Responses of Temperate Forests to Nitrogen Deposition: Testing the Explanatory Power of Modeled Deposition Datasets for Vegetation Gradients

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ABSTRACT

Eutrophication due to increased nitrogen concentrations is known to alter species composition and threaten sensitive habitat types. The contribution of atmospheric nitrogen deposition to eutrophication is often difficult to determine. Various deposition models have been developed to estimate the amount of nitrogen deposited for both entire regions and different landscape surface types. The question arises whether the resulting deposition maps allow direct conclusions about the risk of eutrophication-related changes in the understory vegetation composition and diversity in nitrogen-sensitive forest ecosystems. We combined vegetation and soil data recorded across eutrophication gradients in ten oligo-mesotrophic forest types in southwest Germany with datasets from two different deposition models specifically fitted for forests in our study region. Altogether, 153 forest stands, with three sampling replicates each, were examined. Linear mixed-effect models and NMDS analyses revealed that other site factors, in particular the soil C/N ratio, soil pH and canopy cover, played a greater role in explaining vegetation gradients than nitrogen deposition. The latter only rarely had effects on species richness (positive), nitrophyte cover (positive or negative) and the cover of sensitive character species (negative). These effects varied depending on the deposition model used and the forest types examined. No effects of nitrogen deposition on average Ellenberg N values were found. The results reflect the complex situation in forests where nitrogen availability is not only influenced by deposition but also by nitrogen mineralization and retention which depend on soil type, pH and (micro)climate. This context dependency must be regarded when evaluating the effects of nitrogen deposition.

Key words: Nitrogen; Eutrophication; Atmospheric deposition; Deposition models; Forest vegetation; Indicator species; Ellenberg indicator values.

Author contributions   HP, HGM and MBW conceived the study, MR performed the research and analyzed the data, MR and MH wrote the paper, with input from HP, HGM, MBW and CS.

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HIGHLIGHTS

- Vegetation gradients in 153 oligo-mesophilic forests were compared to N deposition.
- Nitrogen availability in the soil was largely independent from atmospheric deposition.
- The eutrophication gradient in the vegetation was most strongly related to the soil C/N ratio.

INTRODUCTION

Plant growth and vegetation composition are closely related to N availability in many terrestrial ecosystems. Although N is considered to have been a limiting nutrient in most terrestrial ecosystems throughout history (Vitousek and Howarth 1991), elevated atmospheric N deposition, caused by artificial N fixation via the Haber–Bosch process and emission from combustion, has led to an increased N availability in (semi-)natural ecosystems. A surplus of N causes eutrophication which becomes apparent in the vegetation by species composition shifts toward more nitrophytes, the increase in mean Ellenberg indicator values for N, changes in species richness and loss of character species for oligotrophic sites (van Dobben and De Vries 2010; Ewald and others 2013; Bernhardt-Römermann and others 2015). The capability of plants to increase the net productivity under increased N supply is often linked to high photosynthetic capacity (Suding and others 2005). Plant species in oligotrophic ecosystems are, however, mostly adapted to low N levels and cannot invest N as rapidly in growth as generalists. This results in a disadvantage in the competition for light which is a limiting factor in forest understories. Whereas N addition may first increase diversity in oligotrophic communities by allowing also more demanding species to grow, higher addition or addition to already meso-eutrophic systems is likely to decrease diversity due to competitive exclusion (Gilliam 2006; Hautier and others 2009). As such, also evenness or species richness are indicators for eutrophication-caused shifts in species communities. In addition to shifts in interspecific competition, N supply also indirectly affects vegetation via interactions with herbivores, mycorrhizae and pathogens (Bobbink and others 1998; Gilliam 2006). Furthermore, also direct NH_4^+ toxicity (Pearson and Stewart 1993) and soil acidification by N addition and subsequent leaching of plant nutrients like Ca and Mg (De Vries and others 2003) possibly affect species and species composition. A tool often used in vegetation ecology to summarize vegetation responses to environmental factors are Ellenberg indicator values (Ellenberg and others 2001). These values rate the preferences of individual species for nutrients (N), light (L), soil acidity (R) and moisture (F) among others on a nine-point ordinal scale based on an expert assessment. In case of the N-value, for example, 1 represents the most N-sensitive species and 9 indicates plant species with a preference for highly N-enriched habitats.

Although the importance of N availability for plant growth and vegetation composition in most terrestrial ecosystems is undisputed, the contribution of atmospheric N deposition is often less clear. In addition to N inputs from nearby local sources such as agriculture or traffic (Pitcairn and others 1998; Bernhardt-Römermann and others 2006), the main source for external N input into forests is the atmospheric deposition of reactive N transported over short (only in case of NH_x) to large distances (for example, van Dobben and De Vries 2010; Dirnböck and others 2014; van Dobben and de Vries 2017). Atmospheric deposition affects forests more than open areas (for example, agricultural land) due to the large intercepting surface of the canopy (Hasselrot and Grennfelt 1987; Erisman and Draaijers 2003) and the absence of direct fertilizer application. Results of studies on the effects of N deposition on forests tend to be less consistent than those examining open areas (Bobbink and others 2010), mainly due to the larger heterogeneity of the forest structure (for example, tree height, canopy closure). Furthermore, land-use legacies, soil properties and climate influence the partitioning, biochemical conversion and export of reactive N in terrestrial ecosystems, which are all processes that modify the N availability for the vegetation.

For Central Europe, N deposition has been modeled at high spatial resolution, based on monitoring data of N concentration and deposition. The raster cell sizes of the different deposition models vary, depending on the size of the reference area and the dataset, between 50 m (Zirlewagen 2018) or 100 m (StickstoffBW AG1 2017) to 1 km (Builtjes and others 2011; Schaap and others 2015) or even to 50 km (Simpson and others 2012). N deposition models typically distinguish wet deposition, which enters the ecosystem via precipitation, and dry deposition, which includes the deposition of gases and particulate matter (Stevens and others 2011). Because plants can take up N via leaf surfaces and root systems, wet and dry deposition may contribute differently to eutrophication. However, effects may be difficult to disentangle

because dry deposition intercepted by tree crowns may be washed off with precipitation and higher soil water availability favors mineralization processes. Cloud and fog deposition (that is, the deposition of N compounds from fog onto surfaces) was sporadically included in the deposition models (for example, included in the Pollutant Input and Ecosystem [PINETI] model for Germany (Schaap and others 2015), but excluded from the European Monitoring and Evaluation Program [EMEP] model (Simpson and others 2012)). Both the wet and dry deposition of reactive N include reduced (NH_x) and oxidized (NO_y) N compounds, which underlie specific spatial variations in emission and deposition patterns (Holland and others 2005). To regard these deposition forms separately may be interesting, since plant species can vary in their ability to regulate NH_4^+ and NO_3^- uptake in the rhizosphere (von Wirén and others 1997; Glass and others 2002; Neuhäuser and others 2007). As such, preferences of individual plant species for the uptake of reduced or oxidized N might result in differences in the vegetation, even between sites or periods that do not differ in their total N deposition (Stevens and others 2011; van den Berg and others 2016).

