Aboveground persistence of vascular plants in relationship to the levels of airborne nutrient deposition

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Abstract This paper examines whether high atmospheric nitrogen deposition affects aboveground persistence of vascular plants. We combined information on local aboveground persistence of vascular plants in 245 permanent plots in the Netherlands with estimated level of nitrogen deposition at the time of recording. Aboveground persistence of vascular plants was studied using two types of survival statistic technique: Kaplan–Meier analysis and Cox' regression. We expected a link between nitrogen deposition and loss of plant species due to intensified herbivory or other forms of tissue loss that would lead to diminishing local aboveground persistence. This could not be detected. In contrast, a positive relation was found between local aboveground persistence of plants and high levels of ammonia deposition. This result is considered to be an indication of lower colonization access, for example due to limited space (e.g. the chance of successful establishment of individuals from new species is lower). The results are discussed in relation to the extremely high levels of nitrogen deposition in the studied plots. This study provides an indication that management practices aiming for restoration of colonization access (e.g. mowing, grazing and sod cutting) are vital under heavily eutrophied conditions.

Keywords Vegetation change · Competition · Eutrophication · Ammonia · Nitrogen oxides · Herbivores · Soil type · Management practice

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Introduction

Changes in the Dutch flora in the second half of the 20th century have been shown to primarily relate to changes in nutrient availability (Tamis et al. 2005, in a study without consideration of the overarching effects of habitat loss due to land use changes). Also for the UK relationships between increased atmospheric nitrogen (N) deposition and plant species loss (Maskell et al. 2009; McClean et al. 2011) and species number (Stevens et al. 2004) have been established.

Nutrient enrichment may affect plant species through direct toxic effects, changes in their abilities to compete for light and changes in their susceptibility to secondary stress and disturbance (Bobbink et al. 2011). Such changes become visible in the vegetation in two ways: the loss of species and a change in vegetation structure, biomass and density.

Ozinga et al. (2007) analysed a dataset of 845 long-term permanent plots in terrestrial habitats across the Netherlands (Taken from the Dutch National Vegetation Database; Schaminée et al. 2012) and examined which plant traits and habitat preferences best explain local aboveground persistence of the vascular plant species. They define local aboveground presence as the appearance of aboveground parts from year t to year t + 1. Ozinga et al. (2007) found the local

aboveground persistence of plant species to be decreasing with increasing nutrient requirements of the species involved (see Fig. 1). They hypothesized this may be explained by two processes that are not mutually exclusive but which both may be a consequence of higher resource availability due to increased atmospheric nitrogen deposition:

(1) The trade-off hypothesis (Ozinga et al. 2007): a fundamental trade-off between attributes enabling high rates of resource acquisition in productive habitats (high plant growth rates/short lifetime/low persistence) and attributes enabling efficient retention of resources (long lifetime/ high persistence) in unproductive habitats.

(2) The access hypothesis (Ozinga et al. 2007): species with their highest performance in nutrient-poor conditions experience a lower suitability for colonization in enriched areas and are, therefore, declining, thereby selecting for longer aboveground persistence of the resident species (with a preference for nutrient-rich conditions).

In line with the trade-off hypothesis, the efficient retention of resources by plant species of naturally nutrient-poor habitats may be affected by higher

