



## A novel method to estimate the response of habitat types to nitrogen deposition<sup>☆</sup>

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### ABSTRACT

Increasing nitrogen depositions adversely affect European landscapes, including habitats within the Natura2000 network. Critical loads for nitrogen deposition have been established to quantify the loss of habitat quality. When the nitrogen deposition rises above a habitat-specific critical load, the quality of the focal habitat is expected to be negatively influenced. Here, we investigate how the quality of habitat types is affected beyond the critical load. We calculated response curves for 60 terrestrial habitat types in the Netherlands to the estimated nitrogen deposition (EMEP-data). The curves for habitat types are based on the occurrence of their characteristic plant species in North-Western Europe (plot data from the European Vegetation Archive). The estimated response curves were corrected for soil type, mean annual temperature and annual precipitation. Evaluation was carried out by expert judgement, and by comparison with gradient deposition field studies. For 39 habitats the response to nitrogen deposition was judged to be reliable by five experts, while out of the 41 habitat types for which field studies were available, 25 showed a good agreement. Some of the curves showed a steep decline in quality and some a more gradual decline with increasing nitrogen deposition. We compared the response curves with both the empirical and modelled critical loads. For 41 curves, we found a decline already starting below the critical load.

### 1. Introduction

Vegetation changes through atmospheric nitrogen deposition, mainly induced by anthropogenic activities (fossil fuel combustions, agriculture, industrial emissions etc.) is a widespread phenomenon (Stevens et al., 2020). Generally, nitrogen deposition leads to increased

biomass production and a loss of species (Stevens et al., 2010; Etzold et al., 2020; Berendse et al., 2021). Following land use change and climate change, nitrogen deposition is one of the most important threats to terrestrial biodiversity worldwide and negative effects on species presence occur through all major ecosystem types (Sala et al., 2000). A case study for the United Kingdom estimated a species loss of around

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30% due to nitrogen deposition over a range of ecosystems (Payne et al., 2017; Schmitz et al., 2019; Staude et al., 2020). Apart from the direct effect of nitrogen on plant growth and chemical composition of the soil, important secondary effects on higher trophic levels are also likely to occur (Stevens et al., 2018).

A widely used concept to quantify the ecological effects of nitrogen deposition is the critical load (CL). According to the original definition by Nilsson & Grennfelt (1988), a critical load is 'a quantitative estimate of an exposure to one or more pollutants below which significant harmful effects on specified sensitive elements of the environment do not occur according to present knowledge'. In Europe, many studies have been conducted to assess critical loads for a wide range of ecosystems (Van Dobben et al., 2006, Payne et al., 2013; De Vries et al., 2015; Bobbink et al., 2022; Wamelink et al., 2023). The estimated critical loads play an important role in pollution control policy (De Vries et al., 2015). In general, there are two ways to determine critical load values: by simulation, by the SMB model (simple mass balance model, Van der Salm et al., 1993) or using coupled soil-vegetation models (e.g. Van Dobben et al., 2006), or empirically, either by observations in comparable ecosystems at different deposition levels (e.g. Stevens et al., 2010) or through nitrogen addition experiments (e.g. Britton & Fisher, 2007). For the Netherlands, an attempt has been made to integrate these different approaches to a single critical load value per habitat type (Van Dobben et al., 2014; Wamelink et al., 2023). Reported critical loads are primarily in the order of 10–20 kg N ha<sup>-1</sup> yr<sup>-1</sup> for terrestrial ecosystems (Bobbink & Hettelingh, 2011; Bobbink et al., 2022; Van Dobben et al., 2014; Wamelink et al., 2023), although these values may be overestimated (Payne et al., 2013).

From 1984 onward, inorganic nitrogen deposition increased worldwide, except for Europe, where it decreased after 1980 (Ackerman et al., 2019). In the Netherlands, however, the decrease virtually reached a standstill after 2005 (Berendse et al., 2021, CBS and RIVM, 2019), with levels of around 25 kg N ha<sup>-1</sup> yr<sup>-1</sup>. This is well above the above-mentioned critical load range (10–20 kg N ha<sup>-1</sup> yr<sup>-1</sup>). Consequently, widespread negative effects of nitrogen deposition may be expected in the Netherlands (Bobbink et al., 1998; Krepa, 2003). In the EU, the 'habitats Directive' (Council of the European Communities, 1992) requests an increase, or at least a standstill of biodiversity in the 'Natura 2000 network' (Evans, 2012). The National Emissions Ceilings (NEC) Directive (2016/2284/EU) asks for a maximum of nitrogen deposition, which is exceeded on a wide scale in the Netherlands. Therefore, efforts are undertaken to reduce nitrogen emissions in the Netherlands (e.g., Van den Burg et al., 2021; Zara et al., 2021). To assess the effects of nitrogen deposition rate reduction on biodiversity and enable a cost-benefit analysis, there is a strong demand for dose-response relations, even above the critical load. The critical load itself cannot be used for this since it is a single value ('no effect level'). Moreover, it is unlikely that the critical load is a 'tipping point' where exceedance suddenly drives the system into a new state (Van Nes et al., 2016).

The present study aims to derive quantitative relations between nitrogen deposition and habitat quality for the terrestrial habitat types that underlie the Natura 2000 concept (Council of the European Communities, 1992). Here, habitat quality is defined as the expected presence of 'characteristic' species of the habitat type, as a function of nitrogen deposition, considering the rarity of each characteristic species. The latter requires calculated species response curves which we estimated employing the European Vegetation Archive' (EVA) database (Chytrý et al., 2016). They are combined with local estimates of nitrogen deposition resulting from the European Monitoring and Evaluation Programme model (EMEP, Simpson et al., 2012; 2014), with temperature precipitation and soil type as covariates. The characteristic species for each habitat type are based on its definition in the habitats Directive and underlying phytosociological data. The dose variable is the summed deposition of wet and dry and reduced and oxidised nitrogen, averaged for five years. Most of our dose-response curves enclose the critical load, i.e., a response is estimated both below and above the critical load.

Finally, we conducted a plausibility check of the estimated response curves using expert knowledge and field data.

## 2. Methods

### 2.1. Outline of the method

In a first step response curves for plant species for nitrogen deposition were estimated. In a second step response curves for habitat types for nitrogen deposition were estimated based on the normalized response curves of characteristic species per habitat type. Normalization ensures that rare species, with low occurrence probabilities, have a similar weight as more common species. Individual species response curves were estimated employing (1) plot-based presence-absence data extracted from vegetation plots from the European Vegetation Archive (EVA, Chytrý et al., 2016; see Appendix 1) and (2) the nitrogen deposition at the location of the vegetation plots as estimated by the EMEP model (Simpson et al., 2012, 2014). The response curve was corrected for soil type, precipitation and average annual temperature. The resulting response curves for nitrogen deposition for habitat types were evaluated in three different ways: by expert judgement, by comparison with empirical data (statistically and expert judgement) and by comparison with literature.

### 2.2. Characteristic species per habitat type

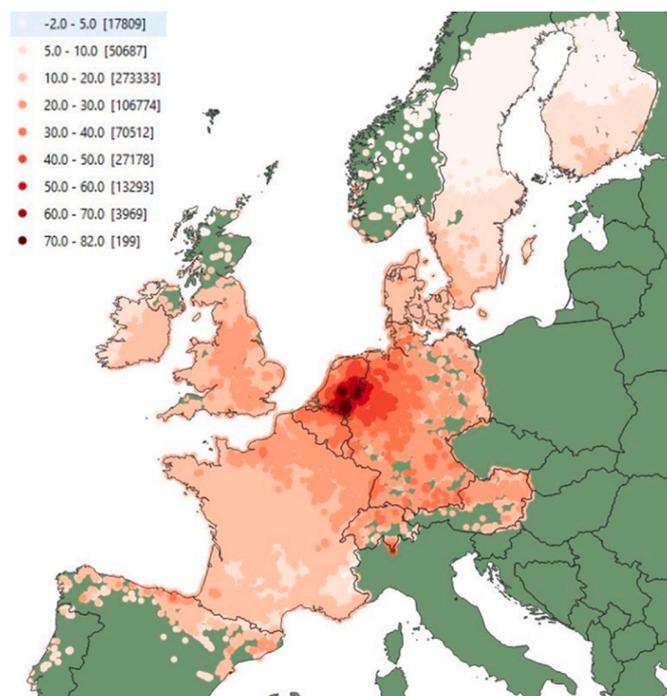
We set up list of characteristic species for each habitat type specific to the Netherlands. The starting point for each habitat type was the list of typical species given by Bal (2007). We supplemented this list by employing the set of plant associations which is linked to each habitat type in the Netherlands (Schaminée et al., 1995; Epe et al., 2009). Each plant association is defined by a large set of Dutch vegetation plots typical for the association which were had picked and reviewed by experts. A species is called characteristic for a plant association, and thus for the associated habitat type, when the frequency and/or mean cover of the species in the defining set of vegetation plots is large enough (see Appendix 2). The resulting list for each habitat type was reviewed by experts.

### 2.3. Selection of plots for each species response curve

A species response curve for nitrogen relates the probability of occurrence of a given target species to a gradient of nitrogen deposition. A response curve can be obtained by fitting a statistical model to presence/absence data of the focal species in a set of plots. We selected plots from the EVA database (Chytrý et al., 2016) within Europe's greater Atlantic region, defined as parts of Spain and Portugal, France, Germany, Belgium, Luxembourg, the Netherlands, the United Kingdom, Ireland, Denmark, and Norway, Sweden and Finland south of the arctic circle (Fig. 1). This set was further limited by selecting plots at altitudes below 500 m a.s.l.

Preferably, only plots within the distribution area of a species should be employed to estimate the response curve. For example, for species with a southern distribution in Europe (e.g., the Iberian Peninsula), plots in the Scandinavian countries should be excluded. To avoid an overload of absence records that would otherwise decrease the species prevalence. Unfortunately, atlas data are not available for all vascular plant species and the native range of most plant species is not exactly known. Therefore, the potential distribution area of a given plant species was defined by the intersection of all occurrence records augmented with circles of a radius of 25 km around the occurrence coordinates (Fig. 2). Only absence records from plots within this distribution area were used to fit the species response curve.

A given species may have a different nitrogen response when it grows in different habitat types, due to, e.g., different competing species or different combinations of other abiotic conditions. For instance, the



**Fig. 1.** Modelled average nitrogen deposition (kg/ha/yr, modified EMEP data; Simpson et al., 2012, 2014) for vegetation plots over the period 1945–2017 after correction for vegetation roughness. Points next to each other may originate from different years. If more than one plot was available per coordinate, then the highest deposition is shown (no plots were omitted from the calculations though). The numbers between brackets in the legend give the number of total plots per deposition class. Green colours indicate either that no plots are available (within the Atlantic region) or that the sites lay outside the Atlantic region. Plots above 500 m altitude within the selected region were omitted. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

response of *Calluna vulgaris* in woodlands may be different from its response in more open habitats like heathlands. Ideally, a species response curve along a gradient of nitrogen deposition should be estimated per habitat type. However, plots have not yet been assigned to habitat types on a European scale. As an alternative, plots were assigned to 11 so-called European Nature Information System (EUNIS) types following the rules of Chytrý et al. (2020) and are supplied by the EVA-database. Habitat types were also assigned to the same EUNIS classification (see Appendix 3). The response curve for a given species within a given habitat type, with its specific EUNIS type, was therefore fitted using only the plots belonging to the corresponding EUNIS type.

#### 2.4. Nitrogen deposition

EMEP provides yearly annual nitrogen (N) deposition data covering Europe at a spatial resolution of  $0.1^\circ \times 0.1^\circ$  for the period 2000–2017 (Tsyro et al., 2018, 2019). Before that period, data on nitrogen deposition were only available in 5-year intervals and at a coarser spatial resolution ( $0.50^\circ \times 0.25^\circ$ ). These nitrogen deposition grids have been generated using the so-called source receptor matrices (SRMs), also produced by EMEP and widely used in the integrated assessment model GAINS (Amann et al., 2011). For nitrogen depositions dating back to 1945 calculations as described in Schöpp et al. (2003) were used. For the whole period 1945–2017, data are separately available for oxidised (NO<sub>x</sub>) and reduced (NH<sub>3</sub>) nitrogen, both wet and dry. The sum of the two gives the total N deposition which was employed as an explanatory variable for fitting species response curves.

The deposition of an atmospheric pollutant depends not only on atmospheric parameters (e.g., wind speed and direction), but also on the

so-called surface roughness (Appendix 3), determined (mostly) by land cover. This is taken into account in the EMEP MSC-W atmospheric transport model, using a European land cover map (LRTAP, Cinderby et al., 2008) as input to the calculations. Thus, the model produces the depositions for forest/non-forests. In addition to the average deposition in a grid cell, separate depositions are used for the (general) classes ‘forests’ and ‘semi-natural vegetation’ (non-forested). The correction for forest results in higher nitrogen depositions due to the relatively higher surface roughness generated by the upper canopy. For a technical description of the EMEP MSC-W model, see Simpson et al. (2012, 2014) and the annual EMEP MSC-W reports for updates ([www.emep.int/mscw](http://www.emep.int/mscw)).

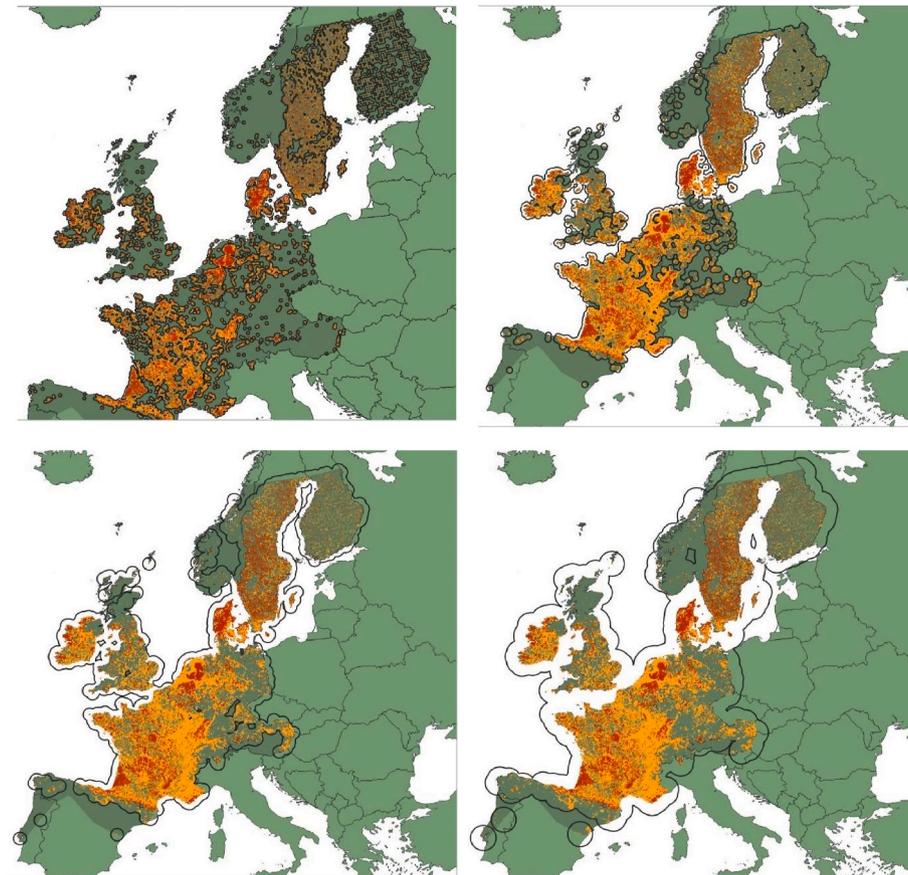
The yearly values of NO<sub>x</sub> and NH<sub>3</sub> deposition for each plot was estimated by using a bi-linear interpolation based on the four surrounding grid cells (Press et al., 1992). Values for years within the 5-year intervals for the period 1945–2000 were estimated by a linear interpolation. Finally, for each plot, the average nitrogen deposition during the year of the vegetation survey and the preceding four years was calculated and used as predictor variable to fit the species response curves.