Modeled N deposition patterns were found to be related to both soil and vegetation patterns in the USA (Simkin and others 2016; Zarfos and others 2019 (the latter combining N and S deposition)). Studies in European forests have been less conclusive so far. Whereas some studies have shown vegetation composition to be related to on-site measurements of N deposition (Seidling and Fischer 2008; Dirnböck and others 2014), other studies using modeled deposition found no or only weak correlations between deposition and vegetation composition (Verheyen and others 2012; Dirnböck and others 2014; Bernhardt-Römermann and others 2015; van Dobben and de Vries 2017). Weak congruence was not only found with coarse (50 km × 50 km) N deposition models but also with the 1 km × 1 km PINETI2 deposition model (Ewald and Ziche 2017). Instead, Ewald and Ziche (2017) found that the Ellenberg N value was mostly correlated with the C/N ratio and base saturation of the upper soil.

In general, there is uncertainty about the importance of N deposition for the vegetation composition relative to other factors, including the nutrient status of the soil, net N mineralization and other environmental factors, which may or may not be related to N supply. Given the sometimes strong impact of N addition on vegetation, the obvious question arises whether deposition models allow direct inferences about the state of the vegetation, especially for N-sensitive (that is, oligo-mesotrophic) ecosystems. The ability to attribute the extent of eutrophication-induced vegetation changes to N deposition with the help of N deposition maps, and to even predict gradients from these maps, would be highly valuable for nature conservation.

In our study, we wanted to test whether it is possible to detect the impact of N deposition against the background of confounding covariates in climate, topography, geology and soil properties. Using two deposition models and ten forest types, which were known to be potentially susceptible to eutrophication-induced shifts in species composition, we conducted a case study in broad-leaved and coniferous forests of southwest Germany. We developed a study design that aimed to increase the probability of finding a significant relationship between vegetation gradients and N deposition. First of all, we selected a study area for which atmospheric N deposition models were available at high spatial resolution to reduce the scale mismatch between vegetation sampling and deposition models. Secondly, we selected the vegetation sampling plots in a stratified random procedure, which should produce the highest possible contrast between eutrophication-affected and unaffected variants of ten different forest types. With our study, we wanted to test the hypothesis (1) that atmospheric N deposition is significantly correlated with the occurrence and cover of N-sensitive vascular and cryptogam plant species in the understory of the studied forest types. As total atmospheric N deposition consists of different components, in terms of both the form of deposition (that is, dry and wet deposition) and the oxidation state (NH_x and NO_y) and as plants differ in their response to various forms of reactive N (Stevens and others 2011; van den Berg and others 2016), we tested hypothesis (2) that different components of the modeled deposition differ in their effects on the occurrence and cover of plant species. Because N indicator values of Ellenberg and others (2001) are often used to identify eutrophication effects on the vegetation, we calculated mean N indicator values for our sample plots to test hypothesis (3) that these mean indicator values are positively correlated with modeled atmospheric N deposition. Our study included the humus form, humus layer depth and the pH, C/N ratio and the total N content of the topsoil as covariates.

MATERIALS AND METHODS

Study Region

The study was conducted in the state of Baden-Württemberg, southwestern Germany (Figure 1). Due to the high topographic heterogeneity of the landscape, temperature and precipitation vary strongly between different regions. Climate ranges from dry–warm conditions in the Rhine valley (mean annual temperature > 11°C; annual precipitation < 700 mm) to cold–humid conditions in the mid-mountain range of the Black Forest (mean annual temperature < 6°C; annual precipitation > 2000 mm) (Hartmann and others 2016). The geological substrates and soils are also highly variable: Whereas siliceous soils prevail in the Black Forest, calcareous soils are common on the Swabian Alb. Accordingly, a wide variety of different forest types and communities exist, with Norway spruce (*Picea abies*) and European beech (*Fagus sylvatica*) as the current most dominant tree species (Kändler and Cullmann 2014).

Modeled Deposition Data

Two datasets of modeled atmospheric N deposition, explicitly developed for forests in the state of Baden-Württemberg, were used for our study, namely the datasets of Zirlewagen (2018) and a dataset provided by T. Gauger (Institute of Navigation, Stuttgart, Germany) which represents an advanced version of the models published by StickstoffBW AG1 (2017). The models are henceforth referred to as 'ZW2018' and 'LUBW2020,' respectively. ZW2018 is a regionalization of N deposition monitoring data based on geostatistical modeling using high-resolution topographic, geologic and climatic data and the EMEP and PINETI2 deposition maps as auxiliary variables (see Table S1 in the electronic supplementary material ESM1). In ZW2018, modeled deposition was available for the years 1881–2016 at a high resolution of 50 m × 50 m. In our analysis, we used the mean annual values for the period 1970–2016. LUBW2020 is using emission, meteorological, air concentration and land-cover data as well as
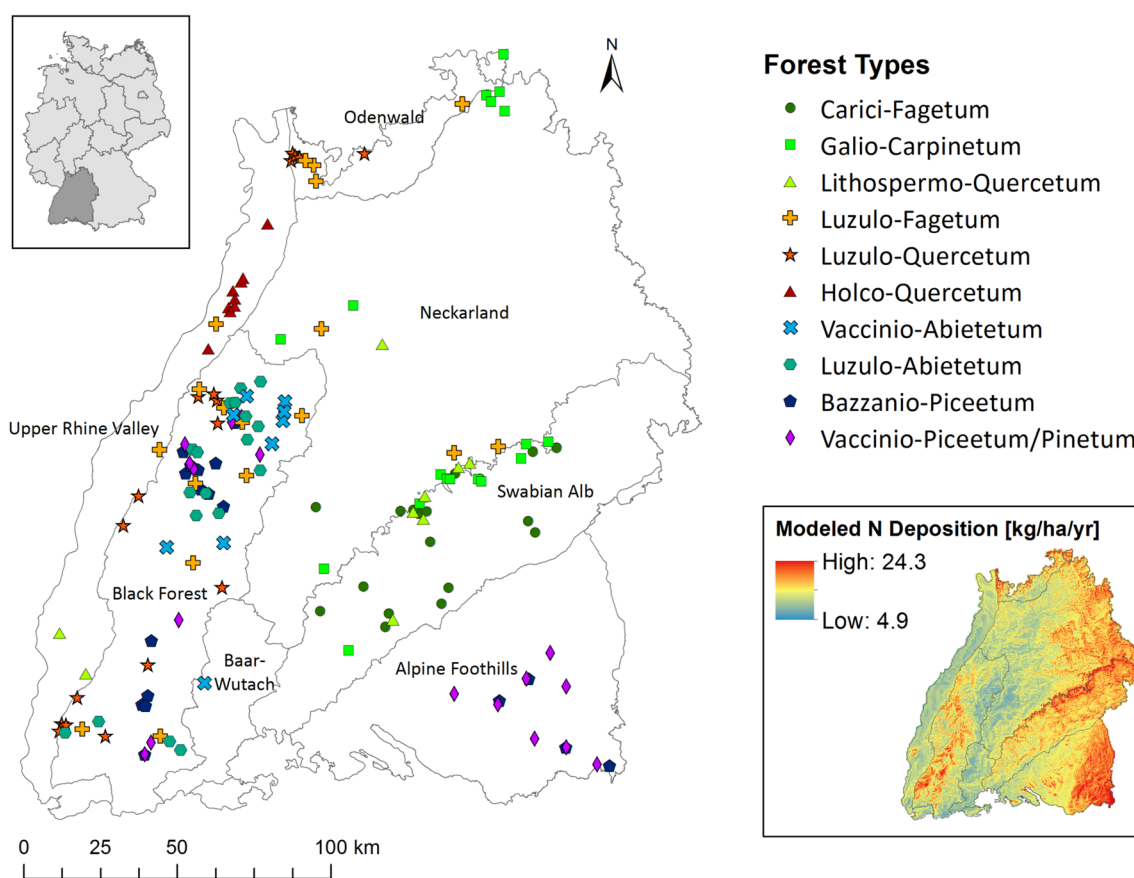