Fig. 1 Trade-off hypothesis. Adapted from Ozinga et al. 2007. Productivity is defined by the Ellenberg indicator values of the species (Nutrient level at which the species has its highest frequency of occurrence; Ellenberg et al. 1991): Low = Ellenberg values 1–4, Intermediate = Ellenberg values 5–6, High = Ellenberg values 7–9. The *red lines* indicate the hypothetical lower local aboveground persistence through elevated nutrient deposition. *N* = number of species
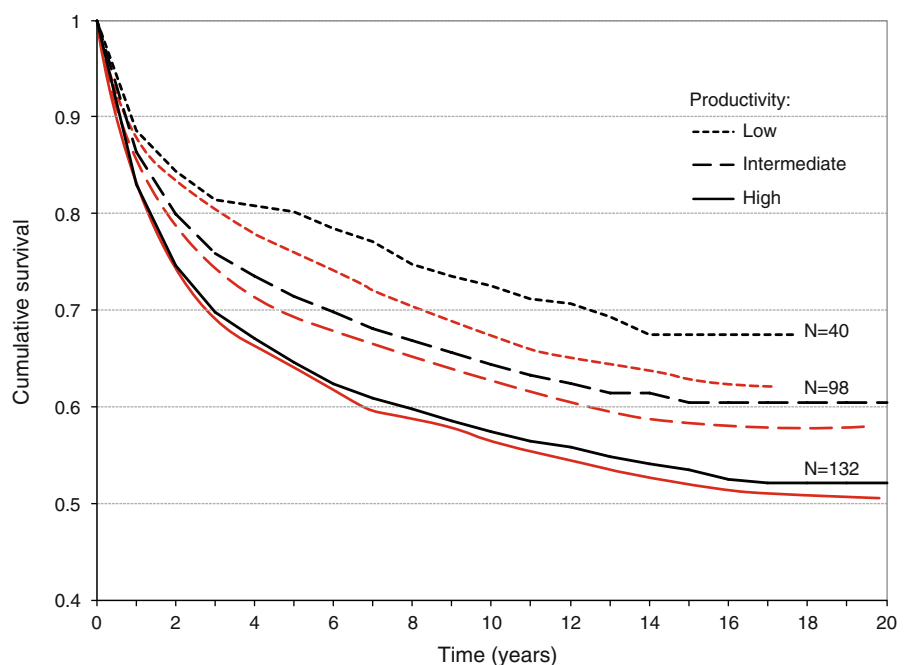
Fig. 2 Access hypothesis Adapted from Ozinga et al. 2007. The *red-dotted line* indicates the expected higher local aboveground persistence under conditions of unnaturally high Nitrogen deposition. Note that the total number of species will be lower then ($N =$ total number of species)
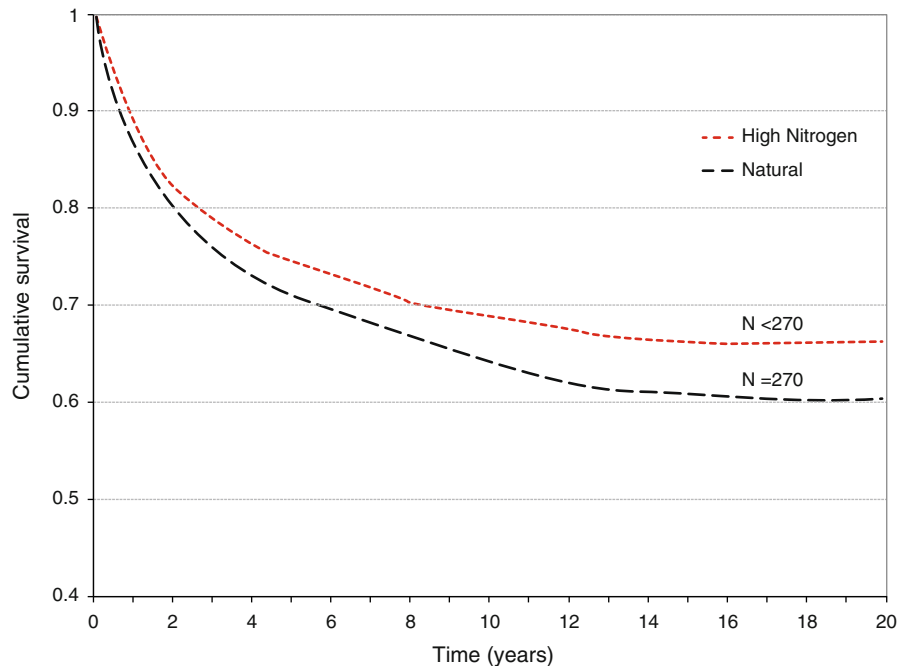
resource availability as a result of higher N deposition rates. Such higher resource availability may cause higher levels of tissue loss due to herbivory (cf. the context dependent defence hypothesis; Hendriks et al. 1999, 2009) or to susceptibility to secondary stress other than herbivory, e.g. frost or drought. This would lead to lower aboveground persistence (Fig. 1; all red lines). This effect is expected to be smaller for species from naturally nutrient-rich environments (Fig. 1; continuous red line) compared to species from naturally nutrient-poor environments (Fig. 1; dotted red line).

