have doubled since 1950 (Gold, Korotkovb & Sasse 2006).

In our study, the decreasing management intensity is reflected in the increase in total canopy cover in most of the study regions and an increasing importance of more shade casting, late successional species such as *Acer pseudoplatanus* and *C. betulus*. Shrubs or small trees such as *Corylus avellana*, *Sorbus aucuparia* and *Crataegus* spp. tended to decrease (Table 3). Similar trends have been reported before in some of the study regions included in this paper (e.g. Meerdaalwoud: Baeten *et al.* 2009; Milovice: Hédl, Kopecký & Komárek 2010; Wytham: Kirby *et al.* 2005; Tournibus & Florennes: Van Calster *et al.* 2008a). Next to a higher litter input due to the increased canopy cover and change in management system, the litter generally also became more decomposable over the years due to the increasing importance of species with good litter quality such as *Fraxinus excelsior*, *A. pseudoplatanus* and *C. betulus* (cf. Jacob *et al.* 2009) in the studied forests. This has also been reported earlier for some of the study regions included (e.g. Dalby: Persson, Malmer & Wallén 1987). Furthermore, active litter removal was also a common practice in the past (e.g. Kirby & Watkins 1998).

The unexpected significant decrease in canopy cover in some study regions, where no management has taken place (Dalby), where management intensity has decreased (Rychlebské hory, Milíčovský les) or remained stable (Elbe-Weser), is related to a series of natural disturbances: canopy tree mortality due to diseases (e.g. tracheomycosis of oaks in Milíčovský les, Dutch elm disease in Dalby), storm damage (Elbe Weser), air pollution-related damage to beech (Rychlebské hory) and mortality due to old age (Elbe-Weser, Dalby and Milíčovský les). It is also likely that the canopy will become more open in other regions as in the next decades, more and more forests are gradually moving towards a canopy breakup stage (*sensu* Peterken 1996).

The trend towards increasing large herbivore densities is being observed across Europe (e.g. Fuller & Gill 2001; Ward 2005; Milner *et al.* 2006; Bláha & Kotecký 2008). The increase is explained by land-use changes, milder winters and changes in game management. Decreasing numbers in three of the studied forest landscapes are due to fencing (Lady Park Wood), targeted hunting (Munich) or the abandonment of a game preserve (Děvín).

In summary, the ecological changes in our study sites reflect some of the major trends that are affecting broadleaved woodland more generally across Europe, and so the changes seen in the understorey in this study are likely to be applicable more generally.

CHANGES IN THE UNDERSTOREY

In 70% of the study regions, the number of species significantly increased or decreased, and almost 30% of the species in the plots has been replaced since the time of the first survey, which concurs with understorey changes reported in other resurvey

Table 3. Overview of the ten most frequent tree and shrub species (across the different studies) in the recent surveys, their average cover in the plots where they occurred and the trends in frequency and cover compared to the old surveys. The species are ranked according to decreasing frequency

Species	Frequency (%) in recent survey	Change in frequency (%) compared to old survey	Cover (%) in recent survey	Change in cover (%) compared to old survey
Quercus robur/petraea	53	+4	38	−2
Fraxinus excelsior	46	+3	44	+4
Coryllus avellana	44	0	36	−2
Acer pseudoplatanus	43	+7	38	+11
Carpinus betulus	31	−1	38	+11
Fagus sylvatica	27	+3	52	−1
Betula pendula/pubescens	20	−2	18	+5
Sorbus aucuparia	19	−1	7	0
Ulmus glabra	17	−1	40	+1
Crataegus spp.	16	−2	13	0

Table 4. Outcome of the general linear mixed models with the response ratio of species richness (RR_s) and the Lennon similarity coefficients between the old and recent surveys as response variables and the deposition (N_{mean}), number of years (no. years), initial Ellenberg indicator values (mL_O, mN_O), climate (MAT, MAP), grazing (density, HERBI−, HERBI+) and canopy variables (RR_{cover}, RR_{litter}, RR_{shade}) as explanatory variables. Each combination of the individual explanatory variables that proved to be equivalent in terms of explanatory power when used in single-variable models (i.e. $\Delta AIC < 4$ than the model with the lowest AIC) is reported