Figure 1. Location of the 153 study sites representing ten forest types in Baden-Württemberg, southwestern Germany and the location of the study region within Germany (inset top left). Inset bottom right: an example of a modeled deposition map for the study region (ZW2018, broad-leaved forest, year 2016).

deposition measurements and combines four different modeling approaches. The main outcome are deposition maps averaged over the 5-year period 2012–2016 with a resolution of 100 m × 100 m (Table S1). Both models resulted in higher levels of estimated total N deposition compared to the coarser-scale models (EMEP or PINETI), particularly in the mid-mountain range of the Black Forest, the urban region in the northwest of Baden-Württemberg and the eastern part of the state. Both datasets included models for wet, dry and total N deposition. LUBW2020 (but not ZW2018) provided separate information for NH_x and NO_y deposition. Considering that each dataset had specific strengths regarding spatial resolution and the details of deposition types and that the datasets were only moderately correlated (see below and Figure S1), we used both datasets in our analyses. Deposition data fitted for coniferous and broadleaved forests were available in both datasets and were used according to the occurrence of the main tree species on our study sites.

The correlation of total N deposition between the two datasets was $r = 0.68$ ($p < 0.001$) (Figure S1). NH_x and NO_y deposition were both correlated with the total N deposition in the LUBW2020 dataset ($r_s = 0.82$ and $r_s = 0.69$, both $p < 0.001$), but were only weakly intercorrelated ($r_s = 0.25$, $p < 0.01$). This indicates that the relative share of NH_x and NO_y for total N deposition was highly variable between the individual study sites. The NH_x/NO_y ratio was generally higher in the east, in drier areas with more intensive agriculture, and lower in the west where precipitation is higher. ZW2018, which covered the temporal variability of N deposition, showed a decrease in the mean total N deposition across all study sites from roughly 25 kg ha^{-1} year^{-1} to less than 20 kg ha^{-1} year^{-1} from the 1980s to 2016 (Figure S2). One potential weakness of ZW2018 is that the model did not account for potential spatial shifts in deposition over time as a result of shifts in emission characteristics (for example, shifts in the location or range of point sources), instead, local deposition just varied as a function of the mean deposition level. Therefore, it was not possible to examine the effect of the length of exposure to certain levels of deposition on the vegetation. Sulfur deposition was not considered in our study since it strongly decreased since the 1980s in Europe and leveled off at low concentrations today (Vestreng and others 2007).

Study Sites for Field Sampling

A total of 153 forest stands representing ten different oligo-mesotrophic forest types were examined. The forest stands were distributed throughout most of the state of Baden-Württemberg (Figure 1, Table 1). The forest types were selected because their ground vegetation layer was noted in the literature as sensitive to eutrophication. It is usually composed of species with low or moderate N requirements and adaptation toward N deficiency (Falkengren-Grerup and Schöttelndreier 2004; Bobbink and Hettelingh 2011; Reger and others 2014). Ranges and the mean of N deposition in the different forest types are presented in Table S2.

Our goal was to test whether variants of the same forest type, which strongly contrast in terms of their signs of eutrophication, can be related to modeled N deposition. Thus, we implemented a strategic selection of study sites over a visible gradient of eutrophication stages to obtain as much N-related variation in the vegetation as possible. Preliminary information on the forest vegetation of Baden-Württemberg was available from the forest habitat mapping of Baden-Württemberg (Kerner and Geisel 2015). This monitoring maps forest types which are generally or regionally rare (that is, in the respective natural region (Michiels 2014); Figure 1) with the purpose of supporting management decisions. In the mapping, forest types are delimited in the field based on site conditions and the occurrence of certain character species which are defined in a mapping manual (Kerner and Geisel 2015). Part of this habitat mapping is the compilation of (incomplete) presence species lists for the vegetation of the stands. For plot selection, these species lists were evaluated for their mean Ellenberg N indicator value and their number of character species for the respective forest types (as defined by the manual). For each forest type, all sites with a size of at least 1 ha were ranked according to each of these two measures. Low ranks were given to (a) plots with low Ellenberg N values and (b) plots with a high number of character species. The two ranks were summed, weighting the ranks of Ellenberg values double and the ranks of character species single. For each forest type, the sites with the six (three) lowest, most central and highest ranks of the final lists were selected as study sites and grouped in the classes L (low), M (medium) and H (high), respectively, resulting in 18 (9) study sites per forest type (Table 1; cf. Figure S3, Table S3).

Table 1. Forest Types, Their Assignment to Forest Type Groups and the Number of Surveyed Study Sites (n), Each with Three Plots for Vegetation Sampling as Subsamples

Forest type group	Forest type	Abbreviation	n
Broad-leaved forests on carbonate soil	Carici-Fagetum	CF	18
	Galio-Carpinetum	GC	18
	Lithospermo-Quercetum	LSQ	9
Broad-leaved forests on acidic soil	Luzulo-Fagetum	LF	18
	Luzulo-Quercetum	LQ	18
	Holco-Quercetum	HQ	9
Coniferous forests on acidic soil	Luzulo-Abietetum	LA	18
	Vaccinio-Abietetum	VA	9
	Bazzanio-Piceetum	BP	18
Bog forests	Vaccinio-Piceetum/Pinetum	VP	18

For three forest types only nine study sites were sampled due to their rarity (LSQ), confined distribution (HQ) and similarity to neighboring forest types (VA).