#### 2.5. Covariables

Species distribution and habitat type quality are not only determined by nitrogen deposition, but also by other environmental factors. To account for some of these factors, the mean annual temperature, total annual precipitation, and soil type of a given plot were added as covariates in the model fitting the species response curve. An multivariate analyses carried out for the model PROPS (Wamelink et al., 2020) with part of the here used database revealed that these factors were the most important ones determining species occurrence. Temperature and precipitation were calculated for the five-year period preceding the year of the vegetation survey. Temperature and precipitation data are based on records collected by weather stations in the EOBS dataset from the UERRA project ([www.uerra.eu](http://www.uerra.eu)), the Copernicus Climate Change Service and the ECA&D project ([www.ecad.eu](http://www.ecad.eu), Cornes et al., 2018). Soil type data was extracted from the European soil atlas which is part of the World Reference Base for Soil Resources (Jones et al., 2015; FAO, 2015). To avoid losing too many degrees of freedom, the many soil types were reduced to five main levels: sand, clay, bog, young soils, and water (Appendix 4). The few plots on loess were added to the sand level and the few plots with a salty soil type were added to the clay level. Plots with soil types that hardly occur in the Netherlands, like rock, were omitted. Plots on impervious soils, like buildings, road verges and pavements, were also excluded.

#### 2.6. Response curves for species and habitats

For each species – EUNIS combination a nitrogen response curve was obtained by fitting a logistic regression model to the binary species presence absence data. The logistic model encompasses nitrogen deposition as a smoothing spline (Hastie and Tibshirani, 1990) with two degrees of freedom and also covariates temperature, precipitation, the interaction between temperature and precipitation, and soil type. The model was fitted employing the GenStat software (VSN International, 2021). Curves were only fitted when a species was present in at least 100 of the selected plots within a given EUNIS type. A response curve along the nitrogen deposition gradient that is representative of the Netherlands was predicted per species – EUNIS combination. To do so, covariates in the fitted model were set to their average temperature (10.6 °C) and precipitation (876 mm) conditions over ten years (2007–2017) using data from the main Dutch weather station: De Bilt in the middle of the country. For soil conditions, a weighted average over soil types was taken with weights according to surf area based on the number of plots per soil type. For species – EUNIS combinations with less than 100 selected plots in the Netherlands, weighting of soils was based on all selected plots. To prevent extrapolation of response curves to very



**Fig. 2.** Estimated distribution area of *Calluna vulgaris* based on circles drawn around each occurrence of the species. The top left panel shows the occupied range based on a radius of 10 km around each occurrence record, the top right panel is based on a radius of 25 km, while the bottom left and right panels are based on radii of 50 km and 100 km, respectively. Dark red points indicate occurrence records for *C. vulgaris* while orange points indicate plots without *C. vulgaris*. The latter are used as absence data values in the logistic response estimation. The black lines indicate the estimated final distribution area of *C. vulgaris*. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

low or large deposition levels, a relevant range of deposition levels was established for each habitat type (Appendix 5).

A nitrogen response curve for a habitat type could be obtained by averaging the predicted response curves for the species that are characteristic for the focal habitat. However, response curves for rare species, with low predicted occurrence probabilities, are then swamped by response curves of the more common species. This implies that rare species have little influence on such a habitat response curve. Therefore, before averaging, each species response curve was normalized by the area under the curve. This ensures that rare and common species have the same weight in the habitat response curve.

#### 2.6.1. Assessment of the curves and evaluation with empirical data

Each habitat curve was plotted alongside the established critical load (Wamelink et al., 2023) and the empirical range for critical load (Bobink et al., 2022). The curves were then assessed by the first author of this paper as either good, reasonable, or bad, by comparing the curve with the critical load and the empirical range for critical load. It was assumed that the critical load and the empirical critical load were correct, and that the response should descent at least in the same range as both versions of the critical load. This as a first assessment of the curves.

Habitat curves were also evaluated by comparing them with habitat quality (i.e. qualifying species richness), or species richness when habitat quality was not available, from nine field studies within nitrogen gradients (Alard, pers comm.; Armitage et al., 2014; Field et al., 2014; Jokerud, 2012; Roth et al., 2013, 2017; Stevens et al., 2010, 2011a; 2011b; Van den Berg et al., 2011; Wilkins & Aherne, 2016). Despite the limited amount of empirical evaluation data, evaluation was possible for

23 out of 60 habitat types with a response curve. Some habitat types could also be evaluated using a subset of species, such as herbs or mosses, resulting in 41 comparisons in total. The habitat curves are dimensionless, making a direct comparison with the experimental data impossible. Therefore, the habitat curves were multiplied by a constant factor so that after multiplication, Lin's concordance correlation coefficient  $\rho$  (Lin, 1989) between the empirical values and the response curve of the habitat type was maximal. The degree of agreement between the empirical values and the multiplied response curves was evaluated by five experts as either good, reasonable, or bad. These ratings were summarised by an overall assessment which also considers the value of Lin's coefficient. For example, if two or three ratings were reasonable and the others were good, the final rating is good when Lin's coefficient was high.

### 3. Results

#### 3.1. Species response curves

We obtained data for 2567 species-EUNIS combinations in the Atlantic Region resulting in 2111 estimated response curves for combinations with 100 or more occurrences per species. Of these combinations, 1220 occur in the Netherlands. An example is given in Appendix 6 for species that are characteristic for 7110ARaised bogs (active bogs).

Species response curves per habitat type are described in Appendix 7, the curves are given in Appendix 8. Most species showed a decreasing probability of occurrence with increasing nitrogen deposition. Yet, it is well known that some species may benefit from nitrogen deposition

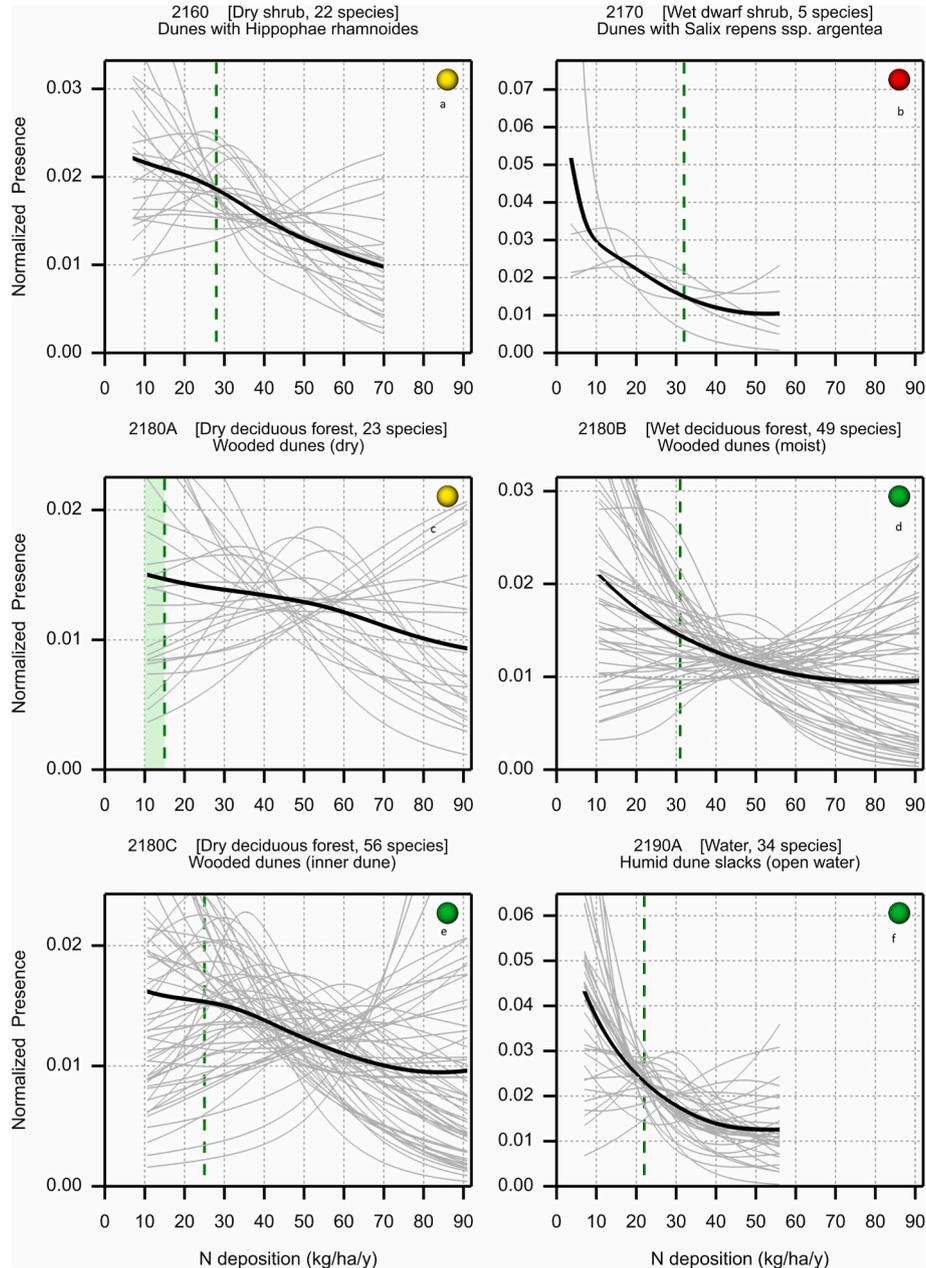
(Krepa, 2003). Some of these species, indeed, show increasing probabilities of occurrence with increasing nitrogen deposition, e.g., *Molinia caerulea* and *Avenella flexuosa* in moist heathland habitats (4010A). However, there are also species that showed an unexpected increase with nitrogen deposition, e.g., *Drosera intermedia* (4010A).

### 3.2. Evaluation of habitat response curves compared to the critical loads and empirical range for critical load

We estimated response curves for nitrogen deposition for 60 habitat (sub)types based on the characteristic species. As an example, six response curves for coastal dune Habitats are given in Fig. 3, including the normalized response curves of the characteristic species. The 60

habitat curves were judged by experts, based on their field knowledge and also based on the goodness of fit and the present-day critical loads, as either good (39 curves), reasonable (9 curves) or bad (12 curves). Evaluation based on the critical loads (Wamelink et al., 2023) and empirical range for critical load (Bobbink et al., 2022) was done by the first author. An increase in habitat quality with increasing nitrogen deposition was obtained for four habitat types, since this is unexpected, these curves were judged as bad. Because these habitat types have a critical load (Bobbink et al., 2022) and are therefore expected to be vulnerable to nitrogen depositions. For Embryonic shifting dunes (2110), no curve could be estimated due to a lack of characteristic species for which a response curve could be fitted.

All the coastal dune habitat types show a more or less decreasing

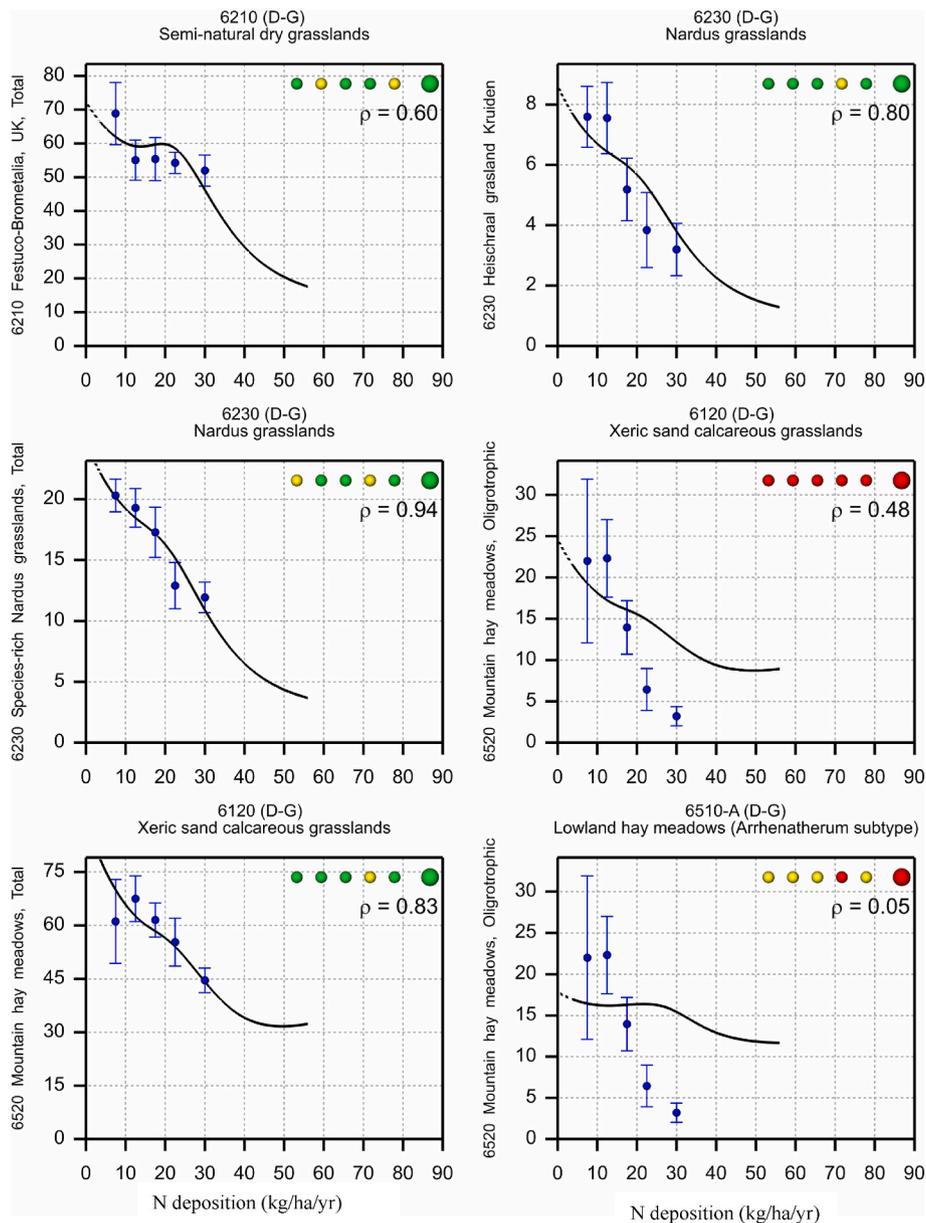


**Fig. 3.** Response curves to nitrogen depositions for six dune habitat types (solid black lines) overlaid on top of the response curves of all the characteristic species (grey line) belonging to the focal habitat type. Other covariates in the model, i.e., mean annual temperature (10.6 °C), annual precipitation (876 mm) and soil type were set to constant values. The dashed vertical green line indicates the critical load (Wamelink et al., 2023), while the green rectangle outlines the empirical critical load range, if available (Bobbink et al., 2022). The heading gives the habitat type number, a short name of the type and between brackets the structure type (for full names see Appendix 3). The coloured dots give the judgment of the curve by one expert (with green = good, yellow = reasonable and red = bad). All responses can be found in appendix 8. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

habitat quality with increasing nitrogen deposition, but both the rate and the amount of decrease varies between the six habitat types. Dunes with *Salix repens* ssp. *argentea* (Salicion arenariae, 2170, Fig. 3b) and the moist dune slacks (subtype open water; 2190A, Fig. 3f) show a steep decline, whereas the dry subtype of Dune forests (2180A, Fig. 3c) and the inner dune subtype of Dune forests (2180C, Fig. 3e) only show a marginal decline. For dunes with *Salix repens* ssp. *argentea* (2170, Fig. 3b), the decline already starts at deposition values far below the Dutch critical load used in legislation. For now, these responses are judged as bad. For moist dune slacks (open water, 2190A, Fig. 3f), the decrease also starts at very low deposition values, but this is in accordance with the critical load. Therefore, this response curve was judged as good.

