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# Evidence for differential effects of reduced and oxidised nitrogen deposition on vegetation independent of nitrogen load

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## ABSTRACT

Nitrogen (N) deposition impacts natural and semi-natural ecosystems globally. The responses of vegetation to N deposition may, however, differ strongly between habitats and may be mediated by the form of N. Although much attention has been focused on the impact of total N deposition, the effects of reduced and oxidised N, independent of the total N deposition, have received less attention. In this paper, we present new analyses of national monitoring data in the UK to provide an extensive evaluation of whether there are differences in the effects of reduced and oxidised N deposition across eight habitat types (acid, calcareous and mesotrophic grasslands, upland and lowland heaths, bogs and mires, base-rich mires, woodlands). We analysed data from 6860 plots in the British Countryside Survey 2007 for effects of total N deposition and N form on species richness, Ellenberg N values and grass:forb ratio. Our results provide clear evidence that N deposition affects species richness in all habitats except base-rich mires, after factoring out correlated explanatory variables (climate and sulphur deposition). In addition, the form of N in deposition appears important for the biodiversity of grasslands and woodlands but not mires and heaths. Ellenberg N increased more in relation to $NH_x$ deposition than $NO_y$ deposition in all but one habitat type. Relationships between species richness and N form were habitat-specific: acid and mesotrophic grasslands appear more sensitive to $NH_x$ deposition while calcareous grasslands and woodlands appeared more responsive to $NO_y$ deposition. These relationships are likely driven by the preferences of the component plant species for oxidised or reduced forms of N, rather than by soil acidification.

## 1. Introduction

There is widespread evidence across the globe, from both experiments and field surveys, of the significant ecological impacts of nitrogen (N) deposition on semi-natural ecosystems of low nutrient status (e.g. Bobbink et al., 2010), which also carries economic costs (Jones et al., 2014). However, interpretation and quantification of these effects, and predictions of the benefits of emission control policies, need to consider the different components of N deposition (Brink et al., 2011). There are two main chemical forms – reduced N (ammonia, $NH_3$ and ammonium, $NH_4^+$) emitted primarily from agricultural sources, and oxidised N (nitrogen oxides, $NO_y$, nitric acid, $HNO_3^-$ and nitrate $NO_3^-$) emitted primarily from fossil fuel combustion. In addition, N deposition may be in the form of dry deposition of gases and aerosols, which is most important close to sources, and in regions of the world with low rainfall, and as wet deposition as snow, dew, cloud or rainwater, which are important in more remote regions and in areas with high rainfall.

The mechanisms underlying the ecological effects of N deposition include direct toxicity, growth stimulation and competitive exclusion, soil acidification and increased susceptibility to other

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abiotic and biotic stresses (e.g. Bobbink et al., 1998; Roem and Berendse, 2000). There are strong reasons, which have been recently reviewed by Stevens et al. (2011), for expecting that there may be different effects of reduced and oxidised N deposition for each of these mechanisms. For example, foliar uptake of gaseous $NH_3$ is more likely to be directly toxic than uptake of gaseous nitrogen oxides, while soil $NH_4^+$ is more likely to be toxic to plant roots than soil $NO_3^-$ (Sheppard et al., 2011, 2014). Plant species also differ strongly in their preference and tolerance for $NH_4^+$ or $NO_3^-$ uptake from soil solution with species of acidic habitats generally more tolerant of higher soil ammonium (Falkengrengrerup and Lakkenborgkristensen, 1994). The soil $NH_4^+/NO_3^-$ ratio is partly a function of the ratio in atmospheric deposition, but also of the degree of nitrification in soils; high rates of nitrification result in a lower soil solution $NH_4^+/NO_3^-$ ratio, which may reduce the risk of direct $NH_4^+$ toxicity but may increase acidification because of the greater oxidation to $NO_3^-$.

Experimental studies provide some evidence of the differential effects of reduced and oxidised N deposition. For example, van den Berg et al. (2008) showed that higher $NH_4^+/NO_3^-$ ratios in deposition to heathland mesocosms had significant adverse effects on acid-sensitive species but not on acid-tolerant species that were also tolerant of high soil $NH_4^+/NO_3^-$ ratios. This effect was lost in limed mesocosms, suggesting that acidification at higher $NH_4^+/NO_3^-$ ratios was the key driving mechanism. By contrast, in Mediterranean maquis vegetation, the application of both $NH_4^+$ and $NO_3^-$ increased biomass but not plant diversity, while $NH_4^+$ alone increased plant diversity but not biomass (Dias et al., 2014); these effects can at least partly be explained by the different responses of individual species to total N inputs or to reduced N deposition specifically.