Vegetation Surveys

At each of the 153 study sites, three sample plots each with a radius of 10 m (area 314 m^2) were established randomly within the forest stand. This sample plot size corresponds with recommended plot areas for vegetation relevés for forest vegetation (Dierschke 1994). The average time used for a relevé was 0.5–1.5 h, depending on the diversity of the vegetation and the cover of the herb layer. To avoid observer bias, all surveys were completed by the same author, partly with the support of student assistants. All plant species in the sample plots were recorded separately for the tree (> 5 m height), shrub (< 5 m height), herb (< 0.5 m height) and cryptogam layers. The cover of individual species within these layers as well as the overall layer cover was estimated using a percent scale, with 1% steps for species with a cover of 1–10% and 5% steps for species covering more than 10% of the sample plot. For species with a cover below 1%, cover values of 0.01% (1–3 plant individuals) or 0.1% (> 3 individuals) were assigned. Nomenclature referred to Breunig and Demuth (1999) for vascular plants, Sauer and Ahrens (2006) for bryophytes and Wirth (2008) for lichens.

To characterize vegetation diversity, species richness (α-diversity, defined as the sum of all vascular plants and cryptogams regardless of their layer), the Shannon–Weaver Index ($H = -\sum_i^S p_i - \ln p_i; p_i = \frac{n_i}{N}$ with $S =$ species richness; $p_i =$ relative abundance of a species i; $n_i =$ number of individuals; $N =$ total number of individuals; Shannon and Weaver (1949)) and evenness ($E = H/\ln(S)$; Pielou (1966)) were calculated.

To test our third hypothesis, log-transformed cover-weighted means of Ellenberg N values (CWM N values) for each plot were calculated combining all understory layers (herb, shrub and cryptogam layer). Likewise, we calculated CWM values for light (L), acidity (R, 'reaction' in Ellenberg and others (2001)) and moisture (F) to assess potential intercorrelations of other site parameters with N availability. Analogous indicator values with a slightly different definition of scales were used for bryophytes (Hill and others 2007) and lichens (Wirth 2010). Species with N indicator values of at least 6 were classified as nitrophytes. The threshold was chosen since already many species with Ellenberg N value = 6, for example, *Rubus fruticosus* or *Impatiens parviflora*, are untypical for the examined oligo-mesophilic forest types. Furthermore, for each forest type, a group of N-sensitive character species was defined, containing species with N indicator values no greater than 3 that are additionally listed as character species for the respective forest type in the forest habitat mapping manual (Kerner and Geisel 2015; see above). Their species number and cover in the herb and bryophyte layer of each sample plot were calculated by simple addition. Cover of sensitive character species thus exceeded 100% in some cases.

Chemical Analysis of the Soil

Disturbed soil samples of the topsoil at a depth of 0–10 cm were obtained and were analyzed separately for each circular plot. Depending on the soil structure, soil samplers (20–30 points per plot), spades (3 points) or pickaxes (1–3 points) were used to collect samples of approximately 300 g. Sample points were equally distributed across the plots with a minimum distance of 1 m to trees. Where the humus layer was less than 10 cm, it was

removed and mineral soil was sampled, and where the humus layer was greater than 10 cm, a humus sample was collected. Humus form and humus layer depth (cumulated depth of the L, Oh and Of layers) were determined in the field. Prior to analysis, samples were dried at 60°C. Mineral soil samples were crushed and sieved (mesh size 2 mm); humus and peat samples were ground to 0.5 mm particle size using a variable speed rotor mill. The samples were analyzed for total N and C via combustion analysis at 950°C using a C/N analyzer (Vario MAX cube, Elementar Analysesysteme, Langenselbold, Germany). For samples with $pH_{(H2O)}$ above 6.2, the content of organic C (C_{org}) was analyzed by combustion analysis at 530°C; for samples with $pH_{(H2O)}$ below 6.2, C_{org} was assumed to equal C_{total}. We refer to C_{org}/N from here on as C/N. Sampling and sample analysis were conducted by the laboratory of the Forest Research Institute of Baden-Württemberg following GAFA (2014) with small adaptations.

Other Site Variables

Plot-specific climate data (mean annual temperature and precipitation averaged over 30 years, 1981–2010) were obtained for the sample plots from modeled climate data provided by the German Weather Service (Deutscher Wetterdienst, Offenbach, Germany). Distances from the sample plots to the nearest forest edge, road or unpaved forest track were calculated in GIS, based on topographic maps and a forest cover layer of Baden-Württemberg. Elevation was measured in the field using a GPS navigation device and slope inclination was measured using a Vertex IV ultrasonic clinometer (Haglöf, Långsele, Sweden). All variables used in the statistical analyses are listed in Table S4.

Statistical Analyses

All statistical analyses were performed using R software. The three vegetation relevés as well as all continuous soil and environmental variables of each stand were averaged prior to all analyses except for the models because they did not represent independent samples. In the models, the replicates were accounted for as random effects. Differences in species richness, evenness, number and cover of N-sensitive character species or nitrophytes, deposition and soil variables between the three vegetation-based classes L, M and H were assessed by Kruskal–Wallis tests and subsequent nonparametric Neyemi post hoc tests since assumptions for parametric tests (that is, homoscedasticity and normal distribution) were not met. Indicator spe-

cies for the three classes were analyzed according to Dufrêne and Legendre (1997) using the R package 'indicspecies' (De Cáceres and others 2010). These analyses identify species that are significantly most abundant in (sensitive) or most restricted to (specific) particular predefined groups. Correlations between individual variables were tested using the Pearson correlation coefficient (r) for normally distributed data with linear relationships; Spearman's rank correlation coefficient (r_s) was used in all other cases. To test the correlation between single species and modeled deposition, Kendall's tau as a more conservative and robust coefficient was used due to low sample numbers and existing outliers.

Non-metric multidimensional scaling (NMDS) using Bray–Curtis distances was performed for the multivariate analysis of the relationships between individual species, the overall vegetation composition and different environmental variables (Leyer and Wesche 2007) using the R package 'vegan' (Oksanen and others 2019). The first three dimensions were considered as they provided suitable goodness of fit according to the stress value (0.11–0.12). Cover values of plant species (D) were log-transformed ($\log(D + 1)$) before analysis to reduce the weight of abundant species. The unconstrained ordination graphs were overlaid with environmental variables to quantify their impact on the species composition using the function 'envfit' (R package 'vegan'). This function fits environmental variables to the site scores of the sampling sites in the ordination space. As summary statistics, the R^2 value and the p value of the underlying regression analysis are presented. NMDS was preferred over other ordination methods as it does not assume a certain data structure, such as normal distribution or homogeneity of variance or any specific response model, thus increasing the robustness of the results (Oksanen and others 2019).