Grassland habitat type curves show unexpected responses in some cases (Appendix 8). For Lowland hay meadows (subtype Sanguisorba

offinalis, 6510A), this unexpected response curve was further investigated. The habitat type 6510A has 36 characteristic species. Fourteen of these have a declining trend with higher nitrogen deposition, 11 are more or less indifferent (including 6 species with an optimum response), and 11 species increase with increasing nitrogen deposition. All 11 increasing species are qualified as stable or increasing and are very common species in The Netherlands (Dutch plant species inventory, <https://www.verspreidingsatlas.nl/vaatplanten>, last accessed 18-7-2022). These species probably profit from higher nitrogen depositions. Out of the 14 species with a descending trend, as nitrogen deposition increases 4 are red list species and 4 show a negative trend in the number of occurrences in the Netherlands since 1950 (25–50% decrease) without yet being considered as a red list species. Surprisingly, also three common species decreased with nitrogen deposition, *Jacobaea vulgaris* ssp. *vulgaris* (increasing in the Netherlands), *Lathyrus pratensis* (species of



**Fig. 4.** Example of the evaluation of the response per habitat type with empirical field data (including 95% uncertainty interval). The coloured dots in the upper right corner give the judgement of five experts (green = good, yellow = reasonable and red = bad) and with a bigger dot for the final score. Also given is Lin's correlation coefficient  $\rho$  of concordance. The dashed vertical green line indicates the critical load (Wamelink et al., 2023), while the green rectangle outlines the empirical critical load range, if available (Bobbink et al., 2022). All evaluation results can be found in electronic appendix 4. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

nutrient rich soils) and *Geranium pyrenaicum* (originally from South Europe). In conclusion, most of these grassland species have a response curve that agrees with field data, but some show unexpected responses. This leads to a more or less constant response for the habitat type because the decreasing and increasing species level out the response curve. Although all species are characteristic for the habitat type, this raises the question whether all species should be included in the selection.

### 3.3. Evaluation with independent field data

The response curves per habitat type were evaluated with independent field data when available. Field data were obtained from the literature for 23 (sub)habitat types. Fig. 4 gives an example of this evaluation for six grassland habitat types. In total, 41 comparisons were made between our response curves at the habitat level and independent field data; a single habitat curve was sometimes compared to field data of different species groups. Of these 41 comparisons, 25 were judged as good, 5 as reasonable and 11 as bad. In general, there is a good agreement between the expert assessment and the evaluation with independent field data (Table 1). For example, three of the raised bog habitats curves (7110A, 7110B and 7120) were judged as reasonable by the experts when compared to the raised bog empirical data from the UK, although the correspondence with field data is quite good (Lin's correlation = 0.64, or higher). The final judgement based on the UK data is therefore 'reasonable'. However, compared to the data from Norway, the judgement is 'good' which leads to an overall judgement of good.

The comparison of the response curves of grassland habitat type curves with empirical data of Montane grasslands is generally bad. Since real montane grasslands do not occur in The Netherlands, this might not be a good or valid comparison.

## 4. Discussion

We were able to estimate response curves for nitrogen deposition for 60 Dutch habitat types that are sensitive to nitrogen deposition and have a critical load. During the evaluation step, the response curves of 39 out of a total of 60 habitat types were judged 'good' while 9 were judged 'reasonable', based on a combination of expert judgement and a comparison with field or experimental data. This reveals that the method we used is able to estimate realistic response curves, but that more work is needed to get good responses for all habitat types. Our results are consistent with the empirical and simulated critical load of the habitat types investigated by and the research carried out by Rosén et al. (1992), Fremstad et al. (2005), Wilkins & Aherne (2016) and Clark et al. (2019). Several aspects can be improved, and this is discussed below.

### 4.1. The decrease starts before the critical load

For several of the habitat response curves, the decrease of the quality of the habitat type already starts below the Dutch critical load used in legislation (Wamelink et al., 2023) or even below the ranges from empirical critical load (Bobbink et al., 2022)). This might seem surprising, but there are several possible explanations.

1. Van Dobben et al. (2006) define the critical load as the level of nitrogen deposition at which 80% of the consisting (sub) associations are protected. Consequently, there are species that already decrease below the CL. Moreover, the CLs were calculated per vegetation type (association). The CL of a habitat type is based on the constituent associations as the average of these associations. Some associations will already start to decline in species composition below this average value.
2. Rosén et al. (1992) show that for several habitat types in Scandinavia the decline in species composition already starts at or just above the background, non-anthropogenic nitrogen deposition. Every amount

above the background deposition could already lead to a change in species composition (Fremstad et al., 2005). For the habitat types mentioned by Rosén et al. (1992) and the constituent species that also occur in the Netherlands, there is no ecological reason why this would be different in the Netherlands. This implies that a decline may start well below the Dutch critical load that is used know in legislation and is well above the natural background deposition.

3. Two other studies, one for Ireland (Wilkins & Aherne, 2016) and one for the USA (Clark et al., 2019), found comparable results. Wilkins & Aherne (2016) estimated responses for nitrogen deposition for species based on Irish data. They did not estimate curves but ranges in which species could occur (see their Fig. 2). They concluded that the decline of several species that are characteristic for a habitat type already starts below the critical load for that focal habitat type, similar to our findings. Clark et al. (2019) investigated the vulnerability of 348 plant species for acid and nitrogen deposition in the USA. They concluded that 70% of the species reacted negatively to nitrogen deposition (measured as the number of occurrences), and a major part of the species already showed a decline at the lowest deposition levels (3.1 kg/ha/y). Overall, the responses curves estimated by Clark et al. (2019) have a strong resemblance to our curves, also with monotonic declines for higher depositions and species that benefit from nitrogen deposition (most notably invasive alien species). Recently, Payne et al. (2020) found a positive response curve for *Nardus stricta* with increasing nitrogen deposition, similar to, what we found.

### 4.2. Evaluation of the response curves

The resulting response curves for nitrogen deposition for habitat types were evaluated in two different ways: by expert judgement, and by comparison with empirical data (statistically and expert judgement). We used critical loads from both van Wamelink et al. (2023) and Bobbink et al. (2022) in our evaluation and considered curves that enclose critical load values reported in either of these papers as reliable. Although these studies have large uncertainties, we believe that agreement between these and our studies strongly adds to the credibility of our results. The curves now judged as reasonable or bad require further evaluation.

### 4.3. Covariables

The covariables temperature, precipitation and soil type were added in our model to account for the effects of these variables on the estimated parameters of the response curve along the nitrogen deposition gradient. This choice of covariables was based on the development of the PROPS model (Wamelink et al., 2020). A multivariate analysis on a subset of the EVA-data showed that average temperature and precipitation sum were good overall predictors of species occurrence. However, the choice of covariables was based on data availability and other important environmental factors are not available. For all vegetation plots. For example, in the Netherlands, intensified management is often used to mitigate the effects of nitrogen deposition on the vegetation. By not correcting for management the effect of nitrogen deposition may be underestimated.

In the model the effect of the covariables was assumed linear and additive. This was done for the sake of simplicity, but it limits their effect on the response curve. Adding interaction terms between the covariates and their interaction with nitrogen deposition and allowing for nonlinearity could result in more reliable and robust response curves.

Not directly a covariable, we decided not to incorporate the effect of the abundance of the species in a plot. Adding it as a weighing factor in the response curve of a species could in theory lead to a better response curve. In principle a species abundance could decrease over time in abundance tremendously without completely disappearing. This could partly explain the poor and unexpected response of some species. We did not include the abundance for now because it complicates the response

**Table 1**

Evaluation of the responses per habitat type based on (1) the empirical values quantified by  $\rho$  Lin's correlation coefficient of concordance (Lin, 1989).and (2) judgement by five experts in three categories good (G, green), reasonable (R, yellow) and bad (B, red). The final column gives the end judgement based on both Lin's coefficient and the experts, when in doubt Lin's coefficient is of greater preponderance as an independent objective measure.

Empirical data vegetation type	EUNIS type	Respons curve habitat type	code	Lin's $\rho$	Judgement experts					final
					1	2	3	4	5	
Grey dunes	B1.4	Grey dunes (chalk rich)	2130A	0.69	R	G	G	R	G	G
Grey dunes	B1.4	Grey dunes (chalk poor)	2130B	0.72	G	G	G	G	G	G
Grey dunes	B1.4	Grey dunes (herbaceous vegetation)	2130C	0.80	R	G	G	R	G	G
Dry heathland	F4.2	Decalcified fixed dunes with <i>Empetrum nigrum</i> (dry)	2140B	0.93	G	G	G	G	G	G
Dry heathland	F4.2	Atlantic decalcified fixed dunes ( <i>Calluno-Ulicetea</i> )	2150	0.97	G	G	G	G	G	G
Dry heathland	F4.2	Dry sand heaths with <i>Calluna</i> and <i>Genista</i>	2310	0.96	G	G	G	G	G	G
Dry heathland	F4.2	European dry heaths	4030	0.92	G	G	G	G	G	G
Chalk rich grassland Mesobromion (H6210) (BEGIN project)	E1.26	Rupicolous calcareous or basophilic grasslands of the Alysso-Sedion albi	6110	0.81	G	R	G	G	R	G
Chalk rich grassland (BEGIN project)	E1.26	Rupicolous calcareous or basophilic grasslands of the Alysso-Sedion albi	6110	0.18			B			B
Chalk rich grassland (H6210) (UK-project)	E1.26	Rupicolous calcareous or basophilic grasslands of the Alysso-Sedion albi	6110	0.66	G	R	G	G	R	G
Chalk rich grassland Mesobromion (H6210) (BEGIN project)	E1.26	Semi-natural dry grasslands and scrubland facies on calcareous substrates ( <i>Festuco-Brometalia</i> )	6210	0.63	G	R	G	G	G	G
Chalk rich grassland (BEGIN project)	E1.26	Semi-natural dry grasslands and scrubland facies on calcareous substrates ( <i>Festuco-Brometalia</i> )	6210	0.29			G			B

Empirical data vegetation type	EUNIS type	Respons curve habitat type	code	Lin's $\rho$	Judgement experts					final
					1	2	3	4	5	
Chalk rich grassland (H6210) (UK-project)	E1.26	Semi-natural dry grasslands and scrubland facies on calcareous substrates ( <i>Festuco-Brometalia</i> )	6210	0.60	G	R	G	G	R	G
Species rich Nardus grasslands, herbs	E1.71 and E3.52	Species-rich Nardus grasslands on siliceous substrates in mountain areas (and submountain areas in Continental Europe)	6230	0.80	G	G	G	R	G	G
Species rich Nardus grasslands, total	E1.71 and E3.52	Species-rich Nardus grasslands on siliceous substrates in mountain areas (and submountain areas in Continental Europe)	6230	0.94	R	G	G	R	G	G
Montane grasslands Oligotrophic species	E2.3	Xeric sand calcareous grasslands	6120	0.48	B	B	B	B	B	B
Montane grasslands total	E2.3	Xeric sand calcareous grasslands	6120	0.83	G	G	G	R	G	G
Montane grasslands oligotrophic species	E2.3	Lowland hay meadows ( <i>Sanguisorba officinalis</i> subtype)	6510A	0.05	R	R	R	B	R	B
Montane grasslands total	E2.3	Lowland hay meadows ( <i>Sanguisorba officinalis</i> subtype)	6510A	0.25	B	B	B	R	B	B
Montane grasslands oligotrophic species	E2.3	Lowland hay meadows ( <i>Alopecurus pratensis</i> subtype)	6510B	0.10	R	B	R	B	B	B
Montane grasslands total	E2.3	Lowland hay meadows ( <i>Alopecurus pratensis</i> , <i>Sanguisorba officinalis</i> )	6510B	0.26	B	B	B	B	B	B
Raised bog (Norway)	D1	Active raised bogs (bog landscape)	7110A	0.70	G	R	G	R	G	G
Raised bog (UK)	D1	Active raised bogs (bog landscape)	7110A	0.64	R	R	R	R	R	R
Raised bog (Norway)	D1	Active raised bogs (heath fens)	7110B	0.70	G	R	G	R	R	G
Raised bog (UK)	D1	Active raised bogs (heath fens)	7110B	0.65	R	R	R	R	G	R
Raised bog (Norway)	D1	Degraded raised bogs	7120	0.80	G	R	G	G	G	G
Raised bog (UK)	D1	Degraded raised bogs	7120	0.72	R	R	R	R	R	R
Atlantic oak forest (characteristic species)	G1.83	Wooded dunes of the Atlantic Continental and Boreal region (dry)	2180A	0.33	S	R	S	R	R	S

Empirical data vegetation type	EUNIS type	Response curve habitat type	code	Lin's $\rho$	Judgement experts					final
Atlantic oak forest (total)	G1.83	Wooded dunes of the Atlantic Continental and Boreal region (dry)	2180A	0.31	B	B	B	R	B	B
Atlantic oak forest (characteristic species)	G1.83	Wooded dunes of the Atlantic Continental and Boreal region (moist)	2180B	0.95	G	G	G	G	G	G
Atlantic oak forest (total)	G1.83	Wooded dunes of the Atlantic Continental and Boreal region (moist)	2180B	0.90	G	G	G	G	G	G
Atlantic oak forest (characteristic species)	G1.83	Luzulo-Fagetum beech forests	9110	0.86	G	R	G	G	G	G
Atlantic oak forest (total)	G1.83	Luzulo-Fagetum beech forests	9110	0.80	G	G	G	G	G	G
Atlantic oak forest (characteristic species)	G1.83	Atlantic acidophilous beech forests with <i>Ilex</i> and sometimes also <i>Taxus</i> in the shrub layer (Quercion robori-petraeae or Ilici-Fagenion)	9120	0.46	R	R	R	R	R	R
Atlantic oak forest (total)	G1.83	Atlantic acidophilous beech forests with <i>Ilex</i> and sometimes also <i>Taxus</i> in the shrub layer (Quercion robori-petraeae or Ilici-Fagenion)	9120	0.42	R	R	R	R	R	R
Atlantic oak forest (characteristic species)	G1.83	Sub-Atlantic and medio-European oak or oak-hornbeam forests of the Carpinion betuli (sand)	9160A	0.95	G	G	G	G	G	G
Atlantic oak forest (total)	G1.83	Sub-Atlantic and medio-European oak or oak-hornbeam forests of the Carpinion betuli (sand)	9160A	0.90	G	G	G	G	G	G
Atlantic oak forest (characteristic species)	G1.83	Sub-Atlantic and medio-European oak or oak-hornbeam forests of the Carpinion betuli (hills)	9160B	0.84	G	G	G	G	G	G
Atlantic oak forest (total)	G1.83	Sub-Atlantic and medio-European oak or oak-hornbeam forests of the Carpinion betuli (hills)	9160B	0.77	G	G	G	G	G	G
Atlantic oak forest (characteristic species)	G1.83	Old acidophilous oak woods with <i>Quercus robur</i> on sandy plains	9190	0.27	R	B	B	R	B	B
Atlantic oak forest (total)	G1.83	Old acidophilous oak woods with <i>Quercus robur</i> on sandy plains	9190	0.26	B	B	B	R	B	B

curve and test in the past did show only limited effect, also given the uncertain nature of the estimation of the abundance, but it is something worth to test.