In contrast, the access hypothesis predicts that N enrichment leads to a lower suitability for colonization for species from nutrient-poor habitats. Due to limited (re)colonization success, species from nutrient-poor habitats will gradually decline (for example due to genetic erosion or stochastic processes). This decline from the total species pool will result in relative higher persistence of species from nutrient-rich habitats. The cumulative survival curve, therefore, will be higher, but it reflects a lower number of species (Fig. 2; dotted line).

In summary, in this paper we explore the possible effects of nutrient availability on local aboveground persistence through spatial differences in airborne nutrient deposition. For this we re-examined the data

that are used by Ozinga et al. (2007), while additionally dividing the permanent plots into subsets of different levels of N deposition.

The main research question of this paper is to evaluate the two hypotheses mentioned above. We expect that high levels of N deposition will have a negative effect on the local aboveground persistence of species in the case of the trade-off hypothesis, while it will have a positive effect in case of the access hypothesis. The subsets of permanent plots (based on different levels of N deposition) where chosen in such a way that the critical loads of N deposition (Bobbink et al. 2011) for the vegetation types in our study were taken into account. The lowest class is a conservative approach to the critical loads range for the vegetation types used in our study, thus also allowing for additional evaluation of the hypotheses in relation to those critical loads.

Methods

Analysis of local aboveground persistence with permanent plot data

Permanent plots can provide important information about the temporal dynamics of plant communities

since they allow for quantification of year to year local persistence of aboveground presence of the different plant species of a community. The permanent plot data we used, however, do not always include the full period of residence for all species. In many cases, we have both complete data of a given species for which we know the exact period of local aboveground persistence (since the moment of aboveground appearance or disappearance is recorded) and incomplete data for which the period of aboveground persistence is at least the observed period, but may be longer. For such incomplete data, a simple regression analysis is inaccurate and may lead to wrong conclusions (e.g. Bressers et al. 1991; Zens & Peart 2003). Therefore, we used statistical techniques ('survival statistics') that account for censored data: Kaplan–Meier analysis and Cox' regression. Two different techniques have been used since Cox' regression allows for testing the relative effect or multiple variables, whereas Kaplan–Meier analysis is better suited to compare groups of plots with different levels of a single variable (see further below, in the section on survival statistics).

We selected plots with a minimal observation period of 5 years from a large survey of permanent plot data in the Netherlands (1933–1999; see Smits et al. 2002 for further details). In all analyses, we excluded species that occurred in less than ten permanent plots and species that are frequently planted (i.e. many tree and shrub species), leaving a total of 523 species. In order to get a more homogeneous dataset regarding environmental conditions and soil conditions, we also excluded aquatic and forested plots and plots on peat soils, leaving a total of 245 mainly dry and moist (in some cases wet) grassland and other low vegetation plots.

Nitrogen deposition

The 245 plots in the analyses represent different sequences of yearly recordings ranging from minimal five sequential years to 25 sequential years spread over the period 1933–1999. For each of the permanent plots, the estimated level of N deposition at the time of recording (estimated deposition in the year that represents the middle of the sequence of recording years of that plot) was derived from the data produced by the Netherlands Environmental Assessment Agency.

Earlier studies have shown clear differences regarding the ecological relevance of the two forms of N deposition: ammonia (NH_y) and nitrogen oxide (NO_x; van den Berg et al. 2008; McClean et al. 2011). Therefore, in the analyses, we used the total N deposition (N-total), NH_y and the ratio of the two forms (NH_y/NO_x). In addition to NH_y, the ratio (NH_y/NO_x) rather than NO_x separately was applied, because the two forms are significantly correlated. Since N-total and NH_y are also correlated, these factors were only included jointly in the first explorative step. Due to the possibility to incorporate historical spatial variation for NH_y deposition rather than N or NO_x deposition, NH_y deposition was used in the final analyses (see below).