We used linear mixed-effect regression to relate each of six response variables (CWM N value, soil N, soil C/N ratio, species richness, share of nitrophytes' and N-sensitive character species' cover of the total herb layer cover) to N deposition and other covariates. We excluded highly correlated variables ($r_s \geq 0.7$ and/or variance inflation factor VIF ≥ 5) to avoid multicollinearity and conducted manual backward variable selection from full models based on Akaike information criterion (AIC) values. To incorporate the dependency among observations caused by the sampling design, we included forest types and forest stands (with three replicates each) as nested random effects with

varying intercepts. Before the analysis we scaled all data. CWM N values and soil measurements were analyzed with linear mixed models (LMMs). For the number of species as a count variable, generalized linear mixed models (GLMMs) with Poisson likelihood and log-link function were used. For cover data, we used binomial or beta-binomial models, depending on the best model fit. In some cases, dependent variables were log- or sqrt-transformed, overdispersion was corrected using an observation-level random effect, or zero inflation was accounted for with a corrective term. Details for each model are given in the electronic supplementary material ESM2. Final models were checked by model diagnostics using residual and qq-plots for LMMs and the DHARMa package (Hartig 2020) for all other models.

For the NMDS analysis and regression models, forest types were grouped into forest type groups of ecologically similar forest types to increase sample size and degrees of freedom via larger datasets; the classification is shown in Table 1. Bog forests and colline broad-leaved forests on acidic soils were excluded because other influence factors than deposition were assumed to drive the eutrophication gradient. In bog forests, most likely draining plays a major role. In the colline broad-leaved forests, there was only a very small deposition gradient (Table S2).

RESULTS

By examining gradients in the vegetation composition, represented by the Ellenberg CWM N value, the cover of N-sensitive character species and nitrophytes, species richness and evenness, we aimed to answer our research question whether vegetation composition was influenced by atmospheric N deposition. To increase the likelihood of results, we covered a eutrophication gradient for each examined forest type.

Vegetation Patterns Along the Eutrophication Gradient

The eutrophication gradient was reflected in the NMDS ordinations where plots were grouped accordingly (Figure S4, Table 2). As expected, CWM N values increased strongly along the eutrophication gradient over the entire dataset (Figure 2a) and were positively correlated with the number and cover of nitrophytes (r_s = 0.82 and 0.76, both $p < 0.001$) and negatively correlated with the number and cover of N-sensitive character species (r_s = − 0.76 and − 0.90, both $p < 0.001$)

in the herb and bryophyte layer. The forest types differed strongly in the richness and cover of species with high and low CWM N values, thus indicating different sensitivities to N deposition (Figure 2a, Figure S3).

Species richness was significantly higher in the vegetation-based eutrophication class L (low) than in class H (high) in broad-leaved forests on carbonate soil, whereas the opposite was true in coniferous forests on acidic soil (Figure 2b). In broad-leaved forests on acidic soil, there was no significant difference in species richness between the two classes. Evenness did not change consistently across the eutrophication gradient in the different forest types (Figure 2c). In addition to the eutrophication gradient, the soil pH, facilitating the occurrence of comparatively few calcifuge species on acidic soils and a more diverse calciphilous vegetation in forests on carbonate soil, was found to determine species richness and evenness (Figure 2b, c).

Relationships Between the Vegetation and Modeled Total N Deposition

In contrast to the expectation that the vegetation-based plot classes L, M and H would be associated with an increase in modeled atmospheric N deposition in the order $L < M < H$, no such consistent trend was visible in our data (Figure 2d, e; Figure S4). Using linear mixed-effect regression models, we found a significant positive influence of N deposition on the cover of nitrophytes and a significant negative influence on the cover of sensitive character species (ZW2018) in coniferous forests on acidic soil (Table 3). In broad-leaved forests on acidic soil, there was an unexpected negative relationship between N deposition (LUBW2020) and the cover of nitrophytes. Furthermore, species richness was positively associated with N deposition in broad-leaved forests on carbonate soil (ZW2018) and coniferous forests on acidic soil (LUBW2020). There was no effect of N deposition on the CWM N values. In general, other explanatory variables, especially the C/N ratio, the pH of the topsoil and the cover of the tree layer, determined the examined vegetation variables (Table 3).

Species composition was not associated with total atmospheric N deposition according to the results of the NMDS ordination (Table 2). In a correlation analysis between the cover of individual plant species and modeled total atmospheric N deposition, only few associated species were found (Table S6). Among them were noticeably many species of the tree regeneration.
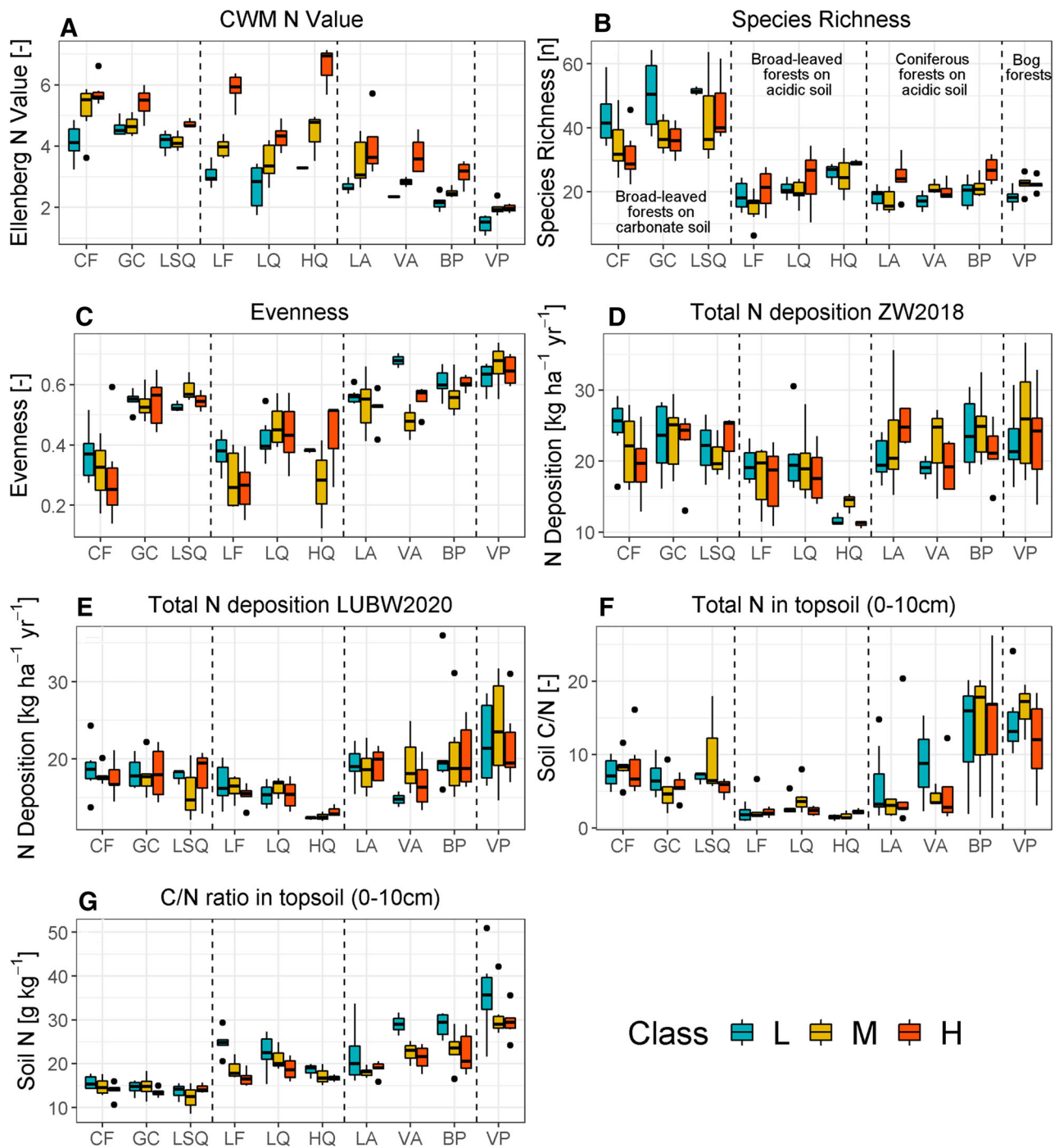
Figure 2. Vegetation changes along the three vegetation-based eutrophication classes *L* (low), *M* (medium) and *H* (high) for the individual forest types. Dotted lines separate the different forest type groups: Broad-leaved forests on carbonate soil (CF = Carici-Fagetum, GC = Galio-Carpinetum, LSQ = Lithospermo-Quercetum), broad-leaved forests on acidic soils (LF = Luzulo-Fagetum, LQ = Luzulo-Quercetum, HQ = Holco-Quercetum), coniferous forests on acidic soil (LA = Luzulo-Abietetum, VA = Vaccinio-Abietetum, BP = Bazzanio-Piceetum) and bog forests (VP = Vaccinio-Piceetum/Pinetum).