RR_S			Lennon		
Variable(s)	ΔAIC	d.f.	Variable(s)	ΔAIC	d.f.
No. years+N_{mean}+mL_o	0.0	6	mL_O + N_{mean} + No. years	0.0	6
No. years + mL_o	1.3	5	mL_o + N_{mean}	0.9	5
N_{mean} + mL_o	3.0	5	mL_o + No. years	2.0	5
No. years + N_{mean}	5.7	5	mL_o	7.8	4
No. years	6.7	4	N_{mean} + No. years	11.3	5
N_{mean}	8.9	4	N_{mean}	11.5	4
mL_o	9.8	4	No. years	11.9	4

Variable	Value	SE	d.f.	*t*-value	*P*-value	Variable	Value	SE	d.f.	*t*-value	*P*-value
Intercept	0.378	0.418	765	0.904	0.367	Intercept	−0.182	0.098	765	−1.848	0.065
No. years	−0.012	0.005	15	−2.166	0.047	No. years	−0.002	0.001	15	−1.601	0.130
N_{mean}	0.023	0.013	15	1.738	0.103	N_{mean}	0.006	0.003	15	1.919	0.074
mL_o	−0.081	0.028	765	−2.843	0.005	mL_o	−0.027	0.007	765	−3.616	<0.001

AIC, Akaike Information Criterion; MAP, mean annual precipitation; MAT, mean annual temperature.
The parameter values of the model that showed the best fit (in terms of AIC value) are shown at the bottom of the table. See Materials and methods for details on the stepwise model building.

studies performed in, for instance, North America (e.g. Taverna, Peet & Phillips 2005; Rogers *et al.* 2008). The large shift in composition could be partly due to the fact that most studies used semi-permanent plots, which might have introduced some relocation error, and because the observers differed between the old and recent surveys. However, the use of presence/absence data partly reduced such sampling error. The fact that the changes in the floristic composition were directional as indicated by the mean Ellenberg value shifts (Fig. 2) also suggests that these are real-world effects. Furthermore, the presence/absence data yield conservative estimates of the plant community change, and it is likely that shifts in species' relative abundances have taken place as well.

The degree to which the species richness and composition changed over time was positively related to the time interval between the old and recent surveys (Table 4), which may be caused by the life span of many forest understorey species that can be as long as several decades (Ehrlen & Lethilä 2002). Therefore, community reorganization is more likely to be detected as the time interval between the two surveys increases. Similar results were, for instance, found by Dupré *et al.* (2010) in acidic grasslands.

In our study, plots with higher initial light availability (expressed as higher Ellenberg L values) showed lower similarity and larger reduction in species richness between the two survey dates. The replacement and filtering of light-demanding

Table 5. Outcome of the general linear mixed models with the response ratio of Ellenberg values for nutrient availability (RR_N) and light (RR_L) as response variables and the deposition (N_{mean}), number of years (no. years), initial Ellenberg indicator values (mL_O, mN_O), climate (MAT, MAP), grazing (density, HERBI−, HERBI +) and canopy variables (RR_{cover}, RR_{litter}, RR_{shade}) as explanatory variables. Each combination of the individual explanatory variables that proved to be equivalent in terms of explanatory power when used in single-variable models (i.e. $\Delta AIC < 4$ than the model with the lowest AIC) is reported

RR_N						RR_L					
Variable(s)	ΔAIC	d.f.				Variable(s)	ΔAIC	d.f.			
$RR_{litter} + RR_{cover}$	0.0	5				$RR_{cover} + RR_{litter} + RR_{shade}$	0.0	6			
RR_{litter}	3.5	4				$RR_{cover} + RR_{litter}$	1.5	5			
RR_{cover}	6.0	4				$RR_{cover} + RR_{shade}$	6.1	5			
						RR_{cover}	6.8	4			
						$RR_{litter} + RR_{shade}$	7.2	5			
						RR_{litter}	9.4	4			
						RR_{shade}	11.2	4			