The distribution of N deposition in the Netherlands has been highly variable in space and time. Data on NO_x and NH_y were generated using N deposition data from 2009 (www.rivm.nl). These data are based upon large-scale emission-data maps, data on additional local emission contributions and data on local concentration measurements (Velders et al. 2010). NO_x deposition estimates for the years 1950–2009 for each 1×1 km grid cell of the map were calculated using a function describing the general emission and deposition trends within the Netherlands over the last one hundred years (Noordijk 2007). A single function was used since we assumed the spatial distribution of the major emission locations (cities and infrastructure) to be generally constant over the time period covered.

For NH_y, estimates for the depositions for the years in the period 1950–2009 for each 1×1 km grid cell were calculated using specific emission–deposition functions for each of the 12 provinces of the Netherlands. These functions were derived from atmospheric transport and deposition relationships in and between provinces and with neighbouring countries in terms of the proportional origins of the depositions (Velders et al. 2010). The emissions are calculated from the amounts of livestock per province, based on numbers of cows, horses, pigs, sheep and poultry over time. Data were taken from Statline (CBS 2012) and historical reports (Noordijk & van der Hoek in prep.). Separate data are collected for different types of cows, horses, pigs, sheep and poultry per province. The emission per province was derived using the same methodology as the general emission and deposition trends within the Netherlands over the last one hundred years. This results in an average deposition value over time for each province. The deposition value for a specific grid cell is casted back in time,

using the time dependent average depositions for the provinces. With respect to the latter, distances and geographical positions relative to the general wind directions determined which provincial times series were selected for the backcasting.

Furthermore, for the purpose of the permanent plot-based persistence analyses, a correction of NH_y deposition levels within the first 1,500 m from the shoreline was applied. Data from local concentration measurements (Stolk et al. 2009) were used to add a location specific increase in NH_y deposition due to inland transportation of NH_y from the surf. This was done in steps: <100, 100–300, 300–700, 700–1,500. Permanent plots closest to the sea were thus corrected with the highest amounts. Two different correction schemes were applied: one for the permanent plots in the Voorne area and near Ouddorp (based on local concentration measurements at Voorne: 2, 1, 0.7, 0.5 kg/m^2 for the above mentioned inland zones) and one in the Meijendel area (based on local concentration measurements in that same area: 2, 1.5, 0.6 and 0.5 kg/m^2, respectively). For plots at >1,500 m from the coast line, no additional NH_y was calculated. Based on the historic development of the eutrophication of the North Sea, this correction was modified for the year of recording of the permanent plots. The above mentioned correction was applied to all plots recorded after 1980. No correction was applied to plots recorded before 1950. Linear interpolation was applied for determining the additional amount of NH_y in the coastal 1,500 m zone between 1950 and 1980. In total, 61 plots were corrected. Two of these were only recorded after 1980, the rest at least partially between 1950 and 1980. One plot in our dataset was recorded before 1950, however, this one was not within 1,500 m from the coast line.

Survival statistics

Cox' regression, also known as Cox's proportional hazards model (with hazard rate being the inverse of persistence), in contrast to Kaplan–Meier analysis allows for testing the relative effect or multiple variables. Both the Kaplan–Meier procedure and Cox regression are based on estimating 'conditional' probabilities at each time interval and taking the product limit of those probabilities to estimate the survival rate (in our case: aboveground persistence) at each point in time and thus to obtain survival curves.

For comparisons of survival curves between groups of plots (grouped according to the estimated levels of deposition or abiotic conditions, see below), the log-rank test within the Kaplan–Meier procedure was used. Pairwise comparisons (Mantel Cox) were performed to explore significance of differences between the survival curves.

All analyses were done in SPSS version 19. For further details on these techniques, we refer to Ozinga et al. (2007). The Kaplan–Meier procedure is only suitable for analyses with just one covariate with a limited number of levels. Therefore, the data on N-total, NH_y and the NH_y/NO_x ratio were divided into three classes (in kg N ha^{-1} y^{-1}) for this procedure (Supporting material, Table S1), the lowest class is a conservative approach to the critical loads range for the vegetation types used in our study. In Cox' regression, the same classes were used. Additionally, in Cox' regression an alternative variant of the three-class division and a two-class division were also applied to explore the sensitivity of the analyses for the definition off the classes (Supporting material, Table S1).

Possible confounding factors

Since the permanent plots were not evenly distributed across the Netherlands (Supporting material, Fig. S2), there may be confounding factors at play which have a spatial correlation with N deposition.