Relationships of the Vegetation with the Wet and Dry Fractions of N Deposition

Concurring with the results for total atmospheric N deposition, also the N loads modeled separately for the wet and dry fractions of N deposition showed only few relationships with the vegetation (Figure S5a–d). NMDS ordinations revealed no relationship between dry deposition and the vegetation of any forest type (Table 2). For wet deposition, only a marginally significant relationship with the vegetation composition of broad-leaved forests on carbonate soil was found (Table 2). Correlation analyses between the cover of individual species and wet or dry N deposition (Table S6) showed more correlations with wet deposition (ZW2018: 17; LUBW2020: 27) than with dry deposition (ZW2018: 11; LUBW2020: 5).

Differences Between the Deposition–Vegetation Relationships for NH_x and NO_y

Regression models for the dependent vegetation variables CWM N and species richness did not reveal any significant influence of neither NH_x nor NO_y deposition. The variables were always excluded during the variable selection process. In the NMDS, species composition and abundance were significantly associated with NH_x deposition in broad-leaved forests on carbonate soils and coniferous forests on acidic soil (Table 2, Figure S4a, c). There were no significant correlations between the vegetation composition and NO_y deposition according to the NMDS ordination.

Relationships of Soil N and C/N Ratio to Modeled Atmospheric Deposition and Vegetation

Like the atmospheric N deposition, the measured soil N content did not increase from vegetation-based plot class L via M to H (Figure 2f). Regression models revealed a significant positive correlation between the modeled total N deposition (ZW2018) and measured total soil N contents in broad-leaved forests on acidic soil (Table 3). According to the regression models, soil N content had a positive effect on species richness in all three forest type groups. In the NMDS ordinations, soil N played a role in explaining the vegetation gradients in the coniferous forests on acidic soil and broad-leaved forests on carbonate soil (Table 2; Figure S4a, c), but not in broad-leaved forests on acidic soil.

In contrast to the total soil N content, the C/N ratio of the topsoil reflected the vegetation-based eutrophication gradient (L, M, H) for most forest types (Figure 2g). This was especially true for both broad-leaved and coniferous forests on acidic soil. In the regression models, the soil C/N ratio was, however, not influenced by the modeled deposition (LUBW2020) or it did even increase with it in broad-leaved forests (ZW2018) (Table 3). In the NMDS ordinations of the forest type groups on acidic soil, the C/N ratio explained some of the variation (Table 2); the gradient was strongly correlated with the distribution of the eutrophication classes (Figure S4b, c). According to the regression models, a wide C/N ratio resulted in lower mean CWM N values and lower cover of nitrophytes in forests on acidic soil and a higher cover of sensitive character species in all forest type groups (Table 3). The C/N ratio itself was negatively influenced by soil N and pH in all forest type groups and also by the humus form in coniferous forests.

Relationships of the Vegetation to Other Site Factors

In the regression models, mostly other variables than N deposition influenced the dependent vegetation variables (Table 3). Besides the C/N ratio, in particular the soil pH value had an effect on the vegetation; it was positively correlated with the species richness and cover of nitrophytes in forests on acidic soil. Other important explanatory variables were the cover of the tree layer (as proxy for light availability) which had a positive effect on the CWM N value and cover of nitrophytes and a negative effect on the cover of sensitive character species in broad-leaved forests. It also had a negative effect on the overall species richness in all three forest types. In broad-leaved forests on carbonate soils, the CWM N value and the cover of nitrophytes decreased with distance to the forest edge. There was also a negative effect of this distance on species richness in forests on acidic soil (Table 3). According to the NMDS analyses, the eutrophication gradient in forests on acidic soils paralleled gradients in the (intercorrelated) CWM N and R values and the soil C/N ratio (Table 2, Figure S4b, c). However, the soil C/N ratio did not contribute to the explanation of the plot gradient in broad-leaved forests on carbonate soils; instead, the CWM F and L values were explanatory variables, in addition to the CWM N value (Figure S4a). The CWM L value had a high explanatory power especially for forests on acidic soil (Table 2) and was, as expected, highly correlated with the cover

Table 2. Explanatory Variables Used in the NMDS Ordination and Their Significance in Explaining Vegetation Gradients in the Three Different Forest Type Groups

Variable	Broad-leaved forests on carbonate soils	Broad-leaved forests on acidic soils	Coniferous forests on acidic soils
Total N deposition (ZW2018)	n.s.	n.s.	n.s.
Wet N deposition (ZW2018)	0.104°	n.s.	n.s.
Dry N deposition (ZW2018)	n.s.	n.s.	n.s.
Total N deposition (LUBW2020)	n.s.	n.s.	n.s.
Wet N deposition (LUBW2020)	n.s.	n.s.	n.s.
Dry N deposition (LUBW2020)	n.s.	n.s.	n.s.
NH_x deposition (LUBW2020)	0.165*	n.s.	0.195*
NO_y deposition (LUBW2020)	n.s.	n.s.	n.s.
NH_x/NO_y ratio (LUBW2020)	0.236**	n.s.	0.176*
Soil C/N ratio	n.s.	0.388***	0.457***
Soil nitrogen	0.494***	n.s.	0.458***
Soil pH	n.s.	0.195*	0.549***
Humus layer depth	0.390***	n.s.	n/a
Cover of the tree layer	0.269**	0.446***	0.335***
Distance to the forest edge	n.s.	n.s.	n.s.
Distance to the nearest road	n.s.	0.258**	n.s.
Distance to nearest unpaved forest track	n.s.	n.s.	0.178*
Elevation	0.385***	0.347**	n.s.
Slope inclination	n.s.	0.241**	0.265**
Precipitation	n.s.	0.184*	n.s.
Temperature	0.432***	0.373**	n.s.
Ellenberg N	0.290**	0.730***	0.793***
Ellenberg L	0.393***	0.674***	0.711***
Ellenberg R	n.s.	0.690***	0.638***
Ellenberg F	0.620***	0.425***	0.345***