#### 4.4. Species selection

The habitat-level response curves were estimated in an indirect way, via the species. To this end we selected species per habitat type based on phytosociological criteria and therefore usually ended up with more species than the list of characteristic species that is given in the standard descriptions of each habitat type (Epe et al., 2009). This was necessary, because the standard descriptions sometimes give only a few or even no plant species. However, a more balanced selection of characteristic species per habitat type may be necessary. Specifically, this is the case for some species that increase in probability of occurrence with nitrogen deposition and may outcompete other species, as e.g., *Molinia caerulea* in heathland habitats. Such species can be typical non-dominant elements within a habitat in its natural state but may become competitors under increased nitrogen deposition. We included these species in the selection, which may result in a flat or weak response at habitat level, while at the species level, a shift takes place from rare species at low nitrogen deposition to common species at high nitrogen deposition. Rowe et al. (2017) et al. already came to the same conclusion and even argued that species number could increase due to nitrogen deposition. They argue that species 'that are distinctive for the habitat but not necessarily scarce may be a more suitable basis for biodiversity metrics'.

#### 4.5. Direct relation between habitat type and nitrogen deposition

A more direct way to relate habitat quality to nitrogen deposition would be (1) to assign a habitat type to each individual plot from the EVA database and (2) to quantify the quality of each plot based on its species composition. The quantified quality could then be directly related to nitrogen deposition for each habitat. This would require a method to link each vegetation plot in the EVA database to a single habitat type. Currently, such a procedure is not available for Europe. As an alternative, the EUNIS types could be used, which could then be linked to the plots. This procedure would skip the difficult step of linking a set of species to a habitat type. The disadvantage of this method,

however, would be that it becomes more like a 'black box'. However, the present method has the advantage of yielding insight into the response of individual species.

#### 4.6. Time period for nitrogen deposition and uncertainty

In this study, we computed the average nitrogen deposition over five years prior to the sampling year of each vegetation plot. This is an arbitrary choice. Annuals will chiefly experience nitrogen depositions during the year they germinate, albeit the long-term history of nitrogen depositions accumulated in the soil until the germination year may also have an impact. On the other end of the spectrum are trees that may have experienced a very long history of both sulphur and nitrogen deposition, and hence might have been influenced by many years of deposition. The five-year average is a compromise between species with a totally different lifespan. Rowe et al. (2017) proposed a 30-year time interval.

An alternative to using the average deposition rate during a given period of five years here could be to use the sum of the deposition that the plot experienced over time. It would reflect the nitrogen load from, e.g., 1950 up to the plot sampling year of the vegetation survey, and thus reflect the total amount of nitrogen added to the system. This might be a better dose parameter for the effect of nitrogen deposition than the five-year deposition that we (and many others) used.

This said, the estimated rate of depositions during the earlier years, especially before the 1980s, are more uncertain than those estimated for the period after 2000. This is the case for at least two reasons: depositions before 2000 are calculated using an older EMEP model at a coarser spatial resolution and emission estimates (especially before 1960) are less reliable. However, it is impossible to give a numerical estimate of the uncertainties involved in the (older) depositions, especially as hardly any field measurements of nitrogen deposition which have their own uncertainties, are available.

#### 4.7. Normalization of the species response curves

Nitrogen response curves were normalized by the area under the curve to ensure that rare and common species have the same weight in the habitat response curves. The so-called Habitat Suitability Index

(HSI), in which each species curve is divided by its maximal predicted occurrence probability, offers an alternative normalization. The HIS normalization turned out to put less emphasis on rare species than the area-under-the-curve and was therefore not used. In a more subjective approach experts could assign a weight to each species response curve separately for each focal habitat, see e.g. Van Dobben et al. (2015). This was considered unfeasible for the present study.

#### 4.8. Concluding remarks

The method we proposed in this study generates habitat-level response curves that, at least partly appear to be reliable and in agreement with other work on this topic. The response curves provide a more detailed insight in the quantitative relationship between habitat quality and nitrogen depositions and can be used in cost-benefit analysis. Both the species level and the habitat-level response curves may also be used to derive data-driven update of the critical load values for nitrogen depositions. They could be used as a third method next to the empirical critical loads and the modelled critical loads, thus strengthening the principle of the critical loads as a way of understanding the negative effects of nitrogen deposition on vegetation quality and the protection of nature in general.

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#### CRediT authorship contribution statement

G.W.W. Wamelink: Writing – review & editing, Writing – original

#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.envpol.2024.123844>.

#### Appendix 1. Data sources used

The data given below were used for this research. All data originate from the EVA-database, except the Swiss database at the end, and most of them also have an entry in the Global Index of Vegetation Data GIVD ([www.givd.info](http://www.givd.info)) database and are accessible there. For each database the owner (all are co-authors of this article) and the number of selected plots are given.

GIVD code	(GIVD) database name	owner	n
	Coastal database Borja Jiménez-Alfaro	Borja Jiménez-Alfaro	49
EU-00-016	Mediterranean Ammophiletea database	Corrado Marcenò	48
EU-AT-001	Austrian Vegetation Database	Wolfgang Willner	6331
EU-00-011	Vegetation-Opname Database of the University of the Basque Country (BIOVEG)	Idoia Biurrun	5204
	GVRD Bogs	Ute Jandt	1328
EU-GB-001	UK National Vegetation Classification Database	John S. Rodwell	21036
EU-00-026	CircumMed Pine Forest database	Gianmaria Bonari	6
EU-CZ-001	Czech National Phytosociological Database	Milan Chytrý	253
EU-DK-002	National Vegetation Database of Denmark	Jesper Erenskjold Moeslund	106850
EU-00-027	European Boreal Forest Vegetation Database	Anni Kanerva Jašková	513
EU-00-017	European Coastal Vegetation Database-A	John Janssen	13
	European Coastal Vegetation Database-B	Corrado Marcenò	38
EU-00-022	European Mire Vegetation Database	Tomás Peterka	306
EU-00-022	European Mire Vegetation Database	Tomás Peterka	133
EU-00-028	European Weed Vegetation Database	Filip Küzmič	1361
	European calcareous fens	Borja Jiménez-Alfaro	664
	Finnish National Forest Inventory	Päivi Merilä	1727
EU-FR-003	SOPHY	Emmanuel Garbolino	72330

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#### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Data availability

Data will be made available on request.

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(continued)

GIVD code	(GIVD) database name	owner	n
	French National Forest Inventory	<a href="https://inventaire-forestier.ign.fr/spip.php?rubrique149">https://inventaire-forestier.ign.fr/spip.php?rubrique149</a>	26142
	GVRD_grasslands	Ute Jandt	10820
EU-DE-014	German Vegetation Reference Database (GVRD)	Ute Jandt	25299
EU-DE-013	VegetWeb Germany	Florian Jansen	14321
EU-DE-013	VegetWeb Germany	Friedemann Goral	4266
EU-DE-013	VegetWeb Germany	Friedemann Goral	454
EU-DE-001	VegMV	Florian Jansen	2118
EU-DE-020	German Grassland Vegetation Database (GrassVeg.DE)	Ricarda Pätzsch	5101
EU-00-025	Gravel bar vegetation database	Veronika Kalnířková	12
EU-HU-003	CoenoDat Hungarian Phytosociological Database	János Csiky	1
EU-BE-002	INBOVEG	Els De Bie	6645
EU-IE-001	Irish Vegetation Database	Úna FitzPatrick	16916
EU-00-031	Masaryk University's Gap-Filling Database of European Vegetation	Milan Chytrý	3
EU-NL-001	Dutch National Vegetation Database	Stephan Hennekens	124999
EU-NL-003	Dutch Military Ranges Vegetation Database (DUMIRA)	Iris de Ronde	9161
EU-00-018	The Nordic Vegetation Database	Jonathan Lenoir	2506
EU-00-002	Nordic-Baltic Grassland Vegetation Database (NBGVD)	Jürgen Dengler	511
	Nordicforests Aune	Jonathan Lenoir	41
EU-PL-001	Polish Vegetation Database	Zygmunt Kaćki	18
	Portugal - Estela database	Jan Jansen	2
	SalineVDB	Daniel Dité	147
EU-DE-040	Database Schleswig-Holstein (Northern Germany)	Joachim Schrautzer	1131
EU-SK-001	Slovak Vegetation Database	Milan Valachovic	72
EU-00-004	Iberian and Macaronesian Vegetation Information System (SIVIM)	Xavier Font	39
EU-00-004	Iberian and Macaronesian Vegetation Information System (SIVIM)	Borja Jiménez-Alfaro	1
EU-00-023	Iberian and Macaronesian Vegetation Information System (SIVIM) – Deciduous Forests	Juan Antonio Campos	229
EU-00-004	Iberian and Macaronesian Vegetation Information System (SIVIM)	Maria Pilar Rodríguez-Rojo	335
EU-00-004	Iberian and Macaronesian Vegetation Information System (SIVIM)	Federico Fernández-González	68
EU-ES-001	Iberian and Macaronesian Vegetation Information System (SIVIM) – Wetlands	Aaron Pérez-Haase	477
	Swedish National Forest Inventory	<a href="https://www.slu.se/nfi">https://www.slu.se/nfi</a>	14259
EU-CH-011	Monitoring Effectiveness of Habitat Conservation in Switzerland	Ariel Bergamini	970
EU-CH-005	Swiss Forest Vegetation Database	Thomas Wohlgemuth	1408
EU-GB-004	UK Floodplain Meadows Database	Irina Tatarenko	26265
	Switzerland grassland database	Unknown	640

## Appendix 2. Selection of species per habitat type

Habitat types are mainly defined by their species composition. For the Netherlands, a list of typical species per habitat type exists (Bal, 2007), which is however too limited for our aim; some habitat types do not have any or only a few plant species. Therefore, we expanded this list using phytosociological techniques (Schaminée et al., 1995), on the basis of vegetation types present in each habitat type (Epe et al., 2009), and the floristic composition of these vegetation types, including mosses and lichens. Each habitat type occurring in The Netherlands is linked with a set of plant associations (Schaminée et al., 1995). Plant associations are defined by vegetation plots that are reviewed by specialists and could get a designated association. This makes it possible to link vegetation plots to habitat types. To expand the list of typical species we selected species that often occur (but not exclusively) in a well-developed Habitat type according to the following criteria.

1.	constancy $\geq$	10%	and	frequency $\geq$	7%
2.	constancy $\geq$	10%	and	mean cover $\geq$	7%
3.	constancy $\geq$	4%	and	frequency $\geq$	30%
4.	constancy $\geq$	2%	and	frequency $\geq$	85%
5.	constancy $\geq$	85%			

With constancy of  $s$  species for a habitat type and fidelity score, based on frequency and mean cover of a species present in a selected set of plots typical for the Habitat type. To be selected a species had to fulfil at least one of the five criteria. Criteria 1–3 were adopted from Smits et al. (2016), criteria 4 and 5 were added to expand the species list for habitat types with few species and to automatically select the typical species. The list of typical species was also used to calibrate the criteria, in order to select the typical species as much as possible. Typical species that still were not selected were added manually to the list. The whole species list was evaluated, and species were removed from the list based on the following criteria.

1. Tree species. Tree species have a long lifespan and therefore their occurrence may be bad characteristics for the effect of nitrogen deposition. They may have germinated under very different circumstances and may persist for a long time under unfavourable conditions. And trees are often planted and thus may not indicate the habitat conditions at the site.
2. The species has a high frequency but is not faithful to the habitat.
3. The occurrence or absence of the species has no influence on the quality of the Habitat type. Species that may be present but are not typical for the habitat type.
4. The species is an indicator for disturbance.
5. The species is a combined species, e.g., *Agrostis canina/vinealis*.

The resulting species list of characteristic species was used to estimate the response curves per habitat type.

### Appendix 3. Classification of habitat types and EUNIS types

Classification of habitat types and EUNIS types in vegetation structure types and roughness class for the calculation of the received nitrogen deposition. The link between habitat type and EUNIS type from the plots can be made via the structure type.

Habitat type	Code	Structure type 1	Structure type 2	Roughness
Salicornia and other annuals colonising mud and sand ( <i>Salicornia</i> )	1310-A	Salt		Low
Salicornia and other annuals colonising mud and sand ( <i>Sagina maritima</i> )	1310-B	Salt		Low
Spartina swards ( <i>Spartina maritima</i> )	1320	Salt		Low
Atlantic salt meadows ( <i>Glauco-Puccinellietalia maritima</i> , outside the dyke)	1330-A	Salt		Low
Atlantic salt meadows ( <i>Glauco-Puccinellietalia maritima</i> , inside the dyke)	1330-B	Salt		Low
Embryonic shifting dunes	2110	Salt		Low
Shifting dunes along the shoreline with <i>Ammophila arenaria</i> ("white dunes")	2120	Dry grassland		Low
Fixed coastal dunes with herbaceous vegetation ("grey dunes", chalk rich)	2130-A	Dry grassland		Low
Fixed coastal dunes with herbaceous vegetation ("grey dunes", chalk poor)	2130-B	Dry grassland		Low
Fixed coastal dunes with herbaceous vegetation ("grey dunes", Nardetea)	2130-C	Dry grassland		Low
Decalcified fixed dunes with <i>Empetrum nigrum</i> (moist)	2140-A	Wet dwarf shrubs		Low
Decalcified fixed dunes with <i>Empetrum nigrum</i> (dry)	2140-B	Dry dwarf shrubs		Low
Atlantic decalcified fixed dunes ( <i>Calluno-Ulicetea</i> )	2150	Dry dwarf shrubs		Low
Dunes with <i>Hippophae rhamnoides</i>	2160	Dry shrub		High
Dunes with <i>Salix repens</i> ssp. <i>argentea</i> ( <i>Salicion arenariae</i> )	2170	Wet dwarf shrubs		Low
Wooded dunes of the Atlantic Continental and Boreal region (dry)	2180-A	Dry deciduous forest		High
Wooded dunes of the Atlantic Continental and Boreal region (moist)	2180-B	Wet deciduous forest		High
Wooded dunes of the Atlantic Continental and Boreal region (inner dune)	2180-C	Dry deciduous forest		High
Humid dune slacks (open water)	2190-A	Water		Low
Humid dune slacks (chalk rich)	2190-B	Wet grassland		Low
Humid dune slacks (chalk poor)	2190-C	Wet grassland		Low
Dry sand heaths with <i>Calluna</i> and <i>Genista</i>	2310	Dry dwarf shrubs		Low
Dry sand heaths with <i>Calluna</i> and <i>Empetrum nigrum</i>	2320	Dry dwarf shrubs		Low
Inland dunes with open <i>Corynephorus</i> and <i>Agrostis</i> grasslands	2330	Dry grassland		Low
Oligotrophic waters containing very few minerals of sandy plains ( <i>Littorelletalia uniflorae</i> )	3110	Water		Low
Oligotrophic to mesotrophic standing waters with vegetation of the <i>Littorelletea uniflorae</i> and/or of the <i>Isoëto-Nanojuncetea</i>	3130	Water		Low
Hard oligo-mesotrophic waters with benthic vegetation of <i>Chara</i> spp.	3140	Water		Low
Natural eutrophic lakes with <i>Magnopotamion</i> or <i>Hydrocharition</i> - type vegetation	3150	Water		Low
Natural dystrophic lakes and ponds	3160	Water		Low
Northern Atlantic wet heaths with <i>Erica tetralix</i> (inland sandy soils)	4010-A	Wet dwarf shrubs		Low
Northern Atlantic wet heaths with <i>Erica tetralix</i> (lowland fens)	4010-B	Wet dwarf shrubs		Low
European dry heaths	4030	Dry dwarf shrubs		Low
<i>Juniperus communis</i> formations on heaths or calcareous grasslands	5130	Dry shrub		High
Rupicolous calcareous or basophilic grasslands of the <i>Alyso-Sedion albi</i>	6110	Dry grassland		Low
Xeric sand calcareous grasslands	6120	Dry grassland		Low
Calaminarian grasslands of the <i>Violetalia calaminariae</i>	6130	Dry grassland		Low
Semi-natural dry grasslands and scrubland facies on calcareous substrates ( <i>Festuco-Brometalia</i> )	6210	Dry grassland		Low
Species-rich <i>Nardus</i> grasslands on siliceous substrates in mountain areas (and submountain areas in Continental Europe)	6230	Dry grassland		Low
<i>Molinia</i> meadows on calcareous peaty or clayey-silt-laden soils ( <i>Molinion caeruleae</i> )	6410	Wet grassland		Low
Hydrophilous tall herb fringe communities of plains and of the montane to alpine levels (dry woodland edge)	6430-C	Dry deciduous forest		High
Lowland hay meadows ( <i>Alopecurus pratensis</i> , <i>Sanguisorba officinalis</i> ; <i>Arrhenatherum</i> subtype)	6510-A	Dry grassland		Low
Lowland hay meadows ( <i>Alopecurus pratensis</i> , <i>Sanguisorba officinalis</i> ; <i>Alopecurus</i> subtype)	6510-B	Dry grassland		Low
Active raised bogs (active bog landscape)	7110-A	Wet dwarf shrubs	Swamp	Low
Active raised bogs (heath bogs)	7110-B	Wet dwarf shrubs	Swamp	Low