One such possible factor is the occurrence of specific management interventions or disturbance events at the permanent plot locations. Therefore, we included in the analysis the occurrence of an abrupt (from one year to the next) change of vegetation type in a permanent plot (yes versus no). The occurrence of abrupt vegetation type changes is defined as the occurrence of multiple vegetation types within the sequence of PQ multi annual recordings of each plot as it is documented in the Dutch National Vegetation Database. The association type denominations in that database were established with the software tool 'Associa' (van Tongeren et al. 2008).

A second issue is the occurrence of spatially unevenly distributed species pools related to differences in abiotic conditions. For this reason, we included soil type in the analysis (based on the 1:50,000 soil types map of the Netherlands from 2006). We analysed sandy soils versus clay soils since

this is the most relevant contrast for the permanent plots in this study. The possible differences in effects of N deposition within these two soil type subsets, however, may also be related to differences in species pool at an even finer spatial scale. Therefore, we alternatively also performed the analyses for subsets of plots within different physical geographical regions of the Netherlands: 'Dunes' and 'Sandy area' which mainly have sandy soils; 'Riverine area,' 'Sea clay area' and 'Hill Country' which mainly have clay soils (Supporting material, Fig. S2, Fig. S3 and Table S4).

Thirdly, since spatial clusters of permanent plots are also clustered in time, the year that represents the middle of the sequence of recording years of each plot was also included into the analyses as a covariate.

Analyses

In a first step, we performed a Cox' regression with the N factors (in the three different class divisions) as well as the possible confounding factors added to an empty model. To evaluate the trade-off hypothesis, the interaction of N-total and of NH_y with the nutrient requirements of the species (based on Ellenberg indicator values; Ellenberg et al. 1991) was included in this Cox' regression. Furthermore in this first step, the factor physical geographical region was included and not soil type.

Secondly, a Kaplan–Meier analysis and a second Cox' regression with physical geographical regions, as strata, were performed.

Finally, another Kaplan–Meier and Cox' regression were performed with the soil types used as strata. In order to exclude the possible confounding effect of differences in local species pools related to the effect of different physical geographical regions, we also included plant species as a categorical variable in this third Cox' regression. Also our main factor of interest, N deposition, was included. As explained above, N-total, NH_y and NO_x are correlated. Therefore, we included NH_y and the NH_y/NO_x ratio. The choice for NH_y (and not N-total) was based on the larger strength of NH_y in the empty Cox' regression model (Table 1).

Results

The first, empty model, Cox' regression revealed the factors that significantly affect the aboveground persistence of the plants (Table 1). It also confirmed the validity of the choice for the 'A' variant of the three classes division (Supporting material, Table S1) to be used in further analyses. Total N deposition, NH_y and the NH_y/NO_x ratio are all significant, both when divided into three classes as well as when analysed continuously. Interestingly also the average year of recording of the permanent plots (ranging from 1939 to 1997), the occurrence of abrupt vegetation changes, the Ellenberg indicator values for nutrient availability (divided in three classes cf. Fig. 1) and three of the physical geographical regions (dunes, sandy area and riverine area) do have a significant effect upon plant species persistence. The interaction of N-total and of NH_y with the nutrient requirements of the species (based on Ellenberg values) was included in the Cox' regression. Neither of these did prove to be significant (data not shown).

Since the physical geographical regions were among the significant factors, we further explored this with a Kaplan–Meier analysis and a second stratified Cox' regression. Pairwise comparisons (Mantel Cox) indeed show significant differences between the survival curves for different physical geographical regions (Supporting material, Fig. S3) and in the Cox' regression significant interactions with these regions occurred (Supporting material, Table S4).

Figure 3 shows the results of the Kaplan–Meier analysis with NH_y classified into three categories. Pairwise comparisons (Mantel Cox) show significant differences between all of the three survival curves ($P < 0.001$).

In figure 4 the survival curves as inferred from the Cox' regression model (taking into account species as a covariate) are displayed. Aboveground persistence is significantly higher in plots on sandy soils compared to clay soils ($P < 0.001$). The patterns within the two soil type strata are similar, for both NH_y (Fig. 4a/c) and for NH_y/NO_x ratio (Fig. 4b/d).