A combination of targeted field surveys and analysis of nationwide surveillance data over the last decade have provided a strong body of evidence of the impacts of N deposition. Strong negative associations between N deposition and species richness have been reported in acid grasslands (Stevens et al., 2004, 2010a; Duprè et al., 2010; Stevens et al., 2010a), grasslands, heathlands and bogs (Maskell et al., 2010; Caporn et al., 2014; Field et al., 2014)and sand dunes (Jones et al., 2004). In acid grasslands, this negative association is linked to declines in forb species richness and a corresponding increase in graminoids (Maskell et al., 2010) with differential responses of individual forb species to N deposition (Payne et al., 2013). In acid grasslands acidification rather than eutrophication may be the main driver of change (Stevens et al., 2010b), but the relative influence of sulphur versus nitrogen as the driver of acidification has not been separated.

However, in some other habitats; for example in calcareous grasslands, gradient surveys have shown no significant association between N deposition and species richness (Maskell et al., 2010). However, high rates of N deposition have been associated in calcareous grassland plots with an increase in grass:forb ratio (Maskell et al., 2010) and a decline in species diversity and in the frequency of characteristic species (van den Berg et al., 2011). This latter study suggests that, while direct effects of N deposition were responsible for shifts in diversity, effects on herb species number reflect indirect effects of both N and S deposition on soil acidity.

These and other findings from field surveys suggest that the responses to N deposition of vegetation characteristics in different habitats may be at least partly explained by differences in the underlying mechanisms of impact of reduced and oxidised N, mediated by soil pH, with acidification effects prevailing in poorly-buffered habitats and eutrophication effects in well-buffered habitats. Few field surveys have tried to separately evaluate the strength of associations with reduced and oxidised nitrogen but were only able to do so with relatively low number of samples/sites (Caporn et al., 2014; Field et al., 2014). Three studies have showed adverse changes in vegetation composition that were significantly correlated with reduced N deposition but not with oxidised N deposition: an increase in mean Ellenberg fertility index in semi-natural grassland and heaths/bogs between 1990 and 1998 in UK Countryside Survey data (Smart et al., 2004); a loss of species with a low Ellenberg fertility index in UK national recording data between 1987 and 1999 (McClean et al., 2011); and increases in graminoid cover and decreases in lichen cover in heathlands (Southon et al., 2013). A further study showed effects only of dry deposition of $NH_x$ and no effect of wet reduced or oxidised N on abundance of N sensitive epiphytic lichens (Seed et al., 2013).

However, interpretation of such field surveys is difficult due to problems of spatial autocorrelation, and the confounding effects of other environmental and land use changes. The levels of reduced and oxidised N deposition are often highly correlated (areas of low reduced N usually have low oxidised N, etc); in addition, the range and spatial variability of reduced N deposition is often greater than that of oxidised N deposition, thereby increasing the probability of detecting a statistically significant association with vegetation characteristics (e.g. Smart et al., 2012). In this paper, we present new analyses of national surveillance data in the UK to provide a more rigorous evaluation of whether there are differences in the effects of reduced and oxidised N deposition that are more robust to statistical limitations. The data that are used here provide a greater sample size and spatial scope that includes almost the complete N deposition range in the UK and allows us to evaluate our mechanistic understanding of the differential effects of the two forms of N deposition in different habitats and on different groups of species. In our analysis we focus on species richness of vascular plants as a measure of biodiversity, Ellenberg N as a measure of nutrient status (Diekmann and Falkengren-Grerup, 2002) and grass:forb ratio as a measure of competitive dominance effects. We hypothesise that:

- The form of N (oxidised $NO_y$, or reduced $NH_x$) in deposition has an effect on vegetation composition that is independent of, and additional to, that of total N deposition.
- Reduced N deposition has a greater impact on vegetation composition than oxidised N deposition.

## 2. Methods

### 2.1. Vegetation data

The effect of N deposition on vegetation was assessed using vegetation data obtained from 6860 plots (2 × 2m) from the UK Countryside Survey 2007 (Carey et al., 2008). For each plot, total species richness, grass:forb ratio and mean Ellenberg N values were calculated. Species richness was defined as the sum of all vascular plants in each 2 × 2 m plot. Grass to forb ratio was based on the cover of grass species (*Poaceae*) divided by the cover of forb species. Cover-weighted average Ellenberg N numbers (Ellenberg et al., 1991) that were modified for the UK (Hill et al., 2004) were calculated based on the cover per 2 × 2 m plot to obtain strong correlates of species responses to nutrient availability and succession (Vile et al., 2006).

The vegetation in each plot was classified according to the UK National Vegetation Classification (NVC) and plots were pooled into broad groups of similar habitat (see Table in supplementary material). Earlier studies have shown that soil pH or base saturation can explain species richness and can affect the responses of the vegetation and the ecosystem to N deposition (van den Berg et al., 2005; Stevens et al., 2006). Therefore, habitats that belong to a similar broad NVC classification but differ strongly in average soil pH and/or base cation content (heaths, mires and grasslands) were