Variable	Value	SE	d.f.	t-value	P-value	Variable	Value	SE	d.f.	t-value	P-value
Intercept	0.040	0.017	764	2.300	0.022	Intercept	−0.0216	0.010	763	−2.180	0.030
RR_{litter}	0.037	0.013	764	2.829	0.005	RR_{litter}	0.0418	0.015	763	2.841	0.005
RR_{cover}	0.020	0.008	764	2.350	0.019	RR_{cover}	−0.0279	0.009	763	−3.037	0.003
						RR_{shade}	−0.048	0.026	763	−1.878	0.061

AIC, Akaike Information Criterion; MAP, mean annual precipitation; MAT, mean annual temperature.
The parameter values of the model that showed the best fit (in terms of AIC value) are shown at the bottom of the table. See Materials and methods for details on the stepwise model building.

species due to a gradual canopy gap closure is likely to account for those patterns (Van Calster *et al.* 2008b). This corroborates the results of Kirby *et al.* (2005) who found a general decrease in understorey species richness, except in sites that were most severely hit by the 1987 storm in the south and east of England.

Unlike studies in grassland (e.g. Stevens *et al.* 2004; Dupré *et al.* 2010), high atmospheric N deposition rates did not have a negative effect on the understorey species richness. By contrast, there was even a (weak) positive effect on species richness, and plots exposed to higher N deposition rates tended to exhibit less floristic changes. Some experimental N addition studies also found positive (Hurteau & North 2008) or mixed (Ostertag & Verville 2002) effects on understorey species richness, whereas others found negative effects (Strengbom *et al.* 2001). Gilliam (2006) discusses N-mediated changes in various processes (e.g. competition, herbivory, mycorrhizal infection), which could all potentially affect forest understorey diversity and composition, but the rather idiosyncratic results of studies so far indicate that the understorey effects of adding a single limiting resource cannot yet be predicted at the community level (see also De Schrijver *et al.* 2011).

The shifts in Ellenberg values, which point to increased shading and nutrient availability, are consistent with those reported elsewhere (e.g. Kirby *et al.* 2005; Baeten *et al.* 2009; Keith *et al.* 2009). The importance of canopy variables to explain the changes in the Ellenberg indicator value for light (Table 5) is consistent with the expectation that more shady conditions, caused by increasing canopy cover and a higher relative importance of shade casting species in the canopy, reduce

the survival chances of more light-demanding species in the understorey plant community. The positive relationship between increasing litter quality and the share of light-demanding species may be related to the difficulties these species experience in germinating and/or establishing on sites where a litter layer has accumulated (Sydes & Grime 1981; Eriksson 1995; Dzwonko & Gawronski 2002; Sayer 2006).

The more frequent occurrence of nutrient-demanding species in the community, detected through the Ellenberg N indicator values, is not directly explained by variation in the N deposition rate. Instead, changes in the canopy seem to be primarily responsible for the observed eutrophication signal. The increased input (and maybe also reduced removal) of litter and the increasing importance of species with faster decomposing litter is likely to have increased the general nutrient availability in the studied forests (cf. Dzwonko & Gawronski 2002; Hofmeister *et al.* 2009). Common garden experiments have shown that tree species differ greatly in their impacts on soil acidity and fertility (e.g. Neirynck *et al.* 2000; Hagen-Thorn *et al.* 2004; Reich *et al.* 2005; Vesterdal *et al.* 2008) with consequent impacts on the understorey vegetation (e.g. van Oijen *et al.* 2005; Wulf & Naaf 2009; Kooijman 2010). Kooijman (2010), for example, specifically focused on litter-generated differences in N cycling under tree species with contrasting litter quality (beech and hornbeam), and the effect on the understorey species composition. The, albeit weak, negative correlation between RR_L and RR_N is consistent with a canopy-induced eutrophication signal as it suggests that the frequency of more nutrient-demanding species has particularly increased in plots where the canopy has become more closed. However, an

indirect effect of N deposition on the forest understorey, caused by increasing forest productivity and the rates of canopy closure (e.g. Hedwall *et al.* 2010) or by changing the foliar nutrient contents and litter decomposition rates (e.g. May *et al.* 2005), cannot be excluded. Indeed, excluding the Elbe-Weser study from Fig. 3a, the results reveal a positive relationship between the N deposition rate and the canopy closure, but further research is needed to confirm this relationship. Nevertheless, interspecific variability in leaf traits will most likely continue to have a dominant impact on litter decomposition (Cornwell *et al.* 2008).