The effect of the factor species is much stronger compared to the effect of N (Table 2). If the species effect is taken into account, the differences between the three NH_y classes, however, remain significant ($P < 0.009$, Table 2). In comparison to a model without the species effect (results not shown), the order stays the same. Most interestingly, the high NH_y class is showing the highest survival rate and the low NH_y class the lowest.

Table 1 Results of Cox' regression when adding the different factors to an 'empty model'. Higher scores explain larger proportions of the variance in the model

	Score	df	Sig.
PGR (all classes)	376.423	5	.000
NHy/NOx ratio (all 3 classes variant A)	369.317	2	.000
NHy/NOx ratio (all 3 classes variant B)	349.996	2	.000
PGR: sandy area	331.136	1	.000
NHy (all 3 classes variant A)	323.072	2	.000
NHy/NOx ratio (high class variant A and B)	303.650	1	.000
NHy (high class variant A)	295.236	1	.000
NHy/NOx ratio (intermediate class variant A)	288.917	1	.000
NHy (all 3 classes variant B)	273.714	2	.000
NHy (intermediate class variant A)	250.586	1	.000
NHy (high class variant B)	248.294	1	.000
NHy/NOx ratio (intermediate class variant B)	248.001	1	.000
N-total (all 3 classes variant B)	234.880	2	.000
PGR: Riverine area	234.300	1	.000
N-total (all 3 classes variant A)	221.582	2	.000
N-total (high class variant A and B)	205.447	1	.000
N-total (intermediate class variant B)	157.440	1	.000
N-total (intermediate class variant A)	154.565	1	.000
NHy (intermediate class variant B)	151.971	1	.000
Vegetation shock	137.069	1	.000
NHy (no classes)	88.420	1	.000
Ellenberg N values (all classes)	78.603	2	.000
N-total (no classes)	63.476	1	.000
NHy/NOx ratio (no classes)	55.437	1	.000
Average year	40.502	1	.000
Ellenberg N high class (Fig. 1)	21.357	1	.000
Ellenberg N intermediate class (Fig. 1)	20.614	1	.000
PGR: Dunes	7.129	1	.008
NHy/NOx ratio (2 classes)	6.259	1	ns
N-total (2 classes)	5.006	1	.025
NHy (2 classes)	5.006	1	.025
PGR: Hill country	2.328	1	ns
PGR: Sea clay area	.899	1	ns

Average year average year in which a series of a permanent plot was recorded, *Vegetation shock* the occurrence of an abrupt (from one year to the next) change of vegetation type in a permanent plot (yes or no); *PGR* physical geographical regions. For the different classes see Supporting material, Table S1
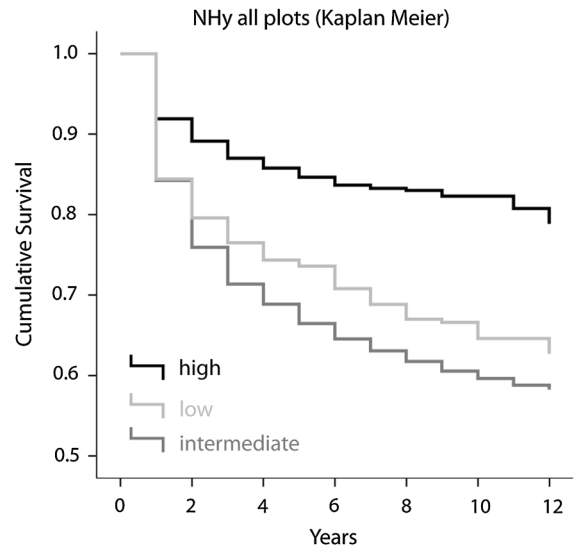
Fig. 3 Aboveground local persistence illustrated with survival curves based on Kaplan–Meier analyses. Analysis with 523 species, 245 plots and 3,842 observed survival times (periods of local aboveground persistence) and 8,932 censored survival times. The *y-axis* gives the cumulative percentage of plots in which the species persists at a given time. All three curves are significantly different ($P < 0.001$). The classifications are all according to the 'A' variant (supporting material, Table S1)

For the NH_y/NO_x ratio, a difference between the highest ratio class and the other two classes is revealed. This difference is significant ($P < 0.027$), whereas the difference between the low and intermediate class is not.