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Habitat type	Code	Structure type 1	Structure type 2	Roughness
Degraded raised bogs still capable of natural regeneration	7120	Wet dwarf shrubs	Swamp	Low
Transition mires and quaking bogs (quacking bogs)	7140-A	Swamp		Low
Transition mires and quaking bogs ( <i>Sphagnum</i> reedland)	7140-B	Swamp		Low
Depressions on peat substrates of the Rhynchosporion	7150	Swamp		Low
Calcareous fens with <i>Cladium mariscus</i> and species of the <i>Caricion davallianae</i>	7210	Swamp		Low
Petrifying springs with tufa formation ( <i>Cratoneurion</i> )	7220	Wet deciduous forest		High
Alkaline fens	7230	Wet grassland		Low
Luzulo-Fagetum beech forests	9110	Dry deciduous forest		High
Atlantic acidophilous beech forests with <i>Ilex</i> and sometimes also <i>Taxus</i> in the shrub layer ( <i>Quercion robori-petraeae</i> or <i>Ilici-Fagenion</i> )	9120	Dry deciduous forest		High
Sub-Atlantic and medio-European oak or oak-hornbeam forests of the <i>Carpinion betuli</i> (sandy soils)	9160-A	Wet deciduous forest		High
Sub-Atlantic and medio-European oak or oak-hornbeam forests of the <i>Carpinion betuli</i> (hills)	9160-B	Dry deciduous forest		High
Old acidophilous oak woods with <i>Quercus robur</i> on sandy plains	9190	Dry deciduous forest		High
Bog woodland	91D0	Wet deciduous forest		High
Alluvial forest with black alder <i>Alnus glutinosa</i> and common ash <i>Fraxinus excelsior</i> ( <i>Alno-Padion</i> , <i>Alnion incanae</i> , <i>Salicion albae</i> ), softwood subtype	91E0-A	Wet deciduous forest		High
Alluvial forest with black alder <i>Alnus glutinosa</i> and common ash <i>Fraxinus excelsior</i> ( <i>Alno-Padion</i> , <i>Alnion incanae</i> , <i>Salicion albae</i> ), ash-elm subtype	91E0-B	Wet deciduous forest		High
Alluvial forest with black alder <i>Alnus glutinosa</i> and common ash <i>Fraxinus excelsior</i> ( <i>Alno-Padion</i> , <i>Alnion incanae</i> , <i>Salicion albae</i> ), beech shore subtype	91E0-C	Wet deciduous forest		High
Riparian mixed forests of <i>Quercus robur</i> , <i>Ulmus laevis</i> and <i>Ulmus minor</i> , <i>Fraxinus excelsior</i> or <i>Fraxinus angustifolia</i> along the great rivers ( <i>Ulmion minoris</i> )	91F0	Dry deciduous forest		High

Classification of EUNIS types into vegetation structure types and their roughness (low or high) used for the calculation of the received nitrogen deposition.

Code	Description	Structure type 1	Structure type 2	Roughness
C	Surface waters	water		low
C11a	Permanent oligotrophic waterbody with very soft-water species	water		low
C11b	Permanent oligotrophic to mesotrophic waterbody with soft-water species	water		low
C12a	Permanent oligotrophic to mesotrophic waterbody with Characeae	water		low
C12b	Mesotrophic to eutrophic waterbody with vascular plants	water		low
C14	Permanent dystrophic waterbody	water		low
C15	Permanent inland saline and brackish waterbody	Salt		low
C21a	Base-poor spring and spring brook	streaming water		low
C21b	Calcareous spring and spring brook	streaming water		low
C22b	Permanent non-tidal, fast, turbulent watercourse of plains and montane regions with <i>Ranunculus</i> spp.	streaming water		low
C23	Permanent non-tidal, smooth-flowing watercourse	streaming water		low
C24	Tidal river, upstream from the estuary	streaming water		low
C25a	Temperate temporary running watercourse	streaming water		low
C35a	Periodically exposed shore with stable, eutrophic sediments with pioneer or ephemeral vegetation	swamp		low
C35b	Periodically exposed shore with stable, mesotrophic sediments with pioneer or ephemeral vegetation	swamp		low
C35c	Periodically exposed saline shore with pioneer or ephemeral vegetation	salt		low
H32b	No description available	dry grassland		low
H32c	No description available	dry grassland		low
MA	Coastal saltmarshes	salt		low
MA221	Atlantic saltmarsh drift line	salt		low
MA222	Atlantic upper saltmarsh	salt		low
MA223	Atlantic upper-mid saltmarsh and saline and brackish reed, rush and sedge bed	salt		low
MA224	Atlantic mid-low saltmarsh	salt		low
MA225	Atlantic pioneer saltmarsh	salt		low
MA232	Baltic coastal meadow	salt		low
N11	Atlantic, Baltic and Arctic sand beach	salt		low
N13	Atlantic and Baltic shifting coastal dune	dry grassland		low
N15	Atlantic and Baltic coastal dune grassland (grey dune)	dry grassland		low
N18	Atlantic and Baltic coastal <i>Empetrum</i> heath	dry dwarf shrub		low
N19	Atlantic coastal <i>Calluna</i> and <i>Ulex</i> heath	dry dwarf shrub		low
N1A	Atlantic and Baltic coastal dune scrub	dry shrub		low
N1D	Atlantic and Baltic broad-leaved coastal dune forest	dry deciduous forest		high
N1H	Atlantic and Baltic moist and wet dune slack	wet grassland	swamp	low
N21	Atlantic, Baltic and Arctic coastal shingle beach	salt		low

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Code	Description	Structure type 1	Structure type 2	Roughness
N31	Atlantic and Baltic rocky sea cliff and shore	salt		low
N34	Atlantic and Baltic soft sea cliff	salt		low
Q11	Raised bog	wet dwarf shrubs	swamp	low
Q12	Blanket bog	wet dwarf shrubs	swamp	low
Q21	Oceanic valley mire	wet dwarf shrubs		low
Q22	Poor fen	swamp		low
Q24	Intermediate fen and soft-water spring mire	swamp		low
Q25	Non-calcareous quaking mire	swamp		low
Q3	Palsa and polygon mires	wet dwarf shrubs		low
Q41	Alkaline, calcareous, carbonate-rich small-sedge spring fen	wet grassland		low
Q42	Extremely rich moss-sedge fen	swamp		low
Q43	Tall-sedge base-rich fen	wet grassland		low
Q44	Calcareous quaking mire	swamp		low
Q45	Arctic-alpine rich fen	swamp		low
Q51	Tall-helophyte bed	swamp		low
Q52	Small-helophyte bed	swamp		low
Q53	Tall-sedge bed	swamp		low
Q54	Inland saline or brackish helophyte bed	salt		low
Qa	Mires	wet dwarf shrubs		low
Qb	Wetlands	wet dwarf shrubs		low
R	Grasslands	Wet and dry grassland		low
R13	Cryptogam- and annual-dominated vegetation on calcareous and ultramafic rock outcrops	dry grassland		low
R1A	Semi-dry perennial calcareous grassland (meadow steppe)	dry grassland		low
R1M	Lowland to montane, dry to mesic grassland usually dominated by <i>Nardus stricta</i>	dry grassland		low
R1P	Oceanic to subcontinental inland sand grassland on dry acid and neutral soils	dry grassland		low
R1Q	Inland sanddrift and dune with siliceous grassland	dry grassland		low
R1R	Mediterranean to Atlantic open, dry, acid and neutral grassland	dry grassland		low
R1S	Heavy-metal grassland in Western and Central Europe	dry grassland		low
R21	Mesic permanent pasture of lowlands and mountains	dry grassland		low
R22	Low and medium altitude hay meadow	dry grassland		low
R35	Moist or wet mesotrophic to eutrophic hay meadow	wet grassland		low
R36	Moist or wet mesotrophic to eutrophic pasture	wet grassland		low
R37	Temperate and boreal moist or wet oligotrophic grassland	wet grassland		low
R42	Boreal and Arctic acidophilous alpine grassland	dry grassland		low
R51	Thermophilous forest fringe of base-rich soils	dry deciduous forest		high
R52	Forest fringe of acidic nutrient-poor soils	dry deciduous forest		high
R54	<i>Pteridium aquilinum</i> vegetation	dry deciduous forest		low
R55	Lowland moist or wet tall-herb and fern fringe	swamp		low
R57	Herbaceous forest clearing vegetation	dry deciduous forest		low
R63	Temperate inland salt marsh	salt		low
S11	Shrub tundra	dry dwarf shrub		low
S12	Moss and lichen tundra	dry dwarf shrub		low
S21	Subarctic and alpine dwarf <i>Salix</i> scrub	wet dwarf shrubs		low
S22	Alpine and subalpine ericoid heath	dry dwarf shrub		low
S23	Alpine and subalpine <i>Juniperus</i> scrub	dry shrub		high
S31	Lowland to montane temperate and sub-Mediterranean <i>Juniperus</i> scrub	dry shrub		high
S32	Temperate <i>Rubus</i> scrub	dry deciduous forest		high
S33	Lowland to montane temperate and sub-Mediterranean genistoid scrub	dry shrub		high
S35	Temperate and sub-Mediterranean thorn scrub	dry shrub		high
S37	<i>Corylus avellana</i> scrub	dry deciduous forest		high
S38	Temperate forest clearing scrub	dry deciduous forest		high
S41	Wet heath	wet dwarf shrubs		low
S42	Dry heath	dry dwarf shrub		low
S91	Temperate riparian scrub	wet deciduous forest		high
S92	<i>Salix</i> fen scrub	wet deciduous forest		high
Sa	Scrub	shrub		high
Sb	Dwarf-shrub vegetation	dry dwarf shrub		low
T11	Temperate <i>Salix</i> and <i>Populus</i> riparian forest	wet deciduous forest		high
T12	<i>Alnus glutinosa</i> - <i>Alnus incana</i> forest on riparian and mineral soils	wet deciduous forest		high
T13	Temperate hardwood riparian forest	wet deciduous forest		high
T14	Mediterranean and Macaronesian riparian forest	wet deciduous forest		high
T15	Broadleaved swamp forest on non-acid peat	wet deciduous forest		high
T16	Broadleaved mire forest on acid peat	wet deciduous forest		high
T17	<i>Fagus</i> forest on non-acid soils	dry deciduous forest		high
T18	<i>Fagus</i> forest on acid soils	dry deciduous forest		high
T19	Temperate and sub-Mediterranean thermophilous deciduous forest	dry deciduous forest		high
T1B	Acidophilous <i>Quercus</i> forest	dry deciduous forest		high
T1C	Temperate and boreal mountain <i>Betula</i> and <i>Populus tremula</i> forest on mineral soils	dry deciduous forest		high
T1E	<i>Carpinus</i> and <i>Quercus</i> mesic deciduous forest	dry deciduous forest		high
T1F	Ravine forest	dry deciduous forest		high
T1G	<i>Alnus cordata</i> forest	dry deciduous forest		high
T1H	Broadleaved deciduous plantation of non site-native trees	dry deciduous forest		high
T27	<i>Ilex aquifolium</i> forest	dry deciduous forest		high
T29	Broadleaved evergreen plantation of non site-native trees	dry deciduous forest		high
T3C	<i>Taxus baccata</i> forest	dry deciduous forest		high

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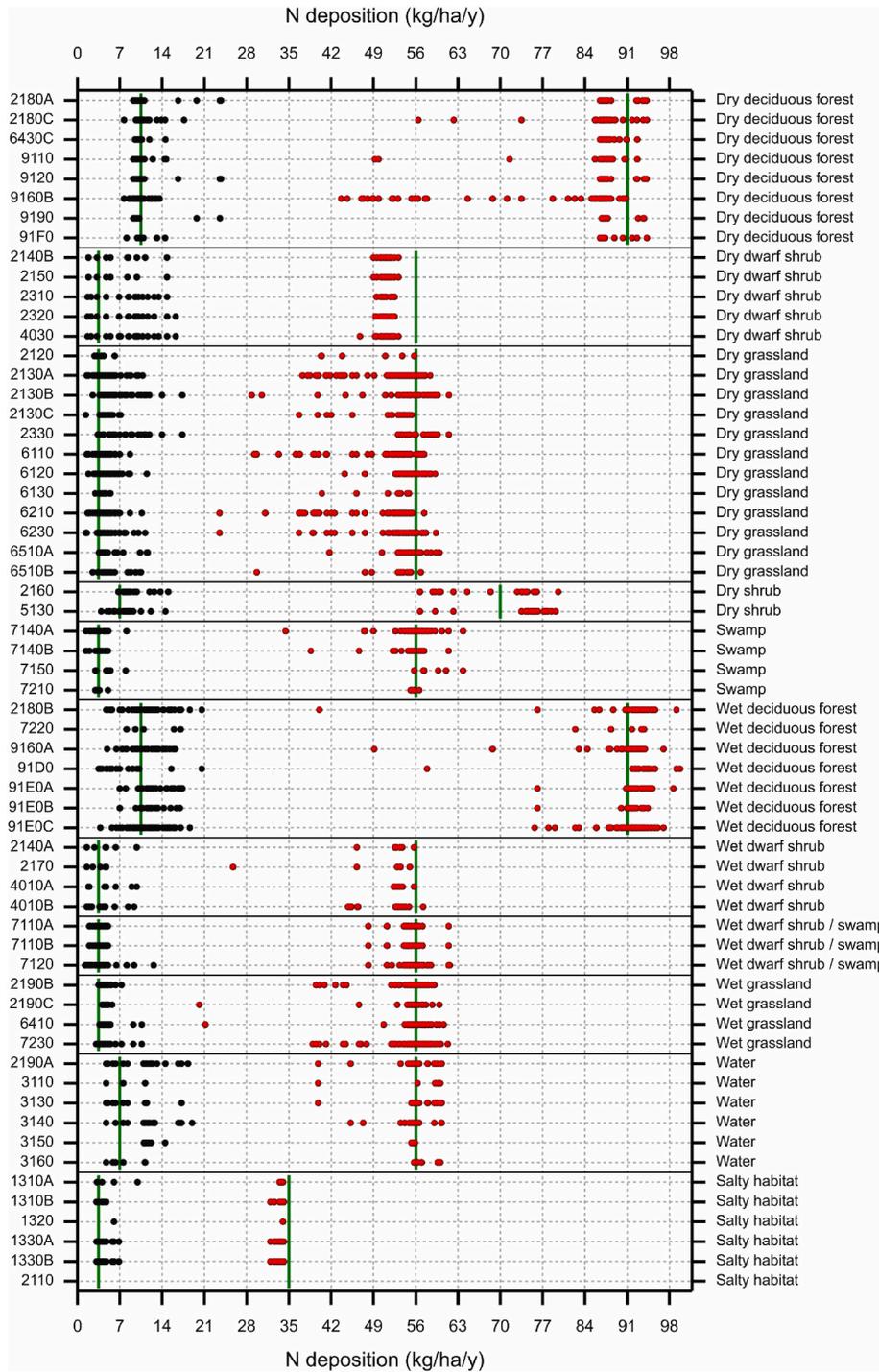
Code	Description	Structure type 1	Structure type 2	Roughness
U	Inland sparsely vegetated	dry grassland		low
U23	Temperate, lowland to montane siliceous scree	dry grassland		low
U27	Temperate, lowland to montane base-rich scree	dry grassland		low
U33	Temperate, lowland to montane siliceous inland cliff	dry grassland		low
U37	Temperate, lowland to montane base-rich inland cliff	dry grassland		low
V34	Trampled xeric grassland with annuals	dry grassland		low
V35	Trampled mesophilous grassland with annuals	dry grassland		low
V39	Mesic perennial anthropogenic herbaceous vegetation	dry deciduous forest		high