Significance levels: ***$p \leq 0.001$, **$p \leq 0.01$, *$p \leq 0.05$, °$p \leq 0.1$.
n.s. not significant.

of the tree layer and the slope inclination. The intercorrelated variables elevation and temperature explained the vegetation gradients in both broad-leaved forest type groups, but not in coniferous forests on acidic soil. A small but significant part of the gradient was also explained by the distance to roads (broad-leaved forest on acidic soil) and unpaved forest tracks (coniferous forest on acidic soil; Table 2), where vegetation was less influenced by N at greater distances to roads and tracks.

DISCUSSION

Our dataset included ten different forest types ranging from bog forests to broad-leaved forests on carbonate soils. The topography, soil chemistry and climatic conditions varied across the observed forest types. For each forest type, we covered a eutrophication gradient to increase the likelihood of detecting relationships between vegetation gradients and N deposition.

Contrary to our first hypothesis, we did not find consistent correlations between species composition and the modeled atmospheric N deposition. Given that our approach, using a strategic plot selection to increase the probability of detecting significant relationships, did not reveal strong correlations, a fully randomized study would be even more unlikely to detect any results. In coniferous, but not in broad-leaved forests, a positive influence of N deposition on nitrophytes and a negative influence on N-sensitive character species were found, suggesting varying sensitivities of different forest types to N deposition. Nevertheless, the general eutrophication gradient underlying our study was neither related to the modeled atmospheric N deposition nor the measured soil N content. This gradient, covering an increasing dominance of nitrophytes and decreasing domi-

Table 3. Estimates of the Final Linear Regression Models After Variable Selection

Target variable	Ellenberg CWM N			Soil C/N ratio			Soil nitrogen		
	BLC	BLA	CA[a]	BLC	BLA	CA	BLC	BLA[b]	CA[a]
Total N Depos. (LUBW2020)	—	—	—	—	—	—	—	—	—
Total N Depos. (ZW2018)	—	—	—	0.45*	1.67***	—	—	0.15***	—
Total N Depos. (ZW2018)^2	—	—	—	—	—	—	—	—	—
Soil C/N ratio	—	−0.58***	−0.05**	—	—	—	−1.41***	−0.10**	—
Soil nitrogen	—	—	−0.03°	−1.40***	−1.52***	−2.18*	—	—	—
Soil pH	—	—	0.07***	−0.91***	−0.65*	−1.17***	0.57**	−0.05°	—
Humus layer depth	0.15*	—	—	—	0.83**	—	—	—	0.72***
Humus form: moder	−0.34*	—	—	—	—	2.18*	—	—	1.93***
Humus form: mor	—	—	—	—	—	9.13***	—	—	2.13***
Humus form: peat	—	—	—	—	—	8.30***	—	—	—
Cover of the tree layer	0.16**	0.29***	—	—	−0.59*	—	—	−0.06°	—
Distance to forest edge	−0.20*	—	−0.03°	—	—	—	—	—	—
Elevation	—	—	—	—	—	—	1.50***	0.16***	0.09°
Precipitation	—	—	−0.05*	—	—	—	−0.72*	—	−0.16**
Slope inclination	—	−0.19*	0.05*	0.52*	−0.61°	−0.91°	—	—	0.15**

Target variable	Species richness			Cover of sensitive character species			Cover of nitrophytes		
	BLC	BLA	CA	BLC	BLA	CA	BLC	BLA	CA
Total N Depos. (LUBW2020)	—	—	0.05°	—	—	—	—	−0.94*	—
Total N Depos. (ZW2018)	0.06*	—	—	—	—	n.s.	—	—	0.63*
Total N Depos. (ZW2018)^2	0.08***	—	—	—	—	−0.28*	—	—	n.s.
Soil C/N ratio	0.09**	—	—	0.60***	0.99***	0.49**	—	−1.93***	−0.52*
Soil nitrogen	—	0.08°	0.08**	n.s.	—	—	—	—	—
Soil pH	—	0.09**	0.13***	0.44*	—	−0.44***	—	—	0.62***
Humus layer depth	—	—	—	−0.52**	—	—	0.19°	−1.01*	—
Humus form: moder	—	—	—	—	—	—	—	2.00**	—
Humus form: mor	—	—	—	—	—	—	—	—	—
Humus form: peat	—	—	—	—	—	—	—	—	—
Cover of the tree layer	−0.06**	−0.05°	−0.06*	−0.34*	−0.57***	—	0.15*	0.61*	—
Distance to forest edge	—	−0.15***	−0.07*	—	—	—	−0.41*	—	—
Elevation	—	—	—	—	—	—	—	0.54°	—
Precipitation	—	−0.13**	—	n.s.	0.82**	0.79***	—	—	—
Slope inclination	—	—	—	n.s.	—	−0.40*	—	—	−0.52*

Comprehensive model results and model diagnostic plots are presented in the electronic supplementary material ESM2.
BLC = Broad-leaved forests on carbonate soils, BLA = broad-leaved forests on acidic soil, CA = coniferous forests on acidic soil.
*Significance levels: ***p ≤ 0.001, **p ≤ 0.01, *p ≤ 0.05, °p ≤ 0.01.*
n.s. = not significant (but not excluded during variable selection).
[a]Dependent variable was log-transformed.
[b]Dependent variable was sqrt-transformed.

nance of N-sensitive character species in the vegetation toward higher eutrophication classes, could rather be attributed to variations in the soil C/N ratio. Similar results were reported by Ewald and Ziche (2017) who found the C/N ratio and the base saturation of the mineral topsoil to be the variables most closely related to average Ellenberg N values. According to Seidling and Fischer (2008), the best single predictor for Ellenberg N in monitoring plots across Europe was topsoil pH, followed by base saturation, both superior to N concentration and plot-specific (measured) N deposition. Other European forest studies confirmed that N deposition was not important in explaining the observed eutrophication signal, but eutrophication was mainly related to shifts toward denser canopies and changed canopy species composition (Verheyen and others 2012) or changes in the light regime and recovery from acidification (Helm and others 2017). A close relationship between canopy cover and vegetation gradients was also found in our study. In contrast, some American studies reported effects of N deposition (Simkin and others 2016) or combined N and S deposition (Zarfos and others 2019) on soil and vegetation patterns in forests. Whereas its role in forests is still debated, N deposition is a known driver of eutrophication in grasslands (Duprè and others 2010; Stevens and others 2010) and heathlands (Bobbink and others 2010), underlining the importance of competition for light. Verheyen and others (2012) highlight the possibility of cumulative long-term effects of N deposition that may show as soon as forest canopies open up.