When we compare the result of the Cox' regressions for NH_y (Fig. 4a/c) with the Kaplan–Meier analysis for NH_y (Fig. 3), the low and intermediate classes switch order.

Discussion

Nitrogen deposition was calculated using spatial variation in historical emission trends for counties in which the permanent quadrats lay. Potentially, this introduces increased variance in the estimation of the nitrogen deposition. However, when only national historic trends would have been used, the deviation from the actual historical deposition rates will be substantially higher since large spatial variation exists.

Fig. 4 Aboveground local persistence illustrated with survival curves based on Cox' regression. Analysis with 523 species, 245 plots and 3,842 observed survival times (periods of local aboveground persistence) and 8,932 censored survival times. The *y-axis* gives the cumulative percentage of plots in which the species persists at a given time. Survival curves for sand ($n = 96$) and clay ($n = 149$) as strata and with plant species included in the model. In 4a/c, species are classified in three NHy classes and in 4b/d three NHy/NOx ratio classes. The classifications are all according to the 'A' variant (supporting material, Table S1)
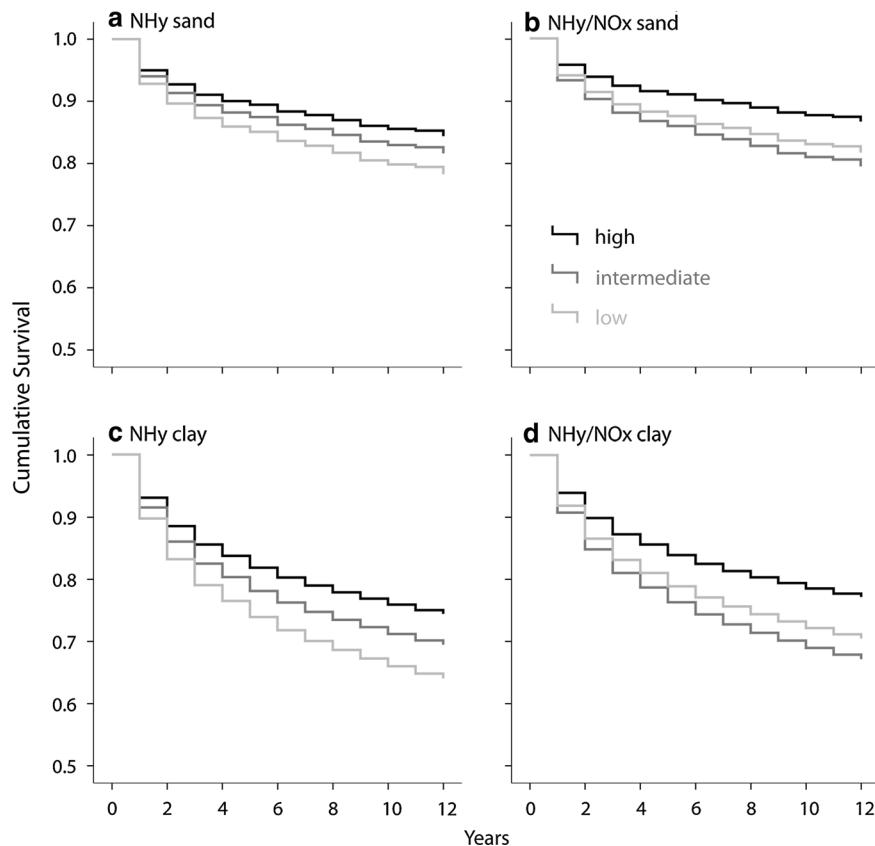
The trade-off hypothesis predicts the effect of atmospheric N deposition to be different for plant species from different natural environments (see Fig. 1). The lack of an interaction between N deposition and the nutrient requirement of the plants suggest that the communities are not assembled based on the trade-off hypothesis. In addition, the trade-off hypothesis predicts the local aboveground persistence of plant species to be lower in case of higher levels of N deposition. Our results indicate that the opposite was true and we can, therefore, not confirm the trade-off hypothesis. The highest N-total or NH_y deposition category consequently also showed the highest local aboveground persistence of the plant species, both with and without the species pool effect taken into account and independent of the soil type. This is in line with the 'Access hypothesis' as formulated in the introduction: elevated nutrient availability might leave less space for colonization by new individuals, i.e. lower colonization access. On the landscape scale this may lead in the longer term to declines of species with

relatively low dispersal abilities (see Ozinga et al. 2009).