#### Appendix 4. Translation of the 30 soil types from the European soil map (Jones et al., 2015) into five types used in this research (sand, water, bog, clay and young soils). The loess plots were added to sand and the salt plots to clay

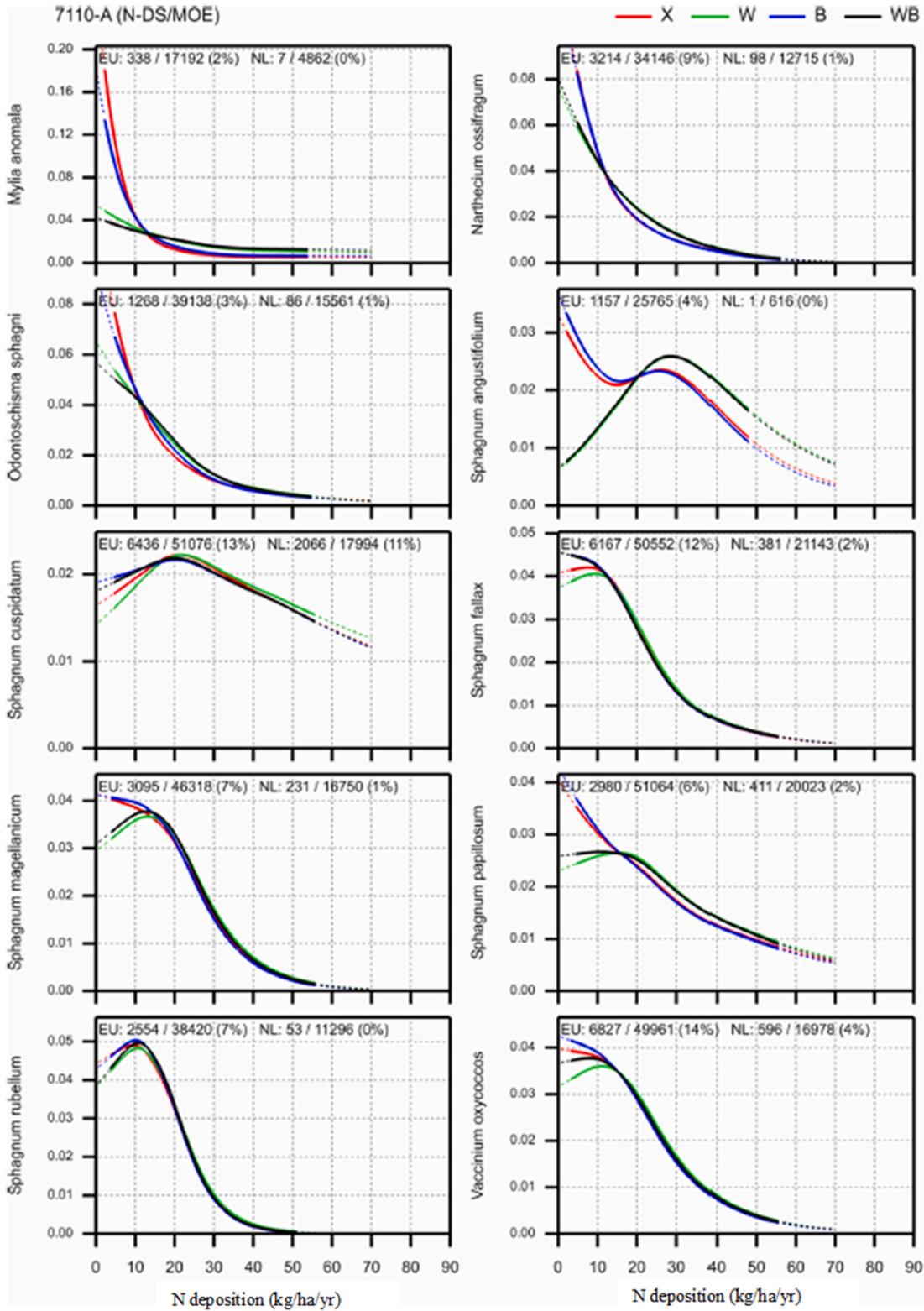
number	description	code	n plots	Reason to remove plots	New soil type
1	Podzol	AB	134838		Sand
2	Water body	AC	3755		Water
3	Andosol	AL	344	NOT in the Netherlands	
4	Cryosol	AN	0		
5	Histosol	AR	34059		Bog
6	Rock outcrops	AT	1012	Not in the Netherlands	Rock
7	Glacier	CH	79	Ice, should not be present in our selection	
8	Gleysol	CL	29008		Clay
9	Leptosol	CM	26401	Not in the Netherlands	Rock
10	Fluvisol	CR	73033		Clay
11	Cambisol	DU	130879		
12	Albeluvisol	FL	7852		
13	Arenosol	FR	11921		Sand
14	Planosol	GL	2159		Clay
15	Phaeozem	GY	1866		Loess
16	Regosol	HS	17188		Young soils
17	Chernozem	KS	1969		Loess
18	Umbrisol	LP	2	Only two sites	
19	Kastanozem	LV	0		
20	Solonchak	LX	474		Salt
21	Solonetz	NT	74		Salt
22	Vertisol	PH	31		Clay
23	Calcisol	PL	4	Only 4 sites	
24	Town	PT	3596		Youn soils
25	#N/A	PZ	629	Could be anything	
26	Soil disturbed by man	RG	293		Young soils
27	Luvisol	SC	83048		Clay
28	Acrisol	SN	0		
29	Marsh	UM	298		Bog
30	Gypsisol	VR	152	Not in the Netherlands	

#### Appendix 5. Estimation of the nitrogen deposition range

Estimation of the nitrogen deposition range where no extrapolation takes place for the response curves per (sub) habitat type (code on the left, vegetation structure type on the right). The black dots indicate plots that are around up the 1 percentiles deposition and the red dots the 99 percentiles. The green lines indicate the chosen upper and lower limits of the range for the response curves. For simplicity reasons limits are the same for groups of habitat types and rounded, based on the values in Kmol/ha/yr. On top of the figures the nitrogen deposition in Kmol/ha/yr and on the bottom the nitrogen deposition in kg/ha/yr is given. On the left Y-axes the habitat type code is given and on the right y-axes the structure type code. For the vegetation structure types: D-B: dry forest, D-DS: dry dwarf shrub, D-G: dry grassland, D-S: dry shrub, Moe: swamp, N-B: wet forest, N-DS: wet dwarf shrubs, N-G: wet grassland, WAT: water and ZOU: Salt.



Appendix 6. Response curves for species to nitrogen deposition for H7110A Raised bog (active bog). The red curve without covariables, the green curve with the climatic covariables (temperature and precipitation), the blue curve with soil type as covariable and the black curve with all covariables. All responses are given in electronic appendix 6



**Appendix 7. Short description of the response curves and their assessment by the first author. The range in which the response curves descent was estimated by the first author and only given in the cases there was a descent**

Code	Name habitat type	Description of the curve	Range decent (kg/ha/yr)	Assessment
1310A	Salicornia and other annuals colonising mud and sand (Salicornia)	Increasing curve, only five species, all species show an increasing response which is unlikely.		Bad
1310B	Salicornia and other annuals colonising mud and sand ( <i>Sagina maritima</i> )	Steadily decreasing response with an increase in decent within the empirical range for critical load (CR) and just below the Critical Load (CL).	30	Good
1320	Spartina swards ( <i>Spartinion maritimae</i> )	Only one characteristic species ( <i>Spartina anglica</i> ), with an inexplicable response (hyperbola).		Bad
1330A	Atlantic salt meadows (Glauco-Puccinellietalia maritimae, outside the dyke)	Descending curve with an increase in decent within the empirical CR and with a larger decent just before the CL.	20	Good
1330B	Atlantic salt meadows (Glauco-Puccinellietalia maritimae, inside the dyke)	Descending curve with an increase in decent within the empirical CR and with a larger decent just before the CL.	20	Good
2110	Embryonic dunes	No characteristic species.		

Code	Name habitat type	Description of the curve	Range decent (kg/ha/yr)	Assessment
2120	Shifting dunes along the shoreline with <i>Ammophila arenaria</i> ("white dunes")	From the lowest deposition a sharp descending curve, descent till the highest deposition. Strong descent before the empirical critical load range. Is the descent too strong in the beginning or is this genuine? The strong descent is mainly caused by <i>Eryngium maritimum</i> and <i>Calystegia soldanella</i> . <i>Eryngium maritimum</i> is a red list species but given its Ellenberg characteristic value for nutrient richness not very sensitive. The same applies for <i>Calystegia soldanella</i> . Maybe vegetation succession interferes with the response here.	15	Reasonable
2130A	Fixed coastal dunes with herbaceous vegetation ("grey dunes", chalk rich)	Descending curve with a stronger descent from the CL on, descending till the lowest deposition. The new empirical CR from Bobbink et al (2022) is more in agreement than the old empirical CR (Bobbink & Hetteling (2011).	50	Good

Code	Name habitat type	Description of the curve	Range decent (kg/ha/yr)	Assessment
2130B	Fixed coastal dunes with herbaceous vegetation ("grey dunes", chalk poor)	Steadily descending curve that slightly evens out at higher deposition. The new empirical CR from Bobbink et al (2022) is more in agreement than the old empirical CR (Bobbink & Hetteling (2011)).	40	Good
2130C	Fixed coastal dunes with herbaceous vegetation ("grey dunes", Nardetea)	Descending curve with a small bend at deposition above the CL. Descent continues till the maximum deposition. The new empirical CR from Bobbink et al (2022) is more in agreement than the old empirical CR (Bobbink & Hetteling (2011)).	40	Good
2140A	Decalcified fixed dunes with <i>Empetrum nigrum</i> (moist)	Descending curve with a small bend at deposition above the CL. Descent continues till the maximum deposition but differences are relatively small.	40	Good
2140B	Decalcified fixed dunes with <i>Empetrum nigrum</i> (dry)	Strong descent before the CL but mostly within the range of the empirical CL. After the CL there is almost no descent. The sharp drop at the lower end is mostly caused by <i>Cladonia</i> species and <i>Viola canina</i> .	20	Good

Code	Name habitat type	Description of the curve	Range decent (kg/ha/yr)	Assessment
2150	Atlantic decalcified fixed dunes (Calluno-Ulicetea)	Strong descent before the CL but mostly within the range of the empirical CL. After the CL there is almost no descent. The sharp drop at the lower end is mostly caused by <i>Cladonia</i> species.	20	Good
2160	Dunes with <i>Hippophae rhamnoides</i>	Steady descent for the whole range with a sharper decrease after the CL. The CL is relatively high, but not reflected in the curve. Many species of which some very strongly react with a sharp descent from the lowest deposition.	65	Reasonable
2170	Dunes with <i>Salix repens</i> subsp. <i>argentea</i>	Strong descent at low deposition levels then gradually less steep descent. Descent starts already at much lower deposition levels than the relative high CL. There are four characteristic species, <i>Empetrum nigrum</i> and <i>Luzula multiflora</i> react as expected, <i>Schoenus nigricans</i> shows a steep descent, fitting for a species which is showing a steep decline in the Netherlands. Also due to the limited number of species this type is cored as bad.	35	Bad

Code	Name habitat type	Description of the curve	Range decent (kg/ha/yr)	Assessment
2180A	Wooded dunes (dry)	Slightly descending curve for the whole deposition range for a type with a low CL. A (stronger) descent was expected. <i>Avenella flexuosa</i> does not react on nitrogen deposition, which we can not explain. Many species of which a part, not unexpected, show a strong increase: <i>Frangula alnus</i> , <i>Holcus mollis</i> and <i>Sorbus aucuparia</i> .	85	Reasonable
2180B	Wooded dunes (moist)	Strong descent starts already before the CL, but the descent continues after the CL to even out at high deposition rates. Many characteristic species.	55	Good
2180C	Wooded dunes (inner dune)	A slight descent before the CL, after the CL a strong descent to even out at the higher nitrogen levels.	50	Good
2190A	Humid dune slacks (open water)	Strong descending response around the CL evening out at high deposition levels.	30	Good
2190B	Humid dune slacks (chalk rich)	Mild descent evening out around the CL. After the CL descending till the maximum nitrogen deposition. Many characteristic species.	35	Good

Code	Name habitat type	Description of the curve	Range decent (kg/ha/yr)	Assessment
2190C	Humid dune slacks (chalk poor)	Strong descent before the CL, before the CL the descent becomes less descending staying the same till the maximum deposition. The curve agrees with the new empirical CR. The strong descent is mostly the result of <i>Empetrum nigrum</i> and <i>Scorpidium scorpioides</i> . Especially the response for the latter, a very rare red list species, is as could be expected.	50	Good
2310	Dry sand heaths with <i>Calluna</i> and <i>Genista</i>	Strong descent before the CL, stabilising just before the maximum value of the empirical critical range. The curve agrees with the new empirical CR. The strong descent at low deposition rate is mainly the result of a number of <i>Cladonia</i> species.	20	Good
2320	Dry sand heaths with <i>Calluna</i> and <i>Empetrum nigrum</i>	Strong descent before the CL, but in agreement with the empirical CR. The strong descent is the result of a large part of the characteristic species.	20	Good
2330	Inland dunes	Gradually descending response over the whole range with a slightly stronger descent after 20 kg/ha/j.	50	Good