Although it is inherently difficult to disentangle acidification and eutrophication using Ellenberg indicator values (e.g. Diekmann & Dupré 1997), it seems that the latter process is more important to explain the patterns observed in this study. The RR_N values equally increased in plots in more acidic ($mR_o \leq 5$) and more base-rich sites ($mR_o > 5$). Also the response ratios for soil reaction (RR_R) increased, but more so in the more nutrient-poor sites ($mN_o \leq 5$) than in the more nutrient-rich sites ($mN_o > 5$) (results not shown). Bürger-Arndt (1994) found similar patterns and considered the increasing mR values in forests that are becoming darker to be an artefact caused by the selective loss of acid-tolerant species that are often light demanding.

SYNTHESIS

Significant shifts have occurred in the understorey vegetation of semi-natural deciduous forest in temperate Europe during recent decades. Whereas no unidirectional shifts in species richness occurred, the relative proportion of nutrient-demanding and shade-tolerant species has clearly increased. Atmospheric N deposition may be one of the (indirect) drivers behind the change, but management-related alterations in the canopy structure and composition appear much more important. This finding is yet another example of the importance of understorey–overstorey interactions in forests (Gilliam 2007).

Our multi-site approach clearly demonstrates that one should be cautious when drawing conclusions about the impact of atmospheric N deposition based on the interpretation of plant community shifts in single sites or regions (e.g. Thimonier *et al.* 1994; Lameire, Hermy & Honnay 2000) due to other concurrent ecological changes. However, even though the effects of many decades of increased atmospheric N deposition are currently overruled by the effects of canopy changes, atmospheric N deposition may still have a significant impact.

Smith, Knapp & Collins (2009) recently proposed a hierarchical-response framework (HR-framework), conceptualizing ecological change as a response to chronic resource alterations. The forest understoreys under study have on the one hand experienced chronic increases of atmospheric N but on the other hand chronic decreases of light availability. These opposing trends in resource availability together with the longevity of forest understorey species and their often slow colonization rates (Verheyen *et al.* 2003; De Frenne *et al.* 2011) may help to explain the apparent resistance of forest understorey plant communities to species losses as a result of chronic N additions. This resistance may change, however, if the forest canopies are opened up again so that light becomes a less limiting resource. The HR-framework would suggest that a strong community reordering and possible species loss could be expected if the N that has built up over decades becomes available for plant growth. Initially, this might mean increases in species richness due to the increased occurrence of disturbance-adapted and non-forest species, but in the longer term, a decline in some forest specialist species through competition with competitive, light-demanding taxa such as *Rubus fruticosus* coll. and several graminoids could be expected. Chronic N deposition might therefore be regarded to as the building up of a 'nitrogen time bomb'.

However, the accumulated N may not become readily available for plant growth due to microbial immobilization and subsequent storage in stable soil organic matter (SOM) pools. Due to, often long term, intensive coppice with standards management, the SOM stocks in many ancient forests in Europe are currently still building up (e.g. Luyssaert *et al.* 2010), generating a higher potential for N immobilization. For instance, McLauchlan *et al.* (2007) demonstrated that N availability for plant growth in a North-American hardwood forest subject to increased atmospheric N deposition has even declined over the past 75 years probably because the system was still recovering from a period of agricultural land use during the 19th century.

Clearly, more research is needed to better understand the current and future impacts that increased N deposition may have on forest understorey communities.

Acknowledgements

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Supporting Information

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Appendix A. Overview of the litter quality index scores.

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