The aboveground persistence being significantly higher in plots on sandy soils compared to clay soils is in line with the predictions of the trade-off hypothesis in the sense that efficient retention of resources through long lifetime/high persistence is favourable in the more nutrient-poor sandy soils. This, however, in itself is not sufficient to confirm the hypothesis.

The fact that NH_y/NO_x ratio is also having an effect indicates that not only the level of N deposition matters, but also its form as was shown in an earlier study by van den Berg et al. (2008). It is possible that NH_y is more relevant to aboveground persistence of plants than NO_x since many of the persistent species are species that are known to prefer NH_y (e.g. Falkengren-Grerup 1995). However, we cannot exclude the possibility that this result is due to the stronger gradient of NH_y (ranging from 4 to 39 kg N ha^{-1}yr^{-1}) in our dataset compared to NO_x (ranging from 2 to 9 kg N ha^{-1}yr^{-1}).

Table 2 Results of Cox' regression for hazard rate (inverse of persistence), with soil type as strata

Variable	β	SE	Wald χ^2	df	Sign.
Plant species	–	–	1940.806	521	.000
NH_y (all 3 classes)	–	–	9.416	2	.009
NH_y (intermediate class)	−.200	.092	4.717	1	.030
NH_y (high class)	−.411	.134	9.407	1	.002
NH_y/NO_x ratio (all 3 classes)	–	–	17.224	2	.000
NH_y/NO_x ratio (high class)	−.332	.150	4.897	1	.027

Based on 523 species, 245 plots and 3,842 observed survival times (periods of local aboveground persistence) and 8,932 censored survival times. For the significant variables that were included in the multivariate model (NH_y, NH_y/NO_x, plant species) the following parameters are given: regression coefficient (β; *negative values* indicate that the variable reduces the hazard rate and thus increases the local aboveground persistence, while *positive values* imply a trade-off), standard error (SE), the Wald test statistics (indication of the relative importance of the effect), and the significance of the regression coefficients β_i. Beta en SE are only relevant for classes within the variables

The fact that the results in this study are pointing in the direction of high nutrient availability leading to lower colonization access rather than loss of species due to intensified herbivory or increased competition for light and space, may very well be related to the severity of eutrophication problems in the Netherlands. Both the intermediate and the high categories of N deposition (total N deposition, supporting material, Table S1) are well above the critical loads of N deposition for most vegetation types (Bobbink et al. 2011 indicate an upper limit of 20 kg N ha^{-1} yr^{-1} for the majority of types). Furthermore, this excessive N deposition in the Netherlands already started in the sixties and peaked in the eighties and since then is very slowly declining (Noordijk 2007). Our dataset also covers a similarly long time span. The significant positive effect of the average recording year (ranging from 1939 to 1997) upon plant persistence (Table 1) probably is the result of this historical correlation. The indication that the critical loads are exceeded, however, does not mean that the exact upper limits of the critical loads ranges can be evaluated with the approach we used. A more refined division into nitrogen deposition-based subsets of the plots, a different statistical method and additional empirical critical loads information for the specific vegetation types in our study would be needed for that.

Another indication of the validity of the access hypothesis is provided by the fact that the occurrence of abrupt (from one year to the next) changes of vegetation type in the permanent plots also showed a significant effect (Table 1) upon plant species persistence. Such abrupt vegetation type changes are likely caused by disturbance events with a positive effect on vegetation accessibility such as accidental fire and management such as sod cutting.

The 'fixation' of vegetation dynamics due to the lower accessibility to newcomers poses an extra threat to species diversity since it may lead to further additional extinction of species due to population dynamic and population genetic effects (Booy et al. 2000). At the same time the results presented here support the notion that management practices aiming for restoration of colonization access (e.g. mowing, grazing and sod cutting) are vital under heavily eutrophied conditions such as in the Netherlands.

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