Code	Name habitat type	Description of the curve	Range decent (kg/ha/yr)	Assessment
3110	Oligotrophic waters	Descending response for the whole range. The CL is lower than the range the response could be estimated for. Only three characteristic species, all three similar.	40	Good
3130	Oligotrophic to mesotrophic standing waters	Evening out descending response curve. The CL is lower than the range the response could be estimated for.	30	Good
3140	Hard oligo-mesotrophic waters	Descending response curve, slightly increasing at the highest nitrogen depositions. The CL is lower than the range the response could be estimated for. See also H3130. <i>Isolepis fluitans</i> has a S-shaped response curve.	30	Good
3150	Natural eutrophic lakes	Slightly descending curve, evening out at higher deposition. Relative high CL, largest descent below the CL. The overall picture may be genuine, but <i>Stratiotes aloides</i> is showing a steady descending trend, surprising for a species of relative nutrient rich water.	40	Bad

Code	Name habitat type	Description of the curve	Range decent (kg/ha/yr)	Assessment
3160	Natural dystrophic lakes and ponds	Strong descent at lower deposition levels, evening out at higher depositions. Four characteristic species with similar curves. Two species show the start of the descending response at the CL.	30	Good
4010A	Wet heaths with <i>Erica tetralix</i> (inland sandy soils)	Light descending curve, with already a descent before the CL. Unexpected increasing response curves for species as <i>Drosera intermedia</i> , <i>Erica tetralix</i> , <i>Gentiana pneumonanthe</i> and <i>Sphagnum compactum</i> . The response curve for <i>Molinia caerulea</i> does not show an increase, also unexpected. All the responses of the species are based on vegetation plots of structure type dwarf shrub. Most likely the heathlands overgrown by <i>Molinia</i> are missing, as they are classified as grassland in the EUNIS typology.		Bad
4010B	Wet heaths with <i>Erica tetralix</i> (lowland fens)	Descending curve then evening out and at high deposition levels slightly increasing. Curve fits better with the new empirical CR.	35	Good

Code	Name habitat type	Description of the curve	Range decent (kg/ha/yr)	Assessment
4030	European dry heaths	Strong descent at low deposition, already below the CL, then evens out. Curve fits better with new CL and new empirical CR.	20	Good
5130	Juniperus communis formations	Gradely descending curve, the differences are relatively small. The biggest descent is within the empirical CR.	65	Good
6110	Rupicolous calcareous or basophilic grasslands	Descending curve, stabilising around the CL and then decreasing further. Curve fits better with the new empirical CR.	50	Good
6120	Xeric sand calcareous grasslands	Descending trend, at higher deposition the curve evens out. Curve fits better with the new empirical CR.	35	Good
6130	Calaminarian grasslands of the Violetalia calaminariae	Descending curve beyond the CL. The most characteristic zinc tolerant species are missing due to lack of data. The result is determined by common species.	35	Reasonable

Code	Name habitat type	Description of the curve	Range decent (kg/ha/yr)	Assessment
6210	Semi-natural dry grasslands and scrubland facies on calcareous substrates (Festuco-Brometalia)	A slight descent at low deposition levels stabilising around the CL and then a steep descent. The curve fits less well with the new lower empirical CR, though there is already a descent in the curve starting from the lowest deposition.	35	Good
6230	Species-rich Nardus grasslands on siliceous substrates in mountain areas (and submountain areas in Continental Europe)	Descending curve The curve fits the new empirical CR well, with a descent at the lowest deposition..	50	Good

Code	Name habitat type	Description of the curve	Range decent (kg/ha/yr)	Assessment
6410	Molinia meadows on calcareous peaty or clayey-silt-laden soils (Molinion caeruleae)	Limited descent, with a minor increase at high deposition levels, where a strong descent was expected. The new empirical CR is lower than the old one, which fits the curve better. The curve of <i>Rhinanthus angustifolius</i> is unexpectedly increasing with nitrogen deposition levels. <i>Carum verticillatum</i> has a very limited range. Most species seem more or less indifferent for nitrogen deposition. It could be that for this habitat type other processes are more important, such as (quality of) seepage, which is not included as covariable.	35	Reasonable

Code	Name habitat type	Description of the curve	Range decent (kg/ha/yr)	Assessment
6430C	Hydrophilous tall herb fringe communities of plains and of the montane to alpine levels (dry woodland edge)	Slightly increasing curve. The increase starts at higher deposition level than the CL. This subtype is now linked to structure type forest. This could lead to a to high estimate of the deposition and thus a wrong response curve. Many very common species of nutrient rich circumstances determine the response: <i>Aegopodium podagraria</i> , <i>Anthriscus sylvestris</i> , <i>Galium aparine</i> , <i>Glechoma hederacea</i> , <i>Lamium album</i> , <i>Rumex obtusifolius</i> , <i>Silene dioica</i> and <i>Urtica dioica</i> . However, the most characteristic species of the type are very rare.		Bad
6510A	Lowland hay meadows ( <i>Alopecurus pratensis</i> , <i>Sanguisorba officinalis</i> ; <i>Arrhenatherum</i> subtype)	At lower deposition levels a straight line, with a descent at deposition levels higher than the CL but within the empirical CL. The new empirical CR fits less well with the curve, the descent starts just outside the range.	30	Bad
Code	Name habitat type	Description of the curve	Range decent (kg/ha/yr)	Assessment
6510B	Lowland hay meadows ( <i>Alopecurus pratensis</i> , <i>Sanguisorba officinalis</i> ; <i>Alopecurus</i> subtype)	Almost no response to deposition, only a slight decrease at the low deposition levels. The new empirical CR borders now the descending part of the curve. The differences are minimal. A part of the species are characteristics of nutrient rich grasslands, which has a major effect on the curve.		Bad
7110A	Active raised bogs (active bog landscape)	A descending curve from the CL onwards, with a stabilisation at high deposition levels.	50	Good
7110B	Active raised bogs (heath bogs)	A descending curve from the CL onwards, with a stabilisation at high deposition levels. The new empirical CR fits better with the curve.	50	Good
7120	Degraded raised bogs still capable of natural regeneration	A descending curve from the CL onwards, with a stabilisation at high deposition levels.	50	Good
7140A	Transition mires and quaking bogs (quacking bogs)	Descending curve evening out at high deposition levels. The decrease is increasing at deposition levels beyond the CL. The new empirical CR fits better with the curve.	50	Good

Code	Name habitat type	Description of the curve	Range decent (kg/ha/yr)	Assessment
7140B	Transition mires and quaking bogs ( <i>Sphagnum</i> reedland)	Optimum curve with an increase way beyond the CL. The descent is quite strong, but only starts at very high deposition levels. Many species show a similar optimum curve. We can offer no explanation for this curve.	30	Bad
7150	Depressions on peat substrates of the Rhynchosporion	Descending response curve for the whole deposition range. The new empirical CR and CL fit better with the curve.	50	Good
7210	Calcareous fens with <i>Cladium mariscus</i> and species of the Caricion davallianae	Strong descending curve below and above the CL. The new empirical CR and CL fit better with the curve. There are only three characteristic species of which two <i>Cladium mariscus</i> and <i>Myrica gale</i> show a strong descent. <i>Thelypteris palustris</i> shows a response fitting with the CL. For <i>C. mariscus</i> , a species of more nutrient rich waters, a less steep response was expected. The CL is based on species for Calcareous fens, for which we could not estimate a response curve.	50	Reasonable

Code	Name habitat type	Description of the curve	Range decent (kg/ha/yr)	Assessment
7220	Petrifying springs with tufa formation (Cratoneurion)	Descending curve. The descent already starts at lower levels than the CL. It is possible that the CL is too high and should be reviewed, especially compared to H7210. There are only five characteristic species.	70	Reasonable
7230	Alkaline fens	Descending curve evening out around the CL. The descent is small but based on many species. Also, here the unexpected increase of <i>Rhinanthus angustifolius</i> at higher nitrogen deposition levels. Also, many species that show an increase at higher deposition levels fitting for species adjusted to nutrient rich circumstances. The effect of these species is masked by the many species that show a descent for nitrogen deposition.	50	Good
9110	Luzulo-Fagetum beech forests	Descending curve for the whole range, evening out at high deposition levels. The new empirical CR and CL fit better with the curve.	70	Good

Code	Name habitat type	Description of the curve	Range decent (kg/ha/yr)	Assessment
9120	Atlantic acidophilous beech forests with <i>Ilex</i> and sometimes also <i>Taxus</i> in the shrub layer ( <i>Quercion robori-petraeae</i> or <i>Ilici-Fagenion</i> )	Slightly descending curve for the whole range. The lower value of the empirical CL is just below the start of the response curve. The new empirical CR and CL fit better with the curve.	75	Good
9160A	Sub-Atlantic and medio-European oak or oak-hornbeam forests of the <i>Carpinion betuli</i> (sandy soils)	Slightly descending response curve, evening out at high deposition rates.	70	Good
9160B	Sub-Atlantic and medio-European oak or oak-hornbeam forests of the <i>Carpinion betuli</i> (hills)	Descending curve for the whole range. The new empirical CR fits better with the curve, both start at 10 kg/ha/y.	75	Good

Code	Name habitat type	Description of the curve	Range decent (kg/ha/yr)	Assessment
9190	Old acidophilous oak woods with <i>Quercus robur</i> on sandy plains	Slightly descending response curve, dropping greater at higher deposition rates (after 60 kg/ha/y). The descent is limited and therefore the response was judged as bad. The shape of the curve could be right though. Most species do not show a response for deposition with the exception of <i>Melampyrum pratense</i> and <i>Polytrichum formosum</i> , both showing a decrease. <i>Avenella flexuosa</i> does not show much of a reaction to nitrogen deposition, which is unexpected, since it is known to profit from nitrogen deposition.	40	Bad
91D0	Bog woodland	Descending curve, evening out at higher deposition rates. The descent starts well below the CL. The steep descent is due to <i>Eriophorum vaginatum</i> , <i>Vaccinium oxycoccos</i> and <i>Vaccinium vitis-idaea</i> . The descent of some species may also be related to the ageing and thus darkening of the forest, which in turn is accelerated by nitrogen deposition.	70	Good

Code	Name habitat type	Description of the curve	Range decent (kg/ha/yr)	Assessment
91E0A	Alluvial forest with black alder <i>Alnus glutinosa</i> and common ash <i>Fraxinus excelsior</i> (Alno-Padion, <i>Alnion incanae</i> , <i>Salicion albae</i> ), softwood subtype	Descent already before the CL, at depositions above the CL no effect. The effects are small. The small effect is caused by species that increase at higher deposition rates, <i>Galeopsis tetrahit</i> , <i>Galium palustre</i> , <i>Iris pseudocorus</i> , <i>Salix alba</i> , and <i>Urtica dioica</i> , all species of nutrient rich circumstances. According to van Wamelink et al. (2023) this habitat type is less/not sensitive for nitrogen deposition; hence the descent is unexpected. However, this conclusion can be questioned, but there are no data yet available to back the found response. Therefore. For now, the curve is judged as bad.	30	Bad
91E0B	Alluvial forest with black alder <i>Alnus glutinosa</i> and common ash <i>Fraxinus excelsior</i> (Alno-Padion, <i>Alnion incanae</i> , <i>Salicion albae</i> ), ash-elm subtype	Descending curve for the whole range, also at lower levels than the CL. A part of the species shows a response that fits well with the CL. The descent is mainly caused by <i>Eurhynchium striatum</i> and to a lesser extent <i>Fissidens taxifolius</i> , <i>Geum urbanum</i> and <i>Rumex sanguineus</i> .	85	Reasonable

Code	Name habitat type	Description of the curve	Range decent (kg/ha/yr)	Assessment
91E0C	Alluvial forest with black alder <i>Alnus glutinosa</i> and common ash <i>Fraxinus excelsior</i> (Alno-Padion, <i>Alnion incanae</i> , <i>Salicion albae</i> ), beech shore subtype	Descending curve, evening out at higher deposition rates.	65	Reasonable
91F0	Riparian mixed forests of <i>Quercus robur</i> , <i>Ulmus laevis</i> and <i>Ulmus minor</i> , <i>Fraxinus excelsior</i> or <i>Fraxinus angustifolia</i> along the great rivers ( <i>Ulmion minoris</i> )	The response shows an optimum curve with a descent at rates above 50 kg/ha/y. The CL is much lower. There are seven characteristic species, of which five show an optimum curve. Two species, <i>Poa nemoralis</i> and <i>Viola odorata</i> , show a descending curve from the beginning.	40	Bad