The close relation between eutrophication gradients in the vegetation and the C/N ratio was confirmed in many studies in Central European temperate forests (Ewald and Ziche 2017; Falkengren-Grerup and Diekmann 2003; Hofmeister and others 2002). The C/N ratio is influenced by the mineral composition of the soil parent material, the (micro)climate and the soil pH, whereby the latter is potentially influenced by N deposition but also by recovery from acidification (Andreae and others 2016; Fleck and others 2019). Furthermore, land-use legacies from historical biomass extraction potentially play a role (Glatzel 1990). The negative effect of soil pH, but also a positive effect of the humus layer depth and less decomposed humus forms in forests on acidic soil, was confirmed in our study. Other factors shaping the C/N ratio were also reflected by the occurrence of light, temperature and moisture conditions (represented by plot-wise means of Ellenberg indicator values) as explanatory variables in the NMDS ordinations. Besides these

factors, in particular the dominant tree species are decisive for the C/N ratio through the litter quality, with broad-leaved trees having easier decomposable litter than coniferous trees, leading to narrower C/N ratios (Andreae and others 2016; Fleck and others 2019). Litter quality has been shown to be a stronger driver of topsoil conditions than land-use legacies or N deposition (Verheyen and others 2012; Maes and others 2019). This provides an opportunity to influence the C/N ratio by managing the tree species composition of forests. The effect of N deposition additionally varies by the fact that it does not only influence the C/N ratio directly but also promotes the decomposition of soil organic matter which releases N but also C and other nutrients, depending on the mineralization potential of the soil. In some studies, an increase in soil C under N deposition was found, caused by a change of microbial composition and a slower C turnover (Treseder 2008; Janssens and others 2010). This might explain the positive relationship between N deposition (ZW2018) and the soil C/N ratio in the broad-leaved forests in our study which is likely also the driver behind the negative correlation between N deposition and nitrophyte cover in broad-leaved forests on acidic soils.

Different components of the total N deposition (wet vs. dry deposition, NH_x vs. NO_y) merely showed very limited specific effects on the vegetation, and thus, we reject our second hypothesis. NMDS indicated that forest vegetation in broad-leaved forests on carbonate soils and coniferous forests on acidic soil was primarily influenced by NH_x deposition, whereas NO_y deposition did not have an influence. The observation that NO_y does not play a role in forests on acidic soil matches with the well-established fact that plants preferentially take up NO_3^- under high-pH conditions and NH_4^+ under low pH conditions (Falkengren-Grerup 1995; Stevens and others 2011). Moreover, the association of plant species composition with NH_x deposition in the coniferous forests on acidic soil may be due to the circumstance that the coniferous forests are aggregated in the most precipitation-rich areas of the study region, where NO_3^- may be readily leached from the soil.

The lack of any positive relationship between mean Ellenberg N values and atmospheric N deposition contradicts our third hypothesis. It is, however, plausible, as we even did not find any consistent direct relationship between species composition and N deposition. Because the Ellenberg indicator values are expert assessments, they add another source of potential imprecision to the insecurities derived from the modeled deposition

data, thus lowering the probability of a significant relationship. Though the overall correlation of modeled atmospheric N deposition with the vegetation was weak, NMDS and regression analyses suggested that the abundance of individual species or species groups (N-sensitive character species, nitrophytes) was influenced by atmospheric N deposition. In addition to the association of some nitrophilous and N-sensitive species with high or low values of modeled N deposition, natural tree regeneration increased in abundance with increasing N deposition for several species, including *Fraxinus excelsior*, *Prunus avium* and *Acer campestre*. Evidence for increased tree regeneration due to increased N deposition from field studies is surprisingly rare in the literature. Pröll and others (2011) found that seedlings of *Fagus sylvatica* and *Acer pseudoplatanus*, but remarkably not *Fraxinus excelsior*, benefitted from high inorganic N soil contents in the Alps.

Our study succeeded in covering a wide range of different oligo-mesotrophic forest types as well as eutrophication gradients in each of these forest types. However, the forest types were naturally not equally distributed across the study region, but strongly depended on the underlying soil substrate and climatic factors. This resulted in an occurrence of some types, especially bog forests and coniferous forest on acidic soils in regions of high deposition, but also in the underrepresentation of the east of the study region where comparatively high deposition prevails but only few of the examined forest types were located. These circumstances lead to some spurious correlations (for example, negative correlations between N deposition and CWM *N* values in Figure S1) when the entire dataset was regarded. Thus, we accounted for the spatial differences by either including the forest types as random effects in our regression models or by using subsets of ecologically similar forest type groups in the NMDS ordination.

Bobbink and Hettelingh (2011) assumed the existence of nonlinear relationships between atmospheric N deposition and shifts in the vegetation composition and used this assumption for defining critical loads of atmospheric N for different vegetation types across Europe based on expert assessments. Whether such deposition thresholds were connected with the correlations found between individual species, functional types or forest types and N deposition, was not specifically investigated in our study. Finding such relationships could provide insights on processes affecting the relationship between N deposition and N surplus and would, thus, be worth further analysis.

CONCLUSIONS

In our study, no close and consistent relationships between N deposition and plant species richness or composition were detected though some relationships, for example, an increasing cover of nitrophytes in coniferous stands, were found. The failure to establish any consistent relationship was most likely not due to imprecisions of the deposition models, which had high spatial resolutions with grid cell edge lengths of 50–100 m. Instead, N deposition has to be regarded as only one subordinate driver of eutrophication and effects are concealed by effects of tree layer composition, land-use legacies and soil pH as main determinants of the soil C/N ratio which was most closely related to the eutrophication state of the vegetation. The finding of effects of N deposition in some forest types and their lack in others reflects a high context dependency which can be ascribed to differences in soil type, pH and microclimate and their influence on N mineralization and retention. Though the impact of N deposition may partly be concealed by these factors, eutrophicating effects of N deposition have widely been proved and should not be underrated. To some degree, silvicultural measures in industrial forestry may counteract eutrophication, for example by optimized stand establishment or replacement of conifers by more nutrient-demanding broad-leaved trees (Ewald and Pyttel 2016). For the preservation of most oligotrophic sites of high conservation value, targeted measures to withdraw nutrients such as raking, forest pasture or coppice may become necessary under ongoing high N deposition.

Compliance with Ethical Standards

Conflict of interest The authors declare that they have no conflict of interest.

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