## Appendix 8. response curves per habitat type and species

### References

- Ackerman, D., Millet, D.B., Chen, X., 2019. Global estimates of inorganic nitrogen deposition across four decades. *Global Biogeochem. Cycles* 33 (1), 100–107.
- Amann, M., Bertok, I., Borcken-Kleefeld, J., Cofala, J., Heyes, C., Höglund-Isaksson, L., Klimont, Z., Nguyen, B., Posch, M., Rafaj, P., Sandler, R., Schöpp, W., Wagner, F., Winarwar, W., 2011. Cost-effective control of air quality and greenhouse gases in Europe: modeling and policy applications. *Environ. Model. Software* 26, 1489–1501. <https://doi.org/10.1016/j.envsoft.2011.07.012>.
- Armitage, H.F., Britton, A.J., van der Wal, R., Woodin, S.J., 2014. The relative importance of nitrogen deposition as a driver of *Racomitrium* heath species composition and richness across Europe. *Biol. Conserv.* 171, 224–231.
- Bal, D., 2007. Selectie van typische soorten voor habitatrichtlijn. Ministerie van Landbouw, Natuurbeheer en Visserij. Directie Kennis (Ede).
- Berendse, F., Geerts, R.H., Elberse, W.T., Bezemer, T.M., Goedhart, P.W., Xue, W., et al., 2021. A matter of time: recovery of plant species diversity in wild plant communities at declining nitrogen deposition. *Divers. Distrib.* 27, 1180–1193.
- Bobbink, R., Hettelingh, J.P. (Eds.), 2011. Review and Revision of Empirical Critical Loads and Dose-Response Relationships. Coordination Centre for Effects, National Institute for Public Health and the Environment (RIVM), p. 244. RIVM report 680359002/2011.
- Bobbink, R., Hornung, M., Roelofs, J.G.M., 1998. The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. *J. Ecol.* 86, 717–738.
- Bobbink, R., Loran, C., Thomassen, H. (Eds.), 2022. Review and Revision of Empirical Critical Loads of Nitrogen for Europe. Umweltbundesamt, Dessau-Roßlau.
- Britton, A.J., Fisher, J.M., 2007. Interactive effects of nitrogen deposition, fire and grazing on diversity and composition of low-alpine prostrate *Calluna vulgaris* heathland. *J. Appl. Ecol.* 44, 125–135.
- Cbs, P.B.L., Rivm, W.U.R., 2019. Stikstofdepositie, 1990-2018. [www.clo.nl](http://www.clo.nl) last accessed 27-1-2022.
- Chytrý, M., Hennekens, S.M., Jiménez-Alfaro, B., Knollová, I., Dengler, J., Jansen, F., et al., 2016. European Vegetation Archive (EVA): an integrated database of European vegetation plots. *Appl. Veg. Sci.* 19, 173–180. <https://doi-org.ezproxy.library.wur.nl/10.1111/avsc.1219>.
- Chytrý, M., Tichý, L., Hennekens, S.M., Knollová, I., Janssen, J.A., Rodwell, J.S., et al., 2020. EUNIS Habitat Classification: expert system, characteristic species combinations and distribution maps of European habitats. *Appl. Veg. Sci.* 23 (4), 648–675.
- Cinderby, S., Emberson, L., Owen, A., Ashmore, M., 2008. LRTAP land cover map of Europe. In: Slootweg, J., Posch, M., Hettelingh, J.P. (Eds.), *Critical Loads of Nitrogen and Dynamic Modelling*, CCE Progress Report 2007, pp. 59–70. MNP Report 500090001/2007. <https://www.pbl.nl/en/publications/Criticalloadsofnitrogenanddynamicmodelling>.
- Clark, C.M., Simkin, S.M., Allen, E.B., et al., 2019. Potential vulnerability of 348 herbaceous species to atmospheric deposition of nitrogen and sulfur in the United States. *Nat. Plants* 5, 697–705. <https://doi.org/10.1038/s41477-019-0442-8>.
- Cornes, R., van der Schrier, G., van den Besselaar, E.J.M., Jones, P.D., 2018. An ensemble version of the E-Obs temperature and precipitation datasets. *J. Geophys. Res. Atmos.* 123, 9391–9409.
- Council of the European Communities, 1992. Council Directive 92/43/EEC of 21 May 1992 on the Conservation of Natural Habitats and of Wild Fauna and Flora, p. 66. Brussels.
- Critical loads and dynamic risk assessments: nitrogen, acidity and metals in terrestrial and aquatic ecosystems. In: De Vries, W., Hettelingh, J.P., Posch, M. (Eds.), 2015. *Environmental Pollution Series*, vol. 25. Springer, Dordrecht, p. 662. <https://doi.org/10.1007/978-94-017-9508-1>. ISBN 978-94-017-9507-4.
- Epe, M.J., Wallis de Vries, M.F., Bouwma, I.M., Janssen, J.A.M., Kuipers, H., Keizer-Vlek, H., Niemeijer, C.M., 2009. Urgent bedreigde typische soorten en vegetatietypen van Natura 2000habitattypen. Alterra-rapport 1909. Alterra Wageningen UR, Wageningen, Netherlands.
- Etzold, S., Ferretti, M., Reinds, G.J., Solberg, S., Gessler, A., Waldner, P., et al., 2020. Nitrogen deposition is the most important environmental driver of growth of pure, even-aged and managed European forests. *For. Ecol. Manag.* 458, 117762.
- Evans, D., 2012. Building the European union's Natura 2000 network. *Nat. Conserv.* 1, 11–26.
- FAO, 2015. World Reference Base for Soil Resources 2014. International Soil Classification System for Naming Soils and Creating Legends for Soil Maps. Update 2015. World Soil Resources Reports 106. FAO, Rome, p. 106. <https://www.fao.org/3/i3794en/i3794en.pdf>.
- Field, C.D., Dise, N.B., Payne, R.J., Britton, A.J., Emmett, B.A., Helliwell, R.C., Hughes, S., Jones, L., Lees, S., Leake, J.R., Leith, I.D., Phoenix, G.K., Power, S.A., Sheppard, L.J., Southon, G.E., Stevens, C.J., Caporn, S.J.M., 2014. The role of nitrogen deposition in widespread plant community change across semi-natural habitats. *Ecosystems* 17, 864–877.
- Fremstad, E., Paal, J., Möls, T., 2005. Impacts of increased nitrogen supply on Norwegian lichen-rich alpine communities: a 10-year experiment. *J. Ecol.* 93, 471–481.
- Hastie, T.J., Tinschirani, R.J., 1990. *Generalized Additive Models*. Chapman and Hall, London.
- Jokerud, M., 2012. Impact of Nitrogen Deposition on Species Richness and Species Composition of Ombrotrophic Mires in Western Norway. University of Bergen, Norway. Master Thesis, Department of Biology.
- Jones, A., Montanarella, L., Jones, R., 2015. Soil Atlas of Europe 293. <https://esdac.jrc.europa.eu/content/soil-atlas-europe>.
- Krepa, S.V., 2003. Effects of atmospheric ammonia (NH<sub>3</sub>) on terrestrial vegetation: a review. *Environ. Pollut.* 124, 179–221. [https://doi.org/10.1016/S0269-7491\(02\)00434-7](https://doi.org/10.1016/S0269-7491(02)00434-7).
- Lin, L.L.K., 1989. A concordance correlation coefficient to evaluate reproducibility. *Biometrics* 45, 255–268. <https://doi.org/10.2307/2532051>.
- Nilsson, J., Grennfelt, P., 1988. Critical loads for sulphur and nitrogen. In: Miljørapport, vol. 15. Nordic Council of Ministers, Copenhagen, pp. 1–418.
- Payne, R.J., Dise, N.B., Stevens, C.J., Gowing, D.J., partners, B.E.G.I.N., 2013. Impact of Nitrogen Deposition at the Species Level, vol. 110. Proceedings of the National Academy of Sciences, pp. 984–987.
- Payne, R.J., Dise, N.B., Field, C.D., Dore, A.J., Caporn, S.J., Stevens, C.J., 2017. Nitrogen deposition and plant biodiversity: past, present, and future. *Front. Ecol. Environ.* 15, 431–436.
- Payne, R.J., Campbell, C., Stevens, C.J., Pakeman, R.J., Ross, L.C., Britton, A.J., 2020. Disparities between plant community responses to nitrogen deposition and critical loads in UK semi-natural habitats. *Atmos. Environ.* 239, 117478.
- Press, W.H., Teukolsky, S.A., Vetterling, W.T., Flannery, B.P., 1992. *Numerical Recipes in C: the Art of Scientific Computing*, second ed. Cambridge University Press, New York, NY, USA, pp. 123–128. ISBN 0-521-43108-5.
- Rosén, K., Gundersen, P., Tegnhamm, L., Johansson, M., Frogner, T., 1992. Nitrogen enrichment of Nordic forest ecosystems: the concept of critical loads. *Ambio* 21, 364–368.
- Roth, T., Kohli, L., Rihm, B., Achermann, B., 2013. Nitrogen deposition is negatively related to species richness and species composition of vascular plants and bryophytes in Swiss mountain grassland. *Agric. Ecosyst. Environ.* 178, 121–126.

- Roth, T., Kohli, L., Rihm, B., Meier, R., Achermann, B., 2017. Using change-point models to estimate empirical critical loads for nitrogen in mountain ecosystems. *Environ. Pollut.* 220, 1480–1487.
- Rowe, E.C., Jones, L., Dise, N.B., Evans, C.D., Mills, G., Hall, J., Stevens, C.J., Mitchell, R. J., Field, C., Caporn, S.J.M., Helliwell, R.C., Britton, A.J., Sutton, M.A., Payne, R.J., Vieno, M., Dore, A.J., Emmett, B.A., 2017. Metrics for evaluating the ecological benefits of decreased nitrogen deposition. *Biol. Conserv.* 212, 454–463.
- Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., et al., 2000. Global biodiversity scenarios for the year 2100. *Science* 287, 1770–1774.
- Schaminée, J.H.J., Stortelder, A.H.F., Westhoff, V., 1995. *De Vegetatie van Nederland; deel 1: Inleiding tot de plantensociologie - grondslagen, methoden en toepassingen*. Opulus Press, Uppsala.
- Schmitz, A., Sanders, T.G.M., Bolte, A., Busotti, F., Dirnbock, T., Johnson, J., et al., 2019. *Environ. Pollut.* 244, 980–994.
- Schöpp, W., Posch, M., Mylona, S., Johansson, M., 2003. Long-term development of acid deposition (1880-2030) in sensitive freshwater regions in Europe. *Hydrol. Earth Syst. Sci.* 7, 436–446. <https://doi.org/10.5194/hess-7-436-2003>.
- Simpson, D., Benedictow, A., Berge, H., Bergström, R., Emberson, L.D., Fagerli, H., Flechard, C.R., Hayman, G.D., Gauss, M., Jonson, J.E., Jenkin, M.E., Nyiri, A., Richter, C., Semeena, V.S., Tsyro, S., Tuovinen, J.-P., Valdebenito, A., Wind, P., 2012. The EMEP MSC-W chemical transport model - technical description. *Atmos. Chem. Phys.* 12, 7825–7865. <https://doi.org/10.5194/acp-12-7825-2012>.
- Simpson, D., Andersson, C., Christensen, J.H., Engardt, M., Geels, C., Nyiri, A., Posch, M., Soares, J., Sofiev, M., Wind, P., Langner, J., 2014. Impacts of climate and emission changes on nitrogen deposition in Europe: a multi-model study. *Atmos. Chem. Phys.* 14, 6995–7017. <https://doi.org/10.5194/acp-14-6995-2014>.
- Smits, N.A.C., Mucher, C.A., Ozinga, W.A., de Waal, R.W., Wamelink, G.W.W., 2016. *Procesindicatoren PAS: rapportage 2016. Bijlage 1 sheet 5*. In: Wageningen Environmental Research Rapport; No. 2771. Wageningen Environmental Research, Wageningen, Netherlands. <https://doi.org/10.18174/401546>.
- Staude, I.R., Waller, D.M., Bernhardt Romermann, M., Bjorkman, A.D., Brunet, J., De Frenne, P., et al., 2020. Replacements of small- by large-ranged species scale up to diversity loss in Europe's temperate forest biome. *Nature Ecology & Evolution* 4, 802–804. <https://doi.org/10.1038/s41559-020-1176-8>.
- Stevens, C.J., Duprè, C., Dorland, E., Gaudnik, C., Gowing, D.J.G., Bleeker, A., Diekmann, M., Alard, D., Bobbin, R., Fowler, D., Corcket, E., Mountford, J.O., Vandvik, V., Aarrestad, P.A., Muller, S., Dise, N.B., 2010. Nitrogen deposition threatens species richness of grasslands across Europe. *Environ. Pollut.* 158, 2940–2945.
- Stevens, C.J., Duprè, C., Dorland, E., Gaudnik, C., Gowing, D.J.G., Bleeker, A., Diekmann, M., Alard, D., Bobbin, R., Fowler, D., Corcket, E., Mountford, J.O., Vandvik, V., Aarrestad, P.A., Muller, S., Dise, N.B., 2011a. The impact of nitrogen deposition on acid grasslands in the Atlantic region of Europe. *Environ. Pollut.* 159, 2243–2250.
- Stevens, C.J., Duprè, C., Dorland, E., Gaudnik, C., Gowing, D.J.G., Bleeker, A., Alard, D., Bobbin, R., Fowler, D., Vandvik, V., Corcket, E., Mountford, J.O., Aarrestad, P.A., Muller, S., Diekmann, M., 2011b. Changes in species composition of European acid grasslands observed along a gradient of nitrogen deposition. *J. Veg. Sci.* 22, 207–215.
- Stevens, C.J., David, T.I., Storkey, J., 2018. Atmospheric nitrogen deposition in terrestrial ecosystems: its impact on plant communities and consequences across trophic levels. *Funct. Ecol.* 32, 1757–1769.
- Stevens, C.J., Bell, J.N.B., Brimblecombe, P., Clark, C.M., Dise, N.B., Fowler, D., et al., 2020. The impact of air pollution on terrestrial managed and natural vegetation. *Philosophical Transactions of the Royal Society A* 378, 20190317.
- Tsyro, S., Aas, W., Solberg, S., Benedictow, A., Fagerli, H., Posch, M., 2018. Chapter 2: status of transboundary air pollution in 2016. In: Fagerli, H., et al. (Eds.), *Transboundary Particulate Matter, Photo-Oxidants, Acidifying and Eutrophying Components*. EMEP Status Report 1/2018. Norwegian Meteorological Institute, Oslo, Norway, pp. 15–40.
- Tsyro, S., Aas, W., Solberg, S., Benedictow, A., Fagerli, H., Scheuschner, T., 2019. Chapter 2: status of transboundary air pollution in 2017. In: Fagerli, H., et al. (Eds.), *EMEP Status Report 1/2019*. Norwegian Meteorological Institute, Oslo, Norway.
- Van den Berg, L.J.L., Vergeer, P., Rich, T.C.G., Smart, S.M., Guest, D., Ashmore, M.R., et al., 2021. Direct and indirect effects of nitrogen deposition on species composition change in calcareous grasslands. *Global Change Biol.* 17, 1871–1883.
- Van den Burg, A.B., Berendse, F., van Dobben, H.F., Kros, J., Bobbink, R., Roelofs, J., et al., 2021. Onderzoek naar een ecologisch noodzakelijke reductiedoelstelling van stikstof: stikstof en natuurherstel. Wereld Natuur Fonds, Zeist, Netherlands, p. 49.
- Van der Salm, C., Voogd, J.C.H., de Vries, W., 1993. *SMB - a Simple Mass Balance Model to Calculate Critical Loads: Model Description and User Manual*. DLO Winand Staring Centre. Technical document no.11.
- Van Dobben, H.F., Posch, M., Wamelink, G.W.W., Hettelingh, J.P., De Vries, W., 2015. Plant species diversity indicators for use in the computation of critical loads and dynamic risk assessments. In: de Vries, W., Hettelingh, J.-P., Posch, M. (Eds.), *Critical Loads and Dynamic Risk Assessments: Nitrogen, Acidity and Metals in Terrestrial and Aquatic Ecosystems*. Springer, Dordrecht, Netherlands, pp. 59–81.
- Van Dobben, H.F., Van Hinsberg, A., Schouwenberg, E.P.A.G., Jansen, M., Mol-Dijkstra, J.P., Wieggers, H.J.J., et al., 2006. Simulation of critical loads for nitrogen for terrestrial plant communities in The Netherlands. *Ecosystems* 9, 32–45.
- Van Dobben, H., Bobbink, R., Bal, D., van Hinsberg, A., 2014. Overview of critical loads for nitrogen deposition of Natura 2000 Habitat types occurring in The Netherlands. *Alterra-report 2488* 46. Wageningen, Netherlands.
- Van Nes, E.H., Arani, B.M., Staal, A., van der Bolt, B., Flores, B.M., Bathiany, S., Scheffer, M., 2016. What do you mean, 'tipping point'. *Trends Ecol. Evol.* 31, 902–904.
- VSN International, 2021. *GenStat for Windows, 21nd Edition*. VSN International, Hemel Hempstead, UK. Web page. <https://www.genstat.co.uk/>.
- Wamelink, G.W.W., Mol-Dijkstra, J.P., Reinds, G.J., Voogd, J.C., Bonten, L.T.C., Posch, M., Hennekens, S.M., de Vries, W., 2020. Prediction of plant species occurrence as affected by nitrogen deposition and climate change on a European scale. *Environ. Pollut.* 266, 115257. <https://doi.org/10.1016/j.envpol.2020.115257>.
- Wamelink, W., van Dobben, H., van der Zee, F., van Hinsberg, A., Bobbink, R., 2023. *Overzicht van kritische depositiewaarden voor stikstof, toegepast op habitattypen en leefgebieden van Natura 2000: Herziening 2023. Rapport/Wageningen Environmental Research; No. 3272*. Wageningen Environmental Research. <https://doi.org/10.18174/633179>.
- Wilkins, K., Aherne, J., 2016. Vegetation community change in Atlantic oak woodlands along a nitrogen deposition gradient. *Environ. Pollut.* 216, 115–124.
- Zara, M., Boersma, K.F., Eskes, H., Denier van der Gon, H., Vilà-Guerau de Arellano, J., Krol, M., van der Swaluw, E., Schuch, W., Velders, G.J.M., 2021. Reductions in nitrogen oxides over The Netherlands between 2005 and 2018 observed from space and on the ground: decreasing emissions and increasing O<sub>3</sub> indicate changing NO<sub>x</sub> chemistry. *Atmos. Environ.* X 9, 100104. <https://doi.org/10.1016/j.aea.2021.100104>. ISSN 2590-1621.